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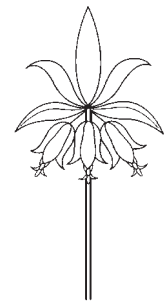

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"Über die Wirkung des Lichtes auf einige höhere Kryptogamen"; A translation of Ivan Borodin's (1847–1930) 1868 paper on fern physiology

Michael Witty

Abstract

Borodin worked in Imperial and Soviet Russia on many botanical issues, including contributions to the central concept of alternation of generations between gametophyte and sporophyte. This is a translation of his 1868 paper, which is still cited but inaccessible to most scientists because Borodin wrote in German, the most important language of botany in the 19th century, whereas most modern botanists read technical manuscripts only in English. Borodin's paper is significant for the history of science and also for the technical descriptions of experiments. Borodin used none of the commercially available equipment with which we are privileged to work today, even to the extent that he made his own light filters starting with common chemical salts. Borodin's 1868 paper reveals part of the history of science and the methods used to make early progress.

Biography

Ivan Parfen'evich Borodin (1847–1930, Fig. 1), who also published under the names Johann Borodin and Johann Parfen'evich Borodin was born in Novgorod, northwestern Russia, in 1847. He survived very turbulent times and obtained great stature as measured by his obituaries (Anonymous 1930a, b, 1948; Druce 1930) and biographical entries in encyclopedias (Barnhart 1965; Prokhorov 1973; Sukachev 1947). His scientific career began with a degree in natural science from St. Petersburg University. He then accepted a post at the St. Petersburg Agricultural Institute and was able to complete a dissertation in botany by 1876 (Sukachev 1947). (I was unable to locate the title of Borodin's dissertation and would welcome any new information.) Borodin's career involved work at several prominent institutions in Imperial Russia. Professors Borodin and Woronin founded in 1906, using their own money (Borodin 1901, 1906), a sophisticated laboratory at Bologoje. This was one of only seven biological stations in Russia at the time (Kofoid 1910).

Borodin's early work as an experimental scientist studying the physiology of ferns was overtaken by an interest in ecology. Before 1917 there were three main schools of environmentalism in Russia: pure scientists; utilitarian environmentalists interested in the economic value of nature; and pastoralists more concerned with the aesthetic and intrinsic value of nature. Borodin is a main example of the pastoralist school (Gare 1993). Borodin went on several expeditions to Siberia and the caucuses (Druce 1930), where he developed early ideas of environmentalism that persist and are cited in modern scientific literature (Anonymous 1930a, Worster 1989). Borodin advocated conservation of natural monuments *(Naturdenkmalen)* because of their beauty rather than utility or a desire to preserve their diversity (Weiner 1982, 1988a, b). One of the chief means of conservation was the creation of national parks *(Zapovedniki)*. This concept was largely overtaken by early Imperial and Bolshevik agronomy and industrialization from the last decade of the 19th century onward (Weiner 1988a). The civil war in 1917 and later rise of Lysenkoism largely eclipsed

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Figure 1. Ivan Parfen'evich Borodin (1847–1930), 1904 (at age 57), photomechanical reproduction of photograph by H. de Mrozovsky published in Ignaz Dörfler, *Botaniker Porträts* (Vienna, Druck von F. Jasper, 1906–1907, no. 14), Hunt Institute for Botanical Documentation Archives portrait no. 1.

pastoralism: attempts to control and conquer nature overshadowed worship of aesthetic beauty after 1928, when Five Year Plans were introduced, controlling land use amongst many other things (Bragg 2008; Medvedev 2000).

Borodin died in Leningrad in 1930, presumably of natural causes considering his advanced age. This was unusual for someone living through the turbulent times that lay between his birth and death and made him more fortunate than some of his colleagues who suffered the tyranny of Trofim Lysenko (1898–1976) or died in Soviet concentration camps (Li 1987). Borodin helped to cause one revolution in scientific thought and survived bloody civil wars, and his ideas persist at the foundation of both plant physiology and environmentalism.

History for fern spore germination studies

Many important aspects of fern reproduction are difficult to see with the unaided eye, and the fern life cycle was unknown until the widespread use of microscopy was established (Raghavan 2005). They are referred to as cryptogams because ferns produce no conspicuous organs of reproduction, such as flowers or seeds with an obvious role in reproduction (Steeves and Sussex 1989). Instead they rely on microscopic spores for most distribution. Many important features of the fern life cycle were first described by John Lindsay (1794), who sowed *Polypodium lycopodioides* spores and observed their germination and growth under microscopy. Surprisingly, development was not directly from spore to adult form. Instead an initial filamentous form grew and developed into a small delicate sheet of tissue that does not resemble an adult fern. Then an unusual observation was made: late in development an anatomically distinct adult form of fern sprouted from the delicate early form and grew into the large and robust adult plant. These two forms were later identified as distinct genetic entities, haploid gametophyte and diploid sporophyte, when the role of motile gametes was shown by Wilhelm Hofmeister (1851). Because of the role of motile gametes, ferns rely on thin films of water for movement of gametes from antheridium to archegonium, which completes their life cycle.

