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STUDIES ON THE VARIATION
OF THE GENUS *DRYAS*
IN GREENLAND

BY

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WITH 47 FIGURES AND 7 TABLES
IN THE TEXT

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CONTENTS

	Page
Abstract	4
I. Introduction	5
II. Morphological characters.....	7
III. Taxonomy	18
IV. Herbarium studies	22
V. Field studies	28
a. Field measurements	28
b. Population samples.....	32
VI. Ecology.....	38
VII. Cytology.....	47
VIII. Discussion	48
Acknowledgements.....	52
Appendix: Authorities of bryophytes and lichens	53
Literature.....	54

Abstract

A short history of the taxonomic treatment of the genus *Dryas* in Greenland is given, stressing the difficulties which have arisen in N. and E. Greenland.

Studies of morphological characters using herbarium material and pressed random samples are described. The most useful characters in the study of Greenland material are presence or absence of branched hairs on the leaves, leaf crenation, and to a lesser extent ratio of leaf width at the middle of the leaf to that at the base. These studies also show that some Greenland specimens, which have been assigned to several taxa, are referable to either *D. integrifolia* VAHL, *D. octopetala* L. or hybrids between these two species. The previous reports of *D. crenulata* Juz. are argued to be large leaved, ecological variants of *D. octopetala* and hybrids of this species with *D. integrifolia*; those of *D. punctata* Juz. and *D. hookeriana* Juz. to be variants within the variation of *D. octopetala*. A herbarium survey of the genus shows that all specimens from S.E. and W. Greenland can be referred to *D. integrifolia*, and those from N.W., N. and E. Greenland to *D. integrifolia*, *D. octopetala* and intermediates. One of these intermediate types has previously been called *D. chamissonis* SPRENG., but this name is shown to have never been validly published.

A field investigation in the Kong Oscars Fjord region, E. Greenland (lat. 72° N.), measuring populations in the field and collecting population samples shows that all populations contain intermediate types and have the characteristics expected of introgressive hybridization between *D. integrifolia* and *D. octopetala*. Floristic lists and soil analyses are given from the localities sampled. These show that variation in population structure is not correlated with any particular vegetation type or soil conditions.

Cytological studies on field material show meiosis to be almost completely regular with $n = 9$.

The described variation is discussed and interpreted as an example of allopatric introgression over a very large area. The question of experimental and formal taxonomic categories is commented upon and it is concluded that it is best to regard *D. octopetala* and *D. integrifolia* as incipient ecospecies and of specific status.

I. INTRODUCTION

Dryas is a small genus in the Rosaceae, widely, but discontinuously distributed in northern temperate and arctic areas. In the southern parts of its range it is confined to mountain areas, but descends to progressively lower altitudes towards the North. In arctic and sub-arctic areas it is often extremely common and found in a wide range of habitats. All species are woody, prostrate undershrubs.

Unlabelled specimens of *Dryas* were first collected in Greenland by PAUL EGEDE in 1739, from Christianshåb and Godthåb. At this time *D. octopetala* L. was the only described species in the genus. In 1798 however M. VAHL described a new species from Greenland, *D. integrifolia*, differing from *D. octopetala* by having narrower, revolute leaves with entire, instead of crenated margins. During most of the nineteenth century Greenland specimens were referred to one of these two species, although opinions differed as to the distinction between them. Thus W. J. HOOKER (1833) considered them quite distinct, while J. D. HOOKER (1861) reported that for *D. integrifolia* he had "vainly endeavoured to find any satisfactory characters for it; the only one of any consequence, derived from the outline, etc. of the leaf, is not only the most inconstant, but presents every transition to *D. octopetala*." In 1884 NATHORST stated that collections from Ivsugigsok (lat. 76°7'–9' N., long. 68°15'–35' W.) included specimens with entire leaves, with leaves having three crenatures, and with completely crenated leaves. He described the plants with intermediate numbers of crenatures as *D. octopetala* f. *intermedia*, and suggested that they might be hybrids. Later HARTZ (1895) transferred f. *intermedia* NATH. to *D. integrifolia* and described its distribution as being from latitudes 70°–72° N. on both the east and west coasts. The inclusion of the west coast is, no doubt, due to the specimens collected by HARTZ from Kingigtok (lat. 70°8' N.) and commented on by ROSENVINGE (1892) who stated that they differ from *D. integrifolia* by the large broad leaves, often dentate at the base. Later, both SIMMONS (1906) working on the Ellesmere Island flora, and M. P. PORSILD (1920) on the flora around Disko considered that such specimens were only ecological variants. OSTENFELD has also recorded *D. integrifolia* f. *intermedia* from North Greenland, both from specimens collected from the Wolstenholme Fjord

area (1923a) and in those of TH. WULFF from the north coast (1923b). He agrees with NATHORST in regarding it as of hybrid origin, but states, in respect of the Wolstenholme Fjord material, that "it does not seem to be a simple hybrid between the two species as it fruits freely, but may be the result of more complicated crossings." In East Greenland all authors have had difficulty in classifying *Dryas*; thus SØRENSEN (1933) working on the flora between latitudes 71°–73° N. comments that "it seems impossible to keep the two *Dryas* species distinct." GELTING (1934) found the variation in *Dryas* between 73°15' and 76°20' such that he included *D. integrifolia* as a variety of *D. octopetala*. SEIDENFADEN and SØRENSEN (1937) working on the flora between latitudes 74°30' and 79° comment (p. 58) that the two species are often difficult to distinguish from one another, and point out later in the same paper (p. 157) that this situation appears to be due to hybridization between them in E. Greenland.

More recently A. E. PORSILD (1947) and HOLMEN in BÖCHER, HOLMEN & JAKOBSEN (1957) have suggested that other *Dryas* taxa are present in Greenland, while HULTÈN (1959), working on herbarium material, has postulated that where *D. octopetala* and *D. integrifolia* overlap there is also present "a hybrid population between these species with several intermediate types not yet stabilized."

It has been emphasised by BAKER (1947) that a study of this type, which considers hybridization as a possible source of variation within the group, should include artificial crosses as well as investigations of natural populations. This paper considers the evidence gained from herbarium studies and field observations. Crossing and culture experiments are in progress and it is intended to report on these in a later paper.

The herbarium studies have been mainly carried out on the extensive collections of *Dryas* in the University Botanical Museum, Copenhagen (C). The field study was carried out in the Kong Oscars Fjord region during the summer of 1962 while the author was a member of the Leicester University East Greenland Expedition 1962.

In the following account it is proposed to refer to *D. integrifolia* and *D. octopetala* as of species rank. The question of their status will be discussed in section VIII.

II. MORPHOLOGICAL CHARACTERS

A number of morphological characters have been studied using random pressed samples collected from populations in the Kong Oscars Fjord region (discussed in detail in section V). These in some cases have been supplemented by herbarium material. Some of the characters have been used in separating *D. octopetala* and *D. integrifolia* and also in the delimitation of a number of other *Dryas* species. These characters and their significance will now be discussed.

Leaf characters

Leaf Length. The leaf lengths of *D. integrifolia* and *D. octopetala* plants are randomly distributed within the population samples with no differences between the grouped measurements of the two species. Also no differences between the species in this respect could be seen in herbarium material. The mean leaf lengths of the population samples are given in table 1. There is some variation between populations which is, at least partially, due to ecological differences. As HARTZ (1895) pointed out the smaller-leaved forms are usually from dry, exposed localities, while plants with larger leaves grow in more sheltered conditions. My observations are in general accordance with these, although microclimatic data would be necessary to establish any close correspondence in this respect. HARTZ (l.c.) also states that such small-leaved plants are not usually covered by snow in the winter. Both he and JESSEN (1921) point out that plants from exposed localities are more strongly revolute than those from sheltered ones. SIMMONS (1906), while stating that *D. integrifolia* characteristically has revolute leaves (also mentioned by VAHL in his original description), describes non-revolute forms from sheltered localities and highly revolute forms of *D. octopetala*. Small-leaved forms of *D. octopetala* have been given a number of names; thus W. J. HOOKER (1824) has described material from Svalbard (not central Europe as HULTÈN (1959) states) as var. *minor*, while NOTØ (1902) has described similar forms from N. Norway as var. *minima*; HEGI (1923) mentions small leaved plants from exposed localities in the Alps as f. *sneznicensis* DERGANC. *D. octopetala* var. *minor* has been applied to E. Greenland

Table 1.
Mean leaf lengths of population samples.

No.	Locality	Mean leaf length (cm)
1	Antarctics Havn	1.00
2	Pictet Bjærge	1.04
3	Mesters Vig	1.56
4	Mestersvig flyveplads	0.98
5	Lower E. Skeldal	1.17
6	Lower E. Skeldal	1.09
7	Lower E. Skeldal	1.13
8	Lower E. Skeldal	1.09
9	Upper W. Skeldal	1.37
10	Kap Petersens	0.96
11	Segelsällskapets Fjord	1.10
12	Schaffhauserdalen	2.07
13	Polhems Dal	1.99
14	Åkerbloms Ø	1.02
15	W. side Holms Bugt, Traill Ø	1.21
16	E. side Holms Bugt, Traill Ø	0.90
17	W. side Karupelv, Traill Ø	1.23
18	N. Karupelv, Traill Ø	1.25
19	Gudenelv, Traill Ø	1.07

plants by HARTZ (1895) and to plants from N.W. Greenland by OSTENFELD (1915).

Leaf length/breadth. In his original description VAHL (1798) writes that the leaves of *D. integrifolia* are three times as narrow as those of *D. octopetala*. The population samples do not give any evidence of this separation, for although there is a good deal of variation in leaf length/breadth ratio there is no correlation between this and the variation in crenation or

Table 2.
Means and standard errors of leaf length/breadth ratios of groups of Dryas specimens from different areas of Greenland.

Taxon	Area	Leaf length/breath ratio and S. E.	No. Plants
<i>D. octopetala</i>	E. Greenland	2.04 ± 0.05	28
<i>D. integrifolia</i>	N. Greenland	2.50 ± 0.06	28
<i>D. integrifolia</i>	S. E. Greenland	2.39 ± 0.07	12
<i>D. integrifolia</i>	W. Greenland	2.15 ± 0.04	56
<i>D. integrifolia</i>	Simiutap kûa, W. Greenland	2.11 ± 0.12	18

presence or absence of branched hairs (both important diagnostic characters discussed in the following paragraphs). Table 2 shows that there are some differences between the mean values of this ratio for the group of *D. octopetala* specimens from E. Greenland and *D. integrifolia* groups from various areas in Greenland. The difference is not significant for the *D. octopetala* group and the W. Greenland *D. integrifolia* groups, but is so for the S.E. and N. Greenland groups. Since no information is available as to whether these differences represent a real genetical dissimilarity or merely an environmental modification, it therefore seems impossible to comment further on this situation. The variation does show, however, that this ratio is not of any use in separating the two species.

Crenation. The number of crenatures along the side of the leaf is an important character in the separation of *D. integrifolia* from *D. octopetala* and in the past has been the chief character used. Thus VAHL (1798) in his description of *D. integrifolia* states that the leaf margins are entire, in contrast to *D. octopetala* which has completely crenated leaves. It is clear from the study of herbarium specimens that crenation is very useful in conjunction with the character of presence or absence of branched hairs on the leaves (see below), and it has therefore been used as one of the co-ordinates in the scatter diagrams of field populations. For these measurements the number of crenatures along one side of the leaf was counted on five of the largest leaves from each specimen and a mean (the crenation index) calculated.

Ratio of leaf breadth at the middle of the leaf to that at the base. It has been pointed out several times that the leaves of *D. integrifolia* are more or less truncate at the base, while those of *D. octopetala* are more or less ovate, thus giving a higher breadth ratio than *D. integrifolia*. This is illustrated in Fig. 1 where values of this ratio are plotted against crenation index on a scatter diagram for a number of specimens of *D. integrifolia* from W. Greenland and a random sample from a population of *D. octopetala* from Kings Bay, Svalbard (leg. D. OGDEN), an area from which *D. integrifolia* is absent. There is a distinct difference between the two sets of measurements. For this reason the breadth ratio has been used as one of the co-ordinates in the scatter diagrams of field populations.

Branched hairs. Branched hairs were first observed in *Dryas* by BABINGTON (1842) who described them as "minute, linear, pellucid, fringed scales." He used them as one of the characters separating some Irish plants as *D. octopetala* var. *pilosa*. This variation will be discussed in a later paper on variation in European *Dryas*. The hairs are typically present on the petioles and the undersides of the prominent main veins

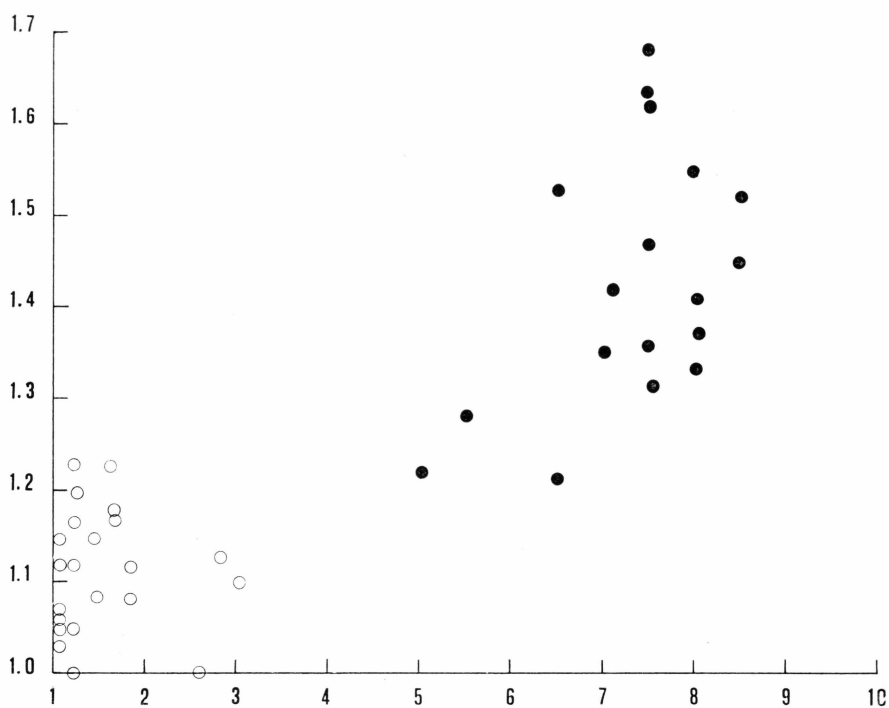


Fig. 1. Scatter diagram of ratio of leaf width at the middle of the leaf to that at the base as ordinate and crenation index as abscissa. ○ measurements of herbarium specimens of *D. integrifolia* from W. Greenland and ● a pressed, random, population sample of *D. octopetala* from Kings Bay, Svalbard.

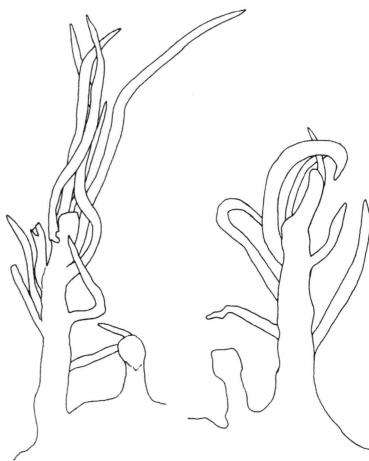


Fig. 2. Branched hairs and glands from lower surface of leaf; specimen of *D. octopetala* from Lower E. Skeldal, Kong Oscars Fjord. $\times 140$.

of the leaves, sometimes also on the lateral veins. Each hair consists of a multicellular stalk, usually brown or yellow in colour, with a variable

number of lateral, single hyaline cells which form the branches. These hairs are characteristically present in *D. octopetala* and absent in *D. integrifolia*, they are illustrated in fig. 2.

