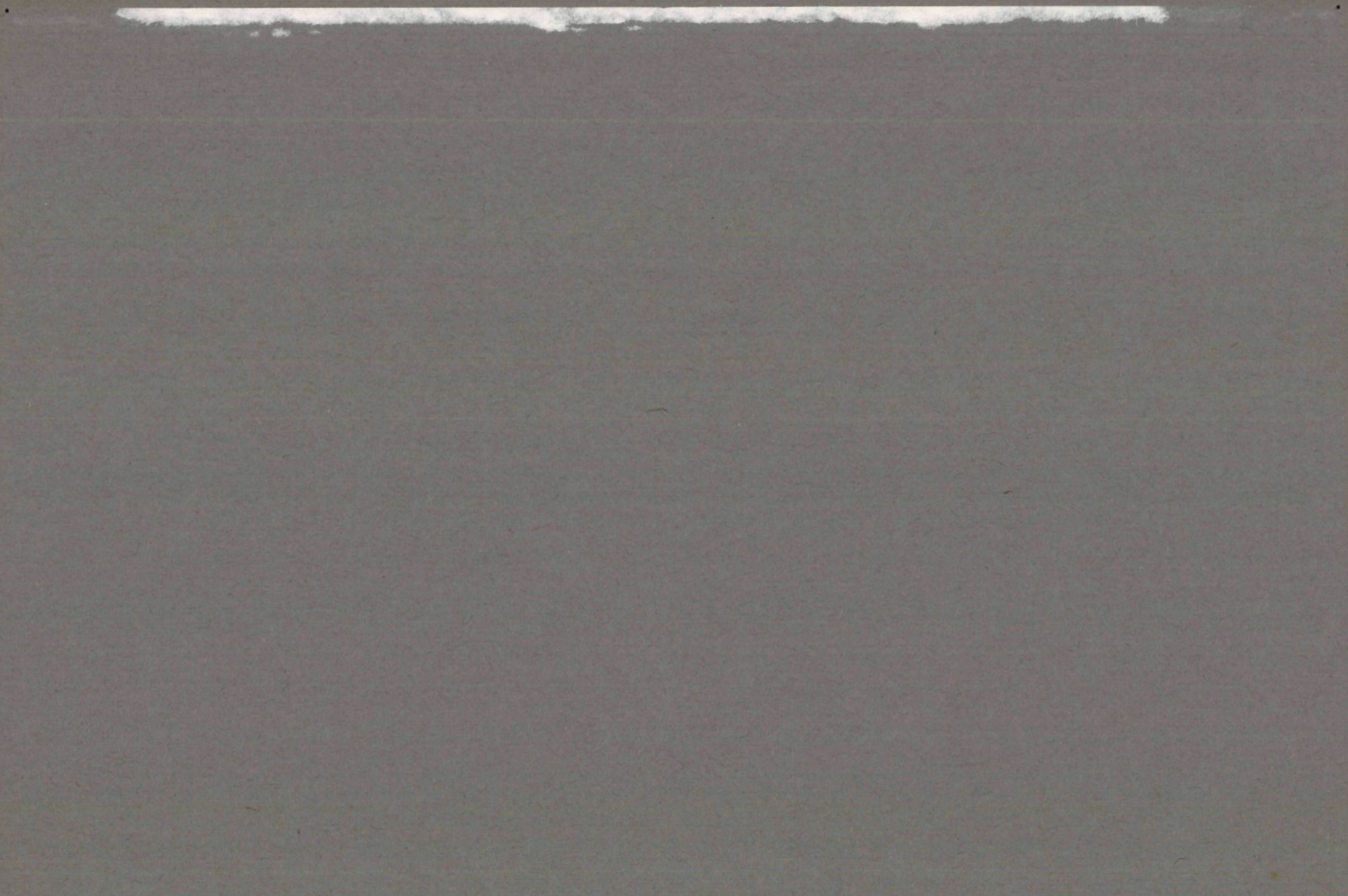

A heath reserve in the Netherlands. The Dwingeloo Heath in full bloom.

(from a water-colour drawing by the author)

CALLUNA

A MONOGRAPH ON THE SCOTCH HEATHER

BY

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WITH 30 PLATES AND 141 FIGURES

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INTRODUCTION.

The name Calluna is derived from the Greek verb kalluno, which has a twofold meaning: to clean and to ornament or adorn [1]).

The first meaning refers to the practical use it has been put to by man, especially in the times when Calluna-heaths still occupied vast regions in north-western Europe and their inhabitants, benefited in manifold ways by its useful properties, remained for centuries in close touch with it, so that in the long run the moors even left their mark on the people as well as on the fauna. The "cleaning" refers to its being used by the heath-dwellers as the material for brooms and brushes. But this, as we shall see later on, is by no means the only way in which this plant has been useful, in fact, this is only a minor part of the significance it has had, and to some extent still has for mankind.

"To ornament" points to its aesthetical value. The beauty of its uncommonly rich bloom, especially the glorious feast of colour, when the wide heath-fields in the countries round the North Sea are in full bloom, never fails to impress us afresh. Not only the many expressions in painting and poetry, referring to heath and the heath-landscape, testify this, but so does Calluna itself as an ornamental plant. For as such it has earned a worthy place in our gardens and parks, particularly in England, where the most notable forms have been cultivated since many years.

Besides these two aspects there is a third, leading to the true estimation, it is the knowledge of its structure, life-history and distribution on the Earth. Through it only it is revealed to us what this form of life contains, how Calluna distinguishes itself from many of its relations, how phylogenetically and also morphologically and physiologically, it presents many as yet unsolved problems.

Its extremely fine structure of a typical "ericoid" character is shared to this extent by only few other phanerogamous plants of the European flora. The structure of its flower and fruit and the number of chromosomes diverge so much from related genera, that from a morphological as well as from a phylogenetic point of view it occupies a somewhat isolated position within the family of the Ericaceae. NORDHAGEN, in his recent work on Calluna (1938, p. 58), rightly remarks: "Calluna ist eine enigmatische, aber sehr wertvolle Pflanze, denn sie bricht die Einförmigkeit der Gruppe Ericoideae und sie lässt uns einen Zusammenhang mit andern, entferntern Bicornesgruppen ahnen." (Calluna is an enigmatical but very valuable

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[1]) Cf.: J. C. LOUDON, Encyclopaedia of the trees and shrubs of Great Britain (1842; p. 559) and Transact. Linn. Soc., 1802, **6**, p. 317.

plant, for it breaks the uniformity of the group Ericoideae and lets us surmise a connection with other more remote Bicornes groups.)

Moreover it has a remarkable, also teratologically important, plasticity of form, manifesting itself in numerous already known abnormal deviations, while at the same time the species shows in the most distant corners of its wide range of distribution an amazing fixity of external form.

Although it has not been much studied as yet physiologically, still it shows such a conspicuous ecological power of accomodation to its surroundings, that again we are surprised by its chemico-physical capacities. As a sclerophytic oligotrophic woody plant with xeromorphic characteristics it is able to live on swampy peat-soil and in the extreme North far beyond the polar circle, as well as under the subtropical summer-heat on the sunny Moroccan rocks and Spanish mountain-slopes. A plant with so large a terrestrial adaptation must have a potential adaptation at least as wide and so deserves the full attention of plant-physiologists. Full of problems is also its non-obligatory, non-cyclical mycorrhiza symbiosis.

Also geographically Scotch heather (ling) is interesting, not so much on account of its extensive area as by its occurrence in such different surroundings as e.g. woods, moors, drift-sands and rocks, and besides by its ability to form mass-vegetations of large extent, in which it then dominates completely. Then it is interesting to note how this species emigrates westward and eastward from its main area in Europe. What DRUDE could still write in 1891 in the first edition of ENGLER–PRANTL's Natürliche Pflanzenfamilien: "Es ist Calluna gewissermassen eine Wappenpflanze für den europäischen Anteil des nordischen Florenreiches" (Calluna is so to speak an armorial plant for the European share in the northern floral kingdom) no longer fully holds nowadays, for in North America it has in numerous places got a firm footing and from these is extending rapidly, as it also seems to do on the East side of the Ural.

The literature on Calluna is already fairly extensive, as may appear from the following list. It is so much scattered, however, that a full summary of our present knowledge on this plant seemed desirable. To be sure, GREVILLIUS and KIRCHNER (1923) and BRAUN BLANQUET (1926) have given good surveys, but these are by no means complete and do not give what may be expected of a monograph. Besides they are already out of date on many points.

An ample discussion of the literature on Calluna cannot be given here, if it were only because of the space it would occupy. So I have restricted myself to a short enumeration of the principal investigators with the dates of their papers, which are mentioned in the bibliography. Only to the more important investigations a few remarks are added. The order of the subjects is the same as in the present paper.

On the habit and organisation of the plant important data are already found with the older morphologists, as e.g.: WIGAND (1854), DÖLL (1859) and WYDLER (1860). MALME (1908) studied more in detail the ramification of the annual shoots, on which data are also found with HAGERUP (1928), BEIJERINCK (1937) and NORDHAGEN (1937/38). Chemical data are given by: ROCHLEDER (1852); PERKIN and NEWBURY (1899); DEKKER (1913); KEEGAN (1916); WEHMER (1931) and NOOIJEN (1936), as far as the more specific organic substances are concerned. Analyses of ash are given, among others, by WOLFF (1871) and VON LINSTROW (1929). Comparative analyses of Calluna at various ages and in different seasons were made by LANDER and COMRIE (1936).

On the abnormities of Scotch heather something is found with: CLOS (1871); MASTERS and DAMMER (1886); ASCHERSON and RUTHE (1901); LINDMAN (1907); PENZIG (1921); JANSEN (1927, 1929, 1935) and BEIJERINCK (1933, 1937).

In 1937/38 NORDHAGEN published his important morphologic-phylogenetic: "Studien über die monotypische Gattung Calluna Salisb.", I—II (Researches on the monotypical genus Calluna Salisb.), in which besides the chief relational and other morphological characteristics also phylogenetic considerations are given.

On the structure of the root data are found with: WARMING (1884); VAN TIEGHEM et DOULIOT (1888); FRÜH and SCHRÖTER (1904) and SYLVÉN (1906).

Stem and wood have been dealt with, among others, by: CHALON (1867); GRIS (1872); SEGERSTEDT (1894); KANNGIESSER c.s. (1906—1914; on the growth in thickness and the age-limit) and KOSTYTSCHEW (1924).

For the structure of the leaf the researches of GRUBER (1882); LJUNGSTRÖM (1883) and DOSE (1904) are of importance, briefer data being found, among others, with HESSELMANN (1904); GERTZ (1906) and BRAUN (1933).

On the flower and its parts several publications exist and new particulars are constantly being discovered. We may mention here the publications of FRITSCH (1845); PAYER (1857); BAILLON (1860); CELAKOVSKY (1875); EICHLER (1875); LIDFORS (1899); CHURCH (1908); VELENOVSKY (1910); HAGERUP (1928); BEIJERINCK (1933, 1937) and NORDHAGEN (1937/38), while more particularly on the structure of the sexual-organs, the fruit and the seed publications were made by: CHATIN (1870; anther); GUÉGUEN (1901; style); ARTOPOEUS (1903; anther and embryo-sac); PELTRISOT (1904; embryo-sac and seed-grain); SAMUELSSON (1913; embryo-sac and anther); NETOLITZKY (1926; seed-grain; survey of the literature) and HAGERUP (1928; chromosomes and fruit-structure).

The biology of the spreading is a.o. dealt with by: WARMING (1904); RIKLI (1916); RIDLEY (1930) and NORDHAGEN (1937/38).

Besides, a fairly comprehensive survey of the life-history, with numerous references to literature, is given in: KIRCHNER, LÖW and SCHRÖTER (1923). More specialised physiological-ecological investigations on our plant were made by TANSLEY (1922); STOCKER (1923); WALTER (1928); FIRBAS (1931); SEYBOLD (1929) and SCHRATZ (1932), chiefly on the water economy, the osmotic values having been studied by THREN (1934); GIROUX (1936) and CARTELLIERI (1936).

For the rest the metabolism has been little investigated as yet. The most important researches are those of SCHÜLLER (1898) and LIDFORS (1907) on the fluctuating sugar and amylum content in the organs, while also the chemical analyses of LANDER and COMRIE (1936) give some information on the metabolism. On the further ecology work has been done a.o. by HINCHCLIFF and PRIESTLEY (1924; fat metabolism) and RAYNER (1911, 1913, 1921, 1922, 1924, 1925). There are relatively many publications on the symbiosis of Calluna with its endotrophic mycorrhiza. We mention the research-reports of: TERNETZ (1907); RAYNER (1915, 1922, 1927, 1929); CHRISTOPH (1921); KNUDSON (1928) and FREISLEBEN (1933—1935).

The periodicity of the vegetation and fructification was dealt with by HAGERUP (1928) and BEIJERINCK (1937).

Of the formation of adventitious organs mention is only made in the works that occupy themselves with the cultivation of Calluna and other Ericaceae in a vegetative way, such as: WAITZ (1805); REGEL (1843) and JOHNSON (1928).

On the geographical distribution more or less elaborate data can be found in numerous floristic works, so that I restrict myself here to a reference to the bibliography given by BEIJERINCK (1938) in his article on Calluna for HANNIG–WINKLER's "Pflanzenareale". As the most important papers on areas must be considered those by: KÖPPEN (1888); WITTICH (1889); HERDER (1892); MATTFELD (1929) and the just mentioned bibliography.

Concerning Calluna heaths and other vegetations rich in Calluna, data are found in several works on plant-geography, as: WILLKOMM (1896); TANSLEY (1911); WARMING–GRAEBNER (1918); RAUNKIAER (1918); DU RIETZ (1925); ALLORGE (1926); BRAUN BLANQUET (1926); FERNALD (1926); WALTER (1927); MATTFELD (1929); ONNO (1933); LÜDI (1933); NORDHAGEN (1927); SCHIMPER–VON FABER (1935) and TÜXEN (1938).

Finally the significance of Calluna for mankind. On this subject scattered data are found with: KÖPPEN (1888); GRAEBNER (1895); JOHNSON (1928) and the numerous works of a more agricultural and horticultural kind. On the cultivation as an ornamental plant all necessary information is found with: WAITZ (1805); REGEL (1843); PAQUET (1844); MAXWELL (1927) and JOHNSON (1928). For data of a more dendrological kind we may here refer to: DON (1834); LOUDON (1838); KIRCHNER (1911); SCHNEIDER (1912); REHDER (1927); BEAN (1919/33) and others.

Data on the heath-reserves in the various countries can be best gathered from the periodicals and publications which, arranged in order of the countries, are mentioned in: BROUWER's "Organisatie der Natuurbescherming in de verschillende landen" (The organisation of Nature Protection in the various countries) (1931; Americ. Ed., 1938).

As to the present publication it may still be remarked that it is partly founded on personal research, where necessary or desirable supplemented with data from already existing literature. The photos and drawings were for the greater part made after originals by the author; when borrowed, this is indicated (see the explanation of the figures at the end).

I wish here to express my sincere thanks to all who have so cordially assisted me with the present work. They were in the first place the gentlemen: L. G. M. BAAS BECKING, Buitenzorg (Netherlands East Indies); A. H. BLAAUW, Oosterbeek; B. H. DANSER, Groningen; J. JANSEN, Malden; H. J. LAM, Leiden; A. A. PULLE, Utrecht; A. DE WEVER, Nuth, and the ladies: N. KRIJTHE, Wageningen and M. KRIJTHE, the Hague, who have more directly assisted me by word and deed. Besides, several foreign scholars have greatly obliged me by their informations and consignments of material. Among others I mention here the gentlemen: W. ARWIDSSON, Stockholm; W. J. BEAN, Kew; J. BORNMÜLLER, Weimar; J. BRAUN BLANQUET, Montpellier; R. FREISLEBEN, Halle; H. GAMS, Innsbrück; O. HAGERUP, Copenhagen; E. HANNIG, Münster in W.; A. W. HILL, Kew; W. E. TH. INGWERSEN, East Grinstead; K. KRAUSE, Ankara; W. LÜDI, Zürich; R. MAIRE, Algiers; J. MATTFELD, Berlin; R. NORDHAGEN, Bergen, Norway; N. E. SVEDELIUS, Upsala; W. T. SWINGLE, Washington; F. WIŚNIEWSKI, Warschau; and the ladies: M. C. JONES-RAYNER, London and L. P. SERGIEVSKAJA, Tomsk. I feel also greatly obliged to Mr. H. LOOSJES for his assistance in collecting the literature and to the translater.

I. STRUCTURE.

A. General Features.

1. THE HABIT AND ORGANISATION.

The usual appearance of Scotch heather is that of a richly ramified, microphyllous dwarf-shrub, mostly of irregular shape and from a foot to over a meter high. In exceptional cases, under favourable circumstances, the shrubs attain a height of 1.5 to over 2 meters. The longest specimens I came across in the Netherlands had a height of 1.75—1.85 m. In the oldest specimens the stems had diameters of over 20 mm and showed at least 20 annual rings.

If it stands free the seedling first develops into a more or less regular spruce-like shape (Pl. I). This shape is the result of the monopodial, rigorously decussate mode of ramification, often showing the most strongly developed side-shoots along the vertical main axis on the basal part. The lateral shoots, inserted on the main axis at angles between 30 and 90°, generally of ± 45°, raise themselves in their further development and the strongest may become as long as the main shoot. Older plants in a cramped position may, by dropping frame-branches, assume a dwarf-tree shape, where a stem, frame-branches and a crown with leafed twigs can be distinguished (see Pl. II).

If the individuals develop freely and unhampered, the natural shape of the plants is more or less hemispherical (Pl. XXIII), but the habit depends very much on the factors of the environment, as illumination, wind-action, drought, etc. Plants that have grown up in the shade of trees are more slender, those that grew in the full sun on open sandy plains or on rocks are more thick-set and cushion-like, which is also the result of animal voracity or exposure to storms.

The ability to form side-shoots on the annual shoot is strongly developed with Calluna. During the same growing-season branches of the 2d and 3d order and in rare cases even of the 4th order may develop on the annual shoot. (Pl. III, 2). Either long-shoots are formed, in which the internodes may attain a length of one to several times that of a leaf, or short-shoots in which the internodes are equal to or shorter than the leaves. Also intermediate shoots, in which the internodes are only little longer than the leaves, occur, especially if the development took place in the shade or in dim light. The lateral shoots of the 2d order may likewise have the character of long-shoots.

The long-shoots are as a rule formed from the hibernating short-shoots with robust terminal buds. These short-shoots stand on the base and on the top part of the hibernated long-shoot, which in its middle part produces the flower-bearing twigs, even if these short-shoots are in their turn ramified.

These flower-bearing twigs usually die within a year, like the long-shoot leaves, from whose axils they sprout, so that a portion of the stem is left bare as a frame-branch.

The most vigorous long-shoots usually develop close together from the top part of the hibernated long-shoots, the result being a storeyed growth, as shown in Fig. 1. Thus, if the development is not disturbed, a foliage zone of increasing density is formed, under which, by the dying off of twigs and leaves, a blank bundle of branches will exist. Weak frame branches also die off when the foliage roof becomes denser, and at last the aged plant has in its lower parts smooth frame branches. This, as we have seen, is especially the case when the individuals stand crowded. When the position of the individuals is sufficiently free, the dwarf-shrub shape may be long retained, as the frame-branches will sag and diverge, thereby causing the more or less hemispherical shape.

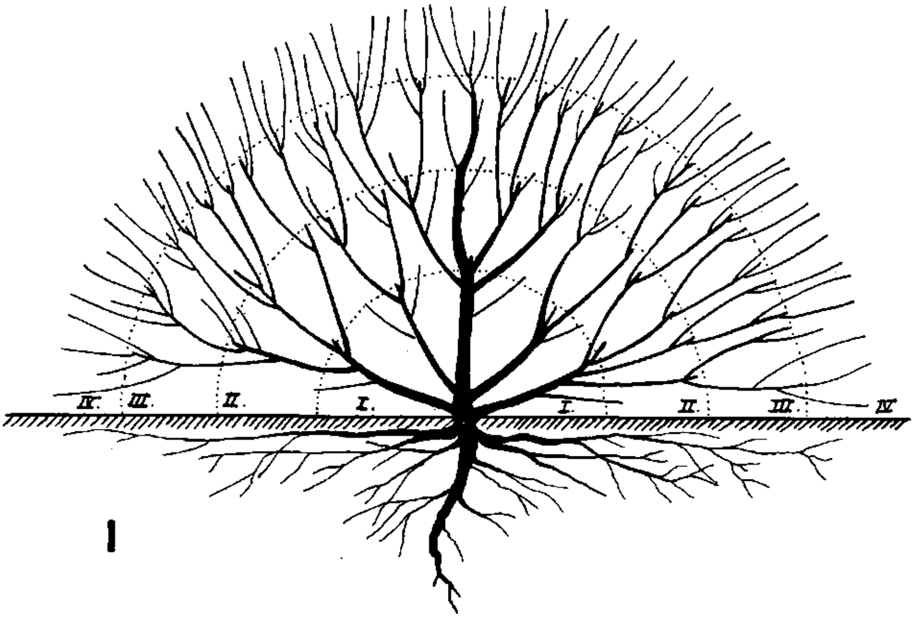

Fig. 1.

Long-shoots may, when opportunity offers, also form at other than the normal points, e.g. where the upper part of the plant has been curtailed or has died off. Even from perennial frame-branches adventitious shoots may develop. Young plants, temporarily injured by frost, often develop a large number of shoots on the root-base, producing in this way a thick, bushy growth.

As will be seen when the abnormities are discussed, still other deviations in habit may occur than the above mentioned more normal ones.

The branch-formation, like the leaf- and flower-formation, is characterised by fineness and numerousness, i.e. the organs themselves are small, but their number on a single individual is large. So the total surface of the assimilating leaves is fairly considerable. In order to obtain an estimate, the robust plant represented in Pl. II, with a height of about 1 meter, was treated in the following way. After having been air-dried the whole plant, including the main roots, was weighed. Then the flowers were carefully stripped and after these the densely leafed short-shoots (assimilation-shoots).

The whole plant weighed air-dry : 261 grams, of which:
branches and roots together : 200 grams;
the leaf-twigs + leaves : 47.5 ,,
the flowers + twigs : 14 ,,

For an approximate determination of the number of leaves and flowers on this plant, the parcels of foliage and flowers were thoroughly mixed and small portions of the mixture were accurately weighed, after which the leaves and flowers of these weighed portions were counted, so that their total numbers could be estimated. The number of flowers amounted to about 7900 and that of the leaflets to about 400.000. Putting the surface of a leaf at 3 mm^2, the total leaf-surface of this plant works out at about 1.2 m^2. The number of seeds, produced by it, may be estimated at 7900 × 20 or about 158.000, i.e. per m^2 (5 plants) at about 800.000 seeds. NORDHAGEN (1937) calculated for Bergen in Norway about 1.000.000 seeds per m^2.

These big numbers of organs are characteristic for the ericoid type, of which Calluna is, also in other respects, a particularly fine representative.

Besides the ordinary assimilating leaves on the short-shoots somewhat differently shaped stem-leaves appear on the long-shoots, while also prophylls and bracts are present. Cotyledons, primary and following-leaves of the seedling form a transition to the ordinary leaves, while the so-called intermediate leaves show a series of forms, merging into the bracts. The bracts in their turn may by an elongate shape and by their colour form transitional stages to the sepals and these again to the petals (Fig. 24). So Calluna presents a continuous series of leaf-forms from the cotyledons to the ovary. The organisation of the flowers is normal and complete, all whorls are present. The flowers are hermaphroditical, obdiplostemonous, sometimes obdiplosepalous (NORDHAGEN, 1937), protandrous, feebly zygomorphous and characterised by a corolla-shaped, coloured, large, loose-leafed calyx and a dehiscent quadrilocular septifragal capsule with fixed septa and basally attached carpels. The seed-box is many-seeded and may contain as many as 28 seeds; with good fertilisation the average number is no more than 20 seeds per capsule, however.

Root-hairs are entirely lacking, while the hair-root system may be uncommonly extensive and finely ramified under certain conditions, as when the plant lives in oligotrophic moss-peat or on barren sand. On the other hand this root-system may be much smaller in extent on a more nutritive soil. Organisation and habit are in so far related that the latter is strongly dependent on the mode of ramification, namely on the formation and distribution of the long- and short-shoots over the corm, therefore on their number and length, but also on their direction and place of insertion. Then the length of the floral zone on the long-shoots has a great influence on the habit, since this zone as a rule no longer furnishes any new long-shoots worth mentioning. And this is exactly the cause of the storeyed growth (Fig. 1), at any rate in normal cases. When the flower-formation remains restricted to a few scattered flowers, this may also bring about a different habit.

Finally, the constitution of the frame-branches affects the habit. If for instance the young frame-branches are thin and limp, so that they will easily bend over by their own weight, quite a different habit will result than with thick and stiff frame-branches, that will keep straight. (Compare e.g. Pl. XI with Pl. VIII, 1).

2. THE CHEMICAL COMPOSITION.

The chemical composition of the cormus of a species depends on: 1. individual differences; 2. the environment, where it grew; 3. the age of the individuals and 4. the time at which the material was collected and examined. The recent analyses of LANDER and COMRIE (1936, l.c. p. 48 ff) give with regard to Calluna a good illustration so far as the differences by age are concerned and those with material collected and examined at different times (see tables I and II), while the analyses of WOLFF and RÖTHE, published by VON LINSTROW (1929, l.c. p. 69) show the difference in the ash-constituents of Calluna with plants from different soils (table III). So there remains the first point, the individual differences. This must be conceived as a fluctuation round a certain average and need not be considered here, so far as for analysis mixtures of several individuals were used, yielding concordant values (see e.g. table I).

In table I plants, obtained from various localities in England and belonging to definite age-groups, have been analysed separately. It appears that the percentages of nitrogen, ash (without SiO_2), lime and phosphorus diminish with advancing age, whereas the percentages of oils and fats (ether extract) and crude fibre increase.

The differences occurring when the material is collected at different times (seasons) are seen from the data of table II. Here the nitrogen percentage is in general lower towards the winter, like the ash content (SiO_2-free). On the other hand the crude fibre content then increases, which is a well-known phenomenon with woody plants.

The average composition of 63 specimens of Calluna is stated by the same investigators as:

	N	Ether extract	Crude fibre	SiO_2 free ash	CaO	P_2O_5
Average	1.29	2.73	25.18	2.13	0.54	0.20
Limits	0.84—2.11	1.41—4.51	18.36—32.19	1.28—3.55	0.38—0.87	0.10—0.41

From these figures one can gather that the fluctuations in the percentages of the various substances may be considerable.

TABLE I.

Influence of age on the composition of Calluna according to LANDER and COMRIE (1936). (In % of the dry mass).

Locality	Age	N	Ether extract	Crude fibre	SiO_2-free ash	CaO	P_2O_5
Bedshiel	seedling	1.35	2.94	20.17	2.31	0.73	0.20
id.	young plant	1.11	3.28	21.51	1.94	0.64	0.15
id.	nesting	0.98	3.38	24.62	1.90	0.60	0.13
id.	old	1.06	3.22	26.08	1.84	0.47	0.13
Hexpath	seedling	1.75	2.09	21.21	2.71	0.76	0.30
id.	young plant	1.26	3.06	22.94	2.01	0.69	0.21
id.	nesting	1.08	3.09	26.39	2.01	0.50	0.15
id.	old	1.08	3.22	28.01	1.69	0.46	0.15
Kettleshiel	1 year	1.70	2.05	21.38	2.54	0.56	0.31
id.	3 years	1.52	2.52	22.11	2.33	0.54	0.26
id.	6 years	1.30	2.73	22.76	2.17	0.57	0.21
id.	10 years	1.26	3.37	25.73	2.09	0.53	0.21
E. Lednathie	young	1.41	2.60	23.15	2.33	0.55	0.23
id	3—5 years	1.26	2.74	25.44	2.17	0.48	0.24
id.	6—10 years	1.26	2.31	25.61	2.26	0.49	0.20
id.	over 10 years	1.24	2.42	26.94	2.05	0.46	0.21
Berryhill	3—4 years	1.34	2.64	27.78	2.38	0.45	0.25
id.	7—8 years	1.18	2.56	25.42	2.20	0.48	0.18
id.	old	1.37	2.71	27.04	2.17	0.42	0.16

Table III shows how very different the composition of the ash can be with plants from different soils. It should be borne in mind, however, that the numbers in the vertical columns cannot be directly compared, since only percentages of the total ash content are given, which fluctuates, so that only the mutual ratios of the numbers in the horizontal rows are significant.

TABLE II.

Influence of the time of collecting on the composition of Calluna according to LANDER and COMRIE (1936). (In $^0/_0$ of the dry mass).

Locality	Date of collecting	N	Ether extract	Crude fibre	SiO_2-free ash	CaO	P_2O_5
Bedshiel	21.6 .'33	1.36	2.31	22.12	2.01	0.63	0.23
id.	26.7 .'33	1.10	3.31	24.33	1.88	0.51	0.14
id.	30.9 .'33	1.05	3.86	23.41	2.28	0.68	0.12
id.	12.1 .'34	0.99	3.20	23.31	1.81	0.60	0.13
Hexpath	21.6 .'33	1.41	2.30	23.29	2.44	0.62	0.22
id.	26.7 .'33	1.44	3.03	27.34	2.00	0.52	0.26
id.	26.9 .'33	1.27	2.54	23.55	2.45	0.69	0.19
id.	12.1 .'34	1.05	3.71	26.19	1.53	0.59	0.14
Kettleshiel	27.6 .'33	1.69	2.62	21.10	2.54	0.57	0.30
id.	16.8 .'34	1.28	2.70	25.60	—	0.54	0.24
id.	12.10.'34	1.37	2.93	22.29	2.02	0.54	0.22
E. Lednathie	7.7 .'32	1.35	2.20	22.44	2.44	0.47	0.17
id.	18.8 .'32	1.23	1.77	26.54	2.24	0.46	0.22
id.	1.11.'32	1.16	2.53	27.31	2.01	0.51	0.24
id.	6.7 .'33	1.39	2.52	23.98	2.34	0.50	0.22
id.	30.8 .'33	1.26	3.17	26.23	1.96	0.45	0.23
Berryhill	28.6 .'32	1.49	1.65	26.08	2.51	0.46	0.22
id.	19.11.'32	1.12	1.84	30.92	1.75	0.51	0.19
id.	14.9 .'33	1.10	3.62	27.41	1.99	0.44	0.17

TABLE III.

Influence of the soil on the composition of the ash of Calluna according to E. WOLFF and L. F. RÖTHE, in v. Linstrow (1929). (In $^0/_0$ of total ash).

Soil	K_2O	Na_2O	CaO	MgO	Fe_2O_3	P_2O_5	SO_3	SiO_2	Cl
Dolomite	4.81	10.23	26.49	8.39	2 71	0.61	5.22	29.78	4.86
id.	2.71	11.93	12.97	10.39	12.77	0.60	2.29	45.81	0.51
Lias sandstone	6.42	5.41	33.48	8.03	2.02	4.01	1.44	32.72	1.83
id.	29.58		15.56	6.67	1.54	5.30	1.03	30.94	4.10
Clay soil	10.65	0.86	12.02	6.70	4.95	10.89	1.73	48.08	—

The water content also is subject to very large fluctuations and is in general smallest during dry and cold periods. An extreme case is mentioned by THREN (1934, l.c. p. 493). He writes: "Auf die lang andauernde Kälte im Februar reagierte Calluna wieder ebenso stark wie schon in Dezember. Proben von Sprossen, die nicht unter Schneeschutz waren, erreichten 37.6 Atm. 1)). Die Blätter dieser Proben waren noch durchaus grün, bzw. an stark lichtexponierten Stellen von Anthocyan stark rot gefärbt. Aus einer Probe vom 1. März war kein Preszsaft mehr zu gewinnen; in der Folgezeit waren dann alle Kurztriebe, die nicht längere Zeit unter Schneeschutz gewesen waren, tot". (On the prolonged cold in February Calluna reacted again as strongly as it did in December. Specimens of shoots that were not protected by snow, reached 37.6 atm. 1)). The leaves of these specimens were still entirely green, where much exposed to light also highly red by anthocyanin. Out of a specimen of March the first no sap could be squeezed; after this all the short-shoots that had not been for a long time under snow-cover, were dead.) Personally I weighed three Calluna plants, about 0.5 meter high, during dry winter-weather in February. The fresh-weight was for the three plants together: 310 grams; air-dried at 98° C: 190 grams, so that the loss of water amounted to only 120 grams or about 40 %. 15.56 grams of fresh Calluna wood then weighed air-dry 9.6 grams. So here the loss of water was about 60 %, or 1.5 times as much as with the whole cormus (with the main roots). See also table IV, showing the sclerophytic character of Calluna.

The total ash content of Calluna ranges from 3.2 to 6.3 % and the ash itself contains up to 48 % SiO_2.

As characteristic substances of Calluna WEHMER (1931, l.c. 2, p. 913) mentions:

in the stem: arbutin, fumaric acid, citric acid, tannic acid, callutanic

TABLE IV.

Survey of the water percentage of the assimilating organs with plants from peat-soils (after FIRBAS, 1931); and some further ecological plant types (after STOCKER and FIRBAS, ibid.).

Species:	Water content in % of the fresh weight	Water content in % of the dry substance.
Empetrum nigrum	46.7 (45.6—53.6)	88
Vaccinium uliginosum	52.4 (48.7—58.2)	110
Vaccinium oxycoccus	52.7 (48.4—55.3)	111
Calluna vulgaris	54.1 (49.7—59.2)	118
Eriophorum vaginatum	55.2 (51.3—59.2)	121
Carex limosa	55.7 (54.6—58.7)	125
Andromeda polifolia	57.0 (55.2—59.8)	133
Eriophorum angustifolium	63.4 (63.1—63.7)	173
Scheuchzeria palustris	67.3 (66.7—68.3)	205
Drosera rotundifolia	81.3 (77.0—88.4)	434

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1) Osmotic value of the press-juice.

TABLE IV (*Continued*).

	in % of the fresh weight		in % of the fresh weight
Viola palustris	79.5	*Viola odorata*	81
Caltha palustris	76.8	*Hieracium umbellatum*	79
Spiraea ulmaria	67.2	*Galium mollugo*	78
Comarum palustre	72.3	*Helichrysum arenaria*	67
Menyanthes trifoliata	80.6	*Corynephorus canescens*	56
Anemone nemorosa	80	*Elymus arenarius*	74
Senecio vulgaris	88	*Ammophila arenaria*	72
Arnica montana	87	*Calamagrostis epigeia*	70
Molinia coerulea	72	*Calluna vulgaris*	55
Aegopodium podagraria	83	*Erica tetralix*	55

acid, quercetin, catechintannin, inulin, ericolin, pentosanes, while in the literature we still meet for the cormus without roots: cutin, quercetin, myricitrin, catechintannin, carotin, resin, fatty oils, pentosanes, amylum, Ca-oxalate, albumins, gums and the enzyme arbutase.

According to KEEGAN (1916, l.c. I, p. 218) Calluna contains: cutin, fatty oils, carotin, some resin, much quercetin, myricitrin, catechintannin (with strong dyeing properties), amylum, Ca-oxalate, pentosanes and gums.

In the Botanical Laboratory at Leiden a number of chiefly microchemical reactions were performed by Miss. M. KRIJTHE in order to obtain some information on the localisation of the more specific substances in the Calluna plant. Her results were the following:

albumin: in the bark and the medullary-ray parenchyma;

fat and suberin: in the wood parenchyma and the medullary-ray cells, the cuticles and the cell-walls of the endoderm;

glycose: in the epiderm, the endoderm, the bark-cells and the medullary-ray cells;

amylum: in the wood parenchyma and the medullary-ray cells;

inulin: in the whole xylem;

tannic acid: in the epiderm, the endoderm, the bark, the periderm, the medullary-rays and the wood-parenchyma;

resin: in the subepiderm;

urson: mainly in the leaves, little in the stem.

On the presence of the following substances no certainty could be obtained: callutanic acid (= quercetin), arbutin and andromedotoxin.

Arbutin, however, ($C_{12}H_{16}O_7$, hydrochinoneglucoside) I could detect indirectly by the method, indicated by TUNMANN, by microsublimation of hydrochinone from dried and pulverised Calluna leaves, collected in October. Small hexagonal prisms and still smaller monoclinic scales crystallised out.

The seeds contain in their endosperm much aleurone and oils.

Gums occur between the cell-wall lamellae of the leaf-epiderm.

Finally BRAUN (1933) a.o. mention oxalate sphaerites, measuring 10—14 μ, in the vicinity of the vascular bundles of the leaves. I have sometimes observed these sphaerites in winter material, without settling their composition. It is possible that here citrates are present instead of oxalates, as has been pointed out by WEHMER (1892, l.c. p. 333).

The wood is characterised by a high percentage of ash and especially of silicic acid (see above). The younger wood has a light green colour, while the nuclear wood of older stems is yellowish to light brown. The light sea-green colouring substance of the Calluna wood slowly disappears when the splitting-plane is exposed to the air and then turns yellow to light brown. The wood has a weak sweetish taste and little smell. Tannin and arbutin and maybe other substances probably prevent the ligno-celluloses from being attacked by wood-fungi and insects, which are not or seldom found in the wood of the living plants. On the content of pectins, hemicelluloses and pentosanes I have no further information.

3. ABNORMITIES.

The great fixity of form within the species is very striking when plants from the most distant corners of the area of distribution are compared, e.g. specimens from Iceland, Lapland, Morocco, Thracia, West Siberia, Spain, Scotland, North America and Central Europe. With normal material it is then not or hardly possible to discover important outward deviations, that might justify the introduction of definite geographical species. On the other hand, especially from Central Europe, a large number of more or less rare deviations from the normal type have become known, which can be united by the word "abnormities", leaving undecided whether they are mutations or modifications, hybrids or monstrosities. These forms, distinctly deviating in size, shape, colour, position, direction, structure and periodicity of the organ-groups, organs or parts of organs, are for the greater part somatically fixed and preserve their characteristics with vegetative reproduction of the plants. In 1937 BEIJERINCK (l.c. p. 445 ff.) gave a survey of these irregularities. It is sufficient here to discuss the just mentioned categories and to give some examples, since a further description and the survey of the forms will be given later on in this paper.

a. *Deviations in the size of the organs.*

Forms with large and small flowers as well as with large and small leaves have become known. The latter mostly bear normal flowers, although a single case has become known where both the flowers and the leaves were small. To this category belong: fa. *grandiflora* mihi, fa. *parviflora* mihi (Pl. VI), fa. *microphylla* mihi (Fig. 2a and b). If the annual shoots are short, so-called dwarf-forms arise (fa. *nana* Kirchner, with the subf. *compacta* (hort.) mihi (Pl. IX, 2). Besides white-flowered and hairy dwarf-forms occur (fa. *pumila* (hort.) mihi and fa. *compressa* mihi). This combined occurrence of several deviations in the same individual is common also with other characteristics.

b. *Deviations in form (polymorphism proper).*

Here the following categories may be distinguished:

1. deviations in the ramification, as with the fa. *decumbens* (Don) mihi (Pl. IX, 1), where the branches are bent down or spread flat, so that the plant shows a cushion-like or drooping habit. The extreme case of the latter is the subfa. *pendula* mihi. When a fa. *decumbens* has at the same time fasciated stalks, it is the subfa. *fasciata* mihi (Pl. IV, 4). The fasciated stalks have a breadth of over 1 cm and are broadened fan-like towards the top.

Further deviations from the normal mode of ramification are the forms:

patula mihi, with widely diverging frame branches (Pl. VIII);

erecta mihi, with steeply erect, closely parallel frame branches;

condensata (Lamt.) mihi, with short, crowded frame branches;

minima (hort.) mihi, with numerous short, vertical frame branches, standing close together, which are limp and easily lie down, after which they will strike new roots and so will present a sod-like habit;

rigida (hort.) mihi, with stiff, thick branches, spreading flat, the result being a broad growth (Pl. X);

elegantissima (Sennen) mihi, with very long, graceful flowering-shoots and a long flowering-zone. At the same time late-flowering (Nov.—Dec.).

2. deviations in the hair of the foliage leaves.

Various forms, provided with more or less hairy foliage leaves, may be united in the variety *hirsuta* Gray (Pl. XXII). The strongly haired, white to grey, felty forms, a.o. from Scotland, England, the Channel Isles and SW France, belong to the fa. *typica* mihi, while short-haired forms, carrying a more or less greyish-green foliage, are indicated as fa. *pilosa* (hort.) mihi. These latter are at the same time white-flowered. A yellow-leafed, white-flowering and feebly haired form is the fa. *lutescens* mihi, while a thick-set form (fa. *compressa* mihi) has already been mentioned. Finally there occur forms with white, dark, pale and double flowers, resp. fa. *albiflora* mihi, *Alporti* (hort.) mihi, *pallens* mihi and *Bealeae* mihi (Pl. XVIII).

3. deviations in the shape of the flowers, with the fa. *campanulata* mihi, where the corolla has relatively shallow incisions and remains closed, while the calyx opens in the normal way; the fa. *brachysepala* J. Jansen, with the subf. *curtisepala* mihi, where the calyx slips are shorter or even considerably shorter than the corolla; the fa. *clistanthes* J. Jansen, where the flower either remains closed or opens just enough to let the stigma free (subf. *ferax* mihi).

c. *Deviations in the number of the organs or their parts.*

Certain organs may be increased, decreased or entirely lacking. We may distinguish:

1. deviations in the number of the foliage leaves on the flower-twigs. Typical is: 2 prophylls + 4 bracts. With the fa.

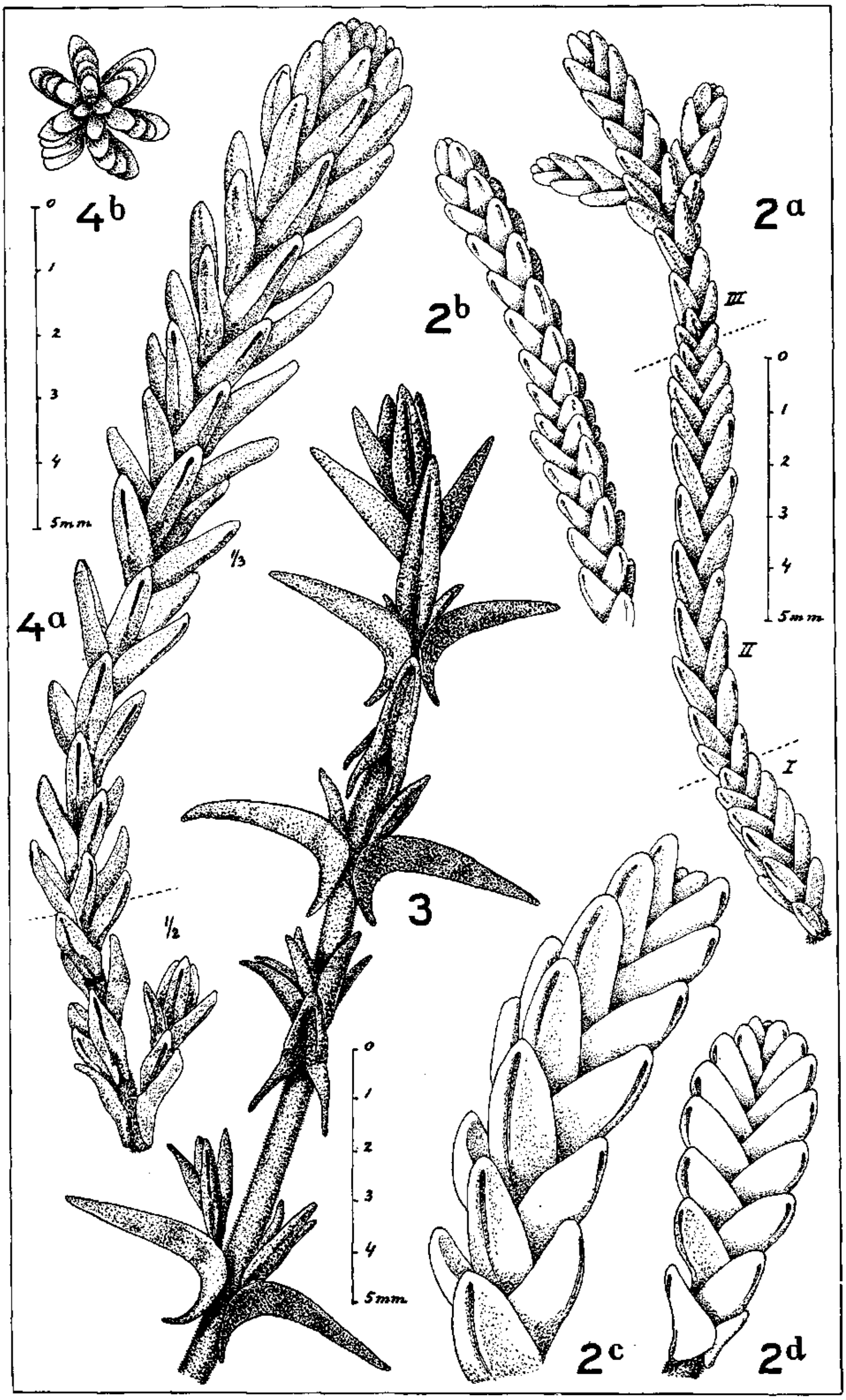


Fig. 2—4.

terminalis J. Jansen the flowers stand at the end of richly leafed short-shoots, bracts being generally absent. I did not observe a total lack of foliage leaves on the flower-twig, neither did NORDHAGEN.

2. deviations in the number of the bracts, preceding the flower. Ordinarily this number is 4 to 12. When more than 12, up to 64 bracts are present, and perhaps still more bracts and transitional or intermediate leaves (Zwischenblätter in NORDHAGEN's sense) which then generally form tight packets, one has to do with the fa. *multibracteata* J. Jansen, of which again several subforms may be distinguished, characterised by the existence of a spiral arrangement of the intermediate leaves (subf. *torta* J. Jansen), the absence of flowers, so that only packets of bracts are formed (subf. *deflorata* J. Jansen), or pentamerous, filled flowers, late flowering, a spread out or steeply erect habit (resp.: subf. *pentamera* J. Jansen, *multiplex* mihi, *serotina* mihi, *extensa* mihi, and *recta* mihi). To this category also belong:

3. deviations in the number of the flower-parts.

When it is only or mainly the sepals which have increased in number, the result being filled, stiff organs, as in everlastings, one has to do with the fa. *polysepala* J. Jansen, when the corolla tips only have been increased with the fa. *polypetala* mihi, while increase in both calyx and corolla is found with the fa. *plena* mihi. Moreover these three forms have still various subforms, mentioned in the subsequent survey; as the names sufficiently indicate the deviation, no further comment is wanted. Plants whose flowers remain closed or open only slightly, while the calyx is doubled and the corolla and stamens are lacking, may be classed with the fa. *diplocalyx* J. Jansen, of which again several subforms are mentioned in the subsequent survey. Finally there occur plants with irregularly deformed flowers, in which one often finds many styles, a larger or smaller number of stamens, more or fewer petal and sepal tips. These may be combined as a fa. *monstrosa* mihi.

With the fa. *gynodioica* mihi on the other hand, the stamens are always lacking, the flowers being otherwise well developed, so that the plants are in fact female. The flowers do not expand quite so far as normal flowers do. A subf. *simplicissima* mihi of this form shows flowers with nothing but four sepals and the female sexual-organs.

4. increase or decrease of the number of flowers leads to the distinction of forms with a particularly rich or a very poor or entirely lacking bloom. (fa. *pauciflora* mihi).

d. *Deviations in the colour of the foliage and flowers, as well as variegation.*

1. deviations in the colour of the foliage occur with the forms: *aurea* (Don) mihi, *cuprea* (hort.) mihi, *incana* mihi and *argentea* (hort.) mihi (Fig. 5), where during the spring the foliage is coloured resp. yellow to golden yellow, red to copper-colour, greyish-green and whitish.

During the summer the tint is more greenish, while during the winter more reddish shades appear with *aurea* and *cuprea*. Besides the fa. *aurea* has still two subforms, the one with twigs that are here and there yellow-leafed, the other with short-shoots with partly yellow leaves (subfa. *aureovariegata* mihi and subfa. *chlorostachys* (J. Jansen) mihi.

2. variegated leaves are found, especially during the early months of the year, with the forms: *variegata* (Regel) mihi with the subfa. *roseovariegata* mihi, spotted resp. white and pink, and the fa. *rhodostachys* mihi, where the youngest leaves are red, the somewhat older ones white and the old ones green, which causes a peculiar multi-coloured effect.

3. deviations in the colour of the flowers there are many; only the principal ones will be mentioned here. These are: fa. *alba* (Don) Braun Blanquet with the subfae.: *erythrostyla* mihi, *aureifolia* mihi, *pumila* (hort.) mihi, *Serlei* (hort.) mihi and *Hammondi* (hort.) mihi, *alboviolacea* mihi, *albopurpurea* mihi and *purpurea* (Don) Braun Blanquet. Besides plants occur, although rarely, with a single branch, carrying flowers of a deviating colour (fa. *bicolor* mihi) or with several colours, by having coloured sectors, as with the fa. *multicolor* mihi.

e. *Deviations in the position of the organs,* among which are to be reckoned:

the plants with a more or less *actinomorphous terminal flower* (top-flower) on the annual shoot, instead of the there normally found assimilation-shoots. Besides, it happens as a very rare exception that *assimilation-shoots of the 4th order* (Pl. III, 2) are formed in one and the same season. Also instead of flower-twigs *small assimilation-shoots* may be regularly formed, as happens with some pauciflorous forms, or the phyllotaxis may change (Fig. 4). In spring certain plants may show phenomena of *prolification,* sometimes coloured calyx- or corolla-like organs are formed first, after which the axis grows on as an ordinary leafed twig (Fig. 6), or, as with the multibracteate forms, new intermediate leaves or packets of bracts develop in spring instead of flowers (Fig. 9). Whether these phenomena, which only appear in places, are also somaticaly fixed, is doubtful.

f. *Deviations in the direction of the organs.*

Partly these have been already mentioned with the deviations in ramification (sub b). Besides, the lateral position of the flowers may be more drooping, as with the fa. *elegantissima* (Sennen) mihi, or more erect, as with the fa. *stricta* mihi. The as a rule adjacent leaves on the short-shoots, which overlap like tiles, may under certain circumstances (a very moist atmosphere) begin to diverge laterally, and at the same time become longer; this is in most cases accompanied by an elongation of the internodes (Fig. 3). Yet there are forms, like *Serlei* (hort.) mihi, where a distant foliage is the rule, also under circumstances when the other forms show a regular foliage. One might speak here of a squarrose foliage. In a few

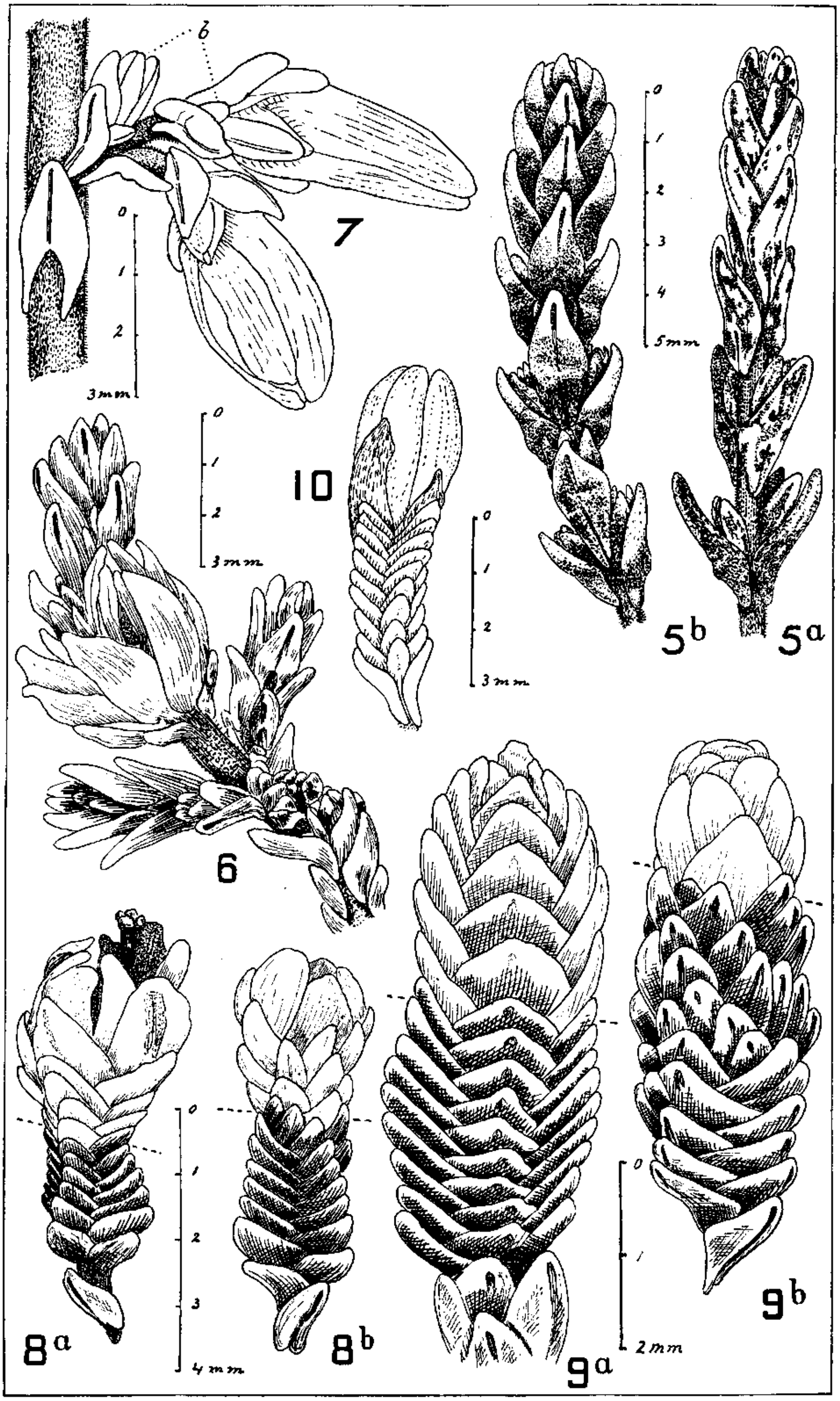

b
7
0
1
2
3 mm
0
1
2
3
4
5 mm
5b
5a
0
1
2
3 mm
10
0
1
2
3 mm
6
0
1
2
3
4 mm
8a
8b
9a
0
1
2 mm
9b

Fig. 5—10.

instances one meets twigs which, instead of a decussate phyllotaxis with pairs of oppositely placed leaves, have *whorls of three leaves*, alternating with each other, so that it seems as if 6 rows of leaves are inserted along the stem (Fig. 4). I also observed this on plants where at the same time the twigs were fasciated.

g. *Deviations in the periodicity.*

Under this heading fall the early and late-flowering forms, resp. fa. *praecox* mihi with the decumbent subfa. *tenuis* (hort.) mihi, which already at the end of June or in the beginning of July open their first flowers, and the fa. *hiemalis* (hort.) mihi, which does not start flowering until half October and continues to flower until stopped by the frost, sometimes as late as the end of December. A little less late-flowering is the fa. *autumnalis* (hort.) mihi. Among the multibracteate forms and those with filled flowers and double calyces likewise very late-flowering subforms occur, while in one case on a multibracteate form which before the winter had not got into bloom, flowers appeared here and there in the spring on the packets of bracts that had been formed in the preceding year. It has already been remarked that the South European form *elegantissima* is likewise a very late-flowering form, also in this country. In the far North (Iceland, Lapland) it seems that, on account of the short season, *Calluna* does not attain bloom for many years in succession. Flowering years have there become exceptions. How such plants behave in our latitude I do not know.

To the temporary deviations, caused by circumstances, still belong: the transient red colour of the foliage; the deformations in the wood and the foliage, caused among other things by wood mites (acc. to DOCTERS VAN LEEUWEN); the cushion-shaped or decumbent habit, caused by the nibbling of rabbits and sheep; the bluish-green colour of the foliage, caused by renewed sprouting on the burnt down heather stubble; small-floweredness, caused by drought during the development of the buds; the morbid variegation of the leaves, of which the cause is unknown to me. By etiolation the colour of the flowers may fade almost to white, so that they will resemble the fa. *bicolor*. It is not certain whether the sometimes frequent occurrence of terminal flowers on the long-shoots of a plant must be classed with the somatically fixed or the temporary deviations.

4. RELATIONAL CHARACTERISTICS.

Although it has been pretty difficult, as one will gather from the following brief historical survey, to obtain a classification based on relationship, of the forms within the larger family-group of the *Bicornes* (Ericales), it proved still more difficult to trace the closer relationships between *Calluna* and the other *Ericaceae* within the *Ericaceae-Ericoideae*, among which also the genera *Erica* and *Calluna* are classed, as the monotypical genus *Calluna* shows considerably deviating characteristics, either entirely disconnected or only found again in otherwise rather distant forms.

In an extensive investigation NORDHAGEN (1937/38) has recently, first morphologically and then phylogenetically, analysed the correlations of Calluna within the *Ericoideae* and the *Ericaceae*. In the main his views will be followed here, since his work must be judged the best we now possess in this field.

LINNÉ, in his Philosophia Botanica (1751), already pointed out the great mutual affinity of the "*Bicornes*", among which he reckoned the genera: *Ledum, Azalea, Rhododendron, Andromeda, Clethra, Erica, Blairia, Myrsine, Memecylum, Santalum, Vaccinium, Arbutus, Royena, Diospyros, Melastoma* and *Pyrola*.

A. L. DE JUSSIEU (1789) united this group to an order (which was then a group between a genus and a class, properly speaking a family) of the *Ericae*. *Erica* in a narrower sense was one of the 16 genera of LINNÉ, while *Rhododendron*, incorporated by LINNÉ with the *Bicornes*, was now distinguished as the family of the *Rhododendrae* with 7 genera.

A. DE CANDOLLE (Prodromus, 1838) combined 52 genera to the family of the *Ericaceae* (after LINDLEY, 1836). DE JUSSIEU's *Rhododendrae* were also incorporated again.

BENTHAM and HOOKER (Genera Plantarum, 1876) founded the family of the *Ericaceae* as the centre of a group of 5 other families, forming together the "*Ericales*".

O. DRUDE (1889), in ENGLER–PRANTL's first edition, divides the "*Ericales*", as the first series of the *Sympetales*, into the following 6 families:

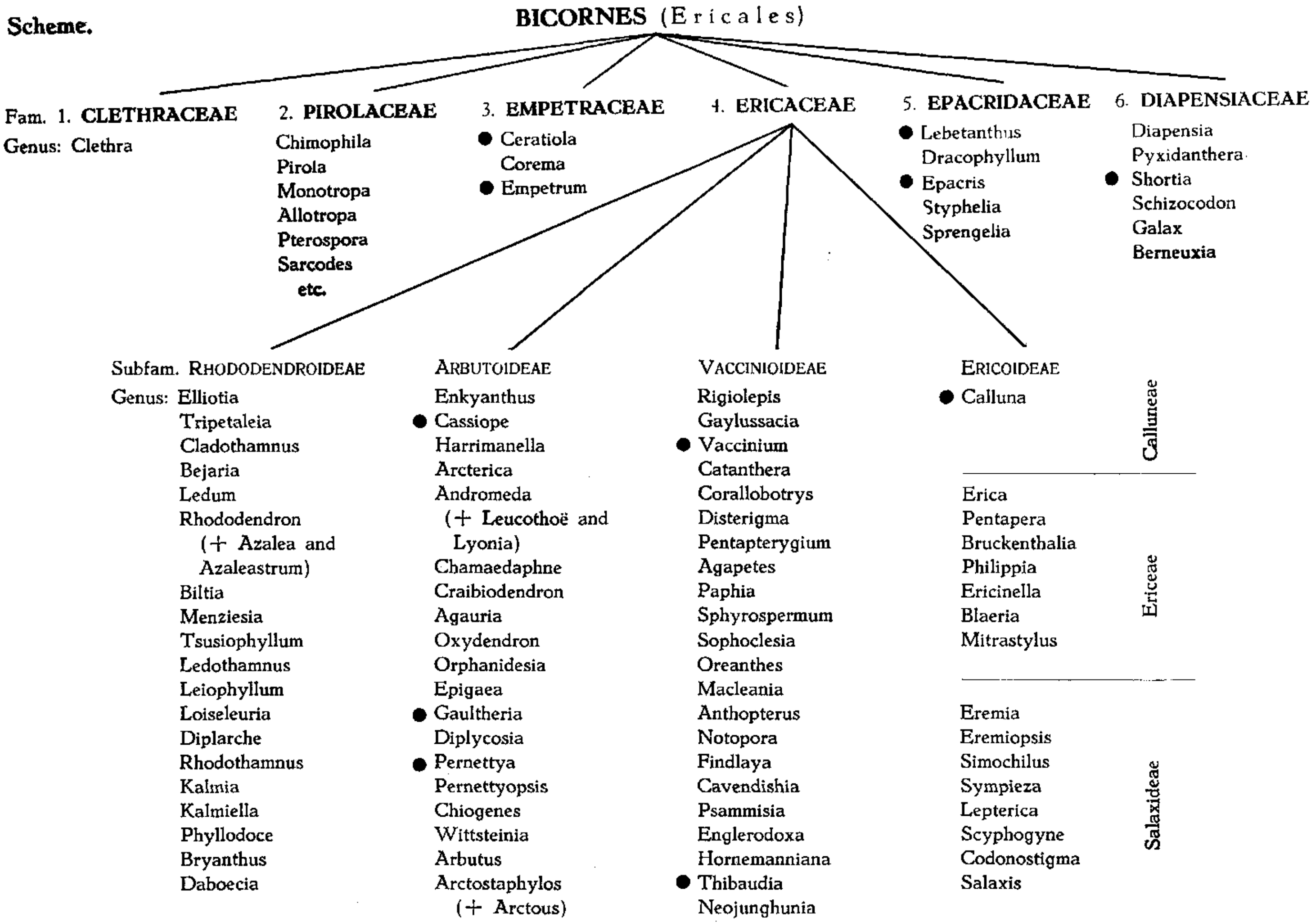
1. *Clethraceae*, 2. *Pirolaceae*, 3. *Lennonaceae*, 4. *Ericaceae*, 5. *Epacridaceae*, and 6. *Diapensiaceae*. The *Lennonaceae* (root parasites) are nowadays classed among the *Tubiflorae* (HALLIER, 1900/01), while the *Empetraceae*, after the elaborate comparative investigations of SAMUELSSON (1913) on the structure of the embryo-sac and some other characteristics with the Bicornes: *Empetraceae* and *Diapensiaceae*, and of HAGERUP (1922; on *Empetrum*) are classed with the *Ericales*, namely between the *Pirolaceae* and the *Ericaceae*. The structure of the style of the *Empetraceae* is closely related to that of *Pirola*, while according to HAGERUP (1922) the flower-diagram agrees with that of certain *Ericaceae*, e.g. *Tripetaleia* Sieb. et Zucc..

