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XXX.—On the development of the Lycopodiaceæ

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edges of the under mandible rather high, and in the hind part very much bent in."

P. 257, line 34, for "Notes, habits, &c. not thoroughly known," read "The notes, habits, &c. were completely recognised."

This supposed variety of *Motacilla alba* is the *M. luzoniensis*, Scop. (*M. leucopsis*, Gould, *M. alboides*, Hodgs.)

No. 25. "*Motacilla flava*" is the *Budytes viridis* (Gm.), (*B. beema*, Sykes).

P. 260, line 34, for "The best are of compact coarse hay," read "They consist of compact coarse hay."

P. 260, last line, for "this seemed the most probable," read "were most frequently seen."

H. E. STRICKLAND.

XXX.—On the Development of the Lycopodiaceæ.

By KARL MÜLLER*.

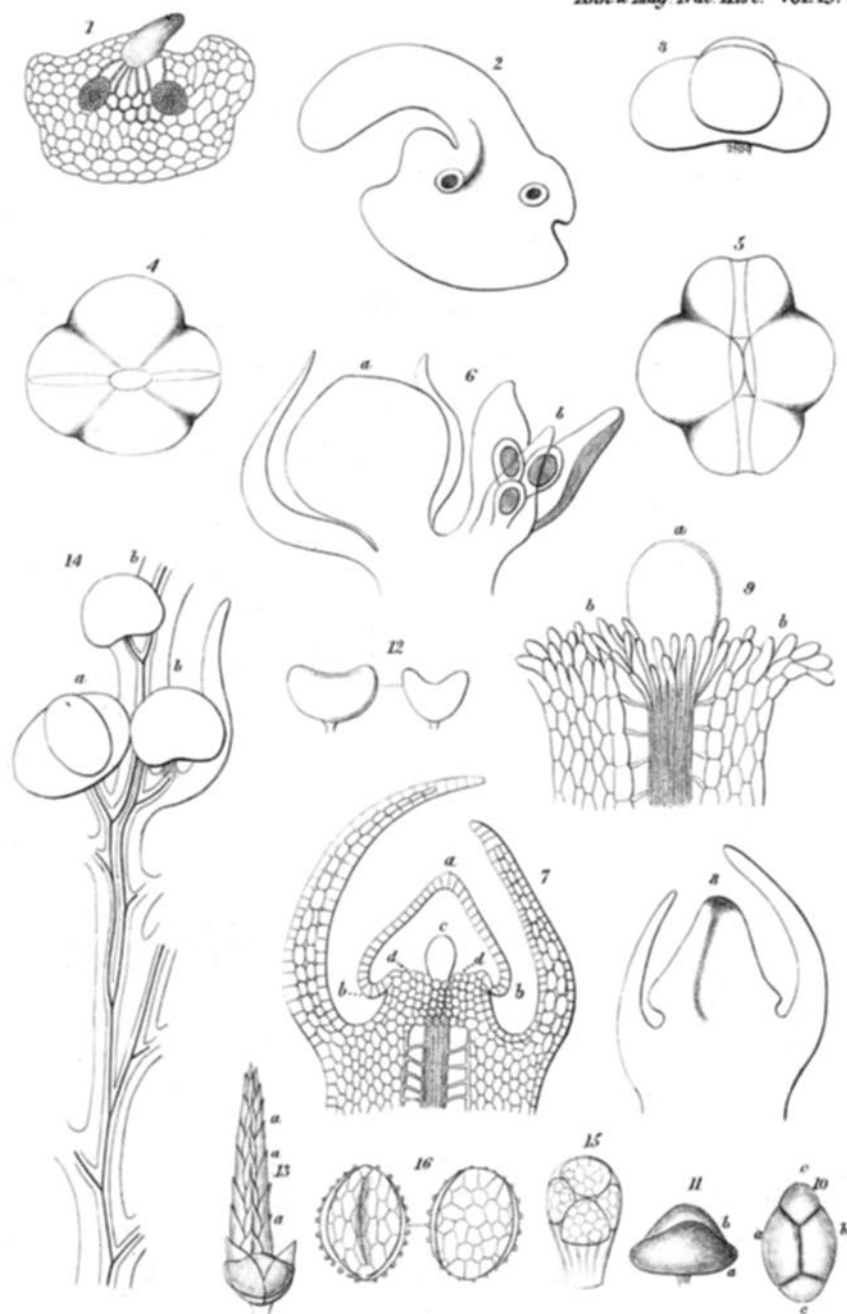
[With five Plates.]

