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THE GROWTH-PROMOTING ACTIVITY OF SOME ALIPHATIC ALDEHYDES ON FUNGI.

BY

NILS FRIES.

Introduction.

The interesting observations by Suolahti (1951) formed the basis of the present investigation. Suolahti found that pieces of wood hanging in the air above a growing mycelium enhanced the growth-rate and stimulated the formation of aerial hyphae by the mycelium. Not all species responded positively, but some wood-rotting fungi seemed to be particularly sensitive. His experiments showed that the stimulation was caused by a volatile substance formed in the wood. They also led to the conclusion that fats and fatty acids, notably unsaturated acids, present in the wood were the material from which the active, volatile substance was formed. The substance was ether-soluble and active at a very low concentration. He was not able to identify it chemically, but its non-identity with a large number of tested organic compounds was ascertained.

Nonanal (pelargonic aldehyde) and nonanoic acid (pelargonic acid) belong to those substances which are formed by oxidation of unsaturated fatty acids (Ellis 1936, Fieser & Fieser 1944, Ralston 1948, Iselin 1949). Therefore I considered it justified to test these compounds, together with a few other chemically related compounds, for activity on wood-rotting fungi. As the test organism, Stereum sanguinolentum was chosen in the first place, since this species had responded most readily to the volatile factor in Suolahti's investigation.

Part of the results reported in the present paper were published last year in a preliminary communication (Fries 1960).

Material.

All the hymenomycetes used in this investigation were obtained from the stock culture collection of the Institute of Physiological Botany. Some species have been maintained in this collection for ten years or more, viz.

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Lentinus omphalodes Fr., Panus torulosus (Pers.) Fr., Mycena adonis (Fr.), M. epipertugia (Scop. ex Fr.), and M. metabolata (Fr.). Others were isolated for this investigation as late as the autumn of 1950, viz. Daedalea unicolor Bull. ex Fr., Fomes annosus (Fr.) Cooke, Polyporus planatus Pers. ex Wallr., P. cerinicus Pers., P. fomentarius L. ex Fr., P. variegatus Schaeff., Lentinus lepideus Fr. and Stereum sanguinolentum Fr. These isolations were performed by Fil. mag. M. Mattson and represent polysporous or tissue cultures. Furthermore, a strain of Coprinus narcoticus (Batsch ex Fr.) was obtained from Dr. Lisbeth Fries and a strain of Boletus variegatus Sw. ex Fr. from Professor E. Melin.

Some fungi belonging to groups other than hymenomycetes were also tested in a few experiments. Most of them were received by courtesy of Dr. D. Lihnell, State Plant Protection Station, Stockholm, viz., Aspergillus niger v. Tiegh., A. alliaceus Thom et Church, Fusarium nivea (Fr.) Ces., Pestalodila cfr. rhododendri and Sclerotinia sp. The others belonged to our above-mentioned stock-culture collection, viz., Fusarium culmorum (W. Sm.) Sacc., Neurospora crassa Shear et B. O. Dodge, Ophiostoma multiannulatum Hedgc. et Davids., and Rhizopus nigricans Ehrenb.

Methods.

The aldehydes were presented to the fungi either in gaseous form, through the air, or dissolved in the liquid nutrient medium.

In the former case the test fungus was inoculated into the centre of an agar plate in a 9 cm Petri dish and allowed to grow out to a size of 1 to 3 cm in diameter. Each plate contained 20 ml agar medium. This medium contained, in addition to 1.5 per cent agar, either malt extract (2 per cent) or a synthetic nutrient solution, “modified medium 3”, of the following composition: glucose 20 g, ammonium tartrate 5 g, KH₂PO₄ 1 g, MgSO₄·7 H₂O 0.5 g, NaCl 0.1 g, CaCl₂ 0.1 g, ZnSO₄·7 H₂O 4.43 mg, MnSO₄·4 H₂O 4.05 mg, FeCl₃·6 H₂O 4 mg, thiamin 40 μg and distilled water 1 litre.

An aluminium cup was then introduced in the Petri dish with the actively growing mycelium. This cup contained a few drops of Tween 40, in which the aldehyde in question was dissolved in a concentration of 1 or 5 per cent. Nonanal, the aldehyde used in most experiments, was a pure sample synthesized in the Institute of Organic Chemistry, University of Uppsala, under the supervision of Professor A. Fredga. The plates were incubated in darkness at +25°C.

At regular intervals, usually two or three times a week, the plates were examined, the response of the fungus was noted and photographs were taken. Of necessity, this way of studying the effects of the aldehydes must be chiefly qualitative.

However, most of the experiments were arranged according to the other mode of approach, where the aldehyde was dissolved in the liquid medium in which the mycelium was cultivated. The dry weight of the mycelia produced should give a quantitative expression of the effect. The difficulty consisted in preparing an exactly known and stable concentration of the aldehyde in question. In the first experiments measured volumes of distilled

water saturated with aldehyde were supplied to the culture, the actual concentrations being rather approximate. In the later experiments the aldehyde was supplied as an exactly prepared 0.1-molar solution in ethanol, ten to fifty microliter solution to each culture.

The initial amount and concentration of aldehyde per culture obtained in this way was undoubtedly exact, but one would suspect that this concentration would decrease at an unknown rate during an experiment lasting more than a week, because of the volatility and oxidizability of the aldehydes. Therefore, in some experiments aldehyde solution was added to the culture flasks not only at the start but also at regular intervals of two or four days during the course of the experiment.

The nutrient media in these flask culture experiments were the same as those used in the Petri dish cultures mentioned above, except that they did not contain any agar. In a few cases other media were used, the composition of which is given in the text. The flasks were of the ordinary 100-ml Erlenmeyer type and each contained 25 ml nutrient solution. After having been sterilized by autoclaving, the flasks were supplemented with a small volume of ethanol with, or without, aldehyde. Each flask was then inoculated with a small square piece (c. 4 x 4 mm) of mycelium cut out from an agar culture of the fungus which was to be tested. Care was taken that the inoculum remained floating on the surface of the nutrient solution. The amount of growth was determined, after a suitable period of incubation, by collecting, drying and weighing the mycelium produced in each flask.

Experiments.

(a) Cultivation on agar plates.

Only six species were tested in this way, all of them being typical wood-rotting fungi. The mode of response to the vapours of aliphatic aldehydes differed considerably from one species to another.

The effect of nonanal was first investigated. Daedalea unicolor showed a very strong positive reaction to nonanal on the synthetic agar medium (Pl. I: a–d). The solution of 5 per cent nonanal caused a much denser growth of the mycelium, a density which increased in the proximity of the cup containing the Tween–nonanal solution. After a week a heavy wall of aerial mycelium had formed against the edge of the cup (Pl. I: e). The hyphae in this wall were more richly branched and more densely interwoven than in the other parts of the mycelium. A similar although much weaker effect was observed on the malt agar plates with the higher concentration of nonanal.

Polyporus appplanatus reacted even more strongly, but in a different way. After four day's growth on the synthetic agar medium one could notice a tendency for the mycelium to develop preferentially towards the cup with the Tween–nonanal solution. After eight days the edge
of the cup was reached. The growth in the other directions was poor (Pl. II: c–e). Finally the mycelium welled up over the brim of the cup. In the control plates with only Tween 40 in the cup almost no growth occurred. On the malt-agar plates, on the other hand, growth was rapid in all cases and the aerial mycelium was well developed. However, a curious effect of nonanal was observed: in the control plates numerous sectors, differing in growth rate, were formed, while in the plates with nonanal the mycelium was almost perfectly circular without any irregularities.

*Polyporus cervinus* showed a reaction to nonanal similar to that of *Daedalea* but less conspicuous (Pl. II: a–b). *Polyporus variegatus* and *Stereum sanguinolentum* did not respond at all.

(b) *Cultivation in liquid media.*

From cultures in liquid nutrient solutions quantitative expressions of the aldehyde effect on the growth rate were obtained. In the first experiments of this sort the aldehyde was added to the medium as a saturated aqueous solution of unknown concentration. To each culture flask containing 20 or 25 ml synthetic nutrient medium 0.2, 1 or 5 ml aldehyde-saturated aqueous solution was added.

Nonanal was tested in the first place. Out of 14 Hymenomycetes six responded positively to an addition of this aldehyde, viz. *Boletus variegatus*, *Coprinus narcoticus*, *Mycena adonis*, *M. metata*, *Polyporus fomentarius*, and *Stereum sanguinolentum* (Table I). The strong response of *Stereum* was surprising, since its reaction to gaseous nonanal had proved negligible, as earlier mentioned. On the other hand, at least two of those species which did not respond to nonanal in liquid medium, viz. *Daedalea unicolor* and *Polyporus cervinus*, were stimulated by this aldehyde in gaseous form, when cultivated on agar plates.

The increase in growth rate caused by nonanal in the liquid medium differed considerably from one experiment to another. This can be exemplified by the behaviour of *Boletus variegatus* in three experiments performed within a period of three weeks (Table II). These differing results were probably caused by the aqueous solution of nonanal not always being saturated, despite all precautions. Another possibility is the physiological variability of the fungus.

Furthermore the experiments showed that the stimulatory effect of nonanal also occurred in media of a more complex composition. Most surprising was the fact that the growth of *Stereum sanguinolentum*
Table I. The growth of 15 different species of Hymenomycetes in liquid nutrient solutions containing nonanal.

Nonanal was added as a saturated aqueous solution at the beginning of the experiment. The figures give the mycelial dry weight as average values from four parallel cultures.

<table>
<thead>
<tr>
<th>Quantity of nonanal added per flask</th>
<th>Boletus vari-&lt;br/&gt;gatus</th>
<th>Coprin. narco-&lt;br/&gt;t.</th>
<th>Daedalea unicolar</th>
<th>Fomes annosus</th>
<th>Lentin. lepid.</th>
<th>Lentin. omphal.</th>
<th>Mycena adonis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Synthetic medium</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No addition</td>
<td>43.0 (15 days)</td>
<td>18.6 (12 days)</td>
<td>14.2 (9 days)</td>
<td>5.4 (11 days)</td>
<td>9.1 (13 days)</td>
<td>2.3 (13 days)</td>
<td>2.6 (12 days)</td>
</tr>
<tr>
<td>0.2 ml nonanal</td>
<td>38.7</td>
<td>18.8</td>
<td>13.3</td>
<td>7.3</td>
<td>9.9</td>
<td>2.3</td>
<td>4.9</td>
</tr>
<tr>
<td>1.0 ml nonanal</td>
<td>49.2</td>
<td>26.8</td>
<td>15.7</td>
<td>3.6</td>
<td>10.2</td>
<td>2.6</td>
<td>7.7</td>
</tr>
<tr>
<td>5.0 ml nonanal</td>
<td>68.1 (34.5)</td>
<td>14.0</td>
<td></td>
<td>3.4</td>
<td>10.3</td>
<td>2.3</td>
<td>7.3</td>
</tr>
<tr>
<td>Malt extract medium</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No addition</td>
<td>15.1</td>
<td>—</td>
<td>25.6</td>
<td>37.7</td>
<td>19.9</td>
<td>23.6</td>
<td>19.7</td>
</tr>
<tr>
<td>0.2 ml nonanal</td>
<td>14.5</td>
<td>15.9</td>
<td>28.8</td>
<td>35.6</td>
<td>21.5</td>
<td>25.1</td>
<td>21.1</td>
</tr>
<tr>
<td>1.0 ml nonanal</td>
<td>13.9</td>
<td>10.9</td>
<td>30.5</td>
<td>35.5</td>
<td>21.1</td>
<td>—</td>
<td>20.9</td>
</tr>
<tr>
<td>5.0 ml nonanal</td>
<td>15.2</td>
<td>10.4</td>
<td>29.1</td>
<td>33.5</td>
<td>19.0</td>
<td>20.8</td>
<td>(15.6)</td>
</tr>
</tbody>
</table>

was promoted by nonanal even in such a rich medium as a 5 per cent solution of malt-extract. In this solution Stereum produced in 12 days without nonanal 9.2 mg mycelium (dry weight); with nonanal 21.3 mg (Table I).

The course of growth with and without nonanal was analysed in an experiment with Stereum sanguinolentum as the test organism. Be-
Table II. The response of *Boletus variegatus* to nonanal in three consecutive experiments.

Average values from five parallels.

<table>
<thead>
<tr>
<th>Quantity of nonanal-saturated aqueous solution added per flask</th>
<th>Dry weight of mycelium per flask</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Expt. 1514 (14 days)</td>
</tr>
<tr>
<td>No addition</td>
<td>9.7 ± 0.6</td>
</tr>
<tr>
<td>0.2 ml</td>
<td>29.7 ± 3.1</td>
</tr>
<tr>
<td>1 ml</td>
<td>46.5 ± 7.4</td>
</tr>
<tr>
<td>5 ml</td>
<td>0</td>
</tr>
</tbody>
</table>

cause of the long duration of the experiment and the volability of nonanal a small volume—0.1 or 1 ml—of freshly prepared nonanal-saturated aqueous solution was added to each culture flask every two days. The ordinary synthetic nutrient medium and a 5 per cent malt-extract solution were used as media.

From Figure 1 it can be seen that growth started very slowly in

![Figure 1](image-url)

*Fig. 1. Growth curves of *Stereum sanguinolentum* cultivated in the synthetic medium (A) or in 5 per cent malt extract solution (B). Each point represents the average dry weight of the mycelia from four cultures. The broken line shows the growth without nonanal, the unbroken lines the growth with 0.1 or 1 ml of nonanal-saturated aqueous solution added per flask every two days.*

Fig. 2. The mycelia of Stereum sanguinolentum produced in 19 days in the synthetic liquid medium with and without nonanal. a, no nonanal added; b, 0.1 ml; c, 1 ml of a saturated aqueous solution of nonanal added every two days. Compare Fig. 1. 1/4 natural size.

the synthetic medium, almost no increase in weight being noted in the control cultures until after 25 days. With repeated additions of 0.1 ml nonanal solution the growth rate was higher, and with the one-milliliter additions the growth curve rose as a straight line after only two weeks, giving mycelial dry weights three to eight times those of the control cultures (see Fig. 2).

In the malt-extract cultures only one-milliliter additions of nonanal solution were tested. During the first two weeks the growth was better without, than with nonanal. Then the two growth curves crossed and the cultures with nonanal continued to give higher yields of mycelium up to the end of the experiment, which lasted 30 days. It seemed as if the higher mycelial weights in the nonanal cultures were, at least partly, the result of a more abundant formation of aerial hyphae in these cultures than in those of the control series.

Still with Stereum as test organism, the effect of octanal and de-
Table III. Effect of octanal, nonanal and decanal on the growth of *Stereum sanguinolentum* in synthetic nutrient solution.

Incubation time 16 days. Average values from five parallels. The samples of octanal and decanal were obtained from Th. Schuchardt, München.

<table>
<thead>
<tr>
<th>Quantity of aldehyde-saturated aqueous solution added per flask every two days.</th>
<th>Dry weight of mycelium per flask</th>
</tr>
</thead>
<tbody>
<tr>
<td>No addition</td>
<td>1.6</td>
</tr>
<tr>
<td>Octanal, 0.03 ml</td>
<td>1.9</td>
</tr>
<tr>
<td>Octanal, 0.1 ml</td>
<td>2.2</td>
</tr>
<tr>
<td>Octanal, 0.3 ml</td>
<td>3.1</td>
</tr>
<tr>
<td>Octanal, 1 ml</td>
<td>1.5</td>
</tr>
<tr>
<td>Nonanal, 1 ml</td>
<td>10.3</td>
</tr>
<tr>
<td>Decanal, 0.03 ml</td>
<td>1.8</td>
</tr>
<tr>
<td>Decanal, 0.1 ml</td>
<td>1.7</td>
</tr>
<tr>
<td>Decanal, 0.3 ml</td>
<td>2.1</td>
</tr>
<tr>
<td>Decanal, 1 ml</td>
<td>2.9</td>
</tr>
</tbody>
</table>

Fig. 3. The mycelia of *Stereum sanguinolentum* produced in 16 days in the synthetic medium with and without aldehydes in saturated aqueous solution. *a*, no aldehydes; *b*, 1 ml solution of nonanal; *c*, 0.3 ml solution of octanal; *d*, 1 ml solution of decanal. These additions were made every two days during the whole period of incubation, viz. 16 days. 1/5 natural size. See Table III.

GROWTH-PROMOTING ACTIVITY OF ALDEHYDES ON FUNGI

Canal was studied, these substances being the nearest lower and higher straight-chain homologues of nonanal. Both were tested in four concentrations and the growth-promoting activity compared with that of nonanal. A new one-milliliter addition of each solution was given every two days. The experiment lasted 16 days (Table III, Fig. 3).

Neither octanal nor decanal gave rise, in any of the tested concentrations, to a growth promotion as high as that of nonanal. Octanal seemed to be inhibitory in its highest concentration.

In order to attain a higher degree of exactitude in administering the aldehydes to the culture flasks, each substance was first dissolved in absolute ethanol. From this rather concentrated solution (0.1 M) a volume of 0.01 to 0.1 ml was added to each flask. Control flasks were supplied with the same volume of pure ethanol.

**Table IV. Growth of Stereum sanguinolentum in synthetic nutrient solution with additions of nonanal in ethanolic solution.**

The nonanal solution was supplied either at the beginning of the experiment (series 1–8) or in portions every two days during the course of the experiment (series 9–16). Incubation time 14 days. Average values from five parallels.

<table>
<thead>
<tr>
<th>Series no.</th>
<th>Composition of each addition</th>
<th>No. of additions</th>
<th>Total amount added</th>
<th>Dry weight mycelium per flask</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ethanol ml</td>
<td>Nonanal µg</td>
<td>µmole</td>
<td>Ethanol ml</td>
</tr>
<tr>
<td>1</td>
<td>0.01</td>
<td>—</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>0.02</td>
<td>—</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>3</td>
<td>0.05</td>
<td>—</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>4</td>
<td>0.10</td>
<td>—</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>5</td>
<td>0.01</td>
<td>142</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>6</td>
<td>0.02</td>
<td>284</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>7</td>
<td>0.05</td>
<td>710</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>8</td>
<td>0.10</td>
<td>1420</td>
<td>10</td>
<td>1</td>
</tr>
<tr>
<td>9</td>
<td>0.01</td>
<td>—</td>
<td>—</td>
<td>6</td>
</tr>
<tr>
<td>10</td>
<td>0.02</td>
<td>—</td>
<td>—</td>
<td>6</td>
</tr>
<tr>
<td>11</td>
<td>0.05</td>
<td>—</td>
<td>—</td>
<td>6</td>
</tr>
<tr>
<td>12</td>
<td>0.10</td>
<td>—</td>
<td>—</td>
<td>6</td>
</tr>
<tr>
<td>13</td>
<td>0.01</td>
<td>142</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>14</td>
<td>0.02</td>
<td>284</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>15</td>
<td>0.05</td>
<td>710</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>16</td>
<td>0.10</td>
<td>1420</td>
<td>10</td>
<td>6</td>
</tr>
</tbody>
</table>

Table IV shows the result of an experiment in which Stereum had been grown for 14 days in culture flasks supplemented with nonanal in this way, either with only one addition at the start of the experiment, or with additions repeated every two days. Growth was more rapid in the latter case than in the former. Thus, in the series (No. 13), where 0.85 mg nonanal had been added in portions of 0.14 mg every two days, growth was considerably better than in the series (Nos. 7 and 8), where 0.71 mg or 1.42 mg nonanal had been added in one portion at the start of the experiment.

From Table V, it can be concluded that out of the five straight-chain aldehydes possessing 7 to 11 carbon atoms, heptanal was most active in promoting growth; in the second place came nonanal,

*Table V. Effect of six different aldehydes on the growth of Stereum sanguinolentum in the synthetic nutrient solution.*

The aldehydes were added in two portions of 0.1 molar ethanolic solution; the first at the start of the experiment and the second after seven days. The quantities given in the table are these two portions added together, i.e. the total amount ethanol and aldehyde given to each culture flask. Incubation time 14 days. Nonanal was the usual synthetic preparation; the other aldehydes, including nonenal (n-nonen-2-al-1), were obtained from Th. Schuchardt.

<table>
<thead>
<tr>
<th>Composition of the additions</th>
<th></th>
<th></th>
<th>Dry weight mycelium per flask</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ethanol ml</td>
<td>name</td>
<td>Aldehyde</td>
<td>mg</td>
</tr>
<tr>
<td>0.02</td>
<td>—</td>
<td>Heptanal</td>
<td>220</td>
</tr>
<tr>
<td>0.04</td>
<td>—</td>
<td>Heptanal</td>
<td>460</td>
</tr>
<tr>
<td>0.10</td>
<td>Heptanal</td>
<td>1140</td>
<td>10</td>
</tr>
<tr>
<td>0.02</td>
<td>Octanal</td>
<td>260</td>
<td>2</td>
</tr>
<tr>
<td>0.04</td>
<td>Octanal</td>
<td>520</td>
<td>4</td>
</tr>
<tr>
<td>0.10</td>
<td>Octanal</td>
<td>1280</td>
<td>10</td>
</tr>
<tr>
<td>0.02</td>
<td>Nonanal</td>
<td>280</td>
<td>2</td>
</tr>
<tr>
<td>0.04</td>
<td>Nonanal</td>
<td>560</td>
<td>4</td>
</tr>
<tr>
<td>0.10</td>
<td>Nonanal</td>
<td>1420</td>
<td>10</td>
</tr>
<tr>
<td>0.02</td>
<td>Decanal</td>
<td>320</td>
<td>2</td>
</tr>
<tr>
<td>0.04</td>
<td>Decanal</td>
<td>630</td>
<td>4</td>
</tr>
<tr>
<td>0.02</td>
<td>Undecanal</td>
<td>340</td>
<td>2</td>
</tr>
<tr>
<td>0.04</td>
<td>Undecanal</td>
<td>680</td>
<td>4</td>
</tr>
<tr>
<td>0.02</td>
<td>Nonenal</td>
<td>280</td>
<td>2</td>
</tr>
<tr>
<td>0.04</td>
<td>Nonenal</td>
<td>560</td>
<td>4</td>
</tr>
</tbody>
</table>
The growth-promoting effect on *Stereum sanguinolentum* of the aliphatic aldehydes with five to eleven carbon atoms. The fungus was grown for 12 days in the synthetic nutrient medium. The aldehydes were added in three portions of a 0.1 molar ethanolic solution; at the start of the experiment, after four days and after eight days. The figures on the abscissa indicate the total amount added per flask in each series. The figures on the ordinate indicate the average dry weight of mycelium per flask produced within each series (comprising five flasks). Each value is reduced by the average amount of dry weight increase caused by the addition of ethanol alone (without aldehyde) as it appeared in the corresponding control series.

and then followed undecanal, decanal, and octanal, these comparisons being made on an equimolar basis. The unsaturated nonenal was just as active as nonanal. In this experiment two additions were made: the first one at the start and the second one seven days later.

Some weeks later, when also pentanal and hexanal were available, this experiment was repeated. This time the aldehyde solutions were added to the culture flasks every four days. With this procedure nonanal seemed to be slightly more potent than heptanal; these two aldehydes, however, were still the most active ones of those tested (Fig. 4). Hexanal and octanal were less active, followed by pentanal, decanal and undecanal. The two last-mentioned ones were inhibitory in the higher concentrations.

In the same way four of the corresponding straight-chain alcohols were tested (heptanol was not available). Decanol and undecanol appeared to be inhibitory, octanol was almost inactive, but nonanol exerted, in the lower concentration, a clear positive effect, inferior, however, to that of nonanal (Table VI).

The reaction of *Stereum sanguinolentum* to nonanal and nonanol, added every four days, was followed for some weeks (Fig. 4). The growth-promoting effect of the alcohol appeared later than that of the aldehyde, the growth rate during the first three weeks being almost the same in the flasks with nonanol as in those without any
Table VI. The effect of aliphatic alcohols with eight to eleven carbon atoms on the growth of *Stereum sanguinolentum* in the synthetic nutrient solution.

The long-chain alcohols and the nonanal were added in three portions of 0.1 molar ethanolic solution; the first at the start of the experiment, the second after four days and the third after eight days. The quantities given in the table are these three portions added together, i.e. the total amount of ethanol and higher alcohols given to each culture flask. Incubation time 12 days. The sample of nonanol was obtained from L. Light & Co., the other alcohols came from Th. Schuchardt.

<table>
<thead>
<tr>
<th>Ethanol ml</th>
<th>Long-chain alcohol or aldehyde</th>
<th>Dry weight mycelium per flask</th>
</tr>
</thead>
<tbody>
<tr>
<td>—</td>
<td>—</td>
<td>1.2</td>
</tr>
<tr>
<td>0.06</td>
<td>—</td>
<td>2.3</td>
</tr>
<tr>
<td>0.03</td>
<td>Octanol</td>
<td>1.8</td>
</tr>
<tr>
<td>0.06</td>
<td>Octanol</td>
<td>2.2</td>
</tr>
<tr>
<td>0.03</td>
<td>Nonanol</td>
<td>3.2</td>
</tr>
<tr>
<td>0.06</td>
<td>Nonanol</td>
<td>2.4</td>
</tr>
<tr>
<td>0.03</td>
<td>Decanol</td>
<td>1.7</td>
</tr>
<tr>
<td>0.06</td>
<td>Decanol</td>
<td>1.2</td>
</tr>
<tr>
<td>0.03</td>
<td>Undecanol</td>
<td>0.8</td>
</tr>
<tr>
<td>0.06</td>
<td>Undecanol</td>
<td>0.5</td>
</tr>
<tr>
<td>0.03</td>
<td>Nonanal</td>
<td>4.1</td>
</tr>
<tr>
<td>0.06</td>
<td>Nonanal</td>
<td>6.1</td>
</tr>
</tbody>
</table>

It should be noted that in this experiment the composition of the medium was not quite the same as in the earlier experiments (see the legend of Fig. 4), as it was arranged to serve another purpose as well.

As the earlier described agar tests showed, none of the phycomycetes, ascomycetes or fungi imperfecti tested responded positively to nonanal. The same species were also tested in liquid nutrient medium to which 1 ml or 5 ml of distilled water saturated with nonanal had been added. In all cases an inhibition was obtained with the 5-ml addition, whereas the 1-ml addition caused a weak or no inhibition, except for *Pestalotia cfr. rhododendri*, which exhibited a slight and questionable increase in growth rate.

Discussion.

The experiments reported above have shown that aliphatic, long-chain aldehydes, notably nonanal, as gases or solutes, stimulate dry matter production and aerial mycelium formation in several wood-
Fig. 5. Growth curves of *Stereum sanguinolentum* cultivated in the synthetic nutrient solution, but with 4 g/l glucose (instead of 20 g/l) and with 3.58 g/l ammonium sulphate (instead of 5 g/l ammonium tartrate). Every four days 0.01 ml ethanol was added to each flask, this supplement containing: in series a no further organic compound; in series b 140 μg (= 1 micromole) nonanol, and in series c 140 μg (= 1 micromole) nonanal. Thus at the end of the experiment 0.09 ml ethanol had been added to all the remaining cultures; and to each flask in the series b and c 1260 μg (=9 micromoles) of nonanol and nonanal, respectively. Each circle represents an average value from four parallel cultures.

destroying hymenomycetes. Although much circumstantial evidence supports the assumption that Suolahti's factor is identical with nonanal, this identification cannot be looked upon as proved. The chemical tests carried out by Suolahti indicated that the active substance could not be an aldehyde. Furthermore, the strain of *Stereum sanguinolentum* used in the present investigation did not respond to gaseous nonanal as did the strain studied by Suolahti, although both strains were strongly stimulated by the respective factors dissolved in the aqueous medium. This question of identity probably cannot be answered definitely until the wood-factor has been isolated and chemically identified.

Be that as it may, nonanal undoubtedly represents a new type of growth factor for fungi, active as a gas as well as a solute. From a quantitative point of view it is less potent than most vitamins. The specificity is low, since other long-chain aldehydes possess a similar, although less pronounced, activity.

Comparatively little has been reported earlier about the effect of

aliphatic aldehydes upon fungi. Germicidal properties have been found in some of them, notably octanal and nonanal (Penfold & Grant 1926, Okazaki & Homma 1954). A stimulating effect of nonanal on the germination of wheat rust spores has been reported by French & Weintraub (1957).

So far, the bioluminescence of bacteria seems to be the only case where a biological effect of aliphatic aldehydes has been studied more closely. A long-chain aldehyde, e.g. dodecanal, is obviously an indispensable component of the bacterial luciferase system (Cormier & Strehler 1953, Cormier, Totter & Rostorfer 1956, McElroy & Green 1955, Rogers & McElroy 1955).

The mode of action of nonanal and other higher aldehydes in the growth processes of fungi is now being investigated in this laboratory and will be dealt with in a forthcoming paper.

Summary.

The aliphatic aldehyde nonanal was found to promote the growth of several hymenomycetes. When acting as a gas upon a mycelium growing on an agar medium, nonanal induced a more abundant development of aerial hyphae. Dissolved in a liquid medium nonanal increased the rate of dry matter production of a mycelium growing in the medium. The latter mode of action was studied in several experiments, Stereum sanguinolentum being the chief test organism.

When the quantity of nonanal or some other homologous aldehyde was added to the culture in portions every two or four days, a stronger effect was obtained than if the total quantity was added at the start of the experiment. This was probably due to the volatility and instability of these compounds. Thus the dry weight of the mycelium was increased several times by an addition of half a milligram of nonanal, supplied in three or more consecutive portions.

The effect was most conspicuous in the synthetic nutrient medium, but occurred in some cases also in the very rich malt extract medium.

Heptanal was about as active as nonanal; after these two came octanal, followed by hexanal and pentanal. Decanal and undecanal, which were the highest homologues studied, were stimulatory only in low concentrations and inhibitory in higher.

Of the four corresponding alcohols tested, only nonanol produced a stimulatory effect, whereas the others were inactive or inhibitory.
The author is indebted to Mrs. Harriette Cedervall for valuable technical assistance and to Professor A. Fredga for a sample of nonanal.

Institute of Physiological Botany, University of Uppsala, November 1960.

REFERENCES.


Explanation of the plates.

Plate I.

*Daedalea unicolor* growing on the synthetic agar medium in Petri dishes. The small cup in each Petri dish contains a few drops of Tween 40 with or without nonanal. 

- *a*, no nonanal (5 days);
- *b*, 5 per cent nonanal (5 days);
- *c*, 2 per cent nonanal (8 days);
- *d*, 5 per cent nonanal (8 days);
- *e*, 5 per cent nonanal (9 days).

*a*-d, half natural size, *e*, double natural size.

Plate II.

*a*, eight day old culture of *Polyporus cervinus* on malt-agar. The small cup to the right in the Petri dish contains a few drops of Tween 40. *b*, as *a*, but the Tween drops contain 5 per cent nonanal.  

*c*, nine day old culture of *Polyporus applanatus* on the synthetic agar medium. The small cup to the left in the Petri dish contains a few drops of Tween 40. *d* and *e*, as *c*, but the Tween drops contain 5 per cent nonanal. *a*-d, half natural size, *e*, double natural size.
N. Fries: Growth-Promoting Activity

MONOGRAPH OF THE GENUS CANARINA L.  
(CAMPANULACEAE).

BY

OLOV HEDBERG.

In collaboration with INGA HEDBERG, BENGT JONSELL, LENA JUNELL, NILS LUNDQVIST, and OLOF OLSSON.

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Preface.

The present publication contains the tangible results of an experiment in teaching taxonomic botany. When the senior author was requested to give during the spring term of 1960 a course in plant-systematic research methods for graduate students at Uppsala University, he decided to follow the advice of Turrill (1950, p. 15), according to whom the best approach is “to teach the student to teach himself the practice of taxonomy and to guide him to an understanding of the fundamental principles of classification.” I also agree with Turrill (loc. cit.) that “lectures in taxonomy should be reduced to a minimum; field and laboratory studies should be encouraged rather than reading”; and that “above all, in teaching taxonomy, as in taxonomic research, the newer methods should be given prominence”. During this course condensed accounts were given not only of the “traditional” methods of plant taxonomy (including the proper handling of herbarium material) but also of the study of variation and correlation by graphical methods, and of recent approaches provided by anatomy, cytology, palynology, etc. All those methods of investigation were applied, as far as possible, to a concrete example—the genus *Canarina* L. In this way we prepared during the course a draft of a monograph of this genus. This was afterwards elaborated by the senior author, who is also alone responsible for the chapters on “systematic position” and “phytogeography”, but his collaborators took part in all the preliminary work with annotation of specimens, tracing of literature, measurements and scoring of various taxonomic characters, tabulation and elaboration of graphs of various kinds, and the drawing of taxonomic conclusions. They have also all perused the final draft, and shared in the proof-reading.

The genus *Canarina* was chosen as a suitable object for this course because (1) no complete revision of it existed (though some useful taxonomic comments had been provided by Burtt, 1938), (2) it is exotic and the number of species described is small, hence the total amount of herbarium material available was deemed to be manageable, (3) part of the genus at least appeared to be critical taxonomically and to pose some nomenclatural problems as well, and (4) its distribution was considered to be phytogeographically interesting. Furthermore, its possession of large and showy flowers makes the genus both agreeable to the student and liable to be observed by

collectors and kept for horticultural purposes. In fact we managed to find material in cultivation of all the species of the genus. The choice of material therefore proved to be very fortunate.

**General part.**

**History of discovery and description.**

The genus *Canarina* was established by Linnaeus in 1771 for a plant from the Canary Islands that he had earlier named in Species Plantarum (1753) *Campanula canariensis*. That species had been in cultivation in Europe since the end of the seventeenth century (cf. Loudon, 1830, p. 139), and seems to have been a popular greenhouse plant (cf. e.g. Curtis, 1799; Don, 1834, p. 736; Planchon, 1856). By a typographical error the generic name was first printed *Canaria* (Linnaeus, 1771, pp. 148, 225), but this was corrected by the author in the Addenda of the same volume. That correction was obviously not observed by Scopoli (1777, p. 150), who proposed to rename the genus *Pernettya*, considering the name *Canaria* impermissible because it differed only in gender from the earlier generic name *Canarium* L. (1754). But the corrected name *Canarina* L. must, of course, have precedence over the later *Pernettya* Scop. (cf. Bentham & Hooker, 1876, p. 558).

At the same time as Linnaeus promoted *Campanula canariensis* to a genus of its own he also provided it with a new specific epithet, calling it *Canarina campanula* L. Under the rules of nomenclature perfected by later generations of botanists this is not permissible, however; the species must keep its older epithet *canariensis* also under the new generic name. This was first pointed out by Vatke (1874, p. 700), although O. Kuntze (1891, p. 379) is usually quoted as the author of this combination. Apart from the two epithets mentioned above, six more are to be found under this genus in Index Kewensis, viz.:

- *C. zanguebar* Lour. (1790)
- *C. moluccana* Roxb. (1814), nom. nud.
- *C. laevigata* G. Don ex Loud. (1830), nom. nud.

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1 Index Kewensis erroneously gives Lamarck as the author of this name.
2 The distorted form *C. "campanulata"*, ascribed by Index Kewensis to Linnaeus, originates, as far as we can find, from G. Don (1834, p. 736; "C. campanulata Lam."; cf. also Baillon, 1886, p. 536.)
C. eminii Aschers. ex Schweinf. (1892)
C. abyssinica Engl. (1902)
C. elegantissima Th. Fr. Jr. (1923)

Two of these names must be discarded as nomina nuda (C. moluccana and C. laevigata), but the other four were validly and effectively published. Loureiro's (1790) "Canarina zanguebar" is known only from the short original description.¹ In the absence of a type specimen this does not allow positive identification with any known species. Its status as a species of Canarina was questioned already by Willdenow (1799, p. 241), and De Candolle (1830, p. 125; 1839, p. 422). According to Merrill (1935, p. 400): "This is apparently neither a Canarina nor a representative of the Campanulaceae." Its taxonomic position must at present be left open, but since the plant in question cannot be a Canarina it need not concern us here. The first reliable record of this genus from the African continent came only in Schweinfurth's paper of 1892 (p. 173), in which a plant from Ruwenzori was described as Canarina eminii. Ten years later Engler (1902, p. 116) described Canarina abyssinica on material from southern Ethiopia, and finally Th. C. E. Fries (1923, p. 392) described Canarina elegantissima from Mt Aberdare (Kenya Colony). Two varieties have furthermore been validly described from East Tropical Africa, viz. C. abyssinica var. umbrosa (Engler, op. cit., p. 116), and C. eminii var. elgonensis (Fries, 1923, p. 395). The typification of the last five names presents no great difficulty (cf. below).

To summarize: In the genus Canarina four valid specific epithets are available, one pertaining to material originating from the Canary Islands, and three to material from East Tropical Africa. To the latter area belong also two valid names of varieties.

Morphological and ecological variation.

Introduction.

Even a cursory examination of the herbarium material of Canarina available in Sweden demonstrated the occurrence of a large variation in a number of characters, some of which had earlier been used for specific distinction. In order to make an adequate revision, it was therefore decided to bring together as much herbarium material as

¹ The notes by Don (1834, p. 736) on its cultivation were probably only an optimistic interpretation of the data supplied by Loureiro (loc. cit).

possible—field studies being, of course, excluded. For that purpose all material available was requested on loan from all larger herbaria of the world where the genus was expected to be represented. Thirteen of these herbaria proved to possess no material at all, whereas a total of 411 specimens was received on loan from thirty-three herbaria, viz. B, BM, BR, BRLU, C, E, EA, F, FI, FR, G, GH, HBG, JE, K, L, LA, LD, LISU, M, MA, NY, P, PH, PRE, S, UC, UPS, US, W, WAG, YBI, and Z (abbreviations according to Lan- jouw & Stafleu, 1959). Furthermore, after our revision was completed one of us (B. Jonsell) during a visit to Russia had the opportunity of working through the Canarina material preserved in Lenin- grad (LE).

When most of the material mentioned had been assembled, we started to sort it into groups according to the general appearance of the whole plant, taking no notice of the names given on the labels. It was soon found that all satisfactory specimens could be fairly easily distributed into three distinct taxa, within each of which the variation appeared more or less continuous. The first taxon, provisionally designated “Group a”, could be distinguished from the other two (b and c) by the shape of its leaves, corolla, and filament bases. It comprised all the material from the Canary Islands, while the others were restricted to East Tropical Africa. The second taxon, “Group b”, was characterized by its long and usually coiled petioles, coiled pedicels, broader ovary, etc. The third one, “Group c”, finally, was found to differ from the other two in leaf shape, seed shape, etc. Later on it was also found to possess a different type of pollen. Unfortunately, some of the best distinctive characters discovered between these three taxa were either available in but a fraction of the specimens (as seeds), or could be studied as a rule only by the destruction of a flower (filament bases), or by microscopic investigation (pollen). We consequently found it desirable to investigate in detail both inter- and intraspecific variation in all characters of potential taxonomic importance, searching for additional specific distinctions as well as for evidence of intraspecific differentiation.

**Variation in gross morphology.**

The main features earlier employed for species discrimination in the genus Canarina are differences in the shape of corolla, ovary, and leaves; differences in the length and width of the sepals; and

Fig. 1. Diagrammatic sketch explaining the dimensions measured in flowers (I) and leaves (II and III): 
a, length of corolla along the axis from the edge of the receptacle to the level of the petal tips; 
b, width of corolla measured halfway along a at right angles to the flower axis; 
c, length of sepals measured from the edge of the receptacle to the tip; 
d, width of sepals measured 1.0 cm above the edge of the receptacle; 
e, width of ovary; 
f, height of ovary; 
g, leaf blade length along the midrib; 
h, leaf blade width halfway along the midrib and at right angles to it, measured between lines connecting the tips of the teeth or crenules.

presence or absence of a twist or coil on the pedicels (cf. Schweinfurth, 1892, p. 173; Engler, 1902, p. 116; Fries, 1923, p. 394; Burtt, 1938). All these features and a few more were studied by us in as many herbarium specimens as possible. Unfortunately, because of incomplete specimens, bad preservation, insect attacks, etc. two thirds of the material available could not be utilized for these measurements. Cultivated specimens were also as a rule excluded. Nevertheless we measured a total of 117 specimens, of which 34 had been classified in Group a, 24 in Group b, and 59 in Group c. Each of these sheets had at least one well-preserved flower and a few well-developed leaves.

The shape of the living corolla cannot, of course, be accurately measured in herbarium specimens—the only data obtainable concern the dimensions of its flattened remains. Its length will perhaps not be much changed in pressing, but its width on a herbarium sheet will probably correspond neither to its width in actual life nor to half of its circumference. Nevertheless some differences in corolla shape can be observed even in herbarium specimens. To get some numerical

expression for these we measured its length along the axis from the base to the level of the petal tips (cf. Fig. 1, Ia), and its width halfway between the base and the level of the petal tips (cf. Fig. 1, Ib). The ratio of those figures was taken as a crude index of its shape. (A better index might have been obtained by means of the width of the corolla at the rim, but the variable position of the petals in the pressed flowers makes such measurements too unreliable, cf. Figs. 4–6.) The variation of this index in the material investigated is shown in Fig. 2, III, and some examples of corolla shape from each of the Groups a, b, and c, are given in Figs. 4–6. The variation in the absolute length of the corolla is shown in Fig. 2, I.

The variation in the length of the sepals, as measured from the base (the edge of the receptacle) to the tip (cf. Fig. 1, Ic), is shown in Fig. 2, II. Because, in some specimens, the sepals are fused at the base, their width could not be measured there; in order to get comparable values we measured it in all flowers 10 mm above the base (the edge of the receptacle; cf. Fig. 1, Id). The result of those measurements is shown in Fig. 3, I. Both corolla length and sepal length are, of course, directly dependent upon the absolute size of the flower, and hence to some extent upon the general vigour of the plant. The ratio of corolla length to sepal length might therefore be expected to be more significant. Its variation is illustrated in Fig. 2, IV.

Also differences in the shape of the ovary are difficult to study in herbarium specimens because of frequent deformation in pressing. Nevertheless, an attempt was made to measure the width and the height of the ovary (cf. Fig. 1, Ie and f) in all specimens studied, taking the ratio of those figures as an index of ovary shape. The variation in this index is shown in Fig. 3, III. Measurements in fresh material would probably have provided a much better distinction, however. The variation in the absolute width of the ovary is shown in Fig. 3, II.

Measurements of leaf shape in *Canarina* do not encounter difficulties of the same kind as provided by the corolla and ovary. But here we find instead such a variability in shape that it is difficult to decide which dimensions should be used (cf. Figs. 7–9). Because of the great variability in leaf size absolute dimensions are evidently of no use for taxonomic purposes. One obvious relative feature is the ratio of leaf blade length to petiole length (g/i in Fig. 1, II and III), illustrated in Fig. 3, V. Another useful ratio might be the length/width index of the leaf blade. But if the maxima of leaf blade length

Fig. 2. Histograms illustrating variation in corolla length (I, in cm); sepal length (II, in cm); corolla shape index, as defined by the ratio $a/b$ in Fig. 1 (III); and in the ratio of corolla length to sepal length (IV); in herbarium specimens of Canarina. Measurements could be made as a rule only in one flower of each collection (rarely 2-3, in which case a mean value was used). Each division of the figure comprises four histograms, the lower of which corresponds to specimens of “Group $a$”, the second lowest to “Group $b$”, and the third one to “Group $c$”, whereas the top one represents $a + b + c$, that is, the sum of all material measured. The specimens measured are listed in Appendix 1, p. 58; out of 117 specimens measured 34 belong to “Group $a$”, 24 to “Group $b$”, and 59 to “Group $c$”.

and width were employed, this index would not account for the differences between the more or less hastate leaves shown in Fig. 7 and the broadly ovate-cordate leaves illustrated in Figs. 8 and 9. For that reason it was decided to employ instead the ratio of the leaf blade length as measured along the midrib from the petiole to the apex (Fig. 1, IIg and IIIg), and the width as measured half-way.
Fig. 3. Histograms illustrating variation in sepal width, measured 1.0 cm above the edge of the receptacle (I, in mm); ovary width (II, in cm); in the ratio of ovary width to ovary height (III); in leaf shape index, as defined by the ratio $g/h$ in Fig. 1 (IV); and in the ratio of leaf blade length to petiole length, as defined by the ratio $g/l$ in Fig. 1 (V). The values under I–III could be obtained as a rule only for one flower of each collection (rarely 2–3, in which cases mean values have been employed). IV and V are based on mean values from measurements on (3–)4–5 well-developed leaves in each collection. For further particulars, see explanation to Fig. 2.

along the midrib at right angles to it (Fig. 1, II h and III h). In order to avoid complications caused by serration etc., the width was measured between lines connecting the tips of the teeth (cf. Fig. 1, II and III). The modified leaf shape index so obtained gives a much better distinction, as shown in Fig. 3, IV.

Fig. 4. Variation in flower shape in *Canarina*, “Group a” (*= C. canariensis*). Contour drawings traced from photographs. The flowers depicted belong to the following collections: a, Tristram 53 (K); b, “Hortus Monac. 1845” (M); c, Bourgeau 171 (G); d, Herb. Webbianum s.n. (FI); e, Bornmüller 2625 (LD).

Fig. 5. Variation in flower shape in *Canarina*, “Group b” (*= C. abyssinica*). Contour drawings traced from photographs. The flowers depicted belong to the following collections: a, Granvik 331 (S); b, Graham 1003 (K); c, Mytton Watson H. 1289-20 (K); d, Rotschild Exped. s.n. (P); e, Ambjörn 37 (UPS); f, Gardner 1377 (K); g, Andrews 1919 (K).

We may then proceed to investigate the variation curves obtained (Figs. 2 and 3). Each portion of these figures gives a series of four histograms (except Fig. 3, V with only three). The lower three (or two, in Fig. 3, V) of those give the variation range for each of the taxa a, b, and c, respectively, starting from the bottom. The uppermost curve gives the variation in the total material. Examination of those diagrams proves that the most useful distinctive characters of those tested are the leaf shape index (Fig. 3, IV), which gives a sharp distinction between “Group a” and the other two, and the ratio of leaf blade length to petiole length (Fig. 3, V), which provides an equally sharp distinction between “Group b” and “Group c”. The distinction in corolla shape index (Fig. 2, III) between “Group a” and the others is not quite so good—there is some overlapping. Even more overlapping occurs in ovary shape index (Fig. 3, III) between “Group b” and the others. Finally, the variation ranges of corolla length (Fig. 2, I) and ovary width (Fig. 3, II) are but slightly overlapping for “Group a” and “Group b”. But this seems to be all that can be deduced from those diagrams.

Correlation of different variates.

Let us then attempt to trace to what extent the morphological distinctions detected may be correlated to each other and to other character differences. The best way to illustrate this seems to be by means of pictorialized scatter diagrams (cf. e.g. Anderson, 1949; Ehrendorfer, 1955, 1958, etc.; O. Hedberg, 1954, 1955a, 1957, 1961a; White, 1957; Monnier, 1957; I. Hedberg, 1961). Fig. 10 shows such a diagram, where the shape index of the corolla (vertical axis) has been plotted against the shape index of the leaf blade (horizontal axis). The shape of the leaf base is shown by the degree of filling of the rings, an open ring standing for cordate leaf base, a half-filled for truncate, and a filled ring for hastate leaf base. Evi-Sv. Bot. Tidskr., 55 (1961) : 1
Fig. 8. Variation in leaf shape in *Canarina*, "Group b" (= *C. abyssinica*). Contour drawings traced from photographs. The leaves belong to the following collections: a, Wilkes 120 K.U. (BM); b, Wimbush 11591 (EA); c, Granvik 332 (LD); d, Cooper B.8035 (EA); e, Ambjörn 37 (UPS).

Fig. 9. Variation in leaf shape in *Canarina*, "Group c" (= *C. eminii*). Contour drawings traced from photographs. The leaves belong to the following collections: a, Lindblom 3/6-20 (S); b, Stolz 1081 (K); c, Kerfoot 155 (EA); d, Robyns 3293 (BR); e, Christiaens 820 (BR); f, Williams 584 (EA); g, Rossignol 250 (BR); h, Fries & Fries 2567 (UPS); i, Ross 468 (BM); j, Tweedie 460 (K); k, Insol 117 (BM).

dently the correlation between corolla shape and leaf shape is quite good in this case. Furthermore, hastate leaves are recorded only for specimens corresponding to the right-hand swarm of dots ("Group a"), whereas cordate leaves are found only in specimens corresponding to the left-hand swarm ("Groups b + c"). The clear discontinuity between the two swarms of dots in this diagram suggests an interspecific boundary, that is, "Group a" should be specifically distinct from the other two.

The interrelations between "Group b" and "Group c" are not so evident from Fig. 10; they are better shown in another diagram, Fig. 11. Here the shape index for the ovary (vertical axis) has been plotted against the ratio of leaf blade length to petiole length. The amount of fusing of the sepal bases is shown by the amount of filling of the dots, a black dot standing for distinctly fused sepals, and a half-black dot denoting sepals fused for little more than 1 mm. Finally, occurrence of distinct coiling in petioles and/or pedicels is marked by a long tail on the dot, whereas a short tail indicates indistinct coiling. Also in this diagram we find good correlation between the character differences studied, and a sharp discontinuity between two swarms of symbols, suggesting an interspecific boundary between "Group b" (left) and "Group c" (right).

Additional distinctions in gross morphology.

Apart from the characters studied above there are a few other morphological distinctions which cannot be studied in all specimens, either because the material is insufficient or because their study necessitates destruction of part of the material. One of those concerns the appearance of the buds. In specimens belonging to "Group b" the sepals seem to be always fused in bud (cf. Plate III), whereas in the other two groups they are free. This difference was found to hold good in all specimens seen possessing well-developed buds. The calyx also provides another character of less diagnostic value: in "Group a" the sepals are often (but not always) dentate and often reflexed, whereas in the other two taxa they are erect or patent, and their margin is always entire.

Another distinction was found in seed morphology (cf. Table I and Fig. 12). Ripe seeds were available in nine sheets of “Group a”, three of “Group b”, and seven of “Group c”. In addition one collection of fresh seeds of “Group a” and one of “Group c” were available. The seeds of “Group c” are elongate with a length/width ratio of about 3 (2.7–3.5), whereas those from the other two groups are ovate with a length/width ratio about 1.5 (1.4–1.9). The surface texture of the former is also different (Fig. 12). The seeds of “Group a” tend to be smaller than those of “Group b”, but their variation ranges are largely overlapping (Table I).

A third distinguishing character is found in the shape of the filaments. During anthesis their lower halves are in all three taxa bent inwards over the top of the ovary, whereas their upper parts are erect. In specimens of “Group a” the lower halves of the filaments are almost linear, about 2 mm wide, and do not overlap at the base. In the other two taxa they are more or less triangular-ovate, about 6 mm wide, and distinctly overlapping from the base (cf. Linnaeus, 1738, Table 8; Gaertner, 1807, Table 211, Canarina, c; De Candolle, 1830, Plate 4B; Engler, 1895, Table 366; Burtt, 1938, Fig. B). This feature can only be studied in dissected flowers, and since few sheets contain more than one or two (usually un-dissected) flowers, it cannot be investigated in all herbarium specimens without

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Table I. Measurements of seed size (length and width) in seminiferous herbarium specimens of *Canarina*. The measurements were made with a binocular lens to the nearest 1/20 of a mm. Ten normal seeds were measured from each collection; the table gives the mean value for each dimension as well as the range of variation.

<table>
<thead>
<tr>
<th>Origin of collection</th>
<th>Seed length, mm</th>
<th>Seed width, mm</th>
<th>Ratio (length/width)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. <em>C. canariensis</em> (&quot;Group a&quot;)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bourgeau 171 (G)</td>
<td>1.53 (1.45–1.65)</td>
<td>1.11 (1.05–1.15)</td>
<td>1.4</td>
</tr>
<tr>
<td>Bourgeau 172 (G)</td>
<td>1.58 (1.45–1.70)</td>
<td>0.94 (0.80–1.05)</td>
<td>1.7</td>
</tr>
<tr>
<td>Bourgeau 1416 (WAG)</td>
<td>1.45 (1.25–1.55)</td>
<td>1.04 (0.95–1.25)</td>
<td>1.4</td>
</tr>
<tr>
<td>Dahlstedt s.n. (UPS)</td>
<td>1.75 (1.70–1.85)</td>
<td>0.91 (0.80–0.95)</td>
<td>1.9</td>
</tr>
<tr>
<td>Gelert 17/597 (G)</td>
<td>1.29 (1.15–1.40)</td>
<td>0.90 (0.85–0.95)</td>
<td>1.4</td>
</tr>
<tr>
<td>Krause s.n. (PRE)</td>
<td>1.35 (1.30–1.40)</td>
<td>0.87 (0.80–0.95)</td>
<td>1.6</td>
</tr>
<tr>
<td>Murray s.n. (BM)</td>
<td>1.74 (1.55–1.80)</td>
<td>1.04 (0.95–1.10)</td>
<td>1.7</td>
</tr>
<tr>
<td>München, cult, &quot;22&quot; (M)</td>
<td>1.43 (1.35–1.60)</td>
<td>0.95 (0.80–1.00)</td>
<td>1.5</td>
</tr>
<tr>
<td>Anonymus s.n. (FI)</td>
<td>1.59 (1.50–1.70)</td>
<td>1.05 (0.95–1.10)</td>
<td>1.5</td>
</tr>
<tr>
<td>2. <em>C. abyssinica</em> (&quot;Group b&quot;)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Davoli 59 (FI)</td>
<td>1.85 (1.55–2.10)</td>
<td>0.99 (0.90–1.15)</td>
<td>1.9</td>
</tr>
<tr>
<td>Lind 262 (K; 8 seeds only)</td>
<td>2.08 (2.00–2.20)</td>
<td>1.28 (1.20–1.35)</td>
<td>1.6</td>
</tr>
<tr>
<td>Thomas 426 (K)</td>
<td>1.78 (1.70–1.85)</td>
<td>1.19 (1.05–1.30)</td>
<td>1.5</td>
</tr>
<tr>
<td>3. <em>C. eminii</em> (&quot;Group c&quot;)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Christiaens 1476 (BR)</td>
<td>2.27 (2.00–2.55)</td>
<td>0.71 (0.65–0.75)</td>
<td>3.2</td>
</tr>
<tr>
<td>Fishlock &amp; Hancock 30 (K)</td>
<td>2.02 (1.95–2.10)</td>
<td>0.66 (0.60–0.70)</td>
<td>3.1</td>
</tr>
<tr>
<td>Gardner 2838 (BM)</td>
<td>2.15 (2.00–2.25)</td>
<td>0.64 (0.55–0.70)</td>
<td>3.3</td>
</tr>
<tr>
<td>Lebrun 4492 (BR)</td>
<td>2.17 (1.95–2.30)</td>
<td>0.81 (0.75–0.85)</td>
<td>2.7</td>
</tr>
<tr>
<td>Scott-Elliot 7958 (BM)</td>
<td>2.55 (2.40–2.75)</td>
<td>0.77 (0.70–0.85)</td>
<td>3.3</td>
</tr>
<tr>
<td>Stolz 1081 (S)</td>
<td>2.38 (2.15–2.55)</td>
<td>0.68 (0.55–0.80)</td>
<td>3.5</td>
</tr>
<tr>
<td>Thomas 340 (K)</td>
<td>2.19 (2.00–2.30)</td>
<td>0.62 (0.60–0.65)</td>
<td>3.5</td>
</tr>
</tbody>
</table>

doing much damage to the material. It was checked in about 5–10 collections of each taxon.

