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MEASUREMENT OF THE BLOOD VOLUME BY MEANS OF BLOOD CORPUSCLES LABELLED WITH P^{32}

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HANS H. BOHR

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Introduction.

As described in several papers by HEVESY[1, 2, 3], it is possible to use radioactive phosphorus (P^{32}) in the determination of the total amount of circulating erythrocytes in the organism by labelling the red blood corpuscles *in vitro*.

The aim of the present work is to point out some circumstances that might contribute to a more rational view both on the labelling of the red blood corpuscles and on the conditions for the preservation of constant activity in the blood corpuscles, thereby considering especially the application of labelled blood corpuscles in the determination of the blood volume.

Earlier investigations by means of this method, primarily by HEVESY and collaborators, have shown that determinations on the same patient can be made with an uncertainty of 5—10 per cent and that the results are consistent with blood volume determination by means of CO and T-1824 on normal persons. NYLIN and coworkers have carried out numerous experiments[4, 5, 6] with the P^{32} method. Thus, NYLIN has determined the changes in the circulating of blood before and after pulmonectomy and before and after application of a tourniquet to an extremity, whereby the blood volume in the lungs and in a limb, respectively, could be measured. Owing to special conditions to which we shall return later, this author finds that in the blood corpuscles the activity remains practically constant for 1—2 hours, and utilizes the experience to examine the changes in the blood volume during this period, e. g. in patients with heart diseases. KELLY et. al.[7] have arrived at results in accordance with those of NYLIN. Recently REEVE and VEAL[8], when comparing the results from the P^{32} method with those gained by means of the T-1824 method, were able to show consistency. However, these authors propose

a technique somewhat different from that used by HEVESY and by NYLIN. After activation of the blood they remove the plasma previous to injecting the sample into the vein. This is done under the consideration that the labelled blood corpuscles alone are indispensable for the determination of the total amount of erythrocytes and that, therefore, the presence of the plasma in activity determinations is superfluous and even harmful. In their investigations REEVE and VEAL find that the cleaned erythrocytes lose some of their activity both *in vitro* and still more *in vivo*, the activity decreasing with 5 and 9 per cent, respectively, within 60 minutes.

Technique.

In our experiments the measurement of the blood volume was carried out in the following way. A sample of blood from a patient is shaken in a bottle containing radioactive phosphorus. Shaking should be performed very cautiously so that the blood corpuscles are kept under as physiological conditions as possible; it has to be done in a thermostat in order that the procedure may pass fairly quickly, cf. HEVESY and HAHN[1]. After two hours' shaking the amount of inactive phosphorus exchanged with active phosphorus is so large that the activity in the corpuscles is about the same as that in the plasma (per cc.). When the activated blood corpuscles are injected into the patients vein and the activity produced in the blood after its complete mixture with the injected sample is measured, it will be possible from the dilution found to calculate the total amount of blood corpuscles according to the following equation

$$X = p \cdot \frac{A}{a}, \qquad (1)$$

where X is the amount of blood corpuscles present, p is the injected amount of blood corpuscles, and A and a are the activities of the blood corpuscles in the injected sample and in the patients blood after the mixing, respectively.

The measurement of the radioactivity in the samples was originally carried out as a determination of the activity per gram of phosphorus. The blood corpuscles were destroyed by

boiling in nitric acid and sulphuric acid, a certain quantity of phosphate was added and, finally, the phosphate was precipitated as ammonium magnesium phosphate with Fiske's solution. Already in 1945 NYLIN suggested to measure the activity on dried and pulverized blood corpuscles. Recently, K. ZERAHN[9] has further simplified the method by measuring directly on the centrifuged blood corpuscles after having placed them in cuvettes. According to ZERAHN, these cuvettes are made of a steel ring with bottom and lid either of cover glass, 0.1—0.2 mm. thick, or of thin aluminium foil. Having acquired some experience one finds no special difficulties in filling and cleaning the cuvettes, which is done through one or two holes in the steel ring. The radioactivity is measured with an apparatus as described by AMBROSEN, MADSEN, OTTESEN, and ZERAHN[10] by means of an automatic arrangement similar to the one described in that paper.

Discussion.

As stated by HEVESY et al. in accordance with HALPERN, EISENMANN et al.[11] and TAYLOR et al.[12], the activation of the blood corpuscles is due to an exchange between the inorganic phosphate of the blood corpuscles and that of the plasma, and by an incorporation of inorganic corpuscle phosphate into organic acid soluble phosphorus compounds. According to HEVESY and ATEN[13], both these processes together are, at least in the beginning, directly proportional to the difference between the specific activity $\left(\frac{P^{32}}{P^{31}}\right)$ of the plasma and the specific activity of the blood corpuscles, depending on a constant denoted as the penetration factor a.

It is evident, however, that the penetration of P^{32} into the blood corpuscles must be a reversible process, radioactive phosphorus from the plasma being exchanged with inactive phosphorus of the blood corpuscles, and vice versa.

This can be expressed more clearly by the following equation:

$$dx = -b \cdot x \cdot dt + a \cdot (1 - x) \cdot dt, \qquad (2)$$

where it is merely indicated that the increase in activity of the blood corpuscles, dx, is the result of P^{32} entering the blood

corpuscles, $a \cdot (1 - x)$, and of P^{32} leaving the blood corpuscles, $b \cdot x$, a and b being coefficients for the processes involved and 1 being the total concentration of P^{32} in the blood.

By integration of equation (2) we obtain

$$X = \frac{a}{a+b} - C \cdot e^{-(a+b)t}, \tag{3}$$

where C is a constant;

if $X = 0$, when $t = 0$, then $C = \frac{a}{a+b}$, and the equation (3) becomes

$$X = \frac{a}{a+b} \cdot (1 - e^{-(a+b)t}); \tag{4}$$

if $X = 1$ when $t = 0$, then $C = \frac{-b}{a+b}$. Subsequently, we obtain

$$X = \frac{1}{a+b} \cdot (a + b \cdot e^{-(a+b)t}). \tag{5}$$

Equations (4) and (5) are expressions of the activation process in blood, starting with the total activity present in the plasma and in the red blood corpuscles, respectively. The coefficients a and b can be explained in the following way. When X is very small, practically no radioactive phosphorus will leave the corpuscles. From equation (2) one gets

$$\frac{dx}{dt} = a \quad \text{for} \quad X = 0;$$

a therefore expresses the slope at the beginning of the curve for the equation (4). Similarly, we get

$$\frac{dx}{dt} = -b \quad \text{for} \quad X = 1,$$

which means that $-b$ expresses the slope at the beginning of a curve representing the diffusion of P^{32} from the corpuscles into the plasma (equation (5)). If, in equations (4) and (5), $t = \infty$, we get

$$X = \frac{a}{a+b}$$

which means that both curves approach this value. For the special problem here discussed, a is much larger than b since the amount of exchangeable phosphorus is much larger in the corpuscles than in the plasma. Fig. 1 gives three examples of curves representing three different sets of values for a and b.

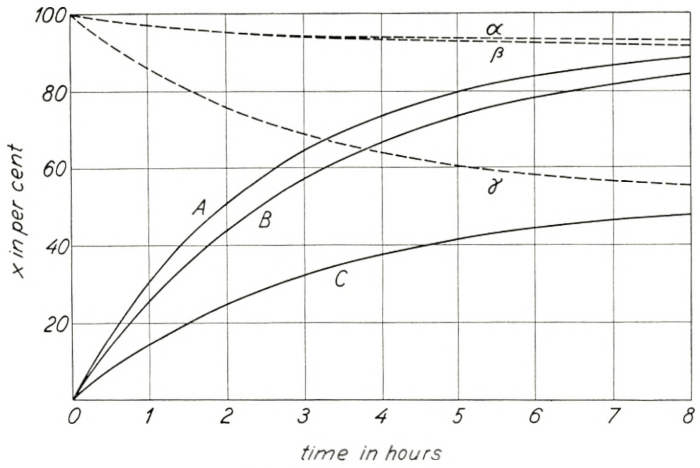

Fig. 1. Theoretical curves.

The lower curves illustrate the equation $x = \frac{a}{a+b}(1 - e^{-(a+b)t})$.

The upper curves illustrate the equation $x = \frac{1}{a+b}(a + b\, e^{-(a+b)t})$.

Curve A and α corresponding to a = 0.37, b = 0.03.
Curve B and β corresponding to a = 0.30, b = 0.03.
Curve C and γ corresponding to a = 0.17, b = 0.16.

From these considerations it appears that the activation process is independent of the absolute activity of the blood corpuscles and the plasma, but dependent only on the relation between the activity of the blood corpuscles and that of the plasma. This means that the course of the process will not be changed when fresh blood from the same person is added, in which case the blood corpuscles and the plasma would be equally diluted. According to the assumptions underlying the calculations above it makes no difference whether the activity is distributed uniformly in the blood corpuscles or some corpuscles have more and some less activity.

If, however, plasma or physiological NaCl solution is added

only, the relation between the activity of the plasma and that of the blood corpuscles will be different and, consequently, the course of the process will be changed.

Experimental.

In order to elucidate whether this theory is in accordance with actual conditions, experiments *in vitro* were carried out. Newly drawn blood kept in paraffinated bottles to which heparin had been added was used. After addition of P^{32} of negligible weight the bottles were carefully shaken in the thermostat at 37° C. At convenient intervals samples were drawn and sharply centrifuged, and the activity of the blood corpuscles and the plasma was determined. Cuvettes of the type described previously were used in these experiments.

Fig. 2 gives an illustration of the increase in activity of the blood corpuscles. By measuring the activity in percentage of the total activity of the blood, the hematocrit value is taken into account and, therefore, more constant conditions are obtained for the individual curves, which still, however, show some differences. The average curve of 12 such experiments is shown and compared with the theoretical curve for $a = 0.37$ and $b = 0.03$. Individual values for four different experimenting curves are given as points of various kinds (Fig. 2 a), the experimenting error being about $\pm 2\ \%$. The value of b is obtained by drawing curves on the diffusion of P^{32} from the blood corpuscles. First, the blood corpuscles are activated; then the blood is sharply centrifuged, the plasma removed with a pipette, and the blood corpuscles are resuspended in a cooled physiological NaCl solution. This process is repeated and, after a second centrifugation and removal of the NaCl solution, inactive plasma from the patient from whom the blood sample was drawn is added. The blood is shaken in the usual way in the thermostat, samples being removed for the determination of the activity of the plasma and the corpuscles. The average for b as obtained from two experiments is 0.03 (Fig. 2 b). Hilde Levi[14] in her experiments has obtained curves only slightly deviating from these.

A comparison between the curves in Fig. 2 shows that the

agreement between the theoretical and the experimental curves is satisfactory. However, the experimental curve does not rise to higher values than 0.86, while the theoretical maximum for a = 0.37 and b = 0.03 is 0.93, according to the above-mentioned expression $\frac{a+b}{a}$. This can be accounted for in the following way. When examining freshly drawn blood, the amount of acid

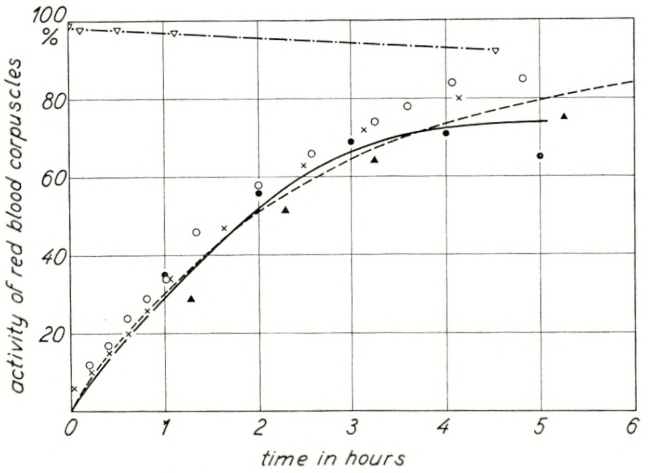

Fig. 2. Experimenting curves.
The lower curves representing Fig. 2 a.
The upper curve representing Fig. 2 b.
The dotted line gives the theoretical curve for a = 0.37, and b = 0.03.
The full line gives the average values for 12 experiments.
The different points showing individual values of 4 experiments.

soluble phosphorus (which includes that amount of phosphorus which is easily exchangeable within the time of observation) in the plasma and the blood corpuscles is found to be about 38 and 3 mg %, respectively. These figures are in good agreement with the values found for a and b. But in the course of 4 hours' incubation at 37° C. some of the phosphorus compounds of the blood corpuscles are destroyed with the result that the amount of inorganic phosphate of the plasma is increased to about 5 mg %,. This phenomenon diminishes the relation $\frac{a}{b}$, and consequently the curve does no more rise to the same level.

Thus, it seems probable that the blood *in vitro* reacts as calculated from the theoretical considerations. Indeed, if some

activated blood is mixed with a larger amount of inactive blood and the activity of the blood corpuscles is investigated, it is found that the changes of the activity are not influenced by this dilution which does not change the relative activities of the plasma and the blood corpuscles.

Different results are obtained when these proportions are changed, for instance by diluting the plasma with physiological NaCl solution, as shown in Fig. 3. Curve 2 makes it clear that if so much NaCl solution is added that the activity of the plasma decreases to $\frac{1}{10}$ of the activity of the blood corpuscles, the activity of the blood corpuscles remains constant. If only half as much NaCl solution is added, the activity of the blood corpuscles is hardly changed either. If we dilute with still less NaCl solution, the activity of the blood corpuscles continues to increase, though more slowly than before. If we dilute so highly that the activity of the plasma decreases to less than $\frac{1}{20}$ of the activity of the blood corpuscles, the corpuscles will lose some activity until a balance is restored (Fig. 3, 3). These experimental results are in agreement with the theoretical considerations outlined above.

When attempting to utilize these experiences at the application of the radioactive blood corpuscles in the determination of the blood volume *in vivo* we find that the blood after activation for two hours is not yet in balance, i. e. the activity of the blood corpuscles is still increasing. On injection in the vein, the radioactive blood will be diluted with inactive blood of the same composition, whereby the activation process will not be affected. However, a special circumstance has to be taken into consideration, viz. the activity of the plasma which is present mainly as inorganic phosphate will, after the injection, distribute *not* only over the plasma, but also over the extracellular fluid and the activity will decrease correspondingly. If we follow the activity of the blood corpuscles and of the plasma after injection of the activated blood, we find that the activity of the blood corpuscles remains constant during the first hour (cf. also (5)), while the activity of the plasma even after completion of the mixing continues to decrease very rapidly during the first 10 minutes; from then on the activity still decreases, though at

a slower rate. The steep decrease in the plasma activity during the first 10 minutes, which is shown in Fig. 7, is an expression of the exchange of inorganic phosphate between plasma and extracellular fluid (cf. HAHN and HEVESY[15]). Thus the activity of the plasma in the course of a very short time will decrease to about one fifth of the activity of the blood corpuscles, and according to results shown in Fig. 2 and 3 the activity of the

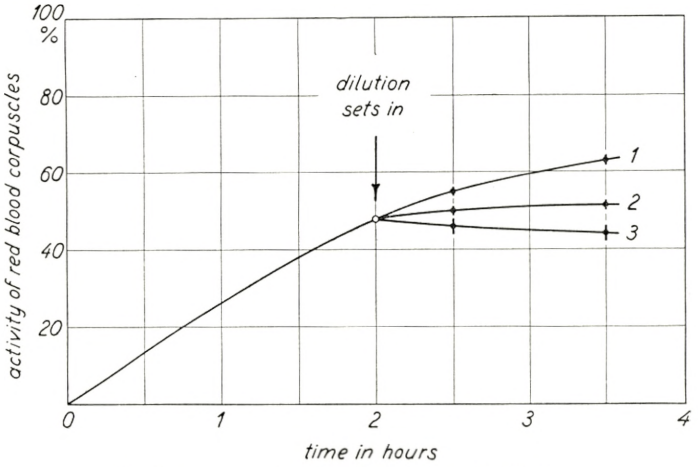

Fig. 3. Curves showing the effect of diluting.
1) 5 cc. labelled blood to 30 cc. inactive blood. (Experimenting error ± 2 %)
2) 20 cc. labelled blood to 50 cc. phys. saline. (— — ± 2 %)
3) 20 cc. labelled blood to 250 cc. — — (— — ± 5 %)
Hematocrit value 44 %.

blood corpuscles will consequently remain almost unchanged. The activity of the plasma, however, will, as mentioned above, continue to decrease as a result of the interchange of the plasma phosphate with intracellular phosphate and through excretion.

If the activity of the plasma decreases much below one tenth of the activity of the corpuscles, then the latter will diminish somewhat. As already mentioned, REEVE and VEAL proposed to remove the plasma from the blood corpuscles prior to the injection. Following this procedure, as was to be expected, a loss of activity is observed in one hour.

As mentioned before, it can be shown that blood kept in a thermostat undergoes a change. If we follow the experimental curve in Fig. 2 for 8—10 hours, we see that it deviates still more from the theoretical curve. Fig. 4 shows how the curve now

begins to fall, reaching quite a new balance which remains constant for more than 48 hours. This fall precedes any hemolysis, since in most cases no red-colouring of the plasma can be observed until after 10 hours' shaking, when it begins very faintly and then increases steadily. Neither does one see any changes in the hematocrit value nor on the red blood picture. The phenomenon must be regarded as an expression of changes

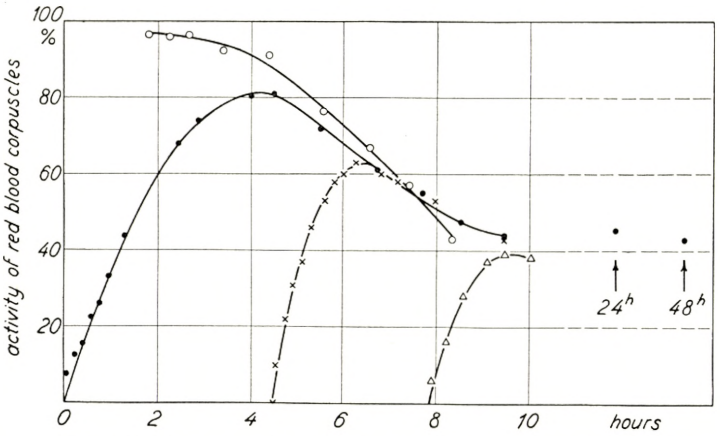

Fig. 4. Curves showing labelling of the red blood corpuscles.
● fresh blood.
× blood stored at 37° for 270 min.
Δ blood stored at 37° for 470 min.
○ blood activated for 37° for 90 min., replacing the plasma with inactive plasma.

inside the blood corpuscles, in the first place probably with regard to the sensitive enzymatic system regulating the phosphorylation processes. This is also indicated by an accompanying steep increase in inorganic phosphate of the plasma, as shown in Table 1.

A closer examination of these conditions shows that the decrease in the activity of the blood corpuscles is directly dependent on the time during which the blood is kept at 37° C. If the blood corpuscles were placed in a thermostat for 4 hours before addition of P^{32}, and then shaken, the result is seen on Fig. 4, which also shows the course of the activation when the blood before activation was kept in a thermostat for 8 hours. A curve like that does not reach beyond the values corresponding to the secondary balance.

The shape of the activation curve of the blood corpuscles treated with P^{32} thus indicates a way of estimating the extent to which the blood is changed during storage.

It might, however, be that such a change was produced as a consequence of the fact that the blood consumed some substance important for the processes involved. Here, one might

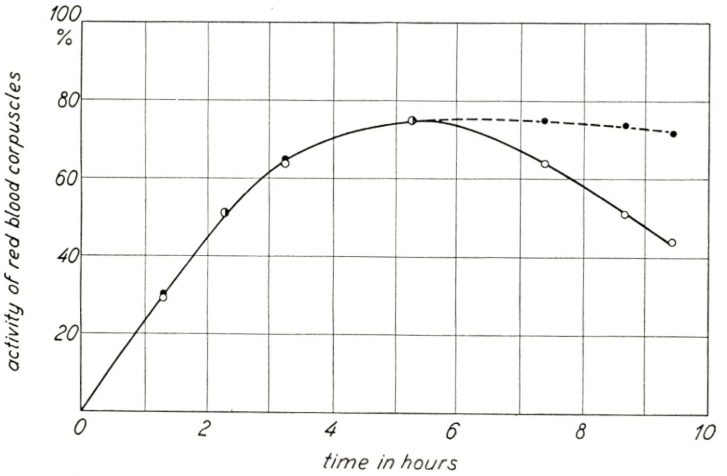

Fig. 5. Activity curves showing the effect of glucose.
Dotted line representing blood to which glucose was added during incubation.
Full line representing blood to which no glucose was added.

think of oxygen, for instance. However, as the bottles containing the blood are made so as to secure an ample supply of oxygen, no analysis of the air was performed. Another substance, the presence of which is of equal importance in this respect, is glucose. As is well known, the glucose content of the blood decreases rather rapidly during incubation at 37°. This is shown in Table 1 where glucose content of the blood is seen to fall from about 80 % to about 20 % in the course of a few hours. The effect of an addition of glucose to the blood is also shown by Table 1, which demonstrates that the presence of a high concentration of glucose in the blood reduces the loss of P^{32} by the corpuscles. But even if the loss of glucose is replaced, the corpuscle activity still decreases as shown in Fig. 5 indicating that some change has taken place in the blood.

If blood is stored at room temperature for 24 hours we obtain

Table 1.

With Glucose			Without Glucose		
Min.	P mg %	Glucose mg %	Min.	P mg %	Glucose mg %
0	2.9	70	0	2.9	70
77	..	29	77	..	54
137	3.1	25	137	3.3	156
316	4.7	..	316	4.4	..
441	8.7	..	441	6.0	..
515	14.7	..	515	8.2	..
563	..	25	563	..	150

an activation curve similar to that of blood kept at 37° C for 8 hours; if however, glucose is added in suitable amounts, the activation curve is found to be identical to that obtained for freshly drawn blood, demonstrating that no irreversible change takes place within 24 hours at room temperature.

It is not surprising that glucose plays an important part in

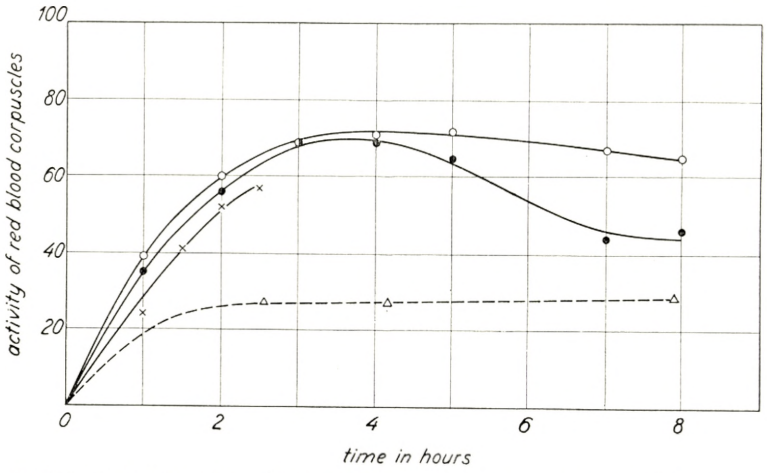

Fig. 6. Curves showing the effect of different agents on the labelling of blood.
● blood with heparin.
○ blood with acid citrate-glucose solution.
× blood with 3 % citrate.
Δ blood with 2 ‰ fluoride.

the activation of the corpuscles as glycolytic processes are involved in the incorporation of P^{32} into the organic acid soluble phosphorous compounds. In an experiment in which fluoride

was added to the blood the rate of intrusion of P^{32} into the blood corpuscles was found to be much reduced. This is shown in Fig. 6, which also demonstrates the behaviour of blood containing 3 % citrate or acid citrate-glucose solution, respectively. None of these substances seem to influence the interchange mechanism of the corpuscles.

Conclusion.

From the results above, the following conclusions may be drawn. To obtain a constant activity of the blood corpuscles, the activity of the blood corpuscles must be about 10 times as large as the activity of the plasma (per cc.). This equilibrium can be temporarily obtained *in vivo* by injecting blood of almost equal activity of the blood corpuscles and the plasma, since the activity of the plasma decreases after an exchange with the extracellular fluid. According to Fig. 2, an activation of about 2 hours at 37° C. is required to obtain this ratio between the activities in the blood. It appears, however, that blood *in vitro* kept at 37° C. gradually undergoes a change, so that a shorter time of activation is prefer-

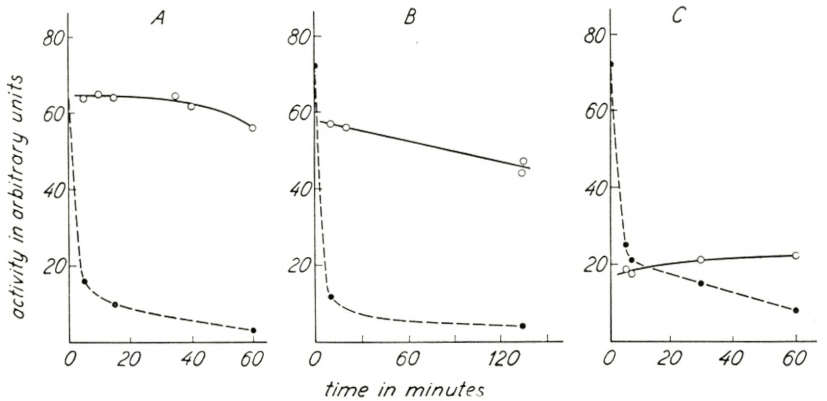

Fig. 7. Curves showing the activity of the blood corpuscles (full line) and the plasma (dotted line) following injecting *in vivo*.
A following injection of blood labelled for 120 min.
B following injection of blood labelled for 75 min.
C following injection of blood labelled for 40 min.

able. By activating for one hour, only, the activity of the plasma appears to be relatively too high in the beginning, but in the course of some minutes it decreases sufficiently not to cause an

increase in activity of the blood corpuscles, due to the continual cellular uptake and excretion of phosphate. If, however, the blood is activated for half an hour only, the activity of the plasma will cause an increase in the activity of the blood corpuscles (Fig. 7). Still, it is possible to reduce the time of activation considerably by removing some of the activity of the plasma. This can be done by centrifuging the blood, as suggested by REEVE and VEAL. But while these authors wash the corpuscles in cooled physiological saltwater to remove all the plasma, thereby easily damaging the red blood corpuscles, the above considerations seem to indicate that it is more reasonable to remove only the greater part of the plasma after very delicate centrifugation. Which method is to be preferred—either activating for one hour or activating for about 20 minutes and centrifuging of the blood — will depend upon the results to be obtained *in vivo* by each method.

Summary.

1. Theoretical considerations in connection with the determination of the blood volume by means of erythrocytes labelled with P^{32} are put forward, and their correctness tested by measurement of the rate of interchange between plasma and blood corpuscles in experiments carried out *in vitro*.

The results obtained permit a satisfactory explanation of the data obtained by various experimenters.

2. The rate of loss of P^{32} by the activated corpuscles was found to increase markedly in blood incubated at 37° for more than 5 hours. Addition of glucose reduces the rate of loss of P^{32} by the corpuscles.

3. The most favourable way of obtaining labelled corpuscles is discussed.

The present investigations were carried out at the University Surgical Clinic C., Copenhagen, and at the Institute for Theoretical Physics, University of Copenhagen. I wish to thank the heads of these institutions, Professor E. DAHL-IVERSEN and Professor NIELS BOHR for their continuous interest and encouragement. I am especially indebted to Professor G. HEVESY for most valuable guidance and advice throughout the work.

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PRODUCTION OF DRY MATTER, RATE OF PHOTOSYNTHESIS AND RESPIRATION, AND DEVELOPMENT OF LEAF AREA IN SOME DIPLOID, AUTOTETRAPLOID AND AMPHIDIPLOID SOLANUMS

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A. Introduction.

A feature, generally much emphasized in the description of polyploid plants, is their so-called "gigas" character. This expression refers to the fact that these plants, like the tetraploid "gigas" form of *Oenothera Lamarckiana* arisen in 1895 in the cultures of DE VRIES, have a more vigorous growth and larger organs than the diploid forms from which they descend. Even though exceptions are known, this feature is characteristic of the majority of polyploid plants. The idea to utilize the luxuriance in plant breeding is quite natural; however, not until recent years methods were developed which permit an experimental formation of polyploid plants to an extent required for an application to plant breeding practice. Since such methods are now at our disposal, these problems were resumed. When investigating the cultural value of a given polyploid plant, primarily its productivity should be compared with that of the corresponding diploid plant; this means a quantitative determination of the "gigas" character. A few such comparisons are available; however, just as previous rough estimates, they seem to refer to individual plants, only, while in agricultural practice, the size of the crop in a stock of plants in the field is the essential point.

A brief report of the main points of the investigations on the production of matter in polyploid plants so far published is given below.

FABERGÉ (1936) found that the tetraploid strains of tomato examined by him showed no greater production of dry matter than the corresponding diploid ones. In the tetraploid strains of tomato examined by SCHLÖSSER (1937), an excess of dry matter of 20—25 per cent as compared with the diploids could be demonstrated in 4 weeks old plants, (in "old" plants the excess was even 74 per cent). When these experiments were repeated (SCHLÖSSER 1940), the maximum excess,

however, in plants somewhat older than 6 weeks was no more than 8 per cent. In another tetraploid strain of tomato, almost 8 weeks old plants showed a deficiency of 18—27 per cent, in proportion to the diploids. It could, however, be stated that the tetraploids were on the point of overtaking the diploids, the *intensity* of their production at the time of investigation being greater than that of the diploids.—Examinations by the same author on tri- and tetraploid sugar beets showed that the production of dry matter in these plants was 12—15 per cent less than in the corresponding diploids. Similarly, the tetraploid *Petunias* examined by HESSE (1938) produced less dry matter than the diploids. This result has been confirmed by PIRSCHLE (1940) through investigations of the same strain as that used by HESSE.—According to GREIS (1940), the yield of straw of tetraploid Kobai barley, at the beginning of the flowering period, was about 50 per cent greater than that of the diploid plants; the formation of grains, on the other hand, was very bad.—The works mentioned have partly been reviewed more thoroughly by PIRSCHLE (1940).

In experiments performed by GYÖRFFY (1941) various autotetraploids were investigated. The majority of these experiments was carried out in greenhouse; unfortunately, no details as to the cultivation method are given, at least not in the English summary. The main results of GYÖRFFY's determinations of the production of dry matter are as follows. In different strains of *Capsicum annuum*, the tetraploids yielded an excess of total dry matter varying from 11 to 79 per cent as compared with the diploids.—In two strains of *Epilobium*, an excess of 8 per cent and of 66 per cent, respectively, was produced by the tetraploids.—With *Hyoscyamus albus* and *H. niger*, converse results were obtained. In the former the tetraploids yielded 7 per cent less, while in the latter the tetraploids yielded 33 per cent more than did the corresponding diploids.—With *Petunia nyctaginiflora* rather inconsistent results were attained, the main point being that a possible excess in the tetraploid was decreasing with age, at last turning into a marked deficiency.

Recently, LEVAN (1942 *a* and *b*) reported some preliminary investigations on the productivity of field-grown polyploid strains of clover and flax. In clover, the tetraploids consistently yielded more green matter than did the diploids, the excess varying from 31 to 40 per cent, and in one case amounting even to 128 per cent. These values correspond with a somewhat smaller excess of dry matter in the tetraploids, since it is stated that their content of dry matter is lowered on an average by 2.1 per cent. The yield of seed in the tetraploids is stated to be "inferior".—In flax, the general viability as well as the fertility was lower in the tetraploids throughout all experiments. The relative dry weight of the tetraploids varied from 42 to 74, the values for diploids being put equal to 100.

Obviously, part of the investigations reviewed above give contradictory information on the productivity of polyploid plants

Fig. 1. *Solanum nodiflorum.* To the left the diploid ($n = 12$), to the right the tetraploid ($n = 24$). ($\times$ 1/16).

Fig. 2. *Solanum gracile.* To the left the diploid ($n = 12$), to the right the tetraploid ($n = 24$). The small number of berries in the tetraploid should be noticed. ($\times$ 1/15).

relative to that of the diploids, although it is the chief impression that the "gigas" character generally does not seem to stand a quantitative examination. Hence, there may be reasons for examining the production of matter of an additional number of species and, particularly, for comparing the yield of diploid and tetraploid plants grown under field conditions; it cannot be taken for granted that the more vigorous development of the individual, solitarily growing plant involves a larger production of leaves, seeds etc., when a multitude of such plants are growing in a stock.

In order to elucidate the problems outlined above the investigations reported on the following pages were carried out. Material of *Solanum* from the cultures of Professor C. A. JØRGENSEN Ph. D. was used. The cultivation of the plants took place in Lyngby, near Copenhagen, in the experimental field of the Laboratory of Genetics of the Royal Veterinary and Agricultural College. The polyploid strains were raised either by the callus method or by a combination of the callus and the colchicine method, as described in detail in the previous paper of this series (JØRGENSEN 1943).

The present investigation was carried out partly on autotetraploid strains of *Solanum*, i. e. pure species in which the chromosome number has been doubled, partly on amphidiploids (allotetraploids), i. e. species hybrids the chromosome number of which has been doubled.

The first group included:

	Haploid chromosome number in diploids	tetraploids
Solanum nodiflorum JACQ.	12	24
Solanum gracile OTTO	12	24
Solanum alatum MOENCH	24	48
Solanum nigrum L.	36	72

The habit of these plants appears from figures 1—4. The plants were photographed on September 7th, 1940, towards the end of their vegetation period. They have been dug out of the field and potted immediately before being photographed.

The diploid and the tetraploid *Solanum nodiflorum* (fig. 1) look very much alike. The tetraploid is not so profusely branched as the diploid. On the other hand, the branches are

Fig. 3. *Solanum alatum*. To the left the diploid ($n = 24$), to the right the tetraploid ($n = 48$). ($\times$ $^1/_{17}$).

Fig. 4. *Solanum nigrum*. To the left the diploid ($n = 36$), to the right the tetraploid ($n = 72$). ($\times$ $^1/_{16}$).

generally somewhat longer. The number of berries is not very different in the two forms. From the habit of the $2n$ and $4n$ strains of this species, only a slight excess of dry matter could be expected in the tetraploid.

The vegetative development of the tetraploid *Solanum gracile* (fig. 2) is much more vigorous than that of the diploid plant, the number of berries, however, is markedly decreased. Nevertheless, according to the appearance of the habit of the plant, a considerable excess of dry matter was to be expected in the tetraploid.

In *Solanum alatum* (fig. 3), the diploid plant is more vigorous both with respect to vegetative growth and to production of berries. In this case, one would expect a pronounced deficiency of dry matter in the tetraploid as compared with the diploid.

Finally, the ratio between the diploid and the tetraploid *Solanum nigrum* (fig. 4) is about the same as in *Solanum gracile*, the tetraploid having the more vigorous vegetative growth and the diploid, in return, the larger amount of berries. (Unfortunately, the latter feature is not so clearly shown in the photo.) The tetraploid, however, is not quite so infertile as the tetraploid *Solanum gracile*. The expectation of a considerable excess in the yield of dry matter in the tetraploid seemed to be justifiable.

About 2500 individuals of each of the two chromosome races of *S. nodiflorum* were used in the experiments; the number of individuals used in the case of *S. gracile* was 1100 of each of the two strains. Of each of the other plants concerned about 600 individuals were grown.

The second group of plants used for the experiments included:

	Haploid chromosome number in	
	parents	amphidiploid hybrids
S. gracile OTTO	12	..
S. insulae-pascalis BITT.	12	..
S. gracile × *S. insulae-pascalis*, amphidiploid	..	24
S. nigrum L.	36	..
S. nitidibaccatum BITT.	12	..
S. nigrum × *S. nitidibaccatum*, amphidiploid	..	48

Fig. 5. To the left *Solanum insulae-pascalis*, (n = 12), in the middle *S. gracile* × *S. insulae-pascalis*, amphidiploid (n = 24), and to the right *S. gracile* (n = 12). ($\times$ 1/19).

Fig. 6. To the left *S. nitidibaccatum* (n = 12), in the middle *S. nigrum* × *S. nitidibaccatum*, amphidiploid (n = 48), and to the right *S. nigrum* (n = 36). ($\times$ 1/19).

Figs. 5 and 6 show the habit of these plants. Both of the amphidiploid hybrids look coarser, more vigorous, and therefore more productive than do the initial forms. About 500 individuals of each of these plants were employed.

The aim of the investigations was, first and foremost, to measure and to compare the production of dry matter in the diploid and tetraploid plants; moreover, it was attempted, through a detailed analysis, to elucidate the causes of the differences expected. However, a thorough analysis of all species examined could not be carried out. For this purpose one species, only, was chosen, viz. *Solanum nodiflorum*, since most material of this species could be supplied. Unfortunately, the course of the production of matter in diploids and tetraploids of this very species proved to be very much alike, practically speaking, no difference being present. For this reason, it might have been better if f. inst. *S. gracile* had been chosen instead. The analysis in itself, however, aimed at a further special achievement, viz. to elucidate whether it is possible to calculate the production of matter in a stock of annual plants on the basis of measurements concerning the rate of photosynthesis and of respiration of the plants, supposed the external factors during the development are known. The latter investigation has already been reported (LARSEN 1941). Only the data concerning the production of matter, i. e. the rate of photosynthesis and of respiration, and furthermore the size of the leaf area will be given here. These quantities were determined in *Solanum nodiflorum* and in some of the other experimental plants. The physiological investigations were carried out at the Laboratory of Plant Physiology of the University of Copenhagen. The present work was supported by a grant from the Carlsberg Foundation to which my best thanks are due.

B. Production of Dry Matter.

I. Methods.

In most investigations mentioned in the introduction the plants were grown either in water culture, in flower pots, or in flat boxes, generally in greenhouse. It was the aim of the present series of experiments to determine the production of dry matter under conditions as similar as possible to practical cultivation. Hence, the plants were grown in stocks under field conditions. This enables us to calculate the results per hectare.

The experiments on autotetraploids were carried out in 1939 and those on amphidiploids in 1940. Three or four weeks before the transplantation to the field, the seeds were sown into earthenware dishes in sifted soil, sterilized previously at 100° C. The dishes were kept in greenhouse during germination. About ten days later, the seedlings were pricked off to flat boxes which were kept in frames under glass for two or three weeks; subsequently, the transplantation took place.

In both years, the field consisting of good, loamy soil was fertilized in the spring with 150 kg. per hectare of superphosphate and 250 kg. of a potash manure containing 40 per cent of K_2O (or 33.2 per cent of potassium). Shortly before transplantation, 200 kg. per hectare of calcium nitrate were sown. (In 1939, on August 4th and 12th, 135 kg. per hectare of calcium nitrate were given in addition.)

The area under experiment was divided into strips, each of which, except the outer ones, was 2.88 m. wide and 25 m. long. Each strip was planted up with plants of the same kind. They were planted by rows at a distance of 32.0 cm. on an average, the interval between two consecutive rows being the same. When one strip was planted up with diploid plants, the next one contained tetraploids of the same species. The strips were subdivided into plots. In the main experiment with *Solanum nodiflorum* and in the majority of the other experiments, the size of each plot was 2.153 sq. m., including $3 \times 7 = 21$ plants. On all sides they were surrounded by protective belts consisting of 2 rows of plants. The external belts, however, included 3—10 rows of plants. In the experiments on autotetraploid *S. gracile*, *S. alatum*, and *S. nigrum*, the size of each plot was 1.536 sq. m., the plot containing 15 plants, only.

The increase in dry weight of the experimental plants was determined at shorter intervals during the whole period of vegetation. Each time 2 replicate plots were reaped. The fresh weight and the dry weight of the roots, the stems, the leaves, and the reproductive organs were determined and the leaf area was measured. "Stems" embraces leaf stalks, too. After having been weighed in fresh state, the plants were transferred to paper bags, previously dried and weighed. Next, they were killed in an oven at 90—100° C, and finally dried to constant weight at 100° C. In this way, the dry weight of the plants and

of their constituent parts was found in grams per 4.305 sq. m., which is the total area of two plots. This value was converted into hectokilograms per hectare by multiplication by the factor 0.02323. For the 1.536 sq. m. plots the corresponding factor is 0.03254.

The soil of the field proved to be not quite uniform. One part of the field in which the plants, diploids as well as tetraploids, developed extraordinarily well was not taken into account at all. Moreover, each time samples were taken, the two plots were chosen as different as possible in order to obtain the most probable average. The difference between such replicate plots appears from tables 1 and 2. As is seen from table 1, the variation of the two replicates in the main experiment in a single case amounted to nearly 30 per cent of the mean. In the experiments represented in table 2 the variation in one case is almost 37 per cent. However, these figures are the maxima, and in most cases, especially towards the end of the experiment, when the most important harvests are taken, the variation is less than 10 per cent. In the main experiment with *S. nodiflorum*, the dry weight in the 6 first harvests was determined directly through drying of the total quantity of roots, of stems, etc. In the next 3 harvests, the roots of the 21 plants from each plot have been desiccated, while the green parts of 11 to 6 plants only have been completely analyzed. The green parts of the rest of the plants have been dried without being specified in stems, leaves, and reproductive organs. The contribution of their individual organs to the total weight could be calculated on the basis of the composition found in the analyzed plants. In the 8 last harvests, only 5 or 4 plants per plot have been completely analyzed and desiccated. The various fresh weights, of course, were determined immediately after the plants had been lifted out of the soil, so that the water content of those analyzed and of those not analyzed was as uniform as possible.

The determination of the weight of the roots took place after the roots had been washed repeatedly with water and wiped with filter-paper. When the plants are dug out, part of the roots is generally left in the soil. In order to determine this fraction some plants with a big rootball were carefully taken out. The soil was removed, the loosened soil being sifted in order to pick up all the torn-off parts of the roots. The dry weight of the roots dug out in this way was found to be on an average 64 per cent higher than that of the roots dug out in the usual way. As an estimation of this kind cannot, of course, be done very accurately, the correction was assumed to be 50 per cent and therefore, all weights of roots have been multiplied by 1.5.

Towards the end of the growth season, some of the species are more or less markedly inclined to shed leaves or fruits, so that a given yield may be less than the preceding one. In such cases, when comparing the yields of the various strains, the highest measurement has been reckoned with. Consequently, some disagreement may be found between the amounts of dry matter evaluated directly, as given

in the tables representing the raw material, and the corresponding amounts in those tables and diagrams which serve for a comparison of the maximum productivity of the strains.

II. Production of Dry Matter in Autotetraploids.

a. The Course of Production of Dry Matter.

As mentioned previously, the main experiment was carried out on *Solanum nodiflorum*. The transplanting to the field took place on May 20th, 1939. The dry weight was determined during the vegetation period at approximately one week intervals. From harvest No. 7 it was no longer possible, due to the increasing amount of work, to reap on the same day the diploid and the tetraploid plots to be compared.—The results of the determinations of dry matter are given in table 1. The yields, calculated

Table 1.

Main experiment. *Solanum nodiflorum*, diploid and autotetraploid. Yield of each of the two replicate plots. Shed parts not included.

Harvest No.	Diploid					Tetraploid				
	Date 1939	Amount of dry matter of the two replicate plots, g.		Average amount of dry matter per plot, g.	Variation, percent of the mean	Date 1939	Amount of dry matter of the two replicate plots. g.		Average amount of dry matter per plot, g.	Variation, percent of the mean
1	May 20	..	..	2.99	..	May 20	..	..	2.84	..
2	May 30	2.82	4.20	3.51	±19.8	May 30	3.87	3.87	3.87	± 0.0
3	June 6	4.75	5.17	4.96	4.2	June 6	3.54	5.46	4.50	21.3
4	June 12	4.81	7.89	6.35	24.2	June 12	5.66	6.42	6.04	6.3
5	June 19	9.54	11.66	10.60	10.0	June 19	10.06	11.06	10.56	4.7
6	June 26	21.4	39.2	30.3	29.4	June 26	19.0	31.4	25.2	24.7
7	July 4	65.1	72.2	68.6	5.1	July 3	50.3	51.5	50.9	1.1
8	July 10	92.9	98.9	95.9	3.1	July 11	67.2	97.0	82.1	18.1
9	July 17	110.7	160.9	135.8	18.5	July 18	127.8	168.8	148.3	13.8
10	July 24	262	268	265	1.0	July 25	245	329	287	14.6
11	July 31	344	456	400	14.0	Aug. 1	467	553	510	8.4
12	Aug. 7	597	705	651	8.3	Aug. 8	489	623	556	12.1
13	Aug. 14	727	813	770	5.6	Aug. 15	632	656	644	1.8
14	Aug. 21	772	820	796	0.3	Aug. 22	800	898	849	5.8
15	Aug. 28	802	854	828	3.2	Aug. 29	766	932	849	9.8
16	Sept. 4	824	848	836	1.4	Sept. 5	798	894	846	5.7
17	Sept. 11	964	990	977	1.3	Sept. 12	905	1031	968	6.5
18	Sept. 18	939	949	944	0.5	Sept. 19	905	1037	971	6.8

per hectare, are rendered in fig. 7, curve *a*. From the 11th harvest and further on, the values of this curve have been gained by summing up the values of the smoothed curves of fig. 13, representing the distribution over the various organs of the dry matter produced. It appears that the course of production of dry matter in the diploid and the tetraploid plants is very much the same. If the relative production of dry matter of the tetraploids is calculated, setting the production of the diploids equal to 100, the result will be the following.

Harvest No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Relative weight of the tetraploids (Diploids = 100):	95	107	92	94	98	84	80	80	100	100	106	87	87	92	96	99	99	99.

The amount of dry matter of the tetraploids, on the day when the diploids were reaped, was read from a curve drawn on a large scale. Only in the second and the 11th harvest the dry weight of tetraploids showed a larger value than did the diploids. In the 9th and 10th harvests, identical figures were found for diploids and tetraploids. Otherwise the tetraploids were always inferior, though the differences on the whole are very small. Hence, the question, whether the tetraploids show a larger production than the diploids, must presumably be answered negatively for this species.

The slope of the drawn curves is an expression of the production intensity at every given moment. During the first 10 periods, both types of plants produce almost equal amounts of dry matter per unit of time. In the beginning of August, the daily production of the diploids reaches the maximum. The intensity of production of the tetraploids, during this period, is less than that of the diploids. The difference, however, will be counterbalanced, during the last half of August, through the increase in production intensity of the tetraploids, the final result in diploids and tetraploids becoming the same.

The results obtained with other species of *Solanum* are given below. The plants were transplanted to the field on May 22nd, 1939. The dry weight was determined only three or four times during the season.

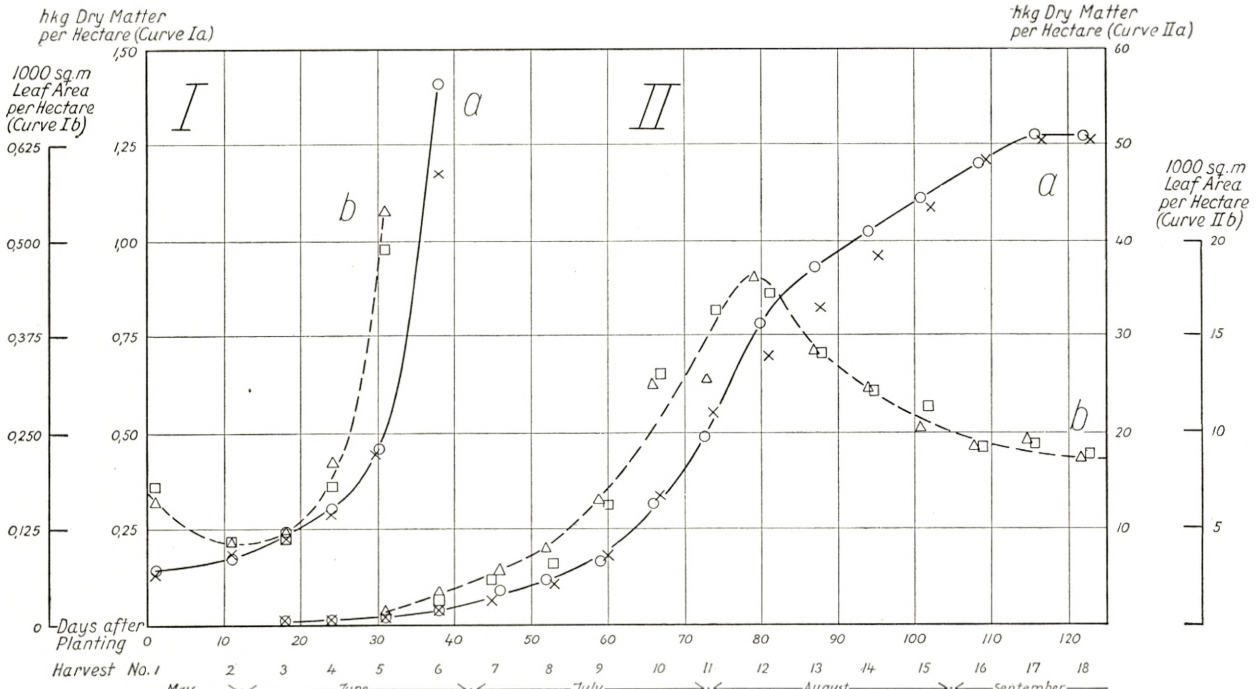

Fig. 7. *Solanum nodiflorum*, diploid and autotetraploid, grown in 1939.

The curves *I* (ordinate to the left) represent the first part of the curves *II* (ordinate to the right) drawn on a larger scale. The points representing the diploids, only, are connected by a line.

a total production of dry matter, hkg. per hectare. o–o diploid, ×× tetraploid.
b leaf area, 1000 sq. m. per hectare; △---△ diploid, □□ tetraploid.

Table 2.

Yield of each of the two replicate plots in *Solanum gracile*, *S. alatum*, and *S. nigrum*, diploid and autotetraploid.

	Date 1939	Diploid				Tetraploid			
		Amount of dry matter of the two replicate plots, g.		Average amount of dry matter per plot, g.	Variation, per cent of the mean	Amount of dry matter of the two replicate plots, g.		Average amount of dry matter per plot, g.	Variation, per cent of the mean
Solanum gracile	May 22	1.53	1.71	1.62	±5.5	1.02	1.34	1.18	±13.8
	June 28	34.3	49.2	41.8	17.9	21.6	23.2	22.4	3.5
	Aug. 31	696	716	706	1.3	754	772	763	1.2
Solanum alatum	May 22	1.97	1.99	1.98	0.5	1.15	1.49	1.32	13.1
	June 28	31.3	38.3	34.8	10.0	8.2	17.6	12.9	36.7
	Aug. 31	714	868	791	9.7	590	636	613	3.7
Solanum nigrum	May 22	5.56	6.58	6.07	8.5	2.67	2.69	2.68	0.5
	June 28	44.0	83.2	63.6	30.8	20.5	25.2	22.9	10.2
	Aug. 31	936	968	952	1.7	770	873	822	6.3
	Sept. 29	946	1021	984	3.8	533	990	762	30.0

The behaviour of *Solanum gracile* appears from table 2 and fig. 8. In the beginning, the amount of dry matter is less in the tetraploids than in the diploids. On the 102nd day, however, an amount of dry matter was gained, larger by 8 per cent in the tetraploids than in the diploids (cf. table 3). In both cases, the variation of the two replicate plots was slight, only 1.2 and 1.3 per cent of the mean, and the difference may thus be a real one.

In *Solanum alatum* and *Solanum nigrum*, on the other hand, the tetraploids were markedly inferior, never reaching the weight of the diploids (cf. tables 2 and 3, and figs. 9 and 10).

A summary of the relation between the productivity of the diploid and the autotetraploid plants examined is given in table 3. A common feature of the four species of *Solanum* examined is that in the beginning the rate of development is slower in the tetraploids than in the diploids, a fact which is also

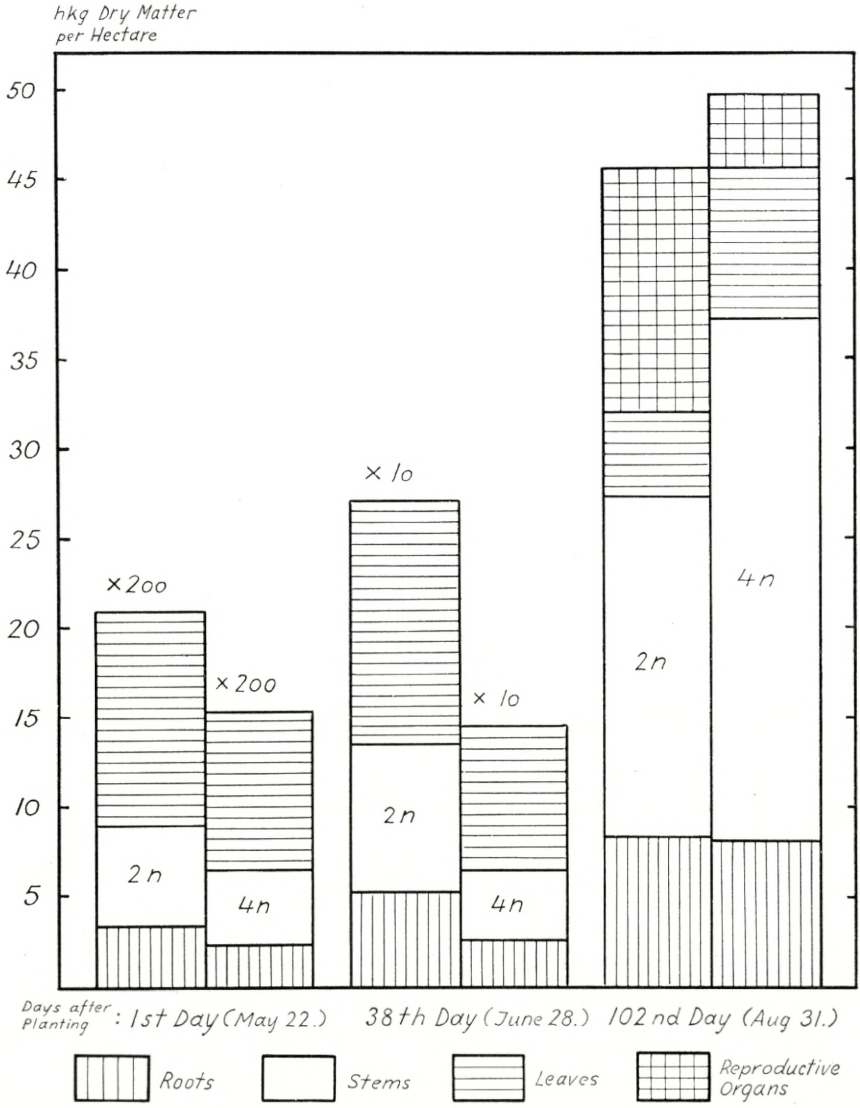

Fig. 8. *Solanum gracile,* diploid and autotetraploid, grown in 1939. Total production of dry matter and distribution of dry matter over the various organs, hkg. per hectare. NB. different scale. In the case of the first and the second pair of columns the readings on the ordinate should be divided by 200 and by 10, respectively.

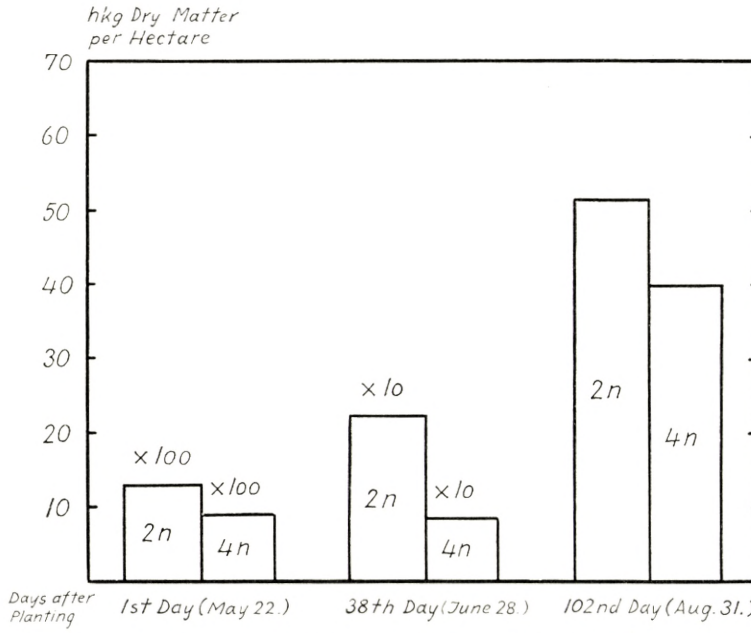

Fig. 9. *Solanum alatum*, diploid and autotetraploid, grown in 1939. Total production of dry matter, hkg. per hectare. NB. different scale. In the case of the first and the second pair of columns the readings on the ordinate should be divided by 100 and by 10, respectively.

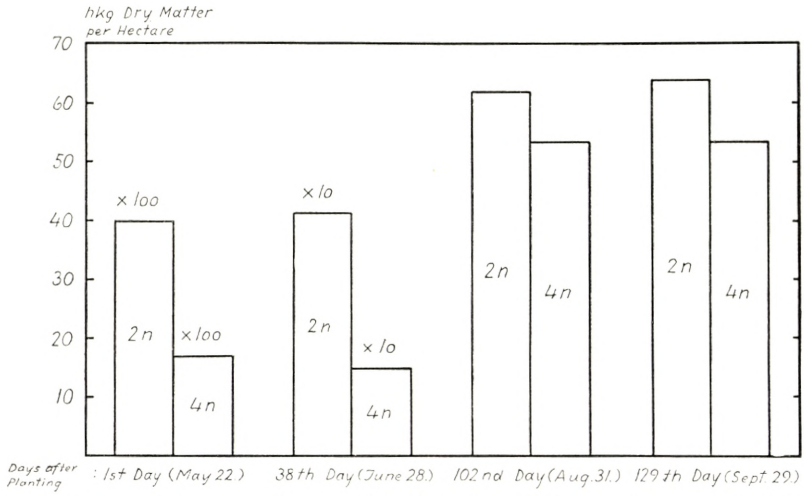

Fig. 10. *Solanum nigrum*, diploid and autotetraploid, grown in 1939. Total production of dry matter, hkg. per hectare. NB. different scale. In the case of the first and the second pair of columns the readings on the ordinate should be divided by 100 and by 10, respectively.

Table 3.

Dry weight of tetraploids, the dry weight of diploids being = 100.

Number of days after transplantation to the field	*Solanum nodiflorum*	*Solanum gracile*	*Solanum alatum*	*Solanum nigrum*
1	95	89	69	44
38	84	54	37	36
102	96	108	78	86
131	—	—	—	84

recognizable directly from the appearance of the plants. From a mere inspection of the field, the following impression of the further development may be gained (comp. also the photographs figs. 1—4): In *S. nodiflorum*, the diploids seem to be reached by the tetraploids. In *S. gracile*, they seem to be overtaken, the tetraploids looking twice as big as the diploids. In *S. alatum*, the tetraploids do not seem to attain the size of the diploids, and finally, in *S. nigrum*, the tetraploids look considerably larger. In the case of *S. nodiflorum* and of *S. alatum*, only, the impression gained in this way is confirmed by the determinations of dry matter. In *S. gracile*, on the other hand, the actual excess of dry matter in the tetraploids was only 8 per cent, and in the tetraploid *S. nigrum* even a deficiency of 14—16 per cent was found. The wrong presumption of a much higher production in the tetraploid *S. gracile* and *S. nigrum* is caused by a change in the distribution of the matter produced, i. e. an alteration of the form of the plant which is to be analyzed in detail in the next section.—An evident change of the luxuriance during the development was shown still more markedly by the tetraploid Kobai barley examined by GREIS (1940).

The growth of plants depends on several external conditions; a change in one or more of them may greatly influence the development of a given plant. From agricultural practice it is well-known that varieties of the same plant species, no more different than diploids and tetraploids, often respond in different ways to a change in external conditions. It might therefore be possible, too, that the proportion between diploids and tetraploids found in the previous experiments would be

different under changed conditions. From this point of view, a few preliminary experiments were carried out in which the plants were grown under conditions different from those in the experiments hitherto described. The effect of the variation of two factors, only, was examined, viz. the planting distance and the supply of nitrogen, both of which are known to be of great importance to the size of the crop.

Experiments on the effect of varying distance between the plants were carried out with diploid and tetraploid *Solanum nodiflorum*.

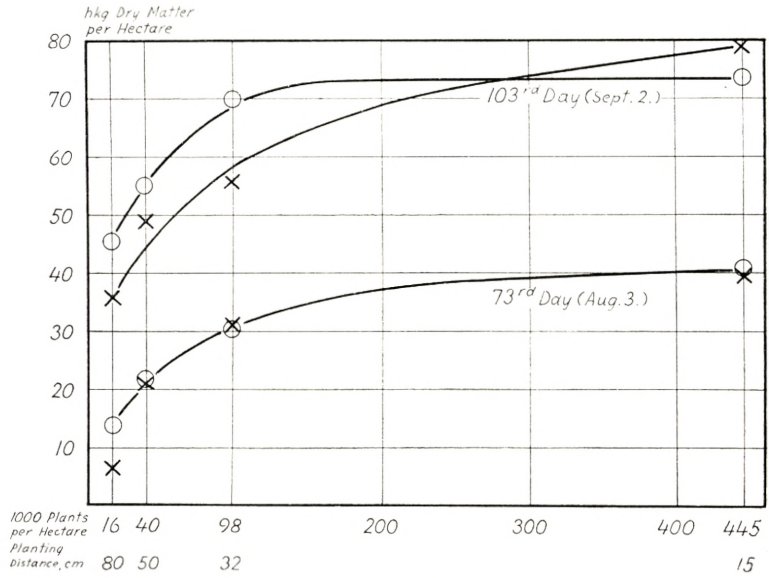

Fig. 11. *Solanum nodiflorum*, 2 *n* and 4 *n*, grown in 1939. Effect of various planting distances on production of matter. oo diploid; ×× tetraploid.

The intervals used were 15, 32, 50 and 80 cm., the size of each plot being 0.876, 1.54, 3.00 and 6.40 sq. m. and the plots including 39, 15, 12 and 10 plants, respectively. One plot, only, of each of the types of plant was reaped on the 73rd and 103rd day of vegetation. The results are represented in fig. 11. As is generally the case, the production increases according to the number of plants per hectare. The tetraploids yielded a small excess (7 per cent) in case of the greatest density of plants. This result is, however, encumbered with great uncertainty.

The influence of varying amounts of nitrogen on the production of dry matter was determined in experiments on *Solanum gracile*, 200, 300, and 500 kg. of calcium nitrate being given per hectare. Before the transplantation of the plants took place, all three experimental areas got 200 kg. per hectare; on the 23rd day of vegetation, two of them got 100 and 300 kg. respectively, per hectare. On the 77th and 103rd day, two plots

of each type of plant were reaped; on the 130th day, however, only one diploid and one tetraploid plot have been harvested. The result is illustrated in fig. 12. The increased supply of nitrogen had a furthering effect on the productive capacity of both types of plants. At a large supply of nitrogen and a prolonged duration of vegetation, the tetraploid *Solanum gracile* will possibly produce a little more than the diploid; analogously, in the last harvest of the previous experiment on this species (p. 16 and fig. 8), the production in the tetraploids was somewhat larger than in the diploids.

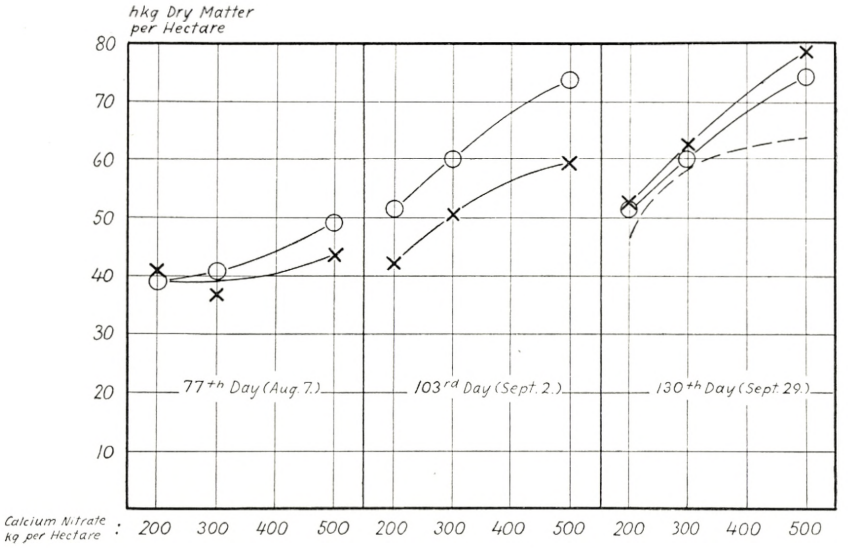

Fig. 12. *Solanum gracile*, 2 *n* and 4 *n*, grown in 1939. Effect of increasing amounts of nitrogen on the production of dry matter. o—o diploid; ×—× tetraploid; – – – diploid, shed parts not included.

b. Distribution of the Dry Matter Produced.

In the previous section, only the total amount of dry matter was considered. By now, the distribution of the organic substance produced is to be studied. The proportion between the quantity of roots, stems, leaves, and reproductive bodies is of interest for two reasons. First it is determinative for the production of matter itself (the more leaves, the more of photosynthates). It would further be of genetical interest to know whether the chromosome doubling has any effect on this proportion, i. e. whether it is capable of modifying the form of plants.

Solanum nodiflorum: The amount of roots, stems, leaves and reproductive organs reaped directly at every second harvest is

Table

Solanum nodiflorum, 2*n* and 4*n*. Dry weight of the individual organs represented. g. per

Harvest No.	1		3		5		7	
Date 1939	May 20	May 20	June 6	June 6	June 19	June 19	July 4	July 3
	2*n*	4*n*	2*n*	4*n*	2*n*	4*n*	2*n*	4*n*
Roots	2.02	1.68	5.32	4,69	9.12	10.06	34.8	29.8
Stems	1.29	1.33	1.98	1,72	4.81	4.21	43.9	29.1
Leaves	2.66	2.66	2.62	2,58	7.26	6.84	56.4	41.9
Reproductive organs	—	—	—	—	—	—	2.0	0.9
Total	5.97	5.67	9.92	8.99	21.19	21.11	137.1	101.7

given in table 4. In fig. 13, the production of the individual plant organs is graphically represented by the results of each harvest, calculated per hectare. The points correspond to the values actually found, while the curves plotted have been smoothed. When smoothing the growth curves of the roots, the average of the two highest values was used as a maximum value. The lower values found after the 13th harvest were not taken into account, since they probably result from the ever increasing difficulty of getting the roots out of the soil, owing to their increasing size. Regarding the leaves, two curves were plotted. One, fig. 13 *a*, represents the amount of the living, the other (*b*) that of the living + dead leaves. Both types of plant, the diploid and the tetraploid, on the whole behave in the same way, particularly during the first part of the vegetation period. Afterwards certain deviations occur which, however, are partly accompanied by incidental fluctuations of the yield, hence being less reliable. Nevertheless, it may be concluded that the tetraploids produce a somewhat larger amount of stems and leaves than the diploids, since in each of the last 5 harvests larger amounts of tetraploid stems were reaped, and the same holds for tetraploid leaves in the harvests 10 to 15.—Until the 70th day, the slope of the curve for the production of flowers and fruits, indicating the intensity of production, for instance per day, is approximately the same in both types of plant. During the next two weeks, a great rise in the production of berries appeared

4.

directly reaped. Shed parts not included. Only every second harvest two replicate plots.

9		11		13		15		17	
July 17	July 18	July 31	Aug. 1	Aug. 14	Aug. 15	Aug. 28	Aug. 29	Sept. 11	Sept. 12
2 *n*	4 *n*	2 *n*	4 *n*	2 *n*	4 *n*	2 *n*	4 *n*	2 *n*	4 *n*
74.5	79.5	183	212	360	290	258	261	264	311
95.0	106.6	327	428	565	500	480	574	559	589
91.2	97.6	208	275	208	236	150	168	151	132
10.8	12.9	81	104	407	262	767	694	980	903
271.5	296.6	799	1019	1540	1288	1655	1697	1954	1935

in the diploids, which was only incompletely compensated by a later increase in the production of berries in the tetraploids. The dry weight of the berries in diploids and tetraploids in the harvests Nos. 17 and 18 is as 100 to 92 and 100 to 86, respectively.

Hence, the diploid and tetraploid strains of *S. nodiflorum* being so much alike in total production of dry matter are also found to be very similar as to the distribution of the substance produced.

Quite another picture is seen in *Solanum gracile* which, however, was reaped only three times. In table 5, the amounts

Table 5.

Solanum gracile, diploid and autotetraploid. Dry weight of the individual plant organs directly reaped. Shed organs not included. g. per two replicate plots.

Date 1939	May 22		June 28		August 31	
	2 *n*	4 *n*	2 *n*	4 *n*	2 *n*	4 *n*
Roots	0.52	0.36	16.5	8.2	258	255
Stems	0.86	0.64	25.4	12.4	581	898
Leaves	1.86	1.36	41.5	24.1	143	260
Reproductive Organs	—	—	—	—	432	113
Total	3.24	2.36	83.4	47.7	1414	1526

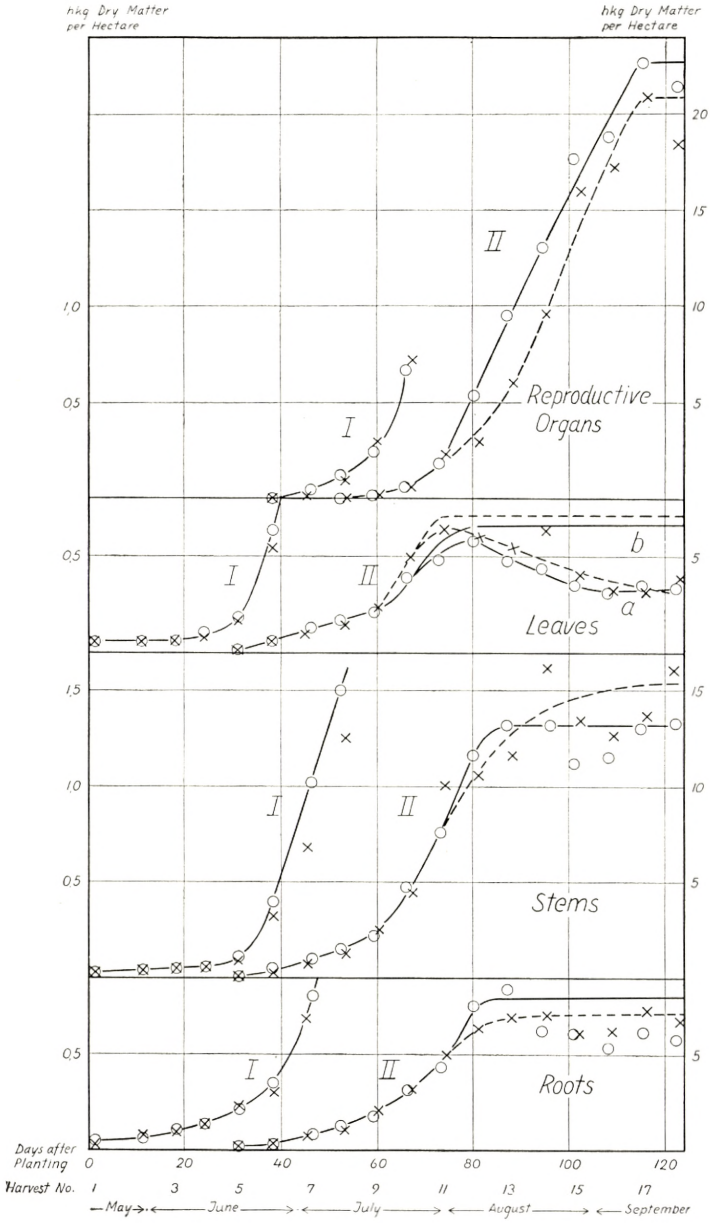

Fig. 13. *Solanum nodiflorum*, 2 *n* and 4 *n*, grown in 1939. Distribution of dry matter produced. The curves *I* (ordinate to the left) represent the first part of the curves *II* (ordinate to the right), drawn on a larger scale. o—o diploid; × – – – × tetraploid. As to the representation of the production of leaves, curve *a* shows the amount of living and curve *b* that of living + dead leaves.

of dry matter actually reaped in each harvest are represented. The production per hectare is shown graphically in fig. 8. In this species, too, until the appearance of the reproductive organs (flower buds) the relative distribution of dry matter is approximately the same in the diploid and the tetraploid plants. At this time, the total weight of the diploids is almost twice that of the tetraploids. Later, when the tetraploids exceed the diploids as to dry weight, the distribution of dry matter in the two types of plant becomes very different. The ratio of dry weight in the fruits of the diploids and of the tetraploids at the end of the experiment is 100 to 27 (cf. also table 19). On the other hand, in the tetraploids the amount of leaves is about twice and that of the stems one and a half times that of the diploids. At a rough estimate in the field, one would judge the total production in the tetraploids considerably higher than that of the diploids. The exact measurement, however, showed but a relatively small superiority in the production of the tetraploids, these plants producing only 8 per cent more than the diploids. The cause of this contradiction has to be sought in the fact that the stems of the tetraploids are stronger and more erect and their leaves are larger and more numerous, which makes the plants look much more bulky. As, however, the diploids simultaneously deposit a large amount of their photosynthates in the berries, the weight of which one is highly inclined to underestimate, their amount of dry matter will be nearly as high as that of the tetraploids.

Solanum nigrum, too, behaves in almost the same way as *Solanum gracile*: in the tetraploids of this species, a considerable excess would be estimated by a mere inspection of the cultures while, on the other hand, the determinations of dry matter showed a deficiency of 14—16 per cent. Unfortunately, determinations of the distribution of matter were not carried out in this plant; but also here the tetraploids produced a by far smaller number of berries than did the diploids.

The change in the form of the plant, which follows the doubling of the chromosome number in species like *S. gracile* (and very likely *S. nigrum*, too), thus involves a more luxuriant development of the vegetative parts, but at the same time a marked

decrease in the amount of fruit produced. In tobacco, cabbage, grass, clover, and other plants, the vegetative parts of which are the aim of cultivation, the possibility of an increased production induced by polyploidy is thus at hand. As far as reproductive organs are concerned, however, the prospects seem rather unpromising.

Table 6.

Diploid and corresponding amphidiploid *Solanum*s. Total yield of dry matter and its distribution throughout the individual plant organs. g. per two replicate plots.

	S. gracile				*S. gracile* × *S. insulae-pascalis*; amphidiploid				*S. insulae-pascalis*			
Date 1939	June 24	Aug. 1–2	Aug. 26–28	Sept. 16–18	June 24	Aug. 1–2	Aug. 26–28	Sept. 16–18	June 24	Aug. 1–2	Aug. 26–28	Sept. 16–18
Days after planting	25	63	88	109	25	63	88	109	25	63	88	109
Roots	13.3	278	580	513	7.1	223	551	704	4.1	112	311	495
Stems	13.6	769	1347	1390	5.3	480	1311	1748	5.6	262	806	977
Leaves	24.6	460	362	107	13.1	474	533	538	13.5	464	406	237
Reproductive organs	0.3	85	486	865	—	24	151	250	—	13	154	232
Total	51.8	1592	2775	2875	25.5	1201	2546	3240	23.2	851	1677	1941

	S. nigrum				*S. nigrum* × *S. nitidibaccatum* amphidiploid				*S. nitidibaccatum*			
Date 1939	June 25	Aug. 5–6	Aug. 27–29	Sept. 17–19	June 25	Aug. 5–6	Aug. 27–29	Sept. 17–19	June 25	Aug. 5–6	Aug. 27–29	
Days after planting	25	67	89	110	25	67	89	110	25	67	89	
Roots	18.2	210	306	304	20.7	297	443	511	11.1	139	158	
Stems	11.7	382	502	408	15.5	736	948	922	17.2	914	670	
Leaves	20.0	316	397	204	30.0	504	482	284	29.7	472	136	
Reproductive organs	5.1	688	1283	1480	2.3	483	1426	1198	7.6	691	566	
Total	55.0	1596	2488	2396	68.5	2020	3299	2915	65.6	2216	1530	

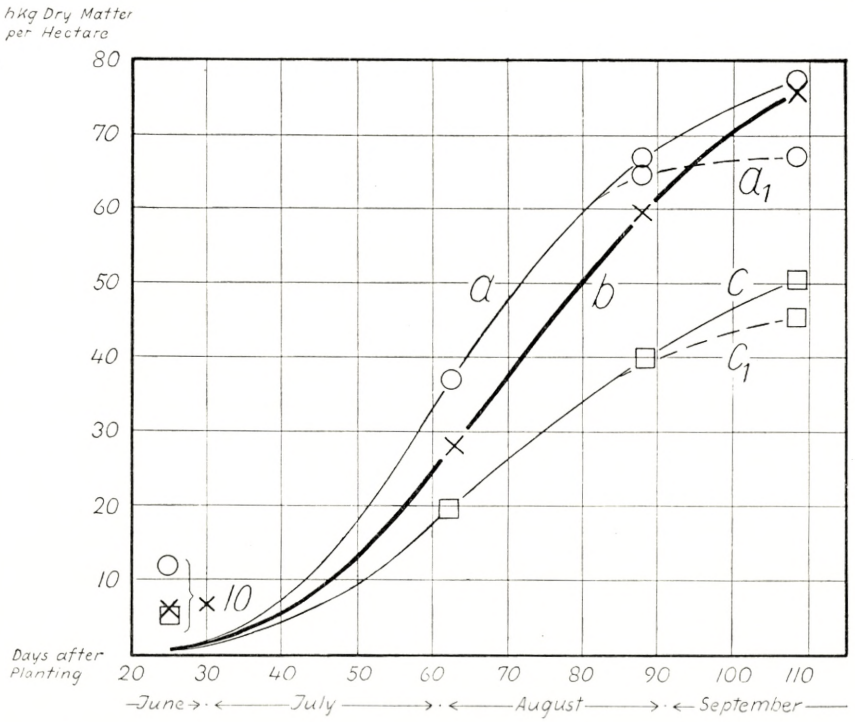

Fig. 14. Diploid and amphidiploid *Solanums*, grown in 1940. Total production of dry matter; hkg. per hectare.

a Solanum gracile; shed organs included (a_1 shed organs not included).

b S. gracile × *S. insulae-pascalis*, amphidiploid.

c S. insulae-pascalis; shed organs included (c_1 shed organs not included).

III. Production of Dry Matter in Amphidiploids.

a. The Course of Production of Dry Matter.

The amphidiploid plants and their parent species were cultivated in 1940. The transplanting to the field took place on June 1st. The amounts of dry matter directly reaped are given in table 6.

The table shows but the sum of the amounts of dry matter reaped in two replicate plots, because the harvest was carried out in the way that one plot, only, of each of the three types of plant to be compared was reaped on the same day; the second of the replicates was reaped one or two days later. Consequently, the difference between the yields of the individual

replicate plots does not give any information as to the variation between the two plots. On the other hand, the figures representing the yield of each of the three types of plant, the parent species, and their amphidiploid hybrid, are fully comparable.

The total production of dry matter per hectare in *Solanum gracile*, *S. insulae-pascalis* and their amphidiploid hybrid is shown graphically in fig. 14. The amount of dry matter of the hybrid, at the beginning, is the same as in *S. insulae-pascalis*, the smaller of the two parent species. The course of its production during the development is intermediate as compared with the parents, its weight in the end being almost the same as the weight of *Solanum gracile*, the more productive of the parent species. The same appears from table 7 which gives the relative weight of the three types of plant.

Table 6 and fig. 15 show the course of the production in *Solanum nitidibaccatum*, *S. nigrum* and the amphidiploid hybrid of these species. *S. nitidibaccatum* develops most quickly, but very early the production is slowed down, and the plant begins to shed berries and leaves. Meanwhile, *S. nigrum* and the amphidiploid hybrid continue to grow, the weight of the hybrid being

Table 7.

Relative dry weight of diploid and corresponding amphidiploid *Solanums*.

Number of days after transplantation to the field	*Solanum gracile*	*S. gracile* × *S. insulae-pascalis*; amphidiploid	*S. insulae-pascalis*
25	224	110	100
63	187	141	100
88	166	147	100
109	153	150	100
	Solanum nitidibaccatum	*S. nigrum* × *S. nitidibaccatum*; amphidiploid	*S. nigrum*
25	119	124	100
67	139	127	100
89	90	134	100
110	—	126	100

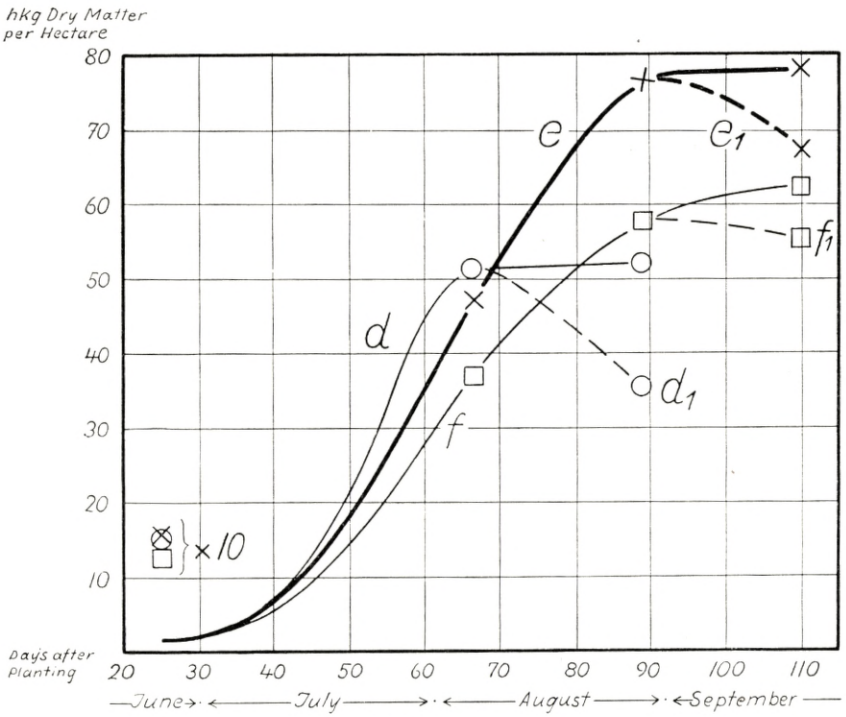

Fig. 15. Diploid and amphidiploid *Solanums*, grown in 1940. Total production of dry matter; hkg. per hectare.
d Solanum nitidibaccatum; shed organs included (d_1 shed organs not included).
e S. nigrum × *S. nitidibaccatum*, amphidiploid; shed organs included (e_1 shed organs not included).
f S. nigrum; shed organs included (f_1 shed organs not included).

the higher one. The proportion of the dry weights of the three types of plant is given in table 7. On the 89th day of vegetation, at any rate, a considerable superiority is found in the amphidiploid hybrid as compared with both initial forms.

b. Distribution of the Dry Matter Produced.

The distribution over the various organs of the matter produced in the amphidiploid plants and the parent species appears from table 6 which shows the amounts of dry matter actually reaped. The values calculated per hectare and corrected for shed organs are represented graphically in figs. 16 and 17.

It is seen that the amphidiploid hybrid between *S. gracile* and *S. insulae-pascalis* produces about the same quantity of roots

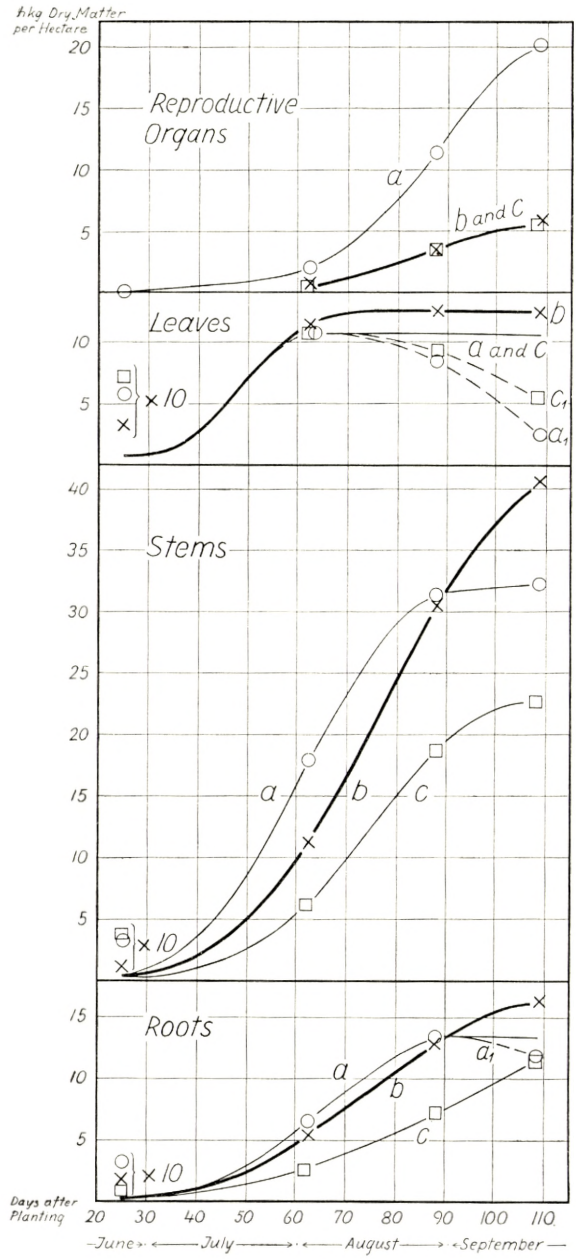

Fig. 16. Diploid and amphidiploid *Solanums*, grown in 1940. Distribution of the dry matter produced.

a Solanum gracile; shed organs included (a_1 shed organs not included).

b S. gracile × *S. insulae-pascalis*, amphidiploid.

c S. insulae-pascalis; shed organs included (c_1 shed organs not included).

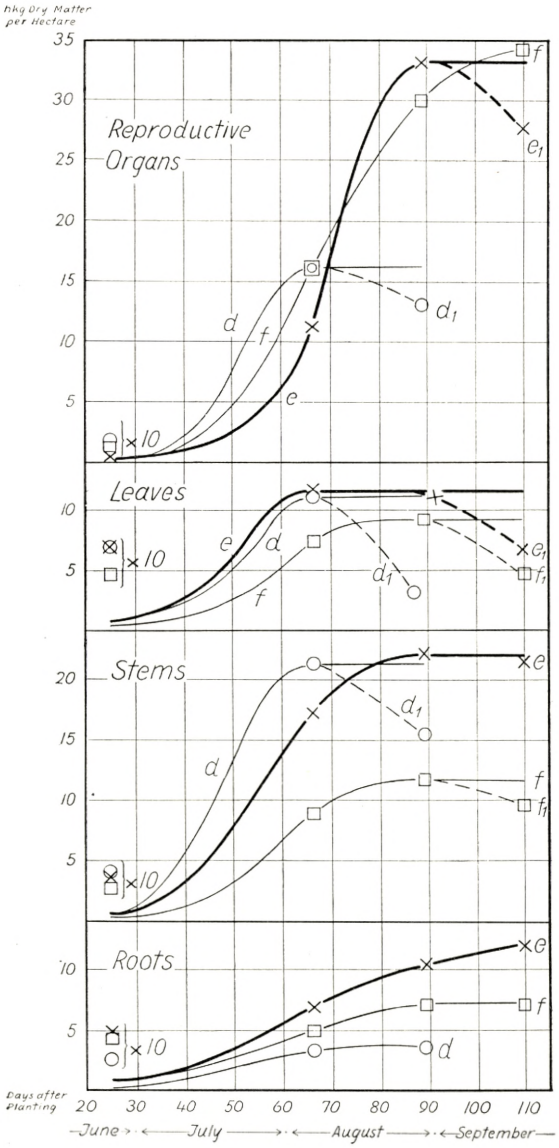

Fig. 17. Diploid and amphidiploid *Solanums*, grown in 1940. Distribution of the dry matter produced.
d Solanum nitidibaccatum; shed organs included (d_1 shed organs not included).
e S. nigrum × *S. nitidibaccatum*, amphidiploid; shed organs included (e_1 shed organs not included).
f S. nigrum; shed organs included (f_1 shed organs not included).

as *S. gracile*, which is considerably more than in *S. insulae-pascalis*. The hybrid further produces a larger amount of stems and, in contradistinction to both parent species, it keeps its leaves until the 110th day at least. At this time, only 50 per cent of the leaves are left in *S. insulae-pascalis* and only 20 per cent in *S. gracile*. The production of berries of the hybrid is exactly consistent with that of *S. insulae-pascalis*, i. e. only about one fourth of that of *S. gracile*.

The production of roots, stems, and leaves in the amphidiploid hybrid between *S. nigrum* and *S. nitidibaccatum* is larger than in *S. nigrum*, while the production of berries is the same. Compared with *S. nitidibaccatum*, the hybrid has twice the production of roots and berries, while the production of stems and leaves is equally large in both forms. As early as after the 66th day *S. nitidibaccatum* begins to shed the older leaves. The hybrid and *S. nigrum*, on the other hand, keep their leaves three weeks longer. *S. nitidibaccatum* is markedly inclined to drop its fruits. In the amphidiploid, too, this inconvenient character is present, though to a less extent, the shedding occurring not until three weeks later.

Of the two amphidiploids investigated the first one represents a case in which the productivity of the hybrid does not exceed that of the parent species. In the last mentioned amphidiploid, *S. nigrum* × *S. nitidibaccatum*, however, an absolute excess of dry matter is produced, which is combined with a remarkable fertility (cf. also table 19). The expectations of many geneticists and plant breeders, that amphidiploids would prove more favourable than their parent species, have thus been realized in this case.

The formation of the amphidiploid plants has been carried out in two steps. First, the two species have been crossed and, next, the chromosome number of their hybrid has been doubled. Which of these steps is responsible for the increased productivity, either hybridization (heterosis) or chromosome doubling ("gigas"-growth), cannot be ascertained, since the productivity of the diploid hybrid itself is unknown. According to the experience with autotetraploid forms of *Solanum*, it is impossible to know *a priori* whether the amphidiploid or the diploid hybrid would have been the superior. From the appearance

of the diploid hybrid, the result is most likely to be taken as an effect mainly of the chromosome doubling and to a minor degree—if at all—of hybrid vigour. As has been demonstrated earlier in this paper, however, the appearance of plants is a rather unsafe basis of estimation of the productivity.—Setting aside whether the diploid or the amphidiploid hybrid is the more productive, the amphidiploid has the indisputable advantage of being fully fertile, while the diploid hybrid is completely sterile.

C. Rate of Photosynthesis.

The determination of the rate of photosynthesis was carried out according to the air current method devised and thoroughly described by BOYSEN JENSEN (1928, 1932, 1933). The most recent alterations of the apparature have been described by ROMOSE (1940).

Through a control by means of BOYSEN JENSEN's stomatometer, it was secured that leaves only with stomata widely opened were used for the determinations of carbon dioxide assimilation.

In the method described, the amount of carbon dioxide taken up by the leaves from outside, the so-called apparent assimilation, is determined. Simultaneously, however, the carbon dioxide produced by respiration is assimilated, too; the rate of real assimilation is then gained by summing up the intensity of respiration per 50 sq. cm. leaf area per hour at 20° C. and the rate of apparent assimilation measured directly. The rate of respiration mentioned is given in the tables as a footnote. Each rate of photosynthesis given in the tables is an average of 2 to 5 individual determinations.

I. Autotetraploids. Table 8 shows the maximum rate of photosynthesis of the leaves of *Solanum nodiflorum* which can be obtained under natural conditions, i. e. the rate of photosynthesis at such an illumination that an increasing light intensity does not cause any increase in photosynthetic activity. In the case of the diploids, this quantity is on an average 12.5 mg. CO_2 per 50 sq. cm. per hour. The values of the 4 individual plants used vary from 12.1 to 13.1 mg. In the tetraploids, on the other hand,

Table 8.

Rate of photosynthesis in *Solanum nodiflorum*.

Plant No.		Maximum rate of real assimilation; mg. CO_2 per 50 sq. cm. leaf area per hour at 20° C. and normal pressure of carbon dioxide. Illumination 17100—23800 BJ-Lux	
Diploid [1]	1	12.1	mean = 12.5
	2	12.4	
	3	12.4	
	4	13.1	
Tetraploid [2]	1	15.4	mean = 11.0
	2	8.9	
	3	14.1	
	4	12.4	
	5 [3]	5.8	
	6 [3]	9.5	

[1] Average rate of respiration = 0.87 mg. CO_2 per 50 sq. cm. per hour at 20° C.
[2] Average rate of respiration = 0.42 mg. CO_2 per 50 sq. cm. per hour at 20° C.
[3] Roundish-leaved type of plant.

the variation is much greater. The maximum rate of photosynthesis of the 6 individuals fluctuates from 5.8 to 15.4 mg. CO_2 with an average of 11.0 mg. It is noticeable that two of the plants have a considerably higher rate of photosynthesis than the diploids. On the other hand, individuals showing a very low rate of photosynthesis are also found. Among the tetraploids, a morphological variation, too, could be observed, manifesting itself particularly through the shape of leaf. In addition to the normal plants with ovate-elliptical leaves, some with coarser, broader, more roundish leaves were found. According to a rough estimate, this type amounts to 10 per cent of the tetraploid plants. Although this morphological variation is not quite parallel to the variation of the rate of photosynthesis, yet the lowest maximum rate of 5.8 mg. CO_2 was measured in the type with roundish leaves.

Moreover, for a comparison with the *Solanums*, the rate of photosynthesis of diploid and tetraploid plants of *Sinapis alba* was determined on material which had been cultivated in well manured garden soil in the Botanical Garden of Copenhagen. The maximum rate of real assimilation of tetraploid plants was found to be on an average 85 per cent of that of the diploids

Table 9.

Rate of photosynthesis in *Sinapis alba*.

Plant No.		Maximum rate of real assimilation; mg. CO_2 per 50 sq. cm. leaf area per hour at 20° C. and normal pressure of carbon dioxide. Illumination 21900 BJ-Lux	
Diploid[1]	1	15.0	mean = 14.9
	2	14.6	
	3	15.2	
Tetraploid[2]	1	12.5	mean = 12.6
	2	12.1	
	3	11.6	
	4	12.6	
	5	14.4	

[1] Average rate of respiration = 0.60 mg. CO_2 per 50 sq. cm. per hour at 20° C.
[2] Average rate of respiration = 0.91 mg. CO_2 per 50 sq. cm. per hour at 20° C.

(cf. table 9). In this case, all measurements in tetraploids are lower than in diploids.

In connection with the examinations on photosynthesis, E. K. GABRIELSEN, Ph. D., the Royal Veterinary and Agricultural College, kindly determined the content of chlorophyll in the leaves of *Sinapis*. The content of chlorophyll (a + b) of the leaves of 6 diploid and 6 tetraploid plants was 2.8 ± 0.12[1] and 2.9 ± 0.07[1] mg., respectively, per 50 sq. cm. of leaf area (measured on one side). The ratio $diff./m_{diff.} = 0.1 : 0.14 = 0.71$. Hence, the difference is not significant. The corresponding figures per g. fresh weight are: diploids 3.2 ± 0.16[1] mg., and tetraploids 2.9 ± 0.08[1] mg. $Diff./m_{diff.} = 1.7$. Accordingly, calculated in this way, the tetraploids have the minor amount of chlorophyll. However, also in this case the difference is insignificant.—These results are in accordance with the majority of the determinations of chlorophyll in various diploid and polyploid plants carried out by Dr. GYÖRFFY and published by PIRSCHLE 1941 (here additional literature).

II. Amphidiploids. The results from determinations of the rate of photosynthesis in leaves of diploid and corresponding amphidiploid *Solanums* are collected in table 10. It appears from the table that, in the case of the amphidiploid hybrid between

[1] The mean error has been calculated after the formula $m = \pm \frac{\sigma}{\sqrt{n \div 1}}$, in which σ is the standard deviation and n is the number of experiments.

Table 10.

Maximum rate of real assimilation in the leaves of diploid and corresponding amphidiploid *Solanums*. mg. CO_2 assimilated per 50 sq. cm. of leaf area per hour at 20° C. and normal pressure of carbon dioxide. Illumination 21900 BJ-Lux. (For rate of respiration, cf. Table 12.)

Plant No.	*Solanum gracile*	*S. gracile* × *S. insulae-pascalis*; amphidiploid	*S. insulae-pascalis*
1	9.1	8.5	9.4
2	8.9	8.7	8.3
3	6.6	11.2	10.2
4	7.5	5.8	—
5	—	11.2	—
Mean	8.0	9.1	9.3

Plant No.	*Solanum nigrum*	*S. nigrum* × *S. nitidibaccatum*; amphidiploid	*S. nitidibaccatum*
1	6.5	5.5	10.8
2	7.9	6.5	7.4
3	8.8	7.7	10.7
4	8.1	6.6	10.2
5	—	7.7	—
Mean	7.8	6.8	9.8

These experiments have been carried out by Dr. V. Romose.

S. nigrum and *S. nitidibaccatum*, the rate of photosynthesis of the amphidiploid was less than that of the parent species. In the case of *S. gracile* × *S. insulae-pascalis*, it was nearly equal to the one of the original species having the highest rate of photosynthesis, viz. *S. insulae-pascalis*.

D. Rate of Respiration.

The rate of respiration of the plant organs was determined by means of the same apparature as used for the determinations of photosynthesis; the plant material was kept in darkness.

Table 11.

Rate of respiration in various organs of *Solanum nodiflorum*, 2 *n* and 4 *n*.

Plant material		Date 1939	Number of days after transplantation to the field	mg of CO_2 given off per g. dry matter per hour at 16° C.	Relative rate of respiration (diploids = 100)
Roots	2 *n*	June 17	29	2.25	100
	4 *n*	June 17	29	1.72 } 1.56	69
	»	June 19	31	1.39 }	
Stems	2 *n*	June 17	29	2.52 } 2.68	100
	»	June 28	40	2.84 }	
	4 *n*	June 17	29	3.04 } 3.26	122
	»	June 28	40	3.47 }	
Leaves	2 *n*	June 22	34	3.06[1]	100
	4 *n*	June 19	31	1.90[1]	62
	2 *n*	Aug. 24	97	2.15	100
	4 *n*	Aug. 24	97	1.45	67
Reproductive organs	2 *n*	June 22	34	3.21	100
	4 *n*	July 3	45	3.38	105
	2 *n*	Aug. 24	97	1.79	100
	4 *n*	Aug. 25	98	1.91	107

[1] Regarding the rate of respiration per 50 sq. cm. leaf area at 20° C., cf. footnote of table 8.

I. Autotetraploids. The results of the determinations of respiration in *Solanum nodiflorum*, carried out at 16° C., are collected in table 11. It appears that the rate of respiration decreased somewhat during the period of vegetation in the diploids as well as in the tetraploids. Otherwise, it is seen from the table that no uniform relation exists between the rates of respiration of the organs of the diploid and the tetraploid plants. While the tetraploid stem in June is respiring at a rate by 22 per cent higher than that of the diploid, the rate of respiration in the roots and leaves of the tetraploids is only 69 and 62 per cent, respectively, of that of the diploids. In the reproductive organs, the rate of respiration in both cases is almost the same. From the rates of respiration and the weights of the individual organs per hectare, the loss of dry matter by

respiration per hectare may be calculated, the temperature being taken into account (cf. LARSEN 1941). From these figures, moreover, the rate of respiration of a whole plant may be calculated, and from the results, the average rate of respiration of a plant, for instance per g. dry matter, may be deduced. For a tetraploid plant, during the first 7 periods (until the middle of July), this quantity was on an average 79 per cent of that of a diploid. During the next month, when the percentage share of the reproductive organs increases, the tetraploid plants have an average rate of respiration of 87 per cent of that of the diploids; during the last part of the vegetation period, when the distribution of dry matter is still more shifted in favour of flowers and fruits which respire at a high rate in the tetraploids, too, the average rate of respiration is equal in both types of plant, the tetraploids respiring at a rate amounting to 99 per cent of that of the diploids.

In the rest of the experimental plants, the rate of respiration was measured in the leaves only, at a temperature of 20° C.

The rate of respiration in the leaves of *Sinapis alba*, cultivated in the Botanical Garden and used for the above mentioned experiments on photosynthesis, was in the diploids 0.60 and in the tetraploids 0.91 mg. CO_2 per 50 sq. cm. per hour. In this case, in contradistinction to *Solanum nodiflorum*, the tetraploid leaves respire at a higher rate. In order to verify this result, determinations were carried out on material from some unpublished experiments on *Sinapis* grown in glazed stoneware pots. According to these determinations, the rates of respiration in leaves of diploids and tetraploids were 0.50 and 0.62 mg. CO_2, respectively. In this case, too, the tetraploid plants show a higher rate of respiration than the diploids, calculated per unit area of leaf. If the latter values are calculated per g. of dry matter, the following rates of respiration will be reached, viz. 3.73 mg. CO_2 in the diploid and 5.07 mg. in the tetraploid leaves. Hence, the latter respire more intensely by 36 per cent.

Also in the leaves of tetraploid ferns examined by HEILBRONN (1933), a higher rate of respiration was found than in the diploids. Through an air current method according to PETTENKOFER, a difference of about 10 per cent was stated. By means of a manometrical procedure according to BARCROFT, on the other

Table 12.

Rate of respiration in the leaves of diploid and corresponding amphidiploid *Solanums*; mg. CO_2 given off per hour at 20° C.

	Solanum gracile	*S. gracile* × *S. insulae-pascalis*; amphidiploid	*S. insulae-pascalis*
per 50 sq. cm. leaf area	0.60	0.78	0.72
per g. dry matter	2.96	3.12	3.55
	Solanum nigrum	*S. nigrum* × *S. nitidibaccatum*; amphidiploid	*S. nitidibaccatum*
per 50 sq. cm. leaf area	0.64	0.53	0.84
per g. dry matter	2.83	2.15	4.18

These experiments have been carried out by Dr. V. Romose.

hand, it was determined to be 62 per cent. Now Heilbronn considers the figures, gained by the Pettenkofer method, the correct ones, because, the results obtained by the other method might have been disturbed by a traumatic stimulus which he

Table 13.

Ratio of the maximum rate of real assimilation of carbon dioxide to the rate of respiration (both per unit leaf area) in leaves of the amphidiploid plants and their parent species.

Solanum gracile	*S. gracile* × *S. insulae-pascalis*; amphidiploid	*Solanum insulae-pascalis*
13.3	11.7	12.9
Solanum nigrum	*S. nigrum* × *S. nitidibaccatum*; amphidiploid	*Solanum nitidibaccatum*
12.2	12.8	11.7

assumed to be the more active in the tetraploids. A detailed analysis of the causes of the deviating experimental results is, however, impossible.

II. Amphidiploids. The rate of respiration in the leaves of the amphidiploid plants and their parent species is given in table 12. The interrelation between these figures nearly corresponds to that of the rates of photosynthesis in the leaves of the same plants (table 10). As is seen from table 13, the ratio: rate of photosynthesis to rate of respiration per unit leaf area in all these plants is an almost constant quantity.

E. Size of Leaf Area.

The size of the leaf area per hectare is highly decisive for the absolute height of production of matter. It was determined on the majority of the experimental plants at each harvest. The procedure was as follows. A sample of leaves was drawn on paper with a known weight of area, the drawings of the leaves were cut out and weighed. When moreover the dry weight of the sample and the weight of living leaves per hectare are known, the total leaf area per hectare may be calculated.

I. Autotetraploids. The leaf area of *Solanum nodiflorum* is drawn in fig. 7. The leaf areas of the diploids and the tetraploids are almost equal during the whole period of vegetation.

In *Solanum gracile*, the proportion between the size of the leaf area of the diploids and the tetraploids changes in the course of the development (table 14). On the 38th day, the

Table 14.

Size of leaf area in *Solanum gracile*, $2n$ and $4n$; 1000 sq. m. per hectare.

Number of days after transplantation to the field	1	38	102
$2n$	0.18	2.37	10.20
$4n$	0.14	1.24	15.16

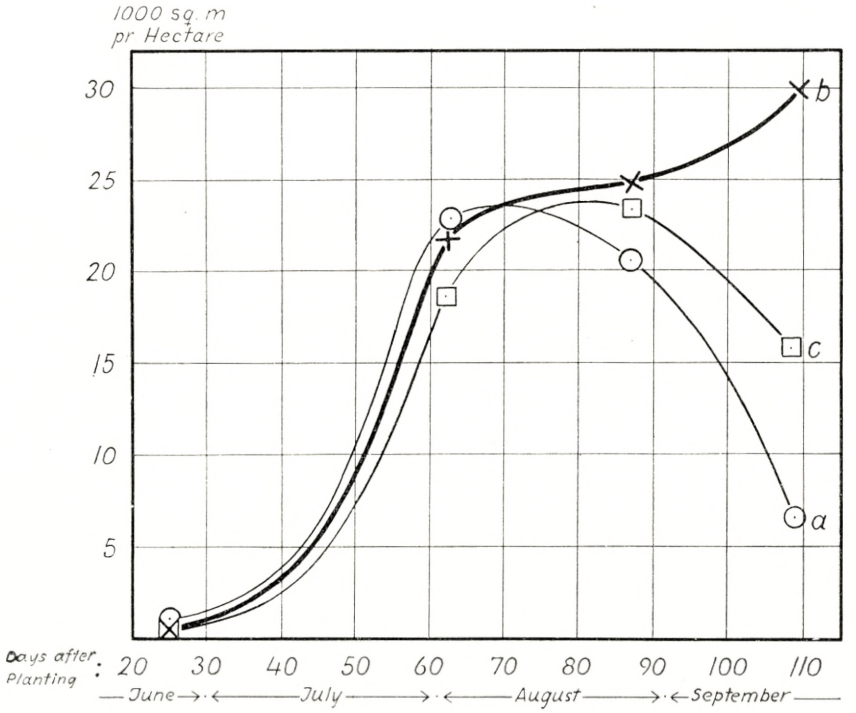

Fig. 18. Diploid and amphidiploid *Solanums*, grown in 1940. Size of leaf area. 1000 sq. m. per hectare.

a Solanum gracile.

b S. gracile × *S. insulae-pascalis*; amphidiploid.

c S. insulae-pascalis.

leaf area in the diploids is twice that of the tetraploids, on the 102nd day, however, the leaf area of the tetraploids is the larger one, viz. one and a half times that of the diploids.

II. Amphidiploids. The leaf areas of the amphidiploid plants and their original species are shown in figs. 18 and 19. It appears from the curves that the amphidiploid hybrid between *Solanum gracile* and *Solanum insulae-pascalis*, in contradistinction to the parent species, at the end of the experiment still possesses a large leaf area which is nearly twice that of *S. insulae-pascalis* and more than four times that of *S. gracile*. This involves the possibility of a longer period of vegetation which, in our lati-

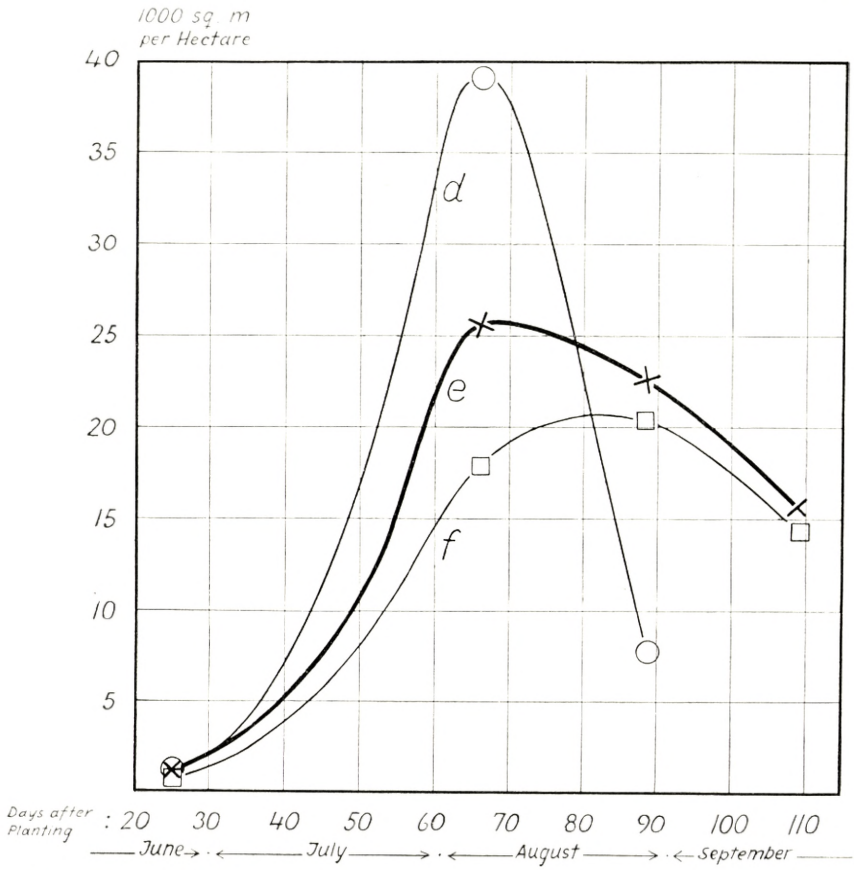

Fig. 19. Diploid and amphidiploid *Solanums*, grown in 1940. Size of leaf area. 1000 sq. m. per hectare.

d Solanum nitidibaccatum.

e S. nigrum × *S. nitidibaccatum*; amphidiploid.

f S. nigrum.

tude, however, soon comes to an end owing to the low temperatures in the autumn.

The leaf area of the other amphidiploid hybrid, *Solanum nigrum* × *Solanum nitidibaccatum*, is intermediate on the 66th day (fig. 19). One of the initial species, *S. nitidibaccatum* after that time sheds the majority of the leaves, while the hybrid and *S. nigrum* do so to a much less extent. At the end of the experiment, the leaf area of the hybrid is only 10 per cent larger than that of *S. nigrum.*

F. Relation between Rate of Photosynthesis and Production of Matter.

As the organic matter of the green plants is produced by photosynthetic assimilation of carbon dioxide, it might perhaps be expected that a proportionality should exist between the rate of photosynthesis and the production of dry matter. As is seen from table 15, this is, however, not the case. The cause hereof will appear from the following.

The yield of a plant stock (the net production) is the difference between the total yield of photosynthesis (the gross production) and the loss by respiration during the period in question:

Net production = gross production ÷ loss by respiration.

The magnitude of the gross production depends on the size of the leaf area and on the rate of photosynthesis per unit of leaf area. The loss by respiration is proportional to the respiring amount of plant and to the rate of respiration. The absolute magnitude of these quantities is of course dependent on the length of the vegetative period.

Table 15.

Comparison between production of dry matter and rate of photosynthesis in the experimental plants.

Year		Total production of dry matter; hkg. per hectare	Maximum rate of real assimilation; mg. CO_2 per 50 sq. cm. per hour
1939	*Solanum nodiflorum* 2*n*	50.9	12.5
	» » 4*n*	50.6	11.0
1940	*Solanum gracile* 2*n*	76.8	8.0
	» *insulae-pascalis* ... 2*n*	50.4	9.3
	S. gracile × *S. insulae-pascalis*; amphidiploid . 4*n*	75.3	9.1
1940	*Solanum nigrum* 2*n*	62.4	7.8
	» *nitidibaccatum* 2*n*	52.0	9.8
	S. nigrum × *S. nitidi-baccatum*; amphidiploid 4*n*	78.8	6.8

These facts must be taken into account if we want to compare the productivity of two or more plants, for instance a diploid and a tetraploid one. It is clear that a simple comparison of the rates of photosynthesis is not sufficient to decide, which of the plants concerned is the more capable of production. Even if the leaf area and the duration of vegetation are taken into account, the gross production only, and yet quite roughly, may be compared. Moreover, at an equally large gross production of two plants, very different amounts of dry matter may be stored as net production dependent on the rate of respiration and on the respiring amount of plant, the total loss by respiration during the season being of the same order of magnitude as the net production itself. Nor is the relation between assimilation and respiration decisive for the magnitude of production. HEILBRONN (1933 p. 431) stated: "Wenn also ein Organismus im Vergleich zu einem anderen pro Zeiteinheit vermehrte Trockensubstanz erzeugt, so muss das Verhältnis von Assimilation zur Dissimilation eine Verschiebung zugunsten der ersteren erfahren haben". This is not necessarily the case. If, for instance, assimilation as well as respiration are doubled, the proportion between these quantities will not be changed; the difference between them, which actually is the net production, will nevertheless be doubled. Hence, if the production capability of two types of plant has to be compared, the absolute magnitude of assimilation and of respiration must be calculated on the basis of measurements, at any rate for a short period, of the rate of photosynthesis, rate of respiration, leaf area, amount of plant substance, illumination, and temperature. Subsequently, the net productions gained by subtraction of these quantities may be compared. This method, however, is much more difficult than the simple statement of the production of dry matter, but it may lead to valuable informations as to the causes of possible differences in the production of dry matter in the plants in question. In this way, the production of matter of *Solanum nodiflorum* during the period of vegetation has been analyzed (cf. LARSEN 1941).

The investigations of photosynthesis and leaf area in the amphidiploid plants and the species compared with them permit

no detailed statements as regards the differences in their capability of production of matter; above all, because determinations of the respiration in various organs are lacking. In this series of experiments, the highest rate of photosynthesis is found in *Solanum nitidibaccatum* which, up to a given time, shows the largest total leaf area of all plants in question. In spite of these facts, the production of dry matter of this species is rather small, because the duration of its vegetation period is short.

G. Addendum.

During the present investigations, various results were gained which had no immediate connection with the production of matter. However, these results may be regarded as contributions to the characterization of the experimental plants. Some of these data will be mentioned in the present section.

It has often been stated that polyploid plants contain more water and less dry matter than normal plants. The dry matter content of various organs of autotetraploid *Solanums*, used in this investigation, relative to those of the diploids is given in table 16. The individual values of the absolute content of dry matter show a considerable variation due to the different wheather conditions on the days of harvest and due to the state of development. The ratio of the percentage content of dry matter in tetraploids and diploids, however, is fairly constant, and, therefore, this ratio is given in the table. It appears from the figures that the differences in *Solanum nodiflorum* (the average of 36 pairs of determinations), *Solanum gracile*, and *Solanum alatum* (6 pairs of determinations for each species) are quantitatively negligible. In *Solanum nigrum* (8 pairs of determinations), on the other hand, the content of dry matter of the tetraploids is lower, the content of water, consequently, being higher than in the diploids. The differences in the *water content*, however, will be very small. If the ratio of the percentage

Table 16.

Relative content of dry matter in autotetraploid *Solanums*, the content of the corresponding diploids = 100.

	Solanum nodiflorum	*Solanum gracile*	*Solanum alatum*	*Solanum nigrum*
Roots	96	96	104	86
Stems	101	101	101	86
Leaves	100	102		
Reproductive organs	98	92		

Table 17.

Relative content of dry matter in diploid and amphidiploid *Solanums*.

	Solanum gracile	*S. gracile* × *S. insulae-pascalis*; amphidiploid	*Solanum insulae-pascalis*	*Solanum nitidibaccatum*	*S. nigrum* × *S. nitidibaccatum*; amphidiploid	*Solanum nigrum*
Roots	130	117	100	86	105	100
Stems	124	102	100	66	103	100
Leaves	119	101	100	94	100	100
Reproductive organs	117	107	100	91	98	100

Table 18.

Comparison of the weight of the berries in the various experimental plants.

	Fresh weight per ripe berry		Dry weight per ripe berry		Number of berries in the sample
	mg.	relative	mg.	relative	
Solanum nodiflorum 2 *n*	232	100	43.6	100	94
» » 4 *n*	235	101	41.2	94	89
Solanum gracile 2 *n*	339	100	73.1	100	91
» » 4 *n*	197	58	34.3	47	56
Solanum gracile 2 *n*	339	90	73.1	134	91
S. gracile × *S. insulae-pascalis*; amphidiploid 4 *n*	522	139	87.4	160	67
Solanum insulae-pascalis 2 *n*	375	100	54.6	100	28
Solanum nigrum 2 *n*	459	100	95.8	100	247
S. nigrum × *S. nitidibaccatum*; amphidiploid 4 *n*	334	72	68.5	72	73
Solanum nitidibaccatum 2 *n*	257	56	52.9	55	201

of dry matter in two types of plant is, for instance, 100 to 85, this may correspond to a dry matter content of about 20 and 17 per cent of the fresh weight. Hence, the water content is 80 and 83 per cent, respectively, of the fresh weight.

Corresponding proportionals for the diploids and the amphidiploids examined are given in table 17. Each figure is the average of 6—8 pair of determinations. The content of dry matter is considerably higher in *Solanum gracile* than in *Solanum insulae-pascalis*. The dry matter content of the superterranean portions of their amphidiploid hybrid is almost the same as in *S. insulae-pascalis*, while the content of the roots is intermediate. In the other amphidiploid hybrid, the content of dry matter is almost th esame as in *Solanum nigrum*, being somewhat higher than in *Solanum nitidibaccatum* especially with respect to stems.

It would also be of interest to compare the size of the fruits of the various diploid and tetraploid strains. Table 18 gives the absolute and the relative average fresh weight and dry weight of the ripe berries. It appears from the table that the size of the berries in *Solanum nodiflorum* remained unchanged despite the doubling of the chromosome number, while in *Solanum gracile*, it decreased considerably. The amphidiploid hybrid beetween *Solanum gracile* and *S. insulae-*

Table 19.

Number of berries per hectare, *medio* September.

Year		Amount of reproductive organs per hectare; hkg. dry matter	Number of berries, (ripe + unripe), millions per hectare
1939	*Solanum nodiflorum* ... 2*n*	22.8	125.6
	» » ... 4*n*	21.0	101.5
1939	*Solanum gracile* 2*n*	14.04	39.6
	» » 4*n*	3.68	19.0
1940	*Solanum gracile* 2*n*	20.17	56.8
	S. gracile × *S. insulae-pascalis*; amphidiploid 4*n*	5.81	10.8
	Solanum insulae-pascalis 2*n*	5.38	13.2
1940	*Solanum nigrum* 2*n*	34.40	40.0
	S. nigrum × *S. nitidi-baccatum*; amphidi-ploid 4*n*	33.18	72.7
	Solanum nitidi-baccatum 2*n*	16.06	33.5

pascalis possesses berries, which are increased in size as compared to the parent species, while on the other hand the size of the berries in the second hybrid, *S. nigrum* × *S. nitidibaccatum*, is intermediate.

In order to make an estimation of the fertility of the various plants feasible, the number of berries per hectare is given in table 19. The calculation of these figures was based on the determinations of the weight of the reproductive organs per hectare (cf. figs. 8, 13, 16, and 17) in connection with counts of the berries per gram of dry matter in the reproductive organs. It must be emphasized that "reproductive organs" include, too, the flower stalks and the fruit stalks. The remarkable fertility of the tetraploid *S. nodiflorum* and of the amphidiploid hybrid between *S. nigrum* and *S. nitidibaccatum*, and the reduced fertility in the tetraploid *S. gracile* appear from the table. The figures would correspond still better to the fertility, if they were completed by counts of the number of seeds per berry. Examinations of this kind will be published by M. WESTERGAARD, Ph. D.