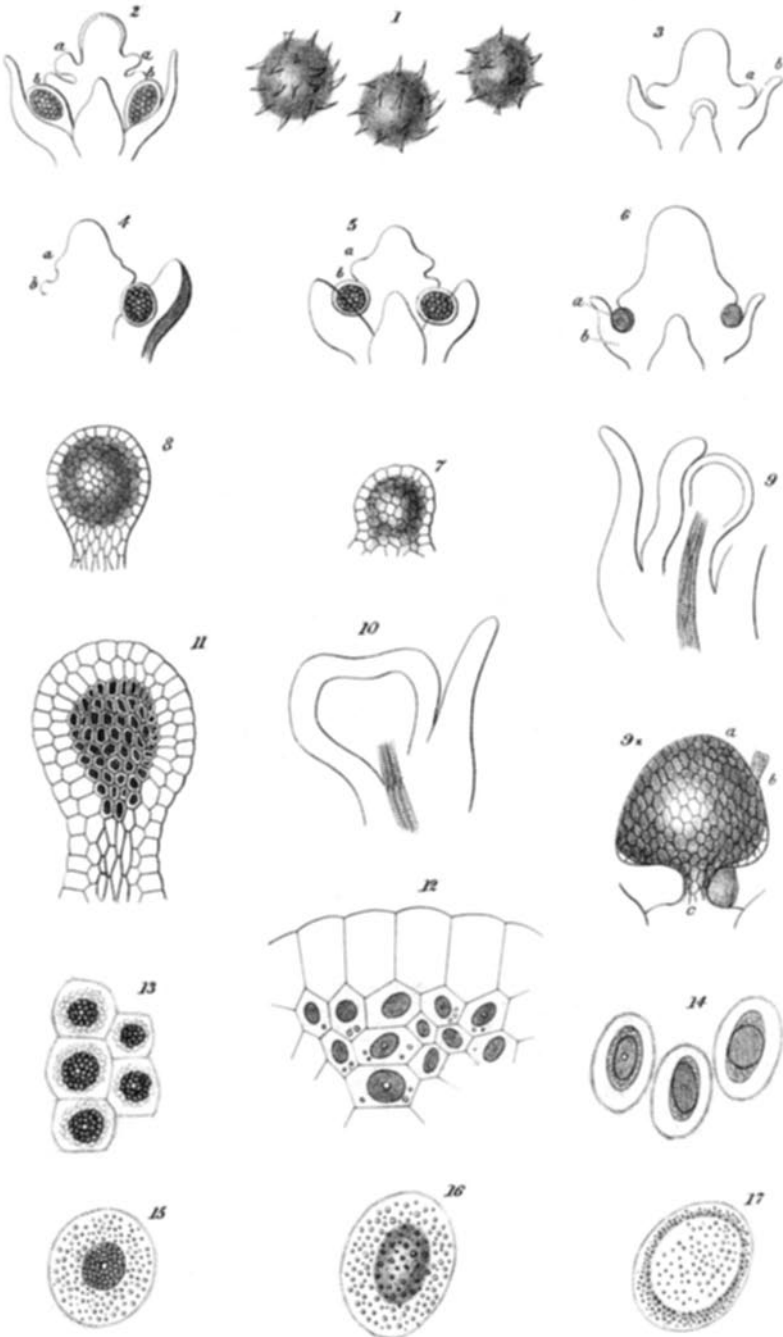
[Continued from p. 120.]

