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XXXV.—On the development of the Lycopodiaceæ

Karl Müller

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cies, and *C. horrens*, an exotic insect, is the type; under these circumstances I consider that it is sufficient to refer to the elaborate generic and specific characters given by Schönherr rather than to transcribe them*.

XXXV.—On the Development of the Lycopodiaceæ.

By KARL MÜLLER†.

[With five Plates.]

[Concluded from p. 249.]

c. The morphological import of the spore. Up to the present time it remains doubtful what purpose is served by the antheridium-spore. One person maintains this opinion, another that. This author declares that he has seen it germinate, the other that he has never been able so to do. Kaulfuss (*Das Wesen der Farrenkräuter*, &c. Leipz. 1827) relates (p. 23) that, first, Fox sowed *Lycopodium Selago*, then Lindsay *Lycop. cernuum* with success, and that *Lycopodium clavatum* had sprung up in abundance with Willdenow. With himself it did not succeed, yet the garden-inspector Otto, at Berlin, raised *Lycop. pygmæum*, Kaulf., from seed, for several years in succession. The last case however is easily explicable, since the *Lyc. pygmæum* which I know by this name from the hands of the exact Kunze, possesses oophoridia also; and that these germinate is known. Here therefore we cannot place full dependence even on the assurance of such an authority as Willdenow.

An observation of Göppert's‡ however is of far greater importance from the fact, that it does not merely amount to a confirmation; this was beholding young plants produced from the antheridium-spores of the same *Lyc. denticulatum*, the development of which we have above become acquainted with. His observations were first published in the 'Übersicht der Arbeiten und Veränderungen der schlesischen Gesellschaft für vaterländische Kultur,' in the years 1841 and 1845. In the latter the author has also, although imperfectly, furnished illustrations to it. The observations were next published in No. 7 of the literary notices in the 'Flora,' p. 110, and lastly by Röper (in the 'Flora Mecklenburg's,' i. p. 126). The passage in question is here transcribed *verbatim* for those who may not have access to any of these books:—

* Syn. Ins. vii. p. 120, 121.

† From the 'Botanische Zeitung,' Oct. 2, 1846. Translated by Arthur Henfrey, F.L.S. &c.

‡ I have only become acquainted with it since the second section was printed.

"Both kinds of spores (in *Lyc. denticulatum*) have already been seen to germinate by Brotero and Salisbury (Trans. of the Linn. Soc. vol. xii. p. 2. tab. 19). The accuracy of these observations was however questioned by G. W. Bischoff (Krypt. Gew. 2 Lief. p. 111), because Salisbury's figures exhibited, throughout, too great an agreement with the germination of a dicotyledonous plant*. In November 1840 I noticed in a flower-pot standing near *Lyc. denticulatum* in the hothouse of our botanical garden, some germinating plants which on closer inspection and their further development I was enabled to recognise as *Lyc. denticulatum*. They exhibited two conditions: *one kind which had been developed from the delicate pulverulent seeds were one-eighth of a line high, and were already thickly clothed from the rootlets upward with alternate leaves, but they did not divide in the bifurcate manner so peculiar to the Lycopodia until they had attained a length of from three to four lines.* The others differed strikingly from these, outwardly, and at the first glance appeared to possess the greatest similarity with a germinating dicotyledonous plant. The outermost envelope of the spore was still adhering to the spot from which the roots, three to four lines long, extended downward, so that no doubt could remain as to the development from it, and from the same envelope was prolonged a perfectly naked stem two to three lines long, projecting above the surface of the ground; the upper part bore the first leaflets, which however did not stand opposite one another like the seed-leaves of the Dicotyledons, but alternate: this however could only be ascertained by a pretty close examination; and therein lies the mistake of the illustrations figs. 2, 4 and 5 of Salisbury, who has represented the leaves as opposite†. Above these leaflets the axis divided into two branches of equal development, so that the dichotomy appeared at once here, while in the former it did not occur until after the development of eight to ten whorls of leaves. Moreover in these the leaflets were also twice or thrice as large as in the others."