Cultivation experiments on European *D. octopetala* have shown that presence and absence of branched hairs is a stable character over several years, no plants having lost their branched hairs if they had them in the wild condition, or developed them if they lacked them when collected. These data indicate that their presence or absence is genetically controlled.

Presence of branched hairs has been scored in all specimens examined. In the field, specimens were scored into three classes, and in herbarium studies, into four classes. Descriptions of the class limits are given in the sections describing these studies.

Glands. Many specimens of Greenland *Dryas* which have branched hairs on the undersides of the leaves also bear, mixed with these, small, stalked glands (fig. 3). In cases where these are abundant on the lower surface they are sometimes also found on the upper surfaces of the leaves (fig. 4). Similar glands are also often found on the upper sides of leaves of *D. octopetala* plants from Europe. HULTÈN (1959) has pointed out that since LINNAEUS 'undoubtedly knew *Dryas* best from the Swedish mountains' the Scandinavian plant must be regarded as the typical one. Glands are therefore illustrated from a Swedish plant (fig. 5).

As in the Greenland material these plants always have branched hairs and similar stalked glands on the lower surfaces of the leaves along the main vein and sometimes lateral veins (fig. 6). Three specimens from the University Museum, Copenhagen have rather different glands on the upper surface. These are from Wollaston Forland, Mt. Zackenberg, lat. 74°28' N., long. 20°38' W., leg. F. SCHWARZENBACH, coll. Aug. 1956; Nordvestkysten Loch Fyne, lat. 73°55' N., leg. SEIDENFADEN, no. 158, coll. 29.7.29, (determined by TH. SØRENSEN 1954 as *D. punctata* Juz.); and Grønne Dal, Clavering Ø, lat. 74°17' N., leg. SEIDENFADEN, no. 726, coll. 20.7.30. The glands on the Wollaston Forland plant range from very large sessile ones (fig. 7) to others somewhat smaller and subsessile (fig. 8). Both extremes are found on the Loch Fyne specimen while the smaller subsessile glands are matched by those found on the specimen from Clavering Ø (fig. 9). Since these specimens have been referred to *D. punctata* Juz. (see p. 20) material of this species was examined. Specimens of *D. punctata* from E. Taymyrland, Arctic Siberia, leg. A. TOLMATCHEV, coll. 4.7.1928 and Maud Harbour, Arctic Siberia, leg. SVERDRUP, coll. 4.8.1919 have similar sessile and subsessile glands (figs. 10 and 11). Amongst the population samples collected, one (no. 16, Holms Bugt, Traill Ø) has specimens with somewhat similar glands. The relation of

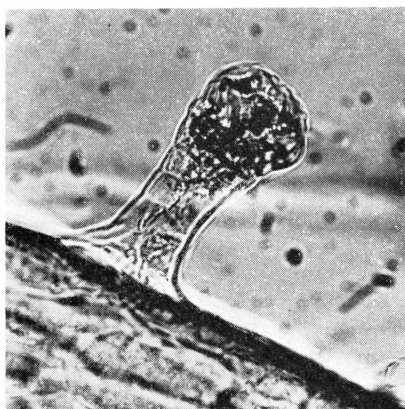


Fig. 3. Small stalked gland, lower leaf surface of *D. octopetala* plant from population 6, Lower E. Skeldal, Kong Oscars Fjord. $\times 750$.

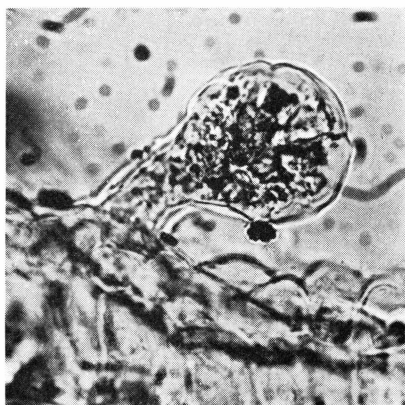


Fig. 4. Small stalked gland, upper leaf surface of *D. octopetala* plant from population 6, Lower E. Skeldal, Kong Oscars Fjord, $\times 750$.

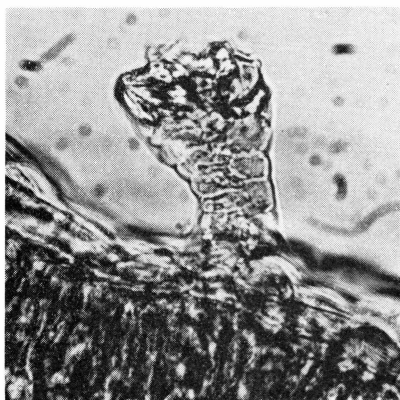


Fig. 5. Small stalked gland, upper leaf surface of *D. octopetala* plant from Vassijaure, near Abisko, N. Sweden. $\times 750$.

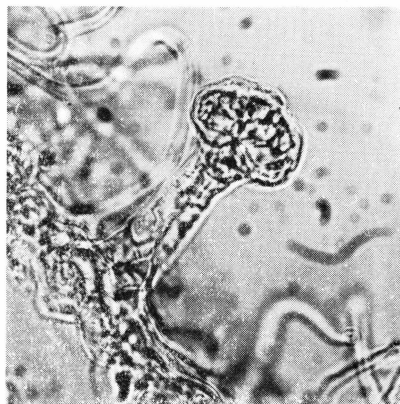


Fig. 6. Small stalked gland, lower leaf surface of *D. octopetala* plant from Vassijaure, near Abisko, N. Sweden. $\times 750$.

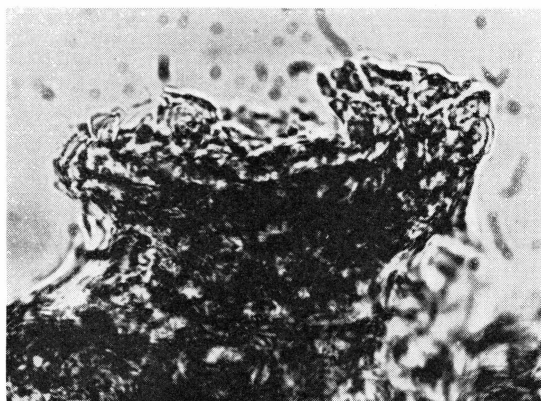


Fig. 7. Large sessile gland, upper leaf surface of *D. octopetala* plant from Wollaston Forland, E. Greenland. $\times 520$.

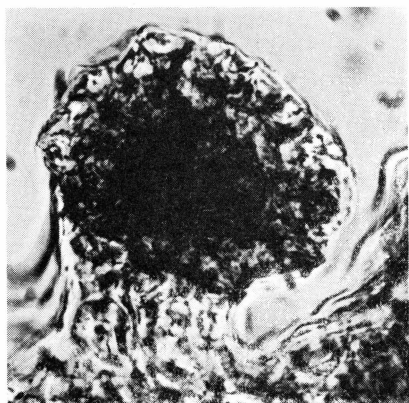


Fig. 8. Subsessile gland, upper leaf surface of *D. octopetala* plant from Wollaston Forland, E. Greenland. $\times 520$.

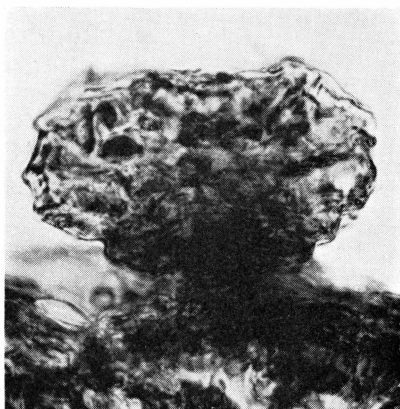


Fig. 9. Subsessile gland, upper leaf surface of *D. octopetala* plant from Grønne Dal, Clavering Ø, E. Greenland. $\times 520$.

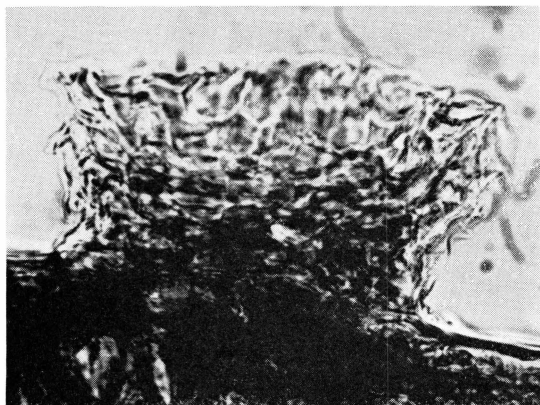


Fig. 10. Large sessile gland, upper leaf surface of *D. punctata* plant from Maud Harbour, Arctic Siberia. $\times 520$.

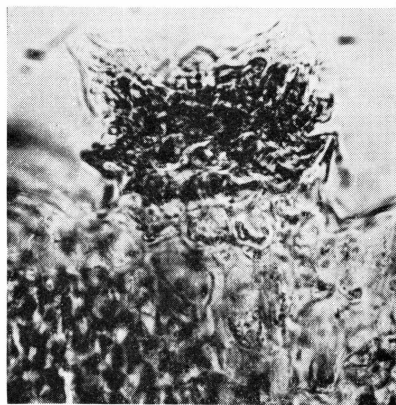


Fig. 11. Small sessile gland, upper leaf surface of *D. punctata* plant from E. Taymyrland, Arctic Siberia. $\times 520$.

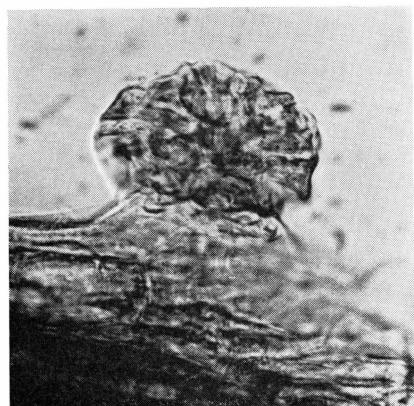


Fig. 12. Subsessile gland, lower leaf surface of *D. octopetala* plant from Grønne Dal, Clavering Ø, E. Greenland. $\times 520$.

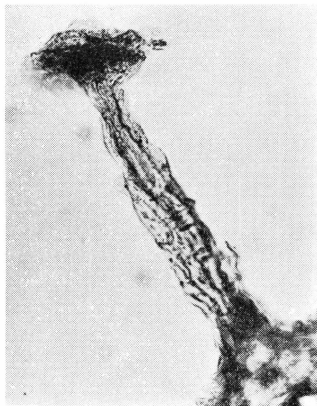


Fig. 13. Large stipitate gland, lower leaf surface of *D. octopetala* plant from Grønne Dal, Clavering Ø, E. Greenland. $\times 175$.

these specimens to *D. punctata* is discussed on p. 20. Similar, though generally smaller, sessile or subsessile glands to those described above can be found on the lower surfaces of leaves from both Greenland and North Russian specimens (fig. 12).

On the lower sides of the leaves from the specimen from Clavering Ø there are also a number of large stipitate glands (fig. 13). These are also present in a number of specimens without punctate glands on the upper surface, in some cases mixed with normal branched hairs and in others without them. In these latter specimens, where most leaves are usually without any glands, the large stipitate glands often have one or two branches.

Similar plants to that from Clavering Ø were found in population sample 10 from Kap Petersens. Here, among a heterogeneous population, otherwise similar to those from other localities in the region, were two distinct plants. One has one leaf with large, purple, stipitate glands and the rest lacking glands; the other plant has one leaf with similar purple glands and the rest bearing a mixture of normal branched hairs and long yellow stipitate glands with one or two branches. The taxonomic position of these plants is discussed on p. 20.

Canescence. All *Dryas* specimens collected from the Kong Oscars Fjord region have at least a few hairs along the impressed midvein on the upper surface, but a number of specimens are more or less canescent on the upper surface. Such specimens in *D. integrifolia* have been described as var. *canescens* by SIMMONS (1906) and in *D. octopetala* as f. *argentea* (BLYTT) by HULTÈN (1959). Although such specimens of *D. integrifolia* are apparently rare in W. Greenland (see M. P. PORSILD 1920) *Dryas* from North and East Greenland is frequently canescent. In the population samples collected the presence of this form is at least partially correlated with the degree of exposure of the plants, as has also been pointed out by SØRENSEN (1933). There is no evidence of any correlation between canescence and presence or absence of branched hairs.

Flower characters

Calyx length and length/breadth ratio. There appears to be no correlation between either of these characters and any other character which varies within a population. Also, although there is some inter-population variability, it has not been possible to correlate this with any other factor or group of factors.

Hypanthium glands. In European *D. octopetala* the hypanthium and calyx are generally covered by long purple unbranched glands which often ex-

tend down the pedicel. It was noticed that some of the plants in the population samples also have branched glands. These are also purple and are usually mixed with unbranched glands. All transitions can be found between these two types and the range of variation is shown in fig. 14. In some cases similar branched glands are also present on the pedicel where they are also mixed with normal unbranched glands. Since this variation has not been noticed in Greenland plants before, the population samples have been scored for presence or absence of branched glands on the hy-

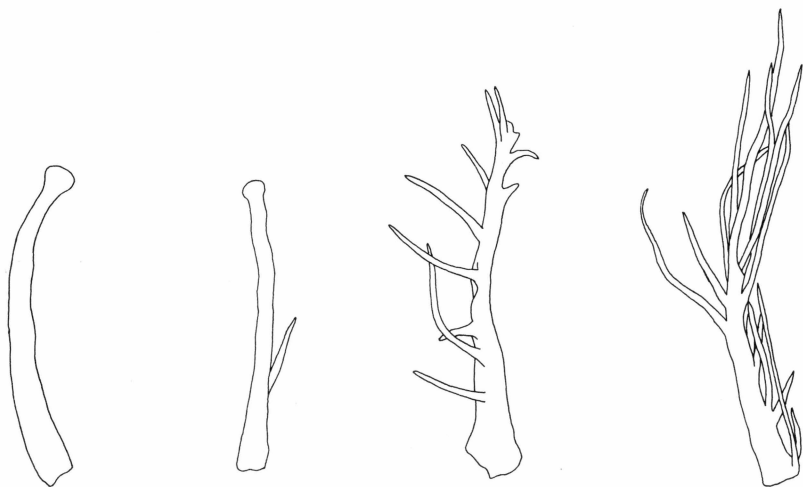


Fig. 14. Variation of unbranched to branched glands removed from hypanthium; specimen of *D. octopetala* from sample 4, Mesters Vig, Kong Oscars Fjord. $\times 65$.

panthium and calyx. The results are given in table 3. The presence of branched glands on the hypanthium and calyx is not correlated with the presence of branched hairs on the leaves. Branched glands on the hypanthium can be found on all types of plants within the populations, although they are generally sparse on *D. integrifolia* plants.

