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LIC. PHIL., MLM

LUND 1922, BERLINGSKA BOKTRYCKERIET



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BY DUE PERMISSION OF THE PHILOSOPHICAL FACULTY OF THE UNIVERSITY OF LUND
TO BE PUBLICLY DEFENDED IN THE BOTANICAL AUDITORY,
DECEMBER 13, 1922, AT 10 O'CLOCK,
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LUND 1922, BERLINGSKA BOKTRYCKERIET

THE GENOTYPICAL RESPONSE OF THE PLANT SPECIES TO THE HABITAT

BY GÖTE TURESSON

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THE study of the variability of the plant species in relation to its environment, or its habitat, might be pursued along two lines of research, viz. the study of the effect of various environmental factors upon the individual plant, and the study of the effect of these environmental factors upon the genotypical composition of a species-population in a certain habitat. The one line of research is primarily a study of the modifications of the plant, the other is manifestly a study of the hereditary variations. The two groups of variation have long ago been dealt with from the point of view of the environment, but while the experimental study of the former problem has received much attention the latter problem, the hereditary variation of wild plants in relation to habitat, has remained experimentally almost unattacked.

The classical transplantation experiments with Lowland plants in Alpine situations performed by KERNER (1891) and BONNIER (1895) belong to the important body of facts relating to the modifications of plants. The modern study of the problem is particularly connected with the names of KLEBS (1903, 1906) and GOEBEL (1908, 1913). Our knowledge of the power of modification, or rather of the range of possible reactions, of the plant when exposed to different environmental factors has been greatly increased by all this work. Its important bearing upon other lines of studies has also been felt, and the data obtained through the experimental inquiries into this field have been extensively employed when attempts have been made to throw light upon less known subjects, especially in the field of ecology. This is particularly true of the cases in which the supporters of the theory of the inheritance of acquired characters endeavour to find new support for the theory in the increasing mass of data obtained (WARMING, 1909, p. 373; WIESNER, 1913, p. 314). That the fact of the great »plasticity» of the plant has led to undue generalizations even in matters of a less speculative nature will be evident from

the following instances, which also serve to bring out the necessity of a closer study of the hereditary variation in relation to habitat.

MASSART (1902), in his well known paper on the modifications of *Polygonum amphibium*, shows that the plant in question might be readily modified into a land form, a water form and a dune form by exposing cultures from one and the same individual to the proper environmental conditions. He then concludes that the three similar forms of this species found in nature are simply modifications of this kind brought about by direct hydromorphosis and aeromorphosis. It is clear, however, that the experiment does not prove anything of the sort. There may exist genotypical differences in the three forms, as found in nature, which would play an important part ecologically. Extensive work — including cultivations under the same conditions of a great number of individuals of the plant, collected in different habitats in nature, and preferably supplemented by breeding experiments — is necessary in order to settle the point. A similar generalization of facts, to give another example, has been made by SCHMIDT (1899). He finds that *Lathyrus maritimus* from the coasts of the Baltic differs in the anatomical structure of its leaves (these being dorsiventral) from the *L. maritimus* found along the North Sea coast of Denmark (which has isolateral leaves). Subsequent experiments with the former plant showed that watering with solutions of sodium chloride induced a leaf structure (viz. isolaterality) typical of the North Sea plant. He concludes that it is to be assumed that the direct effect of the sodium chloride, which is found in a higher percentage in the North Sea than in the Baltic, produces the North Sea type. It is at once seen that this is a generalization of facts similar to that criticised above. It is a generalization of about the same order as the statement that any white flowering *Primula sinensis* has been produced by the cultivation of normal, red flowering *Primula sinensis* at 30° C. Even if it is true that red flowering *P. sinensis* becomes white when cultivated at 30° C it is equally true that there exist hereditary, white *P. sinensis* forms (BAUR, 1914), e. g. white-flowering at a temperature at which the former plant has red flowers (viz. at 20° C).

Thus in the absence of critical acquaintance with the different forms of a plant species met with in nature, much speculation as to the origin of «adaptive» structures is to be found in writings on ecology. The following discussion includes a number of notorious adaptive forms, and an attempt is made to ascertain whether the existence in nature of such forms is the result of an advantageous response on the

part of the individual, or whether these forms are brought into existence through a genotypical response of the species-population to definite habitat conditions.

Before going into details I wish to express my gratitude for the help received from so many sources during my work. The nature of the work necessitated considerable space. Professor H. NILSSON-ENLE, head of this Institute, has not only put the resources of the institute at my disposal; but to him I am also indebted for much inspiring advice given freely during the progress of this study. The necessary green-house space as well as other facilities have been kindly provided for me by Professor S. MURBECK, head of the Botanical Museum and Garden in Lund, who has taken much interest in my work. I also take this opportunity of acknowledging my indebtedness to Professor H. KYLIN, head of the Botanical Laboratory in Lund, for his kindness in promoting these studies in different ways.

The collecting of the various plants in cultivation, discussed in the following, has been done chiefly by myself on journeys some of which have been rendered possible through economical support from the Physiographical Society and the Botanical Club of Lund. However, material of certain forms has also been supplied by friends interested in my work and to them I wish to extend my sincerest thanks for all their kindness. I am under obligation to Messrs. N. STENSSON, and K. B. KRISTOFFERSON, for the necessary photographic work.

I. THE MATERIAL AND THE CULTURES.

Transplantations on a small scale were begun in 1916. At that time isolations were also made of species of the genus *Atriplex*. The necessary ground for these cultures was obtained in my home garden in Malmö. With the increase in the number of cultivated species and in the number of individuals of each species the space became too small, and in 1918 the cultures were moved to the Institute of Genetics at Åkarp. Since then the cultures have much increased; the area covered by individuals of perennials transplanted from various habitats is at present about 25 ares. The soil is a fine loam, and the conditions of the ground show satisfactory uniformity throughout. In order to maintain this uniformity no animal manure is used. The plants in the permanent cultures (that is the perennials) are planted in rows, usually with a distance of 40 cm. between the plants in the row and of 50 cm. between the rows. The more bulky ones are given

distances of 50×60 cm. Each plant has then space enough to increase in size, and the cultivation with tools between the plants becomes easy. The cultures are kept free from weeds and are dug twice a year, in spring and in autumn. Among the species cultivated, only *Leontodon autumnalis* has been found to thrive less satisfactorily. The individuals of this species sometimes suffer badly from the attacks of cutworms (*Agrotis* spp.?) on the roots. A certain type of *Hieracium umbellatum*, viz. the broad-leaved sea-cliff type, is particularly damaged and greedily eaten by rabbits, which has necessitated the fencing of the field.

A few words should be said as to the kind of species used and as to the mode of collecting. It is clear from the nature of the study that only such species have been investigated as are very common and occur in different habitats. Such species are, for instance, *Lysimachia vulgaris*, *Centaurea jacea*, *Solanum Dulcamara*, *Matricaria inodora*, etc. It is further to be expected that if changes in the genotypical composition of a species result in response to climatic or edaphic factors these changes would be most clearly brought out and most easily demonstrated in species which have an extended and uninterrupted distribution running through areas of different climatic and edaphic character. The coast line of southern Sweden, to which region most of the species dealt with in the following are to be referred, is well suited for investigations of this kind. There are marked climatic differences between the east coast and west coast, the latter being more maritime and exposed to the action of strong winds and atmospheric sodium chloride (cf. FRÖDIN, 1912), and the physiographical features of the coast lines vary much, cliffs, dunes and salt marshes alternating. There are plant species which occur throughout this varied stretch of land, and some of these, viz. species of the genus *Atriplex*, *Armeria vulgaris*, *Hieracium umbellatum*, have been found to furnish important data and have therefore been transplanted and cultivated on a large scale.

In the collecting, the individuals of a species from a certain habitat are carefully dug up, care being taken that no selection is made; they are then numbered and packed in sacks and posted. They are immediately planted in the experimental field on arriving. In planting as much soil as possible is removed from the roots. When just planted they are watered once or twice and then left. When treated in this way, only very few of the plants are spoiled and die.

In regard to the notes and measurements of the different cultures discussed in the following it should be said that the values given in

the *Hieracium* tables (placed at the end of the chapter) for the length and width of the middle leaves are average values based upon the measurements of five leaves of each plant. The values given in the same tables of the magnitude of the angles formed by the stem with the perpendicular refer to the angles of the largest stem of the individual. These values have by tests been found to deviate ± 5 degrees from the correct value. Field numbers preceded by one or more 0 indicate that a corresponding number of individuals have died and left gaps in the row. It has been found practical to use this method in checking the individuals. A — in the table columns indicates that measurements or notes have not been taken because of the wilted conditions of the leaves or of the whole plant (or because of damage by rabbits in some cases).

The cross-sections made of different leaves have for technical reasons been collected at the end of the *Hieracium* chapter.

The terminology followed in discussing the distribution of various shore species in the different zones of the shore is that worked out by SERNANDER (1917).

In arranging the material it has been thought best to group it under seven headings, the first four containing the results of the cultivations of shade forms, dwarfs, succulent shore forms of inland species, and halophytes, and the last three containing the data for inland and coast forms of *Sedum maximum*, *Armeria vulgaris* and *Hieracium umbellatum* respectively. The general discussion of the results and the bearing upon the problem which these results imply will then follow.

1. MATERIAL AND CULTURES OF SHADE FORMS OF MESOPHYTIC SPECIES.

A great number of mesophytes are known to develop shade forms in response to subdued light, and the morphological and anatomical changes brought about in such forms, especially in the leaves, are well known. The further question, whether or not all shade forms occurring in nature are shade-modified open air plants, or whether hereditary shade varieties also exist within certain species, has received but little attention. The cultures made in order to settle this point cannot yet be said to be conclusive, since no crossings have been made, but they are calculated to throw some light on the problem. The plants employed are *Lysimachia vulgaris* L., *L. nummularia* L. and *Dactylis glomerata* L.

A. *LYSIMACHIA VULGARIS*.

The extreme shade form of this plant has been found most typically in the moist *Alnus* swamps of Hallands Väderö. The habitus of the shade form differs markedly from the ordinary form, as has already been pointed out, although rather incompletely, by GLÜCK (1911). The stems of the shade form are thin and slack, and, in their upper half, horizontally expanded. The leaves stand horizontally and almost in one plane; they are considerably larger than in the ordinary form but very much thinner. Flowers are rare.

A dozen of these plants, collected in different spots within the swamp area, were brought home in 1920. By the following year (1921) the habitus of these plants was already changed and corresponded now in all essentials with the ordinary form. The changes brought about in the culture are best followed in regard to the leaf structure. Fig. 75 a (p. 329) represents a cross section of a leaf of the shade form. They were found to be between 123—157 μ . thick and did not have any typical palisade layer. The figure to the left is a cross section of a leaf of the same plant from the culture in 1921. The leaf thickness was now found to vary between 358—368 μ ., and powerful palisades in two layers are found throughout. The anatomical leaf structure as well as the habitus of the separate plants belonging to this series do not at present exhibit any observable differences from sets of the ordinary form brought home and transplanted from the beach at Ringsjön (middle part of Scania) in 1920.

It should not be thought that *Lysimachia vulgaris* might not be found to show hereditary shade forms, but the evidence adduced above points to the fact that the Hallands Väderö shade form is merely a shade modification of the ordinary form.

B. *LYSIMACHIA NUMMULARIA*.

Series of this plant were collected and brought home from various points in Scania in 1920. The cultivated material thus includes series from moist pastures at Åkarp, from similar habitats in the neighbourhood of Malmö, and from the woods south of Kivik (on the east coast of the province of Scania). The latter locality is heavily wooded with oak, elm, Norway maple, ash and linden, while the former localities consist of open, grassy, and somewhat moist pastures. Careful examination reveals differences between the pasture *nummularia* and the

plant from the woods. The latter has somewhat larger leaves than the former; they are further convexly bent and of a deep green colour in the woods, while the leaves of the pasture plant are somewhat concave and light green in colour.

The separate plants of the pasture series cannot be seen to differ from each other in culture. The series from the Kivik woods, in all 16 individuals, cultivated at the side of the former does not show any



Fig. 1. *Lysimachia nummularia*. Forest type (the upper) and pasture type.

observable variation within the series either. It is a remarkable fact that the Kivik *nummularia* retains its distinctive marks in culture. The small pieces of turf originally brought home have increased in size ten-fold without showing any tendency to lose their characteristics. Clones raised in 1922 from cuttings from both the pasture and the forest *nummularia* likewise retain the characteristics of the respective mother plants. Fig. 1 represents pieces of the two plants taken from the clone cultures in 1922. The differences between the pasture plant and the plant of the woods as to the leaves are at once seen. Cross

sections of leaves from these cultivated plants show much the same structure (both forms having one layer of palisades), but the cuticle of the upper epidermis is found to be thicker throughout in the cultures of the pasture plant than in those of the plant from the woods. Repeated measurements have given a mean value of 7.8μ for the former and 5.6μ for the latter. The outer wall of the lower epidermis is also thicker in the former than in the latter, especially in places below the vascular bundles, where it attains a considerable thickness and becomes much folded. Thus the results of the cultivations point strongly to the assumption that there are in Sweden at least two hereditary types of this species, the one growing in meadows and pastures, the other in the woods. The differences in the leaves show that the latter is manifestly a shade plant as compared with the former.

DAHLGREN (1922 a) has recently traced the distribution of *L. nummularia* in Sweden and pointed out that the plant has to a large extent been spread by human agency. It remains to be settled whether the above described shade type from the woods is native in our country, while the type from the meadows and pastures is introduced and spread through man, a view, which might be an approximation to the truth. A further point of interest will be afforded by the crossing-experiments between the two types to be started a following year. The experiments made by DAHLGREN (1922 b) have shown that plants from widely different parts in Sweden are sterile when crossed with each other, while fruit develops when Swedish plants are crossed with German and Austrian specimens. It seems reasonable to assume that the failure in the case of the crossings where Swedish material was exclusively used was due to the fact that the plants were members of the same clone, in this case probably the pasture *nummularia*, as this type has no doubt the largest distribution in the country.

It should perhaps be said that the shade variety of *L. nummularia*, discussed above, has not been found described in the literature. DOMIN (1904), who lists a number of forms of the species, does not mention any such form.

C. DACTYLIS GLOMERATA.

A shade form of this grass is known to systematists under the name *D. glomerata* var. *lobata* Drej. It occurs in the beech woods of southernmost Sweden, as well as in Denmark, and differs from the

ordinary type in having culms taller and slacker and loosely tufted, long, drooping and dark or light green leaves, slack, long and somewhat drooping, never violet-coloured, panicles, smaller spikelets, and smooth flowering scales. Sets of this form have been collected and transplanted from Denmark (near Copenhagen) in 1919 (17 individuals), and from Dalby in Scania in 1921 (16 individuals). The changes brought about in the cultivated shade form as compared with the plants in their natural habitat are the following. The culms become more tufted, although the tuftiness of the main type is not attained. Both leaves and the panicles become brightly violet-coloured, and more so than is generally seen in the main type. The thickness of the leaves increases. The mean thickness of the basal leaves of two individuals from the Dalby series was found to be 135–155 μ , and 140–150 μ , in their natural habitat in 1921, while the mean leaf thickness of the same plants the following year (1922) in culture was found to be 150–175 μ , in the one plant and 165–185 μ , in the other. Whether the leaf thickness of the main type, the leaves of which are considerably thicker, has been attained in any of the plants of the Copenhagen series, which has been in culture since 1919, has not been ascertained with exactness, but to judge from superficial examination this is not yet the case.

The length of the culms as well as of the leaves has been found to increase in the cultures. The mean leaf length, for instance, in the Dalby series (measuring 10 of the longest basal leaves of each plant) was found to be 425 mm. in 1921, while it was 530 mm. in 1922. An increase in the length of the panicles has also been found to take place in culture.

The above results favour the assumption that *D. glomerata* var. *lobata* is a hereditary shade variety and not a modification due to the direct effect of the environment. Although undoubtedly certain characteristics ascribed to the form are the results of the extreme environment, as for instance the great looseness of the tuft and the pure green colour of the leaves and panicles, which characteristics disappear in culture, other characteristics, as the length of the leaves, culms and panicles, increase in magnitude upon cultivation. This would not be likely to take place had the plant in question developed its characteristics in direct response to subdued light.

The variation within the series is otherwise rather large. Fig. 2 represents the shape of the panicle in fruit from 4 individuals of the Copenhagen series. The same relation as to the degree of spreading

of the panicle is seen every year in these individuals, so there is little doubt as to the hereditary nature of the variations seen between the different plants. A few of the plants in the series have somewhat hairy flowering scales and should not be referred to var. *lobata* according to the diagnosis given of the form in the floristic handbooks. They correspond in all other respects, however, with the shade variety, and thus illustrate the difficulties — and perhaps the impossibility — with which the systematists are confronted in their efforts to draw



Fig. 2. *Dactylis glomerata*. Illustrating different shapes of panicle found within the shade type.

hard and fast lines between a certain variety and its supposed main type.

It should not be thought that modificatory shade forms of *D. glomerata* do not exist. Such forms are, on the contrary, recorded several times. They are often much like the var. *lobata*, although they are usually furnished with some hairs on the flowering scales. From what has been said above with regard to the occurrence of hairy scaled individuals whithin the hereditary shade variety it will at once be seen that the difficulty with regard to the separating of the modificatory

forms from the hereditary ones without cultivating the plants must be very great, or rather insurmountable.

2. MATERIAL AND CULTURES OF LOWLAND DWARF FORMS.

In our country dwarf forms are especially met with in Alpine habitats, in the so called Alvar vegetation and in the salt meadows along the coast. Representatives of the two former groups have been cultivated for too short a time to be considered here, and therefore only salt meadow dwarfs, already in culture for some years, will be discussed. The plants to be discussed at any length are *Aster tripolium* L., *Succisa pratensis* Moench, and *Centaurea jacea* L.

A. ASTER TRIPOLIUM.

A dwarf form of this plant is known to systematists under the name *A. tripolium* var. *diffusus* DC. It is a much branched plant, not more than 5 cm. high, and occurs in somewhat drier spots of the salt meadow than the ordinary, tall growing *tripolium*. A series of the form (in flower) was collected at Vellinge, south of Malmö, and transplanted in the autumn of 1919 together with a few rosettes of the ordinary form. The latter attained a height of between 45—70 cm. in 1920, then flowered, and died in the autumn. The dwarf, although flowering in 1919, lasted through the autumn and winter and flowered again 1920. The height of the 1919 plants varied between 3—5 cm. The plants grew taller in 1920, and the height now varied between 10—16 cm. They were found to fruit freely. Fruits were collected from one of the individuals; they were sown in the autumn, and the seedlings were forced in the green-house and transplanted into the open in May the following year. They all flowered in the autumn. Fig. 3 illustrates some of the resulting types in the series raised. The height of the plants in the series varies between 8—18 cm. There is great variation between the different individuals, especially in branching. The plant to the left in the fig. has a wholly prostrate main axis, the plant in the middle has a number of ascending, equivalent branches, while the plant to the right has an erect main axis and smaller, ascending side branches. The same characteristics of the different plants both as to height and branching are seen this year (1922). The same is true of the original dwarf's transplanted in 1919, which do not show any tendency to change the habitus attained in the culture 1920.

It seems therefore safe to conclude that the series in question is made up of hereditary dwarfs, which, at least in the experimental fields at Åkarp, are perennials, as distinct from the ordinary tall growing *A. tripolium*. Within the dwarf series, moreover, all kinds of branching types might be found just as in the ordinary form showing



Fig. 3. *Aster tripolium*. Hereditary dwarfs.

that certain characteristics vary as much in the dwarf variety as in the ordinary *tripolium*.

Modificatory dwarfs of *A. tripolium*, called forth by insufficient water and food supply, might also probably be

found in nature. As to modificatory perennials of *A. tripolium* the statement is made by BUCHENAU (1896) that the plant becomes perennial when eaten by animals or cut down. Both modificatory and hereditary dwarfs might be contained in the var. *diffusus* of the floristic handbooks. As to the latter group it should be noted that it is not the dwarf as seen in the culture which conforms to the var. *diffusus*; it is only the plant that results from a modificatory dwarfing of this dwarf in the natural habitat which fulfils the prescription given in the diagnosis.

B. SUCCISA PRATENSIS.

This species is rather common in the upper part of the salt meadows along the coast of Scania. It is usually dwarfed in these localities, and the most extreme form, which only attains a height of at most 85 mm., is known under the name f. *nana* Bolle. Series of this extreme dwarf were collected and transplanted from Torekov and Hallands Väderö (N. W. Scania) in 1919, and a set of the ordinary swamp plant, as found in the inland, was transplanted from Stehag (middle part of the province) in 1920. Table 1 lists some of these series (series 34 from Torekov, 35 from Hallands Väderö, 118 from Stehag) and gives the length (in mm.) of the longest flowering stem of each plant when transplanted and as found in 1921 and 1922.

Fig. 4 illustrates the habitus of the dwarfs used in the series 34 and 35. They have all increased in length under culture, as may be

seen from the table. The increase in the case of series 34 and 35 was greatest the year after the transplanting. The dwarf habit was at that time thought to be an unquestionable case of modificatory dwarfing, which would disappear in time. For this reason no measurements were made in 1920. In 1921 the height of the plants was surprisingly like that already attained the preceding year, and the suspi-

TABLE 1.

Field N:o	Length of stem when transpl.	Length of stem in 1921	Length of stem in 1922	Field N:o	Length of stem when transpl.	Length of stem in 1921	Length of stem in 1922
34,1	43	130	145	35,06	73	325	330
02	61	200	210	7	79	710	740
03	58	140	170	8	82	650	620
4	72	175	180	09	54	490	515
5	84	170	165	10	50	190	200
6	57	155	160	11	63	185	200
7	66	110	120	12	35	200	210
8	68	235	245	13	42	315	360
9	71	200	210	14	63	115	125
010	80	345	370	15	68	145	135
11	34	190	210	118,1	420	400	560
12	48	265	255	2	490	395	645
13	39	325	330	3	535	515	650
14	60	215	220	4	425	435	700
15	55	265	280	5	510	500	635
16	72	125	130	6	590	565	600
35,1	76	390	400	7	635	610	640
2	80	195	210	8	580	535	700
3	34	520	575	9	700	580	690
4	56	570	615	10	620	595	650
5	59	215	210				

cion arose that the variation seen in the series as to the height of the different individuals was of a hereditary nature. The different heights observed in 1921 do not fall much lower than those observed in 1922. As the summer of 1922 was considerably wetter than that of the preceding year the slight increase in the height of most of the individuals in 1922 is most probably due to differences in weather conditions.

It is further seen from the table that series no. 35 includes a

number of individuals much taller than any of those of series no. 34. It would be difficult to understand why this should be the case were



Fig. 4. *Succisa pratensis* f. *nana*. Plant to the left 10 cm. high. Torekov 1919.

it not that the genotypical constitution of the plants differed in the two series. When it is remembered that the series, as well as the different plants of each series, grow under almost identical conditions of culture, little doubt remains as to the hereditary nature of the differences

seen between the plants in these two series, as well as of the differences between these salt meadow series and the inland series (no. 118).

The differences in height between the plants in series nos. 34 and



Fig. 5. *Succisa pratensis*. Behaviour of a dwarf series (no. 35) when cultivated.

35 may probable be accounted for when the nature of the two original habitats is considered. No. 34 comes from a very sterile salt meadow, while no. 35 comes from a much less extreme salt meadow,

where species of the inland swamp (*Ranunculus flammula*, *Lycopus*, *Scutellaria*, *Caltha*, *Comarum* etc.) occur mixed with typical salt meadow plants (*Plantago maritimum*, *Glaur*, *Armeria*). The point in question will be discussed more fully in a following chapter.

Fig. 5 illustrates some of the different types now seen in the cultivated series no. 35. It should not be thought, however, that variation does not occur with regard to other characteristics. Differences between the plants are also seen in the matter of the hairiness of the leaves, in the shape of the leaf margin, in the shading of the blue flower colour, etc. These characteristics have been found to repeat themselves, in those plants observed, every year, and thus strengthen the belief in the hereditary nature of the characteristics in question.

In summarizing the results of the cultivations the following conclusions seem most reasonable. The hereditary variation in height becomes covered by the modificatory dwarfing of the plants when exposed to the more or less extreme conditions in the natural salt meadow habitat, resulting in a seemingly homogeneous population of dwarfs known under the name f. *nana*. When brought into culture, the population breaks up into its component parts, and the great hereditary variation as to height becomes visible. The fact that individuals, found upon culturing to be constitutionally as tall as those of the inland swamp population, are found to be contained in certain dwarf populations, while they are excluded from others, points to the controlling effect of the habitat factors upon the hereditary composition of the population.

C. CENTAUREA JACEA.

This species is also found growing in the salt meadows along the coast in a much dwarfed form, f. *humilis* Schrank., about 10 cm. high, or even less. Fig. 6 illustrates the general appearance of this dwarf as it is found growing at Vellinge. One of these Vellinge dwarfs was brought into culture as long ago as 1916. It increased in height the following year, and then measured about 35 cm. In 1918 it attained a height of about 50 cm., and has since kept this height, with slight fluctuations in response to the yearly fluctuations of weather conditions. The plant was divided in 1920, and fig. 7 represents an individual of the resulting clone. A dwarf transplanted in 1917 from Torekov behaved in a different way. It should be said that f. *humilis* grows abundantly at this place together with the dwarf *Succisa* dealt

with above. It is apparently the locality already mentioned by NEUMAN (1884) as densely populated by *Centaurea* dwarfs. The dwarf could not be seen to differ in any respect from the original Vellinge dwarf, but on cultivation a prostrate habit of growth was taken up. This plant was also divided in 1920, and fig. 8 represents one of the clonal individuals. This clone does not attain half the height attained in the Vellinge clone, and the tall, nearly erect form of the latter individuals contrasts sharply with the prostrate, spreading growth of the Torekov clone.

In the summer of 1919 the Torekov locality was visited once



Fig. 6. *Centaurea jacea* f. *humilis*. Plant in the upper left corner 12 cm. high. Vellinge 1916.

more and a larger collection of the dwarf was made, in order that the nature of the dwarf population might be studied more closely. The collection included 40 individuals, the majority of which, or 35, are thriving well. The behaviour of this population in culture has been found to be much the same as the *Succisa* population, series no. 35. Fig. 9 represents four of the types making up the population. The extremes,

the dwarf in the upper left corner with stems only 15 cm. long, and the ascending-erect plant in the lower right corner with stems 60 cm. long, are rare. The former type, shown in the photograph, is the only one present in the population, while there are four individuals attaining the height of the latter type. The intermediates, two of which are shown in the photograph (pag. 228), predominate. As to the position of the branches, individuals wholly prostrate are in the minority, while plants with procumbent and ascending branches predominate. None has been found to be quite erect. There are additional differences between the plants in this series, involving the hairi-

ness of the leaves, the position of the leaves (prostrate or ascending), the shape of the bracts, etc.

In order to make clear the genotypical constitution of the plant as to the form of growth, a cross was made in 1919 between the nearly erect Vellinge plant (fig. 7) and the spreading Torekov plant (fig. 8). The resulting F_1 was intermediate, none of the bastards obtained (12 in number) being as erect as the one parent, and none as prostrate as the other. Several of the F_1 -plants were crossed with each other (*C. jacea* is wholly self-sterile) but the fruits were found to be eaten by a larva and only one of the plants was found to have some intact fruits left. The 30 fruits sown gave 26 individuals, which were already brought to flower in 1921. They show segregation into 2 nearly erect, 20 intermediates and 4 spreading. Although this F_2 -generation is too small to allow of



Fig. 7. *Centaurea jacea*. Behaviour of Vellinge dwarf in culture.



Fig. 8. *Centaurea jacea*. Behaviour of Torekov dwarf in culture.

any factorial scheme, the segregation evidently involves several factors; it is mentioned here to show the hereditary nature of the characteristics in question. The cross has been repeated this year.

In summarizing the results of the cultivations it should be said that it might be safely assumed that the dwarf *C. jacea* f. *humilis* of the salt meadows is made up of a heterogeneous assemblage of most diverse, genetically different types. They all react upon the extreme habitat conditions with dwarf growth, thus giving the impression of a homogeneous population just as in the case of the dwarf *Succisa*. — The question whether or not the erect *Centaurea jacea* of

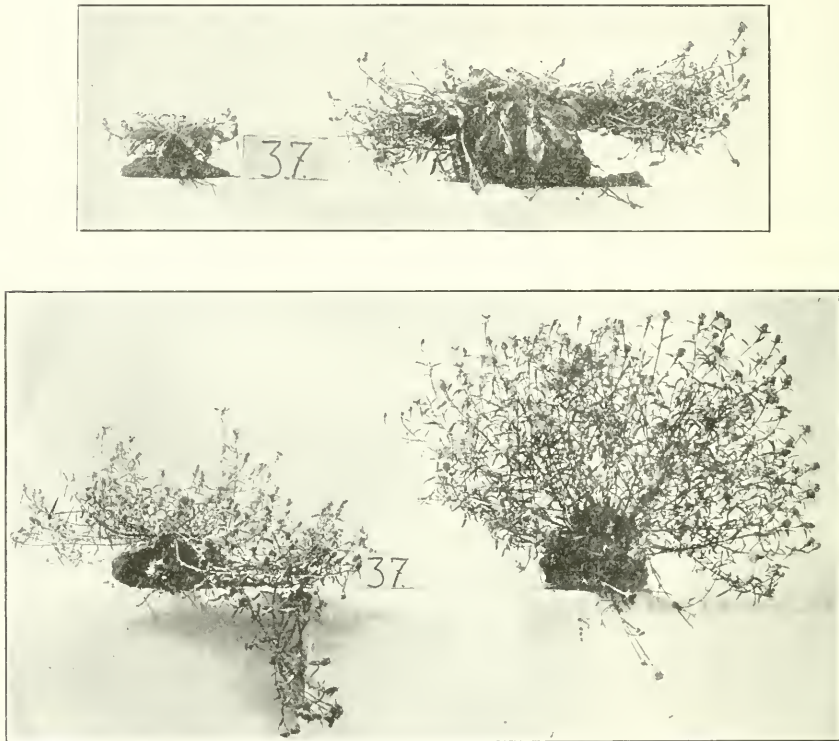


Fig. 9. *Centaurea jacea*. Behaviour of a dwarf series (no. 37) when cultivated.

the inland might in nature become modified to the same extent has not yet been investigated.

Additional dwarf forms, including those of *Veronica spicata* L. from sand dunes, *Achillea millefolium* L. from the same habitat, and *Prunella vulgaris* L. from salt meadows, have all upon culturing been found to be modifications presumably called forth by insufficient water and food supply in the respective habitats (Jost, 1913; Witte, 1906).

3. MATERIAL AND CULTURES OF SUCCULENT COAST FORMS OF MESOPHYTIC INLAND SPECIES.

It is well known from works on ecology that certain species are described as dimorphous (WARMING, 1909), showing a halophytic form with succulent, thick leaves, and an inland form with thin leaves. It is also known (BATALIN, 1876; LESAGE, 1890; BOODLE, 1904 etc.) that fleshiness, increased development of palisades, reduction of intercellular spaces, etc. might be readily induced in many species by watering with solutions of sodium chloride. From these facts it might seem plausible that the halophytic, succulent forms of ordinarily mesophytic, thin-leaved inland species have been called forth by the modificatory action of the salt on the plant when growing in saline soil.

