CANADIAN THESES ON MICROFICHE

THÈSES CANADIENNES SUR MICROFICHE

National Library of Canada
Collections Development Branch

Canadian Theses on
Microfiche Service

Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada
Direction du développement des collections

Service des thèses canadiennes
sur microfiche

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE

NL 339 (r. 86/09)

Canada

0-315-19558-4

National Library of Canada
Canadian Theses Division
Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada
Division des thèses canadiennes

2¹/⁴

67466

PERMISSION TO MICROFILM — AUTORISATION DE MICROFILMER

- Please print or type — Écrire en lettres moulées ou dactylographier

Full Name of Author — Nom complet de l'auteur
James Gregory Harris

Date of Birth — Date de naissance
2 August 1954

Country of Birth — Lieu de naissance
U.S.A.

Permanent Address — Résidence fixe
635 Sagewood Ave.
Provo, Utah 84601
U.S.A.

Title of Thesis — Titre de la thèse
A revision of the genus Braya (Cruciferae) in North America

University — Université
University of Alberta

Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée
Ph.D.

Year this degree conferred — Année d'obtention de ce grade
1985

Name of Supervisor — Nom du directeur de thèse
John G. Packer

Permission is hereby granted to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

L'autorisation est, par la présente, accordée à la BIBLIOTHÈQUE NATIONALE DU CANADA de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans l'autorisation écrite de l'auteur.

Date
1 November 1984

Signature
James G Harris

NL-91 (4/77)

THE UNIVERSITY OF ALBERTA

A revision of the genus *Braya* (Cruciferae) in North America

by

© James Gregory Harris

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Doctor of Philosophy

IN

Botany

Department of Botany

EDMONTON, ALBERTA

Spring, 1985

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR James Gregory Harris

TITLE OF THESIS A revision of the genus *Braya* (Cruciferae) in North America

DEGREE FOR WHICH THESIS WAS PRESENTED Doctor of Philosophy

YEAR THIS DEGREE GRANTED Spring, 1985

Permission is hereby granted to THE UNIVERSITY OF ALBERTA LIBRARY to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

(SIGNED) James G. Harris

PERMANENT ADDRESS:

635 Sagewood Ave.
Provo, Utah 84601
U.S.A.

DATED 30 Oct 1984

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled A revision of the genus *Braya* (Cruciferae) in North America submitted by James Gregory Harris in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Botany.

....

Supervisor

Ruth A. Stockey

....

....

Reed C. Rollins

External Examiner

Date October 30 1984

For Janet Cooper, who opened my eyes to biology. Her evident love of the natural world proved infectious.

Abstract

A revision of the genus *Braya* Sternb. & Hoppe is presented for North America. Studies of the morphology (both traditional herbarium studies and numerical analyses), cytology, ecology, and enzyme chemistry of *Braya* have resulted in a treatment recognizing three sections consisting of seven species and six varieties. The phylogeny [illegible] of these taxa are discussed. Keys to the sections, species, and varieties are provided, along with descriptions, chromosome numbers, distribution maps, illustrations, and comments. The following five undescribed varieties are recognized: ***B. humilis*** (C.A. Mey.) Robins. var. ***ellesmerensis*** Harris, ***B. humilis*** var. ***maccallae*** Harris, ***B. humilis*** var. ***porsildii*** Harris, ***B. glabella*** Richards. var. ***prostrata*** Harris, and ***B. thorild-wulffii*** Ostenf. var. ***glabrata*** Harris. Proposed as a new combination is ***B. glabella*** var. ***purpurascens*** (R.Br.) Harris.

Section *Braya* includes a single North American species, *B. linearis*, of Greenland. Section *Platypetalum* includes *B. fernaldii*, endemic to northwestern Newfoundland; *B. glabella* var. *purpurascens* of wide distribution in the high arctic; *B. glabella* var. *glabella* of wide distribution in arctic, sub-arctic, and alpine regions; *B. glabella* var. *prostrata*, endemic to northern Ellesmere Island; *B. longii*, another northwestern Newfoundland endemic; *B. pilosa* of the Mackenzie Delta area; *B. thorild-wulffii* var. *thorild-wulffii*, an endemic of Greenland and the northern Canadian Arctic Archipelago; and *B. thorild-wulffii* var. *glabrata* of Banks Island and Victoria Island. Section *Sisymbriastrum* includes a single species, *B. humilis*, of four varieties: var. *ellesmerensis*, an endemic of northern Ellesmere Island; var. *humilis*, widely distributed on calcareous soils in northern North America; var. *maccallae*, endemic to the Rocky Mountains in southern Alberta and British Columbia; and var. *porsildii* of the Rocky Mountains and Mackenzie Mountains.

Acknowledgments

I am indebted to many people for their assistance with this project. I would first like to thank Dr. J. Packer, my thesis supervisor, for suggesting the study and for offering advice and counsel when it was needed. Dr. K. Denford provided invaluable assistance with the electrophoretic portion of the study especially, for which I am grateful. Drs. G. Ball, R. Stockey, and K. Denford deserve thanks for acting as supervisory committee members, a task that often required a good deal of time and the alteration of busy schedules. I would also like to thank Dr. R. Rollins for agreeing to act as external examiner.

Several people have collected specimens for me from areas that would otherwis[illegible] gone unsampled. These include D. Taylor, J. Taylor, O. Rønning, J. Poelt, B. Welsh, S. White, S. Welsh, G. Scotter, and B. Johnston. I am grateful to all of them.

I wish to thank the curators of the many herbaria that have loaned me specimens, especially Dr. S. Welsh (BRY), who allowed me to remove seeds for greenhouse studies, chromosome counts, and enzyme analysis.

Field work for the project has been supported by a grant from the Boreal Institute for Northern Studies, by logistic assistance from Polar Continental Shelf Project, Canada, and by NSERC Grant No. A-2582 to Dr. J. Packer. I am grateful to all of these organizations.

Many graduate students have offered valuable advice and suggestions from which I have greatly benefited. I offer my best thanks to all of them, but especially to J. Bain, an inexhaustible source of information about any and all aspects of graduate study at the University of Alberta, and N. Salazar, my office mate of three years, a quiet, kind person who has shared a wealth of insight in areas botanical and otherwise.

I would like to thank R. Kroon and H. Barthel for their advice and assistance in cultivating *Braya* plants in the greenhouse, Dr. D. Vitt for offering me the use of much valuable equipment, Drs. D. Pattie and L. Bliss for giving me the opportunity to tag along with them in their studies in the Canadian Arctic Archipelago and to collect specimens from areas that would otherwise have been inaccessible, and Dr. R. Buck for correcting my Latin

diagnoses.

Finally, I acknowledge with deepest gratitude the many contributions of my wife, Melinda, to the successful completion of this project. Some contributions, like her excellent illustrations for this thesis, are obvious. Others, such as her continual patience, support, and encouragement throughout several years of study, are perhaps not as visible, but they are vastly more important, and they have not gone unnoticed.

Table of Contents

List of Tables

List of Figures

I. Introduction

The family Cruciferae is a large cosmopolitan taxon of approximately 350 genera and 3000 species. Members of the family are distributed mainly in the north temperate regions of the world with the highest concentration of species occurring in the lands surrounding the Mediterranean Basin (Hedge, 1976). The Cruciferae is composed predominantly of annual to perennial herbs, but also includes some small shrubs (Benson, 1959).

The family is economically very important due to the large number of cultivated vegetables included in it. Cabbage, cauliflower, broccoli, Brussels sprouts, kohlrabi, kale, turnips, radishes, rutabagas, water cress, and mustard all belong to the Cruciferae. Of increasing economic importance is the production of canola (rapeseed) oil from some species in the genus *Brassica*.

The Cruciferae appears to be a natural assemblage of taxa with exceptionally distinct family limits. The floral structure of the family is remarkably uniform; only rarely do species deviate from a general family description of the flowers and fruits. Flowers have four free sepals, four free petals, six tetradynamous stamens, and a compound pistil of two functional carpels. The ovary develops into an unusual fruit, unique to the Cruciferae, called a silicle if less than twice as long as broad, or a silique if more than about twice as long as broad, that is divided into two locules by a scarious, translucent septum arising from the center of each of the two parietal placentae, forming a false partition. At dehiscence the valves (composed of ripened ovary wall) fall away leaving the septum, placentae with attached seeds, style, and stigma intact. Although there are exceptions to this floral arrangement (some species may lack the corolla or have six stamens of equal length or more or less than six stamens) and fruit type (some species produce indehiscent fruits or fruits with an incomplete septum or with four fertile carpels), the vast majority are as described. This overall uniformity in attributes considered essential for classification makes it very easy to recognize members of the family, but very difficult to separate the members into tribes, genera, and sometimes species (Rollins, 1959, 1982b; Al-Shehbaz, 1973).[1] Rollins (1982b) has commented on the fact that members of a genus in the Cruciferae will often have just enough features in common to bind them into a separate genus, but individual species may closely approach, morphologically, members of closely related genera. He notes that it is very common for two or more genera to come together at the fringes of their diversity and suggests that this lack of gaps in morphological diversity argues for the relative youth of the family; extinction has not yet had time to remove the evolutionary connections between genera. Stebbins (1950) and Al-Shehbaz (1973) have suggested that this apparent confluence of tribes and genera may be due to a much lower extinction rate in the Cruciferae than in families with more distinctly delimited genera.

Early classifications of the Cruciferae usually stressed one or a few morphological characters and, therefore, differed significantly from one another with regard to the definition and delimitation of tribes and genera (Hedge, 1976). Hooker (1862) stressed fruit length and cotyledon and radicle characters; his classification recognized 10 tribes. Prantl (1891) emphasized indumentum characters and recognized only four tribes. Hayek (1911) placed particular importance on nectary glands and myrosin cells; he recognized 10 tribes.

The two most recent world-wide classifications of the Cruciferae have used a larger number of characters to circumscribe tribes and genera. Schulz (1936), in his treatment of the Cruciferae for the second edition of *Die natürlichen Pflanzenfamilien*, used a variety of flower, fruit, gland, embryo, and indumentum characters to divide the family into 19 tribes and 360 genera. Schulz's system has been criticized for placing too little emphasis on the North American crucifers (Rollins, 1941), and for the delimitation and arrangement of his tribes (Janchen, 1942). Janchen (1942), in his classification of the family, recognized 15 tribes — he consolidated some of Schulz's tribes because he felt that the characters used to separate them were not significant enough to warrant tribal recognition — and changed the sequence of the

---

[1] Generic delimitation in the Cruciferae can be so frustrating that one conservative botanist, Krause (1902), in perhaps the ultimate example of "lumping", proposed that the entire family be consolidated into a single all-inclusive genus *Crucifera*. This obviously is not the solution to the problem and only makes the situation more unwieldy and difficult to deal with, and it would have required hundreds of nomenclatural changes in the literature.

tribes to better reflect their phylogeny. He also transferred several genera into different tribes (Hedge, 1976). Hedge (1976) should be consulted for a more detailed comparison of Schulz's and Janchen's classifications.

Recent authors have commented on the inadequacy of both Schulz's and Janchen's classifications and have continued to redefine tribal and generic boundaries (Vaughan & Whitehouse, 1971; Al-Shehbaz, 1973; Hedge, 1976; Hauser & Crovello, 1982; Rollins, 1982b). Taxonomic problems in the Cruciferae are most pronounced at the tribal and generic levels, but species delimitation also can be difficult in some groups (Al-Shehbaz, 1973). The genus *Braya* Sternb. & Hoppe, in the tribe *Sisymbrieae*, is a good case in point. *Braya* is a rather well-defined genus that includes a number of taxa with very obscure species boundaries.

Braya[2] is a relatively small arctic-montane genus of circumboreal distribution. In the Eastern Hemisphere the genus extends well southward to the mountains of Central Asia, but in North America it is restricted to more northerly regions and extends south of the Fiftieth Parallel only in a few widely-scattered disjunct populations (Figure 1). *Braya* is generally not common within its range and tends to be found in small, isolated populations on suitable habitat. Suitable habitat usually consists of barren, often calcareous soils on gravelbars, riverbanks, shorelines, scree slopes, solifluction lobes, and on disturbed soils along roads and airfields.

Braya is based upon *B. alpina*, a species from the Tirolean Alps. As distinguishing characteristics of *Braya*, Sternberg and Hoppe (1815) listed the closed calyx, very widely-spreading corolla, truncate petals, crowned style, convex and somewhat beaked seeds, and cylindrical, torulose siliques. Subsequent authors (Robinson, 1895; Vasil'chenko, 1939; Hegi, 1958) have pointed out the unique nature of the epidermal cells of the septum. The cells have very thick walls and are elongated transversely or very obliquely in relation to the longitudinal axis of the silique (Figure 2). While there are other cruciferous genera that share one or more of *Braya*'s distinguishing features, none share all of them; and, in combination,

---

[2] Named in honor of Franz Gabriel de Bray, president of the Königliche Botanische Gesellschaft of Regensburg and French Ambassador to Bavaria.

Figure 1. Distribution of *Braya* in North America.

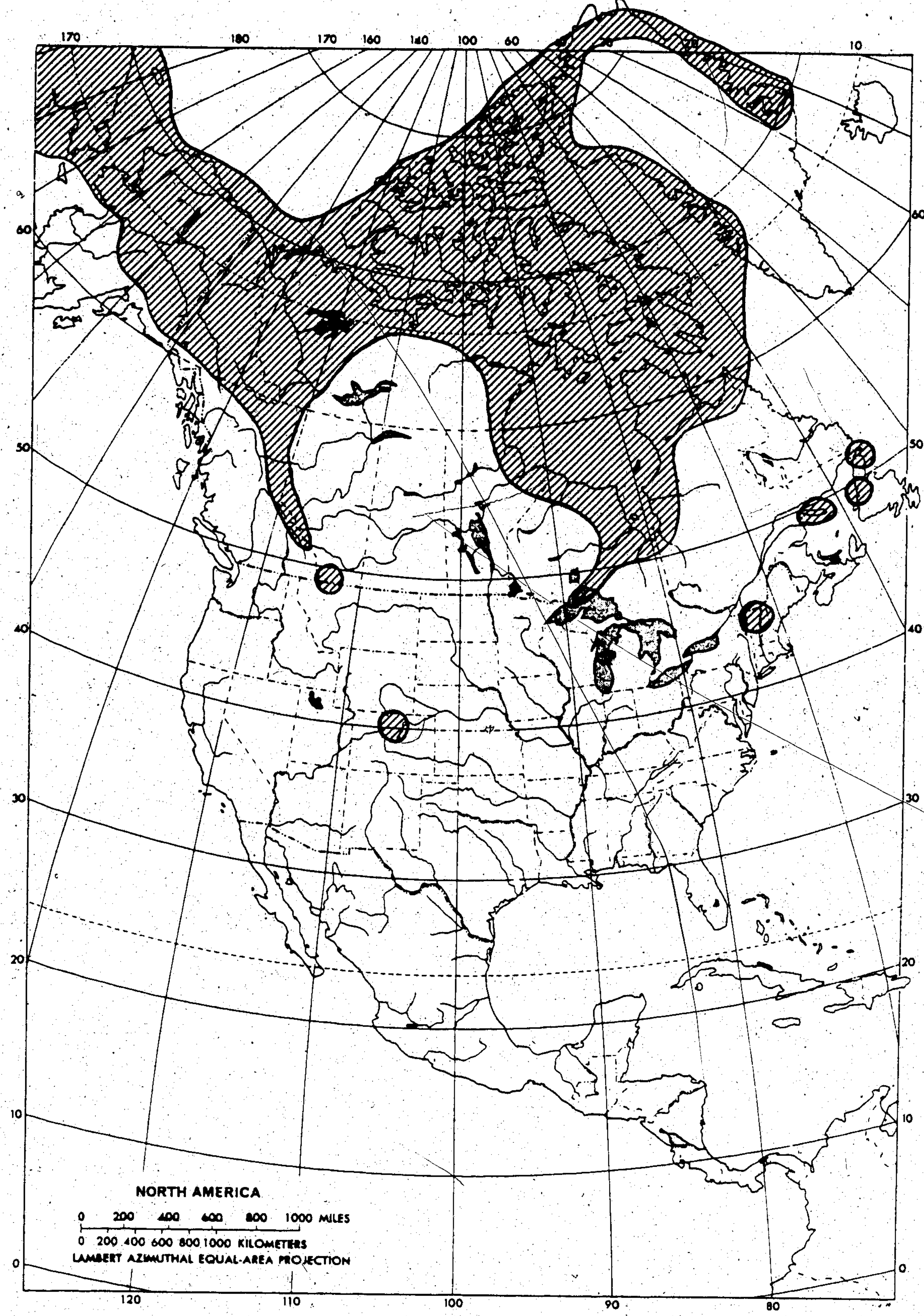
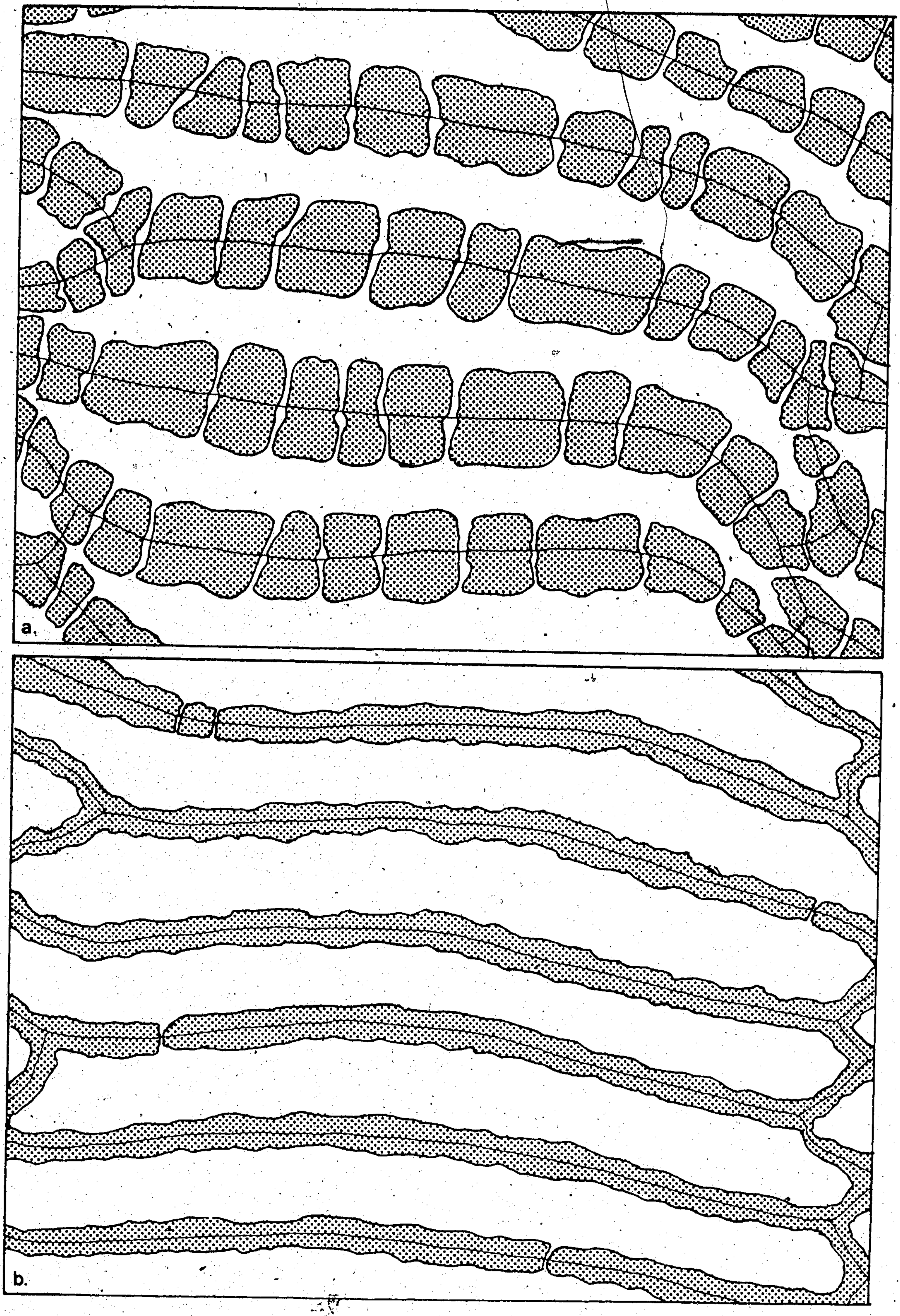

NORTH AMERICA
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
170
180
170
160
140
100
60
10
60
50
40
30
20
10
0
120
110
100
90
80

Figure 2. Epidermal cells of the silique septum in *Braya*; a. *B. humilis* s.l., *B. linearis* Rouy. b. *B. glabella* s.l. (Stippled areas represent cell walls.)


a.
b.

these characteristics delimit the genus very well.

As additional species were described, Sternberg and Hoppe's (1815) original concept of *Braya* had to be enlarged to include taxa obviously closely related to the generic type species, *B. alpina*, but differing somewhat morphologically. Robert Brown (1823) erected the genus *Platypetalum* based upon *P. purpurascens* from Melville Island in the Canadian Arctic, a plant he acknowledged was very similar to *Braya*, but differed in the oval-elliptical shape of the fruits. Bunge (1841) later transferred *P. purpurascens* to *Braya*.

Braya humilis (C.A. Mey.) Robins., from the Altai Mountains of Central Asia, was originally placed in the genus *Sisymbrium* (Meyer, 1830). Robinson (1895) recognized that *Sisymbrium humile* C.A. Mey. ex Ledeb. is morphologically similar to both *Sisymbrium* and *Braya*, but has the septal epidermal cells of *Braya* rather than *Sisymbrium*, and transferred the taxon to *Braya*. Schulz (1924) chose to keep *Sisymbrium humile* separate from *Braya* — largely because the siliques are linear and long and the seeds are arranged in a single row, while the siliques of *B. alpina* are shorter and the seeds appear to be arranged into two rows — and placed it in the newly-erected genus *Torularia*. Currently, some Russian and European herbaria catalog their collections under *Torularia*, but most taxonomists place this taxon within an expanded *Braya*. Even taxonomists with a broad concept of *Braya* recognize that there are at least two, perhaps three, major sections or species groups in the genus in North America: *B. humilis* s.l., *B. glabella* s.l., and *B. linearis* Rouy.

The *Braya humilis* group is characterized by the often sinuate-dentate basal and cauline leaves, leafy stems (usually with three or more leaves per stem), narrow linear siliques (usually 10 - 25 times longer than broad) with uniseriate seeds, and septal epidermal cells with very thick and irregular walls (Figures 2 and 3). Fruit shape, long considered to be of paramount importance in the Cruciferae, is very uniform in the *B. humilis* species group and interpopulation variation is therefore most often treated taxonomically at the subspecies or variety (or even form or race) level. Taxa are usually separated on the basis of minor differences in style length, stigma shape, and silique dimensions and pubescence (Fernald,

Figure 3. Generalized illustration of *Braya humilis* sensu lato.


MWH

1918; Abbe, 1948; Böcher, 1950, 1956; Rollins, 1953; Boivin, 1968, 1969). Twenty-seven nomenclatural combinations in five different genera have been proposed by various authors at various times to categorize the diversity in this species complex in North America (Table 1). Most of the combinations have been proposed because of disagreements over the rank at which a taxon should be treated rather than because of disagreements over taxon recognition.

Abbe (1948), in his treatment of *Braya* in eastern North America, recognized six geographical races in the *B. humilis* complex. These were isolated populations differing somewhat in habit, stigma shape, leaf margins, silique pubescence, and in the dimensions of the style, silique, petals, sepals, and pedicels. Abbe concluded that "there is overlapping of all characters to such an extent that it would be unjustifiable to propose them as varieties or perhaps even as forms"; he simply described and numbered the races, one to six. Subsequent authors have not been at all reticent about proposing names for Abbe's races, which have been recognized as species (Böcher, 1950, 1956; Sørensen, 1954), subspecies (Böcher, 1950, 1956; Rollins, 1953), varieties (Böcher, 1950, 1956; Boivin, 1968, 1969), and forms (Böcher, 1950, 1956).

Very little taxonomic work has been done on the *Braya humilis* species complex in western North America (Hooker, 1830; Robinson, 1895; Rydberg, 1907; Rollins, 1953), even though interpopulation variation appears to be much greater than in the eastern part of the continent and the opportunity for taxonomic interpretation, therefore, more pronounced.

The *Braya glabella* species complex can be characterized by a basal rosette of mostly entire (occasionally with one or two teeth) and somewhat fleshy leaves, a leafless scape (at most with a single leaf or bract subtending the lowermost silique), shorter and broader siliques or silicles (usually 1.5 - 7 times longer than broad) with biseriate seeds, and septal epidermal cells with thinner and more regular walls than those in the *B. humilis* complex (Figures 2 and 4). Fruit shape is generally quite variable in this species group and interpopulation variation is most often treated at the species rank, based principally upon differences in fruit and flower dimensions (Hooker, 1830; Ostenfeld, 1923; Fernald, 1926; Raup, 1934; Abbe, 1948). Eighteen

Figure 4. Generalized illustration of *Braya glabella* sensu lato.


MWH

Table 1. Epithets and nomenclatural combinations proposed for North American members of the *Braya humilis* species complex.

Braya
B. humilis (C.A. Mey.) Robins.
B. humilis ssp. *arctica* (Böch.) Rollins
B. humilis ssp. *arctica* f. *biloba* Böcher
B. humilis ssp. *richardsonii* (Rydb.) Hult.
B. humilis ssp. *ventosa* Rollins
B. humilis var. *abbei* (Böch.) Boivin
B. humilis var. *americana* (Hook.) Boivin
B. humilis var. *arctica* (Böch.) Boivin
B. humilis var. *interior* (Böch.) Boivin
B. humilis var. *laurentiana* (Böch.) Boivin
B. humilis var. *leiocarpa* (Trautv.) Fern.
B. humilis var. *novae-angliae* (Rydb.) Fern.
B. humilis var. *ventosa* (Roll.) Boivin
B. novae-angliae (Rydb.) Sør.
B. novae-angliae ssp. *abbei* Böcher'
B. novae-angliae ssp. *ventosa* (Roll.) Böcher
B. novae-angliae var. *interior* Böcher
B. novae-angliae var. *interior* f. *capitata* Böcher
B. novae-angliae var. *laurentiana* Böcher
B. americana (Hook.) Fern.
B. richardsonii (Rydb.) Fern.
B. intermedia Sør.
B. vestita Porsild (in sched.)*
B. humilis var. *maccallae* Boivin (in sched.)*

Torularia
T. humilis (C.A. Mey.) Schulz
T. humilis ssp. *arctica* Böcher

Pilosella
P. novae-angliae Rydb.
P. richardsonii Rydb.

Sisymbrium
S. humile C.A. Mey. in Ledeb.

Arabidopsis
A. novae-angliae (Rydb.) Brit.

---

*These epithets proposed on herbarium sheets but never actually published.

nomenclatural combinations in two genera have been proposed for this group in North America (Table 2).

Braya glabella Richards. was described in 1823 by Sir John Richardson (1823), Naturalist with Franklin's voyage to the coast of Arctic Canada, from specimens collected on the Copper Mountains between Great Bear Lake and Coronation Gulf. In the same year, Robert Brown (1823) named *Platypetalum* (*Braya*) *purpurascens* from plants collected on Melville Island, Northwest Territories by members of the Parry Expedition. Both taxa are very closely related and belong to the same major species complex, but Brown's *P. purpurascens* represents the more typical and widespread form. Partly for this reason, and because there has been some confusion about which description was published first and which epithet therefore has priority, the name *B. purpurascens* is most often applied to this species group.[3] Nevertheless, it is clear from the original descriptions that although both Richardson and Brown were familiar with each other's work and cite it in their own publications, Richardson is referring to Brown's unpublished manuscript and Brown is referring to Richardson's already published work (he cites final page numbers). The epithet "*glabella*" therefore has priority over "*purpurascens*" and I will refer to this group as the *B. glabella* group or complex from here on.

A third, much smaller group, the *Braya linearis* group, is represented in North America by a single species found on the east and west coasts of Greenland. *Braya linearis* Rouy is also found in northern Scandinavia and, based on some cytological and hybridization studies by Böcher (1966, 1973), appears to be closely related to the type species of the genus, *B. alpina*, from the European Alps. *Braya linearis* bridges the gap, to some extent, between the *B. glabella* and *B. humilis* groups. The fruits are intermediate in length between *B. glabella* and *B. humilis*, but the seeds are arranged roughly into one row as in *B. humilis*. The leaves tend to be long and linear, like *B. glabella*, but with a greater tendency to be toothed, like *B. humilis*. Stems are leafier than those in *B. glabella*, but somewhat less leafy than those in *B. humilis*.

---

[3] In fact, *B. glabella* has occasionally been placed into synonymy under *B. purpurascens* (Robinson, 1895; Scoggan, 1978).

Table 2. Epithets and nomenclatural combinations proposed for North American members of the *Braya glabella* species complex.

Braya
B. glabella Richards.
B. alpina var. *glabella* (Richards.) Wats.
B. alpina ssp. *americana* Hook.
B. alpina var. *americana* (Hook.) Wats.
B. americana (Hook.) Fern.
B. arctica Hook.
B. bartlettiana Jordal
B. bartlettiana var. *vestita* Hult.
B. fernaldii Abbe
B. henryae Raup
B. longii Fern.
B. pilosa Hook.
B. pilosa ssp. *Thorild-wulffii* (Ost.) Petro.
B. purpurascens (R. Br.) Bunge
B. purpurascens var. *dubia* (R. Br.) Schulz
B. purpurascens var. *fernaldii* (Abbe) Boivin
B. purpurascens var. *longii* (Fern.) Boivin
B. purpurascens ssp. *pilosa* (Hook.) Hult.
B. purpurascens ssp. *thorild-wulffii* (Ost.) Hult.
B. purpurascens var. *thorild-wulffii* (Ost.) Boivin
B. thorild-wulffii Ostenfeld
B. thorild-wulffii var. *glabrata* Porsild (in sched.)*

Platypetalum
P. purpurascens R. Br.
P. dubium R. Br.

---

*This epithet proposed on a herbarium sheet but never actually published.

Because from this group only *B. linearis* is distributed in North America, the area addressed in this study, I will refer to this species complex as the *B. linearis* group or complex.

Very few biosystematic studies, other than chromosome counts, have been done on *Braya* in North America. Gaiser (1953) published chromosome counts for *B. humilis* from Colorado and Alaska of $n=32$ and $2n=40$ respectively. Subsequent counts have shown that Gaiser's counts were almost certainly in error (Mulligan, 1965; Böcher, 1966), but they *did* indicate the probability of polyploidy in the genus.[4] Rollins (1953) and Böcher (1956) found a rough correlation between chromosome number and pollen size in the *B. humilis* group and, based on pollen grain measurements, suggested the possibility of lower chromosome numbers eventually being found in Asiatic populations. Mulligan (1965), in a paper providing a number of chromosome counts in *Cardamine* and *Braya*, reported several new chromosome counts from *Braya* populations in Alaska, Northwest Territories, Alberta, British Columbia, and Colorado including the first report of tetraploid members of the *B. humilis* complex (Table 3).

Mulligan (1965) also attempted to cross many of the same *Braya* populations used for chromosome counts, but was only successful in one of them, between a tetraploid *B. humilis* population from the Northwest Territories and a hexaploid *B. humilis* population from British Columbia. He reported that the F_1 hybrids had a chromosome number of $2n=35$ and that meiosis was very irregular; all fruits aborted and no seed was set.

Somewhat surprisingly, by far the greatest amount of biosystematic research has been done on populations from Greenland, one of the least accessible regions of North America. These studies, of course, have been done mostly by Danish botanists such as Holmen (1952), Jørgensen *et al* (1958), and especially Böcher (1950, 1956, 1966, 1973; Böcher & Larsen, 1950). Böcher and Larsen (1950) reported chromosome numbers of two West Greenland taxa, *B. linearis* and *Torularia* (*Braya*) *humilis*, as $2n=42$ and $2n=56$ respectively, firmly establishing $x=7$ as a base number in the genus. Further counts of Greenland *Braya* populations by Holmen (1952) also fell in the $x=7$ pattern. Holmen counted $n=28$ in *B. purpurascens* and

---

[4] Counts of $2n=64$ in *Braya linearis* (Westergaard, 1948) and $2n=32$ in *B. alpina* (Manton, 1932) are also believed to be erroneous (Jørgensen *et al*, 1958; Mulligan, 1965; Böcher, 1966).

Table 3. Chromosome numbers previously reported in *Braya* in North America.

Taxon	n	2n	Locality	Reference
humilis		42	Ellesmere Island, Northwest Territories(3)*	Mulligan (1965)
	14	28	Nahanni, Northwest Territories	Mulligan (1965)
		42	Fort Simpson, Northwest Territories(2)*	Mulligan (1965)
		42	Norman Wells, Northwest Territories(2)*	Mulligan (1965)
		42	Cli Lake, Northwest Territories	Mulligan (1965)
		42	Inuvik, Northwest Territories(3)*	Mulligan (1965)
		56	Carcajou, Northwest Territories	Mulligan (1965)
	14	28	Athabasca River, Jasper, Alberta	Mulligan (1965)
	21	42	Athabasca River, Jasper, Alberta	Mulligan (1965)
	14	28	Kicking Horse River, Yoho, British Columbia	Mulligan (1965)
	21	42	Kinbasket Lake, British Columbia	Mulligan (1965)
		42	MacDonald Creek, British Columbia	Mulligan (1965)
		56	Muncho Creek, British Columbia	Mulligan (1965)
	28	56	Kootenay River, British Columbia	Mulligan (1965)
		56	Hoosier Pass, Colorado	Mulligan (1965)
	21		Northeast Greenland	Jørgensen et al. (1958)
		42	Northeast Greenland	Böcher (1956)
		56	West Greenland(2)*	Böcher & Larsen (1950)
novae-angliae	28	56	West Greenland	Böcher (1956)
		56	West Greenland	Böcher (1966)
		56	Hoosier Pass, Colorado	Böcher (1966)
intermedia	35		Northeast Greenland	Jørgensen et al. (1958)
	35	70	Northeast Greenland	Böcher (1956)
purpurascens	28		North Greenland	Holmen (1952)
	28		Northeast Greenland	Jørgensen et al. (1958)
	28		Northeast Greenland(3)*	Böcher (1966)
		56	Ellesmere Island, Northwest Territories(3)*	Mulligan (1965)
		56	Donnelly, Alaska	Mulligan (1965)
		56	Summit Lake, British Columbia	Mulligan (1965)
thorild-wulffii		28	Ellesmere Island, Northwest Territories(3)*	Mulligan (1965)
		28	Axel Heiberg Island, Northwest Territories	Mulligan (1965)
	14		North Greenland	Holmen (1952)
		28	North Greenland	Böcher (1966)
linearis	21		Northeast Greenland	Jørgensen et al. (1958)
	21	42	West Greenland	Böcher & Larsen (1950)
	21		West Greenland(2)*	Böcher (1966)
linearis x humilis		42	Northeast Greenland	Böcher (1966)

---

*Numbers in parentheses refer to the number of collections counted from that locality.

n = 14 in *B. thorild-wulffii*, the first-reported non-octoploid in the *B. glabella* complex. Jørgensen and Westergaard (1954) reported counts of $2n = 42$ for *B. humilis* in East Greenland and $2n = 70$ for *B. intermedia*, an East Greenland endemic and the only known decaploid in the genus.

In his thorough treatment of the *Braya humilis* complex in Greenland and eastern North America, Böcher (1956), working with plants cultivated in the greenhouse and with wild plants, followed the course of meiosis in West Greenland *B. novae-angliae* and East Greenland *B. intermedia*. He found that meiosis was almost completely regular in *B. novae-angliae*, but much less regular in the decaploid *B. intermedia*. Meiotic irregularity was also evidenced by the high number of dwarfed pollen grains found and by reduced seed fertility. Böcher also conducted cultivation experiments to determine how well phenotypic differences observed in the field would hold up in a common garden. Based on the results, Böcher suggested that East Greenland members of the *B. humilis* complex were distinct from West Greenland members.

Böcher (1966) conducted further cultivation experiments with *Braya* populations from Greenland, Asia, Europe, and Colorado. He recognized that *B. linearis* and *B. alpina* are very closely related, but with enough differences to maintain them as separate species and suggested their close relationship to *B. aenea*, an Asiatic species, and to *B. glabella*, *B. pilosa*, and *B. henryae* from North America. Böcher felt that cultivated plants of *B. novae-angliae* ssp. *novae-angliae* from Greenland appeared to be only subspecifically different from those of *B. novae-angliae* ssp. *ventosa* from Colorado, and that both of these subspecies were closely related to ssp. *abbei* from Newfoundland.

Finally, Böcher (1973) conducted hybridization experiments between *Braya linearis*, *B. alpina*, and *B. rosea*.[5] He found that a *B. linearis* x *B. alpina* cross produced fertile F_1 hybrids, indicating a very close relationship between the two taxa. The *B. linearis* x *B. rosea* cross was much less successful. The F_1 hybrids exhibited meiotic chromosome-pairing disturbances; most chromosomes did not pair properly and the plants were sterile.

---

[5] *Braya rosea* is an Asiatic species.

Chemosystematic studies of *Braya* evidently have never been attempted. This despite the fact that such studies have proved useful in other cruciferous genera. Of particular value in the Cruciferae have been the glucosinolates and seed and leaf proteins.

The glucosinolates are a group of about 85 naturally-occurring anions that upon hydrolysis with myrosinase enzymes characteristically break down into glucose, sulfate, and isothiocyanate (mustard oil). It is the resulting isothiocyanates that are responsible for the pungent aroma and sharp, biting taste associated with plants in the mustard family. The isothiocyanates are found only in very minute quantities or may be completely absent from healthy tissues and are formed only when the tissues are crushed or damaged (Ettlinger and Kjaer, 1968; Al-Shehbaz, 1973).

The glucosinolates have shown some promise for chemotaxonomic studies in the Cruciferae. The order Rhoeadales of Bessey (1915) included the families Papaveraceae, Fumariaceae, Tovariaceae, Moringaceae, Resedaceae, Capparaceae, and Cruciferae. All of these families, with the exception of Papaveraceae and Fumariaceae, contain glucosinolates (Kjaer, 1960). It would seem then that the Rhoeadales is not a natural order and that the Papaveraceae and Fumariaceae should be removed (Kjaer, 1963). Interestingly, the same conclusion was reached by Cronquist (1968, 1981) and Takhtajan (1969) primarily on morphological grounds and they have included only the families that produce glucosinolates in the order Capparales.

While it appears that the Capparales is a natural order, partly on the basis of the presence of glucosinolates, it should be added that several other unrelated families also produce glucosinolates: Limnanthaceae, Caricaceae, Bataceae, Tropaeolaceae, Gyrostemonaceae, Salvadoraceae, Zygophyllaceae, and Euphorbiaceae. Clearly, the glucosinolates do not provide the definitive answer to the classification of families containing these compounds.

Furthermore, the glucosinolates appear to be of very limited value in determining generic and tribal boundaries in the Cruciferae (Al-Shehbaz, 1973). Ettlinger and Thompson (1962) were able to distinguish *Brassica* from *Sinapis* on the basis of differences in glucosinolate content, but Al-Shehbaz (1973) could find no distinct patterns of glucosinolate distribution that set apart the six genera of the tribe Thelypodieae (*Stanleya, Thelypodium, Thelypodiopsis, Caulanthus, Streptanthus,* and *Streptanthella*). It appears that the glucosinolates are much more valuable as taxonomic markers at the interspecific and infraspecific levels (Al-Shehbaz, 1973).

Kjaer and Hansen (1958), in a study of *Arabis*, found that patterns of glucosinolate distribution correlated quite well with morphological differences between taxa. Al-Shehbaz (1973), in his biosystematic treatment of *Thelypodium*, found that, except for a few species, the qualitative and quantitative patterns of glucoside distribution were species-specific. The data provided by the glucosinolates appeared to support the taxonomic decisions arrived at through other types of data.

Rodman (1974, 1980) found that glucoside patterns were very useful for detecting hybrids. He found that *Cakile* plants suspected of being hybrids on morphological grounds were additive for numbers of glucosides (incorporating the glucosides of both parents in the pattern) and intermediate for quantities of glucosides (Rodman, 1980). This indicated quite clearly that the suspected hybrids were in fact of hybrid origin.

