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The Structure and Division of the Vegetable Cell. By J. M. MACFARLANE, B.Sc., Demonstrator of Botany in the University of Edinburgh, (Plates IX. and X.)

(Read April 16 and May 12, 1881.)

Introduction.

During the last six years our knowledge of the animal and vegetable cell has been greatly increased. Previously, it was held by most observers that a typical cell consisted simply of a *wall* or bounding membrane, secreted from the *protoplasm* which filled the cell, a *nucleus* formed of protoplasm of a denser consistence than the surrounding mass. Inside the nucleus a *nucleolus* was supposed occasionally to be present. It is now being gradually discovered that the cell is of a more complicated nature, and is the centre of more complicated changes than had once been imagined. Admirable summaries of the advances made prior to 1878, especially those of Strasburger, have been given* by Priestley and Klein. To summarise briefly their papers, it may be said that a network of fibres can be seen permeating the substance of the cell attached on the inner surface to the nucleus, and that these are merely continuations of a similar network within the nucleus. The former has been termed by Klein the *intra-cellular network*, the latter, the *intra-nuclear network*. It is further stated by Klein that Eimer, Flemming, and himself consider that in the animal cell a *nuclear membrane* is present surrounding the nucleus.

As it is specially with the vegetable cell that I will deal, a more detailed account of Strasburger's investigations is necessary.† This author shows that in division of the cell the nucleus undergoes a series of peculiar changes. At first of a rounded or oval outline, the denser material aggregates to form a dark band—the *nuclear plate*—crossing a clear fusiform area—the *nuclear disc*. The former splits up, each part retreating along the clear area to its extremity, and there form the *daughter nuclei*. These are again united by a fibrous bridge, and in the middle of this a row of granules appear—forming the *cell-plate*—which

* Quart. Journ. Micro. Soc. vols. xvi. and xviii.

† Ueber Zellbildung und Zelltheilung.

in turn eventually split up; and between them the cellulose wall is formed. He does not attach any special significance to the nucleolus. This idea is shared by Klein, who says, referring to the animal cell:—"To every experienced student of histology it must have become apparent that if there is one thing unsatisfactory, unreliable, puzzling, and inconstant about the nucleus of vast numbers of cells, it is this very nucleolus." He concludes that the so-called nucleoli are either thickenings of the intra-nuclear network, or result from "shrivelling up and intimate fusion of a part of the network."

More recently Flemming, Treub, Schmidt, and Hegelmaier have contributed some important observations. Schmidt has shown* that in the cells of the *Siphonææ* and *Siphonocladææ* among Algæ, as also in *Saprolegnia* and the *Myxomycetes* among fungi, instead of one nucleus, many may be present; amounting in the genus *Valonia*, for instance, to several hundreds. He has further proved that various of the simpler algæ and fungi, formerly supposed destitute of a nucleus, possess such a body; and he concludes that in all Thallophytes the cells contain one or more nuclei, organisms destitute of a nucleus being unknown. Treub† points out that not only in Cryptogams do a plurality of nuclei occur, but that in the bast fibres and laticiferous cells of various Phanerogams a like condition is found.

Hegelmaier‡ records observations on the cells of the suspensor in various leguminous plants, and states that in these, numerous nuclei may be present, to the number of twenty, thirty, or more, embedded in a parietal layer of protoplasm. Inside each is a clearly-marked nucleolus; and in old nuclei two nucleoli may be found. He then advances the important fact, which I had previously verified for myself in various plants, that division of the nucleus is always preceded by that of the nucleolus, which elongates, assuming a dumb-bell shape, and then divides. The nucleus next divides, and one nucleolus goes with each half. He notices that while the nucleolus is sharp and clear in outline, the nucleus at its periphery seems to fuse with

* S. B. Niederrhein, "Geo. Natur-u Heilk." Bonn, 1879.

† *Comptes Rendus*, lxxxix. 1879, page 494.

‡ Bot. Zeit. xxxviii. page 513.

the protoplasm. An article by Flemming,* which has recently appeared, will be referred to shortly.

My attention having been given for some time to the study of the vegetable cell, I found on examining the epidermal cells of *Ornithogalum pyramidale*, L., with Hartnack's No. 4 eyepiece and No. 7 objective what seemed a well-marked body inside the nucleolus of a cell. The idea suggested itself to me, Might this be constant? and on carefully examining the others, such was found to be the case. The epidermis was quite fresh, and had been stained in alcoholic solution of eosin—an excellent stain for demonstrating minute structure. Through the kindness of Professor Dickson, I submitted them to a Hartnack's No. 10 immersion objective, and the new structure was well seen. Numerous other flowering plants were examined, and in the whole of these it was found to be present in the cells of the epidermis, lamina, petiole, stem, and root, as also in Cryptogams such as *Equisetum limosum*, *Chara*, *Spirogyra*, &c. All the plants enumerated below show the new structure well; though in some, it is larger and more marked than in others.

DICOTYLEDONS.

Phaseolus multiflorus, stem, petiole, and lamina.

Veronica gentianoides, leaf epidermis.

Polemonium cæruleum, petiole cells.

Rheum officinale, stem, petiole, and lamina.

Rumex acetosella, leaf epidermis.

Asarum Europæum, leaf epidermis.

MONOCOTYLEDONS.

Orchis mascula, leaf epidermis.

Vanilla, sp., leaf epidermis, stem, and aerial root.

Pancratium rotatum, leaf epidermis.

Pancratium caribæum, leaf epidermis.

Eucharis candidissima, leaf epidermis and petiole cells.

Narcissus Pseudo-narcissus, leaf epidermis.

Hyacinthus, leaf epidermis.

Scilla Peruviana and *bifolia*, leaf epidermis, &c.

Allium sativum, leaf epidermis.

Fritillaria imperialis, leaf epidermis.

* Arch. für Mikr. Anat. xviii.

Ornithogalum pyramidale, various.

Colchicum autumnale, leaf epidermis and parenchyma cells.

Pothos, sp., leaf epidermis.

Saccharum officinarum, cells from young stem.

CRYPTOGAMS.

Equisetum limosum, cells from young stem.

Chara fragilis.

Spirogyra nitida.

The cells of the stem and leaf-epidermis of *Fritillaria imperialis* show the largest examples of the new structure, but it is very distinct in *Ornithogalum pyramidale*, and *Narcissus Pseudonarcissus*. In the cylindrical cells of *Spirogyra* there is a difficulty, at times, to demonstrate it owing to their roundness, but in Plate X. fig. 1, it is very evident. Usually there is only one, but it is by no means uncommon to find two, and even three or four. When more than two are present, however, the cells are generally old; and this is a significant fact. The new structure is round or slightly oval in outline, and exhibits a clear bounding-wall differentiating it from the substance of the nucleolus. Aqueous solution of logwood reveals its outline well, still better is a solution of iodine; but I prefer to either of these a $\frac{1}{4}$ per cent. solution of eosin in common methylated spirit.