I have also related this author's observations on the germination of the oophoridium-spores here, because I hold them to be an evidence, that Göppert saw real germinating plants of *Lyc. denticulatum*, and to him the Lycopodial nature of the plants produced from the antheridium-spores must be indubitable. Assuming this, implicit trust may be placed on so accurate an observer as Göppert; yet I cannot suppress some perverse doubt, which his figures have inspired me with. In the first place, they are figured under too small a magnifying power to show more than

* As is well known, Bischoff retracted this in an appendix to his 'Krypt. Gew.,' having himself observed this germination.

† According to my observations Salisbury is quite right.

the branches and leaves. Then, figure 17 appears to me so like a young plant of *Fissidens*, a moss which often enough occurs in flower-pots in our green-houses, that I am involuntarily—I hope M. Göppert will, in such an important circumstance, be charitable enough to pardon me—led to imagine that he may have been deceived. By one single argument however Göppert could free himself at once from this suspicion—if, namely, he can assure us positively that he has seen the antheridium-spore still adherent to the young germinating plant; a condition of which he has made no mention. If this was actually the case, an axis must have been developed at once from the spore, and thus a confusion with a young moss plant would have been impossible; because in this as in many other Cryptogamous families a prothallus is developed first, and then a bud is afterwards produced upon this, from which the axis and the remainder of the plant are developed. Moreover the Lycopodial nature might have been pointed out at once, from the structure of the leaf. But Göppert's figures give nothing of this, and, alas! the subsequent development of the plant is wanting altogether.

Although I do not now throw any doubt on the possibility of the germination of the antheridium-spores, yet one involuntarily asks, how then are the *Lycopodia* without oophoridium-spores propagated? we must still wait for further observations which shall offer a complete history of the development. But it always presents itself to me as a peculiar phenomenon, that some observers have unanimously described plants produced from antheridium-spores, while others again have altogether failed in discovering them. This has been my own case, although I have kept *Lyc. denticulatum* more than half a year in a room, and observed dozens of germinating plants developed from oophoridium-spores and have sown numbers of antheridium-spores. Just the same has occurred to me with the spores of *Psilotum triquetrum*, although, according to Kaulfuss (*l. c.* pp. 10 and 27), the inspector Otto found *Bernhardia dichotoma* quite separate from the parent plants upon roots of plants, in many pots in the Berlin gardens, a phenomenon which Dr. Fischer has also observed upon a palm root in Gorenki. Enough of all these opinions and assurances; they are altogether too doubtful to allow any conclusions to be drawn from them. One can only urgently desire that this important point may right soon be settled.

§ 6. Retrospect.

The following are the points which may be considered as surely proved in the foregoing history of development:—

1. The *Lycopodiaceæ* possess two kinds of organs of fructifica-

tion, antheridia and oophoridia. The spores of the latter certainly germinate; of the former, it is still doubtful.

The *antheridium-spores* correspond to those of such cryptogamia as are formed to the number of four in a mother-cell.

The *oophoridium-spores* correspond to the ovule of the higher plants; nearest to those of the *Rhizocarpeæ* if the ovule is understood as a mother-cell produced by the axis, inside which the plant is formed. It appears to me that nothing can be objected to this: the inner membrane then would correspond to the embryo-sac of the ovule of *Rhizocarpeæ*, and the outer in like manner would be the analogue of the external membrane of the same ovule. Since in these, according to Mettenius (Beitr. z. Kenntniss der Rhizocarpeen), the embryo-sac originates by the deposition of membranous substance, or rather by the secretion of the internal membrane, so also must it be formed in the *Lycopodium* ovule in the same manner, since it is produced at a later period.

If this comparison, of the oophoridium-spore with an ovule, have a good foundation—and I see with pleasure that Spring is of the same opinion, which so much the more strengthens me in my views that I did not yet venture to assert them in the second section, and only determined to regard them as clear and correct after subsequent explanations—the *Lycopodium* ovule thus becomes of as much consequence in a systematic point of view as that of *Rhizocarpeæ* has become since an impregnation has been distinctly pointed out in it. Perhaps I may be allowed to express briefly and conclusively what here presses itself upon us involuntarily as a *necessary consequence*, in propounding here five chief stages in the formation of plants. Four of them have perhaps already been propounded by many authors; but hitherto they have never been displayed in connection with one another.

