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EXPERIMENTAL
AND CYTOLOGICAL STUDIES ON PLANT
SPECIES

IX. SOME ARCTIC AND MONTANE CRUCIFERS

BY

TYGE W. BÖCHER



København 1966
Kommissionær: Munksgaard

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Synopsis

Comparative cultivations and cytological investigations were carried out on a number of arctic or montane species of the genera *Arabis*, *Draba*, *Braya* and *Kernera*. New chromosome numbers were recorded in *Arabis arenicola* ($2n = 16$), *Draba sibirica* ($2n = 16$), *D. lanceolata* ($2n = 32$), *D. gilliesii* ($2n = 48$), *D. aurea* ($2n = 76$), *Braya rosea* ($2n = 42$), *B. alpina* ($2n = 42$) and *Kernera* cfr. *decipiens* ($2n = 14$). In the *Draba cinerea* group the three chromosome levels ($2n = 48$, 64 and 80) are shown to be connected with three taxa for which the names *D. cinerea* Adams, *D. arctica* J. Vahl p. p. ssp. *groenlandica* (Ekm.) comb. nov. and *D. arctica* J. Vahl p. p. are used. *D. arctogena* Ekm. is connected with *D. norvegica* by transitional forms. Both are maintained as species but seem to belong to the same group and not to the *D. cinerea* group. In *D. glabella*, races with $2n = 64$ and 80 have been studied, but so far it has not been possible to divide the material taxonomically into two entities corresponding to the two chromosome numbers. *D. aurea* has a very deviating chromosome number, $2n = 76$, or perhaps $2n = 72 + 4$ extra chromosomes. Clear evidence of small supernumerary chromosomes (B-chromosomes) however, was only found in *D. norvegica*. The material of *Braya rosea* deviates sharply from the description of the type and deserve a closer taxonomical study. In *B. linearis* two strains with B-chromosomes occurred and one of them from Junkerdal in Norway deviated morphologically from the other strains. As this race also can be distinguished in herbarium material it has been described as a new variety (var. *meizophylla*). In *B. novae-angliae*, strains from Colorado and W. Greenland had the same chromosome number ($2n = 56$) but deviated morphologically, the American material belonging to ssp. *ventosa* (Rollins).

In *Draba* there seems to be at least three basic chromosome numbers $x = 8$, 10, and 12 while in *Braya* all species can be arranged in a series with $x = 7$. The evolutionary trends in both genera are discussed on the basis of cytological, morphological and plant geographical evidences. Some of the distributional patterns are illustrated by maps.

1. Introduction

From a taxonomic point of view, some of the most critical genera in the flora of arctic and montane areas are undoubtedly found among the Crucifers. Botanists working in the Arctic agree that the genera *Draba* and *Braya* are particular problematic. In other groups, e.g. the *Arabis holboellii* complex, the situation is complicated by the occurrence of apomixis.

A critical study of arctic *Arabis*, *Draba* and *Braya* was made by GELERT as early as 1898. *Draba* has been studied thoroughly by EKMAN 1912–1941, POHLE 1925, SCHULZ 1927, FERNALD 1934, and HITCHCOCK 1941. More important works and papers concerning *Braya* were published by OSTENFELD 1923, SCHULZ 1924, ABBE 1941, ROLLINS 1953, SØRENSEN 1954, and BÖCHER 1956.

In spite of this extensive taxonomic and cytological literature, our knowledge of these arctic-montane Crucifers is unsatisfactory. We have no real understanding of the micro-evolutionary dynamics which are responsible for the complexity nor the evolutionary trends and the processes leading to species formation. Experimental hybridizations as done by WINGE (1933, 1940) in *Erophila* is one of the most urgent tasks.

The present study is mainly cytotaxonomical. Its purpose is to create a basis for experimental crossings by limiting or elucidating the problems.

The study was considerably facilitated by the improved cultivation possibilities available in the Arctic Greenhouse in the Copenhagen Botanical Garden. This greenhouse was granted by the Carlsberg Foundation and the Rockefeller Foundation.

For material placed at my disposal for the present investigation I wish to express my sincere thanks to Drs. T. T. ELKINGTON, NIELS FOGED, BENT FREDSKILD, KJELD HOLMEN, KNUD JAKOBSEN, MARTIN LEWIS, Professor H. MERXMÜLLER, and Professor TH. SØRENSEN. I am also indebted to the curators of the museums in Bergen, Copenhagen, Stockholm, and Uppsala for loan of important collections of *Draba* and *Braya*. Correction of the english was kindly undertaken by Dr. MARTIN LEWIS, Birmingham.

2. *Arabis*

Arabis arenicola (Rich.) Gelert and *A. petraea* (L.) Link

Material of *Arabis arenicola* from two localities in continental West Greenland has been cultivated in the arctic greenhouse and in pots in frames at the experimental field. The species is not easy to cultivate even in the arctic house as the plants

sometimes die after luxuriant flowering. In pots at the field the plants form small dense cushions with small leaves and few short flowering stems and are also inclined to die after two or a few years.

Chromosome number. Both strains (Cult. No. 4851 from head of Sdr. Strømfjord and No. 6064 from Nunatarujuk at the head of Arfesiorkfjord) had $2n = 16$ or $n = 8$ and quite normal meiosis. (Figs. 1a–b and 10e). The number is the same as that in *A. petraea* (L.) Link. which has been cultivated simultaneously (No. 28 see below) and was already counted by BÖCHER & LARSEN (1950).

Variation. The two strains of *A. arenicola* differed from each other and from *A. petraea* in a number of characters which may be summarized as follows.

No. 4851: First year rosettes vigorous. Second year flowering shoots (5) 8–14 cm long, ascending or \pm upright. Diameter of largest flowers 4–5 mm. Siliques up to 2.1 cm long and 2 mm broad \pm ascending. Leaves \pm entire. 3–5 stem leaves.

No. 6064: First year rosettes slender, second year flowering shoots 7–13 cm long, prostrate. Diameter of largest flowers 4–4.5 mm. Siliques up to 2.0 cm long and 1.7–2.0 mm broad, spreading. Leaves more light green, smaller and sometimes with few shallow incisions. 2–3 stem leaves.

A. petraea (No. 28) from Falljökull in Iceland has also \pm prostrate shoots, but the plants are much larger than those of the two strains of *A. arenicola* and the flowers attain almost double the size. Furthermore the incisions in the rosette leaves are deeper and more numerous. The plants are easy to cultivate.

GELERT (1898) who referred the *Eutrema arenicola* of RICHARDSON, and the *Sisymbrium humifusum* of J. VAHL to the same species of *Arabis*, viz. *A. arenicola*, has discussed the relation between the latter and *A. petraea*. He concludes that the two species replace one another geographically and that *A. arenicola* possibly is a rather young species having evolved from *A. petraea*.

This opinion, however, is not supported by the observations referred to above. Both species are diploids and any estimate of their evolution must therefore at the moment rest upon geographical data.

Arabis petraea is a north-Atlantic European species; it occurs in Iceland, the Faroes, Scotland, Wales, Scandinavia, North shore of lake Onega as well as in the mountains of Central Europe. In Scandinavia its peculiar, disjunct range was studied and mapped by HOLMBOE (1936: 22–24) who concludes that there is every indication that in Norway it must be considered as an interglacial “winterer”. The range of *A. arenicola* is also interesting. It is a NE-American-Greenland endemic (A. E. PORSILD 1964 map 197), today almost exclusively found in areas which previously were glaciated; its present area is also disrupted. Both species are exclusive to open rocks, moraines or sands and show clear preference for basic soils often rich in minerals (serpentine soils, basalt soils etc.). Today in West Greenland *A. arenicola* grows abundantly along the margin of the Inland Ice. It behaves as a glacial plant able to follow retreating ice sheets and fitted for glacial conditions. Similarly *A. petraea* according to HOLMBOE probably reached its stations in the skerries of Ångermanland by late glacial migration from Trøndelag.

It is a striking feature that there are no records of *Arabis arenicola* on the basaltic East Coast of Greenland opposite Iceland (see map in BÖCHER 1952 fig. 9) which would probably be the case if this species had developed from *A. petraea*. Although clearly related the two species are very distinct and neither of them probably young species. If they, as is most likely, are periglacial survivors *A. petraea* has spread from a refuge of an oceanic type (e.g. in Iceland and in Norway) while *A. arenicola* came from continental refuges in Ellesmere-Greenland; the two species became adapted to very different climatic conditions and are therefore allopatric in our day.

3. *Draba*

Draba fladnizensis Wulfen and *D. lactea* Adams

These two species are undoubtedly related. While POHLE (1925: 84) unites them in one species, most recent authors separate them, as did ERMAN 1932. Chromosome investigations clearly show that they are distinct.

Draba fladnizensis seems to be one of the basic diploids within the subsection *Euleucodraba*. $n = 8$ has been counted in material from Dovre (Norway), HEILBORN (1927: 60), NE Greenland (JØRGENSEN et al. 1958: 69), and the Alps (MERXMÜLLER & BUTTLER 1965). The same number also occurs in Spitzbergen. Seeds were collected there by NIELS FOGED 1958 in the Advent Valley (Hotelnæsset $78^{\circ}15'$ lat. N. $15^{\circ}30'$ E.) and plants were grown in the Arctic Greenhouse (Cult. Dr. 8). They resembled *D. lactea* in growth habit but had only simple hairs, mainly as marginal cilia on the basal leaves. JØRGENSEN et al. found some variation in size of the bivalents. The mitotic metaphases studied by the present author (Fig. 1o) do not show much variation in chromosome size indicating that the differences found during meiosis may be due to variation in the number of terminalized chiasmata.

Draba lactea is hexaploid ($n = 24$) according to JØRGENSEN et al. This interesting result based on material from NE Greenland can now be corroborated, again in Spitzbergen material collected by NIELS FOGED. (Two stations in Van Keulenfjord $77^{\circ}37'$ lat. N., $14^{\circ}55'$ E., cult. Nos. Dr. 2 and Dr. 5).

The relation between the two species was discussed by HULTÉN (1958: 226) in connection with his mapping of their world ranges. HULTÉN assumes that the two species cross freely where they are sympatric or rather that *D. lactea* constitutes a hybrid series formed by crossings between *D. fladnizensis* and *D. nivalis*. He has seen a complete series of transitional forms between these two species, in which *D. lactea* occupies a central position. HEILBORN (1927) gives an analysis of the hybrid between the two diploids *D. fladnizensis* and *nivalis*. In spite of the fact that the hybrid had entirely abortive seeds, meiosis in the anthers proceeded normally. EKMAN (1932: 440) also refers to this hybrid and says that it is always sterile.

The available evidence therefore makes any explanation of *D. lactea* as a primary hybrid, unlikely. On the other hand much is in favour of the view that it is an

allohexaploid and a well established balanced species. Morphologically it is much closer to *D. fladnizensis* than to *D. nivalis*, a fact which suggests that it arose after doubling in a triploid hybrid having two '*fladnizensis*' genomes (from an unreduced gamete) and one '*nivalis*' genome.

In this connection some deviating specimens of *D. lactea* from Niaqorssuaq in Nordre Strømfjord, W. Greenland (Altitude 500 m, TWB 1958 No. 812) deserve mention. The rosette leaves have the same mixed pubescence as in *D. lactea*, but the lower part of the stem has a thin covering of very small stellate hairs. The plants seem to be fertile. Such plants and many others belonging to the transitional series mentioned by HULTÉN may not to be new hybrids (back crossings) but the result of some kind of structural change in the chromosomes of the allohexaploid resulting in the occurrence of stellate hairs on the stem, a character which is usually masked in *D. lactea*.

D. lactea has a circumpolar range similar to that of *D. nivalis* but unlike *D. fladnizensis* which is arctic-alpine (montane) and has many disjunct areas. One such area is found in NE Greenland, another in West America. HITCHCOCK (1941) mentions it as a rare plant on the highest peaks of Colorado and Southern Utah and from British Columbia; he adds that the widely separated localities must represent relic stands.

In culture, under uniform conditions, *D. fladnizensis* and *D. lactea* showed clear size differences during flowering (Table 1). The dimensions found in the Arctic Greenhouse were generally smaller than those given by EKMAN (1932) in the diagnose. *D. lactea* flowered a little earlier. Both species produced elongated racemes with short peduncles.

TABLE 1.

Species	<i>Draba fladnizensis</i>	<i>Draba lactea</i>	
Cult. No.	Dr. 8	Dr. 5	Dr. 2
2n	16	48	48
Height of plants cm	3.0-4.0	4.5-6.5	5.0-8.0
Length of sepals mm	1.4-1.5	1.6-2.0	1.6-2.0
Length of petals mm	2.0-2.2	2.8-3.3	2.6-3.0
No. of stem leaves	0-1	0	0
Length of rosette leaves mm	9-11	8-10	8-11
Length of longest cilia at leaf margins mm	0.5-0.6	0.8-1.0	1.0-1.1
Stellate hairs on rosette leaves	none	present	present

***Draba lanceolata* Royle**

This species seems to be identical with *Draba stylaris* J. Gay and *D. thomasii* Koch, see FERNALD (1934: 359). MERXMÜLLER & BUTTLER (1965), however, still uphold *D. stylaris* and have found $2n = 32$ in this taxon from Engadin; this is the

same number as found in the closely related *D. incana* L. from localities in Europe and Greenland. Material of *D. lanceolata* from Angujårtorfik in the hinterland at Søndre Strømfjord, W. Greenland, was also tetraploid ($n = 16$, see Fig. 1c). Thus the entire *D. incana*-complex seems to be tetraploid.

In Greenland *D. incana* and *D. lanceolata* are vicarious, being largely allopatric (BÖCHER 1952 fig. 32 and p. 26). *D. incana* has an atlantic subarctic distribution and is very common in South Greenland. *D. lanceolata*, on the other hand, is confined to continental Central W. Greenland and the interior of the Scoresbysund fjord system. It was recently refound there by HOLMEN and LÆGAARD; an older collection from the same area by N. HARTZ (as *D. arctica*, Head of Gåsefjord, June 2nd 1892) belongs to *D. lanceolata*. The locality in question is described by HARTZ (1895: 248–249). It occurred on moraine soil, probably together with *Calamagrostis purpurascens* and *Kobresia myosuroides*, two species which very frequently occur together with *D. lanceolata* in W. Greenland.

The two species *D. incana* and *D. lanceolata* seem to hybridize in the narrow zone where they are sympatric. In Greenland there are a few transitional forms e.g. in the Godthåbsfjord area.

The Greenland material of *D. lanceolata* (Cult. No. 4884) was grown in the Arctic Greenhouse and in pots at the experimental field together with *D. cinerea*, *D. norvegica* and *D. glabella*. The meiosis in *D. lanceolata* was completely regular. In a young stage there was a good deal of resemblance between *D. lanceolata* and *D. cinerea* but in a flowering fruiting stage these two species are easily distinguished (Plate IV). *D. lanceolata* is coarser, with narrower and longer siliques which are often somewhat contorted. The characters of the cultivated plants appear from Table 3a. They deviate in having only 3–6 cauline leaves, while very often 4–10 are found in herbarium material from other places. They have a dense covering of small stellate hairs but also bear unbranched hairs particularly on the petioles and main stems. The morphological resemblance between *D. lanceolata* and *cinerea* will be discussed below. It may, however, already be pointed out that they also show clear ecological affinities. Both have a low-arctic continental distribution in Greenland and there occur in steppe-like communities.

***Draba norvegica* Gunn. and *D. arctogena* Ekm.**

These two species have much in common. Both have a heterotrichous pubescence and broad, rather short siliques and both are hexaploids.

Draba norvegica. Earlier chromosome counts were made by HEILBORN (1927: 61, 1941: 142) who found $n = 24$ in material with glabrous siliques (Dovre and Jotunheimen, Norway) and in plants with hairy siliques (Scotland, Kisteskarstnuten in Norway, Jämtland in Sweden and Godhavn on Disko, W. Greenland).

Here, material from two West Greenland localities (No. 4772 from Østerlien at Godhavn and No. Dr. 9 from Tupilaq at Egedesminde) has been cultivated and

studied cytologically. Both showed $n = 24$ during meiosis and both had comparatively large flowers (sepals 2.1–2.3 mm, petals 4 mm long, cp. ssp. *grandiflora* Ekm., see EKMAN 1941: 140) a mixture of hair types on the leaves, and broad siliques with mainly bifid hairs (see further Plate Id and Table 2).

Cytologically Dr. 9 differed from 4772. The latter had a regular meiosis (Fig. 1 e–g) although sometimes two pairs were situated so closely together that they might be interpreted as a quadrivalent. One cell had 23 bivalents and 2 univalents (Fig. 1 g). Dr. 9 was interesting in the occurrence of two pairs of minute B-chromosomes. They seemed to be heterochromatic in as much as four minute dark bodies were observed in many resting nuclei. However, they were often difficult to detect during meiosis and may be absent from some of the PMCs (e.g. Fig. 1 h). Figs. 1 i–m show their behaviour at Metaphase I and Telophase I–II. In ana- and telophases the small chromosomes were only seen in cases where they were lagging; Fig. 1 l shows that two of them may even occasionally form a bridge-like configuration.

Draba arctogena. Unfortunately no material was available for cultivation but a comparison of two collections of plants with known chromosome number ($n = 24$) gives some important information.

The material studied cytologically by HEILBORN (1941) was presumably collected by EKMAN at Godhavn (see EKMAN 1929: 490). It corresponds to the type collections kept in the Naturhistoriska Riksmuseet in Stockholm (Plate Ia). These consist of two sheets. Those specimens marked on the label as *D. arctogena* sp. n. were collected on July 26th 1923 in Lyngmarksfjeldet, above Godhavn, Disko. The plants are 12–14 cm high with one stem leaf only. The short pedicelled siliques are up to 9 mm long and 2.5–3.5 mm broad, with a pubescence of bifid hairs. In habit, it is very similar to *D. norvegica*, the main difference being the greater density of the hairs on the leaves.

The plants studied by HOLMEN (1952) originate from Peary Land (Brøndlund fjord, HOLMEN No. 6551). It is a high arctic “condensed” plant, 3.5 cm high with 0–1 stem leaf. The basal leaves are densely covered with long unbranched hairs hiding the mid-nerve. The stems have a mixed pubescence although simple or bifid hairs predominate, but the hairs on the siliques are stellate. The sepals attain a length of about 2 mm and the petals 3–3.5 mm.

A comparison of all high arctic collections of *D. arctogena*, e.g. those studied by HOLMEN (1957: 55–56), shows that the siliques have a mainly stellate type of pubescence. This is also the case with the specimen collected by FREUCHEN (Plate Ib Table 2) which has been determined by EKMAN as *D. arctogena*.

A further examination of hebecarp *D. norvegica* and *D. arctogena* from Greenland shows that the siliques almost always have a mixed pubescence but that the bifid and unbranched hairs predominate in *D. norvegica* and the stellate in *D. arctogena*. There are however, some plants of high-arctic *D. arctogena* (e.g. Rivieradal 80°06' lat. N., leg. SCHWARZENBACH) in which the bifid hairs are most common and some

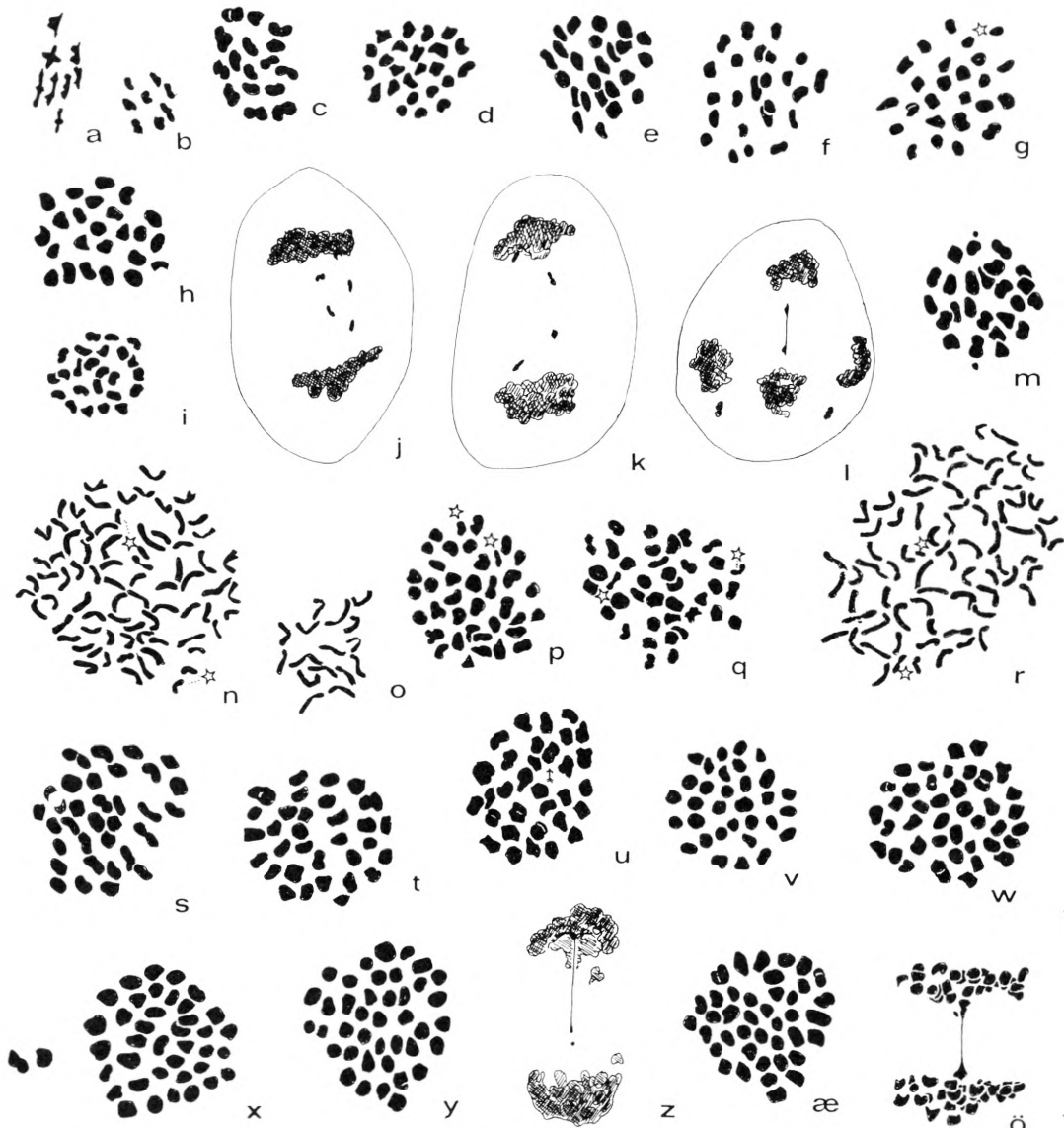


Fig. 1. Chromosomes in *Arabis arenicola* No. 4851 (a-b) and *Draba* (c-ð). — c: *D. lanceolata* (No. 4884, $n = 16$). — d: *D. cinerea* (No. 4813, first anaphase, $n = 24$). — e-g: *D. norvegica* (No. 4772, $n = 24$ (in fig. g one pair of univalents at *)). — h-m: *D. norvegica* (No. Dr. 9, $n = 24 + 4 B$; h and m: first metaphases; i: second metaphase; j-l: telophases I-II showing B-chromosomes; m: the two pairs of B-chromosomes are placed on both sides of the plate of normal bivalents). — n, p-q: *D. aurea* (n , p-q: Nos. 4883; r: No. 4820; $2n = 76$, $n = 38$; particularly small, possibly extra chromosomes are marked with *). — o: *D. fladnizensis* (No. Dr. 8, $2n = 16$). — s-z: *D. glabella*; s-t: No. 6325; u: No. 4814; v: No. Dr. 12; all $n = 32$, in fig. s one pair precociously separated, arrow in fig. u points towards pair displaced from plate; w-z: No. 4788, $n = 40$, in x two displaced pairs drawn separately, in z first telophase bridge and laggard pair. — ð: *D. arctica* (No. Dr. 8b, $n = 40$, in ð first anaphase bridge). — All microtome technique. Scale 10μ .

TABLE 2.

	<i>Draba norvegica</i>		<i>Draba arctogena</i>	
	Cult. 4772	Cult. Dr. 9	Type coll.	Vildtland Plate I b
2n.....	48	48 + ff	48	—
Height in cm	7–8	7–9	9–14	6
Length of ripe siliques mm	6–7	6–7	6–9	5.5–6
Breadth of ripe siliques mm	3.2–3.5	3.3–3.5	2.5–3.5	2.8–3.0
Pubescence of siliques.....	Dense, bifid (-stellate with few large branches)	Not dense, bifid (-stellate with few large branches) subglabrate	Unbranched- bifid	Stellate (-bifid)
Seed length mm	1.1	1.1	1.0–1.1	1.0
Length of lower pedicels mm	3.0	2.0–3.5	2.5	2.0
Leaf pubescence (leaves in all four examples entire):				
Marginal cilia	Unbranched	Unbranched- bifid-stellate	Unbranched (-bifid)	Dense and unbranched
Upper surface.....	Unbranched- bifid	Almost glabrous	Unbranched- bifid, very dense on young leaves	Unbranched (-bifid) very dense
Lower surface.....	Unbranched- bifid-stellate	Stellate-bifid	Unbranched- bifid-stellate, dense on young leaves	Unbranched (-bifid-stellate) very dense

<i>Draba norvegica</i>		<i>Draba arctogena</i>
Stem leaves 0–3	↔	Stem leaves 0–1
Rosette leaves often ± dentate	↔	Rosette leaves entire
Pubescence of rosette leaf surface not dense, some leaves with many stellate hairs, some mainly ciliated	↔	Pubescence of rosette leaf surfaces dense, con- sisting mainly of unbranched hairs, which cover the blades
Siliques usually with mainly bifid hairs	↔	Siliques usually with mainly stellate hairs
Inflorescence mostly elongated	↔	Inflorescence usually only slightly elongated
Low-arctic oceanic	↔	High arctic continental

northern *D. norvegica* plants which also have stellate hairs. According to POHLE (1925: 97) the siliques in *D. norvegica* can have unbranched, bifid or stellate pubescence.

