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The Spiral-growth of Phycomyces

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BY

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Introduction. In one of my experiments on light-growth-responses in *Phycomyces* I was struck by the fact that the otherwise quite globular sporangium showed a small excrescence on one side. The remarkable part of it was that on examining the sporangium sideways with the aid of a cathetometer, this excrescence grew gradually larger, next again decreased in size and finally became quite invisible. After some time, however, the excrescence appeared on the other side of the sporangium to disappear from there likewise after a while. After an other interval of time it appeared on the first side, etc. It was obvious to assume therefore that the sporangium turned round a vertical axis. Various questions now immediately arose. Do all sporangia rotate or is it only an abnormality? Is the rotation connected with the growth in length or does only the sporangium turn and not the sporangiophore? At what rate do they rotate? Before our going into these questions something should be communicated about the method followed.

Method. To render the rotation visible I used very fine glass needles, which I glued to the top of the sporangium with minute drops of saliva or liquid gelatine. Originally I used glass needles of a diameter of $\pm$ 60 μ and a length of about 2 mms. From a calculation it appears, however, that the weight of a similar glass needle means a not to be neglected increase in weight of the sporangium. The sporangia namely have an average diameter of 600 μ. If we put the specific gravity = 1 (which is certainly not to much), such a sporangium weighs $4/3\ \pi\ (0.3)^3$ mgrs = 0.11 mgr., while a glass needle of a length of 2 mms and a diameter of 60 μ, weighs 0.014 mgr., if we put the specific gravity = 2,5.

So the average increase of weight is round 13 %. Afterwards I found in glasswool a material that is thinner yet, but which is consequently much more difficult to handle. The average diameter was 35 μ in this case and the weight of a needle not yet 0.005 mgr., so that the weight of the sporangium is but increased by 4 to 5 %. Subsequent experiments were always made with these lighter needles. A fundamental difference between the two kinds of weight-increases, however, was not stated.

I measured the rotation by means of a horizontal microscope (fig. 1 : a) via a mirror (b) placed over the sporangium at an angle of 45°. Initially the observations were made in a faint white light, falling in the thermostat from above. The light reflected by the needle, however, was quite insuffi-

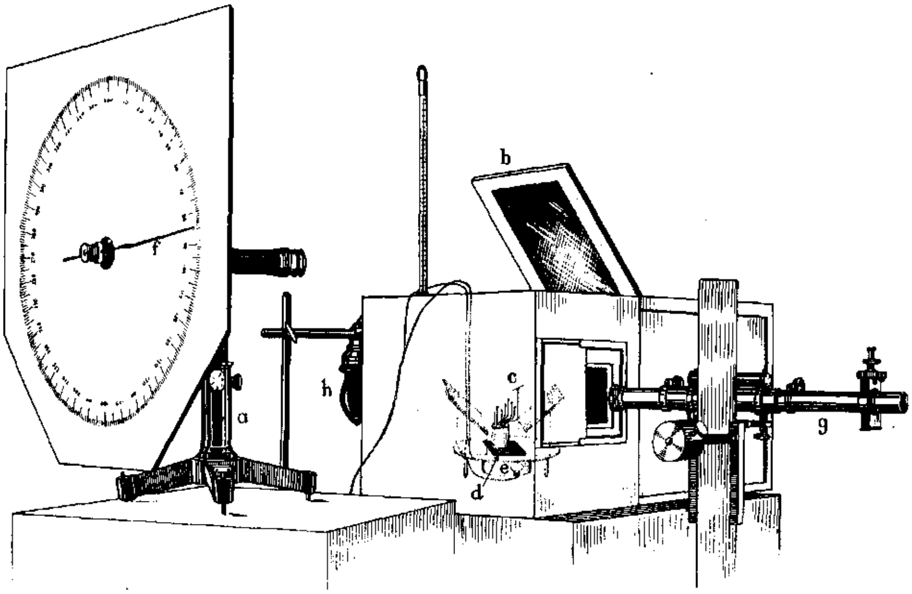


Fig. 1. The apparatus.

