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RENEWED INQUIRIES

CONCERNING

THE SPIRAL STRUCTURE OF MUSCLE,

WITH

OBSERVATIONS ON THE MUSCULARITY OF CILIA.

BY

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[With Two Plates.]

[THESE renewed examinations of muscle, extending over a period of many months, were made in the house of the veteran Purkinje; whose judgement in the matter may be inferred, when it is stated that,—after what he had seen during that long period of almost daily demonstrations by the author, and the devotion of whole mornings to the subject with almost every kind of muscle that could be obtained,—he translated an account of the same into German, printing no fewer than sixty-eight pages.]

Deprived for years of the pleasure of microscopic research by an affection of his sight, the author finds himself in this respect so far restored, that it does not appear necessary to deny himself that pleasure any longer. If he has erred in taking up the microscope again, that is to say, should his sight be thereby injured, he thinks he may well claim to be excused.

For it could not be to him a matter of indifference that his researches on the structure of muscle had not met with the attention he had expected, and which the subject well deserves. He therefore felt driven to renewed research; and, after nine months of still more rigid investigation, does not find occasion to give up his former views. So far from this, indeed, his opinion that muscle has no other than a spiral structure has been even more confirmed. He has met with unexpected states

* Communicated by the Author; being the substance of a paper translated into German by Professor Purkinje, Foreign Member R.S., and by him communicated to Müller's *Archiv*, Heft vi. 1850.

of interlacement, throwing new light upon the whole; and now understands how it was that observers did not see what he has seen. The attention of some at least appears to have been given so exclusively to one or to another of those states of interlacement, that they remained, as it were, at different stages in their attempts at explanation. Probably his double spiral fibril, appeared to most observers too complicated, perhaps too artificial. Now, however, having found and figured transition stages extending to complete relaxation, he hopes that there will be some at least disposed to repeat their examinations, and with more minuteness than before. Then, perhaps, justice may be done to the author's views, instead of having assigned to them the mournful honour of figuring somewhere in history as opinions or even errors. The objects are of extreme minuteness, requiring almost without exception the highest magnifying powers; and they are optically so complicated, that nowhere in the field of microscopic observation is there a subject more difficult than that of muscle.

The principal facts made known by the author in the Philosophical Transactions of the Royal Society for 1842, briefly recapitulated, were these:—The muscular fibril consists of two spiral threads, so interlaced as to present a double cylinder, *i. e.* the fibril appears as if grooved on each side, a transverse section of the fibril being represented by the figure (∞). The fibril of a primitive fasciculus having transverse striæ is usually so situated that one of its edges is directed towards the eye of the observer; whence it comes that usually there is seen the spiral of only one of the cylinders of the fibril. A muscle is thus nothing less than a vast bundle of spirals, appearing short and thick in contraction, long and thin in relaxation. The elliptical winds of the spirals appear to have been mistaken by some observers for "beads," "segments," or "particles." The dark *longitudinal* striæ of the primitive fasciculus are spaces (probably occupied by a lubricating fluid) between the edges of the fibrils. The dark *transverse* striæ are rows of spaces between the winds of the spiral threads constituting the fibrils. If the dark longitudinal striæ are spaces between the edges of the fibrils, the light longitudinal striæ are the edges themselves of the fibrils; and if the dark transverse striæ are rows of spaces between the curves of spiral threads, the light transverse striæ are of course the visible portions themselves of those spiral threads. The contraction of muscle does not require a flattening of "segments" or "particles," as supposed by some, but simply a more transverse direction of the spirals in their curves. Hence in contraction the striæ of a fasciculus are narrow, and in relaxation they are broad, denoting a shortening and lengthening respectively of the fibrils. "Transverse cleavage" of the primitive fasciculus is caused by the spirals giving way at that part where they offer the least resistance, viz. at the part where they cross one another and are in contact. The sarcolemma arises from the coalescence of spirals.

It was by attending to the history of development of muscle, chiefly in the larva of the large toad of Jersey, that the author arrived at a knowledge of the foregoing facts. His observations published in the present paper were made with one of the large compound microscopes of Plössl; and it happened that the instrument was the very last constructed by that justly renowned optician. The following are some of the new facts herewith observed; others will be mentioned further on.

The two spirals of which the muscular fibril consists, run in the same direction, and not in opposite directions, as the author at first supposed. (Plate I. fig. 1.)

These two spirals are united at the end of the fibril, as in a loop. Such at least is the case in one form of muscle, Pl. II. fig. 30, and from analogy it may be presumed to be the same in others.

The fibril, being thus a double or twin spiral, undergoes a stronger twisting in contraction, and an untwisting in relaxation.

When met with in relaxation, the two spirals usually present themselves in a state comparable to that of common twine. (Pl. I. fig. 2.)

Between the untwisting in relaxation and the twisting in contraction, there are several intermediate states. Fig. 3 presents four such intermediate states seen in different parts of the same fibril.

Cilia also are double spiral threads, and thus have a structure like that of the muscular fibril. (Figs. 29, 30, 31, &c.)

The author then describes models of lead wire which he has constructed for the purpose of illustrating the structure of the muscular fibril, fig. 1. These models, though very rude ones, may afford some idea of the different conditions of the fibril in regard to length, breadth, and thickness, in different degrees of contraction, *a*, and relaxation, *b*. (*b*, in the model, fig. 1, represents part of *a*, after the drawing of the latter out*.)

It is an error to suppose it possible to learn how the striæ in muscle are produced, by examining merely the primitive fasciculus. The primitive fasciculus must be, as far as possible, teased out with needles, and the fibrillæ separately examined. To obtain the fibril, muscle should be selected in which the primitive fasciculi are small. For this purpose the heart is especially to be

* [Such models have since been presented to the Royal Society and to the Royal College of Surgeons in London by the Author.—May 1852.]

recommended; because, from the ever-active condition of that organ, its muscle is in a state which he regards as that of continued renewal; and the fibrils are not so very difficult to separate from one another. In no heart that the author has examined are the fibrils seen with more distinctness to be double spirals than in the heart of the common frog. He has frequently found such states of the fibril as those in fig. 2, and fig. 3 *f*, to be seen with remarkable distinctness in muscle from the tail of the Crawfish, *Astacus fluviatilis*. The observer should use for examination the muscle of a healthy animal just killed, and never employ muscle that has been preserved in spirit or in any other fluid. The least degree of decomposition is sufficient to destroy the spirals. Decomposing muscle presents granulated threads enough (fig. 6 *b*), *i. e.* rows of cell-germs, but rarely any trace of spirals. (From this it is seen, and it is important to observe, that the spiral threads are more easy of decomposition, and disappear sooner than the formative cell-germs.)

The accustomed eye can often discern spirals without a chemical reagent; but for those unacquainted with them a reagent is essential. The author provides two solutions; the first a solution containing $\frac{1}{200}$dth of corrosive sublimate in spirit of 0·940 spec. grav., and the second a concentrated solution of corrosive sublimate in distilled water. Having placed a drop of the first of these solutions upon glass, he introduces into it a minute portion of muscle from the heart of the frog, and *immediately* proceeds to carefully spread it out with needles. He then separates longitudinally a portion as minute as possible from the rest, and teases this out in the same drop under a lens *to the very utmost.* The threads thus prepared he removes to another strip of glass upon which he had placed a drop of the solution No. 2, covers them with a bit of the thinnest glass, and views them under the microscope,—at first with a power of about 200 diameters, in order to select the threads best adapted for observation, and bring them into the middle of the field of view. He then applies a power of about 600, and usually finds here and there a fibril sufficiently separated from the rest at the edge of the preparation to enable him to discern its spirals. It is not unimportant to remark, that the muscle must always be first teased out in the solution No. 1, before it is introduced into the solution No. 2; for, besides corroding the needles, and making them quite useless, the solution No. 2 instantly renders the substance of the muscle so compact, that teasing of it out is absolutely impossible. Even the solution No. 1 lays hold of the muscle to a certain extent, so that the observer should proceed as soon as possible to apply the needles. If it be desired to make preparations that are to be preserved for any length of time, the concentrated aqueous solution of corrosive sublimate (solution No. 2) of course cannot be employed, as the fibrils become speedily decomposed and indistinct. For such preparations the author prefers a solution containing $\frac{1}{120}$th of nitrate of silver in distilled water, using this instead of the solution No. 2, but having proceeded as before with the teasing out in solution No. 1. It is true that the nitrate of silver does not show the spirals with the same remarkable distinctness as the solution No. 2, and besides, the preparation is here and there defaced with a precipitate; but for preparations to be preserved for any length of time, it is to be preferred. For immediate examination the author especially recommends the solution No. 2.

