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EXPERIMENTAL AND CYTOLOGICAL STUDIES ON PLANT SPECIES

VIII. RACIAL DIFFERENTIATION IN AMPHI-ATLANTIC *VISCARIA ALPINA*[4]

BY

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København 1963
i kommission hos Ejnar Munksgaard

Synopsis

Cultivation experiments with 14 strains of *Viscaria alpina* have been carried out. All strains had $2n = 24$.

The experiments have demonstrated the existence of a series of races which differ in flowersize, earliness, height, leaf dimensions, morphology of the inflorescence and habit. A very important difference in basal leaf formation is found between Greenland plants and plants of European origin. The most vigorous basal leaf cushions are produced by the boreal European races. The variation may be clinal in areas where the species is frequent, but where it occurs in isolated pockets the clines have become stepped. The clines are broken where the species has crossed the Denmark Strait and at the transition from high mountains to boreal-temperate conditions in Scandinavia. Taxonomically the variation is best described as three subspecies: viz. ssp. *americana* (Greenland-N.E. America), ssp. *alpina* (mountains in Europe), ssp. *boreale* (boreal European areas). The latter subspecies is proposed as a new taxon. The paper is concluded with a discussion of the type of variation, gains and losses of biotypes in refugia or during migration as well as leaf size in relation to environment. *Viscaria alpina* originated in Europe and was able to cross the Atlantic ocean from east to west: it is a genuine Amphi-Atlantic species.

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1. Introduction

The problems concerning Amphi-Atlantic distributions were recently discussed by Hultén (1958). His maps afford a much better basis for such a discussion than has been available hitherto. Hultén also considers briefly the racial differentiation of Amphi-Atlantic species by assuming a diminishing of the contents of biotypes in many species as a result of the changing and often severe conditions of life during the Ice Ages. He thinks that the formerly glaciated areas were "covered with taxa less rich in biotypes than their original Tertiary populations." He also maintains his old theory about the origin of the Amphi-Atlantic distributions by saying that the species in question, with a few exceptions, are remains of species which formerly possessed circumpolar ranges but which have died out in the Pacific sector owing to vicissitudes presumably of climatic nature.

In my paper from 1938 (1938: 268–271) the Amphi-Atlantic distributions were also discussed. It was as inter alia concluded that plants migrating from Europe to Greenland—N. America (or *vice versa*) using the Atlantic Islands (Iceland, Faeroes, British Isles) as their route would be exposed to cold maritime types of climate and thus perhaps lose all continental biotypes during the migrations.

One of the many examples of true Amphi-Atlantic species which have never been found in Asia or Western North America is *Viscaria alpina*. Its range is shown on map No. 49 in Hultén's treatise. On this map the species is differentiated into two taxa, a western one called var. *americana* Fern. occurring in E. America-Greenland and an eastern one, corresponding to typical *V. alpina* which ranges from Iceland to N. Russia and southwards to the Pyrenees and Apennines. Apart from certain lowland occurrences in southern Sweden, *Viscaria alpina* is confined to areas with montane or sub-lowarctic climatic conditions. It is a low-subarctic montane species.

One type of modern gene-ecology deals with the geographical distribution of heritable characters within the range of a species. Such character distributions have mainly been traced in Europe (e. g. *Prunella vulgaris*, *Holcus lanatus*, *Geranium sanguineum*, Böcher 1949, Böcher & Larsen 1958, Böcher & Lewis 1962). In *Plantago maritima* which was closely investigated experimentally by Gregor 1939 it was shown for the first time that certain characters form gradients in the North Atlantic area. Such experimental work is undoubtedly of fundamental importance for the solution of the problems concerning the Amphi-Atlantic distributions and the

Table 1. Cultivated material of Viscaria alpina.

No.	Cult. No.	Origin	Years of cultivation	Figures	Chromosome count
1	1	New Foundland, Bonne Bay, Serpentine slope (upper part) of Table Mt. Seeds from Dr. A. W. H. Damman	1961–63		$2n = 24$
2	4753	W. Greenland, Holsteinsborg	1957–62		$2n = 24$
3	4843	W. Greenland, Head of S. Stromfj.	1957–62	Fig. 1	$2n = 24$
4	29	W. Greenland, Kangersuneq 1	1959–62	Fig. 1	$n = 12$
5	30	W. Greenland, Kangersuneq 2	1959–63	Fig. 1	$n = 12$
6	31	W. Greenland, Sukkertoppen	1959–62		
7	41	S. Iceland, Thorsmork, Seeds from Prof. Morten Lange	1960–63		$2n =$ ca.24
8	36	Norway (seeds collected in nature from Bot. Gard. in Bergen)	1961–63	Fig. 1	$n = 12$
9	37	Norway, Lake Helin (Transplants)	1961–62		
10	38	Norway, Bessheim (Transplants)	1961–62		$2n = 24$
11	27	Sweden, Öland, Vickleby Alvar	1958–63		$2n = 24$
12	33	Alps, Valais, Riffelberg 2600 m.	1960–62		$n = 12$
13	34	Alps, Hortus Vilmorin Verriéres	1960–62		$n = 12$
14	35	Alps, Region du Laûtaret (Seeds from the University of Grenoble)	1960–62		$n = 12$

history and evolution of the plants in question. One of the main aims of this work is to attempt to explain the present distribution of *Viscaria alpina* partly as a result of ecotypic differentiation, partly of race formation either during migrations or due to geographical isolation.

2. Material and Methods

Experimental cultivations of *Viscaria alpina* were carried out in the years 1957–1963. The plants were grown in pots in frames at the experimental field west of Copenhagen (Tåstrup) or in the arctic greenhouse in the Botanical Gardens in Copenhagen. 14 strains from various parts of the range of the species were investigated. As a rule 10–15 plants of each strain were cultivated. Population studies in nature and herbarium studies as well as chromosome counts were undertaken in order to supplement the results obtained from the cultivations. Table 1 gives a survey of the cultivated strains, their origin, years of cultivation and chromosome number.

3. Cytological Observations

2n = 24 (or n = 12) was found in 12 strains, see Table 1. The *number is in* agreement with many previous counts, i. e. by Blackburn (1928), Griesinger (1937), Rohweder (1939), Favarger (1946, material from the Alps), Löve (1956, Iceland material), Blackburn & Morton (1957) and Jörgensen et. al. (1958, material from Disko, Greenland), see Löve & Löve (1961).

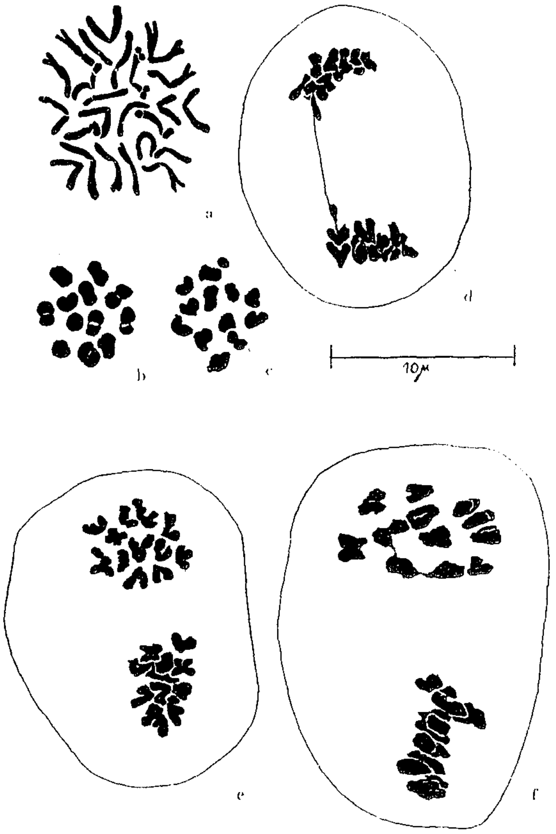

Fig. 1. Chromosomes in Viscaria alpina. — a somatic metaphase from root tip (strain No. 3). — b metaphase I (No. 4). — c anaphase I (No. 5). — d anaphase I with bridge (No. 5). — e metaphase II (No. 4). — f metaphase II (No. 8).

Meiosis was studied in five strains. It appeared to proceed quite normally but in two Greenland strains, Nos. 4–5 from Kangersuneq, evidence of the occurrence of an inversion was found. The number of PMCs with acentrics or bridges, however, was always very low.

Fig. 1 c shows a first anaphase plate with a small fragment which was situated in the middle of the cell and was undoubtedly acentric. The bridges (e. g. Fig. 1 d) were very thin and in most cases seemed to break very soon. In the case illustrated it was impossible to detect any acentric fragment in connection with the bridge.

In four of the strains the orcein squash technique was used. As compared with microtomed Feulgen stained material (Fig. 1 a–e) the squashed PMCs were usually somewhat larger and the chromosomes larger and more swollen (Fig. 1 f). In metaphase II it was sometimes possible to detect very thin chromatin threads connecting the chromosomes. Such connections may break and disappear as a result of a stronger contraction caused by the fixation and embedding technique.

