STUDIES ON THE *EMPETRACEAE*

BY

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CONTENTS

1. Introduction.

For a number of years the small family *Empetraceae* has been subjected to an extraordinary number of investigations. This is due to the fact that it presents several features which are of interest in principle. The chief recent works, given in the subjoined list of the literature, show, amongst other things, that the geographical distribution is fairly well known. Thus Good has charted the genus *Empetrum*'s distribution over the globe, while Arvidsson (1943) in his fine maps has shown the distribution of the two Scandinavian species in Sweden. Similar studies have been made by Duvigneau in Belgium and by Böcher in Denmark. From Iceland, Greenland, North America, and several other countries we also have studies of the distribution and ecology, e. g. by Nordhagen and Marklund.

None of the peculiarities of the family have, however, aroused such interest as the cytological and anatomical features; this applies especially to the structure of the leaves which was closely studied already by Gibelli in 1876, and later by Gruber (1882). In 1894 McEven treated the anatomy both of the leaves and stems in the *Corema* species, while Hasselbaum studied the roots and mycorrhiza. The cytological (Hagerup) as well as the embryological conditions have likewise been well investigated (Samuelsson).

As a systematic unit the family has undergone many vicissitudes, until at last Samuelsson in 1913 introduced several new embryological characters into the discussion. Most investigators have taken no account of the uncertain results of the serum diagnoses (Bry); instead, many have followed Samuelsson and

1*

classed the *Empetraceae* with the *Bicornes*. Below we shall give further support to this view by pointing out various new characters.

It is almost exclusively the genus *Empetrum* that has been studied, while the other two genera are in most respects almost unknown. Thanks to the great help of several investigators it was, however, possible to procure freshly fixed and good material of all the exotic species otherwise not easily accessible. Thus Professor A. FERNANDES sent *Corema album* from Portugal, Professor F. K. SPARROW collected *Corema Conradi*, and Professor J. C. T. UPHOF, *Ceratiola ericoides* in the U. S. A.; while Dr. ERLING CHRISTOPHERSEN gave me his material of *Empetrum rubrum* from Tristan da Cunha. I should like here to thank these investigators for their valuable aid, which was absolutely essential to the carrying through of the present investigation. In addition I have myself collected a large material of *E. nigrum* and *E. hermaphroditum* in Denmark, the Faröe Islands, Iceland, and Greenland, and further I had at my disposal a considerable collection of dried plants in the Botanical Museum of the University of Copenhagen.

It would, however, be highly desirable if the botanists who have an opportunity of studying *Corema* and *Ceratiola* under natural conditions would supply the numerous deficiencies in our knowledge of these two genera.

Where no other particulars are given the information in the sequel only applies to *Empetrum nigrum* which I have had most facilities for studying in nature.

2. The Structure and Pollination of the Gynaeceum in *Empetrum nigrum*.

The development of the gynaeceum begins already in the month of July, the year before the flowering. The placenta is a direct continuation of the axis of the flower, on which the carpels (C in Fig. 2) arise some distance below the apex. The ovula (O in Fig. 2) develop in a ring around the tip of the placenta similarly as the carpels and like leaves on an ordinary vegetative stem. Hence I regard the ovula as homologous with whole independent leaves, as I have explained in more detail in several previous works.

During the continued growth of the carpels (C in Fig. 39) they bend towards each other as well as inwards over the tip of the placenta with the ovula (O) placed on it. However, the carpels do not become attached to the apex of the placenta by their whole surface, a quite narrow channel will always remain free just below the median line of each carpel (Figs. 3 and 6). This channel, which might be called the pollen tube channel,
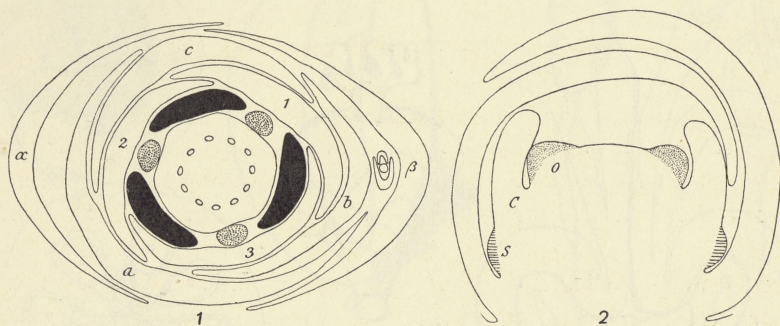

Fig. 1-2. Fig. 1. *Empetrum nigrum.* Transverse section of female floral shoot (from Aug. 1). α and β, bracteoles. a, b, and c bracts. 1, 2, and 3 calyx. Corolla black. Rudimentary stamens dotted. × 80. Fig. 2. Longitudinal section through female flower (from Aug. 1) showing that the ovula (O, dotted) arise at the apex of the floral axis (= the placenta). Rudimentary stamens (S) with horizontal hatching. C, carpel. × 135.

is of great biological importance, because it serves to carry the pollen tubes directly to the ovula.

Nor do the carpels fuse entirely in their upper part, but the style remains tubiform, having a channel in its centre with a peculiar stellate diameter (Fig. 5).

When the pollen germinates on the stigma (Fig. 3) the pollen tubes do not grow into the living tissue of the style but follow the channel in the style vertically downwards to the tip of the placenta. Here, however, lies the above-mentioned channel, and through this the pollen tubes now grow out sideways at right angles, and are carried out to the cavities in the ovary, placing themselves along the upper side of the funicle (Fig. 3). At the hilum there is a constriction and the pollen tubes place themselves in this transverse groove, being thus carried right down to the micropyle.

Thus during their growth the pollen tubes only move in

atmospheric air (and nowhere in the tissue). For comparative purposes I have examined several different genera of *Bicornes* and found quite similar conditions, e. g. in *Monotropa, Pyrola, Calluna, Cassiope, Phyllodoce* and many others, whose placenta has also at the tip quite fine channels which carry the pollen tubes right out to the ovula (HAGERUP 1928).
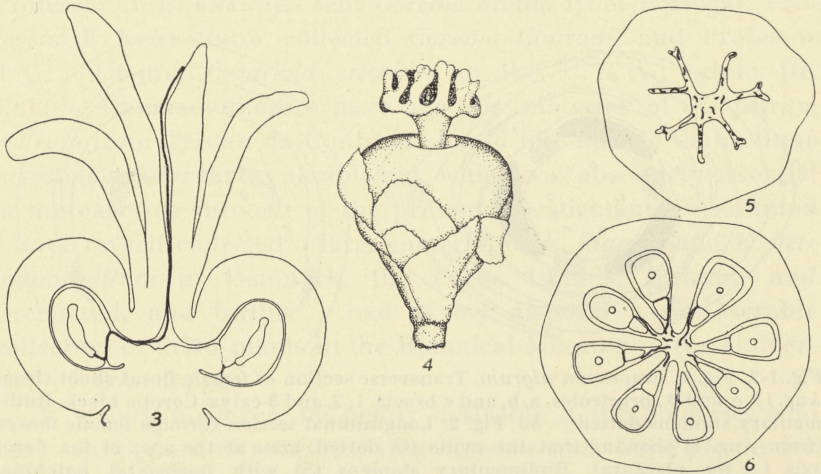
Figs. 3-6. *E. nigrum.* Fig. 3. Longitudinal section of the the gynaeceum showing the path of the pollen tube (heavy black line). × 50. Fig. 4. Female flower (May 15). × 15. Fig. 5. Transverse section from the base of the style with pollen tubes (heavy black lines). × 120. Fig. 6. Transverse section of the gynaeceum showing the path of the pollen tubes (heavy black lines). × 50.

Many other plants have a hollow style through which the pollen tubes grow, e. g. *Orchidaceae, Liliales* etc., but the peculiar channel along the tip of the placenta is not, perhaps, known from other plants than the *Bicornes?*

3. The Seed of *Empetrum nigrum.*

On Danish moors one may often find numerous dark blue excrements derived from various animals. The colour frequently reveals that it is fruits of *Vaccinium* or *Empetrum* that have been eaten, and in that case the "stones" are easy to find. They are so readily observed that in many places they have given rise to the various vulgar names of *Empetrum.* The fruits are eaten

in large amounts—not only by birds, but also by men, foxes, bears etc.

However, only a few seeds germinate (ROSTRUP) and they may lie for several (1—4) years in the earth first. It is not absolutely necessary that the fruits should be eaten in order that
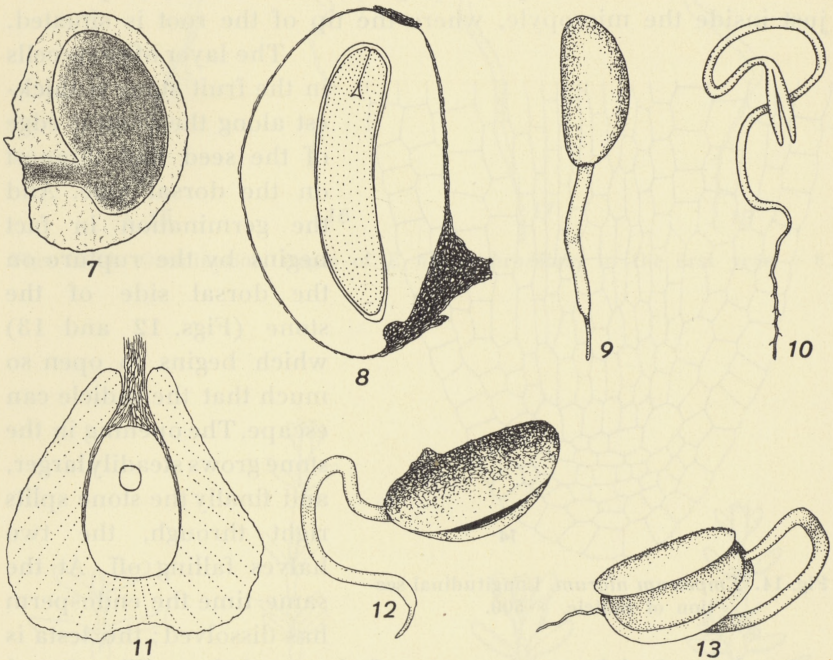
Figs. 7-13. Fig. 7. *E. nigrum*. The cast off hard layer of the stone viewed from within, showing (left) the channel that carries water to the seed. Fig. 8. Longitudinal section of seed (without stony layer). × 35. Fig. 9. The endosperm still adhering to the cotyledons. × 20. Fig. 10. The endosperm absorbed. Fig. 11. Transverse section of stone showing the position of the water channel. × 35. Figs. 12-13. Incipient germination, the stone split at the dorsal edge. × 20.

the seeds may germinate. This appears, amongst other things, from the fact that I have sometimes found entire collections of 8—10 stones situated close together at the base of seedlings that have been dug up. This could hardly have been the case if the fruits had been exposed to the mechanical treatment in the intestinal tract of an animal.

Germination takes place especially in the spring, but in the summer and autumn too quite young seedlings may be found.

4. The Germination of *Empetrum nigrum*.

The hard layer surrounding the seed is pierced by a very fine channel (Figs. 7, 11) in the place where the vascular bundle has entered the funicle; and here water may enter directly into the seed. In the endosperm (Fig. 8) too there is a depression just inside the micropyle,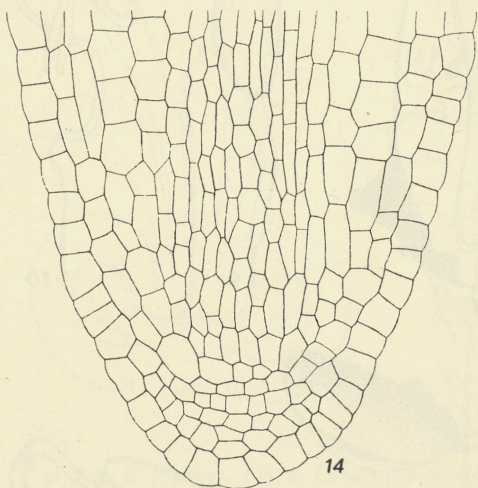 where the tip of the root is situated. The layer of stone cells in the fruit stone is thickest along the ventral edge of the seed and thinnest on the dorsal side. And the germination in fact begins by the rupture on the dorsal side of the stone (Figs. 12 and 13) which begins to open so much that the radicle can escape. The opening in the stone grows steadily larger, and finally the stone splits right through, the two halves falling off. At the same time the endosperm has dissolved; the testa is soon situated right at the apex of the cotyledons (Figs. 9 and 15) and falls off when the latter begin to diverge from each other.

Fig. 14. *Empetrum nigrum*. Longitudinal section of radicle. × 500.

At the same time the stem has bent in different directions and attained a favourable position both for the root and the tip of the stem.

The tip of the root (Fig. 14) has a similar structure as in most other dicotyledons and the root-cap is only a few (3—5) cell layers thick.