Introduction to the translation

Study of historic papers is beneficial for experimental scientists for two particular

reasons. First, it allows us to see examples of work that can be done without the sophisticated modern methods that are often poorly understood by students and scientists and are often conceptualized as "black boxes" that produce results by an unknown mechanism. Second, it is interesting to see what experiments lay at the foundation of modern botany. However, many 19th-century papers are written in languages that are inaccessible to most scientists and in jargon that most modern translators of standard German are reluctant to attempt.

In my literature research into fern biology, I found Borodin (1868) cited as one of the principal scientists involved in the elaboration of gametophyte biology but no information about what he actually did. Borodin has been cited at least 11 times in 20th-century works in English (e.g., von Aderkas and Cutter 1983), and these in turn have been cited 459 times (Bakkalbasi et al. 2006). This large number of scientists has been influenced by Borodin, but I am not sure he has been read so often because I know of no English translation. I am sure exclusively Anglophone cryptogamologists would like to understand what Borodin's work contains and why he is still influential. Borodin's 1868 paper describes in detail some of his procedures for work on fern gametophytes. I was also surprised to discover his exacting work regarding the effects of blue and yellow light on fern spore germination, chloroplast movement, and the relevance of these wavelengths to modern work on phytochrome.

It is surprising to study cryptogams and find that many years ago people did not think as we do; they assumed these plants behaved just like seed plants. It is also surprising to see convinced references to long falsified theories such as "Chemical Radiation" (Chang and Leonelli 2005a, b), an early attempt to account for the chemical effects of infrared and visible radiation. This theory asserts, amongst many other things, that yellow light is particularly weak in terms of chemical activity and that quinine sulfate absorbs chemical rays strongly (Pynchon 1874).

Some minor technical details should also be explained. Borodin refers to *Aneimia Phyllitides* [*sic*], which may be *Anemia phyllitidis,* but no detailed anatomical descriptions are given. This means that defunct fern names are difficult to make correspond to current species names, though where possible they are given in square brackets following the name used in the original manuscript. Borodin also used potassium chromate (K_2CrO_4) because it is a yellow chromium salt useful for making yellow light filters, rather than for chemical purposes. Copper oxide passed through ammonia was used by Borodin to prepare diamminecuprate; this is because Cu_2O dissolves in concentrated ammonia to form the colorless diamminecuprous complex $[Cu(NH_3)_2]^+$ that readily reacts to blue $[Cu(NH_3)_4(H2O)_2]^{2+}$, useful for making blue light filters. Borodin seems to confuse refraction and absorption or uses them interchangeably.

This manuscript is not a literary translation of the words of Borodin by a humanities scholar; it is a description of the deeds of Borodin written by an experimental scientist. My aim was to understand what he did and tell his tale rather than produce a literary work. This distinction is important because translation is more of a creative activity than many people appreciate and often reveals the translator as well as the original text. It depended much more upon my experience looking down a microscope than my knowledge of German (Nirenburg 1989). My method is weak linguistically, but I make up for that by some understanding of both botany and experimental science. Obviously, if I have mistranslated, you must blame me and

not my victim, that is, Borodin, who might say something similar to Martial (Marcus Valerius Martialis, between A.D. 38 and 41–between A.D. 102 and 104):

> If any writing in these sheets seems to you either too obscure or not quite good Latin, the mistake is not mine: the copyist spoiled them in his haste to complete his tale for you (Adapted from Ker 1968).

Translation of Borodin's experiments was generally straightforward for me because I am a plant scientist and experimentalist. Even so, some sentences were almost untranslatable for me. This may be because communication with a pre-Darwinian Russophone writing in formal German one and a half centuries ago is difficult for a modern Anglophone. However, it is worth trying because Borodin did work worth knowing.

Acknowledgments

I thank the reviewers and publisher for helping me to prepare this paper. I am also grateful to George Germeck of the Guggenheim library, Monmouth University for helping me find manuscripts relating to the life of Ivan Borodin. I wish to thank Rudolf Schmid for the bibliographic information on Borodin's 1868 paper.

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115: "If any poems in those sheets, reader, seem to you either too obscure or not quite good Latin, not mine is the mistake: the copyist spoiled them in his haste to complete for you his tale of verses. But if you think that not he, but I am at fault, then I will believe that you have no intelligence. 'Yet, see, those *are* bad.' As if I denied what is plain! They *are* bad, but you don't make better."

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Effects of light on some higher cryptogamae, J. Borodin. (Read on 28 November 1867)

(With one plate [see Fig. 2 for all figures cited in the translation below].)