A fourth distinction was found in the ovary. In specimens of "Group c" this is distinctly six-ribbed on the outside, with thick ribs projecting up into the calyx lobes (Fig. 13; cf. BURTT, 1938, Plate 9531 and Fig. D). In the other two taxa the veins may protrude a little above the outer surface of the ovary, but there are no distinct ribs (cf. DE CANDOLLE, 1830, Plate 4 B: 8; ENGLER, 1910 a, Fig. 116).
Conspicuous as it is in living material this distinction may be difficult or impossible to trace in herbarium specimens because of deformation in pressing (cf. Fig. 16, II).

A fifth difference is found in the arrangement of the leaves, which in vigorous shoots of “Group a” may be ternate, whereas in the other two taxa they are always opposite.

**Variation in microscopical characters.**

Modern taxonomy derives much of its evidence from microscopical characters provided by anatomy, palynology, and cytology. It was therefore attempted to extend our investigations into those fields. Anatomical differences between species of the same genus seem to be uncommon, but the peculiar coiling petioles of “Group b” might be expected to differ anatomically from those of the other two taxa. And petiole anatomy has in other cases provided good hints for taxonomy. Since the only living material available in Uppsala was one collection of “Group a”, we had to rely mainly on herbarium specimens. On the suggestion of Prof. NANNFELDT the dry petioles to *Sv. Bot. Tidskr., 55 (1961)* : 1
be examined were first soaked for one or two days in a mixture of equal parts of aqueous ammonia and water, then thoroughly rinsed, embedded in paraffin, sectioned with a microtome, and stained with safranine. Most of the preparations obtained by this method were quite satisfactory, as can be seen from Plate I, where A was made from fresh material, B and C from herbarium specimens.

As is evident from Plate I, the petiole anatomy of the three taxa is largely similar: all have one open crescent-shaped or horse-shoe-shaped vascular strand. But on closer examination some differences are found. Thus the section at B (belonging to “Group b”) is evenly rounded, whereas the other two are flat or concave on the upper (adaxial) side. This difference can be detected with a hand lens in herbarium specimens. And in C (representing “Group c”) the sides of the crescent-shaped vascular strand converge inwards so much as to make it almost closed, with a couple of detached phloem strands at the top. The material investigated anatomically was unfortunately rather small, consisting of one petiole from each of four collections of “Group a” (Asplund 644, UPS, and 756, G; Bourgeau 171, G; Hedberg 3750, UPS), three of “Group b” (Ambjörn 37, UPS; Tweedie 332, K; Wimbush 11591, EA), and three of “Group c” (Gardner 2838, K; Kerfoot 293, EA; Williams 584, EA). Furthermore some of the preparations were not quite as successful as those pictured in Plate I. The results must therefore not be taken as proof of an absolute distinction in petiole anatomy between the three taxa concerned, even if such a distinction appears plausible. The petiole anatomy has proved useful also for the purpose of tracing the taxonomic relationship of the genus (cf. p. 42 below).

Another rewarding approach was provided by palynology. Pollen grains of *Canarina* were pictured already by De Candolle (1830, Plate 4, B:6), though his picture bears little resemblance to the original. A better picture, showing the spinuliferous exine and three long colpi is found in Gardeners’ Chronicle (Anonymus, 1911). Brief descriptions of the pollen grains in four collections of *Canarina* from the Canary Islands and Tropical East Africa were given by Erdtman (1952, p. 92), who found differences both in pollen shape and in the length of the colpi. In order to study this variation we made permanent slides of acetolyzed pollen grains (cf. Erdtman, op. cit., p. 6 f.) from seven collections of “Group a”, 10 of “Group b”, and 11 of “Group c”. Microscopic investigation of those slides revealed the existence of two distinct pollen types (cf. Plate II). One of those,

Table II. Chromosome counts in the genus *Canarina* L. The count by Raven (No. 5 in the table) was made in a squash preparation of flower buds; all the other counts were made in root tips, fixed in chromoacetic formalin, embedded in paraffin, sectioned, and stained with crystal violet (cf. Fig. 14).

<table>
<thead>
<tr>
<th>Origin of material</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>&quot;Group a&quot; (= <em>C. canariensis</em>)</td>
<td></td>
</tr>
<tr>
<td>1. Uppsala Bot. Garden, &quot;Tenerife 1955: 1&quot; (Ref. Sheet: Hedberg 3750, UPS)</td>
<td>$2n = 34$</td>
</tr>
<tr>
<td>2. Kew Gardens, Temperate House; fixed 8.3.1960. Cf. Fig. 14, III</td>
<td>$2n = 68 \pm, 34$</td>
</tr>
<tr>
<td>3. Kew Gardens, Temperate House, fixed 29.9.1960, specimen 241-53 (Orotava); presumably the same specimen as No. 2 above. Cf. Fig. 14, II</td>
<td>$2n = 34$</td>
</tr>
<tr>
<td>4. Kew Gardens, Tropical House, fixed 29.9.1960</td>
<td>$2n = 34$</td>
</tr>
<tr>
<td>5. Los Angeles, Vavra Estate, March 1959; P. Raven 13828. Cf. Fig. 14, I</td>
<td>$n = 17$</td>
</tr>
<tr>
<td>&quot;Group b&quot; (= <em>C. abyssinica</em>)</td>
<td></td>
</tr>
<tr>
<td>6. Kew Gardens, Tropical House, specimen 128-55 (from Kenya, Endebess, leg. Mrs. Irwin), fixed 29.9.1960</td>
<td>$2n \leq 34 \pm$</td>
</tr>
<tr>
<td>&quot;Group c&quot; (= <em>C. emini</em>)</td>
<td></td>
</tr>
<tr>
<td>8. Ibid., another specimen</td>
<td>$2n = 34$</td>
</tr>
</tbody>
</table>

occurring in "Groups a and b", is subprolate to prolate spheroidal and tricolporate with long colpi (for explanation of palynological terms see Erdtman, *op. cit.*). The second pollen type, characteristic of "Group c", is oblate to suboblate or oblate spheroidal, indistinctly tricolporate with short colpi, or seemingly triporate, the colpi coinciding more or less completely with the pores. A certain variation does occur in the shape of its apertures, as illustrated by Hedberg (1961a, Fig. 6), but in the material investigated the palynological distinction between "Group c" and the other two taxa is quite sharp.

The cytological feature most often utilized by taxonomists is the number (and shape) of the chromosomes (cf. Darlington, 1956). The basic number of a genus may often be a guide to its taxonomic position, and differences in basic number indicate most often generic *Sv. Bot. Tidskr.*, 55 (1961): 1

distinction. A difference in ploidy between two specimens is also of taxonomic interest because it indicates a barrier to interbreeding, which is one of the criteria commonly requested for specific distinction. Through the courtesy of the Director, Royal Botanic Gardens, Kew, we managed to obtain fixed root-tips for chromosome counting from all three taxa of *Canarina*. Chromosome counts of “Group a” were also made in material grown in the Botanical Garden at Uppsala University, and a further count for this taxon was obtained from Dr. Peter H. Raven, Los Angeles. The numbers obtained are given in Table II; cf. also Fig. 14. The basic number of the genus is evidently 17, and all specimens examined are diploid, with one puzzling exception. A specimen of “Group a” in the Temperate House at Kew Gardens provided 2n = 68 ± (Fig. 14, III), and was first believed to be a regular tetraploid. Occurrence of a tetraploid race in a commonly cultivated plant like “species a” appeared a priori very plausible, since fresh polyploids tend to have larger flowers, hence

Fig. 15. Canarina, "Group a" (= C. canariensis). Scatter diagram illustrating weakly correlated variation in pollen diameter (vertical axis) and stomatal (guard cell) length (horizontal axis). Both were measured by means of eye-piece micrometer in lactophenol preparations (cf. Hedberg, 1952, p. 257). The diagram is based on mean values (in scale divisions, each equalling 1.2 μ) of measurements on 25 pollen grains and 10 stomata from each collection. The open ring represents the crucial specimen in the Temperate House, Kew Gardens, some root-tips of which provided metaphases with the tetraploid chromosome number (cf. p. 37). The other specimens measured are listed in Appendix 2, p. 59.

being desirable from a horticultural point of view. Such fresh polyploids seem to have as a rule larger pollen grains and stomata than the corresponding diploids (cf. Noggle, 1946; Stebbins, 1950, p. 302 f.; de Wet, 1954; Maurizio, 1956, p. 68). In order to disclose any occasional tetraploid specimens in the herbarium material available it was therefore attempted to trace discontinuous variation in those features. For that purpose lactophenol preparations were made of pollen and pieces of full-grown leaves from each of altogether 29 collections of "Group a". (The specimens are listed in Appendix 2, p. 59.) The variation in pollen size and stomatal length proved quite continuous, however, as shown in the scatter diagram in Fig. 15. A herbarium specimen of the crucial plant at Kew happened to have the largest pollen grains and the smallest stomata of all specimens sampled. A later fixation of root-tips from what must be the same specimen at Kew gave the diploid number only (2n = 34, cf. Fig. 14, II). The tetraploid number first obtained for this plant had been counted in two different roots of the first fixation, but when Sv. Bot. Tidskr., 55 (1961): 1
another group of roots from that first fixation was sectioned, one of them gave the diploid number also. Barring contamination (which seems improbable in this case because the number 68 is comparably rare) the explanation of this inconsistency may either be sought in endopolyploidy, or else the specimen in question was a chimaera with a tetraploid sector comprising part of the root system. This case demonstrates in any case the danger of relying on a single unchecked chromosome count for a cytotaxonomic conclusion. Another memento is the rather weak correlation between pollen diameter and stomatal size in “Group a”; a similar case has been found by I. Hedberg (1961) in Anthoxanthum odoratum L., s. lat.

Variation in ecology.

To study ecology from herbarium specimens only may appear a precarious undertaking. One important piece of information concerning “Group c” is readily available from collector’s labels, however: this plant occurs most often as an epiphyte on tree stems in montane or riverine forest, more rarely in rock fissures, etc. The other two taxa seem to be always growing on the ground, usually in more open vegetation.

Taxonomic conclusions.

It may now be time to summarize the taxonomic evidence procured. As demonstrated by the scatter diagrams in Figs. 10 and 11 the three taxa “a, b, and c” recognized at the outset are morphologically sharply distinct from each other. Their independence from each other is also supported by some of the additional features discussed above. Thus “Group a” differs from the other two also in its narrower filament bases and in having ternate leaves on vigorous shoots and frequently serrate sepals; “Group b” in its closed aestivation; and “Group c” in its elongate seeds with different surface structure, its pronouncedly ribbed ovary, oblate—brevicolpate pollen grains, and predominantly epiphytic habit. These three taxa must therefore be regarded as very good species. On the other hand, the continuous variation encountered within each of them gives no support for taxonomic subdivision below the species level.

It then remains to establish the correct names for the three species distinguished. As shown above (p. 20) four validly published specific epithets are available. One of these, Canarina canariensis (L.) Vatke, Sv. Bot. Tidskr., 55 (1961): 1
pertains to material from the Canary Islands, that is "species a". As with most other species described by *Linnaeus* no specimen can be automatically designed as a holotype (cf. Stearn, 1957). Since the first reference given by *Linnaeus* in *Species Plantarum* (1753, p. 168) under "*Campanula canariensis*" it would be natural to select a specimen in the Cliffort Herbarium at the British Museum as a lectotype. But unfortunately the *Canarina* specimen in that herbarium has been lost. In the Linnean Herbarium in London there is, however, one specimen, from "Hortus Upsaliensis". Whether that specimen had been acquired before 1753, and hence utilized by *Linnaeus* in making the original description, is difficult to establish. In the absence of contrary evidence we have selected it as lectotype.

The other three names available were all created for material from East Tropical Africa. The oldest of them, *Canarina eminii* Aschers. ex Schweine., obviously refers to our "Group e". The holotype was unfortunately destroyed in Berlin during the second world war, and the original description is very meagre, but an illustration published a couple of years later (Engler, 1895, Table 36) permits identification. This is furthermore the only species of the genus known from Ruwenzori. A specimen from the same part of that mountain as the holotype was compared with it in Berlin by Humbert and found to agree; this specimen (Humbert 8818, P) has been selected as neotype (cf. Plate IV).

The second oldest name from East Tropical Africa is *Canarina abyssinica* Engl., described from Ethiopia. The two syntypes were destroyed in Berlin during the war, but the original description is quite sufficient for identification with our "Group b". (It mentions, *inter alia*, the long petioles, coiled pedicels, broad ovary, and broad seeds.) This identification is also supported by a picture published by Engler (1910 a, Fig. 116). As neotype has been selected a specimen (Ambjörn 37, UPS) from the same part of Ethiopia as the syntypes, which corresponds well to the original description and the illustration just mentioned. In the same paper Engler (*loc. cit.*) described *C. abyssinica* var. *umbrosa* Engl., said to be distinguished by longer internodes, larger leaves, and wider sepals. The variation in these features within *C. abyssinica* is quite continuous, however (cf. p. 21 etc. above), and although the type has been lost, there is no doubt that this variety must be sunk.

mainland is *Canarina elegantissima* Th. Fr. jr. Its type specimen (Fries & Fries 2567, UPS) still exists, and clearly falls within the variation range of "Group c", that is *C. eminii*. Its describer stated it to be "von sämtlichen bisher bekannten Arten der Gattung sehr scharf getrennt" (Fries, 1923, p. 394). He did not specify which characters should be distinctive, however, and in the material now available all features investigated display continuous variation within "Group c". *C. elegantissima* must therefore be reduced to a synonym of *C. eminii*. Because of that continuous variation it is also impossible to maintain the variety *C. eminii* var. *elgonensis* Th. Fr. jr., described in the same paper (op. cit., p. 395).

**Systematic position of the genus Canarina.**

Ever since the genus *Canarina* was segregated from *Campanula* its taxonomic position has been open to debate. **Linnaeus** (1771, pp. 148, 225) considered it to be most closely related to *Campanula*. **Alph. De Candolle** (1830, p. 66) in his monograph of the *Campanulaceae* placed it next to the genera *Campanumaea*, *Codonopsis*, and *Platycodon*, considering this group to be more closely related to *Wahlenbergia* than to *Campanula*. The same arrangement was maintained in the *Prodromus* (De Candolle, 1839, p. 414), where he placed the four genera concerned in the tribe *Wahlenbergiae*. **Reichenbach** (1837, p. 186) also brought *Canarina* and the other three genera mentioned to the same group as *Wahlenbergia*, but separate from *Campanula*. **Bentham & Hooker** (1876, p. 544) follow much the same system, although *Canarina* and *Campanumaea* are placed with *Peracarpa* and *Pentaphragma* in a subgroup of their own because of their "*bacca carnosa v. subsicca, indehiscens*". But these genera are listed immediately after *Codonopsis* and *Cyananthus* and placed nearer to *Wahlenbergia* than to *Campanula* in the linear sequence adopted.

**Schönland** (1889, p. 55), on the other hand, puts *Canarina* with *Campanula* in the group (*Campanuloideae-Campanulaceae*) *Campanulinae*, whereas *Codonopsis* and *Campanumaea* remain with *Wahlenbergia* in the *Wahlenberginae*. The same arrangement has been followed, for instance, by **Diels** (1936, p. 336) and **Skottsberg** (1940, p. 596 f.).

**Heintze** (1927, p. 63), finally, brings *Codonopsis* to *Wahlenbergiae*, *Canarina* and a few others to *Canarineae*, and *Campanumaea* to
Fig. 16. Accessory shoots in Canarina. I, Canarina canariensis, Uppsala Bot. Garden, node of living stem with two vigorous branches projecting from the leaf axils. Below each branch can be seen a rudimentary accessory shoot. Magnification ×1.5. — II, Canarina eminii, detail of herbarium sheet (Hedberg 158, UPS). From the axils of the uppermost pair of leaves below the terminal flower are emitted two vigorous side branches, below each of which projects a small accessory shoot. Magnification ×0.7. This picture also shows to some extent the ribs of the ovary, and the (purplish) mottling on the stem.

Campanuleae. One must object to this classification that, according to Nannfeldt (1931, p. 152), the genera Campanumaea and Codonopsis are so closely related that it might be most logical to unite them. These examples may perhaps be sufficient. Evidently no stable system for the subdivision of this family can be obtained without a thorough revision, utilizing not only the traditional characters of gross morphology, but also data from anatomy, palynology, cytology, etc. In the absence of such a revision no final decision can be made, of course, as regards the position of Canarina. It must suffice for the moment with an attempt to establish whether its greatest affinities are with Campanula or with Codonopsis and Campanumaea.

As regards pollen morphology Erdtman (1952, p. 92) finds Canarina to agree better with Campanumaea, Codonopsis and Platyodon than with Campanula (and Wahlenbergia); cf. Plate II. The petiole anatomy seems to point in the same direction, Canarina having an open, crescent- or horse-shoe-shaped vascular strand (cf. p. 35 above and Plate I) like Codonopsis and Cyananthus, whereas Campanula is said to have cylindric vascular strands in its petioles (Metcalf & Chalk, 1950, p. 811). In Canarina eminii the vascular Sv. Bot. Tidskr., 55 (1961): 1
strand appears to be almost closed, however (Plate I, C). The scandent habit of *Canarina abyssinica* is matched in several species of *Campanumaea* and *Codonopsis*, but not in *Campanula*. The opposite (or ternate) leaves in *Canarina* also point towards *Codonopsis* and *Campanumaea* rather than *Campanula*. The baccate fruit in *Canarina* is matched in *Campanumaea* but not in *Campanula*. The peculiar accessory shoots described by Nannfeldt (1940, p. 383 f., Fig. 1) in *Codonopsis* occur regularly in *Canarina* (Fig. 16; cf. also Anonymus, *Sv. Bot. Tidskr.*, 55 (1961): 1)
1911, Fig.), but may be found also in Campanula (Nannfeldt, loc. cit.). The only character that might suggest closer affinity with Campanula than with the other genera mentioned is the basic chromosome number, which is 17 in Canarina. The same basic number occurs also in Campanula, whereas the basic number 8 has been found in Codonopsis (Darlington & Wylie, 1955, p. 287). But so far only two species of Codonopsis have been investigated cytologically, and this polymorphic genus may well prove to be equally variable
cytologically as *Campanula*, where no less than seven different basic numbers are known (8, 9, 10, 12, 13, 14, 17; cf. Darlington & Wylie, loc. cit.; Larsen, 1954, p. 169). The weight of evidence therefore supports the placing of *Canarina* nearer to *Codonopsis* and *Campanumaea* than to *Campanula*.

**Phytogeography.**

The known geographic distribution of the genus *Canarina* is shown on the map (Fig. 19), and the areas of *C. abyssinica* and *C. eminii* on Figs. 17 and 18, respectively. The latter two are largely overlapping. Both species are common, for instance, in the surround-
Fig. 20. Distribution map for the Old World species of *Sibthorpia* L., after Hedberg, 1955 b, with addition of a few recent collections at Kew. Black dots refer to *S. europaea* L., open rings to *S. africana* L., and the open square to *S. peregrina* L.

ings of Endebess on the lower slopes of Mt. Elgon in Kenya Colony (*fide* Mrs. P. H. Irwin, *in litt.*), but they seem to be ecologically sharply separated, and no hybrids have been encountered. *C. canariensis*, on the other hand, is widely disjunct from the other two.

The area of the genus as a whole is decidedly discontinuous with a wide gap across Sahara (Fig. 19), suggesting a relic distribution. The *Sv. Bot. Tidskr.*, 55 (1961): 1
age of this discontinuity cannot at present be ascertained, but a brief discussion may nevertheless be of interest. Schimper (in Schenck, 1907, p. 333) believed the present species of Canarina to be descendants from some common ancestor belonging to the European warm-temperate Tertiary flora. That flora evidently contained a large number of species identical with (or closely related to) plants now occurring in Makaronesia (Canary Islands, Madeira, and the Azores), especially in the Laurus forests (op. cit.).

A similar type of Makaronesian-afromontane disjunction occurs in the species Sibthorpia europaea L. (map, Fig. 20; cf. Hedberg, 1955b), though that species extends also to West Africa and to south-western and south-eastern Europe, occurring in Makaronesia on the Azores instead of the Canary Islands. Also that species must be expected to have had at one time a less discontinuous distribution. It appears to be more cool–temperate than Canarina, occurring further to the north and higher up the mountains (cf. Hedberg, op. cit.). Two other species of Sibthorpia occur as local endemics on Madeira and on the Balearics, respectively (op. cit.).

A third case of Makaronesian–afromontane disjunction is provided by the well-known Erica arborea L. (cf. map, Fig. 21). Its north-western area extends from Makaronesia around most of the Mediterranean (including the northern parts of Morocco, Algeria, and Tunis; cf. Rikli, 1933), and its south-eastern area extends from southern Tanganyika to northern Ethiopia and Eritrea (cf. also Pichi-Sermolli & Heiniger, 1953, Map 1; Hedberg, 1957, p. 140). Recently a sensational extension of its area was recorded by Bruneau de Miré & Quezel (1959), who report the occurrence of a relic stand of trees on a summit in Tibesti in central Sahara. They also report subfossil Erica arborea pollen in neolithic sediments from four other localities in the Sahara (op. cit., map, p. 67; cf. Fig. 21 here). According to these authors, Erica arborea probably had an almost continuous distribution from the high mountains of East Tropical Africa to the Mediterranean region during the moister phases of the Quaternary. Whether Sibthorpia and Canarina were influenced to the same extent by those climatic changes seems uncertain, however. These genera seem to be more dependent on a moist (local) climate than Erica arborea, and the Saharan interval in their areas may well be of Tertiary age. Relic distributions of similar type are possessed by several taxa in the afroalpine and afromontane floras as well as in the flora of Makaronesia (cf. Hedberg, 1961b).

Fig. 21. Distribution map for *Erica arborea* L. Mediterranean area (hatched) after Rikli, 1933; Ethiopia and Eritrea after Pichi-Sermolli & Heiniger, 1953, map 1; Tropical East Africa after Hedberg, 1957, p. 140 f.; Sahara after Bruneau de Miré & Quezel, 1959. Black dots represent living populations (or at least herbarium specimens), thick open rings denote finds of subfossil pollen tetrads (cf. Bruneau de Miré & Quezel, *op. cit.*).

**Special part.**

**Canarina L.**

*Canarina* L., 1771, p. 148 ("Canaria") et 588. Type species: *C. canariensis* (L.) Vatke.

*Pernettya* Scop., 1777, p. 150 ("Pernetya"), non *Pernettya* Gaudichaud 1825 ("Pernettia").

Glabrous and often glaucous herbs containing abundant white latex, with thick and fleshy perennating roots. Stems seasonal, herbaceous, terete and hollow with incrassate nodes, smooth, with opposite or ternate petiolate leaves, di-(or sometimes tri-)chotomously branched, with branches of second order from leaf axils. Most leaf axils produce also small accessory shoots. Flowers large, solitary in the dichasial forks or terminal on end branches, pendent, hexameric (rarely 5- or 7-merous) throughout, epigynous, protandrous. Filaments more or less broadened at the base. Fruit baccate with persistent calyx, indehiscent. Petiole in transverse section exposing an open crescent-like or horse-shoe-shaped vascular strand with more or less incurved edges. Pollen grains subprolate—spheroidal—suboblate-oblate, about \((45-30) \times (35-40)\mu\), tricolporate-tricolporoidate or seemingly triporate; sexine about as thick as nexine, spinuliferous. Basic chromosome number: \(n = 17\).

Key to the species.

Leaf blade narrowly triangular–hastate with a length/width ratio\(^1\) larger than 2.4; vigorous shoots usually with ternate leaves; corolla campanulate; filament bases almost linear, about 2 mm wide; sepals often dentate

1. *Canarina canariensis* (L.) Vatke

Leaf blade cordate–broadly triangular–ovate with a length/width ratio\(^1\) smaller than 2.4; all shoots with opposite leaves; corolla funnel-shaped; filament bases shield-like, about 6 mm wide; sepals always with entire margin.

Petioles long (ratio of leaf blade length to petiole length\(^1\) smaller than 1.5); peduncles and petioles usually coiled; sepals entirely united in bud; sepal bases usually fused for a few millimetres in open flowers; seeds ovate; ovary cupular

2. *C. abyssinica*

Petioles short (ratio of leaf blade length to petiole length\(^1\) larger than 1.5); peduncles and petioles not coiled; sepals free in bud; sepal bases not fused (for more than 1 mm) in open flowers; seeds elongate; ovary obconical

3. *C. eminii*

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1 Cf. Fig. 1.

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Illustrations. **Linnaeus**, 1738, Plate 8 (as *Campanula foliis hastalis dentatis, caule determinate folioso; flowering branch*). — **Curtis**, 1799, Plate 444 (as *Canarina campanula; flowering branch*). — **Gaertner** 1807, Plate 211 (as *C. campanula; bud, flower dissections*). — **Loddiges**, 1819, Plate 376 (as *C. campanula; flowering branch*). — **De Candolle**, 1830, Plate 4B (as *C. campanula; flower, flower dissections, pollen*). — **Webb & Berthelot**, 1836–1840, frontispiece (as *C. campanula; flowering branch*). — **Planchon**, 1856, No. 1094 (as *C. campanula; flowering branch*). — **Bailon**, 1886, p. 323 (as “*C. campanulata*”; flower). — **Schönland**, 1889, Fig. 31 (as *C. campanula; flowering branch*). — **Engler**, 1910b, Fig. 686 (as *C. campanula; flowering branch—the same picture as in Schönland 1889*). — **Schenck**, 1907, Fig. 50 (as *C. campanula; flowering branch*). — **Anonymous**, 1911 (as *C. campanula; flowering branch, flower dissections, pollen*). — **Söderberg**, 1936, p. 20 (as *C. campanula; flowering branch*).

Seven more illustrations, not seen by us, are listed in **Index Londinensis**.

Terrestrial herb with thick tap-root. Stems up to 3 m tall, erect, scandent, in their lower part usually trichotomously branched with ternate leaves, in their upper part dichotomously forked with opposite leaves. Petiole about half as long as the leaf blade, patent, straight, flattened or concave on the adaxial side. Leaf blades about 5–10 cm long, narrowly triangular-ovate (their length/width ratio as defined by $g/h$ in Fig. 1 larger than 2.4), more or less coarsely dentate or sometimes crenate, usually hastate (cf. Fig. 4). Sepals entirely free from each other; erect, patent or reflexed; often dentate (cf. Fig. 4). Corolla 3–6 cm long, campanulate (cf. Fig. 4), dull yellowish purple-testaceous. Filament bases almost linear, about 2 mm wide. Ovary obconical, indistinctly hexangular in transverse section. Fruit black (*fide Schenck*, 1907, p. 405). Seeds ovate, $(1.3–1.8) \times (0.8–1.1)$ mm, brown, with finely pitted surface (Fig. 12, I). Pollen grains subprolate–prolate spheroidal, tricolporate with long colpi (Plate II A–C). Chromosome number: $2n = 34$.

**Distribution:** Known only from four of the Canary Islands (Palma, Gomera, Tenerife, and Gran Canaria), where it appears to be common in suitable localities. Because of its edible berries it seems to be commonly cultivated in these islands. Known in cultivation in Europe at least since 1695 (cf. **Loudon**, 1830, p. 139), and has been a popular greenhouse plant.

In **Laurus** forest and scrub, at forest margins, in ravines, among shaded rocks, etc., usually between 300 and 800 m altitude. Flowering season November–May(–June).
Canary Islands.

**Palma.** *Los Llanos,* 1928, Praeger s.n. (K); Reg. orient., alt. 100–400 m, Anonymus s.n. (US).

**Gomera.** 1888 (?), Kuntze s.n. (K).

**Tenerife.** *Adeje:* Barranco del Infierno, alt. c. 600 m, 1897, Andreas s.n. (M). — *Anaga:* in dumosis lauretorum scandens, 1855, Perraudière s.n. (F, K, LE); 1901, Murray s.n. (BM). — *Guimar:* Barranco de Badajoz, 1927, Wettstein s.n. (M). — *Icod de los Vinos:* zw. Icod u. Garachico, 1897, Andreas s.n. (M); in rupestribus, 1923, Cool & Tex 409 (L); Barranco de Castello de Daiva (?), in umbrosis, Anonymus s.n. (LISU). — *Laguna:* Barranco de Portezuelo, 1917, Lindinger s.n. (HBG); Mercedes, 1909, Dahlstedt s.n. (UPS); alt. 750 m, lisiére de la forêt, 1905, Pitard 1795 (P); in opacis saxosis convallium, 1855, Bourgeau 1416 (C, E, G, JE, LE, LISU, MA, P, UPS, W, WAG); alt. 700 m, ad marginem silvarum, 1906, Pitard 609 (G, L, P); alt. 800 m, 1855, Perraudière s.n. (P). — *Los Campos:* Bolle s.n. (E). — *Monte Aguirre:* 1900, Cabrera, comm. Bornmüller s.n. (C, LD). — *Nivaria:* in reg. sylvosa, Anonymus s.n. (FI); in sylvis, Anonymus s.n. (FI); Perraudière s.n. (LE).

**Orotava:** Barranco de Llarena, alt. 500–600 m, 1921, Burchard 24a (S); Barranco de Montijo, alt. 500–600 m, 1921, Burchard 24b (E, F, G). — *Rambla:* alt. c. 300 m, 1933, Asplund 756 (G, S). — "*Rocky Dingles*," 1822, Forbes 4 (K). — *San Diego del Monte:* In sylvis caenobi, 1845, Bourgeau 171 (BM, C, E, FI, G, GH, K, P, W); 1845, Anonymus 166 (FI). — *Santa Cruz:* El Campo, 1859, Lowe 180 (BM, K); Valle de San Andres, 1904, Burchard 187 (LA, M). — *Silos:* In dumetis silvosis et ad rupas umbrosas, 1946, Ceballos & Ortuño (MA 122130). — *Taconorte:* Agua Garcia, 1933, Asplund 644 (S, UPS); ibid., 1921, Borgesen 220 (C); Monte del Agua Garcia, 1891, Cabrera s.n. (BM); Agua Garcia, 1930, Herb. Maude s.n. (BM); ibid., 1884, Anonymus s.n. (FI); forêt de l’Agua Garcia, 1911, Anonymus s.n. (LA). — *Taganana:* Las Vueltas, 1851, Bolle s.n. (P); Vuelta, 1890, Herb. Murray s.n. (BM); ibid., 1888, Herb. O. Kuntze (NY). — *Tegueste:* Monte de la Mina, alt. 750 m, 1905, Pitard 245 (G, L, P). — *Val de Guerra:* alt. 450 m, growing over bushes in very stony ravine among brambles etc., 1955, Tristram 53 (K). — *Valle de Agurnía:* 1900, Sabradoz (MA 122331).

— *Without specif. loc.:* Bauden s.n. (P); Berthelot s.n. (GH); 1855, Bourgeau 1416 (W) and s.n. (C); Cabrera (MA 162331); Courant s.n. (LE); 1796, Le Dru 46 (E, P) and s.n. (FI); Lehower (?) s.n. (B); Lemann s.n. (K); Perraudière s.n. (LE); Skinner (?) s.n. (K); 1844, Webb s.n. (G); 1911, Zettrow s.n. (HBG); Herb. de Pitard-Briau s.n. (G); in sylvestribus, Anonymus s.n. (P); Anonymus s.n. (GH, K, L, P).

Mücke 2309 (B); ibid., c. 400 m, climbing plant from waste ground, 1955, Scott s.n. (K). — *Telos*, 1894, Cook 119 (GH, NY, US). — *Teror*: 1887, Anonymus s.n. (E); ibid., “in montosis Canarice”, Anonymus s.n. (FI). — Without specif. loc.: Anonymus s.n. (FI).

*Canary Islands*, without specif. loc.: Courant 188 (G); 1837, Despréaux 269 (G); Despréaux s.n. (PH); Firetay (?) s.n. (K); “Hänge am Hülle”, Krause 229 (PRE).


Another 30 collections of cultivated material without specified locality have been examined.

2. *Canarina abyssinica* Engl. — Figs. 5; 8; 12, II; Plates I B, II G–I, III.


Illustrations. *Engler*, 1910 a, Fig. 116 (flowering branch). — *Jex-Blake et al.*, 1934, Table 5 (flowering branch). The plate seen by us only in reprint.

Terrestrial herb with large bulbous root. Stem richly branched at the base (*fide* Wiltshire No. 76 in herb. Kew), sparsely dichotomously branched in its upper part, up to 2 m long or more, climbing by means of the coiling petioles and peduncles. Leaves opposite through-

out. Petioles of about the same length as the leaf blade (ratio of leaf blade length to petiole length 0.7–1.4), terete, often coiling around twigs of other plants. Leaf blades about 3–8 cm long, their length-width ratio (as defined by \( g/h \) in Fig. 1) smaller than 1.8, variable in shape (pentagonal-triangular–cordate-ovate) though always with cordate base (Fig. 8), obtusely crenate–sharply dentate. In bud the sepals are entirely fused, forming a closed cup-like cover (cf. Plate III); in open flowers they are usually fused for a few mm from the base (cf. Fig. 5) and always erect with entire margin. Corolla 4–7.5 cm long, funnel-shaped–almost cylindrical (Fig. 5), orange and streaked with red, sometimes lighter inside. Filament bases shield-like, about 6 mm wide, appressed to the receptacle. Ovary broad, cupular, terete. Peduncle in older flowers and fruits as a rule spirally coiled (cf. Plate III). Fruit almost spherical, yellow (fide A. S. Thomas, No. 426 in herb. Kew) or pale tomato-coloured (fide Lind, No. 262 in herb. Kew). Seeds ovate \((1.8–2.1) \times (1.0–1.3)\) mm, blackish brown, with pronouncedly pitted surface (Fig. 12, II). Pollen grains sub-prolate–prolate spheroidal, tricolporate with long colpi (Plate IIG–I). Chromosome number: \(2n = 34\).

**Distribution.** Confined to the uplands of East Tropical Africa, occurring in southern Sudan, central and southern Ethiopia, northern and eastern Uganda, western Kenya, and northern Tanganyika (cf. distribution map, Fig. 17). At Kew there is one specimen in cultivation since 1955.

On more or less shady places in sparsely wooded grassland, savanna, or ‘bush’, sometimes on old termite hills and in forest clearings but not in closed forests, recorded only from altitudes between 1500 and 2500 m. Flowers in the rainy season, usually (May–)June–August(–September).

**Sudan.** Imatong Mts, Mt Ongiliro, alt. 1900 m, 1939, Andrews 1989 (K).


1800 m, 1932, Thomas 426 (K); Bulago, bush and forest land, 1800 m, 1917, Snowden 516 (BM, K); Kaphonwa, amongst undergrowth near stream, alt. 2250 m, 1954, Lind 262 (K). — Without prec. loc.: 1903, Longman s.n. (K).


**Tanganyika. Arusha distr., Ngongongare, alt. 1500 m, 1955, Willan 247 (EA, K).**

3. *Canarina eminii* Aschers. ex Schweinf. — Figs. 6; 9; 12, III; 13; 16, II; Plates 1C, IID–F, IV.


*C. eminii* var. *elgonensis* Th. Fr. jr., op. cit. p. 395 & Fig. 2. Orig. coll.: Kenya, Elgon, “an einem Waldbach im Urwald ca 8000 Fuss ü.d.M.”, 23.5.1920, G. Lindblom s.n. (S, holotype).

**Illustrations.** Engler, 1895, Table 36 (flowering branch, style, stamen). — Fries, 1923, Fig. 1 (as *C. elegantissima*; flowering branch) and Fig. 2 (as *C. eminii* var. *elgonensis*; flowering branch). — Burtt, 1938, Table 9531 (flowering branch, bud) and Figs. A (flower with corolla removed), B (stamen), C (ovary in longitudinal section), and D (ovary in transverse section). *Sv. Bot. Tidskr., 55 (1961): 1*
Epiphytic or terrestrial usually glaucous herb with long and thick root, often provided with a corky surface layer. Stem erect and scandent or pendent, dichotomously branched, up to 2 m long, usually with a fine purplish mottling (cf. Fig. 16, II). Leaves opposite throughout. Petioles less than half the length of the leaf blade (ratio of leaf blade length to petiole length 2.1–7.6), flattened or concave on the adaxial side, patent, straight. Leaf blades about 2.5–9 cm long, their length/width ratio (as defined by $g/h$ in Fig. 1) smaller than 2.2, cordate–ovate with cordate or truncate base, obtusely or sharply dentate–doubly dentate or doubly serrate. Sepals entirely free from each other, erect or patent with entire margin (cf. Fig. 6). Corolla 4.3–7.6 cm long, funnel-shaped (Fig. 6), orange–dark salmon with red streaks (cf. Fig. 13). Filament bases shield-like, about 6 mm wide, appressed to the receptacle. Ovary obconical, distinctly six-ribbed on the outside with thick ribs projecting up into the calyx lobes (cf. Fig. 13). Peduncles straight. Seeds elongate, about $(2.0–2.6) \times (0.6–0.8)$ mm, with fine longitudinal striation (Fig. 12, III). Pollen grains suboblate–oblate spheroidal, indistinctly tricolporoidate with colpi little longer than the pores (Plate II D–F). The shape of the apertures is fairly variable (cf. Hedberg, 1961a, Fig. 6). Chromosome number: $2n = 34$.

**Distribution.** Confined to montane areas in East Tropical Africa, occurring in southern Sudan, central and southern Ethiopia, eastern Belgian Congo, Uganda, western Kenya, and southern Tanganyika (cf. distribution map, Fig. 18). Has been kept in cultivation at least at Cambridge (since 1936) and Kew (since 1959).

In montane or riverine forest, or occasionally on shady places in montane grassland (especially on the smaller mountains in northeastern Uganda). Grows most often epiphytically on trees of Hagenia, Conopharyngia, Podocarpus, etc., but may sometimes occur in shaded rock fissures or on the ground in forests. Recorded from altitudes of 1450–3000 m. Flowering probably not restricted to the rainy seasons; flowering specimens seen from all months of the year.

**Sudan.** Imatong Mts, Gilo, 1500 m, common locally in mountain ravine forests, on road from Katire to Gilo, 1947, K. G. M. 29 (K). Equatoria Prov., Didinga Mts, Mt Lotuke, 2400 m, 1939, Myers 10888 (K).

**Ethiopia.** Lake Tana region: Burye-road, alt. 2150 m, 1926, Chessman s.n. (BM). Damot, near source of R. Abai, 1902, Degen s.n. (BM). — *Shea*: Addis Ababa, 1914, Armbruster s.n. (K). Entotto, alt. 2650 m, Negri 1392 (FI). “Rive del piccolo Akaki”, 1887, V. Ragazzi s.n. (FI). Near Kachissy,


Uganda. Imalong Mts: 2600 m, 1938, Eggeling 3604 (K); ibid., Mt Lomwaga, 2600 m, 1945, Greenway & Hummel 7284 (EA, K, PRE); ibid., Langia Mt, 2800 m, 1943, Purseglove 1433 (EA, K). — Mt Rom: Alt. 2150 m, Liebenberg 133 (K). — Mt Moroto: Alt. 2400 m, Eggeling 2985 (K). — E. Karamoja, Mt Kadam: Wilson 769 (K); ibid., about 2 miles NE of Obda summit, near Kyesowe, 1953, Wood 683 (K). — Mt Elgon: W. slope between Bulambuli and Butandiga, alt. 2750 m, 1953, Goodwin 103 (GH). Sebei, N. of Mt Elgon at Kyessweri R. Siti and Kaburunon R. Sundet, 1900 m, 1953, Norman 223 (K). Buginyanya, 1700 m, 1917, Snowden 513 (BM, K). Bumoni, 1800 m, 1924, Snowden 862 (BM, K). Bulago, Bugishu, 1950 m, 1932, Thomas 340 (K). Without detailed locality: 1952, Engholm 119 (K); 2250 m, Irwin 6 (BR, K). — Ruwenzori: Kangasaba, 2450 m, Fishlock & Hancock 30 (K). Mahoma Valley, near Nyabitubu, 2550 m, 1952, Ross 468 (BM). — “Ruwenzori & Mt Elgon”, N. side, 2500–3000 m, climber on tree in bamboo forest, 1949, Osmaston 4009 (K).

Dimbilil River, SW. Mau, Sambset Catchment, 1958, Kerfoot 155 (EA). — Endabarra, Mau forest, 2250 m, 1946, Bally 4790 (K). — Aberdare Range, 2300–2750 m, 1907, Battiscombe 62 (K); ibid., E. slope, “in silva montana”, 1922, Fries & Fries 2567 (S, UPS); ibid., Tuso fishing camp, 2150 m, 1934, Elliot 7192 (EA). — Mt Kenya: Embu Distr., Thiba camp, 1948, Bally 1146 (K); ibid., 1850 m, 1957, Dyson 428 (EA). 37°18' E, 23° S, 2100 m, 1927, Insol 117 (BM). Katamayo, 2150 m, 1934, van Someren 3498 (EA, K) and 6642 (BR).

Uganda or Kenya. Mt Elgon: 1920, Benham s.n. (BM); 1850 m, 1932, Humphreys 1207 (BM); 1850 m, 1933, Jack 498 (EA); 1937, Jex-Blake 6863 (EA); 2750–3000 m, 1921, Lankester s.n. (K).


Cultivated specimen: Cult. in University Bot. Garden, Cambridge, raised from seeds collected in East Africa by Mr. P. M. Synge (K).

Species incertae sedis: Canarina zanguebar Lour., 1790, p. 195.

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Appendix 1.

List of collections measured for the diagrams of Figs. 2–3 and 10–11. Sometimes more than one sheet of the same collection was measured.

1. “Group a” ( = Canarina canariensis).

Asplund 644 (S, UPS) and 756 (G, S), Bornmüller 2625 (G, L, LD, P, W), Bourgeau 171 (BM, E, G, K, W), 1416 (E, G, LISU, UPS, W, 2 sheets) and s.n. (BM), Brooke 91 (BM), Burchard 187 (M), Cool 400 (L) and 698a (L), Despréaux 269 (G), Pitard 609 (L), Herb. Portenschlager (W), Praeger s.n. (K), Scott s.n. (K), Trehewy 177 (K) and s.n. (BM), Tristram 53 (K), Anonymus (L).

2. “Group b” ( = Canarina abyssinica).

Ambjörn 37 (UPS), Andrews 1989 (K), Bogdan 442 (EA), Cooper B8035 (EA, K), Dowson 543 (K), Eggeling 5099 (EA), Gardner 1377 (K) and 1471 (K), Graham 1003 (K), Granvik 331 (LD), 332 (LD) and 333 (S), Jex-Blake 265 (EA) and 3086 (EA), Nissl s.n. (W), Rotschild exp. s.n. (P), Siegenthaler X40 (EA), Thorold H148/51 (EA), Tweedie 332 (K), Webster AH9660 (EA), Wilkes 0120 (BM), Wiltshire 76 (K), Wimbush 11591 (EA).

3. “Group c” ( = Canarina eminii).

Adamson 454 (EA, G), Andersen 327 (S), Armbruster s.n. (K), Bally 1146 (K), Battiscombe 62 (K), Christiaënsen 820 (BR), David 1266B (EA), Degen s.n. (BM, 2 sheets), Eriksson 030 (S) and 373 (S), Fries 2567 (S, UPS), Gardner 2838 (BM, EA, K), Giordano 812 (FI, 2 sheets), Greenway & Hummel 7284 (EA), Hauman 40 (BR, BRLU), Hedberg 158 (EA, S, UPS), Holm 118 (S), Humbert 7468 (P) and 8818 (P), Humphreys 1207 (BM), Insol 117 (BM), Irwin 6 (K), Jack 498 (EA), Jex-Blake 2125 (EA, K) and 6863 (EA), Kerfoot 155 (EA), K. G. M. 29 (K), Lind 119 (K), Lindblom 23.V.1920 Sv. Bot. Tidskr., 55 (1961): i
Appendix 2.

List of specimens of *Canarina canariensis* used for measurements of pollen diameter and stomatal size. Sometimes more than one sheet was measured of one collection (from different herbaria).

Asplund 756 (S), Børgesen 114 (C), Bornmüller 2625 (LD, S), Bourgeau 171 (BM, E), 1416 (E, UPS), s.n. (BM), Burchard 24 (G), 187 (M), Courant 188 (G), Despréaux 269 (G), Herb. Copenhagen, no collector (C), Herb. Desfont. s.n. (FL), Herb. Webb s.n. (FL), Hort. Edinb. s.n. (FI), Hort. Kewens. 1960 (UPS), Labohm s.n. (WAG), Maude s.n. (BM), Perraudière s.n. (P), Praeger s.n. (K), V. Ruejoly s.n. (FI), Scott s.n. (K), Tretheway s.n. (BM), Tristram 53 (K), Zuccarini s.n. (M, two collections).

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Explanations of the Plates.

Plate I.

Microphotographs of transverse sections through petioles of Canarina canariensis (A), C. abyssinica (B), and C. eminii (C). A was taken from fresh greenhouse material, fixed in chromoacetic formalin, B and C from herbarium specimens. The latter petioles were soaked for a day or two in a mixture of equal parts of concentrated NH₃-solution and water and then thoroughly rinsed before they were (as A) embedded in paraffin, sectioned with microtome, and stained with fuchsine. A comes from Uppsala Bot. Garden (reference sheet, Hedberg 3750, UPS), B from Ambjörn 37 (UPS), and C from Kerfoot 243 (EA). Magnification ×45.

Plate II.

Microphotographs of acetolyzed pollen grains of Canarina canariensis (A–C), C. eminii (D–F), and C. abyssinica (G–I), all ×900. A, D, and G show the surface in polar view; B, E, and H show optical section at the equator; C, F, and I show the surface in equatorial view. The pollen was recovered from the specimens Asplund 644 (UPS; C. canariensis), Adamson 454 (G; C. eminii), and Ambjörn 37 (UPS, C. abyssinica). The photographs were taken by Mr. K. E. Samuelsson, through the courtesy of Prof. O. Selting.

Plate III.

Photograph of the neotype of Canarina abyssinica, Ambjörn 37 (UPS). Magnification ×0.4. Note the coiled peduncle and the closed calyx of the buds.

Plate IV.

Photograph of the neotype of Canarina eminii, Humbert 8818 (P). Magnification ×0.4. This specimen was matched by Humbert to the holotype in Berlin–Dahlem, which has since been lost.

TAXONOMICAL NOTES ON ASCOMYCETES.

BY

LENNART HOLM.

IV. Notes on Nodulosphaeria Rbh.

In the author's thesis (1957) the genus *Nodulosphaeria* Rbh. was treated in some detail and I tried to demonstrate that it is a natural group if amended, referring to it quite a few species earlier placed in the genera *Leptosphaeria* and *Ophiobolus*. Since then I have had the pleasure of making acquaintance with still a number of species of this affinity, which will be described and discussed in this paper. First some general considerations.

*Nodulosphaeria* is for several reasons an interesting genus of Pyrenomycetes, morphologically as well as biologically. A remarkable character in common with many species is the occurrence of setae in the apical pore; no doubt they are a sort of persistent periphyses. The tendency to form such setae is an important generic character. There are, however, examples of "species-pairs", i.e. two closely related species, one of which has bristles and the other not, e.g. *N. gallica*--*N. Volkartii*, and *N. aquilana*--*N. ladina*.

Another interesting feature is the common occurrence of terminal gelatinous spore appendages, which offer excellent diagnostic criteria for the delimitation of species. At first one might feel tempted to attach a still greater taxonomic value to these appendages and to try to divide the genus into sections according to the different types of appendages. That would, however, be unjustified. It is quite evident that certain species, differing in appendages, are nevertheless very closely related. There are several such species-pairs, e.g. *N. Cadubriae* and *N. Epilobii* with semiglobose and cylindric, straight appendages respectively, *N. derasa* and *N. robusta* with bent and straight appendages respectively, and *N. gallica* and *N. Volkartii* with and without semiglobose appendages. It seems probable that the presence of the different appendages is determined by a series of alleles.

Biologically many species of *Nodulosphaeria* afford much of interest because of their pronounced specialisation as to the substratum. A survey is given below of the host-plants for the species known to me:

Plurivorous: *N. modesta*, *N. erythrospora*, *N. Niesslii*, *N. Mathieui*.  
**Compositae variae:** *N. dolioloides*, *N. Cirsii*.  
Buphthalmum salicifolium: *N. seplemcellulata*.  
Centaurea Jacea: *N. Jaceae*, *N. pontica*.  
Centaurea scabiosa: *N. Centaureae*.  
Hieracium spp.: *N. aquilana*.  
Inula salicina: *N. franconica*.  
Senecio: *N. derasa*, *N. robusta*, *N. octoseplata*.  
Succisa pratensis: *N. Succisae*.  
Sambucus Ebulus: *N. megalospora*.  
Ballota nigra: *N. ulnispora*.  
Mentha longifolia: *N. pseudaffinis*.  
Ononis spp.: *N. fruticum*.  
Clematis recta: *N. aucta*.  
Epilobium Dodonaei: *N. Cadubriae*.  
Epilobium Fleischeri: *N. Epilobii*.  
Umbelliferae variae: *N. olivacea (?)*, *N. Volkartii*.  
Laserpitium spp.: *N. gallica*, *N. ladina*, *N. Muelleri*, *N. spectabilis*.  
Tofieldia calyculata: *N. submodesta*.  

The list is probably not complete, but I am convinced that the general picture is fair and the host-plants given are the principal ones. Thus some few species are encountered on members of many families of Angiosperms but the majority are restricted to one family and even to one genus or one species. Several families are represented but it is quite evident that two are the principal ones, viz. **Compositae** and **Umbelliferae**. It is interesting to notice that these families are considered to be relatively very modern ones, and I think that *Nodulosphaeria* is also a modern genus among the Pyrenomycetes. And perhaps it is not a mere coincidence that the sporologically most simple and probably most primitive species, *N. submodesta*, is met with on *Tofieldia*, i.e. a genus considered very primitive among the **Liliaceae**, which is a family generally believed to represent basic monocotyledonous stock.

1. *Nodulosphaeria submodesta* (E. Müller) L. Holm n. comb.


Fig. 1. Ascospores of a, *Nodulosphaeria submodesta*; b, *N. Kümmerlei* (middle spore germinating); c, *N. Cadubriae*; d, *N. pseudaffinis*; e, *N. ?Succisa* (Jaap, F. sel. n. 218); f, *N. spectabilis*; g, *N. aucta*; h, *N. megalospora*, i, *N. olivacea*; j, *N. Muelleri* (to the right two schematic spores, the figures indicating the order of the formation of septa); k, *N. gallica*; l, *N. Volkartii*. – The hyaline appendages are indicated with dotted lines.

– About ×650.
Matr.: *Tofieldia calycilata*; caules sicci.
Exs.: 0.
Fig.: 1a.

Ascocarps often thickly scattered, but as a rule mutually free, at first covered by the epidermis, then erumpent, almost semiglobose, 200–250 μ diam., often somewhat depressed, without papilla but the pore coronated by short, stout, brown bristles, about 30 × 6 μ.

Peridium 15–20 μ, made up of about 4 layers of small, ± rounded cells, usually 7–10 μ, with rather thin, darkly pigmented walls.

Asci numerous, 70–85 × 12–14 μ, clavate, almost non-stipitate, 8-spored.

Spores irregularly biseriate, 22–29 × 4.5–5 μ, fusiform, triseptate, pale olive, with terminal hyaline, semiglobose appendages, about 5 μ diam; 2nd cell somewhat inflated.

As I recently suggested (1957, p. 79), this species also belongs to *Nodulosphaeria*. Due to the courtesy of Dr. MÜLLER, I have had the opportunity of examining type-material which has allowed me to establish that, in fact, it is a most interesting member of the genus. So far, it is the only known *Nodulosphaeria* with 4-celled spores, i.e. as regards spore septation it is the most primitive member of the genus. Also some other features may be considered primitive, e.g. the lack of a papilla.

MÜLLER's original gathering is, as far as I know, the only find hitherto reported. I have found a further sample however, among undetermined collections in S, viz.: Switzerland, Bischofsberg, *T. calycilata*, 22.VI.1884, leg. WEGELIN. Perhaps *N. submodesta* is restricted to *Tofieldia calycilata*, as I have looked for it in vain on *T. pusilla* (= *T. borealis*). *Nodulosphaeria modesta* is common on the latter plant.


This species and its nearest relatives present a real challenge to the taxonomist. Important progress towards a better understanding of the group has recently been made through works by MÜLLER and MUNK, but a fully satisfactory treatment of this group does not seem possible as yet. That will hardly be arrived at without a thorough examination of a large material combined with extensive cultural work—that would be a task for a doctor's dissertation. However I have made a number of observations which may be worth mentioning.

In the *modesta* group, the number of spore septa varies from three
(N. submodesta) to at least eight (N. ladina). 4-septate spores with the formula 1–1–3\(^1\) have been considered characteristic of the typical modesta, at least by most modern authors, but one has generally permitted in this species a certain variation, sometimes designating forms with up to 6-septate spores as modesta (cf. Holm 1957). Perhaps that has been somewhat too liberal.

The type material has constantly 4-septate spores and thus forms with such spores are in the first place entitled to the epithet modesta. Moreover I think that it may be possible and justified to reserve it for such forms only. I have the impression that the forms with five and six spore septa are rather restricted to certain host-plants which may make it possible to treat them as separate taxa. Obviously there are such forms, more or less restricted to Hieracium (N. aquilana) and Succisa (cf. N. Succisae). But even if we refine the definition of N. modesta by including in it only forms with 4-septate spores, this species is by no means a uniform one but still displays a considerable variation. This holds true for, e.g. the size of the spores and the appendages, and the presence of germ pores.

Thus spore length can vary at least between 25 and 42 \(\mu\), which is quite considerable. The type represents a large-spored form, with spores 34–40 \(\times\) 5 \(\mu\), and still larger spores are met with in the type material of Leptosphaeria Bupleuri P. Syd. These large-spored forms are, however, not very common, and possibly more specialized as to host-plants. The most common form has small spores, about 30 \(\times\) 5 \(\mu\), and seems to be very homogeneous, and obviously quite polyphagous.

Still more remarkable is the variation in appendage size, which I find quite surprising. The small-spored form, just mentioned, which could perhaps be referred to as the “normal” form, has in my experience always small cushion-like appendages, about 5 \(\mu\) in diam. Large-spored forms may as a rule have larger appendages, but exceptions occur, as can be illustrated by two collections on umbelliferous hosts, distributed in Lundell & Nannfeldt, Fungi exsiccata suecici (cf. Fig. 2 a, b):

- n. 2197 on Laserpitium latifolium. Spores 34–38 \(\times\) 4.5–5 \(\mu\), appendages about 12 \(\mu\) diam.
- n. 2198 on Peucedanum palustre. Spores 34–38 \(\times\) 4.5–5 \(\mu\), appendages about 5 \(\mu\) diam.

\(^1\) This sort of “spore formula” was introduced by the author (1957, p. 92) in order to briefly state the number of cells above and below the inflated one. Thus, e.g. 2–1–3 means that there are two cells above and three cells below the inflated cell.