4. Previous experimental and taxonomic work

Colour of the flower and chlorophyll deficiency. White flowering specimens have been observed frequently in the Greenland population (f. *albiflora* Lange) as well in Iceland, Norway and Sweden. I described a peculiar form from Greenland as f. *chrysochloa* (1952: 21–23). It has yellowish stem leaves but normal green rosette leaves and light pink flowers. It probably represents a double heterozygote as its offspring also gives some white flowering individuals.

Comparison of alpine, montane and lowland races in Scandinavia. Turesson (1927, 1932) compared alpine series from three Scandinavian mountain areas with material from the lowland in Southern Sweden, the Alvar on the Isle of Öland and Vedeby in Blekinge. He concluded that the lowland series from Öland differed from the alpine ones in many characters. Thus he was able to show that the Öland race which had been treated by taxonomists as var. *oelandica* was not a habitat modification.

The Öland race was described as a variety of *Lychnis alpina* L. by Lindström (1817: 17) who said that it differs by being much more pliable and having petals which are pale pink (purpureo-albescentia). Fries (1842: 170) obviously treated the same race as var. *petraea* (Herb. norm. IV). Sterner (1938: 97) referred to the Öland plant as var. *oelandica* (Ahlqu.) Sterner, but the correct name must be var. *oelandica* (Lindstr.) Sterner in spite of the fact that the oldest collections from Öland are labelled "*Lychnis alpina* var. *oelandica*, Oelandia 1814 Abr. Ahlquist" (see further p. 23 and Fig. 8).

The montane Scandinavian plants occurring mainly on serpentine areas in the coniferous forest region (below 500 m) were described by Rune (1953: 56–60) as var. *serpentinicola* Rune. By cultivation experiments Rune, like Björlykke (1938:

115), was able to prove the persistence of all the characteristics of this variety. It has narrow leaves, more or less reduced petals, a slender but stiff stem and a highly branched and elongated raceme. Some plants are apetalous, but a gradual transistion from such plants to plants with normal flowers could be demonstrated. According to RUNE (loc. cit.: 58) var. *serpentinicola* can be distinguished from certain lowland specimens of the species only after cultivation. He mentions a number of features common to the montane and lowland forms but adds, strangely enough, that var. *serpentinicola* seems to have nothing to do with var. *oelandica*.

Comparison of European and American populations. FERNALD (1940) demonstrated the difference between the coarse west-arctic *Viscaria alpina* and the European one. He referred the American-Greenland plants to a separate variety, var. *americana* Fern. All differences between it and the typical plant are quantitative (see Table 2).

Table 2. Viscaria alpina (Data from FERNALD 1940).

	European material	American-Greenland material
Length of radical leaves	1.0–3.5 cm	1.5–6.5 cm
Breadth of radical leaves	2 –5 mm	2 –8 mm
No. of cauline leaves	2 –4 pairs	3 –7 pairs
Length of larger cauline leaves	1 –3 cm	1.5–5.5 cm
Breadth of larger cauline leaves	2 –5 mm	2.5–10 mm
Length of calyx during anthesis	3 –5 mm	5 –7 mm
Length of petals (incl. claw)	6 –8 (9) mm	8.5–14.5 mm
Breadth of petals	3 –3.5 (4) mm	3 –6 mm

There is reason to mention that FERNALD admits that some specimens from Iceland and Norway have flowers approaching those of var. *americana*, and that dwarfed plants (from Greenland) may be as small as some European ones. As already mentioned HULTÉN treats var. *americana* as a geographical race. He suggests, however, that var. *americana* represents a different chromosome race, which is obviously not the case (see Table 1).

5. Experimental cultivations carried out 1957—1962

Comparisons of two Greenland races with the Öland race (Table 3).

This first experiment which started in 1957 unveiled a rather large racial difference between the two Greenland strains and between them and the Öland strain. Typical plants from all three strains are seen on Fig. 2 and the results of the comparisons in Table 3. It appears that No. 2 from Holsteinsborg (coastal mountains)

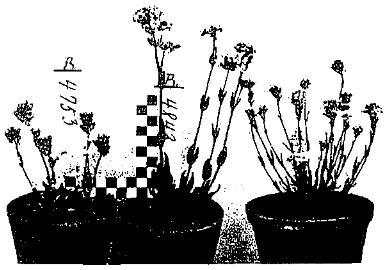

Fig. 2. Culture experiment with two Greenland races and the Öland race (on the right) of *Viscaria alpina*. From the left Nos. 2, 3, and 11 (4753, 4843, and 27). — Phot. June 1st 1959.

approaches the Öland race, No. 11, having pale pink flowers, one terminal inflorescence, intermediate breadth of radical leaves and petal segments. On the other hand it has many characters in common with No. 3 from the extreme continental area at the head of Søndre Strømfjord. The latter matches typical "var. *americana*", being coarse with high content of anthocyanin in leaves and stems and usually two small additional inflorescences supported by the uppermost pairs of leaves. The most striking difference between the two Greenland strains and that from Öland appeared in the number of stems per individual, this number being much higher in the Öland strain. Another important difference concerned the breadth of the stem leaves and the flower size (cp. Table 3).

Comparisons of Greenland races with various European races (Table 4).

Material from three new stations in West Greenland collected as seeds in 1958 (Nos. 4–6) was available for comparison with plants of European origin in the years 1960–62. In 1960 No. 11 from Öland was almost as vigorous as in 1959 but later the height of the plants and the number of stems decreased. As it was very low in 1962 (Fig. 4) it resembled the Iceland dwarf race (No. 7) very much. However, as compared in the second year of cultivation (1960 for No. 11, 1962 for No. 7) the dimensions of the two races are very different.

The three Greenland strains did not differ so much as those used in the first experiment (Table 3). The two strains from the inland area at Kangersuneq near Christianshåb, Nos. 4–5, resembled one another and No. 3 very much while No. 6 from Sukkertoppen (coastal mountains) somewhat approached No. 3 (also coastal) by having narrower and smaller radical leaves (Plate I Fig. 1). This was already obvious the first year (1959) when the plants had only developed basal rosettes. Later, however, this difference was less pronounced.

It appears that the variation among the European plants is large and seems to surpass that found in Greenland. The comparisons of cultures in 1962 (Table 4)

Table 3.

	No. 3 (Greenland continental)	No. 2 (Greenland coastal)	No. 11 (Sweden, Öland, Alvar)
Height of plants in cm	16–19 (1959) 12–14 (1960–61)	8–12 (1959) 9–12 (1960–61)	10–16 (1959) 5–19 (1960–61)
Number of stems per individual	2–4 (1960)	3–6 (1960)	21 (15–29) (1960)
Direction of stems	Rigid, erect	Rigid, erect	Somewhat arcuately ascending
Diameter of stems in mm (middle part)	1.8–2.5	about 2	about 1.5
Breadth of largest cauline leaves in mm	7–9 (1959) 6–7 (1960–62)	7–8 (1959) 8–10 (1960–62)	2–4 (1959) 2–3.5 (1960–62)
Colour of upper cauline leaves	Reddish	Green	Green
Breadth of radical leaves in mm	4–6 (1959) 4–5 (1960–62)	2–4 (1959) 3.5–4 (1960–62)	1–2 1.5–3 (1960–62)
Diameter of flower in mm	14–15	12–15	8–10
Shape of petals	Not deeply 2-cleft segments broad	intermediate	Deeply 2-cleft narrow diverging segments
Colour of petals	Pink	Pale pink	Pale pink
Inflorescence	Usually divided, terminal one not large	One large terminal	Usually one terminal
Earliness and length of flowering period	Relatively late, long flowering period	Very early, short flowering period	Late, very short flowering period

show that the European material can be divided into five types, viz. a Scandinavian mountain type with large flowers (Nos. 8–10), an Alvar type with small flowers and many flowering stems (No. 11), an Iceland dwarf type (No. 7), an alpine tall type (Nos. 13–14) and an alpine low growing type with spreading stems (No. 12), see Figs. 3–4 and Plates I–II.

In order to be able to study the difference between Greenland and European plants in more detail, the various distinguishing characters have been investigated separately. The results may be summarized as follows:

Height. No general differences, but hereditary dwarfs only found in Iceland.

Table

Cult. No.	Start of Cult	Height in cm Averages and ranges (in brackets)				Number of (Averages	
		1960 F	1961 F	1962 F	1962 A	1960 F	1961 F
4	1959	14 (10–18)	12 (7–16)	9 (6–10)	19–22	1.0 (1–1)	2.4 (1–4)
5	1959	16 (10–20)	14 (10–23)	13 (8–16)	11–16	2.2 (1–5)	2.7 (1–5)
6	1959	13 (9–17)	11 (9–13)	10 (7–15)	13–18	1.3 (1–2)	2.6 (1–4)
7	1960		–	3 (2–4)[2]	Rosettes only	–	–
8	1961			9 (7–14)	14–18	—	–
10	1961				12–20	—	–
11	1958	15 (11–19)	7 (5–9)	6 (3–8)	–	21 (15–29)	18 (15–22)
12	1960				12 (8–16)	—	–
13	1960	–	15 (10–22)	13 (7–18)	23 (18–26)	—	1.4 (1–3)
14	1960			–	17 (10–21)	—	—

[1]) Nos. 4–6 from Greenland, Nos. 7–14 from Europe [2])4(3–5) 1963
F = Experimental field (pots in frames)
A = Arctic Greenhouse

Number of flowering stems. The largest number is usually reached in the second year of cultivation. All Greenland strains have few (less than 5–6) flowering stems while most European strains have more, some up to 25–30 flowering stems.