I. The effect of light on the germination of fern spores

All inquiries about germination processes have been limited to the spermatophytes (seed plants). The results thus obtained are sometimes extrapolated, without further examination, to include spores of cryptogams. This is immediately apparent when one considers the available botanical literature for germination of fern spores. Although this subject has often been investigated (for example by Kaulfuss,[1] Leszczyc-Suminski,[2] Thuret,[3] Mercklin,[4] Wigand,[5] Hofmeister[6]), one finds almost nothing about the conditions required for germination. All previous researchers concentrated on the morphology of the process and asserted that germination of fern spores happens by the same processes as seeds of spermatophytes. Mercklin's results[7] clearly show that moisture and an appropriate temperature are required for the development of a prothallus from spores. The probable equivalence of the germination process in spores and seeds was assumed but not examined in detail. If spores and seeds have equivalent germination processes, then spores should germinate in the dark and produce etiolated prothalli.

Most fern spores have ample quantities of fats and oil that gradually disappear during germination[8] and some seeds that have oils as reserve substances. Because ferns and seed plants are quite similar to each other in this respect, it was expected that light would induce germination in fern spores as well as in seeds, though this was not seen by Pringsheim. This was a detailed investigation but led to conflicting results. My own very simple and easily repeatable experiments show that spores do not germinate in the dark. Before I describe these attempts, I will say a few words about the method used. Most often, I sowed spores on water. This method of observing germination and early development has already been applied by von Kaulfuss in his excellent investigations of the development of *Pteris serrulata* [*Pteris multifida*]. Kaulfuss cultivated prothalli on damp cotton in a glass dish.[9] Results were compared for sowing spores on distilled water and on water with earth, and no noticeable difference in germination time was seen, so I always used Neva water [water from the Neva River, St. Petersburg]. Now I will describe my experiments.

First experiment

On 28 March spores of *Aspidium spinulosum* Sw. var. *foenisecii* [*Dryopteris carthusiana*] were sown on water in two equivalent vessels. One vessel was transferred to darkness, the other kept in daylight. On 15 April it was seen that all light-exposed spores were sprouting, while spores kept in darkness showed no change. To find out if dark grown spores retained the ability to germinate, a portion was transferred to a small porcelain cup and exposed to daylight. After nine days entirely normal germination was seen, while the spores left in darkness still showed no trace of germination. The same results were seen when the previous material was sown on wet sand.

Second experiment

On 15 June I sowed spores of *Aneimia Phyllitides* Sw. var. *longifolia* Raddi [*Anemia phyllitidis*], some in light and some in the darkness. A week later, the spores in daylight were sprouting whereas all those in darkness remained unchanged. I moved a portion of the latter into daylight, and after a week they were all sprouting. On 4 July many spores left in darkness were beginning to rot, and when I transferred them to light, only a few were still capable of germination. Similar experiments with spores of *Allosorus sagittatus*, *Aspidium molle*, *Polypodium repens*, *Phegopteris effusa*, *Asplenium alatum*, *Asplenum* sp? [*sic*] and *Asplenium* (*Diplazium*) *lasiopteris* all gave the same results. Thus, it has been proven that the presence of light is a necessary condition for the germination of fern spores. In dark-treated spores even the exine did not burst, and it is clear that the germination process cannot be ascribed to mere absorption of water, though this has repeatedly been asserted.[10]

You may find stated in Leszczyc-Suminski and others that the circumstances favorable for germination of spores include light; but nowhere is it as explicitly mentioned in print as follows: "dormant spores only show their vital force slowly, after sowing in the presence of moisture, warmth, light and other circumstances favorable for their awakening."[11] Wigand does not fully appreciate the influence light has on germination. In his second treatise, "The developmental history of the ferns," Leszczyc-Suminski[12] describes the negative heliotropism of prothalli with these remarks: "In another experiment, the influence of light on the direction of new growth was determined by growth around a transparent window in a darkened drinking glass, though attempts to repeat the experiment were unsuccessful, probably because of poor access to air." However, I believe the true cause of failure in this experiment is poor access of light and not air because the germination of fern spores requires a very small amount of air. The spores of *Aneimia Phyllitides* even germinate under water.[13]

To address the question of which light rays cause germination, I used the lantern light of Prof. Famintzen[14] and carried out the following experiments.

First experiment

On 26 April four equal tubes of water were sown with spores of *Aspidium spinulosum*. One was placed in full lamplight, another under light depleted of most of its heat radiation (through the intervention of a water-filled glass tank). In the other two tubes the effect of light transmitted by a solution of potassium chromate and copper oxide passed through ammonia (diamminecuprate) was examined. Finally, an additional control was sown in daylight. This experiment very clearly showed the influence of temperature. The earliest germination took place in full lamplight, with no heat depletion and 2–3-cell prothalli could be seen on 9 May. It was not until 15 May that germination of spores was seen in heat-depleted lamp light and in yellow light. In blue light no germination was seen by 19 May. For four days, before treating spores with blue light, new spores were kept in darkness. These spores were incubated under blue light to 1 June and then in darkness to 15 June and did not germinate, but when exposed to daylight, they germinated normally after a week.

