

XXXI. *Supplementary Observations on the Development of the Theca, and on the Sexes of Mosses. In a Letter to R. H. SOLLY, Esq., F.R.S. & L.S. By WILLIAM VALENTINE, Esq., F.L.S.*

Read May 7th, 1839.

I FIND, upon resuming the examination of Mosses, which I had given up, that I have not done Mohl justice in the note attached to my paper "on the Development of the Theca and on the Sexes of Mosses," published in the preceding volume of the Society's Transactions. In that note I have stated, that I thought Mohl was mistaken where he describes the sporules as being developed by fours in a mother-cell, believing that he had taken the several masses of granular contents, which may be in many instances observed in a sporule, as so many distinct sporules. I am now bound to confirm the accuracy of Mohl's observation in this respect; and I beg, through you, to offer to the notice of the Society a remarkable instance of the tetrahedral union of the sporules as an appendix to my former paper. The subject of the following account is *Ædipodium Griffithianum*, which, from my residence being near Snowdon, where it is found plentifully, I was enabled to examine in a recent state.

A transverse section of a very young theca (TAB. XXXV. fig. 9.) shows several concentric layers of cells in strict contact with each other. The outer layer is slightly tinged with brown, and is the true theca: the two next, the outer of which is pellucid, and the inner tinged with green granules, constitute the thecal membrane. The succeeding layer of cells also contains green granules, and the next is pellucid; these two form the sporular membrane. Independent of the number and sequence of the layers, by which we may decide in this state of the theca which will ultimately form the distinct sporular and thecal membranes, the presence of the green granules sufficiently identifies them; for if we examine a longitudinal section of a ripe

theca (TAB. XXXV. fig. 8.), we shall find that the space between the thecal and sporular membranes communicates with the loose tissue in connexion with the stomata, so that the air has free access to the opposing surfaces of those membranes; and it is a fact, that all the tissue thus exposed to the action of the atmosphere contains green granules, whilst in those parts of the tissue, the columella for instance, which may be supposed to be inaccessible to the air, the granules are smaller and colourless\*. The proof is then satisfactory, that the last-described layer is the outer surface of the sporular membrane, which consists of certainly not more than two layers of cells; for I am confident, from the great number of species which I have examined in all stages of their growth, that this thickness of the sporular membrane is never exceeded. I have, in many species, had a difficulty in deciding whether there were more than one layer, but never that there were not more than two. It follows, then, that the next layer, after counting two for the sporular membrane, will either be the columella or a tissue occupying the sporular cavity. That this last is the truth, is proved by the fact of the succeeding layer being composed of decided sporules. The cells forming the layer which intervenes between the sporules and the sporular membrane are tinged with yellow, in which respect they resemble the sporules before they have arrived at maturity; and between the columella, which is composed of colourless cellules, and the layer of sporules, are two rows of cells, also coloured yellow similar to the last, and also occupying the sporular cavity. In this stage the sporules already formed consist of a disjointed cell containing a quantity of grumous granular matter. In some of the cells the grains are uniformly scattered, and in others they begin to arrange themselves in groups around four grains of larger development (TAB. XXXV. fig. 10.), which ultimately become four distinct sporules contained in a mother-cell. It is perfectly certain that the single row of sporules which exists in this stage is not equivalent to the thousands of sporules which exist at the time of maturity, and it therefore follows that more must be formed. Now as it has been already proved that the yellow cellules occupy the sporular cavity, and as they are exactly similar

\* This remark, that the columella does not contain green granules, must not be understood as generally applicable, for there are many species in which the columella is crowded with green granules.

to the mother-cells, except that they are more adherent to each other, it is fair to presume that it is by a secretion of granules in their cavities that the additional sporules are formed. I have not been able to find a theca in an intermediate state between the formation of the first layer of sporules and the complete conversion of the yellow tissue into sporules. I am not at all certain by what means the four masses of granules in each mother-cell acquire each a separate envelope. It is certain, however, that they gradually become more and more distinct, and their enveloping membrane becomes more opaque by a gradual deposition of a granular matter on its surface, which at maturity is completely covered. This granular deposit has but a loose connexion with the membrane, and is easily rubbed off in little grains, which are of a brownish colour when mature, and are individually transparent, although when crowded over the surface of the sporule they obscure its contents. The contents of the sporules gradually become less and less granular, the smaller grains being apparently absorbed by the larger one, which at length fills the entire cavity of the sporule\*.

