Cytotaxonomic studies of *Draba nivalis* and its close allies in Canada and Alaska

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The cytotaxonomy of seven closely related species of *Draba* is discussed and a key is given. The species are as follows: *D. fladnizensis* Wulfen ($n = 8$); *D. lactea* Adams ($n = 24$); *D. lonchocarpa* Rydberg ($n = 8$); *D. nivalis* Liljebl ($n = 8$); *D. palanderiana* Kjellman ($n = ?$); ***D. porsildii*** G. A. Mulligan, sp. nov. ($n = 16$); and *D. subcapitata* Simmons ($n = 8$). Characteristics of sterile artificial and of natural hybrids, between some of these species and between them and other species of *Draba*, are discussed. *Draba fladnizensis*, *D. lonchocarpa*, and *D. nivalis* are diploids, each with two homologous sets of eight chromosomes that are partly homologous with sets of the other two species. *Draba porsildii* contains two sets of 16 chromosomes, each with two completely homologous genomes, and each genome from both sets of 16 is partly homologous with either of the genomes in the other set. All four genomes of *D. porsildii* are partly homologous with each genome of *D. fladnizensis*, *D. lonchocarpa*, and *D. nivalis*.

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L'auteur discute la cytotaxonomie de sept espèces étroitement apparentées de *Draba* et présente une clef de détermination. Les espèces étudiées sont *D. fladnizensis* Wulfen ($n = 8$), *D. lactea* Adams ($n = 24$), *D. lonchocarpa* Rydberg ($n = 8$), *D. nivalis* Liljebl ($n = 8$), *D. palanderiana* Kjellman ($n = ?$), ***D. porsildii*** G. A. Mulligan, sp. nov. ($n = 12$) et *D. subcapitata* Simmons ($n = 8$). Les caractéristiques d'hybrides artificiels stériles et d'hybrides naturels entre certaines de ces espèces, ainsi qu'entre elles et d'autres expèces de *Draba*, sont discutées. *Draba fladnizensis*, *D. lonchocarpa* et *D. nivalis* sont diploïdes, chaque espèce ayant deux compléments homologues de huit chromosomes qui sont partiellement homologues avec les compléments des deux autres espèces. *Draba porsildii* a deux compléments de 16 chromosomes; chaque complément contient deux génomes complètement homologues et chaque génome des deux compléments de 16 est partiellement homologue avec l'un ou l'autre des deux génomes de l'autre complément. Les quatre génomes de *D. porsildii* sont partiellement homologues avec chaque génome de *D. fladnizensis*, de *D. lonchocarpa* et de *D. nivalis*. [Traduit par le journal]

Introduction

The present study considers the cytotaxonomy of a group of Canadian and Alaskan species of *Draba*, characterized by having stems usually less than 1 dm tall, zero to two stem leaves, and white petals. They are as follows: *D. fladnizensis* Wulfen; *D. lactea* Adams; *D. lonchocarpa* Rydberg var. *lonchocarpa*; *D. lonchocarpa* Rydberg var. *thompsonii* (C. L. Hitchcock) Rollins; *D. lonchocarpa* Rydberg var. *vestita* O. E. Schulz; *D. nivalis* Liljebl; *D. palanderiana* Kjellman; *D. subcapitata* Simmons; and a new species described as ***D. porsildii*** G. A. Mulligan (Figs. 1–9).

Materials and Methods

Specimens in the following herbaria were studied: Department of Agriculture (DAO) and National Museum (CAN), both in Ottawa, Canada; and University of Alaska, College, Alaska (ALA). Selected specimens were obtained from Herbier Marie-Victorin, Montreal (MT); University of Alberta, Calgary (UAC); University of Alberta, Edmonton (ALTA); University of British Columbia, Vancouver (UBC); McGill University, Ste-Anne-de-Bellevue, Quebec (MTMG); Gray Herbarium, Harvard University, Cambridge (GH); Missouri Botanical Garden, St. Louis (MO); Washington State University, Pullman (WS); University of California, Berkeley (UC); Institute of Systematic Botany, Uppsala (UPS); Naturhistoriska Riksmuseum, Stockholm (S); Botanisk Museum, Oslo (O); and University of Moscow (MW).

Living plants were grown from seed obtained from natural habitats. Artificial first-generation interspecific hybrids were produced in a greenhouse by transferring pollen from one species to the stigma of emasculated flowers of another species. The chromosome number determinations were according to the methods outlined in Mulligan (1970).

KEY TO SPECIES

1. Leaves glabrous...*D. lactea*
1. Leaves pubescent
    2. Leaves lacking stellate hairs; hairs of leaves mostly long and simple, sometimes bifurcate to few-forked.

3. Stem and pedicels glabrous; stem with 0–1 cauline leaf..*D. fladnizensis*
3. Stem and pedicels copiously hairy; stem leafless...*D. subcapitata*

2. Leaves with stellate hairs; sometimes also with leaf hairs simple to few-forked.

4. Large white flowers, sometimes with yellow center; petals up to 5.5 mm long; style usually over ½ mm long; stem leafless; some silicles frequently aborted; pedicels usually longer than sepals.... ....*D. palanderiana*
4. Flowers white, smaller; petals up to 4.0 mm; style less than ½ mm; stem leaves 0–2; silicles never aborted; pedicels shorter to about same length as silicles

5. Stellate hairs less than ¼ mm, rays spreading (Fig. 10)

6. Pedicels glabrous; leaf blade frequently with long simple to few-forked hairs; stellate hairs most frequent on underside of leaf and towards the apex...*D. lactea*
6. Pedicels with copious stellate hairs ¼ mm broad; leaf blade lacking simple to forked hairs; stellate hairs abundant on both leaf surfaces...*D. nivalis*