The use of chemical reagents having been objected to, it may be replied, as suggested to the author by his brother, J. T. Barry, were anyone *denying* the existence of the structure in question, then it might be very proper to object, that reagents had destroyed it; but when the existence of that structure is *affirmed*, it cannot be objected that that structure has arisen through those reagents, especially when, in order to bring it into view, substances so very different have been used, as corrosive sublimate, nitrate of silver, and chromic acid. Least of all can those object to the use of chemical reagents who in such researches employ maceration, which, as is known, does not require much time to produce in organic substance the greatest changes.

Adhering to his original views regarding the situations of the striæ in the fasciculus of muscle, as above quoted, the author gives figures illustrative of the same (figs. 4 and 5). These show the situations of the dark longitudinal striæ to correspond to the spaces between the edges of the fibrils, and the situations of the dark transverse striæ to correspond to the crossing places of the winds of the spirals. It is obvious from the same figures that both the longitudinal and transverse striæ are produced by the refraction of light; for at the very part where the dark striæ present themselves, the rays from the mirror of the microscope fall upon oblique surfaces, where they are diverted from their direct course and do not reach the eye. The dark longitudinal striæ are produced by the cylindrical form of the elementary muscular threads, and the dark transverse striæ arise partly from the same cylindrical form of the muscular threads, but chiefly from the oblique direction of the same at their crossing.

Had observers paid due attention to the history of development, they could not have failed to observe a pellucid gelatinous substance to which the author has given a name suggested to him by Professor Owen, that of hyaline; a name descriptive of the appearance only, though the substance evidently performs functions rendering it in importance second to none. In muscle, this substance, hyaline, is often found within the winds of the spiral threads; often the fibril is enclosed within a cylinder of hyaline, fig. 3. It is very important to be aware of the little difference in refractive power between the hyaline and the substance of the spirals, whereby the outline of the latter becomes almost invisible. This is especially the case when the fibril still lies in the primitive fasciculus, and even occurs after its separation from it. Hence the different views taken by observers of the fibril, especially that assigning to it a structure comparable to a row of varicosities or beads. It is therefore equally important to apply reagents that will serve to introduce a greater difference in the refractive power of the two substances in question, and thus diminish the misleading influence of the hyaline.

This hyaline appears in another way to have misled observers. Where contained within the winds of spiral threads, fig. 6 *a*, it holds together a row of cell-germs; which cell-germs, on the wearing out as contractors of the old spiral threads, give the material for new ones. And some observers, overlooking the spiral threads, probably mistook such rows of cell-germs for fibrils. This mistake is very likely to be made when the muscle has undergone a slight degree of decomposition, fig. 6 *b*, whereby the spiral threads dissolve and disappear sooner, leaving exposed the axis of hyaline with its row of cell-germs. Prof. Bowman appears to have figured such an axis of hyaline containing cell-germs, as a fibril*. It may appear absurd to suppose that any doubt on such a matter can be entertained; and yet, since the mistake in question has been made, the author ventures to ask physiologists which appears to them the more probable: that spirals are formed first in order to produce cell-germs (!), or that cell-germs are first formed in order that they may give origin to spirals? *c* and *d* in fig. 6, show division and subdivision of the cell-germs for the production of minuter spirals. It must be admitted that the changes in the structure of the fibrils, attending their continued composition or decomposition, present a series of transition states such as may mislead all engaged in this most difficult field of observation.

It is known that in some states the primitive fasciculi during manipulation break off short, that is transversely, and that in other states they divide in a longitudinal direction; but it is not known on what this difference depends. The author explains it thus:—He finds the tendency to transverse cleavage to be in proportion to the amount of contraction the muscle happens to

* Cyclopædia of Anatomy and Physiology, article "Muscle and Muscular Contraction," fig. 287 *c*. In his earlier work, Phil. Trans. 1840, no such figure is to be found.

be in at the time of manipulation, while relaxation in the same proportion causes the giving way in a longitudinal direction; and he offers the following as perhaps sufficient to account for the difference. In contraction, where the transverse striæ are narrow, the spirals cross each other (*i. e.* antagonize each other) at the acutest angles; and in such a state of course it is that there occurs most easily a mutual *cutting through*, producing the "discs" of Bowman, to be again referred to. On the other hand, in relaxation the spirals meet only at obtuse angles, whereby the tendency to cutting through is in proportion lessened. The cutting through of the spirals when crossing at acute angles is illustrated by reference to a play with twine, familiar to school-boys.

In the early stages of development, however, fasciculi are sometimes met with in which the fibrillæ are so surrounded with large spirals, that longitudinal cleavage would be difficult however complete the relaxation. Of such large spirals, not merely two, but many interlace,—each surrounding its own cluster of fibrils. These large spirals pass into membrane and form septa*. Now within the winds of the larger spirals there arise smaller ones, which in their turn enlarge and pass into membrane, to be succeeded by another generation, and so on; by which it is easy to understand the prevention of longitudinal cleavage, as well indeed as the difficulty constantly met with when endeavouring to obtain separate fibrils for microscopic examination. Again, the state of the primitive fasciculus in fig. 7 was met with; where the fibrillæ, *c*, were shared by more than one surrounding spiral, *b*; the whole being surrounded by a larger spiral, *a*. Here also cleavage in a longitudinal direction would be very difficult. Further, the author saw states in which there was absolutely no cleavage, the fasciculus before breaking off becoming tapered to a point, fig. 8. This tapering to a point seemed referrible partly to great distensibility of the sarcolemma, and partly to a loose condition of fibrils already somewhat relaxed; and it is beautifully demonstrative of a spiral structure. (See the figure, and contrast the direction of the curves of the spirals at *a* with that at *b*.) Besides, at *a* the fasciculus was thick, while at *b* it was thin; and as the spirals became more and more drawn out, the fasciculus became more and more thin, until it terminated in a point. (The arrow shows the longitudinal direction of the fasciculus.)

It not rarely happens in the breaking off of twine, in which the two threads composing it are of unequal extensibility, that

* Bowman observed that the inner surface of the sarcolemma often presented irregularities, which the author thinks were no other than remains of septa such as those above mentioned.

one of them is more drawn out than the other, which becomes coiled around it as around an axis. Such a state being not unfrequently presented by twine-like muscular fibrils, fig. 9, after the breaking of them up with needles, it is important that the observer should be aware how the appearance is produced; for it may easily mislead him into the belief that he sees a row of alternately longer and shorter "beads."

The author is convinced that, with the exception of one case already mentioned (fig. 6 *b*), in all instances where Prof. Bowman speaks of fibrils, he had before him, without recognising them, nothing less than spirals. "Very reluctantly," says the author, "should I again enter into a controversy with a fellow-countryman whom I much esteem, were I not sure that his desire to arrive at the truth in this matter is quite equal to my own." He then gives copies of five of Bowman's figures, fig. 10 *a, b, c, d, e,* placing beside them five corresponding figures of his own, fig. 11 *a, b, c, d, e,* and showing the former to be, not, as supposed by Bowman, rows of beads, but different states of double spirals. No doubt, it is added, Bowman's fibrils had undergone some change; for three out of five of the preparations from which they were drawn had been preserved in spirit, while the fourth had been exposed to maceration.

What the author states of Bowman's figures of fibrils applies equally to the drawings given by that physiologist of fasciculi, though the latter are on a smaller scale. And no one, he thinks, who will take the trouble carefully to compare Bowman's figures 39 and 40, in his memoir, Phil. Trans. 1840, as well as those in his (Bowman's) Plate 19, in the same memoir, with what has been said in the present paper of the change in breadth of the transverse striæ in consequence of the difference in direction of the winds of the crossing spirals, will refuse to admit that the latter serves fully to explain the former.

We are indebted to Bowman for representations of manifold appearances presented by primitive fasciculi during their contraction and expansion, though from being unacquainted with the spiral structure of muscle he could not explain them, and wisely avoided the attempt to do so, except that he sought to refer the approach towards, and withdrawal from one another of the transverse striæ, to contraction and expansion of his supposed "discs."