Summary.

The production of dry matter in stocks of some diploid and autotetraploid and also of diploid and amphidiploid forms of *Solanum* has been studied in field experiments. Moreover, the rates of photosynthesis and respiration as well as the development of leaf area have been compared in the experimental plants.

A. Autotetraploid Plants.

1. Setting the amount of dry matter of each of the diploid plant species at the end of the season equal to 100, the following relative amounts were found in the corresponding autotetraploids: *S. nodiflorum* 99, *S. gracile* 108, *S. alatum* 78, and *S. nigrum* 84. Hence, in *S. gracile*, only, a small excess was found in the tetraploids. In *S. nodiflorum*, the final result was practically the same in diploids and tetraploids. Otherwise, the capability of production of the tetraploids was smaller than that of the diploids (table 3 p. 19).

2. While the distribution over the individual plant organs of the matter produced was almost the same in $2n$ and $4n$ plants of *Solanum nodiflorum* (fig. 13), a considerable decrease in the production of berries and an increase in the production of stem and leaf were caused in *S. gracile* (fig. 8) and *S. nigrum* through the doubling of the chromosome number.

3. The relative rates of photosynthesis of diploid and tetraploid plants of *Solanum nodiflorum*, on an average, are as 100 to 89. Moreover, the variation is markedly greater in the tetraploids (table 8). (Also in *Sinapis alba*, (table 9), the rate of photosynthesis was found to be smaller in the tetraploids, viz. 85 per cent of that of the diploids.)

4. From May 20th until the middle of June, the average rate of respiration of a whole plant per gram of dry matter was in the tetraploid *Solanum nodiflorum* 79 per cent of that of the diploid; during the next month, this figure was 87 per cent and 99 per cent during the last part of the season.

5. The size of leaf area of the tetraploid *Solanum nodiflorum* was almost identical with that of the diploid during the whole season (fig. 7).—On the 38th day of vegetation, the leaf area of the diploid *Solanum gracile* was almost twice that of the tetraploid, on the 102nd day, however, the leaf area of the tetraploids was $1^1/_2$ times that of the diploids (table 14).

B. Amphidiploid Plants.

1. In the beginning, the amount of dry matter per hectare in the amphidiploid hybrid between *Solanum gracile* and *S. insulae-pascalis* was about the same as in the smaller of the parent species, viz. *S. insulae-pascalis*; however, during the development, it approached gradually that of *S. gracile*, finally becoming almost as high as in this plant (fig. 14 and table 7).—In the amphidiploid hybrid between *S. nigrum* and *S. nitidibaccatum*, the amount of dry matter per hectare during the last part of the experimental period was 25—35 per cent higher than in *S. nigrum*, and much higher than in *S. nitidibaccatum*, which species rather early stopped developing, although it grew very vigorously in the beginning (fig. 15 and table 7).

2. The amphidiploid hydrid between *Solanum gracile* and *S. insulae-pascalis* produced somewhat more stem than did the parent species. The production of berries was exactly that of *S. insulae-pascalis*, amounting to about one fourth, only, of that of *S. gracile* (fig. 16).—The amphidiploid hybrid between *S. nigrum* and *S. nitidibaccatum*, as compared with *S. nigrum*, has a greater production of root, stem, and leaf, while the production of

berries is equal. Compared with *S. nitidibaccatum*, it has twice the production of root and berries, while the production of stem and leaf in these plants is equally great (fig. 17).

3. The maximum rate of photosynthesis of the amphidiploid hybrid between *S. gracile* and *S. insulae-pascalis* was smaller than that of both original species; in the case of the amphidiploid hybrid between *S. nigrum* and *S. nitidibaccatum*, however, it was about the same as in the superior of the two parent species (table 10). The ratio of the maximum rate of photosynthesis of the leaves to that of the respiration of the leaves was about the same in all these plants (tables 12 and 13).

4. During the period of vegetation, the leaf area of the amphidiploid hybrid between *Solanum gracile* and *S. insulae-pascalis* increased continuously, in contradistinction to the original species, in which the leaf area at last had highly decreased (fig. 18). In *Solanum nigrum* and *S. nitidibaccatum* as well as in the amphidiploid hybrid between these species, a shedding of part of the leaves took place during the last part of the experimental period. This shedding was much more marked in *S. nitidibaccatum* than in the two other forms. In this case, too, the hybrid finally had a larger leaf area than any of the parent species (fig. 19).

C. Addendum.

The relative content of dry matter in the various plant organs and also the size and the number of fruits are given in tables 16—19.

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THE ASPECTS OF POLYPLOIDY IN THE GENUS SOLANUM

III: SEED PRODUCTION IN AUTOPOLYPLOID AND ALLOPOLYPLOID SOLANUMS

BY

M. WESTERGAARD

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I KOMMISSION HOS EJNAR MUNKSGAARD
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I. Material and Methods.

The present paper deals with the seed production in a number of *Solanum* species and their polyploid derivatives. The natural species all belong to the Morella group of the genus *Solanum* (basic chromosome number x = 12). The investigation comprises 7 monobasic species (2 n = 24), viz. *S. nodiflorum* Jacq., *S. nodiflorum* var. *dentatum* var. nov., *S. gracile* Otto, *S. Insulæ-pascalis* Bitter, *S. Dillenianum* Polgár, *S. adventitium* Polgár and *S. nitidibaccatum* Bitter; 9 dibasic species (2 n = 48), viz. *S. villosum* Lam., *S. flavum* Kit. in Reich., *S. miniatum* Bernh. in Reich., *S. alatum* Moench, *S. bengalensis* sp. nov., *S. curtipes* Bitter, *S. retroflexum* Dun., *S. rubrum* Mill. and *S. ochroleucum* Bast.; and finally 7 tribasic species (2 n = 72), viz. *S. nigrum* L., *S. nigrum* var. *chlorocarpum* (Spenn.) Boiss., *S. nigrum* var. *gracile* Raddi, *S. nigrum* var. *humile* (Bernh.) Boiss., *S. nigrum* var. *memphiticum* Mart., *S. Roberti-Eliae* Bitter and *S. Guineense* Lam.

The detailed morphology and the relationship of these species will be described elsewhere (C. A. JØRGENSEN, in course of publication). However, a brief outline of the classification of the material is necessary also in this paper: The monobasic species are fairly well defined. *S. adventitium* and *S. nitidibaccatum* are unable to cross with the other monobasic species. The others can be crossed with some difficulty, but the hybrids are sterile, except in the cross *S. nodiflorum* (or *S. nodiflorum* var. *dentatum*) × *S. gracile*, where the hybrids produce a few seeds. The hybrid between *S. nodiflorum* and *S. nodiflorum* var. *dentatum* is entirely fertile.—The dibasic species on the other hand are very closely related except for *S. retroflexum*, which also morphologically takes up a rather isolated position in this group, being the only dibasic species with black berries known to us. *S. retroflexum* crosses

only with difficulty with the other dibasic species and the fertility of the hybrids is rather poor. The other dibasic species cross readily, the hybrids are quite fertile and regular Mendelian segregations are recorded in F_2. Probably all these species should be considered varieties of *S. villosum*. The dibasic species can be crossed to all of the monobasic species except *S. adventitium* and *S. nitidibaccatum*. The hybrids are completely sterile.—The tribasic species are likewise closely related. However, *S. Guineense* and probably *S. Roberti-Eliae* are somewhat isolated from the *S. nigrum* types. Hybrids between *S. Guineense* and *S. nigrum* show reduced fertility and complicated segregations are recorded in F_2, in which also many sterile plants appear. *S. Roberti-Eliae* has not been crossed to the other tribasic species, but is morphologically rather closely related to *S. Guineense*.

Autotetraploids have been produced experimentally from all of the 7 monobasic species (2 n = 48 in the tetraploids), from 7 dibasic species (2 n = 96 in the tetraploids) and from 7 tribasic species or varieties (2 n = 144 in the tetraploids). Crossings between monobasic species with subsequent chromosome doubling of the hybrid produced 6 amphidiploids (2 n = 48). From crossings between monobasic and dibasic species, 24 amphidiploids were raised (2 n = 72). Chromosome doubling of the hybrids between monobasic and tribasic species resulted in 6 amphidiploids (2 n = 96), and crossings between tribasic S. *nigrum* types and the dibasic *S. villosum* and chromosome doubling of the hybrids gave two amphidiploids (2 n = 120). The material thus comprises 21 autotetraploids raised from three different chromosome levels and 39 amphidiploids representing four different chromosome levels. The chromosome doubling was induced by a combination of the callus method (JØRGENSEN 1928) and colchicine treatment. A detailed description of the experiments will follow in C. A. JØRGENSEN's paper.

For fertility determinations five typical plants from field plots have been selected and the total number of berries (ripe + unripe) was counted two or three times until the end of the growing season. The number of berries per plant (Tables 1 *a* and 1 *b*) is the average of these 5 plants. The number of seeds per berry (Table 2 *a* and 2 *b*) have been counted in 100 berries taken from typical plants and the average figure calculated. The number of berries

per plant multiplied by the number of seeds per berry gives the number of seeds per plant (Tables 2 *a* and 2 *b*). The seed weight is determined from the weight of 1000 seeds, and the seed weight multiplied by the number of seeds per plant is the seed weight per plant (Tables 4 *a* and 4 *b*).

II. Results.

Seed production in autopolyploids. Table 1 *a* shows that in all cases but one (no. 11, *S. alatum*) chromosome doubling results in reduced berry production. On an average, the berry production of the tetraploids of the monobasic group is 51 per cent of the diploid species. In the dibasic group the average is 55 per cent and in the tribasic group 32 per cent only; the tetraploid *S. nigrum* var. *memphiticum* is almost sterile and could not be propagated sexually.

In Table 2 *a* it should first be noted that there is no correlation between the seed number per berry and the chromosome level of the species. The two highest figures (nos. 2 and 21) are from a monobasic and a tribasic species, and the two lowest figures (nos. 14 and 7) from a dibasic and a monobasic species. In the monobasic group the average seed number per berry of the tetraploids is 44 per cent of the diploids, in the dibasic group 37 per cent of the fertility is recovered in the tetraploids and in the tribasic group 8 per cent only. The tetraploid S. *Guineense* produces a large number of big parthenocarpic berries without any seeds. The combined effect of the reduction in the number of berries and in the number of seeds per berry is a very drastic reduction in the fertility of the experimental polyploids as compared with the diploid species (Table 2 *a*, the last 3 columns). In the monobasic and the dibasic group 19 and 21 per cent, respectively, of the fertility of the diploids is on an average recovered, and in the tribasic group 4 per cent only is maintained.

Seed production in allopolyploids. In Tables 1 *b* and 2 *b* the seed production of the amphidiploids (designated 4 n, F_1) is compared with the diploid parent species. It should be kept in mind that the F_1 hybrids are completely sterile except for the hybrids *S. nodiflorum* (or *S. nodiflorum* v. *dentatum*) × *S. gracile* (nos. 23 and 25), which both had a few berries with approx-

Table 1 a.
Number of Berries per Plant, Autopolyploids.

Case no.	2 n*	Species	Berries per Plant		4 n in p.c. of 2 n
			2 n	4 n	
1	24	*S. nodiflorum*	2668	1066	**40**
2		*S. nodiflorum* v. *dentatum*	1462	781	**53**
3		*S. gracile*	1368	871	**64**
4		*S. Insulae-pascalis*	341	125	**37**
5		*S. Dillenianum*	296	16	**5**
6		*S. adventitium*	825	348	**42**
7		*S. nitidibaccatum*	1355	1036	**76**
8	48	*S. villosum*	1203	578	**48**
9		*S. flavum*	915	842	**92**
10		*S. miniatum*	853	459	**54**
11		*S. alatum*	1015	1326	**131**
12		*S. bengalensis*	845	425	**50**
13		*S. curtipes*	2065	814	**39**
14		*S. retroflexum*	2001	476	**24**
15	72	*S. nigrum*	1046	847	**81**
16		*S. nigrum* v. *chlorocarpum*	2826	982	**35**
17		*S. nigrum* v. *gracile*	1688	785	**47**
18		*S. nigrum* v. *humile*	1682	229	**14**
19		*S. nigrum* v. *memphiticum*	1617	+	**0**
20		*S. Roberti-Eliae*	1511	434	**29**

* Somatic chromosome number of the diploid species.

imately 6—7 seeds per berry, and the varietal hybrid *S. nodiflorum* × *S. nodiflorum* v. *dentatum* (no. 22), which gave 55 seeds per berry. One of the most striking features in these tables is the complete sterility of the hybrids *S. nodiflorum* × *S. villosum* (no. 29), *S. gracile* × S. *villosum* (no. 36), *S. gracile* × *S. curtipes* (no. 38) and *S. gracile* × *S. retroflexum* (no. 39). To this group of sterile amphidiploids should be added the hybrids, not recorded in the table, between *S. nodiflorum* and the dibasic species *S. rubrum*, *S. ochroleucum*, *S. flavum*, *S. miniatum* and *S. alatum*, all closely related to *S. villosum*, and those between *S. gracile* and *S. rubrum*, *S. ochroleucum*, *S. flavum*, *S. miniatum*, and *S. alatum*. However, these amphidiploids are only male sterile; in the *S. nodiflorum* hybrids the anthers are transformed into petals, and in the *S. gra-*

Table 1b.
Number of Berries per Plant, Allopolyploids.

Case no.	2 n*	Cross ♀ × ♂	Berries per Plant			4 n, F_1 in p.c. of	
			2 n ♀	2 n ♂	4n, F_1	2 n ♀	2 n ♂
23	48	*S. nodiflorum* × *S. gracile*	2668	1368	267	**10**	**20**
24		*S. nodifl.* × *S. Dillenianum*	2668	296	274	**10**	**93**
25		*S. gracile* × *S. nod.* v. *dentatum*	1368	1462	267	**20**	**18**
27		*S. Insulae-pasc.* × *S. nod.* v. *dentatum*	341	1462	550	**161**	**38**
30	72	*S. nodiflorum* × *S. bengalensis*	2668	845	1747	**65**	**207**
31		*S. nodiflorum* × *S. curtipes*	2668	2065	767	**29**	**37**
32		*S. nodiflorum* × *S. retroflexum*	2668	2001	106	**4**	**5**
33		*S. nod.* v. *dent.* × *S. bengalensis*	1462	845	2194	**150**	**260**
34		*S. nod.* v. *dent.* × *S. curtipes*	1462	2065	1116	**76**	**54**
35		*S. nod.* v. *dent.* × *S. retroflexum*	1462	2001	1722	**118**	**86**
36		*S. gracile* × *S. villosum*	1368	1203	+	**0**	**0**
37		*S. gracile* × *S. bengalensis*	1368	845	46	**3**	**5**
38		*S. gracile* × *S. curtipes*	1368	2065	73	**5**	**4**
39		*S. gracile* × *S. retroflexum*	1368	2001	+	**0**	**0**
40		*S. Insulae-pascalis* × *S. curtipes*	341	2065	1271	**373**	**62**
41		*S. Insulae-pascalis* × *S. retroflexum*	341	2001	952	**279**	**48**
42		*S. Dillenianum* × *S. curtipes*	296	2065	768	**259**	**37**
43	96	*S. nigrum* × *S. nodiflorum*	1046	2668	459	**44**	**17**
44		*S. nigrum* × *S. nod.* v. *dentatum*	1046	1462	702	**67**	**48**
45		*S. nigrum* × *S. gracile*	1046	1368	824	**79**	**60**
46		*S. nigrum* × *S. Insulae-pascalis*	1046	341	616	**59**	**181**
47		*S. nigrum* × *S. nitidibaccatum*	1046	1355	938	**90**	**69**
48		*S. nig.* v. *chlorocarp.* × *S. nitidibac.*	2826	1355	1242	**44**	**92**
49	120	*S. nigrum* × *S. villosum*	1046	1203	820	**78**	**68**
50		*S. nig.* v. *chlorocarp.* × *S. villosum*	2826	1203	424	**15**	**35**

* Somatic chromosome number of the amphidiploid (4 n, F_1)

cile hybrids the anthers contain 100 per cent abortive pollen. When pollinated with diploid *Solanum* species with the same chromosome number, these amphidiploids are fertile on the female side (the amphidiploid *S. gracile* × *S. villosum* for instance, when pollinated with *S. nigrum*, gave 24 seeds per berry).

When the fertile amphidiploids only are considered, the berry production of the polyploids, as seen in Table 1 *b*, is generally

Table 2 a.
Number of Seeds per Plant, Autopolyploids.

Case no.	2 n	Species	Seeds per Berry		4 n in p.c. of 2 n	Seeds per Plant		4 n in p.c. of 2 n
			2 n	4 n		2 n	4 n	
1	24	*S. nodiflorum*	59	27	**46**	157412	28782	**18**
2		*S. nod.* v. *dentatum*	88	34	**39**	128656	26554	**21**
3		*S. gracile*	45	12	**27**	61560	10452	**17**
4		*S. Insulae-pascalis*	52	26	**50**	17732	3250	**18**
5		*S. Dillenianum*	73	24	**33**	21608	384	**2**
6		*S. adventitium*	46	43	**93**	37950	14964	**39**
7		*S. nitidibaccatum*	23	3	**13**	31165	3108	**10**
8	48	*S. villosum*	39	12	**31**	46917	6936	**15**
9		*S. flavum*	37	13	**35**	33855	10946	**32**
10		*S. miniatum*	43	15	**35**	36679	6885	**19**
11		*S. alatum*	42	14	**33**	42630	18564	**44**
12		*S. bengalensis*	45	21	**47**	38025	8925	**23**
13		*S. curtipes*	48	18	**38**	99120	14652	**15**
14		*S. retroflexum*	21	9	**43**	42021	4284	**10**
15	72	*S. nigrum*	60	7	**12**	62760	5929	**9**
16		*S. nig.* v. *chlorocarpum*	46	8	**17**	129996	7856	**6**
17		*S. nigrum* v. *gracile*	46	2	**4**	77648	1570	**2**
18		*S. nigrum* v. *humile*	44	5	**11**	74008	1145	**2**
19		*S. nigrum* v. *memphiticum*	44	+	**0**	71148	+	**0**
20		*S. Roberti-Eliae*	56	8	**14**	84616	3472	**4**
21		*S. Guineense*	84	+	**0**	?	+	**0**

much lower than in the diploid parents. In 6 cases, however, (nos. 27, 35, 40, 41, 42, 46) the berry production of the hybrid is higher than in one of the parental species; in 4 of these cases *S. Insulae-pascalis* was one of the parents. In one case (no. 33) the amphidiploid produced more berries than any of the parents. The seed number per berry (Table 2 *b*) is also generally much lower in the amphidiploids than in the parents, but in two cases (nos. 35 and 41) the berries of the hybrid had more seeds than one of the parental species, viz. *S. retroflexum*. The seed production per plant is also much lower in the amphidiploid than in the diploid parental species except in 4 cases (nos. 35, 40, 41, 42, all tribasic amphidiploids), where the experimentally produced

Table 2 b. Number of Seeds per Plant, Allopolyploids.

Case no.	2 n	Cross ♀ × ♂	Seeds per Berry			F_1 in p.c. of		Seeds per Plant			4 n, F_1 in p.c. of	
			2 n ♀	2 n ♂	4 n, F_1	2 n ♀	2 n ♂	2 n ♀	2 n ♂	4 n, F_1	2 n ♀	2 n ♂
22	48	*S. nodiflorum* × *S. nod.* v. *dentatum* ...	59	88	41	**69**	**47**	..	..	..	..	..
23		*S. nodiflorum* × *S. gracile*	59	45	25	**42**	**56**	157412	61560	6675	**4**	**11**
24		*S. nodiflorum* × *S. Dillenianum*	59	73	25	**42**	**34**	157412	71608	6850	**4**	**32**
25		*S. gracile* × *S. nod.* v. *dentatum*	45	88	27	**60**	**31**	61560	128656	7290	**12**	**6**
26		*S. Insulae-pascalis* × *S. nodiflorum*	52	59	14	**27**	**24**	..	..	..	..	..
27		*S. Insulae-pasc.* × *S. nod.* v. *dentatum* ..	52	88	25	**48**	**28**	17732	128656	13750	**78**	**11**
28		*S. Insulae-pascalis* × *S. gracile*	52	45	27	**52**	**60**	..	..	..	..	..
29	72	*S. nodiflorum* × *S. villosum*	59	39	0	**0**	**0**	157412	46817	0	**0**	**0**
30		*S. nodiflorum* × *S. bengalensis*	59	45	19	**32**	**42**	157412	38025	33193	**21**	**87**
31		*S. nodiflorum* × *S. curtipes*	59	48	16	**27**	**33**	157412	99120	12272	**8**	**12**
32		*S. nodiflorum* × *S. retroflexum*	59	21	6	**10**	**29**	157412	42021	636	**0.4**	**2**
33		*S. nod.* v. *dent.* × *S. bengalensis*	88	45	13	**15**	**29**	128656	38025	28522	**22**	**75**
34		*S. nod.* v. *dent.* × *S. curtipes*	88	48	23	**26**	**48**	128656	99120	25668	**20**	**26**
35		*S. nod.* v. *dent.* × *S. retroflexum*	88	21	26	**30**	**124**	128656	42021	44772	**35**	**107**
36		*S. gracile* × *S. villosum*	45	39	+	**0**	**0**	61560	46917	0	**0**	**0**
37		*S. gracile* × *S. bengalensis*	45	45	9	**20**	**20**	61560	38025	+	**0**	**0**
38		*S. gracile* × *S. curtipes*	45	48	+	**0**	**0**	61560	99120	+	**0**	**0**
39		*S. gracile* × *S. retroflexum*	45	21	+	**0**	**0**	61560	42021	+	**0**	**0**
40		*S. Insulae-pascalis* × *S. curtipes*	52	48	26	**50**	**54**	17732	99120	33046	**186**	**33**
41		*S. Insulae-pascalis* × *S. retroflexum*	52	21	30	**58**	**143**	17732	42021	28560	**161**	**68**
42		*S. Dillenianum* × *S. curtipes*	73	48	35	**48**	**73**	21608	99120	26880	**124**	**27**
43	96	*S. nigrum* × *S. nodiflorum*	60	59	15	**25**	**25**	62760	157412	6885	**11**	**4**
44		*S. nigrum* × *S. nod.* v. *dentatum*	60	88	15	**25**	**17**	62760	128656	10530	**17**	**8**
45		*S. nigrum* × *S. gracile*	60	45	23	**38**	**51**	62760	61560	18952	**30**	**31**
46		*S. nigrum* × *S. Insulae-pascalis*	60	52	10	**17**	**19**	62760	17732	6160	**10**	**35**
47		*S. nigrum* × *S. nitidibaccatum*	60	23	22	**37**	**96**	62760	31165	20636	**33**	**66**
48		*S. nig.* v. *chlorocarp.* × *S. nitidibac.*	46	23	21	**46**	**91**	129996	31165	26082	**20**	**84**
49	120	*S. nigrum* × *S. villosum*	60	39	8	**13**	**21**	62760	46917	6560	**10**	**14**
50		*S. nig.* v. *chlorocarp.* × *S. villosum*	46	39	7	**15**	**18**	129996	46917	2968	**2**	**6**

plants are more fertile than one of the parents. In one case, no. 35, this is due to the hybrid producing more seeds per berry than the parent, in the three remaining cases an increased berry production per plant is responsible for the increased fertility.

If the seed production of the amphidiploids is compared with the average production of the two parental species ((♀ + ♂): 2), the 4 dibasic hybrids (nos. 23, 24, 25, 27) on an average produce 9 per cent of the parents. If the sterile amphidiploids are omitted from the tribasic group, the synthetic amphidiploids on an average produce 31 per cent as compared with the parents. In the tetrabasic group 20 per cent of the fertility is maintained, and in the two pentabasic hybrids 7 per cent only.

Comparison between autotetraploids and amphidiploids. The present material offers a very good opportunity of comparing the effect of autopolyploidy versus allopolyploidy on fertility, because in a number of cases the seed production of the amphidiploid can be compared with that of the autotetraploids of both parental species. These cases are grouped in Table 3. In 5 cases (nos. 23, 25, 31, 32, 50) the amphidiploid produces less seeds than any of the two autotetraploids. To this group should be added the sterile amphidiploids between *S. nodiflorum* or *S. gracile* and the dibasic *S. villosum* types, these sterile amphidiploids not being included in Table 3. In 6 cases the seed production of the amphidiploid is intermediate between the two autotetraploids (nos. 24, 27, 34, 43, 44, 49) and in the remaining 10 hybrids (nos. 30, 33, 35, 40, 41, 42, 45, 46, 47, 48) the fertility of the amphidiploid is higher than in any of the autotetraploids, in some cases (especially nos. 35, 40, 41, 42, 45, 47, 48) even very much higher.

Seed weight per plant (Tables 4*a* and 4*b*). Chromosome doubling causes a considerable increase in the weight of the seeds in all cases, and the increase is especially pronounced in some of the amphidiploids. However, in the autotetraploids the increased seed weight cannot compensate for the reduction in seed number, and the seed production of the tetraploids, even when measured by weight, is much inferior to the diploid species; in two cases only, it amounts to more than 50 per cent of the diploids (nos. 6 and 11). In the amphidiploids on the other hand, one of the hybrids yields a higher seed weight than any

Table 3.

Comparison between Seed Production of Autopolyploids and Allopolyploids.

Case no.	2 n	Cross ♀ × ♂	4 n ♀	4 n in p.c. of 2 n ♀	4 n ♂	4 n in p.c. of 2 n ♂	4 n, F_1	4 n, F_1 in p.c. of	
								2 n ♀	2 n ♂
1-3-23	48	*S. nodiflorum* × *S. gracile*	28782	18	10452	17	6675	4	11
1-5-24		*S. nodiflorum* × *S. Dillenianum*	28782	18	384	2	6850	4	32
3-2-25		*S. gracile* × *S. nod.* v. *dentatum*	10452	17	26554	21	7209	12	6
4-2-27		*S. Insulae-pasc.* × *S. nod.* v. *dent.*	3250	18	26554	21	13750	78	11
1-12-30	72	*S. nodiflorum* × *S. bengalensis*	28782	18	8925	23	33193	21	87
1-13-31		*S. nodiflorum* × *S. curtipes*	28782	18	14652	15	12272	8	12
1-14-32		*S. nodiflorum* × *S. retroflexum*	28782	18	4284	10	636	0.4	2
2-12-33		*S. nod.* v. *dent.* × *S. bengalensis*	26554	21	8925	23	28522	22	75
2-13-34		*S. nod.* v. *dent.* × *S. curtipes*	26554	21	14652	15	25668	20	26
2-14-35		*S. nod.* v. *dent.* × *S. retroflexum*	26554	21	4284	10	44772	35	107
4-13-40		*S. Insulae-pasc.* × *S. curtipes*	3250	18	14652	15	33046	186	33
4-14-41		*S. Insulae-pasc.* × *S. retroflexum*	3250	18	4284	10	28560	161	68
5-13-42		*S. Dillenianum* × *S. curtipes*	384	2	14652	15	26880	124	27
15-1-43	96	*S. nigrum* × *S. bengalensis*	5929	9	28782	18	6885	11	4
15-2-44		*S. nigrum* × *S. nod.* v. *dentatum*	5929	9	26554	21	10530	17	8
15-3-45		*S. nigrum* × *S. gracile*	5929	9	10452	17	18952	30	31
15-4-46		*S. nigrum* × *S. Insulae-pascalis*	5929	9	3250	18	6160	10	35
15-7-47		*S. nigrum* × *S. nitidibaccatum*	5929	9	3108	10	20636	33	66
16-7-48		*S. nig.* v. *chlorocarp.* × *S. nitidibac.*	7856	6	3108	10	26082	20	84
15-8-49	120	*S. nigrum* × *S. villosum*	5929	9	6936	15	6560	10	12
16-8-50		*S. nig.* v. *chlorocarpum* × *S. villos.*	7856	6	6936	15	2968	2	6

Table 4 a.
Seed Weight per Plant, Autopolyploids.

Case no.	2 n	Species	Weight of 1000 Seeds		4 n in p.c. of 2 n	Seed Weight per Plant		4 n in p.c. of 2 n
			2 n gms.	4 n gms.		2 n gms.	4 n gms.	
1	24	*S. nodiflorum*	0.23	0.31	**135**	36.2	8.9	**25**
2		*S. nodiflorum* v. *dent.*	0.35	0.57	**163**	45.0	15.1	**34**
3		*S. gracile*	0.45	0.67	**149**	27.7	7.0	**25**
4		*S. Insulae-pascalis*...	0.37	0.47	**127**	6.6	1.5	**23**
5		*S. Dillenianum*.....	0.47	0.69	**147**	10.2	0.3	**3**
6		*S. adventitium*.....	0.47	0.63	**134**	17.8	9.4	**53**
7		*S. nitidibaccatum*....	1.23	1.68	**137**	38.3	5.2	**14**
8	48	*S. villosum*.....	1.25	1.70	**136**	58.6	11.8	**20**
10		*S. miniatum*	1.24	1.74	**140**	45.5	12.0	**26**
11		*S. alatum*	1.12	1.46	**130**	47.7	27.1	**57**
12		*S. bengalensis*.....	0.83	1.10	**133**	31.6	9.8	**31**
13		*S. curtipes*	0.81	0.91	**112**	80.3	13.3	**17**
14		*S. retroflexum*.....	1.06	1.60	**151**	44.5	6.9	**16**
15	72	*S. nigrum*.....	0.88	1.28	**145**	55.2	7.5	**14**
17		*S. nigrum* v. *gracile*..	1.23	1.70	**138**	95.5	2.7	**3**
18		*S. nigrum* v. *humile*..	1.14	1.82	**160**	84.4	2.1	**2**
20		*S. Roberti-Eliae*	0.90	1.13	**141**	76.2	3.9	**5**

of the diploid parents (no. 35), and in 6 cases the yield of the amphidiploid is higher than in one of the parents (nos. 27, 30, 40, 41, 42, 46). In one case the seed weight is almost 6 times as high in the hybrid as in the parent (no. 40, where the amphidiploid gives 38.8 gms. per plant as against 6.6 gms. in the parental species *S. Insulae-pascalis*).

In Table 5 the seed weight of the amphidiploids is compared with that of the experimentally raised tetraploids of the two parental species (cf. Table 3). In three cases the yield is lower in the hybrid than in both tetraploids (nos. 23, 25, 32), in 6 cases it is between the tetraploids (nos. 24, 27, 31, 43, 44, 49), and the 10 remaining hybrids give a higher yield than any of the two tetraploids. In most of these cases the yield is very much higher—about three times as high—as in the tetraploids.

Table 4 b.

Seed Weight per Plant, Allopolyploids.

Case no.	2 n	Cross ♀ × ♂	Weight of 1000 Seeds			F_1 in p.c. of		Weight per Plant			4 n, F_1 in p.c. of	
			2 n ♀ gms.	2 n ♂ gms.	4 n, F_1 gms.	2 n ♀	2 n ♂	2 n ♀ gms.	2 n ♂ gms.	4 n, F_1 gms.	2 n ♀	2 n ♂
22		*S. nodiflorum* × *S. nod.* v. *dentatum* ...	0.23	0.35	0.52	**183**	**149**	..	..	..	..	..
23		*S. nodiflorum* × *S. gracile*	0.23	0.45	0.69	**300**	**153**	36.2	27.7	4.6	**13**	**17**
24		*S. nodiflorum* × *S. Dillenianum*	0.23	0.47	0.69	**300**	**147**	36.2	10.2	4.7	**13**	**46**
25	48	*S. gracile* × *S. nod.* v. *dentatum*	0.45	0.35	0.60	**133**	**171**	27.7	45.0	4.3	**16**	**10**
26		*S. Insulae-pascalis* × *S. nodiflorum*	0.37	0.23	0.53	**143**	**230**	..	..	..	..	..
27		*S. Insulae-pasc.* × *S. nod.* v. *dentatum*..	0.37	0.35	0.55	**149**	**157**	6.6	45.0	7.6	**115**	**17**
28		*S. Insulae-pascalis* × *S. gracile*	0.37	0.45	0.68	**184**	**151**	..	..	..	..	..
30		*S. nodiflorum* × *S. bengalensis*	0.23	0.83	0.96	**417**	**116**	36.2	31.6	31.9	**88**	**101**
31		*S. nodiflorum* × *S. curtipes*	0.23	0.81	0.96	**417**	**119**	36.2	80.3	11.8	**33**	**15**
32		*S. nodiflorum* × *S. retroflexum*	0.23	1.06	1.02	**443**	**96**	36.2	44.5	0.6	**2**	**1**
33		*S. nod.* v. *dent.* × *bengalensis*.....	0.35	0.83	1.03	**294**	**124**	45.0	31.6	29.4	**65**	**93**
34	72	*S. nod.* v. *dentatum* × *S. curtipes*	0.35	0.81	0.95	**271**	**117**	45.0	80.3	24.4	**54**	**30**
35		*S. nod.* v. *dent.* × *S. retroflexum*	0.35	1.06	1.20	**343**	**113**	45.0	44.5	53.7	**119**	**121**
40		*S. Insulae-pascalis* × *S. curtipes*	0.37	0.81	1.16	**314**	**143**	6.6	80.3	38.3	**580**	**48**
41		*S. Insulae-pasc.* × *S. retroflexum*.....	0.37	1.06	1.21	**327**	**114**	6.6	44.5	34.6	**524**	**78**
42		*S. Dillenianum* × *S. curtipes*	0.47	0.81	1.31	**279**	**162**	10.2	80.3	35.2	**345**	**44**
43		*S. nigrum* × *S. nodiflorum*	0.88	0.23	1.06	**120**	**461**	55.2	36.2	7.3	**13**	**20**
44		*S. nigrum* × *S. nod.* v. *dentatum*	0.88	0.35	1.14	**130**	**326**	55.2	45.0	12.0	**22**	**27**
45	96	*S. nigrum* × *S. gracile*.....	0.88	0.45	1.27	**144**	**282**	55.2	27.7	24.1	**44**	**87**
46		*S. nigrum* × *S. Insulae-pascalis*.....	0.88	0.37	1.25	**142**	**338**	55.2	6.6	7.7	**14**	**117**
47		*S. nigrum* × *S. nitidibaccatum*.....	0.88	1.23	1.64	**209**	**133**	55.2	38.3	33.8	**61**	**88**
49	120	*S. nigrum* × *S. villosum*	0.88	1.25	1.70	**173**	**124**	55.2	58.6	11.2	**20**	**19**

Table 5.

Comparison between Seed Weight of Autopolyploids and Allopolyploids.

Case no.	2 n	Cross ♀ × ♂	4 n ♀ gms.	4 n ♀ in p.c. of 2 n ♀	4 n ♂ gms.	4 n ♂ in p.c. of 2 n ♂	4 n, F_1 gms.	4 n, F_1 in p.c. of	
								2 n ♀	2 n ♂
1-3-23	48	*S. nodiflorum* × *S. gracile*	8.9	**25**	7.0	**25**	4.6	**13**	**17**
1-5-24		*S. nodiflorum* × *S. Dillenianum*	8.9	**25**	0.3	**3**	4.7	**13**	**46**
3-2-25		*S. gracile* × *S. nod.* v. *dentatum*	7.0	**25**	15·1	**34**	4.3	**16**	**10**
4-2-27		*S. Insulae-pascalis* × *S. nod.* v. *dentatum*	1.5	**23**	15.1	**34**	7.6	**115**	**17**
1-12-30	72	*S. nodiflorum* × *S. bengalensis*	8.9	**25**	9.8	**31**	31.9	**88**	**101**
1-13-31		*S. nodiflorum* × *S. curtipes*	8.9	**25**	13.3	**17**	11.8	**33**	**15**
1-14-32		*S. nodiflorum* × *S. retroflexum*	8.9	**25**	6.9	**16**	0.6	**2**	**1**
2-12-33		*S. nod.* v. *dentatum* × *S. bengalensis*	15.1	**34**	9.8	**31**	29.4	**65**	**93**
2-13-34		*S. nod.* v. *dentatum* × *S. curtipes*	15.1	**34**	13.3	**17**	24.4	**54**	**30**
2-14-35		*S. nod.* v. *dentatum* × *S. retroflexum*	15.1	**34**	6.9	**16**	53.7	**119**	**121**
4-13-40		*S. Insulae-pascalis* × *S. curtipes*	1.5	**23**	13.3	**17**	38.3	**580**	**48**
4-14-41		*S. Insulae-pascalis* × *S. retroflexum*	1.5	**23**	6.9	**16**	34.6	**524**	**78**
5-13-42		*S. Dillenianum* × *S. curtipes*	0.3	**3**	13.3	**17**	35.2	**345**	**44**
15-1-43	96	*S. nigrum* × *S. nodiflorum*	7.5	**14**	8.9	**25**	7.3	**13**	**20**
15-2-44		*S. nigrum* × *S. nod.* v. *dentatum*	7.5	**14**	15.1	**34**	12.0	**22**	**27**
15-3-45		*S. nigrum* × *S. gracile*	7.5	**14**	7.0	**25**	24.1	**44**	**87**
15-4-46		*S. nigrum* × *S. Insulae-pascalis*	7.5	**14**	1.5	**23**	7.7	**14**	**117**
15-7-47		*S. nigrum* × *S. nitidibaccatum*	7.5	**14**	5.2	**14**	33.8	**61**	**88**
15-8-49	120	*S. nigrum* × *S. villosum*	7.5	**14**	11.8	**20**	11.2	**20**	**19**

III. Discussion.

A more thorough discussion of these data will be postponed until the final paper in this series of publications, when all the cytological and experimental data are available, because one of the most interesting problems, *viz.* the cause of the reduced fertility of the polyploids, must be discussed in relation to meiotic behaviour and pollen formation of the plants.

However, the following general conclusions from the above data may be briefly commented on: The reduction in the fertility of the experimentally produced autotetraploids (Table 2 *a*) is due to a reduction in the berry production as well as to a decreased number of seeds per berry. In the tribasic group only, this reduction is strongly correlated with the chromosome number of the diploid species, whereas in the monobasic and dibasic groups there is a great variation in seed reduction not correlated with chromosome number. The two monobasic species *S. adventitium* and *S. nitidibaccatum* are less fertile than any of the other monobasic or dibasic species. In the first type the reduction is due to a decreased number of berries per plant, whereas in *S. nitidibaccatum* a low number of seeds per berry is the cause. It can be said already that this difference cannot be explained as due to visible meiotic differences between the different types. Hence the effect of chromosome doubling on the fertility of the tetraploids depends upon the genotypic constitution of the diploid more than upon the chromosome number, at least when this is not too high.

In the amphidiploids the fact that some of the artificial, constant hybrids are more fertile than one of the parental species is very important. In all these cases the hybrid has resulted from a cross between two diploid species which show a great difference in seed production. Unfortunately, due to the sterility of the F_1 hybrids, the genetic background of this difference cannot be analysed, but there is good reason to assume that it is under control of polygenes. On the other hand, not all crosses between high and low diploid seed producers resulted in superior amphidiploids, the most striking examples being the sterile amphidiploids in which the very high seed producers *S. nodiflorum* or *S. gracile* are involved. Hence the result again first and fore-

most depends upon the general genotypic constitution of the diploid parents and upon how far the two genomes can harmonize in the hybrid, whereas the meiotic behaviour of the amphidiploids is of secondary importance only. Fertility and sterility are to be explained in genetic terms rather than on a cytological basis, as emphasised by MÜNTZING (1943).

On the basis of this assumption it is not difficult to explain that the amphidiploids are not always more fertile than the autotetraploids (Table 3). In the latter case only one step is involved in the production of the new type, and we are dealing with the same genes as were present in the diploid species. Amphidiploidy on the other hand involves two steps, crossing and chromosome doubling, and the result is therefore likely to be more uncertain.

The problems of the fertility of the artificial polyploids is of great importance for the practical plant breeder, who in recent years on an increasing scale has devoted his attention to experimental polyploids in his breeding work. The fact that it is possible to produce amphidiploids which give a higher yield than one of the diploid parents, and in one case even a higher seed weight than any of the diploid parents, is indeed very encouraging and points towards amphidiploids rather than autopolyploids as material for producing superior plants. However, the utilisation of the autopolyploids and of most amphidiploids will depend upon the extent and speed with which it will be possible to improve their fertility by selection. That such an improvement is possible, and actually has taken place, under the influence of natural selection, is obvious from the fact that the polybasic natural *Solanum* species as well as many other polybasic plant species are as good or even superior seed producers as the monobasic species. However, we do not know whether this process takes thousands of generations or only a few, or how much it can be speeded up by artificial selection. In this laboratory some of the *Solanum* polyploids have been under cultivation for at least 15 generations. No attempts have been made to improve the fertility by selection and there is no indication that the seed production has actually increased. For instance, JØRGENSEN (1928) counted 40—50 seeds per berry in the diploid *S. nigrum* and 10—15 in the tetraploid. The corre-

sponding figures in my investigations are 60 seeds in 2 n and 8 in 4 n *S. nigrum*. The amphidiploid *S. nigrum* × *S. villosum* (*S. luteum* in JØRGENSEN's paper) had 8—11 seeds per berry in 1927 as against 8 in the present investigations. On the other hand other authors have obtained encouraging results in improving the fertility of both autotetraploids (*Zea mays*, RANDOLPH 1941, *Galeopsis*, MÜNTZING 1943, *Secale*, MÜNTZING 1948) as well as amphidiploids (for instance *Triticale*, MÜNTZING 1948) by selection.

IV. Summary.

The seed number and the seed weight per plant have been investigated in a number of *Solanum* species and their artificially produced polyploid derivatives (21 autopolyploids and 39 amphidiploids).

All the autotetraploids produce less than 50 per cent of the seeds of the diploid species. Most of the amphidiploids produce less seeds than any of the diploid parental species, but a few produce more seeds than one of the parents. In one case an amphidiploid yielded a higher seed weight than any of the diploid parents. A group of amphidiploids are completely male-sterile.

A comparison between the seed production of an amphidiploid and that of the autotetraploids of the two parental species shows (Tables 3 and 5) that in some cases the allopolyploid is inferior to the autotetraploids, in others, the fertility of the hybrid is intermediate between that of the two tetraploids, and in others again, the amphidiploid produces more seeds than any of the two related autopolyploids.

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V. Literature.

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DET KGL. DANSKE VIDENSKABERNES SELSKAB

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THRIPS POLLINATION IN *CALLUNA*

BY

O. HAGERUP

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I KOMMISSION HOS EJNAR MUNKSGAARD
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1. Bee Pollination.

In Danish nature perhaps there is no plant the flowers of which may be pollinated in so many different ways as those of *Calluna*. Nearly all the commonest ways of pollination may be found realized in nature.

The heather flowers have both fragrance and honey and attract both man and insects. Hence they are nearly always surrounded by swarms of insects of many different species. The commonest visitors, however, are honey-bees and humble-bees, which with great industry collect the fine aromatic honey, which again is an article much desired by man.

The importance of the visit of the insects to the pollination appears so obvious that hardly anybody will think of doubting it. Still I came to doubt the necessity of the bees' visit during various stays in the Faroes (particularly in 1922—23 and 1947), where there are neither bees nor butterflies in so large a number that they can play any important part to the pollination of *Calluna*. In spite of careful investigation I did not succeed in seeing any large insects visiting the flowers. And still all flowers produced fruits with ripe seeds, and seedlings were of common occurrence in nature in the Faroes.

Visits by the usual large insects thus cannot be necessary to the pollination. But how, then, is the *Calluna* flower pollinated with the automatic certitude with which it takes place in nature? And is the visit by the bees more or less superfluous?

It is important for the pollination that the style should be so long that it projects outside the flower in a similar way as in many anemophilous flowers. This means that the stigma is easily touched by visiting insects. On the other hand the length of the style also makes it difficult for the insects to put their heads into the flowers, thus touching the anthers, which

are short and nearly completely confined in the remarkably small corolla.

When bees and other insects with long proboscises visit the flowers they mostly keep at a suitable distance from it and extend

Fig. 1. *Calluna*. Flowering shoot from the Faroes. × 3.
Fig. 2. *Taeniothrips ericae* pollinating a flower (Denmark). × 12.
Fig. 3. *Erica cinerea* (the Faroes). Longitudinal section of flower-bud in self-pollination immediately before flowering × 12.

the proboscis to its full length. The proboscis is then inserted in the flower from its lower side (L in fig. 6), where there is the greatest space between the corolla and the stamens.

Hence the proboscis is often the only part of the insects which comes into direct contact with the anthers, but this smooth,

thin organ is badly suited for receiving and retaining pollen and carrying it to other flowers.

On the other hand, the proboscises of the insects are rarely (or never?) inserted in the space (M, Q) between style and anthers. And at the bottom of this space a material part of the nectary (N) is hidden and thus inaccessible for the sucking of honey. In a cross-section of the flower (fig. 4) it appears that the nectary has a similar form as a cog-wheel, the anthers being placed in the spaces between the cogs. Only the tips of the cogs can be touched direct by the insects, and here some of the honey oozes out into the bottom of the corolla, which therefore is sticky, and there is always some pollen there.

The anthers split open along the side almost at the same time as the corolla opens; but as the anthers are placed very close together with the sides pressed against each other, very little pollen is liberated at a time. And during the whole flowering period there is constantly some pollen encased in the anthers, and almost everywhere in the interior of the flower some pollen may be found.

However, remarkably little pollen is seen on the insects that have visited *Calluna* only. And the proboscises that have touched the anthers as a rule do not get into contact with the stigmas.

Because of the mentioned structural feature of the flower the visit by the insects is hardly of any appreciable value to the pollination. *Calluna* may even completely do without visits by bees and butterflies (in the Faroes) and still be pollinated with automatic precision.

2. Wind Pollination.

If a person walks through a dense vegetation of flowering *Calluna*, his feet will be powdered with a fine layer of pollen. Also when it is windy, fine clouds of pollen are shaken out of the flowers.

Hence there is hardly any reason for doubting that the flower under certain circumstances can be pollinated by the wind.

But this way of pollination, too, may be uncertain, e. g. during a prolonged period of rain, for in this case the stigma will soon

get wet, so that it can hardly receive pollen, and much pollen shaken into the air will be caught by the raindrops and beaten to the ground, where it perishes.

These drawbacks about wind pollination are particularly conspicuous in the Faroes, where there may at any time be protracted periods with violent rain. I have myself witnessed that it has been raining for five days in succession without any intervals. In such a case probably most of the pollen available will be shaken out of the flowers and be spoiled. And still the fructification is perfect also in the Faroes. Hence there must be securer ways of pollination of the flowers than by the aid of insects and the wind.

3. Self-Pollination.

In *Erica cinerea* (Fig. 3), which in the Faroes is growing together with *Calluna*, the flowers are self-pollinating: the anthers open immediately before the flowers come out, and pollen falls direct on to the stigma, which is also ripe at this early stage. When at length the beautiful hanging flower opens, it emits fragrance, and there is also plenty of honey present; but a possible visit by insects is without any importance to the flower at all, as it has already been pollinated.

In *Calluna* the anthers also open while the flower is in bud. But at this stage the stigma is not yet ripe for being pollinated. Only when the flower has opened (fig. 1), the stigma reaches its full length and then protrudes far out of the flower so that the stigma cannot get into direct contact with the anthers, from which a little pollen is constantly emitted into the air.

Some of the pollen thus liberated will probably be able to hit upon the flower in question itself or neighbouring flowers, i. e. provided that e. g. the very capricious weather of the Faroes does not prevent this somewhat uncertain way of pollination.

But as the flowers are placed so close together, wind-pollination is no doubt more effective than insect pollination, and many flowers inevitably receive pollen produced by themselves.

However, if the plant had exclusively to content itself with wind pollination, the consequence would undoubtedly be that many flowers were not pollinated, as is the case in e. g. *Empetrum*.

4. *Thrips* Pollination.

The above-mentioned three ways of pollination thus all involve a certain uncertainty. As, however, as mentioned, the pollination takes place with automatic certainty, the plant must dispose of other, more certain methods of pollination. But which? In order to obtain an answer to this question I examined the plant in the Faroes in 1947 throughout a flowering season and later supplemented the observations made by investigations in various places in Denmark.

Already Nordhagen discovered and described the curious way in which the corolla opens. This is pressed outwards because it grows very much in thickness at its base, where a circular pad ($A_1 - A_2$ in fig. 6) arises. The inspissation, however, is greatest on the lower side of the corolla (at A_1), the latter thus getting distinctly zygomorphic.

The filaments are just as curious as the corolla, being thin and band-shaped at their bases (figs. 4—6) so that a hinge is formed by which the filament may be moved towards or away from the style.

In the flower not yet full-blown the filament is of nearly the same thickness in its whole length (fig. 5); but when the corolla opens, this is to some degree due to a pressure from the bases of the filaments, these suddenly growing very fast in thickness as indicated by the dotted line in fig. 5. The inspissated part of the filament (U in fig. 6) is situated immediately above the thin hinge mentioned and opposite to the thick pad on the corolla. All these inspissations arise by the cells of the subepidermal layers of cells increasing their volume very considerably.

In a longitudinal section of the flower (fig. 6) it is seen that the inspissations in anthers and corolla are also situated nearly opposite to the thickest part of the ovary. The tensions arising mean that the lower parts of the filaments in the full-blown flower are squeezed very firmly into a definite position, viz. so that the anthers are closely united with their sides against each other. And as the anthers open at the sides (fig. 5) the tense position of the stamens causes that little pollen may be liberated at a time, the possibilities of pollination thus covering a comparatively prolonged period. The upper halves of the filaments, how-

ever, are both thin and S-shaped. Hence the anthers may be tilted to and fro so that the passage between style and anthers is not barred to small insects; but I have never seen large insects sticking their proboscises inside the stamina down to the part of the nectary concealed inside these (N in fig. 6), which is obviously reserved for particularly small insects.

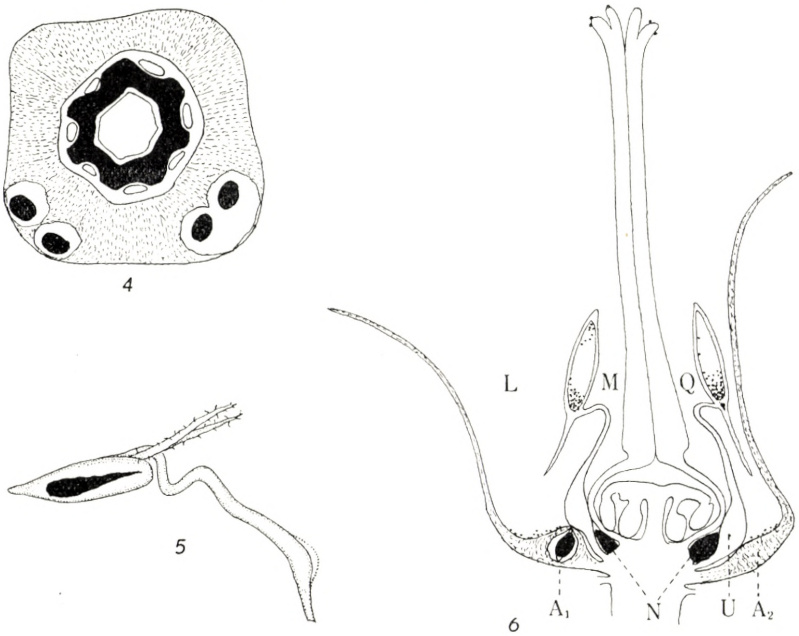

Fig. 4. *Calluna*. Transverse section of old flower with four ova (black) of *Taeniothrips ericae* at the (hatched) base of the corolla. Nectary black. The Faroes. × 15.

Fig. 5. Stamen from bud. × 18.

Fig. 6. Longitudinal section of flower (the Faroes) with ova of *Thaeniothrips ericae* (at A_1) in the (hatched) base of the corolla. A_1—A_2: inspissated pad. N: nectary (black). The proboscis of a bee is inserted at L on the lower side of the flower. At M and Q *Taeniothrips* forces its way down to the nectary. × 15. For further details see text.

On the basis of experiences gained in Danish nature as regards pollination I searched during the flowering season in 1947 in the Faroes for large insects which might play a quantitatively significant part to the everywhere abundant fructification in *Calluna*; but all searching continued being in vain day by day. The riddle could not be solved by any of the usual channels.

The only insects which were common on the Faroese *Calluna* were some remarkably small *Thrips*; but these were only about

1 mm. in length and very slender. A priori it would seem impossible that such small creatures should be able to play the role of a large humble-bee; nor has such a view been advanced in the literature.

However, these small creatures constantly obtruded upon my attention when I examined the flowers; for they were always present, often several (up to 4—6) crawling in a single flower. In spite of their small size I was gradually forced to take the animals seriously and to subject their doings in the flowers to a more detailed examination.

It is not difficult to observe these *Thrips* closely in a magnifying-glass. They are unwilling to leave the flowers even if these are shaken in a collecting box on a long excursion in the mountains. Likewise they are particularly stationary during rain and gales when they have a really good hiding-place at the bottom of the bell-shaped corollas, which because of their position, small size and narrow entrance are not filled with rain-water. I have had flowers of *Calluna* steeped in water (to which was added a little formalin) for three years without any water entering the corollas and the (dead) *Thrips* lying in there.

The corollas do not only offer an ideal hiding-place to these insects during the frequent Faroese storms, but there the *Thrips* may constantly and undisturbed perform their other life functions, both—as we shall see below—eating, copulating, and laying ova at a time when the other types of pollination fail.

Thrips are lively animals, which are constantly moving about the inner parts of the flower, and because of their small size they can even easily crawl into the narrow space between style and stamina (M and Q in fig. 6), where the proboscises of larger insects, as said above, will not go. In this room at the base of the style the animals thus may be sitting quite unmolested, sucking off the whole surface of the nectary (black in figs. 4 and 6), which cannot be touched by bigger insects. Bees can only collect the honey which through the spaces between the bases of the stamens seeps into the bottom of the corolla, but as regards bees a direct contact with the nectary can only take place on the fine tips of the cogwheel-shaped nectary (fig. 4).

However, what is of special interest in this connexion is the fact that *Thrips* cannot reach down to their favourite haunts on

the nectary without touching the anthers, which are just giving off pollen at the same time as the nectary secretes honey. As mentioned above, the anthers open at the sides (fig. 5), but these are set together so closely that very little pollen may be given off at a time, and this particularly takes place when the anthers are pressed apart, as is just the case when a *Thrips* squeezes down into the narrow space between style and stamina. A direct examination actually shows that pollen may be found everywhere on the visiting *Thrips*. The small insects transport few pollen grains at a time, it is true, but then only a small number of ovules (about 20) are found in the ovary, and hence about 5—6 tetrads will be sufficient to fertilize a flower, a quantity of pollen small enough for being easily transported by one *Thrips* at one visit only.

What particularly causes the insects periodically to be restless and to move about not only between the sexual leaves of a single flower, but also to fly about from flower to flower, is the fact that the individuals of one sex—the males—are apterous and comparatively rare, so that the females have to roam about to seek out the males.

Hence it is quite a normal thing to observe a female which has stayed so long on the nectary that it has eaten its fill in its hiding-place inside the filaments. It is now sexually mature, and if it has not been fertilized it will leave the nectary to search for a male, which takes place in the following characteristic way: (1) It leaves its place on the nectary (N in fig. 6), and from here there is generally only one beaten path, which the insect mostly follows slavishly by (2) crawling along the tubular channel (M, Q) between stamens and style. By squeezing through this narrow passage the insect cannot avoid touching the anthers and receiving pollen.

(3) The insect now naturally continues its way along the style, like so many other insects wanting to seek out as spacious a starting-place as possible, where it can freely unfold its wings without these striking against neighbouring objects.

(4) As a matter of fact it is difficult for *Thrips* to get the four wings clear of each other and have them unfolded, because along their edges they are densely set with a fringe of long stiff hairs which clutch each other so that the wings function as if

they were glued together. Hence the insect often sits on the stigma, bending its abdomen up and down in order thus to disengage the pair of wings. During these efforts the insect trips to and fro above the stigma in order to find the most favourable position for its start (Fig. 2). These manœuvres to make the wings ready to start take some time and offer rich opportunities for the pollen which the insect carries with it to be shaken off on the stigma or even be pressed direct on to its sticky surface.

In short, the *Thrips* uses the style in the very same way as the starling utilizes the perch of a starling-box. And exactly in the most spacious place of the flower is the stigma. It has not been possible to see whether arriving insects land on the stigma, too; but during the roaming of the insects both in the flower and from flower to flower, they must be able to transport pollen from the flower in question itself as well as pollen from other flowers and pollinate the stigma with it.

(5) After the vegetative period of the insect on the hidden parts of the nectary the copulation follows, and soon the time approaches when the *Thrips* is to deposit its ova. In these last phases of the insect's life it generally stays outside the stamens at the bottom of the corolla. Here it again takes nourishment, both by sucking honey from the same sources as are utilized by possible bees, but also by gnawing at the juicy tissue which is particularly well developed in the lower parts of the corolla. This tissue formerly served to open the corolla. Now it has been smeared with nectar. Further there are still numerous pollen grains which have stuck in the viscous nectar, and the viscous pollen sticks to the insects when they move about this favourite haunt of theirs and occasionally creep over the anthers on to the stigma in order, perhaps, to attempt a fresh start to another flower.

The juicy tissue which is eaten by the *Thrips* is found not only in the above-mentioned pad (A_1 and A_2 in fig. 6), but also at the base of the stamens (see fig. 5—6). Hence it is often seen that the insects simply fell the stamens by gnawing through the bases of them, which are particularly attractive by being smeared with honey. These overturned stamens particularly easily give off pollen, part of which is caught in the honey, from where it thus may be transported to the stigma.

(6) The *Thrips* does not even leave the flower when it is

going to deposit its ova. But the symbiosis between the insect and *Calluna* is so thorough that the insect sticks its short and sharp ovipositor into the thickest, soft tissue of the corolla, immediately into the above-mentioned pad (A_1 and A_2 in fig. 6), which is the only place in the corolla that affords room for the comparatively large ova.

Calluna is one of the few plants indigenous to Scandinavia the corollas of which generally remain on the plant until the next year. These withered flowers thus contain the ova of the insects that may pollinate the flowers of the coming season. It is true that some of the withered flowers fall to the ground during the following winter, but mostly they remain under the plants in the dense vegetation so that the hidden ova are not removed very far. As regards the flowers which remain on the plants until next year, the tender larvae thus are hatched close to the place where they may spend the rest of their life until oviposition and death.

A series of longitudinal sections through an insect which has stayed inside the stamens showed that the abdomen contained four ova only. And series of transverse-sections through flowers (fig. 4) which had begun withering, further showed that the ova are deposited in pairs in small chambers in front at the base of the corolla, where there is most space. Here the insects remain, safe and independent of storms. They cannot be chased away by an obtrusive proboscis of a bee, and the oviposition may be observed direct through a magnifying-glass. Perhaps the individual insect may lay more than one hatch of ova.

The development of the insect from ovum to imago is not known in detail. The larvae, however, are found in the flowers (together with the imagos), where they move about and also transport pollen so that they may contribute their share to the pollination. Preisner (1926) assumes that the pupation takes place on the ground under the plants, from where the imagos of the *Thrips* after hibernation emerge next summer, when the flowering season approaches. In the Faroes the imagos were already found in the flowers which had come out first. Preisner found the first females as early as May and the last in November. This late occurrence only indicates that *Calluna* is in bloom much later in Southern Europe than in Scandinavia.

It would be interesting to investigate to how high a degree the curious conditions of symbosis between *Calluna* and *Thrips* may be generalized. J. Maltbæk states that all the Faroese *Thrips* belonged to the species *Taeniothrips ericae* Holiday. It is also this species which dominates in the Danish *Calluna*, but here we may also find interspersion of other species (e. g. *Franklini-ella intonsa* Trybom). *T. ericae* is "common in West Jutland, but also elsewhere in Jutland and North Zealand in regions with heath and bog". Its existence is closely connected with

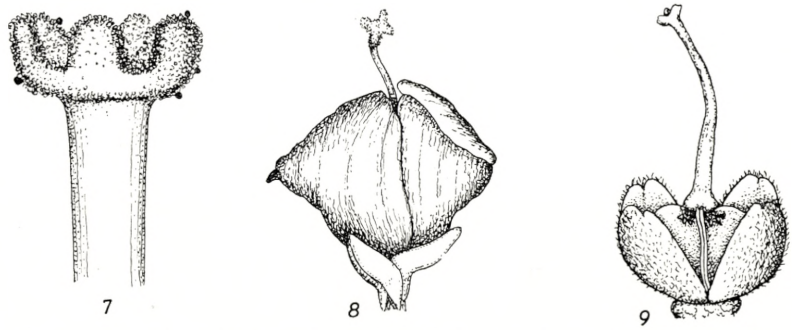

Fig. 7. Stigma with few tetrads pollinated by *Taeniothrips*. The Faroes. × 50.
Fig. 8. Hibernated flower. The Faroes. × 7.
Fig. 9. Hibernated, empty fruit. The Faroes. × 7.

Calluna, even though it also may be found on other plants, particularly such, however, as belong to the *Ericaceae*.

T. ericae is distributed from Northern Iceland to the Mediterranean and from Russia to England (Preisner), thus with a similar distribution as *Calluna* (Nordhagen).

In other species of *Thrips* parthenogenesis is common, and in some species males are even completely unknown.

The fact that *Thrips* are of importance as dispersers of pollen is both recorded in the literature and easy to observe in many different flowers.

Dr. A. Löve has found *T. ericae* in abundance in Iceland, where bigger pollinating insects are absent. Both here and in the Faroes this small insect obviously is one of the conditions that *Calluna* is found at all in the place in question, as both wind- and self-pollination will fail in most normal years because of the climate. Further, if there were no *Calluna* in the Faroes the sheep would

starve to death in unfavourable winters, which again would mean a catastrophe to the population. The Faroes (literally 'the Sheep Islands') would not either have been given this name about a thousand years ago.

The fact that the insect may also occasionally be observed on other plants only indicates the vagabondizing tendencies of this lively animal, which again are due to its search for food and for the other, wingless sex (the males). I have myself found *Thrips* on *Erica*. It should be investigated whether the insect may also deposit its ova in the hibernating corollas of this plant.

Altogether the importance of the various species of *Thrips* to pollination ought to be investigated in more detail. As an illustration of this wish *Silene acaulis* may be mentioned. In the Faroes, where this species is generally distributed, single tufts are often found removed from other individuals. Even when such individuals are purely female, they do set abundant fruit although there are no pollinating insects upon them other than *Thrips*. In a number of *Compositae*, *Armeria* and many others as well, it seems that the flowers may be pollinated by *Thrips*. J. Grøntved further has found many *Thrips* in regions in Greenland poor in insects, where the flowers generally seem to be thrown upon self-pollination.

Hence, continued investigations of the doings of the other *Thysanoptera* in other flowers might open a new chapter in the biology of pollination.

A generalization from morphological points of view seems particularly natural within *Bicornes*, most species of which have stamens reminding of those of *Calluna* by forming a narrow tube encircling both style and nectary, which is accessible just to such small insects as *Thrips*. Hence it should be investigated whether e. g. our native species may occasionally or mostly be pollinated by *Thrips* and, if so, where these insects deposit their ova in the case of the species the corollas of which are dropped immediately after the flowering season. Similarly the flowers of many *Compositae* seem to be adapted to *Thrips* pollination because the nectary in these, too, is hidden at the bottom of a very narrow tube into which only very small insects may squeeze.

It should, however, be emphasized that the way in which a plant is pollinated may change greatly from place to place and

from year to year. *Calluna* is a particularly fine illustration showing how cautious one should be as regards generalizing within floral biology.

The winter of 1946—47 was so unfavourable to the hibernation of *Calluna* that a considerable number of the old plants died in the greater part of Scandinavia. In the few flowers which developed the next summer (1947) there was a nearly normal number of *Thrips*, as some of the ova obviously had been destroyed with the plants killed.

The following summer (1948) the heather had already succeeded in regenerating because the youngest individuals had been able to stand the unfavourable winter. Hence there was a rich flowering in 1948; but now there was a deficiency of *Thrips* because these deposit comparatively few ova and no doubt require several years to reach a normal number of individuals again, which may be of importance to the pollination. However, there were (1948) abundant visits by bees, and hence the stigmata were densely filled with pollen (in Denmark); but at the same time *Calluna* is referred to *Thrips*- or wind-pollination in other regions where larger insects are missing or are rare.

For the further understanding of the value of the various methods of pollination I isolated a flowering plant under glass so that neither wind nor insects might cause pollination. None of the numerous flowers then set fruit.

Other individuals were planted in the open, but 1 km. from the nearest *Thrips* locality. These were pollinated by wind and bees and set abundant fruit.

Hence it follows that *Calluna* cannot fructify without pollination and that according to external conditions pollination may take place either by (1) wind, (2) bees, (3) butterflies, or (4) *Thrips*. According to circumstances the flowers are pollinated by pollen originating from the same flower or from other flowers; but a direct contact between anthers and stigma is unknown. From a genetic point of view, however, the pollination of *Calluna* in many cases must be designated as autogamy.

Summary.

Calluna may be pollinated in many different ways. The one which may be observed most easily is bee-pollination; but this method of pollination fails completely in some regions, e. g. in the Faroes, where large pollinating insects are absent.

In (probably the whole of) the area of distribution of *Calluna* the flowers, however, may be pollinated by a very small insect (*Taeniothrips ericae*), which even deposits its ova in the swollen base of the corolla (figs. 4—6). The stamens form a tube at the bottom of which the greater part of the nectary is hidden in so narrow a room that only very small insects may squeeze in there.

In the corolla the insect seeks shelter (from storms), food, and a breeding-ground. In return it pollinates the flower by creeping on to the stigma (fig. 2), from where the winged females mostly start when flying away from the flower, e. g. in search of the wingless and rarer males.

Without this curious symbiosis there would hardly be any *Calluna* and hence hardly any sheep in the Faroes and other northern regions.

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RAIN-POLLINATION

BY

O. HAGERUP

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
1950

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1. The Problems.

It is a well-known fact that rainy weather may have a very injurious effect on many flowers. The fructification becomes poor and many flowers may be completely ruined during showers of rain because petals are beaten off, stamens and styles rot, and pollen is spoilt and washed away while at the same time visits by insects are prevented.

In nature finer flowers (e. g. those of grasses) may be injured by rain in a similar way as flowers in gardens. In the literature there is plenty of information about such structural features as serve to protect flowers from the injurious influence of rain.

All these questions forced themselves upon me during a year's stay in the Faroes (1922—23), where it is raining—little or much—on most of the days of the year. I have even witnessed that it has been raining incessantly there for five days running. Thus the flowers of the wild plants must be able to stand the rain without the fructification being prevented. In 1947 the Carlsberg Foundation again enabled me to study in the Faroes, where conditions of pollination are much simpler than in Denmark, because the usual big pollinating insects (bees, butterflies) are practically absent. Further the abundance of rain gives good occasion to investigate how the flowers behave in the kind of weather which tempts the floral biologist to keep indoors. Later the observations made in the Faroes were supplemented by studies in Denmark.

The available information of the injuriousness of the rain perhaps might even seem to be in too good agreement; for indeed it is fact that numerous wild flowers are completely open even during the heaviest showers of rain, so that one may ask about the usual injurious effects on e. g. the beautiful abundance

of *Caltha* on Danish meadows when a violent thunder-shower sheds so much water that the open flowers may be filled with water several times. When the storm is over the flowers still appear to have got unhurt through this event, which e. g. to the blossoms of apples and cherries has proved a catastrophe.

Thus there must be some way in which certain flowers may hold their own through showers of rain. But how, then, are these protected from destruction, e. g. in other climates where it is raining much more frequently than in this country? Indeed, some aquatic plants (e. g. *Zostera*) are normally pollinated by

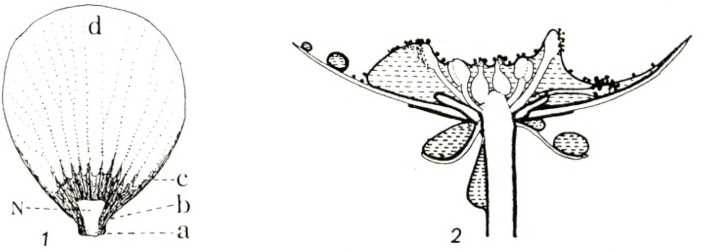


Fig. 1. *Ranunculus repens*. Corolla from the upper surface. N: nectary; a—c: area binding water; in the curve, b, part of the outlet is found; c—d: nonabsorbent area. × 3. Denmark.

Fig. 2. *Ranunculus flammula*. Longitudinal section of flower. Rain-water dotted and with fat contour. On the surface of the water pollen is floating to the stigmas. Surplus water is drained off through the outlet at the bottom. The Faroes. × 5. See further the text.

means of the water. Might it be possible, after all, that some of the terrestrial plants were able to be pollinated by means of rain?

If on a normal spring day one approaches a Faroese settlement, the problems of the rain often arise at once, because the small brooks are bordered by a vivid yellow fringe of *Caltha* on which the rain is pouring down. Later it appears that all the flowers have still been normally pollinated and numerous seeds float on the violently rushing water. The pastures round the houses, too, have a yellowish tinge, originating from the numerous *Ranunculus* flowers, which are not either injured by the rain. And on the untilled parts of the mountains yellow spots of *Narthecium* are seen, the flowers of which are wide open and turned towards the rain. This species, too, fructifies abundantly.

In what follows a few examples will be adduced which go to show how flowers can manage all right in the rain without

having their pollen washed away and spoilt. But beyond having this purely defensive and passive task to perform, some flowers also prove to have a positive faculty of utilizing the rain in the service of pollination.

2. *Ranunculus.*

Among most European peoples the buttercups enjoy a remarkably great popularity, which is reflected in numerous picturesque vulgar names. In the Faroes the flowers thus are called "Sun-eye", which name does not only refer to the colour of the corolla, but also to the bright and glossy surface of the latter, a special quality which is not found to such a pronounced degree in any others of our wild plants. Hence the question naturally arises whether the glossiness of the corolla should somehow be of use to the flower. If one tries to drip water into fresh flowers, it appears at once that the petals are markedly nonabsorbent. The water gathers in nearly spherical drops, which soon trickle down the more or less obliquely upward turned glossy petals until they come to rest at the bases of these.

If one takes a fresh petal and dips it into water, it proves that it is not equally nonabsorbent on the whole of its surface. On the upper side there is at the base a scale which covers a nectary. Here the water is bound very strongly, while the rest of the upper side is the most nonabsorbent part of the corolla.

On its lower side the corolla is also distinctly nonabsorbent on the whole of its outermost broad part; but at the base a darker part is seen (fig. 1), which has a dull surface that binds the water. This curious base is situated immediately above the sepals, for which reason a small room thus forms between calyx and corolla where rain-water may be kept by capillary action.

A stamen is nonabsorbent except at its base and in the places were the anther has opened. Hence pollen is easily washed away from the stamen when it is raining, and water and pollen are distributed among the numerous stamens at the bottom of the flower.

Further, ripe stamens may bend outward and downward when the petals are moist on the upper side. Then they generally lie down right on the surface of the water, which is soon filled

with floating pollen, this being rapidly distributed everywhere in the interior of the flower where there is any water, e. g. between the bases of the stamens and on the petals. At new supplies of rain-water the stranded pollen is again whirled round in the interior of the flower.

In the young flowers the carpels are nonabsorbent at their tips. The flower is then particularly susceptible to insect pollination. But at that time there is little chance of self-pollination, because the youngest stamens, which are closest to the gynaecium, are not yet open, and hence cannot place their pollen direct on the stigmas.

In the fully developed flowers the gynaecium, however, easily gets moist in rainy weather. If a small drop of water is placed on one side of a gynaecium, it is in few minutes sucked down between the carpels, and the water then may be observed direct between these. This absorption of water thus does not take place momentarily as in filter paper. If the water is placed at the base of the gynaecium, where the stamens are situated, it is particularly easily absorbed, as the axis of the flower binds it just at the bases of the stamens. The normal direction of the water in the gynaecium thus is from below upwards; but below we just find pollen floating on the surface of the absorbed water.

If a drop of water is placed on the tip of the gynaecium, it is absorbed slowly between the carpels. This water will not be of any great value to the pollination, either, because it carries no pollen.

The drops of rain which hit the tip of the gynaecium are soon thrown towards the sides by the shakings produced by both wind and rain. Thus pollen may come to float on the water, which is rapidly absorbed between the stamens and soon ends at the bottom of the flower, where it is united with the pollen-bearing water already found there, which is drawn up between the bases of the carpels and further up to the stigmas by capillary action.

The curious capillary absorption of water in the gynaecium is conditioned by the form of the carpels and their mutual position, as illustrated in figs. 2, 3, 4, and 8 (where the paths of the water are indicated by dots). The carpels are placed close together; but still there are quite small channels between their

edges (figs. 4 and 8). Particularly wide are the spaces at the bases of the carpels, where the water may rise along the axis of the flower. From these mains the water flows out through the narrow passage along the inward turned edges of the carpels (fig. 4), but exactly here is the lowest part of the stigma (figs. 3 and 8).

The adhesion of the water to the carpels is facilitated by small fixed glands in the surface of the carpels. These are particularly conspicuous in *R. sardous.*

If this curious flower is exposed to a heavy rain which hits all the parts of the flowers, the open anthers are nearly completely

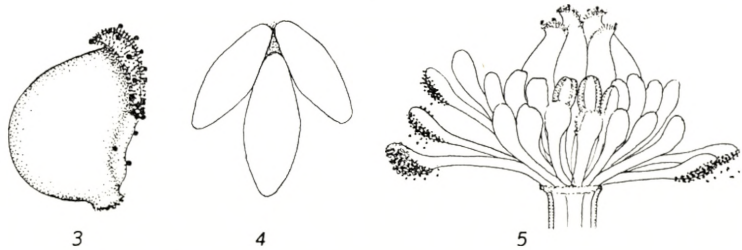


Fig. 3. *Ranunculus bulbosus.* Carpel. × 12. Denmark.
Fig. 4. *Ranunculus bulbosus.* Cross-section of three carpels; path of the water dotted. × 17. Denmark.
Fig. 5. *Caltha palustris.* Flower without petals. × 4. The Faroes.

opened and pollen is flung aside and on to the water at the bottom of the flower, where it floats on the surface, which rises more and more. If the water could fill the flower completely so that it overflowed, the pollen would get lost by being washed away. The flower must have some protection from this catastrophe to the pollination; for during continued rain the amount of water may be so great that all the buttercups in the region in question may even be filled several times and hence are washed out completely. In nature we do not find that the flowers may be brimful of water, either, nor that the water overflows. The amount of water is rarely greater than indicated in fig. 2. In the flowers which have been exposed to rain for a prolonged time we only observe the very thin coat of water which has been bound by capillary action.

The greatest amounts of water are found in the flowers at the beginning of the rain, because the faculty of shedding water is greatest as long as the flower is still dry and young. This

faculty, however, is lost completely or in part during continued rain. Even the upper surface of the petals, which are the most nonabsorbent parts of the flowers, may in time come to bind water (fig. 2 on the left).

Fig. 2 illustrates the first filling of rain-water in *R. flammula*. As described in more detail above, the drops trickle down along the insides of the hollow petals, where they may wash off the pollen which is nearly always futilely sticking here. Other drops wash out nearly all pollen from the open anthers and accumulate at the bottom of the flower to form a connected body of water with abundant pollen on the surface. During continued rain the water rises between the carpels, where the moving grains of pollen soon hit the stigmas and these are pollinated.

Not only the interior of the flower is moistened during heavy rain. The stalk of the flower is moistened as well, even immediately below the flower where no drops fall direct.

If one holds a cut flower of e. g. *R. repens* or *R. bulbosus* vertically between one's thumb and fingers and drips 5 to 10 drops into it, it soon appears that the water can run through the bottom of the flower, which thus must have some outlet of a suitable size.

If the water passed rapidly through the flower, the pollen would be carried away by the stream and be lost; but the outlet at the bottom of the flower is so narrow that most of the pollen on the surface of the water gets stranded on the large number of obstacles at the bottom of the flower or rises again to the surface of the arriving rain-water, from where it has again a chance of getting up to the stigmas.

There is nearly always a little pollen in the water that runs out of the bottom of the flower. This water, however, is comparatively poor in pollen (or completely without it) as compared with the surface water. It is of course of great importance for the pollination that no great quantities of pollen are lost through the outlet.

The narrower and the more sinuous the outlet, the more slowly the water will pass and the less pollen will be lost.

Exactly according to these principles the passage through the bottom of the flower is arranged. Further, the water naturally flows first over the surfaces which bind the water to the highest degree.

In fig. 2 the paths of the streams of water are indicated by water-surfaces being drawn with a fat, black line, while the rest of the water is dotted.

The petals are placed so close together that there is only a narrow fissure between each two. And the passage between them is further made difficult by the fact their edges are nonabsorbent except along the small part where the nectary is situated, and, as appears from fig. 1, there is also here a slight bend (b) of the edge. In this place the first and most difficult passage in the outlet is found, and exactly off and under this place the sepals are situated in the hollow surface of which the water oozing through is collected, often as a big drop that above is bound to the lower surfaces of the petals, which exactly in this place bind the water.

If more rain comes down, some of it may drop down from the tips of the sepals. In most species, however, the water is slowly drained off through the fissures between the sepals. It is then collected at the bases of the sepals, from where it further trickles down the stalk. This passing stream is easy to point out when one holds a flower in one's hand and drops water into it. The water will then soon drop into one's hand.

During natural rain the water which passes through the bottom of the flower generally does not gather into drops, but flows evenly down the stalk. Thus it is avoided that the water by sudden and violent movements tears pollen with it.

This important fact, that the stream is even, has in certain species been secured by various contrivances in the structure of the stalk. The regulating faculty of the stalk is particularly clearly observed in *R. bulbosus* (and *R. repens*), the stalks of which are provided with deep grooves, which are highly conductive to water, as can easily be seen by direct observation.

The capillary action of these grooves may also be demonstrated by placing a gynaecium which has been relieved of all the leaves placed under it, in a glass of water. The water then rises through the grooves where it is kept as a fine stream under numerous hairs along the sides of the grooves which bind the water. By way of the grooves the water is carried right up to the gynaecium the carpels of which the next day prove to have been moistened by water that has been transported through the grooves of the stalk.

One more form of stream regulator is found in the sepals in *R. bulbosus* (figs. 6 and 7), which have a sharp transversal bend so that the outermost and longest parts of the sepals are directed downwards, the tip thus being situated close to the stalk of the flower.

If any water enters this flower, it runs out between the bases of the petals—as in other species—and collects in the space between the bases of petals and sepals. From here the water passes out between the sepals; but then it collects in the large

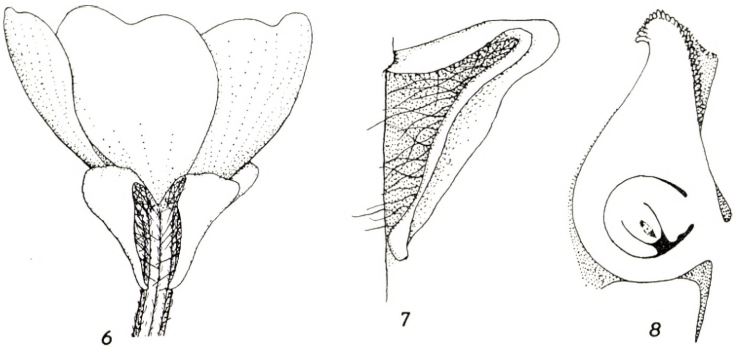


Fig. 6. *Ranunculus bulbosus*. Flower. From the lower surface of the pilose and retroflex sepals surplus water is drained off by the grooves on the stalk. Denmark. × 2.

Fig. 7. *Ranunculus bulbosus*. Sepal with rain-water (dotted) confined under it. Denmark. × 6.

Fig. 8. *Ranunculus acer*. Longitudinal section of carpel in rainy weather. The surrounding water dotted. The Faroes. × 40.

space between the stalk and the lower side of the retroflex part of the sepals, where it is retained between remarkably long and stiff hairs which are found exclusively in this place.

From this curious reservoir under the sepals (fig. 7) the water is carried downwards to the tips of the sepals and from there farther on to the grooves on the stalk. This transport takes place slowly and evenly and in a way which reminds of that in which ink flows from the tip of a fountain pen, where the fluid is bound in a similar way as under the sepal of *R. bulbosus* and is given out in a corresponding continuous manner.

There are considerable differences in the ways of pollination in the various species of *Ranunculus*. Thus they are all visited

by insects, as has been exactly recorded in the literature, which is amply summarized by e. g. Knuth.

R. acer is the species which is visited by most insects. In the Faroes the species particularly grows near inhabited places, where there is a particularly large number of flies, and in most flowers some insect is constantly observed. During rain the thin stalks are bent so that the flower nods and turns the lower side towards the rain. In the dry interior of the flower the insects then find an excellent shelter and food.

The flies generally sit on the petals and thrust their proboscises down to the nectary under the stamens. Often they also creep over the interior of the flower and transfer pollen to the stigmas.

R. acer thus is a typical insect-pollinated flower; but self-pollination may also take place in older flowers by the pollen of the innermost stamens dropping direct on to the stigmas.

During rain and gales the flies remain in their shelters, where they creep about in order to suck all the five nectaries; but at the same time the stigmas are pollinated with the flower's own pollen. Often *Thrips* are also found in the flowers and like the flies give rise to autogamy. Rain-pollination has not been observed in *R. acer.*

In *R. flammula* the pollination (in the Faroes) is quite different from that in *R. acer.* Thus the flowers in *R. flammula* are not bell-shaped, but are formed like a low bowl, because the petals have been spread out nearly horizontally, in which position they can catch the greatest possible quantity of water (figs. 9—10). The thin flexible stalk always bends so that the open flowers are all spread out nearly horizontally. In *R. acer* the flowers in many cases are held in a more or less oblique position and forming a deeper bowl. These differences in the position and form of the flowers is not particularly conspicuous when the two species are growing together.

In Denmark *R. lingua* behaves in a similar manner as *R. flammula.*

The flies have a predilection for *R. acer,* whereas visits by insects are remarkably few in *R. flammula* when the two species are growing together, and when the rain comes, it is the flowers of *R. flammula* which dominate the picture.

The farther one gets away from the Faroese settlements, the fewer pollinating insects are found. *R. acer* disappears with the flies. In remote localities where there are no insects at all, *R. acer* often is completely absent, whereas *R. flammula* may very well be common along the streams. This difference in distribution is no doubt in part conditioned by the fact that *R. flammula* fructifies excellently after rain-pollination.

A third type within the genus is represented by *R. bulbosus*, which is a typical self-pollinator. The chance of insect pollina-

Figs. 9—10. *Ranunculus flammula*. After rain grains of pollen (big dots) may be found everywhere in the flower, also on the stigma. The Faroes. × 5.

tion is small, as the gynaecium is hidden between the remarkably long stamens. As in the other species, however, pollinating *Thrips* often creep about the flower, but they particularly transport the flower's own pollen.

In *R. bulbosus*, too, the outermost stamens open first, while the innermost ones unopened cover the gynaecium. At this stage the flower may be pollinated by rain.

Only when the flower begins withering, the innermost anthers open, and their pollen now falls direct on to the stigmas. But this latter method of pollination is only a last resort, as the flower generally has been pollinated before.

This last-mentioned form of self-pollination may also occur in the other species, but not so conspicuously and functioning so unerringly as in *R. bulbosus*.

In order to investigate the effectivity of rain-pollination a number of large flower-buds of *R. repens* were placed at the same time in two different glasses, where they burst without

being pollinated by insects. One glass with fresh flowers then for an hour was moved out into natural rain, after which it was again placed beside the other so that no insects had admission to the flowers.

In the glass which had been exposed to rain all the flowers fructified; but in the glass which had been isolated from both insects, shakings, and rain it proved that pollination had taken place only exceptionally in a few flowers where a little pollen had dropped from the innermost stamens on to the stigmas.

In order to test the viability of the pollen after rain I collected some flowers of *R. bulbosus* which had been exposed to heavy natural rain in the open for three hours. Both styles and stamens were drenched. The outermost stamens in the usual way had bent down towards the petals, which had plenty of pollen sticking to their insides. Some of this pollen, which was also drenched by rain-water, was placed in ordinary water in a microscopical preparation without addition of sugar or other nourishing substances, and the next day the germination was in full swing.

Another portion of the pollen wetted by the rain was smeared on the stigmas of one side of a flower, while the other side of the flower was not pollinated. Some days after this local pollination it was easy to see that only those carpels which had received the wet pollen had been pollinated and developed seeds.

Thus there is no reason to believe that *Ranunculus* pollen should lose its faculty of fertilizing by being moistened by rain.

3. *Caltha palustris.*

Conditions of pollination in *Caltha* (fig. 5) remind of those observed in the *Ranunculus* species (figs. 1—10).

The remarkably large flowers are highly attractive to flies, a great number of which, in many different sizes, creep about the flowers. As the carpels in the Faroese form are considerably longer than the stamens nearest to them, a pollination as a consequence of direct contact between anthers and stigmas is impossible during the first part of the flowering season. Only towards the period of withering the inmost stamens stretch so

far that they can touch the stigmas; but at that time the stigmas have nearly always been pollinated by insects long ago, and the fructification is always plentiful.

The typical insect pollination is one of the reasons why *Caltha* in the Faroes is especially found near places where the offal and droppings of man and birds are favourable breeding places to flies.

During rain the flowers are wide open and collect a large amount of water. The perianth leaves then are moistened along their insides, as they are not glossy and nonabsorbent like the petals of *Ranunculus*. But the large quantities of water are drained off faster than in the insect-pollinated *R. acer*, because sepals are missing so that the water can easily run out through the base of the perianth, from where it is rapidly transported away through the grooves of the stalk.

Both carpels and stamens also get wet in rainy weather, and pollen is distributed all over the interior of the wet flower so that pollination may also take place if prolonged rain keeps the insects away.

The stalk is so stiff that the flower cannot bend aside a little such as that of *R. acer*, for which reason the flies do not seek shelter in the flowers of *Caltha* during rain.

This species thus can be pollinated in at least three different ways just as the buttercups.

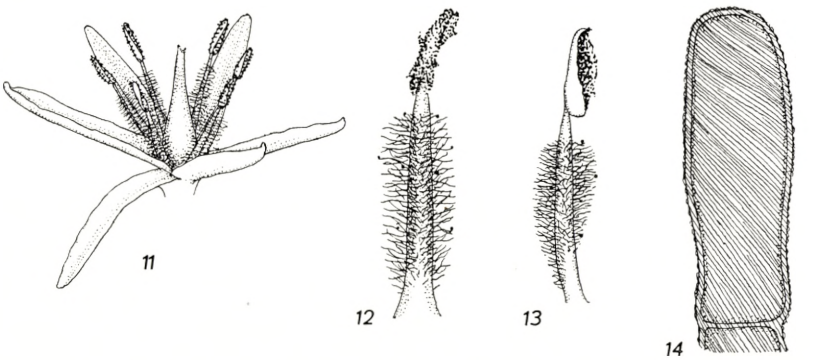
4. *Narthecium ossifragum* (Figs. 11—16).

The method of pollination is mysterious. Knuth has observed the flowers being visited by bees and other insects as well and gives a list of these; but the flowers have no honey, so the insects may have been attracted by the scent or the conspicuous colour.

But insect pollination at any rate is not necessary, for the plant fructifies abundantly in the Faroes, where there are no bees. Only once I have seen a fly on the flowers there, and such a sparing visit by insects cannot play any role worth mentioning to the multitude of flowers found everywhere in Faroes, where I have examined a large material.

Only a few times I have observed spontaneous self-pollination in flowers in which a few anthers had opened in the bud and given off pollen direct on to the stigma. Wind pollination as well is extremely rare. Both this and insect pollination are made difficult by rain, and further the plant fructifies excellently in such localities where there are no pollinating insects.

In the Faroes I witnessed the rare phenomenon that there was no rain for about a fortnight. I then sought out a fairly large population of *Narthecium* with flowers newly out. Half of



Figs. 11—14. *Narthecium ossifragum*. Fig. 11: flower seen obliquely from above. × 4. Figs. 12—13: stamens with nonabsorbent hairs seen from behind (fig. 12) and from the side (fig. 13). After rain pollen may be found everywhere in the interior of the flower. × 7. Fig. 14. Tip of hair on stamen with nonabsorbent spiral ledges. × 800. The Faroes.

the area was now sprinkled with water several times during a few days. After about ten days the flowers that had received the artificial rain had withered because they had been pollinated and the ovaries had begun growing; but the flowers which had not been sprinkled with water were still fresh because they had not been pollinated. Thus there is a probability that *Narthecium* can be pollinated by rain even though artificial sprinkling with water has not quite the same effect as natural rain.

If a whole, young flower is dipped into water it proves to be nonabsorbent in most places, only that it gets moist at the bottom of the flower and on anthers and stigmas. This faculty, however,—as in *Ranunculus*—is lost with age or when the flower has been exposed to plenty of rain. The possibilities of pollination therefore must be investigated in newly opened flowers.

Of particular interest to the pollination are the curious stamens (figs. 12—13), which in nearly the whole of their length are covered by long coloured hairs, which are nonabsorbent. This faculty perhaps (?) is connected with the fact that the surface of the hairs is provided with very fine spiral lines (fig. 14), which make the hairs scabrous, the physical significance of which I have not investigated.

The pollen hangs together in clots, but if it is put into a drop of water, the various grains separate and float on the surface.

If a single drop of water is dripped into the flower, it will mostly come to rest as shown in fig. 15, the stamens forming a partly water-stopping cup of a similar function as the corolla in *Ranunculus*. If more water enters the flower, it collects as a connected ring round the style, which rises above the surface as a skerry (fig. 16).

In natural rain some of the obliquely placed anthers are hit by the drops at an angle of about 45°. By the force of the drops pollen is now flung to the sides, but—because of the oblique position of the anthers—particularly towards the style and on the surface of the water.

The deep red grains of pollen are easy to see in a magnifying glass. They are moving remarkably rapidly, whirling round on the surface of the water, some of them, however, easily getting stranded on the nearest fixed points, viz. anthers and stigma, which thus may be pollinated.

If the rain-water could flow out of the flower at the top, much pollen would be washed away; but this catastrophe is avoided by the flower having a similar outlet at the bottom as *Ranunculus*.

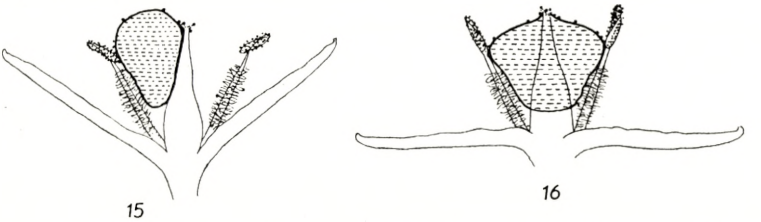
If there is plenty of water in the flower, the blows from falling drops and the water's own weight will force the water down to the bottom of the flower, which is nonabsorbent, among other things because the lower parts of the filaments are without the above-mentioned water-stopping hairs.

When the water has passed the bases of the stamens, the stream is again delayed by the petals found immediately outside, which are also nonabsorbent both inside and outside. However, these are always—even in rainy weather—separated from each other so that all the surplus water can finally leave the flower through the spaces between the petals.

The flowers are always stiffly upright and wide open, so that they receive as much water as possible. After a heavy rain the flower is wet inside. Even the hairs on the stamens have become moist, and if, further, water is dripped into such a moist flower, it runs right through.

After rainy weather pollen may be found everywhere in the interior of the flower, but also on the stigma. The pollination takes place at the beginning of the rain.

From a genetic point of view rain-pollination must be considered autogamy.



Figs. 15—16. *Narthecium ossifragum*. Longitudinal section of flowers with water (dotted), on the surface of which pollen floats from anther to stigma. × 4. The Faroes.

In *Menyanthes* the inside of the corolla is set with similar hairs as are found on the stamens of *Narthecium*. The behaviour of the flower of *Menyanthes* during rain should be explained in detail.

In general it should be investigated what influence is exerted by precipitation on all our flowers, many of which are wide open in rainy weather. Such observations must be considered necessary links in future investigations within floral biology.

5. Summary.

(1) It has been investigated how the flowers of the following species behave during the rain: *Ranunculus* species (figs. 1—10), *Caltha palustris* (fig. 5), and *Narthecium ossifragum* (figs. 11—16).

(2) In *Ranunculus* the flowers of the commonest species may be pollinated in three different ways:

(3) First (entomophily), the just opened flower may be pollinated by insects (particularly flies). The inmost anthers then are unopened

and prevent the outermost open anthers from transferring their pollen directly to the stigmas. Conditions in the Faroes show that several species can completely do without visits by insects, as the flowers can be pollinated by rain.

(4) During heavy rain the flower is not filled with water, which would wash the pollen away.

(5) Only the bottom of the flower is covered with water, on the surface of which pollen is floating (fig. 2). The pollen-bearing water is by capillary action sucked up between the stamens and carpels which are placed close together, and thus pollen gets stranded on the stigmas (figs. 3, 5, 8).

(6) The surplus water is slowly drained off through narrow and sinuous outlets in the bottom of the flower, from where it slowly runs down the stalk.

(7) Insect pollination is most pronounced in *R. acer* (the flower of which bends in the rain). The outlet is most highly developed in species with grooved stalks (figs. 6, 7).

(8) The third method of pollination (autogamy) is used at the very last, if both insects- and rain-pollination have failed, pollen then from the inmost stamens falling direct on to the stigmas.

(9) In *Narthecium* (figs. 11—16) the very hirsute stamens form a water-stopping cup round the style. The flower has a similar outlet at the bottom as that of *Ranunculus*.

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EN METODIK TIL UNDERSØGELSE AF LANDBRUGSPLANTERNES VANDØKONOMI OG STOFPRODUKTION

AF

P. BOYSEN JENSEN

MIT DEUTSCHER ZUSAMMENFASSUNG

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
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A. Indledning.

Den praktiske Betydning af den Del af Plantefysiologien, som vedrører de højere Planter, vil i første Række være den, at dens Undersøgelser og Erfaringer kan medvirke til, at Stofproduktionen hos Kulturplanterne forøges saa meget som muligt, undertiden ogsaa, at uønskede Planter dræbes. For at kunne løse disse Opgaver er det nødvendigt at forstaa Planterne, at vide, hvoraf de lever, og at udrede det Sammenspil mellem de forskellige Planteorganers morfologiske og fysiologiske Egenskaber, som betinger Stofproduktionen.

I Løbet af de sidste 40 Aar er der af nordiske Plantefysiologer udført et meget omfattende Arbejde for at analysere Stofproduktionen hos Planterne. Disse Undersøgelser, hvortil der ikke findes noget Sidestykke andetsteds, er nu i det store og hele ført saa langt frem, som det er muligt i de Laboratorier, der staar til Plantefysiologiens Raadighed, og som her i Danmark er overordentlig beskedent udstyrede. Af Hensyn til den vidtrækkende praktiske Betydning, som disse Undersøgelser har, vil det være ønskeligt at faa oprettet et Laboratorium, hvor de kan føres videre i større Maalestok. Det er da Hensigten med denne Afhandling at undersøge, hvordan et saadant Laboratorium bedst indrettes. Laboratoriet skal først og fremmest undersøge Vandøkonomiens Betydning for Stofproduktionen, men skal ogsaa kunne tage en Del andre Opgaver op.

B. Landbrugsplanternes Vandøkonomi.

Det er i mange Henseender lettere at undersøge Dyrenes Ernæringsforhold end Planternes. Et Dyr er et afgrænset System, man kan tilføre det, hvilke Stoffer man vil, man kan undersøge, hvilke Stoffer der optages og afgives, og samtidig kan man maale Dyrets Vækst.

Under naturlige Forhold vokser derimod mange Planter sammen i en fælles Jordbund. Man kan derfor ikke undersøge den enkelte Plantes Ernæringsforhold, men man maa bestemme Stofoptagelse, Stofafgivelse og Stofproduktion pr. Arealenhed; ofte er disse Størrelser vanskelige at maale. Endvidere ved man ikke, hvor stor en Jordmængde, Planterne udnytter; heller ikke er man i Stand til at maale de disponible Mængder af Vand og mineralske Stoffer i Jorden med særlig stor Nøjagtighed.

Som ovenfor nævnt vil Formaalet med Plantedyrkning hyppigst være den at producere saa meget Stof som muligt. Ved Tørstofproduktionen i en Plantebevoksning forstaar man den Mængde Tørstof, der produceres af den paagældende Bevoksning pr. ha i Løbet af et Aar. Hos Hvede kan det absolut maximale Udbytte, d. v. s. Udbyttet paa de bedste Jorder ved optimal Gødning, naar de ydre Kaar som Lys, Temperatur og Nedbør er særlig gunstige, skønsmæssigt anslaas til 6 ton Kærne + 8 ton Halm; med et Tørstofindhold paa 85 % svarer det til 11,9 ton Tørstof pr. ha. Af Sukkerroer er der høstet 70 ton Rod, svarende til 28 ton Tørstof (Rod + Top) pr. ha.

Man kan tage disse Tal som en Kendsgerning, men man kan ogsaa stille det Spørgsmaal: Hvorfor kan der netop produceres 12 ton Tørstof paa en Hvedemark og ikke f. Eks. 20 eller 30 ton? Dette Spørgsmaal kan kun besvares ved at undersøge, hvilke Faktorer, ydre eller indre, der virker begrænsende paa Stofproduktionens Størrelse. Besvarelsen vil derfor samtidig kunne bidrage til at belyse det Problem, om det ved Ændring af de be-

grænsende Faktorer vil være muligt at forøge Stofproduktionen hos vore Kulturplanter i væsentlig Grad, eller om der muligvis findes en Grænse, som Stofproduktionen ikke kan overskride. Det er Plantevæksten, og da navnlig Landbrugets Planteavl, der er Grundlaget for Menneskets Ernæring, og det er altsaa ogsaa Planteproduktionens Størrelse, der er bestemmende for, hvor mange Mennesker, der kan leve her paa Jorden. Det er derfor af største Betydning at faa Grænserne for Jordens Ydeevne fastslaaet.

Naar man vil forsøge at løse Problemet, hvilke Faktorer der virker bestemmende paa Stofproduktionens Størrelse. maa man begynde med at undersøge, hvad Planterne lever af. En Analyse af Tørstoffet af Hvede viser, at dette har følgende Sammensætning (Ebermayer):

	Kulstof	Brint	Ilt	Kvælstof	Aske
Korn	46,1	5,8	43,4	2,3	2,4
Straa	48,4	5,3	38,9	0,4	7,0

Det fremgaar af Analysen, at over 90 % af Tørstoffet bestaar af Kulstof, Ilt og Brint. Disse Grundstoffer stammer fra Kulsyren i Luften og fra Vandet i Jorden, som med Lyset som Energikilde opbygges til organisk Stof gennem den Proces, der kaldes Kulsyreassimilationen. Naar man derfor spørger, hvorfor der paa den paagældende Hvedemark produceres 12 ton Tørstof pr. ha, maa Svaret blive: I første Instans, fordi den langt overvejende Del af denne Stofmængde er dannet gennem Kulsyreassimilationen.

Foruden det organiske Stof, der aflejres som Tørstof, gaar der en Del organisk Stof tabt ved Respiration i Blade, Akseorganer (Stængler, Rødder) og Fruktifikationsorganer (Blomster, Frugter). Der maa derfor gennem Kulsyreassimilationen dannes en større Mængde organisk Stof, end det, der findes som Tørstof i Planterne. Man kan opstille følgende Ligning:

Bruttoproduktionen (den ved CO_2-assimilationen indvundne Tørstofmængde) — Tørstoftab ved Respiration i Blade, Akseorganer (Stængler, Rødder) og Fruktifikationsorganer (Blomster, Frugter) = Tørstofproduktion i Blade, Akseorganer og Fruktifikationsorganer (Boysen Jensen).

Gennem de ovenfor omtalte Analyser af Stofproduktionen er det blevet muligt at maale de enkelte Størrelser i denne Produk-

tionsligning (smlgn. Poul Larsen 1941), og derved har man faaet et Indblik i, hvilke Faktorer der bestemmer og begrænser Stofproduktionens Størrelse.

Paa den ovenfor omtalte Hvedemark blev der produceret 11,9 ton Tørstof pr. ha. Til denne Produktion er medgaaet 20,5 ton Kulsyre, som er taget fra Atmosfæren. Denne Kulsyremængde er fordelt i 35 Millioner m^3 atmosfærisk Luft, d. v. s. i en Luftsøjle, der har en ha som Basis, og som, hvis Lufttrykket i Søjlen var normal og konstant, har en Højde paa 3,5 km; da Lufttrykket aftager opefter, bliver Højden noget større, mellem 4 og 5 km. Desuden er der assimileret mindst 6 ton Tørstof, som igen er gaaet tabt ved Respiration i de forskellige Planteorganer. Den samlede Bruttoproduktion kan altsaa anslaas til ca. 18 ton Tørstof, og den samlede assimilerede Kulsyremængde er ca. 30 ton.

Endvidere er der ved Kulsyreassimilationen forbrugt ca. 12 ton Vand. Denne Vandmængde udgør dog kun en meget ringe Del af den samlede Vandmængde, som optages fra Jorden. Hvor stor Planternes Vandforbrug er pr. ha, vides ikke nøjagtigt, skønsmæssigt kan den anslaas til 3000 ton; af denne Vandmængde bruges kun ca. 0,4 Procent under Kulsyreassimilationen, en ringe Del er til Stede som frit Vand i saftige Plantedele, den alt overvejende Mængde gaar bort gennem Fordampning fra de overjordiske Dele, navnlig fra Bladene.

Foruden Kulstof, Ilt og Brint indeholder Planten Kvælstof og en Del andre Grundstoffer, af hvilke 11 er uundværlige. Disse Grundstoffer optages fra Jordbunden som Salte sammen med Vandet. Den omtalte Hvedemark har optaget ca. 1 ton Salte (Aske + kvælstofholdige Salte). Disse er som nævnt absolut nødvendige for Planterne, men i Vægt udgør de kun faa Procent af den optagne Kulsyremængde[1].

En Forøgelse af Stofproduktionen hos en Plante kan tænkes opnaaet dels ved en Forbedring af Vækstbetingelserne (d. v. s. de ydre Faktorer) og dels ved en Forædling af Planterne (de indre Faktorer), saa at de er bedre i Stand til at udnytte Vækstbetingelserne.

De ydre Faktorer, der paavirker Stofproduktionens Størrelse, kan deles i 3 Grupper.

[1] Hvis det Tørstof, der produceres paa den paagældende Hvedemark, bredes ud som et ensartet Lag over Marken, vil dette Lag kun være godt 1 mm tykt.

1. De nødvendige Næringsstoffer, nemlig

Kulsyreindholdet i Luften, denne kan ikke ændres.

Vandindholdet i Jorden er bestemt dels af Nedbørens Størrelse og dels af Jordbundens Egenskaber, denne Faktor kan i nogen Grad ændres ved Indgreb fra Menneskets Side.

Indholdet af mineralske Næringsstoffer i Jordbunden, Mængden af disse kan forøges i den Grad, man ønsker, ved Tilførsel af Gødningsstoffer.

Til denne Gruppe af Faktorer maa ogsaa regnes Ilten i Jordbunden, som er nødvendig for Røddernes Aanding. Ved Jordbearbejdning og ved Afledning af skadeligt Vand vil man i Reglen kunne opnaa, at der er tilstrækkelig Ilt i Jorden.

2. Energetiske Faktorer, som er nødvendige for Stofomsætningen. Herhen hører Lyset, som er den nødvendige Energikilde for Kulsyreassimilationen. Denne Faktor kan ikke ændres.

Endvidere Temperaturen; denne virker ikke stærkt paa Kulsyreassimilationen, men derimod paa Væksten, som nedsættes med Temperaturen. Heller ikke denne Faktor kan ændres.

3. Skadelige Faktorer. Denne Gruppe omfatter Faktorer, der kan nedsætte Stofproduktionen. Herhen hører Ukrudt, Angreb af snyltende Svampe og Dyr, endvidere visse klimatiske Faktorer, f. Eks. Vind, der forøger Planternes Vandforbrug, Hagl, stærk Frost o. s. v., samt visse edafiske Faktorer, f. Eks. en ugunstig Brintionkoncentration, Gifte i Jorden o. s. v. Nogle af disse kan ændres, andre ikke.

Enhver af de ovennævnte Faktorer kan virke begrænsende eller formindskende paa Stofproduktionens Størrelse. Af disse Faktorer er det væsentlig de edafiske, der kan ændres. Naar disse er til Stede i Optimum, er det de klimatiske Faktorer, der er bestemmende for Udbyttets Størrelse; da disse Faktorer som nævnt ikke kan ændres ved Menneskets Indgreb, vil en given Plante kun kunne producere en vis maximal Mængde Tørstof pr. ha i Løbet af et Aar.

Den Forøgelse af Tørstofproduktionen, der kan naas ved Forædling, er ligeledes begrænset. Man maa antage, at visse af vore Kulturplanter, f. Eks. Byg, allerede er saa højt forædlede, at deres Ydeevne i Fremtiden kun vil kunne forøges i meget begrænset Omfang.

Konklusionen heraf bliver da den, at selv om det nok vil

være muligt at forøge den maximale Stofproduktion for visse af vore Kulturplanter noget i Fremtiden, vil denne Forøgelse være af begrænset Omfang. Man maa antage, at der for enhver Plante existerer en maximal Stofproduktion, som ikke kan overskrides, hverken ved Forbedring af Vækstbetingelserne eller ved Forædling.

Det er nu imidlertid saaledes, at man i mange Aar ikke naar det maximale Udbytte pr. ha, selv om Indholdet af Plantenæringsstoffer i Jorden, Brintionkoncentrationen o. s. v. er optimal. Aarsagen til Svingningerne i Høstudbyttet fra Aar til Aar skyldes ikke Ændringer i Kulsyrespændingen, som praktisk talt er konstant, heller ikke spiller Vekslinger i Belysning og Temperatur nogen større Rolle. Derimod kan Frost, Insektangreb og Ukrudt i høj Grad bidrage til at formindske Afgrødernes Størrelse. Men den vigtigste Aarsag til Svingningerne i Høstudbyttet er dog utvivlsomt Vandforsyningen, d. v. s. Jordens Indhold af Vand.

Grundlaget for Forstaaelsen af Vandforsyningens Virkning paa Høstudbyttet er Kendskabet til Vandets Betydning for Planterne, som vi derfor nu skal gøre Rede for.

Som omtalt ovenfor anvendes en ringe Del af det optagne Vand til sammen med Luftens Kulsyre af opbygge de organiske Stoffer i Planten, langt den største Del gaar imidlertid bort ved Transpiration fra Bladene. Atter og atter møder man den Opfattelse, at Vandstrømmen gennem Planterne er nødvendig for at transportere de mineralske Stoffer op til Bladene. Denne Opfattelse er ikke rigtig. Ganske vist følger de optagne Mineralstoffer med Vandstrømmen op gennem Veddelen i Ledningsstrengene, men vi ved med Sikkerhed, at der kan ske betydelige Forskydninger af Saltene i Planten, selv om der ikke samtidig foregaar nogen Transpiration. Det stærke Vandforbrug hos Planterne skyldes, at Planterne for at kunne udnytte Lyset maa have en stor ydre Overflade, og at der maa være let Adgang for Luftens Kulsyre til det Indre af Bladene gennem Spalteaabningerne. Da nu Bladene maa have et stort Vandindhold, kan det ikke undgaas, at der samtidig med, at der diffunderer Kulsyre ind, diffunderer Vanddamp ud. Hvis nu Vandtabet under en Tørkeperiode bliver for stort, kan det nedsættes betydeligt ved Lukning af Spalteaabningerne.

Naar der hos Planter med ren vegetativ Udvikling, f. Eks. hos Roer, indtræder en Tørkeperiode, saa at Spalteaabningerne lukkes, vil Kulsyreassimilationen høre op, og Stofproduktionen vil

gaa i Staa. Hvis Tørken ikke beskadiger Planten, fortsætter Stofproduktionen paany, naar der igen kommer Regn, saa at den eneste Virkning af Tørkeperioden er, at dette Tidsrum gaar tabt for Stofproduktionen.

Hos Kornarterne kan derimod Virkningen af en Tørkeperiode være mere kompliceret, idet denne foruden at standse Stofproduktionen kan standse Bladudviklingen og fremme Udviklingen af Akset. Naar denne Omstilling fra ren vegetativ Udvikling til Blomsterdannelse er indtraadt, kan den ikke mere gaa tilbage. Foruden den direkte hæmmende Virkning paa Stofproduktionen, kan Tørkeperioden altsaa hos disse Planter ogsaa have en indirekte Virkning, som bestaar i, at Assimilationssystemet ikke er i Stand til at naa en tilstrækkelig Udvikling, og at Stofproduktionen derfor bliver ringe.

Da baade Transpirationsintensiteten og Kulsyreassimilationen og dermed Stofproduktionen er afhængige af Spalteaabningernes Aabningstilstand, maa man vente at finde en Korrelation mellem Vandforbrug og Tørstofproduktion. Man har bestemt Værdierne af Transpirationskvotienten $\frac{\text{Vandforbrug}}{\text{Tørstofproduktion}}$, begge udtrykt i ton, eller med andre Ord Vandforbruget i ton pr. ton produceret Tørstof. Denne Værdi kan, som det var at vente, variere stærkt; den ligger i humid, tempereret Klima mellem 350 og 700.

Planterne optager det nødvendige Vand fra Jordbunden, men dette stammer igen fra Nedbøren; det vil derfor være formaalstjenligt af begynde med at undersøge Sammenhængen mellem Høstudbytte og Nedbør. En Oversigt over den paagældende Litteratur, findes hos HALLGREN (1947), her skal kun omtales en dansk Undersøgelse, der er udført af R. K. KRISTENSEN paa Askov Forsøgsstation, henholdsvis paa Lermarken og Sandmarken. Denne Undersøgelse er navnlig af Værdi, fordi det Materiale, der ligger til Grund for den, stammer fra en enkelt Lokalitet, saaledes at Ændringer i Gødningstilførslen og Jordbehandlingen ikke kan antages at have spillet nogen større Rolle for Resultaterne. Paa Grund af det nøje Kendskab, som Forfatteren har haft til Afgrødernes Vækst og Udvikling, har han endvidere kunnet udskyde alle de Forsøg, der f. Eks. paa Grund af Frostskade eller Insektangreb, kunde sløre Billedet. Resultatet af Forsøgene svarer i det store og hele til, hvad man vilde vente.

Høafgrøderne er mindst resistente mod Tørke (Bælgplanterne er paa Grund af deres dybtgaaende Rødder dog mere resistente end Græsarterne), Rugen er temmelig uafhængig af Sommernedbøren, for Havren, hvis Udvikling falder om Forsommeren, er Klimaet for tørt, og for Runkelroer og Kartofler, hvis Udvikling hovedsagelig falder om Eftersommeren, har Klimaet gennemgaaende været for fugtigt (eller for koldt).

De Tal, der ligger til Grund for de ovennævnte Undersøgelser, er de maanedlige Værdier for Nedbørens Størrelse, af hvilke der efter bestemte Regler er beregnet Gennemsnit for de Maaneder, hvis Nedbør paa Grundlag af forudgaaende Korrelationsberegninger maa antages at være særlig vigtig for de paagældende Afgrøder. Man kan, som det ogsaa fremhæves af Forfatteren, være noget i Tvivl, om denne Beregning er fin nok. Hvis der falder Regn f. Eks. i Begyndelsen af April og i Slutningen af Juni, kan der i den mellemliggende Tid findes en Tørkeperiode, der kan være langt alvorligere, end man faar Indtryk af ved at se paa de maanedlige Tal for Nedbørens Størrelse.

Den afgørende Faktor for Planterne er nemlig Tørkeperiodernes Længde eller rettere Længden af de Perioder, da Spalteaabningerne er lukkede. Ved at fremstille et Diagram, der viser Nedbørens Fordeling og Størrelse i Løbet af Vegetationsperioden (smlgn. Romose 1940), faar man et Billede, der giver en Forestilling om Længden af Tørkeperioderne. I Fig. 1 er fremstillet Nedbøren i Aalum i Randers Amt i 1946 og 1947. Figuren giver et slaaende Indtryk af den stærke Forskel, der kan være mellem Nedbøren i et fugtigt Aar (1946) og et tørt Aar (1947).

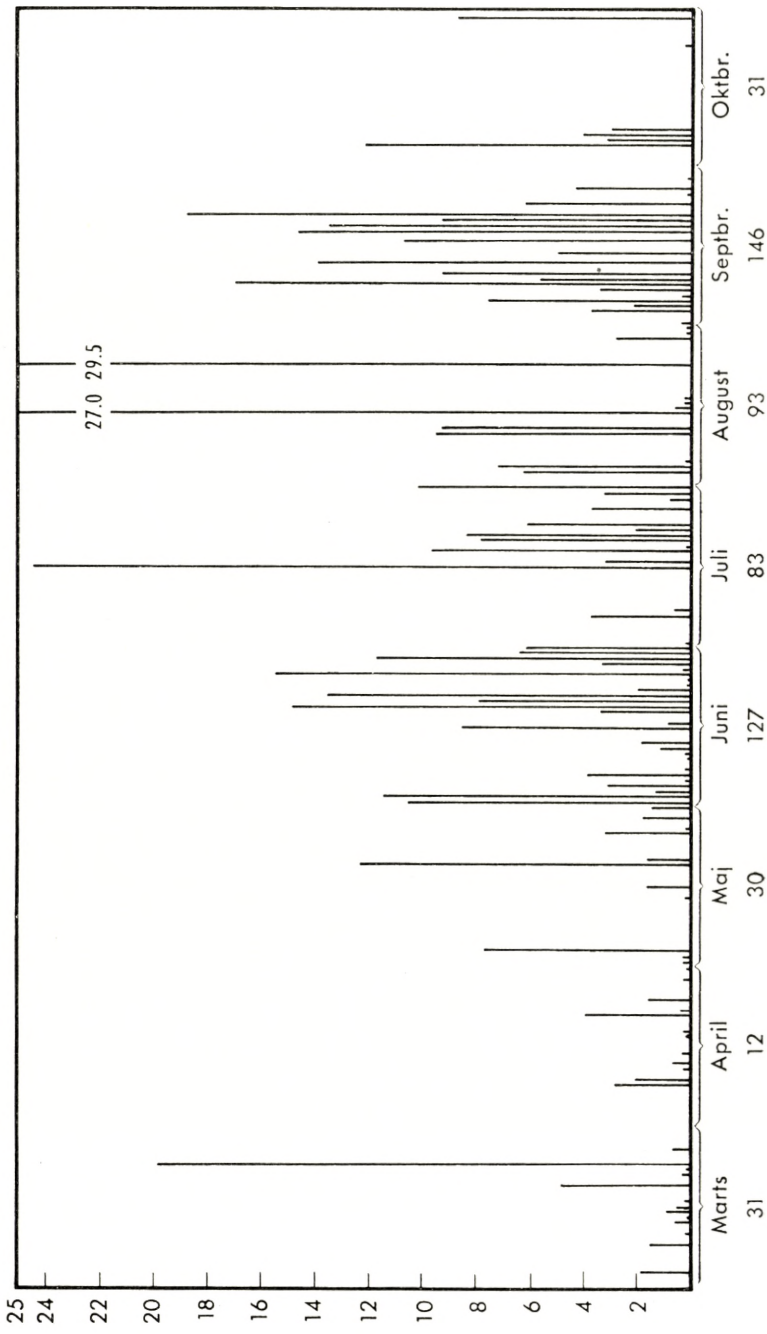
Det kan altsaa fastslaas, at Nedbøren, ihvert Fald for visse af vore Afgrøders Vedkommende, i mange Aar er utilstrækkelig til at give maximalt Udbytte. Nedbøren er man ikke i Stand til at ændre, men man kan stræbe efter at udnytte den saa økonomisk som muligt. Dette kan ske enten ved at nedsætte Planternes Vandforbrug ved Plantning af Læhegn (der ogsaa bidrager til at forhindre eller nedsætte en Vinderosion), eller ved at gribe regulerende ind overfor Vandmængden i Jorden. Det er kun denne Regulering, der omtales i denne Afhandling.

Vandmængden i Jordbunden og dens Betydning for Planternes Vandforsyning. I en større eller mindre Dybde under Jordoverfladen vil man møde Grundvandspejlet.

Naar der efter en Tørkeperiode tilføres Jorden et Overskud af Vand gennem Nedbør, vil en Del af Vandet holdes tilbage af Jorden, medens Resten siver igennem og forener sig med Grundvandet. Den Mængde Vand, som holdes tilbage i Jorden, kaldes den mindste Vandkapacitet; den udtrykkes i Procent af Jordens Volumen. Vandkapaciteten er f. Eks. i let Sandjord 33 %, i Lermuld 46 % og i stærkt lerblandet Humusjord 64 % (Tovborg Jensen 1946). Naar Vandindholdet i Jorden over Grundvandspejlet er mindre end Vandkapaciteten, kan der stige Vand op fra Grundvandet. Stigningshastigheden og den Højde, hvortil Vandet hæves, er forskellig i de forskellige Jordbundsarter. I fint Sand (Kornstørrelse 0,07 mm) steg Vandet i 24 Timer 89 cm, i 8 Døgn 99 cm, i Humus i 8 Døgn 45,4 cm og i Lerjord i 8 Døgn 39,1 cm (Wollny).

Grundvandstandens Højde vil skifte en Del i Aarets Løb. Om Vinteren mættes Jordbunden med Vand fra Nedbøren. Ved Tøbruddet om Foraaret finder der i drænet Jord en meget stærk Vandafstrømning Sted. I Sommerens Løb er Vandforbruget i Almindelighed større end Vandtilførslen, og Grundvandstanden synker ofte betydeligt under Drændybden for dernæst at stige igen om Efteraaret og Vinteren. Grundvandspejlet kan mange Steder ligge adskillige Meter under Jordoverfladen.