The presence of glandular hairs on the pedicel is rather variable within the population samples collected, but could not be correlated with any other character. It is apparent, however, that most herbarium material of *D. integrifolia* from West Greenland has no glands on the pedicels although a number of specimens do have some glandular hairs sparsely distributed on the upper parts of the pedicels. It has been suggested by HARTZ (in a comment on a herbarium sheet from Kingigtok, lat. $70^{\circ}08'$, on the Nûgssuaq peninsula) that this might be due to the influence of *D. octopetala*. HULTÉN (1959) has also made the same suggestion. There are, however, no other traces of characters of this species in the herbarium material, except for an increase of crenation in a number of West Greenland specimens from wet habitats. This is discussed

Table 3.

Presence and absence of branched glands on the hypanthium and calyx in relation to presence and absence of branched hairs on the leaves in the population samples.

Locality Number	No. of plants scored	Percentages of plants			
		Branched hairs present on leaves		Branched hairs absent on leaves	
		Glands present	Glands absent	Glands present	Glands absent
1	23	17	—	66	17
2	22	27	5	50	18
3	24	29	—	46	25
4	25	8	16	24	52
5	25	20	12	44	24
6	21	10	24	28	38
7	24	17	17	37	29
8	25	28	4	48	20
9	25	28	20	44	8
10	23	22	9	56	13
11	24	8	—	75	17
14	24	17	12	38	33
15	25	40	20	32	8
16	23	30	4	39	27
17	21	5	5	48	42
18	25	24	8	44	24
19	14	57	—	43	—

N. B. Number of plants scored is sometimes less than the total population sample due to some plants not flowering or without old flowers.

in section IV where an ecological explanation is suggested as being most likely. Also no specimens with branched hairs on the leaves have ever been collected in West Greenland to the south of Melville Bugt so that it seems unlikely that hybridization has ever taken place in this area.

Petal length and length/breadth ratio. Measurements of these characters show no correlations with any other characters scored in the population samples. Also, although there is some variation between samples, this appears to be random. A number of herbarium specimens of *D. integrifolia* from West Greenland measured for these characters showed no significant differences from the population samples from the Kong Oscars Fjord region.

Petal Pubescence. Occasional specimens in the population samples have a scattered pubescence of single white hairs on the undersides of the

petals. It appears to be of no taxonomic significance, being found on plants which are otherwise morphologically heterogeneous.

Other characters

Several other characters have been mentioned by a number of authors as being of use in the separation of *D. octopetala* from *D. integrifolia*. JESSEN (1921) states in his account of the anatomy and floral biology of arctic *Dryas* that the vein parenchyma of the leaves is more strongly developed in *D. integrifolia* than in *D. octopetala*. No further observations have been made on this difference. SCHWARZENBACH (1961), in his study of the flora of nunatak areas of East Greenland, states that the few entire-leaved plants that he found were not true *D. integrifolia* because the leaves were dull and not glossy on the upper surfaces. While it is true that many specimens of *D. integrifolia* from West Greenland have rather glossy leaves, plants with non-glossy leaves can easily be found, and equally *D. octopetala* specimens from East Greenland often have rather glossy leaves. As W. J. HOOKER (1833) first pointed out, the leaves of *D. integrifolia* are generally smoother, being less impressed along the veins than those of *D. octopetala*. There is however considerable variation in this character and it has not been used in the present study because of the difficulty in scoring. Finally T. PORSILD (1920) obtained some evidence, based on a small number of specimens, for difference in the number of lateral hairs per mm along the style and in style length in *D. integrifolia* and *D. octopetala* from various localities. A survey of these characters was not carried out because of the time that would be required for measurements which would be statistically significant.

III. TAXONOMY

It will be seen from the previous section that the main differences between *D. octopetala* and *D. integrifolia* are as follows:—

- (i) *D. octopetala* has completely crenated leaves, whereas *D. integrifolia* has either entire leaves or leaves with a few crenatures on the lower parts.
- (ii) *D. octopetala* has more or less ovate leaves, while those of *D. integrifolia* tend to be truncate at the base. Specimens of *D. octopetala* therefore have higher values for the ratio of leaf breadth at the middle of the leaf to that at the base, than do those of *D. integrifolia*.
- (iii) *D. octopetala* bears branched hairs on the petioles and the lower sides of the main veins of the leaves, sometimes also on the lateral veins. These hairs are absent in *D. integrifolia*.

A number of other *Dryas* species have been, or possibly could be, applied to Greenland material. The applicability of these will now be discussed.

***D. crenulata* Juz.**

Plants with rather long, crenated leaves and no branched hairs have been compared to *D. crenulata* Juz. by HOLMEN in BÖCHER, HOLMEN & JAKOBSEN (1957) and by SCHWARZENBACH (1961). This is a species originally described from N. E. Siberia by JUZEPCZUK (1929) and mainly characterized by having leaves approximately three times as long as broad, the dimensions being given as 0.6—1.4 cm long and 3—4.5 mm wide. PORSILD (1947), however, in his description of the N. American species gives leaf dimensions of 3—4.5 cm long and 0.6—1.4 cm wide. The correspondence between these two sets of figures is striking; it appears that not only have the figures for length and breadth been exchanged, but that the measurements for width in JUZEPCZUK's account have been changed from mm to cm to allow for their use in this way. It is, however, this description which has been used by HOLMEN (l.c.) for the study of Greenland material. Similar plants to those in question, with leaves up to 3 cm long, were found together with very well grown specimens of *Salix arctica* and *Taraxacum brachyceras* in one locality in Kong Oscars Fjord region, at Skipperdal, Scoresby Land (lat. 72°23' N. long. 24°55'

W.) by a stream on a S.W. slope. This population, however, included plants both with and without branched hairs. The fact that the population only differs from the others in the region by the larger leaf size, a feature which is shared by the other species growing in the immediate area of the stream, suggests that this form is an environmental modification. There is evidence, however, that some degree of genetic fixation of this character has taken place, at least in some populations. Thus SCHWARZENBACH (1961) found large leaved plants at Krumme Langsø (lat. 74°06' N., long. 23°58' W.) were growing together with small leaved ones in sheltered places covered by snow in the winter.

D. chamissonis

This species was first applied to Greenland material by BÖCHER, HOLMEN & JAKOBSEN (1957), the taxon having been first mentioned by JUZEPCZUK (1929) in his survey of the genus. Here it is named "*D. chamissonis* SPRENG. ined. (ex sched. Herb. Horti. Berol.)" and is included within the genus subsection *Tenelleae* JUZ., which is characterized as having leaves entire or crenated only at the base, slightly rugose above, not impressed over the secondary veins, and with no punctate glands. These characters separate the subsection from subsections *Chamaedrifoliae* JUZ. and *Punctatae* JUZ., which are both composed of species with leaves crenately incised along their whole length and deeply impressed over the secondary veins, the former having leaves variably rugose above and without punctate glands, and the latter rugose above and with punctate glands. In PORSILD's (1947) study of the genus in N. America the presence or absence of branched hairs (see p. 9) on the leaves was raised to a subsectional character separating the *Tenelleae*, which lack them, from the subsections *Chamaedrifoliae* and *Punctatae*, which bear them. The typical species of subsection *Chamaedrifoliae* is *D. octopetala* and of the *Tenelleae*, *D. integrifolia*. Although JUZEPCZUK in the subsection description characterizes the *Tenelleae* as being predominantly entire leaved he includes *D. chamissonis* within it, although PORSILD (1947), who names the taxon *D. chamissonis* SPRENG. ex JUZ., describes it as having leaves which are completely crenated, but without any branched hairs. PORSILD states that it is confined to the Bering Strait area both in S.W. Alaska and the Chukotskoi peninsula. HOLMEN (in BÖCHER, HOLMEN & JAKOBSEN 1957), however, claims that this species, here called *D. chamissonis* SPRENG. is also present in Greenland. However none of these authors have given a formal diagnosis so that it appears that this species has never been validly published and can therefore be disregarded. As will be shown, whatever the status of this morphological type in S.W. Alaska, it is not, as HULTÈN (1959) has indicated, to be regarded as a taxonomic entity in Greenland.

***D. punctata* Juz.**

A number of Greenland collections have been identified as this species by PORSILD (1947). According to the original description by JUZEPCZUK (1929), this species which is the typical species of the subsection *Punctatae* Juz., has as its main diagnostic characters punctate glands on the upper surfaces of the leaves and more glandular scapes than *D. octopetala*. Some of the collections mentioned by PORSILD (l.c.) have small stalked glands, which as already mentioned (p. 11), are of the same type as those on the lower leaf surfaces and similar to those found on European plants. It seems clear, therefore, that these Greenland specimens do not differ from typical *D. octopetala* in this respect. As already described, however, (p. 11) a few specimens from E. Greenland have similar sessile or subsessile glands to those found on the leaves of material, named *D. punctata*, from Siberia. Material was examined from this area because JUZEPCZUK gives the distribution of *D. punctata* as Siberia, Mongolia and E. Europe. One of the population samples from Kong Oscars Fjord (no. 16) has specimens with somewhat similar glands; these plants form part of a population which is otherwise similar in composition, with respect to presence of branched hairs and crenation, to others in the region. It would therefore appear most reasonable to regard such specimens from Greenland as a variant of *D. octopetala* in the population not to be regarded as of taxonomic significance. HULTÈN (1959) has suggested that *D. punctata* is not a distinct species and that plants with glands on the upper sides of the leaves should be known as *D. octopetala* var. *viscida*, although he does not mention the variation in gland structure.

***D. hookeriana* Juz.**

This species was reported from Greenland by BÖCHER, HOLMEN & JAKOBSEN (1957) on the basis of some specimens which bear large stipitate glands on the undersides of the leaves (see p. 14 and fig. 13). This species, which has its main area of distribution in western North America, is characterized by the leaves bearing large stipitate glands, but no branched hairs, although HULTÈN (1959) has pointed out that some specimens do have a few branched hairs.

Similar plants have also been found in a population sample from Kong Oscars Fjord (no. 10, Kap Petersens), see p. 14. Because of this variation in one population and since these specimens only occur as isolated individuals within the area of *D. octopetala* in Greenland it seems best to regard them as part of the variation to be found in *D. octopetala* in this area. Similar forms are found in the U. S. S. R. and are discussed

by HULTÈN (l.c.). He comes to the conclusion that they should only be considered of subspecific rank, at least until more material is available for study.

***D. ajanensis* JUZ. and *D. Tschonoskii* JUZ.**

It is convenient to consider these species together since both characteristically have branched hairs on the hypanthia, similar to those described from Greenland material (p. 14). The two species were published by JUZEPCZUK (1929), *D. ajanensis* being described from around the sea of Okhotsk in the east asiatic U.S.S.R. and *D. Tschonoskii* from Japan and Sakhalin. In *D. Tschonoskii* branched hypanthium glands are given as one of the main differential characters of the species; according to the original description they are mixed with purple-black glandular hairs and smaller yellow stipitate glands on the hypanthium, whereas in *D. ajanensis* branched glands may or may not be present. As HULTÈN (l.c.) has pointed out, *D. ajanensis* is intermediate between *D. Tschonoskii* and typical *D. octopetala* and he therefore reduces *D. Tschonoskii* to subspecific rank and makes *D. ajanensis* a variety of this subspecies. The two latter taxa are otherwise distinguished by having different leaf and sepal shapes. Both these characters are however very variable in many populations of *D. octopetala*. It therefore seems unnecessary to give taxonomic rank to the Greenland plants since the presence of hypanthium glands within the populations does not appear to be correlated with any others. Further evidence for this view is given by the fact that plants in cultivation from a number of European localities also have branched hairs on the hypanthia and pedicels.

IV. HERBARIUM STUDIES

A general survey of the variation of the genus in Greenland has been carried out by an examination of the material in the University Botanical Museum, Copenhagen (C). The characters which have been used are presence of branched hairs, leaf crenation and leaf length/breadth ratio.

The measurements have been made as follows:—

(i) branched hairs; each specimen was examined under a binocular microscope and scored into one of the following four classes:

1. Branched hairs present on all leaves, some leaves at least with branched hairs on both the main and lateral veins.
2. Branched hairs present on all leaves, but confined to the main vein.
3. Branched hairs present on some leaves, but not on all.
4. No leaves with branched hairs.

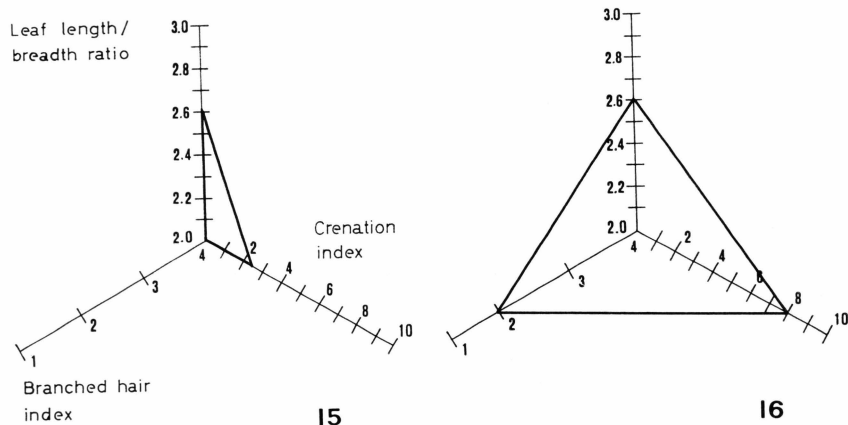
(ii) crenation; the number of crenatures along one side of the leaf was counted on five of the largest leaves from each specimen and a mean calculated. The apex was counted as one crenature so that an entire leaf has a score of one.

(iii) length/breadth ratio; the lengths and breadths of the two largest leaves on each specimen were measured, the length/breadth ratios calculated and the two figures averaged.

Each set of three figures has been plotted along three equiangular axes and these points joined so that a triangle is made for each specimen. Figs. 15 and 16 give typical shapes for *D. integrifolia* and *D. octopetala* respectively. Fig. 17 shows a map of Greenland with triangles for all specimens that have been measured, plotted geographically.