The classification of the *Bicornes* is nowadays, at any rate in its main features, that which is represented in the following scheme. (Page 26).

Now, the family of the *Ericaceae* is characterised principally by:

Mostly actinomorphous, sometimes slightly zygomorphous (*Calluna, Rhododendron*) flowers, as a rule 4 to 5-partite (seldom 2, 3, 6 and 7), of which the sepals are either free or coalesced and the bell-, beaker-, jar- or tube-shaped corolla is only very rarely polypetalous (*Ledum*) or widely opened (*Rhododendron*). Anthers are generally present in twice the number of the corolla-tips or petals, free, obdiplostemonous, inserted along the outer edge of a hypogynous or epigynous, nectar-secreting disc.

Scheme.



BICORNES (Ericales)

Fam. 1. **CLETHRACEAE**
Genus: Clethra

2. **PIROLACEAE**
Chimophila
Pirola
Monotropa
Allotropa
Pterospora
Sarcodes
etc.

3. **EMPETRACEAE**
● Ceratiola
Corema
● Empetrum

4. **ERICACEAE**

Subfam. RHODODENDROIDEAE
Genus: Elliotia
Tripetaleia
Cladothamnus
Bejaria
Ledum
Rhododendron
(+ Azalea and
Azaleastrum)
Biltia
Menziesia
Tsusiophyllum
Ledothamnus
Leiophyllum
Loiseleuria
Diplarche
Rhodothamnus
Kalmia
Kalmiella
Phyllodoce
Bryanthus
Daboecia

ARBUTOIDEAE
Enkyanthus
● Cassiope
Harrimanella
Arcterica
Andromeda
(+ Leucothoë and
Lyonia)
Chamaedaphne
Craibiodendron
Agauria
Oxydendron
Orphanidesia
Epigaea
● Gaultheria
Diplycosia
● Pernettya
Pernettyopsis
Chiogenes
Wittsteinia
Arbutus
Arctostaphylos
(+ Arctous)

VACCINIOIDEAE
Rigiolepis
Gaylussacia
● Vaccinium
Catanthera
Corallobotrys
Disterigma
Pentapterygium
Agapetes
Paphia
Sphyrospermum
Sophoclesia
Oreanthes
Macleania
Anthopterus
Notopora
Findlaya
Cavendishia
Psammisia
Englerodoxa
Hornemanniana
● Thibaudia
Neojunghunia

ERICOIDEAE
● Calluna
Calluneae

Erica
Pentapera
Bruckenthalia
Philippia
Ericinella
Blaeria
Mitrastylus
Ericeae

Eremia
Eremiopsis
Simochilus
Sympieza
Lepterica
Scyphogyne
Codonostigma
Salaxis
Salaxideae

5. **EPACRIDACEAE**
● Lebetanthus
Dracophyllum
● Epacris
Styphelia
Sprengelia

6. **DIAPENSIACEAE**
Diapensia
Pyxidanthera
● Shortia
Schizocodon
Galax
Berneuxia

The genera, marked with a dot, show species with several intermediate leaves.

The thecae are free, bilocular, the points being often bent asunder, and dehiscent with round to oval pores or along a skew or longitudinal slit. Often with two tail-like appendages on the anthers. Anther-wall without or with a reduced endothecium. Pollen in tetrads. Ovary superior or inferior, with 1—12, usually 4—5 loculi. Placentae central, with one to many anatropic or skew amphitropic seed-originations, with mostly epitropic or heterotropic (apotropic) orientation. Embryo mostly short. Endosperm relatively big. Well-developed endosperm-haustoria. The coalesced styles with club-shaped stigma. Fruit a berry, a capsule or a drupe, containing few seeds. Capsule loculicidal or septicidal and only with Calluna septifragal. (see Fig. 60).

Foliage leaves simple, undivided, leathery, stiff, without stipules. Woody plants, mostly dwarf-shrubs or shrubs, seldom trees (*Arbutus, Erica,* a.o.).

The genus *Calluna,* with only a single species, is within this family distinguished from the other genera by:

1. the structure of the fruit, which is a septifragal many-seeded capsule, the style, placenta and septa forming an indissoluble unit, while the four fruit-valves dehisce from above along the septa and diverge in dry weather; in damp weather the capsule is completely closed again by the movable valve-mechanism.

2. the presence of several so-called "intermediate leaves", generally 4 bracts, but occasionally as many as twelve and in the multibracteate forms up to 64 and perhaps still more, lying between the two prophylls and the outer sepals, on the flower-twig. These intermediate leaves (NORDHAGEN's "Zwischenblätter") may have the character of genuine bracts, but also of the ordinary foliage leaves on the short-shoots and between these any transitions exist. Besides, sepal-like transitional leaflets are often found between the bracts and the outer sepals. Their character is more or less intermediate between these two organs.

3. the number of chromosomes, 8, (also found with *Clethra*) deviates from the fundamental number of the Bicornes, which according to HAGERUP is $n = 6$ (found with *Phyllodoce coerulea* and *Diapensia lapponica*). HAGERUP wants to derive the number 8 from 6. Various higher numbers are found with the Bicornes, as: 12, 24, 36, 48, 13 and 16 (8-series), (see the following table, page 28).

4. the structure of the perianth is in so far remarkable, that the calyx has assumed the outward appearance of the corolla. The sepals are loose, longer than the corolla and persisting, like the smaller, fairly deeply incised bell-shaped corolla, which shrivels up, however, whilst the calyx remains smooth (like straw-scales) and plays a curious part in the biology of the speading of the plant. With Calluna the calyx has, as it were, taken over the function of the corolla as a strewing-organ for the seed; the function of the corolla itself is in this respect less important than with other *Ericeae.*

Survey of the chromosome numbers with a few Bicornes, according to HAGERUP (1928)
(Abbreviations: H = HAGERUP; S = SAMUELSSON; L = LONGLEY)

	n		n
Pyrola grandiflora (H, 1928) . . .	23	*Andromeda polifolia* (H, 1928) . .	24
„ *rotundifolia* (H, 1928) . . .	23	*Cassiope hypnoides* (H, 1928) . .	(?) 24
„ *minor* (H, 1928)	23	*Gaultheria shallon* (H, 1928) . . .	48
Rhododendron lapponicum (H, 1928)	13	*Arctostaphylos diversifolia* (id.) . .	13
Ledum groenlandicum (H, 1928) . .	13	„ *uva ursi* (H, 1928) .	26
Phyllodoce coerulea (H, 1928) . .	6	*Arbutus andrachne* (H, 1928) . . .	13
Kalmia latifolia (H, 1928)	12	„ *canariensis* (H, 1928) . . .	13
Kalmia glauca (H, 1928)	24	*Vaccinium vitis idaea* (H, 1928) . .	12
Loiseleuria procumbens (H, 1928) .	12	„ 3 spec. (L.)	12
Leiophyllum buxifolium (H, 1928) .	12	„ 3 spec. and 4 hybr. (L.) .	24
Empetrum nigrum (H, 1927) . . .	13	„ 2 spec. (L.)	36
„ *hermaphroditum* (H, 1927)	26	„ 1 hybr. (L.)	30
Erica tetralix (H, 1928)	12	*Polycodium stamineum* (L.)	12
„ *cinerea* (H, 1928)	12	*Gaylussacia baccata* (L.)	12
„ *arborea* (H, 1928)	12	*Oxycoccus palustris* (H, 1928) . . .	36
„ *arborea* (H, 1928)	12	*Epacris impressa* (S.)	13
„ *hiemalis* (H, 1928)	12	*Clethra arborea* (H, 1928)	8
Calluna vulgaris, v. pubescens (H, 1928)	8	„ *alnifolia* (H, 1928)	16
Bruckenthalia spiculiflora (H, 1928)	18	*Diapensia lapponica* (S., H, 1928) .	6

5. the feebly zygomorphous shape of the flower, with an approximately horizontal position, by which it is possible to retain the function of the anther-appendages as a strewing-mechanism for the pollen. These appendages are only found in the pendent flowers of the Bicornes. In this connection it may also be remarked that with Calluna the anthers do not open at their upper end through pores, but by longitudinal slits, thus making the spreading of the pollen also possible in a horizontal position of the flower.

All these important differences impart to Calluna a quite individual character; on the other hand, however, there are numerous points of agreement with the other *Ericeae* — *Ericoideae* — *Ericales*. Our object here is to find the nearest links by which *Calluna* is connected. NORDHAGEN (1937/38) attaches particular value to the above-mentioned characteristics, especially to the structure of the flower-twigs and of the vegetative-floral zone in their entirety, the occurrence of ramifications of the 3d and 4th order and of intermediate leaves being the most characteristic.

In the above systematic scheme the genera of which it is known that they embrace species where intermediate leaves occur on the flower-twigs, have been marked by a dot. These are:

Empetraceae, with the genera: *Ceratiola* and *Empetrum*;

Ericaceae, with *Cassiope*, *Gaultheria* and *Pernettya*, *Vaccinium*, *Thibaudia*, *Calluna*;

Epacridaceae with *Lebetanthus* and *Epacris*, and finally the genus *Shortia*, belonging to the closely related *Diapensiaceae*.

Especially the manner of flowering of *Ceratiola* and *Empetrum*, with a vegetative-floral zone, with floral-axes even of the 3d order and intermediate leaves, and a basal and a terminal zone of exclusively vegetative character under and above it, is in conspicuous agreement with Calluna. It is true that *Empetrum* and *Calluna* differ in this, that with the former the bracts of the vegetative-floral zone persist, whereas with the latter they are shed simultaneously with the flower-twigs after the seed has ripened, but with *Ceratiola* the agreement is closer in this respect, for there we see the vegetative-floral zone become bare after the fruit has ripened.

NORDHAGEN (1938, p. 25), after an elaborate analysis, arrives at the following statement: "Meines Erachtens dürfte es sich hier um starr fixierte Organisationsmerkmale handeln, die Calluna von ihren Vorfahren übernommen hat. Und die nachgewiesene Uebereinstimmung zwischen *Calluna, Empetrum,* gewissen *Vaccinoideae* und *Arbutoideae* sowie *Epacrideae* betreffs der Zwischenblätter, deutet darauf, es habe einmal eine ganze "Bicornes-Schicht" existiert, deren florale Achsen den Character ± reich beblätterter, vielleicht auch verzweigter Seitensprosse hatten". (In my opinion we may have here rigidly fixed characteristics of organisation, which *Calluna* has taken over from its ancestors. And the proved agreement between *Calluna, Empetrum,* certain *Vaccinoideae* and *Arbutoideae,* as well as *Epacrideae,* with regard to the intermediate leaves, indicates that once there may have existed a whole "Bicornes-stratum", the floral axes of which had the character of ± richly leafed, perhaps also ramified lateral shoots).

The simple flower-stalk with only 2 prophylls (or none), which nowadays is characteristic for the majority of the Ericaceae, makes, according to NORDHAGEN, within the family the impression of a new acquisition. If this view is correct, the *multibracteata* and *terminalis* forms of *Calluna* would make an atavistic impression, — so there might also with *Calluna* have already taken place a reduction of an originally larger number of "intermediate leaves", which is indeed implied in the "attempt at reconstruction" which the same investigator puts in the following words (l.c. p. 27/28): "...... gelangt man zu dem Resultat, dass die nächsten *Calluna*-Vorfahren folgende Eigenschaften aufweisen: nickende, radiäre Blüten mit gespornten Antheren und einem normalen, d.h. kleinen Kelch; eine nur schwach sympetale Krone; eine an den Langsprossen radiäre Verteilung der blühenden Kurzsprosse (etwa wie bei *Empetrum* und *Ceratiola*), aber eine reichere Verzweigung der letzteren; eine noch grössere Zahl von Zwischenblättern oberhalb der Vorblätter als bei den typischen rezenten *Calluna*-Blüten. Vieles bleibt aber selbstverständlich ganz unsicher (die Zahlenverhältnisse der Blüte; die Anordnung der Laubblätter und der Zwischenblätter an ihren Achsen; die Oeffnungsweise der Kapsel und ihre postflorale Lage u.s.w.)". (one arrives at the result that the nearest *Calluna*-ancestors present the following properties: pendent actinomorphic flowers with spurred anthers and a normal, i.e. small calyx; an only feebly sympetalous corolla; on the long-shoots a radial distribution of the short-shoots (resembling *Empetrum* and *Ceratiola*), but a richer ramification of the latter; a still larger number of intermediate leaves above the prophylls than with the typical recent *Calluna*-flowers. Much remains uncertain, of course (the question of the numbers in the flower; the arrangement of the foliage leaves and the intermediate leaves on their axes; the way in which the capsule opens and its post-floral position etc.).

Finally NORDHAGEN, like NIEDENZU (1890) lays strong emphasis on the phylogenetic value of the *Arbutoideae* (l.c. p. 30): "Man bekommt aber den Eindruck, es seien die *Arbutoideae* — *Empetraceae* — *Epacridaceae* — *Calluna* in irgend einer Weise blutsverwandt. Es fehlen aber Zwischenformen, die die Lücke ausfüllen könnten. Nach NIEDENZU (1890) sollten die *Vaccinioideae* von den *Arbutoideae* abgeleitet werden, und weil nun Zwischenblätter auch bei den *Vaccinioideae* — *Thibaudieae* vorkommen, zeigt die "Kompassnadel" hier wieder auf die *Arbutoideae* als eine zentrale Gruppe. Die *Rhododendroideae* sind betreffens des Antherenbaues, des Blütendiagrammes und der Oeffnungsweise der Kapsel von allen diesen Gruppen durch und durch verschieden. Auf die grosse phylogenetische Bedeutung der *Arbutoideae* hat vor allem NIEDENZU in seiner vorbildlichen Arbeit (1890) aufmerksam gemacht. Ihre Ahnen scheinen schon in der Kreidezeit, allerdings nur durch Blatt- und Zweigreste, nachgewiesen zu sein. Es fragt sich, ob nicht der Anschluss für die *Empetraceen, Epacridaceen* und die *Calluna*-Vorfahren bei gewissen *"Ur-Arbutoideen"* gesucht werden sollte. Es ist auch sehr wichtig, dass die Gattung *Erica* sowie die übrigen Gattungen der "*Erica*-Reihe" denselben loculiciden Kapseltypus besitzen, den wir bei den *Arbutoideae-Andromedeae* finden. Bei den *Arbutoideae* treten somit Merkmale auf, die einerseits bei *Calluna* (Zwischenblätter!) andrerseits bei der *Erica*-Reihe (loculicide Kapseln!) vorhanden sind. Auch ericoide Blattformen sind bei den *Andromedeae* repräsentiert (*Cassiope*).

Obwohl die Chromosomenzahlen der untersuchten rezenten *Arbutoideen* recht hoch sind, lassen sich doch dieselben auf die Grundzahl n = 6 zurückführen. Es könnten somit die *"Ur-Arbutoideen"* diese Zahl besessen haben, gleichfalls die *Calluna*-Ahnen; denn nach HAGERUP sollte auch n = 8 von 6 abgeleitet werden". (One receives the impression, however, that between the *Arbutoideae* — *Empetraceae* — *Epacridaceae* — *Calluna* there must be kinship in some way or other. Intermediate forms that might fill up the gap, are lacking, however. According to NIEDENZU (1890) the *Vaccinioideae* should be derived from the *Arbutoideae*, and since intermediate leaves are also found with the *Vaccinioideae* — *Thibaudiaceae*, the "compass-needle" again points to the *Arbutoideae* as a central group. In the structure of the anthers, the flower-diagram and the manner of opening of the capsule the *Rhododendroideae* are thoroughly distinguished from all these groups. Especially NIEDENZU has in his exemplary work (1890) drawn attention to the great phylogenetic significance of the *Arbutoideae*. Their ancestors seem to have been proved as early as the cretaceous period, albeit only by remnants of leaves and twigs. The question arises whether the link for the *Empetraceae*, *Epacridaceae* and the *Calluna*-ancestors should not be sought with certain "*Pre-Arbutoideae*". It is also very important that the species *Erica* as well as the other species of the "*Erica*-series" possess the same loculicidal type of capsule as we find with the *Arbutoideae* — *Andromedeae*. Thus characteristics appear in the *Arbutoideae* which are present on one side with *Calluna* (intermediate leaves!), on the other side with the *Erica*-series (loculicidal capsules!). Also ericoid leaf-forms are represented with the *Andromedeae* (*Cassiope*).

Although the numbers of chromosomes of the investigated recent *Arbutoideae* are rather high, they can be referred to the fundamental number n = 6. So the "*Pre-Arbutoideae*" may have possessed this number, and likewise the *Calluna*-ancestors, for according to HAGERUP also n = 8 is to be derived from 6).)

Also with the *Empetraceae* we see, according to NORDHAGEN, many morphological characteristics combined, such as: choripetalism, trimerous whorls and haplostemony, as in the *Rhododendroideae*; the drupes, functional dioecia and the bracts of the *Arbutoideae*, the drupes and bracts of the *Epacridaceae* — *Stypheliae* and the shoot-structure and the bracts of *Calluna*. To these is to be added the great uniformity in the structure of the style, namely a central air-channel, through which the air has access to the placenta, which reminds us e.g. of the *Gymnospermae*. Also conformity in the structure of the embryo-sac and the presence of urson belong to the relational characteristics.

The subfamily of the *Ericoideae* must, according to NORDHAGEN, be maintained within the family of the *Ericaceae*, although it is not yet sufficiently known in how far we have a natural group here. He assumes that there has existed a group of forms, the "*Pre-Ericoideae*", uniting *Calluna* and *Erica* features. This group might then in its turn have found its origin in the "*Pre-Arbutoideae*". It is pretty obvious that unless supported by palaeontology such working hypotheses do not carry us much forward.

For the future NORDHAGEN prefers a subdivision of the *Ericoideae* into three sub-groups instead of two, about as follows:

A. Capsule septifragal. Above the 2 prophylls several pairs of intermediate leaves (typical are 4 bracts, placed crosswise) are found, forming an adventitious calyx, or even, if the number of intermediate leaves is much larger, packets of bracts or a richly leafed short-shoot...... *Calluneae*.

B. Capsule loculicidal, with several to many seeds in each compartment. Pedicel as a rule with 2 prophylls, sometimes also with an upwardly shifted bract, in this case therefore bearing 3 leaflets, or bare...... *Ericeae*.

C. Fruit septicidal with only one seed-grain in each loculus, breaking up into partial fruits, or otherwise with a non-disintegrating fruit, sometimes without distinct partition-walls, very seldom breaking up into loculi with only one seed-grain each. Flower with 2 prophylls and bract or without adjacent leaves...... *Salaxideae*.

B. The Roots.

We distinguish a main or primary root, the origin of which is already present at germination, and the side-roots, sprouting irregularly from it and finally ending in the extremely thin hair-roots. Besides, the older parts of the stem and especially the root-base often produce adventitious roots (see: formation of adventitious organs). Root-hairs, however, are entirely lacking.

The youngest part of the root shows a very simple structure, as with most other *Ericaceae*; this was pointed out already by VAN TIEGHEM and DOULIOT (1888). The epiderm cells are relatively very big. Their largest diameter is from 10 tot 15 μ, the whole diameter of the young hair-roots being 30—40 μ. With the primary root of the seedling these dimensions are larger. Here the epiderm cells have a largest diameter of 30—40 μ, whilst near the top the root measures 50—75 μ across. So the epiderm cells may reach the same diameter as the whole remaining root-tissue (Fig. 11, 12). They do not show any development into root-hairs. The remaining part of the hair-roots consists of a cortical layer of one cell thickness and a central cylinder with a simple pericambium and two or three phloem- and xylem-hanks, each reduced to a single narrow spiral vessel and two or three libriform fibres with slit-shaped pits, the whole forming a very thin central cylinder.

At the top of the rootlet the epiderm cells divide themselves radially and partly also periclinically, so that periodically a new calyptra is detached (Fig. 13 and 14), consisting of a middle cell and 8 surrounding marginal cells. Sometimes the constriction of the root-caps takes place in rapid succession, so that several of them are present simultaneously. As a rule however they soon decay.

The bark grows longer by radial divisions at the top, whilst the central cylinder proceeds from a single initial cell. With young hair-roots we clearly notice an (apical) division-zone and a (basal) extension-zone (Fig. 12). When the extension has taken place, growth in thickness and the formation of side-roots follow.

The growth in thickness proceeds as follows: we first observe a bast-parenchyma and a closed xylem cylinder. Then the bast-parenchyma with the endoderm dies off from the outside with suberisation, while the cambium forms phloem externally and regular xylem internally. The suberised periderm cracks and comes off, while a new thin layer of cortex comes free again.

When a lateral root is formed the epiderm cells locally diverge and the protuberating bark temporarily comes free in the shape of a root-sac (Wurzelhülle, poche digestive). This protuberance is the result of the cell-divisions in the meristem of the side-root, in which we can soon distinguish epiderm (dermatogen, assise pilifère), bark and a central cylinder. Then the bark cells of the mother-root diverge in their turn and leave a free passage for the side-root (Fig. 11).

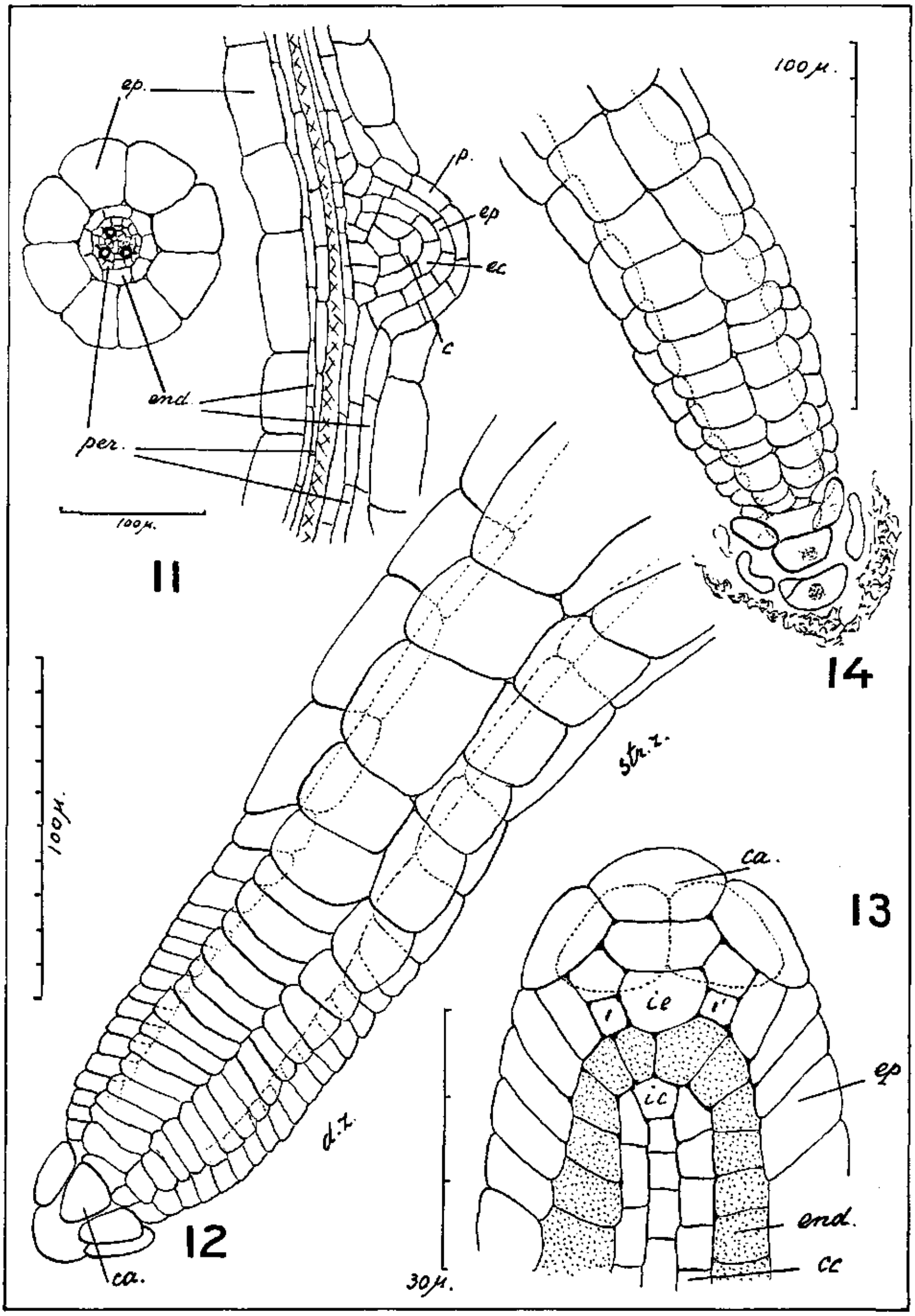


Fig. 11—14.

The xylem of the root shows in the main the same structure as that of the stem. The phloem and xylem bundles are spread at fairly regular distances throughout the wood, the medullary rays of which consist of unicellular radial laminae, the boundaries of the annual rings being indicated by the difference in bore and number of the xylem-vessels.

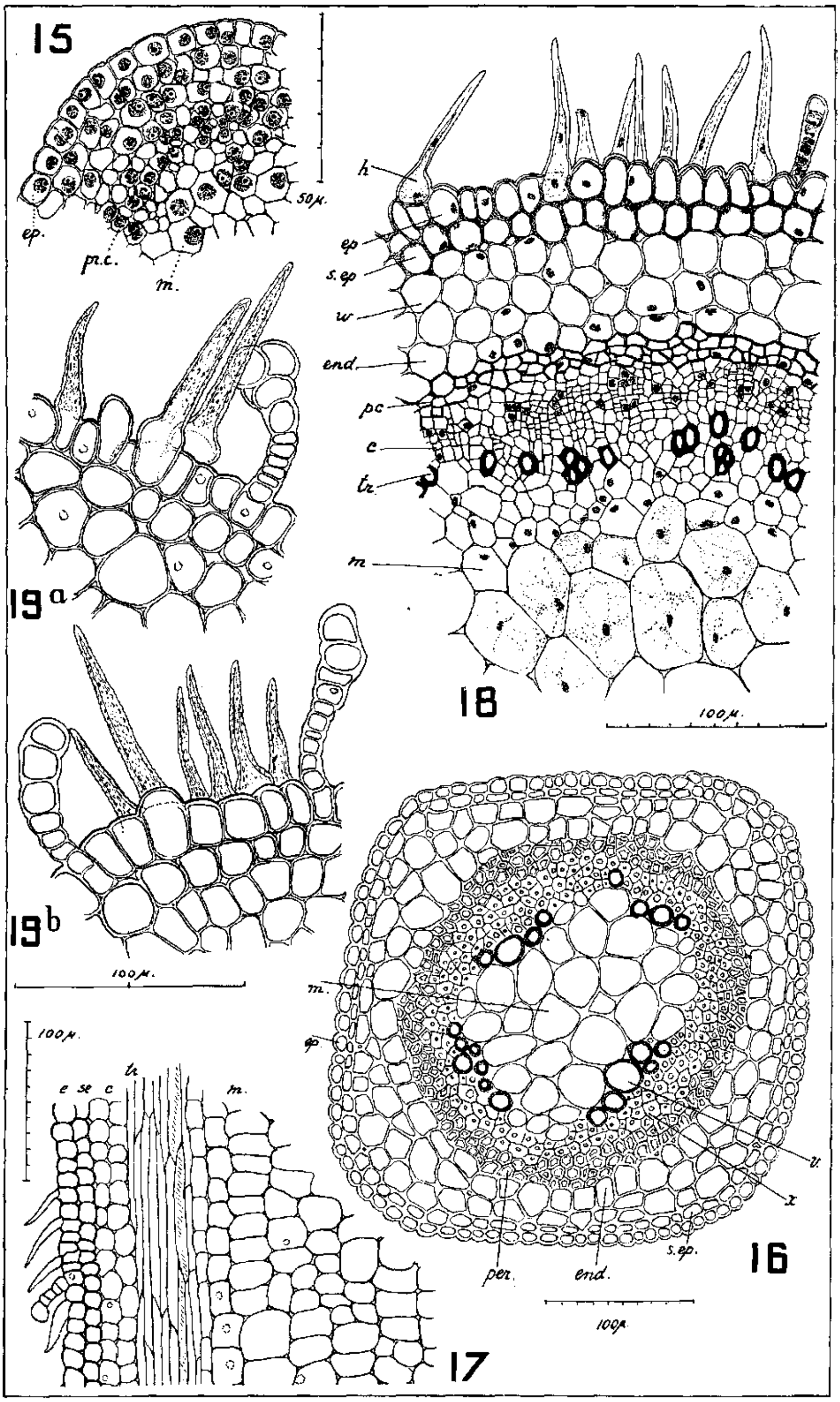
The roots of Calluna may reach a comparatively very great length. I found living Calluna roots at a depth of 2.5 m below the surface. The ramification may under certain conditions be very dense, so that after washing out the soil-particles there remains a very fine, dense texture of large surface. Of this texture the youngest parts, that are still extending, are quite clear and under the microscope beautifully transparent, so that their finer structure can be studied without special precautions. Older, lignified root-parts (duramen) have a light yellow to nearly brown colour. Also the periderm is brown.

C. The stems.

The structure of the stem of Calluna is in the main the same as that of the other *Ericaceae*. It is characterised, however, by a double epiderm, or, to be quite exact, an epiderm and a sub-epiderm, unlike the leaves which always have a simple epiderm. Under the sub-epiderm follows in the younger part of the stem a cortical parenchyma. This tissue consists mostly of 2—4 cell-layers and an endoderm of thin-walled cells (so-called water-tissue) (Fig. 18). The sub-epiderm contains chloroplasts; the cortical parenchyma, as far as my observations go, does not. This latter and the endoderm suberise soon after the formation of the first xylem-cylinder, which with Calluna is already closed at an early date. If the plant develops vigorously this suberised part of the bark cracks already in the same year, otherwise in the second year, and then sets free a new bark, consisting of 5—6, sometimes more, suberised layers of phloem.

The meristem of the vegetation-point of the stem differentiates in the usual way into a dermatogen, periblem and plerom (Fig. 15). This latter then produces a thin-walled, fairly homogeneous medullary-parenchyma of simple structure, while in the mesoderm very soon, close under the vegetation-point, a procambium ring is originated (Fig. 16), in which the primary annular and spiral vessels are differentiated. Also the leaf-traces may be originated early. At the same time a so-called cambial parenchyma is formed, which later becomes irregular, like the indistinct pericycle (Fig. 18). After this also the bast-parenchyma cells and the endoderm begin to suberise. The cambium differentiates a continuous cylinder of xylem internally and phloem externally, of which the 2 or 3 outer cell-layers always die off and suberise, beginning with the pericycle-layer. So the periderm is at first very thin with Calluna. Later on, however, by not being cast off, it continually increases in thickness and cracks off in scales, similarly as with many woody plants.

The wood is of a simple structure, the medullary-rays consist of radial laminae of one cell thickness. The groups of vessels lie spread more or less regularly between the thick-walled wood-fibres, communicating through dotted ducts (Fig. 22). The annual rings are pretty distinctly delineated and can be clearly recognised with low magnifications by the difference in


15
ep.
p.c.
m.
50μ.
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16
100μ

Fig. 15—19.

number and size of the vessels in the winter- and summer-wood; especially when stained they show well. Part of the vascular bundles are perforated ladder-like at the obliquely truncated end (Fig. 21). Spiral as well as annular vessels occur, but also nearly smooth-walled, somewhat narrower libriform fibres, which as it were form a transition to the real wood-fibres (Fig. 21).

The leaf-traces do not leave free leaf-windows in the bark-cylinder, so that this latter is only pierced at the base of the lateral shoots; this is peculiar for *Calluna*. The branch-traces of the lateral shoots, sprouting in the axils of the stem-leaves, have their origin in the stem-cambium, but are nevertheless situated directly above the leaf-traces. The stem-leaf and the little twig sprouting from its axil die off about simultaneously. If however the little twig should remain alive, yet the corresponding stem-leaf generally dies off in the same growing-season. So the stem-leaf soon dies off in any case, the little twig may grow on vegetatively. The flower-bearing twigs as a rule die off after the ripening of the fruit, with the corresponding stem-leaves. The internodes of the long-shoots are short in the basal and terminal part and under normal conditions increase in length towards the middle part (see Fig. 76).

The stems, when young, i.e. before the endoderm with the other bark-parenchyma and the epiderm-layers have suberised, are densely haired and in a moist environment show in places stomata, as also does the unhaired hypocotyl axis (Fig. 23). On the young part of the stem, and also on the leaf-top in the bud, between the other hairs, evolved from an epiderm cell, multicellular club-shaped trichomes are found whose surface is studded with tiny warts (Fig. 19a, b).

The cells of the epiderm, like those of the subepiderm, at first contain fairly much chlorophyll, and under certain conditions also anthocyanin. As long as the stem-members are occluded in the bud and cramped up between the decussately placed bud-leaves, their cross-section is more or less diamond-shaped with rounded corners (Fig. 16). But as soon as the members are freed by extension, the cross-section is circular. With old frame-branches and stems one often notices again a more or less square section with strongly rounded corners. This is probably connected with the scars of the leaves and twigs which are inserted along the stem in four rows, and in those places the growth of the wood is somewhat impeded. These scars are very long preserved and sometimes form small dents in the surface of the stem. Also with cumbent branches an excentric wood-growth is occasionally found, the side, turned towards the earth, showing the broadest annual rings. The increase in thickness of the wood very much depends on circumstances.

The average annual increase in thickness amounts in our climate to about 0.5 mm, so that a twenty year old stem may have a diameter of 2 cm. In the High Alps and in Northern Scandinavia this growth in thickness is considerably less. The one year old twig as a rule attains a diameter

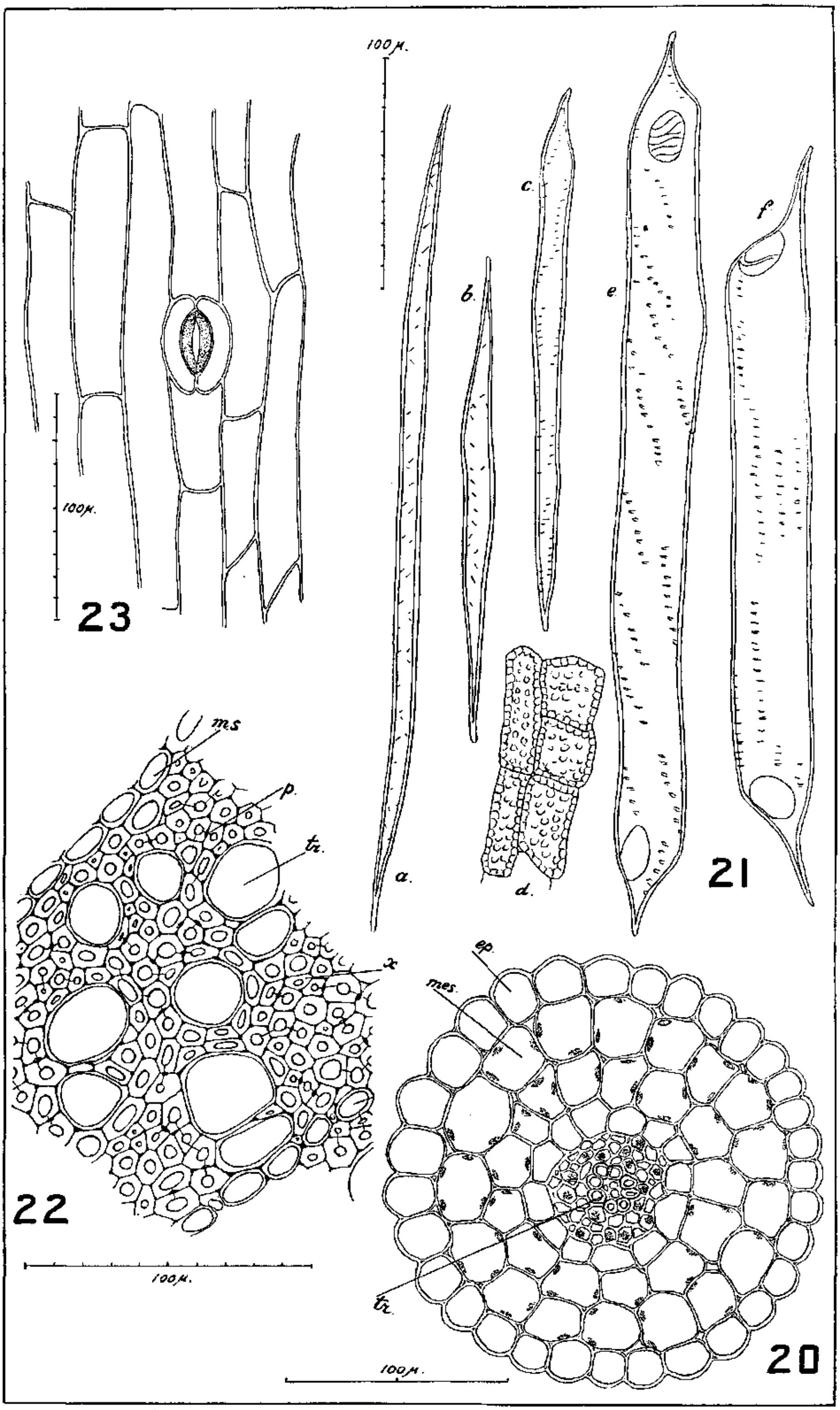

Fig. 20—23.

of 1—2 mm, but under particularly favourable conditions the growth in thickness may be considerably greater, especially during the first years. All this holds for long-shoots. With short-shoots the cross-section of the stem may remain a more or less rounded square, especially when the leaf-arrangement is dense and the internodes consequently short. On the short-shoots the stem-internodes are not directly visible as a rule, since the leaves overlap like tiles (Fig. 2). With young seedlings, where the leaves have the character of primary leaves, and with plants that have grown up in a damp and dark environment, the internodes of the short-shoots are visible. (Pl. I). The short-shoot twigs are likewise provided with a double epiderm and haired, although not as strongly as the young long-shoots. The difference in length of the internodes, as shown by the long-shoots, is not or hardly observed with the short-shoots.

Wood-formation occurs sooner with drought than in damp weather or a moist environment. In our country under ordinary conditions the wood-formation in the long-shoots is already in full progress before blooming begins.

D. The Leaves.

Without doubt the Scotch heather is one of the spermatophytes of the European flora with the smallest leaves, it has true dwarf-leaves. Not only the foliage leaves but also the other leaf-types of this plant excel by their smallness. These types are with Calluna: 1°. cotyledons; 2°. primary and following leaves; 3°. short-shoot leaves (including bud-leaves); 4°. long-shoot leaves and their transitions to the preceding kind; 5°. prophylls; 6°. intermediate leaves; 7°. protecting leaves (bracts) (Fig. 24). Stipules and bud-scales are absent. There is a striking tendency to form transitions between these leaf-types, so that it is often difficult to make out what the type is. The cotyledons present a flat lamina, gradually passing via the primary and following leaves into the more needle-shaped foliage-leaves, deeply grooved on the underside. These latter in their turn quite gradually pass via the intermediate leaves into the more flattened, broad, almost scale-like bracts.

We shall deal with the short-shoot leaves first, as representing the most frequent and at the same time most characteristic type. They are from about 1 to over 3 mm long and 0.5 to 1.5 mm broad, more or less like short needles, unstalked, attached with the middle part of the base, while the two sides are prolonged downwards in a pair of spur-like appendages (see Fig. 24). The cross-section is about trapezoidal with rounded corners. One distinguishes a more or less flat or slightly concave upper surface and two convex sides, converging to the narrow underside, the middle portion of which has the appearance of a white stripe, running from near the top to the place of attachment at the base. This stripe is nothing else but a deep groove, going down to about halfway the thickness of the leaf, and coated with hairs. The epiderm consists of slightly elongate cells of 20—50 μ length with undulated sides (Fig. 30b, c). Between the inner and outer lamellae of the inward-turned cell-wall the third lamella has often become mucilaginous, especially in the epiderm of the sides of the leaf (Fig. 26 and 32). This mucus, which is coloured brown by iodine, probably consists of gums, while the two other lamellae consist of cellulose. The cuticle of the epiderm of the leaf-sides is very thick and has a finely layered structure. On the lower as well as on the upper side of the leaf the epiderm cells are somewhat smaller (Fig. 30b, c), but about similar in shape. The number of stomata is largest in the groove on the underside and on that part of the spurs which is turned towards the stem, and also near the point of attachment of the leaf. Besides, stomata also occur here and there on the upper surface of the leaf, but, as far as I could discover, not on the sides. The stomata in the groove lie in close proximity (Fig. 29) on small wart-like elevations, formed by the adjoining epiderm cells being bent upwards (Fig. 34). The size of the stomata varies from 20 to 25 μ in length and 18 to 20 μ in breadth. In the groove their number per mm^2 will approximately be 1200.

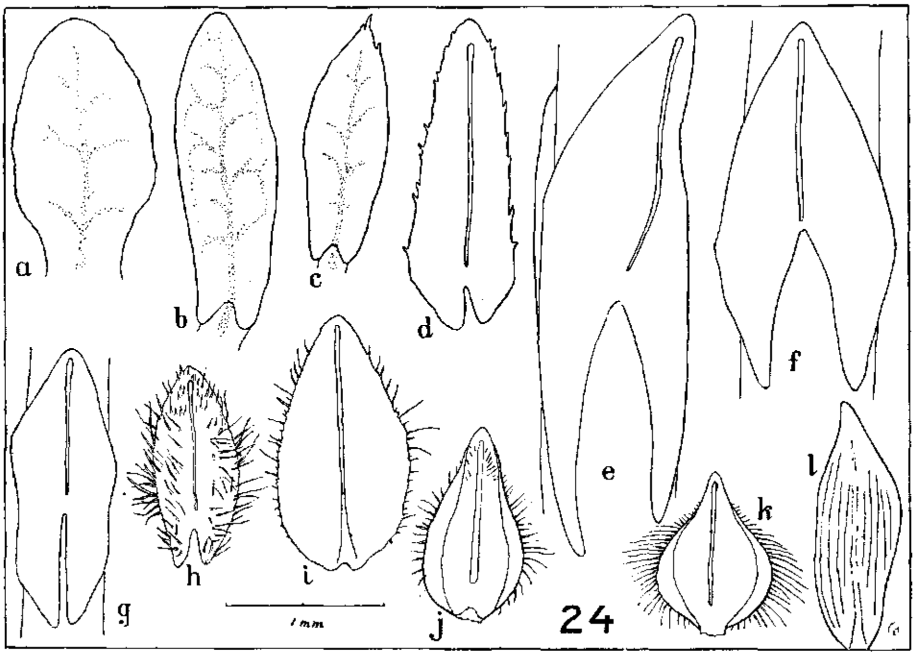

Fig. 24.

The development of the *palisade-tissue* is by far the strongest along the two sides of the leaf. It consists of one, rarely two cell-layers, the cells of which are 3—4 × longer than broad and taper inwardly, so that on the outside of the palisade layer the diameter is about twice that on the inner side. The length of the palisade cells is 40—60 μ and their breadth 18—27 μ. They contain numerous chloroplasts, arranged along the outer

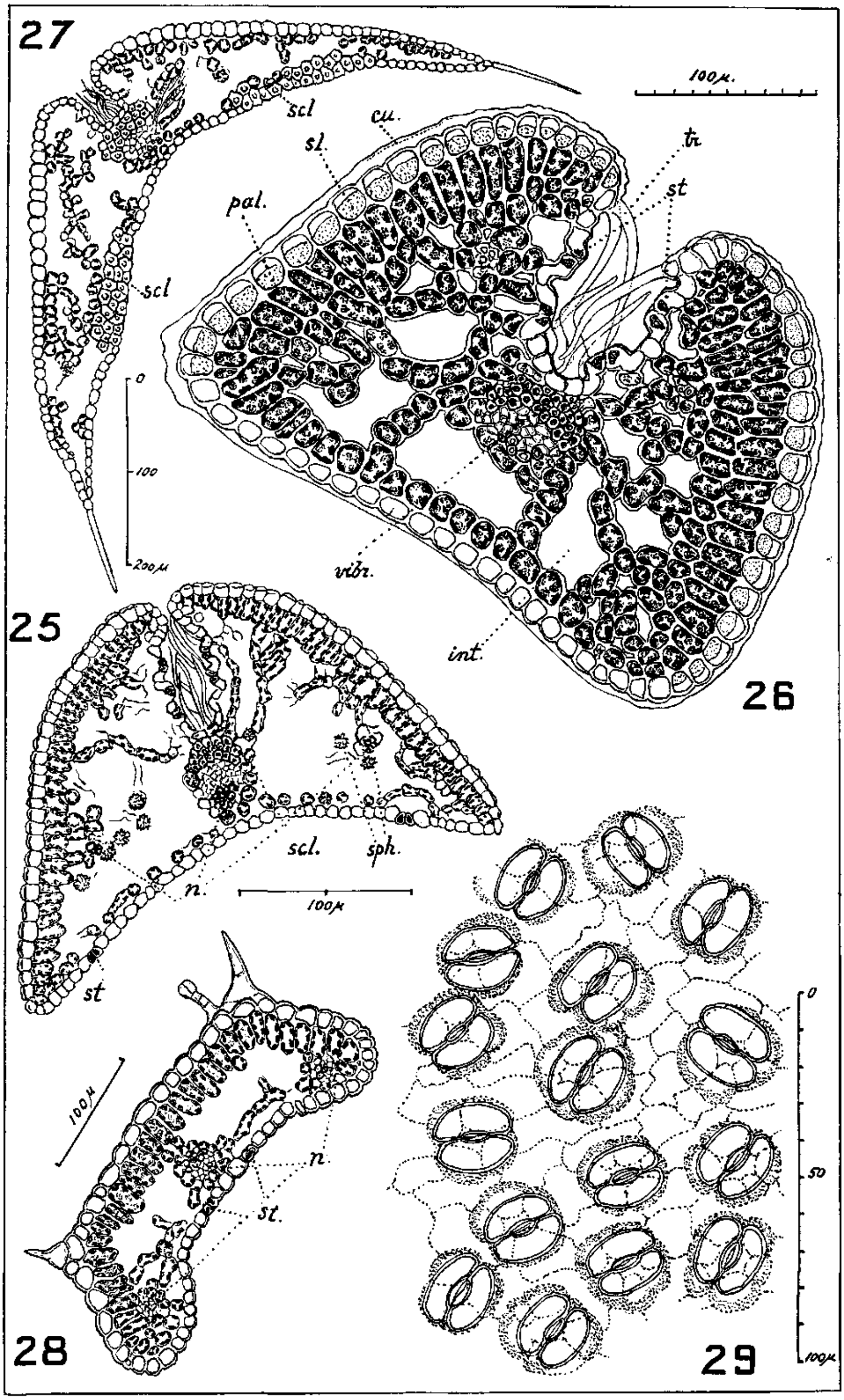
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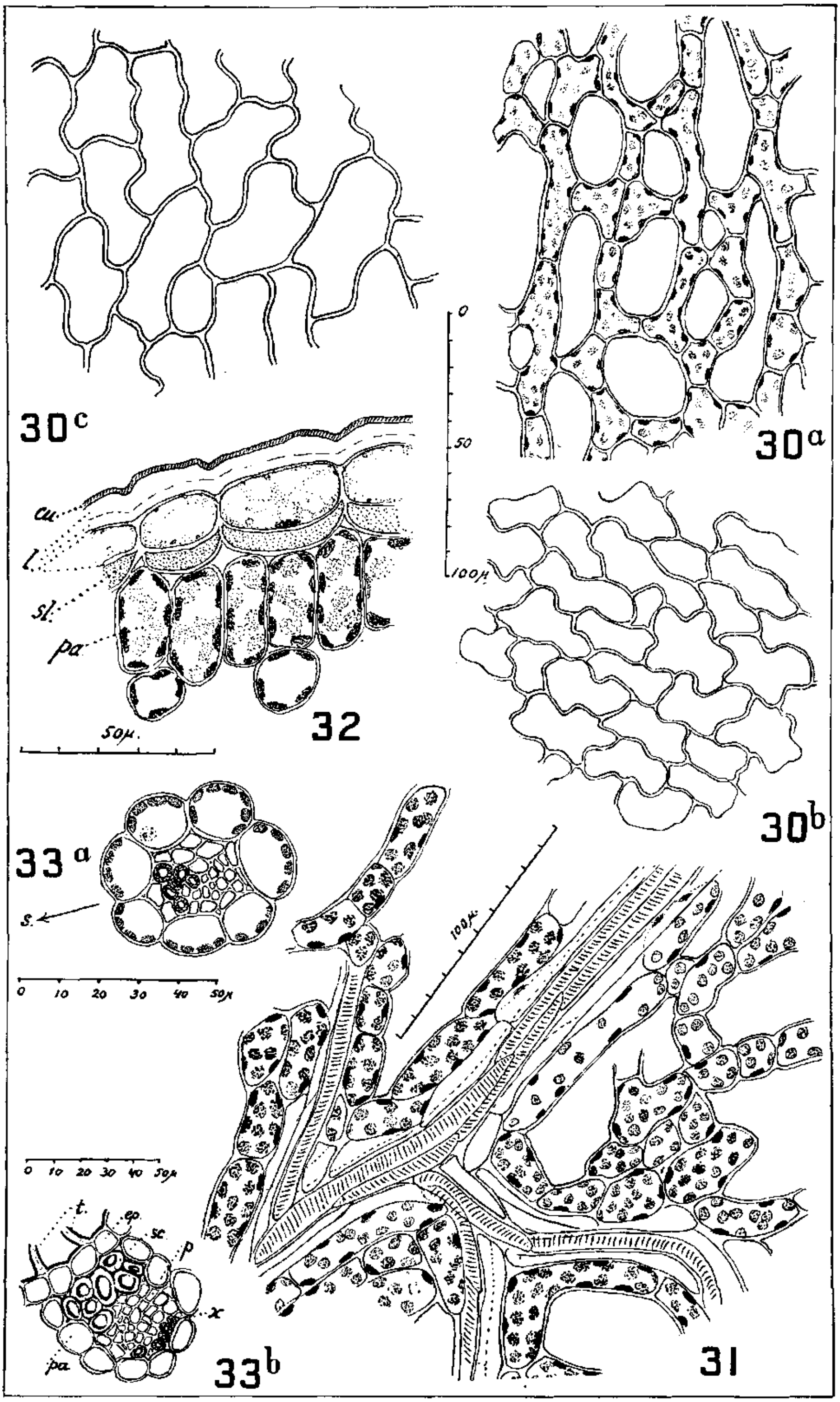
Fig. 25—29.

cell-wall. On the upper surface of the leaf the palisade layer is less distinct and may almost be lacking at the basal end. The cells there have the character of short mesophyll cells.

The mesophyll is a spongy tissue and consists for the greater part of very much elongated, chlorophyll-containing cells, which as a system of ramified threads traverse the interior of the leaf, notable by a relatively very large air-space; they form connections between the veins and the palisade-layers of the sides (Fig. 25 and 26). The vascular bundles of these primitive veins have a small diameter; the number of veins is very restricted. They anastomise with extremely fine veinlets. The principal vein is reinforced underneath by a sclerenchyma mantle, filling the space between this principal vein and the epiderm of the inside of the groove (Fig. 26 and 33b). The remaining part of the principal vein and the side veins are surrounded by a parenchymatous sheath (Fig. 33a), from which the mesophyll chains radiate towards the palisade tissue. Towards the top of the leaf the air-space becomes relatively smaller (Fig. 26). The leaf-spur is collateral as usual, with the lignified vessels directed apically. The veins contain spiral and smooth vessels, more or less obliquely truncated and often of small length (Fig. 31). Sometimes crystal sphaerites occur in the mesophyll of the leaves, but then the adjoining cells have become structureless, so that one receives the impression that this is not a normal condition. Several times I observed these sphaerites in large numbers during the winter months and it seemed to me that there might be some connection between this phenomenon and the dry cold which Calluna cannot endure well. The veins in the spurs and also the other side-veins have no reinforcing mantle of sclerenchymatous cells (Fig. 33a).

Trichomes are especially found along the edge of the upper surface and in the groove of the underside (Fig. 26, 35). They are unicellular, crystal-clear hairs, originating from epiderm cells, and pluricellular club-hairs, formed at the top of the leaf by further divisions of an epiderm cell (Fig. 35). First a row of simple cells is formed and finally on the top part, by longitudinal division, a club-shaped dilatation. These club-shaped trichomes are originated at an early date, as a rule even before the extension of the internodes. I often observed mycorrhiza threads in these club-trichomes, and also hyphen clews (Fig. 35). These trichomes soon disappear after the leaf has become full-grown. Their function is unknown to me. The trichomes in the groove afford a good protection against outside moisture and too strong evaporation inside. Also the trichomes along the edge of the leaf afford in the bud stage a good protection of the vegetation-point. It is quite possible that also the club-shaped trichomes at the top of the young, not yet full-grown leaf have a similar function, but one wonders why they should then differ so considerably in shape from the other hairs beside them. Also on the young part of the stem we find, amidst a large majority of the ordinary unicellular hairs, a fraction of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31

Fig. 30—33.

these club-hairs (Fig. 19), where they also disappear when the internode grows older.

The usual length of the hairs is 30—50 μ, but is very variable. With the var. *hirsuta* Gray the length of the hairs may equal that of the leaves, although as a rule it is much less. The surface of the hairs is studded with tiny warts, the hairs themselves being hollow. There may also be hair on the stems, strongly haired plants may look like grey or white felt.

Broader and somewhat flattened, closely packed short-shoot leaves are found with the fa. *rigida*, more needle-shaped distant leaves occur a.o. with the fa. *Serlei*, and also with etiolated plants. On the whole the shape of the leaves is rather variable (Fig. 24).

The long-shoot leaves distinguish themselves from those of the assimilation-shoots (short-shoots) by their size, shape and duration of life. On the whole the long-shoot leaves are bigger and can reach a total length of 5—6 mm. Further the two spur-like appendages are relatively much longer (Fig. 24e), in extreme cases they may even be longer than the remaining leaf. The long spurs are often of unequal length and, when developed in a dry environment, closely pressed against the stem, whereas with plants, developed in a damp atmosphere, they stand off and may even be more or less curled (Fig. 3). In the latter case also the blade stands off as far as possible, namely at a right angle. By these long spurs, which under ordinary conditions lie against the stem, the leaf receives considerable support and reinforcement, the place of attachment being only small and round. Besides, nearly always side-shoots sprout from the axils of these leaves, so they are at the same time bud-protectors.

As to the duration of life of the leaves, on the short-shoots it is 2½ years at the utmost. In the third year they die off, if this has not happened earlier, although the twig itself may continue to grow at the top. The long-shoot leaves seldom reach an age of a single year; they generally die soon after the fruit has ripened. So they have a subordinate significance as organs of assimilation, but as organs for support and protection they are all the more important.

Especially with young plants and with shadow twigs transitional forms between short- and long-shoot leaves are often met with, as they are also found between the short- and long-shoots themselves. The shape of the leaf seems to be connected with the length of the internodes. If the full-grown internodes are longer than the leaves, one has to do with a long-shoot and with long-shoot leaves. If on the other hand the full-grown internodes are shorter than the blade or about equally long, one has to do with short-shoot leaves with their reduced spurs.

On the short-shoots the leaves as a rule overlap tile-like in four regular rows (Fig. 2b). The number of leaves on a short-shoot usually ranges from 28 to 48 in a growing-season, though there are exceptions; full-grown season-shoots are meant here, of course. The number of internodes and therefore the number of leaf-pairs on the long-shoots is pretty much the same as with the short-shoots, anyhow of the same order of magnitude in one and the same individual.

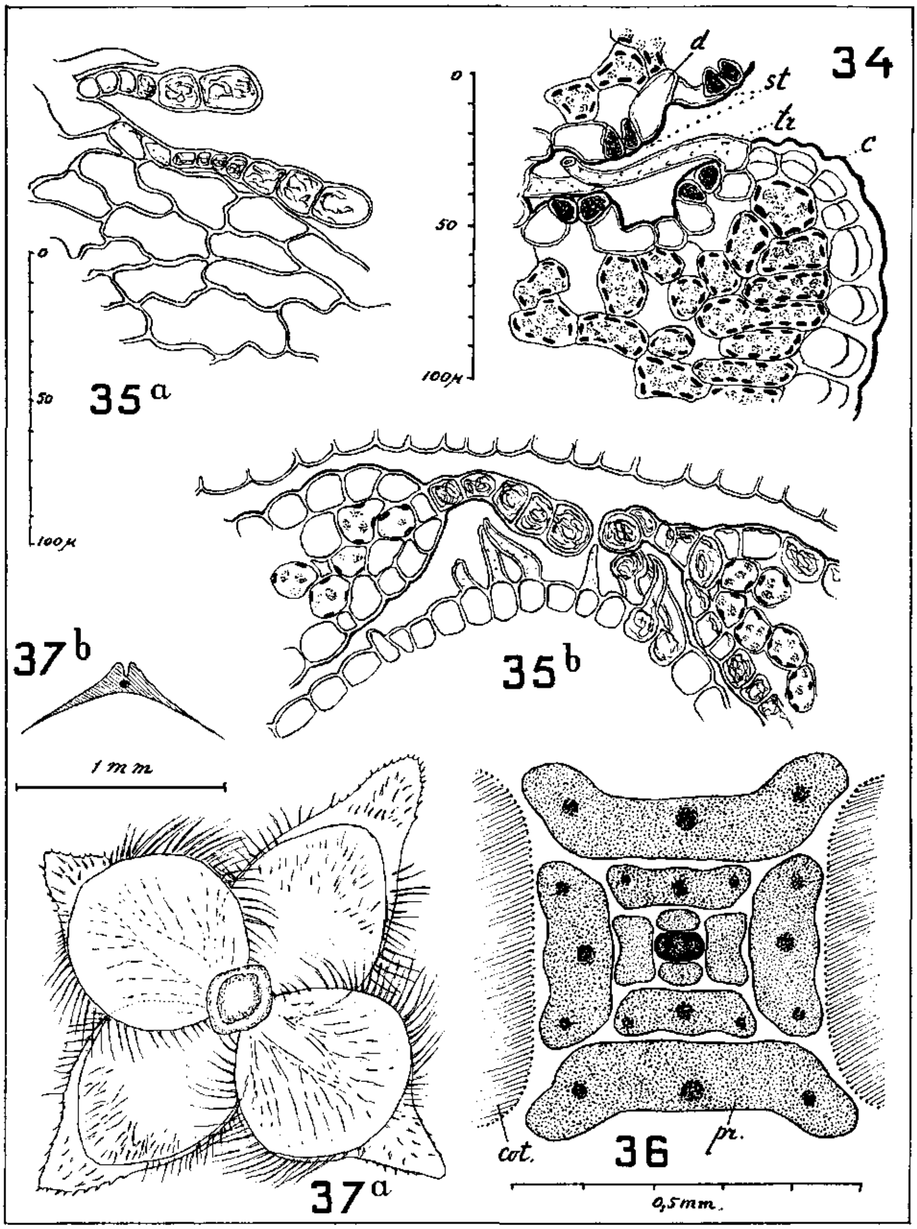


Fig. 34—37.

The winter-bud of *Calluna* is open, i.e. special bud-scales are lacking. The last leaf-pairs remain smaller, also during the following growing-period, and are bent towards each other, thus protecting the vegetation-point during the cold season. For the rest the bud-forming leaves have the same outward appearance as the short-shoot leaves.

Entirely deviating in shape are the two cotyledons, which are simply discs with an egg-shaped circumference and beginning with a slightly lengthened foot, which must be conceived as a short petiole (Fig. 24a). The length and breadth of the cotyledon disc amount to 0.9—1.4 and 0.7—1.0 mm. respectively. The edge is feebly undulated. For the rest the blade has a smooth surface and is provided with stomata, on the underside as well as above. The palisade tissue consists of one cell-layer. The stomata lie mostly on the underside.

The primary and following leaves form distinct transitions to the ordinary short-shoot leaves (Fig. 24b, c). They are rather frequent on the young seedlings and are more or less lancet-shaped with a convex upper surface and a concave underside. A groove has not yet formed here, though on the leaf-base two knobs are already visible where the stem-leaves have spurs, while on the anterior edge a few trichomes may occur in the shape of simple or pluricellular prickles or hairs and clubs. From the central principal vein two or more side-veins run close to the edge (Fig. 25). Feeble anastomoses occur. The primary leaves are already provided with a spongy mesophyll, leaving much air-space inside (Fig. 28). The cell-chains of this mesophyll remind us of multicellular ramified filamentous algae, proliferating within the leaf. Remarkable is the flush situation of the stomata on the underside of these leaves, agreeing in this with the stomata on the inner side of the spurs of full-grown stem-leaves.

E. The Flower.

The arrangement of the flowers on the long-shoot at first sight makes the impression of a raceme or a composite raceme, but on closer inspection it appears to be a raceme-like arrangement of isolated flowers, placed terminally on flower-twigs. Besides, the long-shoot carrying the flower-twigs ends in a few short-shoots with ordinary leaves, therefore without flowers, and this does not occur in a true inflorescence. Each flower is preceded by at least 4 bracts and 2 prophylls, but the number of the bracts and of the intermediate or transitional leaves (NORDHAGEN's Zwischenblätter) between bracts and prophylls varies considerably (see under Abnormities). The flower-twigs sprouts from the axil of a long-shoot leaf, which might be called a protective or supporting leaf. NORDHAGEN speaks of a "Deckblatt" (covering leaf). (1937, l.c. p. 17, Fig. 5).