After verifying its apparent invariable presence in the plant cell, a preparation of cerebellum, which I had made in Professor Rutherford's class of Practical Physiology, was submitted to the microscope. In the large multipolar nerve-cells a nucleolus has long been known to exist, but inside many nucleoli this new structure was quite visible. Dr Priestley informs me that it has been mentioned before casually, but no importance was attached to it. On looking over various zoological works one finds that it is figured repeatedly; as to its presence in the animal cell we may for the time neglect it. To this new factor in the vegetable cell I propose applying the term *nucleolo-nucleus*. My investigations led me strongly to the conclusion that the nucleolus is also an invariable element; in fact all the tissue systems of every plant, which have come under my notice in the present connection, are provided invariably with a nucleus, nucleolus, and nucleolo-

nucleus, *if the cell is still active*. To ascertain, if possible, the function of these, and their rôle in division of the cell, I set about examining various plants. The results obtained have been highly interesting.

*Structure and Division of the Cells of Ornithogalum
pyramidale, L.; Scilla bifolia, L.*

Ornithogalum pyramidale has a much stronger growth than *Scilla bifolia*, and the cells are very much larger, consequently the former has most engaged my attention. By obtaining bulbs in which the young ascending axis had not attained to a great size, and by splitting up these so as to expose the pale actively growing parts, admirable examples were obtained, showing all the stages of cell division. As the epidermis is well suited for study, owing to the largeness of the cells and their local development of stomata, this tissue has principally been chosen. If we carefully strip off a piece of epidermis, say 2 inches long, from the point of union of a leaf with the short underground axis and upwards, and stain with logwood, iodine, or eosin, all the changes in division and new formation of cells can be traced. At the basal part of the preparation will be seen cells quite resembling each other in size and structure, and not as yet indicating any differentiation into stoma mother cells, and cells of the epidermis. The interior is generally filled with protoplasm, containing a nucleus, nucleolus, and nucleolo-nucleus. While in many nucleoli only one nucleolo-nucleus is present, others may be seen with two. Some of the nuclei again, as we pass up the preparation, have two nucleoli with a nucleolo-nucleus in each. Lastly, nuclei may be dividing, or nearly divided, to form two cells, each daughter nucleus carrying with it a nucleolus and nucleolo-nucleus.

One of the two cells thus resulting, we will suppose, elongates to form an epidermal cell, while the other is destined to form a stoma. We will meanwhile trace the latter, superficially distinguished from the former by its increasing little in length, but significantly distinguished by its subsequent history. At first, having only one nucleus, nucleolus, and nucleolo-nucleus, the latter soon

divides. Though, owing to its small size, I have only once seen what appeared to be a median constriction, there can be little doubt that this is the course of events, for two distinct ones can often be discerned in cells about this period. The nucleolus next elongates, and this almost invariably parallel to the plane of the former cell-division. Sometimes it may form an acute angle with it, or even may elongate at right angles, the first, however, is by far the commonest method. A constriction is then carried through the centre of it, which deepens till complete separation into two results, each carrying with it a nucleolo-nucleus (Plate IX. figs. 1 and 2). That increase in its size goes on at this time cannot be doubted, since the two new nucleoli are each nearly of the same size as was the parent one at its initial period of division. The nucleus next elongates slightly in the same plane as did the nucleolus, the protoplasm collects considerably around it; next, by movement of what seems the denser material of the nucleus towards the two poles, a narrow but elongated clear space, traversed by very delicate fibrils stretching from its two halves, appears running at right angles to the plane of elongation of the nucleus, this may be called the nuclear barrel. Shortly, in the middle of it, there can be distinctly seen a double row of close-set dots which, on focussing, seem to change their position, almost giving one, at first glance, the idea of three parallel rows. This results from different parts of the cell-plate being seen as the focus is altered. Along this cell-plate the new cellulose septum is deposited, and after a considerable interval it splits up to constitute the aperture of the stoma. Even before the nuclear disc is visible the two nucleoli take up positions on opposite sides of its area (Plate IX. fig. 3). Such is the course of development as far as I have been able to follow it. Strasburger gives a very similar account, as far as nuclear division goes, of the formation of a stoma in *Iris pumila*. In *Ornithogalum*, however, elongation of the nucleus is not nearly so pronounced as in it.

We may seem now to have exhausted the complete history of stoma development, but in many instances this is not so. Even during the nuclear division one can often observe that the nucleolo-nucleus of each half has again

divided, and by the time that complete separation of the two cells of the stoma has been brought about, the nucleolus also may have divided, giving us two nucleoli in each guard-cell, and this condition may be permanently retained. This may seem an unimportant fact, but it helps us to make a broad generalisation as to division of the cell generally, viz., that the nucleolus, or more probably the nucleolo-nucleus, is the centre of germinal activity, and that as we pass outwards to the periphery of the cell, this reproductive activity becomes less and less. In no other way, to my mind, can the number of nucleoli and nucleolo-nuclei at different ages in the cells of any plant be explained; but regarding this as the true explanation many difficulties vanish. If such, then, be the case, we should expect to find that, occasionally at least, each guard-cell nucleus should split up, and, by formation of a septum, give rise to two cells. Were this morphological change to take place, the physiological function of the stoma would necessarily be destroyed. This interesting pathological change has thrice come under my notice. Ordinarily, as the guard-cells become aged, the nuclei may get shrivelled, and protoplasm, with chlorophyll bodies and starch, greatly fills the interior. They would seem in truth to have played out their important function.