In many respects the transition from *D. norvegica* to *D. arctogena* is clinal, which can be expressed in the scheme following Table 2.

EKMAN (1929: 489) in comparing *Draba norvegica* and *D. arctogena* remarks the pubescence in the latter is much denser. Moreover *Draba norvegica* in

summer develops leaves with stellate hairs and has some dentate leaves. In cultivated specimens of *D. arctogena* only the first eight or nine leaves had stellate hairs and the simple ones appeared already on the tenth or eleventh leaf whereas in *D. norvegica* they made their first appearance with the 25th leaf. Considering the fact that the appearance of unbranched hairs in *D. norvegica* varies considerably (this was later shown by EKMAN (1941: 137)), it seems as if *D. arctogena* might be interpreted as one extreme in a clinal series including both species.

EKMAN (1929) first included *D. arctogena* within *D. groenlandica* as a variety of the latter. But *D. groenlandica* is an octoploid and it belongs clearly to the *D. cinerea* group to which *D. arctogena* scarcely belongs. In any case, the type of pubescence and the habit of *D. arctogena* bears no resemblance with those of hexaploid *D. cinerea*.

The Greenland distribution of *D. norvegica* and *D. arctogena* is of great interest. A detailed map of the Greenland area of *D. norvegica* is found in BÖCHER (1963) while HULTÉN (1958) gives a map of its total range. *D. norvegica* can be classified as north-atlantic low-arctic. In sharp contrast to this *D. arctogena* is high-arctic-continental. It is common in the interior of Peary Land (HOLMEN 1957) and extends south to the nunataks of NE-Greenland (SCHWARZENBACH 1961). In the west it reaches NW-Greenland and Ellesmereland. There are no records between the Thule district and the two occurrences on Disko and at Holsteinsborg. On the map Fig. 5 these two stations are indicated by a special symbol as the specimens in question (hence even the type collection) are transitional between this species and *D. norvegica*. Both stations lie within the northern part of the range of *D. norvegica* where in all probability typical *D. arctogena* is very rare and high-montane as in NE-Greenland. Altogether it is highly probable that the two species where they are sympatric show signs of hybridization or introgression.

At present I am against a reduction of *D. arctogena* to subspecific level. It differs strongly from *D. norvegica* in ecology (distributional type) and it is most likely a comparatively old species with a total area which is almost identical with that of *Braya thorild-wulffii* (see p. 69) and other high arctic relics. Perhaps it survived the last ice-age in ice-free areas in Ellesmere-North Greenland and has only relatively recently come into contact with its southern relative, *D. norvegica*.

Draba arctogena may have evolved from the same group as *D. norvegica* which in itself is very heterogeneous. A partly independent development, however, is not out of the question. Both species are hexaploids and may have reached that level by allopolyploidy after different crossings of species with $n = 8$ and 16 (or perhaps after fertilization between cells with $n = 16$ and 32).

***Draba cinerea* Adams and *D. arctica* J. Vahl**

The *Draba cinerea* group consists of hexaploids, octoploids and decaploids. One of the main problems concerns the identity of *D. arctica* J. Vahl.

According to EKMAN (1912: 3, 1917, 1929: 484) typical *D. cinerea* Adams is

identical with *D. arctica* J. Vahl, a statement which is not in agreement with POHLE (1925: 71) who like BUSCH (1919) tried to maintain *D. arctica* as a sub-group within *D. cinerea*. SCHULZ (1927) in his monograph even maintains *D. arctica* as a separate species.

POHLE considers *D. cinerea* var. *arctica* (J. Vahl) Pohle to be distinguished from *D. cinerea* by lower stems with fewer leaves, larger flowers and siliques and not so dense a covering of stellate hairs. POHLE's view agrees with that of GELERT (1898: 306) who pictures a specimen of *D. arctica* which has the distinguishing characters mentioned by POHLE. EKMAN (1929) cites the diagnosis of *D. arctica* in order to show how it fits in with the type specimens of *D. cinerea*. But the diagnosis contains no measurements and includes the words "*foliis basi ciliatis*" which EKMAN interprets as "a few cilia at their base". EKMAN neglects the treatment of the group in BUSCH (1919: 382) in which ssp. *arctica* (J. Vahl) Busch is described as follows: "*Folia rosularum basi ciliata. Caules ca. 5–7 cm alti, 2–4 phylli, pedunculi fructiferi 2.5–10 mm lg. Siliculae pubescentes, ca. 6 mm lg., ca. 2.75 mm lt.*" BUSCH clearly puts emphasis, on the cilia and he emends VAHL's description by adding the short length of the stems. BUSCH gives stem length of 14–44 cm for *D. cinerea* ssp. "*normalis*".

In my opinion the character *foliis basi ciliatis* refers to the high arctic type found e. g. in Spitzbergen and collected and mentioned by J. VAHL (see Plate IIa–d and Table 4). EKMAN tries to avoid the difficulties by saying that in her view the synonymy of *D. cinerea* and *D. arctica* was confirmed by the specimens collected by VAHL in Greenland and adds: "Those from Svalbard are less typical".

A closer study of *D. arctica* reveals that the description and picture of the species in Flora Danica (39:1840:5, Tabula 2294, see Fig. 2) refer to two widely different plants which are both cited in the description. VAHL mentions in his description first Umanaq in W-Greenland and later Bellsound in Spitzbergen. His collections from both places are found in the Botanical Museums of Copenhagen and Stockholm.

The Umanaq plants (Plate IIe, IIId) have an elongated inflorescence, short peduncles, short and small siliques, short styles, small dense stellate hairs and (1)–2 stem leaves.

The Bellsound plants (Plate IIa) in the Copenhagen herbarium have been severely damaged, probably by the painter who made the plate in the Flora Danica. They have longer pedicels, siliques, styles and the inflorescences have fewer flowers. The stellate hairs are longer and not very dense and the stems are short with few or no leaves. In the Stockholm herbarium there is one low specimen (Plate IIb) which corresponds to that in Copenhagen and one 25 cm tall specimen (Plate IIc) with an elongated raceme, long pedicels and siliques and one stem leaf only. In all the specimens from Bellsound there are some simple hairs on the pedicels and even along the midribs on the lower surface of the rosette leaves. The cilia on these leaves are far more numerous than in the Umanaq plants, see further Table 4.

The main picture on the plate in Flora Danica (Fig. 2) shows a plant which is intermediate between the two collections. It has stem leaves as in the Umanaq



Fig. 2. *Draba arctica* J. Vahl. The plate 2294 in Flora Danica. The pubescence consists of rather large and not very dense stellate hairs and the siliques have long pedicels as in the Spitzbergen material but 1-2 stem leaves as in the Umanaq material. — Scale 10 cm.

plant while the peduncles and siliques correspond to the Spitzbergen plants. The stellate pubescence on the enlarged silique is also as in the Spitzbergen plants but the style is short as in the Umanaq plants.

This shows that VAHL'S *D. arctica* is an ambiguous entity. It includes partly material which must be referred to *D. cinerea* Adams, partly a high-arctic taxon, which corresponds to POHLE'S *D. cinerea* var. *arctica* and which in the following will be mentioned as *D. arctica* J. Vahl (p. p.).

Thus *Draba arctica* which will be described in detail below has now to be based on the collections by VAHL from Bellsound in Spitzbergen, all three specimens serving as lectotypes.

In the following, the taxa in the *D. cinerea* group are arranged according to their ploidy-level.

***Draba cinerea* Adams**

Cytological studies. HEILBORN (1927, 1941) counted $n = 24$ in material from Umanaq and from "Greenland" (without locality, but presumably also from Umanaq). The same number was found in the var. *brachysiliqua* (Mela) Ekm. from the Ladoga area. Concerning the Umanaq material he says that the plants have a few simple hairs on the petioles and somewhat dentate leaf laminae.

The var. *brachysiliqua* (from Mäkisalo, Karelia ladogensis) has a few long and simple hairs on the leaves which otherwise have a very dense covering of small stellate hairs. EKMAN (1917, 1926:42) takes the simple hairs as an indication of some kind of introgression, but HEILBORN (1927) doubts its hybrid nature and suggests it to be a primitive form within the species complex. It has very short siliques while the stems are tall (14–22 cm) with some simple hairs at the base and 2–3 leaves (see Plate III and Table 3b).

Material with the hexaploid number was also collected by the present author at the head of Søndre Strømfjord (Store Saltø), SW-Greenland and was cultivated in the Arctic Greenhouse over several years (Cult. No. 4813). The meiosis proceeded very regularly (Fig. 1 d). The plants in culture maintain small flowers and short siliques and have a dense covering of small stellate hairs and only very few marginal cilia at the base of the petioles. They have usually two stem leaves, see Plate VIb–c and Table 3c.

JØRGENSEN, SØRENSEN & WESTERGAARD (1958:68) refer to material with $n = 24$ which they have called *D. ovibovina* and material with $n = 40$ which they refer to *D. cinerea*. Unfortunately the dried material corresponding to the two fixations had been mixed. It is clearly the hexaploid number which has to be attached to *D. cinerea*. The plants in question are very small (Plate VI, a) but have two stem leaves. They have the dense covering of small stellate hairs and short siliques. Marginal cilia are present on the lower part of the rosette leaves and a few simple hairs also occur on the basal part of the stems, see further Table 3e.

It is very probable that EKMAN's collection from Umanaq W-Greenland (Aug. 1923, Herb. Stockholm) corresponds to the plants which were counted by HEILBORN. The plants resemble VAHL's collection from Umanaq (Plate III d), the dimensions are given in Table 3 d.

Common to all material which has been studied cytologically and shown to be hexaploid, is the dense cover of small stellate hairs (Fig. 3), the short peduncles, the short siliques and the presence of more than one stem leaf.



Fig. 3. On the left three stellate hairs of hexaploid *D. cinerea* (No. 4813); on the right three of octoploid *D. arctica* ssp. *groenlandica* (K. Holmen No. 6712). — Scale 100 μ .

Typical *Draba cinerea*. According to EKMAN (1929:484) the type of *D. cinerea* from Schigansk has short oval siliques and a fine pubescence of stellate hairs. She found some needles of *Larix sibirica* between the rosulate leaves. It was collected 1817 by ADAMS in "locis montosis sterilibus". Schigansk is on the Arctic Circle and south of the timber line.

The type specimen which is illustrated in EKMAN 1917 (Plate 3) is 27 cm high with 3 stem leaves and a long raceme. It differs from the material which was counted in having long pedicels and narrow siliques which have a tapering distal part and fairly long styles. It is clearly the same plant which is mentioned by BUSCH (1919:381) as "ssp. *normalis*". His drawing on p. 383 shows a specimen 16 cm high with 3-4 stem leaves and a raceme of narrow tapering siliques on long pedicels. The diagnosis says "*Pili simplices desunt*", but a few simple hairs are shown on the drawing.

The Stockholm Herbarium contains several sheets collected by N. H. NILSSON from Asia which resemble the type material in every detail. Some measurements of this material are collected in Table 4. It appears that all the plants have narrow and rather long siliques (4.5-9 mm long, 1.5-2 mm broad) and most often long pedicels and 3-4 stem leaves (Plate IV a-b). They correspond to the material studied cytologically in two respects: The small size of the stellate hairs, the very few cilia and the small flowers and seeds.

TABLE 3. *Draba lanceolata* – *cinerea* – *arctica*.

Taxon	Reference to text	2n	Height in cm	Length of rosette leaves mm	No. of stem leaves	Length of longest siliques mm	Length of styles mm
<i>D. lanceolata</i>	a	32	13–21	10–12	3–6	10.5(9–11)	0.3(0.2–0.4)
<i>D. cinerea</i>	b	48	14–19	12–15	2–3	4.4(4–5)	0.5(0.4–0.5)
<i>D. cinerea</i>	c	48	10–16	5–	2–3	4.4(4–5)	0.5(0.3–0.6)
<i>D. cinerea</i>	d	48	12–20	10–15	(1)–2	5.5(4.5–6)	0.6(0.5–0.7)
<i>D. cinerea</i>	e	48	5–6	6	2	4.4(4.2–4.5)	0.5(0.4–0.5)
<i>D. arctica</i> ssp. <i>groenlandica</i>	f	64	4–11	7–10	0–1(2)	7.1(6.3–7.7)	0.3(0.2–0.4)
<i>D. arctica</i> ssp. <i>groenlandica</i>	g	64	8–10	8–10	0–(1)	6.0(5.3–7.0)	0.4(0.3–0.5)
<i>D. arctica</i>	i	80	10	12–15	0	7.2(7–7.5)	0.5(0.4–0.6)
<i>D. arctica</i>	j	80	7–8	5–6	0–1	7.3(6.5–8.0)	0.6(0.5–0.7)
<i>D. arctica</i>	k	80	4	4–5	0	7.4(7–8)	0.7(0.6–0.9)

In spite of the fact that no chromosome count exists for the Siberian population of typical *D. cinerea*, it is most probable that it is hexaploid too. The small stellate hairs and comparatively many stem leaves (more than one) and the small seeds are probably important characters as indicators of the ploidy-level.

Most of the material which was counted can without difficulty be referred to var. *brachysiliqua* (Mela) Ekm. EKMAN (1917:35) says that this variety is very closely related to typical *D. cinerea*. As mentioned already she puts forward the hypothesis that the variety is hybridogenous, originating from crosses between *D. cinerea* and *D. norvegica* (coll.), which is not untenable as both species belong to the same ploidy-level. The occurrence of simple hairs in the Finnish material from Kuusamo as well as in the Ladoga plants may indicate this. However, Greenland plants with almost the same habit (Plate III), are without simple hairs apart from a few cilia on the petioles. In my opinion it is impossible to base hybrid origin on small deviations in the hair cover. We must not forget that hexaploids within the *cinerea* group may have evolved from different crosses or that various cytological aberrations may have had the effect of a repatterning of the chromosome set leading e.g. to difference in the proportion of hair types.

HEILBORN (1927:65) holds the view that the series $n = 24, 32, 40$ has arisen out of two primitive forms, one with 16 and the other with 24 haploid chromosomes. A 16-chromosome form as the hypothetical parental species is, however, as he says, difficult to demonstrate.

As mentioned under *D. norvegica*, plants with $2n = 48$ may have arisen by

Measurements of plants with known chromosome number.

Lowest pedicels (shorter (s) or equalling (e) siliques)	Length of sepala mm	Length of petala mm	Length of ripe seeds mm	Pubescence					Diameter of stellate hairs μ	Illustration
				s: stellate, b: bifid, c: cilia or unbranched ↓: occurring mainly downwards						
				Rosette leaves	Stems	Pedicels	Siliques			
s	2.0	3.5–4.0	0.8–1.1	s(c↓)	sc↓	cb(s)	s	225(125–350)	Plate IVd	
s	1.5	2.2	0.8–1.0	sc↓	sc↓	s(b)	s(b)	230(150–275)	Plate IIIb–c	
s	1.5–2.0	3.0–3.5	0.8–0.9	s(c↓)	s	s	s	235(175–300)	Plate VIb–c	
s	2.1–2.5	3.5–3.6	0.6–0.7	s(c↓)	s(cb↓)	s	s	250(200–300)	Plate IIe, III d	
s	2.0	3.0–4.0	–	s(c↓)	s(c↓)	s	s	250(175–300)	Plate VIa	
s	2.5–3.2	4.5–5.0	0.9–1.0	s(bc)	sc↓	s(b)	s	310(200–375)	Plate Va–c	
s	–	–	0.9–1.0	s(c↓)	s(c↓)	s	s	300(200–425)	Plate VIe	
e	2.3–2.5	4.5	1.1	sbc	s	s	s	375(250–500)	Plate VI f	
s–e	–	–	–	sbc↓	sbc	sc	–	350(150–500)		
s	–	–	1.1	sbc	sbc↓	sbc	s	400(325–550)	Plate VI g	

doubling the chromosomes in a hybrid $n = 8 \times n = 16$ or by crossing between tetra- and octoploids ($n = 16 \times n = 32$). The latter idea has in the case of *D. cinerea* the great advantage that one is dealing with chromosome numbers which are known within the *D. cinerea* group and adjacent groups. PÖHLE (1925:1) groups *D. incana*, *D. lanceolata* (-*stylaris*) and *D. cinerea* together and in SCHULZ (1927:206), *D. cinerea* and *lanceolata* end up in the same part of the key to *Leucodraba*. As $2n = 32$ is found in *D. lanceolata*, we may imagine that typical *D. cinerea* was endowed with erect stems and rather many stem leaves and its dense very small stellate hairs from *D. lanceolata* or its ancestors while other characters were received from the octoploids within the *D. cinerea*-group, e.g. *D. arctica* ssp. *groenlandica*.

EKMAN (1935:352) states that *D. cinerea* due to its pubescence is closely related to *D. lanceolata*. She discusses also a sterile specimen from Sofia's Harbour in continental W. Greenland which she interprets as *D. cinerea* × *lanceolata*. This hybrid would probably be the result of a fertilization between cells with $n = 24$ and $n = 16$.

The geographical distribution of *D. cinerea* s. str. is quite interesting. In Asia it is sub-low-arctic, whilst in N. America A. E. PORSILD (1955:124–125) says that *D. cinerea* s. str. "is a continental, subarctic rather than high-arctic species which, north of the mainland, extends only to the southernmost islands of the Arctic Archipelago." This is in complete agreement with the distribution in Greenland. It is here restricted to the two continental districts CW and CE (cp. BÖCHER, HOLMEN & JAKOBSEN 1966). Most of the material has short siliques, but some specimens, mainly those from North-east Greenland, closely resemble typical Asiatic or North American *D. cinerea*. BÖCHER

(1954: 155, 156, 163) contains some notes about its type of habitats. It is found on dry gravelly slopes together with *Dryopteris fragrans*, *Woodsia ilvensis* and *Saxifraga tricuspidata*. In Greenland typical *D. cinerea* is a low arctic continental species; it seems only to touch higharctic areas and is absent from subarctic—suboceanic environments.

***Draba arctica* J. Vahl p. p. ssp. *groenlandica* (Ekm.) comb. nov.**

Cytological studies. The first count of *Draba groenlandica* was made by HEILBORN (1941: 142). AS EKMAN (1929: 487) includes the chromosome number ($n = 32$) in the diagnosis there is no doubt that this number was found in the type material collected by herself in 1923 at Godhavn, Disko.

The type material (*D. groenlandica* sp. n.) which is kept in the Stockholm Herbarium was collected on June 23th 1923, other specimens (labelled *D. groenlandica* mihi) were collected in August (Plate V, a–c). The plants are 4–11 cm high with 1 (rarely 2) stem leaves. Pedicels are short and the seeds larger than in *D. cinerea*. Some of the rosette leaves are ciliated along their margins and have some simple hairs on the lamina. Usually, there are also simple hairs on the lower part of the stems and on the pedicels. The stellate hairs are larger than in *D. cinerea*. (Fig. 3), Table 3f.

HOLMEN (1952: 13) also reports $n = 32$ in material from Peary Land. This material is closely related to *D. groenlandica*. In his later treatise (1957: 59) he transfers the material to *D. cinerea* coll. which is quite understandable as the pubescence differs from the type material of *D. groenlandica* having fewer simple hairs (cp. Plate VI, e and Table 3g).

The very interesting plants counted by HOLMEN have lead me to the conclusion that the octoploids form a series of plants with different density of simple hairs; none of them, however, have as few simple hairs as typical *D. cinerea*. They are distinguished from typical *D. cinerea* by larger stellate hairs and seeds, fewer cauline leaves, coarser and shorter growth, and in many cases the occurrence of unbranched hairs on the basal part of the stem.

As plants belonging to ssp. *groenlandica* are octoploids they may have reached that level in a less complicated way perhaps more resembling autopolyploid development. We have no knowledge of similar species with $2n = 32$, but they may exist e.g. in Siberia. In the Stockholm herbarium one sheet from Irkaj pij (Tjuch peninsula) ($68^{\circ}55' N.$, $179^{\circ}25' Long.$) collected by KJELLMANN Sept. 1878 was determined by EKMAN as *D. groenlandica*. It has the mixed type of pubescence, short stems and coarse habit, but has small seeds and siliques (see Table 4 No. 6). It is presumably related to *D. parvisiliquosa*. Tolm. from arctic Taymir. According to TOLMACHEV (1932: 142) the type of pubescence in this species is mixed and it has thick siliques 3–4 mm long. It is closely related to *D. cinerea* and occurs on dry stony hillslopes and on the edges of large tundra-hummocks.

As compared with *D. cinerea* the octoploids within *D. arctica* have a much more arctic distribution and at the same time are not so continental in their climatic requirements. In Greenland they are wide ranging with a montane behaviour in the south (Fig. 5). They grow on Disko Island where no true *D. cinerea* is found. A. E. PORSILD (1955: 125–126) mentions ssp. *groenlandica* from the Arctic Canadian Islands from Banks Island to Greenland. His picture (1957: Fig. 40 a–e) agrees with Greenland material of ssp. *groenlandica*.

The octoploids are difficult to separate from *D. arctica* as defined above and would be covered by POHLE's *D. cinerea* var. *arctica*.

Taxonomically, the octoploids may best be distinguished from true *D. arctica* by the shorter pedicels and the shape of siliques. But in many cases the determination will be difficult. In my opinion it is therefore best to treat them as members of a subspecies. In a previous paper (B. 1952) I proposed the combination *D. cinerea* ssp. *groenlandica* but as I consider that the octoploids in many respects resemble *D. arctica* more than *D. cinerea* I now prefer the new combination *D. arctica* Vahl (p. p.) ssp. *groenlandica* (Ekm.).

From the continental area at the head of Søndre Strømfjord and at Arfersiorfjord there are a few collections of plants which have a pubescence closely resembling ssp. *groenlandica* but which differ in habit, having slender, erect stems (Plate V h–i). They have been referred to ssp. *groenlandica* but may perhaps have resulted from a cross between true ssp. *groenlandica* and *D. lanceolata*. In some of the plants the seed-fertility seems to be reduced, in others not. A hybrid of this type would be less puzzling if we suppose that e.g. normal pollen of ssp. *groenlandica* fertilized an unreduced egg cell in *D. lanceolata*.

On the map Fig. 6 specimens which with regard to type of pubescence, correspond to the type of *D. groenlandica* have been indicated with open circles. The majority of specimens resemble the specimen collected by HOLMEN and counted by him (Plate VI e and Fig. 6 solid circles). They might have been referred to a separate variety with fewer unbranched hairs and broader siliques. However, I am unwilling to erect a new taxon as it would involve an unnecessary complication. On the other hand the present treatment involves an emendation of EKMAN's taxon, amplifying it to cover both types of octoploids.

***Draba arctica* J. Vahl p.p. ssp. *arctica* and ssp. *ostenfeldii* (Ekm.) comb. nov.**

Cytological studies. Decaploid plants belonging to the *D. cinerea* group were first found by HEILBORN (1927: 62) working with Spitzbergen material. Morphologically this material differed from typical *D. cinerea* in having simple hairs on the fruiting pedicels. It also had scattered simple hairs on the surface of the leaves as well as stellate hairs. Also FLOVIK (1940: 433) reports $2n = 80$ in plants from Spitzbergen, but has no description of their morphology.

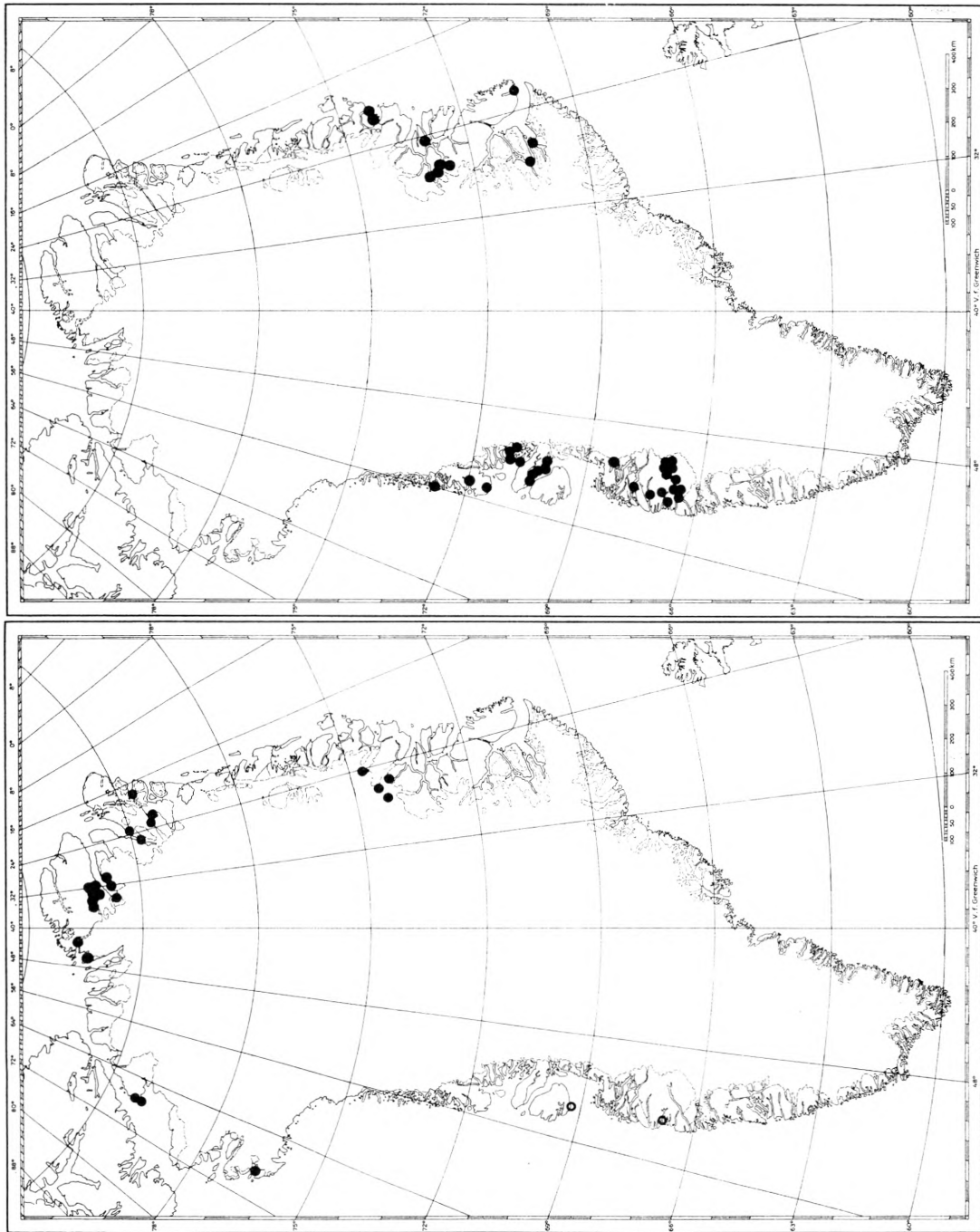


Fig. 4. On the left the Greenland range of *Draba arctogena*, on the right that of typical (probably hexaploid). *D. cinerea*.