3. *The antheridium*.—*a. The formation of the sporangium*. This sporangium has a more simple structure than the oophoridium. It is found, almost universally, under a more or less reniform shape, having at the base a stalk, which is always longer than that of the oophoridium (Pl. V. fig. 9). The membrane is made up of cells almost regularly hexagonal, a structure which is very various in different species. In *L. denticulatum* it dehisces transversely over the vertex when ripe; but this condition is also subject to modification according to the species. In the interior is then found a free pulverulent mass, the well-known so-called *Semen Lycopodii*. As usual, they are tetrahedral cells which only differ in respect to size and nature of surface. In *L. denticulatum* the surface is covered by a number of papillæ which are broad at the base and, diminishing to a point above, are usually somewhat curved (Pl. V. fig. 1). Seen in any quantity, these spore-cells usually appear yellow: this is the case in *L. denticulatum*: in *L. pygmæum* and other species they appear reddish.

These antheridia are produced in considerable numbers on the other branch, opposite to that which is transformed into the oophoridium (Pl. IV. fig. 6). It is thus evident *a priori*, that the antheridia cannot be regarded, like the oophoridium, as metamorphosed terminal buds of a branch.

* From the 'Botanische Zeitung,' Sept. 25, 1846. Translated by Arthur Henfrey, F.L.S. &c.





To trace its origin, we must, as in every case, turn to the terminal bud. It is a cone more attenuated above than below, originally almost transparent, but subsequently becoming opaque through the penetration of water into its internal cavities and substance. This of course occurs through the water applied in the microscopic examination. On this terminal bud, above the youngest leaf and antheridium, at four alternating points around the axis of the branch, two little conical processes are always visible, lying in one plane, *i. e.* one above the other (Pl. V. figs. 2—6, *a b*): they are the youngest parts of the spike, in their earliest condition. The upper process is destined to become a leaf, the lower an antheridium, and both of them are mere processes budding from the axis of the branch. It soon becomes evident that the leaf is increasing in size and exceeding the antheridium in regard to extent of surface, becoming wider at the base and elongated at the apex (figs. 2—6 *b*). This is very natural, since the growth of the antheridium is centralized in its interior, while that of the leaf is more especially directed toward the periphery. The conical process from which the antheridium is to be developed therefore becomes gradually more rounded in its form, and soon appears as a perfect sphere, seated in the axil of the leaf. In this condition both leaflet and antheridium are almost perfectly transparent, like what has been already said of the terminal bud. At a later period however a granular matter makes its appearance, which is seen through the outer and as yet tolerably hyaline membrane of the antheridium, which evidently consists of a layer of denser cells, the granular mass of the antheridium not extending to its external surface (fig. 7). The base of the spherical antheridium is even now tolerably thick, and as it elongates it becomes still more independent (fig. 8). The growth of the antheridium is now particularly directed from the base toward the two sides (fig. 10 *c*). Thus the upper part becomes the more slender, the lower broader, and the form of the antheridium is perfected. It is ovato-reniform, and the peduncle at this time is very slender: this latter often attains a considerable length.

We are now met by the question: What is the import of the antheridium? The reply to this question is somewhat more difficult than to that respecting the oophoridium; yet this much is certain, that the antheridium can be no product from a leaf, since it is formed from the axis contemporaneously with the leaf. As little can we regard it, with Bischoff, as formed by the growing together of leaves. Besides, H. von Mohl has already triumphantly refuted this view. But that we have to do with a metamorphosed bud, on the contrary, cannot be disputed; since the first, rounded antheridium-spherule possesses all the pecu-

liarities of a bud, the epidermis and a formative cell-contents. The only question here is, whether we are to regard this bud as that of a branch, or altogether as an axillary bud like those so often met with in the axils of the leaves. I consider it the *bud of a twig* (*Zweig*), which is only distinguished from the terminal bud of the branch developed into the oophoridium by the circumstance that the latter is a principal branch, which possibly was capable of a more extensive development into branch and foliaceous organs, while the twig which is developed into an antheridium is but a small particle of such a main branch. That it is a twig, appears to me to be shown by the internal structure of the fruit-axis, since from its central vascular bundle are given off real lateral branches to each bud (antheridia). Yet it must be freely admitted, that the vascular bundle does not actually run into the peduncle of the antheridium, but terminates before reaching it, and it is merely elongated cellular tissue which proceeds from the vascular bundle into the peduncle (Pl. IV. fig. 14).