5. Stellate hairs more than ¼ mm broad, rays mostly parallel to leaf surface

7. Stems with 1 or 2 leaves usually more than 2 mm broad; silicles usually appressed to stem; stem and pedicels frequently pubescent............................*D. lonchocarpa* var. *vestita*
7. Stems with 0 to rarely 1 leaf, less than 2 mm broad; silicles usually spreading; upper stem and pedicels usually glabrous

8. Basal leaves with simple, forked and stellate hairs; stellate hairs with 9 or more rays

9. Silicles greater than 2 mm broad...............................*D. lonchocarpa* var. *thompsonii*
9. Silicles less than 2 mm broad...................................*D. lonchocarpa* var. *lonchocarpa*

8. Basal leaves with simple, forked, cruciform and stellate hairs; stellate hairs with 8 or fewer rays..***D. porsildii***

Taxonomy and Distribution

1. *Draba fladnizensis* Wulfen in Jacq., Misc. Austr. Bot. 1: 147. 1778 (for complete synonymy see Buttler, Mitt. Bot. München, 6: 314. 1967).

Draba fladnizensis occurs in the mountains of eastern Alaska, Yukon, northern British Columbia, and western Mackenzie District. It also is found at a few locations at lower elevations in arctic areas of eastern Mackenzie District, Keewatin District, and on the Melville Peninsula, Southampton Island, and Banks Island (Fig. 11). It is an arctic–alpine species that is circumpolar in distribution.

2. *Draba lactea* Adams in Mém. Soc. Nat. Moscou, 5: 104. 1817; ostia Lenae, *Adams* (MW!)—see also Knaben, Bot. Not. 119: 433. 1966.

=*D. allenii* Fernald, Rhodora, 36: 289. 1934; south side of Fernald Pass, Mount Mattaouisse, Que., July 8, 1923, *Fernald, Grissom, Mackenzie, Pease & Smith 25,799* (holotype GH!).

Draba lactea is a common plant of alpine and arctic areas of Canada and Alaska. It occurs from St. Lawrence Island in the west to Labrador in the east, as far north as Ellesmere Island, and south to the Schickshock Mountains of Gaspé, Quebec (Fig. 12). *Draba lactea* is arctic–alpine and circumpolar.

3*a*. *Draba lonchocarpa* Rydb. var. *lonchocarpa*, Mem. N.Y. Bot. Gard. 1: 181. 1900; McDonald's Peak, Mission Mountains, *Canby 27* (lectotype GH!).

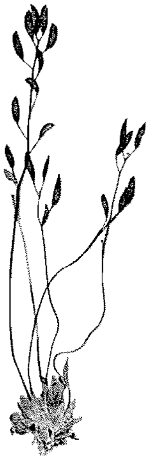
=*D. lonchocarpa* Rydb. var. *exigua* O. E. Schulz in Engler, Pflanzenreich, 89(4, 105): 216. 1927; Sawatsh Range, alpine, *J. S. Brandegee 12714* (lectotype MO!, isolectotype GH!).

=*D. nivalis* Liljebl var. *elongata* Wats., Proc. Am. Acad. 23: 258. 1888 (lectotype not chosen).

=*D. lonchocarpa* Rydb. var. *semitonsa* St. John, Proc. Biol. Soc. Wash. 43: 113. 1930; Mount Rainier, *Piper 2060* (holotype WS!, isotype GH!).

FIGS. 1–9. Pressed specimens of *Draba* species. Fig. 1. *D. fladnizensis*. Fig. 2. *D. lactea*. Fig. 3. *D. lonchocarpa* var. *lonchocarpa*. Fig. 4. *D. lonchocarpa* var. *thompsonii*. Fig. 5. *D. lonchocarpa* var. *vestita*. Fig. 6. *D. nivalis*. Fig. 7. *D. palanderiana*. Fig. 8. *D. porsildii*. Fig. 9. *D. subcapitata*.

PLATE I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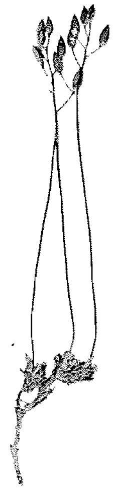
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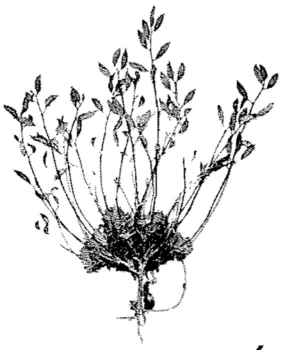
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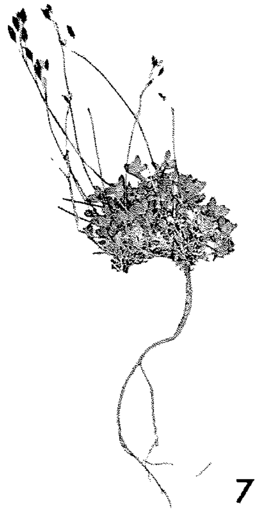
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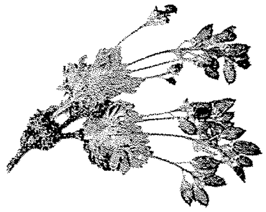
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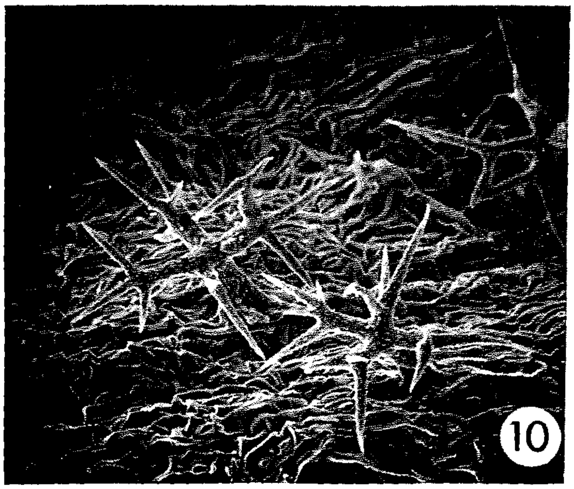


FIG. 10. Stereoscan photomicrograph of *D. lactea* hair, × 180.