The vegetable kingdom commences with a single cell. It becomes a mother-cell, new cells being formed in its interior. The daughter-cells propagate the species in a similar manner, these again also becoming mother-cells. This is the case in the *Bacillariæ* and plants of the genus *Protococcus*. Schleiden will pardon me if I reckon the *Bacillariæ* and *Desmidiaceæ* decidedly among plants. In *Frustulium* I believe that I have distinctly observed a single cell expand itself into the so-called *siliceous lorica*, inside which new chlorophylle-like cells were formed, from which the species was again propagated in the same manner. This I have clearly observed in my *Frustulia polymorpha* from the North Sea—no matter where this be arranged, since my honoured friend Kützing has passed it over in silence in his work on the *Bacillariæ*. I believe that I saw it also in an *Achnanthes*, which appeared to me to be *Ach. panduræformis*. Moreover I have observed in *Closterium Acus* cell-formation in the interior from *cytoblasts*, which wholly

corresponded with that observed by Schleiden himself. In my estimation however, that is a vegetable cell which possesses *no contractility* (like that of the animal), whereby we can at the first glance through the microscope distinguish a simple animal cell, like that of a *Monas*. The development of chlorophylle in the interior of this vegetable cell is to me the second important distinction. A third lies in the colour of the animal cell, which can only be comprehended by actual sight, which cannot be expressed, and varies from the hyaline appearance of the vegetable cell to the reddish colour of cytoblastema.

Next to this structure follows, secondly, the simple spore, from the Algæ to the Ferns. *Here the plant is formed outside the spore*, which elongates in a tubular manner: there are several modifications of this. In the Algæ—e. g. in *Chara*, which I include here on account of the agreement of its fruit with that of *Chatophora*, in *Chatophora tuberculosa* and *endiviaefolia*, where I have distinctly observed it—the whole spore grows out at once into an axis, which is in fact nothing more than a simple tube. Whether the so-called *Florideæ* among the Algæ, ally the true seaweeds, to the following modifications, I know not. In these, as is well known, a proto-thallus is developed and the plant is then produced from a bud which is formed upon it. This occurs from the Fungi—in the Lichens it is only probable—to the Ferns. It is sufficiently known that further modifications occur in the protothallus, that this sometimes appears as a tubular filament, sometimes as a tissue of filaments, according to the more highly developed structure of the family. A higher step is at all events taken by nature if Göppert's observations shall be confirmed—that an axis is developed at once from the antheridium-spore of *Lycopodium*.

To this widely distributed structure succeeds, *thirdly*, the *ovulum* of the *Selaginellæ*. *Here the plant is produced without impregnation in the interior of the ovule, consequently in an embryo-sac, and perfected externally.*

Fourthly, we come to the *ovule* of *Rhizocarpeæ*: *here the plant is produced in the interior of the ovule by impregnation in the manner pointed out by Schleiden, the embryo being formed in the pollen-tube outside the embryo-sac, and the plant perfected on the outside of the ovule; but the acts of impregnation and germination are simultaneous stages.* In the *Rhizocarpeæ* the axis originates free in the germinal "nidus" (*Wulste*) serving as envelope (the germ, *Keimkörper*), which may be compared to the proto-thallus of the preceding Cryptogamia, only that here it is formed in the interior of the ovule. In the ovule of *Lycopodium* the axis still grows in connection with the germinal body. Up to this point no main root occurs, since, according to Mettenius, the root of the *Rhizocarpeæ* is not a main root, as Schleiden considered it.

Lastly, we see in the *fifth* place, that the acts of impregnation and germination have become two independent stages; then the embryo is produced by impregnation inside the ovule, in fact in the embryo-sac, and is at once so fully perfected, that the act of germination is nothing more than an evolution of an already fully-formed part. Here therefore the plant is produced and perfected in the interior of the ovule:

The degree of importance the *Lycopodiaceæ* possess in this series is at once evident. They unite the sexual plants with the asexual (*Agamæ*), the plant being actually formed in the interior of the ovule without the occurrence of impregnation. They possess therefore the ovule of the sexual plants and the gemmation of the asexual, and thus make good their place for ever between *Ferns* and *Rhizocarpeæ*.