If now we endeavour to bring Von Mohl's observations into agreement with the foregoing facts, we are first opposed by the statement that the sporangia are not actually situated in the axils of the leaves. That is subsequently seen to be perfectly correct, but does not testify against the formation of the antheridium from a twig, since the simultaneously-formed antheridia and leaves also *simultaneously* diverge from the fruit-axis, and thus it happens that if a leaf be cautiously detached from the axis, the antheridium also is removed with it, and may then always be observed on the inwardly thickened base of the leaf. We have, therefore, here an actual growing together of the fruit-stalk and the leaf; and if Von Mohl reminds us that the shortness of the fruit-stalk and the absence of it speak to the contrary in *Isoëtes*, we have here on the other hand a fruit-stalk of tolerable length, and it appears rather that *Isoëtes* possesses a different structure. It would be some what different with *Psilotum* if the antheridium were actually formed from the leaf. I have therefore examined this genus in a living state, and found that the condition is exactly the same as in *L. denticulatum*: the earliest development of the antheridia shows their perfect independence of the leaf, and it is only subsequently that the fruit-stalk contracts such union with the leaf that its exceeding shortness causes it to be scarcely noticed. Yet it may always be recognised as independent if we trace the internal structure of the base of the sporangium in a delicate longitudinal section. Here a thick vascular bundle most distinctly proceeds to an internal, chambered cavity, and the length of the fruit-stalk must consequently be defined by the point where the bundle ends (Pl. V. figs. 9—10). The vascular bundle, closely examined, consists of porous vessels, like

that which proceeds into the leaf. That the sporangium of *Psilotum* however is chambered, is not to be explained, as Von Mohl believes, as resulting from a growing together of several sporangia, but by the fact that—as the course of development shows—the sporangium is always simple in the youngest stage, and the several partitions are formed in its interior subsequently, the number often amounting to four. The partitions are formed of parenchymatous cellular tissue, which ramifies in the interior and consists of enlarged cells. These facts I have observed with the greatest certainty, although I cannot declare the law by which the ramification of these layers of cells is governed, and why their cells do not rather become mother-cells for the spores. That the fruit of *Psilotum* is one-, two-, three- or four-chambered, indicates, from what has already been said of it, that a growing together of leaves or sporangia is not to be thought of here. The inconstancy is too great to admit of our believing, that several sporangia can be developed freely in one axil and so grow together. Here in *Psilotum* however it would be more pardonable than in any other case, to explain the formation of the sporangium by the growing together of carpels, since in a tolerably perfect sporangium a pretty distinct furrow runs over each globular protuberance (*Hügel*), which may easily lead an observer to suppose that it is formed of leaves grown together. In this genus indeed a complete history of the development might become in the highest degree interesting. The structure of the antheridium appears to me to be still more clearly evident in *Tmesipteris* than in *Psilotum*, at least from the dried specimens I was able to examine in the Royal Herbarium at Schöneberg near Berlin; for in these the fruit-stalk was often developed to a considerable length and projected beyond the leaf. In fact, we have here as in *Psilotum* a simultaneous formation of sporangia and leaves, so that it is impossible that the former can be composed of the latter, as in such case the sporangia must clearly be formed subsequently.

H. von Mohl also opposes to Bischoff's view, the formation of the spores in the same manner as pollen-grains, &c., which I have already referred to. This cannot be made to contradict my opinion—in fact, it even does not once touch Bischoff's. For where-soever formative substance is present, there cells may be formed. These formed, and a sufficient quantity of the formative matter still present, new cells again may be formed within the first, the mother-cells, and the second generation become perfect simple cells which we then call spores.

Regarding Von Mohl's and Bischoff's opinions therefore, I hope that I have succeeded in displaying in a convincing manner, a different theory of the course of development of the antheridia. As to Schleiden's so very definitely stated views, how-

ever, I can oppose no further reasons to them, since this observer has not unfolded his ideas sufficiently in detail. Meantime the figure of the antheridium of *L. annotinum* which he gives in the second edition of his work is represented in such an advanced state, that it cannot by any means be regarded as a proof of the origin of the antheridium from the leaf. Since the leaf and the antheridium are formed simultaneously, it is naturally the earliest stage alone which can yield evidence in the history of the formation of the two organs.