Cauline leaves. The difference in breadth between Greenland and European plants is significant. Greenland plants have broader leaves (4–13 mm) European narrower ones (2–8 mm), see also Figs. 3–4. The number of leaf pairs varies; there is evidently no general difference between Greenland and European plants but some observations indicate that American plants are often particularly tall and have sometimes up to 6–7 pairs of leaves.

Behaviour of basal rosettes. European plants have green radical leaves which are usually narrow (very narrow in Nos. 11 and 7). Some may be as broad as the broadest ones in the Greenland plants (No. 13). With increasing age European plants are more inclined to form small mounds of many dense leaf rosettes, some of which produce flowering shoots the next year. In the Iceland dwarfs the mounds may approach the appearance of a hemispherical cushion plant (e.g. *Armeria maritima*). In all European strains new basal rosettes are formed as short lateral shoots supported by the leaves in the original basal rosette. The leaves of the new rosettes are very

4.[1]

flowering stems and ranges)		No. of internodia 1962		Breadth of leaves mm		Flower size mm	
1962 F	1962 A	F	A	Cauline	Radical	Length of Calyx	Diameter
2–4	2–4	4–5	4	6–12	2–5	0.8–1.2	1.1–1.5
2.1 (1–4)	1–4	3–5	5	6–13	3–6	1.0–1.3	1.3–1.6
2.7 (1–6)	1–3	3–5	4–5	4–10	2–4 (6)	0.8–1.2	1.3–1.6
2.7 (1–8)[3]	Rosettes only	2–4	Rosettes only	2–4	1–3	0.6–0.7	0.8–0.9
4.0 (1–8)	3–4	3–4	5	3–7	2–4	1.1–1.4	1.3–1.7
—	1–5	—	4	4–6	2–4	0.9–1.1	1.4–1.5
12 (1–30)	—	3–4	—	2–4	1–3	0.5–0.9	0.8–1.0
—	5.8 (3–8)	—	3–5	4–6	3–5	1.0–1.0	1.2–1.3
9.3 (5–26)	6.5 (1–8)	3–6	5–6	4–8	2–5 (6)	0.7–1.2	0.8–1.3
—	4.0 (1–7)	—	5	5–8	3–5	1.0–1.0	1.2–1.5

[3]) 8 (2–14) 1963

narrow, so that in the autumn the basal leaf assemblance is composed of leaves of very different size (cf. Fig. 5).

Greenland plants have most often reddish radical leaves in the autumn. They are broader because the largest ones are comparatively short. The plants form very low or no mounds and old plants have usually rather few basal rosettes (see Fig. 4). A few observations of American plants (strain 1 and some transplants) make it probable that they have longer basal leaves than most Greenland plants.

Flower dimensions and morphology. No general difference but most European plants have smaller flowers. The Norwegian plants have large flowers but these deviate from flowers of Greenland plants by having narrower sepal lobes and petal segments. The latter difference, however, is not quite reliable as some plants of No. 8 have segments which are almost as broad as those in Nos. 4–6.

Some of the European plants with narrow petal segments deviate by a slight outward curving of the segments. This applies to No. 7 from Iceland No. 13 from the Alps, No. 10 from Norway and No. 11 from Öland.

Except No. 7 all strains are protandrous. No. 7 is probably autogamous, its stamens mature allmost at the same time as the styles. Furthermore the anthers and the pollen grains are whitish instead of lilac.

Comparisons of plants in pots in the experimental field and in the Arctic greenhouse. The plants grown in the Arctic greenhouse in the Botanical Gardens (A) in Copenhagen were exposed to light and positive temperatures from May 1st until Oct. 15th. During the first three weeks and the last month the temperature was kept between 1 and 9°C while in the rest of the period the temperature extremes were fixed at 5° and 16°C. Day length was regulated so that it approximately corresponded to conditions in middle Greenland (2 hours darkness in the summer (5th–14th week)).

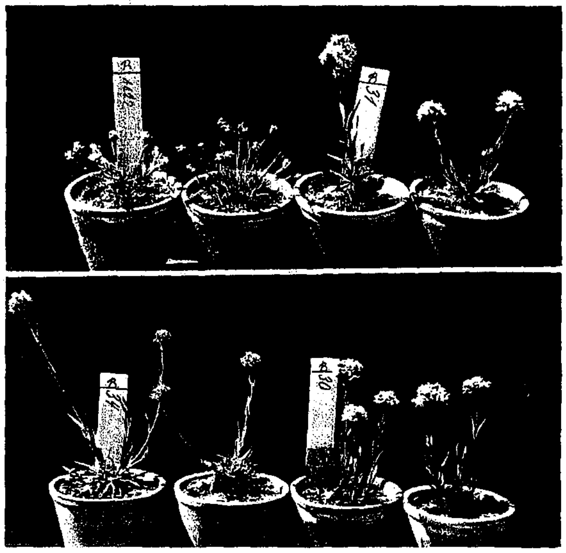

Fig. 3. Two European races of *Viscaria alpina* compared with two Greenland ones (both on the right in the two pictures). Upper row on the left: No. 11 from Öland; on the right: No. 6 (31) from Greenland. Lower row on the left: No. 13 (34) from the Alps, on the right No. 5 (30) from Greenland. — Phot. late May 1961.

In the Arctic house flowering took place late in June or one month later than in the experimental field of Tåstrup (Copenhagen). Comparisons were made with six cult. nos. (Table 4). It appeared that the Greenhouse plants became longer (see Nos. 4, 6, 13) a fact which probably was a result of somewhat reduced light intensity and more sheltered conditions in the Arctic house. The batch of Iceland plants in the Arctic house were all without flowers. The anthocyanin content was low in all plants from the Arctic house.

6. Possible ecological variation

It is difficult to estimate the ecological variation in *Viscaria alpina*. The only way to obtain evidence is by varied environment experiments which unfortunately have not yet been undertaken. The available information about the ecological demands of the species is rather contradictory, indicating different ecological characters in the various races.

Climatic demands. Lid & Zachau (1928: map on p. 75) were the first to give exact information about the distribution in Scandinavia. They regard *V. alpina* as a glacial relic which in lowland areas shows a marked western distribution. A similar trend appears from Hultén's map in which a decreasing frequency eastwards is evident in North Scandinavia (Lofoten → Kola Peninsula). According to Hiitonen (1962: 33 and Fig. 24) *V. alpina* is one of the many species which stop in the Karelian Isthmus. Its southern limit almost coincides with the southeast boundary of the bedrock area. *V. alpina* also shows decreasing frequency from west to east in the Alps.

In America-Greenland *V. alpina* may be composed of maritime and relatively continental races (cp. Table 3). This would explain why the species in Greenland reaches the extreme continental areas at the head of Søndre Strømfjord and penetrates as far as Hudson Bay in Canada.

It is interesting that *V. alpina* is exclusively alpine in the Alps (between 1,900 and 3,100 m above sea level) while it is able to grow in the lowland of Southern Sweden. This discrepancy is explained by the occurrence of special lowland races in Southern Sweden and absence of such races in the Alps.

In all there seem to exist five climatic types connected with different ecological races in *V. alpina*: viz. Continental-lowarctic (e.g. Cult. Nos. 3–5), oceanic-montane-lowarctic (e.g. coastal races in Greenland, mountain races of Scandinavia and South-European mountains), subarctic-subcontinental (races in the coniferous belt in Scandinavia), temperate subcontinentat (No. 11) and finally a subarctic-oceanic type (No. 7).