The typical flower-diagram (Fig. 39 and 51) shows two whorls of 2 sepals each, a bell-shaped corolla with four incisions and 2 whorls of 4 stamens, in reality forming a single whorl. The 4 corolla tips would alternate with the 4 sepals if these latter were situated in a single whorl. Also the 2 × 4 stamens and the quadrilocular ovary alternate, i.e. the inner whorl of stamens (those inserted at the highest level) alternates with the loculi of the ovary, while the 4 outer ones alternate with the 4 inner ones; the 4 outer stamens, however, do not alternate with the 4 corolla tips.

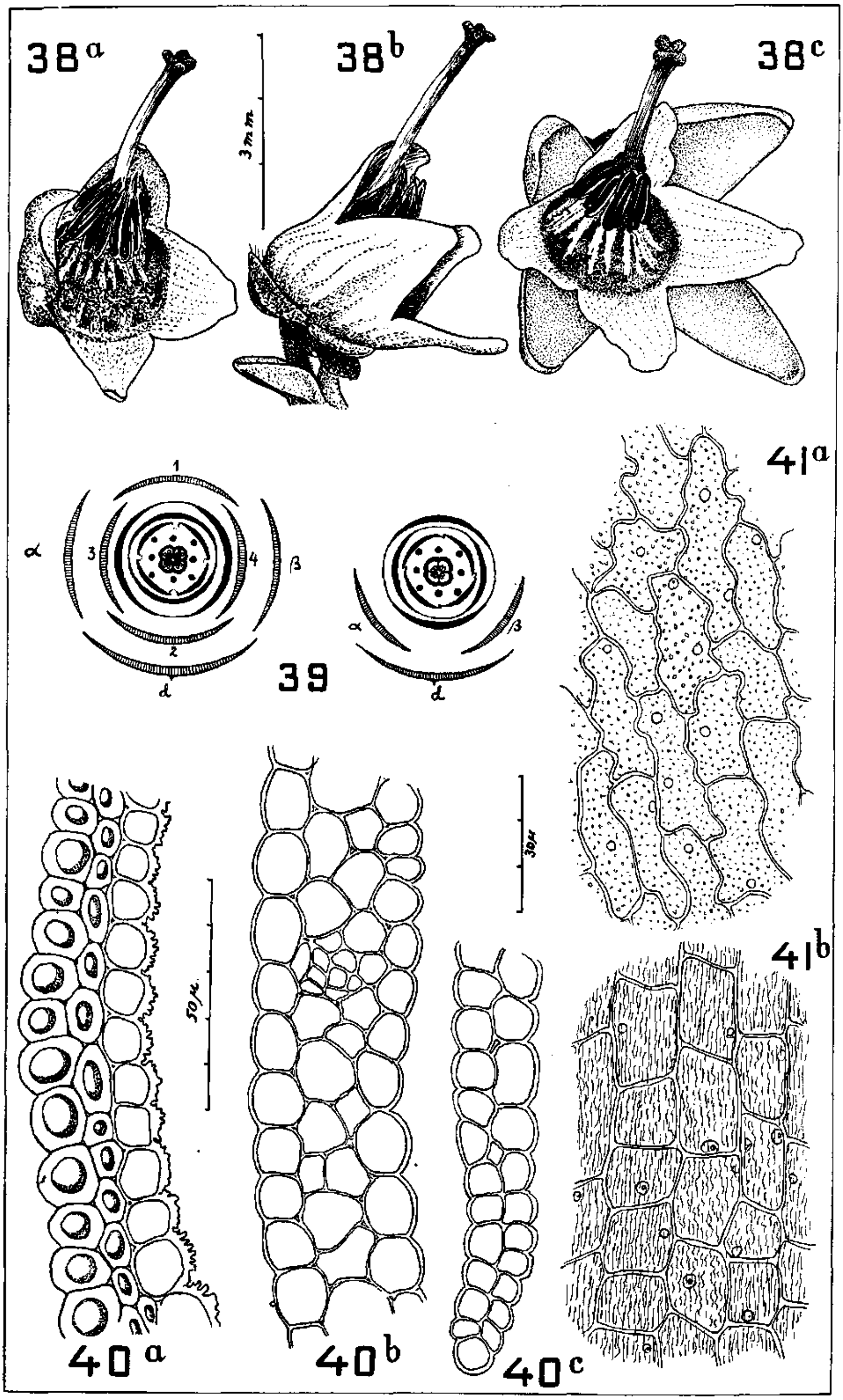


Fig. 38—41.

So this obdiplostemony which is general with the *Ericaceae*, is also present in *Calluna*. Besides it sometimes happens that the two outer sepals do not alternate with the upper pair of bracts, but face them. NORDHAGEN (1937) accordingly speaks of an "obdiplosepalism" with *Calluna* (Fig. 98 and 99). Also in other respects Calluna shows numerous deviations in the situation of the bud. Sepals and corolla tips overlap to the right and to the left. Also intercalated bracts of a sepal-like character are more than once met with (Fig. 10). Five- and even six-partite flowers I repeatedly observed with Calluna and also flowers with irregular whorls of often mis-shapen parts.

The flower-twigs may again be ramified and carry branchlets of the 3d order and a few times there are even side-shootlets of the 4th order, but these appeared to be all of a vegetative character (Pl. III, 2).

If the long-shoot with the flower-twigs stands exactly vertically, the isolated flowers on side-axes of the 2nd order stand away from the main axis in four directions, like the leaves. As soon however as the position of the long-shoot deviates a little from the perpendicular, as it nearly always does, the flower-twigs bend over to the leaning side in such a way that the flowers come to lie in a semi-cylindrical plane, at the underside of the inclining long-shoot (Fig. 58). Normally the direction of the flowers is about horizontal, i.e. laterally distant, this is probably connected with the feeble zygomorphism. In very exceptional cases it occurs that the long-shoot with flower-twigs does not terminate in vegetative shoots, but has a top-flower, by the side of which a reduced terminal bud is often found. Such a top-flower is generally a little bigger and has an actinomorphic structure, it is in a sense a peloria (Pl. XIII).

The sepals are normally violet-pink, like the corolla, they are oblong ovals, the outer surface of which is slightly convex and the edge bent inwards, they exceed the petals in length. The outer surface is more or less glossy and they are constituted like straw, as of the 3 or 4 cell-layers of the sepal the 2 or 3 outer ones are thick-walled and lignified (Fig. 40a). In the inner layer the exposed cell-walls are thickened and rough by protuberances. After the bloom the sepals persist, they retain their gloss though the colour fades, and then enclose the fruit like four straw scales. They then bend sharply inwards about halfway the length, so that the tips overlap and cover the fruit (Fig. 59). In damp and dry weather and even when immersed in water the sepals retain this crooked shape. So they are not hygroscopic, differing in this respect from the carpels, which are highly hygroscopic.

The calyx of Calluna never expands fully. In full bloom two opposite sepals form an angle of 90°—120°. At the top the young sepal has strongly thickened cells, which in the bud-stage of the flower by overlapping reinforce it considerably (Fig. 45), so that the bud of the delicate little flower can stand rough usage by strong wind. Androecium and gynoecium are well protected by this peculiar structure of the sepals, especially against

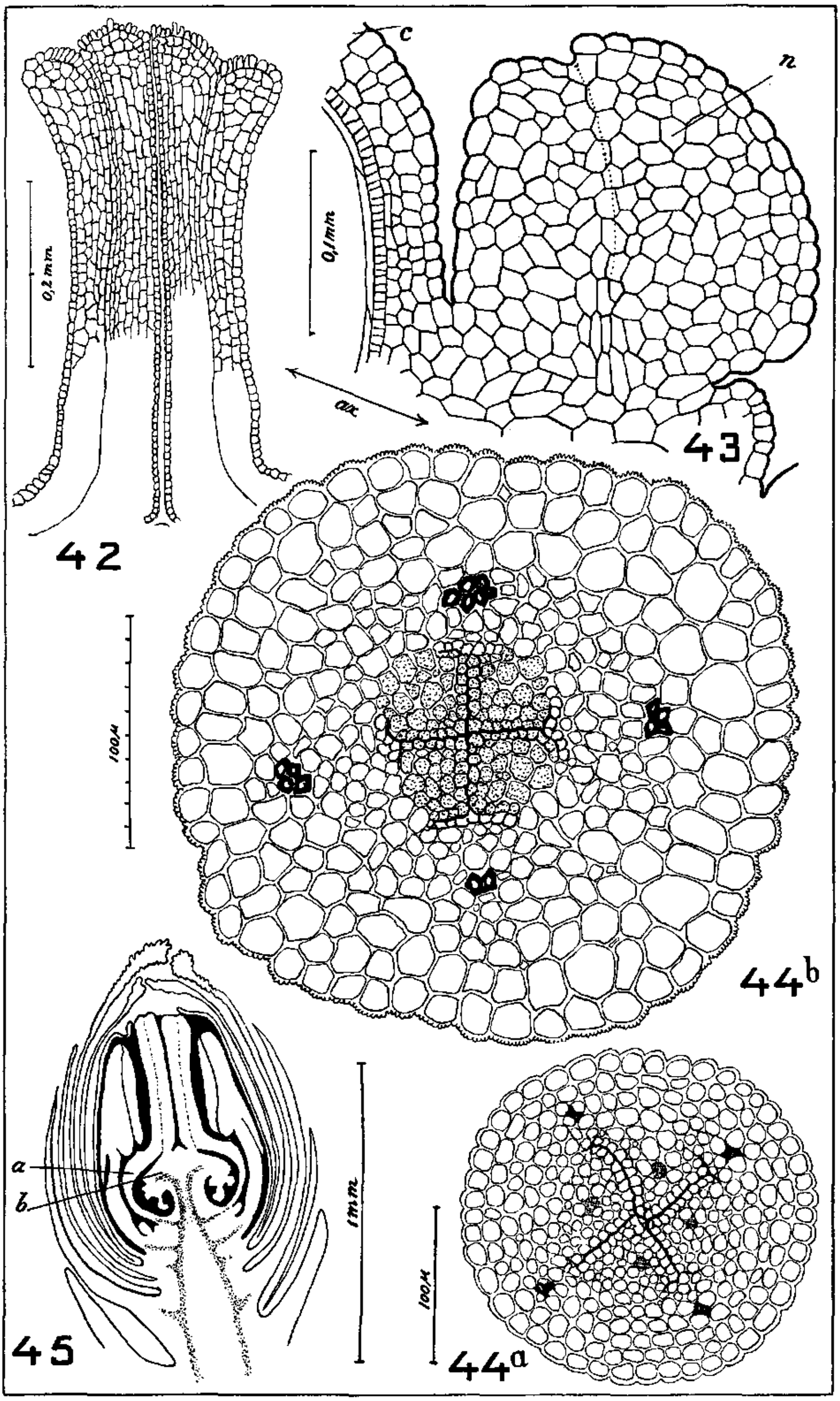


Fig. 42—45.

pressure in the direction of the longitudinal axis. Also the smooth, hard outer surface contributes to this. The two outer sepals may be placed radially as well as tangentially with respect to the main axis.

The corolla is more or less bell-shaped (Fig. 38a, b) and bulges out at the base. Mostly the 4 corolla tips are a little longer than the coalesced part. Their structure is different from that of the sepals, the corolla persists like the calyx, but it shrivels and loses its shape; the thick-walled straw-cells are lacking (Fig. 40b, c). Also the surface is smooth on both sides. The walls of the epiderm cells are scarcely thicker than those of the intermediate cells. At the base of the corolla, where the sutures of the coalesced petals are, cushion-like swellings are found, consisting of so-called swell-tissue (Fig. 99, 100). These pads strongly increase in size against the time the flower expands. By their position just against the sepals they press them outwards and so aid the unfolding of the tightly closing sepals of the bud (Fig. 56). The corolla-tips which at first are bent towards each other and so protect the sexual organs, spread out when the flower opens, and bend outwards. The zygomorphism finds its expression in the lowest corolla tip being bent out a little further and in the sexual organ being more erect. In this way the position of the gynoecium with respect to the opening of the corolla tube becomes excentric. In full bloom the style is a little turned upwards or curved, so that it generally lies along one of the corolla tips (Fig. 38b).

The stamens have their specific structure, like the other parts. They have their origin on the disc, which also carries a vaulted, annular nectary-cushion (Fig. 56b) round the base of the ovary, so that the base of the stamens is embedded in this cushion (Fig. 100). The filament has at its base an almost triangular cross-section, but is soon flattened bilaterally (at the level of the greatest circumference of the ovary) (Fig. 99, 100) and retains this section up to the place of attachment of the anthers. The filament which in the juvenile flower-bud is at first straight, is prolonged in an S-shape, the S being situated over the ovary (Fig. 56a). The anthers are bilocular, but in a ripe condition show no endothecium (Fig. 52). Each theca opens by a longitudinal slit in the side. This is exceptional with the *Ericoideae*, where as a rule the pollen is shed through round pores in the top part of the anthers.

The epiderm, consisting of small, loosely contiguous cells, is dissolved in places (Fig. 52b) and recedes in order to give passage to the pollen tetrads. At the base of the anthers two downward toothed appendages are found, — anther-spurs which, when touched in the flower, cause the anthers to vibrate, by which the pollen is shaken out of the thecae (Fig. 50a, b). The top of the theca ends in a little horn, so that each anther shows two little horns. The name "Bicornes" is derived from this characteristic, because it is frequent in this family-group. The basal portion of the anthers has the greatest capacity, towards the top they become narrower. The colour of the ripe anthers varies from light to dark brown. The

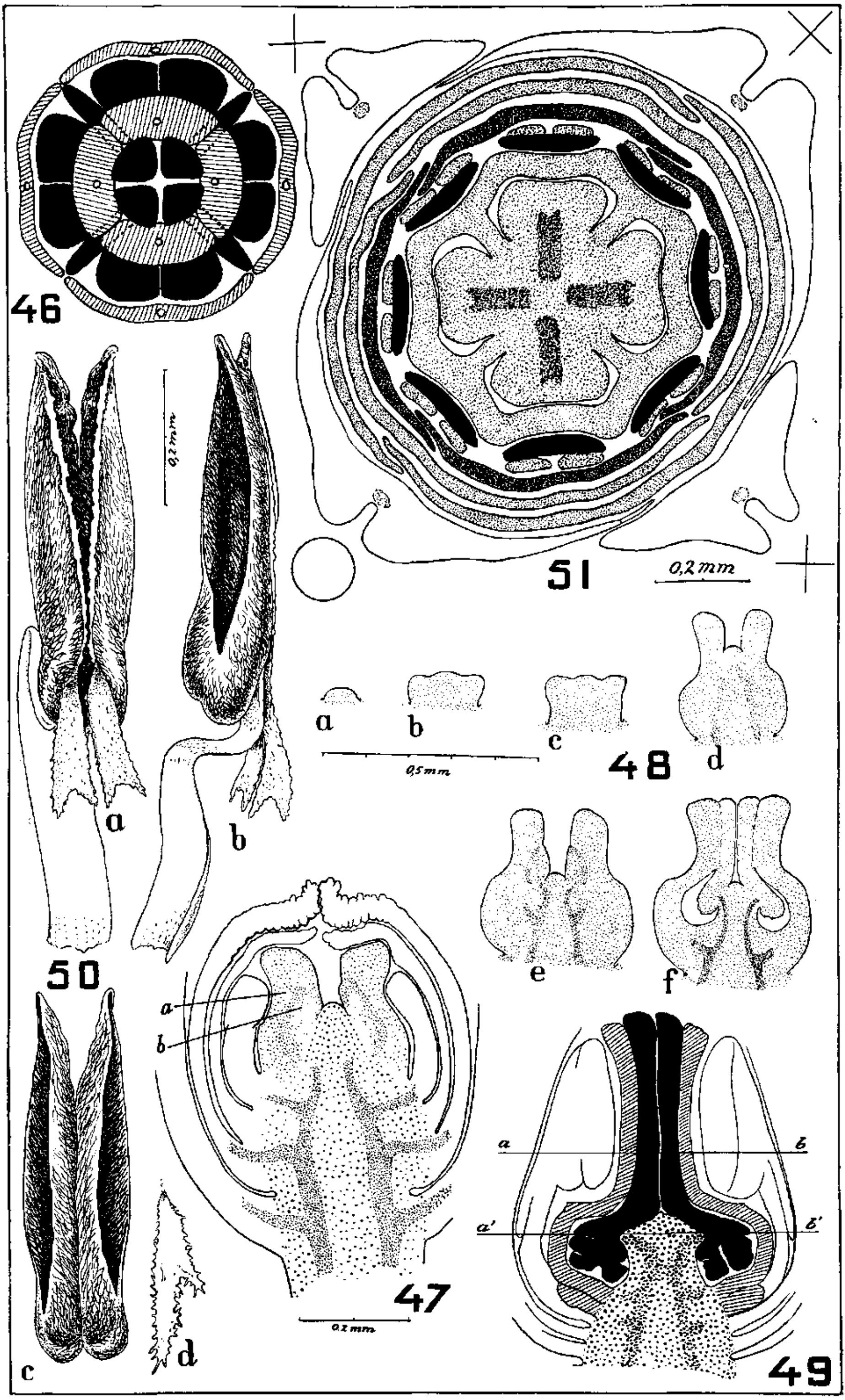
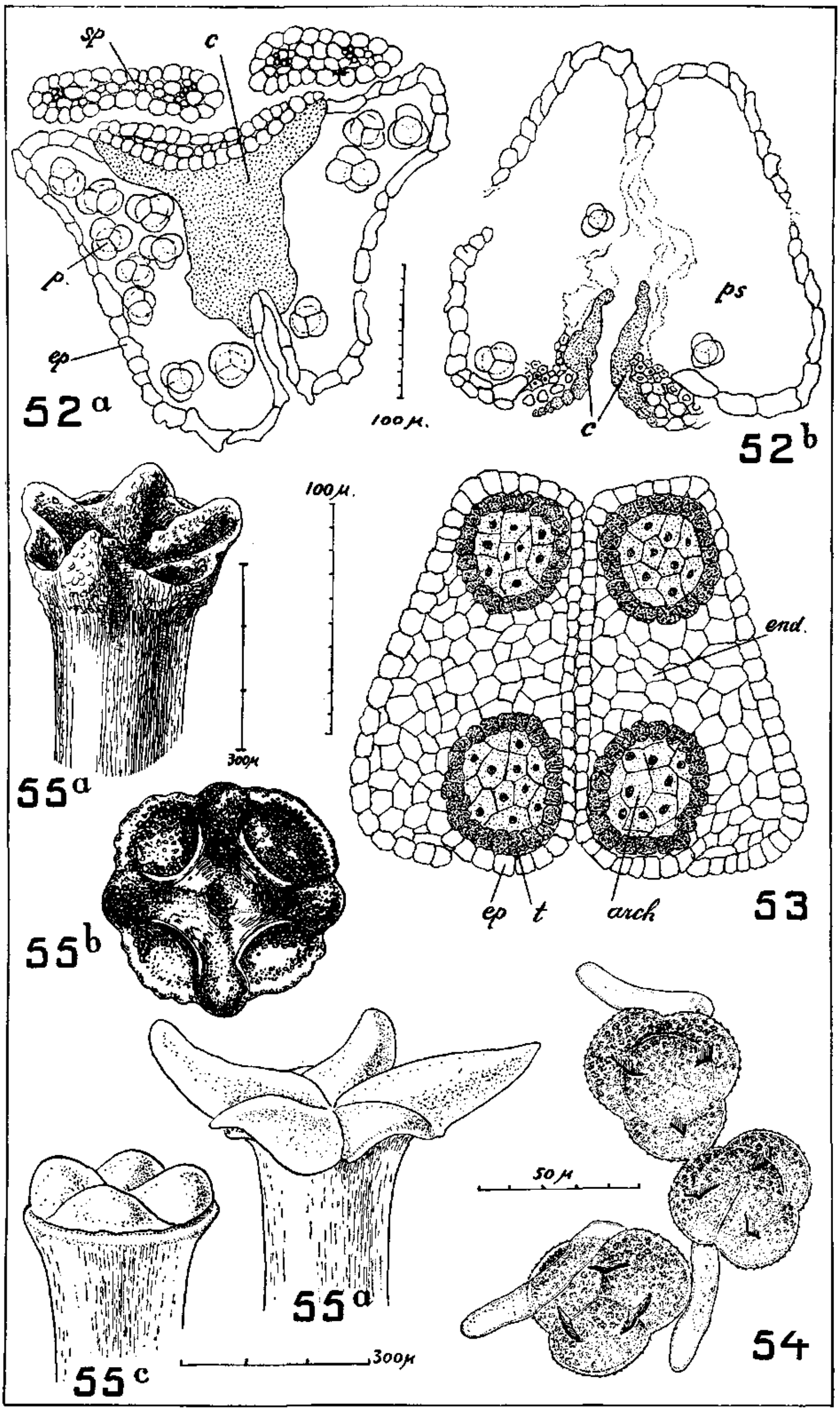


Fig. 46—51.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300μ
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Fig. 52—55.

epiderm cells of the anthers are somewhat elongate with an undulated outline and a dotted outer surface (Fig. 41a). The pollen has a light grey colour and consists of pollen tetrads of 30—40 μ diameter, with a warty surface. The pores are slit-shaped and fit two by two against each other, so that each tetrad has 12 pores and each grain consequently 3 pores (Fig. 54).

The gynoecium is rather complicated and shows some peculiarities by which Calluna occupies a quite individual position among the *Ericaceae* (see also under Fruit and Seed). The ovary is quadrilocular and contains in each loculus several seed-buds, as a rule 6 to 8, seldom 10, of which on an average no more than 4 to 5 become seeds. The orientation of the seed-buds is anatropous, sometimes skewly heterotropous, and they have only a single integument. The micropyle in the newly expanded flower communicates with the loculus of the fruit and this in its turn with the duct in the style and with the open air, so that here a very old, primitive condition has been perpetuated, as it is found with the *Gymnosperms*, namely that the ovule has direct communication with the open air. So the growing pollen tubes need not pierce an obstruction of tissue.

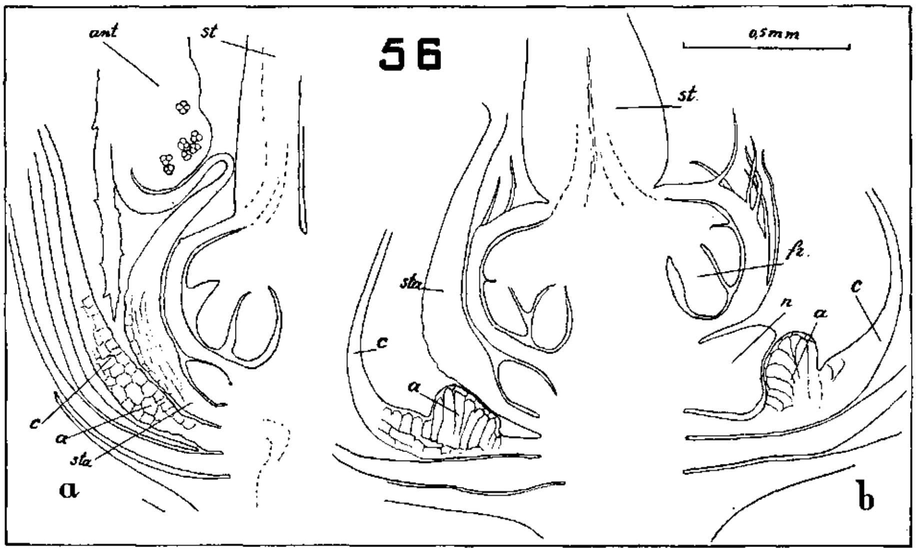


Fig. 56.

The placenta stands perpendicularly to the longitudinal axis and is connected with the median partition-walls of the ovary. The style-duct consists of a central passage and four median side-wing ducts (Fig. 44a, b), issuing into it, each lying opposite a corresponding compartment of the ovary (Fig. 46).

In the opened flowers the style is longer than the sepals and has near the stigma a club-shaped dilatation, consisting of 4 lobes which are slightly concave above and alternate with the compartments of the ovary. The style-duct and its wings are coated with a small-celled epiderm (Fig. 42, 44). Of a mantle-shaped enclosure of the stigma, which is present in many *Ericaceae*, some indication is also found with Calluna, especially in the juvenile stages of the flower-buds (Fig. 48, 49) (see also under: Periodicity of the flower-formation).

F. Fruit and Seed.

The small, melon-shaped capsular fruit has, when ripe, a diameter of no more than 1.5—2 mm. Its cross-section is octagonal (Fig. 51, 98 and 99) and it is always a little broader than high. The somewhat flattened apical part round the insertion of the style is more or less provided with trichomes (Fig. 56b). With strongly haired forms also the sides are sometimes a little hairy, especially along the sutures of the carpels. The four carpels dehisce by detaching themselves from above, as well from the base of the style as from the septa. The central part constitutes with the placenta and these septa a coherent entity, which persists as such after the fruit has shrivelled (Fig. 60a, b).

The fruit-wall consists of a coarse-celled epicarp, a mesocarp with one or a few cell-layers and an endocarp of two layers (Fig. 65a). This endocarp is built up of long-drawn, thick-walled cells, with a narrow lumen and resembling fibres (Fig. 65b). In the two layers these cells lie crosswise, which makes the fruit-wall considerably stronger. Before ripening the mesocarp cells contain chlorophyll and often also anthocyanin. Afterwards the fruit-wall is lignified but retains its shape, even after the seeds have matured.

The entirely different structure of this septifragal capsular fruit of Calluna, which is unique not only within the family of the *Ericaceae*, but even within the family-group of the *Bicornes*, deserves closer attention, as it may give us morphological indications, elucidating the moot problem of the axillary placentae and the occurrence of a so-called "Stengelkrug" (stem-jug, HAGERUP, 1936). Whereas with the *Rhododendroideae* the septicidal and with the *Ericaceae* the loculicidal capsular fruit is found, *Calluna* is the only genus with a septifragal capsular fruit, which is here of the marginal type.

BAILLON, HUISGEN, EICHLER, HAGERUP and others have occupied themselves with the structure of the fruit of the *Ericaceae*. The first two investigators were of opinion that with the *Ericaceae* the placentae were separate formations of the central axis, quite independent of the capsular wall, therefore. EICHLER (1875, p. 341) on the other hand, considered the placentae as well as the fruit-septa as parts of the four carpels, the edges of which would have been folded inwards. HAGERUP (1934, p. 71 and 1936, p. 52) however, seems more inclined to the conception of the former investigators and speaks of a separate central organ in the fruit, the so-called "Stengelkrug" (stem-jug).

Now, in order to make out how the fruit of Calluna is built up, I examined

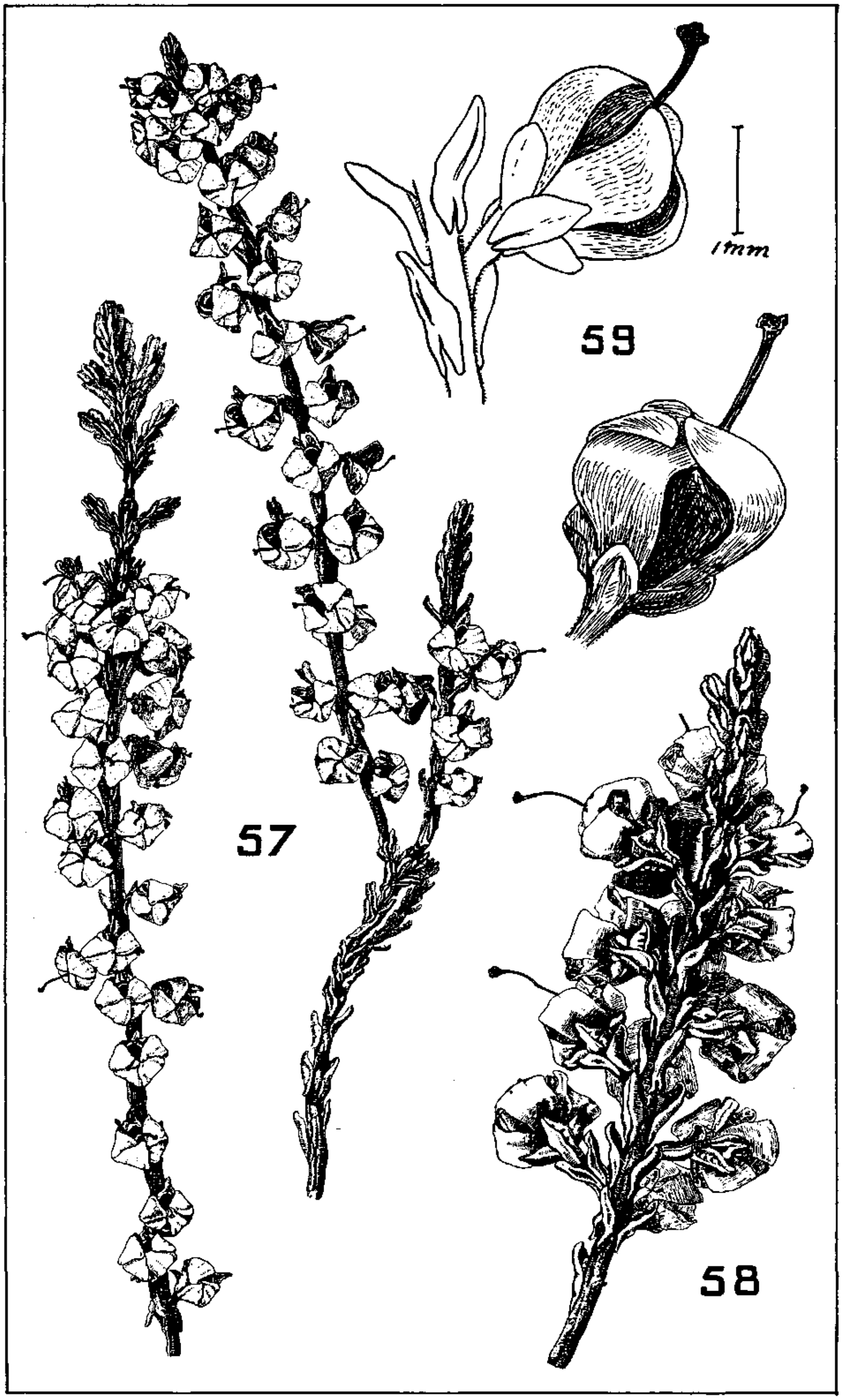


Fig. 57—59.

its development by comparing median longitudinal sections of young flower-buds. The following image is obtained (see Fig. 48). The place where the ovary will be formed is at first the hemispherically vaulted main vegetation-point in the flower-origin. Then upward growth seems to stop, for round this vegetation-point there arises an annular wall, which becomes continually higher and elevates itself far above the apparently stagnant main vegetation-point, so that a cup-shaped hollow is formed (Fig. 48d), probably because the 4 carpel-primordia, which later evolve to the fruit-valves and the style-mantle, have from the outset coalesced along the edges. So the style is at this stage hollow and tubular.

Quite near the stagnant main vegetation-point the feeble outline of a new primordial ring now becomes visible (Fig. 48e). In a somewhat more advanced stage this second carpel whorl has been pushed up into the primary style-cavity and also 4 lobes have grown out sideways (the future septa?). In the 4 spaces, produced in this way inside the ovary, the 4 placentae then grow out sideways. After this the seed-bud primordia are formed at the base of these distant placentae.

This state of things puts BAILLON, HUISGEN and HAGERUP in the right, anyway as far as I could gather from the ontogenetic development.

To this must be added that with a full-grown flower-bud, just before the anthesis, the vascular-bundle cylinder of the flower-twig is continued as such up to the level of the placenta, that is considerably higher than the insertion of the 4 carpels. Now this vascular-bundle cylinder is morphologically typical for a member of a stem and cannot be explained by simply assuming 4 folded carpels, the less so since at the level of the insertion of the carpels 4 separate strands of vascular bundles are clearly seen to branch off (Fig. 49), as it is regularly observed with the whorls of the stamens and the perianth.

The question remains open, however, whether the interior of the ovary has been built up out of a single or out of two separate, successive, at the same time alternating, leaf-whorls of 4.

Perhaps the simplest solution is to assume two whorls of four, situated immediately above one another, namely 4 septa and 4 placentae. This would then be a repetition of the double whorl of 8 stamens. Still, in my opinion, it is quite possible that only 4 metamorphosed leaves have each time given rise to the formation of a septum plus two placenta-halves, lying on either side of it. These latter would then have coalesced, while higher up in the central portion of the style only a coalescence with the style-mantle has taken place, so that 4 flat wings of the style-duct, corresponding to the fruit-loculi, remain free (Fig. 46). The 4 uppermost carpels would then correspond to the style-segments, delineated in the cross-section by the cross-shaped system of the style-duct, and to the 4 septa.

The main point, however, is that, as is also my opinion, the Calluna fruit is not simply built up out of 4 metamorphosed leaves, but contains a central column, which must be regarded as a stem-organ ("Stengelkrug", stem-jug). On this middle column, after the 4 lowest carpels have already coalesced at their edges, a second, and maybe a third, more elevated whorl of carpels is formed, evolving as well to the 4 septa as to the 4 placentae and the inner part of the style (cf also Fig. 66 and 61).

The seeds are minute and of a clear brown colour, sometimes also light or darker brown. According to the measurements of FAUGRI (in NORDHAGEN, 1937, p. 48) their length ranges from 0.278 to 0.715 mm, with M = 0.51 ± 0.1. Their shape is more or less bilaterally flattened with an egg-shaped or ellipsoidal outline, but for the rest is rather irregular (Fig. 62). Generally 5 to 8 seeds develop in each loculus. Under favourable conditions the number of ovules in each loculus may amount to 10.

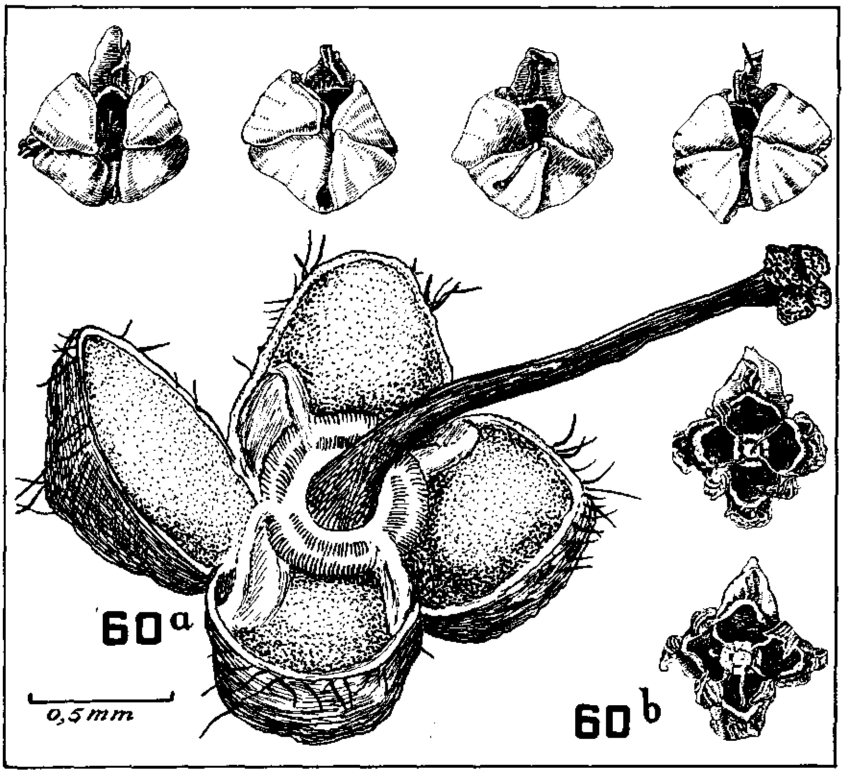
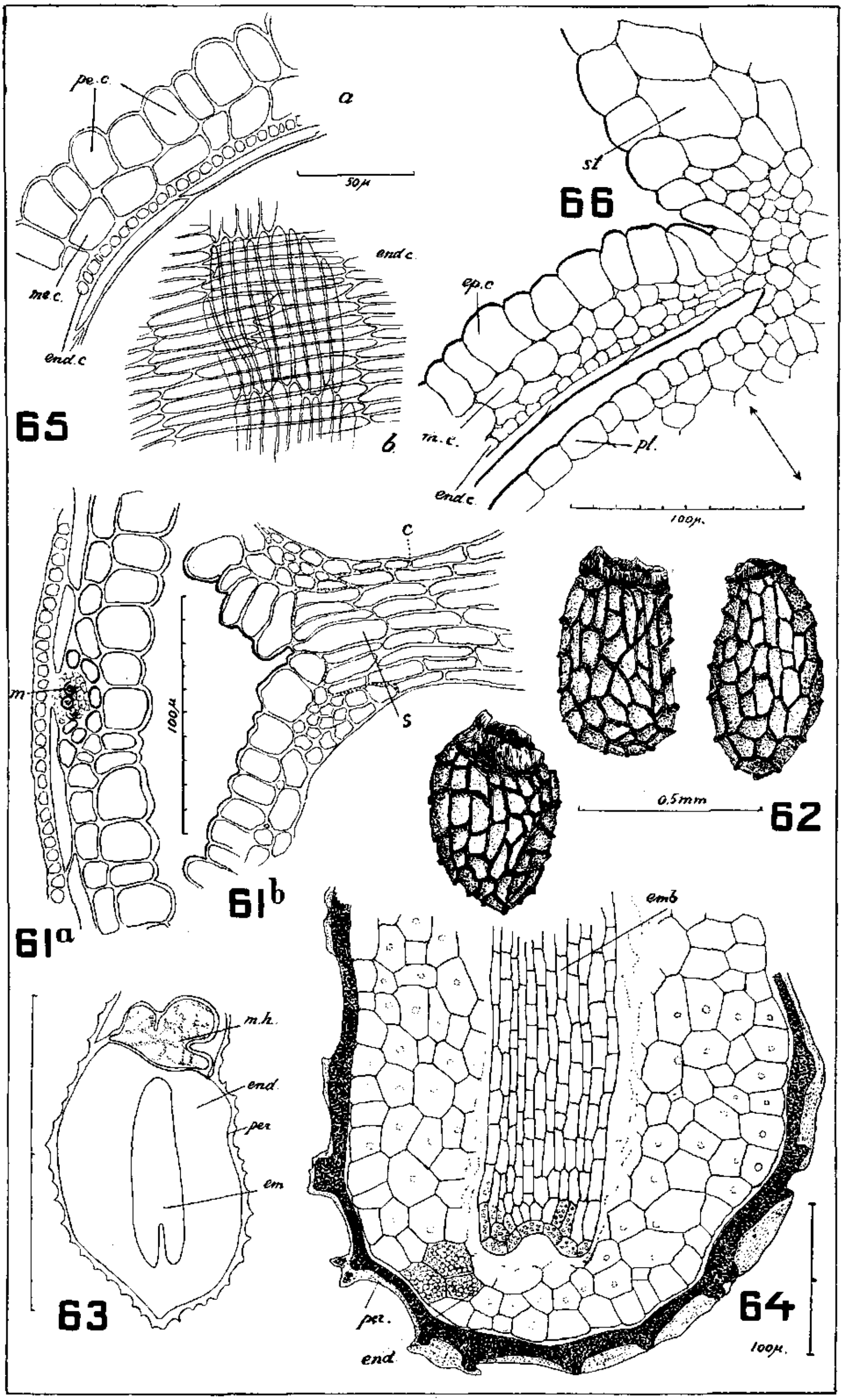


Fig. 60.

The skin is simple and consists of a rather thin wall, developed from the big epiderm cells of the integument, and reinforced by a meshwork of ribs. When these cells have died, their outer wall has come to lie against the inner wall, while the sides have remained (Fig. 64), with the result that a great number of depressions is found where otherwise the contents of the cells would be.

Under the skin lies no layer of air, but the endosperm follows directly, consisting of a very thin-walled parenchymatous tissue, the cells of which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emb
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63
per.
end
64
100μ.

Fig. 61—66.

are filled at first with amylum and later with aleurone grains and oils. In this the whole embryo is embedded, it is built up of considerably smaller, somewhat elongate to polygonal cells, also filled with aleurone and oils. The embryo lies with its root-end towards the micropylar haustorium and is long-drawn and cylindrical, with clearly differentiated cotyledon primordia (Fig. 63).

As soon as the fruit is ripe the sutures between the four carpels mutually and of the 4 septa burst easily, probably because the carpels and septa lignify and in this process shrink or warp a little. Also the style dies soon after fertilization and shrivels a little. In dry weather the carpels then burst at the top and turn over and thus would free the seed, if it were not that the 4 straw-like sepals had already during the maturing of the fruit bent themselves over it, partly overlapping and leaving on the upper side of the horizontal flower a narrow slit, through which the seed-grains may be shed by vibration (Fig. 60b). The carpels react readily on moisture and drought, they shut at once in a moist environment and open again by dryness. So they execute xerochastic movements, in contrast with the 4 folded sepals which always retain their position, even when immersed in water. With *Erica* these xerochastic movements of the carpels do not exist, but they are of less importance there, because after the flowering the urn-shaped, monopetalous corolla affords a much more effective protection against moisture than the polysepalous calyx and the shrivelled corolla of *Calluna* (NORDHAGEN, 1938).

II. LIFE-HISTORY.

A. Spreading and germination of the seed.

When the fruit was just now described, the peculiar function was pointed out of the 4 straw-like sepals as an envelope for the fruit and a strewing-organ for the seed. Only when the flower twigs are shaken by gusts of wind, the seeds are shed and at the same time spread. In our latitude this happens in dry and windy weather in October and November and sometimes begins already in September. With rain and in damp air the carpels shut and the seeds cannot be strewn out. So the carpels carry out xerochastic movements, the calyx capsule however is not affected and the slit on the upper side (Fig. 57) remains open.

According to the countings by NORDHAGEN (1937, l.c. p. 51) the capsules as a rule contain from 20 to 32 seeds. LLOYD PRAEGER (1911, p. 78) states that the seeds of Calluna settle in still air with a velocity of 114.3 cm per second, corresponding to a distribution-radius of about 100 *m*, *if the wind-velocity is* 10 *m/sec*. But the seeds vary much in size, from 0.278 to 0.715 mm, and so the above results are only rough numbers. With wind velocities of 30 to 40 m/sec. the seeds will according to NORDHAGEN be certainly carried to 0.4 km. Of course other factors may hinder or aid the spreading, such as accidented ground, transport by water and animals. Woodgrouse and blackgrouse, for example, often swallow Calluna capsules, and also elks and deer spread the seeds, according to HEINTZE. WARMING states that in a winter-storm Calluna fruits were blown from West Sweden across the Cattegat as far as the Baltic coast of Jutland over a distance of at least 16 miles. Also dropped fruit-capsules may be rolled away by the wind or taken up and carried off. In regions with a prolonged snow-cover during the winter-months the autumnal sowing may be retarded until the winter is over. As the number of seeds produced by each plant and per square meter of heath-vegetation is large, according to NORDHAGEN about a million seeds per m^2, we understand how this species can in oligotrophic regions (sandy plains, high moor-ridges, etc.) occupy the ground very quickly. The numbers, given by NORDHAGEN for the heaths along the Norwegian coast are perhaps rather high, anyway for the optimal heath-regions in N.W. Germany, Holland and East Britain. Basing ourselves on my counts on a robust Calluna plant (p. 12), we may assume that a square meter of a compact field-vegetation holds five plants with 7000 fruits each, which would be a production of ± 800.000 seeds per m^2, or $^4/_5$ of the above-mentioned result. Sometimes large numbers of fruit-capsules are torn off in a storm and, filled with seed, alight on an always moist soil, e.g. moss-peat or humus, where they cannot open. Then the fruits remain shut for a long time and the seeds can only germinate when the fruit-wall has decayed and admits moisture. I repeatedly came across such fruits, from which the seedlings came out in bundles (Pl. V, 6).

The wind is the chief agent in spreading the Calluna seeds. On uneven ground the fruits and seeds will settle in low and sheltered spots and germinate in large numbers. One finds many such germination-beds in dry hollows on peat-moor, in dried up trenches or on moist moss-pads and moist bare heath-soil, overgrown with algae. The remarkable point is that *Calluna* germinates excellently on the humus formed from its own refuse. Generation may succeed generation without a decline in the vegetation being perceptible. As soon as the older plants die off, in our latitude generally when between 15 and 20 years old, and more light penetrates to the soil underneath, the young *Erica* and *Calluna* plants grow up there and fill the open spaces again. This is the process in the region of optimal development of *Calluna*; the vegetation there rejuvenates itself (Pl. XXV). This phenomenon is often met with in oligotrophic media, e.g. in the *Sphagnum* vegetations, the *Erica-tetralix*-fields and suchlike. Much more difficult is the regeneration of the Calluna-vegetation in dry sandy regions, although in a wet sea-climate even on the tops of high dunes, e.g. in the North Sea island Texel, Calluna seeds may germinate and develop into sturdy plants, since in those places the condensed water may keep the sand moist for a long time, while rain and snow soon remove salt concentrations. I observed this effect of condensed water during a prolonged drought in summer. In the forenoon the tops of the dunes were covered with a layer of very moist sand, which could only be explained by the condensation of water-vapour.

In Central Europe the Calluna fruits ripen from half September until the beginning of December. At the end of November by far the greater part of the seed has been strewn. In the middle of October numerous seedlings are already found on damp heath-fields. But the germination, which depends very much on light and moisture, also takes place in the last months of the year and a considerable fraction even germinates in spring. In June I still found young seedlings of Calluna on fairly dry heath-fields, a.o. near Hilversum.

If the sunlight has full access and under otherwise favourable conditions a few seeds germinate already after a week, the great mass however after 2 to 3 weeks. Seeds laid out in the dark hardly germinate at all. According to KINZEL (1913) Calluna seeds, after having lain for two years in the dark, will soon begin to germinate when transferred to light. GREVILLIUS (1928, p. 134) asserts that Calluna seeds, previously heated to 67—70° C for a few hours, germinate more quickly, especially in autumn.

By imbibition the seed-grain swells to about its double volume, after which the seed-coat rips and lets the root free on the upper side (the embryo lies with the rootlet upwards in the endosperm, which is rich in oil). The root first develops to a length of a few millimeters and in doing this soon curves geotropically, in order to penetrate into the substratum and to fasten the young plant. In this it is not always successful, so that the first rootlets grow along the surface until they can somewhere penetrate into it. Then the hypocotyl axis erects itself and the two cotyledons, which for a fairly long time remain enclosed within the seed-coat and the soon consumed endosperm, diverge. The coat is shed or clings for a time to one of the cotyledons and at last drops.

B. Development of the seedling until the flower-formation.

After the cotyledons have diverged they assume a horizontal position ⊥ the hypocotyl axis. The cotyledons are short-stalked or at any rate narrowed, and between the curved leaf-stalks lies the bud, which, being bare, at once grows out by extension and by forming the leaf-primordia near the main vegetation-point (fig. 67). These first leaf-primordia grow out to primary and following leaves, which the young Calluna plant continues to form for a long time. Even the first side-branches of the main axis may still bear leaves of a primary character. The hypocotyl axis remains short and reaches a length of about 0.5 cm, though with etiolated plants it may extend.

The most advanced autumn-seedlings make so-called winter-buds, i.e. the internodes become smaller and smaller and also the size of the leaves decreases against the rest-period in the growth. In the following year this accumulation of smaller foliage-leaves marks the place where the new long-shoot started growing. Hibernated seedlings can often be recognised by this, though not always, as the young seedlings, germinated shortly before the winter, grow on in early spring without a trace of winter-buds being perceptible. Even such plants may attain bloom within the growing-season, although this is exceptional.

The seeds, germinated in late autumn (October—November) hibernate as seedlings, before having formed primary leaves. During the winter all sorts of seedlings are met with, from those with only 2 cotyledons to the more advanced with side-shoots on the main axis. In our country the seeds, germinated in October, may under favourable circumstances bloom in the following year in August and September.

Thus we can distinguish three sorts of seedlings in spring: a. more advanced seedlings with winter-buds, b. young seedlings that hibernated with nothing but two cotyledons, c. juvenile plants, germinated in early spring. This latter category is in diverse stages still met with in June and it is possible, even probable that Calluna seeds germinate throughout the whole year, except during the winter-cold.

When the seedling has advanced so far that side-shoots have formed, on which process the quantity of light has great influence, at a certain moment the manner of growing changes. Up to now there has been a regular constriction of leaf-primordia of primary or following leaves (Pl. I). There is as yet no or very little differentiation in the length of the internodes of the main axis and side-shoots, or in the shape and position of the leaves. Now, during a dry period or by some other external cause (light?), we see the internodes of the main axis become longer and also the foliage leaves, belonging to them, become larger and change their shape. They get long spur-like appendages and begin to differ considerably from the compact short-shoot leaves on the side-shoots, which remain short and stunted. Usually from the lowest side-shoots of the seedlings several erect long-shoots are formed, parallel to the main axis, the result being the shrub-like habit. Often also long-shoots sprout from the root-base and hypocotyl axis, when the seedlings have been frozen up in winter.

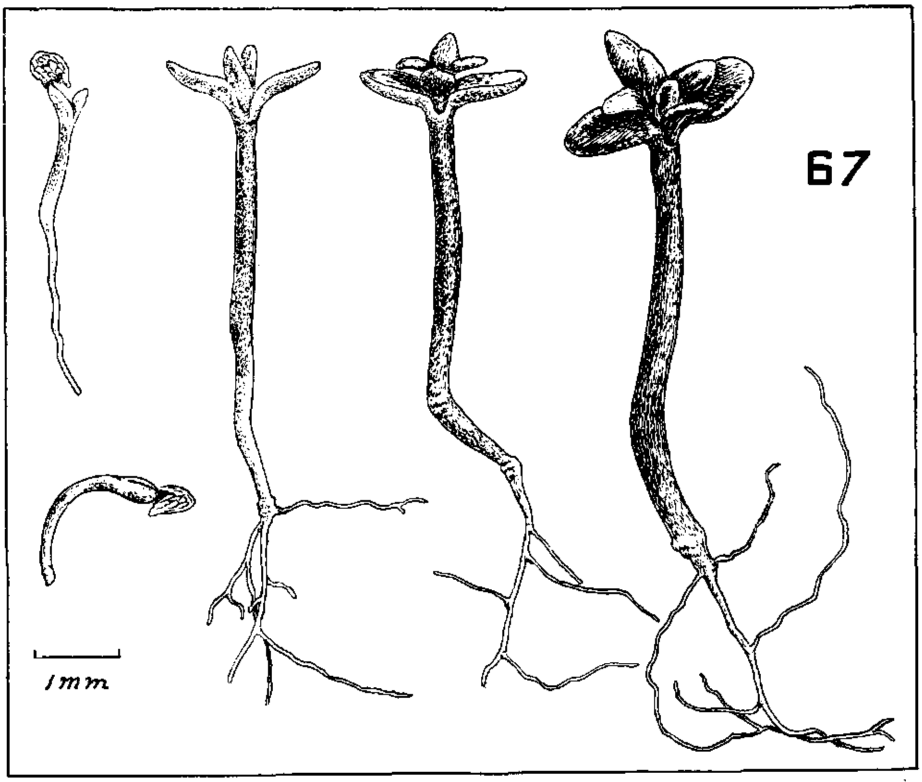

Fig. 67.

When the plants grow more closely together the main stem may at first develop more vigorously, while the side-shoots lag behind. Also the roots often undergo a similar influence. On broad plants one generally finds the root-system grown out in breadth, and conversely plants that have remained narrow have a root-system which has grown out little in breadth, though this means nothing for the depth to which the roots have penetrated into the soil. Nevertheless, I repeatedly met on burnt down heath-fields steep-growing seedlings, although the vegetation could not be called dense there. From the axils of the primary leaves side-shoots sprout by way of exception, but from the axils of the long-shoot leaves they sprout regularly as soon as the internodes have reached a certain length (Pl. I). These side-shoots may be of three kinds. Firstly they may be again long-shoots with foliage-leaves only or partly with flower-bearing twigs. Secondly they may be assimilation-shoots, i.e. densely leafed short-shoots, and thirdly they may be flower-bearing twigs, always ending in a terminal flower-bud. A vigorously developed long-shoot produces in one growing-season assimilation-shoots as well as fructiferous shoots. Usually the short-shoots of the preceding year then die off and are dropped as a whole. Some of these short-shoots however go on growing and may again produce long- and short-shoots. This happens especially in places where enough light has access through openings in the foliage roof.

The long-shoots begin to extend as soon as the winter-buds come out, but the first internodes remain short (Fig. 75). Then their length increases fairly regularly until the vegetative-floral zone has been originated. After this it decreases again up to the winter-bud. By way of exception longer internodes may again develop after the vegetative-floral zone, and a second vegetative floral zone may even be formed, but this is very exceptional and takes place especially if the main vegetation-point is untimely destroyed by mechanical injury.

The intercalary growth was examined by measuring the length of the internodes on a number of full-grown long-shoots, collected after the growing-season (12 January 1935), and stripped of leaves and twigs. At the base of the year-shoot are the closely packed leaves, or their remains, of the short-shoot of the preceding year. These internodes have been disregarded here; the first longer internode was reckoned as the beginning of the year-shoot. In Fig. 76 the lengths have been plotted vertically. Although the measured year-shoots came from different plants, the course of the intercalary growth may on the whole be said to be similar. In a single case a year-shoot showed a deviating course (above point 29). On closer inspection it turned out that by a mechanical disturbance the top had been lost. Then from one of the last eyes a new long-shoot had formed, the internodes of which remained much shorter than on the primary long-shoot.

The number of internodes formed was rather divergent with different individuals and also on one and the same individual. On the examined long-shoots the highest number was 30, the lowest 20. Considerably smaller long-shoots were found, but these were unsuitable for counting because of the small number of internodes.

It has already been pointed out that apparently there is a relation between the shape of the leaves and the length of the internodes. The shorter the internodes, the shorter are also the spur-like appendages of their leaves on the same long-shoot. This does not mean that for a certain length of the internode all individuals always have the same type of leaves, for this depends on individual differences; there are forms where the long-shoot leaves always have relatively short spurs and others where they are particularly long (Fig. 24e and f).

The young parts of the stem are herbaceous and coloured from bright green to reddish brown by a varying chlorophyll and anthocyanin content. During the herbaceous state the stems are very sensitive to drought, soon become limp and then droop. The drooping young stems may retain this position for a long time if lignification sets in soon. In spots with great fluctuations between wet and dry, e.g. along the sides of furrows, one often notices such plants with drooping branches, subject to speedy desiccation, which then imitate the true creeping and pendent forms. It is possible that the true creeping and pendent forms owe their origin to a growth-stage in which the limp herbaceous stems curve by lack of turgor and then are fixed in this state by incipient lignification. So these true creeping and pendent forms would represent an extreme case of the just-mentioned furrow-side plants. Experiments might throw more light on this point.

The young foliage-leaf is as a primordium a more or less oval or long-drawn elevation, which on the side, turned away from the axis, lags behind in growth as soon as a central vascular bundle has originated. The groove formed in this way becomes relatively deeper and narrower, as the two sides and the groove in the leaf (the outside) increase in size (Fig. 80), while between the central vascular bundle and the epiderm of the bottom of the groove a sclerenchymatous, no longer growing tissue has formed as a reinforcing mantle round the ventral side of the principal vein (fibro-vascular bundle) (Fig. 25, 33b). This construction makes the leaf strong and also by the thick cuticle and epiderm layer it is resistant against extraneous violence, especially friction by wind. Calluna may be said to have been built to stand strong wind. By the speedy lignification the fine system of twigs is tough and very flexible, and on account of the smallness of its leaves this necessitates that the leaves are specially adapted against knocks and rubbing. The leaves have no stalks, their base is attached directly to the stem, they have the shape of short needles with a smooth to felty surface, and the two spur-like appendages provide an additional support against tangential movements. Besides, the leaves on the short-shoots are so compact that they overlap, thus constituting a composite organ in the shape of a plain column. The same holds for the long-shoot, which has a large number of not much projecting side-shoots, mostly sprouting from all leaf-axils, except the lowest, the whole showing again the figure of a column. Without doubt this shape is better than any other adapted to the functions which this form of life has to fulfil, namely to resist the action of wind at right angles to the upright frame-branches, the force of which is broken by the combing action of the numberless short-shoots and leaflets; secondly to regulate assimilation and transpiration under strongly varying conditions, which is achieved by a great increase of the total surface and of the palisade-layer of the leaves in a relatively very small space; thirdly to protect the vegetative-floral zone of the new year-shoots by a strengthening of the flower-buds, for which purpose the flower-bud is specially shaped and the sepals are hardened, while also the flower-branchlets are strengthened by numerous leaf-organs, as prophylls, intermediate leaves and bracts.

To this should be added the power to take in water from the atmosphere, independently of the roots.

All this gives us some idea of the wonderfully appropriate structure which this plant has acquired in its medium of optimal development and distribution, namely on poor open plains of sand or peat-moor and on barren humus-covered rocks, or on mountain-slopes without any higher wood-growth, where wind, sunshine, rain and heat-fluctuations have free scope and make high demands on the structure of the there growing types of ericoid dwarf-shrubs (see also under Geography).

C. The formation of the sex-cells.

As soon as the flower-bud has reached a length of about 0.8—1 mm and the bracts, which at first completely enclose the sepals, begin to diverge a little, so that the white smooth little bud just becomes visible between them, the moment has come for the reduction-divisions of the embryo-sac mother-cells and pollen mother-cells.

Because on a long-shoot all sorts of successive stages of the flower-buds occur, and also of the meiosis, it is practical, when investigating chromosomes, to fix a number of successive buds of ± 1 mm length simultaneously in a Carnoy-solution (Alcohol, chloroform, acetic acid : 6 : 3 : 1).

The prophases of the pollen mother-cells are characterised by the chromatin-corpuscles in the nucleus and the subsequent formation of leptome threads (Fig. 68, 1—2). Next follows, by conglomeration of the leptome threads round the nucleolus, the synapsis stage (Fig. 68, 3—4), and then the zygonema stage with the double threads, and the diakinesis stage (Fig. 68, 5—7). During this latter stage the number of gemini (= 8) can as a rule be clearly distinguished. On the diakinesis follows the anaphase (Fig. 68, 11—12), in which the chromosomes arrange themselves according to the nuclear plate and then move towards the two, meanwhile formed, poles of the mother-nucleus and there enter the interkinesis stage (Fig. 68, 13).

Also in this stage the haploid chromosome-number ($n = 8$) can be observed well.

Finally follows the somatic (homotypical) division, resulting in the formation of the tetrad (Fig. 68, 14—15).

The pollen mother-cells of Calluna and their nuclei are remarkably small. In the prophases the nuclei have a diameter of 7—8 μ and in the newly formed tetrads of only 3—4 μ. The chromosomes in the heterotypical

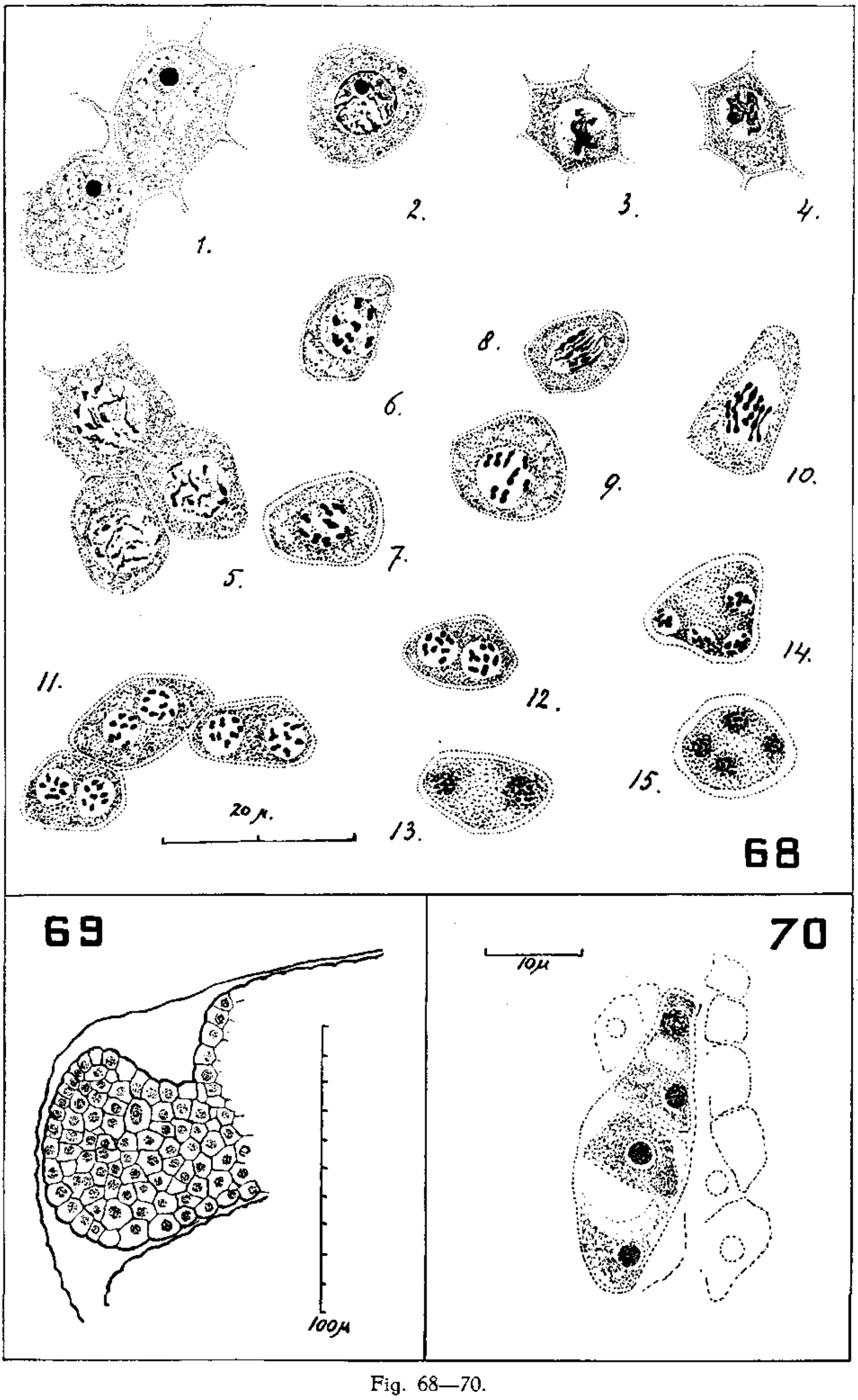

Fig. 68—70.

anaphase have a diameter of ± 0.5—1 μ. They do not show characteristic shapes, they are more or less spherical or drop-shaped, as in many *Bicornes*. As far as can be judged from the restricted number of species up to now studied, the haploid number 8 is an exception, though.