Second experiment

On 9 July spores of *Aneimia Phyllitides* and *Allosorus sagittatus* were sown together in two small bowls of water. One was placed under yellow, the other under blue lamplight. After nine days all spores of *Allosorus* and *Aneimia* under yellow light were sprouting; germination

consisted of prothalli 1–2 cells long. The spores under blue light showed no change, but when the tank with diamminecuprate was replaced with a tank of water, germination of all spores was seen six days later.

Although these experiments were not numerous, they show clearly that germination is caused by less than the whole spectrum of light. The higher radiation refractions seem to behave like darkness, or in any case their effect is much weaker.

It seems easiest to explain the necessity of light and the failure of fern spore germination in darkness as conditions that also prevent chlorophyll synthesis. However, after mature reflection, this explanation seems highly unlikely[15] because in darkness not even the exine bursts during germination and, when germinating spores of *Allosorus sagittatus* are transferred to darkness, normal but weak chlorophyll-free germination is seen. It is likely that germination is caused by a light dependent chemical process. During germination very important changes in reserve substances are expected, so I looked for what was missing in the first cell of the prothallus. In this matter I came to no positive results. Some observations suggest that here too germination resembles oily seeds[16]; oil is depleted in cornstarch, but that does not get us a step further since this process is completely independent of the light.

Thus, we have no neat explanation for the failure of germination in darkness.

The above-documented dependence of germination of fern spores on light cannot be extended to all ferns, without exception. The ophioglossales germinate, as is known, underground. Irmisch and Hofmeister found prothalli of *Botrychium lunaria* 1–3 inches below the surface,[17] in full darkness. However, light is not the only factor necessary for germination. I have shown that spores of *Polytrichum commune* do not germinate in darkness. It seems appropriate to include Unger's observation: *Vaucheria* spores only germinate in the light.[18] Milde[19] also germinated spores of Horsetail in darkness (namely *Equisetum arvense*), but his attempts need confirmation in my opinion.

As an appendix I will cite the following observations.

If you illuminate germinating spores of *Allosorus sagittatus* grown in darkness, the prothallus develops in a very peculiar way. It has been known for a long time that antheridia, not just foliage, are involved in the spread of germinating spores. Nägeli[20] described a filament with only six cells and three antheridia for germinating *Aspidium augescens* Link., and Schacht described[21] even less development with antheridiophore development of *Pteris serrulata*. Wigand found the same for *Blechnum Spicant* Sw.[22] In *Allosorus sagittatus* this phenomenon can be caused artificially, including through early dislocation of light and continued spore germination in the dark. This leads to the normal development of vegetative cells, forming antheridia. Therefore when we remove germinating spores from the influence of light, the remains of the undeveloped portion of the vegetative part germinates. If you sow *Allosorus* spores in light on water and transfer them to darkness 5–6 days later,[23] then most do not germinate. Germinating spores produce protonema, which bear 1–3 antheridia, except those whose exine had already burst in the light, which develop only one cell. The vegetative cell forms mature spore cells. Its content consists mainly of oil not used in germination, which forms a suspension of large and small drops in the cell. In addition, there are often very clear starch granules. Now in the whole process of germination, no trace of chlorophyll is found, as in the spores of *Allosorus*, and in all the fern species examined by me, starch is never encountered; it seems not precipitate from the simultaneous occurrence of oil and starch in a single cell to conclude formation of

the latter from the former. Such germination procedures are very suitable for investigating the structure of antheridia. Thus, it is easy to see the accuracy of the Schacht-Hofmeister model of antheridia and view the structure of their cell walls, and often one sees the radial sidewalls with the greatest clarity (Fig. 3). In darkness antheridia are not open very long, but they may be emptied artificially by moderate pressure on the coverslip, so they release spiral threads of roundish cells, which soon develop into normal and mobile free sperm.

Although the vegetative cells of the three germination systems described often bear antheridia, it is nonetheless a requirement of further development for germinating spores to be exposed to light. Then the vegetative cell, or one of the vegetative cells, grows a lateral outgrowth from the base of the sheath wall. The behavior of ordinary crest cells of the young germinating spores is very similar: they divide initially through transverse walls and later also through longitudinal walls (Fig. 4). In this way completely normal prothalli develop in continuous daylight with one or more, mostly empty, antheridia. For other fern species I did not succeed by early transfer of germinating spores to darkness, and antheridia were only seen for *Allosorus*. I noticed only one significant aspect of vegetative cells grown in light; once or twice transverse division was seen, but further development did not take place. Certainly there is this to say, that *Allosorus* produces antheridia much earlier than other ferns I have investigated. The ferns that developed prothalli on water least were *Aneimia phyllitides* and *Aspidium spinulosum,* and antheridia were never seen while prothalli of *Allosorus sagittatus* grown under the same conditions produced antheridia early. Early development is so constant that even under continuous illumination by lamplight germination takes place.