Det Vand, som holdes tilbage i Jorden, kan dels være til Stede i imbiberet Tilstand i de kolloide Partikler i Jorden, dels som Kapillærvand i Hulrum og Kanaler. Saa længe der er rigelig Vand til Stede i Jordbunden, er dette ikke fastbundet, men efterhaanden som Vandmængden aftager, lægger Vandet sig som en Hinde om Jordpartiklerne og fastholdes ved Adhæsion til disse med en stedse stigende Kraft. Denne kaldes Jordbundens vandbindende Kraft. Et Maal for denne Kraft er Jordbundens Damptryk, som man kan bestemme ved over en Jordprøve, som befinder sig i et lukket Rum, at anbringe Kapillærrør med forskelligt koncenterede Rørsukkeropløsninger og maale, hvilke af disse der tiltager, og hvilke der aftager i Volumen. Paa denne Maade findes Koncentrationen af den Rørsukkeropløsning, der hverken suger Vand til sig fra Jordbunden eller afgiver Vand til den; med denne Opløsning er Jorden altsaa i Ligevægt, og dens vandbindende Kraft kan derfor udtrykkes ved Størrelsen af det osmotiske Tryk af den paagældende Opløsning.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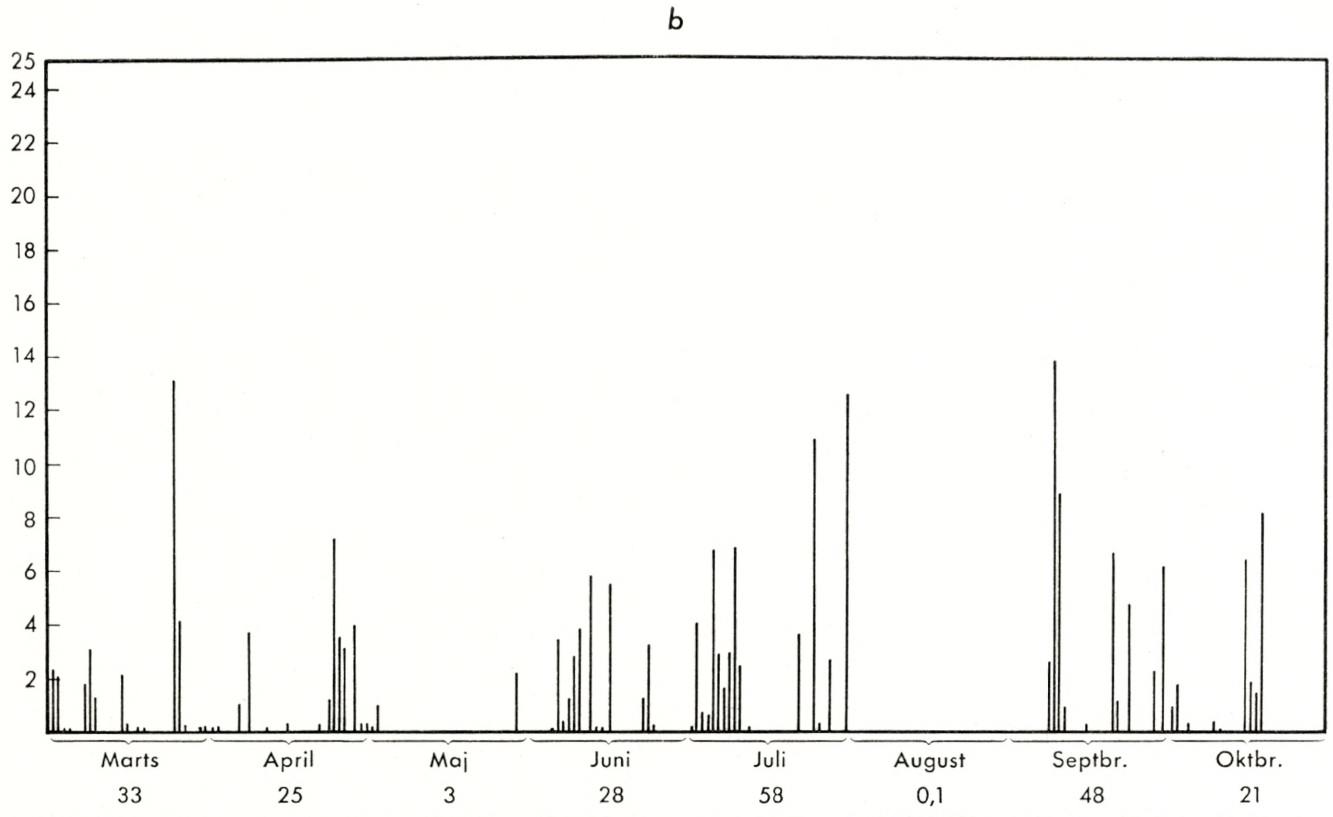


Fig. 1. Nedbøren i Aalum, Randers Amt, i 1946 (a) og 1947 (b). Den samlede Nedbør var i 1946 698 mm (Januar 35, Febr. 35, Novbr. 44 og Decbr. 31) og i 1947 381 mm (Januar 9, Febr. 5, Novbr. 108 og Decbr. 43).

Størrelsen af Jordens vandbindende Kraft i forskellige Jordbundsarter er fremstillet i Fig. 2. Den er i meget høj Grad afhængig af Størrelsen af den indre Overflade i Jorden og er derfor ved samme procentiske Indhold af Vand langt større i en finkornet Jord, f. Eks. Lerjord, end i Sand; en Indblanding af kolloidale organiske Stoffer, hvori Vandet kan imbibere, bidrager i høj Grad til at forøge den vandbindende Kraft.

Det følger heraf, at ikke alt Vand i Jorden kan optages af Planterne; naar Vandindholdet er sunket til en vis Værdi, vil Vandoptagelsen høre op, og Planten begynde at visne. Dyrkes den samme Plante i forskellige Jordbundsarter, viser det sig, som det fremgaar af Tabel 1, at Vandindholdet i Jorden i det Øjeblik, da Planten begynder at visne, er højst forskelligt i de forskellige Jordbundsarter, mindst er det i Sand, størst i Ler eller humusholdige Jorder. Dette forstaas let ud fra det tidligere fremstillede Forhold, at der til samme vandbindende Kraft svarer et meget forskelligt Vandindhold i de forskellige Jordbundsarter.

Tabel 1 (Sachs).

Vandindhold i 100 g Jord ved indtrædende Visning af Tobaksplanter.

Sand + Humus	12,3 g
Ler	8,0 g
Sand	1,5 g

Vandforsyningen i Vegetationsperioden stammer altsaa fra 3 forskellige Kilder:

1. Det disponible Vandforraad, der er til Stede i Jorden ved Vegetationsperiodens Begyndelse (det forhaandenværende Vand — det Vand, som ikke kan optages af Planterne).
2. En Del af Nedbøren (den samlede Nedbør — den Del, der siver igennem til Grundvandet).
3. Den Vandmængde, der stiger op fra Grundvandet[1].

Under en Tørkeperiode er Nedbøren enten 0 eller meget ringe. Den Vandmængde, der da staar til Raadighed, er dels det disponible Vand i Jorden og dels det opstigende Vand. Naar

[1] Naar Grundvandspejlet ligger nogle Meter under Jordoverfladen, spiller den kapillære Opstigning af Vand dog næppe nogen større Rolle.

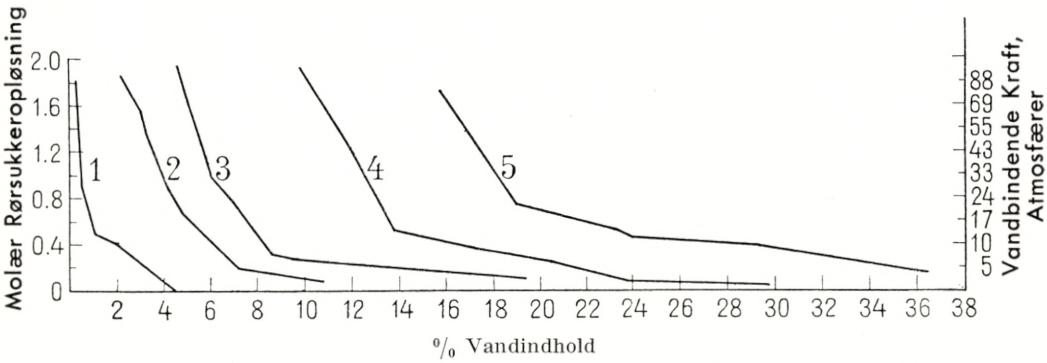


Fig. 2. Størrelsen af den vandbindende Kraft i forskellige Jordbundsarter. 1 Sand, 2 sandblandet Ler, 3 Havejord, 4 Modellerler, 5 Bøgehumus. (H. C. HANSEN).

denne sidste Vandmængde ikke er tilstrækkelig til at dække Planternes Forbrug, vil Vandindholdet i Jorden synke, og naar den er naaet saa langt ned, at den vandbindende Kraft og Modstanden mod Forskydningen af Vandet i Jorden begynder at stige, vil det Tidspunkt nærme sig, da Planten for at opretholde Vandbalancen maa sætte Vandforbruget ned. Dette sker som ovenfor nævnt ved at lukke Spalteaabningerne paa nogle af Bladene eller alle Blade enten nogle Timer om Dagen eller hele Dagen. Naar Spalteaabningerne er lukkede hele Dagen, er Vandforbruget sunket til nogle faa Procent af det normale, men samtidig gaar, som ovenfor nævnt, Stofproduktionen i Staa.

Med Hensyn til Jordens Indhold af Vand kan man skelne mellem to Ydertilfælde.

Jordbunden kan være saa tør, at Planten selv ved ganske kortvarige Tørkeperioder bliver udsat for Vandmangel. Dette er Tilfældet med lette Jorder med lav Vandkapacitet, navnlig naar Grundvandet ligger dybt, saa at den opstigende Vandmængde er ringe.

Af Hedeselskabets Undersøgelser (smlgn. JAKOBSEN 1944) fremgaar det, at den Mængde Vand, der strømmer bort gennem Varde Aa, udgør 50,2 % af Nedbøren i det afvandede Omraade, medens Afstrømningen gennem Tryggevælde Aa kun udgør 34 %. En lignende Forskel findes ogsaa mellem andre Aaer henholdsvis i Jylland og paa Øerne. Den Vandmængde, der bliver tilbage, naar man trækker Afstrømningen fra Nedbøren, udgør for Omraadet

for Varde Aa 367 mm og for Tryggevælde Aa 417 mm. Af disse Vandmængder strømmer noget bort gennem Undergrunden — denne Størrelse kendes ikke —, men største Delen gaar sikkert bort gennem Fordampning fra Jorden og fra Planterne. Selv om man maa benytte de anførte Tal med stor Varsomhed, maa man dog vist kunne slutte, at Grunden til den stærkere Vandafstrømning i Jylland er den, at de jydske Jorder er mere sandede og har en mindre Vandkapacitet end de mere lerede Jorder paa Øerne, og endvidere, at der som Følge af den større Vandkapacitet ogsaa er en større Mængde Vand til Raadighed for Planterne paa Øerne end i Vestjylland.

Da der nu er Sammenhæng mellem Vandforbrug og Spalteaabningernes Aabningsvidde og endvidere mellem denne sidste Størrelse og Stofproduktionen, maa man antage, at en af Grundene til Forskellen mellem de lette og svære Jorders Ydeevne er den, at Vandkapaciteten er mindre hos de første end hos de sidste[1]. Dog spiller sikkert ogsaa det større Antal Næringsstoffer i de svære Jorder og disses større Evne til at tilbageholde opløste Stoffer en vigtig Rolle for deres Frugtbarhed.

Foruden Jordbundens Vandkapacitet er i visse Tilfælde Grundvandstandens Dybde af stor Betydning for Planternes Resistens under en Tørkeperiode. Dette fremgaar af Fejlbergs Undersøgelser over Plantevæksten paa Klitsletterne ved Gammel Skagen (Fejlberg 1891). Naar Grundvandstanden om Sommeren ligger i en Dybde af 3″ (8 cm) findes der Sivvegetation og Mosedannelse, ved 6″ (16 cm) Dybde optræder der Mos og Halvgræsser, men Græsset begynder at komme frem; ved 9″ (24 cm) Dybde er Græsserne fremherskende; ved 12″ (31 cm) er der normal Græsvækst i almindelige Somre; ved 15″ (39 cm) bliver Sæden god, naar Sommeren er lidt varm; ved 18—24″ (47—63 cm) i kolde og fugtige Somre; ved 30—40″ (78—105 cm) er Jorden ubrugelig til Dyrkning af Korn, og der optræder Tørkeplanter.

Jordbunden kan dog ogsaa være for fugtig. Naar Grundvandstanden staar for højt, bliver den Jordmængde, Planterne kan udnytte, altfor lille, da Rødderne ikke vokser ned i Vandet, og den tilgængelige Jord bliver paa Grund af dens altfor store Vandindhold iltfattig og sur.

[1] Rigtigheden af denne Opfattelse støttes af, at Høstudbyttet gennemgaaende er mere stabilt paa Lerjorder end paa Sandjorder (Frode Hansen 1945).

Imellem disse to Ydertilfælde ligger Jordbundens optimale Vandindhold.

En Regulering af Jordbundens Fugtighed kan, hvis Jorden er for tør, ske ved en Tilførsel af Vand, og hvis Jorden er for fugtig, ved en Afledning af Vand.

Forsøg med kunstig Vanding er i Danmark anstillet paa Blangstedgaard og i de sidste Aar paa Forsøgsstationen i St. Jyndevad. I Sverrig er der i Ultuna siden 1941 blevet udført Vandingsforsøg paa gammel Græsmark. Forsøgsmaterialet er endnu ikke saa omfattende, at man kan afgøre, i hvilket Omfang det er rentabelt at vande. Kunstig Vanding vil formentlig kun kunne anvendes med Fordel, naar der er let Adgang til Vand, og der kan faas billig Elektricitet, og den vil af disse Grunde her i Danmark kun kunne faa begrænset Betydning.

Det maa antages, at en kunstig Vanding paa Skøn vil være mere økonomisk end en ren skematisk Vanding, der bringer Nedbøren op paa et bestemt Antal mm pr. Maaned. Naar Jordbunden som Følge af stærk Nedbør i en bestemt Maaned er stærkt mættet med Vand, vil det, selv om den følgende Maaned er noget tør, ofte være overflødigt at tilføre Vand, ja, en Vanding kan maaske virke direkte skadelig. Vand skal som i Havebruget kun tilføres, naar Planten virkelig trænger dertil, og dette Tidspunkt kan formentlig afgøres ved en Undersøgelse af, om Spalteaabningerne er lukkede eller aabne (D. Müller 1946).

Af langt større Betydning er Afvandingen af Jorden. Der er, for en stor Del under Medvirkning fra Hedeselskabet, afvandet meget store Omraader i Danmark (J. J. Hansen 1944). Alligevel skal der i Følge en Undersøgelse, som er udført i Aarene 1915—35, ved hvilken 18 % af det samlede Landbrugsareal blev undersøgt, endnu være 24 % af Danmarks Ager og Eng, der er vandlidende.

En Afvanding bestaar i en Sænkning af Grundvandstanden, hyppigst ved Dræning. Virkningen af en saadan er ikke rent lokal. Naar f. Eks. Vandspejlet i en Sø sænkes, vil ogsaa Grundvandstanden i det tilstødende Jordomraade komme til at ligge lavere.

Selv om det ikke kan dokumenteres med Tal, er det dog utvivlsomt, at de omfattende Dræningsarbejder, der er udført i Danmark, har medført en stærk Sænkning af Grundvandstanden. Dette fremgaar af, at det i de senere Aar ofte har vist sig at være nødvendigt at grave Brøndene dybere. I den tørre Sommer 1947

var det paa visse Steder forbundet med Vanskelighed at skaffe tilstrækkeligt Drikkevand til Mennesker og Husdyr.

Den gavnlige Virkning af en Afvanding træder i de fleste Tilfælde overordentlig tydeligt frem, idet Jordens Ydeevne forhøjes ofte i meget væsentlig Grad.

En Sænkning af Grundvandstanden kan dog uden at være skadelig være overflødig stærk, naar der anvendes et større Antal Drænledninger — og altsaa ogsaa en større Kapital til Arbejdet — end nødvendigt for at bortlede det skadelige Vand.

Afvandingen kan endvidere være saa stærk, at den er direkte skadelig. En skadelig Virkning fremkommer, naar Grundvandstanden sænkes for hurtigt eller for stærkt.

En for hurtig Sænkning af Grundvandstanden om Foraaret kan medføre, at de øverste Jordlag tørrer saa hurtigt ud, at der ikke er Vand nok i Jorden til at sikre Spiringen af Frøet. Muligvis kan der ogsaa opstaa en Vinderosion, der kan bevirke, at en Del af de øverste Jordlag føres bort under de Storme, der kan indtræffe om Foraaret, navnlig paa Steder, hvor der ikke er Læ.

En for dyb Sænkning af Grundvandstanden kan bevirke, at den Vandmængde, der stiger op fra Grundvandet til de Jordlag, hvori Rødderne befinder sig, bliver for ringe, saa at Planterne under en Tørkeperiode er henvist til at klare sig med den Vandmængde, der er til Stede i Jordbunden.

Det er navnlig paa sandede Jorder med ringe Vandkapacitet eller paa Mosejord, hvor den vandbindende Kraft i Jorden er stor, at en Sænkning af Grundvandstanden kan være direkte skadelig.

Formaalet med en Afvanding maa iflg. THØGERSEN (1945) være, »at finde den Afvandingsgrad, der under de givne Jordbundsforhold og Nedbørsforhold vil give de bedste Voksevilkaar for Planterne«. Denne Afvandingsgrad naas vel, naar man, samtidig med at man bortleder skadeligt Vand, udnytter Nedbøren saa økonomisk som muligt[1]. Afvandingen maa ikke være saa stærk, at der i tørre Aar er Fare for Misvækst, selv om man da i fugtige Aar ikke helt kan naa den maximale Afgrøde. Der maa tilstræbes en Udligning mellem de tørre og de fugtige Somre, saa Udbyttet bliver saa stabilt som muligt. Endvidere maa man selvfølgelig tilstræbe den bedst mulige Forrentning af Anlægget.

[1] I denne Sammenhæng maa man som tidligere nævnt ogsaa have Opmærksomheden henvendt paa, at Vandforbruget kan formindskes ved Læplantning.

For at undersøge Virkningen af Dræningen paa Høstudbyttet blev der i 1927—1941 anstillet et Forsøg i Kvorning paa ret stiv, stærkt vandlidende Jord (THØGERSEN 1945). Der blev anvendt 2 Drænafstande, nemlig 11 og 22 m, og 3 Drændybder, nemlig 80, 115 og 150 cm. Et udrænet Areal blev henlagt til Kontrolforsøg.

Grundvandstanden laa i Vækstperioden betydelig under Drænene, i Reglen under en Dybde af 1,5—2 m.

Dræningen medførte, at Udbyttet steg betydeligt. Drændybden var uden Virkning paa Udbyttet. Virkningen af de forskellige Drænafstande var gennemgaaende ret ringe.

Et Forsøg paa Lanna Forsöksgaard i Sverrig paa Agerjord, der karakteriseres som »mullhaltig — mullrik mellanlera« med Lerundergrund gav tilsvarende Resultater.

Der har i de nævnte Forsøg ikke været Tale om en skadelig Virkning af Afvandingen, men Lederen af det svenske Forsøg, Agronom Perman, drager den Slutning, som ogsaa Thøgersen har fremsat, at der vil kunne spares Millionbeløb ved ikke at dræne saa stærkt, som det har været almindeligt. »Tillige vil der i tørre Aar kunne indvindes betydelige Værdier i Form af større Afgrøder, dersom man i højere Grad end det hidtil er sket tog Hensyn til foreliggende Forsøgsresultater paa dette Omraade« (THØGERSEN).

Et andet Afvandingsforsøg, der tillige er Gødningsforsøg, blev anlagt paa en Jordbund, der bestod af Lavmosetørv med en Dybde paa ca. 2 m. Grundvandstanden blev sænket ca. 30 cm til ca. 1 m under Overfladen. Resultatet af Afvandingen var, at Udbyttet af Hø som Helhed har været aftagende med Aarene. Afvandingen har altsaa været for stærk.

Ogsaa Sandjord kan afvandes for stærkt.

Trods de store Kapitaler, der i Aarenes Løb er investeret i Afvanding, trods den store Betydning en rigtig Afvanding har for Stofproduktionen, er det saaledes kun et lille Forsøgsmateriale, der foreligger for at belyse Virkningen af Afvandingens Styrke paa Høstudbyttet. Naar Resultatet af disse Forsøg viser, at Dræningen i et Tilfælde har været overflødig stærk og i et andet, at den har været direkte skadelig, tør det, som det ogsaa stærkt er fremhævet i flere af de ovennævnte Arbejder, være meget paakrævet, at der anstilles yderligere Forsøg.

En Undersøgelse af Virkningen af en Afvanding er forbundet med en Række Vanskeligheder. En optimal Afvanding er forskellig for de forskellige Afgrøder. Planter med dybtgaaende Rødder taaler og behøver en stærkere Afvanding end Planter med et overfladisk Rodsystem, Lerjord med dens store Vandkapacitet behøver og taaler en stærkere Afvanding end Sandjord med dens ringe Vandkapacitet, og først og fremmest træder den skadelige Virkning af for stærk Afvanding kun frem i tørre Aar.

Den Fremgangsmaade, man anvender inden for Landbruget, naar man vil undersøge disse og lignende Problemer, er Markforsøget. Dette har mange og store Fordele, men ogsaa sin Begrænsning. Grundlaget for alt eksperimentelt Arbejde er, at man kun varierer én Faktor ad Gangen, og at man er i Stand til at variere den Faktor, hvis Virkning man vil undersøge. I Markforsøg arbejder man i Reglen med flere variable Faktorer ad Gangen, dels den Faktor, man selv varierer, f. Eks. Gødningsmængden, og dels de variable klimatiske Forhold, navnlig Nedbøren, som man ikke kan beherske. For at komme uden om denne Vanskelighed, gentager man, f. Eks. naar man vil undersøge en Kornsorts Ydeevne, det samme Forsøg gennem en Aarrække, idet man gaar ud fra, at Virkningen af de klimatiske Forhold da vil udlignes, og dette vil vel i Almindelighed ogsaa være rigtigt.

Naar man vil anvende Markforsøg til at belyse Virkningen af Grundvandstand og Afvanding paa Høstudbyttet, møder man som ovenfor nævnt den Vanskelighed, at man ikke kan variere Nedbøren, og at Virkningen af en for stærk Afvanding kun træder frem i tørre Aar, saaledes at man kan komme til at vente mange Aar, før man ser et Resultat af Forsøgene. Heller ikke er det altid helt let at afgøre, hvilke Aar der er tørre, og endelig faar man aldrig to eller flere Aar med ganske de samme Nedbørsforhold, saa man kan kontrollere de Resultater, man har faaet frem i et enkelt Aar. Selv om Markforsøg i høj Grad vil være paakrævet for at løse Problemet om den rigtige Afvandingsgrad, vil det af de anførte Grunde være nødvendigt at supplere dem med Kulturforsøg, ved hvilke man er i Stand til at variere Grundvandstand og Nedbør. Det er en Forsøgsanordning til saadanne Kulturforsøg, som skal beskrives i det følgende.

Som Kulturkar (Fig. 3) anvendes firkantede Beholdere af Metal med en Sidelængde paa 25 cm og en Højde paa 160 cm.

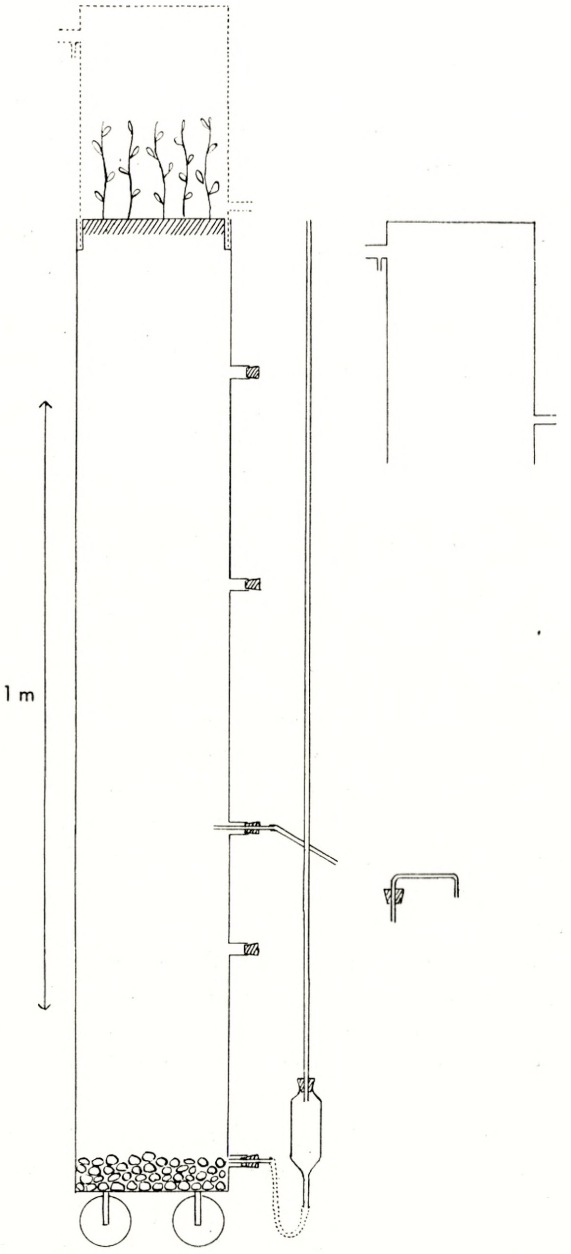


Fig. 3. Kulturkar.

De staar paa Hjul, saaledes at de let kan køres ind paa en Decimalvægt eller paa en lille Transportvogn. I Siderne er der anbragt 5 Aabninger med Bøsninger. Disse anvendes til at udtage Jordprøver til Vandbestemmelse, endvidere kan der indføres Dræn i dem til Afvanding af Jorden. I den nederste Aabning er der indført et Glasrør, som gennem en Gummislange staar i Forbindelse med en Niveaubeholder. I Tegningen er der i Aabningen paa denne indsat et Stigerør, saa man kan følge, hvordan Vandstanden synker i Karret. Naar Vandstanden er sunket til den ønskede Dybde, kan den holdes konstant ved at hælde Vand i Niveaubeholderen, hvis Vandet synker yderligere. Hvis Vandstanden som Følge af Vanding stiger over den ønskede Dybde, kan der i Niveaubeholderen anbringes en Prop med et Glasrør, gennem hvilket Overskuddet af Vand løber bort.

Paa nogle af Kulturkarrene findes der under den øverste Rand en Vandlaas; man kan sætte en Beholder, der foroven er lukket med en Glasplade og forneden er aaben, i Vandlaasen, saaledes at Planterne befinder sig i en afspærret Luftmængde. Efter en af D. Müller udarbejdet, men endnu ikke offentliggjort Metode kan man da foretage en Bestemmelse af Kulturplanternes Assimilationsintensitet ved at lede en Luftstrøm med en bestemt Hastighed og med et kendt Kulsyreindhold fra en Bombe ind gennem den øverste Beholder og foretage en Bestemmelse af den ikke assimilerede Kulsyre i den udstrømmende Luft. Under Forsøget belyses Planterne med elektrisk Lys gennem Glaspladen foroven i Beholderen. I Kulturkarrene kan der i én af Siderne anbringes en Glasplade, gennem hvilken man kan følge Røddernes Vækst[1].

Kulturkarrene anbringes i to Rækker[2] i en Udgravning i Jorden (Fig. 4), saaledes at deres øverste Rand ligger i Niveau med Jordoverfladen. Mellem de to Rækker findes en Løbegang, der ligger lidt dybere, i denne ligger der 4 Skinner, og paa disse

[1] Den Side af Beholderen, hvori denne Glasplade findes, maa hælde svagt indad for at tvinge Rødderne ind mod Glasset.

[2] Det er muligt, at man kunde anbringe to Rækker af Kulturkar paa hver Side af Løbegangen. Kulturkarrene maatte da forbindes to og to med en Gummislange under Bunden, saaledes at man kunde nøjes med at regulere Grundvandstandens Højde i det forreste Kar. Ved Vejningen maatte de to Vægte anbringes ved Siden af hinanden, saaledes at hvert Kar blev vejet paa sin særlige Vægt. Ved denne Anordning vil man spare noget Væksthusareal, men det vil blive besværligere at arbejde med Kulturkarrene.

løber to Decimalvægte (b) til at veje Kulturkarrene samt to Transportvogne (a) til at køre dem ind i Assimilationsrummet A, der ligger for Enden af Karrækkerne; c er Sporskifter. Vægtenes og Vognenes øverste Flade ligger i samme Niveau som den nederste Rand af Hjulene paa Kulturkarrene, saaledes at disse let kan køres ind paa dem.

De to Rækker Kulturkar er dækket med et Glastag, saaledes at de befinder sig i et Drivhus uden Vægge (Fig. 5). De staar saa langt fra Glastagets Yderrande, at det ikke kan regne ned i dem. Glastaget holdes afkølet ved, at der fra en Beholder gennem Røret *a* risler afkalket Vand ned over Glasset, naar Solen skinner. Vandet ledes gennem Samlerør tilbage og ned i en Brønd, hvorfra det pumpes op i Beholderen. I den Jordoverflade, der støder op til Udgravningen, dyrkes der Planter af samme Art som i Kulturkarrene, saaledes at Planterne i disse faar samme Sidelys, som hvis de voksede i en naturlig Bevoksning. Paa den Side af Kulturkarrene, der vender ind mod Løbegangen, anbringes gennemsigtige Skærme, saaledes at Sidelyset ogsaa paa denne Side bliver det samme som under naturlige Forhold.

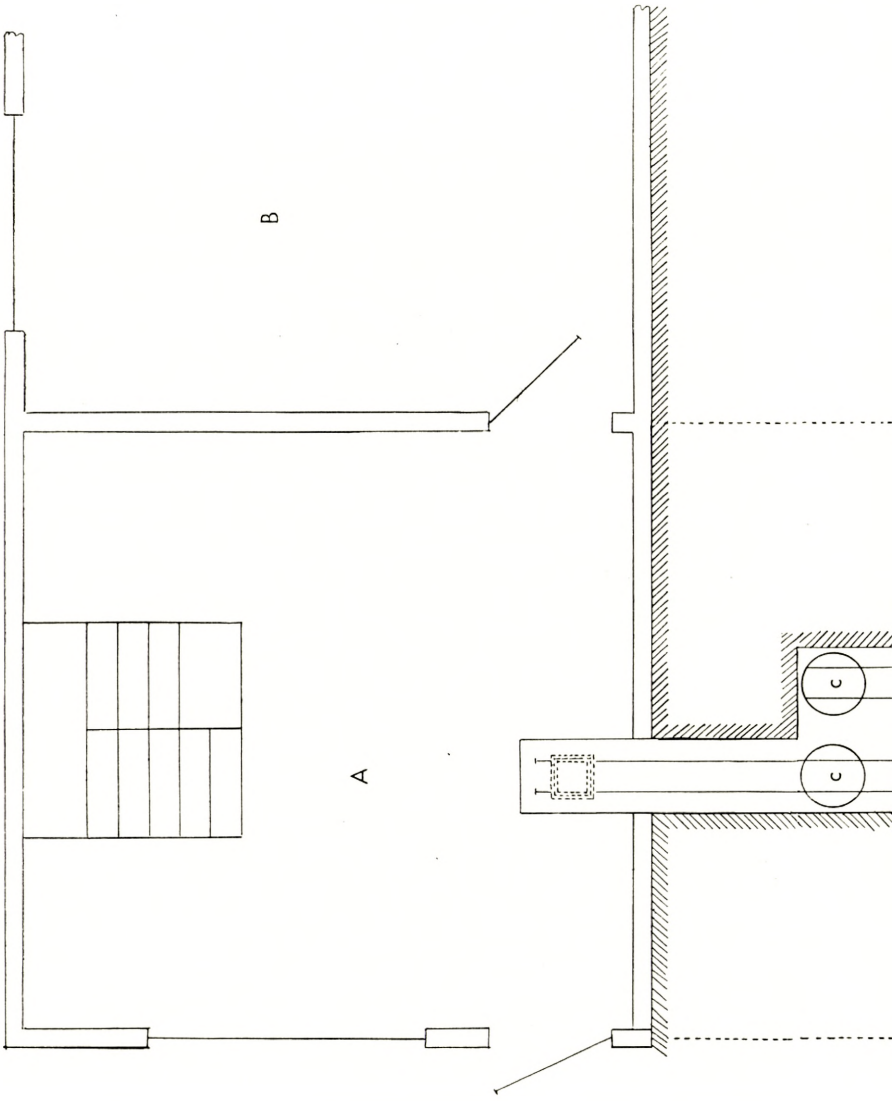
I Hovedbygningen ligger der ved Siden af Assimilationsværelset Rum til Plante- og Jordbundsanalyser samt andre Forsøg (Fig. 4 B etc.). Ved den modsatte Ende af Væksthuset med Kulturkarrene ligger der en Række Bokse til de forskellige Jordarter, som skal benyttes til Forsøgene (C, D).

Eventuelt kan dette Laboratorium suppleres med et Kuldelaboratorium, i hvilket man kan undersøge Planternes Modstandsdygtighed mod lave Temperaturer.

Ved denne Forsøgsanordning kan man variere:

1. Jordbundens Beskaffenhed.
2. Næringsstofferne i Jorden.
3. Afvandingens Hastighed (ved at anbringe et stærkere eller svagere Dræn i Kulturkarrene).
4. Grundvandstandens Dybde.
5. Nedbør (d. v. s. Vandtilførslen).

I et Anlæg som det beskrevne, d. v. s. et aabent Væksthus, vil de klimatiske Faktorer, Lys, Temperatur og Luftfugtighed, ikke være konstant, alligevel vil Anlægget være tilstrækkeligt til


B
A
C
C

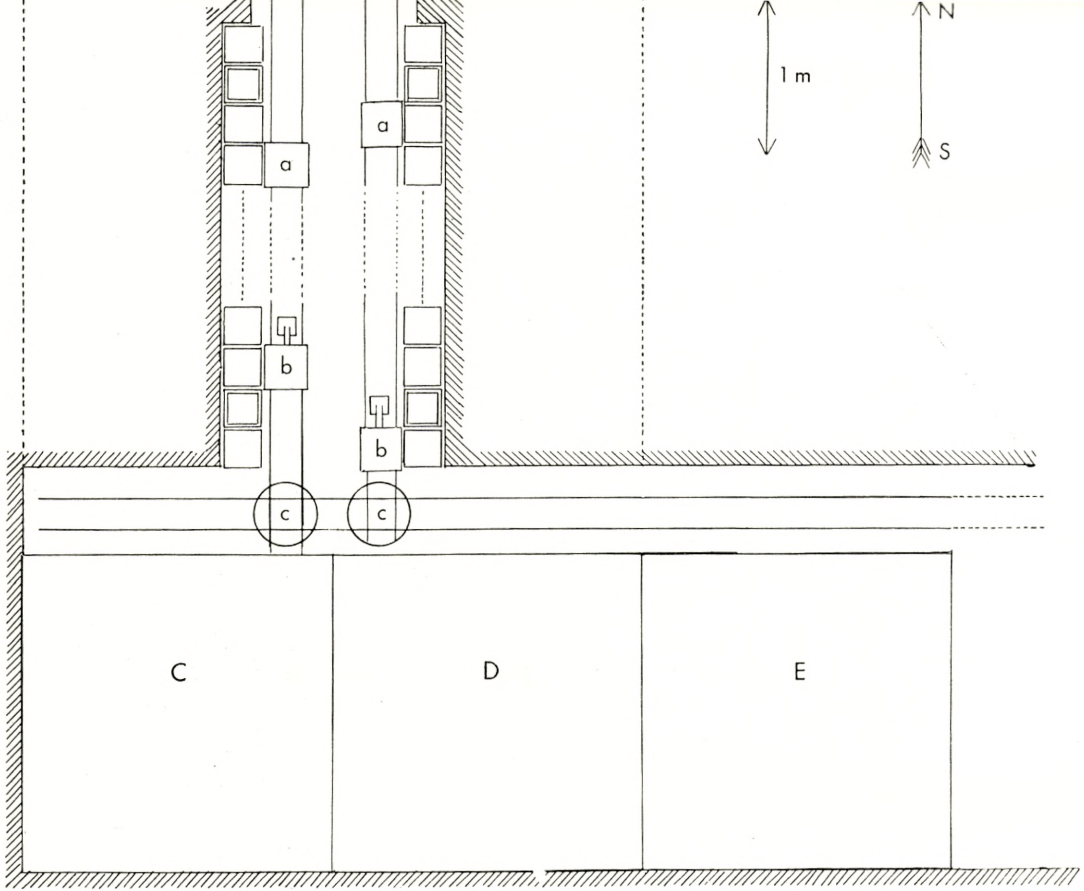


Fig. 4. Laboratorieanlægget, Grundplan.
Mellem de to øverste Sporskifter c skal anbringes to Tværskinner.

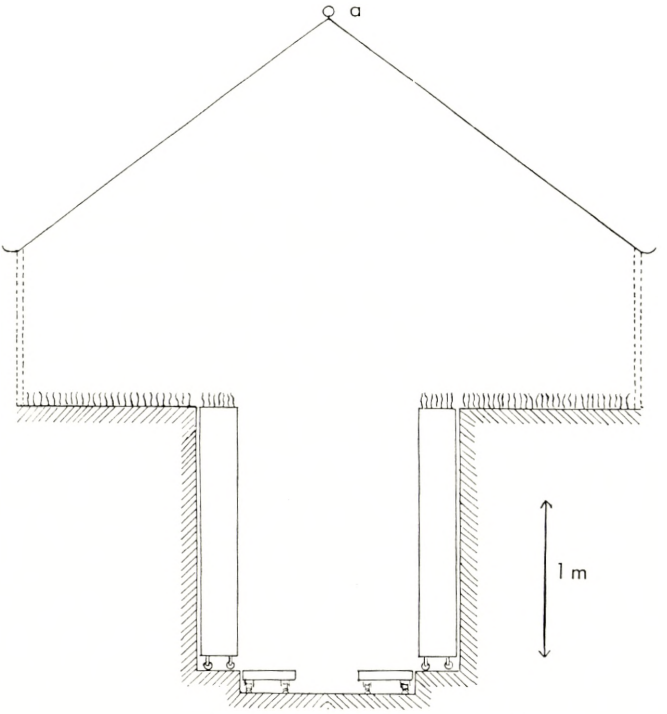


Fig. 5. Laboratorieanlægget, Tværsnit.

at undersøge Vandøkonomien hos Planterne. Der er næppe noget i Vejen for, at man kan indrette et Anlæg, hvor ogsaa Luftfugtighed, Lys, Temperatur og eventuelt Kulsyrespænding kan varieres og holdes konstante. Man maatte da bygge et lukket luft-konditioneret Væksthus. Driften af et saadant vilde imidlertid blive meget kostbart, og man vilde fjærne sig længere fra de naturlige Forhold, end det er ønskeligt.

Man kan maale:

1. Nedbør (d. v. s. Vandtilførslen).
2. Transpiration + Fordampningen fra Jordoverfladen (Vægten ved Forsøgsperiodens Begyndelse + (Vand, der er tilført ovenfra — Vand, der er strømmet ud fra Niveaubeholderen) + Vand, der er tilført gennem Niveaubeholderen — Vægten ved Forsøgsperiodens Slutning).

3. Forandringer i Jordbundens Vandindhold og Vandbindingsevne.
4. Vandhævningen fra Grundvandstanden (den Vandmængde, der er tilført gennem Niveaubeholderen).
5. Spalteaabningernes Aabningsvidde.
6. CO_2 Assimilationen.
7. Stofproduktionen ved Analyse af Udviklingen af Planterne i Kulturkarrene (baade med Hensyn til Bladflade og Tørstof).

Man kan løse følgende Problemer:

Det blev ovenfor fremhævet, at der med Hensyn til Afvanding af Jorden er to Faktorer, som er af Betydning for Planteudviklingen, dels den Hastighed, hvormed en Sænkning af Vandstanden foregaar, og dels Grundvandstandens Dybde under Vegetationsperioden. Det er disse Faktorers Virkning paa Plantevæksten, som det er af Vigtighed at undersøge.

1. Den Hastighed, hvormed Grundvandstanden synker, kan i Kulturforsøgene varieres ved at indskyde Dræn med forskellig Effektivitet, og man kan da undersøge, hvorledes denne Hastighed paavirker Spiringsevnen og Planteudviklingen i dens første Fase. Der er dog Grund til at tro, at dette Problem bedst kan løses ved Markforsøg. Ved Gravning af Brønde kan man let følge Grundvandstandens Bevægelser om Foraaret.

2. Med Hensyn til det andet Problem, Virkningen af Grundvandstandens Dybde, maa det være Hovedopgaven at finde den optimale Grundvandstandsdybde for en bestemt Afgrøde paa en bestemt Jordbund, d. v. s. finde den Grundvandstand, der ikke er højere, end at der i Aar med normal Nedbør kan høstes en god Afgrøde, men som heller ikke er dybere, end at Afgrøden i tørre Aar ikke gaar for langt ned under det normale. Dette Problem kan med Karforsøg løses paa følgende Maade:

Det vil være rimeligt at begynde med Forsøg paa Sandjord, hvor man maa vente at finde de største Udslag. Som Forsøgsplante kan man vælge Byg.

Man begynder da med at fylde et passende Antal Kulturkar, f. Eks. 120, med den paagældende Sandjord. Paafyldningen skal man formentlig helst foretage om Efteraaret, og Karrene staar da hen Vinteren over, for at Jorden kan synke sammen og

faa en normal Lejring[1]. I Forvejen maa man have bestemt den vandbindende Kraft i Jorden som Funktion af Vandindholdet, saaledes at man under Forsøget kan nøjes med at bestemme den sidste Størrelse.

Om Foraaret, naar Forsøget skal begynde, deles Kulturkarrene i 15 Grupper, hver paa 8. Hver Gruppe har altsaa et Areal paa $^1/_2$ m^2 (Tørstofproduktionen er ca. 300—500 g). De tre Grupper er bestemt til at undersøge Udviklingen af Planterne ved en Grundvandstandsdybde paa henholdsvis 50, 90 og 130 cm Dybde og normal Nedbør, de andre Grupper skal anvendes til at undersøge Tørkeresistensen ved de samme Grundvandstandsdybder.

Til at begynde med behandles begge Grupper ens. Karrene drænes til den ønskede Grundvandstandsdybde og Byggen saas. Hver 3die eller 6te Dag tilføres $^1/_{10}$ eller $^1/_5$ af den maanedlige Nedbør. Naar Planterne har naaet en passende Udvikling, ophører den fælles Behandling.

For de tre Grupper med normal Nedbør fortsættes Forsøget uforandret, d. v. s. med Vanding hver 3die eller 6te Dag. Man bestemmer paa den ovenfor angivne Maade, hvor meget Vand der bortgaar ved Transpiration, hvor meget der stiger op fra Grundvandet, og Formindskningen af Vandindholdet i Jorden for hver Forsøgsperiode. Endvidere bestemmer man paa passende Tidspunkter Bladareal og Tørstofmængde i de forskellige Organer samt Bevoksningens Assimilationsintensitet (paa forskellige Tidspunkter af Dagen, eventuelt ved forskellige Lysstyrker) og bliver derved i Stand til at fastlægge Stofproduktionens Forløb i Vegetationsperioden. Denne vil forløbe efter en S-formet Kurve.

Ved Slutningen af Forsøget bestemmer man Planteantal, Buskning, Antal af Aks og Korn samt Tørstofindholdet i de forskellige Organer og beregner disse Størrelser pr. ha.

De 12 andre Grupper anvendes til Undersøgelse af Tørkeresistensen. Da denne (foruden af Luftfugtighed og Vind) er afhængig af Bladarealet, er den ikke alene forskellig for forskellige

[1] Der kan ikke være Tvivl om, at man ved at stampe Jorden fast sammen kan opnaa en lige saa fast Lejring som i naturlig Jordbund. Skulde man alligevel nære Betænkeligheder i denne Henseende, er der intet i Vejen for, at man kan skære Blokke ud af frossen Jord og overføre dem i denne Tilstand i Kulturkarrene; man forandrer da ikke Jordens Struktur i mindste Maade.

Jorden til Forsøgene maa helst tages fra Forsøgsstationer, hvor man gennem mange Aars Forsøgsvirksomhed nøje kender Jordens Ydeevne.

Planter, men sandsynligvis ogsaa noget forskellig paa forskellige Udviklingsstadier. Tillige spiller naturligvis Tørketidens Længde en stor Rolle. For at belyse disse Forhold, kunde man dele de 12 Grupper paa følgende Maade:

1. 1 Maaneds Tørketid, begyndende tidligt (f. Eks. fra 15. April—15. Maj).
   3 Grundvandstandsdybder paa 50, 75 og 125 cm.
2. 1 Maaneds Tørketid, begyndende senere (f. Eks. fra 15. Maj—15. Juni).
   3 Grundvandstandsdybder paa 50, 75 og 125 cm.
3. 2 Maaneders Tørketid, begyndende tidligt (f. Eks. fra 15. April—15. Juni).
   3 Grundvandstandsdybder paa 50, 75 og 125 cm.
4. 2 Maaneders Tørketid, begyndende senere (f. Eks. fra 15. Maj—15. Juli).
   3 Grundvandstandsdybder paa 50, 75 og 125 cm.

Karrene fra alle de forskellige Forsøgsrækker blandes om mellem hinanden.

Under Tørkeperioden bestemmer man ligeledes med korte Mellemrum, hvor meget Vand der bortgaar ved Transpirationen, hvor meget Vand der stiger op fra Grundvandet, og Formindskningen af Vandindholdet i Jorden. Man bliver derved i Stand til at afgøre, hvilken Betydning det disponible Vand i Jorden og Grundvandet har for Vandforsyningen.

Man vil finde, at Transpirationen synker efter en Kurve, som skematisk er gengivet i Fig. 6[1]. Under den første Fase af denne Kurve er Spalteaabningerne endnu helt eller delvis aabne, enten paa enkelte Blade eller i nogle Timer af Dagen. Der finder derfor nogen Kulsyreassimilation og Stofproduktion Sted, men den aftager efterhaanden. Naar Vandindholdet i Jorden er sunket saa stærkt, at den vandbindende Kraft og Modstanden mod Vandforskydningen i Jorden er blevet saa stor, at Vandoptagelsen nærmer sig Nul, træder Udviklingen ind i Fase II. Alle Spalteaabningerne er lukkede Døgnet rundt, Stofproduktionen er standset, men Bladene er levende. Det kan ikke undgaas, at der stadig fordamper Vand fra Bladene gennem Kutikulaen, og naar

[1] Under den første Fase vil Transpirationen dog svinge ret stærkt efter Fugtigheden i Luften.

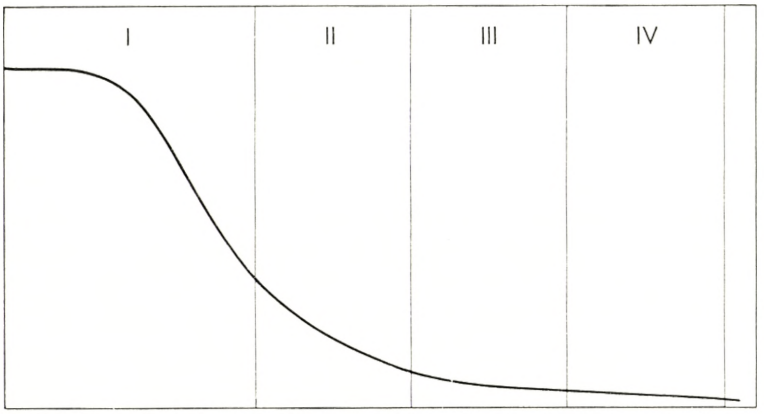


Fig. 6. Transpirationens Forløb under Udtørring.

Vandindholdet i Bladene er sunket til en vis Grænse, begynder de at dø, og Udviklingen træder ind i Fase III. Ved Slutningen af denne er alle Plantens Blade døde, men der er, som paa en Græsmark, Knopper tilbage, disse vil da efterhaanden dø under Fase IV. Saa vidt kommer det imidlertid ikke i Naturen.

I det beskrevne Tilfælde imødegik Planten til at begynde med Udtørringen alene ved at lukke Spalteaabningerne, ofte vil dog Transpirationen nedsættes, ikke alene ved Lukning af Spalteaabningerne, men ogsaa ved Formindskelse af Bladarealet, idet de nederste Blade begynder at dø allerede samtidig med, at Spalteaabningerne holdes helt eller delvis aabne, saaledes at der stadig foregaar en Stofproduktion, der dog er stærkt nedsat. Fase I—III kommer derfor til at glide mere jævnt over i hinanden, men ogsaa i dette Tilfælde faar man en faldende Kurve som Udtryk for, at baade Transpiration og Stofproduktion tager af.

Det er da disse Kurver, der er et Udtryk for den paagældende Bevoksnings Tørkeresistens. Jo brattere Kurven falder, desto hurtigere gør den skadelige Virkning af Vandmanglen sig gældende, og desto mindre er altsaa Tørkeresistensen, omvendt jo langsommere Kurven falder, desto større er Tørkeresistensen. Det, der da skal afgøres ved Forsøgene, er, i hvilken Grad Kurvens Forløb og altsaa ogaa Tørkeresistensen paavirkes af Grundvandstandsdybden.

Tørkeperioden afbrydes ved, at man paany tilfører Vand;

man kan da fastslaa, hvilken Virkning den har haft paa det endelige Høstudbytte.

Paa tilsvarende Maade anstilles Forsøg paa Lerjord og med andre Afgrøder f. Eks. Græs.

3. Det gælder da om, som nævnt, gennem Forsøgene at finde frem til den optimale Grundvandstand, idet man tager Hensyn til Høstudbyttet, ikke alene i fugtige, men ogsaa i de tørre Aar. For at naa dette Maal kunde man ogsaa reproducere Udviklingen af forskellige Afgrøder, f. Eks. af Korn, paa forskellig Jordbund, f. Eks. Sandjord og Lerjord, og med forskellig Grundvandstand i hvilke som helst Aar, f. Eks. i den fugtige Sommer 1946 og i den tørre Sommer 1947, ved at tilføre den Vandmængde, som faldt paa de forskellige Datoer i de paagældende Aar, til Kulturkarrene.

4. Den beskrevne Metode kan endvidere anvendes til at sammenligne Tørkeresistensen hos forskellige Sorter. Ligesom man af Vintersæd fremstiller Sorter, der er særlig modstandsdygtige mod lave Vintertemperaturer, vil det være paakrævet at fremstille Sorter af Sommerkorn, som er særlig resistente mod en Tørkeperiode.

5. Endvidere vil man kunne undersøge Virkningen af Gødningsstoffer under vel definerede Forhold og tillige belyse Samspillet mellem Gødningsmængde og Tørkeresistens.

Man har ofte den Opfattelse, at man betrager Vandet i Jorden som en Gift, som det gælder om at blive af med, og at man tager imod de tørre Aar som en Skæbnens Tilskikkelse, som der ikke er noget at gøre ved. Det er sandt, at Vand kan virke som Gift for Planterne, men Vandet er ogsaa den Faktor, som betinger Liv, og som det derfor er Grund til at økonomisere med saa meget som muligt, det vil sige, man maa ikke bortlede Vand, der kan være til Nytte for Bevoksningen.

Man vil gennem den beskrevne Metodik kunne løse det Spørgsmaal, hvilken Vandstandsdybde, der er den optimale paa forskellig Jordbund og for forskellige Afgrøder. Den praktiske Betydning af Undersøgelsen vil afhænge af, i hvilken Grad man er i Stand til at naa frem til en Afvandingsmetode, der gør det muligt at regulere, eventuelt helt standse Afvandingen, saaledes at

Grundvandstanden kan holdes i en Dybde, som er optimal for den paagældende Afgrøde. Det er maaske ikke udelukket, at dette Maal kan naas ved at indskyde Ventiler paa passende Steder i Drænledningerne.

C. Andre Opgaver.

Foruden de foran omtalte Undersøgelser over Planternes Vandøkonomi er der en Række andre Opgaver, som det vil være naturligt, at Laboratoriet tager op. Her skal kun nævnes nogle enkelte.

1. Undersøgelser over den praktiske Brug af Hormonerne. Disse benyttes i Landbruget for Øjeblikket kun til Bekæmpelse af Ukrudt, det har imidlertid været hævdet, at de ogsaa kan benyttes til at forøge Stofproduktionens Størrelse. Selv om man maa betragte de Undersøgelser, der ligger til Grund for denne Paastand, med en vis Skepsis, er Spørgsmaalet dog af saa vidtrækkende Betydning, at det maa undersøges nærmere.

2. Et andet Problem er dette: Hvori bestaar Forædling? d. v. s. med Hensyn til hvilke morfologiske og fysiologiske Egenskaber adskiller en højt ydende Race sig fra en mindre stærkt ydende? Dette Problem kan løses ved en morfologisk Analyse af en Bestand og en fysiologisk Analyse af Stofproduktionen i denne. En saadan Analyse vil afgive Grundlag for et rationelt Forædlingsarbejde.

D. Zusammenfassung.

Die Abhandlung enthält eine Beschreibung der Einrichtung eines Laboratoriums für Untersuchungen über die Stoffproduktion der landwirtschaftlichen Kulturpflanzen.

Zunächst soll es die Aufgabe des Laboratoriums sein, die Bedeutung der Wasserversorgung für die Stoffproduktion zu untersuchen. Die Pflanzen werden in den in Abb. 3 dargestellten Metallgefässen gezüchtet; durch Zufuhr von Wasser zu dem Niveaubehälter, der durch einen Gummischlauch mit einem in das Kulturgefäss eingeführten Glasrohr verbunden ist, ist es möglich, den Grundwasserstand in einer bestimmten Tiefe zu halten. In dem Wasserverschluss kann eine Stülpe, die oben mit einer Glasplatte verschlossen ist, angebracht werden. Es ist dann möglich die Intensität der CO_2-assimilation nach einer von D. Müller ausgearbeiteten Methode zu messen.

Die Kulturgefässe werden in einer Ausgrabung (Abb. 4) untergebracht. Auf den Schienen zwischen den beiden Reihen von Kulturgefässen laufen zwei Dezimalwaagen und zwei Transportwägen, auf welche die Kulturgefässe eingeschoben werden können. Durch Wägung derselben in gewissen Zwischenräumen kann man die Grösse der Transpiration bestimmen. Die Transportwägen dienen dazu, die Kulturgefässe in den Assimilationsraum einzufahren.

Die Kulturgefässe sind mit einem Glasdach überdeckt, so dass sie sich in einem Gewächshaus ohne Seitenwände befinden (Abb. 5). Sie sind dadurch gegen Regen geschützt, und die Bewässerung kann daher genau reguliert werden. Man ist somit imstande, die Entwicklung der Kulturpflanzen bei verschiedener Tiefe des Grundwasserstandes zu verfolgen, und zwar sowohl bei normaler Wasserzufuhr als auch während einer Trockenperiode,

wenn kein Wasser von oben zugeführt wird; auf diese Weise kann man die Wirkung der letzteren auf Entwicklung und Stoffproduktion der Versuchspflanzen feststellen.

Es ist somit möglich, die optimale Tiefe des Grundwassers für verschiedene Bodenarten und verschiedene Kulturpflanzen zu ermitteln. Die praktische Bedeutung dieser Versuche hängt davon ab, ob es möglich ist, ein geeignetes Drainierungsverfahren auszuarbeiten, so dass man instandgesetzt wird, die Ableitung des Wassers zu regulieren, bezw. ganz zu unterbrechen. Man würde dann mit einer gewissen Annäherung den Grundwasserstand in einer für den betreffenden Bestand optimalen Tiefe halten können.

Daneben soll aber das Laboratorium imstande sein, auch andere Aufgaben, z. B. Hormonuntersuchungen, in Angriff zu nehmen.

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BY

P. BOYSEN JENSEN

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
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1. A Method to Estimate the Increase in Tissue Cultures.

(a) Starting of the tissue cultures. According to WHITE (1939) sterile tissue cultures of *Nicotiana glauca* × *Langsdorffii* can be obtained from young stems of the hybrid by breaking them 4–5 cm. from the tips and removing cones of tissue from the exposed, aseptic surface with a sterile scalpel.

Besides this method I have also used callus produced by seedlings to start the cultures. Seeds of the hybrid were wrapped in moist filter paper and placed in a pulp of crushed tomatoes for 48 hours. Afterwards they could be sterilized in the usual manner with calcium hypochlorite. The sterile seeds were placed in Freudenreich flasks on a semisolid nutrient containing 1 per cent. agar and the usual salts. When the seedlings had developed, the tip was severed from the basal part with a pair of scissors and the callus produced on the cut surface was used for setting up the cultures.

It seems that cultures prepared after the last method (Strain 18 in Table 2) grow a little faster than those prepared after the first one.

(b) Culture technique and nutrients. The cultures were maintained in 100 ml. Erlenmeyer flasks of Duran-, Jena-, or Pyrex glass.

The water used for preparation of the nutrients was tap water distilled first over alkaline potassium permanganate (per l. 7 ml. 0.2 per cent. $KMnO_4$ + 2.5 ml. 10% KOH), then over barium hydroxide (per l. 2.5 ml. 0.8 per cent. $Ba(OH)_2$, and finally without any addition (WHITE 1932).

The following stock solutions were prepared:

I b 0.95 g $Ca(NO_3)_2$
1.7 g $MgSO_4$
0.95 g Na_2SO_4

0.38 g KNO_3
0.31 g KCl
0.08 g KH_2PO_4
500 ml. triple distilled water

II 0.037 g KJ
0.125 g $Fe_2(SO_4)_3$
0.220 g $MnSO_4$
0.075 g $ZnSO_4$
0.080 g H_3BO_3
500 ml. triple distilled water

III a_1 0.03 g glycine
0.005 g thiamin
100 ml. triple distilled water

III a_2 0.03 g asparagine
0.005 g nicotinic acid
100 ml. triple distilled water

III a_3 0.03 g glycine
0.03 g asparagine
0.005 g nicotinic acid
200 ml. triple distilled water

III a_4 0.03 g glycine
0.03 g asparagine
0.005 g thiamin
200 ml. triple distilled water

III a_5 0.03 g glycine
0.005 g thiamin
0.005 g nicotinic acid
200 ml. triple distilled water

III a_6 0.03 g asparagine
0.005 g thiamin
0.005 g nicotinic acid
200 ml. triple distilled water

IIIa_7 0.005 g thiamin
0.005 g nicotinic acid
200 ml. triple distilled water.

The nutrients were made by mixing 100 ml. Ib + 10 ml. II + 10 ml. of one or two of the stock solutions $IIIa_1$—$IIIa_7$ + 20 g sucrose + 800 ml. triple distilled water.

Each culture flask was charged with 8—10 ml. of the nutrient and plugged with non-absorbent cotton, covered with filter paper. Transfers were made at intervals of 10 days, in some periods during the war only once monthly.

The cultures were maintained at room temperature in weak light.

(c) Estimation of the increase. At intervals of about a month the increase of the cultures was estimated in the following way. The tissue fragment from a culture was placed in a small, dry sterilized glass box (fig. 1, diameter 3.0 cm., height 2.5 cm.), and the box with the fragment was weighed; afterwards the fragment was transferred to a culture flask with fresh nutrient, and the box was weighed anew. The difference between the weight of the fragment, estimated in this manner, and the weight a month ago is the increase in mg. in the said month.

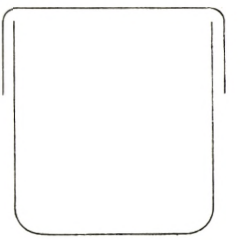

Fig. 1.

The fragments are very seldom contaminated by this procedure.

The method permits consecutive measurements on the same fragment.

(d) Calculations. Blackman (1919) has found that the equation $W_t = W_0 e^{rt}$, which implies that the increase is proportional to the weight in every moment, is applicable for the growth of an annual plant. According to Caplin (1947) this formula is also particularly applicable for describing the growth of tobacco tissue cultures. Still, as the cultures mainly or exclusively grow on the surface, it is more probable that the increase is proportional to the surface and not to the weight of the fragment, and I have therefore preferred to estimate the increase in mg. per day per sq. cm. surface. It is assumed that the fragment is spherical and that the specific gravity is 1.

The calculations are carried out in the following way. Through the method described above the weight of a fragment is estimated. The corresponding surface is taken from the curve in fig. 2,

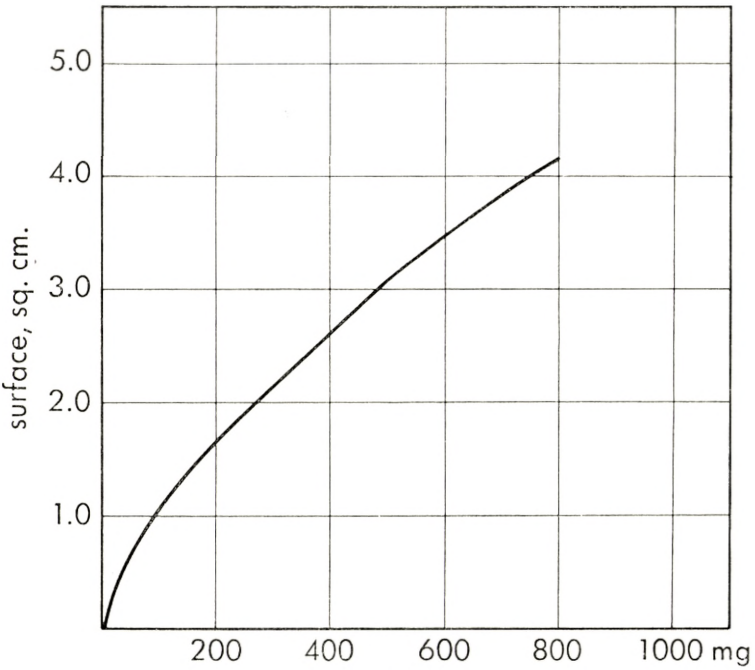

Fig. 2.

in which the surface of a sphere is rendered as a function of its weight in mg. The increase during a period of a month is divided by the surface of the fragment at the beginning of the period. In this way we get the increase in the period in mg. per sq. cm. surface. Next the mean of the increases for the different fragments in a series is calculated; the mean is divided by the number of days in the period, and thus we get the mean increase for a series in mg. per sq. cm. surface and day.

If a fragment breaks, so that there are more than one fragment in a flask, the surface is calculated by adding the surfaces of the single fragments.

Table 1 shows the calculations and results of an experiment with a single fragment for 7 months. Although the increase varies considerably, the accuracy is sufficient to obtain reliable results, when the increase is calculated as a mean of the increases in a series of 5—10 cultures for a prolonged time (cf. Table 2).

Table 1.

1 Weight mg.	2 Surface sq.cm.	3 Increase mg. (7–1)	4 Increase mg. per sq.cm. (3:2)	5 Number of days	6 Increase mg. per sq. cm. per day (4:5)	7 Weight mg.	8 Surface sq. cm.	9 Increase mg.	10 Increase mg. per sq.cm. (9:8)	11 Number of days	12 Increase mg. per sq.cm. per day (10:11)
$^{17}/_{5}$	$^{17}/_{5}$	$^{17}/_{5}$–$^{27}/_{6}$	$^{17}/_{5}$–$^{27}/_{6}$	$^{17}/_{5}$–$^{27}/_{6}$	$^{17}/_{5}$–$^{27}/_{6}$	$^{27}/_{6}$	$^{27}/_{6}$	$^{27}/_{6}$–$^{18}/_{8}$	$^{27}/_{6}$–$^{18}/_{8}$	$^{27}/_{6}$–$^{18}/_{8}$	$^{27}/_{6}$–$^{18}/_{8}$
47	0.63	41.7	66	41	*1.61*	88.7	0.96	48.4	50	52	*0.96*
$^{18}/_{8}$	$^{18}/_{8}$	$^{18}/_{8}$–$^{14}/_{9}$	$^{18}/_{8}$–$^{14}/_{9}$	$^{18}/_{8}$–$^{14}/_{9}$	$^{18}/_{8}$–$^{14}/_{9}$	$^{14}/_{9}$	$^{14}/_{9}$	$^{14}/_{9}$–$^{20}/_{10}$	$^{14}/_{9}$–$^{20}/_{10}$	$^{14}/_{9}$–$^{20}/_{10}$	$^{14}/_{9}$–$^{20}/_{10}$
137.1	1.28	51.1	40	27	*1.48*	188.2	1.59	60.4	38	36	*1.06*
$^{20}/_{10}$	$^{20}/_{10}$	$^{20}/_{10}$–$^{20}/_{11}$	$^{20}/_{10}$–$^{20}/_{11}$	$^{20}/_{10}$–$^{20}/_{11}$	$^{20}/_{10}$–$^{20}/_{11}$	$^{20}/_{11}$	$^{20}/_{11}$	$^{20}/_{11}$–$^{18}/_{12}$	$^{20}/_{11}$–$^{18}/_{12}$	$^{20}/_{11}$–$^{18}/_{12}$	$^{20}/_{11}$–$^{18}/_{12}$
248.6	1.91	38.7	20.3	31	*0.65*	287.3	2.09	70.7	34	28	*1.21*
$^{18}/_{12}$											
358.0	..	..	..	..	..	..	..	..	..	..	..

2. The Influence of Thiamin and Some Amino Acids on the Growth of Tobacco Tissue Cultures.

TATUM and BELL (1946) have shown that different genes are concerned in the synthesis of thiamin in *Neurospora*. The wild type of this fungus does not require thiamin for growth, but four mutant strains have been found, which cannot synthetisize this compound. The strain 18588 can synthetisize pyrimidine, but not thiazole, the strain 9185 can synthetisize both pyrimidine and thiazole, but cannot couple the two compounds. The strains 17084 and 1090 require for growth either thiamin or a mixture of thiazole and pyrimidine. The mutant strains are differentiated from the wild type by single genes.

Thiamin or its precursors are also essential to the growth of roots in organ cultures. For tomato roots growth is obtained by supplying the thiazole portion of the thiamin molecule; hence they must be able to synthetisize pyrimidine and to couple the two compounds (ROBBINS and BARTLEY 1937, 1938, WHITE 1937). The roots of pea require both thiazole and pyrimidine (BONNER 1938). As the green plants are autotrophic we must assume that the thiamin is supplied to the roots from the stem and leaves.

Thus a similar difference exists as to the ability to synthetisize thiamin on the one hand between the wild type of *Neurospora* and the mutant strain 18588, on the other hand between the leaves and the root of a tomato plant. In the first case the difference can be explained by the mutation of a gene. Even if it is probable that genes also are concerned in the synthesis of thiamin in the tomato plant, the inability of the root to build this substance cannot be explained by a difference in the genes in the leaves and the root, because the nuclei in these organs are equivalent. We must therefore assume that besides the genes also a cytoplasmatic factor or a surrounding factor, the effect of which is different in leaves and root, is concerned in the synthesis of thiamin.

It may be possible to elucidate the nature of this factor through studies on the requirement of thiamin in tobacco tissue cultures. We can prepare tissue cultures both from the stem and the root and can therefore investigate if such cultures differ as

to their need of thiamin and if the synthesis of thiamin is influenced by external factors (e.g. light).

Previously HILDEBRANDT, RIKER, and DUGGAR (1946) have studied the influence of thiamin on the growth of tobacco tissue cultures. They found: "thiamine and glycine thus seemed beneficial for tobacco tissue, but, since the L. S. D. values for these media were not significant, the necessity of these vitamins and glycine for these tissues is questionable."

With the method described above I have investigated the necessity of thiamin, nicotinic acid, and some amino acids for the growth of tobacco tissue cultures in light. The results of the experiments are rendered in Table 2.

The basal medium contains the ordinary salts + sucrose + thiamin + nicotinic acid + glycine + asparagine. The difference in the increase for the different strains is not great. The highest increase is found for strain 18, prepared from sterile seedlings.

An omission of one of the vitamins or amino acids does not diminish the increase materially.

The most significant fact is that the increase on a nutrient only containing inorganic salts and sucrose is about the same as in the basal medium (1.26 mg. per sq. cm. per day against 1.31 and 1.35).

The experiment lasted 7 months, during which time the weight of one of the cultures was augmented from 47 to 358 mg. As a diminution of the increase could not be observed (cf. Table 1), a reserve of thiamin in the fragment at the beginning of the experiment cannot be held responsible for the growth of the tissue.

Hence we may conclude that tobacco tissue from the stem can grow in light without any supply of thiamin; therefore it must be able to synthetisize this compound. Still it must be remembered that the increase of a tissue culture is rather small, and the possibility exists that the thiamin produced by the cells would not suffice if the increase was of the same magnitude as in normal plants.

I have made few experiments with roots. SKOOG (1944) remarks that experiments with excised roots of the tobacco hybrid could not be continued "as in all cases roots would eventually produce callus and would then cease to grow". I have got an impression that it will be possible to obtain an unlimited growth

Table 2. Increase, mg. fresh weight per sq. cm. surf. per day.

Strain	Composition of the nutrients	Number of cultures	c. $^{17}/_{5}$ – $^{27}/_{6}$ 1944	c. $^{27}/_{6}$ – $^{19}/_{8}$	c. $^{19}/_{8}$ – $^{15}/_{9}$	c. $^{15}/_{9}$ – $^{20}/_{10}$	c. $^{20}/_{10}$ – $^{18}/_{11}$	c. $^{18}/_{11}$ – $^{17}/_{12}$	c. $^{17}/_{12}$ – $^{26}/_{1}$ 1945	Mean	Composition of the nutrients
18	Ib + II + $IIIa_1$ + $IIIa_2$	5	1.59	2.30	2.51	1.40	1.97	1.45		1.87	} basal medium
18	Ib + II + $IIIa_1$ + $IIIa_2$	3	0.92	2.62	1.70	1.66	2.10	1.81		1.80	
23	Ib + II + $IIIa_1$ + $IIIa_2$	4	1.12	1.26	1.48	1.37	1.76	0.87		1.31	
24	Ib + II + $IIIa_1$ + $IIIa_2$	3	0.76	1.17	2.41	0.97	2.21	0.58		1.35	
25	Ib + II + $IIIa_1$ + $IIIa_2$	5	0.91	1.38	1.73	1.89	1.63	2.30	0.97	1.54	
18	Ib + II + $IIIa_6$	6	1.19	1.55	2.17	2.72	2.36	3.36	2.41	2.25	bas. med. – Glycine
18	Ib + II + $IIIa_5$	6	1.61	1.47	2.00	2.14				1.81	– asparagine
18	Ib + II + $IIIa_7$	5	1.32	0.84	1.30	1.89	1.68	1.61	1.44	1.44	– (glycine + asparagine)
24	Ib + II + $IIIa_3$	5	0.83	1.00	1.22	1.59	1.07	1.30	2.02	1.29	– thiamin
18	Ib + II + $IIIa_4$	6	1.41	2.36	1.63	2.17	2.11	2.68	2.41	2.11	– nicotinic acid
23.24	Ib + II	5	1.32	1.06	1.67	0.92	1.13	1.43		1.26	– (glycine + asparagine + thiamin + nicot. acid)

of the roots by culture on an oblique surface of an agar nutrient in test tubes. Unfortunately I shall not be able to continue these experiments in the future.

3. Differentiation in Tobacco Tissue Cultures.

WHITE (1939) has shown that tobacco tissue cultures when immersed in a liquid nutrient can form leafy branches. He supposes that diminution of oxygen calls forth differentiation. SKOOG (1944) found that also temperature and light influence the organ formation in tissue cultures. In experiments carried out at 33°, 25°, 18°, 12°, and 5° the amount of differentiation reaches an optimum at 18°. Tissue developed in strong light is relatively undifferentiated, in darkness and in weak light development of buds occurred generally.

Also the differentiation in higher plants is influenced by the surrounding factors. Germinating fern spores in weak light develop an undifferentiated tube, in stronger light cell divisions occur, and a prothallium arises. In seedlings of dicotyledonous plants light inhibits elongation of the internodes of the stem, but promotes differentiation. In shoots developed from a stub of a tree and therefore supplied with nutrients and water in abundance the leaves are abnormally large, but the differentiation is inhibited. Humid air and 3-indole acetic acid stimulate the growth of cells and can promote formation of undifferentiated tissue.

Even if there are exceptions a certain correlation seems to exist between growth and differentiation. Factors accelerating growth (weak light, nutrients and water in abundance, stimulants) inhibit differentiation and vice versa. But also other factors are concerned with differentiation. Thus Ca-ions seem to promote formation of root hairs.

SKOOG (1949) has found that tissue cultures never produce roots. In some instances formation of root systems on shoots produced from a tissue culture occurred. I can confirm these results.

I have tried to produce a normal plant from a tobacco tissue culture. The first step was to make the culture grow auto-

trophically. At intervals of 14 days the cultures were transferred from a 2 per cent. sucrose solution to solutions with 1 per cent., 0.5 per cent., and 0.25 per cent. sucrose and at last to a pure inorganic nutrient. The cultures were maintained in rather weak light.

In order to supply the tissue fragments with CO_2 they were placed in Erlenmeyer flasks on the surface of a semisolid substratum which besides the usual salts contained 0.75—1 per cent. agar. The flasks were placed in Fresenius desiccators, which were evacuated and filled with pure CO_2 (prepared from pure Na_2CO_3 and H_2SO_4, washed with a $NaHCO_3$ solution and stored in a flask above $NaHCO_3$) until a pressure of 200 mm. The CO_2 content was renewed twice weekly. The desiccators were maintained in open air in shadow. Gradually the cultures assumed a deep green colour, but they were relatively undifferentiated. An addition of $CaSO_4$ to the nutrient made the cultures form a great number of leafy branches with a length of 1—2 mm., but no roots were produced. Two of the biggest shoots were severed off, and the basal part was covered with a paste containing 3-indole acetic acid to promote the formation of roots. The shoots were planted in soil and covered with a beaker. In some weeks they produced 3—4 small leaves; in the meantime the autumn had come and the experiments had to be finished. One of the shoots produced two roots.

Thus it was possible from an undifferentiated culture to produce an autotrophic plant with leaves, stem, and root. But the growth was very slow, the plant seemed to lack some, probably cytoplasmatic, factor.

4. Summary.

1. A method is described which permits consecutive measurements of the increase of the same fragment of a tissue culture.

2. A tobacco tissue culture from the stem can grow indefinitely in light in a nutrient containing only inorganic salts and sucrose. No addition of amino acids or vitamins is needed.

3. It was possible to produce a normal autotrophic plant from an undifferentiated tobacco tissue culture; but the plant was only a few mm. high, and the growth was very slow.

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A NEW GENUS OF THE *DICTYOTACEAE*

BY

F. BØRGESEN

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
1950

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In a collection of marine algae recently sent to me for determination by Dr. R. E. VAUGHAN, Director of *Mauritius Institute and Public Museum*, Port-Louis, a small brown alga is included which after examination has proved to be the representative of a new genus of the Fam. *Dictyotaceae*.

In September 1938 Dr. VAUGHAN asked me to assist him in determining a collection of marine algae from Mauritius and since then Dr. VAUGHAN with indefatigable eagerness has undertaken collections of marine algae along the shores of the island and sent them to me for determination.

It is therefore a great pleasure for me to name this little interesting alga in honour of Dr. VAUGHAN.

Vaughaniella rupicola Børgs. nov. gen. et nov. spec.

The prostrate, creeping, flattened thallus (Fig. 1—3) of this little *Dictyotacea* is fastened by rhizoids to the substratum. The

Fig. 1. *Vaughaniella rupicola* Børgs. Some fragments prepared out from tufts. Natural size.

thallus has monopodial growth performed by a large lens formed apical cell in the main filaments about 75 μ broad and 35 μ high, from which segments gradually are cut off below (compare

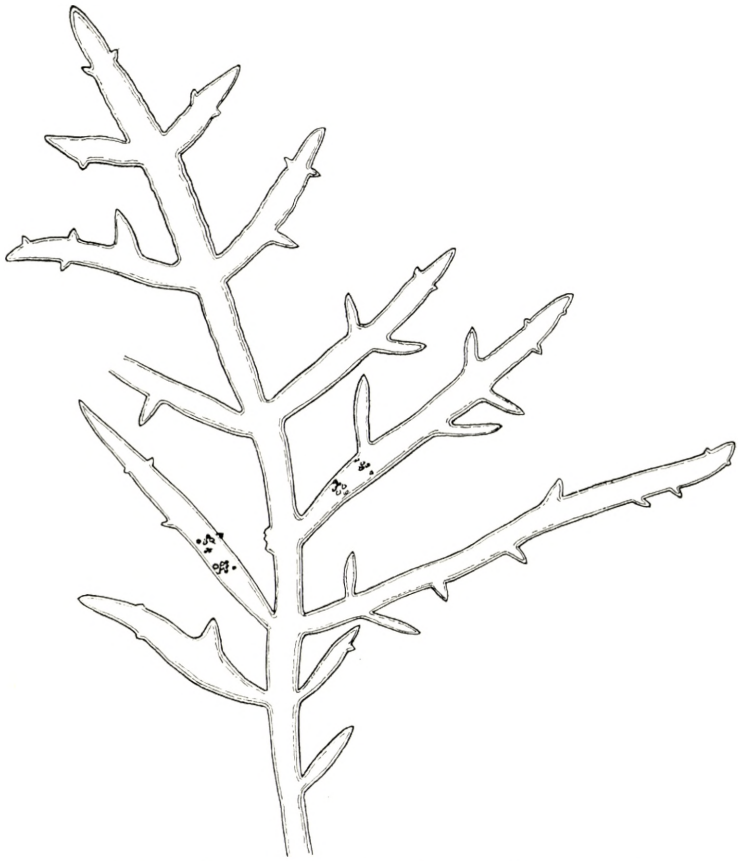

Fig. 2. *Vaughaniella rupicola* Børgs. Part of a specimen with tetrasporangia. (× 6).

Fig. 5 c) in conformity to the apical growth of *Dictyota* (cf. REINKE,[1] 1878).

But while in *Dictyota* the ramification is carried out by longitudinal division of the apical cell, the ramification in *Vaughaniella* takes place by adventitious branches. These originate from an epidermal cell at the edge of the thallus at some distance from

[1] REINKE, G., Entwicklungsgeschichtliche Untersuchungen über die Dictyotaceen des Golfs von Neapel. Nova Acta Leopold.-Carol. Acad. 40, No. 1, 1878.

the apex of the thallus (Fig. 5 *a*). The cell in question gets filled with protoplasma and chromatophores, assuming a darker colour than the surrounding cells, and swells up above these cells; it is then divided by an oblique transverse wall into two cells, the uppermost and larger one being the future apical cell of the new branch; after some divisions it assumes the ordinary aspect

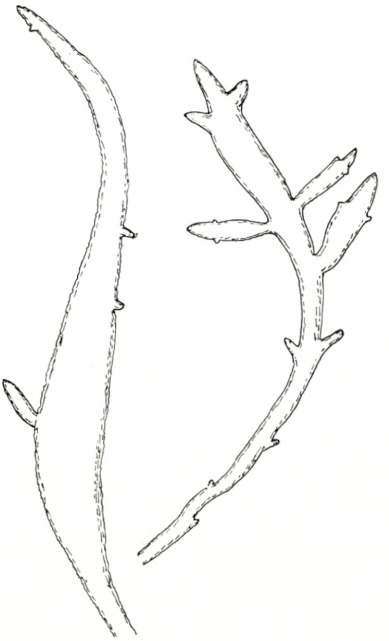

Fig. 3. *Vaughaniella rupicola* Børgs. Two fragments of plant with more irregular growth. (× 10).

of the apical cell (Fig. 5 *c*). Shortly afterwards on the opposite side of the thallus, but not exactly at the same height, a similar development of a marginal cell takes place and becomes the origin of a branch.

In this way of branching the thallus becomes subopposite ly or more irregularly ramified, because it happens that only one of the branches in a pair develops. The branches are again provided with branchlets; these are mostly short, often thornlike only; compare Fig. 2. Now and then a side-branch may grow into a main-branch with continuous growth. The thallus is rather distinctly transversely striated due to the arrangement of

the chromatophores in the medullary layer. The distance between the rows of the chromatophores is about 50—70 μ (Fig. 4 *b*).

The surface of the thallus as well as that of the margins is now nearly even, now slightly undulate (Fig. 4 *b*).

The thallus reaches a breadth of up to 1 mm., it is about 275 μ thick in transverse section, which is broadly oval—lan-

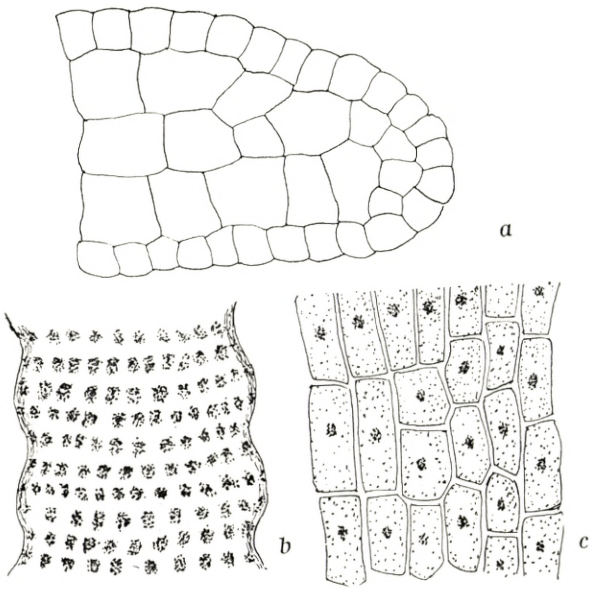

Fig. 4. *Vaughaniella rupicola* Borgs. *a*, part of transverse section of the thallus. *b*, fragment showing the striped thallus. *c*, surface cells of the thallus. (*a*, ×65, *b*, ×20, *c*, ×150).

ceolate in shape (Fig. 4 *a*). The length of the thallus varies much, reaching up to about 3 cm. or more. The branches are shorter and somewhat slender. From the more or less narrowed base they become as a rule a little broader upwards towards the middle, whence they taper to the subacute apex terminated by the large vaulted apical cell. The main filaments together with the branches and branchlets are all in about the same plane.

The thallus forms low cushions on rocks, the branches and branchlets being felted together with those of the neighbouring plants (Fig. 1). It is fastened to the substratum by means of numerous longer or shorter rhizoids (Fig. 6), issuing from the

epidermal cells of the under side either solitarily but mostly sociably in smaller or larger groups; the rhizoids consist of a single row of cells, the length of which is about 150 μ or more; the rhizoids often end in irregularly lobed, coralliformed discs.

The peripheral cells of the thallus (Fig. 4 *c*) when observed

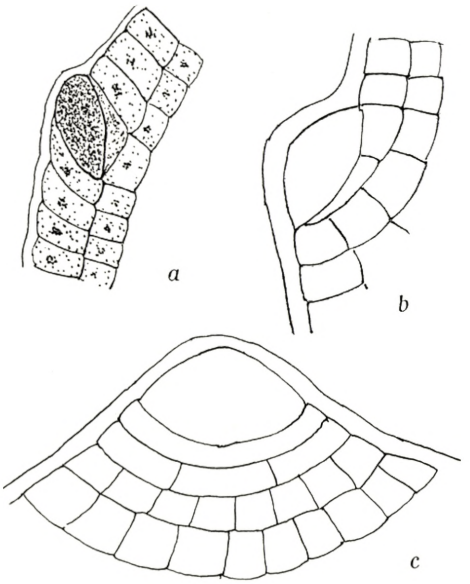

Fig. 5.

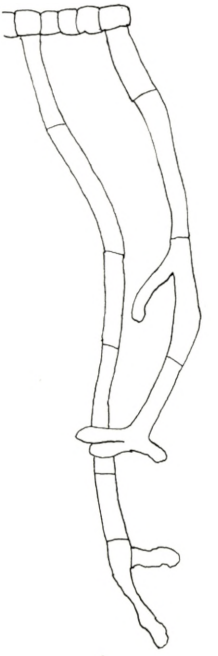

Fig. 6.

Fig. 5. *Vaughaniella rupicola* Børgs. The formation of the adventitious branches. *a*, a marginal cell becomes divided by an oblique wall. *b*, a somewhat more advanced stage. *c*, the fully developed apical cell (× 150).

Fig. 6. *Vaughaniella rupicola* Børgs. Rhizoids. (× 75).

from above are subquadrangular or somewhat lengthened and arranged rather clearly in longitudinal rows; in transverse section about quadrangular, about 40—50 μ broad. The cells in the interior of the thallus (Fig. 4 *a*) are in transverse section irregularly quadrangular or polygonal about 60 μ long and 40—50 μ broad. No midrib is found.

The sporangia (Fig. 7) are cruciately, sometimes also tetrahedrally divided. They occur singly or in small groups scattered

on the upper surface of the thallus (Fig. 2), sometimes also issuing from the margin. They develop from a surface cell which is divided by a transverse wall into two cells, the uppermost of

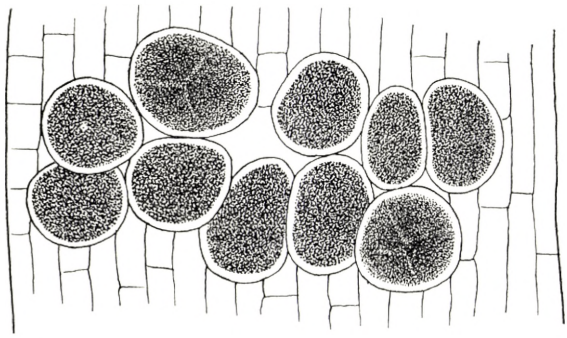

Fig. 7. *Vaughaniella rupicola* Børgs. (×250). Sporangia two of which are divided.

which is the sporangium; this is projecting freely above the surface of the thallus, it is semiglobular in shape and has a diameter of about 75 μ; when several are crowded together more or less polygonal by the mutual pressure.

This is what I am able to say about the asexual reproductive

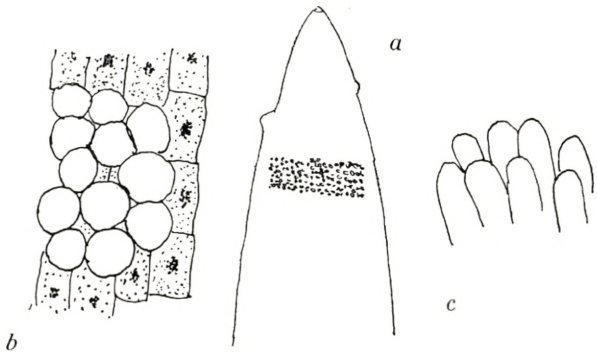

Fig. 8. *Vaughaniella rupicola* Børgs. *a*, apex of frond with a small group of hairs; *b*, a part of this group more magnified. *c*, more developed hairs. (*a*, × 30; *b*, *c*, × 300).

organs; as to the sexual organs the scarce material has brought forward no certain information.

In two of the specimens examined I have in the young parts of the thallus, not far below the apex on the upper side of the

thallus, observed some small groups of densely placed roundish cells issuing from the epidermal ones. Fig. 8 *a* shows such a group: it is oblong in shape, about 200 μ long and 70 μ broad and the cells of which it is composed had a diameter of about 12 μ. The contents in these cells were rather homogeneous and of a lighter colour than that in the epidermal cells since chromatophores were not visible. At first I took these small groups of cells to be young antheridia but later I have given up this idea, when discovering in an other specimen that the small cells become elongated and curved like sausages (Fig. 8 *c*). It seems more likely that they are young hairs, but peculiarly enough I have searched in vain for hairs elsewhere in the specimens.

As to the female organs I have not made any certain observation neither, but the possibility does not seem to be excluded that they occur in a similar way as the sporangia, and when the latter are still undivided, the oogonia might be very like the sporangia.

Because of its apical growth performed by a single large top-cell this new genus is most closely related to the group *Dictyoteae* of the *Dictyotaceae* but it differs fundamentally from this group and others referred to this family because of its dorsiventral creeping thallus, its monopodial growth and its ramification performed by adventitious branches, being in this way the representative of a new group of the *Dictyotaceae*.

Finally a short diagnosis in Latin.

Vaughaniella Børgs. gen. nov.

Frons subplana et sublinearis, ecostata, prostrata et repens, dorsiventralis, rhizoideis ad saxa adfixa, e cellula singula, apicali, per magna creata, polystromatica a cellulis corticalibus minoribus et cellulis interioribus majoribus formata, superficie thalli plus minus sinuosa, transverse evidenter striata, ramosa.

Rami subopposĭti aut magis irregulariter praesentes, adventitii, e cellulis marginalibus orti.

Tetrasporangia sparsa, singula aut plura aggregata, e transformatione cellularum corticalium orta, subsphaerica, cruciatim aut triangule divisa.

Vaughaniella rupicola Børgs. nov. spec.

Frons parva ca. 1—3 cm longa et ca. 1 mm lata et ca. 275 μ crassa, rami tenuiores.

Mauritius: Pointe aux Sables, "growing on rocks exposed at low tide"; March 24, 1945; G. Morin no. 778.

I wish to thank Miss Ingeborg Frederiksen the paintress for her valuable help in producing two of the figures.

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A TETRAPLOID *LARIX DECIDUA* MILLER

BY

H. CHRISTIANSEN

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
1950

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Due especially to the excellent contributions by Sax & Sax (1932, 1933) the chromosome number and chromosome morphology of many coniferous trees are known.

The great majority of the species of coniferous trees agree in being on the same chromosome level, having either $2n = 24$, or $2n = 22$ or $2n = 26$. Polyploidy apparently is an exceedingly rare phenomenon in this group of plants, strictly polyploid numbers being known only for *Sequoia sempervirens, Pseudolarix amabilis* and *Juniperus Chinensis* (see the chromosome list in Darlington & Janaki Ammal, 1945).

These facts justify the conclusion that polyploidy has not been effective in the evolution of the conifers, and have also led to the view that a breeding scheme in conifers based on experimentally produced polyploidy would have little chance of success.

The few polyploid or mixoploid plants of *Picea abies*, raised by colchicine treatment or found by measurements of stomata among seedlings in nurseries, as described in the annual reports of the Swedish Forest Tree Breeding Institute at Ekebo (1946, 1948), proved to be rather dwarfy and far behind the diploid plants in rate of growth.

Much better is the triploid larch hybrid (*Larix decidua* Miller $\times$ *Larix occidentalis* Nutt.) described by Syrach Larsen & Westergaard (1938), but in this case it is open to discussion to what extent the fairly satisfactory growth is due to polyploidy or to heterosis.

Thus the chance of finding in nature a large, old autopolyploid specimen of a coniferous tree would *a priori* seem rather remote, but nevertheless such trees exist, the first one, a tetraploid *Larix decidua*, having been found last year (1949) in the park of the estate Gisselfeld in Sealand, Denmark.

The tree (plate I, fig. 1) stands in a small glade, but a nearby group of deciduous trees to the south gives much shade and has hampered the development of the lower branches of the larch and probably also its growth.

The tetraploid larch is 15.2 m in height and has a straight trunk, which measures 97.5 cm in girth at a height of 1.3 m above the ground.

The branches of the crown are rather sparse, but long and drooping-curved. The lower branches, especially, are very drooping, and the side branches and twigs, which are but sparsely ramified, hang down vertically, giving to the tree a pendulous habit (plate I, fig. 2).

Borings with a sampler near the ground showed the tree to have 54 annual rings, and the total age of the tree may thus be estimated at 56—58 years.

The annual rings in the inner and outer part of the trunk differ much in size as will be seen from the following table:

Mean size of annual rings for periods of 10 years:

(1895—1898	0.7 mm)
1899—1908	3.4 —
1909—1918	3.3 —
1919—1928	2.7 —
1929—1938	1.9 —
1939—1948	0.8 —

It appears from the table, that the tree had a very slow start, but at the age of 8—9 years suddenly put up a much better growth with annual rings measuring on an average more than 3 mm. The good growth continued till the age of about 27 years, and within this period the minimum and maximum size of the annual rings was 0.3 mm (1899) and 6.6 mm (1906), respectively. In later years the growth gradually decreased, and in the last ten years it fell to the level of the starting years. The reason for this decline is not known. A direct comparison with the growth of normal, diploid trees of *Larix decidua* is not possible, since trees of the same age and under similar conditions are not growing in the park of Gisselfeld. The measurements of the growth of

larch found in the Danish forestry literature can hardly be used, partly because they refer to stands, not to single trees, and partly because the soil conditions, exposure, etc., vary much in the different parts of Denmark. It is evident that the dimensions of the trunk of the tetraploid larch tree are inferior to those of well-developed diploid larches; if, however, the former had not slowed down about 1918, but continued to grow at the fast rate till 1948, this would have meant an increase of its diameter by about 40 per cent. and a substantial improvement. In the present circumstances the relative growth rate of diploid and tetraploid larch cannot be determined until comparable plants are cultivated side by side.

The botanical characters described below first made me suggest the tetraploid nature of the tree, and modern methods of plant cytology made it a relatively easy task to confirm the assumption.

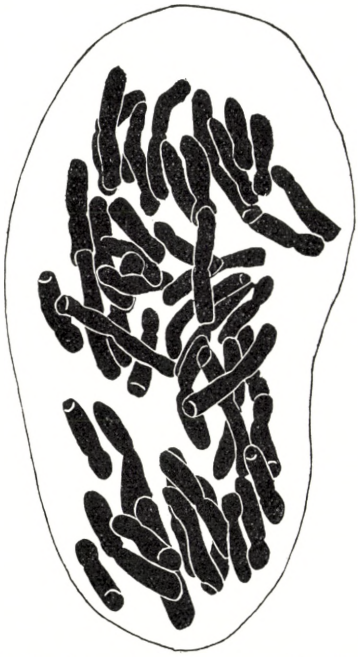
Mitosis in very young needles was studied in iron-aceto-carmine smears by means of the following technique: Tips of young shoots were stripped of all needles except the very youngest at the end, cut in two to ensure a better penetration of the fluid and submersed in 0.3 per cent. colchicine for 5 hours in order to attain a contraction and separation of the otherwise long and tangled chromosomes. Thereafter fixation in Carnoy for 14 hours, maceration in 1 part 96 per cent. alcohol + 2 parts conc. hydrochloric acid for 20 min. and boiling in iron-aceto-carmine for 8 min. If young needles, taken from buds in early spring, are used, boiling in iron-aceto-carmine after Carnoy is usually sufficient.

The best metaphase plate obtained is shown in text-fig. 1. 48 chromosomes are seen, which on closer examination group themselves in two classes of 24 each, one having median to submedian, the other subterminal constrictions. This is in agreement with the idiogram for *Larix* given by Sax & Sax (1933). Due to the large number of 48 chromosomes it was rather difficult to get plates, in which an exact statement of the number and morphology was possible. In fact only 2 plates were completely analysed.

On account of the total absence of male inflorescences in the spring of 1949 no study of the meiosis of the tetraploid larch

could be made at that time. In the spring of 1950, however, male inflorescences are abundant, and a preliminary examination has been made from buds forced at room temperature.

Certain irregularities of meiosis are observed, although fewer than might be expected on account of the apparent seed sterility mentioned below. At diakinesis and metaphase I a number of



Text-figure 1: Mitotic metaphase from young needle after colchicine treatment, 48 chromosomes (× 2000).

tetravalents are found (in the few cells examined the number varies from 10 to 12). At telophase I chromatin-bridges and lagging chromosomes are present, but their occurrence is not very frequent. The "tetrads" of the tetraploid larch are rather irregular. The number of cells varies from monads (often giant cells) to hexades. Micronuclei are observed. There is also, however, a considerable number of apparently normal tetrads, and a quantity of normal pollen may therefore be expected. Pollen-grain mitoses are frequently observed at the tetrad stage, and chromosome counts seem to indicate that cells undergoing mitosis at this stage have irregular chromosome numbers.

The tetraploid larch differs in its botanical characters from typical *Larix decidua* in much the same way as most autotetraploids differ from their diploid ancestors. This will be evident from comparative measurements and illustrations of needles, stomata, and cones. The mean length of the needles of the tetraploid larch is 33.1 mm (350 measurements), that of a nearby diploid 17.6 mm (379 measurements). The tetraploid tree thus has needles of about the double length of the diploid as is clearly seen in the photo plate II, fig. 1. Note also the much bigger size of the terminal bud of the tetraploid.

Measurements of stomatal length of 4n and 2n larches gave the following values: 4n 71 μ (63 measurements), 2n 48 μ (63 measurements).

The cones of the tetraploid tree are large, but vary much more in size than those of normal trees. The greater variation in the case of the tetraploid may be assumed to be due to a deficient seed production, the sparse seeded or seedless cones being more or less dwarfy. The largest cone of 25 measured had a length of 42 mm, the smallest 28, the mean value being 36 mm. The corresponding figures for normal *Larix decidua* are for 25 cones: 38, 22, and 30 mm.

The shape and shape variation of cones of the tetraploid larch will appear from plate II, fig. 2. The cones of this tree are generally broader than those of normal trees and more conical. Often the tetraploid cones are more or less flattened, and not unfrequently twin cones are found (see the second row of cones in the figure). The twin cones are usually curved towards each other.

Scales of the tetraploid cones (left) and diploid (right) are shown in plate II, fig. 2. As will be seen, they are of equal length, but very different in breadth, the broader tetraploid scales often being somewhat emarginate. It should be noted that the tetraploid scales are of a more shiny appearance than the normal ones.

In the record books of the Gisselfeld Gardens the tetraploid larch was first mentioned in 1907 under the name of *Larix europaea*, var. *pendula*. Although the tree does not show all the characters of *L. decidua*, it no doubt belongs to this species. As regards the varietal name, the situation is much more intricate. In the record books of Gisselfeld no author to var. *pendula* is given, and this name has been used profusedly for species and

varieties characterized by a more or less drooping habit of growth. Most of the trees of larch generally referred to as var. *pendula* are apparently simple mutants with drooping growth. The tetraploid var. *pendula* at Gisselfeld, on the other hand, presumably owes most of its pendulous habit to its tetraploid constitution, and if specimens identical with this tree exist, they are likely to be found in English parks. The Gisselfeld estate at the time of the planting of the tetraploid larch had an English head gardener, who is known to have introduced trees from English nurseries.

The seeds of the tetraploid tree appear to be larger than normal seeds, but as most of them, if not all, are empty, it has not been possible to make a true comparison. Whether the sterility (or very low fertility) of the tetraploid larch is due to self-sterility or is caused by the tetraploid nature of the tree, cannot be decided at present.

In order to secure the future existence of the interesting tetraploid larch tree, graftings from it have already been made by Dr. Syrach Larsen at the Forest Tree Breeding Institute at Hörsholm. An additional number will be made next summer and also some rooted cuttings. This material will make it possible to carry out the aforesaid comparison of the growth of tetraploid and diploid young trees. Later, when the graftings start flowering, they will, together with the original tree, be valuable for breeding purposes.

The employment of the tetraploid tree of *L. decidua* may take place in the following two ways:

(1) A direct utilization presents itself if the tree proves superior to diploid larches. In this case vegetative propagation by cuttings or graftings as well as propagation by seeds should be performed. The seedling-method, if practicable, would offer the advantage of producing some variability in the offspring.

(2) Indirectly the tree should prove valuable as a parent in crosses with other larches, *L. decidua* as well as other species. Species hybrids are well known in the genus *Larix*, and the hybrid *L. leptolepis* × *L. decidua* has already proved valuable in Danish forestry (Syrach Larsen, 1937), its growth qualities being superior to those of both parent species.

The present investigation has been made at the Laboratory of Genetics of the Royal Vetr. and Agricultural College, Copenhagen, and the author is much indebted to Prof. C. A. Jørgensen for help and advice.

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Fig. 1. The tetraploid *Larix decidua* var. *pendula* in the park of Gisselfeld, Denmark (photo C. Syrach Larsen 1949).

Fig. 2. The lower part of the tree, showing the drooping side branches.

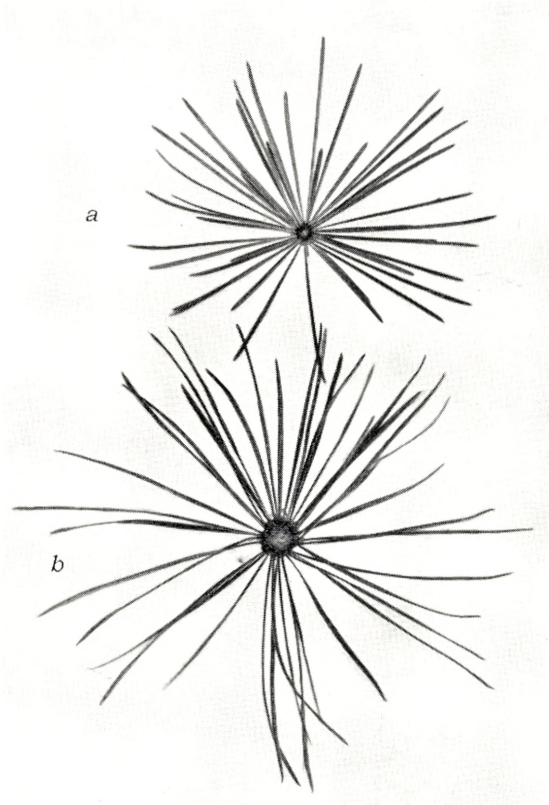

Fig. 1. Dwarf shoot of diploid (*a*) and tetraploid (*b*) larch (× 1).

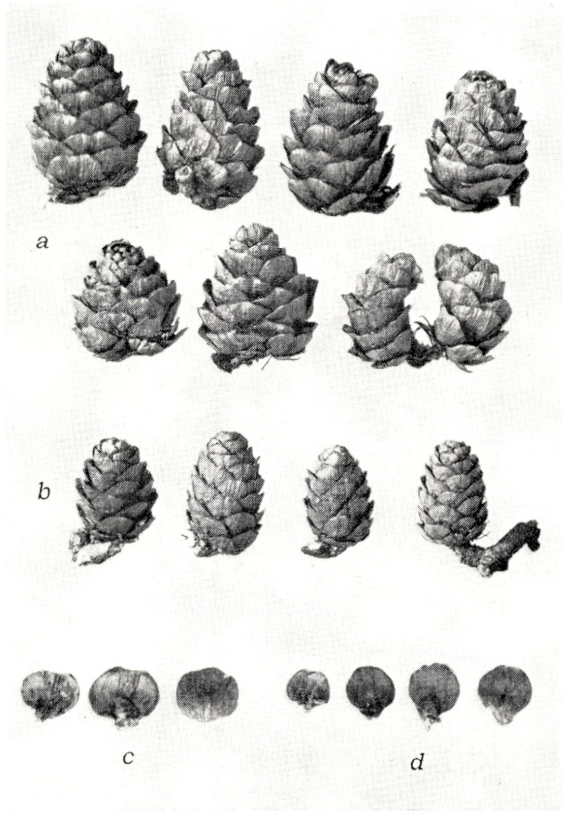

Fig. 2. Cones and scales of diploid and tetraploid larch; (*a*) cones of tetraploid; (*b*) cones of diploid; (*c*) scales of tetraploid; (*d*) scales of diploid. (*a* and *b* × $^{3}/_{5}$, *c* and *d* × $^{2}/_{3}$).

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VON

P. BOYSEN JENSEN

WITH AN ENGLISH SUMMARY

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1. Einleitung.

In einer Abhandlung »A Determination Theory« (1948) stellte ich die Hypothese auf, dass ein lokalisiertes Flächenwachstum der Zellwand, durch welches z. B. die Wurzelhaare gebildet werden, durch eine Anhäufung von Zellulosenbildnern an dem betreffenden Ort zustande kommt.

Dass solche Zellulosenbildner wirklich vorhanden sind, geht aus der Weise, in welcher Stärke gebildet wird, hervor. Cori, Hanes und andere (vgl. Peat 1946) haben nachgewiesen, dass sowohl in Tieren als in Pflanzen Enzyme vorhanden sind, die Polysaccharide, Glykogen und Stärke, aus Glukose-1-phosphat bilden können, und zwar mit besonderer Schnelligkeit, wenn ein Polysaccharidstarter vorhanden ist. Weil der Bau der Zellulosemoleküle eine grosse Ähnlichkeit mit demjenigen der Stärke hat, muss man annehmen, dass auch die Bildung der Zellulose durch enzymatische Vorgänge zustande kommt. Da die Zellulosebildung aus Glukose ein unfreiwilliger Vorgang ist, muss die notwendige Energie durch eine Verknüpfung der zellulosenbildenden Enzymvorgänge mit den Atmungsvorgängen zuwegegebracht werden. Die Enzymkomplexe, die die Zellulosenbildung hervorrufen, sollen als Zellulosenbildner bezeichnet werden.

Um die Zellulosenbildner nachzuweisen, wird man zwei Wege gehen können. Entweder könnte man, wenn sie, wie Farr (1941, 1949) annimmt, in morphologischen Gebilden, d. h. in Plastiden, eingeschlossen sind, untersuchen, ob man diese Gebilde direkt unter dem Mikroskope beobachten kann, oder man würde vielleicht die Lage der Zellulosenbildner durch ihre Wirkung, d. h. durch ihre Fähigkeit Zellulose zu bilden, nachweisen können. Man wird nämlich schliessen können, dass überall da, wo eine Zellulosenbildung vorkommt, nicht nur die Zellulosenbildner,

sondern auch die Stoffe, die für die Zellulosenbildung notwendig sind, anwesend sein müssen.

Eine Zellulosenbildung findet immer während des Wachstums der Zellwand statt. Man könnte daher geneigt sein zu schliessen, dass man einfach das Wachstum als Test für das Vorkommen der Zellulosenbildner benutzen könnte. Es ist aber möglich, dass Zellulosenbildner auch an Orten, wo kein Wachstum stattfindet, vorkommen können. Beispiele dafür sollen später erwähnt werden. Man wird sich daher nach einem anderen Test für das Vorkommen der Zellulosenbildner umsehen müssen.

Durch eine Reihe von Untersuchungen hat sich herausgestellt, dass man durch äussere Eingriffe eine Zellulosenbildung in der Spitze von Wurzelhaaren auf der inneren Seite der Zellmembran hervorrufen kann.

Klebs (1887) hat gefunden, dass Kongorot in eigentümlicher Weise das Wachstum der Zellwände von Algen beeinflusst, indem »das Längenwachstum beschränkt, bez. vollständig verhindert wird, während das Dickenwachstum ungestört, ja um so lebhafter vor sich geht«. Die Einwirkung von Kongorot auf das Wachstum der Wurzelhaare von Lepidium ist von Zacharias (1891) untersucht worden; er fand, dass das Wachstum aufhörte, und dass eine Verdickungschicht in der Spitze der Haare gebildet wurde.

Wortmann (1889) zeigte, dass Wurzelhaare, die in starken Rohrzuckerlösungen kultiviert wurden, sich wiederholt verzweigten. Daneben entstanden starke Verdickungen in den Spitzen, wo das Wachstum aufgehört hatte.

Zacharias (1891) hat nachgewiesen, dass Wurzelhaare von Lepidium, die sich in feuchter Luft entwickelt hatten, aufhörten zu wachsen, wenn sie in Wasser gebracht wurden. In kurzer Zeit wurde eine Verdickung in der Spitze der Wurzelhaare gebildet.

Gorter (1945, 1949) zeigte, dass man auch durch Behandlung der Wurzelhaare von Lepidium und anderen Pflanzen mit Colchicin oder Trijodbenzoesäure neben anderen Wachstumsstörungen Verdickungen in der Spitze der Wurzelhaare hervorrufen kann.

Die Verdickungen färben sich nach Gorter mit Chlorzinkjod, Kongorot und Rutheniumrot, dagegen nicht mit Resoblau. In Cuoxam lösen sie sich nicht.

Die Verdickungen in der Spitze der Wurzelhaare entstehen nach ZACHARIAS (1891) in folgender Weise: »Es ist anzunehmen, dass unter normalen Verhältnissen bei Lepidium Flächenwachstum der Membran nur am Scheitel des Wurzelhaares stattfindet. Die weiter rückwärts gelegenen Theile der Membran des Haares erfahren anscheinend auch kein Dickenwachstum, so dass die Ablagerung von Cellulose sich wahrscheinlich auf die Spitze des Haares beschränkt. Nach dem Übertragen aus Luft in Leitungswasser hört in vielen Fällen das Flächenwachstum der vorhandenen Membran auf, das Haar verlängert sich weder, noch verändert es im übrigen seine Gestalt. Die Bildung von Cellulose wird aber fortgesetzt und es entsteht die Verdickungsschicht, welche meist nur am Scheitel des Haares auftritt. Diejenigen Stoffe, welche unter normalen Verhältnissen für das mit Flächenvergrösserung verbundene Wachstum der Membran am Scheitel des Wurzelhaares verwendet werden, werden auch jetzt am Scheitel des Haares, jedoch für den Aufbau einer in die Dicke wachsenden Neubildung verwendet«.

Nach der von mir vertretenen Auffassung muss man annehmen, dass die Zellulosemassen durch Enzyme, d. h. Zellulosenbildner, erzeugt werden. Wenn man von der Annahme ausgeht, dass das Flächenwachstum in der Spitze der Wurzelhaare durch Intussusception zustande kommt, kann man sich vorstellen, dass die Zellulosenbildner, wenn das Wachstum ungestört ist, in der Membran eingelagert sind, und ferner, dass das Plasma durch Übertragung der Wurzelhaare in Wasser oder in eine Lösung von Kongorot sich aus der Membran herauszieht. Die Zellulosenbildner erhalten dann ihre Lage an der Oberfläche des Plasmas (endo- oder exoplasmatisch) auf der inneren Seite der Membran, wo sie ihre Tätigkeit fortsetzen. Die Zellulosenbildungen, die dabei entstehen, ermöglichen es somit, das Vorkommen der Zellulosenbildner in der Membran nachzuweisen.

2. Versuche.

Als Versuchspflanzen wurden Lepidium und Phleum gewählt. Zwei bzw. vier Samen wurden — ohne eingeweicht zu sein — auf Objektträger, die auf beiden Seiten mit feuchtem Japonais- oder Filtrierpapir bekleidet waren, angebracht. Die Objektträger

wurden senkrecht in viereckige Färbekästchen gestellt. Die Küvetten wurden mit Leitungswasser, das in Kopenhagen stark kalkhaltig ist, beschickt, so dass die Samen sich 0,5—5 cm über die Wasseroberfläche befanden. Im ersten Fall entwickelten die Wurzelhaare sich in Wasser, in den übrigen Fällen in Luft. Die beiden Typen von Wurzelhaaren sollen in dem folgenden als Wasser- bez. Lufthaare bezeichnet werden. Die Keimung der Samen fand bei Zimmertemperatur statt. Die Länge der Wurzeln, die für die Versuche benutzt wurden, betrug etwa 1 cm.

Wenn die Pflanzen sofort, nachdem sie von dem Filtrierpapir abgenommen sind, unter das Mikroskop gelegt werden, findet man nicht (oder jedenfalls sehr selten) Verdickungen in der Spitze der Wurzelhaare oder an den Aussenwänden der Epidermiszellen. Um Verdickungen hervorzurufen muss das Wachstum zum Stillstand gebracht werden. Dies geschah durch eine Vorbehandlung der Pflanzen mit einer Lösung von Kongorot oder Colchicin oder einfach durch Übertragung der Pflanzen in Wasser. In ähnlicher Weise wirken auch Lösungen von β-Indolylessigsäure (im folgenden als βIE bezeichnet). Für die Herstellung der Lö-

Tab. 1.

Vorbehandlung mit der Lösung	Reaktion in der Lösung.
0,01 % Kongorot (30 Minuten)	Leitungswasser 0,01 % Kongorotlösung 0,01 % Kongorotlösung + Dextrose (Konz. 0,1 mol.)
βIE (10, 100 oder 1000 γ pro 100 ccm) 1 Stunde	Dieselbe Lösung wie bei der Vorbehandlung + Dextrose (Konz. 0,1 mol.)
Colchicin (0,05 und 0,5 %) 30 Minuten	Dieselbe Lösung wie bei der Vorbehandlung + Dextrose (Konz. 0,1 mol.)
Leitungswasser (8°—12°) 2 Stunden	0,1 mol. Dextroselösung

sungen wurde Leitungswasser benutzt. Die Vorbehandlung dauerte $^1/_2$—2 Stunden. Nachher wurden die Pflanzen in eine neue Flüssigkeit übertragen, in welcher die Reaktion, die Bildung der Verdickungen, eintrat. Die Flüssigkeit bestand entweder aus Leitungswasser oder aus einer neuen Portion derselben Lösung, die für die Vorbehandlung verwendet wurde. In den meisten Fällen wurde so viel Dextrose zugesetzt, dass die Konzentration 0,1 molar wurde. Ich habe den Eindruck, dass die Zellulosemasse, die sich bildet, durch den Zusatz von Dextrose vergrössert wird. Die Verdickungen entwickeln sich im Laufe von 24 Stunden.

Eine schematische Übersicht der angestellten Versuche findet sich in Tab. 1.

Um das Ergebnis der Behandlung festzustellen, braucht man nur die intakten Wurzeln unter das Mikroskop zu legen. Die Verdickungen in den Wurzelhaaren treten scharf hervor. Noch deutlicher werden sie nach Färbung mit Kongorot oder nach Plasmolyse mit 0,6 mol. Dextroselösung.

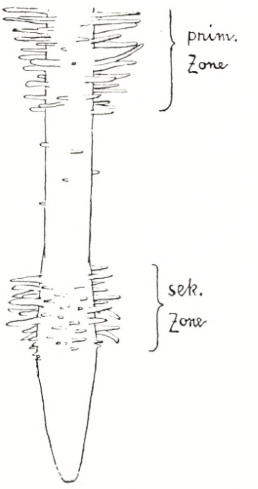

Abb. 1. Wurzel von Lepidium mit einer sekundären Zone von Wurzelhaaren.

Die Verdickungen in den Trichoblasten, die später erwähnt werden sollen, kann man kaum in den Lepidiumwurzeln beobachten, dagegen sehr leicht in den dünnen Wurzeln von Phleum. Diese Pflanze, die neben anderen kleinsamigen Gräsern zuerst von SINNOTT und BLOCH für Untersuchungen über Wachstum und Entwicklung der einzelnen Wurzelzellen benutzt wurde, hat sich als besonders wertvoll für den Nachweis der Zellulosenbildner erwiesen.

Durch die Vorbehandlung wird das Wachstum der Wurzelhaare, die im Begriffe sind sich zu entwickeln, im allgemeinen zum Stillstand gebracht und die Entwicklung neuer Wurzelhaare wird verhindert. Die apikalen Epidermiszellen der Wurzel sind doch mehr resistent als die wurzelhaartragenden Zellen. In einzelnen Fällen sind sie imstande, eine sekundäre Zone von Wurzelhaaren zu bilden (vgl. Abb. 1).

Es sollen nun kurz die Ergebnisse der Versuche dargestellt werden.

a. Versuche mit Kongorot. Die Lösungen von Kongorot werden täglich frisch hergestellt, indem man eine starke Lösung von Kongorot in destilliertem Wasser mit Leitungswasser verdünnt, bis man schätzungsweise die richtige Konzentration erreicht hat.

1. *Lepidium*, Lufthaare.
Vorbehandl. 0,01 %iger Lösung von Kongorot, 30 Min.
Reaktion in Leitungswasser, 24 Stunden.
Schwache Verdickungen in der Spitze der jungen Wurzelhaare.
Keine Verdickungen in den älteren.
Keine nachweisbaren Verdickungen in den Epidermiszellen.
Keine sekundäre Zone von Wurzelhaaren.

2. *Lepidium*, Lufthaare.
Vorbehdl. 0,01 %iger Lösung von Kongorot, 30 Min.
Reaktion in 0,1 mol. Dextroselösung, 24 Stunden.
Starke Verdickungen in der Spitze der jungen Wurzelhaare (Abb. 3, 2, 6).
Vereinzelte Verdickungen in den älteren.
Keine wahrnehmbare Verdickungen in den Epidermiszellen.
Eine sekundäre Zone von Wurzelhaaren.

3. *Lepidium*, Lufthaare.
Vorbehdl. 0,01 %iger Lösung von Kongorot, 30 Min.
Reaktion in derselben Lösung mit Zusatz von Dextrose (Konz. 0,1 mol.).
Mittelgrosse Verdickungen in der Spitze der jungen Wurzelhaare (Abb. 3, 2).
Keine Verdickungen in den älteren.
Keine sekundäre Zone von Wurzelhaaren.

4. *Phleum*, Wasserhaare.
Vorbehdl. 0,01 %iger Lösung von Kongorot, 30 Min.
Reaktion in Leitungswasser, 24 Stunden.
Schwache—ziemlich starke Verdickungen in der Spitze der jungen Wurzelhaare (Abb. 3, 3, 5).
Vereinzelte Verdickungen in den älteren.
Vereinzelte Verdickungen in den Epidermiszellen (Abb. 4 IVa, b).
Keine sekundäre Zone von Wurzelhaaren.

5. *Phleum*, Wasserhaare.
Vorbehdl. 0,01 %iger Lösung von Kongorot, 30 Min.
Reaktion in derselben Lösung mit Zusatz von Dextrose (Konz. 0,1 mol.), 24 Stunden.
Starke Verdickungen in der Spitze der jungen Wurzelhaare (Abb. 3, 3).
Vereinzelte Verdickungen in den älteren.
Vereinzelte Verdickungen in den Epidermiszellen (Abb. 4 II c, III c).
Keine sekundäre Zone von Wurzelhaaren.

Die Epidermiszellen der Wachstumszone war zum grossen Teil zerstört.

b. Versuche mit β-Indolylessigsäure.

1. *Lepidium.* Wasserhaare.
   Vorbehdl. Lösung von β IE, 10 γ pro 100 ccm, 1 Stunde.
   Reaktion in derselben Lösung mit Zusatz von Dextrose (Konz. 0,1 mol.), 24 Stunden.
   Starke Verdickungen in der Spitze der jungen Wurzelhaare (Abb. 3, 2, 3, 5).
   Schwache Verdickungen in den älteren.
   Vielleicht eine vereinzelte Verdickung in den Epidermiszellen.
   Eine sekundäre Zone von Wurzelhaaren, schwache Verdickungen.
2. *Lepidium*, Wasserhaare.
   Vorbehdl. Lösung von β IE, 100 γ pro 100 ccm, 1 Stunde.
   Reaktion in derselben Lösung mit Zusatz von Dextrose (Konz. 0,1 mol.), 24 Stunden.
   Starke Verdickungen in der Spitze der jungen Wurzelhaare (Abb. 3, 5).
   Schwächere Verdickungen in den älteren.
   Vereinzelte Verdickung in einer Epidermiszelle.
   Eine sekundäre Zone von Wurzelhaaren mit schwachen Verdickungen.
3. *Lepidium*, Wasserhaare.
   Vorbehdl. Lösung von β IE, 1000 γ pro 100 ccm, 1 Stunde.
   Reaktion in derselben Lösung mit Zusatz von Dextrose (Konz. 0,1 mol.), 24 Stunden.
   Mittelgrosse Verdickungen in der Spitze der jungen Wurzelhaare (Abb. 3, 3).
   Mittelgrosse Verdickungen in den älteren.
   Vereinzelte Verdickung in einer Epidermiszelle.
   Keine sekundäre Zone von Wurzelhaaren.
4. *Phleum*, Lufthaare.
   Vorbehdl. Lösung von β IE, 100 γ pro 100 ccm, 1 Stunde.
   Reaktion in derselben Lösung mit Zusatz von Dextrose (Konz. 0,1 mol.), 24 Stunden.
   Starke Verdickungen in der Spitze der jungen Wurzelhaare (Abb. 3, 2–8).
   Schwache Verdickungen in den älteren.
   Viele Verdickungen in den Epidermiszellen (Abb. 4, Serie III und IV).
   Keine sekundäre Zone von Wurzelhaaren.

c. Versuche mit Colchicin.