But what are these "discs" of Bowman? Certainly not what he thinks, layers of muscular substance, "primitive component particles," an assemblage of which constitutes the primitive fasciculus. Bowman's discs are really nothing else than the bright parts of the transverse striæ, in which the single winds of the spiral threads are arranged in adjacent order (fig. 5 *a, a, a*), and as it were, into '*étages*' or series. (See fig. 12, where one of these '*étages*,' the lowest, is separated from the rest by the cutting of the spirals at their points of crossing.) The dark places in the transverse striæ correspond to those separating Bowman's discs. They are nothing else than the crossing places of the spiral threads. Here the latter come into immediate contact with one another,—can with pressure be made to exercise a cutting power,—and, as before said, actually to cut each other through. This, too, must take place more or less in stories or '*étages*,' as the points of crossing are for the most part on the same level. And when the cutting through has taken place, each story or '*étage*' represents one of Bowman's discs*. (The author here points out a difference between merely perspective crossing of the spirals, and that crossing where they are in contact; it being of course at the latter only that there can be a cutting through.)

Whence comes it that, as was observed by Bowman, contraction at any part of the primitive fasciculus (characterized as this is by greater nearness of the transverse striæ) is attended, both before and behind that part, in the longitudinal direction, with a separation of the transverse striæ? The cause, according to the author, is simply this: when the spiral threads extend more in a transverse direction at one part than at another, this can take place in no other way than at the expense in the longitudinal direction of their continuations, the winds or loops of which, thereby drawn out of the transverse direction, assume one that is more longitudinal.

Bowman is right in maintaining that contraction of the primitive fasciculus has nothing to do with zigzag inflexions of the same. On the contrary, as Bowman remarks, it has been shown by Owen that it is in *relaxation* that these zigzag inflexions may arise; and not only so, but that in the Filaria they are regularly present in relaxation, being there indeed characteristic of the relaxed state of muscle. The author inquires, How then does it happen that such zigzag inflexions may arise in relaxation? He thinks it may possibly be in the following manner:—Suppose the extreme ends of the primitive fasciculus through any hinderance to remain fixed, and that the fibrillæ, after cessation of the influence of the contractile force, strive by means of their own elasticity, and in consequence of the relaxation of their spiral

* This, however, is not always the case; for at different parts in the breadth of the same primitive fasciculus the fibrils may be in different degrees of contraction, and their points of crossing therefore on different levels. In such states the transverse striæ, viewed with changes of focal distance, are seen to change their place continually, according as viewed near the periphery or at greater depth, as was observed by Bowman, and as every experienced microscopic observer must have noticed.

threads, to gain a greater length; but being prevented from doing so by the hinderance above supposed at their ends, they seek to gain that greater length through lateral inflexions, which in such a case must produce a zigzag form. Were an antagonizing force applied, the elongation could follow without the formation of such zigzags.

We are indebted to Prof. Bowman for many microscopic measurements of the primitive fasciculi in different classes of animals. He found the largest in Fishes; they had a less size in the Amphibia, were smaller in Mammals, and smallest in Birds. Bowman's measurements are very numerous, and were no doubt made with the greatest care. He has, however, omitted to draw general conclusions therefrom, and makes no remark as to the cause of those differences in size. The author in this respect follows the example of Prof. Bowman. He brings forward no general conclusions of his own on the subject, and indeed for this reason: because he thinks that we ought first to have determined the mean size of the primitive fasciculi in the same individual as well as in different individuals of the same species, according to their different manifestations of activity, before we undertake to draw general conclusions. Yet he cannot refrain from here pointing to the following fact, mentioned in a former part of his memoir. According to his observations, the primitive fasciculi are at first merely double spirals, *i. e.* they are no other than fibrils. The metamorphosis of fibrils into primitive fasciculi is especially observable in the heart, where the young fasciculi are found, at first flat and scarcely broader than the fibrils themselves. The cause of these continued changes in the muscle of the heart, as already said, it may well be supposed is no other than the ceaseless activity of that organ. Scarcely is it to be doubted that the same thing takes place in other muscle also, though more slowly. (Certain muscles are then referred to as affording examples of great activity, and it is remarked that in different individuals of the human race the primitive fasciculi in the muscle of certain parts are probably unusually small.) Hence it occurred to the author to offer the following remarks concerning the measurements of Bowman. In Fishes the primitive fasciculi were found the largest, because of the low degree of muscular activity required in the element in which they live (though perhaps the muscles of the fins and gills may be here excepted, and it is known that they present even externally an appearance different from that of the other muscles). In Birds, on the contrary, the primitive fasciculi were found the smallest, as was to be expected from the high degree of muscular activity of this class. Amphibia and Mammals presented a middle average size, from their muscular activity occupying a middle place; but here it must be remarked, that striking differences would certainly have been met with had Bowman's researches been of a more special kind; for it is probable that the salamanders and other naked Amphibia would have presented still larger fasciculi than even Fishes.

Schwann was the first to make us acquainted with the existence of the sarcolemma. An independent discovery of it was made by Bowman, to whom it is that we are indebted for an exact description of that structure and an appropriate name. Its mode of formation out of spirally arranged cells, the author believes to have been first seen and published by himself. That mode of formation of the sarcolemma appears to be as follows:— At *a*, fig. 13, is a coil of young cells (once a column of compound cytoblast, as at fig. 20 *c*). *a*, in fig. 13, is a drawing from nature; *b* in the same figure is a diagram. *a* passes into *b*. That the spirals really do consist of cells is seen from fig. 14, a drawing from nature, in which *a* represents a large double spiral from the tail of the tadpole when very young, and *b* the remains of a similar double spiral after the addition of acetic acid. The acid removed the coalesced membranes of the cells, of which the double spiral *a* was composed, and left the nuclei behind in double spiral order. At *c* is seen the structure of one of those nuclei. They contained the elements of division, by which division the spirals pass into the state of membrane. And fig. 15, also from nature, shows such division to have taken place; this figure representing a stage in the formation of the sarcolemma.

With regard to the function performed by the sarcolemma, no definite opinion appears to have been given. The author believes that its function depends on elasticity. As the walls of the sarcolemma-cylinder are distended during the contraction of the double spiral threads, they return inwards as soon as relaxation comes on. And it is in this manner that the active relaxation of the fasciculus of muscle is to be explained.

Muscle from the thigh of the Grasshopper (of which many individuals, including several species, were examined) having uniformly presented a relaxed state nearly approaching to that in fig. 16 (which, however, is merely a diagram), it appeared to the author probable that such a state was not unconnected with the sudden muscular contractions required by this creature for its leaps. A sudden change from such a state of relaxation to that of extreme contraction must here take place with the greatest facility, and be combined with the manifestation of great power. This opinion having been mentioned to Prof. Purkinje, the latter recommended the author to examine the corresponding muscle from the Flea, in which, from its enormous leaps, something similar would he thought be found. The author accordingly examined some of these, and had the satisfaction to find in them a degree of muscular relaxation even higher than that he had observed in the grasshopper. In the two figures, fig. 16 and fig. 5, the parts in fig. 16 marked *b*, *b*, correspond to *b'*, *b'* in fig. 5. From a comparison of these two figures, it will be at once seen how the extended *b*, *b* in fig. 16, pass in contraction into the narrower *b'*, *b'*, fig. 5. Similar conditions no doubt exist in other animals, but perhaps nowhere are they more remarkable and constant than in those just mentioned. The observation may possibly induce some to bestow their attention upon this subject when examining leaping insects as well as other animals.

The author repeats a drawing he gave in the Phil. Trans. for 1842, of an artery from the pia mater of the Rabbit, fig. 17, of which the following is an explanation :—*a*, longitudinal muscular fibrils, represented merely by rows of dots, except a single one on the left side in which is shown the double spiral; *b*, outline of a fibril surrounding the longitudinal ones; *c*, double spiral structure of *b*; *d*, blood-corpuscles, for the most part young and very small; *e*, a line denoting the inner membrane of the artery. He then gives a figure, fig. 18, representing more distinctly the double spiral structure of such a fibril as *b* in fig. 17.