cient in certain positions of the needle, so that I rejected this method and searched for a method of measuring in light, which is send through the object (just as is done in the case of measuring the growth in length). To attain this end we must have at our disposal sporangia which viewed from above grow over the edge of the culture-pot, so that a source of light can be placed under them. Sporangia meeting with this requirement I obtained by placing the culture-pots horizontally for some time and next putting them vertically again. This treatment produces sporangia that are twice bent (fig. 1 : c.). The pot is placed on a piece of red glass (d) under which a diminutive electric lamp (e) has been put in a closed space. For clearness' sake 2 of the 4 reflecting mirrors have been left out in the drawing. If we subsequently place the culture with its accessories in the thermostat, we look via the mirror down upon the top of the sporangium and the needle, with a red field as background. The rotation was measured by turning the scale of the eyepiece-micrometer in such a way that the strokes of the scale run parallel with the needle, while the angle was read directly from a graduated arc by means of a long hand (f) fixed to the ocular. The size of this graduated arc allowed of a least count of 0.2°. From a non-rotating (mature) sporangium it was determined how great the accuracy of adjustment is. The extreme values differed ± 0.2—0.3° from the average. The accuracy of reading and of adjustment might both be easily increased by a more accurate scale and a higher magnification, but for this research the accuracy attained was amply sufficient.

As fig. 1 shows it is possible to measure the growth in length simultaneously. For this purpose is the cathetometer (g) and the red light (h) mounted behind the thermostat.

A + culture of *Phycomyces Blakesleeanus* Burgeff (see BURGEFF 1925) was used, the same species with which BLAAUW and TOLLENAAR worked under the name of *Phycomyces nitens* and which was cultivated in the way indicated by BLAAUW (1914) in pots with moist bread.

To make the sporangia grow in the desired position (twice bent) they were cultivated in the light. Geotropism by itself does as a rule not suffice to make the sporangia raise themselves quite from their horizontal position. Putting on the needles also occurred in white light. Next the sporangia were placed in the thermostat (described by BLAAUW 1914) at 17.5° in the dark and I waited for at least an hour before I started measuring. Though after one hour the light-sensitiveness has not yet increased to the dark-value, the dark-growth-response is finished by that time and consequently the growth in length has again become about constant.

Rotation a general phenomenon. From more than 20 experiments in constant temperature and from various observations under variable conditions it appears that rotation is a general phenomenon shown by all growing sporangia. (Plate 1). But seldom, and then but for a very short period the rotation is so slight that it is scarcely measurable and accordingly there seems to be *no* rotation.

Before our discussing the measurings of the rotation the question needs first to be put in what part of the sporangium or of the sporangiophore the rotation originates.

The localization of the rotation. Above it was already observed that the rotation occurs in *growing* sporangia and therefore it may obviously be assumed that this rotation occurs in the same zone in which the growth takes place. The growth is confined to a small zone lying at ± ½ to 2—3 mms' distance below the sporangium. (See ERRERA 1884). The following observations and experiments prove this supposition to be correct.

1°. Mature sporangia do *not* rotate.

2°. Sporangiophores which have just formed their sporangium and are therefore in the stage (stage 3 of ERRERA), in which the growth is quite stopped, do *not* rotate. Simultaneously with the beginning of the growth in length (stage 4 of ERRERA), rotation also commences (Fig. 2).

3°. The rotation shows a reaction after exposure to light. This reaction proceeds qualitatively and in the main also quantitatively parallel with the reaction which the growth in length shows after the same exposure. The graphic representations (figs 3 and 4) demonstrate this parallelism clearly. Fig. 3 illustrates the response of a sporangiophore growing in faint white light (± 10 M.C. 4-sided) which was exposed to 40.000 M.C.S. 4-sided. In A the time in minutes has been plotted on the abscis, on the ordinate the

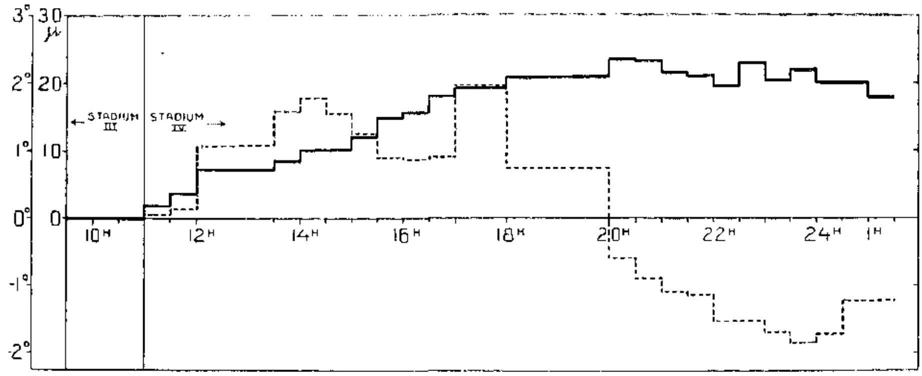


Fig. 2. Rotation and growth in length during the greater part of stages 3 and 4. Abscis: time in hours. Observations were made at points of time marked |. Ordinate: - - - - - Rotation in degrees per min. Left-handed rotation negative. ——— Growth in μ per min.