2. In the formation of the plant in the interior of the ovule all cells originate singly. This is not in opposition to the law laid down by Schleiden, that the cells are developed within cells. Here the ovule is to be regarded as the common mother-cell for many cells. As we here see therefore distinctly that the cells are formed without impregnation, I must mention a phænomenon which Spring relates in his "Monographie de la Famille des Lycopodiacees" in the 'Mémoires de l'Académie Royale de Bruxelles,' tom. xv. He says that R. Brown has often seen the escape of a fovilla-like mass from the spores of *Psilotum triquetrum*, and that he also has often noticed it. This may easily be, since we have above become acquainted with a finely granular matter contained in these spores. I have never seen any fovilla-like mass escape, but certainly the above-described granular contents, which often become elongated and branched. This phænomenon however Spring holds to be very important, without giving any further explanation of it. But if in this importance an intimation is given of anything analogous to an act of impregnation, it disappears of itself before the direct proof that the ovules never open to absorb a fovilla.

Every cell is self-formed, the protoplasma of the ovule being precipitated round a central nucleus, and the outer layer becoming hardened. As in the *Rhizocarpeæ*, where Mettenius (*loc. cit.*) traced the course of formation of the cell, the cells here appear at first as cavities in the protoplasma, since the substance around the nucleus is so transparent that it cannot be detected. An outer ring of protoplasma alone, more granular than the rest, is to be seen, and the outermost layer of this becomes membrane. I have never perceived a cytoblast here in *Lyc. denticulatum*; this structure therefore must be regarded as a modification of cell-formation.

3. The terminal bud alone is formed by the plant inside the ovule.

The rootlets are not formed till afterwards upon the outside of it. Another proof that the *Lycopodia* cannot be said to have a main-root.

4. *The terminal bud becomes inclosed by an envelope (two bud-envelopes, Knospenhüllblättern).* These remind us of the cotyledons of the Dicotyledons. At all events those bud-envelopes are identical with it, which so often occur in the Phanerogamia, *e. g.* in many *Leguminosæ*, as in *Amicia*, *Lathyrus*, *Pisum*, in *Agri- monia*, in *Cunonia capensis*, especially, exactly as in *Selaginella denticulata*, in the Begonias, &c. Here these enveloping leaves have usually been looked upon as stipules. It is impossible that they can be such; for they are distinguished from true stipules, *e. g.* in Roses by the fact that they always inclose axial buds, and always surrounding the stem at the origin of the internode, they persist or drop off (*Cunonia*), while the stipules, mere appendicular organs, rest upon the leaves. This is alluded to in another place.

5. *The Selaginellæ possess a main-axis.* This however remains very short and divides at once in the terminal bud into two branches, which in like manner always divide again dichotomously. Hence the "caulis dichotomo-procumbens."

6. *The leaf is merely an "outshoot" (Auftreibung) of the stem, which expands into a flattened body.*

7. *In Selaginella denticulata an accessory organ also is found between the axis and the leaf; the import of this is as yet doubtful.* In more recent researches in living *Selaginellæ* I found it also in *Selaginella stellata*, *apus* and *viticulosa*, and of exactly the same structure. It thus becomes probable that it extends throughout the whole of the genus *Selaginella*.

8. Among the significant peculiarities in *Selaginella* is also to be included the extremely regular position of the branch-roots. I mentioned above that they are formed upon the upper side of the stem in *Selag. denticulata*, and that Schleiden, without referring to the species, says that he has observed them on the under side. Since this was printed I have become acquainted with several living *Selaginellæ* in the Berlin Botanic Garden, and I found in one of them, in *Selag. stellata*, Spr., a confirmation of Schleiden's assertion. I thus had an opportunity to seek for the law which prevails here. It proves to be as follows: the roots of the branches make their appearance both on the upper and under side of the stem, but always just inferior to the forked division of a branch, and indeed within its last leaf. If this be on the upper side—and then it is a folium intermedium—there, also, the branch-root appears. But if the leaf be on the under side—and it is then a larger leaf—the branch-root also is formed on the under side always between the stem and leaf, consequently as a true branch.