= *D. lonchocarpa* Rydb. var. *dasycarpa sensu* C. L. Hitchock, Univ. Wash. Publ. Biol. 11: 85. 1941, *non* O. E. Schulz in Engler, Pflanzenreich, 89(4, 105): 216. 1927.

The typical variety of *D. lonchocarpa* is common in the mountains of Alberta, British Columbia, Yukon, Mackenzie District, and the southeast corner of Alaska (Fig. 13).

3*b*. *Draba lonchocarpa* Rydb. var. *thompsonii* (C. L. Hitchcock) Rollins, Rhodora, 55: 235. 1953.

= *D. nivalis* Liljebl var. *thompsonii* C. L. Hitchcock, Univ. Wash. Publ. Biol. 11: 85. 1941; high ledges near Mount Stuart, Chelan Co., Wash., at 5500 ft elev, *Thompson 9512*, July 20, 1933 (holotype UC!).

The variety *thompsonii* occurs in the mountains of western British Columbia, from a point opposite the Queen Charlotte Islands southward into the United States (Fig. 14).

3*c*. *Draba lonchocarpa* Rydb. var. *vestita* O. E. Schulz in Engler, Pflanzenreich, 89(4, 105): 216. 1927; summit of Mount Arrowsmith, V.I., crevices of rocks, *Macoun 1929*, July 18, 1887 (lectotype CAN!).

= *D. lonchocarpa* Rydb. var. *denudata* O. E. Schulz in Engler, Pflanzenreich, 89(4, 105): 216. 1927; Muir Glacier, Alaska, *W. Trelease 3911*, June 12, 1899 (isotype MO!).

= *D. nivalis* Liljebl var. *denudata* (O. E. Schulz) C. L. Hitchcock, Univ. Wash. Publ. Biol. 11: 85. 1941.

= *D. nivalis* Liljebl var. *kamtschatica sensu* C. L. Hitchcock, Univ. Wash. Publ. Biol. 11: 83. 1941, *non D. kamtschatica* (Ledeb.) N. Busch, Bull. Acad. Sci. Russ. 5, 12: 1639. 1918.

= *D. lonchocarpa* Rydb. subsp. *kamtschatica sensu* Calder & Taylor, Can. Dep. Agric. Monogr. 4(1): 368. 1968.

The variety *vestita* occurs in the mountains of coastal British Columbia, Vancouver Island, Queen Charlotte Islands, and Seward Peninsula of Alaska (Fig. 15).

4. *Draba nivalis* Liljebl, Vet. Acad. Handl. Stockh. 208, 1793 (for complete bibliography see O. E. Schulz in Engler, Pflanzenreich, 89(4, 105): 209 & 210. 1927).

Draba nivalis is the most widespread member of this group in Canada and Alaska. It is found in almost all arctic and alpine areas (Fig. 16) and is circumpolar in distribution.

5. *Draba palanderiana* Kjellman in Vega-Exp. Vet. Iaktt. 2: 45. 1883; Arktiska America, Port Clarence, *F. R. Kjellman*, July 25, 1879 (holotype UPS!).

= *D. caesia auct. plur.*, *non* Adams in Mém. Soc. Nat. Moscou, 5: 108. 1817.

Draba palanderiana is confined to the mountains of the Mackenzie District, Yukon, and Alaska (Fig. 17).

6. ***Draba porsildii*** G. A. Mulligan, sp. nov.; 8 mi S Highway 1 on Kananaskis–Coleman Road, Alta., alt. 5250 ft, *G. A. & D. G. Mulligan 3472*, Aug. 7, 1969 (holotype DAO!).

Plantae perennes caespitellosae. Folia basilaria integra oblanceolata, 3–12 mm longa, 1.5–2.0 mm lata; paginae pilis simplicibus furcatis cruciformibus et stellatis praeditae; pili stellati 4–8-radiati. Caulis florifer 2.0–6.5 cm altus, glaber vel sparsim pubescens, scapiformis vel folio uno oblanceolato praedito. Pedicelli siliculis breviores. Sepala 1.5–2.0 mm longa. Petala alba, 2.0–3.0 mm longa. Siliculae glabrae obovatae, 4.0–8.0 mm longae, 2.0–3.0 mm latae, 5–9-seminales; styli ca. 0.25 mm longae; semina ca. 1 mm longa.

Plant perennial, caespitellose; basal leaves entire, oblanceolate, 3–12 mm long, 1.5–2.0 mm broad; leaf surfaces with simple, forked, cruciform and stellate hairs; stellate hairs with 4–8 rays; flowering stem 2.0–6.5 cm tall, glabrous to sparsely pubescent, with 0–1 oblanceolate leaf; pedicels shorter than silicles; sepals 1.5–2.0 mm; petals white, 2.0–3.0 mm long; silicles obovate, glabrous, 4.0–8.0 mm long, 2.0–3.0 mm broad, 5–9 seeded; seeds about 1 mm long; styles about 0.25 mm long.

This species is named after Dr. A. E. Porsild, a plant taxonomist who has for many years specialized on plants of the arctic and alpine areas of Canada.

Draba porsildii is a tetraploid species with the base number $x = 8$ and has chromosomes that are partly homologous with those of *D. fladnizensis*, *D. lonchocarpa*, and *D. nivalis*. Morphologically, it most closely resembles the latter two species. It is normally self-fertilized in nature but there is evidence of a small amount of outcrossing.

Draba porsildii occurs in the mountains of Alberta, adjacent British Columbia, northeastern British Columbia, Mackenzie District, and Yukon (Fig. 18).