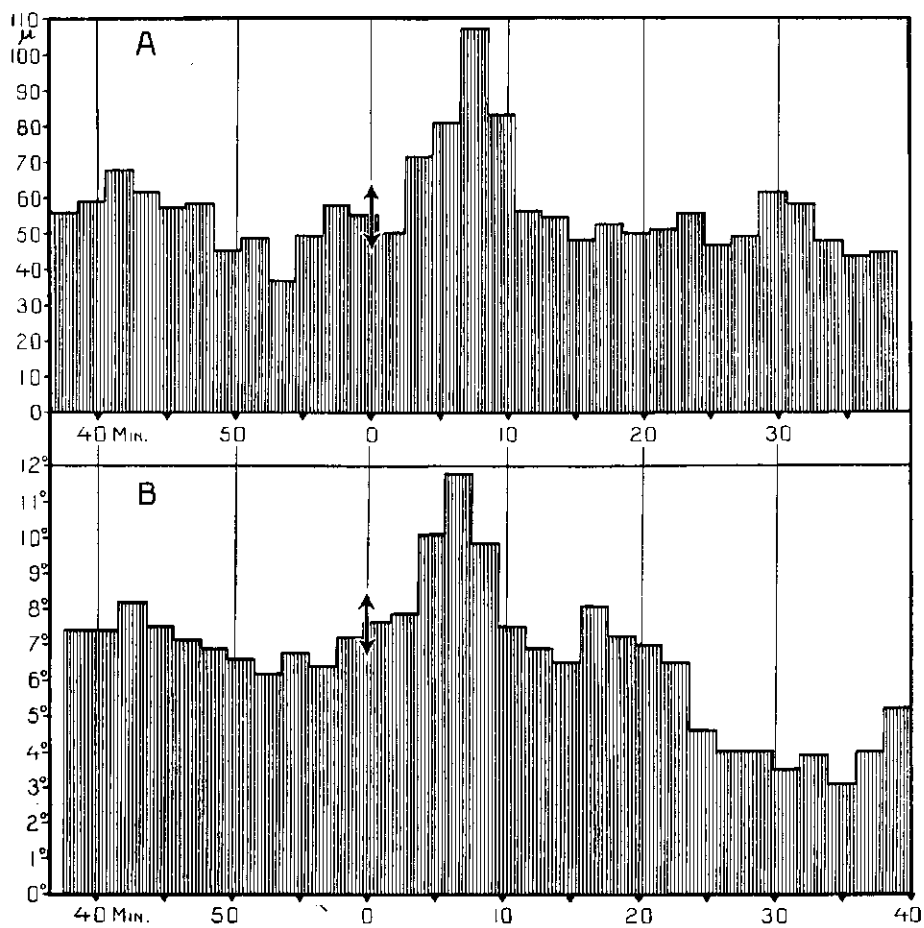


Fig. 3. Light-response of growth (A) and of rotation (B). Abscis: time in min. Ordinate: A. growth in μ per min., B. rotation in degrees per min. Continuous exposure to ± 10 M.C. 4-sided. At time 0 (↕) short exposure to ± 40.000 M.C.S. 4-sided.

increase in length in μ per min. At ↕ (time 0) exposure took place. Observations every 2 minutes. In B. the rotation in degrees per min. of the same sporangium has been plotted on the ordinate. Here too observations