His observations on the history of development of muscle are given in detail, with many illustrative drawings; but as only a part of the latter can be given in this abstract, it is not intended to offer here more than the substance of the principal facts he observed, which were as follows :—

Cells having arranged themselves as at *a*, fig. 19, and their membranes having passed through the states *b* and *c* in the same figure, and a tube having been thus formed (stages known to other observers), columns of compound cytoblasts are seen within the tube, fig. 20 *b*, *c*; which cytoblasts have descended by division from the nuclei of the primitive cells, fig. 19 *a*. (The compound cytoblasts in these columns are arranged with such regularity as to produce, and explain the nature of, the striæ seen by Schwann, fig. 20 *a*.) The membrane of the tube disappears, not forming, as Schwann thought, a permanent sarcolemma; and the columns of compound cytoblasts having passed into coils of cells, fig. 13 *a*, a spiral is formed of them, as shown by the diagram *b* in the latter figure. A central row of cell-germs is left for the formation of future spirals; and the spiral first formed divides, and, as above shown, passes into membrane—the first sarcolemma. Such future spirals in a far later stage are seen in fig. 21; and fig. 22, *a*, *b*, *c*, shows the way in which the cell-germs perpetuate themselves by division and subdivision, every spiral having within its winds the elements of reproduction, fig. 23; and the primitive fasciculus being often found to have preserved cell-germs for a more general purpose in a central line, fig. 21. The reproduction of muscle, when fully formed, is probably no other than a continuation of its history of development, and has been already illustrated in fig. 6. By self-division of its hyaline axis of cell-germs, every fibril may become converted into a primitive fasciculus.

The laws of development in general are best studied in the ovum; and he who holds the wondrous process of cell-formation in the germinal vesicle, *i. e.* the history of development of the germinal spot described by the author in the Philosophical Transactions for 1840 as undeserving of particular attention, may spare himself the trouble of inquiring into the history of development of muscle, or that of any other tissue, as his labour would be thrown away. In that development of the germinal spot, the hyaline in the centre of the spot is obviously the prime mover. It is the hyaline in the centre of the germinal spot that is the substance undergoing fecundation; and no doubt it is the hyaline seen in the head-like extremity of the spermatozoon that is the real fecundating substance. (The author once saw, and figured in the Philosophical Transactions for 1840, what appeared to him to be a spermatozoon in the very act of entering the ovum of the rabbit; its head having already penetrated an orifice discernible for a time in the zona pellucida*.) In the

* He mentions having repeatedly found unaltered spermatozoa in the interior of the ovum in its next stages, after it had passed into the Fallopian tube; and having had the opportunity of showing them to Professor Owen, who declared himself fully convinced of the presence of the spermatozoa within the ovum. Once the author counted as many as seven in a single ovum. (A drawing of that ovum will be found in a paper by him "On Fissiparous Generation," in the Edinburgh New Philosophical Journal, October 1843.) In all instances the spermatozoa were motionless; and not among the cells in which the development of the essential substance was proceeding, but in the colourless fluid between those cells and in the zona pellucida. [While passing through London in May 1852, the author learns that after the lapse of many years these observations have been in two quarters confirmed by others; Dr. Nelson having presented to the Royal Society a paper announcing the presence of spermatozoa in the interior of the ovum of a creature at the other end of the animal kingdom, *Ascaris mystax*; and Mr. Newport having added a postscript to a paper of his on the ovum of the frog, also presented to the Royal Society, in which he candidly acknowledges having erred when, in a former memoir, he questioned the accuracy of the discovery made by the author of the present paper, that entire spermatozoa do actually make their way into the interior of the ovum.]

ovum of the Rabbit, after fecundation, the germinal vesicle returns to the centre of the ovum, and the fecundated hyaline passes to the centre of the germinal vesicle. This hyaline, in consequence of fecundation, now contains substances of two kinds,—one from the female ovum, the other from the male fecundating fluid. Through a process operating in the germinal vesicle before fecundation, the hyaline of the ovum had prepared a sort of pabulum,—minute globules of hyaline. With this pabulum, the new hyaline, a compound of male and female elements, proceeds to nourish itself; or, in other words, proceeds to assimilate the contents of the germinal vesicle, whereby there arises a material for the formation of two cell-germs into which it divides. These two cell-germs grow at the expense of the remaining contents of the germinal vesicle, which are nutrimental cells, until the whole are consumed. The membrane of the germinal vesicle, the mother-cell of the whole body, has now disappeared, and there are seen in the place of that vesicle two young cells, which together constitute the new organic being. How shall we designate the hyaline of this new being? If we call the hyaline of the ovum, hyaline No. 1, and that from the fecundating substance, hyaline No. 2, we have in the new organic being, hyaline No. 3. No. 1 denotes the maternal hyaline, No. 2 the paternal fecundating substance, and No. 3 composed of the first and second, the hyaline of the offspring. Hence it is that the offspring comes to resemble both parents; for, be the resemblance effected as it may, the so compounded hyaline of the offspring will never lose a constitution inherited partly from the father and partly from the mother. And how does the hyaline of the offspring now begin to propagate itself, so that at last a creature shall arise out of it, in stature and other peculiarities like the parents? This is effected by self-division and repeated self-division. Each of the two cells just mentioned, together constituting the new organic being, becomes in its turn a mother-cell, so that now there are four; and in like manner there arise 8, 16, and so on, until the whole assumes the appearance of a mulberry. In the centre of this mulberry-like aggregate of cells there now appears one larger than the rest, like a queen-bee in the hive. This is the only cell in the group that has an enduring existence, *i. e.* in its progeny; all the others serve but a temporary purpose. (We thus have a sort of aristocracy of cells! first manifesting itself in the two above-mentioned as arising in the germinal vesicle, and nourished at the expense of all the surrounding cells.) This large cell now moves from the centre of the ovum towards the periphery, and here takes a fixed station. The hyaline nucleus of this cell is now to be considered as the most peculiar germ of the whole organism. Out of the nucleus of this cell, after many intermediate stages of formation, there at length arises the "primitive trace," and Von Baer's "chorda dorsalis." For other details, the author refers to his researches published in the Philosophical Transactions for 1839 and 1840; not deeming it suitable to the purpose of the present paper to add more, than that the process through which the first and continually repeated self-division of the hyaline is effected, is no other than a repetition of the same process which operates in the germinal spot of the germinal vesicle, as the original cell of the organism; in which process the operation of certain functions required for an increase of substance is implied, viz. absorption, assimilation, and secretion. In the cells thus descending from the original mother-cell down to the remotest generation, it is evident that the same wondrous process is repeated, the same increase of the hyaline; which at first takes a peripheral station in the cell in order through absorption to be newly fecundated (for what in this case is absorption, but the fecundation of the hyaline of the cell through a relatively external substance maintaining the process of division?) Then, after fecundation at the periphery, the hyaline passes into the middle of the cell, there again to divide into new generations of cells, which finally arrange themselves so as to form the various tissues of the organism. But the germinal spot process continues even here. (Compare the contents of the cell in fig. 19 *a*, with the author's delineations of the contents of the germinal vesicle, Phil. Trans. 1840, Plate 22. figs. 159, 160, 162 *c*.)

Every one who has noticed the author's drawings of a certain state of the two cells succeeding the germinal vesicle, must have been struck with the resemblance they bear to corpuscles of the blood. He deems it important in this place to refer to observations he long since published, that both have the same destination; through both these structures, as well the blood-corpuscles as the cells of the ovum, is it intended to reproduce the hyaline,—the one being floating, and the other fixed centres of that process of assimilation which effects the reproduction of the hyaline. The germinal vesicle may be regarded as a living being; and every blood-corpuscle as one of the progeny of the germinal vesicle, reproducing itself, as that vesicle itself does, by division of its fecundated hyaline. We may consider the blood-corpuscles as a floating shoal of Infusoria, receiving as their nourishment the chyle. So nourished, or rather (as regards their hyaline centres) so fecundated, the blood-corpuscles repeat in their interior the whole germinal spot process, since in some of them there proceeds the self-division and repeated self-division of the hyaline, whereby new generations of blood-corpuscles arise, which again repeat the same process; while others deposit upon the walls of the capillaries their hyaline, which operates with fecundating power upon cells lying in the parenchyma of the organs, and becomes assimilated according to the specific constitution of the same. Sometimes, instead of chyle, as the fecundating substance to be assimilated, there reaches the hyaline of the blood-corpuscles quite another heterogeneous substance, for instance some sort of infectious matter, organic or animal poison, &c., whereby there as surely arise diseased processes of formation, which communicate themselves to the remaining portion of the blood or to the parenchyma of the organs.