The whole of the above changes have also been seen in *Scilla bifolia*, except the strongly marked dumb-bell shape assumed by the nucleolus before division. Let us return now to the epidermal cell. When newly cut off it exactly resembles the stoma mother-cell, but is soon distinguished by the great elongation which follows. In some specimens a very pretty alternate arrangement of epidermal and stoma cells, on the principle, so to speak, of the nodal and internodal cells of *Chara*, prevails over the surface, except where fibro-vascular bundles traverse the leaf. If this be the fundamental constitution it is only exceptionally met with, as, by repeated transverse division of the epidermal cells, two or more of these may intervene between two stomata. These divisions are carried out in exactly the same way as in the stoma, only that nucleus, nucleolus, and, I should imagine also, nucleolo-nucleus, elongate, not parallel, but at right angles to the former plane of division, the new partition running, not as in the

stoma, from base to apex of the leaf, but transversely. Though failing to obtain in *Ornithogalum* a good instance of nuclear division, this has been afforded by *Scilla bifolia*, the nuclear disc, when fully established, being nearly as large as either of the elongated daughter-nuclei. In the surface growth of the leaf epidermis, however, it is, to a far greater extent, by elongation of cells which had been cut off in a young state, rather than by actual multiplication, that a greater extent of surface is produced. Now, as these cells, after multiplication and elongation, pass more and more into the permanent state, division of the nucleus, with subsequent formation of a cell-plate, is correspondingly rare; but just as in the guard-cells of the stoma, so here also the nucleolus and nucleolo-nucleus still display a greater reproductive activity, and, as a result, we may find all stages in the dumb-bell shaped division of the nucleolus, which seems now to pass through this change much more sluggishly than in embryonal cells. We therefore find many cell nuclei with two well-marked nucleoli, and one, two, or more nucleolo-nuclei in each. This exactly coincides with the cells of the suspensor of some *Leguminosæ* at a certain period, as described by Hegelmaier; but, whereas, in all the examples of *Scilla* examined only one nucleus was in each cell, in those of the *Leguminosæ* the nuclei were still able to divide, each resulting daughter nucleus carrying with it a nucleolus. This latter state of affairs is, I think, simply a progression on the first, in which the nuclei, as well as nucleoli, go on dividing, without, however, being seemingly able to form septa.

I will now deal very shortly with the ordinary pallisade parenchyma cells of the leaf, as in all essential points they do not differ from those already described. If we take a portion of young epidermis to which patches of these cells are adhering, we immediately notice all steps in the cycle, such as has already been discussed. Some of these cells will contain a nucleus, nucleolus, and nucleolo-nucleus; others a nucleus, nucleolus, and two nucleolo-nuclei, others, again, a nucleus, two nucleoli, with a nucleolo-nucleus in each, while nuclear division may be seen proceeding or completed, each daughter nucleus carrying with it a nucleolus (Plate IX. figs. 12-15). This is there-

fore identical with those previously dwelt upon, and need not further concern us.

A few words now on the nucleus, as to its surface and contents outside the nucleolus. Of recent years it has been regarded by most as possessing a distinct covering, to which the term nuclear membrane has been given. In very young cells of *Scilla*, where the nucleus is densely surrounded by protoplasm, it is difficult to make out a double contoured bounding wall; but as vacuolation goes on, and the protoplasm gets stringy, in like degree does this membrane make itself evident. In epidermal cells of *Scilla*, stained with eosin, it is of a pale homogeneous colour, and doubly refractive, contrasting well with the stringy and granular nuclear substance. In a few cells of *Scilla* treated with alcoholic solution of eosin I have seen it quite detached from the nuclear substance, over the greater part of its surface; the nuclear substance had apparently shrunk from it or the latter had swollen out. In my observations on *Spirogyra* an experiment will be explained whereby the presence of this membrane can be positively demonstrated in one plant at least.

The stringy and granular aspect of the nucleus has lately given rise to much discussion. Butschli, Schwalbe, Hertwig, Eimer, Klein, Flemming, and others, have recently insisted on there being in the animal cell a homogeneous network of fibrils, traversing the nuclear substance, and attached to the inner side of the nuclear membrane. In the young state of *Ornithogalum* and *S. bifolia* one can plainly discern little filaments on the inner surface of the still thin nuclear membrane, which have the same clear homogeneous appearance as it. It is exceedingly difficult, however, to trace the fibrils for any length, since they seem to form a dense plexus. If, however, a piece of pretty old epidermis in which the nuclei are large and well formed be selected, and stained in solution of eosin, or, better still, in a $\frac{1}{4}$ per cent. solution of chromic acid, to which 1 part in 2000 of heliocin is added, this, when submitted to a Hartnack's No. 10 immersion, displays most beautifully a dense reticulum of clear homogeneous fibres, stretching inwards from the equally clear homogeneous nuclear membrane. If, then, the piece of epidermis be subjected to

teasing and rolling with a needle handle, so as thoroughly to set free all loose protoplasmic material, it will still be found that many of the nuclei remain, though broken up, a fibrous network being still discernible, and, what is noteworthy, the nucleoli almost invariably are present as if moored to the nucleus in a definite way.

I would now notice the results at which Flemming has arrived in studying the animal cell. In a paper published in 1879* he considers that two forms of division have been described—the direct and indirect. In the former, “supposed until recently to be the normal one, the nucleolus first divides, then the nucleus, and finally the cell. In the indirect method, the nucleus, first of all, undergoes metamorphosis, separating into a network of highly-refracting filaments, and an intermediate substance not affected by staining fluids. The nuclear network goes through a definite series of changes, and finally divides,”† these masses then representing the two daughter nuclei. Flemming at that time did not believe that direct division ever took place. In a more recent paper‡ he is inclined to suppose that both kinds of division may occur, though the indirect, in his estimation, is by far the commoner. In using these terms he regards them merely as provisional. He further, after describing most carefully the metamorphosis which the nuclear fibres undergo, comes to the conclusion that forces seated in the achromatic, or the nuclear substance component, of the nucleus, are the real initiators and directors of division. But he then propounds the thesis that the function of the nucleoli has in this respect been greatly mistaken, since he supposes that better methods may show that they are not even morphological constituents, but mere thickenings or deposits. It has been my aim to show that it is neither the plan of direct or indirect division, so called, that goes on, but a process compounded of the two, and requiring both of these supposed distinct ones to explain it. Moreover, Flemming himself very beautifully suggests that, to account for the peculiar changes of the nuclear fibres, we require only two

* *Archiv Path. Anat. u. Phys.* (Virchow) lxxvii. 1879, p. 181.

† *Abstract Roy. Micro. Journ.* vol. iii. 1880, p. 51.

‡ *Arch. für Mikr. Anat.* xviii.

agents or forces acting in different directions in the interior of the nucleus; and what can more naturally supply those than the nucleolus after division has taken place, since each daughter nucleolus now acts as a new centre of influence. It may be asked, have I not been able to observe this most characteristic series of movements in the nuclear fibres of *Ornithogalum* during division? I have not; but this can be easily explained when we remember that these fibres in young cells are exceedingly delicate; and, besides, it is not by observing these movements *only* that we can arrive at a right knowledge of the whole process—a fact this acknowledged by Flemming himself, who confesses that the most obvious phenomena of division which he so carefully discriminates have in all probability the least significance.

We will see how well all these propositions can be demonstrated in dealing with *Spirogyra*.