The biosynthesis of glucosinolates is apparently under direct genetic control and the compounds are very stable (Rodman 1974, 1980). Both of these features make the glucosinolates excellent taxonomic markers.

Rodman (1974) found that glucosinolate patterns are often very different between interspecific and infraspecific taxa, but sometimes chemical variation between populations without corresponding morphological differences can occur. He also noticed clinal changes in glucosinolate content and concluded that glucosinolate patterns are another taxonomic character, very similar to other types of characters in their patterns of distribution, susceptibility to variation and taxonomic usefulness.

Unfortunately, plants like *Braya*, with usually limited numbers of rather small seeds, do not lend themselves well to studies of glucosinolate profiles — there simply is not enough seed material available. This is an area of great potential, however, for future long-term taxonomic studies of *Braya* in which adequate quantities of seed might be gathered from populations raised in the greenhouse, or when more sophisticated assaying techniques are developed.

Several serological and electrophoretic studies of seed proteins in the genus *Brassica* have demonstrated the value of these proteins as taxonomic characters in the Cruciferae. Vaughan *et al* (1966) used serological and acrylamide gel electrophoretic techniques in a study of the seed proteins of *Brassica campestris, B. oleracea*, and *B. nigra* to determine the usefulness of these techniques for taxonomic studies of *Brassica*. Their results indicated that all three taxa could be separated immuno-electrophoretically. They also found that *B. oleracea* and *B. campestris* were much more closely related to each other than they were to *B. nigra*. This supports the view of Schulz (1924) that *B. oleracea* and *B. campestris* belong in the section *Brassicotypus* and *B. nigra* belongs in the section *Melanosinapis*.

Vaughan *et al* (1966) also extracted proteins for acrylamide gel separation from seeds and separated them into globulins and albumins by dialysis. It was found that the globulin patterns of *Brassica nigra* were different from those of the other two species, which were indistinguishable from one another, but that all three species had different albumin patterns. Thus, acrylamide gel separation also indicated that *B. oleracea* and *B. campestris* were more closely related to each other than to *B. nigra*. Vaughan *et al* (1966) concluded that the seed protein composition of the three species studied supported the previous classification of these taxa on morphological grounds.

Vaughan and Waite (1967a), using serological techniques, studied the differences in seed proteins between *Brassica* and *Sinapis*. Four *Brassica* taxa and *Sinapis alba* were examined. On the basis of galactosidase, glucosidase, and esterase activity, they determined that *Sinapis* was distinct from the four *Brassica* taxa and that *B. oleracea* and the two *B. campestris* taxa were more closely related to each other than to *B. nigra*. Again, seed [illegible]in studies supported traditional taxonomic methods.

Vaughan and Waite (1967b) used the same serological, electrophoretic, and isoenzyme staining methods to test the hypothesis that *Brassica nigra* (n=18), *B. oleracea* (n=9), and *B. campestris* (n=10) have hybridized to produce the amphidiploids *B. carinata* (n=17), *B. juncea* (n=18), and *B. napus* (n=19). Starch-gel electrophoresis and the identification of the enzyme groups present supported the idea that the three above-mentioned putative hybrids are in fact of hybrid origin. It was found that in each case, most of the enzymes present in the putative parents were also present in the suspected hybrids. (Although in a few instances parent enzymes were not contributed to the hybrid.) On the other hand, enzymes present in the putative hybrids were nearly always present in one or both of the parent species. Only in rare instances did the hybrids contain proteins that were unique. This was taken by Vaughan and Waite to support fairly well the hybridization theory mentioned above.

An additional study by Vaughan and Denford (1968) using acrylamide gel electrophoresis to examine the seed albumins of *Sinapis* and several *Brassica* taxa supported the conclusions reached by Vaughan *et al* (1966), and Vaughan and Waite (1967a, 1967b). In addition, it was found that *B. campestris* contained 100% of the high-frequency enzyme bands found in the other *Brassica* taxa, suggesting that it is most closely related to the ancestral stock of this group.

Vaughan *et al* (1976) have reviewed the studies done using seed proteins as taxonomic indicators in the Cruciferae.

Being under direct genetic control, it would seem that the seed proteins should be extremely valuable in taxonomic studies and, indeed, from the studies cited above, it appears that they have already proved themselves useful in the delimitation of species boundaries in the genus *Brassica*. But the same requirement of reasonably large quantities of seed material for glucosinolate analysis also limits the practicality of seed protein studies in small-seeded genera such as *Braya*. Fortunately, some recent studies have indicated the usefulness of leaf enzymes as possible taxonomic characters in the Cruciferae.

Coulthart (1979) and Coulthart and Denford (1982) successfully used leaf enzymes for electrophoretic analysis of the genetics of an alloploid complex in *Brassica*. Similar techniques, employed in determining electrophoretic banding patterns of leaf enzymes in *Braya*, should prove useful in providing chemotaxonomic characters capable of shedding new light on the taxonomic problems in this genus.

II. Materials and Methods

A. Field Studies and Collections

Field work was carried out during the summers of 1981, 1982, and 1983 throughout a significant portion of the range of *Braya* in North America. Representative plants were collected from forty-nine populations in Alaska, Yukon, continental Northwest Territories, the Canadian Arctic Islands, British Columbia, Alberta, Newfoundland, Vermont, and Greenland. Pressed and dried herbarium specimens were taken from all populations and living plants were collected from some of the populations, especially those that did not have plants with mature seeds. In addition, during the field season of 1981, immature floral buds were collected and fixed in Carnoy's solution for later cytological examination. Information on habitat and plant community type was recorded for each population sampled.

Plants from several other populations in Alaska, Colorado, Baffin Island, Greenland, and Spitzbergen were collected for me by others and those specimens have been included in this study.

B. Morphology

Distribution information and morphological studies were based on my own collections and those of the University of Alberta (ALTA), as well as on more than 1,000 herbarium specimens received on loan from the following institutions:

Biosystematics Research Institute, Agriculture Canada (DAO); National Herbarium of Canada (CAN); Brigham Young University (BRY); Herbier Marie-Victorin, University of Montreal (MT); Gray Herbarium of Harvard University (GH); Kew Herbarium and Royal Botanic Gardens (K); British Museum (Natural History) (BM); University of Copenhagen (C); Botanische Staatssammlung, München (M); Komarov Botanical Institute of the Academy of Sciences of the U.S.S.R. (LE); Academy of Natural Sciences, Philadelphia (PH); University of Michigan (MICH).

Herbarium specimens were examined initially for obvious morphological differences and whether or not these differences correlated with geographic distributions or habitat preferences. In addition to these more general studies, 103 representative specimens (see Appendix 1) were measured and scored for 42 morphological attributes (see Table 4) to be analyzed with a computer classification program, TAXMAP, developed by Dr. J.W. Carmichael of the University of Alberta (Carmichael, 1983). Attributes were chosen from among those which have been most frequently considered valuable in the Cruciferae along with others that appeared useful from my own examination of herbarium specimens. Measurements were taken with a hand rule, with an ocular micrometer in an American Optical dissecting microscope, or with a Houston Instrument Hipad digitizer and Apple II computer using the BIOQUANT II statistical package. Measurements of very small structures (such as seed and style dimensions) were made with the Hipad digitizer and a drawing tube attached to a Leitz dissecting microscope.

TAXMAP calculates the ranges of the attribute values and normalizes the raw data as fractions of the ranges. A weighted average relative proximity is then calculated between each pair of Operational Taxonomic Units (OTU's, or in this case populations or collections) and the OTU's are grouped into clusters according to relative discontinuities in proximities between clusters. A taxometric map is then drawn on a Calcomp plotter. The map is a two-dimensional representation of the relationships of the clusters to each other. Circles represent clusters of more than one OTU and numbered points represent single-member clusters. Arrows indicate the nearest neighbor to each cluster.

C. Greenhouse Studies

Seeds from each collection, when available, were removed from pressed and dried specimens and placed in a freezer for four or five days prior to sowing. Seed germination percentage under these conditions was very high and no further pretreatment experimentation was required; seeds from all populations were routinely exposed to below-freezing temperatures

Table 4. Morphological attributes used in TAXMAP computer analysis.

1. Silique length in mm.
2. Silique width at widest point in mm.
3. Silique width/length ratio
4. Style length in mm.
5. Style width at center in mm.
6. Style width/length ratio
7. Style shape (1=sides parallel, 2=somewhat broader at base, 3=much broader at base)
8. Stigma shape (1=entire, 2=indistinctly bilobed, 3=moderately bilobed, 4=broadly bilobed)
9. Stigma breadth (1=same width as style, 2=slightly broader than style, 3=moderately capitate, 4=broadly capitate)
10. Silique pubescence type (0=none, 1=simple hairs only, 2=mostly simple hairs, some biforked, 3=simple and biforked hairs equal, 4=mostly biforked hairs, some simple, 5=biforked hairs only, 6=biforked hairs, some 3-forked hairs)
11. Silique pubescence degree (0=glabrous, 1=glabrous-extra sparse, 2=extra sparse, 3=sparse, 4=sparse-moderate, 5=moderate, 6=moderate-dense, 7=dense)
12. Fruiting pedicel length in mm.
13. Inflorescence length in cm.
14. Fruiting inflorescence density (average percentage of total siliques arising from the top 1 cm of the inflorescence)
15. Seed row number in siliques
16. Seed length in mm.
17. Seed width in mm.
18. Seed width/length ratio
19. Petal length in mm.
20. Petal width in mm.
21. Petal width/length ratio
22. Sepal length in mm.
23. Sepal width in mm.
24. Sepal width/length ratio
25. Sepal pubescence type (0=none, 1=simple hairs only, 2=mostly simple hairs, some biforked, 3=simple and biforked hairs equal, 4=mostly biforked hairs, some simple, 5=biforked hairs only)
26. Sepal pubescence degree (0=glabrous, 1=glabrous-extra sparse, 2=extra sparse, 3=sparse, 4=sparse-moderate, 5=moderate, 6=moderate-dense)
27. Plant height in cm.
28. Stem leafyness (average number of leaves per stem)
29. Stem branching (average number of branches per stem)
30. Stem rosette formation (0=none, 1=uncommon, 2=common)
31. Stem number per plant
32. Stem pubescence type (1=simple hairs only, 2=mostly simple hairs, some biforked, 3=simple and biforked hairs equal, 4=mostly biforked hairs, some simple, 5=biforked hairs only, 6=mostly biforked hairs, some 3-forked)
33. Stem pubescence degree (1=extra sparse, 2=sparse, 3=moderate, 4=moderate-dense, 5=dense)
34. Basal leaf length in cm.
35. Basal leaf width in cm.
36. Basal leaf width/length ratio
37. Leaf pubescence type (0=none, 1=simple hairs only, 2=mostly simple hairs, some

biforked, 3=simple and biforked hairs equal, 4=mostly biforked hairs, some simple, 5=biforked hairs only, 6=mostly biforked hairs, some 3-forked)

38. Leaf pubescence degree (0=glabrous, 1=extra sparse, 2=sparse, 3=sparse-moderate, 4=moderate, 5=moderate-dense, 6=dense)
39. Basal leaf margin (0=all leaves entire, 1=rare tooth on some leaves, 2=occasional tooth on some leaves, 3=frequent tooth on some leaves, 4=most leaves toothed, 5=all leaves distinctly toothed)
40. Stem habit (1=prostrate-decumbent, 2=ascending-erect)
41. Septum margin base (0=not sack-like, 1=sacklike)
42. Siliques aborted (0=absent or rare, 2=frequent or common)

thereafter.

Seeds were sown under a thin layer of sand in 5-inch plastic pots and the seedlings were later transplanted to 2.5-inch or 3-inch clay pots and placed in the greenhouse in the Biological Sciences Building at the University of Alberta. The temperature in the greenhouse ranged from about 12° - 16°C depending on the outside temperature, and natural lighting was supplemented with artificial lighting to provide about an 18-hour daylength. The intent was not to attempt to simulate any particular environment so much as to provide an environment generally suitable to most *Braya* taxa so that phenological differences observed between populations in the field could be observed in a common garden to see which were environmentally controlled and which were under more strict genetic control. Some specimens from very high latitudes did not do well in the greenhouse and had to be moved to a growth chamber and provided with a 24-hour photoperiod.

Living plants also provided an opportunity for studying the breeding systems of *Braya*. Plants were examined to determine their ability to self-pollinate, and a dissecting microscope and fine forceps were used to carefully remove stamens from plants prior to anthesis to check for any evidence of agamospermous reproduction. A limited number of artificial hybridizations were also attempted by transferring pollen from the anther of a male donor flower to the stigma of an emasculated female recipient flower under a low-power dissecting microscope. It was usually quite obvious under the dissecting microscope if the emasculation of the recipient flower had been unsuccessful and self-pollination had accidentally occurred because the pollen grains were clearly visible on the stigma.

Representative specimens of these cultivated plants have been preserved in the University of Alberta Herbarium (ALTA).

D. Cytology

Meiotic chromosome counts from floral buds fixed in the field were unsuccessful and all counts were made from the somatic cells of root tips of plants transplanted to the greenhouse or raised in the greenhouse from seed.

Mitotic chromosome counting methods were basically those of Tijo and Levan (1950). Root tips were pretreated for 3 - 4 hours in a 0.002 molar solution of 8-hydroxyquinoline at 13° - 17° C, washed for 5 - 10 minutes in distilled water, blotted dry, and stained in a watchglass with a solution of acetic-orecein and 1N HCl (9:1) for 30 - 40 minutes. Three or four times during staining, the root tips and stain solution were warmed gently over an alcohol burner. The root tip meristems were then mounted in 45% acetic acid on a microscope slide and the coverslip was ringed with a mixture of paraffin wax and gum mastic (1:1). The slides remained useable for about 6 - 8 months.

Chromosomes were counted with either the high-power dry objective (788X) or the oil immersion objective (1250X) of a Reichert or Nikon microscope. Voucher specimens for most counts are deposited in the University of Alberta Herbarium (ALTA).[6]

Drawings of some representative preparations were made from photographs taken with a Nikon microscope-camera system. Because of the narrowness of the depth of field of the microscopic image, it was almost always necessary to take a series of three or four photographs while focusing through the chromosome preparation to ensure that all chromosomes had been recorded. Composite drawings were then made from these series of photographs.

E. Enzyme Analysis

Living leaf tissues from *Braya* plants grown from seed were used for electrophoresis. Seeds were obtained from plants collected in the field, as well as from herbarium specimens on loan from Brigham Young University. Seed voucher specimens are listed in Appendix 2.

---

[6] Some counts were made from plants grown from seeds removed from collections on loan from Brigham Young University. These counts are vouched for by specimens at the Brigham Young University Herbarium (BRY).

Several seeds from each population were sown in 5-inch plastic pots onto soil and covered with a thin layer of sand. The seedlings were germinated and raised in a greenhouse under natural lighting conditions[7] at about 25° C (temperature fluctuated somewhat depending on the outside temperature). Plants were well watered.

To ensure adequate material for electrophoresis, entire vegetative basal rosettes were used for enzyme extraction after between 6 and 10 true leaves had developed.[8] Because of the large number of populations sampled and the small amount of plant material available from many of these populations, plants from each population were combined and extracted together.

Leaf extracts were prepared using the extraction buffer (0.06 M Tric-HCl, pH 6.7) and extraction techniques of Coulthart and Denford (1982). The extracts were then quick-frozen in liquid nitrogen and stored frozen in the dark until just prior to electrophoresis.

All enzymes were electrophoresed in polyacrylamide gels, using a single-phase electrophoresis system modified from Denford (1970). A single-density "small pore" gel was cast into 5 mm diameter x 75 mm long glass tubes, to within 1 cm of the top, following the procedure outlined in Coulthart (1979). The gels were then run vertically in a Buchler Instruments "Polyanalyst" apparatus, through which cold tap water was circulated throughout the run. This system allowed 12 gels to be run simultaneously. Enzyme samples in extraction buffer were mixed with 20% sucrose (1:1) to increase the density, and layered under cathode buffer onto the surface of the gels with a pipette. Sample volumes varied from 30 μL to 100 μL per gel, depending on the stain intensity of the enzyme.

Gels were run for 60 to 70 minutes at a constant current of 2.5 mA per tube, until the bromophenol blue marker dye in the cathode buffer had migrated to within 5 mm of the end of the gel. The gels were then removed from the tubes and stained following the procedures and stain recipes of Coulthart (1979). Enzyme banding patterns were carefully compared between

---

[7] Seeds were sown between the first and second week of June and the seedlings were allowed to grow until between the last week of July and the first week of September.

[8] Some previous studies (Coulthart & Denford, 1982) have used only one of the first pair of true leaves to ensure that a uniform phenological stage was sampled, but comparisons of electrophoretic banding patterns of extracts from younger vegetative rosettes and older vegetative rosettes in *Braya* showed no differences.

gels and then recorded as interpretive drawings. A diagram of the banding patterns in the five enzyme systems is included in Appendix 3.

III. Results

A. Morphology

Herbarium specimens were studied in an attempt to determine morphological boundaries between the taxa that have been recognized by various authors in the past (see Tables 1 and 2). The results of these studies to find the obviously delimitable and definable North American *Braya* taxa will be discussed in later sections.

Specimens representing 103 *Braya* populations were scored for 42 morphological attributes and analyzed with the computer classification program TAXMAP. The clusters resulting from the analysis are listed in Table 5. To aid in the interpretation of the clusters, each OTU was named as "glab" (*B. glabella* complex), "line" (*B. linearis* complex), or "humi" (*B. humilis* complex) according to the major species group it appeared to belong to. Following each name is a two-letter code indicating the general location of the population, followed by the collector's(s') name(s) and collection number. For a more complete list of the collection localities for each OTU, as well as the location of the voucher specimens, see Appendix 1. The resulting taxometric map is presented in Figure 5.

TAXMAP recognized 19 clusters and 16 isolated OTU's, or single-member clusters. The first thing that is obvious from the taxometric map is the clear separation of the *Braya glabella* group clusters from the *B. humilis* group clusters. The map is shaped somewhat like a figure 8 leaning to the left. The top of the "8" is composed entirely of *B. glabella* clusters, and the bottom of the "8" consists of *B. humilis* and *B. linearis* clusters. The distinction between the larger species groups is even clearer in the nearest neighbors map redrawn from Figure 5 to show only the relationships of the clusters to their nearest neighbor cluster (Figure 6). The two larger groups (*B. humilis* and *B. glabella*) appear as completely separate entities, with *B. linearis* combining with *B. humilis*.

Within the *Braya glabella* group there are 19 clusters. Many of these clusters are only slightly different from each other and can be categorized together. *Braya glabella* var.

Table 5. TAXMAP cluster analysis of morphological attributes.

```
MAP CLUSTER ANALYSIS:-TAXOMETRIC ANALYSIS OF THE GENUS BRAYA - MORPHOLOGICAL ATTRIBUTES

OTU LISTED AFTER BLANK LINE IS EXCLUDED FROM CLUSTER FOR REASON(S) INDICATED BY FLAG.
FLAG 1 = AVERAGE LINKAGE CRITERION EXCEEDED. FLAG 2 = SINGLE LINKAGE CRITERION EXCEEDED.
FLAG 3 = RATIO CRITERION VIOLATED. FLAG 4 = OTU ALREADY IN A CLUSTER.

(MAXIMUM NUCLEUS 0.152, MAXIMUM RISE 0.0243 BOTH ARE 100% OF NORMAL)
EQUALLY WEIGHTED ATTRIBUTES

CLUS OTU DIST OTU  AVGOF  RISE FAR DIST FLAG NAME OF OTU
TER  NOS BEST BEST  NEW    IN  OTU FAR
NO.      LINK LINK LINKS  AVG.      OTU
-----------------------------------------------------------
  1   75                                    humi BC Harris 1642
      76 0.06                               humi BC Harris 1643
      74 0.07   76 0.073 0.008  75 0.08     humi AL Harris 1640
      73 0.07   74 0.082 0.009  75 0.09     humi AL Harris 1638
      71 0.08   76 0.102 0.019  74 0.12     humi AL Harris 1568
      70 0.09   71 0.107 0.006  75 0.11     humi AL Harris 1566
      80 0.08   70 0.100-0.007  73 0.12     humi AL Harris 1743
      61 0.08   70 0.108 0.007  73 0.13     humi AK Harris 1331
      65 0.08   61 0.117 0.009  73 0.15     humi YT Harris 1465
      57 0.08   61 0.122 0.005  75 0.15     humi AL Dumais 7694
      69 0.09   80 0.103-0.019  71 0.12     humi AL Harris 1554
      56 0.09   69 0.119 0.016  71 0.15     humi CO Johnston 2371
      66 0.10   69 0.118-0.000  57 0.15     humi YT Harris 1470
      60 0.10   61 0.129 0.011  66 0.15     humi AK Harris 1232
      85 0.08   60 0.146 0.017  71 0.18     humi AL McCalla 2272
      84 0.10   80 0.139-0.007  57 0.17     humi GL Schwarzenbach 1253
      93 0.08   84 0.149 0.011  56 0.19     humi GL Seidenfaden 292b
     102 0.10   85 0.156 0.006  73 0.19     humi AS Vereshchagin 372

      83 0.10   80 0.181 0.025  57 0.24 1000 humi AL Harris 1639
-----------------------------------------------------------
  2   18
      19 0.07                               glab AI Harris 1719
       3 0.09   19 0.098 0.031  18 0.11     glab AI Harris 1691
       1 0.07    3 0.102 0.004  18 0.13     glab AK B. Welsh 1247b
       7 0.08    1 0.111 0.009  18 0.15     glab AK Strutz & Shelt. 2240
      54 0.09    3 0.117 0.006  18 0.14     glab AK S. Welsh 20769(a)
       5 0.09    3 0.117 0.000   7 0.13     glab SV  Ronning s.n.
      39 0.09    1 0.121 0.004  54 0.14     glab AK B. Welsh 1246a
       2 0.10    3 0.105-0.017  39 0.12     glab GL M. Porsild s.n.
      28 0.10    2 0.129 0.025  18 0.16     glab AK B. Welsh 1233
       8 0.10    3 0.123-0.007  18 0.16     glab NT Parmelee 3206
      36 0.10    3 0.119-0.004  54 0.14     glab AK S. Welsh 20769(b)
                                            glab NT Larsen & Owen 4261
```

```
    52 0.10   36 0.146 0.027  18 0.19       glab NT Porsild 16828
    27 0.08   52 0.156 0.010  18 0.21       glab NT Porsild 30205
    46 0.10   52 0.130-0.025  28 0.17       glab QU Abbe & Abbe 3819
    32 0.10   18 0.153 0.023  27 0.22       glab AI Senn & Calder 3898
    38 0.11    2 0.133-0.020  27 0.16       glab AK Argus & Chunys 5798
    23 0.11   39 0.139 0.006  54 0.19       glab AL Harris 1555

    22 0.08   23 0.173 0.033  54 0.23 1000 glab AL Harris 1569
-----------------------------------------------------------
 3  33                                      glab NL Fernald et al. 28427
    47 0.07                                 glab NL Fernald et al. 26723
    31 0.08   47 0.095 0.025  33 0.11       glab NL Fernald & Long 28426
    13 0.11   47 0.132 0.038  33 0.16       glab NL Harris 1727

    35 0.11   33 0.158 0.025  13 0.21 1000 glab YT Calder 33952
-----------------------------------------------------------
 4  25                                      glab AK Harris 1330
    26 0.07                                 glab AK Harris 1332
    24 0.09   25 0.099 0.029  26 0.10       glab AK Harris 1371
    34 0.12   26 0.148 0.049  24 0.19       glab GL Meehan 10

    23 0.10   34 0.133-0.015  24 0.16    4 glab AL Harris 1555
     LINK TO CLUSTER  -2
-----------------------------------------------------------
 5  77                                      humi NT Harris 1657
    78 0.07                                 humi NT Harris 1659
    82 0.08   77 0.093 0.022  78 0.11       humi NT Rigby 40
    64 0.10   77 0.111 0.018  78 0.12       humi NT Harris 1432

    88 0.13   82 0.184 0.072  64 0.22 1000 humi AK Welsh & Moore 8633
-----------------------------------------------------------
 6  16                                      glab AI Harris 1724
    30 0.07                                 glab AI Harris 1723
    17 0.09   16 0.093 0.021  30 0.10       glab AI Harris 1720
    35 0.11   16 0.115 0.022  17 0.12       glab YT Calder 33952
    53 0.10   35 0.149 0.033  17 0.18       glab AK Hulten 109
     4 0.09   53 0.164 0.015  30 0.20       glab AK Strutz 2027

     6 0.10    4 0.190 0.026  17 0.25 1000 glab AK Williams 3271
-----------------------------------------------------------
 7  92                                      humi GL Bocher 489
    95 0.08                                 humi ON Dutilly & LP. 15441
    96 0.10   92 0.111 0.034  95 0.12       humi QU Marie-Victorin 24849
    97 0.11   95 0.124 0.014  96 0.15       humi MA Gillett 2242
    94 0.11   95 0.134 0.010  96 0.19       humi ON Dutilly & Fr. 40063
    98 0.11   97 0.143 0.008  96 0.19       humi VT Pringle s.n.
    91 0.12   94 0.143 0.000  96 0.17       humi AK B. Welsh 1199
```

```
     60 0.11    91 0.166 0.023  96 0.19    4 humi AK Harris 1232
      LINK TO CLUSTER  -1
------------------------------------------------------------------
 8   11                                      glab NL Harris 1733a
     50 0.09                                 glab NL Weigand & Long 28440
     10 0.10    11 0.108 0.020  50 0.11      glab NL Harris 1736

     12 0.12    50 0.159 0.052  10 0.18 1000 glab NL Harris 1733b
------------------------------------------------------------------
 9    9                                      glab AK S. Welsh 20769(c)
     44 0.09                                 glab NT Cody 17238

     53 0.11     9 0.124 0.034  44 0.14    4 glab AK Hulten 109
      LINK TO CLUSTER  -6
------------------------------------------------------------------
10   68                                      humi BC Harris 1553
     83 0.09                                 humi AL Harris 1639

     80 0.10    83 0.124 0.031  68 0.14    4 humi AL Harris 1743
      LINK TO CLUSTER  -1
------------------------------------------------------------------
11   63                                      humi YT Harris 1409
     81 0.09                                 humi YT Douglas 10300

     66 0.10    63 0.104 0.011  81 0.10    4 humi YT Harris 1470
      LINK TO CLUSTER  -1
------------------------------------------------------------------
12   41                                      glab NT Cody 17452
     51 0.10                                 glab AK Halliday A220/75

      4 0.10    51 0.131 0.031  41 0.16    4 glab AK Strutz 2027
      LINK TO CLUSTER  -6
------------------------------------------------------------------
13    6                                      glab AK Williams 3271
     22 0.11                                 glab AL Harris 1569

     34 0.12    22 0.143 0.030   6 0.16    4 glab GL Meehan 10
      LINK TO CLUSTER  -4
------------------------------------------------------------------
14   29                                      glab AI Harris 1726
     42 0.13                                 glab NT Parmelee 3004

     32 0.14    42 0.149 0.015  29 0.16    4 glab AI Senn & Calder 3898
      LINK TO CLUSTER  -2
------------------------------------------------------------------
15   40                                      glab AI Malte 120677
     49 0.13                                 glab NT A. & R. Porsild 4698
```

```
       9 0.14    40 0.182 0.047  49 0.23 1004 glab AK S. Welsh 20769(c)
--------------------------------------------------------------------
16   72                                   humi BC Harris 1634
     87 0.14                              humi BC McCalla 7539
     86 0.14   87 0.145 0.009  72 0.15    humi AL Porsild & Br. 16060

     68 0.15   86 0.159 0.014  87 0.19   4 humi BC Harris 1553
      LINK TO CLUSTER -10
--------------------------------------------------------------
17   90                                   humi YT Welsh & Moore 7848
     99 0.14                              humi AK LePage 23861

     56 0.14   90 0.183 0.045  99 0.22 1004 humi CO Johnston 2371
--------------------------------------------------------------
18   58                                   humi AK Harris 1168
    101 0.14                              humi AS Sipliviņsky 5020

     71 0.14  101 0.155 0.011  58 0.17   4 humi AL Harris 1568
      LINK TO CLUSTER  -1
--------------------------------------------------------------
19   88                                   humi AK Welsh & Moore 8633
     89 0.15                              humi AK Harris 1393

    102 0.15   88 0.169 0.023  89 0.19   4 humi AS Vereshchagin 372
      LINK TO CLUSTER  -1
--------------------------------------------------------------

ISOLATED OTU'S (SINGLE MEMBER CLUSTERS)

CLUSTER OTU LABEL
     20  12 glab NL Harris 1733b
     21  14 glab AI Harris 1725
     22  15 glab AI Maher & MacLean 139
     23  20 glab AI Savile 4764A
     24  21 glab NT Richardson s.n.
     25  37 glab NT Cody 17106
     26  43 glab NT Cody 16953
     27  45 glab NT Cody 17653
     28  48 glab NT Cody & Brigham 20413
     29  55 line GL Harris 1790
     30  59 humi AK D. & J. Taylor 1
     31  62 humi AK Harris 1388
     32  67 humi BC Harris 1551
     33  79 humi VT Harris 1742
     34 100 humi NL Fernald & SJ. 10837
     35 103 humi AI Savile 4763
```

Figure 5. Taxometric map of TAXMAP morphological analysis.

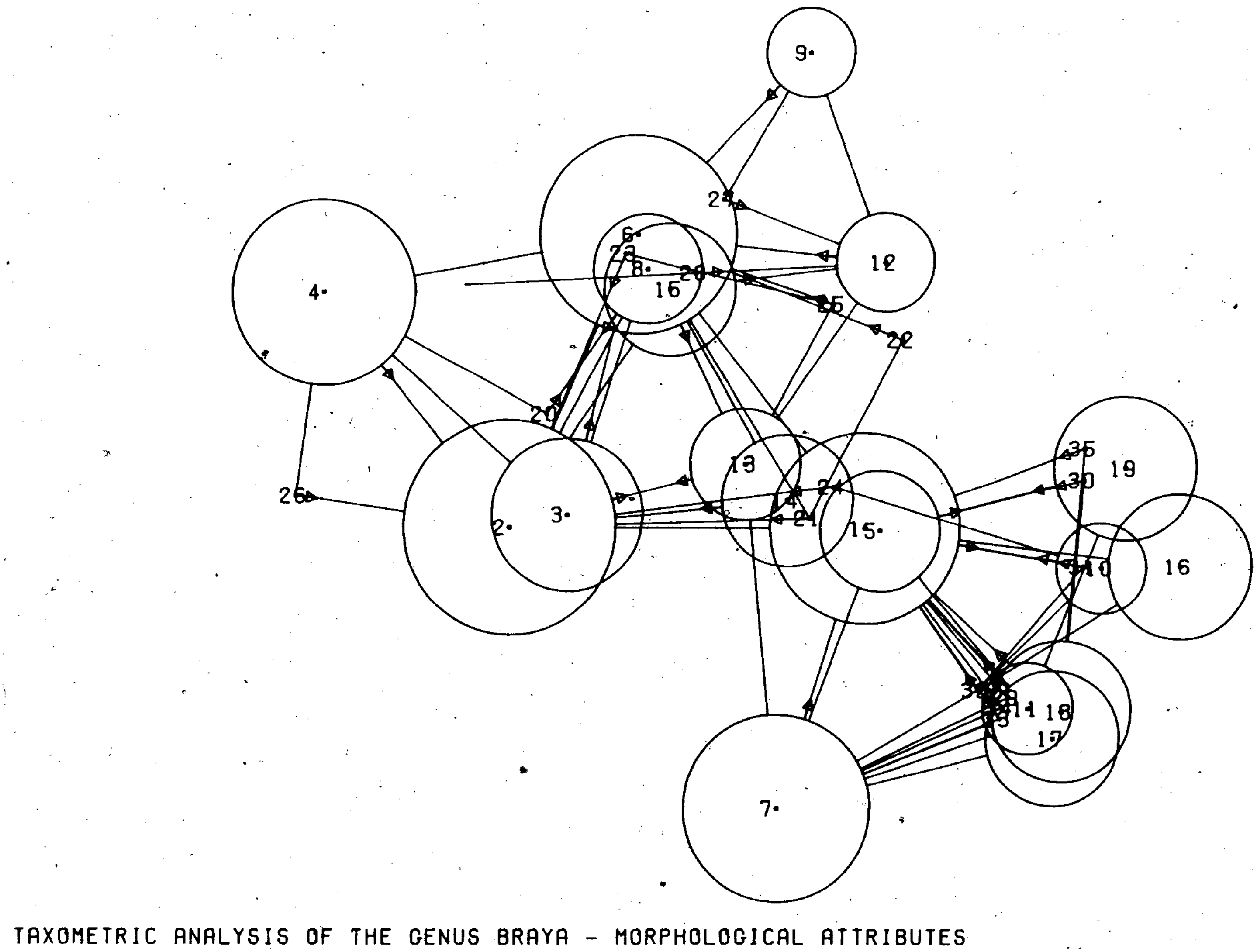
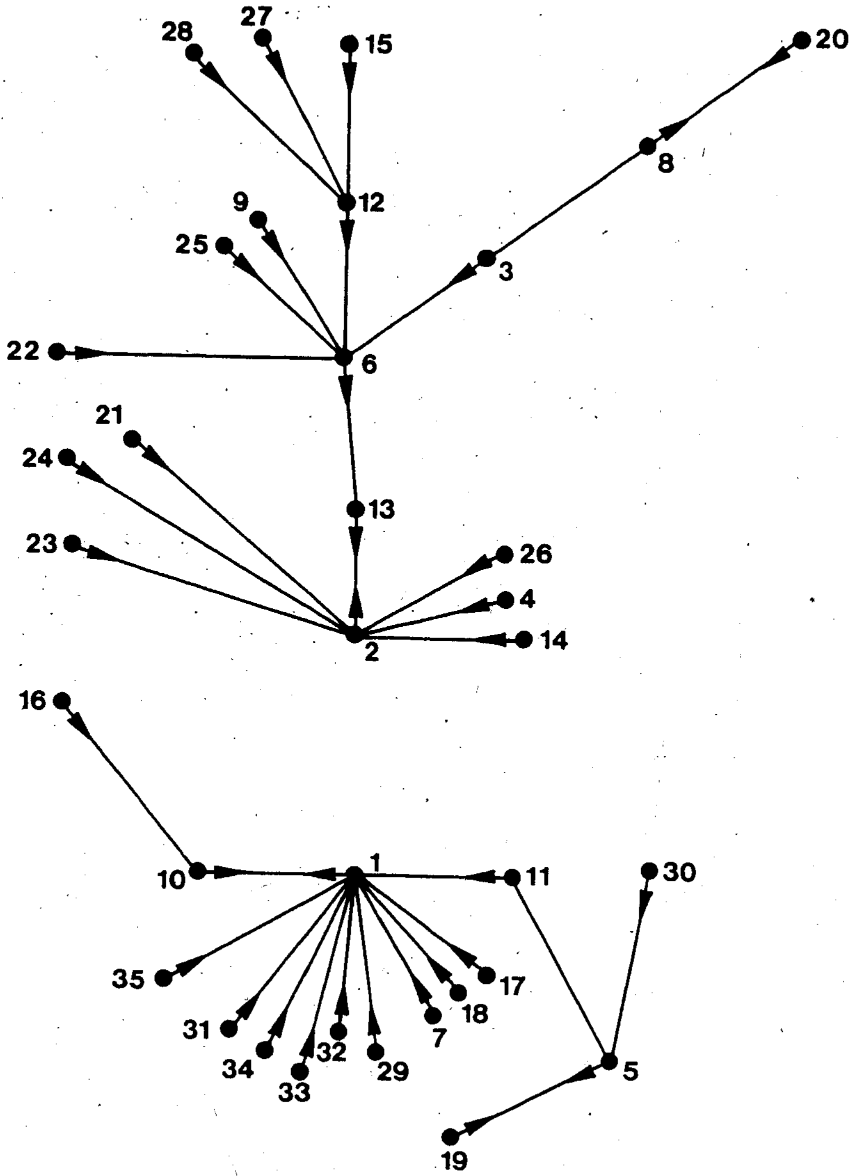


Figure 6. Nearest neighbor diagram from morphological analysis.



purpurascens and var. *glabella* are separated into several clusters and are only partially distinct from one another. It is not surprising, since the two varieties are only weakly separable on the basis of differences in silique shape and compactness of the fruiting inflorescence, that when compared on the basis of 42 morphological attributes, the essential differences between the taxa tend to be swamped among the many other non-essential attributes.

Cluster 15 represents the extreme form of var. *glabella*, and Cluster 14 the extreme form of var. *purpurascens*. These clusters are well separated from one another, but they are linked together by clusters containing OTU's more intermediate in nature. In addition to Cluster 15, clusters 9, 12, 13, 25, 26, 27, and 28 contain OTU's with a more var. *glabella*-like appearance (i.e. longer, narrower siliques and an elongated fruiting inflorescence). Cluster 14 is the only cluster composed entirely of OTU's with a typical var. *purpurascens*-like appearance (i.e. shorter, broader siliques and a compact fruiting inflorescence), but most of the OTU's of Cluster 2 also fall in this category. In addition to Cluster 2, clusters 4 and 6 contain OTU's of both morphological forms. Even though the varieties are mixed in these clusters, the two morphological forms are separated within the clusters; in Cluster 2 the first 11 OTU's are more var. *purpurascens*-like, and the last 7 are more var. *glabella*-like; in Cluster 4 the first three OTU's are more var. *glabella*-like and the last OTU is more var. *purpurascens*-like; in Cluster 6 the first three OTU's are var. *purpurascens*-like and the last three are var. *glabella*-like. The difficulty in reliably separating the two morphological forms is partly due to bridging of clusters caused by OTU's that do not fall clearly into one group or the other.

Clusters 21, 23, and 24 are most closely related to Cluster 2 according to TAXMAP, but all three are well separated and distinct. Cluster 21 includes a single OTU with prostrate stems, globose silicles, and very short styles; it corresponds to the taxon *Braya thorild-wulffii* var. *thorild-wulffii*. Cluster 23 is also composed of a single OTU, this one with prostrate stems, broad leaves, and very long styles; it represents *B. glabella* var. *prostrata*. Cluster 24, consisting also of a single OTU, represents *B. pilosa*; the OTU can be characterized by the very large flowers, globose silicles with very long styles, and the erect stems.

Cluster 22 is most closely related to Cluster 6 according to TAXMAP, but, although not readily apparent from the taxometric map, this cluster is also closely related to Cluster 21. The single OTU making up Cluster 22 is nearly identical to the OTU in Cluster 21 (i.e. it has prostrate stems, globose silicles, and very short styles), but it is almost completely glabrous in contrast to the dense pubescence of the OTU in Cluster 21. Cluster 22 represents *Braya thorild-wulffii* var. *glabrata*.

Cluster 3 includes four OTU's with short, lance-subulate siliques, uniseriate seeds, and a broadly expanded septum margin. This cluster represents *Braya longii*.

Closely related to Cluster 3, are clusters 8 and 20. The OTU's making up these clusters are very similar to those in Cluster 3 except that the floral parts are smaller and the siliques are more pubescent. These clusters represent *Braya fernald*[illegible]

Within the *Braya humilis* group are 15 clusters, one large cluster, Cluster 1, and several other clusters most closely related to Cluster 1. Clust[illegible]1, 17, 18, 31, 32, 33, and 34 are very closely related to each other and represent the highly polymorphic *B. humilis* var. *humilis*. Clusters 5, 19, and 30 are also members of this taxon, but are recognized by TAXMAP as being distinctive enough to require some additional discussion.

Cluster 5 consists of four OTU's, all of them from along the banks of the Mackenzie River or its tributaries. These OTU's clearly fall within the normal diversity of *Braya humilis* var. *humilis*, but they are always grouped separately by TAXMAP (this is also true of the TAXMAP analysis of isozyme profiles). The reason for this is that the four OTU's are so closely related that they group as if they were four individuals from a single population. It is very likely that dispersal along the Mackenzie River took place after these plants had already stabilized into a particular morphological (and enzymatical) form. These OTU's, then, essentially represent a single elongated population. Since TAXMAP clusters OTU's on the basis of relative differences, these OTU's are always kept separate from other var. *humilis* clusters.