The author refers to a full confirmation of his observations on the remarkable process of cell-formation in the germinal vesicle of the mammiferous ovum, by those of Mr. H. D. S. Goodsir on a cystic entozoon. And as this lies at the other end of the series of organic existences, the operation of the process in question there, implies its operation in all intermediate ones.

He then notices an objection made to his observations, published in 1839 and 1840, when making known the fact that cleavage takes place in the *mammiferous* ovum also,—that such cleavage is effected by means of cells; showing that inadequate research led to that objection, and concluding his remarks with the following words:—"After having examined 230 ova found in the Fallopian tube, with the sacrifice of 150 rabbits for embryological research, of which rabbits at least a score were devoted to anatomical inspection for the purpose of enabling me to determine the time at which the ovum leaves the ovary,—no man will wonder that I deem myself competent to judge whether the divisions of the germ are, or are not effected by means of cells. No man who does not examine mammiferous ova in large number immediately before their exit from the ovary, or otherwise through observations on animals or plants make himself acquainted with the germinal-spot-process of division, is able to comprehend the formative process in the mammiferous ovum in any of its earlier or later stages, or indeed *to understand the physiology of cells**."

A former drawing, fig. 13, shows the mode in which a spiral arises out of cells. The following may serve to illustrate the way in which the *twin* or *double* spiral is produced. Every microscopic observer must be familiar with segmented cytoblasts,

* [In the mammiferous ovum there is no substance that can be called a food-yelk. The germ-cells therefore are not there obscured by a surrounding yelk-mass, the cleavage of which they *govern*, as seems to be the case in ova since figured by other observers.]

the annular arrangement of cell-germs in fig. 24, *b, c, d*. Of such rings of cell-germs, two are sometimes met with, connected like two links of a chain, fig. 25. Let the diagram fig. 26 *c* represent a pile of such pairs of connected rings. Now rings such as those in fig. 24 are seen to pass into the state at *h* in the same figure. And this change occurring in each ring of the pile of pairs of rings, fig. 26 *c*, with a uniting at the extremities of rings lying one upon another, would produce the twin or double spiral *d* in the same figure*. Nature, it may be objected, is a more skilful architect. She does not first form rings in order afterwards to divide them and unite their extremities in another way. All is from the first arranged in spiral order. Without denying this, and fully admitting that there is from the first a tendency to arrangement in spiral order, the author still maintains that rings of cell-germs are constantly met with; and that since it is so ordered that spirals shall arise by the union of separate cells, it is in perfect keeping with the form of the cytoblast (fig. 24 *a*), that the germs of those cells when first seen should be arranged in the form of rings. [It must not be forgotten that each of the rings entering into the formation of the spiral has its centre of hyaline, whence the cell-germs of the next generation of spirals. See fig. 13.]

That which in nutrition is ascribed exclusively to the fibrin of the lymph (and which probably corresponds to the author's hyaline), he believes to be derived from the blood-corpuscles themselves. And it is his opinion, that in the coagulation of the blood Nature gives us an example of the coagulation of the blood-corpuscles; for, as he showed in 1842, *many fibres arise through coagulation within those corpuscles*; whereby the latter either pass entirely into fibres, as in the cytoblast blood-corpuscles of the Mammalia, or the coagulation takes place within blood-cells, as in the other Vertebrata.

As already said, the reproduction of muscle seems to take place by a process not differing essentially from that which formed it, a process of division and subdivision of the germs of cells. And what are these germs of cells? They consist of nothing less than that wondrous substance hyaline, the unceasing maintenance of which the author believes to be the main purpose in the formation and division of cells. Each central row of cell-germs within the windings of the spiral threads is really an axis-cylinder of hyaline; and when this divides, there arises a double

* [Or suppose a single pile of such bodies as that at *h* in fig. 24. The union of their extremities would produce a single spiral; and longitudinal division of this single spiral would produce a double one.]

cylinder, and so on. All these rows of cell-germs, arisen through division and subdivision of the nuclei of the primitive cells which arranged themselves in necklace-like order to form the first muscle tubes, as well as the germs of those primitive cells themselves, are descended through division from those substances in the ovum which again had arisen from the fecundated germinal spot or nucleus of the germinal vesicle.

In a brief recapitulation concerning hyaline, the author states his Researches in Embryology as well as his observations on the Corpuscles of the Blood (Phil. Trans. 1838, 1839, 1840, 1841), to have afforded him abundant opportunity for becoming acquainted with it*. He found it in the so-called nucleolus of cells in general, as well as in the germinal spot of the germinal vesicle, to be the point of fecundation,—to be present in the head-like extremity of the spermatozoon,—to constitute as globules, immeasurably minute, the foundation of cytoblasts, these being the real germs of cells. He showed that this hyaline forms as well the membrane as the contents of the cell,—that to it belong the functions of absorption, assimilation, and secretion,—that so long as the vegetative process is in full activity it never ceases to be in operation, but divides and subdivides to form new cells, or rather to reproduce itself. For in the reproduction of cells, the maintenance, the division, and the increase of the hyaline appears to be the main purpose. It may be asked, What is there, then, in the organic body which is not formed through hyaline? Truly nothing. It is the essentially living substance in the body, the whole organism is the product of its formative force. All cell-germs are really, through repeated self-division, effected by a remarkable assimilative process, descendants of the hyaline of the germinal vesicle, this having been fecundated by a substance from the male; whence the resemblance between the offspring and both its parents. Finally, referring to his observations on the mode of origin and structure of nerve and other tissues, the author adds, that were it not that he would probably be blamed for excessive phantasy, he would not hesitate to declare the hyaline, as the foundation of the central nucleus of ganglion globules and of the axis-cylinders of nerves, to be the immediate organ of sensation of every kind.

* See the Edinb. New Phil. Journ. Oct. 1843, a paper "On Fissiparous Generation;" and in the same Journal, Oct. 1847, another "On the Nucleus of the Animal and Vegetable Cell."

On the Muscularity of Cilia.

As his previous observations had led him to expect, cilia were found to be no other than his twin or double spirals. No man, he thinks, will do him the injustice to suppose he maintains the possibility of discerning a double spiral in the minutest cilium. He is as far from maintaining this as he is from asserting the possibility of seeing a double spiral in the minutest muscular fibril. But he does maintain that those who undertake the examination of cilia in the way in which they should set about the examination of all organic tissues, *i. e.* with a desire to know how they originate, what is the history of their development, will certainly find that the double spiral is the fundamental form of all cilia the structure of which can be reached with the microscope, and therefore probably of the most minute. Indeed under favourable circumstances, traces thereof are not so very rarely to be discerned, by the accustomed eye, even in the latter.

In the author's observations he used several bivalve mollusca, including the Oyster, *Ostrea edulis,* and the common Sea Mussel, *Mytilus edulis.* The one last mentioned is to be preferred, because of the bars of its branchial laminæ being most easy of separation. And this mussel is further recommended to those disposed to repeat the author's observations, on account of the excellent description of its gills given by Dr. Sharpey in his Article "Cilia" in Todd's Cyclopædia of Anatomy and Physiology. He recommends the examination of this Mussel when small, because of the branchial laminæ being more transparent than in the larger specimens. He examined some in which the shell measured scarcely two lines in length, they being the smallest he could obtain. The most convenient size, however, he found to be that in which the shell measured in length from $\frac{1}{2}$ to $\frac{3}{4}$ of an inch. Still an examination of the largest should not be omitted.

Convinced by his earlier microscopic labours that it is best to direct the eye for a considerable time exclusively to the same part or set of objects in order to enable it to detect minute differences in the same or in different individuals, the author directed his solely to the branchial laminæ, and here to little more than the sides of those parallel bars of which the branchial laminæ are composed. In this way it was that he became acquainted with the fact, that, as the ever-acting heart requires a continued renewal of its fibrils, so are new generations continually preparing to succeed the indefatigably vibrating cilia.