From the survey on pag. 28 it appears that *Calluna* and *Diapensia* are the only examined *Bicornes* species with the fundamental number 8. With the *Ericaceae* the fundamental number 6 would seem to prevail.

Sometimes the counting of the chromosomes with *Ericaceae* seems to give trouble by their remaining coupled in pairs in the heterotypical metaphase. HAGERUP (1928, l.c. p. 24) says on this point: "This pairing of the chromosomes in the metaphase is particularly marked in *Empetrum hermaphroditicum* and *Arctostaphylos uva ursi*. It may give rise to errors in counting; but in the anaphase the chromosomes are distinctly separate."

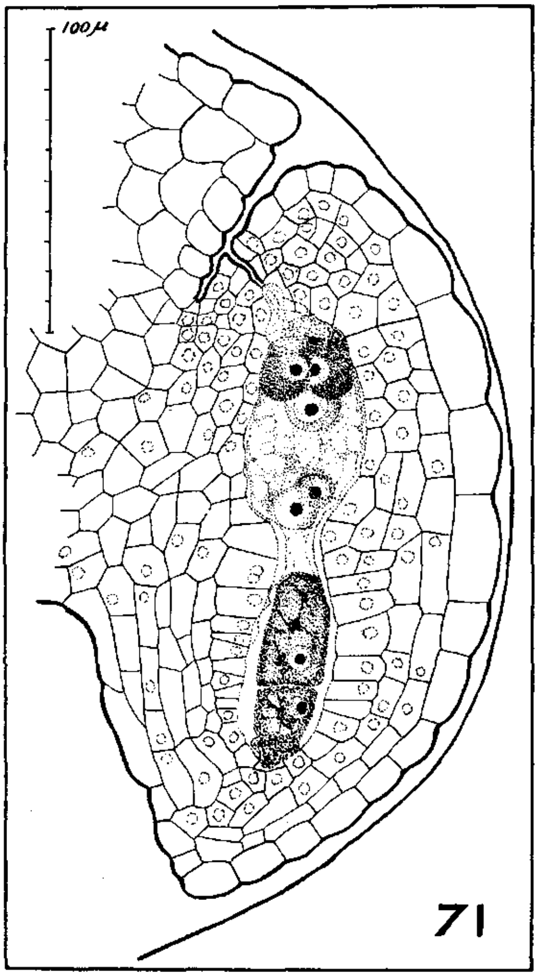

Fig. 71.

Also the conditions under which the plants grow may influence the normal course of the meiosis and according to the same author it would sometimes be impossible to count *Erica*, *Empetrum* and *Calluna*, when grown up in less natural surroundings (l.c. p. 25).

At the same time or somewhat earlier (SAMUELSSON, 1913, p. 108) the nuclei of the embryo-sac mother-cells of Calluna enter the heterotypical prophase. The seed-bud primordia are found as round knobs on the underside of the placenta. Soon after these primordia have become oblong, they curve and at the same time the only integument begins to develop strongly. The archespore is then clearly visible in the longitudinal section as a bigger subepidermal cell (Fig. 69). As soon as the nucleus of the archespore has attained the synapsis stage, also the integument has, according to SAMUELSSON (1933 p. 97 ff.), already developed so strongly that it has reached the top of the nucellus.

With the heterotypical division of the embryo-sac mother-cell the micropyle is already closed and does not seem to re-open until the ovule is ready for fertilization and the stigma for catching pollen, i.e., when the perianth unfolds (Fig. 71).

When the ovules are ready for fertilization they are anatropically orientated, consequently turned 180° (Fig. 71). Characteristic for the *Ericaceae* is the formation of two haustoria, situated at both ends of the embryo-sac. After the quadrinuclear tetrad-stage the archespore already begins to widen towards the micropyle and to replace the adjoining cells of the integument (ARTOPOEUS, 1903, p. 341). After the ordinary further divisions we see the octonuclear stage begin, when the lowermost of the four nuclei has multiplied by rapidly successive divisions. The three other macrospores of the tetrad are completely reduced. I have not personally observed these intermediate stages. The further development of the embryo-sac is either normal, or, as SAMUELSSON (l.c. p. 108) remarks, it is possible that the bi-partition in the upper one of the two mother-cells of the embryo-sac fails to take place, as he believes to have pretty certainly stated also with *Vaccinium uliginosum*. The two haustoria are after their situation respectively called : micropylar and chalazza- (casu quo : antipodial) haustorium. They arise from the adjoining cells of the integument and their function is, according to PORSCH a.o., to provide the embryo with food, at the expense of the tissue of the surrounding nucellus, c.q. integument.

With Calluna the micropylar haustorium is particularly strongly developed. The integument at first develops so strongly that the nucellus proper is entirely superseded by it. The innermost cell-layer of this integument then forms a so-called "mantle-layer" (tapetum, epithelium), a fairly regularly built cell-layer, serving for the nutrition of the endosperm-tissue and the embryo (PORSCH).

The rests of the nucellus are reduced, like the wall of the embryo-sac and of the micropylar duct. Only the middle portion of the embryo-sac has a stronger wall, contiguous with the plasm of the embryo-sac. The two ends of the embryo-sac are transformed into the just-mentioned haustoria. The cells round the micropylar duct become more or less lignified. The two haustoria get a strong wall of cellulose, loosely adjacent against the cuticle-wall of the narrowed middle part of the embryo-sac. From the cellulose-wall of the big micropylar haustorium anastomising threads then spread as a meshwork through the interior. The chalazza-haustorium remains much smaller. In a further advanced stage the narrow connections between the haustoria and the endosperm seem to become entirely filled with cuticular substance, so that the direct connection is stopped (cf. NETOLITZKY, 1926, p. 252).

The egg-apparatus now lies in a dilatation above the mantle-zone of the there narrowed embryo-sac. The antipodes degenerate after fertilization, but are none the less more strongly developed with Calluna than in many other *Ericaceae*. PELTRISOT (1904) has accurately investigated the formation of the endosperm. He is of opinion that it is formed by free cell-formation. SAMUELSSON (1913, l.c. p. 113) on the other hand believes to have observed here a successive cell-division. The just-mentioned dilatation of the embryo-sac begins to enlarge considerably after fertilization and initially contains 2 nuclei (synergids), which are reduced, and the ovule. This state of things arises after the micropylar haustorium has first absorbed the adjoining tissue and has considerably enlarged itself at its expense, by which temporarily more nuclei are incorporated in the haustorium. Then it ceases to grow and the ovule enlarges. Also the endosperm then begins to expand considerably and is only separated from the integument-tissue by a thin brown layer, consisting of cell-wall fragments.

When the embryo has at last reached its true size (rest-stage), also the interior of the micropylar haustorium has become filled with a curious web of threads, while the development of the chalazza-haustorium has entirely lagged behind. According to ARTOPOEUS (1903, p. 340) sometimes a small haustorium has already formed before fertilization.

During the formation of the multicellular embryo the micropylar haustorium has also considerably enlarged. The endothecium is absorbed, only its exterior layer of coarse cells is left. The aperture, connecting micropylar haustorium and endosperm is closed. In the ripe seed the micropylar haustorium is empty, but has partly retained its shape. The chalazza-haustorium and the antipodes-rests have then been reduced to an extremely small volume and are hardly recognisable as such.

On the germinating seeds little is at last left of the micropylar haustorium (Fig. 62, 63), it seems to be played out, however important a function it may have had at first. Endosperm-haustoria seem to be frequent with the *Bicornes* (cf. SAMUELSSON, 1913, p. 114).

The reserve substances of the endosperm and the embryo consist mainly of protein grains and especially of oils.

The shape of the anthers in origin is from more or less globular to that of an inverted egg (Fig. 89, 90). Then an extension takes place; on the cross-section we can distinguish from the outside towards the interior: an epiderm or exothecium, consisting of a single cell-layer, an endothecium, which later on is entirely reduced and vanishes, a tapetum, consisting of a single cell-layer, lying directly round the pollen mother-cells or archespores, which at last completely fill the four locelli (Fig. 53).

When the pollen tetrads are full-grown, the anther-wall is only built up of a single brown cell-layer. The cells along the suture have died and shrivelled a little and are only loosely coherent still (Fig. 52). When the anthers open they dissolve and make free a slit, through which the pollen can come out, usually before the flower-bud has opened.

The pollen tetrads have a diameter of 26.7—36.7 μ, according to OVERBECK (1934), with 31.7 μ as the most frequent value. The simple pollen-grain is flattened on three sides, with which it lies against the other grains in the tetrad. The lines of contact between the 4 pollen grains in a tetrad differ somewhat from the lines of intersection of four spheres in a tetrahedron. Generally the tetrad is more or less irregularly shaped, so that also triple pollen packets are met with (triads), and tetrads in which the cells lie more or less in one plane. The exine of the microspore is provided with an irregular fine network of slightly projecting ridges, which impart to the surface a somewhat rough appearance (Fig. 54). The meshes of this network have a diameter of 1—3 μ, the ridges are thinner than a micron, and the exine is about 1 μ thick. Only when the tetrad has formed, i.e. when the 4 nuclei have formed and taken up their places inside the membrane of the mother-cell, round each nucleus a membrane is formed. These membranes lie close against the membrane of the pollen mother-cell. Not until then a new thicker membrane is formed round each cell-nucleus with its plasm. The double membran consists of a cuticularised outer wall (the exosporium or exine) and the thin cellulose layer, lying inside against it (the endosporium or intine). It is the exosporium that with Calluna shows the fine network structure, at any rate as far as this wall is exposed to the air. In 3 places, where the pollen-tube may come out, the outer wall is very thin or totally lacking, the intine is a little thickened there. These three so-called pores of each pollen-grain are slit-shaped and lie approximately in the middle of each tangent between the tetrad grains, so that there are on a tetrad 12 pores in all, lying two by two against each other (Fig. 54).

D. Anthesis, pollination and fertilization.

The influence of moisture on the anthesis has been dealt with in a former paper (BEIJERINCK, 1935), which is inserted here.

During August 1935 the main flowering-season of the Scotch heather coincided in our country with a prolonged period of drought. Many Calluna plants showed a remarkable development of the flower-buds. The plants were covered at the end of August with nearly all closed, but mature buds of about the same size.

This phenomenon appeared as a more or less simultaneous bud development although it probably was only a retardation in the opening of the buds. Mr. and Mrs. L. G. M. BAAS BECKING communicated to me certain preliminary observations performed in September 1934. 91 Flower-buds on 12 plants were individually marked with pieces of string. At 4.30 p.m. the first buds opened. This continued until the next morning 9 o'clock after which no more buds opened until next evening. Twigs, bearing 70 buds were placed under a glass jar lined with moist filter paper. Both in the light and in the shadow the calyx opened within 30 minutes (17 September 1934). Lowering of the temperature did not cause the buds to open.

These findings are in contrast with the circumstances that caused the opening of the flowers of the tropical orchid *Dendrobium crumenatum*

Lindl. According to J. KUIJPER here lowering of temperature seems to be the stimulus.

If cut twigs of these retarded Calluna-plants were placed in water the flower-buds opened very soon. This warranted the belief that the conduction of water might play an important rôle in the opening of flower-buds in contrast with the cooling effect observed for the tropical orchid *Dendrobium crumenatum* Lindl. 1)

After some preliminary attempts the following course was taken. Twigs were cut below the last annual shoots of one individual with many large closed flower-buds. In this way part of the 1934 long-shoots were gathered too. Twelve twigs of about the same size with closed buds only were placed in glass containers. Six twigs were placed in rain water and six in a moist atmosphere. Eight containers were placed in larger glass jars, partly in dry air (obtained by means of $CaCl_2$) and partly in moist air. In this way direct water supply and moisture of atmosphere were varied. Of every series one glass was placed at higher temperature (18.4—24.9° C) and one glass at lower temperature (15.6—17.0° C). All in dark. The experiment was started August 23 at 18 o'clock. Twice every 24 hours the number of opened flower-buds, humidity and temperature were ascertained. The observations are given in the table. After the number of opened flower-buds the percentage of the total number is given in brackets, the last column of the table gives the total number of flower-buds on every twig. The figure gives the course of the buds opening.

When we keep in mind the preliminary nature of these experiments the following points seem evident:

1. no bud opened in the jars 2, 4, 8, 10 in which there was no direct water-supply; in the dry and in a natural atmosphere;
2. relatively very few buds opened in moist air and without direct water-supply. Opening of these buds happened later, as appears from the table;
3. from the other jars Nos. 5 and 1 with direct water-supply at higher temperature, show the highest number of flowers in a moist atmosphere;
4. the jars placed at lower temperature (thin lines on the figure) seem to lag behind when compared with the partners at higher temperature (heavy lines). An exception to this rule is formed by the case of humid atmosphere without direct water-supply. Here relatively more buds have opened at low temperature.

The opening, although retarded, of the buds without direct water-supply in moist air may be an indication of a possible water intake from the atmosphere, which might be sufficient for the opening of the buds.

The total lack of flowering in dry and in atmospheric air without direct water-supply seems to confirm this point. The observations are in accord with those of Mr. and Mrs. BAAS BECKING.

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1) KUIJPER, J. (1932). Zur Frage der periodischen Blüte von *Dendrobium crumenatum* Lindl. Rec. trav. bot. néerl. Vol. XXX, p. 1—22.

Time Condition		23th Aug.		24th Aug.				25th Aug.				26th Aug.				27th Aug.		Totals
		6 p.m.		9 a.m. I		6 p.m. II		9 a.m. III		7 p.m. IV		10 a.m. V		7 p.m. VI		9 a.m. VII		
1. Dry air + water-supply	warmer (laboratory)		24.9—17.8—47—10.8	5 (4.5)	19.5—14.8—57—9.7	11 (10)	22.4—16.7—53—10.7	21 (19)	19.0—14.4—58—9.4	28 (25.5)	21.2—16.6—61—11.2	41 (37)	18.4—14.2—60—9.5	49 (44.5)	20.5—16.5—64—11.5	54 (50)	19.5—16.9—76—12.7	110
2. Dry air, no water-supply				0		0		0		0		0		0		0		62
3. Ord. air + water-supply				3 (3)		5 (5.5)		6 (6.5)		11 (12)		14 (15.5)		30 (32)		40 (43)		93
4. Ord. air, no water-supply				0		0		0		0		0		0		0		89
5. Moist air + water-supply				2 (4)		5 (10)		6 (12)		12 (23)		18 (34)		29 (55)		37 (70)		53
6. Moist air, no water-supply				0		0		0		1 (1)		2 (2.5)		4 (5)		6 (7)		84
7. Dry air + water-supply	cooler (cellar)		17.0—15.0—80—11.5	1 (1)	17.2—14.0—68—10.0	4 (4.5)	16.0—12.4—63—8.5	6 (6.5)	16.4—13.2—68—9.4	8 (9)	16.2—12.5—62—8.5	16 (17.5)	15.6—13.0—73—9.6	19 (21)	16.8—14.5—76—10.9	28 (31)	16.2—15.0—87—12.0	91
8. Dry air, no water-supply				0		0		0		0		0		0		0		131
9. Ord. air + water-supply				5 (6.5)		6 (8)		8 (10.5)		9 (12)		11 (14.5)		18 (24)		23 (30)		76
10. Ord. air, no water-supply				0		0		0		0		0		0		0		165
11. Moist air + water-supply				11 (8)		20 (14.5)		24 (17)		32 (23)		47 (34)		52 (38)		66 (48)		139
12. Moist air, no water-supply				0		0		0		1 (2)		4 (7)		10 (17)		17 (28)		60

(The four numbers in the narrow columns mean: temperature of dry thermometer, temp. of wet therm., rel. humidity and vapour pressure. The numbers of the last column are the totals of flower-buds on the flowering twigs investigated. The other numbers in the columns are the flower-buds opened and within brackets the %'s of the whole number of the twig, ± 0.5 %).

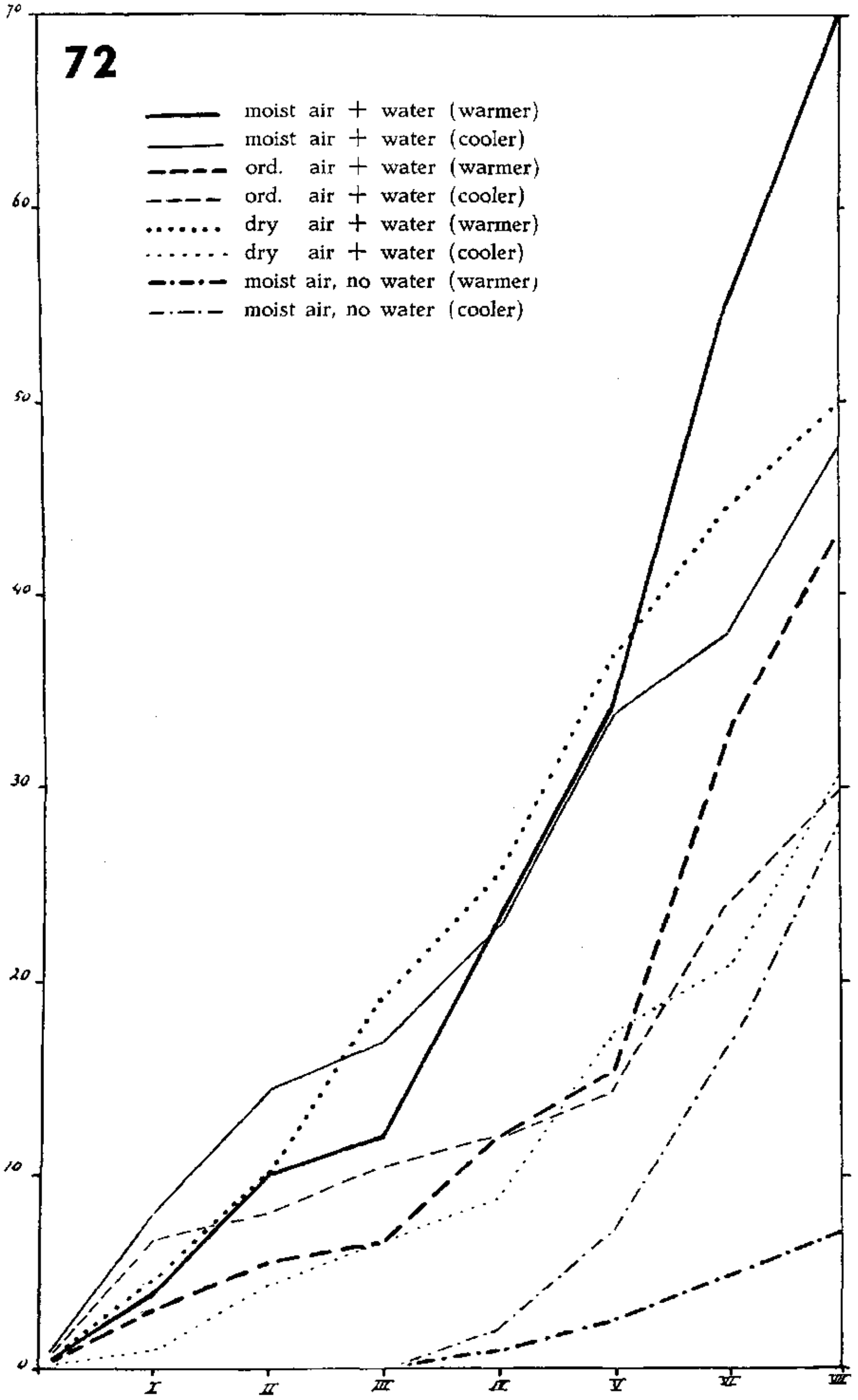

Fig. 72. Vertical: numbers of opened flower-buds in %.
Horizontal: observation-times (see table).

Calluna is generally protandrous, the anthers often open already inside the still closed flower-buds. In the normal anthesis first the sepals recede at the top, because the lengthening style thrusts against them. With a full-grown flower-bud this can be demonstrated by pricking a fine needle from below through the flower. When the point of the needle presses against the cap, formed by the hard reinforced sepals, they burst asunder. If however the perianth consists of 4 whorls of 2 sepals, as with the fa. *diplocalyx*, the style has not sufficient force to burst the bud, which therefore remains closed (so-called bud-flowers), and the lengthening style has two sharp bends, like a bayonet (Pl. IV 2b), unless it has become monstrous, which often occurs with this irregular form. Another reason why the buds do not open is found with the fa. *clistanthes*, where the flowers, although provided with normal whorls, also remain closed or open very little, because the styles remain too short. With the subfa. *ferax* the flowers do open a little at the top, but the short style does not protrude from the calyx, and the surface of the stigma scarcely comes free. Thus the length of the style may determine whether the buds will open or not. Also monstrous styles are often the cause why they remain closed, e.g. with the forms: *diplocalyx, monstrosa, clisthanthes, polysepala, gynodioica,* subfa. *simplicissima*. With this latter subfa. the whole corolla is lacking and therefore ruled out as a factor; the flowers sometimes open partially. With the fa. *gynodioica* the flowers do not open fully; here the whorl of stamens is lacking and it is probably for this reason that the swelling-cushions at the base of corolla cannot thrust aside the sepals, as they normally do. So these pads, which, according to NORDHAGEN (1937, p. 33) govern the unfolding of the corolla, cannot effect the further divergence of the sepals until the bud has burst; opposite sepals will then form about a right angle. At the same time the 4 shorter corolla tips can now bend outwards, thus freeing the genital organs.

The normal position of the flowers is about horizontal, but as the style is curved upwards and the whole genital apparatus placed somewhat excentrically, the flower becomes slightly zygomorphous. The style is now in due time so much lengthened that it protrudes amply from the perianth. It depends on the type of the flower whether the style becomes longer or remains shorter; sometimes the surface of the stigma hardly reaches the top of the sepals, in other cases it may attain a height of about one and a half time the length of the sepals.

By the upward curvature of the whole genital apparatus, which is shared by the whorl of stamens, the lower portion of the flower is more easily accessible to the insects which come to consume the glittering nectar. The secretion of nectar may be so copious, that the bottom of the corolla is quite covered with it. This can be seen if one lets the sun shine into the open flowers. At night temperatures of about 10° C, however, the secretion of nectar is stopped, as it often is after a cooling shower in the late summer or autumn. So there is no question of flowers "à nectar complètement caché", as is stated by MAC LEOD (1894, p. 448). The nectar is chiefly secreted during the night and in the early morning, but, as has been said, this much depends on the surrounding temperature.

The flower, once expanded, remains open also during the night until fertilization has taken place. The anthers are on their exterior side attached to an S-shaped filament, which at the base is more or less triangular and in the middle part flattened in a radial direction, so that radial movements are easier than tangential (Fig. 50). The filament becomes also tangentially narrower towards the place of attachment of the anthers, it is elastic by its S-shape. The spur-like prickly appendages of the anthers are inserted on the exterior base of the thecae and stick out downwards, so that they are easily touched by the insects visiting the flowers. The lightest push, or the wind, is sufficient to make the anthers vibrate, by which the pollen is shed from the long slits in the sides of the thecae. Hymenoptera visiting Calluna are often light grey by pollen. Several species of bees collect this with their legs and carry it home as food for their larvae in small lumps, fixed to the hind-legs in special organs.

Although the haired and powdered insects may unintentionally contribute to the cross-pollination of Calluna, the more so because the stigmas stick out far, yet wind-pollination is probably at least as important. Personally I repeatedly observed how above the vast heath-fields in this country clouds of pollen dust may collect, blown along by the wind, and thus carrying out pollination on such a huge scale and at such a speed that one is reminded of the dust of corn-fields and woods in bloom. The dust over blooming Calluna fields is by no means always visible. Weather conditions must be favourable by alternate lulls and gusts or whirlwinds, which in dry sunny periods are often raised above our heath-fields.

Cross-pollination is the rule. I did not succeed in obtaining self-fertilization in screened flowers. Also the protandry is an obstacle to spontaneous autogamy. Though self-fertile forms of Calluna may exist, yet in nature cross-pollination will by far predominate.

The upper surface of the stigma shows four more or less convex quadrants with a palisade layer (Fig. 42), excreting a liquid on which the pollen tetrads may stick.

Among the visitors of Calluna *Hymenoptera* predominate, although *Diptera* and *Lepidoptera* species are also fairly numerous. O. KIRCHNER (1911, p. 317) therefore classifies Calluna under the so-called "Hymenopterenblumen". According to KERNER (Pflanzenleben, II, p. 128) Calluna belongs to the plants, the flowers of which are at first dependent on pollination by insects, while in a later stage the nectaries cease to secrete nectar and the stamens extend a little more, so that the wind takes over the task of pollination. My own impression is that it depends on the weather conditions whether Calluna flowers will be pollinated more by insects than by the wind.

A survey of the insect species, observed on Calluna, is given below.

The abbreviations refer to the authors, mentioned in a note at the foot of the table. From this list it appears that the *Hymenoptera* species predominate and in the first place the species of humble-bees, although by human apiculture the honey-bee has without doubt become the most important visitor. The names are in alphabetical order.

TABLE VI.

Insects, observed on the flowers of Calluna vulgaris [1].

DIPTERA.

Anthomyia aestiva Meig. (Mc. L.)
„ *radicum* L. (W.)
„ spec. (W.)
Arctophila mussitans F. (A. & H.)
Calliphora erythrocephala Mg. (V., W. & B.)
Cheilosia longula Zett. (M.)
„ *scutellata* Fallen (M.)
Conops quadrifasciatus Deg. (Mc. L., Rich.)
Chrysotoxum festivum L. (A. & H.)
„ *octomaculatum* Curt. (M.)
Dilophus vulgaris Mg. (V.)
Echinomyia grossa L. (A. & H.)
„ *tesselata* F. (A. & H.)
Eristalis arbustorum L. (Mc. L.)
„ *nemorum* L. (Mc. L.)
„ *tenax* L. (K., W. & B., Mc. L.)
Helophilus pendulus L. (Mc. L.)
Limophora spec. (W.)
Lucilia cornicina F. (W. & B.)
Lucilia latifrons Schin. (V.)
Melanostoma mellina L. (Mc. L.)
Melanostoma scalare F. (W. & B.)
Melithreptus scriptus L. (M.)
Platycheirus albimanus F. (W.)
„ *manicatus* Mgn. (W. & B., W.)
„ *peltatus* Meig. (Mc. L.)
Pollenia rudis F. (W. & B., Mc. L.)
Sarcophaga carnaria L. (M., Mc. L.)
Scatophaga stercoraria L. (W.)
Sericomyia borealis F. (M., W. & B., W.)
Siphona geniculata Mg. (Sch.)
Syritta pipiens L. (K., M., Mc. L.)
Syrphus balteatus Deg. (K.)
„ *pyrastri* L. (A. & H.)
„ *Ribesii* L. (Mc. L.)
„ *vitripennis* Meig. (Mc. L.)
„ spec. div. (M.)
Themira minor Hal. (W.)
Volucella bombylans L. (A. & H., Rich.)

HYMENOPTERA.

Ammophila sabulosa L. (Mc. L., Rich.)
Anthrena argentata Sm. (A. & H., Schm., M., Mor., Rich.)
„ *dorsata* K. (M.)
„ *fulvicrus* K. (M.)
„ *fuscipes* K. (M., A. & H., Kr., Schm., Fr., Rich.)
„ *nigriceps* K. (A. & H., Mor.)
„ *parvula* K. (M.)
„ *simillima* Sm. (M., D.)
„ *thoracica* F. (A. & H.)
Apis mellifica L. (K. M., A. & H., Mc. L., de Vr., W., Rich., Beij.)
Athalia lugens Ths. (A. & H.)
„ *rosea* L. (A. & H.)
Bombus agrorum F. (A. & H., L., Mc. L., W. & B., W., Rich.)
„ *alticola* Krchb. (Schl., D. T., G.)
„ *arenicola* Ths. (A. & H.)
„ *cognatus* Steph. (K.)
„ *confusus* Schck. (A. & H., Schl., D. T.)
„ *derhamellus* K. (A. & H.)
„ *distinguendus* Mor. (A. & H.)
„ *hortorum* L. v. *nigricans* Schm. (A. & H., W. & B.)
„ *jonellus* K. (A. & H., Rich.)
„ *lapidarius* L. (A. & H., V., Mch., W. & B., Rich.)
„ *lapponicus* F. (W. & B.)

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[1] Several times I observed Calluna flowers with the anthers gnawed off. According to L. G. M. BAAS BECKING this is done by a beetle (*Antherophagus* spec.), the larvae of which live in humble-bee nests.

Bombus lucorum L. (A. & H., Rich.)
„ *mastrucatus* Gerst. (Schl., D. T.)
„ *muscorum* F. (A. & H., D. T.)
„ *pratorum* L. (W.)
„ *proteus* Gerst. (A. & H.)
„ *silvarum* L. (Schl., D. T.)
„ *scrimshiranus* Kirby (W. & B., W.)
„ *soroensis* F. (Kr.)
„ *subterraneus* L. (de Vr.)
„ *terrester* L. (K., M., A. & H., V., Kr., Schm., de Vr., Mc. L., W. & B., Rich.)
„ *variabilis* Schmied. (A. & H., Kr., Schl.)
Cerceris arenaria L. (A. & H.)
Colletus succinctus L. (A. & H., Fr., Schl., D. T., Sm., Rich.)
Diphysis serratulae Pz. (M.)
Dufourea vulgaris Schck. (A. & H.)
Epeolus variegatus L. (Fr.)
Formica fusca L. (W. & B.)
Halictoides inermis Nyl. (A. & H.)
Halictus calceatus Scop. (A. & H.)
Halictus cylindricus F. (M.)
„ *flavipes* F. (Rich.)
„ *leucozonius* Schrk. (A. & H.)
„ *minutus* Zett. (Rich.)
„ *punctulatus* K. (A. & H.)
„ *rubicundus* Chr. (A. & H., Rich.)
„ *sexnotatulus* Nyl. (A. & H.)
Mellinus arvensis L. (A. & H., S., Mc. L.)
Nomada brevicornis Mosc. (A. & H.)
„ *jacobaeae* Pz. (A. & H., Fr.)
„ *obtusifrons* Nyl. (A. & H.)
„ *roberjeotiana* Pz. (A. & H.)
„ *rufipes* (Rich.)
„ *solidaginis* Pz. (A. & H., Kr., Schm.)
Prosopis pictipes Nyl. (A. & H.)
Psithyrus campestris Pz. (A. & H.)
„ *rupestris* F. (K., A. & H., V.)
„ *vestalis* Four. (Kr.)
Saropoda bimaculata Pz. (M.)
Sphecodes ephippius L. (Sch., D. T.)
„ *gibbus* L. (M., Mc. L.)
Vespa holsatica F. (M.)
„ *vulgaris* L. (W. & B.)

LEPIDOPTERA.

Adopaea thaumas Hfn. (M., Beij.)
Agrotis castanea Esp. (Rössler)
„ *tritici* L. (Rich.)
Anarta Myrtilli L. (Rich., Beij.)
Augiades sylvanus Esp. (Beij.)
Chrysophanus dorilis Hufn. (Beij.)
„ *phlaeas* L. (K., Mc. L., W. & B., Beij.)
Coenonympha pamphilus L. (K., Mc. L., W. & B., Beij.)
Epinephele jurtina L. (Beij.)
„ *tithonus* L. (Mc. L.?, Beij.)
Gelechia ericetella Hb. (Frey.)
Gonopteryx rhamni L. (Beij.)
Grapholitha mendiculana Fr. (Fray.)
Lygris testata L. (Beij.)
Lycaena argus L. (Beij.)
„ *alcon* F. (Beij.)
Pararge egeria L. (Mc. L., Beij.)
„ *megera* L. (Mc. L., Beij.)
Phoxopteryx unguicella L. (Frey.)
Pieris napi L. (Mc. L., Beij.)
Pleurota bicostella Cl. (Frey.)
Plusia gamma L. (K., Rich., Beij.)
Plusia spec. (M.)
Timandra amata L. (Beij.)
Teras aspersana Hub. (W.)
Vanessa io L. (Beij.)
„ *urticae* L. (W. & B., Beij.)

THYSANOPTERA.

Thrips spec. div. (M., Beij.)

ABBREVIATIONS.

K. — P. KNUTH (1899), Hndb. d. Blütenbiologie (Handbook of floral biology), Vol. II, p. 40. (Schleswig Holstein).
M. — H. MÜLLER (1873), Die Befruchtung der Blumen durch Insekten (The fertilization of flowers by insects). Leipzig.

A. & H. — ALFKEN and HÖPPNER, observed near Bremen (cf. Knuth, l.c., p. 40).
S. — SICKMANN, observed near Osnabrück (cf. Knuth, l.c., p. 41).
V. — C. VERHOEF (1891), Biol. Beobacht. ostfr. Inseln (Biol. Observ. of East-frisian isles; Norderney).
L. — E. LOEW (1894), Blütenbiol. Floristik (Flower-biol. floristics) (Brandenburg).
Kr. — R. KRIEGER (1894), near Leipzig (cf. Knuth, l.c., p. 41).
Schm. — O. SCHMIEDEKNECHT (1878), in Thuringia (cf. id., l.c., p. 41).
R. — RÖSSLER, near Wiesbaden (id., p. 41).
Fr. — FRIESE, in Baden (id., p. 41).
Sch. — SCHINER, in Austria (id., p. 41).
Frey — FREY, in Switzerland (id., p. 41).
Schl. — SCHLETTERER, in the Tyrol (id., p. 41).
D. T. — V. DALLA TORRE, in the Tyrol (id., p. 41).
D. — DUCKE, in Austrian Silesia (id., p. 41).
H. — HOFFER, in Styria (id., p. 41).
G. — GERSTÄCKER, in Upper Bavaria (id., p. 41).
Mc. L. — J. MAC LEOD (1893), Over de bevruchting der bloemen in het Kempisch gedeelte van Vlaanderen (On the fertilization of the flowers in the Campine part of Flanders), (Dodonaea, V, p. 449—450).
de Vr. — HUGO DE VRIES (1877), Ned. Kruidkundig Arch., in the Netherlands.
Mor. — MORAWITZ, near Leningrad (cf. Knuth, l.c., p. 41).
Sm. — SMITH, in England (id., p. 41).
W. & B. — J. C. WILLIS & J. H. BURKILL (1895), Flowers and Insects in Great Britain, Prt. I. Ann. of Botany, p. 227—273).
W. — WILLIS (1895), in England (id., p. 41—42).
Rich. — O. W. RICHARDS (1926), Animal communities of the felling and burn successions at Oxshott Heath, Surrey (Journ. of Ecology, XIV, p. 249 ff.)
Beij. — W. BEIJERINCK, in the Netherlands.

When the microspore germinates, the pollen tube, which has a diameter of 9—10 μ, comes out through one of the pores and remains surrounded by the cellulose wall of the intine. The developing pollen grains find their way along the wide style-duct with its four wings, which have a direct outlet into the cavity of the ovary above each of the four placentas. So they must get round these latter in order to reach and to penetrate into the micropyle of the seed-buds. The micropyle of the seed-buds lies on the upper side, i.e. on the side facing the placenta. Directly after fertilization the micropyle, which like the style-duct lies open from the moment the flower begins to expand, closes. The micropylar haustorium and the chalazza haustorium now grow out to their full size, the style soon shrivels and turns brown. Also the corolla becomes limp and dies off. The sepals keep their elasticity by the lignified cell-layers, they bend sharply inwards in the middle, thus protecting the maturing ovary. The pollen-duct with the vegetative nucleus and the two generative or sperm nuclei meets no obstruction by tissue on its way to the ovule, as it does in numerous other *Angiospermae*. On the contrary, in the fully expanded flower, directly before the fertilization, the style-duct and the micropyle are even a little more opened, so that actually the atmospheric air has access to the ovule. This seems to be so in many other *Bicornes*.

HAGERUP (1928, p. 21) remarks on this point: "The lumen of the ovary is thus in direct communication with the atmospheric air, a feature which reminds one of the Gymnosperms. It is evidently a very primitive character and deserves further investigation as to its systematic importance. The cavity is a primary development, originating in the first formation of the flower from the fact that the tips of the carpels only grow together along the edges". The reader is also referred to the description of the fruit and its formation.

E. Water-economy and Metabolism.

SCHRATZ (1932, p. 68) has made a comparative investigation on possible relations between transpiration and leaf-structure with *Ericaceae*. He arrived at the conclusion that the amount of lost water cannot be derived from the morphological leaf-structure alone, so that it cannot be said that species with a thick cuticle or with other properties, counteracting transpiration, must have a smaller transpiration per unit of surface. A comparison of the transpiration per unit of surface with various species of *Ericaceae* led him to the conclusion that the quality of the surface of a leaf, especially the thickness of the cuticle and of the epiderm walls, has no appreciable effect on the total transpiration, anyhow if the experimental plants have a sufficient water-supply. If this supply is deficient, however, the cuticle seems to be an important factor.

In order to compare the transpiration of different plants, STOCKER (1922, p. 16—19) calculated the quantity of water, lost per hour and per unit of surface, which method caused great difficulties and has now lost its significance. He obtained his data by cutting parts of plants above ground and directly weighing them to 0.01 gram, after which he let the twigs evaporate for 1½ hour and weighed them again.

WALTER (1926, p. 46) proposed to express the lost water per gram freshweight of the transpiring organs and re-calculated STOCKER's extensive material in this way. SEYBOLD (1929) followed the same method; his results are given below.

TABLE VII.
Transpiration per gram freshweight. expressed in Erica tetralix = 1, after SEYBOLD (1929).

Species	Ratio	Species	Ratio
Ammophila arenaria	0.58	*Hieracium umbellatum*	1.47
Corynephorus canescens	0.61	*Cakile maritima*	1.59
Elymus arenarius	0.62	*Erica tetralix*	1.0
Calamagrostis epigeios	0.75	*Artemisia maritima*	1.5
Salsola kali	0.82	*Triglochin maritima*	1.9
Suaeda maritima	1.01	*Aster tripolium*	2.1
Honkenya peploides	1.06	*Salicornia herbacea*	2.2
Heliochrysum arenarium	1.18	*Statice limonium*	2.4
Calluna vulgaris	**1.21**	*Glyceria maritima*	**2.4**
Atriplex hastatum	1.30	*Fragaria vesca*	2.7
Galium mollugo	1.46		

From this table we see that Calluna stands pretty near *Erica* and has neither a particularly strong, nor a weak transpiration under the circumstances for which these ratios hold. This does not mean, of course, that under extreme circumstances the ratios might not be very different.

It has been stated that salt-plants have a greater transpiration than plants from moderately dry and sunny localities, e.g. dune-plants [1]. *Erica* and *Calluna* and a few other forms from poor soil keep the mean between these (so e.g. *Hieracium umbellatum* and *Galium Mollugo*). So Calluna seems to have no exceptional transpiration at all, but the aspect becomes quite different when its very small water content is taken into account. The outward structure of Calluna is without any doubt xeromorphic, for it has provisions to enable it to stand severe drought, such as the localization of the stomata, the thick cuticle, the compact short-shoot leaves, etc. The impression is very different if one pays attention to the degree of succulence, i.e. the water content in gr. per dm^2 of the transpiring surface. Putting with STOCKER (1924, p. 289) the succulence of Calluna = 1, the picture is as follows (Table VIII).

TABLE VIII.

Degree of succulence in grams of water per dm^2 of transpiring surface of the plant, expressed in Calluna = 1. after STOCKER and DELF (1924).

Species	Ratio	Type
Calluna vulgaris	1.0	Ericaceae
Erica tetralix	1.5	
Arnica montana	4.4	Mesophytes
Molinia coerulea	3.3	
Corynephorus canescens	0.7	Sandy plain plants
Galium mollugo	3.6	
Hieracium umbellatum	5.1	
Salicornia herbacea (Delf)	6.5	Beach plants
Honkeneya peploides	6.6	
Cakile maritima (Delf)	2.8	
Cereus spec.	52.0	Succulents
Sempervivum tectorum	9.2	
Sedum purpureum	7.9	
Sedum album	4.6	
Elymus arenarius	3.3	Dune-grasses
Ammophila arenaria	5.0	
Calamagrostis epigeios	2.6	
Caltha palustris	6.5	Marsh and Wood plants
Viola palustris	2.3	
Anemone nemorosa	3.4	
Potentilla palustris	1.7	

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[1] Meanwhile recent investigations, a.o. by ADRIANI (1937), have rendered this doubtful. It is even questionable whether the experiments yield results that are entirely comparable.

Here the two *Ericaceae* are far distant from the succulent types, they are rather their opposite and one might call them sapless plants or sclerophytes.

These two facts: an average transpiration and a very low water content, would prove that Calluna must nevertheless have a considerable water-conveyance through its cormus. Now on this point FIRBAS (1931) has made important investigations. He studied the water-economy of peat-moor plants, including Calluna, and, in order to get definite ratios, applied the concepts which HUBER (1928) had already used before: water-conductivity, conducting plane (L = "Leitfläche"), relative conducting plane (r. L.), specific conductivity (L/O), being the ratio between the conducting plane and the surface of the leaf (O = Oberfläche, surface), expressed in mm^2/dm^2 surface, and L/G, expressed in mm^2/grams freshweight (G = Gewicht, weight).

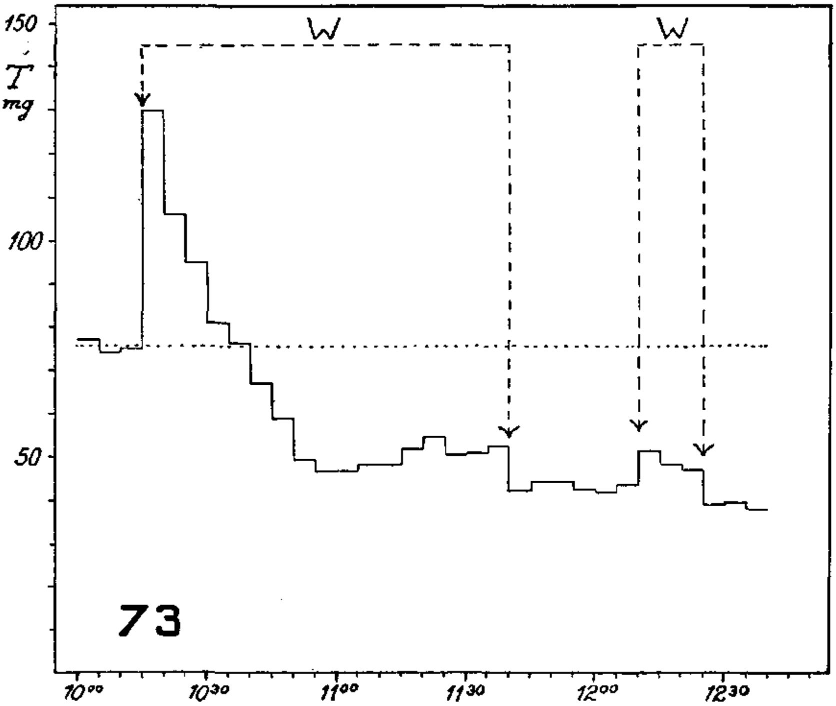

Fig. 73.

Already from HUBER's investigations it appeared that the highest conductivity is found with the *Ericaceae*; they possess a relatively very large water-conveying system. This is especially so with *Vaccinium uliginosum*, then follow *Ledum*, *Andromeda*, *Erica tetralix*, *Vaccinium myrtillus*, *V. oxycoccus*, *Myrica*, *Calluna vulgaris* and *Empetrum nigrum* (see table IX).

By this high conductivity for water Calluna occupies a typical place, like many other peat-moor plants, and may even be compared with the true desert plants; the xerophytes of the steppe-heaths are far surpassed.

TABLE IX.

Relative water-conducting planes with peat-moor plants, (L/G and L/O), after FIRBAS, 1931, l.c. p. 510—512.

Species	L/G	Average for sunny moss-peat	L/O	Number of determinations
Calluna vulgaris (2 y. shoots)	1.81	1.81	—	16
Andromeda polifolia (1—2 y. shoots)	1.89—2.93	2.47	3.61—5.20	37
Vaccinium uliginosum (1 y. shoots)	3.24—5.89	5.38	2.42—7.69	336
Vacc. oxycoccus (1—more y. shoots)	1.13—2.81	2.01	4.92	51
Vacc. myrtillus (1 y. shoots)	1.71—2.01	2.01	1.34—2.24	55
Empetrum nigrum (1—2 y. shoots)	1.41—2.25	1.59	3.14—4.87	135
Ledum palustre (1 y. shoots)	2.81	2.81	5.05	5
Myrica gale (1 y. shoots)	2.0	2.0	2.44	5
Erica tetralix (1—2 y. shoots)	2.24	2.24	—	6
Eriophorum vaginatum (basal leaves)	0.14—0.32	0.16	0.15—0.51	75
Eriophorum angustifolium (id.)	0.31	0.31	0.33	1
Trichophorum austriacum (base of shoot)	0.38	0.38	0.45	6
Scheuchzeria palustris (leaves, base)	0.35	0.35	0.77	4
Carex limosa (id.)	0.36	0.36	0.37	7
Rhynchospora alba (id.)	0.30	0.30	0.41	5
Rubus chamaemorus (1 y. shoot)	0.33—0.74	0.74	0.37—1.61	9
Narthecium ossifragum (basal shoot)	0.46	0.46	0.54	3
Drosera rotundifolia (id.)	0.67—0.84	0.76	2.52	10
Lycopodium inundatum (1 y. shoot)	0.29	0.29	—	2

Under the conditions in the growing Sphagnetum the peat-moor plants have a still more developed system for conveying water and then approach the plants of a sunny dry mineral soil. Although the surface of Calluna is not larger than that of the mesomorphic sun-plants, still on account of its extensive ventilation-system, it is with respect to the volume relatively more active than with the other forms of this moss-peat medium. The adaptability of Calluna is still increased by xerotropic movements of the leaves, by which the transpiring leaves are pressed as a compact mass against the stem. Thus it can live both in wet and dry surroundings. Remarkable also is its power to take in water pretty evenly at low and high temperatures, with an overcast sky as well as in full sunshine. The loss of water, on the other hand, depends very much on the evaporation, which is very high on the peat-moors, especially in the atmospheric layers where Calluna grows. This evaporation in the open air is, according to FIRBAS a.o., much higher than in the swamps and is exceeded by only 20—23 % by the xerophytic vegetation on mineral soil. This explains at once the use of the large water-conveying system. A slight transpiration means for this sclerophyte already a relatively high loss of water, which must be speedily replenished, if catastrophic consequences shall be avoided. For this reason also slight mechanical injuries of this water-conveying system cause the affected parts to die off soon. One observes that during the dry summer-months Calluna soon withers and turns brown, if the plants have been injured by wheels, footsteps or insect voracity.

According to FIRBAS (1931, p. 678) three points are of importance with regard to the water economy:

a. the chemical nature of the substratum immediately causes xeromorphoses (oligotrophy);
b. the water-intake is temporarily diminished in the uppermost, desiccating layers of moss-peat (hummocks) or of humus on podsol and hardpans, probably by a too feeble permeability of the soil;
c. a general relation exists between the food-conditions and the appearance of xeromorphic structures, creating better feeding possibilities by promoting the stomatal gas-exchange.

All this will be made clearer by the following table, containing a comparative survey of the structure, medium and physiological behaviour of, the peat-moor plants, including Calluna, chiefly based on FIRBAS' work (1931).

TABLE X.

Comparative survey of the structure, locality and physiological behaviour of the peat-moor plants, including Calluna, after FIRBAS (1931), with a few alterations.

<table>
<tr><th></th><th colspan="2">All peat-moor plants, except *Drosera*.</th></tr>
<tr><th></th><th>A. the forms of the growing Sphagnum cushions.</th><th>B. the forms of the vegetation-types in which ling has become predominant.</th></tr>
<tr><td>I. **Structure.**
General anatomical character.</td><td colspan="2">As to the epiderm, stomata, leaf-shape, etc. strongly xeromorphic or at least with a few xeromorphic characteristics, the ventilating-system however well developed with all types.</td></tr>
<tr><td rowspan="3">Water-conveying system.</td><td colspan="2">(Calculated as relative conducting-plane). With all peat-moor plants well developed; can only be compared with desert plants.
With *Vaccinium uliginosum, V. myrtillus, V. Oxycoccus, Andromeda*:</td></tr>
<tr><td>A. more strongly developed (partly as on sunny dry mineral soil).</td><td>B. less developed.</td></tr>
<tr><td colspan="2">With *Eriophorum vaginatum* no differences.</td></tr>
<tr><td rowspan="2">Development of surface.</td><td colspan="2">Comparable with the mesomorphic sun-plants, but smaller if calculated on a volume-basis.
With *Vacc. uliginosum, myrtillus* and *Eriophorum*:</td></tr>
<tr><td>A. smaller.</td><td>B. larger.</td></tr>
<tr><td>Size of organs.</td><td>A. smaller.</td><td>B. bigger.</td></tr>
<tr><td rowspan="2">Thickness of epiderm.</td><td colspan="2">With *Vacc. uliginosum* and *myrtillus*:</td></tr>
<tr><td>A. thicker.</td><td>B. thinner.</td></tr>
</table>

TABEL X (*Continued*).

<table>
<tr><td rowspan="3">Number and size of stomata.</td><td colspan="2">In general decidedly high.</td></tr>
<tr><td colspan="2">With <i>Vacc. uliginosum</i> and <i>myrtillus</i>:</td></tr>
<tr><td>A. more numerous and partly bigger.</td><td>B. less numerous and smaller.</td></tr>
<tr><td>II. Locality.</td><td colspan="2"></td></tr>
<tr><td rowspan="3">Temperature conditions.</td><td colspan="2">Extreme, high temperatures especially close to the surface, higher than in the mesotrophic bogs.</td></tr>
<tr><td>A. higher surface temperatures (much higher than the air).</td><td>B. lower surface temperatures.</td></tr>
<tr><td colspan="2">Temporary high air temperatures, temporarily (in comparison with sunny mineral soil continuously) lower temperatures of the deeper root-layers, prolonged frost in the ground.</td></tr>
<tr><td rowspan="3">Evaporation.</td><td colspan="2">On the whole very high, only exceeded by 20—30 % in dry xerophytic vegetations. Especially near the surface higher than in swamps.</td></tr>
<tr><td colspan="2"><i>At the same elevation:</i></td></tr>
<tr><td>A. stronger.</td><td>B. less.</td></tr>
<tr><td>III. Physiological Behaviour.</td><td colspan="2"></td></tr>
<tr><td rowspan="5">Transpiration.</td><td colspan="2">Small absolutely, when referred to the fresh-weight, the surface and the dry-weight, in comparison with mesotrophic sun-plants, and small relatively when compared with the evaporation.</td></tr>
<tr><td colspan="2">With <i>Calluna, Vacc. uliginosum</i> (<i>Empetrum</i>):</td></tr>
<tr><td>A. higher (6—41 %).</td><td>B. lower.</td></tr>
<tr><td colspan="2">With <i>Eriophorum vaginatum</i>:</td></tr>
<tr><td>A. lower.</td><td>B. higher (44 %).</td></tr>
<tr><td>Behaviour of stomata.</td><td colspan="2">Open maximally in dark weather, but are nearly open even at noon on sunny summer-days.</td></tr>
<tr><td>Water content</td><td colspan="2">Very small, considerably less than with swamp-plants; all species have the sclerophytic character. Small daily fluctuations.</td></tr>
<tr><td rowspan="5">Osmotic values. (Press-sap concentrations).</td><td colspan="2">Somewhat higher than with swamp-plants, equal to that of the Central European xerophytes, if the soil is sufficiently wet, generally from 12 to 19 atm.</td></tr>
<tr><td colspan="2">With ever-green species a strong rise during winterfrost. During the vegetation-periods, also after periods of drought, a small rise, slight daily fluctuations.</td></tr>
<tr><td colspan="2">With <i>Calluna, Vacc. uliginosum</i> (a.o.?)</td></tr>
<tr><td>A. lower.</td><td>B. higher.</td></tr>
<tr><td colspan="2">With <i>Eriophorum vaginatum</i> no differences.</td></tr>
</table>

So Calluna is characterised by: a low water-content, a relatively large surface, a large water-conveying system and a large evaporating system. Hence:

1. the absolute amount of its water-circulation and matter-production is small;
2. with respect to the freshweight it has a pretty large transpiration and production of matter;
3. from its xeromorphic structure and xerotropic movements it derives for a great part its power to live between the extremes of humidity and drought, while:
4. its chemical composition without doubt contributes to this.

With a plentiful supply of water from the ground and quick evaporation, (depending on the condition of the surrounding atmosphere, e.g. wind, Fig. 73), it may circulate relatively much water, but with a scanty supply and none the less quick evaporation it can greatly reduce its transpiration, e.g. by xerotropic movements, provided the temperature allows this. If during frost the water-supply through the roots is checked and the transpiration-regulating system retarded or stopped, especially when the frost is severe and dry, conditions become critical for the plant; it shrivels and may die. This danger is much less with great heat, so that even on the hot Moroccan rocks it may hold out by keeping its transpiration-regulating system in working order and living xerophytically; it easily stands summer-drought, but not sudden dry frost.

It is a well-known fact that the changes in the osmotic values pretty accurately reflect the water-relations in the medium. According to WALTER (1929) the course of the osmotic value of the Central European plants during winter would depend on their transpiration and would be directly related to their power to resist cold. THREN (1934) followed for a whole year the course of the osmotic value with various species near Heidelberg, among which Calluna. Only the extreme values are given here, the course over a full year with Calluna is shown in Fig. 74. He found WALTER's statement confirmed in so far that there seems to be a relation between the winter-transpiration and the rise in the osmotic value. The relative transpiration of a few species, examined by THREN during a short cold period, is given by him as follows:

	Relative transpiration (loss of water)
Pinus silvestris	1
Picea excelsa	0.64— 2.09
Fagus silvatica	0.34— 1.07
Quercus sessiliflora	0.52— 1.36
Vaccinium myrtillus	1.51— 3.34
Sarothamnus scoparius	1.68—10.0
Calluna vulgaris	6.12—26.2
Vinca minor	7.63—34.1
Linaria cymbalaria	8.45—33.4

Table XI gives the osmotic values in atmospheres of ecologically divergent plant types, also after THREN. It appears that Calluna may reach particularly high values during periods of severe frost, with the result that the plant is seriously injured.

TABLE XI.

Osmotic values in atm. of a few species, according to Thren (1934).

Species	Number of determinations	Osm. value in summer (summer drought)	Normal winter value	Highest winter value	Injuries during winter
Picea excelsa	38	17.2—20.3	21—22	27.5	none
Pinus silvestris	33	15.7—17.0	18—19.2	22.5	none
Fagus silvatica	22	15.0—18.4	14—15	22.2	none
Quercus sessiliflora	6	—	±16	21.7	none Febr.
Calluna vulgaris	28	10.4—13.1	±17.2	35.2—37.6	many short shs. dead in Febr.
Sarothamnus scoparius	29	10.6—13.1	14.6—14.7	23.1	shoot tops die
Vaccinium myrtillus	31	14.7—17.0	±17	26.9	shoots die
Digitalis purpurea	33	8.5—12.4	10.4	28.8	rosette leaves die
Teucrium scorodonia	30	8.0—11.7	12.4	24.5	young leaves die
Pteridium aquilinum	14	14.0—16.2	—	—	—
Vinca minor	27	9.9—12.1	±17	24.1	
Luzula silvatica	29	10.0—14.2	17.6—18.2	30.8	shoots die after frost period
Linaria cymbalaria	14	8.8—12.1	±11	19.2	shoots die
Parietaria ramiflora	14	13.5—14.7	±14	20.4	shoots die
Sedum reflexum	5	6.7—6.8	10—11	12.1	—

TABLE XII.

Loss of water and osmotic value with a few evergreen species during a cold period (after Thren, 1934).

Species	Beginning of the cold Jan. 9		End of the cold March 1	
	Water content in % of the dryweight	Osm. value in atm.	Water content in % of the dryweight	Osm. value in atm.
Picea excelsa	135.0	21.2	122.0	24.6
Calluna vulgaris	96.6	17.2	56.3	no press-juice
Vinca minor	231.0	18.2	212.0	23.4
Luzula silvatica	182.0	17.4	154.0	25.5

From these two tables one gathers that the relations between winter-transpiration and osmotic winter-values are not quite simple and in any case not direct.

Figure 74 represents a year-cycle of the osmotic value of Calluna; it shows that:

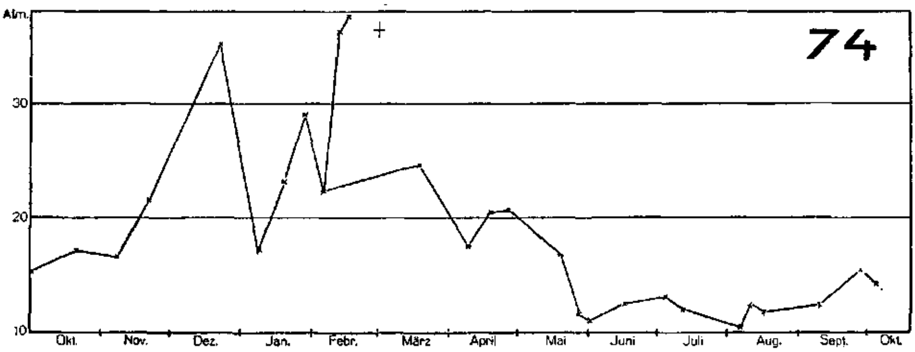

Fig. 74.

1. there is little stability (inertia) in the osmotic value during the winter-months;

2. at the end of May, in the vegetation period, the osmotic value sinks to 11 atmospheres;

3. during summer the oscillations are small; the highest summer-value was 15.5 atmospheres.

To sum up: Calluna is much less sensitive to summer heat than to winter cold. At low temperatures it loses the power to check transpiration; the table shows how very great the loss of water may then be (at the same time the supply from the soil becomes insufficient).

The above may suffice as to the water economy. On the metabolism of Calluna we are not so well informed.

According to SCHÜLLER (1898) the roots of Calluna contain a maximum amount of amylum in autumn, which during the winter disappears completely; in spring there is a new maximum which again decreases, after which during the summer-months amylum is slowly formed and accumulated. Sugars decrease in autumn in the roots, while in the stems there is an increase in amylum which disappears again during the winter. In spring a fair amount of amylum is formed there again; they contain some sugar throughout the year. The leaves are, according to ENGEL (1915), in December nearly and in January entirely free from amylum. The first traces of amylum are found there in mid-February, when the growing-period sets in, but they disappear again by frost.

After the frost-period the amylum continually increases and in the two year-cycles of foliage-leaves reaches a maximum in May and June, when the oldest hibernated leaves begin to die off. In August the young non-hibernated leaves contain very much amylum, the hibernated leaves on the other hand less than in May. In the hibernated leaves the amylum once more increases until October and then is as abundant as in May. The leaves of the new year-cycle then also contain much amylum. Then it decreases to the minimum in December–January. The epiderm contains no amylum. LIDFORS (1907) states that the leaves are very rich in sugar in the beginning of January. According to the investigations of ÅKERMAN (1927), there is a connection between the amount of certain sugars in the cells and the dry substance, and likewise between the resistance to cold and the osmotic pressure. With races of wheat and of numerous other plants there exists a correlation between the resistance to cold and other easily determined factors, such as the osmotic value of the cell-contents at the plasmolytic limit, the amount of reducing sugars, coagulating nitrogenous compounds, dry matter, etc. Whether the forms are winter-proof is closely related with these factors.

Also for Calluna such a relation is likely, as otherwise it is hard to understand why the Portuguese and Spanish forms (fa. *elegantissima*) are not winter-proof at all in our parts, while on the other hand Calluna penetrates as far as the coasts of the Arctic. Probably a selection has taken place in these so far distant climatic regions of the winter-proof races on the one hand and the very late-flowering races on the other (because of the extremely dry hot summers).

It has already been said, when dealing with the chemical composition, that against the winter the nitrogenous compounds (albumins) decrease, and also the total ash content (SiO_2 free). On the other hand the crude fibre content then increases; this is connected with the lignification. Accurate data on the total metabolism are still lacking for Calluna, which is to be regretted, since it is a typical oligotrophic form of life, the metabolism of which might furnish important views on the way in which such plants feed and develop. We know that the evaporation-system is very extensive and that the root-system varies much in size according to circumstances. The utilisation of the mineral substances is subordinate compared with the building up of organic compounds, especially crude fibre substances. So the process of lignification is of primary importance and the quantity of wood is considerable, compared with the other components. Lignification sets in very early, and is generally quickest in rather dry surroundings; it begins directly below the main vegetation-point, where a procambium ring with the necessary vessels is already present. Also the principal vein of the leaves has a sclerenchyma mantle, while lignified cells also occur in the bracts and sepals, and in the fruit. We need not wonder that a plant with such a wood-production (taken relatively) has a large system of evaporation and water-conveyance. On the manner in which the nitrogen economy is maintained we have as yet little information. It is possible that on substrata with hardly or not directly assimilable N-compounds the endotrophic mycorrhiza co-operates, especially in the embryonal organs.

F. Symbiosis.

It has been known for a long time that most *Ericaceae* and many other plant species, growing in an oligotrophic medium with much humus, as peat-moor or sand with much adsorptively unsaturated humus substance and a high concentration of H-ions, live in symbiosis with lower organisms, especially fungi.

TERNETZ (1907) isolated fungi from 5 different *Ericaceae*, among which *Erica tetralix* (but not Calluna), and recognised them as *Phoma* species. After her RAYNER (1911—1929) carried out a series of investigations on the symbiosis of *Vaccinium* and *Calluna*. She came to the conclusion that with these species there was an infection, likewise caused by fungi of the genus *Phoma*. With Calluna this was *Phoma radicis Callunae*. This endotrophic mycorrhiza would not be restricted to the root and stem, but would also occur in the leaves, flowers and fruits and at last infect the testae of the seeds, without penetrating into the endosperm and embryo, however. So there would, according to her, exist a cyclic symbiosis.

These investigations led her to the further conclusion that these fungi possess the power to fix nitrogen, and in this way provide the higher plant with nitrogen. Without this infection by fungi sterile seedlings will not develop, when they are infected they will.