*Structure and Division of the Cells of Spirogyra nitida, Kg.**

The fresh-water alga *Spirogyra* is very convenient for studying the structure and division of the cell, since in its cells the nucleus is isolated from the protoplasm, and is connected with the latter only by delicate radiating strands. The particular species which has been chosen for observation is *S. nitida*, the commonest form in the neighbourhood of our city, and possessing, moreover, a large nucleus, nucleolus, and nucleolo-nucleus.

1. *Structure of the Cells*.—Like all the species of the genus it is a filamentous alga, made up of a large number of simple cylindrical cells, joined end to end. Each cell-wall has the usual homogeneous appearance. Immediately inside it, and forming a complete interior lining, is a thin layer of pale, homogeneous, or but slightly granular protoplasm. Embedded in this are four spirally-arranged bands of chlorophyll. Thanks to the researches of Pringsheim † we are now well acquainted with the structure of these. Each band is studded at intervals with rounded, hollow, or cup-shaped structures, which hold in the cavity a smaller

* Kützing, "Species Algarum," 1849.

† Annals and Mag. Nat. Hist., v. 1880. Pringsheim's "Jahrbücher," xii. heft 3.

body—a starch centre. Certain of the cup-shaped structures are continuous with, and apparent expansions of, the fibres which suspend the nucleus in its place (Plate X. fig. 1).

Occupying the centre of the cell is a large oval or spherical nucleus, quite free, ordinarily, from the peripheral protoplasm, but moored in its position in the way already described. Inside is a large spherical nucleolus. Let us now study the structure of the nucleus a little more closely. The surface of it is seen to be bounded by a clear hyaline zone exhibiting a double contour. With the outside of this the radiating threads *seem* to be fused; but the strong probability is—judging from homologies with animal cells, and their behaviour, as subsequently brought out—that these *pass through, and are continuous with*, those inside the nucleus.

A most remarkable and instructive result was obtained on trying the effect of endosmosis and simultaneous staining on the cells. A fresh filament was adjusted under the field of the microscope near the edge of the cover glass, so that the nucleus of a particular cell was well defined. A few drops of alcoholic solution of eosin were then allowed to fall on the slide at the edge of the glass, care being taken that in the currents set up the definition of the nucleus remained clear. Endosmosis was very speedily effected, the elongated cylindrical cells swelling out notably, while by the action of the stain the nucleus and nucleolus became more distinctly visible; owing to the swelling out of the protoplasmic lining, and the carrying with it of the chlorophyll bands, a strong tension was set up in the connecting threads. This became so great that these suddenly ruptured simultaneously or in rapid succession, one or two remaining attached on one side only to the bands, and towards this side the nucleus, after tumbling about in a confused manner, settled down. The broken and curled-up ends of the threads could, for a moment or two, be noticed surrounding the hyaline zone, but soon the latter detached itself with a sudden jerk and swelled out, forming a translucent sphere attached on one side to the nuclear substance, which now took on rather a shrivelled outline (Plate X. fig. 2.) To the swollen and spherical zone, which goes on increas-

ing till three or four times the diameter of the nucleus, most of the curled-up threads could be seen adhering. This experiment was so novel and magical, if I be allowed the expression, that I repeated it frequently, and in the presence of various gentlemen who were quite satisfied with it; and subsequent repeated trials have given unvarying results both on isolated nuclei and aggregate masses. Any one can verify the facts for himself, by attending merely to the points mentioned.

The structure, thus demonstrated in so positive a manner, clearly corresponds to the nuclear membrane of animal cells as described by Klein* and others. Now Klein has asserted that in cells from the stomach of the newt the "nuclear membrane is composed of an outer thicker portion, which is the limiting membrane proper, and, closely connected with it, of an inner—more or less incomplete, probably because reticular—delicate layer, which is, properly speaking, a peripheral condensation of the intranuclear network." The cells of the alga, now under consideration, are identical in their anatomical details, for after the outer nuclear membrane has detached itself and increased considerably, one can plainly see a clear but rather irregular band enveloping the nucleus. A matter, however, rather difficult of solution now suggests itself. Why, on rupture of the radiating threads, does the outer membrane detach itself? If we suppose that these threads really pierce the latter, and are continuous with the intranuclear fibres, on rupture of them the nucleoplasm would probably incline to shrink, endosmosis setting in would expand the outer membrane and at the same time contract the apertures in it through which the threads pass; on the membrane swelling out then some of the threads at least would tend to snap and be carried with it in expanding. This attempted explanation is given as the only one which seems feasible, and in harmony both with the phenomena here observed and those accompanying division of the cell. In treating of cell division the nature and origin of the nuclear membrane will further be discussed.

The nuclear substance of cells which have been stained with logwood, eosin, chromic acid solution of heliocin, or

* Quart. Micro. Jour. 1878

iodine solution, when looked at with a power of 300° , is granular; consisting of clear spots, not distinguishable optically from the nuclear membrane; and of intervening parts more deeply stained; but when magnified 450° , these appearances are seen to be due to the presence of an inter-lacing network (intranuclear network of Klein), the meshes of which are filled by the more deeply stained "ground substance." One can further notice the fibres stretching inwards from the inner nuclear membrane with which they seem to fuse; while from the outer surface of the nucleolus like processes pass outwards. Professor Rutherford, who has thoroughly examined the nuclei of animal cells, confirms the preceding observation. But even though unable to demonstrate directly the existence of an intranuclear network, the behaviour of the nuclei and nuclear contents would lead to such a conclusion; for in nuclei which have been isolated, torn, and split asunder, the nucleolus may protrude prominently without any indication of passively separating; shreds of the intranuclear network are also encountered adhering to the nuclear membrane. Now, even although the nuclear substance is hardened by the decolorising or staining agent, this hardening could not alone account for conditions such as have been mentioned; I therefore strongly incline to the opinion that the filaments of the intranuclear network stretch inward from the inner layer of the nuclear membrane, and are finally attached to the outer surface of the nucleolus, thus holding the latter in position. Further proof of this will be adduced in studying the division of the cells.

The nucleolus of *Spirogyra* is very large, and is a morphological entity, not in any way to be confounded with a local thickening of the intranuclear network. A nucleolar membrane, quite as evident, but scarcely equal in width to that of the nucleus, surrounds it. With the outer surface of this the nuclear fibres *seem* to fuse. Its inner surface is smooth, and does not show that it gives off processes into the interior. Instead of having a granular or reticulated aspect like the nucleus, it gives the impression that it is a pretty homogeneous body.

The nucleolo-nucleus, as before mentioned, is sometimes

obscured, owing to the rotundity of the cell, nucleus, and nucleolus, but in the great majority of cells it is very apparent, and attains a much larger size than in any other plant, excepting *Fritillaria*, which has come under my notice.