II. The effect of light on the location of chloroplasts within cells

On a small, but already bilobate prothallus of *Aspidium spinulosum*, which had germinated under lamplight and was then transferred to darkness for about two weeks, I noticed that chloroplasts entirely occupied the side of cells, while the upper and lower surface of each cell appeared free of chlorophyll. Since a similar distribution of chloroplasts was also seen recently in *Mnium* leaves by Professor Famintzin,[24] I hoped to find light dependence for the position of chloroplasts in fern prothalli. I was, several times, very successful using many water germinated spores of *Aspidium spinulosum*, as well as those of the *Allosorus sagittatus*, observing light-dependence on the location of chloroplasts within cells. A more detailed investigation of the chloroplast distribution shows they follow this rule: In darkness they are only seen near cell walls that border neighboring cells; in light on the other hand, they are seen near walls with cell-free surfaces. This rule, which also applies to expanding *Mnium* leaves, occurs with the greatest clarity in fern prothalli.

For peripheral cells in darkness with chloroplasts along three internal side walls (Figs. 5–7), the fourth free side wall and upper and lower cell surfaces are chlorophyll free. The peripheral cells have papilla-shaped hairs, for example in *Aspidium spinulosum* (Fig. 7), where you can see little hairs of the peripheral cell separating the sidewalls and also associated with chloroplasts. In filamentous cells of young germinating *Allosorus* (Fig. 5), the chloroplasts cover only the transverse walls while the free cylindrical side walls are entirely without chloroplasts.[25]

The position of chlorophyll at night has been described very well by Mercklin regarding germinating spores of *Pteris vittata* and *Pteris vespertilionis*,[26] but since then no

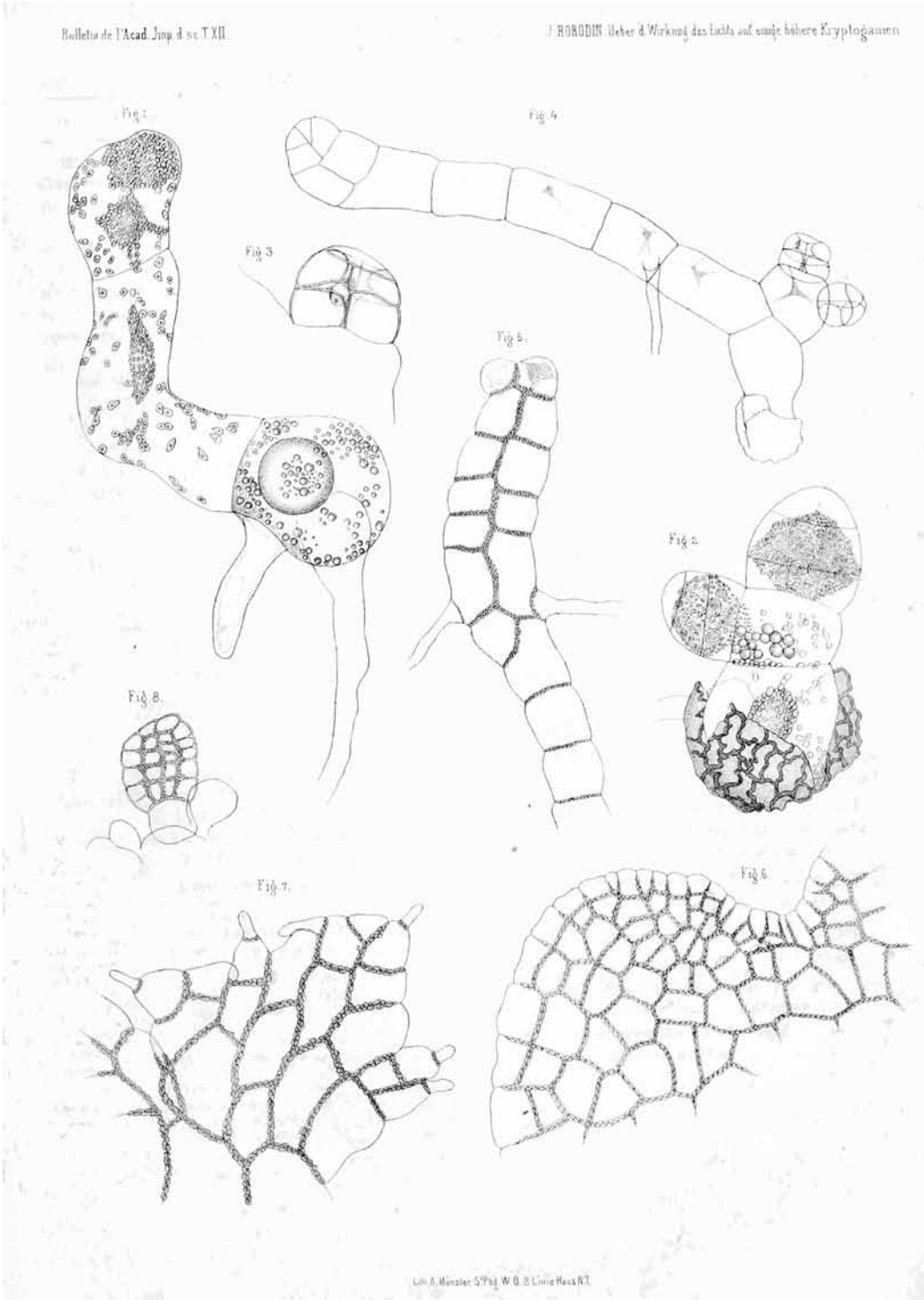
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Fig. 1.
Fig. 4.
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Fig. 2.
Fig. 8.
Fig. 7.
Fig. 6.
Lith. A. Münster St. Pbg. W. O. 8 Linie Haus N. 1.