Quite different results, however, were obtained by CHRISTOPH (1921), KNUDSON (1928) and FREISLEBEN (1933—1935). CHRISTOPH rejected the obligatory mycotrophy of *Calluna vulgaris* and *Erica carnea*, both would be facultatively mycotrophic. On dry soils, poor in humus, the mycorrhiza was often entirely absent. Moreover this investigator denies that one has to do here with a cyclic symbiosis, basing himself on his culture experiments, which RAYNER (1922) has never conclusively disproved.

More important still are the investigations of KNUDSON, who after successful experiments on asymbiotic germination of orchid seeds, published in 1928 a communication on Calluna seedlings with a normal root-system, obtained in a rigorously aseptic way. On the ground of this result he was convinced that for the development of Calluna seedlings the fungus may be dispensed with, to which conclusion also CHRISTOPH (1921) had arrived. In other words, the fungus may be replaced by certain chemical substances, added to the substratum. Still the fact remained that the Calluna seedlings in a pure culture, inoculated with the endophyte, but without fixed nitrogen (total concentration 0.05 %; 1.2 % agar), developed well. These plants were even healthier and of a brighter green than the checks on substrata with nitrogen (RAYNER, 1922). This latter series of experiments was carried out with great care, on a substratum of silicic acid instead of agar and with specially purified chemicals.

Especially FREISLEBEN (1933, 1934 and 1935) has studied the real significance of the *Ericaceae* symbiosis. He arrives at the following, in part remarkable, results:

1. It appears that arbitrary soil-fungi, forming no mycorrhiza, may have an analogous growth-promoting action on *Vaccinium* seedlings as the true endophytes.

2. The seed-infection, mentioned by RAYNER, does not exist with the genus *Vaccinium*, so that there is no cyclic symbiosis either.

3. The root-fungi of the *Vacciniums* considerably stimulate the growth of their hosts. With various species of *Ericaceae* they are interchangeable.

These results with the *Vacciniums* FREISLEBEN could confirm for numerous other *Ericaceae*. He also noticed that *Ericaceae*, kept in pure culture on a mixture of humus and sand, showed impeded growth. This was stated with 21 species from 13 genera. Only *Arbutus unedo* and *Arctostaphylos uva ursi* grew well in these pure cultures. Normal growth could with all the other species be restored by inoculating the substratum with root-fungi or any soil-fungi. With most species it was possible to obtain mycorrhizas experimentally with the endophyte "*M. R. Myrtilli a*". With the two *Arbuteae* this did not succeed. FREISLEBEN then concludes (1935, p. 457—458): "Es ist wahrscheinlich, dass der Familie der Ericaceen eine Gruppe von Pilzen gegenübersteht, die sich in ihrem physiologischen Verhalten so ähnlich sind, dass ein Austausch der Pilze unter den verschiedenen Wirtspflanzen möglich ist. Das Misslingen einer Mycorrhiza-Bildung bei den untersuchten Arbuteen hängt vielleicht mit dem anderen Mycorrhiza-Typus dieser Arten zusammen" (It is probable that parallel with the Ericaceae family there is a group of fungi, so similar in their physiological behaviour, that they may be interchanged among the different hosts. That the formation of a mycorrhiza with the investigated Arbuteae was unsuccessful is perhaps related with the different type of mycorrhiza of these Arbuteae.)

He then tries to detect the causes of this check on the growth of *Vaccinium myrtillus* and *Calluna vulgaris*. An asymbiotic culture on a suitable agar substratum proved feasible, although growth was less vigorous than with the infected plants. By using different substrata it could be made probable that organic substances of unknown composition acted as "retarders". Such retarding substances would be present in varying amounts in peat-extracts, peptone, malt-extract, potato-agar and fungus-extracts. His final conclusion is (l.c. p. 458): "Die förderende Wirkung der Pilze auf das Wachstum von Ericaceen beruht infolgedessen nicht auf einer direkten Beeinflussung, etwa durch Ausscheidung wachstumförderender Stoffe, sondern auf einer Inaktivierung, Zerstörung oder Absorption der Hemmungsstoffe. Es wird angenommen, dass auch in natürlichen Böden die Wurzelpilze und die Bodenpilze, die als Komponenten einer peritrophen Mycorrhiza auftreten, für die Ericaceen eine ähnliche Bedeutung haben." (Consequently the stimulation of the growth of Ericaceae by fungi is not a direct influence, e.g. by the secretion of growth-substances, but an inactivation, destruction or absorption of the retarding substances. It is assumed that also in natural soils the root-fungi and soil-fungi, which we find as components of a peritrophic mycorrhiza, are of a similar importance for the Ericaceae.) Heterauxin and similar growth-substances are, according to FREISLEBEN, not decisive for the mycotrophy of the *Ericaceae* (communication by letter). Still this new point of view does not solve the question: "Has the endotrophic mycorrhiza of the *Ericaceae* a definite significance for the nutrition of the host that lodges it, and if so, what is this significance?"

It has already been remarked that at first, after RAYNER's culture experiments, it seemed very likely that the mycorrhiza fungi supplied the higher plant with nitrogen. It is by no means settled, though, whether this supply actually takes place and, if it does, whether it is direct or indirect. It is not sure even that this possible fixation of nitrogen by the endophyte is sufficient to satisfy the requirements of the higher plant. Anyhow, with respect to *Vaccinium macrocarpon* it appeared from the investigations of ADDOMS and MOUNCE (1931) [1]) that: "The small amount of vegetative growth in the minus-nitrogen series indicated that if nitrogen-fixation by the endophyte (*Phoma radicis*) occurred, it was quite inadequate as a source of nitrogen for the cranberry plant".

The same authors also point out (l.c. p. 654—655) that with this *Vaccinium* the mycelium of the endophytic fungus was found throughout the stem-tissue, especially in the parenchyma and in the cells of the vegetation-points ("embryonic tips"). The quantity of mycelium seemed to be directly related to the vigour of the vegetative growth, it was namely plentiful in the grow-tops of vigorously developed plants and less abundant or partly lacking in these tops with weaker specimens.

This observation seems to me to be important; I noticed something similar with Calluna. There also in the young, vigorously growing shoots cells are often seen that are entirely filled with hyphae-clews. Also the pluricellular trichomes are there often full of hyphae (Fig. 35). On their real function nothing is known as yet. More extensive investigations will be required to shed some light on this symbiosis of Calluna and other *Ericaceae*, which in any case is not obligatory and not cyclical. Another open question is whether other symbioses occur with Calluna, e.g. with bacteria and actinomycetes.

However, the above-mentioned investigations of KNUDSON and FREISLEBEN have made it probable that, viewed from the side of food-physiology, this symbiosis is not so important as was at first supposed.

G. The periodicity of growth and flowering.

Calluna hibernates with open flower-buds. The youngest leaves bend towards each other over the terminally situated main vegetation-point, and,

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[1]) ADDOMS, R. M. and MOUNCE, F. C., Notes on the nutrient requirements and the histology of the Cranberry. (Plant Physiology, 1931, 6, 653—668.)

helped by the trichomes on their tops, protect it against moisture and outside damage.

Besides this terminal growing-point on the densely leafed short-shoot, there are often lateral growing-points in the axils of the leaflets. These leaflets have the shape of short needles, overlap like tiles and are decussately placed (Fig. 2 and 3).

In spring as soon as weather- and other conditions allow it, in our latitude sometimes as early as February, the bud-internodes and young leaflets extend, while also divisions take place in the meristem of the growing-points, by which new leaf-primordia are differentiated. This first extension, however, takes place by "fits and jolts", depending on the weather-conditions (Fig. 75).

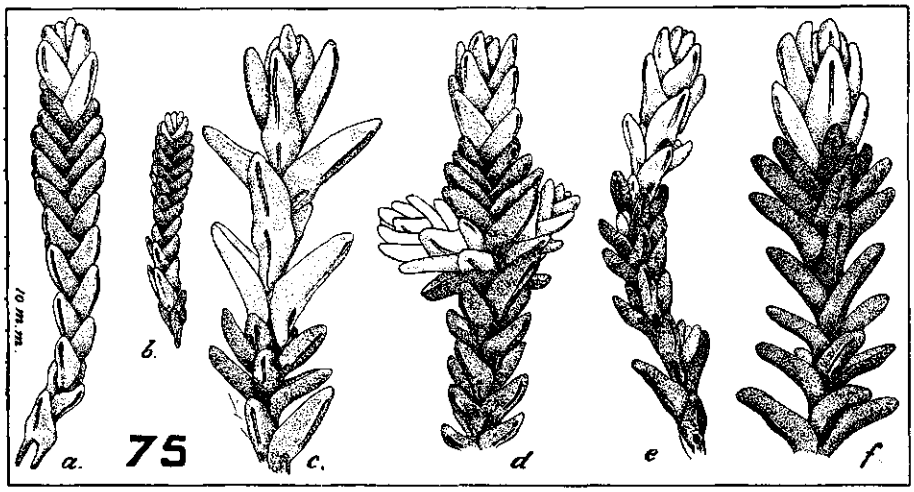

Fig. 75.

The lateral vegetation-points, like the terminal one, may produce long-shoots or short-shoots, which in their turn may ramify in the same growing-season, forming shoots of the second, third and very rarely of the fourth order. There are also transitions between long- and short-shoots, or a long-shoot may for a time grow on as a short-shoot, which is common in autumn, or conversely a short-shoot may grow on as a long-shoot, which is common in spring.

Against the winter both internodes and leaves become smaller, so that the hibernating foliage-leaves, densely packed and smaller towards the apex, mark in the following growing-season the spot where the winter-bud has lain. The leaves on the short-shoots may remain green for 2—2½ years, whereas long-shoot leaves, from whose axils the side-shoots sprout, mostly die off within the growing-season. By way of exception the long-shoot leaves on vigorously developed plants hibernate alive and die in the following spring.

Calluna forms richly ramified year-shoots. In the flowering period in

August or September a well-developed year-shoot generally reaches a length of 15—20, exceptionally 50—55 cm. Three zones can be distinguished on them:

1. a basal part with only assimilation-shoots of the 1st, 2d, rarely of the 3d order;
2. a middle part with side-shoots of the 2d, 3d and rarely of the 4th order, bearing both leaves and flowers;
3. an apical part, again with assimilation-shoots only and therefore without flowers.

The flowers always stand terminally on leafed short-shoots or, what comes to the same, on flower-twigs with nothing but 2 prophylls and a few pairs of bracts. The fairly regular arrangement of the flowers on the short side-shoots of the much longer year-shoot suggests a raceme, but in spite of this appearance is nothing but a raceme-like arrangement of terminal isolated flowers. For the apical part of the year-shoot continues to grow and in the following growing-season generally produces several long-shoots from the short-shoots there present.

In the quicker or slower longitudinal growth of the year-shoots, which in the Netherlands lasts from March till September, there is one period in which flower-buds are formed from the terminal growing-points of the side-shoots. In this country this period falls in the month of June, i.e. not until then the first recognisable sepal-primordia are separated from the meristem.

Of Calluna a number of forms are known with widely divergent flowering-times. In the Netherlands the earliest unfold their flowers already by the end of June and in the first days of July. One of these early-flowering garden-forms, the fa. *tenuis*, as a rule flowers a second time with flowers spread here and there on the ends of richly leafed short-shoots. On the other hand there are very late-flowering forms, the first flowers of which do not open until the second half of October and which then go on flowering until stopped by severe frost; the plants then still have many closed buds. If winter sets in late they are still flowering at Christmas and even later. Especially South European forms of Calluna, as the fa. *elegantissima* (Sennen) from Spain and Portugal behave in this way.

Still more extreme was the behaviour of a plant from Drente [1]), belonging to the form-group of the *multibracteata*. This plant showed before the winter nothing but packets of bracts and not a single flower. In the following spring (May—June), however, here and there expanding flowers developed, which in other respects were normal. All these forms, deviating from the type in the periodicity of the flower-formation, are passed by here.

Normally the first perianth whorls are present in the beginning of June. It is difficult, though, to detect the first originated flower-primordia on the richly ramified year-shoots, since the basal part has assimilation-shoots

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[1]) A province of the Netherlands.

only, as we have seen. Moreover the flower-buds formed on the side-shoots of the 2d and 3d order lag behind those formed more apically on the side-shoots of the 1st order. This is clearly demonstrated in vigorously developed plants in the beginning of the flowering period. The buds on the ramified side-shoots do not open before the lowest flowers on unramified side-shoots are already in full bloom or even off flowering. One gets the impression that the time, required for the origination of the numerous leaf-primordia on these ramified side-shoots, has retarded the formation of the flower-buds on them.

The flowers of Calluna do not originate simultaneously but successively over a period which may certainly last a few weeks, depending on the length of the year-shoot, the number of flowers to be formed, and other conditions. Fig. 77 represents this successive formation of the flower-buds. It is a median longitudinal section through the apical part of a year-shoot on June 25, and already shows an almost complete series of flower-bud stages, from growing-points on which no primordia of flower-parts can as yet be recognised to already closed buds.

The minuteness of the first flower-bud stages and their very rapid succession, which probably is allied to their smallness, would make their detection difficult, if not, exactly during the origination-period, regular compact rows of all sorts of stages were found on the top part of the year-shoots. This circumstance enables us to slice on the microtome whole series of buds in successive stages at the same time and to make out by extrapolation, where an undifferentiated flower-bud primordium is still

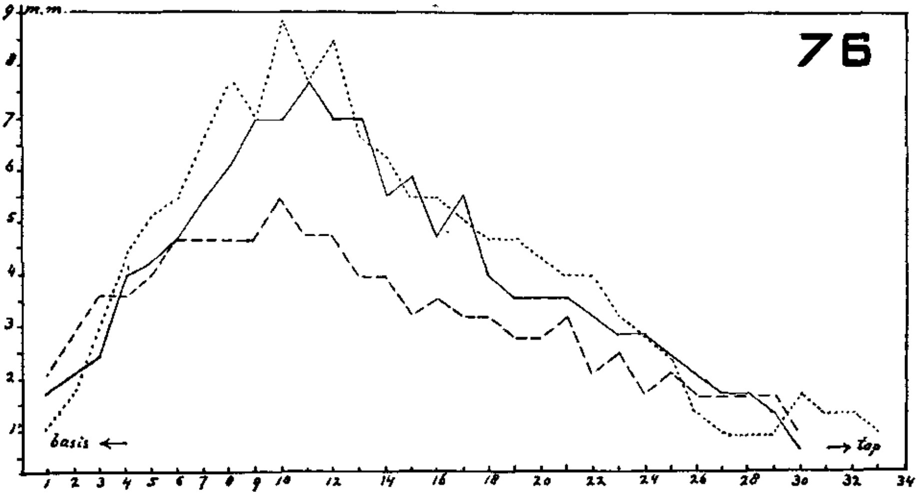

Fig. 76.

present; this is where the last pair of bracts has just been separated (Fig. 81) and where the origin of the first perianth whorl is visible.

We shall now describe 10 successive stages, which are distinguished for

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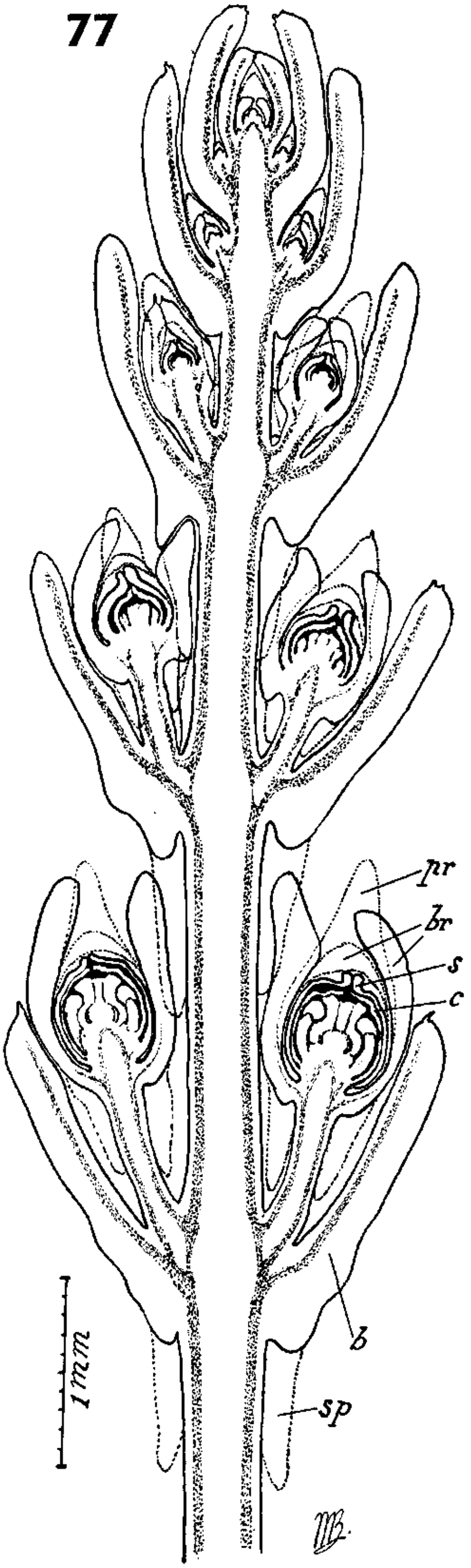

Fig. 77.

convenience' sake, but are by no means points of stagnation. Stagnations perhaps occur, but then depend on external causes, as cold, drought, lesions, etc. As a stage we here designate a state of development, characterised by the first appearance of definite primordia, organs or parts of organs. Between the stages lie periods of development.

STAGE I. (See Fig. 81). Here the last pair of bract-primordia has been differentiated, i.e. has become visible. The ± hemispherical vegetation-point is still smooth and has a diameter of 60—70 μ, so it is a little larger than the ordinary vegetative growing-points, whose diameter is 40—60 μ at the moment that another pair of leaf-primordia has just been differentiated, as in Fig. 80 (see explanation of the figures).

STAGE II. (Fig. 82). The four sepal primordia are visible. As in Fig. 81 the flower-primordium is preceded by 3 pairs of bracts and one pair of prophylla. This complex fills the leaf-axil of an ordinary long-shoot leaf and lies between the long-shoot internode, the stem-leaf and the two spurs of the stem-leaf above it. The scarcely differentiated growing-point within the 4 sepal primordia has now got a diameter of about 100 μ and begins to show a slight conical vaulting.

STAGE III. (Fig. 83 and 86). The 4 corolla tip primordia have become visible in the angles between the sepal-primordia, with which they therefore alternate. Also the corolla wall is just visible, while of the stamen-primordia not much is to be seen as yet, although they are present, as is proved by fig. 83. Here the impression is that the stamen-primordia originate before or at the same time as the corolla tip primordia, which has also been stated with other *Ericaceae* (LUYTEN and VERSLUYS (1921), p. 108 and Fig. 15). The growing-point is now drawn up a little and has a diameter of ± 120 μ, that of the whole flower-bud being ± 200 μ.

STAGE IV. (Fig. 87). I have been unable to find a stage in which only one whorl of 4 stamens, without more, was visible. Still this condition is likely to exist at a certain moment. Probably the formation of the minute primordia here takes place in very rapid succession, so that this intermediate stage has eluded observation and the 8 stamen-primordia seem to appear simultaneously. Neither could it be settled which whorl lay lowest, the epipetal or the episepal. With *Rhododendron* the episepal one, alternating with the corolla tips, seems to be present first. The stamen-primordia now have a diameter of 30—50 μ, while the meristem-cells in the division-zone are 4—5 μ long. The nucleus then nearly fills the whole cell. The number of cells in a stamen-primordium is about 50.

I therefore chose as STAGE IV that condition of the bud in which the whorl of 8 stamen-primordia can be well distinguished. It is notable that the 4 episepal bumps are rounded off more spherically, whereas the epipetal ones have a more oval cross-section. But from this no conclusion can be drawn, as the difference in shape may be caused as well by the pressure conditions at that moment round the primordium, as by a higher or lower position. This could not be made out by means of the microtome sections, which could be used only. There is no question yet of a differentiation of the gynoecium. The flower-bud has now a diameter of 250—300 μ. We note that the longitudinal sections of Fig. 83 and 84 refer to flower-buds, preceded by two pairs of bracts only, whereas in the transverse sections of Fig. 86 and 87 three pairs of bracts are seen. The number of bracts is rather variable with Calluna, even on the same individual.

STAGE V. (Fig. 85). The primordium of the gynoecium can now be recognised by being apically flatter and broader. As is already visible in Fig. 83 and 84, the upper pair of bracts has vaulted over the flower-bud, but also the sepals have now reached each other and cover the other parts, at first by gliding over one another with their tops, as is seen in Fig. 85. The diameter of the bud is now about 350 μ.

STAGE VI. (Fig. 88 and 92). On the tops of the stamen-primordia the bumps of the anthers have not formed yet, but the corolla tips begin to bend over the surface of the stigma, while in the ovary-primordium the four loculi of the ovary are feebly outlined, thus indicating at the same time the obdiplostemony as it is found with the *Ericaceae*. The gynoecium has extended together with the whorl of stamens and corolla, but a real differentiation between ovary and style is not noticed yet. The surface of

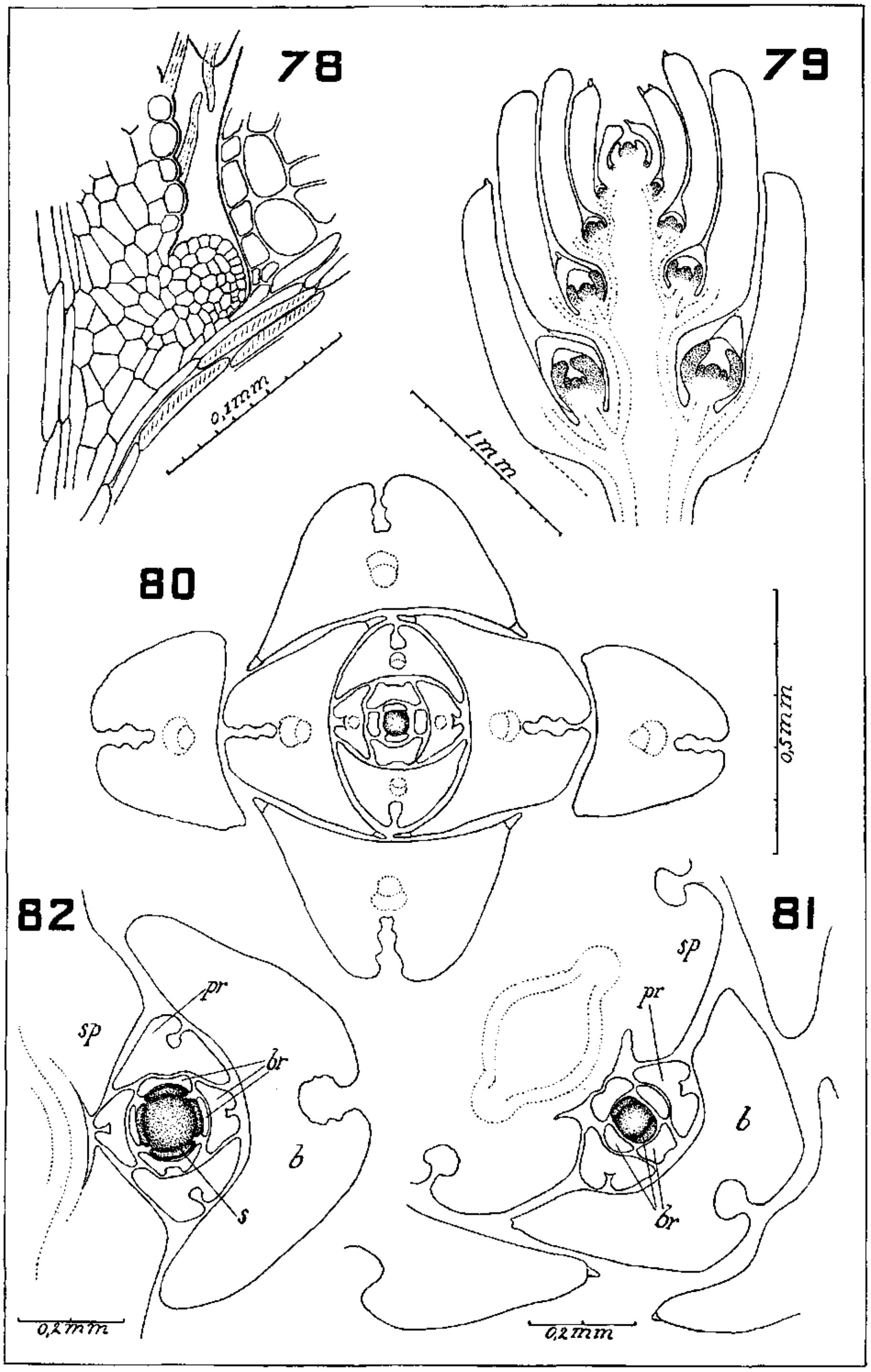

Fig. 78—82.

the stigma, however, begins to show a cup-like depression. The flower-bud now has a diameter of ± 380—400 μ. In Fig. 92 it is preceded by several ordinary foliage-leaves, which is of frequent occurrence.

STAGE VII. (Fig. 89). The primordia of the anthers can now be clearly recognised, but without the appendages. The placenta cannot be seen well, but the folds of the style-duct and the first origination of the nectaries are distinct. The corolla tips have now nearly reached each other above the stigma. At the top of the sepals cushion-like swellings have formed (see also Fig. 90 and 91). The broadening sepals begin to overlap where they are broader than half the circumference. The diameter of the flower-bud is now about 0.5 mm.

STAGE VIII. (Fig. 90). Also the appendages of the anthers now become visible, while the placenta and nectaries are likewise clearly observed. The whole flower-bud begins to extend, the style remains longer than the stamens. The bracts diverge more and more. The diameter of the flower-bud is now about 0.7 mm.

STAGE IX. (Fig. 91). The whole flower-bud has broadened as well as extended. The sepals have become longer than the bracts; they assume a whitish tint and by the divergence of the bracts are directly visible on the plant. At this stage the reduction-divisions of the pollen tetrads take place and the embryo-sac mother-cell is present. Diameter of flower-bud ± 1 mm.

STAGE X. (Fig. 94). The flower-bud is now full-grown and 3—5 mm long. The sepals have a pink-violet hue. The filaments have assumed their peculiar S-shape. The appendages of the anthers are toothed (Fig. 50d), while most anthers have already opened with a lateral slit, through which the pollen tetrads come out. Everything is ready now for the anthesis, which in our latitude normally takes place from the middle of July to the end of August or the beginning of September.

It has already been remarked that the time of flowering of Calluna fluctuates from the end of June until the new year and even the following spring. These differences in the time of flowering are not uncommon with the *Ericales*. *Erica carnea*, for example, also forms its first flower-buds in June (see CHURCH, 1908, p. 138, Fig. 2) and hibernates normally with complete flower-buds in the last-mentioned stage X. Still this species has forms which either bloom before the winter or later in spring. *Erica tetralix* often flowers twice in the same season, while the blooming-period of the several forms of *Erica cinerea* may extend from June till winter. Calluna, however, has the widest range, unless the reason is that this species has been studied best.

A shifting of the flowering-time of Calluna is caused by different elevations on the mountains. In the Alps, at a height of 1000—1200 m, it commonly blooms already in the middle and at the end of July. A plant from Grindelwald (1057 m), transported to the Netherlands, has there for

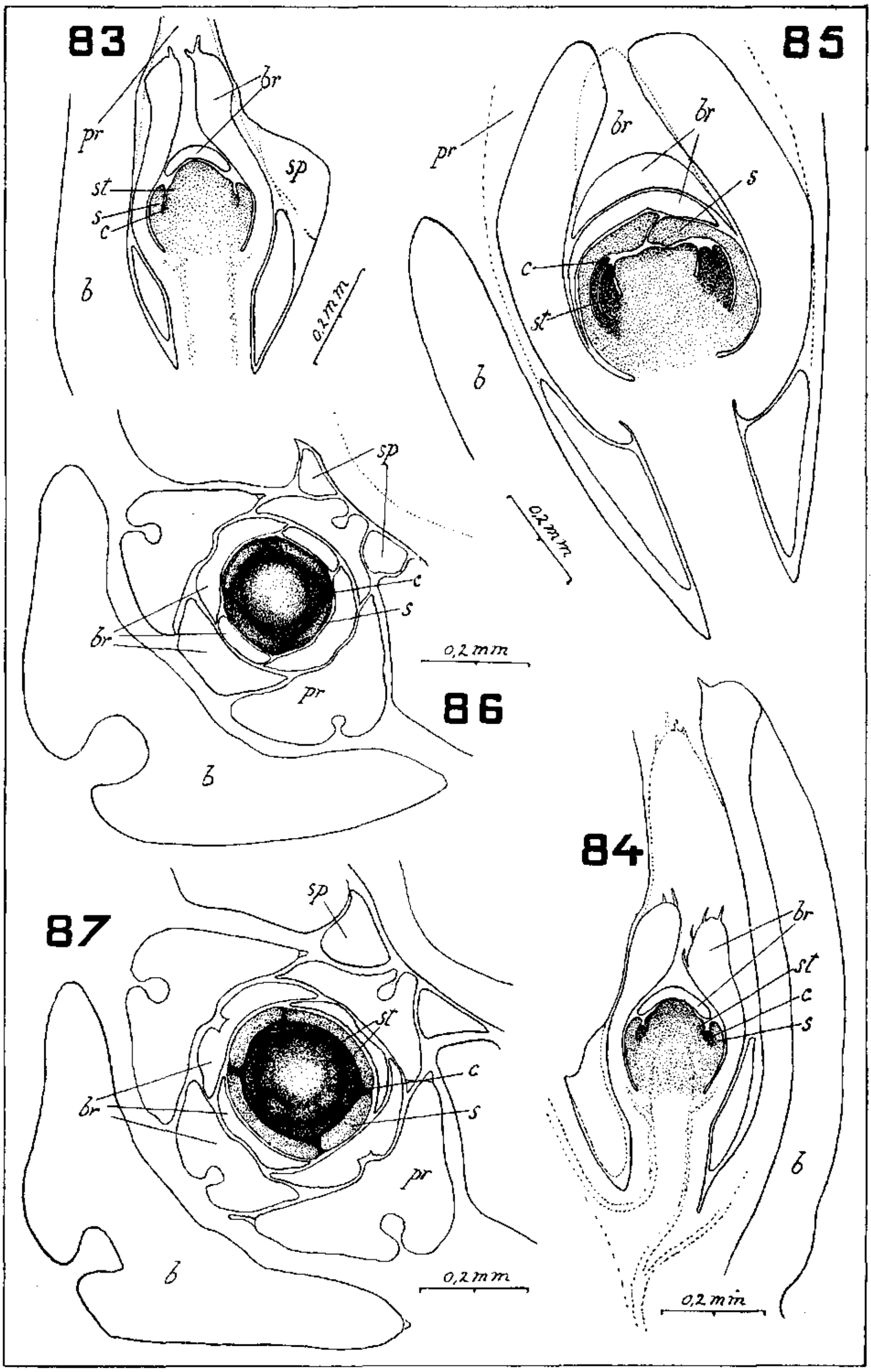
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Fig. 83—87.

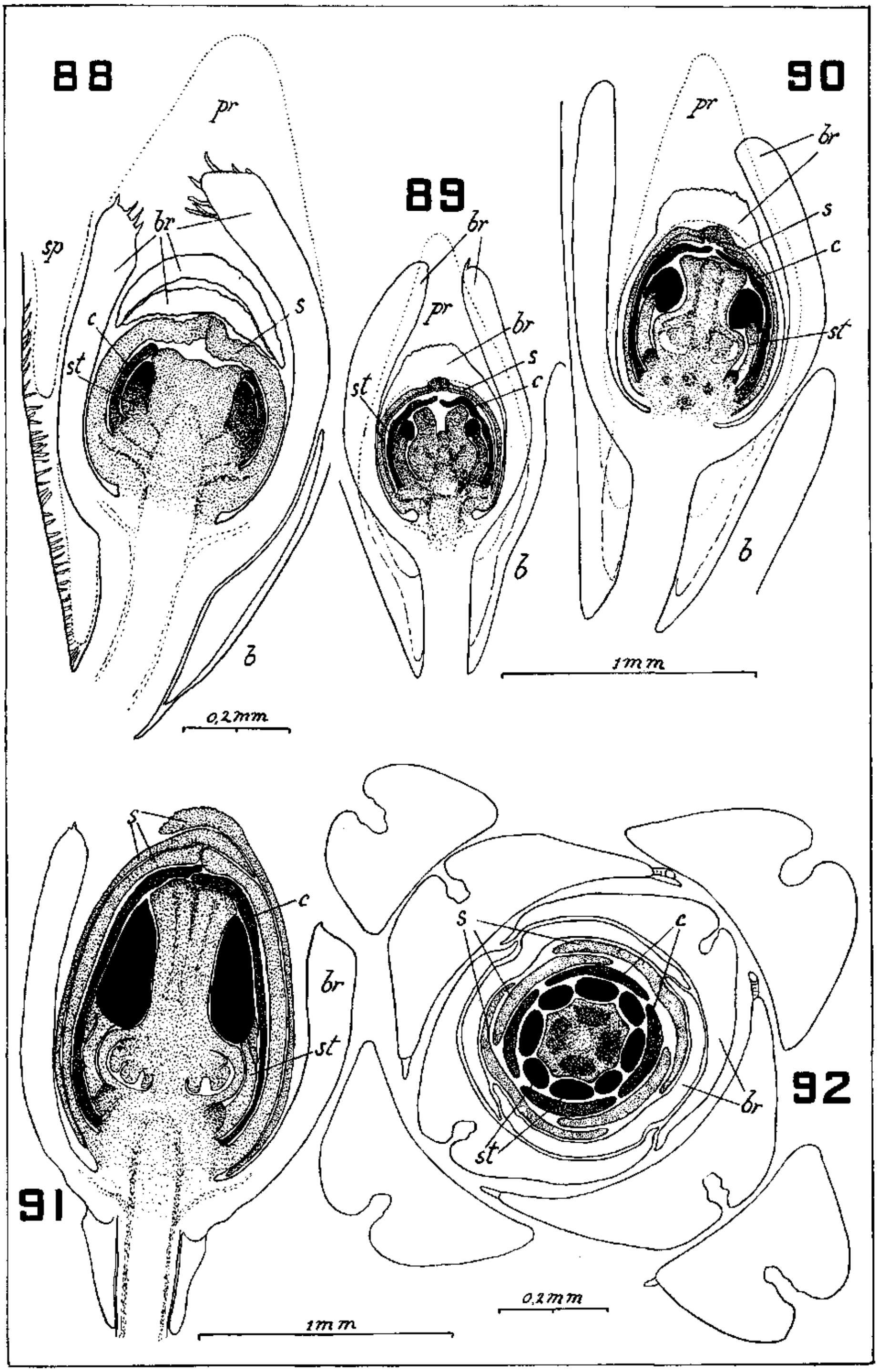
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Fig. 88—92.

some years been the earliest to flower, the first flowers opened at the end of June or in the beginning of July.

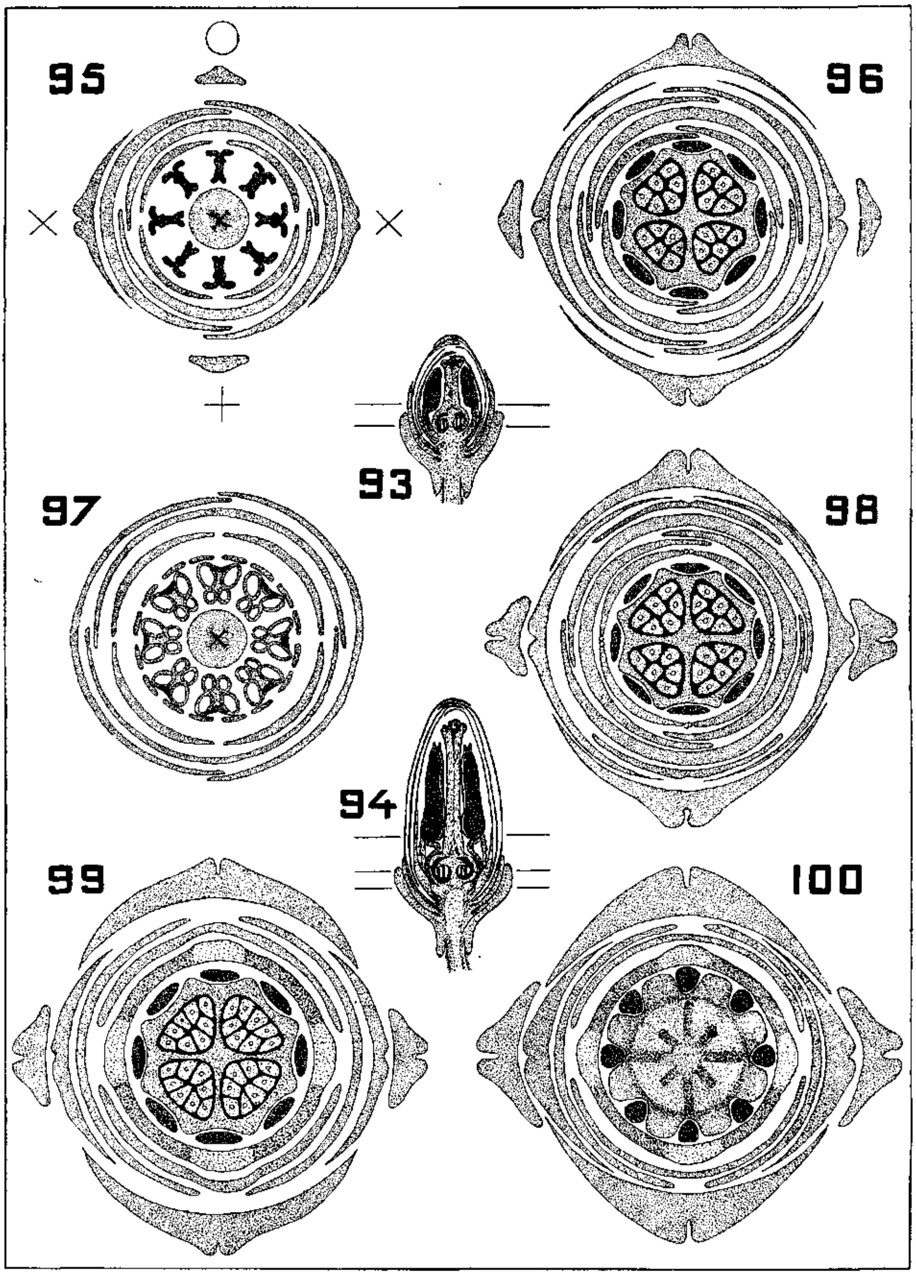

Fig. 93—100.

At an elevation of 2000 m however, in the East Alps, Calluna seems not to flower before the end of August (cf. SCHIMPER and v. FABER, 1935, II, p. 1287). So a difference in elevation of 800—1000 m brings about a considerable difference in the time of flowering. Still wider apart are the flowering-times of the Mediterranean region, Central Europe and Lapland. In Morocco and South Spain Calluna does not flower until November and December, while in Central Europe this time lies between 15 July and 15 September. In Swedish Lapland, near the polar circle, I saw Calluna in full bloom at the end of July. Having returned a few days later to the Netherlands, I was greatly surprised that the heath-fields of Drente showed hardly any bloom yet. In the most northern places, as the Varanger Fjord, at the end of July no trace of flower-formation could be seen. It seems that there, on the farthest northern border of the region of distribution, no flowers and certainly no fruits can by any means be formed every year. According to WARMING this is one of the factors that prevent further spreading to the north.

H. Formation of adventitious organs.

One year old seedlings as well as older plants may on the root-base and in other places along the stem and root develop adventitious shoots, generally in the shape of leafed short- and long-shoots, but also as adventitious roots. These organs are formed in the following ways:

1. from a wound cambium, as the result of mechanical injuries (true adventitious organs),
2. from so-called "dormant" eyes on the stem below places where there have been injuries or disturbances (seemingly adventitious organs),
3. from parts of the stem or root, by the influence of the environment, without lesions or disturbances (true adventitious organs).

1. This case is frequent in nature when the very tender young seedlings have been injured, e.g. by freezing up in winter or by being trodden down and probably also by snow-pressure and voracity of animals. A condition in all these cases is that the environment allows the development of these organs. Thus, adventitious organs will rarely develop in dry surroundings, whereas they readily do so in the always moist atmosphere of the moors. There even gnawed off or broken twigs may strike root again and go on growing, for Calluna is a woody plant that easily grows from cuttings, if certain conditions are fulfilled as to time of the year, size, age and place of the cutting, the substratum and other factors of the medium. (Ch. III).

2. If during the vernal growing-period (March—July) long-shoots are pruned or by some other mechanical cause the main vegetation-point is destroyed or if it dies off, at a short distance below it still dormant or feebly developed eyes, which regularly exist in the axils of the long-shoot leaves, will sprout vigorously, generally forming one or more new long-shoots. Pl. III, 1, represents a case where the intercalary growth was interrupted by fire. The original long-shoot was here continued by a number of smaller but typical long-shoots. The further backwards an

extending long-shoot is lopped, the more vigorously the new shoot will generally develop. This is typical for regenerating long-shoots. Short-shoots regenerate with much more difficulty or not at all. However, the wound-surfaces of the clipped side-shoots and stem-leaves, even of the short-shoot leaves, may develop adventitious roots under favourable circumstances, e.g. when slipped in an always moist but well aired locality.

3. Frequently older and younger parts of stems and roots develop very thin rootlets, especially if the root-system no longer functionates normally, if, for example, a thick moss-cover or accumulating humus threatens to smother it. In Plate IV, 1, to the right, an over ten years old Calluna stem is represented, from which in a number of places young roots have come forth without any perceptible outside injury. Here a vigorous growth of moss round the plant had been the cause; in a high moss-cushion of *Entodon Schreberi* and *Hypnum cupressiforme* the plant was already so deeply imbedded that it stood in danger of being overgrown. This often happens in peat-moors, where the *Sphagnum* cushions sometimes grow up at a prodigious rate, choking those species that are unable to develop quickly enough new adventitious roots at a higher level. Most peat-moor plants, such as *Eriophorum, Drosera, Vaccinium oxycoccus, Betula, Andromeda polifolia,* and others, have the power to form adventitious roots, like Calluna. Plants that cannot do this speedily enough, will perish there. Such are: *Pinus silvestris, Picea excelsa, Rhynchospora, Carices.*

This ability to form adventitious organs in many places of the cormus greatly increases the resistance of Calluna. Perhaps for this reason it is eminent as a former of peat, at least in regions where it thrives. Cumbent forms may take root over and over again and so creep on and spread. This is not observed in dry sandy regions, however.

These examples confirm that: 1. from wound-tissue new vegetation-points can develop as true adventitious organs; 2. from so-called dormant eyes, already present in origin, suddenly (seemingly adventitious) organs can come into being; 3. from apparently healty cambium new (truly adventitious) shoots can develop.

If one cuts off a short-shoot and strips the lowest leaf-pairs, the planted cutting will develop roots from the ring of wound-cambium, formed round the scars. But also if the lowest leaf-pairs are not removed and the cutting is put halfway in sand, the rootlets grow out from the axils.

In the latter case either the tissue at the insertions of the leaflets has been damaged and this injury has been sufficient to stimulate the evolution of roots, or the dormant eye in the leaf axil develops into a root.

Leaves and flowers, as far as my observations go, do not form adventitious organs. In theory it is possible, though, because of the remarkable structure of the ovary, that shoots might develop from the flower-origin of a slipped flower-twig, provided it bears enough leaves and the flower-bud is in an early stage.

There is still another way in which adventitious shoots may be formed in large numbers and on a large scale in the field, namely after heath-fires. In Plate III, 1 a plant is pictured which was burnt down and charred above ground in the spring of 1938. The photo was taken on September 19 of the same year. Within half a year the adventitious shoots had vigorously developed and attained a rich bloom.

The dotted line marks the burnt surface. Both stems and roots have developed close together just below the surface.

III. GEOGRAPHY.

A. Main area and further distribution on the Earth.

The main area of Calluna extends over a large part of Europe with the exception of the south and east of the Mediterranean region. Over smaller areas and in isolated places it also grows in the adjacent parts of Asia and Africa and in North-America.

In Europe the northern boundary runs from the extreme north of Norway (Magerö, 71° 5′ North latitude) over the Varanger-Fjord to Alexandrovsk (ISATSHENKO, 1927) and further to the south-east via Yokanskoe in North-Kola (POHLE, 1898) to the Kanin peninsula, where according to SCHRENK and POHLE the northern limit lies between 67° and 69° North lat. In the northern part of the Rybatshi (Fishermen) peninsula and in the island of Heinäsaari I did not find Calluna any longer, but I did near Kirkenes (South-Varanger). From Kanin, where Calluna penetrates into the tundra, as it does in Kola, the northern boundary runs steadily south-east, to the banks of the Rotshuga and the western slopes of the Timan Range, and through the former district of Wologda (BÜCHER, 1882) as far as the Ural. It passes this mountain range approximately in the direction Tsherdyn—Werkhoturj (Ural region), and then, according to the extensive newer data of KRYLOV, proceeds eastward in West-Siberia via Turinsk as far as Tobolsk. Here the northern boundary, running south-east, meets the southern, running from south-west to north-east. It begins in Morocco in the coastal area from Tanger (MAIRE) to Tetuan (HOOKER, 1871; TRITTENY, 1934), runs over Corsica and Central Italy (BERTOLONI) through Dalmatia to Bosnia (Serajewo-district and Zepec, after SMITH and KUTTALY) and then to the north through Slavonia. Avoiding the Bakony Wood and the Hungarian Plain (NEILREICH) it goes in a wide arch southward through Siebenburgen (FUSS & SCHUR), bends to the north again through Rumania, west of the Moldau, and then via Khotin (BODE, 1856) to Wladimir. From there the boundary of the area bends eastward, round Podolia, and follows the 50th parallel at some distance via Ostrog and Shitomir to Kiev (acc. to KÖPPEN, 1881). KÖPPEN's further data for South-Russia indicate that the boundary of the closed area runs from Kiev to the north-east via Glukhov, Trubtshevsk, Bjelev and Alexin (south of Moscow) and from there eastward in the direction of Kazan as far as Alatyr. According to the same author, HERDER and WITTICH, Calluna grows in several isolated spots in the districts Poltawa, Kursk, Woronesh, Tambov, Saratov and Penza. These spots have not been marked on the map, because in my opinion it then better shows that the

Ural-Wolga basin, like the basins of the Don, Dnjepr, Dnjestr and Danube are all avoided with wide arches. On the further course of the southern boundary of Calluna in Russia, east of the line Balashov (ZINGER) — Alatyr (KÖPPEN), the data of KÖPPEN (1888), WITTICH (1889) and HERDER (1892) do not agree. According to GAMS (communication by letter) the southern boundary in Russia nearly coincides with the limit for *Pinus silvestris*. KÖPPEN draws a pretty well straight eastern boundary from Alatyr northward across the Wolga west of the district Wjatka, to Ustsyssolsk as far as the Timan Range, probably based on the older data of A. MEYER and KRYLOV. According to KRYLOV's more recent data this line cannot be right. WITTICH draws the southern boundary from Spask (district Tambov) to Laishev (distr. Kazan) further eastward, north of the river Belaja, via Serapol and Krasno Ufimsk (distr. Perm) to Ekaterinenburg. From there it runs further eastward via Shadrinsk, Kurgansk and Yalatorovsk to Tobolsk. WITTICH's boundary is indicated on the map.

In the west the area is bounded by the Atlantic and the Arctic. The islands in the Atlantic are isolated parts of the European area, in few of them Calluna is lacking.

From the Azores, notably from Pico and Terceira, it is repeatedly reported (SEUBERT and HOCHSTETTER, 1843, 1844; GUPPY, 1917). In the British Isles (incl. the Channel Isles, Hebrides, Orkneys and Shetlands), as well as on the Faröer (OSTENFELD and GRÖNTVED, 1934) Calluna is spread everywhere. In Iceland it is only absent in the north-west (acc. to HAGERUP and OSTENFELD). Some herbarium material from the neighbourhood of Constantinople, kept in the Vienna herbarium (leg. J. NEMETZ, 1896), was collected in a wood near Bagdshe Kai. According to MATTFELD (1929) and STEFANOFF (1924) a separate area extends in East-Thracia from near Constantinople to just south of Burgas.

The only known African area has already been mentioned in connection with the European main area. In the Tingitan peninsula Calluna is found in the Djebel Kébir near Tanger (GAY, 1925; PITARD, 1913 and MAIRE, 1929) and near Tetuan (TRITTENY, 1934).

In Asia, outside the mentioned West-Siberian offshoots of the main area in the Ural region, only a few isolated habitats are known, near Perm, Tjumen and Tobolsk, of which that in the district Tomsk in the neighbourhood of the village Berdskii Obi, mentioned by KRYLOV, is the most eastern one. The specimen in the Leningrad Herbarium, labelled: "Yakutsk (?), Strutshkov", probably is a mistake, according to E. BUSCH (1910), although STRUTSHKOV has indeed collected plants there and sent to Petersburg in 1856. From the North of the district Akmolinsk KRYLOV reports another find-place in the district Koktshetavskaja in the neighbourhood of the village Borowii.

The most south-eastern find-places are in the Pontian mountains, near Lazistan-Trebizond, on the mouth of the river Of, at 41° North lat. and 40° East long. (K. KOCH, 1837; BALANZA, 1866, and HANDEL-MAZETTI,

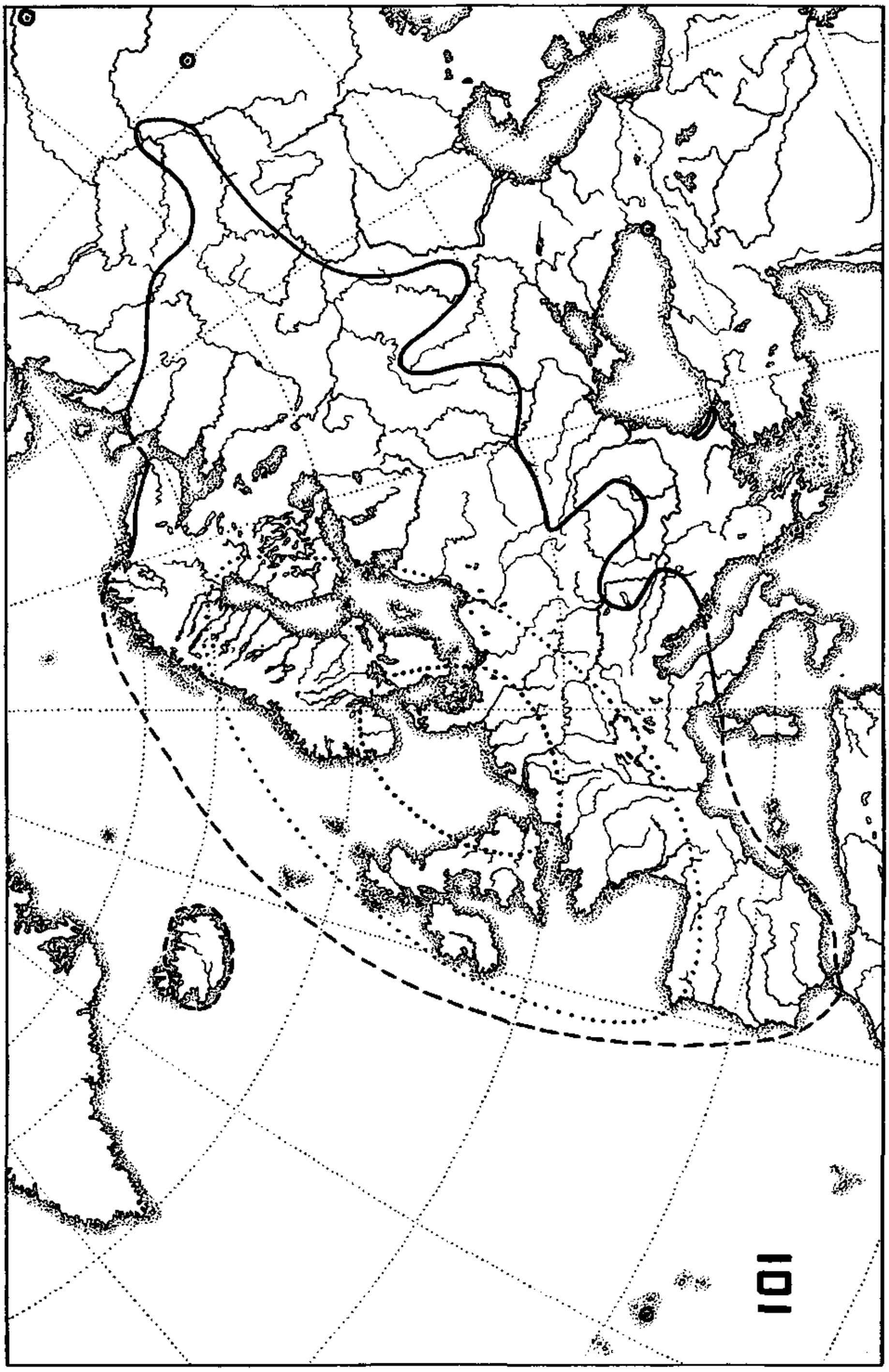

Fig. 101.

1907). Here, as in Thracia, Calluna belongs to the Végétation colchique (communication by WIŚNIEWSKI).

The Americans are at present inclined to consider Calluna in North-America as an adventive plant, probably introduced by the old settlers. Assuming this to be true, because no original habitats have become known with certainty, we may state that it has become well naturalised and thrives in several places on the Atlantic coast between Quebec and New Jersey.

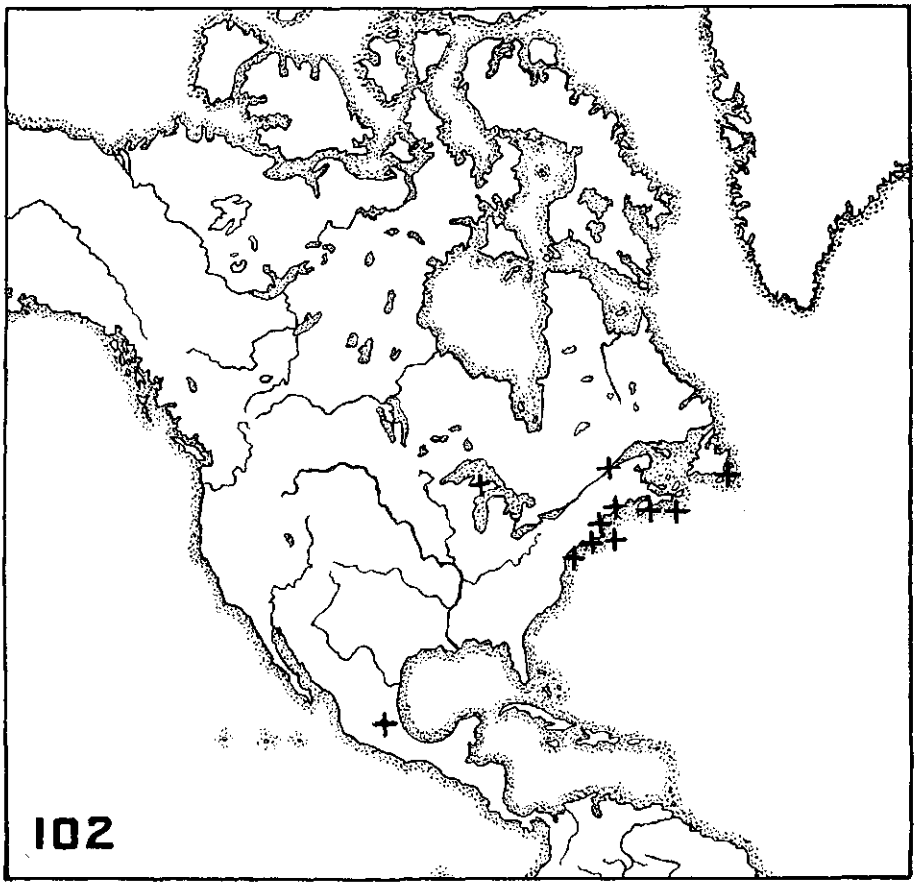

Fig. 102.

It is even found near Marquette (Michigan), and seems to be spreading. In the Gray Herbarium I found specimens from Calvert (Caplin Bay, S. New Foundland); Whitborne; Sable Island; Halifax, N. Sc.; Portland; Chathamport (Mass.); Tewksbury (Mass.); Nantucket; Edgartown (Mass.); Egg Harbor City (New Jersey). The Kew Herbarium contains a plant from Cape Breton Island (1862). The Berlin Herbarium even has a plant with the inscription: "Mexico, Queretaro, leg. UHDE, comm. NIEDERLEIN", without further comment. In the State Herbarium at Leiden there is a specimen with the annotation: "Labrador?, comm. KRAEPELIN", also without further comment. It is obvious that such material is of no great use.

On the geographical distribution of the varieties and forms little is known as yet. The var. *hirsuta* (WAITZ) GRAY with dense hair over the whole surface of the leaf, which makes the plant look like white or grey felt, seems to be spread over England and Scotland and also occurs in France (especially Central France and the Landes), the Channel Isles, the northern Fore-Alps, Bohemia to Silesia, and more rarely in Germany, the Netherlands, Danmark and Lithuania. Among the rich Scandinavian material I noticed only one feebly haired specimen from South-Sweden (Ronneby, leg. LINDBLOM, 1845). In the Finnish and Russian material it was entirely absent, and likewise in the South-European. The richest findings come from Central England and Scotland and from the Channel Isles. The comparatively scanty material from America contained three hairy specimens; possibly this is connected with the import of English and French plant-trees in the last century.

The white-flowering form of Calluna (fa. *alba* (WAITZ) DON) was amply represented especially in the Fennoscandinavian material, a good many specimens also came from England and Central-Europe, very few from Russia and South-Europe, none from Spain, for example. KUJALA (1929) reports from Virtaniemi (Finnish Lapland) the frequent occurrence of white-flowering heather. Also from Swedish Lapland I saw several specimens in the Stockholm herbarium.

The purely female form (fa. *gynodioica* W. BEIJ.) is up to now only known from the Netherlands, several other forms, characterised by deviating flowers, only from England and the Netherlands, and a few (fa. *diplocalyx* and fa. *multibracteata*) also from NW-Germany. The fa. *polypetala* with its subforms is in the wild state up to now only known from England. It is possible, of course, that a closer search will reveal the presence of these forms elsewhere. Separate mention deserve the very late-flowering South-European forms, among which the fa. *elegantissima* Sennen from Spain, Portugal and Morocco, which flower in November and December, also in the Netherlands. The late-flowering Calluna-forms *multibracteata*, *diplocalyx*, *polysepala* and *hiemalis* are indigenous in England and the Netherlands.

B. Horizontal and vertical distribution within the main area.

Within the main area Calluna is on the whole restricted to those parts where the following conditions are satisfied:

1. a small quantity of assimilable mineral salts (oligotrophy).
2. a hydrogen-ion concentration of the soil between pH $= 3.5$ and 6.7.
3. no excessive fluctuations in the humidity of air and soil.
4. in the far North and in the high mountains, a protecting snow-cover during the winter-months.
5. enough light.

These are the chief, though not the only, factors. So Calluna is lacking horizontally and vertically:

a. on the clay-soils of river-valleys and coastal areas.

b. on strongly alkaline soils (marl, lime, etc.), if there is no acid cover of humus in which the plant can strike root.

c. in regions with a pronounced continental and steppe climate, without an efficient screen, e.g. of trees.

d. on exposed places in the mountains where the winter-storms sweep away the snow.

e. in dark woods or other badly lighted places.

But where the above conditions are satisfied Calluna can exist, if the rivalry of other forms of life and the remaining factors of the environment allow it. Besides the competition of other plants and animals it has above all been man, who from times immemorial has strongly influenced the extension of the Calluna-vegetations in some places and their disappearance elsewhere. Their distribution within the main area is nowadays quite different from what it was one or more centuries ago. Extensive heaths in South Sweden, Danmark, North Germany, the Netherlands, England, Belgium and France have now disappeared by reclamation, while during the Middle Ages and long before, in prehistoric times, by repeated dis-afforestation, either wilful or by wood-fires, large areas were prepared for a heath-vegetation. Still, in my opinion, this latter point of view is sometimes exaggerated. It is unlikely that only the destruction of woods should have given rise to all the Calluna-heaths of Europe. Without the interference of man also nowadays heath-vegetations form again and again on virgin soil, which may be grounds, shifted and transformed by Nature, as dune- and drift-sands, mountains above the tree-line, in the far North (Lapland), shifted and washed out valley-sands, and peat-moors, when raising and draining of the surface begins to hamper the growth of mosses. A condition in all these cases is that a sufficient source of seed is close by.

Ecologically heath- and Sphagnum-moor vegetations are closely connected and often pass imperceptibly into each other. The oligotrophy, the hydrogen-ion concentration in the root-layer and the illumination are about the same. Only the humidity diverges rather strongly and therefore is of primary importance. The oligotrophic heath- and Sphagnum-vegetations in our country are perhaps the most striking examples of the connection between the factors of the medium and the vegetation-cover, for the scantiness of the food and a greater or smaller accumulation of adsorptively unsaturated humus-substances alone suffice to cause a rigorous selection of the plant-types. Moreover the surviving flora-elements are so sensitive to further small differences in the medium, that they may become locally predominant, or be entirely absent, or live together with other species. WARMING rightly sees in the possibility for the seedlings in the heath to develop one of the most important criteria. Also the micro-climate of the growing-place is significant. The course of the temperature there strongly reminds of a continental climate by its wide fluctuations. It differs entirely from that in a swamp, for example. The humus-cover is a bad conductor of heat, so that a rise of temperature does not penetrate far below the surface. So high temperatures by day and low at night are characteristic. Night-frosts are much more frequent than in other regions. The daily amplitude sometimes amounts to 27—30° C., especially on the true Sphagnum-moor. In proportion as the humus-cover becomes thinner and contains more sand, the extremes differ less. The chief cause of all this is the difference in humidity. The ecological saturation-deficit (= max. vapour-tension with respect to the moist thermometer) gives an idea of the transpiration-possibilities of the damp Sphagnum cushions on the one hand and the Calluna vegetation on the other. The ratio between the precipitation (in mm) and this saturation-deficit, the so-called water-balance quotient, is according to LEICK (1930) a good standard for the water-conditions of a region and indicates pretty accurately where a Sphagnetum can or cannot maintain itself, so that other plants, better adapted to dryness, begin to predominate. The evaporation-gradient in the peat-moor is very great, in the heathfields smaller, but in both is subject to wide fluctuations. Also the condensation of water in the form of dew is an important factor in the heathfield as well as in the Sphagnum-bog. According to LEICK the survival of a moor may depend on it alone. In either region the layer with the roots may for a time become so dry that the plants would not be able to keep their water-economy balanced, if the xeromorphic character of most peat-moor plants and heathfield-plants, with the exception of the mosses (*Sphagnaceae*), did not save them.