In order to test to what extent such forms are merely modifications or hereditary, some species showing «dimorphism» in this characteristic were brought under culture. The species to be dealt with at some length in the following are *Solanum Dulcamara* L., *Matricaria inodora* L., *Leontodon autumnalis* L. and *Melandrium rubrum* (Weig.). Garcke.

A. SOLANUM DULCAMARA.

Sets of this widely distributed plant have been collected in the inland and at different points on the east and west coasts. The inland series (coll. at Krageholm, Scania 1919 and at Stehag, Scania 1920) include plants (20 in all) with smooth and rather thin leaves. Fig. 75 b illustrates the anatomical structure of the inland leaf type as seen in the cultures in 1922. The thickness of the middle leaves has been found to vary between 193 μ . and 245 μ . The sets from the east coast of Sweden (from Geta, 1920 and Västervik, 1920) include plants with both hairy and smooth leaves. The leaves of this type are usually somewhat thicker than the inland type both in the natural habitat and in the cultures. The most remarkable type, however, is the one that inhabits the west coast of Sweden. The leaves of this type are more than twice as thick as those of the inland type and always more or less hairy. It is found on the exposed, rocky shore (in the upper supralittoral belt) from north-western Scania and north-wards. A series of 16 plants of this type from Hallands Väderö was brought under culture in 1919. These 16 plants have all retained their hairy and fleshy leaves, although the fleshiness is somewhat less in the cultures than in the natural habitat. One of the plants with very thick

leaves, field no. 11, has been specially followed as to this point. The thickness of the middle leaves of this plant was found at the time of collecting to vary between 560 μ . and 613 μ . The value of the leaf thickness of the same plant in the culture in 1921 was found to vary between 438 μ . and 507 μ . In 1922 the value was found to be about 500 μ .

Another proof of the hereditary nature of this succulent type is given by the cultural experiments with shade forms of the same type. Such shade forms are found growing in the *Alnus* swamps of Hallands Väderö a few hundred metres distant from the shore. The leaves of these plants (the physiology of which has been discussed by LUNDEGÅRDH, 1919) are thin and smooth. Fig. 75 e represents a cross section of a typical leaf of the shade form, showing that it is considerably thinner than the leaf of the cultivated inland type. A series of these thin-leaved shade forms has been cultivated since 1920. Fig. 75 f shows the appearance of the leaves the following year (1921). The increase in thickness is considerable, and it is now found to be much thicker than the leaf of the inland type. It has also become hairy. In 1922 the thickness shown in fig. 75 g, which is a cross section of a leaf of the same plant, is attained. The original thin-leaved shade plant has now attained the same fleshiness of leaves as has been found typical of the fleshy coast (and sun) plant when cultivated, thus showing that the shade form in this case is a shade-modified plant of the coast type. It is seen from the figure that the thickness of the leaf is brought about by an elongation of the palisades and an enlargement of the sponge cells.

The great differences in the anatomical structure of *Dulcamara* leaves from inland and coast habitats have been particularly discussed by WARMING (1906), although the question as to the hereditary nature of these differences has had to be left unanswered by him. The results of the above mentioned cultivations, however, favour the following conclusions as to the presence of different, hereditary types within *S. Dulcamara*:

a. *The inland type*, as found in natural habitats in the interior of Scania. The type in question has smooth and rather thin leaves, both in the habitat and in cultures.

b. *The succulent type of the west coast*. This is a hairy leaved and fleshy type (probably identical with the var. *marinum* Bab. of systematic handbooks) which upon culture has been found to retain its hairiness and most of its fleshiness. Shade forms of this type

have been found to be smooth-leaved and much thinner than cultivated plants of the inland type. When cultivated under ordinary field conditions, however, the hairiness and fleshiness of the leaves typical of the type are soon developed.

c. *The type of the eastern coast.* This type includes both smooth- and hairy-leaved forms. The leaves, both of cultivated individuals and plants in the natural habitats, are usually thicker than those of the cultivated inland type. None have been found as thick-leaved as the west coast type.

B. MATRICARIA INODORA.

A succulent, halophytic variety of this species is known to systematists under the name var. *maritima* (L.). It differs also from the inland form growing as a weed throughout Sweden in being perennial and bushy in growth, in having bracts with broad, dark-coloured margins and, usually, in having broader and shorter rays and less erect growth. It is for the rest rather variable as to the length and shape

TABLE 2.

Field no	Position of stems	Length of leaf segments	Thickness of leaf segments in μ	Place of collection	Year of collection
1	Erect	Long	385—440	Lund	1921
2	Procumbent	Short	965—1050	Hall. Väderö	1919
3	Prostrate	»	1025—1230	»	»
4	»	»	915—985	Kristineberg	1921
5	Ascending	Elongated	620—695	Stockholm	1920
6	»	»	635—745	Västervik	»

of the leaf segments and rays, etc. (see NEUMAN, 1882). The different forms of this variety are common on the west and east coasts of Sweden, and series of these forms have been transplanted from Hallands Väderö, Kullen and Kristineberg in Bohuslän (on the west coast) and from the islands off Stockholm, Karlskrona and Västervik (on the east coast). Some of the original plants have been divided and clones have been raised. Table 2 gives the characteristics of five of these clones (with 10—20 individuals in each) as seen in the cultures in 1922, together with the place and year of collection. Field no. 1 represents the ordinary inland weed type growing on the same bed, and raised from seed collected in 1921 at Lund.

There are additional differences between the clones, but those

cited are the most characteristic as to the vegetative parts. The differences between the inland type and the succulent type are striking enough and need not be further discussed. The point of interest is the difference between the var. *maritima* from the east coast and from the west coast. The latter have thicker and shorter leaf segments and

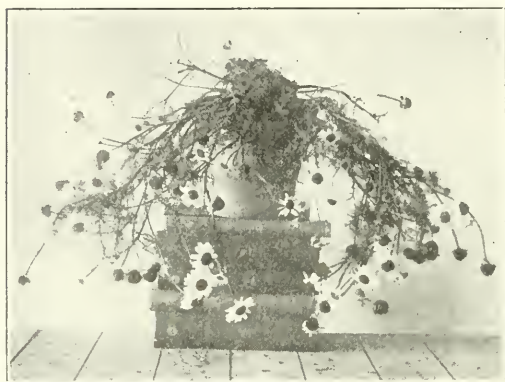


Fig. 10. *Matricaria inodora*. Prostrate form of the coast type from the west coast.



Fig. 11. *Matricaria inodora*. Procumbent form of the coast type from the west coast.

are more depressed. These differences are seen not only in the above clones but also in most of the cultivated single plants transplanted from both coasts. The west coast forms have been found throughout to represent more extreme forms than those of the east coast, as compared with the inland type. Less prostrate and less fleshy-leaved forms may also be found on the west coast, and prostrate and very fleshy-leaved forms may conversely be found on the east coast, but west coast sets have always been found to contain more numerous individuals of the latter type, and vice versa with regard to east coast sets.

The anatomical structure of the leaf of the inland type differs much from that of the *maritima* type. Fig. 74 a represents a cross-section of the marginal part of a leaf segment belonging

to a plant raised from seed collected from the cultivated Hallands Väderö series in 1919, from which the clones represented in field nos. 2 and 3 have been raised. As regards shape and leaf thickness it much resembles the clone represented in field no. 2. Fig. 74 b is a cross-section of a leaf segment from the inland type raised from seed

collected at Lund in 1919 and grown on the same bed as the former. Besides the very great difference in thickness the *maritima* leaf is found to be isolateral, while the inland leaf is found to have only one layer of palisades on the lower side.

Fig. 10 represents an individual from one of the clones cultivated in 1922 (viz. field no. 3), and fig. 11 shows an individual from another clone (field no. 2). This latter was crossed in 1920 with the inland type. The F_1 -generation was found to be uniform and intermediate as to shape and thickness of leaf segments. The plants were as erect as the inland type, and, like the latter, had a single main axis, but the crown of the plants was very bushy. Fig. 12 illustrates one of these F_1 -plants. They all died in the autumn, thus being annual like the inland type.

The F_2 -plants obtained in 1922 from the crosses between F_1 -individuals (the plants were found to be wholly self-sterile) is at this mo-



Fig. 12. *Matricaria inodora*. A F_1 -plant from a cross between the inland type and the shore type represented in fig. 11.

ment still in the rosette stage. However, segregation is very evident. As to the shape of the leaf segment there are (out of a total of 163 plants) 28 short and blunt (like the *maritima* parent), 56 short and pointed, 58 elongated, 17 long segmented (like the inland parent), and 4 very long and narrow. The segregation is evidently polyhybrid showing transgression in one direction. The grouping of the individuals as to leaf thickness is rather peculiar: there are 9 very thick and fleshy (transgressions), 62 thick-leaved (like the *maritima* parent), 59 intermediately thick and 33 thin leaved (like the inland parent). The segregation, although probably polyhybrid, is presumably disturbed by modificatory influences. It will be followed up closely when flow-

ering has commenced, but it is mentioned here as a proof of the hereditary nature of the characteristics involved.

The different hereditary forms of *Matricaria inodora* transplanted from various places are thus found to group themselves into the following types according to the habitat:

a. *The inland type.* This is an annual weed with an erect habit of growth. The leaf segments are long and thin. Only known as an anthropophyte.

b. *The type of the west coast.* This type includes perennial, halophytic forms with thick, short and blunt leaf segments. They are more or less depressed and have a bushy growth. The rays of the flowers are shorter and broader than those of the inland type, and the bracts have a broad and dark coloured margin. There is moreover a great variation within the type, involving hereditary differences as to morphological details of leaves and flowers.

c. *The type of the east coast.* This type includes perennial, halophytic forms the leaf segments of which come between the inland type and the b-type in point of length and thickness. While most of the forms of the b-type are prostrate or procumbent, the majority of forms belonging to this type are ascending.

It should be added that in places where cultivated fields run down to the shore bastards representing different combinations of the inland and the halophytic types might be found.

C. LEONTODON AUTUMNALIS.

Sets of this plant have been collected from beach habitats as well as from the inland in 1919, 1920, and 1921, and important differences are seen in the cultures between some of these sets. This is particularly true of the series transplanted in 1920 from the coast at Kullen and Arild (N. W. Scania). The plants included in these series are all smooth with coarsely dentated or nearly entire leaves. The plants making up the series transplanted from inland meadows in Scania have mostly pinnatifid leaves, usually somewhat hairy. These plants are also taller than the coast plants. The cultivated coast plants from Kullen and Arild, furthermore, have been found to flower about two weeks before the inland plants. Clones have been raised from individuals of these different series. Fig. 13 (to the left) represents an individual from a clone obtained in 1921 by dividing a plant typical of the Kullen series (transplanted 1919), while the plant to the right

illustrates the individuals in a clone obtained the same year by dividing an inland meadow plant (transplanted 1919). The differences as to height and shape of leaves are plainly seen. The anatomical structure of the leaves of these clones is also different, as is seen in figs. 75 c and d. The cross-sections are made from leaves taken from the cultures in 1922. There is a slight but distinct difference in thickness. The thickness of the inland clone has been found to vary between $250\ \mu$. and $300\ \mu$., while the Kullen clone varies between $285\ \mu$. and $350\ \mu$. The loose tissues rich in intercellular spaces, which are typical of the inland leaf, contrast strongly with the compact tissues of the Kullen leaf. These differences in the anatomy of the leaf have been found to be very typical of other series from the coast (Varberg,



Fig. 13. *Leontodon autumnalis*. The type of the coast (to the left) and the inland type.

Bohuslän) and the inland. In places where meadows and pastures run down to the shore, there is a great confusion of different forms, as series from such localities show. Such series have been transplanted from Vellinge and Hallands Väderö on the west coast, and from Västervik on the east coast. They apparently represent different combinations between the coast type and the inland type.

Plants from the clones represented in fig. 13 have been crossed. The F_1 -generation is multiform with regard to hairiness and to the shape of the leaf. The further discussion of the segregation will be put off till the next generations have been raised. It should be said, however, that in the F_1 -generation already produced types of leaves have appeared which differ from both of the parents, for instance pinnate types with extremely narrow lobes (identical with the f. *coronopifolius* Lge. of the floristic handbooks).

A few words should be said in regard to the treatment by systematists of some of the forms of *L. autumnalis*. NEUMAN (1882—83), in our country, has discussed the various forms. The above coast type from Kullen, Arild and Varberg is apparently identical with the form described under the name f. *salinus* Aspegr. There is another similar form, which NEUMAN describes as f. *robustior*. It differs from *salinus* mainly in being shorter in stature and in having more succulent leaves. There seems to be little doubt that this form is merely a habitat modification of the former. For it has been found that plants answering to the description of f. *robustior* at the time of collecting have become taller and less fleshy upon cultivation as early as the year after transplantation. It is equally true, however, that the characteristics of these cultivated plants, which now match the plants of the coast type described above, are genotypically founded and are not to be regarded as modifications of inland plants.

In summarizing the results of the cultivations the following conclusions as to the existence of different hereditary types of *L. autumnalis* seem to be justified.

a. *The type of the interior of Scania.* The type includes rather tall plants with pinnatifid and usually hairy leaves. The leaf is composed of very loose tissues rich in air spaces.

b. *The type of the coast,* as obtained from Kullen, Arild, and Varberg. This is composed of plants lower in stature than the inland type. The leaves are coarsely dentated or almost entire, and always smooth. The leaf is composed of very compact tissues, poor in air spaces, and is somewhat thicker than the leaf of the inland type. The plants of this type flower about two weeks earlier than the inland type. The f. *salinus* Aspegr. of systematic handbooks seems to cover this coast type.

It may safely be held that the number of types characteristic of *L. autumnalis* in nature is not exhausted by these two. In sandy places along the coast plants with depressed, pinnate leaves are found, which have been described as f. *coronopifolius* Lge. The cultivated material of this form is too young, however, to permit of any definite conclusions as to the nature and importance of the form. The same is true of cultivated material of the Alpine forms of the species. It may be said, however, that the compactness and slight succulence of the leaves, characteristic of the coast type, seem to be characteristics of the Alpine forms as well, and are even more pronounced here than in the coast type.

D. MELANDRIUM RUBRUM.

No succulent coast form of this species seems to have been recorded. Such a form grows, however, on the sea cliffs of Kullen in N. W. Scania. It has been in culture for two years and does not yet show any decrease in thickness. Fig. 76 f represents a cross-section of a leaf of the ordinary type, cultivated since 1920, so common in the beech woods of Scania. Fig. 76 e shows a cross-section from the cultivated, succulent Kullen type made in 1922. The thickness of the leaves of the cultivated type of the beech woods varies between 295μ . and 350μ ., while the leaves of the cultivated plants belonging to the type from Kullen vary between 575μ . and 615μ . The measurements refer to well-developed rosette leaves in autumn.

Great variation is found within both types in regard to the shape and hairiness of the leaves, the shading of the red colour of the flower, etc., but the characteristics of the leaf thickness are peculiarly uniform in each of the two types.

It should not be thought that succulence is characteristic of the coast type of Kullen only. Alpine varieties of this species, now brought under culture, seem to be still more fleshy. The material is too young to allow definite conclusions to be drawn, but a few plants belonging to this Alpine type, transplanted from Jämtland in 1918 and cultivated by Professor NILSSON-EHLE in the same field as the above-mentioned Lowland types, have been examined as to leaf succulence this autumn (1922). The leaf thickness was found to vary between 645μ . and 735μ . Fig. 76 d represents a cross-section of a rosette leaf from one of these plants.

There are, no doubt, additional examples of thin-leaved inland plants represented by succulent types both along the coast and in the mountains. Preliminary work on *Rumex acetosa* L. seems to point in this direction. These coast and Alpine types of one and the same species represent an interesting illustration of the fact so well known among plant geographers that one and the same species may be found both along the coast and in the Alpine regions (SCHIMPER, 1908). It has yet to be shown, however, that these species really are represented by the same hereditary type in both localities. That this is not so in the case of the above-discussed plants seems certain.

The results of the cultivation of succulent coast types discussed above leave little room for doubt as to the genotypical differences between these types and the corresponding inland types. That the

presence of sodium chloride, in the amount found in the coast habitats, should in certain cases modify these coast types towards a degree of succulence not attained in the cultivated series (as we have found in the case of *Solanum Dulcamara* and *Leontodon autumnalis*) is not surprising when it is known that a great number of non-halophytic plants are also thus modified. There is — even in those series which have been found to be less succulent in the cultures than in their natural habitats — a distinct difference as to the thickness of the leaf between the cultivated coast types and the cultivated inland types from the Lowland. When the latter have been found to be thin-leaved, while the former, cultivated in the same bed under the same conditions, are found to be succulent, genotypical differences between both types as to leaf thickness must, no doubt, exist. This is made all the more plausible when the F_2 -segregation from the cross between the two *Matricaria* types, as well as the behaviour of the cultivated shade form of the Väderö *Solanum*, are remembered. The existence of succulent Alpine forms of some of these species also speaks in favour of the assumption that succulence by no means stands in any direct proportion to the quantity of mineral salts present in the different soils.

This does not lessen the importance of the fact of the modificatory action of salt upon the plant: it must be emphasised, however, that the results of the cultivations do not support the idea that the halophytic forms of thin-leaved inland species, found habitually along the coast, are modifications called forth in direct response to the saline soil. The classification of these forms into a group of »facultative» halophytes (WARMING, 1906) must therefore be refrained from. They are, on the contrary, to be considered as obligatory as most of the well-known species confined in nature to saline situations.

4. MATERIAL AND CULTURES OF DIFFERENT SPECIES OF HALOPHYTES.

The cultural experiments with species of halophytes have been largely confined to the genus *Atriplex*, and the discussion pertaining to this topic will therefore be limited to species belonging to that genus. *Atriplex patulum* L., although not a regular halophyte, has also been included in the discussion.

No other genus would seem so suitable for investigations of this kind as *Atriplex*. They are annuals, and several species of the genus have long been known to be exceptionally polymorphic. Various

forms, dwarf forms, forms presumably adapted to live on sandy shores, on rocky shores, on sea-weed banks, etc. have been distinguished within several species and named by systematists. The polymorphism has also been assumed to be due, to a certain degree, to the occurrence of hybrids between some of the species. The method largely employed in my own work has been to collect series of young plants of the various forms and species from different points on the Swedish coast for my cultures. As many as possible of these transplanted individuals have then been isolated with pergamin bags at the stage of flowering, and the offspring has been compared with the mother-plants. All the species investigated seed perfectly well when isolated in that way. The isolations have been continued for several years and a considerable number of biotypes have been isolated from the different species. A remarkable multitude of different hereditary forms have thus been found to build up the species in nature. The frequent self-fertilization, occurring also in nature, tends to preserve these different forms, thus giving rise to the perplexing polymorphism found. That this polymorphism is sometimes increased by crossings between different species, and by the direct influence of environmental factors upon the plants will also be shown. It has been thought best to discuss the different species separately.

A. ATRIPLEX LITORALE.

The species occurs commonly along the Swedish coast. It has a shallow root-system and is therefore limited to the lower portion of the beach, where it often roots in the sea-weed banks thrown up. Farther up on the sandy beach only dwarfed forms are produced. The plant flourishes best in sheltered places and keeps away from the most exposed localities (cf. also TURESSON 1919 a). It reaches its best development along the Sound, especially on the beach-lines bordering the bays and coves, where masses of *Fucus* and *Zostera* have collected. The dimensions reached by the plant along the Sound are not attained on the coast farther to the north, e. g. in Halland and in Bohuslän. The forms met with in sheltered places along the Sound are often tall, erect, and very robust, while the forms farther up on the more exposed west coast are lower of stature and more spreading. The question arose whether these differences between the forms of the Sound and those of the coast line to the north are hereditary or only modificatory and wholly due to differences in the environment. In

order to answer the question collections of seed and small plants were made in the years 1916, 1917 and 1918 from various places along the Sound and the coast strip of Halland and Bohuslän. A great many of the plants raised were isolated with pergamin bags during these and the following years and a representative collection of different biotypes was obtained. It was thus found that the *A. litorale* populations both of the Sound and of the Halland-Bohuslän coast were made

TABLE 3.

Field no	Middle length of main axis (in mm)	Middle length of basal branches (in mm)	Position of main axis	Position of basal branches	Leaf margin	Bractlets	Flowering	Place and year of coll. of the mother plant
171	1005	1035	Ascending	Ascending	Denticulate	Closed	Late	The Sound, 1916
172	980	965	Erect	»	Dentate	»	»	» »
175	970	990	»	Erect	Almost entire	»	»	» »
176	945	970	»	»	»	Spreading	»	» »
169	885	925	»	»	Entire	Closed	»	» »
170	860	870	»	Ascending	Almost entire	»	»	» »
177	810	840	»	»	»	Spreading	»	» 1917
178	805	825	»	Erect	Denticulate	»	Intermediate	» »
168	635	715	»	Ascending	Dentate	Closed	Late	» »
173	580	595	Ascending	»	»	»	Early	Bohuslän, 1918
174	540	600	»	»	»	Spreading	»	» »
155	510	545	»	»	Entire	Closed	Intermediate	Halland, 1917
159	425	430	Procumbent	Procumbent	Almost entire	Spreading	Early	» »
160	410	460	Prostrate	Prostrate	»	»	»	» »
156	405	480	Procumbent	»	Dentate	»	Intermediate	Bohuslän, 1917
158	375	415	»	»	»	»	Late	The Sound, 1916
157	330	405	Prostrate	»	»	»	Intermediate	» »

up of a large number of biotypes often differing noticeably from each other in various respects. It was also found that certain biotypes, representing certain combinations of characters, could be repeatedly isolated from the population of the Sound but not from the Halland-Bohuslän coast. The additional fact was also brought to light that certain combinations very characteristic of the northern coast strip occurred but sparsely along the Sound. Table 3 gives the characteristics of 17 biotypes, most of them in culture since 1916—1917. The middle values of the length of the main axis and of basal branches have been based upon the measurements of the first

30 plants in the row of each biotype. The angle taken up by the main axis and the basal branches (columns 4 and 5) has been indicated by the terms erect, ascending, procumbent and prostrate. The measurements were made in 1921, and the different biotypes are arranged as to the length of the main axis (column 2).

The biotype represented by field no. 169 is figured in fig. 14. field nos. 170 and 168 are shown in figs. 15 and 16, and nos. 159 and



Fig 14. *Atriplex litorale*, field no 169. Plant to the left raised under ordinary field condition; the plant to the right raised in sand culture.



160 in figs. 17 and 18. The biotypes represented are selected so as to give an idea of the great variability in branching habit. It should also be said that each of the 17 biotypes in the list appear to be constant throughout, the small differences seen between the individuals of the same type being certainly due to fluctuations in soil etc. They resemble in all essentials the separate mother-plants from which they originated. This fact speaks in favour of the assumption that autogamy is the rule in this species. A few mother-plants have upon iso-

lation given offsprings showing segregation as to branching habit, time of flowering, colour of leaves, shape of leaf margin, etc., but these families have been found to be in a decided minority.

The pure cultures of biotypes of *A. litorale* comprised in 1921 36 different kinds. About half of the number of the pure cultures comprised only 15—25 individuals in each family and have on this account been excluded from the table. The number of isolated bio-



Fig. 15. *Atriplex litorale*, field n:o 170.

types could easily have been increased were it not for practical difficulties with regard to the space of ground needed and the care required for a greater number of isolations. The material at hand, however, is quite sufficient to make clear the marked hereditary differences between the different biotypes. In the 17 cultures of biotypes none is found to represent the combination of characters typical of another. Between some of them only small differences are seen, but these differences repeat themselves with absolute exactness every year.

The variations as to branching habit, leaf character, bractlets, etc.

seen in a natural population of *A. litorale* are probably in most cases due to the occurrence in the same habitat of a mixture of distinct biotypes each representing a distinct combination of hereditary characteristics. It should not be thought, however, that environmental factors may not influence the habitus. Modificatory dwarf forms are often developed in the upper part of the beach, probably on account of an insufficient water supply. Similar plants differing much in size from individuals of the

same biotype growing under ordinary field conditions are invariably produced when allowed to develop in sand culture. Fig. 14 shows the habitus of two individuals belonging to the same biotype (field no. 169) of which the one to the left has developed under the normal conditions of the experimental fields, while the dwarf to the right has been raised in sand culture.

There is also ano-

ther group of modifications, viz. the modificatory prostrate forms, which afford much interest. The prostrate habit of growth, which in some biotypes is a hereditary character (as in field no. 160, fig. 18) might sometimes, especially in exposed localities, become developed as a result of response to environmental factors. I have in a former publication tried to show (Turessox 1919 a) that exposure to great light intensity produces this modificatory prostrateness. Species belonging to the genus *Atriplex* were also mentioned which possessed different

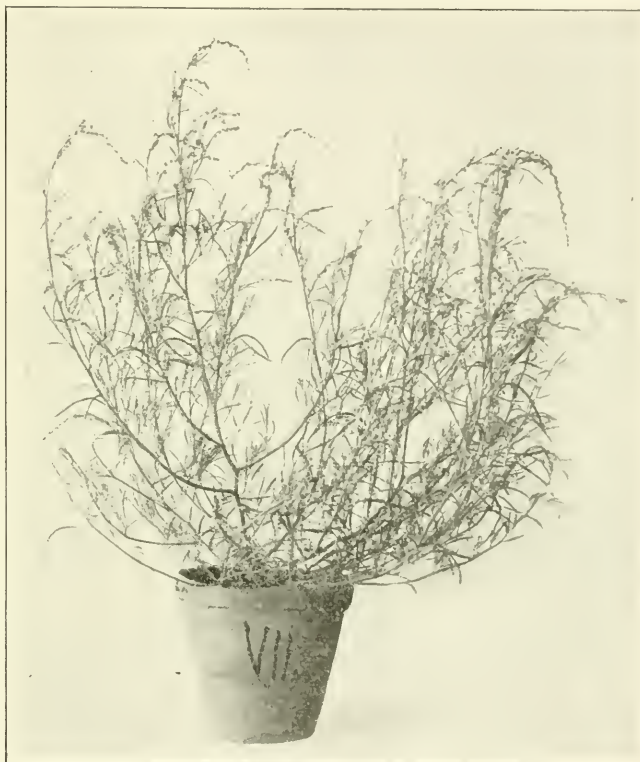


Fig. 16. *Atriplex litorale*, field no. 168.

hereditary branching types, one erect in ordinary light and one prostrate in ordinary light (*A. latifolium* and *A. patulum*), of which the former type could be induced to become more or less plagiotropic when exposed to light of great intensity. An erect type of *A. litorale* was also experimented with on that occasion, but this was found to be the least sensitive of the different forms (belonging to other species) tried. Since then instances of modificatory prostrateness have also



Fig. 17. *Atriplex litorale*, field no. 159. The upper plant grown under ordinary field condition; the lower plant raised in sand culture.

been found in *A. litorale*. It is especially the procumbent biotypes which are apt to become modified in that way. Prostrate modifications almost always result when individuals belonging to these types are allowed to develop in the sand

culture, where much light is reflected from the white sand and where the plants, because of their reduced size, do not shade one another. Fig. 17 shows the habitus of two individuals belonging to the same biotype (list no. 159) of which the upper plant has been raised in the ordinary field culture, while the lower plant

illustrates the modificatory prostrate habit of growth attained in the sand culture. When modificatory and hereditary prostrates occur together on the exposed beach some difficulty is experienced in separating the different types, and the cultivating of the forms becomes necessary. Prostrate modifications of erect types have not been found. The ascending types may become influenced to a limited degree and are then hard to distinguish from the procumbent types. These latter are most readily induced to become prostrate.

The distribution in nature of the different types of branching is very interesting. The erect type of branching so characteristic of the types of the Sound has not been found in any of the series of young plants and seed collections obtained from the Halland-Bohuslän coast. The tall and erect branching type, if not entirely lacking, must be but sparsely distributed in that region. Extensive series from Kristineberg and Marstrand in Bohuslän and from Varberg, Falkenberg, Halmstad, Båstad and other places along the Halland coast have upon cultivation only given plants belonging to the ascending, procumbent and prostrate types of rather low stature. A few of these types are still being kept in pure cultures (see the table). There is another characteristic of these types. They have been found to flower earlier than most of the types occurring along the Sound. The difference in the time of flowering for in-

stance, between field no. 169 from the Sound and list no. 173 from Bohuslän (see the table) amounts to about 14 days. As has been remarked this difference in flowering-time may become less distinct in certain



Fig. 18. *Atriplex litorale*, field no. 160.

years, but in years with normal weather conditions the difference is always seen. The difference in flowering-time between the Sound types and the Halland-Bohuslän types is generally less than 14 days; there is usually about a week's difference between the two groups.

The tall, erect types are the most common in the Sound region, the ascending ones are somewhat less frequently distributed, while the procumbent and prostrate types are very rare. The gigantic dimensions attained by the *A. litorale* vegetation along sheltered sea-weed banks of the Sound, both as to height and as to extent, are thus seen to be due not only to the occurrence of more favourable localities for the plant in this region as compared with the more exposed northern coast strip but also to the occurrence of hereditarily more robust and taller types than are found in the populations to the north.

The limited number of cultivated types from the eastern coast

strip seems to indicate that the *A. litorale* types inhabiting this coast strip differ genetically both from the plants typical of the Halland-Bohuslän coast and from those of the Sound region.

B. *ATRIPLEX BABINGTONII* WOODS.

This species occurs along the west coast as far to the south as Kul-len. It is only found sporadically along the Sound. It has also been found quite typically at Stenshuvud on the east coast of Scania, and occurs

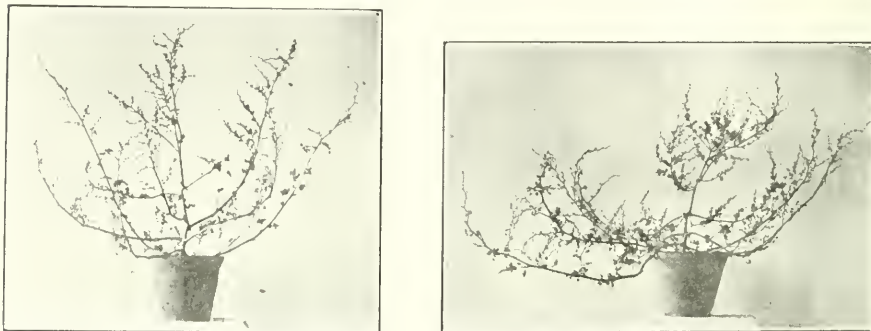


Fig. 19. *Atriplex Babingtonii*. Ascending and procumbent types.

likewise on Öland and Gotthland. The plant has a deep-ground root-system and generally occupies the upper supralittoral belt of the beach. A number of biotypes have been isolated from this species also but no

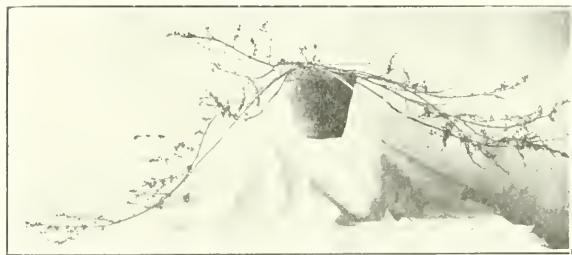


Fig. 20. *Atriplex Babingtonii*. A prostrate type.

differences in the geographical distribution of the types have been found. Populations from Bohuslän, Halland and Gotthland show the same mixture of types as to branching habit, leaf margin, bractlets, etc. Auto-

gamy does not seem to be the rule in this species. In all localities where *A. Babingtonii* co-exists with other species of the genus, for instance with *A. latifolium* Wg., hybrids are found. The hybrids are in fact much more common on our west coast than *A. Babingtonii* itself. It is only in places, where the zones of the beach for some reason or other are devoid of other *Atriplex* species, that *A. Babingtonii* is found in its typical form.