9. *The oophoridium in Selaginella denticulata, and all those Selaginellæ where it stands at the base of the spike, is always a metamorphosed main-branch.* This is the case in *Selag. ferruminata*, Sprg. (= *elongata*, Klotzsch), *lucidinervia*, Sprg. (= *pedata*, Kl.), *conduplicata*, ej., *distorta*, ej., *Poppigiana*, ej., *sulcata*, ej., *stolonifera*, ej., *deliquescens*, ej., *puberula*, Kl., *lævigata*, Sprg., *articulata*, &c. Whether this law may be modified in those species where antheridia and oophoridia occur on one spike, whether it is here a transformed secondary branch, e. g. in *S. stellata*, Sprg., *pygmaea*, ej., *helvetica*, ej., &c., yet remains to be investigated. In other *Selaginellæ*, the fruit of which is diœcious, where therefore oophoridia and antheridia occur on distinct spikes, the oophoridium appears to be a metamorphosed main-branch, e. g. in *S. selaginoides*—certain it is however that the oophoridium is never a leaf-product.

The oophoridium-spores, more properly the ovules, are formed at the extremity of the vascular bundle which projects free into the interior of the oophoridium as a hollow mother-cell. The course of its development still requires to be more minutely investigated.

10. *The antheridium is a metamorphosed twig-bud* (Zweignospe) developed simultaneously with the leaves from the axis, a twig here being understood to be a secondary branch.* The antheridium is never a leaf-product. Here refer also the sporangium of *Psilotum* and *Tmesipteris*.

The antheridium-spores originate by fours in a mother-cell, and certainly by cytoblast-formation as understood by Schleiden (formation of a membrane around a nucleus), never by division of the cytoblastema.

EXPLANATION OF PLATES II. TO VI.

PLATE II.

Fig. 1. The germinating spore: *a*, the rootlet; *b*, the terminal bud; *c*, the germ. 250 †.

Fig. 2. The terminal bud so seen that the other branch-bud lies behind the one *a*. 250.

Fig. 3. The same, unfolded artificially. 250.

Fig. 4. The whole germinating plant, removed from the spore: *a*, the point of vegetation for the stem and root; *b*, the germ (*Keim-körper*). 50.

Fig. 5. The germinating plant with the bud-leaves. 10.

Fig. 6. A bud-enveloping leaf, with a branch-bud *a*; *b*, an accessory organ. 250.

Fig. 7. The base of the bud-envelope. 400.

* The word *Zweignospe*, literally twig-bud, is here used in distinction to *Astknospe* or branch-bud, which latter may be regarded as determining the bifurcation of the main axis, while the former is a secondary ramification.—Tr.

† The figures give the magnifying power.

- Fig. 8.* The branch-bud from *fig. 6 a*, unfolded; *a*, pre-formed leaf. 250.
Fig. 9. The same unfolded, with the terminal bud of the young branch *a*. 250.
Fig. 10. The last magnified 400 times.
Figs. 11—19. Germinating plants, more or less developed, magnified 5 to 10 times.

PLATE III.

- Fig. 1.* Accessory organ of the leaf. 250.
Fig. 2. The same cut across between the leaf and branch parenchyma. 400.
Fig. 2a. The same cut across between a leaf and branch. 50.
Fig. 3. The same, magnified, at the apex, 400 times.
Fig. 4. The same, bifurcate. 250.
Fig. 5. The same cut lengthways. 400.
Fig. 6. The same in its earliest development on a young leaf from the terminal bud of germinating plant, seen laterally. 400.
Fig. 7. The same, seen crossways. 400.
Fig. 8 and 8a. The same in course of development on the youngest branch of the perfect plant. 250.
Figs. 9 and 10. The same, isolated and more developed. 250.
Fig. 11. Longitudinal section of the axis-branch, to show the various anatomical relations: *a*, accessory organ with its basilar cells; *b*, cortical layer of the branch; *c*, inner leaf-cells; *d*, the elongated base of the leaf. 250.
Fig. 11x. Longitudinal section of the leaf. 50.
Fig. 12. Cross section of the axis-branch. 250.
Fig. 13. Longitudinal section of the apex of the branch. 50.

PLATE IV.