In the far north Calluna is lacking in places where during the long severe winter with its desiccating winds there is no sufficient snow-cover. On such exposed places Calluna is replaced by species like: *Loiseleuria procumbens, Empetrum hermaphroditum,* lichens and other less sensitive species. More to the south it prefers a pronounced Atlantic climate and avoids the regions with a continental climate. With sufficient atmospheric humidity it can penetrate far south, as we see demonstrated in the coastal areas of Morocco, Lazistan and Strandzsha along the Black Sea and in the Azores. There are in the south a larger number of competing species, though, e.g. from the Maquis flora and the mountain-wood flora, so that Calluna mostly occupies a secondary place there, as it does in the extreme north. Towards the continental east (Russia) Calluna becomes more or less a wood-plant and is seldom found in the open field. Along the coasts of the North Sea is the area of its optimal development (inner dotted line on the map), where it may occur in strange places, on the thin humus-cover of the chalk-cliffs of South England or on the half-washed valley-sand of the plain of the Rhine; even on the clay of Seeland (Danmark) there are places, where a very thin acid cover is sufficient to call a Calluna vegetation into being. In South-Norway with its exceptionally high rainfall of over 2000 mm, Calluna grows, like various other plants, on the roofs of the houses. In this country I found small young Calluna plants on the hood of the fungus *Polyporus perennis*, rooted in the half-decayed tissue of the fungus. So we see that with an otherwise favourable factor-complex the substratum is relatively unimportant.

Within the optimal region the true Calluna fields extend, which in their purest form contain this species only or at most a slight admixture of some other species, like *Erica tetralix, Genista pilosa* and *Genista anglica*. The farther one comes outside this region the greater the admixture will be, until outside the second dotted line in the main area hardly any extensive Calluna-fields are met with, at best vegetations with an admixture of Calluna. An exception to this, however, are the areas and localities outside the main area, such as East Thracia and the Azores, where the conditions may locally be so favourable that the same heath-fields as in the second zone may come into being. In the Central Alps Calluna ascends near the snow-limit, which it never reaches, though. In Tessino it is found from 205—2600 m above sea-level (CHEVENARD, 1910), in the Grisons as high as 2670 m (RÜBEL and BRAUN), in the Puschlav district up to 2250 m (BROCKMANN–JEROSCH, 1907). In South Spain on the other hand it is stated not to occur above 350 m (WITTICH, 1889). In the British Isles it is found up to 600 m, in Scotland up to 975 m (GRISEBACH, 1884) and in South Norway it is mentioned up to about 1250 m (BLYTT, 1861). In Central Scandinavia it occurs in places from sea-level to 1200 m (SMITH). In the north of Lapland I found Calluna at about 100 m above sea-level here and there on the coast-fjells, e.g. near Kirkenes. In Morocco it grows between 50 and 400 m (MAIRE's "étage méditerranéen humide"). In the isle of Pico (Azores) it climbs to the highest top of the volcano, 2222 m above sea-level (GUPPY, 1917). In the Central European mountains it nearly everywhere reaches the highest tops and on a boggy substratum often forms field-vegetations on the crest, so e.g. on the Hautes Fagnes and in the Black Forest on the Hornisgrinde.

C. Vegetation-types, in which Calluna is found.

Calluna, owing to its physiological and morphological properties, such as its ecological plasticity, abundant seed-production and good spreading-possibilities, inhabits an extensive area. Consequently it is found under very different climates, under the temperate rainy climate of Western Europe, the humid boreal climate of East- and partly North Europe, and the Mediterranean sea-climate, which is also a moderately warm wet climate, but with hot and dry summers and wet winters. Calluna may therefore meet all sorts of vegetation-types, peculiar to these climates. In the following survey first floristically different vegetation-types with a Calluna admixture are summed up, without any pretence to completeness. Then the ecologically different combinations of species are mentioned, in which Calluna occurs, and finally the successions in which the true heathfields participate. In most of the following lists a figure behind the name indicates the degree of covering, this being the surface occupied by that species. BRAUN–BLANQUET's five subdivisions 1) have been used. RAUNKIAER's data from Danmark are only provided with a frequency-index, i.e. the number of times a species was observed in different vegetations. In a few lists, borrowed from literature or in some cases from communications by letter, for lack of further data only an enumeration of the species could be given. We shall start in the extreme north.

I. Heath, rich in lichens, on the Kaunispää in Finnish Lapland, 68° 30′ N. lat., 505 m above sea-level. (BEIJERINCK, 1934).

Empetrum hermaphroditum 3
Vaccinium myrtillus 2
Vaccinium vitis idaea 2
Vaccinium uliginosum 1
Loiseleuria procumbens 1
Calluna vulgaris 1
Andromeda polifolia 1
Phyllodoce coerulea 1
Linnaea borealis 1
Festuca ovina fa. 1
Deschampsia flexuosa 1
Nardus stricta 1
Carex rigida 1
Rubus chamaemorus 1
Pedicularis lapponica 1
Bartschia alpina 1
Orchis maculata, var. *lapponica* 1
Sphagnum fuscum 1
Sphagnum Warnstorfii 1
Sphagnum Wulfianum 1
Cladonia alpestris 4
Cladonia rangiferina 2
Cetraria nivalis 1
Cetraria islandica 1

II. Calluna-heath, rich in species, N.E. of Nedalen in the Sylene-district in Central Scandinavia, 850 m above sea-level. (NORDHAGEN, 1927).

Calluna vulgaris 5
Arctostaphylos alpina 1
Loiseleuria procumbens 1
Vaccinium myrtillus 1
Vaccinium uliginosum 1
Vaccinium vitis idaea 1
Empetrum nigrum 2
Betula nana 1
Juniperus nana 1
Lycopodium alpinum 3
Deschampsia caespitosa 1
Deschampsia flexuosa 1
Agrostis tenuis 1
Nardus stricta 1
Carex rigida 1
Carex sparsiflora 1
Bartschia alpina 1
Campanula rotundifolia 1
Galium boreale 1
Hieracium spec. 1
Pedicularis Oederi 1
Pinguicula vulgaris 1
Polygonum viviparum 1
Potentilla erecta 1
Selaginella spinulosa 1
Solidago virga aurea 1
Polytrichum alpinum 1
Hylocomium Schreberi 1
Hylocomium splendens 1
Lophozia lycopodioides 1
Ptilidium ciliare 1
Cladonia silvatica 1
Cladonia rangiferina 1
Cladonia alpestris 1
Cladonia coccifera 1
Cladonia gracilis 1
Cladonia pyxidata 1
Cetraria islandica 1

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1) 1 = less than 1/20 of the surface; 2 = 1/20 to ¼; 3 = ¼ to ½; 4 = ½ to ¾; 5 = more than ¾.

III. Bare Calluna-heath in South Norway. Lowest alpine zone in the Tron-district, 900—950 m above sea-level (after DU RIETZ, 1925). Two counts.

Calluna vulgaris	5	5	*Festuca ovina*	—	1
Empetrum nigrum	2	2	*Luzula pilosa*	—	1
Linnaea borealis	—	1	*Dicranum scoparium*	1	1
Vaccinium myrtillus	1	2	*Hylocomium parietinum*	—	1
Vaccinium vitis idaea	2	1	*Jungermannia* spec.	—	1
Antennaria dioica	1	—	*Polytrichum* spec.	1	—
Deschampsia flexuosa	1	2	*Cetraria islandica*	1	1
Cladonia coccifera	1	1	*Cladonia rangiferina*	1	1
Cladonia crispata	1	1	*Cladonia silvatica*	2	1
Cladonia degenerans	1	—	*Cladonia squammosa* f.	1	—
Cladonia gracilis f.	—	1	*Cladonia uncialis*	1	—
Cladonia pyxidata	1	1	*Peltigera aphtosa*	1	—

IV. Jutland heath-types according to RAUNKIAER (1918).

	Frequency of the species			
	Group A	Group B	Group C	Group D
Calluna vulgaris	100	100	96	92
Arctostaphylos uva ursi	36	92	12	—
Empetrum nigrum	40	60	100	24
Erica tetralix	—	—	4	88
Genista anglica	—	20	—	—
Genista pilosa	—	8	—	—
Vaccinium uliginosum	—	—	—	4
Vaccinium vitis idaea	—	—	36	—
Salix repens	—	—	—	4
Aira flexuosa	—	4	4	—
Molinia coerulea	24	52	8	24
Scirpus caespitosus	—	4	8	12
Juncus squarrosus	—	—	4	—
Carex Goodenoughii	—	—	24	—
Carex panicea	—	8	16	16
Carex pilulifera	—	8	—	—
Potentilla erecta	—	8	—	—
Arnica montana	4	12	—	—
Majanthemum bifolium	—	8	—	—
Orchis maculata	—	8	—	—

Cryptogamia have not been included. Group A: heath south of Varde; B and C: heaths north of Varde; D: heath near Grinsted.

More to the north-east, in Finland, Russia and to some extent already in Brandenburg, Pomerania and West-Prussia Calluna is accompanied by a few other species, as:

Ledum palustre
Chamaedaphne calyculata
Pinus silvestris

V. True Calluna heaths in the Netherlands and N.-W. Germany, after BEIJERINCK, 1934 (1, 2), TÜXEN, 1937; VAN DIEREN, 1934 (10); and DIEMONT (1937).

Species \ Localities	1	2	3	4	5	6	7	8	9	10
Pinus silvestris	+—1	+—2	+	—	+—1	—	—	—	+—2	—
Juniperus communis	+—2	—	+—2	—	+	—	—	—	+—2	—
Betula pub. et alba	+	+	+	—	+—1	+—1	+	+	+	—
Quercus robur	+	+—1	+	—	+	—	—	+	+—1	—
Sorbus aucuparia	+	+—1	—	—	+	—	—	—	+	—
Vaccinium myrtillus	—	—	—	—	—	—	—	+—1	—	—
Vaccinium vitis idaea	—	—	—	—	—	—	—	—	+—2	—
Empetrum nigrum	—	—	—	+—5	—	—	—	—	2—5	+—2
Arctostaphylos uva ursi	—	—	—	1	—	—	—	—	—	—
Calluna vulgaris	4—5	3—5	4—5	2—5	2—5	2—4	4—5	1—5	2—5	5
Erica tetralix	1—3	+—3	+—1	+	+—3	1—3	—	—	+—3	+—2
Genista anglica	2—3	+—2	+—1	+—1	+—1	+—2	—	—	1	+
Genista pilosa	1—2	+—2	+—2	+—2	+—1	+—1	1	+—2	—	—
Myrica gale	—	—	—	—	—	—	—	—	—	+
Salix repens	—	—	—	—	—	+—1	—	—	—	+—2
Salix aurita	—	—	—	—	+	—	—	+	+	—
Deschampsia flexuosa	—	—	+—2	+—2	—	—	—	+—2	—	—
Agrostis alba	—	+—3	+—1	+—1	+	+	+	+—1	+—1	—
Anthoxanthum odoratum	—	—	—	—	—	—	—	+	—	+
Festuca ovina	+—1	+—5	+—1	+—2	+—1	+—1	+—1	+—2	+—1	+—2
Sieglingia decumbens	—	+—1	+—1	+—1	+—1	+—2	+—3	+—2	—	—
Ammophila arenaria	—	—	—	+—2	—	—	—	—	—	+—2
Molinia coerulea	+—1	+—1	—	—	+—2	+—2	—	—	1—3	—
Nardus stricta	—	+—1	—	+	+—1	+	—	+—4	—	—
Juncus squarrosus	+	—	—	—	+—1	+—1	—	—	—	—
Trichophorum caespitosum	+	—	—	—	+	+	—	—	+	—
Carex panicea	+	—	—	—	—	—	—	—	—	—
Carex pilulifera	+—1	+—1	+—2	—	+—1	+—1	+—1	—	+—1	—
Carex arenaria	—	—	—	+—2	—	—	—	—	—	1—3
Carex trinervis	—	—	—	—	—	—	—	—	—	+—1
Luzula campestris	—	—	—	+—1	+	—	+—1	+—1	—	—
Lycopodium clavatum	+	—	—	—	+	—	4	+—2	—	—
Lycopodium complanatum	—	—	—	—	—	—	—	1	—	—
Orchis maculata	—	—	—	—	—	+—1	—	—	—	—
Platanthera bifolia	—	—	—	—	—	+	—	—	—	—
Rumex acetosella	—	+—1	—	—	—	—	+	—	—	—
Potentilla erecta	+—1	+—1	+—1	+—1	+—1	+—1	—	+—1	+—1	+—1
Epilobium angustifolium	+—1	+	—	—	—	—	—	—	—	—
Polygala serpyllifolia	—	—	—	—	—	+—1	—	—	—	—
Rubus fruticosus	—	+	—	—	—	—	—	—	—	—
Veronica officinalis	—	—	—	—	—	—	—	+	—	—
Pedicularis silvatica	+	—	—	—	—	+—1	—	—	—	—
Cuscuta epithymum	—	+	+—1	+	+	+—1	—	—	—	+
Lotus corniculatus	—	—	—	—	—	—	—	—	—	+
Rosa spinosissima	—	—	—	—	—	—	—	—	—	+
Galium verum	—	—	—	—	—	—	—	—	—	+
Galium mollugo	—	+	—	—	—	+	—	+—2	+—1	—
Campanula rotundifolia	—	+	—	+	—	—	+—1	+—1	—	—

V. (*Continued*).

Localities / Species	1	2	3	4	5	6	7	8	9	10
Gentiana pneumonanthe	+	—	—	—	—	+—1	—	—	—	—
Succisa pratensis	—	—	—	—	—	+	—	—	—	—
Solidago virga aurea	+—2	—	—	—	—	+	—	—	—	—
Arnica montana	1	—	—	—	—	+—2	—	—	+—1	—
Scorzonera humilis	—	—	+	+	+	—	—	—	—	—
Leontodon autumnalis	—	+—1	—	—	—	—	+	—	—	—
Hypochoeris radicata	—	+—1	—	—	—	+	+	+	—	—
Achillea millefolium	—	—	—	—	—	—	+	+	—	—
Antennaria dioica	+	—	+	+	+	+—1	+—3	+—2	—	—
Hieracium umbellatum	+—1	+—1	—	+—1	—	—	—	+—1	+—1	—
Hieracium pilosella	—	+—1	—	—	—	—	+—1	+—1	—	—
Hieracium levigatum	—	—	—	—	—	+	—	—	—	—
Hypnum Schreberi	+—2	+—1	+—5	+—4	+—4	+—3	+—4	+—5	1—5	
Hypnum cupressiforme f.	+—2	+—1	+—3	+—5	+—4	+—2	+—2	+—3	+—4	
Hypnum imponens	—	—	—	—	+	—	—	—	—	
Polytrichum commune	+—2	—	—	—	—	—	—	—	+—1	
Polytrichum juniperinum	—	+—2	—	—	+	—	+—1	+—1	—	
Polytrichum piluliferum	—	—	—	—	—	—	+	—	—	
Polytrichum attenuatum	—	—	—	—	—	+—1	—	—	—	
Dicranum scoparium	+—3	+—1	+—2	+—3	+—1	+—1	—	+—2	—	
Dicranum spurium	+—1	—	—	+—1	+	—	—	—	+—2	
Dicranum undulatum	—	—	—	—	—	+—2	—	—	—	—
Leucobryum glaucum	+—2	—	—	—	+—1	+—1	—	+—2	—	
Pohlia nutans	—	—	—	—	+	—	—	—	—	
Ceratodon purpureus	—	+—1	—	—	—	—	—	—	—	
Hylocomium proliferum	—	—	—	—	—	—	—	+	—	
Cephalozia bicuspidata	—	—	—	—	—	—	—	—	+—1	
Ptilidium ciliare	—	—	+—2	+—2	+—3	+	—	—	—	
Scapania nemorosa	—	—	—	—	—	—	—	—	+—1	
Cladonia rangiferina	1—2	+—5	—	—	—	+	—	—	+—4	
Cladonia furcata	—	—	—	—	—	—	—	—	+—1	
Cladonia gracilis	—	+—1	+—1	—	+—1	+—1	1—2	—	—	
Cladonia uncialis	—	—	+—2	+—1	+—1	+	—	—	—	
Cladonia pyxidata	+—1	—	—	—	—	—	—	—	—	
Cladonia macilenta	+—1	—	—	—	—	—	—	—	—	
Cladonia mitis et impexa	—	—	+—4	—	—	—	—	—	—	
Cladonia cornuto-radiata	—	—	+—1	—	—	—	—	—	—	
Cladonia chlorophaea	—	—	+	+	+—1	—	—	—	—	
Cladonia glauca	—	—	+	—	—	—	+	—	—	
Cladonia silvatica	—	—	+—5	1—4	+—1	+—2	+—2	+—2	—	
Cladonia squamosa	—	—	+	+	+	+	—	—	—	
Cladonia impexa	—	—	—	+—4	+—5	1—2	+—1	—	—	
Cladonia Floerkeana	—	—	—	—	+—1	+	—	—	—	
Cladonia fimbriata	—	—	—	—	—	—	+—1	+—1	—	
Cornicularia aculeata	—	—	+—2	+	+—2	—	+	—	—	
Parmelia physodes	+—1	+—1	+—2	—	+	—	—	—	+—2	
Cetraria islandica	—	—	—	—	+—1	—	—	—	—	
Baeomyces roseus	—	+—2	—	—	—	—	—	—	—	

while, as in nearly the whole of Scandinavia, the *Genista*'s are lacking, except in some places in Germany and Poland. GRAEBNER (1925) still mentions for certain districts of North-Germany (Rügen, Pomerania, Posen, Lübeck, Stralsund, etc.) the occurrence in mass of ***Pulsatilla vulgaris*** and ***Pulsatilla pratensis*** in the Calluna-heaths on loamy hill-slopes. In Karelia and Russia Calluna retreats more and more into the fir-woods. Very likely this must be attributed to the more continental climate with its severe dry winters.

On pp. 115—116 a more elaborate survey is given of the true Calluna heaths in their optimal area, namely in North-West Germany and the Netherlands. The figures for the covered portions are the highest and lowest value of several determinations. Where only one value resulted a single figure is given; a + sign indicates that the species was only sporadic.

VI. Calluna heath with much *Erica cinerea* in England, after SUMMERHAYES (1924).

Calluna vulgaris
Erica cinerea
Erica tetralix
Ulex nanus
Ulex europaeus
Genista anglica
Deschampsia flexuosa
Festuca ovina
Aira praecox
Molinia coerulea
Juncus squarrosus
Scirpus caespitosus
Carex pilulifera
Potentilla erecta
Cuscuta epithymum
Rumex acetosella
Alchemilla arvensis
Cerastium triviale
Hypochoeris radicata
Myosotis versicolor
Ornithopus perpusillus
Rubus fruticosus
Sagina subulata
Senecio jacobaea
Spergularia rubra
Plantago coronopus
Sphagnum compactum
Leucobryum glaucum
Polytrichum juniperinum
Polytrichum commune
Hypnum cupressiforme v. ericetorum
Dicranum scoparium
Hypnum Schreberi
Barbula cylindrica
Brachythecium purum
Campylopus flexuosus
Funaria hygrometrica
Polytrichum formosum
Cladonia pyxidata
Peltigera canina

As typical for the British Calluna-heaths are also mentioned:

Agrostis setacea
Carex binervis
Ulex Gallii
Wahlenbergia hederacea
Listera cordata

To these must be added in South England: *Erica vagans* and *Erica ciliaris*, while in Ireland *Daboecia cantabrica* and *Erica vagans* are an important constituent.

VII. Heath-type with much *Ulex* and *Sarothamnus* from the "Massif de Multonne" in France, according to ALLORGE (1926).

Ulex europaeus
Ulex nanus
Sarothamnus scoparius
Erica cinerea
Erica tetralix
Calluna vulgaris
Salix repens
Salix aurita
Genista anglica
Sieglingia decumbens
Anthoxantum odoratum
Agrostis vulgaris
Molinia coerulea
Nardus stricta
Scirpus caespitosus
Luzula multiflora
Potentilla tormentilla
Stellaria graminea
Polygala serpyllacea
Viola lancifolia
Veronica officinalis
Euphrasia nemorosa
Galium saxatile
Jasione montana
Scorzonera humilis
Achillea millefolium
Hypochoeris radicata
Hieracium pilosella
Solidago virga aurea
Carum verticillatum
Pimpinella saxifraga
Pedicularis silvatica
Hypericum pulchrum
Lobelia urens
Scabiosa succisa
Serratula tintoria
Sphagnum compactum
Hypnum purum
Hypnum Schreberi
Hypnum cupressiforme
Leucobryum glaucum
Dicranum spurium
Cladonia furcata
Cladonia spec.

Further to the south-west, in the Landes, in Portugal and North Spain, Calluna becomes more and more a subordinate constituent of the heath-vegetation, which there is composed of a number of other dwarf-shrubs. In the Landes e.g. Calluna occurs together with other *Erica* species.

VIII. Landes (Fr.), according to A. H. BLAAUW (1935). (Comm. by letter).

Erica cinerea
Erica ciliaris
Erica tetralix
Erica scoparia
Erica lusitanica
Ulex europaeus
Ulex nanus
Rubus spec.
Solidago virga aurea
Ruscus spec.

TH. WEEVERS (1938, p. 116) found in the Landes, round Mont de Marsan, Calluna associated with: *Ulex europaeus, Erica cinerea, Pteris aquilina, Erica scoparia, Erica tetralix, Agrostis vulgaris, Helianthemum alyssoides, Erica ciliaris, Erica vagans, Pinus maritima, Quercus Robur, Quercus Tozza, Solidago virga aurea, Festuca ovina, Molinia coerulea, Potentilla Tormentilla, Betula* spec., *Hypnaceae*. For the Landes are still mentioned: *Ulex nanus, Agrostis setaceus* and *Polygala dunensis.*

This vegetation forms as it were a transition to the South-European "Maquis" flora along the Mediterranean. The Atlantic heaths of Spain and Portugal are, according to WILLKOMM (1896), characterised by the large number of *Erica* species. We have e.g. the following association:

IX. North Spain (Biscay), according to WILLKOMM (1896).

Erica cinerea
Erica ciliaris
Erica vagans
Erica lusitanica
Erica scoparia
Erica tetralix
Erica arborea
Erica aragonensis
Calluna vulgaris
Genista leptoclada
Genista florida
Ulex nanus
Ulex europaeus
Sarothamnus cantabricus
Quercus pedunculata
Quercus Ilex
Quercus Tozza
Crataegus monogyna
Adenocarpus complicatus
Cytiscus lusitanicus

X. In Asturia and Galicia (Cantabria) WILLKOMM (1896) states true Calluna heaths in which often fairly large plots are still occupied by ling alone.

Calluna vulgaris
Erica cinerea
Erica vagans
Erica aragonensis
Genista obtusiramea
Genista leptoclada
Vaccinium myrtillus
Vaccinium uliginosum
Thymelaea nivalis
Ulex nanus
Campanula adsurgens
Dianthus Planellae

XI. In South Spain especially the Cistus heaths are important, likewise according to WILLKOMM (1896).

Cistus laurifolius
Cistus ladaniferus
Cistus monspeliensis
Cistus populifolius
Cistus salvifolius
Halimium ocymoides
Halimium occidentale
Pistacea Terebinthus
Rhamnus Alaternus
Phillyrea angustifolia
Phillyrea media
Erica scoparia
Calluna vulgaris

XII. For the Sierra de Valdemeca the same author gives:

Erica australis
Erica scoparia
Calluna vulgaris
Genista anglica
Genista pilosa
Halimium umbellatum
Quercus Tozza
(near Montalvan still *Betula verrucosa, Pinus silvestris, Erica arborea, Erica lusitanica, E. scoparia, E. umbellata, Genista hirsuta* and *Cistus* spec. div.)

According to BRAUN-BLANQUET (1926) true Calluna-heaths are also found at the southern foot of the Alps, in the Pyrenees, Cevennes and Apennines. As an example of the heaths of southern France one of his tables is given here.

XIII. An *Erica scoparia* and *Lavendula Stoechas* vegetation with much Calluna, in the Bois de Lamoure near Mauguio, Dép. de l'Hérault, 10 m above sea-level (after BRAUN-BLANQUET, 1926).

Erica scoparia (for the most part)
Calluna vulgaris (much)
Cistus salvifolius (much)
Cistus monspeliensis
Lavendula Stoechas
Quercus coccifera
Genista pilosa
Quercus Ilex
Juniperus communis
Osyris alba
Daphne Gnidium
Rosa spinosissima
Dorycnium suffructicosum
Phillyrea angustifolia
Thymus vulgaris
Rubia peregrina
Anthoxanthum odoratum
Andropogon Gryllus
Brachypodium ramosum
Carex Halleriana
Ranunculus monspeliacus
Potentilla hirta
Potentilla verna
Polygala vulgaris
Hypericum perforatum
Vincetoxicum officinale
Teucrium Chamaedrys
Betonica officinalis
Plantago lanceolata
Aster acris
Andryala sinuata
Crepis taracifolia
Hypochoeris radicata
Hieracium pilosella
Aira caryophyllea
Erophila spec.
Euphrasia exigua
Myosotis versicolor
Polytrichum juniperinum
Stereodon cupressiforme
Funaria mediterranea
Tortella tortuosa
Cladonia endivaefolia
Cladonia rangiformis
Cladonia furcata
Cladonia pyxidata

On burnt down plots Calluna alone may predominate here, the heath is then poorer in species but contains much Polytrichum juniperinum.

In the West and Central Alps Calluna heaths occur again up to considerable altitudes. As an example the results are given, obtained by W. LÜDI (1934) for two vegetations.

XIV. Calluna-heaths in the Aar mountain-complex (Pörtlialp) at two altitudes; a. at 2120—2150 m. and b. at 2100 m above sea-level.

	a.	*b.*
Juniperus nana	2	1
Rhododendron ferrugineum	1	1
Loiseleuria procumbens	—	1
Vaccinium vitis idaea	2	1
Vaccinium myrtillus	2	1
Vaccinium uliginosum	2	2
Calluna vulgaris	4	5
Anthoxanthum odoratum	1	—
Agrostis tenella	2	—
Deschampsia flexuosa	2	1
Avena versicolor	1	—
Carex sempervirens	1	—
Luzula silvatica	1	—
Luzula lutea	2	—
Juncus trifidus	—	1
Silene inflata	1	—
Silene rupestris	+	—
Anemone sulfurea	2	—
Sempervivum montanum	1	—
Ranunculus montanus	1	—
Sieversia montana	2	—
Hieracium intybaceum	+	—
Polytrichum juniperinum	1	2
Hylocomium Schreberi	—	1
Dicranum scoparium	—	1
Potentilla aurea	+	—

XIV. (*Continued.*)

	a.	b.		a.	b.
Alchemilla alpina	+	—	*Phyteuma betonicifolium*	1	—
Trifolium alpinum	1	—	*Campanula barbata*	1	—
Lotus corniculatus	1	—	*Campanula Scheuchzeri*	+	—
Bupleurum stellatum	+	—	*Solidago virga aurea*	1	—
Laserpitium Halleri	2	—	*Homogyne alpina*	1	1
Gentiana (purpurea)	1	1	*Arnica montana*	2	—
Gentiana ramosa	1	—	*Senecio doronicum*	2	—
Ajuga pyramidalis	+	—	*Hypochoeris uniflora*	1	—
Rhinanthus glacialis	2	—	*Leontodon pyrenaicus*	2	1
Pedicularis tuberosa	1	—	*Cladonia silvatica*	—	3
Galium pumilum	1	—	*Cladonia gracilis*	—	+
Phyteuma orbiculare	+	—	*Cetraria islandica*	—	2

These two plots were situated at a relatively short distance, the first measured 200 and the other 100 m^2. This shows how very variable the composition of the species is in the Alps.

In the Colli Euganei near Padua Calluna is found in the region of the chestnut woods.

XV. Vegetation, rich in Calluna, on the Monte Ortone near Teoli (Colli Euganei) 50—100 m above sea-level, according to BÉGUINOT (1915).

Calluna vulgaris
Cistus salvifolius
Erica arborea
Arbutus unedo

In the forests near San Remo GAMBLE (1901) met Calluna at 900—1000 m above sea-level.

According to a written communication of Prof. R. MAIRE at Algiers Calluna occurs in the North African region in the "étage méditerranéen humide", of which an example is given here.

XVI. Maquis-vegetation on the Mont aux Singes near Ceuta (Morocco), at 340 m above sea-level (annual rainfall 800 mm, according to Maire, 1934).

Quercus suber
Erica arborea
Erica scoparia
Erica umbellata
Erica australis
Calluna vulgaris
Arbutus Unedo
Cistus populifolius
Cistus salviifolius
Cistus ladaniferus
Cistus crispus
Halimium eriocephalum
Helianthemum tuberaria
Myrtus communis
Lavandula stoechas
Cytiscus tridentatus
Quercus coccifera
Pistacia Lentiscus
Teucrium fruticans
Teucrium baeticum
Genista triacanthos
Eupteris aquilina
Agrostis setacea
Stachys Betonica, var.
Polygala baetica
Calamintha baetica
Pedicularis lusitanica

XVII. Heath-fields, rich in Calluna, in the Strandsha (East Thracia), according to MATTFELD (1929).

Erica arborea
Erica verticillata
Calluna vulgaris
Arbutus unedo
Cistus creticus
Juniperus oxycedrus
Quercus sessilis; Q. cerris
Fraxinus Ornus

In some places *Erica verticillata* and Calluna predominate entirely and form true heath-fields over considerable distances (Mount Sheremed). *Erica verticillata*, however, always prevails, sometimes with an admixture of *Osyris alba*. The two Erica's, mentioned in the list, are typically mediterranean; *Erica verticillata* forms true heath-fields in SW Thracia, near Xanthi. It is East-Mediterranaean and is in the West replaced by *Erica vagans*. Calluna is here, as in the Pontus, a constituent of the Colchian flora (after STEFANOFF, 1924, and MATTFELD, 1929), of which the following species are members: *Fagus orientalis, Rhododendron ponticum, Prunus laurocerasus, Daphne pontica, Epimedium pubigerum, Vaccinium arctostaphylos, Psilostemon orientale, Hypericum calycinum* and *Smilax excelsa*.

According to HANDEL-MAZETTI (1907) Calluna occurs on the Pontus (Trebizond) in the Rhododendreta on eruptive rocks, up to ± 1100 m above sea-level. According to KRAUSE (communication by letter) it is found there associated with *Ulex europaeus*.

On the Azores vegetations, rich in Calluna, are found on the mountain slopes as high as 2200 m above-level.

XVIII. Volcano Pico (Azores) near the top, (according to GUPPY, 1917).

Calluna vulgaris
Thymus serpyllum, v. *angustifolius*
Menziesia polifolia
Polygala vulgaris
Agrostis castellana
A little lower also: *Pteris aquilina*

In the moorland region between 700 and 1300 m:

Calluna vulgaris
Anagallis tenella
Erythraea massoni
Hydrocotyle vulgaris
Luzula purpureo splendens
Lysimachia nemorum v. azorica
Lycopodium Selago
Blechnum Spicant
Menziesia polifolia
Polygala vulgaris
Potentilla Tormentilla
Sibthorpia europaea
Thymus serpyllum, v. *angustifolium*
Viola palustris
Carex flava
Polytrichum spec.
Sphagnum spec.

For the east coast of America the following association of species is typical, in which Calluna and *Erica tetralix* both occur as non-endemic forms.

XIX. Vegetation with Calluna at Chathamport, Mass., according to M. L. Fernald (1927).

Erica Tetralix
Myrica pensilvania
Calluna vulgaris
Polytrichum ("carpet")
Rhus Toxicodendron
Smilax rotundifolia
Rubus hispidus
Vaccinium macrocarpon etc.

Fernald here remarks: "in dryish sandy and peaty margin of boggy-shore".

If we now overlook all these vegetation-types, it appears that by their floristic composition, as well as by their geographical distribution, in Europe the following groups of vegetations with much Calluna may be distinguished.

1. *The boreal and Alpine heaths,* characterised by the presence of: *Empetrum hermaphroditicum, Vaccinium myrtillus, Vacc. vitis idaea, Vacc. uliginosum, Juniperus nanus* a.o. They are spread over Fennoscandinavia and in the higher Alps. According to the classification of vegetation-types after Braun-Blanquet they belong to the order of the *Vaccinio-Piceetalia* (Braun-Blanquet, 1938). In these Calluna is found as a locally characteristic species in the Juniperon nanae union, a.o. in the Central Alpine valleys, such as the Engadin.

2. *The Atlantic Calluna-heaths of Central Europe,* which, according to recent views, are classed with the order of the *Calluneto-Ulicetalia* (Quantin, 1935, Tüxen, 1937). In these Calluna appears as a locally characteristic species, e.g. in the *Ulicion* union (Malquit, 1929), together with *Genista anglica, Genista pilosa, Sieglingia decumbens, Antennaria dioica* and others. This vegetation-type comprises also the true Calluna-heaths of the optimal region round the North Sea.

3. *The South European Cistus-heaths,* of which the Mediterranean *Cistion ladaniferi* is sometimes very rich in Calluna. As locally characteristic species may be mentioned: *Cistus ladanifer, Cistus salvifolius, Erica arborea, Erica scoparia,* and others.

These three well-characterised types agree with their geographical situation. Within the unions, however, several other local types may be distinguished, so e.i. in England and Scotland the Calluna-heath with *Ulex nanus* and *Erica cinerea*; in South England, West France and North-West Spain the heath, rich in Calluna, with *Erica vagans* and *Erica ciliaris,* in Ireland with *Daboecia cantabrica,* etc. Also within the South European *Cistus*-heaths there exist separate types, so e.g. in Morocco and along the Baltic (see above). About the East European Calluna-vegetations little is known to me. It seems that there Calluna becomes more and more of secondary importance, e.g. in the pine-woods (*Piceetalia excelsa* a.o.). Moreover in the north Calluna occurs in the *Oxycocco-Empetrion,* which belongs to the order of the *Ericeto-Ledetalia palustris,* while in the Alps it also appears in the *Rhodoreto-Vaccinion* or related vegetations. Also in some other unions it may occur, such as the *Quercion*-unions, but is generally of secondary importance then.

According to the medium we may distinguish: 1. sand-heaths; 2. moor-heaths; 3. wood-heaths; 4. mountain-slope heaths. Of course, between these many transitions exist, as there are between the above-mentioned vegetation-types. Characteristic for the sand-heaths is the great difference in moistness of the root-layer in summer and winter, especially where the humus-sandstone banks ("humus hardpans") lie at a small depth. Then in summer the layer above them may become very dry, while after a rainy period the water cannot sink away.

Apparently the moistness of the moor-soil is more equable, and one might suppose the water-supply to be much more regular. But this is not so. During the summer-months evaporation at the surface is, as we have seen, very great, while replenishment from below seems to be inadequate (FIRBAS, 1931), so that during periods of drought desiccation-phenomena are often observed. Especially the plants with shallow roots, like the *Ericaceae*, suffer from this, and also the mosses. Both the moor-heath and the sand-heath regions are subject to great fluctuations of temperature. Much less pronounced are the changes in temperature and moistness in the wood, but there insufficient light may hamper the growth of Calluna, which needs much light.

In the heaths on mountain-slopes drainage is generally good, atmospheric humidity is high (foggy days) and alternates with dry winter-storms. These latter are as a rule the restrictive factor, only where in winter a sufficient cover of snow accumulates Calluna will be able to maintain itself in the high and secondary mountains. Light is on the whole more intense there than in the plains, to this we must probably ascribe the remarkable differences in flowering-time in the zones at different altitudes, which will also depend on the duration of the snow-cover.

D. Calluna-heaths proper and their origination (successions).

As we have seen, the true Calluna-heaths are in the main restricted to the countries round the North Sea and the Channel. To be sure, outside this optimal area of development heath-fields are here and there found, in which ling predominates, but these do not attain the extent which the former have, or rather had, for a considerable portion of them has nowadays disappeared through reclamation.

To the question, why this species is more than any other able to occupy whole districts, a simple answer cannot be given. Adapted to the oligotrophic Atlantic medium, it can do this on account of an intricate complex of circumstances, in which man has always been an important agent. It has a great physiological plasticity and the power to progagate at a quick rate by its enormous production of seed and the easy spreading of it by the wind. Where within the optimal area impoverishment of the soil, or rather of the surface of the substrate, and destruction of forests go hand in hand, it will extend its domain very quickly, provided a sufficiently large Calluna-nucleus be present.

The true Calluna-heaths can hold their own for a very long time by their power to grow on their own humus and so to rejuvenate continually. Various oligotrophic species, particularly the true peat-formers, possess this property. In the Lüneburg district in N-W Germany Calluna-fields have become known, which have maintained themselves since many centuries (GRAEBNER, 1925). A sort of unstable equilibrium has then established itself between the vegetation and its environment. This equilibrium is by no means final, for another vegetation may already arise if only a single one of the factors of the medium is changed. The concept of successions has become necessary in order to understand how in nature different types of vegetation succeed each other after changes in the medium. Evidently these alterations (successions) need not always be in the same direction. A forest may turn into a heath [1] and conversely, a graminaceous, moor or drift-sand vegetation may become a heath, but also the reverse. A general scheme of vegetations is: halophytic ⇄ dune ⇄ heath ⇄ forest ⇄ moorland ⇄ heath ⇄ drift-sand ⇄ halophytic ⇄ mud-flat ⇄ clay ⇄ moorland-vegetations, and so on. In short: all vegetations on the Earth may gradually be transformed into each other by changes in the medium. However, in order to pass from the vegetation of a brackish mud-flat to an oligotrophic sphagnum-bog or a heath-vegetation, a great trophic change is required, which nature accomplishes slowly and with intermediate steps. The same holds for the great climatic periods in some area in the course of centuries. More sudden changes are caused by catastrophic destruction of forests by fire, by floods or sand-drifts, and the resulting changes in level and trophic conditions.

So it seems probable that the Calluna-fields are a natural and original type of vegetation from times immemorial, like so many wood-, dwarf-shrub-, and steppe-vegetations. That accidentally by the action of man heath-fields became predominant over considerable areas and have again disappeared by the effect of human culture, does not alter the case. The mere fact that Calluna-fields form again and again without the intervention of man, e.g. on dune-sands, peat-moors, mountain-slopes and rocky plains, points to a natural type of vegetation, which may have gradually formed through the ages by selection and adaptation to a certain environment. This power to dominate under favourable circumstances is shared by many other plant-species; it makes no difference in principle whether only a few square meters or large areas are dominated by one and the same species. For a closer study of the optimal natural medium of a species it is therefore important to trace these one-species vegetations ("Einarter"). On this subject little is known as yet.

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[1] TÜXEN, DIEMONT a.o. have e.g. pointed out the connection between the *Querceto-Betuletum* and the *Callunetum Genistetii*.

IV. SIGNIFICANCE FOR MANKIND.

A. Technical use.

Seeing, how nowadays the Calluna-heaths are converted at great speed into cultivable land, one would be inclined to believe that there is no more useless plant in the whole flora.

In the Netherlands, as late as the 19th century (1833), it occupied, alone or with a slight admixture of other species, over 6000 square kilometers, about a fifth of the total area of the country, then amounting to a little more than 30.000 square kilometers. In 1907 these Calluna-fields had by reclamation been reduced to about 4500 km^2, of which at present no 1000 are left, and will at this rate have shrunk within a few years to about 200 km^2, which will perhaps be spared through considerations of national defence or nature-protection. Only the larger of these heath-fields will be of lasting importance for biology, as the smaller ones are likely to be transformed in the long run into wood, arid grass-vegetations or suchlike.

In fact, the appreciation of the Scotch heather has in the course of time had ups and downs. For centuries Calluna reigned supreme over large areas of N-W Europe, where its dense and peculiar vegetation left its mark on the people who dwelt there. After man had in previous times, by destroying woods and by draining peat-moors, predestined huge stretches of land to become heath-fields, he afterwards fully adapted himself to the environment, created by his own hands, and with him the animal world. The territory of the Calluna-heaths, as it had its largest extent in previous centuries in South Sweden, Danmark, the Netherlands, Belgium, Scotland, England, Ireland and West France, was characterised by a modified climate with much wind, great fluctuations in the moistness of the soil, high atmospheric humidity with much fog, and by wide plains, covered with a sombre and monotonous vegetation. If by stagnation the level of the subsoil water rose, peat was formed on a large scale, by which the already bad inhabitability was made worse. No wonder that all this reacted on the inhabitants, attached to their native soil, and that in the small settlements, lying as oases amid the wide plains, mostly hidden under trees, people lived of a modest character, adapted to a hard and sober life, attached to each other within their small communities and resembling in many respects the arctic primitive races and the steppe-dwellers.

The wonderful plant-species, dominating this whole landscape, was turned to good account in various ways. The heaths were a pasture for sheep, sometimes for cattle and goats, and long before that were perhaps hunting-fields. Near the settlements the heath soon disappeared, first on the broad tracks along which the flocks went and came. There, by trampling and nibbling, and by manure, a poor meadow of sand-grasses and herbs was formed. This gradually became a better pasture, thus initiating the more natural reclamation of the heath-fields, which in this form was continued even in the second half of the preceding century, until a more rational use of manures became general and a more systematic improvement of the soil began.

In the form of cut sods ling served as the material for building the poor hovels and for covering roofs. Only a few years ago such hovels, built of heath-material, could here and there be seen in this country, at present they are practically gone.

Infusions of Calluna were used as a remedy against gout and renal calculi. A tea is sometimes made of the dried flowers, while tradition has it that the Picts prepared a drink from it. We quote from R. L. STEVENSON's poem "Heather Ale" [1].

"From the bonny bells of heather
They brewed a drink long-syne,
Was sweeter far than honey,
Was stronger far than wine.
They brewed it and they drank it,
And lay in blessed swound
For days and days together
In their dwellings underground."

But ling had more useful applications. The Scots tanned their leather with it and the result is said to have been at least as good as with oak-bark. Also a kind of rope was made of it. From the wood a red and a yellow dyeing-substance were prepared, with which the Scots dyed their wool.

For bee-keeping the rich bloom and nectar-production were of much importance and are so still in the surviving heath-fields.

In the warm ashes of the burnt down moor-heath the heath-farmers sowed their buckwheat, known as "moor-buckwheat".

The thin strong twigs were and are still used for besoms and brushes, and formerly for filling mattrasses of the same elasticity as is now obtained by means of metal springs.

Important was the use of heath-sods as fuel. Especially in wet and level fields the formation and accumulation of humus-substances by Calluna is so considerable, that a thin layer of peat is formed. After the ling has been burnt down in winter or in early spring, when the ground is still frozen or wet, the humus-layer with as little sand as possible is cut in rectangular sods of ½ by 1 foot and 2 to 4 inches thick, piled up and dried, after which it is fit for fuel. From 7 to 10 years later the process may be repeated.

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[1] From A. T. JOHNSON, 1928, p. 107.

This cutting of small sods for fuel and large flakes for manure and the periodic burning of the heath in order to obtain a fresh vegetation for feeding sheep, have both been very important for the preservation and extension of the heath-fields. They prevented the formation of wood, which is much slower, while also accumulation of more soluble nutrients and trophic changes were prevented. Thus between the field-vegetation and its utilization an equilibrium was established, which often lasted for centuries and kept out other, more natural, successions.

As an adornment at festivities flowering heather is still popular and dry bouquets are in demand, especially in foreign parts.

In spite of all this it is being completely ousted because of the higher claims, put to the productivity of the soil, anyhow in the densely populated countries of N-W Europe. But to the very last its good properties are turned to account. So in agricultural and sylvicultural meliorations Calluna is used:

1. For draining. Bundles of old long shrubs are laid on the bottom of the drainage furrows and covered with moss and sand,

2. For checking sand-drifts. Cut or mown heather is stuck in a row in the sand; often a blanket of mown heather is laid on the sand and kept in place by putting a shovelful of sand on it at distances of half a meter. In dusty wood-plantations heath-sods are laid to prevent the roots of the young plants from being laid bare and dried out,

3. For making loose sandy tracks passable. If no loam or gravel is available, heather laid across a sandy bicycle-track will keep it passable.

4. In former days heath-sods were piled up as partition-walls between fields. In the fence was a nucleus of sand in which wood was planted. These are the old wood-walls which are even now found in many heath-regions, and are a characteristic feature of the landscape.

5. Also for strengthening the sides of ditches and trenches the tough heath-sods are often used, because the fine and dense network of hair-roots prevents the sand from being washed down by rain-water. The author has also seen the slopes of canals reinforced with these sods.

6. Before the advent of artificial manures the heath-farmers used to cut thin irregular, more or less rounded sods with living heather.

In the stables these were trampled down by the cattle and mixed with their manure. This gave an excellent voluminous manure, rich in humus, which afterwards was prepared more simply and better by means of moss-litter, but which has done good service for long times. This voluminous sod-manure was every year put on the land. Hereby the level was gradually raised, and what was more important, the cultivable layer became thicker, an advantage that was more often than not lost by too shallow cultivation, for deep-ploughing on these old fields did not begin until much later.

With a view to future possibilities the cultivation of ling as an ornamental plant will be dealt with separately.

B. Calluna as a horticultural plant.

1. *Cultivation.*

As a richly flowering evergreen dwarf-shrub, Scotch heather, like many other *Ericaceae*, has gained a firm footing in gardens and parks by its easy culture, moderate size and long, rich bloom. For ever so long the English have appreciated it as a garden-plant, especially the white-flowering forms, "lucky heather", are popular there. Nurserymen have always had an eye for its richness in forms and nowadays the catalogues of the big nurseries offer a large assortment. Most of these forms have been traced in the English heath-fields by so-called "heath-hunters", and reproduced vegetatively, either by layering or by cuttings. This latter method is the usual one nowadays, as stronger and more regularly developed plants are obtained by it than with layers. We have seen that Calluna easily grows adventitious roots from one and two year old wood. Intentional cross-breeding presents great difficulties and has not been applied yet, but spontaneous crosses and their sowings are frequent in the nurseries.

WAITZ (1805) and REGEL (1843) already published elaborate instructions for cultivation, as well as data on the propagation of the *Ericoideae* by cuttings. These methods have in the main been taken over and improved by the present English, German and Dutch nurserymen (Cf. e.g. JOHNSON, 1928, p. 24—30, and MAXWELL, 1927, p. 80—84).

Ordinary high-shaped flower-pots are filled to 2—3 cm below the brim with heath-earth, covered with a thin layer of clean sand. The cuttings are short-shoots or apical ends of long-shoots, 1—3 cm long, cut off with a sharp knife and then put directly in the pots to halfway their length at distances of 2 cm. This must be done carefully so as not to injure the tender twigs, which would entail failure. The cuttings should be taken from sound and vigorous twigs, if they are from weak or unsound wood they will not root. On the application of special growth-substances in the slipping of *Ericaceae*, nothing is known yet, although it may become feasible in the future.

When the cuttings have been planted, the pots are placed in rain-water up to the level of the earth inside, so that they become soaked. When they are taken out the superfluous water flows out and the earth becomes compact, by which the cuttings take root more easily. The pots are embedded in a hothouse or greenhouse, kept moist with rain-water and during the first weeks covered with glass.

The best time for slipping is from May to August. Light is at first screened off, but soon full light can be admitted. Within three weeks most cuttings have already developed rootlets and are then placed each in a separate small slip-pot, also filled with heath-earth. In about 3 months' time well-developed plants will already have a length of 10 cm and more, and if the slipping was done early enough some of them may flower in the same season.

After having hibernated under glass, the plants, after a little hardening, are planted out in the open in beds (Pl. XXII, 2), and there grow up for the market. The price of such biennial slipped plants nowadays varies from —/—/5 tot —/10/— apiece, according as it is an ordinary plant or a novelty.

It has already been remarked that most of these forms were found in the fields by so-called "heath-hunters". However, of late years new forms repeatedly come from the nurseries, where they arise spontaneously. In my own collection of forms I discovered between the old plants a new form, a white-flowering creeping one. Also yellow leaves (*aurea*) and white flowers (*alba*) seem to be easily combined by crossing. White-flowering plants generally give a numerous offspring of white seedlings. In a heath-field near Borger (Drente) I once found a number of white-flowering plants together in a group. In a less degree this is also seen with other forms, as: *diplocalyx, multibracteata, polysepala,* of which often a number are found near together. One gets the impression that such cases are sowings of definite crosses.

2. *Survey of the varieties and forms.*

Under the heading "Abnormities" a short summary was given of the different forms of Scotch heather, which have become known. A more elaborate description will now follow of those forms that retain their characteristics when reproduced vegetatively. This is intended at the same time as an identification-table on behalf of dendrology and horticulture.

When identifying a specimen a choice is made between the two varieties I and II and the table referring to this variety is followed, always taking the first deviation mentioned, without paying attention to other deviations.

I. Foliage leaves unhaired or with only a few small prickles or hairs along the edge. .... Var. **genuina** Regel, 1843.

II. Foliage leaves either densely haired, like felt, or less densely haired. (For this test it is advisable to use young leaves as the hairs of older and perennial leaves have often been rubbed off by the wind.) .... Var. **hirsuta** Gray, 1821.

I. Var. **genuina** Regel, 1843.
(= C. v. var. *glabra* Neilreich, 1859.)

1a. Flowers deviate by their size, number, position, direction or shape 2
b. Flowers deviate by their colour 8
c. Foliage leaves deviate in size, colour or pattern 9
d. Ramification of the plants deviates 10
e. Time of flowering deviates 11
2a. Sepals 5 mm long or longer ... Fa. **grandiflora** W. Beijerinck, 1937. Pl. VIa and Fig. 132. Breadth of the sepals varies. Plants of ordinary size and shape. In a single case a specimen was found with abortive

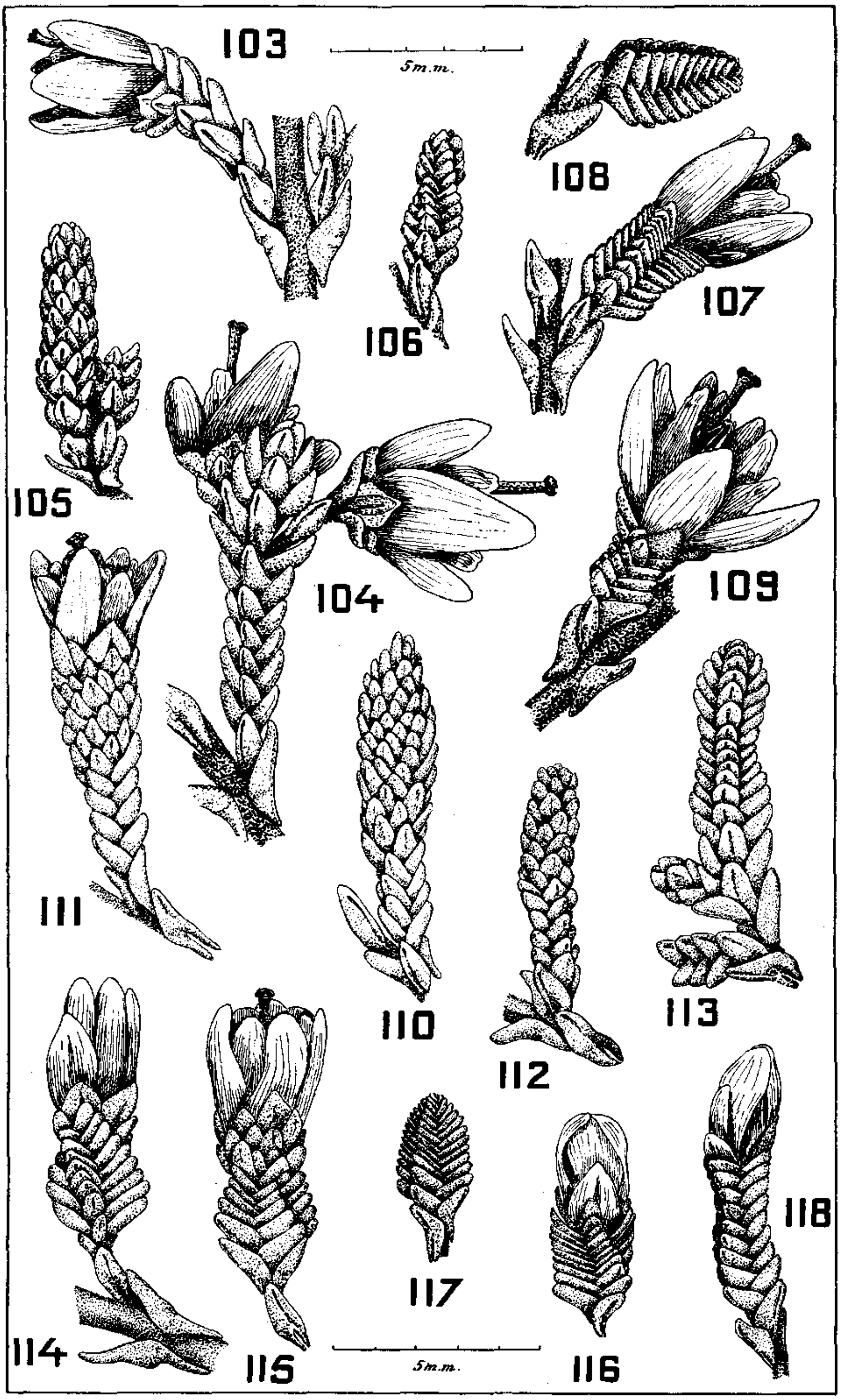

103
5 m.m.
108
107
106
105
104
109
111
110
112
113
118
114
115
117
5 m.m.
116

Fig. 103—118.

empty anthers. This specimen also flowered late. (October). In culture an English form with fairly large but scarcely 5 mm long flowers is met with (*C. v. Serlei grandiflora*). Also in the Netherlands it was sometimes found. From Finland 1 specimen. (Åbö, leg. E. LINDSTROM, 1906).

b. sepals shorter 3

3a. Flowers small, sepals at the utmost 4 mm long, but always longer than the corolla .... Fa. **parviflora** W. Beijerinck, 1937. Pl. VIb and Fig. 133. Flowers light violet-pink, very small, mostly 2—3 mm long. Short-shoot leaves also small, ± 1 mm long. The twigs bend and the plant spreads when it has reached a height of 2 dm. Blooms richly in Aug.-Sept. Only once found in the Netherlands. Must not be confounded with modifications that have been hampered by drought and then flower late with small flowers, but when transplanted at once produce larger flowers.

b. Sepals as long as or shorter than the corolla ....
Fa. **brachysepala** Joh. Jansen, 1935.
Pl. VIc and Fig. 135. Plant of ordinary size or smaller. By the short sepals flowers rather small to very small. Repeatedly found in our country. The following subforms may be distinguished:

Subfa. **microsepala** W. Beijerinck, 1937. Pl. V, 1, centre above, and Fig. 134. With very small sepals and a longer projecting corolla. Sepals do not diverge but narrowly enclose the corolla. Repeatedly found in the Netherlands; not known to me from other countries.

Subfa. **densa** W. Beijerinck, 1937. Plant of squat low habit, ± 1—3 dm high, part of the flowers deformed. Found only once in this country, known as a garden-form under the name *C. v. darleyensis* hort.

c. Flowers or flower-twigs deviate in some other respect 4

4a. Flowers not as usual directed sideways but more or less erect ......
Fa. **stricta** W. Beijerinck, 1937.
Plant with erect closely parallel frame-branches. Flowering-time normal. Not to be confounded with the subfa. *recta* of the Fa. *multibracteata*, which is always characterised by a large number of bracts on the flower-twigs.

b. Flowers on rather long, curved flower-twigs, spaced on the elegantly bent long-shoots, which may be over 50 cm long. Very late-flowering form (Nov.-Dec.) . Fa. **elegantissima** (Sennen) W. Beijerinck, 1937. This form, found in the Iberian Peninsula also seems to occur in Morocco and Italy. The plant flowers late in our latitude as well, where in the open it is as a rule overtaken by the winter-cold and freezes. In 1928 this form was introduced into England by W. E. TH. INGWERSEN and since then is known there as a "show"-plant, because of its very different flowering-time. When cultivated in the open it should be well covered with spruce in winter.

c. Plant with hardly any flowers or with none at all. In the places of the flower-twigs small short-shoots with extremely small leaflets are formed .... Fa. **pauciflora** W. Beijerinck, 1937. During flowering-time these evergreen plants, like some non-flowering or late-flowering multibracteate forms, are conspicuous in the heath-fields. Repeatedly found in the Netherlands. The characteristic is retained in culture.

d. Flowers preceded by a large number of closely packed bracts, attached to the flower-twig. The number of bracts exceeds 12 ......
Fa. **multibracteata** Joh. Jansen, 1935.
Pl. IV, 2; V, 2; V, 3; XVI; and Fig. 105—118. Of this form, which is repeatedly met with in the Netherlands and NW Germany, but apparently is not yet known from other countries, several subforms exist, namely:

Subfa. **torta** Joh. Jansen, 1935. Fig. 114, 115. Bracts partly or wholly arranged in spirals along the flower-twig.

Subfa. **deflorata** Joh. Jansen, 1935. Pl. XVI, 2 and Fig. 106, 110, 112, 113. Packets of bracts are present, but no real flowers.

Subfa. **pentamera** Joh. Jansen, 1935. Pl. IV, 2; Pl. V, 2 and Fig. 109. Flowers often with a pentamerous, sometimes hexamerous perianth. Besides, the packets of bracts are as a rule more or less twisted.

Subfa. **multiplex** W. Beijerinck, 1937. Flowers filled by multiplication of the sepals.

Subfa. **extensa** W. Beijerinck, 1937. Plant with far extending twigs, grows out in breadth.

Subfa. **recta** W. Beijerinck, 1937. Frame-branches stiff and vertical, in a close bundle.

Subfa. **serotina** W. Beijerinck, 1937. Flowering-time from October right up into the winter. Flowers more or less violet-pink.

All these subforms are known from the Netherlands; from England I did not see a single specimen yet of this form or its subforms.

e. Flowers at the end of richly leafed short-shoots, i.e. flower-twigs with more than three ordinary leaf-pairs. Bracts generally lacking ...
Fa. **terminalis** Joh. Jansen, 1935.
Pl. V, 5. Plant for the rest of ordinary size and shape. Repeatedly found in the Netherlands, not known from other countries.

f. The flowers themselves deviate in some respect or other from the shape of the type 5

5a. Flowers remain closed, so-called "bud-flowers", or open only slightly. For the rest the flower-parts are present in normal numbers.........
Fa. **clistanthes** Joh. Jansen, 1935.
Pl. XVII, to the left, and Fig. 128. If the flower-buds open a little,

the surface of the stigma generally comes free, so that fertilization can take place. This deviation is to be distinguished as Subfa. **ferax** W. Beijerinck, 1937, Fig. 131. The typical form with entirely closed flowers as well as the subfa. *ferax* were repeatedly found in the Netherlands. Flowering-time as a rule somewhat later than with the ordinary Scotch heather, so that when the fields are nearly off flowering this form is conspicuous by the fresh colour of its flowers, as also the late-flowering subforms of *multibracteata, diplocalyx* and *polysepala* sometimes are.

b. Likewise bud-flowers, but these are either incomplete or show an increase in the number of certain flower-parts and sometimes deformations 6

c. Flowers do open, but deviate in some other respect 7

6a. Bud-flowers, consisting of 8 sepals with gynoecium, thus without corolla or stamens. By way of exception a corolla and stamens are nevertheless present, while also the style is often deformed. The number of sepals, however, is always doubled ....
Fa. **diplocalyx** Joh. Jansen, 1935.

Pl. XV, XVII to the right and Fig. 129, 139. Of this form, which is known from England (*C. v. David Eason* hort.), Germany and the Netherlands, in the latter country a number of subforms were found, namely:

Subfa. **hermaphrodita** W. Beijerinck, 1937. Flowers with stamens and pistil, but with doubled calyx and flowers that generally remain quite closed.

Subfa. **polystyla** Joh. Jansen, 1935. Fig. 128. Style deformed, mostly split into a number of thinner styles, sometimes a very thick short style. With the typical form there is inside the bud-flower a bayonet-shaped or crooked style of normal dimensions (Pl. IV, 2). Evidently the style grows to the normal length and is bent or crooked because it is locked up.