The branching types usually found in *A. Babingtonii* are the ascending and the procumbent ones (fig. 19). The prostrate (fig. 20) type is less common. No biotype characterized by wholly erect growth has yet been isolated.

C. ATRIPLEX PATULUM L.

This species has been considered to be one of the most variable in the genus, and forms presumably adapted to live on cultivated ground, on sandy shores, and on rocky shores, etc. have been distinguished and named by systematists. I have shown in a previous paper (TURESSON, 1919 b) that the great variability assumed by some

TABLE 4.

Field no.	Position of main axis	Position of basal branches	Leaves with or without scurf	Margin of the terminal part of the basal leaves	Bractlets
6	Erect	Ascending	Almost without	Denticulate	Small
7	»	»	»	Entire	»
8	»	Procumbent	With	Dentate	»
3	»	Prostrate	Almost without	Entire	»
4	»	»	Without	»	»
5	»	»	Almost without	Denticulate	»
209	Prostrate	»	With	Entire	»
211	»	»	Without	»	»
212	»	»	»	»	Leafy

writers to be peculiar to *A. patulum* has been due to a confusion of this species with forms belonging to another species, which is strictly confined to the salt water shores. This species will be dealt with in the following.

A. patulum, on the contrary, is a typical anthropophyte, which only goes down on the beach in places, where cultivated fields are close by or where refuse and rubbish has collected. Autogamy seems to be the rule in this species, and numerous biotypes, different as to branching habit, leaf character, bractlets etc., are easily raised, when different mother-plants are isolated. A great number of such isolations were made in 1916 and 1917. A few of the resulting pure cultures are still kept. Table 4 shows the combination of the most important characters realized in these different pure cultures.

Fields nos. 6 and 3 are shown in figs. 21 and 22, and field nos. 5 and 209 in fig. 24 (the main axis of this type is erect but it is sooner

or later bent by the wind) and in fig. 23. When growing, as it usually does, on much trodden road-sides or in crowded fields it becomes sometimes much dwarfed. The erect type will then in most cases

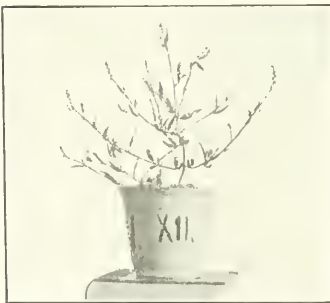


Fig. 21. *Atriplex patulum*, field no. 6. The upper under normal field conditions, the lower under sand culture conditions. Pots 12 cm. high.

have an appearance corresponding with the lower plant in fig. 21, which belongs to the same biotype as the upper plant (field no. 6). It has been raised in sand culture. Plants belonging to the



Fig. 22. *Atriplex patulum*, field no. 3.



Fig. 23. *Atriplex patulum*, field no. 209. The upper under normal field conditions, the lower under sand culture conditions. Pots 12 cm. high.



prostrate type will similarly take on the habitus shown by the lower plant in fig. 23, which is a modification of the upper plant (field no. 209) and is raised in sand culture. These prostrates become even more stunted and dwarfed when growing as a weed in the corn-fields of southern Sweden; they often do not exceed 10 cm. when spread out.

The different biotypes occur almost indiscriminately through southern and middle Sweden in cultivated places. There is one habitat, however, which has been found to exclude all types which do not



Fig. 24. *Atriplex patulum*, field no. 5.

show a prostrate habit of growth. In the stubble-fields of southernmost Sweden, where *A. patulum* grows as a weed, only the prostrate races of the species are found, together with other annuals low in stature, such as *Anagallis*, *Odontites*, *Euphorbia exigua*, *Stachys arvensis* etc. The offspring from isolated mother-plants collected in the stubble-fields might vary as to all other characters, in the shape of the leaves, in characters of leaf margin, in the size of the bractlets, etc., but they all show the prostrate habit of growth. They escape, apparently, the fatality which inevitably meets the erect races in this habitat, viz. that of being cut down and deprived of fructification.

A. patulum var. *erectum* Huds. of the floristic handbooks includes most of the types with an erect habit of growth, while the var. *angustifolium* J. E. Sm. comprises a great assemblage of prostrate types together with dwarfs and hunger forms of the preceding types.

D. ATRIPLEX SARCOPHYLLUM.

The *A. patulum*-like shore Atriplices with thick and fleshy leaves are here grouped under this preliminary name. I have shown in a former publication (TURESSON, 1919 b) that these forms have been erroneously grouped with *A. patulum*, which species they resemble in the shape of the leaves. They form together one of the most distinct species in the genus, systematically and ecologically, and occur almost along the whole Swedish coast, occupying the zone nearest to the water (the lower supralittoral belt), where no other species of the genus thrives well. They flower earlier than any other species of the genus, as early as May and June. Sets of seeds and young plants of forms belonging to this species have been collected from some thirty different localities and cultivated, and a remarkable hereditary variation has been found to occur. Furthermore, the geographical distribution of the various forms is of great interest. It is found that the eastern coast strip is inhabited by a certain group of forms distinctly different from the population inhabiting the Sound region, and both these groups of forms differ again from the forms found on the western coast strip. It is preferable to discuss these different geographical groups separately.

a. *The type of the eastern coast strip.*

The forms of this type have the general characteristics of the whole group: thick and fleshy, rhombic-lanceolate leaves; long, unbranched and, in the upper part, leafless inflorescences; early flowering etc. The eastern forms differ from the rest in the branching: they are erect, with the basal branches ascending. They have in addition somewhat thicker leaves than the forms of the Sound and the western coast (see figs. 74 e and f). The mean leaf thickness of the east coast type has been found to vary between 945 μ , and 1155 μ ., while that of the Sound type varies between 893 μ , and 1667 μ . For purpose of comparison it may be mentioned that the thickness of *A. patulum* has been found to vary between 315 μ , and 525 μ . The values refer all to cultivated biotypes. The fruiting bractlets of these eastern forms are



Fig. 25. *Atriplex sarcophyllum* from the east coast (Oxelösund).
Pot 12 cm. high.



Fig. 26. *Atriplex sarcophyllum* from the east coast (Gottland). Pot 10 cm. high.

often smaller in size and more fleshy than in the other forms. When it is examined in the field, an impression of the great homogeneity of the type is obtained. When brought into culture, however, a number of different forms can be isolated. The offspring obtained from isolated plants appears to agree in all details with the respective mother-plants, indicating autogamy in a state of nature also. The following enumeration refers to biotypes now kept

in pure cultures. The place and year of collection of the original mother-plants are also given together with short notes (taken in 1922)

on the characteristics of the resulting pure cultures. The number of individuals in each pure culture varies this year between 15—25.

- Nämnö, off Stockholm, 1920; plants of rather low stature; leaves deep blue-green.
- Oxelösund, Södermanland, » ; plants stouter and considerably more branched than the former; not quite as blue-coloured. Shewn in fig. 25.
- Getå, Östergötland, » ; plants resembling in all essentials the Nämnö form.
- Västervik, Småland, » ; plants resembling in all essentials the Nämnö form.
- Kalmar, Småland, » ; plants more slender than any of the former; the margin of the fruiting bractlets denticulated.
- Kastlösa, Öland, 1918; low of stature compared with most of the other forms; inflorescences short and contracted.
- Slite, Gotland, 1920; low of stature; leaves and stems brightly anthocyan coloured. Illustrated in fig. 26.

The individuals of these cultivated biotypes differ markedly only in one respect from the plants in the natural habitat, viz. in size. The »wild» plants are dwarfs compared with the plants obtained in the cultures. The thickness of the leaves is often greater in the cultivated biotypes than in the plants from the natural habitat, apparently because of the better development of the former plants. The thickness of the leaf attained in the cultivated Kastlösa forms, for instance (prepared from the cultivated material, 1922) has not been found in any material from natural habitats, where the thickness of the leaves varies around 1000 μ . In the Kastlösa form the leaf thickness has been found to attain 1155 μ .

The forms making up this eastern type of *A. sarcophyllum* have been followed from the islands outside of Stockholm to Karlskrona in Blekinge (the province east of Scania). The group has been described under the specific name of *A. praecox* by HÜLPHERS (LINDMAN, 1918), and a form with contracted inflorescences apparently belonging to this group (and perhaps identical with my cultivated Kastlösa form) has been described by JOHANSSON (1897) from Gotland under the name *A. patulum* f. *globosum*.

b. *The type of the Sound region.*

When collecting material for my cultures in 1916 I was much struck by a small *Atriplex* form growing abundantly along the marshy shore line at Limhamn, near Malmö. It was already in flower in May and had thicker leaves than other forms of the genus growing in the same place. Several of these Limhamn plants were isolated and pure cultures were obtained, some of which are still being kept. The



Fig. 27. *Atriplex sarcophyllum* from the Sound; field no. 45; ascending-erect form. Pot 12 cm. high.

material has been increased by forms collected in their natural habitats from the following additional places: Vellinge, Klagshamn, Arlöv, Lomma, and Landskrona. A number of biotypes, differing in small points, have been isolated from this material. They resemble the forms of the eastern coast type in being early (they are even somewhat earlier than these), in having thick, fleshy leaves (see fig. 74 f) and with regard to the form of the leaves as well as of the inflorescences. There are, however, some important differences between the two groups of forms. Towards maturity the oldest fruiting bractlets in the inflorescences of these forms become large and leafy, and their petioles elongate, attaining a length of sometimes up to 3 cm. These charac-

teristics are also seen in individuals collected in the natural habitat. Another point of difference from the preceding type is the colour of the leaves, which is almost always bluish-green in the *praecox*-type but dark green in the Sound type, both cultivated and »wild». The branching habit, which in the *praecox*-type is ascending-erect, is often procumbent, or even prostrate, in the Sound type. The margin of the leaves as well as of the bractlets may vary as in the case of *praecox*, but it is most often entire. Fig. 27 (field no. 45) shows one of the ascending-erect biotypes and fig. 28 (field no. 30) one of the prostrate ones, both isolated and pure cultured from the original Limhamn



Fig 28. *Atriplex sarcophyllum* from the Sound; field no. 30.
Prostrate form. Pot 12 cm. high.

plants. It should be said that long-stalked fruiting bractlets are also developed when the plants are allowed to develop in sand culture.

Two individuals, one from a pure culture of field no. 45, the other a pure culture of the *Kastlösa-praecox* (see above) were isolated within the same pergamin bag in 1920 with the object of procuring hybrids between the two types¹. A large number of seeds were obtained and sown, and 60 individuals from these cultures were isolated in 1921. Only one of these isolated plants has shown segregation this year, the rest are either typical no. 45 or typical *Kastlösa-praecox*. The

¹ Castrations, unfortunately, cannot be made in the genus *Atriplex* because of technical difficulties.

segregating plant differed from the rest even in 1921, and aroused the suspicion of being a bastard-plant between the two types. It showed the branching habit of no. 45, but the fruiting bractlets resembled the *praecox*-type, with the exception of a few, which showed a tendency to become leafy. Fig. 29 shows this plant. The offspring of the plant shows segregation with regard to branching habit, bractlets, leaf colour etc., and a few of the individuals have much resemblance to the parent plants. A full account of this segregation, however, must be postponed until the next generation has been grown.

The Sound type of *A. sarcophyllum* was held to be a mere modifi-



Fig. 29. *Atriplex sarcophyllum*. A F_1 -plant from the cross between the east coast and the Sound types.

cation in one of my former publications (TURESSON, 1919 b), as a result of insufficient experience in regard to the behaviour in culture of the types of the eastern and western coast strips. The hereditary nature of the characteristics peculiar to the Sound type is now beyond all doubt. The forms belonging to this type grow abundantly on the marshy coast strip along the Sound. A form belonging to the group was described as long ago as 1838 by DREJER from near Copenhagen under the specific name *A. longipes*. The name has disappeared from modern handbooks, or else it has been discarded with the remark that it refers to abnormal plants of other species, the »abnormal» charac-

teristic meant being the long-stalked, leafy fruiting-bractlets. Probably the name *A. patulum* f. *hololepis* Fenzl., current in some of the systematic handbooks, also belongs to this type.

c. The type of the western coast strip.

Forms belonging to this type are already found in the region of Kullen, in north-western Scania, and they extend at least as far as to the middle part of Bohuslän. Cultivated material from along this coast strip shows a great hereditary variation. Individuals with leafy, long-stalked fruiting bractlets are entirely absent. The forms of this type show most resemblance to the *praecox*-type as to fruiting bractlets, but the branching habit is different. They are usually much branched at the base and most often prostrate both as to main axis and as to basal branches. A number of biotypes have been isolated since 1917, when the first individuals of this type were brought into culture. Table 5 characterizes the most important biotypes now in culture, and gives information as to the place and year of the collection of the original mother-plants.

TABLE 5.

Field no.	Position of main axis	Position of basal branches	Colour of leaves	Nature of leaf margin	Place and year of coll. of mother-plant
63	Ascending-erect	Procumbent	Blue-green	Entire	Marstrand, Boh., 1920
64	Procumbent	»	»	»	Varberg, Hall., 1919
65	»	»	Dark-green	Denticulate	» » »
66	Prostrate	»	»	Entire	» » »
67	»	»	Blue-green	»	Falkenberg, Hall., 1919
120	»	Prostrate	Dark-green	»	Hall. Väderö, Scania 1917
122	»	»	»	Denticulate	» » » »
125	»	»	Blue-green	Dentate	» » » 1918
128	»	»	»	Entire	» » » »

Field nos. 63 and 64 are shown in figs. 30 and 31, and field nos. 120 and 128 in figs. 32 and 33. Some of the isolated plants gave an offspring which corresponded in every characteristic with their original mothers indicating autogamy, others showed segregation as to leaf colour, leaf margin, and branching habit. Self-fertilization seems to be the rule in most of the forms, however, as cases of vicinism are very rare in the plants sown from seed harvested from unprotected individuals in the cultures, where a number of different biotypes are grown close by.

The biotypes tabulated above differ in a number of characters not indicated in the table. The width and length of the fruiting bractlets, for instance, vary with the different biotypes within narrow but distinct limits. The length of the fruiting bractlets of the biotypes represented by field nos. 63, 66 and 120 are given here. The fruiting bractlets are taken from one individual in the case of no. 63 and from three individuals (a, b, c) each of nos. 66, 120. The measurements were

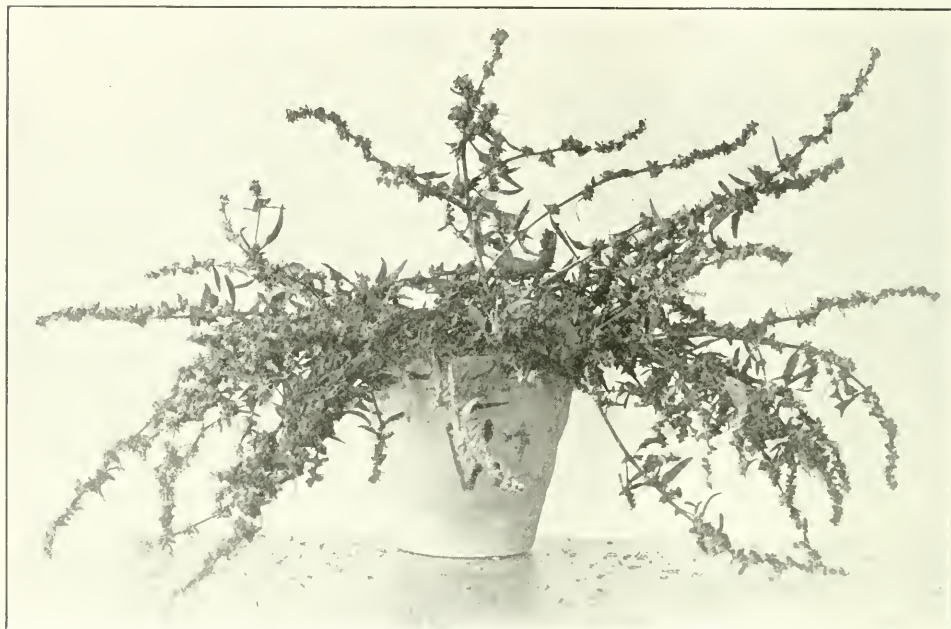


Fig. 30. *Atriplex sarcophyllum* from the west coast; field no 63. Ascending-erect form. Pot 12 cm. high.

made in 1921 from the pure cultures, and 300 fruiting bractlets were taken from each individual. The distribution in the different length classes (in mm.) is as follows:

	2	4	6	8	10	12	14
no. 63			152	100	38	7	3
no. 66 a	112	159	25	4			
b	107	158	29	6			
c	104	147	35	12	2		
no. 120 a	65	195	30	6	2	2	
b	72	180	29	10	5	4	
c	63	170	37	15	9	6	

There are also additional small points of difference between the different biotypes, although they are immaterial in this discussion.



Fig. 31. *Atriplex sarcophyllum* from the west coast; field no. 64. Procumbent form. Pot 12 cm. high.

They all differ from the *praecox*-type in having a procumbent or a prostrate mode of growth. In rare cases the main axis may be nearly erect (cf. field no. 63) but the basal branches show in all cases a powerful development as compared with the main axis. The thickness of the leaves is about the same as in the



Fig. 32. *Atriplex sarcophyllum* from the west coast; field no. 120. Prostrate form. Pot 12 cm. high.

Sound-type. The time of flowering is somewhat later than in the case of the *longipes*- and *praecox*-types. It falls in the latter part of June, sometimes as late as in the first part of July.

In certain places on the western coast, where an abundance of other species of the genus, such as *A. Babingtonii* and *A. latifolium*, occur, hybrids between the west coast type and these latter species become so frequent that it is sometimes difficult to find typical individuals of the type in question. This is the more remarkable as cases of vicinism have been very few in my cultures (see above). Different forms of the type might behave differently as to the mode of fertilization. The relatively late flowering probably favours a certain degree of hybridism with other species. The western type flowers late enough to find particularly early individuals of other species flowering at the same time.

The northern limit of extension of the forms belonging to this western type has not yet been determined. They have been found to



Fig. 33. *Atriplex sarcophyllum* from the west coast; field no. 128.
Prostrate form. Pot 12 cm. high.

be common at least to the middle part of Bohuslän. Undoubted intermediates between this type and the Sound type have been found this year at Helsingborg. Their behaviour will be followed in cultures. As to the systematics of the forms belonging to the western type of *A. sarcophyllum* the name *A. hastifolium* Salisb. has been adopted to cover the group (by LINDMAN, 1918). The name *A. patulum* var. *sarcophyllum* Neum., covers some of the forms characteristic of the type.

5. MATERIAL AND CULTURES OF INLAND AND COAST FORMS OF *SEDUM MAXIMUM* (L.) SUTER.

The material of *Sedum maximum* comprises about 300 individuals transplanted from their natural habitats and now growing in the experimental field. They come from Bohuslän, from Halland, from several points in Scania, from Småland and from the islands off Stock-

holm. A few of the series cultivated since 1919 and 1920 (the years of transplantation) will be briefly dealt with below.

My attention was first drawn to the plant in 1919 at Kullen in



Fig. 34. *Sedum maximum*. The sea cliff type of the west coast.



Fig. 35. *Sedum maximum* from Hallands Väderö.

N. W. Scania. Small, stunted plants of the species grow here in the crevices of the exposed sea cliffs. The leaves of these individuals were found to be folded and brightly anthocyanic in colour. They were at that time thought to be modifications of the green or glaucous, flat-

leaved inland-*maximum* called forth by the extreme habitat conditions of the sea cliff. A few of the cliff individuals were excavated and brought home in order that the reversion to the inland form might be followed more closely. This reversion has not yet taken place, however. The plants have, on the contrary, developed their original peculiarities still more with increasing age and growth. Fig. 34 (to the right) shows one of the plants, once a stunted, single stemmed dwarf,



Fig. 36. *Sedum maximum* from Stenshuvud (to the left) and from S:t Olof (to the right).

now one of the largest in culture. The leaves are permanently dark red in colour and much folded, as is plainly seen from the photograph. A second series from this locality composed of 26 individuals was brought home in 1920. The slight variation within this series, as seen in 1922, may be briefly noted: the number of flat-leaved individuals is two, the rest have folded leaves; the pure green-leaved individuals number 6, the rest have dark red leaves. The series further includes plants with ascending and with erect stems (fig. 34, to the left) in about equal number.

It is thus seen that when a greater number of plants is taken, individuals with the characteristics of the inland form are also found to occur. It is, however, a point of much interest that these latter occur in a decided minority. The same has been found to be true of cliff series from Varberg in Halland and from Bohuslän. The *Sedum maximum* vegetation of the rocky shores of Hallands Väderö, which would be expected to come close to that of Kullen, is made up of individuals the majority of which are flat-leaved and glaucous. It should be remembered, however, that the rich, herbiferous woods making up the interior of that island and in close touch with the rocky shore include a multitude of *Sedum maximum* much resembling in certain characters the ordinary inland type, which, no doubt, incessantly recruits the shores with individuals of its own type. The leaves of the plants from the woods have a typical shade-leaf structure, as has already been pointed out by LUNDEGÅRDH (1919), while the plants from the rocky shores have sun-leaf structure. The shade-leaf structure of the woodland plants is only a modification, which had entirely disappeared in 1922 in all individuals brought home from the island in 1919. Fig. 35 shows two plants, one prostrate, the other almost erect, both belonging to this woodland series.

The folded leaf *maximum* typical of the exposed sea cliffs of the west coast has also been found on the east coast of Scania, viz. on the cliffs at Stenshuvud. The folded individuals, however, are here mixed with flat-leaved in about equal proportions. The folding, further, is not so pronounced in the Stenshuvud plants as in the west coast plants. Fig. 36 (to the left) shows a leaf-folded individual from Stenshuvud. The colour of the leaves of these plants is pure green, not anthocyanic except towards autumn. The Stenshuvud series is thus seen to be rather different from the west coast series, even if certain characteristics of the west coast cliff type may be traced in some of the individuals.

The series cultivated and examined from further up the east coast, viz. from Oskarshamn and Västervik in Småland and from the islands off Stockholm have only been found to comprise rather long-stemmed, flat-leaved individuals, the majority of which have been found to be glaucous. Some series, for instance those from Stockholm, show all kinds of branching habit. Fig. 37 illustrates 3 plants belonging to a series of 15 brought home in 1920 from Nämndö (an island off Stockholm). The prostrate plant is the only one in the collection, the erect habit characterizes a few, while the ascending habit predominates.

Inland *maximum* has been collected in several places in Scania.

Series from mountain hills in N. E. Scania (e. g. Balsberg, not far from Christianstad) include individuals with somewhat folded green leaves and rather varying branching habit (erect and ascending), while those series collected in the southern part of the province (e. g. 10 km. to the east of Malmö, in the vicinity of St. Olof, and at Hörby) only include green, flat-leaved, tall and erect individuals. The latter series have been found growing along road sides and cultivated fields and may be garden escapes, although this point is very difficult to settle. In fig. 36 (to the right) a plant from the St. Olof series is shown. It has the typical habitus of the Lowland series of the interior, flat, pure green (sometimes indistinctly glaucous) leaves, and taller stems than in



Fig. 37. *Sedum maximum*. The type of the eastern coast strip of middle Sweden. the plants of the west coast series. It has furthermore an erect habit of growth (the angle of the base of the stem is brought about by wind action).

In summarizing the results of the cultivation of different inland and coast forms of *Sedum maximum* the following grouping of the forms with regard to their natural habitats might be made:

a. *The type of the exposed sea cliffs of the west coast.* The leaves of this type are in the majority of cases folded and permanently dark red (anthocyanic) in colour.

b. *The mixed type of Stenshuvud and the interior of N. E. Scania.* The series of this type is made up of individuals both with folded and with flat leaves. There is no red colour in the leaves except occasionally in autumn.

c. *The type of the eastern coast strip of middle Sweden.* The plants of this type are somewhat more long-stemmed, have flat and glaucous leaves.

d. *The type of the cultivated regions of the southern interior of Scania.* This is taller than any of the preceding types, has an erect habit of growth and flat, green (rarely indistinctly glaucous) leaves. The type may be a garden escape, although evidence in that direction has not been forthcoming.

6. MATERIAL AND CULTURES OF INLAND AND COAST FORMS OF *ARMERIA VULGARIS* WILLD.

Sets of turfs of this variable species have been collected in the years 1918—1922 from various places along the coast and from the interior and grown in cultures. The sets obtained from the west coast, viz. from Marstrand, Bohuslän, 1920; Varberg, Halland, 1920; Hallands Väderö, Scania, 1919 and Vellinge, Scania, 1918 show a remarkable variation as to the scape (hairy and smooth), length and shape of the bracts, hairiness of the calyx etc. Plants transplanted from localities on the south and east coasts of Scania, viz. from Trelleborg and Löderup (brought under culture in 1919 and from Vik, Vitemölle and Åhus (brought under culture in 1919) do not vary to the same extent. Cultivated material from the east coast farther to the north shows again some variation, viz. the set from Karlskrona, Blekinge (transplanted in 1920) and the set from Kalmar, Småland (also transpl. in 1920), while the sets obtained north of Kalmar, viz. from Oskarshamn (in 1920) and Västervik (in 1920) show but small variation. The same is also true of cultivated material from the interior, which includes series from Vombsjön (Öved) and Tollarp in Scania (brought under culture in 1919), from Jönköping in Småland (cultivated since 1920) and from Flottsund, Uppland (cultivated since 1921). Besides the cultivated collections mentioned above, smaller ones comprising only few individuals have been grown from additional localities. Cultivated series collected in 1922 include material from several points on the Norwegian coast (Bergen, Aalesund, Molde), but these will not be considered here at any length.

In order to make clear the different degree of variability within cultures from different localities a few of the series are tabulated below. In the following table (table 6) the individuals from the Marstrand culture are put together.

The only character changed through the cultivation is the length of the scape and the leaves (not shown in the table). The other characteristics typical of the different individuals have not undergone any observable changes during cultivation. Even such characteristics

as the time of flowering and the colour shade of the flowers, to be discussed in the following, have kept constant. The tabulated plants show, for the rest, very different combinations of characters; hairy scape, blunt bracts, and hairiness along the calyx ribs (field no. 1); smooth scape, blunt bracts, calyx hairy throughout (field no. 2); smooth scape, short bracts (e. g. bracts somewhat more elongated than in the case of the blunt ones) and hairiness of calyx mostly collected along the ribs (field no. 8), etc. In order to demonstrate the variation within

TABLE 6.

Field no	Length of longest scape in 1922 (in mm.)	Length of longest scape in 1920 (in mm.)	Character of scape (Hairy or Smooth)	Length of bracts	Shape of bracts	Hairiness of calyx
1	146	96	Hairy	Shorter than the head	Blunt	Along ribs
2	198	149	Smooth	» » » »	»	Hairy throughout
3	212	148	»	» » » »	»	Mostly along ribs
4	206	180	Hairy	» » » »	Short	»
5	188	146	Smooth	» » » »	»	Along ribs
6	202	186	»	» » » »	Blunt	»
7	218	211	»	» » » »	»	»
8	200	151	»	» » » »	Short	Mostly along ribs
9	168	98	Hairy	» » » »	Blunt	Along ribs
10	212	145	Smooth	» » » »	»	Mostly along ribs
11	225	172	Hairy	» » » »	»	»
12	211	183	»	» » » »	»	Along ribs
13	205	194	Smooth	» » » »	Short	»
14	216	159	»	» » » »	»	»
15	205	177	»	» » » »	»	»
16	195	165	Hairy	» » » »	Blunt	»
17	178	150	»	» » » »	»	Mostly along ribs

a set of plants collected farther to the south the Hallands Väderö culture is tabulated below (table 7).

The culture from Hallands Väderö differs in some points from the Marstrand culture. The length of the scape is longer in the Hallands Väderö culture, and the length of the bracts is variable. There is, moreover, a considerable variation as to the combination of characteristics typical of the different individuals in the series. As to the changes brought about through cultivation only the length of the scape has been influenced; it has become longer as have also the leaves. No other changes from 1920 to 1922 have been observed. There are,

however, some additional points of differences between the Väderö and the Marstrand cultures not shown in the tables. The leaves of the Marstrand plants are throughout narrower but thicker than those of the Väderö culture. They are about 2 mm. wide in the latter but hardly 1 mm. in the former plants. The anatomical structure of the leaf is also totally different in the two cultures. Fig. 74 c is a cross section of a leaf from a Marstrand plant taken from the culture in 1922. There are 3—4 layers of palisades on the upper side but none

TABLE 7.

Field no	Length of longest scape in 1922 (in mm.)	Length of longest scape in 1920 (in mm.)	Characters of scape (Hairy or Smooth)	Length of bracts	Shape of bracts	Hairiness of calyx
1	248	228	Hairy	Shorter than the head	Short	Along ribs
2	273	218	»	» » » »	Blunt	»
3	259	245	Smooth	» » » »	»	»
4	268	208	Hairy	» » » »	Short	Mostly along ribs
5	167	124	»	» » » »	Blunt	Along ribs
6	361	250	Smooth	» » » »	»	Hairy throughout
7	238	202	Hairy	As long as the head	Short	Mostly along ribs
8	300	252	»	Longer than the head	Long and pointed	Along ribs
9	234	140	Smooth	Shorter than the head	Blunt	»
10	305	168	Hairy	» » » »	»	Hairy throughout
11	260	164	»	» » » »	Short	Along ribs
12	339	185	»	» » » »	Blunt	Mostly along ribs
13	220	190	»	» » » »	»	Along ribs
14	226	200	Smooth	As long as the head	Short	»
15	294	260	Hairy	Shorter than the head	»	»

in the lower. The plants collected on the Norwegian coast seem to correspond with the Marstrand plants as to the length of the scape and with regard to the anatomical structure of the leaves. The Väderö plants resemble more the inland form of *Armeria vulgaris* as to the structure of the leaves. The leaf structure of the inland form (from the Tollarp culture, 1922) is seen in fig. 74 d. There is here a tendency to isolaterality, two layers of palisades being the rule on the upper side and 1—2 layers on the lower side. The Väderö plant has most often one layer of palisades on the lower side (cf. WARMING, 1897). The colour of the flowers is another point of difference; it is deep red in

the Marstrand plants but rose-coloured or pink in the Väderö plants. This difference is as plain now as it was in the first year of culturing the plants. When examined in the field it is found that the plant along the coast of Norway and in Bohuslän has this characteristic colour, while the change to the rose colour probably takes place in Hal-

TABLE 8.