Unfortunately these appendages are somewhat troublesome to examine as they are hardly visible except in India ink, for which reason they are impractical as taxonomic characters. In old material they are often in bad condition, as in the type-material of *N. modesta*, where they seem to be 6–8 μ in diam.

Some large-spored forms are also characterized by the fact that the spores have thin-walled terminal areas, which obviously are germ pores. (In *N. spectabilis* the germ pores are of constant occurrence and are marked by a peculiar annular ridge.) Thus they are rather well-developed in, e.g. the type material of *Leptosphaeria Sileris* Bresadola 1926, p. 16, a name which is herewith included in the wide synonymy of *N. modesta*. (Type collection: Italy, Maranza pr. Trento, *Laserpitium Siler*, leg. Bresadola, BPI). *Leptosphaeria Sileris* has, as far as I know, been completely neglected by mycologists, perhaps partly due to its being described in a paper not readily available to the mycological public. It may be worth mentioning that some statements in the diagnosis are fallacious, e.g. "peritheciis ... glabris". On the contrary the fruit bodies have the apical bristles characteristic of the *modesta* group. Furthermore, Bresadola writes: "sporidiis 36–50 = 4–5 mmm., 3–5 septatis, generatim 4 septatis". These figures are somewhat striking, but I cannot confirm them, since I have seen no spores longer than 42 μ or with more or less than 4 septa. The spores have terminal appendages but they are in bad condition. They seem to have been semiglobose, about 6 μ diam. As stated above, there are fairly distinct germ pores, which are marked by traces of the annular ridge, met with in *N. spectabilis*. Bresadola does not mention the germ pores, though his description otherwise is rather suggestive of *N. spectabilis*, and one should perhaps not exclude the possibility that Bresadola had both species under his eyes, when writing his description. In the type material examined by me there is, however, no *spectabilis*.

As to the germ pores, I must point out that I am very much in doubt as to what diagnostic value can generally be attributed to them in *N. modesta*. Several times I have noticed spores with and without germ pores in one and the same preparation. The latter possibly were unripe, but I would not consider it improbable that the presence of germ pores in *modesta* is due to a single Mendelian factor, sorted out at meiosis. If so, the pore has, of course, very little taxonomical significance.

Finally I wish to emphasize that it seems probable that at least...
some of the large-spored forms of _modesta_ are more closely related to _N. aquilana_ and _N. Succisae_ than to the common small-spored _modesta_. It seems highly probable that the two last-mentioned species derive from a large-spored _modesta._


**Coll. orig.:** The Faeröes; Strómö, Langesand, _Succisa pratensis_, 3.VIII. 1938, leg. F. H. Møller.

**Matr.:** _Succisa pratensis_; caules sicci.


**Fig.:** 3e.

This species was described on the basis of the type-collection only, which unfortunately has not been available for study. No further find has been reported. Judging from the description _N. Succisae_ seems to be characterized above all by its spores which are said to be 38–45 × 5–7 μ, and constantly 6-celled in accordance with the formula 1–1–4. Spore appendages are said to be lacking but they may have escaped notice.

In consequence of Munk's interesting report my attention was drawn to _Succisa_ as a host-plant of special interest, and so I have scrutinized the material of _Nodulosphaeria_ on this substratum in S and UPS, and, of course, also looked for the species in nature. The result was rather surprising. Besides a couple of collections, undoubtedly belonging to the ordinary _modesta_, the material in question—listed below—represents a species of its own, which, however, rather annoyingly, does not agree very well with Munk's description. It is a large-spored form too, with spores 38–46 × 6–7 μ, with terminal semiglobose appendages, 6–9 μ in diam., and terminal germ pores, and, what is interesting, a trace of an annular ridge of the type met with in _N. spectabilis_. These details might perhaps be present in typical _N. Succisae_ too. But what does not match that species is the remarkable variation as regards spore septation. Perhaps the most common spore type is 2–1–4, but 1–1–4, 2–1–3, and 1–1–3, are also frequently met with. This variation occurs in one and the same ascocarp and also, at least to some extent, in one and the same ascus. I think this variation has a genetical basis, and that the material is heterokaryotic with regard to the genes for spore septation.
It is still an open question how to denominate this material. I do not feel justified in naming it *N. Succisae*, as that species is expressly stated to have constantly 5-septate spores. Dr. Munk, who has kindly examined the material of Jaap, F. sel. n. 218, shares my hesitation. I think that we cannot settle this question until we have a better knowledge of *N. Succisae* and its range of variation, which will require examination of ample material of the *modesta*-group on *Succisa* from the Faeroes.

**Material examined.** Besides the above-mentioned exsiccata, I have seen the following collections of *N. cfr Succisae*. 


4. **Nodulosphaeria spectabilis** (Niessl) L. Holm n. comb.


**Matr.:** *Laserpitium gallicum, L. latifolium, L. Siler; caules sicci.*

**Exs.:** 0.

**Fig.:** 1f, 2c.

Ascocarps scattered to subgregarious, somewhat innate, mostly 200–300 μ in diameter, 200–300 μ high, ± pyriform, with a distinct papilla, 50–100 μ high and thick; pore with stout brown bristles, about 40 × 5 μ, occasionally with a septum.

Peridium 15–20 μ, made up of about 4 cell-layers; the outer cells ± globose, usually about 10 μ in diam., the inner cells prismatic, up to 15 μ. Cell wall pigmented rather thin. No scleroplechtenychymа.

Asci numerous, cylindric-clavate, 100–125 × 14–17 μ, shortly stipitate, 8-spored.

Spores irregularly bi- to triseriate in the upper part of the asci, uniseriate below, (36–)40–45(–50) × 5–6 μ, fusoid, brownish olive, 4(–5)-septate, multi-guttulate, with terminal germ pores surrounded by an annular border and semiglobose gelatinous appendages, 10–15 μ in diam. 2nd (3rd) cell basally somewhat inflated.

It is surprising that this peculiar species, so characteristic by its unique spore type, was not really distinguished until Müller published his paper of 1953. It is true that Niessl described it earlier but, though otherwise so keen-eyed, he obviously overlooked the annular borders of the spores, as he does not mention them. To judge from the original description *L. spectabilis* seems to be a mere form of *N. modesta* and so it has generally been interpreted. However, examina-

tion of the type material reveals at once the identity with *L. cornuta* Müller, and in consequence, Niesl's epithet takes precedence, though Müller is the spiritual father of the species.

There can be no doubt that *N. spectabilis* is closely allied to the *modesta* group. The peculiar spore type can be easily derived from the spore encountered in such a *modesta* form as is represented by the type specimen of *Leptosphaeria Sileris*.

The finds of *N. spectabilis* are still rather few. In 1953 Müller reported three finds, all from Switzerland and with *Laserpilium Siler*.

as host-plant. In addition to the above-mentioned type collections I can announce five more finds, two of which have been kindly communicated by Dr. Müller:


Coll. orig.: Albania, “Montes Korab, in lapidosis graminosis declivium cacuminis altissimi ad pagum Radomir (alt. ca 2800 m)”, in foliis radicalibus emortuis Campanulae alpinae, leg. Kümmerle (BP!).

Exs.: 0.

Fig.: 1b, 2d.

Ascocarps scattered, immersed in the foliar tissue, pyriform, 100–150 μ in diameter, 150–200 μ high, with a distinct protruding papilla, 50 μ thick, 50–100 μ high, apically passing into some brown rather weak bristles, up to 30 × 5 μ. No bristles in the pore.

Peridium rather poorly developed, of uniform width, about 10 μ, formed of 1–2 layers of rounded cells, about 10 μ, or the interior cells often more elongate, 15 (–20) μ. Cell membrane somewhat thickened and pigmented.

Asci rather few, broadly cylindric, 90–105 × 25–27 μ, almost sessile, 8-spored.

Spores irregularly 2–3-stichous, fusiform, pale olive, 35–45 × 7.5–10.5 μ, 5-septate, with terminal almost globose appendages, 7–9 μ in diam.; the 2nd cell is distinctly inflated.

N. Kümmerlei is known only from the type-collection. It is quite an interesting little fungus which in some respects holds a unique position within Nodulosphaeria. Nevertheless I think that Moesz was quite right when referring it to this genus. The apical bristles and the spore appendages justify placing it here. But the species shows also features alien to Nodulosphaeria, e.g. its being foliicolous. The small number of the asci and the “square-built” spores are more characteristic of Wettsteinina. It would indeed be very interesting if we found here a connection between Nodulosphaeria and Wettsteinina; I hope to have the opportunity of investigating that problem later. Anyhow it is obvious that the species is closely related to Wettsteinina engadinensis E. Müller and I consider it probable that they are conspecific. There are, however, some minor differences, e.g. as regards the appendages. Leptosphaeria morthieriana Sacc. also belongs to the same form group. For the present I have had too

little material available for the study of these forms to enter upon a
discussion of their mutual relations, so I treat here only *N. Kümmerlei*,
which will not require a new combination.


*Leptosphaeria aucta* Niesl. ap. RBH., F. eur. n. 2240 (1877) (=orig.

**Matr.:** *Clematis recta*; caules sicci.

**Exs.:** Crypt. vindob. 619 a, b, (c) — KRieg. F. sax. 1777—LINH., F.
hung. 165 — PETR., F. pol. 424 — RBH., F. eur. 2240 — REHM, ASC.
488 — SYD., Myc. march. 2423.

**Fig.:** 1g.

Ascocarps densely scattered, often covering large areas of the substratum,
subepidermal, ± semiglobose, 200–300 μ diam., with a minute papilla; pore
coronated by coarse, brown bristles, about 30 × 6 μ.

Peridium about 15 μ, composed of about 4 cell layers; outer cells rounded,
about 10 μ wide, somewhat thick-walled; inner cells more prismatic up to
15 μ, thin-walled.

Asci numerous, clavate, 90–105 × 10–12 μ, almost sessile, 8-spored.

Spores ± quadri-septate in the upper part of the ascus, uniseriate below,
cylindric-fusoid, 35–45 × 5–5.5 μ, 6-septate, indistinctly guttulate, with
terminal germ pores and terminal, cushion-shaped hyaline appendages,
about 2 μ diam., the 3rd cell somewhat inflated.

This species is no doubt closely related to *N. aquilana* and its
spore type can easily be derived from *aquilana*’s—we may assume
that the basal cell in the *aquilana*-spore has been divided by a
septum. It should further be noticed that *N. aquilana* also has
terminal germ pores (at least the type-specimen).

*N. aucta* gives a very uniform impression and seems to be re-
stricted to *Clematis recta*. As regards peridial anatomy the species
is hardly distinguishable from *N. aquilana*. BERLESE (Ic. F. I, p. 71)
erroneously identifies the species with *N. spectabilis*.

**Material examined:** 14 collections from Germany, Austria, Czechoslovakia,
Italy, Hungary, Poland, Russia.

7. *Nodulosphaeria Cadubriae* (Speg.) L. Holm n. comb.

*Leptosphaeria Cadubriae* Speg. 1881, p. 55. — Coll. orig.: Italy, Fortogna,
Cadore, *Epilobium Dodonaei*, 17.IX.1879, leg. SPEGAZZINI (LPS!)

**Matr.:** *Epilobium Dodonaei*; caules sicci.

**Exs.:** 0.

**Fig.:** 1c.

Ascocarps scattered, at first covered by the epidermis, then erumpent,
more or less lageniform, 200–300 μ diam., about 300 μ high, with a generally

distinct papilla, up to 75 μ thick and 100 μ high. Pore lined with brown setae, about 40–50 × 4–5 μ.

Peridium rather strongly developed, of varying thickness, 25–50 μ, made up of several layers of rather rounded cells up to 15 μ, most of them with rather thin, not very pigmented walls.

Asci numerous, clavate, 70–110 × 14–15 μ, shortly stipitate, 8-spored.

Spores irregularly quadriseriate in the upper part of the ascus, uniseriate below, cylindric-fusoid, 35–48 × 5–6 μ, olive-brown, without distinct guttules, 8–9-septate, with almost globose terminal appendages, about 7 μ diam. The 4th cell is slightly inflated.

As I pointed out in my dissertation (1957, p. 92) this species is closely akin to *Nodulosphaeria Epilobii* but due to insufficient knowledge I then only mentioned it in passing. Since then, I have seen further material, viz. Austria, Tyrol pr. Waidbruck, *E. ?Dodonaei*, IX. 1907, leg. H. Rehm, sub nom. *Leptosphaeria Cadubriae* (S). This material is in excellent condition and confirms the fact that the two species are nearly related but plainly distinct, and also easily recognized by their spores. They are shorter in *N. Cadubriae*, with fewer septa, and the inflated cell is as a rule the 4th one, while it is the 5th one generally in *N. Epilobii*. Above all, the spore appendages are quite different: almost globose in *N. Cadubriae*, almost cylindrical in *N. Epilobii*. The appendages of *N. Epilobii* are visible in water-mounts, while those of *N. Cadubriae* can only be seen in India ink.


Exs.: RbH., F. eur. 2049.

Fig.: 1h.

Ascocarps ± thickly scattered, subepidermal, lageniform, 150–300 μ diam., about 300 μ high, with a distinct papilla up to 85 μ wide, 150 μ high, terminating in coarse, brown bristles. Pore clothed by bristles, 25–40 × 5 μ.

Peridium 10–15 μ, made up of about 4 layers of cells, 10–15 μ, rounded to prismatic, with rather thin, pigmented walls.

Asci numerous, clavate, 95–120 × 17–20 μ, hardly stipitate, 8-spored.

Spores parallel, 70–80 × 6 μ, 12–14-septate, olive brown, with terminal hyaline, cushion-shaped appendages, about 1.5 μ diam.

The above description is based on the type gathering, which is the only material studied by me. It agrees, however, fairly well with descriptions given by Berlese and Bresadola (1889, p. 35) and *Sv. Bot. Tidskr.*, 55 (1961): 1
Müller (1950, p. 304), founded on Italian and Swiss material, respectively, except for the hyaline appendages which as stated by these authors are almost cylindrical. As regards peridial anatomy the species resembles *N. Mathieui* rather closely, but I think it derives from the vicinity of *N. robusta*.

It is possible that *N. megalospora* is a rare species; anyhow there are only a few statements about it in the literature. Winter reported it (1880, p. 167) from *Achillea* and *Senecio*, due probably to a misidentification. Further Petrak (1940, p. 135) claimed to have found it on *Senecio Fuchsi*ii. Judging from his description, I think that the fungus in question belonged to another species, say *N. robusta*.


**Matr.**: *Carum Carvi, Agastache urticifolia* (fide Wehmer 1946); caules sicci.

**Exs.**: 0.

**Fig.: 1 i.**

Ascocarps thickly scattered beneath the epidermis, ca. 400 μ in diameter, slightly depressed; papilla generally small (to 75 μ high), without bristles, but with distinct periphyses in the pore. Substratum slightly blackened.

Peridium ca. 20 μ wide, formed of 3–4 layers of cells, 7–15 μ, ± globose to elongate. No pseudosclerenchyma.

Asci numerous, clavate, very shortly stipitate, 120–150 × 12–18 μ, 8-spored.

Spores parallel, elongately cylindric-fusoid, pale olive-brown, 70–78 × 5–6 μ, 6-septate, obscurely guttulate, with terminal, hyaline subglobose appendages, about 5 μ diam.; 3rd cell basally inflated.

Ellis’ original description was obviously based on two collections, now preserved in the Herbarium of the New York Botanical Garden, and which I have had the privilege of examining: (1) the one cited above and here proposed as lectotype, and (2) Utah, Pleasant Valley, II.1882, S. J. Harkness no. 95. Both gatherings are on unidentified host-plants. As far as I know this species had fallen more or less into oblivion when Wehmeier published a study of it (1946, p. 238), on the basis of five collections from Wyoming. He quite correctly interpreted Ellis’ description and on the whole I agree with him, though he seems to have overlooked the spore appendages. But I cannot share his opinion that the species is closely akin to *Leptosphaeria Erigerontis* Berl., which is a typical member of *Sv. Bot. Tidskr.*, 55 (1961): 1
Leptosphaeria s. str. There can be no doubt of its being a true Nodulospheria. The spore type could be regarded as a much elongated aucta spore.

Of Wehmeyer's collections, two were on "Umbellifer stems", two on Carum Carvi, and one on Agastache urticifolia. Through the courtesy of Dr. Wehmeyer I have received duplicate material of his no. 1132, on Carum Carvi. It agrees completely with the type material. So far this but little noticed species is known only from Utah and Wyoming. A peculiar statement is made by Berlese, Ic. Fung. II, p. 132. He examined the original collection of our species but did not find it. Instead he found another Pyrenomycete, Ophiobolus ellisianus Berl.

10. Nodulosphaeria Muelleri L. Holm n. sp.

Exs.: 0.
Fig.: 1j.
Matrix: Laserpitium gallocum, L. latifolium, L. Siler; caules sicci.
Ascocarpia sat dense dispersa, sed vulgo non confluentia, subepidermalia, ± pyriformia, (300–)350–450–(500) μ diam., ad 550 μ alta, collo distincto ad 200 μ alto et 150 μ crasso, extus hyphis sparsis brunneis crassis instructo. Substratum saepe paullo nigrifactum.
Peridium fere pari latitudine, 20–30 μ latum, e seriebus nonnullis cellularem parvorum; cellulae externae plus minusve globosae; cellulae internae elongatae, in stratum fibrosum transeuntes. Membrana cellularum tenuis, sed in collo subpseudosclerenchymatico.
Asci numerosi, clavati, distincte pedicellati, 130–140 × 14–15 μ, octo-spori.
Sporae subcylindricae, parallelae, lutescentiae, 75–85 × 5 μ, 6-septatae (an semper?), guttulatae, quaque cellula guttulis 2 instructa, sine appendicibus terminalibus; cellula tertia apice inflata.
Hanc speciem cl. E. Müller, investigatori assiduo mycoflorae Alpium, dedico.

This species comes close to N. olivacea but is plainly distinct, inter alia, due to the lack of spore appendages. Moreover the 3rd cell is apically inflated, while basally in N. olivacea. The differences are small but significant. None of them has bristles in the pore, nor does the papilla protrude into bristles.

N. Muelleri is, so far, only known from the Alps, where Müller has collected it several times; some of his finds have been published (1955, p. 7) sub nom. Ophiobolus olivaceus.

Besides the type-collection, I have seen some other gatherings, listed below. The material, studied by me, looks very uniform.

This species differs from most *Nodulosphaerias* by the enlarged spore cell being apically inflated—as a rule in this genus the cell in question is either uniformly or basally inflated. But otherwise the spores are just true *Nodulosphaeria* spores, as is shown by, e.g. the order of the formation of septa (cf. Fig. 1j). As is apparent, the septa are formed according to the scheme characteristic of the genus, the lower wall of the inflated cell always being the first septum formed (cf. Holm 1957, pp. 78–79). Cf. also *N. Volkartii* and *N. pseudaf fimis*.


11. **Nodulosphaeria Volkartii** (E. Müller) L. Holm & E. Müller n. comb.


**Matr.:** *Chaerophyllum temulum*, *Peucedanum Ostruthium*; caules sicci. (According to Müller 1952, p. 314, also *Adenostyles Alliaria*.)

**Exs.:** 0.

**Fig.:** 1.l.

Asccarps scattered, somewhat immersed, pyriform, 400–500 μ in diam., by 500–600 μ high, with a distinct papilla, 100–120 μ thick, by 100–150 μ high. No apical bristles.

Peridium of rather uniform thickness, about 40 μ, formed of about 8 layers of cells, up to 20 μ; the outer ones more or less globose, with a somewhat thickened and pigmented membrane; the inner ones elongated, hyaline.

Asci numerous, subcylindrical, attenuating into a short pedicel, 175–210 (~240?) × 15–20 μ, 8-spored.

Spores parallel, cylindrical, 135–160 × 5 μ, 7–9-septate, yellowish with obscure guttules and no terminal appendages; a distinct subapical enlargement in the 3rd or 4th cell.

Besides the type material, I have also seen another collection of this species, viz. SWEDEN, Öland, pr. Borgholm, *Chaerophyllum temulum*, 8.VI. 1928, leg. A. G. Eliasson, sine nomine, (S). This Swedish material agrees perfectly with the Swiss type.

12. **Nodulosphaeria gallica** L. Holm n. sp.

**Exs.:** 0.

**Fig.:** 1.k.

**Matrix:** *Laserpitium gallicum*, *L. Siler*; caules sicci.

Ascocarpia sparsa vel laxe gregaria, subepidermalia, pyriformia, 350–450 \( \mu \) diam., (300–)400–500 \( \mu \) alta, collo 100–150 \( \mu \) alto et crasso intus et extus setulis brunneis ad 50 \( \times \) 10 \( \mu \) instructo, praedita.

Peridium fere pari latitudine, 25–30 \( \mu \), e c. 5 seriebus cellularum compositum; cellulae externae saepe minores et plus minusve globosae, cellulae internae prismatice ad 15 \( \mu \). Collum ex pseudosclerenchymate typico compositum.

Asci numerosi, subcylindracei, (160–)200–250 \( \times \) 13–15 \( \mu \), breve stipitati, octospori.

Sporae cylindricae, parallelæ, lutescentiae, 130–200 \( \times \) 5–6 \( \mu \), 8–10-septatae, appendicibus terminalibus gelatinosis, semiglobosis, 4–6 \( \mu \) diam. instructæ, multiguttulatae, quaque cellula guttulis 2 distinctis et nonnullis indistinctis instructa; una cellula (plerumque quarta) apice inflata.


This species is, of course, closely akin to *N. Volkartii* but there are some differences which I think justify its recognition as a separate taxon. Thus the fruit bodies are provided with apical bristles (lacking in *N. Volkartii*) and further more we can find some minute but I think important spore characters: the spores have terminal appendages and distinct guttules, and last but not least, the 4th cell is inflated just below the apical septum, whereas this swelling is sub-apical in *N. Volkartii*.

*N. gallica* is hitherto known only from the French Alps, thanks to some collections by MÜLLER. Besides the type-gathering I have studied the following material:


13. **Nodulosphaeria pseudaffinis** (PETR.) L. HOLM n. comb.


**Matr.:** *Mentha longifolia*; caules sicci.

**Exs.:** 0.

**Fig.:** 1d.

Ascocarps scattered, subepidermal, rather flattened, 200–350 \( \mu \) in diam., 200–250 \( \mu \) high, with a distinct, often somewhat eccentric papilla, up to 100 \( \mu \) high and wide. No bristles.

Peridium 15–20 \( \mu \) wide, made up of 3–4 layers of cells; the exterior ones about 10 \( \mu \), ± globose, the interior ones up to 15 \( \mu \), hyaline, with somewhat thickened and pigmented walls.

Asci numerous, almost cylindrical, 110–135 × 8–9 μ, attenuating into a short pedicell, 8-spored.

Spores parallel, cylindrical, 90–105 × 3–3.5 μ, yellowish with obscure guttules and several (about 10) more or less obscure septa; the 3rd or 4th cell is apically somewhat inflated.

The proper place of this little known species no doubt is in the vicinity of *N. Mathieui*, and in fact the two species agree in most respects. We can distinguish them on the spores, however. Both species have one inflated spore cell, or more exactly, one cell has an inflation. In *N. pseudaffinis* this inflation is subapical, just below the upper wall of the cell in question, whereas it is in the middle of the cell in *N. Mathieui*. The difference is minute but I think it is sufficient to keep them separate, and is a reliable taxonomic character, cf. the couple *N. olivacea*–*N. Muelleri*, and *N. Volkartii*–*N. gallica*. Petrar overlooked this important character, stating in his diagnosis that the spores were “ohne vorspringende Knotenzelle”.

It is reasonable to assume that this species is identical with *Ophiobolus affinis* (Sacc.) Sacc., reported on *Mentha rotundifolia*, and Petrar himself suggests this possibility. Due to the courtesy of Dr. C. Cappelletti of Padova, I have had the opportunity of examining the type collection of *O. affinis* (France, on stems of *Mentha rotundifolia*, leg. Brunaud). This material is in rather bad condition and hardly permits an accurate determination. However, I am pretty sure that it is not *N. pseudaffinis*, but rather *N. Mathieui*.

It is quite striking that the material of *N. pseudaffinis*, which I have seen is heavily infested by *Didymosphaeria conoidea* Niessl, a parasite often encountered also in *N. Mathieui*.

Besides the typematerial I have seen three collections of this species, viz.


**Acknowledgements.**

The present study is based primarily on the material in the Herbaria of Stockholm (S) and Uppsala (UPS). Furthermore I have had the privilege of studying a number of specimens obtained on loan from the Herbaria of Budapest (BP), Beltsville (BPI), La Plata (LPS), Munich (M), New York

(NY), Padova (PAD), Paris (PC) and Zürich (ZT). My sincere thanks are due to the directors of these Institutes. The reader will notice my obligation to Dr. Emil Müller, in Zürich, for his pioneer work and unstinted helpfulness in placing his material at my disposal.

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NOTES ON THE AFRICAN SPECIES OF TRIGLOCHIN.

BY

HENNING HORN AF RANTZIEN (†).

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Introduction.

The scope of this paper is primarily to describe and discuss a new African species of Triglochin and to compare this with the other African bulbiferous representative, T. bulbosum. The three non-bulbiferous species are discussed in considerably less detail. Two among them (T. palustre, T. striatum) are well known, and study of a representative material did not furnish any new facts of interest in this connection. A third species (T. elongatum) cannot be discussed in the same detail as the bulbiferous because of fragmentary information about its characteristics and variation.
The investigation is based on material from the herbaria of Kew and Stockholm. It would certainly have been profitable to include further collections, but the time available did not permit revision of the whole extensive material of African *Triglochin* species. It follows from the above that this is not intended as a general revision of the African species.

The investigation was temporarily finished at the end of 1952. In 1959 this study was taken up again in the writer's spare time. Specimens recently collected were included. The manuscript was entirely rearranged and new illustrations prepared.

When collecting in Northern Rhodesia in 1937–1938, Mr. E. Milne-Redhead, Royal Botanic Gardens, Kew, found a bulbiferous *Triglochin*, which differed from the common *T. bulbosum* in its flowers and fruits. When he returned to Kew, Mr. Milne-Redhead made a search for similar plants among the material available of *T. bulbosum* and found such specimens from Southern Rhodesia, Tanganyika, Angola, and Natal. In the spring of 1952 the present writer was asked to study the material and to describe the plant if it proved distinct.

In order to study the differences between this new species of *Triglochin*, and those previously known, it was necessary to investigate flowers and fruits of all African species in detail, especially in respect of the variation of certain characters.

As indicated above, there are five African species of *Triglochin* (*T. milnei* n.sp., *T. bulbosum*, *T. palustre*, *T. striatum*, and *T. elongatum*). *T. bulbosum*, a variable and widely distributed species, is divided into five subspecies (*bulbosum*, *tenuifolium*, *barrelieri*, *maurum*, and *laxiflorum*). Some South African specimens were impossible to refer for the present to the species previously known. They may be two further *species novae* or may represent aberrant forms of other species. Only about five specimens were available of each form, and this material is decidedly too small for specific descriptions in such a variable group as *Triglochin*. These plants are briefly discussed under the designations *Species A* and *B* at the end of this paper.

*Triglochin* is of considerable interest from the view of phytogeography. This matter cannot be dealt with here to any large extent but some brief notes seem to be justified because of the absence of previous analyses of the areal patterns. Judging by their actual distribution, the Scheuchzeriaceae (taken in the same broad sense as that of Wettstein 1935, pp. 974–975; cf. also Lawrence 1951, *Sv. Bot. Tidskr.*, 55 (1961) : 1.
NOTES ON THE AFRICAN SPECIES OF TRIGLOCHIN

pp. 379–380) are of Antarctic origin. From a former primary centre of distribution they spread to other parts of the southern hemisphere, where there are three present centres (about fifteen species in the Australian temperate region, five in extratropical South America, four in South Africa). Some species apparently migrated northwards from these austral centres to the northern hemisphere, probably along the mountain ranges. Within the secondary distribution area developed in the north, there are three species of wide distribution and some others of local range. Since no Pre-Quaternary occurrences of the Scheuchzeriaceae are known (Gothan & Weyland 1954, p. 365) this interpretation is exclusively based on analysis of the actual ranges of the respective genera and species. These general features of distribution, the same as those displayed in a more manifest way, for instance by the Droseraceae, can be traced also in the ranges of the African species of Triglochin. Only T. palustre and three subspecies of T. bulbosum occur in the northwestern part of the continent and thus belong to the secondary, northern distribution area. The remaining species and subspecies are exclusively South African (Cape, Natal) except T. milnei n.sp., which extends into the Tropical African Flora. The last-mentioned species accordingly occupies an unusual position in respect of its distributional pattern.

All measurements relative to floral and fructificational morphology refer to material originally preserved in liquids or to dry material which was soaked in water before investigation.

Acknowledgements.

This investigation was carried out at the Botanical Department, Riksmuseum, Stockholm. To the Director of this Department, Prof. E. Hultén, I wish to extend my cordial thanks for help, interest, and encouragement. I am also much obliged to Dr. G. Taylor, Director of the Royal Botanic Gardens, Kew, for the loan of a representative material of the T. bulbosum group. My cordial thanks moreover go to Mr. E. Milne-Redhead of Kew for kindly asking me to study this interesting material and for permitting me to describe it.

The present study was financially supported by a grant from Stockholm University relative to doctoral theses. For this great favour I tender my respectful thanks.

Key to the African species of Triglochin.

African species of Triglochin are very variable, and the diagnostic characters are not especially well suited to a dichotomous key like

the present. Aberrant specimens are not rare. They may be difficult to determine, particularly if underground parts are lacking in the herbarium material. In South African specimens of *T. bulbosum* about 40% are transitional between subspecies, in North African 20–30%.


2. Flowers as a rule less than 3 mm long. Tepals of outer cycle less than 2½ mm long. Fruits with strong walls, not easily compressed, linear to narrowly lanceolate, less than 2 mm broad. — A variable species represented by five subspecies. *T. bulbosum*

3. Flowers averaging 2 mm in length. Anthers of outer cycle circular to reniform. Fruits linear, slightly or not at all tapering towards apex. Follicles rarely keeled dorsally, with tips as a rule slightly recurved. — South African subspecies.

4. Plant large or medium-sized, 20–50 cm high. Fruits approximately 10 mm long and 1 mm broad, on pedicels shorter than the fruits. — Cape, Natal; marshes. *T. bulbosum* ssp. *bulbosum*

5. Fruits averaging 6 mm in length, pedicels short (2–4 mm). — Libya, Algeria; Mediterranean of Europe and Asia. *T. bulbosum* ssp. *barrelieri*

6. Fruits averaging 10 mm in length, pedicels comparatively long (3–7 mm). — Morocco; transitions to ssp. *barrelieri* in Algeria. *T. bulbosum* ssp. *maurum*


2. Flowers large, 2½–5 mm long. Tepals of outer cycle 2½–4 mm long. Anthers of outer cycle 1½–3 mm long, broadly ovoid to circular. Fruits broadly lanceolate to ovate, 7½–13 mm long, 2–4½ mm broad, distinctly

NOTES ON THE AFRICAN SPECIES OF TRIGLOCHIN

Triglochini milnei n. sp.

1. Species with slender rhizomes. Bases of stems not surrounded by dense layers of fibrous sheaths.

2. Rhizome with thin, weak stolons, the apices of which are incressate and form small, hibernating bulbs. Fruits linear, pressed to stem when mature. Follicles smooth dorsally, their tips parallel, erect. — Morocco, at high altitudes; northern hemisphere; South America. *T. palustre*

3. Fruits globular to lanceolate; when lanceolate, tips of follicles distinctly recurved. Follicles keeled dorsally.

3. Fruits lanceolate, 6–9 mm long. Pedicels more than 3 mm long, their upper parts parallel to the stem. Tips of follicles comparatively long, distinctly reflexed. — Cape, (?) Natal. *T. elongatum*

Descriptions and discussions of the African species.


Derivation of specific name. — Named for Mr. E. Milne-Redhead, Royal Botanic Gardens, Kew, Great Britain.


Holotypus Milne-Redhead 3012, vide infra.

*Plant* perennial, bulbiferous, slender. *Bulbi* single or few, surrounded by dense layers of the strongly fibrous leaf-bases. *Stem* terete, exceeding the leaves, bearing a many-flowered spike. *Upper leaves* linear, slightly flattened,

ventrally canaliculate, with a short sheathing part. Lower leaves linear, flat, keeled, with a comparatively long sheathing part and a shorter laminar one. Flowers 2½–5 mm long, diameter of the perianth 2–5 mm, pedicels up to 3 mm long. Outer tepals 2½–4 mm long, 1½–2½ mm broad, conchiform, ovate, apex as a rule broadly acute. Inner tepals conchiform. Outer anthers ovoid, flattened, 1½–3 mm long, 1½–2½ mm broad, approximately 1 mm thick. Inner anthers broadly ovoid, flattened. Fruits 7½–13 mm long, 2½–4½ mm broad, broadly lanceolate to narrowly ovate, strongly tapering upwards, composed of three sterile and three fertile follicles, and with the walls thin and delicate, hence easily compressed. Fertile follicles lanceolate, tapering towards the tips which are distinctly recurved, narrowly triangular to circular in cross-section, lateral side 1½–2 mm broad, dorsal side about 1 mm broad, keeled along their whole length. Pedicels of the fruits 2–5 mm long, directed somewhat irregularly obliquely upwards from the stem, not pressed to it, nor patent.

Holotype: Milne-Redhead 3012, see below.

Differential diagnosis. — Differs from all subspecies of its nearest ally, T. bulbosum, by flowers as a rule more than 3 mm long, tepals of outer cycle more than 2½ mm long, by fruits thin-walled, not easily compressed, broadly lanceolate to narrowly ovate, and more than 2 mm broad; differs from South African subspecies of T. bulbosum moreover in fruits distinctly tapering towards the apices, and follicles dorsally strongly keeled with tips distinctly recurved; differs from the remaining African Triglochin species by the subterranean parts forming bulbs. See moreover under Affinities (p. 101).

Holotype. — Milne-Redhead 3012 (holotype in K, isotype in S).

Type locality. — Northern Rhodesia: Mwinilunga District, half a mile south of Matonchi farm, c. 1350 m. alt., in shallow, peaty moist soil on "laterite" in open, Oct. 30, 1937, fl.


Fig. 1. Triglochin milnei n.sp. Left-hand specimen: Milne-Redhead 3012, Northern Rhodesia, Mwinilunga District, Matonchi (isotype, S). Right-hand specimen: Milne-Redhead 3693, same locality (paratype and locotype, S). Both figures 2½. Photo K. E. Samuelsson.

Notes on the African Species of Triglochin


Occurrence. — Tanganyika, Angola, Northern Rhodesia, Southern Rhodesia, Natal.

Description of holotype. — Plant 20—30 cm high, perennial, slender, bulbiferous. Bulbs single or few (1—3), surrounded by dense layers of the brownish, strongly fibrous leaf-bases. Stem 15—25 cm high, \( \frac{1}{2}—1 \text{ mm in diam.} \), terete, exceeding the leaves, bearing 10—15 comparatively large flowers. Upper leaves 5—25 cm long, less than \( \frac{1}{2}—1 \text{ mm in diam.} \), slightly flattened, ventrally canaliculate. Lower leaves 3—8 cm long, 4—6 mm broad, flat, keeled, with a comparatively long sheathing part and a shorter laminar one. Flowers green (perianth and styles tinged mauve in life), comparatively large, 3—4 mm long, diameter of the perianth 4—4.5 mm, pedicels of the young flowers very short or failing, of the mature ones growing up to 3 mm long. Outer tepals 3—4 mm long, 2—2.5 mm broad, conchiform, ovate, with a cuculate, broadly acute apex. Inner tepals 2—2.5 mm long, 1.5—2 mm broad, conchiform, more rounded than the outer, apex erect, semitubular with the upper margin irregularly dentate or shortly fimbriate. Outer anthers sessile, 2-locular, ovoid, flattened, 2—3 mm long, 1.5—2 mm broad, approximately 1 mm thick. Inner anthers sessile, 2-locular, broadly ovoid, flattened, 1—1.5 mm long, 1 or slightly more than 1 mm broad, up to 3 mm thick. Pollen spherical, nonaperturate, reticulate, 24—28 \( \mu \) in diam. Gynaecium of mature flowers approximately 2.5 mm long, provided with three free styles, spreading, recurved. Fruits absent.

Supplementary description of fruits of the paratype and locotype Milne-Redhead 3693:

Fruits yellowish green (in life), 11—12 mm long, 2—3 mm broad, broadly lanceolate, distinctly tapering towards the apices, composed of three sterile and three fertile follicles, and with the walls thin and delicate, hence easily compressed. Sterile follicles much reduced, acicular. Fertile follicles lanceolate, tapering towards the tip which is distinctly recurved, narrowly triangular in cross-section, lateral side 1.5—2 mm broad, dorsal side approximately 1 mm broad, keeled along their whole length, the keel as prominent apically as basally. Pedicels of the fruits 2—5 mm long, directed somewhat irregularly obliquely upwards as compared with the stem, not pressed to it, nor taking a straight angle to it, nor patent.

Variation. — The variation in a number of characters of the specimens examined are illustrated by the Tables I—IV to which reference is made for details.

Fig. 2. Triglochin milrtei n.sp. Bullock 2364, Tanganyika, Ufipa District, Sumbawanga (paratype, S). 2/1. Photo K. E. Samuelsson.

The biggest specimens seen are those in the two collections from Angola (Gossweiler s.num., Welwitsch 3017) and moreover Robinson 969 and Eyles 4587. These plants average 45 cm in height; they are also characterized by strong stems (up to 3 mm thick) and leaves (upper leaves up to 2 mm broad). As to their heights most other paratypes are intermediate between the holotype and the specimens now described. The holotype and, among the paratypes, Richards 2310 and 2312, Wild 2260, being 15–30 cm high, are small as compared with the others.

The number of flowers and fruits, respectively, per stem (10–15 in holotype) varies between rather wide limits in the others but is probably correlated in some extent to the general size. Thus big specimens (Welwitsch 3017, Eyles 4587) tend to bear more flowers, up to 24 and 31, respectively, than the medium-sized (Bullock 2354: 5–11, Rudatis 440: 17–23) and small plants (e.g. Wild 2260: 8–12).

The holotype is characterized by well-developed bulbs, surrounded by dense and strong, fibrous sheaths, blackish or brownish in colour. As a rule there are two or more bulbs under each plant. The bulbs are still stronger in Wild 2260. The specimens Welwitsch 3017 and Eyles 4587 agree with the holotype as to their underground parts. In some specimens, for instance Bullock 2364, Gossweiler s.num., and Milne–Redhead 3693 only single bulbs were observed. The last-mentioned specimens are locotypes. The fact that they differ from the holotype and isotypes in the number of bulbs seems noteworthy. Some specimens of Bullock 2364 are characterized by weakly developed bulbs and enveloping sheaths, superficially these do not differ very much from thick rhizomes.

The lengths of the flowers in the paratype collections range from $2\frac{1}{2}–4$ mm (Eyles 4587), $3–4$ mm (Gossweiler s. num., Richards 2312), $3\frac{1}{2}–5$ mm (Wild 2260, King 403) to $4–5$ mm (Bullock 2354, Welwitsch 3017, Rudatis 440, Robinson 969, Milne–Redhead & Taylor 7934). The unusually small flowers of Eyles 4587 seem to be immature. The transversal diameter of the perianth varies in relation to the flower length from 2 to 5 mm. Also other floral measurements vary proportionally to the flower length. The lengths of the outer tepals range from $2\frac{1}{2}$ to 4 mm, and their widths from $1\frac{1}{2}$ to $2\frac{1}{2}$ mm. Corresponding figures for the inner tepals are $1\frac{1}{2}–2\frac{1}{2}$ mm and $1\frac{1}{2}–3$ mm, respectively. In all these respects the paratypes agree well with the holotype. The outer anthers show a more noticeable variation. In the holotype these are $2\frac{1}{2}–3$ mm long and $1\frac{1}{2}–2$ mm broad, the ratio $100 \times$ anther length/anther width being 150. In the paratypes the lengths of the outer anthers vary from $1\frac{1}{2}$ mm (Bullock 2354, Richards 2312, Robinson 969) to $2\frac{1}{2}$ mm (Rudatis 440), whereas the widths range from $1\frac{1}{2}$ mm (Eyles 4587) to $2\frac{1}{2}$ mm (Rudatis 440). The ratio mentioned above varies a great deal: 133 (Welwitsch 3017, Eyles 4587, Wild 2260, King 403), 100 (Gossweiler s.num., Rudatis 440, Richards 2312, Robinson 969, Milne–Redhead & Taylor 7934), and 75 (Bullock 2354). Conformably with this varying ratio, the anthers vary from subreniform to

![Fig. 3. Triglochin milnei n. sp. Milne–Redhead & Taylor 7934, Tanganyika, Songea District, Songea (paratype, S). 2/1. Photo K. E. Samuelsson. Sv. Bot. Tidskr., 55 (1961): 1](image-url)
Fig. 4. *Triglochin milnei* n.sp. Milne-Redhead 3012, Northern Rhodesia, Mwinilunga District, Matonchi (holotype, K). a, Outer tepal, adaxial view. b, Outer tepal, lateral view. c, Outer anther, adaxial view. d, Outer anther, abaxial view. e, Inner tepal, adaxial view. f, Inner tepal, lateral view. g, Inner anther, abaxial view. h, Inner anther, adaxial view. All figures 7/1.

ovate. In most paratypes the inner anthers are weakly developed to rudimentary; in Gossweiler s.num. the best developed ones are slightly less than $1\frac{1}{2}$ mm long to slightly less than 1 mm broad, in Robinson 969 slightly more than 1 mm long and broad, and in Rudatis 440, Richards 2312, and Milne-Redhead & Taylor 7934 they are approximately $1\frac{1}{2}$ mm long and 1$\frac{1}{2}$ mm broad.

The outer tepals are of rather uniform shape, being ovate and more or less distinctly conchiform. In the specimens Welwitsch 3017 and Gossweiler s.num. they are more shallowly conchiform than in the others. In the holotype (and in Rudatis 440) the apices of the outer tepals are

NOTES ON THE AFRICAN SPECIES OF TRIGLOCHIN

Fig. 5. *Triglochin milnei* n. sp. MILNE-REDHEAD & TAYLOR 7934, Tanganyika, Songea District, Songea (paratype, S). Complete, normally developed flower, lateral view. 12/1.

cucullate and broadly acute, in other paratypes they are erect (BULLOCK 2354, WELWITSCH 3017, EYLES 4587, GOSSWEILER s. num., MILNE-REDHEAD & TAYLOR 7934, RICHARDS 2312, ROBINSON 969), more or less rounded (WILD 2260, KING 403), or blunt to slightly semitubular (EYLES 4587, GOSSWEILER s. num.). In BULLOCK 2354 the apices of the outer tepals are erect and broadly acute. Considerable variation was observed in the three outer tepals of one flower of GOSSWEILER s. num. with the erect apices broadly acute, blunt, and semitubular, respectively. The inner tepals were observed in only few flowers. They correspond to those of the holotype and show the same characteristic strong dentation of the upper margin. The outer anthers were flattened in all cases observed, but otherwise vary in shape. In the holotype and some paratypes they are ovate, others are broadly ovate to circular. In BULLOCK 2354 the outer anthers are subreniform with the width larger than the length. Also in this respect some variation in one and the same flower was observed. Thus in WELWITSCH 3017 anthers of the same flower vary from ovate to circular, and in EYLES 4587 from ovate to broadly ovate. The inner anthers were only rarely observed. These vary from ovate to circular but generally are more rounded than the outer. The gynaecium exhibits some variation as to length but it is in other respects of uniform appearance. The free, somewhat recurved styles constitute one of the most important characters of this species.

Abortion of parts of flowers seems to be more common in *T. milnei* than in any other species of *Triglochin*. Rudimentary development or abortion of various floral members was reported previously for the Scheuchzeriaceae (BUCHENAU 1882, p. 495, 1903, p. 5; SAUNDERS 1939, p. 537) and was especially observed in *Scheuchzeria palustris*. Flowers of *Triglochin* are composed by six trimerous cycles, the two outer forming the perigon, the two next the androecium in the axes of the tepals, and the two innermost the gynaecium. The outer gynaecium cycle is regularly sterile in *Triglochin*. In *T. milnei* tendencies to irregular development were observed in the inner perigon

cycle, in the inner androecium cycle, and, rarely in the inner gynaecium cycle. No abortion or rudimentation was observed in the three flowers from different specimens examined of the holotype collection or in the paratypes Rudatis 440, Richards 2312, and Milne-Redhead & Taylor 7934. The other paratypes showed irregular floral development to various extents. This appears from Table III, to which reference is made for details. In the single flower examined of Bullock 2364 there was no inner perigon or inner anthers, but the flower appeared normal in other respects. Wild 2260 exhibited some low protuberances on the place of the inner androecium and inner perigon, but it could not be decided in this mature floral stage which among these cycles the respective protuberances represented. The two flowers dissected of Eyles 4587 lacked the inner androecium and the inner perigon; in one protuberances were found similar to those observed in Wild 2260. In the flower of Eyles 4587 provided with protuberances one of the three fertile carpels was moreover abnormally developed as a small acicular object, fairly similar to the sterile carpels. The single flower examined of Gossweiler s.num. was normal apart from one inner gynaecial member being rudimentary. The latter was unlike the rudimentary carpel of Eyles 4587, being as thick as the cycle mates but only half their length. It may have been sterile. In one flower of Welwitsch 3017, the inner perigon and the inner androecium were reduced to a row of low and inconspicuous protuberances; in another flower of the same collection, the inner perigon was represented by three lanceolate scales, only about \( \frac{1}{3} \) mm long.

Though the present material is much too small for illustrating the general extent of partial floral abortion or rudimentation in *T. milnei*, the examples *Su. Bot. Tidskr.*, 55 (1961) : 1
NOTES ON THE AFRICAN SPECIES OF TRIGLOCHIN

Table I. Variation in 14 collections of *Triglochin milnei* n.sp.: stem and leaves.

<table>
<thead>
<tr>
<th></th>
<th>Plant</th>
<th>Stem</th>
<th>Lower leaves</th>
<th>Upper leaves</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Height, mm</td>
<td>Diam., mm</td>
<td>Length, mm</td>
<td>Width, mm</td>
</tr>
<tr>
<td><strong>Holotype and isotypes</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Milne-Redhead 3012</td>
<td>200-300</td>
<td>1-1</td>
<td>30-80</td>
<td>6-6</td>
</tr>
<tr>
<td><strong>Paratypes</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bullock 2364</td>
<td>250-350</td>
<td>1-1$\frac{1}{2}$</td>
<td>45-55</td>
<td>3-6$\frac{1}{2}$</td>
</tr>
<tr>
<td>Eyles 4587</td>
<td>450</td>
<td>2$\frac{1}{2}$</td>
<td>30-55</td>
<td>4$\frac{3}{4}$-7</td>
</tr>
<tr>
<td>Gossweiler s.num.</td>
<td>450</td>
<td>3</td>
<td>40-50</td>
<td>2-4</td>
</tr>
<tr>
<td>King 403</td>
<td>200-400</td>
<td>1-1$\frac{1}{2}$</td>
<td>35-50</td>
<td>3-5</td>
</tr>
<tr>
<td>Milne-Redhead 3693</td>
<td>200-300</td>
<td>1-1$\frac{1}{2}$</td>
<td>30-40</td>
<td>3$\frac{1}{4}$-4$\frac{1}{2}$</td>
</tr>
<tr>
<td>Milne-Redhead &amp; Taylor 7934</td>
<td>300-500</td>
<td>1-2$\frac{1}{2}$</td>
<td>35-65</td>
<td>2$\frac{3}{4}$-4$\frac{1}{2}$</td>
</tr>
<tr>
<td>Richards 2310</td>
<td>150-200</td>
<td>1$\frac{1}{2}$</td>
<td>30-40</td>
<td>3$\frac{1}{4}$-5</td>
</tr>
<tr>
<td>Richards 2312</td>
<td>150-250</td>
<td>1-1</td>
<td>50-65</td>
<td>3-4</td>
</tr>
<tr>
<td>Robinson 969</td>
<td>350-500</td>
<td>2-2$\frac{1}{2}$</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Robinson 2730</td>
<td>300-400</td>
<td>1$\frac{1}{4}$-2</td>
<td>45-50</td>
<td>3$\frac{1}{2}$</td>
</tr>
<tr>
<td>Rudatis 440</td>
<td>300-400</td>
<td>1-1$\frac{1}{2}$</td>
<td>35-50</td>
<td>2$\frac{1}{4}$-3$\frac{1}{2}$</td>
</tr>
<tr>
<td>Welwitsch 3017</td>
<td>450</td>
<td>3</td>
<td>40-50</td>
<td>2-4$\frac{1}{2}$</td>
</tr>
<tr>
<td>Wild 2280</td>
<td>200-300</td>
<td>1-1$\frac{1}{2}$</td>
<td>35-40</td>
<td>3$\frac{1}{4}$-4$\frac{1}{2}$</td>
</tr>
<tr>
<td><strong>Range</strong></td>
<td>150-500</td>
<td>1$\frac{1}{4}$</td>
<td>30-80</td>
<td>2-7</td>
</tr>
<tr>
<td><strong>Accuracy of measurements</strong></td>
<td>50</td>
<td>$\frac{1}{4}$</td>
<td>5</td>
<td>$\frac{1}{4}$</td>
</tr>
</tbody>
</table>

quoted from Table III certainly indicate that there are considerable such tendencies in this species. Nothing comparable is known from other *Triglochin* species. It should be admitted, however, that few if any similar investigations on *Triglochin* species have been carried out (cf., though, Hill 1900, p. 83 for *T. maritimum*; Buchenau 1882, pp. 494 foll. for *T. striatum* var. *montevidensis*; Saunders 1939, p. 537, and some further papers quoted there, for *T. martitium*, *T. palustre*, *T. bulbosum* ssp. *barrelieri*, and *T. "montevidense"*).

The fruits show less variation than the flowers. Mature fruits are lacking in the holotype. Fruits considered typical of *T. milnei* occur in the locotype *Milne-Redhead* 3693. The latter are broadly lanceolate, considerably tapering upwards with the follicular tips free and distinctly spreading. They are 11-12 mm long and 2-3 mm broad. A slightly different shape of the fruit was observed in Bullock 2364, being shorter (8-10 mm) and broader (3-4 mm) and more ovate than lanceolate. In the same collection there are also fruits which are transitional to those of *Milne-Redhead* 3693. The broadest fruits met with occur in Robinson 2730 (up to 4$\frac{1}{2}$ mm broad).
Table II. Variation in 11 collections

<table>
<thead>
<tr>
<th>Flowers</th>
<th>Outer tepals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length, mm</td>
<td>Width, mm</td>
</tr>
<tr>
<td>Holotype and isotype</td>
<td></td>
</tr>
<tr>
<td>Paratypes</td>
<td></td>
</tr>
<tr>
<td>Bullock 2364</td>
<td>4–5</td>
</tr>
<tr>
<td>Eyles 4587</td>
<td>2½–4</td>
</tr>
<tr>
<td>Gossweiler s.num.</td>
<td>3–4</td>
</tr>
<tr>
<td>King 403</td>
<td>4</td>
</tr>
<tr>
<td>Milne-Redhead &amp; Taylor 7934</td>
<td>5</td>
</tr>
<tr>
<td>Richards 2312</td>
<td>3½</td>
</tr>
<tr>
<td>Robinson 969</td>
<td>4½</td>
</tr>
<tr>
<td>Rudatis 440</td>
<td>4–5</td>
</tr>
<tr>
<td>Welwitsch 3017</td>
<td>4–5</td>
</tr>
<tr>
<td>Wild 2260</td>
<td>3½–5</td>
</tr>
<tr>
<td>Range</td>
<td>2½–5</td>
</tr>
</tbody>
</table>

Accuracy of measurements

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of *Triglochin milnei* n.sp.: flowers.

<table>
<thead>
<tr>
<th>Inner tepals</th>
<th>Outer anthers</th>
<th>Inner anthers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length, mm</td>
<td>Width, mm</td>
<td>Length, mm</td>
</tr>
<tr>
<td>2–2½</td>
<td>1½–2</td>
<td>2½–3</td>
</tr>
<tr>
<td>—</td>
<td>—</td>
<td>1½–2</td>
</tr>
<tr>
<td>2</td>
<td>2½</td>
<td>2½–3</td>
</tr>
<tr>
<td>1½</td>
<td>1½</td>
<td>1½–2</td>
</tr>
<tr>
<td>2</td>
<td>1½</td>
<td>2½–3</td>
</tr>
<tr>
<td>2</td>
<td>1½</td>
<td>1½–2</td>
</tr>
<tr>
<td>2</td>
<td>1½</td>
<td>1½–2</td>
</tr>
<tr>
<td>2½</td>
<td>3</td>
<td>2½–3</td>
</tr>
<tr>
<td>—</td>
<td>—</td>
<td>2½–3</td>
</tr>
<tr>
<td>1½–2½</td>
<td>1½–3</td>
<td>1½–2½</td>
</tr>
</tbody>
</table>

*7 – 61173301*  
Table III. Observations on irregular morphology in 15 flowers of *Triglochin milnei* n.sp.

The flowers listed below were chosen at random from the material available and examined with an ordinary dissecting lens. In most collections time permitted only one flower to be examined for morphological irregularities. The data cannot hence be expected to give an adequate expression of the frequency and distribution of such irregularities in *T. milnei*.

<table>
<thead>
<tr>
<th>Holotype and isotypes</th>
<th>Outer perigon cycle</th>
<th>Inner perigon cycle</th>
<th>Outer androecium cycle</th>
<th>Inner androecium cycle</th>
<th>Outer gynaecium cycle</th>
<th>Inner gynaecium cycle</th>
</tr>
</thead>
<tbody>
<tr>
<td>Milne-Redhead 3012</td>
<td>Normal</td>
<td>Normal</td>
<td>Normal</td>
<td>Normal</td>
<td>All members sterile</td>
<td>Normal</td>
</tr>
<tr>
<td>Flower A</td>
<td>Normal</td>
<td>Normal</td>
<td>Normal</td>
<td>Normal</td>
<td>All members sterile</td>
<td>Normal</td>
</tr>
<tr>
<td>Flower B</td>
<td>Normal</td>
<td>Normal</td>
<td>Normal</td>
<td>Normal</td>
<td>All members sterile</td>
<td>Normal</td>
</tr>
<tr>
<td>Flower C</td>
<td>Normal</td>
<td>Normal</td>
<td>Normal</td>
<td>Normal</td>
<td>All members sterile</td>
<td>Normal</td>
</tr>
</tbody>
</table>

Paratypes

| Bullock 2364          | Normal              | All members abortive | Normal                 | All members abortive | All members sterile    | Normal                 |
| Eyles 4587            | Normal              | All members abortive or rudimentary | Normal                 | All members abortive or rudimentary | All members sterile    | Normal                 |
| Flower A              | Normal              | All members abortive or rudimentary | Normal                 | All members abortive or rudimentary | All members sterile    | Normal                 |
| Flower B              | Normal              | All members rudimentary | Normal                 | All members rudimentary | All members sterile    | One member rudimentary |
| Gossweiler s.num.     | Normal              | Normal               | Normal                 | Normal                 | All members sterile    | One member rudimentary |
| King 403              | One member abortive | Normal               | One member rudimentary | Two members abortive  | All members sterile    | Normal                 |
| Milne-Redhead & Taylor 7934 | Normal | Normal               | Normal                 | Normal                 | All members sterile    | Normal                 |

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* Normal indicates in this connection that the writer found no deviations from the normal state in the respective flower, neither in respect of the number of members, nor in their appearance.