1. *Lepidium*, Wasserhaare.
   Vorbehdl. 0,05%iger Lösung von Colchicin, 30 Min.

Reaktion in derselben Lösung mit Zusatz von Dextrose (Konz. 0,1 mol.), 24 Stunden.
Die jungen Wurzelhaare stark deformiert und verzweigt mit mittelgrossen Verdickungen.
Mittelgrosse Verdickungen in den älteren.
Keine nachweisbaren Verdickungen in den Epidermiszellen.
Eine sekundäre Zone von Wurzelhaaren, dieselben waren stark deformiert und verzweigt mit Verdickungen in der Spitze.

2. *Lepidium*, Wasserhaare
Vorbehdl. 0,5%iger Lösung von Colchicin, 30 Min.
Reaktion in derselben Lösung mit Zusatz von Dextrose (Konz. 0,1 mol.), 24 Stunden.
Starke Verdickungen in der Spitze der jungen Wurzelhaare (Abb. 3, 5).
Schwache—mittelgrosse Verdickungen in den älteren.
Keine Verdickungen in den Epidermiszellen.
Keine sekundäre Zone von Wurzelhaaren.

d. Versuche mit Wasser. Die Pflanzen müssen ziemlich trocken gezüchtet werden. Wenn die Zimmerluft feucht ist, muss der Deckel der Färbekästchen abgenommen werden.

1. *Phleum*, Lufthaare.
Vorbehdl. Leitungswasser, 2 Stunden.
Reaktion in einer 0,1 mol. Dextroselösung, 24 Stunden.
Starke Verdickungen in der Spitze der jungen Wurzelhaare (Abb. 3, 3).
Mittelgrosse Verdickungen in den älteren.
Viele Verdickungen in den Epidermiszellen (Abb. 4, Serie II und V).

Aus obigen Angaben geht hervor, dass man durch die betreffende Behandlung die angeführten Ergebnisse erhalten kann, nicht aber, dass man sie immer erhält. Die Wurzelhaare sind sehr empfindliche Organe, die nicht immer in derselben Weise reagieren. Es tritt im allgemeinen als Folge der Vorbehandlung ein Stillstand des Wachstums ein, aber man kann auch beobachten, dass einzelne Wurzelhaare das Wachstum fortsetzen, ja sogar, dass bestimmte Konzentrationen von βIE und Colchicin das Wachstum beschleunigen können. Entsprechend findet man, dass zwischen Wurzelhaaren mit starken Verdickungen auch solche ohne Verdickungen vorkommen können. Im allgemeinen tritt jedoch die Reaktion mit ziemlich grosser Sicherheit ein. Die zuverlässigste Methode, die Verdickungen bei Phleum hervorzurufen, ist die Behandlung mit Kongorot; aber auch bei Übertra-

gung der Pflanzen in Wasser erhält man durchgehend gute Erfolge. Wurzeln, die sich 4—5 cm über die Wasseroberfläche entwickelt haben, geben fast immer Verdickungen.

Weshalb die Wurzeln, die von Filtrierpapier in Wasser übertragen werden, aufhören zu wachsen, ist noch nicht geklärt. Es findet in den Wurzelhaaren eine starke Wasseraufnahme statt, die zu einer vorübergehenden Stockung der Plasmaströmung, in einigen Fällen auch zu einer Plasmoptyse führen kann. Es ist wahrscheinlich, dass die durch diese Wasseraufnahme hervorgerufenen Störungen Ursache des Stillstands des Flächenwachstums in den Wurzelhaaren sind.

Dass grössere Konzentrationen von βIE und Colchicin das Wachstum aufheben und dadurch Verdickungen in der Spitze der Wurzelhaare hervorrufen können, ist leicht verständlich. Es ist wohl auch recht einleuchtend, dass Kongorot dadurch, dass es an die in der Zellwand vorhandenen Zellulosefäden haftet, das Auseinanderrücken derselben unmöglich machen kann, und dass es auf diese Weise das Flächenwachstum der Zellwand zum Stillstand bringen kann. Die Behandlung mit Kongorot wirkt somit als eine Abfangmethode.

Die chemische Beschaffenheit der Wandverdickungen. Bei mikroskopischer Untersuchung ungefärbter Wurzelhaare mit Verdickungen kann man keine Trennungslinie zwischen Primärmembran und Verdickung beobachten, und man hat, namentlich bei kleinen Verdickungen, den Eindruck, dass dieselben durch Einlagerung von Stoffen in die Primärmembran entstanden sind. Eine Trennungslinie tritt aber sofort auf, wenn man mit Kongorot färbt, und namentlich, wenn man die Wurzelhaare im Dunkelfelde untersucht, indem nur die Primärmembran aufleuchtet, während die Verdickung dunkel ist. Die Verdickungen bestehen somit aus organischen Massen, die der inneren Seite der Primärmembran angelagert sind. Die Verdickungen werden mit Kongorot intensiv rot und mit Anilinblau (in 3 %iger Essigsäure gelöst) blau gefärbt. Mit Rutheniumrot färben sie sich kaum.

Es wird von verschiedenen Forschern behauptet, dass die Verdickungen sich mit Chlorzinkjod blau färben. Das stimmt nicht ganz zu meinen Erfahrungen. Der grösste Teil der Verdickungen, die mit βIE oder Wasser erzeugt sind, wird, sowohl bei Lepidium als bei Phleum, mit Chlorzinkjod entweder nicht

oder sehr schwach blau gefärbt, der innere Saum der Verdickungen, der unmittelbar an das Plasma stösst, wird dagegen in vielen Fällen intensiv blau gefärbt. Mit Jodjodkalium und Schwefelsäure erhält man dasselbe Ergebnis.

Im Dunkelfelde leuchtet, wie oben erwähnt, die Primärmembran stark auf, während die Verdickungen dunkel sind. Daneben tritt in vielen Fällen auch der innere Saum der Verdickung als eine leuchtende Linie hervor (Abb. 2). Der leuchtende Teil der Verdickung ist offenbar derselbe, der durch Chlorzinkjod blau gefärbt wird.

Abb. 2. Die leuchtenden Linien eines Wurzelhaares von Phleum in Dunkelfeldbeleuchtung.

Im Polarisationsmikroskop kann bei gekreuzten Nicols und Einschaltung eines Quarzplättchens (Rot I Ordnung) in dem unteren Teil der Primärmembran eine Doppelbrechung nachgewiesen werden. Die Verdickungen geben weder Additions- noch Subtraktionsfarben.

Aus dem angeführten wird man schliessen können, dass die Verdickungen aus den gewöhnlichen Bestandteilen der Zellwand aufgebaut sind. Der grössere Teil enthält nur eine geringe Menge Zellulose, möglicherweise gar keine. Dieser Teil ist wahrscheinlich ziemlich locker gebaut und kann somit nicht mit den Zelluloseschichten, die bei dem gewöhnlichen Dickenwachstum entstehen, verglichen werden.[1] Der innere Saum der Verdickung dagegen hat eine festere Konsistens und besteht vorwiegend aus Zellulose.

Zusammenfassung. Wie frühere Forscher gefunden haben, können durch verschiedene äussere Einwirkungen Verdickungen in der Spitze der Wurzelhaare hervorgerufen werden. Diese Verdickungen bestehen aus einem Gemisch verschiedener Verbindungen der Zellulosengruppe.

Nach meiner Auffassung sind die Verdickungen ein Beweis dafür, dass in der Spitze der Wurzelhaare Zellulosenbildner vorhanden sind, d. h. Enzymsysteme, die entweder aus Verbindungen, die dort vorkommen, oder aus Stoffen, die künstlich zugeführt

[1] Verdickungen, die mit Kongorot hervorgerufen und mit diesem Stoffe gefärbt sind, erhalten mit Chlorzinkjod häufig eine blaue Farbe; in einigen Fällen wird doch nur der innere Saum blau gefärbt, während der übrige Teil der Verdickung die rote Farbe behält. Es ist möglich, dass die mit Kongorot hervorgerufenen Verdickungen mehr Zellulose enthalten als diejenigen, die mit Wasser oder βIE erzeugt sind.

werden, Verbindungen der Zellulosengruppe bilden können. Die Bildung der Verdickungschichten kann somit als ein qualitativer Test für die Anwesenheit von Zellulosenbildnern benutzt werden.

Wie oben erwähnt können Verdickungen auch in den Epidermiszellen auftreten.

Es soll nun im folgenden eine Übersicht über das Vorkommen und die Lage der Verdickungen gegeben werden. Es wird sich zeigen, dass es möglich ist, der Lösung des Problems, in welcher Weise die Wurzelhaare erzeugt werden, einen Schritt näher zu kommen.

3. Vorkommen und Lage der Zellulosenbildner in Wurzelhaaren und Trichoblasten.

Wurzelhaare mittlerer Länge. Wie HABERLANDT (1887) und andere nachgewiesen haben, wachsen die Wurzelhaare durch Spitzenwachstum. Man darf daher erwarten, dass auch das Vorkommen der Zellulosenbildner auf die Spitze beschränkt ist. Das ist tatsächlich auch der Fall; die Verdickungen werden ausschliesslich in der Spitze erzeugt. In vielen Fällen sind sie so stark entwickelt, dass die ganze Spitze ausgefüllt ist. Die wachsende Zone beträgt bei Polygonum fagopyrum nach HABERLANDT 0,013 mm, die Länge der Verdickungen bei Lepidium etwa 0,015 mm, bei Pleum etwa 0,017 mm (vgl. Abb. 3, 5), in einigen Fällen können sie etwas kürzer oder länger sein. Die Länge der Wachstumszone und der Verdickungen ist somit von derselben Grössenordnung.

Es erhebt sich nun die Frage, ob die Zellulosenbildner, welche die Verdickungen erzeugen, an der inneren Seite der Primärmembran oder an oder in der Oberfläche des Plasmas liegen. Die erstere Annahme ist nicht wahrscheinlich. Die erst gebildeten Verdickungsschichten müssten dann an der inneren Seite der Verdickung liegen, und man müsste erwarten, dass sie stark gefaltet wären, was nicht der Fall ist. Direkt widerlegt wird diese Annahme durch ein Versuch von WORTMANN (1889). Wurzelhaare von Lepidium, die in 6—9 %iger Rohrzuckerlösungen kultiviert waren, wurden plasmolysiert und nachher in einer Lösung, in welcher die Haare wieder turgescent wurden, weiter kultiviert. Das Ergebnis der Versuche beschreibt er mit folgenden Worten: »In allen, auch den jüngsten Haaren, haben sich lebhafte Mem-

branverdickungen am Scheitel eingestellt, wobei in vielen Fällen durch allmähliches Zurückweichen des Plasmas vom Scheitel 2—3 Membrankappen gebildet waren, diese entweder zwischen sich einen freien Raum lassend, oder auch, wie in einigen Fällen beobachtet werden konnte, durch weniger dichte Cellulose continuirlich mit einander verbunden«. Aus diesem Versuch kann man schliessen, dass die Zellulosenbildner an der Oberfläche

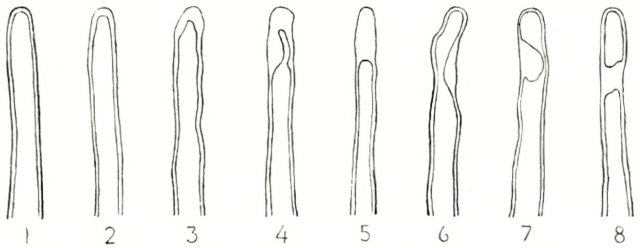

Abb. 3. Verdickungen in der Spitze von Wurzelhaaren mittlerer Länge von Phleum. 1 Kontrolle, 2–8 Wurzelhaare mit Verdickungen, alle aus derselben Wurzel. Die Verdickungen sind mit βIE hervorgerufen. (Vergr. $\frac{400}{1}$).

des Plasmas liegen, ob endo- oder exoplasmatisch mag vorläufig dahingestellt bleiben.

Die Form der Verdickungen kann sehr verschiedenartig sein. Man wird jedoch vielleicht zwei Gruppen unterscheiden können.

In der ersten Gruppe (Abb. 3, 2—5) befindet die Hauptmasse der Verdickung sich in der Spitze des Wurzelhaares und nimmt entweder abwärts allmählich ab (2—3) oder die ganze Spitze ist von der Verdickung ausgefüllt (5); doch kann im letzteren Fall ein Kanal, der mit Plasma gefüllt ist, sich in die Verdickung hineinerstrecken (4). Man darf annehmen, dass in dieser Gruppe die Zellulosenbildner sich hauptsächlich an der Spitze des Plasmas befinden, an der Stelle, wo das Flächenwachstum der Zellmembran am stärksten ist.

In der zweiten Gruppe (Abb. 3, 6—8) wird die Hauptmasse der Verdickung unterhalb der Spitze gebildet. Entweder entsteht eine einseitige Verdickung oder ein ringförmiger Wulst ungefähr an der Grenze, wo das Flächenwachstum des Wurzelhaares aufhört (6, 7). Die Wülste können zu einem geschlossenen Zylinder zusammenfliessen, so dass zwischen Spitze der Primärmembran und Verdickung ein mit Plasma gefüllter Raum eingeschlossen

wird (8). Man darf annehmen, dass in dieser Gruppe eine Verschiebung der Zellulosenbildner stattgefunden hat, so dass sie sich an der Basis der Wachstumszone angehäuft haben. Dieser Typus ist weit seltener als der erst erwähnte.

Weiter unten im Wurzelhaar finden sich nicht oder jedenfalls ausserordentlich selten Verdickungen.

Ältere Wurzelhaare. Auch in älteren Wurzelhaaren, sowohl von Lepidium als von Phleum, können Verdickungen gebildet werden, dieselben sind jedoch meistens kleiner als in den jüngeren. Es ist wahrscheinlich, dass Wurzelhaare Verdickungen bilden können, auch nachdem sie aufgehört haben zu wachsen; sie enthalten somit auch Zellulosenbildner. Wenn sie trotzdem nicht wachsen, ist die Ursache wahrscheinlich in dem Mangel an Stoffen zu suchen, die für das Flächenwachstum notwendig sind.

Junge Wurzelhaare und Trichoblasten von Phleum. Die Lage der Verdickungen in denselben ist in Abb. 4 dargestellt. In dem jungen Wurzelhaar (IIa) liegt eine kugelförmige Verdickung in der Spitze. Wenn man nun von diesem Wurzelhaar weiter in Richtung auf die Wurzelspitze geht, trifft man auf ein jüngeres Stadium (IIb); in dieser Zelle ist die Aussenwand nur schwach vorgewölbt, sie enthält aber eine Verdickung von ungefähr derselben Grösse wie in IIa. Die jungen Wurzelhaare liegen an dem apikalen Ende der Zellen. In den folgenden Stadien ist die Aussenwand der Epidermiszellen vollkommen plan. Von ganz besonderer Bedeutung ist es nun, dass man auch in einigen von diesen Zellen an der inneren Seite der Aussenwand kegelförmige oder halbkugelförmige Verdickungen von ganz derselben Beschaffenheit wie in den jungen Wurzelhaaren finden kann. Sie färben sich mit Kongorot und liegen ebenfalls mit seltenen Ausnahmen an dem apikalen Ende der Zellen (IIc, d). Es finden sich alle Übergänge zwischen diesen Verdickungen und den Verdickungen in den jungen Wurzelhaaren, und man wird daher nicht bezweifeln können, dass sich ein Wurzelhaar an diesen Stellen gebildet hätte, wenn die Entwicklung nicht abgebrochen worden wäre. Die in den Serien III und IV dargestellten Entwicklungsreihen entsprechen ganz derjenigen in Serie II. Nur sind die Verdickungen in den Trichoblasten mehr länglich.

Wie Sinnott und Bloch (1939) nachgewiesen haben, teilen

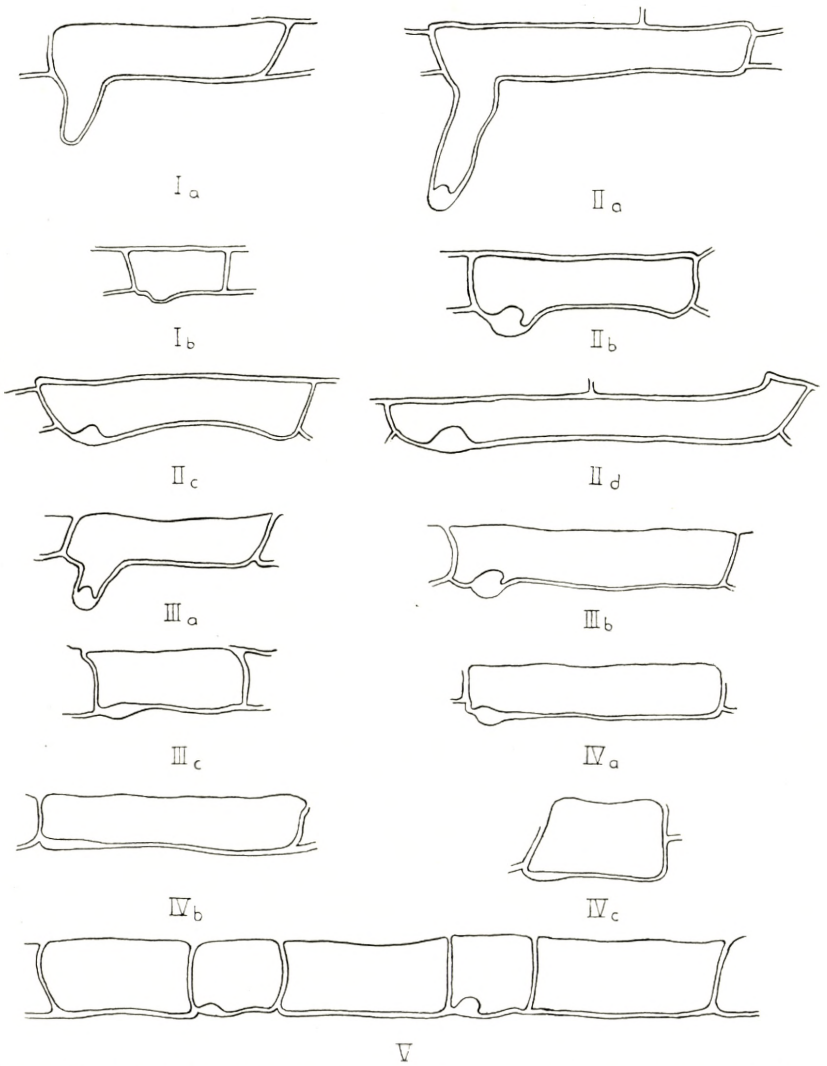

Abb. 4. Verdickungen in jungen Wurzelhaaren und Trichoblasten von Phleum. Die Wurzelspitze liegt links. Jede Serie enthält Abbildungen von Zellen aus derselben Wurzel in der Reihenfolge Basis→Spitze. Serie I Kontrolle. In den Serien II und V sind die Verdickungen durch Wasser und in den Serien III und IV durch βIE hervorgerufen. (Vergr. $\frac{400}{1}$).

sich die Zellen der Phleumwurzeln in einigem Abstand von der Spitze in zwei ungleichartige Zellen, eine kürzere apikale, die ein Wurzelhaar bilden kann, und eine längere basale, die sich streckt. In einem Fall (Abb. 4, V) ist es gelungen zu zeigen, dass

die Verdickungen in kurzen Zellen, die zwischen längeren Zellen eingeschoben sind, entstehen können.

Da man annehmen muss, dass die Verdickungen in der Spitze der Wurzelhaare durch Zellulosenbildner hervorgerufen sind, wird man weiter schliessen müssen, dass die Verdickungen in den Zellen, die noch kein Wurzelhaar gebildet haben, von Zellulosenbildnern, die an dem betreffenden Ort angehäuft worden sind, erzeugt sind. Bei normaler Entwicklung würden diese Zellulosenbildner die Zellwand eines Wurzelhaares gebildet haben, bei Abbruch der Entwicklung entsteht dagegen eine Verdickung.

Bei Wurzelhaaren besteht somit die Determination, d. h. das Wesen der Vorgänge, welche die bei der Entwicklung der Haare stattfindende Differenzierung hervorrufen, in einer Anhäufung von Zellulosenbildnern an dem Ort, wo das Wurzelhaar gebildet werden soll. Die von dem Verfasser aufgestellte Determinationstheorie (Boysen Jensen 1948) hat somit Gültigkeit für die Bildung der Wurzelhaare.

Dem pflanzenphysiologischen Laboratorium der Universität und dem Carlsbergfond, die mir die für die Untersuchungen notwendigen Instrumente zur Verfügung gestellt und mich auch in anderer Weise unterstützt haben, spreche ich meinen besten Dank aus.

Meiner Tochter, Frau Margrete Ehlers, die mich mit unermüdlicher Gewissenhaftigkeit bei der Ausführung der Versuche unterstützt hat, möchte ich auch an dieser Stelle herzlich danken.

In einer folgenden Abhandlung soll untersucht werden, ob es möglich ist, die Zellulosenbildner direkt unter dem Mikroskope zu beobachten.

4. Summary.

The cellulose masses produced in the tips of the root hairs of *Lepidium* and *Phleum* by the influence of Congo red or 3-indole acetic acid, or simply by placing plants cultivated on filter paper in water demonstrate that cellulose-building enzymes are located in the tips. Generally a thickening on the inner side of a cell wall can be used as a test indicating that such enzymes are present there.

Besides in the tip of a root hair a cellulose mass can also be produced as a small cone on the inner side of the outer wall of hairless epidermis cells. Such a cone indicates that cellulose-building enzymes have been accumulated in this place and that a root hair would have been produced there, if the development had not been arrested.

Hence it appears that the process determining the development of a root hair is an accumulation of cellulose-building enzymes in a definite place at the apical part of the outer wall of an epidermis cell.

The investigations support the determination theory advanced by the author (Boysen Jensen 1948).

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SOME MARINE ALGAE FROM MAURITIUS

ADDITIONS TO THE PARTS PREVIOUSLY PUBLISHED. II

BY

F. BØRGESEN

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
1950

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The present part with a single exception contains additions to Part 2, 1943, and Part 3, 1944, dealing with the *Gelidiales, Cryptonemiales, Gigartinales*, and the *Rhodymeniales*, respectively.

In all 32 species are mentioned and of these 10 species have not previously been recorded from Mauritius. To the remaining species various information, as to their structure, biology, etc., is added, this being made possible by means of new material arrived from the island.

Because of Dr. VAUGHAN's visit to Europe last summer I have not recently received any new material from the island.

The small dredge which, as mentioned in the paper of 1949, I have sent to Mauritius has at last arrived there and according to a letter recently received from Dr. VAUGHAN some algae from deeper water not yet met with have been gathered by means of the dredge.

To the Trustees of the Carlsberg Foundation I am much indebted for a continued grant for algological investigations.

Nemalionales.

Fam. 1. ***Chaetangiaceae.***

Actinotrichia Decsne.

1. **Actinotrichia fragilis** (Forssk.) Børgs.

Alg. Mauritius, III, 1, 1942, p. 44.

Some well developed specimens have lately been received from Mauritius. Most regrettably the specimens are sterile.

Mauritius: Pointe aux Cannoniers, Febr. 16, 1946, R. E. V. no. 535.

Gelidiales.

Fam. 1. ***Gelidiaceae.***

Gelidiella Feldm. & Hamel.

1. **Gelidiella acerosa** (Forssk.) Feldm. & Hamel.

Alg. Mauritius, III, 2, 1943, p. 5.

Having formerly seen very little material of this species I have in a later collection received a well developed specimen (no. 477) of this species.

Nothing is said about the locality.

Mauritius: Without locality 1943, C. Neyroles, no. 477.

Gelidium Lamour.

1. **Gelidium pusillum** (Stackh.) Le Jolis.
var. **pulvinatum** (Ag.) Feldm.

Alg. Mauritius, III, 2, 1943, p. 6, fig. 1.

Of this small rather variable plant several specimens are found in a later received collection.

The specimens had rather narrow tongue-shaped lobes.

It was growing "in rock crevices exposed to waves".

Mauritius: Ilôt Brocus, March 10, 1948. R. E. Vaughan, no. 855.

Cryptonemiales.

Fam. 1. ***Rhizophyllidaceae.***

Desmia Lyngb., J. Ag.

1. **Desmia Hornemanni** Lyngb.

Alg. Mauritius, III, 2, 1943, p. 13.

Some few well prepared specimens have been received from Mauritius in recently received collections.

Mauritius: Grande Rivière, Nov. 11th, 1941. G. Morin, no. 419.

Fam. 2. ***Corallinaceae.***

Amphiroa Lamour.

1. **Amphiroa fragilissima** (L.) Lamour.

Alg. Mauritius, III, 2, 1943, p. 17.

Some specimens of this species have lately been received. An examination shows that the padlike swollen ends of the joints, a characteristic feature of this species, were not developed in the specimens or in any case very little. As to the central strands these were very alike in the specimens, having 4—5 rows of long cells interrupted by a row of short ones.

One of the specimens (no. 580) was in all respects larger, forming tufts up to 6 cm high and with joints in the thallus reaching a length of 5 mm or even more. This specimen was gathered in shallow water in a lagoon. Another specimen (no. 353) was growing in a lagoon and mixed with sea-grasses. And a third one (no. 821) was found on exposed rocks, mixed with other algae.

Mauritius: Pointe aux Sables, Aug. 1939, R. E. V. no. 353. Gris-Gris near Souillac, June 20, 1946, R. E. V. no. 850. Ilôt Barkly, May 24, 1948, R. E. V. no. 821.

Cheilosporum (Decsne) Aresch.

1. **Cheilosporum acutilobum** Decsne.

Alg. Mauritius, III, 2, 1943, pp. 19—21, fig. 5.

Of this beautiful species of which I formerly have seen only some few small specimens, a collection including several fine specimens is present in a gathering no. 754 of a late date.

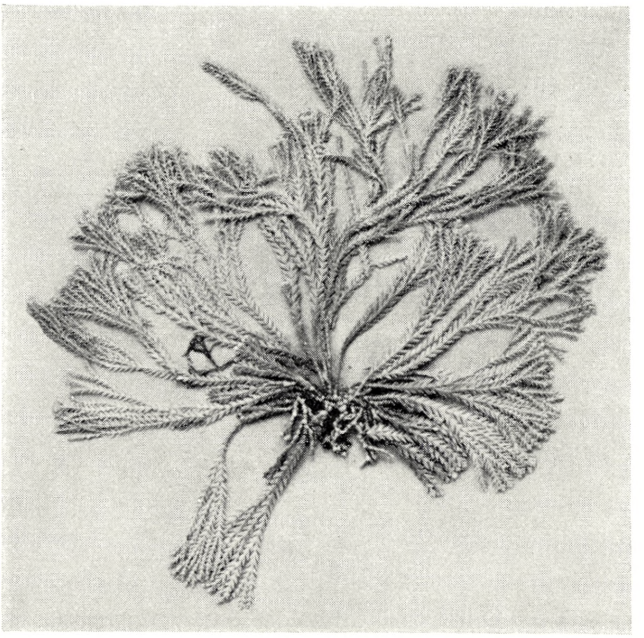

Fig. 1. *Cheilosporum acutilobum* (Decsne) Aresch. Natural size.

Fig. 1 shows the habit of a specimen.

The colour of the dried specimens is very beautiful, changing from a whitish rosy-red to a light-green.

The specimens were sterile.

As to its near relationship to several similar species compare my remarks *l. c.*

It was growing on a reef.

Mauritius: Pointe aux Roches, Nov. 17, 1947. R. E. V. no. 754.

2. **Cheilosporum jungermannioides** Rupr.

Ruprecht, in Areschoug, J. E., *Corallineae* in J. Agardh. Spec. Alg., II, 2, p. 546.

Of this tiny elegant *Corallinacea* a small tuft was found in a collection of algae from Mauritius. The specimen is in good conformity with several specimens from Tahiti received some years ago from Setchell, Tahiti being the type-locality of the species; later it has been found by Yendo in Japan and on the south coast of Java by Weber v. Bosse.

The specimen forms a dense tuft, the much ramified filaments being felted together. Most regrettably any information as to the locality is not given.

Mauritius: Without locality and date, C. Neyroles, 1943, no. 433.
Geogr. Distr.: Tahiti, Japan, Java.

Corallina Lamour.

1. **Corallina polydactyla** Mont. et Mill.

Alg. Mauritius, III, 2, 1946, pp. 21—22, fig. 6.

In collections recently received from Dr. Vaughan several specimens of this variable species are present.

As fig. 6 a (*l. c.*) shows, a trait of character in this species is that several pinnae, two to three, often are given off from the upper edge on both sides of the joints in the mid-rib; in *Corallina mauritiana* a single and less developed pinna, only, as a rule is developed from the upper edge of the joint on both sides.

Some of the specimens formed tufts up to 7 cm high. The specimens were growing upon reefs in exposed localities; one, no. 758, was an epiphyte upon stems of *Cymodecea* growing in a lagoon and accordingly the thallus was more flabby.

Mauritius: Pointe aux Roches, May 3, 1947, R. E. V. no. 688. Same locality, Nov. 17, 1947, R. E. V. nos. 758 and 759.

Jania Lamouroux.

1. **Jania tenella** Kütz.

Alg. Mauritius, III, 2, 1946, p. 26.

Some few small specimens of this tiny species have lately been received.

They were epiphytes upon pieces of larger algae.

Mauritius: Without locality and date, C. Neyroles, 1943, no. 434.

Fam. 3. ***Grateloupiaceae.***

Halymenia J. Ag.

1. **Halymenia maculata** J. Ag.

Agardh, J., Till Algernes Systematik, Nya bidrag. 4de afdl. VII. Florideae, 1884, p. 12; Analecta Algologica, 1892, p. 53.

Besides some smaller fragments I have for examination had an, as it seems, entire large lamina of a specimen measuring 45 × 28 cm. And finally, just when the paper was going to be printed, a small, complete specimen fixed to a piece of a coral and preserved in formol has been received from Mauritius.

By means of this specimen I have been able to examine the base of the plant. The specimen, about 25 cm high, has a quite short stipe scarcely 1½ cm long and is fastened to a piece of coral by means of a flattened, irregularly lobed disc. From the lower part of the terete stipe several small 2—3 cm broad irregularly shaped lamina-like lobes are given out. Above, the stipe makes an abrupt transition in the cordate base of the thallus, the decumbent edges of which near the stipe are smooth without

proliferations. The laminae of the specimens are in the most irregular way lobed and sinuated in larger and smaller cuneate lobes with roundish bases between them and their margins are again provided with densely placed irregularly shaped fimbriate

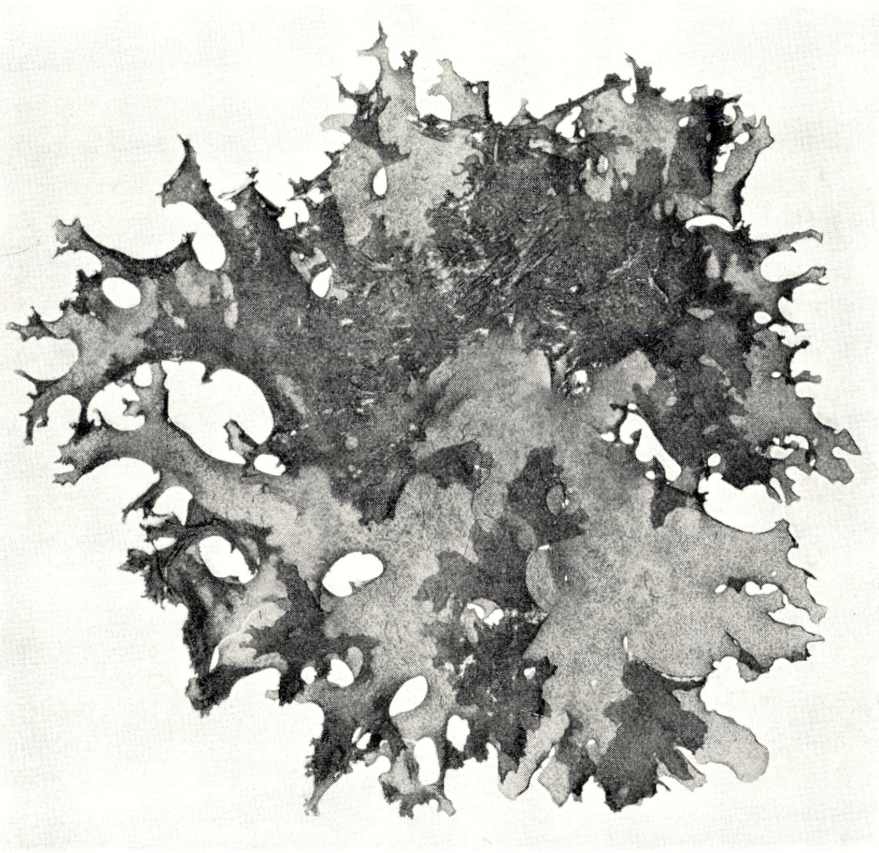

Fig. 2. *Halymenia maculata* J. Ag. Lamina of a small specimen. About $\frac{1}{2}$ size.

proliferations (Fig. 2). In a dry condition the outmost lobes are often quite narrow and nearly thornlike, but when moistened they become much broader and roundish, the whole thallus at the same time swelling highly, becoming soft and slimy.

The lamina in a dried condition is darkish purple; its surface is densely maculated by quite small roundish or polygonal spots gathered more or less densely into larger ones. The spots are due

to the fact that the surface is more or less densely wrinkled and bullate with small bulges, assuming a darker colour in the swelled parts.

A transverse section (Fig. 3) of the thallus shows that the epidermal layer consists of elongated papilla-like cells about 20 μ long, emerging from oblong-ovate cells, from which there is an even transition to larger ones lower down, the cells gradu-

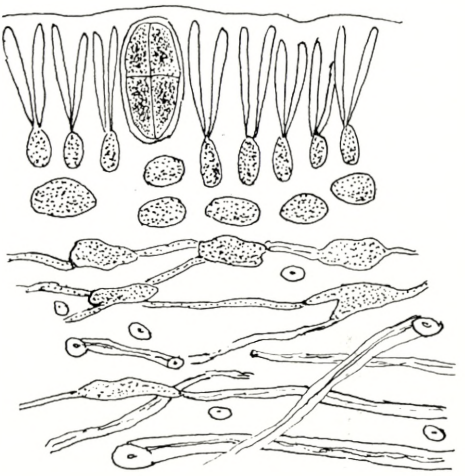

Fig. 3. *Halymenia maculata* J. Ag. Transverse section of the thallus with a sporangium. ($\times$ 600).

ally assuming an elongated more or less stellate appearance and giving out filaments from the projections; the medullary layer is filled with slime in which filaments are running in all directions.

The specimens are tetrasporic. The cruciately divided sporangia are about 30 μ long and 15 μ broad and developed in the upper part of the cortical layer from cells below the papilla-like epidermal ones, being more or less embedded among them.

The plant is endemic in Mauritius, being called there "Red Sea Lettuce", and is said to be common in places, but any information about its habitat, f. in. if it is found in the littoral or sublittoral zone or in exposed or sheltered places is not given.

Mauritius: Ilôt Barkly without dates, Fr. Neyroles, no. 431. Cassis, Jan. 7, 1947, G. Morin, no. 627.

Geogr. Distr. Endemic.

Carpopeltis Schmitz.

1. **Carpopeltis rigida** (Harv.) Schmitz.

Alg. Mauritius, III, 3, 1943, p. 27, fig. 9.

In later received collections some more specimens of this species are included, but none of them have been collected in situ; all are said to have been washed ashore.

As mentioned in the former part and said by JADIN this species occurs on exposed coast in the violent surf.

Mauritius: Pointe aux Roches, May 3, 1947, R. E. V. no. 687. Cassis, Jan. 1, 1948, G. MORIN nos. 772 and 773.

Gigartinales.

Fam. 1. ***Nemastomaceae.***

Titanophora (J. Ag.). Feldmann.

1. **Titanophora Pikeana** (Dickie) Børgs.

F. BØRGESEN, Alg. Mauritius, III, 2, 1943, p. 31, figs. 10—12. — *Titanophora Pikeana* (Dickie) Feldm. p.p., Remarques sur les Nemastomacées, 1942, p. 111.

During the war FELDMANN in the year 1942 in his above quoted paper pointed out that J. AGARDH's subgenus *Titanophora* ought to have generic rank; but since my paper quoted above and dealing with the same matter did not appear till 1943 FELDMANN has the priority.

While FELDMANN followed WEBER in considering the plant from New Guinea to be the same as that from Mauritius, I came to the result that Mme WEBER's plant specifically was different from that from Mauritius.

The species has not been rediscovered since Colonel PIKE collected it.

Fam. 2. ***Solieriaceae.***

Sarconema Zanard.

1. **Sarconema filiforme** (Sonder) Kylin.

Alg. Mauritius, III, 2, 1943, p. 39.

In the paper quoted above a fragment of a specimen from Réunion was referred to this species, but in a later collection some specimens of this species have been received from Mauritius also. When compared with specimens I have collected in Bombay and referred to this species (Kew Bulletin, 1934, p. 11, fig. 7) the specimens from Mauritius agree quite well with the Indian ones; but it cannot be denied that they are also very like *Sarconema indicum* (J. Ag.) Kylin, 1932, p. 22, pl. 8, fig. 17, where the original specimen found in J. Agardh's herbarium is reproduced; these two species are surely very closely related, and their size and shape upon the whole alters surely much as to the more or less exposed localities in which they occur.

In the above quoted paper I gave a transverse section of the Indian plant (fig. 7); as compared with a section of the plant from Mauritius, the cells of the medulla in the latter are smaller, having only a diameter of up to 90 μ.

The specimens were washed up by the waves.

Mauritius: Cassis, Jan. 28, 1948, G. Morin, no. 765.

Solieria J. Ag.

1. **Solieria robusta** (Grev.) Kylin.

Kylin, H., Die Florideengattung Gigartinales, 1932, p. 18. — *Dumontia robusta* Grev., Alg. Brittan., 1830, p. LXII. *Solieria australis* Harv., Phycol. Austr., tab. 149. *Rhabdonia robusta* J. Ag., Spec. Alg., II, p. 355.

f. *flagelliformis* J. Ag., Kylin *l. c.* pl. 5, fig. 9.

Two specimens found in the collections from Mauritius agree quite well with the figure of Kylin reproduced from the original specimen of this form in J. Agardh's Herbarium in Lund.

One of the specimens is tetrasporic.

Mauritius: Ilôt Barkly, Aug. 26, 1941, G. MORIN, no. 420. The other specimen, no. 435, was collected by Father C. NEYROLES, but is without locality and date.

Geogr. Distr.: Australia, Japan, Malayan Archipelago, India.

Eucheuma J. Ag.

1. **Eucheuma serra** J. Ag.

Alg. Mauritius, III, 2, p. 43.

Some few specimens (no. 892 a) coming near to those I formerly referred to this species have recently been received from Mauritius.

Besides the short spines characteristic of this species, long ones are present in places, reminding of those figured by KÜTZING in his figure of *Grateloupia opposita* Kütz., Tab. Phycol. vol. 17, pl. 31 referred by DE-TONI to *Eucheuma jugatum* J. Ag. in Sylloge Alg., vol. IV, 1, p. 371.

Another feature which was not found in the specimens of Dr. MORTENSEN is that the uppermost parts of some of the filaments are curved like tendrils. This is yet more the case in two smaller specimens (no. 892 b) which are better referred to *Eucheuma jugatum*.

The thallus of the specimens is terete.

The specimens were collected in a lagoon and have been laid dry at low tide.

Mauritius: Mahébourg, Aug. 1948, I. VINSON, no. 892.

2. **Eucheuma jugatum** J. Ag.

Alg. Mauritius, III, 2, 1943, p. 47.

Some specimens of *Eucheuma* (no. 893) together with the above-mentioned two smaller ones (892 b) are referable to this species, being in good accordance to the original specimen of this species found in AGARDH's Herbarium in Lund, of which a photo has been published by KYLIN, Gigartinales, 1942, p. 23, pl. 9, fig. 20.

The characteristic feature of this species is the numerous

sharp, in most cases rather short (1—1½ mm long), spines placed densely all round the thallus; but some few longer spines are found now and then.

But as said in my paper (1943) this species together with the above-mentioned one and furthermore *Euch. nodulosum* Aresch. and *E. horridum* (Harv.) J. Ag. are most probably only forms of a very polymorphic species.

The specimens were collected in the same locality as the above-mentioned species.

Mauritius: Mahébourg, Aug. 1948, I. VINSON, nos. 892 b and 893.

Fam. 3. ***Rhodophyllidaceae.***

Gelidiopsis Schmitz.

1. **Gelidiopsis variabilis** (Grev.) Schmitz.

SCHMITZ, FR., Marine Florideen von Deutsch-Ostafrika, 1895, p. 148. FELDMANN, J., Remarques sur les genres *Gelidium* Lamour., *Gelidiopsis* Schmitz et *Echinocaulon* (Kütz.) Feldm., 1931, p. 6. — *Gigartina variabilis* Grev. mscr., *Gelidium variabile* J. Ag., Epicrisis, p. 547, KÜTZING, Tab. Phycol., XIX, tab. 23, figs. C. D.

Several specimens (nos. 457, 538, 629, 638, 847) are referable to this species, agreeing quite well with KÜTZING's figures referred to above.

The breadths of the thallus of the different specimens varied from about 110 μ in the thinner filaments to about 250 μ in the thick ones.

As to the habitat of the species it is said about one specimen only: "On rocks and in pools near reef."

Mauritius: Cassis, Jan. 18, 1947, G. MORIN, nos. 629 and 630. Grand Baie, Febr. 16, 1946, G. MORIN, no. 538. Ilôt Brocus, May 9, 1948, R. E. V. no. 847.

Geogr. Distr.: Indian Ocean.

Fam. 4. ***Hypnaceae.***

1. **Hypnea charoides** Lamx.

Alg. Mauritius, III, 2, 1943, p. 56.

In later received collections from Mauritus several specimens referable to this very variable species were found.

Characteristic of this species is the fact that the branches are more or less densely clad with short acute branchlets.

Cystocarpic and tetrasporic specimens are met with.

As was stated already by JADIN this species is surely common at the shores of Mauritius.

Mauritius: Cassis near Port Louis, G. MORIN, nos. 421, 428, 429, 430. Ilôt Barkly, April 1, 1946, G. MORIN, nos. 520, 516, 517. Pointe aux Sables, March 30, 1947, G. MORIN, no. 665. Ilôt Barkly, March 25, 1948, G. MORIN, no. 781.

2. **Hypnea Valentiae** (Turn.) Mont.

Alg. Mauritius, III, 2, 1943, p. 58.

Some few specimens (no. 126) were found in lately received collections. The specimens agree with those I have formerly mentioned, being easily recognized by means of the stellate bulbils developed more or less densely over the thallus.

Mauritius: Pointe aux Vaeao, March 1, 1931. R. E. V. no. 126.

3. **Hypnea Esperi** Bory.

BORY, Voyage de Coquille, p. 157. KÜTZING, Spec. Alg. p. 759; Tab. Phycol., vol. 18, pl. 26. GRUNOW, Alg. Novara, p. 79. BØRGESEN, Alg. Easter Island, p. 306, fig. 48. TANAKA, The Genus Hypnea from Japan, 1941, p. 243, fig. 16.

Some sterile specimens of this small species were found in later received collections.

Mauritius: Cassis, Apr. 24, 1940, G. MORIN, no. 427.
Geogr. Distr.: In most warm seas.

4. **Hypnea nidulans** Setchell.

Setchell, W. A., American Samoa, 1924, p. 161, fig. 30. Weber, A., Alg. Siboga, 1928, p. 454, fig. 192, Tanaka, T., The Genus Hypnea from Japan, 1941, p. 246, figs. 18—19.

Some small specimens (no. 850) are referable to this species.

This characteristic species was first described by Setchell (*l. c.*), having earlier been distributed by Harvey in his Friendly Island Algae as *Hypnea pannosa* J. Ag. It has later been found to be common in the Malayan Archipelago by Mme Weber and in Japan by Tanaka.

The specimens from Mauritius are tetrasporic, the tetrasporangia being found in saddle-like nemathecia upon the ramuli as figured by Setchell and Tanaka.

Mauritius: Ilôt Barkly, May 10, 1948, G. Morin, no. 850. Grand Baie, Febr. 16, 1946, G. Morin, no. 546.

Geogr. Distr.: Pacific and Indian Oceans.

5. **Hypnea Cenomyce** J. Ag.

Agardh, J., Spec. Alg., II, 1852, p. 452. Epicrisis, 1876, p. 564. Tanaka, T., The Genus *Hypnea* from Japan, 1941, p. 250, fig. 21.

Some few specimens (no. 807) forming low, dense tufts produced by the entangled, irregularly ramified filaments are referable to this species.

Characteristic of this species is the fact that the sporangia develop in the basal swollen parts of the short lateral ramuli emerging from the branches; compare Tanaka *l. c.* p. 249, fig. 21 A. But nearly the whole material is sterile and I have seen only a very few fertile branchlets.

This author mentions that in the Japanese specimens the branchlets often instead of being acute are provided with a small disc. This was not observed in the Mauritian specimens.

The plant was found "upon block of old cement".

Mauritius: No locality, April 24, 1948, G. Morin, no. 807.

Geogr. Distr.: Australia, Japan.

6. **Hypnea**(?) **horrida** (Ag.) J. Ag.

Alg. Mauritius, III, 2, 1943, p. 62, fig. 32.

Having formerly seen only some small bleached specimens cast ashore of this species endemic to Mauritius I have recently received some few small but well prepared specimens from the island. The colour of the specimens is dark red.

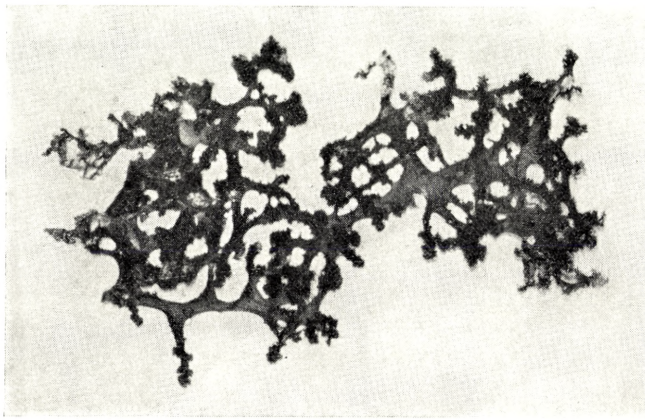

Fig. 4. *Hypnea horrida* (Ag.) J. Ag. Natural size.

Fig. 4 shows one of the specimens, demonstrating the very irregular ramification of the main branches from which short side branches are given out, the branchlets towards their summits being crowned by densely placed thorny, short outgrowths.

The anatomical structure agreed with my former description.

The plant is never found fruiting and the specimens mentioned here were sterile, too.

As to the habitat of the specimens no information is given, but according to JADIN it grows on reefs.

Mauritius: Pointe d'Esny, Aug. 17, R. E. V. no. 714.

Fam. 5. ***Sphaerococcaceae.***

Caulacanthus Kütz.

Caulacanthus ustulatus (Mert.) Kütz.

Kützing, Phycol. gener. p. 395; Spec. Alg., p. 753; Tab. Phycol., vol. XVIII, pl. 8. J. Agardh, Spec. Alg., vol. II, p. 433. Bornet et Thuret, Notes algal., p. 55, pl. 19. — Fucus ustulatus Mert. fide Kützing.

A small alga recently received from Mauritius is according to its structure a *Caulacanthus* and most probably referable to *C. ustulatus*, agreeing quite well with the description and beautiful figures of Bornet (*l. c.*).

For the use of later comparison, when better material is to be had, I give here some few figures of the plant. A small piece of the thallus is seen in Fig. 5, showing the irregular ramification. The thallus is mostly terete, but here and there some of the branchlets are flattened (Fig. 6 b).

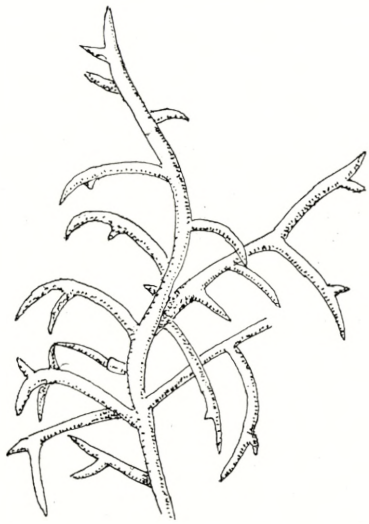

Fig. 5. *Caulacanthus ustulatus* (Mert.) Kütz. Habit of a fragment of the thallus. (× 15).

The plant is fixed to the substratum by means of short rhizoidal discs (Fig. 6 b, c, d) formed by coherent rhizoids breaking out from the epidermal cells, some of them also fixing themselves to neighbouring filaments.

Upon a transverse section (Fig. 6 a) of the thallus the thick-walled axis is seen in the middle; a longitudinal section shows that it is composed of cylindrical cells about 4—5 time as long as broad; from these cells a single or two filaments issue from

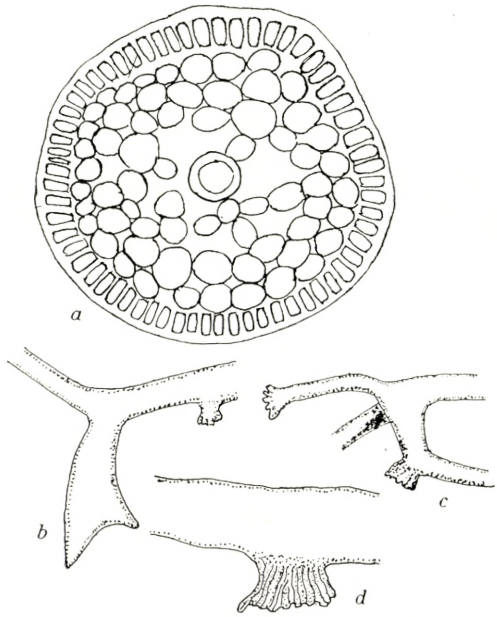

Fig. 6. *Caulacanthus ustulatus* (Mert.) Kütz. *a*, transverse section of the thallus. *b*, fragment of the thallus with a flat branchlet. *c*, *d*, fragments with rhizoids. (*a*, × 250; *b*, *c*, × 20; *d*, × 50).

each cell on all sides, which by their ramification form the peripheric tissue.

As to the size of the Mauritian plant the main filaments are about 250 μ thick, but some parts may be more than 300 μ and the thinner ones about 150 μ only. The plant was sterile.

Several species are described of the genus; they all seem to be very closely related; besides the size of the thallus the most essential characters are whether the thallus is more or less flattened or whether the discs are more or less numerous or the ramification more or less dense, etc.; this also applies to *C. divaricatus* (Suhr) Papenfuss, Notes on South African Mir. Alg. II, 1943, p. 86, originating from South Africa. A critical revision of the genus based upon original specimens is surely much

needed; compare also my remarks about Indian specimens in the Kew Bulletin, 1933, p. 115.

As to its systematic relationship *Caulacanthus* has formerly been placed in the fam. *Gelidiaceae*; but FELDMANN and HAMEL, 1934, p. 15, point out that the right place of the genus is in the Fam. *Sphaerococcaceae* near the genus *Heringia*, basing this view upon the facts that the apical cell is divided by oblique walls, that the sporangia are zonately divided and that the cystocarp shows a great resemblance to that of the genus *Heringia*.

And in a later paper FELDMANN, 1938, p. 298 about the germinating of the tretraspores of *Caulacanthus ustulatus* arrives at the result that the development of the spores is carried out in a way often found in the *Gigartinales*, but very different from what is the case in the *Gelidiales*.

Still I want to point out that the plant from Easter Island I (1920, p. 280, fig. 27) referred to *Caulacanthus spinellus*, because of its massive thallus surely is not this genus, but should rather be considered a small *Hypnea*; as said above the plant was sterile.

The specimens were collected: "In rock crevices exposed to waves."

Mauritius: Ilôt Brocus, May 9, 1948, R. E. V. no. 845.
Geogr. Distr.: Widely distributed in warmer seas.

Fam. 6. ***Sarcodiaceae.***

Sarcodia J. Ag.

1. **Sarcodia ceylanica** Harv.

Alg. Mauritius, III, 2, 1943, p. 66.

From Dr. VAUGHAN I have in recent years received some few specimens of *Sarcodia*, but all are fragments and most probably cast ashore. Some of the specimens may show some likeness to the small fragments upon which J. AGARDH based the species *Sarcodia Gattyae* (J. Ag.) Kylin and *S. ceylonensis* (J. Ag.) Kylin, 1932, p. 56, pl. 21, figs. 51 and 52, both species I feel inclined to refer to *S. ceylanica*.

Upon the whole, according to the few specimens I have

seen, a great variability as to the shape of the thallus seems to reign in this genus, making a large number of specimens necessary to be able to clear up the delimitation of the species.

As a characteristic of the 3 species: *S. Gattyi*, *S. Montagneana* and *S. ceylanica* KYLIN points out (*l. c.* p. 56) the presence of stellate cells in the medullary layer of these species and I have

Fig. 7. *Sarcodia* spec. Natural size.

also mentioned this in the above quoted paper. But as to these "stellate cells" Professor PIERRE DANGEARD, Bordeaux, in a letter asking me about a specimen of *Sarcodia*, remarks, referring also to KYLIN, that it is the contents of the cells which are stellately contracted not the cell wall, and in this I quite agree with Professor DANGEARD.

Fig. 7 shows a small specimen (no. 468) recently received from Mauritius. The thallus in this specimen is much furcated and divided and the lobes are again provided with small irregular projections along the margins. The plant is cystocarpic; the structure of the plant is rather like that of *Sarcodia ceylanica* (*l. c.* fig. 34) but the contents of the cells in the medullary layer are, especially regarding the outmost ones, less stellately con-

tracted. A transverse section of the cystocarp shows that it is very like that pictured by OKAMURA, Icones Jap. Alg., vol. IV, 1921, pl. 178, fig. 10. The parenchymatic tissue in the cystocarp in this specimen had cells with less stellately contracted content than I have found for instance in *S. ceylanica*.

Another specimen (no. 464), being most probably the same species as that mentioned above, is tetrasporic. Fig. 8 shows a

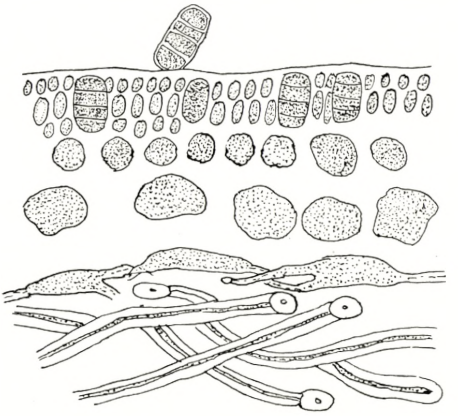

Fig. 8. *Sarcodia* spec. Transverse section of a tetrasporic specimen (no. 464). (× 250).

fragment of a transverse section of this specimen. The oblong cylindrical, transversely divided tetrasporangia, about 38 μ long and 13 μ broad, are formed in the epidermal layer composed of oblong densely placed small cells which are more elongated below. In the medullary tissue below the cell-contents in the uppermost cells are only contracted in a less degree, somewhat more in those lower down.

The two specimens were collected by Father NEYROLES, but are without locality and dates.

There is of course a possibility that the two small specimens represent a new species.

Mauritius: Without localities, C. NEYROLES nos. 464 and 468.

Fig. 9. *Corallopsis Opuntia* J. Ag. Fragments of a specimen (no. 536) preserved in formol. Natural size.

Fam. 7. ***Gracilariaceae.***

Corallopsis Grev.

1. **Corallopsis Opuntia** J. Ag.

Alg. Mauritius, III, 2, 1943, p. 67.

Referring to what I have previously said about this species and its relationship to *Gracilaria crassa* (Harvey) J. Ag. (compare my papers: Some Marine Algae from Ceylon 1936, p. 86 and Contributions to a South Indian Marine Algal Flora, II, 1937, p. 328) the recently received material from Mauritius has confirmed my supposition that the two species belong together, as even transitions occur from forms with a quite or nearly cylindrical thallus to such ones as have a markedly constricted thallus.

One of the specimens (no. 536) is a larger form, the thallus of which in parts is quite cylindrical, in others with more or

less distinct narrowings. Because of the very thin walls of the large cells in the medulla and the great contents of water, the plant shrivels very much when it is dried and it is also very little capable of assuming its original shape even when boiled in water, but fortunately some small fragments have been preserved in formol and seawater, a piece of which is seen in Fig. 9. As the figure shows, parts of the thallus are cylindrical,

Fig. 10. *Corallopsis Opuntia* J. Ag. Habit of a specimen. Natural size.

others are constricted. When the constrictions are much developed a form like the figure (Fig. 10) is the result; this figure originates from a specimen collected by JADIN and is preserved in my herbarium.

Another specimen (no. 731) is a more poorly developed form, having most probably been growing upon rocks in an exposed locality. The thallus in this form is more irregularly ramified and likewise more irregularly constricted; it is thinner, often with short internodes and curved branches.

A third specimen (no. 885) agrees very well with the latter; some fragments of this specimen have been preserved in formol and seawater and have thus kept their original shape. They show that the terete, ab. 4 mm thick, fleshy thallus is very irregularly ramified, often curved, in parts nearly cylindrical, in others

irregularly constricted. About its habitat, habit, and colour it is said by the collector: "Forms large cushions or mats up to 50 cm broad. Thallus smooth, terete, purple-yellow."

Mauritius: Pointe aux Cannoniers, Febr. 16, 1946, R. E. V., no. 536. Pointe d'Esny, Aug. 17, 1947, R. E. V., no. 731. Ilôt Barkly, Sept. 19, 1948, R. E. V. no. 885.

Gracilaria Grev.

1. **Gracilaria Millardetii** (Mont.) J. Ag.

Alg. Mauritius, III, 2, 1943, p. 72, figs. 36—40.

Of this species, originally described by MONTAGNE upon a unique fragment only, I have lately received a rather large material, but in spite of this a complete specimen with basal disc has been searched for in vain. And most regrettably the information about the localities and the external conditions in which the specimens have lived is also rather insufficient.

J. AGARDH (1884, p. 64) enumerates 3 forms of this species. The first of these is the forma *Millardetii* J. Ag. of which MONTAGNE's fig. 3, pl. XXV shows a fragment of the thallus with rather broad lobes. In the rather rich material I have got now any form answering exactly to MONTAGNE's specimen is not found, all the specimens having much narrower lobes; and this also applies to the small specimen, fig. 36, in my former paper (1943), which I with doubt referred to this form. Hence, even if I presume that MONTAGNE's specimen and those I have got now belong together, I prefer to consider the latter as representing a form of its own for which I propose a special name, forma *exposita*.

Fig. 11 shows a specimen of this form; it appears surely as low, 5—6 cm high, dense, firm tufts on rocks and corals in the littoral zone fixed to the substratum by a vigorous disc, thus being able to endure the violent surf of the ocean. The thallus is very irregularly divided and lobed, provided along the margins with numerous proliferations and teeth of variable shape and size. When dry the thallus has a dark red-brown colour and a horny-cartilaginous consistence. In the female specimens the large, about 1 mm broad, semiglobular cystocarps are scattered

Fig. 11. *Gracilaria Millardetii* (Mont.) forma *expositа* Børgs. Natural size.

over the flat sides of the thallus. Compare MONTAGNE and MILLARDET's figs. 3 a and 3 c *l. c.* 1862, pl. XXV.

The other two forms described by J. AGARDH, namely f. *crenulata* and f. *linearifolia* have proportionally narrow thalli with longer distances between the furcations; they have also a

much thinner thallus and their colour is lighter red. These forms surely live in more sheltered localities with more or less stagnant water or they have been cast ashore by the surf and carried into lagoons and other sheltered places, assuming the altered shape algae adopt when living in such places. In my paper (1943) figs. 39 and 40 give illustrations of these forms such as I have understood them without having been able to see AGARDH's specimens.

Finally several larger specimens are found in the later received collections which are in good conformity with the unique specimen which I in my former paper, p. 76, presumed to be *Gracilaria denticulata* (Kütz.) Schmitz, but which I now after examination of the recently received large material by means of intermediate forms consider a more broad-lobed and robust form of this highly variable species.

Fig. 12 shows a specimen of this form (nos. 417 and 774) for which I propose the name of forma *latifolia*. The specimens have a rather thick cartilaginous thallus and a dark red colour; it is irregularly lobed with narrower or broader lobes, up to $1\frac{1}{2}$ cm broad, cuneately narrowed towards their base and along their margins more or less densely provided with irregularly shaped proliferations or teeth. The tetrasporangia are scattered in the surface of the thallus and likewise the cystocarps.

At last I want to point out that by means of the large material available to me it has appeared that the different forms mentioned above are linked together by means of intermediate forms (figs. 13—14), an even transition being met with forms with narrow lobes and forms with broader ones, with much divided thalli and less divided ones, with numerous proliferations and fewer ones and so on.

Having nearly brought to an end the examination of the material of this polymorphous species I received E. JALE DAWSON's interesting paper, "Studies on the Northeast Pacific Gracilariaceae" (1949) and occasioned by this I have re-examined the material with reference to DAWSON's observations.

For more details referring to the treatise itself I shall mention only here that DAWSON with starting-point in SJÖSTEDT's (1926, p. 51) thorough examinations of 3 *Gracilaria*-species arrives at he result that one of these species, namely that which SJÖSTEDT called *Gr. robusta*, but which KYLIN (1930, p. 55) later described

Fig. 12. *Gracilaria Millardetii* (Mont.) J. Ag. forma *latifolia* Børgs. Natural size.

as *Grac. Sjöstedtii*, is the representative of a new genus: *Gracilariopsis*. This new genus is especially characterized by the want of the nutritive filaments arising from the gonimoblast and

Fig. 13. *Gracilaria Millardetii* (Mont.) J. Ag. Intermediate from approaching forma *crenulata* J. Ag. and f. *linearifolia* J. Ag. Natural size.

piercing the pericarp which are found in *Gracilaria confervoides*, the type species of the genus and therefore to be expected also in other species of *Gracilaria*, and furthermore the gonimoblast in the new genus is dome-like and formed by small cells densely filled with protoplasma. Regarding the shape of the thallus all the species in the new genus are cylindrical.

Fig. 14. *Gracilaria Millardetii* (Mont.) J. Ag. Intermediate form (tetrasporic specimen) approaching f. *latifolia* Børgs. Natural size.

However, by the examination of some cystocarps of *Gracilaria Millardetii* and comparing them with those of a specimen of *Gr. confervoides* collected by ROSENVINGE at Biarritz I was unable in the Mauritian specimens to find the nutritive filaments which are so common in the upper part of the cystocarps in *Grac. confervoides*. And furthermore I also found that the cells of the gonimoblasts were smaller in *Gr. Millardetii* than those in *Gr. confervoides* and moreover it also struck me that the innermost cells in the rows of cells forming the pericarp, into which the nutritive filaments penetrate, in *Gr. confervoides* were much larger and filled with protoplasma forming a much softer parenchyma than in *G. Millardetii*. Finally in the latter species the base of the gonimoblastic parenchyma was much broader than in *Gr. confervoides*.

Because of these rather essential differences I wrote to Dr. DAWSON about the matter, at the same time sending him some material of a cystocarpic specimen of *Gr. Millardetii*.

Most kindly Dr. DAWSON answered me that he had found the nutritive filaments in the specimen, but adds:

"I was surprised somewhat at the position of the nutritive filaments. You probably missed finding them by looking for them in the upper parts of the pericarp. I find no nutritive filaments in the region of the ostiole and very few in the upper two thirds of the pericarp. However, the nutritive filaments are both abundant and large in the lower parts of the pericarp. In some sections I can count six or seven, most of them descending and invading the tissue lateral to the base of the large celled gonimoblast-parenchyma. Some of them even invade the margins of the platform of small cells beneath the gonimoblast-parenchyma. The gonimoblast-parenchyma is relatively small in the specimens, but the cells are quite large, especially in the middle. In my opinion *Gracilaria Millardetii* is a true *Gracilaria* in every respect, though the cystocarp differs from *G. confervoides* in the position of the majority of the nutritive filaments."

So far Dr. DAWSON. After re-examination of the cystocarps of *Gracilaria Millardetii* and staining the sections with anilin blue, I have also found the nutritive filaments to be present, often in a great number, but all or nearly all emerging from the bottom of the gonimoblasts, penetrating the lowermost parts of the pericarp, or turning downwards, invading the small-celled paren-

chyma below the gonimoblastic tissue (Fig. 15). Only in a few cases I have met with nutritive filaments higher up in the pericarp and in a single case only a small one quite near the ostiole. Even if, like Dr. DAWSON, I still want to place *Gr. Millardetii* in the genus *Gracilaria* it seems to me that the deviating occurrence of the nutritive filaments in connection with the above-mentioned differences, e. g. the greater breadth of the gonimoblastic parenchyma being composed of smaller cells and the firmer consistence

Fig. 15. *Gracilaria Millardetii* (Mont.) J. Ag. Transverse section of a cystocarp. Nutritive filaments are seen emerging downwards from the basal part of the gonimoblast-parenchyma. (× 75).

of the pericarp are rather essential, and if future examinations should substantiate that other species of this genus rich in species should agree with this one they ought perhaps to be considered as a distinct group of the genus.

Having found the above-mentioned peculiarities in female specimens of forma *exposita* and forma *latifolia* and in intermediate forms, this strengthens my supposition that the, as to habit, rather different forms rightly are to be referred to *Gracilaria Millardetii*.

Another peculiarity which I have met with in the cystocarps I have examined of this polymorphous species was that the cell-contents not only in the cells of the pericarp, but also in most cells elsewhere in the cystocarps, were stellately contracted; in the tissues of the cystocarp of *Gr. confervoides* in the specimen I have examined this was not found.

Regarding the antheridial bodies I have formerly (1943, p. 74) met with them once in the forma *linearifolia*. And in the mate-

rial later received I have found them in a specimen of f. *exposita* (no. 469 a, Fig. 16) in which specimen the peculiarity was present that tetrasporangia as well as antheridia occurred mixed together in great number. Like those in the above specimen the antheridia were developed upon the walls of small cavities (Fig. 17).

These were scattered over the surface of the thallus solitarily

Fig. 16. *Gracilaria Millardetii* (Mont.) J. Ag. f. *exposita* Børgs. The specimen with tetrasporangia and antheridial bodies. Natural size.

or gathered in small irregular groups which protrude cupola-like above the surface. When placed solitarily the caves are broadly urn-shaped, when packed together oblong. They have above a somewhat narrowed opening and are about 70—80 μ deep.

The occurrence of sexual and asexual organs in the same plant is by no means any rare phenomenon. According to CHURCH, "Historical Review of the Florideae", II, p. 332, note 1 "in *Gracilaria confervoides* tetraspores, antheridia, carpogonial branches and cystocarps may all occur in the same individual". And FRITSCH in his important work "The Structure and Reproduction of the Algae", vol. II, 1945, p. 725, mentions a number of such instances in different *Florideae*, but in most cases some few

tetrasporangia were present only in the cases of an antheridial plant and conversely in the opposite case. In the present one both kinds of reproductive organs were abundantly present and mixed densely together, even if in places the sporangia were

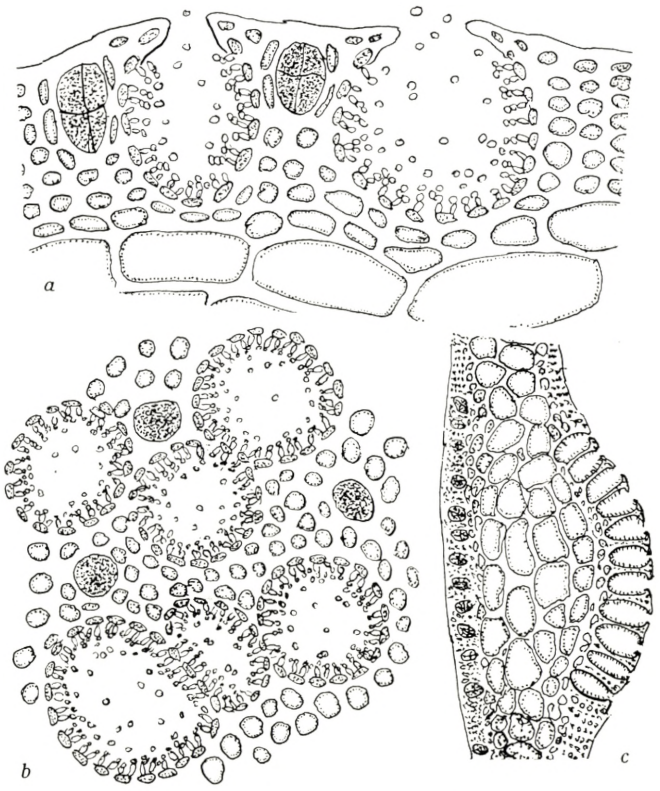

Fig. 17. *Gracilaria Millardetii* (Mont.) J. Ag. f. *exposita*. Tetrasporangia and antheridial bodies mixed together in great number. *a*, transverse section of the thallus, *b*, view from above, *c*, transverse section of thallus with tetrasporangia on the one side and antheridial bodies on the other. (*a*, *b* × 300, *c* × 60).

present in greater number on one side of the thallus and the antheridia on the other (Fig. 17 a).

In continuation of the above I want to mention that I, when examining, as said above, for comparison with *Gr. Millardetii* a cystocarp of *Gr. confervoides*, in the wall of the pericarp to my great surprise found two well-developed antheridial bodies, the female organ thus on her back carrying the male one (Fig. 18).

The tetrasporangia are scattered in the surface of the thallus and each tetrasporangium is surrounded by more or less marked paraphysis-like filaments.

Fig. 19 shows a tetrasporangium with surrounding cells of forma *latifolia*, and those of f. *exposita* are very like that.

Closely related to *Gracilaria Millardetii* if not identical seems *Gracilaria purpurascens* (Harvey) J. Ag. to be, of which species AGARDH says ("Till Algernes Systematik", VII, 1884, p. 63) that

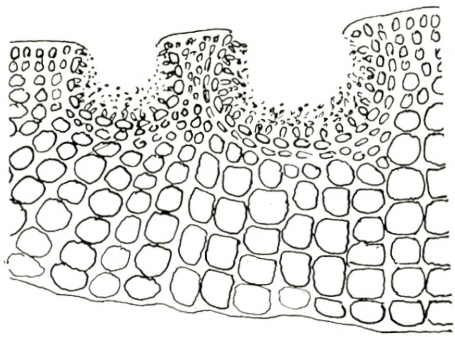

Fig. 18. *Gracilaria confervoides* (L.) Grev. Two antheridial cavities on the pericarp of a cystocarp. (× 150).

he has seen numerous specimens from Mauritius. HARVEY distributed this species as *Rhodymenia purpurascens* in "Alg. Ceylon Exsicc." no. 96. I have not seen any specimen of it nor any of J. AGARDH's, but according to the description it seems to come very near to the variable *Gracilaria Millardetii*. And a figure of an alga referred by YAMADA (*l. c.* p. 125, pl. XXV, 1) to *Gracilaria purpurascens* also shows a very great likeness to this species.

And yet another species described upon specimens from Mauritius, namely *Gracilaria Protea* J. Ag., "Species Alg.", III, 4, 1901, p. 58, which I have once seen in AGARDH's herbarium in Lund, seems to me to be at any rate closely related to this species. And Dr. PAPENFUSS has most kindly sent me a fragment of a specimen he has collected in South Africa and referred to *Gr. Protea* (1948, p. 87), a specimen which seems to me to be closely related to if not identical with certain forms of *Gracilaria Millardetii* as I interpret the species.

And finally, as pointed out by DAWSON (*l. c.* p. 28), the Pacific species *Gracilaria crispata* Setch. and Gard., 1924, p. 453,

pl. 44, and especially *Gr. lacerata* Setch. and Gard. ibd., p. 755, pl. 51 C, are very like the Mauritian species, but in one respect at any rate a difference is present, viz. the antheridia in *Gracilaria crispata* "are borne in small shallow, well-defined depressions" and not in cavities.

As said above, the information regarding the external conditions in which the different forms were growing is rather scanty, but some is found.

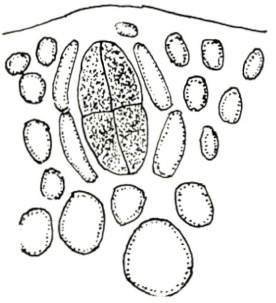

Fig. 19. *Gracilaria Millardetii* (Mont.) J. Ag. A tetrasporangium. (× 500).

As to *exposita*, which I presume to be a form occurring in exposed localities, it is said about no. 830 that it is "growing on rocks and corals", about nos. 476 and 787: "growing on old pieces of cement", and about nos. 769 and 853: "washed up by waves". Considered together I think these observations may be indicative of a locality exposed to the surf.

Regarding specimens of forma *latifolia* it is said about no. 785: "Growing on coral in one foot of water at low tide" and about no. 774: "washed up by waves": This I think is to be interpreted in the way that this form grows in rock pools in localities exposed to the surf in the upper sublittoral zone in contradiction to forma *exposita*, which I presume is found in exposed localities in the littoral zone, being a surf-form.

About no. 663, being referable to forma *linearifolia*, it is said only: "in lagoon", and about no. 853, a somewhat larger form with a somewhat firmer and darker red thallus, it is said: "on rocks and old pieces of coral". This form and forma *crenulata* with their narrow thalli are surely forms from protected places in lagoons, where they very probably are found also lying loose in more or less stagnant water.

Mauritius: Forma *exposita*. Ilôt Barkly, 19.3.45, G. MORIN, no. 530. Cassis, 28.1.48, G. MORIN, no. 769. Ilôt Barkly, 25.3.48. G. MORIN, no. 776. Ilôt Brocus, 20.3.48. G. MORIN, no. 787. Ilôt Barkly, 24.3.48, R. E. V., nos. 830, 831. Ilôt Barkly, 10.5.48. G. MORIN, no. 851. Cassis, 28.1.48. G. MORIN, no. 853.

Forma *latifolia*. Cassis, 5.5.40. G. MORIN, no. 417. Cassis, 7.1.47. G. MORIN, no. 636. Cassis, 1.1.48. G. MORIN, no. 774. Ilôt Barkly, 25.3.48. G. MORIN, no. 785. Ilôt Barkly, 10.5.48. G. MORIN, no. 860.

Forma *crenulata*. Pointe aux Sables, 30.3.47. G. MORIN, no. 666. Without locality and date, C. NEYROLES, no. 443.

Forma *linearifolia*. Pointe aux Sables, 4.4.47. G. MORIN, no. 663. Ilôt Barkly, 10.5.48. G. MORIN, no. 853. Without locality and date. C. NEYROLES, no. 444.

2. **Gracilaria arcuata** Zan.

Alg. Mauritius, III, 2, 1943, p. 69.

Var. *typica*.

In later received collections several specimens referable to this species are found, two of which belong to var. *typica*. One of the specimens (no. 426) is a large specimen, the other (no. 478) smaller; the latter is cystocarpic and quite agrees with FELDMANN's figure of a specimen from Tunis, (Algues marines de Tunisie, 1931, p. 14, fig. 4); compare also my figure of a specimen from Karachi in the Kew Bulletin, 1934, p. 9, pl. III.

Var. *Snackeyi* Web. v. Bosse.

The Mauritian specimens referable to this variety are in good accordance with Mme WEBER's figure; the specimens have terete, fleshy, very irregularly divided branches, being more or less arcuately bent and tapering abruptly towards the apices.

The plant has a purple colour, often turning into greenish, and occurs in pools.

Mauritius: var. *typica*: Cassis, 20.7.40, G. MORIN, no. 426. Without locality: Father C. NEYROLES, no. 478. var. *Snackeyi*: Port Louis, 1.10.40, G. MORIN, no. 424. Pointe aux Cannoniers, 16.1.1946, R. E. V. nos. 539 and 544.

Genus incertae sedis.

Wurdemannia Harv.

1. **Wurdemannia miniata** (Drap.) Feldm. & Hamel.

Feldmann & Hamel, Observations sur quelques *Gélidiacées*, 1934, p. 17, and *Floridées* de France, *Gélidiales*, 1936, p. 260, where literature is mentioned. — *Wurdemannia setacea* Harv., Nereis Bor.-Amer., part 2, 1853, p. 245.

After examination of a specimen of *Fucus miniatus* Drapernaud (*Gigartina miniata* Lamouroux) found in Museum National d'Histoire Naturelle, Paris, Feldmann & Hamel have found that this plant is the same as *Wurdemannia setacea* from the West Indies, where it seems to be much distributed, I myself having found it in the former Danish Islands. Later I have also found it in the Canary Islands. And according to Feldmann & Hamel it is much distributed in the Mediterranean Sea. It is therefore of interest that it also occurs at the shores of Mauritius.

The specimens quite agree with my figures of the West Indian specimens as described and figured in "Mar. Alg. D. W. I.", vol. II, p. 368, figs. 360—1. The plant forms low carpets or tufts composed of the much intricated filaments firmly connected by the numerous short hapteres formed everywhere where the filaments come near each other. The filaments have a breadth about 200—300 μ. The specimens were sterile. Kützing in "Tab. Phyc.", XIX, pl. 21 gives a figure of the zonately divided sporangia found in specimens from Kew West, Florida, but elsewhere it is always found only as sterile. Because of the absence of cystocarps its systematic position is uncertain.

Mauritius: Near Gris-Gris, Souillac, June 6, 1947, R. E. V. no. 692.
Geogr. Distr.: West Indies, Canary Islands, Mediterranean Sea.

Rhodymeniales.

Fam. 1. ***Rhodymeniaceae.***

Coelothrix Børgs.

Coelothrix indica Børgs.

Alg. Mauritius, III, 3, 1944, p. 14, fig. 9—11.

When in 1944 I described this species I had only a single dried, sterile specimen to rely on and the differences I found when comparing the Mauritian plant with *Coelothrix irregularis* (Harv.) Børgs. were upon the whole small, but to these came at any rate also the geographical distribution.

I was therefore gladly surprised, when, in recently received material from Mauritius, I found some very good and even fertile (tetrasporic) specimens (no. 667 A). By means of this material I have not only been able to correct my former description, but have also found characters which strengthen the proposing of the Mauritian species.

In the description of the new species I pointed out that I had not been able to find any of the rhizoidal discs by means of which the filaments in the West Indian plant are fixed together. A search in the new material has shown that they are present, although less numerous than in the West Indian plant.

I shall not dwell on the remaining differences pointed out in the description, but mention only that the Mauritian plant seems to be somewhat slenderer than the West Indian one. But are these differences in the vegetative thallus small, then those as to size and shape of the stichidia in the West Indian and Mauritian plants are so much more essential.

Collins in his paper "The Algae of Jamaica", 1901, p. 225, describes the stichidia in this way: "the modified portions of the branches being ovate or subspherical rather than lanceolate". And according to Taylor's description and figures (The Marine Algae of Florida, 1928, p. 160, pl. 22, fig. 19 and pl. 23, fig. 18) "the tetrasporangia are carried in short swollen, ovoid pedicillate branches".

In the specimens from Mauritius the stichidia (Fig. 20) are elongated, clavate, tapering upwards to an obtuse, occasionally

almost subacute apex (fig. 21 a). The stichidium pictured in fig. 21 *a* has a length of 2.1 mm and a breadth of 580 μ, where it is thickest, and those seen in fig. 20 are about 1950 μ long and about 600 μ broad; the pedicels carrying these stichidia were

Fig. 20. *Coelothrix indica* Børgs. Fragments of the thallus. (× about 4).

about 750 μ long, but that carrying the stichidium shown in fig. 21 *a* was 3 times this length.

A great difference regarding the length of the pedicel and the shape of the stichidia of the West Indian plant as compared with that from Mauritius is thus present, separating the latter clearly from the former.

Regarding the division of the tetrasporangia, this is carried out in different ways, some being tetrahedrally divided, but most of them cruciately or more irregularly, rather many like that shown in fig. 21 *b*.

In continuation of what was said in my former paper (1944, p. 17) about the question of the systematic position of this genus, I want to state that it seems to me that it can remain in the group *Rhodymenieae* of the fam. *Rhodymeniaceae* until

further observations also regarding the cystocarps (cfr. COLLINS, 1901, p. 55) are brought forward; we know only what has been stated by COLLINS.

At last follows a new altered and augmented diagnosis of the species:

Thallus plus minus dense caespitosus, suberectus, ca. 5—6 cm

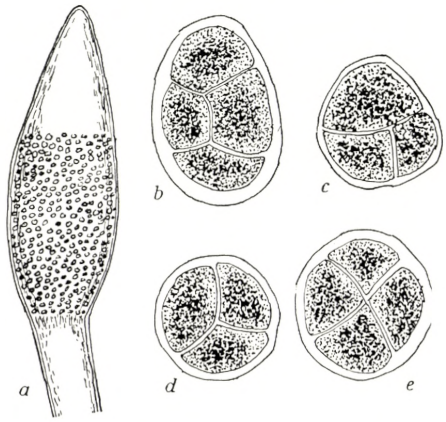

Fig. 21. *Coelothrix indica* Børgs. *a*, a stichidium; *b—e*, tetrasporangia (*a* × 20, *b—e* × 250).

altus, irregulariter ramosus, exfilamentis 240—500 μ latis, rhizoideis sparsis connectis, compositus.

Stichidia pedicellis plus minus elongatis instructa, elongata-subpyriformia, ad apicem obtusa aut subacuta, ca. 2 mm longa et 500—600 μ lata.

Tetrasporangia cruciatim, triangule aut magis irregulariter divisa.

Mauritius: Pointe aux Sables, in lagoon, April 4, 1947, G. MORIN nos. 667 and 667 A. A specimen no. 471 was collected by C. NEYROLES, but is without locality and dates.

Geogr. Distr.: Mauritius.

Botryocladia (J. Ag.) Kylin.

1. **Botryocladia Skottsbergii** (Børgs.) Levr.

LEVRING, T., Die Meeresalgen der Juan Fernandez-Inseln, 1941, 645. FELDMANN, G., Revision du genre *Botryocladia* Kylin, 1945, p. 55. — *Chrysymenia Skottsbergii* Børgs., Alg. Easter Island 1920, p. 317, figs.

44—50. *Chrysymenia Kuckuckii* Weber, Alg. Siboga, 1928, p. 466, fig. 799. *Botryocladia Kuckuckii* (Weber) Yamada et Tanaka, Mar. Alg. Yonakuni, 1938, p. 77, figs. 8—9. BØRGESEN, Alg. Mauritius, 1944, p. 23, figs. 16—48.

In my paper (1944) named above I, not without much hesitation, referred some few small specimens of a *Botryocladia* to *B. Kuckuckii* (Weber) Yamada et Tanaka, but at the same time printing out that it seemed to me very questionable whether the

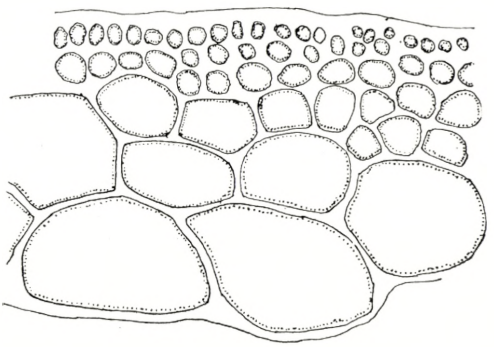

Fig. 22. *Botryocladia Skottsbergii* (Børgs.) Levring. Transverse section of a vesicle. (× 350).

species of WEBER was to be kept separate from *B. Skottsbergii* Børgs. from Easter Island described in 1920. When describing her species Mme WEBER did not take my species into consideration. In reality it is only some minor differences, in the more or less thick wall of the inflated branchlets and the size of specimens, upon which the separation of the species depends; the differences are in reality unessential and surely due to the external conditions under which the specimens have lived.

My paper was published during the war and the same is the case with that of Mme FELDMANN quoted above. In this the author points out that the differences between the two forms are insignificant and hence refers WEBER's plant to *B. Skottsbergii*. Had Mme FELDMANN not done so I had at any rate done so now as in recently received material from Mauritius I have been able to examine some few specimens, rather small of size, showing the variability of this plant.

The height of these specimens was only 1—1½ cm and the inflated branchlets 3—4 mm long and up to 3 mm broad. A

transverse section of the latter shows that their wall is firmly built, about 150 μ thick, and composed of several layers of cells; the innermost ones facing the cavity are large, the following ones decreasing gradually in size to the quite small densely placed peripheral ones (Fig. 22).

About the character of the locality in which the latest received specimens are found it is said: "On rocks exposed to waves", and if this has been a coast open to the violent surf of the Indian Ocean, it is no wonder that the specimens have been small with a firm structure; compare also JADIN's description (1934, p. 166) of the locality of *Chrysyminia obovata*, as said in my former paper (1944, p. 26) to be the present species.

Mauritius: Ilôt Brocus, May 9, 1948, R. E. V. no. 842.

Geogr. Distr.: Easter Island, Malayan Archipelago, Japan, Mascarene Island.

Fam. 2. ***Champiaceae.***

Champia Desv.

1. **Champia parvula** (Ag.) Harv.

Alg. Mauritius, III, 3, 1944, p. 30.

Having formerly seen only some few small specimens I have in a recently received collection found some well developed large specimens of this species.

They were growing "in calm water in a lagoon".

Mauritius: Ilôt Barkly, 19.9.48, R. E. VAUGHAN, no. 888.

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Additions to the lists in the former parts.

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INDEX OF SPECIES

together with some synonyms, the latter printed in italics.

Indleveret til selskabet den 14. marts 1950.
Færdig fra trykkeriet den 5. juli 1950.

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PHYTOPLANKTON STUDIES

1. *NITZSCHIA FRIGIDA* GRUN., AN ARCTIC-INNER-BALTIC DIATOM FOUND IN DANISH WATERS

BY

JUL. GRØNTVED

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
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1. Introduction.

In 1896 P. T. Cleve (1896b, pp. 3—4) published a report on the discovery in the Baltic of some pelagic species of diatoms, previously known only from Arctic seas: *Coscinodiscus lacustris* var. *hyperboreus*, *Achnanthes taeniata*, *Chaetoceros septentrionalis* (? *C. gracilis Schütt*) and *Navicula septentrionalis* (= *N. Vanhöffenii* Gran).

The intensive plankton investigations of the following decade gave information regarding the occurrence of still other Arctic plankton forms in the Baltic during the winter and spring, but also showed that some of the species in question occurred in the waters which now connect the Arctic seas with the Baltic. Referring here only to the diatoms of the plankton, the following species may be regarded as having a bicentric distribution, being stationary on the one hand in the Arctic seas and on the other in the Baltic: *Achnanthes taeniata* Grun., *Melosira arctica* (Ehrh.) Dickie, *Navicula Vanhöffenii* Gran and *Nitzschia frigida* Grun. Where they have been observed outside these areas, they may be regarded as more or less chance occurrences, even though they may locally occur in great abundance where the ecological conditions have at times been favourable for their reproduction.

According to more recent investigations (Leegaard 1920; Cleve-Euler 1937) this group also includes *Fragilaria cylindrus* Grun., *F. islandica* Grun., *F. oceanica* Cleve, *Thalassiosira hyalina* (Grun.) Gran and possibly a few more.

The Baltic species referred to may be regarded as relicts of the time when there was a direct connection between this sea and the Arctic waters (Cleve 1897, p. 8; Jørgensen 1912, p. 10; Leegaard 1920, p. 39).

The present work received its stimulus from finding *Nitzschia frigida* in Danish waters in Kattinge Bight, one of the innermost branchings of the Isefjord water system. The sample in question, given me by Dr. Aa. Jensen, Dansk Biologisk Station, for investigation, consisted of melting water from the underside of an ice-layer which was about 70 cm. thick, coloured greenish in the lowermost few cm. by the organisms contained in it. I owe thanks to Dr. Jensen for giving me the sample together with Table 2 displaying the hydrographical conditions at the spot where the sample was taken. To Dr. K. J. Purasjoki, Helsingfors, too, who has put me in possession of *Nitzschia frigida* material from Levander's collections in the Gulf of Finland, I would tender my best thanks. During the preparation of this work I have had the opportunity of seeing slides from E. Østrup's great collections of diatoms, now found in the Botanical Museum of Copenhagen University; I wish to thank the Inspector of the Museum, Dr. phil. O. Hagerup, for the loan of these slides.

2. The Morphology of *Nitzschia frigida.*

Nitzschia frigida Grunow 1880, p. 94, Taf. V, Fig. 101. — ? Østrup 1895, p. 447, T. VIII, Fig. 99. — Cleve 1896a, p. 12. — Vanhöffen 1897, p. 264, T. IV, Fig. 1. — Gran 1897a, p. 10, T. I. Fig. 11. — Gran 1905, p. 129, Fig. 173. — Jørgensen 1905, pp. 103—104. — Meunier 1910, p. 335, Pl. XXXIV, Fig. 36. — Lebour 1930, p. 212, Fig. 177. — Ussatschew 1935, p. 75.

Original diagnosis: Bisher nur in ganzen Frusteln beobachtet, welche stets in der Mitte etwas weiter wie an den Enden sind. Kielpunkte klein, 7—9 in 0.01 mm., die mittleren zwei entfernter, mit Andeutungen eines Centralknotens zwischen ihnen, Querstreifen sehr zart, über 35 in 0.01 mm. Länge 0.045—0.075 mm., Breite 0.008—0.0125 mm. Karisches Meer. Eine ähnliche Form mit 9—10 Kielpunkten sah ich von Novaja Semlja.

Description: The form of the cell in valve view is linear, narrowing towards the ends (Fig. 1 (right)); in girdle view the cell form is approximately linear-lanceolate (cp. Pl. I, Fig. 2f). Length[1]: 33—81 μ; breadth (in valve view): 5.6—12.5 μ; 2 chrom-

[1] As in the diagnose the cell length and breadth here mean the length of the apical and transapical axis respectively.

atophores separated by the cell nucleus lying centrally; the valve is linear with truncated ends (Fig. 1 (left)). Breadth[1]: 4.5—5.5 μ; keel eccentric with 7—10 keel-points in 10 μ; there is a weakly developed central nodule between the 2 midmost keel-points (Fig. 1); the striae of the valves are very faint[2]; the cells form irregular colonies which at some places are branched like a tree, in other parts the cells are connected linearly or in zig-zag formation (Pl. I, Fig. 1).

In a diatom material from an East Greenland coastal area (73°14′ — 75°37′ N. Lat.) ØSTRUP found a species which he refers—with some doubt—to *Nitzschia frigida* (ØSTRUP 1895, p. 447, T. VIII, Fig. 99a—e); ØSTRUP's figures are reproduced here in Fig. 2a—e. 2a is undoubtedly *N. frigida*, but 2d showing a valve view and 2b—c showing an oblique position are not this species; it has a rhomboid form with central keel, whilst *N. frigida* has a linear valve with eccentric keel. ØSTRUP states that the species in question usually took up the position in the slides shown in Fig. 2a, but it was also sometimes observed in an oblique position, as shown in 2e; it was only in special preparations that he succeeded in seeing it in valve view (Fig. 2d). If ØSTRUP's Figs. 2a and 2d represented the same species, practically all solitary cells (and ØSTRUP no more than the original diagnosis mentions formation of colonies) would take up the position shown in Fig. 2d, as they will settle on the broadest side; however, the opposite was the case, and it may be concluded from this alone, that Figs. 2a and 2d do not belong to the same species. ØSTRUP does not seem to have seen cells like Fig. 2d in girdle view and he has not seen isolated *N. frigida* valves.

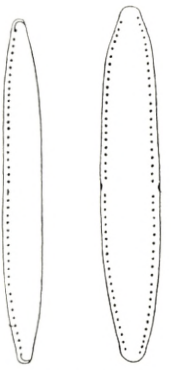

Fig. 1. *Nitzschia frigida;* valve (left) and frustula (in valve view). Kattinge Bight $^5/_3$, 1947. (×1000).

A transverse section of the *N. frigida* cell shows a rhomboid figure with diagonally placed keels at the pointed angles of the rhomboid; in glow preparations isolated cells almost always are placed on one of the valves and the keels are lateral; in

[1] Neither Grunow nor any of the other authors dealing with the morphology of the species has seen isolated valves; the breadth given here for the valve comes from measurements on the Kattinge Bight population, which consisted of rather small cells; thus it cannot be taken to cover the whole range of variation.

[2] Apart from the original diagnosis there is nowhere any information about the number of striae, and the present author has not been able to determine it either.

colonies, on the other hand, where the single cells are held in position by their connection with the neighbouring cells, the keels are not rarely seen centrally in the cell, which in this position has an almost linear-lanceolate circumference (cp. Pl. I, Fig. 2f). MEUNIER (1910) in a drawing of an *N. frigida* colony (Pl. XXXIV, Fig. 36) shows some cells in this position and regards it as a valve view; it is an oblique girdle view.

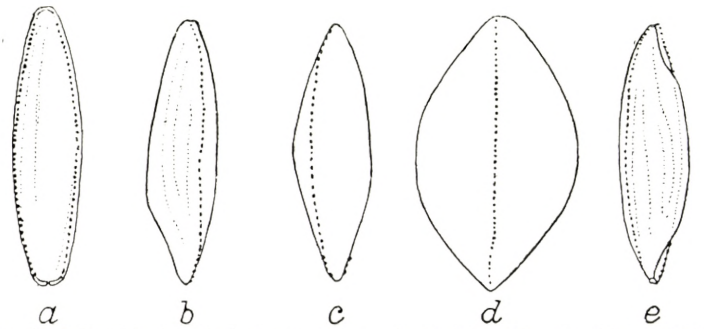

Fig. 2. *Nitzschia frigida*? (from Østrup 1895, T. VIII, Fig. 99). (×600).

3. The Geographical Distribution of *Nitzschia frigida*.

The geographical distribution of *N. frigida* is shown in Figs. 3 and 4, where a filled-in circle marks a finding place with this position; in Fig. 3 also shaded places indicate areas within which the species is said to be found, but without precise information about the localities; not marked in this Fig. we have the following summary data of finds of *N. frigida:* CLEVE and GRUNOW 1880, p. 94 (Novaja Semlja, Karisches Meer); CLEVE 1898, p. 26 (Barents Meer). When CLEVE (1883, p. 481) gives the species from Discovery Bay this seems to be a mistake and the locality in question therefore is not marked on the map.

The sources in the literature forming the basis of the distribution maps are the following; for the Arctic region (Fig. 3):

ØSTRUP 1895, p. 447; CLEVE 1896, p. 12; VANHÖFFEN 1897, p. 264; GRAN 1897a, pp. 2, 10; GRAN 1897b, p. 133; CLEVE 1900a, p. 6; CLEVE 1900b, p. 334; GRAN 1900, pp. 62—63; GRAN 1902, p. 181; Bulletin des Résultats, etc. Année 1902—1903, p. 163; GRAN 1904, pp. 515, 544; JØRGENSEN 1905, pp. 76, 80, 84, 103, 104; BROCH 1909, Table I; OSTENFELD 1910, p. 281; MEUNIER 1910,

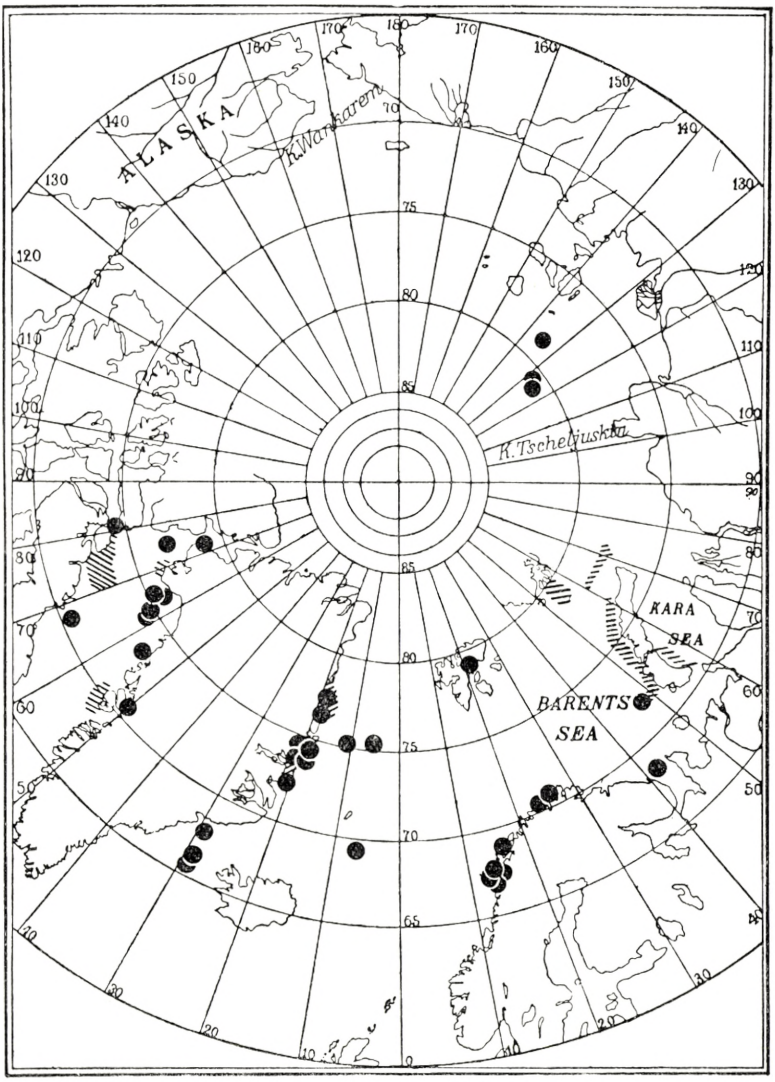

Fig. 3. Distribution of *Nitzschia frigida* in Arctic seas.

p. 336; Ussatschew 1935, pp. 14, 30, 75; Braarud 1935, pp. 97, 138, 160, 164; Grøntved and Seidenfaden 1938, pp. 52 seq., 137 seq., 350, 363, 366.

And for the Baltic distribution (Fig. 4):

Bulletin des Résultats, etc. Année 1902—1903, p. 148; Année 1903—1904, pp. 148, 150, 152; Année 1904—1905, p. 138. Bulletin

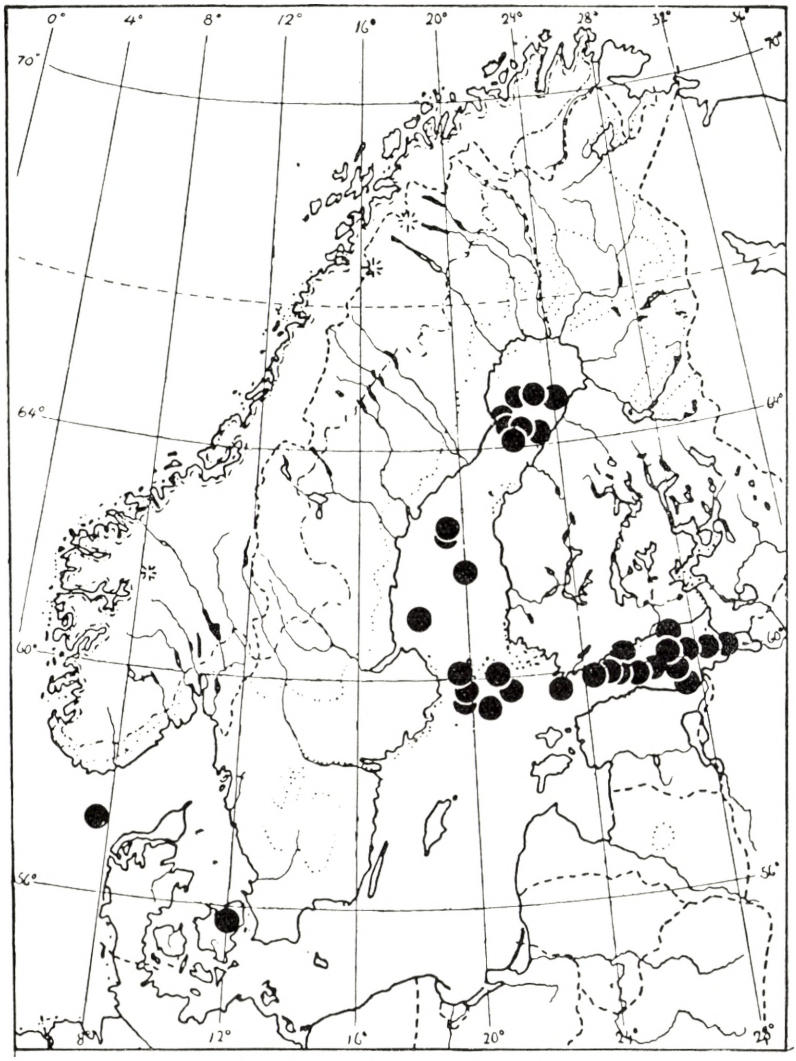

Fig. 4. Distribution of *Nitzschia frigida* in the Baltic; on the chart also the Danish finds in Kattinge Bight and one in the North Sea.

Trimestriel, etc. Année 1905—1906, pp. 96, 98. Bulletin Planktoniques, etc. Années 1908—1911, pp. 23, 24—25. VÄLIKANGAS 1926, p. 279, LEVANDER 1947, pp. 5, 7, 13, 19, 21, 31, 32, 35, 39.

Fig. 4 likewise shows the Danish finds in Kattinge Bight; furthermore one made in the North Sea (57°32′ N.; 7°36′ E.) in November 1906, which is mentioned in the Bulletin Trime-

striel, etc. Année 1906—07, p. 53; this may have been an occasional occurrence, probably carried out by the current from the Baltic.

The two distribution maps (Figs. 3 and 4) show that *N. frigida* has a bicentric distribution; apart from the larger area in the Arctic it occurs also in the smaller inner-Baltic; in the latter it seems reasonable to regard it as a relict (see Introduction).

Nitzschia frigida is a neritic species, but like a number of other Arctic-neritic diatoms it is "in irgend einer Weise vom Eise abhängig" (Gran 1904, p. 545); when it has been found far from the coast it has always been with or near the ice.

4. *Nitzschia frigida* in Kattinge Bight.

Kattinge Bight is a small sheltered bight in the innermost part of Roskilde Fjord (Fig. 5), which again branches off from the Isefjord; the latter has its outlet on the north coast of Sealand and thus stands in direct communication with the Kattegat. In a small central part the depth in the bight is ca. 12 m., but for the rest the bottom is fairly level outside the 4-m. curve, which runs at a short distance from the shore; there is a freshwater inlet in the south-western corner, to the east it has a narrow connection with Roskilde Fjord, ca. 3 km. from the place where the fjord receives the sewage of the town of Roskilde.

On $^5/_3$, 1947, when Roskilde Fjord and Kattinge Bight were covered with ice about 70 cm. thick, Dr. Aa. Jensen carried out hydrographical investigations under the ice at Stations 1—4 (see Fig. 5 and Table 2); at St. 3 and St. 4 the underside of the ice was strongly green-coloured in a layer of some cm.s thickness; a sample of the melting water from this coloured ice from St. 3 was preserved and given to the present author for examination; the sample proved to contain *Nitzschia frigida* cells to the number of ca. 1.1×10^6 per cm^3, in addition a green flagellate also in strong concentration; otherwise no plankton organisms were present.

In the rich *N. frigida* material there was a good opportunity of making a morphological study of the species; reference to this has been made in a previous section; here it is only necessary to

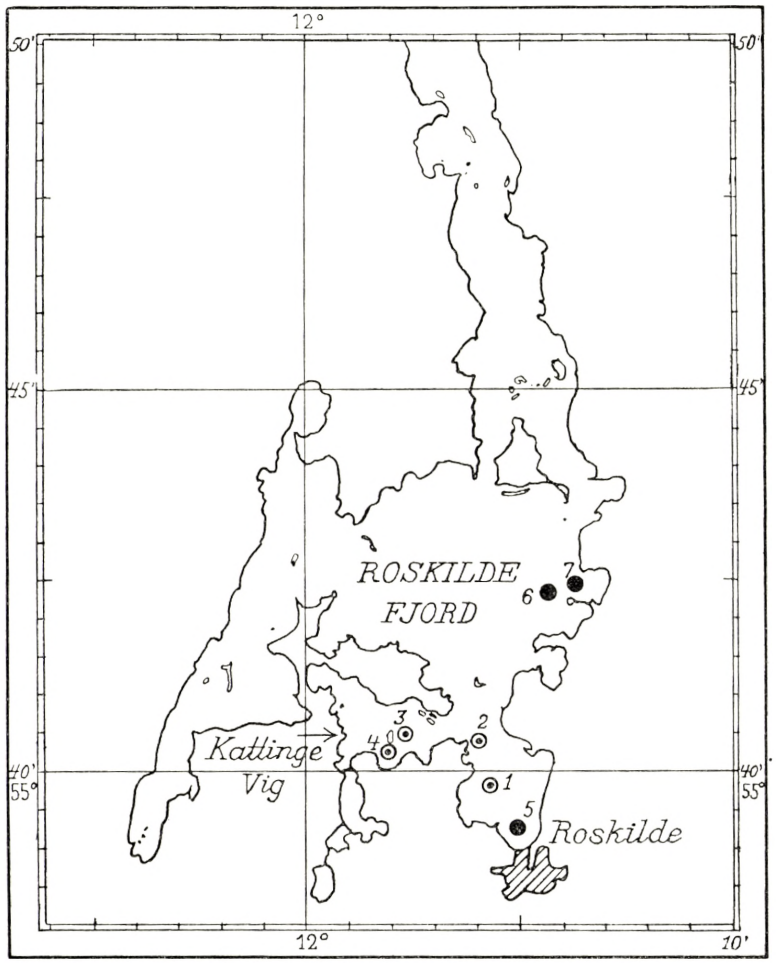

Fig. 5. Chart of the inner part of Roskilde Fjord with Kattinge Bight, showing the stations (1—7) where collections were made—$^{5}/_{3}$ and $^{18}/_{3}$, 1947.

give the results of measurements of the cell length in this population and—for comparison—the corresponding values from a plankton sample from the inner-Baltic area of the species.

Only one specimen was measured in each colony; in the somewhat sparse Porkala material 200 measurements were made as against 1000 in the sample from Kattinge Bight.

The length of the Kattinge Bight cells varies from 38 to 50 μ, whilst the variation in the Porkala material covers a range from 33 to 70 μ; such a difference between a uniform and a more mixed

Table 1. The cell length of *Nitzschia frigida* from Kattinge Bight ($^{5}/_{3}$—47) and from Porkala in the Gulf of Finland ($^{20}/_{4}$—04).

Units of measurement 2.5 μ	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	Total number
Kattinge Bight.....			2	53	357	417	155	16									1000
Porkala	1	5	22	22	34	32	20	23	15	10	7	5		2	1	1	200

population might be expected; Kattinge Bight is a fairly isolated area and *N. frigida* is not known in its neighbourhood, whereas the plankton station in Porkala stands in open connection with the rest of the Finnish coastal waters where the species has often been observed. It should be noted, however, that the measurements from the two localities are not directly comparable, since the Porkala material was taken by means of a plankton net, which filters a relatively large mass of water, whereas the sample from Kattinge Bight came from melting water from the underside of the ice and the measurements in this sample thus are only average values for the 100 cm^3 mass of water contained in the sample bottle. The result of the measurements cannot, therefore, be taken as decisive evidence that the stock in Kattinge Bight, in agreement with the small variation in size of individuals, comes from a single or some few mother cells, and that the Porkala material has a more diverse origin. The measurements only apply to the two available samples, but these are not to the same degree representative of the populations in question as a whole.

There can be no doubt that the development of the stock of *N. frigida* found in the Kattinge Bight actually occurs on the spot and that the density of the organisms has been greatest in the uppermost layer, where the light is relatively strong, though reduced by the passage through the ice. With regard to the need for light, to judge from the occurrence in Kattinge Bight and elsewhere (e. g. Vanhöffen 1897, p. 264; Gran 1897 a, p. 2), *N. frigida* may be considered a "shadow-species", which carries on assimilation by very faint light. Directly under the ice cell division has continued in rapid succession, a considerable number of individuals being in process of dividing up, and the development of the numerically strong population must have taken place in a fairly short time, as is also evident from the fact that organisms in

macroscopically appreciable quantities were only found in the lowermost few cm. of the ice.

In addition to the light the content of dissolved nutrient salts is a factor with a direct influence on the plankton production and the development of a plankton like the one in question must have required a great consumption of nutrient materials. In culture experiments ATKINS (1923, pp. 22—23) found that 1.12 mlgr. P_2O_5 is necessary for the production of 1×10^9 *Nitzschia closterium* individuals; *N. frigida* can hardly be supposed to have smaller requirements and in the uppermost parts of the productive layer the amount of P_2O_5 must have been more than 1 mlgr. per litre for such a stock of *N. frigida* to have developed as that found in the sample examined, provided that no phosphates had been added during the period in which the stock was under development. Eutrophication of the water in Kattinge Bight takes place in several ways; in the first place through the current in Roskilde Fjord which carries waste water from the town of Roskilde; *N. frigida* is certainly not an organism which keeps to unclean water, but we are here so far from the source of contamination that it obviously can make use of the food brought to it without being damaged by the other stuffs found in the waste water; further nutrient materials are brought to Kattinge Bight from the freshwater inlet in the inner part and it is possible that dissolved nutrient salts rise to the upper layers from the bottom, where in the deeper middle part a certain amount of self-contamination takes place. In spite of the great eutrophication a nutrient content of the dimensions noted for the phosphates seems improbable and additional nutriment must therefore have come during the development of the population; since—in spite of the currents—it has been able to keep its place, this may be connected with the biological condition that the species is inclined to attach itself to the underside of the ice; when the colonies are anchored here they are fixed in place; their further growth downward then takes place at a rate corresponding somewhat to the increasing thickness of the ice.

N. frigida is fairly indifferent to the salinity of the water; it thrives in the brackish waters of the Finnish coasts and in the Arctic it occurs both at places where the salinity is $34\,^0/_{00}$ and in ponds on the ice not communicating with the sea (GRAN 1900,

p. 62), thus in water of a very low salinity; on the other hand it seems to be stenothermal, as we do not know any dense concentration where the temperature is over 3°.

The mass occurrence of *N. frigida* in Kattinge Bight, under conditions where no other diatoms occur, shows that it is a species with an ecological constitution different from the plankton diatoms which generally live here and in similar localities on our coasts.

Along with Dr. Aa. Jensen the present author on $^{18}/_{3}$, 1947, made an excursion to Roskilde Fjord and collected plankton and hydrographical samples under the ice at Sts. 5, 6 and 7 (Fig. 5); at St. 5 there was a great undersaturation of oxygen, especially at the bottom; in the plankton there were several specimens of *Euglena* sp. and a strong concentration of bacteria; a considerably higher degree of oxygenation was found at St. 6, without reaching saturation; no plankton organisms were found in the samples from here; at St. 7, which has a fairly sheltered position, the oxygen content was slightly higher than at St. 6, but saturation had not been reached; the underside of the ice was fairly strongly coloured and in samples from this melting ice there were green flagellates in considerable concentration; further a few colonies of *N. frigida*; in the water samples from this station some flagellates were found, but otherwise no plankton; here, therefore, a short time before the excursion was made, there has been a considerable production of plankton; that the stock had suddenly disappeared may probably have been due to the fact that the ice had become covered with a good layer of snow, which of course reduced the amount of light under the ice.

The mass occurrence of *N. frigida* in the inner part of Roskilde Fjord in March 1947 seems, according to these investigations, to have been restricted to Kattinge Bight, where it was observed on $^{5}/_{3}$.

With the object of making further investigations on *N. frigida* a collection of plankton samples was made in Kattinge Bight $^{18}/_{3}$, 1948. The temperature at the surface varied between 3°,94 and 4°,02. *Sceletonema costatum* dominated the plankton and *Melosira moniliformis* was fairly abundant, but *N. frigida* was not found; it was also absent in some small samples taken of the bottom-material.

N. frigida was again sought for in Kattinge Bight on $^{23}/_{11}$, 1948, special attention being paid this time to the collection of bottom

samples. A special procedure was used, as shown in the sketch Fig. 6; a heavy piece of iron with irregular edges was used to stir up the bottom material and a fraction of the suspended material was collected by a plankton net with silk-gauze no. 25. The length

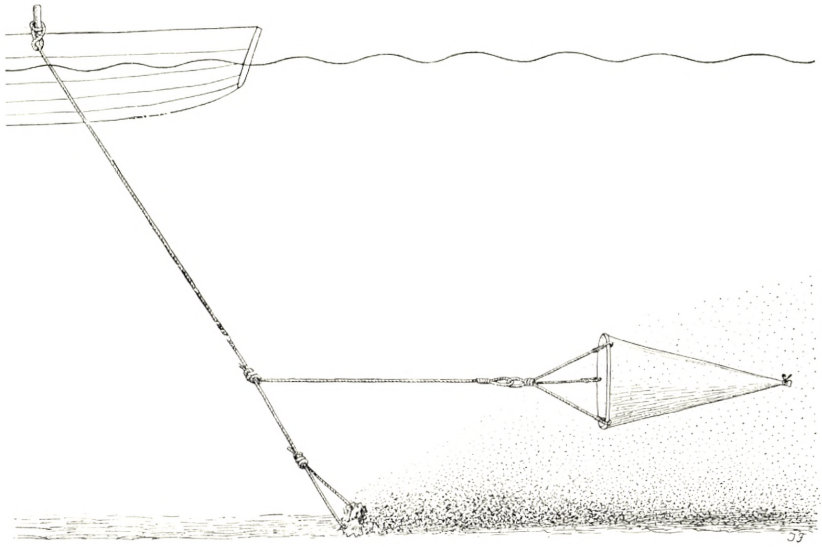

Fig. 6. Sketch to illustrate the procedure used in making collections of bottom diatoms (see text).

and fixing point of the line connecting the plankton net with the line of the iron-piece can be adapted for the object of the collecting; the finer the fraction of the bottom-material required, the longer the plankton net line must be; further attention has to be paid to the speed of the boat, depth of the water and nature of the bottom. When it is not a question of quantitative collecting of bottom diatoms, this method is quite applicable and it has the advantage over the usual bottom sampler, that the material is sorted out and the possibility is increased of obtaining rare species, a relatively great area of the bottom being searched over. In the bottom samples collected in this way a few solitary *N. frigida* cells were found, varying somewhat more in size (45—60 μ) than was the case in the population found in the ice in this locality $^{5}/_{3}$, 1947; otherwise the cells had the same appearance.

In the plankton from this excursion no specimen of *N. frigida* was found; the most abundant species were *Melosira moniliformis*

and *Synedra crystallina*. The temperature at the surface varied between 4°,35 and 4°,75.

On $^{22}/_{3}$, 1949, *N. frigida* was again sought for in Kattinge Bight; the temperature at the surface was 2°,80, at the bottom 2°,60; in the plankton, which was not specially rich, *Diatoma elongatum*, *Melosira moniliformis*, *Synedra* sp. and *Dinobryon* sp. were fairly frequent; *N. frigida* was not seen here, but a few solitary cells of this species were found in the bottom mud, of which samples were taken in the same way as on the previous excursion; no resting spores were found and there is every probability that *N. frigida* outside its flowering periods lives at the bottom as solitary cells, morphologically not different from those which form colonies in the plankton during the flowering period.

A biological importance of a flowering of the winter plankton, as that observed in Kattinge Bight in March 1947, is shown in Table 2, a survey of the temperature of the water, salinity, and oxygen content. Considering here the oxygen content: at Sts. 1 and 2 both lying in the current carrying the waste water of Roskilde northwards, the water of all depths is undersaturated with oxygen,

Table 2. Hydrographical investigations at St. 1—4; $^{5}/_{3}$, 1947.

Station No.	Depth m	Temperature °C	Salinity ‰	Oxygen cm³/litre
1	1	÷ 0.65	13.33	3.93
«	2	1.61	14.36	3.64
«	3	2.18	15.37	1.28
2	0.75	÷ 0.69	13.48	6.26
«	2	0.90	14.24	6.36
«	3	0.62	15.50	7.44
«	4	0.90	15.99	4.63
3	0.75	0.25	13.39	13.89
«	2	1.61	14.22	6.97
«	2.25	1.42	14.25	7.02
«	2.50	1.05	..	7.02
«	3.50	0.78	14.96	7.16
«	4.50	0.62	15.93	6.32
4	0.75	÷ 0.56	13.33	15.40
«	1.25	1.00	13.53	13.41
«	2	1.89	14.15	5.30

most at St. 1, which lies nearest the sewage outlet. At St. 3, at a depth of 0.75 m., that is just under the ice, there is a considerable oversaturation, but from 2 m. to the bottom there is a less degree of undersaturation. The melting water with the rich content of *N. frigida* came from this station; at the shallow-water St. 4 there is a supersaturation with oxygen directly under the ice and at 1.25 m.; at 2 m., as at St. 3, there is undersaturation; no samples for plankton investigations were taken at St. 4, but according to information from Dr. Aa. Jensen the underside of the ice and the uppermost layer of water had the same green colour as at St. 3; both stations have undoubtedly been populated with the same plankton organisms, which in a layer of almost 1 m. in depth have been able to utilize the weak light for photosynthesis, whereby the water has become enriched with oxygen, so that fishes and other animals could live there during an otherwise critical period; that such a dense stock of phytoplankton may play a considerable part as nutrient source for plankton animals emphasizes further the importance of a plankton flowering in the winter.

The occurrence of *N. frigida* in the Kattinge Bight seems to be due to an immigration from the inner-Baltic area, from where the species probably has been carried by the currents to the Kattegat and from there into the Isefjord; the pelagic mode of life offers great opportunity for spreading in the case of marine organisms; it cannot be considered improbable, that the species occurs in other Danish fjords and bays in the Kattegat and the Baltic, but when—as in the present case—its flowering period does not come before the ice has reached a considerable thickness, it is conceivable that it has not been observed in previous investigations in our inner waters. It may be mentioned in this connection, that the present author, immediately after the finding in Kattinge Bight in March 1947, sought for the species in Præstø Fjord, an area which has considerable exchange of water with the Baltic and plankton with a partly Baltic character (Grøntved 1950)—but with negative results.

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Explanation of Plate I.

Microphotographs of *Nitzschia frigida* GRUN. Except Fig. 2 *a*, which is from a plankton sample from Porkala in the Gulf of Finland (LEVANDER $^{20}/_{4}$, 1904), all the figures are from material from Kattinge Bight (AA. JENSEN $^{5}/_{3}$, 1947).