5. The Seedling.

The first few years the seedling develops with remarkable slowness and the first winter the cotyledons only enclose a very small bud (Figs. 17, 18), which merely contains 2—4 very small
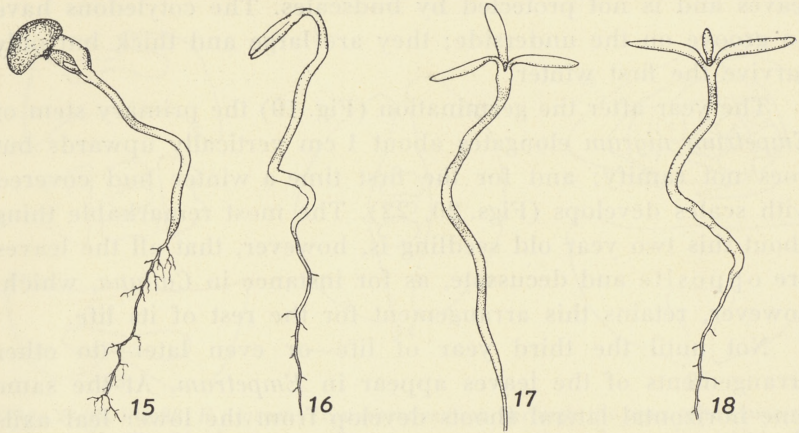
Figs. 15-18. Germination stages of *E. hermaphroditum* in the first year. × 8.
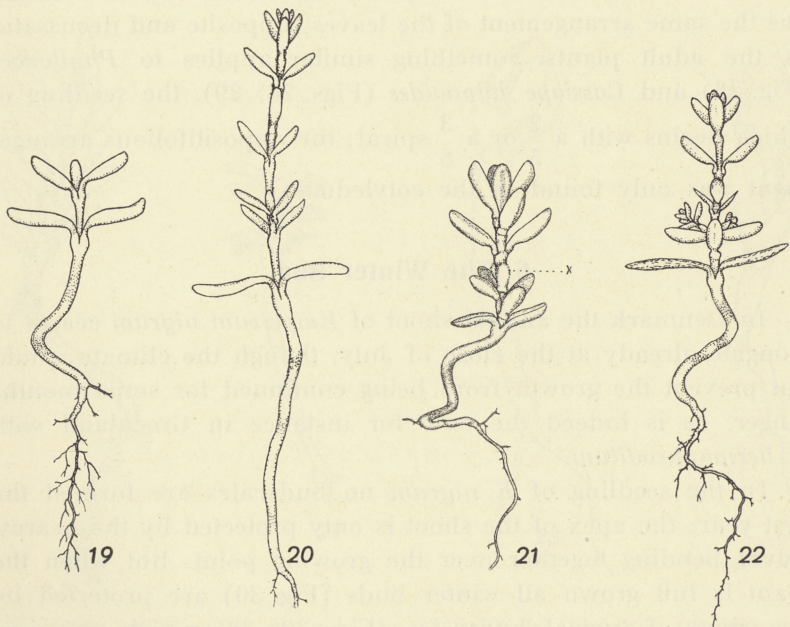
Figs. 19-22. *E. hermaphroditum*. Seedlings in the second year. The leaves opposite and decussate. × boundary between the annual shoots. Fig. 22. Lateral shoots have begun to develop.

leaves and is not protected by budscales. The cotyledons have
no groove on the underside; they are large and thick but only
survive the first winter.

The year after the germination (Fig. 19) the primary stem of
Empetrum nigrum elongates about 1 cm vertically upwards but
does not ramify; and for the first time a winter bud covered
with scales develops (Figs. 20, 22). The most remarkable thing
about this two year old seedling is, however, that all the leaves
are opposite and decussate, as for instance in *Calluna*, which,
however, retains this arrangement for the rest of its life.

Not until the third year of life—or even later—do other
arrangements of the leaves appear in *Empetrum*. At the same
time horizontal lateral shoots develop from the lower leaf axils
(Fig. 22); soon the primary axis ceases to elongate very much
more, and later it perishes and is replaced by lateral shoots
which creep sideways along the ground.

For comparison I collected seedlings of various other *Ericaceae*
in Greenland and found that in *Loiseleuria* (Fig. 27) the seedling
has the same arrangement of the leaves (opposite and decussate)
as the adult plants. Something similar applies to *Phyllodoce*
(Fig. 26) and *Cassiope hypnoides* (Figs. 28, 29), the seedling of
which begins with a $\frac{2}{5}$ or a $\frac{3}{8}$ spiral; the oppositifolious arrange-
ment was only found in the cotyledons.

6. The Winter Bud.

In Denmark the annual shoot of *Empetrum nigrum* ceases to
elongate already at the close of July, though the climate would
not prevent the growth from being continued for some months
longer, as is indeed the case for instance in Greenland with
E. hermaphroditum.

In the seedling of *E. nigrum* no budscales are formed the
first year; the apex of the shoot is only protected by the nearest
leaves bending together over the growing point. But when the
plant is full grown all winter buds (Fig. 30) are protected by
two rings of typical budscales (Figs. 33—38) which are very
different from the foliage leaves in a morphological respect. The
budscales are small, brown, and membranaceous, with a broad
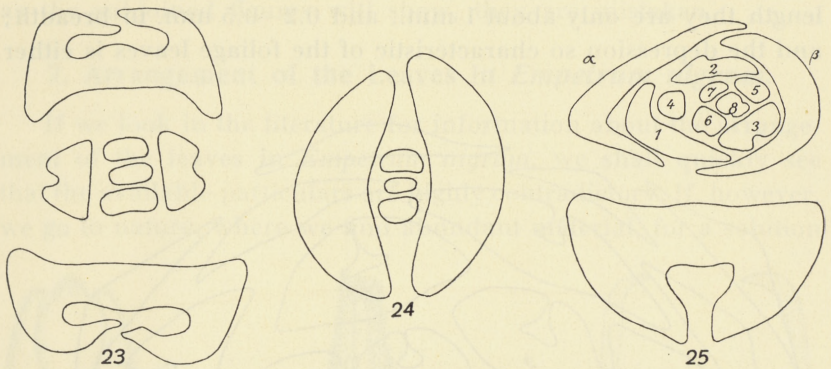
Figs. 23-25. Fig. 23. *E. nigrum*. Transverse section through the apex of the primary axis. × 75. Fig. 24. *E. nigrum*. Transverse section through growing point of a young seedling. × 65. Fig. 25. *E. rubrum* (Tristan da Cunha). Transverse section of lateral bud with supporting leaf. *α* and *β*, bracteoles. 1-8, primordia. × 75.
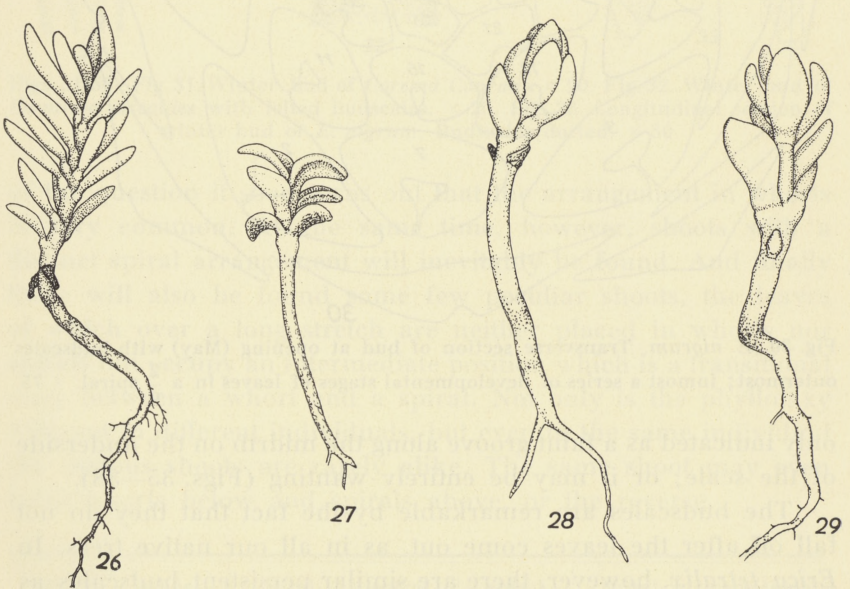
Figs. 26-29. Seedlings in the first year of *Phyllodoce coerulea*. (Fig. 26) with leaves in $\frac{2}{5}$ spiral. × 10. Fig. 27. *Loiseleuria procumbens*, leaves opposite. × 15.

Figs. 28-29. *Cassiope hypnoides*, leaves in spiral. × 17.

thin margin covered with long white woolly hairs (Fig. 34). In length they are only about 1 mm., and 0.2—0.5 mm. in breadth; and the depression so characteristic of the foliage leaves is either
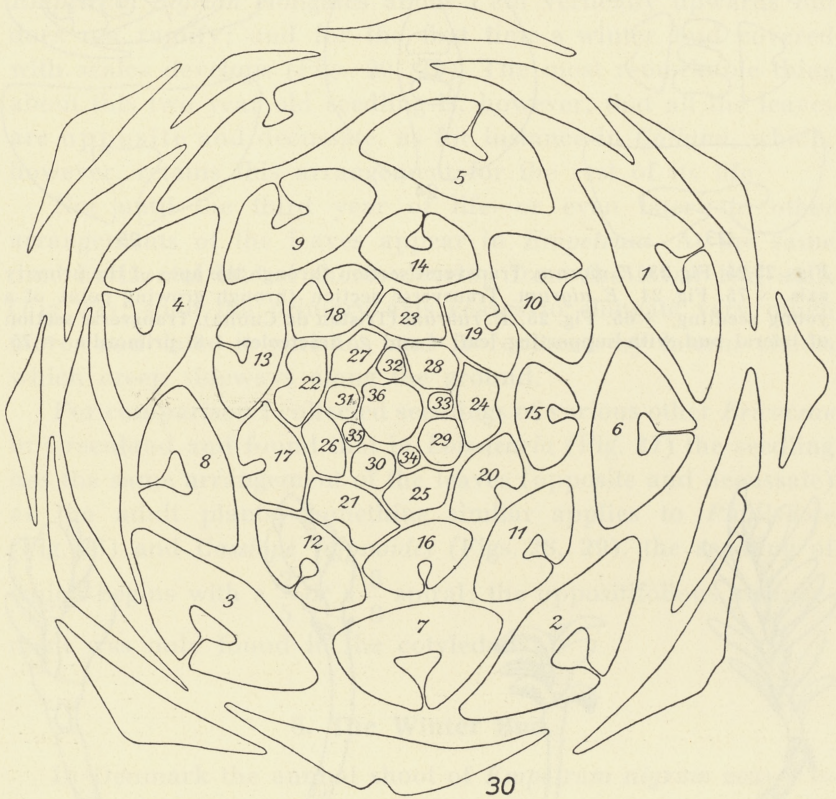
Fig. 30. *E. nigrum.* Transverse section of bud at opening (May) with budscales outermost; inmost a series of developmental stages of leaves in a $\frac{2}{9}$ spiral. × 75.

only indicated as a faint groove along the midrib on the underside of the scale; or it may be entirely wanting (Figs. 35—38).

The budscales are remarkable by the fact that they do not fall off after the leaves come out, as in all our native trees. In *Erica tetralix*, however, there are similar persistent budscales as in *Empetrum*.

In all the other species of the family (Figs. 31, 32 and 41—42), too, I have found similar distinct budscales as in *Empetrum*.

Various authors have denied the existence of budscales, but as the subjoined figures will show, they are mistaken.

7. Arrangement of the Leaves in *Empetrum nigrum*.

If we look in the literature for information about the arrangement of the leaves in *Empetrum nigrum*, we shall quickly see that the available particulars are highly contradictory. If, however, we go to nature, where we find abundant material, for a solution

Figs. 31-33. Fig. 31. Winter bud of *Corema Conradi*. × 20. Fig. 32. Winter bud of *Ceratiola ericoides* with felted budscales. × 20. Fig. 33. Longitudinal section of winter bud of *E. nigrum*. Budscales dotted. × 50.

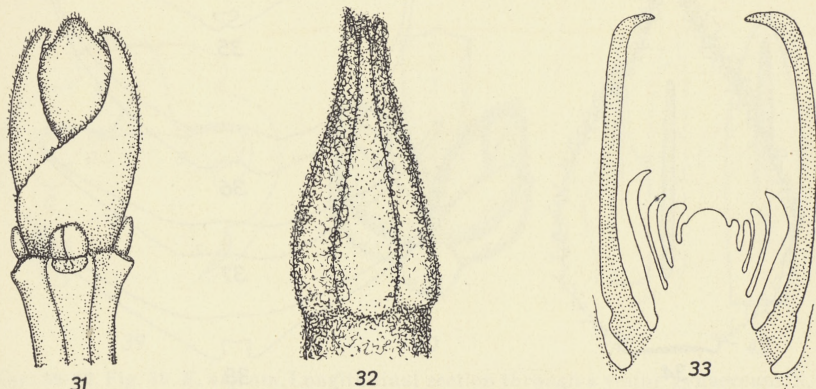of the question it soon turns out that the arrangement in whorls is very common. At the same time, however, shoots with a distinct spiral arrangement will inevitably be found. And finally there will also be found some few peculiar shoots, the leaves of which over a long stretch are neither placed in whorls nor spirals but occupy an intermediate position which is a transitional stage between a whorl and a spiral. Not only is the phyllotaxy different in different individuals, but even in the same individual the various shoots are rarely alike. The same shoot may even have whorls below and spirals above, or the reverse.

whorl 4-leaved	whorl 5-leaved	spiral $^2/_5$	spiral $^2/_7$	spiral $^2/_9$	spiral $^2/_{11}$	transitional stages
20 %	31 %	1 %	8 %	20 %	7 %	13 %

The frequency of the various arrangements of the leaves in 100 long shoots is tabulated above, p. 13.