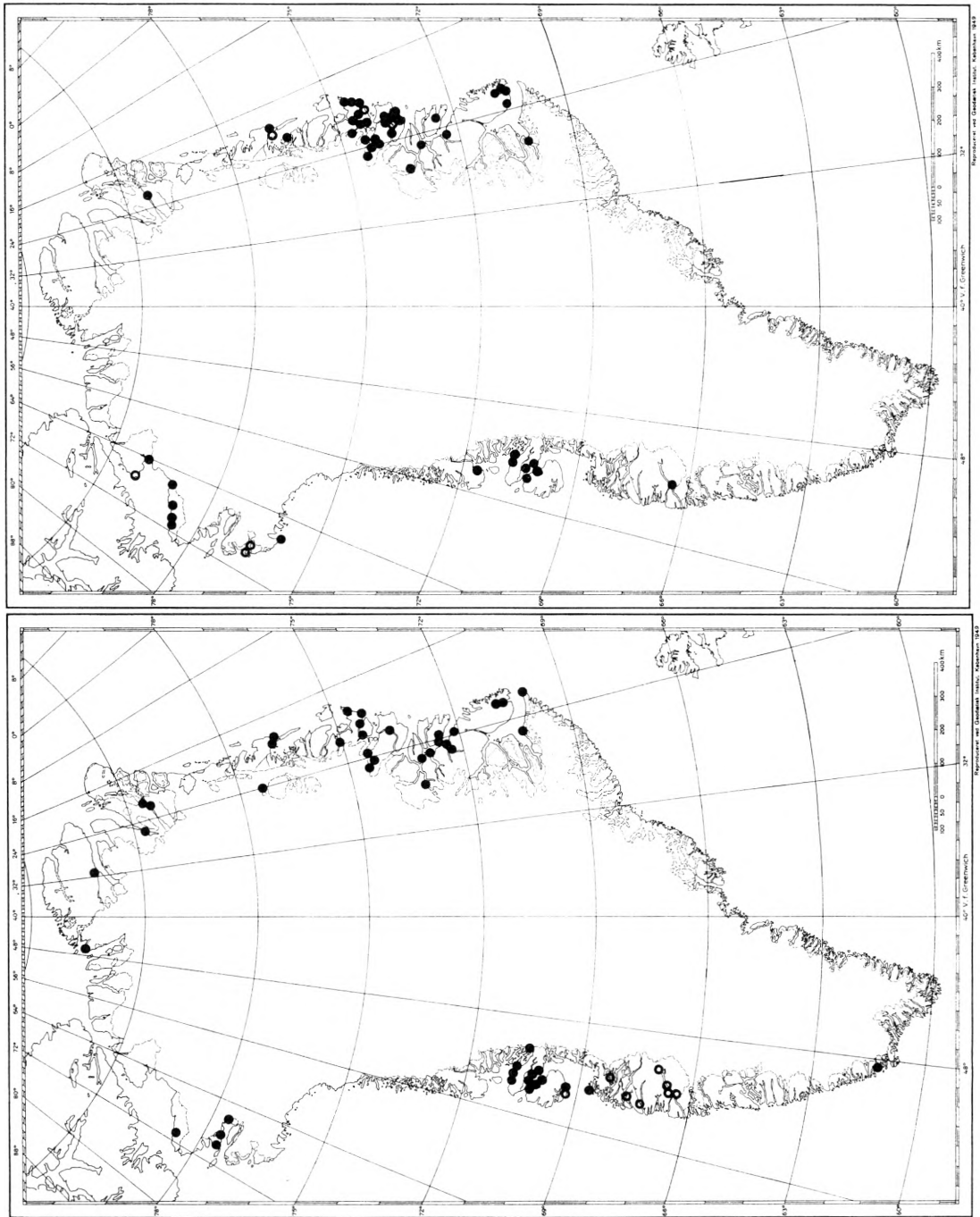


Fig. 5. On the left the Greenland range of *Draba arctica* ssp. *groenlandica*, on the right that of *Draba arctica* ssp. *arctica* (solid dots) and ssp. *ostefeltii* (open rings).

A third count ($n = 40$) was made by the present author in material collected in the Advent Valley on Spitzbergen by NIELS FOGED and cultivated as Dr. 8b. In most PMCs meiosis appeared regular (Fig. 1æ) but in a few cells inversion bridges with fragments occurred at first anaphase (Fig. 1ö). Most loculi had normal tetrads but not infrequently dyads and giant pollen grains were formed, see Fig. 6. Smaller deviations such as elimination of single univalents or exclusion of a single chromosome at Metaphase I occurred occasionally. Also, in a few loculi a degeneration of the PMCs took place. In such loculi, anaphase I cells had sometimes numerous bridges due to stickiness of some kind.

The plants in question have stellate pubescence on the rosette leaves intermixed with a few simple hairs. They were compared with *D. cinerea* No. 4813 which was cultivated simultaneously:

No. Dr. 8b: Largest rosette leaves frequently more than 3 mm broad, green; the stellate hairs do not cover the surface and the interstices are often broader than the hairs. The stellate hairs coarser on relatively long and broad hairstalks. Unbranched hairs along leaf margin (cilia) reach middle part of leaf. Young leaves grey, with much denser hair cover. 0–1 stem leaf, large flowerbuds. Difficult to cultivate.

No. 4813: Largest rosette leaves usually less than 3 mm broad, grey. Almost covered by smaller and more slender stellate hairs with thin and short hairstalks. Marginal cilia on petiole only. Up to 3 stem leaves, small flowerbuds. Easy to cultivate.

The first decaploid material from Greenland was reported by JØRGENSEN et al. from two places on Clavering Island in N.E. Greenland. As mentioned under *D. cinerea* (p. 14) one part of the dried material of the fixed plants had been mixed. Accordingly the decaploid number has almost certainly to be attached to two somewhat different plants, one (k) belonging to EKMAN's taxa. *D. ostenfeldii-ovibovina*, the other (j) to *D. arctica*.

(j) 7–8 cm high with 0–1 stem leaf. Rosette leaves 5–6 mm long with large stellate hairs. Marginal cilia present, which in the upper part are often replaced by bifid hairs. In young leaves cilia also along the upper margin and some bifid hairs between the stellate ones on the laminae. Siliques 7.3 mm. Pedicels with stellate hairs and few simple ones (see Table 3 j).

(k) Plants 4 cm high without stem leaves. Rosette leaves 4–5 mm long covered with large stellate hairs intermixed with a few bifid hairs, cilia along margin and below on midrib. Siliques 7.4 mm long with large stellate hairs. Pedicels also with simple hairs (see Plate VI g and Table 3 k).

The difference between j and k is not striking and can be characterized as a difference in the amount of simple and bifid hairs.

A third fixation of material from Kap Oswald, NE Greenland was made by KJELD HOLMEN who kindly placed imbedded buds and a dried specimen (Plate VI f) at my disposal. Unfortunately most buds were too old, but in one flower some unclear second anaphase plates were studied. They showed that the number was about 40. The dried material has long siliques and cilia (Table 3).

The Spitzbergen material of *D. arctica*

Three fixations from Spitzbergen all showed the same number $2n = 80$. The lectotype collected by VAHL is from Spitzbergen and agrees completely with other material from the Svalbard area. The very comprehensive collections from Spitzbergen kept in the Stockholm herbarium show that the species is particularly uniform in that part of the Arctic. We may therefore use a detailed study of this material as a starting point for a discussion of the decaploid section of the *D. cinerea* group. On the basis of the material in Table 3-4 the following description can be given:

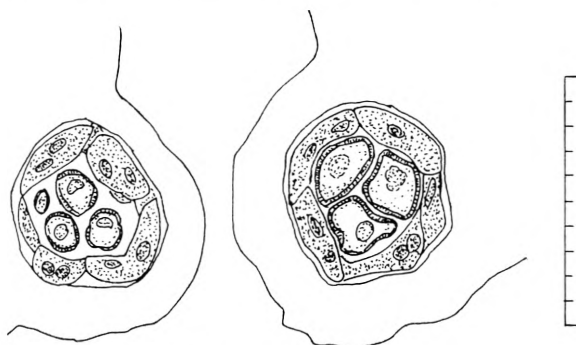


Fig. 6. Two loculi in two adjacent anthers in *Draba arctica* (Dr. 8b) showing giant pollen (on the right) and normal pollen as well as one dwarf grain (on the left). — Scale 100 μ .

3-15 (-25) cm tall with many ascending-erect stems bearing 0-1 (2) leaves. Full-grown rosette leaves greenish, usually 4-6 mm long, covered with large stellate hairs, ciliated at base or up to the middle part of the leaf and sometimes with some few simple or bifid hairs even on the lamina. Stems with stellate pubescence, in the lower part intermixed with simple hairs. Pedicels with stellate hairs usually also with some bifid or simple hairs, the lower pedicels almost as long as the siliques. Sepals 2.5-3 mm, petals 4-5 mm long; large ripe siliques 7-11 mm long, broadest below, tapering; styles 0.5-0.9 mm long. See further Plate VI h-i.

The taxonomic status of *D. ostenfeldii* Ekm. and *ovibovina* Ekm.

In high arctic areas some deviating plants occur, which appear to be over-nourished, possibly by guano (Plate VII). They have broader leaves and the hair cover is more soft and some of them have larger flowers. It is impossible without cultivation experiments to decide whether such plants are modifications due to enriched soil conditions or not. EKMAN (1929) referred them to a new species *D. ostenfeldii* Ekm. with large flowers (Petals 4.5-5.25 mm) and comparatively many simple and bifid hairs on the leaves and to its var. *ovibovina* with predominantly stellate hairs on the leaves and flowers of the same size as in *D. arctica* (see above) This latter

TABLE

Collection	Taxon	Origin and Collector	Height in cm	No. of cauline leaves	Length of longest siliques mm	Length/Breadth of siliques	Lowest pedicels shorter (s) or equalling (e) siliques	Length of sepala mm
1	<i>D. cinerea</i> var. <i>cinerea</i>	Jakutsk, Kumach Sur. 71°30' N. H. Nilsson	17-29	2-4	5.5-7.5	3.2-3.8	e	1.8-2.0
2		Jakutsk, Balaganach 71°35' N. H. Nilsson	15	3-4	4.5-6.0	3.0-4.0	e	2.1-2.4
3		Tuharunach, 71°50' N. H. Nilsson	15-19	1-2	7.5-9.0	3.5-4.5	e	-
4		Bulun, 70°43' N. H. Nilsson	19-24	3-4	7.0-10.0	4.0-4.5	e	-
5		East Taymir, 74°27' A. Tolmatchev No. 43 . . .	ca. 8	2-3	-	-	-	1.5
6	<i>D. cfr. parvisiliquosa</i>	Irkajpij, 68°55' F. R. Kjellman	6-8	1-2	3.8-4.2	1.8-2.9	s	-
7	<i>D. cinerea</i> var. <i>brachysiliquva</i>	Kuusamo, Aulaukajoki, A. L. Backman	15-18	2-3	3.3-4.5	1.8-2.0	s	1.8
8		Kuusamo, Ruskeakallio, J. Montell	13-23	2-(4)	5.0-5.5	2.0-2.5	s	2.0
9		Ladoga, Mäkisalo A. L. Backman	22	1-3	3.5-4.5	1.8-2.0	s	1.3
10		W. Greenland, Strömfjordshavn, TWB . . .	16-25	2	4.0-4.5	2.0-2.2	s-e	-
11		W. Greenland, Umanaq, J. Vahl	8-12	2-3	4.0-5.5	2.0-2.5	s	1.8
12		W. Greenland, Umanaq, Enander	6-13	1-2(3)	4.0-5.5	2.6-2.8	s-e	2.0-2.5
13	<i>D. arctica</i> ssp. <i>groenlandica</i>	W. Greenland, Godhavn, J. Lagerkranz	7-10	0-1	6.0-7.0	2.5-3.0	s	-
14		E. Greenland, Skeldal, T. T. Elkington	7-10	0-1	6.0-7.5	2.4-3.0	s-e	-
15	<i>D. arctica</i> ssp. <i>groenlandica</i> (deviating)	W. Greenland, Tunertoq TWB & Lægaard	14	2	7.0-10.0	4.0-5.0	s	-
16		W. Greenland, East of Mt. Hassel, TWB	10	1	8.0-9.0	4.0-4.3	s	-

1) s = stellate; b = bifid; u = unbranched; c = marginal cilia; ↓ means that the hair type occurs downwards

4.

Length of petals mm	Length of ripe seeds mm	Pubescence ¹⁾					Reference to Figures	Remarks
		Rosette leaves	Main stems	Pedicels	Siliques	Size of stellate hairs		
3.0	—	s c ↓	s	s	s	small	Plate IV a	
3.5–3.8	—	s c ↓	s	s	s	small		
—	0.7	s c ↓	s(u–b ↓)	s	s	small		
—	0.7–0.8	s c ↓	s	s	s	small		
2.5	—	s c ↓	s	s	s	small		
—	0.6–0.7	s, u, b, c ↓	s	s	s	small		
2.5–3.0	0.7–0.8	s c ↓	s(u ↓)	s	s	small	Plate III a Plate III d	(Type material)
4.0	0.7	s c ↓	s(u ↓)	s	s	small		
2.0–2.2	0.7–0.8	s c ↓	s(u ↓)	s	s	small		
—	0.6–0.8	s c ↓	s	s	s	small		
2.0	0.6–0.7	s c ↓	s	s	s	small		
3.5–3.8	—	s c ↓	s	s	s	small		
—	1.0	s c b	s(u ↓)	u–b(s)	s	intermediate	Plate V d–f	
—	1.1	s c ↓	s(u ↓)	s(b)	s	intermediate	Plate V j	
—	—	s c b	s(u ↓)	s(u)	s	intermediate	Plate V h–i	
—	—	s c ↓	s	s(u)	s	intermediate		

(continued)

on the organ.

TABLE

Collection	Taxon	Origin and Collector	Height in cm	No. of cauline leaves	Length of longest siliques mm	Length/Breadth of siliques	Lowest pedicels shorter (s) or equalling (e) siliques	Length of sepala mm
17	D. arctica ssp. arctica	Spitzbergen, Bell Sound, J. Vahl	8-10(25)	1-2	7.0-8.5	3.0-3.7	e	2.0
18		Spitzbergen, Sassenberg, E. Jørgensen	7-10	0-1	9.0-10.0	2.8-3.0	e	1.7-2.0
19		Spitzbergen, Advent Bay, E. Jørgensen	6-10	0-1	7.0-9.0	3.3-3.5	s-e	2.5
20		Spitzbergen Isfjord, Advent Bay, J. Lagerkranz	10-15	0-1	8.0-11.0	3.7-4.4	e	3.0
21		Spitzbergen, Middlehook, I. A. Bjørling	3-5	0-1	6.0-7.0	2.4-3.0	e	2.5
22		Spitzbergen, Longyearbyen, J. Lagerkranz	6-16	0-1	8.0-10.0	3.8-4.0	e	2.5
23		E. Greenland, Ostenfeld Nunatak, Schwarzenbach	23	0-1(2)	8.0-11.0	3.8-4.0	e	-
24	D. arctica ssp. arctica (deviating, approach. typical D. cinerea)	W. Greenland, 900 m, Sdr. Strømfjord, Beschel	18-21	1-2(3)	6.5-9.0	3.2-3.4	e	2.2
25	D. arctica ssp. ostenfeldii	W. Greenland, Sounders Isl., P. Freuchen	4-10	2	8.0-9.0	3.4-3.0	s	4.0
26	D. arctica ssp. ostenfeldii	Spitzbergen, Longyearbyen, J. Lagerkranz	5-8	0(1)	7.0-8.0	3.2-3.4	s-e	-
27	D. arctica ssp. ostenfeldii var. ovibovina	Ellesmereland, Fram Hb. H. G. Simmons	10-15	1-2	7.0-9.0**	2.3-3.0	s-e	3.0
28	D. arctica ssp. ostenfeldii var. ovibovina (ad groenlandica)	Ellesmereland, Fram Hb. H. G. Simmons	12	0-1	7.5-8.5**	2.5-2.8	e	-

¹⁾ s = stellate; b = bifid; u = unbranched; c = marginal cilia; ↓ = means that the hair type occurs downwards on

rather doubtful taxon was later promoted to a separate species by EKMAN (1941: 135). Common to both is a soft pubescence of mixed hairs (unbranched, bifid, stellate) on the pedicels.

The chromosome counts of $2n = 80$ in very small plants of the *ovibovina* type, which clearly have not been affected by enriched soil (Plate VIg) makes it most probable

4 (continued).

Length of petala mm	Length of ripe seeds mm	Pubescence ¹⁾					Reference to Figures	Remarks
		Rosette leaves	Main stems	Pedicels	Siliques	Size of stellate hairs		
3.2	1.0	s(u)c ↓	s	s(u)	s	large	Plate IIa-d	(Type material)
3.5-3.7	1.0-1.2	s c ↓	s	s	s	large	Plate VI	
4.0	1.0	s(u)c ↓	s(u) ↓	s(u)	s b	large	Plate VI	
4.5-5.0	1.0-1.1	s b c ↓	s u(↓)	s	s b u	large		
4.0-4.5	1.0	s b u c ↓	s(u) ↓	s b	s b	large		
4.0-4.5	1.1-1.2	s b u c ↓	s(u) ↓	s b u	s	large		
-	1.0-1.1	s(b u)c ↓	s(u) ↓	s u	s	large	Plate VI d	
3.0	0.9-1.0	s(b) c ↓	s(u) ↓	s	s	interm.-large		
5.0-6.0	-	s*b u c ↓	s b u	u s	s b	large	Plate VIIa	(Type material)
-	1.0-1.1	s(c) ↓	s(u) ↓	u s	s	large	Plate VIIb	
4.0-4.5	1.0	s b(c) ↓	s b u c ↓	u s	s b	large	Plate VIIc	(Type material)
-	1.0	s u b(c) ↓	s(u) ↓	u s	s	large	Plate Vg	

the organ. * stellate hairs with long stalks. ** very short styles.

that genetically deviating decaploids exist which ought to be considered taxonomically. However, the type of pubescence is not widely different from that found in typical *D. arctica*. As long as it is completely obscure whether *D. ostenfeldii* represents a modification of *D. ovibovina*, it may not be practical to abandon it. Therefore, it is proposed provisionally to consider both as was proposed by EKMAN (1929) but at the same time

reducing *D. ostenfeldii* to subspecific rank as the new combination, *D. arctica* J. Vahl p. p. subsp. *ostenfeldii* (Ekm.). Var. *ovibovina* Ekm. belongs to this subspecies; see further Plate VII c.

Key to the Greenland taxa of the *Draba cinerea* group

The key given here summarizes the points made in the preceding section. *Draba arctogena* and *D. dovrensis* Fries which are mentioned in EKMAN'S key (1941: 135) are omitted. The former because it is considered to be closely related to *D. norvegica*, the latter because it is connected with *D. glabella*, see p. 29.

- A₁ Stem leaves 2–4. Stellate hairs small, about $\frac{1}{4}$ mm in diameter, always dense, covering leaves and siliques. Very few cilia on petioles. Flowers small, seeds 0.7–0.8 mm long. *D. cinerea* Adams.
 B₁ Siliques narrow and tapering towards the apex, lowest pedicels equaling the siliques. *D. cinerea* Adams, ssp. *cinerea* (Plate IV a–c).
 B₂ Siliques short, not tapering, with almost obtuse apices, pedicels short $2n = 48$ *D. cinerea* Adams ssp. *brachysiliqua* (Mela) Ekm. (Plate III).
 A₂ Stem leaves 0–1 (2). Stellate hairs large, flowers large, seeds about 1–1.1 mm long. Pubescence on siliques (sometimes on leaves) less dense.
 *D. arctica* J. Vahl p. p.
 C₁ Pedicels short, rarely equaling the siliques. Siliques usually not tapering towards the apex, but not obtuse. Stellate hairs about $\frac{1}{3}$ mm in diameter. Basal leaves with a varying (sometimes locally abundant) number of unbranched cilia or hairs along the leaf margins, as well as on the petioles. Basal part of stem usually with some unbranched hairs. $2n = 64$
 *D. arctica* J. Vahl p. p. ssp. *groenlandica* (Ekm.) Böch. (Plate V).
 C₂ Lowest pedicels equaling the siliques which taper towards the apex. Stellate hairs about $\frac{1}{2}$ mm in diameter. Pubescence on leaves, stems and pedicels mainly stellate. Some bifid or unbranched hairs are often found intermixed with stellate hairs on the leaf surfaces. $2n = 80$
 *D. arctica* J. Vahl p. p. ssp. *arctica* (Plate VI d, f, h, i).
 C₃ Lowest pedicels shorter or equaling the siliques, which are slightly or not tapered towards the apex. Stellate hairs about $\frac{1}{2}$ mm in diameter, often long-stalked. Leaves, stems and pedicels with a mixed pubescence. Dense well-developed cushions of broad rosette leaves.
 *D. arctica* J. Vahl pp. ssp. *ostenfeldii* (Ekm.) Böch.
 D₁ Many unbranched hairs on the leaves, flowers large
 var. *ostenfeldii* (Plate VII a, b).
 D₂ Predominantly stellate hairs on the leaves, flowers of normal size $2n = 80$ var. *ovibovina* Ekm. (Plate VII c).

***Draba glabella* Pursh**

Draba glabella Pursh, which according to FERNALD (1934: 333–334) covers *D. hirta* of many authors and *D. daurica* DC., is another very polymorphic species. In many respects, it constitutes a series of forms which is parallel to the *D. arctica* complex, in that both species include both octoploids and decaploids. The main difference between the two series is difficult to define in as much as *D. glabella* s. l. also embraces forms with more or less hirtellous siliques. However, *D. arctica* is a member of a xerophytic group which ecologically differs from the *D. glabella* group, the latter being mesophytic with greenish leaves and with sparsely pubescent scapes and usually almost glabrous siliques.

Previous chromosome counts. There are many counts of $n = 32$ in the *D. glabella* complex. HEILBORN (1927: 62, 1941: 142) found this number in “*D. magellanica* ssp. *borea* Ekm.” from Swedish Lappland, Umanaq in W. Greenland (two strains, one being a *condensata*-form), Atanikerdluk in W. Greenland (var. *lutescens* Ekm.) and Godhavn, Disko. Also the populations of *D. glabella* in the Søndre Strømfjord area (67° lat. N.) in spite of attaining very different heights (BÖCHER 1952 Fig. 10) are octoploids. Three strains were counted by BÖCHER & LARSEN (1950: 19). According to JØRGENSEN et al. (1958: 68) material from NE Greenland studied by HOLMEN also belongs to the octoploid series.

Draba dovrensis Fries (*D. hirta* var. *dovrensis*), which resembles *D. dasycarpa* Mey. of Altai and seems to be closely related to *D. glabella*, has $n = 32$ (HEILBORN 1927 in material from Kongsvold in Dovre). It has hairy siliques and was interpreted as a hybrid between *D. cinerea* and *D. glabella* (*hirta*) by EKMAN (1935), but HEILBORN reports no meiotic irregularities which might indicate hybrid origin and there are no *D. cinerea* or *D. arctica* in southern Scandinavia where it occurs.

Also *D. magellanica* Lam. from the straits of Magellan has $n = \text{ca. } 32$ (HEILBORN 1941) which agrees with the fact that this species resembles *D. dovrensis* (EKMAN 1933: 479).

Decaploid strains were hitherto only found in Greenland material, i.e. from Godhavn by HEILBORN (1927: 62) and Clavering Island, NE. Greenland, by JØRGENSEN et al. (1958).

Cytological observations. New material of the *D. glabella* complex has been studied from five very different localities. In three of the cases the plants were octoploid, i.e. Cult. No. Dr. 12 from Finland (Turku Bot. Gardens) No. 6325 from rocks at Percé (Gaspé Peninsula, Canada) and No. 4814 from head of Søndre Strømfjord, W. Greenland. One culture No. 4788 from Godhavn was decaploid as was a plant fixed in N.E. Greenland by KJELD HOLMEN (Holmen No. 261, see Fig. 7).