There are a number of points of interest. In S.E. Greenland the genus is absent except for a small area around Angmagssalik where *D. integrifolia* is present. A considerable number of species have isolated occurrences in the Angmagssalik area and BÖCHER (1956) has argued that this is due to survival through the last glacial period on nunataks which he has proposed on topographical evidence. In W. Greenland the genus is

represented by *D. integrifolia*. In the southern part it is rather rare and scattered, but further north it becomes common and is an important component of a number of types of vegetation (see BÖCHER 1954). Some specimens from between 69° and 73° latitude had a rather high number of crenatures. A number of specimens from Simiutap kûa (lat. 71°58' N., long. 54°41' W.), collected by the Danish geological expeditions to N.W. Greenland and kindly made available by K. JAKOBSEN, show that plants with more crenatures than usual occur with normal plants in the same area. Such plants have a mixture of leaves with one or two crena-



Figs. 15 & 16. Diagrams of equiangular axes and scales used for the general survey of *Dryas* herbarium material. Typical triangular shapes for specimens of *D. integrifolia* (fig. 15) and *D. octopetala* (fig. 16) superimposed.

tures and leaves with up to six or seven crenatures. It has been suggested (see p. 13) that this is due to hybridization with *D. octopetala*. Plants with the highest crenation (mean between four and five) have a low length/breadth ratio; such plants, according to K. JAKOBSEN, are from wet marshes and are almost certainly an ecological variant caused by the wet conditions. In support of this hypothesis no specimens with branched hairs or with all leaves regularly crenately incised have ever been recorded from this area. There is no ecological information on other herbarium specimens having a similar pattern of crenation. As previously mentioned some specimens from this area have pedicels bearing black glandular hairs, but this feature is not thought to be of any significance (see p. 15). M. P. PORSILD (1920) has recorded similar crenated forms from wet shaded localities and gravelly banks of river beds on Disko and the adjacent mainland. He also thinks that they are ecological variants, but compares such variants with *D. octopetala* var. *intermedia* NATH., but as already mentioned (p. 5) this variety was described from

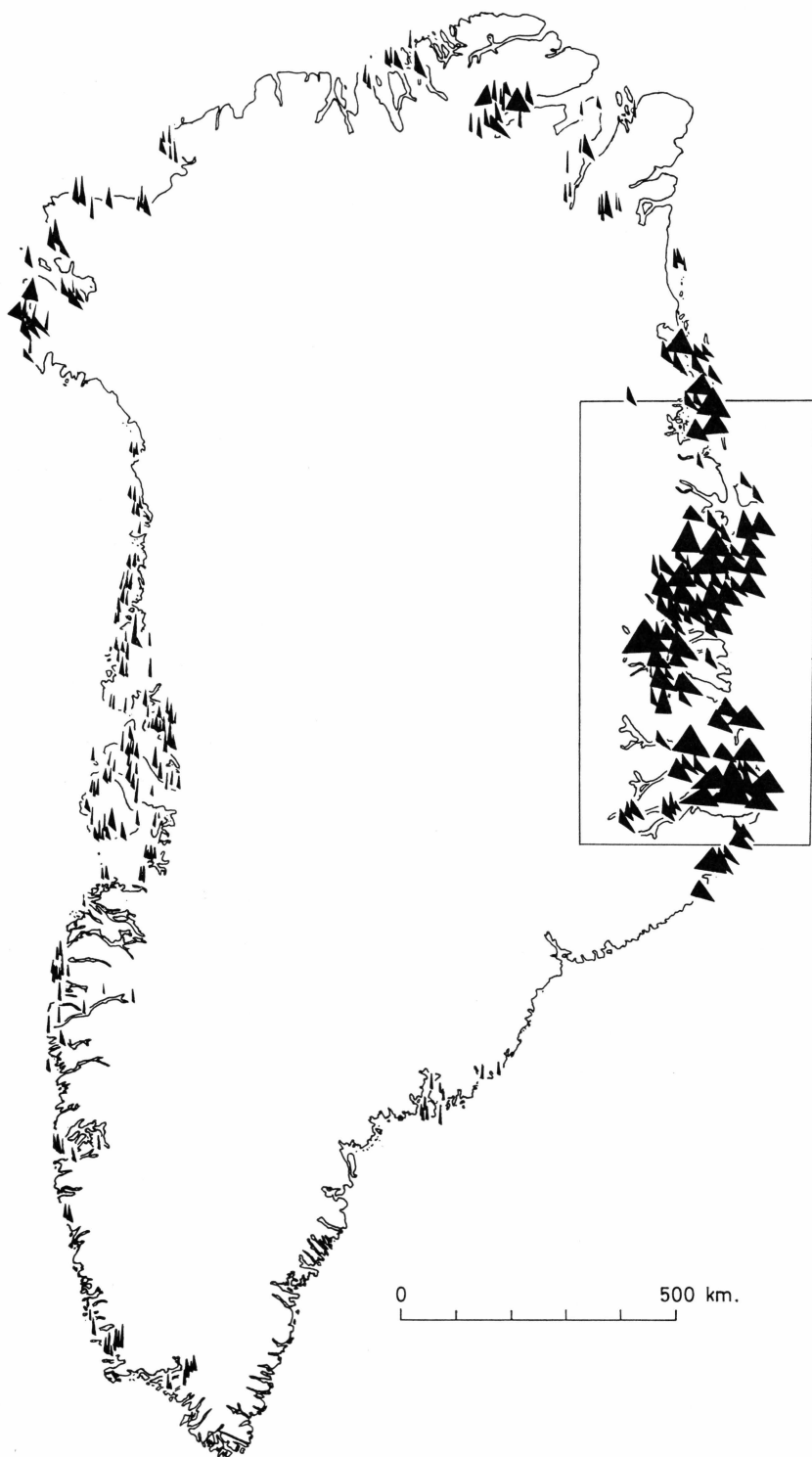


Fig. 17. Outline map of Greenland with triangular representation of *Dryas* herbarium material from the University Botanical Museum, Copenhagen. Inset shows area of fig. 18.

N.W. Greenland where *D. octopetala* is also present and, as discussed later, the pattern of variation and the reasons for it are different, so that this is not a good comparison.

Further to the north there appears to be a small gap in the distribution area between approximately latitudes 75° and 76° in the Melville Bugt region. In this area the ice cap is more or less coastal with icefree land confined to scattered semi-nunataks and small islands. There have been few botanical collections from this area, however, (see SØRENSEN 1943), so that *Dryas* may be present in at least some localities. The coastal ice cap will produce at least some breaks in the distribution area and this is reflected in the fact that immediately north of Melville Bugt evidence for the presence of *D. octopetala* has been found. In the material available two specimens with branched hairs have been found, both being scored in class 3 for this character. These are from E. end Saunders Ø, lat. $76^{\circ}30' N.$, long. $68^{\circ}50' W.$, leg. CROCKERLAND, and N.W. Granville Fjord, lat. $76^{\circ}50' N.$, leg. ERICHSEN. Typical specimens of *D. integrifolia* are present in the same area and also plants the leaves of which are completely crenated along the whole of the margins, but have no branched hairs. OSTENFELD (1923a) recorded *D. octopetala* from both Wolstenholme Fjord and Inglefield Land on the N.W. coast, but the specimens cited do not, on re-examination, bear any branched hairs and are also of this type. Fig. 17 shows that such plants extend round the north of Greenland and down the E. Greenland coast south to the Blosseville coast where the area of the genus is interrupted. They thus completely overlap the distribution of *D. octopetala* in Greenland and are not present outside it. *D. integrifolia* is also represented in the rather scanty material available from North Greenland and according to HOLMEN (1957) no other forms besides this and plants with completely crenated leaves and without branched hairs are found in Peary Land. Re-examination of the material from this area has however disclosed two interesting specimens. One, from Jørgen Brønlund Fjord, Heilprin Land, lat. $82^{\circ}10' N.$, long. $31^{\circ} W.$, has a few very small branched hairs on a few of the leaves, while the other, collected from Midsommersøen, Baggården, lat. $82^{\circ}16' N.$, long. $35^{\circ}45' W.$, has a few leaves with long, multicellular hairs with one or two side branches on the underside of the main vein. They indicate that *D. octopetala* is present in North Greenland although it may be rather rare. From approximately $78^{\circ} N.$ south to $69^{\circ} N.$ *D. octopetala* is well represented in the herbarium collections and *D. integrifolia* is also present although not so commonly. Fig. 18 shows the central part of E. Greenland on a larger scale with a nearly complete representation of the material in the Copenhagen collections. The material available is not sufficient to draw any conclusions as to whether there is any pattern in the distribution of the different types,

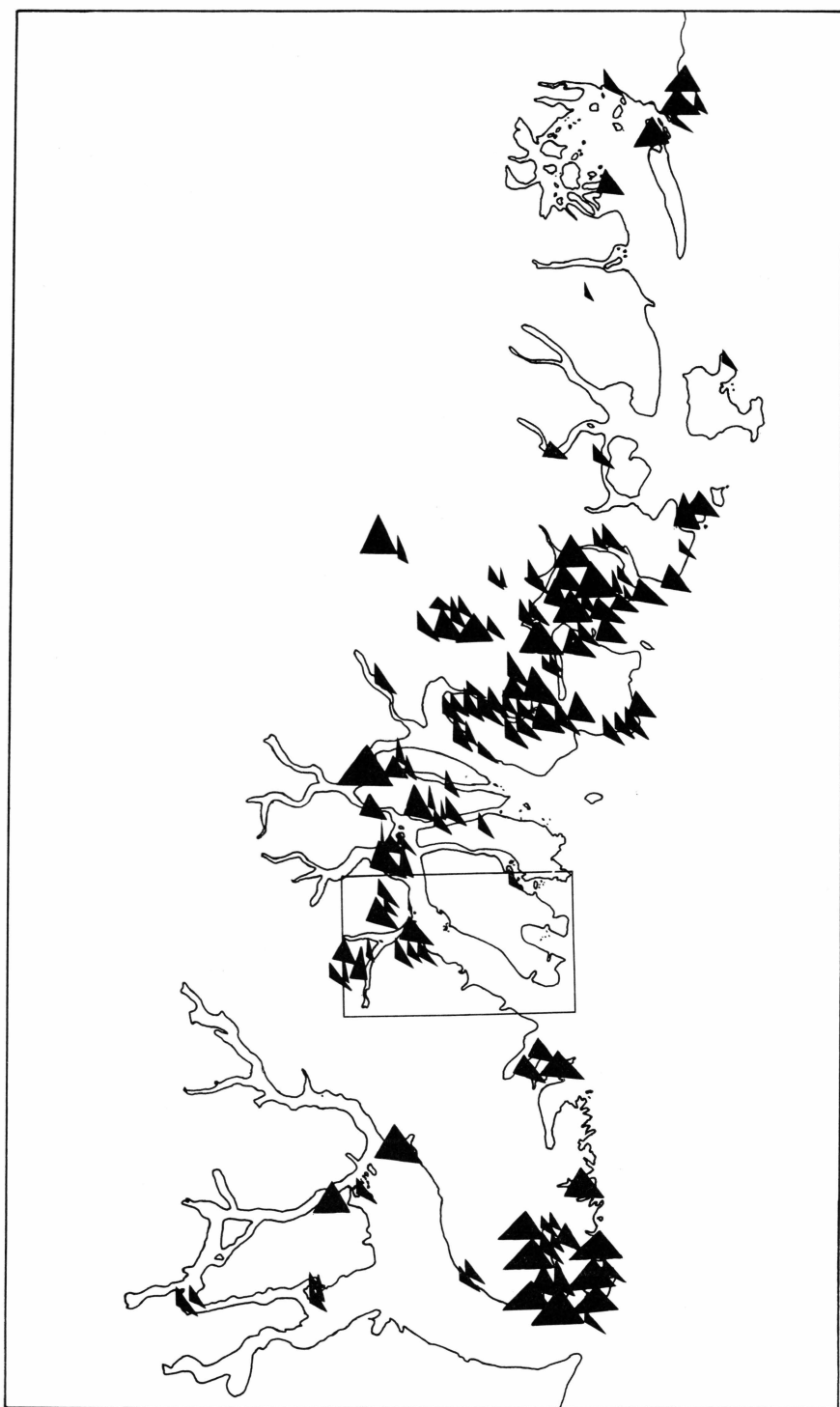


Fig. 18. Outline map of central East Greenland with triangular representation of *Dryas* herbarium material from the University Botanical Museum, Copenhagen.
Inset shows area of fig. 19.

either latitudinally or from the outer coastal to the inner fjord areas (as suggested by VAAGE (1932) and SEIDENFADEN & SØRENSEN (1937)). The presence of intermediate types in the outer coast areas, however, suggests that *D. integrifolia* plants may be present in these areas.

The sudden interruption of the genus' distribution and the southern limit of *D. octopetala* on the Blosseville coast have been discussed by BÖCHER (1938), who considers that explanations based on topographical barriers or limitation due to lack of time since immigration (including the limitation of dispersal) are insufficient. He believes that the limit of *D. octopetala* is physiological in nature, the species being represented by a high arctic race unable to survive in sub-arctic areas.

V. FIELD STUDIES

A. Field Measurements.

In order to study the variation found in the herbarium material a population study was carried out during an expedition to the Kong Oscars Fjord region of East Greenland, lat. approximately 72° N. In all, seventeen populations were studied, the localities being shown in fig. 19 and listed, together with an indication of the vegetation type and topographical situation in table 4. In addition collections from Polhems Dal (loc. 13) and Schaffhauserdalen (loc. 12), collected on the Leicester University East Greenland Expedition 1961, were kindly made available to me. At each locality a population sample of 25 branches was collected at random in the population. A description was also made of the vegetation and a soil sample collected for analysis. The methods used and the results obtained are described in the ecological section.

At selected localities, field measurements were made along belt transects to study the population variation in situ. A line of ten, contiguous, one metre quadrats was laid out and the position of each plant marked on a sketch map. Five of the largest leaves were picked and scored into one of the three following classes for branched hairs: —

1. Branched hairs on all leaves.
2. Branched hairs on some leaves only.
3. Branched hairs on no leaves.

The number of crenatures down one side of each leaf was counted and the mean calculated. The lengths and breadths of the two largest leaves were measured and a mean length/breadth ratio calculated. These observations were then used to construct triangles in the the same way as for the herbarium material. The results, for four of the seven populations studied in this way are given in figs. 20–23. It should be mentioned that in comparison with the random samples collected from the same populations and scored in the laboratory there is often an under-representation of plants with branched hair class 2. This is the result of not seeing the branched hairs on these specimens when working in poor weather. These plants are thus included in class 3 for this character, but this error does not affect the general picture or the interpretation