The four sporules in each mother-cell are piled on each other, so as to form a cone with a triangular base (TAB. XXXV. fig. 12.), and they appear to be connected with each other in the young state by a very minute stalk which is situated at the conjunction of three radiating lines (TAB. XXXV. fig. 13, 15

\* I have described the contents of the sporules as they appeared at the time; it did not occur to me, until I had no longer the power of applying it to this species, that sulphuric acid might perhaps have some effect on the sporules of Mosses. From its effects on *Gymnostomum truncatulum* and several other species, I am now certain that these large apparent granules are globules of fluid surrounded by a thicker grumous viscid fluid, or I believe I may say, in other words, that they are particles of that fluid separated from its more solid constituents, which separation takes place gradually; and the globules thus formed, as they increase in size, combine with each other until there is but one large globule remaining, which occupies the entire cavity of the sporule, and is surrounded by the viscid matter of the fluid, which is consolidated into a most delicate translucent pellicle, that forms an elastic internal lining to the sporule. In the cavity thus formed is finally secreted the slimy granular matter, which in *Gymnostomum truncatulum* consists of a few granules only; in *Tortula ruralis* var. *laevipila*, the granules and globules of fluid are in about equal proportion; in *Orthotrichum striatum* the granules predominate; and in *Jungermannia complanata* I cannot discover any traces of fluid, the cavity being filled with granular matter. This fluid is easily observed on account of its immiscibility with water or sulphuric acid. This account of what I conceive to be the *modus operandi* is of course quite hypothetical.

& 18.). This connexion is, perhaps, in most instances dissolved at an early period, and the sporules recede a little from each other, but are still kept in the triangular form by the mother-cell (TAB. XXXV. fig. 13.). It is not uncommon, however, to find the connexion unbroken after the sporules have arrived at maturity; and in these instances there seems to be a general adhesion at the opposing faces of the sporules (TAB. XXXV. fig. 17.). When these adhesions are broken by violence, the adherent surface of the sporule is seen to be transparent, and altogether deficient of the granular deposit which covers the rest of the sporule, and the three radiating lines are most easily seen in this state of the sporule (TAB. XXXV. fig. 18.). The mother-cell remains entire until the sporules have nearly arrived at maturity, but as to what finally becomes of it I have no evidence. When it is ruptured by external violence it assumes a shrivelled appearance, as if it had been on the stretch and had contracted on the removal of the distention (TAB. XXXV. fig. 15.). I have observed several instances in which the mother-cell contained but one sporule, which was in all the cases round, and did not exhibit any signs of a stalk or of radiating lines on its surface (TAB. XXXV. fig. 16.).

I shall conclude this paper with some observations on the analogy that exists between sporules and pollen, which is so remarkable, and the particulars so numerous, that the essential identity of the two can, as I conceive, be scarcely a matter of opinion. In the first place, the sporules are formed in thecæ which have a great resemblance to some anthers. They are in most instances surrounded by a perichætium, which is a collection of modified leaves analogous to the perianth. They are either sessile, or seated on a stalk or seta, which may be named the filament. In *Sphagnum* the theca is elevated on a pedicel or leafless prolongation of the axis, of which peculiarity the anther of *Euphorbia* is a parallel instance. The thecæ are one-celled, yet they have a columella, which may be likened to the connectivum; and although the connectivum usually divides the anther into two cells, *Callitriche* is an instance in which there is but one cell; and there are examples in which the cavity is spuriously divided into four cells, as in *Tetratheca*, which in this respect resembles the theca of *Polytrichum*; and in the fact of evacuating its contents by a single pore, resembles the general structure of thecæ. All thecæ are lined by a distinct membrane, and so nearly does this resemble the endo-

thecium of an anther, that in *Jungermannia multifida* its tissue is fibrous. The remarkable manner of the development of sporules and pollen is a most convincing analogy; they are developed in unions of fours in the *cavities* of simple cellules; in fact, they are secretions in the cellules which occupy the interior of the theca or anther, and are the only instances on record within my knowledge, of organized secretions in the cavities of simple cellules. Although the tetrahedral union of both sporules and pollen is almost always dissolved at an early period, yet in some instances, as in *Ædipodium* and *Erica Tetralix*, it remains at maturity. Again, neither sporules nor pollen ever have the slightest apparent organic connexion with the parent plant,—a most remarkable coincidence, and a fact which has never been insisted on as a distinguishing character between sporules and seeds\*.