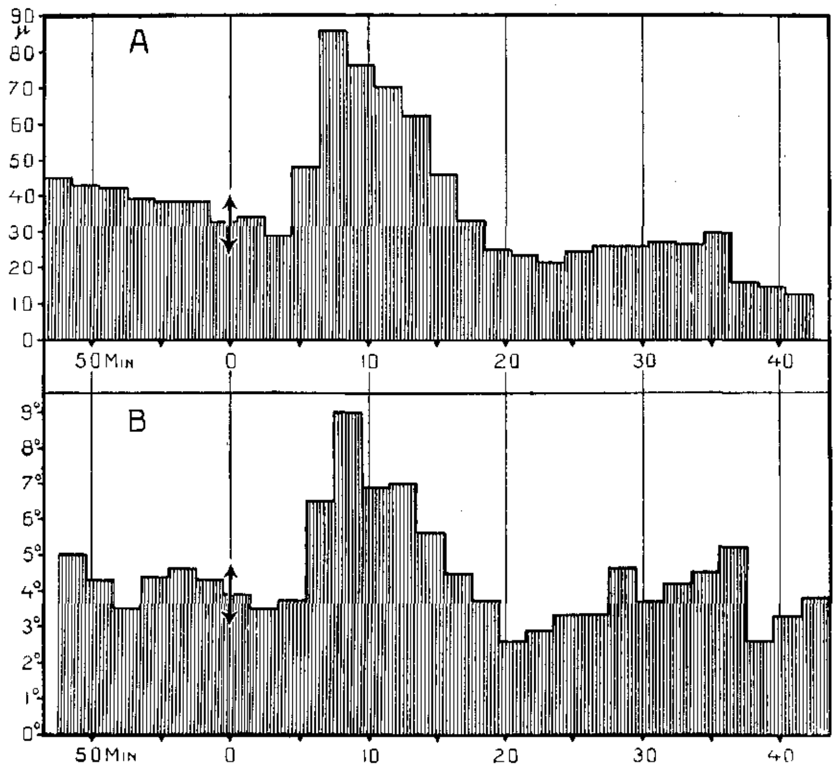


Fig. 4. Light-response of growth (A) and rotation (B). Sporangium in the darkness At time 0 (↕) exposure to $\pm$ 160 M.C.S. 4-sided. Further as in fig. 3.

were made every 2 minutes ; it should, however, be noted that the periods of observation alternate with those concerning the growth in length. One minute an observation was made through one microscope, the next minute through the other microscope.

Fig. 4 gives the responses of a sporangiophore growing in the darkness, which at ↕ (time 0) was exposed to $\pm$ 160 M.C.S. 4-sided. A again gives the increase in length in μ per min. B. the rotation in degrees per min. We see that the curves of A and B in both figures especially as regards the maximum run beautifully parallel. After that the agreement is less perfect, but it frequently occurs that at this very point of time (so after the maximum) little curvatures appear, which will affect both the measuring of the growth in length and that of the rotation, that is now in the same sense, now in the reverse sense.

Even if these first 3 arguments are not absolute evidence, because two simultaneous events need not necessarily happen in the same place, the last (4th) argument leaves no doubt about it.

4^0. If we apply glass needles in and below the growing zone, it appears that needles below the growing zone do not turn, whereas needles in the growing zone initially rotate fairly rapidly, later slower and finally stop altogether. The needle has turned out of the rotating zone and also out of the growing zone, for at the same time the increase in length of the zone lying below the needle has also been reduced to nil. Rotation and growth, therefore, take place in the same zone. The above has been schematically represented in fig. 5 *a, b* and *c*. In *b* we see a sporangiophore with three needles, one on the top, one in the zone of growth and one below the zone of growth. In *c* we see the same sporangium some time later. The sporangiophore has grown a great deal, while simultaneously a rotation of nearly 180° has taken place. The lower part of the zone of growth (below the middle needle) has grown less, while the rotation is also slighter (nearly 90°). The lower needle shows that below the zone of growth no rotation takes place. Fig. 5d shows the path described by a point on the wall above the zone of growth when we think the cylinder of the sporangiophore spread out in one plane and when we regard it from the outside.

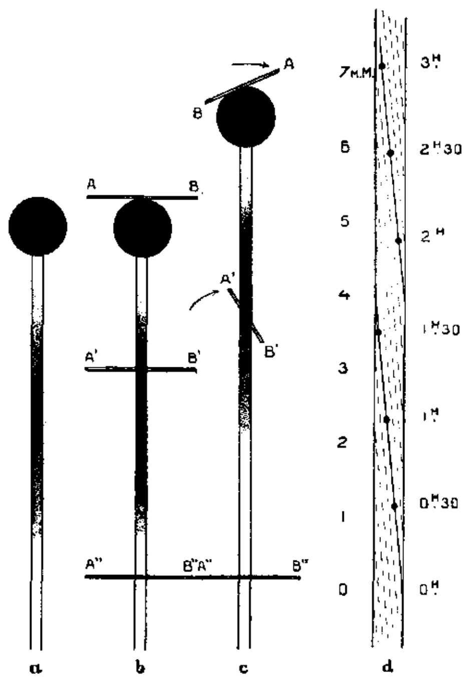


Fig. 5. Schematical representation of spiral-growth. *a.* Sporangiophore with zone of growth; *b.* with needles above, in and below the zone of growth; *c.* the same sporangiophore some time after; *d.* the path of a point above the zone of growth, when we think the cylinder of the sporangiophore spread out in one plane and when we look from the outside.