But by this history of the mode of formation, moreover, the independence of the family of *Lycopodia* is shown most indubitably, and the gap which formerly existed between them and the Ferns is again established (compare Röper in the 'Flora Meklenburgs.,' 1 Th., 1843, p. 127). More of this however hereafter.

b. The formation of the spores. That which is now perfected in the interior of the antheridium is the so-called spore. The essential points relating to its form have already been given in the commencement of these observations on the development of the antheridia. I pass therefore to the history of their development.

According to H. von Mohl the spores are formed here exactly in the same manner as pollen-grains, and this has already been pointed out above in that observer's own words. From my own researches I can of course confirm that here also the spores are formed in mother-cells; meanwhile I have not attained to a complete history of the development in *L. denticulatum*, because in fact I neglected it. The reason however was this: I wished to give a perfect history of the formation in a Lycopodiaceous plant with very large spores; thus to make certain at once, in what peculiar manner the contents of the mother-cells become divided into four parts—whether this, as some observers hold, occurs through division by means of septa, or whether, as others will have it, it is effected through the agency of cytoblasts. To this end I traced the formation of the spores in *Psilotum triquetrum*, which I obtained in a living state through the kindness of Prof. Kunze of Leipzic. In the first place, however, two words on the internal structure of the antheridium of *L. denticulatum*. If once successful, after many long preparations, in obtaining a very fine longitudinal section of the antheridium in a very young condition, we notice a threefold layer in its internal cavity (Pl. V. fig. 11). First the outermost or true epidermis: this is composed of a layer of parenchyma of some density which passes off to the fruit-stalk. To this follows a second layer of empty, transparent and delicate parenchymatous cells: this is continuous with the elongated cells in the fruit-stalk. Then comes the third layer which

occupies the whole of the interior: this also consists of delicate parenchymatous cells, which are very densely filled with a formative matter (reddish cytoblastema): they are the mother-cells of the spores. By the examination of the interior we now understand, why the layer of mother-cells of the spores is often compressed in an evident degree, and why, when seen through the young and delicate membrane of the antheridium, they appear globular. The greater or less degree of compression depends of course on the thickness of the epidermis and the subjacent cellular layer.

Passing to *Psilotum*, we find, in a delicate longitudinal section of the sporangium, the same layer of mother-cells which we meet with in *L. denticulatum* (Pl. V. fig. 12). However, the layer of empty cells which follow close upon the epidermis of *L. denticulatum* does not exist here. The mother-cells, tolerably regular in form and of large size, lie closely upon the very thick epidermis of the sporangium of *Psilotum*; they are also distended by a reddish mass, which, agglomerated into a spherical form, may clearly enough be perceived to consist of cytoblasts. If the cytoblast has been cut through a little out of the centre, the central nucleus also is perceived in its granular, distinctly evident substance. These mother-cells are therefore formed through cytoblasts in the first instance, and fill the interior of the sporangium as a large-celled parenchymatous tissue.

The sporangium now swells, and this process depends on the expanding mother-cells (fig. 13). This swelling out and extension act in such a manner that the membranes of the mother-cells acquire an extraordinary degree of transparency, which may be so increased in later stages, that unless one has very sharp eyes and observes with great attention, the cell-walls will be certainly overlooked. I shall return once more to this. The expansion of the mother-cells is combined simultaneously with that of the cytoblasts contained in their interior: this is in consequence of their outer borders becoming dissolved or rather macerated in water, since the softened mass is almost always granular. The latter thus becomes mucilaginous. The cytoblast becomes gradually smaller, but is usually so equably dissolved that it always appears globular (fig. 13). Sometimes however it is oval (fig. 14): this only occurs if the mother-cells no longer lie, as in the former case (fig. 13), one upon another as tumefied cellular tissue, but when the individual cells have become perfectly separated from each other, and thus lie so much freer in the interior of the sporangium. That the sporangium undergoes proportional expansion with the actual enlargement of the mother-cells is to be understood in all cases.