Explanation of figures

Figure 1. A normal germinating spore of *Allosorus sagittatus* on water at daylight. The exine has been lost. The basal cell has unused oil.

Figure 2. A young protonema of *Allosorus sagittatus*, in the shadow of an early developing antheridium.

Figure 3. An emptied antheridium.

Figure 4. A protonema of *Allosorus sagittatus* similar to Figure 2, but further developed in daylight.

Figure 5. A protonema of *Allosorus* showing the nighttime position of chloroplasts. At the upper end two antheridia are developing.

Figure 6. As Figure 5, but with a much larger protonema, partially shown.

Figure 7. Protonema of *Aspidium spinulosum* showing the nighttime position of chlorophyll.

Figure 8. A young gemma, still attached to the bottom of a gemmae cup of *Marchantia polymorpha*. Nighttime position of chlorophyll; individual chloroplasts were not seen.

Figure 2. *Left,* Figures 1–8 for Ivan Parfen'evich Borodin's "Über die Wirkung des Lichtes auf einige höhere Kryptogamen" in *Bulletin de l'Académie impériale des Sciences de St-Pétersbourg* [Sér. 3] (St. Petersbourg, 1868, pl. after p. 447). Image courtesy Biodiversity Heritage Library (http://www.biodiversitylibrary.org).

more has been found, and it is not surprising that this phenomenon remains unexplained. When a germinating spore with chlorophyll in its nighttime position is brought into the light, there is movement of chloroplasts to the free cell surfaces, and after some time they cover them fully while the side walls are free of them. This distribution of chloroplasts was sometimes found throughout germinating spores and sometimes only in individual portions. When the above *Aspidium* prothallus, which I for the first time noticed the nocturnal position of chlorophyll, was cut lengthwise into two halves and one of these portions was cut again, all three pieces showed the same movement of chloroplasts when conditions were alternated between darkness and light, as in intact prothalli.

To explore the effect of colored light, I took germinating spores of *Aspidium* and *Allosorus* grown in darkness, with their chloroplasts in the nighttime position, and transferred some prothalli to full light lamp, with heat radiation shielded (in full light germinating spores died rapidly because of the high temperature), some to yellow and some to blue light. The results thus obtained were completely consistent with those of Famintzin. In blue light and in full lamplight the daytime position prevailed, and in yellow light the position of chloroplasts remained unchanged.

Next, I investigated the role that chemical rays play in the movement of chloroplasts. It is indeed possible that yellow light behaves like darkness because it contains no chemical radiation. Incidentally, chemical rays of very low kerosene lamplight destroyed the night position of the chloroplasts even faster than daylight, and it is very likely that here, as in so many other of the light-dependent life processes of plants, chemical rays play no important role. In order to be completely clear, I examined the chemical rays of full and blue lamplight as much as possible. For this purpose, I used the well-known property of quinine solutions in sulfuric acid; they absorb most chemical rays. The experiments were performed in the following way. I let lamplight pass through one vessel containing quinine solution and another containing water. The germinating spores were in small porcelain bowls covered with glass plates. At the beginning of the experiment, I prepared photographic paper and took a piece of it into the light to check its sensitivity. The other piece was placed on the glass plate covering the bowl; after 12 hours of exposure to light passed through the quinine solution, only a very minor blackening was seen. Several repeated comparative tests showed that the efficacy of the lamp light was not weakened in the least by the depletion of its chemical rays.

Prothalli developed on water went through the movements of their chloroplasts relatively slowly. At least three illuminations were necessary to achieve a complete cycle of movement of chlorophyll from the nighttime to the daytime position.

Reversed chloroplast position often comes only after standing 24 hours in darkness. I believed this slowness must be due to weak life processes of the vegetative protonemae germinating on water. Therefore I repeated the experiment and observed only germinating spores that were the most normal looking in development. By Mr. Rosanoff's kindness, I received from the local botanical garden a significant quantity of different fern prothalli. I quickly noticed the same movements of chlorophyll as before, although most were not distinct, especially in large prothalli; this movement took place only in the youngest, under the dividing clefts of prothalli, often with not all chloroplast moving to the sidewalls in darkness.