Field n:o	Length of longest scape in 1922 (in mm.)	Length of longest scape in 1919 (in mm.)	Characters of scape (Hairy or Smooth)	Length of bracts	Shape of bracts	Hairiness of calyx
1	415	245	Smooth	Longer than the head	Long and narrow pointed	Along ribs
2	346	302	"	" " " "	" " " "	"
3	270	218	"	As long as the head	" " " "	"
4	429	285	"	Shorter than the head	Long and pointed	"
5	508	315	"	" " " "	Long and narrow pointed	"
6	440	298	"	" " " "	" " " "	"
7	405	325	"	Longer than he head	Long and pointed	"
8	412	317	"	" " " "	" " " "	"
9	333	297	"	As long as the head	Long and narrow pointed	"
10	369	316	"	" " " " "	" " " "	"
11	415	295	"	" " " " "	" " " "	"
12	412	288	"	Shorter than the head	" " " "	"
13	424	312	"	As long as the head	" " " "	"
14	368	314	"	Longer than the head	Long and pointed	"
15	495	287	"	" " " "	" " " "	"
16	367	310	"	Shorter than the head	Long and narrow pointed	"
17	418	219	"	" " " "	" " " "	"
18	426	245	"	" " " "	" " " "	"
19	505	275	"	" " " "	Long and pointed	"
20	492	300	"	As long as the head	" " " "	"

land. In Varberg and Falkenberg rose-coloured and deep red-coloured individuals are intermingled. The point to the south where the deep red-coloured plants disappear has not yet been determined. The rose colour is not only typical of the west coast plants to the south but also of the plants of the east coast and of the interior.

There is still another point of difference between the *Armerias* of the northern and southern parts of the west coast. The Bohuslän plant flowers in June and begins about two weeks earlier than the plant of the southern districts. The *Armerias* of the east coast and of the interior correspond in this respect with the plant of the southern

west coast. This difference in earliness is seen most beautifully in the cultures every year.

We are now ready to discuss the *Armerias* of the south coast and east coast of Scania, as well as the inland form. A culture from the east coast (from Vitemölle, cultivated since 1919) will serve to demonstrate the important characteristics. Table 8 lists the individuals of that culture.

It is at once seen from table 8 that the length of the scape is longer in this culture than in the west coast cultures; it is also seen that cultivation has increased the length of the scape considerably. There are certain characteristics common to all the individuals in the culture, viz. the smooth scape and the calyx rib hairiness, while the characters of the length and shape of the bracts vary and combine in different ways in the different individuals.

The cultures from the south coast and east coast of Scania, with the exception of one, to be dealt with below, show similarly a long and smooth scape and the hairiness of the calyx confined to the ribs. The *Armerias* of this nature begin to appear on the south coast of Scania. The exact point has not yet been determined but at Trelleborg the large majority of the plants already possess the characteristics in question. *Armerias* of this nature are now the only ones found along the sandy shores of southern and eastern Scania. There is one exception, as has just been said. Individuals with hairy scapes occur mixed with smooth ones on the flat rocks which make up the shore at Brantevik in eastern Scania (just south of Cimbrishamn). *Armeria* grows here as a chasmophyte in the upper supralittoral belt. On the sandy bluffs facing the sea, about 100 metres above the cliff locality, only smooth scaped plants have been found.

The cultivated material from Blekinge (the province to the east of Scania) is rather scanty. Small cultures from Karlshamn and Karlskrona include hairy individuals, however, and these are also found in cultures from Kalmar, on the east coast of Småland, and from the shores of Öland, although their number is few. These hairy scaped individuals from the east coast are by no means identical with the hairy individuals from the west coast (the scapes of the former attain, for instance, the length typical of the *Armerias* of the east coast in general, cf. fig. 38) but it is a remarkable fact that east coast sets with hairy individuals also include individuals which resemble the west coast *Armerias* with regard to the shape and length of the bracts. The *Armeria* population examined north of Kalmar has been found to agree

with the ordinary type of the southern and eastern coast of Scania as to scape and hairiness of calyx. The inland cultures of *Armeria vulgaris* also show a smooth scape and a calyx hairiness confined to the ribs. There are, however, considerable differences in other characteristics between the cultures of the inland form from the southern and middle parts of the country.

In the further discussion of the different forms of *Armeria vulgaris* reference will be made to table 9. This table lists the results of the examination of *Armerias* from 16 different localities (with 100 individuals from each locality) as to the character of the scape, length



Fig. 38. *Armeria vulgaris* from cultivated series. The type of the northern part of the Swedish west coast (to the left); the type of the southern part of the Swedish west coast (in the middle); and the type of the cliffs and salt meadows of the eastern coast (to the right). The three figured individuals have all hairy scapes.

and shape of the bracts, and as to hairiness of calyx. The material was collected in 1922, in great part by other persons, (viz. nos. 2, 3, 4, 5, 7, 10, 11, 12, 14, 15 and 16) who were carefully instructed, however, so as to ensure that no selection was made in collecting. Only one scape, the longest one, was taken from each turf. The length of the bracts has been graded in 3 classes, and the shape of the bracts in 4, beginning with the shortest and bluntest ones. The hairiness of the calyx has been graded as to the distribution of the hairiness, viz. throughout the calyx, mostly confined to the ribs and exclusively confined to the ribs. Nos. 1—12 refer to coast form collections, nos. 13—16 to inland

form collections. Among the former collections nos. 1—6 come from the west coast, nos. 7 and 8 from the south coast of Scania, and nos. 9—12 from the east coast.

In Bergen, on the west coast of Norway, only hairy individuals are found, which have short and mostly blunt bracts. On the west coast of Sweden the proportion between hairy and smooth-scaped in-

TABLE 9.

The variation of Armeria vulgaris in different habitats.

No.	Place of collection	Character of scape		Length of bracts			Shape of bracts				Character of calyx		
		Hairy	Smooth	Shorter than the head	As long as the head	Longer than the head	Blunt	Short	Longer and pointed	Longer and narrow pointed	Hairy throughout	Hairy mostly along the ribs	Hairy only along the ribs
1	Bergen, Norway. ...	100	—	91	8	1	67	27	6	—	37	20	43
2	Kristineberg, Boh.	12	88	95	2	3	55	38	7	—	11	10	79
3	Marstrand, »	38	62	100	—	—	58	35	7	—	11	37	52
4	Varberg, Hall.	55	45	99	1	—	88	10	2	—	18	16	66
5	Hall, Väderö, Scania	62	38	95	5	—	47	49	4	—	28	16	56
6	Limhamn, »	28	72	73	24	3	48	46	6	—	23	23	54
7	Trelleborg, »	—	100	91	9	—	38	61	1	—	1	7	92
8	Löderup, »	—	100	46	29	25	—	—	34	66	—	—	100
9	Vik, »	—	100	33	34	33	—	—	14	86	—	—	100
10	Kalmar, Smål.	5	95	75	22	3	36	51	12	4	5	16	79
11	Oskarshamn, »	—	100	6	28	66	—	—	32	68	—	—	100
12	Västervik, »	—	100	2	25	73	—	1	24	75	—	—	100
13	Vombsjön, Scania...	—	100	25	47	28	—	—	11	89	—	—	100
14	Vickleby, Öland	—	100	15	46	39	—	19	22	59	—	—	100
15	Mörbylånga, »	—	100	6	38	56	—	6	52	42	—	—	100
16	Flottsund, Uppl. ...	—	100	6	17	73	—	—	10	90	—	—	100

dividuals varies, and this is also the case with the shape of the bracts, while the length of bracts is rather uniform, being in the large majority of cases shorter than the head. At Trelleborg, on the south coast, only smooth-scaped individuals have been found, but the length of the bracts is still that typical of the west coast *Armerias*. At the next station on the south coast, Löderup, the length of the bracts is rather varying; the change in the form of the bracts is also marked, these being longer and more pointed in this collection. The changes seen in the rest of the coast collections (with the exception of the Kalmar collection) run in the same direction, that is, towards longer

and more pointed bracts. The characteristics typical of these latter collections, viz. smooth scape, bracts longer than the head and pointed, have, together with a few other characteristics which these collections also show, viz. tall scapes, and hairy calyx ribs, been attributed to the var. *elongata* Hoffm., sometimes considered a species, *A. elongata* (Hoffm.) Koch. The inland collections listed in the table sometimes resemble this *elongata* (no. 16), but in the majority of the individuals examined, the bract do not attain the length prescribed (nos. 13 and 14).

The cultures from the east coast, where hairy individuals occur scattered in the population, have been discussed above. A collection from Kalmar including such individuals is listed in the table (no. 10). The chief characteristic of these plants is perhaps the great mass of individuals with short and blunt-short bracts. The *Armerias* at Kalmar occupy the upper supralittoral belt of a marshy coast strip and grow in a salt meadow. The small cultures from Karlshamn and Karlskrona, which also included hairy and short-bracted *Armerias*, come, as was mentioned above, from exposed sea cliffs. *Armeria* grows here in large quantities. The locality at Brantevik, where hairy individuals also occurred, has already been dealt with. It should be remembered that the *Armerias* from southern and eastern Scania (excepting the Brantevik *Armerias*) come from the sandfields typical of these regions. The inland *Armerias* have been collected on sandfields or on gravelly hill slopes.

A few words should also be said as to the nature of the *Armeria* localities on the west coast. The low, hairy and thick leaved individuals exclusively found around Bergen grow as chasmophytes on the exposed sea cliffs typical of the shore line in this region. *Armerias* of exactly the same habitus grow in similar habitats around Molde and Aalesund. The mixed *Armeria* populations nos. 2—5 have been collected in similar habitats, while nos. 6 and 7 come from salt meadow with closed turf.

The regional grouping of the different forms of *Armeria vulgaris* growing within the area dealt with may be illustrated by the following types, which are intended to cover, to some extent, the grouping of the forms in nature:

a. *The type of the Norwegian coast*, as found at Bergen, Aalesund and Molde. The scape is rather short and densely clothed with hairs. The leaves are thick, narrowly linear (cf. fig. 74 c), and the bracts

are short and blunt in the majority of cases. It flowers early and has deep red flowers.

b. *The type of the northern part of the Swedish west coast.* This type closely resembles the former. However, smooth scaped and hairy scaped individuals occur mixed.

c. *The type of the southern part of the Swedish west coast.* Individuals with smooth and hairy scapes occur mixed. They are taller than the preceding types, and have flat and broader leaves, resembling those of the inland and sandfield type. The length of the bracts is about the same as in the preceding types, but individuals with the bracts blunt shaped and short shaped occur in about the same proportions. This type flowers about two weeks later than the preceding types, and the flowers are rose-coloured or pink.

d. *The type of the interior and of the sandfields of the southern and eastern coasts.* The scape of this type is quite smooth and taller than in any of the preceding types. The leaves are flat, and the anatomical structure of the leaf is very different from that of the types a and b, or almost isolateral (see fig 74 d). The length and the shape of the bract vary; they are in most cases, however, longer and more pointed than in the preceding types. The hairiness of the calyx is confined to the ribs. The colour of the flowers and the time of flowering correspond with type c.

e. *The type of the cliffs and salt meadows of the eastern coast.* Differs from the preceding mainly in regard to the bracts, which are shorter than the head, in the majority of the plants examined. The shape of the bracts is most often blunt-short. Hairy scaped individuals are found intermingled in a limited number with smooth scaped. — The type may be interpreted as an eastern representative of the west coast type c.

A few words should be said of the treatment of *Armeria vulgaris* by systematists. The extreme forms of the west coast (with short, hairy scapes; blunt bracts) have been called *A. maritima* (Mill) Willd., while the smooth scaped, tall and long-bracted forms, especially typical of the inland, have been brought together under the specific name *A. elongata* (Hoffm.) Koch. The number of »transitional forms» found in certain localities led systematists back to the Linnean one-species-conception and called the plant *Statice Armeria* L. or *Armeria vulgaris* Willd. This course has in our country been followed by WINSLOW (1879), who examined *Armerias* on the Swedish west coast and found the characteristics ascribed to *A. maritima* and *A. elongata*

combined in different ways. A similar course has been followed by NEUMAN (1883, 1887), who examined *Armerias* from Väderö, Kalmar and Öland and also found the characteristics combined in different



Fig. 39. *H. umbellatum*. Cult. cliff type from Hallands Väderö.



Fig. 40. *H. umbellatum*. Cult. dune type from Torekov.

ways. The subsequent treatment of the species in his flora (NEUMAN — AHLFVENGREN, 1901) closely follows the scheme adopted by MARSSON (1869), who recognizes one species, *A. vulgaris*, and three main varieties: *elongata*, *intermedia* and *maritima*, with additional forms subordi-

nated under these supposed main varieties. The difficulties led Focke (1902) to advocate another course. He recommends the keeping apart of *A. maritima* and *A. elongata*, which he considers «good» species, and the bringing together of the variable rest under a third species: *A. ambifaria*.

The treatment of the species in the systematic literature thus differs according as the region covered by the handbook corresponds with a region covered by mainly one form or by many. NEUMAN and MARSSON have felt the difficulties of the latter case, while for instance BLYTT, (1874), writing upon the flora of Norway, where the above type a has the largest distribution, readily makes this type a species (*A. maritima*) under which the remaining rarer forms are without trouble subordinated as less important varieties.

7. MATERIAL AND CULTURES OF INLAND AND COAST FORMS OF *HIERACIUM UMBELLATUM* L.

My attention was first drawn to the great variability of this species in 1917 while studying the distribution of different shore forms of inland species along the north-west coast of Scania. Two types occur in this region both differing from the ordinary inland form growing in Scania. The latter is a tall plant, erect or almost erect, with lanceolate leaves, about 10 mm. wide, and with rather contracted inflorescences. It is a typical woodland form and occurs throughout the province, except for a narrow stretch of land along the sea and a few isolated localities in the interior to be dealt with in the following. The two types found along the north-west coast were both confined to distinct habitats, the one occupying rocky and much exposed points on the coast strip, the other growing on sand dunes in the epilittoral belt. In a previous publication (Tureson, 1919 a) both forms were preliminarily classed as *Hieracium umbellatum* var. *dunense* Reyn. On that occasion the zonal distribution of plants accompanying the two forms was also dealt with (l. c. pp. 5 and 6).

Most of the individuals belonging to the sand dune form have less erect stems — some are more or less prostrate — and somewhat narrower leaves and less contracted inflorescences than the inland form. The cliff form is also more or less prostrate and has a bushy growth. When grown in cultures the leaves become much broader than those of the inland form. The inflorescences are also more expanded in the cliff form than in the inland form.

There are three points within this north-west region where the

massive rock appears, viz. at Kullen, where partly wooded mountain hills attain a height of 80—190 m. above the sea, at Hofs Hallar, to the north of Kullen, and on the west side of Hallands Väderö, the small island lying off the coast about 5 kilometres from Hofs Hallar. The cliff form is the only *Hieracium umbellatum* form found in these three localities. Typical sand dunes within the region are found at Torekov, a small fishing village about 4 kilometres to the south of Hofs Hallar, at Skelderviken, situated at the head of the bay with the same name, and at Nyhamn, about 10 kilometres to the south of Kullen. The sand dune form is strictly confined to these localities. In order to test the nature of these forms seeds were collected in 1917 from the cliff form of Hallands Väderö (seed collected from 10 turfs) and from the sand dune forms of Torekov and of Skelderviken (also from 10 turfs).



Fig. 41. *H. umbellatum*. Cult. dune types from Skelderviken (to the left) and from Nyhamn.

Before discussing these preliminary trials with *Hieracium umbellatum* a short account of the material of this species, now in culture, will be given.

It was soon found that the species in question was well suited to investigations of this kind. It has an extensive and almost uninterrupted distribution in Scandinavia and occurs in widely different habitats. Efforts were therefore made to obtain the plant from as many different localities as possible. The collection brought together since 1918 comprises at present more than 1200 well-developed turfs collected in different regions in Scandinavia and in different habitats within one and the same region. Beginning on the west coast the collection includes series from different points on the Norwegian coast — Trondhjem, Molde, Aalesund, Bergen. From the Swedish west coast series

List no.	Locality	Coll. no.	Year of transplant.	Number of cultivated individuals	Fig. nos. of cult. plants	Fig. nos. of leaves from cult. plants	Table no.
1	Kristineberg, Bohuslän	61	1921	12	—	—	10
2	» »	62	»	13	48	—	»
3	Marstrand, »	52	1920	13	49	—	—
4	Varberg, Halland	60	»	21	47	—	—
5	Falkenberg, »	63	»	20	46	67	11
6	» »	64	»	18	—	—	»
7	Halmstad, »	65	»	28	—	68	12
8	Hofs Hallar, Scania	130	»	15	—	—	13
9	Torekov, »	135	1918	21	40	69	14
10	Hallands Väderö, »	30	»	11	39	62	15
11	Skelderviken, »	138	»	28	41	70	16
12	Kullen, »	145	1920	12	43	63	17
13	» »	147	»	10	»	»	»
14	Nyhamn, »	154	»	26	41	71	18
15	Sofiero, »	157	»	19	44	—	—
16	Falsterbo, »	158	1918	20	—	—	—
17	Ystad (Nybroån), »	28	1919	21	—	—	—
18	Sandhammaren, »	26	1920	16	—	72	19
19	Skillinge, »	126	»	15	—	—	—
20	Cimbrishamn, »	124	»	12	—	—	—
21	South of Vik, »	125	»	9	—	—	—
22	North of Vik, »	123	»	11	—	—	—
23	Stenshuvud, »	164	1919	4	—	—	—
24	» »	119	1920	22	54	64—65	20
25	» »	120	»	20	—	—	»
26	Vitemölle, »	24	1919	15	—	—	21
27	» »	25	»	17	—	—	»
28	» »	96	1920	15	—	66	29
29	Åhus, »	31	1919	18	—	—	22
30	» »	32	»	21	50	—	»
31	East of Falkenberg, Halland	166	1920	10	44	—	—
32	Åstorp, Scania	159	»	23	»	—	—
33	Stehag, »	170	»	33	»	59—61	23
34	Vombsjön, »	48	»	22	55	73	24
35	St. Olof, »	27	1919	18	45	—	—
36	Kivik, »	121	1920	23	53	—	25
37	Torup, »	104	»	23	52	—	26

have been brought together from different points in the provinces of Bohuslän, Halland and Scania. The southern coast strip is also represented in the collection, and the east coast collections comprise series

from the southernmost point (Sandhammaren) to Stockholm. The inland series are best represented from Scania, but collections have been made in several other provinces, including Jämtland.

About half of the number of series has been in culture during only one vegetation period. These series are therefore excluded from the discussion and only those which have been in culture for at least two vegetation periods are here discussed at any length. In order to facilitate the survey of the material to be treated in the following the series are tabulated above. The place of collection, collection number, year of transplantation, number of cultivated individuals in each series,



Fig 42. *H. umbellatum*. Dried specimen from Hofs Hallar.

figure and table numbers — in the case of series figured or tabulated — are also given. The last seven series in the table pertain to inland and mixed series, and list nos. 9, 10, 11 and 18 refer to series raised from seeds.

We shall now examine the results of the cultivation of list nos. 9, 10 and 11. These were all raised from seeds. Although the number of plants obtained is rather limited, important differences are seen between the cliff material (list no. 10) and the sand dune material (list nos. 9 and 11). The former material (table 15, fig. 39) contains

only bushy broad-leaved forms, none narrower than 13 mm. The magnitude of the angles formed by the stems with the vertical varies with different individuals, and the same is the case with the characters of the leaf margin. The character of the inflorescence is uniform within the material, the shape of the inflorescence being umbelloid and expanded-spreading. The sand dune material from Torekov and Skelderviken (tables 14, 16; fig. 40, 41) differs much from the Hallands Väderö plants just discussed. The width of the leaves furnishes the most striking point of difference. In the material from Torekov only four individuals are more than 10 mm. wide, and in the material from Skelderviken none attains the width of 10 mm. Other characters vary

much within the two sets. As to the characters of the inflorescence the expanded inflorescence predominates while semi-umbelloids and, in the case of the material from Skelderviken, non-umbelloids occur



Fig. 43. *H. umbellatum*. Cult. cliff type from Kullen.



Fig. 44. *H. umbellatum*. Cult. inland types from east of Falkenberg (to the extreme left), Sofiero, Åstorp and Stehag.

mixed with the umbelloids. This is not the case in the Hallands Väderö material, where only umbelloids are found.

Besides Hallands Väderö there are, as has been mentioned above, two more points in the district where the massive rock appears on the coast, viz. Hofs Hallar and Kullen. *Hieracium umbellatum* is here a

rather common chasmophyte in the epilittoral belt and it also occurs higher up in the gnarled and wind-broken woody vegetation. A typical *H. umbellatum* chasmophyte from Hof's Hallar is seen in fig. 42. The leaves of these plants seldom exceed a width of 8–10 cm. in their natural habitat. When cultivated the leaves increase in width even in the first year after the transplanting. Table 13 shows the behaviour



Fig. 45. *H. umbellatum*. Cult. inland type from S:t Olof.

of *H. umbellatum* chasmophytes from Hof's Hallar which have been kept in culture during three vegetation periods. The leaves do not attain the length of the Väderö plants (which fact may be due to the younger age of the material) but the width of the leaves varies within about the same limits as in the Väderö plants. The stems are often more depressed than in the Väderö plants and deviations from the average of these plants are also seen in the characters of the leaf margin and of the inflorescence.

The *H. umbellatum* growth in the isolated sand dune fields between Hof's Hallar and Kullen has already been dealt with. The sea cliffs of Hallands Väderö and of Hof's Hallar reappear in more gigantic dimensions at Kullen. The list nos. 12 and 13 belong to series brought home from this

locality and cultivated since 1920. Table 17 (fig. 43) gives the characters of the separate individuals in these series. The similarity between these series and the Hof's Hallar collection is at once seen. The average width of the leaves is about the same, and the characters of the leaf margin and of the inflorescence vary much in the same way.

The cliff region of Kullen ceases abruptly to the south and the

sandy beach typical of the larger part of the coast strip of Halland and Scania becomes prevalent. At Nyhamn, about 10 kilometres to the south of Kullen, extensive fields of *H. umbellatum* are found. It grows here in the epilittoral dunes. Table 18 (fig. 41) gives the result of the cultivation of a series of individuals from this locality, which were brought home in 1920. When this series is compared with the material from Skelderviken, table 16, the nearest sand dune region to the north, the similarity in characters is found to be striking. This



Fig. 46. *H. umbellatum*. Cult. dune type from Falkenberg.

is true not only of the width of the leaves but also of the characters of the leaf margin and of the inflorescence.

It has already been stated that the dune form and the cliff form of this region differ widely from the form growing in the interior of Scania. It will be convenient at this stage to discuss this inland form more fully. The most important point of difference between the inland form and the coast forms just discussed is the erect habit of growth in the former and the more or less plagiotropic growth of the latter. The stems of the inland type may form an angle with the vertical but only at the very base. By far the greater part of the stem stands erect or almost erect in most of the inland individuals, as is clearly seen in the photographs (figs. 44, 45). The average width

of the leaves of the inland form is somewhat greater than in the extreme sand dune form but considerably smaller than in the cliff form. The characters of the leaf margin vary with the individuals much in the same way as in the coast forms, but the characters of the inflorescence is peculiarly uniform, the umbelloid and contracted inflorescence being the rule. The type occurs as a woodland plant in most parts of the province, and series belonging to this type have been collected at various points. List no. 35 belongs to a series cultivated since 1919 and collected at St. Olof, a village situated in eastern Scania about 9 kilometres from the sea. A plant belonging to this series is represented in fig. 45. Another series of the inland form, brought



Fig. 47. *H. umbellatum*. Cult. cliff type from Varberg.

home from woodlands at Stelhag (in the middle part of the province), is tabulated in table 23 (shown to the extreme right in fig. 44). The characteristic features of the type are clearly seen in these plants, which have been in culture since 1920.

We are now ready to examine the cultivated material of *Hieracium umbellatum* brought home from various places on the coast strip to the north and south of the north-west region of Scania discussed above. The coast to the north is a sandy beach running through the southern and middle part of Halland, while the coast strip of the northern part of this province, as well as that of Bohuslän, is much broken and rocky. We should accordingly expect to find the dune form distributed in the southern and middle parts of Halland and the cliff form in the northern part of Halland and in Bohuslän. This is just what happens. The

dune form starts a few kilometres north of Båstad and runs through the whole southern and middle parts of the province, occupying its usual habitat in the epilittoral belt of the beach. It is succeeded by the cliff form somewhere between Falkenberg and Varberg. Three series of the sand dune form are tabulated here, viz. list no. 7 from Hahnstad (table 12), situated between Båstad and Falkenberg, and list nos. 5 and 6 from the latter place (table 11, fig. 46). List no. 5 includes some rather broad leaved individuals to be discussed more fully in the following. Fig. 44 (the plant to the extreme left) shows a plant belonging to the inland form (list no. 31) collected about 10 kilometres to the east of Falkenberg in the inland, where the dune form typical of the beach is entirely wanting. The cliff form takes the place of the dune



Fig. 48. *H. umbellatum*. Cult. cliff type from Kristineberg.

form somewhere north of Falkenberg, as stated above. Fig. 47 shows a typical plant from the series from Varberg cultivated since 1920 (list no. 4). On the rocky coast of Bohuslän the cliff form is the only one hitherto found. List nos. 1, 2 and 3 refer to cultivated series from this coast strip (figs. 48, 49). The first two series have been tabulated in table 10. While as a whole these series much resemble the former cliff form series, some characteristics, for instance the width of the leaves, seem to differ. The leaves in rather many of the individuals are of less than the average width in former cliff form series. This is probably due to the fact that the series in question have been in culture only for a relatively short time, or since 1921. The plants were all more narrow-leaved at the time of transplanting from their natural habitat. The average width of ten leaves on each of the first five individuals of list no. 1 were ascertained in 1921 at the time of collecting:

these values (in mm.) compared with those obtained from the same individuals in the culture of 1922 (cf. table 10) are given below:

Field no.	01	02	3	4	5
1921	10	11	12	13,5	13
1922	13	—	17	16	17

The increase in the width of the leaves after the cultivation of the plants forms an analogue to the Hof's Hallar plants mentioned above (cf. also fig. 42). For a further discussion of the same topic see below.

The *H. umbellatum* vegetation south of the northwest region of



Fig. 49. *H. umbellatum*. Cult. cliff type from Marstrand.

Scania already discussed is of much interest. The detailed discussion of the plants collected here (list nos. 15 and 16) as well as of the plants from the southern coast of the province (list no. 17) will be deferred to a following chapter. It suffices to state here that the plants belonging to these series show resemblance with the inland form, the result being a limitation of the distributional area of the *H. umbellatum* growth on the beach in these places.

We shall instead examine the distribution of *H. umbellatum* forms on the east coast of Scania. A small belt of *H. umbellatum* runs along the entire length of this coast strip from the extreme southern point (Sandhammaren) to Blekinge, the province to the east of Scania.

It is much to the purpose to start with the description of *H. umbellatum* from the northern part of this eastern coast strip of Scania and then to proceed southwards. List nos. 29 and 30 refer to series from Åhus, the former series collected in the epilittoral belt, which is here composed of an almost closed turf of vegetation, the latter series collected in the moss-carpeted floor of the planted pine woods some hundred metres from the beach. Table 22 gives the result of the cultivation of these series, which were started in 1919. The similarities as to the characters of leaf, leaf margin and inflorescence between these series and the dune form series from the west coast is at once seen. There is, however, one striking point of difference between the ma-

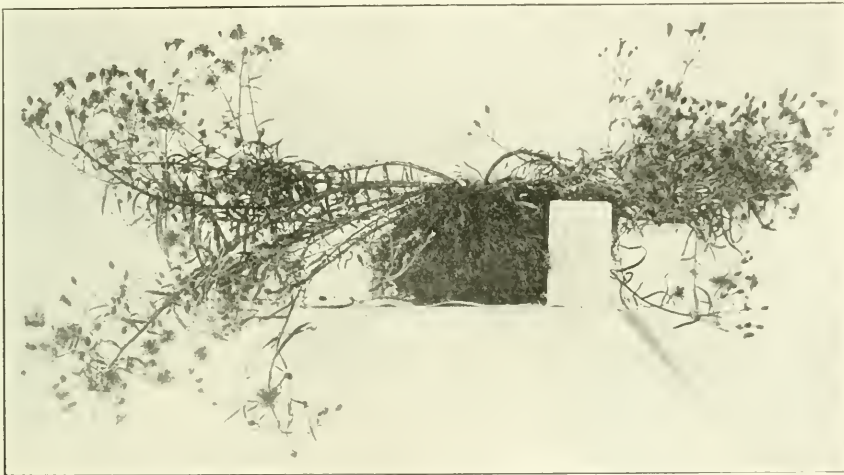


Fig. 50. *H. umbellatum*. Cult. dune type from Åhus.

terial from Åhus and the west coast dune forms. The large majority of the individuals from Åhus show extreme prostrateness of their stems and keep the terminal part of the stems at an angle of about 45° with the vertical (see also fig. 50). The same extreme prostrateness may be found in the west coast dune series but the regularity of this feature is much greater in the former series than in the latter. There is another point of difference between the two series, which is not shown in the tables. The west coast dune forms show a marked shoot-regenerating power during autumn, while the eastern dune representative does not show any, or a very weak, power of regeneration. The distribution of this characteristic form is rather extensive. It occurs frequently in the sand field area of north-eastern Scania and ceases to the west, where the sand fields cease, grading into the inland form of the

woodlands. Large collections have been made in the neighbourhood of Christianstad, and these contain apparently all kinds of types as to angles of stem and leaf characters, making a very strong impression of a population composed of hybrids between the inland form and the prostrate dune form and their segregates. These series have been in culture during only one vegetation period and are therefore not discussed any further here. The same is true of series brought together from the eastern limit of the area in Scania occupied by the prostrate form. It occurs sporadically in its typical habitus to about Skräbbe-

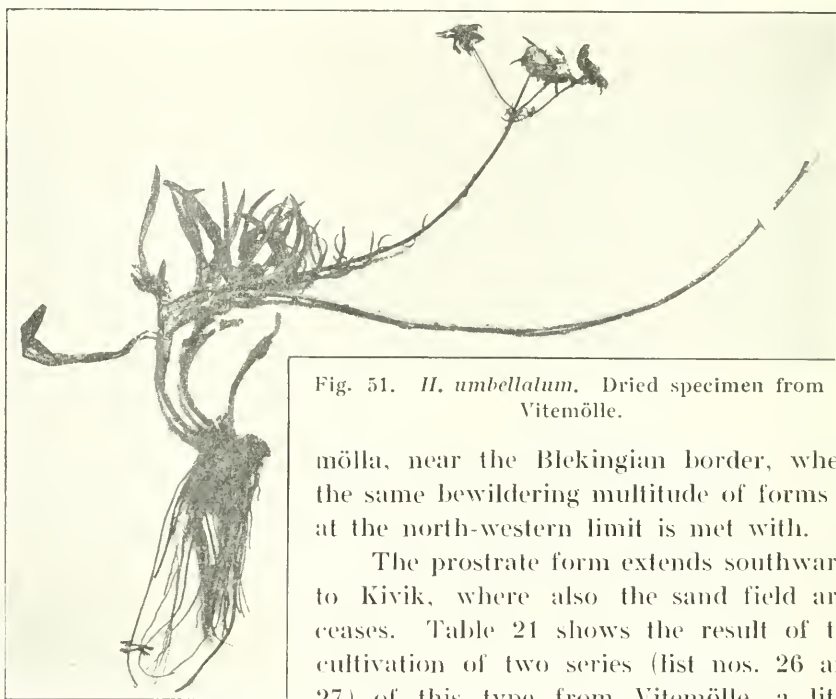


Fig. 51. *H. umbellatum*. Dried specimen from Vitemölle.

mölle, near the Blekingian border, where the same bewildering multitude of forms as at the north-western limit is met with.