7. *Draba subcapitata* Simmons, Rep. Second Norw. Exped. Fram, 1: 91. 1906; Ellesmereland, Yellow Hill, *Simmons 3591* (lectotype O!, isolectotype DAO!).

Draba subcapitata is found on the high arctic islands of Canada, the Melville Peninsula, and Southampton Island (Fig. 19). It is an amphi-Atlantic species.

Chromosome Numbers

Voucher Specimens for Chromosome Counts

D. fladnizensis, $n = 8$. YUKON: St. Elias Range, 61°33′ N, 140°23′ W, alpine community, altitude 4300 ft, *George W. Scotter 20875 & 20862* (DAO); Tundra communities near Bonnet Lake, 68°11′ N, 137°52′ W, *G.W.S. 20707* (DAO).

D. lactea, $n = 24$. ALASKA: Gaedtuk, St. Lawrence Island, Bering Sea, *S. B. Young 1380* (DAO); McCarthy Quad., vicinity terminus of Sheep Glacier, upper White River valley, 61°42′ N, 142°39′ W, *D. F. & B. M. Murray 2267* (DAO, ALA). FRANKLIN DISTRICT, NORTHWEST TERRITORY, BAFFIN ISLAND: Longstaff Bluff, 68°56′ N, 75°18′ W, *J. A. Parmelee & J. R. Seaborn 4082A* (DAO); Cape Dyer, 66°35′ N, 61°37′ W, *J.A.P. & J.R.S. 3760* (DAO); Inugsuin Fiord, 69°37′ N, 70°02′ W, *J.A.P. & J.R.S. 3922* (DAO). KEEWATIN DISTRICT, NORTHWEST TERRITORY, HUDSON BAY: SE tip Split Island, North Belcher Islands, *P. F. Maycock & J. Op de Beck 10482* (DAO), (plant completely glabrous); just south of NW extremity of Johnson Island, North Belcher Islands, *P.F.M. & J.O. 10751* (DAO), (plant completely glabrous); just SE of NE extremity of Split Island, North Belcher Islands, *P.F.M. & J.O. 10335* (DAO); Sleepers Islands, *P. Morisette 70/156* (DAO).

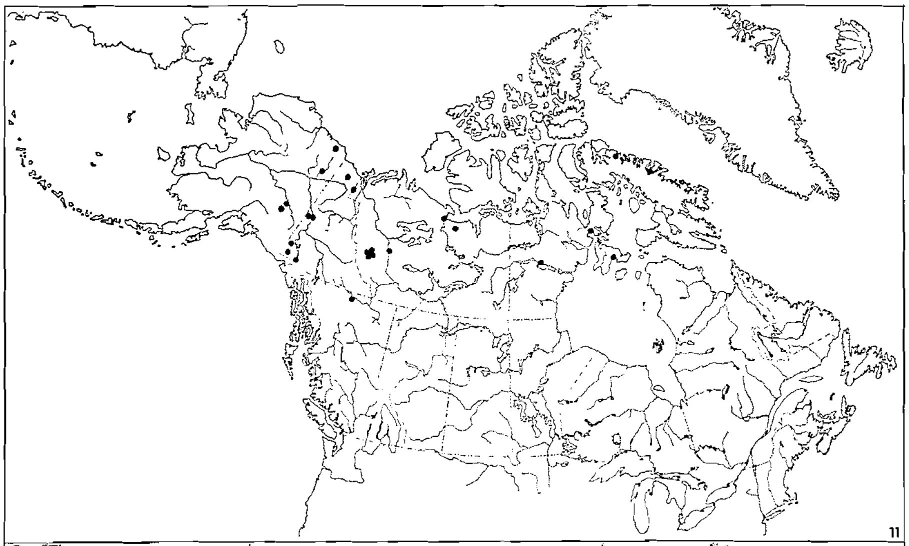
D. lonchocarpa var. *lonchocarpa*, $n = 8$, $2n = 16$. YUKON: Ogilvie Mountains, *R. T. Porsild 1698* (CAN). ALBERTA: ENE Saskatchewan Glacier near Sunwapta Pass, Banff National Park, *J. A. Calder & K. T. MacKay 32710A* (DAO); Snow Creek Pass, 30 mi N Banff, Banff National Park, *G. A. & D. G. Mulligan 3488* (DAO); Sulphur Mountain, near Banff, *G.A.M. & D.G.M. 3494* (DAO); 8 mi S junction of Highway 1 and Kananaskis–Coleman Road, *G.A.M. & C. Crompton 3219* (DAO); 8 mi S junction of Highway 1 and Kananaskis–Coleman Road, *G.A.M. & D.G.M. 3474* (DAO). BRITISH COLUMBIA: Below Stanley Peak, Kootenay National Park, *J.A.C. & K.T.M. 32771* (DAO) & *G.A.M. & D.G.M. 3459* (DAO); Fairy Lake, SSW Fort Nelson, *J.A.C. & I. Kukkonen 27216* (DAO).

D. lonchocarpa var. *vestita*, $n = 8$. BRITISH COLUMBIA: Queen Charlotte Islands, about 3 mi W of head of Cumshewa Inlet below north face of Mount Moresby, Moresby Island, *J.A.C. & R. L. Taylor 36382* (DAO).