Meiosis was regular in No. 6325 (Figs. 1, s–t). In No. 12 one univalent (and possibly a trivalent) occurred in a very few cells. In No. 4814 one pair was often placed above or below the first metaphase plate. Meiosis proceeded here mostly normally but in

TABLE 5. Cultivations of *Draba glabella*.

Cult. No.	Origin	2n	Height of plants in cm	Number of stem leaves	Length of ripe siliques, mm	Length of ripe seeds mm	Other characters
6325	Gaspé Peninsula Canada	64	12(10–16)	2–3(4)	9–10	1.0–1.2	Rosette leaves more narrow mostly with two opposite teeth, ciliation often restricted to petiole or as in No. 2325, sometimes also reaching higher up. Flowering once a year.
Dr. 12	Turku Bot. Gardens Finland	64	15(9–20)	2–4	7–10	0.9–1.1	
4814	Sondre Strømfjord W. Greenland	64	11(7–15)	(1)2–3	6–9	0.9–1.0	
4788	Godhavn, Disko W. Greenland	80	7(6–8)	(0)1–2	5–8.5	0.9–1.0	Rosette leaves rather broad more green almost entire, ciliated up to middle part. Flowering twice a year.

some of the anther loculi dyad formation occurred indicating apomeiotic development. Some of the dyad cells developed into giant pollen grains. In the decaploid No. 4788 displacement of one or two bivalents from the equatorial plane took place in some PMCs (Fig. 1 x) while in others a pair of univalents were observed outside the plate. Occasionally a quadrivalent configuration occurred. Most anaphases appeared normal but Fig. 1 z shows that laggards and bridges occur although probably rarely.

Morphology of material with known chromosome number. The octoploid strains were all relatively tall with 2–4 cauline leaves and the racemes became elongated at fruiting stage resulting in a rather remote positioning of the siliques (Fig. 7). The decaploid No. 4788 was low in culture with (0) 1–2 leaves and its raceme was denser on a longer peduncle (Table 5). The East Greenland decaploid plant (Holmen No. 261) has also the dense terminal raceme and 0–2 cauline leaves (Fig. 7 on the left).

It proved impossible to demonstrate any distinct differences between octoploids and decaploids with regard to size of stellate hairs and seeds but there seemed to be a slight difference in the shape of the fruits and the breadth of the rosette leaves (Table 5). The siliques are lanceolate, subacute in the octoploids, while they may be elliptic and slightly obtuse in the decaploids (Fig. 7). The longest siliques are 6–8.5 mm in the latter and 9–10 mm in the octoploids. The cauline leaves are broader near the base in the plant from NE. Greenland, and \pm cuneate in most octoploids. The latter distinction corresponds to that used by SCHULZ in his attempt to distinguish



Fig. 7. *Draba glabella* Pursh. On the left decaploid from Kap Oswald, Ella O, East Greenland (leg. K. HOLMEN Aug. 1960), on the right single shoot and new rosette from hexaploid cultivated material (Cult. No. Dr. 12 from Finland). — Scale 10 cm.

between *D. hirta* and *D. daurica* and appears also from the pictures of *D. hirta* and *D. daurica* in BUSCH (1919: 351 and 357). However, as pointed out by FERNALD (1934 Plate 308) it is impossible to use this difference between two species as the type material of *D. daurica* has cuneate stem leaves as has that of *D. glabella*. Although the shape of the stemleaves may be of some importance it is certainly not a reliable character and seems not to be clearly correlated with differences in chromosome number.

The octoploids vary in degree of pubescence. No. 6325 and 4814 have almost glabrous upper stems and leaves and completely glabrous siliques, while in Dr. 12 the siliques have some unbranched or bifid hairs along the margins. Both decaploids have glabrous siliques.

Almost the same pattern of variation in pubescence is found in dried material of plants with unknown chromosome number. Most specimens have completely glabrous siliques and scattered stellate pubescence on pedicels and stems. Deviations from this may be exemplified as follows:

- 1) Scattered unbranched (-bifid) hairs mainly along the margins of the siliques as in Dr. 12. Examples: Spiret, N. Strømfjord (leg. F. Salomonsen 1954), Qapiarfik (leg. TWB 1958), Godhavn (leg. G. Kleist 1904; NB. siliques broad and obtuse, probably var. *brachycarpa*, see below), Pröven 72°22' (leg. I. A. Björling, determined as *D. hirta* var. *hebecarpa* Lindbl. but later as *D. cinerea* × *daurica* by EKMAN, Herb. Stockholm).
- 2) More dense pubescence on the siliques of unbranched and bifid hairs. Examples: Upernivik Ø, 71°10' (leg. M. P. & R. T. Porsild 1929, determined as *D. cinerea* × *daurica* by EKMAN, Herb. Stockholm), Sermermiut (leg. S. B. 1870, by TOLMATCHEV 1927 determined as *D. hirta*, by EKMAN as *cinerea* × *daurica* and on the label with the remark "corresponds to *D. dovrensis*", Herb. Stockholm). These two collections are almost identical with plants from Knutshö and Kongsvold in Dovre.
- 3) Glabrous siliques but with long unbranched hairs on the pedicels: Some of the rosette leaves ciliated with unbranched hairs. Type of *D. daurica* var. *rupestriformis* Ekm. (EKMAN 1930: 286, Umanaq, leg. B. Floderus 1929, Herb. Stockholm). ± Ciliated rosette leaves also seen in Cult, No. 6325 from Gaspé, Canada.

Taxonomical remarks. JØRGENSEN et al. (1958: 68) express the view that "*D. hirta* perhaps covers two species with $n = 32$ and 40 respectively, but add that until more material has been collected, it is impossible to settle the discrepancy between chromosome number and taxonomical demarcation". The new material now available has not contributed a great deal to the solution of the problems. The morphological differences found between octo- and decaploids are too vague. FERNALD's treatment (1934: 333) of the polymorphy within *D. glabella* deserves, however, to be discussed in this connection. FERNALD operates with four varieties arranged into two groups. His var. *typica* and var. *orthocarpa* may belong to the octoploid series while var. *brachycarpa* (Rupr.) Fern. and his var. *megasterma* are possibly decaploids with $n = 40$ or in the case of the latter even higher numbers. His pictures of *D. glabella* var. *brachycarpa* (Plate 310) from Greenland show plants which resemble the decaploids studied cytologically although the plants chosen by FERNALD have particularly broad and obtuse siliques. On the other hand, his pictures of typical *D. glabella* from

Labrador (Plate 307) resemble octoploids from Greenland (e. g. as No. 4814) while his var. *orthocarpa* from Quebec (Plate 309) has much in common with the octoploid material from Finland (Dr. 12). FERNALD'S distinction between the two groups, however, is based on differences found between morphologically extreme specimens and these also show some difference in the size of the seeds. It must therefore be remembered, that octoploids show clear differences in the size of the seeds (Table 5).

At the present stage of our knowledge it is preferable to refrain from erecting any taxa (e.g. varieties or subspecies) to cover the decaploids. It seems clear that typical *D. glabella* specimens are octoploid and have a relatively southern sub-low arctic distribution. One part of the decaploids, on the other hand, seems to constitute a high arctic group which so far is not found south of Godhavn on Disko.

Relationship between the *Draba glabella*, the *D. cinerea*, and the *D. norvegica* group

Hybrids between *D. glabella* (*daurica*) and "*D. cinerea*" were discussed in EKMAN'S earliest papers and in EKMAN (1930). HITCHCOCK (1941) also tackled the problems by saying that he is inclined to consider *D. cinerea* as merely a very pubescent form of *D. glabella*. He also mentions *D. cinerea* var. *kamschatica* (Regel) Schulz which has glabrescent siliques. In Greenland, however, there is no reason to unite any species of the *D. cinerea* group with *D. glabella* s. l. in spite of the existence of some forms considered by some to be intermediate.

Some of the hybrids mentioned by EKMAN (1930) seem from a cytological point of view rather unlikely, e.g. *D. glabella* × *norvegica*, *D. arctogena* × *glabella* and *D. cinerea* (typical) × *daurica*, all of which would involve crossings between plants with $n = 24$ and $n = 32$. On the other hand are hybrids at the octo- or decaploid level more probable. In fact EKMAN assumes a rather frequent occurrence of the hybrid *D. arctica* ssp. *groenlandica* × *daurica* and thinks this hybrid is identical with *D. dovrensis*.

On p. 287 EKMAN expresses the view that it may be difficult to decide whether the other parent plant is *D. arctica* ssp. *groenlandica* or *D. norvegica* as pubescent siliques may have been inherited from either of these species. But in specimens where the rosette leaves are ciliated, she adds "the other parent plant is in most cases *D. norvegica*". This remark is curious as *D. arctica* ssp. *groenlandica* often has ciliated basal leaves. Obviously plants interpreted as *D. glabella* × *norvegica* are suspect and need a closer study. In fact *D. glabella* s. l. includes an octoploid form with cilia on the rosette leaves (e.g. Cult. No. 6325); this culture originates from a locality outside the known area of *D. norvegica* (A. E. PORSILD 1957: 184, HULTÉN 1958 map 14).

Also the presumed hybrid *D. arctica* ssp. *groenlandica* × *glabella* needs corroboration. *D. dovrensis* shows no meiotic irregularities and occurs outside the area of ssp. *groenlandica*. A striking fact is that *D. dovrensis* has simple or bifid hairs on the siliques, not stellate as in ssp. *groenlandica*. If the plants determined by EKMAN are hybrids it is necessary to assume inheritance of hair type from *D. glabella* and high hair density on the siliques from ssp. *groenlandica*.

At the head of Søndre Strømfjord where octoploid *D. glabella* is sympatric with hexaploid *D. cinerea* there were no signs of hybridity between these two species. The presumed hybrids are all from areas where octoploids or decaploids within the *glabella*- and *cinerea*-group occur together. This makes introgression a possibility but there is no substantial evidence.

***Draba sibirica* (Pallas) Thell.**

Material of this species was obtained as seeds from the Botanical Gardens of Strassbourg, Halle and Moscow. Unfortunately no seed from nature was available. The plants were easily grown in pots in the Experimental Field and all three samples (Nos. 7647, 7667, 7671) flowered already in the autumn of the first year of cultivation. Morphologically there was no difference between them and all had the chromosome number $2n = 16$ (Fig. 10, h-i).

According to SCHULZ (1927: 79) *D. sibirica* belongs to the section *Chrysodraba*, and is the first diploid found in this section. It is an Asiatic-East European subarctic-subalpine species, although extending to low arctic areas, e.g. in Middle East Greenland and also to temperate areas in Middle Russia. All the high arctic representatives of *Chrysodraba* are polyploids (see e.g. *D. bellii*).

The material from the Botanical Gardens which is very uniform may have originated from localities of southern type. In Halle *D. sibirica* was observed growing abundantly in the Rock Garden thus certainly not behaving as an arctic species. Morphologically *D. sibirica* deviates from all high arctic species of *Chrysodraba* by being loosely tufted, its vegetative shoots being elongated and stolonlike (GELERT 1898: Fig. 9).

***Draba bellii* Holm**

Material of this species from Spitzbergen (Cult. No. Dr. 1, Kongsfjord, W. Spitzbergen) collected as seeds by Dr. N. FOGED and grown in the Arctic Greenhouse appeared to be 16-ploid with $2n = 128$. The root tip mitoses could not be counted with absolute certainty but the clearest metaphase had $2n = 128 \pm 2$ chromosomes. HOLMEN (1952) has found a similar high chromosome number in material from Peary Land ($82^{\circ}10'$ lat. N.). He first referred the plant to the closely related taxon *D. macrocarpa* Adams. Later, however, (1957) he expresses doubt about the taxonomical status of his material and is inclined to refer it to *D. bellii*. Dr. HOLMEN has kindly lent me his pressed material thus enabling me to make a comparison between the two 16-ploid plants from Spitzbergen and N. Greenland (Table 6).

According to HOLMEN (1957: 57-58) *Draba bellii* has a great range of variation. In many ways this variation appears also from a comparison of the two strains which were studied cytologically. The Spitzbergen plants have longer, more numerous, unbranched hairs and have narrower leaves and petals and smaller flowers. In most

TABLE 6.

	<i>Draba bellii</i> from Spitzbergen Kongsfjord (NB. cultivated material; Dr. 1.)	<i>Draba bellii</i> from Peary Land, HOLMEN No. 6594 (collected in nature)
Height and habit	3–5 cm, densely caespitose no stem leaves	5–6 cm, densely caespitose no stem leaves
Basal leaves	Narrowly spatulate, weakly acute marginal cilia 1–1.2 mm. Lamina glabrescent above with few scat- tered bifid and unbranched hairs, below with stellate and bifid hairs	Spatulate, obtuse, marginal cilia 0.6–0.9 mm. Lamina above with mixed pubescence of stellate hairs (near margin) bifid and unbranched hairs, below also mixed but with more stellate hairs
Stems and pedicels	Dense covering of ca. 1 mm long unbranched or bifid hairs	Mixed dense pubescence of mainly unbranched-bifid hairs
Flower	Sepals 2.5 mm, Petals 4 mm rather narrow and emarginate, pale yellow	Sepals 3 mm, petals 5–6 mm broad and emarginate, pale yellow
Siliques (without style)	8.5 mm long, 2.5 mm broad. Pubescent with ca. 0.4 mm long unbranched hairs which are partic- ularly dense along the margin. Seeds 1.2–1.3 mm long. Siliques sometimes solitary on short peduncles between basal leaves	8–9.2 mm long, 4–5 mm broad. Pubescent with ca. 0.4 mm long unbranched hairs. No seeds available
Style and stigma	0.5 mm long style and capitate stigma	0.5 mm long style and capitate stigma

characters this strain corresponds to *D. bellii* var. *svabardensis* Ekman (see EKMAN 1931: 470), while the material from Peary Land may be referred to “f. *typica*”. It differs from the description of *D. macrocarpa* in having emarginate petals and stellate hairs (with more than two-three branches). Considering, however, the great range of variability in *D. bellii* as found in Greenland and Spitzbergen and the slight morphological difference between *D. bellii* and *D. macrocarpa* it seems probable that these two species ought to be united. If so the species has to be called *D. macrocarpa* Adams. From a phytogeographical point of view this *D. macrocarpa* s. lat. would be circumpolar high arctic. The great range of variation in the complex is not surprising as it is composed of 16-ploids and may have been formed as a result of allopolyploid evolution. TOLMACHEW (1932: 52) has a map of the world range of *D. macrocarpa*. It shows stations for this species in NE. Greenland, NW. Greenland, the American Arctic Archipelago, Arctic Siberia and Novaja Semlja. This shows that TOLMACHEW included in *D. macrocarpa* specimens which others e.g. A. E. PORSILD (1955: 123–214, 1957: 95) have referred to as *D. bellii* Holm.

***Draba aurea* M. Vahl**

This is a West American species occurring in forests and montane regions from Alaska to New Mexico, Southern Utah and the higher mountains of Arizona. In East America it is confined to a few stations in Northern Labrador and a single one in Ungava (James Bay), see HITCHCOCK (1941: 26), FERNALD (1934 map p.: 299). In East and West Greenland, however, it has a wide range extending to 70–71° n. lat., see Fig. 8. In continental West Greenland it occurs mainly in the lowland and often in connection with dry willow scrubs (BÖCHER: 1954). The type of distribution within Greenland is low-subarctic and subcontinental.

Chromosome number. The first count of this species was made by BÖCHER (1958: 351) in plants from the Botanical Garden in Copenhagen. The material was very small as it was only possible to count one megaspore mothercell at diakinesis. 32 chromosome pairs were found. During examination of the slide the cell was not found again; it is therefore impossible to say more than the haploid number was at least 32 and probably not much higher. This remark is necessary as the new material clearly had more than 32 bivalents.

Two strains from W. Greenland (Fig. 9, Cult. Nos. 4883 and 4820) had the unusual number $2n = 76$ or $n = 38$. While somatic plates distinct enough for safe countings were rare (Fig. 1 n, r), the meiotic metaphases showed clearly that the haploid number was 38, see fig. 1 p–q. According to SCHULZ (1927: 173) *D. aurea* belongs to the section *Phyllodraba* which contains 11 species from mountains of N. America and 17 montane asiatic species but no true arctic species, *D. aurea* being the only one which reaches sub-lowarctic Greenland. The possibility exists, therefore, that the *Phyllodraba* section has another basic number, which may be 19 or perhaps 12, see p. 64. In the latter case *D. aurea* would have $2n = 72 + 4$ small extra chromosomes. In fact in two of the plates, fig 1 p–q, two small pairs are seen (☆) which supports this explanation without of course giving any kind of proof. With 12 as the basic number *D. aurea* is a type of decaploid with extra-chromosomes whilst with 8 it is a secondary decaploid by loss of two pairs. In this connection it is perhaps of some importance that small extra chromosomes occur in other species in the genus (e.g. *D. norvegica*, Fig. 1j–m).

Variation. EKMAN (1934) classifies *D. aurea* as perennial and HITCHCOCK (1941) describes it as an erect to decumbent perennial but adds biennial with a question-mark. The material from Greenland cultivated by me was biennial or pauciennial as the plant died after prolific fruiting. HITCHCOCK also makes a remark about the variation which deserves comment. Undoubtedly, he says, *D. aurea* is more variable than any other of our western North American species, but I am convinced that much of this variation is due to local ecological conditions. According to him only one variant deserves taxonomic recognition viz. *D. aurea* var. *leiocarpa* (Payson & St. John) Hitchc. Also FERNALD is of the opinion that the West-American material which customarily is referred to *D. aureiformis* Rydb. is not specifically distinct from *D. aurea*. From the

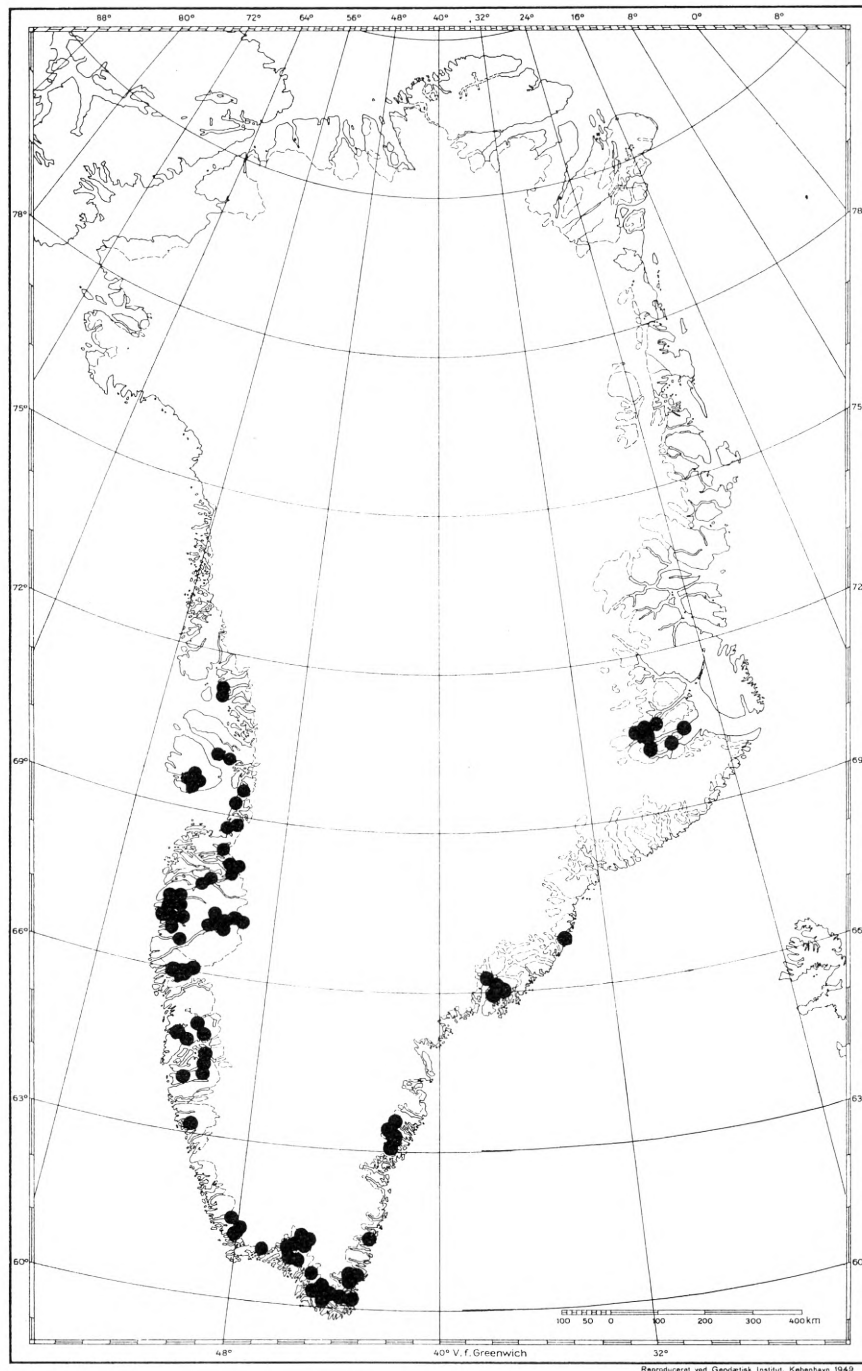


Fig. 8. Greenland range of *Draba aurea*.

treatise in SCHULZ 1927 and the discussions in HITCHCOCK and FERNALD, however, it seems quite clear that *D. aurea* is polymorphic in its West-American main area while it is evident that the range of variability in Greenland is much smaller. Decumbent plants have never been found in Greenland while plants with glabrous siliques were interpreted as *D. aurea* × *glabella* by Ekman (1934: 78). The two strains from West Greenland which were cultivated simultaneously were not morphologically



Fig. 9. *Draba aurea* from W. Greenland. No. 4883 from N. Isortoq is early flowering with light yellow flowers and many stems while No. 4820 from Søndre Strømfjord is late flowering with ochre-yellow flowers and fewer stems. — 8/5 1959.

identical but deviated from one another in flowering time—one being almost a week earlier (Fig. 9)—in branching and in colour of the petals, one being more deeply yellow than the other.

No. 4883 is from a place not far from the outer coastal mountains while No. 4820 is from the extreme continental inland. Studies in the Greenland herbarium in Copenhagen shows that the plants from the most continental areas, e.g. Scoresbysund and the Strømfjord hinterland all belong to the type with few or no branches on the lower part of the inflorescence and few basal shoots. The branched type however is found in many places in South and West Greenland from N. Isortoq southwards. Very vigorous specimens of both types are shown in Plate VIII. The paler flowers in No. 4883 perhaps deserve attention. If EKMAN is right in her opinion that *D. aurea* can cross with *D. glabella*, such pale plants might be results of some kind of introgression. The cytological observations referred to above, however, do not suggest easy hybridization and there are glabrous fruited specimens found in Western America which are not referred to any hybrid (HITCHCOCK 1941).

***Draba gilliesii* Hook. & Arn.**

Material of this species collected by Dr. JOSÉ DIEM in Parque Nacional Nahuel Huapi in the provinces Neuquén and Rio Negro in Argentina was cultivated in the Botanical Garden in Copenhagen. The plants were quite typical, 12–13 cm high with 5, remotely dentate cauline leaves, white flowers and 3 mm long styles on the ripe siliques. In all parts the plants were densely covered by stellate hairs. According to SCHULZ (1927: 156–158) the species is polymorphic. The material studied by me belongs clearly to var. *rosulata* (Phil.) Reiche.

Numerous PMCs were studied at diakinesis in orcein squash slides. 24 bivalents were found. One large pair (☆ in Fig. 10 c) had one terminalized and one non-terminalized chiasma, its two free ends being often less condensed. In root tip squashes 48 chromosomes occurred (Fig. 10 b) among which two were large and showed a high degree of splitting. They may correspond to the deviating pair. The species belongs probably to a series with 12 as basic number (cp. p. 64).

4. *Braya*

***Braya thorild-wulffii* Ostf.**

This high arctic species was first counted by HOLMEN (1952) in material from Peary Land and later by K. JAKOBSEN in plants from Nugsuaq, West Greenland (JØRGENSEN et al. 1958: 73). Quite recently $2n = 28$ was counted by MULLIGAN (1965) in plants from Northwest Territories (see Postscript). The present writer received seeds collected in Peary Land by BENT FREDSKILD (Slope at Kedelkrogselven, FREDSKILD No. 2715). The plants were grown as Cult. No. 7327 in the Arctic Greenhouse and counted in root tip squashes. $2n = 28$ was found thus corroborating earlier counts.

HOLMEN (1952, Fig. 18) pictures a first metaphase plate in which one large bivalent is seen in the center and another rather large one at the top. In the clearest plate studied by me (Fig. 10 a) there are two particularly large chromosomes with submedian centromeres (marked with black asterisks), about 8 which are intermediate in size and about 18 which are much smaller. It was not possible to detect four large chromosomes with submedian centromeres, a fact which may be of some importance in indicating that the species is not an autotetraploid.

B. thorild-wulffii No. 7327 was grown simultaneously and together with three strains of *B. purpurascens* (see Table 10). The plants appeared to be very clearly separated from the latter species, having i.a. ciliated leaf margins and more greyish green leaves. Most of the plants did not flower but formed cushions of small rosettes at the same time as the strains of *B. purpurascens* were luxuriantly flowering.