Thus whorls are the most frequent (51 $^0/_0$), then spirals (36 $^0/_0$), and finally 13 $^0/_0$ of the shoots showed transitional stages.

In *Empetrum* I have found more than 10 different arrangements of the leaves. Below I shall try to show how these positions change and merge in each other during the development of the
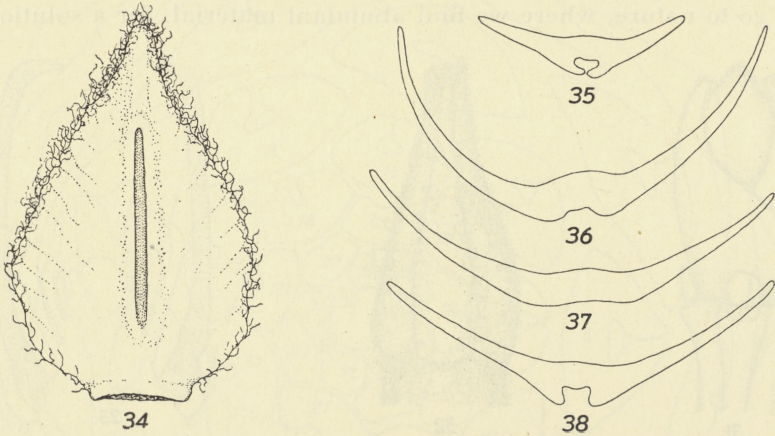
Fig. 34-38. Budscales of *Corema Conradi* with broad edges and faint dorsal groove. Fig. 34. × 50. Figs. 35-38. Transverse sections. × 80.

plant from seedling to adult. For the sake of clarity it will, however, be convenient to denote the different positions of the whorls by fractions with the numerator 2 and a denominator which is numerically double the number of leaves in the whorl in question; e. g. the 4-leaved whorl will be denoted by $\frac{2}{8}$. The positions are briefly designated by the usual series of Braun. In both notations the denominator will then also indicate the number of orthostichies.

On the primary axis of the plant the leaves are always opposite and decussate; the same is the case with most of the shoots developing the next year. But in the most vigorous shoots of individuals 2—3 years old there are often only 4 orthostichies at the base, and 5 at the apex of the shoot. In that case, close examination will show that the phyllotaxy has been changed from $\frac{2}{4}$ (whorl) to $\frac{2}{5}$ (spiral).

In a somewhat older plant it is not difficult to find shoots in which the position of the leaves is $\frac{2}{5}$ below and $\frac{2}{6}$ above (= 3-leaved whorls). Finally shoots may readily be found in which the position of the leaves is changed from $\frac{2}{6}$ to $\frac{2}{7}$; and thus the evolution may continue until whorls with 6 leaves occur $\left(\frac{2}{12}\right)$. Whorls of more than 6 leaves I have never found. The

39   40   41   42
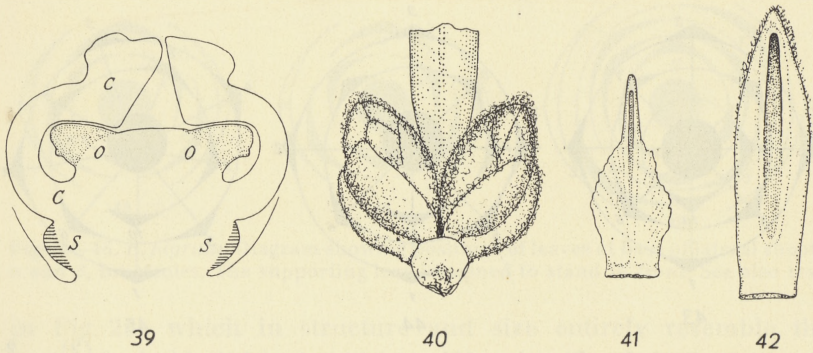
Figs. 39-42. Fig. 39. *E. nigrum*. Longitudinal section through a young gynaeceum. S, rudimentary stamens. C, carpels, O, ovula. × 75. Fig. 40. *Ceratiola ericoïdes*. 2 male flowers in the axil of a leaf viewed from above. Figs. 41-42. *Empetrum rubrum*, budscales with broad edges and distinct dorsal grooves. × 17.

changes in the positions of the leaves occurring during the continued development of the seedling may be briefly described by the following series:

$$\frac{2}{4} \to \frac{2}{5} \to \frac{2}{6} \to \frac{2}{7} \to \frac{2}{8} \to \frac{2}{9} \to \frac{2}{10} \to \frac{2}{11} \to \frac{2}{12}.$$

The transition from whorl to spiral, and conversely, often takes place in the same annual shoot; and the two different positions are frequently connected by even transitions covering a stretch of 1—4 cm. according to the length of the internodes. Below (Figs. 43—45) we exemplify the transition from $\frac{2}{8}$ whorl to $\frac{2}{9}$ spiral which is one of the most frequently occurring changes.

Stage I: Fig. 43 is a diagram of the position of the leaves in two whorls with 4 leaves each, the relative age of the leaves

being determined by their vertical distance from each other; these conditions are indicated by the figures (1, 2, 3, 4) and (5, 6, 7, 8). Of the third whorl above this, only the two eldest leaves (9, 10) are drawn.

The first step from the $\frac{2}{8}$ whorl towards the $\frac{2}{9}$ spiral is brought about by the following whorls (cp. Fig. 52 A, the inner ring) not being exactly horizontal; but of the 4 leaves in a whorl, 2 (or merely 1) of the neighbouring leaves are on a higher level than

43   44   45
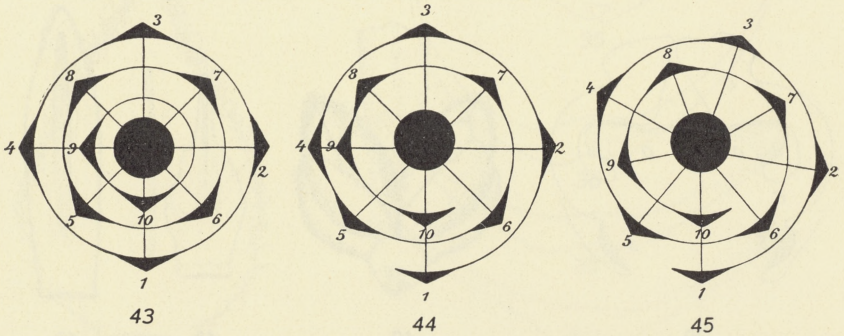
Figs. 43-45. *E. nigrum.* Diagrams of the transition from 4-leaved whorl $\left(\frac{2}{8}\right)$ to $\frac{2}{9}$ spiral. The orthostichies indicated by straight lines. See also text.

the other two leaves of the whorl. Further, in the next whorls leaf 2 is slightly higher up than leaf 1, leaf 3 a little higher than leaf 2, and again leaf 4 a little higher than leaf 3. This position may be denoted as:

Stage II. This is shown in Fig. 44. The whorl has been broken, the leaves in the numerical order indicated having a constant vertical distance from each other, which means that the leaves in the individual whorls are placed on part of a spiral line. The individual whorls, however, are only broken in a particular place, so that, for instance, the leaf which takes the uppermost position in a whorl (4 in Fig. 44) will be nearest to the lowermost leaf (5) in the "whorl" above. The position shown in Fig. 44 is not any typical spiral position, however, because all the leaves are not at the same angle of divergence from each other.

Stage III, Fig. 45. Here the leaves are placed in such positions that all the successive leaves are both at a constant vertical and

also at a constant horizontal distance from each other; a spiral line through the leaves will thus have a continuous course. At the same time as the angle of divergence of the leaves from each other has become constant, one more orthostichy has been added.

Hence the final result of this development is that a **whorl has been altered to a spiral.**

When lateral shoots develop, these always begin with 2 transversally placed, brown, scale-shaped bracteoles (a and β
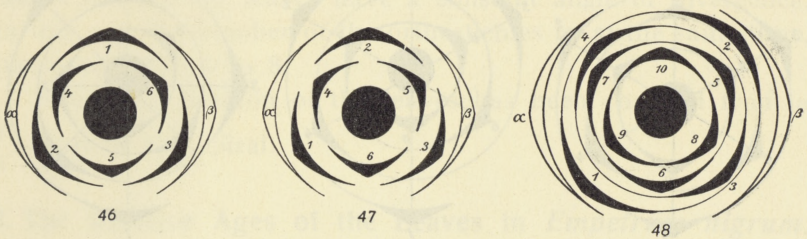
Figs. 46-48. *E. nigrum.* Diagram showing positions of leaves at base of lateral shoots. a and β, bracteoles. The supporting leaf imagined to stand in front. See also text.

in Fig. 25) which in structure and size entirely resemble the budscales and the bractae situated under the flowers, and are generally at different levels, so that their relative ages can readily be determined. After the bracteoles there may follow from 0 to 3 whorls with two leaves, alternating with each other, and whose leaves may more or less show a transition to a $\frac{2}{5}$ spiral. After the whorls with two leaves there may follow some with three leaves and finally some with four leaves. But a stretch with a spiral arrangement may also be interposed etc. The lateral shoots show great variation in the position of the leaves; but the transitions between these are not so smooth as in the long shoots. Here, too, the relative ages of the foliage leaves are often easily determined, because the individual leaves—even in the case of whorls—have some little vertical distance between them.

I. If there are not any other whorls with 2 leaves than those of the bracteoles, whorls with 3 leaves will directly follow β, and the first of the foliage leaves will then as a rule be placed on the posterior part of the axis (Fig. 46) but may also sometimes be found on the anterior part obliquely opposite β (Fig. 47).

II. When there is one whorl with two leaves between the

bracteoles and the whorls with 3 leaves, then the first leaf of
the latter is placed medially on the anterior part; and the first
leaf in the whorls with three leaves may then be placed obliquely
on the anterior part on the same side as β.

III. If there are 2 whorls with 2 leaves above the bracteoles
(Fig. 48) then they will be placed diagonally, so that the first
foliage leaf (1) will be placed anteriorly, obliquely opposite to β,
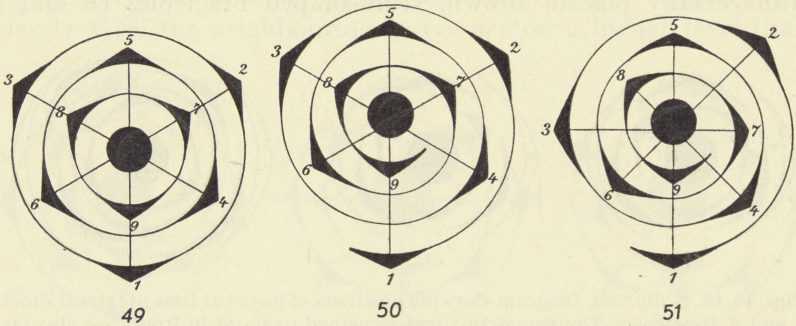
Figs. 49-51. *E. nigrum*. Diagrams of the transition from whorls with 3 leaves $\left(\frac{2}{6}\right)$ to $\frac{3}{8}$ spiral. Orthostichies indicated by straight lines. See also text.

while a leaf in the lowermost whorl with 3 leaves will be placed
anteriorly and medially. As this position is of interest if we want
to understand the morphology of the floral shoot, it is shown in
the subjoined diagram (Fig. 48). But the position of the whorls
with 2 and 3 leaves at the base of the lateral shoots differs just
as much as the position both of the bracts and the sepals in
the floral shoots; and the cases mentioned above are merely
examples among many others.

When whorls with 3 leaves continue their development they
become $\frac{2}{7}$ spirals in the long shoots; but in the short shoots a $\frac{3}{8}$
spiral will often develop from the whorls with 3 leaves. This
development, which is shown in the diagrams in Figs. 49—51,
indeed resembles the above-described transition from $\frac{2}{8}$ to $\frac{2}{9}$ so
much that the stages are given the same designation.

Stage I (Fig. 49). These whorls are characterized by small
vertical displacements so that the relative ages of the individual
leaves can be determined.

Stage II (Fig. 50). In this transitional stage the vertical displacements have become so considerable that a spiral line through the base of the leaves shows a gradual rise and a continuous course. But at the transition from the spiral fragment developed out of one whorl to the next one (from leaf 3 to 4), the spiral line does not pass to the leaf (5 og 6) which has the smallest angle of divergence, but to the most distant (4).

Stage III (Fig. 51) is characterized by such horizontal distances that all the leaves have a constant angle of divergence. In this way the number of the orthostichies is, at the same time, increased from 6 to 8.

Hence the position of the leaves has been changed from a $\frac{2}{6}$ whorl to a $\frac{3}{8}$ spiral.

8. The Relative Ages of the Leaves in *Empetrum nigrum*.

In order to decide what is the order of succession of the individual leaves in the various leaf-arrangements, we may either examine how the edges of the leaves overlap each other or we may study the position of the embryonic leaves at the apex of the stem. In the spiral arrangement the leaves arise in the order in which they occur in the spiral. In the whorl position we meet with the difficulty that when the foliage leaves are fully developed they do not overlap, because they are too narrow. But if the plant has winter buds, it is easy to see from a transverse section how the broad edges of the budscales overlap.

Only in few instances does a true whorl position occur, recognisable by the fact that all the leaves of the whorl have one free and one covered edge (Fig. 52 A). In by far the greater number of cases the leaves of the whorl do not appear at the same time but in a spiral line, and at least one leaf then has both its edges free, while one or several others have both edges covered.