D. nivalis, $n = 8$, $2n = 16$. YUKON: Ogilvie Mountains, *R. T. Porsild 464* (CAN). MACKENZIE DISTRICT, NORTHWEST TERRITORIES: Mackenzie Mountains, 62°42′ N, 126°40′ W, *W. J. Cody 17628* (DAO); Anderson River, 69°40′ N, 128° 57′ W, *G. W. Scotter 6462a* (DAO). KEEWATIN DISTRICT, NORTHWEST TERRITORIES: Baker Lake, *E. Whitton Aug. 30, 1967* (DAO); Johnson Island, North Belcher Islands, Hudson Bay, *P.F.M. & J.O. 10805* (DAO); Moore Island, South Belcher Islands, *P.F.M. & J.O. 11014* (DAO); Innetalling Island, South Belcher Islands, *P.F.M. & J.O. 9832* (DAO); Flaherty Island, South Belcher Islands, *P.F.M. & J.O. 11073* (DAO). FRANKLIN DISTRICT, NORTHWEST TERRITORIES: Baffin Island, 66°35′ N, 61°37′ W, *J. A. Parmelee & J. Seaborn 4177* (DAO); Baffin Island, 68°37′ N, 71°08′ W, *J.A.P. & J.S. 4027* (DAO). ALBERTA: Mount Rae, Highwood Pass, 7900 ft, *G. Trottier in 1971* (DAO). BRITISH COLUMBIA: Anahim Lake, *R. L. Taylor 5713* (DAO).

D. porsildii, $n = 16$, $2n = 32$. YUKON: Kluane National Park, 60°45′ N, 138°34′ W, 4500 ft, *G. W. Scotter, Aug. 4, 1972* (DAO). ALBERTA: 7½ mi S junction Highway 3 and Kananaskis–Coleman Road, *G.A.M. & C. Crompton 3220* (DAO, holotype); Plateau Mountain, E. Wilkinson Summit on Kananaskis Road, *J. A. Calder 37299a* (DAO); 8 mi S of Highway 3 on Kananaskis–Coleman Road, *G.A.M. & D.G.M. 3472* (DAO); Snow Creek Pass, 30 mi N Banff, *G.A.M. & D.G.M. 3491* (DAO); Fairy Lake, SSW Fort Nelson, 57°20′ N, 123°55′ W, *J.A.C. & I.K. 27184A* (DAO).

FIGS. 11–19. Distribution in Canada and Alaska, from herbarium specimens. Fig. 11. *D. fladnizensis.* Fig. 12. *D. lactea.* Fig. 13. *D. lonchocarpa* var. *lonchocarpa.* Fig. 14. *D. lonchocarpa* var. *thompsonii.* Fig. 15. *D. lonchocarpa* var. *vestita.* Fig. 16. *D. nivalis.* Fig. 17. *D. palanderiana.* Fig. 18. *D. porsildii.* Fig. 19. *D. subcapitata.*



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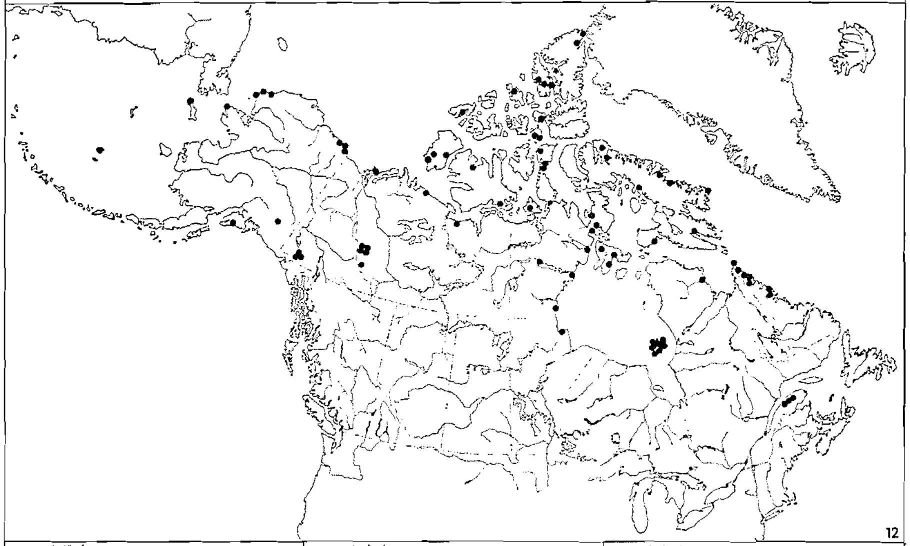

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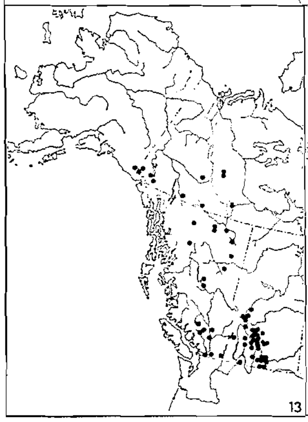

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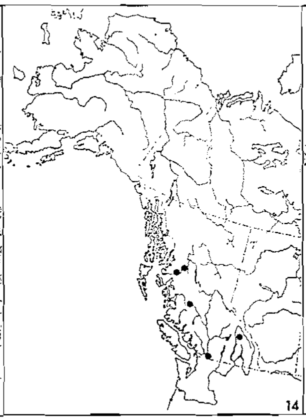

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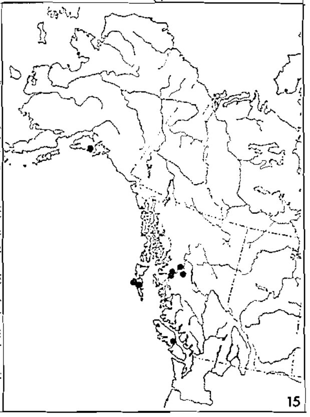