Edaphic demands. The plants of the Alps are said to occur on rocks poor in lime (Hegi). This statement is in agreement with the behaviour of plants in the Scandinavian mountains. According to Nordhagen (1936) *V. alpina* shows a strong preference to the acidophilous communities of his *Juncion trifidi*, but it also enters communities like the *Carex rupestris-Encalypta*-soc. and *Alchemilla alpina-Deschampsia flexuosa*-soc., which fact points towards a rather wide soil tolerance (see details in Nordhagen 1943). Knaben (1950: 100) also found it on many types of rock. The curious fact is that the species seems to be most abundant on serpentine and is able to tolerate high concentration of copper, see Vogt (1942), who describes it as a copper pyrite indicator, and Coombe & White (1951: 50) who found it the only representative of flowering plants on refuse heaps at copper mines in Norway. According to Rune (1953: 105) *V. alpina* in the district of Bergslagen occurs abundantly and disjunctively on ore and slag deposits. It is very frequent on minerals containing copper, lead, and zinc at the Garpenberg mines. *V. alpina* is also connected with serpentine or heavy metal soils in Scotland and Raven & Walters (1956: 109) suggest that it can only survive in soil conditions that are so repugnant to the majority of plants that any severe competition is eliminated. No doubt the var. *serpentinicola* is closely connected with serpentine (RUNE 1953). The conclusion may therefore be drawn that typical *V. alpina* is a little acidophilous although with a rather wide tolerance, while var. *serpentinicola* and related races are in any case able to grow on a number of ultrabasic rocks. However according to RUNE (1953: 44) the pH values of the root horizon in stands containing *V. alpina* on ultrabasic rocks are not particularly high. The pH range which he found is between 6.3 and 7.2 or almost exactly the same as that given by STERNER (1938: 97) for var. *oelandica*. (pH 6.0–7.1). On the other hand, NORD-

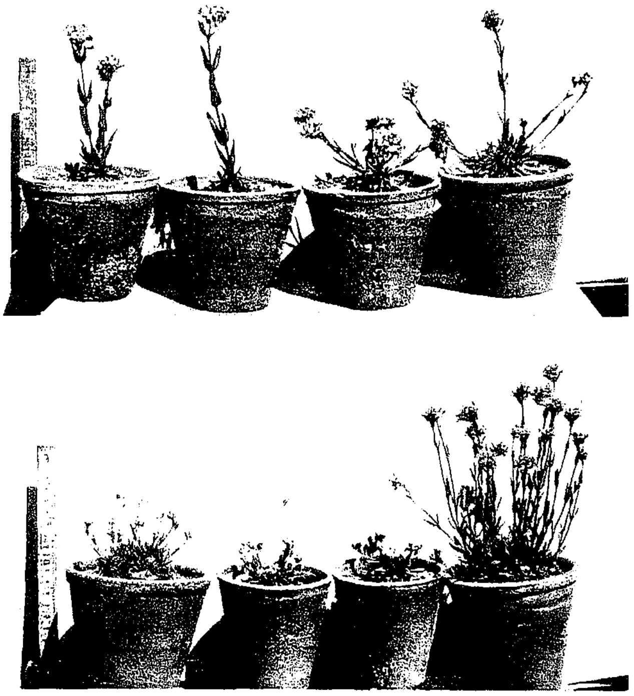

Fig. 4. Upper row on the left No. 5 from Greenland, on the right No. 8 from Norway. Lower row from the left No. 11 (one pot) from Öland, No. 7 (two pots) from Iceland, and No. 13 from the Alps. Note strong basal leaf formation in all except No. 5. — Phot. June 8th 1962.

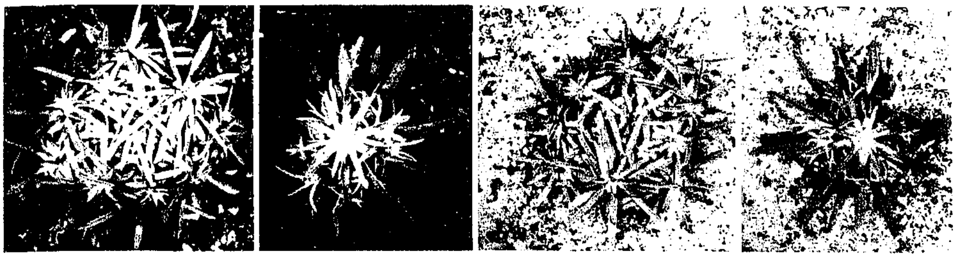

Fig. 5. Basal leaf mounds of *Viscaria alpina* from Iceland (No. 7). Two photos of one large mound which next year will produce several flowering stems and one young and small showing the formation of new narrow-leaved rosettes. Cultures from the Arctic Greenhouse. – Phot. Sept. 1962.

HAGEN (1943) found *Viscaria alpina* in *Juncion trifidi* on soil with pH values between 4 and 5.3.

In America and Greenland the soil requirements of *V. alpina* may not be much different from those found in Europe. It is true that FERNALD (1907) found *V. alpina* confined to basic or neutral soils in the Gulf of St. Lawrence region, but the species is abundant in the bedrock areas of Greenland and does not seem to prefer basalt to gneiss. So far, I have found it in Greenland on soils with pH values between 6.0 and 7.0 but it was seen in some communities which presumably occur on more acid soils, i.e. *Juncus trifidus-*, *Empetrum-* or *Loiseleuria* sociations (see B. 1954: 32, 39, 118) and on lichen heaths in southern-most Greenland. It never grows on peaty and acid soils or on ultrabasic, more or less saline soils at the salt lakes in continental West Greenland. On the other hand it is particularly abundant in places where rocks are disintegrating (Fig. 10) or in areas disturbed by bulldozers, occurring for example in hundreds of tall specimens on sloping, partly disturbed ground at Vandsoen (the Water Lake) near Holsteinsborg. Huge specimens have been found on bird cliffs in Greenland (see Plate I Fig. 2) and a particularly high frequency was noticed on gravel near the top of Præstefjeldet, Holsteinsborg, at a place where a calciphilous species like *Potentilla vahliana* also grows (see population No. 2 Table 5).

Altogether it is most probably that the various races in *V. alpina* have different soil requirements. All three subspecies (cp. p. 27), however, are found in abundance on serpentine soils. Thus they may all possess some biotypes which are particularly tolerant of serpentine soils. This question, however, can only be solved by experiments like those carried out by KRUCKEBERG (1951, 1954), who found serpentine- and non-serpentine races in several species in California. It is most likely that var. *serpentinicola* is a serpentine race and that the typical alpine races of Scandinavia are better adapted to non-serpentine soils, but some American races (e.g. the tall race from the serpentine areas of Mount Albert, Tab. 5 No. 1) may also be serpentine races in spite of the fact that they morphologically are just forming the other extreme from var. *serpentinicola*.

Table 5. Viscaria alpina. Larger population samples.

Population No.	Origin and collectors	No. of specimens	Height in cm Mean and range	Broadest cauline leaves mm Mean and range	Broadest radical leaves mm Mean and range	No. of internodia below inflorescence Mean and range	Basal leaf formation index (p.2[illegible])	No. of flowering stems Mean and range	Morphology of inflorescence[1]	Size of flowers	Contents of Anthocyanin
1	Canada, Gaspé Penins. Mt. Albert. Collins, Fernald and others	29	18 (11–30)	3.5 (2–7)	3.1 (2–6)	4 (3–5)	C	1.3 (1–5)	sh-ah	large	interm.
2	W. Greenland, Præstefjældet 550 m above sea level. P. Frederiksen	18	9 (5.5–12)	3 (2–4)	3 (3–4)	3 (3–4)	C	1.1 (1–2)	sh	large	interm.
3	N.E. Greenland, Upper E. Skeldal. T. T. Elkington	20	14 (9–17)	5.8 (3–8)	3.3 (2–4)	3 (2–4)	C	1.3 (1–4)	ah (sh)	large	high
4	S.E. Greenland, Angmagssalik. Kruuse, Rüttel & Pedersen	15	9 (5–13)	3.3 (2–4)	3.1 (1–4)	3 (2–4)	B	2.5 (1–6)	sh (l)	large	interm.
5	N. Iceland, Hof, Horgardal. Olafur Davidsson	18	7 (3.5–10)	1.4 (1–2)	1.8 (1–3)	3 (2–4)	A	1.3 (1–2)	ah-sh	small	interm.
6	Norway, Kongsvoll, Dovre. Grevillius and Kindberg	15	13 (6–20)	3.8 (3–5)	3.1 (2–4)	3 (2–4)	C–B	1.4 (1–3)	sh (ah-l)	interm.	low-interm.
7	Sweden, Torneträsk, Valfojokk. E. Asplund	19	11 (7–16)	2.8 (1–4)	2.6 (1–4)	3 (2–4)	C (B)	1.1 (1–2)	sh (ah)	small	interm.
8	Sweden, Lycksele Lapmark. Olaf Rune	16	8 (6–10)	1.5 (1–2)	1.2 (1–2)	3 (2–4)	B	2.1 (1–7)	sh (ah)	small	interm.
9	Sweden, Dalarne, Alvesta. C. Indebetou	21	12 (8–22)	2.1 (1–4)	1.2 (1–1.5)	3 (2–4)	B	1.5 (1–4)	l (sh)	small	low
10	S. Sweden, Vämö, Karlskrona. Bjørn Holmgren	18	11 (7–17)	2.8 (1–5)	2.0 (1–3)	3 (2–3)	B–A	1.8 (1–8)	sh (ah)	small	low
11	S. Sweden, Öland, Möckelmossen. T. T. Elkington & M. C. Lewis	17	7 (3–22)	3.0 (1.5–5)	2.3 (1.5–4)	3 (2–5)	A	4.1 (1–16)	sh	small	low
12	S. Sweden, Öland, Vickleby Alfvar. T. T. Elkington and M. C. Lewis.	17	10 (3–17)	2.9 (1.5–5)	1.6 (1–2.5)	3 (3–5)	A	5.4 (1–19)	sh (ah)	small	low
13	Switzerland, Zermatt and Riffelberg Marret, Davall, Gugly et al.	22	6 (3–9)	2.6 (1.5–5)	2.7 (2–3)	3 (2–4)	C–B	1.6 (1–4)	sh	small	very low

Table 6. Viscaria alpina. Small population samples.