According to the number of leaves forming the whorls different combinations will arise. And even if the number of leaves is the same in different whorls, the order in which they cover each other may still be so different that it may be difficult to see the various observations from the same point of view. Fig. 52 shows some examples of the position of the two whorls of budscales:

I. In the whorls with 2 leaves in the seedlings there is no overlapping of the leaves, but both in the vegetative and the floral shoots the bracteoles of the same whorl do not arise at the same time.

II. Whorls of 3 leaves are likewise best examined in the
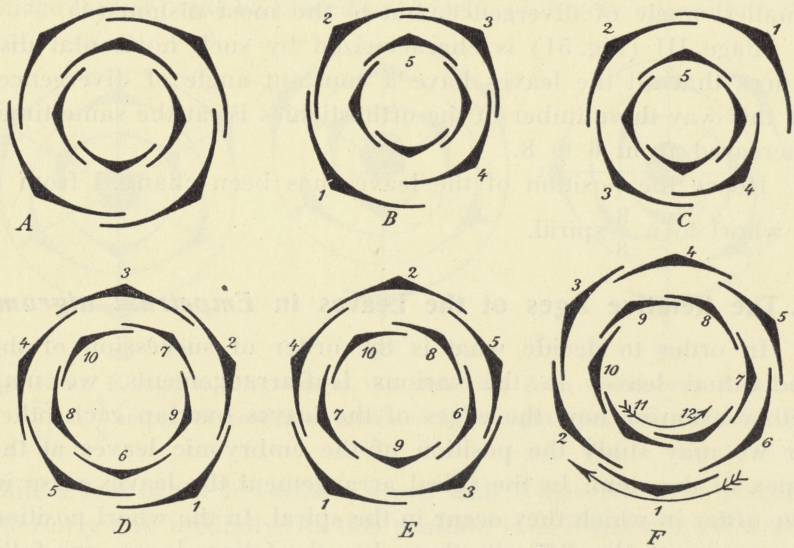
52

Fig. 52. *E. nigrum*. Diagrams of the imbrication of the budscales.

floral shoots, where the bracts as a rule arise according to a $\frac{1}{3}$ spiral. That nevertheless the position of the leaves should be regarded as a whorl will appear from the fact that the individual whorls alternate, so that the number of orthostichies will be 6 and not 3 as in a $\frac{1}{3}$ spiral.

III. Fig. 52 A, B, and C are diagrams of the positions of the budscales in 3 different winter buds with 4 leaves. In the inner ring the overlapping of the leaves is the same. And as regards the inner ring the 3 figures are turned in the same direction so as to show the differences in overlapping in the outer ring which in Fig. 52 A exhibits a true whorl, while B and C show that the leaves in the outer ring arise in a spiral line. If—like EICHLER,

for instance—we take the shortest way between two leaves, it will also be seen that the outer rings in B and C are antidromous; but in spite of this the inner rings are alike both in overlapping and orientation. The order of overlapping for instance resembles the overlapping in the corolla of the *Papilionaceae*, and this means a similar relative difference in age between the leaves as may often be observed in the long shoots at the transition from whorl to spiral.

IV. Figs. 52 D and E show that a whorl with 5 leaves may arise as "zweiumläufig" (EICHLER), the numerator of the fraction for this position being 2; but that this need not always be the case is again seen from the outer ring in Fig. D.

V. Fig. 52 F shows a diagram of budscales arranged in whorls with 6. The leaves arise on a spiral line, but the whorls are antidromous, as shown by the arrows.

9. Changes in the Directions of the Spirals.

As shown above, the changes in the position of the leaves arising on the long shoots during the development of the individual may be expressed by the following formula:

$$\frac{2}{9} \rightarrow \frac{2}{5} \rightarrow \frac{2}{6} \rightarrow \frac{2}{7} \rightarrow \frac{2}{8} \rightarrow \frac{2}{9} \rightarrow \frac{2}{10} \rightarrow \frac{2}{11} \rightarrow \frac{2}{12}$$

When the ramification is monopodial the position of the leaves is changed at most once in the same annual shoot, which therefore can only have 2 successive links in the series above. And one of these two positions of the leaves must then be a whorl. The case is otherwise when the ramification is sympodial. For then the position of the leaves at the base of the lateral shoot is $\frac{2}{4}$ (the bracteoles), while the apical leaves of the annual shoot in question may be for instance in the position $\frac{2}{6}$ or $\frac{2}{7}$. Lateral shoots therefore have often several different positions of the leaves; but these are as a rule not connected by smooth transitions as was the case with the monopodial ramification. In lateral shoots the transition from one position to another often takes place quite suddenly without the least suggestion of tran-

sitional stages. If the two leaf-arrangements are both spirals, it will now be possible to determine whether they turn in the same direction. The interesting observation will then constantly be made that every time a spiral is changed to another spiral, it will change its direction. If for instance the first $\frac{2}{5}$ position in a seedling is a dextrorse spiral, then the formula quoted above will be changed into:

$$\frac{2}{4} \rightarrow \frac{2}{5}r \rightarrow \frac{2}{6} \rightarrow \frac{2}{7}l \rightarrow \frac{2}{8} \rightarrow \frac{2}{9}r \frac{2}{10} \rightarrow \frac{2}{11}l \rightarrow \frac{2}{12}$$

r denoting right and l left.

10. Changes in the Position of the Leaves in other Plants.

Hence it has been seen that in *Empetrum* there is a greater abundance of different leaf-arrangements than in any other Danish ligneous plant. It would, then, be interesting to learn whether analogous conditions are known anywhere else in the plant world.

An examination of the other genera belonging to the family showed that in the *Corema* species there were both whorls and spirals. On the other hand, there were only whorls in the rather sparse material of *Ceratiola*. The varying phyllotaxy of these species should be investigated under natural conditions.

For a number of other plants some observations are already available in Braun (pp. 334—338), who found varying positions of the leaves either in various individuals of the same species or on the different axes of the same individual. An alternation between whorls and spirals was thus found in *Lycopodium, Salix, Carex, Acorus, Cactus, Euphorbia, Linaria, Sedum* and others. Braun thinks that the spiral position is the simplest intermediate position between the whorls (p. 355), whereas Eichler supposes that the whorls are compact spirals.

In recent times Goebel and others have found both whorls and spirals in different plants without, however, having investigated the intermediate stages more closely. Of changes in the direction of the spiral in the same annual shoot I have not been able to find anything in the literature, however.

11. Periods in the Development of the Annual Shoot.

As a typically arctic plant, *Empetrum* can already begin its vital activity at comparatively low temperatures, and thus it becomes one of our vernal plants. Already in April, while patches of the last snow of the winter may still be left between the heather plants *Empetrum* enlivens the moor by its pretty little red flowers.

Almost simultaneously with the flowering the leaves begin to shoot too, the tip of the stem elongates and the budscales open. However, a new formation of cells does not at once take place at the growing point; but the bud increases in circumference because the cells which were already formed the year before merely elongate very considerably and form the lowest and oldest part of the annual shoot, the vernal shoot.

Hence the vernal shoot is formed of the contents of the winter bud, and is therefore 6 months older than the rest of the annual shoot. Normally the vernal shoot does not develop lateral shoots or flowers. Evidently its chief function is merely to start the assimilation of CO_2. In a couple of months the vernal shoot is fully developed, and the longitudinal growth temporarily stops until the middle of June. But then the new cells again begin to form in quantity at the apex of the stem; and a long piece of stem with appertaining leaves develops. This youngest and upper-most part of the annual shoot is termed the summer shoot; its cells have not rested for any length of time in the bud, but have elongated immediately after they were formed at the growing point. Already before August the summer shoot has developed, and the winter bud terminates the annual shoot. With this the longitudinal growth stops for the year.

At the boundary between the vernal and summer shoots there are no budscales; the two parts of the annual shoot pass into each other, and it is not always easy to see where one begins and the other ceases. They are most readily distinguished in the winter stage; for then, owing to its considerably greater age, the outermost cortical layer of the vernal shoot is already dying, so that the colour changes from green or red to brown. The cortex of the summer shoot, on the other hand, is alive and red (or green) in the winter. The boundary between the cortices of the two parts of the shoot is often very sharply marked off by

a dark brown ridge running round the stem between two whorls
of leaves.

The leaves too may show various differences (Fig. 53), the
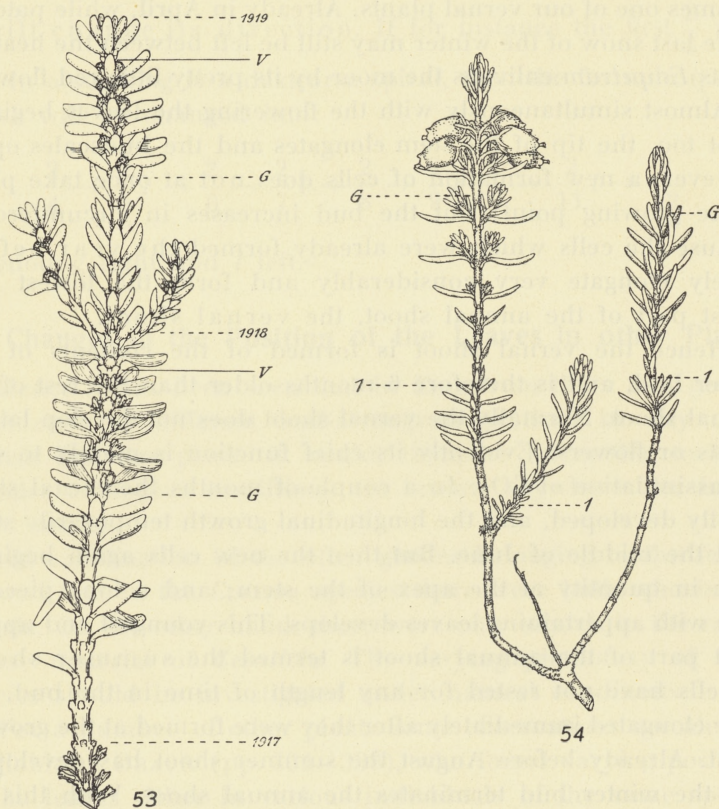
Figs. 53-54. Fig. 53. Male shoot of *E. nigrum* in the winter stage. The years
indicate the boundaries between the annual shoots. G, boundary between
spring and summer shoots. V, boundary between the second (floral) and the
third vegetative section of the annual shoot. × ³/₂. Fig. 54. *Erica cinerea*.
Twig with a vegetative and a flowering branch. 1, Boundary between the
annual shoots. G, Boundary between vernal and summer shoots. Faröes,
August 23, 1922, × 2.

leaves of the summer shoot being comparatively thick and
obtuse; in addition, owing to the difference in age, they are less
wrinkled and lighter in colour than the leaves of the vernal
shoot. The direction of the leaves may also be somewhat different;
the leaves of the summer shoot (especially in short shoots) are

almost horizontally divaricate, while in the vernal shoot they are obliquely upward-directed.

The most conspicuous difference, however, is that the flowers occur exclusively on the summer shoot, never on the vernal shoot. But flowers are never found right up to the winter bud, for the upper 1—2 mm. long tip of the summer shoot only bears vegetative buds in the axils (Fig. 31). Nearly all the vegetative lateral shoots of the plant therefore arise directly below the winter bud (Fig. 53), a fact that influences the branching which may be typically umbellate. In many cases the leaf-arrangement is the same in vernal and summer shoots. Often, however, the above-described changes in the position of the leaves occur precisely at the transition from one section of the shoot to another.

The two parts of the annual shoot are almost of the same length; if there is any difference, it is nearly always the summer shoot which is longest.

While in most of our trees and shrubs summer shoots only develop from a few buds, in *Empetrum* it is all the annual shoots that develop in the above-described characteristic way. This peculiar development of the shoots actually corresponds to what takes place in many trees in the tropics; this rhythm also occurs in Greenland.

In the other *Empetraceae*, too, the annual shoots consist of these three different sections. NORDHAGEN found something quite similar in *Calluna*; and *Erica* (Fig. 54) too shows corresponding conditions. Perhaps this tripartition is a property that is characteristic of certain *Bicornes*; or perhaps it may also be found in the annual shoots of other plants? This point should be more closely investigated.

The terminal bud of the long shoots continues its growth monopodially, even if the shoot ramifies and flowers. This is the case not only in all species of *Empetrum*, but also in *Ceratiola*.

In *Corema*, the third of the genera of the family, the ramification is quite different (Fig. 56), it recalls conditions in the *Rhodoraceae* (Fig. 55), the flowers being gathered in a dense terminal inflorescence which terminates the long shoot, so that the growth of the latter is continued the following year by means of lateral shoots which arise directly under the flowers. Thus in *Corema* the floral axis is a sympodium, whereas it is

a monopodium in *Empetrum* and *Ceratiola* whose flowers arise
in the axils of the ordinary foliage leaves. The supporting leaves
of the flowers of *Corema* are moreover scale-like bracteae; and

Figs. 55-56. Fig. 55. *Phyllodoce coerulea.* Opening of buds. The axis terminates in an
inflorescence, distinct boundaries between annual shoots. Greenland Aug. 10,
1925. × 2. Fig. 56. *Corema Conradi.* Structure and ramification of shoot (Sym-
podium) as in the preceding example (Fig. 55) × 2.

its winter buds resemble the corresponding organs in *Rhodo-
dendron, Phyllodoce* (Fig. 55) and others, whose main axis
remains as a small dead stick in continuation of the annual
shoot.