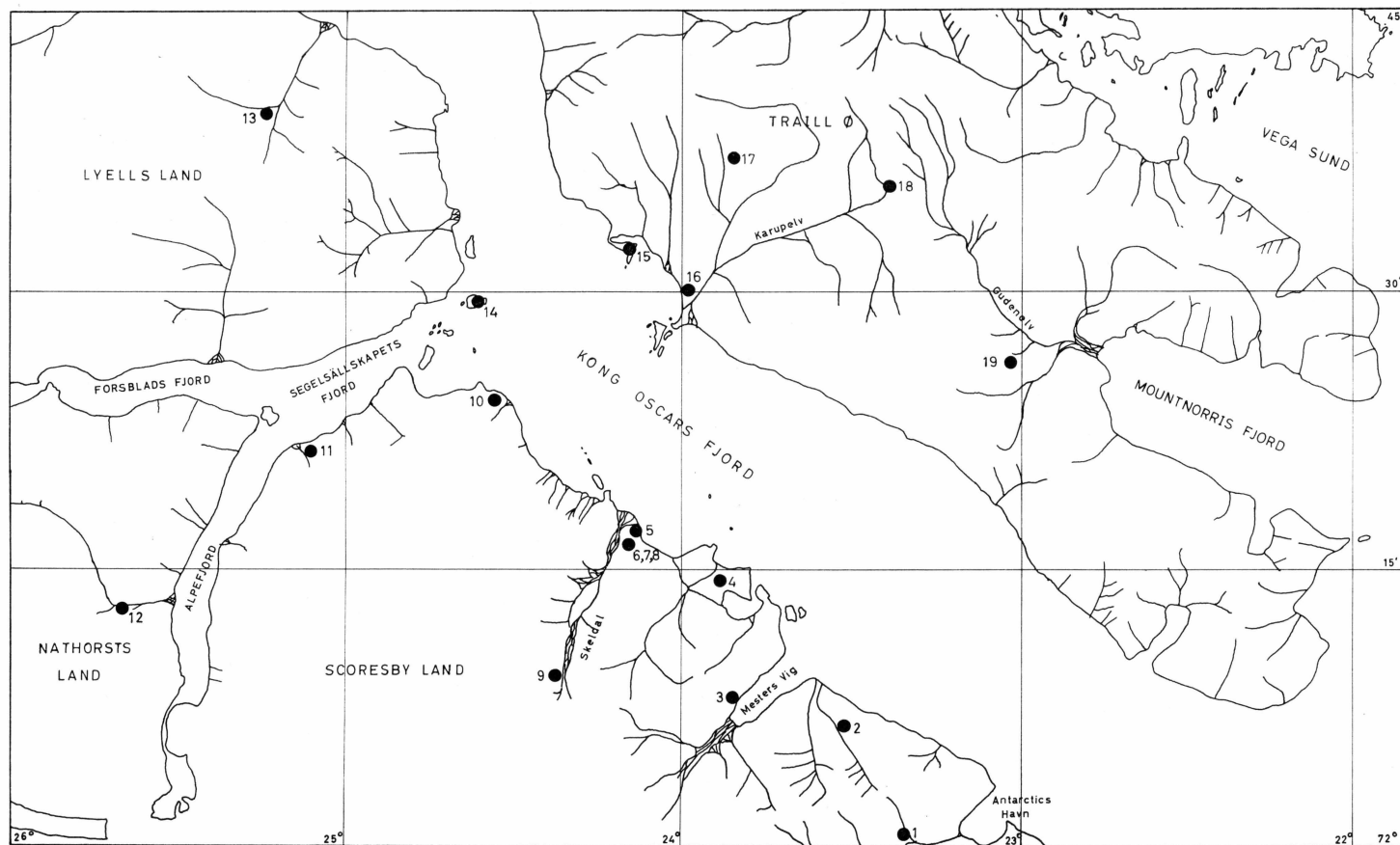


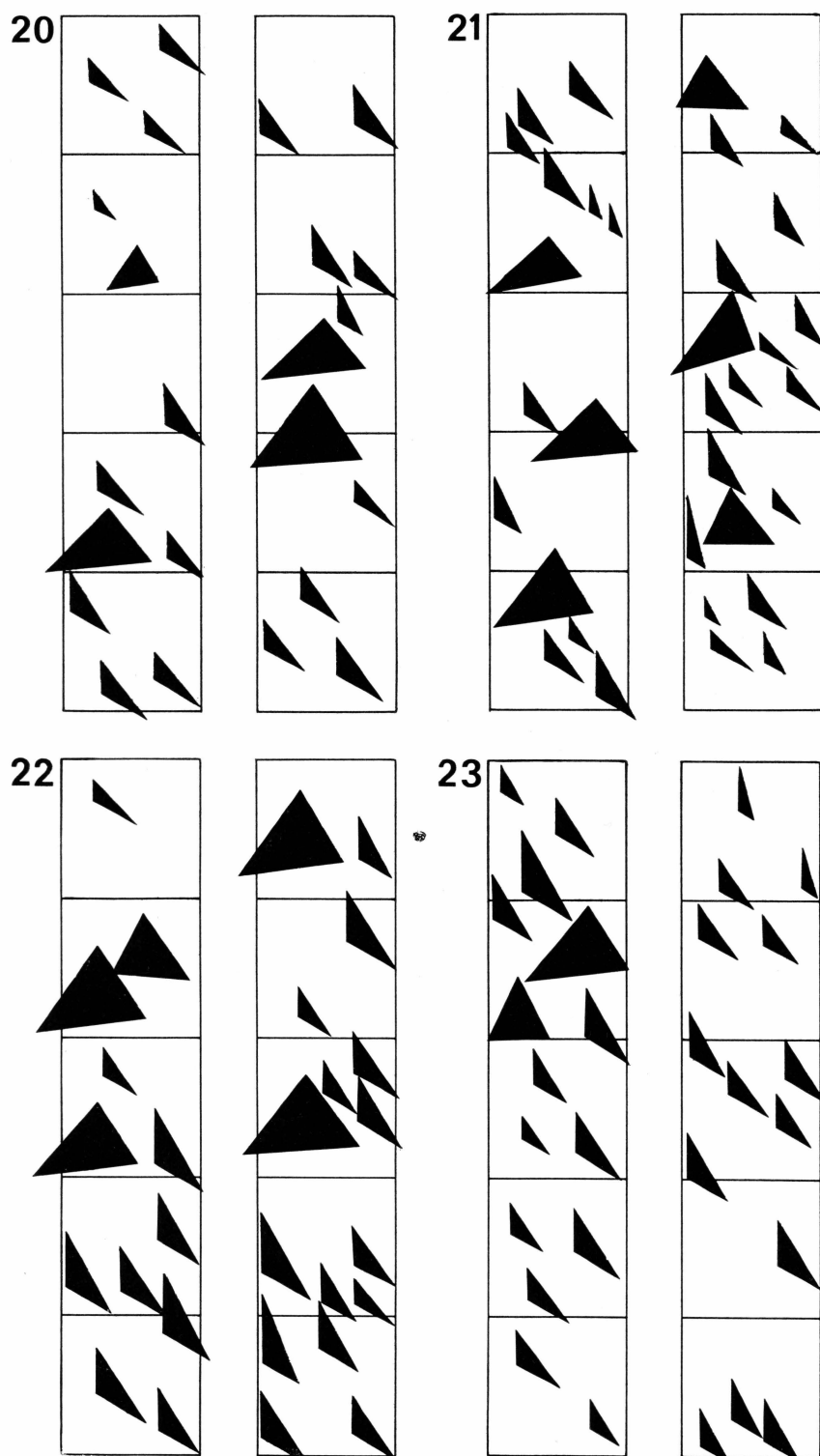
Fig. 19. Localities of populations sampled in the Kong Oscars Fjord region of East Greenland.

Table 4.

List of localities with latitudes and longitudes, together with an indication of the vegetation type and topographical situation.

-
1. Antarcities Havn; lat. 72°01' N., long. 23°22' W.; fell field on old river flood plain.
 2. Pictet Bjærge; lat. 72°06' N., long. 23°32' W.; *Dryas* heath on mountain slope.
 3. Mesters Vig; lat. 72°08' N., long. 23°52' W.; fell field on stony raised beach.
 4. Mestersvig flyveplads; lat. 72°14' N., long. 23°55' W.; lichen-rich *Dryas* heath on raised fjord floor.
 5. Lower E. Skeldal; lat. 72°17' N., long. 24°08' W.; wet hummock marsh on raised fjord floor.
 6. Lower E. Skeldal; lat. 72°16' N., long. 24°10' W.; open herb mat on bank cut into alluvial deposit by stream.
 7. Lower E. Skeldal; lat. 72°16' N., long. 24°10' W.; *Dryas* heath on patterned ground, originally fjord floor.
 8. Lower E. Skeldal; lat. 72°16' N., long. 24°10' W.; open herb mat on weathered dolerite outcrop.
 9. Upper W. Skeldal; lat. 72°09' N., long. 24°23' W.; fell field on mountain slope.
 10. Kap Petersens; lat. 72°24' N., long. 24°33' W.; scree on frost shattered limestone.
 11. Segelsällskapetets fjord, Scoresby Land; lat. 72°21' N., long. 25°06' W.; dry heath on mountain slope.
 12. Schaufhauserdalen, Nathorst Land; lat. 72°13' N., long. 25°40' W.
 13. Upper Polhems dal, Lyells Land; lat. 72°40' N., long. 25°15' W.; fell field on exposed ridge.
 14. Åkerbloms Ø, Kong Oscars fjord; lat. 72°29' N., long. 24°36' W.; wet *Dryas* – *Salix arctica* heath on raised fjord floor.
 15. Holms Bugt, Traill Ø; lat. 72°32' N., long. 24°08' W.; dry heath on dolerite outcrop.
 16. Holms Bugt, Traill Ø; lat. 72°30' N., long. 24°00' W.; dry grassland on raised beach.
 17. W. side Karupelv, Traill Ø; lat. 72°37' N., long. 23°50' W.; fine scree below dolerite outcrop.
 18. N. Karupelv, Traill Ø; lat. 72°36' N., long. 23°23' W.; heath – grassland mosaic on steep ravine.
 19. Gudenelv, Traill Ø; lat. 72°26' N., long. 23°02' W.; fell field on weathered dolerite outcrop.
-

of the results. A consideration of the figures shows that, in all cases, both plants with and without branched hairs are present within ten sq. m. In three populations, 6, 7 and 16 of which no. 7 is illustrated (fig. 22), all the leaves of plants without branched hairs are completely crenately incised, but in the other populations sampled e.g. no. 10, fig. 23, intermixed with these are a small proportion of *D. integrifolia* plants. Two populations, numbers 1 and 4 (figs. 20 and 21), are of special interest since they contain plants with few crenations, but with branched hairs (population 1, quadrat 2, plant with crenation mean 3.4, branched hair



Figs. 20-23. Triangular representation of field measurements in selected populations along belt transects of ten, contiguous, one metre quadrats. Fig. 20 - population 1; fig. 21 - population 4; fig. 22 - population 7; fig. 23 - population 10.

class 2; population 4, quadrat 8, plant with crenation mean 3.4, branched hair class 1). Such plants are not represented in the Copenhagen museum collections, but have been mentioned by HULTÈN (1959) p. 538. It seems apparent from the field observations that these populations consist mainly of specimens intermediate between *D. integrifolia* and *D. octopetala* with typical specimens of these two species being in a small minority. Thus within a distance of 10 m. the total variation known in Greenland *Dryas*, with respect to crenation and presence of branched hairs, can be demonstrated. This variation is such as would be expected from introgressive hybridization between the two species.

B. Population samples.

The variation in the population samples collected has been expressed using two dimensional scatter diagrams, the coordinates being crenation mean and the ratio of leaf width at the middle of the leaf to that at the base. Each specimen in every sample has been scored for branched hairs and the two largest leaves have been removed and measured for the coordinate characters. Branched hairs have been scored into four classes using the same limits as in the study of herbarium specimens. They are indicated on the diagrams by shaded sectors as in fig. 24. The resulting

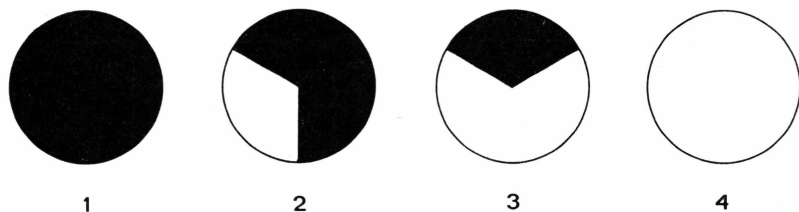


Fig. 24. Sector representation of the four branched hair classes used in the scatter diagrams of population samples.

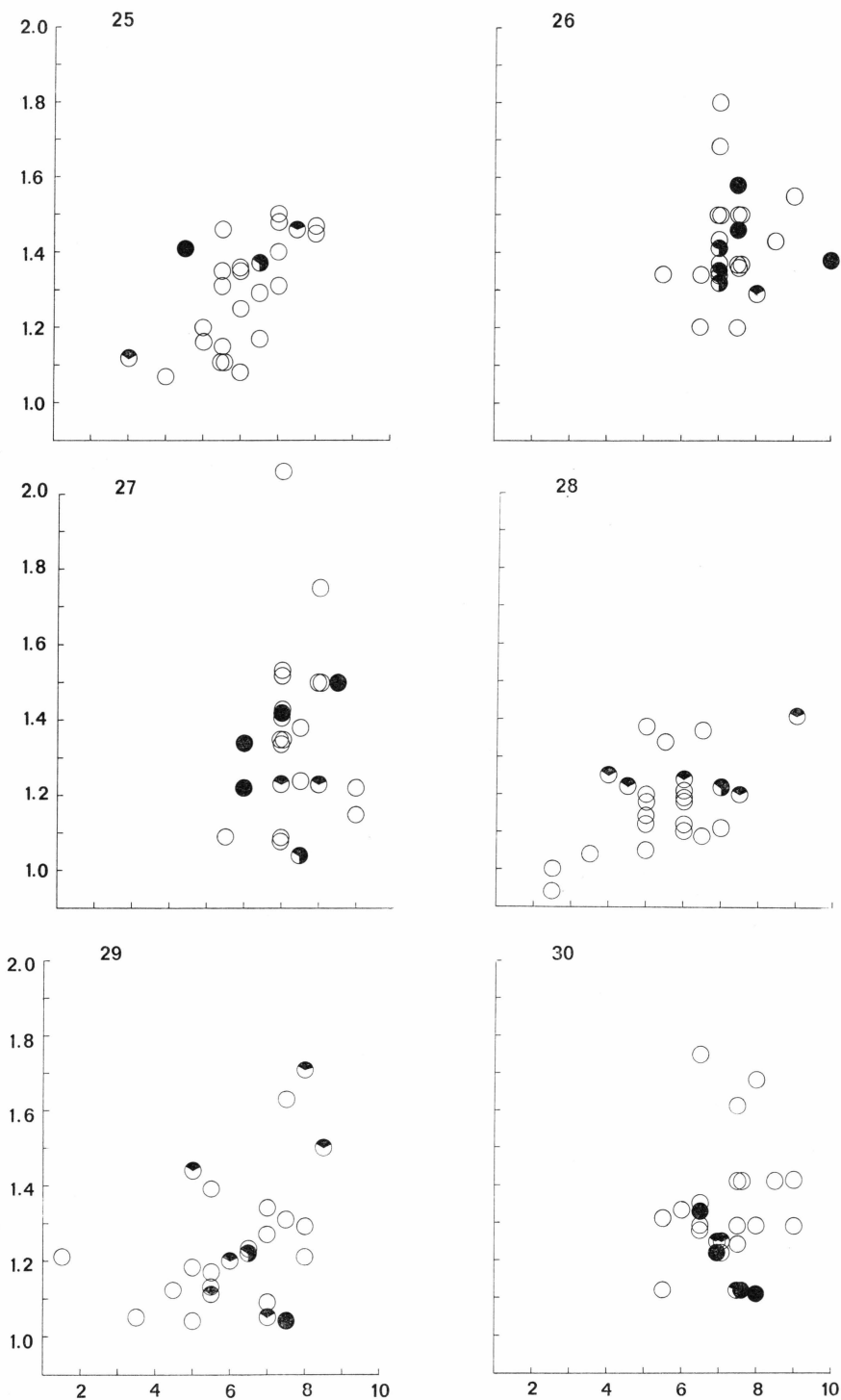
diagrams are shown in figs. 25 to 43. The results are similar to those obtained from the field measurements. When compared to fig. 2, a diagram which is made up of two groups of specimens one of *D. octopetala* and one of *D. integrifolia*, each from an area where only that species is present, it will be seen that these diagrams span the complete range. The diagrams show the characteristics that would be expected if introgressive hybridization were taking place between *D. integrifolia* and *D. octopetala* and it seems most reasonable to regard them as examples of this process. It is possible to divide the populations into groups corresponding with degrees of hybridization. Thus populations such as those from localities 2 (Pictet Bjærge) and 6 (Lower E. Skeldal, alluvial terrace) (figs. 26 and 30) have a predominance of *octopetala* forms with no plants

of low crenation mean. Others such as 5 (Lower E. Skeldal, fangsthytte) and 11 (Segelsällskapets Fjord) (figs. 29 and 35) indicate a preponderance of *D. integrifolia* biotypes since they have a number of plants of low crenation mean without branched hairs. A third group e.g. 15 (Holms Bugt, Traill Ø) (fig. 39) also has plants of low crenation mean, but some of them have branched hairs. This variation in population structure appears to be random, there being no correlations with geographical distribution within the area, or with ecological difference.