Cluster 19 consists of two OTU's from the banks of the Yukon River at Eagle, Alaska. These are very large, robust plants with exceptionally large flowers. The reason for the large flowers is unclear. No chromosome counts have been made from plants in this area, but it may well be that they will turn out to be tetraploid; large flowers seem to be correlated with a low ploidy level in *Braya*. These OTU's have been left in var. *humilis* because other plants from this area show a wide variation in flower size, from flowers typical of other var. *humilis* populations to flowers much larger than average. Additional cytological and phytochemical study of plants from this area may indicate the need for taxonomic recognition as a separate variety of *B. humilis*.

Cluster 30 consists of a single OTU, a large hexaploid plant very similar to var. *humilis* populations from other parts of Alaska and Northwest Territories, but with the odd attribute of leaf pubescence of simple hairs. TAXMAP apparently groups the OTU separately because of this unusual attribute. In all other morphological attributes, this OTU is well within the range of diversity of *Braya humilis* var. *humilis*.

Cluster 10 consists of two OTU's with very large flowers, often abortive siliques, and very dense pubescence. This cluster represents *Braya humilis* var. *porsildii*.

Cluster 16 is closely related to Cluster 10. It consists of three OTU's, also with very large flowers and often abortive siliques, but with much less pubescence than those in Cluster 10. These OTU's represent *Braya humilis* var. *maccallae*.

Cluster 35 is a single-member cluster. Plants of this OTU have prostrate stems and very broad siliques. This cluster represents *Braya humilis* var. *ellesmerensis*.

Cluster 29, the only representative of *Braya linearis*, is shown by TAXMAP to be most closely related to Cluster 1.

The TAXMAP morphological analysis is useful for visually demonstrating the relationships of the various morphological forms in *Braya*, but it is of much less value in the actual delimitation of the taxa. Taxa which TAXMAP recognizes as clearly separable are usually already clearly separable by more traditional methods of morphological comparison.

These easily classified clusters tend to maintain themselves intact despite alterations of the TAXMAP data base in the form of additions of OTU's or attributes. The more difficult groups (e.g. *Braya humilis* var. *humils*, *B. glabella* var. *glabella*, and *B. glabella* var. *purpurascens*) show wide fluctuation in patterns of grouping with alteration of the data base. These difficult taxa are morphologically highly variable and seem to sort themselves into closely related clusters of slightly differing morphological form. The addition of OTU's may bridge the gaps between some clusters, but, because clustering is based on relative similarity, segments of other clusters break away to form new clusters.

Another problem with numerical analyses is the swamping of distinguishing attributes by less significant attributes. This can be overcome to some extent by a weighting of attributes, but this, in turn, allows the possibility of bias entering into the weighting procedures. The problem of swamping of distinguishing attributes can be especially frustrating in a family like the Cruciferae, where taxa are often separated on the basis of a small number of differing characteristics. The clustering of *Braya thorild-wulffii* var. *thorild-wulffii* and var. *glabrata* is a good example. Despite the fact that these taxa are obviously very closely related, TAXMAP does not group them as nearest neighbors. This is because they differ in the degree of stem, leaf, sepal, and silicle pubescence, all attributes of very limited value in comparison to the shared attributes of stem orientation and silicle shape.

B. Greenhouse Studies

The opportunity to observe plants from many different North American *Braya* populations growing in a common garden proved very useful in determining the extent of between- and within-population variation in the genus. It was immediately obvious, as soon as the first true leaves of the *Braya* seedlings began to develop, that there were several very distinct morphological differences, even at the seedling stage, between the members of the *B. glabella* complex and the *B. humilis* species complex. The former had long, narrow, fleshy; and usually erect leaves; the latter had shorter, broader, thinner, more spreading, and usually more pubescent leaves. As usual, *B. linearis* fell somewhere in between the other two groups; the very young seedlings looked like those of *B. glabella* s.l.; but, as they matured, they became more *B. humilis*-like.

Mature plants of the *Braya glabella* species complex generally looked quite similar in the greenhouse to their parents in the field. Silique size and shape, style length, and inflorescence arrangement were usually fairly stable, indicating that these attributes are probably among the most useful taxonomically. Leaf dimensions, plant height, and habit were much less stable. Plants from all populations generally had much larger, wider leaves and taller stems in the greenhouse than in nature. Many stems became so tall that they could no longer support their own weight and they would bend down until they rested on the edge of the pot and, with this new support, begin growing upright again. The end result was often a bent or wavy stem, unable to support its own weight.

In general, in the *Braya glabella* group, deviation in the greenhouse from the morphology of the naturally-occurring parents tended to unify the populations and obscure the differences observed in the field. *Braya thorild-wulffii, B. longii,* and *B. fernaldii* maintained their distinctiveness in the common garden, but populations which in the past would have been separated into *B. glabella* s. str. and *B. purpurascens* seemed to intergrade considerably. Populations from the Seward Peninsula in Alaska, for instance, were virtually identical in the greenhouse with those from Alberta, though this had not been the case in the field. There was, however, a tendency for high arctic populations to look more *B. purpurascens*-like, and for lower arctic and montane populations to resemble *B. glabella*.

The patterns of variation in *Braya humilis* in the greenhouse were much more complicated. Greenhouse-grown plants generally bore very little resemblance to their naturally-occurring parents, and each population, in the vegetative stages, seemed to be somewhat different from the next. Within three or four weeks of germination, it was possible to recognize and separate most of the various *B. humilis* populations on the basis of minor differences in leaf shape, dentation, arrangement into rosettes, and pubescence degree and type.

Many of these differences were obscured somewhat as the plants matured, but it was common for groups of populations from the same geographical region to maintain a certain distinctiveness throughout the life cycle. Differences observed in the field in naturally-occurring *B. humilis* populations generally held up, or actually increased, in a common garden. This was not always true, however, in an outdoor garden.

In the fall of 1983, I moved a number of potted *Braya humilis* plants to a *Sphagnum* bed on the roof of the Biological Sciences Building at the University of Alberta to allow them to overwinter. Plants from many of these populations did not survive the winter (the surviving plants were almost all from Alberta and British Columbia populations), but those that did survive appeared to be much healthier than greenhouse plants and they tended to be more uniform in their appearance. Almost all were very erect with erect siliques and long styles. This contrasted sharply with some of the naturally-occurring parent populations, some of which were composed of short plants with ascending stems, and often somewhat spreading siliques with shorter styles. Most of these cultivated plants looked very similar to *B. humilis* populations from eastern North America. The outdoor garden suggested that environmental factors can have a great deal of influence on the *B. humilis* phenotype.

Greenhouse studies also indicated that the age of the plant can have a profound effect on plant habit in *Braya humilis*. Plants from some populations were kept alive through three growing seasons. Stems appeared to become greater in number, less erect, and more branched with increasing plant age.

Plants from the single *Braya linearis* population cultivated, looked much like their wild parents except that the leaves were longer and broader in the greenhouse.

Greenhouse plants also were used to study the breeding systems in *Braya*. Rollins (1953) hypothesized that apomixis might be present in *Braya*, and that apomixis coupled with polyploidy would explain "the distinct, but only slightly different populations of *B. humilis*" Abbe (1948) had described from eastern North America. Results of this study produced no evidence of agamospermy in *Braya*. Emasculated flowers never produced seeds or fruit.

Rather than being due to agamospermy and polyploidy, this study suggests that the peculiar patterns of morphological variation noted for the small, isolated populations of *Braya* may be due to polyploidy coupled with autogamy. Greenhouse observation showed *Braya* to be almost completely autogamous. Almost without exception, as soon as the flowers would begin to open, the anthers would come into contact with the stigma and self-pollination would occur. This was especially true in members of the *B. glabella* species complex; fruit set from self-pollination was almost 100% successful. The same was generally true of the *B. humilis* populations, but I found that a few populations (Harris 1409, 1470, 1465, and, to a lesser extent, 1554) would produce normal, self-fertilizing flowers during part of the flowering cycle and protogynous flowers at other times, either before or after the normal flowers.

There has been a recent renewed interest in protogyny in the Cruciferae (Rollins, 1971; Al-Shehbaz, 1977). Bateman (1955) stated that there is no protogyny in the Cruciferae, but this has been shown to have been too broadly stated. Rollins (1971) found protogynous flowers to occur in *Arabis constancei*, Johnson (1971) in *A. holboellii* and *A. sparsiflora*, and Al-Shehbaz (1977) in 24 of 91 cruciferous species examined from 472 populations in Iraq. These 24 species represented 19 different genera.

Al-Shehbaz (1977) summarized the previously reported occurrences of protogyny in the Cruciferae and found that, if a broad definition of protogyny is accepted (this would include cases where the anthers have not yet dehisced when the flowers have fully opened), protogyny had been reported in at least 61 species from 33 genera and nine different tribes, including a report of protogyny in *Braya alpina* (Kerner, 1895). Protogyny in the Cruciferae is evidently much more common than once believed.

The cases of protogyny I have observed in *Braya humilis* appear to be more pronounced than most. Not only does the stigma protrude from the unopened bud, as it does in most other reported instances of clear-cut protogyny, but often the flower never opens at all. The sepals, petals, and stamens with undehisced anthers simply wither and die in bud. In the greenhouse, with no available pollinators, these protogynous pistils never set seed on their own. If artificially pollinated with pollen from normal autogamous flowers, they set seed and produce normal fruit. It would appear that some *B. humilis* populations have developed protogyny as a means of promoting outcrossing in these normally self-pollinating populations.

Another exception to the general rule of autogamy occurs in *B. humilis* varieties *maccallae* and *porsildii*. These tetraploid taxa produce flowers about twice the size of those in var. *humilis* and are evidently almost completely self-incompatible. Members of these varieties, at least in the greenhouse, almost never set seed from self-pollination.[9] This is not due simply to mechanical problems with the anthers contacting the stigma; even when artificially self-pollinated, seed set does not occur. When the flowers are artificially cross-pollinated with pollen from other populations normal fruit development takes place. This is similar to the situation observed in some other genera (*Oenothera, Trifolium*) where artificially-induced autotetraploids remain self-incompatible, at least in part, due to dominance of one of the S alleles present in the diploid pollen grain, so that there is a full reaction of the dominant allele with the style, just as would be the case in diploids (Lewis, 1947; Pandey, 1956).

This pattern of xenogamy in tetraploids[10] with large flowers, reduced seed set, reduced fruit maturation, and narrow distribution; and autogamy in higher polyploids with smaller flowers, normal seed set, consistent fruit development, and wider distribution follows closely the characters outlined by Ornduff (1969) as common in xenogamous and autogamous plants. It should be pointed out, however, that not all tetraploid populations were self-incompatible. One tetraploid population of *Braya humilis* var. *humilis* (Harris 1168, from Alaska) had smaller flowers and regularly developed mature fruits with viable seed as a result of self-pollination.

There seem to be no cross-compatibility barriers, or at most only very weak barriers, in the genus. Crosses between different *Braya* populations were almost always successful. This

---

[9] Very rarely, fruit will develop in these varieties with no apparent cross-pollination having taken place. But this may be due simply to the occasional accidental introduction of insect vectors into the greenhouse.

[10] They are probably very old tetraploids, because diploids are unknown in the genus, and are likely behaving as diploids.

was even true of crosses between populations with different chromosome numbers, and between populations from different species groups. In almost all cases, viable seed would result.

The F_1 offspring of interpopulational crosses between populations of the same chromosome number were usually fertile, but this was not always the case. Some populations, even though members of the same taxon and morphologically very similar, produced sterile F_1 offspring. In all of the few cases observed, sterility was due to aborted pollen grains and the female gametes were apparently normal; when backcrossed with male gametes of either of the parental populations, normal seed set and fruit development took place. It is probably to be expected that these normally isolated, self-pollinating populations are often different enough genetically to show reduced fertility in the F_1 generation when crossed, and this might well be typical of a significant portion of the isolated populations in the genus. Crosses between populations of different chromosome numbers that resulted in odd ploidy levels (i.e. 5n) in the F_1 also produced vigorous F_1 individuals, but these were always sterile.

A few hybridizations of populations from different species groups were also attempted. Crosses between tetraploid *Braya humilis* populations and octoploid *B. glabella* populations produced seeds, but these seeds have not yet been sown. The intermediate nature of the hexaploid *B. linearis* makes the idea appealing that it may have arisen from a similar hybridization between members of the *B. glabella* and *B. humilis* complexes. Whether such a hypothetical hybridization was between a tetraploid *B. humilis* and an octoploid *B. glabella* is, of course, speculation. It is equally possible that such a hybridization could have been between a tetraploid *B. glabella* and an octoploid *B. humilis*. The fact that *B. thorild-wulffii*, a tetraploid member of the *B. glabella* complex, and octoploid *B. humilis* are both found in Greenland, the only locality of *B. linearis* in North America, perhaps makes the latter alternative more plausible. In any case, it will be interesting to note any similarities between the F_1's of these artificial hybridizations and naturally-occurring *B. linearis*.

C. Cytology

Somatic chromosome counts were made for 44 North American *Braya* populations. A complete list of these counts as well as information on the collection locality of each is included in Table 6.

Some difficulty was experienced in obtaining counts due to the fairly high numbers of relatively small chromosomes in *Braya*. A certain count from a taxon with 56 somatic chromosomes usually required that several hundred dividing cells be examined before a "perfect" squash was located. While there is some room for error due to the possibility of overlapping chromosomes, no evidence of aneuploidy was found in any of the populations counted; all counts were multiples of the previously-reported base number of 7 in the genus (Böcher & Larsen, 1950; Holmen, 1952; Jørgensen & Westergaard, 1954; Böcher, 1956, 1966; Mulligan, 1965).

When counting chromosomes in *Braya*, it is at once obvious that there is a great difference in size between the largest and the smallest chromosomes in each species (Figure 7). The largest chromosomes appear to be about twice the size of the smallest in *B. humilis* s.l. and *B. glabella* s.l., and about three times the size of the smallest in *B. linearis*. This disparity in chromosome size has been reported by other workers (Böcher & Larsen, 1950; Böcher, 1956, 1966; Jørgensen et al., 1958; Mulligan, 1965) and has been suggested as a possible cause of the several erroneous counts published for *Braya* (Mulligan, 1965).

Mulligan (1965) has also commented on the difference in size between somatic chromosomes of *B. humilis* s.l. and *B. glabella* s.l. — chromosomes of the *B. glabella* group are somewhat larger than those of the *B. humilis* group (Figure 7). This observation was borne out in the present study.

North American members of the *Braya glabella* species group are octoploid with the exception of *B. thorild-wulffii*, a tetraploid.

B. fernaldii

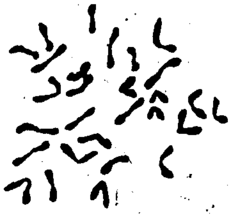
Table 6. New chromosome counts for North American *Braya* populations.

Taxon	2n	Locality	Voucher
B. fernaldii	56	NFLD, Cape Norman	J. Harris 1736
B. glabella var. *glabella*	56	ALTA, Cardinal River, ca. 19 km due SSE of Cadomin	J. Harris 1555
	56	ALTA, Jasper Natl. Park, Athabasca Glacier	J. Harris 1569
	56	ALASKA, Anvil Mt. near Nome	J. Harris 1332
	ca. 56	ALASKA, Anvil Mt. near Nome	J. Harris 1330
B. glabella var. *dubia*	56	NWT, Ellesmere Island, Alexandra Fjord	J. Harris 1720
	56	NWT, Ellesmere Island, Alexandra Fjord	J. Harris 1723
	56	NWT, Ellesmere Island, Alexandra Fjord	J. Harris 1724
	ca. 56	NWT, Ellesmere Island, Grise Fjord	J. Harris 1691
	56	ALASKA, Prudhoe Bay	B. Welsh 1233
	56	ALASKA, Prudhoe Bay	B. Welsh et al. 1246a
	56	ALASKA, Prudhoe Bay	B. Welsh et al. 1247b
	56	ALASKA, Prudhoe Bay	A. Strutz 2240
	ca. 56	ALASKA, Prudhoe Bay	S. Welsh 20769
B. humilis var. *humilis*	28	B.C., Muncho Lake Prov. Park	J. Harris 1551
	28	B.C., Yoho Natl. Park, Kicking Horse River near Chancellor Pk. Campground	J. Harris 1627
	28	ALASKA, confluence of Copper and Chitina Rivers	J. Harris 1168
	42	ALTA, Banff Natl. Park, head of Bow Lake	J. Harris 1638
	42	NWT, Mackenzie River Delta at Inuvik	J. Harris 1432
	ca. 42	NWT, Liard River at Mackenzie Hwy. crossing	J. Harris 1659
	ca. 42	NWT, Mackenzie Hwy. at Trout River	J. Harris 1670
	42	YUKON, Ogilvie Mts., km 160 on Dempster Hwy.	J. Harris 1470
	42	YUKON, Windy Pass, km 155 on Dempster Hwy.	J. Harris 1409
	ca. 42	YUKON, Richardson Mts., Rock River at km 438.6 on Dempster Hwy.	J. Harris 1465
	42	ALASKA, Anvil Mt. near Nome	J. Harris 1331
	42	ALASKA, 5.5 km N of Denali Natl. Park turnoff on G. Parks Hwy.	J. Harris 1232
	42	ALASKA, Tanana River, ca. 2 km below Delta Junction	J. Harris 1388
	42	ALASKA, above the Chitina River, ca. 10 km from Copper River Bridge on road to McCarthy	D. & J. Taylor 1
	42	VERMONT, Willoughby Cliffs of Mt. Pisgah above Willoughby Lake	J. Harris 1742
	56	ALTA, Cardinal River, ca. 19 km due SSE of Cadomin	J. Harris 1554
	56	ALTA, Jasper Natl. Park, Sunwapta River, ca. 16 km due SE of Sunwapta Falls	J. Harris 1566
	56	ALTA, Jasper Natl. Park, Athabasca Glacier near Sunwapta Lake	J. Harris 1568
	56	ALTA, Banff Natl. Park, Bath Creek, ca. 5 km E of Kicking Horse Pass	J. Harris 1640
	56	ALTA, Ram Mt., SW of Nordegg	M. Dumais 7694
	ca. 56	ALTA, Banff Natl. Park, Parker Ridge	J. Harris 1743

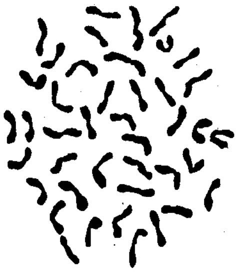
	ca. 56	B.C., Kootenay Natl. Park, Vermilion River near the Paint Pots	J. Harris 1642
	ca. 56	COLORADO, Hoosier Pass	B. Johnston 2371
B. humilis var. *mccallae*	28	B.C., Yoho Natl. Park, head of Emerald Lake	J. Harris 1629
	28	B.C., Yoho Natl. Park, Kicking Horse River ca. 2 km above Field	J. Harris 1634
B. humilis var. *porsildii*	28	ALTA, Banff Natl. Park, terminal moraines of Victoria Glacier	J. Harris 1639
	28	B.C., Stone Mt. Prov. Park, slopes above Summit Lake	J. Harris 1553
B. linearis	42	GREENLAND, Sondre Stromfjord	J. Harris 1790
B. longii	56	NFLD, between Point Savage and Sandy Cove	J. Harris 1727
B. thorild-wulffii	28	NWT, Ellesmere Island, Eureka	J. Harris 1725

Figure 7. Illustration of mitotic chromosomes of *Braya* species; a. *B. humilis* var. *porsildii* (Harris 1639); b. *B. humilis* var. *humilis* (Harris 1232); c. *B. humilis* var. *humilis* (Harris 1568); d. *B. glabella* var. *glabella* (Harris 1569).

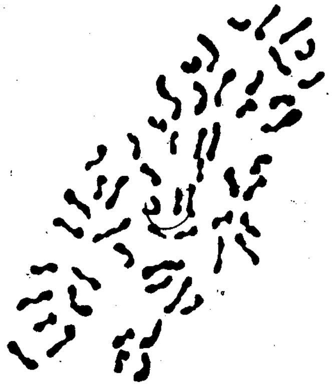
Braya humilis s.l.



a 2n=28

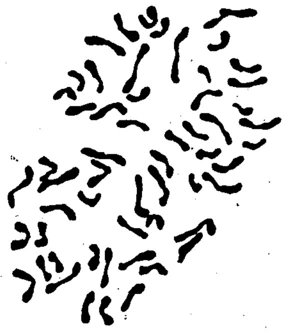


b 2n=42



c 2n=56

Braya glabella s.l.



d 2n=56

One count is reported for *B. fernaldii*. This is the first reported chromosome count from this species. As expected, *B. fernaldii* is octoploid, as are most other members of this complex.

B. glabella var. *purpurascens*

Nine new counts were made for this variety; all are octoploid. Four of the counted populations are from Ellesmere Island, and the other five are from Prudhoe Bay, Alaska.

B. glabella var. *glabella*

Four new counts of var. *glabella* are reported. Two counts are from Alberta and the other two are from the Seward Peninsula in Alaska. All counts are 2n=56, octoploid.

B. longii

A single count was made for *B. longii*. It is octoploid. This is the first reported chromosome count for this species.

B. thorild-wulffii var. *thorild-wulffii*

A single count is reported for this species. The population counted is from northern Ellesmere Island; it is tetraploid. This count is in accord with several other counts in this species of n=14, 2n=28 reported by Mulligan (1965), Holmen (1952), and Böcher (1966).

The *Braya linearis* species group, represented in North America only by *B. linearis*, is evidently uniformly hexaploid. The great disparity in chromosome size noticed in this species (Böcher, 1966) may be the result of hybridization between *B. glabella* s.l. and *B. humilis* s.l.

B. linearis

A single count is reported, from Sondre Stromfjord in western Greenland. The count was 2n=42 as expected from previous counts of this species (Jørgensen et al., 1958; Böcher & Larsen, 1950; Böcher, 1966).

North American members of the *Braya humilis* species complex form a polyploid series comprised of tetraploids (2n=28), hexaploids (2n=42), octoploids (2n=56), and decaploids (2n=70).

B. humilis var. *humilis*

Twenty-three counts are reported for this variety. Three of the populations are tetraploids; two are from British Columbia and the third is the first-reported tetraploid population of *B. humilis* from Alaska. Twelve populations are hexaploid, mainly from Alaska, Yukon, and Northwest Territories, but also including a single count each from Alberta and Vermont. Eight populations from Alberta, British Columbia, and Colorado are octoploid.

B. humilis var. *maccallae*

Two counts of var. *maccallae* were made. Both counts are from British Columbia and both are tetraploid. These agree with previous counts in this variety by Mulligan (1965), with the exception of a single count of 2n=42 by Mulligan from a population in Jasper National Park, Alberta (J.A. Calder & K.W. Spicer 33838 DAO 278310). Mulligan's annotation on the voucher reads, "n=21 II (metaphase I), 2n=42 on plants taken from this location June 28, 1962". Two duplicate sheets of this collection (DAO 278302, 278303) are not annotated. It appears that this is a mixed collection; DAO 278302 and 278303 are clearly *B. humilis* var. *humilis* and DAO 278310 is *B. humilis* var. *maccallae*. Mulligan's count of n=21, 2n=42 almost certainly came from var. *humilis* individuals rather than from var. *maccallae* plants. Unfortunately, the annotation label has been placed on the var. *maccallae* sheet. *Braya humilis* var. *maccallae* is apparently always tetraploid.

B. humilis var. *porsildii*

Two counts are reported from var. *porsildii*. Both counts, one from Alberta, the other from British Columbia, are tetraploid. These counts agree with previous counts in this group by Mulligan (1965). *Braya humilis* var. *porsildii* appears to be invariably tetraploid.

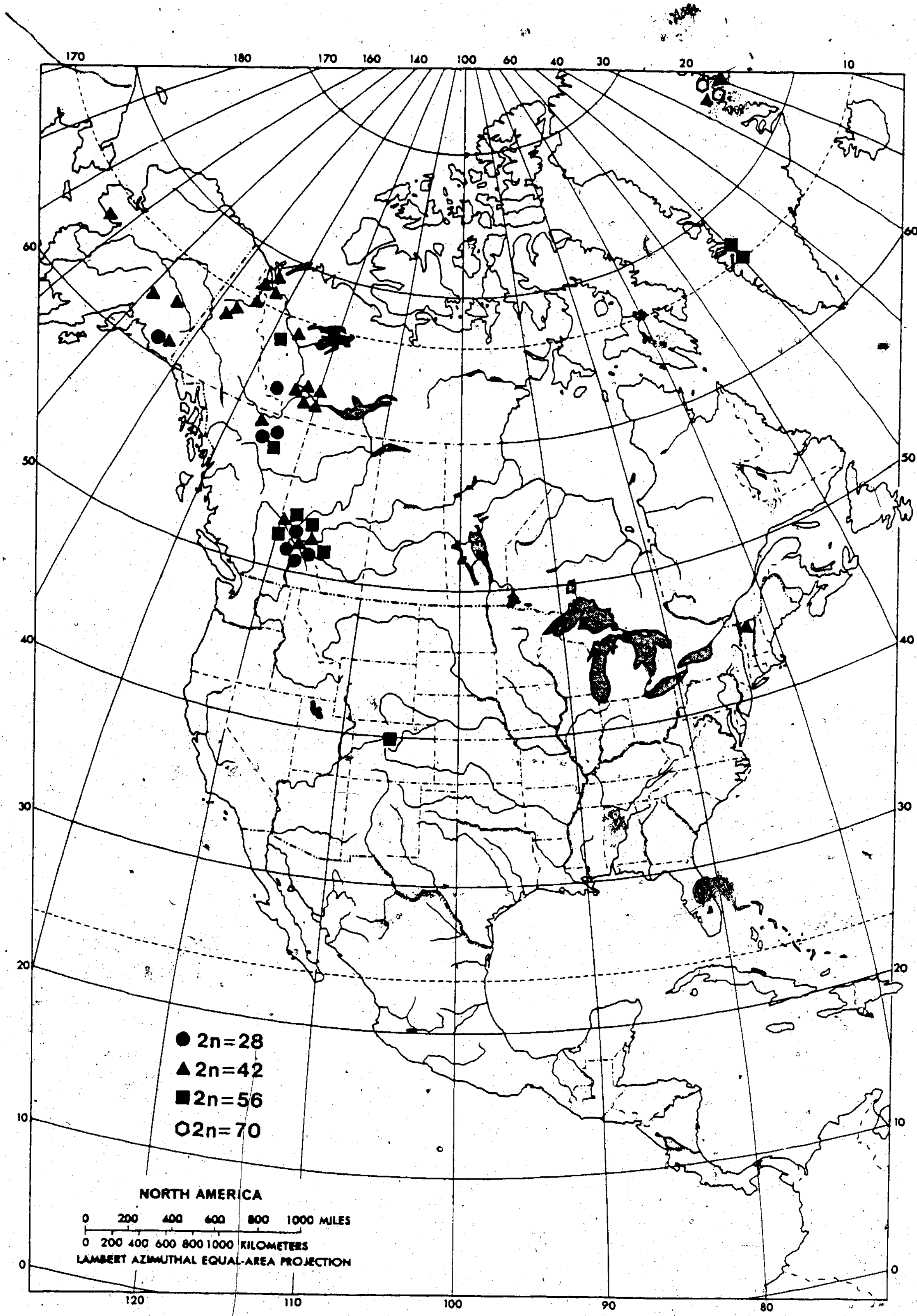
Tetraploids are the lowest known ploidy level in *Braya*. The distribution of tetraploid populations of *B. humilis* in North America is very restricted in comparison to the distribution of hexaploids and octoploids (Figure 8). Tetraploids are known from the Rocky Mountains in Alberta and British Columbia, from the southern Mackenzie Mountains in Northwest Territories, and from a single population along the Copper River in southeastern interior Alaska.

Hexaploids, on the other hand, are found in the same areas as tetraploids, but also extend north and west through Alaska, Yukon, and western Northwest Territories to Ellesmere Island and northeastern Greenland. The only known count from eastern continental North America, from Vermont, is also hexaploid.

Octoploids, though perhaps not as widespread as hexaploids, are also distributed more broadly than tetraploids. They are known from the Rocky Mountains of Alberta and British Columbia, the Mackenzie Mountains in Northwest Territories, from an isolated population in the Rocky Mountains of Colorado, and from western Greenland. Whether hexaploids are actually more widespread than octoploids remains to be seen however; counts from most of the *B. humilis* populations in eastern continental North America have never been made. These will almost certainly prove to be either hexaploid or octoploid.

Decaploids ($2n=70$) are extremely restricted in their occurrence, being known only from northeastern Greenland.

Figure 8. Distribution of chromosome numbers of *B. humilis* in North America.


● 2n=28
▲ 2n=42
■ 2n=56
○ 2n=70
NORTH AMERICA
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
170
180
170
160
140
100
60
40
30
20
10
60
50
40
30
20
10
0
120
110
100
90
80

D. Enzyme Analysis

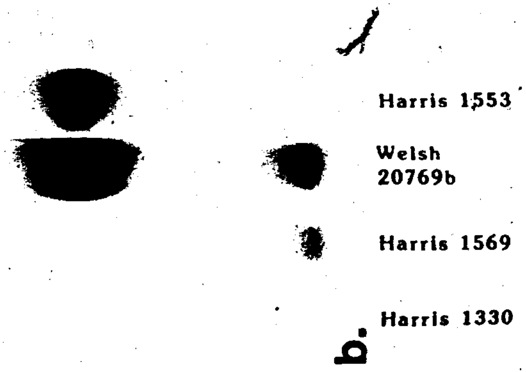
Plants from 46 *Braya* populations and one *Draba* population were analyzed for differences in leaf enzyme composition in five enzyme systems: esterase (EST), isocitrate dehydrogenase (IDH), phosphoglucomutase (PGM), phosphoglucose isomerase (PGI), and superoxide dismutase (SOD).

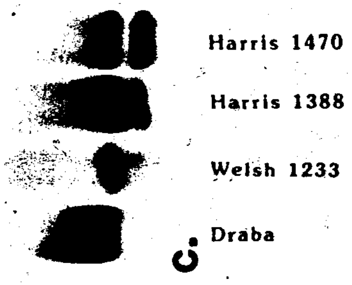
The purpose of the analysis was not to determine the genetics of various *Braya* populations. This would require breeding studies to determine which bands are due to allozymic variation at a single locus and which are due to the presence of multiple loci (Gottlieb, 1977; Soltis, personal communication), and is beyond the scope of this study. Rather, the patterns of enzyme banding were used as independent taxonomic attributes (Figure 9). To aid in determining similarities in banding patterns between populations, each band was treated as a separate attribute and scored according to relative density (i.e., 0 = band absent, 1 = light band, 2 = medium band, 3 = dark band). The banding scores for each population were then analyzed using TAXMAP. Each enzyme system was run separately and then all five were run together.

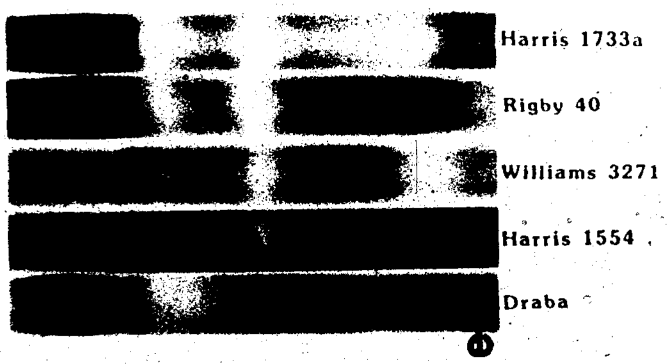
The results of the computer analyses of banding patterns in the IDH, PGM, PGI, and SOD gels were completely chaotic; populations were clustered in an apparently random fashion (Figure 10). Banding patterns in these four enzymes did not correlate with major species groups, chromosome numbers, or geographical distribution (Table 7). The results of the EST TAXMAP analysis, on the other hand, correlated well with the division of the genus into major groups based on morphology, with chromosome number, and with geographical distribution. Apparently, EST is much more useful as an indicator of taxonomic relationships in *Braya* than are IDH, PGM, PGI, or SOD. A possible reason for this will be discussed later in the text. The results of the esterase TAXMAP analysis are found in Table 8, and the corresponding taxometric map in Figure 11.

The EST analysis (as well as the morphological analysis) points out the distinct separation of the *Braya glabella* and *B. humilis* species groups and the intermediate position of

Figure 9. Photographs of representative electrophoretic gels.


b.
Harris 1553
Welsh 20769b
Harris 1569
Harris 1330


c.
Harris 1470
Harris 1388
Welsh 1233
Draba


e.
Harris 1733a
Rigby 40
Williams 3271
Harris 1554
Draba


a.
Harris 1553
Rigby 40
Harris 1554
Harris 1569
Harris 1725
Draba

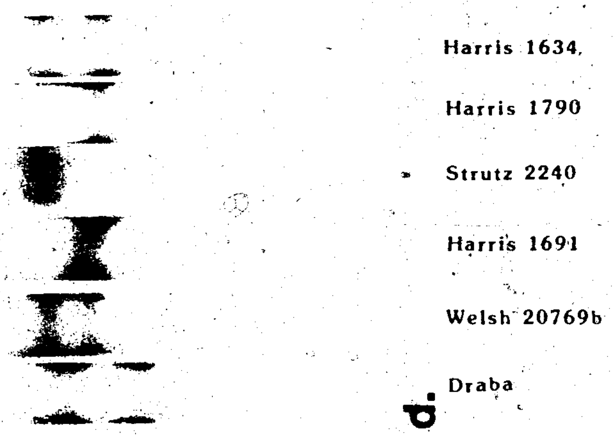

d.
Harris 1634
Harris 1790
Strutz 2240
Harris 1691
Welsh 20769b
Draba

Figure 10. Taxometric map of TAXMAP IDH, PGM, PGI and SOD analysis.

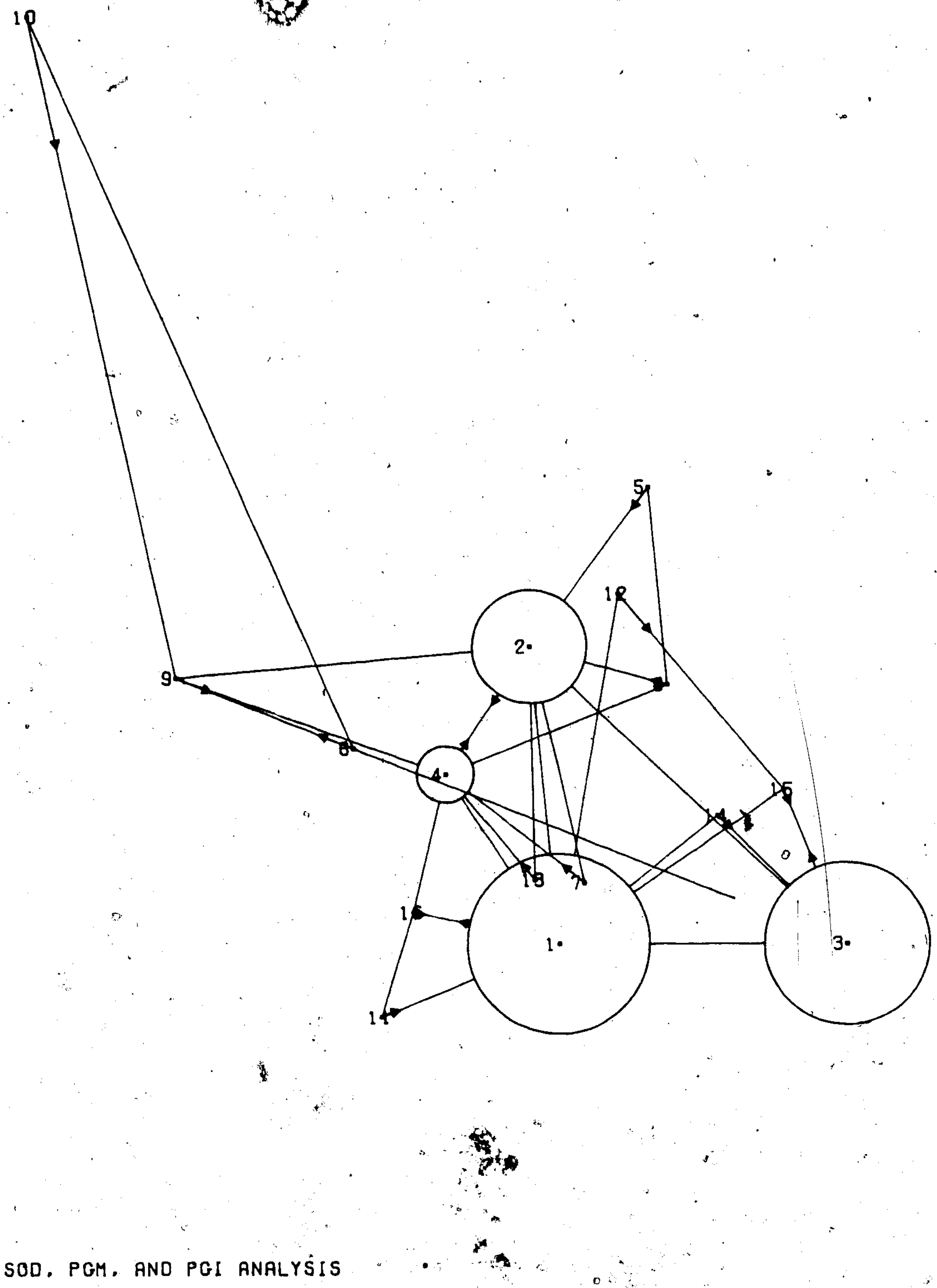


Table 7. TAXMAP cluster analysis of IDH, PGM, PGI and SOD attributes.

```
MAP CLUSTER ANALYSIS:-IDH, SOD, PGM, AND PGI ANALYSIS

OTU LISTED AFTER BLANK LINE IS EXCLUDED FROM CLUSTER FOR REASON(S) INDICATED BY FLAG.
FLAG 1 = AVERAGE LINKAGE CRITERION EXCEEDED, FLAG 2 = SINGLE LINKAGE CRITERION EXCEEDED,
FLAG 3 = RATIO CRITERION VIOLATED, FLAG 4 = OTU ALREADY IN A CLUSTER.

(MAXIMUM NUCLEUS 0.071, MAXIMUM RISE 0.0313 BOTH ARE 100% OF NORMAL)
ATTRIBUTES WEIGHTED BY CALCULATED INFORMATION CAPACITY


CLUS OTU DIST OTU  AVGOF  RISE FAR DIST FLAG NAME OF OTU
TER  NOS BEST BEST  NEW    IN  OTU FAR
NO.      LINK LINK LINKS  AVG.      OTU
------------------------------------------------------------
  1   34                                   humi NT Harris 1432
      35 0.0                               humi NT Rigby 40
      40 0.03   34 0.030 0.030  35 0.03    humi AK Harris 1331
      23 0.02   40 0.040 0.010  34 0.05    humi AL Harris 1566
      30 0.0    23 0.030-0.010  35 0.05    humi AL Harris 1638
      38 0.04   40 0.060 0.030  34 0.07    humi YT Harris 1470
      37 0.0    38 0.050-0.010  34 0.07    humi YT Harris 1409
      29 0.0    37 0.043-0.007  35 0.07    humi AL Harris 1743
       8 0.04   37 0.056 0.013  35 0.07    glab AK S. Welsh 20769(c)
      41 0.0     8 0.050-0.006  34 0.07    humi AK Harris 1388
      22 0.0    41 0.045-0.005  35 0.07    humi BC Harris 1553
      44 0.02   22 0.064 0.020  35 0.10    humi AK Harris 1168
      39 0.02   44 0.079 0.015  35 0.12    humi YT Harris 1465
      33 0.02   44 0.067-0.012  34 0.12    humi VT Harris 1742
      31 0.03   44 0.083 0.017  35 0.13    humi BC Harris 1634
      17 0.04   41 0.067-0.016  31 0.09    glab AI Harris 1725

      43 0.04   33 0.100 0.032  34 0.16 1000 humi AK D. & J. Taylor 1
------------------------------------------------------------
  2   12                                   glab AK Strutz 2027
      13 0.0                               glab AI Harris 1724
      14 0.0    13 0.0   0.0    12 0.0     glab AI Harris 1719
       4 0.02   14 0.020 0.020  12 0.02    glab NL Harris 1733a
       9 0.02    4 0.035 0.015  12 0.04    glab AK S. Welsh 20769(a)
      16 0.04   13 0.052 0.017   9 0.08    glab AI Harris 1691
       3 0.02   16 0.050-0.002   9 0.06    glab NL Harris 1727

       6 0.05    3 0.090 0.040  12 0.11 1000 glab AK Harris 1371
------------------------------------------------------------
  3    1                                   glab AL Harris 1555
      10 0.0                               glab AK Strutz & Shelt. 2240
      45 0.07   10 0.067 0.067   1 0.07    humi YT Douglas 10300
      15 0.0    45 0.045-0.022  10 0.07    glab AI Harris 1720
```