The prostrate form extends southwards to Kivik, where also the sand field area ceases. Table 21 shows the result of the cultivation of two series (list nos. 26 and 27) of this type from Vitemölle, a little north of Kivik. They were brought under culture in 1919. List no. 27 comes from the closed dunes and arenacious fields a few hundred metres from the beach, and list no. 26 contains individuals collected on the *Elymus*-dune of the beach, where this form grows but very sparsely. When these series are compared with the series from Åhus the close correspondence between the two sets is at once seen.

The morphological features of the plant in culture differ somewhat from the habitus characteristic of the plant growing in its natural habitat. Fig. 51 gives a picture of a typical plant as found in the field. A more or less horizontal position is taken up by the stem as

soon as the shoot reaches the surface of the ground. Usually not more than one stem develops in each vegetation period. The plant illustrated was collected in 1920. The stem belonging to the shoot generation of the preceding year is still attached to the plant as well as the one from 1918 (the stump to the right). The leaves are smaller and more narrow than in the cultivated plants, etc. In order to follow the changes of the plants when moved to the experimental field 15 specimens were measured and characterized in their natural habitat (Vitemölle) in 1920; they were then put into culture and noted in 1921 and 1922. Table 29 (list no. 28) summarizes the results. The increase in the growth of the stem is already considerably in 1921. The magnitude of the angle of the stem base is about the same in 1920 and



Fig. 52. *H. umbellatum*. Cult. mixed population from Torup.

in 1921, but the terminal part of the stem has turned upwards in almost every case. It is now kept at an average angle of less than 40° with the vertical and this angle is about the same in 1922. The change in the width of the leaves is also remarkable: in 1921 the have already attained more than twice their original width, while the change in 1922 is slight. As to the characters of the leaf margin slight changes have taken place, but the characteristics attained in 1921 remain unchanged in every case in 1922. The *reaction-type* (Tureson, 1922) of this prostrate dune form as well as of the forms of Hof's Hallar and Kristineberg discussed above is thus seen to be rather different in different habitats even if such extreme stages as those typical of *Centaurea jacea* and *Succisa pratensis* in certain habitats do not become realized in the case of *Hieracium umbellatum*.

The sandfield area at Vitemölle is narrow. Woodlands already

replace the sandfields at about 3.5 kilometres from the sea. The prostrate dune form is found quite typically 1.5 kilometres from the sea. At Torup, due west of Vitemölle and 3.5 kilometres from the coast, the woodlands are found to harbour a mixed population. Table 26 (list no. 37) tabulates the results of the cultivation of a number of individuals from this locality, which have been in culture since 1920. It seems more than probable that this collection includes mongrels between the prostrate dune form and the erect inland form and their segregates. Fig. 52 gives a picture of two extremes and one intermediate plant (as to angle of stem), all three members of this collection. The intermediate zone, where the mixed population occurs, is probably



Fig. 53. *Hieracium umbellatum*. Cult. mixed population from south of Kivik.

quite narrow, as cultivated material collected at random at a distance of less than 1 kilometre to the west of Torup contains the typical woodland variety only. The southern limit of the extensive sandfield area touches Kivik, as has been said before, and then the woods begin. Here again mixed *H. umbellatum* populations are found. List no. 36 refers to a collection of plants made 0.5 kilometre to the south and a little to the west of Kivik. Table 25 (fig. 53) gives the result of the cultivation of these individuals, which have been in culture since 1920. The table includes extremes, as to the angle of stem, as well as intermediates. The width of the leaves is on the average greater than in the mixed population from Torup, which is probably due to the fact that the *H. umbellatum* form inhabiting the woody coast region to the south of the sandfield area is a broad-leaved type to be discussed more fully in the following. The extension of the intermediate zone harbouring this multitude of

forms differing as to angle of stem, width of leaf, and characters of inflorescence has not been determined. The woody coast strip to the south, which replaces the sandfields, terminates in Stenshuvud, a hill rising 150 m. above sea. The steep slopes towards the sea are covered with beech, oak, aspen, ash etc., and *Hieracium umbellatum* is found growing here in the supralittoral and epilittoral belts of the rocky beach. A few individuals of the plant were brought home and put under culture in 1919 (list no. 23). The remarkable habitus called for another visit to the locality and in 1920 the region was once more investigated and a larger collection was made and put under culture (list nos. 24 and 25; fig. 54). Table 20 summarizes the results. The remarkable width of the leaves, equaling that of the cliff forms from the west coast, is here combined with an almost erect growth. It is not only in this latter character that this variety resembles the inland variety, but also as to the more or less contracted inflorescences. The broadness of the leaves was not as well marked in the natural habitat as it has since become in the cultures, the plant resembling in this respect the behaviour of the cliff form representative of the west coast. The average width of ten leaves (the middle ones) on each of the first five individuals of list no. 24 was ascertained in 1920 before transplanting; these values (in mm.) compared with the values obtained from the same plants in culture in 1921 and 1922 are given here:



Fig. 54. *H. umbellatum*. Cult. cliff type from Stenshuvud.

Field no.	1	2	3	4	5
1920	15,5	18	12	14	16
1921	17	24,5	19	19	19,5
1922	18	23	16	20	21

The region south of Stenshuvud is a sandy beach with scantily wooded epilittoral bluffs, rising about 20 m. List no. 22, collected 1 km. north of Vik, comes from this region. This series does not contain any plant that attains the great leaf width of the broadest Stenshuvud plants; it includes, on the contrary, a few individuals which are more narrow-leaved than any of the plants contained in the Stenshuvud collection. A small area of much fissured rock 1 km. south of Vik has been found to harbour a *H. umbellatum* chasmophyte which in culture (list no. 21) is found to be almost prostrate with rather broad leaves, although of less width than the broader leaved Stenshuvud plants. Farther to the south, between Baskemölla and Cimbrishamn and about 9 kilometres from Stenshuvud, closed dunes and beach flats covered with a low vegetation, mainly composed of an often continuous turf of mosses and lichens, begin to appear. The prostrate dune variety from the closed dunes and arenacious fields north of Kivik reappears here in its most typical form. List no. 20 refers to a collection of this form brought home in 1920 from the locality in question. It is not to be distinguished from the variety found north of Kivik. It is therefore a natural assumption that the indistinct *H. umbellatum* forms found on the coast strip between Stenshuvud and this point represent mongrels between the erect, broad-leaved Stenshuvud variety and the prostrate dune variety of the southern centre of distribution.

The closed dunes and the beach flats continue southwards. List no. 19 refers to collection made at Skillinge. This series is made up of the typical prostrate dune form. At a point situated about 5 kilometres to the south of Skillinge the large drift-sand region of Sandhammaren begins. This region was visited in 1919 and seeds from a number of plants of *H. umbellatum* growing in the drifting sand were brought home. A series of individuals raised from these seeds is tabulated in table 19. Important differences between these plants and the prostrate dune variety are at once seen. The variation in the magnitude of the angle of the stem is rather large, but the extreme prostrateness characteristic of the prostrate dune variety is not attained in any of the plants. The Sandhammar form shows greater similarity

to the west coast dune form in this respect, and the same holds true as regards the power of regeneration in autumn, which equals, if it does not surpass, that of the latter form. The considerable length of the leaves of these plants should also be noted. Series of the Sandhammar form have also been collected on the dunes at Löderup on the southern side of the drift-sand region. These series show exactly the same characteristics. The extent of the area covered by the *H. umbellatum* form in question has also been determined. It extends from a little to the west of Löderup on the south side to a point on the east side due east of Kylsgård; the form covers, in other words, almost exactly the area occupied by the drift-sand. The prostrate dune form of the north and the Sandhammar form of the south meet on the beach at Kylsgård, and series from this place show a strongly mixed population. These latter series have only been in culture during one vegetation period and are therefore not tabulated



here; however, no doubt remains as

Fig. 55. *H. umbellatum*. Cult. dune type from Vombsjön.

to the mixed character of the series in question. The *H. umbellatum* population at Kylsgård will be referred to once more in a later chapter.

A dune form from the interior of the province has also been located. This is found growing on the lacustral dunes at Vombsjön near Öved station together with *Carex arenaria*, *Elymus arenarius*, *Corynephorus*, etc. Table 24 (list no. 34; fig. 55) gives the results of the cultivation of a series from this locality cultivated since 1920. It should be said that the ordinary, erect inland form grows abundantly close by, for instance at Skartofta, at a distance of about 4 kilometres from the lake locality.

Before summarizing the facts with regard to the different forms of *H. umbellatum* a few words should be said of the castration experiments and the crosses made. It is known that nearly all the species belonging to the subgenus *Archieracium* are apogamic; *H. umbellatum* belongs to the very few sexual ones (OSTENFELD, 1906, 1921). The castrations I have made in order to find out whether this rule holds for the different forms of the species in my cultures includes trials with two individuals (5—10 flower-heads on each plant) each from the list



Fig. 56. *H. umbellatum*. *Fi*-plants from a cross within the Falkenberg dune type.

nos. 3, 10, 11, 16, 18, 26 and 33. The upper half of the unopened flower-heads was cut off with a razor in the way recommended by OSTENFELD. The results were in all cases negative; no fruits developed. Other experiments with the same plants in the same year (1921) showed that these plants were self-sterile when isolated with pergamin bags. In a few heads (list nos. 26 and 33) the seeds seemed at first to begin to ripen but none gave full fruits capable of germination. Crosses between some of the varieties were made during the summer of 1922, and these will be followed up later on. A few crosses between different plants of the same variety were made in 1921. Although the number

of plants obtained as a result of these crosses is too small to be of any great value, two series of these crosses are tabulated here. Table 27 shows the composition of the offspring from a cross between two individuals belonging to the Falkenberg dune variety. Fig. 56 gives a picture of some of the one year old F_1 -plants from this cross. Table 28 tabulates the individuals obtained from a cross between two plants belonging to the Kristineberg cliff form, and fig. 57 shows some of the



Fig. 57. *H. umbellatum*. F_1 -plants from a cross within the Kristineberg cliff type.

young F_1 -plants. Fig. 58 illustrates a few F_1 -plants (the first row still in the rosette-stage) obtained by a cross within the prostrate dune variety from Vitemölle. The distinctive characters of the cliff form (broad leaves, contracted growth) and of the dune forms (narrower leaves, slender growth) are clearly seen from the photographs. Furthermore, the results of the breeding experiments show sufficiently clearly that the characters typical of these varieties are hereditary and are not modifications due to the direct effect of the environment.

In order to bring out the differences in the leaves between the

different *H. umbellatum* forms dealt with above I have thought it well to reproduce some series of leaves collected from the cultivated material in October, 1922. No selection has been made in collecting the material, but any plant with leaves in good conditions at that time has been included in the series. The leaves have then been approximately arranged according to their width starting with the broadest ones. Three or four leaves of different sizes have been taken from each plant, and the numerals at each of the leaf groups on the photographs refer to the field numbers of the plants in the tables. These photographic reproductions run from figs. 59—73.



Fig. 58. *H. umbellatum*. *F*₁-plants from a cross within the Vitemölle dune type.

It should not be thought that the points of difference between the above discussed *H. umbellatum* forms are exhausted by the distinctions already made and shown. There are marked differences in the anatomical structure of the leaf in the various forms. The cultivated inland form of the woodlands has generally two, at the most three, layers of palisades (fig. 76 a). Cross sections of leaves of the cultivated Sandhammar dune form (list no. 18) generally show four layers of palisades (fig. 76 b), and both the dune form from the west coast and the prostrate dune form from the eastern coast have generally 3—4 of these layers. Leaves of the cultivated cliff forms from the west coast have about the same thickness as those of the dune forms, but the cells, even those

of the upper epidermis, are considerably distended (fig. 76 c). The Stenshuvud cliff form has leaves of about the same thickness and structure but the cells are less distended than in the west coast cliff forms.

There are also marked differences in the time of flowering and fruiting in the different forms. The dune forms begin to fruit as soon as the first part of September, while the cliff forms do not reach this stage until the last part of September or the first part of October. The inland form is intermediate in this respect.

The above discussed cultivations of *Hieracium umbellatum*, collected in different habitats, tend to bring out the facts that the hereditary variation within the species is considerably marked and that the variations occurring within the limited geographical area dealt with roughly group themselves in five types, viz.:

a. The *dune type of the shifting dunes* from the drift-sand and white dunes along the western coast and the Sandhammar region. This type comprises individuals with rather narrow leaves and slender, less erect, sometimes more or less prostrate, stems. The power of shoot-regeneration during autumn is marked. The rather tough and thick leaf shows 3—4 layers of palisades. The fruiting stage is reached in the first part of September. — The form growing on the lacustral dunes at Öved is probably to be referred to this type.

b. The *dune type of the arenaceous fields* and stationary dunes from the eastern coast strip of Scania. The individuals of this type closely resemble the dune form of the shifting dunes but differ in the extreme prostrateness of their stems. The power of shoot-regeneration during autumn is less marked or is entirely wanting.

c. The *sea-cliff type of the west coast*. This type comprises broad-leaved individuals, more or less prostrate. The cells of the leaves are considerably distended. The growth-form of the plants is contracted and bushy. The fruiting stage is first reached in the latter part of September or in the beginning of October.

d. The *sea-cliff type of the east coast* (Stenshuvud) resembles the preceding form as to the broadness and thickness of the leaves. The growth-form, however, is quite different: the plants are tall and almost as erect as plants of the inland type. The fruiting stage is reached at the same time as in type c.

e. The *woodland type of the interior* from open, herbiferous

woods. This type comprises stout, erect plants with lanceolate leaves of intermediate width. They are tough but considerably thinner than the leaves of the preceding types and have only two, at the most three, layers of palisades. The inflorescences are generally umbelloid and contracted. The fruiting stage is reached in September.

Additional forms will probably become added when the complete collection of Scandinavian *H. umbellatum* material has been tried in cultures. As to the systematic and nomenclative side of the question no efforts have been made to ascertain whether or not forms similar to those discussed above have been distinguished and named by systematists. To judge from the characteristics of the forms described in Scandinavian manuals, viz. *f. coronopifolium* (Gmel) Fr., *f. dunense* Reyn., *f. filifolium* Fr. and *f. humile* Schum., no difficulty would probably be encountered in finding all these forms growing together on the same spot.

TABLE 11. *Hieracium umbellatum* Nos. 63 and 64. Falkenberg.
Plants in culture since 1920. Notes taken 1922.

Field number	Angle of stems		Characters of leaves		Characters of leaf margin			Characters of inflorescence	
			Length in mm.	Width in mm.	Curved. Straight.	Ciliolate. Almost Smooth. Smooth.	Entire. Denticulate. Dentate. Laciniate.	Umbelloid. Semi-umbelloid. Non-umbelloid.	Contracted. Expanded. Spreading.
	At base	At top							
63,1	50	20	102	8	Straight	Ciliolate	Dent.-Laciniate	Semi-umbelloid	Expanded
2	45	30	120	12	»	»	Laciniate	Umbelloid	»
3	80	45	73	7,5	Curved	»	Dentate	Semi-umbelloid	»
4	70	60	105	10	»	»	Laciniate	Umbelloid	Spreading
5	80	45	92	12	Straight	»	»	—	—
6	50	10	101	7	»	»	Entire	»	Contr.-Expanded
7	65	10	86	9	»	Smooth	Laciniate	»	Expanded
8	80	30	100	13	»	Ciliolate	»	—	—
9	65	60	—	—	—	—	—	—	—
10	—	—	—	—	—	—	—	—	—
11	30	10	85	7	»	Smooth	Dentate	»	»
12	90	90	83	6	Curved	Ciliolate	Dent.-Laciniate	»	»
13	45	20	—	—	—	—	—	—	—
14	70	45	105	9	Straight	»	Laciniate	»	Exp.-Spreading
15	85	45	98	6,5	»	Smooth	»	»	Expanded
16	65	10	—	—	—	—	—	—	—
17	60	45	—	—	—	—	—	—	—
18	15	0	—	—	—	—	—	—	—
19	85	45	66	7,5	»	Ciliolate	Dentate	»	Expanded
20	60	20	115	8,5	Curved	»	Laciniate	»	Contr.-Expanded
64,1	90	45	75	6,5	»	»	Dentate	»	Expanded
2	55	45	112	8	Straight	»	»	—	—
3	70	45	81	10	Curved	»	Dent.-Laciniate	»	Contr.-Expanded
4	75	30	96	5,5	Straight	»	Dentate	»	Expanded
5	80	20	—	—	—	—	—	»	Contr.-Expanded
6	85	45	100	9,5	»	»	Dent.-Laciniate	—	—
7	60	45	—	—	—	—	—	»	Expanded
8	45	30	—	—	—	—	—	—	—

Field number	Angle of stems		Characters of leaves		Characters of leaf margin			Characters of inflorescence	
	At base	At top	Length in mm.	Width in mm.	Curved. Straight.	Ciliolate. Almost Smooth.	Entire. Denticulate. Dentate. Laciniate.	Umbelloid. Semi-umbelloid. Non-umbelloid.	Contracted. Expanded. Spreading.
9	85	45	—	—	—	—	—	Umbelloid	Expanded
10	90	80	—	—	—	—	—	»	Exp.-Spreading
11	70	10	87	8	Curved	Smooth	Laciniate	»	Expanded
12	—	—	—	—	—	—	—	—	—
13	60	60	—	—	—	—	—	—	—
14	70	30	—	—	—	—	—	—	—
15	65	45	—	—	—	—	—	»	Contracted
16	80	0	—	—	—	—	—	»	Expanded
17	90	20	78	6	»	Ciliolate	Dentate	»	»
18	60	45	90	6	»	»	Dent.-Laciniate	»	Contracted

TABLE 12. *Hieracium umbellatum* No. 65, Halmstad.

Plants in culture since 1920. Notes taken 1922

1	45	45	90	7	Straight	Ciliolate	Dentate	Umbelloid	Expanded
2	45	0	—	—	—	—	—	»	»
3	45	10	80	7	Curved	»	»	»	Contr.-Expanded
4	80	0	—	—	—	—	—	»	Expanded
5	—	—	—	—	—	—	—	—	—
6	45	0	110	10	»	»	Denticulate	Non-umbelloid	Contr.-Expanded
7	—	—	—	—	—	—	—	—	—
8	70	30	—	—	—	—	—	Umbelloid	Expanded
9	80	45	—	—	—	—	—	Semi-umbelloid	»
10	80	45	75	7.5	Straight	»	»	»	»
11	70	30	86	10	Curved	»	»	Umbelloid	»
12	65	15	—	—	—	—	—	»	»
13	90	10	74	7	Straight	»	»	»	»
14	45	10	98	10	Curved	»	Dent.-Laciniate	»	»
15	90	25	80	6	»	»	Entire	»	»
16	90	20	—	—	—	—	—	—	—
17	—	—	—	—	—	—	—	—	—
18	45	0	—	—	—	—	—	Semi-umbelloid	»

Field number	Angle of		Characters of leaves		Characters of leaf margin			Characters of inflorescence	
	Stems		Length in mm.	Width in mm.	Curved. Straight.	Ciliolate. Almost Smooth. Smooth.	Entire. Denticulate. Dentate. Lacinate.	Umbelloid. Semi- umbelloid. Non- umbelloid.	Contracted. Expanded. Spreading.
	At base	At top							
19	90	45	—	—	—	—	—	Umbelloid	Expanded
20	80	20	—	—	—	—	—	"	"
21	75	15	105	7	Straight	Ciliolate	Dentate	"	Exp.- Spreading
22	45	0	76	7.5	Curved	"	"	"	Expanded
23	—	—	—	—	—	—	—	—	—
24	70	0	—	—	—	—	—	—	—
25	80	45	—	—	—	—	—	—	—
26	45	30	72	7	Straight	"	"	Umbelloid	"
27	70	45	75	7	Curved	"	"	"	"
28	45	10	—	—	—	—	—	"	Exp.- Spreading

TABLE 13. *Hieracium umbellatum* No. 130. Hojs Hallar.

Plants in culture since 1920. Notes taken 1922.

1	25	10	74	22	Straight	Ciliolate	Dentate	Umbelloid	Expanded
2	90	20	56	17	"	"	"	"	"
3	—	—	—	—	—	—	—	—	—
4	90	50	88	21	"	"	"	"	"
5	90	40	63	19	"	"	"	"	"
6	75	20	48	16	"	"	Denticulate	Semi- umbelloid	"
7	90	55	75	19	Curved	"	"	Umbelloid	"
8	—	—	—	—	—	—	—	—	—
9	90	30	63	17	Straight	Almost Smooth	Dentate	"	Exp.- Spreading
10	90	20	62	20	"	Ciliolate	Denticulate	"	Expanded
11	90	15	82	17	"	"	Dentate	"	"
12	90	50	65	19	"	"	Denticulate	Umbelloid	"
13	90	40	63	20	"	"	Dentate	"	"
14	90	30	52	15	"	"	Denticulate	Non- umbelloid	"
15	70	30	73	19	"	Almost Smooth	"	Umbelloid	"

TABLE 14. *Hieracium umbellatum* No. 135, Torekov.

Plants raised from seeds, coll. 1917. Notes taken 1922.

Field number	Angle of stems		Characters of leaves		Characters of leaf margin			Characters of inflorescence	
	At base	At top	Length in mm.	Width in mm.	Curved. Straight.	Ciliolate. Almost Smooth. Smooth.	Entire. Denticulate. Dentate. Laciniate.	Umbelloid. Semi-umbelloid. Non-umbelloid.	Contracted. Expanded. Spreading.
1	90	20	66	10	Straight	Ciliolate	Dentate	Umbelloid	Expanded
02	90	20	—	—	—	—	—	»	»
03	90	10	50	7	»	»	»	Semi-umbelloid	»
4	45	20	56	10	—	—	—	Umbelloid	Exp.-Spreading
5	—	—	—	—	—	—	—	—	—
6	60	45	92	15	»	»	Laciniate	»	Expanded
7	90	20	80	8	»	»	Dentate	»	»
8	60	0	65	8	»	»	»	»	»
9	65	25	67	12	»	»	»	Semi-umbelloid	»
10	90	20	56	10	»	»	»	Umbelloid	»
11	50	0	71	8	»	Almost Smooth	Denticulate	»	»
12	90	30	75	10	»	»	»	»	»
13	55	10	78	7	Curved	Smooth	Dentate	»	»
14	90	20	64	13	Straight	Ciliolate	Denticulate	Semi-umbelloid	»
15	90	10	57	8	»	Smooth	»	Umbelloid	»
16	65	45	68	9	»	Almost Smooth	Denticulate	Semi-umbelloid	»
17	90	35	64	13	»	»	»	»	»
018	75	45	50	6	Curved	Smooth	Entire	Umbelloid	»
19	40	25	76	10	Straight	Ciliolate	Dentate	Semi-umbelloid	»
0020	90	60	—	—	—	—	—	Umbelloid	»
21	45	0	77	12	»	»	»	»	»

TABLE 15. *Hieracium umbellatum* No. 30, Hallands Väderö.

Plants raised from seeds, coll. 1917. Notes taken 1922.

1	45	30	75	20	Curved	Ciliolate	Dentate	Umbelloid	Expanded
2	70	45	70	17	»	»	Dent.-Laciniate	»	Exp.-Spreading
3	90	45	80	22	»	Smooth	Dentate	»	Expanded

Field number	Angle of stems		Characters of leaves		Characters of leaf margin			Characters of inflorescence	
	At base	At top	Length in mm.	Width in mm.	Curved. Straight.	Ciliolate. Almost Smooth. Smooth.	Entire. Denticulate. Dentate. Laciniate.	Umbelloid. Semi-umbelloid. Non-umbelloid.	Contracted. Expanded. Spreading.
20	70	20	56	6,5	Curved	Almost Smooth	Entire	Non-umbelloid	Expanded
21	—	—	—	—	—	—	—	—	—
22	55	10	76	5	Straight	Ciliolate	Denticulate	Umbelloid	„
23	90	0	66	6	Curved	Almost Smooth	„	Non-umbelloid	—
24	—	—	—	—	—	—	—	—	—
25	70	0	53	8,5	Straight	Ciliolate	„	„	„
026	20	0	54	8	„	Almost Smooth	„	„	„
27	45	10	75	4,5	„	„	Entire	Semi-umbelloid	„
28	55	10	84	7	„	Ciliolate	Laciniate	Umbelloid	„

TABLE 17. *Hieracium umbellatum* Nos. 145 and 147, Kullen.
Plants in culture since 1920. Notes taken 1922.

145,1	90	50	75	22	Straight	Ciliolate	Dentate	Non-umbelloid	Expanded
2	35	35	48	20	„	„	Denticulate	„	„
03	90	0	70	20	„	„	„	Umbelloid	„
4	70	20	69	19	„	„	Dentate	„	„
5	10	10	65	18	„	„	Denticulate	„	„
6	45	15	45	17	„	„	„	Non-umbelloid	„
7	45	25	54	20	Curved	„	Dentate	Umbelloid	„
8	90	10	60	20	Straight	„	Denticulate	„	„
09	90	45	53	16	„	Almost Smooth	„	„	„
010	25	10	35	16	„	Ciliolate	„	„	„
011	60	45	63	22	„	„	Dentate	„	„
12	55	0	59	16	Curved	Almost Smooth	Denticulate	„	„
147,1	90	55	60	21	Straight	Smooth	Dentate	„	„
2	90	90	55	21	„	Ciliolate	„	„	„
3	90	60	50	22	„	„	„	„	Exp.-Spreading
4	90	90	58	24	„	„	„	„	Expanded

Field number	Angle of stems		Characters of leaves		Characters of leaf margin			Characters of inflorescence	
	At base	At top	Length in mm.	Width in mm.	Curved. Straight.	Ciliolate. Almost Smooth. Smooth.	Entire. Denticulate. Dentate. Laciniate.	Umbelloid. Semi-umbelloid. Non-umbelloid.	Contracted. Expanded. Spreading.
5	90	55	56	17	Straight	Ciliolate	Dentate	Semi-umbelloid	Expanded
6	90	80	57	22	»	»	Denticulate	Umbelloid	Exp.-Spreading
007	90	60	48	18	»	»	Dentate	»	»
008	90	80	50	18	»	»	»	»	»
09	70	55	51	18	»	»	»	»	Expanded
010	70	40	41	18	»	»	»	»	»

TABLE 18. *Hieracium umbellatum* No. 154, Nyhamn.
Plants in culture since 1920. Notes taken 1922.

1	45	10	87	9	Straight	Ciliolate	Dent.-Laciniate	Semi-umbelloid	Expanded
2	90	10	72	6,5	»	»	Denticulate	Umbelloid	»
3	20	10	60	3,5	Curved	Smooth	Entire	»	Contr.-Expanded
4	70	50	73	5	Straight	Almost Smooth	»	»	Expanded
5	—	—	—	—	—	—	—	—	—
6	20	10	84	9	Curved	Ciliolate	Dent.-Laciniate	Semi-umbelloid	»
7	80	45	63	8	»	»	Dentate	Non-umbelloid	»
8	45	0	75	8,5	Straight	Almost Smooth	Denticulate	Semi-umbelloid	»
9	60	20	84	7	»	Ciliolate	Dent.-Laciniate	»	»
10	45	10	82	7	»	»	Dentate	Umbelloid	»
011	40	25	80	6	»	Almost Smooth	»	»	»
12	45	45	80	7	»	Ciliolate	»	»	»
13	45	15	74	7	»	»	Dent.-Laciniate	»	Exp.-Spreading
14	90	10	87	8,5	»	Smooth	»	»	Expanded
15	50	25	86	5,5	»	Almost Smooth	»	Semi-umbelloid	»
16	50	30	65	6	»	Smooth	Entire	Umbelloid	»
017	40	0	73	6,5	»	Ciliolate	Dentate	»	»

Field number	Angle of stems		Characters of leaves		Characters of leaf margin			Characters of inflorescence	
	At base	At top	Length in mm.	Width in mm.	Curved. Straight.	Ciliolate. Almost Smooth. Smooth.	Entire. Denticulate. Dentate. Laciniate.	Umbelloid. Semi-umbelloid. Non-umbelloid.	Contracted. Expanded. Spreading.
18	30	0	83	7	Straight	Ciliolate	Dentate	Umbelloid	Expanded
19	35	20	—	—	—	—	—	»	»
20	35	0	77	5,5	»	Almost Smooth	Dent.-Laciniate	»	»
21	50	20	—	—	—	—	—	»	»
22	70	0	71	9	»	Ciliolate	Dentate	»	»
23	70	0	70	6	Curved	»	Denticulate	»	Contr.-Expanded
24	25	0	74	9	Straight	»	Dentate	»	»
25	45	20	95	6,5	»	»	Entire	»	»
26	45	0	65	6	»	»	Dentate	»	»

TABLE 19. *Hieracium umbellatum* No. 26, Sandhammaren.

Plants raised from seeds, coll. 1919. Notes taken 1922.

1	70	30	117	7	Curved	Smooth	Dentate	Semi-umbelloid	Contr.-Expanded
02	30	30	125	13	Straight	Ciliolate	Dent.-Laciniate	Umbelloid	Expanded
3	70	20	130	6,5	Curved	Smooth	Laciniate	Semi-umbelloid	Contracted
4	35	10	123	7,5	Straight	»	Dentate	Umbelloid	Contr.-Expanded
5	30	25	125	7	Curved	Ciliolate	Laciniate	»	Contracted
6	30	10	115	8	Straight	»	Dent.-Laciniate	»	»
7	35	20	108	8	—	—	—	—	—
8	40	15	—	9	Curved	»	Dentate	Semi-umbelloid	Contr.-Expanded
9	70	45	117	8	»	»	Dent.-Laciniate	Umbelloid	Expanded
10	45	20	118	12,5	Straight	Smooth	»	»	»
11	20	10	112	5	Curved	»	»	»	Contracted
12	45	10	120	7	»	Almost Smooth	»	Semi-umbelloid	Contr.-Expanded
13	35	0	—	8,5	»	»	Denticulate	Umbelloid	»

Field number	Angle of stems		Characters of leaves		Characters of leaf margin			Characters of inflorescence	
	At base	At top	Length in mm.	Width in mm.	Curved. Straight.	Ciliolate. Almost Smooth. Smooth.	Entire. Denticulate. Dentate. Laciniate.	Umbelloid. Semi-umbelloid. Non-umbelloid.	Contracted. Expanded. Spreading.
14	45	25	85	8	Straight	Almost Smooth	Dentate	Semi-umbelloid	Contr.-Expanded
15	70	30	110	7	»	Ciliolate	Dent.-Laciniate	Umbelloid	Expanded
16	40	0	103	6	Curved	»	Laciniate	»	Contr.-Expanded

TABLE 20. *Hieracium umbellatum* Nos. 119 and 120. Stenshuvud. Plants in culture since 1920. Notes taken 1922.