* The term rudimentary means that the respective cycle or member is imperfectly developed and its appearance distinctly deviating from that of the normal cycle or member.

* Abortive indicates absence of the respective cycle or member; it was accordingly not encountered at the examination. In some cases where both the inner perigon and inner androecium cycles are suppressed a row of low protuberances was observed, representing either or both cycles. However, these protuberances could not be determined to belong to any particular cycle by outer appearance only. In such cases the expression abortive or rudimentary was inserted in the respective columns.

Table III cont.

<table>
<thead>
<tr>
<th></th>
<th>Outer perigon cycle</th>
<th>Inner perigon cycle</th>
<th>Outer androecium cycle</th>
<th>Inner androecium cycle</th>
<th>Outer gynaecium cycle</th>
<th>Inner gynaecium cycle</th>
</tr>
</thead>
<tbody>
<tr>
<td>Richards 2312</td>
<td>Normal</td>
<td>Normal</td>
<td>Normal</td>
<td>Normal</td>
<td>All members sterile</td>
<td>Normal</td>
</tr>
<tr>
<td>Robinson 969</td>
<td>One member abortive</td>
<td>One member abortive</td>
<td>One member abortive</td>
<td>One member rudimentary</td>
<td>All members sterile</td>
<td>Normal</td>
</tr>
<tr>
<td>Rudatis 440</td>
<td>Normal</td>
<td>Normal</td>
<td>Normal</td>
<td>Normal</td>
<td>All members sterile</td>
<td>Normal</td>
</tr>
<tr>
<td>Welwitsch 3017</td>
<td>Flower A</td>
<td>Normal</td>
<td>All members abortive</td>
<td>All members abortive</td>
<td>All members sterile</td>
<td>Normal</td>
</tr>
<tr>
<td></td>
<td>Flower B</td>
<td>Normal</td>
<td>All members rudimentary</td>
<td>All members abortive</td>
<td>All members sterile</td>
<td>Normal</td>
</tr>
<tr>
<td>Wild 2260</td>
<td>Normal</td>
<td>All members abortive or rudimentary</td>
<td>Normal</td>
<td>All members abortive or rudimentary</td>
<td>All members sterile</td>
<td>Normal</td>
</tr>
</tbody>
</table>

other extreme is represented by Robinson 969 with fruits only 2–2.5 mm broad and lanceolate instead of broadly lanceolate. The longest fruits (13 mm) were observed in Welwitsch 3017. Fruits of remaining paratypes are largely similar to those of Milne-Redhead 3693. In the latter collection the follicles are triangular in cross-section and keeled along the whole dorsal side; the keel does not become more prominent towards the apex. Follicles triangular in cross-section were also observed in Robinson 969, but the keels were distinctly stronger apically. Other paratypes were characterized by follicles more or less circular in cross-section and as a rule with keels becoming more prominent towards the follicular tips. The last-mentioned characteristic was not shared by Robinson 2730. The transversal follicular shapes could not be determined of the few fruits of Welwitsch 3017 available for examination.

Field characteristics. — From the labels accompanying the various collections of *T. milnei* listed above one gets the impression that this species is most characteristically developed on wet, seasonally flooded meadows and similar localities. Some specimens, for instance Richards 2310 and 2312, were collected in much drier biotopes, on sandy open spaces, and such plants are small and slender, superficially resembling *T. bulbosum* ssp. *tenuifolium*, which is also found in comparatively dry habitats. However, it seems probable that dry places in which *T. milnei* occurs are exposed to annual inundations during the rainy season if also of brief duration.

*T. milnei* is generally 20–35 cm high, though specimens up to 45 cm are not rare. The variation in size is probably correlated to some extent to the availability of water and fertility of soil in the respective habitats. The stems

Table IV. Variation in seven collections of *Triglochin milnei* n.sp.: fruits.

<table>
<thead>
<tr>
<th>Paratypes</th>
<th>Mature fruits</th>
<th>Foliaces</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Length, mm</td>
<td>Width, mm</td>
</tr>
<tr>
<td>Paratypes</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bullock 2364</td>
<td>7½–10</td>
<td>2½–4</td>
</tr>
<tr>
<td>Eyles 4587</td>
<td>9½–11</td>
<td>2½–3½</td>
</tr>
<tr>
<td>Milne-Redhead 3693</td>
<td>11–12</td>
<td>2–3</td>
</tr>
<tr>
<td>Milne-Redhead &amp; Taylor 7934</td>
<td>10–11</td>
<td>3–3½</td>
</tr>
<tr>
<td>Robinson 969</td>
<td>10½–11½</td>
<td>2–2½</td>
</tr>
<tr>
<td>Robinson 2730</td>
<td>11–12½</td>
<td>3½–4½</td>
</tr>
<tr>
<td>Welwitsch 3017</td>
<td>12–13</td>
<td>2½–4</td>
</tr>
<tr>
<td>Range</td>
<td>7½–13</td>
<td>2–4½</td>
</tr>
</tbody>
</table>

Accuracy of measurements: ½ ½ — — —
towards the apices. The follicles are keeled and their tips characteristically recurved.

The colours of the living plant are very well illustrated by an annotation made by Mr. E. Milne-Redhead and Mr. P. Taylor in 1955 (Milne-Redhead & Taylor 7934): “Bulb covered by dark brown fibres; sheaths pinkish below; leaves terete, green; scape yellow-green; tepals green below, dull purplish above; anthers greenish tinged and shaded dull purple; style green.”

Affinities. — T. milnei is a bulbiferous species. According to the account of Triglochin given by Buchenau the succession and the arrangement of shoots and the occurrence of rhizomes or tubers is a natural basis of classification. There is only one further bulbiferous Triglochin species in Africa, viz. T. bulbosum, divided into five subspecies. Only one of these, ssp. bulbosum occurs in the distribution area of T. milnei; another, ssp. tenuifolium, is more southern. Remaining subspecies are North African. T. milnei shows little resemblance to bulbiferous species of Triglochin from other parts of the world.

T. bulbosum ssp. bulbosum is distinct from T. milnei in quite a number of characters. The flowers are generally smaller, 2–3 mm long. Also the members of the floral cycles are of smaller dimensions than in T. milnei. The outer tepals do not usually exceed a length of 1½ mm. The outer anthers are approximately 1 mm long and 1½ mm broad, they are accordingly strongly reniform. The inner anthers do not exceed 1 mm in length or width. The styles of the gynaecium are erect and united to the outermost tip. The fruits are moreover different, in ssp. bulbosum linear, not at all or only slightly tapering towards the apices, about 10 mm long and 1–1½ mm broad, the tips of the follicles gently spreading but not distinctly recurved.

T. bulbosum ssp. tenuifolium is still more different from T. milnei.

With respect to the North African subspecies there are certain points of similarity between ssp. barrelieri and T. milnei. The flowers of ssp. barrelieri are slightly larger than in ssp. bulbosum, averaging 3 mm in length. The fruits are lanceolate, 5 mm long and 1 mm broad being the most common dimension. The fruits are accordingly very much smaller in ssp. barrelieri than in T. milnei.

Considering species developing rhizomes T. milnei is superficially alike T. elongatum of South Africa. However, this species is characterized by narrower fruits (5–9 mm long and 1–2 mm broad) which are appressed to the stem when mature.

Triglochin bulbosum L.

T. bulbosum comprises a puzzling array of forms. Previous interpretations are controversial. By some authors this complex is considered to include four species, T. bulbosum L., T. barrelieri Lois., T. laxiflorum Guss., and T. tenuifolium Adams. More frequently one or two of them have been subordinated to T. bulbosum. Close study reveals that these four taxa are not specifically distinct. Though
not a few specimens fit the published descriptions well, others intergrade. In identifications statements on locality, habitat, and time of anthesis are of more use than those on morphological characters.

*Triglochin bulbosum* s. str. is a South African plant, particularly characteristic of marshes. The other South African representative, *T. tenuifolium*, is probably closely allied to the former but restricted to drier habitats (mountain slopes). Several specimens are difficult to distinguish from *T. bulbosum*, and *T. tenuifolium* is possibly a depauperate modification of that species. In the absence of observations on its constancy in culture, it is provisionally interpreted as an ecologically vicarious subspecies of *T. bulbosum*. In the Mediterranean area there is a bulbiferous *Triglochin* designated *T. barrelieri* Lois. Most material of this common plant is morphologically separable from the South African *T. bulbosum*. However, transitions occur and the differences are but slight. For these reasons *T. barrelieri* is considered a subspecies of *T. bulbosum*, geographically isolated from it and morphologically not quite constant. *T. laxiflorum*, finally, is a seasonal dimorphism of ssp. *barrelieri*, differing from it morphologically only to a slight extent. Also this is interpreted here as a subspecies (biological race) of *T. bulbosum*.

The following is a brief review of the previous interpretations of this group.

Micheli (1881, pp. 98 foll.) reported *T. bulbosum* L. (syn. *T. barrelieri* Lois.) from Algeria, Morocco, Cape, Natal, and Angola, and *T. laxiflorum* Guss. from Algeria. The same statements were repeated by Buchenau (1881, p. 510). Battandier & Trabut (1895, p. 5) listed *T. laxiflorum* and *T. barrelieri* as belonging to the Algerian flora. Durand & Schinz (1895, pp. 491–492) recorded *T. bulbosum* (syn. *T. barrelieri*) from Morocco, Algeria, Libya, Angola, Natal, and Cape, and *T. laxiflorum* from Morocco and Algeria. Bonnet & Baratte (1896, p. 429) stated occurrences of *T. barrelieri* in Tunisia, Tripolitania, Algeria and Morocco and of *T. laxiflorum* in Algeria and Tunisia. Bennett (1897, p. 42), besides the common *T. bulbosum*, also reported *T. laxiflorum* from South Africa (Natal) for the first time. The same author (1901, pp. 215–216) confirmed the occurrence of *T. bulbosum* in Angola. In his monograph of the Scheuchzeriaceae, Buchenau (1903) reexamined the previous records. *T. bulbosum* (syn. *T. barrelieri*) and *T. laxiflorum* were reported both for North Africa and for South Africa; *T. laxiflorum* was listed from a Cape locality; Bennett's record of 1897 from Natal was omitted as probably due to misidentification.

A new grouping of these forms was published by Rouy (1912, pp. 270–272). He distinguished the Mediterranean *T. barrelieri* as a subspecies from the South African *T. bulbosum*. According to Rouy, the latter is characterized by the hard, long, woody fibers of the leaf bases and the prolonged
T. laxiflorum was interpreted as another subspecies of *T. bulbosum* but it was not reported from Africa by Rouy. Pau (1914, p. 425) described a Moroccan *Triglochin* as *T. barrelieri* var. *maurum*. Jahandiez & Maire (1931, pp. 20–21) did not accept Rouy’s arrangement of the *T. bulbosum* group. *T. laxiflorum* was interpreted as a distinct species with an African range comprising Algeria, Morocco, and Tunisia. *T. barrelieri* was considered worth specific distinction too; it was reported from the whole of northwestern Africa from Libya to Morocco. The variety *maurum* was stated to be a Moroccan endemic, known only from the type locality. Nor did Pampañini (1930, pp. 92–93) adopt the views of Rouy; the Libyan plant reported by him was designated *T. bulbosum* (syn. *T. barrelieri*). Jahandiez & Maire (1934, p. 859) stated that all the Moroccan records of *T. barrelieri* were var. *maurum* Pau. Algerian specimens were referred to the typical form of the species (*T. barrelieri* var. *genuinum* Maire). Some of these approached var. *maurum*, however. Emberger & Maire (1941, p. 922), Maire (1952, pp. 212–213), and Cuenod (1954, p. 44) adopted the grouping of Rouy (but not as to *T. laxiflorum*) the first-mentioned authors referring the specimens quoted in 1931 to “*Triglochin bulbosa* L. (1) ssp. *Barrelieri* (Lois.) Rouy, et var. *maura* (Pau in Font-Quer) Maire, comb. nov.”

The first (and only) discussion of South African *Triglochin* since Bennett’s treatment (1897) in Flora Capensis was given by Adamson (1939, pp. 29–31). A new species, *T. tenuifolium* Adams., was described on the basis of ten collections from the Cape Peninsula and Caledon. *T. bulbosum* (syn. *T. barrelieri*) was reported as “found in several inland stations but commoner near the coast”. The statements of Bennett (1897) and Buchenau (1903) on the occurrence of *T. laxiflorum* in South Africa were considered erroneous, and that taxon was excluded from the South African Flora.

**Triglochin bulbosum** ssp. **bulbosum**.

*Triglochin bulbosum* Linnaeus 1771, p. 226.

*Triglochin bulbosum* ssp. eu-bulbosum Maire & Weiller in Maire 1952, p. 212.

**Selected references.** — Micheli 1881, p. 99; Durand & Schinz 1895, p. 490; Bennett 1897, p. 42; Buchenau 1903, p. 11; Adamson 1939, p. 30.

**Specimens examined.** — Of a large material, mainly from the Cape Peninsula, and including a number of intergrades, the following are typical:


Typification and description. — The type of this species in the Linnean Society Herbarium, London, is from the Cape of Good Hope. The type material has not been examined in the present connection. It is said to comprise rather weak specimens; the delimitation of this towards the ssp. *tenuifolium* is accordingly somewhat obscure. One of the plants quoted above, collected by C. Wright in Cape (K) was compared by N. E. Brown on July 24, 1917, with the type collection of *T. bulbosum* according to annotation on that sheet. The said specimen was stated to agree well with the type. In view of that, and since the writer had no opportunity to see the latter, Wright's specimen is taken to be representative of *T. bulbosum*. It is described below to serve as a basis for comparison with other African *Triglochin*.

Plants 20–25 cm high, perennial, slender, bulbiferous. *Bulbs* single, terminal, surrounded by dense layers of strongly fibrous leaf-bases. *Stems* 1–1½ mm in diam., terete, exceeding the leaves, with 11–17 flowers. *Upper leaves* 10–14 cm long, ½–1 mm wide, flattened, distinctly canaliculate on ventral side. *Lower leaves* (only one observed) 50 mm long, 4 mm wide, flat, keeled. *Flowers* greenish, 2–2½ mm long, perianth 1½–2 mm in diam., pedicels of young flowers short or absent, in mature flowers up to 3 mm long. *Outer tepals* 1½ mm long, 1 mm broad, conchiform, apices broadly acute, in some slightly cucullate. *Inner tepals* 1 mm long, 1 mm broad, conchiform, more rounded than the outer, apices erect, rounded or obtuse, slightly dentate, indistinctly semitubular. *Outer anthers* sessile, 2-locular, reniform, flattened, 1 mm long, 1½ mm broad, ½ mm thick. *Inner anthers* sessile, 2-locular, reniform, flattened, ½ mm long, 1 mm broad, less than ½ mm thick. *Pollen* spherical, nonaperturate, reticulate, 21–26 μ in diam. *Gynaecium* 2 mm long, the three styles erect, united to the apex. *Fruits* 9–11 mm long, approximately 1 mm broad, linear, slightly or not at all tapering towards the apex, composed of three sterile and three fertile follicles. *Sterile follicles* much reduced, needle-shaped. *Fertile follicles* subrectangular in cross-section, lateral side less than ½ mm broad, dorsal side ½ mm broad, unkeeled but with a dorsal groove along the whole length, linear, only slightly tapering towards the style which is erect or only slightly spreading. *Fruit pedicels* 3–4 mm long, directed irregularly obliquely upwards, not appressed to stem.

Affinities and variation. — This subspecies is variable, especially as to size. The above description refers to a rather common, weak form. Transitions to ssp. *tenuifolium* are frequently met with. Within the area of typical ssp. *bulbosum* there also occurs a larger and stouter plant which may appear strikingly different. However, this intergrades with the former. It may be a modification ecologically corresponding to more favourable soil and water conditions. The differences in size refer to stem height, stoutness of stems and leaves, and other vegetative characters, whereas the size and shape of the flowers and fruits are similar to those of the type. Several specimens of this big *T. bulbosum* were examined particularly from the vicinity of Cape Town. Garside 1139 is one of the most characteristic of these plants, others are Echlon 569 and Drège 1840. The first-mentioned is very briefly described below with special reference to the differences from *Sv. Bot. Tidskr.*, 55 (1961) : 1.
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typical ssp. *bulbosum*. It deviates too little from the latter to need a Latin designation.

*Plants* stout, 35–50 cm high. *Stems* 2–3 mm in diam., with 20–50 flowers. *Upper leaves* up to 35 cm long, 1–3 mm wide, more flattened than in typical form. *Lower leaves* as in typical form. *Flowers* and *fruits* agreeing with those of typical form except in the longer fruit pedicels, 4–7 mm.

The subspecies of *T. bulbosum* differ from each other mainly in the shapes, sizes, and positions of their fruits. The flowers and general appearances of plants are comparatively similar throughout this species. Characteristic of typical specimens of ssp. *bulbosum* are the linear fruits, approximately 10 mm long and 1 mm broad, slightly tapering towards the tips, less so or not at all towards the bases, directed more or less obliquely upwards on pedicels shorter than the fruits. The follicular tips are erect. In several specimens there is a characteristic dorsal groove on the follicles instead of a keel. These statements refer to mature fruits.

However, the fruits vary a great deal within the individual collections. In DnèÈgë 1840, besides quite typical fruits, there are also shorter (8 mm long) ones which should be described as narrowly lanceolate instead of linear. Others (Bolus 2850, Hafström & Lindberg s. num.) have some fruits only 7 mm long and lanceolate; such may be strikingly similar to those of ssp. *barrelieri*. In the Zeyher specimens from Branfontein the pedicels are as long as the fruits or somewhat exceeding them and the follicular tips are more reflexed than usual. Generally, these tips are long and can be examined without a lens; in Ecklon 569 they are quite short, hence approaching those of ssp. *barrelieri*. A few fruits are somewhat assymetrical (as in ssp. *laxiflorum*), but very rarely they are pressed to the stem as in the last-mentioned subspecies. The most frequent cases of deviating fruits in the area of ssp. *bulbosum* occur in specimens also in other respects transitional to ssp. *tenuifolium*; these are linear but very small.

The flowers of most specimens of ssp. *bulbosum* are comparatively small, 2–3 mm long. Those of ssp. *barrelieri* are as a rule larger, and those of ssp. *tenuifolium* generally smaller, but exceptions occur. The outer anthers of most flowers are 1 mm long, but in some up to 1½ mm; they are reniform or circular. The floral characters seem somewhat unstable and it is hardly possible to identify the subspecies of *T. bulbosum* solely on account of the flowers. Abortions are less common than in *T. milnei*; they were observed in Bolus 2850 and Ecklon 569. In both the inner anthers were absent and the inner tepals reduced to scales.

Doubtless ssp. *bulbosum* is close to ssp. *tenuifolium*. The three Mediterranean forms *barrelieri*, *maurum*, and *laxiflorum* are somewhat more remotely allied; most South African specimens differ in the linear, symmetrical fruits and the long follicular tips. *T. milnei* differs considerably in the fructificational characters quoted under that species and in the constantly larger flowers.

References to *T. bulbosum* from Tropical Africa (Rendle 1899, p. 93, Bennett 1901, p. 215) apply to *T. milnei*; those from North Africa (for instance Pampanini 1930, p. 92) to ssp. *barrelieri*.

**Triglochin bulbosum** ssp. *tenuifolium* (Adamson) n. comb.

*Triglochin tenuifolium* Adamson 1939, p. 30.

*Triglochin bulbosum* Bennett 1897, p. 42, in part.


Adamson (l.c.) reports this from eight further localities on Cape Peninsula and one in Caledon Division.

**Typification and description.** — The holotype (Adamson 986, BOL) of this South African *Triglochin* originates from the western slopes of Table Mountain, Cape Peninsula. This specimen was not examined in the present connection. In order to complete the short original description and to facilitate comparison with other subspecies one of the paratypes (Schlechter 1540) is described below.

Plants 6–11 cm high, perennial, slender, bulbiferous. Bulbs small, single or in groups, surrounded by dense layers of brownish or greyish, fibrous leaf-bases. Stems 4–9 cm high, $\frac{3}{4}$–1 mm in diam., terete, as a rule shorter than the leaves, with 7–19 flowers. Upper leaves 5–11 cm long, $\frac{1}{4}$–1 mm wide, almost terete, not distinctly canaliculate on ventral side. Lower leaves mostly withered, only remnants left, about 2 mm wide, flattened. Flowers greenish, 1$\frac{1}{2}$–2$\frac{1}{2}$ mm long, perianth 1$\frac{1}{2}$–2 mm in diam., pedicels of young flowers short or absent, in mature flowers up to 2 mm long. Outer tepals 1–1$\frac{1}{2}$ mm long, 1$\frac{1}{4}$–2 mm broad, comparatively broader than in ssp. *bulbosum*, distinctly conchiform to hemispherical, with apices erect, broadly acute. Inner tepals 1–1$\frac{1}{2}$ mm long, approximately 1 mm broad, conchiform but less distinctly than the outer, apices erect, distinctly dentate, semitubular. Outer anthers sessile, 2-locular, reniform, flattened, slightly less than 1 mm long, 1 mm broad, less than $\frac{1}{4}$ mm thick. Inner anthers sessile, 2-locular, broadly ovoid to somewhat reniform, flattened, about $\frac{1}{2}$ mm long and broad, less than $\frac{1}{4}$ mm thick. Pollen spherical, nonaperturate, 24–29 μ in diam. Gynaecium 1$\frac{1}{2}$–2 mm long, the three styles erect, united to the tip. Fruits 6–7 mm long, approximately 1 mm broad, narrowly lanceolate, slightly tapering towards base and apex, composed of three sterile and three fertile follicles. Sterile follicles much reduced, needle-shaped. Fertile follicles triangular in cross-section, lateral and dorsal sides less than $\frac{1}{2}$ mm broad, not distinctly keeled nor grooved, narrowly lanceolate, tapering towards the base and style, the latter only slightly spreading. Fruit pedicels 6–8 mm long, directed irregularly obliquely upwards, taking an angle of 25–40° to the peduncle, not appressed to this.

The description of the holotype differs in some minor respects from the above description. In the holotype the bulbs are said to occur in groups,
the leaves are longer (14–15 cm), the fruits slightly larger (7–8 mm long) with longer (8–12 mm) pedicels, distinctly exceeding the fruits in length. These differences are within the variation exhibited by ssp. *tenuifolium*.

**Affinities and variation.** — Principal distinguishing characters of this subspecies are furnished by the fruits. The small (6–8 mm long and \(\frac{1}{2}\)–1 mm broad), narrowly lanceolate to linear fruits on pedicels equaling or exceeding them are particularly diagnostic. Some mature fruits are still smaller, 5 mm long (*Schlechter* 8979). In *Zeyher* 1735, the fruits are somewhat lanceolate, 5 mm long, but the pedicels are only 2–4 mm long. The follicular tips are generally slightly spreading. In some fruits (*Hutchinson & Pillars* 104) they are short and inconspicuous. The follicles are generally more or less distinctly triangular in cross-section. Most are neither grooved nor keeled dorsally.

In most specimens the flowers are characteristic too, being smaller than those of ssp. *bulbosum*, as a rule less than 2 mm long and with the outer anthers \(\frac{1}{2}\) to slightly less than 1 mm long. In one collection (*Hutchinson & Pillars* 104) there are larger flowers, up to 3 mm, with outer anthers 1–1\(\frac{1}{2}\) mm. The outer tepals generally agree with those of the paratype described, being rounded, comparatively broader, and more conchiform than those of ssp. *bulbosum*; exceptions occur, however. No partial floral abortions were observed. They were not especially looked for and might be found in a large material.

This is a much smaller plant than ssp. *bulbosum*, the stems of most specimens being 5–10 cm high (*Ecklon & Zeyher* s. num. and 620, *Schlechter* 8979), or 10–15 cm (*Schlechter* 1540, *Penther* 352, *Zeyher* 1735). The stem and leaves are very slender, less than 1 mm in diam. The leaves are spreading and early withered. They equal the stem in length or exceed it and the comparatively long leaves constitute a diagnostic character of most specimens. The bulbs are single or in groups, minute, and surrounded by fibers in some blackish and woody, in others brownish or greyish and softer.

*Adamson* (1939) considered the most useful characteristics of *T. tenuifolium* the “pale green colour, small fusiform tubers, which often occur in groups and are surrounded by a brown fibrous sheath, the very slender spreading flexible leaves, few-flowered spikes, and fruits narrowed at both ends on long stalks”. However, *T. tenuifolium* intergrades with *T. bulbosum* when and where these plants meet, and some of the characteristics quoted by *Adamson* are subject to considerable variation as is evident from the present, rather restricted material. Many South African specimens are accordingly transitional and it is a matter of opinion to which of the two taxa they should be referred. Typical specimens of ssp. *tenuifolium* differ from those of ssp. *bulbosum* in most or all of the following characteristics: plants approximately 10 cm high with stems and leaves very slender and the tubers minute; stems equal to or shorter than the leaves; flowers less than 2 mm long with outer anthers less than 1 mm long and with outer tepals very distinctly conchiform; fruits linear, 5–8 mm long and less than 1 mm broad, on pedicels equal to or exceeding the fruits in length.

bulbosum is essentially an inhabitant of marshes, it appears probable that ssp. tenuifolium replaces the former in dry habitats of the extreme south of the bulbosum area. With respect to the considerable morphological intergradation of the two, it is doubtful whether the present plant can be maintained as a subspecies. It may be a depauperate modification of ssp. bulbosum. As there are no observations on its constancy in culture, this question cannot be decided here.

**Triglochin bulbosum ssp. barrelieri** (Loiseleur) Rouy.

Triglochin barrelieri Loiseleur 1807, p. 725.
Triglochin barrelieri var. genuinum Maire in Jahaniez & Maire 1934, p. 859.
Triglochin bulbosum ssp. barrelieri Rouy 1912, p. 271.

**Selected references to African specimens.** — Micheli 1881, p. 99; Buchenau 1881, p. 510; Durand & Schinz 1895, p. 491; Battandier & Trabut 1895, p. 5; Bonnet & Baratte 1896, p. 428; Buchenau 1903, p. 11; Pampinini 1930, p. 92; Jahaniez & Maire 1931, p. 21; 1934, p. 859; Eemberger & Maire 1941, p. 922; Maire 1952, p. 212; Cuenod 1954, p. 44.

**Specimens examined.** — A large material particularly from the Mediterranean of Europe. This plant is distributed from Portugal and southwestern France through Italy and the Balkans to Asia Minor and Cyprus, and in North Africa from Benghazi and vicinity eastwards into Algeria. Moroccan specimens are considered to belong to ssp. maurum. African specimens seen: Tunisia: Sandwith 2845, salt-marshes between Tunis and Carthage, April 28, 1939, flfr. (K). — Murbeck s. num., Tunis, March 17, 1896, flfr. (S).

**Typification and description.** — *T. barrelieri* was described by Loiseleur from the vicinity of Arles, Mediterranean France. A specimen from the Swartz herbarium (S) may belong to the type collection. The label bears no data to that effect, but the handwriting is very similar to that of Loiseleur. This represents a weak form with immature fruits. The description below is based on three collections (S) from southern France, viz. the Swartz specimen just mentioned (abbr. SW), a flowering plant from Montpellier, Palaoas, collected by Lenander in April 1939 (LR), and nine fruiting specimens from Ande, leg. Sennen in April 1903 (SN).

Plants 10–15 cm high, perennial, stouter than ssp. bulbosum, bulbiferous. Bulbs single, terminal, in some one additional lateral bulb present, surrounded by dense layers of brownish, strongly fibrous leaf-bases. Stems 7–13 cm high, 1–1 1/2 mm in diam., terete, in some exceeding the leaves in length, with 8–11 (SW), 15 (LR) or 4–14 (SN) flowers. Upper leaves 3–11 cm long, 1/2–1 1/2 mm wide, flattened, canaliculate on ventral side. Lower leaves 5–9 cm long, 1/2–2 mm wide, flat, keeled, with a longer laminar, and a shorter sheathing part than in ssp. bulbosum. Flowers greenish, 3 1/2–4 mm long, perianth 3–4 mm in diam., pedicels of young flowers very short or absent, in mature flowers up to 3 1/2 mm long. Outer tepals 2 1/2–3 mm long, 1 1/2–2 mm broad, conichiform with slightly acute to rounded, distinctly ciliate apices. Inner tepals 1 1/2–2 mm long, 2–2 1/2 mm broad, conichiform, *Sv. Bot. Tidskr., 55 (1961): 1*
more rounded than the outer, apices obtuse, somewhat dentate, not semi-tubular. *Outer anthers* sessile, 2-locular, broadly ovoid, slightly flattened, $1\frac{1}{2}-2$ mm long, $1\frac{1}{2}-2$ mm broad, $1\frac{1}{2}$ mm thick. *Inner anthers* sessile, 2-locular, broadly ovoid to reniform, flattened, $1-1\frac{1}{2}$ mm long, approximately $1\frac{1}{2}$ mm broad, almost $1$ mm thick. *Pollen* spherical, nonaperturate, 27–30 $\mu$ (LR) in diam. *Gynaeicum* $2\frac{1}{2}$ mm long, the three styles erect, united to the tip. *Fruits* (SN) 4–6 mm long, $\frac{1}{2}-1\frac{1}{2}$ mm broad, lanceolate, tapering towards the apex, composed of three sterile and three fertile follicles. *Sterile follicles* much reduced, needle-shaped. *Fertile follicles* almost circular in cross-section, diam. almost $1$ mm, keeled along their whole length, the keels more prominent upwards, narrowly lanceolate, tapering towards the styles which are slightly spreading. *Fruit pedicels* 2–4 mm long, directed obliquely upwards, taking an angle of approximately $30^\circ$ to the peduncle. 

**Affinities and variation.** — Ssp. *barrelieri* is generally low and stout with succulent stems and leaves and with a few flowers which are larger as a rule than those of the other subspecies of *T. bulbosum*. The floral size cannot be used for identification, however, since there is considerable variation in the material. The lengths of the flowers range from 2 to 4 mm, and the lengths of the outer anthers and outer tepals vary conformably from 1 to $2\frac{1}{2}$ mm and from $1\frac{1}{2}$ to 3 mm, respectively. As usual in *T. bulbosum*, the fruits furnish the best characteristics. In typically developed specimens they are 5–7 mm long and $1-1\frac{1}{2}$ mm broad and, because of that, appear comparatively stout. They are lanceolate, tapering towards the apices and bases. The follicular tips are short and slightly spreading; the follicles are keeled in their whole length. The pedicels are characteristic: 2–5 mm long, generally shorter than the fruits, fairly stout, and directed obliquely away from the peduncle. Also the fructificational characters show some variation. Some specimens are provided with very small fruits, approximately 4 mm long and almost ovate in shape. Though most fruits are symmetrical, more or less distinctly assymmetrical ones are not rare. They are never so conspicuously assymetrical as in ssp. *laxiflorum*, however. The follicles of some fruits have longer tips than usual and, in those cases, are similar to those of ssp. *bulbosum*. Pedicels which are as long or slightly longer than the fruits were particularly observed in specimens from the Balkans and Asia Minor. In some plants the pedicels are appressed to the stem.

Differences relative to the leaf sheaths between Mediterranean and South African *T. bulbosum* as quoted by Rouy (1912) are unreliable. This subspecies comes rather close to ssp. *laxiflorum*. Quite a few specimens of ssp. *barrelieri* must be identified solely on account of the flowering season, being morphologically almost indistinguishable from the autumnal form. Moreover, ssp. *barrelieri* seems to be close to the Moroccan endemic ssp. *maurum*. Most Mediterranean specimens can be distinguished from South African *T. bulbosum* by their fruits or, in the absence of them, by their flowers which are larger as a rule. However, in spite of the geographically isolated ranges there is considerable morphological intergradation. Because of that these two taxa cannot be interpreted as separate species.

Triglochin bulbosum ssp. maurum (Pau) n. comb.

Triglochin barrelieri var. maurum Pau in Font Quer 1914, p. 425.
Triglochin bulbosum var. maurum Maire in Emberger & Maire 1941, p. 922.


Specimens examined. — Morocco: Font Quer 16, inter Ceuta et Tetauen, loco dicto Rincón de Medik, alt. 4 m s. m., in arenosis humidis, March 13, 1930, flfr. (S). — Font Quer 17, ad ripas fl. Lukos, juxta El Araix, in paludosis, May 1, 1930, fr. (S).

Remarks. — This is stated to differ from ssp. barrelieri in mainly two respects, expressed by Font Quer (l.c.) as “los pedúnculos mayores y casi rectos, con frutos doble mayores” (cf. also Maire 1952, p. 213). Its tenability is difficult to decide from the brief description and scanty material examined. Of the two sheets available, identified by Font Quer, only Font Quer 17 agrees with the original description, the fruits being 9–11 mm long and the pedicels 3–7 mm. Font Quer 16, with fruits 5–7 mm long, are fairly similar to specimens of ssp. barrelieri.

The rise of this as a subspecies is mainly based upon its supposed inhabiting a separate geographical range to the exclusion of ssp. barrelieri. It was interpreted as a Moroccan endemic (Jahandiez & Maire 1931), widely distributed in that country (Jahandiez & Maire 1934, Maire 1952). Algerian plants are ssp. barrelieri but some are stated to be reminiscent of ssp. maurum (Jahandiez & Maire 1934). The taxonomy and affinities of this form are still unsufficiently known.

Triglochin bulbosum ssp. laxiflorum (Gussone) Rouy.

Triglochin laxiflorum Gussone 1825 (not seen); 1827, p. 451.
Triglochin bulbosum ssp. laxiflorum Rouy 1912, p. 272.

Selected references to African specimens. — Micheli 1881, p. 101; Buchenau 1882, p. 510; Battandier & Trabut 1895, p. 5; Durand & Schinz 1895, p. 490; Bonnet & Baratte 1896, p. 428; Buchenau 1903, p. 11; Jahandiez & Maire 1931, p. 20; 1934, p. 858; Emberger & Maire 1941, p. 922; Maire 1952, p. 213; Cuenod 1954, p. 44.

Specimens examined. — A large material from Sicily and Sardinia, Mediterranean France and Portugal.

range of ssp. laxiflorum is stated to comprise Tunisia, Constantine, Algeria, Oran, and Morocco (Maire 1952, p. 214).

**Affinities and variation.** — This is a seasonal dimorphism of ssp. barreleri and is very similar to the latter from a morphological point of view. It is characterized by its autumnal anthesis as contrasted with the vernal season of flowering of ssp. barreleri. The flowers seem indistinguishable from those of the latter, but the fruits differ to some extent. These are 5–6 mm long and slightly more than 1 mm broad; the pedicels are comparatively short (2–3 mm). The fruits taper more distinctly towards the spreading stylar tips than those of ssp. barreleri. Owing to hemicircular curvation of the pedicels towards the peduncle, the fruits become appressed to this. This peculiar curvation is striking but hardly constant; in some plants, particularly from Sicily, the fruits are divergent from the peduncle as in ssp. barreleri. Most specimens are more gracile and less succulent than those referable to ssp. barreleri; generally, the spikes consist of fewer (5–10) flowers than in the latter. The Moroccan and Algerian specimens collected by Gattefossé and Tribout, respectively, are exceptional in that respect, being big and succulent plants well comparable with the largest barreleri examined, and the spikes contain a considerable number of flowers. Without information on the time of anthesis these two taxa are difficult to distinguish in several cases. Some Italian and Albanian specimens of ssp. barreleri match ssp. laxiflorum in all respects, except in the time of flowering, whereas others agree with the later in one or two of the characters mentioned.

The assignment of this autumnal plant as a subspecies of T. bulbosa or T. barreleri is generally adopted for the present. It seems somewhat debatable, however. The actual concept of subspecies is primarily geographically defined, involving as criteria, for instance, distinct areas of distribution bordered by transitional zones of morphological intergrades. The autumnal plant discussed occurs in a considerable part of the distribution range of its vernal ally. The morphological differential characteristics seem insignificant and unstable to a degree that makes one favour the idea of subordinating the autumnal plant to ssp. barreleri as a variety or still lower category.

However, reasons may be advanced for an opposite view. There is a current tendency among taxonomists to regard seasonal dimorphism as specifically distinct, when the seasons of anthesis differ sufficiently to prevent any crossing. The slight and inconstant morphological differences and the overlapping areas of distribution are not considered decisive in such cases.

Records of ssp. laxiflorum from Tropical Africa (Bennett 1901) and South Africa (Bennett 1897, Buchenau 1903) are due to misidentifications.

**Triglochin palustre L.**

*Triglochin palustre* Linnaeus 1753, p. 338.

**Selected references to African specimens.** — Jahandiez & Maire 1931, p. 21; Eemberger & Maire 1941, p. 922; Maire 1952, p. 212.

**Specimens examined.** — No African specimens seen. According to Jahandiez & Maire (1931) and Eemberger & Maire (1941), this species occurs in about ten localities on lake shores and in marshes at altitudes of

1400-2000 m s.m. in the Atlas Mountains of Morocco. MAIRE (1952) states that it is met with in wet meadows and along rivulets and that it is not rare in suitable localities in the Moven Atlas and eastern Grand Atlas; it is also found on one locality in Rif. T. palustre has a circumboreal distribution in the northern hemisphere (see HULTÉN 1941, p. 107). HULTÉN (1950) places it among the boreal-circumpolar plants lacking large gaps in their area. Besides, there is an isolated distribution area in the southern hemisphere, viz. in South America. The species occurs here in the Andes from the Atacama Desert and Cordillera de la Rioja southwards to Tierra Fuegia.

Remarks. — T. palustre is a distinct and well-known species, described repeatedly, and a detailed discussion is hence superfluous. Among the species producing rhizomes it might be mistaken for the exclusively South African T. elongatum. T. palustre differs from that in narrower fruits, conspicuously tapering towards the bases, and in constantly erect stylar tips; mature fruits are distinctly apressed to the stem. The flowers are much smaller than those of T. elongatum and their pedicels shorter. The stolons of the short rhizome are fugaceous and rarely to be observed in herbarium specimens; their apices are incrassate. The rhizome of T. elongatum is longer, and the stolons resistant. All tuberous African species differ from T. palustre in their basal morphology. In the absence of basal parts, T. palustre is superficially alike T. bulbosum ssp. bulbosum and laxiflorum but both differ from the former in respect of their fruits.

Records of T. palustre from Algeria (MICHELI 1881, p. 98, DURAND & SCHINZ 1895, p. 491) probably refer to T. bulbosum ssp. laxiflorum.

Triglochin striatum Ruiz & Pavon.

Triglochin striatum Ruiz & Pavon 1802, p. 72.

Selected references to African specimens. — MICHELI 1881, p. 101; BUCHENAU 1882, p. 502; DURAND & SCHINZ 1895, p. 491; BENNETT 1897, p. 42; 1901, p. 216; BUCHENAU 1903, p. 10; ADAMSON 1939, p. 29.

Specimens examined. — A comprehensive material from southwestern Europe, North and South America, and Australia. T. striatum is widely distributed, particularly in the southern hemisphere. In Africa it is found from Angola (Mossamedes) and Durban to the Cape Peninsula with increasing frequency southwards; in Australia along the coast from Western Australia to southern Queensland, moreover on Tasmania, New Zealand (North and South Islands), Chatham Islands, and Stewart Island; in South America from southwestern Brazil and northern Chile southwards through Uruguay, Argentine, and Chile; and in North America finally as a Coastal Plain species from Maryland to Louisiana, and moreover in California and Mexico. Finally, T. striatum occurs in slightly saline marshes of southern Portugal; it was first found in Minho, later during the thirties and forties also in Beira and Estremadura but was considered to have been introduced there.


Remarks. — *T. striatum* is perhaps the most characteristic and most easily identified of the African species. The minute flowers and the small globular fruits on short pedicels, crowded in dense and compact spikes, make this species easily recognized. It grows especially in dry borders of swamps, slightly wet meadows, and similar biotopes but is also met with in shallow pools. Specimens growing in water look unusual: the spikes become lax and the stems and leaves long, flaccid, and slender. A somewhat aberrant modification of this kind is represented in the material by Rudatis 1612.

Except when growing as an aquatic plant, *T. striatum* is not very variable and in this respect differs a great deal from *T. bulbosum*, for instance. Micheli (1881) and Buchenau (1882, 1903) divided *T. striatum* into three varieties (vars. *triandra*, *montevidensis*, and *filifolia* of Buchenau), based upon the heights of the stems and the widths of the leaves. These varieties were stated to have different ranges of distribution. Results of the present examination do not support Buchenau’s segregation; this does not appear congruent with the slight infraspecific variation occurring. Among these varieties, var. *filifolia* Buch., a small plant with leaves less than 1 mm broad, seems to be that which deviates most from the common African form. It is stated to occur “vorzugsweise in Neuholland, Tasmanien, Neuseeland; entsprechende Formen aber auch aus Chile” (Buchenau 1903, p. 10). A rather similar form from South Africa (Zeyher 814) is provided with a long, unusually well-developed rhizome, and has probably grown in a rather dry habitat.

In conformity to *T. milnei* and *T. bulbosum*, *T. striatum* tends much to partial abortion of the flowers (cf. Buchenau 1882, pp. 494 foll., and Saunders 1939, p. 537). Several flowers were examined in which the inner tepals and the inner anthers were rudimentary or absent. In some, the members of these cycles were represented by small verruciform extensions. One of the flowers examined (Acock 3027) lacked the inner tepal cycle, one of the outer anthers, and all inner anthers; besides, one of the three fertile carpels was of abnormal shape and probably sterile.

The outer tepals are as a rule orbicular; in some flowers they are provided with a lingulate extension above. Buchenau considered this typical of the variety *montevidensis*. However, this characteristic is also observed in other plants and is probably accidental; it cannot be correlated with the variations of other characters.

South African specimens of *T. striatum* have been erroneously identified with *T. maritimum* (Thunberg 1794, p. 67, Meyer 1832, p. 131). The last-mentioned differs from *T. striatum* by developing six follicles in the fruits and by the much larger flowers.
Triglochin elongatum Buchenau.

Triglochin elongatum Buchenau 1903, p. 10.

Selected references. — Buchenau 1903, p. 10; Adamson 1939, p. 30.

Specimens examined. — Cape of Good Hope: Malmesbury Division, Acock 2962, Kuils River, on outcrop of Malmesbury Series clay, May 1932, flfr. (S, as T. laxiflorum). — Uitenhaage Division, Ecklon s. num., on the shore of Swarzkopfrivier, fr. (S, as T. palustris). — Cheeseman, herb. Acock 7678, clay flats by the roadside near Tulbagh, Sept. 21, 1935, fl. (S, as T. bulbosum) may be this species but it is too fragmentary to be referred to it with absolute certainty.

T. elongatum is exclusively South African. It was recorded by Buchenau (1903) for Malmesbury Division (Bachmann 1692, 1693), Pondoland (Bachmann 309), and, with some hesitation, from Natal, Durban (Rehmann 8581, Wood 925) according to statements by Bennett (1897). Adamson (1939) quoted localities from the Cape Peninsula and Uitenhaage Division.

Remarks. — T. elongatum appears to be a rare species and herbarium materials are mostly scanty. On this account the morphology and variation are insufficiently known. To judge from Buchenau's description there are several points of similarity to T. bulbosum ssp. bulbosum. No type specimens of T. elongatum were examined in the present connection. The collections quoted above show some minor deviations from the type description and type figure of T. elongatum.

Flowers examined resemble those of T. bulbosum ssp. bulbosum except in the fact that the anthers are larger, 1–2 mm, as a rule approximately 1½ mm long. The fruits differ considerably from those of T. bulbosum, however. Those of the type material of T. elongatum (Bachmann 1692, 1693, 309, herb. B) were described by Buchenau (l.c.) as follows:

"Fructus 6 usque 9 mm longi, rhachi paralleli (fere adpressi) elliptico-lineares, sursum sensi attenuati, apice tridentato; pedunculi 3 usque 4 mm longi, oblique erecti; carpidia dorso laevia, medio dorsi indistincte, superne manifestius carinata."

It should be added to this description that, according to Buchenau's illustration, the fruits taper towards their bases and are slightly more than 1 mm broad. Those of Acock 2962 and of Ecklon s. num. agree well with the above description. Fruits of T. bulbosum ssp. bulbosum are generally slightly larger, 7–11 mm long and 1 mm broad, linear, and do not taper notably towards their tips and bases.

References to occurrences of T. laxiflorum in South Africa (Bennett 1897, p. 42) refer, at least in part, to T. elongatum.

Unidentified specimens.

The South African species of Triglochin are still insufficiently known. There are two plants in the material examined which could not be referred to any species included here. They may be aberrant forms of other species or represent undescribed taxa. The available Sv. Bot. Tidskr., 55 (1961) : 1
NOTES ON THE AFRICAN SPECIES OF TRIGLOCHIN

material is insufficient to decide this and it is to be hoped that taxonomists resident in this area will pay attention to them.

One of these, provisionally designated Species A, is represented by some specimens labelled "Triglochin bulbosum L., South Africa, sandy, stony lower slopes at "Tierbos", Hout Bay, 24-IV-1934, JOHN P. H. ACOCK no. 6883" (S). This collection comprises three specimens, one with undeveloped flowers, the second with young, and the third with mature fruits. The plants are 20–35 cm high, gracile (stems up to 1 mm in diam., leaves approximately 1/3 mm broad), and distinctly bulbiferous. The plants approach T. milnei in general appearance. Considering their stage of development, the flowers are very small, about 1/3 mm long. Similarly developed flowers in the holotype of T. milnei are at least 3 mm long. The flowers are not well preserved and no detailed studies can be carried out; however, the styles show the same recurvation as in T. milnei. The outer anthers, which attain their final shape and size at an early stage in Triglochin, are less than 1 mm long. The fruits are lanceolate; they are narrower and smaller (5–7 mm long and 1/3 mm broad) than those of T. milnei. Though in some other respects reminiscent of T. milnei fruits, they moreover differ in being erect and appressed to the stem. These plants also show superficial similarity to T. bulbosum ssp. laxiflorum. References to the latter from the Cape Peninsula, for instance by BENNETT (1897, p. 42), may, at least in part, refer to specimens of this kind. ACOCK 6883 seems, however, more allied to T. milnei than to T. bulbosum. It cannot be identified with the Mediterranean ssp. laxiflorum of the latter, which is characterized by much larger flowers, and as a rule assymmetrical fruits. The present plant may be an ally of T. milnei, but its taxonomical position cannot be decided on the base of the material at hand.

The collection preliminarily designated Species B is labelled "Triglochin laxiflora Guss., mountain areas near Cape Town, alt. 2000 ft., ZEYHER 4324" (S). It resembles T. elongatum and was first tentatively referred to that; close inspection revealed several differences which prohibit identification. This plant is primarily characterized by its fruits. These are broadly lanceolate to ovate, 5–7 mm long and 2 mm broad, sessile or on pedicels less than 1 mm long. The fruits taper distinctly towards the apices and bases. Tips of the follicles are very short and erect. The dorsal sides of the follicles are distinctly, though not prominently keeled. The flowers are large and resemble those of T. bulbosum ssp. bulbosum.

This form shows similarity to T. bulbosum and particularly to ssp. barrellieri, strange to say. But the fruits are so peculiar that one feels tempted to describe it as a species. The material is too scanty and fragmentary for such an action.

Species to be excluded from the African flora.

*T. maritimum* L.

References to South African specimens. Thunberg 1794, p. 67; Meyer 1832, p. 131.

References to Algerian specimens. — Munby 1857, p. 31; Battandier & Trabut 1895, p. 5; Durand & Schinz 1895, p. 491; Rouy 1912, p. 271.

References to Tunisian specimens. — Bonnet & Baratte 1896, p. 428; Maire 1952, p. 211; Cuenod 1954, p. 44.

South African references are due to a misidentification and apply to *T. striatum*.

All references to the occurrence of *T. maritimum* in Algeria are based upon the same original record by Munby (l.c.). Since the species has not been re-found on the locality stated in spite of much searching, the record was probably based on an erroneous determination. It is not settled to which species Munby’s observations apply; no specimens seem to have been preserved.

The original statement on the presence of *T. maritimum* in “marais et lieux humides du littoral” at La Goulette in Tunisia (Bonnet & Baratte l.c.) has been quoted up to the present time as an indication that *T. maritimum* is a member of the North African flora. However, both Maire (l.c.) and Cuenod (l.c.) point out that the species has not been recovered in this locality and that the record is unverified. The present state of *T. maritimum* in Tunisia is accordingly very uncertain and, though there is nothing to disprove its existence in that country, this species had better be excluded from the North African flora until some positive evidence has been produced on its occurrence there.

University of Stockholm, June 1960.

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CYTOTAXONOMIC STUDIES IN ANTHOXANTHUM ODORATUM L. S. LAT.

1.

MORPHOLOGIC ANALYSIS OF HERBARIUM SPECIMENS.

BY INGA HEDBERG.

Introduction.

The occurrence of more than one chromosome number within what has been considered one and the same species offers some interesting problems. In many cases the discovery of such a difference has lead to the splitting of the species in accordance with cytological evidence. Connected with the cytological distinction there have in such cases evidently been some constant morphological differences. These differences should doubtless make it possible to classify herbarium material without knowing the chromosome number of each specimen or its place of origin. There are, however, examples of differences in chromosome number unaccompanied by morphological distinctions (cp. Darlington 1937, p. 227; Larsen 1957). A comparison between a few specimens of different ploidy will often give the impression that morphological differences exist between the polyplotypes. But an investigation of sufficiently large population samples may reveal that all characters show such a degree of variation in the species as a whole as to make a distinction on a morphologic basis difficult or impossible. The present paper illustrates such a case in the genus Anthoxanthum L.

Previous investigations.

The first report on different chromosome numbers within Anthoxanthum odoratum L. s.lat. was given by Östergren (1942), who reported the diploid number \((2n = 10)\) for material from alpine and subalpine localities in Norway, northern Sweden, and Switzerland and the tetraploid number \((2n = 20)\) for lowland material.

Table I. Survey of the differences between *Anthoxanthum odoratum* L. (s. str.) and *A. alpinum* Löve & Löve according to the authors enumerated.

<table>
<thead>
<tr>
<th>Author</th>
<th>2n = 20</th>
<th>2n = 10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Östergren</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Different ecological and geographical distribution</td>
<td>Not so tall</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Narrower leaves</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Smaller floral parts (spikelets)</td>
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<tr>
<td></td>
<td></td>
<td>The awn usually protrudes more</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Colour of the ripe panicle often warmer (more like gold)</td>
</tr>
<tr>
<td>Löve &amp; Löve</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Folliis angustioribus et erectoribus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Spiculis minoribus et compactioribus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Aristis longioribus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Semina minora</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Stramenta minus floccata</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Spicae maturae aureae</td>
</tr>
<tr>
<td>Tutin</td>
<td>Leaves of vegetative shoots (2-) 3-5(–10) mm wide</td>
<td>Leaves of vegetative shoots 1–3 mm wide</td>
</tr>
<tr>
<td></td>
<td>Leaves usually spreading Inflorescence (3–)4–6(–7) cm long</td>
<td>Leaves usually erect Inflorescence 1.5–3 cm long</td>
</tr>
<tr>
<td></td>
<td>Spikelets 7–9 mm long</td>
<td>Spikelets 5–6.5 mm long</td>
</tr>
<tr>
<td></td>
<td>Longer awn equalising or rarely slightly exceeding the upper glume</td>
<td>Longer awn 2–3 mm longer than the upper glume</td>
</tr>
<tr>
<td></td>
<td>Pedicels hairy, glumes with at least a few rather long hairs</td>
<td>Pedicels and glumes glabrous</td>
</tr>
<tr>
<td></td>
<td>Caryopsis 2–2.2 mm long</td>
<td>Caryopsis 1.5–1.75 mm long</td>
</tr>
<tr>
<td></td>
<td>Length of guard cells in mature leaves 48–54 μ</td>
<td>Length of guard cells in mature leaves 37–42 μ</td>
</tr>
<tr>
<td>Rozmus¹</td>
<td>Spikelets 5–7 mm long</td>
<td>Spikelets 6–7.5 mm long</td>
</tr>
<tr>
<td></td>
<td>Pubescence on glumes weak, coarsely pubescent along the nerves</td>
<td>Pubescence on glumes somewhat stronger</td>
</tr>
<tr>
<td></td>
<td>Upper awn twice as long as lower awn</td>
<td>Upper awn three times as long as lower awn</td>
</tr>
<tr>
<td></td>
<td>Pubescence of sterile lemmata (&quot;pair of upper glumes&quot;) strong, reaching the top</td>
<td>Pubescence of sterile lemmata (&quot;pair of upper glumes&quot;) strong, surface coarse near the top</td>
</tr>
<tr>
<td></td>
<td>Fertile lemmata (&quot;lemmata&quot;) glossy</td>
<td>Fertile lemmata (&quot;lemmata&quot;) coarse</td>
</tr>
</tbody>
</table>

¹ The terminology used by Rozmus is a little bewildering. Thus what is called "pair of lower glumes" must refer to lower and upper glume, "pair of upper glumes" must be the two sterile lemmata (see also Fig. 1 in Rozmus op. cit.) and "lemmata" must refer to fertile lemmata.

Later on Löve (1945) listed the diploid as “subspecies” and a few years later Löve & Löve (1948) made it a new species. Their original description is, however, mainly a recapitulation of the relative differences already given by Östergren (op. cit.; cp. also Knaben 1950, p. 132; Jørgensen, Sørensen & Westergaard 1958, p. 12). Comparisons made by Tutin (1950) between British tetraploid Anthoxanthum and diploid Anthoxanthum from Switzerland revealed some additional differences. Finally Rozmus (1958) gives the result of a morphologic and cytologic investigation of diploid and tetraploid Anthoxanthum from Poland. The differences between the diploid A. alpinum Löve & Löve and the tetraploid A. odoratum L. s.str. as stated by these authors are enumerated in Table I.

**Morphologic variation within Anthoxanthum odoratum L. s. lat.**

Since the possibilities of distinguishing between the two ploidy types in Sweden on a morphologic basis seemed to be doubtful (see also Östergren op. cit. and Hylander 1953, p. 346) a thorough morphologic investigation was carried out on a representative herbarium material from different parts of Sweden. At my request one of my colleagues at the Institute of Systematic Botany, Uppsala, took out 35 sheets covering all the main parts of Sweden¹ (cp. Table III) and covered the labels so that the place of origin should not be allowed to interfere with my conclusions. On this material all characters mentioned in Table I were measured or scored except the height of the plant and the width of the leaves, as these features are highly dependent, *inter alia*, on soil and water supply in the place were the plant is growing (cp. Hubbard 1954, p. 245). In addition width of panicle, length of lower glume, length of anthers, and size of pollen grains were measured and the presence or absence of scabrities on the fertile lemma was noted. Unfortunately the length of the anthers could not be used consistently on this material because of the age of the specimens. Most of the stamens were already more or less emptied and thus their length reduced.