Fig. 1. Colony formation. The cells are connected irregularly so that the colony is at some places branched like a tree; in other parts the cells are placed linearly or in zig-zag formation. Glow preparation. (×160).

Fig. 2 *a*—*b*. Frustules, seen in valve view. Glow preparations. (2 *a* × ca. 1300; 2 *b* × ca. 1350.

Fig. 2 *c*. The two valves are separated at the ends of the frustule. Glow preparation. (× ca. 1350).

Fig. 2 *d*. On preparation the two valves have become more separated. Material treated with nitric acid. (× ca. 1300).

Fig. 2 *e*. An isolated valve. Material treated with nitric acid. (× ca. 1300).

Fig. 2 *f*. Frustule; through connections with neighbouring cells it is held in a position which represents an oblique girdle view; the transapical concavity to the left is due to preparation. Glow preparation (× ca. 1300).

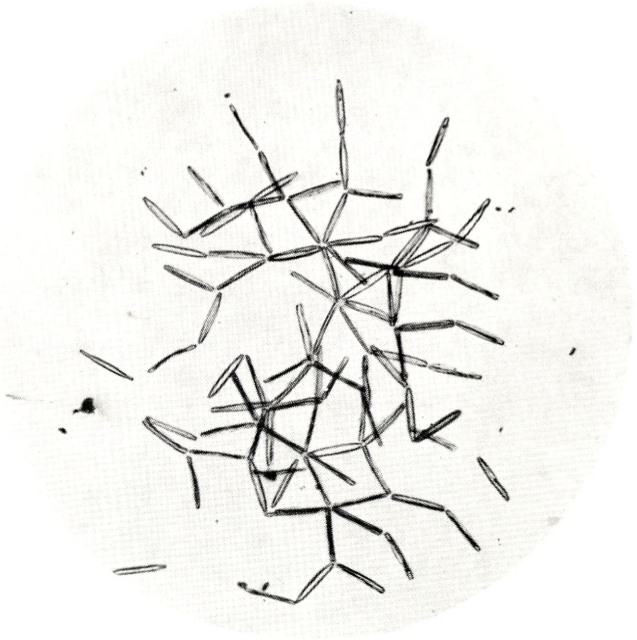
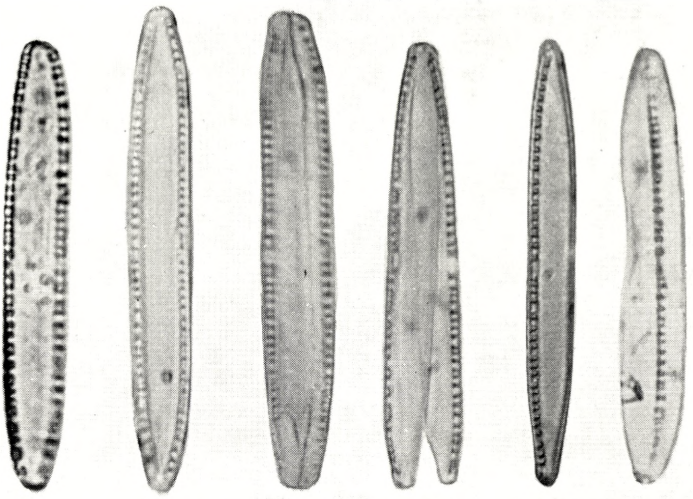


Fig. 1.



a *b* *c* *d* *e* *f*

Fig. 2.

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BY

TYGE W. BÖCHER

København
i kommission hos Ejnar Munksgaard
1951

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Introduction.

A series of morphological progressions consists of forms which morphologically become more and more complicated. Morphology is here used in the widest sense of the word, thus including anatomy, cytology, and cell-physiological conditions underlying morphological differences. The series of morphological progressions does not require genetic relationship between its steps. It may serve the understanding of the evolution that has taken place, but is not necessarily an evolutionary series. The evolutionary series, on the other hand, requires genetic relationship. It is not always a series of morphological developments, and in respect of the morphological factors may be either progressive or regressive or both, because some organs may develop into a more and more complicated structure, while at the same time others are simplified. To the question of the purpose of distinguishing between morphological progression and evolution this answer may be given: the introduction of the concept of morphological progression means a simplification: the material is considered from one point of view, only, viz. the morphological point of view. At each stage in the series a change takes place which may be defined and mostly demonstrated on recent material. The progression may be briefly expressed through these definitions and these, again, may be used to establish the degree of organisation of a group of plants. By definitionally keeping morphological progression apart from the concept of evolution we obtain a breadth of outlook which is not only of interest in itself, but which may probably be of a certain importance for the theory of evolution as well since the stages of morphological progression have no doubt been traversed by the world of plants during the history of the earth.

At the definitions of the various stages of progression conditions of polarity play a decisive part. Unfortunately the physiological aspect of polarity is not sufficiently known at present. Hence some of the views advanced here will perhaps prove premature or erroneous.

The Main Series of Morphological Progressions.

The main series is used here to denote the series in which there are most stages or steps and in which the final stage comprises plants with the greatest possible morphological differentiation. Besides the main series there are several others, which seem to end at a comparatively low stage of organization.

(0), (1), and (2). From Homopolarity to Heteropolarity.

Certain forms of virus are considered by many research-workers to have a primitive form of life. The complicated, chemically very active substances of which the virus consists have the quality of being able to propagate themselves. The individual molecule forms another molecule of the same type as itself. On the whole the same thing happens when a chromatin apparatus in a cellular organism divides. Every molecule in that apparatus may re-form. The chromatin regulates the processes taking place around it in the rest of the living substance. When by the reformation of the chromatin apparatus in a cell two similar chromatin masses have developed, there are really two centres, and if these move apart, two poles are formed in the cell in connexion with the two centres. The plant forms in which the polarity in the cell is connected with the process of cell division no doubt represent the most primitive of all types.

Such genera as *Lamprocystis* among the sulphur bacteria or *Microcystis* among the blue-green algae may serve as instances of the most primitive stages that can be established in plants. The cells divide in every direction and are without special organs of locomotion. The *Microcystis* cell is built centrically with an external photosynthetic plasma and an interior in which i. a. the chromatin is found. The photosynthesis conditions a growth

of the cell. One might suppose that the cell increased in size during its growth,—that the ball expanded. But this does not happen[1]. It extends in one direction and then divides. We may imagine that certain substances on which the growth depends accumulate in two poles in the cell orientated in opposite directions. These poles are alike. We may term this phenomenon *homopolarity*.

It seems that in the homopolar organization we have found a primitive starting-point; for it is hardly possible to visualize an apolar organism. GEITLER (1936 p. 24), it is true, applies the term apolar to homopolar blue-green algae, but adds that this does not mean that these are without predetermined planes of division. Even spherical cells at any rate at times have an axis, i.e. a line between two poles. For that matter apolar organization seems impossible, if only from the following consideration. The form, size, and structure of the undivided spherical cell depend on the genes of the chromatin apparatus. When during the growth of the cell the genes have re-formed so that there are two sets of them, each of these will have properties conditioning the formation of cells of the same size, form, and structure. Therefore the cell does not expand in all directions, but extends and divides into two. ROBINOW's investigations (1947) of cell divisions in the rod-shaped bacteria are very interesting in this connexion. He has been able to show that the rod-shape was highly the result of an extension of coccoid cells in connexion with rapid successive divisions of chromatinic bodies without a simultaneous division into new cells. In *Escherichia coli* there is a chromosome-like body which splits longitudinally, and the homopolarity of the cell seems completely in accordance with the bipartition of the chromatinic bodies.

The establishment of the fact that homopolarity may change direction is of importance for our understanding of the most primitive homopolar state. The axis connecting the poles may change its situation and e. g. turn through an angle of 90°.

[1] HEITZ (1940, 1942) supposes that the polarity is due to accumulation of growth substance in one part of the cell, thinking of the heteropolarity frequently found in mosses (see below). Starting from this point of view he tried to prevent germination of heteropolar spores of moss by many-sided artificial addition of growth substance. By means of β-indolyl acetic acid he succeeded in making spores develop into larger balls of a volume 40—50 times as large as that of the original spores.

In *Bacterium megathericum* ROBINOW (*loc. cit.* p. 377) by cultivation on 2 per cent. malt agar succeeded in producing sarcina-like clusters by the plane of cell division being turned through 90°. A homopolarity which might be shifted in any direction is probably the most primitive type. Perhaps it corresponds to what was termed radial polarity by SCHUSSNIG (1938). And it may be influenced by external conditions. However, SCHUSSNIG confuses various things since under radial polarity he classes partly the *Chroococcaceae*, partly the *Fucus* zygote. The *Fucus* zygote is not homopolar, but heteropolar. Its polarity appears only at the germination (see INOH 1935) and the division plane of the cell depends on various external conditions, e. g. the direction of incidence of light, *p*H, differences in temperature, influence of certain chemical substances (see ROSENVINGE 1888, LOWRANCE 1937, WHITAKER 1942, WHITAKER and BERG 1944). A similar development is found in *Equisetum* spores (cf. MOSEBACH 1942).

SCHUSSNIG in his work also mentions the existing criteria of polarity in unicellular plants. There are partly morphological, partly physiological criteria, among which he reckons the direction of motion. A flagellate with flagella at one pole here has a distinct front part, thus even if the flagellate is swimming backwards, with its front part behind. In this I agree with him, but when in the same context he mentions a bacterium with flagella at both ends and assumes that only the direction of motion can decide which is the anterior and which is the posterior part, I think he attaches too great importance to the direction of motion. Instead of supposing that the polarity in such a bacterium incessantly changes its direction, I should prefer to consider the bacterium as homopolar, as both ends of it may function as front part, and which end at the moment in question will have the strongest effect, will depend on the stimulation to which the bacterium is exposed. It must be the morphological polarity which is decisive, not a fortuitous state which is made possible by the special structure of the cell.

The transition from a homopolar to a heteropolar state in unicellular plants can no doubt be best studied in bacteria, where the flagella may be placed on all sides (peritrichous), at both ends (amphitrichous), or at one end. Among these the peri-

trichous type—if existing at all—must be placed first as any polarity as regards flagella is here absent. Next comes the amphitrichous type with homopolar insertion of the flagella, and finally the forms which have one flagellum or a cluster of flagella placed onesidedly. These monotrichous or lophotrichous forms are heteropolar. The transition which can be studied here is not influenced by external conditions. It is a question of different stages of organization.

After these considerations we can more closely define the first stages in the main series of morphological progressions:

(0) Shifting homopolarity.

The plane of division of the cell is not fixed, but can theoretically be in all directions. Polarity closely connected with differences arising in connexion with the mechanism of cell division.

(1) Fixed homopolarity.

The plane of division of the cell is fixed. Morphologically distinct poles are found, which have the same structure. Polarity not always connected with differences arising in connexion with the mechanism of cell division.

(2) Heteropolarity.

Morphologically distinct poles of different structure. The plane of division of the cell is fixed or shifting by the influence of external conditions. Polarity as a rule independent of the mechanism of cell division.

An organism like *Chroococcus turgidus* is at a transitional stage between (0) and (1). Here the plane of cell division is regularly turned through ab. 90°. If the first division is in one direction, the following ones will as a rule take place in a direction transverse to that of the first division. The shifting polarity here is restricted to several definite planes. In *Eucapsis* there are three planes of division at right angles to each other and hence cubical colonies, in *Merismopedia* only two such planes and square-tabular colonies. Finally there is one plane, only, in plants forming catenulate colonies, and here we may therefore use the term of fixed homopolarity.

It is more difficult to find forms showing the transition between homo- and heteropolarity, (1) and (2). We must resort to pluricellular forms, i. e. forms belonging to Stage (3), to

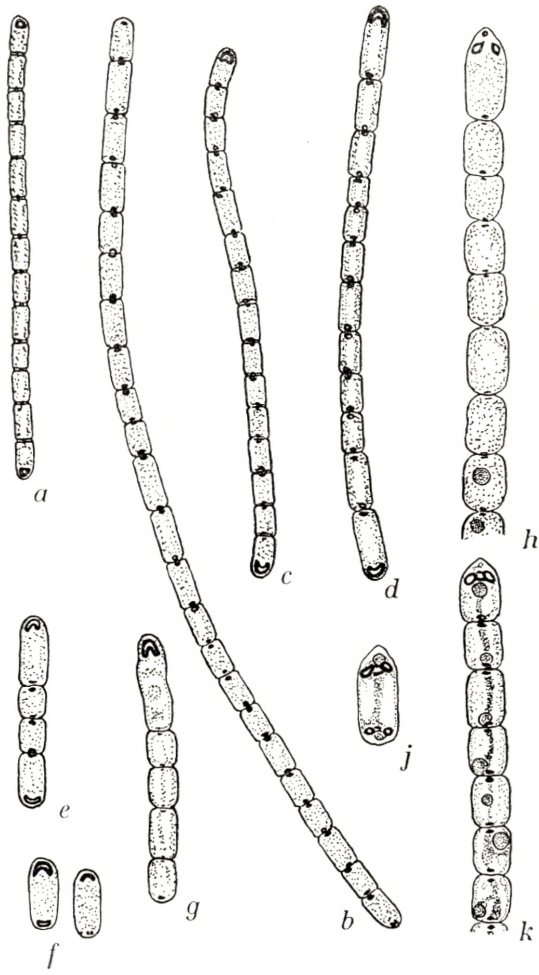


Fig. 1. a—g *Pseudanabaena galeata*, h—j—k *Pseudanabaena biceps*, f and j unicellular "hormogonia" (detached terminal cells). × 1700. After BÖCHER 1949 a.

illustrate this transition. *Pseudanabaena biceps* and *galeata* are particularly suitable. They are unramified, filiform, with specially equipped terminal cells in which the polarity particularly appears in the terminal placement of the gas vacuoles (BÖCHER 1949 a). In both species the terminal cells may be detached and grow

into new filaments. At the detachment the cell is heteropolar, but soon after it develops in a homopolar direction, small gas vacuoles developing at the end which before the detachment was turned away from the apex. The cell now gets two similar ends, which are distinct from the middle of the cell. Then it divides and the wall develops in the central part, which no doubt both structurally and chemically differs from the ends. The wall comes to separate two heteropolar cells, the polarity of which is diametrically opposite. Taken as a whole the filament is homopolar, but its various cells are heteropolar. The filament may move in both directions, but as in a train on the suburban railway we cannot speak of a front part and a hinder part. The above-mentioned transformation of the polarity in a detached terminal cell suggests that after the detachment certain chemical changes take place which result in the formation of gas vacuoles in the end just detached. In *Pseudanabaena biceps* this end gradually becomes bright and tapering. The substances most probably existing which give rise to the development of the special structure in the terminal cells may be called terminal substances. As long as the terminal cells are connected with the other cells the terminal substances will have a retarding effect on the pole turning away from the apex. After the detachment the terminal substances will gradually be distributed more and more evenly to the poles until homopolarity has been obtained. To go from a homopolar to a heteropolar state we need only think of a constant retardation of one pole or a constantly unequal distribution of such terminal substances.

In its structure *Pseudanabaena* reminds of a *Streptococcus*, and it was mentioned above that rod-shaped bacteria in certain cases might be regarded as undivided chains of coccoid units. In such forms, too, it may therefore be supposed that there are differences of polarity of the same type as that mentioned. The question now arises whether the heteropolarity arising in such threads can be supposed to be the source or a condition of the heteropolarity occurring in unicellular plants, e. g. in monotrichous bacteria. This can hardly be excluded, but it will mean that heteropolarization follows after trichomatation: trichomatation will be Stage 2 and heteropolarization Stage 3. In this connexion it should be kept in mind that most heteropolar

unicellular organisms, e. g. flagellates, have an extremely complicated, greatly differentiated cell structure. However, in numerous cases it is hardly possible to imagine the heteropolarity as having arisen with trichomic forms as intermediate stages, and perhaps this is not necessary, either. When a unicellular heteropolar organism divides, such as e. g. *Ochromonas granularis*, it passes through a homopolar state in the anaphase. The difference between the *Ochromonas* species and a *Pseudanabaena* is that the former after the detachment of the cells does not regenerate a terminal pole in the detached end. Immediately before the detachment of the cells these have opposite polarity, a—b, b—a, and this is maintained. In *Pseudanabaena* we also in a detached terminal cell find the distribution a—b, but here the state then is changed in the direction a—b—a.

(3) Trichomatation.

Already in diplococci or blue-green algae such as *Synechocystis* we find the first beginnings of trichomatation. Trichomatation also takes place in diatoms and desmids, but here the trichomes are considered to be in the nature of colonies or cenobia, while e. g. in the *Oscillatoria* they represent a genuine pluricellularity. The criterion of genuine pluricellularity must be the mutual physiological interdependence of the cells. Visible evidence of a dependency or a collaboration appears in the existence of pores and plasmodesms between the cells. However, it cannot be concluded from the absence of plasmodesms that there is no interdependence of the cells, for it may be assumed partly that there are often submicroscopical plasmodesms present, partly that there may be permeation of substance through the cell wall. Hence it may sometimes be difficult or impossible to decide whether an organism is organized as a filiform colony or as a trichome.

The above-mentioned homopolar trichome found in the *Oscillatoriaceae* will not be mentioned in detail here. It only belongs to the main series provided that it represents a stage which is lower than the heteropolarization. On the other hand the trichome which has a heteropolar structure with a base (attachment cell) and a part growing upwards clearly represents a

higher stage in the progressive main series. Such a heteropolar trichome is found already in blue-green algae, such as e. g. *Endonema* (see PASCHER 1929) and here has its starting-point in a spherical endospore. In the green algae, on the other hand, the starting-point is a swarm cell of a heteropolar structure which attaches to a substratum and germinates. SCHUSSNIG (*loc. cit.* p. 229) mentions that the swarm cell is attached at the front part and that the rear end then grows into a filament. He is of opinion that the polarity in the cell thus obtains an opposite direction. Here it should be noted that the cell is still heteropolar and that we can hardly compare "front" and "rear" in a swarmer with base and apex in a algal trichome. Recent investigations (KOSTRUN 1944), indeed, have shown that the polarity of the swarmer in green algae mostly is in good accordance with the polarity of the filament. In the cases in which only one swarmer is formed in each mother cell, the longitudinal axis of the swarmer will correspond to the transverse axis of the mother cell. If such a swarmer is attached by the front part, the contents in the part containing the chromatophore are turned through 90°, so that the original polarity of the mother thread is retained. Other swarmers are attached at the flank and grow out without any turning of the contents. Finally there are forms in which the longitudinal axis of the swarmer comes to correspond to the longitudinal axes of the germling without it being possible to see whether there have been any changes in the contents of the cell. KOSTRUN here supposes that there may be submicroscopical plasmatic changes corresponding to a turning of polarity through 180°. It seems easier to me merely to think of the front part of the swarmer as physiologically corresponding to the basal end of the trichome.

(4) Simple Ramification.

A next important stage is reached when the trichome ramifies. The ramification which takes place in blue-green algae, both the genuine and the false ramification, however, does not belong to the main series, as even the "genuine" ramification here is of another and more primitive character than that found in other Thallophyta. It is characteristic of most of these that the ramification starts from the upper end of the cell (fig. 2). Only

Fig. 2. Examples of simple ramification. A. *Callithamnion tetragonum* var. *fruticulosa*. Upper part of sterile branch. Branches of the first order are numbered. The branches marked with × are of the second order. — B. *Anthithamnion boreale*. Distichous ramification having arisen by the formation of two opposite a_1 poles. Below, rhizoids issued from b poles. A × 200, B × 95. (After Rosenvinge).

in certain much derived forms such as e. g. *Bostrychia*, where the branches form a cortical covering around a central cell filament, the rows of cells corresponding to branches may issue from basal parts of the cells (FALKENBERG 1901). In forms of algae in which rhizoids or so-called hyphae develop by ramification, these as a rule are given out from the lower parts of the cells. In both cases the ramification must be supposed to be due to a division of the existing poles into an axial and a lateral pole. When the lateral pole is formed in the upper part of a cell, a lateral branch develops. If it is formed at the base, a rhizoid may develop. No real repolarization has taken place, but there is a division of the existing poles. Now it appears that the branches mostly grow obliquely upwards and grow less intensely than the main filament. Thus, at the division of the poles two similar upper poles and two similar lower ones have not developed, but the lateral ones are slightly different from the axial ones. A difference in polarity has arisen transversely to the longitudinal axis, this difference being maintained together with the longitudinal or axial polarity. In the diagrammatical figures (fig. 4) the axial polarity is termed a—b, the transverse or radial polarity a_1—a_2—a_3, etc.

In a very great number of uniseriate filiform algae with a heteropolar structure the very lowest cells at the ramification are apt to form rhizoids or attached branches only, while the upper cells form obliquely upwards growing lateral branches only (fig. 2 B). This may be supposed to be due to a different concentration of the substances determining the poles. The "a-substances" are in excess in the whole of the upper region, the "b-substances" in the lower cells. According to this theory the a-substances in a homopolar filament will have the intensest concentration at the ends, which undeniably goes very well with the appearance of *Pseudanabaena* (figs. 1 and 7 A). Conditions of ramification in a number of *Chaetophoraceae*, e. g. *Stigeoclonium lubricum*, are interesting in this connexion (see figures in BERTHOLD 1878). At the germination of the zygote a plagiotropic filament creeping in both directions develops, thus a homopolar filament. Provisionally disregarding the upright branches and only looking at those creeping like the mother filament, it may be established that the lateral branches towards the two ends are

given out typically from the distal end of the cell, while those in the middle of the mother filament are issued medianly. The midmost cells in such a filament will be more or less homopolar with two comparatively weak poles and a median "pole" which is unimpaired or even strengthened (cf. fig. 7). Therefore it is this median "pole" which here gives rise to the lateral ramification, and the branches morphologically develop like the other distally issuing lateral branches, but the branches from the central cells grow out at right angles to the mother filament. In the diagrammatical figures the poles are marked with α and β in order to show that this is a slightly different type of polarity, which is horizontal, or, better, depends on the plane of the substratum.

(5) Pluripolar Ramification.

In *Stigeoclonium*, however, also upright shoots are given out and it now appears that these, like the branches reduced into hairs, issue from the middle of the cells. This shows that besides the poles α and β a new pole must have developed in these cells, upwards and in the middle of the cell. Here there is no division of an axial pole, but a new-formation.

Before going on, a consideration of the red alga *Trailliella intricata* is of importance, because this alga besides creeping filaments with α—β-polarity has upright main filaments and downwards turned filaments forming haptera (fig. 3). These hapteron shoots like the erect ones issue from the middle of the cells, but diametrically opposite to the former. This clearly

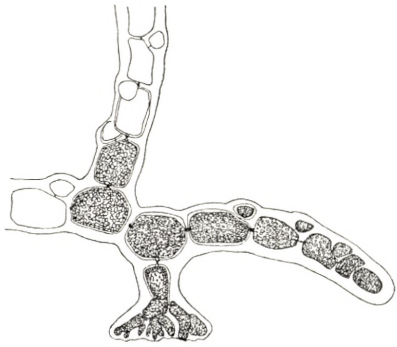


Fig. 3. *Trailliella intricata*. Creeping filament with erect filament and hapter. × 260. After ROSENVINGE.

shows that the cells must have four main poles and two crossing axes. They have a horizontal α—β-polarity and a vertical a—b-polarity. As both in the horizontal plane and in an upward and downward direction lateral branches may be given out (often

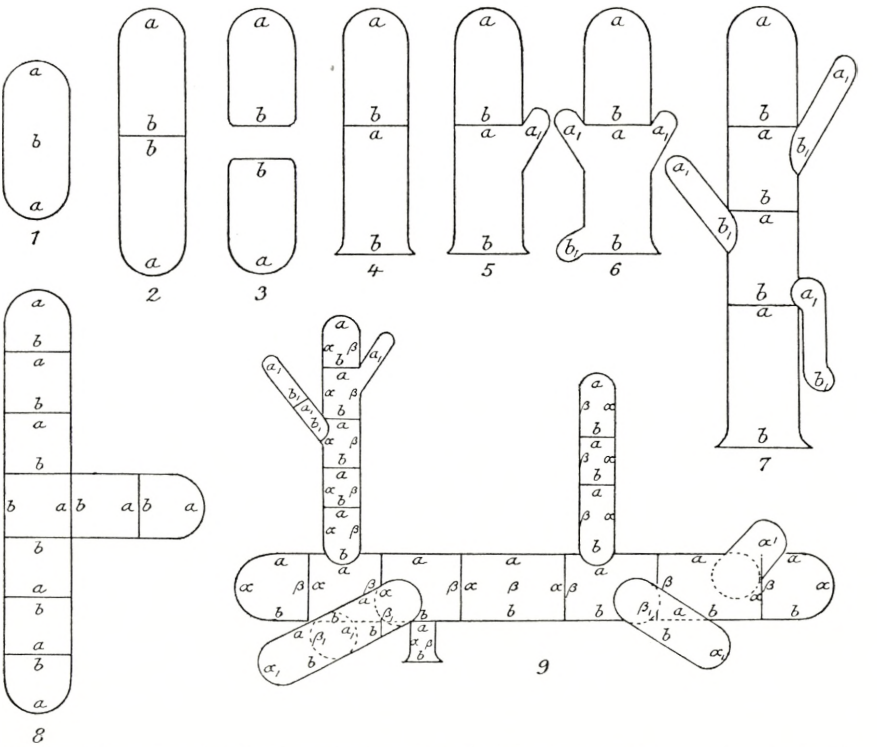


Fig. 4. Diagrammatic figures showing the theoretical conditions of polarity in algae which are unicellular or consist of one row of cells. 1 homopolar unicellular, 2 homopolar bicellular, 3 heteropolar unicellular, 4 heteropolar bicellular, unramified, 5 heteropolar with incipient simple onesided ramification, 6 the same with two-sided simple ramification and rhizoid formation, 7 heteropolar with simple ramification, 8 homopolar with ramification due to turning of polarity (*Stigonema* type), 9 pluripolar ramification (as in *Stigeoclonium lubricum* or *Trailliella intricata*).

in the form of small gland cells) which are placed regularly near α-, a-, or b-poles, this shows that here we have to do with a very complicated form of polarity. This is the one which is the cause of pluripolar ramification.

The morphological stage of algae of this type is very important as it is possibly a condition of a further progression. It will not be possible to illustrate this until an account has been given of the next stage.

(6) Simple and Pluripolar Syntagmation.

Syntagma is used by SCHUSSNIG to mean "alle jene Thallusbildungen deren anatomischer und organogenetischer Aufbau die Zusammensetzung aus mehreren bis zahllosen, zunächst gleichartigen, später differenzierten Faden oder Schlaucheinheiten erkennen lässt". SCHUSSNIG here is thinking of the thallus as a whole, in the algae, if anything, OLTMANNS' "Springbrunnentypus" and derived forms, and the thallus in lichens and in the fruit body of mushrooms. The peculiarity about the syntagma type is the coalescence of single filaments into larger bodies. Such a feature may also be observed in plants built on other principles. In e.g. *Polysiphonia* and *Delesseria* there are main axes from which lateral axes issue. These, however, do not develop as free cell filaments, but either coalesce into cylindrical bodies or into flat leaf-like bodies. Any form of sideways coalescence of originally similar filaments into firmer bodies may be termed *syntagmation*.

We may now distinguish between a syntagmation of filaments with simple ramification, and syntagmation of filaments with pluripolar ramification. These two types may be termed *simple* and *pluripolar syntagmation*. They cannot be regarded as two independent stages, for it is highly questionable whether the simple syntagmation belongs to the main series. Indeed, it is not necessary to think of simple syntagmation as the basis of the pluripolar one, even if a close connexion between these types is not excluded.

Simple syntagmation is found e.g. already in the cortical zones of a *Ceramium*. Here, however, only primary pores are found between the cells, i. e. the original branches indeed have coalesced, but physiologically they still seem to constitute connected systems of cells. In *Polysiphonia* the syntagmation is more intimate as secondary pores develop between cells which do not belong to the same original system of branches. At the secondary pore formation i. a. *a cell fusion* takes place through which the most intimate contact is obtained. In *Delesseria* as well, which has simple syntagmation, there are plenty of secondary pores (ROSENVINGE 1909—31, p. 466). In the genus of green algae *Coleochaete* there are in the plagiotropic thallus pressed against

the substratum all possible transitions between quite free cell filaments and cell discs which have arisen by fusion of plagiotropic filaments (cf. SCHUSSNIG, *loc. cit.* pp. 276—277 "Nematoparenchym").

Among the kind of forms which show pluripolar syntagmation there are also degrees of the intimacy of the coalescence. In a "fountain type" like *Furcellaria fastigiata* it is still easy to pursue the individual filaments and their ramifications and there do not seem to be any secondary pores. In other, more derived forms there is a more intimate contact; the cells communicate through numerous prolongations penetrating the very thick walls (e. g. in *Eucheuma speciosum*, fig. 22 in BÖRGESEN 1943). It is no doubt correct to speak about a higher degree of contact, for the filaments in a *Furcellaria* are hardly without contact, the reason being that even though there may not be any secondary plasmodesms between parallel filaments, neither microscopical nor submicroscopical ones, the occurrence of a mutual influence by secretion and absorption from the cells is not excluded. Unfortunately too little is known about this feature.

The germination of the spores and the first stages of growth are of the greatest importance for our understanding of pluripolar syntagmation. In a great number of forms a compact cell disc or hemispherical body closely attached to the substratum develops. Such a basal disc must have developed by divisions partly in a horizontal, partly in a vertical direction, and thus may be regarded as a syntagmation of filaments with both α—β- and a—b-polarity.

Later the erect, pluriaxial main shoots are given out from the basal disc. We may now, no doubt rightly, assume that previously several differences in polarity have arisen between the cells in the basal disc, which grows up to the erect shoots. The probable difference in substances determining the poles in a homopolar, plagiotropic filament was mentioned above. In quite a corresponding way it may be supposed that there are differences in concentration between the central parts of the basal disc and the peripheral parts, which, as said above, correspond to ends of filaments. The appearance of the erect shoot therefore has been determined already in the basal disc. A chemical influence from filament to filament therefore, as assumed above, is hardly the

most decisive factor for the morphological development of the plant body. The mutual relation between the filaments—the radial polarity—is determined already before they shoot up. It seems possible to derive this radial polarity from homopolarity during plagiotropic growth by coalescence of plenty of filaments and branches with such growth.

In species with apical or intercalary meristems there is at the development of the meristem a similar radial polarity as in the basal disc, and in these cases it spreads downwards or both up and down, as e. g. in *Nereia filiformis*, which was thoroughly investigated by KUCKUCK (1929).

Forms with large top cells, as found e. g. in *Sphacelariales*, *Dictyota*, and *Fucus*, might seem greatly deviating from forms with meristems. However, there are a great many features which indicate that growth of a top cell is not a primary, but a secondary phenomenon. As regards *Dictyota* and *Fucus* SCHUSSNIG supposes that the top cells have arisen by sideways "fusion" of several meristem cells. On the other hand, he keeps the *Sphacelariales* outside such a view because in the case of this group he imagines the radial polarity to have arisen in connexion with a suppressed lateral ramification from a main filament (changed central axis type). However, the development of a basal disc in *Sphacelariales* and the transition within this order from the uniseriate *Sphacella* to the pluriseriate *Sphacelaria*, if anything, indicates that the *Sphacelariales* belong to the stage of pluripolar syntagmation. Hence the large top cell may here, too, be interpreted as a "fusion product", which, however, should not be regarded as referring to a real fusion, for what has happened is probably one or more mutations, which have caused plants with genes for a multicellular meristem of pluripolar cells to develop into plants with genes for a single pluripolar top cell. Top-cell growth thus may have developed on the basis of meristem growth, but nothing has happened to justify a reference of forms with top cells to a higher stage in the series of morphological progressions. A *Fucus* or a *Dictyota* with top cell is not at a higher stage than a *Laminariacea* with an intercalary meristem. Besides, it should here be noted that forms with top cells do not belong to the main series.

Already a cross-section of an erect shoot in an alga with a

comparatively simple structure like *Furcellaria fastigiata* shows a clear anatomical tripartition of the shoot into a central string of very long, narrow cells, an inner cortex of rather large, short cells, and an outer cortex of small, assimilating cells. The zones are not well-defined and can easily be connected with the above-mentioned radial polarity. In other red algae the differences become more pronounced. As an example may be mentioned

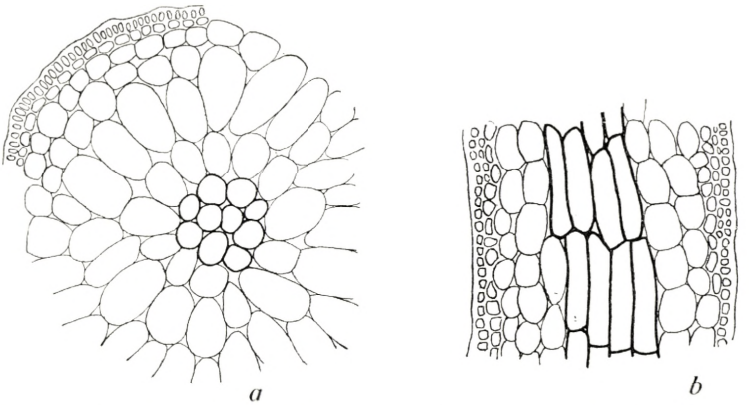


Fig. 5. *Mychodea chamaedoridis* Börgs. a transverse section, b longitudinal section of the thallus. × 60. After BÖRGESEN.

Mychodea chamaedoridis described by BÖRGESEN (1943); see fig. 5. Here there is nearly a tripartition into stele, cortex, and epidermis, and at any rate a close approach to the anatomical differentiation found in stems and roots of primitive archegoniates (cf. p. 21).

(7) Differentiation of idioblasts and formation of cell patterns.

With this stage we are no doubt for the time being at the limit of what on the basis of morphological investigations we dare imagine as regards conditions of polarity. A number of algae both morphologically and anatomically reach a very high degree of differentiation presupposing a further complication of conditions of polarity. We may remind of the sieve-tubes and mucilage canals in *Laminariales* and conceptacles (incl. cryptoblasts) and air bladders in *Fucus*. Also the thalli of macrolichens and the fruit bodies of macromycetes reach very high stages. They

represent stages above syntagmation itself, but they do not belong to the main series.

The fundamentally new about these forms in relation to such as only reach syntagmation itself is the development of idioblasts or special systems of tissue which collaborate in such a way that we can begin talking about vegetative organs.

The development of conceptacles in the *Fucaceae* is very instructive. The hair pits are found distributed on the surface of the plants and at more or less regular distances from each other. At certain definite intervals initial cells arise which cause the development of these organs. It very much reminds of the development of lip cells in the epidermis in the cormophytes. Such a differentiation within the same anatomical area in certain definite places (formation of a cell pattern) presupposes a form of polarity on a somewhat higher plane than the above-mentioned forms of polarity. It must be admitted that even in blue-green algae, which otherwise have a very simple structure, there are regularly intercalary cells of a deviating structure (heterocysts). Also hair shoots may occur with great regularity in many algae. However, the conceptacles in *Fucus* and the lip cells with the air-chambers behind them have the character of multicellular organs and may be the result of more complicated cell differentiations.

Cell differentiations or the formation of patterns seem to be connected with growth substances with a retarding effect. Bünning & Sagromsky (1948) in the case of the stomata were able to show that round the individual stoma there is an inhibition zone in which no stomata developed. This was connected with the development of a growth substance which prevented such differential cell divisions as resulted in the formation of new initials for lip cells. On the whole the differentiation of idioblasts in plant tissue (lip cells, root-hair cells, passage cells, or e. g. trichosclereids in air roots (cf. Bloch 1946)) to begin with seems to be inhibited by such substances as may be supposed to be produced by the meristem cells. Only when the concentration of these substances has become sufficiently low, a differentiating, unequal cell division may take place through which an idioblast-initial cell particularly rich in plasma is formed. But this, again, has recovered its embryonal character and now gives off the

same kind of substances as inhibit the development of new initial cells in its surroundings.

Such primitive archegoniates as *Rhynia* clearly belong to the same stage as the most highly organized algae. ZIMMERMANN (1930, p. 104) writes about this primeval terrestrial plant that its "Gesamttracht war noch ausgesprochen thallophytisch". What distinguishes it from the algae was tissues or cell types connected with its terrestrial life: the stomata in the epidermis, the tracheids in the simply built protostele, and the water-absorbing cells on its plagiotropic shoots.

According to ZIMMERMANN *Rhynia* was built of telomes, which according to him are uniaxial sections of shoots anatomically consisting of a stele, cortex, and epidermis. *Rhynia* had horizontally creeping and erect shoots which branched by simple bifurcation. As regards ramification it was at a lower stage than e. g. *Polysiphonia*.

(8) Telome-Syntagmation.

ZIMMERMANN regards the telome as a morphological basic element in the cormophytes. According to his theory telomes can form "telome clusters" and the individual telomes in such clusters can coalesce into larger bodies. In a similar way as lateral branches in a *Delesseria* with sideways coalescence form a flat leaf-like organ, so telomes are united into blades, e. g. in *Sphenophyllum* and *Ginkgo*. Basal parts of telomes in telome clusters coalesce into stems with actinostele and still more complicated forms of stele.

In the section on syntagmation the peculiar conditions in the brown algae were mentioned that we should probably consider forms with an apical meristem as most original and forms with a top cell as derived. Hence it is interesting that the same process seems to take place in connexion with the telome syntagmation. In the telome plants with the lowest organization, the *Rhyniaceae*, there was a large number of initial cells at the top of the shoots, while in a great many of the cormophytes with a higher organization there are large top cells. But not in this case either does the top cell represent decisive progress. Indeed, we see that both *Lycopodium*, eusporangiate ferns, and phanerogams have retained the large number of initial cells.

Conditions of polarity of course with the renewed syntagmation have become considerably more complicated and escape any possibility of more detailed investigation from a morphological point of view. On the other hand, it will be possible to make further advances by means of physiological experiments. Many experiments have already been made which show that the a—b-polarity is still present in cormophytes with a higher organization; but this does not mean much. Tissue cultures and influencing these with growth substances are probably the road leading to a profounder understanding.

(9) Axillary Concatenation.

This concept has been taken over from ZIMMERMANN, who points out that any form of ramification from axils is absent in more primitive cormophytes. In phanerogams, on the other hand, axillary concatenation is a typical feature. It is also found in *Equisetum*, ferns, and in the strobili of the *Lycopodiales*. ZIMMERMANN (*loc. cit.* fig. 21) points out three possibilities by which axillary concatenation can arise from ordinary lateral ramification. In all the three cases there must be a suppression of growth in a definite part of the stem.

The question then arises whether this axillary concatenation can be characterized as a new morphological stage of progression. As to this there can hardly be any doubt, for if ZIMMERMANN is right in his interpretation of the origin of the axillary position, the latter must presuppose an inhibition of growth at every single node, which, again, means a further complication of the chemical basis of the morphological differentiation.

(10) Cambial Differentiation.

The secondary growth which is due to cambia and phellogens represents the next stage. It is true that cambia develop from special embryonal cells placed peripherically and formed by the growing-point cells which arising by radial polarity during the development of the growing-point have already obtained a certain lateral determination. Something similar applies to phellogen cells, for even if these are formed secondarily from cells already rather well-developed, it should be kept in mind that the cells

which develop into phellogen are placed in the periphery of the plant body in question and thus originate from cells at the growing-point which had obtained a lateral determination by radial polarity. The fundamentally new about the secondary growth—what particularly causes it to represent a new stage—is the fact that cambia and phellogens in all probability are highly active in the processes of morphological differentiation. In plants with secondary growth the morphological development, the differentiation through differences in polarity, besides in shoot- and root-tips is also laid in the lateral meristems.

The lateral differentiation due to cambia is very heterogeneous. Perhaps we ought to distinguish two stages, which might be termed simple and complicated cambial differentiation. In the first case the differentiation mainly consists in different cells developing in a centrifugal and centripetal direction (phloëm and xylem, phellem and phelloderm); in the other case also considerable differences arise between the cells developed on the same side. The numerous elements in the xylem and phloëm of the deciduous trees of our day are the result of such a complicated cambial differentiation. The reason why I have not distinguished these stages more closely is that it is difficult to find a boundary between them.

Cambial differentiation is the highest stage. Possible higher stages are not clearly developed. It is quite interesting to remember that in ligneous lianas there may be a third syntagmation with several trunks growing together. Some deviating specimens of certain trees (e. g. *Fagus silvatica*), too, behave peculiarly and form numerous anastomoses and coalescences of the trunks. However, it is of course impossible to know whether such variants signify the introduction to a new stage of progression.

In what precedes we have nearly exclusively kept to vegetative characters. These are decidedly the easiest to survey, and it seems as if the progression that can be ascertained as regards the structure of sexual organs and organs of reduction division hardly differ on essential points from that which may be ascertained in the vegetative parts. But sexual organs and to a still higher degree organs of reduction division (meiotangia) nearly always represent a higher stage than that reached in the vegetative parts in the same organism. Some examples will illustrate this:

Ectocarpus. Vegetative: Stages 4—5 (plagiotropic filaments are found to have been developed in some species). Sexual organs: with little difference from the vegetative filaments, but a stage above these, as the cells are divided into a great many small cells each of which is changed into a gamete. Organs of reduction division: egg-shaped or spherical organs very different from the vegetative filaments, cell-formation in the organ without simultaneous wall-formation.

Lycopodium. Vegetative: Stage 8. Organs of reduction division (strobili): Stage 9.

Helianthus. Vegetative: Stage 10 (intrafascicular cambium with complicated cambial differentiation). Organs of reduction division: Stage "11". The head is a very complicated formation which presupposes a third syntagmation of inflorescence stems simultaneously with growth retardations in keeping with those described in connexion with Stage 9.

Lateral Series.

The present paper is not intended as a general morphology. Hence, only some examples will be adduced which are of special interest in connexion with the discussion of the stages of the main series. Among lateral series which will not be discussed in detail we may mention the morphological stages of progression that may be ascertained in fungi, lichens, and bryophytes.

(a) Lateral Ramification with Simple Turning of Polarity.

The turning of the plane of cell division through 90° in bacteria and *Chroococcaceae* was mentioned above. In the group which formerly was called *Hormogonales* there are filamentous forms, thus Stage 3 in the main series. But the *Stigonemaceae* take a step further and have "genuine ramification". A close comparison of this ramification with that mentioned in the case of the main series (Stage 4) shows a fundamental difference. The lateral branches in the *Stigonemaceae* are given out from the whole cell, not from its upper or lower part. The uniseriate filament is shaped like a hormogonium and hormogonia have a

clearly homopolar structure. A turning of polarity through 90° takes place in connexion with divisions transverse to the longitudinal axis of the filament, a process which presumably corresponds to the turning found in bacteria and *Chroococcaceae*. The ramification may be referred back to the shifting homopolarity and therefore in itself is not something fundamentally new. Hence, the *Stigonemaceae* do not reach Stage 4 and even though the plants may sometimes be heteropolar (*Nostochopsis*, *Doliocatella*) the ramification is not in this case, either, due to the development of any new lateral pole. In *Hapalosiphon* it can be shown that the ramification is initiated in sections of filaments cut off from the end of the filament by a heterocyst. The heterocyst can here be supposed to stop or change the substances conditioning the longitudinal polarity in the filament and thus create a possibility of lateral ramification (Böcher 1950). The heterocysts, however, are not an absolute condition of the lateral ramification. Thus, in the genus of *Doliocatella* there are no heterocysts and in *Stigonema* the lateral ramification is often completely independent of the heterocysts. Here the polarity is turned some little distance behind the apex of the trichome. It may be supposed that the substances of polarity passing in a longitudinal direction are soon weakened behind the apex, while in others it is weakened slowly or only by insertion of heterocysts. Perhaps the chief purpose of the heterocysts is that of regulating, changing, or stopping substances of polarity. A large number of occurrences of heterocysts can be interpreted in this way. For instance the spore formation near heterocysts in *Anabaena* may be due to the heterocysts neutralizing the longitudinal polarity and themselves producing substances conditioning spore formation. But it is difficult to explain the purpose of lateral heterocysts in *Stigonema mamillosum*, *Nostochopsis*, and *Mastigocoleus*. In the last-mentioned genus the heterocysts, however, terminate short lateral branches. In other words, they stop the growth of the lateral branch. Long branches bearing hormogonia or long attenuated branches develop where there is no formation of heterocysts. In *Stigonema mamillosum* the typical place of the heterocysts is outermost in the cell families developing by the transverse growth of the segments. The cell families can be apprehended as contracted systems of branches, and the hetero-

cysts therefore also here "stop" the further growth of certain lateral branches. CANNABAEUS' (1929) studies on the heterocysts show that physiologically these behave differently from ordinary cells. In any case their appearance must be due to a sudden change in the longitudinal polarity, and this fact causes forms with heterosysts to be at a higher stage of morphological progression than forms without heterocysts. The *Oscillatoriaceae* therefore are more primitive than the other groups frequently included among the "*Hormogonales*" (cf. further p. 34).

(b) Lateral Ramification in Connexion with Stoppage of Longitudinal Polarity.

In most forms of "*Hormogonales*" there is a so-called false ramification. This seems to be completely dependent on the occurrence of heterocysts or intercalary dying cells. In a *Rivularia* a heterocyst will interrupt the longitudinal polarity, after which the cell below the heterocyst will behave like a new apex and grow past the heterocyst. In *Scytonemaceae* two sections of filament between two heterocysts separated by a dying cell will be able to grow into two branches. As in the case of hormogonium formation the longitudinal polarity is interrupted. Two homopolar sections of filament will develop and two poles with opposite orientation will be placed opposite to each other at the place of ramification. Intercalary dying cells and separation discs as well as heterocysts must no doubt be due to a change of the longitudinal polarity and hence the false ramification like the lateral ramification in the *Stigonemaceae* mean progression. Biologically the lateral series a and b replace Stage 4 in the main series. None of them seems to lead on to new stages. And still one might feel tempted to apprehend cases of accumulation of trichomes within the same system of sheaths as a kind of syntagmation (see e. g. the very peculiar *Fischerellopsis* described by FRITSCH 1932).

(c) Turning of the Plane off Cell Division without Turning of Polarity in Bipolarly Heteropolar Plants.

It should first be noted that turning of polarity here means a sudden turning by which two adjacent cells get different polarity.

In *Volvox* the zygote is clearly heteropolar, with hyaline plasma in what corresponds to the front part. At the first cell division the zygote is split into two hemispheres each with an equal share in the front part. At the next division the plane of

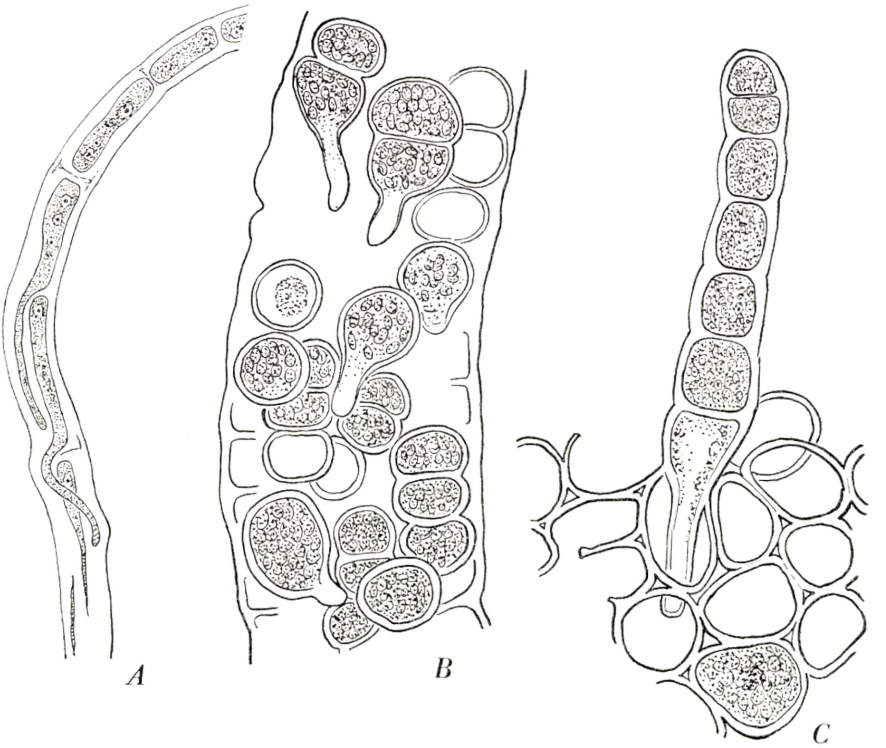


Fig. 6. A, *Chaetomorpha* sp. The basal cell-like sections are heteropolar; the b-poles develop rhizoid-like extensions growing past the section under them. — B—C *Enteromorpha* sp. B, mucilaginescent end of an old filament. Many of the cells have changed into akinetes; some of these have died later and have become empty, others are germinating. C, among many empty rounded cells (akinetes) there are an ungerminated and a germinating akinete growing into a uniseriate heteropolar filament. × 625.

division is turned through 90°, but the four cells still each get their share of the front part of the original cell. At the following divisions, too, the plane of division is turned without the polarity being changed. A cell plate develops which curves and gradually comes to encircle a cavity. At last we get a blastula-like organism of heteropolar cells, which are laterally connected by plasmodesms.

In *Ulva* and *Enteromorpha* the zygote at the germination forms a heteropolar cell filament. A two-layered plate-shaped body or

a tubular body with one-layered walls develops by longitudinal divisions in which the plane of division is turned through 90°. The cells in these forms of thallus are all heteropolar and are no doubt unidirectional as regards polarity, as is seen, i. a., when akinetes originating from the ordinary cells germinate (fig. 6 B—C). At the base of the thallus the cells are able to give out descending rhizoids, which contribute to the attachment. These in *Ulva* either grow down between the two layers of cells or externally. They obviously come from the lower pole of the cells, but as there are cells immediately under them, they cannot grow downwards vertically, but have to bend in one direction or the other to get round those under them.

Under the apical cell in a *Sphacelaria*, too, longitudinal walls soon develop which separate cells with the same type of polarity. In this case matters, however, are quite different because the cells are pluripolar (cf. pp. 14—15). *Sphacelaria* is undoubtedly a derived type which does not belong to the main series, but the lateral series of which it is a representative proceeds from a higher stage than the lateral series to which *Volvox* and the *Ulvaceae* belong. These plants are but bipolarly heteropolar and the lateral series in contrast to *Sphacelaria* do not lead to higher stages of morphological progression.

(d) Regular Alternation between Cells with and without Ramification.

In *Sphacelaria* the apical cell gives off segment cells which before longitudinal walls develop are again divided into an upper and a lower segment cell. Now it appears that lateral branches only develop from cells originating from the upper segment cell. This may be explained by means of the theory of differences in concentration of the substances determining the poles mentioned on p. 13. At the formation of a segment cell this as usual will get an upper and a lower pole (a and b). At the division of the segment cell two cells arise, both with a—b-polarity, but with weakened or inhibited polarity around the new wall, so that we have a—(b) in the upper and (a)—b in the lower segment cell. As lateral ramification in simple ramification takes place near the a-pole, only cells originating from

the upper segment cell are able to give out branches. Cells originating from the lower segment cell in some species, e. g. *Sphacelaria plumigera*, can give out cortical filaments directed downwards. The peripheral cells of the lower segment here are divided into four storeys of cells, and the filaments directed downwards always issue from the uppermost storey but one, thus from cells with a comparatively high concentration of b-substances. Strangely enough, they are not given out from the lowest storey, where one would expect to find most b-substance. This may be connected with the fact that these cortical filaments on the analogy of other species within the order are not genuine rhizoids, but hold a peculiar intermediate position between rhizoids and lateral branches. In other species the system of cortical filaments becomes very complicated as even a lateral meristem (meristoderm) may develop, which gives rise to secondary growth. Secondary growth in the main series was considered the last stage, which followed after axillary concatenation and telomic syntagmation. In *Sphacelariales*, too, it signifies a higher stage of progression, but there it probably follows after pluripolar trichome syntagmation, only not directly, as previously a stage has developed with alternation of segments with mainly a-polarity and segments with mainly b-polarity. For that matter, the secondary growth is very primitive as compared with that mentioned under Stage 10, the so-called meristoderm giving off cells only centripetally and chiefly giving off only one kind of cells. Thus there is a wide gulf between this form of lateral differentiation and that achieved by cambium in a dicotyledonous ligneous plant. What resembles the secondary growth in *Sphacelariales* most perhaps is the growth which in *Lepidodendron* was due to the phellogen and which chiefly consisted in a development of cells in a centripetal direction. An intermediate stage, however, is clearly missing. Perhaps such a stage was found in *Protolepidodendron* or still older forms. If so, another stage with primitive secondary growth without material differentiation of cells and possibly only with a centripetal development of new cells should be added to the main series.

In connexion with the theory advanced as to the differences in concentration *Cladostephus verticillatus* is particularly interesting. Sauvageau's thorough investigations (1906, 1914) show that at

some distance from the apex secondary lateral shoots originate from the upper cells within the originally inferior segments. Other weaker secondary lateral shoots develop from the third storey of cells arising from an originally superior segment and from the

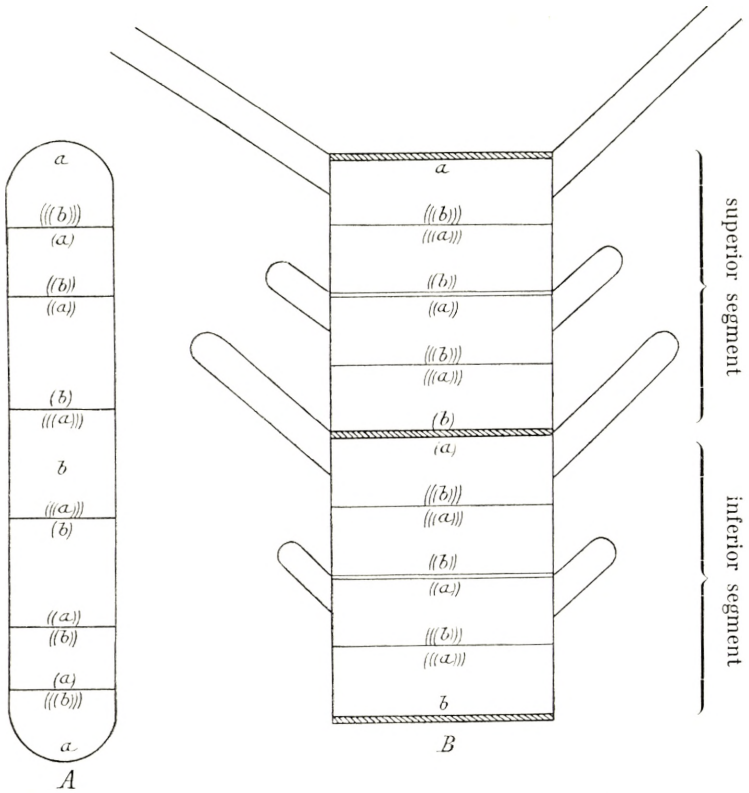


Fig. 7. Diagrammatical figures illustrating the theory on differences in concentration in respect of substances determining the poles. A homopolar filamentous alga with one row of cells (*Pseudanabaena*). The differences are supposed to have arisen by a movement of substance directed from the poles towards the centre and perhaps simultaneously a passage of substance in the opposite direction, towards the poles. B highly organized alga with pluripolar cells (*Cladostephus*), the ramification of which indicates differences in concentration. The boundaries here are not between cells, but between segments and subsegments.

third storey arising from an originally inferior segment. The strength of these lateral shoots is excellently explained by the theory of differences of concentration as, with four storeys of cells in each segment, we get three degrees of a-polarity. Denoting the degree of inhibition by 1, 2, or 3 parentheses, we get (cf. fig. 7):

a	pole	forming main lateral branches (primary lateral branches)
(a)	pole	forming large secondary lateral branches
((a))	pole	forming small secondary lateral branches
(((a)))	pole	provisionally forming no lateral branches

The *Charales* morphologically behave in a similar way as the *Sphacelariales*. The nodal cells correspond to the upper segments and the internodal cells to the lower segments. The main difference is that these two types of cells in the *Charales* are not subdivided further, that the nodal cells remain short cells, while the internodal cells stretch very much, and that the branches from the nodal cells are not given out from the upper part of the cell but from the whole cell. As, however, the branches behave like lateral branches from heteropolar plants and grow obliquely upwards, there is hardly any reason to imagine a turning of polarity at every change. It is more probable that a further inhibition or weakening has taken place, perhaps a total disappearance of the pole-determining substances around the wall separating the nodal and internodal cells so that in the upper cell, the nodal one, there are only (or nearly exclusively) a-substances and in the lower cell, the internodal one, only (or nearly exclusively) b-substances. In the nodal cell a formation of some lateral a_1-poles takes place around the axial a-pole, but these lateral poles are not shifted towards the upper part of the cell as there is no pronounced b-pole. In *Cladostephus* secondary lateral shoots could develop from upper cells in lower segments. In the *Charales* such a process does not take place. Here the regular alternation of cells with and without ramification is absolutely firmly established and as there is even a morphological difference between two cells following each other, we may say that the *Charales* represent a further stage in the lateral series introduced with types corresponding to the *Sphacelariales*.

Coenocytic Lateral Series.

Green algae with a coenocytic structure by virtue of their special cytological conditions belong to lateral series. Within the *Cladophorales* there are uniseriate filaments in *Chaetomorpha* in

which the basal segments show b-polarity by giving out descending rhizoids issuing from the lower parts of the segments (fig. 6 A). Furthermore there is simple ramification in *Cladophora* with ascending branches and descending rhizoids from respectively upper and lower parts of the coenocytic segments. Within the *Siphonales* there are simple forms such as *Protosiphon*, forms with simple ramification (*Vaucheria*), with ramification according to the central axis principle (*Dasycladaceae*), forms with clear pluripolarity (with repent and erect shoots, e. g. *Caulerpa*), and syntagmatic forms (*Codium*), indeed, even forms with systems of repent and erect syntagmatic thallus segments (*Udotea Desfontainii*). Thus it seems that among the coenocytic algae there are stages of progression corresponding completely to the stages of the main series, a fact that appears very interesting.

Phylogeny and Progression within some Groups of Thallophytes.

A number of phylogenetic and systematic conditions are set in a new light if we study the height of organization of the various forms on the scale of progressive stages. In what follows we shall discuss some examples from the taxonomy of the thallophyta.

(1) Monera.

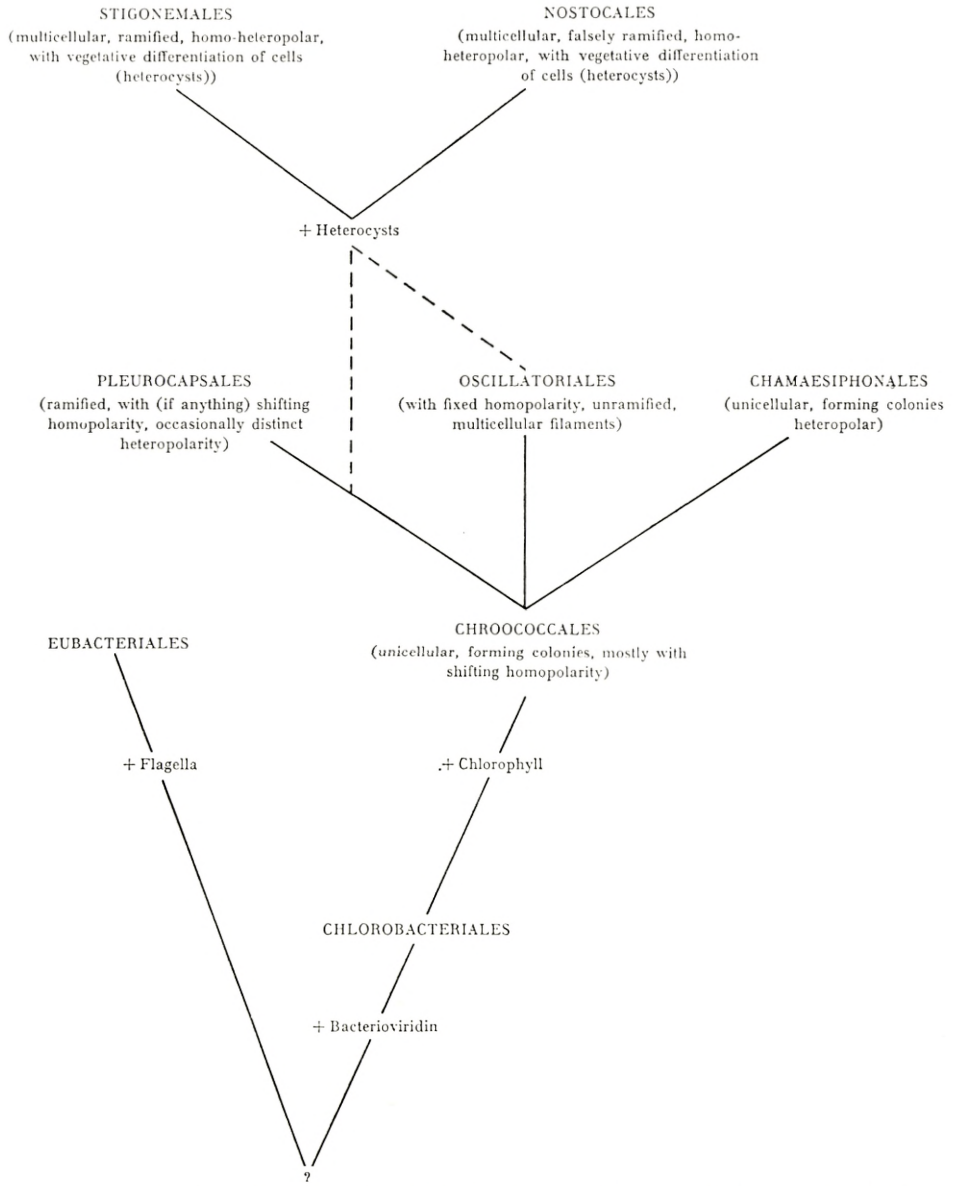
Copeland (1938) in accordance with Haeckel (1866) has proposed this name for the group of *Schizomycetae* and *Myxophyta* (*Cyanophyceae*), i. e. the anuclear plants or *Schizophyta*. Later Stanier & Van Niel (1941) have tried to set up a natural system for the kingdom *Monera*. This attempt has aroused general interest and, with the phylogenetic lines to which they have called attention, marks a phase of progress in relation to previous times, more practically arranged bacterial classifications, and one thing is particularly interesting: the greatest importance is attached to morphological criteria, and the groups to a certain degree are arranged progressively morphologically. Stanier & Van Niel's fig. 1 is a survey of the phylogeny of the *Eubacteriales*. The branches of the genealogical tree are based on morphology.

The starting-point is a primitive coccus, thus an immotile organism with shifting homopolarity. From there issue partly a branch of immotile forms, ending with *Sarcina*, partly a branch with polarly flagellated rods, which ends in the morphologically most derived forms, the spirilla. This series is Gram-negative. The third branch is fairly heterogeneous and hardly quite natural. It ends in ramified bacteria and is carried further to the likewise frequently ramified *Actinomycetales*. Finally there is a branch of peritrichous, rod-shaped groups. All these branches end in forms of a higher stage of progression, as flagellate bacteria must have a higher organization than non-flagellate ones. Among the motile bacteria the heteropolar mono- or lophotrichous forms must be at a higher stage than the homopolar (bipolar) mono- or lophotrichous ones. As stated by STANIER & VAN NIEL, it is probable that future work will show the necessity of drastic revisions. The importance of the genealogical table therefore at the present stage is chiefly in the discussion it may bring about. A very important contribution to a greater discussion has recently been made by PRINGSHEIM (1949). Whereas STANIER & VAN NIEL like several other workers point to a close affinity between *Chroococcales* and *Eubacteriales*, PRINGSHEIM arrives at the view (*loc. cit.* p. 87) that "there is no affinity between Bacteria and Myxophyceae". Even though I completely accept PRINGSHEIM's attempt at a circumscription of bacteria and blue-green algae, I do not see that he has produced evidence of anything but the fact that the highly organized bacteria and the highly organized blue-green algae are essentially different. Both groups include several stages of morphological progression and the lowest of these (the immotile coccoid type) is common to both groups. As this lowest stage even cytologically proves to be of a low organization, and this in the same way (absence of a genuine cell nucleus, sap vacuoles, and plastids as well as important accordances with regard to the chromatin apparatus; cf. also NEUGNOT (1950)), it is hardly premature to assume affinity in the form of common origin between bacteria and blue-green algae at the lowest stage of organization. It is evident that the groups besides, during their evolution, have parted. The same applies to the algae, among which forms of low organization within several series indicate a common origin, without our daring otherwise to attempt giving

a detailed account of the affinity. A common origin of blue-green algae and bacteria thus is still very probable. On the other hand we are on unsafe ground in attempts at finding out whether blue-green algae or bacteria are the oldest forms. According to STANIER & VAN NIEL the *Chroococcales* may be supposed to have developed from the *Eubacteriales*, as they, with OPARIN (1938), are of opinion that there was a chemical synthesis of organic substance on the earth before the first organisms showed signs of life. These, therefore, might be heterotrophic. This view is inconsistent with experiences from the other parts of the vegetable kingdom, where colourless forms must always be derived from forms containing chlorophyll. VAN NIEL has himself later (1944) in his discussion of the *Pseudomonadales* found it necessary to regard the photosynthetic forms as progenitors of the non-photosynthetic forms. If, therefore, the blue-green algae are to be derived from the bacteria, it must be from such as are morphologically of low standing and which likewise are photosynthetic. Here the group of interest would seem to be the *Chlorobacteriales*, which consist of immotile cocci (*Chlorobium*, cf. NADSON 1912) or rods, which may sometimes assume coccoid forms (BÖCHER 1949a) and which therefore possibly consist of chains of undivided coccoid units (cf. above p. 5).

The genera *Beggiatoa* and *Oscillatoria* have the same structure of cells and the same type of motility. Both STANIER & VAN NIEL and PRINGSHEIM are of opinion that they are related and the *Beggiatoaceae* therefore can be apprehended as apochlorotic colourless blue-green algae. They belong to an order which I propose to term *Oscillatoriales* and which in regard to height of organization (absence of heterocysts) is below the other groups often classed together as "*Hormogonales*". These may suitably be termed *Nostocales* (including all forms bearing heterocysts and with false ramification; cf. p. 26) and *Stigonemales* (mostly forms bearing heterocysts and with ramification by turning of polarity; cf. pp. 24—26).

The *Pleurocapsales* are peculiar by having plagiotropic filaments from which branches may be given out laterally, upwards and downwards (i. e. into the substratum). Conditions may remind of pluripolar ramification and syntagmation, but to all appearance the ramification is of the same type as in the *Stigonemales*



Diagrammatic representation of the phylogeny of the *Cyanophyceae* according to the theory advanced by the present writer.

and is due to a turning of polarity, which in addition seems capable of taking place in any direction, thus a structure greatly reminding of shifting homopolarity. Because of the similarity as regards ramification, the *Stigonemales* may be supposed to have been derived from forms from which the *Pleurocapsales*, too, originated. Only after the two groups had parted, forms with heterocysts arose, and then one branch specialized on false ramification while another retained ramification by turning of polarity. The strange *Fischerellopsis* (FRITSCH 1932) has both false ramification and *Stigonemales* ramification.

In my previous paper (1949a) I pointed out the possibility of deriving the *Oscillatoriales* from the *Chroococcales* through the medium of such genera as *Synechococcus*, *Synechocystis*, and *Pseudanabaena*. FRITSCH (1945, p. 859) entertains a similar idea when writing: "from the primitive coccoid type, there may have originated an extinct series of multicellular forms, one branch of which led to the *Oscillatoriaceae*, while another, after the evolution of the heterocyst, gave rise to the other three families of *Nostocales*." This point of view is the direct opposite of that of GEITLER (1925), who is of opinion that the *Oscillatoriaceae* is the most advanced group among the *Hormogonales*. Like FRITSCH I go in for the abandonment of the name of *Hormogonales* and instead operate with *Nostocales*, *Stigonemales* (proposed by FRITSCH), and *Oscillatoriales*. On p. 35 there is a survey of my theory of the phylogenetic conditions in the *Cyanophyceae*.

(II) Algae.

A number of instances of the placement of nuclear autotrophic thallophytes in the scale of morphological progression have already been discussed. Some comments on phylogenetic conditions follow.

Great interest attaches to the occurrence of homopolar forms. Whereas in anuclear organisms these were predominant they constitute rather a subordinate element among the nuclear forms. In itself this is not very strange. If unicellular flagellate forms, as supposed by many workers, form a number of primary groups, from which the majority of other groups should be derived, then the starting-point is heteropolar.

Among the great number of different groups there are only two mainly homopolar ones, viz. *Conjugatophyceae* and *Bacillariophyceae* (the diatoms). Furthermore a few red algae have homopolarity and such a form as *Raphidonema nivale*, which belongs to the *Chaetophorales*, is clearly homopolar. The latter species can easily be dispatched, as it is evidently a greatly reduced type. Above, p. 15, plagiotropic homopolar shoots forming the basis of erect shoots were mentioned just as occurring among the *Chaetophorales*. A type like *Raphidonema* can be assumed to have arisen by the loss of such erect shoots. *Pleurococcus vulgaris*, too, is a very primitive type, which can only with difficulty be regarded as heteropolar, but which may remind of plants with shifting homopolarity. However, its divisions on three planes can easily be derived from forms with pluripolar ramification. This, too, is apprehended as a reduced form within the group of *Chaetophorales* (see FRITSCH 1935).

Conditions are quite different in diatoms and conjugates. These are two groups rich in species in which the homopolarity is nearly universal. In no place homopolarity is more beautifully demonstrable than in *Closterium*, where the poles have vacuoles with oscillating crystals of gypsum. At the cell division in *Cosmarium* we see something corresponding to the division of a detached cell in *Pseudanabaena* (fig. 1). Between the two a-poles in *Cosmarium* there is a "b-pole", which, however, is not retained, because the cells are separated by the division. The b-pole is at once changed into two new a-poles in the new halves of the two cells detached from each other. But in the *Zygnemaceae* there is a development of filaments composed of cells which mostly are homopolar and not attached. There is, however, an interesting progression to be observed here. The *Zygnema* cell with its two stellate chromatophores is clearly homopolar and accordingly the cell produced by the germination of the zygote is also homopolar (see KURSSANOW 1912). *Spirogyra* has spirally placed ribbons of chromatophores running from one end of the cell to the other. The cell here is not clearly homopolar, and at the germination of the zygote it appears (see e. g. TRÖNDLE 1911) that there is a difference between the two ends of the cell, the rear end being colourless and rhizoid-like. In the genus *Spirogyra* we just find attached forms (*S. adnata*, *S. fluviatilis*) with a basal

cell equipped especially for attachment. Here heteropolarity has developed within an otherwise homopolar group.

Apart from conditions of polarity in a cytological respect the *Conjugatophyceae* are more highly organized than the homopolar blue-green algae. And the cells of the *Bacillariophyceae* seem still more complicated. Both conjugates and diatoms, therefore, are highly organized homopolar groups. They are no doubt final stages in two otherwise separate evolutionary series beginning with simple homopolar forms[1]. The *Mesotaeniaceae* are more closely related to these unknown primitive forms than the other groups of *Conjugatophyceae*.

By their homopolar organization together with many other properties both the *Conjugatophyceae* and the *Bacillariophyceae* hold a very isolated position among the nuclear plants. I see but a slight possibility of finding a transition to the heteropolar forms, where the flagellate cell type is completely prevalent. Even if *Spirogyra* reaches heteropolarity, this avails little as it forms no swarmers and has neither flagella nor eye-spots. The facts adduced e. g. by FRITSCH (1935 p. 361) in favour of a connexion with the other green algae carry little conviction. He derives a sideways fusion of two immotile or amoeboid, mostly homopolar gamete cells from a fusion of two a-poles in two heteropolar flagellated gametes, which seems rather artificial. He mentions that also in the *Chlorococcales* there is absence of motile reproductive stages, but in this group plants without motile stages obviously are due to reduction of forms with motile stages, and there is no indication of such a process of reduction in the *Conjugatophyceae*. In another modern manual, SMITH (1938), it is attempted to derive the *Conjugatophyceae* either from the *Volvocales* or the *Tetrasporales*, thus from pronounced heteropolar forms. This is no doubt done on the basis of the view that "the evolutionary possibilities along the tetrasporine line are infinite. A tendency for the vegetative cells to become non-flagellated but to return directly to the motile condition is found in the tem-

[1] Having finished this paper I received the very interesting paper on radiation of desmids by TEILING (1950). According to this author it is possible among the desmids to distinguish between several types of radiation (that structural element which is decisive in the shape of the desmids according to their vertical symmetry-planes) and these types seem to form a regressive series. Finally TEILING uses the radiation types or steps as a basis for a phylogenetical survey of the desmids.

porary *Palmella* stages of many unicellular *Volvocales*." But when an alga enters a *Palmella* stage and loses its motility, it does not at the same time become homopolar.

A possibility of finding a transition between the *Conjugatophyceae* and the other green algae is no doubt to be sought in possible homopolar ancestors of the latter group. But even in *Hormidium*, which in many respects seems primitive as its filaments may come to small pieces which are apparently homopolar, there are biciliate heteropolar zoospores and gametes. Thus there are no forms now living which fulfil the conditions as connecting links between the *Conjugatophyceae* and the *Chlorophyceae*, and hence it is presumably most natural to regard the *Conjugatophyceae* as an independent group. Thus I do not subscribe to the view of all the present-day phycologists which according to SMITH have abandoned the former practice of placing the *Conjugatophyceae* in a special subclass. We shall probably go right back to a homopolar, unicellular, nuclear organism, something like a primitive *Mesotaeniacea*, before obtaining a connexion between the *Conjugatophyceae* and the *Chlorophyceae*.

A similar taxonomic position is held by the diatoms. PASCHER (1921) has advocated the view that the diatoms should belong to a division of "*Chrysophyta*", among which also the *Xanthophyceae* (*Heterocontae*) and *Chrysophyceae* should be classed. The chief correspondences are in the brown colours in the chromatophores and the occurrence of fat oils and not starch as assimilation product. The majority of *Xanthophyceae* and all *Chrysophyceae*, however, are heteropolar, whereas the diatoms are homopolar. A possible connexion between the groups, therefore, must be through the homopolar *Xanthophyceae*. A genus like *Centritractus* set up by LEMMERMANN, the cell wall of which is composed of two similar halves and which has no flagellated stages, might very well be related to the forms from which partly the *Xanthophyceae* and *Chrysophyceae*, partly the *Bacillariophyceae* originated.

Whereas the brown algae probably originate from unknown brown flagellate-like algae, things are quite different as regards the red algae, in which flagella are completely absent. The red algae on the whole are heteropolar, but it is an interesting fact that within the primitive group of the *Bangiales* there are uni-

to bicellular, clearly homopolar forms (*Porphyridium cruentum* and *Chroothece*), a few of which (*Chroothece mobilis*; see PASCHER & PETROVA 1931) can move by secreting mucilage, particularly at the poles. The apical attachment filaments found both in *Kyliniella*, which belongs to the *Bangiales*, and in floridean forms like *Spermothamnion repens* and *Trailliella intricata* is probably a character pointing to homopolar ancestors.

Particularly KYLIN (1930, 1943) has advanced the view that the red algae should be descended from blue-green algae; but this view has been opposed by GEITLER (1944) and has not been accepted by FRITSCH, either. Reference has especially been made to the more highly organized cell structure of the red algae (cell nucleus, chromatophores). The similarity between the most highly organized blue-green algae and certain primitive red algae, such as e. g. *Goniotrichum* (see ROSENVINGE 1909, p. 76), however, is very great. Apart from the cell nucleus and the chromatophores in the latter, they belong to the same stage of progression. As an important addition to the points of resemblance adduced by KYLIN between *Cyanophyceae* and *Rhodophyceae* now comes the homopolarity which occurs both in *Stigonemales* and in *Bangiales*, while the fact that the *Cryptophyceae* are markedly heteropolar weakens GEITLER's theory of a relationship between these and the red algae. But the finding of missing links in the form of a *Cyanophycea* with cell nucleus or a red alga with a primitive chromatin apparatus or a *Stigonemacea* with incipient division of the chromoplasm into chromatophores will be necessary to form a secure basis of the theory of an evolution from blue-green algae to the red algae. SPEARING's cytological investigations (1937) of *Stigonema mamillosum* would seem to indicate that in this species there are certain signs of nucleus formation, as e. g. nucleolus-like bodies and a system of chromatinic filaments reminding of a prophase in a typically nuclear plant have been found there. It will be a very important task for cytology thoroughly to compare the *Cyanophyceae* and the most primitive red algae. A bridge made between the *Monera* and the other plants will open up considerable new vistas, for if typical cell nuclei can have been formed by evolution from the chromatin apparatus in a *Monera* type in one place, this may have happened in other places, too, and the bridge will also give evolution a possibility

of following the series of progression in quite another way than may be done when the nuclear or anuclear organisms are considered apart, and this, of course, seems very pleasant, as the assumption of several separate series of living organisms, several "creations" is a hypothesis of little probability. Copeland (1938, fig. 8), too, assumes the nuclear organisms to have developed from anuclear ones.

If it proves possible to derive the red algae from the blue-green algae, the brown algae will come to hold a comparatively more isolated position, for the most primitive among these are already at Stage 5. The absence of Stages 3 and 4 prevent a contact with the flagellates.

The stoneworts (*Charales*) also hold an isolated position, but here, at any rate as far as morphological conditions are concerned, a connecting link with the other green algae has been found. The genus *Draparnaldiopsis* found by Smith & Klyver (1929) and later by Bharadwaja (1933) and belonging to the *Chaetophorales*, as compared with the other forms of this order signifies a further advance. Here are the long axes composed of alternating long internodal and short nodal cells, and the branches are formed only on the short cells and arise from their median region. The laterals may develop into rhizoid-like filaments, which sometimes form a dense cortical covering around the main axis. Viewed from the stages of progression included in the order, the *Chaetophorales* seem to hold a very important position. It is here the pluripolar structure appears, and furthermore there is in respect of the differentiation of the main axes a progression reminding of that mentioned in connexion with the brown algae (uniseriate, primitive forms—*Sphacelaria*—*Cladostephus*). The *Chaetophorales* show a clear phylogenetic connexion with the *Ulotrichales*, which are at a lower stage of progression, and with *Draparnaldiopsis* as connecting link there is a possibility of a distant relationship with the *Charales*, which include higher stages of progression. Finally, perhaps with a starting-point in *Coleochaete*, there is a possibility of relationship with the forms of green algae which must have existed and which formed the basis of the most primitive archegoniates.

Concluding Remarks.

The concept of morphological progression is here first kept distinct from the concept of evolution, then used for a critical appraisal of certain phylogenetic trends. An unravelment of the relation between morphological progression and evolution seems urgent. In works dealing with evolution, e. g. HUXLEY (1945), the concept of evolutionary progress is mentioned. In the animal world this ends with man, and many biologists, among them HALDANE (1932), call attention to the fact that when speaking of evolutionary progress "we are already leaving the relatively firm ground of scientific objectivity for the shifting morass of human values". No organism is "high" or "low", for they are all results of an evolution and are to an equally high degree adapted to the surrounding nature. HUXLEY opposes this view and is of opinion that evolutionary progress can be defined and studied on an objective basis. To him evolutionary progress consists in "a raising of the upper level of biological efficiency, this being defined as increased control over and independence of the environment, . . . progress is all-round biological improvement". It is very probable that the morphological progression represents a biological improvement. In many cases, however, it is difficult objectively to define the improvement; nor is it easy to find criteria of increased control over the environment. Add to this that the word *improvement* does not exactly tally with the fact that all organisms—including the extinct ones—are or were to an equally high degree adapted to the environments. In the face of these facts morphological progression seems to hold a strong position in respect of objectivity. The concept can be kept clear of the concept of evolution, and the material underlying it can be studied on an exact basis. It must be admitted that my investigations of the stages of progression are but intro-

ductory and that future investigations no doubt will modify many details and perhaps result in a subdivision of the stages into more stages; but this does not alter the fact that morphological progression can be studied objectively and used for an appraisal of phylogenetic theories. It seems evident that the world of plants as a whole has passed through the whole series of progression, but that the single trend in some respects may have developed progressively, in others regressively. The species of *Rafflesia* have a very highly organized flower, but their vegetative, myceloid body by regressive development has dropped far down in the progressive series of stages.

A progressive development accordingly becomes a rise in respect of morphological complication continued through the history of the world. As behind greater complication of the external forms there is a corresponding greater complication of conditions of polarity (the morphological differentiation as a physiological process), it is evident that our eye must be directed towards the results to be obtained from growth-substance research as regards morphological differentiation. Furthermore it will naturally be directed towards such mutations as are capable of surviving (ecologically possible) and at the same time result in a greater complication of the structure of the plants. Behind each stage in the progressive scale there are one or more mutations, which change the cells and plants as a whole so that the structure gets more complicated; but even if perhaps some mutations have been necessary for the development of each of the ten stages mentioned in the main series, it seems that the progression in itself is due to comparatively few, but then very important, mutations. Only an infinitesimal number of the mutations taking place result in types capable of surviving and, particularly, of competition, and an even smaller number of the mutations result in morphological progression. The nearly countless number of variations displayed by the species in the world of plants put together, therefore are presumably in the first place due to non-progressive mutations. It seems as if the progression drags along, whereas the formation of species and the ecological specialization is fast.

The progression in respect of the structure of the reproductive organs seems closely connected with the vegetative progression,

these organs, however, as a rule being somewhat more complicated than the vegetative ones in the same organism. We should here speak of reproductive organs, not of sexual organs, since the latter, as in the cormophytes, may undergo a considerable regressive development. It is the aggregate reproduction apparatus of the plants which is developed progressively. Within the group of cormophytes we see how the organs of reduction division develop slowly, but progressively, gradually taking over the function of the sexual organs. Exactly because reproductive organs follow the slow progression, they seem conservative and homogeneous as compared with the vegetative organs. They are rigid, whereas the vegetative organs are plastic, and hence they are the fixed data to which taxonomists and phylogeneticists must cling in the rough sea of vegetative variation.

This can also be illustrated through the fairly numerous available studies of race biology. Such a species as *Prunella vulgaris* e. g. in respect of vegetative development can be extremely heterogeneous. It consists of races which are cushion plants, repent, erect, annual, biennial, perennial, etc.; but in floral characters it varies little (cf. Böcher 1949b). An annual and a perennial race belong to two different life forms. We see that the ecological race, the ecotype, as it has been termed by Turesson, is a forerunner of the life form. Widely different groups of plants in respect of vegetative characters are plastic, and by convergent development produce a number of life forms corresponding to certain external conditions; but this development does not affect the floral characters. Such a group as the *Leguminosae* has developed trees, shrubs, dwarf shrubs, and annual and perennial herbs. This development is a fast-going, ecologically stamped evolution, whereas the development by which the *Leguminosae* arose from *Rosales*-like ancestors is a slow progressive or phylogenetic trend.

Out of consideration to the clearness of the discussion, we shall finally for a moment distinguish between the mutations producing new progressive stages from these which mainly takes place within the same stages and result in ecotypes, species, and life forms. The latter appear in great numbers of small hereditary changes which in some cases do not result in a subdivision into races, but in the appearance of nearly continuous character-

gradients or clines. The former, the progressive mutations are very little known. If they are of the same order of magnitude as the others, they will easily escape observation as the appearance of the progressive stage to which they were to contribute probably extends over a considerable period. The chance of coming across them therefore is small, and as they represent small deviations from the norm, only, they will be difficult to discover. However, it is not certain at all that they are always small. The undoubtedly rare mutants capable of living and competing which include several genes, perhaps are of the greatest importance exactly for the progressive evolution[1]. Within the animal kingdom there has been a development from an earth-bound existence to a flying life in insects, reptiles, and mammals. Here already the first mutation must have resulted in a type which was capable of using its transformed limbs for something which perhaps was not exactly flying, but e. g. keeping hovering for a short time, thus being able to escape a pursuer. But such a mutation is very comprehensive. As an instance of great deviation (probably a mutation) of a progressive type I may mention a strange *Myosotis* plant which some years ago I found among hundreds of normal plants in a garden (fig. 8). Unfortunately it was not fertile, but it was very interesting by showing vegetative as well as floral progression. The flowers were 8—10-merous and in the vegetative parts an umbelliform inflorescence with formation of involucres, i. e. a development indicating a *local* process of growth inhibition similar to that mentioned in the chapter on axillary concatenation (p. 22) and in the brief section on the inflorescence in *Compositae* (p. 24).

But even though there may be quantitative differences in respect of the mutations which give rise to the two forms of evolution, the adaptive and the progressive evolution, it is evident that this is not a case of quite different things. Conditions in the algae seem particularly suitable to illustrate this. FRITSCH (1935, pp. 26—27) has some interesting surveys of parallelism in evo-

[1] Recently GOLDSCHMIDT (1948) has advanced views which on some points are in agreement with mine. He does not think that small mutations, selection, and isolation result in anything but ecotypes, whereas macromutations are needed to produce species. GOLDSCHMIDT writes: "Major systematic differences and adaptions can only originate in single major steps which establish at once the main features of the new organizational and physiological pattern."

lution in the algae. His types of construction (e. g. "heterotrichous filament", "crust or cushions", "multiaxial compact type") are a kind of life forms. We have heterotrichous filaments e. g. in *Stigeoclonium*, *Ectocarpus*, and *Chantransia*, crusts or cushions in e.g. *Pleurocapsa*, *Pseudopringsheimia*, *Ralfsia*, and *Hildenbrandia*, the "central axial type" is realized in *Batrachospermum* and *Draparnaldiopsis*, etc. The crust-cushion type is no doubt a good life-form as it is specialized for epiphytic or epilithic life, and we see that the most different groups of algae convergently have reached this life form. However, this type is also of a very high progressive significance as a prostrate growth is a condition of radial polarity (p. 13) and of the formation of a larger attachment disc which enables growth of larger algal bodies (p. 18). The "fountain type", too, is a kind of life form which is found realized both in red and brown algae, and which is approximately reached by the *Rivulariaceae*. Coenocytic green algae like *Codium* as well belong to this type, and furthermore we must assume that cellular unknown green algae have reached this life form; but only in the last-mentioned case the fountain type became of fundamental importance for evolution as the algae in question became the first stages of the scale of progression which was later continued in the cormophytes. These instances show that progressive development in many cases—perhaps always—coincides with adaptive development, and indeed it is evident that the progressive mutations must also be ecologically important. For reasons of selection it cannot be otherwise. If they were not ecologically well-equipped, they would perish.

As a main result it may be stated that the majority of mutations capable of surviving are not progressive; they do not result in new stages. As for the vegetative parts the non-progressive evolution results in the formation of a great number of ecotypes and species and—in the long run—life forms, which give the species and groups of plants a possibility of living in different environments. Few of the vegetative, ecologically important mutations are *also* progressive, resulting in new stages or parts of them. As for the reproductive organs, e. g. the flowers, great numbers of varieties with different colours and sizes of the flowers, properties of fragrance, etc., corresponding to the ecotypes will develop in the non-progressive evolution and give the species a possibility

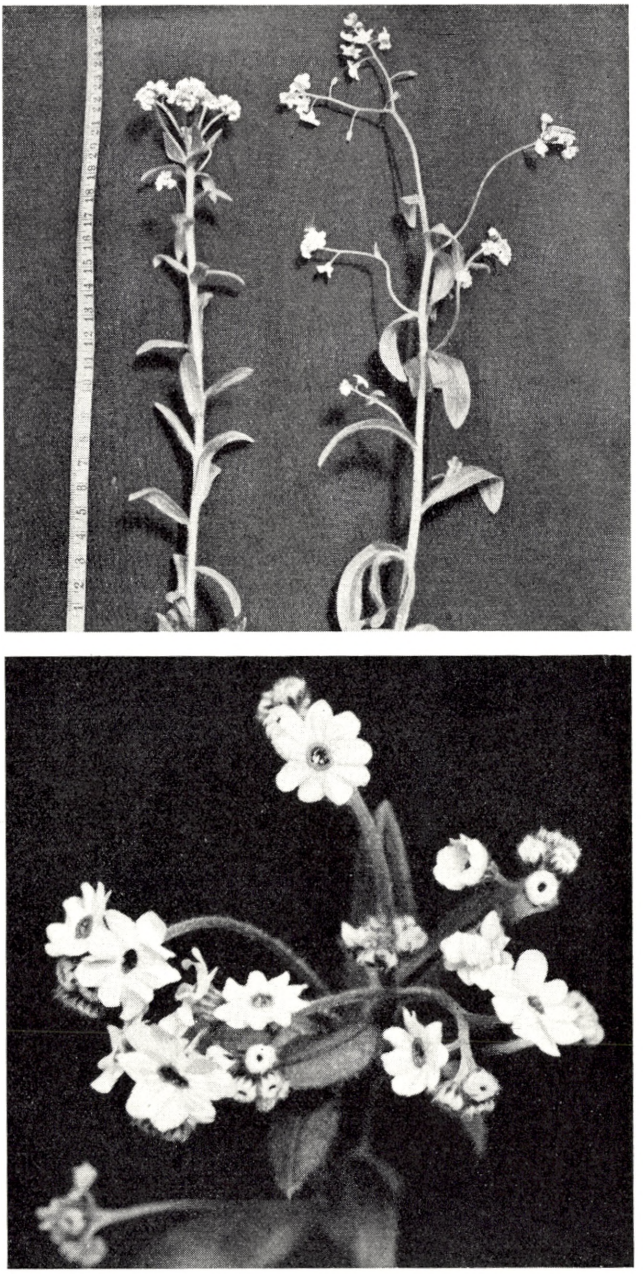


Fig. 8. Above, on the right, normal garden variety of *Myosotis silvatica*, on the left greatly deviating plant with umbelliform cluster of the helicoid cymes and 8—10-merous flowers. Below, the same seen from above. TWB. phot. 1934.

of managing i. a. under different conditions of pollination. But very few mutations are *also* progressive, leading to reproductive organs of a more complicated structure. As these mutations are also important from the point of view of floral biology (ecologically), the result will be that at each stage of progression an advantage is obtained from the point of view of floral biology. Therefore we find simultaneously with the morphological progression in the reproductive organs of the plants an increasing degree of care for the embryos culminating in epigynous forms in the angiosperms.

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THE ENZYMATIC OXIDATION OF 2-AMINO-4-HYDROXY-6-FORMYLPTERIDINE

BY

HANS KLENOW

København
i kommission hos Ejnar Munksgaard
1951

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THE ENZYMATIC OXIDATION OF 2-AMINO-4-HYDROXY-6-FORMYLPTERIDINE

BY

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København
i kommission hos Ejnar Munksgaard
1951

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Introduction.

It has been shown that pteroylglutamic acid (synthetic folic acid) can be converted to an aldehyde which has been proved (1) to be 2-amino-4-hydroxy-6-formylpteridine (6-aldehyde). The transformation can be brought about either by treatment with sulphurous acid (1) or by irradiation with ultraviolet light (2). The conversion product is an extremely effective inhibitor of the oxidation of some purines and pteridines by xanthine oxidase from milk (3 and 4). The inhibitory potency is eliminated by incubation of the 6-aldehyde with xanthine oxidase (3 and 4). From studies of the absorption spectrum of the enzymatic conversion product of the inhibitor LOWRY *et al.* (2) conclude that 2-amino-4-hydroxy-6-pteridine carboxylic acid was formed by an enzymatic oxidation of the corresponding 6-aldehyde.

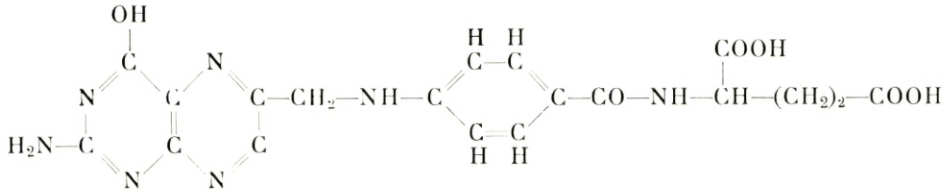
The aim of the present work is to establish that the enzymatic conversion of the inhibitor is 1) of an oxido-reductive nature and 2) that an acid is formed as result of this oxidation.

The relation between the substances mentioned is indicated in the following diagram.

Materials and Methods.

The 2-amino-4-hydroxy-6-formylpteridine used was initially prepared in this laboratory by sulphurous cleavage of folic acid, later Dr. T. H. JUKES, Lederle Laboratories, kindly supplied us with a solid product prepared according to the method of WALLER *et al.* (5). The aldehyde was estimated as the 2,4-dinitrophenylhydrazone according to the method previously described (4).

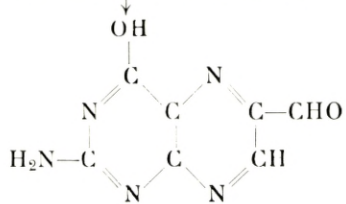
The enzymatic conversion of the aldehyde was followed fluorometrically (4). In a 0.1 M pyrophosphate buffer about pH 9



Pteridine part — p-Amino benzoic acid — Glutamic acid

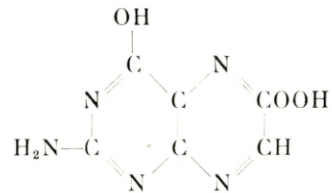
Folic acid

Sulphurous acid or | ultra violet light

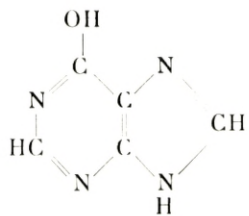


6-Aldehyde

Xanthine oxidase →

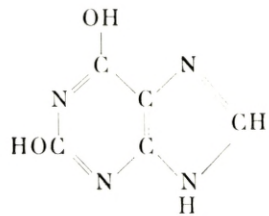


2-Amino-4-hydroxy-6-pteridine carboxylic acid.



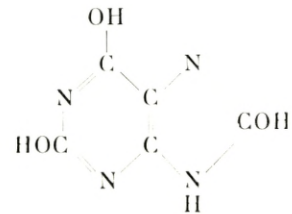
Hypoxanthine

Xanthine oxidase →



Xanthine

Xanthine oxidase →



Uric acid

the increase in fluorescence brought about by the enzymatic reaction was approximately 90 per cent of the original fluorescence. In a 0.1 M glycine buffer about pH 9, however, a decrease in fluorescence took place, corresponding to about 27 per cent of the fluorescence of the original solution of the aldehyde. The fact that the change in fluorescence does not necessarily go in the same direction must be ascribed to a difference in the proportion of the quenching effect of the two buffer solutions on the aldehyde and the corresponding conversion product.

Properties of the Enzyme.

The differential fluorometric analysis was used as a test for the enzyme. The enzyme was found in milk and the activity always accompanied that of xanthine oxidase prepared from cream. The enzyme was purified as previously described for xanthine oxidase (4). It has not been possible to separate the activity of the two enzymes. About the possible identity of the enzymes the reader is referred to LOWRY *et al.* (3). The enzyme which acts on the aldehyde in question here was practically

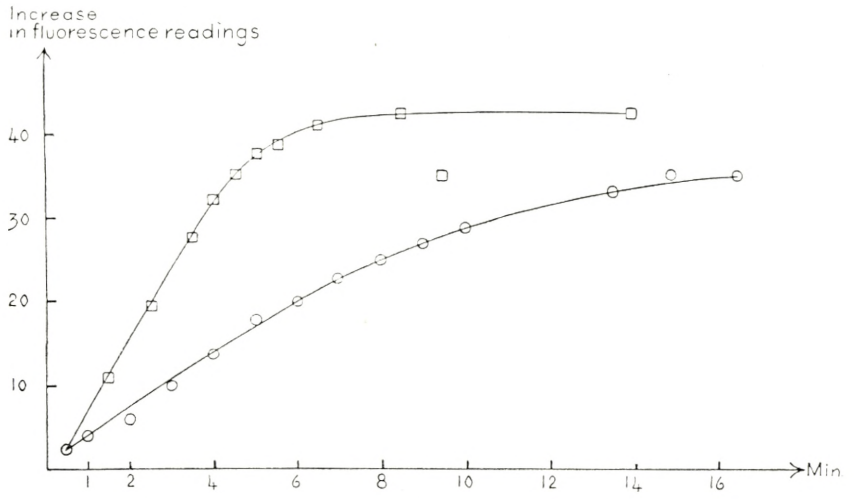


Figure 1. Inhibition of the enzymatic conversion of 2-amino-4-hydroxy-6-formylpteridine by guanine. □ 0.73×10^{-9} moles of the aldehyde per ml of pyrophosphate buffer pH 9. ○ the same with 6.6×10^{-9} moles of guanine added per ml of the mixture. Xanthine oxidase added at zero time. Abscissa: time of incubation. Ordinate: readings at the fluorometer.

inactive at pH 7.5 and the pH optimum of the enzyme was found to be located at about pH 9.

The most purified preparations of the enzyme are able to convert about 1.1×10^{-8} mole of the aldehyde per hour per mg of protein at 20° C. It was found that the activity of the enzyme is inhibited by the presence of guanine. Thus in a sample containing about 0.73×10^{-9} moles of the aldehyde per ml the activity of the enzyme towards the aldehyde is reduced to about 50 per cent of the original activity by the presence of about 6.6×10^{-9} moles of guanine per ml of the mixture (see figure 1).

Type of Reaction Involved in the Enzymatic Conversion of the Aldehyde.

Absorption Spectra.

In figure 2, 3 and 4 the absorption spectra of the aldehyde and of the corresponding oxidation product at different pH values are recorded. It is seen that the characteristics of the shapes of the absorption curves of the conversion product are approximately unchanged at pH ranging from 3 to 9. The absorption curves of the aldehyde at pH 9 is much like those of the conversion products, whereas at pH 3 and 7,7 the curves are almost alike but differ from that at pH 9.

Disappearence of the Aldehyde Group.

The increase in fluorescence during enzymatic conversion of 6-aldehyde can be shown to be directly proportional to the disappearance of the aldehyde as measured by the specific colorimetric method. This is graphically illustrated in figure 5. The experiment was performed in the following way. At fixed time intervals as indicated in the figures, aliquots of the enzyme-aldehyde mixture were deproteinized with perchloric acid. The fluorescence and the hydrazone-color in these aliquots were measured in the usual way. The measurements obtained expressed as percentages of the final values were plotted against the time of incubation.

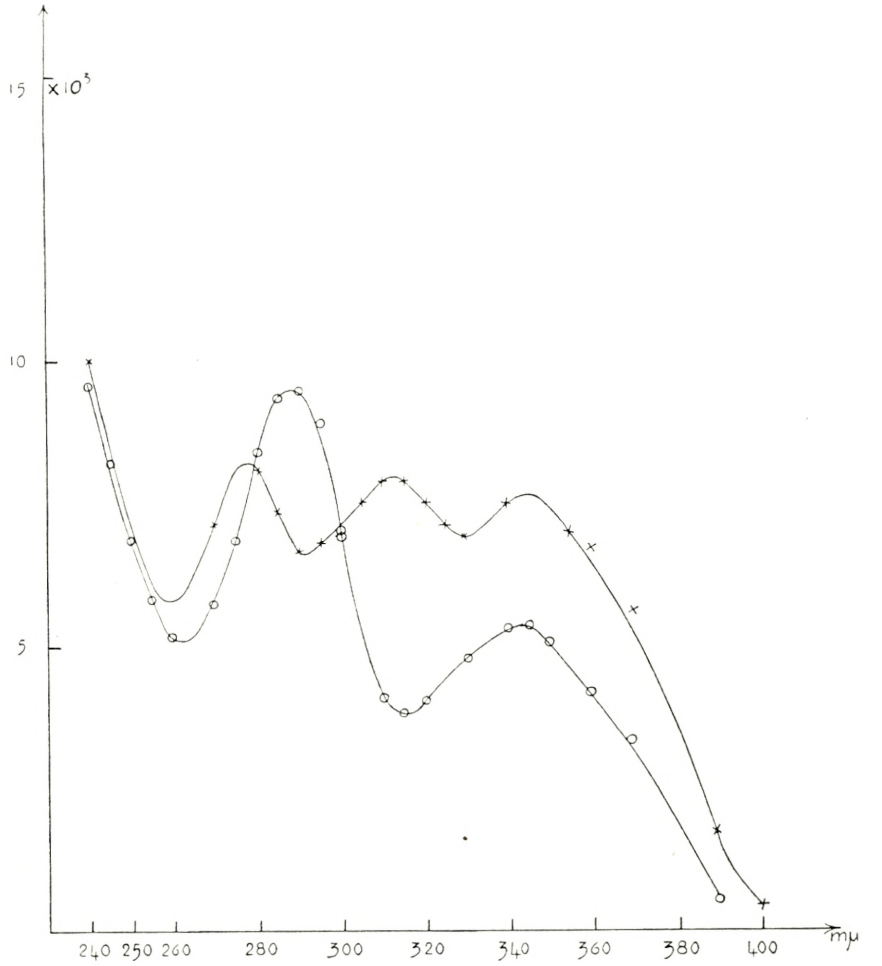


Figure 2. Molar extinction curve of 2-amino-4-hydroxy-6-formylpteridine and of the enzymatic conversion product. M/5 glycine buffer pH 3.0. × 2-amino-4-hydroxy-6-formylpteridine. ○ Enzymatic conversion product. Abscissa: Wavelength in mμ. Ordinate: Molar extinction.

Formation of an Acidic Group.

It seemed probable that the enzymatic conversion of the aldehyde group was due to an oxidation or a dismutation. It was not, however, possible to demonstrate the formation of an acidic group by means of pH indicators. The appearance of an acidic group was established by estimating the distribution coefficient between aqueous buffer solutions and butanol of the aldehyde

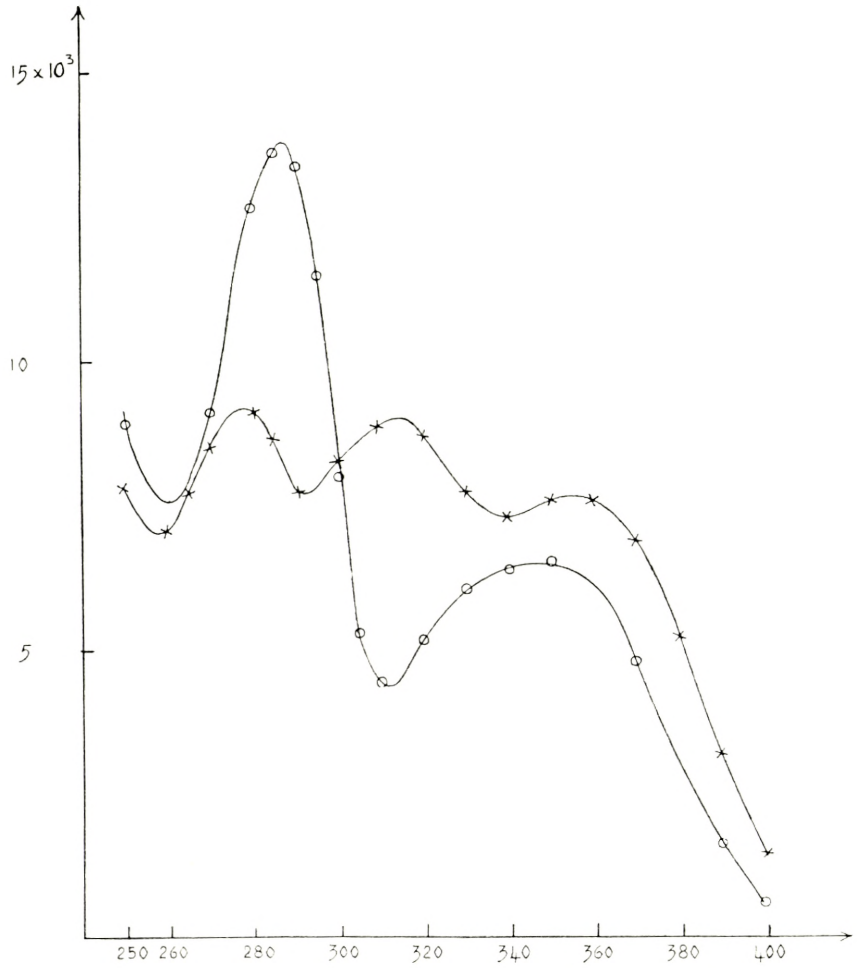


Figure 3. Molar extinction curve of 2-amino-4-hydroxy-6-formylpteridine and of the enzymatic conversion product. M/5 glycine buffer pH 7.7. × 2-amino-4-hydroxy-6-formylpteridine. ○ Enzymatic conversion product. Abscissa: Wavelength in mμ. Ordinate: Molar extinction.

and that of the enzymatic conversion product. The two pH values selected were pH 3 and pH 7. This shift in pH should not affect the distribution coefficient of the aldehyde. However, an acidic group of a pK between 3 and 7 should be extracted much more into the butanol layer at pH 3 than at pH 7 since it is dissociated at the latter pH.

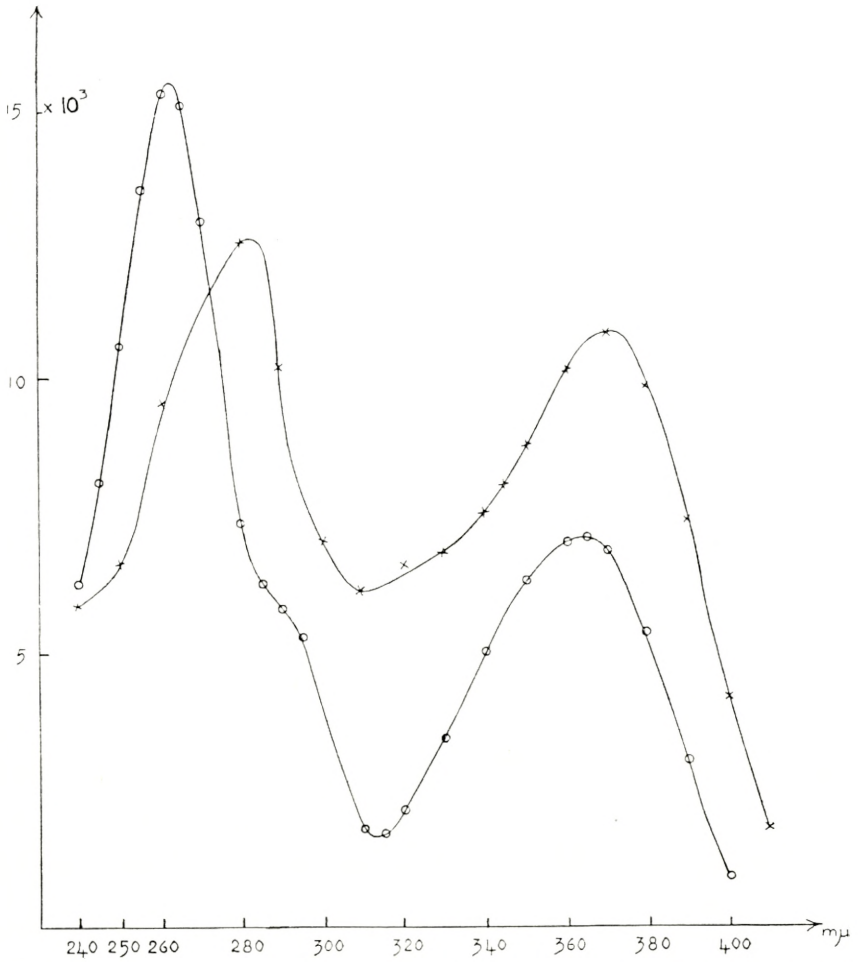


Figure 4. Molar extinction curve of 2-amino-4-hydroxy-6-formylpteridine and of the enzymatic conversion product. M/5 pyrophosphate buffer pH 9.0. × 2-amino-4-hydroxy-6-formylpteridine. ○ Enzymatic conversion product. Abscissa: Wavelength in mμ. Ordinate: Molar extinction.

The distribution coefficients of the compounds were obtained by measuring the decrease in fluorescence in the buffer solutions during a number of extractions with butanol.

In the case of the enzymatically transformed aldehyde the experiments were performed in the following way. The buffer solutions (saturated with butanol) containing the enzymatic conversion product of the aldehyde were extracted about ten

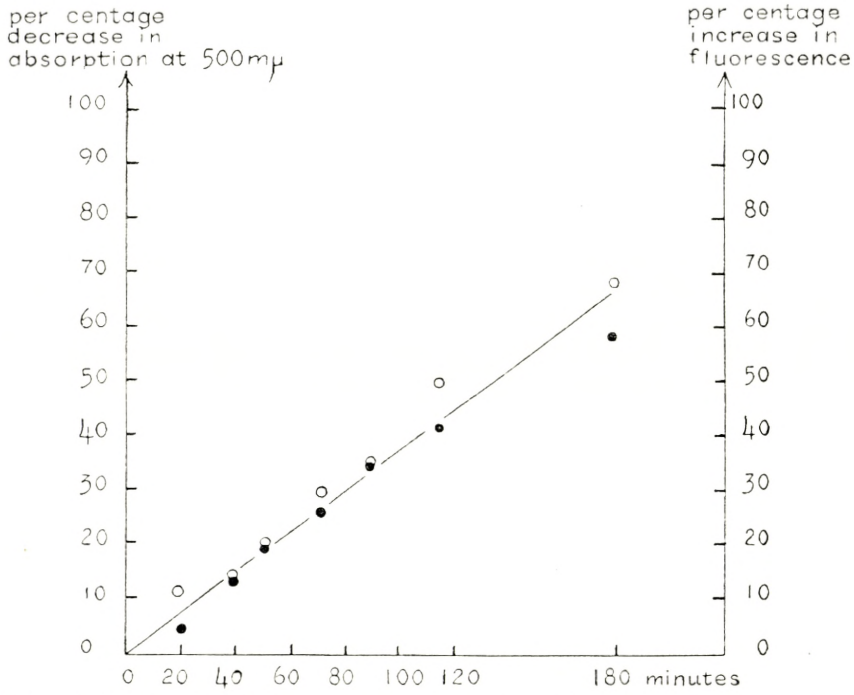


Figure 5. The relation between the disappearance of the aldehyde group and the increase in fluorescence during incubation with 2-amino-4-hydroxy-6-formylpteridine with xanthine oxidase. Abscissa: time of incubation. Ordinate: increase in the fluorescence of aldehyde solution (Ō) and decrease in absorption (at 500 mμ) of alkaline phenylhydrazone (●), expressed in percentages of terminal changes (after 24 hours).

times with the equal volumes of butanol (saturated with the appropriate buffer solution). After each extraction small samples were taken from the aqueous layer and were blown out into 0.1 M pyrophosphate buffer pH 9.0 and the fluorescence of these solutions was measured. The logarithm of the fluorescence was plotted against the number of extractions (cf. fig. 6).

The same technique was used in the extraction of the unreacted aldehyde. In this case, however, also a determination of the concentrations of the aldehyde present in the final pyrophosphate solutions was performed by enzymatic differential fluorometry. When the logarithm of these concentrations is plotted against the number of extractions a straight line is obtained. The slope of this line gives a specific value for the distribution coefficient

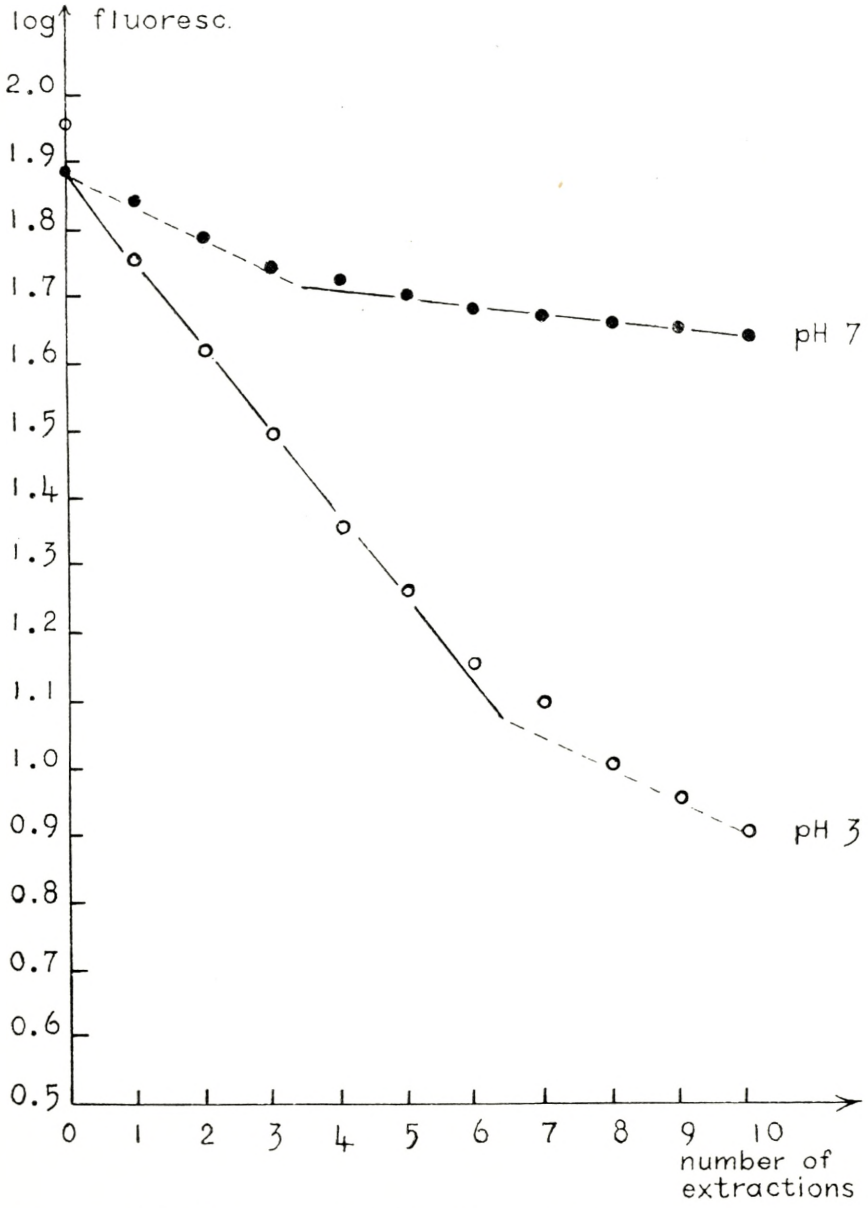


Figure 6. Butanol extraction of buffer solutions containing enzymatic digest of 2-amino-4-hydroxy-6-formylpteridine (about 1×10^{-6} moles per ml). ○ extraction at pH 3.0 (citrate buffer). ● extraction at pH 7.0 (phosphate buffer). Abscissa: number of extractions with equal volume of butanol. Ordinate: the logarithm of the fluorometer readings of the aqueous phase at pH 9.0 (pyrophosphate buffer).

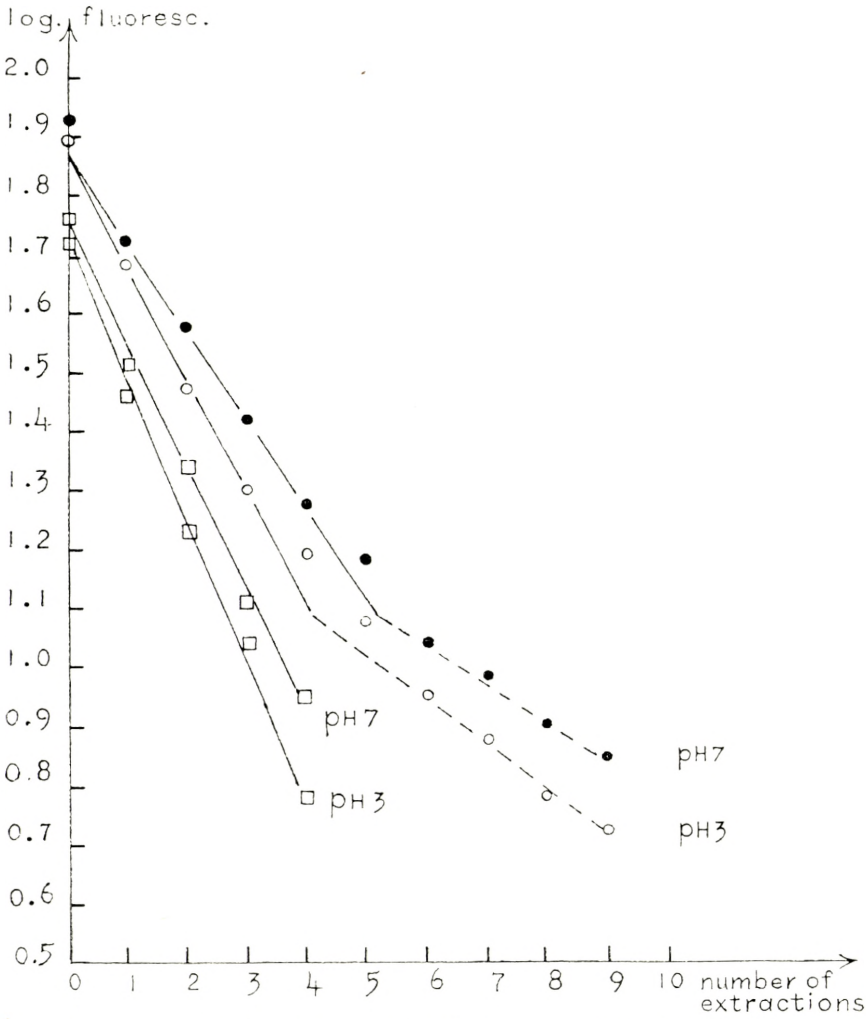


Figure 7. Butanol extraction of buffer solutions containing 6-amino-4-hydroxy-6-formylpteridine (about 1×10^{-6} mole per ml). ○ extraction at pH 3.0 (citrate buffer). ● extraction at pH 7.0 (phosphate buffer). Abscissa: number of extractions with equal volume of butanol. Ordinate: the logarithm of the fluorometer readings of the aqueous phase at pH 9.0 (pyrophosphate buffer). □ the amount of the aldehyde present in the aqueous phase during extraction (at pH 3.0 and at pH 7.0, respectively) as measured by increase in fluorescence due to enzymatic conversion. Ordinate: the logarithm of the increase in the fluorescence of the aqueous phase at pH 9.0 (pyrophosphate buffer).

of the aldehyde, independent of the possible presence of other fluorescent compounds in the solution (cf. fig. 7).

The curve obtained from the extraction experiments can be

interpreted on the following assumption. When the logarithm of the fluorescence of a solution of the aldehyde is plotted against the number of extractions, according to the law of constant distribution, a straight line should be obtained. The slope (a) of the line gives a value for the distribution coefficient (K), which can be calculated from the equation: $K = \frac{1}{10^{-a} - 1}$.

As is evident from the figures, some of the curves obtained may conceivably have been made up of two straight lines. This indicates that the corresponding solutions contain two fluorescent components, the distribution coefficients of which can be read from the slopes of the two lines, respectively.