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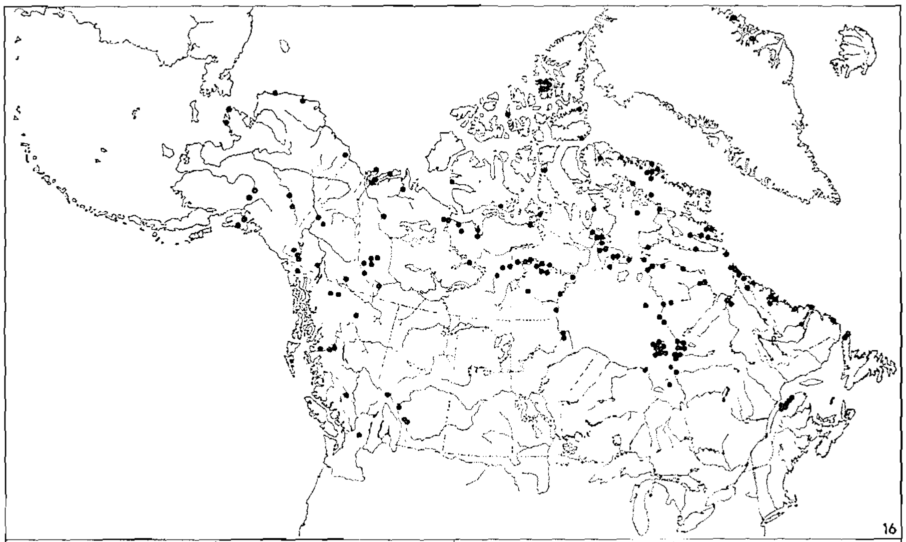

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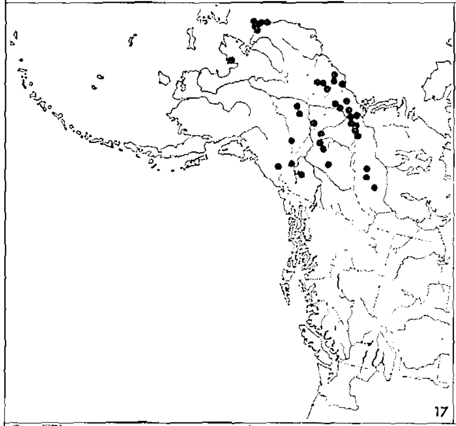

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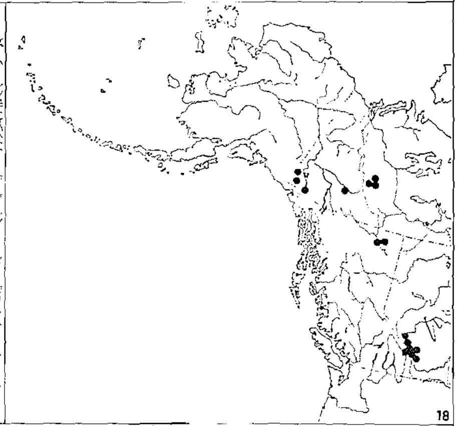

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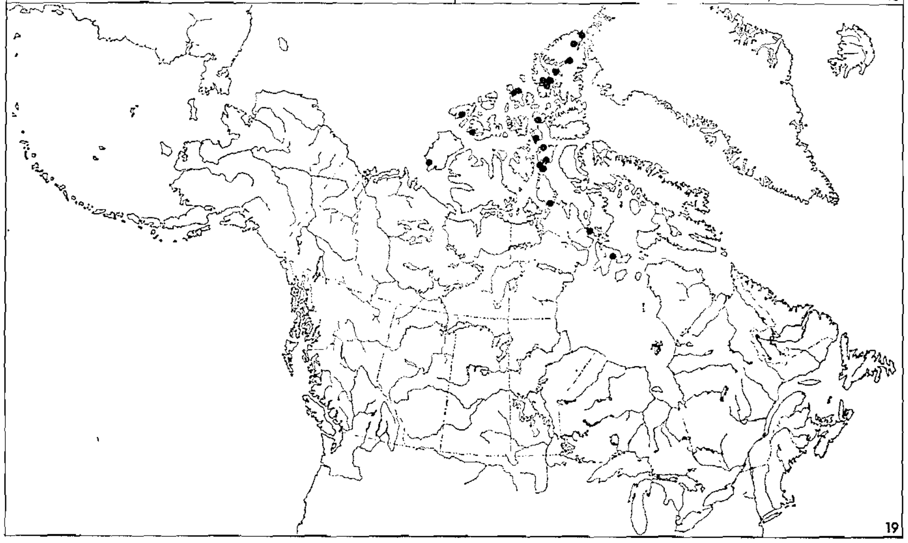

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D. subcapitata, $n = 8$. FRANKLIN DISTRICT, NORTHWEST TERRITORIES: Masik River, Banks Island, *W. Mason 69* (DAO).

Previous chromosome numbers reported for members of the *D. nivalis* group are as follows: *D. fladnizensis*, $2n = 16$, Greenland, Iceland, Norway, alps of Central Europe and Chukhotsk Peninsula of U.S.S.R. (Heilborn 1927; Löve and Löve 1956; Jørgensen *et al.* 1958; Merxmüller and Buttler 1964; and Zhukova and Tikhonova 1973); *D. lactea*, $2n = 48$, Greenland and Norway (Jørgensen *et al.* 1958; and Knaben 1966); *D. lonchocarpa*, $2n = 16$, Canada and Chukhotsk Peninsula of U.S.S.R. (Mulligan 1966; Taylor and Mulligan 1968; and Zhukova and Tikhonova 1973); *D. nivalis*, $2n = 16$, Alaska, Greenland, Iceland, Norway, Sweden, and Wrangel Island and Chukhotsk Peninsula of U.S.S.R. (Heilborn 1927; Löve and Löve 1956; Jørgensen *et al.* 1958; Zhukova 1965; Knaben 1966; Johnson and Packer 1968; Bolkhovskikh *et al.* 1969; Zhukova and Petrovsky 1971; and Zhukova and Tikhonova 1973); *D. palanderiana*, $2n = 32$ & 64, U.S.S.R. (Zhukova 1968; Zhukova and Tikhonova 1971; and Zhukova and Petrovsky 1972); *D. subcapitata*, $2n = 16$, Greenland (Holmen 1952; and Jørgensen *et al.* 1958).