The results of the measurements are shown in Table II. As can be seen from this table, the variation range in most features is wide. In order to trace any discontinuous variation as regards measurable characters histograms were made for all these characters (Figs. 1 and 2). The presence of two different taxa within the material would then be expected to reveal itself in a more or less marked minimum

¹ and one from Norway.

CYTOTAXONOMIC STUDIES IN ANTHOXANTHUM ODORATUM

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Table II. Measurements in herbarium specimens of Anthoxanthum

odoratum L. s.lat.
The reference number given in the first column refers to Table III. A = width of panicle
B = length of panicle, C = length of spikelet, D= length of lower glume, E= length of
longest awn, F=length of shortest awn (all in mm), G = E/F, H=length of protruding
part of longest awn (in mm), I = pollen size (in scale divisions, each equalling 2.45 ju),
J= length of guard cells (in scale divisions, each equalling 1.05 fi). K and L give the
pubescence on pedicels (K) and glumes (L): + = dense pubescence, (+) = a few hairs,
“glabrous; M = presence (+) or absence (-) of scabrities on fertile lemma, N ='
caryopsis length (in mm). A-H and N refer to mean values of three measurements
within each collection, and I-M to measurements in one and the same specimen, where
I and J give the mean value of 25 measurements. The pollen measurements were
made in lactophenol preparations (cp. Hedberg 1952, p. 257), and the guard cells
were studied according to the method used by Prat (1948).
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32
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34a
34b
35
36

A

B

9.3 44.5
11.3 29.3
10.0 31.7
6.7 29.0
10.3 42.3
7.3 30.3
10.3 24.7
9.0 43.0
9.3 32.0
11.7 24.3
11.7 30.3
6.7 39.7
8.7 33.3
5.7 26.3
11.3 35.7
8.6 31.7
16.0 48.0
5.3 28.8
5.0 24.8
8.3 37.7
9.0 33.0
9.0 21.8
5.3 33.8
7.0 24.8
9.3 24.3
6.0 41.5
6.3 31.2
5.3 25.8
9.0 33.8
9.7 35.8
6.6 28.8
7.7 25.2
5.3 32.3
7.3 23.7
9.3 38.2
5.7 33.0
7.3 34.0

G

D

E

8.1
7.0
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7.8

F

G

H

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I

J

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13.4
17.8
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12.7
15.2
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K

L

41.2
+
44.0
+
43.7
+
45.5
+
46.4
+
41.2
+
49.8
+
50.2
-tu.2
+
45.1
+
42.6
+
47.3
+
48.6
+
43.8
+
46.2
+
54.2
+
49.0
+
50.1
+
_
36.0
48.0
+
50.2
+
_
45.0
38.0 ( + )
46.7 ( + )
43.6
+
—
39.1
_
44.8
_
42.2
_
44.7

+
+
+
+
+
+
+
+
+
+
+
+
+
+
+
+
+

____

_

13.8
15.4
16.1
15.1
13.7
15.0
13.9

41.0
50.3
46.4
34.3
37.8
40.8
42.2

+
+

_
_

1.8

_
_

2.5

_
_
_
_
_
_
_

2.0
2.2

_
_

2.1

_
_

1.9

_

+

2.0

_

2.3

_

_

(+)

+
+

(+)
+
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_

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+
+
+

_
_

_
_
_
_

2.0

_

_

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(+)
(+)

N

_
_

_

(+)
+
(+)
(+)

M

2.0

_

+
+

_

-

—



Fig. 1. Histograms illustrating variation ranges for measurable characters given in Table II. A = width of panicle, B = length of panicle, C = length of spikelet, D = length of lower glume, E = length of longest awn, F = length of shortest awn, H = length of protruding part of longest awn.

in at least some of the histograms. As can be seen from these, none of the measurable characters earlier given to distinguish between the polyplotypes shows such a minimum.

The length and width of the panicle are very variable and certainly dependent on the conditions where the plant is growing which makes them rather unsuitable for taxonomic use (cp. Fig. 1A and B). The length of the spikelets shows no discontinuous variation (Fig. 1C). The limits given by Tutin (op. cit.) in this respect are not relevant to Swedish material, the variation range being 5.9–8.7 mm without any possibility of splitting the material. On material from Poland Rozmus (op. cit.) has found that the tetraploid has in general shorter spikelets than the diploid, their variation ranges, however, overlapping. His conclusion in this respect is thus contrary to those of Tutin (op. cit.) and Östergren (op. cit.). As regards the awns,
stated by Löve & Löve (1948) to be longer in the diploids, no difference can be found in the present material (Fig. 1E and F). The relation between the awns given by Rozmus (op. cit.) as a distinction (longer awn three times as long as the shorter one in alpine material, twice as long in material from lowland localities) does not hold in my material, where in the bulk of the specimens the longer awn is between two and three times as long as the shorter one (cp. Table II:G). In a few samples the ratio rises above three, most of those being, however, from lowland localities. The part of the longest awn protruding above the upper glume is said by Östergren (op. cit.) to be usually longer in alpine material, and the difference in this respect is given by Tutin (op. cit.) to be about 2–3 mm. As can be seen from Fig. 1 H, there is no such difference in the present material. The length of the protruding part seems to be highly dependent on the age of the spikelet and may vary considerably in one panicle (cp. Fig. 3). As the spikelet ripens, it opens up more and more so that the longer awn no longer follows the keel of the glume but bends outward. This feature will certainly add to the impression of a longer protruding part in very ripe specimens, as does also the colour of the awn.

Ripe grains were available only in 10 of the collections, but
already these few values show that the distinction claimed by Tutin (op. cit.) does not hold in Swedish material (cp. Table II: N).

Pollen size and length of guard cells show a great variation in the present material, not only between different populations but also within one and the same specimen (cp. Fig. 2), and none of them can alone be used for taxonomic distinction.

The presence or absence of hairs on pedicels and glumes is used by Tutin (op. cit.) as a main distinction between the tetraploid and the diploid. In Swedish material these characters are, however, extremely variable (cp. Hylander loc. cit.) and not directly correlated to each other, as also shown by Knaben (op. cit.) on material from Norway. In the present material one can find specimens with hairy and glabrous pedicels on the same herbarium sheet and hence this character seems not to be very useful. The pubescence of the glumes is also very variable. In the same sheet one can find some panicles with densely pubescent spikelets, while others are practically glabrous. Also in this respect Rozmus’ (op. cit.) conclusion seems to be contrary to that of Tutin (op. cit.). The statements “weak, coarsely pubescent along the nerves” in the tetraploid and “somewhat stronger” in the diploid (Rozmus op. cit., p. 178) must, as far as I can see, refer to the pubescence of the glumes.

The difference between alpine and lowland material from Poland as regards pubescence of sterile lemmata claimed by Rozmus (op. cit.) does not occur in Swedish material. In none of the specimens investigated does the pubescence reach the top (cp. Pl. I: A–B). The uppermost part is always glabrous, as seems to be the case also in British material (cp. Hubbard op. cit., p. 245).

The occurrence of scabrities on the fertile lemma (cp. Pl. I: C–E) seems to be to some extent correlated with the absence of hairs on the glumes but there is no absolute correlation, non-scabrous lemmata being found in glabrous spikelets and vice versa (cp. Table II).

Evidently no single character shows such a discontinuity in the present material as to support taxonomic segregation. Specimens

Fig. 4. Pictorialized scatter diagram illustrating the combined variation in mean length of guard cells (horizontal axis), mean size of pollen grains (vertical axis), pubescence of glumes, and presence or absence of scabrities on the fertile lemma. Filled circles refer to specimens with more or less pubescent glumes, open circles to specimens with glabrous glumes, and half-filled circles to specimens with just a few hairs on the glumes. The presence of scabrities on the fertile lemma is indicated by a tail. (Based on values from Table II.)

from the northern half of Sweden tend to have in general somewhat smaller pollen grains, however (cp. Tables II and III), and since pollen size as well as the size of guard cells often show correlation to chromosome number, these features were combined in a scatter diagram together with presence or absence of hairs on glumes and presence of scabrities on the fertile lemma (Fig. 4). From this diagram it is evident that there is a strong tendency for specimens having small pollen grains and guard cells to have glabrous glumes and also to some extent to have scabrities on the fertile lemma. Because of the relation of cell size to chromosome number mentioned above, such specimens should a priori be supposed to represent diploids. The absence of hairs on the glumes is not a character exclusive to material from alpine regions, however (cp. Table II), and the amount of scabrities is quite variable in such material (cp. Pl. I:C–E). Furthermore, amongst the supposed diploids with small pollen grains etc. some specimens are found which in every other respect correspond to the lowland type.

Thus in spite of a careful analysis no sharp morphological distinction can be drawn and it seems impossible to decide in many cases whether a herbarium specimen belongs to the diploid or the tetraploid race without having access to the chromosome number.

In a later contribution I am going to test the morphological characters reported here on cytologically examined material, and to map the distribution of the two chromosome races in Sweden.

Summary.

A thorough morphologic investigation of a representative herbarium material of *Anthoxanthum odoratum* L. s. lat. from various parts of Sweden has demonstrated that neither the morphological differences claimed by Löve & Löve (1948) and other authors (cp. survey in Table I) nor other morphological features studied permit reliable distinction between (diploid) *A. alpinum* Löve & Löve and (tetraploid) *A. odoratum* L. s. str. in herbarium specimens.

Acknowledgements.

This investigation has been carried out at the Institutes of Genetics and of Systematic Botany of the University of Uppsala, partly during the tenure of a scholarship from Uppsala University (“licentiand-stipendium”). For advice and information I am indebted to Dr. A. Nygren, Prof. J. A. Nannfeldt, and my husband Dr. O. Hedberg. The English text was revised by Mrs. C. Hörner, Uppsala.

REFERENCES.

Hedberg, O., 1952: Cytological studies in East African mountain grasses. — Hereditas 38, pp. 256–266.


**Explanation of the plate.**

Photographs illustrating the pubescence of sterile lemmata (A–B) and the occurrence of scabrities on the fertile lemma (C–E).
A, Sterile lemma from lowland material (No. 12 in Table III), ×20.
B, Sterile lemma from alpine material (No. 26 in Table III), ×20.
C–E. Fertile lemmata from alpine material, ×55. C from No. 28, D from No. 26, and 
E from No. 31 in Table III.
INGA HEDBERG: ANTHOXANTHUM ODORATUM

PHYSIOLOGICAL STUDIES ON FUNGI ISOLATED FROM SLIME FLUX.

BY

BRITA NYMAN.

Introduction.

When a deciduous tree has been felled, the sap rises in the stump the following spring, forming a damp surface which may constitute the habitat of various fungi. A similar habitat is formed on a wounded stem. Fungi growing on this slime flux seem to be especially common on birches.

This paper deals with the nutritional requirements of some fungi isolated from slime flux.

Isolation of test material.

The fungus material is to be found on the stump or stem as a slimy mass, white, yellow, or pink in colour. A sample of such a mass was scraped off with a scalpel which had been dipped in 70 % ethanol. The sample was later suspended in distilled water, and five different dilutions were made. 1 ml of a dilution was pipetted into a sterilized Petri dish. The sterilized and melted agar medium was then added, and the dish was rotated in order to distribute the suspension evenly. The temperature of the agar was about 40°C. The single cells or hyphae grew out, forming isolated colonies which could be transferred to malt agar plates. This method of making sterile pure cultures can be used for phycomycetes and ascomycetes.

The following agar media were used for the isolations:

1. Malt agar
   - Malt extract: 25 g
   - Agar: 15 g
   - Dist. water: 1000 ml

2. Lactose
   - 10 g
   - NH₄H₂PO₄: 2.37 g
   - KH₂PO₄: 1 g
   - Na₂HPO₄: 2.25 g

9 – 61173301

When isolating microorganisms from soil, WARCUP (1951) treated samples of soil with steam at 100°C. He found that many species were killed by steaming for 3–5 min. On the other hand, he was able to isolate various species which had not been detectable in untreated samples.

WARCUP’s method was applied to the material collected from slime flux in the following way. A glass flask containing a sample of the fungus material was placed in a vigorously steaming autoclave. It appeared that no microorganisms survived even such a brief exposure to the steam as 1 min, so the isolations of pure cultures had to be made from untreated samples.

The fungus strains were kept as stock cultures on malt agar at about 8°C. Prior to the first experiment with a particular strain, a new cell suspension was made, 1 ml was pipetted into a Petri dish, malt agar was poured on and the fungus was isolated from one of the colonies growing out.

This investigation comprises the following strains:

<table>
<thead>
<tr>
<th>Host</th>
<th>Locality</th>
<th>Agar medium of isolation</th>
</tr>
</thead>
<tbody>
<tr>
<td>3b <em>Rhodotorula</em> sp. a</td>
<td>Hornbeam Uppland, Funbo parish</td>
<td>1</td>
</tr>
<tr>
<td>3c <em>Rhodotorula</em> sp. a</td>
<td>Hornbeam Uppland, Funbo parish</td>
<td>1</td>
</tr>
<tr>
<td>7a <em>Rhodotorula</em> sp. a</td>
<td>Birch Skåne, Toßjö parish</td>
<td>1</td>
</tr>
<tr>
<td>18b <em>Rhodotorula</em> sp. a</td>
<td>Birch Västmanland, the town of Västeräs</td>
<td>1</td>
</tr>
<tr>
<td>33a <em>Rhodotorula</em> sp. a</td>
<td>Birch Dalecarlia, Mora parish</td>
<td>2</td>
</tr>
<tr>
<td><em>Phialophora</em> sp. b</td>
<td>Oak Uppland, Funbo parish</td>
<td>1</td>
</tr>
<tr>
<td><em>Dipodascus aggregatus</em> b,c</td>
<td>Dalecarlia, Mora parish</td>
<td>?</td>
</tr>
</tbody>
</table>

*a Kindly determined by Dr. R. SANTESSON, Uppsala.
*b Kindly determined by Dr. A. KÄÄRIK, Stockholm.
*c Kindly determined by Dr. L. R. BATRA, Swarthmore, Pa. U.S.A.

Methods.

Prior to use, all glass vessels were cleaned with a sulphuric acid-dichromate solution, then thoroughly rinsed with hot tap-water and allowed to stand filled with hot (softened) water for about 24 hours. Then they were rinsed

with distilled water and allowed to stand filled with distilled water for a few hours.

The chemicals used were of the highest purity obtainable.

The sterilization of the solutions was generally performed by autoclaving up to 120°C and sometimes by filtering through a sterilized glass filter “Jena G5”.

The pH values were determined by means of a potentiometer 22, Radiometer, Copenhagen. The readings could be made with an accuracy of about 0.03 pH units.

**Rhodotorula.** In all experiments with liquid media the fungi were cultivated in glass tubes with a diameter of 20 mm. Triplicates were made in each series.

The empty culture tubes were autoclaved. In all experiments the medium was composed of different solutions which were autoclaved separately and mixed after autoclaving and cooling. 10 ml of the complete medium were then aseptically added to each culture tube. The tubes were inoculated with 0.5 ml of a suspension prepared by scraping yeast cells from a malt agar plate with the aid of a platinum needle and suspending them in sterilized distilled water. The malt agar culture was generally 3–7 days old.

The culture tubes were continuously shaken at 20°C and growth determined turbidimetrically. These determinations were made partly by means of a photometer constructed by Åberg & Rodhe (1942) and partly by means of an Engel colorimeter (Kipp, Delft) at 610 μm. This wavelength was chosen with regard to the absorption spectra of the pigments shown in Rhodotorula cells (Goodwin, 1952). Unless otherwise stated, the photometer of Åberg & Rodhe has been used.

The extinction values have been expressed according to the relation

\[ Z = (e_t - e_0) \times 10^3, \]

where \( e_t \) = extinction at time \( t \) and \( e_0 \) = extinction at time 0 (initial extinction). The various extinction values may be calculated from the formula

\[ e = \log \frac{I_0}{I}, \]

where \( I_0 \) = intensity of incident light and \( I \) = intensity of transmitted light.

The initial pH value was determined from the uninoculated medium of a series, the final pH from the liquid of one tube of the series.

**Phialophora and Dipodascus.** The fungi were cultivated at 25°C in 100 ml glass flasks containing 25 ml of liquid nutrient solution. Six replicates were made in each series.

The inoculations were made from malt agar plates (N. Friis, 1938), as a rule 3–7 days old. The inocula were about 3 x 3 mm, and were immersed in the liquid.

The initial pH was determined from the uninoculated solution, the final pH from the pooled liquids from the flasks of a series.

The experiments with Phialophora proceeded for 8 days, the ones with
*Dipodascus* for 21 days. Upon harvesting, the mycelia were thoroughly washed with distilled water, dried at 100°C for about 24 hours and weighed.

The weight value given for a series is the mean dry weight of the mycelia from all the replicates. The standard error of the mean ($\varepsilon$) was calculated from the formula

$$
\varepsilon = \pm \sqrt{\frac{\Sigma (m - M)^2}{n(n-1)}},
$$

where $m$ = dry weight of the mycelium from one particular flask, $M$ = mean value of the dry weights of the mycelia from the series and $n$ = number of flasks of the series.

Nutrient solutions:

<table>
<thead>
<tr>
<th>Medium A 1</th>
<th>(modified from L. Fries, 1955)</th>
</tr>
</thead>
<tbody>
<tr>
<td>p-Glucose</td>
<td>10 g</td>
</tr>
<tr>
<td>K-Na-tartrate</td>
<td>0.76 g</td>
</tr>
<tr>
<td>KH$_2$PO$_4$</td>
<td>1 g</td>
</tr>
<tr>
<td>Na$_2$HPO$_4$•2H$_2$O</td>
<td>2.25 g</td>
</tr>
<tr>
<td>Na$_2$SO$_4$</td>
<td>0.28 g</td>
</tr>
<tr>
<td>Vitamin mixture</td>
<td>10 ml</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Medium A 2</th>
<th>(modified from L. Fries, 1955)</th>
</tr>
</thead>
<tbody>
<tr>
<td>NH$_4$H$_2$PO$_4$</td>
<td>2.37 g</td>
</tr>
<tr>
<td>KH$_2$PO$_4$</td>
<td>1 g</td>
</tr>
<tr>
<td>Na$_2$HPO$_4$•2H$_2$O</td>
<td>2.25 g</td>
</tr>
<tr>
<td>Na$_2$SO$_4$</td>
<td>0.28 g</td>
</tr>
</tbody>
</table>

| Medium A 3          |                                |
|---------------------|                                |
| L-Asparagine       | 1 g                            |
| KH$_2$PO$_4$        | 0.15 g                         |
| K$_2$HPO$_4$        | 0.35 g                         |
| Na$_2$SO$_4$        | 0.28 g                         |

<table>
<thead>
<tr>
<th>Medium B</th>
<th>(L. Fries, 1955)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CaCl$_2$•H$_2$O</td>
<td>116.2 mg</td>
</tr>
<tr>
<td>MgCl$_2$•6H$_2$O</td>
<td>410 mg</td>
</tr>
<tr>
<td>Ferricitrate</td>
<td>5.31 mg</td>
</tr>
<tr>
<td>Citric acid</td>
<td>5.31 mg</td>
</tr>
<tr>
<td>MnSO$_4$•4H$_2$O</td>
<td>4.43 mg</td>
</tr>
<tr>
<td>ZnSO$_4$•7H$_2$O</td>
<td>4.05 mg</td>
</tr>
<tr>
<td>Dist. water</td>
<td>40 ml</td>
</tr>
</tbody>
</table>

Medium B was always autoclaved separately. The quantities of distilled water were adjusted so that 1000 ml was added to the complete medium, e.g. medium A2 + medium B + a solution of glucose.

<table>
<thead>
<tr>
<th>Vitamin mixture</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Biotin</td>
<td>2 µg</td>
</tr>
<tr>
<td>Ca-pantothenate</td>
<td>400 µg</td>
</tr>
<tr>
<td>Inositol</td>
<td>2000 µg</td>
</tr>
<tr>
<td>Niacin</td>
<td>400 µg</td>
</tr>
<tr>
<td>p-Aminobenzoic acid</td>
<td>200 µg</td>
</tr>
<tr>
<td>Pyridoxine hydrochloride</td>
<td>400 µg</td>
</tr>
<tr>
<td>Thiamine hydrochloride</td>
<td>400 µg</td>
</tr>
<tr>
<td>Riboflavin</td>
<td>200 µg</td>
</tr>
</tbody>
</table>

The concentrated stock solution contained these quantities per 10 ml. Ten millilitres of this solution was added to 1 l of nutrient solution.

Buffer solutions:

<table>
<thead>
<tr>
<th>No.</th>
<th>ml of $\frac{1}{15} M$ KH$_2$PO$_4$</th>
<th>ml of $\frac{1}{10} N$ HCl</th>
<th>ml of $\frac{1}{15} M$ KH$_2$PO$_4$</th>
<th>ml of $\frac{1}{15} M$ Na$_2$HPO$_4$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>75</td>
<td>75</td>
<td>149.5</td>
<td>0.5</td>
</tr>
<tr>
<td>2</td>
<td>129</td>
<td>21</td>
<td>131.5</td>
<td>18.5</td>
</tr>
<tr>
<td>3</td>
<td>144</td>
<td>6</td>
<td>110</td>
<td>40</td>
</tr>
<tr>
<td>4</td>
<td>146</td>
<td>4</td>
<td>93</td>
<td>57</td>
</tr>
<tr>
<td>5</td>
<td>149.5</td>
<td></td>
<td>55</td>
<td>95</td>
</tr>
<tr>
<td>6</td>
<td>131.5</td>
<td></td>
<td>24</td>
<td>132</td>
</tr>
<tr>
<td>7</td>
<td>110</td>
<td></td>
<td>14</td>
<td>140</td>
</tr>
<tr>
<td>8</td>
<td>93</td>
<td></td>
<td>3</td>
<td>147</td>
</tr>
<tr>
<td>9</td>
<td>55</td>
<td></td>
<td>10</td>
<td>140</td>
</tr>
<tr>
<td>10</td>
<td>24</td>
<td></td>
<td>34</td>
<td>116</td>
</tr>
<tr>
<td>11</td>
<td>14</td>
<td></td>
<td>60</td>
<td>90</td>
</tr>
<tr>
<td>12</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>10</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>34</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>60</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Rhodotorula.**

1. Growth with different nitrogen sources.

Investigations on the ability of various yeasts to utilize different nitrogen sources have been performed by several scientists, e.g. Wickerham (1946), who dealt with strains of *Torulopsis*, *Kloeckera*, and *Candida* as to their utilization of ammonium sulfate, asparagine, urea, and peptone. Lodder & Kreger-van Rij (1952) in defining the species of the genus *Rhodotorula*, made use of their varying ability to utilize nitrate. Husain & Hardin (1952) cultivated *R. gracilis* with six different nitrogen compounds: asparagine, urea, ammonium sulfate, ammonium chloride, yeast extract, and Bactopeptone. They found the use of asparagine produced the highest yields of both cell mass and lipids.

**Experiment 1.**

*Strain. Rhodotorula* 3b.

*Nitrogen sources tested.* KNO$_3$, KNO$_2$, NH$_4$H$_2$PO$_4$, (NH$_4$)$_2$-tartrate, l-asparagine, l-aspartic acid, urea.

Fig. 1. Growth of *Rhodotorula 3b* with different nitrogen sources.

Final pH. 6.20–8.60.

Nutrient solution. Medium A1 + B.

The nutrients of medium A1 were dissolved in 80% of the final amount of distilled water. For each series 100 ml of this solution was autoclaved. A solution was prepared from each nitrogen compound containing 105 mg of nitrogen per 100 ml. The pH was adjusted to 6.80–7.00. All the solutions were autoclaved except that of urea which was sterilized by filtering. When the solutions had cooled, 5 ml of medium B + 25 ml of “nitrogen solution” (in the control series 25 ml of distilled water) were added to each flask containing medium A1. The nutrient solutions contained 202 mg of nitrogen per l.

Experiment 2.

Strain. *Rhodotorula* 18b.

Nitrogen sources tested. KNO₃, KNO₂, NH₄H₂PO₄, (NH₄)₂-tartrate, L-asparagine, L-aspartic acid, urea.


Nutrient solution. Medium A1 + B.

The solutions were prepared as in Experiment 1 except that the solutions of the nitrogen compounds contained 131.3 mg of nitrogen per 100 ml. After autoclaving, 5 ml of medium B + 20 ml of "nitrogen solution" (in the control series 20 ml of distilled water) were added to each flask containing medium A1. The nutrient solutions contained 210 mg of nitrogen per l.

As can be seen from Fig. 1, the strain 3b produced good growth with all the nitrogen compounds investigated. Similar results were found with the strain 3c and also with 7a and 33a, although in these strains growth was slower with nitrate and nitrite.

The strain 18b, on the other hand, was unable to grow with either nitrate or nitrite as the nitrogen source, as is shown by Fig. 2. Be-
cause of the shortcomings of the photometer, the values of $Z$ exceeding 1000 must be considered uncertain.

In the following experiments, ammonium dihydrogen phosphate was chosen as source of nitrogen. All the strains made good growth with this compound and, because it does not contain carbon, it can be used for experiments with different carbon sources.

2. Growth with different mono- and disaccharides.

The schemes for determining the species of the genus *Rhodotorula* published by LODDER (1934) and LODDER & KREGER-VAN RIJ (1952) are, among other things, founded upon their ability to utilize different sugars. LODDER chiefly made use of an auxanographic method for the tests. HUSAIN & HARDIN (1952) investigated the effect of some sugars on *R. gracilis* in an asparagine medium and found that glucose produced the highest yield of cell mass, while sucrose gave the highest content of lipids. According to LÖHR (1953), the sugars present in sap are glucose, fructose, and traces of sucrose.

*Table I. Growth of Rhodotorula 3c with different sugars (Experiment 3).*

<table>
<thead>
<tr>
<th>Hexose</th>
<th>Value of $Z$ after 70 hours</th>
</tr>
</thead>
<tbody>
<tr>
<td>None</td>
<td>25</td>
</tr>
<tr>
<td>D-Glucose</td>
<td>1723</td>
</tr>
<tr>
<td>D-Fructose</td>
<td>1545</td>
</tr>
<tr>
<td>D-Mannose</td>
<td>1689</td>
</tr>
<tr>
<td>D-Galactose</td>
<td>243</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Disaccharide</th>
<th>Values of $Z$ after 71 hours</th>
</tr>
</thead>
<tbody>
<tr>
<td>None</td>
<td>31</td>
</tr>
<tr>
<td>Maltose</td>
<td>1684</td>
</tr>
<tr>
<td>Sucrose</td>
<td>1630</td>
</tr>
<tr>
<td>Lactose</td>
<td>29</td>
</tr>
<tr>
<td>Cellobiose</td>
<td>355</td>
</tr>
</tbody>
</table>

*Experiment 3 (Table I).*


*Final pH.* 3.10–6.70.

*Nutrient solution.* Medium A 2 + B with 10 ml of vitamin mixture per l.

The nutrients of medium A2 were dissolved in 80% of the final amount of distilled water. For each series 100 ml of this solution was autoclaved. Solutions with a content of 5 g per 100 ml of each sugar were prepared. The hexoses were autoclaved while the disaccharides were sterilized by filtering. After autoclaving, each flask containing medium A2 was supplied with 5 ml of medium B + 25 ml of a sugar solution (in the control series 25 ml of distilled water). The nutrient solutions contained 9.62 g of sugar per 1.

Table II. Growth of *Rhodotorula* 18b with different sugars (Experiment 4).

<table>
<thead>
<tr>
<th>Sugar</th>
<th>Value of Z after 114 hours</th>
</tr>
</thead>
<tbody>
<tr>
<td>None</td>
<td>9</td>
</tr>
<tr>
<td>D-Glucose</td>
<td>1400</td>
</tr>
<tr>
<td>D-Galactose</td>
<td>4</td>
</tr>
<tr>
<td>Maltose</td>
<td>39</td>
</tr>
<tr>
<td>Sucrose</td>
<td>799</td>
</tr>
</tbody>
</table>

Experiment 4 (Table II).

*Initial pH. 6.50–6.70.*

*Nutrient solution. Medium A2 + B with 200 μg PABA and 400 μg thiamine hydrochloride per l.*

The solutions were prepared as in Experiment 3, except that the sugar solutions contained 6.25 g per 100 ml. After autoclaving, 5 ml of medium B + 20 ml of a sugar solution (in the control series 20 ml of distilled water) were added to each flask containing medium A2. The nutrient solutions contained 10 g of sugar per l.

The Engel colorimeter was used.

The strain 3c produced good growth with glucose, fructose, mannose, maltose, and sucrose. Growth was less with galactose and cellobiose. No growth was produced with lactose.

The behaviour of the strain 3b was shown to be similar to that of 3c. The strain 7a resembled 3c, too, except that growth was also good with cellobiose.

The strain 18b produced the best growth with glucose as the carbon source. With sucrose, growth was somewhat poorer. This fungus was unable to grow with galactose and maltose. With these carbon sources, no growth could be observed even after 16 days. According to earlier experiments, 18b could utilize fructose, mannose, and possibly cellobiose to a small extent, but was unable to utilize lactose.

3. Growth with glucose of varying concentrations.

When the sap has ceased rising in a stump, the damp surface gradually dries up. Thereby, of course, the substrate is changed for the fungi being nourished upon the slime flux. This will be still more concentrated as to the nutrients, and the osmotic pressure will rise considerably.

Numerous so-called osmophilic fungi and bacteria are known. They can stand or even require substrates possessing a high osmotic pressure. Such organisms have been found e.g. in honey and in brine. A survey of earlier investigations of osmophilic fungi and bacteria was made by Kroemer & Krumholz (1931). According to Zopf (1892), the water bacterium Bacillus disciformis was capable of growing in a solution of nearly 55% glucose. (By % Zopf probably meant the number of g per 100 g of solution. The following percentage values refer to the number of g per 100 ml of solution.)

Among the osmophilic fungi, Aspergillus repens is worth mentioning (Klebs, 1928). The limiting concentration of growth for this fungus was said to be as high as 95% glucose or 100% sucrose. Growth was more abundant in a solution containing 80% sugar than in one containing 20%. According to Laurent (1890), 55% invert sugar can be regarded as the upper limiting concentration for yeasts.

The effect of a concentrated nutrient solution upon an organism is not only due to the osmotic pressure but also to the compounds causing this pressure. For the experiments with the fungi isolated from slime flux, glucose was chosen because this sugar is abundantly found in sap.

Table III. Concentrations of glucose tested in Rhodotorula 7a and 18b (Experiment 5). % = g per 100 ml of nutrient solution.

<table>
<thead>
<tr>
<th>% of d-glucose</th>
<th>Initial pH</th>
<th>Final pH</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>7a</td>
</tr>
<tr>
<td>0</td>
<td>6.35</td>
<td>6.40</td>
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<td>1</td>
<td>6.40</td>
<td>3.30</td>
</tr>
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<td>2</td>
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<td>3.45</td>
</tr>
<tr>
<td>50</td>
<td>5.85</td>
<td>3.85</td>
</tr>
</tbody>
</table>

Fig. 3. Growth of *Rhodotorula* 7a with D-glucose of varying concentrations.

**Experiment 5 (Table III).**

*Nutrient solution.* Medium A2 + B with 10 ml of vitamin mixture per l. Medium A2 with 20% of the final amount of distilled water was autoclaved. 162.5 g of glucose was dissolved in distilled water up to a volume of 250 ml. In addition, by diluting this 65% solution, glucose solutions

Fig. 4. Growth of *Rhodotorula* 18b with D-glucose of varying concentrations.

with the following concentrations were prepared: 26%, 13%, 6.5%, 2.6%, and 1.3%. 100 ml of each solution (in the control series 100 ml of distilled water) was autoclaved and then supplied with 25 ml of medium A 2 + 5 ml of medium B.

As can be seen from Fig. 3, the strain 7a produced fairly good growth with 20% glucose, although growth was still better with the lower concentrations. This fungus was able to grow even with 50% glucose. At this concentration however, the lag period was about three days as compared with the normal period of less than one day. Strains 3b and 3c proved to agree with 7a.

Fig. 4 shows that growth of strain 18b was considerably retarded when the glucose concentration reached 20%. With 50% no growth was obtained after seven days.

4. Growth with different vitamins.

The vitamin requirements of yeasts have been the subjects of several investigations. Many strains of the genus *Saccharomyces* have been found to require one or more of the following vitamins: biotin, pantothenic acid, inositol, niacin, pyridoxine, and thiamine (Leonian & Lilly, 1942; Burkholder, McVeigh & Moyer, 1944).

Several species of *Rhodotorula* have also been investigated as to their vitamin requirements. Schöpfer (1937, 1938) found that *R. rubra, R. mucilaginosa* and *R. flava* required thiamine or the pyrimidine moiety of this vitamin and that *R. aurea* and *R. glutinis* were able to grow without the addition of vitamins. Robbins & Ma (1944) showed that *R. aurantiaca* required thiamine + p-aminobenzoic acid (PABA) for growth. It was unable to grow with thiamine replaced with pyrimidine, thiazole or pyrimidine + thiazole.

**Experiment 6.**

*Strain. Rhodotorula 3b.*  
*Vitamins tested. Ca-pantothenate (400 μg per l), niacin (400 μg per l), PABA (200 μg per l), riboflavin (200 μg per l), vitamin mixture.*  
*Initial pH. 6.35–6.40.*  
*Final pH. 2.90–3.00.*  
*Nutrient solution. Medium A 2 + B with 1% glucose.*  

The salts of medium A2 were dissolved in 70% of the final amount of distilled water. For each series, the amount of vitamins corresponding to 1 l of nutrient solution was dissolved in 100 ml of distilled water. 5 ml of vitamin solution (in the control series 5 ml of distilled water) was added to *Sv. Bot. Tidskr.*, 55 (1961): 1
35 ml of medium A2, and the mixtures then autoclaved. A solution of glucose containing 6.25 g per 100 ml was autoclaved separately. After autoclaving, each flask containing medium A2 + vitamins was supplied with 2 ml of medium B + 8 ml glucose solution.

**Experiment 7.**

*Strains.* Rhodotorula 7a and 18b.

*Vitamins tested.* The vitamin mixture complete, as well as with each individual vitamin excluded.


*Final pH.* 3.50–6.40.

*Nutrient solution.* Medium A2 + B with 1% glucose.

Fig. 6. Growth of *Rhodotorula* 7a with the vitamin mixture added to the medium and the effect of excluding each individual vitamin of the mixture. The growth curves devoid of markings refer to inositol, niacin, PABA, pyridoxine, and riboflavin excluded.

The salts of medium A2 were dissolved in 60% of the final amount of distilled water. For each series, the amount of vitamins corresponding to 1 l of nutrient solution was dissolved in 160 ml of distilled water. 16 ml of vitamin solution (in the control series 16 ml of distilled water) was added to 60 ml of medium A2. The mixtures were autoclaved. A 5 g per 100 ml glucose solution was autoclaved separately. After cooling, 4 ml of medium B + 20 ml glucose solution were added to each flask containing medium A2 + vitamins.

Fig. 5 shows that the strain 3b could grow without the addition of vitamins. Growth was, however, considerably accelerated in the presence of Ca-pantothenate. This substance alone stimulated growth to the same extent as the vitamin mixture.

As can be seen from Fig. 6, strain 7a produced no growth beyond that of the control series when thiamine was excluded. Growth was very slow in the series without biotin. In the series where Ca-pantothenate was excluded, growth was not as good as in the other series with vitamins added. Strain 7a seems to require thiamine and to be considerably stimulated by biotin and Ca-pantothenate.

As shown by Fig. 7, strain 18b produced no growth beyond that of the control series when PABA or thiamine was excluded. This strain therefore seems to be deficient for these two vitamins.

5. Attempts to replace vitamins with certain other substances.

a. Biotin.

Du Vignaud et al. (1942) reported that pimelic acid could replace biotin for a strain of the diphtheria bacterium. The authors supposed pimelic acid to be a precursor of biotin in this organism. According to Eakin & Eakin (1942), the synthesis of biotin in Aspergillus niger is considerably increased in the presence of pimelic acid. Cysteine or cystine enhanced this effect. Robbins & Ma (1942) studied 13 biotin-deficient fungi as to the utilization of pimelic acid alone and
together with L-cystine, glutathione or methionine. It turned out that none of these additions was able to replace biotin for any one of the fungi investigated.

The *Rhodotorula* strain 7a, which had proved to be greatly stimulated by biotin, was subjected to an attempt to replace the biotin (2 µg per l) with 1.31 µg pimelic acid per l, 1.31 µg pimelic acid per l + 0.99 µg L-cysteine per l and 1.31 µg pimelic acid per l + 990 µg L-cysteine per l. No growth was obtained with any of these alternatives.

Several investigators dealing with biotin-deficient fungi have reported that the concentration of biotin in the nutrient solution can be decreased if aspartic acid is added. Mathiesen (1950) found that in *Ophiostoma pini* both aspartic acid and oleic acid entirely replaced biotin. Later, the same author (Käärik, 1960) studied 10 different blueing fungi deficient for biotin, most of them species of *Ophiostoma*. This investigation showed that the effect of aspartic acid and oleic acid on the different fungi was very divergent. For most species, however, growth was considerably more abundant with biotin than with aspartic or oleic acid.

The growth of strain 7a in a medium lacking biotin was not increased by the addition of L-aspartic acid (400 µg per l), oleic acid in the form of Tween 80 (about 400 µg oleic acid per l) or both. The experiment was carried out at three different pH values: 4.20, 4.65 and 6.35.

**b. Pantothenic acid.**

Weinstock et al. (1939) reported that a strain of *Saccharomyces cerevisiae* synthesized pantothenic acid if cultivated in a medium containing β-alanine. According to Lilly & Barnett (1951), β-alanine is generally not so effectively utilized as pantothenic acid.

**Experiment 8.**

*Strain. 7a.*

*Substances tested.* β-alanine (149.6 µg per l) and Ca-pantothenate (400 µg per l).

*Nutrient solution.* Medium A2 + B with 1 % glucose, 2 µg biotin per l and 400 µg thiamine hydrochloride per l.

The nutrient solutions were prepared in the same way as in Experiment 6.

As shown by Fig. 8, the same growth for strain 7a was obtained with Ca-pantothenate as with an equivalent amount of β-alanine. The values of \( Z \) exceeding 1000 are uncertain.

Further experiments with strain 3b showed that Ca-pantothenate (400 \( \mu \)g per 1) was entirely replaced by an equivalent amount of \( \beta \)-alanine, or even half this amount. This, however, does not necessarily mean that the fungus utilized \( \beta \)-alanine as well as or even more effectively than pantothenate, for the latter may have been present in excess.

The strains 3c and 33a were found to agree with 3b in making the same growth with Ca-pantothenate (400 \( \mu \)g per 1) as with the vitamin mixture. The pantothenate could be entirely replaced with the equivalent amount of \( \beta \)-alanine, or half this amount.

\[ \text{So. Bot. Tidskr., 55 (1961): 1} \]
c. p-Aminobenzoic acid.

The results of some experiments with the strain 18b as to the effects of PABA, pteroylglutamic acid, purines, amino acids and thymine, as well as the inhibiting effects of sulphadiazine will be published later.

Davis (1950) reported that some mutants of *Escherichia coli* required *p*-hydroxybenzoic acid for growth. PABA could be utilized too, but *p*-hydroxybenzoic acid was much more active. According to this, PABA might be a precursor of *p*-hydroxybenzoic acid.

Strain 18b produced no growth when the PABA of the nutrient solution was replaced with an equivalent amount of *p*-hydroxybenzoic acid.

d. Thiamine.

Experiment 9.

*Strain*. 7a.

*Substances tested*. Pyrimidine (250 μg per l), thiazole (170 μg per l), pyrimidine (250 μg per l) + thiazole (170 μg per l), thiamine hydrochloride (400 μg per l).


*Nutrient solution*. Medium A2 + B with 1% glucose, 2 μg biotin per l, and 400 μg Ca-pantothenate per l.

The salts of medium A2 were dissolved in 60% of the final amount of distilled water. For each series, the amount of vitamins corresponding to 1 l of nutrient solution was dissolved in 60 ml of distilled water. 3 ml of vitamin solution (in the control series 3 ml of distilled water) was added to 30 ml of medium A2 and the mixtures autoclaved. A solution of glucose containing 1 g glucose per 30 ml was autoclaved separately. After autoclaving, each flask containing medium A2 + vitamins was supplied with 2 ml of medium B + 15 ml glucose solution.

Experiment 10.

*Strain*. Rhodotorula 18b.

*Substances tested*. Pyrimidine (250 μg per l), thiazole (170 μg per l), pyrimidine (250 μg per l) + thiazole (170 μg per l), thiamine hydrochloride (400 μg per l).

*Initial pH*. 6.95–7.00.


*Nutrient solution*. Medium A3 + buffer + B with 1% glucose and 200 μg PABA per l. Buffer solution: 114 ml \(\frac{1}{10} M\) Na₂HPO₄ + 66 ml \(\frac{1}{15} M\) KH₂PO₄.

The salts of medium A3 were dissolved in 28% of the final amount of distilled water. For each series, the amount of vitamins corresponding to 1 l of nutrient solution was dissolved in 20 ml of distilled water. For each series, 14 ml of medium A3 + 30 ml buffer solution + 1 ml vitamin solution (in the control series 1 ml of distilled water) were mixed and then autoclaved.

Fig. 9. Growth of *Rhodotorula* 7a with thiamine replaced with its moieties, single and together.

A glucose solution containing 5 g per 30 ml was autoclaved separately. After autoclaving, each flask containing medium A3 + buffer + vitamins was supplied with 2 ml of medium B + 3 ml glucose solution.

In this experiment inoculation was performed with cells grown in a liquid medium lacking thiamine and its moieties. The cells were separated from the nutrient solution by centrifugation and then suspended in sterilized distilled water.

As can be seen from Fig. 9, strain 7a produced the same growth with pyrimidine and with pyrimidine + thiazole as with thiamine. With thiazole, no growth beyond that of the control series was made. The growth in the control series was probably due to an extraordinarily high content of vitamins in the inoculation suspension. The suspension may have been denser than usual, or it may have contained traces of malt agar.

Fig. 10 shows that, for the strain 18b, thiamine could be entirely replaced by pyrimidine + thiazole. With pyrimidine alone and thiazole alone growth was very slow. The values of $Z$ exceeding 1000 are uncertain. The experiment was performed at pH 2.90 in the same way with similar results.

Fromageot & Tchang (1938) reported that Rhodotorula sanniei could not utilize glucose as the carbon source without the addition of thiamine or pyrimidine. On the other hand, it was able to grow with glycerol without thiamine added. The glycerol was carefully purified. Moreover the authors compared the course of growth first with glucose + glycerol as the carbon source and secondly with glucose + thiamine. The course of the growth curves was rather different, which was thought to indicate that the effect was not due to a contamination from thiamine or pyrimidine.

Experiments with the thiamine-requiring Rhodotorula strains 7a and 18b proved that none of them was able to grow with glycerol without the addition of thiamine.

6. Growth at different pH values.

The effect of the pH on growth (rate and total amount) of *Rhodotorula gracilis* was investigated under controlled conditions of aeration by Spotholz, Litchfield & Ordal (1956). They tested different pH values between 2.5 and 7.5 at 32°C. The optimum value of pH was found to be 4.5.

*Table IV.* Buffer solutions added to the nutrient solution for cultivating *Rhodotorula* 7a and 18b at different pH values. Final pH values for 18b are lacking (Experiment 11).

<table>
<thead>
<tr>
<th>Buffer solution no.</th>
<th>7a</th>
<th>18b</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Initial pH</td>
<td>Final pH</td>
</tr>
<tr>
<td>1</td>
<td>2.00</td>
<td>2.05</td>
</tr>
<tr>
<td>2</td>
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</tr>
<tr>
<td>14</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>15</td>
<td>8.90</td>
<td>8.40</td>
</tr>
</tbody>
</table>

*Experiment 11 (Table IV).*

Nutrient solution: Medium A3 + buffer + B with 1% glucose and the necessary vitamins.

The salts of medium A3 were dissolved in 30% of the final amount of distilled water. For each series and strain, 15 ml of medium A3 (with vitamins) was added to 30 ml of buffer solution and then autoclaved. A solution of glucose containing 5 g per 30 ml was autoclaved separately. After cooling, each flask containing medium A3 + buffer was supplied with 2 ml of medium B + 3 ml glucose solution.

At pH values exceeding 7-8, a precipitate was formed in the medium. In these series, of course, the values for Z were affected not only by the growth of the fungus but also by the successive dissolving of the precipitate as the salts were consumed.

Fig. 11 shows that strain 7a grew at all pH values investigated between 2.90 and 7.95. The most rapid growth was obtained at 7.00. The values for Z exceeding 1000 are uncertain.

The strains 3b and 33a proved to be similar to 7a as to the pH

Fig. 11. Growth of *Rhodotorula* 7a at different pH values. The numbers refer to the initial pH values of the nutrient solutions.

range for growth. These strains, however, produced the most rapid growth at pH values about 5.

As can be seen from Fig. 12, strain 18b could grow at the pH values investigated between 2.90 and 7.00. There was no growth at pH 7.65. The most rapid growth was obtained at pH 5.45. The values for $Z$ exceeding 1000 are uncertain.

Fig. 12. Growth of *Rhodotorula* 18b at different pH values. The numbers refer to the initial pH values of the nutrient solutions.

Fig. 13. Growth of *Rhodotorula* 7a determined turbidimetrically (open circles) and by weighing the dried cells of duplicate samples at each time (filled circles).

7. Comparison between turbidimetric determinations and dry weight determinations.

Fig. 13 shows growth of strain 7a measured both turbidimetrically with the aid of the Engel colorimeter and by weighing the cells. After each turbidimetric determination from 47 hours, two culture tubes were harvested. The cells were centrifuged in tubes of known weight, washed three times with distilled water and dried for two days at 100°C. The tubes were then weighed.

The scale of the dry weights has been chosen in such a way that the dry weight of the cells from one of the tubes harvested after 47 hours is coincident with the value for Z at the same time. The dry weights of the cells from the two tubes harvested after 71 hours were exactly the same.

8. Discussion of the experiments with Rhodotorula.

Lodder & Kreger-van Rij (1952) differentiated the genus Rhodotorula into seven species and one variety. This classification was founded mainly upon physiological characteristics, viz. the ability to utilize nitrate as the single nitrogen source and to assimilate certain sugars.

Skinner & Huxley (1956) made an investigation on 99 strains of Rhodotorula. They classified the cultures according to Lodder & Kreger-van Rij and then studied the effect of 21 carbon sources in addition to the compounds used for differentiating the species. A few other physiological properties were also investigated. Except for tests which were all negative or all positive, there was no consistency in the tests, nor was there any correlation between tests, with few exceptions. Thirty cultures were able to utilize nitrate as the nitrogen source, and all these cultures also grew without the addition of vitamins. Strain 7a of the present investigation was, however, not able to synthesize its own vitamins, although it was able to utilize nitrate as the single nitrogen source. Skinner & Huxley pointed out that if the species of the genus Rhodotorula were characterized with the aid of some other carbon compounds than the ones used by Lodder & Kreger-van Rij, a quite different system would be obtained. In characterizing the species, Lodder & Kreger-van Rij also made use of differences in size and shape of the cells. Skinner & Huxley, however, could find no definite morphological differences. These authors were of the opinion that sufficient support for a natural Sv. Bot. Tidskr., 55 (1961): 1
differentiation of the genus *Rhodotorula* was lacking, and therefore suggested that the genus should, at least at the present time, be considered as monotypic.

Hasegawa (1958) studied 46 *Rhodotorula* strains. Among other things, he reached the same conclusion as Skinner & Huxley concerning the validity of differentiation by the shape and size of cells as made by Lodder & Kreger-van Rij. Thus *R. aurantiaca* and *R. glutinis var. rubescens* should be synonymous with *R. glutinis* and *R. mucilaginosa* with *R. rubra*.

Hasegawa, Banno & Yamuchi (1960) suggested a differentiation of the genus *Rhodotorula* into two subgenera: *Rubrotorula* for red species and *Flavotorula* for yellow species. This differentiation was founded upon different absorption maxima of petroleum ether extracts of *Rhodotorula*as cultivated on potato-yeast medium. However, when this medium was replaced with a synthetic medium containing vitamins, the absorption maxima for some of the red species were changed so that they agreed with the maxima for the yellow species. Furthermore, the authors were of the opinion that there is a difference in vitamin requirements between the two groups, so that the red species requiring thiamine can grow with pyrimidine alone while the yellow species require pyrimidine + thiazole. Two of the three yellow species investigated, however, made fairly good growth with pyrimidine alone.

Several new species of *Rhodotorula* have been described by different authors since the publication of the work of Lodder & Kreger-van Rij.

Some of the results of the physiological experiments with the *Rhodotorula* strains of the present investigation are summarized in Table V. 3b and 3c utilized nitrate and the sugars glucose, galactose, sucrose, and maltose. The size of the cells on malt agar was $2.6 \pm 0.2 \times 4.0 \pm 0.3 \mu$ and $2.9 \pm 0.2 \times 4.6 \pm 0.3 \mu$ respectively. According to Lodder & Kreger-van Rij, these strains should be classified as *R. glutinis var. rubescens*. Strains 7a and 33a also utilized nitrate. 7a assimilated the same sugars as 3b and 3c, but no experiments with different sugars were performed with 33a. Probably both 7a and 33a should be classified as *R. glutinis var. rubescens*. The size of the cells in these strains was, however, not measured. According to Hasegawa, all these strains ought to be named *R. glutinis*.

The strain 18b did not utilize nitrate or any of the sugars used for classification except glucose and sucrose. None of the species recog-
Table V. Growth of the different *Rhodotorula* strains with nitrate, certain carbon sources, with certain vitamins excluded, as well as the pH ranges for growth and the pH values for the most rapid growth.

<table>
<thead>
<tr>
<th>KNO₃</th>
<th>d-Glucose</th>
<th>d-Galactose</th>
<th>Sucrose</th>
<th>Maltose</th>
<th>Lactose</th>
<th>d-Glucose 50%</th>
<th>Pantothenate excluded</th>
<th>Pantothenate replaced with β-alanine</th>
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<tr>
<td>3 b</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>(−)</td>
<td>+</td>
</tr>
<tr>
<td>3 c</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>(−)</td>
<td>+</td>
</tr>
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<td>7 a</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>+</td>
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</tr>
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<td>18 b</td>
<td>−</td>
<td>+</td>
<td>−</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>+</td>
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<tr>
<td>33 a</td>
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<td>+</td>
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<table>
<thead>
<tr>
<th>Biotin excluded</th>
<th>PABA excluded</th>
<th>Thiamine replaced with pyrimidine</th>
<th>Thiamine replaced with thiazole</th>
<th>Thiamine replaced with pyrimidine + thiazole</th>
<th>pH range for growth</th>
<th>Optimum pH</th>
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<td>3 b</td>
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<td></td>
<td>2.95–8.25</td>
<td>4.55, 5.15</td>
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<td>3 c</td>
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<td>+</td>
<td>+</td>
<td></td>
<td>2.90–7.95</td>
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<tr>
<td>7 a</td>
<td>(−)</td>
<td>+</td>
<td>−</td>
<td></td>
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<tr>
<td>18 b</td>
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<td>−</td>
<td>−</td>
<td>(−)</td>
<td>2.80–8.05</td>
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<tr>
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<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

+ = growth, − = no growth, (−) = growth considerably retarded.

The vitamin requirements of the strains investigated proved to be rather different. 3b, 3c, and 33a were all stimulated by pantothenate, which could be replaced with β-alanine. This was also true of 7a, but this strain required biotin and thiamine (or the pyrimidine moiety) in addition. 18b proved to be deficient for PABA and thiamine (or pyrimidine + thiazole). ROBBINS & MA (1944) reported *R. aurantiaca* to be totally deficient for PABA and thiamine. The intact thiamine molecule was required. As shown above, 18b could not be classified, but *R. aurantiaca* differs from 18b in being able to utilize nitrate as well as galactose and maltose.

Cultivating the *Rhodotorula* strains at different pH values indicated that 3b, 7a, and 33a resembled each other as to the range where growth took place. The upper pH limit for these strains was about 8. 18b, however, did not grow at pH 7.65, and even at pH 7.00 growth was considerably retarded. 18b required thiamine or pyrimidine + thiazole for growth. Thiamine is unstable at neutral and alkaline pH values, probably because the thiazole moiety is destroyed. Fil. mag. L. Hultgren, Uppsala (personal communication) investigated the stability of thiamine when autoclaved at different pH values using *Lactobacillus viridescens* as a test organism. He found that a large part of the thiamine was destroyed even at pH 7. This might explain the inability of 18b to grow in alkaline solutions. 7a was deficient for thiamine too, but this strain was able to grow with pyrimidine only. 7a grew very well at pH 7.00 and fairly well even at pH 7.95.

**Phialophora sp.**

The conidia of the *Phialophora* strain investigated here are rather slender (5.1 x 2.1 μ) and mostly rod-shaped. Dr. A. Käärik (personal communication) reports that it resembles *Phialophora repens* (Davidson) Conant macroscopically but that the spores are larger and not curved. According to Dr. Käärik, this fungus is found in Sweden on birch and aspen. It has a very constant morphology both macroscopically and microscopically.

1. Growth with different nitrogen sources.

*Table VI. Growth of Phialophora sp. with different nitrogen sources (Experiment 12).*

<table>
<thead>
<tr>
<th>Nitrogen source</th>
<th>Initial pH</th>
<th>Final pH</th>
<th>Dry weight of mycelium in mg per flask</th>
</tr>
</thead>
<tbody>
<tr>
<td>None</td>
<td>7.00</td>
<td>6.95</td>
<td>0.8</td>
</tr>
<tr>
<td>KNO₃</td>
<td>6.95</td>
<td>8.10</td>
<td>78.3</td>
</tr>
<tr>
<td>KNO₂</td>
<td>6.95</td>
<td>8.20</td>
<td>86.1</td>
</tr>
<tr>
<td>NH₄H₂PO₄</td>
<td>6.80</td>
<td>5.40</td>
<td>77.5</td>
</tr>
<tr>
<td>(NH₄)₂-tartrate</td>
<td>6.95</td>
<td>4.90</td>
<td>83.5</td>
</tr>
<tr>
<td>L-Asparagine</td>
<td>6.95</td>
<td>6.95</td>
<td>74.9</td>
</tr>
<tr>
<td>L-Aspartic acid</td>
<td>6.95</td>
<td>7.80</td>
<td>93.5</td>
</tr>
<tr>
<td>Urea</td>
<td>7.00</td>
<td>7.30</td>
<td>86.8 ± 1.7</td>
</tr>
</tbody>
</table>

Melin & Nannfeldt (1934) studied the growth of Cadophora (=Phialophora) fastigiata with different nitrogen compounds. They reported that this fungus produced good growth with nitrate and nitrite, but grew poorly with ammonium chloride and urea. Brewer (1959) investigated several isolates of P. fastigiata and P. richardsiae. He tested 16 different sources of nitrogen, among them ammonium tartrate, potassium nitrate, asparagine, and aspartic acid. He found that all compounds investigated except cysteine could be utilized.