- Fig. 1.* Cross section of a branch at a node with the branch-root forming. 50.
Fig. 2. The same. 50.
Fig. 3. The oophoridium, *in situ*. 50.
Fig. 4. The same, seen from beneath. 50.
Fig. 5. The same, seen from above. 50.
Fig. 6. Two branches producing, *a*, an oophoridium, and *b*, a spike with antheridia. 250.
Fig. 7. An oophoridium in longitudinal section, in a very young condition: *a*, the epidermis of the oophoridium; *b*, the same, produced downward at the base; *c*, mother-cell of the spores; *d*, contents of the future fruit-stalk. 250.
Fig. 8. The same, seen from behind. 250.
Fig. 9. A similar one with a more highly magnified mother-cell *a*; *b*, cells on the base of the interior of the oophoridium. 400.
Fig. 10. An oophoridium, very young, *in situ*, seen from above. 10.
Fig. 11. The same, the longer side. 10.
Fig. 12. The same, the shorter side. 10.
Fig. 13. The spikelet with the oophoridium. 10.
Fig. 14. Oophoridium *a*, and antheridia *b*, *in situ* on a fruit-axis cut longitudinally. Only the central portion, represented with the cortical layers of the axis removed. 50.
Fig. 15. Mother-cells from the oophoridium of *Lyc. selaginoides*, with four young spores. 250.
Fig. 16. The last magnified 400 times.

PLATE V.

- Fig. 1.* Spores from the antheridium.
Figs. 2—6. The terminal bud of the antheridia-spike, with the antheridia forming upon it. 400.
Fig. 7. An antheridium, more perfect. 400.

Fig. 8. Another still further developed. 56.

Fig. 9*. Perfect antheridium *a*; accessory organ *b*; base of the leaf *c*. 50.

Figs. 9 and 10. Longitudinal sections of the sporangium of *Psilotum*. 50.

Fig. 11. Longitudinal section of an antheridium of *Lycopodium denticulatum*. 400.

Fig. 12. Cross section from the sporangium of *Psilotum*. 400.

Figs. 13—17. Forms of the development of the spores of *Psilotum triquetrum*. 400.

PLATE VI.

Figs. 1—28. Forms of the development of the spores of *Psilotum triquetrum*. 400.

XXXVI.—On the Discovery of Silurian Rocks in Cornwall. By Sir RODERICK IMPEY MURCHISON, G.C. St. S., F.R.S., V.P.G.S. & R. Geogr. S., Honorary Member of the Royal Geological Society of Cornwall, Mem. Imp. Acad. Sc. St. Petersburg, Corr. Roy. Inst. France, &c. In a Letter addressed to Sir C. Lemon, Bart., M.P., President of the Royal Geological Society of Cornwall.

MY DEAR SIR CHARLES,

IN compliance with the promise I made when attending your last anniversary meeting at Penzance, I now give you a more decided opinion than I was then enabled to do, respecting the age of the lowest and oldest of the sedimentary rocks of Cornwall.

Not having seen the fossils collected by Mr. Peach on the south coast of Cornwall, I then found it difficult to come to any other conclusion than that at which Professor Sedgwick and myself had long ago arrived; viz. that with the exception of the presence, in the north-eastern extremity of the county, of a portion of the culmiferous (carboniferous) trough of central Devon, the remaining and underlying strata of Cornwall were of the age of the Devonian or Old Red system. The few Cornish fossils which were then shown to me in your museum, were unquestionably similar to those with which I was formerly familiar in Devonshire and North Cornwall, as well as with those of the Rhenish provinces and the Eifel, which Professor Sedgwick and myself had shown to occupy a like geological position. They were, in fact, forms of the same type as those which, at the suggestion of Mr. Lonsdale and with the assistance of Mr. James Sowerby on one occasion†, and with the help of MM. de Verneuil and d'Archiac on another‡, we had published as characteristic of a group of intermediate characters, pertaining to strata lying *beneath* the carboniferous rocks and *above* the Silurian system. In a word, they were identical with some of the numerous fossils of Devon and North Cornwall, published in the work of Professor

† Trans. Geol. Soc. n. s. vol. v. p. 633.

‡ Ibid. vol. vi. pp. 221, 303.