Before detailing his observations, the author states what others should do who may be disposed to repeat the examinations. A small piece, about a square line, having been cut from the marginal-edge of the gill and placed upon glass, he adds to it a drop of the fluid, which, on the mussel being opened, collects in the shell, gently and to a small extent separates the bars from one another with fine needles, and places them under the microscope without the addition of any covering such as glass or mica. It is soon seen that some of the bars, wedge-like in their transverse sections, present the thicker of their edges to the eye, fig. 37, while others are lying on their sides, figs. 41, 36. Both should be examined with especial reference to the cilia on the two sides of the bar. Of these cilia there are three sets, and not two only, as hitherto supposed; one set uppermost when the thicker edge of the bar is directed towards the eye, and marked *m* in the figures just referred to; the second occupying a middle place, and marked *n* in the same figures; the third lowest, and marked *o*.

Concerning these cilia, the author states the following as new facts:—In the *first* place, these cilia, and from analogy probably all cilia, consist of double spiral threads, and thus have a structure like that of the muscular fibril; *secondly*, the cilia *m*, fig. 36, &c., present merely stages in the development of the cilia *n*; *thirdly*, the cilia *o*, in the same figures, hitherto either overlooked or held to be identical with the cilia *n*, are really not so,—they are the counterpart thereof. And he then proceeds to establish these three positions in the order here laid down, as follows:—

Separated from their localities by manipulation, and strewn through the field of view among the fragments of the gill, are seen simple cells, several of which are represented in outline in fig. 27. In the interior of such cells the young cilia are indicated. They push before them the membrane of the cell, so that it appears pointed; and afterwards present themselves, as in fig. 28, of a club-like form*. Sometimes this club-like form appears referrible to a provision of plastic substance at the extremity for the lengthening of the cilium, and sometimes to a bending down of the extremity hook-like upon itself. Up to this time the membrane of the cell appears in some instances to continue entire,—the young cilium, though coming into view, being as it were still unborn. At length the membrane is ruptured, and the bent down extremity of the cilium gradually developes and unrolls itself like a young fern, fig. 29. This figure, fig. 29, represents part of a large fragment, several of which were found in substance scraped from the gill of the Oyster. They contained at the margin numerous cells. The middle

* Probably Valentin saw the same stage of development in *Unio pictorum*, where he mentions it (the "club-like form") as an unusual shape ("ausnahmsweiser Gestalt").—R. Wagner's *Handwörterbuch der Physiologie*, p. 500.

space presented none. On the nature of these large fragments the author has for the present nothing further to remark, than that they afforded him an invaluable contribution towards the history of development of cilia; for of that development they presented with distinctness a very early stage. The minute cells in their interior seemed destined to give origin to cilia, which here and there, fig. 29, were seen to have been already formed and to have burst through the membrane of their cells. One of these, the interior of which was seen with rare distinctness, is represented on a larger scale in fig. 30. The young cilium here drawn consisted of two spirals, within the winds of which was a pellucid substance corresponding to that which the author above and elsewhere has termed hyaline. At the extremity the two spirals passed into one another, and were bent over hook-like towards one side. At the base they separated, to bestride, as it were, the contents of the cell in which the cilium had been formed*. Perhaps these two separate threads may be considered as the radical ends of the cilium, in which growth first of all takes place somewhat in the following manner:—The extremity of each of these two threads draws into itself new substance from the nucleus of the cell. And now as the cilium is alternately in the states of twisting and untwisting, it gradually spins up into its substance those after-threads, and in this manner elongates.

Drawings are then given of stages following those just described, of which figs. 31, 32, 33, and 34 present a selection. These different appearances evidently denote different degrees of development. [Corresponding differences were noticed in their movements. None of them, however, were in a perfect state. For the movements of even the most advanced were awkward, showing them to be, as it were, still in their apprenticeship.] Now to all of these cilia, making allowance for differences in the degree of development, may be applied the description just given of fig. 30; though it is only here and there that a trace of connexion with the cell, such as that in fig. 30, can be distinctly seen. The author thinks that no observer can attentively examine such cilia without seeing, as he did, that each of them consists of a double spiral thread, having therefore a structure like that of the muscular fibril, and thus establishing his position No. 1.

The broad cilia of which examples have been given in Beroë and other ciliograde Mollusca,—where, instead of cilia of usual form and arrangement, there are found rows of broad flat flaps each of which is said to consist of a row of single cilia,—appear to

* [It will be observed, that each of these separate threads is twisted on itself.]

the author to consist of *fasciculi* of cilia; and if this be the case, their mode of reproduction is probably the same as that of other muscle. He found the bulb at the base of some cilia much smaller than at that of others. This may have arisen from division,—a larger bulb together with its cilium dividing into two; or it may have arisen from consumption of the bulb, through nourishment and growth of the cilium. In other cases the bulb had entirely disappeared, and the cilia arose from a common ground, fig. 35 *h*. Here it is possible that after the bulbs had been entirely spent from the growth of the cilia, all trace thereof had disappeared.

Notwithstanding all that he has said, both in this treatise and in former ones, on the necessity in all researches on the structure of tissues of attending to the history of their development, the author adds that he feels called upon candidly to acknowledge cilia to present in this respect a difficulty such as perhaps is scarcely to be found elsewhere. Here the observer has it not in his power to *begin* with the history of development; for after what has been above stated of a continued renewal of the cilia, and of several stages in their development being sometimes met with even in the same bar, it cannot be expected that the younger cilia will necessarily be found in the younger mussels. The few facts in their development recorded in this memoir, were not fully ascertained until after a long series of measurements and observations on movements, and on forms of cilia met with *quite at random*. The author trusts his descriptions and drawings of the several stages may be useful to others in following out the history of development; but it is a misfortune for him not to have it in his power to say just where the younger and most convincing stages are to be found, such as would enable others so easily to confirm his observations on their spiral structure. It is added: "You may open a very large number of mussels, and devote whole days to the examination, before you find an example for demonstration. If, however, you are so fortunate as to meet with a stage such as that in fig. 30, you feel richly rewarded for all the labour."

The author then proceeds to establish his position No. 2, that the cilia marked *m* in fig. 36, &c. are merely different stages in development of the cilia *n* in the same figures. To this unexpected observation he was led by the following facts.

In the *first* place, the cilia *m* and *n*, see fig. 36, have a common place of origin, their roots arising mixed together in the same field. *Secondly*. You here and there see one of the cilia *m* flexed at its base, by which its extremity is made to approach the extremities of the cilia *n*; but it instantly returns to its previous state, to be immediately afterwards depressed again as before; and so on*. *Thirdly.* You sometimes meet with states in which this depression of some of the cilia *m* is permanent. See *m'* in the same figure. *Fourthly.* As already mentioned, the cilia *m* in different individuals present very different states, figs. 31, 32, 33, 34, 39, 40. Their lengths differ, some being very short; sometimes they are straight, sometimes curved; sometimes they are found moving, sometimes motionless. The movements are generally quite irregular. There is nothing like a common purpose in them; certainly no combination for the production of a current. In some they are such as to suggest the idea of efforts to become unbent at their extremities, fig. 32; and in others no longer bent at their extremities, the movements seem made for the purpose of becoming elongated, fig. 40. You sometimes meet with the two last-mentioned states in the same bar, fig. 39. In short, these different appearances and movements evidently denote different degrees of development. Not until they reach the state in fig. 36 can the cilia *m* be said to have attained maturity, and to exhibit a common purpose in their movements. But even then their movements are not so vehement as to be likely soon to wear them out. Why, then, are they so constantly renewed? The fact is, that by flexion at the base, the cilia *m* (see fig. 36) pass, one after another, into the vehemently vibrating cilia *n*, which they succeed as a later generation. For this purpose they are formed, and then for the first time do they perform really efficient action. Thus it was that the author was led to his position No. 2.

In his third conclusion, he stated that the cilia *o* in fig. 36, &c., hitherto either overlooked or held to be identical with the cilia *n*, are really not so,—they are the counterpart thereof. This will be immediately made clear if attention be paid to their origin and the function they perform.

The roots of these two lines of cilia are separated by a broad pellucid space, fig. 36 *h*, in which are no cells such as those (*p*) giving origin to the cilia in question. The cilia of the two lines, proceeding from opposite sides of the pellucid space, arch over it, their extremities meeting in the middle line, where they, alternating with one another, like the fingers of the two hands, form

* The movements of the cilia *m* are described by Sharpey merely as follows:—"The more opake cilia, or those of the exterior range, appear and disappear by turns, as if they were continually changing from a horizontal to a vertical direction and back again."—*L. c.* p. 622. And the author says, he is not aware that any other author has given more exact information concerning them.

a sort of tunnel, through which water is driven by their vehement movements. So much for conclusion No. 3*.