S p i r a l - g r o w t h. From the conclusion: "growth and rotation always go together and are confined to the same zone", it follows that the actual direction of growth does not coincide with the longitudinal direction of the sporangiophore, but forms a definite angle with it. The direction of growth, therefore, runs spirally round the cell. Accordingly we have called the phenomenon s p i r a l - g r o w t h.

We will now further analyse this spiral-growth. When measuring the rotation, properly speaking we measure the width-component of growth [1])

[1]) One might be inclined to speak of g r o w t h in width, but we had better avoid this term. For the growth (increase in volume of cell-wall) exclusively takes place in a longi-

and when we know the diameter of the sporangiophore (which was measured at the end of each experiment), we can express this width-component in μ per min. instead of in degrees. From the ratio of the length- and the width-component, which were measured at the same time, the angle can then be computed which the main direction of growth forms with the longitudinal axis.

In table 1 the results of more than 20 experiments have been resumed. When first we observe the direction of the rotation, it strikes us that it is right-handed [1]) in 17 cases. In the other 5 cases the rotation is partly right-handed and partly left-handed. (In the table and also in fig. 2 left-handed rotation has been marked —). Sporangia rotating exclusively left-handed or not rotating at all were not found. Accordingly the spiral can change its direction and pass from right-handed to left-handed of from left-handed to right-handed. But it is indeed obvious that the right-handed spiral is being preferred. It is not yet possible to explain the reason why one sporangiophore behaves differently from another. Therefore I will here only indicate some points that may probably throw light on this question. If beside the rotation we also consider the growth in length, it strikes us that the sporangiophores with exclusively right-handed rotation as a rule grow most rapidly (30—60 μ per min.), while most sporangia with left-handed and right-handed rotation grow much slower (10—20 μ per min.) and consequently we get the impression that there is something wrong with the growth in these sporangia. We should then have to consider the sporangiophores with alternate left-handed and right-handed rotation as abnormal cases.

This assumption is strongly supported by the process of the growth of sporangium N⁰. 1 from table 1. Initially the growth was normal and the rotation right-handed. Both, however, decreased till at a certain moment both stopped altogether. I thought the sporangiophore had arrived at the end of the grand period, but after a short time the growth recommenced and so did the rotation, but it was now left-handed. Growth and rotation, however, were slow (respectively 10—15 μ per min. and $1^{\circ}.5$—3° per min.). In normal cases no stagnation of growth occurs in the grand period; it is, therefore, not strange to regard left-handed rotation in this case as abnormal. The growth of the sporangiophores nos 8, 14, and 19 is now comparatively slow, only N⁰. 13 with an average growth of 47 μ per min. forms an exception. In sporangium N⁰. 19, of which the greater part of the

tudinal direction. By growth in width one should rather understand an increase of circumference of the sporangiophore. This would result in a widening of the sporangiophore towards the top, which occurs for instance in *Pilobolus* and some varieties of *Phycomyces Blakesleeanus*. This growth in width is here out of the question.

[1]) We call a spiral right-handed, when the observer who considers it as a winding stair-case and ascends it, has the right hand at the inside. When we look down on the sporangium from above we see in the case of a right-handed spiral the needles on the top of the sporangium move like the hands of a clock.

TABLE 1.

N⁰. exper.	Duration exper. in hours	Average growth in length in μ min.	Direction of rotation	Average rotation in degr. min.	Min. and max. rotation in degr. min.	Diameter sporangiophore in μ	Average width-component in μ min.	Average $\angle \alpha$ in degr.
1*	3	—	R—L	—	—4.5—0—9.0	—	—	—
2*	$1\frac{1}{2}$	55	R	6.7	5.0—8.2	—	—	—
3*	$1\frac{1}{4}$	—	R	3.6	2.3—4.7	—	—	—
4	2	46	R	4.5	2.4—6.7	—	—	—
5	$3\frac{1}{2}$	37	R	2.1	1.2—3.1	90	1.6	2.5
6*	4	46	R	1.5	0.2—3.7	108	1.4	1.8
7	4	33	R	2.6	1.4—3.3	120	2.7	4.7
8*	$4\frac{1}{2}$	15	L—R	—	—5.3—0—7.0	64	—	—
9	$1\frac{1}{2}$	40	R	7.1	5.8—10.7	156	9.7	13.5
10*	$2\frac{1}{2}$	18	R	1.1	0.0—2.0	—	—	—
11	1	40	R	2.9	2.2—5.1	120	3.0	4.3
12	1	26	R	3.5	2.3—4.8	136	4.2	9.2
13*	3	47	R—L—R	—	—1.3—0—1.8	162	—	—
14*	6	13	L—R	—	—5.6—0—1.1	97	—	—
15	$\frac{1}{2}$	—	R	2.7	—	—	—	—
16	2	63	R	4.8	3.2—8.5	83	3.5	3.2
17	6	43	R	2.9	1.0—4.5	102	2.6	3.5
18	$3\frac{1}{2}$	12	R	1.6	0.9—2.5	110	1.5	7.1
19*	16	21	R—L	—	—1.9—0—2.0	—	—	—
20	$\frac{1}{2}$	3	R	0.5	—	—	—	—
21	5	54	R	6.9	3.8—9.5	98	5.9	6.2
22	4	36	R	4.4	3.1—5.3	130	5.0	7.9
Average *		39.1		3.65		113.9	3.74	5.81