Finally, I would speak of the result of staining agents such as those already referred to. The whole of these, if the solution be not too strong, stain the peripheral protoplasm scarcely at all; the nuclear substance is slightly stained, the nucleolus rapidly absorbs and soon assumes a brilliant hue, while the nucleolo-nucleus has a deeper tint imparted to it. The general character of these, in fact, when treated chemically, lead to the conclusion that each is a more richly differentiated mass of protoplasm than that by which it is surrounded.

2. *Cell Division*.—My study of cell division in *S. nitida* has been carried on wholly by chromic acid preparations slightly stained with heliocin. The material was obtained in a state of division, by placing quantities of it in 1 per cent. solution of chromic acid, during different hours of the night, that gathered at 3 A.M. giving the best results.

Taking as our starting-point a typical cell just initiating the dividing process, the first change observable is the aggregation, on two opposite sides of the nucleus, and in a line with the long axis of the cell, of a quantity of pale, slightly granular protoplasm, which seems to be derived from the peripheral layer, and to travel along the radiating threads, for during aggregation little masses can be seen here and there along the course of the threads in addition to that already massed. Coincident with this, or soon thereafter, a very curious movement is set up in the nucleolus, the exact course of which it is rather difficult to follow; one or two very clear preparations, however, made by Mr Jackson, a senior member of the University Practical Botany Class, as also several of my own, have helped me to gain a definite idea of what now goes on.* The nucleolus swells out on opposite sides into two protuberances, in line with the aggregating protoplasm; these do not seem to

* I would here express my indebtedness to Mr Jackson for the use of about two dozen slides—prepared in connection with the class—of nuclei quite isolated from their cells, and remarkably fine for exact definition.

represent the denser material of the nucleolus, since it forms a bridge-like connection between (Plate X. figs. 3*a* and 3*b*). It will be noticed that in fig. 3*b* two nucleolo-nuclei are visible on opposite sides of the dense portion; further, the nucleolar membrane has, *as far as can be seen*, disappeared, but, as stated below, this again makes itself visible; I therefore think it probable that these swollen sac-like expansions are inflations of the nucleolar membrane, and that during this period division of the nucleolo-nucleus is carried out, since, in all subsequent changes, two nucleolo-nuclei are present. The nucleolus again assumes its normal shape, its membrane reappearing, and as well defined as in a resting state. After this it increases markedly in size, as if an abundant nutrient supply were being handed on to it; and this may furnish an explanation of, and reason for, the aggregation of the protoplasm, since there would then be provided a source of nutritive material immediately round the centre of increase and action.

The next step in the process of division is a very striking one, and enables us somewhat to realise how little is our knowledge of the vital energies which reside in living matter, while it teaches us that in bodies *apparently* structureless profound molecular changes may be going on. The nucleoplasm is forced through the nuclear membrane, and aggregates itself on the two opposite sides, where the protoplasm had already accumulated, giving the idea, now no longer, of two pale masses of almost homogeneous protoplasm, but of dark and closely packed amœboid-looking lumps; *and to these* (not to the nuclear membrane) *the radiating threads are attached*. These sides we may now term the poles of the nucleus. The nucleoplasm of the poles is still connected with the nucleolus by fibres, which pass through the nuclear membrane (Plate X. fig. 4). The question may now suggest itself, Why do we believe that the nucleoplasm is forced, rather than pulled out? To this we reply that the only *visible* agents by which this could be effected, are the radiating threads; but at this time, instead of being tense, they are loose and flaccid. The whole after behaviour of the nucleolus, moreover, confirms the supposition, that it now is the centre of two opposing

forces, acting along the long axis of the cell; in fact, that from this point onward the nucleolus presides over, guides, and impels the movements of the nucleus. Owing to Strasburger's attaching no special importance to the nucleolus, and his observation of the cells with rather a low power, he, while figuring pretty correctly the phenomena already described, does not fully appreciate their importance. Probably also, from the latter reason, he has not noticed the formation of the beautiful nuclear barrel, and succeeding cell plate, which is, however, only a confirmation of his renowned researches on other plants. But he describes and figures very carefully the evolution from the peripheral protoplasm, of what is at first a single row of minute spots or granules, as seen in Plate X. fig. 6, but which increase afterwards so as to form a double row, or even an irregular belt. These granules, first seen when the nucleoplasm is forced out, but frequently not appearing till a later stage, mark the area where subsequent folding in of the protoplasm takes place, with coincident formation of the cellulose septum.

As in *Ornithogalum*, so here also the nucleoplasm is densest on the sides away from the nucleolus.

Hitherto the nuclear membrane has not in any way altered, but soon at the two poles a solution of its continuity becomes apparent, while, as indicated in Plate X. fig. 5, a slight elongation of it is also effected; this breaking up at the poles goes on till the nuclear membrane is undistinguishable. After dissolution at the poles is accomplished, the appearance is such as is represented in Plate X. fig. 6; the polar masses are, especially towards the outer sides, dark, compact, fibrous, amoeboid-like lumps, giving off on their inner sides fibrous strands which run to the nucleolus, while above and below are two darker strands—the remains of the nuclear membrane. This fibrous area constitutes, from this period onwards, the *nuclear barrel*.

The nucleolus next splits into two daughter nucleoli, each of which seems to carry along with it a nucleolo-nucleus, since one at least is usually to be made out in each sister form. It is important to notice now how completely these regulate the movements of the polar masses and nuclear barrel. As they retreat from each other they drive the

polar masses before them, thereby elongating the nuclear barrel; this is pretty well brought out in Plate X. figs. 7 and 8; but the repulsive influence now acts, not in a straight line only. It radiates out all round, driving asunder the fibres of the nuclear barrel, so that widening as well as elongation occurs at the same time. In fig. 7 the elongation is very pronounced, but the widening has just begun; in figs. 8*a* and 8*b* the process is continuing, while in fig. 9 it has reached its maximum. It should here be noted that the nuclear barrel of figs. 8*a* and 9, while of an average size, is not to be compared with figs. 8*b* and 10; but these and some succeeding ones are on the whole exceptionally large specimens. For the clear and telling preparation from which the drawing of fig. 8*b* was made, I am again indebted to the ingenuity of Mr Jackson. The nucleoli at length advance to the polar masses and bury themselves in the nucleoplasm of these. A redistribution of nucleoplasm now takes place; from being heaped up or compacted on the sides away from the centre of action, it now spreads round and covers in the nucleoli.