On the subject of functions it is also to be remarked, that the pellucid space, fig. 36 *h*, over which these two lines of cilia, *n* and *o*, move so vehemently, belongs to the membrane of the bar (known to be considered as a vessel of the gill), which membrane is probably destined to absorb oxygen from the water and communicate it to the blood. This would be materially assisted were the stream of water accelerated, and a fresh supply of oxygen constantly afforded.

It must further be remembered, that, as is known, the direction of the current in neighbouring bars is different. If in one it is from the base of the gill towards its margin, in the next it is from the margin towards the base; in the one case appearing to end at a round projection covered with vibrating cilia, fig. 41 *qq*,—in the other appearing to begin there. The direction of the currents now mentioned as opposite in neighbouring bars, is also opposite on the two sides of the same bar, figs. 37, 38†. The round projection, fig. 41 *qq*, just referred to, Sharpey has not particularly mentioned. It seems to be of the same nature as his "round projections," *q* in the same figure, with this difference, that where the two bars pass into one another at their ends, two round projections pass into one. Hence the larger size of that at *qq*, fig. 41.

The marvellously complicated movements of the cilia *n* and *o*, figs. 36, 37, 38, 41, the author says he has very often observed, continuing to watch them until they became slower, and at length ceased. At last only groups of them are seen thus moving, then not more than two or three together, and finally single ones.

* The cilia *o*, as an independent line, Sharpey appears not to have observed; he mentions and figures merely the cilia *n*, as is evident from the following:—"The motion of the other set consists in a succession of undulations, which proceed in a uniform manner along the sides of the bar from one end to the other. It might be very easily mistaken for the circulation of globules of a fluid within a canal, more especially as the course of the undulations is different on the two sides of the bar, being directed on one side towards the edge of the gill, and on the other towards the base. But besides that the undulations continue for some time in small pieces cut off from the gill, which is inconsistent with the progression of fluid in a canal, the cilia are easily distinguished when the undulatory motion becomes languid. When it has entirely ceased, they remain in contact with each other, so as to present the appearance of a membrane (*d, d*, fig. F)."—Sharpey, *l. c.* p. 623.

So far Dr. Sharpey. And the author adds, that he is not aware of any other observer having made any mention of them,—the cilia *o*.

† [This fact also is already known.]

When the movements have entirely ceased, the two lines of cilia lie nearly parallel, fig. 36, *n*, *o*, and somewhat bent, with the convexity almost always in the same direction as the current their movements had occasioned.

It remains to be added respecting the cilia *n* and *o*, that when their movements have terminated, and the cilia are left in a state of relaxation, they often in a short time entirely disappear. Probably most of them break off at their roots, as indeed may constantly happen during life, when the old ones become replaced by new, the former going off when worn out, being carried away by the stream, and thrown out at the excretory orifice.

As nothing until now was known regarding the structure of cilia, everything brought forward as to the cause of their movements has been conjecture only. Having found in them a structure adapted for contraction and relaxation, the author has much pleasure in thus showing that his fellow-countryman, Professor Sharpey, was right when in the year 1836 he thought it probable that the moving power of cilia lay in the cilia themselves, and was referrible to a substance contained in more or less of their length, like that of muscle.

The undulatory movements of cilia,—compared by Sharpey, when many were seen together, to those produced by the wind on a field of corn,—the author on two occasions witnessed when performed by cilia in a single line, and when most perfect; on one of which occasions he had the pleasure of showing the rare spectacle to Purkinje. In both instances this living mechanism was seen at the marginal end of the bar, and in the line of cilia *m*, fig. 41; in one instance at the point *r*, in the other at the point marked *s*. The rough diagram, fig. 42, will scarcely serve to convey an idea of these undulatory movements, for the appearance was exceedingly delicate and beautiful. The undulating cilia in the two instances were in different conditions. In the one instance they had their spirals in a twine-like state, as in fig. 40, and were permanently contracted at no part; in the other instance they were permanently contracted at the base, as at *m* in fig. 36. In the first case the movements may have consisted merely of a shortening and lengthening in the axis of the cilia; in the second, of flexion at the base. Further, the cilia in the two instances in question were of different forms; in one instance being straight, as in fig. 40,—in the other curved, as in fig. 36 *m*. As now the contraction of a double spiral implies a twisting of the same, the extremity when bent must describe a course spirally infundibular, not represented in the diagram. [The author observed very young cilia, fig. 43, which evidently showed in their movements a shortening and lengthening. No definite order, however, such as that implied by undulation, was observed. Perhaps a disturbance had occurred through manipulation.]

It is important, the author thinks, to have seen these undulatory movements performed by the cilia *m*, fig. 36; for, as successors to the cilia *n*, the cilia thus undulating were about to arrange themselves in one of the two lines above mentioned as combining to form a sort of tunnel, through which by their extremely vehement movements to drive a rapid current. And the following occurred to him as possibly sufficient to explain the appearance presented by these movements,—which have been aptly compared to the rapid flow of globules of a fluid. The cilia *n*, fig. 36, are all bent in the same direction; they are arranged in a line, and perform their swinging or lashing movements in an undulatory manner according to the order of their positions in that line. Like movements, and in the like order, are performed by the cilia *o* in the opposite line; their extremities alternating with the extremities of the cilia *n* in the first line, like the fingers of the two hands, and moving without the slightest mutual interference. Now were the movements throughout the whole phalanx of cilia contemporaneous, there would be presented to the eye a permanent line of swinging movements. As, however, those swinging movements are performed by the cilia one after another in the order of their positions in the line, they assume the appearance of a row of roundish waves, following, or as it were chasing, and uninterruptedly passing into one another; not rarely appearing to the eye like a long revolving screw. The difference between rows of globules (the appearance most frequently presented by the movements in question) and screw-cylinders, may be supposed to arise as follows:—When the swinging movements are of different extent at different parts, we have the appearance comparable to a row of globules; when those movements pass uniformly into one another, there is seen the long-revolving screw*.

Having found the cilia on the branchial laminæ of Mussels to consist of double spirals, the author deems it scarcely needful to remark, that he infers a like structure in other cilia, exist where they may. As, however, in the course of these researches he has very often had the opportunity of examining cilia of Infusoria, several species of which are met with in the fluid of the Mussel's shell, he cannot refrain from making known the fact, that in these cilia also he finds his double spiral. Often did he