Experiment 12. (Table VI).

Nutrient solution. Medium A1 + B.

The nutrients of medium A1 were dissolved in 80% of the final amount of distilled water. 20 ml of this solution was added to each culture flask and then autoclaved. The solutions of the nitrogen compounds were prepared in the same way as in Experiment 1. After autoclaving, each flask containing medium A1 was supplied with 1 ml of medium B + 5 ml of "nitrogen solution" (in the control series 5 ml of distilled water). The nutrient solutions contained 202 mg of nitrogen per l.

Phialophora sp. made good growth with all the nitrogen sources tested. Unfortunately all the mycelia of each series were mixed by mistake before weighing, and only the mycelia cultured with urea were weighed separately.

2. Growth with different mono- and disaccharides.

Melin & Nannfeldt (1934) stated that Cadophora (=Phialophora) fastigiata utilized maltose and sucrose as well as monosaccharides. This species made no growth with lactose as the carbon source. Brewer (1959) reported that P. fastigiata and P. richardsiae could utilize 10 different carbohydrates, among them glucose, galactose, mannose, fructose, sucrose, maltose, and cellobiose. Arabinose could not be utilized.

Table VII. Growth of Phialophora sp. with different sugars (Experiment 13).

<table>
<thead>
<tr>
<th>Sugar</th>
<th>Initial pH</th>
<th>Final pH</th>
<th>Dry weight of mycelium in mg per flask</th>
</tr>
</thead>
<tbody>
<tr>
<td>None</td>
<td>6.50</td>
<td>6.50</td>
<td>0.3</td>
</tr>
<tr>
<td>D-Glucose</td>
<td>6.50</td>
<td>3.55</td>
<td>51.2 ± 1.1</td>
</tr>
<tr>
<td>D-Fructose</td>
<td>6.50</td>
<td>6.00</td>
<td>26.3 ± 5.1</td>
</tr>
<tr>
<td>D-Mannose</td>
<td>6.50</td>
<td>3.95</td>
<td>74.8 ± 2.3</td>
</tr>
<tr>
<td>D-Galactose</td>
<td>6.45</td>
<td>4.45</td>
<td>62.0 ± 3.9</td>
</tr>
<tr>
<td>Maltose</td>
<td>6.45</td>
<td>5.30</td>
<td>49.8 ± 4.1</td>
</tr>
<tr>
<td>Sucrose</td>
<td>6.50</td>
<td>3.60</td>
<td>59.1 ± 1.6</td>
</tr>
<tr>
<td>Lactose</td>
<td>6.50</td>
<td>6.25</td>
<td>11.5 ± 0.5</td>
</tr>
<tr>
<td>Cellobiose</td>
<td>6.50</td>
<td>5.20</td>
<td>72.6 ± 5.7</td>
</tr>
</tbody>
</table>

Experiment 13 (Table VII).

Nutrient solution. Medium A2 + B with 10 ml of vitamin mixture per l. The solutions were prepared in the same way as in Experiment 3. Each culture flask was supplied with 20 ml of medium A2 and autoclaved. After cooling, 1 ml of medium B + 5 ml of a sugar solution (in the control series 5 ml of distilled water) was added. The nutrient solutions contained 9.62 g of sugar per l.

Phialophora sp. grew well with glucose, mannose, galactose, maltose, sucrose, and cellobiose, but poorer with fructose. Least growth was obtained with lactose as a carbon source.

3. Growth with glucose of varying concentrations.

Table VIII. Growth of Phialophora sp. with D-glucose of varying concentrations (Experiment 14). % = g per 100 ml of nutrient solution.

<table>
<thead>
<tr>
<th>% D-glucose</th>
<th>Initial pH</th>
<th>Final pH</th>
<th>Dry weight of mycelium in mg per flask</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>6.50</td>
<td>6.50</td>
<td>0.2</td>
</tr>
<tr>
<td>1</td>
<td>6.50</td>
<td>3.80</td>
<td>67.8 ± 1.6</td>
</tr>
<tr>
<td>2</td>
<td>6.45</td>
<td>3.90</td>
<td>65.5 ± 2.9</td>
</tr>
<tr>
<td>5</td>
<td>6.40</td>
<td>3.70</td>
<td>65.2 ± 2.4</td>
</tr>
<tr>
<td>10</td>
<td>6.30</td>
<td>5.10</td>
<td>49.6 ± 6.0</td>
</tr>
<tr>
<td>20</td>
<td>6.20</td>
<td>5.65</td>
<td>38.9 ± 7.4</td>
</tr>
<tr>
<td>50</td>
<td>5.90</td>
<td>5.80</td>
<td>0.4</td>
</tr>
</tbody>
</table>

Experiment 14 (Table VIII).

Nutrient solution. Medium A2 + B with 10 ml of vitamin mixture per l. The solutions were prepared according to Experiment 5. Each culture flask was supplied with 20 ml glucose solution (in the control series 20 ml of distilled water) and autoclaved. After cooling, 5 ml of medium A2 + 1 ml of medium B were added.

Phialophora sp. produced about the same growth with 1%, 2%, and 5% glucose. Growth was less abundant with 10% and still somewhat less with 20%. No growth was obtained with 50% glucose.

4. Growth with and without vitamins.

Rennerfelt (1938) reported that Cadophora (= Phialophora) fastigiata grew poorly on media lacking vitamins. Vitamins of the “bios” group exerted a favourable influence upon growth. Brewer

(1959) found that *P. fastigiata* produced good growth without the addition of vitamins, while *P. richardsiae* required the addition of biotin.

**Table IX. Effect of vitamin mixture upon growth of Phialophora sp. (Experiment 15).**

<table>
<thead>
<tr>
<th>Vitamins</th>
<th>Initial pH</th>
<th>Final pH</th>
<th>Dry weight of mycelium in mg per flask</th>
</tr>
</thead>
<tbody>
<tr>
<td>No vitamins</td>
<td>6.60</td>
<td>4.20</td>
<td>59.6±3.2</td>
</tr>
<tr>
<td>Vitamin mixture</td>
<td>6.60</td>
<td>4.30</td>
<td>60.2±2.6</td>
</tr>
</tbody>
</table>

**Experiment 15 (Table IX).**

*Nutrient solution.* Medium A2 + B with 1 % glucose.

The nutrients of medium A2 (with and without vitamins added) were dissolved in 80 % of the final amount of distilled water and autoclaved in the culture flasks, 20 ml per flask. A 6.25 g per 100 ml glucose solution was autoclaved separately. After cooling, each flask containing medium A2 was supplied with 1 ml of medium B + 4 ml glucose solution.

*Phialophora* sp. grew as well in the series where vitamins were lacking as in the one with vitamin mixture added.

**Dipodascus aggregatus.**

The species *Dipodascus aggregatus* was recognized by Francke-Grosman (1952). She found the fungus in pinewood where it occurred in the canals made by the larvae of a bark beetle.

The cells of the strain studied in the present investigation proved uninucleate, which is also mentioned by Batra (1959) as a characteristic of the species.

1. **Growth with different nitrogen sources.**

Dulaney & Grutter (1950) reported that *Dipodascus uninucleatus* was unable to utilize nitrate as the sole nitrogen source. Batra (1959) stated that *D. albidus* and *D. aggregatus* could not reduce nitrate, whereas *D. uninucleatus* could. Kuehn (1960) investigated the growth of *D. uninucleatus* with 24 different nitrogen sources. L-Aspartic acid proved to be weakly assimilable while no growth was obtained with nitrate, nitrite or urea. Ammonium sulfate produced good growth.

### Table X. Growth of *Dipodascus aggregatus* with different nitrogen sources (Experiment 16).

<table>
<thead>
<tr>
<th>Nitrogen source</th>
<th>Initial pH</th>
<th>Final pH</th>
<th>Dry weight of mycelium in mg per flask</th>
</tr>
</thead>
<tbody>
<tr>
<td>None</td>
<td>6.95</td>
<td>6.75</td>
<td>0.4</td>
</tr>
<tr>
<td>KNO₃</td>
<td>6.95</td>
<td>6.75</td>
<td>0.4</td>
</tr>
<tr>
<td>KNO₂</td>
<td>6.95</td>
<td>6.75</td>
<td>0.4</td>
</tr>
<tr>
<td>NH₄H₂PO₄</td>
<td>6.85</td>
<td>5.80</td>
<td>36.5±0.6</td>
</tr>
<tr>
<td>(NH₄)₂-tartrate</td>
<td>6.90</td>
<td>4.85</td>
<td>24.6±1.6</td>
</tr>
<tr>
<td>L-Asparagine</td>
<td>6.95</td>
<td>6.70</td>
<td>29.7±0.5 (5 replicates)</td>
</tr>
<tr>
<td>L-Aspartic acid</td>
<td>6.90</td>
<td>7.05</td>
<td>13.2±0.4</td>
</tr>
<tr>
<td>Urea</td>
<td>6.95</td>
<td>6.70</td>
<td>12.3±0.4</td>
</tr>
</tbody>
</table>

**Experiment 16 (Table X).**

*Nutrient solution. Medium* A1 + B.

The solutions were prepared according to Experiment 2. 20 ml of medium A1 was added to each culture flask and autoclaved. After cooling, 1 ml of medium B + 4 ml of “nitrogen solution” (in the control series 4 ml of distilled water) were added. The nutrient solutions contained 210 mg of nitrogen per l.

*Dipodascus aggregatus* produced good growth with ammonium dihydrogen phosphate, ammonium tartrate, and L-asparagine. With L-aspartic acid and urea, growth was poorer, and with nitrate and nitrite it was nonexistent.

### 2. Growth with different mono- and disaccharides.

**Table XI. Growth of *Dipodascus aggregatus* with different sugars (Experiment 17).**

<table>
<thead>
<tr>
<th>Hexose</th>
<th>Initial pH</th>
<th>Final pH</th>
<th>Dry weight of mycelium in mg per flask</th>
</tr>
</thead>
<tbody>
<tr>
<td>None</td>
<td>6.35</td>
<td>6.45</td>
<td>0.1</td>
</tr>
<tr>
<td>D-Glucose</td>
<td>6.35</td>
<td>3.90</td>
<td>22.4±1.4</td>
</tr>
<tr>
<td>D-Fructose</td>
<td>6.35</td>
<td>4.60</td>
<td>25.4±0.7</td>
</tr>
<tr>
<td>D-Mannose</td>
<td>6.35</td>
<td>4.00</td>
<td>16.9±1.3</td>
</tr>
<tr>
<td>D-Galactose</td>
<td>6.35</td>
<td>3.95</td>
<td>17.0±1.6</td>
</tr>
<tr>
<td>Disaccharide</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>None</td>
<td>6.40</td>
<td>6.40</td>
<td>0.1</td>
</tr>
<tr>
<td>Maltose</td>
<td>6.40</td>
<td>5.75</td>
<td>14.9±4.7</td>
</tr>
<tr>
<td>Sucrose</td>
<td>6.40</td>
<td>6.35</td>
<td>0.2</td>
</tr>
<tr>
<td>Lactose</td>
<td>6.40</td>
<td>6.35</td>
<td>0.1</td>
</tr>
<tr>
<td>Cellobiose</td>
<td>6.40</td>
<td>6.35</td>
<td>0.2 (3 replicates)</td>
</tr>
</tbody>
</table>

Kuehn (1960) tested 37 different carbohydrates as sole carbon sources for Dipodascus uninucleatus. This fungus produced good growth with glucose, maltose, and sucrose. Galactose, lactose, and cellobiose supported no growth.

**Experiment 17 (Table XI).**

*Nutrient solution.* Medium A2 + B with 10 ml of vitamin mixture per l. The nutrient solutions were prepared in the same way as in Experiment 13 except that the sugar solutions contained 6.25 g per 100 ml. After autoclaving, each flask containing medium A2 was supplied with 1 ml of medium B + 4 ml of a sugar solution. The nutrient solutions contained 10 g sugar per l.

*Dipodascus aggregatus* proved to be able to grow with all the hexoses tested, but the best growth was obtained with glucose and fructose. The only disaccharide utilized was maltose.

**3. Growth with glucose of varying concentrations.**

*Table XII.* Growth of Dipodascus aggregatus with D-glucose of varying concentrations (Experiment 18). % = g per 100 ml of nutrient solution.

<table>
<thead>
<tr>
<th>% D-glucose</th>
<th>Initial pH</th>
<th>Final pH</th>
<th>Dry weight of mycelium in mg per flask</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>6.45</td>
<td>6.50</td>
<td>0.3</td>
</tr>
<tr>
<td>1</td>
<td>6.45</td>
<td>4.25</td>
<td>31.0 ± 1.4</td>
</tr>
<tr>
<td>2</td>
<td>6.45</td>
<td>3.60</td>
<td>33.7 ± 2.3</td>
</tr>
<tr>
<td>5</td>
<td>6.40</td>
<td>3.55</td>
<td>26.5 ± 0.7</td>
</tr>
<tr>
<td>10</td>
<td>6.30</td>
<td>3.55</td>
<td>14.0 ± 0.6</td>
</tr>
<tr>
<td>20</td>
<td>6.20</td>
<td>3.55</td>
<td>1.4</td>
</tr>
<tr>
<td>50</td>
<td>5.90</td>
<td>5.75</td>
<td>4.2</td>
</tr>
</tbody>
</table>

**Experiment 18 (Table XII).**

*Nutrient solution.* Medium A2 + B with 10 ml of vitamin mixture per l. The nutrient solutions were prepared according to Experiment 14.

*Dipodascus aggregatus* made good growth with 1%, 2%, and 5% glucose, poorer with 10%. In the series with 20% glucose, very weak growth in the form of oidia was obtained. The fungus did not grow with 50% glucose. The relatively high value of the mean dry weight of this series was probably due to glucose remaining on the inocula.

4. Growth with different vitamins.

Dulaney & Grutter (1950) reported that a strain of Dipodascus uninucleatus that they had isolated required biotin and thiamine for growth. Batra (1959), on the other hand, found that D. albida, D. uninucleatus, and D. aggregatus were deficient for biotin only. Kuehn (1960) reported that D. uninucleatus failed to grow in the absence of either biotin or thiamine, while growth was stimulated by niacin.

The effect of the eight vitamins of the vitamin mixture on the growth of my isolate of D. aggregatus was studied. This strain was shown to be deficient for biotin only, which agrees with the results of Batra. Attempts were made to replace biotin with pimelic acid and pimelic acid + L-cysteine as well as with oleic acid and L-aspartic acid of the same concentrations as with Rhodotorula 7a. No growth was obtained with any one of the compounds tested.

5. Growth at different pH values.

Table XIII. Effect of pH on growth of Dipodascus aggregatus with L-asparagine and L-aspartic acid, respectively, as the nitrogen source (Experiments 19 and 20).

<table>
<thead>
<tr>
<th>Buffer solution no.</th>
<th>Experiment 19 (nitrogen source L-asparagine)</th>
<th>Experiment 20 (nitrogen source L-aspartic acid)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Initial pH</td>
<td>Final pH</td>
</tr>
<tr>
<td>1</td>
<td>2.00</td>
<td>2.65</td>
</tr>
<tr>
<td>2</td>
<td>2.90</td>
<td>3.30</td>
</tr>
<tr>
<td>3</td>
<td>4.15</td>
<td>4.85</td>
</tr>
<tr>
<td>4</td>
<td>4.85</td>
<td>5.20</td>
</tr>
<tr>
<td>5</td>
<td>5.50</td>
<td>5.55</td>
</tr>
<tr>
<td>6</td>
<td>6.05</td>
<td>6.05</td>
</tr>
<tr>
<td>7</td>
<td>6.40</td>
<td>6.30</td>
</tr>
<tr>
<td>9</td>
<td>6.95</td>
<td>6.85</td>
</tr>
<tr>
<td>11</td>
<td>7.50</td>
<td>7.25</td>
</tr>
<tr>
<td>13</td>
<td>8.05</td>
<td>7.55</td>
</tr>
<tr>
<td>15</td>
<td>8.90</td>
<td>8.10</td>
</tr>
</tbody>
</table>
Nutrient solution. Medium A3 (in Experiment 20, the 1 g L-asparagine used in Experiment 19 was replaced with 1 g L-aspartic acid) + buffer + medium B with 1% glucose and 2 µg biotin per l.

The nutrients of medium A3 were dissolved in 28% of the final amount of distilled water. 7 ml of medium A3 (with biotin) + 15 ml buffer solution were added to each culture flask and then autoclaved. A glucose solution containing 12.5 g per 100 ml was autoclaved separately. After autoclaving, 1 ml of medium B + 2 ml glucose solution were added to each culture flask.

The variation in growth of Dipodascus aggregatus with pH for the two nitrogen sources investigated is illustrated in Fig. 14.

6. Discussion of the experiments with Phialophora and Dipodascus.

As can be seen from the experiments and from the summarizing Table XIV, Phialophora sp. proved to be a very tolerant fungus, being able to utilize all the nitrogen sources tested as well as all the sugars, although growth was poor with lactose. The strain was able to grow with 20% glucose, but not with 50%. No vitamins were required.

Dipodascus aggregatus, on the other hand, was unable to grow with nitrate or nitrite as the nitrogen source. All the hexoses studied could be utilized, but the only disaccharide producing growth proved to be maltose. With sucrose, lactose, and cellobiose no growth at all was obtained. The fungus was unable to grow with 20% glucose. Biotin was required for growth.

Schmalfuss & Mothes (1930) studied the breakdown of asparagine by Aspergillus niger. They stated that this breakdown is carried out in different ways at different pH values. In acid solutions, the amino nitrogen is disengaged, and the amido nitrogen is simultaneously liberated. In alkaline solutions, the amino group is extremely slowly liberated, while the amido group is rapidly disengaged with the aid of an enzyme, which, in A. niger, proved to be active between pH 6 and pH 10 with the optimum at pH 7.7—7.8. L. Fries (1955) reported that certain Coprinus strains produced far more abundant growth with asparagine than with aspartic acid at pH 4.5—8.0.

Growth of Dipodascus aggregatus at different pH values is shown in Fig. 14. With asparagine as the nitrogen source, the growth curve has a maximum at about pH 4, a minimum at about pH 5.5 and a second maximum at about pH 7. This agrees well with the theory.
Fig. 14. Growth of *Dipodascus aggregatus* at different pH values with L-asparagine (unbroken lines) and L-aspartic acid (broken lines) as the nitrogen source.

of Schmaljuss & Mothes. The second maximum would hence be due to an enzymatic liberation of the amido group.

With asparagine replaced by aspartic acid, it is true that there is also a tendency towards two maxima in the growth curve. Considering the standard errors of the mean, however, one might establish that the yield was highest and practically constant between pH 3.4 and

Table XIV. Growth of *Phialophora* sp. and *Dipodascus aggregatus* with nitrate, certain carbon sources, with vitamins lacking and with biotin added.

<table>
<thead>
<tr>
<th>Fungus</th>
<th>KNO₃</th>
<th>d-Glucose</th>
<th>d-Fructose</th>
<th>d-Manose</th>
<th>d-Galactose</th>
<th>Maltose</th>
<th>Sucrose</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Phialophora</em> sp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Dipodascus aggregatus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Fungus</th>
<th>Lactose</th>
<th>Cello-biose</th>
<th>d-Glucose 20 %</th>
<th>d-Glucose 50 %</th>
<th>Vitamins lacking</th>
<th>Biotin added</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Phialophora</em> sp.</td>
<td>(-)</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Dipodascus aggregatus</em></td>
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+=growth, -=no growth, (-)=growth considerably retarded.

and 6.4. Passing from 6.4 towards higher pH values, growth decreased continuously.

In the experiments with the *Rhodotorula* strains at different pH values with asparagine as the nitrogen source, no minimum corresponding to the one found in the growth curve of *D. aggregatus* was observed. This may be due to the presence of some amino- or amido-liberating enzyme being active also within the pH range of 4.5–6.5 in *Rhodotorula*.

### Summary.

Five strains of the genus *Rhodotorula*, one strain of the genus *Phialophora* and one of *Dipodascus aggregatus* were isolated from the slime flux of various deciduous trees. The present investigation consists of physiological studies on these fungi.

Four of the *Rhodotorula* strains could utilize seven different nitrogen sources investigated, among them nitrate and nitrite. Three of these strains could also grow with seven sugars tested, among them glucose, galactose, maltose, and sucrose. Lactose could not be utilized. They could also grow in a nutrient solution containing up to 50% glucose. The fourth strain was not tested in these respects.

The remaining strain of *Rhodotorula* was unable to utilize nitrate and nitrite, nor was it able to grow with galactose, maltose, or lactose as the carbon source, or in a solution containing 50% glucose.

Of the four strains that could reduce nitrate, three proved to be deficient for pantothenate (or β-alanine). The remaining strain required pantothenate (or β-alanine), biotin, and thiamine (or pyrimidine) for growth. The strain that could not utilize nitrate was deficient for PABA and thiamine (or pyrimidine + thiazole).

Three of the four strains reducing nitrate produced growth within a pH range of about 2.9–8.0. The remaining strain was not investigated in this respect. The strain which did not reduce nitrate was unable to grow at a pH of 7.65 or higher.

The connection between the ability to utilize nitrate as the nitrogen source and vitamin autotrophy found by Skinner & Huxley (1956) for 30 Rhodotorula strains proved invalid for one of the strains of the present investigation. The physiological properties of another strain (the one which was unable to grow with nitrate) did not agree with any one of the species recognized by Lodder & Kreger-van Rij (1952) nor with any one of the species described later.

The Phialophora strain investigated could utilize all seven nitrogen sources tested and all eight sugars investigated, although growth was weak with lactose. No growth was obtained with 50% glucose. The Phialophora strain produced good growth in a medium lacking vitamins.

The Dipodascus aggregatus strain proved to be unable to utilize nitrate and nitrite. Of the sugars investigated, sucrose, lactose, and cellobiose could not be utilized. The fungus was unable to grow with 50% glucose, and even with 20%, very weak growth was obtained. This strain required the addition of biotin. The varying growth of D. aggregatus at different pH values with two different nitrogen sources, asparagine and aspartic acid, is demonstrated in the investigation.

Acknowledgements.

I wish to express my deepest gratitude to Professor Nils Fries for invaluable discussions and helpful criticism.

Institute of Physiological Botany, University of Uppsala, November 1960.

LITERATURE CITED.


FUNGI ISOLATED FROM SLIME FLUX


OVARIAN MORPHOLOGY AND TAXONOMICAL POSITION OF SELAGINEAE.

BY

SVEN JUNELL.

Introduction.

At the outset of the present investigation, I was interested mainly in studying the embryology of *Hebenstreitia dentata*, one of the few species of the tribe *Selaginaceae* cultivated in our Botanical Gardens. It soon appeared, however, that valuable information about the relationships of these plants could be obtained by widening the scope of the investigation to include the structure of the flower in general and the morphology of the ovary in particular. In similarity to numerous other sympetals with 2- or 1-ovuled ovaries, *Selaginaceae* have been given different taxonomical positions by various workers. I reproduce here the following excerpt from *Stapf* (1932) because it makes this clear and also because it adequately describes the general appearance and geographical distribution of these plants.

The family *Selaginaceae* ... represents a very natural group of plants, mostly South African (over 200 out of 230), the remainder being confined to Tropical Africa, where they occur chiefly in countries around Lake Nyassa, a very few being found farther north. Of the seven genera of the family, *Selago* is by far the largest, comprising over 140 species. They are all more or less of the heath-type and when growing gregariously may cover extensive stretches of land.

Jussieu suggested already in 1806 that *Selago* might be the type of a new and distinct family, relying mainly on the orientation of the embryo with its superior radicle. It was, however, Choisy who in 1823, in his memoir on the *Selaginaceae*, actually proposed and described the family as such, impressed by its homogeneity and the well-defined general aspect of its members, although he was aware of its affinity to *Verbenaceae* and its relations to certain *Scrophulariaceae* and *Acanthaceae*. Bentham accepted Choisy’s concept of the family. ... More recently Wettstein and Hallier have reduced the family to a tribe of *Scrophulariaceae*. Theoretically there

may be some justification for this reduction, but the family as proposed by Choisy is geographically and, in a general way also, morphologically so well defined that we ought to acknowledge this fact by giving the group the status of a family.

A few additional examples of how the group has been dealt with in various handbooks will now be given. In his analysis in De Candolle's "Prodromus", Choisy (1848) retained Selagineae as a distinct family. On the other hand, Bailon (1882) distributed the genera on the tribes Selagineae and Hebenstreitieae within the family Scrophulariaceae. Wettstein stated in Engler & Prantl's handbook that Selagineae was a tribe in the subfamily Antirrhinoideae. Rolfe (1901) and Levyns (1950), just as most British authors, accepted in "Flora Capensis" and in "Flora of the Cape Peninsula" Selagineae as a distinct family. Conversely, Phillips (1951) included the group in the Scrophulariaceae. In the latest edition of "The Families of Flowering Plants", Hutchinson (1959) let the Order Lamiales comprise Myoporaceae, Selagineae, Globulariaceae and Labiatae. (Strangely enough, Verbenaceae should not belong to this Order when it does include Labiatae. True, as I have shown previously (1934), Verbenaceae is not a homogeneous family, but some groups exhibit such a close affinity to Labiatae that I consider it justified to include them therein.)

The fact that the Selagineae usually have been treated as a family distinct from the Scrophulariaceae must surely be due to the belief that none of these plants ever have more than two ovules in the ovary. Actually this is a misconception, however, for types transitional to the typical Scrophulariaceae do exist which have four ovules.

By virtue of the great generosity of the Botanical Museums at Stockholm (abbreviated S in the list of species), Uppsala (U), Lund (L), Gothenburg (G), Kew (K), and the National Botanical Gardens of South Africa at Kirstenbosch (Ki), I have been afforded the opportunity of examining a very comprehensive series of specimens. To facilitate such examination, I have adopted the procedure described previously (1934), viz. flowers and fruits were first digested in warm water for a day or two and then embedded and sectioned on a microtome.

Almost without exception the illustrations depict either transverse or longitudinal sections of flowers, ovaries or fruits. The orientation of the transverse sections is such that the anterior of the two carpels

is the one nearest the bottom of the page. Moreover, whenever serial sections are illustrated, they are numbered from the top downwards. Unless otherwise stated, the longitudinal sections are from the median plane and they are oriented to place the anterior carpel on the left side. In some figures the nature of the illustrated parts is indicated by abbreviations, bract being designated "br", calyx and its lobes "sep", corolla and its lobes "pet", and stamens "st".

To enable the ovary of the Selagineae group to be compared with that of some typical Scrophulariaceae, I have examined some genera belonging to the tribe Manuleae in the subfamily Antirrhinoideae. The two groups are alike in being composed chiefly of South African genera and also in having monotheeous stamens.

Ovarian Morphology of Some Typical Scrophulariaceae.

The material used was as follows:

*Glumicalyx montanus* Hiern, Nat. Herb. Pretoria n. 1826 (K).
*Manula cheiranthus* L., Acock 563 (S).
*Polycorea heterophylla* (L. f.) Levyns, Hafström et Acock 1235 (S).
*Sutera antirrhinoides* (L. f.) Hiern, fixed material.
*S. brachiata* Roth forma, Hafström et Acock 1163 (S).
*S. foetida* (Andr.) Roth, fixed material.
*Zaluzianskya capensis* (L.) Walp., fixed material.

A selection of transverse serial sections through a young flower of *Zaluzianskya capensis* is depicted in Figs. 1 a1–a4. In Fig. 1 a1 (drawn at lower magnification than the others) one sees the two inferior anthers in cross-section, and it is evident that two pollen sacs are present in the theca. The other sections have passed through the ovary, and what levels they come from may readily be established by referring to the longitudinal section shown in Fig. 1 b. The most striking feature is the conspicuous nectariferous gland at the base of the ovary. It is composed of cells rich in plasma and here and there on its surface large glands are found. The vascular bundle supplying the nectariferous gland is the one continuing upwards along the midline of the posterior carpel. Within the gland it ramifies and several discrete bundles are consequently seen in transverse sections.

Figs. 1 a2 and a3 disclose that the ovary is 2-chambered and consists of two carpels. Their margins have a large number of slightly curved, anatropous ovules. Whilst only a few ovules are cut nearly lengthwise in either longitudinal or transverse sections, all but the *Sv. Bot. Tidskr.*, 55 (1961): 1
uppermost ones are pendulous and have the micropyle directed more or less upwards. The uppermost ovules project into the ovarian cavity and have the micropyle directed downwards. Accordingly we have here a case of heterotropy. The other species examined have a similar ovarian morphology. In Fig. 1c, depicting a longitudinal section through a young ovary from *Sutera antirrhinoides*, the majority of ovules are oriented horizontally. The nectariferous

gland is less distinctly demarcated laterally and in *Manulea cheiran-thus* it is rather inconspicuous.

Longitudinal and transverse sections through the ovary of *Gluma
calyx montanus* are illustrated in Figs. 1* d, e and f*. Apart from its much smaller number of ovules, the features of this species are strikingly similar to those described in the foregoing. When describing this monotypical genus, *Hiern* (1903) reported that it shows the closest affinity to *Digitalis* and *Isoplexis*. Without going into the particulars of its relations, I would point out, however, that the stamens are stated to be monotheccous. *Phillips* (1951) positioned the genus immediately after the *Selagineae* group.

**Ovarian Morphology in *Selagineae*.**

1. *Selago*.

The material used was as follows:

*S. asperuloides* Schlecht., Schlechter 25.8.97 (L).
*S. Buchananii* Rolfe, Stolz 1388 (S).
*S. Burmannii* Choisy, Drège, Giftberg (S det. Norlindh, L).
*S. corymbosa* L., Wall 27.11.37 (S), Oldevig-Roberts Feb. 1951 (S), Hélne 286 (U).
*S. diffusa* Thunb., Zeyher, Stellenbosch (L).
*S. Forbesii* Rolfe, Sidey, 3102 (S).
*S. fruliculosa* Rolfe, Wilman 860 (det. Esterhuysen, G).
*S. Galpinii* Schlecht., Kotze 889 (L).
*S. geniculata* Choisy, Herb. Retzii (L).
*S. glutinosa* E. Mey., Penther 2371 (S), Codd (U).
*S. lepidioides* Rolfe, Rudatis 592 (S).
*S. Millotii* Rolfe, Sidey, 3102 (S).
*S. Holubii* Rolfe, Sidey, 3102 (S).
*S. hyssopifolia* E. Mey., Penther 2371 (S), Codd (U).
*S. lamprocarpa* Schlecht., Schlechter 1.11.96 (G), Pl. Schlecht. 10047 (S).
*S. lepidoides* Rolfe, Rudatis 592 (S).

S. cf. minutissima Choisy, Wall 18.9.38 (S).
S. namaquensis Schlecht., Pl. Schlecht. 8179 (S).
S. punctata Rolfe, Galpin 1809, 1924 (K).
S. quadrangularis Choisy, Ecklon 732 (det. Norlindh, S)
S. racemosa Bernh., Wood 6421 (L).
S. ramosissima Rolfe, Wall 18.9.38 (L), 1349 (det. Esterhuysen, L).
S. ramulosa E. Mey., Acock 15373 (L).
S. scabrida Thunb., Wall 29.11.37 (S).
S. serrata Berg., Örtendahl (fixed material), Acock 3973 (S).
S. spuria L., Wall 19.11.38 (det. Norlindh, S)
S. Thunbergii Choisy, Ecklon et Zeyher, Caledon Botrivier (L, S).

The floral morphology in this genus, the largest in the Selagineae, is of the scrophulariaceous type with respect to the orientation and numbers of sepals, petals and stamens (five, five and four in number, respectively). In the other genera a reduction has taken place in one or more of these whorls.

Just as in Scrophulariaceae generally, the ovary consists of two median carpels, but it differs—in those species I accept as belonging to Selago—in the sense that it contains merely two ovules. The nectari­ferous gland at the base of the posterior carpel is usually well deve­loped and sometimes nectariferous disc tissue grows out sideways, occasionally extending right round to the anterior aspect of the ovary.

Fig. 2a illustrates a median longitudinal section through S. serrata and shows how the two anatropous ovules are suspended from a placental tissue which occupies a large part of the superior portion of the ovary and has a coating of transmitting tissue with papillate cells. Since the ovular median plane is approximately perpendicular to the ovarian median plane, it is impossible in longitudinal sections to trace the vascular bundles all the way down to the ovules. This can be done more readily in the series of transverse sections (Figs. 2b1–b4).

In Figs. 2e and 2g are shown median longitudinal sections through ovaries from S. corymbosa and S. quadrangularis. These species are the opposites of one another with respect to the orientation of the ovules. In the former, the funiculus is directed away from the central part of the ovary, the ovules thus being apotropous. In the latter, on the other hand, the funiculus is directed inwards and in consequence the ovules are epitropous. When, as in S. serrata, the median plane

Fig. 2. Longitudinal and transverse sections of flowers, ovaries and fruits. a–c, Selago serrata. a, longitudinal section with approximate levels of the transverse sections $b_1$–$b_4$ indicated; c, longitudinal section of ovule; d, S. scabrida; e–f, S. corymbosa (section f includes only one of the ovules, which has a megaspore mother cell); g, S. quadrangulartis; h, S. glutinosa; i, S. Holstii; k–l, S. fruticosa, longitudinal and transverse sections of immature fruits (k and l are from the lower part of the fruit; pieces of the gland are visible). k, l, ×35; a–e, g, h, ×45; c, i, ×55; f, ×90.

of the ovule is perpendicular to the median plane of the ovary, I designate the orientation of the ovules as pleurotropous (cf. Gușu-Leac, 1937).

I have examined a large number of ovaries in various stages of development from *S. corymbosa* and found an apotropous position in all of them. Fig. 2f illustrates an ovary with an ovule at the megaspore mother-cell stage. In Figs. 2h and 2i, showing transverse ovarian sections from *S. glutinosa* and *S. Holstii*, the posterior ovule is apotropous whilst the anterior one is pleurotropous. I have also encountered such transitions between apotropy and pleurotropy in *S. albida*, *S. foliosa* and *S. geniculata*.

The majority of species seem to be pleurotropous, and undoubtedly this is the most primitive position. Besides in *S. serrata*, I have observed it in *S. Burmannii*, *S. elata*, *S. guttata*, *S. lamprocarpa*, *S. spuria* and *S. Thunbergii*. More or less distinctly apotropous species in addition to those mentioned already are *S. Forbesii*, *S. lepidioides* and *S. ramulosa*. To my knowledge the only epitropous species is *S. quadrangularis*. The ovaries of the apotropous species are as a rule more or less rounded (in the median plane).

The position of the ovules—which is often unvarying throughout entire families—is, and probably rightly so, accorded considerable taxonomical significance. But at the same time it by no means rarely varies within one and the same group. I have personally demonstrated (1934) that both epitropy and apotropy may occur concomitantly within the same genus of the family *Stilbaceae*. Samuelsson (1913) pointed out that among those plants with a reduced number of ovules which have originated from a group with heterotropy one might find different types of ovular position.

Apart from the position of the ovules, the ovarian morphology is similar in all members of the genus. The ovarian morphology in *S. glomerata*, *S. Nelsoni*, *S. spuria*, *S. triquetra* and *S. verbenacea* is practically identical to that in *S. serrata*. In some species, for example *S. foliosa*, the ovaries are unusually tall, whereas in others, for example *S. Holubii* and *S. geniculata*, they are nearly round (in median sections). The two ovarian chambers are nearly equally deep in *S. serrata* and *S. glutinosa*, but the anterior chamber is deeper in most species. This is the case especially in species having a well-developed nectariferous gland such as *S. scabrida* (Fig. 2d), *S. canescens* (Fig. 3b) and *S. triquetra*. In *S. Holubii* the gland extends like a lingual projection from beneath the round ovary.

Despite the fact that the taxonomical literature states that the bract is not adnate to the calyx in *Selago*, I have established that that is precisely what it more or less distinctly is in *S. Burmannii*, *S. cane-
Fig. 3. Longitudinal and transverse sections of ovaries and flowers. a, Selago Thunbergii; b, S. canescens; c–d, S. geniculata; e–f, Cromidon corrigoioides (= S. corrigoioides, cf. p. 177); g, Walafrida nitida; h, W. cinerea; i, k, W. saxatilis. b, c–g, i, ×35; a, h, ×45.

scens (Fig. 3b), S. corymbosa, S. decumbens, S. geniculata (Fig. 3c), S. heterophylla, S. quadrangularis, S. racemosa, S. scabrida, S. serrata, S. spuria, S. Thunbergii (Fig. 3a) and S. verbenacea. As I shall explain later, I have also seen such deviations in other genera which are assumed to be homogeneous in this respect.

In some species, most obviously in S. glomerata and S. fruticosa, the basal portion of the ovary underlying the nectariferous gland becomes markedly woody when flowering is over. In Figs. 2k and

one sees in the latter species this tissue sticking up like a plug intruding between the two halves of the fruit.

2. *Cromidon.*

The material used was as follows:

*C. corrigioloides* (Rolfe) Compton, Compton 11171 (K), Örterndahl 386 (G).

When Compton (1931) described this genus on the bases of *Selago corrigioloides*, he emphasized that this plant differed from *Selago* in the adnate bract, from *Microdon* in the unequally lobed calyx and the equally 2-lobed ovary, from *Walafrida* in the 5-lobed calyx and adnate bract, and from all three in the 4-lobed corolla.

The ovarian morphology (Fig. 3f) is of the usual *Selago* type and concerning the cited difference from *Selago*, I have just pointed out that numerous *Selago* species have the bract adnate to the calyx and then usually more conspicuously than in *S. corrigioloides*. In my opinion, therefore, everything suggests that this species may be included in *Selago*, as also Phillips (1951) does.

As Compton states, the posterior sepal is the smallest, the posterolateral larger and the two anterior largest. Fig. 3e, illustrating a transverse section through a flower on a level with the upper part of the ovary, discloses that even at this high level the two anterior sepals are united, and on the right side also with the next sepal. As the section lies at a higher level on the left side, the corresponding sepal here is free. In a few series of sections I have found neither a free portion nor any remains of the vascular bundle of the posterior pair of sepals. This makes the calyx resemble the 3-lobed *Walafrida* calyx. The 4-lobed nature of the corolla seems to be due to the fact that the posterior petals are united.


The material used was as follows:

W. *albanensis* (Schlecht.) Rolfe, Sidey 3145 (S).
W. *cinerea* (L. f.) Rolfe (det. Norlindh, S).
W. *decipiens* (E. Mey.) Rolfe, Ecklon et Zeyher (det. Norlindh, S), Levring 1.10.47 (G).
W. *densiflora* Rolfe, Schlechter 3807 (U).
W. *Dinteri* Rolfe, Dinter 7695 (S).
W. *Goelzei* (Rolfe) Brenan, Crook M. 93 (S).
W. *nittida* E. Mey., Drege, Ecklon et Zeyher (S).

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W. paniculata (Thunb.) Rolfe, Örtendahl 11.7.31 (S).
W. saxatilis (E. Mey.) Rolfe, Wall 13.11.38 (G).

This genus differs from Selago in having a 3-lobed calyx. The posterior sepal is often smaller and, reportedly, may be missing. It is difficult to determine the nature of the lateral sepals but it seems likely that they are homologous to the anterior pair in Selago, whereas a reduction of the posterior pair has taken place. In transverse sections through flowers from W. decipiens and W. nitida, I have occasionally observed a supernumerary, smaller vascular bundle in the posterior part of the lateral sepals. In a slide from W. decipiens this bundle occurred in only one of the two sepals. In my opinion this bundle suggests that sometimes a remnant of the posterior pair of sepals may persist. Just as detailed above in the case of Selago (Cromidon) corrigioloides, the two lateral sepals of W. Dinteri are united anteriorly.

In a number of Walafrida species, e.g. W. nitida (Fig. 3g), W. paniculata and W. saxatilis (Fig. 3i), the bract is adnate to the calyx.

Although the fruit of W. nitida is practically round, its ovary is unusually elongated (Fig. 3g). A voluminous placental tissue occupies the superior portion of the ovary. The other species instead have remarkably short ovaries which as a rule are broadest towards the base or, as in W. densiflora and W. Dinteri, practically round (in the median plane), the ovules in the latter case being curved.

As one might have surmised from the shape of the ovary, the ovules are in most instances more or less distinctly apotropous. I have examined a great number of slides of W. cinerea, the funiculus in all of them being directed outwards (Fig. 3h). Similarly, I have observed apotropy in W. decipiens, W. Dinteri, W. paniculata and W. rotundifolia, although they often present transitions towards pleurotropy which seems to be the rule in W. saxatilis and, above all, in W. nitida (Fig. 3g).

From W. albanensis, W. cinerea, W. Dinteri, W. nitida and W. paniculata, I have examined young fruits (Figs. 4a, b and c). The cells of the inner layers of the fruit wall enlarge and develop thick walls. This makes the mature fruit separate into distinct cocci, the same thing reportedly occurring throughout the genus.

When E. Meyer originally founded this genus, its only member was W. nitida, which is characterized by a pair of additional spurious cells in the cocci at adjacent margins. No evidence of these cells Sv. Bot. Tidskr., 55 (1961): 1
appears in the young ovary but they are distinctly visible in young fruits (Figs. 4a and b). Whilst the vacuoles in the younger fruit (Fig. 4a) are wholly occupied by large, thin-walled, empty, rounded cells, only remnants of the walls of these cells remain in the older fruit.

4. **Hebenstreitia and Dischisma.**

The material used was as follows:

*Hebenstreitia comosa* Hochst., Ecklon et Zeyher 36 (U).

*H. dentata* L. (fixed material).


*H. integrifolia* L., Meeuse 9280 (U).

*H. repens* JAROSZ, LINDEBERG 30.8.36 (S).


*Dischisma arenarium* E. Mey. (fixed material).

*Dischisma ciliatum* (BERG.) CHOISY, WALL 29.11.38 (det. NORLINDH, S).

These genera differ from *Selago* chiefly in the morphology of the calyx and the corolla. Both have a corolla which anteriorly is divided down to the middle of the tube and posteriorly expands in four lobes. In sections through the tube no vascular bundle can be seen anteriorly, suggesting that the anterior petal is missing as a rule. It has been reported, however, that a fifth minute lobe occasionally is present in the fissure of the tube.

The two genera are distinguished from one another by the calyx. *Dischisma* has two sepals which are separated almost down to the base; and, judging by transverse sections of young buds (Fig. 4e), they are the persisting posterior pair of originally five sepals. In *Hebenstreitia* the calyx is spathaceous, only a few cell layers thick, and adnate marginally to the bract (Fig. 4d). Transverse sections normally present two vascular bundles but residual traces of a third occasionally occur centrally, suggesting that remnants of the posterior sepal sometimes may persist.

These genera both develop four stamens and, as usual, their anthers are monothecous. I have observed in a few specimens of *H. dentata* remnants of a fifth posterior stamen in the form of a filament. Although it was unlike the others, an anther actually had developed in one of these specimens (Fig. 4d). The pollen grains were abnormally small and surrounded by a highly vacuolized plasma. In addition to two distinct chambers, there was a third which extended inwards and at one side apparently communicated with the pollen sac lying outside it. The series of sections was unfortunately incomplete, but

Fig. 4. a–b, Walafria nitida, transverse sections of immature fruits; c, W. cinerea, transverse section of immature fruit (the posterior sepal fails to reach the section level); d, f, g and i, Hebenstreitia dentata; d, transverse section of a bud (besides the four ordinary stamens, there is a posterior abnormal one); f, longitudinal section of a bud (one of the ovules with a dyad and the other with a tetrad); g, i–l, longitudinal and transverse sections of ovaries (in g the approximate levels of the transverse sections are indicated); h, H. repens, longitudinal section of ovary; e, k and l, Dischisma arenarium; e, transverse section of a bud; k, l, transverse and longitudinal sections of immature fruits with embryo and endosperm. l, × 25; a–e, g, h, k, × 35; f, × 45; i, × 55.

this fifth anther nevertheless gave the impression that it might be
dithecouc.

Fig. 4\textit{f} shows a median longitudinal section through a young bud
from \textit{H. dentata}. One ovule contains a dyad and the other a tetrad
of megaspores. Of the normal tenuinucellate type, the nucellus is
directed obliquely upwards. At the base one perceives the first hint
of the nectariferous gland. Longitudinal sections of mature ovaries
(Figs. 4\textit{g} and \textit{h}) resemble those in \textit{Selago serrata} (Fig. 2\textit{a}) apart from
having epitropous ovules. With rare exceptions the median plane
of the ovule coincides fairly closely with the median plane of the
ovary.

I have noted only minor differences between the various species.
Thus, for example, \textit{H. comosa} and \textit{H. integrifolia} have a remarkably
tall and \textit{H. hamulosa} an unusually low ovary. As appears from Fig.
4\textit{h}, the placental tissue of \textit{H. repens} is very voluminous.

Figs. 4\textit{k} and \textit{l} show transverse and longitudinal sections from a
fruit of \textit{D. arenarium}. The transverse section includes the embryo’s
cotyledons. The embryo has consumed part of the endosperm tissue.
The cell walls are thickened in the inner cell layers of the fruit wall.

**B. The Ovary with One Ovule.**

1. \textit{Microdon, Gosela, Agathelpis} and \textit{Globulariopsis}.

The material used was as follows:

\textit{Microdon linearis} Choisy, Zeyher 1385 (S).
\textit{M. lucidus} (Vent.) Choisy, Schlechter 1897 (U).
\textit{M. orbicularis} Choisy, Pl. Schlecht. 8478 (K).
\textit{M. ovatus} (L.) Choisy, Acock 3409 (S).
\textit{M. polygaloides} (L. f.) Norl. (=\textit{M. cylindricus} E. Mey.), Hagström et
Acock 9.9.38 (S), leg. et det. (\textit{M. cylindricus}) Esterhuysen 15905 (G).
\textit{Gosela eckloniana} Choisy, Ecklon et Zeyher 36 (U), Wall 1936 (S).
\textit{Agathelpis brevifolia} E. Mey., Acock 1380 (det. Norlindh, S).
\textit{A. dubia} (L.) Hutch. (=\textit{A. angustifolia} Choisy), Wall 19.11.38 (S), Drège
(U), Lam et Meeuse 1938 (U).
\textit{A. nitida} E. Mey. Drège (U), Ecklon et Zeyher (S).
\textit{Globulariopsis wittebergensis} Compton, Compton 9983 (Ki).

According to Phillips (1951), \textit{Microdon} comprises six or seven and
\textit{Agathelpis} three or four species. The other two genera are both mono-
typical. It is stated in the handbooks—e.g. Rolfe’s and Phillips’s—
that the ovary is 2-celled in the first three genera. Thus, Phillips
described the ovary as “2-chambered, with one chamber smaller

Fig. 5. Longitudinal and transverse sections of flowers, ovaries and young fruits. a–b, Microdon polygaloides; c–d, M. lucidus; e, M. linearis; f–k, Globulariopsis wittebergensis (sections h and i are not median). e, ×25; c, d, i, k, ×35; a, b, f, g, ×45.

and containing an abortive ovule” in Microdon; as “2-chambered with a solitary ovule in each chamber” in Gosela; and as “2-chambered with only one ovule developed” in Agathelpis. Despite the large number of slides that had to be prepared for most species, I have never obtained even a single slide where there was any sign of the posterior ovule or its chamber. But the fact that the ovary still contains a good deal of the posterior carpel is demonstrated clearly by, for example, Figs. 6 b and c, where one sees the vascular bundle.
of the posterior carpel, and by Fig. 5d, showing a transverse section from the superior portion of an ovary where the boundary between the two carpels appears as a distinct constriction of the wall.

The ovary is of the same type in all these genera. The Microdon species (Figs. 5a, b and c) differ only in minor details. M. orbicularis and M. ovatus, for example, have ovaries which are unusually compact near the base. The same applies to the surrounding corolla tube and the thereto adnate filaments of the two posterior stamens. The cells in large portions of the ovary contain raphides or become stony in character. Such sclerenchymatous cells occur also in other parts of the flower, particularly in the bract which they render minutely puncticulate. Moreover, the epidermal cells of the bract and calyx acquire massive cuticular thickenings. Especially in older ovaries and fruits these thickenings give rise to considerable difficulty in cutting serial sections. Such sclerenchymatous cells are less conspicuous in M. ovatus.

Generally the ovules are pleurotropous, but the raphe is not seldom directed more or less straight forward, and so one has ovules of types intermediate to the distinctly apotropous. A nectariferous gland is invariably present and is most highly developed in M. polygaloides (Fig. 5a). As appears from the longitudinal section of a young fruit from M. linearis in Fig. 5e, fibrillar thickenings develop in the wall of the fruit.

Sclerenchymatous cells occur rather sparsely in Gosela. A median longitudinal section of the ovary is shown in Fig. 6c. On it are marked those levels which correspond to the transverse sections in Fig. 6d. In addition, three frontal longitudinal sections are depicted in Figs. 6e to f3.

The morphology of the ovary is very uniform in Agathelpis, the ovary of the illustrated A. dubia (Figs. 6a and b) being practically indistinguishable from that in Microdon polygaloides. All parts of the flower contain raphides or sclerenchymatous cells in abundance (but are not included in the figures).

In Globulariopsis sclerenchymatous cells are less conspicuous. As in Microdon the position of the ovules is pleurotropous or apotropous (Figs. 5f to k). The transverse section in Fig. 5g shows the vascular bundle of the ovule lying nearly in the median line. Fig. 5i depicts a longitudinal section of a young fruit. Several cell layers in the fruit wall exhibit striate thickenings of the same character as in Microdon (cf. Fig. 5e). Unfortunately this longitudinal section did not lie

precisely in the median plane, but the extent of these layers can be estimated by comparison with the corresponding transverse section (Fig. 5k).

The Microdon species and Globulariopsis have four stamens, Gosela possesses two stamens and two staminods, and the Agathelpis species are provided with two stamens only. In M. polygaloides, M. lucidus and M. orbicularis the anterior, very short but more or less projecting stamens are attached in the throat of the corolla, at or just below the base of the anterior corolla lobe. The posterior stamens are attached farther down. The free part of the filament is short but can be discerned as a ridge-like fold passing along the tube to its base (Fig. 5b). In Globulariopsis the two anterior stamens protrude quite far. The stamens in Gosela and Agathelpis are located a good way down the tube but they are discernible right down to the base of the tube in these genera too. They are homologous with the posterior pair in Microdon. The anterior pair in Agathelpis is completely aborted but persists in Gosela as staminods which sometimes protrude slightly but also may be reduced to insignificant evaginations of the throat. Whilst the anthers are short and more or less oval in Microdon and Globulariopsis, they are long and thin in the Agathelpis species and Gosela.

Since available information about the calyx in Gosela is somewhat contradictory, I would emphasize that the two anterior lobes are united up to a fairly high level, whereby a bifid anterior lobe is formed.

Their dense inflorescence as well as their greatly enlarged and peculiarly formed bracts suggest that Microdon linearis, M. orbicularis and M. ovatus are highly specialized plants. Specialization in another direction has led to the evolution of flowers having a very narrow and long tube, and this has resulted in the development of the genera Gosela and Agathelpis. The Agathelpis species—especially A. dubia and A. brevifolia—resemble Microdon polygaloides very closely in habit and ovarian morphology, but the flowers of the former have acquired a long and narrow tube, which, in turn, has naturally led to the reduction of one pair of stamens. This is another occasion when—as often happens—some readily observable character (here the number of stamens) divides a group representing a homogeneous line of development into separate genera.

When Compton (1931) described *Globulariopsis wittebergensis*, he placed the new genus *Globulariopsis* in the family *Selagineae*, although this plant was unlike other members of this family in having opposite leaves. The unilocular anthers were certainly a character of importance for this decision, but the following citation shows that it was not made without some hesitation: “Its nearest affinity would appear to be with the *Globulariae* in which it would probably be included on account of its ovary, if this family were kept up.” As we have seen, the morphology of its ovary is the final proof that the plant should be included among the *Selagineae*, and its close relationship to *Microdon* is obvious. Compton pointed out that *Globulariopsis* is distinguished from *Microdon* by the bract being not at all adnate to the calyx. But in both *M. linearis* (Fig. 5e) and *M. ovatus* these components are either wholly free or at most united deep down near the base. However, as I have only had the opportunity of studying the morphology of the flowers, I shall merely draw attention to the close affinity to *Microdon*.

2. *Selago tephrodes.*

The material used was as follows:

*Selago tephrodes* E. Mey., Wall 2.9.38 (S).
Drège, Paarlberg, Sept. (S), Nieuwekloof, Oct. (S).
s.n. *S. laxiflora* Choisy, with following comment by Rolfe: “This was probably collected by Zeyher, at Brak Fontein, Olifants River. According to Choisy, Zeyher collected this species” (K).
Compton 22952 (det. Willemis, Ki).
Henderson 1168 (det. Compton, Ki).
Martin 532 (det. Johnson, Ki).
Middlemast 1881 (det. Barker, Ki).
Bond 598 (det. Compton, Ki).
Compton 4980 (s.n. *S. laxiflora*) (Ki).

Also in this species the posterior ovule is completely aborted. Longitudinal and transverse sections of the ovary are depicted in Figs. 6f and g. As in *Microdon* and *Agathelpis*, the tissues are rich in sclerenchymatous cells. That part of the ovary which is obviously composed of the posterior carpel is distinguished from the anterior portion by having considerably larger cells. The ovules are pleurotropous and the nectariferous gland is conspicuous.

Fig. 6. Longitudinal and transverse sections of flowers and ovaries. a1–a3, b, Agathelpis dubia; c–e, Gosela eckloniana; c, median section (the approximate levels of the transverse sections d1–d4 are indicated); e1–e3, frontal sections of ovary (e1 has gone through the ovule and e3 through the gland (the dots over the gland are pollen grains), in e2 one can see a part of the vascular bundle in the posterior carpel). f–g, Selago tephrodes (H. Norm. Austr. Afr. 847). × 46.

Hoping to establish whether the ovarian morphology outlined above is a constant character in this species, I have gone to great lengths to amass as representative a material as possible for study. Another reason for doing so was that I wished to unravel how this species should be distinguished from closely related ones, specifically S. laxiflora Clossy. All the collections I have had access to were strictly consistent as regards ovarian morphology and other habits, even if some of them might have exhibited minor variations in such matters as pubescence.

very few collections, among them ZEYHER 26! Clanwilliam, Brak Fontein, near Olifants River. On the single sheet of this species in the Kew museum an annotation—written by ROLFE—states that the specimen probably has been collected by ZEYHER at the aforementioned locality (see my index of collections). The plant was actually *S. tephrodes*, as its ovarian morphology and general appearance otherwise proved.

Collections from Botrivier labelled *S. tephrodes* by ECKLON et ZEYHER, ROLFE determined as *S. Thunbergii CHOISY*. The specimens from that locality which I have examined also clearly indicate that it is out of the question to identify them as *S. tephrodes*. Excellent slides were prepared from the specimens from Lund (Fig. 3a), those from the Botanical Museum at Stockholm were less well preserved. The ovaries from both these collections were of the usual *Selago* type. Furthermore the bract was adnate to the calyx, which is not the case in *S. tephrodes*.