119,1	25	0	86	18	Straight	Ciliolate	Dentate	Umbelloid	Contracted
2	20	0	70	23	»	»	Denticulate	—	—
3	30	0	76	16	»	»	»	»	»
4	10	0	75	20	»	Almost Smooth	Dentate	»	Contr.-Expanded
5	15	0	71	21	»	»	»	Semi-umbelloid	Expanded
6	10	0	77	19	»	Ciliolate	Denticulate	—	—
7	10	0	65	18	»	»	»	—	—
8	30	0	100	30	»	»	Dentate	Umbelloid	Contracted
9	25	10	99	26	»	»	»	»	Expanded
10	25	0	76	21	»	Smooth	»	»	»
11	20	0	90	15	Curved	Almost Smooth	»	»	Contracted
012	60	30	75	14	»	Smooth	»	»	Contr.-Expanded
13	10	0	94	20	Straight	Ciliolate	»	»	Contracted
14	45	0	90	22	»	»	»	»	Contr.-Expanded
15	70	10	72	13	»	»	»	»	»
16	25	0	61	15	»	Almost Smooth	»	»	»
17	30	0	74	17	»	Ciliolate	»	»	Contracted
18	30	0	92	20	»	»	»	»	Expanded
19	20	0	90	21	»	»	»	»	»
20	0	0	66	16,5	»	»	»	»	Contr.-Expanded
21	35	0	111	17	»	Almost Smooth	»	Semi-umbelloid	Expanded

Field number	Angle of Stems		Characters of leaves		Characters of leaf margin			Characters of inflorescence	
	At base	At top	Length in mm.	Width in mm.	Curved. Straight.	Ciliolate. Almost Smooth. Smooth.	Entire. Denticulate. Dentate. Laciniate.	Umbelloid. Semi-umbelloid. Non-umbelloid.	Contracted. Expanded. Spreading.
22	45	20	76	17	Straight	Ciliolate	Denticulate	Semi-umbelloid	Contracted
120,1	60	10	75	12	Curved	Smooth	Dentate	Umbelloid	Contr.-Expanded
2	30	0	81	18	Straight	»	Denticulate	Semi-umbelloid	»
3	20	0	84	19	»	»	»	»	Contracted
04	25	0	85	25	»	Ciliolate	»	»	»
5	0	0	52	16	»	Almost Smooth	»	—	—
06	45	10	87	13	»	Smooth	»	—	—
7	30	0	105	17	»	»	»	Umbelloid	Contracted
8	15	0	66	21	»	Ciliolate	Dentate	Semi-umbelloid	»
9	40	0	90	20	Curved	Smooth	»	Umbelloid	Contr.-Expanded
10	30	0	88	18	Straight	Ciliolate	»	»	»
011	20	0	68	15	»	Smooth	»	»	Contracted
012	60	45	75	18	»	Ciliolate	»	»	Expanded
13	0	0	74	28	»	»	»	»	Contracted
14	0	0	105	18	»	»	»	»	Contr.-Expanded
15	45	20	106	23	Curved	Smooth	Denticulate	»	Contracted
16	0	10	—	—	—	—	—	—	—
17	25	0	93	20	Straight	Ciliolate	Dentate	»	»
18	40	0	82	17	»	Almost Smooth	»	Non-umbelloid	»
19	10	0	80	18	»	»	»	Umbelloid	»
20	40	20	95	17	»	»	»	»	Contr.-Expanded

TABLE 21. *Hieracium umbellatum* Nos. 24 and 25, Vitemölle.

Plants in culture since 1919. Notes taken 1922.

24,1	90	35	67	9	Curved	Cilolate	Dentate	Semi-umbelloid	Expanded
2	90	60	90	7	»	»	Dent.-Laciniate	Umbelloid	»

Field number	Angle of stems		Characters of leaves		Characters of leaf margin			Characters of inflorescence	
	At base	At top	Length in mm.	Width in mm.	Curved. Straight.	Ciliolate. Almost Smooth. Smooth.	Entire. Denticulate. Dentate. Laciniate.	Umbelloid. Semi-umbelloid. Non-umbelloid.	Contracted. Expanded. Spreading.
0015	70	40	88	9	Curved	Ciliolate	Dent.- Laciniate	Umbelloid	Exp.- Spreading
16	90	50	47	6,5	Straight	»	Dentate	Semi-umbelloid	»
017	90	55	75	10	»	»	Laciniate	»	Expanded

TABLE 22. *Hieracium umbellatum* nos. 31 and 32, Åhus.

Plants in culture since 1919. Notes taken 1922.

31,1	55	40	56	8	Curved	Smooth	Dentate	Umbelloid	Spreading
2	90	45	62	9	»	Ciliolate	Dent.- Laciniate	»	Expanded
3	90	60	101	6	»	»	»	»	Spreading
4	90	30	65	12	»	Smooth	Dentate	»	»
5	90	50	80	7	»	Ciliolate	Entire	»	Exp.- Spreading
6	90	20	53	8	»	»	Dentate	»	Expanded
7	90	55	70	8	»	Smooth	»	»	»
8	90	35	67	8	»	Ciliolate	»	»	»
9	90	70	80	7	»	Almost Smooth	Entire	»	Spreading
10	80	50	68	5,5	»	Ciliolate	Dentate	»	Expanded
011	90	70	72	9	»	»	»	Semi-umbelloid	»
12	90	45	58	6	»	»	»	Umbelloid	Spreading
13	—	—	—	—	—	—	—	—	—
14	90	45	—	—	—	—	—	»	Exp.- Spreading
15	90	50	60	8	»	Smooth	»	»	Expanded
16	90	55	102	10	»	Ciliolate	Dent.- Laciniate	Semi-umbelloid	»
17	35	35	115	6,5	»	»	»	Umbelloid	Exp.- Spreading
018	70	30	—	—	—	—	—	»	»
32,1	90	45	78	7	Straight	»	Dentate	»	Expanded
2	90	60	95	7	Curved	»	»	»	»
3	90	45	90	8	»	»	Entire	»	»
4	90	45	64	7,5	»	»	Dentate	»	»
5	90	40	96	8	»	»	Entire	»	»

Field number	Angle of stems		Characters of leaves		Characters of leaf margin			Characters of inflorescence	
	At base	At top	Length in mm.	Width in mm.	Curved. Straight.	Ciliolate. Almost Smooth. Smooth.	Entire. Denticulate. Dentate. Laciniate.	Umbelloid. Semi-umbelloid. Non-umbelloid.	Contracted. Expanded. Spreading.
6	90	45	78	8	Curved	Ciliolate	Dentate	Umbelloid	Expanded
7	90	50	85	8	Straight	»	»	Semi-umbelloid	Spreading
8	90	45	86	6	Curved	»	»	Umbelloid	Expanded
9	75	30	65	7	»	»	»	»	Spreading
10	75	20	92	8,5	»	Smooth	Laciniate	»	Exp.- Spreading
11	70	45	75	6	»	Ciliolate	»	»	Expanded
12	70	50	78	7	»	»	Dentate	»	Spreading
13	90	45	72	5	»	Smooth	»	»	Expanded
14	70	20	92	6,5	Straight	»	»	»	»
15	—	—	—	—	—	—	—	—	—
16	90	60	74	12	»	Ciliolate	»	»	Spreading
17	90	55	65	8	Curved	»	»	»	»
18	90	50	—	—	—	—	»	»	Expanded
19	90	90	80	7	»	Smooth	Laciniate	»	»
20	90	40	94	7,5	»	Ciliolate	»	»	Spreading
21	90	90	75	8	»	»	»	»	Expanded

TABLE 23. *Hieracium umbellatum* No. 170, Stehag.

Plants in culture since 1920. Notes taken 1922.

1	10	0	67	9,5	Curved	Ciliolate	Dentate	Umbelloid	Contracted
2	15	0	70	8,5	»	»	Denticulate	»	»
3	25	0	68	8	Straight	Almost Smooth	Dentate	»	»
04	20	0	80	14	»	Ciliolate	Denticulate	»	»
5	35	0	81	10	»	Almost Smooth	»	»	»
6	15	0	72	8	»	»	Dentate	»	»
7	30	0	76	8,5	»	»	Entire	»	»
8	25	0	67	9	»	Ciliolate	Dentate	»	»
9	35	0	76	8	»	Almost Smooth	»	»	»
10	20	0	80	9,5	»	Ciliolate	Denticulate	»	»
11	30	20	75	15	»	»	Dentate	»	»
12	45	10	100	14	Curved	»	»	»	»
13	10	0	83	9	»	Almost Smooth	»	»	»

Field number	Angle of stems		Characters of leaves		Characters of leaf margin			Characters of inflorescence	
	At base	At top	Length in mm.	Width in mm.	Curved. Straight.	Ciliolate. Almost Smooth. Smooth.	Entire. Denticulate. Dentate. Laciniate.	Umbelloid. Semi-umbelloid. Non-umbelloid.	Contracted. Expanded. Spreading.
14	10	0	—	—	—	—	—	Umbelloid	Contracted
15	45	35	73	10	Curved	Ciliolate	Dentate	»	Contr.-Expanded
16	30	15	103	15	Straight	»	»	»	Contracted
17	45	10	72	9	Curved	Smooth	Denticulate	»	»
18	20	0	100	10	»	Almost Smooth	Dentate	»	»
19	25	0	85	11	»	Ciliolate	Denticulate	»	»
20	30	10	78	9	Straight	Almost Smooth	»	»	»
21	20	0	81	11,5	Curved	Ciliolate	Dentate	»	»
22	25	0	80	9	Straight	Almost Smooth	»	»	»
23	15	0	90	12,5	»	Ciliolate	Denticulate	»	»
24	35	0	80	10	Curved	»	Dent.-Laciniate	»	»
25	50	20	90	10	»	»	Dentate	»	Exp.-Spreading
26	10	0	90	9,5	Straight	Almost Smooth	Denticulate	»	Contracted
27	5	0	84	11	Curved	»	Entire	»	»
28	25	0	76	8	Straight	»	Dentate	»	»
29	45	10	90	13	Curved	Ciliolate	»	»	Expanded
30	30	0	82	12,5	Straight	»	»	»	Contracted
31	25	0	86	10	»	Almost Smooth	»	»	»
32	20	0	77	11	»	»	Denticulate	»	»
33	10	0	85	11	»	»	»	»	»

TABLE 24. *Hieracium umbellatum* No. 48, Vombsjön.

Plants in culture since 1920. Notes taken 1922.

1	70	20	78	8	Curved	Ciliolate	Laciniate	Umbelloid	Expanded
2	60	45	85	7	Straight	Smooth	»	»	Contr.-Expanded
3	35	0	76	9,5	Curved	Ciliolate	»	»	Expanded
4	75	30	—	—	—	—	—	»	»
5	50	30	74	8	»	»	Denticulate	»	»
6	45	20	75	8	»	»	»	»	»

Field number	Angle of stems		Characters of leaves		Characters of leaf margin			Characters of inflorescence	
	At base	At top	Length in mm.	Width in mm.	Curved. Straight.	Ciliolate. Almost Smooth. Smooth.	Entire. Denticulate. Dentate. Laciniate.	Umbelloid. Semi-umbelloid. Non-umbelloid.	Contracted. Expanded. Spreading.
7	55	—	89	7	Curved	Ciliolate	Denticulate	—	—
8	45	—	82	10	»	Smooth	Laciniate	—	—
9	50	20	85	6	»	Ciliolate	Dentate	Semi-umbelloid	Expanded
10	70	30	—	—	—	—	—	Umbelloid	»
11	45	—	98	11	»	»	Laciniate	—	—
12	60	—	90	9	»	»	Dent.-Laciniate	—	—
13	70	20	77	8	»	»	»	Umbelloid	Exp.-Spreading
14	45	—	75	8	»	»	»	—	—
15	45	20	—	—	—	—	—	»	Expanded
16	70	10	—	—	—	—	—	»	Contr.-Expanded
17	30	—	—	—	—	—	—	—	—
18	40	25	—	—	—	—	—	»	Expanded
19	80	45	—	—	—	—	—	»	»
20	80	45	90	8	»	Smooth	Laciniate	»	Exp.-Spreading
21	80	—	—	—	—	—	—	—	—
22	80	0	—	—	—	—	—	»	Expanded

TABLE 25. *Hieracium umbellatum* No. 121, Kivik.

Plants in culture since 1920. Notes taken 1922.

1	80	45	86	13	Straight	Smooth	Dentate	Umbelloid	Exp.-Spreading
2	0	0	85	17	»	Ciliolate	»	»	»
3	45	10	84	10,5	»	»	»	—	—
4	30	10	91	13	Curved	Smooth	»	—	—
5	70	0	—	—	—	—	—	—	—
6	20	0	86	16	»	Ciliolate	»	»	Expanded
7	90	45	87	12	»	Smooth	»	»	Contracted
8	45	10	—	—	—	—	—	—	—
9	45	10	—	—	—	—	—	—	—
10	60	20	75	10	»	»	Denticulate	»	Contr.-Expanded
11	70	20	78	7	»	»	Dentate	—	—

Field number	Angle of stems		Characters of leaves		Characters of leaf margin			Characters of inflorescence	
	At base	At top	Length in mm.	Width in mm.	Curved. Straight.	Ciliolate. Almost Smooth. Smooth.	Entire. Denticulate. Dentate. Laciniolate.	Umbelloid. Semi-umbelloid. Non-umbelloid.	Contracted. Expanded. Spreading.
012	50	15	84	10	Curved	Ciliolate	Dent.-Laciniolate	Umbelloid	Exp.-Spreading
13	80	20	86	6	Straight	Smooth	Dentate	"	Contr.-Expanded
14	65	0	—	—	—	—	—	"	Expanded
15	60	0	65	13	Curved	Ciliolate	Laciniolate	—	—
16	20	0	71	10	"	Smooth	Denticulate	"	"
17	20	0	86	13,5	Straight	"	"	"	Contr.-Expanded
18	70	45	82	8	"	Ciliolate	Dentate	"	Expanded
19	45	0	63	10,5	"	"	Dent.-Laciniolate	"	Contracted
20	50	20	80	9	Curved	Smooth	"	"	"
21	35	10	92	14	Straight	"	"	"	"
22	10	0	76	9	"	"	"	"	Contr.-Expanded
23	20	0	78	10	"	Ciliolate	Dentate	"	Contracted

TABLE 26. *Hieracium umbellatum* No. 104, Torup.

Plants in culture since 1920. Notes taken 1922.

1	70	10	70	8	Straight	Ciliolate	Dentate	Umbelloid	Contracted
2	65	10	72	12	"	Smooth	Dent.-Laciniolate	"	Contr.-Expanded
3	70	10	85	6,5	Curved	Ciliolate	"	"	Contracted
4	45	10	75	12,5	"	Smooth	Dentate	—	—
5	30	30	64	10	"	Ciliolate	"	—	—
6	90	20	65	6	"	"	"	"	Contr.-Expanded
7	90	45	80	6,5	"	"	"	"	Contracted
8	90	10	75	5	"	Smooth	"	"	Contr.-Expanded
9	90	50	65	7,5	"	Ciliolate	"	"	"
10	35	10	70	6	"	Smooth	Dent.-Laciniolate	Non-umbelloid	Expanded
11	45	0	85	8	"	"	Denticulate	Umbelloid	Contracted
12	30	10	90	13	Straight	"	Laciniolate	—	—
13	90	25	72	9	Curved	"	"	"	Expanded

Field number	Angle of stems		Characters of leaves		Characters of leaf margin			Characters of inflorescence	
	At base	At top	Length in mm.	Width in mm.	Curved, Straight.	Ciliolate, Almost Smooth, Smooth.	Entire, Denticulate, Dentate, Laciniate.	Umbelloid, Semi-umbelloid, Non-umbelloid.	Contracted, Expanded, Spreading.
14	45	0	86	7,5	Curved	Smooth	Dentate	Non-umbelloid	Contracted
15	90	0	77	5,5	»	Almost Smooth	»	Umbelloid	Expanded
16	45	15	90	7	»	»	Dent.-Laciniate	»	»
17	70	10	66	9	»	Ciliolate	Dentate	Semi-umbelloid	»
18	50	20	83	6,5	»	Almost Smooth	Denticulate	»	»
19	20	10	71	8	»	Smooth	Dentate	Umbelloid	Contracted
20	70	0	84	6,5	»	Ciliolate	»	»	»
21	45	0	65	7	»	»	»	—	—
22	80	45	72	6	»	»	»	»	Exp.-Spreading
23	90	45	—	—	—	—	—	»	»

TABLE 27. *Hieracium umbellatum* No. 63, Falkenberg.Field nos. 11 and 12 (see table 11) crossed in 1921. F_1 -notes taken 1922.

Field number	Angle of stems		Characters of leaves		Characters of leaf margin		
	At base	At top	Length in mm.	Width in mm.	Curved, Straight.	Ciliolate, Almost Smooth, Smooth.	Entire, Denticulate, Dentate, Laciniate.
1	90	80	96	7	Straight	Ciliolate	Dent.-Laciniate
2	65	75	80	6	»	»	Laciniate
3	60	40	76	9,5	»	»	»
4	90	65	68	10	Curved	»	Dentate
5	75	45	88	9	Straight	Almost Smooth	»
6	60	45	72	8,5	Curved	Ciliolate	»
7	80	20	66	6	»	»	Laciniate
8	85	10	80	5,5	Straight	»	»
9	70	50	76	9	»	Smooth	»
10	90	80	69	7	»	»	Dent.-Laciniate
11	45	20	59	5	Curved	Almost Smooth	Dentate
12	90	45	60	6,5	Straight	»	Laciniate

Field number	Angle of stems		Characters of leaves		Characters of leaf margin		
	At base	At top	Length in mm.	Width in mm.	Curved. Straight.	Ciliate. Almost Smooth. Smooth.	Entire. Denticulate. Dentate. Lacinate.
13	60	30	64	9	Curved	Smooth	Denticulate
14	—	10	76	6	»	Ciliate	Dentate
15	30	10	72	7	»	»	»
16	70	25	65	7,5	Straight	»	»
17	80	30	68	6	Curved	»	»
18	90	20	91	9	»	Smooth	Dent.-Lacinate

TABLE 28. *Hieracium umbellatum* No. 61, Kristineberg.Field nos. 01 and 3 (see table 10) crossed in 1921. F_1 -notes taken 1922.

Field number	Angle of stem at base	Characters of leaves		Characters of leaf margin		
		Length in mm.	Width in mm.	Curved. Straight.	Ciliate. Almost Smooth. Smooth.	Entire. Denticulate. Dentate. Lacinate.
1	rosette	45	12	Straight	Ciliate	Dentate
2	»	77	16	»	Smooth	»
3	45	90	17,5	Curved	»	»
4	55	72	18	Straight	Ciliate	»
5	rosette	51	16	»	»	»
6	»	53	13	»	»	»
7	»	62	12	»	»	»
8	»	46	15,5	»	Almost Smooth	»
9	50	97	18	»	Smooth	Lacinate
10	60	71	17	»	»	Dentate
11	90	62	13	Curved	»	»
12	35	72	13	»	»	»
13	90	84	17,5	Straight	Ciliate	»
14	rosette	54	18	»	»	Dent.-Lacinate
15	45	80	16,5	»	»	Dentate
16	30	63	17	Curved	»	Dent.-Lacinate
17	rosette	66	11	Straight	»	Dentate
18	70	58	11	Curved	Smooth	»
19	65	56	16,5	»	Ciliate	»
20	70	57	13	»	Almost Smooth	Denticulate
21	90	68	18,5	»	Smooth	Dent.-Lacinate
22	65	63	12	»	»	»
23	80	78	15	Straight	»	Dentate

TABLE 29. *Hieracium*
Plants measured and characterized in their natural habitat

Field num- ber	Length of stem in mm.			Angle of stems						Characters of leaves						C h a r a c t e r s	
	1920	1921	1922	1920		1921		1922		1920		1921		1922		1920	
				At base	At top	At base	At top	At base	At top	Length in mm.	Width in mm.	Length in mm.	Width in mm.	Length in mm.	Width in mm.	Curved. Straight.	Ciliolate. Almost Smooth. Smooth.
1	166	—	—	90	55	—	—	—	—	37	4	—	—	—	—	Curved	Ciliolate
2	165	310	458	90	40	90	40	90	45	36	4	55	7	63	8	"	"
3	227	275	413	90	90	90	60	90	75	41	3,5	75	11	80	10	"	"
4	164	380	465	90	70	90	30	90	30	51	4,5	92	8	95	9,5	"	"
5	210	522	586	90	55	90	45	90	40	42	3	95	8	94	7,5	Straight	"
6	235	436	510	90	60	75	50	85	50	46	3,5	110	10	98	9	Curved	"
7	170	212	388	90	75	90	55	90	60	48	4	62	7	68	6,5	"	"
8	212	421	460	80	35	70	10	75	20	57	4	101	6,5	93	5,5	Straight	"
9	180	—	—	90	80	—	—	—	—	42	3	—	—	—	—	"	"
10	253	597	619	90	50	75	40	85	35	43	4,5	90	11	104	10	Curved	"
11	175	430	481	90	80	90	30	90	30	41,5	4	83	9	92	9	"	"
12	302	525	600	90	90	90	35	90	35	53	4	105	9,5	96	10,5	"	"
13	167	—	—	90	85	—	—	—	—	40	3,5	—	—	—	—	"	"
14	200	304	389	90	80	90	45	90	50	45	3	80	8	73	7	"	"
15	256	340	378	90	45	90	30	80	40	47	4	71	9	69	9	"	"

umbellatum no. 96, (Vitemölle).

in 1920, then in culture and noted in 1921 and in 1922.

o f m a r g i n

1920		1921		1922		
Entire. Denticulate. Dentate. Laciniate	Curved. Straight.	Ciliolate. Almost Smooth. Smooth.	Entire. Denticulate. Dentate. Laciniate.	Curved. Straight.	Ciliolate. Almost Smooth. Smooth.	Entire. Denticulate. Dentate. Laciniate.
Dentate	—	—	—	—	—	—
»	Curved	Ciliolate	Dentate	Curved	Ciliolate	Dentate
»	»	»	Dent.- Laciniate	»	»	Dent.- Laciniate
»	»	»	»	»	»	»
»	»	Smooth	Laciniate	»	Smooth	Laciniate
»	»	Ciliolate	»	»	Ciliolate	»
Denticulate	»	Almost Smooth	Dentate	»	Almost Smooth	Dentate
Dent.- Laciniate	Straight	»	Dent.- Laciniate	Straight	»	Dent.- Laciniate
»	—	—	—	—	—	—
Dentate	Curved	Ciliolate	»	Curved	Ciliolate	»
Dent.- Laciniate	»	»	»	»	»	»
Dentate	»	»	Denticulate	»	»	Denticulate
»	—	—	—	—	—	—
»	Straight	»	»	Straight	»	»
»	Curved	»	»	Curved	»	»

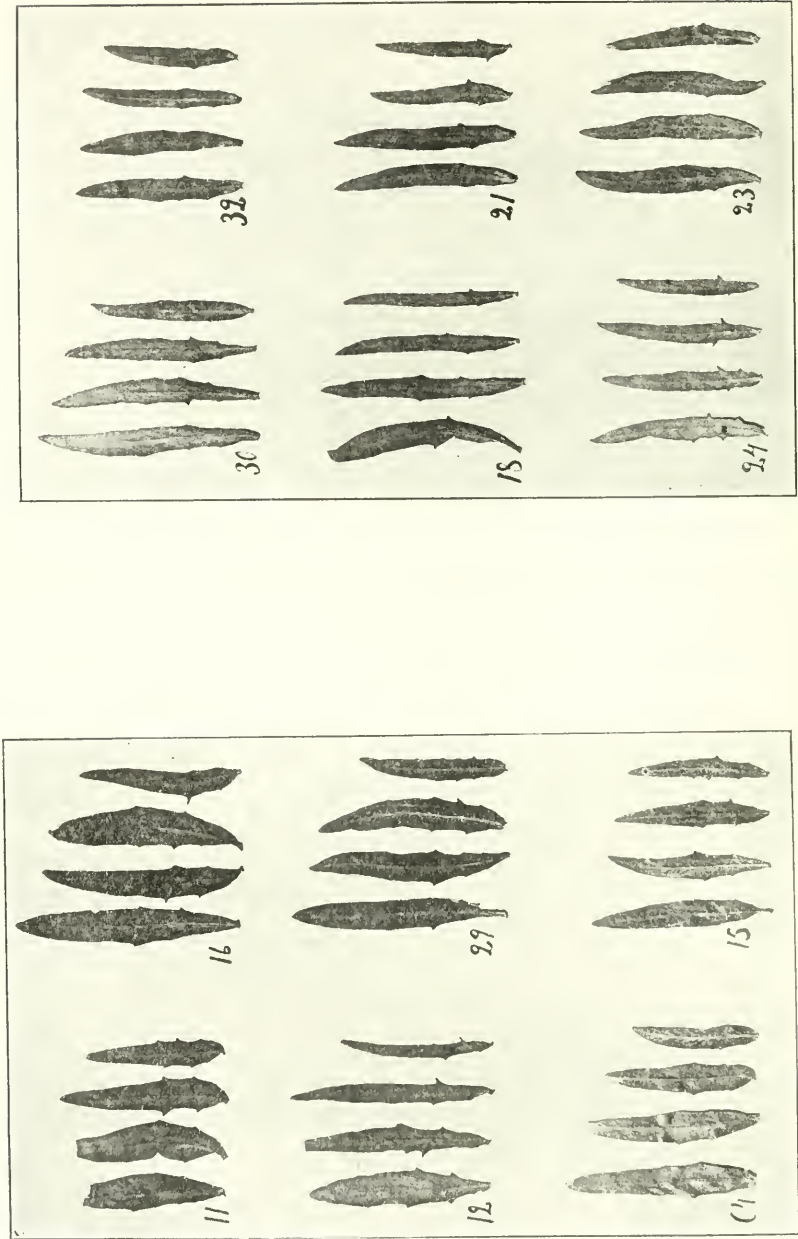


Fig. 59. *H. umbellatum*. Leaves of cult. Stehag inland type (list no. 33).

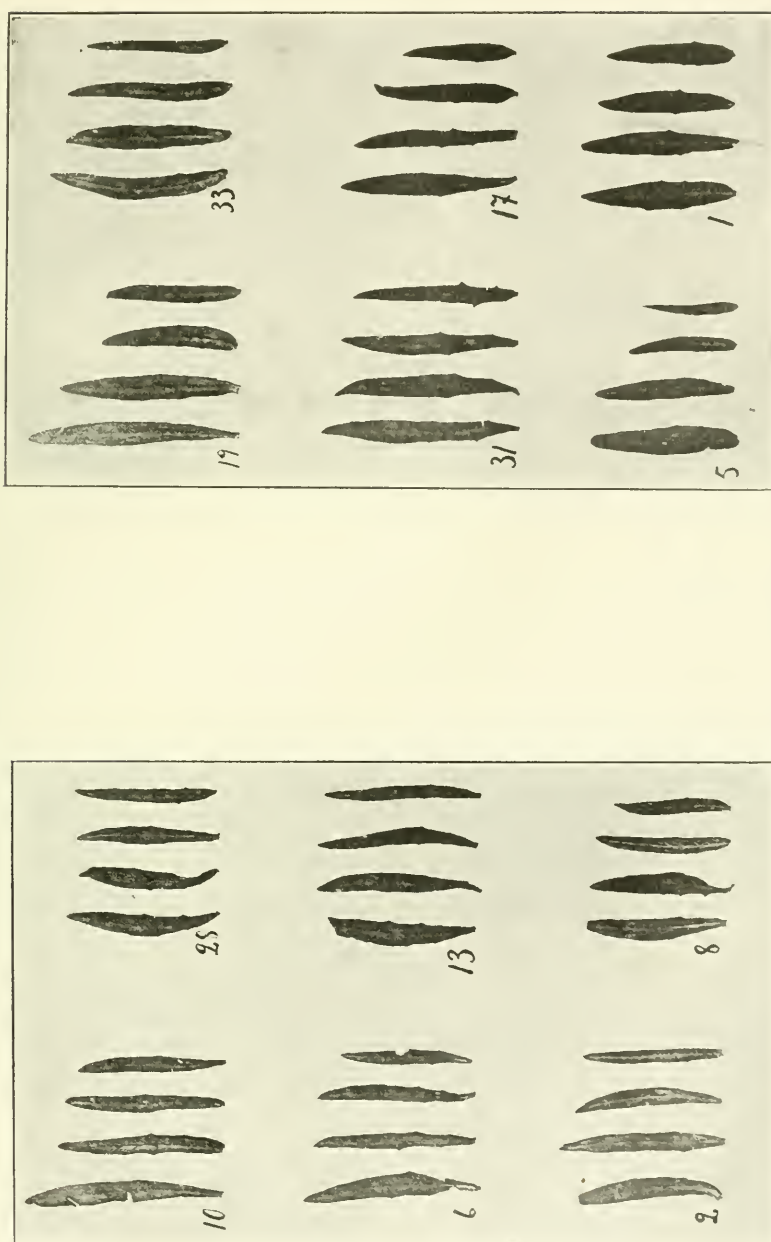


Fig. 60. *H. umbellatum*. Leaves of cult. Stehag inland type.

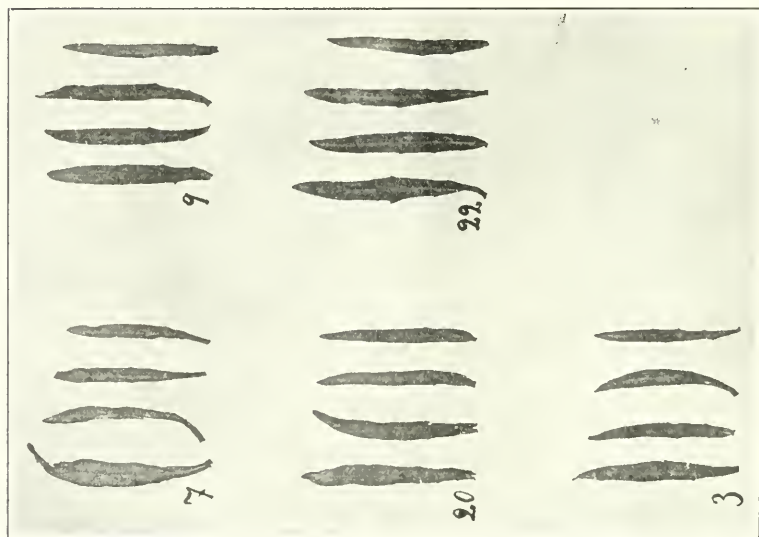


Fig. 61. *H. umbellatum*. Leaves of cult.
Stehag inland type.

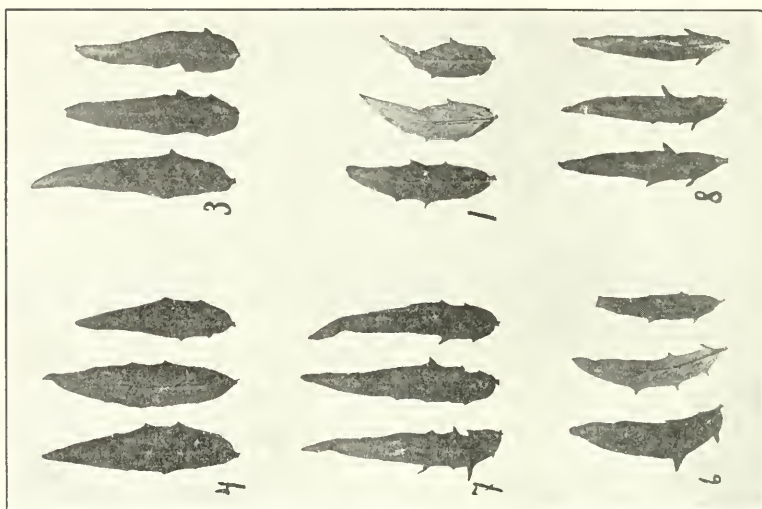


Fig. 62. *H. umbellatum*. Leaves of cult. Hallands
Väderö cliff type.