The expansion of the mother-cells proceeds with continually

accelerating rapidity, and with it that part of the cytoblast also becomes more fluid which in the foregoing stages was becoming softened at the periphery (fig. 15). Now it appears as a mass composed of very small granules in a state of fine division in a mucilaginous fluid. The end of the next stage is, that the whole cytoblast has become dissolved in the said fluid (Pl. V. figs. 16, 17, and Pl. VI. fig. 1). It very seldom happens, however, that the mass becomes so fluid that granular points are no longer perceptible in it (Pl. VI. fig. 1).

In the same figure we see, moreover, that the whole mass has become more agglomerated. That is a further stage, and is always met with before the division of the cell-contents into several portions. The whole mass has returned into the condition of cytoblastema*. Thereupon it becomes retracted either on to the walls of the cell, or, as more rarely happens, into the centre.

The mass is now seen to be collected into four parts (fig. 2). Thereby either the whole substance is appropriated, or the four portions are formed inside the mass. This is easily explicable. Each of the portions is a cytoblast: it increases in size in the latter case, because that portion of the mass which has not been appropriated in the formation of cytoblasts becomes deposited upon its external surface (Pl. VI. figs. 3—6).

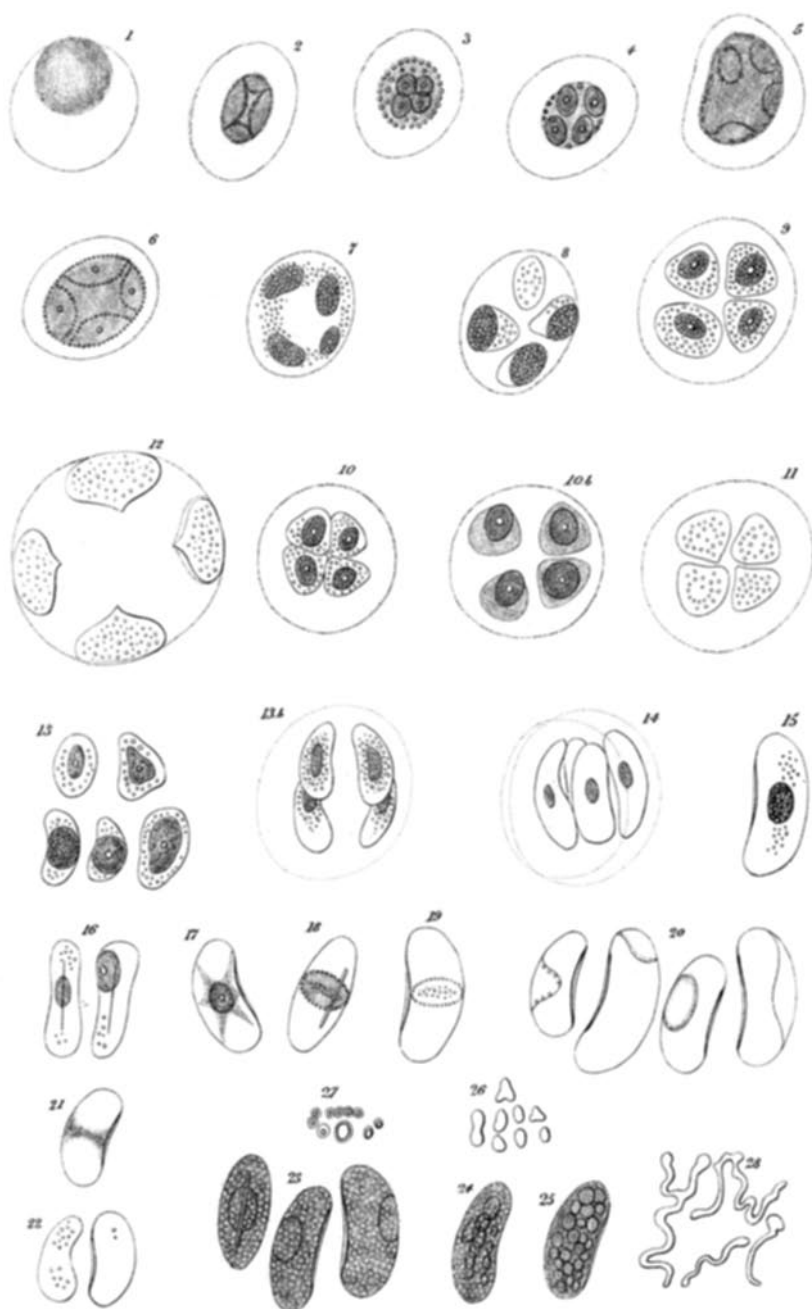
The substance of the cytoblast is still visibly very mucilaginous. In the interior of it is seen the central nucleus as a simple granule (*Kern*). Around it the mass of cytoblastema is so deposited that its outer contour is composed of granules lying heaped together, *i. e.* very closely applied upon one another (fig. 6).