Superficially and vegetatively *S. tephrodes* resembles several species of *Selago*, but owing to the morphology of its ovary, it occupies a unique position, and hence the plant ought to be withdrawn from the genus. A convenient solution would then be to include the plant in *Globulariopsis*, although to me the relationship between *S. tephrodes* and *Globulariopsis wittebergensis* does not seem particularly close. Surely the two species are descended from separate parts of *Selago*. For the time being I shall let *S. tephrodes* remain within *Selago*.

C. The Ovary with Four Ovules.

The material used was as follows:

*Selago aggregata* ROLFE, MEEUSE 9972 (S).
*S. longituba* ROLFE, EXENS 2032 (L), ROGERS 29484 (S).
*S. natalensis* ROLFE, WALL 6.3.49 (S), CODD 9577, 9665 (U), SIDEY 1604 (S), Wood 12982 (S), 4863 (K); GERRARD et MCKEN (K), SLEWADT 95 (K).
*S. Wilmsii* ROLFE, WILMS 1163 (K).

The following description of the ovarian morphology refers specifically to *Selago natalensis* but is in all essentials equally applicable to the other species. As usual the ovary has a conspicuous nectariferous gland at its base and is divided into an anterior and a posterior chamber but, unlike all other *Selagineae*, each of these chambers contains two ovules. These are located at two levels (Figs. 7a and b). The two occupying the bottom storey are disposed in the

same manner as in other Selagineae, viz. they are pendulous and the micropyle is directed upwards. The two in the top storey are placed so that they become the mirror image of the lower ones, in other words they are erect and with the micropyle directed downwards. As appears from the transverse sections depicted in Fig. 7 d₁, the ovules are, like those in Selago serrata (cf. Fig. 2 b₄), oriented with their median plane perpendicular to the median plane of the ovary.

In Figs. 7 c₁ to c₃ the two ovules in the same storey are disposed
with the raphes facing opposite directions and each of the two ovules in the top storey has its raphe directed away from that of the ovule in the bottom storey of the same chamber. However, Fig. 7d discloses that the two ovules in the same storey may be codirectional.

The wall of the ovary is composed of four, or in some parts five cell layers. The innermost layer—which is most easily studied in longitudinal sections cut along a plane tangential to an ovarian chamber—is made up of very elongated, uniformly thick, roughly horizontal cells with a high plasma content. Consequently the inside of a chamber takes on a finely striped appearance. The other layers of the ovarian wall are composed of isodiametric cells.

Shortly after fertilization the cells in the layer next to the innermost become considerably enlarged and develop fibrous, striate thickenings. The cells in the other layers become vacuolized and more or less deformed. The transverse section of a fruit depicted in Fig. 7e shows that the central waist of the ovary remains on the whole unchanged in girth whilst, on the other hand, the portions on either side of it expand greatly owing to distension of the chambers. That a single layer of the fruit wall undergoes such a transformation is something I have never observed in any other species. In Globulariopsis and Microdon the fibrous layers of the wall acquire a structure which is fairly like that of this single cell layer (cf. Figs. 5e, i and k). In those species of Selago and Walafrida whose fruit wall I have studied certain cell layers become lignified (cf. Figs. 4b and c) but the ovary preserves its shape.

Unfortunately I have had no opportunity to study mature fruits but a median longitudinal section of a fruit that has attained a fairly advanced stage of development is illustrated in Fig. 7f. Every ovule contains an embryo and has remnants of a micropylar haustorium. There is no wall separating the upper ovule from the lower. The two lobes of the ovary are still firmly attached to one another, but since the fibrous layer of the wall almost wholly coats each lobe the prerequisites for an ultimate division of the fruit into two parts each with two seeds would seem to be present. Judging by the oldest fruits I have examined, however, the fruit would appear to have no pronounced tendency to divide in such a manner. Externally young fruits exhibit not only the deep furrow marking the boundary between the two halves but also a shallower furrow along the median line of each carpel, that on the anterior part being more distinct. (In Fig. 7e this shallow furrow faces the front.)

The highly remarkable ovarian morphology of these four species puts them in a distinctive position which is extraordinary enough to warrant their being segregated in a genus of their own. I am constrained to base a description of this genus solely on my knowledge of its ovarian morphology. During my studies of the genus *Selago*, I have often investigated detached flowers without being able to compare simultaneously an adequate number of complete specimens. Clearly, however, these four species form a natural and homogeneous group. Their habits are very similar: their leaves are all more or less lanceolate and toothed, their flowers are aggregated in dense corymbs, and the bract is adnate to the calyx.

The number of ovules is unfortunately a character that cannot readily be checked. Nevertheless the differences between this new genus and *Selago* seem greater than those between *Walafrida* and *Selago*, or between *Dischisma* and *Hebenstreitia*, or amongst *Microdon*, *Gosela* and *Agathelpis*.

*Tetraselago* S. Junell, gen. nov.

Genus sicut *Selago* ovario biloculari instructum, ab illo ovulis in quoque loculo binis distinctum, superiore adscendente, micropyle deorsum versa, inferiore pendulo, micropyle sursum versa.

Typus generis: *Tetraselago natalensis* (Rolfe) comb. nov.

Syn.: *Selago natalensis* Rolfe 1901, p. 151.

The Taxonomical Position of the *Selagineae* with an Outline of the Evolution of the Ovary.

The *Selagineae* are in many ways similar to the *Manuleae*. Both have their centre of distribution in South Africa and their anthers are monotheceous. The greatest difference—apart from the morphology of their ovaries—would appear to be that as a rule the plants in the former group have alternate leaves and those in the latter opposite leaves. But exceptions to this rule occur in both groups.

Within the *Manuleae* there is a tendency towards reduction of the number of ovules. It has been reported, for example, that some species of *Phyllopodium* have only a few ovules. In my opinion it must be from such a scrophulariaceous type that the ovary of *Tetraselago*, with its four ovules, is to be derived. Those *Manuleae* species I have studied had the upper ovules erected with the micropyle directed downwards, whilst the lower ovules were pendulous with
the micropyle directed upwards (Fig. 8a). The ovary of *Tetraselago* contains two ovules of each of the two types (Fig. 8b). In ovaries with only two ovules (Figs. 8c–e, these are pendulous and obviously homologous to the lower pair in *Tetraselago*. The placenta often seems needlessly large, and this is so certainly because the ovary is to be derived from an ovary with several ovules. By abortion of the posterior carpel we have finally the one-celled ovary with its solitary ovule (Fig. 8f).

The morphology of the ovary obviously confirms the opinion that *Selagineae* is a tribe within the *Scrophulariaceae*.

The four ovules in the *Tetraselago* ovary have their median planes more or less perpendicular to the median plane of the ovary. The same position (pleurotropy) is also common in ovaries with two ovules, (Fig. 8c) and seems to me to be the most primitive. It is also very common in *Selago* and *Walafrida* to find the funiculus directed more or less straight away from the centre of the ovary (apotropy, Fig. 8d). The ovules in *Selago quadrangularis*, *Hebenstreitia* and *Dischisma* are turned so that the funiculus is directed towards the centre (epitropy, Fig. 8e).

**Summary.**

1. The taxonomical position of the *Selagineae* and the morphology of their ovary have been briefly outlined in the preceding paragraphs. Hence I shall here merely refer to them.

2. For generic delimitation great weight has often been attached to the bract being or not being adnate to the calyx. The presence of an adnate bract was thus the character mainly responsible for the separation of *Cromidon* from *Selago*. But as *Selago* as well as *Wala-
frida and Microdon, are far from homogeneous in this respect. Cromidion cannot be maintained as a genus.

3. The floral morphology has been studied in genera with one-celled ovaries and the generic differentiation has been discussed. Gosela and Agathelpis are surely derived from Microdon. The flower morphology of Globulariopsis resembles that of Microdon. However, the delimitation of Globulariopsis is doubtful because it is based on whether or not the bract is adnate to the calyx. Selago tephrodes is unique among the species of Selago in having a one-celled ovary.

Gothenburg, October 1960.

REFERENCES.


TWO PEDICULARIS SPECIES FROM NW. AMERICA,
P. ALBERTAE N. SP. AND P. SUDETICA SENS. LAT.

BY
ERIC HULTÉN.

During the excursion of the Ninth International Botanical Congress to Jasper and Banff parks in the Rocky Mountains of Alberta a Pedicularis species that is unknown to science was collected and photographed in colour (Pl. I) by the present author in the Snow Creek Pass at the western end of the Cascade Valley by a tributary of the Red Deer River about 65 km north-west of Banff.

It is closely related to P. flammea L., an arctic plant reaching westwards in America to Great Bear Lake and southwards to James Bay (Fig. 1). P. flammea is in its entire range a completely glabrous plant. As is seen from the photograph, the new species has a white-woolly spike. Judging from the numerous particles adhering to it, it is somewhat viscosce. The basal leaves have an oblong ovate outline, the pinnulae are more dissected than in P. flammea with one to two pairs of broad, short, serrulated lobes, and the teeth of the calyx are broader and less acute.

The bracts have a membranaceous, broad base and a much smaller leaf-like tip than in P. flammea.

In spite of these differences it is a clear counterpart to P. flammea — an interesting fact, as it grows at a distance of about 1500 km from the nearest known station for that species.

Pedicularis albertae n. sp.

Humilis, erecta, 5–10 cm alta; folia pinnatisecta ambitu ovato-lanceolata, segmentis 12–14 suboppositis, pinnato-incisis, pinnis denticulatis; racemus brevis, inferne interruptus, lanatus; bracteae apice brevi foliaceo calyce longiores; flos pedicellatus, calyx cylindricus, lanatus, dentibus triangularibus subacutis instructus, corolla dorso subcurvato, galea obtusa, edentata, lutea, apice purpureo, labium inferius trilobatum duplo superans, filamenta glabra.

Alberta, Snow Creek Pass, July 27, 1959, leg. E. Hultén (S). Known only from the type locality.

The races of *Pedicularis sudetica* Willd. sens. lat.

During trips to Arctic Canada in 1959 and to Point Barrow and other parts of Arctic Alaska in 1960, the latter sponsored by the Arctic Institute of North America, it was noted that the plant called *Pedicularis sudetica* looked strikingly different from the *P. sudetica* which the author had seen growing in south-eastern Alaska, in Kamchatka and in eastern Kola Peninsula. The flowers of the Arctic American plant had a rose-coloured galea with dark purplish tip and nearly white or faintly rose-coloured lip, with dark oblong spots, larger on the lower side, while the others had dark purplish single-coloured flowers. A difference was apparent, and at first I had the impression that the Arctic American plant was a distinct species. Revision of a large material, however, made it clear that the line of demarcation between the taxa, which are closely allied to *P. sudetica* Willd., is somewhat fluent, and here therefore I regard them as races, subspecies, of *P. sudetica*.

P. sudetica was described by Willdenow (L. Sp. Pl., ed. 4, III:1, 1800, p. 209) from "Sudetis inque Sibiria" as having "corolla purpurea", as is also shown in the colour pictures in Reichenbach, Icon. Bot. Pl. Crit. IV, 1826, tab. CCCXC, Reichenbach, Icon. Fl. Germ. Helv. 20, 1862, tab. MDCCCL and Schlechtendal, Langenthal u. Schenk, Fl. Deutschl. 17, 1884, tab. 1719. A specimen labelled P. sudetica mihi by Willdenow, without any locality given, in the Stockholm herbarium agrees completely with the plant from the Giant Mountains. They have in outline ovate lanceolate to lanceolate basal leaves with a fairly broad rachis and with 11–15 subopposite pairs of segments, and a toothed apex. The bracts have a dilatated base and a prolonged toothed apex (Fig. 2). The inflorescence is short in the flowering state. The calyx is inflated with short triangular acute lobes entire or somewhat serrulated in the margin reaching to the end of the tube.

The lip is short, denticulated in the margin with a median lobe with so narrow a base that it sometimes almost looks as if it were stipitated. This is P. sudetica subsp. sudetica, restricted to the Sudetes only.

The corresponding plant from easternmost Kola Peninsula, southern Novaya Zemlya and the northern Urals differs in having markedly lobed bracts often without a prolonged apex (Fig. 1). The inflorescence is often but not always somewhat more pubescent than in subsp. sudetica; nearly glabrous specimens occur. Especially in the northern part of the area the plant is often somewhat decumbent. The flowers are purplish, single-coloured, and the median lobe of the lip has a narrow base. For this taxon I propose the name subsp. arctoeuropaea.

In Novaya Zemlya, on Vaigatch and Kolgujev as well as in the northernmost Urals another closely related taxon occurs with very broad bracts with broad short lobes, triangular calyx lobes, large flowers with a large lip having a median lobe that is narrow at the base, and thick galea. It has a strongly yellowish or brownish pubescent spike.

The colour of the flower is difficult to judge from dried material, but it seems to be rose-coloured with a somewhat lighter coloured lip. For this taxon I propose the name subsp. noviae-zemliae.

Along the Arctic Coast from Yenisei and eastwards to the Bering Sea two other taxa occur, one with a more northern and another with a more southern area. The more southern taxon has lower
bracts with small basal lobes, long caudex and unbranched median and upper bracts.

The inflorescence is, contrary to what is the case in the preceding taxa, usually prolonged already during anthesis.

The rachis of the leaves is narrower than in the preceding taxa, the tube being on an average somewhat longer and the lip smaller. Especially Hudson Bay specimens have small flowers and small lip and might possibly be distinguishable as a slightly different race. As this type approaches the taxon growing in interior Alaska I propose to call it subsp. interioroides.

The pubescence is variable but both fairly pubescent and nearly glabrous specimens occur.

In interior Alaska a fourth taxon occurs, characterized even in anthesis by prolonged inflorescence and long narrow bracts lacking long lateral lobes. The top of the inflorescence is pyramidal, and it is a tall slender plant. The tube of the purplish corolla is long, the median lobe of the lip has a broad base and the leaves have a narrow rachis and more numerous, often short, pinnae. It was described by the present author as P. sudetica var. interior in Fl. Alaska and Yukon and is here regarded as a subspecies.

North of the area of subsp. interior and subsp. interioroides, but overlapping their range, a fifth taxon occurs. It is usually low-growing, often decumbent and somewhat tufted with large flowers and large lip. The lower bracts are lobed, dilatated below, the upper ones with single lobes, often broad ovate lanceolate or ovate. The galea is rose-coloured with dark purple tip, and the lip white or faintly pink with oblong spots larger on the lower side (Pl. I). The spike is always woolly pubescent. For this taxon occurring from Yenisei eastwards to the Bering Sea and to Ellesmere Land and Baffin Land I propose the name subsp. albolabiata. It is most closely related to subsp. noviae-zemliae.

Where its area overlaps that of subsp. interioroides and subsp. interior intermediates occur both on the coast of Siberia and in northern Alaska.

Lastly, a sixth taxon belonging to this affinity occurs on the southern coast of Alaska in the Bering Sea area and in Kamtchatka.

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Fig. 2. Races of Pedicularis sudetica: a, subsp. sudetica from the Sudetic Mts.; b, subsp. arctoeuropaea (type); c, subsp. noviae-zemliae (type); d, subsp. albolabiata (type); e, subsp. interioroides (type); f, subsp. interior (Donnelly Dome, Richardson Highway at 145°45' W.); g, subsp. pacifica (type).

Svensk Botanisk Tidskrift, 55 (1961): 1
Its bracts are somewhat like those of subsp. *albolabiata*, dilatated at the base and with single long lobes, but the corolla is very large with large lip often overlapping the galea, and purplish flowers in a flat-topped glabrous or somewhat short pubescent inflorescence. The calyx teeth are long and tend to be somewhat leaf-like in the *Sv. Bot. Tidskr., 55* (1961): 1
apex. The leaves have a broad rachis and, on an average, fewer segments than in subsp. sudetica. The median lobe of the lip has a fairly broad base. For this taxon I propose the name subsp. pacifica. In Kamtchatka it was common within a small very restricted area in the southern mountains, thus showing the same tendency in this respect as subsp. sudetica.

Unfortunately no specimens were seen from the isolated area of P. sudetica in the central Asiatic mountains. The population there must be expected to belong to a separate race, probably to a race similar to subsp. sudetica or subsp. pacifica.

Nor was the Saghalin plant seen, but it may be expected to belong to subsp. pacifica.

Of earlier described varieties of P. sudetica var. gymnostachya Trautv. (Acta Hort. Petrop. 5, 1897 p. 550) is considered in Fl. SSSR to be the hybrid P. langsdorffii × sudetica. Var. gymnocephala Trautv. (loc. cit.) was described from material from Sredne-Ko-

lymsk and is certainly referable to subsp. interioroides, var. "δ bicolor" Walpers (Rep. Bot. Syst. 1844 p. 422) and probably also "γ lanata" Walpers (loc. cit.), are referable to subsp. albolabiata. δ bicolor is described as having "Corolla flava, galea purpurea" and in Fl. SSSR the colour of the flowers of *P. sudetica* is said to be "pink or purplish or sometimes yellow with purplish galea" (translated from the Russian text). However, it is very difficult to judge the colour of the flowers from dried material. Yellow flowers hardly occur in *P. sudetica*. The flowers of subsp. albolabiata may sometimes appear as if they were yellow in dried material.

Var. *macrodonta* Karel. et Kiril. (Walpers loc. cit.) is a plant habitually similar to *P. sudetica* from Dschungarski Alatau, with glabrous calyx, long tube of the corolla as compared with the calyx and two of the stamens with pubescent filaments. It is not regarded as being closely related to *P. sudetica* in Fl. SSSR and is there called *P. songarica* Schrenk.

A species closely related to *P. sudetica* is *P. nasuta* M. à B., occ-
Above: *Pedicularis albertae* n. sp. Type specimen.
Below: *Pedicularis sudetica* ssp. *albolabiata* n. ssp. Type specimen.

Photo E. Hultén.
occurring in NE. Siberia. It lacks the teeth of the galea always present in \textit{P. sudetica}, and has very narrowly winged rachis and linear lanceolate segments of the leaves. \textit{P. villosa} \textit{Ledeb.}, also closely related to \textit{P. sudetica}, also has a narrow rachis, shorter teeth of the bracts, short calyx as compared with the tube and entire margin of the lobes of the lip. It occurs in central Asia from Pamir to Dahruria.

In Montana and Wyoming a related plant, \textit{P. cystopteridifolia} \textit{Rydb.}, occurs. It differs a good deal from \textit{P. sudetica} in its broad and short, more or less cuneate-based, incised leaf-segments, short calyx as compared with the tube and long bracts with laciniated base and long entire caudex.

The conditions described above within the \textit{P. sudetica} complex should be interpreted in the following way. The area of the preglacial \textit{P. sudetica} was split up into several separate areas during the glacial periods, one of them in the unglaciated Arctic archipelago. Slightly different populations developed in each of these areas. In interglacial and postglacial time the species has spread again from these centres and formed one continuous range, with the exception of the small population isolated in the Sudetic Mountains and the larger central Siberian one. In the circumpolar area formed by the merging populations the variation of the distinguishing characters is large, especially where the ranges overlap, and it is most reasonable to regard the present taxa as major races, subspecies, of \textit{P. sudetica}, which is the oldest species name in the complex. It is possible that subsp. \textit{interioroides} was formed through interchange of genes between subsp. \textit{interior} and subsp. \textit{albolabiata}.

The differentiation within the nearly circumpolar \textit{P. sudetica} might serve as an example of the line along which the circumpolar plant species are built up.

As intermediates occur it is hardly possible to give a key from which all specimens can be determined with certainty, but the distinguishing characters are given below.

\textbf{Key to the subspecies of \textit{Pedicularis sudetica}.}

A. Bracts not widely dilatated at the base, basal bracts lacking long lobes (exceptionally with long branches), middle ones lacking lobes, flowers purplish.

B. Inflorescence flat-topped in flower, median lobe of the inflorescence
narrow at the base, tube of corolla short compared with the calyx, leaves with broad rachis. subsp. *sudetica*

B. Inflorescence with pyramidal top often prolonged already in flowering state, tube of corolla longer as compared with the lip, plant taller, more slender, levaes with narrow rachis. subsp. *interior*

A. Bracts strongly dilatated, often hyaline, at the base, basal bracts broad, hyaline at the base with apical or lateral lobes, flowers purplish, or purple with white lip.

C. Lower bracts with small basal lobes and long caudex, the middle and upper ones entire, flowers comparatively small, plant tall, straight, flowers purple. subsp. *interioroides*

D. Profusely lanate-pubescent spike, bracts short, with the exception of the lowest, lacking prolonged apical lobe.

E. Lobes of the bracts very broad, calyx teeth broad triangular, flowers probably pink. subsp. *novaiæ-žemliae*

E. Lobes of the bracts narrow, calyx teeth narrow, flowers with pink galea with purple apex and white or faintly pink, spotted lip. subsp. *albolabiata*

D. Less pubescent spike, bracts with long apical lobe.

F. Calyx glabrous or slightly pubescent, often with leaf-like tips of the teeth, flowers very large. subsp. *pacificæ*

F. Calyx more or less pubescent, exceptionally glabrous, with narrowly triangular, acute teeth. subsp. *arctoeuropaea*

**Systematical survey of *Pedicularis sudetica* Willd. sens.lat.**

Systematically the above reasoning may be summarized as follows:


Type from the Giant Mts.

Distribution: isolated in the Sudetic Mts.

*P. sudetica* subsp. *arctoeuropaea* nov. subsp.

Erecta vel interdum adscendens; racemus plerumque quam apud subsp. *sudetica* lanatior; bracteae parte basali dilatatae lobis lateralis angustis; flores purpurei.

Type from E. Kola Peninsula, Triostrova, leg. E. Hultén (S).

Distribution: from E. Kola Peninsula to Jalmal and in the northern Urals.

*P. sudetica* subsp. *novaiæ-žemliae* nov. subsp.

Robusta, circiter 10 cm alta; racemus lanuginoso dense luteola usque sub-fusica tectus; bracteae lobis latis brevibus; corolla rosea labio pallidiore.

TWO PEDIULARIS SPECIES FROM NW. AMERICA

Type: Matotchkin Shar, Aug. 7, 1891, Ekstam (S).
Distribution: southern half of Novaya-Zemlya, Kolgujev I., the northernmost Urals.

P. sudetica subsp. **interioroides** nov. subsp.

Alta, erecta; inflorescentia jam sub flore extensa; bracteae inferiores pinnis lateralis longis, mediae et superiores integrae. 

Type: Lower Yenisei, Dudinka 1876 leg. Arnell (S).
Distribution: from lower Yenisei to southern Hudson Bay.

P. sudetica subsp. **albolabiata** nov. subsp.

Saepe procumbens; racemus semper densissime lanatus; corolla magna, galea crassa, inferne rosea, superne purpurea, labium album maculis oblongis obscuro-purpureis, bracteae basin versus valde dilatatae, et inferiores et superiores pinnatisectae.

Type: Victoria Land: Cambridge Bay, Hultén, Aug. 12, 1959 (S).
Distribution: from lower Yenisei to northern Bering Sea and eastwards to Ellesmere Land and Baffin Land. Intergrades with subsp. interioroides and subsp. interior where the areas overlap.

P. sudetica subsp. **interior** comb. nov.

Type from Whitehorse, upper Yukon R., EASTWOOD 621 (US).
Distribution: central Alaska and Yukon south to S. British Columbia.

P. sudetica subsp. **pacifico** nov. subsp.

Erecta, circiter 18 cm alta, glabra; corolla magna, galea crassa, labium latum interdum galea longius, bracteae parte inferiores dilatatae, lobis basalius lateralibus longis paucis instructae, calyx glaber, superne dentibus saeppe foliaceis gerens, corolla purpurea, lobus medius labii basin versus sublatus.

Type from St. Paul I., HULTÉN 7246 (S).
Distribution: from northern SE. Alaska to Unalaska and shores

of Bering Sea and Chukchee Sea, Kamtchatka and the northern Kuriles.

The type has glabrous calyx but specimens with pilose calyx occur, var. *pilosicalyx* nov. var.

Differt a typo calyce piloso.

Specimens from the isolated area in central Siberia not seen. The present study is based on the material in the botanical museums in Stockholm, Uppsala, Lund and Copenhagen.
SOME NEW AMERICAN SPECIES OF HEPATICS.

BY

SIGFRID ARNELL.

When examining old material in the Paleobotanical Department of the State Museum of Natural History, Stockholm, I found some specimens containing species new to the science. I will here give descriptions of them.


Dioica. Minor, gracilis, flavicans. Caulis ad 2 cm longus, dilute brunneus, simplex vel pauciramosus. Folia caulina ad 1.5 mm longa, 0.6 mm lata, remotiuscula vel contigua, ventre parum decurrentia ibidemque parum recurvula et concava, stricta, oblique patula (angulo 50–60°), marginibus nudis, sub apicis paucidentatis, apice truncato-rotundato, 3–5 dentato. Folia ramulina simillima. Cellulae marginales 20 × 34 μ, mediae 28 × 40 μ, parietibus tenuis, trigonis nullis. Folia floralia caulinae majorae, obovato-obcuneata, longe spinosa. Perianthia (juvenilia) ore crebre spinoso-dentato. Androecia non observata.

Dioicous, small, ± flaccid, yellowish green-pale brown. Stem up to 2 cm long, pale brown, simple or once branched. Stem leaves to 1.5 mm long and 0.6 mm broad, lingulate-longly obtuse, margins ± parallel (especially in the lower leaves, in the upper leaves the base is generally somewhat narrower than in the distal portion), apex rounded-truncate, with 3–5 teeth, generally 3–5 cells long and acute. Basal part of the margins somewhat incurved and the leaves basally somewhat concave. Margins ± dentate in the subapical portion, basal portion entire. Marginal cells about 20 × 34 μ, cells in the middle of the leaf about 28 × 40 μ, walls ± thin, trigones absent. In the leaves and bracts occur single cells with stronger coloured (pale brown) walls and rounded papills of the cuticle. Cuticle else smooth. Female bracts larger than the leaves, obovate-obcuneate, margins and especially apex with long acute teeth. Perianth (young) with mouth longly dentate. Male plants not observed.

The plant belongs to the section *Angustifoliae* of *Stephani* and differs from the Brazilian and West Indian species by the large, thin-walled cells. No representative of this group was earlier known from southern South America.

Lophocolea boliviensis S. Arn. nov. spec. — Bolivia: Tegumendama 2500 m. s. m. leg. Lindig. Type specimen in the Paleobotanical Department of the State Museum of Natural History in Stockholm.

Dioica, minor, pallide virens, terricola. Caulis ad 15 mm longus, repens. Folia caulina superiora 0.5 mm longa, 0.25 mm lata, subplana, subrecte patula, alternantia, rectangularia, apice truncata, margine integra. Folia inferiortea apice truncata — bidentata. Cellulae marginales 18 × 18 to 20 × 20 μ, mediae 14 × 14 to 18 × 18 μ, trigones parvis acutis, cuticula leviter papillata. Amphigastria magna, libera, profunde bifida. Androecia intercalaria, longa, bracteis apice truncato-emarginato. Cetera desunt.

Dioicous, small, pale green, procumbent or slightly ascending on soil. Shoots up to 15 mm long. Upper leaves 0.5 mm long, 0.25 mm broad, almost plane, approximate, alternate, erecto-patent, apex truncate, margin entire, lower margin slightly decurrent. Lower leaves of varying appearance, almost rectangular, apex truncate, emarginate or bilobed, lobes obtuse — subacute. Marginal cells 18 × 18 to 20 × 20 μ, cells in the middle of the leaf 14 × 14 to 18 × 18 μ, walls thin, trigones small, cuticle slightly papillose-smooth. Amphigastria rather large, deeply bifid, lobes ending with a slime papilla, margin of the basal part of the amphigastrium often with a marginal tooth. Androecia intercalary, rather long. Bracts with apex of the lobe truncate, lobule rather large, apex rounded. Antheridia solitary. Female plants not observed.

Differs from Lophocolea granatensis G., L. irrigata Spn. and L. pyenorhiza Spn. by smaller size and smaller cells.

Fig. 2. *Lophocolea boliviensis* S. Arnell. — *a*, Apex of a shoot; *b*, leaves from the basal portion of the stem; *c*, amphigastria; *d*, male bract; *e*, marginal cells from a leaf.

Fig. 3. *Anastrophyllum guadelupensis* S. Arnell. — *a*, Leaf; *b*, marginal cells from the leaf.

Fig. 4. Stephaniella mexicana S. Arnell. — a, Plants in dorsal view, 1.5/1; b, cross-section of the plant, 100/1; c, leaves, 100/1; d, marginal cells, 250/1; e, cells from the mid of a leaf, 250/1; f, paraphyll, 100/1.

botanical Department of the State Museum of Natural History in Stockholm.

Sterilis, maxima, robusta, purpurascens. Caulis ad 4 cm longus, fuscus et durus, simplex. Folia conferta, subamplexicaula, e basi vaginante curvatim patula, postice ampliata caulique appressa, antice incurva, valde concava, ad medium biloba, lobis ovatotriangulatis, apice acuto, margine paucidentato. Cellulae $20 \times 30 \mu$, basi majores, parietibus incrassatis, trigonis nullis, cuticula leviter verrucosa. Cetera desunt.

Anastrophyllum guadelupensis differs from the other species of the genus by the dentate margin of the leaves.

Fig. 5. *Plagiochila socia* L. et G. var. *longidentata* S. Arnell. — *a*, Leaf; *b*, marginal tooth of a leaf.

Popocatepetl, forest limit, leg. H. Fröderström et E. Hultén 4.3.1932. Type specimen in the Paleobotanical Department of the State Museum of Natural History in Stockholm.


Sterile, 6–8 mm long, 0.8 mm broad, creeping on black soil, almost terete, simple or once or twice dichotomously branched, whitish, pale purple towards the apex. No subterranean flagellae observed. Rhizoids pale brown, long, generally in fascicles from the ventral face of the stem. Leaves densely imbricate, reniform–orbiculare, concave, in the median portion of the plant up to 1 mm broad and 0.25 mm long, in the apical portion less broad, hyaline except in the median portion of the base, where the cells are chlorophyllose. Apical leaves and the upper portion of the other leaves often purple. Margin entire. Inner face of the leaves with 2–5 blunt, longitudinal and parallel ridges or low lamellae of chlorophyllose cells. Cells thin-walled, in the upper part of the margin elongate, especially in the basal portion, where they measure up to 20 × 100 μ, length gradually diminishing backwards to the middle of the leaf, where the cells measure about 26 × 40 μ. Chlorophyllose cells about 28 × 28 μ. Cuticle smooth. Leaf-like paraphyllae from the plane dorsal face of the stem, provided with ridges and lamellae as the leaves. Amphigastria lacking.

Differs from *Stephaniella paraphyllina* Jack by lacking filiform paraphyllae and by longer marginal cells of the leaves, from *S. hamata* St. by

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the shape of the leaves and the parallel longitudinal ridges of the interior face of the leaves.

*Plagiochila socia* L. et G. var. *longidentata* S. ARNELL nov. var. — Brasilia, Sta Catharina, Porto Bello leg. Dr. BILLBERG 1826. Type specimen in Paleobotanical Department, State Museum of Natural History, Stockholm.

Folia caulina 2.5–3 mm longa, 1–1.2 mm lata, plana, margine longe dentato.

Differing from the main species by the long, ciliate teeth in the margin of the leaves.


The male bracts only have one basal amphigastrium and no amphigastria in the distal portion of the branch. The species thus belongs to the genus *Leucolejeunea*, and the name must be *Leucolejeunea rotalis* (Tayl.) S. ARNELL nov. comb.
HYLANDRA—A NEW GENUS OF CRUCIFERAE.

BY

ÅSKELL LÖVE.

One of the few species which are endemic to northwestern Europe is a small plant of the Cruciferae, typical of peaty or gravelly soils in a limited area in central Sweden, southern Finland, and adjacent parts of the Soviet Union (cf. HULTÉN, 1950). It is doubtfully native in more northern and more southern regions in Scandinavia where it is confined to railway banks or their proximities. Although inconspicuous and non-aggressive, this small plant, which rarely exceeds 20 cm in height and usually grows much lower, has a complicated nomenclatural history, as related by HYLANDER (1957), and its generic relationship has been disputed ever since it was first named by FRIES (1843, 1845).

The first name with which the plant in question was identified seems to be either Sisymbrium arenosum, mentioned by LINNAEUS (1755) in the second edition of his Flora Suecica, or, maybe even the earlier Turritis minima used by LINNAEUS in his Iter Lapponicum (cf. HYLANDER, 1957). The use of both these names for the plant in question was, however, caused by a mistake, and it was FRIES (1843) who first realized that this was a taxon in its own right, so he named it Sisymbrium thalianum var. lyratum, thus indicating its characteristic leaf form. A little later, FRIES (1845) replaced this name with Arabis thaliana suecica. As shown by HYLANDER (1957), the binomial Arabis suecica, attributed to Fries, was repeatedly used from 1846 in Swedish publications, though it has been difficult to date its valid publication. It may have been validated by HARTMAN (1849) as a synonym for Arabis arenosa β macilenta, whereas HYLANDER (l.c.) thinks it was validated first by NYMAN (1854–55) in his Sylloge,

although Nyman (l.c.) lists the combination without a reference to the basionym and as if it had been validated at the species level by Fries (1845). The plant was transferred to the genus Arabidopsis as A. suecica (Fr.) Norrl. by Norrlin (1878). The taxon has also been transferred to the genus Cardaminopsis in synonymy with Arabis suecica by Hitonen (1933, 1934), and the combination C. suecica (Fr.) Hirt. was accepted by Hylander (1941), who gave A. suecica as its synonym elsewhere in his checklist of Scandinavian plants in order to establish the validity of this transfer. The major points in the history of the nomenclature of this plant are given by Hylander (1957), whereas the details of understandings and misunderstandings of this taxon have never been narrated.

Morphologically, the taxon named by Fries (l.c.) is related not only to that part of Arabis which was separated as the section Cardaminopsis by Boissier (1867) and later recognized as the genus Cardaminopsis by Hayek (1912), but is also related to the genus Arabidopsis, distinguished from Arabis and Sisymbrium by Heynhold (in Holl & Heynhold, 1842). This almost intermediate position has caused considerable discussion as to the wisdom of separating these genera, although the species is in fact intermediate in morphological characters only between the species Cardaminopsis arenosa and Arabidopsis thaliana and not between other species of these genera, as demonstrated by Hylander (1957). It is, however, closer to A. thaliana in several essential characters as well as in some physiological qualities: both A. thaliana and C. suecica are hapaxanthic annuals or, the latter, occasionally biennial, whereas C. arenosa is pollakanthic and perennial, at least in central Europe (cf. Laibach, 1958) and also when cultivated in eastern Canada, although it seems to be biennial only in Sweden (Hylander, in litt.).

The chromosome number of Arabidopsis thaliana is 2n = 10, as has been demonstrated by a number of students investigating material from different populations (Laibach, 1907; Winge, 1925; Jaretzky, 1928; Mattick, in Tischler, 1950; Langridge, 1955; Böcher & Larsen, 1958; Löve, here published). Other species of the genus in its strict sense remain cytologically unknown. Species of Cardaminopsis so far studied have, however, 2n = 16 or 32 chromosomes. C. petraea (L.) Hirt. is a diploid, as shown by Knaben (1950), Böcher & Larsen (1950), and Löve & Löve (1956), and so is C. Halleri (L.) Hayek, as counted by Jaretzky (1928) and Mattick (in Tischler, 1950). C. arenosa (L.) Hayek is reported to be diploid So. Bot. Tidskr., 55 (1961): 1
in Hungary, according to Baksay (1956) and Soó & Javorka (1951). It is tetraploid in Sweden (Hylander, 1957) and also somewhere in central Europe according to Soó & Javorka (1951) and Mattick (i.e.). The last author gives the number $2n = 28$ and not 32, but the number $2n = 32$ is correct according to studies by the present writer on material of Scandinavian and German origin.

The chromosome number of Cardaminopsis suecica was reported as $2n = c. 28$ by Jaretzky (1932) and as $2n = 26–28$ by Manton (1932). A more exact count was reported by Hylander (1957), who found it to be $2n = 26$. This has been verified on Swedish material by the present writer who found, however, that small deviations from this most common number occur, at least in germinating seeds, so that a very low percentage of the plants may have 27 or 28 and, occasionally, only 25 chromosomes.

Based on these cytological results as well as on the morphological indications given above, Hylander (1947) concluded that C. suecica most likely should be regarded as an allotetraploid between A. thaliana and a diploid C. arenosa. Diploid C. arenosa is reported only from Hungary as mentioned above and does not occur close to the area of C. suecica at least as far as is known at present. Hybridization experiments between the three species in question were performed by Laibach (1958), and they may support the conclusion that C. suecica has originated by hybridization and chromosome number duplication from the other two species. Hybrids between C. suecica and either of the putative parents have been produced successfully, whereas Laibach (i.c.) was unable to obtain hybrids between C. arenosa and A. thaliana.

Although there can hardly be any doubt as to the origin of C. suecica and the correctness of the hypothesis by Hylander (i.c.), a small modification of it may be made. It is perhaps more likely that the allotetraploid taxon has not been formed in two steps, i.e., through a sterile hybrid between diploid taxa of its putative parents, but rather in a single step, by pollination of a normal, and therefore diploid, egg cell in the tetraploid C. arenosa with an abnormally diploid and unreduced pollen grain from A. thaliana. This hybrid would, most likely, be a fertile, alloploid plant with $2n = 26$ chromosomes from which the new species could propagate and disperse. This modified hypothesis is supported by the observation by the present writer of occasional unreduced pollen grains in A. thaliana, and also by experience from frequent productions of experimental

allopolloids in other plants by aid of a previous duplication of the chromosome numbers of the parents. It is also corroborated by the fact, that the meiosis in *C. suecica* populations of Swedish origin shows the high degree of regularity expected in a panallopolloid originating from parents with regular meiosis, though a very low frequency of quadrivalents has also been observed in some of the plants. The fact that the new plant is able to hybridize with each of the putative parent species, though these are completely incompatible with each other, also supports this hypothesis.

Hylander (1957) was of the opinion that his observations did not support the inclusion of *Cardaminopsis suecica* in the same genus as *C. arenosa* unless both were included in the same genus as *Arabidopsis thaliana*. Such a solution would, however, create other problems because of the distinction of this larger genus from *Arabis*, in addition to the fact that it would be highly heterogeneous and clearly artificial. The other solution, favoured by Hylander (l.c.) and in full accordance with modern views on genera as evolutionary homogeneous units, is to separate *C. suecica* from *Cardaminopsis* and *Arabidopsis* as a genus of its own, monotypic and intermediate though distinct (cf. Stebbins, 1953), and at the same time increase the homogeneity of both the genera of the putative parents. It was felt by Hylander (l.c.) that additional evidence was needed before such a step could be taken. Since new data from the experimental studies by Laibach (1958) and the present writer add considerable strength to this conclusion, such a new genus is hereby proposed and named after Dr. Nils Hylander, its discoverer and an eminent specialist on the Scandinavian flora and its nomenclature.

**Hylandra** Löve, gen. nov.


Typus generis: *Hylandra suecica* (Fr.) Löve.

The only species of the genus *Hylandra* so far known is:

Hylandra suecica (Fr.) Löve, comb. nov.


The type of the taxon must be selected from specimens in a copy of Fries' Herbarium Normale, fasc. X, no. 34 (from Strängnäs in the province of Södermanland), cited in the original publication by Fries (1845). Therefore, the writer proposes that the copy preserved in the Botanical Museum of Uppsala be chosen as the type.

The monotypic genus consists of hapaxanthic plants which are annual rather than biennial, with ramified hairs mixed with single hairs, and with light-green stems, leaves and fruits. The rosette leaves are incised lyrate rather than lyrate-pinnatifid, the end lobe large and not clearly distinct (cf. Fig. 174e in Lid, 1952). The petals are 4–5 mm long, pure white with a yellow base. The siliques are 2–3 cm long, broad-oval in cross-section, and the dissepiment is only slightly narrower than the diameter between the valve backs. The pedicel that supports the base of the fruit is equally broad from base to tip. The septum cells are elongated with moderately undulated and straight walls apparently haphazardly mixed. The cotyledon is incumbent, and the seed coat becomes clearly papillous when soaked. The basic chromosome number of the genus is $x = 13$.

The Scandinavian distribution area of the genus indicates that it has been formed in late-glacial or post-glacial times somewhere in central Sweden or southern Finland, though an exact determination of its place and time of origin is not possible without palynological and paleobotanical studies. It is probably somewhat younger than the recently discovered allopolyploid Saxifraga osloëensis (Knaben, 1954). That species seems to be a hemiallopolyploid which may perhaps have been formed more than once in the past where its parental species have met since primary hybrids between them still occur. Although Hylandra suecica has been reported (on the authority of Dr. Hylander) to occur also in Belgium (Lawalrée, 1957), this can be left out of the discussion, since Dr. Hylander (in litt.) has later found this to be based on a misidentification of a race belonging to C. arenaria; therefore, the area of the species seems to be continuous and restricted to central Sweden, southern Finland and the Baltic parts of the Soviet Union. To the present writer it seems highly unlikely that the Swedish-
Baltic population of *Hylandra suecica* has been produced more than a single time as an extreme panalloploid from an extremely rare fertilization of a normal egg in its tetraploid mother species by an occasionally formed unreduced pollen grain from its diploid father.

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SMÄRRE UPPSATSER OCH MEDDELANDEN.

Föreningens medlemmar uppmanas att till denna avdelning insända meddelanden om märkliga växtfynd o.d.

Preliminär översikt av vegetation och vegetationshistoria på halvön Näset vid Tullgarn.


De faktorer som i första hand synas ha präglat Näsets vegetation är å ena sidan topografin och med denna sammanhängande förhållanden, t. ex. markfuktigheten, å den andra områdets ekonomiska exploatering, dvs. om marken har upptägits av äng, betesmark, åker eller skog. I våra dagar existerar endast de tre sistnämnda brukningsformerna.


också för största delen av betesmarken och en väsentlig del av lövskogen. Även bergen är beväxta med lövskog, där så är möjligt. I sen tid avsatt lera (m. e. m. gyttjebländad) bildar stora ytor i sydöst, vilka oftast är täckta av olika våtängssamhällen men som också kan sakna slutet vegetation. Dessa områden skall inte behandlas här. I vissa svackor i och intill det största skogspartiet är markfuktigheten konstant hög. Detta har betingat uppkomsten av några alkärr.

Huvuddragen av Näsets vegetationshistoria kan skildras på följande sätt. (Då mycket återstår att göra på detta område sker det dock med reservation för att kommande undersökningar kan komma att rucka på vissa uppgifter och lämna ytterligare upplysningar.)

Den äldsta kartan över Näset är från 1685 (avbildad i RYBERG 1956, s. 181) och visar ett brett balte av äng som sträcker sig tvärs över halvön. Söderut består denna dämrot av delvis bergigt mark med lövskog mellan bergen. Åker finns något långt i norr. Alltför stora krav på kartans förmåga att ge besked om den exakta fördelningen av skog och ev. förekommande öppen mark får man dock ej ställa.


Den ekonomiska kartan av 1904 är alltför schematisk för att kunna ge några upplysningar. Då är det bättre att gå direkt till fotobilden av 1945, som finns reproducerad i RYBERG (1945). Holmarna i öster och längst i väster har i stort sett samma utseende som för omkring 200 år sedan, men i den mellersta delen har de smått ihop till ett enda stort skogsparti, i fortsättningen kallat »stora skogen«. (Märk att bildens längsida sammanfaller med nord-sydriktningen.)

Detta parti, som nu ska behandlas mer utförligt, är ungefär 700 × 400 m i omkrets. Den mörka färgen på skogen avslöjar att granen intar en framträdande ställning bland träderna (syns tyvärr sämre på reproduktionen än på originalen). Lövträd är emellertid också vanliga och företräds av samtliga de ädla lövträderna vid sidan av björk, asp, rönn, apel, hagtorn, sälj och al.

Hasseln dominerar ofta och särskilt i skogens perifera delar. Igenväxningen har här gått längre än på andra delar av Näset, där huvudparten av 1773 års äng fortfarande är öppen mark, som dock sedan lång tid tillbaka nyttjats uteslutande som bete. (Någon äng finns ej angiven på den ekonomiska kartan och ej heller minns nu levande personer från trakten att ångslätter ägt rum på Näset under deras livstid.)


På de fuktigaste ställena tog alen överhand. Ruggar av Carex caespitosa, C. elongata, Urtica dioica, Filipendula ulmaria och olika högbunkar eller också mer jämnt utbredda bestånd av Lysimachia vulgaris, Naumburgia, Carex vesicaria, Calamagrostis lanceolata m. fl. ersatte då de ovanmäntade arterna. Till de mossiga trädbaserna tydde sig smärre arter som Adoxa och Stellaria nemorum.


Detta kan främst skyllas på betesskador samt på konkurrensen med örter och gräs på de öppna fläckarna och med slyskogen (som växer betydligt snabbare än eken). Vad betet beträffar är detta visserligen avlyst för kreaturen del i den »stora skogens«, men den rikliga tillgången på vilt är tillräcklig för att hålla tillbaka eken i oskyddade lägen. Intill snär och slypartier klarar sig eken bra, i synnerhet om den står i små grupper. Även inne i slyet finns ungplantor av ek (särskilt i nordöst), och med försiktig röjning borde många av dessa kunna utveckla sig tillfredsställande. Underligt vore också annars, eftersom Näset är en utpräglad ekskogsmark. De kvarstående stora ekarna är ett gott bevis på detta. Konkurrensen med högörterna är värre, men också här är det troligt att eken skulle ha nätt längre, om den inte hejdat i växten och temporärt försvagats genom avbetning.


Undervegetationen har nämnts i olika sammanhang men alltid helt flyktigt. Till vad som ovan har sagts skall endast fogas följande synpunkter, som samtidigt kan tjäna som sammanfattning.

1. Inga arter tycks ha försvunnit till följd av de våldsamma ingreppen, men deras frekvens har ofta förändrats. Överhuvud taget är markflorans sammansättning mycket labil och i hög grad avhängig av ljuset, dvs. skogens täthet. Exempel har ovan nämnts i fråga om kolonisationen av hyggesmark eller röjda fläckar.

2. I den täta slyskogen växer samma arter som på mark med glesare skogsskikt, fastän frekvensen växlar. En tydlig samhörighet råder sålunda mellan olika delar av den forna granskogs-ångsmarken. Undantag bildar de svackor som har kärrartad karaktär.

för den »stora skogen«. Sådana arter förefaller därför att vara känsliga för slätter. Man kan då undra hur det kommer sig att de tål betespåverkan och vidare, varför de inte under den långa tid som förflyttit sedan slätterna upphörde förmått vandra ut på f.d. ängsmark, som ju också använts till bete. En förklaring är att lokala arterna på holmarna är mer skyddade; örterna växer där under träd, bland torniga buskar, på avsatser och i skrevor och på andra ståndorter, där djuren (nötkreatur, hästar) ej så lätt kommer åt dem. På Näset finns också gott om öppen gräsmark på jämnt underlag, där djuren företrädesvis uppehåller sig. För vissa arter kan också gälla att de föredrar den högre belägna och ofta stenbundna marken av andra skäl (mindre fuktighet, svagare konkurrens etc.). Hur det än må vara med detta, är det tydligt att röjning och slätter, som utgör så uppskattade moment i modern »naturvård», ingalunda är av godo för alla »lundväxter«. Flera av dessa tillhör den mellansvenska lundvegetationens värdefullaste inslag (t.ex. Galium odoratum, Campanula latifolia, Actaea, vissa lundgräs m.fl.).


Ett helt annat utförande äger den nordöstligaste hagen, »Munthes hage«, i vilken vårens exkursion tog sin början. Det är det enda parti av Näset som påminner något om den mellansvenska hagen. Spridda hängbörkar svarar för detta inträffande. Men likheten är endast ytlig beroende på den för den typiska björkhagen onormalt frittvegetationen. Hagen består av två parallella höjder åtskilda av en låg svacka. Kullarna är klädda med hassel-


På flygfotot i Ryberg (1945) gör hagen intryck av att vara endast glett trädebufvuxen. Detta är emellertid missvisande. Utvecklingen från 40-talets mitt fram till 1959 har nämligen kännetecknats av en snabb igenväxt av de öppna ytorna. Som exempel på igenväxtning till följd av för lågt betestryck är hagen utomordentligt väl lämpad. Även markvegetationen har förändrats av samma orsak. Åggrässet har brett ut sig över stora ytor i den fuktiga svackan. När nu betet åter har ökat och snären delvis röjts bort kan man hoppas att hagen så småningom kommer att återta sin föregående skepnad.


Litteratur.


Måns Ryberg.
Floristiska anteckningar från södra Öland.

Nedanstående anteckningar hänför sig till under åren 1955–1960 gjorda strövtåg på skilda delar av södra Öland (Stora alvaret med angränsande områden).

**Fynd av Alnus incana.**


**Floran i alunskifferbrotten vid Degerhamn.**

Mycket intressanta ur botanisk synpunkt är de gamla alunskifferbrotten vid Degerhamn och de därmed sammanhängande högarna av skiffergrus och annat brottmaterial, vilka tillsammans upptar ett betydande område i nord-sydlig riktning. Alunskifferbrytningen torde ha upphört för åtminstone hundra år sedan, varefter området ifråga i stort sett synes ha fått utvecklas ostört. Flera av sluttningarna är mycket branta; en del sticker upp som rundade fristående högar, andra utgör brytningssidor i den ursprungliga marken. Där brytningen har gått djupast ner i marken har den t.o.m. gått under grundvattennivån, så att små sumpmarker och sjöar uppstått. På syd-, väst- och ostsluttningarna av de olika högarna och branterna råder en mycket stark insolation vars verkningar kraftigt förhöjes av den i detta område mycket ringa årsnederbördens. När nederbörd kommer, rinner den


*Hornungia petrea* (L.) Reichb. är karaktäristisk för torr grusmark med gles vegetation, där den på höst och förrömmaren förekommer i stor ymnighet, mycket erinrande om dess förekomst på vissa slag av alvarmark. Bland övriga inom området ifråga förekommande växter må nämnas *Centaurea scabiosa*, *Anthemis tinctoria* (riklig), *Echium vulgare* (riklig),

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1 V. V. ALECHIN (Vvedenie vo floru Tambovskoj gubernii, Moskva 1915) nämner, att *Hesperis tristis* i guvernementset Tambov växte på sydslutningen av en höjd, som stack upp ur den kringliggande ängsstäppen. Där växte den tillsammans med *Astragalus austriacus*, *Phlomis pungens*, *Androsace maxima* och *Linosyris villosa*, samtliga (inklusive *Hesperis tristis*) växter, som där ej fanns på den plana stäppen utan var karaktäristiska för de sydligare fjädergrässtäpperna. På nordsidan av nyssnämnda sluttning växte bl.a. *Pranella grandiflora*.

Verbascum thapsus, V. nigrum, Artemisia absinthium, Convolvulus arvensis (ställvis riklig), Arabis hirsula, Medicago falcata (riklig), Victoria tenuifolia, V. angustifolia, Lathyrus silvestris, Daucus carota (riklig), Conium maculatum (åtskilliga exemplar), Potentilla collina, Sedum album, Chamaemelum angustifolium (ställvis riklig), Isatis tinctoria, Alyssum syssoides, Diplotaxis tenuifolia, Cardaria draba, Camelina microcarpa, Lepidium campestre, Anthyllis vulneraria, Hyssopus officinalis, Asparagus officinalis och Bromus inermis, samtliga toormarksväxter.

I fuktiga eller vattenfyllda sänkor i brotten växer bl. a. Orchis incarnata, Epipactis palustris, Iris pseudacorus, Typha latifolia, Lythrum salicaria, Eriophorum angustifolium, Triglochin palustre och Centaurium sp.

### Fynd av Stachys arvensis, Kickxia elatine och Euphorbia exigua.


Spridda växtfynd.


*Stellaria neglecta* Whe. — I Albrunna lund, 1957. Denna finnes hos *Sterner* ej angiven för Albrunna lund utan blott för några längre norr ut belägna lundar.


*Buplerum tenuissimum* L. — Växte under sommaren 1960 i stora mängder på flera ställen av Stora alvaret, både inom Södra Möckleby och Grågårds socknar. Den rikliga förekomsten under detta år är dock ej förvånande med hänsyn till den ovanligt regnrike sommaren, som har tillåtit denna annuella växt att utvecklas på de eljest under denna årstid uttorkade och förbrända alvarmarkerna.


*Verbascum phlomoides* L. — På kulturpåverkad mark i Vickleby samhälle, 1955 (ett exemplar, tydligt skilt från *V. thapsiforme*). Hos *Sterner* upptages endast ett tvivelaktigt fynd av *V. phlomoides*.


L. Rodenborg.

**A new species of Cuscuta from Paraguay.**

*Cuscuta longiloba* Yuncker n. sp.

Caules tenues. Flores 5-divisi, circa 2 mm longi ab floris base ad corollae sinus, pedicellis aequantes aut longiores quam Flores; calyeis longior quam corolla, alte divisus, lobi angusto-lanceolati acuminati; corollae lobi lanceolati acuminati tubo campanulato aequante; scalarum fimbriatae ad stamina attingentes. styli tenues longori quam ovarium globosum.

Stems slender, orange-red when dry. Flowers reported as white when growing but becoming reddish when dry, somewhat glandular, membranous, 5-parted, up to about 2 mm long from the pedicel to the corolla sinuses, or 4-5 mm long over-all, on equal or slightly longer pedicels in umbellate-cymose few-flowered clusters. Calyx deeply divided, the lobes acuminate and narrowly lanceolate, scarcely overlapping at the base, longer than the corolla tube. Corolla lobes lanceolate, acuminate, about equaling the campanulate tube, the tips slightly inflexed. Stamens much shorter than the corolla lobes, the filaments rather stout, about equaling the oblong anthers. Scales about reaching the filaments, commonly somewhat broader toward the top, fringed with medium-length processes, bridged below the middle. Styles slender, as long as to much longer than the globose ovary.


The deeply divided calyx with long narrowly lanceolate lobes is a distinctive feature of this species and differentiates it from other possibly related species. It resembles *C. burrellii* Yun. of Gualas, Brazil, in some respects but differs in its entirely smooth flower parts and pedicel, narrower calyx lobes, and less caudately pointed corolla lobes. From *C. rojasii* Hunziker, also from Paraguay, it differs in the shape and proportions of the perianth parts, longer filaments, and with the scales reaching the stamens.

No mature capsules are present on the material studied and it is not known whether they are circumscissile or not.

T. G. Yuncker.

**Mossor från västra Jämtland.**

I Svensk Botanisk Tidskrift 1957 (s. 613) har jag lämnat en förteckning över några intressantare mossfynd från västra Jämtland. Då jag därefter
under flera nya exkursioner inom samma område insamlat mossor, lämnar jag nedan en komplettering till den föregående artlistan. Beläggexemplar ha tillställts Naturhistoriska Riksmuseum, Stockholm.

**Musci.**


*Cnestrum schisti* (Wo) HAG. Mörsil: Storboströmmen nedom Storbofallet c.fr.


Pseudoleskea patens (Lindb.) Limpr. Åre: Åreskutan.


Stegonia latifolia (Schwaegr.) Vent. Undersåker: Norra Ristafallet c.fr.


Weisia wimmeriana (Sendtn.) Br. & Sch. Åre: Mörvikshummeln c.fr. Tagen av Arnell och Jensen på Lillskutan, där jag återfann den på sydsidan.