*) Observations. Left-handed rotation negative.

No. 1. Average growth during $1\frac{1}{2}$ hours 43 μ, next stopping of growth followed by slow growth of 12 μ min. and slow rotation L. (see also text). Continuous light 10 M.C.

No. 2. Continuous light 10 M.C.

No. 3. Measured from photographs of plate 1. Temp. 16°.

No. 6. Rotation short time almost 0.

No. 8. During $1\frac{1}{4}$ hours L., then $3\frac{1}{4}$ hours R. Growth in length slight.

No. 10. Rotation during short time practically 0.

No. 13. During $1\frac{1}{2}$ hours R., then 1 hour L., next $\frac{1}{2}$ hour R.

No. 14. During $2\frac{1}{2}$ hours L., then $3\frac{1}{2}$ hours R. Average growth in length slight!

No. 19. Average growth computed after last 9 hours. During 9 hours R., then $5\frac{1}{2}$ hours L. See fig. 2 and text.

* The average was computed from 11 experiments; rotation exclusively R. viz. Nos. 5, 6, 7, 9, 11, 12, 16, 17, 18, 21 and 22.

grand period was measured, the rotation was first right-handed for nearly 9 hours, next for 5½ hours left-handed (see fig. 2), but here too the average growth is subnormal and the final length of the sporangiophore amounted only to 3.5 cm, 10 cms being normal. The culture employed was comparatively old, so that a deficit of nutrient substances or water may be the cause of this abnormal behaviour.

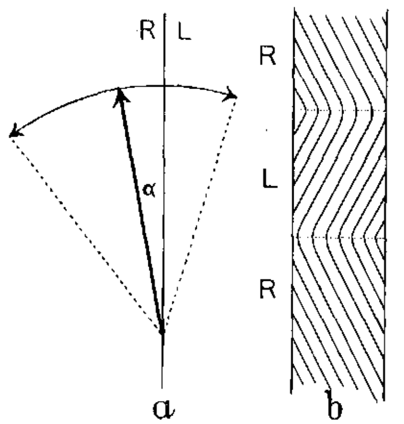


Fig. 6. *a*. Possible explanation of alternating R and L rotation by oscillations in the direction of growth round an average direction forming a definite angle ($\angle \alpha$) with the longitudinal axis. *b*. The direction of growth of a R—L—R rotating sporangiophore drawn on the wall, viewed from the outside. Both schematically.

These are the arguments supporting the supposition that the left-handed spiral probably does not occur but in abnormal cases.

Regarding fig. 2 more closely, we see that in the positive part of the curve considerable oscillations occur in the rate of rotation. It also appears from the other experiments (table 1) that the rate of rotation is not constant. These oscillations proceed gradually and the maxima and minima are at least two hours, frequently much farther removed from each other. Besides long periods occur in which oscillations fail to appear. From these oscillations the left-handed rotation can now also be explained. We must then assume that the average main direction of growth forms a definite small positive angle (α) according to a right-handed spiral with the longitudinal axis, but that the oscillations can be so large that temporarily negative angles can also occur, that is left-handed rotation can take place. This has been schematically represented in fig. 6: a. A good explanation of the rotation of sporangiophore N⁰. 13 (schematically represented in fig. *6b)* might be given in this way.

This also applies to the sporangiophores Nos 6 and 10, the rotation of which is indeed always right-handed, but which for a short period hardly rotate at all. If the oscillation had been a little stronger a left-handed spiral would have occurred for some time. But if we now regard fig. 2 it appears that the above does not give a satisfactory explanation for all cases, because in this case the left-handed rotation continues too long for that. Growth and rotation, therefore, belong together, but as the steepness of the spiral in one and the same cell varies in the course of the hours and also among the different cells, there is no fixed relation between the velocity of growth in length and that of rotation. The rotation, however, does increase and decrease along with the growth, just as in the case of the response to light.