In a more advanced stage the cytoblast exhibits an enveloping membrane (*Haut*) which is as yet very delicate and mucilaginous (fig. 8). It is now manifestly undergoing extension, and the cell-membranes approach toward each other with increasing pace for the tetrahedral junction† (figs. 6—11).

In fig. 8 *a, b, c*, we find also how the membrane is formed and extends from the cytoblast on one side only, therefore in the same manner which Schleiden first described. Subsequently however the membrane is detached and expands all round the cytoblast (figs. 9—10 *b*). Frequently it becomes detached at an earlier period, as in figs. 11 and 12.

* Cytoblastema and protoplasma (incl. mucilage, *Schleim*) are essentially one and the same; yet both names may be used, the latter for the oleaginously fluid, mucilaginous mass, the former for the granular and coagulated.

† This is well-known as an expression proposed by H. von Mohl for that position of the secondary cells where their faces, directed toward the centre of the mother-cell, become pyramidally pointed through their reverse superposition, while the outer faces remain spherical.



The whole of the contents of the mother-cell being now appropriated in the formation of the secondary cells and the membrane of the latter quite complete, without their form being as yet necessarily perfected, the mother-cells expand in an extraordinary degree, and the secondary cells become more widely separated (fig. 12). It is worthy of remark here that the secondary cells are usually quite free, rarely (as in fig. 12) occurring on the wall of the mother-cell. There are no signs of their being retained in their position by filaments or similar means of attachment; we must therefore attribute all to the contents of the mother-cell, and assume that the same is of sufficient specific gravity and thickness to maintain this position. I say we must assume it, since in reality it is not to be observed, for no contents can be made evident in the mother-cells even when the strongest tincture of iodine is applied. This is also always the case with the membrane of the mother-cell: this may equally be treated with the most concentrated tincture of iodine, and it remains transparent and so clear, that, as I have already remarked, it is only to be traced by the closest attention. When one of these mother-cells is beheld for the first time beneath the microscope, the appearance has something very striking about it, since the four cells are always seen in one and the same position without the mother-cell being at all perceived. This definite position of the secondary cells is retained even when the mother-cells are moved backward and forward in the water under the microscope. The separation of the secondary cells from each other is however very variable in regard to distance.

Now commences a new process in the history of the formation of the secondary cells, relating to their form. They do not, like the spores of other *Lycopodiaceæ*, remain tetrahedro-spherical, but become elongated (Pl. VI. fig. 13) and form *bean-shaped* cells. On the ventral surface, *i. e.* on the side of the tetrahedral junction, occurs a double border (*Leiste*) in a straight line, whence it appears as though the interior of the cell was open (figs. 15—25). The border however does not extend the whole length of the cell, but at most $\frac{2}{3}$ rds or $\frac{3}{4}$ ths of it.

This mode of formation of the spores is so much the more striking, that it is in Ferns alone, for instance in *Polypodium Dryopteris*, that we find anything exactly corresponding. At the same time it appears to me, that it already entitles us to give the *Lycopodiaceæ* a higher place than, for instance, Schleiden is inclined to do, who rather places them (Grundzüge, ed. 1. part ii. 80) in the vicinity of Mosses and *Hepaticæ*. However, as I have said, more on this matter hereafter.

The bean-shaped cells lie for some little time in the mother-cell, only, repeating the former condition, they soon become

more (fig. 14) or less (fig. 13 *b*) grouped together. At a subsequent period the absorption of the membrane of the mother-cell takes place.