12. The Ericoid Leaf.

The anatomy of the leaf has long been well known, good
studies of it being available already from the last century by
GIBELLI, GRUBER, LJUNGSTRÖM and others.

There is still a great difference of opinion as to the mor-
phology of the leaf, however, and more especially as to how
the peculiar central cavity within the leaf should be interpreted.
Though for instance GIBELLI and GRUBER had already arrived
at reliable results, not a few recent investigators (e. g. TROLL)
think that the leaf has merely broad revolute edges which meet
on its underside, thereby forming a cavity under it.

The reason for this disagreement is no doubt that we are
not in possession of a sufficient number of detailed investigations
carried out according to modern methods, and comprising not
only the development of the leaf in *Empetrum* but also that of
ericoid leaves in general.

In order to throw light on the problems concerning the mor-
phology of the ericoid leaves, I have studied the genesis of the
above-mentioned cavity in quite thin microtome sections (6 μ)
through the growing points of various species, most of which I
have collected in Denmark or in Greenland. Investigations on
the actual nature of these cavities can best be carried out by
means of transverse sections, as shown in the subjoined figures.

The most easily studied of the species with ericoid leaves that
came under investigation is *Phyllodoce,* the development of whose
leaves is shown in Figs. 60 and 62. The youngest primordia are
almost circular in transverse section (20 in Fig. 60) but soon
they become flattened and develop a keel (11 in Fig. 60) on the
dorsal side on a level with the place where the midrib is formed.
These primordia are easy to homologise with the usual types of
leaf primordia which they entirely resemble. The edges of the
flat primordia are also easy to identify, and if you wish especially
to examine how the cavity is formed, the section drawn in Fig. 60
shows that the edges of the leaves, far from being revolute, on
the contrary are directed somewhat upwards towards the upper
side.

Moreover, the outermost leaves in Fig. 60 plainly show the
first suggestion of the genesis of the disputed cavity, two ridges
being formed on the underside of the leaf parallel to the midrib.
One of the decisive stages has been drawn under higher power
in Fig. 62, which plainly shows the margins of the leaf marked
by 1—2 rows of cells directly under the epidermis. Quite in-
dependently of the edges and a good distance from them, the
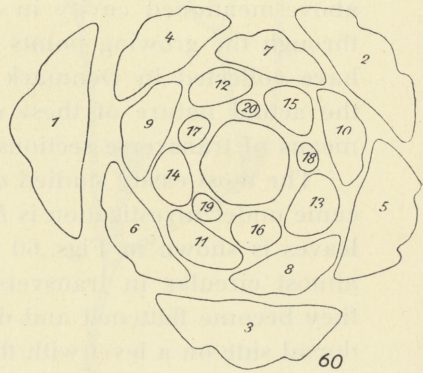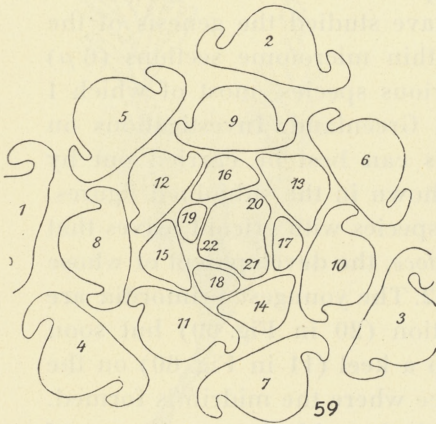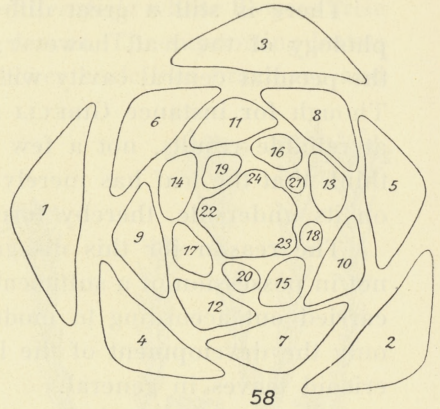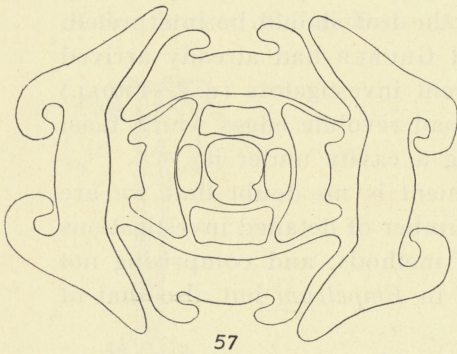
Figs. 57-60. Evolution of leaf. Transverse section of apices of shoots of various *Bicornes*. Fig. 57. *Cassiope tetragona*. × 60. Fig. 58. *Cassiope hypnoides*. Position of leaves $\frac{2}{7}$ spiral. × 100. Fig. 59. *Ledum decumbens*. Revolute edges. Position of leaves $\frac{2}{7}$ spiral. × 50. Fig. 60. *Phyllodoce coerulea*. Position of leaves in $\frac{5}{13}$ spiral. × 100. See also text.

ridges on the underside of the leaf develop. In Fig. 62 the mother cells of the ridges are marked by dotting, and it is distinctly seen that the ridges originally arise in the subepidermal layer of cells, by one or a few rows of cells beginning to divide by walls that are almost parallel with the underside of the leaf. This peculiar formation might also with some justice be called a local growth in thickness.

During the further development the ridges still behave like

separate formations independent of the edges of the leaves. They grow higher and higher until they finally approach each other and enclose the intermediate cavity.

Fig. 30 and Figs. 64, 65, 66, and 68 show that the cavity arises in quite the same way in the leaf of *Empetrum* (*nigrum* and *rubrum*); only the edges of the foliage leaves are barely as
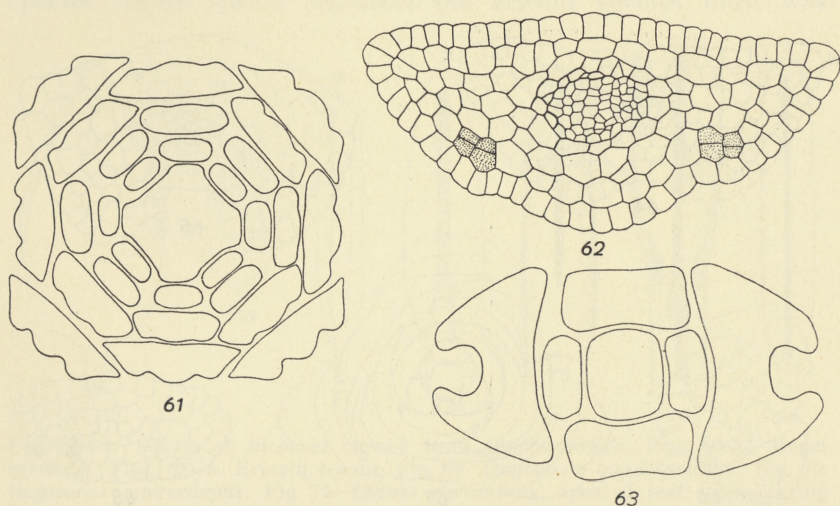
Fig. 61-63. Fig. 61. Transverse section of shoot apex of *Erica tetralix*. × 140. Fig. 62. Transverse section of young leaf of *Phyllodoce coerulea*. The first suggestions of the two ridges on the underside of the leaf are dotted. × 350. Fig. 63. Transverse section of apex of shoot of *Calluna vulgaris*. × 200. The edges of the leaf do not participate in the bounding of the groove on the underside.

broad as in *Phyllodoce*. But here, too, the ridges arise on the underside and distinctly enough some distance from the edges of the leaf in the subepidermal layer.

In transverse sections of winter buds (Fig. 30) interesting views of the budscales are obtained; they have particularly broad edges but also a larger or smaller groove or cavity on the underside of the leaf. It is distinctly seen that the ridges still lie quite close to the midrib but do not follow the edges of the leaves and do not form part of these, as for instance TROLL thinks.

In order to investigate the possibility of a generalisation including other ericoid leaves I have studied several species which are shown in the subjoined figures. It will be seen that the leaves of *Erica* (Fig. 61), *Calluna* (Fig. 63), and *Cassiope tetragona*

(Fig. 57) are in the main constructed and developed in quite
the same way as those of *Phyllodoce* and *Empetrum*.

For comparison Fig. 59 shows the development of genuine
revolute edges in *Ledum decumbens*. It will be seen that here it is
the entire edge that grows downwards and finally inwards to-
wards the midrib. This type of comparatively broad, not ericoid
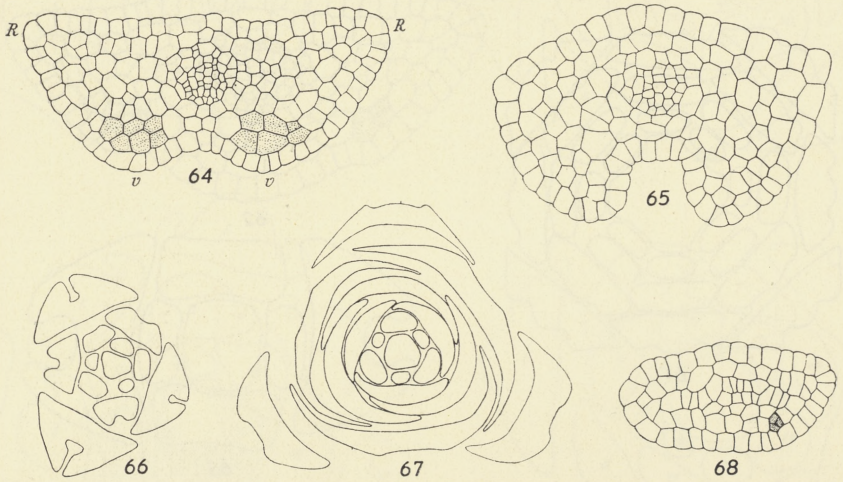
Figs. 64-68. Transverse section of young leaves and shoots showing the genesis
and appearance of the groove and revealing that the edges of the leaves do
not take part in the formation of the groove. Fig. 64. *E. rubrum*. The mother
cells of the ridges dotted. × 300. Fig. 65. *E. nigrum*. × 300. Fig. 66. *E. rubrum*.
Fig. 67. *Corema Conradi*, winter bud. × 100. Fig. 68. *E. rubrum*, mother cell
of ridge dotted. × 300.

leaves, with revolute or flat edges, occurs in the majority of the
Bicornes, as e. g. *Rhododendron, Oxycoccus, Vaccinium, Kalmia,
Arbutus, Andromeda* and many others. In by far the greater part
of the species of *Ericaceae* it is easy to decide directly whether
or not the leaves are ericoid. One of the few questionable cases
is drawn in Fig. 71, which exhibits a leaf (viewed from below)
of a quite narrow-leafed species of *Ledum*. The edges are re-
volute all round the lamina, even the tip is bent, so that this
leaf comes to resemble, e.g. the leaf of *Phyllodoce*. That this is
not a true ericoid leaf can, however, be shown in the first place
by studying the development. But it can also be seen directly
from the bud scales, which have broad flat edges and, in

addition, lack a dorsal groove, which is found in the budscales of ericoid species.

Now there are also in many other plants than the *Bicornes* small and narrow leaves, especially in Australian species. Of these I examined the living species in the Botanical Gardens of Copenhagen; but none of these had true ericoid leaves. The species whose leaves resemble the ericoid species most was
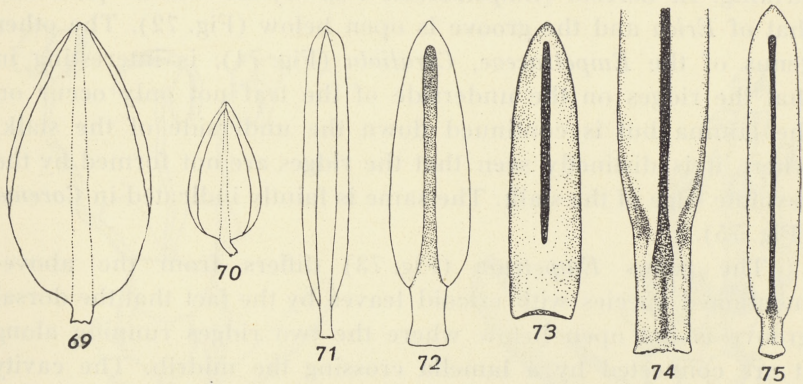
Figs. 69-75. Leaves of *Bicornes* viewed from the underside. Figs. 69-71. Edges revolute. Figs. 72-75. Ericoid leaves. Fig. 69. *Oxycoccus quadripetalus*. Fig. 70. *Oxycoccus microcarpus*. Fig. 71. *Ledum decumbens*, apex of leaf participating in the rolling. × 4. Fig. 72. *Acrostemon equisetoides Kl. (Ericaceae)*. × 20. Fig. 73. *Empetrum rubrum*. Edge of leaf broad, groove closed below. Fig. 74. *Ceratiola ericoides*. Base of leaf. The ridges are continued down the stalk. × 16. Fig. 75. *Corema Conradi*. × 10.