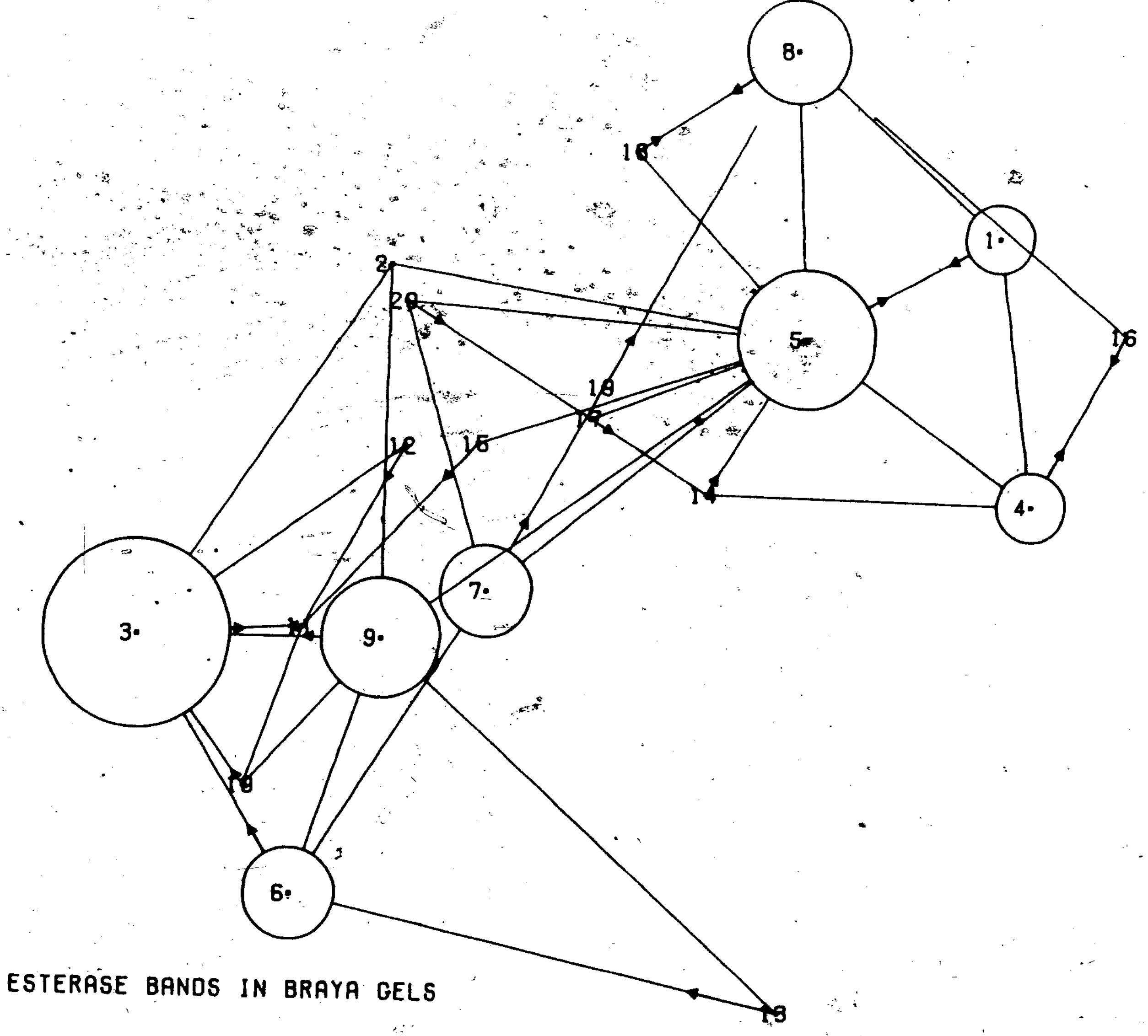
```
       28 0.03    15 0.063 0.019   10 0.10       humi BC Harris 1643
     . 24 0.05    45 0.080 0.017    1 0.11       humi AL Harris 1568

       42 0.06    24 0.113 0.033   28 0.14 1000 humi AK Harris 1232
-------------------------------------------------------------
  4     6                                        glab AK Harris 1371
       26 0.02                                   hu[illegible] AL Harris 1640
       21 0.02     6 0.030 0.010   26 0.04       humi AL Harris 1639
       32 0.02    21 0.027-0.003    6 0.04       humi CO Johnston 2371

        3 0.05     6 0.067 0.041   32 0.09     4 glab NL Harris 1727
        LINK TO CLUSTER  -2
-------------------------------------------------------------
ISOLATED OTU'S (SINGLE MEMBER CLUSTERS)

CLUSTER OTU LABEL
      5   2 glab AL Harris 1569
      6   5 glab AK Harris 1330
      7   7 glab AK Harris 1332
      8  11 glab AK B. Welsh 1233
      9  18 glab SV Ronning s.n.
     10  19 Drab YT Harris 1406
     11  20 line GL Harris 1790
     12  25 humi AL Harris 1554
     13  27 humi BC Harris 1642
     14  36 humi NT Harris 1657
     15  42 humi AK Harris 1232
     16  43 humi AK D. & J. Taylor 1
```

Table 8. TAXMAP cluster analysis of EST attributes.

```
MAP CLUSTER ANALYSIS:-ESTERASE BANDS IN BRAYA GELS

OTU LISTED AFTER BLANK LINE IS EXCLUDED FROM CLUSTER FOR REASON(S) INDICATED BY FLAG.
FLAG 1 = AVERAGE LINKAGE CRITERION EXCEEDED. FLAG 2 = SINGLE LINKAGE CRITERION EXCEEDED.
FLAG 3 = RATIO CRITERION VIOLATED. FLAG 4 = OTU ALREADY IN A CLUSTER.

(MAXIMUM NUCLEUS 0.108. MAXIMUM RISE 0.0431 BOTH ARE 100% OF NORMAL)
ATTRIBUTES WEIGHTED BY CALCULATED INFORMATION CAPACITY


CLUS OTU DIST OTU  AVGOF  RISE FAR DIST FLAG NAME OF OTU
TER  NOS BEST BEST  NEW    IN  OTU FAR
NO.      LINK LINK LINKS  AVG.      OTU
------------------------------------------------------------
  1   39                                     humi YT Harris 1409
      40 0.0                                 humi YT Harris 1470
      41 0.06   39 0.055 0.055  40 0.06      humi YT Harris 1465

      30 0.09   41 0.129 0.074  40 0.15 1000 humi AL Harris 1638
------------------------------------------------------------
  2   35                                     humi NT Harris 1432
      36 0.0                                 humi NT Rigby 40
      37 0.0    36 0.0   0.0    35 0.0       humi NT Harris 1657
      38 0.0    36 0.0   0.0    35 0.0       humi NT Harris 1659

      42 0.19   36 0.195 0.195  38 0.19 1200 humi AK Harris 1331
------------------------------------------------------------
  3    5                                     glab AK Harris 1330
       6 0.0                                 glab AK Harris 1371
      16 0.02    6 0.018 0.018   5 0.02      glab AI Harris 1691
      12 0.02   16 0.031 0.012   5 0.04      glab AK Strutz 2027
      11 0.02   16 0.032 0.002   5 0.04      glab AK B. Welsh 1233
      10 0.03   12 0.053 0.021   6 0.06      glab AK Strutz & Shelt. 2240
      15 0.04   11 0.069 0.016  10 0.10      glab AI Harris 1720
      14 0.0    15 0.059-0.010  10 0.10      glab AI Harris 1719
       9 0.04   11 0.061 0.002  10 0.10      glab AK S. Welsh 20769(a)
       4 0.04   10 0.075 0.014  15 0.10      glab NL Harris 1733a
       3 0.02    4 0.086 0.011  14 0.12      glab NL Harris 1727
       7 0.04    6 0.074-0.012  14 0.11      glab AK Harris 1332
       1 0.04    7 0.105 0.031  14 0.15      glab AL Harris 1555
       2 0.04    7 0.071-0.034  15 0.11      glab AL Harris 1569

      13 0.06   14 0.132 0.061   1 0.21 1000 glab AI Harris 1724
------------------------------------------------------------
  4   27                                     humi BC Harris 1642
      28 0.04                                humi BC Harris 1643
      23 0.06   27 0.055 0.018  28 0.06      humi AL Harris 1566
```

```
      32 0.13    23 0.166 0.111   27 0.18 1200 humi AL Dumais 7694
------------------------------------------------------------
  5   24                                       humi AL Harris 1568
      25 0.06                                  humi AL Harris 1554
      26 0.07    24 0.085 0.026   25 0.10      humi AL Harris 1640
      30 0.07    26 0.093 0.009   24 0.11      humi AL Harris 1638

      41 0.09    30 0.162 0.069   24 0.20 1004 humi YT Harris 1465
------------------------------------------------------------
  6   21                                       humi AL Harris 1639
      22 0.07                                  humi BC Harris 1553

       2 0.13    22 0.147 0.074   21 0.17 1204 glab AL Harris 1569
------------------------------------------------------------
  7   43                                       humi AK Harris 1388
      44 0.07                                  humi AK Harris 1232

      46 0.15    43 0.188 0.114   44 0.22 1200 humi AK Harris 1168
------------------------------------------------------------
  8   42                                       humi AK Harris 1331
      45 0.08                                  humi AK D. & J. Taylor 1

      34 0.11    42 0.152 0.069   45 0.19 1000 humi VT Harris 1742
------------------------------------------------------------
  9   18                                       glab SV Ronning s.n.
      20 0.10                                  line GL Harris 1790

       9 0.11    20 0.140 0.044   18 0.17 1004 glab AK S. Welsh 20769(a)
------------------------------------------------------------

ISOLATED OTU'S (SINGLE MEMBER CLUSTERS)

CLUSTER OTU LABEL
     10   8 glab AK S. Welsh 20769(c)
     11  13 glab AI Harris 1724
     12  17 glab AI Harris 1725
     13  19 Drab YT Harris 1406
     14  29 humi AL Harris 1743
     15  31 humi BC Harris 1634
     16  32 humi AL Dumais 7694
     17  33 humi CO Johnston 2371
     18  34 humi VT Harris 1742
     19  46 humi AK Harris 1168
     20  47 humi YT Douglas 10300
```

Figure 11. Taxometric map of TAXMAP EST analysis.



B. linearis. Most members of the *Braya glabella* species group are placed in a single cluster, Cluster 3. The only exceptions are a population from Svalbard, which groups with *B. linearis* to form Cluster 9; single-member clusters 10 and 11, which are most closely related to Cluster 3; and Cluster 12, a population of the tetraploid *B. thorild-wulffii*. The grouping of the single population of *B. linearis* included in the analysis with *B. glabella* clusters suggests that, at least on the basis of EST isozymes, it is most closely related to the *B. glabella* species complex.

The members of the *Braya humilis* species complex are grouped into seven major clusters that can be correlated with geographical distribution and chromosome number. Cluster 1 includes hexaploids from Yukon Territory, Cluster 2 includes hexaploids from Northwest Territories,[11] Cluster 4 is made up of octoploids from Alberta, Cluster 5 is composed mainly of octoploids from Alberta, but includes a single hexaploid from Alberta, Cluster 6 includes a tetraploid from Alberta and one from British Columbia, and Cluster 7 and 8 are made up of hexaploids from Alaska. Of the single-member clusters, Cluster 17, an octoploid from Colorado, is most closely related to Cluster 14, an octoploid from Alberta; Cluster 18, a hexaploid from Vermont is most closely related to Cluster 8, hexaploids from Alaska, as is Cluster 19, a tetraploid from Alaska; Cluster 20, a hexaploid from Yukon Territory, is most closely related to Cluster 17, the Colorado octoploid. Surprisingly, Clusters 6 and 15, both tetraploids from Alberta and British Columbia, are most closely related to clusters belonging to the *B. glabella* species complex.

Cluster 13, the *Draba* population included for comparison, is very isolated from any of the *Braya* clusters. This limited evidence supports the notion that the taxa in *Braya* form a natural group and are more closely related to each other than they are to members of other related genera.

The simplest patterns in the EST gels are found in tetraploid populations from Alberta and British Columbia. This suggests that polyploidy has probably contributed to the increased

---

[11] Cluster 2 appears as a single dot rather than as a circle in the taxometric map, even though it is composed of four populations. This is because the EST banding patterns were identical in these populations and, therefore, there is no interpopulation variation in the cluster.

isozyme complexity in higher polyploids. Two tetraploid populations (Harris 1168 and 1634), however, have EST isozyme patterns at least as complex as those in the higher polyploids. The reason for this is unclear, but possibly could have been caused by hybridization of these populations with other tetraploid populations of different isozyme make-up.

The patterns of clustering in the EST analysis show that, at least within *Braya humilis*, populations from the same geographical region often have fairly similar esterase profiles, and that these enzyme similarities may correspond to morphological similarities (e.g. clusters 1, 2, 4, 5 and 7). This is not always the case, however; Cluster 8 includes two widely separated populations, one from the Seward Peninsula and the other from south-central Alaska, which are morphologically quite different. Taylor 1 is a large, robust plant with many multi-branched stems and Harris 1331 is a small plant with one or few simple stems. The closest neighbor to this cluster is Cluster 18, a single-member cluster from Vermont.

Similar esterase profiles in plants from the same area probably indicate that dispersal within the area has occurred since the EST isozymes stabilized into a more or less uniform pattern. This is especially apparent in the taxa comprising Cluster 2, all from along the Mackenzie River, and all with identical EST patterns.

Probably because there is only a single ploidy level in the group (except for *Braya thorild-wulffii* which groups separately), populations of the *B. glabella* complex show much less variation in EST banding patterns than do *B. humilis* populations. Populations from across North America all tend to cluster together, or very near one another. This contrasts with the TAXMAP analysis of morphological attributes, which showed a greater range of diversity in the *B. glabella* group than in the *B. humilis* group.

Patterns of EST banding are very useful as an independent indicator of relatedness between populations, especially in cases where this is not apparent from the morphology. EST profiles have, in some cases, indicated a close relationship between morphologically different populations and a lesser degree of relatedness between some morphologically similar populations. This information is very important for determining phylogenetic relationships in the genus and will be discussed in later sections.

IV. Discussion

It is clear, based on morphology and enzyme chemistry, that the genus *Braya* can be divided into three distinct groups, to this point referred to simply as the *B. glabella, B. linearis*, and *B. humilis* species groups. It would seem useful and desirable to recognize these groups taxonomically as separate infra-generic taxa within *Braya*. Turczaninow (1842) has provided names for three sections within *Braya* which correspond well with the three groups envisioned within the genus in this study: section *Platypetalum* for the *B. glabella* group, section *Braya* (*Eubraya*) for the *B. linearis* group, and section *Sisymbriastrum* for the *B. humilis* complex. I will use Turczaninow's section names throughout the the following discussion. A key to the sections, as well as a description and discussion of each are provided in the Taxonomy section of this work.

The North American members of *Braya* sect. *Platypetalum* can be divided into four distinct morphological subgroups. The tax[illegible] of the section, to this point, is straightforward; the four subgroups are well-defined and readily separable. Likewise, the first two subgroups present no real taxonomic problems. The first subgroup of the section *Platypetalum* consists solely of *B. pilosa*, a rare and unique species of very limited distribution. The second subgroup includes *B. thorild-wulffii*, a very distinctive high arctic endemic of North America, which can be divided into two consistently distinct, geographically separate varieties.

Real taxonomic problems in the section *Platypetalum* are almost entirely within the third subgroup, consisting of *Braya glabella* and its varieties. *Braya glabella* is a wide-ranging species composed of many isolated, inbreeding and somewhat distinct populations. None of these populations, however, can be consistently grouped into subgroups distinctive enough to warrant taxonomic recognition at the species level. It seems wisest, and certainly most practical, to recognize a single polymorphic species.

There are some general morphological trends in *Braya glabella* that correlate with geographical distribution. Three of the most distinctive morphological forms have been recognized in this treatment as varieties of *B. glabella*. Two of these varieties, var. *glabella* and var. *purpurascens*, are not always completely distinct, and it would be equally tenable to unite them into a single variety. I have chosen to recognize both varieties, in part, because this reflects a more traditional approach to the classification of this group. A more detailed discussion of the classification of *B. glabella* follows in the Taxonomy section of this work.

The last subgroup of *Braya* sect. *Platypetalum* includes two species, *B. longii* and *B. fernaldii*, both of limited occurrence in northwestern Newfoundland. Both species are apparently closely related to *B. glabella*, but they are readily separable from that species by a number of attributes of the fruits and inflorescence. *Braya longii* and *B. fernaldii* are also very closely related to each other, close enough that they could well be treated as a single species of two varieties. However, they are consistently distinguishable one from another, though admittedly only on the basis of characters subject to a great deal of variation in other taxa in this section, and equally well-treated as separate species. I have chosen the latter alternative, at least in part, because it is in accord with traditional treatments of these taxa by previous authors (Fernald, 1926; Abbe, 1948) and I see little reason to muddy the nomenclatural water in a case that could be argued equally well either way.

Braya sect. *Braya* is represented in North America by a single species, *B. linearis*, of Greenland. There has been some confusion in the past about the relationship between *B. linearis* and *B. glabella*, and whether the species might be conspecific (Gelert, 1898; Geltung, 1934; Seidenfaden, 1930, 1931; Ostenfeld, 1926). Crossing experiments by Böcher (1966), as well as evidence from the wall thickenings of the epidermal cells of the silique septum, have shown *B. linearis* to be very closely related to *B. alpina* of Europe, the type species of this section and of the genus, and both of these species to be much closer, morphologically, to *B. humilis* than to *B. glabella*. *Braya linearis* seems to be clearly distinct from both *B. glabella* and *B. humilis*, enough so that it presents few problems of classification.

I have not seen sufficient Asian material to state unequivocably that the section *Sisymbriastrum* is monotypic, but, at least in North America, this appears to be the case. There seems to be no reliable way of separating the section into groups distinctive enough to warrant specific or, in most cases, even subspecific or varietal recognition.

The problem of classification stems from the tendency of *Braya humilis* to form small populations, of fairly uniform individuals, that are each somewhat different from the next population (Rollins, 1953), but may be quite similar to some distant populations. Böcher (1956) has recognized eight taxa among the slightly differing populations of Greenland and eastern North America. Böcher's classification is essentially unworkable, even in eastern North America, where the populations are geographically separate; but in the West, where the distribution of *B. humilis* is more continuous, a classification based on similar criteria would be valueless. The minute morphological differences used to separate eastern populations are [illegible] western populations, randomly scattered; dozens of sympatric and partially sympatric taxa would have to be recognized if a similar classification were undertaken.

Judging from the three Central Asian *Bra*[illegible] collections I have at hand, similar patterns of interpopulation variation are also fo[illegible]pecies there, so that a classification based on minor morphological variation between populations would almost certainly require the recognition of widely dispersed subspecies or varieties, spanning continents, and obviously not more closely related to each other than to other nearby populations of slightly different appearance.

This tendency in *Braya humilis* for some widely separated populations to resemble one another more than they do many nearby populations may be due to several factors. Some Alaskan populations provide evidence to suggest that separate hybridization events may, at times, lead to similar morphological forms. Hexaploid populations probably often arise through hybridization of tetraploid and octoploid populations. Hexaploids from along the Mackenzie River and throughout central Alaska are often very large, robust plants with large, toothed leaves and multi-branched stems. It would seem likely that all of these morphologically similar hexaploids are closely related and arose from a single hybridization event, but leaf pubescence and ES[illegible] evidence indicate that this is probably not the case. Throughout *B. humilis*, leaf pubescence of bifurcate hairs is the general rule. These hairs may be accompanied by a few simple or trifurcate hairs, but bifurcate hairs are almost always dominant. There are, however, at least five populations from south-central interior Alaska with leaf pubescence essentially entirely of simple hairs (Harris 1168 & 1174 ALTA; H.M. Laing 90 CAN; L.A. Spetzman 561 CAN; W.J. Cody & T.J.M. Webster 5876 DAO; D. & J. Taylor 1 ALTA). One of these populations (Harris 1168) grows along the banks of the Copper River near Chitina, Alaska and is tetraploid. Another population (D. & J. Taylor 1), this one hexaploid, grows nearby on the high, sandy banks of the Chitina River, near the confluence with the Copper River. These populations differ morphologically. The hexaploid is a very large, robust plant, much like other hexaploid populations from along the Mackenzie River. In fact, it is with these populations that it is most closely related according to the TAXMAP analysis of morphological attributes (see Table 5). The tetraploid is much smaller, with smaller leaves and fewer stem branches; it looks more like some Rocky Mountain populations than it does its hexaploid neighbor. Yet these Alaskan populations have simple hairs. It is unlikely that this attribute arose independently in each of these populations, and these Alaskan populations of differing ploidy level must be more closely related to each other than they are to other morphologically similar, but geographically distant populations of matching ploidy level.[12] It would appear that hybridization in different areas may have produced hexaploids which bear some morphological characteristics attributable to ploidy level. Mulligan (1965) has noticed that hexaploids are more variable than tetraploids and octoploids in style length, pod size and shape, and life span. Although some general patterns of morphological appearance are apparently dependent on ploidy level, it should be stressed that, most often, differences in chromosome number are not accompanied by obvious morphological differences. It makes little practical sense to recognize separate species simply because of a difference in ploidy level when it is not possible to distinguish the chromosome races morphologically. Indeed, in *Braya*, such a classification would not be functional; in the Canadian Rocky Mountains, tetraploid, hexaploid, and octoploid populations of *B. humilis* var. *humilis* are scattered in an apparently

---

[12] This is borne out by the TAXMAP analysis of EST isozyme patterns (see Table 8). The Alaskan tetraploid is shown to be most closely related to the neighboring hexaploid.

random fashion into small, isolated populations which form assorted morphological forms with little or no regard to ploidy level.

Similarities between widely scattered *Braya humilis* populations are caused also by phenotypic plasticity; plants growing in similar habitats often have a tendency to resemble one another. Evidence of this, provided by common garden studies of eastern and western *B. humilis* populations, has been discussed previously.

Some morphological similarities between distant populations are likely caused by the fixation, following establishment by one or a few individuals and subsequent inbreeding, of similar alleles in different populations. Although this may account for some long-distance interpopulation similarities, paradoxically, it is probably this same process of genetic depletion and fixation, postulated and demonstrated in many groups of flowering plants (Stebbins, 1942, 1957; Solbrig, 1972; Babbel & Selander, 1974; Nevo, 1978; Soltis, 1982), that is most responsible for the distinctiveness of many *Braya humilis* populations. It seems probable that the variation between populations of *Braya humilis* is best explained by the dispersal of segments of the overall species diversity, perhaps often as single colonizing, autogamous individuals, rather than by divergence due to allopatric speciation. This founder effect, coupled with autogamous reproduction, has led to a situation essentially the same as that in some apomictic groups; the species is composed of many small, fairly uniform, and often isolated, populations of slightly different morphology. Some evidence for this dispersal theory of variation is found in the essentially random distribution patterns of the various isozymes in the IDH, PGM, PGI, and SOD enzyme systems. All of these enzymes have very critical and specific functions in the metabolic pathways of plant cells, and have apparently tolerated very little isozyme alteration in *Braya* as the group has evolved. It appears that all of the variation in these enzymes found in the genus today has been present since the group diverged, and that isozyme patterns in various *Braya* populations are due to random patterns of dispersal of the diversity rather than to the highly unlikely parallel evolution of these isozymes in widely scattered populations and in distantly related taxa within the genus.

I have chosen then, to follow what seems to be the most logical course, and I have recognized a single species, *Braya humilis*, in this section. The vast majority of North American populations of *B. humilis* have been placed in a large polymorphic variety, var. *humilis*. Only the most distinctive groups of variants, those consistently separable from var. *humilis*, have been recognized as three additional varieties of the species.

Phylogeny

Braya appears to be a natural group with well-defined generic boundaries. It is very unusual for members of other cruciferous genera to be confused with *Braya*, or for *Braya* species to be confused with other genera. On occasion, *Arabis lyrata* can look superficially very much like *B. humilis* var. *humilis*, and the two species may at times be found growing in close proximity to each other. Upon closer examination, however, it is clear that *A. lyrata* and *B. humilis* differ sharply in critical attributes of the silique; the siliques of *A. lyrata* are somewhat flattened parallel to the septum, and the epidermal cells of the silique septum are thin-walled and isodiametric in contrast to the terete siliques and thick-walled, elongated septal epidermal cells of *B. humilis*. This coupled with the fact that *A. lyrata* has a base chromosome number of x=8, and *Braya* a base number of x=7, indicates that any superficial morphological similarity between the two species is due to convergence rather than relatedness. Which genus is most closely related to *Braya* is not clear. Most of the genera placed by Schulz (1924) with *Braya* in the subtribe *Brayinae* are South American, Mediterranean, or Asian in distribution, and I have not had an opportunity to compare any of them with *Braya*. These genera are grouped together on the basis of their simple leaves, non-glandular hairs, small seeds that are non-mucilaginous when moistened, non-cordate leaf bases, and non-connecting nectar glands. Given the limited number of characters used to circumscribe the subtribe, it is not at all certain that *Brayinae* is a natural group.

Based on cytological data (Rollins, 1953; Böcher, 1956) and the supposition that the greatest species diversity in *Braya* is found in the mountains of Central Asia (Gams, 1933;

Handel-Mazzetti, 1941; Böcher, 1966, 1973), this region is considered to be the area of origin of the genus. It remains to be seen, however, if species diversity is actually greatest in Central Asia. It is very likely that many of the Central Asiatic taxa will turn out to be conspecific with North American plants when compared in detail, and it may well be that species diversity is actually higher in northwestern North America than in Asia. The area of greatest species diversity, however, is not necessarily the center of origin of a genus, so the geographical origin of *Braya* could well be in Asia or North America regardless of the number of species presently found in each area.

There are many problems in reconstructing the phylogeny of *Braya*. The first is the lack of a fossil record. The present-day distribution of *Braya* is very similar to that of many other genera believed to have formed the Arctotertiary Geoflora, and it is very likely that the genus arose during this time period. Many contemporaneous woody plants have left abundant fossils, but most of the herbaceous plants of the Tertiary, often components of drier, more upland habitats, have left little or no fossil record.

Another problem is the lack of information about the Asian *Braya* species, particularly their cytology and phytochemistry. Detailed morphological comparisons of Asian and North American taxa are also required to determine the sectional status of the Asian plants. It is presently difficult to unravel the relationships between the three sections of *Braya* when it is uncertain whether all three sections, or perhaps additional sections, are present in Asia.

Additional insight into the relationships of the sections could probably also be gained if diploid taxa were known. Unfortunately, this is not the case. However, very few chromosome counts of Asian populations have been made, so it is possible that diploids will eventually be found there. As mentioned earlier, pollen measurements of Asiatic *B. humilis* populations (Rollins, 1953; Böcher, 1956) suggest that some may indeed be diploid.

There is also some evidence that *Braya pilosa*, a North American species of very limited distribution, may be diploid. The large flower size and blossom fragrance found in plants of this species suggest that it is of a lower ploidy level than other members of the section

Platypetalum. Large flowers are correlated with lower chromosome number in *B. humilis*; and fragrance (otherwise unknown in *Braya*), as well as large flower size, have been correlated with xenogamy and lower chromosome number by Ornduff (1969) in a number of flowering plants. Unfortunately, there are no recent collections of *B. pilosa*, so I have not been able to obtain a chromosome count for this species. A survey of pollen sizes in the section *Platypetalum* indicates, however, that *B. pilosa* may have a very low chromosome number. Pollen grains averaged 26.9 x 25.6 μ in *B. pilosa* (Richardson s.n. K), compared with 31.9 x 26.25 μ in the tetraploid *B. thorild-wulffii* (Harris 1725 ALTA), 34.5 x 32.3 μ in one population of the octoploid *B. glabella* var. *glabella* (Harris 1330 ALTA), and 36.5 x 32.8 μ in another population of *B. glabella* var. *glabella* (Cody & Webster 5859 DAO). The measurements show a reasonable correlation in pollen size and chromosome number, similar to that found by Rollins (1953) and Böcher (1956) in *B. humilis*, and suggest that *B. pilosa* may have a lower chromosome number than the tetraploid *B. thorild-wulffii*.

Braya also does not lend itself well to a cladistic approach to phylogenetic interpretation, primarily because of insufficient information about an out-group. This makes it very difficult to ascertain which character states are ancestral and which are derived. Hauser and Crovello (1982) list 32 characters from the Cruciferae and the states of these characters in two hypothetical ancestors of the Thelypodieae (i.e. *Cleome* from the Capparaceae, and *Macropodium*, the only Asian representative of the Thelypodieae), considered by some to be the most primitive tribe in the family. In addition, Hauser and Crovello list the states considered to be primitive by several taxonomists such as Rollins (1939, 1942, 1956), Payson (1923), Al-Shehbaz (1973), Hedge (1976) and Cronquist (1968). Unfortunately, almost all of these 32 characters are non-deviating in *Braya* and provide little information about the direction of evolution in the genus.

The highly reticulate patterns of speciation in *Braya*, due to hybridization, also make cladistic analysis difficult. It is very common for well-differentiated species to form fertile seed when hybridized, and some geographically distant species (e.g. *B. linearis* and *B. alpina*) will even produce fertile F_1 offspring. Even intersectional crosses are possible, and may have led to the formation of new sections. Thus, the patterns of speciation in the genus are much more complicated than the regular dichotomous branches envisioned in most cladistic phylogenies.

Despite the difficulties in authenticating the phylogeny of *Braya*, it is still possible, especially within sections, to note obvious evolutionary trends and to suggest, based on the evidence available, what seems the most pausible evolutionary history of the taxa in the genus. Additional evidence, particularly that of a cytological or phytochemical nature, will undoubtedly demand alterations, perhaps very significant alterations, of the hypotheses presented here.

It is natural to assume that taxa of lower chromosome number are more ancient than higher polyploids and that the taxa of lowest chromosome number in sections *Platypetalum* and *Sisymbriastrum* are probably more closely related to the ancestral stock than are the taxa of higher ploidy level from each section. This would also imply that the taxa of lowest chromosome number from each section should be more closely related to members of the opposite section than should the higher polyploids. The TAXMAP analysis of EST enzyme patterns provides some evidence that this may be the case (see Figure 11). Cluster 6 consists of two tetraploid members of the section *Sisymbriastrum*, and Cluster 15 is a single tetraploid member of the same section. Both Cluster 6 and Cluster 15 are most closely related, on the basis of EST profiles, to Cluster 3 (or the closely related Cluster 11), the cluster containing the bulk of the members of the section *Platypetalum*.

As has been mentioned, sect. *Braya* seems to be intermediate to sections *Platypetalum* and *Sisymbriastrum*, but it is not certain whether this is because sect. *Braya* is ancestral to the other two sections, or whether it is of recent origin and arose through hybridization of the other sections. The only taxa known to belong to sect. *Braya* are *B. linearis*, of East and West Greenland and Scandinavia, and *B. alpina*, of the Tyrolean Alps. Böcher (1973) has shown that the two species are very closely related; they form fertile F_1 offspring upon hybridization.

It is clear that *B. linearis* and *B. alpina* arose from a common ancestor. How then can their present distributions be explained?

Gams (1933) has suggested that one line of the ancestral stock migrated northwest from Central Asia, becoming *Braya linearis*, and that another line migrated through the mountains of Asia and Europe, becoming *B. alpina*. If this were correct, it would suggest an ancient origin for sect. *Braya*; the species would be paleopolyploids (sensu Favarger, 1961), having once been widely distributed, but now restricted to a few small areas and having lost all of their diploid ancestors. This would mean that sect. *Braya* would likely be ancestral to the other sections of the genus, and it would explain the intermediate nature of this section.

Handel-Mazzetti (1941) proposes a similar migration from Central Asia northwest to Greenland in Pliocene or early Pleistocene time and the subsequent migration south to the Tyrolean Alps early in the Pleistocene, at a time when conditions were favorable. Later glaciations isolated the two segments of the population and isolation has since led to the divergence of the two species.

Böcher (1973), on the other hand, favors the alternative view, that the ancestor of *Braya linearis* and *B. alpina* arose in North America/Greenland and that migration has been from west to east across the North Atlantic. In support of this theory, Böcher points to the distribution of several east-arctic species (e.g. *Draba sibirica, Ranunculus auricomus* var. *glabratus, Arenaria pseudofrigida,* and *Carex parallela*) that only reach East Greenland, unlike *B. linearis*, which is also found in West Greenland. Böcher also lists several species (e.g. *Carex nardina, C. scirpoidea, Arenaria humifusa, Draba crassifolia, Erigeron humilis,* and *Campanula uniflora*) believed to be west-arctic in origin that probably reached Scandinavia from the west along the same pathway as that envisioned for *B. linearis*-*B. alpina*. As arguments against an east to west migration from Central Asia, Böcher draws attention to the large gaps in the distribution of *Braya* to the east of both *B. linearis* and *B. alpina*, as well as to the fact that the hybrid of *B. linearis* and the Asiatic *B. rosea* is sterile, while the F_1 hybrid of *B. linearis* x *B. alpina* is fertile. This would suggest a more recent connection between *B.*

linearis and *B. alpina* than between either of these species and Central Asiatic species. (It should be pointed out, however, that the Asiatic species have not been compared extensively with North American species and they are inadequately known cytologically; it is possible that a closer relative to *B. linearis* and *B. alpina* may eventually be identified in Asia.)

Böcher (1973) suggests that *Braya linearis* and *B. alpina* may have been more widespread in Europe as a hexaploid complex during late glacial times, before leaching of the soils, and that "The original populations disappeared from the lowlands and became restricted to small niches in the mountains where they finally attained their present status as two closely related geographically separated taxa."

I tend to favor the view of Böcher, that *Braya linearis* and *B. alpina* arose from a North America/Greenland ancestor. Johnson and Packer (1967), in reviewing Favarger's (1961) criteria for determining the age of polyploids, list as being likely paleopolyploids, "polyploid species forming a particular section of a genus in which the diploid species, if they occur, are classified in another section and differ too markedly to be considered ancestors of the polyploids." *Braya linearis* and *B. alpina* do form a particular section of *Braya*, one with no known diploids or lower polyploids, and the diploids, or at least the lower polyploids, are classified in another section. These lower polyploids, however, do not "differ too markedly to be considered ancestors". I think it very likely that the species of sect. *Braya* are mesopolyploids, and that they arose through hybridization between species of sections *Platypetalum* and *Sisymbriastrum*. As has already been mentioned, *B. linearis*, the only North Amerian species of sect. *Braya*, appears to be somewhat intermediate to *B. glabella* and *B. humilis* and it has often been confused with these two species (Abbe, 1948). The results of the two TAXMAP analyses presented in this work also suggest the intermediate nature of *B. linearis*. The TAXMAP analysis of EST profiles groups *B. linearis* with sect. *Platypetalum*, but the TAXMAP analysis of morphological attributes groups it with sect. *Sisymbriastrum*.

A simple hybridization of a tetraploid *Braya* from section *Platypetalum* or *Sisymbriastrum* with an octoploid *Braya* from the opposite section would account for the chromosome number of $2n=42$, as well as for the great disparity in chromosome size in *B. linearis*. As mentioned in the Results section of this text, similar artificial crosses have been successful in the greenhouse, but F_1's have not yet been cultivated from the seeds. With the abundance of chromosome races in both sect. *Platypetalum* and *Sisymbriastrum* in northern North America, at least at the present time, it is not difficult to imagine such a hybridization taking place. This would support Böcher's (1973) postulated North American/Greenland origin of a *Braya linearis*-*B. alpina* ancestor and obviate the necessity of explaining the absence of *Braya* between Europe and Central Asia. As Handel-Mazzetti (1941) and Böcher (1973) have pointed out, this ancestor must have crossed the Atlantic in early Pleistocene times to have had the time required to become as morphologically distinct, following subsequent isolation, as the two extant species now are.

Some of the difficulties encountered in determining the phylogeny of the sections of *Braya* are alleviated, to some extent, within the sections. Since diploids, or lower polyploids, almost certainly gave rise to the higher polyploids, character states in the lower polyploids can be considered ancestral to those in the higher polyploids. Some general trends in character state transformations in *Braya* can be identified with this method.

A decrease in flower size and a simultaneous loss of self-incompatibility are trends common to sections *Platypetalum* and *Sisymbriastrum*. In sect. *Platypetalum*, a loss of blossom fragrance accompanies reduction in flower size. The siliques of sect. *Sisymbriastrum* are fairly uniform, but in sect. *Platypetalum* there is a transformation series from globose silicles with often fenestrate septae to narrow lance-subulate siliques with entire septae.

Within sect. *Platypetalum*, there appear to be four distinct subgroups. The first subgroup consisting of *B. pilosa*, perhaps a diploid; the second of *B. thorild-wulffii*, a tetraploid; the third of *B. glabella*, an octoploid; and the last includes *B. longii* and *B. fernaldii*, both octoploids. Assuming that it can eventually be shown that *B. pilosa* is actually diploid, this species is the logical place to start in discussing the phylogeny of the section.

Braya pilosa has only been found in an unglaciated area near the Mackenzie Delta. It may be that this species, as well as other diploid species, extended south along the Rocky Mountains and gave rise to many of the extant polyploid *Braya* taxa. Favarger (1961) and Packer (1974) have commented on the relatively large number of diploid species in the Alps and in the Rocky Mountains, and Johnson and Packer (1967) have demonstrated that diploids tend to occur more frequently in more stable habitats, such as unglaciated mountains and other stable environments, and that polyploids are more frequent in less stable environments, such as lowland glaciated areas. It may be that polyploid *Braya* taxa arose from montane diploids and then moved out onto newly exposed habitats as they became available as the ice receded. No diploid *Braya* taxa are now known from the Rocky Mountains, but the taxa of lowest known chromosome number, tetraploids, are located in and near areas believed to have escaped glaciation.

It is not difficult to imagine *Braya thorild-wulffii* arising from *B. pilosa*, or a *B. pilosa*-like ancestor; both species have globose silicles (usually densely pubescent) and both sometimes have a fenestrate septum. In addition, the septal epidermal cell wall thickenings in *B. pilosa* and *B. thorild-wulffii* are somewhat thicker and more irregular than those in other members of the section. On the other hand, the erect habit, large flowers, and very long styles in *B. pilosa* are certainly very different from the prostrate habit, small flowers, and often almost non-existant styles of *B. thorild-wulffii*; the phylogenetic connection between the two species is probably not very recent or very direct. Böcher (1966) found only a single pair of large chromosomes in *B. thorild-wulffii*, so it is unlikely that the species arose as a simple autopolyploid.

Braya thorild-wulffii var. *glabrata* is very closely related to var. *thorild-wulffii*, differing only in degree of pubescence. The fact that lower polyploids, as well as most other *Braya* taxa, are distinctly pubescent, indicates clearly that var. *glabrata* arose as a minor variant of var. *thorild-wulffii*.

How and when *Braya glabella* may have arisen is not clear. Variety *purpurascens* is closest morphologically to *B. pilosa* and *B. thorild-wulffii*, and it is probably ancestral to the other varieties of the species, but whether it arose directly from *B. thorild-wulffii* or from other extinct diploids or tetraploids is uncertain. The differences in silique shape and stem habit between var. *purpurascens* and extant taxa of lower ploidy level suggests an allopolyploid origin involving at least one extinct taxon.