One of the plants formed flowers on 0.5–0.8 cm high pubescent stems which were almost hidden among the rosette leaves. These were up to 1.6 cm long. The sepals were 3 mm long, with some few hairs usually near the top. They were spreading and persistent during ripening of the siliques. The petals equalled or were shorter



Fig. 10. — a: *Braya thorild-wulfii* (No. 7327, $2n = 28$). — b-c: *Draba gilliesii*; b: root tip mitosis, $2n = 24$; c: diakinesis $n = 24$. — d: *Arabis arenicola* (No. 6064, $2n = 16$). — e: *Braya linearis* (No. 7388, $n = 21$). — f-g: *Braya alpina* (No. 6988; f: $n = 21$; g: $2n = 42$). — h-i: *Draba sibirica* Nos. 7647, 7671, root tip mitoses, $2n = 16$. — j-k: *Braya purpurascens*; j: No. 7114, $n = 28$; k: No. 7368, $2n = 56$. — All orcein squashes, the mitotic cells after pretreatment with α monobromnaphthalin. — Scale 10μ .

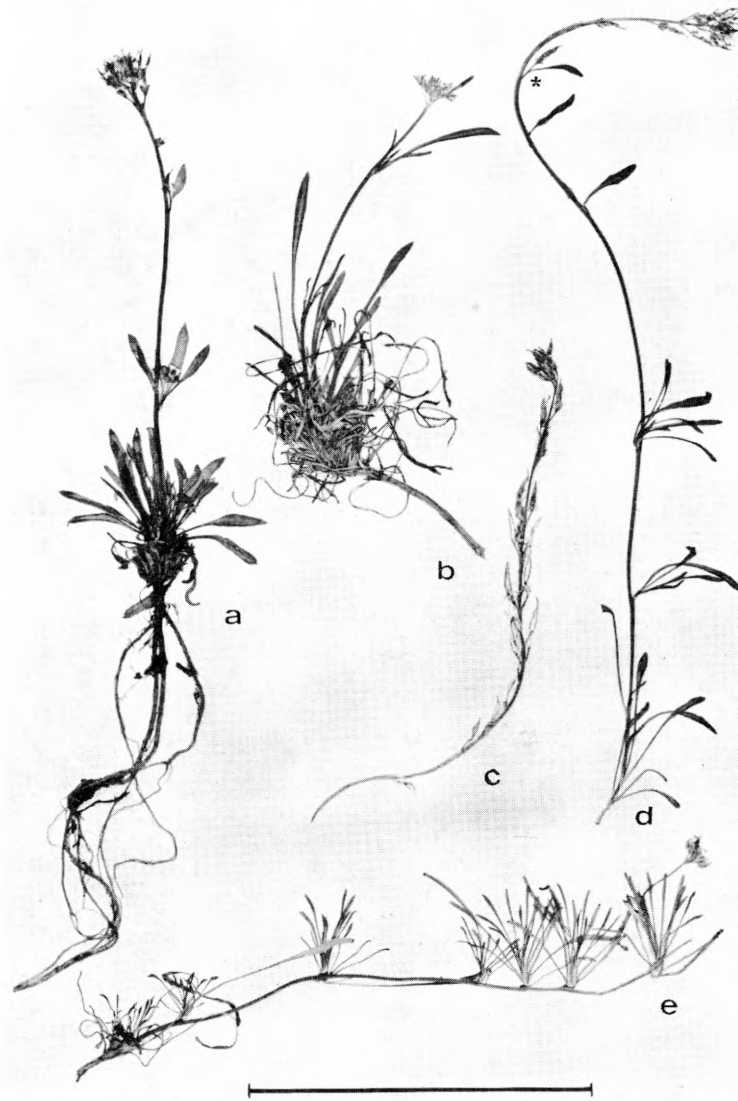


Fig. 11. Material of *Braya rosea* grown as Br. 4 in the Arctic Greenhouse. — a-b: Normal appearance at flowering stage. — c-e: Later stage with elongated decumbent stems producing leaf rosettes in leaf axils and ascending sometimes elongated racemes with long siliques (c). In d fusion between proximal part of pedicel and subtending leaf (marked with*). — Scale 10 cm.

than the sepals, 1.6–3 mm long and not rarely fewer than four. The siliques were densely pubescent, up to 8 mm long and 3.2 mm broad, with 0.4 mm long styles and 1.2–1.4 mm long, finely dotted or granulate seeds. In a few flowers the two carpels were not united and of unequal size, the short style being borne on the larger carpel.

***Braya rosea* (Turcz.) Bunge**

According to SCHULZ (1924: 232) this is a central asiatic montane species but belonging to a species aggregate comprising also *B. aenea* Bunge. *B. angustifolia* (N. Busch.) Vass. has also now to be referred to this aggregate (see KOMAROV-BUSCH Flora URSS VIII, 1939).

Chromosome studies. Counts were made in meiotic material of plants raised from seeds obtained from the Botanical Gardens in Leningrad. $n = 21$ was found in numerous cells (Figs. 12 a–f). Some deviations were noticed such as a pair of univalents (Fig. 12 d), occasional laggard bivalents at first anaphase and bridge formation at second anaphase. Fig. 12 f shows one acentric fragment and a dividing persistent double bridge connecting three of the resulting chromosome groups. The size difference between the bivalents is rather conspicuous.

Cultivation. The plants were cultivated as Br. 4 together with *B. linearis* and *B. novae-angliae*. They showed some resemblance to *B. linearis* but were much coarser with broader siliques and upright-ascending, always entire, rosette leaves, cp. Table 7 and Plate IX d–h. Both species had a clear tendency towards additional rosette formation in the axils of stem leaves, but in *B. rosea* this axillary rosette formation became abnormally prolific late in the year (August) in the batch cultivated in the Arctic Greenhouse (Fig. 11). Some of the rosettes were cut off and planted as cuttings but were unable to produce roots.

Morphology. Table 8 contains a summary of the description given by SCHULZ (1924) compared with measurements of herbarium material from Asia and the Cult. Br. 4. The cultivated plants greatly exceed the dimensions given by SCHULZ and have 2–6 stem leaves. The inflorescence is elongated but terminates in a dense or capitate part. The siliques are 6–12 mm long and the styles are either narrow along their entire length or expanded below the stigma. In some specimens a number of new axillary rosettes were concentrated on the main stem as a new basal rosette separated from the first formed rosette by an elongated internodium (Fig. 11). The difference between such plants and those with many rosettes in stem leaf axils depends only on an elongation of the internodia between the leaves which subtend the short rosette shoots.

Another character which is not mentioned in the description by SCHULZ nor appears from his drawings (Fig. 47 L–N) is the occurrence of fusions between the proximal parts of the pedicel and the subtending leaf.

The degree of pubescence varies within the population. Some plants were completely glabrous (cp. var. *glabra* Regel & Schmalh.).

Taxonomy. Some of the deviations from typical *B. rosea* found in Br. 4 may be due to better growing conditions in culture, but the longer siliques and larger number of stem leaves deserve attention. In height Br. 4 resembles *B. aenea*, but not in the breadth of the rosette leaves and the siliques. It therefore probably represents a new taxon but any description has to be postponed until more information is available.

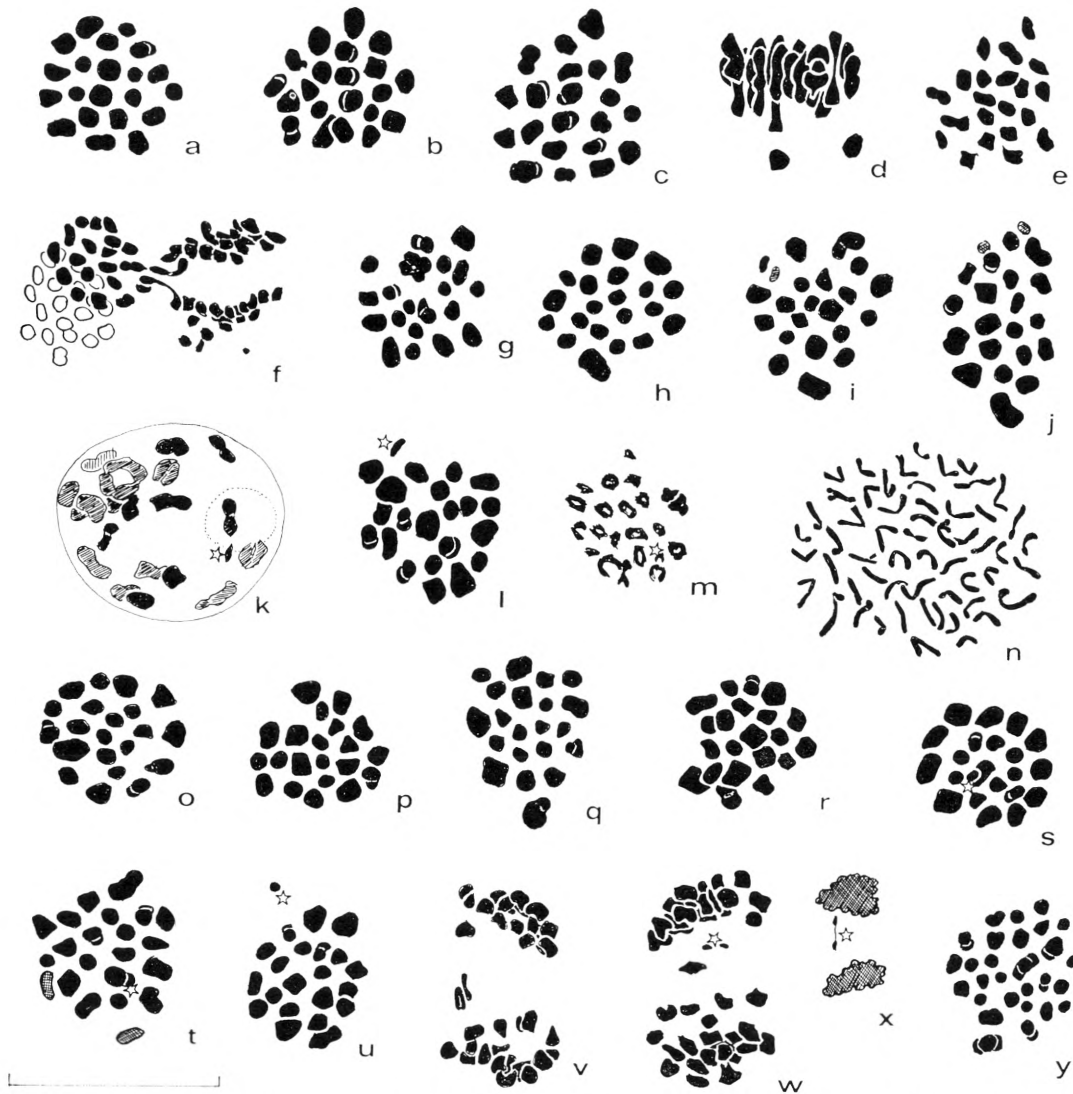


Fig. 12. Chromosomes in *Braya*. — a-f: *B. rosea* (No. Br. 4, $n = 21$; a-d: Mataphase I; e: anaphase I; f: anaphase II with dividing bridge and acentric fragment). — g-m, o-x: *B. linearis* ($n = 21$; g: No. 845 with one ring of four; h-j: No. 4855 in i with precousciously separated pair, in j with one pair of univalents; k-m: No. 4811 with one B, marked ☆; k: diakinesis; l: metaphase I; m: prometaphase II; o-x: var. *meizophylla* No. Br. 3; one B chromosome, marked ☆, in division or divided during anaphase I in v-w); — n and y: *B. novae-angliae*; n: ssp. *ventosa*, $2n = 56$; y: ssp. *novae-angliae* $n = 28$. — All microtome technique. — Scale 10μ .

Braya linearis Rouy

This species is restricted to the continental parts of W. and E. Greenland and Scandinavia, where it has a bicentric distribution (HULTÉN 1958: 82).

Chromosome studies. *B. linearis* is another hexaploid with $n = 21$ as found in material from two collections from Sdr. Strømfjord (BÖCHER & LARSEN

TABLE 7. Cultivations of *Braya*

Cult. No.	Taxon	Origin	2n	Diameter of first year rosettes, cm (Exp.: E*)	Rosette characters (first year)
6788	<i>B. alpina</i>	Gross Glockner, Austria	42	5.6(4.1–6.6)	Adpressed. Leaves entire, lanceolate, hairy
Br. 3	<i>B. linearis</i> var. <i>meizophylla</i>	Junkerdal, Nordland, Norway	42 + B	3.5(2.0–6.0)	Adpressed. Leaves variable. Entire-incised, glabrous-hairy, lanceolate to ovate-lanceolate
Br. 7	<i>B. linearis</i>	Sordal, Troms, Norway	42	5.0(3.0–7.0)	Adpressed. Leaves ± incised at distal end, lanceolate with marginal hairs
7388	<i>B. linearis</i>	Bovertun, Oppland, Norway	42	2.8(2.0–4.0)**	Small and adpressed lanceolate, slightly incised; hairy
4811	<i>B. linearis</i>	Store Saltso, W. Greenland	42 + B	4.6(1.6–7.0)	Adpressed. Leaves ± incised at distal end, lanceolate with marginal hairs
4855	<i>B. linearis</i>	Lille Saltso, W. Greenland	42	1.5(0.5–2.5)	Small and adpressed. Leaves entire-slightly incised, lanceolate-ovate lanceolate glabrous
Br. 4	<i>B. rosea</i>	Leningrad, Bot. Gardens	42	7.5(4.0–11.0)	± Upright. Leaves entire lanceolate, ciliated at base, shiny

* Experiments: A–D: In pots in frames at the Experimental Field (A 1959, B 1962, C 1964, D 1965). E–G: In pots lowest flower between rosette leaves.

1950), one from Ella Ø, NE. Greenland (JØRGENSEN et al. 1958) and one from Jotunheimen, Norway (KNABEN in JØRGENSEN et al.). New material of this species consisted of plants raised from seeds from five places viz.

No. 4811. West Greenland. Shores of Store Saltso at Sdr. Strømfjord.

No. 4855. West Greenland. Shores of Lille Saltso at Sdr. Strømfjord.

No. Br. 3 Norway, Junkerdalen Nordland (see text).

alpina, *B. linearis* and *B. rosea*.

Height of plants with ripe siliques cm, experiments A-G*	Breadth broadest stem leaf mm	Length of ripe raceme cm	Length of ripe siliques mm	Petal size mm L Length B Breadth	Other characters
C: 4 (3-5) D: 5 (4-6)		D: 1.8-2.0	C: 8-9 D: 10-11	L: 0.9-1.2 B: 1.1-1.5	Petals pale lilac, slightly emarginate. Sepals ± persistent
B: 6 (3-9) C: 7 (5-9) D: 7 (5-9) E: 25 (16-31) F: 16 (11-21) G: 24 (22-27)	D: 2-3.5 E: 2-3.5 G: 2-3	D: 4 (2.5-6) E: 7 (5-10) G: 8 (4-11)	D: 10 (9-11) E: 12 (11-13) G: 11 (11-12)	L: 1.0 B: 1.0	Petals white (-very pale lilac) emarginate. Hairy siliques. Stem leaves long and spreading sometimes subtending small rosettes
C: 7-8 F: 17-18 G: 23	F: 1-1.5 G: 1-1.5	G: 6	G: 11	L: 1.0 B: 1.0	Very slender, greener and later flowering. Weak; few plants reached flowering stage
D: 6 (4-10)	D: 1-1.5	D: 4 (3-5)***	D: 8 (7-9)	L: 1.0 B: 1.0	Stem leaves few and short. Petals white (-very pale lilac) emarginate
A: 3.8 (2-8) C: 6.0 (3-8) D: 5.0 (3-6) E: 18 (14-23) F: 16-20 G: 21 (12-25)	E: 1.3-1.5	E: 7 (5-9) G: 8 (3.5-10)	A: 10 C: 9 (8-11) E: 8 (7-9) G: 11 (8-12)	L: 1.0 B: 1.0	Petals white (-very pale lilac), not or very slightly emarginate. Siliques ± spreading
A: 2.9 (1.5-4) E: 16 (13.5-18) F: 16-25 G: 20 (11.5-26)	E: 1.0-1.5	E: 6 (4-11) G: 6 (4-11)	A: 7 E: 8 (7-9) G: 10 (9-11)	L: 1.0 B: 1.0	As the preceding but siliques ± upright, curved. Plants more slender
B: 14 (5-17) E: 33 (26-42) F: 12-21		E: 10 (5-17.5)	E: 9 (7-12)	L: 2.0	Petals white, not emarginate. See further Table 8

in the Arctic Greenhouse (E 1961, F 1962a, G 1962b). ** Experiment D. *** Entire stem often occupied by raceme;

No. Br. 7 Norway, Sørødal, Troms (coll. by Dr. G. Halliday).

No. 7388 Norway, Høirokampen, Oppland (seeds from Bergen; probably the same population as studied by Dr. G. KNABEN).

All five had $n = 21$ (Figs. 10 e, 12 g-m, o-x) but in two, viz. No. 4811 and Br. 3 a supernumerary small chromosome occurred. The difference in size between the bivalents is striking. One bivalent seemed to exceed all the others. This size dif-

Table 8. *Braya rosea* and *B. aenea*.

Origin	Height in cm of plants	Rosette leaves	No. of stem leaves	Inflorescence	Sepal length mm	Petal length mm	Siliques		Style length mm	Axillary rosettes
							Length mm	Breadth mm		
<i>B. rosea</i> . Description in Schulz 1924: 231	2-5 (-10)	Lanceolate (obverse lanceolate obtusiuscula), mostly entire, glabrous; petioles ciliated	0-1	Capitate with remote flower in stem leaf axil	2.5	3.5	4-6	1.5	0.5-1.0	
<i>B. rosea</i> f. <i>albiflora</i> Maxim. Valley of Dar river, Margelan Distr. Fergana Prov. N. Dessiatoff, 1913, No. 1368, Bot. Museum, Stockholm	2-5	Spathulate-lanceolate, 2 cm long, entire ± glabrous; petioles ciliated	0-1	Capitate very short	2.0-(2.5)	3-(3.5)	Broadest at base, not ripe		-	
<i>B. rosea</i> . Altai, near glacier, P. Krylow, 1900, Herb. Flor. Russ. Fasc. XXIII No. 1105 (distrib. as <i>B. aenea</i>), Bot. Museum, Copenhagen	5-9	Spathulate, 1.5 cm long entire, glabrous; petioles ciliated	1-(2)	Lowest flower removed from capitate inflorescence	2.0-2.5	2.2-3.5	4-6	Above 1.3, below 1.6-1.9	0.4-0.8	+
<i>B. rosea</i> Cult. No. Br. 4 see p. 42 and Fig. 11	5-42 see Table 7	Lanceolate spathulate glabrous; petioles sparsely ciliated	(1)2-6	Raceme capitate or with several flowers below. Racemes 5-17.5 cm long	2.5-3.0	3.3-4.0	6-12	Above 1.2, below 2.0	1.0-1.5	+
<i>B. aenea</i> . Description in Schulz 1924: 232	4-10 (-12)	Linear, with narrow petiole	-	-	2-2.5	3.0-3.5	4-6.5	1.2	More slender than in <i>B. rosea</i>	
<i>B. aenea</i> . Jakutsk, Sibiria oblastia, Balaganach. N. H. Nilsson 1898, No. 7135, Bot. Museum, Stockholm	7-17	Almost linear	1-2 very narrow	Lowest flower much removed from capitate inflorescence	2.0	3.0	10-15	Above 0.5-0.6, below 0.8-1.0	0.8	
<i>B. aenea</i> . Jakutsk, Sibiria oblastia, Kumach Sur (ca. 71°30'). N. H. Nilsson, 1898, Bot. Museum, Stockholm	11-20	Linear-lanceolate narrowly, spathulate, glabrous; petioles ciliated	2-3	Lowest flower from ± capitate inflorescence	1.6-2.5	3.0-4.0	7-12	1-1.1	0.4-0.7	+



Fig. 13. Variation in Norwegian *Braya linearis*. Two specimens on the left var. *meizophylla* (Type of the variety) from Junkerdal (leg. Peters & Petterson July 1904, Bergens Museum). On the right three specimens from Bardu in Troms Fylke. Lundeng in Sordal (leg. A. Blytt July 1891, Bot. Museum, Copenhagen), cp. Cult. Br. 3 and 7 and Plates IX-X. - Scale 10 cm.

ference was also found by JØRGENSEN et al. It is greater than in *B. rosea* (Br. 4). One possible quadrivalent or association of four was seen in some PMCs of No. 845 which was studied by BÖCHER & LARSEN 1950 (see Fig. 12 g). In No. 4855 two small chromosomes may be precociously separated (Fig. 12 i) but in one cell (Fig. 12 j) behaved as true univalents; two larger univalents were observed occasionally in Br. 3 (Fig. 12 t).

The small extra chromosome in No. 4811 during diakinesis was placed near or in connection with one of the chromosomes of a pair (Fig. 12 k). It was detected in some first metaphase plates (Fig. 12 l) and could be traced through first anaphase to the second prometaphase (Fig. 12 x). Its later fate could not be followed. In Br. 3 from Norway the small extra chromosome was sometimes easy to see during first metaphase (Fig. 12 s-u) but mostly it was impossible to detect and was assumed either to be absent from some of the PMCs or was sticking to one of the chromosome pairs (see e.g. Fig. 12 q below). At first and second anaphase it was sometimes observed dividing or divided and often in connection with a lagging chromosome (Figs. 12 v-x).

TABLE 9.

Origin	Height in cm of plants	Rosette leaves	Pubescence of stems	No. of stem leaves
Norway. Oppland. Bøvertun valley Høirokampen, K. Fægri & R. Nordhagen 1932, Bot. Museum, Bergen, 6 specimens (and for average heights 26 specimens from Bøvertun)	9 (5-15)	Narrowly spathulate, entire or with 1 (-2) pair of teeth	Hairy	2-3
Norway. Nordland. Junkerdal, scree, Joh. Dyring, July 1893, Bot. Museum, Bergen, 25 specimens	12 (5-26)	Narrowly spathulate, entire or with few shallow teeth	Hairy	1-3
Norway. Troms Fylke. Sørødal. Bardudalen, Axel Blytt, July 1891, Bot. Museum, Bergen and Copenhagen, 22 specimens	8 (4-14)	Lanceolate entire and short	Hairy	0-2
W. Greenland, Store Saltso near head of Sdr. Strømfjord. TWB. Aug. 1946, Nos. 499-500. Bot. Museum, Copenhagen, 11 specimens	10 (7-16)	Linear-narrowly lanceolate (-spathulate)	Hairy	1-2 (3)
W. Greenland. Head of Sdr. Strømfjord, Roadside near Airbase, TWB. Aug. 1946, No. 493, Plate Xa. Glabrous form	(10-14)	Linear-lanceolate (-spathulate)	Glabrous	1-2

In Br. 3 a tendency towards a peripheral positioning of the large pairs was particularly pronounced (see e.g. Fig. 12 s).

Cultivation. The four strains cultivated simultaneously exhibited some differences which deserve consideration (cp. Table 7).

The Norwegian strains Br. 3 and 7 were clearly very different, Br. 7 being much more slender and difficult to cultivate (Plate IX a, c, p, q, Plate X e, f). Only a few specimens completed a normal life cycle, and many died as rosette plants. The few specimens with ripe siliques attained similar heights to No. 3 but the stem leaves were much narrower and aggregated towards the base. The first year rosettes, on the other hand, were broader.

The Greenland strains No. 4811 and 4855 closely resembled one another. Some small differences appear from Table 7. In almost all characters No. 4855 is slightly smaller than No. 4811. The largest difference was found in the first year rosette diameters.

In both Norwegian strains the petals were slightly emarginate while they were

Braya linearis.

Longest stem leaf		Sepal length mm	Petal length mm	Longest siliques (without style)		Style length mm	Axillary rosette	Persistence of sepals and petals
Length cm	Breadth mm			Length mm	Breadth mm			
1-3	0.4-1.1	2.0-2.3	3.2-3.4	6.2-7.2	1.1-1.4	0.1-0.3	+	±
2-5.5	1.5-3.0	2.2-2.3	3.5-3.6	8.3-11	1.2-1.5	0.3-0.5	+	+
0.8-1.5	0.2-1.0	1.7-1.8	? 2.5	7.5-9.0	1.1-1.2	0.3-0.5	(+)	÷
2.5-3.0	1.0-1.4	1.7-2.2	2.5-3.5	7.5-11	1.4-1.4	0.2-0.5 (0.6)	(+)	÷
2.5-2.6	1.0-1.5	-	-	10-12	1.2-1.4	0.4-0.5	+	÷

entire in those from Greenland; otherwise there was no general difference between the plants from the eastern and most western populations of the species.

Taxonomy. The only difference which may deserve taxonomic recognition is that found between Br. 3 and the other strains. The material of Br. 3 was received as seeds in 1959 from the Botanical Gardens of Bergen. Professor KNUT FÆGRI and professor PER WENDELBO have kindly tried to trace the origin of the seeds and came to the conclusion that they were collected on plants either from Jotunheimen (Høyrokampen) or from Nordland (Junkerdaalen). A comparison of the material of Br. 3 with a great number of herbarium sheets in the Botanical Museums in Bergen, Oslo and Uppsala revealed that Br. 3 closely resembles plants from Junkerdaalen. Likewise a large number of specimens from Sørdaalen in Troms were very similar to Br. 7 being small and slender. Some of the observations are collected in Table 9. It appears that the specimens from Junkerdaalen are larger, with longer and broader stem leaves and often with elongated racemes, just as in Br. 3. The plants from Jotunheimen are small with very narrow leaves, as in the cultivated specimens from that

locality (Table 7). Almost all plants from Troms, Finmark and Jotunheimen have narrow leaves and are comparatively low as are some from Nordland (e. g. Bindalen, Knurvig, Ravatnet in Vefsen). The broad-leaved type occurs in Junkerdalen and Saltdalen but closely similar specimens were also collected in Lule Lapmark in Sweden more to the east (Aresvare north of Vastenjaure, leg. T. Å. Tengwall 1913). Even specimens from Jukkasjärvi (leg. H. Smith 1920) may be related.