Phylica eriophora (*Rhamnaceae*); but a study of the development showed something quite similar to *Ledum* (Fig. 53), and revealed that there were merely revolute leaf edges.

Even among the *Bicornes* ericoid leaves are comparatively rare. In the rather abundant collection of *Ericaceae* belonging to the Botanical Museum of Copenhagen I found true ericoid leaves in the following genera:

Acrostemon, Anomalanthus, Blaeria, Bruckenthalia, Calluna, Cassiope, Coilostigma, Erica, Ericinella, Grisebachia, Lagenocarpus, Pentapera, Philippia, Phyllodoce, Salaxis, Scyphogyne, Simocheilus, Sympieza, Syndesmanthus, Thoracospermum, Thamnus.

The ericoid leaves are strikingly alike (Figs. 72—75). The groove on the underside is delimited above by the cucullate tip of the leaf, while below it opens freely at the limit between stalk

and lamina. The leaves in the large genus *Erica* and many of the types grouping themselves around it often have this appearance. Among the *Rhodoraceae* (e. g. *Phyllodoce*) ericoid leaves more rarely occur.

As far as I know, genuine ericoid leaves do not occur in other plants than the *Empetraceae* and within the *Ericaceae*? But in these two related families the similarity of the leaves is indeed striking. In *Corema* (*Empetraceae*, Fig. 75) the leaf is quite like that of *Erica* and the groove is open below (Fig. 72). The other genus of the *Empetraceae*, *Ceratiola* (Fig. 74), is interesting in that the ridges on the underside of the leaf not only occur on the lamina but is continued down the underside of the stalk, where it is distinctly seen that the ridges are not formed by the revolute edge of the stalk. The same is faintly indicated in *Corema* (Fig. 75).

The genus *Empetrum* (Fig. 73) differs from the above-mentioned species with ericoid leaves by the fact that the dorsal groove is not open below where the two ridges running along it are connected by a lamella crossing the midrib. The cavity of the leaf is therefore closed at both ends, so that it only communicates directly with the atmospheric air by a narrow fissure. A similar leaf also occurs in certain *Erica* species (e. g. *E. mediterranea* and *carnea*). And within this large and difficult genus the delimitation of the dorsal groove will no doubt prove a character of great systematic value.

The forms of leaves so characteristic of the *Epacridaceae* are rare within the *Ericaceae*, though they do occur, for instance in *Cassiope hypnoides* (Fig. 58). In addition to this there are at least two entirely different types of leaves within the *Bicornes*. And by the structure of the ericoid leaves the *Empetraceae* also show that they belong to the *Bicornes*.

Thus the ericoid leaf seems to represent a peculiar type. For that a green leaf has a kind of secondary growth in thickness is in itself something rare, but a local thickening of the kind described above, leading to the formation of the aforementioned ridges, is perhaps only known from ericoid leaves.

The ridges in the ericoid leaves might with some justice be termed organs sui generis, and in accord herewith these leaves might be regarded as a special morphological type, different

from other small and narrow leaves with a groove on the under-
side. Future investigations must decide whether ericoid leaves
occur in other plants than *Ericaceae* and *Empetraceae*.

13. The Floral Shoot.

The floral dwarf-shoot only attains a length of 1.5—2.5 mm.
Below it bears 5—6 scale-like small bracteae which in rare cases
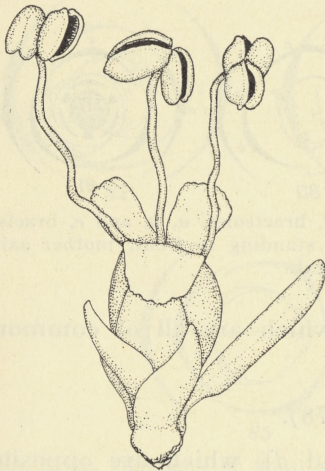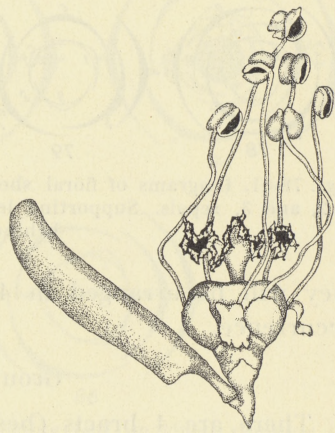
<p style="text-align:center">76   77</p>

Figs. 76-77. Fig. 76. *Empetrum rubrum*. Male flower. Fig. 77. *E. hermaphroditum*.
Supporting leaf with floral shoot, 6 stamens. × 10. Faröes, May 15, 1922.

may support a laterally placed flower; and finally the dwarf-
shoot ends in a terminal flower (Figs. 76—77).

Three different investigations are available on the morphology
of the floral shoot; but since the investigators have arrived at
entirely different results, I have studied the problems anew by
means of microtome sections, this technique being much more
certain than the methods of the earlier authors. My results are
shown in the subjoined diagrams, which are all placed in such
a position that the supporting leaf is in front and the mother
axis behind. For the sake of clarity the first bracteole, *a*, is
throughout drawn on the left. The rest of the bracts are denoted
by small letters and the sepals, denoted by the figures 1, 2, 3,
are given in outline.

Like the vegetative lateral shoots, the floral shoots also bear
below 2 bracteoles, α and β, which are either placed laterally
or are shifted a little backward towards the mother axis. The
anterior edges of the bracteoles do not cover each other, but this
is often the case with the posterior edges, which makes it possible
to determine the difference in age between α and β.

After the bracteoles there follow another 3 or 4 bracts which
may be placed in so many different positions that in the sequel
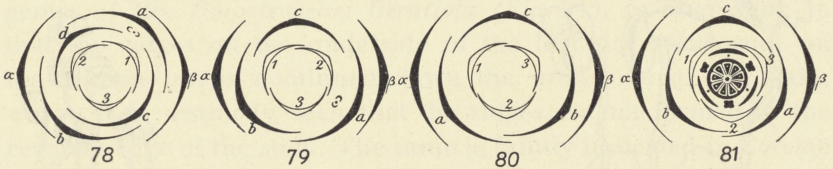
Figs. 78-81. Diagrams of floral shoots. α and β, bracteoles. a, b, and c, bracts.
1, 2, and 3, sepals. Supporting leaf imagined standing in front, mother axis
behind. See also text.

they will be arranged in 4 groups which are all of common
occurrence.

Group I (Fig. 78).

There are 4 bracts (besides α and β), which are opposite
and decussate and placed diagonally between the supporting leaf
and the mother axis. The first bract may either be placed in
front or behind and the median sepal in front. Of this position
Strandmark has given a diagram. For comparison Fig. 48 shows
the position of the leaves at the base of a vegetative lateral shoot.
In this group the plane of symmetry is placed medially.

Group II (Figs. 79-81).

There are only three bracts, the third of which (c) is placed
medially behind, and with an angle of divergence of 120° follow
a and b in front in such a way that the first one (a) may be
placed obliquely opposite either α (Fig. 79) or β (Fig. 80). In
this diagram the median sepal is in front; if this leaf has
No. 1, the diagram of the flower will be almost as in the Mono-
cotyledons. The plane of symmetry in this group is placed
medially.

Group III (Figs. 82-86).

The 3 bracts have a mutual angle of divergence of 120°, but none of them is placed in the median line. The plane of symmetry of the flower lies transversally through the bracteoles. As in group II the first bracteole (a) in front is either placed on the same, or more often on the opposite side of β. Then follows the second bract (b) placed opposite one of the bracteoles (a or as
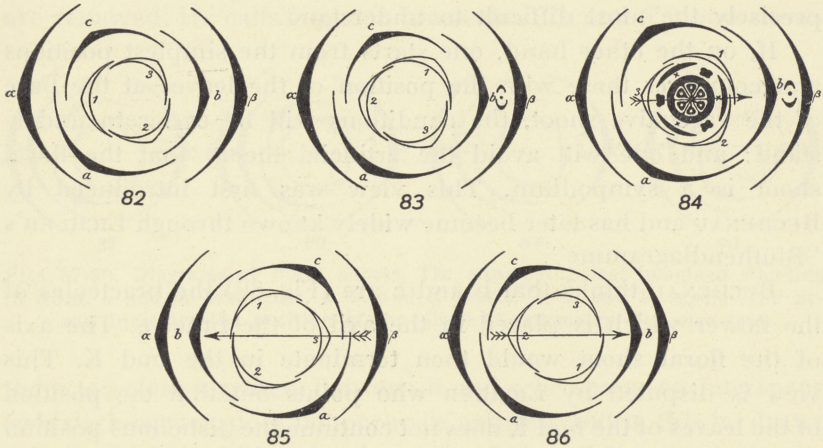
Figs. 82-86. Diagrams of floral shoots. Supporting leaf imagined standing in front. α and β, bracteoles. a, b, and c, bracts. 1, 2, and 3, sepals. The arrows indicate the position of the plane of symmetry. See also text.

a rule β), after which the third bract (c) comes to stand obliquely towards the back. Diagrams of this group have been drawn both by STRANDMARK and by BUCHENAU.

The transversal position of the plane of symmetry in a floral diagram is rare in the Dicotyledons, though present, e.g. in the *Fumariaceae*.

Group IV (Figs. 87-90).

On close analysis this group shows similarities to the preceding one in that the plane of symmetry is transversally placed; further the diagram of the calyx is the same in both groups. But group IV is strikingly different from all the other groups in that the mutual angle of divergence of the 3 bracts (a, b, and c) is not constant. a is directly above a; and on the same side we have both b and

c with a mutual distance of 120°. As a rule b is in front and c behind, but the reverse may also be the case (Fig. 90).

Such diagrams have been found both by STRANDMARK and by BUCHENAU. EICHLER's diagram is identical with Fig. 89. All these three authors have attempted to interpret the diagram of the floral shoot, but they have arrived at different results, none of which is probably quite correct, because they have all been led astray by starting from diagrams of group IV, but these are precisely the most difficult to understand.

If, on the other hand, one starts from the simplest positions and compares these with the position of the leaves at the base of the vegetative shoot, the conditions will be easier to understand; and one will avoid the artificial theory that the floral shoot is a sympodium. This view was first introduced by BUCHENAU and has later become widely known through EICHLER's "Blüthendiagramme".

BUCHENAU thinks that b and c are (Fig. 89) the bracteoles of the flower which is placed in the axil of the bract a. The axis of the floral shoot would then terminate in the bud K. This view is disputed by EICHLER who points out that the position of the leaves of the bud K does not continue the distichous position started with α, β and a. Moreover, a distichous position is not found either in the vegetative or the other three groups of floral shoots. b and c always converge towards the front, towards a, which is never the case with the bracteoles found elsewhere in the plant; such indubitable bracteoles always converge towards the back. In addition a often supports a bud (K), and in that case there will be two buds in the axil of a. But on the vegetative branches and in the other groups of floral shoots there are no accessory buds. Finally a, according to BUCHENAU's interpretation, would assume a position highly peculiar in a dicotyledonous plant and—apart from the bracteoles and perianth—be the only leaf of the axis.

EICHLER, on the other hand, thinks that K is a lateral bud and that the relative mother axis is quite suppressed. He also supposes that the flower is placed laterally in the axil of β, and that b and c are the real bracteoles of the flower. In other respects EICHLER accepts BUCHENAU's interpretation. But that this explanation cannot be right, either, is seen already from the fact

that if β were the supporting leaf, a would stand between the bracteoles and the supporting leaf, which position is not known in any other Dicotyledon.

STRANDMARK's interpretation does not differ essentially from the preceding ones. He too thinks like BUCHENAU that the apex of the axis is in the bud K. Incidentally, as a rule STRANDMARK has not been able to ascertain the difference in age between b and c, though the imbrication is easily seen when α and a are removed. He calls b and c bracteoles ("α and β") and shows
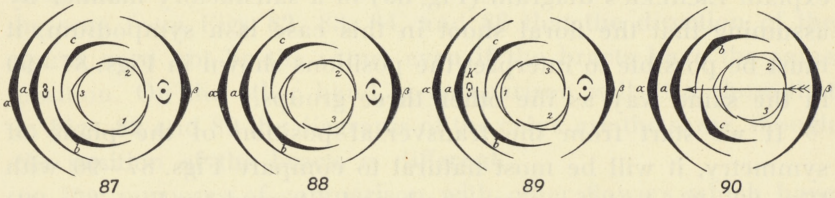
Figs. 87-90. Diagrams of floral shoots. The supporting leaf imagined standing in front. α and β, bracteoles. a, b, and c, bracts. 1, 2, and 3, sepals. The arrow indicates the position of the plane of symmetry. See also text.

them too close together. Between b and c he shows an interspace (which, however, does not occur in nature), and in this he draws a bud which is said to be the apex of the relative mother axis. This bud is perhaps the one which in nature is placed in the axil of the leaf nearest under it. Microtome sections show very plainly that none of STRANDMÀRK's figures of one-flowered shoots is quite correct.

In order to understand the ramification of the floral shoot it will be best to begin by examining the simplest diagrams and then, proceeding from these, try to understand the curious EICHLER diagram (Fig. 89). As a good control the position of the leaves in the vegetative shoots may always be used, since the floral and the vegetative shoots as a rule have almost the same position of the leaves at the base.