Though up to this point not the least trace of a cellulose septum is visible, changes in the peripheral protoplasm have not been wanting. The row of spots before mentioned, and delineated in fig. 6, has increased to a double series, or may form a strong band of irregularly disposed granules as in Plate X. fig. 9. But after this three important and simultaneous actions are induced,—(a) the polar masses, or, as we may now term them, the daughter nuclei, have a new membrane secreted round them; (b) the cellulose septum is faintly foreshadowed by a delicate ring of cellulose deposited in the middle of the granules; (c) the nuclear fibres in the middle of the barrel are sundered, or separate, and at a slightly later period develop a double row of small discs—the cell-plate, between which still later the cellulose septum will grow in. All these conditions are fairly illustrated in fig. 10, and we will now handle them in detail.

(a) By botanists the nuclear membrane, even when believed in, has been regarded, and perhaps naturally so, as a pellicle that has formed on the exposed surface of the nucleus. My preparations show that it is laid down inside a quantity of protoplasm which envelopes it; and we can

scarcely imagine two substances of similar chemical constitution, the denser of which had a pellicle formed round it while inside the lighter. The nuclear membrane, in truth, in *Spirogyra* at least, must be considered to be something as carefully constructed as any other part of the cell; in other plants, or in cells whose nuclei are always more or less surrounded by protoplasm, it may not be found requisite thus to view it, but in the case before us its importance is too great to be lightly estimated.

(b) The cellulose septum in being laid down is earliest seen as a clear pale thread of more highly refractive material than the protoplasm, running through the middle of the granules, and compassing the entire circumference of the cell. As I shall afterwards proceed to prove, it results as a secretion from the protoplasm, the edge of it when formed being laid up against the cell-wall all round, and plastered on to it by some agency unknown. Growth is carried on centripetally, so that as additions are being made to it the protoplasm bends in all round, and thereby carries inwards the granules as well as the chlorophyll bands. The septum, therefore, from being a mere thread, soon deepens into a ring, and next into a shelf or ledge running round the interior of the cell, the edge of it now touching the cell-plate (fig. 11a), the consideration of which we will now take up.

(c) About the time that the first faint indication of the commencing septum is visible, it can occasionally be seen that a splitting is taking place in the middle of the fibres of the nuclear barrel; in others again further advanced there are two lines of granules separated from each other by a clear space. How these granules are formed I am unable to say. It may be that the broken ends of the fibres coil up, or even have material accumulated at their ends to assist in forming the septum; however it be, I am strongly inclined to think, both from their appearance, time of formation, connection with the septum, and optical properties, that they perform in the cell-plate exactly the part played by the granules in the protoplasm, in the formation of the septum; in other words, that the granules in the cell-plate are present for the same end as are those in the protoplasm.

Here we may appropriately notice the result of the

growth of the septum on the chlorophyll bands. These, along with the protoplasm, bend inwards for a certain length, their continuity not being at all interfered with, so that, on focussing down, one can catch a clear image of the outer edge of the septum, and also many of the chlorophyll bands, but one or more are indistinct as they approach the septum, and further focussing must be resorted to ere their complete course is traced (Plate X. fig. 12). About the time that the septum has grown in to meet the cell-plate they are severed in a very inexplicable way, the severed edges giving the impression that they are neatly cut or gnawed through, not at right angles to the bands, but obliquely, though quite in a line with the advancing septum. These cut ends must continue to grow, since, later on, instead of their being opposite each other, one may be considerably prolonged round the interior of the cell.

The nuclear barrel, as far as we have yet considered it, may be said to have passed through the *waxing phase*, but henceforth it gradually diminishes in width, and may appropriately be described as assuming the *waning phase*. We for the time left studying the septum, after watching it till it had grown in to meet the edge of the cell-plate all round. As growth in width proceeds, it passes into the clear band between the granules of the cell-plate, and these, as I suppose, taking on the function of the protoplasmic granules, advance centripetally with the growing edge of the septum, causing thereby a waning of the barrel. The first part of this condition of things is brought out in Plate X. fig. 11b, copied from a most beautiful isolated nucleus in one of Mr Jackson's slides. Here we see the part of the septum, formed by infolding of the peripheral protoplasm, protruding on each side, as viewed optically, or projected flat, though it is in reality a circular projecting rim. From its being projected flat, it is of course impossible to bring out—what is easily accomplished by gradual focussing down—the appearance of a centripetal development of it. In Plate X. figs. 13 and 14, this is partially successful, as by compression the cells are pressed slightly to one side. Waning of the nuclear barrel and deepening of the septum continue till the two daughter

nuclei are connected only by a narrow band, a small spherical part in the centre of the septum being yet in process of formation (Plate X. fig. 14). Finally, when the septum is completed, the two perfectly-formed sister nuclei—each suspended in its own cell—may indicate their relationship by a connecting protoplasmic strand exactly like those which moor the nucleus in its place (Plate X. fig. 15).

An interesting question is here opened up. Whence are these threads or strands derived, and what is their functional value? From the examination of a large number of my preparations, I can scarcely resist the conclusion that they are fibres of the nuclear barrel, and therefore—to trace back their parentage further—fibres of the intranuclear network, which, as the barrel wanes, are detached from it, and in some way or other become united to the chlorophyll bands. Certain it is that new ones do originate, and it is possible that they may be formed by splitting or bifurcation of the older ones, this being continued to the base of attachment of the filament. At the same time it is equally probable that their origin is to be traced in the manner previously indicated. Would these threads then constitute the intracellular network of Klein? In working at vegetable cell-structure I confess that the idea of a distinct series of fibres permeating the cell has appeared to me scarcely tenable, the apparent network in many cases resulting from mere vacuolation of the protoplasm. In *Spirogyra*, however, one cannot quite get rid of the fact that these threads do not result thus, and that they play so important a part in the life history of the cell; in truth, it seems that here an intracellular network exists. Some rather novel views have recently been propounded as to the function of this network in animal cells. In *Spirogyra* I can only say that these seem to be (a) to moor the nucleus in the centre of the cell; (b) to supply it with nutrient matter when in the ordinary resting state; and (c) to convey a plentiful supply when division is going on.