All members of the *D. nivalis* group have the base number $x = 8$. Mulligan (1966, 1971) has shown that many other North American species of *Draba* have higher base numbers. *Draba fladnizensis*, *D. lonchocarpa*, *D. nivalis*, and *D. subcapitata* are diploid, *D. porsildii* is tetraploid, *D. lactea* is hexaploid and *D. palanderiana* is hexaploid and (or) octoploid.

Artificial Hybrids

Artificial hybridization was attempted, in greenhouses at Ottawa, between *D. nivalis*, *D. lonchocarpa*, *D. porsildii*, and *D. lactea* and between these species and other *Draba* not in the *D. nivalis* group. Flowering material of other members of the *D. nivalis* group was not available when these crosses were being attempted. All of the successful crossing, involving members of the *D. nivalis* group, are listed in Table 1. The table includes information on the chromosome numbers of parents, chromosome numbers of interspecific hybrids, the percentage pollen fertility and seed set of the hybrids, and also data on the meiotic configurations found in the hybrids. Some of the hybrids grown in the greenhouse are shown in Figs. 20–22.

Pollen fertility of the first-generation hybrids was zero or nearly so and all the pods aborted at a very early stage. In other hybridization experiments it was found that hybrids between all Canadian species of *Draba* behave in a similar manner. Only first-generation interspecific hybrids are possible in *Draba*. These hybrids can easily be recognized by their aborted pods and low pollen fertility.

Although pollen sterility is complete and

TABLE 1

Artificial interspecific F_1 hybrids in *D. nivalis* group

Hybrid and somatic chromosome number of parents	Chromosome number of hybrid, $2n$	Pollen fertility, %	Seed set	Configurations at metaphase I of meiosis
nivalis (16) × *lonchocarpa* var. *lonchocarpa* (16)	16	0	0	All 8 II
nivalis (16) × *porsildii* (32)	24	0	0	8 III – 3 cells; 7 III + 1 II + 1 I – 9 cells; 6 III + 2 II + 2 I – 10 cells; 5 III + 3 II + 3 I – 2 cells; 4 III + 4 II + 4 I – 1 cell
lonchocarpa var. *lonchocarpa* (16) × *porsildii* (32)	24	0	0	8 III – 3 cells; 7 III + 1 II + 1 I – 6 cells; 6 III + 2 II + 2 I – 14 cells; 5 III + 3 II + 3 I – 1 cell; 4 III + 4 II + 4 I – 1 cell
porsildii (32) × *lactea* (48)	40	13.5	0	Very irregular, mostly univalents, few bivalents
porsildii (32) × *praealta* Greene (56)	44	0	0	Very irregular, could not interpret
porsildii (32) × *kananaskis* Mulligan (64)	48	0	0	Very irregular, could not interpret
porsildii (32) × *stenoloba* Ledeb. (40)	36	0	0	Very irregular, could not interpret
lactea (48) × *praealta* (56)	52	0	0	Very irregular, could not interpret
lactea (48) × *longipes* Raup (64)	56	0	0	Very irregular, could not interpret

silicles abort in artificial first-generation hybrids between *D. nivalis* ($2n = 16$) and *D. lonchocarpa* ($2n = 16$), chromosomes of the hybrid form eight bivalents at metaphase I of meiosis (Figs. 23 and 24). Similarly, the sterile hybrids *D. nivalis* ($2n = 16$) × *D. porsildii* ($2n = 32$) and *D. lonchocarpa* ($2n = 16$) × *D. porsildii* ($2n = 32$) form up to eight trivalents (Figs. 25–28). Heilborn (1927) states that the hybrid *D. nivalis* ($2n = 16$) × *D. fladnizensis* ($2n = 16$) had aborted silicles and formed eight bivalents at meiosis. *Draba nivalis*, *D. lonchocarpa*, and *D. fladnizensis* form 8 bivalents at meiosis and *D. porsildii* forms 16 bivalents. The pairing of chromosomes in the hybrids can be explained as follows.

If the genome of *D. porsildii* is designated as N_1N_1 N_2N_2, the pairing of the two sets of homologous genomes, N_1N_1 and N_2N_2, would form the 16 bivalents observed at meiosis. When *D. porsildii* (N_1N_1 N_2N_2) is crossed with *D. nivalis* (N_3N_3) or *D. lonchocarpa* (N_4N_4) the sterile first-generation hybrids would possess three partly homologous genomes, $N_1N_2N_3$ and $N_1N_2N_4$ and, in the absence of completely homologous sets of chromosomes, form up to eight trivalents at meiosis. According to Stebbins (1971), partly homologous chromosomes may pair with each other if two homologous chromosomes are not present in the same cell. The sterile first-generation hybrids *D. nivalis* × *D. lonchocarpa* and *D. nivalis* × *D. fladnizensis* (Heilborn 1927) would each have two sets of partly homologous chromosomes and would form the observed eight bivalents at meiosis. *Draba fladnizensis*, *D. lonchocarpa*, and *D. nivalis* are diploids, each with two completely homologous sets of eight chromosomes that are partly homologous with sets of the other two species. The formation of up to three trivalents in *D. porsildii* × *D. nivalis* and *D. porsildii* × *D. lonchocarpa* and 16 bivalents in *D. porsildii* indicates that *D. porsildii* contains two sets of 16 chromosomes, each with two completely homologous genomes (N_1N_1 and N_2N_2), and that either genome from both sets of 16 is partly homologous with either of the genomes in the other set. Each of the four sets of eight chromosomes in tetraploid *D. porsildii* is apparently partly homologous to each set of eight chromosomes in the three diploids, *D. fladnizensis*, *D. lonchocarpa*, and *D. nivalis*.