I want here to merely quote a series of experiments, all at the same time, unfortunately using germinating spores that were moved

frequently. In the next few lines just some of these experiments are cited.

In the morning of 23 September, germinating spores clearly showed the night position of chloroplasts (after previously standing approximately three days in the dark).

When they were in water drops on a microscope slide without a full coverslip and exposed to lamplight, it was three hours before the daytime position of chloroplasts was adopted. Then the microscope slide was moved into darkness, and by the following morning, 24 September, the nighttime position of chloroplasts had been restored. By 4:00 P.M. germinating spores in the porcelain bowl described above and illuminated with a lamp deprived of chemical radiation were removed from this condition. After two hours, the photographic paper was unchanged, and during these days the daytime position of chlorophyll was seen overall. Afterwards, I darkened it again, and at midnight the nighttime position was observed again. The same morning, 25 September, I found that at daylight they moved quickly into the daytime position.

A new period of darkness induced the nighttime position again, which on 26 September at daylight reverted to the daytime position. By 4:00 P.M. I returned the germinating spores to darkness, and by 6:00 P.M. all chloroplast were on the side walls. Then the germinating spores on the microscope table were illuminated by tallow [stearin] light; by 7:30 P.M. they were in the daytime position. On the same evening they were in the nighttime position again. On 27 September by 6:30 P.M., the effect of exposing the yellow light bulb to germinating spores at the microscope table was examined. Even by 6:30 A.M. on 28 September, after 12 hours of illumination, chloroplasts were observed in the nighttime position. But when the yellow light bulb was swapped with the blue, chloroplasts covered the whole of the free cell walls after one hour. At 9:00 A.M. I interchanged the blue light with the yellow, and after three hours the chloroplasts had adopted the nighttime position. This experiment clearly shows that yellow light really behaves like darkness.

Repeating illumination by blue light brought back the daytime position. The dependence of chloroplast position on light seems, at least among the cryptogams, to be a widespread phenomenon. According to my observations, it is present in the leaves of many mosses similar to *Mnium* with leaves composed of large parenchymatous cells, as well as long and narrow cells. The leaves of leafy liverworts act similarly, including those of *Alicularia scalaris*. However, this occurs not just in plant parts with only one cell layer. Such chloroplasts may also be found in multilayered tissues. In the last case, they are limited to only the most superficial layer of cells, although the distribution of chloroplasts follows the same law: in darkness the outer walls of the cells are chlorophyll-free. This circumstance is also seen in fern prothalli, particularly in the multilayered padding tissue, where archegonia develop and are seen. Quite the same is observed more clearly in the gemmae of *Marchantia polymorpha*. Here the difference between the night and daytime position of chlorophyll is very obvious; in light the free outer walls of superficial cells are densely covered with chloroplasts, while in darkness they appear completely free of chlorophyll, and only the side walls, as well as the inner walls are lined with chloroplasts, and at low magnification the gemma appear foamy. Very young gemmae that were still attached to the bottom of the gemmae cup often adopted the nighttime position of chlorophyll, although individual chloroplasts were not distinguished (Fig. 8). In the thallus of *Pellia epiphylla* and *Blasia pusilla* with gemmae cups, I have seen very similar movement of chloroplasts.

Since the mosses are particularly suitable to such studies, I have done some experiments with the leaves of *Funaria hygrometrica* to explore further the complete dependence on light for chloroplast location. The moss vegetation used was abundant and had formed on a plate on earth in a dense lawn.

The leaves showed daily periodic migration of chloroplasts. In November the transition from daytime into nighttime position was observed by 6:00 P.M., and in many leaves all the chloroplasts had already migrated to the sidewalls while from 6:00 A.M. to 7:00 A.M. the daytime position gradually occurred. To observe these chloroplast movements a weak magnification is not enough so, as an experiment, I placed a carefully excavated plantlet on soil moistened with water in a small porcelain cup, which I then covered with a glass plate. I convinced myself that under these conditions the plantlets behaved exactly the same as normal vegetation for a long time because when they were left in daylight the leaves performed their periodic migration of chlorophyll regularly. However, when they were placed in darkness, the chloroplasts changed to their nighttime position. On the other hand, leaf chlorophyll can be kept in the daytime position as long as you want by continuous illumination. If in the evening a fresh plantlet, which under normal circumstances has the nighttime position for chlorophyll and preserves this position until morning, is exposed to full lamplight or blue lamplight, the daytime position is observed after one hour. When yellow light is used, the daytime position is not seen after more than 24 hours, and the nighttime position is unaltered. In this way, it is possible, by means of alternating blue and yellow light to cause the same migration as by periodic changes of light and darkness. Thus it is completely proved that yellow light behaves like darkness.