It can be concluded from the extraction curves of the experiment with the aldehyde that the preparation contained two fluorescent components both of which have about the same solubility in butanol at pH 3 and at pH 7. It also appears that the fluorescent component which is most soluble in butanol and which corresponds to the curves with the greatest slope is identical with the aldehyde, as these curves have about the same slope as the curves obtained from the enzymatic estimation of the amount of aldehyde present in the final solutions. The occurrence of the curves having the slightest slope may possibly be ascribed to the presence of fluorescent impurities.

The solution containing the enzymatic conversion product of the aldehyde also contains two fluorescent components, as appears from fig. 6. From the points of intersection of the lines with the ordinate the proportion between the fluorescence of the two components in the original solution can be calculated thus, the fluorescence of the substance which is most soluble in the aqueous layer at pH 7 (K is about 44) and the fluorescence of that which is least soluble in the aqueous layer pH 3 (K is about 2.5) are calculated to amount in both cases to about 70 per cent of the fluorescence present in the original solutions. These two components, consequently, must be identical. The proportion of solubilities of this component is characteristic of an organic acid with $3 < pK < 7$. The other fluorescent substance present in these solutions is supposed to be identical with the non-aldehyde component found in the aldehyde preparation since these two compounds exhibit about the same solubility in the two solvents.

It appears from these extraction experiments that by enzymatic conversion of 6-aldehyde only one fluorescent substance is formed and that this has acidic properties.

Reduction of Methylene Blue.

Using the methylene blue technique as previously mentioned (6) the amount of hydrogen released during the conversion of the 6-aldehyde was measured. The experiment was performed under strictly anaerobic conditions in 0.1 M pyrophosphate buffer pH 9. The following controls were run: 1) Aldehyde plus methylene blue 2) enzyme plus methylene blue. From figure 8 it is seen that on the assumption that two hydrogen atoms are taken up per mole of the methylene blue preparation used, about 0.75 moles of hydrogen are transferred per mole of aldehyde when the aldehyde is converted into the acid.

Conclusion and Discussion.

From the experiments mentioned above it appears that when 2-amino-4-hydroxy-6-formylpteridine is enzymatically converted the aldehyde group disappears and an acidic group is formed. From the methylene blue experiment it appears, moreover, that the reaction is a dehydrogenation. The fact that apparently not 1.0 but only about 0.75 moles of hydrogen are transferred per mole of aldehyde might be partly due to common experimental errors and partly to impurities in the methylene blue and in the aldehyde preparation used. The reaction therefore is supposed to be an aldehyde dehydrogenation. In conformity with LOWRY *et al.* (2) the reaction product is concluded to be 2-amino-4-hydroxy-6-pteridine carboxylic acid.

From the absorption spectra of the 2-amino-4-hydroxy-6-formylpteridine it might be assumed that it exists in two tautomeric forms, the prevailing form being dependent on the pH of the solution in which the compound is dissolved. It seems reasonable to assume that the tautomerism is an enol-keto shift at position 4 in the pteridine molecule. The enol form then should be present at pH 9 and at more alkaline reactions. As the curves

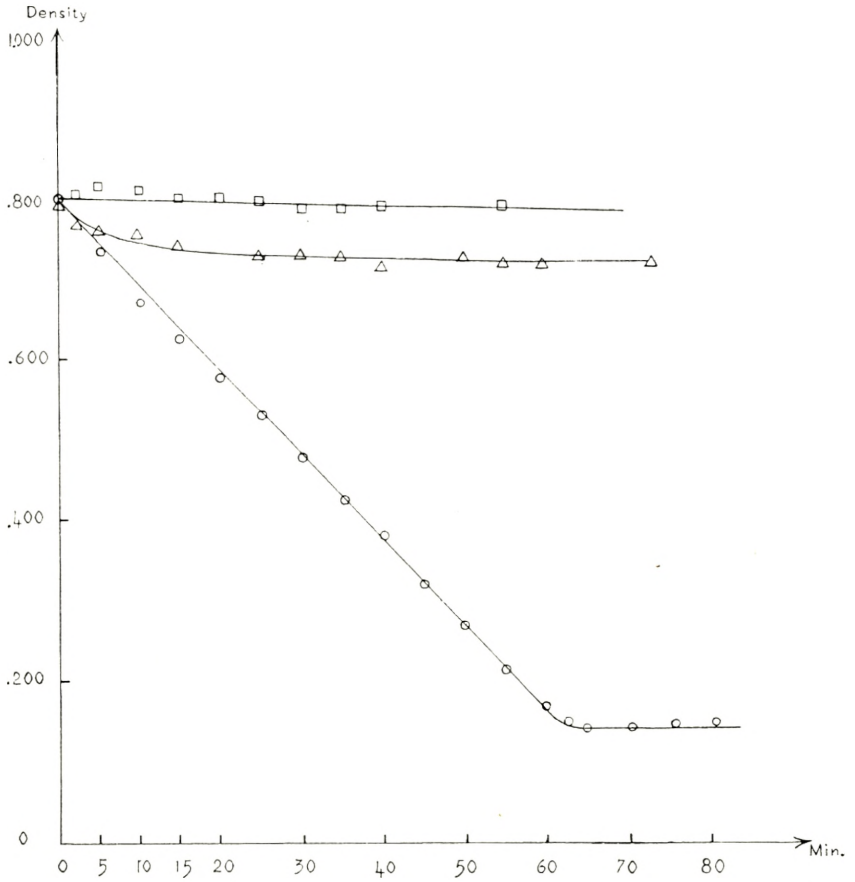


Figure 8. Reduction of methylene blue under anaerobic conditions. 2-amino-4-hydroxy-6-formylpteridine: 1×10^{-8} mole per ml, methylene blue: 1×10^{-8} mole per ml, xanthine oxidase: about 1.5 mg of protein per ml, buffer: M/10 pyrophosphate pH 9.0. ○ Enzyme plus aldehyde plus methylene blue. △ Enzyme plus methylene blue. □ Aldehyde plus methylene blue. Abscissa: time of incubation in minutes. Ordinate: density at $\lambda = 660$ mμ. Measured in a Coleman spectrophotometer.

of the acid have about the same characteristics as that of the aldehyde at pH 9 (and this is even more pronounced at more alkaline reaction) it is possible that the acid is present only in the enol form at pH 3 and at more alkaline reaction.

I am greatly indebted to Dr. H. M. KALCKAR for valuable suggestions and guidance in the performance of the experiments and for the preparation of the manuscript.

Summary.

1. 2-amino-4-hydroxy-6-pteridylpteridine(6-aldehyde) is oxidized by xanthine oxidase from milk to the corresponding acid. The oxidation is characterized partly by the disappearance of the aldehyde group and partly by the formation of an acid group and finally by the reduction of methylene blue under anaerobic conditions.
2. The aldehyde is supposed to exist in two tautomeric forms (in an enol and in a keto form) according to the pH of the solvent.

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Institute of Cytophysiology,
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BY

O. HAGERUP

København
i kommission hos Ejnar Munksgaard
1951

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POLLINATION IN THE FAROES - IN SPITE OF RAIN AND POVERTY IN INSECTS

BY

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København
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1. The Problems.

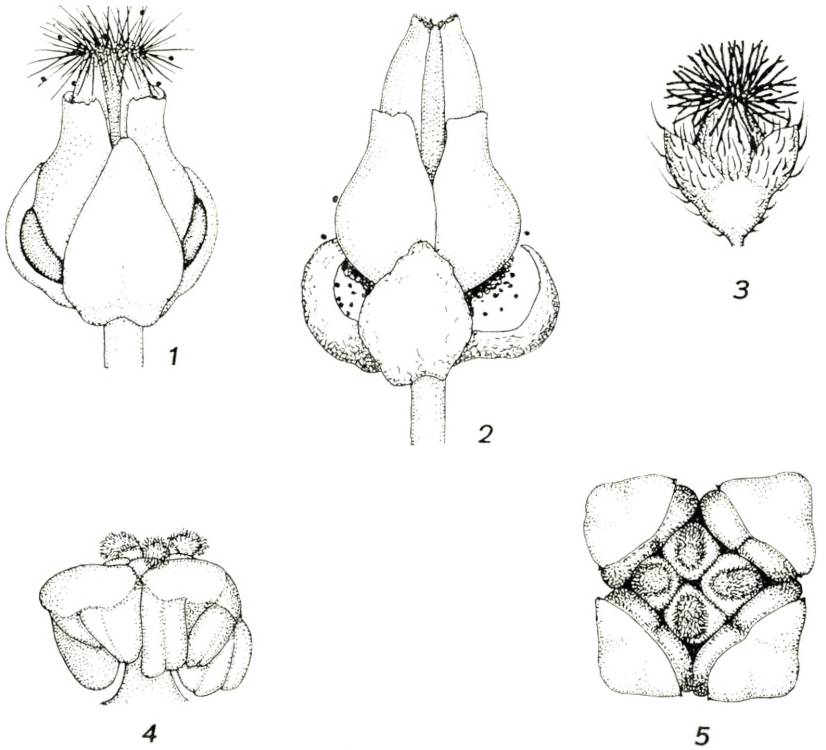
During a stay in the Faroes in 1922—23 it struck me that a number of plants were found there which in Denmark were considered typical entomophiles, such as *Calluna, Lychnis flos cuculi, Ranunculus* species, *Hypericum pulchrum, Armeria*, and others. But in the Faroes bees and butterflies are nearly completely absent, or they are present in so small numbers that they practically do not play any part in the pollination. In nature in the Faroes there are therefore particularly good opportunities to investigate the importance of insects for pollination.

From observations in nature in Denmark one is easily tempted to form a high estimate of the importance or even the absolute necessity of insect pollination; but conditions in the Faroes, Greenland, and other regions in the north poor in insects made me doubt the universal validity of the views mentioned above. During a stay in the Faroes in 1947 it proved that some plants can be pollinated in several different ways, which are realized in accordance with conditions in the various habitats. Thus *Calluna* in Denmark is mostly pollinated by bees and butterflies, but this does not take place in the Faroes. Other species are self-pollinating if cross-pollination fails.

In what follows instances will be adduced of conditions of pollination in a typical Faroese locality, viz. the neighbourhood of Thorshavn, where I have examined practically all the species growing in the environs of the town within a radius of up to one mile.

The world of insects is remarkably poorly represented in the Faroes, as appears from the list of names in Nielsen (1908). Very few species are present in so great numbers of individuals that they can be of any importance to the pollination worth mentioning. During a month's stay in the Faroes in the middle of

the flowering season (July 1947) I observed neither humble-bees (*Bombus*) nor honey-bees (*Apis*). In the same period only one butterfly was present in rather a large number, viz. the little grey *Cidaria albulata* SCHIFF. (*Geometridae*), but this rarely sucks



Figs. 1—5. Anemophilous flowers. Figs. 1—2, *Triglochin palustre* at a female (fig. 1) and a male stage (fig. 2). ×12. Fig. 3, *Urtica dioica*. ×40. Figs. 4—5, *Potamogeton polygonifolius*, side view (fig. 4) and seen from above (fig. 5). ×12.

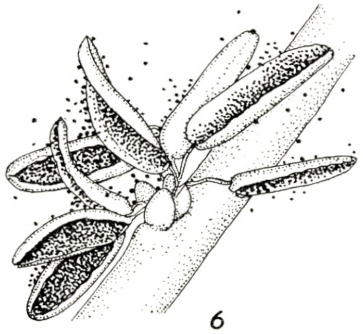
honey from the flowers. Because of the small numbers in which they occur neither bees nor butterflies nor most of the other large insects usually occurring in the Faroes are of any appreciable importance for the pollination.

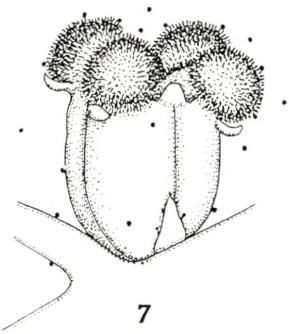
The flies are an exception. Travelling in the Faroes one arrives at the result that the only insects present in so great amounts that they can really play any part in the pollination, are certain rather big flies (*Diptera*).

The importance of the flies, however, is remarkably restricted by the fact that generally they are abundant only in rather sharply

defined localities, which again is due to the conditions of breeding of the flies.

Certain significant rather large species are particularly found near the dwellings of man, where dung and refuse from animals and man are present. (The dunghills are not covered.) On the bird-cliffs, too, the insects are attracted by the dung; finally in places where seaweeds are rotting, e. g. on low beaches and on cultivated fields.





Figs. 6—7. Anemophily in *Myriophyllum alterniflorum*. Male (fig. 6) and female (fig. 7) flower. ×20.

The dung of the sheep is so widely spread on the mountains that there is almost no pollinating insects (only a few flies) or —in certain places—no pollinating insects at all.

There is, therefore, a remarkably great difference between the vegetation on isolated, uncultivated mountains and the flora growing near the villages (the home-field), on the bird-cliffs, and on low beaches. These differences are of course chiefly conditioned by the supplies of dung, but also by the flies, as certain plants the fructification of which succeeds only after pollination by flies, are particularly found in the three localities mentioned, but are rarer or completely absent in the hill pastures.

Pollination by flies is, however, greatly influenced by rain and gales, which for a long time can prevent the activities of the insects. During storms the animals sit still and hide e. g. in the nodding flowers of *Ranunculus acer*, or they allow the rain to pour down upon them in the open flowers of *Archangelica*.

The rain may last for days. In such cases the plants must be capable of self-pollination without the assistance of insects.

We shall therefore examine the individual species and shall see that most Faroese species can really have autogamy, as already suggested by WARMING (1908).

2. Wind Pollination.

Numerically the Faroese vegetation is dominated by *Gramineae*, *Cyperaceae*, and *Juncaceae*. Some of these may be autogamous, but most of them are anemophilous. There is always plenty of wind in the Faroes. The value of this way of pollination is, however, greatly reduced during the constant and prolonged heavy showers of rain, which beat the suspended pollen to the ground.

The defects of wind pollination are illustrated in an interesting manner by conditions within the genus *Empetrum*, represented in the Faroes by two species, which often grow promiscuously. They are closely related, but *E. nigrum* has unisexual flowers, while *E. hermaphroditum* is bisexual. The latter fructifies abundantly, because its flowers either pollinate themselves or receive pollen from neighbouring flowers on the same shoot.

The pollen of the dioecious species must be transported a relatively long distance through the air, and the defects of this method of pollination manifest themselves in the fact that the species fructifies poorly in the Faroes. In Denmark, where conditions of the weather are much more favourable to wind pollination the same species mostly fructifies abundantly.

In spite of the difficulties of wind pollination, many Faroese species are exclusively anemophilous. This is unmistakable e. g. in the protogynous flowers (or inflorescences) of *Potamogeton polygonifolius* (figs. 4—5), *Triglochin palustre* (figs. 1—2), *Myriophyllum alterniflorum* (figs. 6—7) and *Plantago major*, the methods of pollination of which, for that matter, are well-known.

Potamogeton polygonifolius POURR. figs. 4—5.

Such amounts of pollen are transferred that the whole inflorescence is powdered over. Furthermore there is a great waste of pollen, which floats on the surface of the water. In this way there will hardly be any pollination as the spikes are raised out of the water during the flowering. Mostly few of the carpels are pollinated. This may be due to the fact that the flowers producing

pollen are situated below the flowers which are in a female stage.

Juncus squarrosus L.

The large protogynous flowers are wide open and during rain are filled with water. Great quantities of pollen may be found everywhere in the interior of the flower after a shower. In not a few cases, however, the flowers were visited by flies. Still, wind pollination is no doubt the commonest method of pollination,

Figs. 8—9. Anemophilous flowers. Fig. 8, *Agrostis canina*, ×18. Fig. 9, *Rumex domesticus*, ×13.

even though the other methods may now and then be used. In many flowers the ovary withers without developing seeds.

Many species of *Glumiflorae* have not only a chance of wind pollination when the flower opens in favourable weather; but if they are homogamous there is also a valuable possibility of autogamy (see fig. 8). As most of the species have dense inflorescenses, they may also have geitonogamy. The fact that there are so many different possibilities must involve increased certainty of obtaining a favourable pollination in spite of the fact that conditions are both variable and often direct unfavourable.

The possibility of wind pollination even at comparatively long distances is seen in *Rumex* (fig. 9), among the species of which (*R. domesticus, crispus, obtusifolius, acetosa, acetosella*) there are frequently hybrids.

Plants with unisexual flowers also show the value of wind pollination, e. g. *Callitriche*, *Atriplex glabriusculum*, *Litorella*, and *Urtica dioica* (fig. 3).

Furthermore wind pollination is found in *Oxyria digyna*, *Thalictrum alpinum*, and occasionally in *Calluna*.

Within the family of grasses autogamy is found e. g. in *Poa annua*, the flowers of which are nearly always closed. Cross-pollination is typical of protogynous species, e. g. *Alopecurus pratensis*.

In *Festuca rubra* the spikes are non-absorbent because they are covered both with hairs and a thin layer of wax. Therefore open flowers are not spoilt by rain. The relation to rain of the other common grasses requires further investigation.

3. Insect Pollination.

In accordance with the statements above as to the areas of distribution of pollinating insects, entomophilous plants are found remarkably locally, and furthermore are few in number.

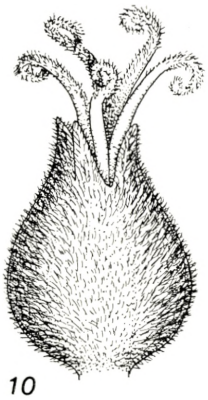
As mentioned above, most of these flowers are particularly found near (1) inhabited places, (2) bird-cliffs, and (3) low beaches with rotting seaweed and animals.

Such plants as can only be pollinated by bees, butterflies, and wasps are not found in the Faroes. The possibility of other forms of insect pollination in this climate, which is so difficult to insects, is clearly illustrated by the fact that some of the entomophilous plants are dioecious (e. g. *Melandrium dioicum*, *Sedum roseum*) and by the fact there is a hybrid, *Orchis maculatus* × *O. purpurella*. The pollinators in this case are flies.

The only insects playing any quantitative role as pollinators worth mentioning are a few big flies. A list of the names of these is found in I. C. Nielsen (1908). There are also many small *Diptera* occurring abundantly in damp places and e. g. seen continually on the leaves of *Pinguicula*. It is particularly a question of various *Chironomidae*, which are also often found sticking to the stigmata of *Orchis*, the honey of which they have tried to get at in the spur. The wings of the insects then have touched the stigmata, but the animals cannot pollinate the flower as they are too small to remove and transport the pollinia.

Archangelica officinalis HOFFM.

This is the Faroese species whose fly pollination is most easily observed. Even at a distance one may often observe a dark layer of insects covering the inflorescences. It is found either near inhabited places or on bird-cliffs, where also *Angelica silvestris* and *Haloscias scoticum* can be found. All these three *Umbelliferae* are pollinated by flies (WARMING 1908, p. 1060).



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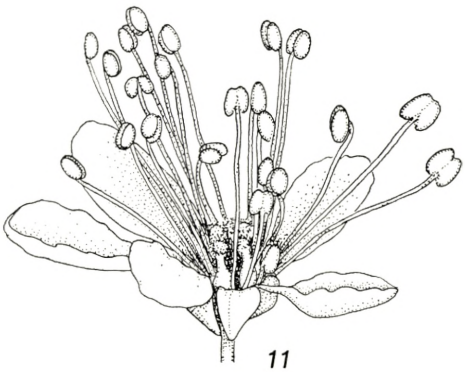

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Fig. 10. *Melandrium dioceum*. Female flower (corolla removed), ×3.
Fig. 11. *Filipendula ulmaria*, anemophilous flower, ×5.

Geranium silvaticum L.

This is also found both on bird-cliffs and near inhabited places where numerous flies swarm about it. Only on one single occasion I have seen a flower pollinate itself by direct contact between anther and stigma. Flowers which are isolated in a room do not fructify. Often some of the flowers are unisexual, and in the bisexual flowers the anthers are turned away from the stigmata so that visits by insects must normally be considered necessary for pollination.

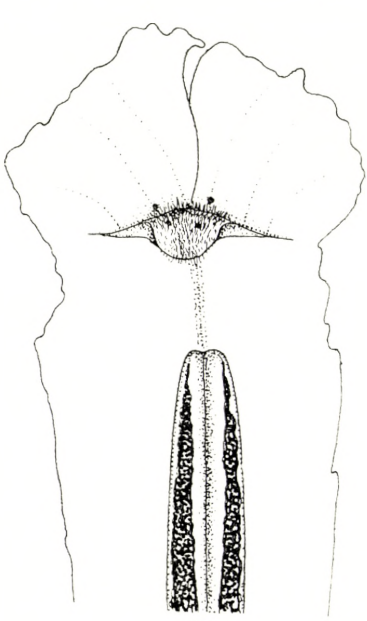
Melandrium dioecum L. (fig. 10).

This also grows in the fly areas on bird-cliffs and near inhabited places. The corollas are conspicuous and spread out flat so as to form a convenient landing-place for the flies, which easily strike against the projecting anthers or stigmata. The stigmata are twisted and long so that the flies can hardly avoid touching them when landing on the flower. During pairing flight the flies

roam about fast between the male and female flowers as very effective pollinators.

Filipendula ulmaria L. (fig. 11).

In accordance with the pollination by flies the plant is particularly found near inhabited places. The fragrant and conspicuous flowers are frequently visited by flies which with vigorous



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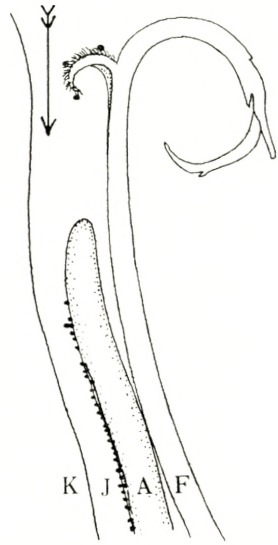

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Figs. 12—13. *Iris pseudacorus*. Fig. 12, style seen from below. Fig. 13, longitudinal section of style (F) and anther (A). The arrow indicates the route of the insect (J); K, corolla. ×3.

movements work about the inflorescences touching the anthers, the light pollen thus being shaken out in all directions so that it can both hit the flower itself (autogamy), the neighbouring flowers (geitonogamy), or the flowers below. Furthermore the insects are powdered over and may perform normal entomogamy.

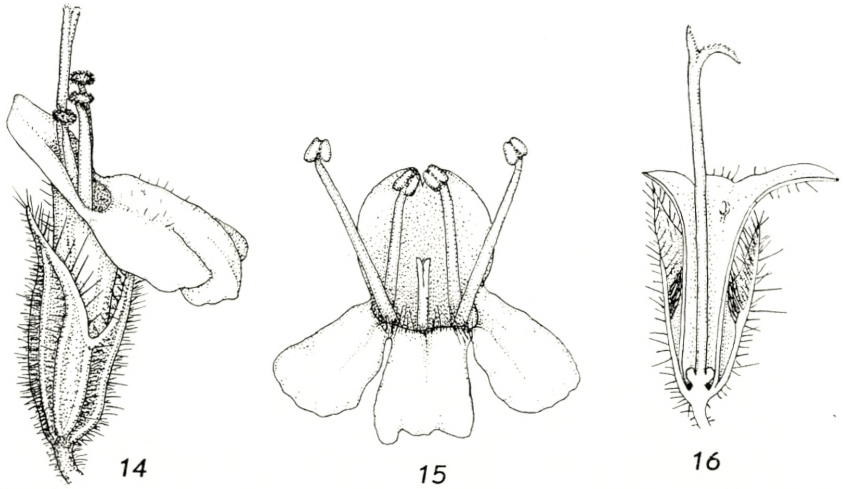
In Denmark the plant is pollinated as in the Faroes.

No doubt wind pollination is of the greatest importance for the flowers. If these are shaken, clouds of pollen are thrown into the air from the long and mobile stamens. In the damp Faroese climate this method of pollination is hardly so secure as in Denmark.

Iris pseudacorus L. (figs. 12—13).

The pollination takes place in the well-known way that flies crawl down into the cleft between style (F) and perianth (K). The route of the insect is in fig. 13 indicated by an arrow. There the animals have a good hiding-place during any kind of storm. Homogamy.

Thymus serpyllum L. var. *prostrata* HORNEM. (figs. 14—16). Even in purely female flowers (fig. 16) there is often pollen



Figs. 14—16. *Thymus serpyllum*. Fig. 14, bisexual flower at the female stage. Fig. 15, bisexual flower at the male stage. Fig. 16, female flower. ×6.

on the stigma. Visits by insects have been observed by both WARMING and me. The plant has plenty of nectar and the big *Eristalis intricarius* may be seen crawling over the dense inflorescences.

In the bisexual flowers the anthers dehisce first,—already while the style is still quite short (fig. 15). Later the style grows up among the anthers and the stigmas spread out so that autogamy may be obtained if insect pollination should fail.

Orchis maculatus L. (figs. 17, 19, 57).

The very complicated structure and function of the flower has rightly made it an object-lesson of insect pollination; but MARTENS (1926) has shown that even this ingenious flower may have autogamy like a number of other orchids. In the Faroes, where

O. maculatus is very abundant, I have been unable to find any form of self-pollination in this species; but still numerous fruits develop without any visits by bees and butterflies.

Observations in nature by R. RASMUSSEN and me have shown that *Orchis* is visited and pollinated by a big and long-haired fly, *Eristalis intricarius* L. (fig. 57), which strangely resembles a small dark humble-bee, a resemblance expressed in the synonym *Eristalis bombyliformis* FABR. This big beautiful fly can easily pull out pollinia and carry them to the stigmata of other flowers.

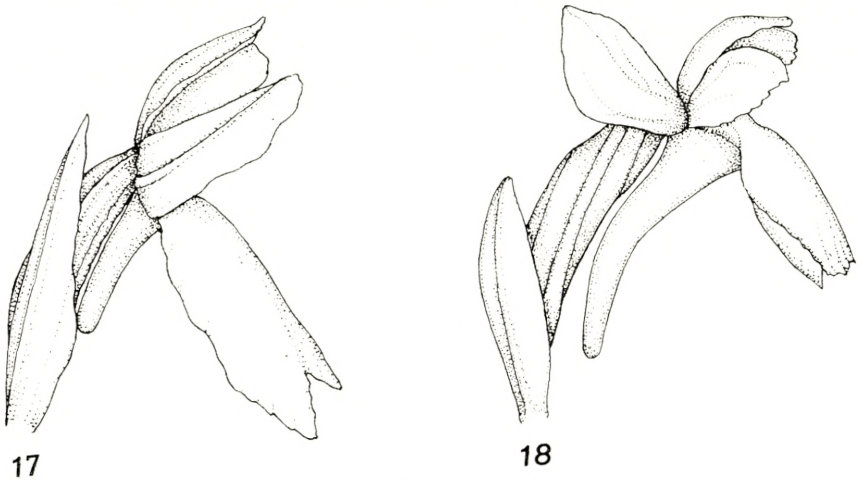


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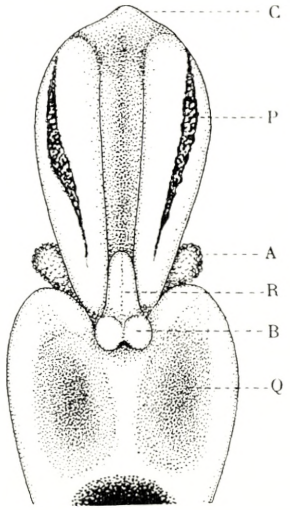
Fig. 17. *Orchis maculatus*; exterior perianth leaves directed forward. Fig. 18. *Orchis purpurella*; exterior perianth leaves directed backward. × 3.

On a single occasion I have also seen the minor species, *Eristalis lucorum* MEDG. on the flowers.

Eristalis intricarius is nearly 1½ cm long and just under 1 cm broad. The body is densely set with long stiff hairs, which make it non-absorbent; but the insect prefers flying in dry weather and then sweeps fast through the air in wide turns. It breeds in damp places, preferably near human dwellings. During the pairing flight it generally lands on the large leaves of *Caltha*; but when the insect wants to eat it roams about and searches many different flowers, e. g. *Ranunculus*, *Thymus*, *Orchis*. This fly is perhaps the most important of all the pollinating insects in the Faroes. It also occurs in Denmark and is distributed from Northern Scandinavia to Italy. Without it the magnificent abundance of *Orchis* flowers was hardly found in the Faroes.

The Faroese form of *O. maculatus* has so short a spur that its bottom can be reached by the proboscis of the fly. This can be stretched out remarkably far (3—5 mm), so that the fly can easily reach the bottom of the spur when squeezing its head into the flower, which is thus pollinated in the usual way. On the very hairy head of the fly there is a hairless spot at the very place where the adhesive disk of the pollinia is touched and sticks fast (fig. 57).



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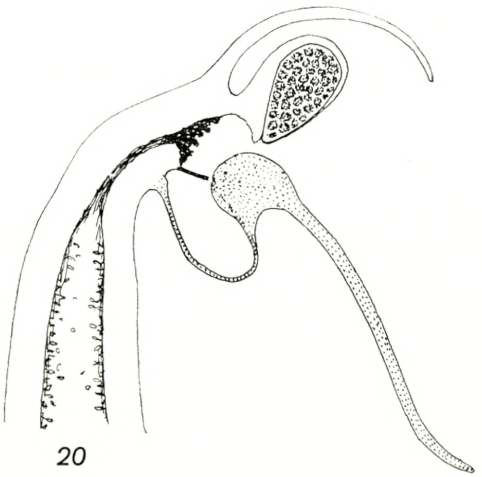

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Fig. 19. *Orchis maculatus*. Flower with perianth leaves removed. A, auricula; B, bursicula; C, anther; P, pollinium; Q, stigma; R, rostellum. ×20.
Fig. 20. *Habenaria viridis*. Median longitudinal section through flower. Entrance to spur closed with membrane (black). ×16.

The Faroese *Orchis maculatus* flowers further seem to be especially adapted to hold their own in rainy weather; for they are assembled much more densely than on the Danish plant. Therefore the lip of one flower hangs as a protecting roof over the flower below, and drops of rain trickle from one lip to the next without penetrating into the interior of the flowers. Not rarely it happens that some of the flowers in the short dense spikes cannot get room enough to unfold themselves completely. The outer leaves of the flower then cannot bend back as is normally the case, but are directed forward so that they, too, can protect the interior of the flower from drops of rain coming from the side. This forward-directed position is also particularly con-

spicuous in *Coeloglossum* (*Habenaria*) *viride*, which looks as if the flower is always in bud.

Coeloglossum (*Habenaria*) *viride* L. (figs. 20—24).

The entrance to the flower is extremely narrow so that only the heads of small insects can be introduced into it. That the flower has come out at all only appears from the fact that the long narrow lip hangs obliquely downwards when the flower can be pollinated. The narrow aperture of the flower somewhat reminds of the entrance to a mouse-trap and it may be surmised that a visiting insect must struggle to get out of the flower, there being thus a greater chance of having some pollinium removed.

The flower being nearly completely closed does not mean that it is autogamous, at any rate not always. I have found a few pollinated flowers which had all of their own pollen situated in its original place, for which reason the pollen found on the stigma must have been transferred from another flower by an insect. I have not, however, seen any insect visit the flowers. There are still some traits missing in our knowledge of the biology of this strange species. An account of these will be published later.

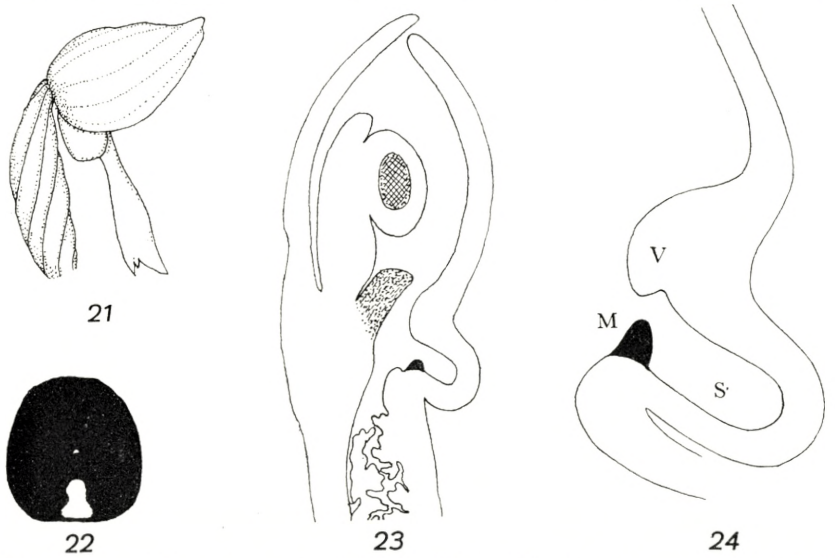
In order to examine the peculiar short spur from which the plant has got its name, I cut some series of sections medianly through the flower. It then appeared that the broad entrance to the saccate spur is closed with a thin membrane, a fact which has never been recorded from any other orchid.

In order to get hold of the nectar in the spur, the visiting insect must first squeeze its proboscis through the membrane, which effort increases the chance that the insect both receives and gives off pollen. It is not necessary, however, that it should be insects with pricking mouth-parts which perforate the membrane, for such insects do not occur in the Faroes, where all the pollinated flowers examined had a burst membrane. Direct observation in nature has provided interesting information of the process of the visit by the insect (Silén, 1906). Only when a non-pollinated flower begins withering (with age) the membrane bursts without the action of insects.

The morphology of this peculiar spur was examined in series of young stages of development. The membrane is started very early as a nearly crescent-shaped circular pad round the entrance

to the spur so that the membrane is broadest at the back and has a narrow aperture in front. In the full-blown flower the membrane covering the entrance to the spur looks as shown in fig. 22, where the perforation is white. It is somewhat triangular in shape and is situated in front.

The lip is peculiar by having a median vertical pad at the base of the upper side. This pad swells greatly during the flowering



Figs. 21—24. *Habenaria viridis*. Fig. 21, flower. Fig. 22, the membrane (black) over the entrance to the spur is perforated in front. ×12. Fig. 23, median longitudinal section of young flower with initial development of the membrane (black). ×28. Fig. 24, median longitudinal section through spur (S) with initial development of membrane (M); V, circular pad. ×50.

season, thus forcing the lip down vertically when the flower comes out. It projects over the hole in the membrane, which thus becomes more difficult to find by a visiting insect.

The inconspicuous flower of *Coeloglossum* thus makes a fresh contribution to the curious pollination biology of the orchids.

Habenaria albida L.

For comparison it may be mentioned that *Habenaria albida* (L.) has a short saccate spur similar to that of *Coeloglossum*, but it is not closed with a membrane. Preliminary investigations of *H. albida* made in Denmark show that the flowers are autogamous and accordingly have a rich fructification. Conditions of pollina-

tion need further investigations and therefore will be discussed in a paper to be published in the future.

Caltha, *Ranunculus*, and *Calluna*, which have previously been described (Hagerup 1950) should be mentioned among the entomophilous plants. Particular attention should be given to the pollination by means of *Thrips*, which was previously nearly unknown, but which is probably rather widely distributed and valuable, e. g. in *Compositae*. In the Faroes *Thrips* thus was found in a number of flowers the pollination of which seems somewhat puzzling, e. g. *Silene acaulis*, *Armeria*, *Leontodon*, and others which need further investigations.

4. Geitonogamy.

In most plants with fairly large, dense inflorescences it cannot be avoided that neighbouring flowers should pollinate each other. This applies to *Glumiflorae*, *Rumex*, *Filipendula*, and others, thus both anemophilous and entomophilous plants. Geitonogamy is particularly conspicuous in *Umbelliferae*, where flies crawl from flower to flower all over the umbel.

Cornus suecica L. (fig. 26).

The stamens are directed obliquely outward and half way over the adjoining flowers so that the heavy pollen will drop direct on to the stigmata when the flowers are shaken by wind, insects, or rain. The fructification is abundant in the centre of the inflorescence, where most of the anthers are assembled. The marginal flowers are often sterile.

The flowers are non-absorbent, surplus rain water being drained off along the stalk of the inflorescence, which is remarkably stiff, grooved, and hairy, a fact which reminds of the rain pollination in certain *Ranunculaceae* (Hagerup, 1950).

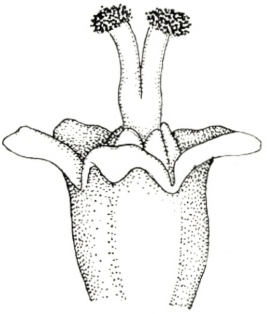
Leontodon autumnalis L.f. *nigro-lanata* Fr. (fig. 27).

The pollination takes place already when the first corollas open; for when the flower head takes up its night position it closes and then all the long projecting styles, which have pollen on the outside, are squeezed among each other in a dense con-

fusion so that they cannot avoid having the pollen of the neighbouring flowers left on their stigmata.

Furthermore autogamy will easily take place, because the two long stigma lobes have papillae right out to their margins, where pollen has often stuck fast when the styles grew out among the anthers.

Particularly in the centre of the flower head there are often exclusively female flowers and the fructification is poor.



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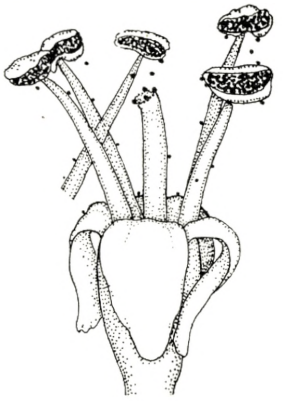

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Fig. 25. *Matricaria ambigua*. The flower's own pollen is seen on the apical stigma. ×20.
Fig. 26. *Cornus suecica*. Geitonogamy. ×12.

In Denmark the pollination takes place in a way similar to that in the Faroes. Here, too, visits by big insects are comparatively rare; but *Thrips* individuals are often found in the flowers.

5. Autogamy.

In the Faroes there is a good number of flowers characterized both by fragrance, colour, and size; but in spite of this the insects present are not attracted. Many of the most beautiful flowers of the Faroes call in vain and are not visited by insects. In many conspicuous flowers a visit by insects would, indeed, be in vain because the flower pollinates itself either (1) before, (2) during, or (3) after flowering, when the corolla has withered and the beauty is gone. Such futile visits by insects are, however, of frequent occurrence. Thus a fly may settle almost anywhere on

a plant or other objects without this visit necessarily having anything to do with pollination. Therefore visits by insects and pollination should not be identified as a matter of course.

Still, one of the rare and accidental visits by insects may, to a normal autogamous flower, mean a chance of cross-pollination, which perhaps is not always without importance.

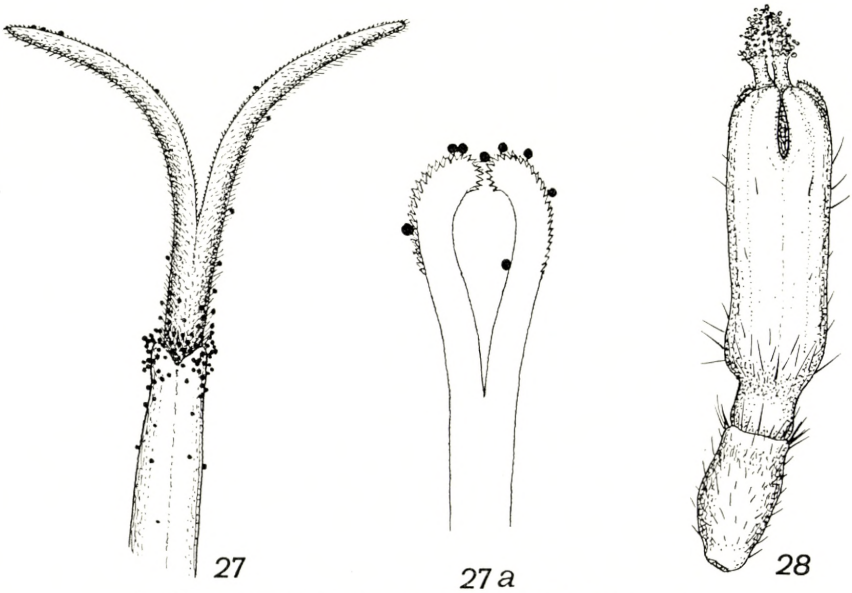


Fig. 27. *Leontodon autumnalis*. Stigma and anthers. ×25.
Fig. 27 a. *Bellis perennis*. Longitudinal section of stigma.
Fig. 28. *Bellis perennis*. Projecting stigma covered by the flower's own pollen. ×25.

A. Pollination after Flowering.

Hypericum pulchrum L. (figs. 29—30).

At a first view of this large, pretty flower it is tempting to assume insect pollination. Indeed, I have on rare occasions seen a fly moving about the long erect stamens in search of nectar. But it soon disappeared, and visits by insects are of no value for the pollination as the anthers are closed and the stigmata unable to receive pollen as long as the flower is open. In spite of assiduous search the pollination of this flower long continued being a puzzle to me.

The fructification is perfect. Every flower develops a large capsule which remains on the plant during the winter until the next flowering season or sometimes still longer (two years). Strangely enough the withered corolla (as on *Calluna* and *Erica*) remains round the wintering capsule.

During the flowering both the corolla and the outer stamens are spread out horizontally; but when the flower for a few days has in vain displayed its tempting beauty, the corolla rather

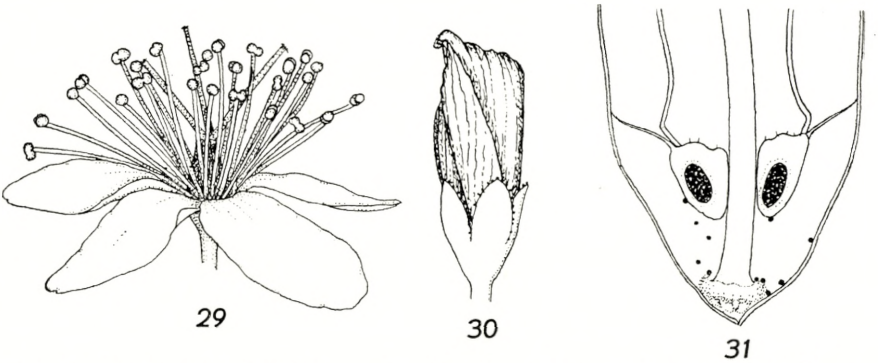


Fig. 29—30. *Hypericum pulchrum*. Fig. 29. Before pollination the flower is open, but the anthers are closed. ×3. Fig. 30. At the stage of pollination the corolla is closed, but the anthers have dehisced. ×3.
Fig. 31. *Erica cineria*. Longitudinal section of bud in autogamy immediately before it comes out. ×12.

suddenly closes tightly by the perianth leaves standing up vertically, and by the withering movements the tips of the corollas twist themselves round each other so as to form a remarkably firm knot, which is not opened later. The bases of the corollas do not work loose, and the stamens remain in their original places. By the vigorous movements of the withering corolla all the stamens are squeezed densely together into a bunch in the centre of the flower, where the three styles are also imprisoned and are squeezed in among the stamens, whose anthers do not dehisce until then. The interior of the withered flower thus is filled with pollen and at the same time the stigma becomes susceptible to pollination, which is performed with automatic certainty. Without any inconvenience caused by bad weather the stigmata are covered with pollen and the fructification is secured.

The Faroese plant is a special variety. It should be investigated how the species is pollinated in other countries, in particular whether it may also have a chance of cross-pollination.

Some individuals were planted in the Botanical Garden of Copenhagen. The plants throve and in the flowering season (in 1949) the weather was both dry and warm with plenty of sunshine. Under these conditions unusual to a Faroese plant, the flowers opened much more than in their native country so that the petals even were somewhat retrorse. It is, however, of special interest that the anthers were open already during the flowering (thus not only when the flower had faded, as in its native country), i.e. that the pollen on possible visits by insects had a chance of being transferred to other flowers and pollinating these. There is no chance like this in the comparatively damp and cold Faroese climate poor in insects and sunshine, in which the flower is autogamous.

Lychnis flos cuculi L. (figs. 33, 34).

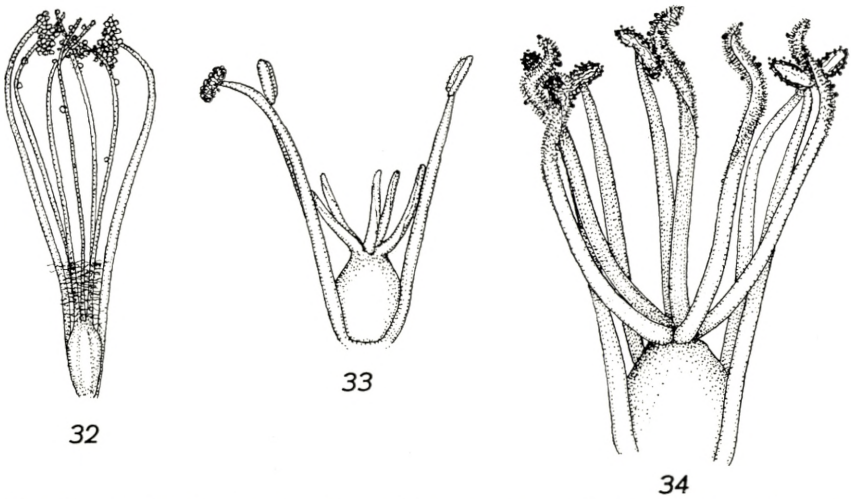
This well-known large, beautiful flower embellishes the Faroese meadows and fields in such a way as to suggest entomogamy. It was, however, impossible, in spite of intense search, to ascertain the occurrence of visits by insects. Furthermore, the flower is so deep that none of the insects present have proboscises long enough to reach the bottom of the calyx. Consequently the flower must somehow be autogamous.

Knuth has a long list of insects which in countries farther south visit the flower, but it should be verified whether these insects are of any importance for the pollination. In the Faroes, at any rate, such visits would be of no value as the stigma is not at all mature for receiving pollen during the flowering (fig. 33). The styles then are quite short and without any developed papillae. The plant, however, fructifies abundantly and at a ripe stage bears numerous large capsules tense with seeds and suggesting that there is an absolutely effective pollination.

During the flowering season the anthers are open and project high above the short styles, which are hidden in the flower.

If rainy weather sets in (as very often happens), some of the pollen is washed down into the flower, where it gets stranded on the inside of the corolla, the lower parts of the stamens, etc. Still, the greater part of the pollen remains in the anthers.

When the flower begins withering, the styles start growing vigorously in length. During this growth, however, they wind several times round their own axis, and furthermore the stigma bends aside. During these characteristic growing movements the papillae develop on the stigma, which is then receptive to pollination. When the stigma moves up through the narrow tube of the corolla, it will touch the organs placed there, which are mostly set with pollen that has dropped down or been washed down.



Figs. 32—34. Pollination in withered flowers, the corolla having been removed. Fig. 32. *Armeria vulgaris*. ×8. Fig. 33. *Lychnis flos cuculi*. Flowering stage with undeveloped stigma, but some dehisced anthers. ×4. Fig. 34. *Lychnis flos cuculi*. Pollination in withered flower. ×6.

The growth of the stigmata stops when they have got on a level with the anthers. Then stamens and styles are twisted round each other and this bunch is squeezed into a dense lump by the withering petals bending towards the centre of the flower. Finally the stigmata have clasped the stamens as with the arms of an octopus so that autogamy is performed with perfect certainty.

Danish individuals are pollinated quite like the Faroese ones.

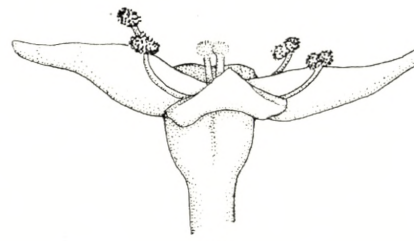
Armeria vulgaris WILLD. (fig. 32).

As this flower has already been described by WARMING (p. 1056), I shall confine myself to the following additions:

In the full-blown flower there is a chance of avoiding auto-

gamy as the styles are bent aside and can only with difficulty touch the anthers. But I have never been able to observe any visit by insects.

When the flower withers the styles and stamens bend closely together in the centre of the flower and are further squeezed together by the petals which surround this "bud" as a tight



Figs. 35—36. Pollination before the flower comes out. Longitudinal section of buds of *Galium saxatile* (fig. 35, ×40) and *Potentilla erecta* (fig. 36, ×12).
Fig. 37. *Galium saxatile*. The flower has already been pollinated when it opens. ×12.

protecting cover inside which autogamy is inevitable as the stigmata have fresh papillae and the anthers still contain pollen. According to IVERSEN the flower's own pollen yet does not germinate upon its own stigmata. It is markedly self-sterile. I do not know how the transport of foreign pollen takes place. It may be the flies of the coastal area which perform the pollination. This needs further investigation. The plant propagates exclusively by seeds, which are present in abundance.

Danish individuals showed the same conditions of pollination as the Faroese ones.

There are probably more flowers than the three mentioned here which have "withering pollination" at last if the other methods of pollination should fail.

B. Pollination before Flowering (Bud-Autogamy).

There was a number of other Faroese flowers whose conditions of pollination to begin with seemed unintelligible, e. g.

Galium saxatile L. (figs. 35 and 37).

Already WARMING (1908, p. 1059) investigated this species, but he did not find out the method of pollination, because the stamens in the open flower are bent outward and away from the styles. Still, such a multitude of fruits is produced that all flowers would seem to have been pollinated.

The numerous flowers are gathered in dense growths, which make the plant conspicuous, and it belongs to the commonest species. In the flowering season, however, the anthers are nearly emptied of pollen and it is extremely rare that a casual insect should be allured by the flowers. Visits by insects are of no value at all for the flowers, which for that matter not only are conspicuous, but also have a large circular nectary which is quite open and easily accessible even to insects with short proboscises (flies).

In order to discover the method of pollination the flower must be examined while it is still in bud shortly before it comes out. Fig. 35 shows a longitudinal section of such a bud. It is seen that the anthers are pressed tightly against the stigmata, which have long papillae. The anthers have dehisced and large quantities of pollen pour out on to the stigmata. This is a very secure form of autogamy. The stamens cannot at that stage be damaged by rain.

During rain the flowers are wide open and the last pollen is washed away, but as the flower has already been pollinated before it opens, its possibilities of fertilization are not reduced by storms.

KNUTH (1898, p. 548) supposes that the plant reproduces by geitonogamy and gives a list of visiting insects; but at any rate in the Faroes visits by insects are of no value whatever.

Potentilla erecta L. (fig. 36).

This is one of the commonest species in the Faroes, which embellishes the vegetation with its numerous yellow flowers. These are wide open and apparently ready to receive visits by insects. But insects are seen so rarely on the flower that they cannot be of any importance worth mentioning for the pollination. In the full-blown flower the stamens, in addition, are turned away from the styles so that they cannot leave pollen direct on the stigmata. Still, all flowers are fertilized and seedlings are common.

WARMING tried in vain to discover the method of pollination, which also at first seemed puzzling to me until the buds were examined immediately before they opened. It then appeared that the innermost anthers were already open and bent towards the stigma where they leave pollen. This mechanism functions very securely and all carpels are fertilized.

Danish individuals have bud-pollination in the same way as the Faroese ones.

Erica cinerea L. (fig. 31).

This is one of the most beautiful species of the Faroese flora. It has not only colour and beauty of form, but it also has a pleasant fragrance and a well developed nectary. Besides, the anthers are provided with the horns so characteristic of most Bicornes, which—in other species perhaps rightly—are considered an adaptation to entomophily.

One would therefore beforehand be inclined to consider it a matter of course that the flower should be entomophilous, and indeed KNUTH gives a long list of visiting insects.

In spite of this no insects are seen on the flowers. Even though there may be flies in the neighbourhood these will not be allured by *Erica cinerea*, but seek out certain other species (e. g. *Umbelliferae*).

There does not seem to be any pollen on the sticky stigma of the full-blown flower either. Furthermore the anthers have long been open and have already given off most of their content.

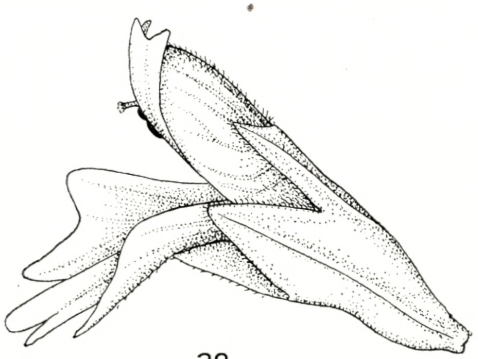
The flower hangs obliquely downwards already while in bud. The stigma is placed in its very lowest tip. The anthers dehisce before the corolla and pollen at once falls into the funnel-

shaped cavity between the tips of the petals, where the sticky stigma cannot avoid being filled with pollen, which is absorbed so quickly in the mucilage that it cannot immediately be seen in the full-blown flower.

This bud-autogamy functions so securely that all possible later visits by insects seem of no use for the pollination. It would be interesting to investigate whether the species is pollinated by insects in other countries.

Euphrasia borealis (TOWNS.) WETTST. (figs. 38, 39).

This flower has already been described by WARMING (1908, p. 1059), who found that the stigma at the flowering stage projects



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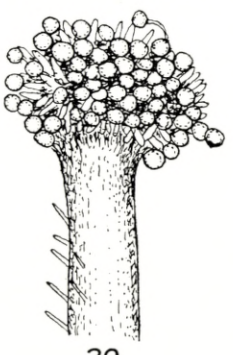

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Figs. 38—39. Autogamy. *Euphrasia borealis*.
Fig. 38. Full-blown flower after pollination. ×5.
Fig. 39. Stigma with the flower's own pollen prepared from bud. ×50.

in front of the anthers so that no self-pollination can take place.

However, if the bud is examined immediately before it opens it appears (fig. 39) that the stigma is already full of pollen from the flower's own anthers. This pollen has already germinated.

The corolla always keeps dry because it is covered by non-absorbent hairs. The upper lip is spatulate and envelops the anthers, which in the bud are pressed close together round the stigma.

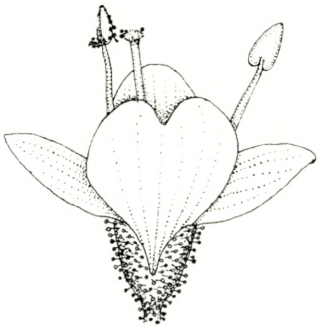
The pollen is dry and in the bud is found everywhere between anthers and stigma. The anthers are densely hairy so that pollen does not spread too much in the anterior of the bud, but is kept together near the stigma. Abundant fructification.

Alectorolophus (Rhinanthus) minor EHRH. (fig. 42).

This flower has a bud-autogamy reminding very much of conditions in *Euphrasia*. See further WARMING 1908, p. 1055.

Veronica beccabunga L. (fig. 41).

In the bud the anthers are pressed tightly against the stigma. They open inward immediately before the flower comes out and then pollen is with great certainty left on the stigma.



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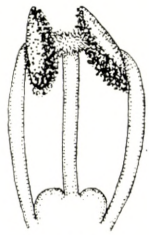

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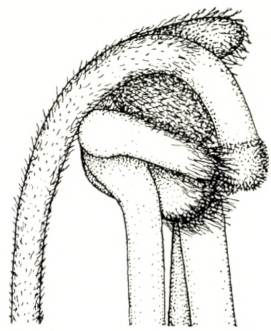

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Figs. 40—42. Autogamy. Fig. 40. *Veronica officinalis*. ×7. Fig. 41. *Veronica beccabunga*. ×18. Fig. 42. *Alectorolophus minor*. Stigma bending in among the anthers. ×12.

In the open flower the stamens are moved somewhat outward and inward.

Once I have seen a small moth, *Cidaria albulata* SCHIFF., flying from flower to flower and sticking its proboscis into the corollas; but such visits are of no importance to the plant as the flowers have already been pollinated.

The Danish plants are different from the Faroese ones both in appearance and biologically. The flowers are smaller and not so purely blue as in the Faroes. In Denmark the anthers do not dehisce in the bud, but only when the flower has come out. In the young flower there is a chance of insect pollination because the anthers are turned outward and away from the style. As a last chance of pollination, however, the stamens in the older flower bend inward and leave pollen on the stigma.

Cerastium caespitosum GILIB. var. *fontanum* BAUMG. (fig. 43).

The Faroese form has relatively large corollas, which often open more than in Denmark. I have not, however, seen any

insects on the flower. Still, there may be a chance of cross-pollination in other countries richer in insects (Norway) where var. *fontanum* also occurs.

In the Faroes the anthers dehisce immediately before the flower comes out and pollen is then left direct on the stigma because the anthers are still pressed tightly together round the stigmata. Fructification is abundant.

Stellaria media (L.) VILL.

It has bud-autogamy like *Cerastium*, and all flowers fructify.

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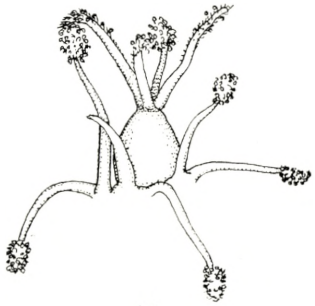

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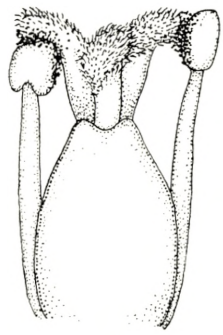

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Figs. 43—45. Autogamy. Fig. 43. *Cerastium caespitosum*. ×5. Fig. 44. *Stellaria uliginosa*. An anther pollinating a stigma. ×12. Fig. 45. *Sagina procumbens*. ×18.

Lotus corniculatus L. f. *carnosa* PERS. (figs. 50—52).

Pollination has been studied thoroughly in Central European localities. As to the main species e. g. KNUTH (1898, p. 303) has arrived at the result that it can only be pollinated by insects. This is not correct at any rate as regards the Faroese form, for this form does not receive visits by insects and besides none of the insects occurring there are heavy and vigorous enough to start the well-known mechanism of pollination. And even if they would have been able to do so it would be too late; for already before the flower opens, the stigma is completely surrounded by large amounts of pollen, which is ready to germinate on the stigma as soon as it becomes susceptible.

It should be investigated whether this form of autogamy is something special to the Faroese variety. KNUTH's long list of visiting insects need not mean that these are necessary for pollination.

A. PEDERSEN (1949, II, p. 311) writes about the form cultivated in Denmark that it is "pronouncedly self-sterile". Pollination in the different forms of this greatly polymorphous species should obviously be studied in more detail. It fruits sparingly.

C. Autogamy during Flowering.

Most of the species belonging here are homogamous and the pollination takes place during the flowering itself. If the flower opens, there is a possibility of insect pollination in such coun-

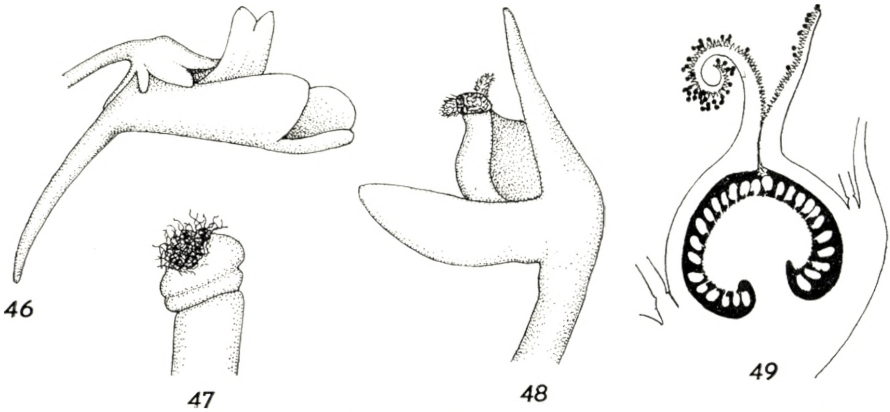


Fig. 46—49. Autogamy. *Pinguicula vulgaris*. Fig. 46, flower in stage of fertilization. ×3. Pollen germinates in the anther (fig. 47, ×16), which is pressed tightly against the stigma (fig. 48, ×6). Fig. 49, longitudinal section of gynaecium. ×14.

tries in which there are many insects; but as this is not the case in the Faroes, cross-pollination is without practical importance there.

In a number of species the flower is open in rainy weather and a filling with water will then often cause pollen to be transported to the stigmata. Autogamy functions with great precision and fructification is abundant. Most of the Faroese species which are not anemophilous belong here.

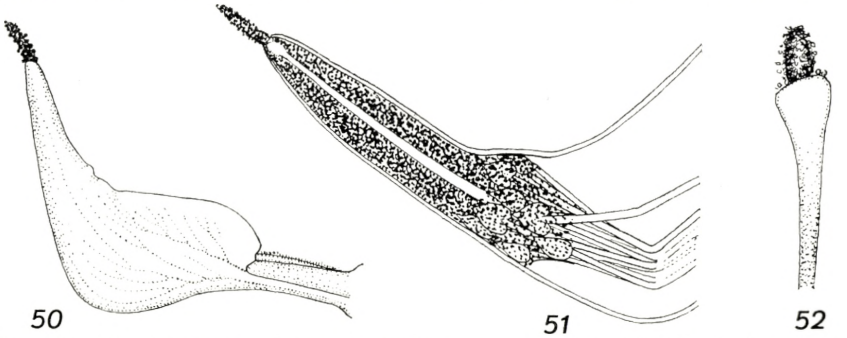
(a) The flower is open during pollination and has a slight chance of cross-pollination.

Pinguicula vulgaris L. (figs. 46—49).

There is some uncertainty as to the pollination, as KNUTH is of opinion that autogamy is excluded. WARMING (1912, p. 389), on the other hand, assumes that both insect- and self-pollination can be practised.

In the Faroes I examined a large material in nature without observing conditions which might in any way support KNUTH's views. Still, it should be investigated how pollination takes place in localities farther south, where KNUTH made his studies.

The anthers of the Faroese plant press tightly against the stigma, which is soon covered with pollen. If one pulls at a stamen it appears that it clings to the stigma and this adhesion is due to the fact that all pollen grains have germinated even though they remain in the anther. Pollen tubes form a dense cotton-like mass of fine interwoven filaments most of which have



Figs. 50—52. Autogamy. *Lotus corniculatus* var. *carnosa*. Fig. 50, carina, ×3. Fig. 51. Longitudinal section of apex of carina showing stigma surrounded by masses of pollen. ×6. Fig. 52. Filament with tumid apex. ×17.

penetrated into the stigma. At high magnification it is easy to follow the tracks of the pollen tubes among the long papillae of the stigmata and farther down to the ovules. The autogamy of the Faroese plant functions very precisely and seedlings are abundant. Once I even found a capsule the seeds of which had not even been dispersed but which had germinated inside the fruit.

Danish individuals showed quite the same conditions of pollination as the Faroese ones.

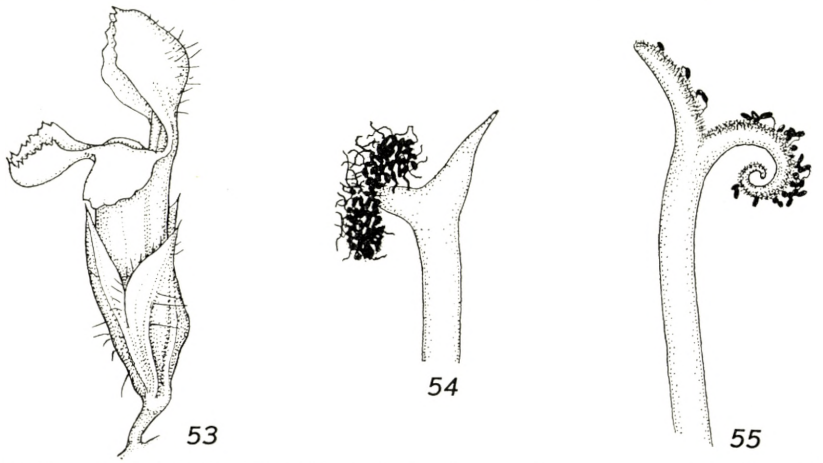
Vicia sepium L.

This species is also generally considered exclusively entomophilous in Central Europe. Not so in the Faroes, where pollen is left direct on the stigma in the homogamous flowers. Fructification is abundant although I have not seen insects on the flowers. The current view of the pollination may also in the case of this species be based on the tempting confusion of visits

by insects with pollination. Flowers from Denmark behave almost in the same way as the Faroese ones. The anthers are open and the stigma is pollinated before the flower opens. The chance of cross-pollination is very poor.

Trifolium repens L.

This species, which is dominant on the low-lying Faroese pastures, is autogamous in a similar way to the two preceding



Figs. 53—55. Autogamy. *Prunella vulgaris*. At the flowering stage (fig. 53, ×5) the pollen tubes have already grown out of the anthers (fig. 54, ×20) and have penetrated into the stigma (fig. 55, ×20).

Papilionaceae, as the ripe stigma is jammed in between the open anthers. The strong fragrance and conspicuous colour of the flower do not attract the few insects. Rain does not penetrate into the flower in *Papilionaceae* because of the form of the petals and their mutual position.

A. Pedersen (1949, II, p. 298) states about the forms cultivated in Denmark that they are "pronouncedly self-sterile". The various forms of the species thus ought to be investigated thoroughly and apart as they may show different conditions of pollination. It fruits sparingly.

Prunella vulgaris L. (figs. 53—55).

The large coloured inflorescences everywhere embellish the Faroese pastures, thus in advance suggesting insect pollination, a view which is indeed shared by the early floral biologists (Knuth, 1898—99, p. 283). Warming (1908, p. 1057), on the

other hand, states the occurrence of autogamy. As a matter of fact the Faroese flies are not attracted by the flowers.

The position of the flower is nearly horizontal, and the stamens are protected from rain by the vaulted upper lip, which on top is set with non-absorbent hairs.

The anthers are pressed firmly against the stigma, which is mature simultaneously with the release of pollen. The pollen germinates quickly. Even if it remains in the anther, pollen tubes grow to the stigma. As in *Pinguicula* the lowest branch of the stigma rolls back spirally, thus obtaining an extra chance of being powdered with the pollen. The mechanism of autogamy functions perfectly, and seedlings are common.

Still, it is possible that some of the southern forms of this polymorphous species can be pollinated by some of the numerous insects included in KNUTH's lists. The Danish flowers, however, behave like the Faroese ones. If an anther is taken out with a pair of tweezers, pollen tubes may already be seen in a magnifying glass. Furthermore, the Danish flowers are much smaller than the Faroese ones and have hardly any chance of cross-pollination worth mentioning.

Galeopsis tetrahit L. (fig. 56).

Autogamy mainly takes place as in *Prunella*. Two of the anthers press tightly against the stigmata and pollen is left upon these. I have not observed any visits by insects in the Faroes, but in Central Europe the flowers are visited by humble-bees (KNUTH, p. 264).

Fructification is plentiful.

In the Danish flowers the anthers are far from being so tightly pressed against the stigma. Hence there is presumably a much greater chance of cross-pollination than in the Faroes.

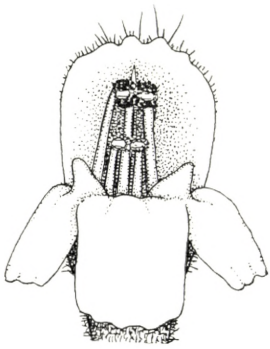
Polygala serpyllacea WEIHE. (figs. 58—60).

Although the flower both in form and colour seems to have been made for insect pollination it is an inveterate self-pollinator. Visits by humble-bees have been observed in localities farther south (KNUTH, p. 153), but in the Faroes I have never seen any insect on the flower and still fruit is developed by nearly all flowers. (Furthermore, the seeds are remarkable by having elaiosome, although there are no ants.)

Already WARMING (1908, p. 1062) found autogamy in *Polygala*. I shall therefore only refer to the figures below. The thick layer of pollen on the stigma exclusively derives from the flower's own anthers.

Veronica officinalis L. (fig. 40).

The corolla is funnel-shaped and directed obliquely upwards. Inside it is non-absorbent like the anthers, but outside it gets wet in the rain. The two anthers, which do not open at the same



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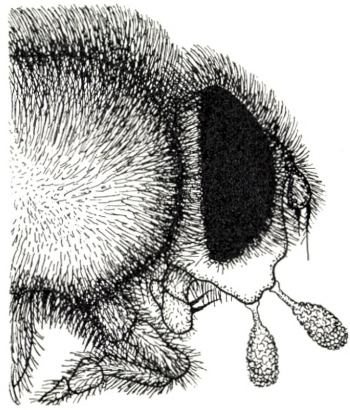

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Fig. 56. Autogamy. *Galeopsis tetrahit*. The anthers pressed against the stigma. ×4.
Fig. 57. Pollinia of *Orchis purpurella* on head of *Eristalis intricarius*. ×6.

time, are both of the same length as the style; but at the beginning of the flowering they are bent outwards and away from the stigma. So at this stage the flower has a chance of insect pollination. In the Faroes, however, I have never seen any insect on the flowers.

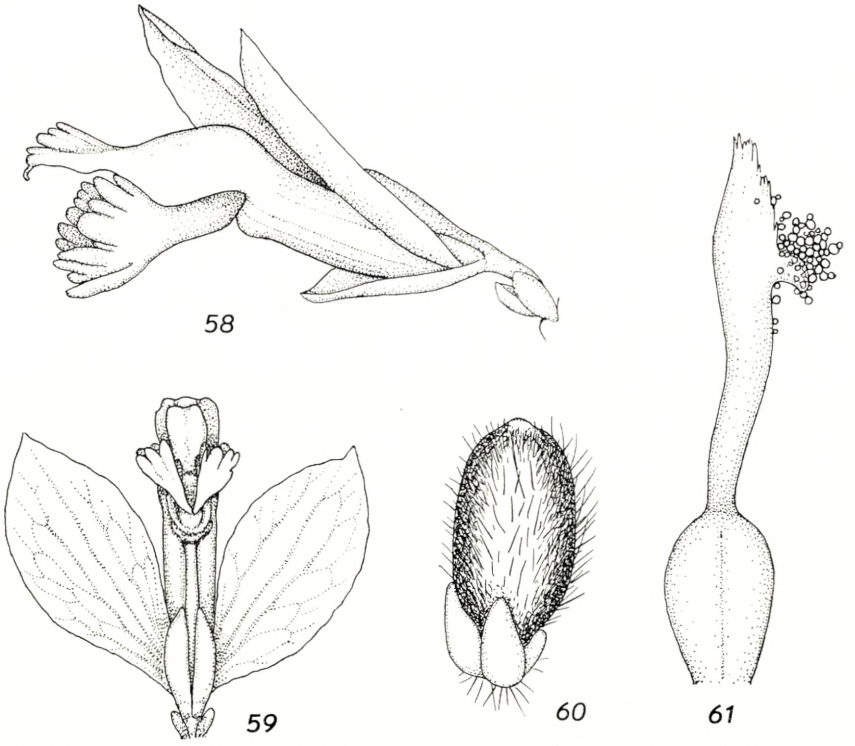
When the flowering is being finished the anthers move towards the centre of the flower and the anther is pressed against the stigma, which in this way receives pollen. This form of autogamy thus is the last chance of the flower, and it is probably nearly always efficient.

The style, too, may move a little aside and towards the anthers.

The Danish plants behave nearly as the Faroese ones, but are more open and have a greater chance of insect pollination in the beginning of the flowering.

Veronica serpyllifolia L.

The corolla is wide open, but the stamens are mostly upright, with the anthers being placed very close to the stigma, autogamy thus being secured.



Figs. 58—61. Autogamy. *Polygala serpyllacea*. Fig. 58. Side view of flower. ×12. Fig. 59. Flower seen from below. ×6. Fig. 60. Seed. Fig. 61. Stigma with the flower's own pollen prepared from bud. ×16.

The flower is self-pollinating in Denmark as well, often before the corolla is quite open. The stamens make spontaneous movements. The anthers dehisce simultaneously with the corolla or shortly before.

Viola Riviniana Rchb. (figs. 62—64).

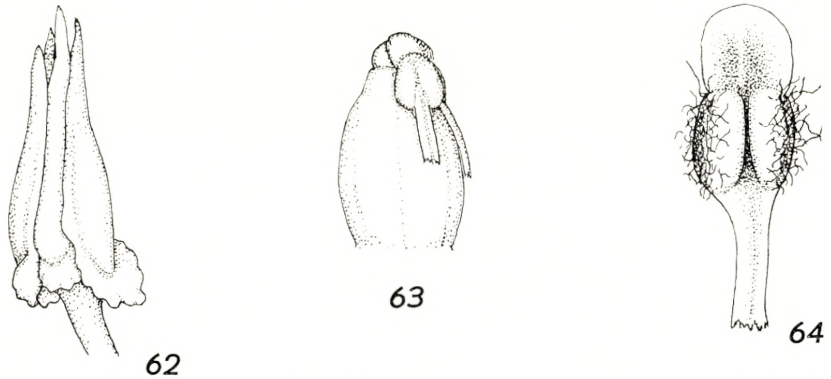
The Faroese plants have closed flowers similar to e. g. the Danish ones. Pollen germinates in the anthers and pollen tubes grow direct down into the stigma.

See further Knuth's account (1898, pp. 138—140).

Bellis perennis L. (fig. 27 a).

This species is abundant in the meadows and its fructification is plentiful; but only rarely a stray fly is seen on the flowers, and if so, it does not pollinate them. During rain or in the dark the inflorescences close nearly completely.

The stigma is strange because it is not, as in other *Compositae*, situated on the inside of the apex of the style. But the sticky papillae are placed both on the apex and on the outside of the



Figs. 62—64. Autogamy. *Viola Riviniana*. Fig. 62. Flower at stage of fertilization. ×7. Fig. 63. Anthers sticking to stigma. ×13. Fig. 64. Pollen tubes growing out of anthers. ×20.

style. When the latter grows up through the tube formed by the stamens, the anthers have already dehisced on the inside, and great quantities of pollen are transferred to the stigma.

From localities farther south KNUTH reports plenty of visits by insects. He does not count on a possibility of autogamy. Danish individuals behave like the Faroese ones.

Senecio vulgaris L.

This species has autogamy similar to *Bellis*. KNUTH counts on autogamy, but also reports scarce visits by insects.

In Denmark, too, the species is autogamous.

Matricaria ambigua (LEDEB.) (fig. 25).

This species is pollinated in a way similar to *Bellis*. The stigma, however, is placed only on the extreme apex of the style, which is pushed like a piston through the anther tube, where it receives plenty of pollen. In Denmark the same method is found in the case of the inner flowers of the main species. The marginal

flowers have spread-out styles, which have a great chance of being insect-pollinated, e. g. by *Thrips*, which often—in great amounts and powdered over by pollen—crawl about the flowers.

Cirsium palustre L. (SCOP.) (figs. 65—66).

In structure the style reminds of the ordinary style of *Compositae*, as on the outside it is set with stiff hairs which sweep the pollen out of the anther tube, while the stigmatic papillae are found to be covered on the inside of the style, autogamy thus generally being avoided.

In the present species, however, there are stigmatic papillae not only on the inner surface, but right out to the margin of it and even some short distance down the outside surface. Indeed, it is just along the margins that the germinating pollen grains are found and perform this special form of autogamy.

The flowers have both fragrance and nectar, and KNUTH gives long lists of visiting insects from southern localities, assuming that the flower is entomophilous. This needs critical investigation.

In Denmark numerous *Thrips* powdered over with pollen move about the flowers. Visits by larger insects are often seen, too.

Flowers from all localities were peculiar by the two stigma branches (facing each other) during the greater part of the flowering season being pressed tightly together. Only during the last stage of the flowering the two branches bend a little apart, but then only at their extreme tips. So at this late stage there is a chance for the flower to receive pollen from other flowers; but as a rule there is still some of the flower's own pollen on the back of the stigma. This is easily transferred to the margin of the stigma, which may thus be pollinated, e. g. when the long stalks are shaken by the wind. Conditions in the Faroes at any rate show that visits by insects are not necessary for the pollination.

One of the two stigmata is nearly always longer and broader than the other (fig. 66). Consequently both apex and margins are exposed during the whole flowering season. The flower's own pollen is often found in the places mentioned, having been left there at an early stage when the flower was coming out, for which reason possible later visits by insects are hardly of

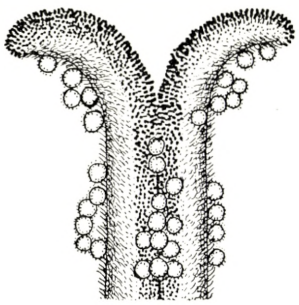
any appreciable importance for the pollination. Autogamy is probably the normal.

Sedum villosum L.

The flower has been described by WARMING (1908, p. 1064). In the stellate flower the stamens are moved inward towards the centre, where they cannot avoid touching the stigma. Autogamy thus is normal.

Saxifraga stellaris L.

As in *Sedum villosum* the stamens make great movements,



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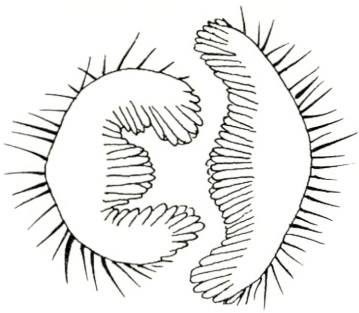

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Figs. 65—66. *Cirsium palustre*. Fig. 65. Apex of stigma with pollen. ×90. Fig. 66. Cross-section of stigma. ×200.

ending in the anthers touching the stigma, where they leave pollen. Abundant fructification.

KNUTH reports visits by insects and states that as a rule the species is not autogamous.

Stellaria uliginosa MURR. (fig. 44).

Pollination in this species reminds remarkably of pollination in *Sedum* and *Saxifraga*. The flower is wide open and the stamens make great movements to and fro so that some of them may be bent right back, while at the same time others are nearly upright in the middle of the flower; but just there the stigma is found and is inevitably pollinated. All flowers set fruit.

Autogamy in this species was described by KNUTH, who also, however, observed visits by insects.

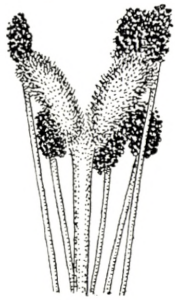
Polygonum aviculare L. (fig. 69).

In fine weather the flower is wide open and the stamens are

first bent outwards; but when the anthers dehisce, they bend one by one towards the middle of the flower and leave pollen on the stigma. Finally the whole flower closes, all the stamens are pressed tightly together, and autogamy is secured.

Epilobium montanum L. (fig. 67).

The flower has already been examined by KNUTH and WARMING, who found that the anthers even adhere to the stigma. The Danish flower has a considerably greater chance of cross-pollination as both stigma and anthers are spread out much more widely than in the Faroes.



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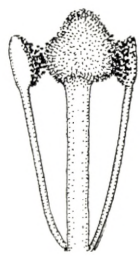

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Figs. 67—69. Contact-autogamy. Fig. 67. *Epilobium montanum.* ×5. Fig. 68. *Epilobium palustre.* Fig. 69. *Polygonum aviculare.* ×16.

Epilobium palustre L. (fig. 68).

This species shows a form of autogamy similar to *E. montanum.* The anthers are open already in the bud and pressed tightly against the stigma. On Danish material the style is somewhat longer than on the Faroese material. Thus at any rate the apex of the style can be receptive to cross-pollination. The flowers are rarely visited by insects; but in Denmark they are more open than in the Faroes and the stamens are also spread out more.

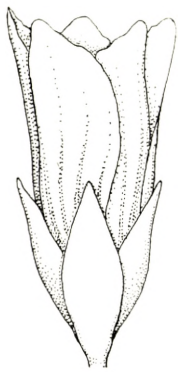
Myosotis palustris (L.) var. *strigulosa* (RCHB.).

When the sun shines on the dense carpets of the conspicuous, beautiful flowers, big flies roam about in the air. They often with predilection settle on *Myosotis* and place their proboscises in the entrance to the narrow corolla tube. In a *Myosotis* locality it is thus possible to observe the humble-bee-like *Eristalis intricarius,* which is of so great importance for the pollination of *Orchis.*

The flower is wide open, the large corollas thus offering good landing-stages for insects; but the insects cannot reach the bottom of the corolla tube with their proboscises because the entrance is completely barred by the stigma and anthers.

The stamens together form a narrow tube similar to that of the *Compositae* and the stigma grows up through this like a piston. During its growth the anthers are open and inevitably leave pollen on the stigma.

The visits by insects, however, offer a chance of cross-pollina-



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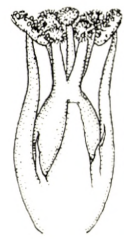

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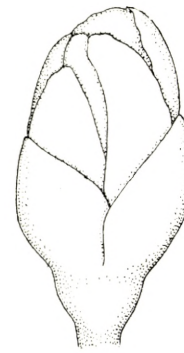

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Figs. 70—72. Autogamy. Fig. 70. *Linum catharticum*. ×8. Fig. 71. *Linum catharticum*. The anthers place pollen on the stigma. ×16. Fig. 72. *Montia lamprosperma*. ×20.

tion which perhaps is not quite without importance even though autogamy is the normal, particularly in bad weather. Rain water cannot penetrate into the narrow aperture of the corolla tube. Therefore the well-protected anthers are always dry, even if the exposed parts of the petals get wet.

The Danish flowers behave like the Faroese ones.

Myosotis arvensis (L.).

This smaller species has a spontaneous autogamy similar to that of *M. palustris*. I have never seen insects on the small flowers.

Linum catharticum L. (figs. 70—71).

The flowers do not open so wide as in Denmark and have hardly any chance of cross-pollination.

The dehisced anthers are tightly pressed against the stigmata, which are pollinated with great certainty.

Cochlearia officinalis L. (figs. 73—74).

At the stage when the flower is opening, there is, in the Faroes, a direct contact between the mostly just dehisced anthers and the stigma, autogamy thus being inevitable in bad weather.

If the air is dry, the flower comes out earlier and the stamens are not pressed so tightly against the stigma. The petals spread out horizontally and the anthers get more space. Autogamy then can easily be avoided. On a dry sunny day in the Faroes the conspicuous flowers are not rarely visited by flies, thus getting a chance of cross-pollination. This possibility is still more pronounced in Denmark.

The species often grows in the coastal fly areas.

Cardamine hirsuta L.

In the Faroes neither calyx nor corolla open, but they are pressed together to form a tube. By this means the anthers of the four long stamens (the anthers dehisce inward) are pressed tightly together in the middle of the flower, but exactly there the stigma is found both before and during the flowering. Autogamy thus is inevitable, and all flowers set fruit.

In Denmark the flowering is somewhat different, the flowers here opening completely as shown in figs. 75—76. This may possibly mean a chance of cross-pollination, which is not possible in the Faroes. Furthermore, the stigma on the Danish plants is found a little higher than the anthers so that as a rule these cannot reach high enough to leave pollen direct on the stigma.

Cardamine silvatica Link.

The flower is a little more open than that of *C. hirsuta*, but still autogamy is practised in the same way in Denmark and in the Faroes.

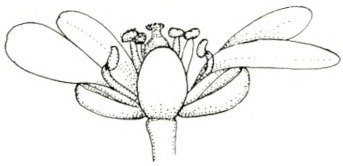
Cardamine pratensis L.

The large beautiful flowers also in the Faroes are wide open, but still they pollinate themselves in the same way as the two preceding species.

In southern localities insect pollination according to KNUTH is the commonest method, and he mentions visits by many different insects.

Capsella bursa pastoris (L.) MOENCH.

In the Faroes mostly in part closed and autogamous. In Denmark visits by insects to the open flowers are not rare, but also there the flowers nearly always pollinate themselves.



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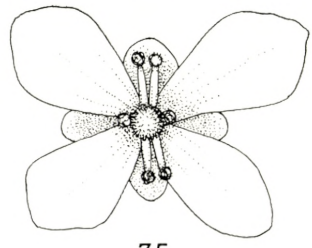

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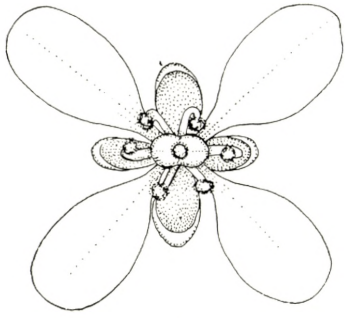

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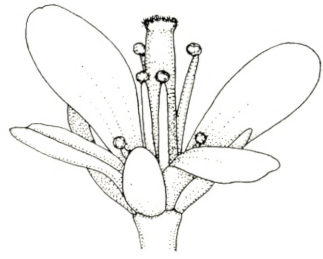

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Figs. 73—74. *Cochlearia officinalis*, side view of flower (fig. 73), flower seen from above (fig. 74). Figs. 75—76. *Cardamine hirsuta*. × 10.

(b) The flower is closed during pollination so that no cross-pollination can take place.

Koenigia islandica L.

In Greenland the flower is completely open in fine weather so that the three yellow nectaries can be seen; but still the anthers touch the stigma and places pollen direct upon it.

In the Faroes the flower is nearly always closed and the mechanism of autogamy functions with great certainty.

Sagina procumbens L. (fig. 45).

In Denmark it sometimes happens that the flower of this species is slightly open; but in the Faroes it is always closed firmly.

By this means the anthers are pressed against the stigma and places pollen direct upon it. The flower always sets fruit. When this is mature, the valves spread like a star. In other countries visits have been observed by flies and bees, and even ants have been seen in the flowers, which have nectaries.

Montia lamprosperma (CHAM.) (fig. 72).

The small white flowers are always closed and the anthers cannot avoid touching the stigma. In Denmark the flowers open somewhat in dry weather and in Scotland visits by flies have even been observed (KNUTH, II, 1, p. 424).

6. General Remarks.

A study of conditions of pollination in the individual species in a Faroese local flora thus has shown that many of the species are not pollinated in the same way as in southern localities.

The present investigations were made in a locality where a number of apparently entomophilous species fructify excellently without visits by insects, the purpose being to find out of how great or small importance visits by insects may be. Some flowers (e. g. those of *Erica*) have both fragrance, nectar, and colour, but they tempt insects in vain. Detailed morphological investigations of such structural features as invite interpretation as adaptations to entomophily (WARMING) thus may actually lead the student astray. This applies e. g. to the horns on the stamens in *Erica cinerea*, the flowers of which are pollinated before the horns can be touched by any insect. The horns in *Calluna* and many other "adaptations" in other flowers are just as superfluous in the Faroes.

Morphological investigations indoors thus are not sufficient. The decisive observations must be made in nature, where the student should not least be attentive to the question whether species considered autogamous really produce seed capable of germinating after self-pollination.

The methods of pollination may be very different in different localities within the total area of distribution of the species. This is most clearly illustrated by *Calluna* (HAGERUP, 1950), the flowers of which may be pollinated by e. g. bees, butterflies, *Thrips*, wind, and autogamy. The method to be realized depends

on ecological conditions in the various stations, e. g. by wind and weather and the species of insects found in the place. These circumstances may again vary from year to year. Consequently the flower need not be pollinated in the same way every year. Thus, if continuous rain sets in, the insects are prevented from flying about and no air transport of pollen can take place. The flower then must fall back on one of the other methods of pollination, e. g. by means of *Thrips* or autogamy. But then, if the weather is dry next year during the flowering, the same individuals perhaps are pollinated in quite different ways, e. g. by bees or the wind.

In the damp climate of the Faroes *Calluna* thus is pollinated by *Thrips* or the wind, while in Denmark the species is often pollinated by bigger insects. In some localities the morphological adaptations then may be of importance while elsewhere they seem of no value. There is thus a certain plasticity in the conditions of pollination of certain flowers, a fact of which already WARMING was aware. The somewhat schematic and stiff descriptions of conditions of pollination in certain textbooks should sometimes be taken with a grain of salt, and many of the classic observations of floral biology should be taken up for renewed investigations. The necessity of this is illustrated e. g. by conditions in *Orchis*, which, indeed, is a classic example of one of the most ingenious forms of entomophily; but here MARTENS has found occasional autogamy, as is also found normally in a number of other orchids (*Epipactis*, *Liparis*, etc.), which indeed have just as ingenious morphological "adaptations" as *Orchis*. All the usual strange forms of pollination in orchids are superfluous in the case of this species. Still, the flower receives visits by insects (just as *Taraxacum* does).

The discrepancies between the observations of pollination in the various species in the Faroes and in southern localities need not be due to erroneous observations, but may simply be due to the fact that various species (e. g. *Prunella*) have developed particular autogamous races in the Faroes, whereas e. g. in Germany they are visited more or less frequently and perhaps also may be pollinated by insects.

The fact that flowering and pollination can be influenced direct by the climate (and thus need not be exclusively genetic-

ally conditioned) is beautifully illustrated by conditions in the Faroese form of *Hypericum pulchrum* (see above, pp. 18-20).

Self-sterility is a possibility which should be considered in the case of the relatively small number of entomophilous species. Thus it is stated that *Ranunculus acer* is sometimes self-sterile; but the great number of autogamous species which are not visited by insects cannot be self-sterile, as it is always easy to find the flower's own pollen germinating on the stigma. Such autogamous species have a remarkably rich fructification.

The flora of the Faroes in respect of nutrition offer conditions of a much richer fauna of insects than is actually found there. In the great number of fragrant, coloured, and attractive flowers there are quantities of pollen and nectar which are not used as food, but simply are wasted (e. g. in *Erica*). For comparison it may be mentioned that in Greenland, in latitudes much farther north, there is a relatively much greater number of pollinating insects (e. g. humble-bees and butterflies) than in the Faroes. This poverty in insects in the Faroes should be investigated by zoologists. The causes may be either the present climatic conditions or conditions of immigration.

In corresponding latitudes on e. g. the west coast of Norway there is also a much richer fauna of insects than in the Faroes.

Similar problems crop up concerning the fly areas which —as mentioned above—are so characteristic of the closest surroundings of (1) inhabited places, (2) beaches with rotting plants and animals, and (3) bird-cliffs and the flora conditioned by these.

Have the inhabitants of the fly areas been imported by man or do these insects belong to the original fauna of the islands as it existed already before man immigrated? Both possibilities seem to have been realized. The house-fly (*Musca domestica*) has obviously immigrated in the company of man. The same perhaps also holds good of other flies whose larvae live in the dung of human beings or domestic animals (sheep). When the domestic animals were imported it was necessary to import fodder for them, too, and this may have contained both the brood of flies and seeds of the plants of the fly areas.

Høeg writes the following passage about the corresponding conditions in Spitsbergen, which in a remarkable degree remind of the above-mentioned conditions in the Faroes:

"This abundance of flowers may indeed arouse feelings of summer; but still it is as if something is missing: all the pullulating life of insects which belongs to our picture of a summer's day and which is part of its atmosphere. Not one honey-bee, not one humble-bee or a butterfly. The flowers come out in vain. They smarten themselves up, tempt and pose,—and then there is nobody for which to pose. Only some disgusting big, fat flies fly about. They are said to have come to Spitsbergen in recent years and now the mining towns teem with them, at any rate Longyear City, so that they sweep them up with vacuum cleaners.—Looking more closely, one finds some small flies and some other still smaller vermin. That is all—indeed nothing to pose for! The poverty in the insect world is very remarkable in the pronounced arctic regions."

But besides all the species imported in the company of man, there are also such carnivorous and coprophagous flies as may very well have been established inhabitants of the bird-cliffs before man immigrated.

I am therefore of opinion that the fly areas house both imported and spontaneous species of pollinating insects as well as plants.

The question whether a given imported species can continue existing in the Faroes thus is conditioned by the possibility of its managing the problems of pollination in spite of the poverty in insects and the bad weather.

7. Summary.

1. The present work is a study on the pollination of the species in a local flora (around Thorshavn) in the Faroes where poverty in insects and violent and prolonged rains and gales put obstacles in the way of cross-pollination.

2. Therefore most plants must either be able to pollinate themselves or utilize the wind.

3. Anemogamy: Some of the flowers pollinated by means of the wind are protogynous, e. g. *Myriophyllum*, *Triglochin*, *Plantago*, *Potamogeton*. Others are homogamous and then mostly autogamous, e. g. *Rumex* and many *Glumiflorae*.

4. Entomogamy: The only insects playing any significant

part in the pollination are some species of flies. These *Diptera*, however, are very local in distribution because their larvae subsist on putrefying animal substances. Therefore there are entomophilous flowers particularly near (1) human dwellings, (2) on bird-cliffs, and (3) on beaches with putrefying algae and animals.

5. No plants collect so many flies as *Archangelica* and other *Umbelliferae*. *Orchis* is pollinated by *Eristalis intricarius*. Fly-pollination is furthermore found in *Geranium*, *Sedum*, *Ranunculus acer*, *Caltha*, *Thymus*, *Melandrium*, *Filipendula*, and *Iris*. *Calluna* is pollinated by *Thrips* and the wind (Hagerup, 1950).

6. A particularly strange species is *Coeloglossum* (*Habenaria*) *viride*, in which the entrance to the spur is closed by a membrane which the insect must penetrate before it can reach the nectar.

7. Rain can pollinate certain flowers: *Ranunculus* sp., *Narthecium*, and *Caltha* (Hagerup, 1950).

8. Autogamy: Most flowers can occasionally or always pollinate themselves. This mostly takes place by the anthers placing pollen direct on the stigmata of homogamous flowers: *Prunella*, *Montia*, *Caryophyllaceae*, *Polygala*, *Cardamine*, *Epilobium*, *Euphrasia*, *Galeopsis*, *Koenigia*, *Linum*, *Lotus*, *Matricaria*, *Myosotis*, *Pinguicula*, *Rhinanthus*, *Trifolium*, *Veronica*, *Vicia*, and *Viola*. In these species pollination takes place during the flowering.

9. Bud-Pollination: In some species the flower is pollinated already while it is in bud (thus before flowering): *Erica*, *Galium*, *Potentilla*.

10. "Withering-Pollination." In some species the flower is not pollinated until the perianth is withering (thus after flowering): *Lychnis*, *Hypericum*.

11. Geitonogamy. The dense inflorescences are closed in the dark, the styles and stamens thus touching and effecting pollination (*Leontodon*): night-pollination. Neighbouring flowers also pollinate each other in a number of other species with dense inflorescences: *Cornus* and many *Glumiflorae*.

12. The faculty of managing by means of autogamy and anemogamy is characteristic of the original species of the Faroes, whereas some entomophilous species presumably have been imported by man.

13. In many cases the Faroese plants are systematically different from the corresponding southern species and should

be subjected to detailed taxonomic and cytological investigations.

14. The characteristic conditions of pollination in many species are genetically conditioned, whereas e. g. autogamy may be due to the direct influence of ecological factors (p. 18-20).

15. The main rule thus is that entomogamy is remarkably rare. The greatest part by far of the area of the Faroes is covered by autogamous and anemophilous plants.

To judge from WARMING's investigations in Greenland autogamy (and anemophily) is to a remarkable degree predominant in other arctic regions poor in insects—even in *Bicornes*.

Acknowledgments.

It has only been possible to complete the present work with assistance from many quarters. The Carlsberg Foundation has given the necessary economic support. Mr. R. RASMUSSEN, Folk High School Director, put his unique knowledge of Faroese nature at my free disposal. The difficult conditions of billeting were met only by the effusive hospitality of a number of friends, among whom I should especially mention the Rev. K. KEIDING of Midvaag, Mr. A. PETERSEN, Missionary, of Klakksvik, and the Management of the Sailors' Home at Torshavn. Mr. NIELS HAISLUND, M. A., has translated this work into English. For all this assistance I beg to offer my respectful and cordial thanks.

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SOME MARINE ALGAE FROM MAURITIUS

ADDITIONS TO THE PARTS PREVIOUSLY PUBLISHED, III

BY

F. BØRGESEN

København
i kommission hos Ejnar Munksgaard
1951

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Some collections of algae from Mauritius recently received from Director, Dr. R. E. VAUGHAN not only contain some new species but also several species not yet recorded from the island, or others of which I formerly have had fragmentary specimens only and of which I can add information in various ways. This is done in the part published here.

In all 29 species are mentioned in this part. Of these 3 species are described as new and when dealing with the species of *Trichogloea* from Mauritius, a new species from Java of this genus is described as an addition.

When working with the species of the genus *Trichogloea* it was of a special importance for me to be able to see the original specimens of *Trichogloea Requienii* Montagne kept in the Muséum National d'Histoire Naturelle, Paris. I am very much indebted to the Director, Professor R. LAMI, who upon my application most kindly allowed me to have the loan of these specimens together with some specimens of *Trichogloea* from Mauritius and some other species of *Trichogloea* here in Copenhagen.

As I also wanted very much to see a specimen of a *Trichogloea* collected by Colonel NICHOLAS PIKE in Mauritius and kept in the Kew Herbarium, the Director, Dr. E. J. SALISBURY kindly permitted me to see the specimen here, for which I likewise want to express my sincere thanks.

Since it was also of much interest for me to be able to see the small specimen of *Trichogloea Requienii* of which KÜTZING in Tabulae Phycologicae, vol. VII, tab. 92, fig. II has given an illustration I am much indebted to Professor H. G. LAM, Director of the Rijksherbarium, Leiden, and to the Curator, Dr. Jos^{e} TH. KOSTER for permission to see the specimen.

Further, Professor W. RANDOLPH TAYLOR, Ann Arbor, Michigan, most kindly sent me a type-written duplicate of a not yet

published paper on *Trichogloea Herveyi* Setch, together with some dried specimens of this species endemic in the Bermudas.

Dr. ISABELLA ABBOTT, Hopkins Marine Station, Pacific Grove, California, who has made the study of the genus *Liagora* a speciality, has most kindly given me valuable information about species of this genus.

The lady artist Miss INGEBORG FREDERIKSEN has most kindly drawn most of the figures and for this valuable help I thank her most heartily.

To the Trustees of the Carlsberg Foundation I am much indebted for a continued grant.

CHLOROPHYCEAE

Siphonocladales.

Fam. 1. Siphonocladaceae.

Siphonocladus (Schmitz) Børgs.

1. **Siphonocladus tropicus** (Crouan) C. Ag.

Alg. Mauritius, Addit. List, 1946, p. 14.

Of this species rather common in the West Indies of which I formerly from Mauritius have seen only a single specimen preserved in JADIN's collection, I have in a lately received collection met with some few more.

As the species has not yet been recorded from other localities in the Indian Ocean than Mauritius a new locality there is of course of interest.

About the locality is said only: "Epiphyte, near reef".

Mauritius: Riambel, 8-12-50, G. MORIN, no. 1006.

Valoniopsis Børgs.

1. **Valoniopsis pachynema** (Martens) Børgs.

BØRGESEN, F., Some Marine Algae from the Northern Part of the Arabian Sea, 1934, p. 10, figs. 1—2. — *Bryopsis pachynema* Martens, Die Preussische Expedition nach Ostasien, Bot. Theil, Die Tange von G. v. MARTENS, p. 24, pl. IV, fig. 2, 1866.

In a lately received collection of algae from Mauritius a large specimen of this species is found which has not earlier been recorded from there.

The specimen forms a large tuft more than 20 cm broad consisting of entangled filaments fixed together by means of the numerous rhizoids issuing from the filaments. The latter are about 300 μ to about 1 mm broad.

About the locality is said: "Forms large cushion-like mats on rocks exposed to surf at low tide".

Mauritius: Riambel, 24-10-50, R. E. V. no. 954.

Geogr. Distr.: Rather widely distributed in the Indian and Pacific Oceans, and the Bermudas in the Atlantic Ocean.

Dasycladales.

Fam. 1. ***Dasycladaceae.***

Acetabularia Lamouroux.

1. **Acetabularia Moebii** Solms.

Alg. Mauritius, I, 1940, p. 44.

Of this diminutive *Acetabularia* I have formerly, when visiting the Kew Herbarium, seen there only some few specimens collected by Colonel PIKE. It was therefore interesting to receive, sent by air-mail from Dr. VAUGHAN, a small tube containing 3—4 tiny specimens (Fig. 1).

When compared with the description of SOLMS (1895, p. 30, fig. 1, pl. IV) based upon PIKE's specimens and a single one collected by MOEBIUS some differences are present in the specimens I have just received.

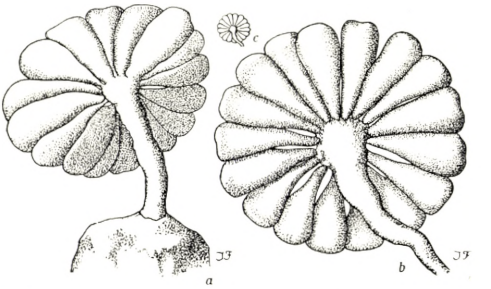

Fig. 1. *Acetabularia Moebii* Solms. *a*, a specimen fixed to a piece of rock; *b*, a disc seen from below; *c*, same specimen in natural size. *a* and *b*, ×7; *c*, ×1.

The discs have in the specimens examined 17 rays, while SOLMS says about 15, and the ends of the rays are in most cases broadly rounded but in a few of the rays they were a little emarginate.

In the coronal knobs mostly six scars, sometimes only 5, were found after the deciduous hairs, while SOLMS says 5 only (Fig. 2).

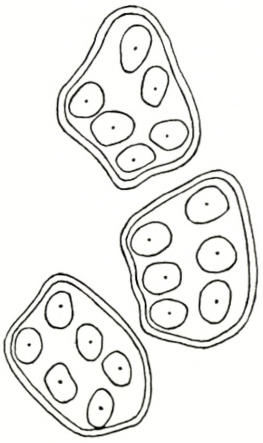

Fig. 2. *Acetabularia Moebei* Solms. Coronal knobs showing hair scars (×300).

And while SOLMS describes the hair scars as "very delicate", those in the specimens just received are thick-walled.

About the chalk-incrustation SOLMS says that the lateral walls of the rays are united by strong calcification; in the specimens examined by me the rays were also in most cases knitted together with chalk but some rays were free.

The stipe, present in one of the specimens only, was $3\frac{1}{4}$ mm long and rather bent and uneven; above, below the disc, it was thickened which is most probably due to remaining parts of a dropped disc. According to SOLMS two discs were found in the single specimen of MOEBIUS.

The specimens were sterile.

Okamura in "Icones of Japanese Algae", vol. II, p. 184, pl. 100, figs. 7—11 has described a small *Acetabularia, A. minutissima* which according to his description and figures seems to be the same as the Mauritian one even if some minor differences are present.

About the locality Dr. VAUGHAN writes in a letter received later:

"We have found it in several localities at Riambel at Mahébourg. It occurs as scattered isolated plants attached to rocks and old pieces of corals on the lagoon side of the reef protected from strong surf, it is usually densely entangled with or covered by other algae".

Mauritius: Riambel at Mahébourg, R. E. V. no. 1059.

Siphonales.

Fam. 1. ***Caulerpaceae.***

Caulerpa Lamouroux.

1. **Caulerpa Webbiana** Mont.

forma *tomentella* (Harv.) Weber.

Alg. Mauritius, Addition. List, I, 1946, p. 36.

In a lately received collection from Mauritius several large, fine specimens of this little *Caulerpa* are found of which I have formerly seen very small fragments only.

Five to six ramuli are found in each whorl in the present form of this variable plant.

About its habitat Dr. Vaughan writes: "On rocks or growing in coral sand exposed to strong surf. Very firmly rooted and difficult to separate from other algae." And on another locality Mr. G. Morin says: "Growing in sand, in one foot deep water at low tide".

Mauritius: Riambel, near Souillac, 24-10-50, R. E. Vaughan, nos. 948, 949. Ile d'Ambre, 2-7-50, G. Morin, no. 968.

2. **Caulerpa brachypus** Harv.

var. *mauritiana* Børgs.
f. *exposita* nov. forma.

In a lately received collection of algae from Mauritius a small *Caulerpa* is found which I consider to be a forma *exposita* of the Mauritian variety.

Fig. 3. *Caulerpa brachypus* Harv. var. *mauritiana* Børgs., forma *exposita* (×1).

As shown in the fig. 3 the erect assimilators are only $\frac{1}{2}$—1 cm high. The margins of the assimilators are somewhat sinuate, but I have been searching for any dentation of this in vain.

The plant was "growing in small ponds constantly swept by water."

Mauritius: Ile Bernache, 26-2-49, G. Morin, no. 969.

3. **Caulerpa cupressoides** (Vahl) Ag.

Alg. Mauritius, I, 1940, p. 50. Add. List, 1946, p. 38.

var. *typica* Weber.

Of this species I have formerly seen only very small and poor specimens. It was therefore of interest in a new collection

sent from Mauritius to find several well developed specimens of var. *typica* Weber.

It was "growing on coral and sand in 1—2 feet of water at low tide in calm water".

Mauritius: Ile d'Ambre, 18-6-50, G. MORIN, no. 973.

4. **Caulerpa racemosa** (Forssk.) Weber v. Bosse.

var. *uvifera* (Turner) Ag.

WEBER, A., Monogr. d. Caulerpes, 1895, p. 362, pl. 33, fig. 24.

This small form, the assimilators of which have a height of about 1 cm, seems to agree quite well with the figure of Mme WEBER referred to above.

The plant was collected on a reef.

Mauritius: Poudre d'Or, 18-6-50, G. MORIN, no. 975.

5. **Caulerpa peltata** Lamour.

var. *stellata* (J. Ag.) Weber.

Caulerpa stellata (J. Ag.), Till Alg. Syst., 1872, p. 38.

Some specimens of a small form of *C. peltata* Lamour. seem to be referable to this variety.

From the delicate creeping rhizome fastened to the substratum by numerous rhizoids short assimilators up to 1 cm high are given out consisting of 1—3, rarely more, discoid ramuli, the uppermost of them issuing from the margin of a disc below. The discs, about 4 mm broad, have a more or less crenulated margin and are now and then dentate.

The plant was found "creeping on rocks and old corals densely entangled with other algae".

Mauritius: Riambel, 23-11-50, G. MORIN, no. 978.

PHAEOPHYCEAE

Dictyotales.

Fam. 1. ***Dictyotaceae.***

Padina Adans.

1. Padina spec.

Vaughaniella rupicola Børgs. A new genus of the Dictyotaceae, 1950.

From the very beginning, when examining this little curious plant, I had great troubles about it. Was it in reality an independent form at all, being for instance homologous to the prostrate rhizome of *Padina Pavonia*? But having been unable to find any trace of *Padina* in the material and especially relying upon the fact that the plant was fertile I gave up my doubts. In this connection I also want to point out that I have collected *Padina* in many places in the tropics, but nowhere I have met with such a striking development of the prostrate filaments, as in the Mauritius plant according to the observations of Dr. VAUGHAN.

Shortly after I had sent out my paper I received from several algologists in Australia and New Zealand letters in which I was told that my paper was of great interest to them, that the plant was well known in Australia, and one of them even wrote that "it solves one of my outstanding problems". Nevertheless I still had my doubts and already before I had sent my paper to Dr. VAUGHAN I asked him to look for *Padina* in connection with *Vaughaniella* and to send me some more material in the hope also perhaps to be able to find the sexual organs. According to my wish Dr. VAUGHAN already last summer sent me some large tufts (Fig. 4) of the plant collected May 3, 1950, no. 917, and as to the locality he wrote: "On flat-topped rocks exposed at low-tide, forms flat moss-like cushions." The examination of this

Fig. 4. *Padina* spec. (*Vaughaniella rupicola* Børgs.). Small bits of the thallus (×1).

material did not show any trace of *Padina*, but neither any sexual or asexual organs.

However, in the beginning of 1951 I received an air-mail letter from Professor ALAN B. CRIBB, Cronulla, N.S.W., dated 13th Jan. 1951, in which he writes: "While I was on holidays in Queensland at Christmas time I was struck by the similarity between *Vaughaniella rupicola* and the basal creeping rhizomatous portion of *Padina Commersonii*. I therefore made careful collections, and after examining the specimens I am of the opinion that *Vaughaniella* is in fact the prostrate juvenile stage of *Padina Commersonii*." And at the same time Prof. CRIBB most kindly sent me some fragments of the rhizome from the

apical tips of which small *Padina*-thalli emerged profusely in various size and development.

An examination of the thallus showed a great likeness to that of *Vaughaniella*, but it was more robust in all respects and not so markedly striated, and the thallus is thicker. Furthermore, a great many apices of the filaments were turned upwards and the tips transformed into smaller or larger juvenile *Padina*-thalli. Professor CRIBB collected the specimen in Weyba Creek, Nossa, Queensland.

Shortly afterwards I received from Mauritius a new larger collection of *Vaughaniella* gathered by Dr. VAUGHAN at Roche Noine, Port Louis, 11-11-50, no. 959. About the locality it is said: "On flat-topped rocks exposed at low tide, calm water." In this collection I have after much search succeeded in finding a quite small *Padina*-thallus emerging from a tip of *Vaughaniella*; besides this some few quite small specimens of *Padina* were found in which I have not been able to observe the connection with the thallus of *Vaughaniella*.

Having thus stated with certainty the connection of *Vaughaniella* with *Padina* I wrote immediately to Dr. VAUGHAN about the fact and in a letter dated Port-Louis 2-3-51 Director VAUGHAN answers: "The information about *Vaughaniella—Padina* is very interesting—but I must say that their habitats are quite different; *Vaughaniella* forms large moss-like growths often several feet square, closely adpressed to flat-topped rocks exposed at low-tide. *Padina* on the other hand likes shallow sandy water in sites usually just covered at lowtide and is often attached to old pieces of rocks and coral debris in the lagoon; one of its favourite habitats here is at the foot of the beach where the lagoon begins. In fact I have never seen them growing together—but in view of your remarks I will make careful note of their association."

So far Dr. VAUGHAN about the habitat of this little peculiar plant. Even if, as said above, *Vaughaniella* is the rhizome of a *Padina*, it seems also to be able to live independently, forming extensive carpets on rocks where *Padina* otherwise does not occur. It is not yet evident what species of *Padina* we have to do with, and an attempt to establish this might perhaps be difficult, when the declaration made above by Dr. VAUGHAN about the occurrence of the two forms, is taken into consideration.

Postscript.

Also the question as to what species of *Padina Vaughaniella* belongs to has been solved, as a specimen (no. 1118) sent in a letter dated june 6, 1951 from Dr. VAUGHAN has shown that the plant is *Padina Commersonii* Bory, thus the same species as that Professor CRIBB has found in Queensland.

The locality of no. 1118 was, according to Dr. VAUGHAN: "at the gently sloping edge of the beach where the lagoon begins—here there are a number of flat-topped, sand covered basalt rocks exposed at low tide and seldom subjected to strong surf or currents. The site was more sheltered than where *Vaughaniella* was previously found; there was in addition well developed thalli of *Padina* growing in the same site (vide specimen enclosed)".

RHODOPHYCEAE

FLORIDEAE

Nemalionales.

Fam. 1. ***Helminthocladiaceae.***

Trichogloea Kütz.

During the war I referred a single specimen of *Trichogloea* in JADIN's collection to *Tr. Requienii* (Alg. Mauritius, III, 1, 1942, p. 17), having at that time no possibility to compare the specimen with authentic material. I have now been able to do so and the result is that the Mauritian plant has turned out to be a new species; but before I enter upon a description of it I shall at first briefly describe the Red Sea plant.

Trichogloea Requienii (Mont.) Kütz.

KÜTZING in Bot. Zeit., vol. 5, 1947, p. 54. ZANARDINI, J., Plant. mar. rubr., 1855, p. 67, tab. V, fig. 1. AGARDH, J., Epicrisis, 1876, p. 514. Non BØRGESEN, Alg. Mauritius, III, 1, 1942, p. 17. — *Batrachospermum Requienii* Mont., Quatrième Centurie Plantes exotiques nouvelles (Ann. sciences nat., II sér., vol. XX, Paris 1843, p. 355).

As it is the first described species of *Trichogloea* it has of course been of a special interest to me to see MONTAGNE's original specimens from the Red Sea, and I am very much obliged to Director, Professor, Dr. R. LAMI, Muséum National d'Hist. Nat., Paris, for permitting me to have them on loan here in Copenhagen.

Two specimens of *Batrachospermum Requienii* Mont. are found in the herbarium; one of them female, the other male. The specimens are fragments only; the ramification is very

irregular, branches issuing without any order with shorter or longer interstices between them and are again provided with branchlets. The thallus is in the thicker parts about 2 mm thick, tapering slowly upwards, the tips of the branches being subacute. The colour of the filaments is whitish-yellowish-olivegreen.

Howe in his paper "Hawaiian Algae", 1934, p. 36, fig. 3,

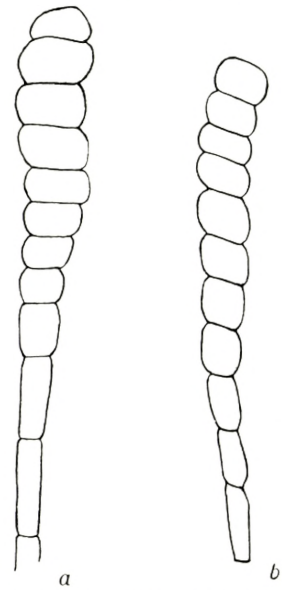

Fig. 5. *Trichogloea Requienii* (Mont.) Kütz. Apical ends of assimilating filaments. (ca. ×350.)

gives a photographic illustration of the female specimen of Montagne. And Zanardini's fig. of a specimen in "Pl. mar. rubr.", p. 67, tab. V, fig. 1, presents quite a good illustration of the plant, only its colour is too green.

The peripheral cells in the assimilating filaments of the thallus are short, especially in the female plant, in which the uppermost ca. 10 cells in the filaments are much broader than the height, about 20 μ broad and 15 μ high (Fig. 5). Another characteristic feature is that in many of the assimilating filaments the transverse walls are oblique (Fig. 5b). In the male plant the sterile assimilating filaments are of about the same shape; but in the fertile filaments the cells become longer, about 10—15 μ or more. Zanardini's figure (pl. V, figs. 3—4) gives quite a good picture of their shape. A. H. Nasr (Synopsis, 1947, p. 95) in his

figure 17 of a gonimoblast of *Tr. Requienii* has drawn the uppermost cells in the assimilating filaments for the most part oblong. No exact information is given as to the question if the plant is dioecious or not.

The occurrence of the antheridial bodies in the assimilating filaments is rather variable, in some cases a single or a few sterile apical cells are found. In others up to 5—6 of the distal cells are fertile and it may happen that the apical cell is fertile, then 1—3 cells are sterile and followed by a row of fertile ones.

In the female plant the gonimoblasts in most cases are dome-like, about 150 μ broad and 125 μ high, but when older often somewhat more irregularly shaped and up to 200 μ broad. The stalk is about 20—30 μ thick; from the uppermost 3 cells in this the nutritive filaments[1] are given out. The uppermost are as a rule the most developed; in rare cases I have seen the uppermost whorl being somewhat upward curved and in that case encircling the base of the gonimoblasts, but most often they are straight outwardly directed like the two smaller ones below, the lowermost ones often consisting only of the basal cells; these are large, nearly ball-shaped, about ca. 20 μ broad. I have not seen any fusion of the cells in the stalk below the gonimoblasts; but this is often difficult to observe because the nutritive filaments cover them.

In the above description I have taken the plant to be dioecious, but this being based upon the two specimens of MONTAGNE only, an examination of more Red Sea material is necessary for confirmation. To be sure, PAPENFUSS (1946, p. 419) found the plant from Hawaii he referred to *Triochigloea Requienii*, in most cases to be dioecious (l. c. p. 425), but I do not feel quite sure about the referring of the Hawaiian plant to the species of the Red Sea, as some differences seem to be present; for instance the shape of the assimilating cells and the fusion of the cells in the stipe of the gonimoblasts which take place in the Hawaiian plant, I have not been able to observe in the Red Sea plant.

The plant PILGER in his papers: "Ueber Trichogloea Kütz.", 1908 refers to *Trichogloea Requienii* is scarcely rightly referred

[1] These filaments are often called sterile filaments, but in my opinion and in conformity with that of PAPENFUSS (1946, p. 431) the purpose of these filaments is that of nursing the gonimoblasts.

to this species to judge from his description and figures of the single specimen he had for examination. Most probably it is referable to one of the species found in Mauritius, but an examination of the specimen is necessary to make this out.

1. **Trichogloea Jadinii** nov. spec.

Trichogloea lubrica Jadin, Algues des Iles de la Réunion et de Maurice, 1934, p. 162. *Trichogloea Requienii* Børgs., Alg. Mauritius, III, 1, 1942, p. 117, fig. 7.

Planta caespitosa, ca. 17 mm alta, in sicco pallide olivacea, calcificatione minore, irregulariter ramosa, ramis majoribus identidem ramulos gerentibus, majoribus in sicco ad 4 mm latis, minoribus tenuioribus, ramis et ramulis ad apicem versus tenuioribus, superne subacutis.

Filamenta assimilationis ca. 600—700 μ longa, in partibus basalibus tenuiora, superne crassiora ex cellulis elongatis oblongisque, ca. 8—12 μ latis composita.

Planta monoica.

Antheridia in filamentis corticalibus, cellulis apicalibus 1—3 sterilibus evoluta. Gonimoblasti subglobosi ca. 150 μ lati et 125 longi, in stipitibus terminales orti. Stipes ca. 20—25 μ latus, cellulis 3 superioribus stipitis filamenta nutritiva in verticillis orta gerentibus.

Mauritius: Flacq, September 1890, JADIN, no. 458. As to the locality JADIN writes: "Sur les récifs, balayés par le courant violent des lames, mais du côté intérieur regardant la lagune."

Of this species (Pl. I) I have had for examination two specimens most probably originating from the same plant, one of these being found in the Muséum National in Paris, the other in my herbarium; and furthermore a large, more ramified specimen and 3 small fragments, all in the collection of the Paris Muséum and collected by JADIN.

From the most probably discoid base a number of erect shoots arise, having a length of up to 20 cm and forming a dense bushy tuft. In the large, by far mostly ramified specimen a great number of side branches issue from the main branches on all sides, bearing again numerous shorter branchlets, often provided

with smaller ones again. Both branches and branchlets are given out in the most irregular way with longer or shorter interstices between them on all sides, but sometimes also unilaterally in shorter or longer rows. The main branches are in a dried condition up to about 4 mm thick. Upwards the branches and branchlets taper to a subacute apex. In a dried condition the colour of the large specimen is olive-yellowish-greyish; and rather much calcified, while the two smaller specimens have a yellowish-brown colour and less calcification.

The plant is monoecious, but the male and female organs are not always found together, very often the female ones are found in one part of the thallus, the male in another.

The assimilating filaments are up to about 700 μ long; when issuing from the medulla they are thin, 3—4 μ thick, becoming slowly thicker and more ramified upwards until near the periphery, where the assimilating parts begin, here being about 8—12 μ thick, and the cells of which they are composed are about double this length.

The antheridial bodies (Fig. 6), being very like those found in other species of *Trichogloea*, are developed near the distal end of the assimilating filaments, leaving in most cases a single or 2—3 apical cells sterile; but it may happen that the apical cell is fertile; 2—4 up to 10 cells in a row may be fertile.