The broad leaved and relatively robust race is concentrated in Junkerdal-Saltdal, but the genes which distinguishes it may be traced as introgressions in some Swedish populations. Not all specimens from Junkerdal-Saltdal correspond to Cult. Br. 3. Some have long erect red peduncles and leaves aggregated below (e. g. specimens collected by Mörner 1885 and E. Jørgensen 1923). Thus the population here is not uniform. In some cases relatively broad and long stem leaves may be found in single specimens from outside Junkerdal-Saltdal (e. g. Troms-Målselven, leg. I. M. Norrman, Bjørkåsen, leg. Andr. Notø; Sør-dal: Sørgaard, leg. Andr. Notø and Sørmo, leg. Peter Beum, all Herbarium Oslo). They may represent modified specimens of the normal type or be genetically related to the Junkersdal-Saltdal-race.

In order to stimulate a further study I have chosen to describe the Br. 3 type as var. *meizophylla* var. nova. *Differt a var. linearis foliis caulinis usque ad 3 mm latis, 5.5 cm longis, racemis elongatis. Habitat in vallibus Junkerdalen et Saltdalen, Norvegiae. Typus in valle Junkerdalen Norvegiae a Peters & Petterson lectus in Museo Botanico Bergensi depositus, in Fig. 13 depictus.*

The occurrence of var. *meizophylla* coincides with a number of very rare arctic plants which in Norway has been considered as "interglacial survivals". According to NORDHAGEN (1935: 135) there are here isolated occurrences of *Arenaria humifusa*, *Carex scirpoidea*, *Saxifraga aizoon* (ssp. *laestadii*, see HOLMBOE 1936 map. Fig. 12), *Papaver radicum* ssp. *subglobosum*, to which may be added *Potentilla hyperborea* (*emarginata*), found on the Swedish side, and the southern group of localities of *Pedicularis flammea* (see NORDHAGEN 1933 Fig. 5). These striking isolated assemblages make the occurrence of var. *meizophylla* particular interesting as it seems to indicate that it constitutes an old population which perhaps was isolated in an ice-free pocket during the last glaciation.

The scree vegetation on limestone and mica-schists with *Braya linearis* var. *meizophylla* was described by NORDHAGEN (1954: Fig. 3 and Table 2). Fig. 4 in the same paper shows typical specimens of the variety growing in the scree of Baatfjell, Junkerdal.

***Braya alpina* Sternb. & Hoppe**

Braya alpina is an endemic east-alpine species, a character species of calcareous screes (*Leontodontetum montanei*) cfr. GAMS (1936: 49). Material was obtained from the Grossglockner area (seeds kindly collected at "Wasserfallsee" by Dr. ZOLLITSCH and sent by Prof. H. MERXMÜLLER). The plants Cult. No. 6788 were grown together with *B. linearis* (see Table 7).

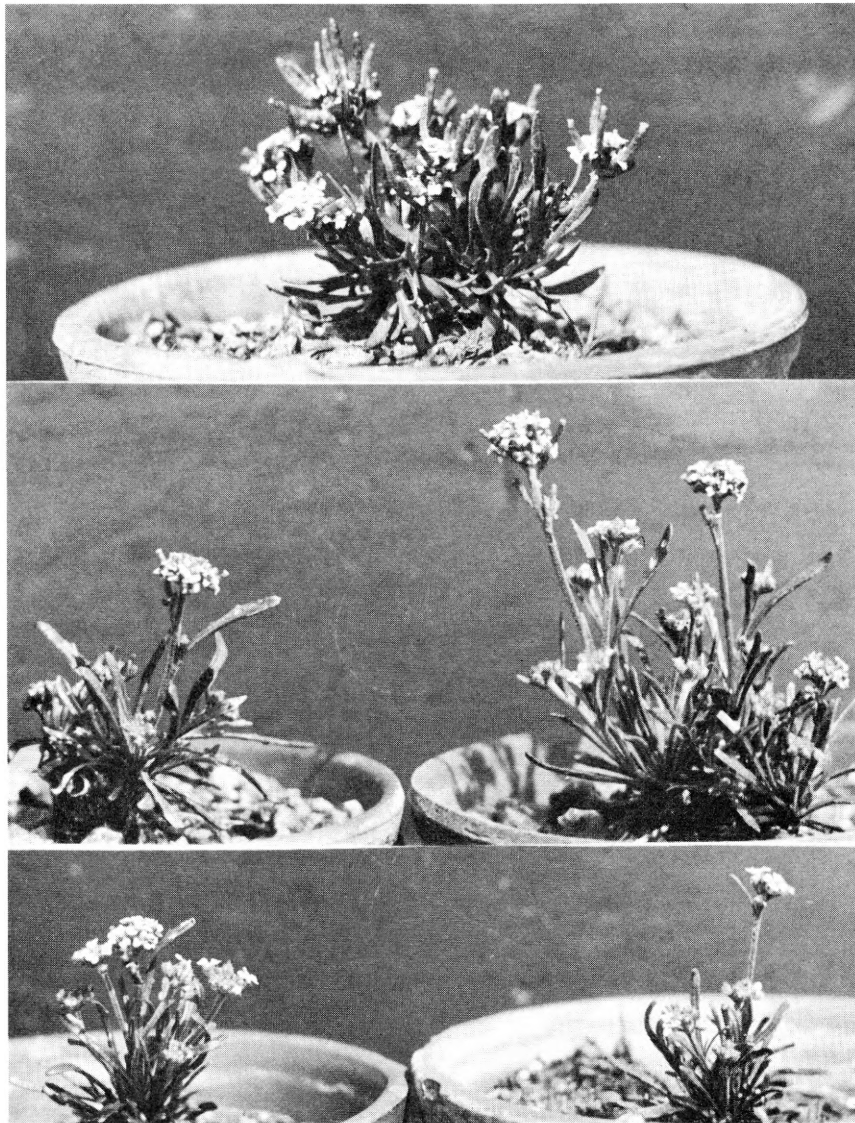


Fig. 14. Above *Braya alpina* (No. 6788) compared with two specimens of *B. linearis* var. *meizophylla* (Br. 3, middle row) and two of *B. linearis* (No. 7388, below). All cultivated simultaneously in pots at the experimental field. May 1965.

Chromosome number. The old count of $2n = 32$ (MANTON 1932: 545) could not be verified, the error being perhaps due to falsely identified plant material. Squashes of PMCs and root tips of No. 6788 showed 21 bivalents or 42 chromosomes (Figs. 10 f-g), the same number as in *B. linearis* which has been considered by some as a variety of *B. alpina* (var. *rivularis* Fries). In the plate pictured by MANTON (1932 Fig. 24) the chromosomes are only slightly different in size almost as in the genus

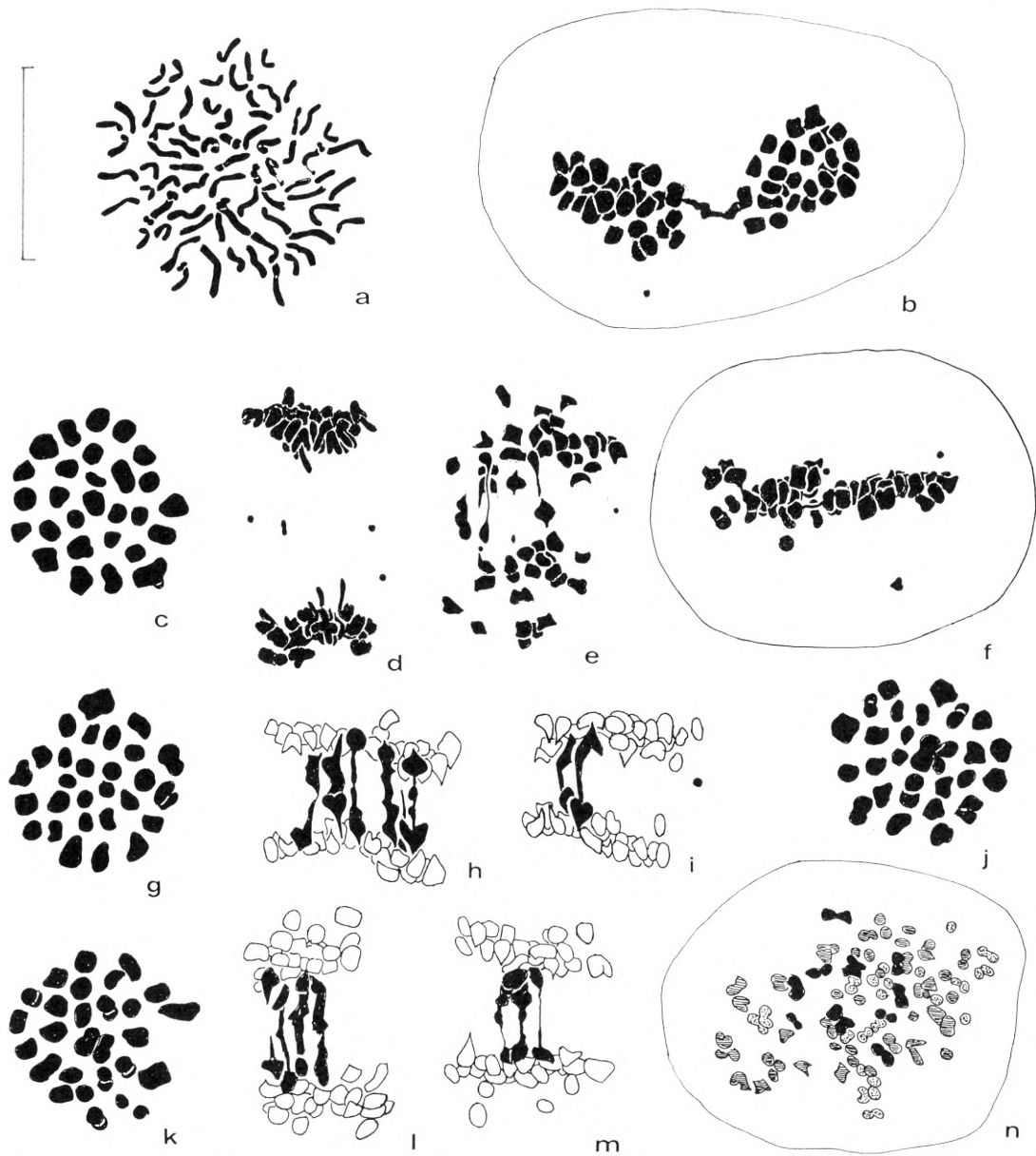


Fig. 15. *Braya*. — a: Metaphase plate in root tips, *B. intermedia* from NE. Greenland ($2n = 70$, cp. Böcher 1956). — b–n: PMCs in *B. purpurascens*; b–f: Cult. No. KJ 54; g–i: Cult. No. KJ 53, both from Nugsuaq, W. Greenland; k–n: Cult. No. 6356 from Spitzbergen; c, g, j, k: first metaphase; d, e, h, i, l, m: first anaphase; b, f: second metaphase; n: restitution nucleus (see text). Inversion bridges and acentric fragments in b, d, e, f and i; bridges due to stickiness in h, i, l, m (see Text). — All microtome technique. Scale 10μ .

Draba. According to MANTON the basic number in many other genera of the tribe *Alysseae* is seven, thus e.g. $2n = 14$ in *Chorispora tenella* which is referred to the subtribe *Braginae*.

Cultivation. In the first year rosette stage there was a clear difference between *B. alpina* and *B. linearis*. *B. alpina* had more vigorous rosettes and its leaves were entire and hairy (along the margins and on the lamina) while in *B. linearis* they were often incised, glabrous or if hairy mainly along the margins. Both species had \pm depressed rosettes. The leaves of *B. alpina* are broader and more succulent and anatomically distinguished by a more dorsiventral structure. *B. linearis* has almost isolateral leaves. Second year flowering plants differed from *B. linearis* in the following characters: petals larger and pale lilac, sepals (and some petals) often persisting below ripening siliques which are shorter and a little broader. *B. alpina* is earlier, all plants having ripe siliques by June 5th, while three strains of *B. linearis* still had flowers and unripe fruits. *B. alpina* is lower and its inflorescence more dense and capitate. Finally the styles in *B. alpina* (No. 6788 and herbarium material) are broader and more often tapering.

The comparative cultivation makes it evident that *B. alpina* and *B. linearis* are clearly distinct species. They are obviously related as are *B. linearis* and *B. aenea*, cp. p. 71.

***Braya purpurascens* (R. Br.) Bunge**

This species was studied in the Arctic Greenhouse in plants from East Greenland and Spitzbergen. Additional material from Nugssuaq W. Greenland was kindly placed at my disposal by Dr. KNUD JAKOBSEN. Unfortunately, many plants which were brought into culture in order to compare W. Greenland, East Greenland and Spitzbergen material died early in a rosette stage. A more detailed comparison therefore was made impossible. The general impression, however, is that *B. purpurascens* is a very polymorphic species and this seems to be explained by its meiotic behaviour. Six strains were examined: viz. two cultivated by KNUD JAKOBSEN as KJ 53 (from Store Dal, Nugssuaq) and KJ 54 (Marrait, Nugssuaq), three strains from Mestersvig in NE. Greenland (Nos. 6679 and 7114, seeds collected by Dr. T. T. ELKINGTON, No. 7368 from Central Skeldal at Mestersvig, D. SPEARING and N. LASCA No. 767), and one strain No. 6356 from W. Spitzbergen, Kongsfjord $78^{\circ}58' N.$, $12^{\circ}10' E.$ (seeds collected 1958 by Dr. NIELS FOGED).

Cytological observations. *B. purpurascens* is an octoploid with $n = 28$. This number was first counted by HOLMEN (1952) in material from Peary Land and later by JØRGENSEN et al. in material from Clavering Island NE. Greenland and by MULLIGAN (1965) from Northwest Territories, Alaska and British Columbia (see Postscript). The six new strains to be discussed here had also $n = 28$ (Fig. 10 j-k and 15).

It was particularly interesting that three of them proved to be structurally deviating in various ways.



Fig. 16. Variation in *Braya purpurascens*. — a: NE. Greenland, Nordfjord (P. J. Povelsen June 1949). — b-c: N. Greenland, Peary Land, Brønlund Fjord (K. Holmen Nos. 6757 and 687). — d: NE. Greenland, Strindberg Halvo (Th. Sorensen No. 3566). — e: W. Greenland, Ignerit Fjord, Magdlâq (M. P. & R. T. Porsild July 1929). — f: Baffin Isl. Frobisher Bay (H. A. Senn & I. A. Calder No. 4020). — g: Alaska, Atkasuk 70°28' (K. Holmen & Olle Mårtensson No. 61-1526). — h: Alaska, Utokok River, 68°55' (K. Holmen, August 1960). The latter belongs probably to *B. glabella*, but in shape of the siliques it is approached by the specimens a, and e-g while specimens b-d have siliques which clearly are broadest in the middle part. Specimen d shows an extreme case with headlike inflorescence. — All specimens from the Bot. Museum in Copenhagen. Scale 10 cm.

No. KJ 54 (Figs. 15 b–f). In this strain bridges and acentric fragments occurred with great frequency, the number of bridges per cell at first anaphase often amounting to four. In some cells one bridge persisted until the second metaphase (Figs. 15 b, f) and was in one case (Fig. 15 f) very short almost uniting the two plates. At second telophase two or three bridges were seen with a corresponding number of acentrics. Laggards occurred in a few cells, while 1–2 univalents were not infrequently placed outside the two nuclei in PMCs at interphase.

Nos. KJ 53 (Figs. 15 g–i) and 6356 (Figs. 15 k–n) resembled each other but deviated from the preceding by the rare occurrence of bridges due to inversions. On the other hand there was sometimes an abundance of bridges which seemed to be due to stickiness, probably mainly localized stickiness resulting from sub-chromatid exchanges (see EVANS 1962, BÖCHER 1964). In Fig. 15 h the bridge on the far right has clearly two side arms as found in plants with localized stickiness. The bridges were often found in a central position in the separating chromosome plates, and the same position was held by some groups of four chromosome at metaphase I (Fig. 15 j–k) which were not assumed to be quadrivalents. In fig. 15 l–m there seemed to be a connection at one end between two of the bridges which makes it probable that the groups of four are held together by sticky connections.

The highly deviating cell fig. 15 n represents probably a rare case. It was found among young pollen tetrads and its chromosome content resembled a giant restitution nucleus. Most chromosomes were dividing (second division). A neighbouring cell had some lagging bivalents surrounded by scattered univalents. Perhaps division into four pollen cells is inhibited in such cells which finally will develop into giant pollen grains, which sometimes are found in *Braya purpurascens*.

It is difficult to estimate to what extent and in which way such cytological disturbances influence the variational pattern. However, it is not too speculative in this case to state that the species as compared with e.g. *B. linearis* is cytologically more unstable and morphologically more variable. In many respects it resembles the high polyploid complex species of *Draba*.

Cultivations. The Spitzbergen strain No. 6356 was slender as compared with the West Greenland plants KJ 53–54 which were cultivated at the same time in the Arctic Greenhouse. Unfortunately all plants of No. 6356 died after having set fruit and could not be compared with the East Greenland plants. In 1965 the two series from Mestersvig (No. 6679 and 7114) were relatively robust and almost identical while No. 7368 from Skeldal was much more slender with smaller flowers. The dimensions appear from Table 10. All three strains had glabrous siliques, while the West Greenland strains KJ 53–54 had hairy siliques and KJ 53 longer siliques (up to 10–11 mm long).

Variation. If taken in a very wide sense this complex would be a species aggregate consisting of the octoploid *B. purpurascens*, the tetraploid *B. thorild-wulfii* (see OSTENFELD 1923) and probably *B. glabella*, *B. pilosa* and *B. henryae* (see RAUP 1934), which are unknown cytologically. Taken in a more restricted sense, however,



Fig. 17. *Braya glabella* Rich. Authentic, specimen kept in the Naturhistorisches Reichsmuseum in Vienna. The type specimens kept at Kew from the Franklin Expedition correspond to this specimen although in one of the plants there is one large stem leaf in the middle part of the stem subtending a very remote silique. The Copenhagen Herbarium contains two specimens of the type collection, a very small one and a larger which, however, is without the terminal part of the inflorescence.

Table 10.

Cult. No.	Origin	Height cm	Dia- meter of stem mm	Breadth of broadest rosette leaf mm	Dia- meter of flower mm	Length of lowest siliques mm	Breadth of broadest siliques mm	Other characters
6679-7114	Mestersvig Damp soil	9(6-13)	1.5	5-7	(4)5-6	8-9 (Style 1 mm)	3	Siliques glabrous. Not infrequently with one stem leaf subtend- ing remote flower
7368	C. Skeldal Heavily cracked clay mounds	9(6-10)	1.0	3-(4)	(2)3-4	8-9 (Style 0.6-0.9 mm)	2	Siliques glabrous. Very rarely with one stem leaf. Sometimes flowering at the basal rosette

B. purpurascens is very complex in itself (Fig. 16), but it is here, as in *Draba glabella* and *D. arctica*, difficult or impossible to find dividing lines enabling a sensible taxonomic subdivision. ABBE (1948) is not inclined to recognize any of the variants which SCHULZ (1924) has accepted. A. E. PORSILD (1955: 133) discusses the badly defined var. *dubia* (R. Br.) Schulz, which he would like to be able to use as a name for certain high arctic compressed and decumbent forms. Otherwise he describes the variation as very considerable as to stature, shape and degree of pubescence of the siliques, length of style and length of flowering and fruiting axes. Even within the same population, plants with pubescent siliques might be as common as those with perfectly glabrous ones. HOLMEN (1957: 52) on the other hand says that *B. purpurascens* in Peary Land varies somewhat, but that this variation is due to differences in environmental conditions. *B. purpurascens*, therefore, may locally appear rather uniform, but studied in its total range, it is clearly polymorphic. This impression is based on studies of the style lengths and shape of the stigma (see BÖCHER 1956 Fig. 8 b-d) and on the preliminary observations of cultivated plants mentioned above.

***Braya glabella* Rich.**

No living plants have been available for study, but in the Vienna Herbarium a specimen was found which most probably is authentic. It is labelled "*B. glabella* North America, Hooker" (see Fig. 17) and it corresponds entirely with the description given by SCHULZ (1924: 230).

ABBE (1948: 9) concludes that *B. glabella* falls in the *B. purpurascens* complex more than it does in the *B. linearis* group and this agrees with the opinion set forth by JØRGENSEN et al. (1958). In BÖCHER (1956: 13) *B. glabella* was assumed to have resulted from a cross between *B. linearis* and *B. purpurascens*, but this idea has now

clearly lost much credibility, as the authentic material resembles *B. pilosa* and *B. henryae* and also approaches *B. rosea-aenea*. Furthermore the established localities for *B. glabella* are West-American and *B. linearis* is unknown west of West Greenland. *B. glabella* resembles what ABBE pictures as the "robust phase" of *B. purpurascens*, but has an elongated inflorescence. It also resembles plants from Southampton Island collected by MALTE and referred by him to *B. glabella* but by ABBE to the above mentioned "robust phase". A. E. PORSILD, however, referred MALTE's plants to *B. pilosa* (1943: 46). A recent collection by K. HOLMEN from Utokok River in Alaska (68°55' N., 161°10' W., Aug. 1960) and kindly placed at my disposal (Fig. 16 h) was recently determined by A. E. PORSILD as *B. glabella*. It has 1 mm long styles with capitate stigmas and glabrous 10 mm long siliques. The petals are 3.5–4 mm long and reddish. The stems have scattered hairs and the leaves are narrowly spatulate, glabrous but ciliated on the petioles. The racemes are elongated and the lower siliques are remote from the terminal part as in *B. rosea*. The appearance of this plant as well as of the material from Vienna suggests that it belongs to a separate species closely related to *B. purpurascens*. The identity of *B. glabella*, however, is still problematic and the questions cannot be answered before material has been cultivated along with the "robust phase" of *B. purpurascens* and chromosome studies have been made.

***Braya novae-angliae* (Rydb.) Th. Sør.**

Braya novae-angliae is another polymorphic species. In the previous paper (B. 1956) it was divided into three subspecies and its ssp. *novae-angliae* into three varieties, this division being partly based on the geographical races mentioned by ABBE (1948).

The chromosome number of *B. novae-angliae* was first counted by BÖCHER & LARSEN (1950) who found $2n = 56$ in material from continental West Greenland. In the paper of 1956 this number was corroborated by studies of meiosis where a number of distinct metaphase plates clearly had 28 bivalents. New material from West Greenland collected in 1956 at Tarajonitsup (Salt lake area at Strømfjordshavn) has now been cultivated for several years (No. 4885) including 1962–65 when it was grown together with Br. 6 originating from Colorado.

The material from Colorado was collected in 1960 by Dr. K. HOLMEN on the summit of North Star Mt., Hoosier Pass, 1200', 150 km SW of Denver. It is obviously the type locality for *B. novae-angliae* ssp. *ventosa* (Rollins) Böch. cp. ROLLINS (1953: 114) to which taxon the material belongs.

Chromosome number. As might be expected the Greenland plants (No. 4885) had the same number as those counted previously. Much more interesting, however, was that $2n = 56$ was established also in the Colorado sample (Fig. 12 n) in spite of the fact that ROLLINS in plants from the same area found $n = 32$. It is almost impossible to misinterpret a somatic plate like that in fig. 12 n. But according to my experience it is sometimes difficult to count meiotic stages in *Braya* because



Fig. 18. Simultaneously cultivated specimens of *Braya novae-angliae* var. *interior* (Cult. No. 4885, upper row) and ssp. *ventosa* (Cult. No. Br. 6, lower row). Arctic Greenhouse, Copenhagen July 1964. — Scale 10 cm.

so often some of the small chromosome pairs separate precociously (Fig. 12). The fact that ssp. *ventosa* has $2n = 56$ removes any doubt about its taxonomical status; it is closely related to ssp. *abbei* Böch. from Newfoundland, but is not an independent species, see remark p. 6 in BÖCHER 1956.

MULLIGAN (1965, see Postscript) also counted $2n = 56$ in plants from North

Table 11. *Braya novae-angliae*. Comparative cultivations.

	<i>Ssp. novae anglica</i> var. <i>interior</i> Cult. No. 4885	<i>Ssp. ventosa</i> Cult. No. Br. 6
First year rosettes	Adpressed, leaf colour variable between green and dark red-green, leaves (anthocyanin) in most cases with few hairs and little toothed. Diameter of rosettes 3.9 cm (2.5–6.0 cm)	Adpressed-ascending, leaves dark red-green, hairy, broadly ovate. First leaves ± entire, but increase in incision in later leaves which also are more hairy. Diameter of rosettes 4.2 cm (3.0–5.0 cm)
Later rosettes	Leaves lanceolate-narrowly spathulate, entire or with a few, broad and shallow teeth, reddish (or green), almost glabrous. Longest leaf 2–4 cm	Leaves spathulate, entire or rarely with 1–3 small sharp teeth, green, with scattered bifid (2-3-pronged) hairs along margin and unbranched cilia along petiole. Longest leaf 2.5–3.5 cm.
Stems	Stems 5–12(17) cm long, ± erect with ± dense pubescence of bifid (2–3-pronged) hairs; 3–11 narrow leaves, the largest being 1.5 cm long and 1.5 mm broad, often with 2 small teeth and scattered bifid hairs	Stems rather coarse 3–10 cm long, ± ascending with dense pubescence of bifid (2–3 pronged) hairs; 3(–5) leaves, entire, ± spathulate, the largest being 1.5 cm long and 2 mm broad with very few bifid hairs
Flower: Sepals Petals	2.5 mm long, with red spots 4–5 mm long, white with pink claw	3 mm long, green, persistent 5 mm long, white with pink claw
Pedicels	Obliquely upright, 2–4 mm	Divaricate, slightly curved 2–4 mm
Siliques	Max. length (without style) 13 mm, almost straight or slightly curved. Max. breadth 0.7–1.0 mm. Valves ± tapering above. Style 0.7 mm long, 0.3–0.4 mm broad. Stigma 0.5–0.7 mm broad. Seeds about 1.0 mm long	Max. length (without style) 16–19 mm, more curved than in No. 4885. Max. breadth 0.9–1.2 mm. Valves more rounded above. Style 0.8–1.0 mm long, 0.3–0.5 mm broad. Stigma 0.5–0.7 mm broad. Seeds about 1.0 mm long
Earliness	Much later in flower than Br. 6	Early

Star Mountain, Colorado. He has not subdivided *B. humilis* coll. and refers the material to this species aggregate. However, there is no doubt, that all specimens from Colorado belong to *B. novae-angliae* ssp. *ventosa*. MULLIGAN also states that the somatic chromosomes in *B. humilis* coll. are smaller than those in e.g. *B. purpurascens*, a fact which is in accordance with observations made by the present author (cp. Fig 12y).