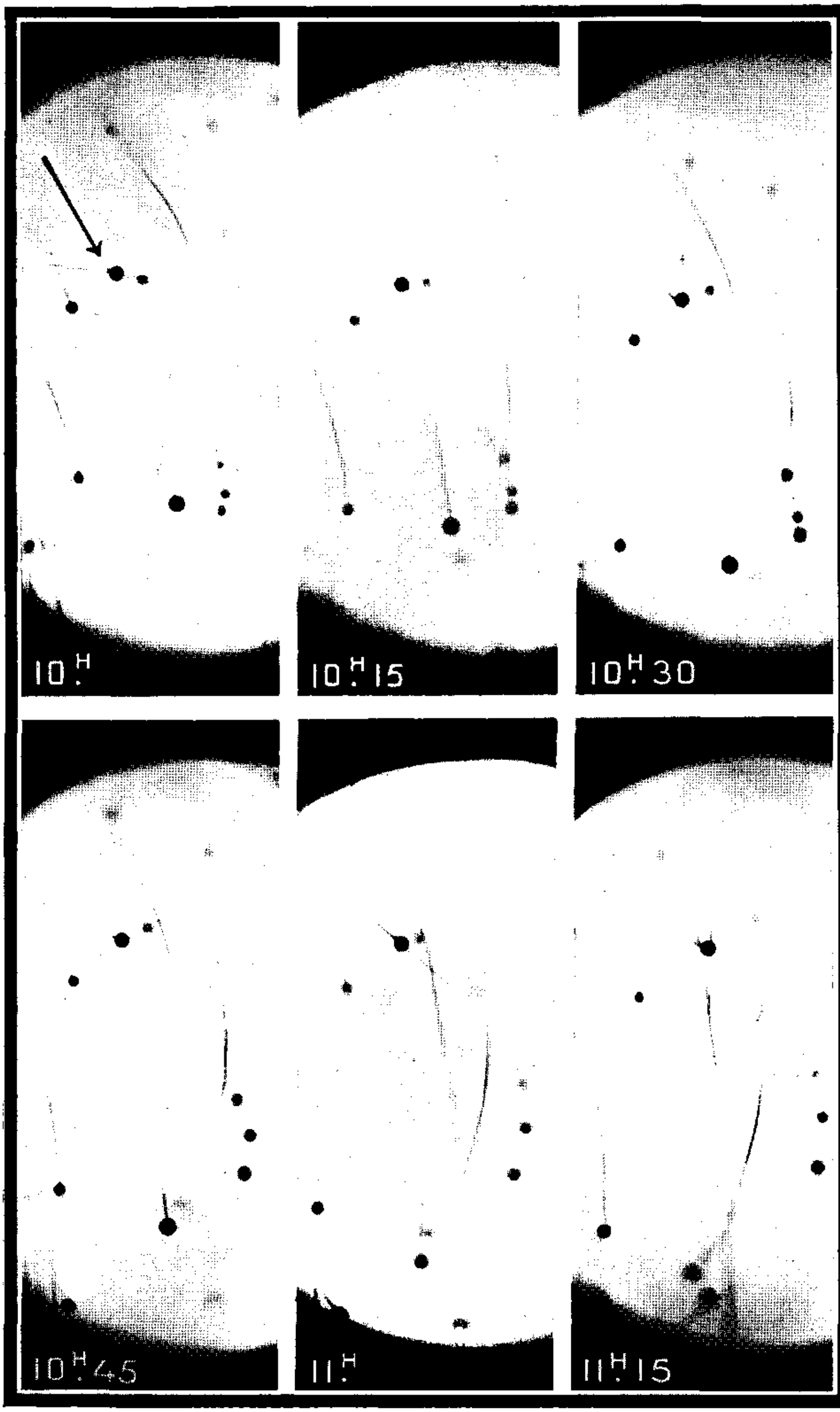
At what rate does the rotation take place? The table may give us a notion of this, but for the reader it is easier to form an idea of the rate of the spiral-growth with the aid of some round averages. For these averages I only made use of the sporangia with right-handed rotation. The average growth amounts to 40 μ per min., the average rotation to 4° per min. With a circumference of the sporangiophore of 360 μ, the component of width then amounts to 4 μ per min. The angle the main direction of growth forms with the longitudinal axis ($\angle \alpha$) is then $\pm$ 6°. Such a sporangium will have made a complete revolution in 1½ hours, the increase in length in that period amounting to 3.6 mms. If we now put the increase in length during the grand period at 8 cms, the end of the cell with the sporangium, there fore, turns more than 20 $\times$ round its axis during that period.