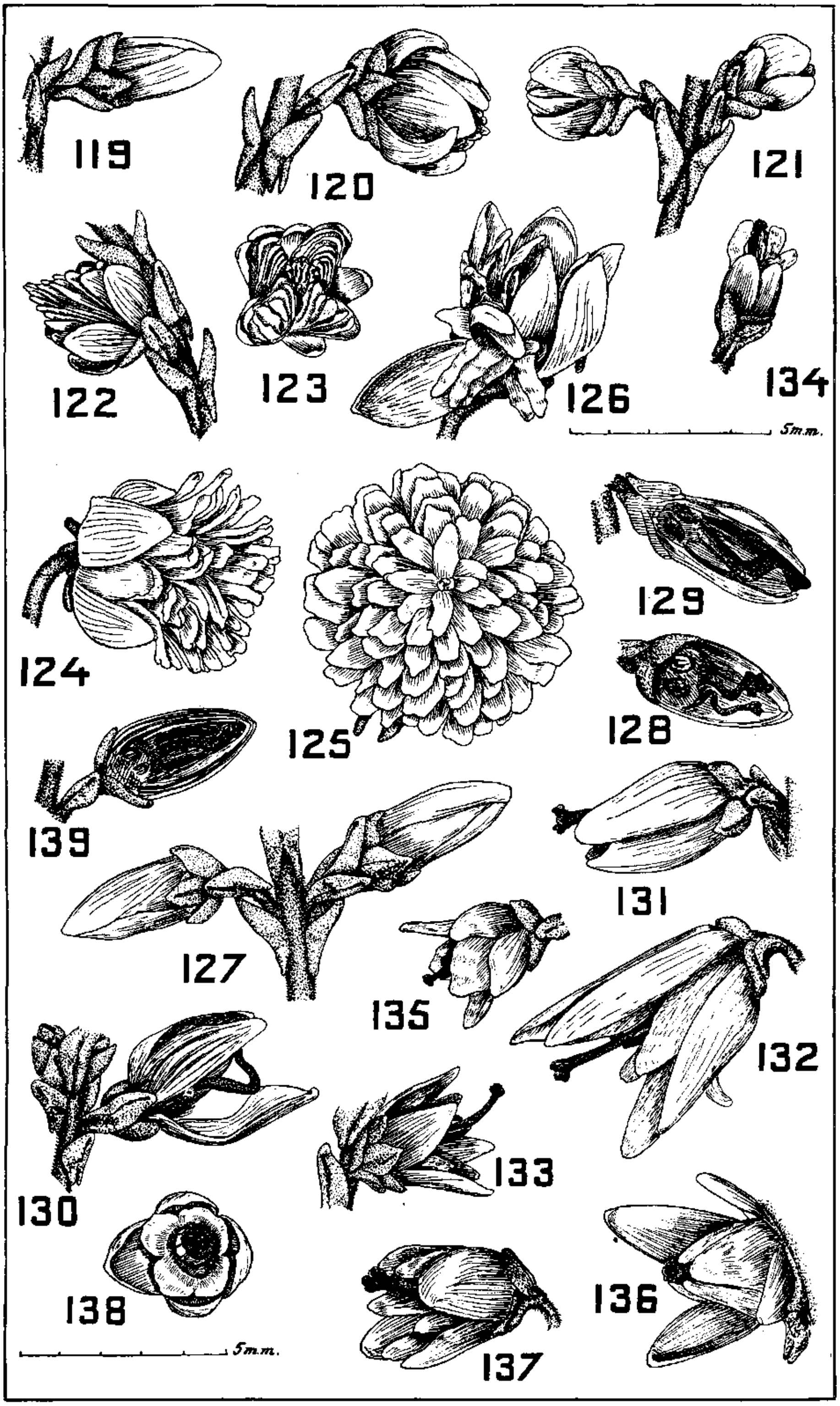
Subfa. **fertilis** W. Beijerinck, 1937. Bud-flowers slightly open at the top, so that the stigma-surface comes free and fertilization may take place.

Subfa. **carnea** W. Beijerinck, 1937. Colour of the flower pure or yellowish pink, without a trace of violet.

Subfa. **elata** W. Beijerinck, 1937. Stems stiff and erect, in a close bundle.

Subfa. **gracilis** W. Beijerinck, 1937. Plant with limp, curved stems, habit more or less cushion-like.

b. Bud-flowers quite or partly filled by multiplication of the sepals. Sometimes style and stamens more or less deformed. By the large number of compact sepals (straw-flowers) the outer sepals sometimes stand out, so that the bud-flowers are half-open, stiffly filled and of various shape .... Fa. **polysepala** Joh. Jansen, 1935.


119
120
121
122
123
126
134
5 m.m.
124
125
129
128
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127
131
135
132
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133
138
137
136
5 m.m.

Fig. 119—139.

Pl. IV, 2, 3; Fig. 120. With fa. *multibracteata, diplocalyx* and *alba* it belongs to the most frequent deviations of Scotch heather in the Netherlands. From other countries, however, this form is not yet known to me. In England on the other hand the fa. *polypetala* (see below) seems to be pretty frequent, which I do not know from this country. Also the fa. *polysepala* shows a few subforms, namely:

Subfa. **gemmata** W. Beijerinck, 1937. Bud-flowers narrow and tapering, in shape similar to normal flower-buds. They are filled, however, and therefore very hard. Colour violet-pink to nearly violet. Pl. XVII, centre. Fig. 119.

Subfa. **pilulifera** W. Beijerinck, 1937. Small bud-flowers, spherical because the sepals are very convex and clasp each other tightly. Fig. 121.

Subfa. **conica** W. Beijerinck, 1937. The numerous sepals are more or less decussately inserted and towards the centre longer, so that the filled flower becomes conical. Pl. V, 1 and Fig. 122, 123.

Subfa. **subplena** Joh. Jansen, 1935. The filled bud-flowers have a somewhat deformed style, sometimes also deformed stamens. Is, as it were, a transition to the forms: *monstrosa* and *plena* (see below).

Subfa. **adscendens** W. Beijerinck, 1937. Frame-branches vertical, close together.

Subfa. **curvata** W. Beijerinck, 1937. Frame-branches divergent and curved. Habit more or less cushion-like.

Subfa. **tardiflora** W. Beijerinck, 1937. Late-flowering, October—November.

All these subforms, like those of *diplocalyx,* kept their colour for a long time, which made it possible to detect them when flowering in the heath-fields was over. Until now the subforms have only been found in the Netherlands.

7a. Flowers resemble small filled roses, on account of the multiplication of the corolla tips. Calyx consists of four large relatively broad sepals .... Fa. **polypetala** W. Beijerinck, 1937. Pl. XIX, 1 and 2; Fig. 124, 125. Very conspicuous form, which by its big filled flowers and beautiful play of colours from white via pink and violet-pink to purple-violet, has already long drawn the attention of the nurserymen and as a garden-form is known under various fine names. As far as I could discover most specimens come from England. In a German nursery only the new white subform seems to have originated, of which further on separate mention is made under the new acquisitions of this year. From this country this form is not yet known in the wild state. Of this form, occasionally indicated in the gardens as C. *v., plena* Regel, 1843, C. *v., flore pleno,* Don, 1834, the following subforms may be distinguished:

Subfa. **rosea** W. Beijerinck, 1937. Flowers bright pink, almost without any admixture of violet. Sepals very glossy, nearly white. Plant does not become high, habit somewhat cumbent. Was originally found on Mount Maughan (Yorkshire) and was introduced into culture by Maxwell & Beale under the name *Mrs. Hamilton* hort. It is one of the finest double-flowered forms.

Subfa. **lilacina** W. Beijerinck, 1937. Flowers very big, more violet-pink. Found in gardens as C. *v., Camla Var.* hort. A similar more cumbent subform with long horizontal flowering-twigs is in the trade under the name *County Wicklow.*

Subfa. **candida**, nov. subfa. Flores sepalis 4 latis lucidis, superea petalis numerosis pleni; floribus albis. (See below).

It was for the first time introduced into the trade in 1938 as: C. *v., alba plena* hort.

b. Flowers less widely opened than with the former, sepals as well as petals multiplied .... Fa. **plena** W. Beijerinck, 1937. Pl. XX and Fig. 126. In the Netherlands found only once in Drente; I have never seen another specimen of it. Flowers purple-violet.

c. Flowers for the greater part deformed, with pentamerous or hexamerous corolla, mis-shapen stamens and styles, etc. ....
Fa. **monstrosa** W. Beijerinck, 1937.

As this phenomenon is recurrent on one and the same individual and on the plants, obtained from it by cuttings, I have combined these plants, bearing more or less mis-shapen flowers, as a form, although, strictly speaking, also many of the other forms are monstrosities or abnormalities. To these also the fa. *apetala* Joh. Jansen, 1935, may be reckoned, which on the same plant only here and there shows flowers without a corolla. It has been repeatedly found in the Netherlands, but can only be discovered by very accurate searching.

d. Flowers without stamens, sometimes also without a corolla, but with a simple calyx .... Fa. **gynodioica** W. Beijerinck, 1937. Fig. 137, 138. So the plants of this form are purely female. As no male plants are known, the word gynodioica has been applied. Up to the present it has been found five times in the heath-fields of Drente. As a rule the flowers do not open entirely. One must be careful not to be misled by plants, where the stamens have been eaten by insects (*Antherophagus*). Reproduced in a vegetative way, the form fully retains its characteristic. As a subform may be distinguished:

Subfa. **simplicissima** W. Beijerinck, 1937. Fig. 130. Here also the corolla is lacking, so that the flowers consist of nothing but a calyx and a gynoecium. Until now only a single specimen was found in Drente.

e. Flowers of which the calyx opens, but the corolla remains nearly closed or does not open until later ....
Fa. **campanulata** W. Beijerinck, 1937.

Fig. 136. Was only found once in Drente. Flower light violet-pink. For the rest normal. In culture the characteristic was retained.

8a. Flowers with white calyx and corolla. Style and stigma green or with a violet-pink shade ... Fa. **alba** (Don) Braun–Blanquet, 1926. One of the most frequent forms of Calluna, especially in Fenno-Scandinavia and England. Less general in Central and East Europe. Not known to me from South Europe. In horticultural literature also under the names: *Er. vulg., alba* Waitz, 1805; *C. v., albiflora* Michot, 1845; *C. v., fl. alba* Dippel, 1889. The foliage of this form keeps in winter a remarkably fresh green colour, whereas the other forms fade to brown-green, yellow-green or red. The following subforms may be distinguished:

Subfa. **erythrostyla** W. Beijerinck, 1937. Style and stigma more or less red. Perianth white.

Subfa. **aureifolia** W. Beijerinck, 1937. Young foliage-leaves yellow-green to yellow. Flowers white with a yellow shade. In gardens under the name: *C. v. alba aurea* hort. The form *lutescens* of *var. hirsuta*, also indicated as *Serlei aurea*, resembles it, but has hairy young leaves. Neither is known to me in the wild state, but only as garden-forms.

Subfa. **pumila** (hort.) W. Beijerinck, 1937. Plant remains small, height from 1 to 2 dm, with erect branches. Flowers of normal size. Garden-form.

Subfa. **Serlei** (hort.) W. Beijerinck, 1937. Robust plant of 0.5—1 m height. Frame-branches feathered with a fine regularity by short-shoots with distant leaves. Flowers late, Sept.—Nov., English garden-form, indicated in the catalogues as *C. v. Serlei alba* hort.

Subfa. **Hammondi** (hort.) W. Beijerinck, 1937. Vigorous plant with leaves of a fine dark or slightly yellowish green (*Hammondi aureifolia* hort.). Big flowers, reaching a length of about 5 mm. Flowering-time normal. Richly and beautifully flowering garden-form, which is also found in the open field.

b. Flowers light lilac to almost white. Sometimes the corolla is of a somewhat darker shade than the calyx ....
Fa. **alboviolacea** W. Beijerinck, 1937.

Not rare, especially on the moorlands in the north of the Netherlands.

c. Flowers bright pink to almost white ....
Fa. **albopurpurea** W. Beijerinck, 1937.

As a garden-form also under the name: *C. v., Kynance* hort.

d. Flowers rather dark purple-violet, mostly tending to purple ....
Fa. **purpurea** (Don) Braun–Blanquet, 1926.

As a garden-form under the names: *C. v., rubra* Kirchner, 1864; *C. v., C. W. Nix* hort.; the foliage-leaves are not hairy, as distinct from the form *Alporti*, which likewise has dark flowers.

e. On the same plant flowers of two colours are found, mostly on separate branches .... Fa. **bicolor** W. Beijerinck, 1937. C. A. LINDMAN, 1908, described a similar plant from Sweden, denoting this phenomenon by the word: amphichromism. Known from England, the Netherlands and Sweden. The most frequent form is that in which suddenly a white-flowering branch appears on a plant, flowering in the ordinary manner. But also plants occur with darker and lighter flowers on different twigs. (see also the following form).

f. Plants with flowers of a lighter as well as of a darker shade, as well as with flowers where the sepals are coloured in sectors .... Fa. **multicolor** W. Beijerinck, 1937. Found only a few times in the provinces of Gelderland, Limburg and Drente.

9a. Short-shoot leaves very small, ± 1 mm long or still shorter .... Fa. **microphylla** W. Beijerinck, 1937. Fig. 2a. Not to be confounded with the microphyllous drought-forms, which develop bigger leaves again when transferred to moister surroundings. Found a few times in this country.

b. Short-shoot leaves have ivory-white tops during the summer. Plant with limp frame-branches, which soon lie down .... Fa. **argentea** (hort.) W. Beijerinck, 1937. Fig. 5b. As contrasted with the next, this form has no variegated leaves. Known to me only as a garden-form.

c. Short-shoot leaves variegated in spring ... Fa. **variegata** Regel, 1843. Fig. 5a. Generally the leaves loose their variegation in summer. Young slip-plants are therefore finest in spring. As a garden-form also known under the following names: C. *v., foliis variegatis* Loudon, 1838, and C. *v., foliis variegatis* Don, 1834. Of this there is a subform with pink and green instead of white and green spotted leaves, namely subfa. **roseovariegata** W. Beijerinck, 1937. The typical form was found several times in the wild state in this country, the subform only once.

d. Short-shoots ending in leaflets of a bright pink, by which the plant, especially during winter and spring looks as if it were blooming ... Fa. **rhodostachys** W. Beijerinck, 1937. As a graceful but rather weak garden-form known under the name: C. *v., Mrs. Pat* hort. Also known from Sweden (Småland, Lofta, leg. C. LINDMAN, 1931).

e. Short-shoot leaves all or part of them coloured golden-yellow to light-yellow, or in summer also greenish-yellow .... Fa. **aurea** (Don) W. Beijerinck, 1937. The typical form during the cold season and especially in spring gets a beautiful golden-yellow colour, mixed with some red, but in summer turns more greenish-yellow. As a garden-form also under the name of: C. *v., lutescens* Dippel, 1889. Pretty rare in the wild state, but much cultivated in gardens. It has the following subforms:

Subfa. **aureovariegata** W. Beijerinck, 1937, with partly yellow-leafed twigs. Only once found in Drente.

Subfa. **chlorostachys** Joh. Jansen, 1935. With short-shoots, the leaves on which are partly yellow, so that the plant has a many-coloured appearance. Found a few times in Gelderland, as yet not known to me as a culture-form.

f. Short-shoot leaves beautifully red in spring, in summer turning yellowish-green, as with *aurea* ....
Fa. **cuprea** (hort.) W. Beijerinck, 1937.
Squat habit with vertical frame-branches. Short-shoot leaves small. Well known as a garden-form, not found by me in the wild state. Not to be confounded with the plants in dry sunny places, which sometimes are red for a time, but soon loose their colour when transplanted.

g. Colour of foliage greyish-green ... Fa. **incana** W. Beijerinck, 1937. Was only once found in Drente. The colour of the foliage strongly reminds of the fa. *pilosa* of the var. *hirsuta*, but the foliage-leaves are entirely without hair.

10a. Habit more or less cushion-shaped. Frame-branches grow out laterally, cumbent or curved ....
Fa. **decumbens** (Don) W. Beijerinck, 1937.
Pl. IX, 1 and XIV. Colour of the flowers ordinary, seldom white or light violet-pink. Fairly frequent form, known as a garden-form under the names: *C. v., prostrata* Kirchner, 1864; *C. v., Erikae* Ascherson, 1899; and *C. v., Kuphaldti* hort. Is found in the heath-fields of North Germany, the Netherlands and England. Not to be confounded with the pseudo-creeping forms, caused by the nibbling of rabbits or sheep, which at once begin to grow upwards when they are transplanted. This form has two subforms:

Subfa. **pendula** W. Beijerinck, 1937. Pl. XI and XII. Frame-branches hang straight down (Pl. XI). Especially conspicuous along steep edges.

Subfa. **fasciata** W. Beijerinck, 1937. Pl. IV, 4. Frame-branches partly broadened fan-like to over 1 cm. Plant grows cushion-like. Flowers light violet-pink. Found only once. Lost its fasciations temporarily in culture, on transplantation they returned. Fasciated cuttings produced again strongly fasciated plants.

b. Frame-branches, although straight, stand out wide. Plant grows out in breadth .... Fa. **patula** W. Beijerinck, 1937. Pl. VIII, 1. Pretty general in the Netherlands.

c. Frame-branches close together, vertical ....
Fa. **erecta** W. Beijerinck, 1937.
Pl. VIII, 2. As the preceding one.

d. Frame-branches short, but richly ramified, so that the leaves form a

dense roof. Height of the plant normal ....
Fa. **condensata** (Lamt.) W. Beijerinck, 1937.
Observed only a few times. I have not been able to settle whether this form is permanent on further cultivation.

e. Frame-branches and short-shoots very short, long 1—3 cm and 0.5 cm respectively. Plant remains small, reaches a height of 1—2 dm. Dense squat habit, more or less cushion-like ....
Fa. **nana** (Kirchner) W. Beijerinck, 1937.
This dwarf-form seems to be rare in the open field. Perhaps it is suppressed by the more quickly growing plants around. Is found in gardens in a few little divergent subforms, under the names: *C. v., pygmaea* hort.; *C. v., hypnoides* hort.; *C. v., minima* hort. This latter has a somewhat different habit (see below). Also as a scarcely flowering dwarf-form: *C. v. Smith's Var.* hort.
Among these dwarf-forms a separate place may be assigned to the following subform, growing still more compactly and forming small hemispherical cushions ....
Subfa. **compacta** (hort.) W. Beijerinck, 1937.
Pl. IX, 2. It is brought out under the names: *C. v., Foxii* hort. and *C. v., Foxii nana.* It is not known to me in the wild state.

f. Plant forms sods. Frame-branches 1—2 dm high, erect, easily striking new roots with the curved lower part, which leads to a sod-like habit. Dense and regularly ramified frame-branches ....
Fa. **minima** (hort.) W. Beijerinck, 1937.

g. Plant spreads out, with thick straight standing out frame-branches. Leaves relatively broad and densely packed on the short-shoots, fresh green colour, also in winter. Flowers white or very light lilac
Fa. **rigida** (hort.) W. Beijerinck, 1937.
Pl. X. Known to me only as a culture-form, under the name *C. v., tetragona* hort.

11a. Bloom sets in very early, in this country usually at the end of June or early in July .... Fa. **praecox** W. Beijerinck, 1937.
Scarce in the Netherlands, only a few specimens were found. Perhaps the early flowering plants from the Alps should be placed in this form. In my garden such a plant from Grindelwald was the first to flower for years in succession, at the end of June. This form has a
Subfa. **tenuis** (hort.) W. Beijerinck, 1937, with a more or less cushion-shaped habit, because of the bent frame-branches. Flowers purple-violet. Second bloom in October with a large flower here and there on richly leafed short-shoots. Garden-form.

b. Flowering-time from mid-September to November ....
Fa. **autumnalis** (hort.) W. Beijerinck, 1937.
As a garden-form under the names: *C. v. hibernica* hort.; *C. v. Serlei grandiflora* hort.; *C. v. Serlei rubra* hort.

c. Flowering-time from mid-October up into the winter .... Fa. **hiemalis** (hort.) W. Beijerinck, 1937.
Flowers tinted more or less violet. Plant grows vigorously and regularly with relatively thick frame-branches. As a rule the later flower-buds freeze in our climate. Introduced as a garden-form under the name: C. *v. Johnson Var.* hort., after the English connoisseur A. T. JOHNSON at Conway, N.-Wales.

II. Var. **hirsuta** Gray, 1821.

(= *Erica vulgaris, hirsuta* Waitz, 1805; C. *v., tomentosa* Don, 1834; C. *v., pubescens* Koch, 1837; C. *v., ciliaris* Döll, 1843; C. *v., incana* Reichenbach, 1855.)

1a. Plant haired as a grey to nearly white felt. Stems, leaves and bracts are all densely covered with hair ... Fa. **typica** W. Beijerinck, 1937.
Pl. XXII, 1. The most densely haired plants I saw from Scotland, England and the Channel Isles. Also from Fontainebleau, Léon (Fr.), Budweis (Bohemia) and Lithuania. Less hairy specimens here and there in Central Europe. Seems not to have been found yet in N-Scandinavia, Finland, Russia and S-Europe. Rare in the Netherlands (on the Veluwe near Nijmegen).

b. The greyish-green foliage has somewhat shorter hair, flowers white, plant remains smaller than the type of the variety .... Fa. **pilosa** (hort.) W. Beijerinck, 1937.
Only known to me as a culture-form under the same name.

c. Colour of the foliage in spring bright yellow, during the summer more yellow-green. Young leaflets hairy. Flowers white .... Fa. **lutescens** W. Beijerinck, 1937.
Is only known to me as a garden-form under the name of *C. v., Serlei aurea* (hort.). Probably originated in an English nursery. Fine and robust form with good pollen and fertile, so that it may be considered for cross-breeding.

d. Plant remains low, 1—1.5 dm, very squat growth, forms small grey cushions, flowers violet-pink ... Fa. **compressa** W. Beijerinck, 1937.
Was found on serpentine rocks in Cornwall and called after the finder: *Sister Anne* hort. Was brought into culture by W. E. TH. INGWERSEN.

e. Flowers white. The hair on the rather robust plant is a grey felt or somewhat thinner. Flowers late, September—October .... Fa. **albiflora** W. Beijerinck, 1937.
Also known in horticulture as *C. v., alba pilosa* hort. and *C. v. serotina* Loudon, 1838. Also known from Scotland and the Landes.

f. Flowers pale violet-pink to nearly white .... Fa. **pallens** W. Beijerinck, 1937.
Known to me only from England and the Landes.

g. Flowers dark purple-violet. Vigorous plant. Richly flowering, but not always equally densely haired .... Fa. **Alporti** (hort.) W. Beijerinck, 1937.

According to KIRCHNER (1864) an old culture-form, originating from England, where even now it is found in the wild state, though, e.g. in Surrey. In literature also indicated as C. *v., atro rubens* Loudon, 1838. As a subform we distinguish:

Subfa. **coccinea** (hort.) W. Beijerinck, 1937, which shows a more cumbent growth and is rather strongly haired. The flowers have the colour of the form. To me only known as a garden-plant under the same name.

h. Flowers filled by multiplication of the corolla tips, light violet-pink tint. In the shadow they may become nearly white. The flowers form a closed column. Late-flowering ... Fa. **Bealeae** W. Beijerinck, 1937 Pl. XVIII. Unless the reverse is expressly stated, all the above forms and subforms have been propagated by me vegetatively, in order to find out, whether the characteristics were hereditarily fixed. With the sole exception of the fa. *condensata* they all kept their characteristics.

In the new nursery-catalogue of Maxwell & Beale Ltd 45 different forms of *Calluna vulgaris* alone are offered, among which a few new ones, which I have not had an opportunity yet to examine, namely: *C. v., alba plena, C. v., Tib* and *C. v., Tom Thumb.* The first of these is recommended as follows: "This fine double heath originated in Germany and is a sport of *Calluna vulgaris alba elegans.* It produces spikes about 8—10 inches long of pure white flowers even more double than *vulgaris H. E. Beale*". This latter is the *C. v., hirsuta,* fa. *Bealeae,* mentioned above.

List of the varieties, forms and subforms of **Calluna vulgaris** (L.) Hull, 1808. (= *Erica vulgaris* Linnaeus, 1753; *Calluna Erica* De Candolle, 1805; *Calluna sagittaefolia* Gray, 1821; *Calluna ciliaris* Schur, 1866; *Calluna atlantica* Seemann, 1866; *Erica Eremocharis* Gandoger, 1875; *Calluna Beleziana* Rouy, 1895; *Calluna elegantissima* Sennen, 1930.)

Var. *genuina* Regel, 1843 (C. v., v. glabra Neilreich, 1859).
- Fa. *grandiflora* W. Beijerinck, 1937.
- Fa. *parviflora* W. Beijerinck, 1937.
- Fa. *brachysepala* Joh. Jansen, 1935.
  - Subfa. *microsepala* W. Beijerinck, 1937.
  - Subfa. *densa* W. Beijerinck, 1937.
- Fa. *stricta* W. Beijerinck, 1937.
- Fa. *elegantissima* (Sennen) W. Beijerinck, 1937.
- Fa. *pauciflora* W. Beijerinck, 1937.
- Fa. *multibracteata* Joh. Jansen, 1935.
  - Subfa. *torta* Joh. Jansen, 1935.

  - Subfa. *deflorata* Joh. Jansen, 1935.
  - Subfa. *pentamera* Joh. Jansen, 1937.
  - Subfa. *multiplex* W. Beijerinck, 1937.
  - Subfa. *extensa* W. Beijerinck, 1937.
  - Subfa. *recta* W. Beijerinck, 1937.
  - Subfa. *serotina* W. Beijerinck, 1937.
- Fa. *terminalis* Joh. Jansen, 1935.
- Fa. *clistanthes* Joh. Jansen, 1935.
  - Subfa. *ferax* W. Beijerinck, 1937.
- Fa. *diplocalyx* Joh. Jansen, 1935 (*C. v., David Eason* hort.)
  - Subfa. *hermaphrodita* W. Beijerinck, 1937.
  - Subfa. *polystyla* Joh. Jansen, 1935.
  - Subfa. *fertilis* W. Beijerinck, 1937.
  - Subfa. *carnea* W. Beijerinck, 1937.
  - Subfa. *elata* W. Beijerinck, 1937.
  - Subfa. *gracilis* W. Beijerinck, 1937.
- Fa. *polysepala* Joh. Jansen, 1935.
  - Subfa. *gemmata* W. Beijerinck, 1937.
  - Subfa. *pilulifera* W. Beijerinck, 1937.
  - Subfa. *conica* W. Beijerinck, 1937.
  - Subfa. *subplena* Joh. Jansen, 1935.
  - Subfa. *adscendens* W. Beijerinck, 1937.
  - Subfa. *curvata* W. Beijerinck, 1937.
  - Subfa. *tardiflora* W. Beijerinck, 1937.
- Fa. *polypetala* W. Beijerinck, 1937 (*C. v., plena* Regel; *C. v., fl. pleno* Don).
  - Subfa. *rosea* W. Beijerinck, 1937 (*C. v., Mrs. Hamilton* hort.).
  - Subfa. *lilacina* W. Beijerinck, 1937 (*C. v., Camla Var.*; *C. v., County Wicklow* hort.).
  - Subfa. *candida* W. Beijerinck, nov. nom. (*C. v., alba plena* hort.).
- Fa. *plena* W. Beijerinck, 1937.
- Fa. *monstrosa* W. Beijerinck, 1937 (incl. fa. *apetala*, Joh. Jansen, 1935).
- Fa. *gynodioica* W. Beijerinck, 1937.
  - Subfa. *simplicissima* W. Beijerinck, 1937.
- Fa. *campanulata* W. Beijerinck, 1937.
- Fa. *alba* (Don) Braun-Blanquet, 1926 (*Erica vulgaris, alba* Waitz, 1805; *C. v., albiflora* Michot, 1845; *C. v., fl. alba* Dippel, 1889).
  - Subfa. *erythrostyla* W. Beijerinck, 1937.
  - Subfa. *aureifolia* W. Beijerinck, 1937 (*C. v., alba aurea* hort.; *C. v., Hammondi aureifolia* hort.).
  - Subfa. *pumila* (hort.) W. Beijerinck, 1937 (*C. v., alba pumila* hort.).

Subfa. *Serlei* (hort.) W. Beijerinck, 1937 (*C. v., Serlei alba* hort.).
Subfa. *Hammondi* (hort.) W. Beijerinck, 1937 (*C. v., alba Hammondi* hort.).
Fa. *alboviolacea* W. Beijerinck, 1937.
Fa. *albopurpurea* W. Beijerinck, 1937 (*C. v., Kynance* hort.).
Fa. *purpurea* (Don) Braun–Blanquet, 1926 (*C. v., rubra* Kirchner, 1864; *C. v., C. W. Nix* hort.).
Fa. *bicolor* W. Beijerinck, 1937.
Fa. *multicolor* W. Beijerinck, 1937.
Fa. *microphylla* W. Beijerinck, 1937.
Fa. *argentea* (hort.) W. Beijerinck, 1937.
Fa. *variegata* (Regel) W. Beijerinck, 1937 (*C. v., fol. variegatis* Loudon, 1838; *C. v., foliis variegatis* Don, 1834).
Subfa. *roseovariegata* W. Beijerinck, 1937.
Fa. *rhodostachys* W. Beijerinck, 1937 (*C. v., Mrs. Pat* hort.).
Fa. *aurea* (Don) W. Beijerinck, 1937 (*C. v., lutescens* Dippel, 1889).
Subfa. *aureovariegata* W. Beijerinck, 1937.
Subfa. *chlorostachys* Joh. Jansen, 1935.
Fa. *cuprea* (hort.) W. Beijerinck, 1937.
Fa. *incana* W. Beijerinck, 1937.
Fa. *decumbens* (Don) W. Beijerinck, 1937 (*C. v., prostrata* Kirchner, 1864; *C. v., Erikae* Ascherson, 1899; *C. v., Kuphaldti* hort.).
Subfa. *pendula* W. Beijerinck, 1937.
Subfa. *fasciata* W. Beijerinck, 1937.
Fa. *patula* W. Beijerinck, 1937.
Fa. *erecta* W. Beijerinck, 1937.
Fa. *condensata* (Lamotte) W. Beijerinck, 1937.
Fa. *nana* (Kirchner) W. Beijerinck, 1937 (*C. v., pygmaea* hort.; *C. v., hypnoides* hort.; *C. v., minima* hort.; *C. v., Smith's Var.* hort.).
Subfa. *compacta* (hort.) W. Beijerinck, 1937.
Fa. *minima* (hort.) W. Beijerinck, 1937.
Fa. *rigida* (hort.) W. Beijerinck, 1937 (*C. v., tetragona* hort.).
Fa. *praecox* W. Beijerinck, 1937.
Subfa. *tenuis* (hort.) W. Beijerinck, 1937.
Fa. *autumnalis* (hort.) W. Beijerinck, 1937 (*C. v., hibernica* hort.; *C. v., Serlei grandiflora* hort.; *C. v., Serlei rubra* hort.).
Fa. *hiemalis* (hort.) W. Beijerinck, 1937 (*C. v., Johnson Var.* hort.).
Var. *hirsuta* Gray, 1821 (*Er. vulg., hirsuta* Waitz, 1805; *C. v., tomentosa* Don, 1834; *C. v., pubescens* Koch, 1837; *C. v., ciliaris* Döll, 1843; *C. v., incana* Reichenbach, 1855).
Fa. *typica* W. Beijerinck, 1937.
Fa. *pilosa* (hort.) W. Beijerinck, 1937.

Fa. *lutescens* W. Beijerinck, 1937 (*C. v., Serlei aurea* hort.).
Fa. *compressa* W. Beijerinck, 1937 (*C. v., Sister Anne* hort.).
Fa. *albiflora* W. Beijerinck, 1937 (*C. v., alba pilosa* hort; *C. v., serotina* Loudon, 1838).
Fa. *pallens* W. Beijerinck, 1937.
Fa. *Alporti* (hort.) W. Beijerinck, 1937.
    Subfa. *coccinea* (hort.) W. Beijerinck, 1937.
Fa. *Bealeae* W. Beijerinck, 1937 (*C. v., Mrs. Beale* hort.).

Nearly all the here enumerated varieties, forms and subforms are present and living in the garden of the Biological Station at Wijster (Drente, the Netherlands), and have been reproduced vegetatively. A complete herbarium-material is found at the said station, while the greater part of these forms is also present in the herbaria at Kew and Leiden (State Herbarium).

3. *Nomenclature of the species and its forms.*

The original name *Erica* (*'Ερείκη*), given to it by THEOPHRASTUS 1) and also used by DIOSCORIDES (PEDANIUS, 1—64 after Christ) and PLINY 2), is in the older herbals used for ling (Calluna). So one finds in the Herbal: "De historia stirpium" of LEONHARTUS FUCHSIUS, 1542, the name "Erice" with a fine picture of ling (Fig. 140).

HIERONYMUS BOCK (= TRAGUS) first mentions the name "*Erica vulgaris*" in 1552. After that we meet it more often, e.g. with JOH. THAL in his Harzflora (1577), with JOHN GERARD (Herbal, 1597) and with CASPAR BAUHIN (Pinax, 1623).

The genus *Erica* was first drawn up by TOURNEFORT (1700) with only 29 species, including *Andromeda*. It was introduced by LINNÉ (1737) without this genus.

Not till 1802 the genus Calluna was separated from the genus *Erica* by R. A. SALISBURY and received the name Calluna 3).

The name Calluna (*Καλλύνω* = I clean) must refer to the making of brooms. To this LOUDON (1842) remarks (l.c. p. 559): The name of Calluna is derived from Kalluno, which, as Sir J. E. Smith observes, "is doubly suitable, whether, with Mr. Salisbury and Dr. Hull, we take it to express a cleansing property, brooms being made of ling, or whether we adopt the more common sense of the word, to ornament or adorn, which is very applicable to the flower."

So the old name *Erica vulgaris* L. has been superseded by *Calluna vulgaris*. However, since SALISBURY only split the genera and did not use this combination, the priority belongs to HULL, who was the first to give

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1) THEOPHRASTUS OF ERESUS, 370—285 before Christ. A Latin translation of his work was published at Amsterdam in 1644: "De historia plantarum libri decem".

2) Cf. C. F. WAITZ, 1805, p. 8 and A. M. CHURCH, 1908, p. 150.

3) In: Transact. Linn. Soc., VI, 1802, p. 317.

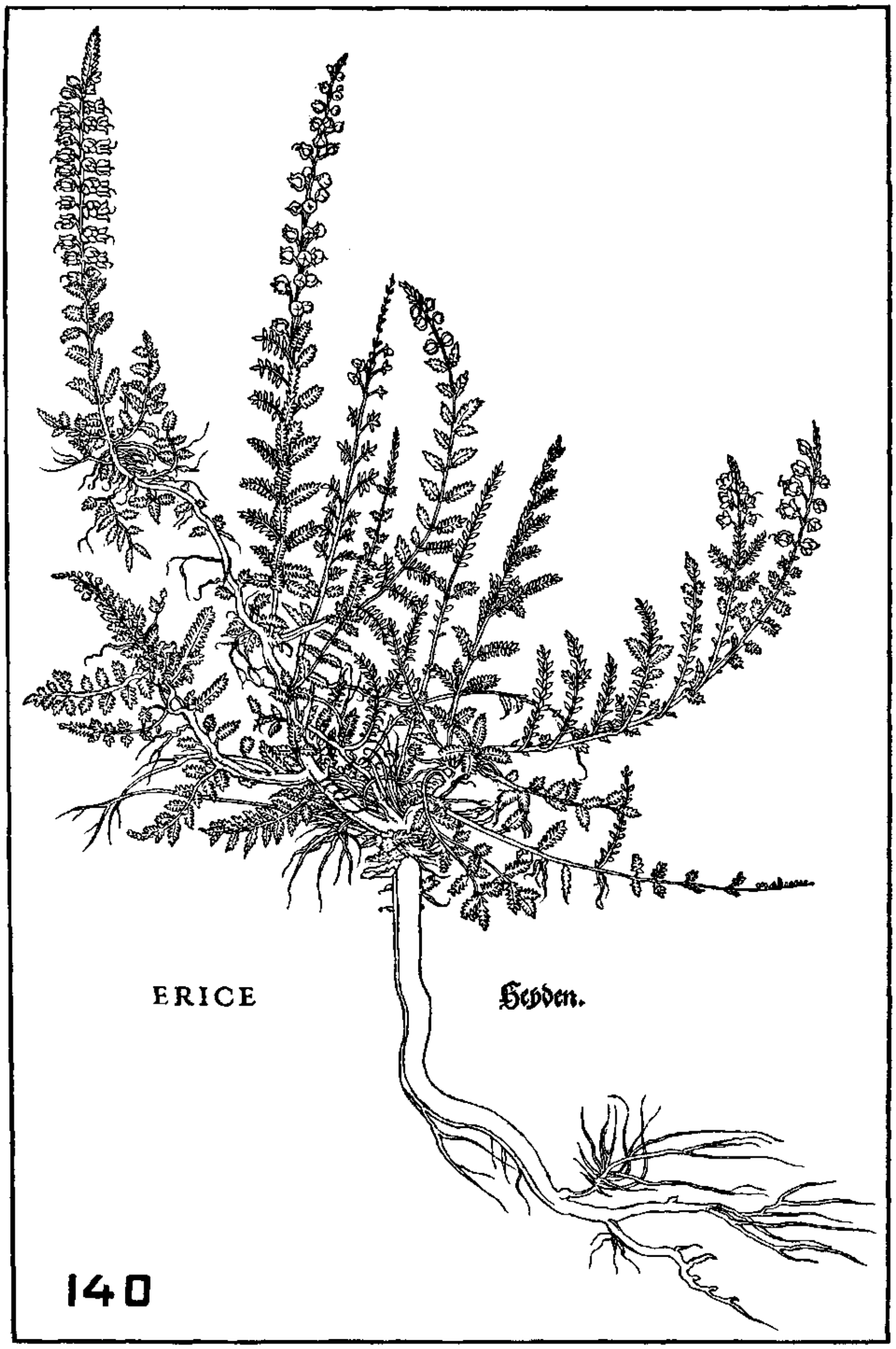

Fig. 140.

this name, with a diagnosis, in his British Flora, 2nd. Ed., 1808, Tome I, p. 114. At the present day the nomenclature is therefore:

Calluna vulgaris (L.) Hull, 1808.

The Linnean diagnosis of the species runs (Spec. Plant., Ed. 1, p. 352):

Erica.

* *Antheris bicornibus.*

vulgaris. 1. **Erica** antheris bicornibus inclusis, corollis inæqualibus campanulatis mediocribus foliis oppositis sagittatis.

Erica foliis quadrifariam imbricatis triquetris glabris erectis, corollis inæqualibus calyce brevioribus. *Hort. cliff.* 146. *Fl. suec.* 309. *Roy. lugdb.* 442.

Erica vulgaris glabra. *Bauh. pin.* 485. *Fl. lapp.* 141.

Habitat in Europæ *campestribus sterilibus frequens* ♄.

Comparativa mediocris, longior, brevior *corollæ* respicit *proportionem ad calycem.*

In England the most current popular names for this species are: *ling* — *common heath* — *common heather* — *Scotch heather* — *sweet broom* — *furze.*

In Germany: *Heidekraut* — *Besenheide* — *Bessenheide* — *Brandheide* — *Kuhheide* — *Kruse Hede* (in Westphalia) — *Krause Heide* — *Ramhäd* (Nahe district) — *Binnheidi* — *Hoaderer* (Bavaria) — *Rinkheiser* — *Ringheiss* — *Rinkheide* — *Rindsheide* (Baden).

In Austria and the Tyrol: *Sendel* — *Sendach.*

In Switzerland: *Brüsch* — *Brensch* — *Gaissbrüüsch* — *Prisi* — *Prig* — *Prisch* — *Bäseries* — *Bruig* — *Brui* — *Brucha* — *Bruoch* — *Bruèl.*

In Italy: *erica minore* — *cecchia* — *scopa* — *brughiera* — *brentoli* — *grecchia* — *sorcelli* — *brüg* (Tessino).

In Spain: *brezo.*

In Portugal: *urze.*

In France: *bruyère commune* — *brande* 1) — *bérée* — *béruère* — *breuvée* — *bruc.*

In the Netherlands and Belgium: *struikheide* — *gewone heide* — *bezemheide* — *heet* — *hiet* — *hied* — *riegheide* — *knopheet* — *kooheet.*

In Danmark and Norway: *röslyng* — *lyng* — *bustelyng.*

In Sweden: *ljung.*

In Iceland: *beitilyng* — *beitibuski.*

In the Faroe Isles: *lyngur* — *heidalyngur.*

In Finland: *kangas* — *kanerwa* — *kanarwa.*

In Finnish Lapland: *liuridne* — *taggnas.*

In Esthonia: *kmarik* — *kanarik* — *kanarpik* — *nömme rohi* — *kana-arg.*

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1) The name is also used for Erica scoparia.

In Latvia: *wirsnes mallohtni* — *malna ahle* — *garsas.*

In Poland: *wrzos.*

In Lithuania: *brizdzei* — *wirzei* (acc. to Hagen).

Samoyeds: *szyts* (acc. to Annenkof).

In Russia: *weresk* — *weress* — *borowitsa* — *borowika* (in the former prov. Wladimir, from bor, a pine-forest) — *yornik, kanabra* — *kanibra* (in the former prov. Olonets; also in Finnish) — *worobjinaja Gretshucha* (i.e. sparrow-buckwheat; in the former prov. Wologda) — *ryssken* (in the prov. Moscow).

Concerning the nomenclature of the varieties, forms and subforms it may be remarked that already Waitz (1805), Don (1834), Loudon (1838) and Regel (1843) have given enumerations of the then known forms of Calluna, but without mentioning the authors. To this Waitz (1805) makes an exception, but his older data from the pre-Linnean period (before 1753) are no longer of value for nomenclature. Also the forms mentioned by the older dendrologists as Kirchner (1864), Koch (1872) and Dippel (1889) either lack the names of the authors, or the diagnoses are insufficient, while the data in the older and more recent botanical and dendrological works, as De Lamarck and De Candolle (1805), Rouy et Foucauld (1908), C. Schneider (1912), Braun-Blanquet (1926) and Rehder (1927) contain many wrong names and garden-names. So a revision was much needed. From the chaos of names finally the following 34 remained:

genuina Regel, 1843
hirsuta Gray, 1821
alba (Waitz) Don, 1834
purpurea Don, 1834
aurea Don, 1834
variegata Regel, 1834
nana Kirchner, 1864
elegantissima Sennen, 1929
polystyla Joh. Jansen, 1935
clistanthes Joh. Jansen, 1935
brachysepala Joh. Jansen, 1935
polysepala Joh. Jansen, 1935
subplena Joh. Jansen, 1935
chlorostachys Joh. Jansen, 1935
compacta hort.
minima hort.
rigida hort.
decumbens Don, 1834
condensata (Lamotte) Rouy, 1908
multibracteata Joh. Jansen, 1935
torta Joh. Jansen, 1935
deflorata Joh. Jansen, 1935
pentamera Joh. Jansen, 1935
terminalis Joh. Jansen, 1935
diplocalyx Joh. Jansen, 1935
tenuis hort.
hiemalis hort.
pumila hort.
Serlei hort.
Hammondi hort.
argentea hort.
cuprea hort.
pilosa hort.
Alporti hort.

The following list contains the names of Calluna-forms, sometimes met with in literature or in gardens, either insufficiently described or given as nomen nudum in catalogues of nurserymen, etc. In order to prevent further confusion it would be recommendable to cancel these names. They are:

alba West
alba dumosa hort.
alba elata hort.
alba erecta hort.
alba gracilis hort.
alba minor hort.
alba pyramidalis hort.
alba tenella hort.
albivariegata hort.
apetala Joh. Jansen, 1935
carnea hort.
coerulea Koch, 1872 (not fixed)
dumosa Kirchner, 1864
elata hort.
elongata hort.
gracilis Kirchner, 1864
grandiflora hort.
hirsuta Presl, 1819
longisepala Rouy, 1898
Mair's Var. hort.
minima Koch, 1872
Mullion hort.
multiplex Loudon, 1838
Olbiensis Albert
patula Rouy, 1908
Penhale hort.
plena hort.
plena Regel, 1843
pumila hort.
pygmaea alba hort.
regina Kirchner, 1864
serotina Loudon, 1838
spicata Don, 1834
spuria Don, 1834
stricta hort.
tenella hort.
tomentosa Bréb.
and all other names which do not accord with the rules of international nomenclature.

In the preceding identification table the principal synonyms are given in brackets behind the names of the forms.

C. Heath-reserves.

In the densely populated civilised countries of Central and West Europe the transformation of the natural or historically grown landscapes by man assumed in the beginning of the twentieth century such enormous proportions that, as a reaction, a wide-spread movement came up to protect and preserve parts of these landscapes, out of pure veneration or from ethical, aesthetical, scientific or hygienic motives.

This utterance of civilisation, the wish to protect nature, to save the individual forms of life and their communities, as they have evolved through the ages, met with a general response and led to legislation and government care for the preservation of nature in many states, so in the Scandinavian countries (in Sweden already in 1909), Germany, England, America and Russia, to mention only a few.

Among the hundreds of nature-reserves which Europe counts at present, a fair number are chiefly occupied by Calluna-heaths with the corresponding fauna and flora, or by vegetations more or less rich in Calluna. They lie mainly in districts within the optimal area for this plant.

It is difficult to give a full enumeration, as a sufficiently accurate inventory of the reserves is not always at one's disposal and it cannot always be ascertained how far a reserve is really safeguarded. Besides, the character of the vegetation often changes quickly, so that heath-fields may become woods, grass-vegetations and suchlike. Nor could the size be always given accurately, it was sometimes missing in the data at my disposal.

In the following survey of the reserves that are of importance for the vegetation-types rich in Calluna, completeness has not been aimed at; it is a list of the scientifically important and largest plots. These lie mostly in N-W Europe, it seems that in other parts, such as S-W France and the Iberian Peninsula, not much has been done in this respect.

The reserves are summed up country by country, the sources of information are given. For general orientation the reader is referred to: G. A. BROUWER, De Organisatie der Natuurbescherming in de verschillende landen (the Organisation of Nature-protection in different countries), Amsterdam, 1931, American edition 1938. This contains extensive literary data.

Many of the following data I owe, with sincere thanks, to l'Office International pour la Protection de la Nature, Rue Montoyer 21, Bruxelles.

Belgium.

Up to now there is not a single heath-reserve. The foundation of such a heath- and moor-reserve in the Hautes Fagnes (Spa—Verviers) is at present being studied.

Danmark.

With the Netherlands Danmark belongs to the countries with the relatively largest number of heath-reserves. They are mostly situated in Jutland, some of them on the islands, as Bornholm and Möen. The principal ones are: *Borris Hede* in W. Jutland, 1875 H.A. 1), also used for military purposes; *Vrögum Plantage,* Jutland, 44 H.A.; *Slotslyngen* on Bornholm, 114 H.A.; *Rebild Bakker,* Jutland, 110 H.A., a national park; *Nörholm,* Jutland, 350 H.A.; *Röde Mölle,* Jutland; *Tolne Bakker,* Jutland; *Randbölhede,* Jutland, 600 H.A.; *Vindbläs Hede,* Jutland; *Gern Bakker,* id. 20 H.A.; *Hjelm Hede,* Jutland; *Hjerl Hede* and *Flyndersö,* Jutland, 760 H.A.; *Bramslev Bakker,* Jutland; *Ibsker Höilyng,* Bornholm, 36 H.A.; *Ulfshale,* Möen. In preparation is a heath-reserve in N. Jutland, the *Hald Hede* and the *Hald* Lake. Lit.: "Dansk Naturfredning", 1924—1938.

Germany.

Among the numerous heath-reserves the moorlands rank first in number. With a view to the protection of the heath-field vegetations themselves several larger and smaller "Naturschutzgebiete" have been reserved. Such are: *Hildener Heide* (Rhine Province); the *Juniper* reserve in the Eifel; the moor near *Roda* (Hessen); the *Gelmerheide*; *Deutener Moor*; *Schwarzes Venn* near Velen; heath near *Ramsdorf*; Moorgebiet *Kletterpoth*; heath near *Stuckenbrock*; *Siemelkenmoor* near Rhaden, all in Westphalia. In

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1) 1 Hectare = 10.000 m^2 = $\frac{1}{100}$ km^2 = 0.00386 sq mile.

Hanover: *Pastorendiek* near Südwalde; *Oberharzer Hochmoore* on the Brocken and Bruchberg; Naturschutzgebiet *Lüneburger Heide*, about

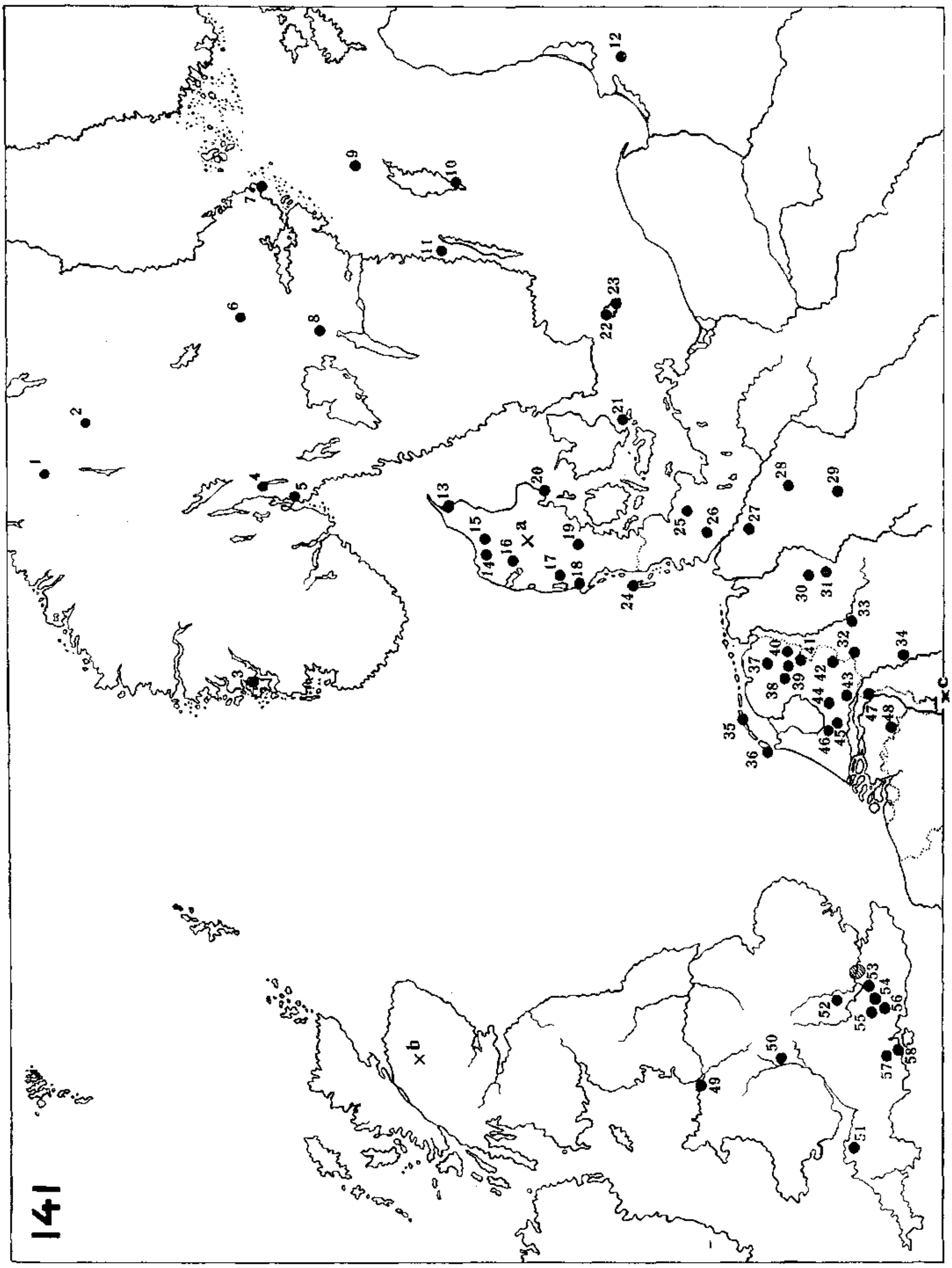

Fig. 141. (Explanation on page 156.)

4000 H.A. round the Wildseder Berg; Juniper vegetation near *Betzhorn*; Hochmoor am *Ewigen Meer*. In Schleswig Holstein lie: *Lister Dünen* and

Morsumkliff on Sylt; heath near *Kellinghusen*; heath near *Brekendorf*; *Salemer Moor*; Eichenkratts in the *Hunsum* heath-district; Eichenkratt on the *Lockstedter Lager*. In East Prussia: the *Zehlau Bruch* near Königsberg, 2360 H.A., etc. Lit.: Beiträge zur Naturdenkmalpflege der Staatlichen Reichsstelle f. Naturdenkmalpflege in Preussen; Nachrichtenblatt f. Naturdenkmalpflege, idem; Merkbuch f. Naturdenkmalpflege, idem, Berlin, 1925; Blätter f. Naturschutz u. Naturpflege, München; SCHOENICHEN, Naturschutz im Dritten Reich, Naturschutzbücherei.

Finland.

Although no sufficiently detailed data on the nature-reserves of this large country are at my disposal, it is pretty certain that in the huge national parks, such as the *Pallas-* and *Ounastunturi* district (85.000 H.A.), the *Kuolajärvi* reserve (28.500 H.A.) and the *Oulankajoki* reserve (23.500 H.A.), also portions will be found that are rich in Calluna. Lit.: E. HÄYREN, Finlands naturskyddsområden, in: Sveriges Natur, vol. 19, 1928.

France.

As far as is known to me not a single heath-reserve exists, which is rather surprising, because there are extensive heath-regions, especially in the South-West. Possibly Calluna will also be found in places in the extensive *Parc National de Pelvoux* (12.982 H.A.) in the Départements Isère and Hautes Alpes. Its existence there is not known to me, however.

England and *Scotland.*

The National Trust for the Places of Historic and National Beauty has among its numerous possessions also several characteristic Calluna-fields and reserves with much Calluna, such as: *Ashridge — Berkhamsted — Common* (2500 acres); *Hackhurst Down* (13 acres); *Hightown Common*, Ringwood (40 acres); *Hindhead Common* (750 acres); *Holnicote Estate*, Exmoor (6500 acres); *Hydon Heath* (92 acres); *Kinver Edge* (200 acres); *Irby Hill* and *Thurstanton Heath, Wirral Properties* (34.5 acres); *Witley Common* (240 acres); *Milford Common* (137 acres). In Scotland the foundation of a nature-reserve in the *Cairn Gorms* is under consideration. Lit.: Annual Reports of the National Trust, 1895—1938; Handbooks of the Royal Society for the Promotion of Nature Reserves in the British Isles, 1923—1938).

The Netherlands.

The principal heath-reserves are the property either of the State, (indicated by S), or of the Vereeniging tot Behoud van Natuurmonumenten in Nederland (Society for the preservation of nature-monuments in the Netherlands, indicated by N). For some reserves, such as the *Leusden Heath*, the *Park de Hooge Veluwe* and the *Gooi reserve*, foundations exist. Others were founded by the Nederlandsche Heidemaatschappij (Netherlands Heath Society), the A.N.W.B. (General Netherlands

Cyclists' and Tourists' Union), the Life-Insurance Co Utrecht, and by private people. The most important of these are: the *Kootwijker Zand* and *Gerritsflesch* on the Veluwe (S), together 760 H.A.; the nature-reserve "*Veluwezoom*" (N), 2439 H.A.; *Dwingeloosche Heide* (N), 750 H.A.; *Mookerheide* (70 H.A.); *Cartierheide* near Hoogeloon (N), 145 H.A.; *Buurser-Zand* near Haaksbergen, 311 H.A.; *Tondensche Heide* near Brummen (N), 10 H.A.; *Balinger-* and *Mantinger Zand* (N), 50 H.A.; *Fochteloër Veen* (N), 150 H.A.; *Lheebroeker Zand* (S), 26.7 H.A.; *Westerveen* and *Kibbelhoek* (S), 15 H.A.; *Aekingerzand* near Appelscha (S), 77 H.A.; *De Tweelingen* near Schoonlo (S), 23 H.A.; *Zeijer Veld* (S), 90 H.A.; *Elper Meer* (S), 29 H.A.; *De Hooge Stoep* near Gees (S), 65 H.A.; *Sleenerzand* (S), 6 H.A.; *De Geul* and *Westerduinen* on Texel (S), 1800 H.A.; *Landrummer Heide* on Terschelling (S), 14 H.A.; *Peelven* with heath (S), 15.4 H.A.; *Hapertsche Heide* (S), 62 H.A.; *Laagveld* near Leende (S), 14.8 H.A. Besides there are several smaller parcels of heath amid the moors and drift-sands, of which a fuller account is found in: G. J. VAN OORDT, De Staatsnatuurreservaten, 1935; Gedenkboek Staatsboschbeheer 1899—1939; G. A. BROUWER, De Organisatie der Natuurbescherming in de verschillende landen, 1931; Annual Reports of the Ver. tot Behoud v. Natuurmonumenten in Nederland.

The private reserves, belonging to the above-mentioned bodies, are: *the Lemeler Mount* (*Park 1813*), the Estate *De Utrecht*, and others.

Norway.

Also in this country, favoured with a grandiose natural beauty, several reserves, rich in Calluna, are found, of which the principal are: *Tofteholmen*, on the Oslo-fjord, 11 H.A.; *Rössvassholmen*, prov. Nordland, 25 H.A.; *Bekkenesholmen*, Nordland, 4 H.A.; *Stubberud*, prov. Akershus near Oslo, 10 H.A.; *Rundeholmen*, prov. Hordaland; *Mölen*, Oslo-fjord, 17 H.A.; *Nedalen nature-reserve* in the Sylene district, 5500 H.A. Lit.: Norge, Tidskrift om vart land, Vol. 1—14 (1925—1938).

Sweden.

This country, excelling by its vast arctic and subarctic national parks, where already on June 23, 1909, a law was passed for the protection of nature, must necessarily have preserved a number of landscapes with Calluna-heaths, such as: *Gotska Sandö Nationalpark*, prov. Kalmar, 40 H.A.; *Ängsö Nationalpark*, prov. Stockholm, 75 H.A.; *Blaa Jungfrun Nationalpark*, 46 H.A.; *Hamra Nationalpark*, prov. Gävleberg, 20 H.A.; *Garphyttan Nationalpark*, prov. Örebro, 108 H.A.; *Norra Kvill Nationalpark, prov.* Kalmar, 27 H.A.; *Töfsingdalen Nationalpark*, prov. Kopparberg, 1365 H.A.; *Sonfjället Nationalpark*, 2700 H.A.; *Peljekaise Nationalpark*, 14.600 H.A. In this latter more northern region Calluna only occurs in places. Lit.: K. Svenska Vedensk. Akad., s. Skrifter i Naturskyddeärenden.

Switzerland.

Although there are no special heath-reserves, Calluna is without doubt sufficiently represented in the *Unter Engadin Nationalpark* (14.500 H.A.) and, as it is pretty general in the Alps, will probably also occur in other reserves.

From the remaining countries no data on heath-reserves are known to me. There is a chance that by the foundation of a large *Tatra National Park* Calluna will be preserved in the Czecho-Polish region. Also in the Austrian Alps Calluna will be found in the numerous smaller reserves, nearer information is lacking, however.

From this summary, although far from complete, one may gather that Calluna is protected in a number of places. Under very different conditions and as a constituent of different vegetation-types it can maintain itself there and be studied, in spite of the serious reduction of its domain during the last half century. It is to be hoped that also in S-W Europe the heath-vegetations will be protected in time, since exactly on the Iberian Peninsula heath shows the greatest diversity and Calluna lives there under quite different conditions and in totally different vegetation-types than in the North.

Names of the nature-reserves, rich in Calluna, shown in the situation-map, Fig. 141.

1. Nedalen Naturpark (5500 H.A.).
2. Sonfjället Nationalpark (2700 H.A.).
3. Rundeholmen.
4. Stubberud.
5. Mölen.
6. Töfsingdalen Nationalpark (1365 H.A.).
7. Ängsö Nationalpark.
8. Garphyttan Nationalpark (108 H.A.).
9. Gotska Sandö Nationalpark.
10. Hamra Nationalpark.
11. Blaa Jungfrun Nationalpark.
12. Zehlau Bruch (2360 H.A.).
13. Tolne Bakker.
14. Vindbläs Hede.
15. Nörholm (350 H.A.).
16. Hjerl Hede, Flyndersö (760 H.A.).
17. Borris Hede (1875 H.A.).
18. Vrögnum Plantage.
19. Randböl Hede (600 H.A.).
20. Hjelm Hede.
21. Ulfshale.
22. Slotslyngen, Bornholm (114 H.A.).
23. Ibsker Höilyng, idem.
24. Lister Dünen, Sylt.
25. Heide bei Brekendorf.
26. Heide bei Kellinghusen.
27. Lüneburger Heide (4000 H.A.).
28. Juniperus Heide bei Betzhorn.
30. Siemelkenmoor bei Rhaden.
31. Heide bei Stuckenbrock.
32. Ramsdorfer Heide.
33. Gelmer Heide.
34. Hildener Heide.
35. Landrummer Heide (Terschelling).
36. Westerduinen (Texel).
37. Zeijer-Veld.
38. Fochteloër-Veen (150 H.A.).
39. Dwingeloo'sche Heide (750 H.A.).
40. Balinger- en Mantinger Zand.
41. Hooge Stoep bij Gees.
42. Buurser Zand (311 H.A.).
43. Reservaat Veluwezoom (2430 H.A.).
44. Kootwijker Zand en Gerritsflesch (760 H.A.).
45. Leusdener Heide.
46. Gooisch Natuurreservaat (1100 H.A.).
47. Mookerheide.
48. Cartier Heide (145 H.A.).
49. Thurstanton Heath and Irby Hill.
50. Kinver Edge.
51. Holnicote Estate, Exmoor (2600 H.A.).
52. Ashridge-Berkhamsted Common (1000 H.A.).
53. Hackhurst Down.
54. Hydon Heath.
55. Witley Common (100 H.A.).
56. Hindhead Common (300 H.A.).
57. Hightown Common, Ringwood.
58. Milford Common.

a. proj. Hald Hede reserve.
b. proj. Cairn Gorms National park.
c. proj. Hautes Fagnes Reserve.

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EXPLANATION OF THE FIGURES.

Fig. 1. Schematic representation of the storeyed growth of a four year old Calluna plant (I—IV = annual accrescence; long-shoots only have been drawn).

Fig. 2a. Perennial short-shoot, 2½ years old, of fa. *microphylla.*

b. Short-shoot of the same form, with a disturbance in growth just below the middle.

c. Extending short-shoot.

d. Short-shoot of the fa. *rigida* with compact leaves.

Fig. 3. Long-shoot, grown in an always very damp environment. Leaves bent away from the stem. The groove in the leaf is widened; the small spurs are bent off.

Fig. 4. Twig with abnormal arrangement of the leaves, passing from $^1/_2$ into $^1/_3$.

Fig. 5. a. Leaves variegated (fa. *variegata*); b. Leaves white-tipped (fa. *argentea*).

Fig. 6. Petalomania and prolification. Out of the abnormal accumulation of buds 3 shoots have developed, of which the middle one bears first a few bract-like organs; then follow a coloured corolla or petal-like organs, succeeded again by green leaves.

Fig. 7. Flowering-twig with two flowers and two leaf-buds (b).

Fig. 8. Proliferated packets of bracts, which after the winter-rest have begun to form flowers (condition in May); a. decussate phyllotaxis has been retained; b. more irregular phyllotaxis.

Fig. 9. a. Proliferated packet of bracts, without flower-formation and with unchanged phyllotaxis ½; b. the same, with spirally arranged bracts.