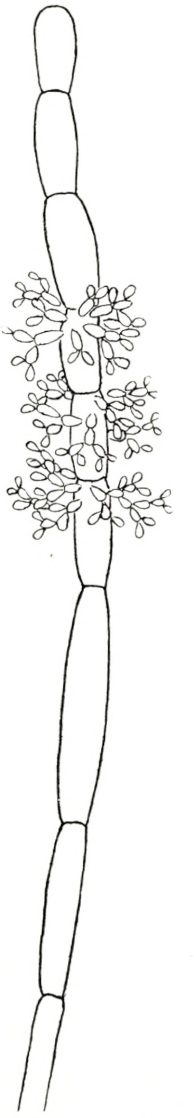

Fig. 6. *Trichogloea Jadinii* n. spec. Assimilating filaments with antheridia. (× ca. 400.)

The young gonimoblasts are about globose, the older ones dome-like, about 150 μ broad and 125 μ high, often also more irregularly shaped and more loosely built, showing also in later stages the branched filaments of the gonimoblasts.

From the vigorous, rather long and thick stipe, in older gonimoblasts up to 40 μ thick, 3—4 but not rarely up to 5 and even 6 whorls of nutritive filaments are given out, the uppermost or sometimes also the second being the largest (Fig. 7). The

filaments are mostly straight outwardly directed, bristly, downwards with increasing distances between the whorls. The basal cells in the nutritive filaments are often large and ball-shaped,

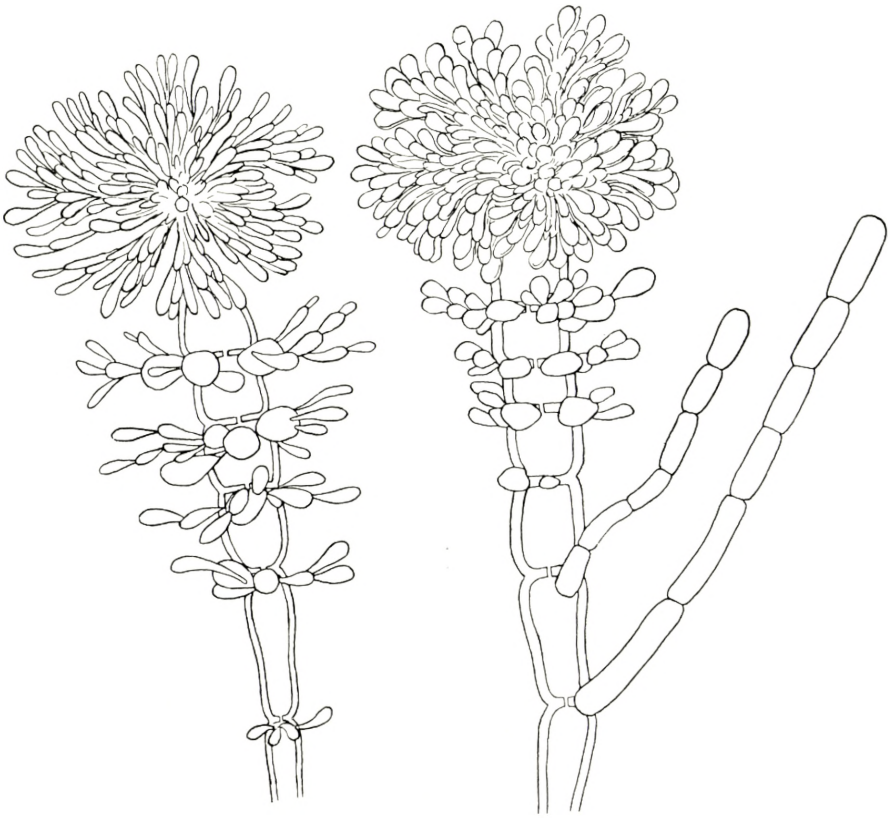

Fig. 7. *Trichogloea Jadinii* n. spec. Two gonimoblasts. (× ca. 400.)

up to about 30 μ broad; then the cells in the filaments decrease in size to the distal ones; downwards the filaments become shorter, the lowermost one consisting of the basal cell only.

The 3 small specimens or fragments only are whitish-rosy of colour, but as far as I have seen sterile.

No fusion of the cells in the stipe has been observed.

At a first glance the large and the two small specimens must be said to be rather distinct, but on closer examination also of the structure I have arrived at the conclusion that they are the same species. It is of course always a drawback to have so little

material to work with and still more when it surely has been more or less decayed, which in the tropics rapidly takes place with algae, especially in the case of such soft, fleshy forms as *Trichogloea*.

Still I want to remark that the gonimoblast figured by OKAMURA in "Icones", vol. IV, p. 188, tab. 197, fig. 6, of an alga he refers to *Trichogloea lubrica* shows much likeness to the Mauritian species, but the habit figure of the Japanese plant seems rather deviating.

2. **Trichogloea** spec.

Myriocladia capensis Dickie, Algae of Mauritius, 1873, p. 191.

Professor W. RANDOLPH TAYLOR in a letter dated 5 Oct. 50 most kindly called my attention to a plant which NICHOLAS PIKE in 1869 had collected in Mauritius and of which 4 specimens are found in the herbarium of the New York Botanical Garden, being named *Myriocladia capensis* by DICKIE (Algae of Mauritius, 1873, p. 191). And Professor TAYLOR wrote about them: "The specimens seem to me to be *Trichogloea*."

Occasioned by this I wrote to Miss DICKINSON, Keeper of the Algal Herbarium at Kew, asking her if a specimen collected by PIKE and determined as said by DICKIE was found in the herbarium. In a letter of Dec. 12 Miss DICKINSON most kindly informed me that such a specimen was found there and that it was laid in the *Trichogloea lubrica* cover. By permission of Director, Sir EDWARD SALISBURY, Kew, I have had the privelege of having it on loan here.

I had of course expected that the plant collected by PIKE should be the same as that of JADIN mentioned above, but a glance at it was enough to show that in reality it is, indeed, a *Trichogloea*, though not JADIN's species but rather a new species of this genus. In the following I shall give a short description of it.

The specimen, or more correctly only a fragment of a specimen, is about 20 cm high. From the main axis the side-branches are given out more or less verticillately with a distance of about 1 cm or more irregularly. The side-branches are again branched and ramuli are given out from the latter. In the middle of the

thallus several small branchlets issue from the main axis between the larger ones. The main stem is about 4 mm thick and all branches and branchlets taper towards the rather blunt apices. The colour of the dried plant is a dirty olive-green.

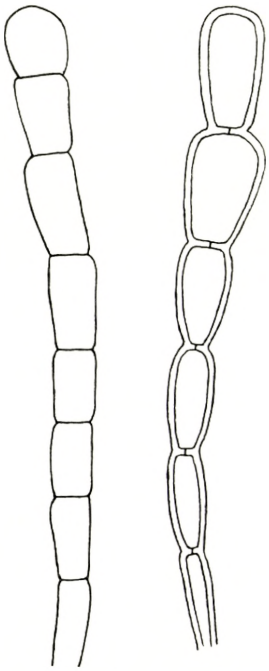

Fig. 8. *Trichogloea* spec. Apical ends of assimilating filaments. (× ca. 350.)

An examination of a small fragment of the specimen has shown that it is most probably sterile.

Regarding the structure of the plant I shall therefore restrict myself to mention that the distal part of the assimilating filaments is composed of cells often nearly cylindrical or also somewhat broader above, having a breadth of about 10—12 μ and 2 to 3 times this length (Fig. 8).

Besides, the specimen seems to be in rather a bad condition, having surely been much decayed before preparation.

Mauritius: Near Barkly Island, July 1870, Colonel PIKE, no. 194.

When treating the species of *Trichogloea* from Mauritius I shall in this connection also mention a characteristic species of this genus

I have several years ago received from Mme WEBER VAN BOSSE and which Mme WEBER had determined as *Tr. Requienii* (Mont.) Kütz.; the specimen was collected in Java by the Swedish botanist HJALMAR MØLLER in the year 1897.

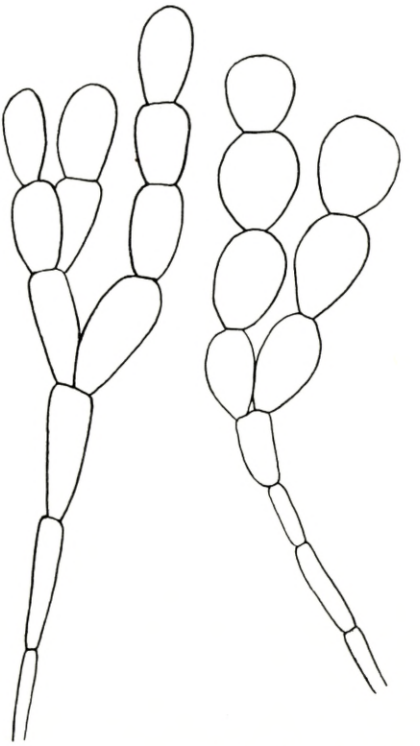

Fig. 9. *Trichogloea javensis* nov. spec. Apical ends of assimilating filaments. (× ca. 350.)

The shape and appearance of this species is very deviating from that of the present known species of *Trichogloea*, reminding, when superficially observed, very much of a brown alga for instance an *Eudesme* or *Chordaria*.

Pl. II shows the habit of the plant. The specimen consists of several fragments mounted together. From the main branches short branchlets, 3—10 mm long, issue in all directions with a distance between them of a few mm. The main branches are 1—1½ mm thick, while the branchlets are only half this breadth. The consistency of the plant is firm and the calcification moderate; the colour of the thallus is dark-brownish.

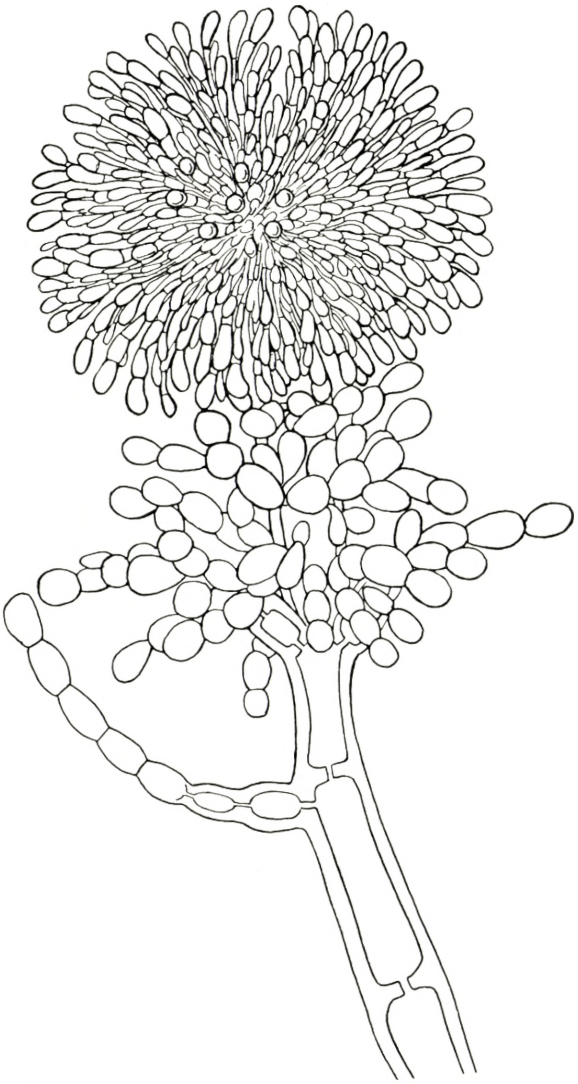

Fig. 10. *Trichogloea javensis* nov. spec. A gonimoblast. (× ca. 400.)

An examination of the structure of the plant has shown this to be in good accordance with that of other species of *Trichogloea*, but in detail characteristic differences are present.

The assimilating filaments are about 600 μ long and repeatedly forked, thin at the base and there composed of long cells; upwards the filaments become gradually thicker and the

cells shorter, in the assimilating part they are moniliform with oblong cells about 15—25 μ thick and 20—30 μ long; (Fig. 9) the uppermost, often nearly ball-shaped, cells are mutually more or less coherent, even after decalcification.

The plant is most probably dioecious, in any case the specimen I have seen is female. No trace of antheridia has been observed.

The gonimoblasts are subglobose-domelike, about 150 μ broad and a little less high; but larger ones, especially broader ones, are found, for instance one was 200 μ broad and 110 μ high and their shape may be rather irregular (Fig. 10).

The stalk is up to about 30—35 μ thick; from the upper cells in this the nutritive filaments are given out, forming a dense more or less compact and broadly expanded collar below the gonimoblasts; but in rare cases the uppermost whorl may be somewhat upward bent towards the base of the gonimoblasts.

The nutritive filaments are often longer than the breadth of the gonimoblasts, those in the figure reaching a length of about 175 μ, and the cells of which they are composed are oval, to pyriform, large, up to about 20 μ broad; the apical cells in the filaments are more or less mutually coherent.

Besides the very characteristic appearance of the thallus of this species, it is characterized by the broadly oval cells in the distal parts of the assimilating filaments, which give them a moniliform appearance, the domelike robust gonimoblasts and the vigorously developed nutritive filaments being densely gathered just below the gonimoblasts.

At last a description in Latin of the species.

Trichogloea javensis nov. spec.

Specimen unicum observatum ex fragmentis majoribus compositum. Rami majores plus minus ramosi et ramulosi, ramulis brevibus numerosis ca. $\frac{1}{2}$—1 mm longis sparse ortis.

Thallus teres, rami majores ca. $1\frac{1}{2}$—2 mm, ramuli ca. $\frac{1}{2}$ mm in sicco lati, superne subacuti. Consistentia thalli firmior, calcificatione moderata.

Filamenta assimilationis ex medulla orta, ca. 600 μ longa ad

apicem moniliformia, ex cellulis oblongis-subovatis composita, ca. 12—17 μ crassis et 20—22 μ longis, cellulis apicalibus inter se plus minus cohaerentibus.

Planta ut videtur dioica, antheridia in fragmentis thalli praesentibus non observata.

Gonimoblasti subglobosi, ca. 150—200 μ lati et ca. 100—130 μ longi, stipites firmi ca. 30—35 μ lati; filamenta nutritiva praesentia ex cellulis superioribus stipitis orta, verticellata, expansa, robusta ca. 175 μ longa, ex cellulis oblongis 5—7 μ latis composita.

JAVA, Zandbaai, Tjisolok, 29-7-1897, legit HJ. MØLLER.

Liagora Lamouroux.

1. **Liagora decussata** Mont.

MONTAGNE, C., in Ann. Sciences Nat. Bot., 1849, p. 64. KÜTZING, Spec. alg., 1849, p. 538. AGARDH, J., Spec. alg. vol. II, 1852, p. 429. YAMADA, Y., The Species of Liogora from Japan, 1938, p. 22, pl. VII and figs. 13—14.

I have lately received some beautiful specimens of this species from Dr. VAUGHAN. The specimens form large dense tufts up to 17 cm high composed of the much ramified filaments.

The plant is strongly calcified becoming rather much longi-

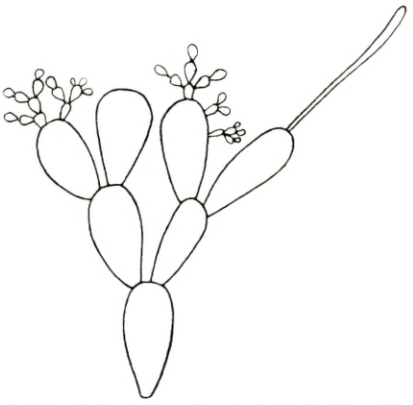

Fig. 11. *Liagora decussata* Mont. Apical ends of assimilating filaments with antheridia and a hair. ($\times$ ca. 350.)

tudinally shrivelled in a dried condition. The colour of the dried specimens is rosy-whitish.

When decalcified the thallus is rather tough and the assimilating filaments, being much entangled in their distal ends, are rather difficult to separate from each other.

From the apical cells in the assimilating filaments numerous hairs are given out. The apical cells are oblong-pyriform, above 7—10 μ thick.

Only male specimens are found. Fig. 11 shows the antheridial bodies together with a hair emerging from the assimilating filaments.

As to the locality it is said: "In deep pools behind reef often epiphytic."

Mauritius: Riambel, 23-11-50, R. E. V. no. 991.
Geogr. Distr.: West Indies, Formosa.

2. **Liagora ceranoides** Lamx.

Alg. Mauritius, III, 1, 1942, p. 28. Additions, I, 1949, p. 32.

A fine specimen of the var. *pulverulenta* (Ag.) Yamada, Spec. of *Liagora* from Japan, 1938, p. 21, pl. VI, is found in a newly received collection of algae from Mauritius.

Mauritius: Pointe aux Roches: "In shallow water near shore", 10-9-50, R. E. Vaughan, no. 939.

3. **Liagora mauritiana** Børgs.

Alg. Mauritius, III, 1, 1942, p. 32, figs. 15-10, pl. II, fig. 3.

This species was described upon a single, rather badly preserved specimen found in Jadin's Herbarium in Paris. In a collection of algae recently received from Mauritius several fine specimens of a *Liagora* are found which seems to me referable to the species in question.

The specimens were found as epiphytes on *Cymodocea* and formed roundish dense tufts with a diameter up to about 10 mm (Plate III).

Their colour is dark-reddish, which is due to the fact that the tips of the assimilating filaments protrude above the surface

of the chalk incrustation forming a rather dense cover above it, as was also found in the original specimen.

And furthermore, to judge from the outside of the thallus, the recently received specimens in a dried condition show the same characteristic parallel arrangement of the branches and

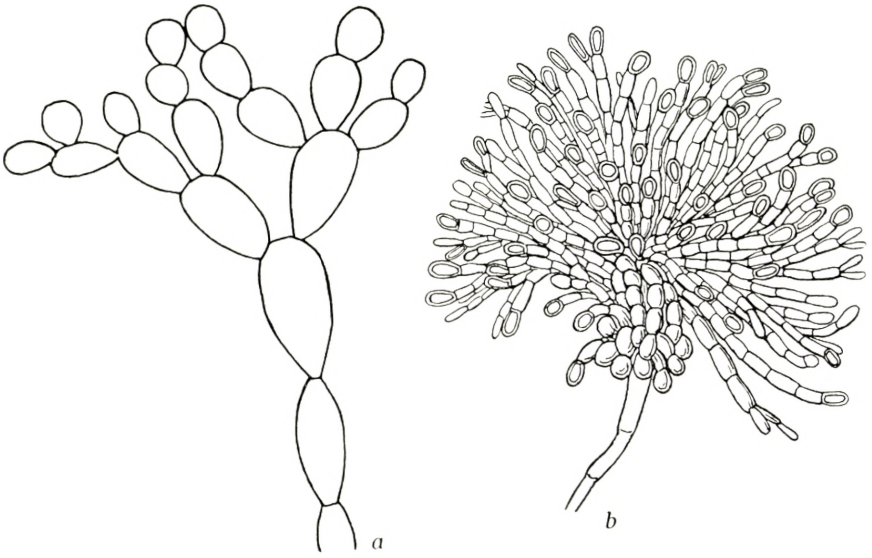

Fig. 12. *Liagora mauritiana* Børgs. *a*, upper parts of assimilating filaments; *b*, a gonimoblast. (× *a*, about 400; *b*, about 250 μ.)

branchlets as is clearly seen in the right part of JADIN's specimen reproduced in pl. II, fig. 3 b, c.

The structure of the thallus likewise seems to be in good accordance with what is said in the description of the species.

The assimilating filaments (Fig. 12) are very alike, composed in their basal part of rather thick cylindrical cells, in their upper part of pyriform, at the top nearly globular cells (Fig. 12 a).

In the semiglobular gonimoblasts the involucral filaments are not much developed and a cell-complex of longer or shorter filaments is found at the base of the gonimoblasts (Fig. 12 b).

In the Latin diagnosis of the species it is said that it is monoecious; but in the specimens I have now examined I have not been able to find any antheridia.

I want to point out that I have sent a fragment of one of the specimens together with a small bit of the type-specimen to

Dr. J. ABBOTT, Hopkins Marine Station, California, asking Mrs. ABBOTT whether in her opinion they are the same species or not. She has most kindly answered me as follows: "No. 992 from Mauritius I believe, as you do, is similar to *L. mauritiana*, and any differences I have observed I feel are minor ones."

About the locality Dr. VAUGHAN writes: "Grows on stems of *Cymodocea* on the lagoon side of reef."

Mauritius: Riambel near Souillac, 28-11-50, R. E. V. no. 992.

4. **Liagora Vaughani** nov. spec.[1]

Frons caespitosa, teres, valde calce incrustata, subfragilis, ca. 10—11 cm alta, alba rosea, superficie thalli in sicco farinaceo-scabrida, ramosa.

Rami et ramuli repetite furcati, majores ca. $1\frac{1}{2}$ mm, minores ca. $\frac{3}{4}$ mm crassi.

Axis centralis frondis ca. 300 μ latus ex filamentis ca. 20 μ latis compositus.

Stratum periphericum ex filamentis assimilationis subdichotomis ca. 300 μ longis, cellulas in parte basali subcylindricas ca. 8—10 μ latas, ad apicem filamentorum versus oblonge ovales, superne subpyriformes continentibus, formatum.

Rami carpogonici robusti, ca. 15—20 μ lati, recti aut fere recti, ex 5 in casu 4 cellulis brevibus compositi; cellula carpogonica conica in trichogynum longum productum.

Gonimoblasti subglobosi aut magis irregulariter formati ex filamentis sterilibus circumcincti.

Mauritius: Riambel, near Souillac. "In deep pools near reef or on the stems of *Cymodocea* and *Sargassum*", 23-11-50, R. E. V. no. 990.

This species (Plate IV) forms a large, dense, paniculate tuft about 10—12 cm high, and is composed of repeatedly furcated, more or less curved branches and branchlets giving the thallus on umbellate appearance. The thicker branches are about $1\frac{1}{2}$ mm thick, tapering very slowly upwards to about $\frac{3}{4}$ mm near the tips.

The calcification is strong, the uppermost tips of the assi-

[1] Named in honour of Director, Dr. R. E. VAUGHAN.

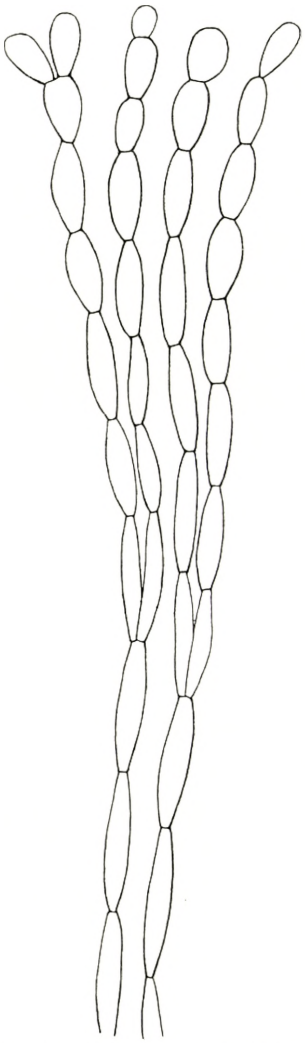

Fig. 13. *Liagora Vaughani* nov. spec. Assimilating filaments. (× ca. 250.)

milating filaments protruding very little or not at all above the chalk incrustation.

The colour of the thallus in a dried condition is whitish-rosy. The surface of the thallus is uneven with numerous small pits given it a mealy appearance, and especially in the younger parts of the thallus is rather much shrivelled.

The central axis of the thallus is composed of nearly cylindrical filaments about 20 μ thick. The assimilating filaments are about 300 μ long; in the younger parts of the thallus the filaments are straight upward directed, closely placed, and nearly parallel (Fig. 13); in their proximal ends they are composed of nearly cylindrical cells upwards becoming gradually ellipsoidal, the apical ones more shortly oval or pyriform, 7—10 μ thick; when older the distal parts of the filaments become more irregularly corymbose and mutually entangled, and after decalcification are pasted together with a tough slime, and rather a strong pressure is necessary to separate them.

The apical cells of the assimilating filaments are provided with numerous hairs in the young parts of the thallus.

The species is most probably dioecious, in any case no antheridial bodies have been observed in the single specimen found.

The carpogonial branches are laterally placed upon a cell above the dichotomy in the assimilating filament; they are nearly straight or very little curved, robust, about 15—20 μ thick and provided with a long trichogyne. It is usually composed of 5 cells, more rarely of 4 only (Fig. 14a).

In the younger gonimoblasts (Fig. 14b) the involucral filaments are obliquely upward directed, encircling the rather densely

placed gonimoblast-filaments; when older the involucral filaments become more outwardly spread.

In the course of time a good many species related to *L. valida* have been described and the species described here seems also

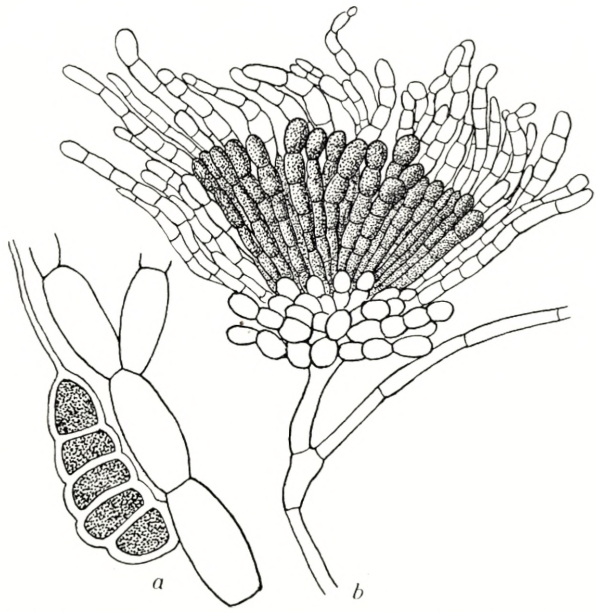

Fig. 14. *Liagora Vaughani* nov. spec. *a*, carpogonial branch; *b*, a gonimoblast. (*a*, × about 400; *b*, × about 200.)

referable to this group, but in one respect in any case it seems to be distinct from the many species referred to this group, namely by the shape of the carpogonial branch which otherwise in this group is curved. But having only one specimen to rely on I wanted to hear Dr. ABBOT's opinion about its specific value, and she has most kindly informed me that it ought to be described as a new species.

5. **Liagora farinosa** Lamx.

Alg. Mauritius, III, 1, 1942, p. 36 and Additions, 1949, p. 33.

Some very fine material of this species has lately been received from Mauritius. A female plant (no. 950) forms a large tuft about 15 cm high. Two other specimens (no. 952) are smaller and seem to be sterile, but material preserved in formol and

seawater, also numbered 952, is loaded with the characteristic antheridial bodies.

The specimens were gathered "in deep pools" and about no. 952 it was added: "often attached to other algae".

Mauritius: Riambel, near Souillac, 24-10-50, R. E. V. nos. 950, 952.

6. **Liagora Pikeana** nov. Spec.

Frons caespitosa, teres, verisimiliter mollisima, incrustatione calcarea nulla aut minima, ramosa, ramificatione irregulariter subfurcata aut alternata.

Rami majores in parte basali frondis nudi, ca. 1 mm lati, apicem versus filamentis assimilationis dense instructi ca. $\frac{1}{2}$ mm latis apicibus ramulorum obtusis.

Color thalli in sicco sordide roseus. Axis centralis thalli ca. 150 μ latus ex filamentis subcylindricis, ramosis, inter se contectis compositus.

Filamenta assimilationis ca. 150—200 μ longa, repetite furcata, in parte basali ex cellulis subcylindricis, sursum pyriformibus, ca. 7—10 μ latis in apice subglobosis formata.

Species verisimiliter dioica, antheridiis non observatis.

Rami carpogonici non visi.

Gonimoblasti subsphaerici, ca. 135—170 μ alti et 170—200 μ lati, ex filis carposporiferis compositi, filamentis involucralibus, ex cellulis infra ramos carpogonici ortis, plus minus circumcincti.

Mauritius: No locality is recorded. Colonel NICHOLAS PIKE legit.

In part III, 1, 1942, p. 40, pl. I, fig. 1 I erroneously referred a single specimen of *Liagora* collected by NICHOLAS PIKE to *Liagora lurida* Dickie, but in Additions I, 1949, p. 34 I corrected this mistake, pointing out that DICKIE's *L. lurida* in reality was a variety of *L. farinosa*.

In a later collection of algae received from Dr. VAUGHAN and collected by PIKE a specimen of the *Liagora* in question is also included, as far as I am aware being not yet described, beyond the quite short description given by myself, I shall in what follows redress this want.

As has already been stated the plant has in a living condition

had a soft, mucous thallus very little incrusted by chalk. Both specimens are fragments only, so it is not possible to say anything about the size of the plant. The specimens are much ramified; compare the habit-figure in part III, pl. I, fig. 1; from the thin, scarcely 1 mm broad, main stem numerous branches and

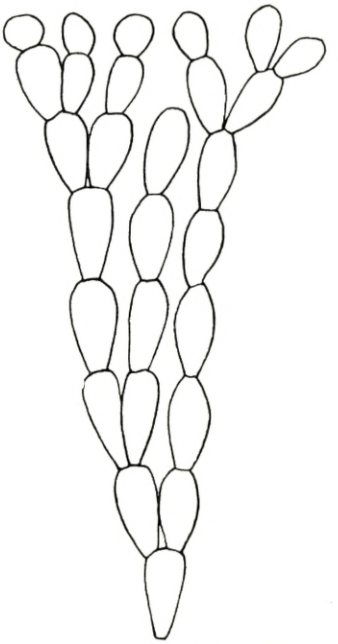

Fig. 15. *Liagora Pikeana* Børgs. Assimilating filaments. (× about 300.)

branchlets are given out, alternating irregularly or secund.

Below the main branches are naked without assimilating filaments, higher up the branches and branchlets are densely covered with these, getting a breadth of about $\frac{1}{2}$—$\frac{3}{4}$ mm and keeping this breadth upwards to the roundish apex.

As to the structure of the thallus the central strand, composed of densely packed filaments, is about 150 μ thick. The assimilating filaments are about 150—200 μ long, often furcated and composed upwards of elongated pyriform cells about 7—10 μ thick, the uppermost one being shorter, subglobose to pyriform (Fig. 15).

No carpogonial branches have been found. The gonimoblasts (Fig. 16) are domelike or subglobase, about 170—200 μ broad

and 135—170 μ high, forming rather a dense mass. The involucral filaments are well developed, reaching a length of up to 200 μ. The uppermost of these are bending upwards round the base of the gonimoblasts, those in the middle are more or less straightly outward directed and the lowermost are bending downwards.

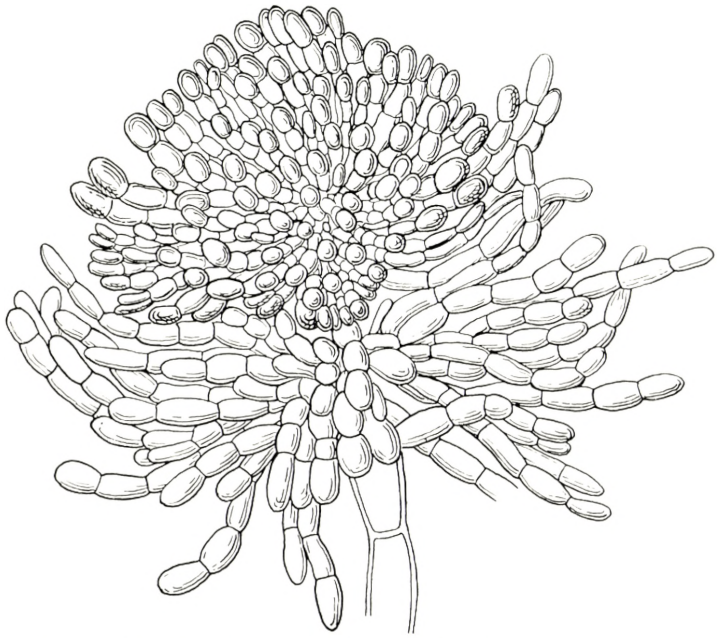

Fig. 16. *Liagora Pikeana* Børgs. A gonimoblast. ($\times$ ca. 1100.)

The plant is most probably dioecious, in any case I have not met with any antheridial bodies in the specimens.

I want to add that the specimens are densely filled with hyphae of fungi and surely must have been much decayed when they were prepared, why they are not very suitable for examination.

Compared with other not or very little calcified *Liagora* species, *Liagora pectinata* Collins and Herv. from Bermuda differs essentially by its in all respects larger thallus, the ramuli for instance being more than 1 mm thick and tapering to the subacute apices, while in *Liagora Pikeana* these are only about half this breadth and keeping this size upwards to their rounded apices.

Likewise the two Japanese species: *Liagora mucosissima* Yam. and *Liag. formosana* Yamada. The species of *Liagora* from Japan,

1938, p. 30 and p. 32, are easily discernible from the Mauritian plant, the first named by the absence of any involucral filaments, while in the latter species the involucral filaments are short and more or less pendent.

Fam. ***Chaetangiaceae.***

Actinotrichia Decsne.

1. **Actinotrichia fragilis** (Forssk.) Børgs.

Alg. Mauritius, III, 1, 1942, p. 44; Additions, II, 1950, p. 5.

Some very fine, large, roundish tufts of this species are found in collections received lately, but to my great disappointment they are all sterile.

Fertile specimens are rarely met with. They ware first discovered by Mme WEBER (Alg. Siboga, p. 207); C. K. TSENG in his paper: Studies on the *Chaetangiaceae* of China, p. 96, mentions that he has found antheridial bodies; compare his figure 8c.

The specimens have a very fine rosy-red colour. The tufts reach a diameter of up to about 12 cm.

As to the locality it is said: "Forms large roundish cushions in shallow water near shore", and upon another label: "Near shore in shallow water: Fish-landing station."

Champia parvula was found intermingled among the thallus of *Actinotrichia*.

Flic-en-Flacq, 3-5-50, R. E. V. no. 916.

Galaxaura Lamouroux.

1. **Galaxaura mauritiana** Børgs.

Alg. Mauritius, Additions, I, 1949, p. 35.

Not without doubt I refer some lately received specimens of *Galaxaura* (no. 920) to this species, because short assimilating filaments containing 4 cells are rarely found and in the few cases in which I have met with them the supporting cell was not de-

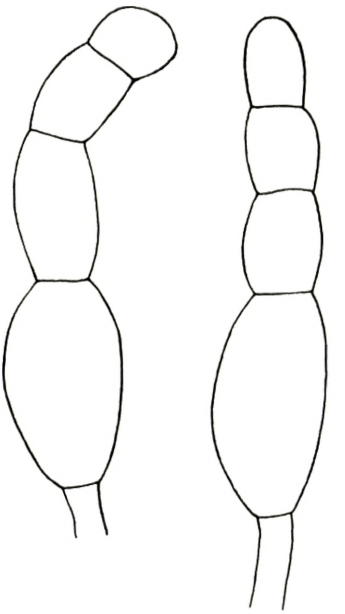

Fig. 17. *Galaxaura mauritiana* Børgs. Two short assimilating filaments. (× about 300.)

veloped (Fig. 17). But apart from this defect the specimens in question were in good conformity with those which I formerly have seen.

Mauritius: Flic-en-Flacq, 3-5-50, R. E. V. no. 920.

2. **Galaxaura oblongata** (Ellis et Sol.) Lamx.

Alg. Mauritius, III, 1, 1942, p. 49; Additions I, 1949, p. 41.

In a collection of algae received from Dr. VAUGHAN in the autumn of 1950 several well developed specimens of a *Galaxaura* are found which in conformity with my former conception of the species I refer to *Galaxaura oblongata*.

The specimens when living must have formed semiglobular balls, the larger ones about 12 cm broad. The specimens are sexual, some female and some male.

As to the locality in which the specimens were found Dr. VAUGHAN remarks: "in channels between rocks in swiftly flowing

water"; during ebb-tide upon a sloping exposed coast such small streams are often found, being outflow from higher lying rock-pools.

Mauritius: Flic-en-Flacq, 3-5-50, R. E. V. no. 921.

3. **Galaxaura umbellata** (Esper) Lamx.

Lamouroux, J. V. F., Extrait etc. 1812, p. 185; Histoire des polypiers coralligènes flexibles, Paris 1816, p. 262. Chou, Ruth Chen Ying, Pacific Species of Galaxaura, II. Sexual Types, 1945 (published 1947), p. 14, pl. V, figs. 1—6, pl. XI, fig. 1. — *Galaxaura obtusata* (Sol.) Lamx., Howe, M. A., A Note on the structural Dimorphism, etc. 1917, p. 621. Svedelius, N., Critical Notes, etc., 1945, p. 52.

For more literature see the papers quoted above.

In Alg. Mauritius, III, 1, 1942, p. 54 I referred a sterile specimen of *Galaxaura*, having the structure of that found in the group *Cameratae* of Kjellman, containing only tetrasporic individuals, to *G. breviarticulata* Kjellm.

It is therefore of interest that in a recently received collection of *Galaxaura* I have found the sexual form of the species, namely *G. umbellata* (Esper) Lamour. syn. *G. obtusata* (Sol.) Lamour., belonging to the group *Spissae* Kjellm. containing sexual forms only.

When, as done above, I have named the species *G. umbellata* (Esper) Lamour. it is according to the observation of Ruth Chou (Pacific Species of *Galaxaura*, II, 1945, p. 14), that the name of Esper has the priority.

Svedelius in his elaborate paper: Critical Notes on some Species of *Galaxaura* from Ceylon, 1945, p. 52, has given a very detailed description of this species to which I refer here, pointing out only that Svedelius has been able to examine several type-specimens of Kjellman's new species of the Sectio *Dichotomaria* comprising the groups *Cameratae* and *Spissae* and has found that they are to be referred to the present species.

The very fine specimens were gathered by Dr. Vaughan in "calm water near shore".

Mauritius: Les Salines, Roche Noire, Port Louis, 11-11-1950, R. E. V. no. 965.

Geogr. Distr.: Found in most tropical seas.

Fam. ***Bonnemaisoniaceae.***

Asparagopsis Mont.

1. **Asparagopsis taxiformis** (Delile) Collins et Herv.

Collins, F. S. and A. B. Hervey, The Algae of Bermuda, 1917, p. 117. Børgesen, F., Mar. Alg. D. W. I., 1919, p. 352, figs. 347—351. Feldmann, P. J., et Geneviève Feldmann, Recherches sur les Bonnemaisoniacées et leur Alternance de Générations, 1942, p. 75. — *Fucus taxiformis* Delile, Flore d'Egypte, 1813, p. 151.

For more synonyms and literature see the above mentioned papers.

In the paper quoted above Jean Feldmann et Mme Feldmann have published their highly interesting observations on the genera *Asparagopsis* and *Falkenbergia*, making it clear that the genus *Falkenbergia* formerly considered as autonomic in reality comprises the tetrosporophytes of the genus *Asparagopsis*. And furthermore they have demonstrated that the number of species known of *Asparagopsis* are to be reduced to two: the above mentioned *Asp. taxiformis* and *Asp. armata* Harv. and in conformity with this that the species of *Falkenbergia* likewise are to be reduced to two: *Falk. Hillebrandii* (Barnet) Falkeb. and *Falk. rufolanosa* (Harv.) Schmith, the former being the tetrasporophyte of the species of *Asparogopsis* mentioned here.

Asparagopsis taxiformis has not previously been found in Mauritius. About the locality where it was found Dr. Vaughan writes: "In shallow water near shore attached to old coral."

Mauritius: Pointe aux Roches, 10-9-50, R. E. V. no. 938.
Geogr. Distr.: Widely distributed in warm seas.

Gelidiales.

Fam. 1. ***Gelidiaceae.***

Gelidiella Feldm. et Hamel.

1. **Gelidiella acerosa** (Forssk.) Feldm. et Hamel.

Alg. Mauritius, III, 2, 1943, p. 5. Additions, II, 1950, p. 5.

Of this species I have formerly seen only rather poorly developed specimens; but in a recently received collection of algae several well developed specimens are included.

As to the locality it is said: "In crevices of large rocks near reef."

Mauritius: Flic-en-Flacq, 10-9-50, R. E. V. no. 945.

Cryptomeniales.

Fam. 1. Callymeniaceae.

Callymenia J. Ag.

1. **Callymenia Morelii** (Mont. et Millardet) Børgs.

Pachycarpus Morelii Mont. et. Mill.

Montagne, C. et M. Millardet, Algues, in Maillard, Notes sur L'ile de la Réunion, Paris 1862, p. 6, pl. XXVI, fig. 2.

In a collection of algae lately received from Mauritius several specimens of a small species were included of which some of the more poorly developed specimens in a striking way reminded of the picture of an alga which Montagne et Millardet in their above quoted paper have called *Pachycarpus Morelii*. About this plant De-Toni in Sylloge Alg., vol. IV, 1897, p. 254 writes: "est forsan *Callymeniae* sp." An examination of the structure of the plant has shown that it is that of *Callymenia*. Therefore even if I have not been able to compare the specimens from Mauritius with authentic material I do not hesitate to refer the plant from Mauritius to that from Réunion.

In the specimens (Pl. V), the largest ones about 7—8 cm high, the bases are missing, but according to the description the plant is fixed to the substratum by a plexus of decumbent stipes from which the wedge-shaped upwards more or less broadened thallus arise.

Upwards and along the upper margin the thallus becomes divided in the most irregular way in a greater or smaller number of lobes just as likewise often numerous proliferations of various size are given out from the edge, the thallus in this way getting a lacerate and flabby appearance.

The thallus is flexible and tough, slippery when wet, thus splendidly fitted to live in strong surf.

As to the structure of the thallus a transverse section shows that this agrees completely with that which KYLIN (1928, p. 59, fig. 1) has given of *Callymenia reniformis*; below the small cortical cells 3—4 layers of larger cells follow, from the lowermost of which ramified filaments are given out, forming the medullary layer.

In the material at hand I have found only female specimens; the large cupola-like cystocarps are scattered over the surface of the thallus.

A transverse section of a cystocarp demonstrates that they are built quite in conformity with those of *Call. reniformis* according to KYLIN's fig. 37 c (l. c.), viz. several large groups of carpospores separated from each other by a tissue of rhizoid-like filaments.

Unfortunately no tetrasporic specimens are included in the collection; according to the description of MONTAGNE and MILLARDET the sporangia are scattered over the surface of the thallus; they are said to be triangularly divided, but this is surely wrong, as the sporangia in the *Callymeniaceae* are cruciately divided.

As to the localities it is said about no. 943: "Exposed places, washed by strong surf", and about no. 957: "firmly attached to rocks in exposed localities washed by strong surf."

Mauritius: Savinia, 17-9-50, R. E. V. no. 943. Riambel, 24-10-50, R. E. V. no. 957.

Geogr. Distr.: Réunion.

Gigartinales.

Fam. 1. ***Soliceriaceae.***

Eucheuma J. Ag.

Sectio I. *Axifera.*

1. **Eucheuma horridum** (Harv.) J. Ag.

Alg. Mauritius, III, 2, 1943, p. 44, figs. 17, 18.

Of this species endemic in Mauritius some fine specimens are found in a recently received collection; Pl. VI shows one of these. As appears from this, the specimens are in good conformity with the type-specimen of Harvey in Herb. Kew. This species

comes near to some forms of *Eucheuma muricatum*, but its thallus is slender and the spines smaller, slender, and undivided.

About its occurrence Dr. VAUGHAN says that it grows in rock crevices on reefs.

Mauritius: Flic-en-Flacq, 3-4-50, R. E. V. no. 902 and the same locality, 3-5-50, R. E. V. no. 924.

Fam. 2. Gracilariaceae.

Corallopsis Grev.

1. **Corallopsis Opuntia** J. Ag.

Alg. Mauritius, III, 2, 1943, p. 47; Additions II, 1950, p. 24, figs. 9—10.

Some fine specimens are found in a collection of algae lately received from Dr. VAUGHAN.

The specimens were collected in shallow water, just behind reef.

Mauritius: Flic-en-Flacq, 3-5-50, R. E. V. no. 923.

Gracilaria Grev.

1. **Gracilaria dura** (Ag.) J. Ag.

AGARDH, J., Alg. Mediterranea, 1842, p. 151; Spec. Alg., II, 2, 1852, p. 589; Epicrisis, 1876, p. 419. — *Sphaerococcus durus* Ag., Spec. Alg., 1821, p. 310.

Some specimens quite recently received from Mauritius seem to agree quite well with the description of this species, but I have not been able to compare the specimens with authentic material. It is characteristic of this species that unilateral branchlets placed in short rows are given out here and there from the main filaments; compare Pl. VII.

KÜTZING's figures in Tab. Phycol., vol. 18, tab. 78 and tab. 76 (as *Sphaerococcus Sonderi*) are not very characteristic.

A transverse section of the thallus shows that the cells near

the periphery are quite small, increasing in size towards the middle of the thallus, where they have a diameter of about 500 μ.

In the tetrasporic specimens the sporangia are scattered in the cortical layer. While the thallus in the tetrasporic specimens reaches a breadth of about 2 mm, that in the female plant is somewhat thicker, about $2\frac{1}{2}$ mm; the cystocarps are scattered over the thallus.

The plant was collected in "calm waters near the shore attached to corals".

Mauritius: Flic-en-Flacq. "Near shore in shallow water at low tide", 3-5-50, R. E. V. nos. 907, 918, and 919.

Rhodymeniales.

Fam. 1. ***Rhodymeniaceae.***

Coelothrix Børgs.

1. **Coelothrix indica** Børgs.

Alg. Mauritius, III, 3, 1944, p. 14, figs. 9—11. Additions, II, 1950, p. 40, figs. 20, 21.

Some fine, but most regrettably sterile specimens of *Coelothrix* have been sent lately from Mauritius. The specimens form rather large, dense tufts of a dark red-brown colour.

About the locality it is said: "Upon rocks on reef exposed to surf. Often epiphytic upon *Digenea*, etc."

Mauritius: Flic-en-Flacq, 3-4-50, G. Morin, no. 908.

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Index specierum.

with some few synonyms, the latter printed in italics.

Chlorophyceae

Phaeophyceae

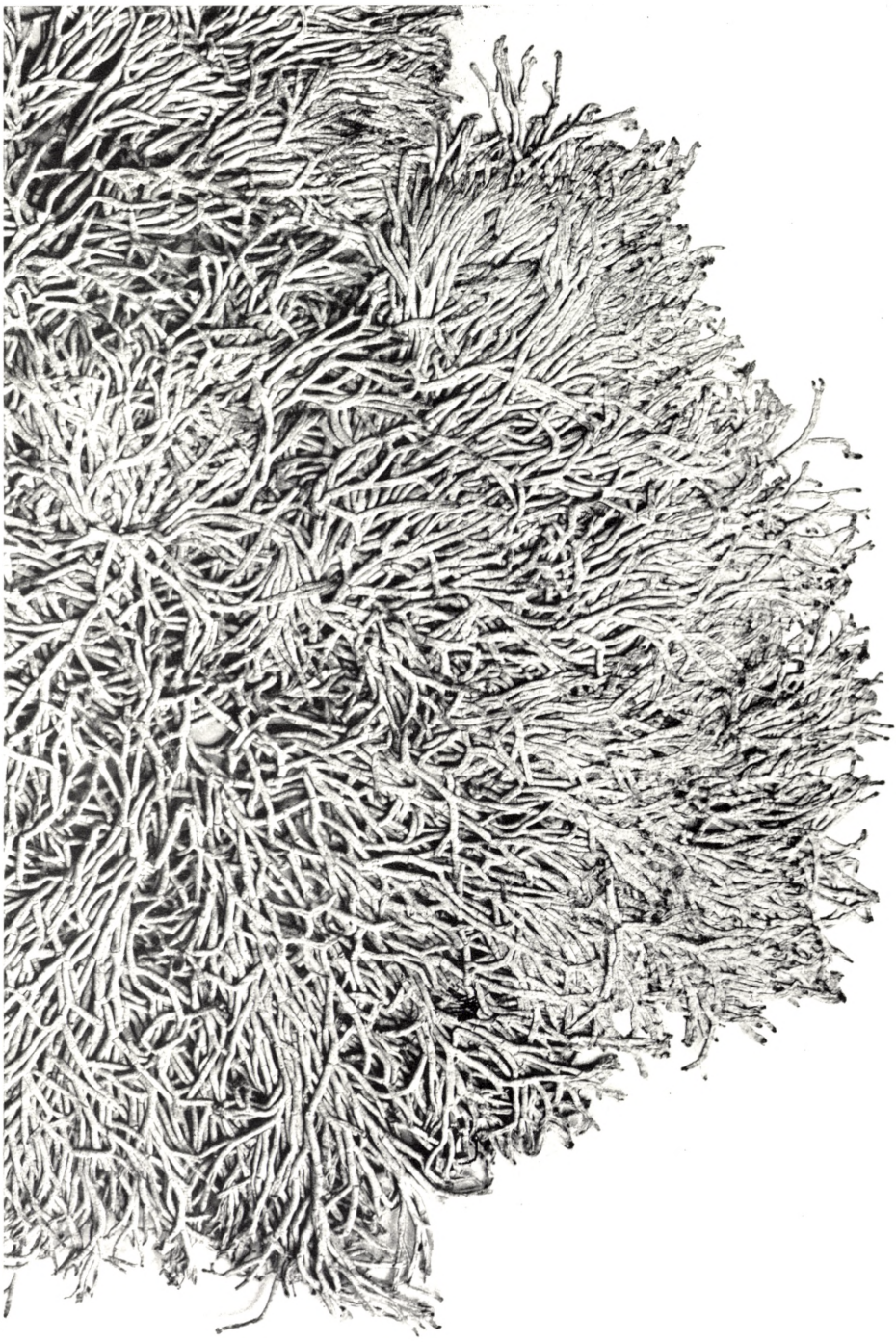
Rhodophyceae

Indleveret til selskabet den 25. april 1951.
Færdig fra trykkeriet den 13. august 1951.

Trichogloea Jadinii nov. spec. (× 1).

Trichogloea javensis nov. spec. (× 1).

Liagora mauritiana Borgs. (× 1).



Liagora Vaughani nov. spec. (× 1).

Callymenia Morelii (Mont. et Millard.) Borgs. (× 1).

Eucheuma horridum (Harv.) J. Ag. (× 1).

Gracilaria dura (Ag.) J. Ag. (× 1).

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PHYTOPLANKTON STUDIES

2. A NEW BIOLOGICAL TYPE WITHIN THE GENUS *CHAETOCEROS*, *CHAETOCEROS SESSILIS* SP. NOV.

BY

JUL. GRØNTVED

København
i kommission hos Ejnar Munksgaard
1951

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Bianco Lunos Bogtrykkeri.

Introduction.

The *Chaetoceros* species to be described in what follows was found in the southern North Sea in May 1948. At that time phytoplankton samples were collected simultaneously at a great number of stations covering the North Sea, the Skagerrak, the Norwegian Sea and the Faroe—Shetland Channel, furthermore on the following sections: The Faroes—the Hebrides and the Shetland—Orkney Islands. This plankton sampling took place coincident with hydrographic investigations initiated by THE INTERNATIONAL COUNCIL FOR THE EXPLORATION OF THE SEA; at sea the work of the combined investigations was performed by Danish, Swedish, Norwegian, English, and Dutch research ships, which simultaneously made cruises in different parts of the area of investigation. As to the working up of the plankton material the present writer examined the samples collected in the southern North Sea in May 1948 (Sections R, S, T, U; see fig. 7) furthermore a number of samples collected by the Danish research ship DANA in May 1947 (Sections Q, R, and S). The results of the quantitative examination of the whole material will be published later by T. BRAARUD, K. RINGDAL GAARDER, and the author; what follows is an account of a taxonomical study.

For the microscopical examination of the said plankton material I have received economic support from THE RASK-ØRSTED FOUNDATION, which also, together with FONDET FOR DANSK-NORSK SAMARBEJDE, paid travelling expenses in connection with the work. My best thanks are due to the directors of these foundations for the aid rendered to me.

Further I am greatly indebted to Dr. CHR. BROCKMANN, Bremerhaven, for having seen my *Chaetoceros sessilis* preparations and for good informations.

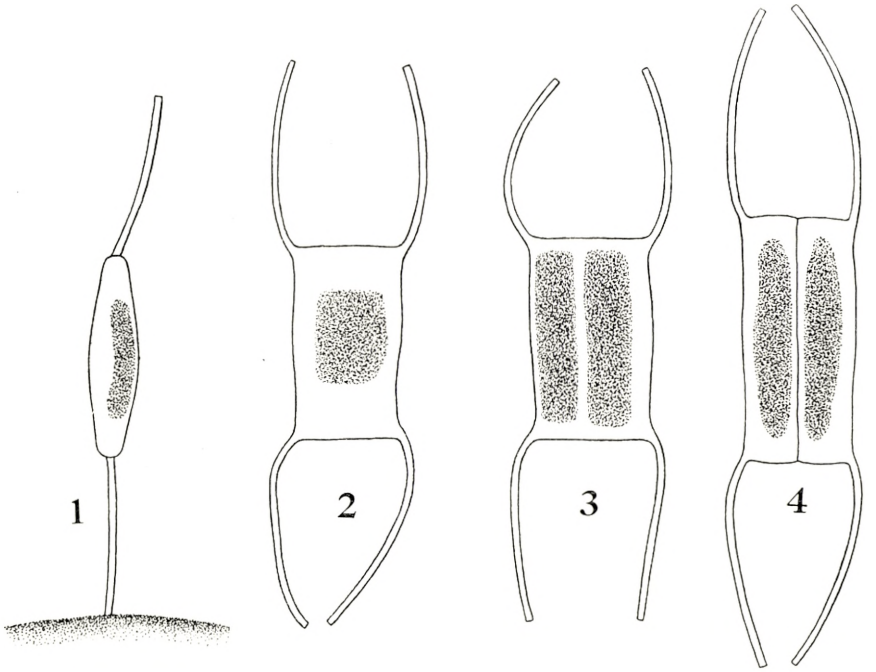
Taxonomy and Occurrence of *Chaetoceros sessilis* sp. n.

The shape of the valve is linear-lanceolate; in broad girdle view the cell is rectangular, being considerably broader than long; the girdle zone could not be distinguished from the valve mantles; the bristles are short and thick, arising from the valve corners; their basal part curved, directed diagonally outwards; distally they are straight, parallel to the apical axis, or irregularly curved; often the bristle of one valve is directed towards or even cross that of the other; they are blunt, open at the tips. The cell wall is slightly siliceous. One large chromatophore is situated on the broad girdle side. Resting spores were not observed. As to dimensions the following measures were found: Apical axis: 18—33 μ, transapical axis: 7—9 μ, length of the bristles: 16—35 μ.

Only solitary cells were seen, most frequently they occurred attached to spherical bodies, one or, generally, two of the bristles touching the substratum with the tips, which are mucous and adhere to it (see Pl. I); the cells are not embedded in mucilage, only the distal parts of the bristles are adhesive and here the mucilage is often seen as a thickening; probably it is secreted through the open tips of the bristles. The cells of *Chaetoceros sessilis* seem to be well adapted to the attached mode of life: when two of its bristles adhere to the substratum there is always one from each valve, thus after cell division the two daughter cells are from birth attached to the same body as the parent cell. Even if chains of two or a few cells are to be found in the case of *Chaetoceros sessilis* individuals being rapidly dividing up, yet, the formation of real chains seems impossible in this sessile species, each valve of the cell being attached by one of the bristles to the substratum.

Fig. 1—5. *Chaetoceros sessilis* from St. S_3. ($\times$1000). — 1. Cell in valve view, adhering to the substratum. 2—5. Cells in broad girdle view, 3 and 4 showing early divisional stages. 5. Glow preparation; in the slightly siliceous cells the bristles are flattened by the glowing and the girdle region shows an elongation, likewise due to preparation; junction between the girdle zone and the valve mantles not to be distinguished.

Fig. 6. The spherical body which serves as a substratum to the *Chaetoceros sessilis* individuals found at St. S_3; this one without covering of diatoms; the body has got a crack from the pressure of the cover glass; perforations are seen on the surface. ($\times$275).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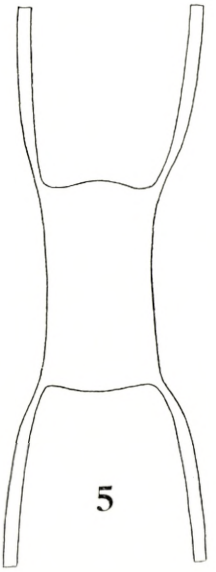
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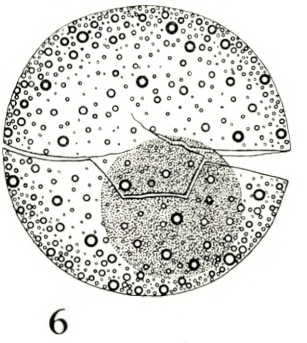
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Latin diagnosis.

Chaetoceros sessilis species nova.

Frustulis e facie connectivali visis rectangularibus, latioribus quam longioribus; valvis lineari-lanceolatis, ad 18—33 μ longis, 7—9 μ latis; setis e margine frustulae orientibus, crassis, plus minus curvatis, 16—35 μ longis. Phaeophora laminiformia, singula, zonae connectivali adposita. Sporis perdurantibus non observatis. Frustulis parce siliceis, solitariis vel binatim conjunctis, ad corpuscula natantia adhaerentibus.

Habitat in mari Germanico; rarissime.

As to the taxonomical position of our species the character of its being attached by the bristles to deposited or floating bodies is so far unknown within the genus *Chaetoceros*; however, we are not justified in setting up a new genus on account of this biological character, and as it is possible to refer it to *Chaetoceros* for morphological reasons, this has been done; within this genus it belongs to the subgenus *Hyalochaete* on account of its single, large chromatophore; further we may place it in the section *Simplicia* as no chain formation was observed.

It is well-known that many *Chaetoceros* species show great morphological variation, and this fact must be taken into consideration when new species are set up; *Chaetoceros sessilis*, however, does not only differ from the other species within this genus with regard to morphological characters, but also in its attached mode of life, and this is one reason why we regard it as a distinct species.

Chaetoceros sessilis was found at two localities, *viz.* at Stations S_3 and 6844 (see fig. 7); at the former station, where plankton was sampled on 8th May 1948, the individuals were attached only to one kind of substratum: hollow, spherical bodies (see fig. 6), their diameters being 100—200 μ; the walls, which are provided with perforations of various sizes, seem to be slightly silicified; the origin of these bodies is unknown to me; they were found only at this station and only in the net sample, thus under pelagic conditions; most of them were without any covering but about thirty were found covered with *Chaetoceros sessilis*, generally without other diatoms being present; however, a few were observed covered with this species together with pennate bottom diatoms; in this case it is probable that the substratum had been deposited on the bottom when the diatoms attached themselves to it. In the net sample

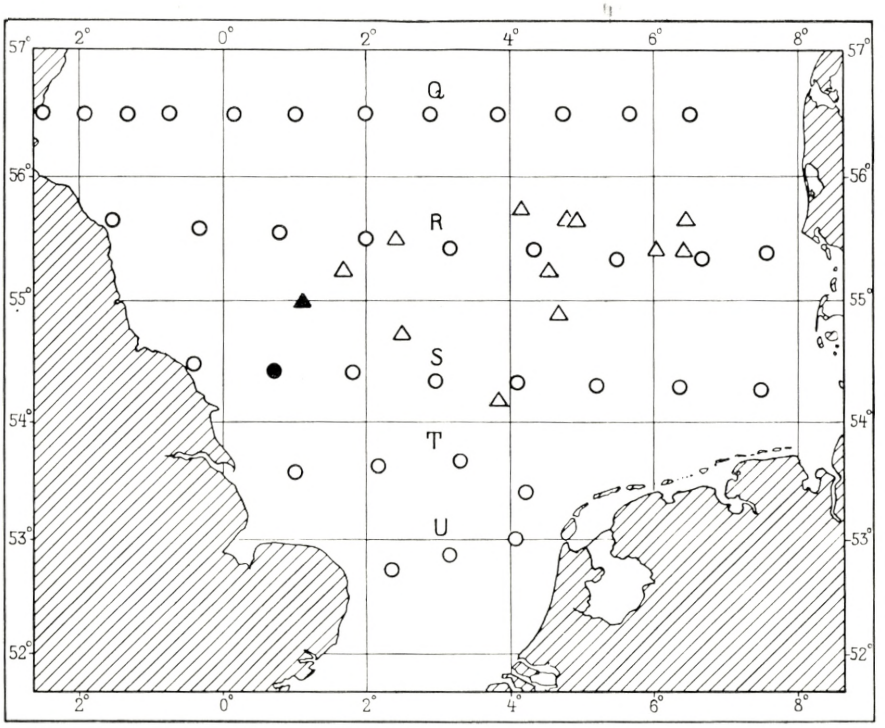


Fig. 7. Map of the southern part of the North Sea showing the positions of the plankton stations in May 1948; at the stations marked with open circles water samples were collected at the following depths: 0, 10, 20, and 50 m. (or bottom); further net sampling took place in the surface at the stations of Sections R and S; with Δ are marked stations for net sampling only. The filled-in circle and triangle indicate St. S_3 and St. 6844 respectively, where *Chaetoceros sessilis* was found in May 1948. In May 1947, when plankton was sampled along Sections Q, R and S, this species was observed at St. 6572 (55° 25′ N. Lat.; 1° 27′ W. Long.). (See postscript).

from St. 6844 gathered on 23rd May 1948, *Chaetoceros sessilis* was found together with numerous pennate bottom diatoms fixed to other sorts of suspended matter, without doubt lately arisen from the bottom; also the spherical substratum from St. S_3 may properly belong to the bottom deposits; thus it seems likely that *Chaetoceros sessilis* has a preference for living on the bottom, and perhaps the circumstance that in our material only a few cells were dividing up is due to the floating condition; but nothing can be said with certainty as to its proper habitat; it is a rare species in our area in the spring plankton, being found only in two of the numerous samples collected all over the North

Table I. Hydrographical Conditions at the Sts. where *Chaetoceros sessilis* was Found.

St. S_3. $^8/_5$, 1948. (Depth 63 m).

Depth in metres	0	10	20	30	50	60
Temperature, °C	9.21	8.04	7.52	7.50	7.47	7.47
Salinity, per mille	34.43	34.51	34.51	34.55	34.51	34.57
σt	26.66	26.91	26.98	27.01	26.98	27.03

St. 6844; $^{23}/_5$, 1948. (Depth 40 m).

Depth in metres	0	38
Temperature, °C	10.38	8.21
Salinity, per mille	34.71	34.69
σt	26.67	27.02

Sea in May 1948; and in May 1947, when plankton was sampled in the southern part of this area (Sections Q, R and S; see fig. 7), it was met with only at one St. (see postscript).

The hydrographical data from the two positive stations in 1948 are recorded in Table I; it appears from this table that the water masses show a certain degree of stratification; consequently the possibilities of bottom diatoms being brought up in water by turbulent activities were not great; at St. 6844 no water samples were collected, but in the water samples from St. S_3 the following species of littoral diatoms were found: *Actinoptychus undulatus, Campylosira cymbelliformis, Cocconeis scutellum, Navicula distans, Pleurosigma angulatum, Rhaphoneis surirella.* As the total number of diatom species in these samples amounted only to 14, the littoral forms were fairly well represented; probably they had been carried by horizontal currents to this place from bottom habitats in more shallow parts, and it does not seem improbable that the *Chaetoceros sessilis* individuals found originate from the same or similar biotopes; possibly the species has a wider di-

stribution on the bottom than that indicated on the map (fig. 7), but no samples were collected here during our investigations.

As a matter of fact little is known about the microflora living on the bottom of the North Sea, apart from the Waddensea and the coastal waters outside it; yet, BROCKMANN (1937)[1] examined samples of bottom material from several stations near the Dogger Bank; and in one locality, at a depth of 46 m, he found an autochthonous diatom flora rich in species; it appears from this that great areas of the sea bottom in the southern and central part of the North Sea are within the euphotic zone in so far as the benthic diatoms are concerned, and it would be of great interest to have made investigations on the diatom populations living here.

[1] Küstennahe und küstenferne Sedimente in der Nordsee.—Abhdl. Nat. Vereins Bremen. Bd. 30, Heft 1—2.

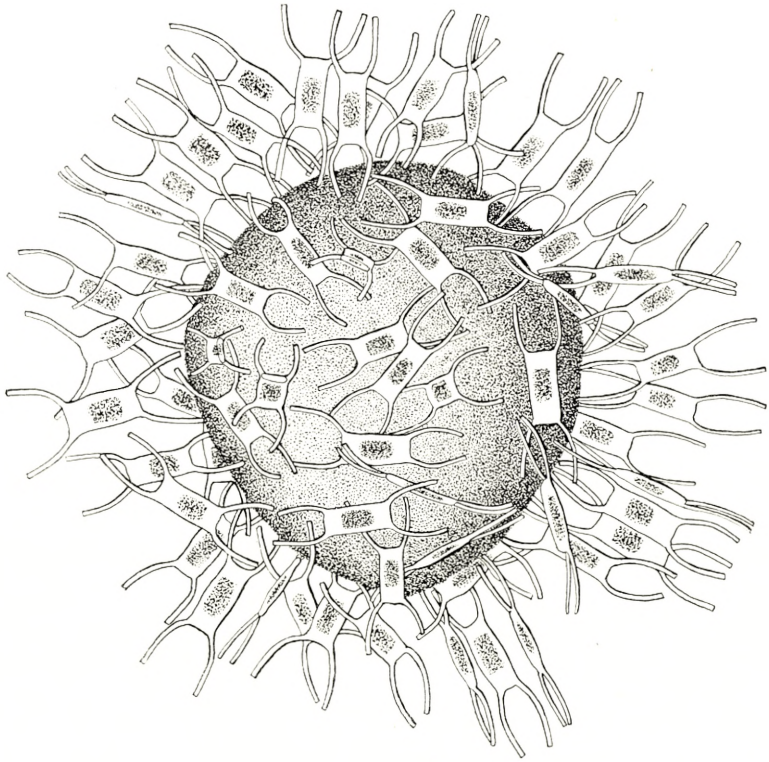
Postscript.

After printing of the preceding pages I have on a special occasion made a renewed examination of the surface net samples from the plankton stations of the Sections Q, R and S, May 1947. In one of the samples, that from St. 6572 (55°25′ N. Lat.; 1°27′ W. Long.), I found *Chaetoceros sessilis*; only one "secondary colony" like that shown in Plate I was observed.

Indleveret til selskabet den 6. juni 1951.
Færdig fra trykkeriet den 15. september 1951.

Explanation of Plate I.

Chaetoceros sessilis individuals from St. S_3, attached to the spherical substratum; the *Chaetoceros* cell adheres to the foreign body with the tips of one or two of the bristles; in the preparation some of the individuals are lying with their bodies close to the substratum, this is due to pressure from the cover glass, the spherical substratum has become somewhat deformed on the same account; the sculpture of its surface is not drawn. ($\times 500$). Drawn by Miss INGEBORG FREDERIKSEN.



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UNTERSUCHUNGEN ÜBER DIE BILDUNG DER GALLE VON *MIKIOLA FAGI*

VON

P. BOYSEN JENSEN

With an English Summary

København
i kommission hos Ejnar Munksgaard
1952

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1. Einleitung.

Es wird im allgemeinen angenommen, dass die Wespen- und Mückengallen durch spezifische, gallenbildende Stoffe, die von den Larven abgegeben werden, erzeugt werden. Diese Auffassung ist nicht stichhaltig. Zwar produziert die *Mikiola*larve, wie der Verfasser (Boysen Jensen 1948) nachweisen konnte, wuchsstoffähnliche Stoffe, die Zellteilungen und Zellstreckungen hervorrufen können. Diese sind aber nicht spezifisch in dem Sinne, dass sie, wenn sie in einer Paste verteilt auf ein junges Buchenblatt aufgetragen würden, ein organisiertes Gebilde, wie es die Galle darstellt, erzeugen können. Die Entstehung derselben wird, wie es in dieser Abhandlung gezeigt werden soll, dadurch ermöglicht, dass die Larve imstande ist, von ihrem Instinkte geleitet, die von ihr abgegebenen Stoffe an bestimmten Stellen an der Unterseite eines jungen Buchenblattes und an der inneren Wand der sich entwickelnden Galle zu secernieren. Diese Stoffe rufen in geordneter Weise Zellteilungen und Zellstreckungen hervor, und es entsteht so nach und nach auf dem Buchenblatte eine Galle von der charakteristischen Gestalt[1].

Um die Fähigkeit der Larve, die Wuchstoffe in spezifischer Weise zu verteilen, nachzuweisen, ist es von besonderer Bedeutung, die Schliessung der jungen Galle und die Regenerationsfähigkeit der geschlossenen Galle zu untersuchen samt die Bewegungen der Larve in der Galle zu verfolgen. Es ist das Ziel der vorliegenden Untersuchung Beiträge zur Aufklärung dieser Probleme zu geben.

Junge, offene oder soeben geschlossene Gallen kann man auf vier verschiedene Weisen erhalten.

[1] Kloft (1951) hat nachweisen können, dass Wuchsstoffe auch bei der Entstehung der Blutlausgallen und der Wucherungen der Wurzelreblaus mitwirken, und zwar können durch Konzentrationsunterschiede gegensätzliche Wirkungen hervorgerufen werden.

1. Man kann sie in der Natur aufsuchen. Mustert man in den Tagen, wenn die Buchenknospen sich entfalten, an Stellen, wo normalerweise viele Gallen vorhanden sind, die jungen Buchenblätter durch, findet man gelegentlich ganz junge Gallen.

2. Man kann Buchenzweige, auf deren Knospen Larveneier abgesetzt worden sind, mit nach Hause nehmen und treiben lassen. Wahrscheinlich werden einige Larven in die Knospen eingedrungen sein. Wenn die Knospen sich entfalten, kann man die jungen Gallen finden. Nach meinen Erfahrungen empfiehlt es sich, die Zweige etwa 10—14 Tage vor der normalen Entfaltung einzusammeln.

3. Man kann eingesammelte Eier auf Knospen eingetopfter Buchen anbringen. Die Knospen werden in Präparatengläser, die innen mit feuchtem Filtrierpapier bekleidet sind, eingeschlossen. Wenn der Versuch gelingt, dringen einige Larven in die Knospen ein und rufen an den jungen Blättern Gallenbildungen hervor, die man, wenn die Knospen sich entfalten, für weitere Versuche benutzen kann.

4. Man legt gebrütete Larven auf einen Baumwollstopfen, der in einem engen Glasrohr untergebracht ist. Dann wird ein Blatt in einer Knospe, die sich noch nicht entfaltet hat, freigelegt, und das Glasrohr mit den Larven wird auf der Unterseite des Blattes mit Agar festgeklebt, so dass die Larven sich zwischen der Blattoberfläche und dem Baumwollstopfen befinden. Gelingt der Versuch, kann man auf dem Blatte, wenn es sich zu entwickeln beginnt, junge Gallenstadien finden.

Ich habe mit allen vier Methoden Erfolg gehabt. Die zweite Methode ist aber diejenige, die sich am leichtesten handhaben lässt, und es ist ausschliesslich diese Methode, die bei den in dieser Abhandlung beschriebenen Versuchen angewendet worden ist.

Um bei den Versuchen die Zweige (Länge etwa 10 cm) mit den gallentragenden Blättern mit Wasser zu versorgen, werden dieselben am besten durch durchgeschnittene Korkstopfen in Präparatengläser (2×4 cm), die mit Wasser beschickt sind, eingeführt. Wenn die Gläser in einem Stativ angebracht werden, kann man die Gallen leicht unter dem Stereomikroskop untersuchen.

Die Gallen erreichen, weil sie sich an Blättern abgeschnittener

Zweige befinden, nur eine Länge von 1—2 mm. Dies ist jedoch für die hier behandelten Probleme ohne Belang.

Bei der Schneidung der Gallen muss man dafür Sorge tragen, dass die Schnittebene mit einer Ebene, die durch die Längsachse der Galle gelegt werden kann, parallel ist. Man erreicht dies dadurch, dass man den Blattstreifen, der mikrotomiert werden soll, senkrecht auf einer Ebene, die durch die Längsachse der Galle gelegt werden kann, herausschneidet. Die Schneidung der Gallen ist mit einigen Schwierigkeiten verbunden; am besten geht es, wenn die Galle nicht fixiert ist.

2. Die Schliessung der Gallen.

Die *Mikiola*galle ist anfangs eine flache, offene Schale an der Unterseite des Blattes. Die Schliessung der Schale geht normaler-

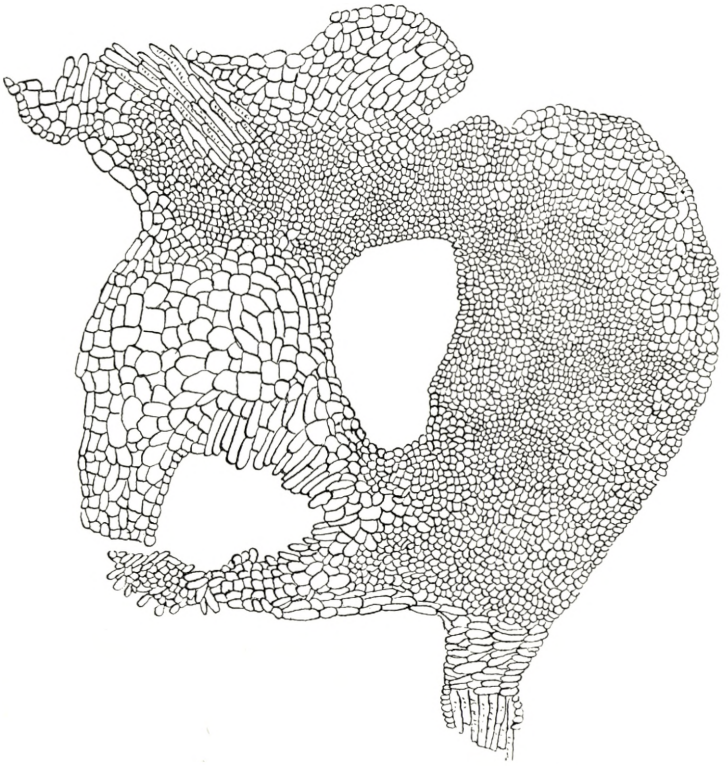

Abb. 1. Abnorme Schliessung einer *Mikiola*galle. (Vergr. $\frac{52}{1}$). Die Larve liegt in einem anderen Teil der Galle. (Vgl. die normale Schliessung in Abb. 2).

weise folgendermassen vor sich. An dem Schalenrande wachsen Papillen nach innen aus, teils horizontal und teils schräg nach unten. Die Öffnung verengert sich nach und nach zu einem Kanal; zuletzt schliesst auch dieser sich, und die Gallenhöhle ist nun durch ein kegelförmiges Gebilde, das an der Unterseite des Blattes hervorragt, nach aussen abgegrenzt (Abb. 2). Bei der weiteren Entwicklung der Galle kann sich der kegelförmige Boden etwas ebnen.

Ein Beispiel soll zeigen, dass die Ausbildung und Schliessung der Gallen in abnormer Weise verlaufen kann.

Wenn man in dem Stadium, wo das kegelförmige Gebilde noch von einem Kanal durchsetzt ist, die Galle unter dem Stereomikroskope anbringt, wobei die Öffnung der Galle nach oben gekehrt und belichtet wird, hören bisweilen die Papillen im äusseren Teil des Kanals zu wachsen auf, während sie im inneren Teil desselben das Wachstum fortsetzen. Es wird somit nur der innere Teil des Kanals verschlossen, während in dem äusseren Teil desselben eine Höhlung zurückbleibt (Abb. 1).

3. Regeneration der Gallen.

a. *Versuche mit jungen Gallen.*

1. Entfernung des Bodens der Galle. An einigen Gallen wurde, kurz nachdem sie nach unten verschlossen waren, der kegelförmige Teil, der auf der Unterseite des Blattes hervorragt, und der den Boden der Galle ausmacht, mit einer Rasierklinge abgeschnitten, so dass die Gallenhöhle wieder nach aussen offen wurde. Die Grösse der Öffnung betrug 0.2—0.3 mm. Die kleinen Zweige mit den gallentragenden Blättern wurden wie oben beschrieben in Präparatengläser mit Wasser eingeführt. Die Gläser wurden horizontal gelegt, so dass die Öffnung der Galle entweder nach oben oder unten kehrte. Die Versuche werden am besten bei schwachem Lichte ausgeführt. In vollständigem Dunkel kann jedoch auch eine Regeneration stattfinden; die Blätter werden aber leicht geschädigt. Die umgebende Luft darf nicht zu feucht sein, weil sonst Intumescenzen entstehen können, die mit dem Regenerationsgewebe verwechselt werden können.

α) *Die Gallenöffnung kehrt nach unten.* Um zu verhindern, dass die Larve die Galle verliess, wurde in den beiden ersten

Versuchen die durch die Operation entstandene Öffnung mit einer kleinen Zellophanplatte, die an den Wundrändern mit 10 $^0/_0$iger Gelatine festgeklebt wurde, verschlossen. Es zeigte sich aber bald, dass diese Massnahme eine Schliessung der Galle verhinderte und dass sie auch überflüssig war, da die Larve im allgemeinen in der Galle verbleibt, auch wenn die Öffnung derselben nicht verschlossen ist.

Im Jahre 1950 wurden im ganzen 3 Versuche, in denen die Larve in der Galle verblieb, angestellt. In allen Fällen trat eine Regeneration ein, indem die Galle durch neugebildetes Gewebe teilweise oder vollkommen wieder verschlossen wurde.

Um zu verstehen, wie der Regenerationsvorgang verläuft, beginnt man am besten mit der Betrachtung einer jungen Galle, die sich soeben geschlossen hat. Ein Längsschnitt durch eine solche Galle findet sich in Abb. 2. Man sieht, dass der Boden der Galle wie oben erwähnt in einen kurzen Kegel, der aus langgestreckten parallel verlaufenden Zellreihen gebildet ist, ausgezogen ist. Wenn man mit einem Rasiermesser den Kegel abschneidet, kann man eine Galle, wie sie in Abb. 3 dargestellt ist, erhalten. Sowohl die Schnittfläche wie die Öffnung der Galle treten deutlich hervor. Es sind die Öffnungen solcher Gallen, die durch neugebildetes Gewebe verschlossen werden können.

Die drei Gallen, an denen eine Regeneration stattgefunden hatte, wurden mikroskopisch untersucht. Das Ergebnis dieser Untersuchung war das folgende:

Es konnte festgestellt werden, dass in 2 Fällen die Öffnung vollkommen verschlossen war, im dritten Fall war eine sehr kleine Öffnung zurückgeblieben. Es ist nicht immer möglich genau festzustellen, wo die Grenze zwischen dem ursprünglichen und dem neugebilden Gewebe verläuft; meist ist jedoch das letztere lockerer gebaut, es besteht, soweit sich beurteilen lässt, aus mit einander verflochtenen Zellreihen.

Bei der ersten Galle (Abb. 4) betrug die Öffnung etwa 0.2 mm im Diameter. Der in der Abbildung dargestellte Schnitt geht ungefähr durch die Mitte der Öffnung. Die Schnittfläche tritt deutlich hervor. Das mit $\times$ bezeichnete Gebilde ist ein eingetrockneter Fetzen, der an der Grenze der Schnittfläche liegt. Die Öffnung liegt zwischen der punktierten Linie und dem Pfeil. Man sieht, dass die Regeneration ausschliesslich von dem linken Rande der

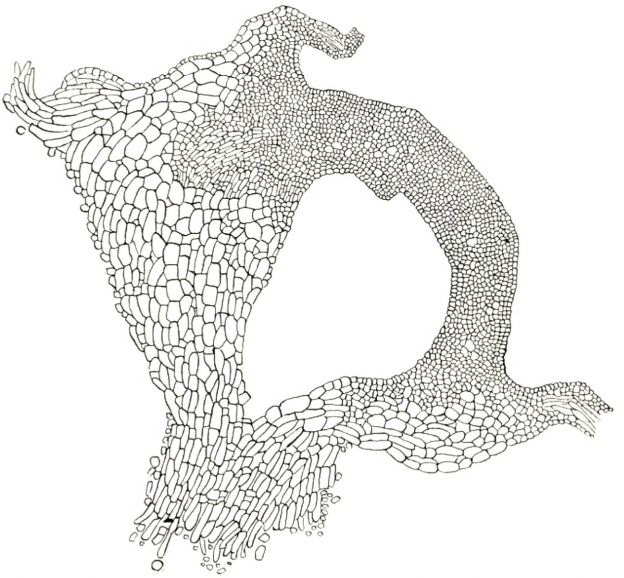

Abb. 2. Längsschnitt durch eine Galle, die sich soeben geschlossen hat. (Vergr. $\frac{43}{1}$). Die Larve liegt in einem anderen Teil der Galle.

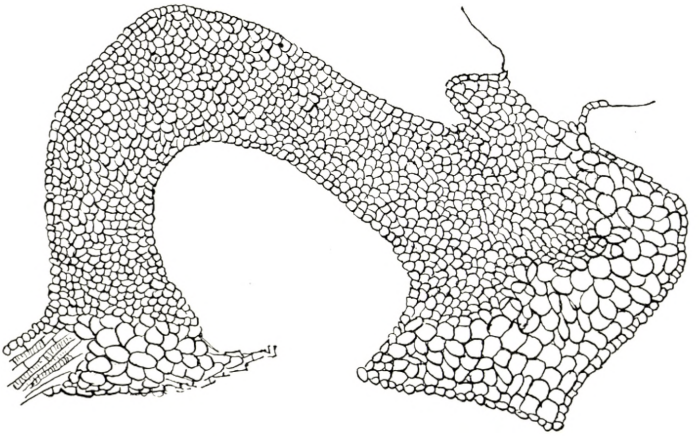

Abb. 3. Eine Galle, deren Boden abgeschnitten worden ist, 4 Tage nach der Operation. Die Larve hat die Galle verlassen; eine Regeneration hat nicht stattgefunden. (Vergr. $\frac{64}{1}$).

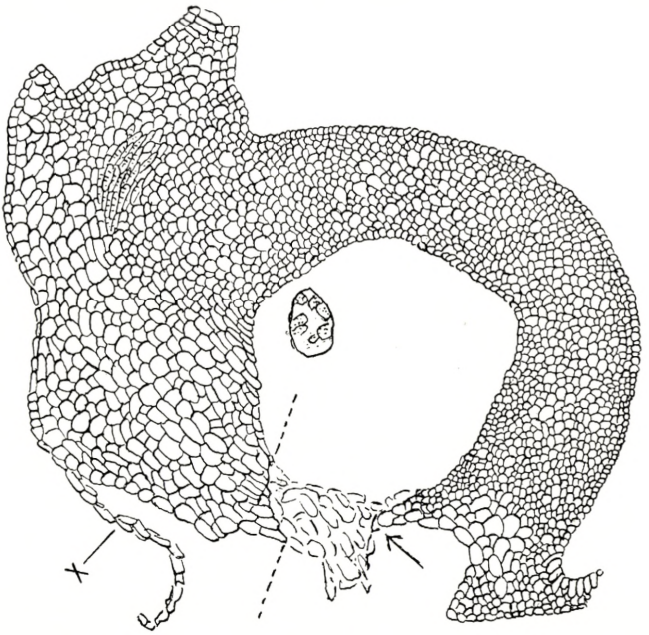

Abb. 4. Eine Galle, deren Boden abgeschnitten worden ist, 4 Tage nach der Operation. Die Öffnung ist wieder verschlossen. Näheres im Text. (Vergr. $\frac{70}{1}$).

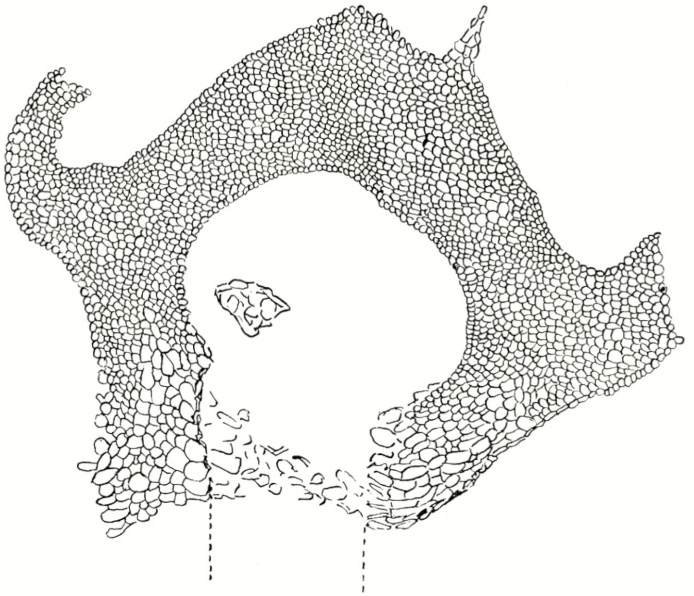

Abb. 5. Eine Galle, deren Boden abgeschnitten worden ist, 4 Tage nach der Operation. Die Öffnung ist wieder verschlossen. Näheres im Text. (Vergr. $\frac{87}{1}$).

Öffnung ausgegangen ist. Von dort hat sich eine Membrane vorgeschoben, die, wenn sie den gegenüberliegenden Rand erreicht, etwas nach aussen gebogen ist. Auch der rechte Rand ist nach aussen gebogen und eingetrocknet. Der Pfeil zeigt die Stelle, wo die Membrane den rechten Rand erreicht. Dass die gegebene Deutung richtig ist, konnte durch Untersuchung mit dem Polarisationsmikroskop bestätigt werden. Die Dobbelt-

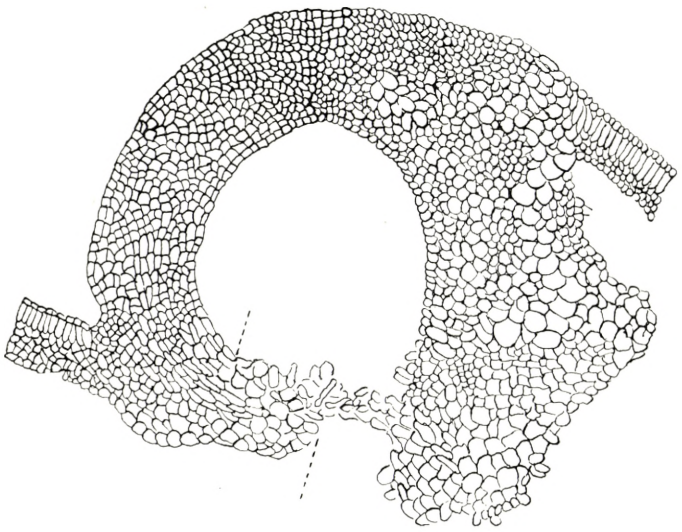

Abb. 6. Eine Galle, deren Boden abgeschnitten worden ist, 4 Tage nach der Operation. Die Öffnung ist wieder verschlossen. Näheres im Text. (Vergr. $\frac{66}{1}$). Die Larve liegt in einem anderen Teil der Galle.

brechung ist in dem neugebildenen Gewebe bedeutend schwächer als in dem ursprünglichen.

Bei der zweiten Galle (Abb. 5) ist das neugebildete Gewebe sehr scharf von dem ursprünglichen geschieden. Die Schnittfläche tritt deutlich hervor. Die Öffnung liegt zwischen den beiden punktierten Linien. Unmittelbar innerhalb der beiden Schnittflächen hat sich eine aus sehr lockerem Gewebe bestehende Membrane entwickelt, die die Öffnung überbrückt. Die Öffnung ist jedoch nicht ganz geschlossen. In den folgenden Schnitten wird die Brücke allmählich dünner und weist in der Mitte eine Öffnung auf. Nachher schliesst sie sich wieder und wird gleichzeitig dicker.

Bei der dritten Galle (Abb. 6) können das neugebildete und

das ursprüngliche Gewebe nicht scharf voneinander getrennt werden, und die Regenerationsvorgänge sind daher schwierig zu deuten. Wie sich durch eine Vergleichung zwischen dem in Abb. 6 dargestellten und den vorhergehenden Schnitten feststellen lässt, ist auf der rechten Schnittfläche eine aus grosszelligem Parenchym bestehende Zellwucherung entstanden. Die ursprüngliche Schnittfläche tritt daher nicht hervor. Die Öffnung lag wahrscheinlich zwischen der Zellwucherung und der punktierten Linie. Es scheint, dass sich von beiden Seiten eine Membrane vorgeschoben hat, wodurch die Öffnung überbrückt worden ist. Die Brücke ist aus unregelmässigen Zellen aufgebaut, zeigt aber eine etwas festere Konsistenz als bei den beiden oben erwähnten Gallen.

Es wurde oben erwähnt, dass die Larven im allgemeinen in der Galle verbleiben, wenn der Boden derselben entfernt ist. Eine Ausnahme bildet die in Abb. 3 dargestellte Galle, die von der Larve verlassen ist. Eine Regeneration ist daher auch nicht eingetreten, und dieser Versuch bildet somit eine Kontrolle zu den in den Abb. 4—6 dargestellten Versuchen.

In einem Versuch wurde die Öffnung einer operierten Galle mit 10 $^0/_0$iger Gelatine bedeckt, so dass die Larve nicht mit der Schnittfläche und dem angrenzenden Teil der Gallenwände in Berührung kommen konnte. In diesem Falle wurde kein Regenerationsgewebe gebildet.

Es wurde im Jahre 1951 versucht, die Regenerationsversuche zu wiederholen, leider aber mit wenig Erfolg. Die jungen Gallen waren in diesem Jahre schlecht entwickelt, wahrscheinlich weil das Wetter in der letzten Aprilhälfte ziemlich kühl war. Die Gallen an den sich entfaltenden Blättern waren meist offen und schlossen sich langsam und unvollständig. Auch draussen in der Natur fanden sich ungewöhnlich viele fehlgeschlagene Gallen. Die Gallen, deren Boden entfernt wurde, wurden häufig von den Larven verlassen, in mehreren Fällen färbten sie sich dunkel, und die Zellen starben ab. Nur in einem Falle konnte eine Regeneration beobachtet werden; die Öffnung wurde aber nicht vollständig geschlossen.

β) Die Öffnung der Galle kehrt nach oben. Es wurde im Jahre 1950 an 3 Gallen der Boden abgeschnitten, und die gallentragenden Blätter wurden so orientiert, dass die Öffnung nach oben

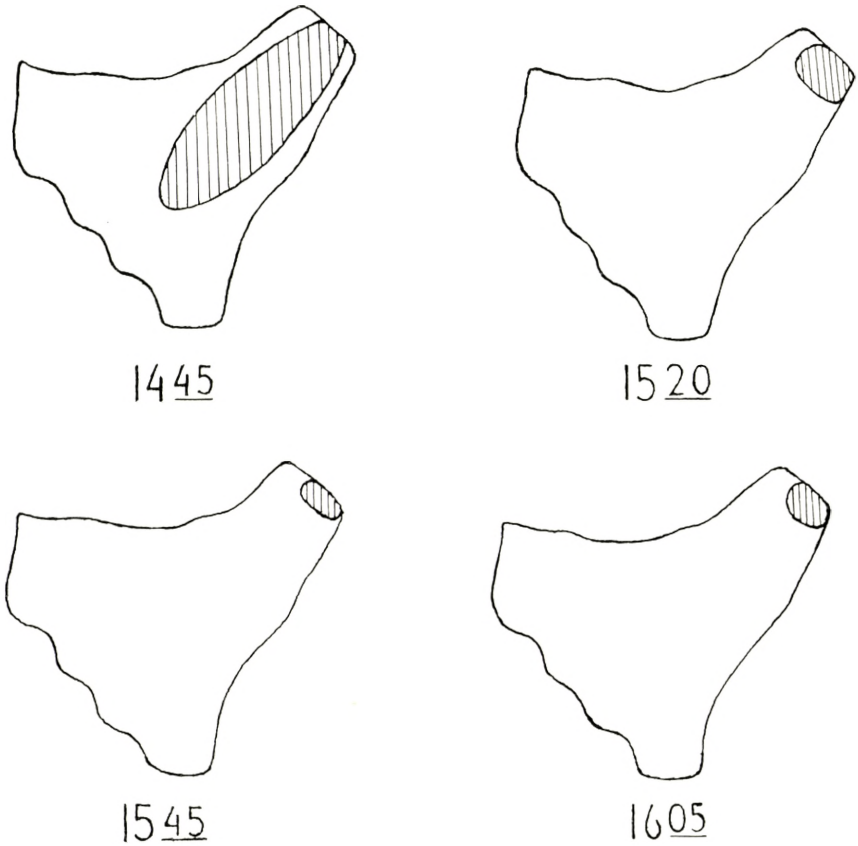

Abb. 7. Die Lage einer *Mikiola*larve in einer offenen Galle zu verschiedenen Zeitpunkten. Die äussere Linie ist der Umkreis der Gallenöffnung, der schraffierte Körper ist die Larve. In Bild 1 sieht man die ganze Larve, in den anderen nur ihren Kopf, der übrige Teil des Körpers ist in die Gallenhöhle hineingekrümmt.

kehrte. Die Larven blieben in den Gallen, eine Regeneration und Schliessung der Öffnung trat aber nicht ein. Die Ursache der fehlenden Regeneration ist vielleicht, dass die Gallen zu stark belichtet sind, wenn die Öffnung nach oben kehrt.

2. Entfernung der Spitze der Galle. Es wurde gleichfalls im Jahre 1950 an zwei Gallen die Spitze der auf der Oberseite des Blattes hervorragenden Galle abgeschnitten, so dass eine kleine Öffnung entstand. Die Blätter wurden in inverser Lage untergebracht, so dass die Öffnung nach unten kehrte. In keinem Falle trat eine Schliessung der Öffnung ein.

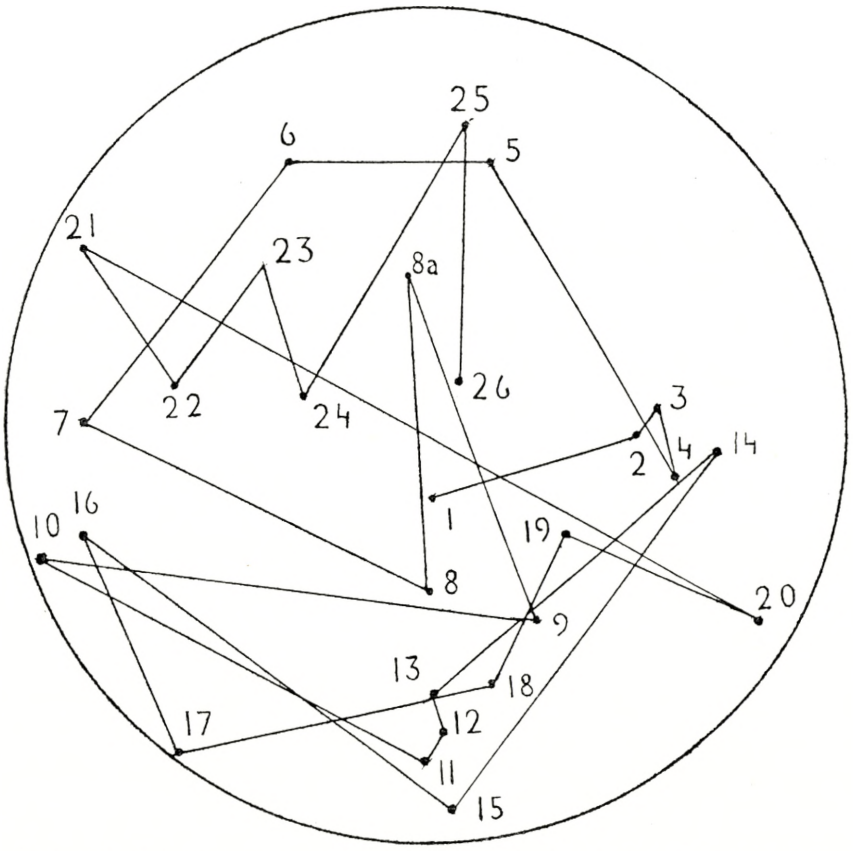

Abb. 8. Die Bewegungen der Larve in einer geschlossenen Galle. Die Zahlen zeigen die Lage der Larve zu den verschiedenen Zeitpunkten an: *1* 15^{30}, *2* 15^{40}, *3* 15^{50}, *4* 16^{00}, *5* 16^{10}, *6* 16^{20}, *7* 16^{30}, *8* 16^{40}, *8a* 16^{50}, *9* 17^{00}, *10* 17^{15}, *11* 17^{40}, *12* 17^{50}, *13* 18^{00}, *14* 18^{10}, *15* 18^{20}, *16* 18^{30}, *17* 18^{40}, *18* 18^{50}, *19* 19^{00}, *20* 19^{10}, *21* 19^{30}, *22* 19^{40}, *23* 19^{50}, *24* 20^{00}, *25* 20^{20}, *26* 20^{30}.

b. *Versuche mit älteren Gallen.*

Regenerationsversuche mit älteren Gallen lassen sich nicht im Walde durchführen, weil die Gallen, wenn der Boden derselben entfernt wird, von Blattläusen besiedelt werden. Man muss daher die Versuche mit abgeschnittenen Zweigen mit gallentragenden Blättern im Laboratorium durchführen.

An 5 Gallen wurde Anfang Juni 1950, als die *Mikiola*gallen etwa einen Monat alt waren, die Böden der Gallen abgeschnitten. Die Gallen wurden so angebracht, dass die Öffnung nach unten

kehrte. Nach 8 Tagen wurden die Gallen untersucht. Nur in zwei Gallen war eine Larve in der Galle anwesend. In keinem Falle hatte eine Regeneration stattgefunden.

4. Die Bewegungen der Gallenlarven.

a. *Offene Gallen.*

In jungen, noch nicht geschlossenen Gallen kann man die Bewegungen der Larve direkt unter dem Stereomikroskop verfolgen.

Die Bewegungen der Larve in diesem Stadium sind sehr unregelmässig. Bisweilen bleibt die Larve, wie es in Abb. 7 dargestellt ist, längere Zeit an derselben Stelle; der Kopf befindet sich an dem Rande der Gallenöffnung. Zu anderen Zeiten bewegt die Larve sich sehr stark umher.

b. *Geschlossene Gallen.*

In jungen geschlossenen Gallen ist die Wand der Galle so dünn, dass man die Lage der Larve als einen kleinen roten Fleck an der inneren Seite der Gallenwand von aussen feststellen kann, wenn man den Teil der Galle, der auf der Oberseite des Blattes emporragt, mit einer starken Lupe betrachtet. Wenn man sich ferner ein Koordinatensystem, etwa eine N-S Achse, die mit der grössten Länge des Blattes zusammenfällt, und dazu senkrecht eine O-W Achse in die Galle hineingelegt denkt, kann man feststellen, in welchem Abstande und in welcher Richtung vom Zentrum aus die Larve sich zu jedem Zeitpunkte befindet. Wenn man ferner die Lage der Larve auf eine Ebene, die die Basis der Galle darstellt, mit Zwischenräumen von 10 Minuten projiciert, und die eingetragenen Punkte durch Linien verbindet, erhält man ein Diagramm, das die Bewegungen der Gallenlarve wiedergibt. Ein solches Diagramm ist in Abb. 8 dargestellt.

5. Schlussfolgerungen.

Wenn die Galle durch einen spezifischen, gallenbildenden Stof, den die Larve abgibt, erzeugt würde, müsste man erwarten, dass die Gallenbildung in ähnlicher Weise wie die Bildung der Organe der Pflanze im grossen und ganzen immer in derselben Weise verlaufen würde, selbst wenn sie möglicherweise nicht

immer zu Ende geführt würde. Es zeigt sich jedoch, dass man durch äussere Einwirkungen auf die Larve eine abnorme Schliessung der Galle hervorrufen kann, indem nicht der ganze Kanal, der in die Galle hineinführt, geschlossen wird, sondern nur der innere Teil desselben. Dies erklärt sich am leichtesten durch die Annahme, dass der äussere Teil des Kanals wegen der Belichtung unzugänglich für die Larve wird, wodurch dieselbe verhindert wird, die von ihr abgegebenen Stoffe in der üblichen Weise auf die gesamte innere Oberfläche des Kanals zu verteilen. Dieselben werden dann ausschliesslich an den inneren Teil des Kanals secerniert, und nur an dieser Stelle findet eine Gewebebildung statt.

Die Fähigkeit der Larve, durch Ausscheidung von Stoffen lokale Zellteilungen hervorzurufen, geht besonders schön aus den Regenerationserscheinungen hervor. Bei zwei Gallen, deren Boden abgeschnitten wurde, ist an den Wundrändern neues Zellgewebe entstanden, so dass die Öffnungen wieder verschlossen wurden. Bei einer dritten Galle wurde gleichfalls eine Zellbrücke gebildet; die Öffnung wurde aber nicht ganz verschlossen. Dass das neugebildete Zellgewebe durch die Larve erzeugt worden ist, geht daraus hervor, dass es nur entsteht, wenn eine Larve in der Galle anwesend ist.

Wenn der Rand der Öffnung mit Gelatine bedeckt wird, treten keine Regenerationserscheinungen ein. Damit eine Schliessung der Galle erfolgen soll, muss somit die Larve imstande sein, die Wuchsstoffe direkt auf die Gallenwände am Rande der Öffnung unterzubringen.

Die lokale Verteilung der Wuchsstoffe findet besonders in dem ersten Stadium der Gallenentwicklung statt, wenn die Galle verschlossen werden soll. Wie aus Abb. 7 hervorgeht, sieht man häufig, dass die Larve in längerer Zeit an derselben Stelle verweilt, und dass der Kopf der Larve mit dem Rande der Öffnung in Berührung ist. Offenbar werden die Wuchsstoffe nur an dieser Stelle secerniert. Von Zeit zu Zeit wechselt die Larve ihren Arbeitsplatz. Die Konturen der Öffnung sind häufig sehr unregelmässig, und man darf daher wohl schliessen, dass die Verteilung der Wuchsstoffe an dem Rande ziemlich zufällig ist.

In dem späteren Stadium ist das Wachstum der Galle mehr gleichmässig, und es müssen daher die Wuchsstoffe über die

gesamte innere Oberfläche verteilt werden. Wie aus Abb. 8 hervorgeht, wird dies dadurch ermöglicht, dass die Larve sich unaufhörlich mit ziemlich konstanter Geschwindigkeit an der inneren Oberfläche der Galle umher bewegt. Die Bewegungen sind anscheinend vollkommen regellos, die Geschwindigkeit ist aber so gross, dass die Larve in wenigen Stunden mit der gesamten inneren Oberfläche der Galle in Berührung kommt. Es besteht jedoch eine Ausnahme. In den geschlossenen Gallen kriecht die Larve immer an den Wänden, und niemals auf dem Boden der Galle umher. Die Wände sollen sich ausdehnen, der Boden dagegen ist fertig gebildet. Bisweilen kann man beobachten, dass auch ein bestimmter Teil der eigentlichen Gallenoberfläche längere Zeit hindurch von der Larve nicht aufgesucht wird.

Man hat vermutet, dass die Larve die Zellen auf der inneren Oberfläche der Galle anzapft und den austretenden Saft aufleckt. Diese Annahme ist kaum richtig. Die Larve bewegt sich so schnell, dass sie die Epidermiszellen nicht anzapfen kann. Weit mehr wahrscheinlich ist es, dass die Larve einen Stoff secerniert, der bewirkt, dass die Zellen einen Teil des Zellinhaltes ausscheiden, und dass die Larve sich von dem austretenden Saft ernährt.

Aus den angeführten Beobachtungen muss man folgern, dass die Gallenbildung in folgender Weise zustande kommt.

Die Larve secerniert Stoffe, Meristine und Auxine, die Zellteilungen und Zellstreckungen in dem Buchenblatte erzeugen. Es ist jedoch möglich, dass diese beiden Wirkungen nicht durch zwei verschiedene Stoffe, sondern durch ein und denselben Stoff in verschiedenen Konzentrationen hervorgerufen werden.

Diese Stoffe werden in spezifischer Weise auf dem Buchenblatte und an der inneren Oberfläche der Galle verteilt. Die Larve beginnt damit, auf eine kreisförmige Fläche an der Unterseite des jungen Buchenblattes Stoffe abzuscheiden, die zahlreiche Zellteilungen hervorrufen. Der betreffende Blattteil wölbt sich nach oben, so dass eine nach unten offene flache Schale gebildet wird. An dem Rande der Schale werden Stoffe abgegeben, die starke Zellstreckungen hervorrufen. Es wachsen lange Papillen nach innen aus, die schliesslich ein zusammenhängendes Gewebe bilden, das die Gallenöffnung nach unten abschliesst. Später werden auf der inneren Seite der Gallenwand Stoffe ab-

gegeben, die eine Streckung der Zellen in der Gallenwand hervorrufen; wenn diese Streckung beendet ist, ist die Galle fertig ausgebildet. Im Herbst werden dann wahrscheinlich an der Basis der Galle Stoffe ausgeschieden, die eine Streckung der dort gelegenen Zellen hervorrufen. Es wird hierdurch eine Trennungsschicht gebildet.

Die Verteilung der Stoffe wird durch die Bewegungen der Larve ermöglicht.

Ein Vergleich zwischen der Bildung einer Seitenwurzel und einer Galle ergibt folgendes.

Eine Wurzelbildung kann durch verschiedene Stoffe, z. B. durch β-Indolylessigsäure, β-Indolylbuttersäure und α-Naphthylessigsäure, hervorgerufen werden. Diese Stoffe wirken in der Weise, dass sie eine Tendenz zur Wurzelbildung, die in dem endogenen Dauer- oder embryonalem Gewebe des Stengels vorhanden ist, auslösen. Die Spezifität der Organbildung liegt somit in dem Reaktionssystem, in dem Stengel, die auslösenden Stoffe sind dagegen nicht spezifisch.

Die Gallenbildung wird gleichfalls durch Stoffe, die Zellteilungen und Zellstreckungen hervorrufen können, hervorgerufen. Diese Stoffe sind nicht spezifisch, d. h. sie können nicht geordnete Zellteilungen und Zellstreckungen hervorrufen und können somit nicht ein kompliziertes Gebilde, wie es die Buchengalle ist, erzeugen. Auch das Buchenblatt hat natürlich in sich keine Tendenz zur Gallenbildung, die durch Stoffe ausgelöst werden konnte. Die Vorgänge, durch welche eine organisierte Galle erzeugt wird, werden somit durch den Gallenbildner, die Insektenlarve, geregelt, indem diese, von ihrem Instinkte geleitet, wuchsstoffähnliche Stoffe in spezifischer Weise auf der Unterseite des Buchenblattes und an der inneren Wand der sich entwickelnden Galle verteilt. Die wuchsstoffähnlichen Stoffe der Gallenlarve sind somit Werkzeuge, mit denen die Insektenlarve aus den Zellen des Buchenblattes die Galle herausmodelliert.

6. Summary.

If an open gall is illuminated, the outer part of the canal leading into the cavity of the gall can be made inaccessible to the larva, which therefore gives off growth substances only to the

inner part of the canal. Only the bottom of the canal will therefore be closed (fig. 1). Hence it appears that the larva can produce a localized growth.

The ability of the larva to distribute the growth substances to definite places is demonstrated especially clearly by the regeneration that takes place if the bottom of a recently closed gall is excised. A proliferation can then arise on the edge of the cut surfaces and the opening can be closed (fig. 4—6). The regeneration does not occur when the larva leaves the gall (fig. 3). If the edge of the cut surfaces is covered with gelatine and thus made inaccessible to the larva, the opening will not be closed.

A localized growth takes place particularly in young, open galls when the opening is to be closed. In such galls the larva often remains for a prolonged time in the same place, its mouth being in contact with the edge of the opening (fig. 7); the growth substances given off by the larva will then produce a localized growth. From time to time the larva changes its working-place and gradually the opening will be closed.

In closed galls the growth is more uniform. In such galls the larva incessantly moves about in order to distribute the growth substances over the whole inner surface of the gall (fig. 8). The movements are apparently accidental, but the speed is so high that the larva in a short time touches the whole surface.

These findings support a theory previously advanced by the author. The formation of the gall is caused by growth substances given off by the larva; these substances can produce cell divisions and cell stretching, but not an organised growth. Neither has the beech leaf a tendency to gall formation which could be released by the larva. The divisions and stretching of the cells are regulated by the larva which, guided by its instinct, moves about in the gall and secretes growth substances in definite places on the beech leaf and in the gall, thereby making the latter adopt its special form. Thus the growth substances are tools by mean of which the gall larva models a gall from the cells of the beech leaf.

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SOME MARINE ALGAE FROM MAURITIUS

ADDITIONS TO THE PARTS PREVIOUSLY PUBLISHED, IV

BY

F. BØRGESEN

København
i kommission hos Ejnar Munksgaard
1952

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During the past year I have received several collections of algae from Mauritius, and by examining the specimens they contained I have found several interesting species, among them also some new ones.

The algal flora of the island must be said to be very rich, particularly considering that the deeper growing sublitoral algal vegetation has not yet, or at any rate but sparely, been the object of exploration.

As a result of the examination of the collections received lately, and leaving out of consideration the species more commonly found which have been mentioned previously, the present part contains 53 species, 20 of which have not previously been found in the island; 12 of these species are recorded as new species or varieties.

It is of special interest that Dr. VAUGHAN and his assistant, Mr. G. MORIN, have succeeded in finding a specimen of *Trichogloea* which turned out to belong to the same species as that of the Red Sea, *Trichogloea Requienii* (Mont.) Kütz., the type species of the genus.

Besides the dried specimen some material preserved in formol and seawater was also sent, and the examination of this has confirmed my supposition that *Trichogloea Jadinii* is a distinct species to be kept separate from *Tr. Requienii* and that thus two species of this genus are found in Mauritius. I am now inclined to consider the *Trichogloea* specimen collected by Colonel PIKE to be the same as *Tr. Requienii,* but since the specimen is sterile an exact determination is excluded.

Having received this new material from Mauritius I very much wanted to make a renewed examination of Colonel PIKE's specimen of *Trichogloea,* and upon my request Director, Dr. E. G.

Salisbury most kindly permitted me to have on loan here again the specimen of Pike being preserved in the Kew Herbarium. Besides this specimen I have borrowed two other specimens of algae; for this obligingness I wish to express my hearty thanks.

The material of *Ceramium* has in the previous parts been worked out by the late Dr. Henning E. Petersen. Having during the last years received more material of this genus I am very much indebted to Mme Geneviève Feldmann-Mazoyer for undertaking this determination. In the rather scarce material Mme Feldmann has found 7 species 3 of which are new to science.

As, for comparison with some specimens of the genus *Sarcodia*, I very much wanted to see a specimen of *S. Gattyae* (J. Ag.) Kylin, I asked Miss Dickinson of the Kew Harbarium whether a specimen of this species was to be found there. This not being the case Miss Dickinson was so very kind as to inquire where a specimen is found and stated that such a one was found in the algal herbarium of the British Museum, Natural History, Kensington, London. As it is not permitted to lend out determined specimens from the Museum, the Keeper of the Algal Herbarium, Miss Linda M. Newton, upon my request most kindly compared one of the Mauritian specimens with the specimens of *S. Gattyae* in the Museum and thus has given me very valuable help.

The lady artist Miss Ingeborg Frederiksen has drawn the great majority of the figures in this part, for which help I thank her very much.

I am much indebted to the Trustees of the Carlsberg Foundation for a continued grant.

CHLOROPHYCEAE

I. Chaetophorales.

Fam. 1. Chaetophoraceae.

Bolbocoleon Pringsh.

1. **Bolbocoleon piliferum** Pringsh.

Pringsheim, N., Beiträge zur Morphologie der Meeresalgen, 1862, p. 1—4, pl. 1. Huber, J., Contributions à la connaissance des Chaetophorées, Paris 1893, p. 308, pl. XIII, figs. 8—12.

This little plant was found abundantly in the wall of *Gracilaria spinuligera* nov. spec.

Flic-en-Flacq, 3-5-51, R. E. V. no. 922.
Geogr. Distr.: Wide spread.

II. Siphonocladales.

Fam. 1. Valoniaceae.

Dictyosphaeria Decsne.

1. **Dictyosphaeria cavernosa** (Forssk.) Børgs.

Alg. Mauritius I, 1940, p. 12. Addit. List, 1946, p. 13.

var. *bullata* nov. var.

A forma *typica* praecipue differt superficie thalli irregulariter bullata.

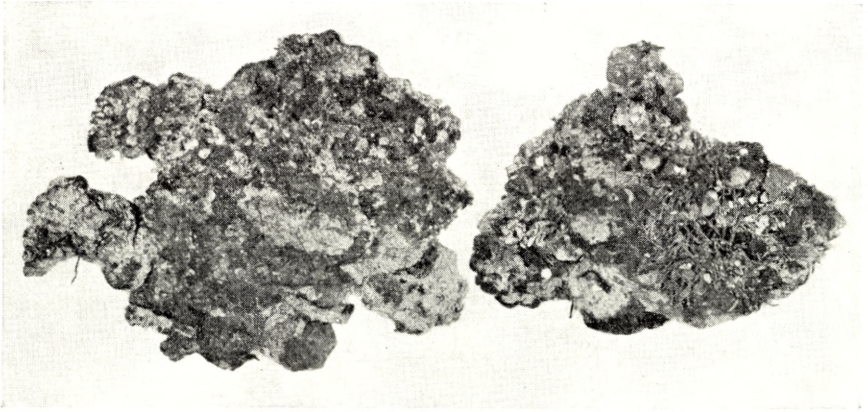

Fig. 1. *Dictyosphaeria cavernosa* (Forssk.) Børgs. var. *bullata* nov. var. Two specimens. (×1).

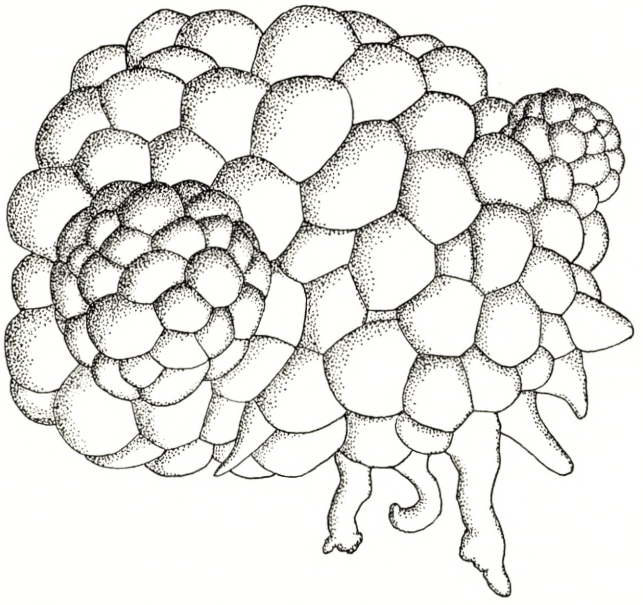

Fig. 2. *Dictyosphaeria cavernosa* (Forssk.) Børgs. var. *bullata* nov. var. (× c. 10). A fragment of a specimen.

This variety forms very irregular bodies because of the many outgrowths of variable size issuing from the thallus (Fig. 1).

These outgrowths are due to the fact that here and there a coenocyte by segregative division becomes divided into a number

of small ones which during their growth gradually form semi-globular outgrowths (Fig. 2) small or large, here and there in the thallus giving it a highly irregular shape. The outgrowths often become rather large, their diameter reaching up to about 2 cm or more.

The thallus ordinarily consists of a single layer of coenocytes, but because of the often large outgrowths broadening out over the underlying layer of coenocytes and perhaps also more or less becoming fixed to it, it may in places appear to be formed by two or more layers.

The diameter of the single coenocyte varies much, reaching up to nearly two mm. Needles are not found.

The plant is fixed to the rocks by means of rhizoids issuing from the base.

As to the locality where the plant was found it is said: "On rocks near reef exposed at low tide."

Mauritius: Riambel, 8-2-51, R. E.V. no. 1035.

Fam. 2. ***Boodleaceae.***

Struvea Sonder.

1. **Struvea anastomosans** (Harv.) Piccone.

Piccone, A., Alghe in E. D'Albertes, Crociera del Corsaro alle Isole Madera e Canarie, Genova 1884, p. 20. Børgesen, Some Chlorophyceae from the Danish West Indies, II, 1912, p. 268; Mar. Alg. D.W. I., p. 54. — *Cladophora*(?) *anastomosans* Harv. in Transact. R. I. Acad., vol. 22, p. 565; Phycologia Australica, vol. II, pl. 101. — *Struvea delicatula* Kütz., Tab. Phyc., vol. 16, tab. 2. Murrey and Boodle, A structural and systematic account of the genus Struvea in Annals of Botany, vol. 11, p. 277, pl. 16, figs. 6—8.

Some few specimens of this delicate plant not earlier recorded from Mauritius were contained in a recently received batch of algae from the island.

Being mostly rather small, the blade-like part in a single specimen (Fig. 3) was about $2\frac{1}{2}$ cm broad and the reticulum rather densely ramified. The stalk is often ramified in the specimens.

Fig. 3. *Struvea anastomosans* (Harv.) Piccone. A large specimen. ($\times 1\frac{1}{2}$).

As to the locality it is said: "Base of large rocks in calm water."

Mauritius: Pointe aux Sables, 22-6-51, R. E. V. no. 1150.
Geogr. Distr.: Most warm seas.

Fam. 3. ***Cladophoraceae.***

Rhizoclonium Kütz.

1. **Rhizoclonium grande** Børgs.

Alg. Mauritius, 1946, p. 31; Additional List, 1948, p. 6.

Some fine specimens of this characteristic species were found in a recently received collection.

As to the locality it is said: "Base of large rocks in calm water."

Mauritius: Pointe aux Sables, 22-6-51. G. Morin, no. 1151.

III. Siphonales.

Fam. 1. Caulerpaceae.

Caulerpa Lamouroux

1. Caulerpa crassifolia (Ag.) J. Ag.

Agardh, J., Till Algernes Systematik, I, p. 13. Howe, M. A., Phycological Studies, II, 1905, p. 574. Børgesen, F., Mar. Alg. D.W.I., Vol. I, 1913, p. 130. — *Caulerpa pinnata* Weber, Monogr. des Caulerpes, 1898, p. 289, pl. XXIV, figs. 1—4.

Two small specimens (no. 1128) (Fig. 4) are as to the shape of the pinnules to be placed near the forma *typica* of this species. They are peculiar in having, besides the usual marginal pinnules, oppositely placed along the margins of the midrib, also such ones issuing without order from the flat sides of the assimilators (Fig. 5).

The pinnules are about 1—1½ mm long and about 450 μ broad and several of them are a little narrowed at their base.