Then to apply, as it were, the precision of a chemical test, if sulphuric acid be applied to the sporules, the same phenomena occur as when it is applied to pollen. The effects of this test vary according to the nature of the contents of the sporule and the manner of its application, which must be carefully regulated to ensure a satisfactory result. If the sporules of *Gymnostomum truncatulum*, the contents of which are almost entirely fluid (TAB. XXXV. fig. 1.), be submitted to its action, they will burst, and a portion of the fluid will be discharged in various-sized globules (TAB. XXXV. fig. 2.). No precaution that I know of will ensure a different result in this species; but if sporules whose contents are chiefly granular, such as those of *Leskea sericea*, *Tortula ruralis* var. *lævipila*, or *Tortula rigida*, be submitted to the action of the acid, which must be added to the water very cautiously and gradually,

\* I am aware that the sporules of *Anthoceros punctatus* are described by Hooker as being attached by a stalk to a central columella; and also, that Dr. Lindley has described the sporules of *Andræa* as being attached to the columella. Dr. Lindley also describes from Brongniart and Bauer the sporules of *Salvinia* and *Azolla* as stalked. In the case of *Andræa* he is certainly incorrect; and it is quite evident, from the account he has given of the latter plants, that their structure is involved in much obscurity. If it should be decided that these bodies are really attached by a stalk to a placenta, I should be inclined to suspect that they were not *mere* sporules, for it seems improbable that bodies, developed as sporules are in the cavities of cellules, should be attached by a stalk. May not what is called the theca be an involucre, and the supposed sporules, each of which in *Anthoceros* is described as being compounded of three or four smaller bodies, be thecæ, each containing either a single union of four sporules, like *Lycopodium selaginoides*, or only one sporule, the rest being abortive, like *Pilularia*?

a few minutes being allowed to intervene between each addition, the outer coat only of the sporules will be ruptured and the contents will be ejected in the mass, being still enveloped by the delicate internal lining membrane of the sporule. Notwithstanding all the care that may be employed, a large majority of these sporules will have both their coats ruptured, and the contents will consequently be scattered. The sporules of *Jungermannia complanata* and *J. dilatata* are much better fitted for the experiment. The sporules of the former species, in their natural state, are of a rich olive-brown colour, and are completely filled with minutely granular matter (TAB. XXXV. fig. 1.). On the addition of a small portion of acid a few of them immediately burst and the contents are scattered (TAB. XXXV. fig. 6.), but the majority acquire a border of a deep-red colour, the contents appearing to be collected more towards the centre of the cavity, and they become more irregular in shape, with a projection on one side (TAB. XXXV. fig. 2.). Upon the addition of a little more acid the outer coat is slowly ruptured, and the contents are gradually squeezed out, the passage appearing to be a work of great labour, giving an observer the idea of parturition in animals (TAB. XXXV. fig. 3.). When the contents are nearly out the action is more rapid, and they are ejected with force, the sporule recoiling and contracting the fissure with a spring, unless, as is sometimes the case, the sporule is so much lacerated as to lose its elasticity. Whilst the contents were passing out they were forcibly compressed by the orifice into an oblong shape; or, if the fissure happened to be small, they would be pressed into the form of an hour-glass; but the moment they are free they resume the globular form, and appear like a spherical mass of slimy granules of a faint greenish-blue colour (TAB. XXXV. fig. 5.). The fact of the granules being evacuated in the mass, together with the peculiar appearances which they present in the act of passing out, fully impress the observer with the belief that they are held together by some power either of a gelatinous cohesion of the granules amongst themselves, or by their being inclosed in a membranous sac. This last supposition is proved to be the real fact, by allowing the sporules to remain in the acid for twenty-four hours, when the mass of granules will be found to have contracted into a smaller and apparently organized body, which in some of the instances may be clearly ascertained to be surrounded by a highly delicate translucent membrane in the form of a hollow sac, about