The outer membrane of the bean-shaped secondary cells is exceedingly delicate and transparent, almost as clear as glass, and thus they produce a very pleasant impression on the eye. The contents consist at present of the cytoblast: this now undergoes a new series of essential changes, into which I will therefore enter more minutely.

It either lies upon the wall, or attached upon a mucilaginous mass more in the centre of the cell (fig. 17). The other characters of position are also excessively variable; sometimes it is in the midst of the cell, sometimes more approached toward the end or in the end itself (figs. 15—20). In the stages where the membrane of the mother-cells is undergoing absorption and the secondary cells come to lie free in the sporangium, the cytoblast becomes altered. Its substance is dissolved, and this usually occurs in such a way that its external border remains behind appearing like a mucilaginous membrane (figs. 18—20). The cytoblast often disappears altogether (figs. 21 and 22).

The mucilaginous fluid originating from the solution of the greater part of the cytoblast passes now into a new structure. It becomes deposited in the shape of exceedingly delicate, minute globules, again coagulated, round the whole internal periphery of the bean-shaped secondary cell or spore, and appears like a very fine precipitate giving the spore a grayish-coloured aspect, produced by the shades the single globules cast around them, whereby of course a peculiar mingling of dark and bright points is necessarily brought about. The outline of the cytoblast is often still to be observed, usually in a roundish form (fig. 23). Before long, the granular contents swell into larger globules which are more or less closely assembled together (figs. 24 and 25). If, in this condition, the membrane of the spore is cut through, a most distinct conviction may be obtained that the remaining space is empty, and that it is from the granular cell-contents alone that the larger globules have originated. At the same time it is seen that the spore-membrane is simple and apparently tolerably tough.

Lastly, the termination of the whole formation is a contraction and corrugation of the hard spore-membrane. It also tears in places, and now occurs a very remarkable phenomenon. The globules (Pl. VI. fig. 26), which, when treated with very concentrated tincture of iodine, appear distinctly hollow (fig. 27) and more or less round, begin to elongate into thick filaments (fig. 28). These frequently branch in the most manifold curves with thick prolongations, and thus usually grow through the

corrugated and torn spore-membrane. I have not succeeded in discovering any purpose whatever in it, striking as the appearance is.

All these observations on the formation of spores confirm the *general results* which H. von Mohl laid down in his memoir on the development of the spores of *Anthoceros lævis*, Linnæa, 1839, vol. xiii. p. 273—290.

1. *Four spores are always developed in a mother-cell.*

2. *Previously to their development, a granular fluid matter is contained in the mother-cell.* Here it may be added, that this same is formed of the dissolved cytoblasts.

3. *The four spores are formed at the same time, and certainly not, as Mirbel believed, by the mechanical division of the cell-mass into four parts by septa, these septa proceeding from the membrane of the mother-cell, but in an independent manner.* To this it may be added, that actual cytoblasts are simultaneously produced in the cell.

The chief conclusion therefore is, *that the process of spore-formation does not differ from the formation of cells through cytoblasts.* *Psilotum* cannot be too highly recommended for the observation of all these facts, as we here possess extraordinarily large mother-cells which allow all the alterations in their interior to be perceived with the greatest distinctness.

Diversity in the peculiarities of the formation of spores in *Psilotum* from that in *Anthoceros* and other Cryptogamic plants, is of course owing to family and generic differences.

[To be continued.]

XXXI.—On the Siliceous Bodies of the Chalk and other Formations, in reply to Mr. J. Toulmin Smith. By J. S. BOWERBANK, F.R.S. &c.

IN the last January Number of the 'Annals and Magazine of Natural History' there are some observations by Mr. J. Toulmin Smith on the Formation of the Flints of the Upper Chalk, in which the author combats certain conclusions of mine published in the 'Transactions of the Geological Society,' vol. vi. new series, p. 181, relative to the spongy origin of the flinty bodies of the chalk, greensands, and oolites. Had the differences between the author and myself been merely matters of opinion, I should not have occupied your valuable pages on the present occasion, especially as he has declared* that "it is not his intention to dispute the particular facts stated by myself as applying to the cases

* Page 2.