Braya glabella var. *prostrata* is clearly closest to var. *purpurascens* on the basis of silique shape and style length, but it shares some attributes with *B. thorild-wulffii* which suggest that introgression with this species has contributed to its divergence as a separate taxon.

Braya glabella var. *prostrata* is known only from northern Ellesmere Island, where it grows in very close proximity to *B. thorild-wulffii* var. *thorild-wulffii*, and it is the only *B. glabella* taxon that exhibits the prostrate stems, thin leaves, and robustness of *B. thorild-wulffii*. It seems more than a coincidence that the only variety of *B. glabella* to share attributes with *B. thorild-wulffii* is found growing in the same localities as that species. It must be mentioned though, that the morphological similarities between *Braya thorild-wulffii* and *B. glabella* var. *prostrata* could also be accounted for by a genetic response to similar environmental conditions. This seems unlikely, however, because populations of *B. glabella* var. *purpurascens* from the same area, and from other areas inhabited by *B. thorild-wulffii*, do not show these similarities.

Braya glabella var. *glabella* has siliques generally somewhat narrower and longer than those in var. *purpurascens*, and it has obviously arisen from that variety. Separation of the two varieties is not entirely complete, in fact, and they often exhibit somewhat overlapping morphological forms.

Braya longii and *B. fernaldii* are known only from a few restricted localities in northwestern Newfoundland. These species are obviously very closely related, and both differ from *B. glabella* in the size and shape of the siliques and in the shape of the septum margin. The septum margin in *B. longii* and *B. fernaldii* is very broadly expanded, so much so that it usually forms a sack-like pouch surrounding the base of the lowermost seed in each locule.

Morphology and EST patterns clearly show that both of these species are most closely related to *B. glabella* var. *glabella* and almost certainly diverged from that taxon. The TAXMAP analysis of morphological attributes suggests that *B. longii* is more similar to *B. glabella* than is *B. fernaldii* and it may, therefore, be the connecting link between the latter two species.

The phylogenetic relationships between the taxa in sect. *Sisymbriastrum* are somewhat more apparent than those in other sections. This is probably because the entire section consists of a single species with four fairly closely related varieties. The low chromosome number (2n=28) and self-incompatibility of *B. humilis* var. *maccallae* and var. *porsildii*, and the simple EST profile of var. *porsildii*, suggest that they are more primitive than varieties *humilis* and *ellesmerensis*. The two varieties look very similar morphologically, differing only in the degree of pubescence, but EST isozyme profiles in the two taxa are quite different, suggesting that the two varieties are not as closely related as they appear. Perhaps they represent separate lines from the ancestral stock.

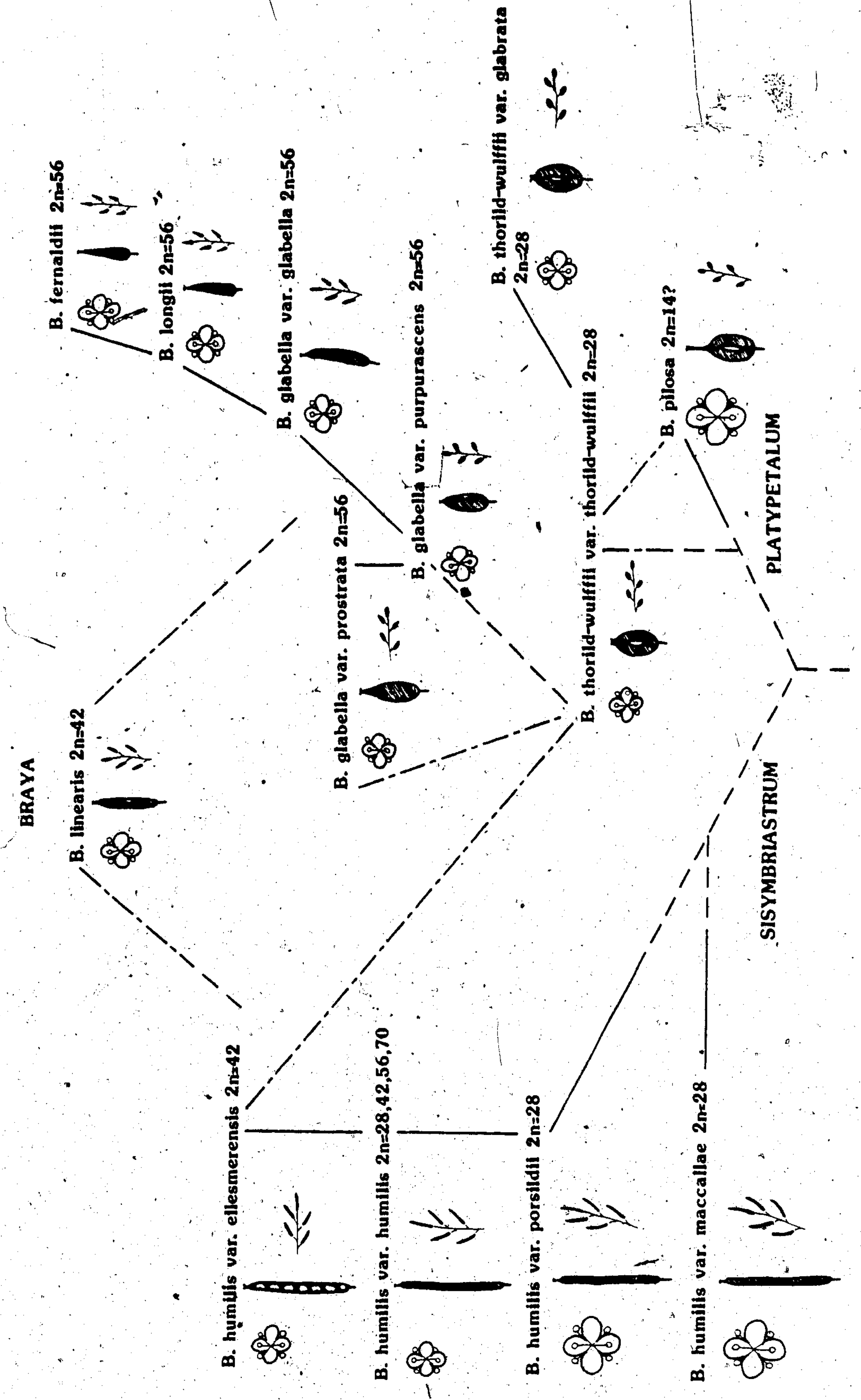
Braya humilis var. *porsildii* seems to be closer morphologically to var. *humilis* than does var. *maccallae*. Variety *humilis* probably arose directly from var. *porsildii* or from a *porsildii*-like ancestor.

It seems reasonably certain that *Braya humilis* var. *ellesmerensis* arose relatively recently from var. *humilis*, since it is restricted to the high arctic and it is geographically isolated from all other varieties. Variety *ellesmerensis* is also closer morphologically to var. *humilis* than it is to other varieties. It seems likely that introgression between *B. humilis* and *B. thorild-wulffii* may have played a role in the formation of var. *ellesmerensis* as a distinct variety. This possibility is discussed in some detail in the Taxonomy section of the thesis.

Based on the conclusions in the preceding discussion, a diagram illustrating the most likely evolutionary history of *Braya* is presented in Figure 12.

Figure 12. Diagram of postulated evolutionary history of North American *Braya* species.

(Even dashed lines indicate uncertain connections; broken dashed lines indicate hybridization or introgression.)


BRAYA
B. fernaldii 2n=56
B. longii 2n=56
B. glabella var. glabella 2n=56
B. thorild-wulffii var. glabrata 2n=28
B. glabella var. purpurascens 2n=56
B. linearis 2n=42
B. glabella var. prostrata 2n=56
B. thorild-wulffii var. thorild-wulffii 2n=28
B. pilosa 2n=14?
PLATYPETALUM
SISYMBRIASTRUM
B. humilis var. ellesmerensis 2n=42
B. humilis var. humilis 2n=28,42,56,70
B. humilis var. porsildii 2n=28
B. humilis var. maccallae 2n=28

Phytogeography

Looking at the present discontinuous distribution of *Braya* species, it is not difficult to imagine that in pre-Pleistocene times they, or their ancestors, had a much more continuous distribution across northern North America. Glaciation removed *Braya* from much of its former range and the genus has been only partially successful in [illegible] areas in post-glacial times.

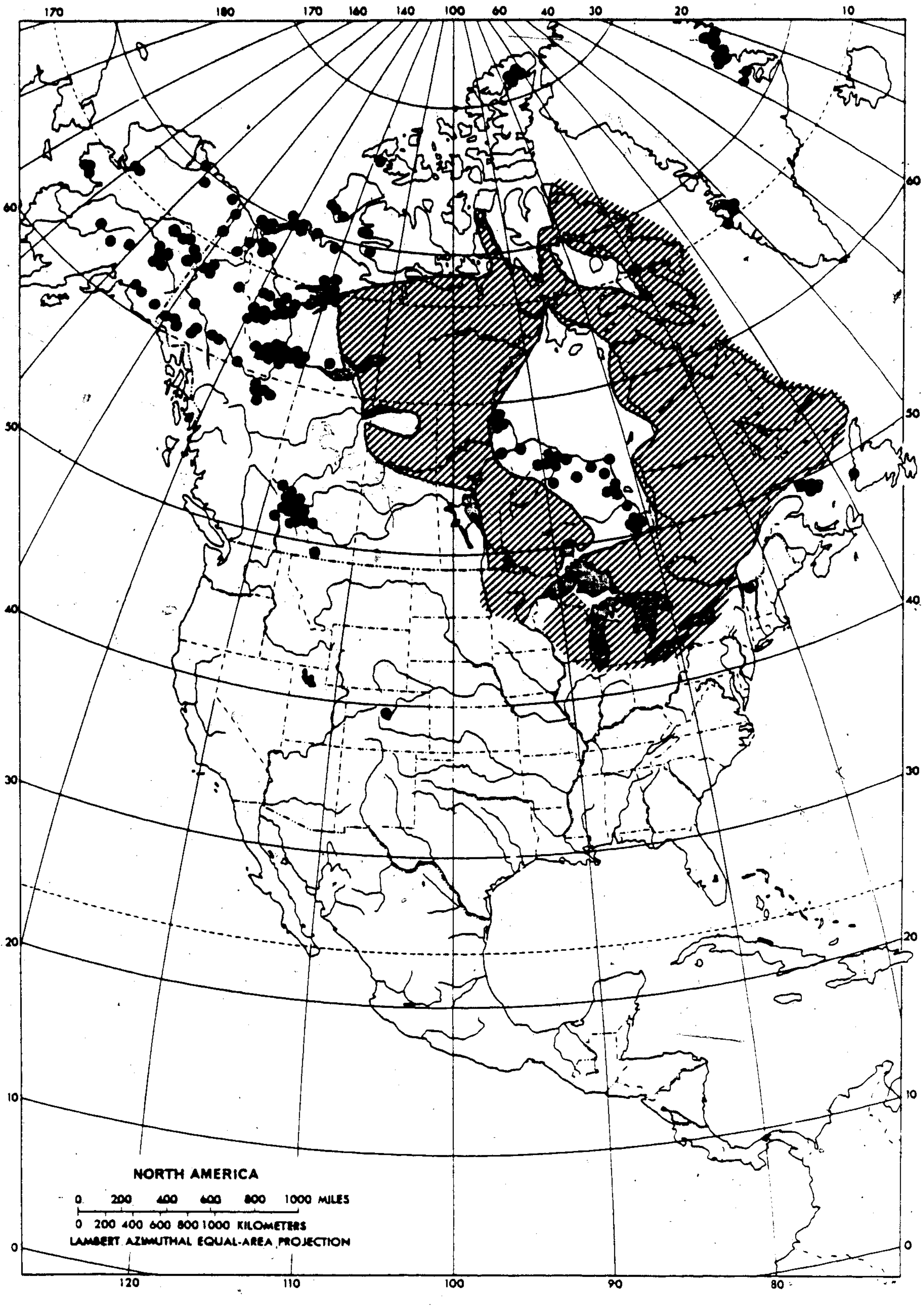
Part of this lack of success has likely been due to the absence of long distance dispersal mechanisms in *Braya*, but by far the most important factor has been the glacial eradication of the edaphic conditions required by the genus from a large portion of its former range. Members of the genus *Braya* are almost entirely, if not entirely, restricted to calcareous soils. *Braya humilis* is perhaps the most striking example, being widely distributed on sedimentary soils in western Canada and Alaska, but completely absent from the granitic rock and soils of the Canadian Shield. Figure 13 shows the distribution of *B. humilis* superimposed on the approximate limits of the granitic bedrock of the Canadian Shield.

Especially striking is the occurrence of *Braya humilis* in eastern North America only on anomalous areas of sedimentary rock within the Shield along the southwestern coast of Hudson Bay, and along the margins of the Shield in western Newfoundland, Anticosti Island, Quebec, and in northern Vermont. The sharply-defined distribution limits of *B. humilis* in Ontario and Manitoba attest to the inability of this species to invade regions of granitic soils.

Braya glabella is also almost entirely absent from the Canadian Shield, but it does encroach slightly onto the margins of the Shield at Bathurst Inlet, Spence Bay, Rankin Inlet, Repulse Bay, the Ungava Peninsula, and southern Baffin Island. The lack of widespread migration onto granitic soils, however, indicates the likelihood that these borderline populations may in fact be growing on local anomalous areas of calcareous soil within the more widespread granitic soils.

In order to adequately explain the present-day distribution of *Braya* in North America, it is necessary to postulate the survival of segments of the population in unglaciated areas to the

Figure 13. Distribution of *Braya humilis* in relation to approximate limits of granitic soils of the Canadian Shield (cross-hatched area).


170
180
170
160
140
100
60
40
30
20
10
60
50
40
30
20
10
0
120
110
100
90
80
NORTH AMERICA
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

north and south of the ice-sheet, as well as in localized refugial areas that escaped glaciation even though surrounded by ice.

The idea of glacial refugia has long been invoked to explain the high incidence of endemic and disjunct taxa in the Gulf of St. Lawrence region of eastern Canada with counterparts in western North America (Fernald, 1925; Marie-Victorin, 1938; Morisset, 1971). Morisset (1971) has noted that geological evidence suggests a much more extensive glaciation in the Gulf of St. Lawrence than originally envisioned, and that this casts some doubt on the validity of Fernald's "nunatak theory". He also points out that the extreme environment likely to have prevailed in these nunatak refugia precludes the survival of the many delicate disjuncts and endemics found in the area.

The periglacial environment of nunatak refugia at full glaciation may indeed present a problem in explaining the survival of many of the Gulf of St. Lawrence- Newfoundland endemics, but this is certainly not the case with *Braya*. *Braya* species are well-adapted to extreme environments in the Arctic and are found at the limits of land in Canada and Greenland.

Whether these nunatak refugia existed or not in eastern North America will probably remain controversial for some time, but there is a general consensus of opinion that these disjunct and endemic species must have survived glaciation somewhere in the area. Ives (1963) and Morisset (1971) suggest that large areas of the continental shelf must have been dry land during glaciation and that plants may have survived in these fairly mild coastal refugia.

Wherever the refugia may have been located in eastern North America, it appears inescapable that at least *Braya longii* and *B. fernaldii*, and perhaps also *B. humilis*, survived glaciation in close proximity to their present-day distributions in Newfoundland and the Gulf of St. Lawrence region. Given their very specific edaphic requirements, which would have prevented step-wise migration across large areas of granitic soil, the only other alternative to explain the distribution of *B. longii* and *B. fernaldii* is long distance dispersal. Long distance dispersal is simply not adequate to explain the distributions of the many endemic and disjunct plants (including *B. fernaldii* and *B. longii*) found growing in the same general region.

The distribution of *Braya humilis* along the southwestern coast of Hudson Bay requires a different explanation. This area was completely glaciated, with no chance of plant survival anywhere in the area. There appear to be only two possible explanations for the present-day distribution of *B. humilis* in the region.

The most likely one is that *Braya humilis* migrated southward with the advancing ice and has gradually moved northward again in post-glacial times along the narrow corridor of sedimentary bedrock extending from Hudson Bay down past the limits of glaciation in Minnesota and Wisconsin (see Figure 13). Although I have not seen specimens of *B. humilis* from the Lake Superior region, populations have been reported from as far south as Isle Royale, Michigan and from the north shore of Lake Superior (Fernald, 1950; Gleason, 1952; Scoggan, 1978). It is not difficult to imagine that *B. humilis* could have moved northward relatively rapidly along this corridor along the many rivers and streams in the area.

Another possible explanation is long distance dispersal. It must be admitted that *Braya humilis* — or any *Braya* species for that matter — does not make a likely candidate for long distance dispersal. There are no obvious morphological adaptations for dispersal of any kind, short or long range. On the other hand, self-compatibility is the general rule in *Braya*, so that even a single introduction, regardless of how remote the likelihood, would stand a good chance of being successful. It is not unreasonable to suggest that transport of propagules from populations in western Canada conceivably could have taken place along the waterways leading to Hudson Bay in early post-glacial time, or that birds might have ingested seeds or carried them along these same waterways and deposited them near Hudson Bay.

The distribution of the extremely disjunct populations of *Braya humilis* var. *humilis* in central Colorado suggest that *Braya* also moved south in western North America as suitable environmental conditions developed. Until recently, only a single Colorado population was known. It consisted of approximately 500 individuals restricted to about 0.77 hectares of frost-scarred calcareous slope at 3700 m in elevation. Since 1980, four or five additional populations have been discovered in the high mountains of Colorado (Johnston, 1984). These Colorado populations are probably isolated relicts left behind on small areas of favorable alpine habitat as the climate warmed and other *Braya* populations in the region became extinct.

The area of greatest diversity in *Braya humilis* in North America is centered in the Canadian Rocky Mountains. The distribution of both *B. humilis* and *B. glabella* support the now generally accepted view that portions of the Rocky Mountains and adjacent foothills remained unglaciated at the peak of the Pleistocene glaciations (Packer, 1971; Packer and Vitt, 1974; Wolf *et al*, 1979).

Of the four North American varieties of *Braya humilis*, three are found in the Canadian Rockies. Of these three varieties, one, var. *maccallae*, is strictly endemic to the Rockies. Another, var. *porsildii*, is found in the Rockies of southern Alberta and then again in the northern Rockies of British Columbia northward into the Mackenzie Mountains of Northwest Territories. A single record from Graham River, British Columbia (Mrs. J.N. Henry 501 PH) falls between the two main centers of distribution. These varieties have the lowest chromosome number (2n=28) known in the species, as well as distribution ranges much more restricted than the higher polyploid members of var. *humilis* (Fig. 8). This follows the pattern noted in many other polyploid complexes, where polyploids tend to be more aggressive and better able to expand their range than their diploid (or in this case, functional diploid) progenitors.

The simplest method of explaining the distribution of these two varieties is to assume that they survived glaciation in the same general areas where they are now found, either in the Rocky Mountains, or in the Mackenzie Mountains, or in both places. It is known that much of the Mackenzie Mountains remained unglaciated (Prest, 1969; Cody, 1971) and it is very likely that *Braya humilis* populations survived there. Assuming post-glacial migration south to the Rocky Mountains would explain the distribution of *B. humilis* var. *humilis* and var. *porsildii* but would not be adequate to explain the distribution of var. *maccallae*. Esterase isozyme evidence suggests only a distant relationship between *B. humilis* var. *maccallae* and var.

porsildii, too distant to have arisen since glacial times by a recent Rocky Mountain divergence. It is much more likely that *B. humilis* populations survived glaciation in both the Mackenzie Mountains and Rocky Mountains.

Since these tetraploid varieties obviously did not arise from more widespread hexaploid and octoploid *Braya humilis* populations, the only other explanation possible for their present-day distributions is to assume that tetraploids survived in unglaciated portions of Alaska or the Yukon, migrated south in post-glacial times, and subsequently became extinct in the north. This explanation requires some causative hypothesis for the selective extinction of tetraploids in the north, as well as for their survival in the same regions of the Rockies, and seems highly improbable.

The concentration of *Braya glabella* var. *glabella* in areas of the Rocky Mountains suspected, on the basis of geological and other botanical evidence, of having escaped glaciation (Packer and Vitt, 1974) strongly suggests that this species, as well, survived in the Rockies during the Pleistocene.

The wide distribution of *Braya* populations on appropriate habitats in unglaciated parts of Alaska and Yukon is undoubtedly due to pre-glacial establishment in these areas. This region has almost certainly served as an important center for migration of *Braya* back into glaciated parts of Alaska, Yukon, and at least the southern parts of the Canadian Arctic Archipelago.

Another important center of migration, at least for the Arctic Archipelago, may have been within the archipelago itself. Hultén (1937), Porsild (1955), Packer (1963), and Brassard (1971) have suggested that ice-free areas must have existed in the high arctic to account for the incidence of endemic and disjunct species there. Prest (1969), on the basis of geological evidence, has indicated that parts of the coast near the Mackenzie River Delta, Banks Island, as well as smaller areas in northern Ellesmere Island remained free of ice during the last glaciation. These refugial areas would have served as centers of migration for plants after glaciation.

The results of this study support the hypothesis that these high arctic refugia existed. Brassard (1971, Fig. 1) has produced a map showing equiformal progressive areas of endemic plant species of the North American Arctic. Three of these areas in the Arctic Islands are particularly rich in endemic plants and include all 21 of the endemics recognized by Brassard. It is interesting to note that two of the endemic taxa recognized in this study (*B. glabella* var. *prostrata* and *B. humilis* var. *ellesmerensis*) occur in, or very near, one of these three areas, in northern Ellesmere Island. It would seem that the only reasonable explanation for this high incidence of endemism is the survival of these taxa at or near their present areas of distribution during the last glaciation. Plants from these refugial areas were probably important in the recolonization of much of the Arctic Archipelago and perhaps also parts of Greenland.

In summary, the distribution of *Braya* in North America was probably more continuous at one time than it is today. Glaciation eliminated *Braya*, as well as all other plant and animal life, from most of its former range and, at the same time, altered the bedrock composition in a significant part of boreal North America, making it unsuitable for recolonization by calcicolous plants. Populations of *Braya* survived glaciation to the north and south of the ice-sheets, and in unglaciated refugial areas within or between the ice-sheets. *Braya* has been fairly successful in recolonizing appropriate habitat in glaciated areas where the required calcareous substrate still remains.

V. Taxonomy

Braya Sternb. & Hoppe

Denkschr. Kgl. Bot. Gesellsch. Regensburg. I. 1:65. 1815.

Perennial, or rarely biennial, herbs, pubescent with branched or simple hairs or rarely essentially glabrous, often purple-tinged; caudex simple or branched; stems erect, ascending or decumbent, simple or branched, foliate or scapose; leaves alternate, basal or basal and cauline, simple, entire, dentate, or pinnatifid, sessile or rarely petiolate, sometimes fleshy; flowers in dense subcapitate or corymbose racemes, the pedicels ascending or erect, not subtended by bracts (except occasionally the lowermost); sepals 4, erect or slightly spreading, ovate, subequal, with a scarious margin; petals 4, widely-spreading, truncate, white or purple-tinged, especially the claw; stamens 6, tetradynamous; anthers cordate, obtuse; styles variable in length; stigma bilobed or entire; fruits siliques or silicles in a compact or elongate raceme, 1.25-many times longer than broad, terete or slightly compressed parallel to the septum, ovoid, oval-elliptic, oblong or linear and subcylindrical, often torulose; septum epidermal cells thick-walled and elongated transversely or obliquely in relation to the longitudinal axis of the fruit; seeds 10-many, uniseriate or biseriate, oval-ovate, slightly convex, somewhat beaked; cotyledons incumbent; $x=7$.

Type species: *Braya alpina* Sternb. & Hoppe. Figure 14.

A fairly small genus of circumboreal arctic, sub-arctic, and alpine distribution.

Key to the North American sections of *Braya*

1a. Stems leafy (usually 2 or more leaves per stem); fruit a silique, linear, subcylindrical, 9 - 33 times longer than broad; seeds uniseriate (at least in North American species) 2

1b. Stems scapose (occasionally with a single leaf or leafy bract); fruit a silique or silicle, ovoid to oblong-lanceolate, never linear, 1.25 - 8 times longer than broad; seeds biseriate (except in *B. longii* and *B. fernaldii*) ....section *Platypetalum*

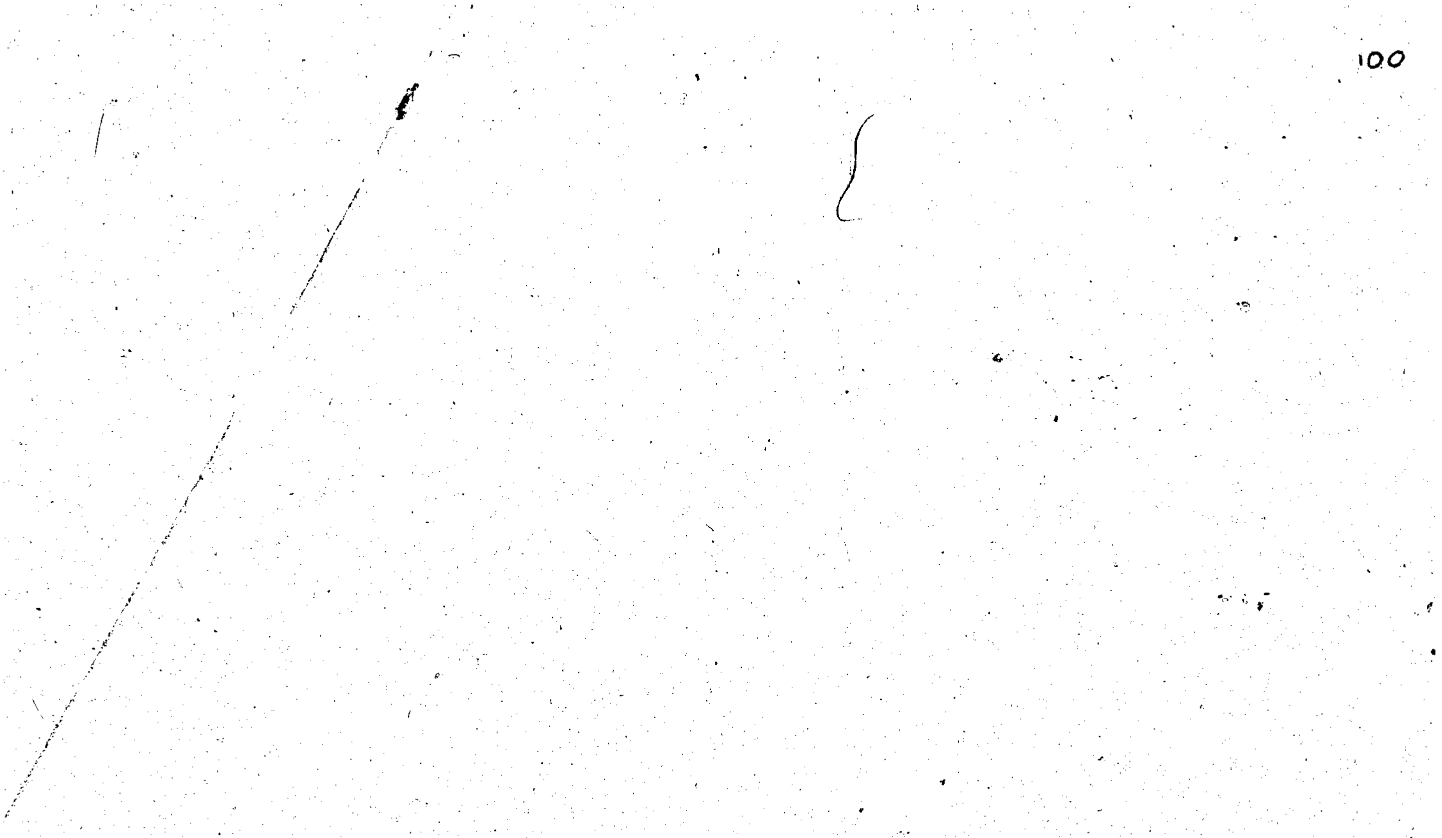


Figure 14. Type specimen of *Braya alpina* Sternb. & Hoppe.

HERBARIUM REGIUM MONACENSE.

Braya
alpina
[illegible]
in alpe
[illegible]

2a. Cauline leaves usually 3 or less per stem; basal leaves usually more than 20 times longer than broad; fruiting inflorescence usually dense and crowded near top of stem; mature siliques usually less than 12 mm long, 9 - 10 times longer than broad............................section *Braya*

2b. Cauline leaves usually 3 or more per stem; basal leaves usually less than 20 times longer than broad; fruiting inflorescence rarely dense and usually scattered along the stem; mature siliques often more than 12 mm long, 12 - 33 times longer than broad....section *Sisymbriastrum*

Braya sect. **Braya**

Braya sect. *Eubraya* Turcz., Bull. Soc. nat. Mosc. XV. 2. p. 280. (1842)

Stems more or less leafy, with 1 - 3(4) leaves per stem, usually simple; basal leaves linear to linear-spatulate, dentate with 1 or 2 teeth per side or entire, usually more than 20 times longer than broad; cauline leaves often indistinctly petiolate; fruit a silique, linear, sub-terete, torulose, 9 - 10 times longer than broad; septum epidermal cell wall thickenings very thick and irregular; seeds more or less uniseriate (at least in North American representatives).

Type species: *Braya alpina* Sternb. & Hoppe

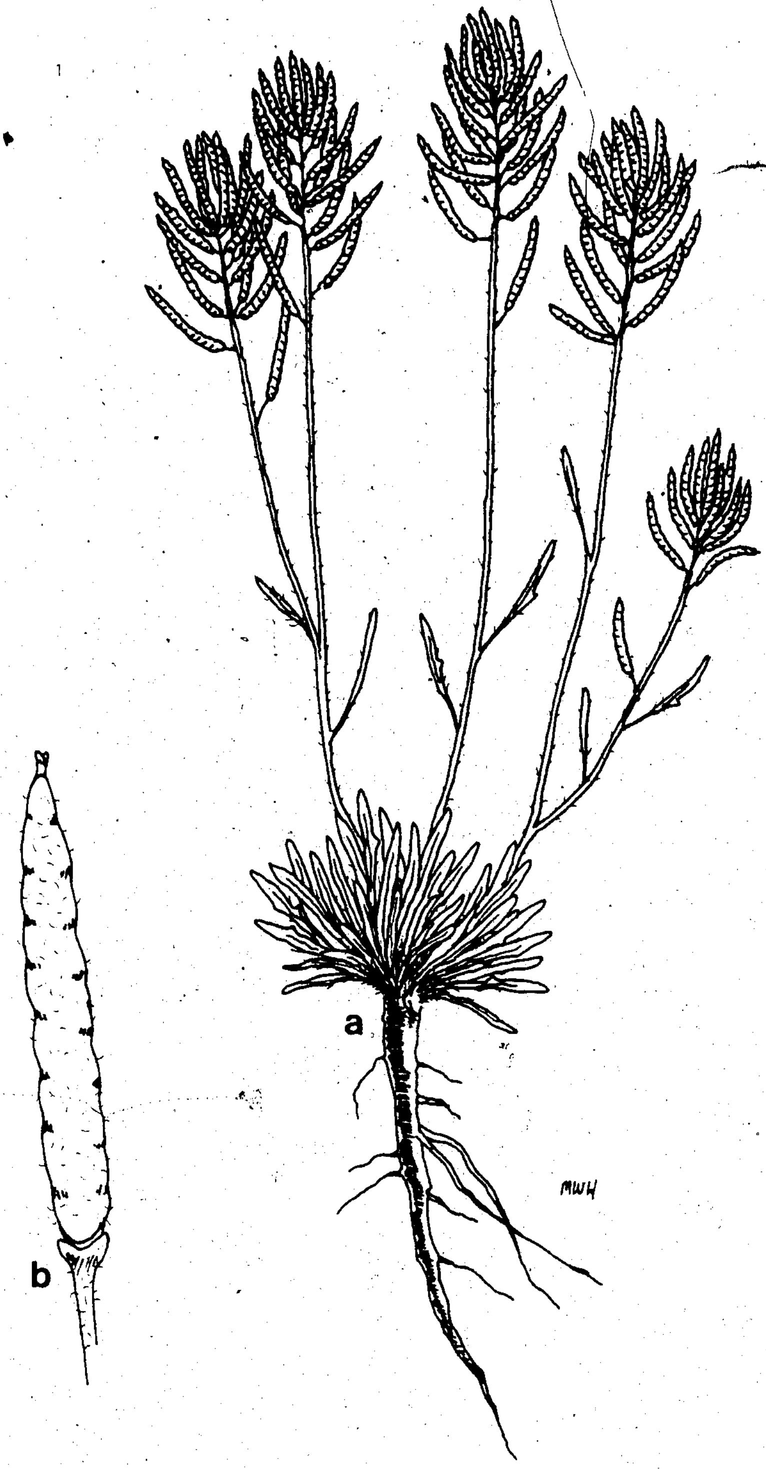
The section *Braya* is represented in North America by a single species, *B. linearis* Rouy.

Because the name of Turczaninow's section *Eubraya* contravenes Article 21 of the International Code of Botanical Nomenclature (1978), I have adopted the section name "*Braya*" in accordance with Article 22 of the Code. The type species is automatically the same as the type species of the genus.

Braya linearis Rouy, Illustr. pl. Europ. rar. XI:84, Tab. CCLIV. (1899) Figure 15.

Plants perennial from a taproot, (4)7 - 14(18)cm tall; caudex simple or branched; stems 1 to several, erect, mainly simple (occasionally branched), leafy, usually deep purple,

Figure 15. Illustration of *Braya linearis*; a., entire plant (natural size); b., silique (x 6).


a
b
MWH

moderately pubescent with mostly bifurcate appressed hairs; basal leaves linear to linear-spatulate, obtuse, dentate with 1 or 2 teeth per side or entire, 5 - 30 mm long, 0.5 - 2.0(3.0)mm broad at widest point, green to deep purple, glabrous to sparsely pubescent with bifurcate and simple hairs; cauline leaves 1 - 4 per stem, similar to basal leaves, but often narrowed at the base to form an indistinct petiole; flowers several, arranged in a dense capitate raceme; pedicels spreading-erect, 0.5 - 2.0 mm long in flower, 1.0 - 4.5 mm long in fruit, pubescent; sepals 1.8 - 2.8 mm long, 1.0 - 1.4 mm broad, obtuse, green to purple-tinged with a scabrous margin, glabrous to lightly pubescent with simple and bifurcate hairs; petals 2.5 - 3.5(4.0) mm long, 1.3 - 2.0 mm broad, white or purple-tinged, especially the claw; fruiting raceme densely compact to elongated; siliques linear, cylindrical, straight or often somewhat curved, more or less torulose, (5)9 - 12(14) mm long, 0.9 - 1.3 mm wide, erect or ascending, deep purple to greenish, glabrous to lightly pubescent with simple and sessile bifurcate hairs; style 0.3 - 0.5 mm long, stout; stigma weakly bilobed to entire; seeds 0.8 - 0.95 mm long, 0.35 - 0.55 mm wide, uniseriate to weakly biseriate.

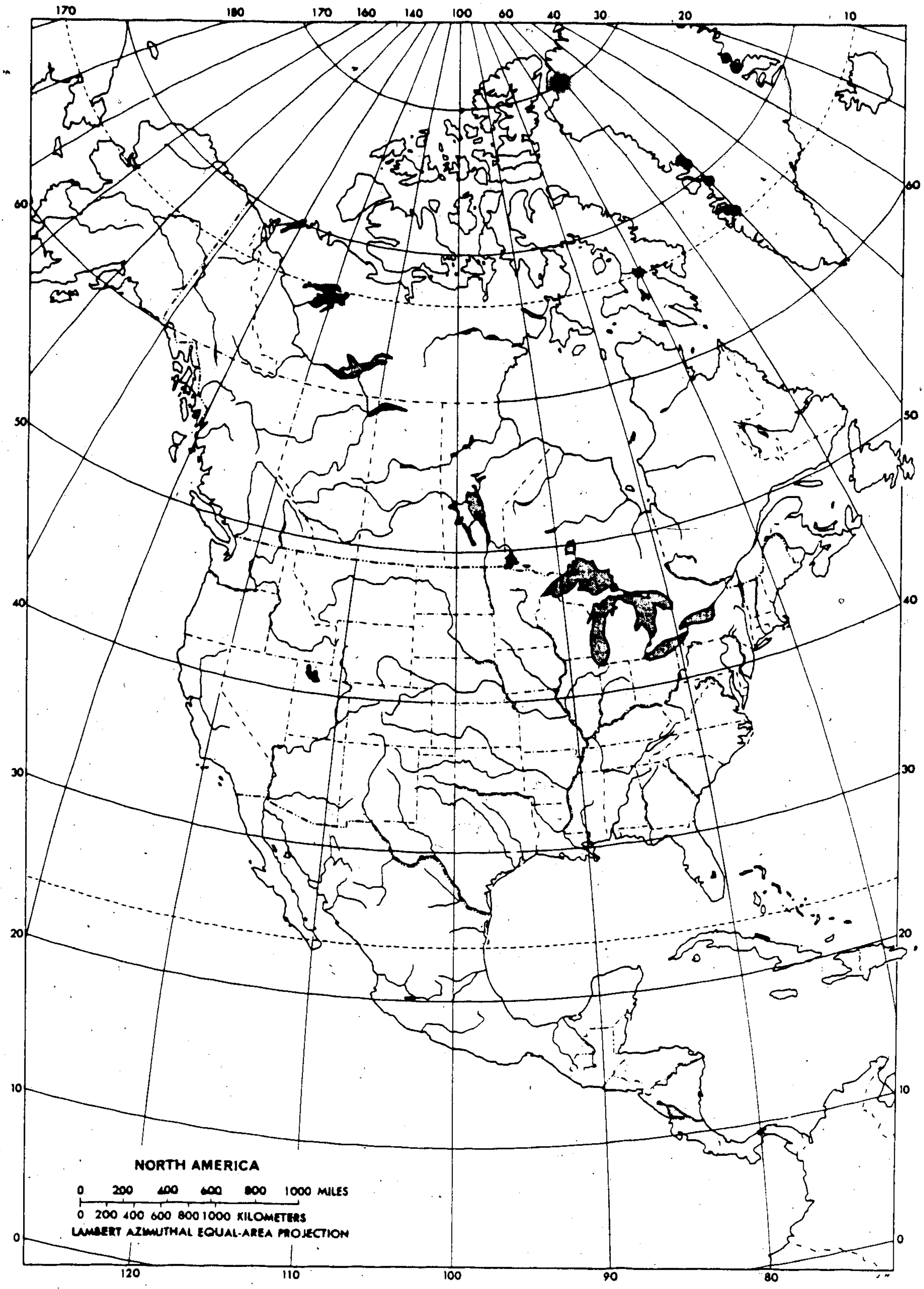
Dry or moist calcareous soils, and alkaline clays and sands at margins of evaporation pools on riverbank terraces and moraines. Western Greenland between 66° - 72° N lat., eastern Greenland between 72° - 74° N lat., and northern Scandinavia. Figure 16.

N=21, 2n=42.

Type: Norway, western Finmark, île Huko, *J.-M. Norman s.n.*, LY (holotype), photo in Rouy l.c.!

Braya linearis extends from the west and east coasts of Greenland to northern Scandinavia. The species is apparently very closely related to *B. alpina* of Europe. Both of these species are probably of hybrid origin; it appears that the species of section *Braya* most likely arose through hybridization between members of the sections *Platypetalum* and *Sisymbriastrum*.

Figure 16. Distribution of *Braya linearis* in North America.


NORTH AMERICA
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
170
180
170
160
140
100
60
40
30
20
10
60
50
40
30
20
10
0
120
110
100
90
80

Braya linearis tends to look more like *B. humilis*, and *B. alpina* more like *B. glabella*. Esterase isozyme studies of *B. linearis* indicate a closer relationship to *B. glabella* than to *B. humilis*. This contradictary morphological and enzyme evidence suggests the intermediate nature of *B. linearis*.

Despite the somewhat intermediate appearance of *Braya linearis*, it can usually be readily distinguished in the field from both *B. glabella* and *B. humilis*.