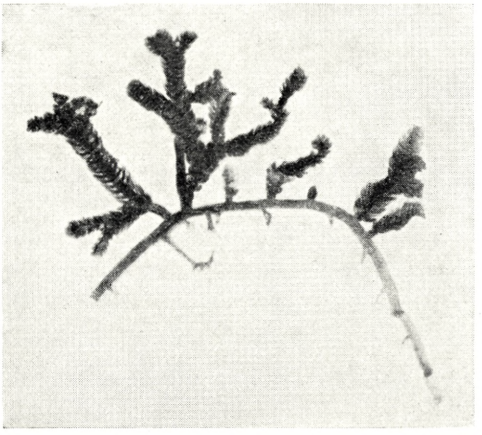

Fig. 4. *Caulerpa crassifolia* (Ag.) J. Ag. Natural size.

The midrib is about 1200 μ broad and the longest assimilator in the specimens only 2½ cm high; they are rather much ramified.

The specimens answer best to Kützing's Fig. 2 in Tab. Phycol., vol. 7, pl. 5 which is called *C. mexicana* there, but as pointed

out by Mme WEBER in her monograph, this figure represents the forma *typica*, while Fig. 3, which KÜTZING calls *C. Herveyana*, is forma *mexicana*.

About the locality it is said: "Near shore, on flat-topped rocks." *Champia parvula* was found together with it.

Another small specimen (no. 1085) is referable to the var.

Fig. 5. *Caulerpa crassifolia* (Ag.) J. Ag. A form with pinnules given out also from the flat sides of the thallus. (× ca. 3).

mexicana (Sond.) Weber, having the pinnules narrowed at their bases.

The specimens, when compared with the West Indian ones, are very small, the breadth of the assimilators reaching only a length of about 3 mm and the highest assimilators $2\frac{1}{2}$ cm only, while in West Indian specimens the assimilators are up to about $1\frac{1}{2}$ cm broad and their length proportional to this.

In a collection of algae from Australia, which Professor A. B. CRIBB most kindly has sent me, a very similar small form of this species was contained, collected on rocks at Colundra, Queensland.

This small form which seems to be characteristic of the southern part of the Indian Ocean I propose to call forma *minima*.

Mauritius: Pointe aux Roches, 1-5-51, R. E. V. no. 1128. Mahébourg near Ile aux Aigrettes, 21-3-51, G. MORIN no. 1085.

Geogr. Distr.: Wide spread in tropical seas.

2. **Caulerpa peltata** Lamour.

var. *typica* Web. v. Bosse.

Alg. Mauritius, I, 1940, p. 51; Add. List, 1946, p. 39; Additions, III, 1951, p. 10.

Some very beautiful specimens were collected in a deep pool behind reef.

Mauritius: Flic-en-Flacq, 22-5-51, R. E.V. no. 1053.

3. **Caulerpa racemosa** (Forssk.) Weber v. Bosse.

Alg. Mauritius, I, 1940, p. 51; Add. List, 1946, p. 39, and 1948, p 32; 1949, p. 14; 1951, p. 10.

In a collection of algae lately received from Mauritius several gatherings of *Caulerpa racemosa* are included. The specimens are referable to the following varieties: var. *clavifera* (Turn.) Web. v. Bosse nos. 1052, 1079; var. *laetevirens* (Mont.) Web. v. Bosse, no. 1066; var. *microphysa* (Web. v. Bosse) Taylor nos. 1051, 1058. But as has often been pointed out, thus lately by Taylor (1942, p. 34), it is an exceedingly variable species and the varieties are united by intermediate forms.

Mauritius: var. *clavifera*, Flic-en-Flacq, near reef submerged at low tide, 22-2-51, R. E.V. no. 1052. Mahébourg, Ile aux Aigrettes, on reef near lagoon, 26-3-51, R. E.V. no. 1079; var. *microphysa*, small form growing densely entangled with no. 1052, R. E.V. no. 1051; Flic-en-Flacq, near reef, 22-2-51, R. E.V. no. 1058; var. *laetevirens* (Mont.) Web. v. Bosse, Mahébourg, reef near Ile aux Aigrettes, 8-3-51, R.E.V. no. 1066.

4. **Caulerpa lentilifera** J. Ag.

forma *parvula* Børgs.

Alg. Mauritius, Additions, I, 1949, p. 15, figs. 5—7.

Some few specimens of this small form were recently received from Mauritius.

As to the locality it is said: "Dredged at 2—3 fathoms."

Mauritius: Tombeau Bay, 30-5-51, R. E.V. no. 1139.

Spongocladia vaucheriaeformis Aresch.

Alg. Mauritius, Additional List, 1948, p. 23, figs. A, B.

Accidentally I have come to examine some material of *Spongocladia vaucheriaeformis* Aresch., the algal symbiont of which I think is a *Cladophoropsis*, and when examining the very irregular and peculiar shape of the cells of the alga in the basal part of the symbiont, it became clear to me that the peculiar bodies which were found in the material preserved in formol of *Cladophora Vaughani* (Alg. Mauritius, 1948, p. 15, 16) and which I presumed to be akinete-formations of this species, in reality are fragments of the much transformed basal filaments of the *Cladophoropsis*.

Most probably the *Cladophora* has been growing near the *Spongocladia* and some of the basal filaments of the *Cladophoropsis* have been mixed with those of the *Cladophora*.

RHODOPHYCEAE

Florideae.

I. Nemalionales.

Fam. 1. Chantransieae.

Acrochaetium Nägl.

1. Acrochaetium subseriatum Børgs.

Alg. Mauritius, III, 1, 1942, p. 15, fig. 6.

Several specimens of this species are found among some epiphytes upon old filaments of *Valoniopsis pachynema*. The specimens formed tufts up to 1 mm high. Many of the sporangia placed unilaterally in long rows are pedicellate.

The species is surely closely related to the West Indian species *Acroch. seriatum* Børgs.

Mauritius: Riambel, 18-12-50, R. E. V. no. 1018.

2. Acrochaetium Trichogloeae nov. spec.

Thallus parvus, ca. 200—300 μ altus, caespitosus, endophyticus, in mucum hospitis (*Trichogloeae Requienii*) immersus.

Sporangia permanentia, magna ca. 20 μ lata et 25 μ longa, germinantia in duas partes divisa, ex parte inferiore filum decumbente inter filamenta assimilationis hospitis emittente, ex parte superiore filamenta erecta.

Fila erecta e basi ramosa, ramis alternis aut magis irregulariter ortis.

Cellulae subcylindricae, ca. 7—8 μ latae et 20 μ longae, chromatophorum axilem, pyrenoide centrali instructum, continentes.

Pili perlongi hyalini plus minus numerosi ex cellulis apicalibus filamentorum orti.

Monosporangia sessilia aut pedicellata, obovata, ca. 8—9 μ longa et 14 μ lata.

Antheridiis in glomerulis parvis pedatis formata.

Mauritius: Barkly Island, 30-10-51, G. MORIN no. 1171a.

This small *Acrochaetium* (Fig. 6) was found abundantly in a specimen of *Trichogloea Requienii* received from Mauritius. It was

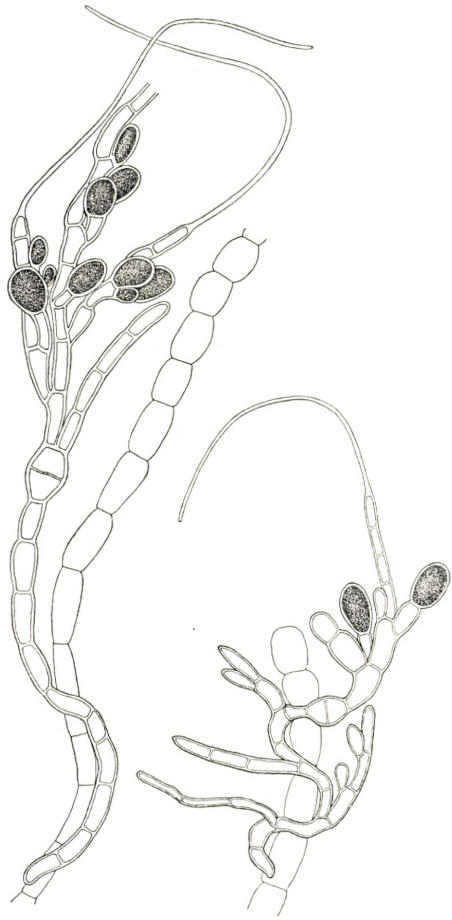

Fig. 6. *Acrochaetium Trichogloeae* nov. spec. Two specimens clinging to the assimilating filaments of the host. (× ca. 400).

quite imbedded in the slime of host, clinging to the assimilating filaments of the host by means of its decumbent filaments.

The germinating spore is permanent. When germinating the spores at first become divided by a transverse wall into two cells from the lowermost of which the downwards growing filaments issue; the filaments are about 5 μ thick and composed of rather long cells.

From the upper cell of the spore the erect filaments are given out; they are ramified from below and form a more or less branched tuft about 200—300 μ high. The ramification is in most cases alternating. The cells of which the filaments are composed are often a little thickened, having above a breadth of 7—8 μ and being 2—3 times as long; they contain an axial cromatophore.

The apical tips of the filaments carry long hairs about 2—3 μ thick and 200—300 μ long.

The ovate monosporangia are sessile or borne upon a short stalk, mostly consisting of a single cell. The sporangia are relatively large, ovate, about 8—9 μ broad and 14 μ long.

Antheridia (Fig. 7) were also found; they form small pedicellate clusters about 25 μ high. As a rule they are present upon separate specimens, but in rarer cases also together with sporangia.

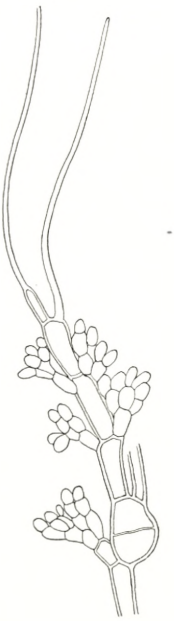

Fig. 7. *Acrochaetium Trichogloeae* nov. spec. A specimen with antheridial bodies. (×ca. 400).

Cystocarpic specimens are not found.

As to its appearance and mode of living this species reminds of *Acrochaetium Collinsianum* Børgs. (syn. *Acr. Liagorae* Børgs.) Mar. Alg. D.W.I., p. 57, figs. 60—62, p. 451.

Fam. 2. ***Helminthocladiaceae.***

Trichogloea Kütz.

Last year I had the great privilege of having on loan here the two original specimens of *Trichogleoea Requieni* (Mont.) Kütz. preserved in the Muséum National d'Histoire Nat., Paris, and as a result of the examination of the specimens I arrived at the

conclusion that the plant JADIN had collected in the island could not be referred to the Red Sea plant and furthermore that PIKE's specimen found in the Kew Herbarium could scarcely be referable to *Tr. Requienii*. Because of this I named it only *Trichogloea* spec. in Additions III, 1951, p. 21.

However, as I last autumn had the pleasure to receive from Dr. VAUGHAN a specimen of *Trichogloea* collected in Mauritius I can state that this specimen is in good accordance with the original specimens of *Tr. Requienii* preserved in Paris.

And since the specimen received from Mauritius seemed to me to show some likeness to PIKE's specimen I therefore asked Director, Professor E. G. SALISBURY to have it on loan here again to make a renewed examination of it; according to this I am now much inclined to consider PIKE's plant as referable to *Tr. Requienii*. Before reporting the results of the examination of the specimens I want to point out that the material has comprised only a single specimen of each form except *Tr. Jadinii*, of which I have seen two specimens, one preserved in Paris and one here in Copenhagen.

As to the most valuable specific characters of *Trichogloea* these seem to be found in the shape and development of the nutritive filaments and the cells of which they are composed.

1. **Trichogloea Requienii** (Mont.) Kütz.

Alg. Mauritius, Additions, III, 1951, p. 15.

Last autumn, as stated above, I received from Dr. VAUGHAN a single small but nicely prepared specimen of *Trichogloea* (Pl. I), and when comparing it with the habit figure of one of the specimens of *Tr. Requienii* preserved in Paris and found in M. A. HOWE's paper on Hawaiian algae, 1914, no. 36, fig. 3, showing the female specimen, it immediately struck me that the specimen from Mauritius was the same species as that from the Red Sea.

In both specimens the branches are given out from the main axis in all directions, the lowermost oppositely, and the branches are in both specimens more or less densely covered by short, worm-like bent branchlets tapering towards their subacute apex. Furthermore the main branches become furcated near their distal

ends more or less in two or three branches; in the lowermost branch on the left in HOWE's photo this is also found.

Comparing the specimen from Mauritius with the figure of ZANARDINI, Plant. Mar. Ruber, 1858, p. 67, tab. V, fig. 1, of a specimen of *Tr. Requienii*, collected by PORTIER "ad scopulos circa Tor", we find the branches issuing from the main axis densely clad with similar small worm-like filaments.

Together with the dried specimen I also from Dr. VAUGHAN received a small sample of it preserved in formol and sea water.

An examination of this material has quite confirmed my supposition that the specimen from Mauritius is *Trichogloea Requienii*.

The examination has brought forward that the specimen is monoecious; the sexual organs may be found mixed, but often they are also found separated in groups here and there.

Fig. 8 shows the upper parts of some of the sterile assimilating filaments. The cells of which they are composed are uppermost subglobose, about 6—8 μ broad, becoming gradually longer downwards. The apical cells in the assimilating filaments are a little longer than those in the original specimens and I have not been able to find here the oblique walls often found in the original specimens. The filaments are about 800 μ long. The chromatophores are hood-shaped with short elongations below.

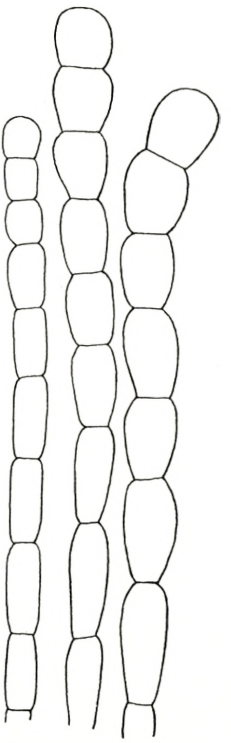

Fig. 8. *Trichogloea Requienii* (Mont.) Kütz. Distal ends of assimilating filaments. (× ca. 300).

The antheridial filaments have as a rule 2 to 5—6 fertile cells in a row below the uppermost sterile ones. Only in a few cases I have found the apical cell to be fertile. In two cases I have found the fertile filaments ramified; in one of these filaments two branchlets were issued, one from the 4th apical cell and one from the 6th; the uppermost branchlet had two fertile cells and the other 4 fertile cells; below in the filaments the cells had only some few antheridial bodies.

The gonimoblasts (Fig. 9) are subglobose when young, when

older broadly dome-like or more irregularly shaped, up to about 200 μ in diameter.

The nutritive filaments as a rule are given out from 3—4, sometimes 5—6, cells in the stipe below the gonimoblasts. As a

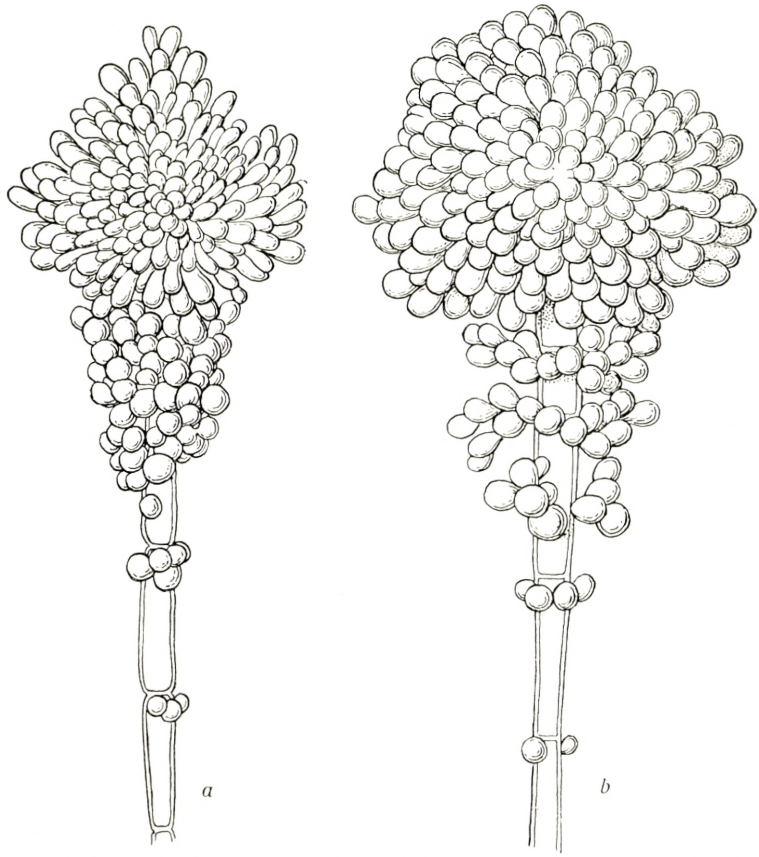

Fig. 9. *Trichogloea Requienii* (Mont.) Kütz. Two gonimoblasts. (× ca. 300).

rule the uppermost whorl is the largest and is often pressed up against the base of the gonimoblasts. The following 2—3 whorls become gradually shorter and are likewise in most cases mutually pressed densely together with the uppermost one in that way covering the whole stipe (Fig. 9*a*); but specimens are also found in which the whorls are more or less separated and the stipe visible (Fig. 9*b*). The lowermost whorls are reduced to a single or a few cells only.

The terminal cells in the nutritive filaments are globose or globose-pyriform about 5—6 μ broad.

In most cases the stipe does not become much thicker during the growth, but it may become so, in such cases reaching a breadth of about 25 μ uppermost. As the nutritive filaments nearly always cover the stipe densely, it is difficult to observe if the cells above in the stipe coalesce during the growth, as found by PAPENFUSS (1946, p. 428, fig. 25) in the *Trichogloea* which he refers to *Tr. Requienii*; but when the nutritive filaments do not cover the stipe densely, it is easily observed that in some cases 2—3 cells in the uppermost part of the stipe become connected by wide canals and often at last coalesce completely.

When this description of the specimen from Mauritius is compared with that of the original specimens (Additions III, 1951, p. 15), it is especially the somewhat shorter cells in the distal parts of the assimilating filaments of the type-specimens which show a deviation from the Mauritian specimen; but the long period of having been dried up might perhaps in any case to some extent be the explanation. Otherwise it must be said that the structure of the Mauritian specimen regarding the antheridial bodies as well as the female ones and the shape and development of the nutritive filaments are in good accordance with the same organs of the typical specimens.

As to the fact that the specimen from Mauritius is monoecious, while the type-specimens are considered to be a male specimen and a female one, this is surely a supposition only, not to be relied on, as one often in parts of a specimen of *Trichogloea* finds only male organs, in other female ones, and because the type-specimens are small, they have been examined carefully only in the same parts of the thalli.

By the fact that the nutritive filaments are pressed more or less up against the base of the gonimoblasts and upon the whole the dense growing together of the nutritive filaments often densely covering the stipe, — in these features *Trichogloea Herveyi* Taylor according to the detailed description and figures of TAYLOR (1951, p. 113) reminds of *Tr. Requienii*, only that these characters are much more fully developed in the plant from Bermuda.

Trichogloea spec.

Alg. Mauritius, Additions, III, 1951, p. 21.

As said above, I have had again the specimen collected by Colonel PIKE on loan here and have made a thorough examination of it, if possibly to find sexual organs in it, but this has been in vain.

Being from Mauritius the specimen is of special interest and a figure of it is therefore given here (Plate II).

From this it appears that the habit of PIKE's specimen, when superficially observed, is rather different from that of the small specimen from Mauritius mentioned above and likewise from ZANARDINI's figure (1858, Tab. V, fig. 1). But after a more thorough examination I have gradually arrived at the conclusion that the differences are not so essential that a referring of it to *Tr. Requienii* is out of the question.

Thus in the small fragment of a specimen of *Tr. Requienii* received from Dr. VAUGHAN the branches issuing from the main stem are more or less oppositely placed and many of the branches are near their distal ends furcated in a way very similar to that in PIKE's specimen and these features are found also in the original specimen of which HOWE has published a figure. And finally the small characteristic worm-like branchlets given out from the main branches and being so characteristic of *Tr. Requienii* are also found in the PIKE specimen.

As to the structure the distal parts of the assimilating filaments in PIKE's specimen are very like those in Dr. VAUGHAN's specimen, but in both plants they are longer than those in the original specimens.

As a result of this comparison I am therefore now highly inclined to consider PIKE's plant to be referable to *Tr. Requienii*, even if an examination of a rich material, comprising the various forms and with fertile specimens, is necessary to make this sure.

Yet I want to point out that the fact that the small lately found specimen occurred in the same locality, Barkly Island, as where PIKE gathered his specimens, this also supports the supposition that both belong to the same species.

As to the colour of the living specimen Dr. VAUGHAN writes: "Colour very pale pinkish-brown" and regarding the locality: "Somewhat calm water, 2—3 feet deep at low tide behind reef."

Mauritius: Barkly Island, 30-10-51, G. MORIN no. 1172a.
Geogr. Distr.: Red Sea, Hawaii.[1]

2. **Trichogloea Jadinii** Børgs.

Alg. Mauritius, Additions, III, 1951, p. 18, figs. 6—7, pl. 1.

In the autumn of 1951 I received from Dr. TANAKA a paper: Studies on Some Marine Algae from Southern Japan, I, Dec. 1950, in which is described a new species of *Trichogloea*: *Tr. Papenfussii*. This species especially as to shape and arrangement of the nutritive filaments seems to show a very great likeness to *Tr. Jadinii*; but the upper cells in the assimilating filaments are shorter and the habit of the thallus seems to differ from *Tr. Jadinii*.

When TANAKA in the same paper, p. 175 refers *Trichogloea lubrica* Okamura (Icones of Japanese Algae, vol. IV, 1930, p. 183, pl. 197, figs. 1—8) to *Tr. Requienii* I cannot follow him. In any case, as said already in my paper of 1951, p. 21 OKAMURA's fig. 6 showing a gonimoblast, the shape of the nutritive filaments in this figure are in good accordance with those of *Tr. Jadinii* and not like those of *Tr. Requienii*; on the other hand the habit fig. 1 on the same plate reminds by the presence of the numerous small branchlets of *Tr. Requienii*.

Liagora Lamouroux.

1. **Liagora rugosa** Zan.

Alg. Mauritius, III, 1, 1942, p. 30, fig. 14; compare also: Additions, 1949, p. 28.

In a recently received batch of algae from Mauritius a small *Liagora* (Fig. 10) is found which I take to be referable to *Liagora rugosa* Zan.

[1] In Additions, Part III, 1951, p. 17 I have expressed some doubts whether the plant from Hawaii is the same as that from the Red Sea. According to my renewed examinations also of the specimen collected by Colonel PIKE I now feel more uncertain whether my doubts are justified.

Most probably all the specimens belong together, having formed a low roundish tuft about 3 cm high.

The thallus is rather regularly di—trifurcated and has in a dried condition a whitish-grey colour with a reddish tinge, while the upper young parts are red; it is rather much shrivelled.

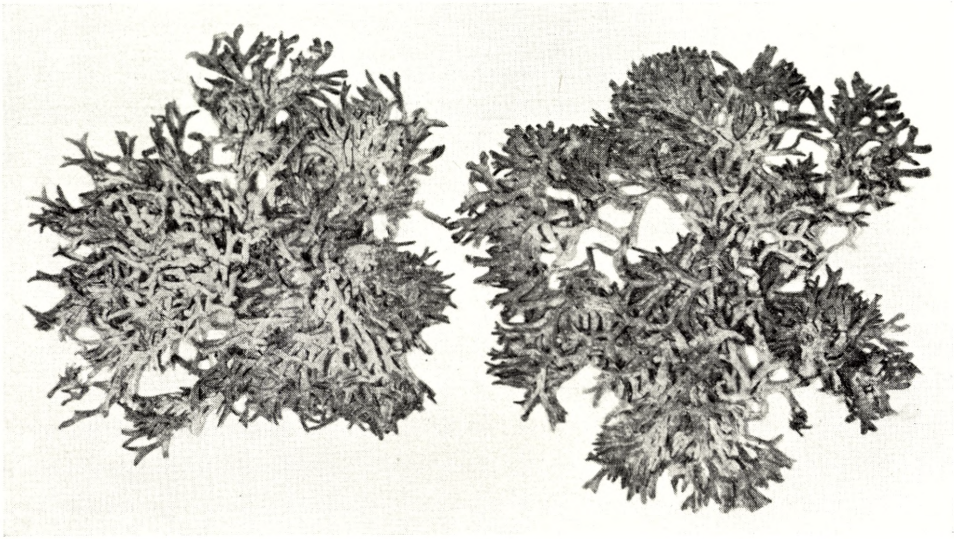

Fig. 10. *Liagora rugosa* Zan. Two specimens. (×1).

The specimens are all antheridial. The antheridial bodies are given out from the uppermost 1—2 cells below the apical ones in the assimilating filaments (Fig. 11). When compared with those formerly figured (1942, p. 30), the shape of the cells in the distal ends of the assimilating filaments of the specimens now found differs somewhat: thus the apical cells are more elongated pyriform, about 25 μ long and 12 μ broad, and the cells below, carrying the antheridial bodies, are also slenderer and longer.

Referring to my remarks quoted above about related forms it must be pointed out that new, especially female, material and examination of ZANARDINI's specimen are necessary to be able to clear up the relationship to the species.

Mauritius: Blue Bay, 8-5-51, R. E. V. no. 1119.

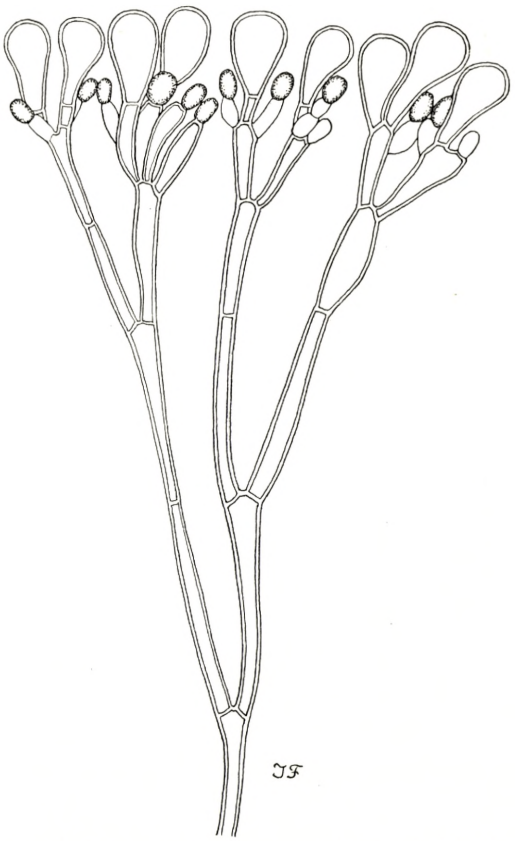

Fig. 11. *Liagora rugosa* Zan. Assimilating filament with antheridial bodies. (× ca. 500).

2. **Liagora mauritiana** Børgs.

Alg. Mauritius, III, 1, 1942, p. 32, figs. 15—16; Additions, III, 1951, p. 27, fig. 12.

In a collection received later a single specimen of this species is found. As previously stated, the species is monoecious and in the specimen received just now well developed antheridia are present in great number while I earlier have seen few. Fig. 12 shows some of the antheridia issuing from the apices of the assimilating filaments.

About the locality it is said: "Pools behind reef attached to stems of *Cymodocea*."

Mauritius: Riambel, 8-2-51, R. E. V. no. 1041.

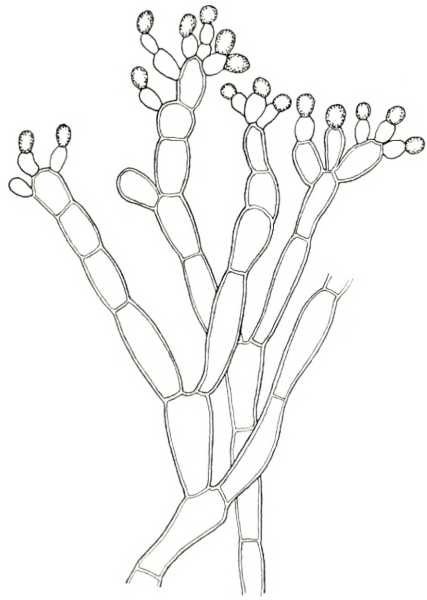

Fig. 12. *Liagora mauritiana* Børgs. Assimilating filaments with antheridia. (× ca. 500).

Gelidiales.

Fam. 1. ***Gelidiaceae.***

Gelidiella Feldm. et Hamel.

1. **Gelidiella acerosa** (Forssk.) Feldm. et Hamel.

Alg. Mauritius, III, 2, 1943, p. 5; Additions, II, 1950, p. 5 and III, 1951, p. 38.

Some few gatherings of this species are included in later received collections of algae from Mauritius.

No. 1045 forms "dense mats entangled with other algae", and as to no. 1050, a very similar form, it is said about the locality and habit: "Forms a dense entangled flat mat-like growth on large rocks protected from strong surf."

No. 1112 is a small, 2—3 cm high, robust form, about the locality of which it is said: "On rocks submerged at low tide."

And finally no. 1076 is a larger form with few, shorter and rather distantly placed ramuli. About this is said only: "Attached to old pieces of corals."

Mauritius: Riambel, 8-2-51, G. MORIN no. 1045. Flic-en-Flacq, 22-2-51, R. E. V. no. 1050. Mahébourg, 26-3-51, R. E. V. no. 1076. Pointe aux Sables, 24-4-51, G. MORIN no. 1112.

Gelidium Lamouroux.

1. **Gelidium pusillum** (Stackh.) Le Jolis.

Alg. Mauritius, III, 2, 1943, p. 5, fig. 1.

Some specimens in a later received collection agree very well with KÜTZING's figures in Tal. Phyc., vol. 15, tab. 37, fig. i.

The specimens were collected: nos. 1102 and 1103 in "2' water at low tide growing on rocks", and no. 1182, "usually attached to large pieces of dead corals, and no. 1113 "submerged at low tides, on rock".

Mauritius: Pointe aux Sables, 24-4-51, G. MORIN nos. 1102, 1103, 1113. Ile aux Aigrettes, Mahébourg, 26-3-51, G. MORIN no. 1082.

Genus incertae sedis.

Wurdemannia Harv.

1. **Wurdemannia miniata** (Drap.) Feldm. et Hamel.

Alg. Mauritius, Additions, II, 1950, p. 39.

Of this species some fine specimens were recently received from Mauritius. The specimens formed densely felted tufts in which also *Champia parvula* (Ag.) Harv. and a small sterile *Hypnea* showing much likeness to *H. nidulans* Setch. were included.

All these small, creeping species, richly provided with hapters given out here and there from the thalli and by means of which they are firmly attached together, share in the formation of the cushions.

About the habitat of the specimens is said: "On flat topped basalt rocks exposed at low tide."

Mauritius: Flic-en-Flacq, 20-5-51, R. E. V. no. 1137.

II. Gigartinales.

Fam. 1. Solieriaceae.

Sarconema Zanard.

1. **Sarconema filiforme** (Sonder) Kylin.

Alg. Mauritius, III, 2, 1943, p. 39; Additions, II, 1950, p. 13.

Some small specimens with filaments nearly as fine as a hair are contained in a collection received later.

The specimens were growing on an old pier.

Mauritius: Ilôt Barkly, 1-4-46, G. Morin no. 514.

Gilidiopsis Schmitz.

1. **Gelidiopsis scoparia** (Mont. et Mill.) Schmitz.

Schmitz, Fr., Marine Florideen von Deutsch-Ostafrika, 1895, p. 149. Feldmann, J., Remarques sur les genres *Gelidium* Lamour., *Gelidiopsis* Schmitz et *Echinocaulon* (Kütz.) emend., 1931, p. 7. — *Gelidium scoparium* Mont. et Millardet, Algues de la Réunion, p. 13, tab. 27, fig. 1. Kützing, Tab. Phyc., vol. XVIII, tab. 46, fig. 2.

Fig. 13. *Gelidiopsis scoparia* (Mont. et Mill.) Schmitz. (×1).

A fine collection of specimens of this characteristic species described upon specimens from Réunion was lately received from Mauritius.

Most regrettably no base of the plant is found in the specimens, but according to the description of MONTAGNE and MILLARDET the erect filaments issue in great number "d'un même point", most probably a disc, thus forming a tuft about 5—6 mm heigh. Referring otherwise to the author's description I shall mention only that the filaments usually begin to be divided at a height of 1—1½ cm. The divisions occur in the way that the apices of the branches become broadened out and flattened and then furcated in a number of lobes (mostly 4), as seen uppermost in fig. 13. This process may be repeated several times.

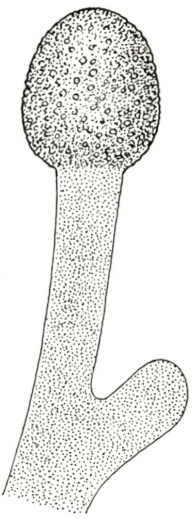

Fig. 14. *Gelidiopsis scoparia* (Mont. et Mill.) Schmitz. A stichidium. (× ca. 20).

The thallus is flattened, about 300 μ thick and its breadth is rather variable, increasing in the places where divisions have taken place.

The plant has hitherto been found sterile only, but in the material now received I have found several stichidia (Fig. 14). These are terminally placed upon a branchlet; they are heart-shaped, ca. 500 μ broad and 750 μ long and densely studded with sporangia.

About the locality it is said: "on large rocks submerged at lowtide."

Mauritius: Pointe aux Sables, 24-4-51, R. E. V. no. 1115.
Geogr. Distr.: Réunion.

Fam. 2. ***Hypneaceae.***

Hypnea Lamouroux.

1. **Hypnea nidulans** Setch.

Alg. Mauritius, III, 2, 1943, p. 62; Additions, II, 1950, p. 17.

Several fertile specimens of this species (no. 1107) were found in a lately received collection of algae.

As to the locality it is said: "On rocks exposed at low tide."

Some other, but sterile, specimens (no. 1145) are surely also referable to this species, but being sterile they cannot be determined with certainty.

As to the locality it is said: "Forms dense moss-like growths on rocks near shore exposed at low tide."

Mauritius: Pointe aux Sables, 24-4-51, G. MORIN no. 1107. Same locality, 22-6-51, R. E. V. no. 1145.

2. **Hypnea**(?) **horrida** (Ag.) J. Ag.

Alg. Mauritius, III, 2, 1943, p. 62, fig. 32; Additions, II, 1950, p. 18, fig. 4.

Two large fine specimens of this endemic species are contained in a lately received collection. The colours of the dried specimens is a splendid deep red. As usually the specimens are sterile.

As to the locality it is said: "On lagoon-side of reef exposed at low tide."

Mahébourg, 26-3-51, R. E. V. no. 1081.

Fam. 3. ***Sphaerococcaceae.***

Phacelocarpus Endl. et Dies.

1. **Phacelocarpus tristichus** J. Ag.

Alg. Mauritius, III, 2, 1943, p. 65, fig. 33.

Of this species endemic in Mauritius I have in collections received recently found some fine specimens, having formerly seen some quite small fragments only.

The specimens reach a height of about 8—9 cm and the plant forms a dense roundish tuft arising from the upwards increasingly dense ramification.

The specimens are most regrettably sterile.

As compared with the specimens mentioned in the previous paper, Fig. 33, the appearance of those now received are more robust.

KYLIN (1932, p. 51, pl. 19, fig. 15) gives an illustration of the original specimen found in J. AGARDH's herbarium in Lund agreeing very well with the specimens now received.

As pointed out by J. AGARDH, Till Algernes Systematik, 1884, p. 57, the Mauritian species is closely related to *Phacelocarpus tortuosus* Endl. & Dies. known from Cape and Port Natal, but according to AGARDH the African species is in all respects larger than the Mauritian one.

As to the locality it is said: "In rock cavities near reef, submerged at low tide."

Riambel, 8-12-50, G. MORIN no. 1000.

Fam. 4. ***Sarcodiaceae.***

Sarcodia J. Ag.

Sarcodia mauritiana nov. spec.

Frons ca. 6 cm alta, plana, carnoso-membranacea, irregulariter palmatim divisa et furcata, e segmentis ca. 1 cm et magis latis, ex marginibus proliferis, cuneato-linearibus aut apicem versus magis expansis, superne plus minus late rotundatis aut in lobulos subacutos divisis composita.

Cystocarpia permagna, globosa, e marginibus et pagina thalli orta.

Tetrasporangia et antheridia non observata.

Color thalli sicci fuscus.

Mauritius: Pointe aux Sables, 22-11-51, G. MORIN no. 1147d.

The specimens, which I take to be the representative of a new species, are somewhat fragmentary as no basal discs are found; but most probably the plant forms 5—6 cm high tufts upon rocks.

The thallus (Pl. III) is very irregularly divided several times in oblong or more or less elongated-cuneate lobes having narrow bases and becoming broader upwards. Lobes or proliferations issue from the margins. And to this irregularity comes the fact that the thallus, as appears from the material preserved in formol, is much sinuated. The large globular cystocarps issuing in

great number from the flat sides of the thallus as well as from the edges augment the irregularity, at the same time giving the thallus a very elegant appearance.

As to the anatomy a transverse section of the thallus shows that the epidermal cells are elongated and very densely placed; then follows a layer of small roundish cells gradually becoming longer inwards and followed by, first, polygonal, then stellate or irregularly shaped cells, the innermost issuing long arms, from which the filaments traversing the slimy interior are given out.

Upon a longitudinal section of the cystocarps it is seen that they have a thick peripheral wall consisting of densely placed rows of small cells; above a peristome is present. A tissue of roundish cells is present in the base of the cystocarp, being a continuation of the cortical layer; above this, near the middle of the cystocarps, a tissue of irregularly formed cells are found from which the much divided carposporic filaments are given out. OKAMURA in Icones Jap. Alg., vol. IV, p. 110, pl. 178, fig. 10 gives a picture of the cystocarps of *Sarcodia Montagneana* J. Ag. which shows a great likeness to that of the present species.

Some few of the dried specimens are tetrasporic (Plate III, the specimen below on the left). These specimens have somewhat broader lobes and upon the whole the thallus is not so much divided. The sporangia are transversely divided, about 30—35 μ long and 15 μ broad, and formed in the cortical layer.

As this species seemed to me to show much likeness to *Sarcodia Gattyae* (J. Ag.) Kylin from Arabia (Aden), compare KYLIN, 1923, p. 56, pl. 21, fig. 51, showing the specimen upon which J. AGARDH described the species I asked Miss DICKINSON, the Kew Herbarium, whether any specimens of this species were found there; this not being the case Miss DICKINSON most kindly stated that a specimen was found in the Natural History Museum, London. As determined specimens are not allowed out on loan from the museum, I sent a specimen of the species from Mauritius to the keeper of the Herbarium, Miss L. M. NEWTON, asking her if she would compare my plant with the specimens of *S. Gattyae*. And Miss NEWTON most kindly answered: "Miss GATTY's plant is very much smaller, is slightly thinner in texture and a lighter red in colour; the cystocarps are borne only on the edges of the frond, not scattered over the thallus." According to this valuable in-

formation the Mauritian plant must be said to be well separated from *Sarcodia Gattyae*.

The previously received material of *Sarcodia* (compare Alg. Mauritius, III, 2, p. 66, fig. 34 and Additions II, 1950, p. 21, figs. 7—8), as said in the papers, consisted only of fragments and specimens cast ashore and my referring of them to *S. ceylanica* Harv. is surely wrong, most specimens perhaps being most probably referable to the species described here.

Fam. 5. ***Gracilariaceae.***

Gracilaria Grev.

1. **Gracilaria spinuligera** nov. spec.

Frons ut videtur decumbens, caespites rotundatos, depressos formans. Thallus teres carnosus, ca. 4 mm latus, ramosus, ramio principalibus ramulos breviores, ca. 3 cm longos spinuliferos gerentibus.

Substantia carcososa-cartilaginea. Color in sicco brunneo-ametysthinus.

Stratum corticale in sectione transversali ex cellulis angustis,

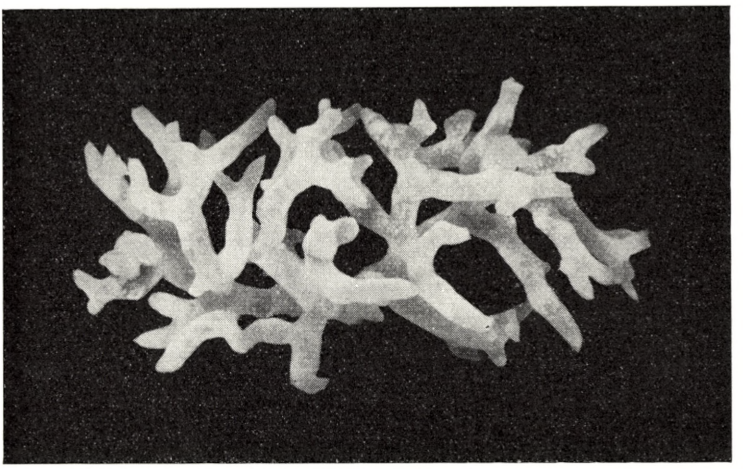

Fig. 15. *Gracilaria spinuligera* nov. spec. Fragment of a specimen preserved in formol and sea water. (×1).

parvis, elongatis compositum; medulla ex cellulis subglobosis exterioribus parvis, interioribus ad 800 μ latis formata.

Tetrasporangia in strato corticali praesentia, cruciatim divisa, ca. 50 μ longa et 25 μ lata.

Mauritius: Flic-en-Flacq, near reef, 3-5-50, R. E. V. no. 922.

According to the material consisting of a single dried specimen (Pl. IV) and a smaller part preserved in formol (Fig. 15), this

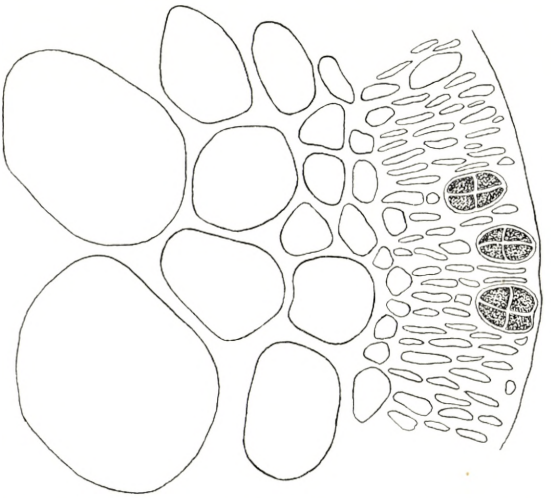

Fig. 16. *Gracilaria spinuligera* nov. spec. Transverse section of the thallus with tetrasporangia. (× ca. 200).

species most probably forms a low somewhat expanded roundish tuft upon rocks.

It has a terete, fleshy, ca. 4 mm thick thallus (Fig. 15) here and there a little narrowed; it is much ramified, from the main branches giving out about 3 cm long, more or less curved branches upwards and outwards. The lowermost half of these branches are naked, then a single short spine-like branchlet is given out, a little higher up another, and the apices of the branches end with a spine or often two, more or less curved. Generally the ramification occurs like this; but it varies much from branch to branch.

A transverse section of the thallus (Fig. 16) shows that the peripheric tissue is about 100 μ thick and consists of densely

placed narrow, thick-walled, ellipsoidal cells, about 5—6 μ broad and twice as long and rather irregularly placed. Then follows a layer of, first, quite small, but gradually larger roundish cells with thick walls; the contents of these cells are stellately contracted from the pores, reminding of what for instance takes place in *Eucheuma*. Then the real medulla begins with rather thin-walled globular cells increasing in size inwards, the innermost having a diameter up to about 800 μ.

The specimen is tetrasporic; the crauciately divided sporangia are formed in the peripheric layer; they are oblong-oval, about 50 μ long and half this breadth.

About the locality of this species it is said only "near reef", but according to its habit and structure the plant surely has its home in very similar localities to those of *Gracilaria crassa* Harv., viz. localities exposed to strong surf.

2. **Gracilaria crassa** Harv.

HARVEY, W. H., Alg. Ceylon exsic., no. 29. J. AG., Epicrisis, p. 417. BØRGESEN, F., Some Marine Algae from Ceylon, 1936, p. 86, fig. 8. — *Corallopsis Opuntia* J. Ag., Epicrisis, p. 409. BØRGESEN, Alg. Mauritius, III, 2, 1943, p. 69; Additions, II, 1950, p. 24, figs. 9—10 and Additions, III, 1951, p. 41.

In the papers mentioned above dealing with the algae of Mauritius and also in earlier papers quoted in the paper from 1950, I have pointed out that in my opinion *Corallopsis Opuntia* J. Ag. cannot be kept separate from *Gracilaria crassa* Harv. Referring to what is said in my former papers I now go the whole length, calling the species *Gracilaria crassa* Harv.

I have been induced to do so by a statement in a letter from Miss LINDA M. NEWTON, the British Museum, in which she writes: "I have read with interest your remarks on *Gracilaria crassa* and *Corallopsis opuntia* and agree with you that they seem to be the same thing. But I think they might belong to the genus *Gracilaria* and not *Corallopsis*." In this I quite agree with Miss NEWTON; being in accordance with my treating of the question in the above quoted paper on algae from Ceylon and also confirmed by examination of later received algae from Mauritius. And since

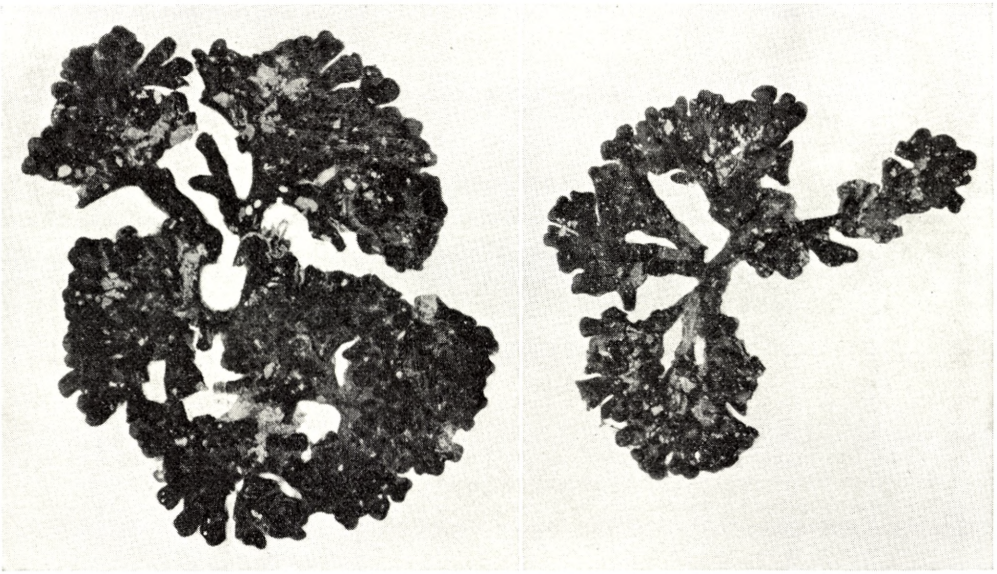

Fig. 17. *Gracilaria crassa* Harv. forma *conglomerata* n. form. (×1).

Grac. crassa Harv. has no. 29 in HARVEY, Ceylon Alg. Exsicc. and *Corallopsis Cacalia* Harv. (= *Corallopsis Opuntia* J. Ag.) is no. 30 the former name must be preferred.

Forma *conglomerata* n. form.

Of this variable species I have in a batch of algae lately received from Mauritius found an interesting form growing upon rocks in an exposed locality.

To judge from the specimens, both dried (Fig. 17) and preserved in formol and seawater (Fig. 18), the plant has formed a low dense, firm cushion on the rocks composed of the much and densely ramified branches firmly entangled.

The thallus is up to 3 mm broad, here and there with narrowings and with blunt, broadly rounded apices.

A transverse section of the thallus shows that the cells in the medulla have very thin walls, the largest in the middle of the thallus are about 350 μ broad.

Corallopsis reptans Weber, 1926, p. 146, fig. 37, shows some

Fig. 18. *Gracilaria crassa* Harv. forma *conglomerata* nov. form. Fragment of a specimen preserved in formol and seawater. (×1).

likeness to this form, but I have not observed rhizoids in the Mauritian plant.

Mauritius: Mahébourg, "reef near Ile aux Aigrettes—exposed to strong surf", 26-3-51, R. E. V. no. 1078.

3. **Gracilaria arcuata** Zan.

Var. *Snackeyi* Weber.

Alg. Mauritius, III, 2, 1943, p. 69, fig. 35.

In collections received later several specimens very like those I formerly have referred to this variety are found. The gathering reminding most of the description and figure given by Mme Weber is no. 1077, of which I give a figure of some specimens here (Fig. 19). The thallus is fleshy, about 4 mm thick; the tips of the thallus are now acute, now roundish. In the female specimens the semiglobular sporangia are very protruding, $\frac{1}{2}$—$\frac{3}{4}$ mm broad.

A transverse section shows that the cells in the middle of the thallus are very large, up to 600—700 μ in diameter.

Another gathering, no. 1064, was more densely branched with shorter branchlets and mostly with broadly rounded apices.

Fig. 19. *Gracilaria arcuata* Zan. var. *Snackeyi* Weber. (×1).

Finally a third gathering, no. 1065, had longer, slenderer branchlets tapering slowly towards the acute apices.

Mauritius: Ile aux Aigrettes near Mahébourg; no. 1077 "exposed at low tide; thallus fleshy, red purple and green", R. E. V., 26-3-51; no. 1064 "exposed at low tide, thallus deep red or reddish-green", G. MORIN, 8-3-51; no. 1065, "lagoon edge of reef", R. E. V., 8-3-51.

Gracilariopsis Dawson.

1. **Gracilariopsis dumosa** (Harv.) comb. nov.

Gracilaria dumosa Harv., Friendly Island Alg., no. 37. AGARDH, J., Epicrisis, p. 416. KÜTZING, Tab. Phycol., vol. XIX, tab. 21, figs. e–f.

The specimens from Mauritius are in good agreement with a specimen in HARVEY's "Friendly Island Algae", no. 37, found in the herbarium of the Botanical Museum. And likewise they agree very well with the description given by J. AGARDH, *l. c.*, and with the habit figure of a fragment of the thallus in KÜTZING's Tabulae.

To judge from the dried specimens (Pl. V), the plant forms much entangled tufts; as the basal discs are wanting I cannot make any statement about their height. The breadth of the thallus is up to about 2 mm. The upper branches taper upwards, ending in pointed apices, but in some cases the filaments in the upper parts become a little thicker and then tapering rather abruptly near the upper ends.

The ramification is very irregular, furcated with shorter or longer distances between the divisions, in places also secund; near the upper ends of the branches the ramification becomes often very dense, nearly tufted.

The colour of the older parts of the thallus in a dried condition is dark brown-violet, in the younger parts yellowish-violet.

A transverse section of the thallus shows that the medulla consists of roundish cells, the largest ones, in the middle, having a diameter up to about 300—400 μ; as is shown in KÜTZING's figure f the walls are rather thick, about 5—7 μ.

In one of the specimens a branch with cystocarps is present; these are not very high, but rather broad. A transverse section shows that the parenchyma in the gonimoblast consists of rather small cells with rich contents and furthermore that nutritive filaments are absent. Because of this, as already stated above, the present species is no *Gracilaria*, but is referable to the genus *Gracilariopsis* Dawson, 1949, p. 3.

Most regrettably I have not found any tetrasporangia, nor antheridia.

As to the locality it is said: "In calm water near shore."

Mauritius: Les Salines, Roche Noire, Pt. Louis, 11-11-50, G. MORIN no. 912.

Geogr. Distr.: Friendly Islands.

III. Rhodymeniales.

Fam. 1. Rhodymeniaceae.

Coelothrix Børgs.

Coelothrix indica Børgs.

Alg. Mauritius, III, 3, 1944, p.14 and Additions, II, 1950, p. 40.

A fertile specimen with the characteristic elongate, clavate stichidia was found as an epiphyte upon *Digenea simplex*.

Mauritius: Flic-en-Flacq, 22-2-51, R. E. V. no.1055.

Erythrocolon J. Ag.

1. Erythrocolon podagricum (Harv.) J. Ag.

Agardh, J., Analecta Algologica, 3, 1896, p. 90. Kylin, H., Die Florideengattung Rhodymeniales, 1931, p.14, fig. 4AB, tab. 6, fig.13. — *Chylocladia podagrica* Harv., Friendly Island Algae, no. 50. J. Agardh, Epicrisis, p. 302. — *Chrysymenia podagrica* (J. Ag.) Weber, Alg. Siboga, p. 471, fig. 204.

Some specimens of this species are found in a collection of algae lately received from Mauritius. The shape of the specimens is in good agreement with Agardh's description and with the figure given by Kylin of the specimen in Agardh's Herbarium, and likewise the structure agrees well with Kylin's figures and description.

As we had not here in Copenhagen any specimen of Harvey's plant I am much indebted to Director Salisbury for the permission to have had on loan here a specimen for comparison with that from Mauritius. This has brought out that the plant from Mauritius is in good agreement with that of Harvey, differing only by its much smaller size, for which reason I propose to name it forma *minor*.

But I want to point out that the plant I in part 3, *Rhodymeniales*, 1944, p. 18, referred to *Coelathrum Boergesenii* Weber is not rightly referred to that species, but is the present one.

When the habit figure given there (Fig. 12) is compared with HARVEY's plant, its much smaller size is clearly seen.

About the locality it is said: "Sea edge of reef exposed to strong surf, rare."

Mauritius: Blue Bay, 8-5-51, G. MORIN no. 1121. Dr. MORTENSEN's specimen was collected at Flatt Island.

Geogr. Distr.: Friendly Islands, Malayan Archipelago.

Champia Desv.

1. **Champia parvula** (Ag.) Harv.

Alg. Mauritius, III, 3, 1944, p. 30.

This species was found intermingled in the thallus of *Actinotrichia fragilis*.

Furthermore it occurred in densely felted clumps of *Wurdemannia miniata* and other algae.

Mauritius: Flic-en-Flacq, 3-5-50, R. E. V. no. 916. Same locality, 20-5-51, R. E. V. no. 1137.

IV. Ceramiales.

Fam. 1. Ceramiaceae.

Subfam. 1. Crouanieae.

Antithamnion Nägeli.

1. **Antithamnion elegans** Berth.?

BERTHOLD, G., Über die Vertheilung der Algen im Golf von Neapel, 1882, p. 516. FUNK, G., Über einige Ceramiaceen aus dem Golf von Neapel, 1922, p. 241, pl. V, fig. 17, BØRGESEN, F., Mar. Alg. Canary Islands, III, 3, 1930, p. 56, figs. 21—23. FELDMANN-MAZOYER, GENEVIÈVE, Recherches sur les Ceramiacées, 1940, p. 267, figs. 100—102.

The reason why I have put a ? after the specific name of the species is that I have found only sterile specimens. But since the vegetative structure of the plant—,more especially the characteristic position of the gland-cells is in good conformity with that found

in this species, I have in reality no doubt as to the referring of the Mauritian plant to this species. The short description below of the Mauritian plant will show it.

The plant was found creeping upon a cable in Port Louis harbour. The tufts had a height of about 1 cm.

Near the base the erect filaments are about 80 μ thick, tapering slowly upwards; the cells have a length of about 300 μ.

In accordance with the vigour of the specimens only two oppositely placed simple branchlets are given out in the poorest ones, while 3—4 to 5 ramified branchlets, verticillately placed, are present in the vigorous filaments.

The gland cells are oblong, about 11 μ long and 6 μ broad, and placed on the ventral side of a single cell, being a little shorter than this. This cell is nearly always the basal cell in a branchlet; generally only a single gland-cell is found in each branchlet.

Mauritius: Port Louis harbour, 28-5-51, G. Morin no.1136.

Geogr. Distr.: Western part of the Mediterranean Sea. Canary Islands.

Subfam. 2. Ceramieae.

Ceramium Lyngbye.

Par Mme Dr. Geneviève Feldmann-Mazoyer.

1. **Ceramium Codii** (Richards) G. Mazoyer.

Mazoyer, G., Céramiacées Afrique du Nord, 1938, p. 324. Feldmann-Mazoyer, G., Recherches sur les Céramiacées de la Méditerranée occidentale, Alger (1940) 1941, p. 285, figs. 40, 59, 105. — *Ceramothamnion Codii* Richards, A new Rhodophyceous alga, 1901, p. 257—265, pl. 21—22. — *Ceramothamnion adriaticum* Schiller, Schussnig, Österreichische botanische Zeitschrift, 1914, p. 85—93.

Sur des échantillons de *Codium dichotomum* (Huds.) S. F. Gray, j'ai observé quelques filaments de cette espèce assez répandue sur le même hôte en Méditerranée. Les filaments rampants à la surface des utricules de l'hôte mesurent environ 80 μ de diamètre et présentent des nœuds à cortication très réduite d'où peuvent naître des rhizoïdes s'insinuant entre les utricules du *Codium*.

La plante de l'Ile Maurice ne me parait différer en rien de celle de la Méditerranée, bien caractérisée en particulier par le très faible développement des cellules corticales des nœuds.

D'après les notes que m'a communiquées le Dr. Børgesen, certains échantillons de l'Ile Maurice étaient pourvus de tétrasporanges, je n'en ai pas observés sur les échantillons que j'ai examinés, mélés à divers épiphytes et en particulier à un *Polysiphonia*.

Ile Maurice: Par 1—2 milles SSW de Round Island, Juin 2, 1948, F. D. Omaney, n° 838.

Distribution géogr.: Baltique (Danzig), Bermudes, Méditerranée.

2. **Ceramium Camouii** Dawson.

Dawson, Y., Marine algae of the Gulf of California, 1944, p. 319, pl. 51, figs. 2—3; 1950, Review of *Ceramium*, 1950, p. 129.

Je rapporte au *Ceramium Camouii* décrit du Golfe de Californie par Dawson, un petit *Ceramium* qui semble bien correspondre à la description et aux figures publiées par Y. Dawson.

Ce petit *Ceramium* (Fig. 20) se présente sous forme de filaments lâches, ne dépassant guère plus de 3,5 mm, rampant sur le *Codium Vaughani* Boerg., auquel il se fixe par des rhizoïdes naissant au niveau des nœuds de la région inférieure de la fronde.

Les entre-nœuds sont bien nets sur toute l'étendue de l'algue et ils sont 2 à 4 fois plus hauts que les nœuds, sauf tout à fait au sommet des rameaux.

Les bords inférieurs et supérieurs des nœuds sont nettement délimités et les cellules corticales, plus ou moins anguleuses, sont disposées d'une manière irrégulière. Les extrémités des rameaux sont droites. Le diamètre des filaments est sensiblement le même sur toute leur étendue et atteint une soixantaine de μ au niveau des nœuds stériles qui sont légèrement renflés. Les nœuds fertiles sont très nettement renflés, déformés et lobés, ils atteignent 130 μ de large.

Les tétrasporanges de cette espèce sont verticillés par 4 ou 5 sur un rang, en partie recouverts par les cellules corticales. Ils sont subsphériques ($45 \times 50\ \mu$ de diamètre environ).

L'échantillon présentait des spermatanges situés tout autour des nœuds supérieurs.

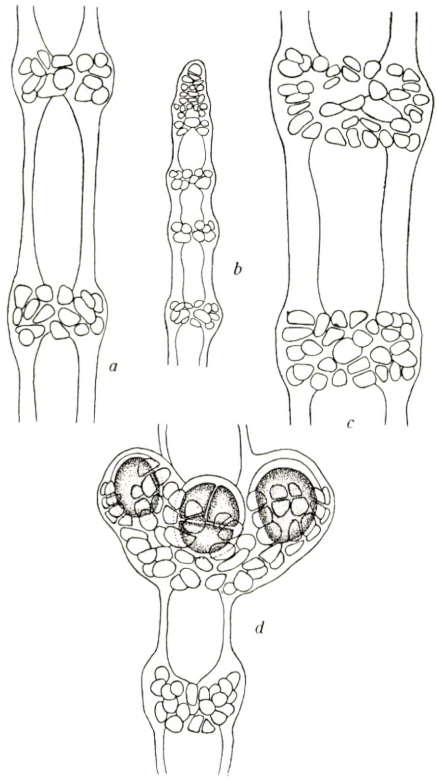

Fig. 20. *Ceramium Camouii* Dawson. *a* et *c*: nœuds de la région supérieure et moyenne; *b*: sommet d'un rameau; *d*: nœudsfertile avec 3 tétrasporanges. *a*, *c* et *d* ×230 env. *b* ×135 env.

Cette espèce est à rapprocher du *Ceramium Codii* mais en diffère par sa cortication plus développée, la largeur de ses entre-nœuds et surtout la disposition de ses tétrasporanges régulièrement verticillés sur des nœuds fortement renflés.

Ile Maurice: Dans une cuvette rocheuse, l'Ilot Brocus (R. E. Vaughan n° 163).

Distribution: Golfe de Californie.

3. **Ceramium gracillimum** (Griff.) Harv.

var. *byssoideum* (Harv.) G. Mazoyer.

Mazoyer, G., Céramiacées Afrique du Nord, 1938, p. 323. Feldmann-Mazoyer, G., Céramiacées de Villefranche, 1939, p. 8; Céramiacées de la Méditerranée, p. 293—295, fig. 109. — *Ceramium byssoideum*

Harvey, Nereis Bor. Amer., pt. II, p. 218; Howe in Britton, Flora of Bermuda, 1918, p. 351. — *C. transversale* Collins et Harvey, Algae of Bermuda, 1917, p. 145, pl. 5, figs. 29—31. Børgesen, Marine Algae in Ostenfeld, Plants from Beata Island, St. Domingo, 1924.

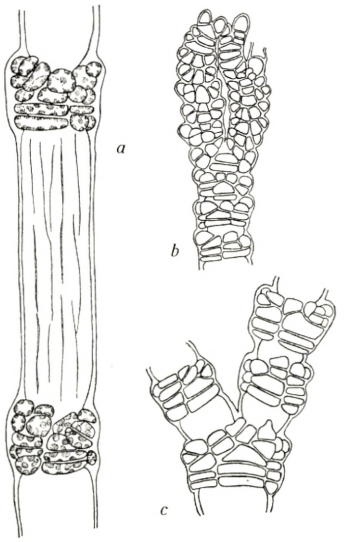

Fig. 21. *Ceramium gracillimum* (Griff.) Harv. var. *byssoideum* (Harv.) G. Mazoyer. *a*: région moyenne de la fronde; *b*: sommet d'un rameau; *c*: région supérieure d'un rameau. × 230 env.

Les échantillons (Fig. 21) de l'Ile Maurice que j'ai examinés, correspondent bien à ceux de Méditerranée; la disposition des cellules corticales des nœuds, allongées transversalement, est particulièrement bien nette.

Ile Maurice: Août 1939, Fort William et Barkly Island, par R. E. Vaughan, n° 327.

Distribution: Semble exister dans toutes les mers chaudes.

4. **Ceramium macrotrichum** G. Feldm. nov. spec.

Frondes pusillae, ad folias Cymodoceae, caespitulos usque ad 3—4 mm altos formantes, filamentis repentibus, rhizoidibus affixis, et filamentis erectis dichotomis, patentibus, constitutae.

Filamenta erecta, apicibus rectis aut paulo incurvis, ad apicem versus 75—80 μ lata, in partibus adultioribus usque ad 100—200 μ lata.

Zonae corticales fere usque ad apicem distinctae, interstitiis pellucidis 4—5 plo longitudinem zonarum superantibus, separatae.

Cellulae corticales majores, in parte inferiori zonarum, rectangulares et transversaliter elongatae. Cellulae corticales superiores zonarum, pilum hyalinum, robustum gerentes.

Tetrasporangia subsphaerica, tetraedrice divisa, 75 μ diam.

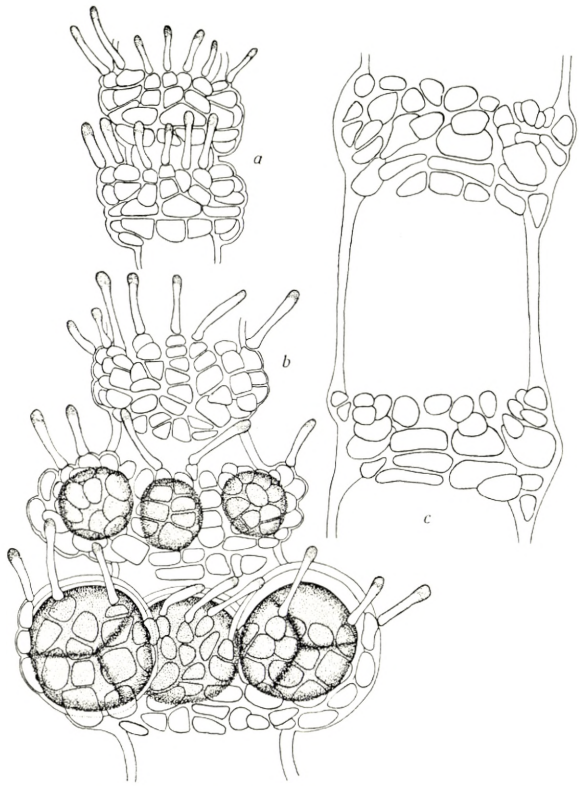

Fig. 22. *Ceramium macrotrichum* G. Feldm. *a*: nœuds situés vers le sommet montrant la disposition des poils; *b*: nœuds de la région supérieure montrant la disposition des tétrasporanges et des poils; *c*: cortication de la région moyenne de la fronde montrant la présence de cellules transversale. × 230 env.

ad zonas eximie inflatas regulariter verticillata et cellulis corticalibus fere omnino obtecta.

Habitat ad folias *Cymodoceae*, in Oceano Indico ad Insulam Mauritii.

Ce petit *Ceramium* (Fig. 22) croît sur les feuilles de *Cymodocea*, formant des petites touffes hautes de 3 à 4 mm. La base des

rameaux est rampante et adhère au substratum par des rhizoides digités, larges d'environ 25 μ naissant des nœuds.

Les rameaux sont irrégulièrement pennés à filaments larges de 100 à 200 μ vers leur base et de 75 à 80 μ vers leurs extrémités. Les cellules axiales peuvent atteindre 450 μ de haut et 125 μ de large vers la base de l'algue, leur hauteur étant 4 à 5 fois égale à celle des nœuds. Les extrêmités sont généralement droites ou à peine recourbées.

La disposition et la forme des cellules corticales rappellent beaucoup celles du *C. gracillimum* bien que la cortication soit plus développée que chez ce dernier.

La limite inférieure et supérieure des nœuds est nettement délimitée. Dans la moitié inférieure des nœuds, on observe des cellules rectangulaires allongées transversalement. Je n'ai pas constaté la présence de cellules sécrétrices qui ont pu éclater dans le liquide fixateur.

Les nœuds des régions supérieures présentent de magnifiques poils disposés en verticilles tout autour des nœuds et naissant des cellules corticales délimitant leur bord supérieur. Cette disposition parait bien régulière chez l'échantillon étudié. Bien que la présence ou l'absence de poils hyalins unicellulaires ne puisse généralement être considérée comme un caractère systématique constant; ce caractère semblant lié à l'état physiologique ou à l'habitat de l'algue envisagée, ceux du *Ceramium machrotrichum* me paraissent bien caractéristiques de cette espèce car ils diffèrent des poils hyalins unicellulaires d'autres *Ceramium* par leur situation régulière, leur diamètre plus grand et leur persistance plus prolongée sur les nœuds assez âgés.

Parmi les échantillons examinés, certains présentaient des tétrasporanges à peu près sphériques (75 μ de diamètre) verticillés par 3 ou 4 et immergés dans le cortex toujours bien développés. D'autres individus étaient sexués et portaient soit des gonimoblastes, soit des spermatanges situés sur le côté externe des nœuds de la région supérieure.

Cette espèce est à rapprocher du *C. gracillimum* dont elle se distingue nettement, comme on le verra en comparant les figures 2 et 3, par le diamètre beaucoup plus grand de ses filaments, ses entre-nœuds plus courts ainsi que la disposition de ses tétrasporanges.

Par ce dernier caractère, le *Ceramium macrotrichum* se rapproche d'une espèce de Californie jusqu'ici confondue avec le *C. transversale* (= *C. gracillimum* var. *byssoideum*) et que Y. Dawson (loc. cit. 1950) a décrit sous le nom de *C. Masonii* et qu'il distingue nettement du *C. transversale* par les tétrasporanges recouverts par les cellules corticales. A en juger par la description qu'il en a donné, la plante de Californie est plus voisine du *C. transversale* que de l'espèce de l'Ile Maurice.

Loc.: Riambul le 8 décembre 1950 sur les feuilles de *Cymodocea* par R. E. Vaughan n° 955 et n° 995.

5. **Ceramium Saviniae** G. Feldm. nov. spec.

H. E. Petersen (Alg. Mauritius III, 4, 1945, p. 10) a considéré que deux specimens de la collection du Dr. Vaughan (n° 281 et n° 307) se rapportaient avec certitude au *C. Johnstonii* Sach. et Gard. Cette espèce de Californie caractérisée notamment par sa fronde entièrement corticuée a été réunie par Dawson (1950) à titre de variété au *C. sinicola* Set. et Gard. Je n'ai eu entre les mains que le n° 307 du Dr. Vaughan provenant de Savinia (août 1939). Cette algue n'a certainement aucun rapport avec le *C. Johnstonii* et le *C. sinicola*. Elle me parait se rapporter au groupe d'espèces que l'on réunit souvent sous la dénomination de *C. diaphanum* mais elle me parait suffisamment différente des formes européennes que j'ai observées pour la considérer comme une espèce distincte: le *C. Saviniae* nov. sp. dont voici la diagnose:

Frons pulvinata usque ad 2 cm. alta e filamentis usque ad 300 μ diam., apiculis attenuatis et eximie forcipatis, dichotomis aut raro ramulos laterales gerentibus, constituta.

Zonae corticales usque ad apicem distinctae, haud inflatae, 2—3 plo latiores quam altae, interstitiis pellucidis, longitudine semper aequali per totam frondis (i. e. versus basin frondis haud elongatis) 2—3 plo altitudinem zonarum superantibus, separatae.

Cellulae corticales sine ordine dispositae, in parte inferiore zonarum saepe paulo majores.

Tetrasporangia subsphaerica, tetraedrica divisa, 45—50 μ diam., verticillata et cellulis corticalibus obtecta.

Habitat in Oceano Indico, ad Insulam Mauritii.

Le *C. Saviniae* (Fig. 23) forme des touffes gazonantes dont les filaments dressés n'atteignent pas 2 cm. de haut, souvent ramifiés

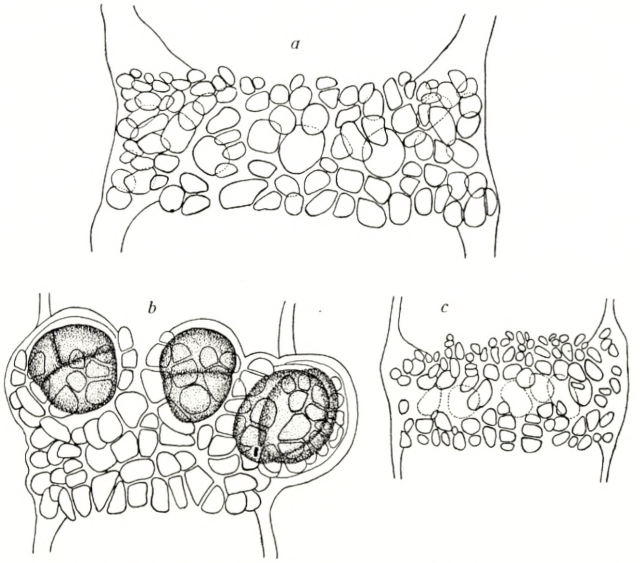

Fig. 23. *Ceramium Saviniae* G. Feldm. *a* et *b*: nœuds situés dans la région moyenne de la fronde; *c*: nœud de la région supérieure présentant 3 tétrasporanges. *a* et *b* $\times$230 env. *c* $\times$130 env.

dichotomiquement, 2 à 3 dichotomies et quelques rares rameaux adventifs latéraux. Dans les régions bien développées le diamètre atteint 300 μ, les extrêmités ne mesurent plus que 75—100 μ de diamètre, leurs sommets sont fortement recourbés en tenaille. Les nœuds sont nettement séparés sur toute la longueur de la plante et nettement distincts même au sommet où ils sont presque contigüs. Les nœuds dont le diamètre ne dépasse pas celui des entre-nœuds, toujours plus larges que hauts (2 à 3 fois plus larges que hauts) atteignent dans les parties moyennes 70—100 μ $\times$ 200—210 μ.

Les entre-nœuds sont d'une longueur relativement constante dans toutes les parties moyennes de l'algue, ils sont en général

2 à 3 fois plus longs que les nœuds ne s'allongeant pas considérablement du sommet vers la base comme c'est le cas par exemple chez le *Ceramium diaphanum*.

La structure des nœuds rappelle celle du *C. diaphanum* étant constitués par plusieurs assises de cellules corticales dont les plus externes sont plus petites et disposées sans ordre apparent. Les cellules corticales sont nettement plus grandes dans la région inférieure des nœuds que vers le sommet de ceux-ci. Sur les bords inférieurs et supérieurs, les cellules sont généralement disposées d'une manière assez ordonnée par suite du recoupement des cellules qui se fait à peu près dans le même sens.

Les tétrasporanges sont disposés en verticilles sur un rang vers la région supérieure des nœuds vers le sommet de la fronde où ils déterminent des renflements. Leur diamètre est de 45—50 μ.

Les échantillons présentaient également des gonimoblastes entourés de 4 à 5 rameaux involucraux.

6. **Ceramium diaphanum** (Roth) Harv. f.a *indica* G. Feldmann.

A typo differt statura mediocri interstitiis pellucidis brevioribus, cellulibus corticalibus paulo majoribus.

Je rapporte au *Ceramium diaphanum* une petite forme (Fig. 24)

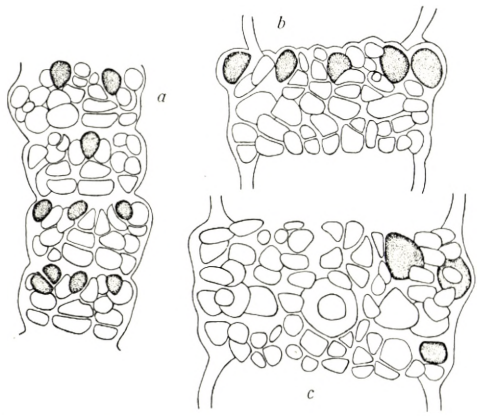

Fig. 24. *Ceramium diaphanum* (Roth) Harv. forma *indica* G. Feldm. *a*: nœud de la région supérieure présentant des cellules parasites (en pointillés) par un Phycomycète; *b* et *c*: nœuds de la région moyenne présentant également des cellules parasitées. ×230 env.

de quelques millimètres de haut présentant les caractères généraux du *Ceramium diaphanum* mais assez différente des formes européennes de cette espèce très polymorphe. Elle s'en distingue en particulier par sa ramification dichotome et ses entre-nœuds sont une à une fois et demi plus hauts que les nœuds. La fronde mesure de 60 à 70 μ vers le sommet et de 150 à 175 μ de diamètre dans les régions moyennes.

Les cellules corticales sont disposées d'une façon quelconque et ne forment pas un cortex très développé. Parmi ces cellules corticales, un certain nombre d'entre-elles présentent un contenu granuleux plus ou moins brunâtre qui rappelle beaucoup celui observé chez les échantillons de *C. mauritianum* et qui est dû vraisemblablement à la présence d'un Phycomycète parasite.

Ile Maurice: Mahebourg reef, G. Morin n° 1068.

7. **Ceramium mauritianum** G. Feldm. nov. spec.

Frons intricata, epiphytica e filamentis repentibus rhizoidibus affixis et filamentis erectis dichotomis et ramulis lateralibus praeditis, constituta.

Filamenta erecta, 150—200 μ lata, apicibus rectis, abrupte attenuatis, zonis corticalibus, usque ad apicem distinctis, interstitiis pellucidis 2—4 plo longiores, separatis.

Zonae corticales e cellulis parvis pro maxima parte rotundatis, inferioribus minoribus, longitudinaliter eximie elongatis, in unam vel duas series dispositis.

Tetrasporangia 50 μ diam., in parte superiora zonarum verticillatim inserta, proeminantia, omnino nuda.

Habitat in Oceano Indico ad Insulam Mauritii.

Sur diverses algues (*Laurencia*, *Corallina*) s'observe un petit *Ceramium* (Figs. 25 *a* et 25 *b*) à ramification dichotome et à ramules latéraux, vivant sous forme d'individus densément enchevêtrés, d'abord rampant sur le substratum où ils se fixent par des rhizoides digités. Les filaments dressés sont souvent non ramifiés ou à peine ramifiés.

Vers les extrémités qui sont droites et brusquement atténuées les nœuds sont extrêmement rapprochés les uns des autres. Dans les parties complètement développées, la hauteur des entre-nœuds

est de 2 à 4 fois égale à celle des nœuds (400 μ de long pour des nœuds de 100 μ de haut par exemple).

Le diamètre des filaments est compris entre 150 et 200 μ dans les régions moyennes et inférieures et entre 100 et 120 μ dans

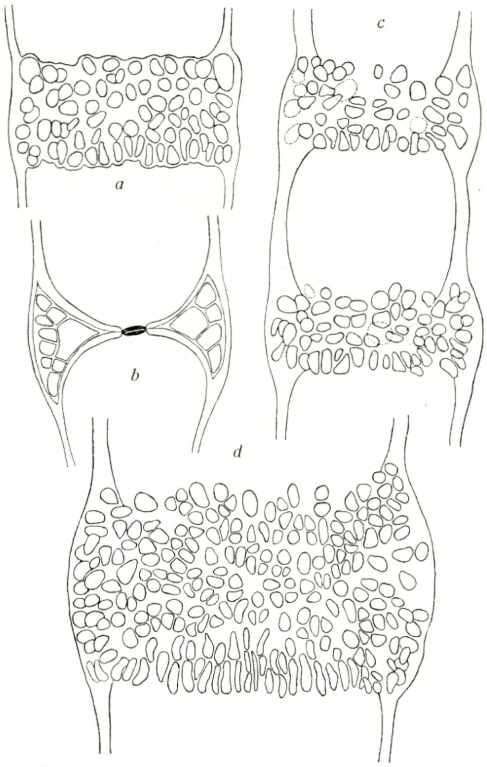

Fig. 25, I. *Ceramium mauritianum* G. Feldm. nov. sp. A gauche, extrémité d'un rameau; à droite jeune nœud portant un tétrasporange et des cellules parasitées figurées en pointillés. × 230 env.

les régions supérieures. La cortication des nœuds est nettement délimitée sur le bord supérieur, elle l'est moins sur le bord inférieur quoique cette cortication ne soit jamais basipète comme elle s'observe chez le *Ceramium circinatum* J. Ag. de Méditerranée par exemple.

La cortication du *Ceramium mauritianum* est bien caractérisée grâce à la forme allongée longitudinalement vers le bas des nœuds des cellules disposées en une ou deux séries parallèles à l'axe du filament.

Les cellules corticales sont relativement petites, celles des parties moyennes des nœuds sont plus ou moins arrondies ou anguleuses, mesurant 4 à 10 μ de diamètre, les inférieures allongées mesurant en moyenne 5×20 μ.

Parmi les échantillons examinés certains présentent de curieuses cellules à contenu brunâtre parfois granuleux disposées selon plusieurs verticilles et que l'on pourrait prendre pour des cellules sécrétrices ou des cellules-mères de tétrasporanges. En

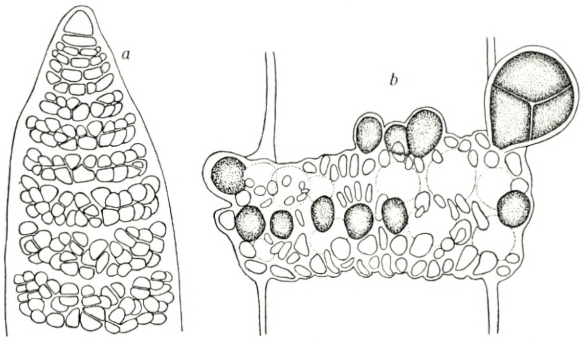

Fig. 25, II. *Ceramium mauritianum* G. Feldm. nov. sp. *a* et *d*: nœuds de la région moyenne et inférieure; *b*: coupe optique d'un nœud; *c*: nœuds de la région supérieure. $\times 230$ env..

réalité il semble s'agir de cellules hypertrophiées par un Phycomycète parasite dont on connait des expèces vivant dans les cellules corticales de *Ceramium* dont il détermine une hypertrophie (*Eurychasmidium tumefaciens* (Magnus) Sparrow par exemple).

Un parasite analogue se retrouve également dans le *Ceramium diaphanum* forma *indica* de l'Ile Maurice. Chez cette algue on peut observer des cellules corticales hypertrophiées renfermant un sporocyste vidé du Phycomycète pourvu d'un tube de décharge des zoospores.

En réalité, malgrè la rareté des tétrasporanges mûrs, ceux-ci sont localisés à la partie supérieure des nœuds, verticillés, font saillie à l'extérieur et ne sont pas recouverts par le cortex. Ils atteignent une cinquantaine de μ de diamètre.

Je n'ai pas observé d'organes femelles mais seulement des plantes mâles dont les rameaux terminaux étaient recouverts de spermatanges.

Ile Maurice: N° 995, 384, 915, 1138.

Subfam. 2. Spyridieae.

Spyridia Harv.

1. Spyridia filamentosa (Wulf.) Harv.

Alg. Mauritius, III, 4, p. 11.

Some few specimens are contained in a collection lately received. One of these, no. 934, was "growing on sand near shore in calm water".

Another specimen (1094) was tetrasporic; it was like the form with short and thick branchlets which I have mentioned in Mar. Alg. D.W.I. p. 234, fig. 224. It was found "attached to blocks of cement, near reef".

Mauritius: Flic-en-Flacq, 29-7-50, R. E. V. no. 934. Ilôt Barkly, 7-4-51, G. Morin no. 1094.

Subfam. 3. Spongoclonieae.

Haloplegma Mont.

1. Haloplegma Duperreyi Mont.

Alg. Mauritius, III, 4, Ceramiales, 1945, p. 11, figs. 3—8.

Some very fine material (Fig. 26) of this species are contained in collections lately received.

In the paper quoted above I have made references to some other species of *Haloplegma* to which I refer here, only pointing out that in some of the specimens recently received, the young tissue was very similar to Kützing's figure in "Tabulae Phycologicae", vol. XII, pl. 63, fig. e of a plant which he calls *Halopl. africanum*, but which surely is the same species as that mentioned here.

Some of the specimens were tetrasporic.

About the locality it is said: no. 977: "in deep pool near reef" and no. 999: "on rocks and old coral; near reef".

Mauritius: Riambel near Souillac, 23-11-50, R. E. V. no. 977 and same locality, 8-12-50, R. E. V. no. 999.

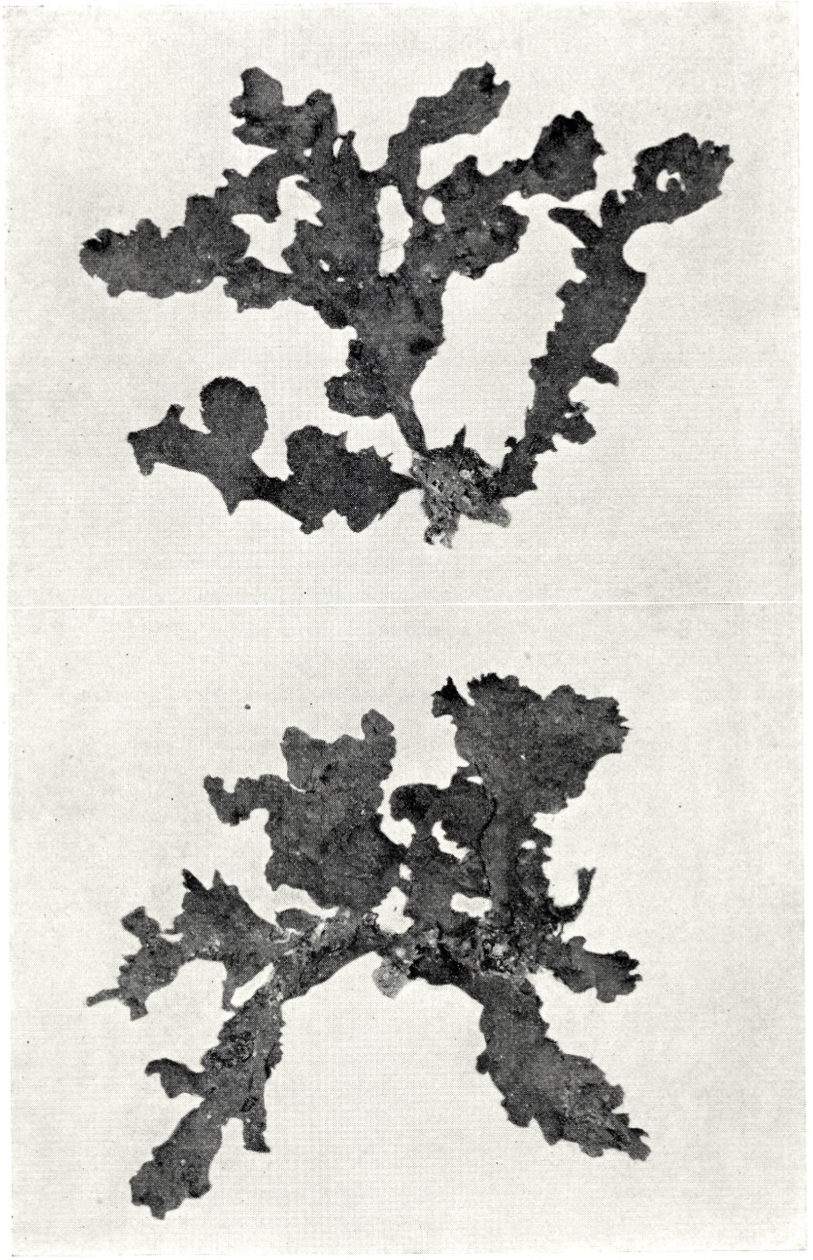

Fig. 26. *Haloplegma Duperreyi* Mont. (×1).

Subfam. 4. Spermothamnieae.

Spermothamnion Areschoug.

1. Spermothamnion Cymodoceae nov. spec.

Frons filiformis, ca. 1—1½ cm alta, ex filamentis repentibus, rhizoideis brevibus substrato (*Cymodoceae ciliatae*) adfixis et filamentis erectis, in parte basali simplicibus, ca. 50 μ latis, apicem versus ramosis, gradatim tenuioribus, ramis sparsis vel in parte superiore unilateralibus composita.

Tetrasporangia oblongo-rotundata, ca. 70 μ longa et 50 μ lata, pedicellis portata.

Pedicelli e partibus apicalibus cellularum vegetativarum orti, plerumque singuli, interdum bini, oppositi, rarissime terni, verticillati, septis transversalibus cellularum suffultoriarum adjacentes praeter nonnumquam alios infra ortos.

Antheridia obovato-elongata, ca. 80 μ longa et 40 μ lata in latere ventrali pinnularum evoluta.

Gonimoblasti subgloboso-depressi, ca. 150 μ alti et 200 μ lati, nunc nudi, nunc 1—3 ramulis involucralibus involuti, terminales, in ramulis brevibus, 1, raro 2 cellulas continentibus, evoluti.

Organa fructifera in plantis inter se diversis orta.

Mauritius: Riambel, 8-12-50, R. E. V. no. 996.

The plant forms dense, soft tufts, 1—1½ cm tall upon *Cymodocea*.

The creeping, basal filaments are composed of cells up to about 100 μ long and 40 μ broad and are fixed to the host plant by means of short, unicellular rhizoids about 100 μ long and terminated by a broad disc (Fig. 27 *a*).

From the creeping filaments the erect ones are given out; in their lower part the filaments are about 50—80 μ broad and composed of cells about 250 μ long; from their middle the filaments taper slowly upwards to about 10—12 μ and are ended with obtuse tips. The wall of the main filaments is in the lower part of the thallus about 25 μ thick.

While the filaments in the basal part are simple or very little ramified, the ramification becomes profuse from about their

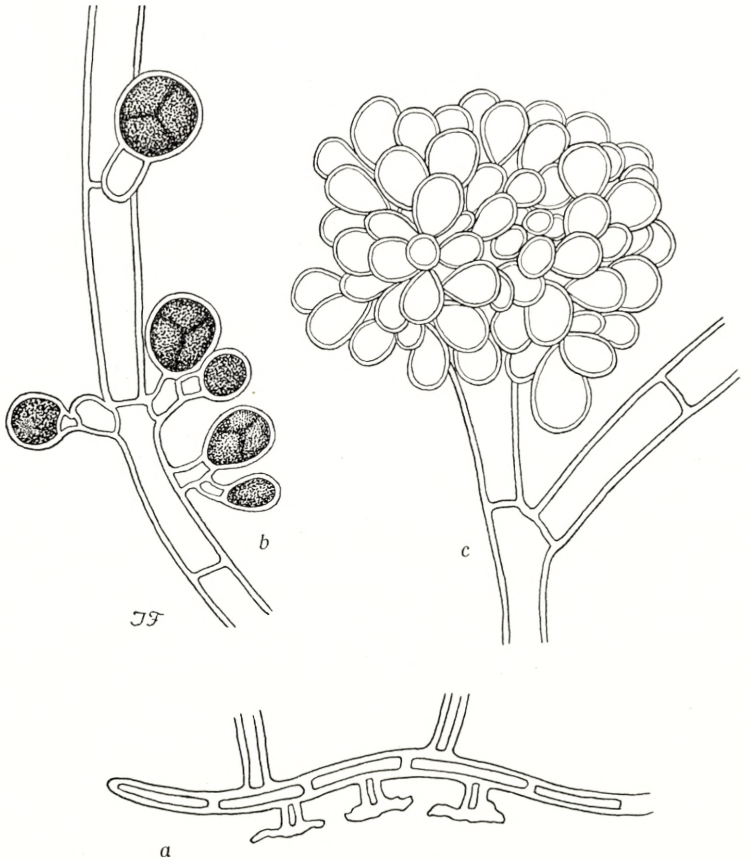

Fig. 27. *Spermothamnion Cymodoceae* nov. spec. *a*, fragment of the base; *b*, tetrasporangia; *c*, a gonimoblast. (*a*, ×125; *b*, *c*, ×400).

middle upwards. The ramification is rather irregular in all directions, in the upper parts unilateral. The branches are given out at acute angles.

The fructiferous organs are found in separate specimens.

I have seen few tetrasporic specimens. The tetrahedrally divided sporangia (Fig. 27 *b*) are stipitate, the pedicels issuing singly, sometimes oppositely and sometimes 3 in a whorl, are given out from the upper end of the mother cell. And in a few cases I have found one and even two pedicels with sporangia issuing in a row below that given out at the upper end of the cell. The same is the case for instance in *Aglaothamnion neglectum* Feldmann-Mazoyer, Ceramiacées, p. 460, fig. 181. The tetraspo-

rangia are often solitarily placed upon the pedicel, but often also a new pedicel with a sporangium is given out below the first or even more.

The sporangia are oblong-roundish about 50 μ broad and 70 μ long, and have thick walls; the pedicels are about 30—50 μ long.

Fig. 28. *Spermothamnion Cymodoceae* nov. spec. *a*, branchlets with antheridial bodies. *b*, branchlets with procarps; (*a*, *b*, ×450).

In the male specimens the subcylindrical, antheridial bodies (Fig. 28 *a*) are about 80 μ long and 40 μ broad; they are sessile, issuing from the ventral side at the upper end of the cells.

The procarps (Fig. 28 *b*) are terminally placed upon short branches issuing unilaterally. The gonimoblasts (Fig. 27 *c*) form large subglobose bodies about 200 μ broad and 150 μ high.

Some of the gonimoblasts are naked, but often a single, two, or three filaments are given out from the cell below the gonimoblasts; these branches in most cases grow into long shoots.

The large pyriform carpospores are about 50 μ long and 25 μ broad.

This species is surely closely related to *Spermothamnion repens* (Dillw.) Rosenv., "Mar. Alg. Denmark", Rhodophyceae, p. 298, fig. 202—211, but when compared in more detail several essential differences become evident.

Thus the Mauritian plant is much smaller than *Sp. repens*, which reaches a height of 5 cm and more.

Tetrasporangia sometimes issue in a row below each other upon a single cell, a pecularity which is not observed in *Sp. repens*.

The antheridial bodies are in *Sp. repens* both sessile and stipitated, while in the plant from Mauritius they are always sessile. Furthermore the antheridial bodies are ovate in *Sp. repens*, but in *Sp. Cymadoceae* ovate-cylindrical.

And lastly the gonimoblasts in *Sp. repens* are as a rule surrounded by a whorl of involucral filaments, while in *Sp. Cymodoceae* none or a few only are found.

A mixture of tetrasporangia, antheridial bodies, and gonimoblasts, as found in *Sp. repens*, has not been found in the Mauritian plant.

Subfam. 5. Lejolisieae.

Lejolisia Bornet.

1. **Lejolisia mediterranea** Bornet.

Bornet, E., Nouv. genre de Floridée, 1859, p. 91, pl. 1—2. Feldmann-Mazoyer, Geneviève, Recherches sur les Ceramiacées de la Mediterranée occidentale, Alger 1940, p. 198—99, figs. 77—78, et p. 377—79, fig. 148. Jean et Geneviève Feldmann, Sur la structure du procarpe et le développement du gonimoblaste chez *Lejolisia mediterranea*, Paris 1940.

In two collections from two different localities I have found this small alga, in both places it formed low soft tufts upon *Actinotrichia fragilis* (Forssk.) Børgs. As compared with the detailed description by Mme Feldmann-Mazoyer in her very valuable monograph of the *Ceramiaceae* p. 377 the Indian plant (Fig. 29) must be said to agree quite well with the Mediterranean one.

The creeping filaments are about 30 μ thick and the erect ones 14—20 μ near their base, 5 μ or less near their apical ends, reaching a length of up to 1 mm.

The great majority of the specimens were tetrasporic. The tetrasporangia develop upon short branchlets issuing from near the basal end of the erect filaments or more rarely also from the creeping filaments. The branchlets are often undivided, composed of a single or two cells provided with a

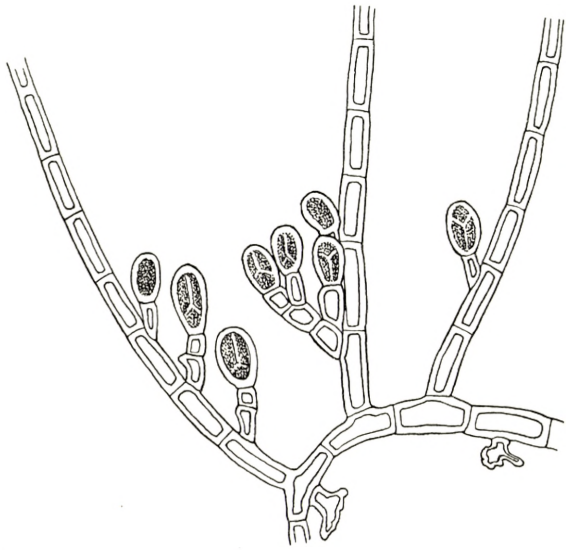

Fig. 29. *Lejolisia mediterranea* Bornet. Basal part of a specimen with tetrasporangia. (×200).

few ramuli. The sporangia are ovate, about 50 μ long and 30 μ broad.

In one of the collections (no. 751) some few procarps were found, but none of the small beautiful cystocarps (compare the above-mentioned figures of FELDMANN) were met with.

The specimen (no. 751) was gathered at a depth of 5—6 fathoms.

Mauritius: Pointe aux Roches, Dec. 12, 1947, R. E. V. no. 749. Port Louis Harbour, Aug. 21, 1947, F. D. OMMANEY no. 751.

Geogr. Distr.: Mediterranean Sea, Indian Ocean (Somali).

Subfam. 6. Wrangelieae.

Wrangelia C. Ag.

Wrangelia Argus Mont.

Alg. Mauritius, III, Ceramiales, 1945, p.18.

Having formerly seen only some fragments of this small alga I have lately received from Mauritius several specimens. Nearly all of these were tetrasporic, only once I have met with an antheridial specimen. As compared with the figure of the antheridia of *Wr. penicillata* I have published in Mar. Alg. D.W.I. vol. II, p.121, fig.132, several differences are found. Thus those in *W. Argus* are much larger, having a diameter of up to 100 μ; they are more densely built and the enveloping filaments are larger, often branched, composed of several cells, and forming rather an open cover round the antheridia, while those in *Wr. penicillata* consist of a single curved cell only.

The antheridial bodies are placed upon short branchlets.

When sterile *Wr. Argus* is easily known by the small acute cells ending the filaments.

As to the localities it is said: no. 1093 "attached to old block of cement, near reef"; no. 1111 "on rocks submerged at low tide"; no. 1123 "entangled with other algae".

Mauritius: Ilôt Barkly, 7-4-51, G. Morin no.1093. Pte aux Sables, 24-4-51, R. E.V. no.1111. Blue Bay, 8-5-51, R. E.V. no.1123.

Subfam. 7. Callithamnieae.

Aglaothamnion Feldm.-Mazoyer.

1. **Aglaothamnion Sarcodiae** nov. spec.

Frons caespitosa, ca. $\frac{1}{2}$ cm alta, non corticata, erectiuscula, ramosa, ramis spiraliter ortis aut superne alternis.

Axis centralis ex cellulis cylindricis compositus, in parte basali brevioribus, ca. 80—100 μ latis, in media parte crassioribus, ca. 125—150 μ latis, apicem versus gradatim tenuioribus, filamentis superioribus ramosissimis, cellulis apicalibus 8—10 μ latis. Pili hyalini praesentes.

Tetrasporangia subgloboso-pyriformia, ca. 50 μ longa et 35 μ lata, tetraedrice divisa, ex lateribus ventralibus ramorum orta.

Antheridia pulvinos elongatos in lateribus ventralibus ramorum formantia. Gonimolobi gemini, subgloboso-polygonui at sublobati, ca. 200 μ lati.

Mauritius: Riambel near Souillac, 23-11-50, R. E. V. no. 982.

Upon a specimen of *Sarcodia* spec. (no. 892) a small epiphyte formed smaller or larger soft tufts. I take it to be a new species of the genus *Aglaothamnion*.

The plant has a height of about 4—5 mm and is fastened to the host by means of rhizoids growing out from the lowermost cells in the main stem (Fig. 30 *a*); the rhizoids are irregularly ramified and by means of their pointed terminal cells well apt

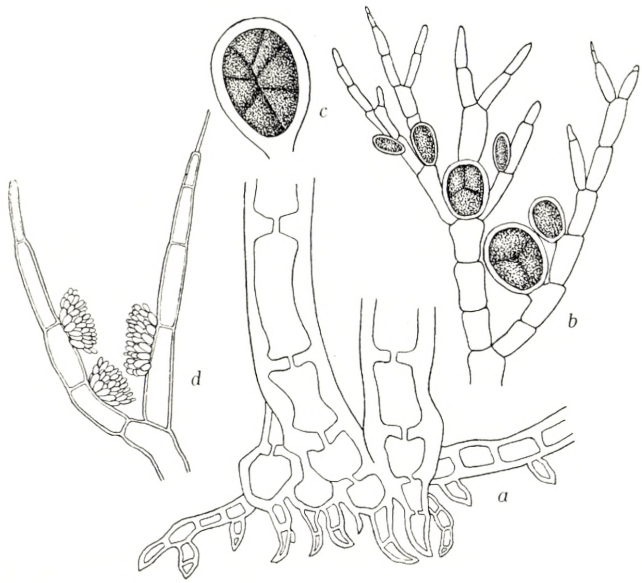

Fig. 30. *Aglaothamnion Sarcodiae* nov. spec. *a*, base; *b*, part of a tetrasporic specimen; *c*, a sporangium with many spores; *d*, part of an antheridial specimen. (*a*, × about 300; *b*, × 400; *c*, × 600; *d*, × 400).

to penetrate into the cortical layer of the host. The specimens occur singly, but often also crowded together and in that case their bases are fused, forming larger or smaller discs.

The size of the plant varies much, the tetrasporic specimens

seem to be most vigorously developed. Thus a tetrasporic specimen was nearly $\frac{1}{2}$ cm high and had a main stem which in the lower half was about 200 μ broad with cells about 100 μ long only. But as a rule the cells of the stem near the base are about 80—100 μ broad, increasing upwards to about 125—150 μ near the

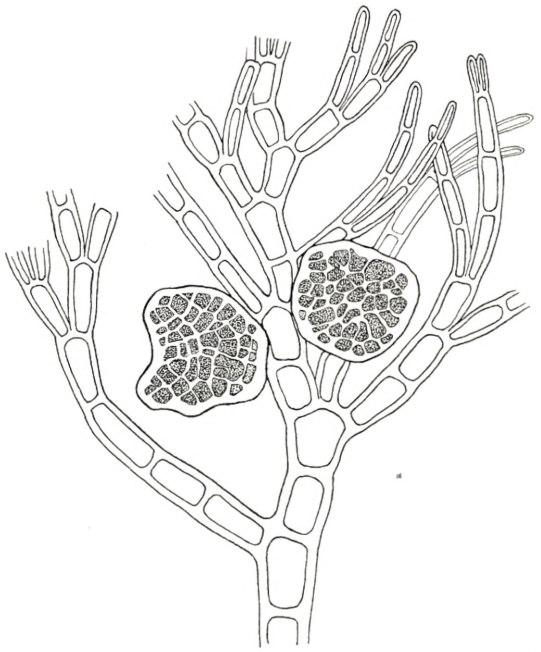

Fig. 31. *Aglaothamnion Sarcodiae* nov. spec. Part of a specimen with gonimolobes. (× about 300).

middle of the thallus, whence the breadth of the stem slowly decreases towards the tips, which are about 8—10 μ broad only; in the basal part of the stem the cells are shorter than their breadth, upwards increasing slowly in length, in the uppermost tips 3—4 times longer than the breadth. The tips of the apical cells are obtuse; some of the apical cells are terminated by hairs ca. 40—50 μ long and 3—4 μ broad. The walls of the cells are very thick in the lower part of the plant, about 20 μ, decreasing slowly upwards in the thallus. As to the ramification the branches are in the lower part of the thallus placed in a screw to the left, branches issuing in vigorous specimens from each joint; higher up in the thallus it becomes alternating.

The chromatophores are elongate ribbon-like or broader and more irregularly lobed; the cells have a single nucleus.

The tetrasporangia (Fig. 30 *b*) are placed in short rows upon the ventral sides of the branchlets, a single one given out from each cell; when young the sporangia are elongate-oblong. They are up to 50 μ long and 35 μ broad, roundish-pyriform in shape and have a thick wall. A vigorous tetrasporic specimen is crowded with sporangia.

The antheridial bodies (Fig. 30 *d*) form elongate tufts mostly upon the ventral sides of the cells; the tufts are about 20 μ high.

In a few cases 1—3 tetrasporangia were found in an antheridial specimen; but the sporangia were not normally divided, having several smaller spores (Fig. 30 *c*).

The gonimoblasts (Fig. 31) are formed by two gonimolobes the shape of which is roundish-polygonal or sublobed; the breadth of the gonimoblasts reaches a length of up to 200 μ.

Regarding related forms this species as to the shape of the gonimoblasts shows some likeness to the West Indian species *Callithamnion cordatum* Børgs., Marine Algae of the Danish West Indies, vol. II, p. 216, which Mme FELDMANN refers to her new genus *Aglaothamnion* (1940, p. 456—7). But being a deep-sea plant the West Indian plant differs much from the Mauritian one.

The small *Aglaothamnion monopodon* Børgs. described in Part III, 4, 1945, p. 19, differs so much from the much larger species described here, that I need not make any more detailed comparison between them.

The species described here was an epiphyte upon a specimen of *Sarcodia* spec. As to the locality it is said: "On seawaved slope of reef exposed to strong surf."

Fam. 2. ***Delesseriaceae.***

Subfam. 1. Nitophylleae.

Martensia Hering.

Martensia elegans Hering.

Alg. Mauritius, III, 4, 1945, p. 27.

Of this species, of which I have formerly seen very little material, I have recently received several fine specimens.

Many of the specimens were tetrasporic.

Regarding the place in the thallus in which the tetrasporangia are formed, SVEDELIUS in his large thorough work on *Martensia* (*l. c.* p. 27) points out that they are met with not only in the reticular part of the thallus but also in the coherent, not reticular part.

This was also the case in the specimens received lately, sporangia being present also in the coherent part of the thallus; but they are most numerous by far in the reticular part.

As to the locality it is said: "at base of large rocks submerged at low tide."

Mauritius: Pointe aux Sables, 24-4-21, G. MORIN no. 1100.

Subfam. 2. Sarcomenieae.

Claudea Lamouroux.

1. **Claudea multifida** Harvey.

HARVEY, W. H., in Hooker Journal. Bot., Vol. VI, p. 145; Ceylon Alg. Exsicc. no. 2. KÜTZING, Tab. Phycol., vol. XIX, pl. 56, fig. a—c. PAPENFUSS, G., Structure and Reproduction of Claudea multifida, Vanvoorstia spectabilis, and Vanvoorstia coccinea, 1937, p. 5.

This beautiful small alga originally found in Ceylon by HARVEY, where for instance near Galle it is rather common, I have later found in a collection of algae from South India gathered by Prof. PARTHASARATHY IYENGAR, and now some small specimens are present in a collection of algae from Mauritius.

Papenfuss in the paper quoted above has given a detailed description of this species to which reference is made here.

The specimens from Mauritius were sterile.

They were found as epiphytes upon pieces of *Valoniopsis pachynema*.

Mauritius: Riambel, 8-12-50, R. E. V. no. 1018.
Geogr. Distr.: Ceylon, South India.

Fam. 3. ***Rhodomelaceae.***

Subfam. 1. Laurencieae.

Laurencia Lamour.

1. **Laurencia papillosa** (Forssk.) Grev.

Alg. Mauritius, III, 4, 1945, p. 58.

Several specimens of this species are found in collections received later. I shall mention some of them.

No. 1944 is a small form, most probably from exposed shore; as to the locality it is said: "On reef in crevices of rocks."

No. 1947 on the other handis a large form, about the locality of which it is said: "Foot of beach in shallow sandy water."

No. 1054 is a smaller, more compact form which was "growing between large rocks near reef exposed at low tide".

And finally no. 1126 is a compact form growing on "Reef subjected to strong surf".

Mauritius: Riambel, near Souilla, 8-2-51, G. Morin no. 1044. Riambel, 8-2-51, R. E. V. no. 1047. Flic-en-Flacq, 22-2-51, G. Morin no. 1054. Blue Bay, 8-5-51, R. E. V. no. 1126.

2. **Laurencia nidifica** J. Ag.

Alg. Mauritius, III, 4, 1945, p. 47, figs. 21—24.

A small *Laurencia* found in a collection recently received from Mauritius shows a great likeness to the plant I referred to this species in the paper mentioned above.

The specimens are tetrasporic and the shape of the stichidia agrees very well with those pictured in fig. 23*a*.

The specimens were creeping "on block of old cement".

Mauritius: Ilôt Barkly, 7-4-51, G. MORIN no.1096.

3. **Laurencia decumbens** Kütz.

Alg. Mauritius, III, 4, 1945, p. 50, figs. 25—27.

Some small specimens (no. 1130) recently received agree very well with those which I formerly referred to this species.

As to the locality it is said: "Reef near Blue Bay, exposed site."

Mauritius: Blue Bay, 8-5-51, R. E.V. no.1130.

4. **Laurencia distichophylla** J. Ag.?

AGARDH, J., Spec. alg., vol. 2, p. 755; Epicrisis, p. 656. YAMADA, Y., Notes on Laurencia, 1931, p. 235.

Some few specimens (no. 1080) recently received from Mauritius are, I think, referable to this species, answering rather well to the descriptions of J. AGARDH and YAMADA; but having not seen any authentic specimens to compare with it I have put a ? after the specific name.

Fig. 26 shows one of the specimens; regarding the habit of this I want to point out immediately that the specimens surely have been dried under strong pressure and because of this the thallus has become broader than it actually is.

YAMADA, who has seen the specimens in AGARDH's Herbarium in Lund, gives (*l. c.*) a short description of one of the specimens (no. 37171) saying, "it is a very nice specimen, being about 7 cm high, flattened in frond, about 1.5 mm wide in the widest part, distichously pinnately branched, branches often *alternate*! with round angles and with stichidial branchlets arranged corymbosely." The specimens when compared with this description certainly in most respects show much likeness to this description, but some differences are present, thus the specimens are only ca. 5 cm high and having been pressed so much, their breadth has become greater than it actually is, but otherwise they agree

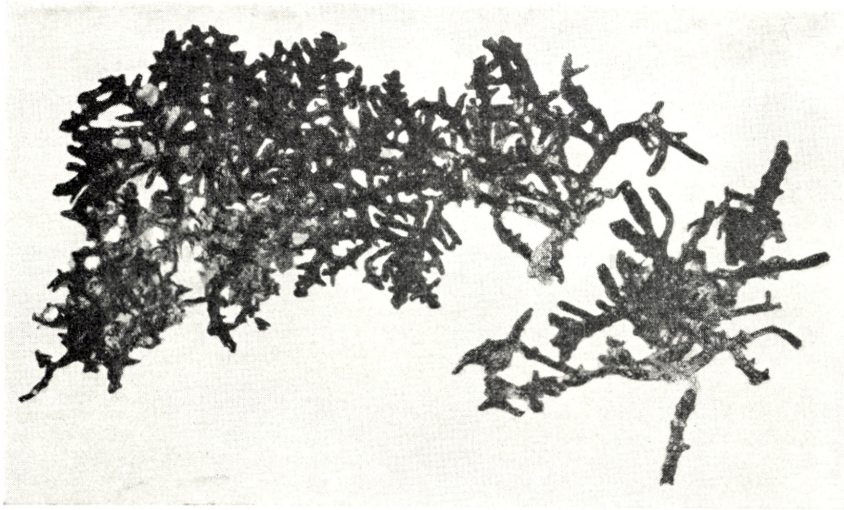

Fig. 32. *Laurencia distichophylla* J. Ag.? Habit of a specimen. (×1).

quite well with the description of the original specimens; most regrettably the specimens from Mauritius are sterile.

Regarding the structure of the thallus this, too, seems to be in good agreement with the description of YAMADA. Thus no thickening of the walls of the cells in the medulla is found, and the surface cells are not palisade-like.

While some of the specimens are from New Zealand those upon which YAMADA has based his description are "an e Cap b. Spei".

About the locality of the specimens is said only: "Closely adpressed to rock crevices."

Mauritius: Reef near Ile aux Aigrettes, 26-3-51, G. MORIN no. 1080.
Geogr. Distr.: New Zealand, Cape(?).

5. **Laurencia flexilis** Setch.

Alg. Mauritius, III, 4, p. 56, figs. 31—33.

Some well prepared specimens of this species has recently come from Mauritius.

Referring to my former description and figures of this plant I shall here restrict myself to giving only a habit figure of a well prepared tuft of the species (Fig. 33).

Laurencia tropica Yam. (1931, p. 233, figs. P, Q) seems ac-

Fig. 33. *Laurencia flexilis* Setch. Habit of a specimen. (×1).

cording to a specimen Professor YAMADA most kindly has sent me to come close to SETCHELL's species, but on the other hand the habit-figure of YAMADA's species (Pl. 20) is rather deviating.

The plant was collected in an exposed locality.

Mauritius: Riambel near Souillac, 8-2-51, G. MORIN no. 1046.

6. **Laurencia obtusa** (Huds.) Lamour.

var. *natalensis* (Kylin) Børgs.

Alg. Mauritius, III, 4, 1945, p. 59.

Some specimens (no. 1338) found in a collection of algae recently received from Mauritius seem to agree quite well with

the description and figures of *Laurencia natalensis* Kylin, which I (1945, p. 59) referred as a variety to *Laurencia obtusa*.

A transverse section of the thallus has shown that no special thickenings of the cell walls in the medulla are found.

About its habit and habitat it is said: "Dark greenish-brown, firmly attached to rocks exposed to surf."

Mauritius: Riambel, near Souillac, 8-2-51, R. E. V. no. 1038.

Fam. 3. ***Rhodomelaceae.***

Subfam. 1. Amansieae.

Amansia Lamour.

1. **Amansia glomerata** Ag.

Alg. Mauritius, III, 4, 1945, p. 43.

Two gatherings of this species are found in collections received later from Mauritius.

One of these, no. 665, most probably collected in an exposed locality, is quite typical, having a thallus forming small dense rosettes some few cm high and broad only.

The other specimen, no. 542, on the other hand, has long flattened branches, 3—4 cm long, but the characteristic arrangement of these in rosettes is well marked. This specimen reminds much of that mentioned in the paper quoted above p. 43 and which JADIN has referred to *Amansia multifida* Lamour but which I take to be a form of *A. glomerata* showing much likeness to HARVEY's figure in "Algae of Mauritius", 1834, p. 151, pl. 126.

The deviating appearance of this specimen is surely due to the fact that it has grown in a sheltered locality; but unfortunately no information about the locality is given.

Mauritius: Ilôt Barkly, 4-2-46, G. MORIN no. 542. Trou d'Eau Douce, 22-3-47, R. E. V. no. 655.

Subfam. 2. Polysiphonieae.

Roschera Sonder.

1. **Roschera glomerulata** (Ag.) Weber v. Bosse.

Weber van Bosse, A., Algues Siboga, p. 359. *Hutchinsia glomerulata* Ag., Systema Algarum, 1824, p. 158.
For more literature see Weber *l. c.* p. 359—362.

The specimens from Mauritius are in good apreement with Weber's description. They are without trichoblasts and no anastomoses between the apical cells of the branchlets are present. The Mauritius plant agrees quite well with that which I have gathered in India near Dwarka (Kew Bulletin, 1931, Nr. 1, p. 17, fig. 11) with the exception that in the Indian specimens numerous, long trichoblasts were present; but the Indian plant was also a male plant, the oblong, oblique antheridial bodies being formed by the trichoblasts.

With reference to the locality in which the plant was collected Dr. Vaughan writes: "Rather rare, grows on rocks exposed to strong surf."

Mauritius: Pointe aux Sables, 4-3-50, R. E. V. no. 903. Mahébourg reef, near Ile aux Aigrettes, 26-3-51, G. Morin no. 1084.
Geogr. Distr.: Widespread in Indian and Pacific Oceans.

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Additions to the lists in former parts.

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Index specierum.

with some few synonyms, the latter italicized.

Chlorophyceae.

Rhodophyceae.

Indleveret til selskabet den 3. april 1952.
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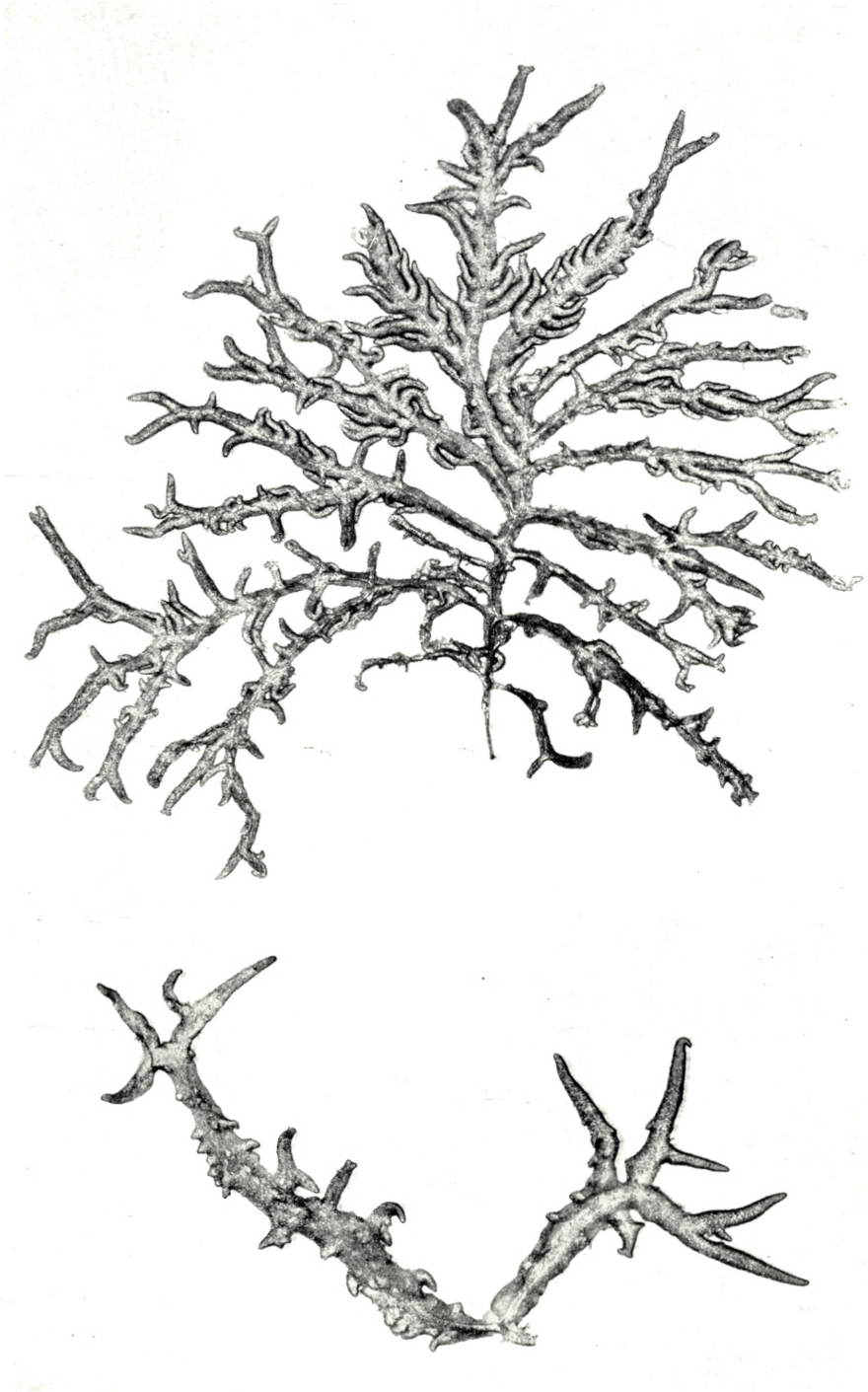

Trichogloea Requienii (Mont.) Kütz.
Above, a specimen ($\times {}^{2}/_{3}$). Below, a fragment of a specimen ($\times 1$).

PLATE II

Trichogloea spec. The specimen collected by Colonel *Pike* and found in the Kew Herb. (×about $\frac{2}{3}$).

Sarcodia mauritiana nov. spec. (×1).

Gracilaria spinuligera nov. spec. (×1).

Gracilariopsis dumosa (Harv.) nov. comb. (×1).

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