Population No.	Origin and collectors	No. of specimens	Height in cm	Broadest cauline leaves mm	Broadest radical leaves mm	Number of internodia below inflores-	Basal leaf formation index	No. of flowering stems	Morphology of inflorescence[1]	Size of Flowers	Contents of Anthocyanin
14	Canada, E. Coast Hudson Bay. Baldwin et al.	7	(5)12–28	4–5	3–4	3–4	C	1–2	sh-ah	large	high
15	Canada, Labrador, Anatolak. C. S. Sewall	5	12–26	3–6	2–4	4–5	C	1–4	sh	large	low-interm.
16	W. Newfoundland, Blomidon Mts. Fernald & Wiegand	6	20–32	4–6	3–4	3–6	C	1–4	sh-l	large	high
17	S. Greenland, Igaliko. Deichmann, Grøntved et al.	12	11–27	4–7	3–6	3–5	C	1	sh-ah	large	interm.
18	W. Greenland, N. Strømfjord. Nordmann	7	10–21	5–7	3–5	3–4	C	1	sh (ah)	large	high
19	W. Greenland, Præstefjeldet. A. Lundager	9	7–17	4–8	4–5	3–5	C–B	1–3	sh (ah)	large	interm.
20	E. Greenland, Antarctic Hb. T. T. Elkington	6	7–14	3–5	2–3	2–3	B	1	sh	large	high
21	N.W. Iceland, Lambadal. C. H. Ostenfeld	10	5–12	2–3	2–3	2–3	A	1–2	ah	small	low
22	S.W. Iceland, Hafnarfjørdur. T. W. Böcher	12	5–15	2–4	1.5–2	2–3	A	1–6	sh-ah (l)	small	high
23	N. Norway, Alten Kaafjord. Lalin & Warming	8	8–18	2–3	2–3	2–4	B–A	1–4	sh-l (ah)	small	interm.
24	N. Norway, Lyngen, Lyngseidet. J. Holmboe	8	9–14	2–2.5	1.5–2	2–3	C–B	1–2	ah	small	low
25	S. Norway, Dovre. I. C. Lindeberg	11	10–22	2–5	2–4	2–4	C–B	1–4	sh (ah)	small	interm.
26	S. Norway, Hallingdal (1200 m). C. H. Ostenfeld	11	11–16	3(4)	2–3	3(4)	B	1–4	sh	small	low
27	S. Norway, Haukelifjeld (1000 m). Fr. Svendsen	7	7–17	2–4	1.5–3	3–4	C	1–3	sh (ah)	small	low
28	N. Sweden, Smeorajokk-Lullehatjåkko. E. Asplund	11	9–16	2–3	2–4	3–4	C–B	1	sh (ah)	small	interm.
29	N. Sweden, Lule Lpm. Gällivare. Serpentine rocks. Olaf Rune	8	9–18	1–2.5	0.5–1.5	2–3	C–B	1–10	ah-l	small	low (interm.)
30	W. Sweden, Koön, Marstrand. Bolander & Johnson	10	(5)10–13	3–4	2–3	3(4)	B–A	1–5	sh (ah)	rather large	low (interm.)
31	S. Sweden, Blekinge, Boråkra. B. A. Söderholm	13	10–18	2–3	2–4	2–3	B–A	1–26	ah (l)	small	low
32	S. Sweden, Öland, Skogsby. Anders Holmertz	13	1.5–6	1–3	1–3	1–3	A	1–12	sh (ah)	small	low
33	S. France, Valle d'Eyne. Alfr. Meebold	9	6–13	2–2.5	1.5–2.5	2–4	B	1–2	sh (ah)	small	low
34	S. France, Gèdre (1430 m). Bordère	11	5–12	1.5–4.5	1–2.5	2–4	C–B	1	sh (ah)	small	low

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[1] sh single terminal head; ah additional small heads below terminal one; l loose and elongated inflorescence.

Viscaria alpina occurs in America, Greenland, and Scandinavia on relatively dry soil, while, in the Alps, it is connected with moister habitats (see p. 24). This divergence may be explained by the existence in the two areas of races with different moisture demands.

7. Population studies

As soon as the heritable background of morphological characters has been tested by culture experiments the same character can, with due consideration to environmental influences, be studied with good results on population samples of various sizes. In *Viscaria alpina* samples from nature for the purpose of population studies were collected by Dr. T. T. ELKINGTON, M. C. LEWIS, B. Sc., and myself. However, as *V. alpina* is a small plant, several herbarium collections contain a large amount of specimens which show the characters of the population in question and their variation. Such herbarium sheets were also sorted out and used for measurements. In some cases specimens from the same station, but collected by more than one person, were used, but only if the specimens resembled one another very much. All measurements were made on dried and pressed material.

In addition to the population samples herbaria were used in order to estimate the range of variation in such large geographical areas as Greenland, Scandinavia etc. The collections in the following museums were used:

National museum of Canada, Ottawa, Canada
Universitetets Botaniske Museum, Copenhagen, Denmark
Botaniska Museet, Uppsala, Sweden
Botanische Staatssamlung, Münich, Germany
Naturhistorisches Museum, Vienna, Austria.

North-east American populations, Plate III Fig. 1.

Tall plants are particularly common in N. America. This appears also from the measurements of the Mt. Albert population (Table 5, No. 1) and the populations from Hudson Bay, Labrador and W. Newfoundland (Table 6, Nos. 14–16) which all contain specimens more than 25 cm high and very few or none lower than 11 cm. As compared with most Greenland specimens the leaves are relatively long in proportion to their breadth. The flowers are large and the inflorescence usually dense. The population from Blomidon Mts. (Newfoundland, No. 16) is deviating as several specimens have a very loose and elongated inflorescence. The formation of new basal rosettes is relatively weak and most specimens accordingly have only one or few flowering stems.

Greenland populations, Plate III Fig. 2.

Some few specimens from Greenland are very tall and vigorous, 30–35 cm high and with up to 12 mm broad leaves (Plate I Fig. 2), but they have been collected on manured soil (bird cliffs) and do not express the normal size of the plant. In South Greenland (Table 6, No. 17) some populations resemble the East American ones very much and have also comparatively long leaves. Taken as a whole, Greenland plants are intermediate in height but have large flowers and broad comparatively short leaves (Fig. 10). The tallest plants e.g. population No. 18, Table 6 and No. 3 in Table 5 come from the inland areas and correspond to my culture No. 3 (Table 3) and Nos. 4–5 (Table 4). Four typical specimens from Qeqertalik, collected by Brummerstedt (1890), are 21–26 cm high with 4–5 and 3–5 mm broad cauline and radical leaves. Such plants from inland areas have usually two additional heads under the large terminal head. The lower coastal race is exemplified by population No. 2 in Table 5. It corresponds to my culture No. 2 in Table 3 and have frequently only one terminal head.

Fig. 6. Two different races from the Alps cultivated in the Arctic Greenhouse. Two specimens of No. 12 (left) and two of No. 13 (right). — Phot. June 22th 1962.

As already pointed out by Fernald some Greenland plants approach European mountain plants very much. In the Copenhagen Herbarium specimens of this type are mainly from the southernmost part of Greenland, i.e. from Tunugdliarfik fjord (legit J. Vahl 1828, T. W. Böcher 1946, J. Grøntved 1953), Frederiksdal (J. Vahl 1828), and Ivigtut (Lindhard 1899, A. E. & M. P. Porsild 1925, R. Bøgvad 1931) but may even occur as far north as Sarkak in W. Greenland (J. Vahl 1835) and Sydkap Ø at lat. 71°20′ N. in East Greenland (Th. Sørensen 1937). The Angmagssalik population (No. 4 in Table 5) seems to approach European ones by its basal leaf tussocks and rather abundant flowering stems.

Iceland populations, Plate IV.

There is a striking difference between the Greenland and the Iceland material. Of 70 collections in the Copenhagen Herbarium 67 per cent consist of small, slender plants, 43 per cent have two or more flowering stems and in 40 per cent the inflorescences are rather loose and elongated although usually with a terminal assemblage of flowers. It is characteristic that strong Iceland specimens have elongated inflorescences and vigorous rosettes with long narrow leaves a fact which appears from the comparison with vigorous Greenland specimen in Plate I Fig. 2. Many specimens resemble var. *serpentinicola* of Scandinavia and many of the dwarfish populations are very similar to var. *oelandica*. Thus, the population from Hof in Horgardal, No. 5 in Table 5, has been determined by Olafur Davidsson as var. *petraea* Fr.

It is difficult to find Iceland specimens which correspond to Scandinavian mountain plants. I have seen a few from Siglufjörður and Goðafoss in northern Iceland.