Representative specimens: **GREENLAND:** Ingnerit Fjord, Magdlâq, 71° 7′ N., *M.P. Porsild & R.T. Porsild s.n.* (MT, CAN); Gem. Umanak: Vorzugsweise N-geneigte Hänge S über Marmorilik, *J. Poelt & H. Ullrich 55/83* (ALTA); Sondre Stromfjord, ca. 3 km E of airfield along river, *J.G. Harris 1765* (ALTA); Sondre Stromfjord, ca. 2.5 km E of airfield along river on old riverbank terrace, *J.G. Harris 1790* (ALTA); Pakitsupilordlia, Qinqua Kujadleg, *Beschel 12107, 12108* (CAN); the S coast of Andrée Land, 73° 18′ N 25° 52′ W, *Seidenfaden 434b* (CAN); Ella Isl., Cape Oswald, *T. Sørensen 3577a* (CAN).

Braya sect. **Platypetalum** Turcz., Bull. Soc. nat. Mosc. XV. 2. p. 279. (1842)

Stems scapose (occasionally with a single leaf or leafy bract subtending the lowermost flower or fruit); leaves entire or occasionally with 1 or 2 weak teeth per side, often fleshy; fruit a silique or silicle, ovoid to oblong-lanceolate, 1.25 - 8.0 times longer than broad; septum epidermal cell wall thickenings quite regular; seeds biseriate, or rarely more or less uniseriate.

Type species: *Braya glabella* Richards.

Braya sect. *Platypetalum* corresponds to the *B. glabella* species complex discussed previously in this work. In North America the section is composed of five species and three additional varieties.

Turczaninow (1842) did not designate a type species for any of the three sections he erected in *Braya*, necessitating the designation of a type. He described *Braya* sect. *Platypetalum* as having oval-oblong siliques and listed *Platypetalum purpurascens*, *P. dubium*, and *B. rosea* as members of the section. It is clear that Turczaninow did not have a clear understanding of the relationship between *P. purpurascens* and *B. glabella* and of the nature of the siliques in this group — he included *B. glabella* in his section *Eubraya* (along with *B. alpina*) on the basis of the "linear-elongate" siliques, an inaccurate description of the siliques of both *B. glabella* and *B. alpina*. It is now obvious that *B. glabella* and *B. alpina* are very different from each other, and that *B. glabella* and *P. purpurascens* are conspecific. *Braya glabella* is therefore the oldest legitimate species in this section and the obvious choice to serve as the type species.

Key to the North American species of *Braya* sect. *Platypetalum*

1a. Fruit a silicle, the length 1 - 2 times greater than the width; stems erect and the petals longer than 4.7 mm *or* stems decumbent to prostrate and the petals shorter 2

1b. Fruit a silique or long silicle, the length 2.5 - 8 times greater than the width; stems erect or ascending (rarely decumbent to prostrate) *and* the petals mostly shorter than 4.7 mm 3

2a. Petals 4.7 - 6.6 mm long, 3.0 - 5.1 mm broad; style 1.25 - 2.0 mm long, slender; stems erect; plants of Mackenzie River Delta region .... *B. pilosa*

2b. Petals 2.0 - 3.7 mm long, 1.0 - 1.5 mm broad; style 0.25 - 0.75 mm long, stout; stems decumbent to prostrate; plants of northern Greenland and northern and western Canadian Arctic Archipelago .... *B. thorild-wulffii*

3a. Siliques lance-subulate; the margin of the septum very broadly expanded at the base and forming a sack-like pouch enclosing the base of the lowermost seed in each locule; seeds few, arranged more or less in a single row 4

3b. Siliques oval-elliptic to oblong-lanceolate; the margin of the septum expanded, or not at all expanded, at the base, but never forming a sack-like pouch around the lowermost seed; seeds few to several, arranged more or less in 2 rows .... *B. glabella*

4a. Petals 2.8 - 3.7 mm long, 1.0 - 1.3 mm wide, not distinctly divided into blade and claw; siliques pubescent .... *B. fernaldii*

4b. Petals 3.7 - 4.8 mm long, 1.5 - 2.3 mm wide, distinctly divided into blade and claw; siliques glabrous (or essentially so)... *B. longii*

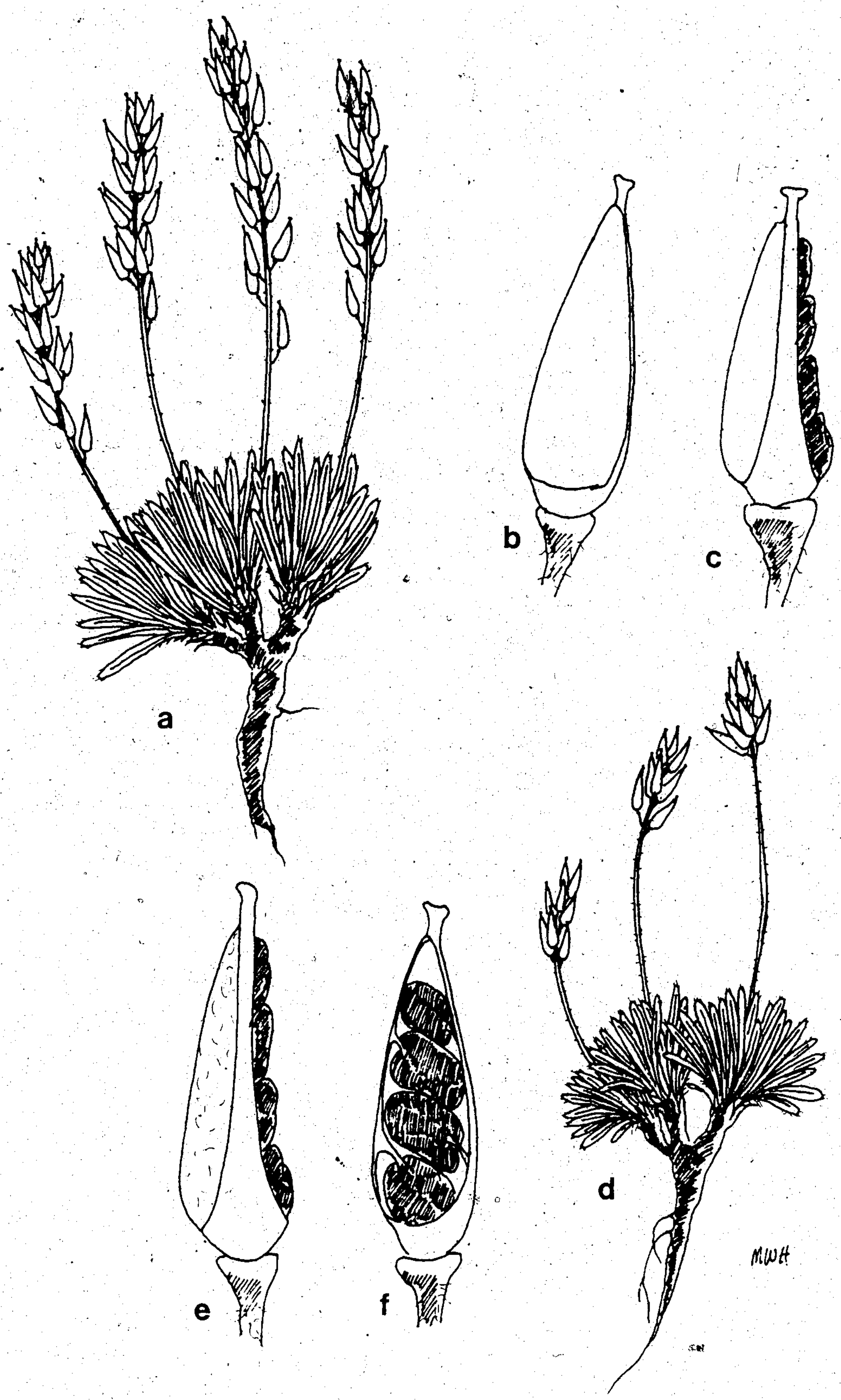
Braya fernaldii Abbe, Rhodora 50:12. (1948) Figure 17.

B. americana (Hook.) Fern., Rhodora 28:203. (1926) in part

B. purpurascens var. *fernaldii* (Abbe) Boivin, Le Natur. Canadien 94, p. 646. (1967)

Plants perennial from a taproot; caudex simple in younger plants but becoming multi-branched with age; stems 1 to many, erect, scapose (occasionally with a single leaf or leafy bract subtending the lowermost flower or fruit), 2.0 - 7.0 (10.0) cm tall, moderately to densely pubescent with bifurcate and simple hairs, often purple or purple-tinged; leaves basal, entire, narrowly spatulate-oblanceolate, obtuse, (5) 10 - 30 (40) mm long, 1.0 - 3.0 mm broad at widest point, sparsely ciliate along lower margins, green to purple-tinged; leaf bases membranous and broadly expanded near point of attachment; flowering inflorescence densely capitate; sepals 2.0 - 2.6 mm long, 1.0 - 1.4 (1.5) mm wide, obtuse, sparsely pubescent with simple hairs or glabrous, green or purple-tinged, with a scarious margin; petals 2.8 - 3.7 (4.0) mm long, (0.85) 1.0 - 1.3 mm wide, gradually and indistinctly divided into blade and claw, white or rose-purple; fruiting inflorescence dense and congested with overlapping siliques, capitate or elongated; pedicels 1.0 - 2.6 mm long, erect-ascending; siliques lance-subulate, (3.6) 4.0 - 7.0 mm long, (0.7) 1.0 - 1.5 (1.7) mm wide at the widest point, densely to moderately pubescent with bifurcate and simple hairs; septum margins broadly expanded at the base, encircling the base of the silique and forming a sack-like pouch around the bottom of the lowermost seed in each locule; style (0.55) 0.65 - 1.0 (1.2) mm long; stigma narrow or broad, bilobed to entire; seeds (0.9) 1.0 - 1.3 mm long, (0.4) 0.5 - 0.65 (0.75) mm broad, more or less uniseriate.

Figure 17. Illustration of *Braya longii* and *B. fernaldii*; a. *B. longii* (natural size); b. silique, dorsi-ventral view (x 7); c. silique, lateral view (x 7); d. *B. fernaldii* (natural size); e. silique, lateral view (x 9); f. silique, dorsi-ventral view (x 9).


a
b
c
d
e
f
MWH

Limestone barrens. Northwestern Newfoundland. Figure 18.

2n=56.

Type: Newfoundland, Pistolet Bay, boggy depressions in limestone barrens, Cape Norman, 18 July 1925, *Wiegand, Griscom & Hotchkiss 28434*, GH! (holotype), PH! Figure 19.

Braya fernaldii Abbe is one of two closely-related northwestern Newfoundland endemics. *Braya fernaldii* and *B. longii* share a number of attributes that separate them from the other members of the *B. glabella* species complex. Both species have short, narrow fruits densely crowded into congested racemes (the apparent congestion is accentuated by the arrangement of the fruits; they are erect-ascending, almost appressed to the scape, and overlapping those above); both have short, narrow, lance-subulate siliques with more or less uniseriate seeds; and both have a unique silique septum margin, broadly expanded, almost winged, at the base, encircling the base of the lowermost seed in each locule in a sack-like pouch and contributing to the lance-subulate shape of the siliques in lateral as well as dorsiventral view (see Figure 17).

Braya fernaldii differs from *B. longii* in the shorter, narrower petals, which are not separated into a distinct blade and claw, and in the fairly densely pubescent siliques.

Fernald (1926), mainly on the basis of style length, felt that *Braya fernaldii* was conspecific with Hooker's (1830) *B. alpina β americana* of Alberta, and proposed the new combination *B. americana* (Hook.) Fern. for the Alberta and Newfoundland populations. Abbe (1948) subsequently pointed out the differences between the Alberta and Newfoundland plants and the obvious interrelatedness of Fernald's *B. longii* and *B. americana*, and proposed the epithet *B. fernaldii* in recognition of Fernald's contributions to our understanding of the Newfoundland flora.

Representative specimens: **CANADA: NEWFOUNDLAND:** Cooks Harbour (about 3.5 miles south of), *E. Rouleau & P. Morisset 8519* (MT); Burnt Cape, Pistolet Bay, *J.G. Harris 1733* (ALTA); Cape Norman, *J.G. Harris 1736* (ALTA); Straits of Belle Isle, one mile back

Figure 18. Distribution of *Braya fernaldii*.

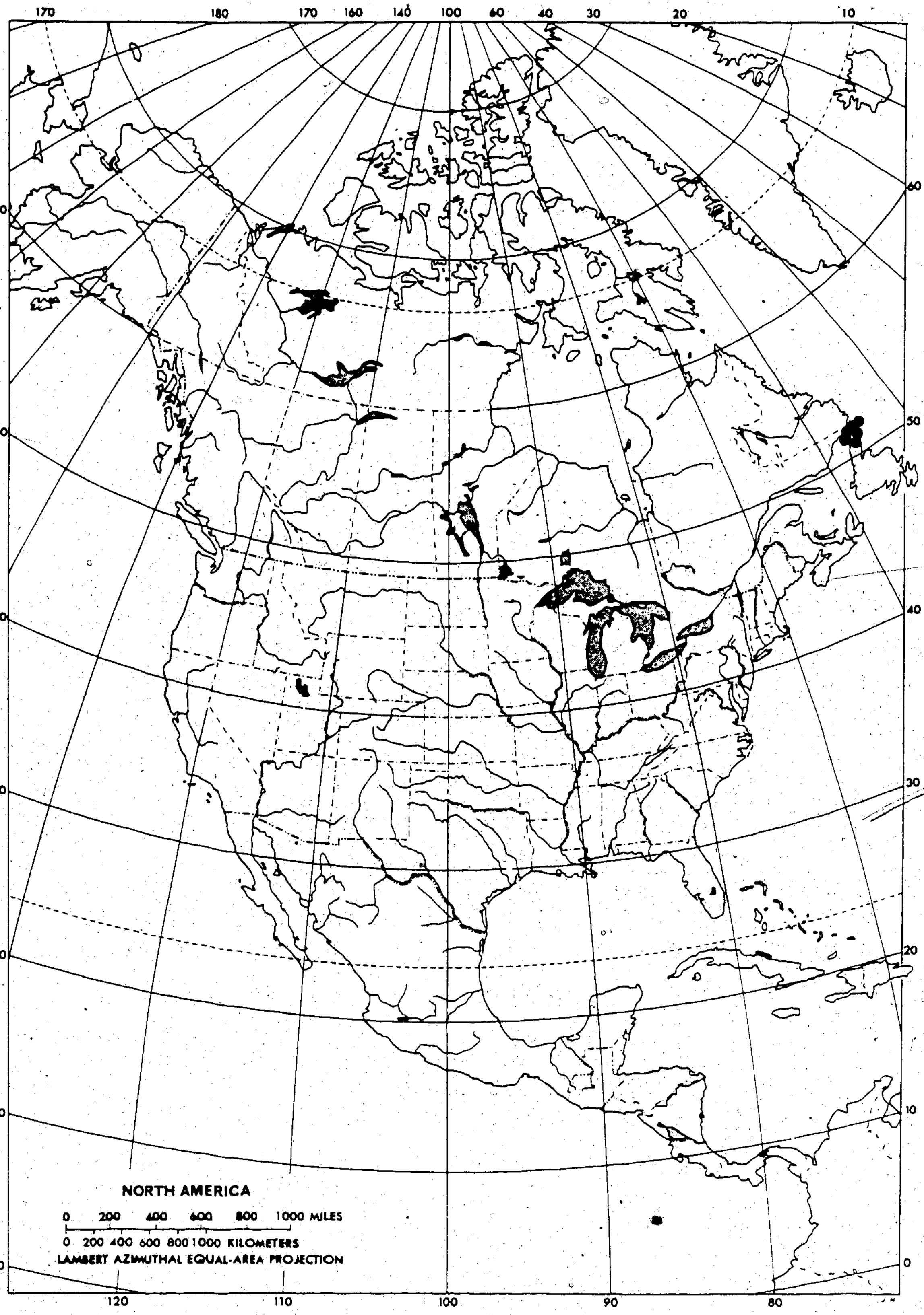

NORTH AMERICA
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
170
180
170
160
140
100
60
40
30
20
10
60
50
40
30
20
10
0
120
110
100
90
80

Figure 19. Type specimen of *Braya fernaldii* Abbe.

PISTOLET BAY

No. 28433

Braya americana (Hook.) Fern.

[illegible] rocks and [illegible] Norris

[illegible]

July [illegible]

ANNOTATION LABEL

ERNST C. ABBE 194

TYPE

Braya Fernaldii Abbe, n. sp.

E. C. A. 1947

FLORA OF NORTHWESTERN NEWFOUNDLAND

PISTOLET BAY

No. 28434

Braya americana (Hook.) Fern.

Boggy depressions in limestone [illegible]

[illegible]

July [illegible]

of Savage Cove, *M.L. Fernald & B. Long 28428* (GH, CAN, DAO-photo), *M.L. Fernald, A.S. Pease & B. Long 28438* (GH); St. Barbe Bay, limestone barrens near Ice Point, *K.M. Wiegand, F.A. Gilbert, Jr. & N. Hotchkiss 28429* (GH); Straits of Belle Isle, limestone barrens back of Big Brook, *M.L. Fernald & B. Long 28431* (PH); Pistolet Bay, northern half of Burnt Cape, *M.L. Fernald, K.M. Wiegand, A.S. Pease, B. Long, L. Griscom, F.A. Gilbert, Jr. & N. Hotchkiss 28432* (PH); Pistolet Bay, Cape Norman, *K.M. Wiegand, L. Griscom & N. Hotchkiss 28433* (GH); Straits of Belle Isle, limestone gravel barrens, Boat Harbor, *M.L. Fernald, K.M. Wiegand & B. Long 28435* (GH, PH); Straits of Belle Isle, swale near mouth of brook, Watts Bight, *A.S. Pease, L. Griscom, F.A. Gilbert, Jr. & N. Hotchkiss 28436* (GH); Straits of Belle Isle, gravelly limestone barrens, Four Mile Cove, *M.L. Fernald, K.M. Wiegand & B. Long 28437* (GH); Pistolet Bay, Cape Norman, *K.M. Wiegand & B. Long 28440* (GH).

Braya glabella Richards., Bot. App., Franklin's Narr. Jour. Arctic Sea, ed. 1, p. 743. (1823)

Plants perennial from a thick taproot; caudex simple or branched; stems 1 to many, erect or ascending (rarely decumbent to prostrate), scapose (often with a single leaf or leafy bract subtending the lowermost flower or fruit), (1.2) 3.5 - 17.0 (22.7) cm tall, lightly, moderately, or densely pubescent with simple, bifurcate, or trifurcate hairs, often purple or purple-tinged; leaves basal, entire or sometimes weakly toothed with 1 or 2 teeth per side, linear-oblanceolate to broadly spatulate, obtuse, often somewhat fleshy, (4) 8 - 60 (79) mm long, (0.3) 0.6 - 4.0 (6.0) mm wide at widest point, sparsely to moderately pubescent with simple or bifurcate hairs, often with a tuft of long simple hairs at the apex, green to deep purple; leaf bases membranous and broadly expanded near point of attachment; flowering inflorescence mostly capitate; sepals (1.6) 1.9 - 3.7 mm long, (0.7) 1.0 - 2.0 mm wide, obtuse, sparsely to densely pubescent with simple, or occasionally bifurcate hairs or glabrous, green or purplish, with a scarious margin; petals (2.1) 2.4 - 4.5 (4.7) mm long, (0.75) 1.0 - 3.0 (3.2) mm wide, abruptly and distinctly divided into blade and claw or gradually and only indistictly divided into blade and claw; white to purple-tinged; fruiting inflorescence dense and capitate to scattered and elongate; pedicels (0.9) 1.9 - 7.5 (8.6) mm long, ascending-erect to spreading; siliques oval-elliptic, oblong-cylindrical or narrowly lanceolate, somewhat torulose or not at all, (3.0) 5.0 - 12.5 (15.0) mm long, (0.8) 1.1 - 3.0 (3.6) mm wide at widest point, sparsely to densely pubescent with simple, bifurcate, or occasionally trifurcate hairs or glabrous, green to dark purple; style (0.35) 0.5 - 1.6 (2.0) mm long; stigma narrow or broad, bilobed to entire; seeds (0.75) 0.9 - 1.6 (1.7) mm long, 0.4 - 0.8 (0.9) mm broad, biseriate.

Braya glabella Richards. is perhaps the most poorly understood *Braya* species. It is extremely variable from one population to another and, to some extent, even within populations. Previous authors have split the species into several taxa on the basis of differences in silique shape and pubescence, style length, stigma breadth and lobing, leaf shape and dentation, and inflorescence length. While it is true that many populations of *B. glabella* appear to be strikingly distinct on the basis of these attributes, when a large number of specimens are examined from throughout the entire range of distribution the perceived morphological gaps quickly blur into a bewildering array of overlapping forms.

Richardson's original collections of *Braya glabella* and the original collections of Brown's *Platypetalum purpurascens* happen to fall near the opposite edges of the spectrum of diversity in the species. It is not at all surprising that Brown (1823, 1824), as well as the overwhelming majority of subsequent authors, recognized the two taxa as separate and distinct species; indeed, the type specimens of *B. glabella* and *P. purpurascens* appear to be very different. But, when the entire range of variation is observed, the two morphological forms flow together to the point that it is impossible to draw a sharp boundary line between them.

Abbe (1948) commented on the range of variation to be found in this group even within a single population. He collected 58 individuals from a population at Richmond, P.Q. (E.C. & L.B. Abbe 3819) and found that the plants ranged from specimens that fell very nicely within the range of variation of "typical" *Braya purpurascens* as described by Brown (1823) and illustrated by Hooker (1830, Tab. XXIII) "...into the robust type of specimen from Southampton Island...". Had Abbe had access to authentic fruiting material of *B. glabella*, he almost certainly would have realized that the robust specimens from Southampton Island (for example, Malte 120677) are near perfect matches for "typical" *B. glabella*. This, in fact, appears to be the pattern in the group; specimens from the North American high arctic are more or less *B. purpurascens*-like, and plants from lower arctic, sub-arctic, and montane regions are generally more *B. glabella*-like, but it is almost always possible to find plants in any population that look somewhat out of place and approach, morphologically, plants of the alternate morphological form. The populations on and near the northern coast of continental North America appear to be in the zone of overlap, and it is here that the greatest difficulty is encountered in attempting to segregate specimens into one or the other of the two forms. This is especially true in disturbed areas (such as bulldozed areas near DEW line sites and around the Prudhoe Bay oilfields, and along roadways), where normally inbreeding, isolated populations come together as they move onto the newly available habitats, gene flow again begins to take place, and plants from the same population may exhibit an extreme range of diversity. A collection from Prudhoe Bay, Alaska (Welsh 20769, BRY) serves as an excellent example (see Figure 20). The collection consists of three fruiting specimens, all remarkably different from each other. The upper left plant is quite tall with a greatly elongated inflorescence (characteristics usually attributed to *B. glabella*) and oval-elliptic fruits (a characteristic usually attributed to *B. purpurascens*); the upper right plant is much shorter and less erect, with very broad, extremely bilobed stigmas; the lower left plant has very erect stems, a more condensed fruiting inflorescence, oblong to oblong-lanceolate siliques, and exceptionally long styles with much narrower, less bilobed, stigmas.

On the basis of morphological and chemical evidence, it is difficult to justify the recognition of more than one species in this very plastic group, but it *does* seem desirable to divide the species into three rather weak varieties. Many populations will be readily separable into one of these three varieties, but other populations will undoubtedly defy unequivocal placement, particularly those from areas where the ranges of the varieties meet.

Figure 20. Photograph of S.L. Welsh 20769 (BRY).

224806

BRIGHAM YOUNG UNIVERSITY
HERBARIUM
PROVO, UTAH

Alaska, USA [illegible]

Braya glabella Richardson

T11N, R15E, Sec 20, Prudhoe Bay, ca 1 [illegible]
ENE of SeaHorse Airport

Gravelly bluffs, marginal Sagavanirktok River

S L Welsh
20764 5 August 1981

HERBARIUM OF BRIGHAM YOUNG UNIVERSITY
PROVO, UTAH

Key to the varieties of *B. glabella*

1a. Siliques oblong to narrowly oblong-lanceolate, 3.5 - 8.3 times longer than broad; mature fruiting inflorescences often loosely elongated; plants of lower arctic, sub-arctic, and montane distribution .... var. *glabella*

1b. Siliques oval-elliptic to oblong-elliptic (rarely broadly oblong-lanceolate), 2.5 - 3.7 times longer than broad; mature fruiting inflorescences often densely compact; plants of high arctic distribution 2

2a. Stems ascending to erect; leaves usually somewhat fleshy, at most 4 mm wide; siliques 5 - 10 mm long; styles 0.5 - 1.2 mm long; plants of wide distribution in high arctic ....var. *purpurascens*

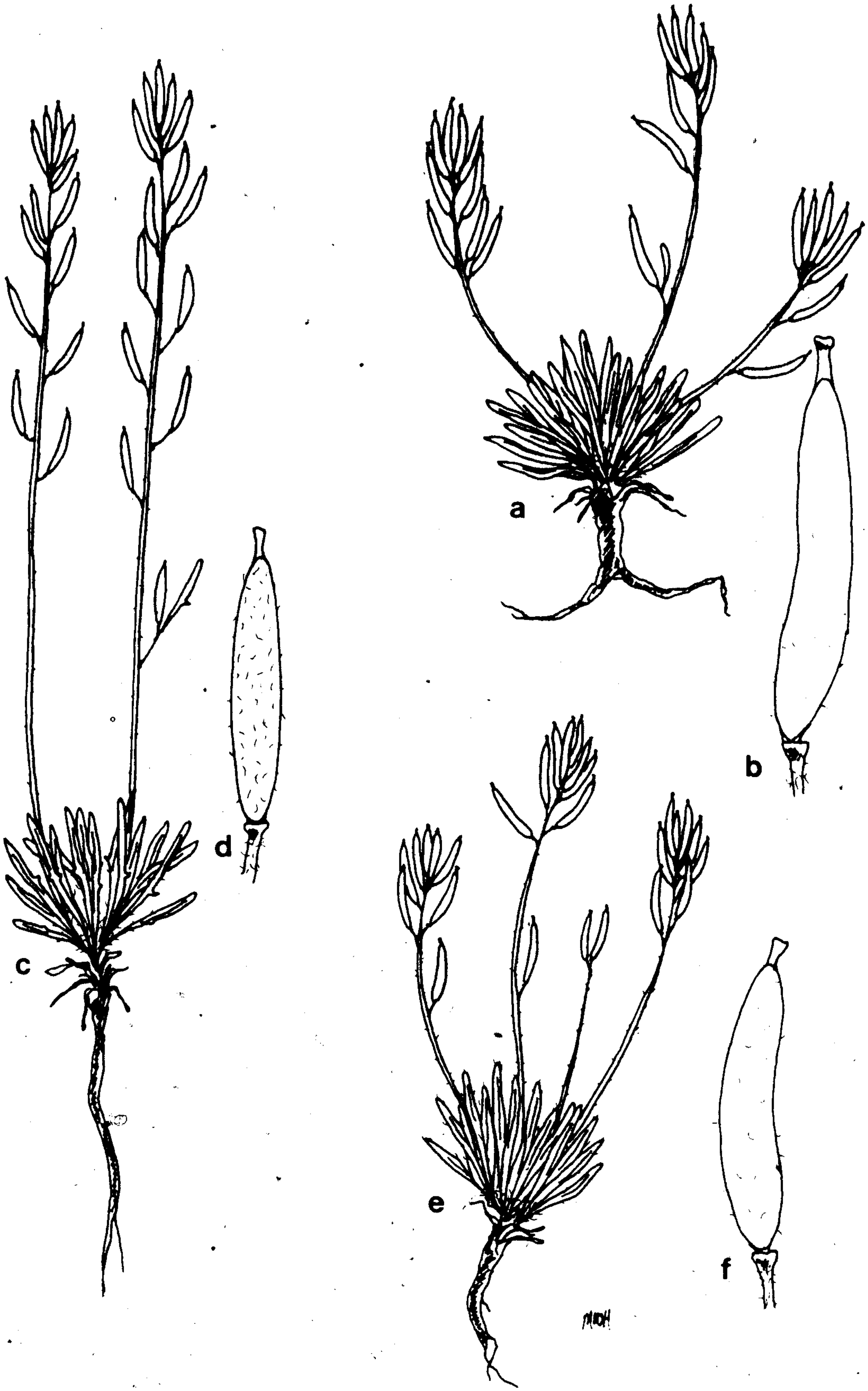
2b. Stems decumbent to prostrate (occasionally weakly ascending); leaves not fleshy, up to 6 mm wide; siliques 8 - 12 mm long; styles 0.8 - 1.8 mm long; plants of northern Ellesmere Island .... var. *prostrata*

Var. **glabella** Figure 21.

B. alpina var. *glabella* (Richards.) Wats., Bibl. I. N. Amer. Bot. p. 51. (1878)
B. alpina var. *americana* (Hook.) Wats., Bibl. I. N. Amer. Bot. p. 51. (1878)
B. alpina β americana Hook., Fl. Bor.-Am. I. p. 65. (1830)
B. americana (Hook.) Fern., Rhod. 23:203. (1926) in part.
B. bartlettiana Jordal, Rhod. 54:36. (1952)
B. bartlettiana var. *vestita* Hult., Ark. f. Bot. 7, 1, p. 66. (1968)
B. henryae Raup, Contrib. Arn. Arb. VI. p. 167. (1934)

Plants 4.7 - 17.0 (22.7) cm tall; stems usually erect, sometimes ascending; leaves occasionally with 1 or 2 weak teeth per side; fruiting inflorescence often loosely elongated; siliques oblong to narrowly oblong-lanceolate, 3.5 - 8.3 times longer than broad, often curved.

Figure 21. Illustration of *Braya glabella* var. *glabella*; a., c., and e. entire plants (natural size); b., d., and f. siliques (x 5).


a
b
c
d
e
f

Usually barren, often calcareous, soils and gravels on gravel bars, disturbed sites, lake and sea shores, scree slopes, and solifluction lobes. Southernmost islands of the Canadian Arctic Archipelago south through the Mackenzie and Rocky Mountains to Athabasca Glacier and Cardinal River, Alberta, west to Seward Peninsula, Alaska, east to Hudson Bay. Figure 22.

$2n=56$.

Type: Copper Mountains, Northwest Territories, *Richardson s.n.*, BM! (holotype). Figure 23.

An admittedly very heterogeneous taxon, var. *glabella* has sometimes been divided into two or three species on the basis of slight differences in silique shape and structure.

Hooker (1830) felt that plants from the Rocky Mountains were only infraspecifically distinct from the European *Braya alpina* and erected the infraspecific taxon *β americana* under that species. Hooker based his *β americana* on the longer styles found in the North American plants. It is now clear that *B. glabella* differs from *B. alpina* in several fundamental attributes, as has been discussed previously in this work, and that the two species are only distantly related.

Raup (1934) described *Braya henryae* from plants collected in northern British Columbia (Mrs. J.N. Henry 347, PH!), distinguishing it from other populations on the basis of the long siliques, conspicuously broader at the base, and the long styles. While it is true that Raup's type material looks noticeably different from most other *B. glabella* populations, these attributes — style length, silique length, and even silique shape — are extremely variable in the group and show very little correlation with each other. Many populations, in an apparently random distribution, may show one or the other of *B. henryae*'s distinguishing attributes, and a few scattered populations (Harris 1569, ALTA!; Strutz 2027, BRY!; Williams 3271, BRY!) are near perfect matches with the type material of *B. henryae*. But esterase profiles show that these isolated populations are always most closely related to other nearby non-*B. henryae*-like

Figure 22. Distribution of *Braya glabella* var. *glabella* in North America.

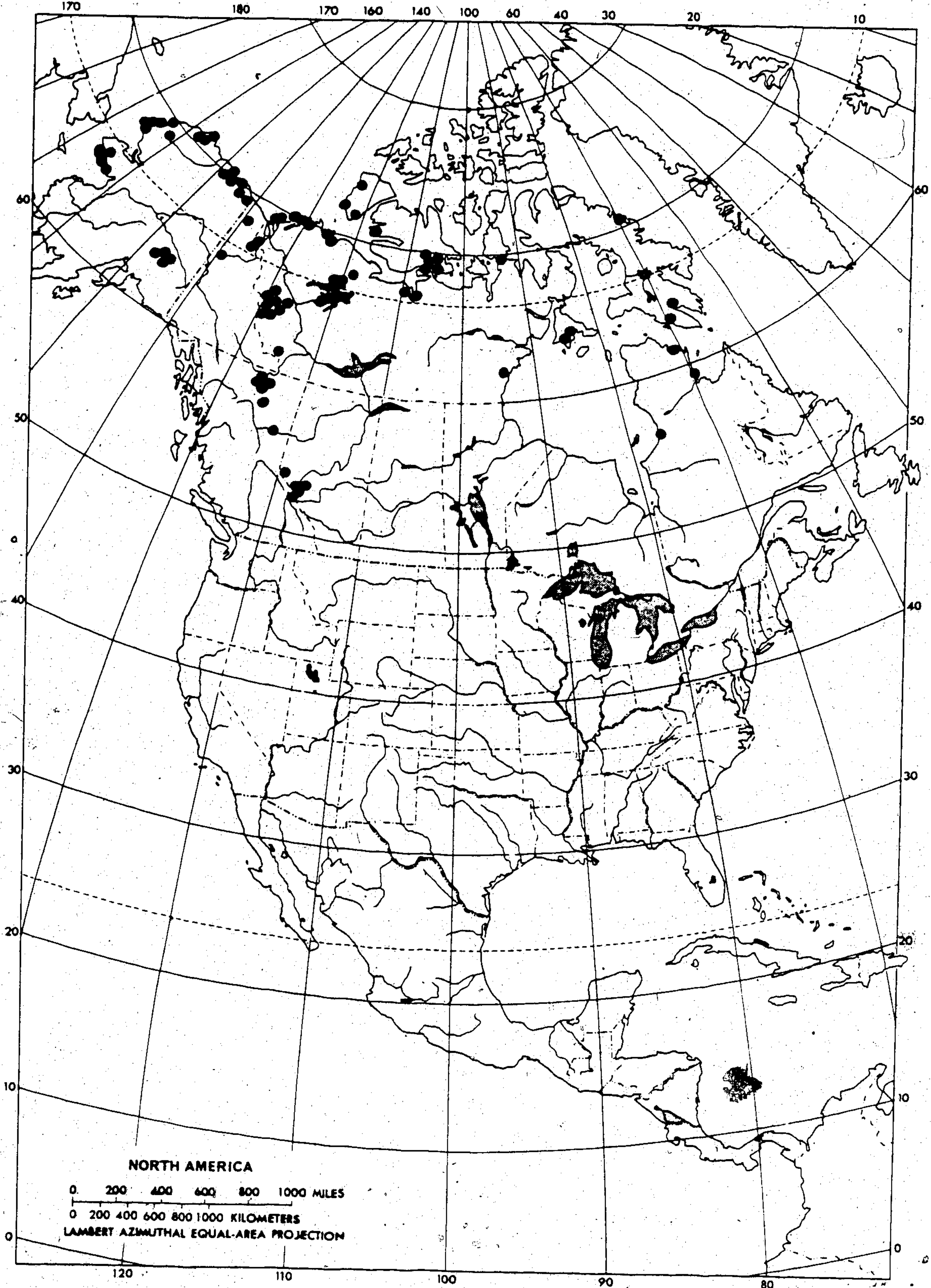
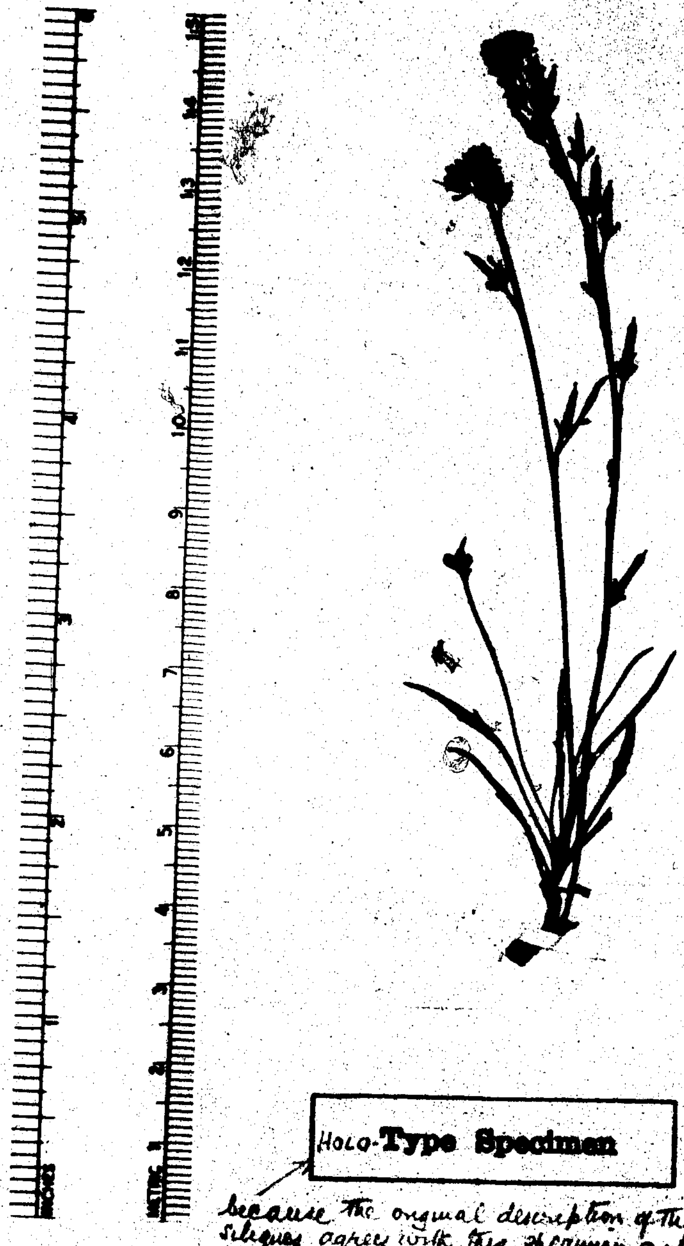

NORTH AMERICA
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
170
180
170
160
140
100
60
40
30
20
10
60
50
40
30
20
10
0
120
110
100
90
80

Figure 23. Type specimen of *Braya glabella* Richards. var. *glabella*.



HOLO-**Type Specimen**

because the original description of the siliques agrees with this specimen only.

[A. J. Wilmott

B. glabella populations rather than to each other.

Similarly, Jordal (1952) described *Braya bartlettiana* from a small population of plants from the Brooks Range, Alaska (L.H. Jordal 2291, MICH!) on the basis of the very indistinct septum midnerve and the glabrous siliques, both highly variable characters of very little taxonomic value in the group.

The supposedly distinguishing attributes of *Braya henryae* and *B. bartlettiana* are within the normal genetic diversity of *B. glabella* var. *glabella* and appear randomly in isolated populations throughout the range of the variety. It is not at all unexpected or surprising that populations of plants in a genus such as *Braya*, with a distribution pattern and breeding system of small, scattered and isolated, self-pollinating populations, likely often founded by one or a few individuals, would show only a part of the variation of the entire species or variety. Attempting to provide epithets for each of these small, variant populations makes little practical sense.