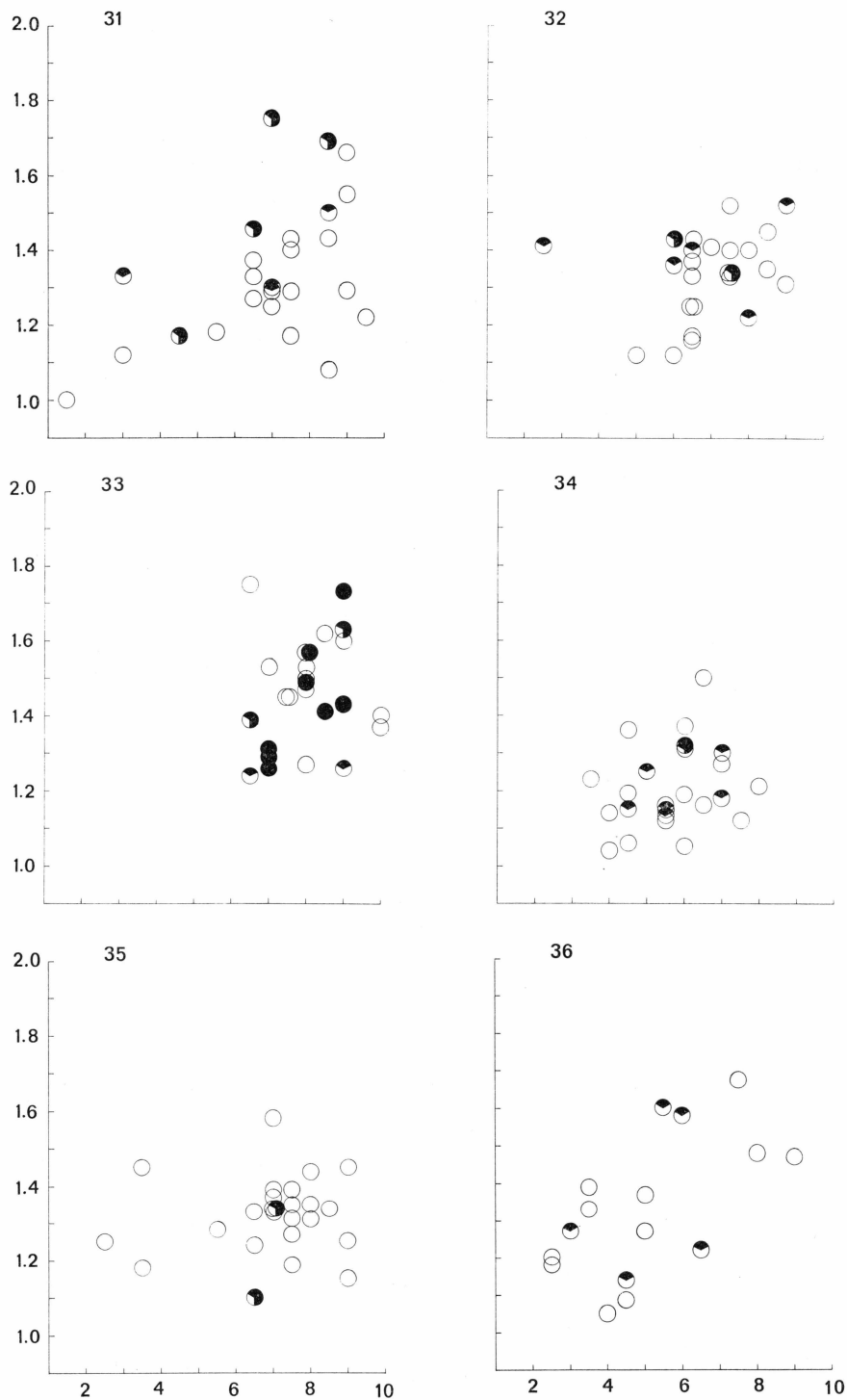
A few of the population samples show some correlation between the leaf breadth ratio and crenation mean e.g. samples 14 and 15, figs. 38 and 39. It is evident that in a mixed population of these two species without interbreeding, correlation will be high for these two characters.

Table 5.
Vegetation types of population samples divided into three arbitrary groups based on variation of morphology in the samples, showing that there is no correlation between these groups and the vegetation type.

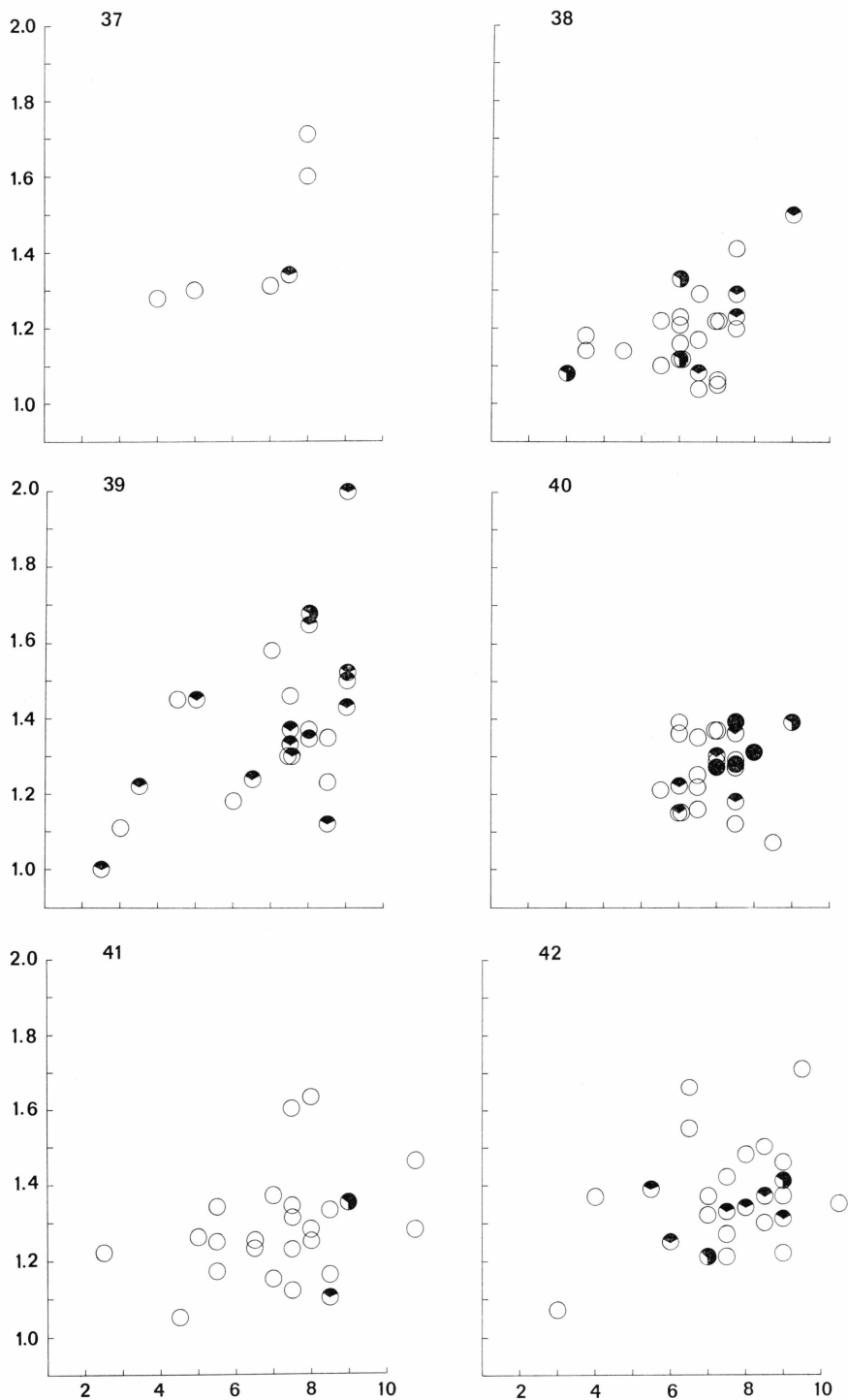
Population	Fig.	Community
Populations with all plants having a crenation mean of 5 or more.		
2	26	<i>Dryas</i> heath
3	27	Fell field
6	30	Open herb mat
9	33	Fell field
16	40	Dry grassland
Populations including plants with a crenation mean of 4 or less; some of these bearing branched hairs on the leaves.		
1	25	Fell field
4	28	Lichen-rich heath
7	31	Patterned <i>Dryas</i> heath
8	32	Open herb mat
12	36	—
14	38	Wet <i>Dryas</i> — <i>Salix arctica</i> heath
15	39	Dry heath
Populations including plants with a crenation mean of 4 or less; none of these bearing branched hairs on the leaves.		
5	29	Wet hummock marsh
10	34	Scree on limestone
11	35	Dry heath
13	37	Fell field
17	41	Scree on dolerite
18	42	Heath — grassland mosaic
19	43	Fell field



Figs. 25-30. Scatter diagrams of population samples 1-6 respectively. Ordinate, ratio of width at the middle of the leaf to that at the base and abscissa, crenation index. Branched hair class of each specimen represented by sectors as in fig. 24.



Figs. 31-36. Scatter diagrams of population samples 7-12 respectively.



Figs. 37-42. Scatter diagrams of population samples 13-18 respectively.

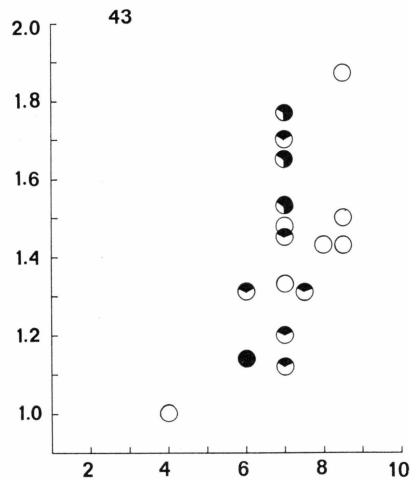


Fig. 43. Scatter diagram of population sample 19.

With progressive interbreeding and increasing recombination, however, this correlation will become less. It is possible therefore that populations which show correlation in this way are less introgressed than those which do not show any such correlation.

The groups are not correlated with any one vegetation type, each of them being found in a range of communities. This is shown in table 5, where the samples, which have been divided into three arbitrary groups, are listed with the vegetation type of each locality. Details of these communities together with soil analyses are given in section VI.

VI. ECOLOGY

Vegetation analyses have been made at nearly all localities from which population samples were collected. The descriptive method which has been used, is based on that of POORE (1955). The details are as follows. A floristic list is made of a 1 sq. m. quadrat; this is then doubled in area twice and additional species added to the list. Cover-abundance of each species is scored using the Domin scale: —

Cover about 100 %	10
Cover greater than 75 %	9
Cover 50–75 %	8
Cover 33–50 %	7
Cover 25–33 %	6
Abundant, cover about 20 %	5
Abundant, cover about 5 %	4
Scattered, cover small	3
Very scattered, cover small	2
Scarce, cover small	1

Notes of the aspect, slope and altitude are also made, a soil sample taken for analysis, and bryophytes and lichens collected for later identification. Bryophytes and lichens not noted in the field, but identified later are denoted in the floristic lists by x.

The floristic results are given in table 6, the species being arranged alphabetically within the following classes: — dwarf shrubs, pteridophytes, grasses, sedges and other monocotyledons, dicotyledonous herbs, mosses, hepatics and lichens. The list of species is preceded by the habitat details of each locality. A list of localities is given in table 4. Localities have been given the same reference number as the population samples collected from them, as have the soil samples.

Soil samples were collected from the rooting layer under *Dryas* plants and air dried as soon as possible. After further air drying in the laboratory the samples were passed through a 2 mm sieve to remove stones and large roots. Humus content was estimated by the Walkley-Black wet oxidation method, pH electrometrically on a 1:2 soil: water

Table 6.

Floristic lists from localities where population samples have been collected.

Locality	1	2	3	4	5	6	7	8	10	11	14	15	16	17	18
Altitude (m)	100	100	50	40	20	100	100	100	50	100	30	50	30	750	350
Aspect	E	NW	SE	—	NE	WNW	NE	W	S	NW	NE	—	W	SSW	E
Slope (degrees)	5	20	10	—	5	25	10	5	5	25	5	—	5	10	20
Cover (%)	75	100	50	100	100	100	60	100	10	75	50	70	100	5	90
Plot area (sq. m)	4	4	4	4	2	4	4	4	4	4	4	4	4	8	4
<i>Cassiope tetragona</i>	—	—	4	—	7	—	1	—	—	3	—	—	—	—	—
<i>Dryas</i> spp.	5	8	5	5	5	6	7	4	4	7	6	5	5	2	6
<i>Rhododendron lapponicum</i> .	—	—	—	—	—	—	—	—	—	2	—	2	—	—	—
<i>Salix arctica</i>	4	2	4	4	3	2	2	—	2	2	5	2	4	1	1
<i>Vaccinium uliginosum</i>															
ssp. <i>microphyllum</i>	2	—	—	—	4	—	1	—	—	5	—	4	—	1	5
<i>Equisetum arvense</i>	—	—	—	—	4	—	—	—	—	—	—	—	—	—	—
<i>Equisetum variegatum</i>	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Woodsia glabella</i>	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—
<i>Colpodium vahlianum</i>	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—
<i>Festuca brachyphylla</i>	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—
<i>Hierochloë alpina</i>	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—
<i>Poa glauca</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
<i>Trisetum spicatum</i>	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Carex bigelowii</i>	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—
<i>Carex capillaris</i>	—	—	—	—	—	—	—	—	—	3	—	2	—	—	—
<i>Carex misandra</i>	—	—	—	—	—	—	—	—	—	2	1	—	—	—	—
<i>Carex nardina</i>	—	—	2	—	—	—	2	3	1	5	—	—	3	2	—
<i>Carex rupestris</i>	—	—	—	—	—	3	—	3	1	3	3	—	5	—	4
<i>Carex scirpoidea</i>	2	3	2	—	—	—	—	—	—	—	—	—	—	—	4
<i>Carex supina</i>															
ssp. <i>spaniocarpa</i>	—	—	—	—	—	—	—	—	—	—	—	6	—	—	—
<i>Eriophorum triste</i>	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—
<i>Kobresia simpliciuscula</i>	—	—	—	—	—	—	—	—	—	—	1	3	—	—	—
<i>Luzula confusa</i>	—	—	—	1	—	—	—	—	—	—	—	—	2	—	—
<i>Tofieldia coccinea</i>	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—
<i>Tofieldia pusilla</i>	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Antennaria canescens</i>	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
<i>Antennaria porsildii</i>	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Arenaria pseudofrigida</i>	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
<i>Arnica alpina</i>	—	3	—	—	—	3	—	—	—	—	—	—	—	—	—
<i>Campanula rotundifolia</i> coll.	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cerastium alpinum</i>															
ssp. <i>lanatum</i>	—	2	—	—	—	3	—	—	—	—	—	—	—	—	—
<i>Chamaenerion latifolium</i> ...	—	—	—	—	—	2	—	2	—	—	—	—	—	—	—
<i>Draba</i> spp.	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1
<i>Lesquerella arctica</i>	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
<i>Minuartia rubella</i>	—	—	—	1	—	—	—	1	—	—	—	—	—	—	—
<i>Oxyria digyna</i>	—	—	—	1	—	—	—	—	—	—	—	—	1	—	—
<i>Papaver radiculatum</i>	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
<i>Pedicularis flammea</i>	—	—	—	—	—	—	1	—	—	2	2	—	—	—	—

(continued)

Table 6 (continued).