Scandinavian populations, Fig. 7 and Plates V–VI.

Thanks to access to comprehensive collections in the Uppsala Botanical Museum, it has been possible to survey the range of variation, which appears to be very wide. Three main types corresponding to the three varieties *alpina*, *serpentinicola* and *oelandica* can be distinguished.

(1) Mountain type (var. *alpina* and related races). Typical populations are found in Table 5, Nos. 6–7, and Table 6, Nos. 25–28. They correspond to my culture numbers 8 and 10 (Table 4). Many mountain plants have fairly large rosettes and more than one flowering stem thus matching the specimen illustrated by Nordhagen (1943 Fig. 51). The radical leaves are usually narrow and the anthocyanin contents clearly lower in Greenland plants. Many collections, however, strongly resemble Greenland plants although they may deviate by one or several characters particularly by having smaller flowers. The following specimens were selected as approaching var. *americana* most: Norway, Lomsfjellene (leg. Zetterstedt), Finsehögda (leg. G. Samuelsson), Dovre, Vårstien (leg. Kindberg), Dovre Kongsvold (Table 5 No. 6). Sweden, Torne Lappmark, Shore of Torneträsk (leg. Carl G. Alm), Torneträsk (Table 5 No. 7). Further specimens from Lycksele Lappmark, Tjajtåsen and Neadalen in Jämtland and Skarffjället in Härjedalen.

Some specimens from Scandinavia are 25–30 cm high. They were collected on lowland, e.g. in Finmark, sometimes along rivers or at the mouth of rivers. Lid & Zachau (1928: 72–73) mention that *V. alpina* has migrated down from the mountains along the rivers and has reached the skerries at the Gulf of Bothnia. The very tall specimens might be interpreted as lowland modifications but they are presumably derived from such mountain populations as are heriditarily rather tall (cp. Cult. Nos. 8 and 10, Table 4). Specimens from Helsingland, Sweden (e.g. Ljusdal, legit Carl Hartman and K. F. Dusén) reach 34 and 42 cm. Their appearance is so striking that the question of some kind of introgression from *Viscaria viscosa* is raised.

Fig. 7. Vigorous *Viscaria alpina* from the West Coast of Sweden (Solberga, Röstången, legit Harald Fries 1923) Herb. Uppsala. Population No. 30 (Table 6). × about 1/2.

The typical mountain variety is also found in Russian Lapland and it seems to have migrated southwards along the Swedish west-coast to Bohuslän. Most specimens from this part of Sweden are coarse with broad leaves and large flowers (see Fig. 7 and population No. 30 in Table 6).

(2) Boreal gravel type (var. *serpentinicola* and related races). Björlykke (1938) was the first to pay attention to this type. His picture (Fig. 10b) from the olivine area of Almklovdalen greatly resembles my pictures of similar Iceland specimens (Plate IV) and Rune's picture of the type of var. *serpentinicola* from Gällivare. In Alklovdalen in Norway *V. alpina* grows in places where the wood is open, e.g. on gravelly slopes. The same is the case in Sundal and many other places investigated by Björlykke in Norway and by Rune in Sweden. The flora which occurs together with *V. alpina* is boreal-temperate with some few arctic-montane species.

Rune (1953: 60) has a list of stations for var. *serpentinicola*. I have studied his type collection and the plants he collected at Rönnbäck (Brandberget, 500 m above sea level), see Table 5, No. 8 and Plate V Fig. 1. It is impossible to distinguish between plants from these stations and plants from some other places in Scandinavia not included in Rune's list. In Uppsala and Copenhagen there are fine collections from Alvesta in Dalarne (leg. C. Indebetou), see No. 9, Table 5, Plate V Fig. 2, which must belong to var. *serpentinicola*; the same is the case with a collection made by G. Samuelson (1935) in Raudabygd at Nordfjord, Norway (780–800 m above sea level). More interesting perhaps is an old record found on a sheet in the Uppsala Museum and labelled *Lychnis alpina* var. *gracilis*. It is from Karesuando in Lapland and was collected by Laestadius in 1830 (Herbar. Wahlenberg). No doubt the determinator had the same idea as Rune did later by referring such slender narrow-leaved plants with loose inflorescences to a separate variety. There are transitional plants available from a number of stations indicating that var. *alpina* and var. *serpentinicola* exchange genes where they meet. Examples of such transitions are the following: Dalarne, Norrbärka (legit Cedergreen and Hägerström, both collections with a terminal assemblage of flowers), Norrbotten, Törendö Village (legit Carl G. Alm (1958), deviating by having 4 mm broad cauline leaves), Mt. Kaunispää, 68°30′ Lapponia pokojnensis (leg. H. Steffen 1930), Norway, Kaafjord, Alten (leg. Lalin (1883) and Warming (1884), cfr. Table 6, No. 23).

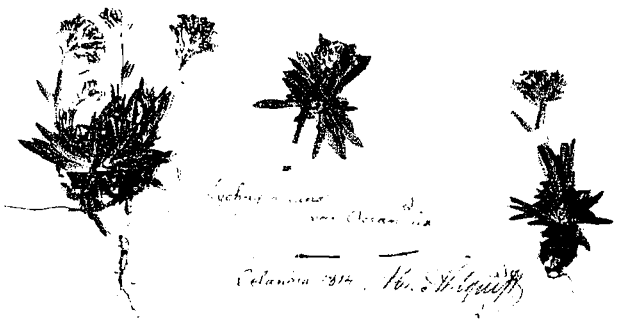

Fig. 8. Probably specimens of the type collection of *Viscaria alpina* var. *oelandica*. Herb. Copenhagen (slightly reduced).

(3) Sandfield and Alvartype (var. *oelandica* and related races). Three Öland populations were studied (recent collections made by Dr. T. T. Elkington and M. C. Lewis), see Nos. 11–12 in Table 5, and an old collection by Anders Holmertz from Skogsby (Table 6, No. 32). While the first ones contain a good deal of large and

Fig. 9. Material from the Alps of *Viscaria alpina*. Upper row four slender specimens from Bormio region (Livigno, nei prati legit M. Longa Herb. Münich). — Lower specimen from Berger Alpe near Kals (legit Hornschuch, Herb. Copenhagen). × 1/3.

vigorous plants the latter is composed of dwarfish 1.5–6 cm high plants (Plate VI). They are indistinguishable from the old collection by AHLQUIST (1814) which may represent the type of var. *oelandica* (Fig. 8). All Ölandic plants have headlike terminal inflorescences, very many flowering stems from vigorous basal leaf cushions and the flowering stems are slender and often arcuate, not erect. Almost the same habit is found in the Blekinge populations, see Table 5, No. 10 from Vämö, Karlskrona, and Table 6, No. 31 from Boråkra. Some of the plants from Blekinge, however, have a rather loose inflorescence or very narrow leaves and thus approach var. *serpentinicola*. The Vämö population is interesting as it contains a slender group collected by B.

Holmgren (Table 6, No. 10) or N. Hylander and a group which approaches typical *V. alpina* by their coarser habit and broader leaves.

Population in the Alps and the Pyrenees. Fig. 9.

The following note was made after a study of the herbarium of the Naturhistorisches Museum in Vienna in 1959: Slender and small specimens occur in the Alps, the Pyrenees, Iceland, and Dalarne in Sweden, robust specimens with broad stem leaves and large flowers in Greenland and North America but some specimens from Dovre and Lapland approach the west-arctic plants in dimensions. Some Swedish plants are slender and narrow-leaved but vigorous e.g. specimens from Pajala collected by Lagerkrantz 1951 and specimens labelled "*Lychnis suecica*" from Avesta Dalarne (Dalecarlica). Among the plants from the Alps those from Tyrol appear to be larger than the others approaching closely the normal Scandinavian mountain plants.

This picture was not modified after a study of the material in Munich and Copenhagen. The collections from Wallis (Valais; Zermatt-Riffelberg) are ± uniform, no specimens being more than 9 cm high (Table 5, No. 13); this is the lowgrowing race described in Table 4 (Cult. No. 12) and seen in Fig. 6 (on the left). Other plants from the Alps are taller, 17–23 cm high, but very slender with small heads and narrow leaves (e.g. Livigno near Bormio, N. Italy, Fig. 9) or fairly robust and with green somewhat succulent leaves (e.g. plants from Berger Alpe at Kals (see Fig. 9) and Algauer Alpen). These may correspond to the taller races in Table 4. According to Dalla Torre (1899: 86) *V. alpina* is 4–9 cm high and in Hegi (Ill. Flora) 15 cm is mentioned as its maximum height. These statements are in agreement with the majority of collections. In culture, however, under optimal conditions or in certain natural environments (Livigno material) greater heights are attained and some races are clearly tall (Table 4, No. 13).

From the Pyrenees two populations have been studied (Table 6 Nos. 33–34). Both consists of small slender plants.