Representative specimens: **CANADA: ALBERTA:** Persimmon Range, Wilderness Prov. Park, *J.G. Packer 3381* (ALTA); Cardinal River, ca. 19 km due SSE of Cadomin, *J.G. Harris 1555* (ALTA), *G. Pegg 3352* (ALTA); Cardinal Divide, ca. 12 mi S of Cadomin, *M.G. Dumais & G. McPherson 5143* (ALTA, CAN), *M.G. Dumais & J. Traquair 6391* (ALTA); Prospect Mtn., 10 mi SW of Cadomin, *P. Mortimer 305* (ALTA); Cataract Creek near Pinto Lake, *S. Brown 1459* (PH); Jasper Natl. Park, Athabasca Glacier, next to small pond, *J.G. & M. Harris 1569* (ALTA); **BRITISH COLUMBIA:** pass NE of Robb Lake, *Mrs. J.N. Henry 347* (PH); mountain near source of Akie River, *Mrs. J.N. Henry 590* (PH); Alaska Hwy., Summit Mt., *A.E. Porsild & A.J. Breitung 11946* (CAN), *H.M. Raup & D.S. Correll 10482, 10594* (CAN); Alaska Hwy., W end of Summit Lake, *J.A. Calder & I. Kukkonen 27446* (DAO); Racing River at mi 418 Alaska Hwy., *J.A. Calder & J.M. Gillett 24671* (DAO); **NORTHWEST TERRITORIES:** Mackenzie Mountains, near Little Divide Lake, *W.J. Cody 16701, 16577, 16653* (DAO); Mackenzie Mountains, near June Lake, *W.J. Cody 19863, 17061, 17106, 17238, 17452* (DAO); Mackenzie Mountains, 10 mi NE O'Grady Lake, *W.J. Cody 16953* (DAO); Mackenzie Mountains, mi 44 Canol Rd., *W.J. Cody & R.L. Gutteridge 7720* (DAO); Mackenzie Mountains, Plains of Abraham, *W.J. Cody 19080* (DAO); Mackenzie Mountains, Carcajou Lake, *W.J. Cody & F.M. Brigham 20507* (DAO); Mackenzie Mountains, Mirror Lake, *W.J. Cody & F.M. Brigham 20413* (DAO); Nahanni Natl. Park, Nahanni Plateau, *G.W. Scotter 23571B* (DAO); Great Bear Lake, N shore of Dease Arm, *A.E. & R.T. Porsild 4698* (ALTA, MT, C, CAN), *4699* (CAN); Rankin Inlet, *J.M. Gillett 15765* (CAN); Cape Dalhousie, 70° 20′ N 129° 55′ W, *A.E. & R.T. Porsild 2760* (CAN, ALTA, C); Tuktoyaktuk Penin., *C.B. Larsen & W.H. Owen 74-4261* (DAO); Sea Coast of Arctic America, *J. Richardson s.n.* (BM, K); Bathurst Inlet, near Goulburn Lake, *G.W. Scotter & S.C. Zoltai 31730* (DAO), *R.E. Miller 220* (CAN); Spence Bay, *D.B.O. Savile 3870* (DAO); Cape Parry Penin., *G.W. Scotter & S. Zoltai 25553, 25904, 25790* (DAO); Atkinson Point, *A.E. & R.T. Porsild 2621* (CAN); Liverpool Bay, Nicholson Island, *A.E. & R.T. Porsild 2889, 2889A* (CAN), *G.W. Scotter 7185* (DAO); Mackenzie River

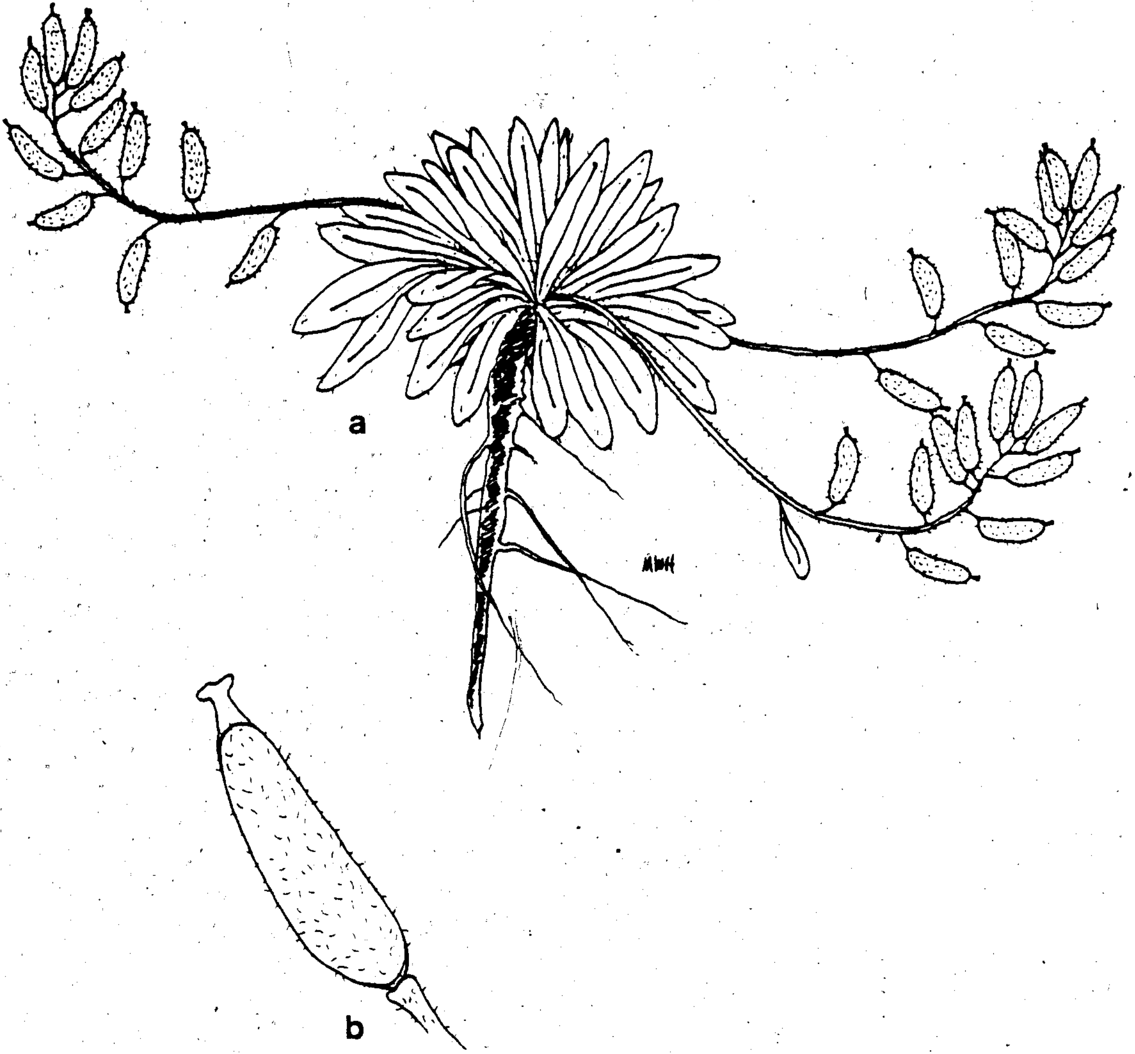
Delta, N end of Richards Island, *A.E. & R.T. Porsild 2229* (CAN, MT), *A.E. Porsild 16828* (CAN, MT); Baffin Island, Lake Harbour, *N. Polunin 1121* (CAN); Baffin Island, Frobisher Bay area, *V.C. Wynne-Edwards 9183* (CAN); Banks Island, 122° 35′ N 71° 12′ W, *S.M. Stirling s.n.* (CAN); Banks Island, Mary Sachs, *J.D. Lambert s.n.* (DAO); Banks Island, Bernard River, *W.J. Maher & S. MacLean 147A, 148-B* (CAN); Victoria Island, Minto Inlet, *Anderson s.n.* (K); Victoria Island, Cambridge Bay, *R. Marris 11802* (BM), *A.E. Porsild 21620, 21619* (CAN), *S. Stephens 1137, 1038, 1051, 1069* (CAN); Victoria Island, vicinity of Holman Island trading post, *A.E. Porsild 17290* (ALTA, CAN); Southampton Island, Air Base, *D.K. Brown, B.R. Irvine & B.A. Oaks 1627* (CAN); Southampton Island, Southampton, *M.O. Malte 120677* (CAN, MT, C); **QUEBEC:** Hudson Bay, Richmond Gulf, S side of Gulf Hazard, *E.C. & L.B. Abbe 3819* (DAO, PH, BM); Wakeham Bay, Hudson Strait, *M.O. Malte 120191* (CAN); SW coast of Ungava Bay, near Tasiujaq, *K.L. MacInnes 5140* (MT); **YUKON:** Ogilvie Mtns., Dempster Hwy. mi 110, *A.E. & R.T. Porsild 23630, 23629, 23628* (CAN); Richardson Mtns., on Yukon-Mackenzie border, *J.A. Calder 34216* (DAO); Richardson Mtns., 5 mi N of Horne Lake, *J.A. Calder 33952* (DAO); ca. 13 mi due W of Sam Lake, *S.L. Welsh & J.K. Rigby 10345* (BRY); U.S.A.: **ALASKA:** Prudhoe Bay, *K. Ostler & B. Welsh 2074* (BRY), *M. Williams 3484* (BRY), *R. Marris 19410, 19350* (BM), *G. Halliday A220/75* (BM); Seward Penin., Teller Rd., mi 44, *M. Williams 3389* (BRY); Seward Penin., Teller Rd., mi 18, Cleveland Creek, *M. Williams 3268, 3271, 3382* (BRY), *A. Strutz 2027, 2092* (BRY); Seward Penin., Teller, *Walpole 1934* (CAN), *A. Strutz 353* (BRY); Seward Penin., Kigluaik Mtns., mi 49 on Nome-Taylor Hwy., *J.G. Harris 1371* (ALTA); Seward Penin., near Bluff, *A.E. & R.T. Porsild 1239* (CAN); Seward Penin., Anvil Mtn., ca. 7 km NNE of Nome, *J.G. Harris 1330, 1332* (ALTA), *E. LePage 23884* (GH), *A. Strutz 1118* (BRY), *S.L. Welsh 5924* (BRY); Seward Penin., Cape Nome, *E. LePage 23824* (GH); about 12 km SE of Cape Sabine on northwest coast, *S.G. Shetler & K.J. Stone 3201* (CAN); Arctic Coast District, Cape Beaufort, *E. Hultén s.n.* (BRY); Ogotoruk Creek, 68° 06′ N 165° 46′ W, *A.M. Johnson 339* (ALTA), *J.G. Packer 2362, 2098* (ALTA), *2098* (DAO); Utukok River, Driftwood Camp, 68° 55′ N 161° 10′ W, *K. Holmen s.n.* (C); Alaska Range, Upper Dry Creek, *L.A. Viereck & K. Jones 5953* (CAN); Donnelly, mi 240 Richardson Hwy., *W.J. Cody & T.J.M. Webster 5859* (DAO); Donnelly Creek Campground, mi 237.9 Richardson Hwy., *A.R. Batten, J.C. Dawe & D.F. Murray 78-75* (DAO); Whistler Creek floodplain, mi 223 Richardson Hwy., *A.R. Batten & J.C. Dawe 78-151* (DAO); Alaktak Half-Moon 3, 70° 45′ N 155° 00′ W, *L.A. Spetzman 2513* (BRY, CAN); Meade River, 70° 40′ N 156° 55′ W, *R.D. & M. Wood 372* (CAN); about 110 km SSW of Point Barrow, *S.G. Shetler & K.J. Stone 3452* (CAN); Arctic Natl. Wildlife Range, Ambresvajun (Last) Lake, *A.R. & C.G. Batten 75-476* (DAO); Kongakut River, 152 mi NNE of Arctic Village, *L.R. Hettinger 291* (ALTA); Bullen, 70° 10′ N 146° 50′ W, *G.W. Argus & W. Chunys 5798* (CAN).

Var. **prostrata** J.G. Harris *var. nov.* Figure 24.

Differt a var. *glabella* et var. *purpurascenti* caulibus prostratis et foliis latioribus tenuioribus.

Stems decumbent to prostrate or weakly ascending, 3.5 - 15 cm tall, moderately to densely pubescent with long simple, and at times bifurcate hairs; basal leaves usually broad and not particularly fleshy, 9 - 45 mm long, 1.5 - 6.0 mm wide, glabrescent with a few scattered,

Figure 24. Illustration of *Braya glabella* var. *prostrata*; a. entire plant (natural size); b. silique (x 4.5).


a
AMH
b

long, simple (or rarely bifurcate) hairs mainly along the margins; leaf bases very broadly expanded, often wider than the leaf blades, membranous; sepals 2.4 - 3.7 (4.0) mm long, (1.0) 1.4 - 2.0 mm wide, glabrescent with a few scattered, long, simple hairs; petals (3.0) 3.5 - 4.7 mm long, 1.6 - 3.0 (3.2) mm wide; siliques oblong-elliptic to broadly oblong-lanceolate, straight or curved, not torulose, (6.8) 8.0 - 12.0 mm long, 2.5 - 3.6 mm wide, sparingly to moderately pubescent with stiff simple or occasionally bifurcate hairs; style 0.8 - 1.8 mm long, stout; stigma capitate to not at all capitate, bilobed to sub-entire; seeds 1.4 - 1.7 mm long, 0.7 - 0.9 mm broad.

Dry or damp sand and silt on barren slopes and plains. Known only from the type locality and nearby areas on northern Ellesmere Island. Figure 25.

2n=56.

Type: Canada, Northwest Territories, Ellesmere Island, Hazen Camp, 81°49′ N 71° 21′ W, "sandy level delta plain, 1 1/2 mi. WSW of Camp", 28 July 1962, *D.B.O. Savile 4764A* DAO! (holotype). Figure 26.

Braya glabella var. *prostrata* is one of three high arctic *Braya* endemics in North America. The variety is, in most instances, readily separable from var. *purpurascens*, its closest relative, on the basis of the decumbent to prostrate stems, the broader, less fleshy leaves, the larger siliques, and the longer styles.

Representative specimens: **CANADA: NORTHWEST TERRITORIES:** Ellesmere Island, Fosheim Penin., Slidre Fjord, *S.D. MacDonald 297* (CAN); Ellesmere Island, Fosheim Penin., 79° 57′ N 85° 02′ W, *P.F. Bruggemann 835* (DAO); Ellesmere Island, Eureka, *P.F. Bruggemann 818* (DAO).

Var. **purpurascens** (R. Br.) J.G. Harris, *comb. nov.* Figure 27.

Basionym: *Platypetalum purpurascens* R. Br., Chloris. Melvill. p. 9 & 50. (1823)

P. dubium R. Br., Chloris. Melvill. p. 9. (1823)

Figure 25. Distribution of *Braya glabella* var. *prostrata*.

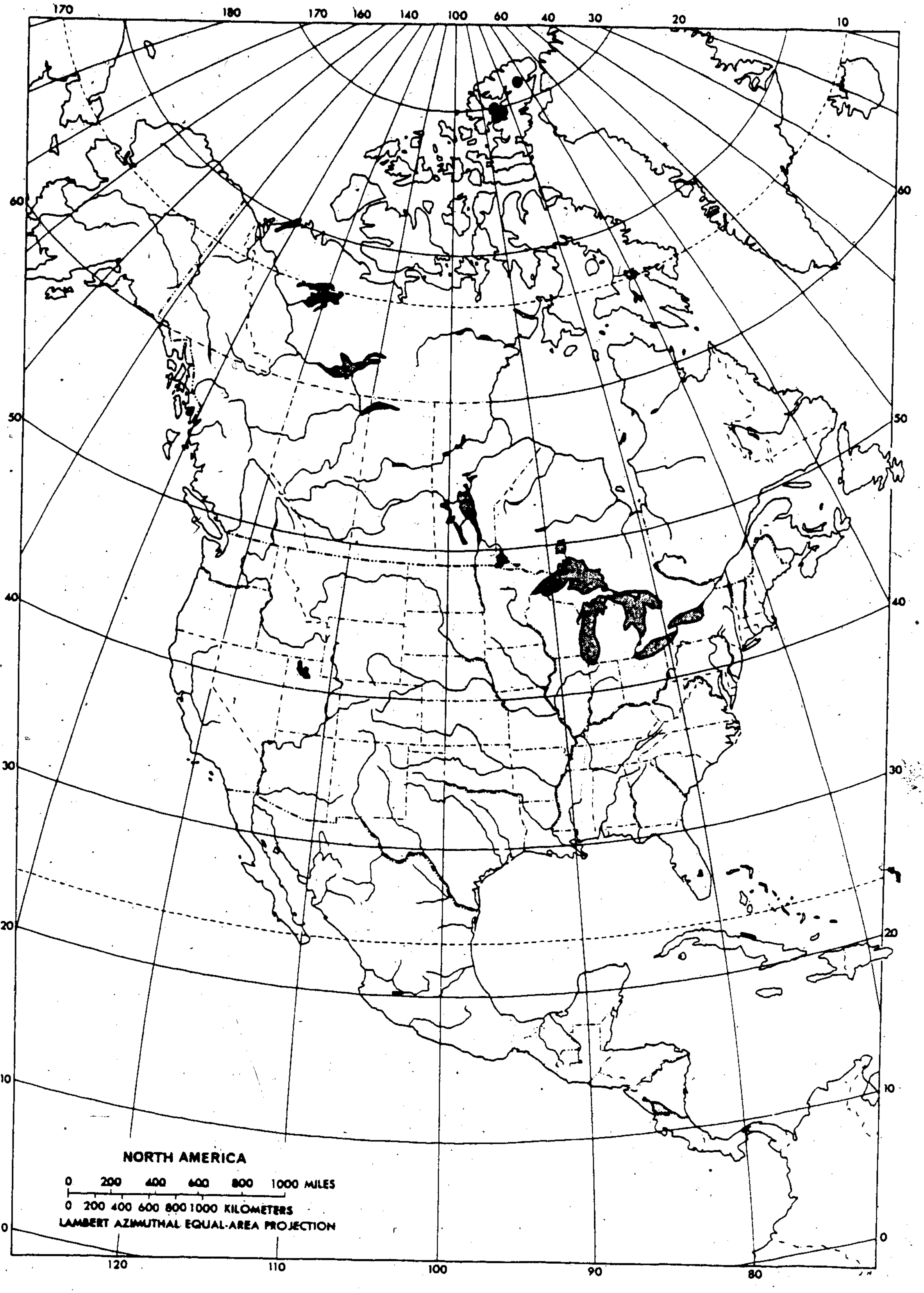

NORTH AMERICA
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
170
180
170
160
140
100
60
40
30
20
10
60
50
40
30
20
10
0
120
110
100
90
80

Figure 26. Type specimen of *Braya glabella* var. *prostrata* Harris.

Braya glabella var. prostrata [illegible]

[illegible]

DETERMINED J. R. Harris DATE [illegible]

Annotated by G. A. Mulligan
Department of Agriculture, Ottawa

PLANTS OF FRANKLIN DISTRICT
NORTHWEST TERRITORIES, CANADA
ELLESMERE ISLAND
Hazen Camp, 81°49'N 71°21'W

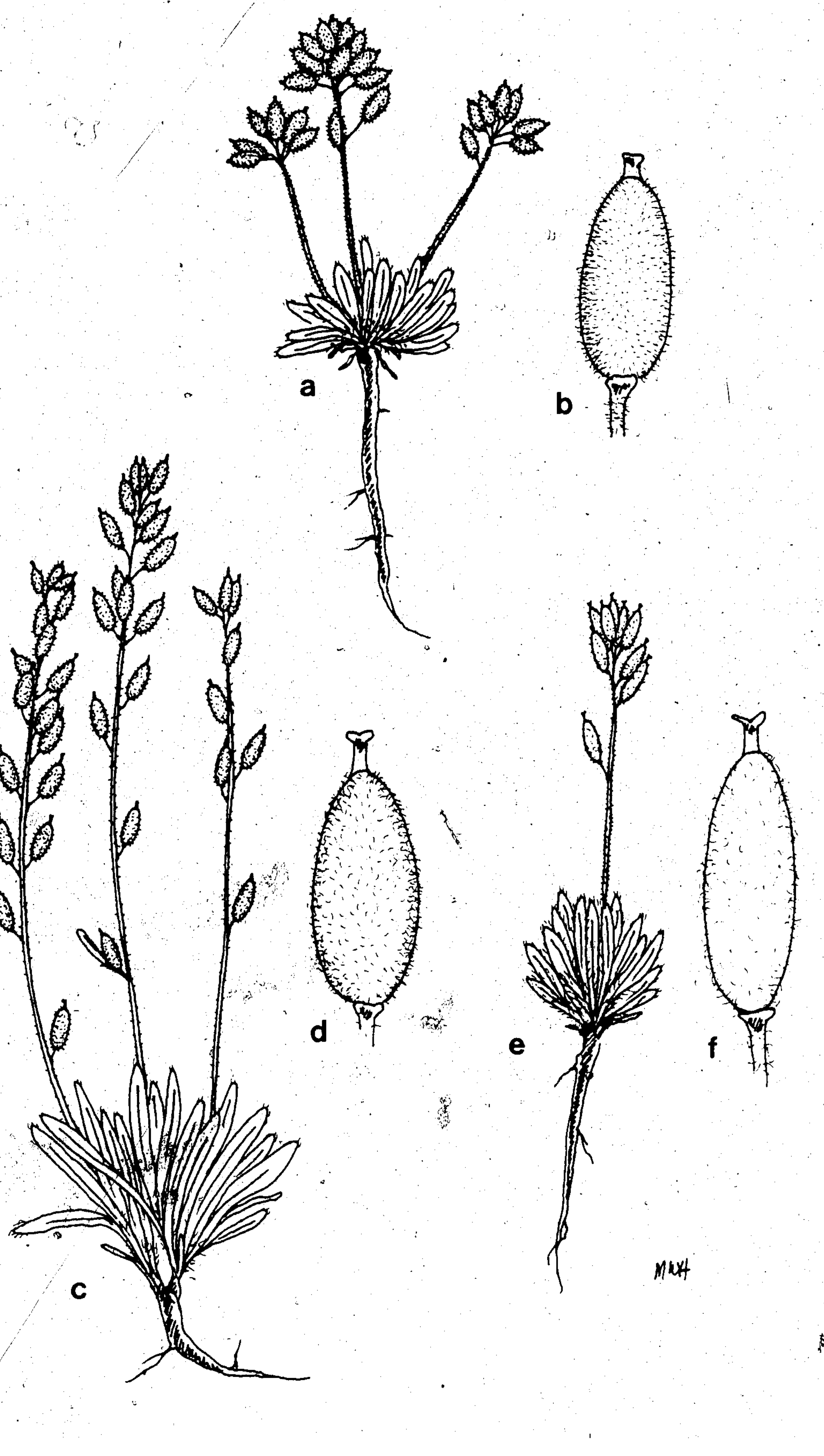
Braya purpurascens (R. Br.) Bunge

Few prostrate plants on sandy level delta plain, 1½ mi. WSW of Camp.

No. 4764A D.B.O. Savile 28 July, 1962

PLANT RESEARCH INSTITUTE
DEPARTMENT OF AGRICULTURE, OTTAWA

Figure 27. Illustration of *Braya glabella* var. *purpurascens*; a., c., and e. entire plants (natural size); b., d., and f. siliques (x 5).


a
b
c
d
e
f

B. purpurascens var. *dubia* Schulz, Pflzrch. IV. 105. pp. 235 & 364. (1924)

B. arctica Hook., Parry's 2nd Voy. App. p. 387. (1825)

B. purpurascens (R. Br.) Bunge ex Ledeb., Flor. Ross. 1:195. (1841)

Plants 3.5 - 10.5 (12.8) cm tall; stems usually ascending, sometimes erect; leaves often fleshy, usually entire (rarely with 1 or 2 weak teeth per side); fruiting inflorescence often densely compact; siliques oval-elliptic to oblong-elliptic, 2.5 - 3.7 times longer than broad, usually straight.

Usually barren, often calcareous, soils and gravels on solifluction lobes, gravel bars, disturbed sites, rocky slopes, and sea shores. Northern coast of continental North America north through the Canadian Arctic Archipelago to the limits of land; circumpolar. Figure 28.

N=28, 2n=56.

Type: "Melville Island", *Mr. James Ross s.n.*, BM! Figure 29.

Robert Brown (1823) originally placed this taxon in his newly erected genus *Platypetalum*. In his view, it differed from *Braya* in the oval-elliptic and convex, rather than oblong and sub-cylindrical, shape of the fruits. As more collections of *Braya* became available, it became obvious that the genus included taxa with a variety of silique shapes, and Bunge (1841) transferred *P. purpurascens* and *P. dubium* to *Braya*, the latter as a synonym of *B. rosea*. *Platypetalum dubium*, segregated from *P. purpurascens* by Brown (1823) based on the entire, rather than bilobed, stigma, the shorter style, and the more pubescent scapes, appears to be only a minor variant of typical *P. purpurascens* — style length, stigma lobing, and scape pubescence are extremely variable in this group, even within a single population — and has been placed into synonymy under an enlarged *Braya purpurascens* by most subsequent authors. I will, therefore, refer to the two taxa as *B. purpurascens* in the following discussion.

Abbe (1948), even with only very limited material to work with, realized the close relationship between *Braya glabella* and *B. purpurascens* and became suspicious that the two

Figure 28. Distribution of *Braya glabella* var. *purpurascens* in North America.

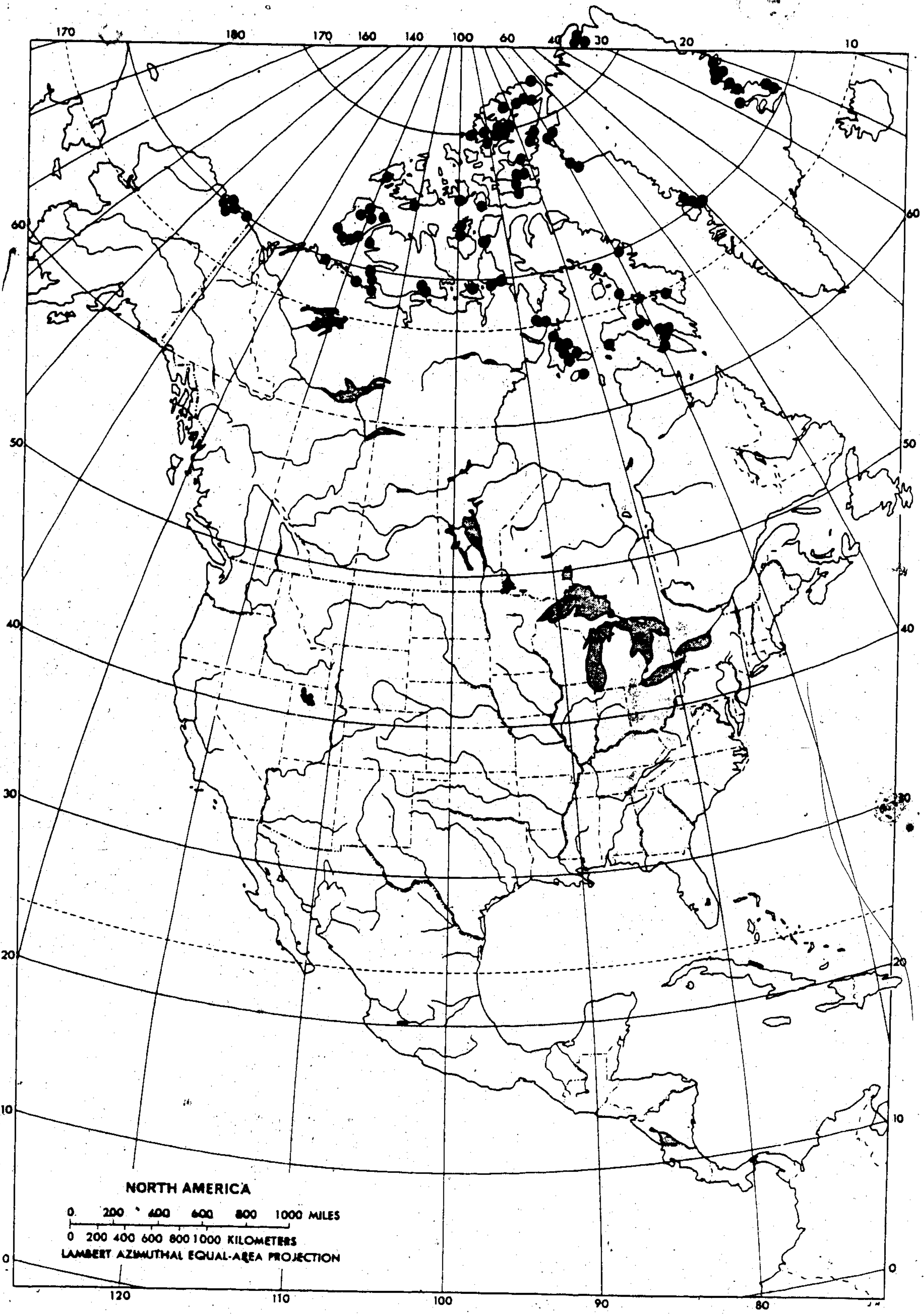

NORTH AMERICA
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
170
180
170
160
140
100
60
40
30
20
10
60
50
40
30
20
10
0
120
110
100
90
80

Figure 29. Type specimen of *Braya glabella* var. *purpurascens* (R. Br) Harris.

[illegible]

Melville Isd.
Mr. Edwards

[illegible] Sabine

Melville Isd.
Mr. Fisher

Type Specimen

PARRY'S 1st VOYAGE 1819
MELVILLE ISLAND

might comprise a single species:

> "There is no evidence against *Braya glabella* of Richardson being conspecific with *B. purpurascens* (R. Brown) Bunge. The chief difficulty is the lack of positive evidence concerning the nature of the mature siliques and of their arrangement on the scape. Should these support the possibility that the two are conspecific, then the name *B. glabella* would have to be substituted for *B. purpurascens*."

It appears that *B. glabella* and *B. purpurascens* are indeed conspecific and only warrant recognition as being varietally distinct. Because the epithet "*glabella*" (Richardson, 1823) was validly published before the epithet "*purpurascens*" (Brown, 1823), *B. glabella* has nomenclatural priority over *B. purpurascens*. This is somewhat unfortunate; *B. purpurascens* is much better known in the literature than *B. glabella* and the plants in this variety are more widely distributed than those in var. *glabella*.

CANADA: NORTHWEST TERRITORIES: Bernard Harbour, *F. Johansen 320* (CAN), *320a* (CAN, BM); N shore of Lake Ferguson, *R. Hainault 2090* (DAO); Spence Bay, *D.B.O. Savile 3829* (DAO); Boothia Isthmus, Tareornitiok, *C. Laverdière 97* (CAN); Repulse Bay, Melville Penin., *P.F. Bruggemann 35, 55* (DAO); Cape Parry, *J.A. Parmelee 2945, 3004* (DAO), *2944* (DAO, ALTA); Clinton Point, *J.A. Parmelee 3206* (DAO); Axel Heiberg Island, Thompson Valley area, *M. Kuc 251* (CAN), *Beschel 10913, 11107* (CAN), *10786* (CAN, DAO); Axel Heiberg Island, NW of Middle Fjord, *Beschel 13152, 13186* (CAN); Axel Heiberg Island, vicinity of Upper House, *M. Kuc 548, 254, 252* (CAN); Axel Heiberg Island, Diana Lake at head of Mokka Fjord, *A.E. Porsild 18673* (CAN); Axel Heiberg Island, Crusoe River, *M. Kuc 202* (CAN); Baffin Island, Frobisher Bay, *J.M. Gillett 8550* (DAO), *H.A. Senn & J.A. Calder 4020* (DAO, MT), *3898* (DAO, PH, BM), *D.D. Bartley 110* (CAN); Baffin Island, Longstaff Bluff, *J.A. Parmelee & J.R. Seaborn 4071(a)* (DAO); Baffin Island, Arctic Bay, *N. Polunin 2524* (CAN); Baffin Island, Col de Pangnirtung, *J-L. Blouin 722* (CAN); Baffin Island, head of Clyde Inlet, *V.C. Wynne-Edwards 8851, 9027, 8922* (CAN); Baffin Island, Lake Harbour, *M.O. Malte 120294* (CAN); Baffin Island, Tavener Bay, *E.W. Manning 69* (CAN); Baffin Island, N side of Mallik Island, *R. Hainault & R. Norman 5944* (CAN); Banks Island, 73° 30′ N 118° 05′ W, *G.W. Scotter 20692, 20690* (DAO); Banks Island, 73° 06′ N 118° 53′ W, *G.W. Scotter & S.C. Zoltai 31356* (DAO); Banks Island, 73° 30′ N 120° 20′ W, *G.W. Scotter & S.C. Zoltai 31101A* (DAO); Banks Island, 73° 29′ N 115° 21′ W, *G.W. Scotter & S.C. Zoltai 31343* (DAO); Banks Island, De Salis Bay, *T.H. Manning & A. Macpherson 39* (CAN), *A.E. Porsild 17626, 17625* (CAN); Banks Island, N of Cape Lambton, *A.E. Porsild 17567* (CAN); Banks Island, Cape Kellett, *M. Kuc s.n.* (CAN); Banks Island, Bernard River, *W.J. Maher & S. MacLean 27* (CAN); Bathurst Island, 75° 42′ N 98° 40′ W, *M. Gauthier BI-74-27* (DAO); Coats Island, east coast, *A.E. Porsild 5904* (CAN, MT); Cornwallis Island, Resolute Bay, *J.G. Harris 1726* (ALTA), *W.B. Schofield 613* (DAO); Devon Island, Truelove Lowland, *J.G. Harris 1719* (ALTA), *P. Pakarinen s.n.* (ALTA), *G. Courtin 14* (ALTA); Ellesmere Island, Eureka, *C.R. Harington 329, 330* (ALTA); Ellesmere Island, Hazen Lake, Hazen Camp, *D.B.O. Savile 4545* (DAO); Ellesmere Island, Craig Harbour, *M.O. Malte 118933* (MT, CAN), *R.W. de F. Feachem 364*

(BM); Ellesmere Island, Grise Fjord, *J.G. Harris 1691* (ALTA); Ellesmere Island, Hilgard Bay, *C.R. Harington 33* (CAN); Ellesmere Island, S shore of Hawkins Lake, *P.F. Bruggemann 222* (DAO); Ellesmere Island, Fosheim Penin., *P.F. Bruggemann 825* (DAO); Ellesmere Island, Alert area, *C.R. Harington s.n.* (ALTA); Ellesmere Island, Alexandra Fjord, *J.G. Harris 1720, 1723, 1724* (ALTA); Ellesmere Island, head of Tanquary Fjord, *G.R. Brassard 1966* (CAN); Ellesmere Island, Bache Penin., *M.O. Malte 118896* (CAN); Ellesmere Island, 8 km due E of head of N arm of Makinson Inlet, *W. Blake, Jr. 6* (DAO); King William Island, 68° 47′ N 97° 40′ W, *J. Woodruff s.n.* (DAO); Melville Island, Winter Harbour, *G.A. McMillan 77297* (CAN); Prince of Wales Island, 72° 35′ N 98° 55′ W, *E. Macpherson 193* (CAN); Prince of Wales Island, 72° 42′ N 98° 14′ W, *J. Edmonds 48* (DAO); Prince Patrick Island, Mould Bay, *S.D. MacDonald 114* (CAN); Somerset Island, N shore of Hazard Inlet, *D.B.O. Savile 3812, 3592* (DAO); Southampton Island, Coral Harbour, *R. Marris 9377* (BM), *W.J. Cody 1947, 1618, 1583, 1200* (DAO), *1545, 1194* (DAO, MT), *S. White 761040, 761032* (DAO), *J.A. Calder, D.B.O. Savile & I. Kukkonen 24235* (DAO), *A.E. Porsild 21748, 21749, 21750, 21751, 21752, 21753* (CAN); Southampton Island, Snafu, *D.K. Brown 557* (CAN); Southampton Island, 2 mi N of foot of Duke of York Bay, *D.K. Brown 1753* (CAN); Southampton Island, Munn Bay, *R. Marris 9528, 10298, 10297* (BM); Southampton Island, Kirchoffer River, *R. Marris 9659* (BM); Victoria Island, Wollaston Penin., *A.E. Porsild 17218* (CAN); Victoria Island, Cambridge Bay, *Beschel 13481* (CAN), *J.A. Calder, D.B.O. Savile & I. Kukkonen 24187* (DAO), *S. Stephens 1034, 950* (CAN); Victoria Island, Walker Bay, *A.E. Porsild 17493B* (CAN); Victoria Island, Read Island off S coast of Wollaston Penin., *A.E. Porsild 17195* (CAN); **GREENLAND:** Nûgssuaq Halvø, Kugssinerssuaq, *M.P. & R.T. Porsild s.n.* (MT); Umanak area, S of Marmorilik, *J. Poelt & H. Ullrich 56/83* (ALTA); Atanikerdluk, Nuqsuak Penin., *C.O. Erlanson 3258* (DAO); Thule, *G.A. Kingston s.n.* (CAN), *W.B. Schofield 630* (DAO); Inglefield Land, Reuselaer Bay, *J.C.F. Jedrow s.n.* (CAN); Inglefield Land, Robertson Bay, *N. Humphreys 21* (DAO); Polaris Bay, *J.M. Powell 419* (CAN); Hold With Hope, E shore of Loch Fyne, *A.H.F. Webbe & R. Marris 6226, 6178, 6224* (BM); Hudson Land, Stordal Delta, *A.H.F. Webbe & R. Marris 6628* (BM); Hudson Land, Lower Stordal, *A.H.F. Webbe & R. Marris 6614* (BM); Hudson Land, Upper Dybendal, *R. Marris 6593, 6594* (BM); E. Jameson Land, Klitdal, *R. Marris 1431* (BM); Wollaston Forland, W side of Lindemanspasset, *R. Marris 5833* (BM); Scoresby Land, Fleming Fjord, *R. Marris 660, 653, 723, AR465, H75* (BM); Erik Raudes Land, Mackenzie Bay, Myggbukta, *C.G. & E.G. Bird 282, 327, 218, 301* (BM); Erik Raudes Land, Payer Land, Revet, *C.G. & E.G. Bird 5* (BM); Ella Island, Cape Elisabeth, *Seidenfaden 1030* (CAN); Clavering Island, *T. Sørensen 4240* (CAN), *J. Vaage s.n.* (CAN), *C.G. & E.G. Bird 33, 39* (BM); S of Musk-ox Fjord, *G. Seidenfaden 1009* (MT); Charcots Land, *K. Holmen & S. Lægaard 52* (DAO, CAN); Heilprin Land, Brønlund Fjord, *K. Holmen 6008* (CAN), *B. Fredskild 281* (CAN); Heilprin Land, Kedelkrogelv, *B. Fredskild 245* (CAN, DAO); **U.S.A.: ALASKA:** Arctic Natl. Wildlife Range, Nuvagapak Point, *D.F. Murray 3132* (BRY, DAO); Prudhoe Bay, *B. Welsh et al. 1247b, 1246a, B. Welsh 1233* (BRY), *A. Strutz & J. Shelton 2240* (BRY), *M. Williams 3483* (BRY).

Braya longii Fern., Rhodora 28:202. (1926) Figure 17.

B. purpurascens var. *longii* (Fern.) Boivin, Le Natur. Canadien 94, p. 646. (1967)

Plants perennial from a taproot; caudex simple in younger plants but becoming multi-branched with age; stems 1 to many, erect, scapose (occasionally with a single leaf or leafy bract subtending the lowermost flower or fruit), 3.0 - 11.0 (15.0) cm tall, lightly pubescent with simple and bifurcate hairs, often purple or purple-tinged; leaves basal, entire, narrowly spatulate-oblanceolate, obtuse, (5) 10 - 30 (50) mm long, 1.0 - 3.5 mm broad at widest point, sparsely ciliate along lower margins, green to purple-tinged; leaf bases membranous and broadly expanded near point of attachment; flowering inflorescence densely capitate; sepals 2.0 - 3.0 (3.5) mm long, (1.1) 1.2 - 1.7 mm wide, obtuse, sparsely pubescent with simple hairs or glabrous, green or purple-tinged, with a scarious margin; petals 3.7 - 4.8 (5.0) mm long, 1.5 - 2.3 mm wide, distinctly and abruptly divided into blade and claw, wholly white or the blade white and the claw purple-tinged; fruiting inflorescence dense and congested with overlapping siliques, capitate or elongated; pedicels (1.2) 1.5 - 4.5 (4.9) mm long, erect-ascending; siliques lance-subulate, (3.0) 4.0 - 8.0 (10.0) mm long, (0.7) 1.0 - 1.5 (1.7) mm wide at the widest point, glabrous or occasionally very sparsely pubescent; septum margins broadly expanded at the base, encircling the base of the silique and forming a sack-like pouch around the bottom of the lowermost seed in each locule; style 0.5 - 1.0 (1.2) mm long; stigma narrow or broad, bilobed to entire; seeds 1.0 - 1.4 mm long, 0.5 - 0.85 (1.0) mm broad, more or less uniseriate.

Dry limestone barrens. Known only from near the type locality at Sandy Cove, Straits of Belle Isle, Newfoundland. Figure 30.