Comparison of simultaneously cultivated plants. Table 11 contains a comparison of a number of characters in the two subspecies of *B. novae angliae*. It

appears that the main difference is expressed in the growth habit the leaf shape and colour, and the dimensions of flowers and siliques.

Of particular interest is the relation between ssp. *ventosa* and ssp. *abbei*. From a comparison of the information in Table 11 it appears that there is very little morphological difference between ssp. *abbei* and ssp. *ventosa*. This means that the suggestion expressed earlier (BÖCHER; 1956: 9) that ssp. *abbei* perhaps ought to be considered as a variety of ssp. *ventosa* might be discussed. At the present stage, however, I see

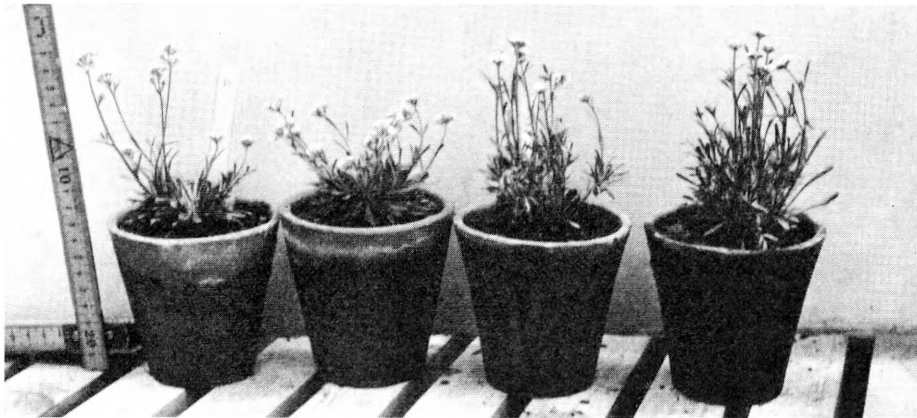


Fig. 19. *Braya novae-angliae* in full flower. On the left two pots with No. Br. 6 from Colorado, North Star, Mt., on the right two of No. 4885 from W. Greenland, Tarajonitsup. Arctic Greenhouse. 22th of June 1962.

no advantage in reducing ssp. *abbei* to varietal rank as it seems distinguished at least by one character: a higher number of stem leaves. From the picture in BÖCHER 1956 Fig. 3 of the type collection of ssp. *abbei* it appears that even small specimens of ssp. *abbei* may often have more than five leaves while cultivated specimens of ssp. *ventosa* did not have more than 3 leaves. Otherwise the two subspecies are widely separated geographically, ssp. *ventosa* being the only representative of *B. novae-angliae* in Western America.

5. *Kerneria*

Material of *Kerneria* collected by Dr. M. LEWIS in the Pyrenees (Garvarnie) was cultivated as No. 7332 and flowered abundantly in the Arctic Greenhouse as well as in pots at the Experimental Field. Root tips were squashed and the chromosome number determined as $2n = 14$ (Fig. 20).

The plants resembled *K. saxatilis* (L.) Rchb. but deviated in some characters from this species, which according to CHIARUGI (1933) has $2n = 16$ and perhaps $2n = 32$ (MATTICK in TISCHLER 1950). $2n = 14$ corresponds to the number found by CHIARUGI (1933) in *Rhizobotrya alpina* Tausch (= *Kerneria alpina* (Tausch) Prantl.), a relic species restricted to the southern Alps (Dolomiti occidentali).

CHATER & HEYWOOD (1964) in their treatise of *K. saxatilis* remark that further investigations especially on plants from the Pyrenees are needed and they discuss the identity of plants from that area which have been referred to *K. decipiens* (Wilk.) Nym. (*Cochlearia decipiens* Willkomm, see WILLKOMM 1852: 12). In such plants the cauline leaves are sagittate and amplexicaule at the base, and the siliques are ellipsoid-obovoid, not orbicular. They add that such plants tend to have somewhat showier petals but they do not list *K. decipiens* as a separate species.

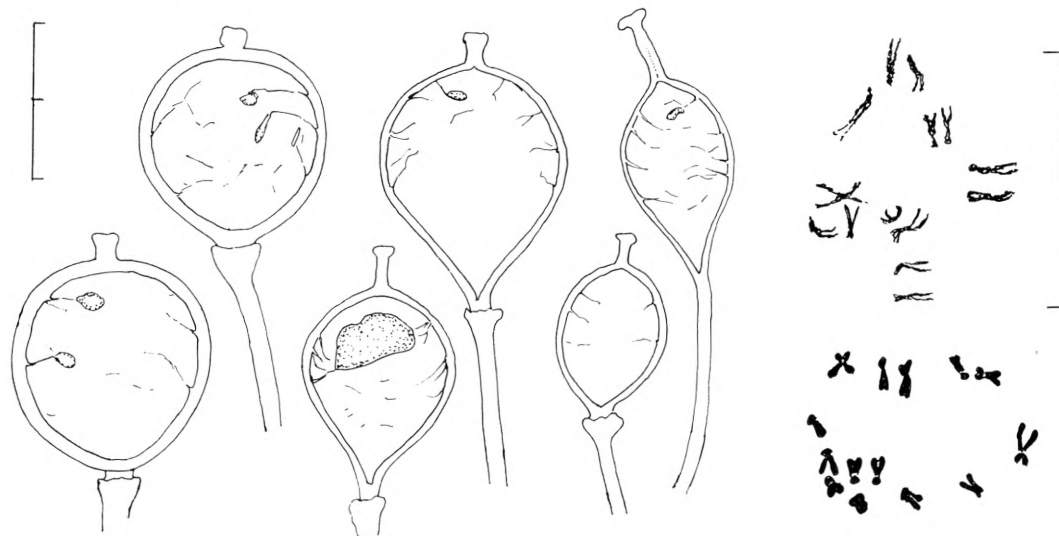


Fig. 20. *Kerneria*; from the left drawings of ripe siliques: two siliques of *K. saxatilis* (from river Drava at Feistritz, leg. J. Vahl 1824), two of *K. cfr. decipiens* (Cult. No. 7332) and two of *K. boissieri* (Sierra Nevada, Mt. Dornajo, leg. Campo 1852). Scale 2 mm. — On the right No. 7332, late prophase and metaphase from mitoses in root tips (orcein squash technique). Scale 10 μ .

The cultivated plants correspond to *K. decipiens* although the stem leaves are hardly sagittate, but clearly amplexicaul. The flowers are a little larger than most flowers in *K. saxatilis*, but the latter contains races with different flower size which makes it difficult to distinguish it from plants of the *K. decipiens* type.

The Copenhagen Museum contains some sheets from the Pyrenees and S. France which closely resemble Cult. No. 7332 (thus Fond des Comps, Pyren. leg. Blytt; St. Guilhem du Desert, leg. Ibérault(?), Inst. Bot. Montpellier; Pic Lhièris, Pyren. Centr. Gall. Sept. 1851 leg. Joh. Lange; Cevennes, Herbar. Liebm.). A comparison of this material with the cultivated plants seems to justify regarding *K. decipiens* as a separate taxon and the deviating chromosome number does not support its reduction to a subspecies of *K. saxatilis*.

It is not easy to distinguish *K. cfr. decipiens* from *K. saxatilis* morphologically, but two characters which appear from the material mentioned above seem to be important additions to the characters mentioned by WILLKOMM (1852) and WILLKOMM & LANGE (1880). First the number of stem leaves is higher and the internodia shorter

in *K. cfr. decipiens*, and the siliques of this taxon have thinner walls and the styles are longer.

With regard to the shape of the fruits *Kernera cfr. decipiens* is intermediate between *K. saxatilis* and *K. boissieri* Reuter from Sierra Nevada in Spain (see Fig. 20). Also *Rhizobotrya* (or *Kernera*) *alpina* has longer styles than *K. saxatilis* (CHIARUGI 1933: 70) and its siliques are not orbicular but broadly ovate and the style may be slightly tapering just as in the available material of *K. boissieri* and to some extent also in Cult. 7332 (*K. cfr. decipiens*).

The above mentioned herbarium material which probably is referable to *K. decipiens* indicates a certain variability in this species. The plant collected by JOHAN LANGE has broader, nearly spherical siliques and approaches thereby *K. saxatilis*, and the plants from the Cevennes are almost glabrous thus in this respect resembling *K. boissieri* which seems to deserve species rank being characterized by thick rhizomes, spatulate rosulate leaves and glabrous stems and leaves (see description in WILLKOMM & LANGE 1880: 842).

The discovery of plants with $n = 7$ in a *Kernera* should prompt further cytotaxonomical studies e.g. of *K. boissieri* and other highly deviating plants. At the same time it has weakened the theories about the evolution of the *Thlapsidinae* mentioned by CHIARUGI and also the justification of maintaining *Rhizobotrya* as a separate genus, the latter being mainly distinguished by having bracteate racemes.

6. Evolutionary trends

Draba

Chromosome numbers

From earlier studies, supplemented by some recent investigations, (e.g. MERXMÜLLER & BUTTLER 1965) a long series of euploid chromosome numbers is presented, the basic number of which is in most sections clearly 8. Counts have been made within eight of the 17 sections (subgenera) mentioned by SCHULZ 1927. In all, the numbers of 46 species and subspecies are known ranging from diploids ($2n = 16$) to sixteenploids ($2n = c. 128$).

In the section *Aizopsis* ($x = 8$) 10 species have been counted, of which 8 are diploids and 2 tetraploids ($x = 8$) (see SKALINSKA (1964), MERXMÜLLER & BUTTLER (1965)).

The section *Chrysodraba* ($x = 8$) goes a step further in having a high polyploid level throughout, the only exception being *D. sibirica* which is diploid. There are two species found at the octoploid level, and one sixteen-ploid, while in one complex species, *D. alpina*, different strains have been counted with $2n = 64, 80,$ and 112 . However, the tetraploids in the section *Aizopsis* seem to form a transition between *Aizopsis* and the high polyploid *Chrysodraba* (cp. MERXMÜLLER & BUTTLER 1965).

The large section *Leucodraba* ($x = 8$) falls into two subsections which differ cytologically. *Euleucodraba* behaves almost as *Aizopsis* in the dominance of diploids

(7 species) but it also contains four hexaploids, of which at least two (*D. norvegica* and *D. arctogena*) are closely related to the species of the other subsection *Holarges*. This section on the other hand has no diploids but four (three) tetraploids, one (or three) hexaploids, six octoploids, 4 decaploids and one duodecaploid ($2n = 96$).

The three species of the section *Drabella* are diploid, tetraploid and perhaps pentaploid ($2n = 40$, *D. crassifolia*, cp. HEILBORN 1941 and below). The diploid and tetraploid species belong to a series with $x = 8$.

In the Central- and South American yellow-flowering section *Adenodraba* only one species, *D. jorullensis* H.B. Kth., has been counted. BEAMAN et al. (1962: 43–46) reports $n = 12$ in material from Mexico (Alt. 3980–4160 m) and they discuss this interesting number saying that it could be interpreted as an additional basic number of $x = 6$ or 12. They also discuss the possibility of a connection between this new number and arctic *Draba* species with $n = 24$. However, while the latter might be a stabilized allohexaploid in a series with $x = 8$, it is difficult to imagine *D. jorullensis* being a triploid. I therefore agree with the opinion that *D. jorullensis* is either a diploid or a tetraploid in a series with $x = 6$ or 12.

Quite recently $2n = 24$ was also reported in one species of the white-flowering section *Rhabdocarpa* (*D. pickeringii* Abrey from Peru, FAVARGER & HUYNH in TAXON 14: 88, 1965). *Rhabdocarpa* is also a purely American section with 10 species in the Andes.

Finally the number $2n = 48$ found in *Draba gilliesii* (see p. 39) may indicate a further evolution within a series with 12 as basic number. The species in question belongs to the section *Calodraba* which is purely South-American (14 species in Andes-Patagonia).

The question of the occurrence of more than one basic number in *Draba* has further been accentuated from a closer study of *Draba aurea* Vahl. This species belongs to another, mainly yellow-flowering section *Phyllodraba* which according to SCHULZ contains 29 species from East Asiatic and North Pacific American mountains extending southwards to California and Northern Mexico (*D. helleriana*). As mentioned on p. 36 *D. aurea* has either $2n = 76$ ($x = 19$) or perhaps $2n = 72 + 4$ small extra chromosomes. *D. aurea* might therefore be interpreted as a secondary hexaploid (perhaps allohexaploid) in a series with $x = 12$.

As pointed out above *D. crassifolia* may possibly be interpreted as a pentaploid in a series with $x = 8$; the only reason for this is that two other species of *Drabella* have this same basic number. However, it is more probable that the species is a tetraploid member of a 10-series. This opinion is held by JØRGENSEN et al. (1958: 143).

Most facts point towards the conclusion that in *Draba* there are at least three basic numbers, viz. 8, 10, and 12.

The very specialized dense cushion plant, *Lithodraba mendocinensis*, from the South American Andes has $2n = 64$ according to BOELCKE (1951), a fact which is of some interest as its nearest relatives *Eudema* and *Xerodraba* are referred by SCHULZ (1924) to the *Brayinae* which is a group with seven as the basic number (see later).

Species formation

According to SCHULZ (1927: 7) *Draba* flowers are adapted to cross-pollination. However, there is strong evidence for assuming a high degree of selfing and inbreeding in many arctic species resulting in a number of uniform and true-breeding lines within each species. The many hybrids which are described indicate occasional cross-pollination, but as already suggested many specimens which have been interpreted as hybrids might as well be considered as extreme variants within one complex species which owes its complexity to a high degree of structural changes in its chromosome complement.

It became evident from the cytological analysis of a number of *Draba* species with a high ploidy-level that polyvalent chromosome associations are very rare, if present at all. This fact which also appears from Fig. 92–99 in JØRGENSEN et al., strongly suggests allopolyploid evolution. In the preceding sections allopolyploid evolution was suggested in hexaploids, e.g. *D. lactea*, *D. norvegica*, *D. arctogena* and *D. cinerea* ($8 \times 16 \rightarrow 24 \rightarrow 48$) and it may well also have been involved in the formation of the decaploids ($24 \times 16 \rightarrow 40 \rightarrow 80$). In the case of octoploids and 16-ploids autopolyploidy is perhaps a little more likely, but octoploid plants also lack polyvalents. What is needed is of course evidence based on experiments and so far we have only one example of known allopolyploid evolution in the closely related genus *Erophila* (WINGE 1933). MANTON (1950: 14), however, suggests that the proportion of allopolyploids in the *Cruciferae* is high.

Now, if we assume allopolyploid evolution as the most important type we may imagine that the same species arose by chromosome-doubling in various parts of the arctic zone resulting in several different \pm sterile primary hybrids. As the parental species themselves often were tetraploid or even of a higher level and already rather complex it seems entirely apprehensible that the resulting high polyploid species became very intricate making the work of taxonomists troublesome and perhaps sometimes impossible. Any deviating type which might owe its origin either to an independent allopolyploid evolution or to changes in chromosome structure within some of the established allopolyploids would probably in a high arctic environment be maintained for long periods as an independent entity. Its features—e.g. type of pubescence—would be maintained because self-pollination was predominant and if cross-pollination took place it would most probably be between plants of the same inbreeding line. Isolation in small pockets of vegetation in the high arctic deserts would further favour differentiation into small units which some taxonomists would evaluate as species and others as varieties or perhaps even forms of little taxonomic importance.

The distribution of species belonging to different chromosome levels is interesting. It appears from the work of MERXMÜLLER & BUTLER (1965) that the majority of alpine species are diploid. Among the arctic species, on the other hand, only four species, *D. fladniansis*, *D. nivalis*, *D. subcapitata* and *D. sibirica*, are diploids. In *Draba*, therefore, the mountains south of the arctic area seem to constitute centers of origin,

a view which corresponds with that of SCHULZ who mentions the mountains which surround the Mediterranean Sea as "ein abgeschlossenes Schöpfungszenrum." *Draba* is sub-divided into so many widely different sections, that it seems reasonable to postulate more than one center of origin, and perhaps a polyphyletic origin. In this connection the deviating chromosome numbers of *D. jorullensis*, *D. pickeringii*, *D. gilliesii*, and *D. aurea* are of particular interest.

There is no indication of any area in the Arctic which could have been a center of origin for species with basic or low chromosome numbers. *Draba sibirica* is an Asiatic-East European subalpine species ranging to subarctic or low arctic areas. *Draba fladnizensis* occurs in Eurasian and North American mountains and *D. nivalis* and *D. subcapitata* have close relatives among the species in Central Asia.

Montane North-American species have reached the Arctic areas, e.g. *D. aurea* which has its eastern limit in Scoresbysund (Fig. 8), and *D. crassifolia* which extends across the North Atlantic Ocean and reached Northern Norway (HULTÉN 1958, map 174). On the other hand, there is no doubt that, in case of the polyploids within the sections *Leucodraba* and *Chrysodraba*, the Arctic zone is a recent center for speciation. The species are all very complex, but the entities are comparatively young and often not yet sufficiently distinct to deserve species rank. Isolating forces such as self pollination, geographical barriers, and chromosome barriers, however, are clearly operating and will probably gradually lead to better defined demarcations.

Polyploidy and distribution

There has been much discussion about the high frequency of polyploids in the Arctic (e.g. works of HAGERUP, TISCHLER, LÖVE & LÖVE). Recently JOHNSON & PACKER (1965) have made an interesting contribution to our understanding of this phenomenon. They found a particular high frequency of polyploids on cold, wet soils in which frost action plays an important rôle and conclude that newly formed polyploids were successful pioneers on newly exposed glaciated surfaces. This success is explained by assuming that polyploids are at a selective advantage in having a higher genetic variability.

If the taxa treated in the present paper are considered we find some agreement with these ideas as certain of the high polyploids (octoploids or higher levels) are found on solifluction soils (e.g. *Draba alpina*, *D. bellii*) while some of the tetra- and hexaploids are found on stable, dry and warm soils (e.g. *Draba lanceolata*, *D. cinerea*).

What is more striking, however, is the fact that all taxa at the high ploidy-levels (8x or more) have high arctic distributions, while species with sub-low-or medium arctic distribution do not reach more than the hexaploid level. In two groups this trend is very clear as relatively southern taxa or races have lower numbers than the northern ones (*Draba cinerea* → *D. arctica*; *Draba glabella* $2n = 64 \rightarrow 2n = 80$). In both these groups a higher chromosome level is correlated with a morphological

change, the high arctic representatives being more compressed and with fewer stem leaves.

But it should be emphasized that not less than three diploids (*D. subcapitata*, *D. fladnizensis* and *D. nivalis*) and two hexaploids (*D. arctogena* and *D. lactea*) reach the high arctic areas, and that some of them (*D. subcapitata* and *arctogena*) are almost restricted to the northernmost parts of the Arctic. They are therefore probably old species, perhaps tertiary relics; they are certainly what JOHNSON & PACKER regard as "old species sufficiently rich in biotypes to adjust". Such species are relatively important in NW. Alaska which was never glaciated, and they are also present in N. Greenland where the existence of such unglaciated areas is also assumed.

Braya

Chromosome numbers and species formation

A critical summary of *Braya* species with known chromosome numbers is presented in table 12. Apart from some countings of $2n = 32$, 40, and 64 which probably are due to various kinds of error (see later), all numbers can be arranged in a series with the basic number of 7. HOLMEN (1952) was the first to find a species at the tetraploid level, viz. *B. thorild-wulffii* with $2n = 28$. The hexaploid level is the most common in the material studied at present.

In table 12 the species are arranged in three groups; the first corresponds to *Torularia humilis*, the second to *Braya* in SCHULZ (1924: 223–227). The third group comprises only one decaploid species, *B. intermedia* Th. Sør., an endemic species of NE. Greenland (cp. SØRENSEN 1954). This species is difficult to place as it combines characters from *B. humilis* and *B. linearis* or *B. purpurascens*, or both, being perhaps a triple-allodecaploid. This latter idea which was proposed by the present author in 1956 presupposes a very intricate process of formation. It is however a fact that *B. linearis* and *B. humilis* in NE. Greenland are hexaploids and the easiest way of obtaining a plant with $2n = 70$ would be fertilization between an unreduced gamete of a hexaploid and a normal reduced gamete of an octoploid. In NE. Greenland only *B. purpurascens* is octoploid. *B. intermedia* resembles *B. humilis* and *linearis* but approaches also *B. purpurascens* and might be interpreted as *B. humilis* × *linearis* (unreduced: 42) × *B. purpurascens* (reduced: 28). A fact which supports this complicated species formation is that species of *Braya* have similar rather narrow ecological ranges and therefore very often grow together. This is striking e.g. at the saltlakes in continental West Greenland.

The first metaphase plate of *B. intermedia* pictured by JØRGENSEN et al. (1958 fig. 107) contains exclusively bivalents indicating a regular meiosis and no or very few multivalents. Also in the polyploid *Braya* species studied by the present author true associations of more than two chromosomes were very rare if present at all.

These facts and the occurrence of two large chromosomes only in the tetraploid *B. thorild-wulffii* favour the view that allopolyploid evolution has been as important in *Braya* as it was assumed to be in *Draba*.

Evolution in relation to geographical distribution

In Table 12 and Fig. 21 are summarized the distribution of all known species and subspecies in the genus *Braya* (incl. *B. humilis* and *B. novae-angliae*). Europe is very poor in species while the Central Asiatic mountains harbours 10 species and may constitute the center of origin of the genus.

B. rosea is the only central-asiatic species with known chromosome number; almost nothing therefore can be said about the chromosome level of the asiatic group of species which may contain some relatively ancient diploids. In the case of the *B. humilis* group, however, measurements of pollen size (ROLLINS 1953: 112 and BÖCHER 1956, Fig. 2) have shown four size classes of pollen grains and here the two largest sizes are connected with the hexaploids and octoploids. The two smallest size classes may therefore correspond to diploids and tetraploids. All three samples of small sized pollen studied by the present author originated from central asiatic plants.

If the central asiatic high mountains are considered as the place of origin we may imagine that some species migrated from the center in various directions. One possible way was towards NE. in the highland east of river Jenisei to Arctic Siberia and further to N. America and Greenland. Another way would perhaps be through the mountain ranges towards the west.

The *B. humilis* group is undoubtedly one phylogenetic line. As illustrated in BÖCHER (1950: 40) and Fig. 21 in the present paper, this species group is found in the unglaciated highland area of Siberia west of river Lena from where it extends to arctic coast. One branch of hexaploids (ssp. *arctica*) continued along the Arctic Sea and reached NE. Greenland while another branch probably of octoploids (*B. novae-anglica*) reached southwards to Colorado and eastwards to Hudson Bay, Newfoundland and Continental Middle West Greenland. But the range of *B. novae-angliae* is split up into at least 8 disjunct areas. Being almost exclusively found in previously glaciated areas, the disjunctions are most probably due to postglacial extinction in connection with forest expansion and soil leaching.

The other group, the *B. alpina*-group, probably followed the same route towards NE. This is indicated by the distribution of species like *B. aenea* extending from Pamir to Arctic Siberia and *B. siliquosa* which from Altai reaches the Lena-Kolyma river area in the north and Okotsk and westernmost Alaska in the east.

In the case of *Braya* the unglaciated highlands east of Jenisej have undoubtedly served as an important route for migration of high montane asiatic species to Arctic Siberia (cp. the ideas proposed by TOLMATCHEV (1960: 272)). At an early stage the ancestors of the *B. purpurascens* group may have reached the Arctic area and were able to establish a circumpolar range. One ancient tetraploid (*B. thorild-wulffii*) is now connected with the high arctic parts of the American Arctic Archipelago and Greenland. The *B. glabella-pilosa* complex may represent another ancient group.