The diagram drawn in Fig. 78 is perhaps the easiest to understand if also compared with the diagram of a lateral vegetative shoot drawn in Fig. 48. As usual both these shoots begin with two transversal bracteoles α and β. Next follow two pairs of opposite and decussate leaves, and finally a whorl with three leaves is drawn. In Fig. 78 there is a bud in the axil of a. There

is no reason to believe that the axis of the floral shoot is a sym-
podium; and there is nothing that tells against the flower being
terminal on the axis.

In the case drawn in Figs. 79, 80, and 81 a comparison with
Figs. 46 and 47 shows that instead of 2 whorls of 2 leaves there
may be a whorl with 3 leaves. But here too the axis is no doubt
a monopodium. And the positions shown in Figs. 82—86 may
easily be interpreted in a similar way.

Since, then, as shown above, it has not been possible to
explain EICHLER's diagram (Fig. 89) in a satisfactory manner by
assuming that the floral shoot in this case is a sympodium, it
must be possible to interpret the positions shown in Figs. 87—90
in the same way as the other three groups.

If we start from the transversal position of the plane of
symmetry, it will be most natural to compare Figs. 87—90 with
Figs. 82—86. And if we imagine b and c turned (in Figs. 87—90)
through an angle of 180° round the axis of the shoot (cf. the
relation between Figs. 85 and 86), by which these bracteoles
would come to stand on the opposite side of the flower, then
Figs. 82—86 and Fig. 87 would be nearly the same, since a, b,
and c would then have a constant mutual angle of divergence.
It is not easy to decide how the position of these 3 leaves is to
be interpreted, but since the angles of divergence differ so much,
the position can neither be termed a whorl nor a spiral.

However, the position of the bracts is best interpreted in the
cases shown in Figs. 87-90, the axis of the one-flowered shoot must
always be a monopodium. Thus *Empetrum* has not 3 axes, as
was previously supposed, but only 2, like *Corema* and *Ceratiola*.

In the axils of all the bracts there may be buds which may
develop into lateral flowers. These are remarkable by not having
other bracts than α and β, like the 2 other genera of *Empetraceae*.

14. The *Lobelia*-Diagram?

In investigations on the relationship of the *Empetraceae* it is
also of considerable value to know the diagram of the calyx.
In the above we have already shown 10 different positions of
the calyx, but in nature there are 24 in all. It is evidently the
bracts which are responsible for the many different positions of

the calyx; for a comparison of the figures will show that when there is a three-leaved whorl of bracts the sepals are always placed opposite the interspaces between these. But except in this single particular the bracts do not seem to have any influence on the position of the calyx. For if we compare Figs. 82, 83, 84, and 86 it will be seen that, though all the bracts in these 4 diagrams are in the same position, the first sepal (1) may be placed opposite any of the 3 interspaces between the bracts below. And if, in order to draw comparisons with Eichler's diagrams, we follow the shortest way between the sepals it will be seen from Figs. 82, 83, 84, and 86 that the direction of the spiral need not be the same, even if the bracts have the same position. On the other hand, a comparison will also show that in Figs. 82 and 89 the diagrams of the calyx are the same, though the position of the bracts is different.

For purposes of comparison with other flowers which have no other bracts than the bracteoles, it is therefore sufficient to decide where the plane of symmetry would lie in an *Empetrum* flower without other bracts than α and β; and at the same time it would have to be examined whether the median sepal would then be placed anteriorly or posteriorly in the diagram.

Not rarely the floral shoot develops a few lateral flowers which are remarkable by the fact that they have no other bracts than α and β. But in other respects these lateral flowers have exactly the same structure as the terminal ones. Fig. 91 is a diagram of such a flower placed in the axil of the supporting leaf S, and the bracteoles of which, α and β stand so far towards the back that the angle of divergence between S, α, and β is almost always 120°. Since these three leaves thus in this respect are like a whorl with 3 leaves, the 3 sepals (1, 2, and 3) are also placed opposite the interspaces between S, α, and β, where there is most room. The plane of symmetry has thus a median position, and the first sepal (1) is placed towards the back in the diagram. There are, however, often flowers, whose first sepal is placed towards the front (Fig. 94). The same calyx diagram normally occurs in *Corema*, which has no other bracts than α and β.

Figs. 46 and 47 further show that the base of the vegetative shoots may have a diagram quite similar to that drawn in Figs. 91 and 94.

If we attempt to interpret the diagram in Fig. 91, it will at
once strike us that the first sepal (1) is placed towards the back.
And if we draw a spiral through the leaves in the order in which
they arise, it will be necessary to follow the long way between
the bracteoles (α and β) if we would go by the short way between
the sepals and not reckon with any change in the direction of
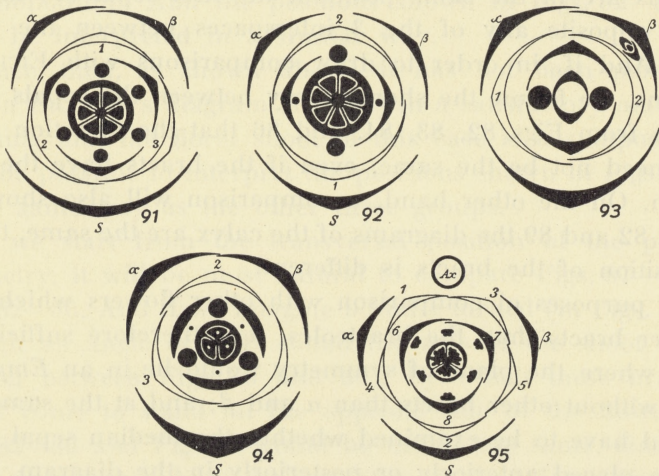
Figs. 91-95. Diagrams of flowers of various *Bicornes* and *Empetraceae*: Fig. 91.
Empetrum hermaphroditum. Lateral flower with 6 stamens. Fig. 92. *E. herma-
phroditum*. Lateral flower with 2 stamens. Fig. 93. *Ceratiola ericoides*. Male
flower. Fig. 94. *Corema Conradi*. Flower imagined bisexual. Fig. 95. *Tripetalia
paniculata* Sieb. et Zucc. S, supporting leaf. α and β, bracteoles. 1-5, sepals.
6-8, petals. See also text.

the spiral. But these are the very features that are characteristic
of the *Lobelia*-diagram, which otherwise is only known from the
Rhodoraceae (Eichler) and the true *Ericaceae* (Hagerup 1922
and 1928). It is, however, always the case in the *Bicornes* that
the *Lobelia*-diagram occurs together with the normal position of
the calyx in which it is sepal 2 that is placed medially towards
the back (Fig. 98). In addition there are also other calyx diagrams
in a given species of *Bicornes*. Such a rich variety of different
calyx diagrams within the same species is shown in the appended
Figures 96—101 of *Erica cinerea*.

However, no 3-merous flower with a *Lobelia*-diagram is known
which can be directly compared to the typical *Empetraceae*
diagram (Figs. 91—94). But among the *Rhodoraceae* there is a

small genus, *Tripetaleia* (Samuelsson), which is 3-leaved in all
the whorls except the calyx, which is 5-leaved; and moreover
the leaves of the latter are united, so that their imbrication cannot
be decided.

By means of microtome sections it was possible to determine
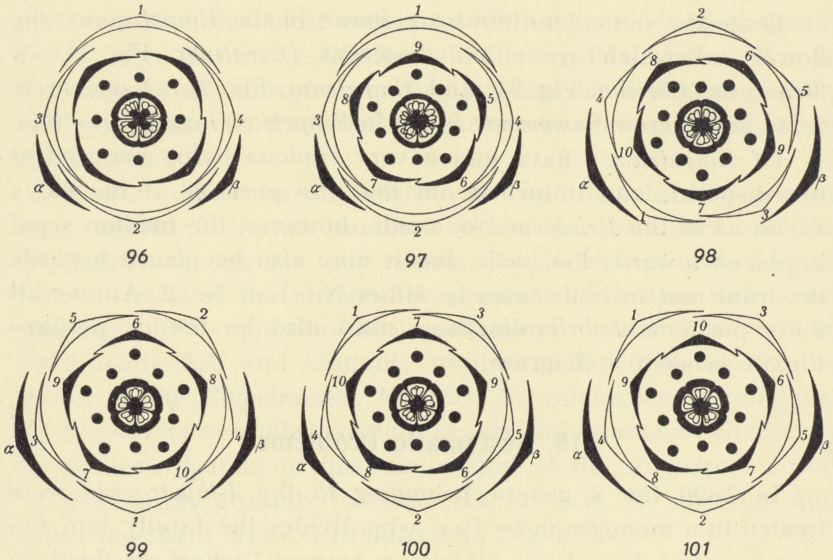
Figs. 96-101. *Erica cinerea*. Floral diagrams. Figs. 100-101. *Lobelia*-diagrams. α and
β, bracteoles. Sepals only outlined. Petals black. Supporting leaf imagined stand-
ing in front. See also text.

the position of the other leaves in the flower of *Tripetaleia*. And
as it turned out that the plane of symmetry had the same position
as in *Rhododendron*, I have in Fig. 95 numbered the sepals as
usual in inverse diagrams and do not think that in so doing I
have committed any error.

If now we compare the diagram of *Empetrum* (Fig. 91) with
that of *Tripetaleia* (Fig. 95), they show good agreement in the
position both of the corolla, the bracteoles, and the stamens, as
well as in the position of the plane of symmetry. It therefore
seems natural to suppose that a *Tripetaleia* with a calyx of 3
leaves would have had this in the same position as in *Empetrum*
and with the median sepal towards the back.

As shown in Figs. 96—101, it is, however, characteristic of

the *Bicornes* that the calyx may occupy many different positions
in one and the same species; the median sepal may both be
placed towards the front and towards the back, and may be
both No. 1 and No. 2. Among these positions we find both *Lobelia*-
positions (Figs. 100 and 101) and normal diagrams (Fig. 98),
which may have either 4 or 5 leaves.

Quite the same conditions are found in the *Empetraceae*, the
flowers of which are either dimerous (*Ceratiola*, Fig. 93) or
3-merous (*Corema*, Fig. 94, and *Empetrum*, Fig. 91). Very rarely
2-, 4-, or 5-merous flowers are found in *Empetrum hermaphroditum*.

Of *Empetrum* I have had a very copious living material at
my disposal, and it turned out that the position of the calyx
varies as in the *Ericaceae*. As a rule, however, the median sepal
is placed towards the back; but it may also be placed towards
the front and in both cases be either No. 1 or No. 2. Among all
these positions *Lobelia*-diagrams must also be found; perhaps
Fig. 91 is such a diagram.

15. Systematic Problems.

In 1890 the 3 genera belonging to the *Empetraceae* were
treated in a monograph by PAX, who divides the family into *Co-
remateae* and *Empetreae*, which are termed "scharf geschiedene
Gruppen". In the *Coremateae* only the genus *Corema* is included
(2 species) and to the *Empetreae* are referred the other two
genera, *Empetrum* and *Ceratiola*.

But this grouping is only based on the axis numbers, the
Coremateae being regarded as biaxial, while the *Empetreae* are
considered triaxial, since PAX accepts BUCHENAU's theory of the
floral shoot being a sympodium. Above it was, however, shown
that BUCHENAU's theory is wrong, as the floral shoot is a mono-
podium both in *Empetrum*, *Ceratiola* and *Corema*. Hence PAX's
grouping too must be abandoned.

The members of the family are all closely related and together
form a rounded-off whole, so that I have hardly here committed
any great error by regarding the single genus *Empetrum* as a
typical representative of the whole family, this genus being
morphologically the richest of them all.

The genus *Empetrum* was erected by LINNÉ; and JUSSIEU

regarded it as related to the *Ericaceae*. But since then the family has undergone many vicissitudes in a systematic respect; it has even once been classed among the *Coniferae* (NUTTALL, 1818). In 1827 DON referred our present 3 genera to the same family, which, however, he thinks is related to the *Euphorbiaceae* and the *Celastrineae*; and for a long period that view was widely accepted. However, most authors admit that there is no foundation for it (e. g. WARMING). On the other hand, PAX writes; "Lange Zeit wurden die Empetraceen in die Nähe der *Ericaceae* gestellt, mit denen sie in keinerlei erkennbaren verwandtschaftlichen Beziehungen stehen."

Recent authors have especially assumed that the *Empetraceae* were related to certain families within the *Geraniales* and the *Sapindales*, though the only reason they have been able to give for this view is the absence or presence of certain individual characters. To supply the above-mentioned need SAMUELSSON in 1913 made full and valuable studies of the evolution of the flower in the *Empetraceae, Bicornes, Geraniales,* and *Sapindales*. In this way he was able to include several important new characters in the investigation of the relationship of the *Empetraceae* and to give ample grounds for referring them to the *Bicornes* and removing them from *Geraniales* and *Sapindales*.

Of special interest are SAMUELSSON's studies on the embryology. And with respect to the endosperm of *Empetrum* he states (p. 177) that "An entirely corresponding evolution has not so far been observed in any single plant belonging to any other group of related genera" than the *Bicornes*.

Referring to several plants that unquestionably belong to the *Bicornes* SAMUELSSON points out that the features most character-istic of the *Empetraceae* are also—though sparsely—found among the *Bicornes*.

Therefore SAMUELSSON with good reason arrives at the view that the *Empetraceae* are so closely akin to the *Ericaceae* that he would think it reasonable to unite the two families. "Die Familien-diagnose brauchte zu diesen Zweck kaum erweitert zu werden" (p. 180).