the same size as the mass of granules before it had contracted (TAB. XXXV. fig. 8.). This sac is so extremely pellucid, that it requires an excellent lens and of great power to exhibit it, and the observer will perhaps have to examine many masses of granules before he will find one inclosed in this sac. I am at a loss to account for the fact of so few of the masses exhibiting the sac, unless it be that the sac is ruptured by the contraction of the granules. Many of the sporules will not evacuate their contents by the action of the acid; and the same contraction of the mass of granules takes place in these, although, from being surrounded by the outer coat of the sporule, the delicate internal sac cannot be seen (TAB. XXXV. fig. 7.)\*. The empty shell of the sporule is dotted all over on its outer surface with minute brick-red coloured particles, which become of a more dingy colour the longer they are exposed to the acid (TAB. XXXV. fig. 4 & 7.). After the sporule is evacuated, or even when not empty, if it has been exposed a short time to the action of the acid, the projection which was mentioned before (TAB. XXXV. fig. 2.) may be ascertained to be more transparent than any other part of the surface, and to be marked by three radiating lines (TAB. XXXV. fig. 7 a.), which, I presume, indicate the point of attachment to the three other sporules that formed the tetrahedral union in the young state. The sporules of *Orthotrichum striatum* (TAB. XXXV. fig. 1.) are an instance in which the strongest acid seems scarcely to have sufficient power to rupture the outer coat, for it is only after a little maceration in the acid that a few of them are ruptured (TAB. XXXV. fig. 3.) and discharge their contents in the mass (TAB. XXXV. fig. 4.). The contents of these sporules are very much contracted by the acid before their expulsion, but immediately expand to their original size on gaining their liberty. TAB. XXXV. fig. 5. represents an unruptured sporule after a maceration of twenty-four

\* This is not the cause of the internal sac being concealed; for I find upon washing the sporules free from the acid and adding diluted spirit, that the internal sac becomes visible; from which I conclude, that the sac was in close apposition with the outer coat until the contracting influence of the spirit on the membrane separated it.

In the course of these experiments I have ascertained that sulphuric acid is a valuable agent in the analysis of the peristomes of Mosses. In common with my friend Mr. Wilson, (who, however, is entitled to the merit of priority,) I have long entertained the opinion that all single peristomes are in reality double, but in a state of cohesion; and I find that sulphuric acid, in the case of *Tortula rigida*, the only instance I have tried, destroys this cohesion, causing the hitherto supposed single peristome to split up into an internal and external layer, the former of which is nearly white and the latter red.

hours, in which the red granules on the surface appear to have been partially removed by the action of the acid. It is clear, from this instance, that the outer coat is in itself colourless and pellucid.

Lastly, to complete the analogy, the sporules of Mosses and of some other tribes commence their germination by the emission of the internal lining membrane in the form of a tube, which is exactly analogous to the pollen-tubes. In the Mosses these tubes increase by the addition of a series of fresh tubes at their extremities, and at length a bud containing the rudiments of stem, leaves and roots is formed, which may be considered analogous to the embryo or young bud in the seed of the more highly organized plants.

Tintinhull, near Ilchester,  
Feb. 18, 1839.

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### EXPLANATION OF THE PLATES.

#### TAB. XXXV.

Fig. 1. Plants of *Ædipodium Griffithianum*, of the natural size.

Fig. 2. A plant magnified.

*The following Figures are all highly magnified.*

Fig. 3. A leaf.

Fig. 4. Apex of a leaf.

Fig. 5. One of the gemmiform bodies which are found in the axillæ of the leaves.

Fig. 6. Transverse section of the same.

Fig. 7. Calyptra.