I would now revert to the formation of the cell-septum by the protoplasm, and the attaching or plastering of this to the cell-wall. In *Spirogyra* it has generally been accepted that the septum arises as a process inwards from

the latter, and that its ingrowth is probably fed by the protoplasm mantling its edge. What one sees after ingrowth has proceeded to a considerable extent is a circular shelf, *as thin, or even thinner*, at its point of junction with the wall as throughout its free part. But this of itself is not enough, for there are often figured in our botanical manuals drawings of this, and allied mesocarpous algæ, with the protoplasm retracted, but still retained to the free edge of an apparent ingrowth of the cell-wall. The reagents in these cases which retract the protoplasm, such as alcohol, do so comparatively gently, and as a consequence it shrinks from the cell-wall generally, and masses round the area of division, where it is attached to the ingrowing septum. It will thus be seen that no special strain acts on the septum to rupture it. On the other hand, by such reagents as chromic acid the cell contents are fixed as in the living state. Preparations then, which have been thus treated, on being teased and twisted about, invariably have one or more cells with a forming septum and the protoplasm displaced. *In such a case the latter unfailingly carries the former with it.* One from many such preparations in my possession is represented in Plate X. fig. 17. Again, if an undisturbed cell which has been in chromic acid have its walls subsequently expanded by endosmotic action, the protoplasm and chlorophyll bands will likewise swell out; but if a forming septum be present, it—instead of swelling out—detaches itself from the wall, and forms a clear annular constriction in the middle of the swollen cell (Plate X. fig. 16).

Even while the protoplasm is rendered firm by the acid, one would still expect, according to the generally-accepted theory, that the septum would part from it rather than from the cell-wall, but this is not so. In *Spirogyra*, therefore, a familiar and demonstrable proof exists, of the formation of cellulose by protoplasm, and the fusing of this with the pre-existing cellulose of the wall.

Having now passed in review the phenomena attendant on division, there are some broad questions which we might with advantage linger on. That the nucleolus and—very probably—the nucleolo-nucleus are invariable cell-factors has already been postulated. While of recent years the

nucleus has gained in importance, in like ratio, we might say, has the nucleolus declined. Some patent reasons can be given for this course. I have already asserted of *Ornithogalum* and *Scilla* that the nucleus is the last of the three factors to divide, and—though at first sight it might not strike one—the same is true of *Spirogyra*; further, that an influence radiates from the centre outwards, and this influence is placed in the nucleolus. It may be that the nucleolo-nucleus has a phylogenetic rather than a functional interest; but, granting this, the nucleolus remains. We have seen that previous to its fission the nucleoplasm was repelled on each side; that on these sides the nuclear membrane first dissolved; that on division the nucleoplasm still further retreated; that as the daughter nucleoli moved apart a radiant repelling influence originated the broad nuclear barrel; and that only after these had buried themselves in the polar masses of nucleoplasm did the latter close up and subsequently form an encircling membrane. It may be said that agents simultaneous with, but separate from those in the nucleolus were at work in the protoplasm forming the granular aggregations first noticed by Strasburger, but not a trace of these is observable when the changes shown in Plate X. figs 3a and 3b, are progressing; as well, therefore, may an impulse travel out setting up a series of movements in the protoplasm, as does the aggregation along the threads towards the nucleus indicate a similar impulse in the opposite direction, propagated, in all probability, originally from the centre.

Though the nucleolus is a smaller body than the nucleus, we must not on that account throw it aside. Nothing, in truth, has struck me more than the firm solid consistence it has when stained, compared with the latter, and quite different from the staining of the intranuclear network. Still more in *Spirogyra* the nucleolus is not insignificant, as it occupies from one-fourth to one-sixth of the area of the nucleus. We can, therefore, no longer regard it as a trifling factor in the life of the vegetable cell, and I hope soon to point out that the same holds true of the animal cell.

It must have been observed that in the foregoing descriptions of cell-division no phase corresponding to Strasburger's

nuclear plate and nuclear spindle is mentioned. In *Ornithogalum* and *Scilla*, if such exists, I have not seen it; in *Spirogyra* it is certainly wanting. In *Equisetum limosum*, however, all these phenomenal stages are passed through, and we will now shortly notice them.

Structure and Division of the Cells of Equisetum limosum, L.

The study of *E. limosum* was made from specimens gathered about 11 A.M. in June of last year, and preserved in alcohol. Longitudinal sections were made of young growing shoots which had just appeared above ground.

The hypodermal and fundamental cellular tissue round the nodes abounded with dividing cells in all stages, four or six sometimes being in the field at once. The cells of the hypodermal tissue were quite filled with protoplasm, containing a nucleus at least half the size of the cell, with nucleolus and nucleolo-nucleus. They were closely packed, and seemed to be multiplying rapidly. On the contrary, the fundamental tissue cells, even at the upper or lower parts of the nodes, were considerably or greatly vacuolated, and had a nucleus not more than one-fourth the size of the cell, with two to four nucleoli. Essentially the same appearances were seen in both kinds at the same stage of division, though in the fundamental tissue-cells certain important steps were traced which were absent from the others. On this account they have been chosen for a short description. The first movement that has been noticed is a massing of the nucleoplasm to form a clear, broad, hyaline band across the centre of the nucleus, the poles of which are left as pale conical projections from the sides of the band (Plate IX. fig. 21). The nucleoplasm thus aggregated is very pellucid and highly refractive, so much so, contrasted with neighbouring nuclei not dividing, that one can easily, after shifting the preparation under the field, find it again by this property. That it is the surface alone which thus refracts, is proved on attempting to focus so as to examine the contents, the result being that a general glairy indistinctness takes the place of the former brilliance, so that if definable structures were in the interior at this time it is impossible to see them. This pellucid band is Strasburger's *nuclear plate*, while the pale

poles together are his *nuclear disc*. This latter is a pale area traversed by delicate threads meeting at the opposite ends. The central band then breaks up, and flows irregularly towards the two poles (Plate IX. fig. 22) along the pale threads, and there aggregates to form the masses of the two daughter nuclei (Plate IX. fig. 23). These have the same shining surface which the nuclear plate had, and only in some cases have I managed by staining to reveal nucleoli in the interior. Connecting the daughter nuclei is a fibrous bridge, the *nuclear barrel*, and there early appears in this one or two rows of granules, the *cell-plate* (Plate IX. fig. 24). The nuclear barrel, from being about one-third the width of the cell, is expanded till it completely spans the latter, or nearly so (Plate IX. figs. 25-29), the cell-plate keeping pace with it. Along the cell-plate the new septum is laid down, after which the halves of the nuclear barrel fuse with the surrounding protoplasm, and two sister nuclei in sister cells now bring the cycle of change to a close.

Though on first formation of the daughter nuclei they are pellucid and difficult to resolve, as increase of the nuclear barrel goes on this passes off; and then it is seen that frequently two nucleoli are in each nucleus (Plate IX. figs. 25-29). In the hypodermal cells only the steps from formation of daughter nuclei onwards are traceable; these cells therefore correspond to those of *Spirogyra*, *Ornithogalum*, and *Scilla*, in having no nuclear plate phase. How then is this difference in the two kinds of cell to be accounted for? As yet I do not venture to reply, since my study of the plant is not completed.