Locality	1	2	3	4	5	6	7	8	10	11	14	15	16	17	18
Altitude (m).....	100	100	50	40	20	100	100	100	50	100	30	50	30	750	350
Aspect	E	NW	SE	—	NE	WNW	NE	W	S	NW	NE	—	W	SSW	E
Slope (degrees)	5	20	10	—	5	25	10	5	5	25	5	—	5	10	20
Cover (°/o).....	75	100	50	100	100	100	60	100	10	75	50	70	100	5	90
Plot area (sq. m.)	4	4	4	4	2	4	4	4	4	4	4	4	4	8	4
<i>Pedicularis hirsuta</i>	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
<i>Polygonum viviparum</i>	3	2	1	2	3	—	2	1	1	3	2	3	2	—	3
<i>Potentilla hyparctica</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
<i>Potentilla nivea</i>	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—
<i>Pyrola grandiflora</i>	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—
<i>Saxifraga aizoides</i>	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—
<i>Saxifraga cernua</i>	—	2	1	—	—	—	—	1	—	—	—	1	1	—	1
<i>Saxifraga nivalis</i>	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—
<i>Saxifraga oppositifolia</i>	3	3	3	3	3	—	2	2	2	3	3	3	3	1	3
<i>Silene acaulis</i>	4	2	2	4	3	1	—	1	—	2	2	1	4	—	—
<i>Aulacomnium turgidum</i>	—	—	—	—	4	—	—	—	—	—	—	—	—	—	—
<i>Babula recurvirostris</i>	—	—	×	×	—	—	—	—	—	×	—	×	×	—	—
<i>Brachythecium groenlandicum</i>	—	—	—	—	×	—	—	—	—	—	—	—	—	—	—
<i>Brachythecium salebrosum</i>															
var. <i>binervulum</i>	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—
<i>Brachythecium turgidum</i>	×	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Bryum argentum</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	×
<i>Bryum</i> spp.....	×	—	—	—	—	—	×	—	—	×	×	×	—	×	×
<i>Campylium stellatum</i>	×	—	—	×	—	—	—	—	—	—	—	—	—	—	—
<i>Ceratodon purpureus</i>	—	×	—	—	—	×	—	—	—	—	—	—	—	—	×
<i>Cnestrum alpestre</i>	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—
<i>Dicranoweisia crispula</i>	—	—	×	—	—	—	—	—	—	—	—	—	—	—	—
<i>Dicranum scoparium</i>	—	—	×	—	—	—	—	—	—	—	—	—	—	—	—
<i>Dicranum spadiceum</i>	—	—	—	—	×	—	—	—	—	—	—	—	—	—	—
<i>Distichium capillaceum</i>	×	—	×	×	×	—	×	—	×	×	×	×	×	—	×
<i>Ditrichum flexicaule</i>	×	—	—	×	×	—	—	×	—	—	×	—	×	—	×
<i>Drepanocladus badius</i>	—	—	—	—	×	—	—	—	—	—	—	—	—	—	—
<i>Encalypta alpina</i>	—	—	—	×	×	—	—	—	—	—	—	—	—	—	—
<i>Encalypta brevicolla</i>	—	—	—	—	—	—	—	×	×	—	—	—	—	×	—
<i>Encalypta rhabdocarpa</i>	—	—	—	—	—	—	—	×	—	—	—	—	—	—	—
<i>Encalypta</i> sp.	—	—	—	×	—	—	—	—	—	—	—	—	—	—	—
<i>Fissidens osmundoides</i>	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—
<i>Hypnum bambergeri</i>	×	—	—	×	×	—	—	—	—	—	×	—	—	—	—
<i>Hypnum revolutum</i>	—	—	—	—	—	—	×	—	—	×	—	—	—	—	—
<i>Isoterygium pulchellum</i>	—	—	—	—	×	—	—	—	—	×	—	×	—	—	—
<i>Meesia uliginosa</i>	—	—	—	—	×	—	—	—	—	×	—	—	—	—	—
<i>Mnium hymenophylloides</i> ...	—	—	—	—	×	—	—	—	—	×	—	—	—	—	—
<i>Myurella julacea</i>	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—
<i>Oncophorus wahlenbergii</i>	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—
<i>Orthothecium chryseum</i>	—	—	—	—	×	—	—	—	—	—	—	—	—	—	—
<i>Orthothecium strictum</i>	—	—	—	—	×	—	—	—	—	—	—	—	—	—	—
<i>Orthotrichum killiasii</i>	—	—	—	—	—	—	—	—	—	×	—	—	—	—	—
<i>Pohlia cruda</i>	—	—	—	—	—	—	—	—	—	—	—	×	×	—	—
<i>Pohlia gracilis</i>	—	—	—	—	—	—	—	—	—	—	—	×	—	—	—

(continued)

Table 6 (continued).

Locality	1	2	3	4	5	6	7	8	10	11	14	15	16	17	18
Altitude (m)	100	100	50	40	20	100	100	100	50	100	30	50	30	750	350
Aspect	E	NW	SE	—	NE	WNW	NE	W	S	NW	NE	—	W	SSW	E
Slope (degrees)	5	20	10	—	5	25	10	5	5	25	5	—	5	10	20
Cover (%)	75	100	50	100	100	100	60	100	10	75	50	70	100	5	90
Plot area (sq. m.)	4	4	4	4	2	4	4	4	4	4	4	4	4	8	4
<hr/>															
<i>Pohlia</i> c. f. <i>nutans</i>	—	—	—	—	—	×	—	—	—	—	—	—	—	—	—
<i>Pohlia</i> sp.	—	×	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Pogonatum capillare</i>	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—
<i>Polytrichum alpinum</i>	—	—	2	3	—	—	—	—	—	—	—	—	—	—	—
<i>Polytrichum juniperinum</i> ..	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—
<i>Polytrichum piliferum</i>	—	—	—	—	—	5	—	3	—	—	—	2	—	—	—
<i>Polytrichum strictum</i>	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—
<i>Stegonia latifolia</i>	—	—	—	×	—	—	—	—	—	—	—	—	—	—	—
<i>Tomenthypnum nitens</i>	×	—	—	—	9	—	×	—	—	—	—	—	—	—	—
<i>Tortella fragilis</i>	—	×	×	×	×	—	×	—	×	×	—	×	—	×	×
<i>Tortula ruralis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	×	×
<hr/>															
<i>Blepharostoma trichophylla</i> .	—	—	—	×	3	—	—	—	—	—	—	×	—	—	—
<i>Cephaloziella</i> sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	×
<i>Odontoschisma macounii</i> ...	—	—	—	—	×	—	—	—	—	—	—	—	—	—	—
<i>Riccardia pinguis</i>	—	—	—	×	×	—	—	—	—	—	—	—	—	—	—
<i>Sphenolobus minutus</i>	—	—	—	—	×	—	—	—	—	—	—	—	—	—	—
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<i>Bacidia</i> c. f. <i>muscorum</i>	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—
<i>Buellia disciformis</i>															
var. <i>muscorum</i>	—	—	—	—	—	×	—	—	—	—	—	—	—	—	—
<i>Candelariella epixantha</i>	—	—	—	—	—	—	—	×	—	—	—	—	—	—	—
<i>Candelariella placodizans</i> ..	—	—	—	—	—	—	—	—	—	—	—	—	×	—	—
<i>Cetraria crispa</i>	—	3	3	—	×	3	—	—	—	2	—	—	—	—	—
<i>Cetraria delisei</i>	4	—	3	4	×	—	—	—	—	—	—	×	—	—	—
<i>Cetraria nivalis</i>	—	—	—	—	×	2	—	3	—	×	—	×	—	—	—
<i>Cladonia coccifera</i>	—	—	—	—	—	5	—	—	—	—	—	—	—	—	—
<i>Cladonia pyxidata</i>	—	9	—	×	×	5	5	×	—	×	×	×	—	—	×
<i>Cladonia</i> spp.	—	—	5	—	—	4	—	—	—	—	—	—	—	—	—
<i>Collema</i> sp.	—	—	—	—	—	—	—	—	—	—	×	—	—	—	—
<i>Cornicularia aculeata</i>	—	3	×	—	—	2	3	3	—	—	—	×	3	—	—
<i>Lecanora epibrya</i>	—	—	—	×	—	—	×	—	—	×	—	—	—	—	—
<i>Lecanora verrucosa</i>	—	—	—	—	—	—	×	—	—	—	—	—	—	—	—
<i>Lecidea decipiens</i>	—	—	×	×	—	—	—	—	—	×	—	×	—	—	—
<i>Ochrolechia frigida</i>	—	—	—	—	—	—	—	—	×	×	×	×	×	—	—
<i>Peltigera aphthosa</i>	—	—	—	—	×	—	—	—	—	—	—	—	—	—	—
<i>Peltigera rufescens</i>	×	×	×	×	—	×	—	—	—	—	—	—	—	×	×
<i>Pertusaria</i> sp.	×	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Physcia muscigena</i>	—	—	—	—	—	—	—	—	—	—	—	×	—	×	—
<i>Solorina bispora</i>	—	—	—	—	—	×	×	—	—	—	×	—	—	—	—
<i>Solorina octospora</i>	—	—	—	—	—	—	—	×	—	—	—	—	—	—	—
<i>Stereocaulon alpinum</i>	—	5	4	2	—	2	3	×	—	—	—	—	×	—	—
<i>Thamnia vermicularis</i>	—	—	—	—	—	—	2	1	—	—	—	—	—	—	—

Nomenclature of vascular plants according to BÖCHER, HOLMEN and JAKOBSEN (1957).

Nomenclature of bryophytes and lichens according to appendix, p. 53.

suspension, and conductance as micromhos per cm, at 20° C., on a 1:5 soil-water suspension.

Exchangeable ions were extracted by leaching with 1M ammonium acetate solution buffered to pH 7. Exchangeable sodium and potassium were estimated by emission spectrophotometry. Exchangeable calcium and magnesium were determined on the same leachate by E.D.T.A. titration. Ca and Mg were first collectively estimated using Eriochrome black T as indicator and then Ca only using H H S N N as indicator. Exchangeable manganese was determined colorimetrically using the method of sodium paraperiodate oxidation in phosphoric acid solution. Colour density was estimated with a Coleman photoelectric colorimeter at a wavelength of 540 mμ. Total exchangeable capacity was determined by sodium saturation (c.f. JACKSON 1958, p. 65). 'Inorganic phosphorus' is the amount soluble in 0.2 N sulphuric acid after 24 hours, measured as molybdophosphoric blue colour.

The results of these soil analyses are presented in table 7.

The most open communities, which are also the most species-poor, are those from localities 10 and 17, the former locality being illustrated in fig. 44. This is on frost shattered limestone slopes and 17 on a fine

Table 7.
Chemical analyses of soil samples from localities described floristically.

Sam- ple num- ber	pH	Con- duct- ance	Hu- mus %	m. eq./100 g soil					Total ex- change- able metals	Cation capa- city	Base sa- tura- tion %	Inor- ganic P (mg/ 100 gms. soil)
				Ca	Mg	Na	K	Mn				
1	6.4	48	3.6	10.40	1.00	0.11	0.17	0.03	11.71	21.11	55.5	28.7
2	6.0	26	2.5	8.26	0.67	0.11	0.22	0.02	9.28	20.00	46.4	20.0
3	6.3	48	6.7	15.80	0.20	0.10	0.30	0.06	16.46	32.00	51.4	26.2
4	6.3	32	3.8	11.80	0.20	0.11	0.15	0.04	12.30	22.86	53.8	9.0
5	6.2	33	6.6	11.60	2.00	0.11	0.21	0.02	13.94	30.00	46.4	7.0
6	5.7	22	3.4	5.06	0.27	0.08	0.18	0.01	5.60	18.20	30.8	23.7
7	8.1	82	2.5	16.80	2.10	0.34	0.51	0.10	19.85	15.60	100.0	80.0
8	6.5	22	1.5	4.13	0.54	0.05	0.14	0.02	4.48	10.00	44.8	15.0
10	7.3	45	1.8	7.00	2.40	0.05	0.05	0.04	9.54	7.30	100.0	3.8
11	6.5	62	15.7	28.00	2.40	0.15	0.26	0.05	30.86	53.33	57.8	7.1
14	6.8	48	13.7	28.00	10.80	0.15	0.16	0.01	39.12	53.33	73.3	4.0
15	5.7	32	10.4	11.80	2.00	0.18	0.25	0.02	14.25	45.00	31.7	4.0
16	5.5	21	3.2	4.80	0.93	0.05	0.13	0.03	5.94	18.00	33.0	2.0
17	7.0	22	0.6	12.80	4.60	0.09	0.22	0.02	17.73	31.43	56.4	15.3
18	6.0	64	11.1	21.20	6.80	0.12	0.50	0.06	28.68	43.33	66.2	8.5



Fig. 44. Frost shattered limestone slopes at locality 10, near Kap Petersens, Kong Oscars Fjord.



Fig. 45. Open, species-rich herb mat community on dolerite outcrop at locality 8, Lower E. Skeldal, Kong Oscars Fjord.

scree below a dolerite outcrop. The soil samples from both have a very low humus content, but due to the high base content of the bed-rock the amount of exchangeable cations is not low and this is reflected in the relatively high pH. Inorganic phosphorus is also low in 10. No. 8 (fig. 45) is also from a dolerite outcrop, but here an open, species-rich, herb mat community has developed, with lichens giving a more or less closed cover between the herbs.

The habitat has a close resemblance to the "Dry Disintegrating Summits and Crests ecosystem" described by SØRENSEN (in SEIDENFADEN & SØRENSEN 1937) from E. Greenland. He associates it with areas of crystalline rock, particularly granite gneiss, but the mode of formation by intense frost shattering, is the same in both cases.

Several of the localities, numbers 1, 3, 9, and 19, bear open vegetation poor in phanerogam species, but often relatively rich in lichens. Such habitats have often been called fell field. They are closely related to the mixed barrens described and illustrated by POLUNIN (1948) from south Ellesmere Island. The communities at localities 2 and 4 are closely related to them. They are closed *Dryas* heaths with a continuous lichen cover, the community at locality 2 being developed on a mountain slope and at 4 on a flat, post-glacially raised, fjord floor. It is not clear whether these are later stages in succession to the fell field communities which have been analysed (at localities 1 and 3) or if the latter are degenerative stages from the closed heath type. Two other types of dwarf-shrub heath are included in the communities analysed. At locality 14 the vegetation is a wet, rather open, *Dryas-Salix arctica* heath. The soil has a high humus percentage and a high exchangeable calcium and magnesium content, due to downwash from a limestone outcrop above the heath area. The sample also has a low inorganic phosphorus content. Localities 11 and 15 are both in the continental, inner fjord region and they support a dry heath community, *Rhododendron lapponicum* being a particularly characteristic species. *Tofieldia coccinea* is also present in 15, this being a species restricted to the inner fjords in this area.

Locality 16, which is from a raised beach, has a dry grassland community (using grassland in the wide sense to include vegetation dominated by sedges). *Carex rupestris* is co-dominant with *Dryas* and *Salix arctica*. The base-poor character of the soil is shown by the relatively low pH and conductance; inorganic phosphorus content is also very low. The *Dryas* heath rich in glumiflores mentioned by GELTING (1937) from Clavering Ø is obviously very similar to this community. Locality 18, near the bottom of a steep ravine, has a heath-grassland mosaic community, the floristic list having both heath, e.g. *Vaccinium uliginosum* ssp. *microphyllum*, and grassland species, e.g. *Carex rupestris*. The soil has a relatively high humus content with a high exchangeable cation total and an associated high conductance.