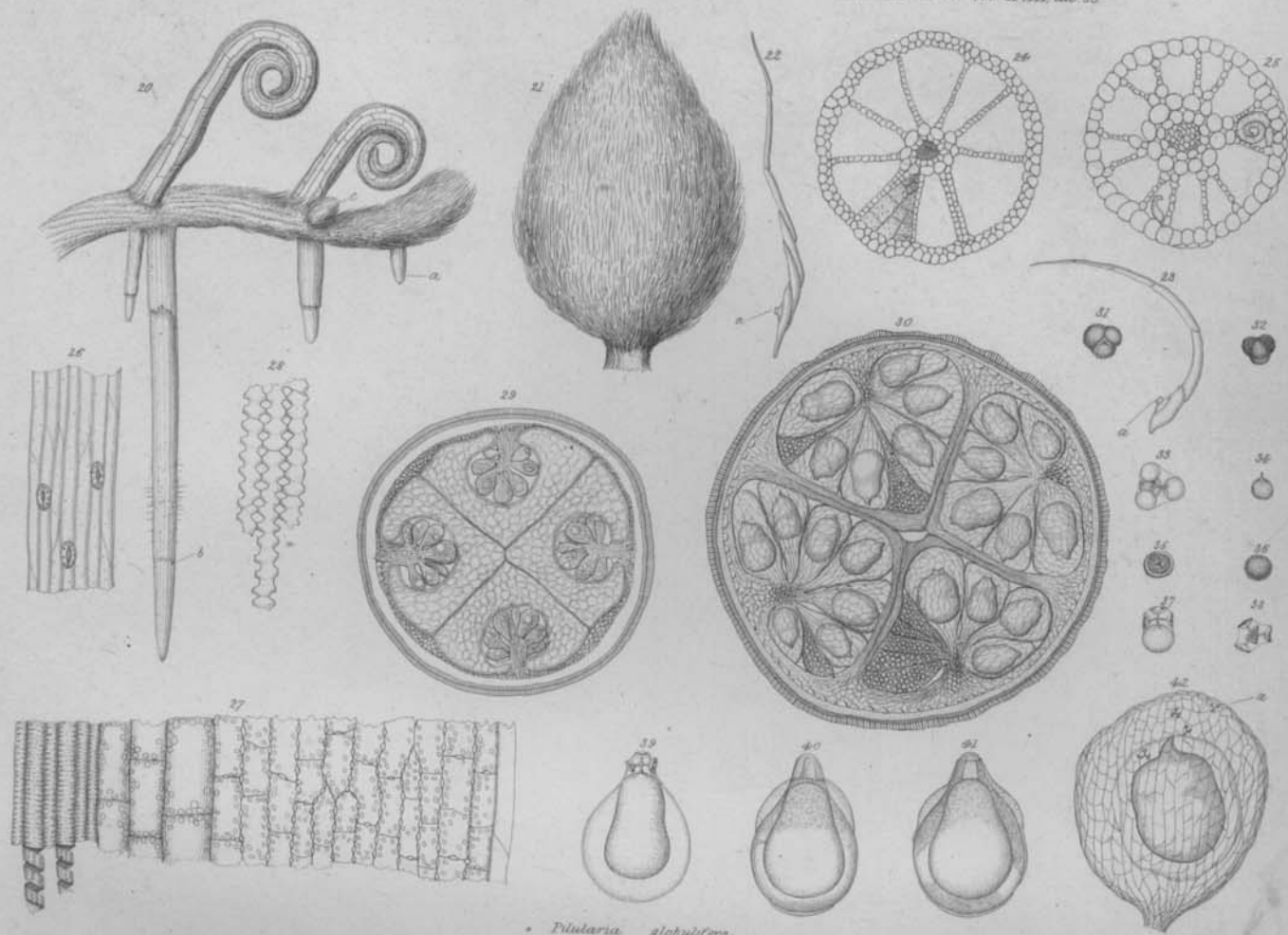
Fig. 8. Longitudinal section of a mature theca and upper part of the seta, passing through three of the stomata.

Fig. 9. Transverse section of a very young theca. *a.* The two layers of the thecal membrane. *b.* The two layers of the sporular membrane. *c.* A layer of sporules. *d.* Three layers of mother-cells, in which the sporules have not yet been secreted. *e.* The columella.