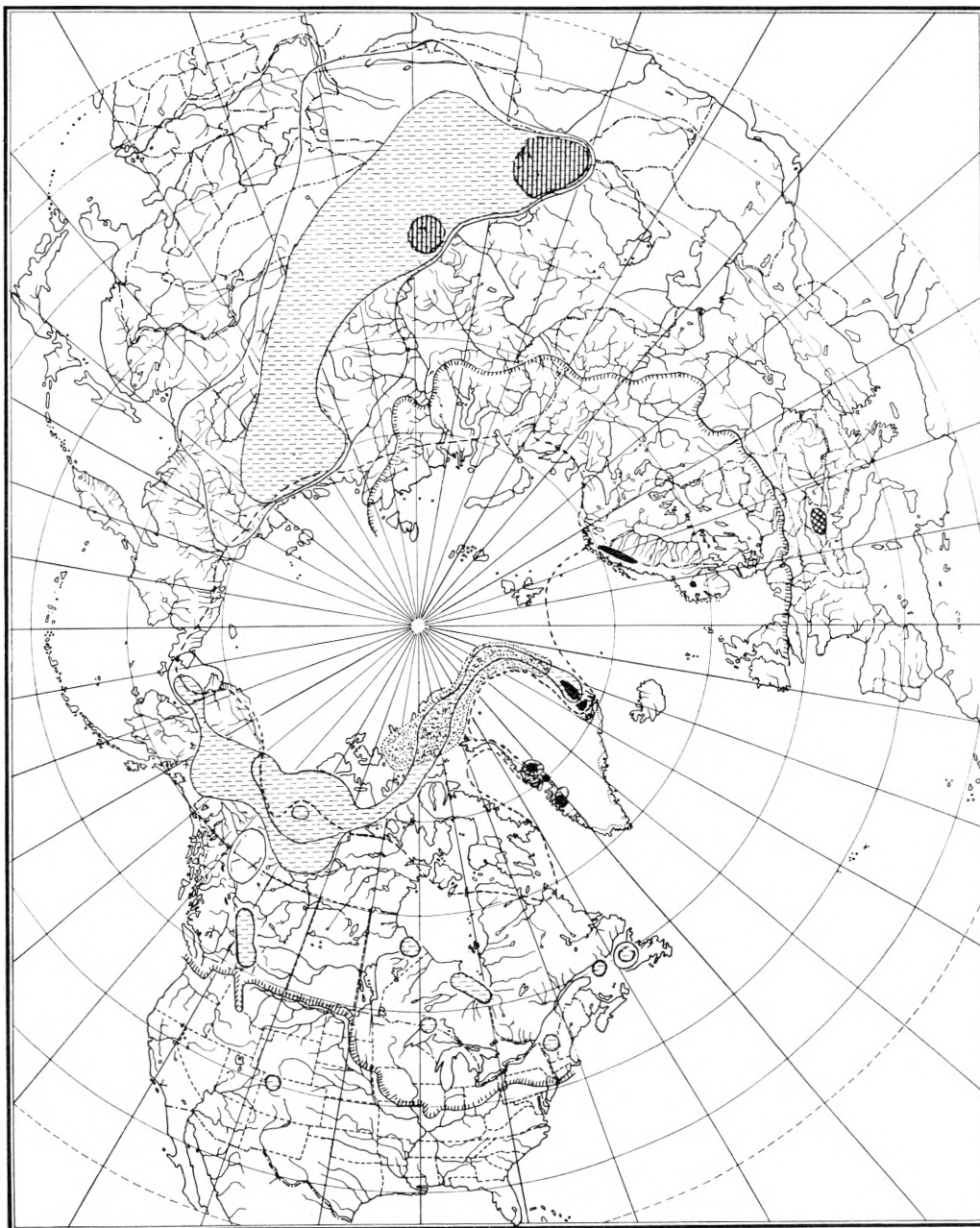


Fig. 21. World distribution of the genus *Braya* and border of greatest extension of larger quaternary ice-shields (|||||). Areas with horizontal hatching (horizontal short lines) are occupied by the *B. humilis*-*B. novae-angliae* complex. The broken line shows the approximate southern limit of the circumpolar *B. purpurascens* while the dotted area shows the distribution of *B. thoriid-wulffii*. The areas of *B. linearis* are black while the east-alpine area of *B. alpina* is cross-hatched. The continuous line in Asia shows the limits of the whole genus while the small vertically hatched areas shows that parts where the concentration of species is greatest. Here we have the following endemic species: *B. pamirica*, *B. scharnhorsti* and *B. brachycarpa*. In the Angara-Sajan district the Komarov-expedition has found the endemic *B. angustifolia* and south of latitude 50° the following wider ranging endemics occur: *B. tibetica*, *B. oxycarpa* and *B. rosea*. In Alaska and Eastern Chuch peninsula there are small areas of *B. pilosa*, *B. glabella*, *B. henryae*, and *B. siliquosa*. *B. glabella* has another occurrence north of Great Bear Lake and *B. henryae* in British Columbia.

TABLE 12.

Taxon	2n	Ploidy level	Geographical area														
			Spitzbergen	Scandinavian Mountains	Central European Mountains	Central Asiatic Mountains	Central North Siberia	NE. Asia	W. North America	E. North America	Arctic Alaska	Arctic Canada	Middle W. Greenland	NW. Greenland	N. Greenland	NE. Greenland	
<i>Braya humilis</i> (C. A. Mey.) Robins. ssp. <i>humilis</i>	28 ¹					x	x		x ¹								
<i>Braya humilis</i> (C. A. Mey.) Robins. ssp. <i>arctica</i> (Bösch.) Rollins	42	6x							x ¹		x	x				x	x
<i>Braya novae-angliae</i> (Rydb.) Th. Sør. ssp. <i>novae-angliae</i>	56	8x					x			x			x	x			
<i>Braya novae-angliae</i> (Rydb.) Th. Sør. ssp. <i>abbei</i> Bösch.										x							
<i>Braya novae-angliae</i> (Rydb.) Th. Sør. ssp. <i>ventosa</i> (Rollins) Bösch.	56	8x							x								
<i>Braya alpina</i> Sternb. & Hoppe	42	6x			x												
<i>Braya linearis</i> Rouy	42	6x		x									x	x			x
<i>Braya glabella</i> Richards																	?
<i>Braya pilosa</i> Hook.											x	x					
<i>Braya henryae</i> Raup								x	x		x						
<i>Braya aenea</i> Bge.						x	x	x									
<i>Braya angustifolia</i> (N. Busch) Vass.								x									
<i>Braya rosea</i> (Turcz.) Bge.	42	6x				x											
<i>Braya longii</i> Fernald										x							
<i>Braya fernaldii</i> Abbe										x							
<i>Braya thorild-wulfii</i> Ostenfeld	28	4x										x		x	x	x	
<i>Braya purpurascens</i> (R. Br.) Bge.	56	8x	x	(x)			x	x			x	x		x	x	x	
<i>Braya siliquosa</i> Bge.						x		x			x						
<i>Braya brachycarpa</i> Vass.						x											
<i>Braya pamirica</i> (Korsh.) Fedsch.						x											
<i>Braya tibetica</i> Hook.						x											
<i>Braya oxycarpa</i> Hook.						x											
<i>Braya scharnhorstii</i> Regel & Schmalh.						x											
(?) <i>Braya limosella</i> Bge. (see SCHULZ 1924)						x											
<i>Braya intermedia</i> Th. Sør.	70	10x															x
No. of species		*	1	2	1	10	3	5	2	4	6	5	2	4	3	5	

¹ Data from MULLIGAN (1965, see Postscript), where however *B. humilis* is treated as a collective species.

In both cases some of the present day stations lie within areas which are believed to have been unglaciated. The successful polymorphic octoploid *B. purpurascens*, however, was able to invade greater parts of the previously glaciated areas.

The most problematic species within the genus are undoubtedly *B. linearis* and *B. alpina*. As may appear from Fig. 21 the similarity between certain races of *B. aenea* and *B. linearis* is great enough so suggest that these two taxa have common ancestors and perhaps it will prove justified to regard, as POLUNIN does (1959), *B. glabella*, *B. pilosa*, *B. linearis*, *B. alpina*, *B. aenea* and *B. henryae* as one huge complex with common origin. If so this complex may have established a circumpolar distribution comparatively early but the area was later disrupted and at the same time the isolation of the separated populations led to speciation. This, however, implies that the present species are largely relics. *B. linearis* may be connected with the arctic circumpolar branch of the complex while *B. alpina* might be regarded as an isolated westerly survival of an Eurasiatic high montane branch (cp. HULTÉN 1937). GAMS (1933: 29) lists it among the tertiary relics of the Alps as one of the species with south-siberian origin. The relic hypothesis for *B. linearis* in Norway has been supported by NORDHAGEN (1935) while the relic nature of its Greenland populations was discussed in BÖCHER (1956). In a case like *B. linearis* it is certainly impossible to classify it as either west- or east-arctic. Its present day north Atlantic areas are probably to be explained as remains of a more continuous area. The species may have arisen as a north Atlantic geographical race within the complex. However, this race was by no means ecologically connected with oceanic climatic conditions. It is a typical member of the genus which in its entirety avoids areas with an oceanic type of climate. This fact also points towards Central Asia as the place of origin.

In several species of *Braya*, isolation in various kinds of refugia has played an important rôle in the formation of species or lower entities. Within *B. linearis*, the Junkerdal race (var. *meizophylla*) may be one such unit which was isolated in an ice age refugium, whilst in the complex octoploid species, *B. novae-angliae*, the various subspecific units were probably isolated later.

Species pairs like *B. glabella*-*B. pilosa* and *B. aenea*-*B. linearis* may represent relic populations of extinct species which now as a result of isolation over long periods are just distinct enough to be regarded as separate species.

Postscript

After having finished this work a paper by MULLIGAN (1965) appeared. It has been possible in the first proof to incorporate a number of references to this important contribution by MULLIGAN. Most interesting is his countings of plants belonging to the *Braya humilis* complex. Tetraploids ($2n = 28$) were found in Mackenzie District, Alberta and British Columbia, hexaploids in the same areas as well as in Franklin District, Northwest Territories. Finally octoploids occurred from Mackenzie District southwards to Colorado. A taxonomical treatment of the three cytotypes is clearly desirable.

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PLATES

PLATE I

a-c: *Draba arctogena*, d: *Draba norvegica*. — a: Type of *D. arctogena* Ekman (Godhavn, W. Greenland leg. Elis. Ekman Aug. 1923, Riksmuseet, Stockholm). — b: Material determined by Mrs. EKMAN as *D. arctogena* (N. Greenland, Navy Cliff Land, Vildtlands western part leg. P. Freuchen, Aug. 1912, Bot. Museum, Copenhagen). — c: *D. arctogena* from Centrum Lake, NE. Greenland 80°07' leg. Schwarzenbach 1952, Bot. Museum, Copenhagen). — d: *Draba norvegica*, Cult. No. 4772 (from Godhavn, W. Greenland). — Scale 10 cm.



PLATE II

Draba arctica J. Vahl p. p. Type material from Bell Sund, Spitzbergen and below on the right (e) *D. cinerea* Adams from Umanaq. W. Greenland collected by J. Vahl and considered by him as identical with his *D. arctica*. — a: *D. arctica* mihi (200 feet above the sea, Bell Sund, August 1938, Bot. Museum, Copenhagen). — b, c, d: Bell Sund material of J. Vahl in the Riksmuseum, Stockholm; b: *D. arctica*, Bell Sund fl. Spitzberg. Vahl jun. scripsit et misit; c: *D. arctica* Vahl Spitzb. misit auctor. On the label of Elis. Ekman: 'This form deviates somewhat from *D. arctica* Vahl from Greenland by being more pilose and having more simple hairs on the fruit stalks'. e: Belongs to the same collection as shown in Plate III d. Note: Many stem leaves, short and short peduncled siliques. — Scale 10 cm.



a

Handwritten notes:
2. 4. 1874
1874
1874
1874



b

Handwritten notes:
1874
1874
1874

Handwritten text:
Arctic
H. H. Hansen



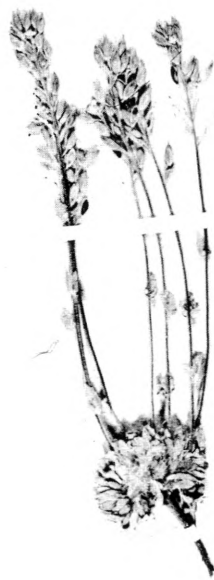
c

Handwritten text:
Arctic
Spitzberg



d

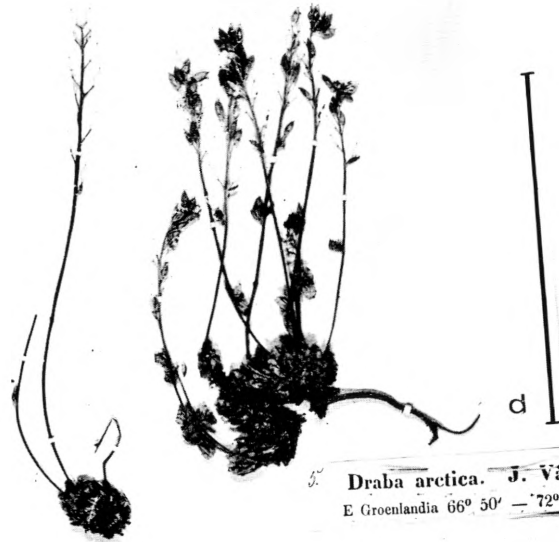
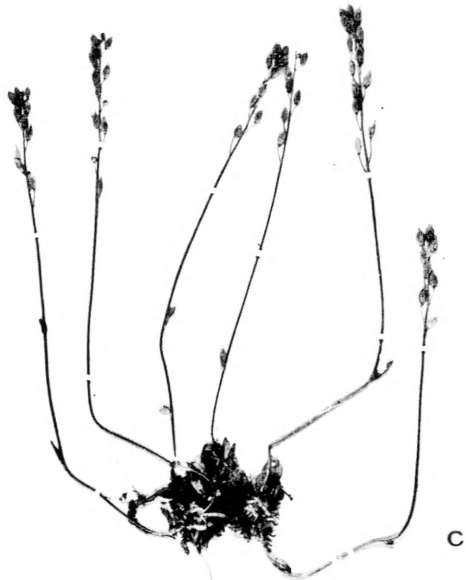
Handwritten text:
Arctic
Spitzberg
det. Elisabeth Ekman



e

PLATE III

Draba cinerea Adams ssp. *brachysiliqua* (Mela) Ekm. — a: At the road between Stromfjordshavn and the Airbase (leg. Aug. TWB. Aug. 1946). — b–c: Karelia Ladogensis, insula Mäkisalo (leg. G. Lång, June 1898, Plantae Finlandiae Exsiccatae No. 244). — d: Part of VAHL's type collection of *Draba arctica* (corresponding to that in Plate IIe). On the label below is written *Draba incana?* Linné, but *incana* is struck out and substituted by *arctica*. Below, referring to the collection No. 5, is added "in locis subhumidis tam ad pedestum ad latera inferiora alpinum, distr. Colon. Umanaq: 1834 Juli J. Vahl". All Collections in the Botanical Museum, Copenhagen. — Scale 10 cm.



Draba arctica. J. Vahl.
E Groenlandia 66° 50' — 72° 48'

Draba arctica
From the high mountains of Greenland
near the Arctic circle
J. Vahl, Copenhagen 1804

PLATE IV

Draba cinerea Adams ssp. *cinerea*. — a-b: Siberia, Jakutsk distr., Bulun 70°43' N. (leg. H. Nilsson, July 1898, Riksmuseet, Stockholm); b: Ignerit Fjord, Magdlaq, West Greenland 71°7' N. c: Nugssuaq, Pâtût 70°15' N. (leg. M. P. & R. T. Porsild, July 1929, Riksmuseet, Stockholm). — d: *D. lanceolata* Royle from W. Greenland, Cult. No. 4884. — Scale 10 cm.

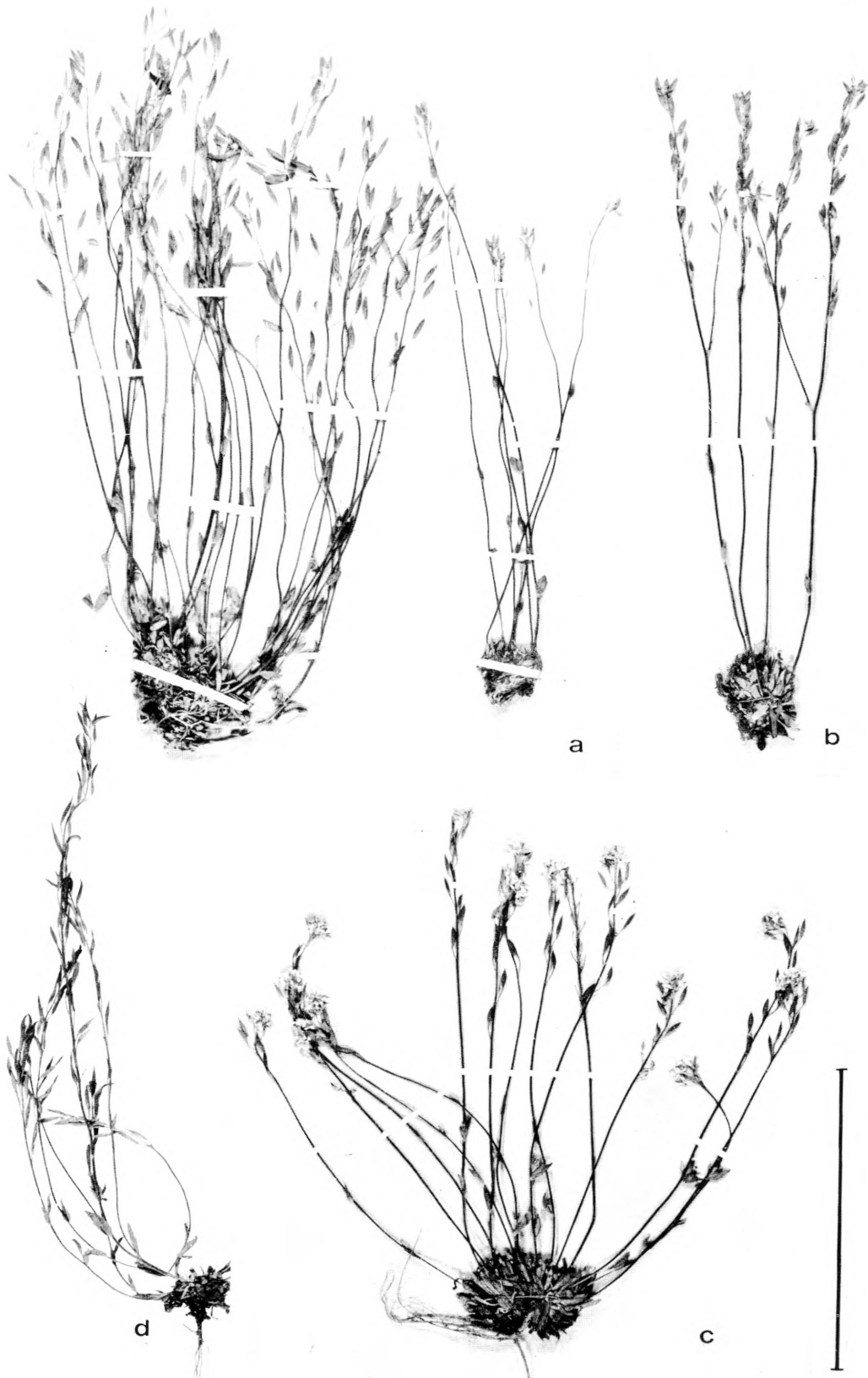


PLATE V

Draba arctica J. Vahl p. p. ssp. *groenlandica* (Ekm.) Böch. — a-c: Type material of *D. groenlandica* Ekm. W. Greenland, Godhavn (leg. Elis. Ekman, Aug. 1923, Riksmuseet, Stockholm). — d-f: Godhavn (leg. J. Lagerkranz 1934). — g: According to determination by Ekman transitional type between *D. groenlandica* and *D. ostenfeldii*, Ellesmereland, Fram Harbour (leg. H. G. Simmons July 1899 (No. 1092)). — h-i: Deviating type with erect, very slender stems; h: Mountain east of Mt. Hassell, Søndre Strømfjord (leg. T. W. Böcher, Aug. 1946); i: Tunertoq, Arfersiorfik (leg. T. W. Böcher & S. Lægaard Aug. 1961). — j: Sandy bank, Lower E. Skeldal, Kong Oscars Fjord, NE. Greenland (leg. T. T. Elkington July 1962). — d-i: from the Botanical Museum, Copenhagen. — Scale 10 cm.



PLATE VI

Draba cinerea Adams ssp. *brachysiliqua* (a-c) and *Draba arctica* J. Vahl p. p. (d-i). — a: Clavering Island NE. Greenland n = 24 (leg. Th. Sørensen). — b-c: Store Saltso, Central West Greenland, cultivated material (No. 4813), n = 24. — d: Vigorous specimen of *D. arctica* from Ostenfeld Nunatak, NE. Greenland, 74°18' N. (leg. F. Schwarzenbach Aug. 1956). — e: *D. arctica* ssp. *groenlandica* from Jørgen Bronlund's Fjord, Peary Land (leg. K. Holmen No. 6712, 2n = 64 cp. HOLMEN 1952: 13). — f: *D. arctica* from Ella O, Cape Oswald (leg. K. Holmen 1950 n = ca. 40). — g: *D. arctica* ssp. *ostenfeldii* var. *ovibovina* from Clavering Island NE. Greenland, n = 40 (leg. Th. Sørensen). — h: *D. arctica* from Sassenbay, Spitzbergen (leg. E. Jørgensen). — i: *D. arctica* from Adventbay, alt. 400 m, Spitzbergen (leg. E. Jørgensen). d-f, h-i; from the Botanical Museum, Copenhagen. — Scale 10 cm.



PLATE VII

Draba arctica J. Vahl ssp. *ostenfeldii* (ekm.) Böch. — a: Type of *D. ostenfeldii* Ekm. Sounders Island, Cape York, NW Greenland, 14. July 1914 (leg. P. Freuchen) first determined by C. H. Ostenfeld as *D. hirta* ssp. *arctica* (Vahl) Wats. — b: Isfjorden, Longyearbyen (leg. Lagerkranz 1932, Loco palætræ). — c: Type of var. *ovibovina* Ekm. Fram Harbour Ellesmereland 20. July (leg. H. G. Simmons, No. 1092). — a and e: Bot. Museum, Copenhagen; b: Riksmuseet, Stockholm.

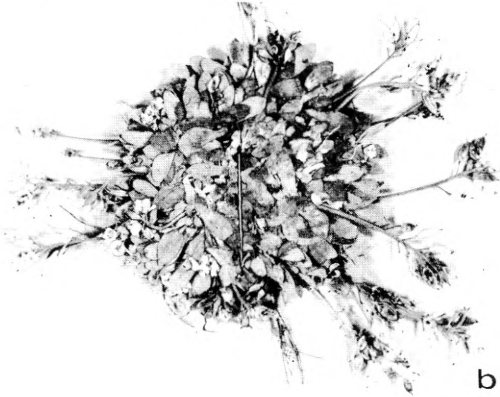


a

Araba O. Lomha del noro.

det. Elisabeth Exman/1929

TYPUS



b



c

TYPUS
Araba O. Lomha del noro.
var. *subarctica*



PLATE VIII

Draba aurea M. Vahl. — a: Unbranched vigorous specimen from continental West Greenland (Søndre Strømfjord, eastern part of Sandflugtsdalen, Southern slope, Aug. 19, 1946 (leg. T. W. Böcher No. 637). — b, c, d: Branched vigorous specimens with broad leaves from Narsarssuaq, Tunugdliarfikfjord, South Greenland, July 13, 1946 (leg. T. W. Böcher No. 621). — Scale 10 cm.



PLATE IX

Experimental cultivations with *Braya linearis* and *B. rosea*. All, except d-e, from the Arctic Greenhouse. — Two specimens of *B. linearis* var. *meizophylla* (Br. 3); b: typical specimen from W. Greenland (No. 4811); c: Troms (Br. 7); Scale 10 cm. — d-e: Two specimens of *B. linearis* (d: Br. 3) compared with *B. rosea* (e: Br. 4); second year plants in their first flowering stage (June 1961, Exp. field). — f-h: One specimen of *B. linearis* from Greenland (f: No. 4811) and two of *B. rosea* (g-h: Br. 4) second flowering (June 1962). — i-k: Two W. Greenland plants of typical *B. linearis* (i: No. 4855, j: No. 4811) compared with var. *meizophylla* (k: Br. 3), the latter being higher with elongated raceme and longer and broader leaves. — l-m: Two specimens of *B. linearis* var. *meizophylla* (l: Br. 3) and two typical ones of No. 4855 from W. Greenland (m). — n-q: n: No. 4811; o: No. 4855 (both W. Greenland); p: Br. 3 (var. *meizophylla*); and q: Br. 7 from Troms (June 1962).

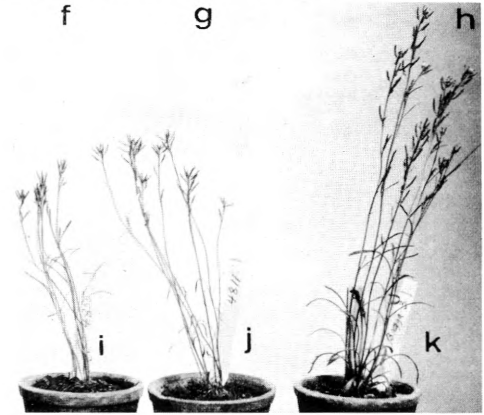


PLATE X

a–b: *Braya linearis*; a: Head of Søndre Strømfjord, W. Greenland at the airbase (leg. T. W. Böcher Aug. 1946); b: Store Saltø near head of Søndre Strømfjord (leg. T. W. Böcher Sept. 1956, Bot. Museum, Copenhagen). — c: *Braya aenea* from Kumach Sur, c. 71°30' Sibiria, oblastia Jakutsk (leg. H. Nilsson, July 1948, Riksmuseet, Stockholm). — d: Specimen of *B. linearis* var. *meizophylla* No. 3 from Junkerdal, Norway, cultivated in the Arctic Greenhouse. — e: Another specimen of this variety cultivated in pots at the experimental field together with the specimens shown in f–g. — f: *B. linearis* No. 7 from Sordal, Troms, Norway. — g: Two specimens of *B. alpina* from the Grossglockner area (No. 6788). — Scale 10 cm.



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