Hepaticae.


Cololejeunea calcarea (Lib.) Schiffn. Mattmar: Storboströmmen nedom Storbofallet.

Moerchia hibernica (Hook.) Gottsche Mörsil: Kvarntjärn, södra stranden.
Scapania aspera Bernet Mörsil: mellan Fiskhusberget och Kvarntjärn.
Nils Hakelier.

Två för Närke nya geoglossacéer.


Geoglossum glabrum Pers. ex Fr. Kil: ca 1 km V om Hammarboda på en liten myr; ca 500 m VSV om Skrikarboda vid bäcken till St. Ryssjön, där den rinner ur en liten tjärn; vid bäcken mellan St. Ryssjön och Boekshosjön. Tysslinge: V. Ånnabodasjön, västra sidan; Fisklösen, rikligt vid norra sidan. Svampen förekom på alla lokalerna — som alltid — i ganska blöta Sphagnum-samhällen.


Nils Hakelier.

Monoblepharis i Uppsalatrakten.

Inte sedan 1899, då Lagerheim publicerade en uppsats om Monoblepharis, synes detta svampsläkte ha påträffats i Sverige. Trots att svampen troligen är ganska vanlig, åtminstone i Uppsalatrakten, är den mycket svår att upptäcka i naturen.


vara utom räckhåll för betande boskap, emedan spillningen tycks hindra svampens uppträdande. pH bör ligga mellan 6,4 och 7,5.


Ovan angivna metod anger PERROTT som den hästa, när det gäller att få svampen att växa ut. Hon anser att den låga temperaturen hindrar andra phycomyceter att tränga ut den mera långsamt växande Monoblepharis.

Då PERROTT tillämpade denna metod (dock modifierad såtillvida, att ingen blandning av vatten utan endast destillerat vatten användes), kunde hon iakttaga svampen efter 2–4 veckor. En del kvistar förvarades i stället i skålar med vanligt oblandat och osterilt vattenledningsvatten vid rumstemperatur. Hyftofsar med oosporer hade här i ett fall bildats redan efter fem dagar. På dessa oosporer kunde släktet lätt igenkännas. Från tre av de sex insamlingsplatserna erhölls svampen. Endast en art, Monoblepharis polymorpha, kunde med säkerhet identifieras.

Någon skillnad mot den förstnämnda metoden beträffande påväxten av andra phycomyceter kunde ej observeras.

En av mina fyndplatser utgjordes av några tillfälliga vattensamlingar i sank björkskog. En annan bestod av ett uttorkande dike i kanten av en åker. Svampen fanns också i en permanent damm omgiven av klibbal. Kvistarna tillhörde i första och andra fallet Betula verrucosa, i det tredje Alnus glutinosa.

Dessutom har svampen iakttagits i material (bladskaffet av al) från en beständig vattensamling intill en aldunge (assistent SVEN NILSSON, Uppsala, muntlig uppgift).

**Summary.**

The genus Monoblepharis found in the vicinity of Uppsala. — Species of the genus Monoblepharis were searched for in pools near Uppsala (central Sweden). On twigs, brought into the laboratory and put into petri dishes filled with water, tufts and oospores of M. polymorpha were found after some days in room temperature.

**LITTERATUR.**


Uppsala, Institutionen för fysiologisk botanik. **Torgny Unestam.**

Tillägg till Sveriges rödalgsflora.
(Preliminärt meddelande.)

1. Om *Bertholdia neapolitana*, *Antithamnion tenuissimum* och *Polysiphonia nigra* i Bohuslän.

Vid ett föredrag i Algologföreningen i Uppsala den 10 december 1958 över havsalgerna på skalbottnar vid Gullmaren och Väderöarna demonstrerade undertecknad bl.a. några rödalgsarter, som förut icke påvisats i Sverige, nämligen *Bertholdia neapolitana* (BERTHOLD) SCHMITZ, jämte en obeskriven art av samma släkte, vidare *Antithamnion tenuissimum* (HAUCK) SCHIFFNER och *Polysiphonia nigra* (HUDSON) BATTERS (mera känd som P. atrorubescens).

Släktet *Bertholdia* utmärkes av att gonimoblasten utvecklas ute på själva förbindelsestråden långt från auxiliarcellerna, en unik företeelse bland rödalgsarna och av stort teoretiskt intresse; se J. FELDMANN: Recherches sur la structure et le développement des Calosiphoniacées (Rhodophycées — Gigartinales). — Revue Générale de Botanique. 61. 1954.


Att *B. neapolitana* växer i Sverige var visserligen mycket oväntat. Men ändå mera överraskande är att vi har en art till i Sverige, en obeskriven, tredje art av släktet *Bertholdia*, som vi tillsvidare äro ensamma om. Den uppträder på samma skalbotten vid Södra Väderöarna men dessutom på Kostergrundet.

*Antithamnion tenuissimum*, en exklusiv Medelhavsart, som vi trodde, påträffades 8 oktober 1958 på grus med skal från 8 m i Nordströmmarna, en av Kristinebergs dragningsplatser. Teckningar och exemplar av denna gracila, delvis nedliggande tofsalg ha sänts till Madame GENEVIÈVE FELDMANN, som bestyrkt min bestämning. *A. tenuissimum* är förövrigt känd från Adriatiska havet, Neapel, Banyuls sur Mer etc. och Algeriet.


2. Om Dumontia-kustan och andra rödalgskrustor i Bohuslän.


Rödalgskrustorna finna vi i ett oroligt avsnitt av rödalgssystemet, där centralträds- och springbrunnstyperna växla, liksom formen av tetrasporangier. Kustorna fördelas på två ordningar: Cryptonemiales, med bl. a. lithothamnierna (som här icke behandlats) och Gigartinales. Rödalgerna i dessa bägge ordningar förete så stora likheter med varandra, att man skulle vilja föra dem till en enda ordning, vore det icke så att hos dem som föres till Cryptonemiales, auxiliarcellen finnes anlagd i särskilda grenar redan före befruktningen, medan hos Gigartinales en vanlig interkalar cell bland andra vegetativa får tjäna som auxiliarcell.


Cruoriella codana insamlades redan i juli 1941 under mina dykningar omkring Stora Bornö i Gullmaren från en berghylla mellan 7 och 9 meter, täckt med grus och block. Algen var då steril och omöjlig att bestämma. Först 1959, den 18 november, erhölls honplantor vid en draggnings, som träffade exakt samma berghylla vid den branta ön. De bildade överdrag på skall av levande Modiolus och på stenblock, där den vinröda krustan nådde en diameter på ett par decimeter. Algen skiljes från vår vanliga Cruoriella Dubyi genom sina långcelliga och smala parafyser, som omge gonimoblasterna. Om artens uppträdande är icke mera känt än Kolderup Rosenvinges danska originalfynd från 23,5 meters djup nära Trindelen i Kattegatt och här meddelade fynd vid Bornö.

Cruoriopsis danica insamlades på skalbotten vid Väderöarna och utanför Gullmaren, där den även växte på Laminaria hyperborea-stammar. Även denna art, som i motsats till den förra är mycket späd, är beskriven av Kolderup Rosenvinge på material från några få ställen i danska farvattnen, i Limfjorden, Kattegatt och Lille Belt.

Cruoria rosea, som bildar mycket små och ljusröda fläckar på kalkalger, insamlades på skalbotten vid Södra Väderöarna. Arten är uppgiven från bägge sidorna av Engelska Kanalen (den beskrevs från Rade de Brest av bröderna Crouan) och från Helgoland (under namn av Cruoria stilla Kuckuck). I Norra Ishavet finns en Cruoria arctica, vars skillnad från C. rosea jag ännu icke kommit underfund med.


Uppsala universitets växtbiologiska institution, i januari 1961.

Mats Wärn.


När presidenten i »Linnean Society of London» den 24 maj 1859 gjorde en återblick på den gångna sessionens förhandlingar, beklagade han att denna passerat utan någon sådan fundamental upptäckt som kunde lämnat ett bestående intryck på vetenskapen. Man måste hålla med utgivaren av den här recenserade boken om att få omdömen varit så felaktiga — denna session omfattade nämligen bl.a. ett bidrag av Charles Darwin och Alfred Wallace, »On the tendency of Species to form Varieties«. En andra etapp i utvecklingslärans genombrutt kom nästa år med Darwins »Origin of Species«. Med tanke på det oerhörda inflytande som utvecklingsläran haft på biologisk forskning och dess betydelse för vår kultur i allmänhet är det lätt begripligt att hundraårsminnet av dess framläggande blivit mycket uppmärksammad. Föreliggande volym är en av de vid detta tillfälle publicerade böckerna.

Varje skolbildad människa i våra dagar känner till namnet Charles Darwin och förknippar det med begreppet utvecklingslära. Men om hans verksamhet på andra områden vet de flesta inte mycket. Darwin var dock en synnerligen mångsidig man som gjorde pionjärinsatser inom en rad olika vetenskapsgrenar. Denna hans mångsidighet belyses mycket väl i föreliggande volym, där sex olika författare i var sin essä behandla olika delar av hans produktion och sätta hans resultat i relation till såväl äldre författares rön som senare erfarenheter.

Det första bidraget, av P. R. Bell, behandlar »The movements of plants in response to light«. Här kommenteras Darwins bok »The Power of Movements in Plants«, i vilken denne redovisade resultaten av en mängd sinnrika experiment utförda under fem års tid tillsammans med Francis Darwin. Deras resultat banade väg för den på senare år så betydelsefulla gren av växtfysiologien som sysslar med tillväxthormoner. Bell ger även en fyllig redogörelse för den senare utvecklingen på detta område.

Nästa avsnitt, av J. Challinor, behandlar »Paleontology and Evolution«. Darwin var bl.a. en av sin tids främsta geologer. Ett av de förhållanden som ledde honom att tro på organisk utveckling var förekomsten i geologiska lagerföljder av sten efter utdöda djur och växter, bland vilka i en del fall kunde spåras utvecklingsserier ledande mot nu levande arter. En av de största svårigheterna för utvecklingsläran var att de geologiska ur-
kunderna var så bristfälliga, och så bristfälligt kända. Detta gäller fortfarande, även om mycket nytt material frambragts under det senaste seklet. Orsakerna till dessa förhållanden utredas här av Challinor, och vidare ges översikter av de fossila vittnesbördens om utvecklingen inom olika djurgrupper.

Den tredje uppsatsen, av J. B. S. Haldane, kallas »Natural Selection». Författaren påpekar först att utvecklingslärans genombrott till stor del berodde på att Darwin gav en acceptabel förklaring på hur utvecklingen kunde ha föriggått, men att situationen i våra dagar i viss mån är omkastad: nästan alla biologer accepterar att en utveckling ägt rum, men detta innebär inte att Darwins förklaring till hur den skett behöver vara tillfyllest. Efter en kort översikt över genetikens principer och en redogörelse för hur man definierar och mäter selektion ger så förf. en rad exempel på olika typer av selektion och dess resultat. Mycket av detta kapitel är hårdsaml för en vanlig biolog, men en del av exemplen är synnerligen intressanta. Inte minst gäller detta de melanistiska mutanter av vissa fjärilar som under det sista seklet utbrott sig i Englands nedsotade industridistrikter.

I den fjärde essän behandlar P. Marler »Developments in the study of animal communication». Även på detta område var Darwin en pionjär, med sin bok »The Expression of the Emotions in Man and Animals» (1872), men det dröjde länge innan hans verk fortsattes. Marler ger här en översikt av olika typer av «communication», genom lukt, smak, syn och hörsel. Bl. a. får man veta att höns och vissa fiskar liksom människan i första hand rättar sig efter ansiktets uteende för att särskilja andra individ. De grafiska illustrationerna av fågelsång te sig för en lekmann ganska svårbedömda, men många av de detaljer som meddelas om fåglarnas sång är mycket fascinerande, bl. a. uppgifterna om lokaliserbarheten för olika sorts ljud, och att fågelsången är mycket individuell. En bofinkhona uppges sannolikt på sången kunna känna igen sin make från föregående år. Detta anses vara av positivt selektionsvärde eftersom erfarna fåglar kan producera större kallar än nybörjare, och eftersom »considerable adjustment is needed when a pair forms for the first time».


Det sjätte och sista bidraget, av J. S. Wilkie, behandlar »Buffon, Lamarck and Darwin: the originality of Darwins theory of evolution.».

Efter en sakkunnig och ingående analys av vad som framskymtar om utveckling i Buffons och Lamarcks arbeten konstaterar förf., att dessa otvivelaktigt i viss mån berett vägen för Darwin, så att den som så önskar kan säga att den senare endast fullbordade den byggnad som andra under större svårigheter påbörjat. Men faktum är att det var han som fullbordade den.

»Darwin’s Biological Work« är, såvitt recensenten kan bedöma, en bok av genomgående hög kvalitet. Redigeringen är mycket välglord — en belysande detalj är att de sex uppsatserna är nästan exakt lika långa. Illustrationerna är till större delen bra — utom »Plate V«, där ett par av fotografierna är misslyckade. Som sammanfattande omdöme måste sägas att boken är en värdig tribut till Darwin’s minne.

Olov Hedberg.


Proportionerna i artantal mellan grön-, brun- och rödalger är de för tropiska hav karakteristiska (inom parentes motsvarande artantal i den inledningsvis nämnda 2. uppl. av floran över Nordamerikas nordligare atlantkust, se Skottbergs rec. i SBT 52: 3): grönalger 201 (105), brunalger 101 (132), rödalger 450 (165) arter. Taylor beräknar det rent karibiska

artelementet till 28%. Han för 11% till ett nordligare element, 33% till ett sydligare och betecknar resten, 28% som mera kosmopolitisk.

*Vaucheria* räknas, såsom i regel numera, till heterokonterna, det alltjämt gängse inkorrekt namnet på ordningen, *Heterosiphonales*, bör dock bytas ut mot det 1901 av Knut Bohlin enligt nu gällande regler korrekt uppställda *Vaucherialae*.

Cyanofyceerna är utelämnade — såsom i regel i floror av detta slag.

En behandling av de få marina fanerogamerna i ett tillägg hade varit nyttig. De växer tillsammans med algerna — eller tjänar rent av som substrat för dem — men behandlas i floror, som algologerna mera sällan har tillgängliga i fält.

Figurerna är ägnade att hjälpa vid bestämningen av mera storvuxna arter, de mikroskopiska detaljbilderna är tyvärr få. Litteraturförteckningen (338 referenser) är utförlig. Kapitlen om algståndorter, alginsamling och -konservering i tropiska förhållanden ökar florans värde för nybörjare — och för algologer från kallare hav.

Med sina två algfloror, som omspänner Atlantkusten från Amerikas polartrakter uppe i norr ned till Brasiliens sydgräns har Taylor skapat förutsättningar för en intensivare utforskning av hela Atlantens algvärld. Även på Atlantens östkust skulle en av politiska gränser oberoende Flora Atlantica vara mycket behövlig — en motsvarighet till den Flora Europaea som för kärlväxternas del är under arbete. Men det är väl knappt möjligt att för en sådan uppgift finna någon, som skulle ha den förmåga, uthållighet och tid och de resurser som för Taylor möjliggjort skapandet av den tropiska algfloran.

Hans Luther.


Med häfte 20 är »Vår svenska flora i färg« fullbordad. Uppställning, bilder och text har varit föremål före ommärkande vid två tidigare tillfällen (Bd 51, h. 2, 1958 och Bd 53, h. 4, 1959). Det finns därför inte mycket att tillägga i dessa avseenden.

Vegetationsbilderna i färg som ingick i häfte 2 har kompletterats med en lika stor svit (16 helsidesbilder) i häfte 20. Tillsammans med de föregående planscherna lämnar de en mycket tilltalande provkarta på skandinaviska vegetationstyper eller snarare landskapstyper, eftersom de ger åskådarna ett utpräglat helhetsintryck av landskapet, däremot sällan några detaljer.

En redaktionell nyhet må anföras. Till medarbetarna har för den svenska upplagan fogats ett nytt namn, docent Sten Ahlner, som biträtt huvudredaktören vid redigeringen och översättningen av den danska texten.

Färgplanscherna har åtminstone i anmälarens tycke överlag fått en kla- rare och hårdare ton än vad de haft tidigare. I regel har växterna inte förlo- rat på denna behandling — märkligt nog, eftersom de förhållandevis ony- anserade färgerna kontrastera mot den mycket naturalistiska teckningen.

Tvärtom har färgåtergivningen blivit allt bättre, även om man — och annat vore egendomligt — kan dra fram ett eller annat exempel, där färgerna slagit slint. Som exempel kan nämnas det alltför smörgula hos Myosotis discolor, blomman hos Lobelia samt Artemisia maritima, som av någon anledning förlorat sin gränsna prägel.


Denna brist är så mycket sorgligare som texten tål att läsas både en och flera gånger, framför allt för sin rikedom på upplysningar av allmän eller kulturhistorisk art. Sådana uppgifter är ofta svåra att få tag på, när man behöver dem. Det verk som det ligger närmast att jämföra »Vår svenska flora i färg» med är Nymans gedigna men föråldrade »Sveriges fanerogamer». De rent morfológiska beskrivningarna kan däremot stundom förmodas bereda en i terminologin otränad läsare vissa bekymmer. Vad är t.ex. en »översittande blomma» (Hippuris) för något?

Utbredningsuppgifterna måste av naturliga skäl göras så kortfattade som möjligt. Ändå undrar man, om det inte ibland hade varit möjligt med mindre standardiserade uttryck. Om många arter sägs, att de växer i södra och mellersta Sverige, vilket i och för sig kan vara sant, men inte dess mindre blir missvisande. Att växter som Marrubium och Anthemis cotula i våra dagar växer här och där i landskapen kring Mälaren innebär sålunda en avsevärd överdrift. Förmodligen är de utdöda annat än som tillfälliga gäster. I samlingen tittar man dock framhållas, att texten betonar, att de blivit allt sällsyntare.

En sak som man fäster sig vid i detta sammanhang är det stora antal arter som förekommer dels på havsstränder, dels som ogräs. Detta är ju ingalunda någon nyhet, men man undrar hur man i somliga fall så säkert kan skilja nären från gettern, d.v.s. sådana som är inhemska på stränderna från på dessa lokaler naturaliserade arter. Antagligen kommer många frågor av detta slag att förblå obesvarade. I detta sammanhang får de sitt största värde genom att visa hur texten kan ge anledning till reflexioner och stimulera till vidare studier. »Vår svenska flora i färg» bör ha alla möjligheter att öka intresset för studiet av den inhemska växtvärlden.

Måns Ryberg.

Av miss Ross-Craigs tecknade flora över brittiska växter föreligger nu ytterligare tre häften, sedan verket senast anmäldes i denna tidskrift (Bd. 59, h.4, 1959).


Måns Ryberg.
Enligt avskrift:

**Govert Indebetou.**

18/2 1875—26/7 1955.

Av

Carl Malmström.


Carl Daniel Govert Indebetou var född den 18 februari 1875 på Forssa bruk i Östra Vingåker sn. Efter skolgång i Nyköping anställdes han 1892 i den av hans morbror Georg Strandberg ägda fondmäklerifirma Georg Strandberg i Stockholm. Sedan morbroder är 1906 dragit sig tillbaka och firman samtidigt ombildats till aktiebolag, blev Indebetou bolagets verkställande direktör. På denna plats stannade han t.o.m. 1946, då bolaget upphörde och rörelsen uppgick i Svenska Handelsbanken.

Inom den ekonomiska världen erhöll Indebetou flera andra uppdrag. Han var under flera år styrelseledamot i Stockholms stads sparbank och i Stockholms stads brandstodsbolag. Vidare var han fullmäktig i Stockholms handelskammare och under en följd av år ordförande i Svenska fondhandlareföreningen.

Indebetou var också mycket verksam som person- och kulturhistoriker. Han medarbetade flitigt i Personhistorisk tidskrift och lämnade talrika och viktiga bidrag till olika biografiska verk. Han utgav även flera större biografiska arbeten, såsom över Berghögskolans och Bergsskolans elever och Teknologföreningens ledamöter (tills. med E. Hylander), samt tvenne minnesskrifter över sparbanker. — Han var vidare under många år verkställande ledamot i direktionen för Hallwylska museet och följde med stor sakkunskap utarbetandet av museets omfattande katalog.

Botaniken ägnade Indebetou ett livslångt intresse, och han var redan som ung en god växtkännare. Det botaniska intresset var utmärkande för hans släkt sedan generationer tillbaka.

Redan som 18-åring eller år 1893 kom Indebetou in i Botaniska Sällskapet i Stockholm, där han snart fick en framträdande ställning. Sålunda blev han bl. a. invald i den kommitté, som sällskapet tillsatte år 1902 för utgivandet av «Stockholmstraktens växter». I denna kommitté spelade han en mycket aktiv roll och bidrog jämte apotekare John Hamner och pro-
fessor Nils Sylvén verksam till att arbetet år 1914 blev slutfört. När sällskapet år 1929 beslöt, att en andra, omarbetad upplaga av »Stockholms­
traktens växter« skulle ges ut, utsågs Indebetou till ordförande i den
kommitté, som skulle leda arbetet. Mellan åren 1905–09 var han också Bo-
taniska Sällskapets skattmästare.— På grund av sina insatser för sällskapet
utsågs han år 1943 till dess hedersledamot.

Indebetou har även betytt mycket för Svenska Botaniska Föreningen. Han
var en av föreningens stiftare och blev föreningens första skattmästare. 
Som skattmästare fungerade han under sex år eller mellan åren 1907–12.

Även sedan han lämnat styrelserna för Botaniska Sällskapet i Stockholm 
och Svenska Botaniska Föreningen, deltog han gärna i föreningarnas sam-
mankomster.

Indebetou var en sällsynt kunnig, vidsynt och välbalanserad människa. 
Sin omgivning visade han alltid stor välvilja och osjälvisk hjälpksamhet. 
Många äro de som i honom hade en klok rådgivare och ett fast stöd.

ERIK SÖDERBERG.

21/6 1890—15/6 1959.

AV

CARL MALMSTRÖM.


Erik Sigurd Söderberg var född i Stockholm den 21 juni 1890. Efter studentexamen vid Högre allmänna läroverket å Södermalm studerade han vid Stockholms Högskola, där han år 1921 avlade fil. kand.-examen.

Tre år före sin kandidatexamen, eller 1918, hade Söderberg börjat sin bana vid Bergianska trädgården, först som amanuensvikarie under ett år och därefter som ordinarie amanuens. Amanuenstjänsten ombildades sedermera till en assistentbefattning, och på denna plats stannade han livet ut.


Sitt stora trädgårdsintresse och kunnande visade Söderberg dessutom genom artiklar i pressen och genom utgivandet av ett flertal rikt och vacker illustrerade blomsterböcker. De viktigaste av dessa äro de stora, högt skattade, hos AB Svensk Litteratur utgivna praktverken »Blommor, en bok om odlade växter« (1942) och »Trädgårdsblommor« (1946), men även hans


Söderberg framträdde som vetenskaplig forskare inom såväl den systematiska som den mer allmänna botaniken. Sålunda har han publicerat artiklar i Svensk Botanisk Tidskrift, Acta Horti Bergiani och i en del andra vetenskapliga publikationer. De viktigaste av dessa arbeten är:

(tills. m. G. Täckholm) Über die Pollenentwicklung bei *Cinnamomum* nebst Erörterungen über die phylogenetische Bedeutung des Pollentyps. — Arkiv f. Bot., Bd 15 (1917); N:o 8, sid. 1–14.
(tills. m. O. Langlet) Über die Chromosomenzahlen einiger Nymphaeaceeen. — Acta Horti Bergiani, Bd 9 (1927), sid. 85–104.
Dendrologiska data. — Lustgården, Årg. 27 (1946) [tr. 1947], sid. 141–152.

År 1922 utsågs Söderberg till lärare vid Stockholms borgarskola och S:t Eriks folkhögskola och kvarstod i dessa tjänster till sitt frånfälle. Hans lärargärning där rönte stor uppskattning.

En annan uppgift, som i hög grad fångade Erik Söderbergs intresse, var sekreterarsskapet i Botaniska Sällskapet i Stockholm. Han tillträdde denna befattning år 1928 efter att ha tillhört Sällskapet sedan år 1914.


HENNING HORN AF RANTZIEN.

7/4 1922—14/9 1960.

AV

HANS TRALAU.

Det var på eftermiddagen den 15 september förra året, som vi genom Sveriges radio nåddes av det tragiska budskapet, att Henning Horn af Rantzien på en sedan länge planerad och av honom efterlängtat forskningsresa förolyckats vid ett ras i ett stenbrott vid Montmorency i närheten av Paris i en ålder av endast 38 år. Hans maka och en av hans franska vänner, som varo i hans sällskap, undkommo med livet i behåll. Han efterlämnar förutom makan Anna, född Arrhenius, fem minderåriga barn.

Henning Horn, som vid sin död var huvudman för sin ätt, en gammal adelssläkt från svenska Pommern, var son till gymnastikdirektören Irene Horn af Rantzien och hans maka Fanny Lucia, född Löding. Eftersom det är omöjligt för författaren att lämna en framställning av Horns personlighet i alla dess skiftningar, då vår bekantskap ej varade längre än fyra år, skall jag i korthet huvudsakligen redogöra för Henning Horns vetenskapliga utveckling.


År 1948 åtog han sig det ansvarsfulla och inte alltid så lättbemästrade uppdraget att vara redaktör och ansvarig utgivare för denna tidskrift. Detta uppdrag innehade han i fyra år. Medlem av vår förening var han sedan 1942.

Under den internationella botanistkongressen 1950 i Stockholm ledde han den limnologiska exkursionen till Vitträsk i Runmarö. Förutom i Sverige


Horn började sin vetenskapliga verksamhet med floristiska undersökningar i Stockholmstrakten, varom några uppsatser i denna tidskrift bära vittnesbörd. Den första av dessa skrev han vid endast 19 års ålder.

Mycket snart började han även intressera sig för systematik och växtgeografi. Han publicerade säkunda 1947 och 1948 två arbeten om Pleurospermum austriacum, vilken som bekant har ett isolerat utbredningsområde i de östliga gränstrakterna mellan Södermanland och Östergötland. Artens övriga utbredning är kontinentalt-eurasiatisk. Även om de av Horn vid detta tillfälle bl.a. framförda teorierna om artens invandring i Sverige ej skulle visa sig hållbara (den danske forskaren Jøns Iversen har 1954 kunnat påvisa Pleurospermum i fossilt tillstånd från englaciala avlagringar på Själland), så är dock dessa uppsatser i flera avseenden värdefulla bidrag till kändedom om denna art. Vid samma tid publicerade han även en ingående systematisk och växtgeografisk utredning av Phleum arenarium.

Under samma period skönja vi hos Horn ett tilltagande intresse för vattendjur — både kryptogama och fanerogama sådana — och hans undersökningar på detta område resulterade i en rad publicationer om vattendjur från olika delar av jorden, t.ex. om släktena Tristicha, Najas och Siro-


Sin breda botaniska kunskap visade han inte minst genom de två förträffliga avhandlingar, som fingo titeln »Macrophyte vegetation in lakes and temporary pools of the Alvar of Öland, South Sweden», där han ger växtsociologiska analyser inte enbart för kärlväxterna utan även för mossorna och characeerna.

De recenta characeéerna fångade hans intresse redan före år 1949 och det var genom denna växtgrupp, som han leddes över till den paleobotaniska forskningens område. Så flyttade han år 1951 över till Riksmuseets paleobotaniska avdelning på förslag av dess föreståndare, professor Olof H. Selling, för att påbörja jämförande undersökningar av fossila och recenta kransalger. Han fick där ett för honom betydelsefullt ideellt stöd av avdelningens föreståndare och vittgående möjligheter att utnyttja avdelningens resurser.

Svårigheterna att jämföra de fossila gyrogoniterna med motsvarande recenta fruktifikationsorgan voro emellertid stora, emedan en hanterlig terminologi saknades, och det var Horns förtjänst att början till en sådan skapades.

I sin gradualavhandling ansåg sig Horn vara tvungen att avstå från att försöka skapa ett naturligt system för de fossila kransalgerna. Han lade i stället ned mycket arbete på beskrivning av morfologiska typer, av vilka de recenta väl motsvarade den allmänt accepterade systematiken. Det fossila materialet grupperades i artificiella organsläkten (med tillhörande arter) efter kalkskalsons utformning. Senare, vid hans död ej slutförra undersökningar över bältsformologien skulle ge svar på de rent systematiska frågor, som väntade på sin lösning. Dessa undersökningar voro framförallt av betydelse på grund av att Horn trodde sig kunna konstatera, att de tertiära gyrogoniterna visade kalkskalsformer, som ej hade motsvarigheter hos de recenta typerna.


Henning Horn af Rantzien efterlämnar minnet av en tillbakadragen, men mot sin omgivning vänlig och tjänstvillig människa. Sin forskning var han i hög grad hängiven och trogen. Med hans alltför tidiga bortgång slöts en forskarbana, på vilken man med allt fog kunnat ställa stora förhoppningar.

FÖRTECKNING ÖVER HENNING HORN AV RANTZIENS TRYCKTA SKRIFTER


Om Pleurospermum austriacum (L.) Hoffm. emend. Turcz., dess taxonomi, utbredning och ekologi. — Ibid., 40, p. 179–213, 7 fig., 1 tab. (Engl. summ.).


Macrophyte vegetation in lakes and temporary pools of the Alvar of Öland, South Sweden. II. The aquatic vegetation. — Ibid., 45, p. 483–497, 3 fig.
Certain aquatic plants collected by Dr. J. T. Baldwin, Jr., in Liberia and the Gold Coast. — Bot. Notiser, 1951, p. 368–398, 2 fig.

1952. On some Charophyta from the Pleistocene of New Mexico. — Ibid., 1952, p. 58–66, 1 fig.

1953. Staining and plastic embedding of small mineralized plant fossils. — Nature (St. Albano), 171, p. 516, 2 fig.


I vetenskapliga tidskrifter publicerade recensioner under åren 1944–1953:

SAMMANKOMSTER ÅR 1960.

Algologföreningen i Uppsala.

Den 2 februari 1960.

Fil. lic. KUNO THOMASSON visade färgbilder av algvegetationen i thermal-
källor i Yellowstone.

Docent NILS QUENNERSTEDT visade bilder och algmaterial från nord-
svenska älvar.

Den 17 februari 1960.

Docent LISBETH FRIES: Odling av marina rödalger i axeniska kulturer.
Fil. lic. ELISABET HENRIKSSON: Blågröna alger i symbios.
Fil. mag. BJÖRN LINDBLAD: Osterilt odlingsförfarande av Enteromorpha
linza.

Den 16 mars 1960.

Docent HENNING HORN AF RANTZIEN, Stockholm, talade om evolutions-
studier av fossila charophyter.

Den 8 april 1960.

Fil. mag. TOM FLENSBURG talade över ämnet »Mikrovegetationen, särskilt
desmidiaceer, i Kävsjön, Småland« samt visade talrika mikrofotografier
(sammanträde tillsammans med Växtbiologiska seminariet).

Den 4 maj 1960.

Docent MAJ-BRITT FLORIN visade och kommenterade ett antal färgfoton
av alger från sjöar inom Södertäljeområdet samt demonstrerade den nya
kvartärgeologiska institutionen.

Den 16 november 1960.

Docent MATS WÆRN: Benthiska chrysophycéer i havet.

Den 14 december 1960.

Fil. lic. TORBJÖRN WILLÉN talade över ämnet »Växtplankton och vatten-

Sammandrag av docent MATS WÆRNS föredrag i Algologföreningen den 10
december 1958 och 2 december 1959 återfinnas under Smärre uppsatser och
meddelanden i detta hälte (sid. 234).

17-61173301 

Autoreferat av föredrag hållt i Algologföreningen den 16 november 1960.

Mats Wärn: Benthiska chrysophycéer i havet.

Inom flagellat-gruppen Chrysophyceae finns även typer, som övervägande föra ett fastsittande (benthiskt) liv, icke blott som enkella utan även som flercelliga i coccoidea eller palmelloidea kolonier eller i enkla trådförmiga eller parenkymatiska förband. Med sina bruna kromatoforer bli de siste-nämnda förvillande lika enkla brunalger (Phaeophyceae).


Till sist demonstrerades ett antal till havslistan nyttillkomna arter, som påträffats i *Chara tomentosa* -ängarna och på vassarna i Öregrunds inre skärgård i fjärdarna med *Vaucheria dichotoma*. Endast 2 av dessa till ett tiotal uppgående arterna har kunnat identifieras med beskrivna arter nämligen Correns' ovan omtalade *Naegeliella flagellifera* (som också påträffats i Hosjön vid Knutby i Uppland) och *Sphaeridiothrix compressa*, känd genom Pascher och Vlk från en salthaltig myr med högt pH vid Lissa an der Elbe i Böhmen. *Sph. compressa* är en liten grenig, trådförmig alg med något till-plattat rundade celler. Av samma släkte sågs ytterligare en grenig art med mindre och kulformade celler, som uppträder i några olika storlekssformer, möjligtvis småarter, varav en även upptäckts i Uppsala botaniska trädgårdens damm.

Botaniska Föreningen i Göteborg.

Den 29 januari.

Fil. lic. B. Peterson, Lund, höll ett föredrag »Från en växtgeografisk resa till Sydafrika«.

Den 26 februari.

Civilingenjör G. TENGSTRAND, Göteborg, berättade om »Några sällsynta växter från Lappland«.

Den 24 mars.

Professor B. LINDQUIST, Göteborg, talade om »Boreala bergsfloror«.

Den 28 april.

Professor E. HULTÉN, Stockholm, skildrade sina intryck »Från en botanisk resa till arktiska Kanada«.

Den 27 maj.

Företogs en vandring i Botaniska trädgården under ledning av intendent B. PETERSON.

Den 30 september.

Rektor M. OHLANDER, Göteborg, berättade »Om några intressanta växtfynd«.

Amanuens T. NITZELIUS, Göteborg, talade »Något om Rhododendronsläktets systematik och utbredning«.

Den 31 oktober.

Professor E. HULTÉN, Stockholm, berättade om »En botanisk resa till Alaska sommaren 1960«.

Den 29 november.

Överläkare G. LUNDGREN, Djursholm, visade »Nordens orkidéer i färg«.

Föreningens styrelse, bestående av ordf. professor B. LINDQUIST, v. ordf. lektor S. SUNESON, sek. apotekare S. HOLMDAHL, kassör godsägare L. EKMAN samt docent G. DEGELIUS och folksskollärare St. NILSSON, omvaldes. I styrelsen nyinvaldes dessutom intendent B. PETERSON och lektor V. GILLNER.

Exkursioner.

Föreningen företog sin vårexkursion till Björkö i Göteborgs norra skärgård. Ett tjugoålt medlemmar deltog.

Bland förut kända arter som iakttoogs märktes Asperugo procumbens, Carex paleacea, Carex recta, Cerasitum tetrandrum, Stellaria holostea m.fl. Ny för ön var Thlaspi alpestre.

Föreningens höstexkursion ägde rum söndagen den 28 augusti under ledning av folksskollärare Stig WOLDMAR, Uddevalla.

Den var förlagd till trakten av Uddevalla; 20 medlemmar deltog.

Först studerades den rika lundvegetationen vid Bratteröd strax söder om staden. Här återfanns Festuca altissima, Brachypodium silvaticum, Bromus Benekeni och Carex silvatica. Nästa anhalt blev skalgrusbankarna vid Bräcke och Kuröd. Vegetationen var redan på upphällningen, men delta-garna kunde glädja sig åt massförekomster av Galeopsis angustifolia, Echium

vulgare, Alyssum alyssoides, Inula salicina m.fl. I Hjärtums socken besöktes en Cladium-lokal i en liten skogstjärn öster om Öresjön.

Exkursionen avslutades med ett besök vid sjön Utby-Lången i samma socken. Här noterades Stratiotes aloides, Potamogeton crispus m.fl. förut kända arter.

Botaniska Sektionen av Naturvetenskapliga Studentsällskapet i Uppsala.

Den 26 januari.

Professor Eric Hultén talade över ämnet »Botanisk resa i arktiska Canada«. Föredraget illustrerades med vackra färgbilder.

Den 9 februari.

Docent Hans Runemark höll ett föredrag betitlat »De europeiska littorala Agropyron-arterna«. Föredraget illustrerades med bilder och herbariematerial.

Den 24 februari.

Botaniska sektionen gjorde ett besök på naturvårdsutställningen i Uppsala Folkets hus. Ciceron var fil. mag. Tord Ingmar, som också höll ett offentligt föredrag över ämnet »Uppländsk natur i stöpsleven«.

Den 8 mars.

Laborator Henning Virgin talade över ämnet »Klorofyllbildningens fysiologi«. Föredraget illustrerades med kurvor och diagram.

Den 31 mars.

Fil. stud. Ingvar Nordin höll ett föredrag betitlat »Vegetationen i Rhône-deltat«. Föredraget illustrerades med färgbilder och herbariematerial.

Docent Rolf Santesson demonstrerade lavar i ultraviolett ljus.

Fil. kand. Jonas Normann utreddde det fysikaliska skeendet vidfluorescens.

Den 12 oktober.


Den 25 oktober.

Docent Henry Rufelt höll ett föredrag över ämnet »Tillväxt och geotropism — några kritiska synpunkter«. Föredraget illustrerades med kurvor och diagram.

Docent Magnus Fries talade över ämnet »Höst i Minnesota« och visade vackra färgbilder.

Den 8 november.

Fil. mag. Bengt Jonsell höll ett föredrag betitlat »Några glimtar från en Rysslands-resa«. Föredraget illustrerades med vackra färgbilder.

Bokauktion.

Den 23 november.

Den 7 december.

Fil. lic. SVEN NILSSON talade över ämnet »Glimtar från resor i Venezuela». Föredraget illustrerades med vackra färgbilder. Julfesten firades.

/ 

Botaniska Sällskapet i Stockholm.

Den 16 februari.

Professor ERIC HULTÉN höll ett med färgbilder illustrerat föredrag: »Om floran på Capri.«

Sällskapets stadgar, som hade översatts och omarbetats, godkändes nu i sin nya form. Styrelsen, som hittills bestått av fyra ledamöter, utökades härigenom med ytterligare fyra sådana, representerande olika grenar av den systematiska botaniken.

Den 24 mars.

Docent GUNNAR LOHAMMAR höll ett föredrag: »Från en resa genom U.S.A. och Canada.« Föredraget illustrerades med talrika vackra färgbilder.

Den 3 maj.

Professor FOLKE FAGERLIND höll föredrag om den botaniska trädgården i Bogor på Java, vilken föredragshållaren senast besökt under december 1959 och januari 1960. Föredraget illustrerades med talrika vackra färgbilder.

Enligt Sällskapets nya stadgar, antagna vid sammanträdet den 16 februari 1960, skulle Sällskapets styrelse utökas med fyra ledamöter. Kompletterande styrelseval förrättades, och valda blev professor FOLKE FAGERLIND, intendent TORSTEN E. HASSELMAN, lektor EDVARD VON KRUSENSTJERNER, civilingenjör SVEN NILSSON och civilingenjör fil. kand. OLLE PERSSSON.

Den 29 maj.


Den 7 oktober.

Civilingenjör fil. kand. OLLE PERSSSON lämnade en översikt över utforskan- det av Stockholmstraktens storsvampflora och angav några riktlinjer för fortsättningen av detta arbete.

Trädgårdsmästare KARL RODHE berättade om en nyförgreningen av detta arbete.

till några botaniska trädgårdar i Storbritannien och Holland, med korta besöket även i Hamburg och Köpenhamn, samt visade ett stort antal mycket vackra färgbilder.

**Den 29 november.**

Professor CARL MALMSTRÖM redogjorde för planerna att för vattenkraftsansändamål bygga ut Torneträsk samt Torne och Kalix älvar och de starka farhågor, som dessa planer väckt hos vetenskapsmän, naturvårdare, näringsidkare och andra. (Se KVA:s Skrifter i naturskyddsärenden Nr 50, Uppsala 1960.)

Professor CARL OLOF TALL berättade med färgbilder om skogsexkursioner i Förenta Staterna, som han deltagit i under aug. och sept. 1960 i samband med VII Internationella Marklärekongressen i Madison, Wisconsin, och V Världsskogskongressen i Seattle.

Till styrelse valdes: ordf. professor CARL MALMSTRÖM, v. ordf. professor ERIK BJÖRKMAN (efter professor RUDOLF FLORIN, som undanbett sig återval), sekret. läroverksadjunkt INGMAR FRÖMAN, skattm. rektor KARL-GUSTAV KÖKERTZ, samt intendent TORSTEN E. HASSELROT, lektor EDVARD VON KRUSENSTJERNEN, civilingen. fil. kand. OLLE PERSSON och docent MÄNS RYBERG (efter professor FOLKE FÄGERLUND, som undanbett sig återval). Revisorer blevo lektor ARVID HEDELIUS och revisor JAN KNÖPPEL (efter bankdirektör VERNER BJÖRKLUND, som undanbett sig återval) och revisors-suppl. jägmästare STEN NORDENSTAM och byråinspektör BENGT ROSENBerg (efter revisor JAN KNÖPPEL).

**Botanistklubben vid Stockholms Universitet.**

**Den 22 februari.**

Ph. D. NICOS G. MARINOS höll ett föredrag om »Dormancy in plants and its possible control by native growth substances«.

**Den 16 mars.**

Visning av Genetiska Institutionen vid Statens Skogsforiskningsinstitut. En inledande orientering gavs av professor ÅKE GUSTAVSSON.

**Den 31 mars.**

Professor D. MÜLLER höll ett föredrag om »Stofproduktion i tropisk regnskog i Côte d'Ivoire«.

**Den 22 april.**

Fil. stud. RAGNAR WIEDERSHEIM-PAUL talade över ämnet »Frosttorka hos Betula nana«.

**Den 2 maj.**

Professor M. G. STÅLFELT redogjorde för »Metoderna för mätning av växternas vattenkonsumtion«.

**Den 21 oktober.**
Laborator H. Wirsing höll ett föredrag betitlat »Om klorofyllbildningens fysiologi«.

**Den 2 november.**
Visning av Statens Centrals Frökontrollanstalt med inledningsanförande av professor G. Nilsson-Leissner.

**Den 8 december.**
Docent Bengt Pettersson höll ett föredrag över ämnet »Om kalkflora i Sydeuropa och vid Östersjön«.
Styrelsen har under året utgjorts av fil. kand. Arne Holst (ordf.), fil. kand. Christian Matthiesen (v. ordf.), fil. kand. Britt Jonsson (sekt.) och fil. mag. Lennart Boo (skattml.).

**Societas pro Fauna et Flora Fennica.**

**Den 5 februari.**
Professor Håkan Lindberg höll ett med färgbilder beledsagat föredrag: »Biologiska exkursioner i Portugal«.
Framlades Flora Fennica 2: Alvar Palmgren, »Carex-gruppen Fulvellae Fr. i Fennoskandien. I«.
Inlämnades till tryck ett arbete av fil. dr Brör Pettersson: »Amiral Etholéns växtsamling i Botaniska Museets i Helsingfors herbarium generale«.

**Den 4 mars.**
Fil. dr Henrik Wallgren höll ett föredrag: »Rubbningar i beteende och nervfunktioner vid alkoholrus«.

**Den 1 april.**
Fil. dr Sten Bergman (Stockholm, Rönninge) höll ett med färgbilder beledsagat föredrag: »Två år i Nya Guineas urskogar«.

**Den 6 maj.**
Docent Hans Luther höll ett med färgbilder illustrerat föredrag: »La Laguna di Venezia«.
Fil. stud. Gunnar Weckström redogjorde för ett fynd av mossan Fissidens jullanus i Kvarnforst i Kervo å vid Helsinge kyrkby.
Docent Hans Luther meddelade, att den i Finland såsom antropokort införd påträffade Gladiolus-art, som identifierats med G. imbricatus, torde höra till den sydösteuropeiska ras, som i Ukraina beskrivits som G. apiterus. I avvaktan av en närmare utredning om sambandet mellan denna och

G. imbricatus — de synas tillhöra samma formkrets — betecknas den i Finland funna rasen G. imbricatus var. apterus. Introduktionen i Finland har uppenbarligen skett med säd från SE Ryssland, till en del synbarligen i samband med missväxter i Finland kring 1800-talets mitt.

**Den 13 maj.**

Årsmöte. Upplästes av professor Alex. Luther författade minnesord över Sällskapets korresponderande ledamot, professor August Thiennemann. Inlämnades till tryck ett meddelande av Nandor och Göran Stenlid: "Om förekomsten av Crambe maritima i Ålands sydöstra skärgård."

Docent Ilmari Hintonen anmälde till tryck: "Beiträge zur Kenntnis der Salix-Flora von Finnland. I."

Ett arbete av fil. dr Bror Pettersson anmältes till tryck: "Notes on Some Plants from Porto Santo and the Dezertas.

Vid förrättade val återvaldes Sällskapets funktionärer.

**Den 7 oktober.**

Fil. kand. Samuel Panelius holl ett av färgbilder beledsagat föredrag: "Om naturen på Jurmo i Korpó."

Sällskapet hedrade minnet av sin hedersmedlem och forne viceordförande, professor Toivo Henrik Järvi och av sin hedersmedlem, professor Nils Eberhard Svedelius.


Framlades Acta Societatis pro Fauna et Flora Fennica 76: 1, innehållande: Henrik Skult, "Om kärlväxtfloran i Korpó Brunskär."

**Den 4 november.**

Upplästes av docent Hans Luther författade minnesord över Sällskapets avlidne korresponderande ledamot, professor Eduard Rübel.

Meddelades att professor Rübelns arvingar till hedrata av hans minne och följande hans önskan hade tillställt Sällskapet 1000 schweiziska francs. Beloppet kommer att fonderas.

Fil. dr Lars Fagerström förevisade exemplar av de för landets adventivflora nya arterna Ipomoea nil, I. lacunosa och Datura tatula, vilka av fröken Alli Väre blivit funna i Jockis och Ypääjä såsom inkomna med nordamerikansk majs, importerad till Jockis sirapsfabrik. Majsavfall från sirapsfabriken har sålts till traktens jordbrukare, varigenom dessa och många andra antropokorer fått avsevärd spridning.


Sammanfattning årsberättelse 1960

Den 2 december.

Professor Alf Johnels (Stockholm) höll ett med färgbilder illustrerat föredrag: »Fiskar i vått och torrt. Djur och klimat i Gambia, Västafrika».


Till korresponderande ledamot invaldes professor Otto Jaag (Zürich).

Svenska Växtgeografiska Sällskapet.

Den 10 februari.

Sällskapets årsmöte. Styrelseval, varvid den avgående styrelsen i sin helhet återvaldes.

Till hedersledamot valdes Sällskapets sedan 1937 korresponderande ledamot, professor Carl Troll, Bonn.

Föredrag av docent Hans Runemark, Lund: »Flora och vegetation på Cycladerna.»

Den 21 oktober.

Ordf. hyllade minnet av Sällskapets hedersledamot, professor Eduard Rübel, Zürich, docent Henning Horn af Rantzien, Stockholm, förste bibliotekarie Erik Marklund, Göteborg, läroverksadjunkt Carl-Axel Hellhagen, Vimmerby, apotekare Karl Holm, Härnösand och direktör Erik Wall, Stockholm.

Till hedersledamot valdes professor Reinhold Tüxen, Stolzenau, samt till korresponderande ledamöter professor Åskell Löve, Montreal, och dr Steindór Steindórsson, Island.

Föredrag av professor The Svedberg: »Bilder från Spetsbergen».

Av Acta Phytogeographica Suecica har Sällskapet under året utgivit ett band:


SVENSKA BOTANISKA FÖRENINGEN.

Revisionssammanträdet 1960.

Föreningen sammanklädde den 21 april å Stockholms Högskola under ordförandeskap av professor R. Florin.

Ordföranden meddelade, att föreningen sedan föregående sammanträde genom döden förlorat tre av sina medlemmar, nämligen professor Peter Boysen Jensen (korresponderande ledamot), professor Carl G. Dahl och dr Robert W. Kolbe. Ordföranden erinrade om de bortgångnas botaniska gärning och lyste frid över deras minne.

De nya medlemmar, som av styrelsen invalts i föreningen, anmäldes.

Revisionsberättelsen för år 1959 upplästes av kamrer P. Olrog. På revisorernas hemställan beviljades styrelsen och skattmästaren full ansvars­frihet.

Ett förslag till stadgeändring, innebärande att medlem, som tillhört föreningen i 50 år, därefter skulle vara befrid från skyldigheten att erlägga medlemsavgift, bordlades.

Ett inkommet, av styrelsen varmt förordat förslag om kallelse av föreningens förutvarande ordförande, professor Elias Melin, till dess heders­ledamot bifölls med acklamation. Ett hyllningsteleram avsändes till professor Melin, som på grund av utlandsresa var förhindrad närvara.

Professor Eric Hultén höll ett med talrika färgbilder illustrerat föredrag med titeln: »Botanisk resa till arktiska Canada.»

Sammanträdet bevisades av 52 personer.

Årsmötet 1960.

Föreningen sammanklädde den 18 november å Stockholms Universitet under ordförandeskap av professor E. Hultén.


De nya medlemmar, som av styrelsen invalts i föreningen, anmäldes.

Ett från föregående sammanträde bordlagt förslag till stadgeändring godkändes av föreningen. Förslaget innebar ett tillägg av följande lydelse till § 7 i föreningens stadgar: »Medlem, som under 50 år erlagt stadgad avgift, skall därefter åtnjuta befrielse från denna skyldighet.«
SVENSKA BOTANISKA FÖRENINGEN


Docent Gunnar Harling höll ett med talrika färgbilder beledsagat föredrag över ämnet: »Från regnskog till páramo. Glimtar från en botanisk forskningsresa i Öst- och Central-Ecuador.«

Sammanträdet bevisades av 73 personer.

Föreningens vårexkursion till Näset vid Tullgarn 1960.


Vid framkomsten gav docent Måns Ryberg en kort översikt av vegetation och flora med tonvikt på den skogshistoriska utvecklingen. Stora förändringar i skogens sammansättning hade inträffat sedan 1945, då vår-exkursionen också hade Näset som mål. Om dessa förändringar kan läsas på annat ställe i detta häfte. Under den följande rundvandringen besöktés större delen av halvön.

I redogörelsen för exkursionen 1945 (Svensk bot. tidskr. 39, s. 447, 1945) återfinns flertalet arter, som har påträffats på Näset, och följande rader utgör därför närmast en komplettering av dessa uppgifter.


På de öppna betesmarkerna, som avlöste lunden, hade växtligheten ännu knappast kommit i gång och var f. ö. av mycket trivial karaktär. Mer fanns att välja på i närheten av alkäret, som gränsade till det stora centrala skogpartiet. Där växte t. ex. Adoxa, Melandrium rubrum, Thalictrum flavum, Carex caespitosa, Poa remota och stora bestånd av Struthiopteris. Deltagarna


På de vidsträckta strandängarna i söder och sydost hade vegetationen knappast kommit igång. Ute på några hällar av urkalksten på sydspetsen var förhållandet ett annat, och här kunde deltagarna se flera kalkgynnade växter, såsom *Saxifraga tridactylites*, *Cerastium glutinosum*, *Polygala amarella*, *Geranium columbinum* och *Hornungia petraea*. Myosurus var mycket allmän.

På återvägen kunde vi studera ett stort bestånd av hybriden mellan vit- och gulsippa i lundkanten.

Varken tiden eller vädret tillåt några ytterligare exkursionsmål, och när bussarnas äntligen lyckats trassla sig upp på fast väg, fortsatte färden till Trosa, där middagen väntade på stadshotellet. Återkomst till Stockholm vid niotiden.

**Måns Ryberg.**

**Nya medlemmar.**


British Columbia, Canada, University of Otago, Dunedin, New Zealand; på förslag av professor E. Hultén: signor Francesco Catanzaro, Mazara del Vallo (Trapani), Italien.


Till författare i Svensk Botanisk Tidskrift.

Enligt styrelsens beslut (den 19 november 1948) får avhandling, för att intagas i tidskriften, i regel leke överskrider 3 ark (= 48 trycksidor). Uppn de mer än 8 ark, kan tidskriften leke åta ga sig omkostnaderna för den överskjutande delen, såvida styrelsen leke efter särskild prövning bestämmer annorlunda.

Korrigeringskostnad, som överstiger 10 % av sättningskostnaden, betalas av vederbörande författare, likaså extra kostnad för sättning av svårligg sligt manuskript. Detta bör därför vara maskinskriptet.

Av större uppsatser och avhandlingar lämnas kostnadsfritt 100 separat och omslag utan tryck; för tryck på omslag debiteras 18 kr. Extra separat kunna beställas mot särskild avgift. Av smärre uppsatser och meddelanden, liksom av recensioner, lämnas särtryck endast efter överenskommelse.

För utformning av text gäller följande:

Avhandlingar av mera allmänt vetenskapligt innehåll böras publiceras på engelska, franska eller tyska; i varje fall skola de föres med en sammanfattning på något av dessa språk. Manuskript på främmande språk skall vara granskat av sakkunnig språkman, vars namn meddelas redaktören.

Koncentration i utformningen av all text eftersträvas, och, där så kan ske utan olägenhet för läsaren, användas förkortningar (t. ex. frekvens- och lokaluppgifter i artillstör). Noter under texten torde undvikas.

Tabeller förses med kort rubrik och numreras med romerska siffror.

Erforderliga bibliografiska uppgifter om citaterade arbeten sammanföras i en till avhandlingen bifogad litteraturförteckning, där de ordnas alfabetiskt efter författarnamn och uppställas enligt följande exempel:


Citeras två eller flera avhandlingar av samma författare och med samma tryckår, betecknas de med a, b, c etc. Dessa beteckningar införs omedelbart efter tryckåret; i texten enligt exempel: (RAUNKIÆR 1912 a, s. 45), I litteraturförteckningen:

RAUNKIÆR, C., 1912 a: — — —

2. Latinska växtnamn i text och figurförklaringar sättas med kursiv stil (understrykas med ett streck).

Text, som skall spärras, understrykas med en bruten linje (- - -).

Illustrationer bifogas manuskriptet i sådant skick, att de omedelbart kunna klicheras. Retusch betalas ej av tidskriften, ej heller montering av planscher eller sammanställning av textfigurer, som omfatta flera små bilder.

För klichering avsedda fotografier utföras i svart-vitt på blankt papper.

Figurer i texten numreras med arabiska siffror och förses med kort förklaring. Sammanföras flera bilder under samma figurnummer, betecknas de enskilda bilderna med bokstäver, ej med siffror.

Planscher numreras med romerska siffror (en nummerföljd för varje uppsats). Omfatta de flera figurer, numreras dessa med arabiska siffror (en nummerföljd för varje uppsats, ej för varje plansch).

I tidskriftenens ärenden träffas redaktören efter överenskommelse, måndagar och tisdagar kl. 14—15 på Riksmuseets Botaniska Avdelning (tel. 32 12 19, växel).

Manuskript, korrektur och skrivelser angående uppsatser sändas till redaktören under adress: Riksmuseets Botaniska Avdelning, Stockholm 50.

Direkt förbindelse mellan författaren och tryckeriet får icke äga rum.

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