Almost all plants from the Alps and the Pyrenees have one terminal inflorescence. Very rarely the two uppermost leaves support two small additional inflorescences or single flowers. All have a very low anthocyanin content and the difference in breadth between cauline and radical leaves is very small or none. The green somewhat fleshy habit of many Alpine specimens is striking, but may be explained by a differential ecological behaviour in the arctic-boreal area and the Alps. While in the north *V. alpina* is common on dry rocks and gravel slopes, it is in the Alps a plant of the "Alpenmatten" i.e. the fairly wet meadows. The alpine population may not contain biotypes fitted for the "schutthalden". If such plants were present the species would probably be much more frequent in the Alps.

8. Summary of variational pattern

In Table 7 the most important morphological characters in *V. alpina* are surveyed. The available information from the cultivation experiments and the population studies is arranged geographically in order to examine the variation in relation to geographical distribution. Each character is expressed by three grades: A means a high, B intermediate and C low value or degree. By totalling up the number of signs for the various geographical areas the conclusion may be reached that the variability is largest in Scandinavia and lowest in E. America and the mountains of Middle- and Southern Europe. All the characters show a tendency to change in a west-east direction and from north to south in Europe. The variation can be expressed as a number of character gradients or topoclines in spite of the fact that these clines in certain places are broken by some degree of discontinuity.

Table 7 (explanation in the text).

	E.America	Greenland	Iceland	Scandinavia	Alps and Pyrenees
Size of plants	A-B	A-B	(A) B-C	A-B-C	A-B-C
Breadth of leaves	A-B	A-B	B-C	B-C	B
Basal leaf formation	B-C	B-C	A-B	A-B-C	B-C
No. of flowering stems	C	B-C	B-C	A-B-C	B-C
Morphology of inflorescence cp. Tables 5–6	sh-ab (l)	sh-ab (l)	sh-ab-l	sh-ab-l	sh (ab)
Size of flowers	A	A (B)	B-C	A-B-C	B-C
Contents of Anthocyanin	A-B	A-B	A-B-C	B-C	C
Sum of signs (Nos. in brackets omitted)	12	13	16	19	12

9. Intraspecific taxonomy

The Greenland-American populations of *Viscaria alpina* differ from the European populations with regard to a number of characters. The difference seems to be great enough to justify the maintenance of a separate taxon. As this can be distinguished by several characters and occupies a separate geographical area it ought to be given subspecific rank.

At the same time, however, it must be admitted that the Greenland population comprises some biotypes which approach European ones and that certain montane

European plants resemble Greenland plants in flower size and breadth of the cauline leaves.

The cultivations and herbarium studies, however, clearly show that the European material falls also into two groups which are distinguished by a number of characters and behave differently ecologically and in their distribution. This means that the range of variation in *Viscaria alpina* ought to be expressed taxonomically by three subspecies. As the montane European material corresponds to ssp. *alpina* another subspecific name has to be found for the boreal-temperate group with very narrow basal leaves forming dense persistent leaf cushions and with a clear tendency towards the formation of many stems and elongation of the inflorescence. The latter subspecies described below as ssp. *borealis*, covers several minor units which might be maintained as varieties. As mentioned already it is difficult to separate Swedish lowland races (var.

Fig. 10. *Viscaria alpina* ssp. *americana* Basalt rocks facing the Denmark Strait. Cape Daussy, East Greenland 68°43′ lat. N. (from B. 1933).

oelandica) from the var. *serpentinicola* and the latter closely resemble the Iceland plants. The differences between the units within ssp. *boreale* seem to be of the same magnitude as those found between certain Greenland races (see Table 3) or between the American and the Greenland races.

Viscaria alpina (L.) Don subsp. *borealis* subsp. nov.

A subsp. alpina statura dense caespitosa ut foliis basalibus angustissimis differt. Folia rosularia plantarum vetustiorum in hemisphaeram fere congesta, unde caules floriferi complures vel multi, erecti vel subadscendentes, capitulo quisque terminatus, infra illud saepe capitula accessoria parva vel flores singulos in axillis superioribus gerens, capitulis in plantis nonnullis satis laxis. Typus 6–12 cm altus, caulibus floriferis 1–7, foliis basalibus 0.1–0.2 cm, caulinis 0.2–0.4 cm latis.

Habitat in Islandia, ut in regione coniferina scandinavica, ut in Blekinge et Öland Sueciae meridionalis.

Typus (Plate IV Fig. 1) *mense Julio anni 1962 in loco e sinu islandico Hafnarfjördur meridionali ab auctore lectus, in Museo Botanico Hauniensi depositus.*

KEY TO SUBSPECIES AND VARIETIES

1. Cauline leaves often 5 mm broad or broader. Flowers relatively large. ssp. *americana* (Fern.) Plate II.
1. Cauline leaves 1–4 mm rarely 5 mm broad. Flowers usually smaller.
   2. Radical leaves not particularly narrow. Inflorescence usually dense with a terminal headlike part. ssp. *alpina* Plate II Fig. 1; textfig. 7 and 9.
   2. Radical leaves narrow forming dense persistent cushions. Inflorescences often elongated and sometimes loose. Flowers small. ssp. *borealis* Plates IV–VI.
      3. Stems erect.
         4. Stems rigid, often low. Inflorescences usually rather dense with small additional ones or single flowers supported by uppermost stem leaves. var. *borealis* Plate IV.
         4. Stems slender. Inflorescences usually elongated and loose. Petals sometimes reduced or missing. var. *serpentinicola* Rune Plate V.
      3. Stems ±arcuate. Old specimens with particularly many flowering stems. Inflorescence usually rather dense. var. *oelandica* (Lindstr.) Sterner Plate VI.

10. Evolutionary trends in Viscaria alpina

The genus Viscaria and the origin of V. alpina.

Viscaria Bernh. is a small genus containing two species only viz. *V. viscosa* (Scop.) Aschers. and *V. alpina* (L.) Don. A third species *V. intermedia* Ledeb. has been transferred to the genus *Silene* (*S. chamarensis* Turcz.). *V. viscosa* and *V. alpina* are frequently united with some other species in the genus *Lychnis* L. In the manuscript to the "Flora Europaea" O. CHATER has included 8 species in *Lychnis* and among them the two species of *Viscaria*. *V. viscosa* (*Lychnis viscaria* L.) is said to be very variable. Two species described from the Balkan peninsula, *V. atropurpurea*

Griseb. and *V. sartorii* Boiss. are referred by Chater to one subspecies (ssp. *atropurpurea*) of *Lychnis viscaria*.

Both *V. viscosa* and *V. alpina* have the chromosome number $2n = 24$ and occasionally form hybrids, e.g. in Sweden according to Lindman (1926: 270) and Sterner (1938: 97). As a rule hybridization in the *Lychnideae* takes place very easily even between taxa referred to different genera (Nygren 1957, Kruckeberg 1962).

As *V. viscosa* and *V. alpina* are able to cross and both occur in Europe and as apart from *V. alpina* ssp. *americana* no indigenous American *Viscaria* is known, it is very probable that *V. alpina* originated in Europe. This is supported by the fact that Europe harbours a related species viz. *Lychnis nivalis* Kit. in Schult. (or *Viscaria siegeri* Griseb.),[1] only known from Mt. Rodnei in Rumania. Further support is given by the fact that *V. alpina* has its centre of diversity in Scandinavia (Table 7) while according to Chater, this centre in *V. viscosa* is situated in Macedonia. All available evidence implies a European origin for *V. alpina* and that this species was able to cross the North Atlantic Ocean from east to west. There is no evidence indicating that the species formerly had a circumpolar range and has died out in the Pacific sector as claimed by Hultén for the majority of species with this type of distribution. *Viscaria alpina* is what might be called a genuine Amphi-atlantic species.

Type of variation.

In the preceding section it was proposed to divide *V. alpina* into three subspecies. This was done because at our present stage of knowledge the variation appears to be particularly abrupt in two areas: (1) At the transition from Iceland to Greenland, (2) At the transition from high montane to boreale and temperate situations in Scandinavia.

Within all three subspecies the variation seems to be fairly evenly graded, although clearly less so in ssp. *borealis*. In this subspecies geographical ecological isolation has probably been operative over a long period of time. The differentiation between plants from Iceland, Öland and the Scandinavian coniferous belt may be ecotypical in nature but as the habitats are clearly demarcated (oceanic-volcanic soil, continental-calcareous soil (Alvar), boreal-serpentine soil) we find a stepped ecological gradient (cp. Heslop-Harrison 1953: 57) and distinct ecotypes. Owing to geographical isolation the race differentiation in this case has been particularly strong. It might perhaps be possible to promote var. *oelandica* and var. *serpentinicola* to subspecific rank. In some ways it is justifiable but this would mean having to operate with a natural group of subspecies within a species which would be less clear or practical. Also in ssp. *americana* we have ecotypical variation (see e.g. Table 3 and Fig. 2), but the variation at least within Greenland appears to be truly clinal. In North-America likewise there are all transitions from tall to medium high races. On the other hand the Mt. Albert population is fairly isolated and may possess some independent

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[1] Also known as *Polyschemone nivalis* (Schott) Nym. & Kotschy.

characters. My impression is that the variation in *Viscaria alpina* is clinal in areas where it is a frequent species, e.g. most parts of its Greenland range. However, where the species occurs in a number of isolated pockets the clines have become stepped or broken.