Fig. 63. *H. umbellatum*. Leaves of cult. Kullen cliff type.

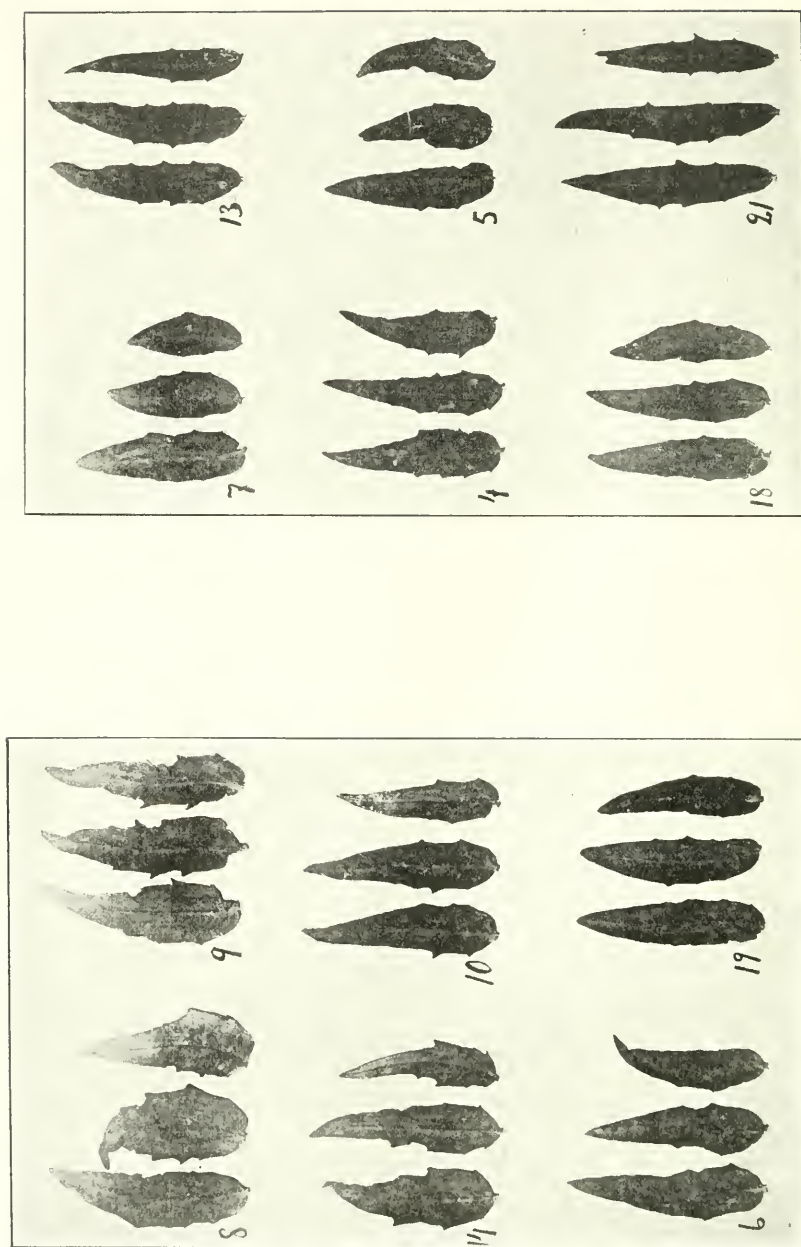


Fig. 64. *H. umbellatum*. Leaves of cult. Stenshuvud cliff type.



Fig. 66. *H. umbellatum*. Leaves of cult.
Vitemölle dune type.

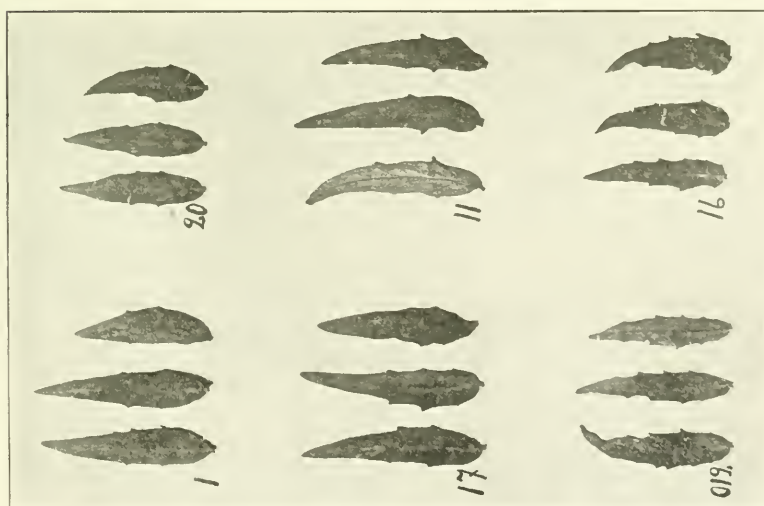
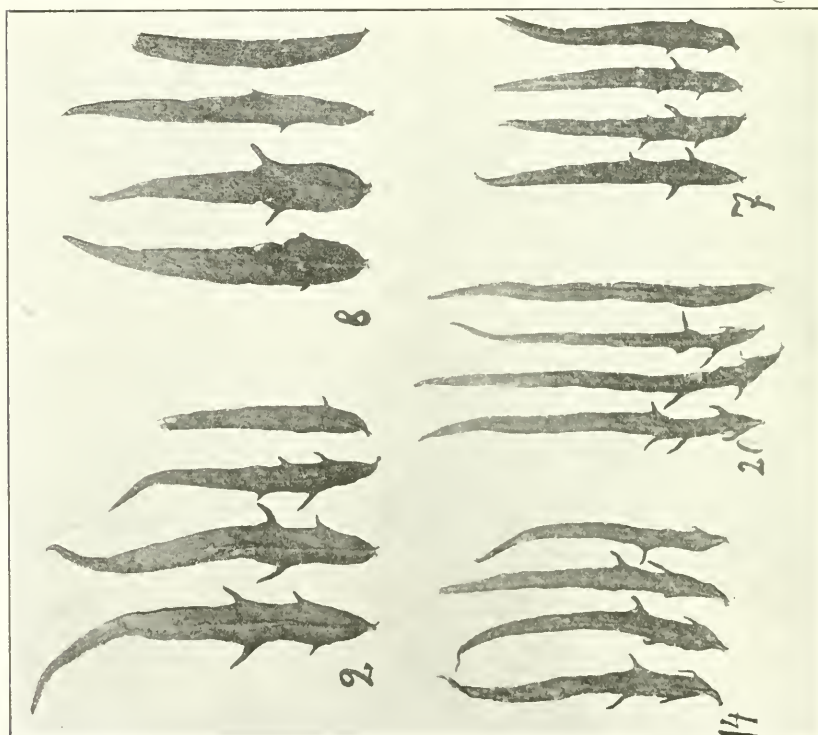
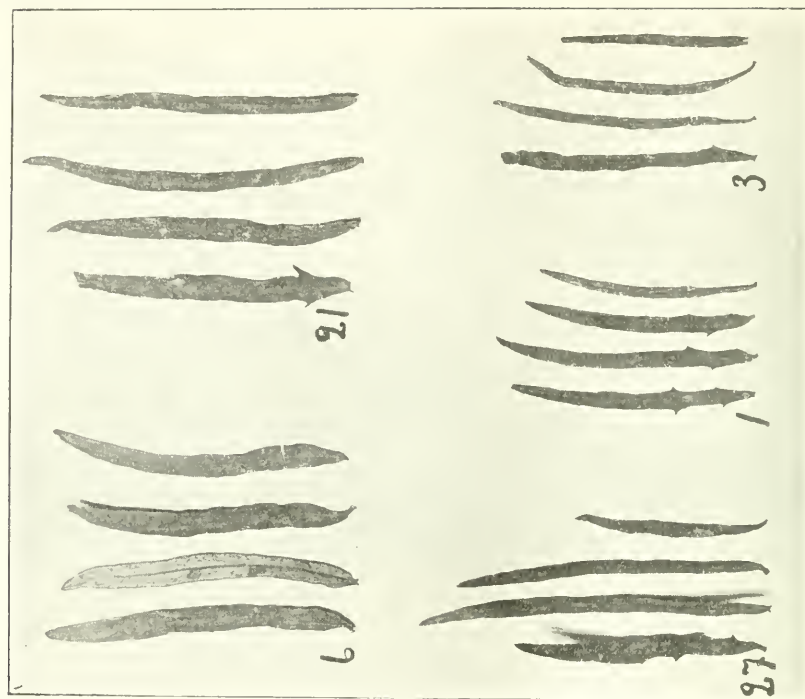


Fig. 65. *H. umbellatum*. Leaves of cult.
Stenshuvud cliff type.

Fig. 67. *H. unbellatum*. Leaves of cult. Falkenberg dune type.Fig. 68. *H. unbellatum*. Leaves of cult. Halmstad dune type.

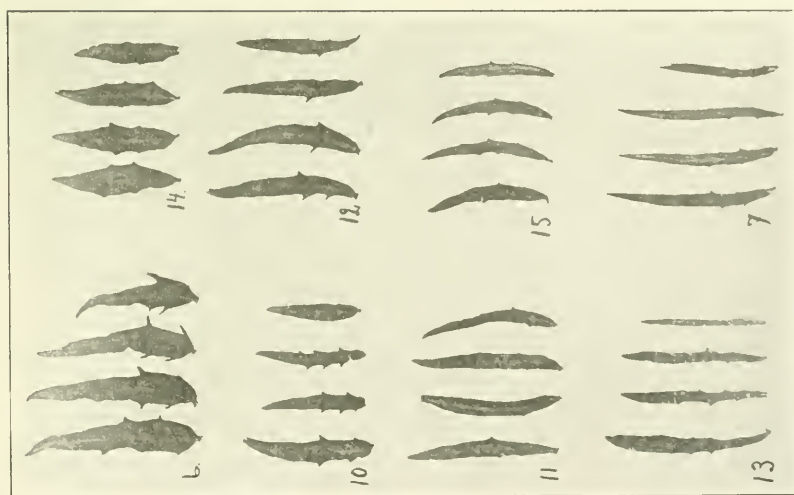


Fig. 69. *H. umbellatum*. Leaves of cult.
Torekov dune type.



Fig. 70. *H. umbellatum*. Leaves of cult.
Skelderviken dune type.

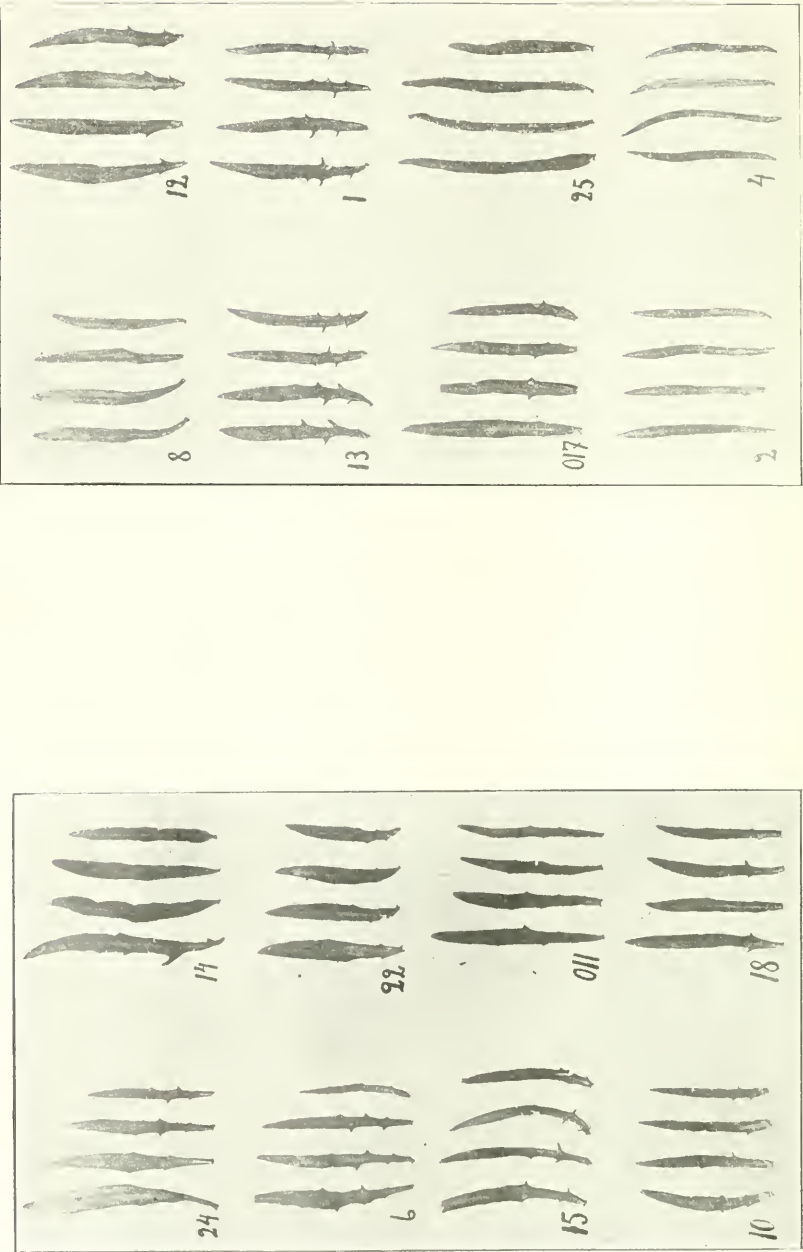
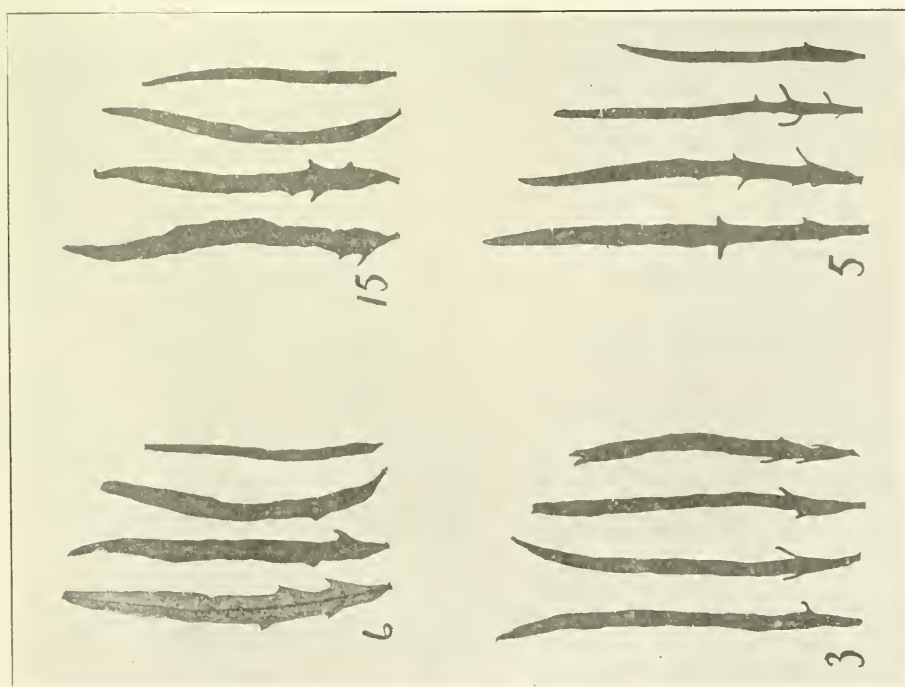
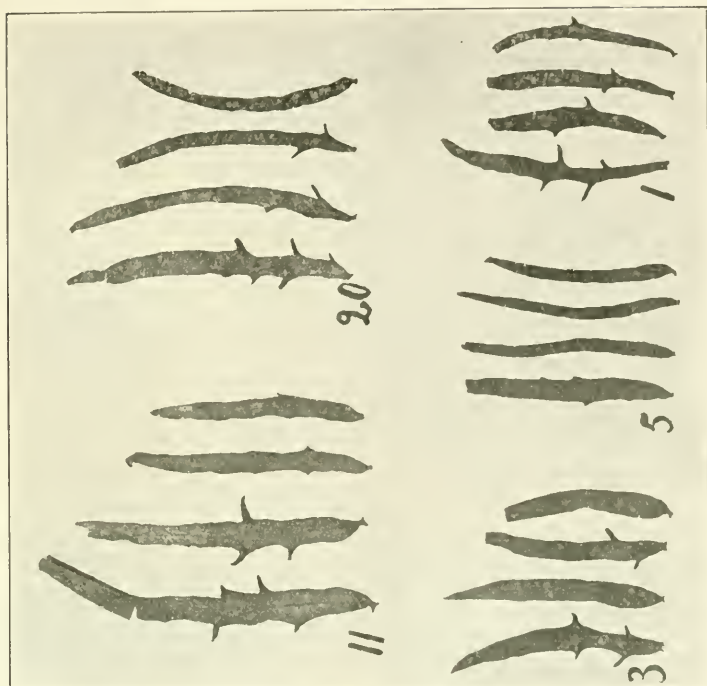


Fig. 71. *H. umbellatum*. Leaves of cult. Nyhamm dune type.

Fig. 72. *H. umbellatum*. Leaves of cult. Sandhammar dune type.Fig. 73. *H. umbellatum*. Leaves of cult. Vombsjön dune type.

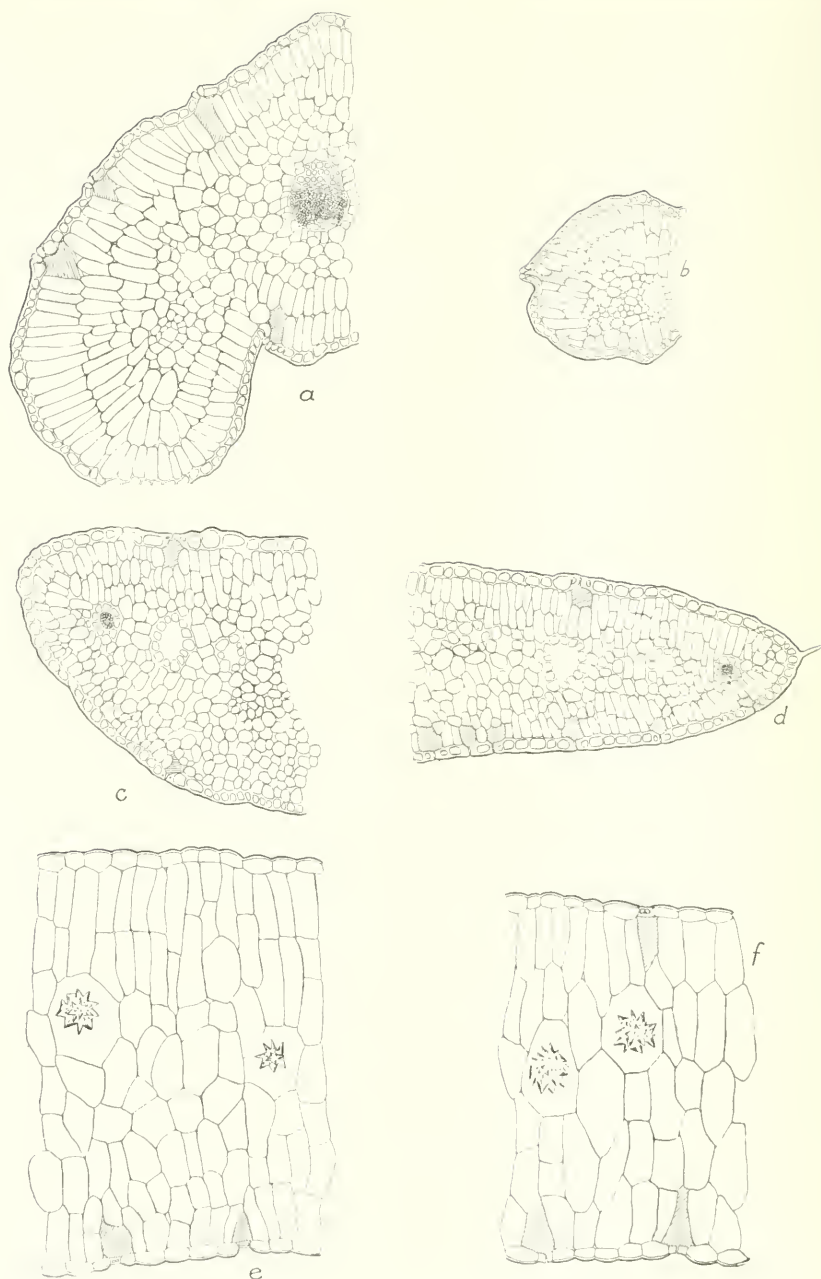


Fig. 74. Cultivated coast type (a) and inland type (b) of *Matricaria inodora*, and of *Armeria vulgaris* (c and d). Cult. east coast type of *Altriplex sarcophyllum* (e), and the Sound type (f). Figures drawn with a Zeiss camera lucida. $\times 60$.

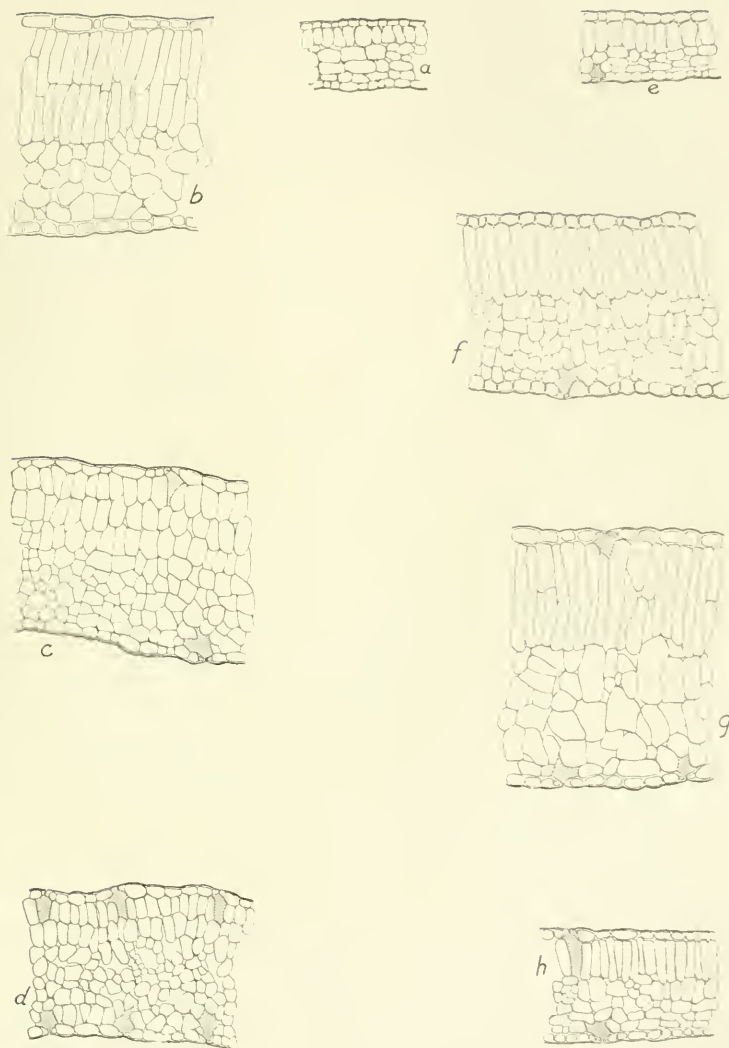


Fig. 75. Shade leaf (a) and leaf of the same plant in the experimental field (b) of *Lysimachia vulgaris*. Cult. coast type (c) and inland type (d) of *Leontodon autumnalis*. Shade leaf of the coast type of *Solanum Dulcamara* (e) and leaves of the same plant in the experimental field in 1921 (f) and 1922 (g). Leaf of the cultivated inland type of the same species (h). Figures drawn with a Zeiss camera lucida. $\times 80$

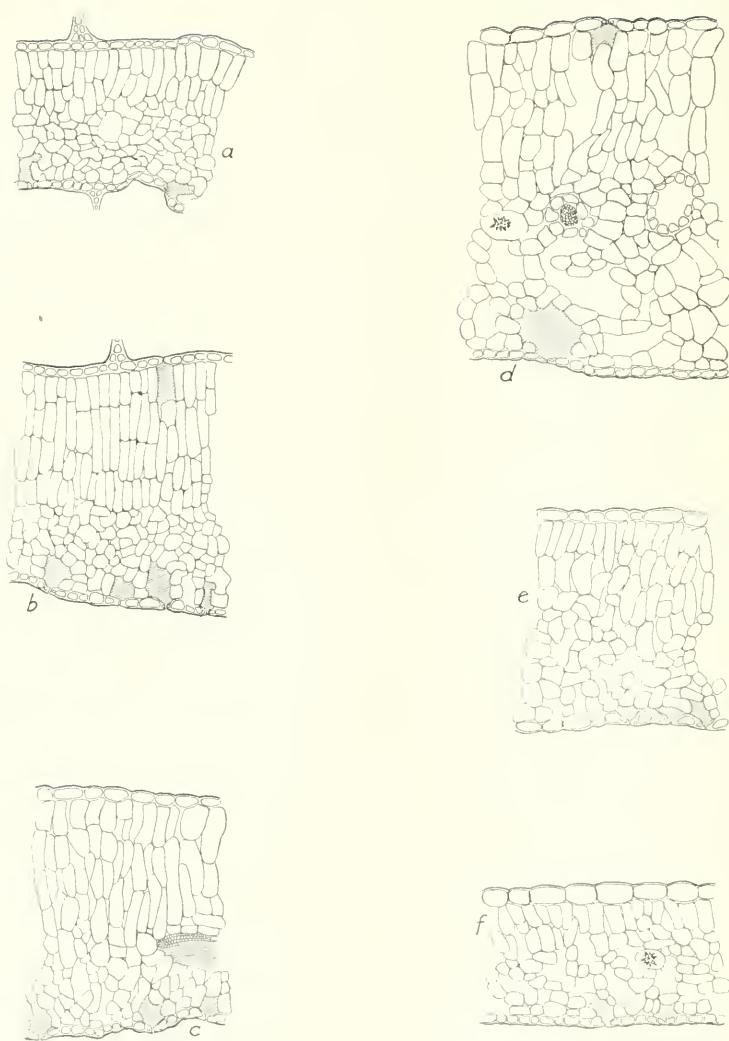


Fig. 76. Leaves of cultivated inland type (a), dune type (b), and sea-cliff type (c) of *Hieracium umbellatum*. Leaves of cult. forest type (f), coast type (e), and Alpine type (d) of *Melandrium rubrum*. Figures drawn with a Zeiss camera lucida. $\times 60$.

II. THE CONTROLLING EFFECT OF THE HABITAT FACTORS UPON THE GENOTYPICAL COMPOSITION OF THE SPECIES-POPULATION.

In the above an attempt has been made to show to what extent the behaviour of a plant species in different habitats is the result of a direct response to the environment on the part of the individual plant, and to what extent it is due to the presence in the different habitats of different hereditary variations. While in some cases the observed characteristics were found to be purely modificatory, the differentiation of the species-population into different hereditary variations in the various habitats was found to be the rule in the majority of cases. Although the conclusive proof of this latter proposition, viz. breeding experiments, has so far been presented in but very few cases, little doubt remains as to the hereditary nature of the characteristics seen in the cultures. The case of *Hieracium umbellatum* may be taken as an example. In the cases where plants have been raised from seeds (tables 14, 15, 16, 19, 27, 28) the results corroborate the view based upon the experiments with the transplantations. A further corroboration of the facts is furnished by the series which show an increase in the prominence of the habitat characteristics when cultivated, which increase has been shown to be present, in regard to the width of the leaves, in the case of the sea-cliff type from Hof's Hallar, Kristineberg and Stenshuvud. The opposite view, that this broad-leaved cliff type is for instance a habitat modification of the inland type, cannot possibly be upheld in the face of such facts. The behaviour in nature of the different types in places, where they come into contact with each other and more or less overlap, furnishes another proof. Mixed populations from such zones of contact have been discussed in the above and listed in tables 25 and 26. The argument increases in strength when it is seen that in a strictly intermediate area between two habitats of different nature and populated by two different types no intermediate population is found but on the contrary individuals of the two definite types and bastards between them appear. A such neutral zone, into which habitats of different nature insensibly grade, has been located on the eastern coast of Scania at Kylsgård (see above, pag. 291), where the drift-sand region of Sandhammar merges into the arenacious fields of the north. If the dune types of the drift-sand region and of the arenacious fields were but modifications, a third intermediate habitat modification would most probably be met with in this intermediate

area. This is not the case. A field examination of 86 individuals from this zone gave the following classes: 8 more or less erect, 31 ascending, and 47 prostrate. A similar classification of 112 individuals within the drift-sand region proper (at Löderup) gave the following result: 44 more or less erect, 61 ascending, and 7 prostrate. An examination of 119 individuals at Vitemölle, in the area of the arenacious fields, resulted in the following relations: 7 ascending, and 112 prostrate. The different groups found in the population at Kylsgård substantiate the view that the intermediate zone between the areas occupied by the dune forms of the drift-sand and of the arenacious fields respectively is inhabited by fragments of these two types and, probably, by bastards between the two types. The population in question conforms to that which is to be expected in the case of hereditary forms meeting in a transitional belt. It thus confirms the statement to the same effect already made by NÄGELI (1866), and also the opinion expressed by BATESON (1913) that in the area of intergradation of two hereditary types no uniformly intermediate population is found but, on the contrary, fragments of the two types together with mongrels between them.

It does not seem necessary to review once more the question of the hereditary nature of the types of different species distinguished above. The data collected from the cultural experiments furnish ample evidence of the hereditary differences between the different types. Certain characteristics usually common to all or to the majority of the individuals of a certain habitat have facilitated their grouping into habitat types, in spite of the hereditary differences seen between the individuals of the same type. These habitat types may sometimes appear more homogeneously in the field than in the cultures, as has been shown to be the case with the *Centaurea* and *Succisa* dwarfs of the salt meadows as well as with the *Hieracium* population at Vitemölle (table 29). The masking of the hereditary differences between the individuals of such types by the modifying effect of extreme habitat factors is readily revealed upon culturing the types. When, nevertheless, the individuals of a type of a definite habitat so often appear to be "fixed" as to certain characteristics, the factor responsible for this fixity becomes of great interest.

To take refuge in the Lamarckian view of the origin of the characteristics in question seems wholly futile. It must suffice here to refer to the current handbooks (JOHANNSEN, 1913; BAUR, 1914) for a full account of the difficulties met with when the attempt is made to make this

theory a basis for the explanation of the facts. From an ecological point of view the arguments already raised against such a theory by NÄGELI (1866) may still be considered valid. We have found that the habitat type — even if it may appear to be quite homogeneous in its habitat — is made up of a number of individuals of which — in the case of allogamous plants — none may represent the genotype of another. These individuals are nevertheless exposed to the same environmental factors and should in time become identical with one another, according to the Lamareckian view. NÄGELI denies — and surely upon good grounds — any such effect of the environmental factors. NÄGELI says further that when for some reason two varieties are each confined to a special habitat, there is not found an intermediate variety in the transitional area between the two habitats, which most likely would have been the case had the varieties been direct products of the habitat. The force of this argument has been especially appreciated by BATESON (1913). It applies with equal strength to the *Hieracium* population in the transition area dealt with above, and will probably also be found to hold good in the great majority of cases which involve the distribution of 'climatic varieties', as is repeatedly maintained by BATESON.