Fig. 46. Hummock marsh at locality 5, Lower E. Skeldal, Kong Oscars Fjord, looking north to Traill Ø. *Cassiope tetragona*, *Dryas* and *Salix arctica* dominant on hummocks.



Fig. 47. Clay area patterned by solifluction, locality 7, Lower E. Skeldal, Kong Oscars Fjord. Vegetation, with flowering *Dryas* dominant, restricted to the peripheries of the polygons.

Localities 5, 6, and 7, all from Lower East Skeldal, show a wide range of habitat conditions and vegetation. Five, which is illustrated in fig. 46, bears a hummock marsh community with hummocks up to 2 m across, separated from one another by channels with surface water. The channels support an open vegetation of scattered *Eriophorum triste*, *Equisetum arvense* and *Carex bigelowii* plants, with *Scorpidium scorpioides* as the dominant bryophyte. The hummocks themselves support a heath vegetation with a very rich bryophyte flora. Locality 6 is a bank cut by a stream into an old alluvial deposit. It bears an open herb community rich in lichens. Locality 7 is an old marine clay area now strongly patterned by solifluction. It is shown in fig. 47. It only bears vegetation along the margins of the polygons, which have an average diameter of about one metre. The vegetation is a rather species-poor heath with *Dryas* dominant. The soil analysis shows that the clay is strongly saline, having about three times as much exchangeable sodium as any other sample. The value for exchangeable calcium is higher than the total determined cation exchange capacity, which is almost certainly due to the presence of free calcium carbonate. It is, no doubt, derived from mollusc shells which can be commonly found in a more or less complete state in the clay. The values for exchangeable potassium and manganese are also the highest recorded in the samples. As expected from these figures the sample has the highest pH and conductance found in the samples analysed. A very similar community in Svalbard, developed on boulder clay, is illustrated by SUMMERHAYES & ELTON (1928).

It is clear from these comments and tables 6 and 7 that *Dryas* is present in a considerable range of communities and grows under a variety of soil conditions in the field study area. SUMMERHAYES & ELTON (1928) have discussed the soil requirements of *D. octopetala* in Svalbard and state that, although it is apparently indifferent to the presence of calcium as such in the soil, "it cannot tolerate an acid reaction". The pH range in my samples is from 5.5 to 8.1, which may indicate that *Dryas* in East Greenland has a greater tolerance to variation in soil conditions.

LUNDE (1962), however, has recorded a variation in the pH of soil samples from the rooting layer of *D. octopetala* plants of from 4.5 to 8.3, in his investigations in the Troms area of N. Norway. This species together with *Cassiope tetragona* showed the greatest variation in pH of the 17 species studied in this respect in the area.

It has not been possible (see section V, p. 33) to find any correlation between the population composition and any ecological factors which have been measured. The proportions of both species and the intermediate types do not, as far as can be seen, depend on a particular vegetation type or soil conditions.

VII. CYTOLOGY

Buds from plants with crenate leaves both with and without branched hairs, were fixed in the field in a mixture of 3:1 alcohol, glacial acetic acid. Squash preparations were made and stained with orcein. In all cases observed, except one, meiosis was regular with nine bivalents at first metaphase. In one P.M.C., from a plant without branched hairs, an anaphase bridge was seen at second metaphase. The very low frequency of irregularities is reflected in the high percentage of stainable pollen. Thus plants with and without branched hairs from locality 4 had percentage good pollen stainabilities of 92–95 % and 94–100 % respectively. This high pollen fertility may be a result of high fertility of the original hybrids as is known in a number of species groups; alternatively if the original hybrids had a high degree of pollen sterility hybridization has presumably continued for a sufficient time for selection of populations characterised by a low percentage of irregularities in meiosis.

JØRGENSEN, SØRENSEN & WESTERGAARD (1958) have studied P.M.C. material from Clavering Ø, N.E. Greenland and record $n = 9$ in first metaphase. No irregularities are mentioned. BÖCHER & LARSEN (1950) have made one count of *D. integrifolia*, from Ivigtut, S.W. Greenland and here $2n = 18$ also. These Greenland counts are the same as counts which have been made elsewhere over the range of the genus, except for a count of $2n = 36$ made by BÖCHER & LARSEN (1955) from plants at Col du Pillon, Switzerland. This is regarded by BÖCHER (1959) as an example of an accidental tetraploid strain to be regarded as an example of differentiation at the racial level only.

VIII. DISCUSSION

It seems clear that the population structure found both by the field measurements and the population sampling can best be explained by a process of introgressive hybridization between *D. integrifolia* and *D. octopetala*. All the specimens except for those which have large punctate glands on the upper surface of the leaves, can be referred to these two types or are to some degree intermediate between them. Since plants with large punctate glands have been found as a component of a population which is otherwise similar to others in the area it seems best to regard them as a variation within *D. octopetala*. It seems likely that the herbarium specimens of this form seen were collected from similar mixed populations because in all cases non-glandular specimens from the same recorded locality are present.

It has not been possible so far to carry out experimental crossings using Greenland material, but crosses between *D. integrifolia* from Canada and European *D. octopetala* have given seed which has a variable, but substantial germination. These plants are not large enough to make morphological observations, nor have they flowered yet.

HULTÈN (1959) has also come to the conclusion, from a study of herbarium material, that '*D. chamissonis*' and *D. crenulata* in Greenland are hybrids of *D. octopetala* and *D. integrifolia*, the former name having been given to broad leaved and the latter to narrow leaved hybrids, both with completely crenated leaves without branched hairs.

The process causing this variational pattern has been called introgressive hybridization in this paper and it is necessary to discuss whether or not it may be regarded as an example of this process. HEISER (1949) in his review of natural hybridization defines introgression as 'the transfer of genes from one species to another by means of hybridization and backcrossing'. It is clear that the variation described fits this definition. STEBBINS (1959), however, has also considered this process and regards three phases as being essential, these being (a) the initial formation of F_1 hybrids, (b) their backcrossing to one or the other of the parental species, and (c) natural selection of certain recombinant types. This third point further restricts the use of the term introgression, in comparison with both HEISER's definition and that of ANDERSON (1949) in his mono-

graphic survey. ANDERSON takes as his basic example the classic work of RILEY (1938) on hybridization between *Iris fulva* and *Iris hexagona* var. *giganticaerulea* in the Mississippi Delta. Here no evidence is presented for selection of particular recombinants and one population (H1) contained a complete range of intermediates between the two parental types. It does not, therefore, seem justifiable to limit the use of the term introgression in this way. This is not to say that selection does not frequently take place. ANDERSON stresses that hybridization is limited by the number of intermediate habitats available between those of the parental species. If, however, there is either a full range of intermediate habitats, or, if both the parental species are present together in a number of habitats, habitat restriction will not necessarily be a limiting factor.

ANDERSON (1953) in a review of introgression has divided the examples known into two groups, depending on whether they exhibit sympatric or allopatric introgression. Sympatric introgression is defined as involving species which have much the same geographical distribution, but are separated ecologically. Breakdown of these ecological barriers allows introgression to take place. Allopatric introgression occurs between those species which were originally native to different areas. ANDERSON (l.c.) has pointed out the importance of this latter type of introgression in speeding up evolution and in creating a wide band of intermediates many kilometres wide.

In Greenland it seems reasonable to suppose that the situation in *Dryas* is a result of allopatric introgression, the two species at one time having been separated. The question of the directions of migration of the Greenland flora is very difficult, but it seems credible that *D. integrifolia* is a western species, which immigrated from Canada and spread round Greenland to be isolated at some time in the Angmagssalik area, possibly in the last Glacial period as suggested by BÖCHER (1956). This hypothesis is based mainly on the fact that *D. integrifolia* is not found east of Greenland while having an extensive North American distribution. The origin of *D. octopetala* is far more problematic, but it seems more likely to have immigrated from the East than from the West since *D. octopetala* is not found in the eastern part of Canada. There are two possible immigration routes from the East, one from Iceland and the other from Svalbard, both these islands being on undersea ridges between Greenland and Europe. *D. octopetala* on Svalbard is very similar to Greenland material in leaf morphology, whereas that from Iceland has large leaves and is more similar to material from the Faeroe Islands and Britain. It therefore seems more likely on this evidence that *D. octopetala* immigrated across the northern ridge from Svalbard. This hypothesis has also been put forward by SEIDENFADEN & SØRENSEN (1937) p. 157, who also suggest that *D. integrifolia* is the older species in Greenland.

At present it seems best, for the reasons outlined above, to regard the two species as being originally allopatric, but without strong sterility barriers so that when they came into contact introgression took place. This process seems to have continued to the present day and has undoubtedly been of great evolutionary significance in an area of rapid climatic shifts and unstable habitats.

The question arises as to how widespread introgression is between *D. octopetala* and *D. integrifolia* in Greenland. The map of herbarium specimens (fig. 17) shows that intermediate specimens are found over the whole range of *D. octopetala* i.e. from N.W. Greenland around the north and east coasts to the southern limit on the Blosseville coast, a distance of some 3000 km. It therefore seems probable that introgression takes place over the whole range of *D. octopetala* in Greenland.

Similar variation patterns in *Dryas* to those described for Greenland have been recorded from other areas e.g. Alaska and Yukon (see HULTÈN 1959) thus pointing to similar processes being at work in these areas.

It is possible to regard the East Greenland *Dryas* populations as being composed of a single, variable species, as in fact a number of authors have done (see Introduction). DOBZHANSKY (1941) has suggested this as one result of introgression although in general this seems to be uncommon as a number of barriers may act to preserve the integrity of the parent species. HEISER (1949) has discussed these in some detail. There is no evidence in *Dryas* for, or against the existence of some of the barriers e.g. partial sterility, while for others e.g. differences in flowering time, there appear to be no real differences between the species.

It is clear from the evidence presented that only a few characters really separate *D. octopetala* and *D. integrifolia*. These are leaf crenation, presence or absence of branched hairs and to a lesser extent the ratio of leaf breadth at the middle to that at the base of the leaf. It is, however, possible to define them taxonomically on this basis. There are also striking differences in the general distribution, *D. integrifolia* being the only taxon over Eastern and Central Canada while at least in Europe *D. octopetala* only is present.

From the viewpoint of experimental taxonomy it seems clear that the two lie on the borderline between ecotypes and ecospecies as defined by CLAUSEN et al. (1945). In discussing these categories VALENTINE (1949) has pointed out the difficulties in coming to a conclusion about several critical cases. Thus D. LÖVE (1944) investigated *Melandrium album* (MILL.) GARCKE and *Melandrium rubrum* (WEIG.) GARCKE and found that they were completely inter-compatible and inter-fertile; she therefore came to the conclusion that they were ecotypes and subspecies of one species. More recently BAKER (1948) studying these forms in Britain found introgression between them, but points out that although

M. rubrum is native in Britain, *M. album* is a recent invader found only on cultivated ground. The two have thus only been brought together by man's activities and VALENTINE therefore regards them as incipient ecospecies, which had they been isolated longer, might have developed a genetical isolation mechanism. In the case of *Dryas* there is no evidence as to whether there is any degree of genetical isolation, but if any does exist it is clearly incomplete. It is therefore possible to regard the two as ecotypes of a single ecospecies. Due to the differences in distribution, however, it seems best to regard them as incipient ecospecies, which in the areas where they are isolated, may develop a genetical isolation mechanism in time.

From a taxonomic point of view it is a matter of opinion whether they should be given subspecific or specific status. This is a question which has often arisen with taxa having a circumboreal distribution. In the case of *Dryas* a separation on the species level seems most reasonable and here SIMMONS (1906) has summed up the situation in the following words: "To a plant form, which has a great continual area of distribution, where it totally excludes another allied one, which on the other hand, is the ruling one in other equally wide tracts with similar conditions of life, I must, for my part, concede the right of being looked upon as a good species, even if the morphological characters are not so very distinct".

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APPENDIX

Authorities of bryophytes and lichens

- Aulacomnium turgidum* (WG.) SCHWAEGR.
Barbula recurvirostris (HEDW.) DIX.
Brachythecium groenlandicum (C. JENS.) SCHLJAK.
Brachythecium salebrosum (WEB. & MOHR) BR. & SCH. var. *binervulum* BRYHN.
Brachythecium turgidum (HARTM.) LINDB.
Bryum argenteum HEDW.
Campylium stellatum (HEDW.) J. LANGE & C. JENS.
Ceratodon purpureus (HEDW.) BRID.
Cnestrum alpestre (WAHLENB.) NYH.
Dicranoweisia crispula (HEDW.) LINDB.
Dicranum scoparium HEDW.
Dicranum spadiceum ZETT.
Distichum capillaceum (HEDW.) BR.
Ditrichum flexicaule (SCHLEICH.) HAMPE
Drepanocladus badius (HN.) ROTH
Encalypta alpina SM.
Encalypta brevicolla BRUCH
Encalypta rhabdocarpa SCHWAEGR.
Fissidens osmundoides HEDW.
Hypnum bambergeri SCHIMP.
Hypnum revolutum (MITT.) LINDB.
Isopterygium pulchellum (HEDW.) BROTH.
Meesia uliginosa HEDW.
Mnium hymenophylloides HÜB.
Myurella julacea (HEDW.) BR. & SCH.
Oncophorus wahlenbergii BRID.
Orthothecium chryseum (SCHWAEGR.) BR. & SCH.
Orthothecium strictum LOR.
Orthotrichum killiasii C. MUELL.
Pohlia cruda HEDW.
Pohlia gracilis (SCHLEICH.) LINDB.
Pohlia c. f. nutans (HEDW.) LINDB.
Pogonatum capillare (MICHX.) BRID.
Polytrichum alpinum HEDW.
Polytrichum juniperinum HEDW.
Polytrichum piliferum HEDW.
Polytrichum strictum SM.
Stegonia latifolia (SCHWAEGR.) VENT.
Tomenthypnum nitens (HEDW.) LOESKE
Tortella fragilis (DRUMM.) LIMPR.
Tortula ruralis (HEDW.) SCHWAEGR.
Blepharostoma trichophyllum (L.) DUM.
Odontoschisma macounii (AUST.) UNDERW.
Riccardia pinguis (L.) S. F. GRAY
Sphenolobus minutus (CRANTZ) STEPH.
Bacidia c. f. muscorum (SW.) MUDD
Buellia disciformis (FR.) MUDD var. *muscorum* (HEPP) VAIN.
Candelariella epixantha (ACH.) SANDST.
Candelariella placodizans (NYL.) MAGN.
Cetraria crispa (ACH.) NYL.
Cetraria delisei (BORY) TH. FR.
Cetraria nivalis (L.) ACH.
Cladonia coccifera (L.) WILLD.
Cladonia pyxidata (L.) FR.
Cornicularia aculeata (SCHREB.) ACH.
Lecanora epibrya ACH.
Lecanora verrucosa (ACH.) LAUR.
Lecidea decipiens (EHRH.) ACH.
Ochrolechia frigida (SW.) LYNGE
Peltigera aphthosa WILLD.
Peltigera rufescens (WEISS) HUMB.
Physcia muscigena (ACH.) NYL.
Solorina bispora NYL.
Solorina octospora ARN.
Stereocaulon alpinum LAUR.
Thamnotia vermicularis (SW.) ACH.

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