The main results of this investigation can be briefly summarized as follows:

1. An essential condition for the germination of fern spores is the presence of light. In darkness fern spores do not germinate.
2. The germination of fern spores is caused entirely by part of the radiation spectrum. Blue light behaves like darkness in germination experiments.
3. Bursting of the exine during germination cannot be ascribed to the mere absorption of water.
4. During the germination of spores it seems that oil is transformed to starch.
5. By early transfer of germinating spores to darkness one can cause development of antheridia in some ferns (*Allosorus sagittatus*).
6. The dependence of chloroplast position on light is a widespread phenomenon in the higher cryptogams. It is seen not only in single but also in multilayered plant organs.
7. In darkness chloroplasts move to cell walls that have neighboring cells, but, on the other hand, in light, they move to free cell surfaces.
8. The daily position change of chloroplasts is caused by strong rays of lamplight, not the whole spectrum, yellow light is like darkness.
9. Chemical rays seem to play no important role.

Footnotes from Borodin 1868

[Translator's Comment: Borodin's references in the footnotes are not translated, but his comments in footnotes 13, 14, 15, 23 and 25 are translated.]

1. Kaulfuss. Das Wesen der Farrnkrauter, 1827, S. 59 u. ff.
2. Leszczyc-Suminski. Zur Entwickelungsgeschichte der Farrnkrauter. 1848, S. 8.
3. Thuret. Note sur les antheridies des fougeres. Ann. d. sc. natur. 3 Serie. T. XI.
4. Mercklin, Beobachtungen an dem Prothallium der Farrnkrauter. 1850. S. 5 u. ff.
5. Wigand. Botanische Untersuchungen. 1854. S. 34.

6. Hofmeister. Vergleichende Untersuchungen. 1851. S. 78 u. f.
7. l. c. S. 5.
8. Vergl. Sachs. Uber die Stoffe u. s. w. in Pringsheim's Jahrbuchern. Bd. III. S. 190.
9. Kaulfuss, l. c. S. 60. Tome XII.
10. Vergl. z. B. Mercklin, l. c. S. 6 und Durchartre, Elements de Botanique. 1867. S. 891.
11. l. c. S. 8.
12. l. c. S. 36.
13. In water, protonema develop in a peculiar way. They grow to an extraordinary length. For example, spores sown on the surface of water on 1 July had sprouted by 15 September and grew as very long, pale filamentous structures at the bottom of the tank. They all showed significant negative heliotropism: all grew away from the window. Microscopic examination showed that these were merely a series of cells connected to the spore at one end. The threads of cells contained round nuclei, very small chloroplasts and were very long; I counted over 20 in one thread. There was accumulation of chlorophyll in crest cells. By 29 October above 40 cells per filament could be counted, but they were almost completely without content.
14. The description of the apparatus can be found in Famintzin In Mem. de l' Acad. Imper. de St.-Petersbourg. Vol. VIII. No 15, p. 13 and in Pringsheim's Yearbook Vol. VI. p. 32.
15. The easiest way would be to investigate spores such as those from *Osmunda regalis* and extract oil containing chlorophyll (Fischer v. Waldheim, Pringsheim's Yearbook Vol. IV, p. 374). Unfortunately I was not able to do this.
16. Sachs l. c. S. 213 u. f.
17. Hofmeister. Beitrage zur Kenntniss der Gefass-Kryptogamen. II. S. 657.
18. Unger. Die Pflanze im Moment der Thierwerdung. 1843. S. 66.
19. Milde. Zur Entwickelungsgeschichte der Equiseten und Rhizocarpeen. Nova-Acta Acad. L. C. T. XXIII. p. II.
20. Nägeli. Bewegliche Spiralfaden an Farren. Zeitschr. f. wiss. Bot. Heft I, Taf. IV, fig. 2.
21. Schacht. Beitrag zur Entwickelungsgeschichte der Farrnkrauter. Linnaea. 1849. Taf. V, Fig. 1 u. 2.
22. l. c. S. 42.
23. It should be noted that the germination period, even for the same batch of spores, varies greatly with the season, probably due to variations in light intensity, and spores that in summer germinate in 6–7 days often require about 2 weeks in the winter.
24. Famintzin. Die Wirkung des Lichtes und der Dunkelheit auf die Vertheilung der Chlorophyllkorner in den Blattern von *Mnium* sp.? [*sic*] Pringsheims Jahrb. Bd. VI. S. 50.
25. Almost all researchers describe the rhizoids as free diverticula of prothallial cells. Henfrey, for example, refers to them explicitly: "their tubular cavities are freely open into those of the cells from which they arise." (Transactions of the Lin. Soc. Vol. XXI. 1855. P. 119). Often, however, the sidewall and the base of the root hair are very clearly seen.
26. l. c. Taf. I, Fig. 4, Taf. III, Fig. 19, Taf. V, Fig. 1.