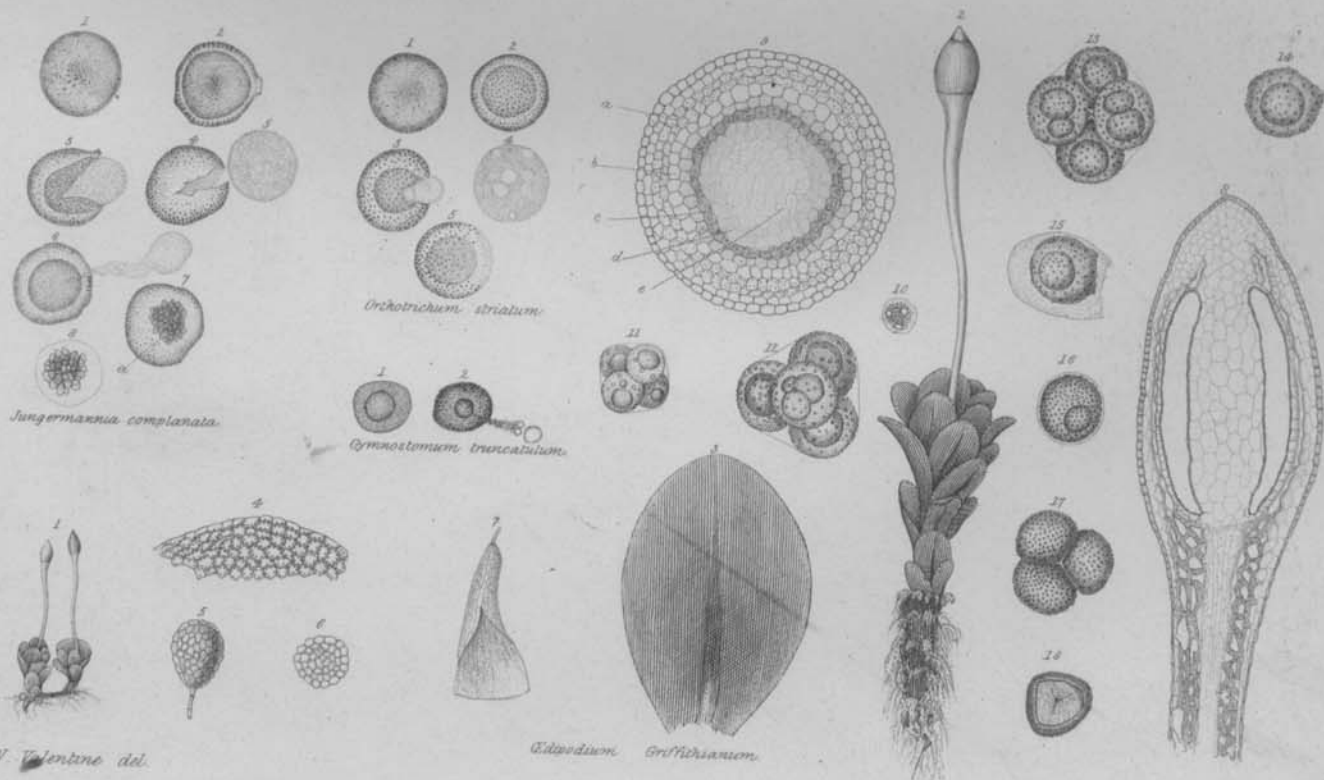
Fig. 10. One of the mother-cells, with its partially developed sporules removed and more highly magnified.



- Fig. 11. A quaternary union of sporules in their mother-cell, somewhat advanced ; each sporule contains globules of fluid and a few granules.
- Fig. 12. A more advanced union of sporules.
- Fig. 13. A different view of sporules in the same stage. The two minute points on the opposed faces of the upper sporules I believe to be analogous to the stalks which connect the sporules of *Pilularia* in the young state.
- Fig. 14. A sporule, which has separated from the others by the bursting of the mother-cell.
- Fig. 15. A sporule, which has been separated by a forcible rupture of the mother-cell, a portion of which still surrounds the sporule, but in a shrivelled state, appearing as if it had been overstretched.
- Fig. 16. An instance in which only one sporule has been developed in a mother-cell. I could discover no signs of the stalk or radiating lines.
- Fig. 17. Ripe sporules. This is an instance where the union has not been dissolved, as it perhaps usually is at an earlier period. The surface of the sporules, at least as much as is exposed, is completely covered with brownish granules. There are no signs of the mother-cell.
- Fig. 18. One of the last sporules, forcibly separated to show the three radiating lines and the minute stalk. No granules could be deposited on the surface at this point on account of the cohesion of the sporules.



*Pilularia globulifera.*



*Jungmannia complanata.*

*Orchotrichum striatum.*

*Gymnostomum truncatulum.*

*Edwardsia Griffithsiana.*