S p i r a l - g r o w t h a n d s p i r a l - s t r u c t u r e. In the literature on the growth and structure of the cell-wall cells are repeatedly mentioned showing a spiral-structure; but no quantitative data about spiral-growth are found. The word spiral-growth however is used several times. But in most cases the word is used for organs, which are composed out of more cells and so it is dubious if we may compare these cases directly with the spiral-growth of *Phycomyces*. Yet I have to mention the investigations of PRINGSHEIM und LANGER (1924) on *Bacillus mycoides* and those of KLUYVER und VAN NIEL (1926) on *Bacillus funicularis*, especially where the autors speak about "Zopfbildung". It is hardly possible to explain this "Zopfbildung" otherwise than through the spiral-growth of the bacteria-threads. Also I have to mention an observation of BURGEFF (1914 p. 279) on *Phycomyces nitens var. piloboloides* which I quote here: "Es entsteht unter einer Dehnung der Membran (des Sporangiumträgers) eine blasige Anschwellung unter dem Sporangium. Während dieser Dehnung erleidet der blasig werdende Teil des Trägers eine Torsion von links nach rechts, die an den in ihm spiralig ausgespannten Plasmafäden sichtbar wird." It is not quite clear if BURGEFF really observed a torsion, but according to this observation about the direction of the plasma-threads it is very probable that this variety also will show spiral-growth.

As regards spiral-structure we find it for instance very common in fibres. (FREY 1926 and 1927). In many cases this structure can already be recognized by striation or by the direction of bordered pits, but with the aid of the polarization-microscope the structural direction can always be determined more exactly. For according to NÄGELI's micellar theory all cellwalls have been constructed from submicroscopical crystalline particles, the so-called micellae. Whether these micellae consist of one single large molecule or of a number of molecules, is not yet known, because the molecular weight of substances as cellulose and chitin is not known. The particles are, however, crystalline which appears from the fact that they show double refraction and yield X-ray interferences.

In many cases the crystals would show the shape of rods [1]), of which

[1]) See also BAAS—BECKING and WAYNE GALLIHER.



Photographs of the rotation, taken in red light; magnification almost 5 ×. Time of exposure 1/2 minute; exposures every 15 min. Temp. 16°.

the longitudinal direction coincides with the greatest coefficient of refraction, that is with the axis of the (approximately uniaxial) crystal. The rods (micellae) now always point more or less in a certain direction and the direction coincides with the direction of a striation or of thickening ridges. Accordingly the structural direction can be determined and as already stated it appears that a spiral-structure frequently occurs. Within this scope I cannot enter into this question further. A good survey of various structures is found in VAN ITERSON (1927) and FREY (1930). Here we also find additional literature.

I have dwelled upon the micellar theory, because it may obviously be assumed that spiral-growth and spiral-structure are connected and that direction of growth and of structure coincide. In this case these cells of *Phycomyces* would be an example in which the spiral-structure is manifested *in the growth,* — owing to their being free cells. Theoretically, however, direction of growth and structure need not coincide. It may for instance be imagined that the direction of growth coincides with the longitudinal axis, while the particles stand obliquely with respect to this axis. Compare for instance a herring-bone clinker-pavement. This is a case in which the parts (clinkers) are orientated obliquely with respect to the main direction in which the "growth" took place during the formation. In the same way we might picture to ourselves a cell with spiral growth, the parts of which are orientated in the longitudinal direction.

In connection with this I also wish to point out the relation found by different investigators (CRÜGER 1855, DIPPEL 1868, STRASBURGER 1882) between the protoplasmic streaming and the structure. Here too further researches on *Phycomyces* will be capable of throwing light on the question whether the streaming of the protoplasm determines the direction of growth.

As to the alternate right-handed and left-handed rotation of *Phycomyces* it is interesting to point to the "reversions" found in the structural direction of cotton-hair (see on this subject VAN ITERSON 1927).

Moreover I also wish to point out here that the phenomenon of spiral-growth in *Phycomyces* appears in its simplest form. Organs constituted of more cells often show a spiral-structure as for instance the stalks of creepers, stems of trees. It is not impossible that the spiral-growth of one single cell, as shown by *Phycomyces,* is the elementary phenomenon from which these more complicated phenomena of growth might be explained.

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Laboratory for Plantphysiological Research.

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