Fig. 10. Transitions between bracts and sepals with fa. *multibracteata.*

Fig. 11. Hair-root in transverse and longitudinal section; ep. = epiderm; end. = bark (v. Tieghem's endoderm); per. = pericycle; p. = root-sac of the radicel; ec. = bark of the radicel; c. = central cylinder (stele) of the radicel. (after VAN TIEGHEM and DOULIOT, 1888).

Fig. 12. Top part of the main root of a seedling; ca = calyptra; d.z. = division-zone of the cells; str. z. = extension-zone of the cells.

Fig. 13. Top of a young hair-root with: ca. = calyptra; ep. = epiderm; end. = endoderm; cc. = central cylinder (stele); i.c. = initial cell of the central cylinder; i.e. = initial cell of the epiderm and the calyptra (1 and 1′).

Fig. 14. Hair-root, grown along glass, with remnants of several laterally shed calyptras, shoved forward in the direction of growth.

Fig. 15. Cross-section through the meristem of part of a young stem, directly below the vegetation point; ep. = epiderm mother-cell; pr.c. = procambium, highly divided (extremely small cells); m. = medulla.

Fig. 16. Cross-section of a short-shoot stem, close below the vegetation-point. A ring of wood with vessels (libriform) has already formed; ep. = epiderm; s.ep. = sub-epiderm; end. = endoderm; per. = pericycle; x. = xylem; v. = vessels; m. = medulla (pith).

Fig. 17. Longitudinal section through a young flowering-twig; ep. = epiderm; s.ep. = subepiderm; c. = water-tissue (parenchyma); tr. = tracheae; m. = medulla or pith.

Fig. 18. Cross-section through a juvenile long-shoot, with incipient lignification; h. = trichomes; ep. = epiderm; s.ep. = subepiderm; w. = water-parenchyma of the primary bark; end. = endoderm; p.c. = pericycle; c. = row-cambium (bast); tr. = tracheae; m. = medulla.

Fig. 19. Uni- and pluricellular trichomes on the young long-shoot.

Fig. 20. Cross-section through the hypocotyl axis of the seedling in the stage with four leaves; ep. = epiderm; mes. = bark; tr. = tracheae of the central vascular bundle.

Fig. 21. a—c = libriform fibres; e—f = tracheae with laddered perforations at the extremities; d. = medullary-ray cells. From material macerated with nitric acid.

Fig. 22. Cross-section through the wood; ms. = medullary ray; p. = pits; tr. = tracheae; x. = xylem.

Fig. 23. Stoma on the hypocotyl axis of the seedling.

Fig. 24. Different shapes of Calluna leaves. a. cotyledon; b. primary leaf; c. following leaf; d. short-shoot leaf; e., f. and g. long-shoot leaves; h. short-shoot leaf of var. *hirsuta*; i. and j. transitional leaves (intermediate leaves); k. bract; l. transition to sepal.

Fig. 25. Cross-section through the middle of a long-shoot leaf, during winter; of the mesophyll many cells have died, while crystal-sphaerites (sph.) of Ca-oxalate (?) are visible; n. = leaf-veins; st. = stomata; scl. = sclerenchyma mantle round the main vein.

Fig. 26. Cross-section through the top-part of a short-shoot leaf, with more mesophyll and a double palisade layer along the sides; cu. = cuticula; sl. = mucilaginous mantle of the epiderm cells; pal. = palisade cells; vibr. (read fibr.) = fibrovascular bundle; int. = intercellular air-space of the mesophyll; st. = stomata; tr. = trichomes.

Fig. 27. Cross-section through a bract with longish hairs on the edges and sclerenchymatous reinforcing tissue (scl.), which sometimes is more voluminous (straw-scales).

Fig. 28. Cross-section of a primary leaf of the seedling; st. = stomata; n. = veins.

Fig. 29. Crowded stomata along the inner side of the groove of a long-shoot leaf.

Fig. 30. a. Mesophyll-layer directly under the epiderm; b. = epiderm on the upper side of the leaf; c. = epiderm on the edge of the leaf.

Fig. 31. Mesophyll with leaf-veins.

Fig. 32. Cells of leaf-epiderm with gum-formation; cu. = cuticle; l. = the three lamellae of the epiderm cell-wall; sl. = mucilaginous middle lamella; pa. = palisade cells.

Fig. 33. a. Vein in the leaf-spur. Transverse section with a mantle of parenchyma around; b. Main vein of a stem-leaf; pa. = parenchyma; x. = xylem; p. = phloem; sc. = sclerenchyma; ep. = epiderm; t. = trichome.

Fig. 34. Transverse section across the leaf-groove with stomata (st.) and trichomes (tr.); c. = cuticle; d. = supporting-cells of the stomata.

Fig. 35. Endotrophic mycorrhiza in the pluricellular trichomes along the edge of the leaf (a) and on the top of the young leaves (b).

Fig. 36. Transverse section just across the vegetation-point of a young seedling; cot. = cotyledon; pr. = primary leaf; enclosed: following leaves and vegetation point.

Fig. 37. a. Bracts after removal of the flower; b. cross-section of one of the outer (lowest) bracts.

Fig. 38. a. and b. Flower after removal of the calyx; c. = complete flower shortly after opening.

Fig. 39. Flower-diagram of Calluna and *Erica cinerea* (to the right), after NORDHAGEN, 1937.

Fig. 40. Cross-section through a sepal (a) and a corolla tip (b and c). In 40a the two (to several) lignified thick-walled cell-layers are seen.

Fig. 41. a. Epiderm of the anther; b. epiderm of the style.

Fig. 42. Longitudinal section through the style. In the middle the duct with small-celled epiderm.

Fig. 43. Longitudinal section through a nectary-cushion; n. = nectary; c. = wall of the ovary; ax. = direction of longitudinal axis of flower.

Fig. 44. a. Cross-section through the style near the base; b. through the middle part.

Fig. 45. Longitudinal section through a flower-bud, about the time of formation of the sex-cells; a. outermost carpel; b. innermost carpel.

Fig. 46. Transverse section through the ovary at the two levels a—b and a′—b′ of Fig. 49, schematized.

Fig. 47. Longitudinal section through a young flower-bud; a. outer carpel; b. differentiation of the inner carpel.

Fig. 48. Six stages of development of the ovary, showing the gradual formation of the two carpels.

Fig. 49. Schematized longitudinal section through a flower-bud, showing how the two carpels have coalesced, a—b and a′—b′ mark the levels, combined in Fig. 46.

Fig. 50. a—b. stamens in different aspects; c. anther, front view; d. spur-like appendage of the anther (after J. J. TER PELKWIJK).

Fig. 51. Cross-section through a flower-bud at the level of the placenta, shortly before anthesis. The four bracts are blank, then follow 4 lightly shaded sepals and 4 darker corolla tips. Anthers black, each with two lightly shaded spur-like appendages. In the centre the ovary with the placenta and four septa.

Fig. 52. Cross-sections through ripe anthers; a. near the base. b. near the top. c. = connective; ps. = pollen-sac; sp. = spur-like appendage; p. = pollen tetrad; ep. = epiderm.

Fig. 53. Cross-section through young anther with 2 thecae and 4 pollen-sacs, in which the archespores (arch.); ep. = epiderm; t. = tapetum; end. = endothecium.

Fig. 54. Pollen-tetrads of Calluna, just germinated on saccharose-gelatine. The intine has come out through one of the three pores in the exine and appears as pollen-tube.

Fig. 55. Four stages of the stigma; a—c shortly after anthesis; below to the right: in full bloom (after TER PELKWIJK).

Fig. 56. Longitudinal sections through an opening flower; ant. = anther; st. = style; fr. = ovary; n. = nectary; a. = swelling-cushion tissue; c. = corolla: sta. = stamen; a. the swelling-cushions still inactive; b. the same, functionating.

Fig. 57. Two twigs with matured fruits. The upper petal as a rule remains visible in the slit, left open by the bent sepals when shedding the seeds (after NORDHAGEN, 1938).

Fig. 58. The flowers on a twig turned to one side (after NORDHAGEN, 1938).

Fig. 59. Flowers after fertilization. The four sepals are bent over the young fruit.

Fig. 60. a. Fruit-capsule after the seed has been strewn. Placenta and septa form an indissoluble whole with the central column.
b. Fruits of Calluna, above with the calyx present, below with the calyx removed (after NORDHAGEN, 1938).

Fig. 61. Transverse sections through the fruit-wall; a. with mid-rib (m.) in the carpel; b. joint of two carpels with the septum (s.). At c. the disruption, marked by a dotted line, begins.

Fig. 62. Seeds of Calluna in three of the most common types.

Fig. 63. Longitudinal section through a seed-grain (according to ARTOPOEUS, 1903); m.h. = wall of the micropylar haustorium; end. = endosperm; per. = perisperm; em. = embryo.

Fig. 64. Longitudinal section through the basal part of a seed-grain with stronger magnification; emb. = embryo; per. = perisperm; end. = endosperm-cells with albumins and oils. Round the embryo part of the cells has been taken up as food and dissolved.

Fig. 65. a. Median section through the fruit-wall; b. the endocarp, consisting of two cell-layers; pe.c. = pericarp; me.c. = mesocarp; end.c. = endocarp, consisting of fibrous cells in two layers, crossing at nearly right angles.

Fig. 66. Median section through fruit-wall, style (st.) and placenta (pl.), showing the carpel curving against the style; ep.c. = epicarp; m.c. = mesocarp; end.c. = endocarp.

Fig. 67. Stages in the development of the seedling.

Fig. 68. Stages in the formation of tetrads in the pollen mother-cells; 1—2, heterotypical prophase; 3—4, synapsis; 5, beginning of the zygophase; 6—7, diakinesis; 8—10, heterotypical metaphase; 11—12, heterotypical anaphase; 13, interkinesis; 14—15, tetrad-formation (homotypical division-stages). Heidenhain staining.

Fig. 69. Seed-bud with uninucleate embryo-sac mother-cell.

Fig. 70. Quadrinucleate stage of the embryo-sac mother-cell.

Fig. 71. Octonucleate stage of the embryo-sac mother-cell, just before fertilization.

Fig. 72. Diagram of the opening of the flower-buds under controlled circumstances (see text).

Fig. 73. Course of the transpiration of Calluna with sudden wind (after FIRBAS, 1931).

Fig. 74. Osmotic value of Calluna during the course of a year (according to THREN, 1934).

Fig. 75. Vernal extension with short-shoots of various forms (condition on April 30). a. *alba Hammondi*; b. *microphylla*; c. *roseovariegata*; d. *rhodostachys*; e. *elegantissima*; f. *aurea*.

Fig. 76. Diagram of the intercalary growth with 3 long-shoots, measured by the length of the internodes (in mm. on the ordinate), number of the internodes on the abscissa.

Fig. 77. Flowering-twig with buds in various stages of development. Median longitudinal section; pr. = prophyllum; br. = bracts; s. = sepalum; c. = corolla; l. = stem-leaf; sp. = spur of the same.

Fig. 78. Median section through a lateral axillary bud in winter (Jan. 5).

Fig. 79. Median section through the top-part of a long-shoot, before the flower-primordia can be recognized (early June).

Fig. 80. Transverse section across the terminal main vegetation-point of a short-shoot.

Fig. 81. Transverse section across a flower-origin, directly after the formation of a pair of bracts (Stage I).

Fig. 82. Transverse section across a flower-origin, after differentiation of the four sepal-primordia (Stage II).

Fig. 83. Median section through a flower-origin, after formation of the primordia of sepals and corolla-tips; those of the stamens can already be distinguished (Stage III).

Fig. 84. Like the preceding one, but a little later; the corolla-tip primordia already somewhat bigger.

Fig. 85. Median section through a flower-bud, after formation of the stigma-primordium; the tops of the sepals have met (Stage V).

Fig. 86. Cross-section through a flower-origin with the corolla-tip primordia formed; those of the stamens were hardly visible here (Stage III).

Fig. 87. Cross-section through a flower-origin with 8 stamen-primordia, placed in a whorl (Stage IV).

Fig. 88. Median section through an already closed flower-bud, at the moment the corolla-tips begin to vault over the stigma, the stamens have lagged behind (Stage VI).

Fig. 89. Median section through a flower-bud after origination of the anther-primordia and of the style-duct (Stage VII).

Fig. 90. Median section through a flower-bud with incipient placenta and anther-spurs.

Fig. 91. Median section through a flower-bud of 1 mm diameter; the sepals have developed and become tinted, the bracts diverge and the bud has lengthened considerably.

Fig. 92. Cross-section through a flower-bud in Stage VI. Here the bud stands at the end of a short-shoot with several leaves. The obdiplostemony can be seen from the quadrilocular fruit-origin.

Fig. 93—94. Longitudinal sections through flower-buds in Stages IX and X (full-grown); the levels of the transverse sections of Figs. 95—100 are indicated. In Stage X the filaments are crooked (S-shaped) and the anther-spurs fully developed; often the anthers have already opened before the anthesis.

Fig. 95—100. Somewhat schematized transverse sections through flower-buds, showing the situation of the parts. Fig. 96 and 98 refer to two differently built buds, the level of the section being about the same. In Fig. 98 the level has been hit where the corolla-tips happen to be still coalesced, 3 pairs of bracts are present here instead of 2. The rest follows from the figures.

Fig. 101. Map of the main area of Calluna in Europe and its distribution in adjacent regions.

Fig. 102. Distribution of Calluna in North America.

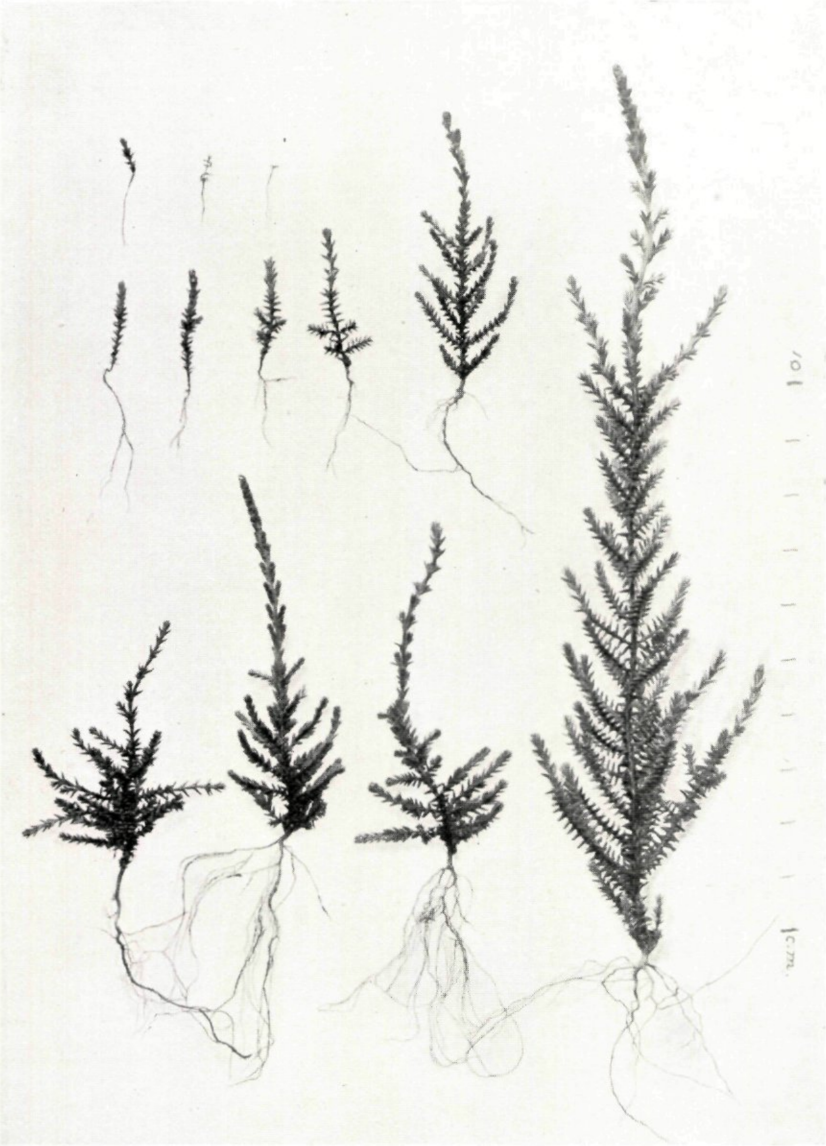
Fig. 103—118. Polymorphism of the Calluna flower and its bracts; 103, fa. *terminalis*; 104, var. *genuina*, type; 105 and 106, fa. *multibracteata*, subfa. *torta*, packets of bracts; 107—108, fa. *multibracteata* with decussately placed bracts; 109, fa. *multibracteata*, subfa. *pentamera*; 110—111, fa. *multibracteata*, subfa. *pentamera*, with partly spirally placed bracts; 112—118 different types of the packets of bracts with fa. *multibracteata*.

Fig. 119—139. Further polymorphism of the Calluna flower. 119, fa. *polysepala*, subf. *gemmata*; 120, fa. *polysepala*, type; 121, fa. *polysepala*, subf. *pilulifera*; 122—123, fa. *polysepala*, subf. *conica*; 124—125, fa. *polypetala*; 126, fa. *plena*; 127, fa. *diplocalyx*; 128—129 subf. *polystyla*; 130, fa. *gynodioica*, subf. *simplicissima*; 131 and 139 fa. *clistanthes*; 132, fa. *grandiflora*; 133, fa. *parviflora*; 134, fa. *brachysepala*, subf. *microsepala*; 135, fa. *brachysepala*; 136, fa. *campanulata*; 137—138, fa. *gynodioica*.

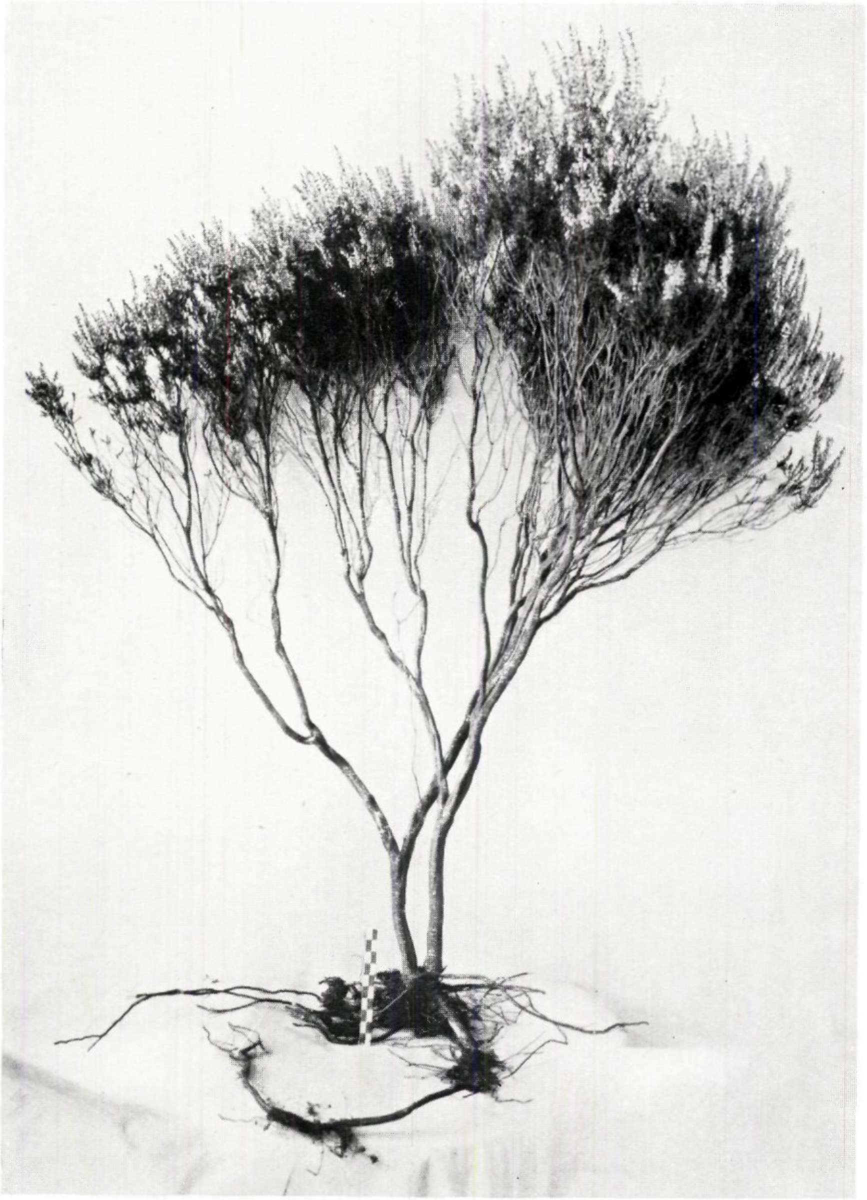
Fig. 140. Picture of "Erice" (= *Calluna vulgaris*), from the herbal of Leonhard Fuchs, entitled: "De historia stirpium commentarii insignes, maximis impensis et vigiliis elaborati, adjectis earundem vivis plusquam quingentis imaginibus, nunquam antea ad naturæ imitationem arteficiosius effectis & expressis, Leonharto Fuchsio medico hac nostra ætate longê clarissimo, autore." Basiliæ, in officina Isingriniana, 1542.

Fig. 141. Map, showing the situation of the principal heath-reserves in N.W. Europe. For a nearer explanation of the numbers see page 156.

PLATE I.



Stages in the development of Calluna from the young seedling with two cotyledons until the two-year-old, not yet flowering plant.



Old Calluna plant, about 1 m high, with trunk-like stem.

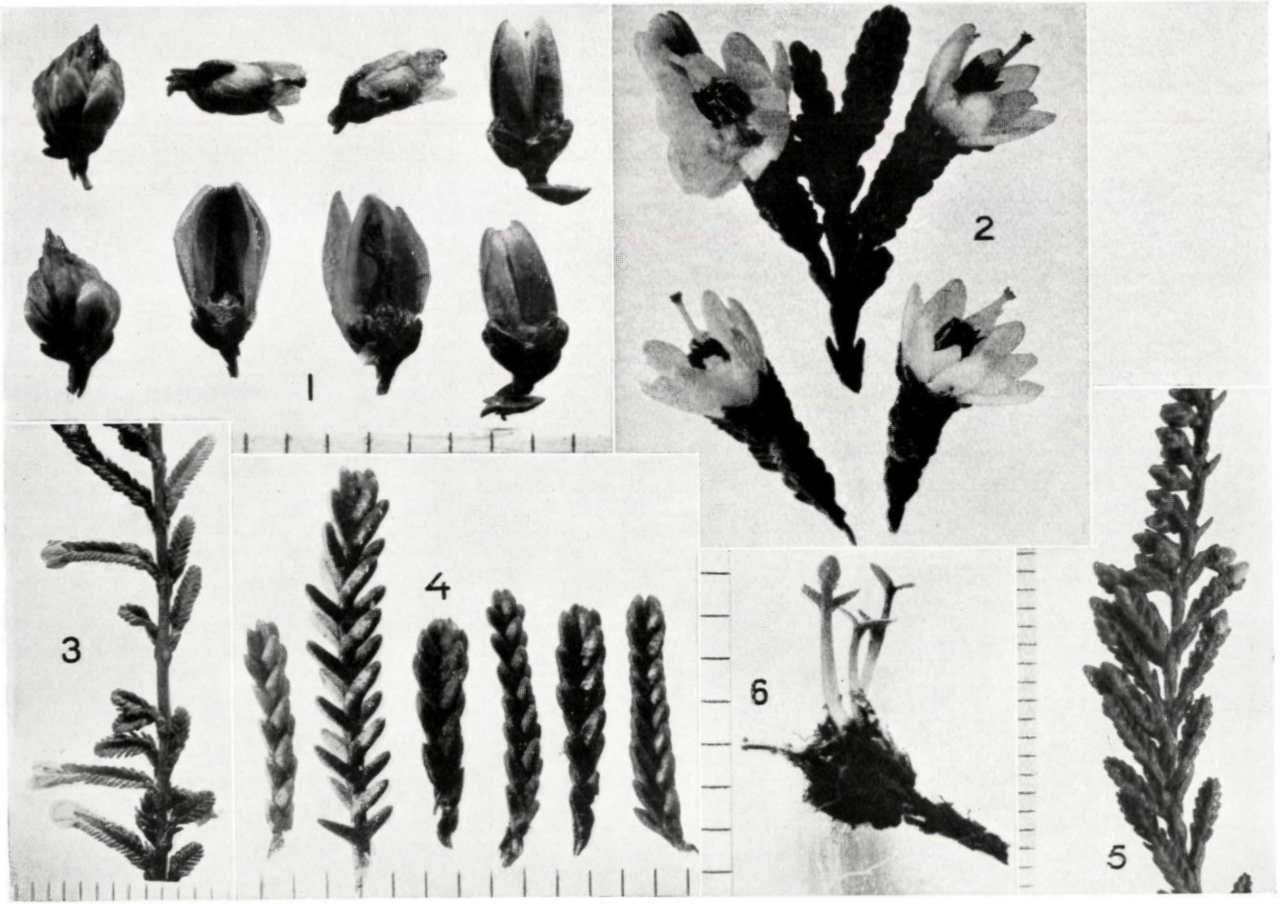
PLATE III.

1. Burnt down Calluna plant, which within six months flowered again with adventitious shoots. 2. Richly ramified annual shoot with side-shoots of the 4th order (at a); b: winter-bud. 3. Well-developed annual shoots, 46 and 43 cm long respectively (b: winter-buds).

PLATE IV.

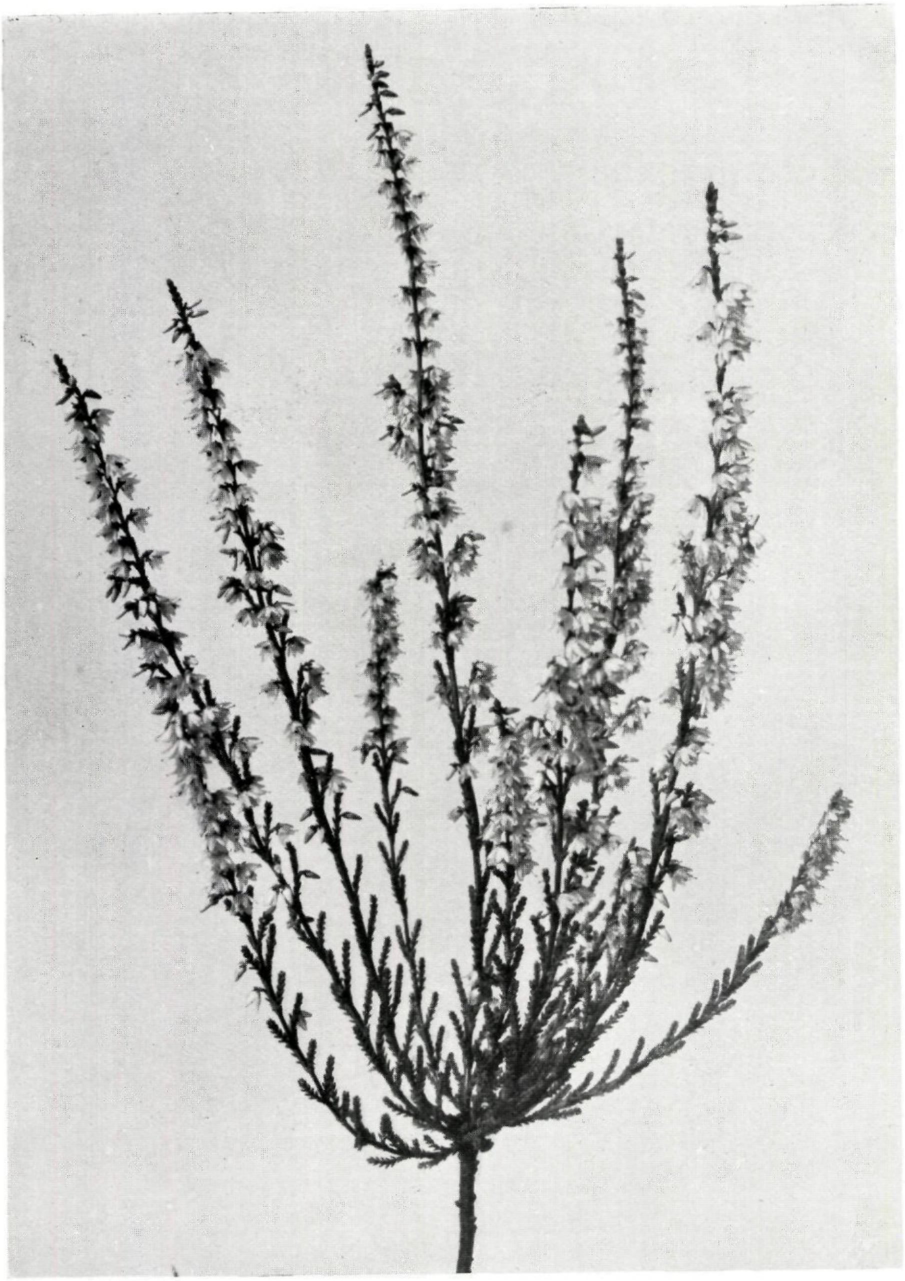
1. Formation of adventitious roots from perennial, up to ± 10 years old frame-branches. 2. a. Polysepalous flower, expanded and closed (below). b. Bud-flower of fa. *diplocalyx*, with bayonet-shaped style. c. Pentamerous flowers of fa. *multibracteata*. 3. Fa. *polysepala* with big filled flowers. 4. Fasciated branches of the fa. *decumbens*, subf. *fasciata*.

PLATE V.



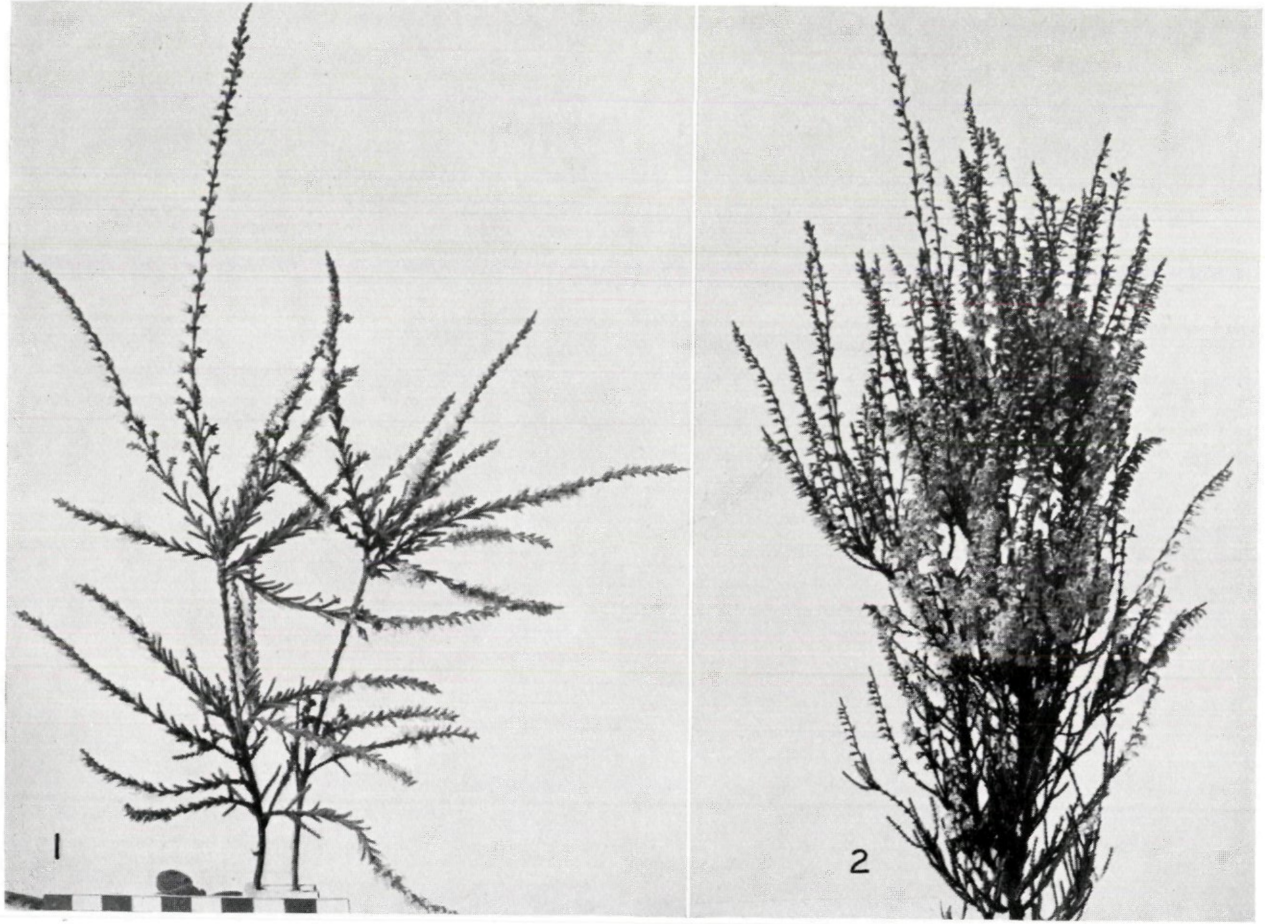
1. To the left: two flowers of fa. *polysepala*, subf. *conica*; to the right: two flowers of fa. *polysepala*, subf. *subplena*: centre, above: two flowers of fa. *brachysepala*, subf. *microsepala*; centre, below: two flowers of fa. *diplocalyx*, subf. *polystyla*. 2. Hexamerous flowers of fa. *multibracteata*. 3. Fa. *multibracteata* with many bracts. 4. Winter-condition of the short-shoots on different Calluna plants. 5. Fa. *terminalis*. 6. Dropped fruit with seedlings, germinated from it.

a. Fa. *grandiflora*; b. Fa. *parviflora*. c. Fa. *brachysepala*.



Typical flowering-twigs of var. *genuina* Regel.

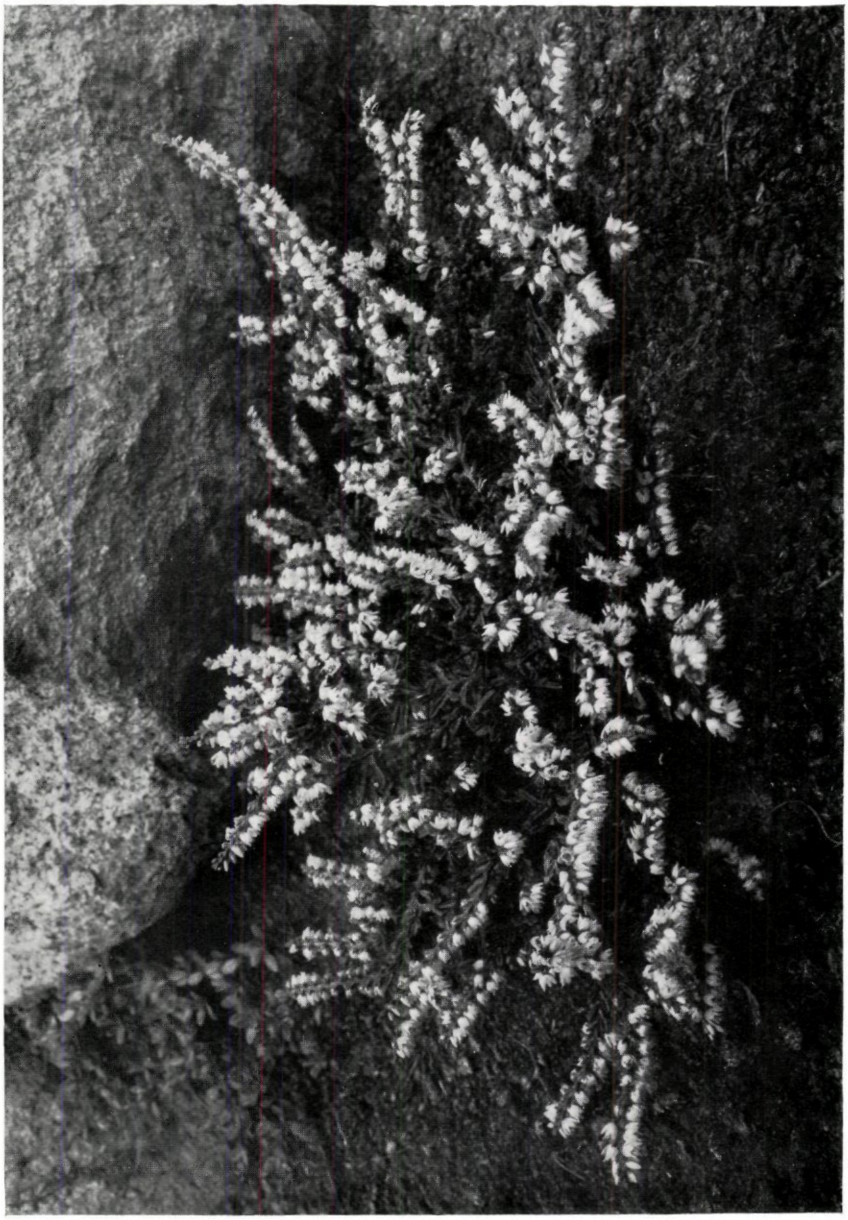
PLATE VIII.



1. Forma *patula*. 2. Forma *erecta*.

PLATE IX.

1. Forma *decumbens*. 2. Forma *nana*, subf. *compacta* (photo A. DE WEVER).



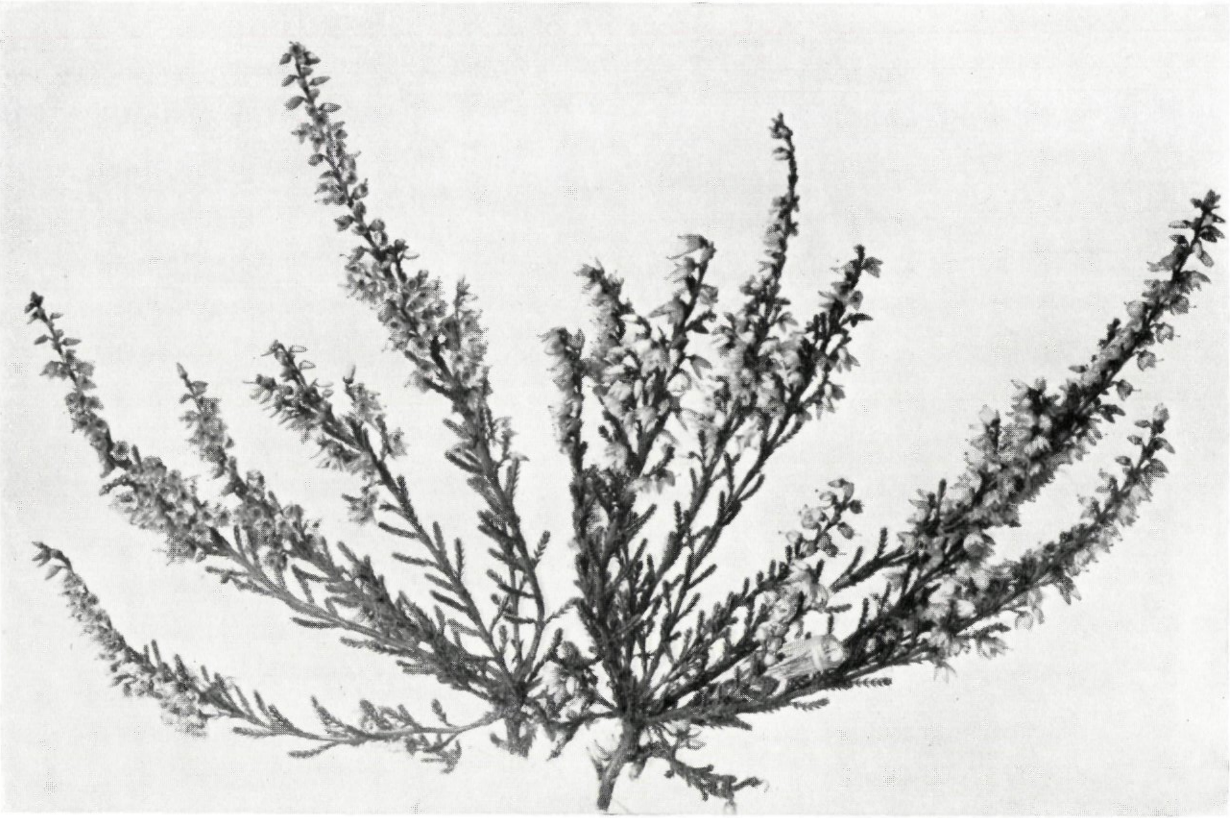
Forma *rigida.*

PLATE XI.

Forma *decumbens,* subf. *pendula,* before blooming.

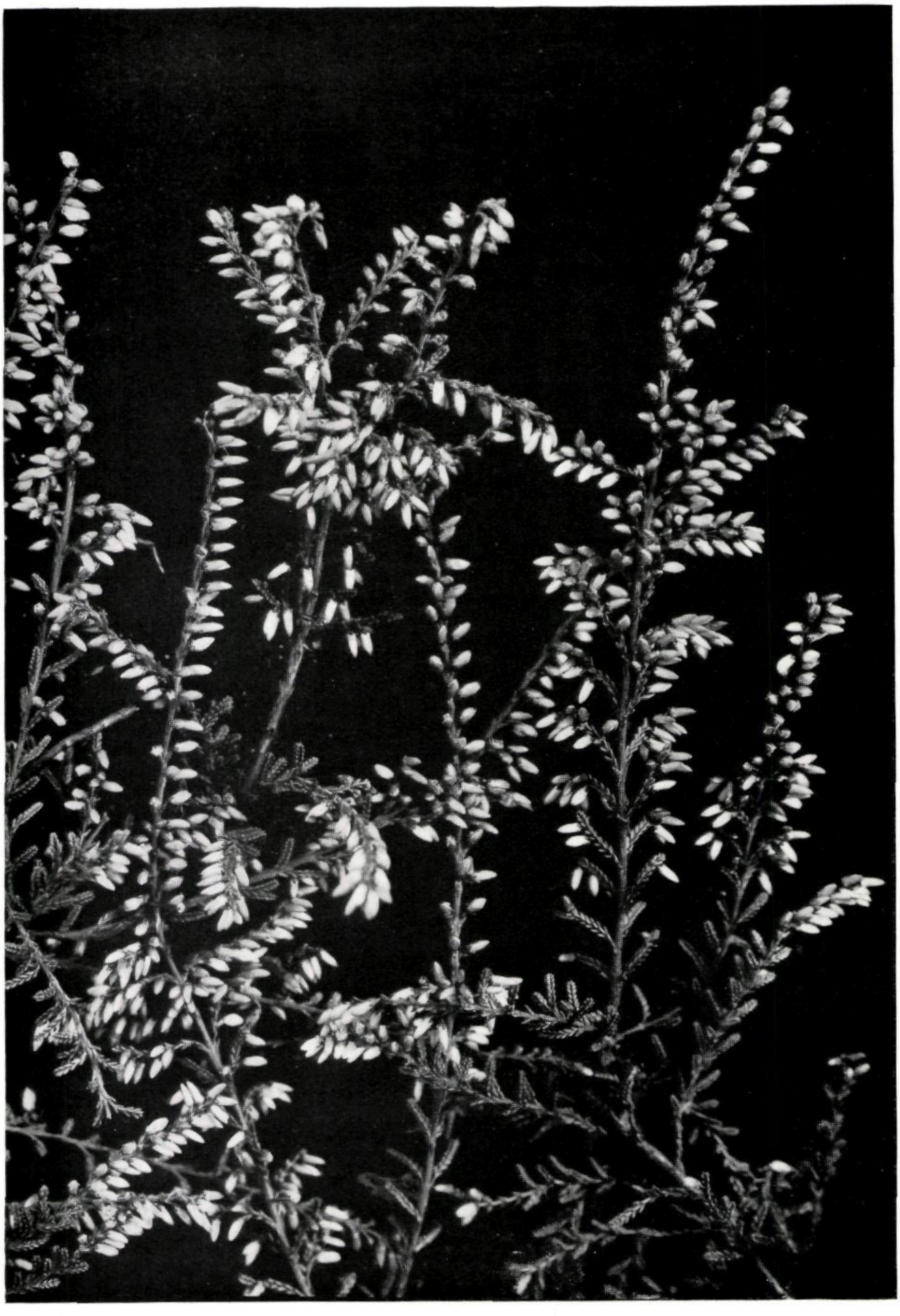
Forma *decumbens*, subf. *pendula*, in bloom.

PLATE XIII.



Flowering-twigs with terminal flower, which sometimes is actinomorphic.

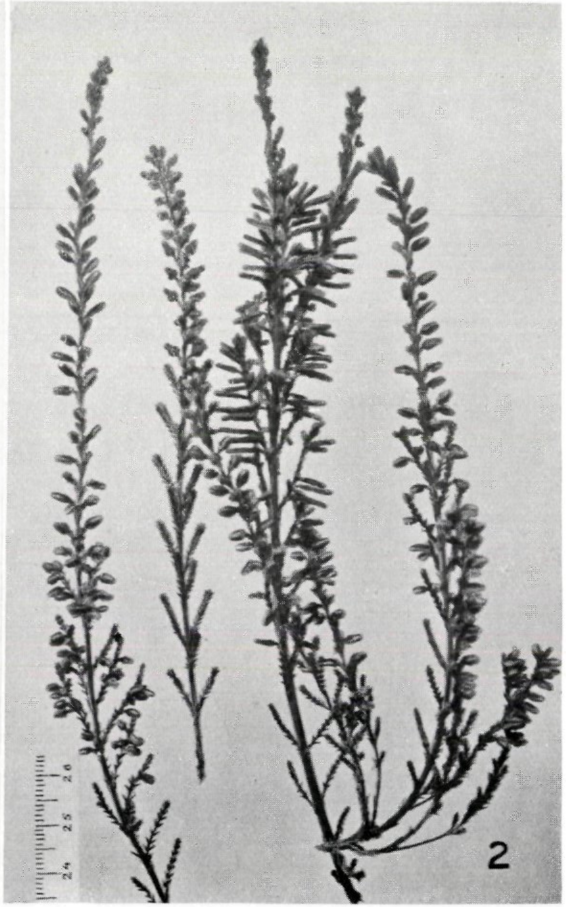
Fa. *decumbens* with less compact growth (photo A. DE WEVER).



Fa. *diplocalyx*, with non-expanding bud-flowers (photo A. DE WEVER).

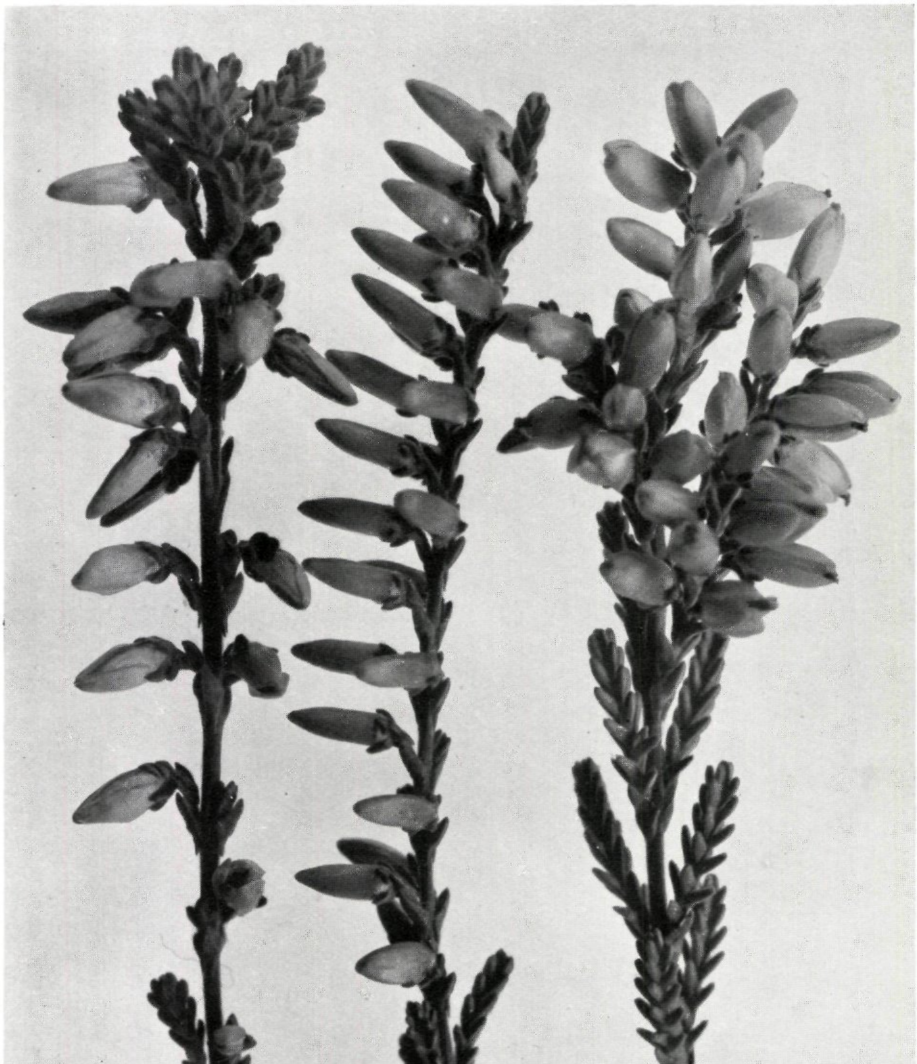
PLATE XVI.


1

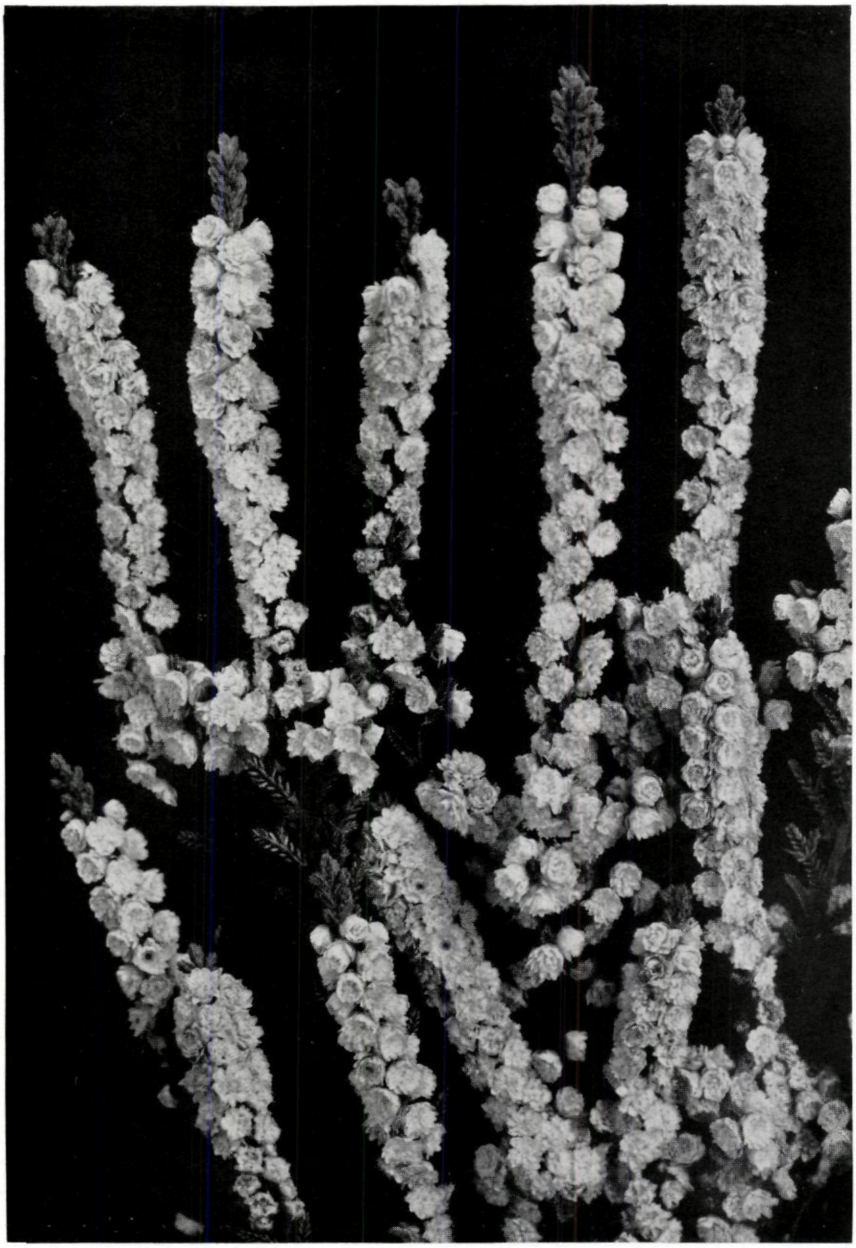

2

1. Fa. *multibracteata*. The two outer ones in bud, the inner ones both subf. *deflorata*, with short packets of bracts.

2. Fa. *multibracteata*, subf. *deflorata*, with various types of packets of bracts.

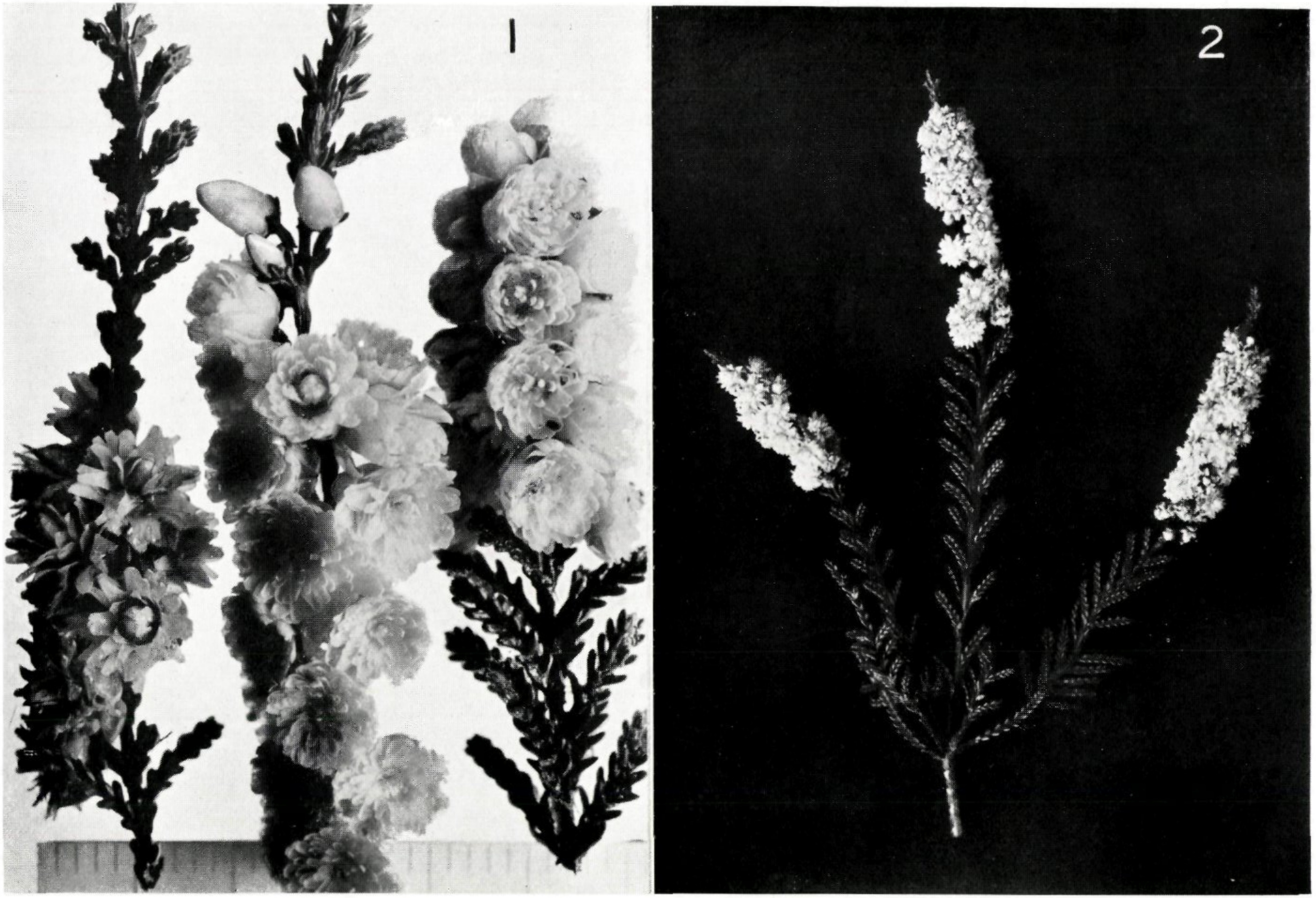


To the left: fa. *clistanthes*, with closed bud-flowers; centre: fa. *diplocalyx*, with closed bud-flowers; to the right: fa. *diplocalyx*, subf. *fertilis*, with slightly opened bud-flowers and exposed stigma.



Var. *hirsuta*, fa. *Bealeae*, with filled, closely set flowers (photo A. DE WEVER).

PLATE XIX.



1. Var. *genuina*, fa. *polypetala*. To the left: type. Centre: subf. *lilacina*; to the right: subf. *rosea*. 2. Var. *genuina*, fa. *polypetala*, type (photo A. DE WEVER).

Fa. *plena*, with the sepals as well as the corolla tips multiplied.

PLATE XXI.

Different tomentous types of the var. *hirsuta* GRAY.

PLATE XXII.

1. Var. *hirsuta*, fa. *pallens*. 2. Seed-bed with one year old slip-plants of Calluna forms, in the garden of the Biological Station at Wijster.

Calluna-plants on bare soil, standing free, near Denekamp, the Netherlands (photo W. H. DINGELDEIN).

PLATE XXIV.

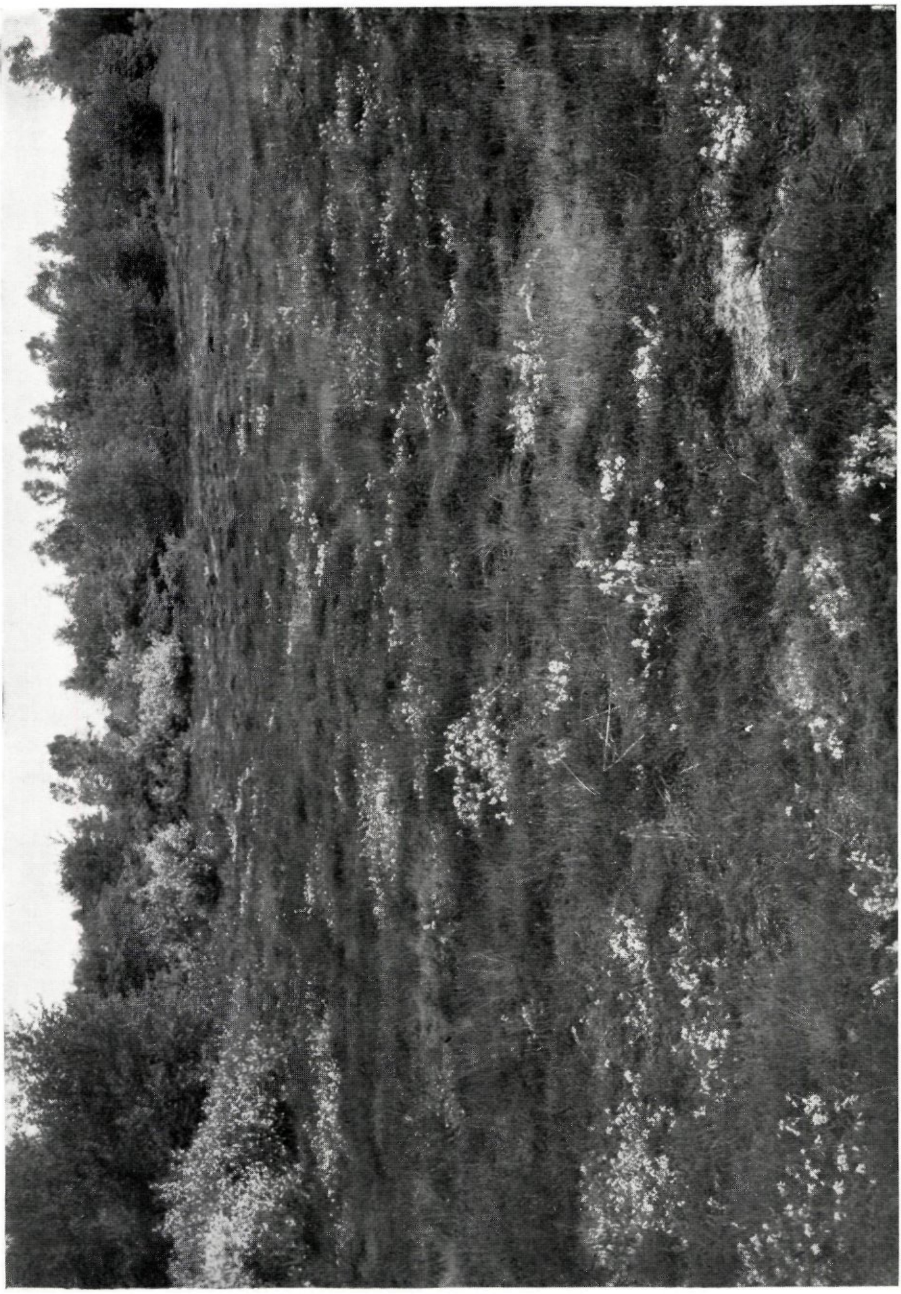
Old Calluna-vegetation with hardly any admixture of other phanerogamous species (Wijster, Dr., the Netherlands).

PLATE XXV.

Old Calluna-vegetation with an undergrowth of much *Cladonia rangeferina.* Young plants shoot up between the dead clumps.

PLATE XXVI.

Extensive Calluna-heath of about 15 square kilometers. View on the Dwingeloo Heath; partly nature-reserve.



Young Calluna-heath with much *Genista pilosa* (in bloom), near Denekamp (photo W. H. DINGELDEIN).

Calluna in drift-sand as a dune-former (photo A. DE WEVER).

PLATE XXIX.

Calluna-heath with much *Empetrum nigrum* and *Juniperus communis* (State Nature-reserve Lheebroeker Zand near Dwingeloo, the Netherlands).