Although hybrids between *D. fladnizensis*, *D. lonchocarpa*, *D. nivalis*, and *D. porsildii* are sterile and are distinct morphologically, the pairing of chromosomes of meiosis suggests that they are very closely related. The pollen fertility of 13.5% in the *D. porsildii* × *D. lactea* hybrid shows that *D. lactea* also belongs to this group. Unfortunately no living material of *D. fladnizensis*, *D. palanderiana*, and *D. subcapitata* was available when the crosses were being made. The pairing of the chromosomes of hybrids from crosses between *D. porsildii* or *D. lactea* and *D. praealta*, *D. kananaskis*, *D. stenoloba*, and *D. longipes* supports morphological evidence suggesting that these species are not members of the *D. nivalis* group.

Natural Hybrids

Herbarium specimens of the following natural first-generation hybrids were recognized: *D. lonchocarpa* × *D. porsildii*, Moose Mountain, Alta., *C. D. Bird 8799a* (DAO); *D. porsildii* × *D. nivalis*, Sewki Mountains, Mack. Dist., N.W.T., *W. J. Cody 17447* (DAO); *D. lonchocarpa* × *D. fladnizensis*, Ogilvie Mountains, Yukon, *J. A. Calder & J. M. Gillett 25958A* (DAO); *D. nivalis* × *D. lactea*, Mount Logan, Que., *A. L. Fernald & A. S. Pease 25101* (CAN). All natural hybrids had complete pollen sterility and aborted silicles. Both parental species were present at the sites where the hybrids were collected. Jørgensen *et al.* (1958) reported the sterile natural hybrid *D. nivalis* × *D. fladnizensis* from Greenland and Heilborn (1927) and Knaben (1966) recorded the same natural hybrid in Norway. Since these hybrids are sterile there is no evidence of interspecific gene exchange in nature.

All members of the *D. nivalis* group, except possibly *D. palanderiana*, are self-pollinating and self-compatible. There is evidence that *D. palanderiana* is a self-incompatible outcrosser. Although *D. fladnizensis*, *D. lonchocarpa*, *D. nivalis*, and *D. lactea* are normally self-pollinated in nature, Mulligan and Findlay (1970) have shown that in most *Draba* flowers the stigma is receptive and exposed for at least 5½ h before the pollen in adjacent stamens is deposited on it and thus outcrossing might occur. Since pollinating insects visit *Draba* flowers under some conditions, they suggest that some cross-pollination occurs in the period between the opening of the

PLATE III

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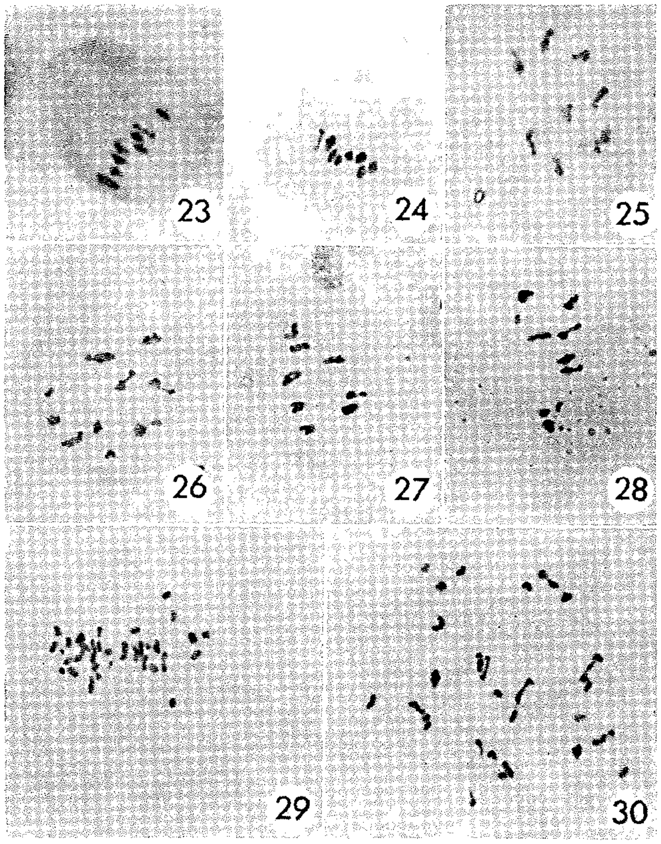
FIGS. 20–22. Some artificial first-generation hybrids grown in a greenhouse. Fig. 20. Left, *D. nivalis* × *D. lonchocarpa* (sterile); center, *D. porsildii* (fertile); right, *D. porsildii* × *D. lonchocarpa* (sterile). Fig. 21. Left, *D. porsildii* × *D. lonchocarpa* (sterile); right, *D. porsildii* × *D. nivalis* (sterile). Fig. 22. *D. lactea* × *D. lonchocarpa* (sterile).

PLATE IV



FIGS. 23–30. Meiotic configuration of artificial first-generation hybrids. Fig. 23. *D. lonchocarpa* × *D. nivalis*, 8 II. Fig. 24. *D. nivalis* × *D. lonchocarpa*, 8 II. Fig. 25. *D. porsildii* × *D. nivalis*, 8 III. Fig. 26. *D. porsildii* × *D. nivalis*, 6 III + 2 II + 2 I. Fig. 26. *D. porsildii* × *D. lonchocarpa*, 8 III. Fig. 28. *D. porsildii* × *D. lonchocarpa*, 6 III + 2 II + 2 I. Fig. 29. *D. lactea* × *D. lonchocarpa*. Fig. 30. *D. lactea* × *D. lonchocarpa*.

flower and when pollen from the adjacent stamens is deposited on the stigmas. The presence of natural F_1 hybrids in these primarily self-pollinating species is positive evidence that outcrossing sometimes occurs in nature.

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