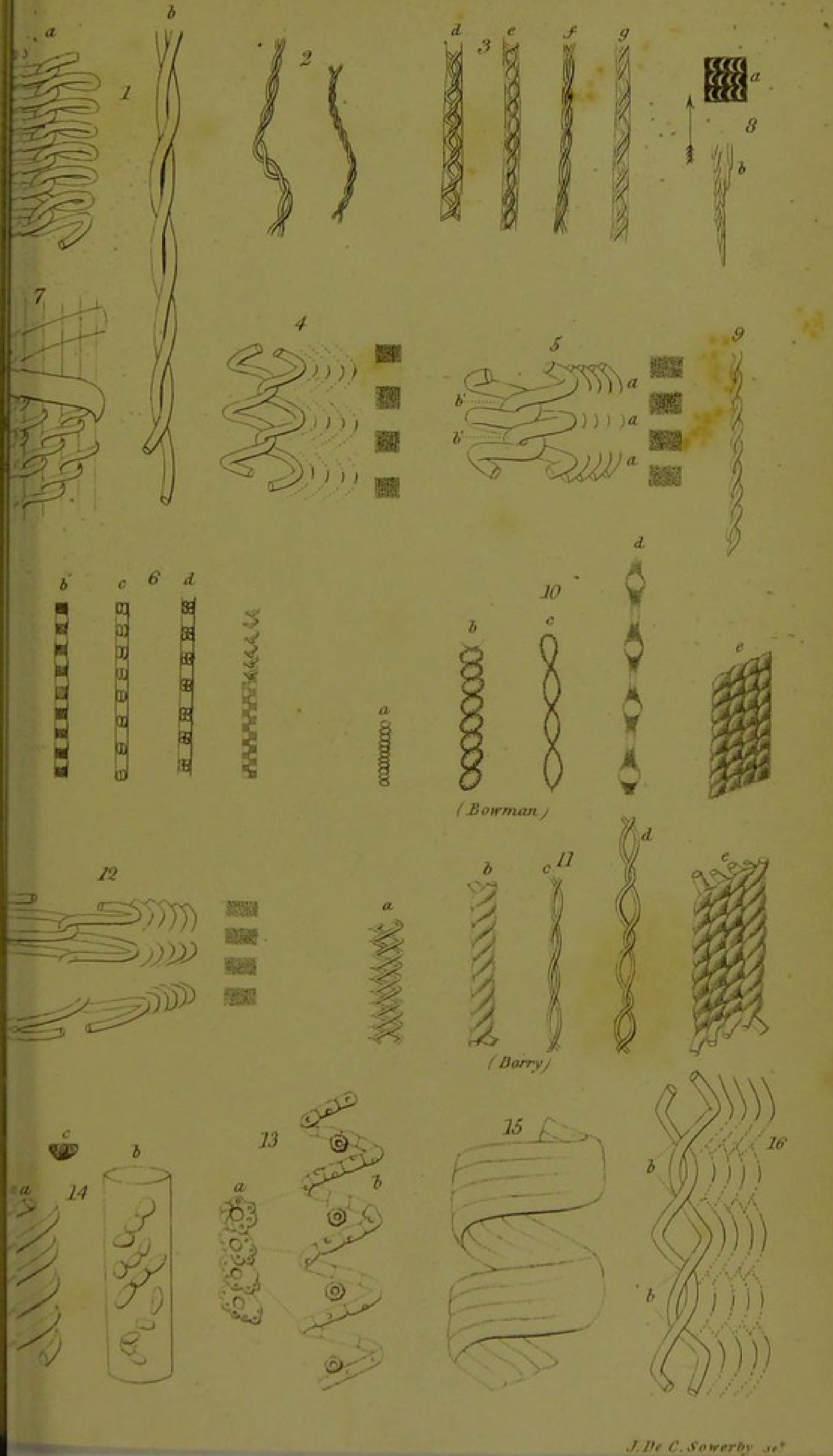
* [The screw probably exhibiting the normal, and the row of globules a disturbed state.]

see in them the spiral structure with such distinctness, as to feel astonished at its not having been long since observed. As the tails of spermatozoa of course correspond to cilia, their structure must be essentially the same. He states it to be now nine years since he published his observation of the spiral structure of the tail of the mammiferous spermatozoon (Phil. Trans. 1842, p. 107). It is probably owing to a like refractive power in the spirals and in the hyaline which lies between them, that the spirals are so difficult to distinguish in the tails of spermatozoa; and hence it no doubt is that they were not observed before.

The subject of the present paper being the structure of muscle, the author has avoided the special mention of other tissues. Lest, however, from this omission it should be supposed that he has abandoned his views,—that the structure of all the elementary fibres, as well of plants as of animals, is originally spiral,—he thinks it right before concluding briefly to declare that those views remain unchanged. Bowman says: "Dr. Barry might as well have entitled his paper 'On the Spiral Structure of the Organic World*.'" To this title, satirically proposed by Bowman, the author remarks that he has not the least objection; so far, indeed, is he from being thereby annoyed, that he thanks him for it. He thanks Prof. Bowman for having thus recorded in the Cyclopædia of Anatomy and Physiology, as far back as in the year 1842, that his (Dr. Barry's) views in regard to the spiral structure of organic fibre were universal in their character; "and I am convinced," it is added, "that the day will come when my views will be as universally adopted by physiologists, as I myself am convinced that the spiral structure is universal. Let it only be fully understood what those views are. What I maintain is, that the spiral form of fibre everywhere is the original and incipient form; and that if this form be lost in many tissues in the course of their special development, it remains permanent in the fibre of muscle as a necessary attribute of its function."

In a postscript it is added, that in the contractile stem of the Bell polype (*Vorticella convallaria*), of which several specimens were examined, the author found his double spiral. In relaxation, this double spiral lay in its extended cylindrical gelatinous sheath, (which he regards as its elastic sarcolemma) in [elongated] spiral winds. In contraction, it presented itself in a manner about the same as that in fig. 18; with this difference, that the double spiral in the polype was enclosed in its gelatinous sarcolemma, which that figure, representing quite another object, does not show.

* Cyclopædia of Anat. and Phys., art. "Muscle and Muscular Motion," p. 511.



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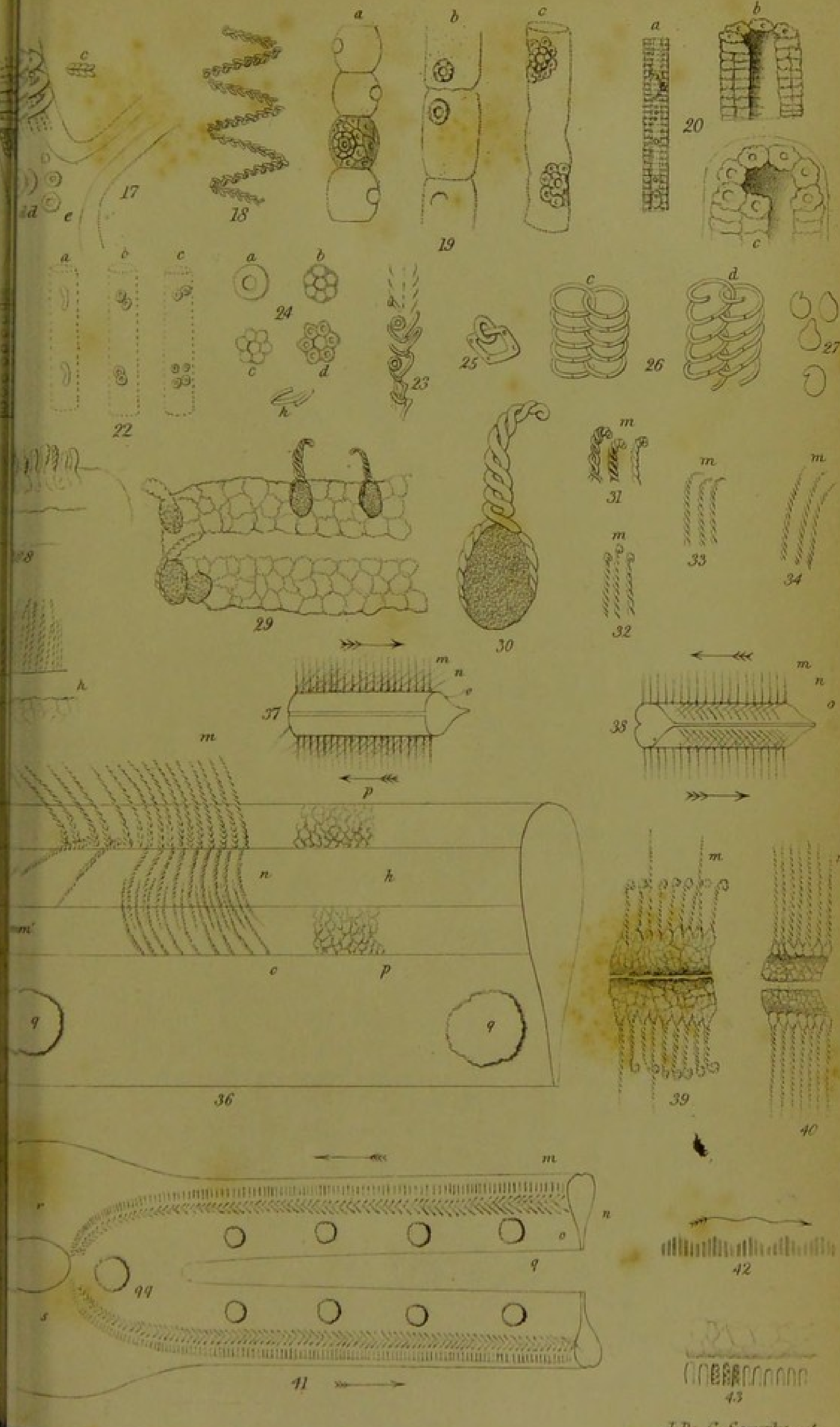

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