Types of isolation. Gain and loss of biotypes in refugia or during migration.

The sharp difference between the Greenland and the Iceland populations is of particular interest. According to the collections in the Copenhagen Museum most Iceland material belongs to ssp. *borealis*. Typical plants (ssp. *alpina*), however, may occur in the highland, but this is uncertain at the moment. One thing is evident: Ssp. *borealis* did not cross the Denmark strait. It must have been fairly broadleaved plants which crossed i.e. plants approaching ssp. *alpina*. As mentioned already certain Norwegian mountain plants closely resemble ssp. *americana* in their flower size and leaves. If similar plants immigrated to Greenland they would here escape hybridization with narrow leaved and small flowered biotypes. Thus they would maintain at least their leaf and flower size. But if the immigrating population included particularly broad-leaved biotypes or if such biotypes arose by mutation in Greenland, this would lead to a population structure as that found in Greenland today. In that case we would have to assume that the broad leaved biotypes in Greenland were at a selective advantage seeing that the Greenland population, with very few exceptions, has broad cauline leaves.

Similar reasonings may be made when considering the immigration from Greenland to Labrador. The Greenland population is composed mostly by plants of medium height but with some rather low and tall ones. If tall plants for some reason were selected for in a more southern environment this would make the occurrence of so many vigorous American specimens more conceivable. A selection of this type is paralleled by that found in species having tall lowland races and low montane ones.

Another possible explanation is that montane plants corresponding entirely to ssp. *americana* did occur also in the Scandinavian mountains at a time when *Viscaria alpina* was a young species with a more continuous range. They were more adapted to relatively continental climatic conditions. All the montane biotypes migrated early westwards crossing the north Atlantic and the broad leaved types established themselves in America-Greenland while in Europe they became exstirpated or modified as a result of crossings later. This theory implies different climatic conditions in the refugia available for montane races of *V. alpina* during the last glaciation and consequently a different selective pressure of the climate on the persisting populations.

In Europe the three races of ssp. *borealis* are now completely separated. Ecologically they are related being boreal not arctic-montane and perhaps by having similar soil requirements. It is therefore not unlikely that they represent the remains of one continuous population which during glacial and late glacial conditions in Europe had a wider and continuous area probably along the southern margin of the Ice sheet. They followed the retreating ice but during post glacial forest expansion the area became disrupted and the three groups began to develop independently. Iceland today has many lowland areas with subarctic climate but which have never been covered by *continuous woodlands*. Also the Alvar of Öland was never totally covered. About the serpentine area Rune (1957) says that even in low-altitude serpentine areas birch-trees are restricted to favourable habitats with deep soil. *Pinus silvestris* is the only tree able to form forest on serpentine in N. Sweden, but the trees grow slowly and their trunks are often stunted or broken. Rune has some fine pictures (Plate V, Figs. 25–27, 32) showing recent localities of his var. *serpentinicola*. It grows in bare rocks or crevices or on gravelly slopes with solifluction surrounded by forest, sometimes it may even enter the light forest flor together with e.g. *Aspelenium viride*. This type of occurrence reminds a good deal of that of ssp. *borealis* in Iceland The type collection (Plate IV) is from a wind-swept lowland area with volcanic patterned solifluction soil. The vegetation in question was not arctic but temperate with a few low-arctic elements. The most abundant plants associated with *Viscaria* were: *Dryas octopetala*, *Thymus drucei*, *Armeria maritima*, and *Anthyllis vulneraria*. *Alchemilla alpina*, *Galium verum*, *Silene maritima*, *Kobresia myosuroides*, *Festuca vivipara*, *Sesleria coerulea*, *Agrostis* sp., and *Platanthera hyperborea* var. *minor* were also very common. Vegetation of this kind is very common in Iceland. The unstable soil conditions and the strong wind are unfavourable to forest growth. In any case birch has never formed continuous woods in such areas.

It is possible to explain the variational pattern found in *Viscaria alpina* today by assuming a splitting up of a species which started as one polymorphic group with clinal variation. The boreal biotypes of *V. alpina* were unable to make the crossing to America via Southern Greenland; the low arctic-montane climate of S. Greenland would have eliminated them.

The European montane population was split up and depauperated during the last Ice Age. One group have persisted in the Pyrenees another in the Western Alps while some persisted in coastal mountain refugia in Norway, e.g. in the Möre region, where the species occurs at present on several high peaks near the coast. In these refugia only relatively oceanic biotypes survived. A theory of this kind would explain why the species has not extended further towards the east along the Arctic coast. On the other hand relatively continental broad leaved biotypes reached Greenland-America prior to the last Ice Age and were later able to penetrate to Hudson Bay and to the head of Sondre Strømfjord.

The Greenland population was probably able to survive the last glaciation in various types of refugia. Now the species is found e.g. on the steep slopes of Kap Daussy in East Greenland together with such a rare relic plant as *Ranunculus lyngei* H. Smith (*R. auricomus* var. *glabrata* Lynge), see maps in Böcher 1938: 89 and Hultén 1958: 30, and Fig. 10. In West Greenland it is abundant on coastal mountain tops (e.g. population No. 2) and in South Greenland it is a species of open exposed habitats.

The boreal European population had probably a continuous range on open areas along the southern margin of the ice cap. Boreal biotypes may have reached Iceland during the late-glacial period or have survived the last Ice Age in Iceland. Some of the more continental groups of biotypes are now isolated from one another by wooded areas; one group being restricted to southernmost Sweden and another to the coniferous region on open serpentine areas. Hybridization and introgression is probably now going on where the montane and boreal biotype meet in middle and North Scandinavia. In the case of the boreal population it may be assumed that the relatively continental biotypes survived the glaciation in the areas along the ice sheet. It is generally accepted that the ice margin climate at least in Middle and East Europe was dry and continental. In the case of var. *oelandica* STERNER (1944: 222) and later SELANDER (1950: 62) proposed a survival in Central East Europe and a similar post glacial history as many of the rare eastern species in Öland (e.g. *Artemisia laciniata*).

11. Leaf size and environment

The possible connection between clines in leaf size or in breadth of leaf sections and climatic differences was recently discussed by BÖCHER & LEWIS (1962). In the case of *Viscaria alpina* a series of races with different leaf sizes (leaf breadths) have been demonstrated, and it was proposed that the broad-leaved western races were perhaps adapted to relatively continental climatic conditions. This may be true. On the other hand very narrow leaves characterize all the boreal European races of which the Öland race and the serpentine race grow under relatively continental conditions. This makes any simple climatic adaption uncertain and supports the idea that the leaf characters are non-adaptive. Thus, the abrupt leaf size cline in the North-Atlantic area may be merely a topocline and not what might be called a "topo-eco-cline", viz. a geographical character gradient dependent on a parallel ecological gradient.

Considering, however, the clear correlation between narrow radical leaves and the formation of vigorous basal leaf cushions, it is possible in *Viscaria* to look upon the leaf size as a secondary concomitant character. The two specimens seen in Plate I Fig. 2 demonstrate that in robust specimens of the very different Greenland and Iceland populations broad stem leaves are associated with weak basal rosettes and narrow leaves with strong rosettes. The strong basal leaf cushions (Fig. 5) may be a character of fundamental importance only for the boreal races which grow on unstable solifluction soils or in any case soils which are unfavourable to forest vegetation or other types of dense vegetation.

In Greenland *Viscaria alpina* hardly occurs on solifluction soils or very loose screes. It is mainly connected with stable conditions in rock fissures and rock ledges or sandy or gravelly dry areas.

The narrow leaves of var. *serpentinicola* deserve special attention. Together with the slender stems and the reduced petals, narrow leaves may be a response to the serpentine soil. Several serpentinomorphoses are known with narrow leaves (stenophyllism, see Pichi-Sermolli 1948, Vergnano 1958). According to Pichi-Sermolli (op. cit. p. 292) serpentinomorphoses include heriditary fixed changes (e.g. the soil ecotypes found by Kruckeberg) as well as non-heriditary modifications. Going through the collections of var. *serpentinicola* (population 8 and 29) some specimens appear particularly weak with extremely narrow leaves and very thin stems (Plate V Fig. 1). They are clearly narrow-leaved modifications of a variety which is also hereditarily relatively narrow-leaved. This gives us another example of parallelism between morphological inter-race pattern and reaction pattern in a species (cp. Böcher & Lewis 1962: 12). At the same time it makes it clear that angustifoliate varieties can be looked upon as ecological races, sometimes connected with unfavourable chemical soil properties, sometimes perhaps with particularly dry habitats, or other environmental conditions.

At our present stage of knowledge the relations between leaf size—or leaf breadth in *V. alpina* and the environment are doubtful or unclear. The only way to unravel the interesting problems are comparative eco-physiological experiments using members of the various leaf type races as test plants.

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