Looking now at the four plants passed under review, the general results as to division, applicable in all, may be summed up as follows:—

(a) In division of the cell the nucleolo-nucleus probably divides first.

(b) The nucleolus undoubtedly divides next, and this is followed by division of the nucleus.

(c) During division of the nucleus a nuclear plate with nuclear disc is formed occasionally.

(d) If a septum is laid down, this is always preceded by formation of a nuclear barrel and cell-plate.

The general facts which have been advanced as to cell-

structure and division have also been verified in *Chara*, an account of which will be given in a future paper.

These investigations have been carried on in the Botanical Laboratory of the University under the direction of Professor Dickson. I am indebted to Mr Geddes for various kind helps readily given, to Professor I. B. Balfour of Glasgow for explanations and references, and last, though perhaps not least, to Mr Sadler, for liberty to obtain fresh specimens, which have been plentifully supplied to me by Mr Lindsay.

The Society's thanks are due to Mr Kidston, for his faithful transference to stone of the drawings which make up Plates IX. and X.

EXPLANATION OF PLATES.

PLATE IX.—Figs. 1–3. Epidermis of *Ornithogalum pyramidale*, $\times 400$. Fig. 3 is a patch of cells which show not only normal stoma phases, but also several interesting from a teratological and pathological aspect.

Figs. 4–8. Cells from epidermis of *Scilla bifolia*, $\times 900$, showing successive division of the nucleolo-nucleus, nucleolus, and nucleus of the stoma mother cell. In fig. 8 the nucleoli of each daughter nucleus have re-divided.

Figs. 9–11. Cells from epidermis of *Scilla bifolia*, showing division of the ordinary epidermal cells, $\times 450$.

Figs. 12 and 13. Parenchyma cells from leaf of *Ornithogalum pyramidale*, $\times 400$.

Figs. 14 and 15. Parenchyma cells from leaf of *Ornithogalum pyramidale*, $\times 900$. Explanation in text, p. 200.

Figs. 16–20. Ordinary epidermal cells from rather old leaf of *Ornithogalum pyramidale*. Stages in division of the nucleolus; the process not proceeding further. The nucleus exhibits a very clear nuclear membrane and intranuclear network.

Figs. 21–29. Fundamental tissue-cells of *Equisetum limosum* dividing. Explanation in text, $\times 400$.

PLATE X.—Fig. 1. Single cell from filament of *Spirogyra nitida*. This one is exceptionally large, having been drawn in winter when many seem to have a tendency to extreme elongation without division. The filaments connecting the nucleus with the chlorophyll bands are very evident.

Fig. 2. Single cell from filament of *Spirogyra nitida*. The nucleus alone is represented as showing the effect of endosmosis on it.

Figs. 3*a*, 3*b*. Nuclei isolated, and exhibiting changes preparatory to division. At this time the nucleolo-nucleus probably divides. From Mr Jackson's cabinet.

Fig. 4. Single cell, with nucleus, &c., alone shown. The nucleoplasm has been expelled on each side of the nucleolus through the nuclear membrane, but is still connected with the nucleolus by delicate threads.

Fig. 5. Single cell, with nucleus, &c., alone shown. The nuclear membrane has fused with the nucleoplasm at the poles.

Fig. 6. Single cell, with nucleus, &c., alone shown. The nucleolus is now dividing, the forming daughter nucleoli being still connected by delicate threads. Crossing the diameter of the cell is a row of granules embedded in the peripheral protoplasm of the cell.

Fig. 7. Single cell, with nucleus, &c., alone shown. The daughter nucleoli are now retreating along the nuclear barrel, and in their course scatter its filaments.

Fig. 8*a*. Single cell. The daughter nucleoli have now reached the polar masses of nucleoplasm, which for a time had been driven before them.

Fig. 8*b*. Isolated nucleus showing appearances at this period. From Mr Jackson's cabinet. It will be observed that a nucleolo-nucleus has been detected in most of the nucleoli hitherto.

Fig. 9. Complete cell with peripheral protoplasm, chlorophyll bands, &c. The single row of granules has now increased to an irregular band, and among the granules the septum will soon form. The barrel has greatly increased in width.

Fig. 10. The septum is now laid down as a narrow circular rim inside the wall, and the peripheral protoplasm is infolding as growth of its edge continues.

Fig. 11*a*. The septum has now grown in and united with the outer edge of the nuclear barrel, and will pass in between the halves of the cell plate.

Fig. 11*b*. Isolated nucleus septum with attached and projecting. The nuclear barrel is now about to wane. From Mr Jackson's cabinet.

Fig. 12. Portion of cell with ingrowing septum. The chlorophyll bands, previous to fission, are being slightly pushed in.

Fig. 13. The septum has increased to a deep shelf, while a coincident waning of the nuclear barrel has taken place.

Fig. 14. The septum is nearly completed, the nuclear barrel being now reduced to a narrow irregular band.

Fig. 15. The septum is here completed, and only a filament or two remain as relics of the nuclear barrel.

Fig. 16. Cell from a filament, the walls of which have been swollen by endosmotic action. The nearly completed septum has been detached from the wall, and is held in position merely by the cell contents.

Fig. 17. Cell which has been tumbled about, and whose contents have been crushed. The chlorophyll bands are not represented. Here also the septum has been displaced from the walls by contraction on crushing of the protoplasm.

Notes on the Flora of the Islands of Colonsay and Oransay.
(Part II.) By SYMINGTON GRIEVE.

(Read 14th July 1881).

When we read our first notes on the flora of these islands, which commence at page 66 of this volume, we expressed the hope that we might be able during future visits to complete the list of plants. We have now had four other collecting excursions, and it is probable we have got a comparatively complete note of the whole flora, though doubtless some plants have escaped notice; but if any visitors to this interesting locality should find plants not on our lists, we should esteem it a favour if they will send us specimens.

Those we have noted have been most carefully verified; and we have to acknowledge, with our best thanks, the aid we have received in this work from Mr Charles P. Hobkirk of Huddersfield, and Mr Andrew Moffat of the Edinburgh Naturalists' Field Club. But we must also place on record the kindly interest manifested, and assistance given, by two eminent botanists now dead. We refer to the late Mr H. C. Watson, of Thames Ditton, and Mr F. M. Webb, of the Edinburgh Herbarium.

We have made detailed remarks regarding a number of the plants upon the appended lists; but let us add that none are specially rare, though some are not very common in Scotland, and we believe here reach nearly their extreme northern limit. Such plants as *Hypericum elodes*, *Scutellaria galericulata*, and *S. minor* are quite abundant; and we have discovered on Oransay a new station for *Orchis pyramidalis*, which was previously only known to exist in the west of Scotland at one station on Colonsay. At neither