When the Lamareckian view must thus be discarded as an explanation of the characteristics which, in spite of the hereditary differences present, are common to the separate individuals of one and the same habitat type, reference must be made to the Darwinian theory of selection. The attempt to make selection responsible for the definiteness of a certain type has been made over and over again. We know now for certain, however, that definiteness of a type does not necessarily mean that the special characteristics exhibited by the type in question have made possible or have contributed to the survival of that type in a certain habitat. When a few individuals or a colony become isolated and remain isolated from intercrossing with the multitude of the species-population, the chances are that these isolations will in time exhibit peculiarities of characters not found in the rest of the population. For a full account of the problem reference should be made to BATESON (1913). Illustrative examples of the origin of 'species' due to the existence of barriers to intercourse are furnished by the Hawaiian snails of the genus *Achatinella* (GULICK, 1905), by the aberrant rat colonies which LLOYD (1912) found confined to isolated buildings in the towns of British India, or again by the aberrant rat populations

each confined to a certain farm house or a certain steamer as mentioned by HAGEDOORN (1921), etc.

That the differentiation of the plant species into the different hereditary habitat types discussed in the first part of this paper cannot be adequately accounted for by recourse to such sporadic variability preserved by chance isolation will be made clear in the following. On the contrary it will be established that these habitat types in all probability represent definite genotypical responses of the plant species to definite habitat factors. The data bearing upon this question have been collected under four headings.

1. THE SPECIALIZATION OF THE HABITAT TYPES TO DOMINANT HABITAT FACTORS.

The effort so often made by ecologists to interpret the habitus and the morphological details of a plant as adaptations has no doubt led to undue generalization of the facts. It is evidently the genotypical constitution of the plant which is the point of primary importance. It is a generalization of the facts to maintain that the prostrate habit of growth enables the prostrate forms of *Atriplex sarcophyllum* to live on the exposed Swedish west-coast while erect forms of the same species, because of their erectness, are expelled from this coast strip. Comparative physiological experiments with individuals differing genotypically from each other only as to the factor or factors responsible for the difference of growth would probably yield some information as to this point. It must be remembered, however, that it is the sum total of the genes, the *Gesamtgenotypus* (JOHANNSEN, 1914), which doubtless determine the presence or absence of a certain form in a certain habitat.

Thanks to their genotypical constitution — and not necessarily on account of certain phenotypical, morphological characteristics — these prostrates support life where the erects do not. In some cases, however, a special habitus seems so related to definite habitat factors that we are compelled to assume that it is the particular reaction type of a particular genotype that enables the organism in question to live in a certain habitat. Such is the case with some of the above-discussed *Hieracium* habitat types. The dune type of the arenacious fields differs from the type of the shifting dunes mainly in the extreme prostrateness of the stems. It grows well in the grassy plains and stationary dunes but avoids the shifting sand dunes, where it would probably be sand-covered and die (since the power of shoot-regeneration is very limited in this type, though it is on the contrary most pronounced in the type of the

shifting dunes). At Vitemölle the type abounds on the stationary dunes some hundred metres from the beach, while it occurs but rarely on the outer dune bank of the beach, where the substratum is moving and not stable. The same phenomenon may be seen on the coast just north of Cimbrishamn. The inference that it is only the specialized type of the shifting dune which is able to inhabit the moving dune banks of the beach is further strengthened by the examination of the *Hieracium umbellatum* population on certain points on the south-coast of Scania, viz. at Falsterbo and Ystad (list nos. 16 and 17). Although some of these individuals are procumbent, the structure of the leaves of these populations is that of the inland type. The type growing in the woods in close proximity to these beach localities also shows most resemblance to the inland type. The plant is extremely rare on the outer beach dune at Falsterbo. The case is the same at Ystad (Nybroån), where only 7 individuals were found on a 5-metre broad stretch of 300 metres' length. For the sake of comparison it may be mentioned that a similar stretch at Löderup (in the Sandhammar region), where the type of the shifting dune begins, an average of two individuals to the square metre were found growing on the outer beach-dune. It seems clear from this that the inland form is unable to populate the dune banks. It may also be suggested that the reason why a dune type has not become differentiated from the species-population in these localities lies in the fact that the woods harbouring the inland type run down to the beach. It is probable that an incessant intercrossing between the individuals which have succeeded in establishing themselves on the dune and the rest of the population is maintained, and thus the isolation of a specialized dune form is prevented.

The same inability of the inland type to populate the beach is found at Sofiero (on the Sound), where the type covers the *Calluna* bluffs, about 50 metres distant from the beach proper, and extends inwards through the woodland. In this locality not a single individual is found to have established itself on the sandy beach below the bluffs.

The intimate relation between type and habitat is also apparent in the case of the so-called climatic varieties (BATESON 1913; NILSSON-EHLE, 1914). The zonation of a species-population into coast types and an inland type, repeatedly discussed in the first part of this paper, furnishes an example of the same order, as does also the occurrence of different types on the east-coast and on the west-coast of Sweden (*Atriplex sarcophyllum*, *Matricaria*, *Solanum* etc.). It would seem to

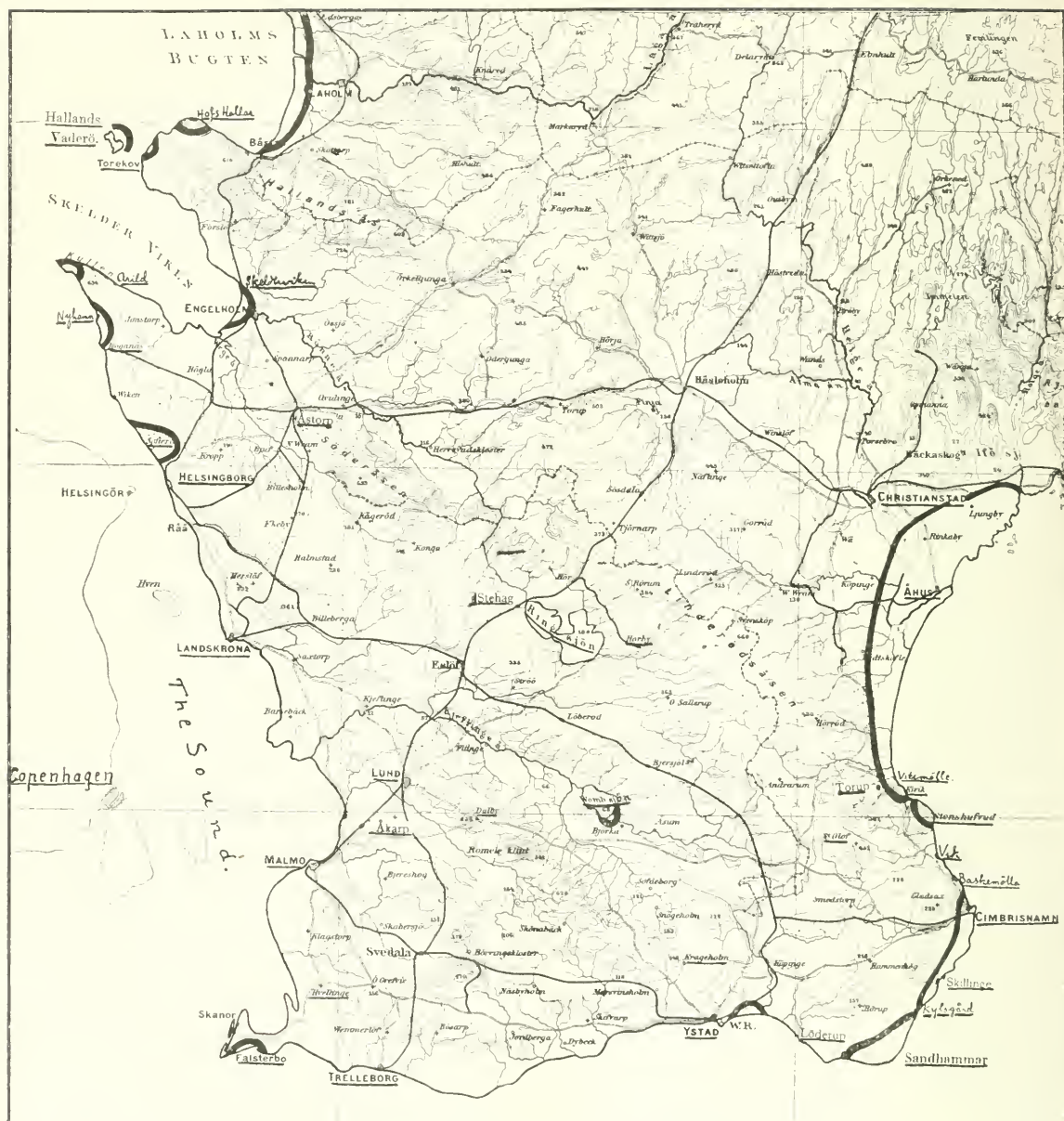


Fig. 77. Province of Scania. The distribution areas of the different coast types of *Hieracium umbellatum* marked schematically with heavy lines. Scale 1:1000000.

be a difficult task to deny that these types are specialized to their respective regions. The influence of the habitat factors upon the composition of the species-population is perhaps best illustrated in the case of *Armeria vulgaris* on the west-coast of Scandinavia. This coast strip runs through climatically widely different latitudes, and the population differs accordingly, as has been shown above. The northernmost type of the species is the var. *sibirica* Turcz. The succession of *Armeria* types on the Scandinavian coast-line partly repeats itself on the coast of Greenland, where the »*maritima*» type is confined to the southernmost portion of the coast, while the var. *sibirica* succeeds it to the north (KOLDERUP ROSENVINGE, 1896).

2. THE CORRESPONDENCE BETWEEN THE ALTERNATION OF HABITAT AND HABITAT TYPE.

The controlling effect of environmental factors on the composition of a species-population is most clearly brought out in the cases where the reappearance of a distinct locality occasions the reappearance of the habitat type typical of that locality. The different *H. umbellatum* types furnish good evidence on this point. The alternation of sea-cliffs and shifting beach-dunes on the Swedish west-coast gives rise to a corresponding alternation of the bushy, broad-leaved sea-cliff type and the dune type. Wherever the *H. umbellatum* population on that coast strip has been investigated, the sea-cliff localities (Kristineberg, Marstrand, Varberg, Hof's Hallar, Hallands Väderö, Kullen) have been found to harbour only the broad-leaved sea-cliff type. The beach dune localities investigated (Falkenberg, Halmstad, Torekov, Skelderviken, Nyhamn), which alternate with the cliff localities, have conversely been found to harbour the dune type.

That a similar correspondence in the alternation of habitat and habitat type may take place within a geographically very limited area is seen from the distribution of the *H. umbellatum* types in the south-east corner of Scania. The successions of habitat types described below take place within an area found to be about 35 kilometres in extent. The prostrate dune type of the arenaceous fields is the only type found at Vitemölle, as was stated above. This type is succeeded by the Stenshuvud sea-cliff type south of Kivik, which again is replaced by the first-mentioned type a little farther to the south, where the sand-fields reappear. The type in question now flourishes as far south as the extent of the sandfield area, but is replaced by the type of the shifting dune as soon as the drift-sand of the Sandhammar region be-

gins (at about Kylsgård). The mixed populations in the transition belts between the distribution areas of the different types have already been discussed.

The map of Scania (fig. 77) reproduced here and showing schematically the distribution areas of the different coast types of this province should be consulted in this connection.

3. THE LOCAL DIFFERENTIATION OF THE HABITAT TYPE FROM THE SPECIES-POPULATION.

When, in passing from South to North or from the plains into Alpine levels, a zonation of a species-population into different climatic types, corresponding to the changes in climate, is found to take place, the conviction is forced upon us that these types are intimately related to the different external factors. The repetition of the zonation in regions far distant from each other, as for instance the zonation of *Armeria vulgaris* on the coasts of Norway and Greenland, increases the strength of this assumption. The further question whether this repetition is due to a local differentiation of the respective types from the species-population, or is the result of a migration of an once differentiated type into suitable habitats, becomes of great interest in this connection. In the following an attempt will be made to throw some light upon this question by the aid of the cultivated habitat types of *H. umbellatum*.

It is convenient to start with the type of the shifting beach-dunes. If the collections of leaves of this type (figs. 67—72) are examined, it is at once seen that the series from the various places exhibit considerable differences. While the series from the Sandhammar set (fig. 72) fairly closely resembles the Halmstad set (fig. 68), important differences as to leaf shape are seen in the Falkenberg set (fig. 67). These individuals do not have the linear leaves typical of the first series, but have leaves which are much pointed and remarkably broad in their lower part. Even in the individuals with quite narrow leaves the characteristic leaf-base is always to be seen. Thus these leaves show resemblances both to the cliff-type (which has the leaves broadest in the lower half) and to the dune type at Halmstad and Sandhammar (which has long and narrow leaves). Now when the Falkenberg dune population *as a whole* shows these undoubtedly non-essential leaf-characteristics, the assumption appears most reasonable that the type in question has become locally differentiated from a mixed population of the cliff-type (which is already found typically at Varberg) and of the dune type of the south.

The Torekov set (table 14, fig. 69) is very interesting in this connection because of its close proximity to the broad-leaved cliff-type of Hof's Hallar and Hallands Väderö, which has already been discussed. The collection raised from seeds includes individuals with varying shape and width of leaf. Some show resemblance to the cliff-type leaf, others to the leaf of the inland-type (broadest in the middle). When it is found (cf. tables 13, 15; fig. 62) that the Torekov set includes individuals with a leaf narrowness only exceptionally found in the cliff series, we may well assume that the Torekov type has been differentiated locally from the *H. umbellatum* population of that region in response to dune conditions. The individuals with leaves resembling the inland type have the leaf-width typical of the most narrow-leaved individuals of that type (cf. figs. 59—61). As to leaf-width only the most narrow-leaved individuals seem thus to have been favoured, while the particular shape of the leaf, broadest in the lower portion or in the middle, does not seem to be of any moment.

There are also dune types consisting almost entirely of individuals with leaves of a shape typical of the woodland type of the interior, e. g. with leaves broadest in the middle. These are the series from Nyhamn and Skelderviken (figs. 70—71). Inspection in the field of the *H. umbellatum* population in these localities has also brought out this peculiarity.

The narrow-leaved type of the shifting dunes is thus seen to differ in different places in regard to the detailed shape of the leaves. It may have exclusively linear leaves (Halmstad, Sandhammar), or the leaves broadest towards the base suggestive of the particular shape of the cliff type (Falkenberg), or may be made up almost exclusively of individuals with leaves broadest in the middle and may thus resemble in this character the inland type (Skelderviken, Nyhamn). It may finally be composed of individuals some of which resemble the cliff type, others the inland type, in regard to this characteristic (Torekov).

I do not think that these findings are consistent with the generally accepted migration theory. The differences observed, which must be considered quite non-essential to the existence of the plant in the various dune localities, go to show that the dune type has on the contrary become differentiated separately at different points, as a response on the part of the species-population to dune conditions.

The broad-leaved sea-cliff type of Stenshuvud illustrates, I think, much the same thing. The important characteristics of this type, which distinguish it from the cliff type of the west coast, viz. the

erect growth and the more contracted inflorescence, also characterize the woodland type of the interior. This latter type grows, as has been mentioned before, not far from Stenshuvud. It therefore appears probable that the Stenshuvud cliff type has become differentiated from the local species-population without the intervention of the cliff type of the west coast. Different crosses now being made are expected to give some information in the near future as to this point.

4. THE PARALLELISM BETWEEN THE MODIFICATION AND THE HEREDITARY VARIATION.

The morphological parallelism between the modification and the hereditary variation offers an additional proof of the control of the environmental factors upon the direction of the differentiation process of the habitat types. The structural characteristics brought about when a non-halophyte is allowed to develop in solutions of sodium chloride, when a Lowland mesophyte is exposed to an Alpine climate, or when a land-plant is submersed, are all in the nature of reaction structures arising through reaction to environmental changes. When it is found that these same habitats, which lead to modificatory succulence, dwarfness, etc. in some forms of the species, are habitually populated by other forms of the species in which these morphological characteristics are hereditary, no doubt would seem to remain as to the influence of the habitat factors upon the genotypical composition of the species-population present in a certain habitat. That this controlling influence may be more or less close has been alluded to in the case of the *Succisa* populations treated above, as well as in the treatment of *Atriplex* and *Matricaria*. The groups dealt with in the first part of this paper furnish, for the rest, ample evidence of the parallelism between modifications and hereditary habitat types.

The fact that in the majority of the cases investigated not the habitat modification of the plant but the corresponding hereditary type of the species has been found to populate the habitat leads to a brief consideration of the theory of adaptive response. If organisms are able to respond directly and advantageously to changed conditions, we should certainly expect to find that the habitat which calls for changed structures on the part of the organisms in order to become inhabitable would be populated with organisms thus modified. When this only to a limited degree seems to be the case, the course followed being rather a genotypical differentiation of the species-population into

different, hereditary habitat types, the advantage of such responses on the part of the individual becomes highly questionable. The conclusions to be drawn from the data presented in this work point rather to an interpretation of the habitat modification opposite to the theory of adaptive response.

The question may be made clearer by the assumption that the same characteristic which in one form of the species (the resulting modification) requires the exposure to an environmental factor of high intensity in order to become developed, may in another form (the hereditary variation) result as a response to a very much lower intensity of this factor (TRESSON, 1919 a). It is conceivable that the habitat factor responsible for the development of the characteristic in question may at the same time act as a limiting factor upon the general development in the case of the modification, while no such limiting action results in the hereditary variation because of the promptness with which it responds to this same habitat factor. The readiness with which an extreme habitat so often is populated by the hereditary habitat type to the exclusion of the parallel habitat modification indicates precisely this nature of the »adaptiveness» of the both forms.

The general results obtained by KÜSTER (1916), DETTO (1904) and other investigators, who have attacked the problem from other aspects, seem to be consistent with the view developed above.

III. THE SPECIES AND THE VARIETY AS ECOLOGICAL UNITS.

It should not be thought that the differentiation of a species-population into hereditary habitat types is a phenomenon peculiar to the species discussed above. The cultivations hitherto made of other species, including for instance *Rumex acetosa* L., *Solidago virgaurea* L., *Artemisia campestris* L., *Campanula rotundifolia* L., *Ranunculus acer* L., indicate precisely the same behaviour. The same will very likely be found to hold true for the majority of common plant species. It is in fact to be assumed that the rarity of certain species is in great measure due to a decreased power of genotypical response to habitat differences, climatic and edaphic, within their area of distribution.

Thus, as a result of genotypical responses of the species-population to different habitats, isolated units are formed within the species much in the same way as contemplated by JORDAN (1905) and HAGEDOORN (1921). However, to speak of such units as »species».

as is done by these writers, is largely to strip the ordinary species, as found in nature, of one of its most characteristic qualities, viz. the ability to respond genotypically to a wide range of different habitats with such units or habitat types, representing various combinations of Mendelian factors. The further discussion of this subject leads to a consideration of the species and the variety as ecological units.

The concept of the species has undergone various changes since the time of LINNAEUS. Darwinism, as also Lamarckism before it, by the nature of the theory led to the conception of the species as mere conventions, set up in order to facilitate a classification of ever-changing and therefore not clearly defined groups. The genetical analyses of Linnean species have again brought about a change; the genotype has now become the real unit, while the "collective" species is still to a large extent considered a conventional conception. This general notion is also reflected in the species-concepts recently propounded (LOTSY, 1916; HAGEDOORN, 1921). Whether this is a legitimate procedure, or whether it does not at the same time reflect the failure on the part of these investigators rightly to appreciate the ecological side of the species problem may perhaps be gathered from the following. It is well known that during the last two decades great progress has been made with regard to the experimental study of the species problem from the genetical point of view. Not only has Mendelism gone far to show that species follow the same laws as varieties with regard to segregation and combination; it has also been able to demonstrate and to a certain extent copy Nature's own course in the building up of new species. This has been admirably shown by LOTSY (1916) in the well known case of *Antirrhinum rhinanthoides*, produced from a cross between *A. glutinosum* and *A. majus* and so different from its parents that a trained botanist would refer it rather to the genus *Rhinanthus* than to *Antirrhinum*. It is constant in certain characters but varies in other in the same way as the Linnean species. The extravagant types produced by HERIBERT-NILSSON (1918) from various *Salix* crosses belong to the same category of facts. All of them (*Salix amerinoides*, *S. pendulifolia*, *S. monandra*) demonstrate in a striking way the process by which new and morphologically very remarkable organisms arise.

Thus, while the belief that the Linnean species of the present genetically represent complicated products of recombined Mendelian factors, or genotype compounds, has been strengthened, few would

maintain that the problems connected with the formation of the Linnean species are exhausted by this demonstration. Most of these species are, as every earnest inquirer will find, in their natural areas of distribution rather circumscribed products, which do not live in any extensive connubium with congeners of other species. The bridgeless gaps found between species of the same genus, the final moulding of the Linnean species, remain then to be explained. The Darwinian idea of selective processes at present offers to most minds a plausible explanation of the differentiation of Linnean species. Although very little is known with regard to the actual play of these selective processes, certain facts likely to demonstrate the complex nature of selection have been brought to light. KÖLREUTER (1761) showed that a species pollinated simultaneously with its own pollen and pollen from another species breeds true to type, in spite of the fact that it otherwise gives hybrids when crossed with that species. That the native pollen is favoured as compared with foreign has been shown by HERIBERT-NILSSON (1920) in the case of *Oenothera Lamarckiana*. He found that pollen tubes of *O. gigas* grew more slowly in the styles of *O. Lamarckiana* than the *O. Lamarckiana*'s own pollen tubes. The terms elimination, certation, prohibition, and substitution discussed by HERIBERT-NILSSON refer to phenomena which give rise to aberrant types of segregation. The importance of such gametic and zygotic complications has been discussed more recently by NILSSON-EHLE (1921). They are all particularly well calculated to throw light upon selective processes of great weight. To whatever extent this «pre-natal selection» may limit the output of new organisms, hybrids between already existing species would no doubt be more numerous and more widely distributed in nature were it not for the controlling effect of living and non-living factors of the outer world. Various disturbances involving different organs are frequently seen in hybrids and in «artificial» species, and this fact does not support the idea that such organisms are able to hold their own with nature. We are thus forced to the conclusion that the present-day species represent the necessary outcome of the complex processes of selection in this epoch of the earth's history (cp. HERIBERT-NILSSON, 1918). As a natural consequence we are led to the inference that a change in the non-living world brings about a corresponding change in the living, inducing a recombination of Mendelian factors now distributed in organisms, and resulting in the formation of new genotype compounds or species (= evolution).

The species problem is thus seen to be in a large measure an ecological problem. As such it has hitherto remained almost un-attacked from an experimental point of view. While at present the purely genetical side of the problem is fairly well understood, we have only to a slight extent been able to arrive at an understanding of the ecological questions involved. So much appears certain, however, that the Linnean species are units of the same importance ecologically as their constituent elements are genetically. In view of the necessity of keeping the distinction between ecological and purely genetical units

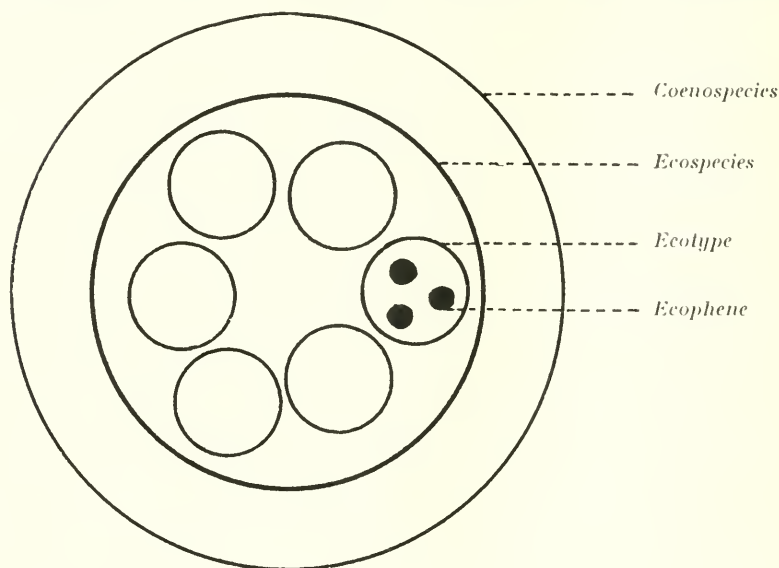


Fig. 78.

in mind, the term *ecospecies* has been proposed (TURESSON, 1922) to cover the Linnean species or genotype compounds as they are realized in nature.

It is evident that we do not find realized in nature the whole possible range of combinations within such an ecospecies because of the control of living and non-living factors of the outer world. If the ecospecies be subjected to artificial crossing or withdrawn from the close control of some of these controlling factors, as is already accomplished to a certain extent when the species is brought under culture by man, the great number of possible combinations within the ecospecies might be brought to light. Such an extension of the limits ordinarily set by nature might also, as is well known, be attained when

different species become crossed. It seems appropriate — for theoretical reasons — to denote the total sum of possible combinations in a genotype compound by the term *coenospecies*¹. The ecospecies is then the genotype compound narrowed down to the ecological combination-limit.

The ecological sub-units of the ecospecies distinguished in the first part of this work have now to be briefly considered. They have been spoken of as types or habitat types. These terms for several reasons, and especially because of their vagueness, do not seem appropriate. The term »variety» might have been employed.

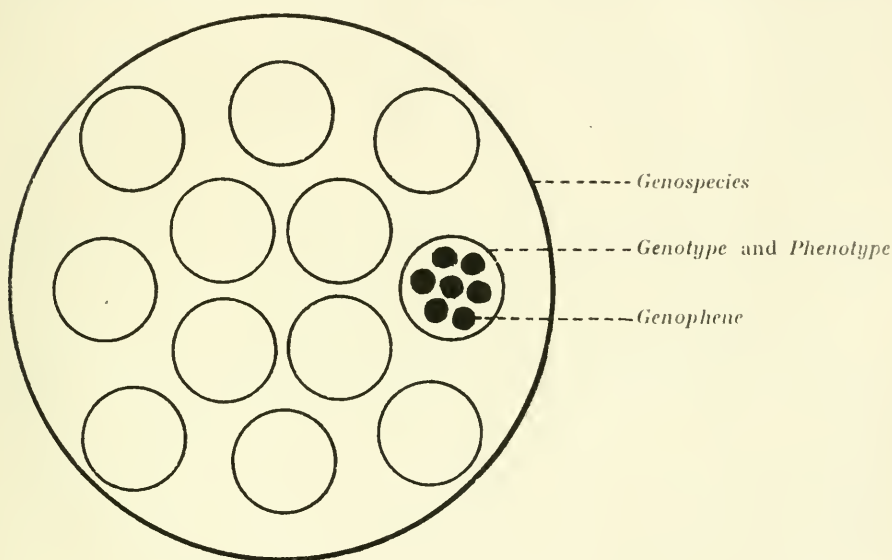


Fig. 79.

It is obvious, however, that this term gives an inadequate conception of the result of the genotypical reaction of an ecospecies to a specific habitat. It is rather arbitrarily used to denominate different kinds of hereditary deviations from a valid or supposed type, and cannot therefore be advantageously employed in any ecological sense. The term *ecotype* seems to be an adequate expression, and is therefore proposed for the ecological unit, to cover the product arising as a result of the genotypical response of an ecospecies to a particular habitat (cp. TURESSON, 1922).

¹ I take the opportunity of thanking Mr. OTTO R. HOLMBERG, Conservator of the Botanical Museum of Lund, for the coining of this term.

The importance from an ecological point of view of the differing genotypical reactions of the ecospecies, when distributed over a continuous area comprising different types of localities, seems to have been sufficiently demonstrated at this stage. We have been able to show, by the help of the cultures made, and by the differentiation of dune-ecotypes, sea cliff-ecotypes etc. that one and the same ecospecies succeeds in populating widely different habitats. It should not be argued, however, that the differing phenotypical reactions may not also be of great moment from an ecological point of view. This is all the more the case when it is found that a population in an extreme habitat responds as a whole with a reaction-type which is suggestive of a specialized ecotype, although it may be found upon culturing to be wholly or partly due to the modificatory effect of the particular habitat factors. The cases of the shade forms of *Lysimachia vulgaris* and *Solanum Dulcamara* on Hallands Väderö, and the *Centaurea* and *Succisa* dwarfs, analysed above, illustrate this mode of behaviour. The reaction-types of the ecotypes called forth by the modificatory influences of extreme habitat factors may appropriately be termed *ecophenes*.

It becomes necessary briefly to consider the genetical analogues of these units. The term *genospecies* has been proposed (cp. TURESSON 1922) to embody the facts of the genotypical construction of the ecospecies. The term, however, is properly to be employed for the genetical analogue of the coenospecies. The *genotypes* (JOHANNSEN, 1909) are, further, the Mendelian sub-units of the genospecies, as the ecotypes are the ecological sub-units of the ecospecies. The various reaction-types of one and the same genotype might be termed *genophenes*. The inclusion of the different genophenes of a genotype becomes then the *phenotype* (JOHANNSEN, 1909). The different units distinguished thus group themselves in the following series:

<i>coenospecies</i>	<i>genospecies</i>
<i>ecospecies</i>	
<i>ecotype</i>	<i>genotype, phenotype</i>
<i>ecophene</i>	<i>genophene</i>

Figs. 78 and 79 may facilitate the survey of the both unit-groups.

It should be said in conclusion that the study of the species along the lines developed in the present work is intended to furnish a necessary complement to the Mendelian study of the species pro-

blem. The importance of this line of research for the understanding of bio-geographical and bio-sociological questions is also evident.

SUMMARY.

1. Material of a number of Linnean species, brought under culture, has revealed the presence of a considerable hereditary variation within each species.
2. The hereditary variations of the species have been found in nature to be grouped into different types confined to definite habitats. Certain characteristics have been found to be common to all or to the majority of the individuals of each type, while other characteristics vary.
3. The following facts bring out particularly well the intimate relation of these habitat types to the habitat factors:
 - a) The characteristics of the types are apparently such that they specialize the types for certain habitats.
 - b) With regard to *Hieracium umbellatum* a close correspondence is found between the alternation of habitat and habitat type.
 - c) Cases have been found where a local differentiation of the habitat type from the species-population has in all probability taken place.
 - d) There is a morphological parallelism between the modification and the hereditary variation.
4. The evidence at hand does not support the idea that the habitat types have originated through sporadic variations preserved by chance isolation. On the contrary the facts go to show that the habitat type represents the genotypical response of the species-population to a definite habitat.
5. The Linnean species represents an ecological unit of great importance. It is specified as a *coenospecies* (defined above), narrowed down to the ecological combination-limit. A genotype compound of this order is here termed an *ecospecies*.
6. The term *ecotype* is used as an ecological sub-unit to cover the product arising as a result of the genotypical response of an *ecospecies* to a particular habitat.
7. The term *ecophene* is proposed to cover each of the reaction-types of the ecotypes arising through the modificatory influences of the combinations of extreme habitat factors given in nature.

8. The genetical analogues of these units are briefly considered, and the concepts of the *genospecies* and the *genophene*, defined above, are introduced.

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