Thus in the embryology there is nothing of importance that would prevent us from referring the *Empetraceae* to the *Bicornes* (SAMUELSSON). The cytological conditions too point in the same

direction, the basic number of the family being 13 (HAGERUP), as in many *Rhodoraceae* and some few *Ericaceae*. Polyploidy is only known in *Empetrum hermaphroditum*, which is the only bisexual species in the family. Simultaneously with the rise of polyploidy the ecological and geographical orientation of the plant has changed, the main area of distribution of *E. herma-phroditum* being more northerly than that of *E. nigrum*. It is possible, however, that *E. hermaphroditum* is the most original type of the family from which the others have been derived?

For the elucidation of the relationship it may then further be added that *Empetrum* may have a *Lobelia*-diagram just like *Rhodoraceae* and *Ericaceae* (though it may also have other diagrams).

There are several other characters which would seem to indicate a closer relationship with the *Rhodoraceae* than with the *Ericaceae*, thus the absence of an appendage to the anthers, which, further, open by means of longitudinal fissures, e. g. in *Loiseleuria* and others. A single whorl of stamens is found e. g. in *Azalea* and *Loiseleuria*, the latter genus may also have a 3-merous gynaeceum. A larger number of carpels than petals is only present in the *Rhodoraceae*. The two genera *Ledothamnus* and *Leiophyllum* which are related to *Phyllodoce* are sympetalous and the carpels open by longitudinal fissures. In *Leiophyllum* the stamens are also longer than the corolla as in *Empetrum*, and the gynaeceum is 2—3-merous.

The whole group of the *Ledeae* is choripetalous. Of the genera belonging to it *Elliottia* has only one ovulum in each of the chambers of the gynaeceum just like *Empetrum*. *Tripetaleia* is sometimes included in this genus; as already stated, it is interesting by having three leaves in all the floral whorls except the calyx, so that the diagram of the flower is very like that of *Empetrum*.

It is especially the 3-merous flower as well as the fact that it is unisexual which is the real reason why *Empetrum* has been regarded as related to the *Euphorbiaceae*, from which, however, the *Empetraceae* deviate much by having a quite different structure of the ovula (WARMING). It is clear, however, that the unisexuality is a secondary character, for the flowers of all the *Empetraceae* show large remnants of the other sex. In addition *E. herma-phroditum* is normally bisexual.

Within the *Bicornes Epigaea* is functionally unisexual. Numerous species of *Erica, Epacridaceae* and others have stamens projecting far outside the corolla and a pollen which is dispersed by the wind. *Calluna* too is often pollinated by the wind just like *Empetrum*.

The appearance of the *Empetraceae* is not a merely accidental outward resemblance to the *Ericaceae*. This is shown by the many vegetative characters which we examined in the preceding part. Among these we must especially emphasise the characteristic development of the ericoid leaves. The peculiar periodical development of the annual shoot and its division into three sections highly different in a morphological and functional respect is also in the main the same in *Empetrum* and e. g. *Calluna* (NORDHAGEN).

Thus it is not merely in outward appearance that the *Empetraceae* are akin to the *Bicornes* (only the uncertain serum reactions differ). In addition there are distinct points of resemblance in cytology, embryology, anatomy, ecology, geography, structure of the flower, and also in the morphology of the organs and in the substances contained.

They bear the greatest resemblance to the *Rhodoraceae*, close to which the *Empetraceae* should be placed in the system, as a merely biologically deviating type.

16. Summary.

1. These studies have been carried out with *Empetrum* as the main subject and form a supplement to the publications already available, mentioned in the list of literature.
2. The pollen tubes do not penetrate into the tissue of the style but grow down to the ovules exclusively through fine channels filled with atmospheric air (Figs. 3—6).
3. The water necessary for the germination is carried down to the seed through a fine channel through the stony layer (Figs. 7 and 11).
4. The germination and the seedling are shown in Figs. 9—24.
5. All the members of the family have typical winter buds covered with broad-edged scales (Figs. 30—42).
6. The position of the leaves in the seedling is always opposite

and decussate (Figs. 19—24). But during the development of the individual the position of the leaves undergoes great changes and whorls may occur with $3\left(=\frac{2}{6}\right)$, $4\left(=\frac{2}{8}\right)$, and $5\left(=\frac{2}{10}\right)$ leaves.

7. Intermediate between these whorls there are $\frac{2}{5}, \frac{2}{7}, \frac{2}{9}, \frac{2}{11}$-spirals respectively.

8. Sometimes a spiral position may be changed to another without the interposition of any whorl, but then the spiral changes its direction (from right (r) to left (l) or the reverse). These changes are shown in the diagrams Figs. 43—45 and Figs. 49—51.

9. The changes in the position of the leaves which take place during the development of the individual may be expressed schematically as follows:

$$\frac{2}{4} \rightarrow \frac{2}{5}r \rightarrow \frac{2}{6} \rightarrow \frac{2}{7}l \rightarrow \frac{2}{8} \rightarrow \frac{2}{9}r \rightarrow \frac{2}{10} \rightarrow \frac{2}{11}l \rightarrow \frac{2}{12}.$$

10. In *Corema* the inflorescence is terminal (Fig. 56) as in *Rhododendron*, and the ramification is sympodial. In *Ceratiola* and *Empetrum* (Fig. 53) the flowers are inserted in the axils of leaves, and the ramification is monopodial. All the species are biaxial.

11. In the ericoid leaves the central hollow is not bounded by "the revolute edges of the leaf" but by 2 ridges which grow out at right angles from the underside of the lamina on either side of the midrib (Figs. 30, 66, 68). The real edges of the leaves are not revolute but flat (Figs. 34—38).

12. The ericoid leaves (Figs. 72—75) are a sharply delimited morphological type probably (?) not found in plants outside the *Bicornes* and the *Empetraceae*, and are therefore of great systematic value.

13. The ericoid leaf is distinguished from most other small and narrow leaves by the underside of the tip being cucullate.

14. The groove on the underside of the leaf is bounded by a transverse ridge at the base of the lamina in *Empetrum* (Fig. 73) and some *Erica* species. In most other ericoid leaves the groove is open below (Fig. 72). This systematic-

ally important character should be used within the genus *Erica*.

15. The structure of the floral axis is shown in Figs. 76—90. This is a monopodium (not as previously supposed (Buchenau, Eichler), a sympodium).

16. The chief floral diagrams of the family are shown in Figs. 91—94.

17. The position of the calyx is just as variable as in the *Bicornes* (Figs. 96—101).

18. Among the various calyx diagrams the *Lobelia*-position also occurs both in the *Bicornes* and the *Empetraceae*. The occurrence of this rare position is regarded as evidence of relationship.

19. The characters peculiar to the *Empetraceae* recur so distinctly in the *Bicornes* that these families must be regarded as closely allied to each other.

Literature.

ARVIDSSON, TH. (1935): *Empetrum hermaphroditum* (LANGE) HAGERUP och *E. nigrum* L. s. str. i Norden. Bot. Notiser.

— (1938): Einige neue Gesichtspunkte zu den Chromosomenzahlenbestimmungen. Svensk bot. Tidskrift, Bd. 32, S. 191.

— (1943): Studien über die Gefässpflanzen in den Hochgebirgen der Pite Lappmark. Acta phytogeographica Suecica. XVII, S. 125.

BLACKBURN, K. B. (1938): On the occurrence of a hermaphrodite plant of *Empetrum nigrum* L. Journ. of Bot. Vol. 76, p. 306.

BÖCHER, T. W. (1937): Om Udbredelsen of *Ericaceae, Vacciniaceae* og *Empetraceae* i Danmark. Bot. Tidsskrift. Bd. 44.

— (1938): Biological distributional types in the flora of Greenland. Medd. om Grønland. Bd. 106, Nr. 2.

BRAUN, A. (1830): Die Ordnung der Schuppen an den Tannenzapfen etc.

BRY, H. (1930): Systemat. Stellung der *Empetraceae*. Dissertation Berlin.

BUCHENAU (1862): Der Blüthenstand von *Empetrum*. Bot. Zeitung, p. 297.

CARMICHAEL, D. (1918): Some account of the island of Tristan da Cunha and of its natural productions. Trans. Linn. Soc., Vol. XII, p. 484—513.

DON (1826): On affin. of *Empetreae*. Edinb. New phil. Mag., p. 59.

DRUDE O., (1891): *Ericaceæ*. Nat. Pflanzenfam. von ENGLER u. PRANTL.

DUVIGNEAU, P. (1943): Les associations à *Empetrum* en Belgique. Bull. Soc. R. Bot. Begique, Bd. 75, 2 Sér., 25, p. 39—43. 1 Tab.

EICHLER, A. W. (1875—78): Blüthendiagramme. I—II.

ERDTMAN, O. G. E. (1943): An introduction to pollen analysis. New Ser. of Plant Science Books, ed. by F. VERDOORN. Printed in U. S. A.

FERNALD, M. L. and WIEGAND, K. M. (1913): The genus *Empetrum* in North America. Rhodora. Vol. XV, p. 211—217.

— (1925): Persistence of Plants in Unglaciated Areas in Boreal America. Mem. of the Am. Ac. of Arts and Sciences. Bd. 15, III, p. 241.

GIBELLI, G. (1876): Di una singolare struttura delle foglie delle *Empetraceae*. Nuovo giorn. bot. Ital., VIII, p. 49.

GOEBEL, K. (1913): Organographie der Pflanzen. I.

GOOD, R. D'O. (1927): The genus *Empetrum*. Journ. Linn. Soc., Vol. XLVII, p. 489—523.

GREVILLIUS, A. J. und KIRCHNER, O. (1925): *Empetraceae*. Lebensgeschichte der Blütenpflanzen Mitteleuropas von O. KIRCHNER, E. LOEW und C. SCHRÖTER. Bd. IV, 1, S. 165—181.

GRUBER, G. (1882): Anatomie und Entwickelung des Blattes von *Empetrum nigrum* und ähnlicher Blattformen einiger Ericaceen. Inaug. diss. Königsberg.

HAGERUP, O. (1922): Om *Empetrum nigrum* L. Botan. Tidsskrift. Bd. 37.
— (1927): *Empetrum hermaphroditum* (LGE.) HAGERUP. A new, tetraploid, bisexual species. Dansk Bot. Arkiv. Bd. 5, No. 2.
— (1928): Morphological and cytological studies of *Bicornes*. Dansk bot. Arkiv. Bd. 6, No. 1.
— (1941): Zytoökologische *Bicornes*-Studien. Planta. Bd. 32, S. 6.
HASSELBAUM, G. (1931): Cytologische und histologische Studien zur ericoiden endotrophen Mykorrhiza von *Empetrum nigrum*. Bot. Archiv. 31, S. 386.
DE JUSSIEU, A. L. (1791): Genera plantarum secundum ordines naturales disposita. Turici Helvetorum.
LINSBAUER, K. (1900): Zur Anatomie der Vegetationsorgane von *Cassiope tetragona* DON. Sitz. K. Akad. Wiss. Wien. math.-nat. Kl. Bd. 109, Abt. I. S. 685.
LJUNGSTRÖM, E. (1883): Bladets byggnad inom familien *Ericaceæ*. Lunds Univ. Årsskrift. Tom XIX.
MALTE, M. O. (1934): Critical Notes on Plants of Arctic America. Rhodora. Vol. 36, p. 172.
MARKLUND, G. (1940): Beobachtungen über *Empetrum hermaphroditum* (LANGE) HAGERUP und *E. nigrum* L. S. str. Memoranda Soc. Fauna et Flora Fennica. Vol. 16, p. 74—76.
McEWEN, M. C. (1894): The Comparative Anatomy of *Corema alba* and *C. Conradi*. Bull. Torrey Bot. Club. Vol. 21, p. 277—285.
MENTZ, A. (1912): The Structure and Biology of Arctic Flowering Plants. I, 3. *Empetraceae. Empetrum nigrum* L. Medd. om Grønland. Bd. 36.
NORDHAGEN, R. (1937-38): Studien über die monotypische Gattung *Calluna* SALISB. I—II. Bergens Museums Årbok. Naturv. rekke No. 4/₁.
— (1943): Sikilsdalen og Norges Fjellbeiter. Bergens Museums Skrifter. No. 22.
NUTTALL, Th. (1818): The genera of North American plants, II. Philadelphia.
PAX, F. (1896): *Empetraceae*. Nat. Pflanzenfam. von ENGLER und PRANTL. III, 5.
PETERSEN, H. E. (1912): The biological anatomy of the leaves and the stem (*Ericineae*). Medd. om Grønland. Bd. 36.
ROSTRUP, O. (1900): Aarsberetning fra Dansk Frøkontrol for 1898—99. S. 50—51. København.
SAMUELSSON, G. (1913): Studien über die Entwicklungsgeschichte der Blüten einiger *Bicornes*-Typen. Svensk Bot. Tidskrift. Bd. 7, Hf. 2.
SKOTTSBERG, C. (1921): Phanerogams of Juan Fernandez Islands. Uppsala.
STRANDMARK, P. W. (1880): Blomställningen hos *Empetrum nigrum* L. Bot. Notiser.
SYLVÉN, N. (1906): Om de svenska dicotyledonernas första förstärkningsstadium. Kungl. svenska vet. akad. handl. Bd. 40.
TROLL, W. (1939): Vergleichende Morphologie der höheren Planzen. I, 2. S. 1107.
WARMING, E. (1912): Frøplanterne. København.