2n = 56.

Type: Newfoundland, Straits of Belle Isle, gravelly and peaty limestone barrens, Sandy (or Poverty) Cove, 25 July 1925, *Fernald, Long & Gilbert 28424*, GH! (holotype), PH! Figure 31.

Braya longii Fern. is a very narrow endemic species of calcareous soils in northwestern Newfoundland. It is very closely related to the somewhat more widely distributed *B. fernaldii*, sharing the shape and arrangement of the siliques, the more or less uniseriate seeds, and the unique nature of the silique septum margin. *Braya longii* differs from *B. fernaldii* in the

Figure 30. Distribution of *Braya longii*.

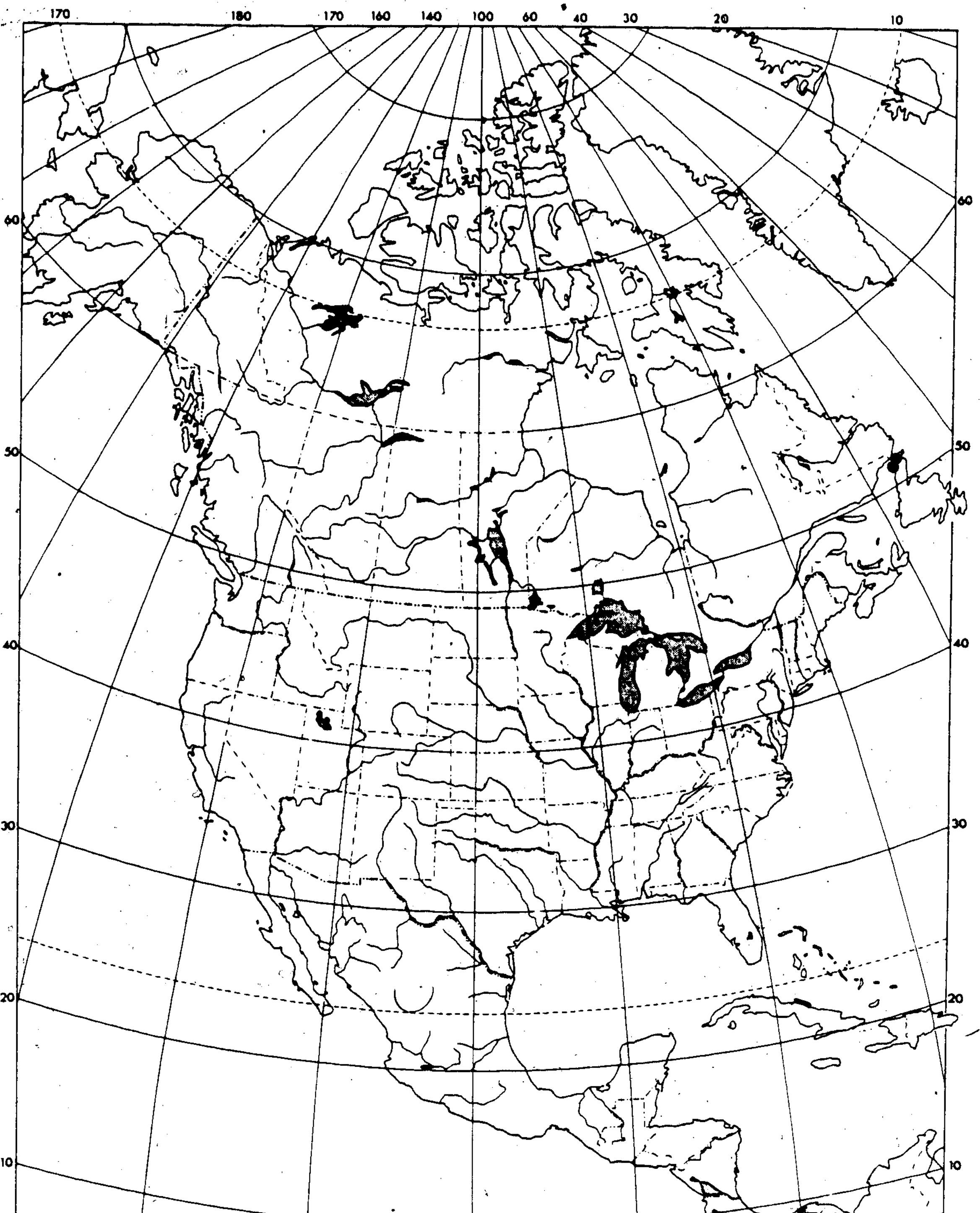

170
180
170
160
140
100
60
40
30
20
10
60
60
50
50
40
40
30
30
20
20
10
10
0
0
120
110
100
90
80
NORTH AMERICA
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
LAMBERT AZIMUTHAL-EQUAL-AREA PROJECTION

Figure 31. Type specimen of *Braya longii* Fern.

FLORA OF NORTHWESTERN NEWFOUNDLAND Type
STRAITS OF BELLE ISLE

No. 28424
Braya Longii Fernald, n. sp.

Gravelly and peaty limestone barrens, Sandy [illegible]

M. L. Fernald, Bayard Long and
[illegible]

longer and broader petals, which are separated into a distinct claw and blade, and in the glabrous, or nearly glabrous, siliques.

Fernald (1926) named the species in honor of its discoverer, his friend and traveling companion, Bayard Long.

Representative specimens: **CANADA: NEWFOUNDLAND:** between Savage Point and Sandy Cove, *J.G. Harris 1727* (ALTA); Straits of Belle Isle, Sandy (or Poverty) Cove, *M.L. Fernald, B. Long & B.H. Dunbar 26723* (GH, PH), *M.L. Fernald & L. Griscom 28423* (GH, PH); Straits of Belle Isle, Savage Point, *M.L. Fernald, K.M. Wiegand, A.S. Pease, B. Long, F.A. Gilbert, Jr. & N. Hotchkiss 28425* (PH, CAN), *M.L. Fernald & B. Long 28426* (GH, CAN, DAO-photo); Straits of Belle Isle, Yankee Point, *M.L. Fernald, K.M. Wiegand & B. Long 28427* (PH).

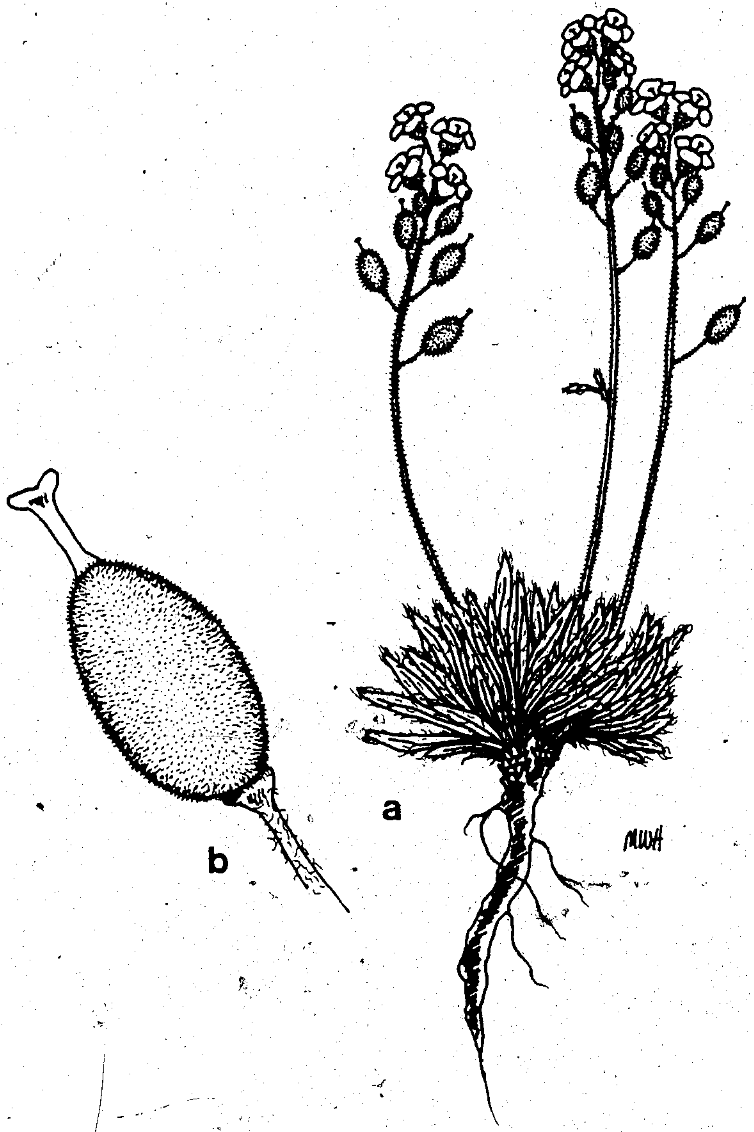
Braya pilosa Hook., Fl. Bor.-Am. I:65, Tab. XVII A. (1830) Figure 32.

B. purpurascens f. *pilosa* (Hook.) Schulz *In* Pflanzenreich 86 (IV.105):235. (1924)

B. purpurascens subsp. *pilosa* (Hook.) Hultén, Circumpolar plants II. P. 18. (1970)

Plants perennial from a stout taproot; caudex branched and usually covered with a thick, rough layer of marcescent leaf bases; stems 1 to several, erect to ascending, scapose (occasionally with a single leaf or leafy bract subtending the lowermost flower or fruit), 4.5 - 9.5 cm tall, lanate-pilose; leaves basal, entire, moderately to densely pilose mainly at margins and apex with mostly simple hairs (a few bifurcate hairs also may be present), linear to linear-spatulate, obtuse, 7 - 20 (30) mm long, 0.7 - 2.0 mm broad at widest point and gradually tapering towards the base; leaf bases membranous and broadly expanded near point of attachment; flowers 5 to many in a dense corymbose raceme (inflorescence somewhat more elongated in fruit); pedicels spreading-erect, 1 - 6 mm long, moderately lanate; sepals 2.8 - 3.5 mm long, (1.3) 1.6 - 2.5 mm broad, obtuse, with a scarious margin, lightly to moderately pubescent with simple and bifurcate hairs; petals entire, 4.7 - 6.6 mm long, 3.0 - 5.1 mm broad, with a short claw and broad orbicular blade, white; silicles ovoid, about 5 mm long, 3 mm broad; valves distinctly convex, densely pubescent when immature and becoming more moderately pubescent when mature with short simple and bifurcate hairs; style 1.25 - 2.0 mm

Figure 32. Illustration of *Braya pilosa*; a. entire plant (natural size); b. silicle (x 7).


b
a
MWH

long, slender; stigma broadly expanded, obscurely bilobed; seeds ca. 0.8 mm long, 0.5 mm broad, about 8 per locule, biseriate.

Sandy seashores. Known only from the type locality at the mouth of the Mackenzie River and areas in close proximity along the coast of the Beaufort Sea between the Mackenzie River delta and Cape Bathurst. Figure 33.

Type: Arctic Sea coast (according to Hooker, "Mouth of Mackenzie River, lat. 70°"), *Richardson s.n.*, K! (holotype) Figure 34, CAN!

Braya pilosa Hook. is a very distinctive, but poorly understood taxon. When he described the plant, Hooker (1830) had only flowering individuals with immature silicles to work from and he was apparently uncertain whether or not the plant was actually a *Braya*. He placed a question mark behind the genus name and stated, "... in all probability, it ought to constitute a new genus". And, indeed, without the advantage of mature fruits for examination, Hooker's suggestion of a new genus would seem justified. The flowers are much larger than those in any other *Braya* and, according to Richardson (1830), they are fragrant, with a smell similar to lilac blossoms. Fragrance has not been associated with any other members of the genus. In addition, the ovaries are ovoid, nearly globose, in shape with markedly convex valves and an exceptionally long style, over half the length of the ovary.

Lack of fruiting material has continued to cause confusion about this taxon. Porsild (1943) reported the collection of fruiting specimens of *Braya pilosa* from a number of localities near the Mackenzie Delta (Porsild 2229, 2621, 2760, and 2889 CAN!). He based his identification upon perceived differences between these specimens and typical *B. glabella*, noting the "...short, soft pubescence of simple and bifurcated gray hairs", the less elongated fruiting inflorescence, the broader siliques, the somewhat longer styles, and the paler seeds.

An examination of authentic fruiting specimens of *Braya pilosa* (Richardson s.n., 1848 K!; Pullen s.n., 1850 K!)[13]

---

[13] These specimens are included on a single, very congested, herbarium sheet at Kew, apparently mixed with the holotype specimens, and it is impossible to be certain which individuals are part

Figure 33. Distribution of *Braya pilosa*.

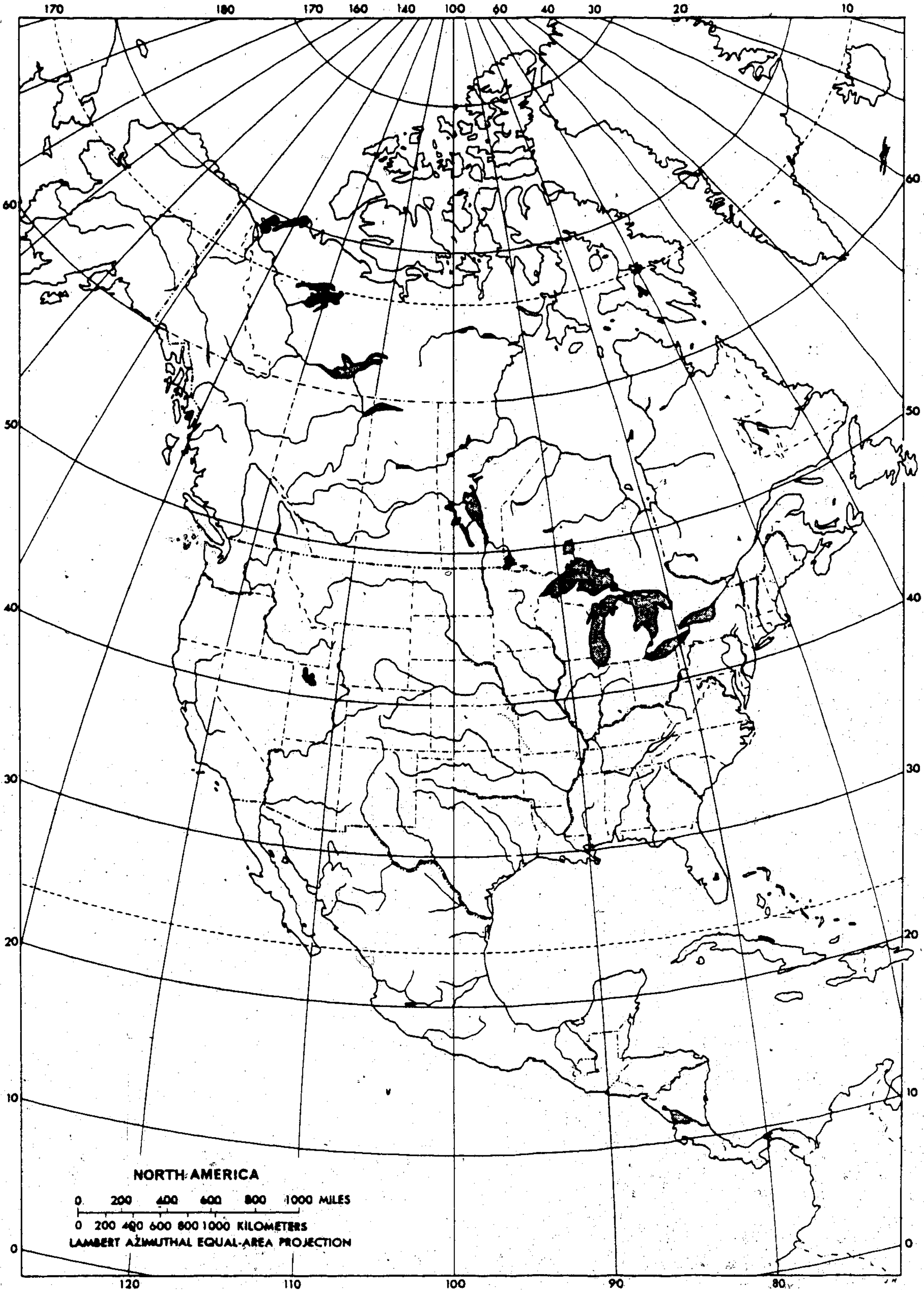
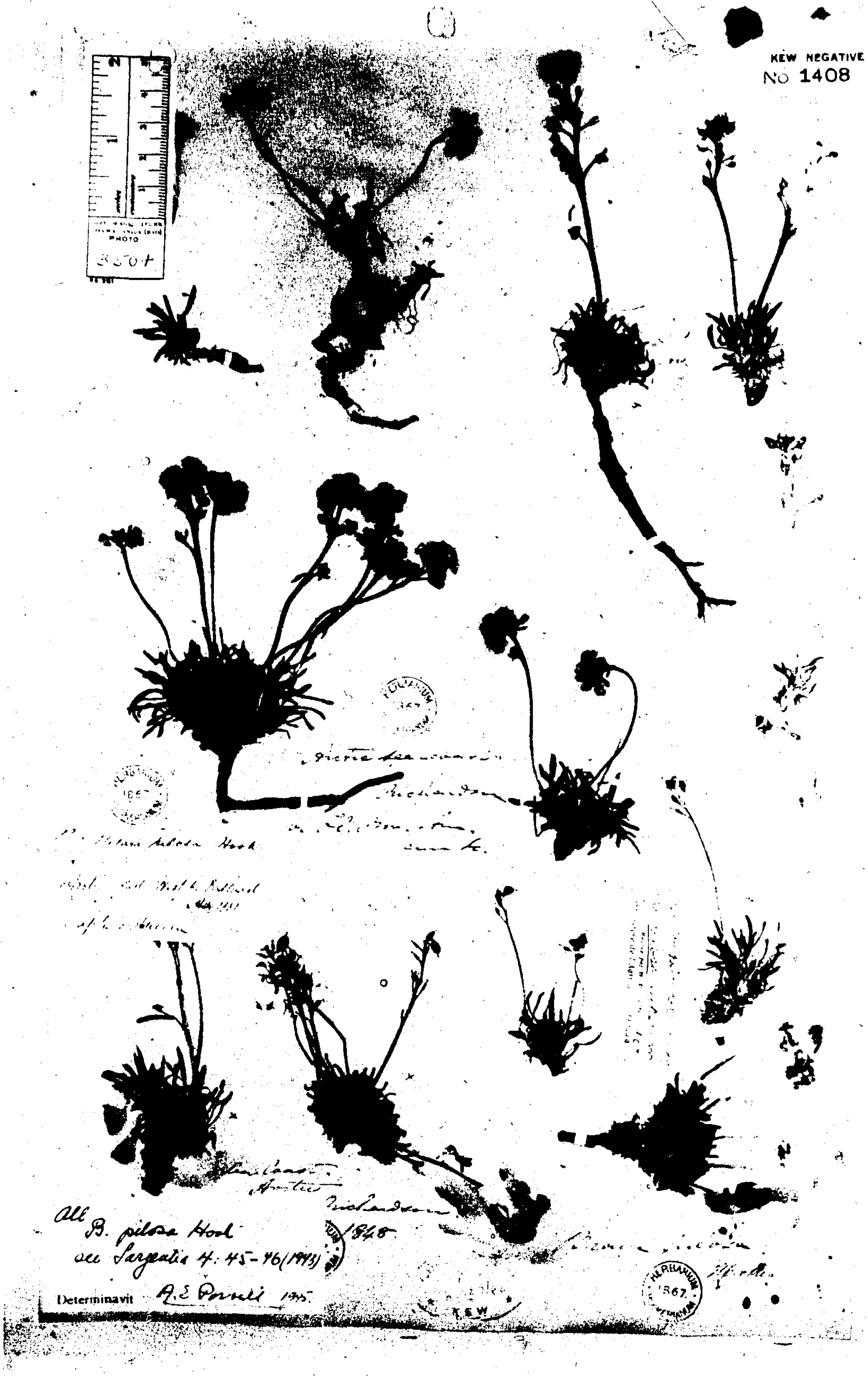

170
180
170
160
140
100
60
40
30
20
10
60
50
40
30
20
10
0
60
50
40
30
20
10
0
NORTH AMERICA
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
120
110
100
90
80

Figure 34. Type specimen of *Braya pilosa* Hook.

KEW NEGATIVE
No 1408



Arctic Sea coast
Richardson

B. pilosa Hook

Arctic
Richardson
1848

All B. pilosa Hook
see Sargentia 4: 45-46 (1943)

Determinavit A. E. Porsild 1945

quickly dispels any doubt about the nature of the species. Although Hooker's illustrations (1830, Tab. XVII A) of *B. pilosa* were of specimens with immature fruits, his drawings of the silicles match perfectly with more mature fruits. By way of contrast, the specimens cited by Porsild (1943), supposedly representing fruiting specimens of *B. pilosa*, bear very little resemblence to Hooker's illustrations of the species, and, in fact, are much closer to Hooker's illustration (1830, Tab. XXIII C.) of *Platypetalum purpurascens*.

In addition, Porsild's specimens are not at all pilose; the styles, though some are quite long, are extremely variable in length; the basal leaves are often toothed, much like the leaves of typical *Braya glabella*; the siliques are extremely variable in shape and many are distinctly narrowly oblong-lanceolate and near perfect matches for typical *B. glabella* siliques; and the withered flower parts, still present on some specimens, are obviously nowhere near as large as those in *B. pilosa*.

Murray (1983) has suggested that Richardson's collections do not belong to *Braya* at all, but rather are specimens of *Draba corymbosa* R. Br. ex DC. and that the normally yellow *Draba* petals have faded to off-white upon drying.

Fruiting specimens of *Braya pilosa* differ significantly from *Draba corymbosa*. The leaves of *D. corymbosa* are much shorter, wider, thinner, more acute, and more densely pubescent than those in *B. pilosa*; the styles of *D. corymbosa* are much shorter than those of *B. pilosa*; the valves of the silicles of *D. corymbosa* are distinctly flattened while those of *B. pilosa* are distinctly convex; the epidermal cells of the septum in *D. corymbosa* are thin-walled, isodiametric, and irregular-shaped (typical *Draba* epidermal cells), while those in *B. pilosa* are very typical *Braya* epidermal cells, characteristically thickened and transversely or obliquely elongated. *Braya pilosa* is undoubtedly a *Braya*.

Why there are no recent collections of *Braya pilosa* is unclear. I have seen no authentic specimens of this species collected since 1850. Perhaps the plant is of extremely limited and sporadic occurrence. Perhaps it is extinct.

---

[13] (cont'd)of the various collections represented. Fortunately, all of the specimens are very clearly members of the same taxon.

Representative specimens: **CANADA: NORTHWEST TERRITORIES:** Arctic coast, W of Cape Bathurst, *Captn. Pullen s.n.* (K, CAN-photo); Sea Coast, Arctic, *J. Richardson s.n.* (K, CAN-photo); Arctic America, *Franklin Exp. s.n.* (K).

Braya thorild-wulffii Ostf., Medd. Grønl. *64*, p. 176. (1923)

Plants perennial from a long taproot; stems 1 to many, simple, decumbent to prostrate or occasionally ascending, often bent or wavy, scapose (rarely with a single leaf or leafy bract subtending the lowermost flower or fruit), (3.0)5.0 - 9.0(14.0) cm long, quite densely villous with simple and bifurcate hairs or essentially glabrous, green to purple-tinged; leaves basal, entire, spatulate to linear-spatulate, obtuse, (5)10 - 30(40) mm long, 1 - 4 mm broad at widest point, ciliate with long, mostly simple, hairs and often with a tuft of hair at the apex, green to purple-tinged; leaf bases membranous and broadly expanded near point of attachment; inflorescence of 3 to many flowers, densely clustered in flower, becoming elongated in fruit; pedicels spreading-erect, almost non-existant in flower, 1.5 - 4.0 mm long in fruit, densely lanate or glabrous; sepals 2.0 - 3.5 mm long, 1.0 - 2.0 mm broad, obtuse, pilose or glabrous, green to purple-tinged; petals entire, scarcely longer than sepals, 2.0 - 3.7 mm long, 1.0 - 1.5 mm broad, not distinctly divided into claw and blade, but tapering gradually from the narrow blade to the base, white to purplish; silicles ovoid to globose, (4)5.0 - 8.0(10) mm long, (2.5)3.0 - 5.0 mm broad, densely pubescent with bifurcate and simple hairs or glabrous; style short, from almost non-existant to 0.75(1.0) mm long, stout; stigma broadly bilobed to entire; seeds (1.1)1.2 - 1.4(1.5) mm long, (0.5)0.7 - 0.8(0.95) mm broad, biseriate.

Key to the varieties of *B. thorild-wulffii*

1a. Scapes, pedicels, sepals, and silicles densely pubescent ....var. *thorild-wulffii*

1b. Scapes, pedicels, sepals, and silicles essentially glabrous............................ var. *glabrata*

Var. **glabrata** J.G. Harris *var. nov.* Figure 35.

Plantae similis var. *thorild-wulffii* sed differt in inflorescentiis fructiferis glabris.

This variety is similar in all repects to var. *thorild-wulffii* except that the scapes, inflorescence, and silicles are almost completely glabrous, in sharp contrast to the densely pubescent scape, inflorescence, and silicles of the latter.

Dry sand (and clay?). Banks Island and Victoria Island. Figure 36.

Type: Canada, Banks Island, Bernard River, 73°22′ N 121°47′ W, 6 August 1963, *Maher & MacLean cat. no. 139* CAN! (holotype). Figure 37.

I would in some cases be rather hesitant to recognize a new variety solely on the presence or absence of pubescence, particularly in light of Rollins's (1958) work in *Dithyrea*, where he found that silicle pubescence was controlled by a single gene. The situation in *Braya thorild-wulffii* is somewhat different from that in *Dithyrea* however; mixed populations of glabrous and pubescent individuals have never been reported in *B. thorild-wulffii* and the two varieties are evidently completely allopatric. It seems wisest to recognize these two geographically isolated, strikingly different morphological forms as separate varieties pending genetic studies possibly indicating only minor genetic differences.

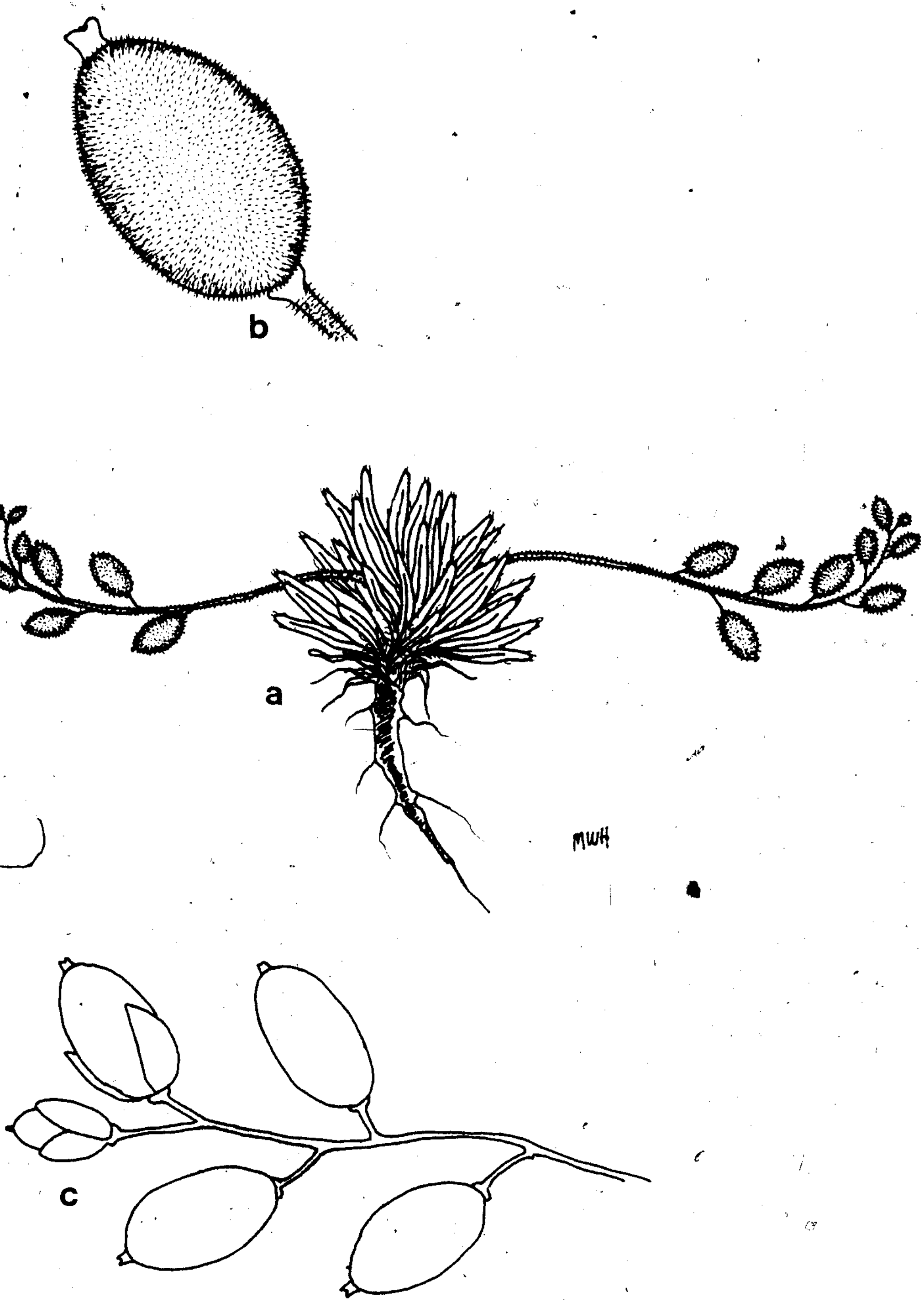
This taxon was first recognized as distinct by Porsild, who proposed the epithet "*glabrata*" on the type specimen, but never actually published the name.

Representative specimens: **CANADA: NORTHWEST TERRITORIES:** Banks Island, 73° 13′ N 119° 32′ W, *G.W. Scotter & S.C. Zoltai 31227* (DAO); Victoria Island, 70° 40′ N 107° 23′ W, *W.D. Stretton 18* (DAO).

Var. **thorild-wulffii** Figure 35.

B. purpurascens Porsild *pro parte* (*non* Bunge), Sarg. IV. p. 46. (1943)

Figure 35. Illustration of *Braya thorild-wulffii*; a. var. *thorild-wulffii*, entire plant (natural size); b. silicle (x 6); c. var. *glabrata*, fruiting stem (x 3).


b
a
MWH
c

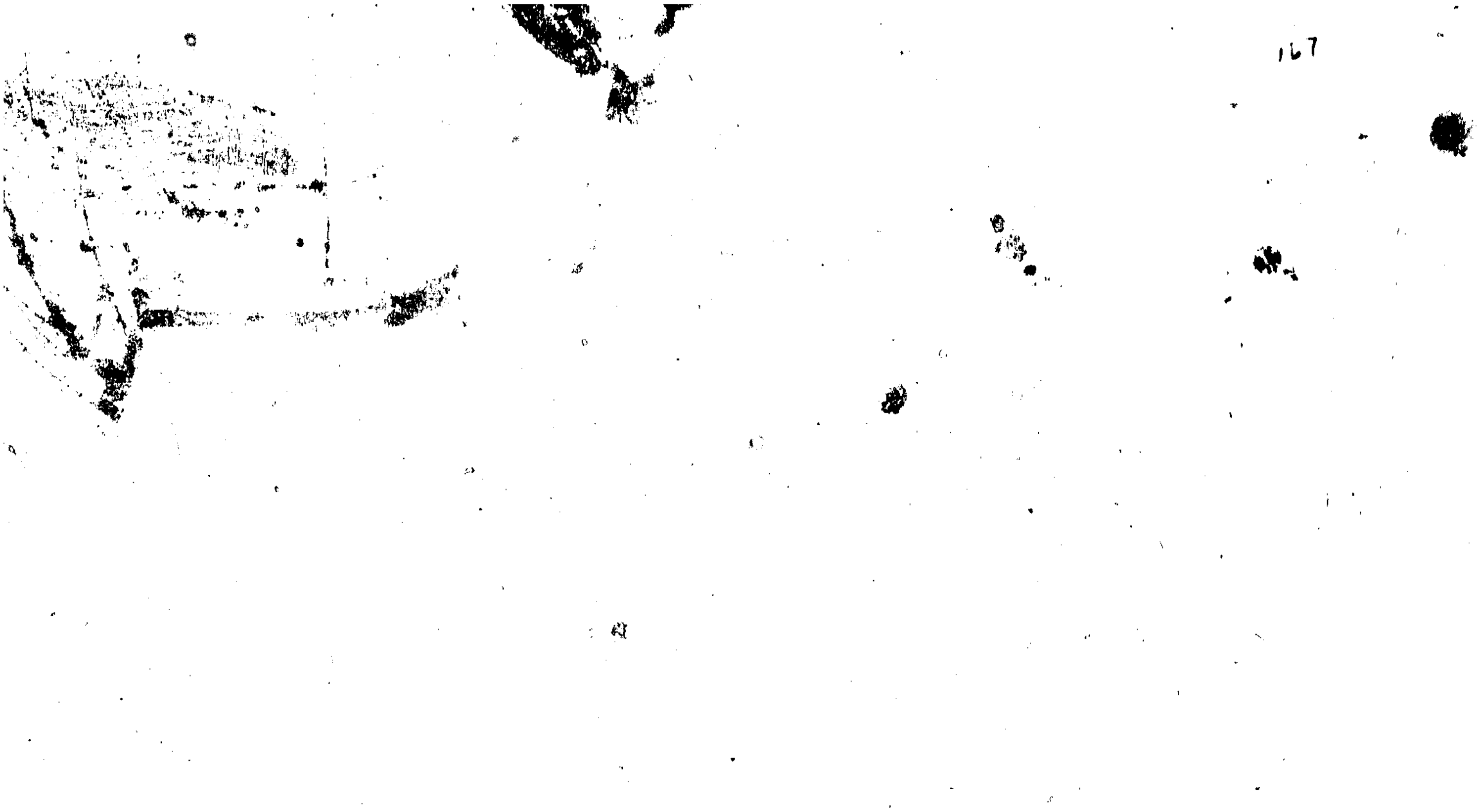
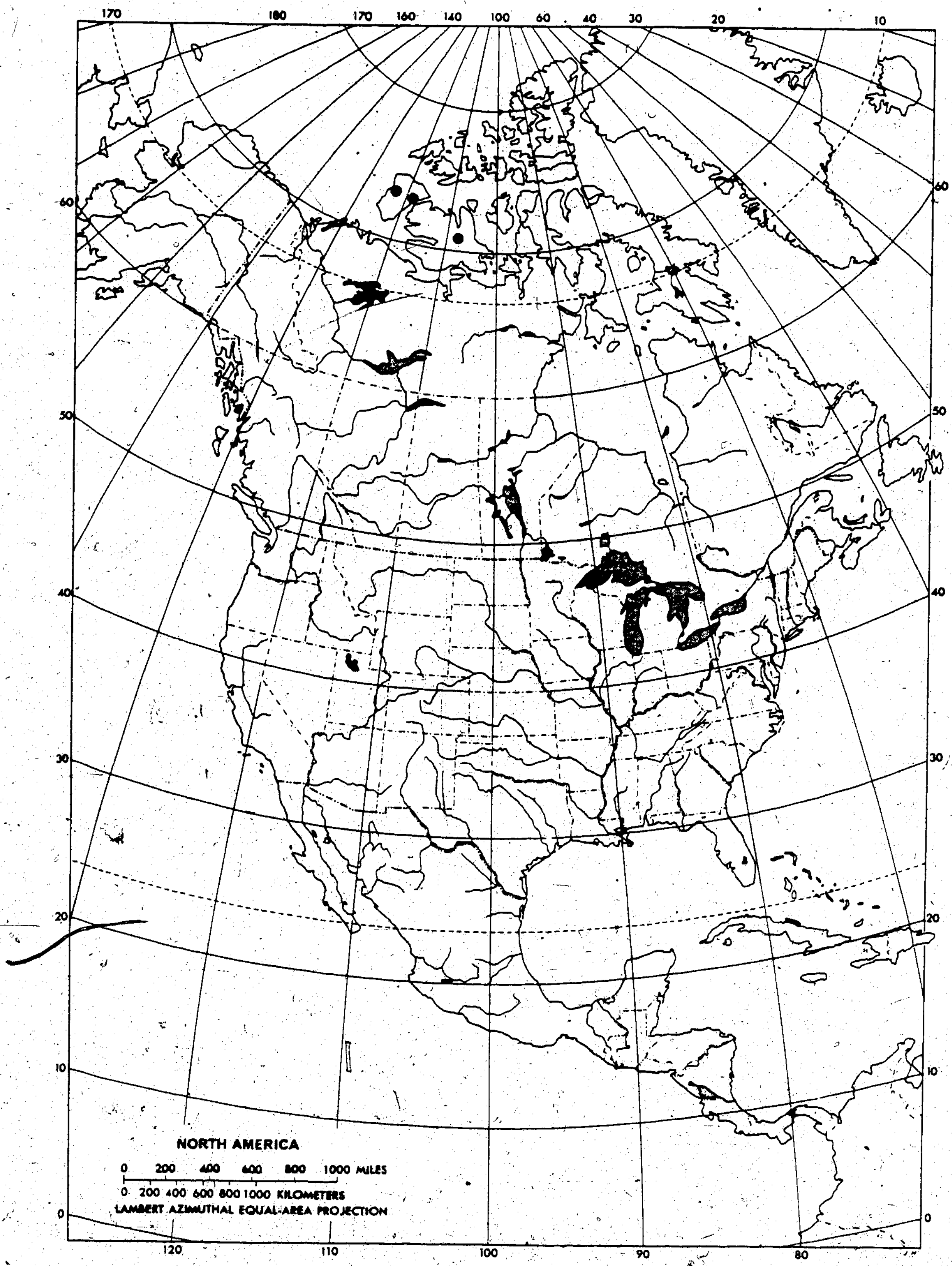


Figure 36. Distribution of *Braya thorild-wulffii* var. *glabrata*.


NORTH AMERICA
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
170
180
170
160
140
100
60
40
30
20
10
60
50
40
30
20
10
0
120
110
100
90
80

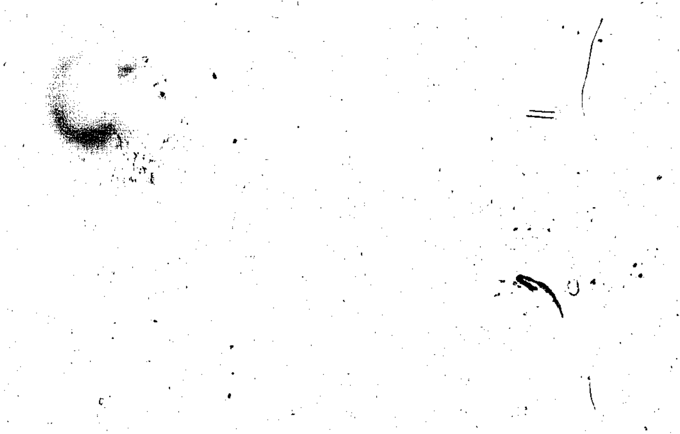


Figure 37. Type specimen of *Braya thorild-wulffii* Ostenf. var. *glabrata* Harris.

Braya thorild-wulffii var glabrata var nov

HOLOTYPE

DETERMINED J. G. Harris DATE August 1986

FLORA OF NORTHWEST TERRITORIES
Banks Island

Cat. No. 139 Braya [illegible]

BERNARD RIVER:~ 73 22' N. Lat., 121 47' W. Long

Collectors: W. J. Maher & S. MacLean Aug. 6th, [illegible]
Identified by:

B. purpurascens subsp. *thorild-wulffii* (Ostf.) Hultén, Circum. plants II. p. 18. (1970)

B. purpurascens var. *thorild-wulffii* (Ostf.) Boivin, Le Natur. Canadien 94, p. 646. (1967)

B. pilosa subsp. *thorild-wulffii* (Ostf.) Petrovsky, Flora Arct. URSS, p. 52. (1975)

Dry, often calcareous, gravel, sand, and clay barrens, often on south-facing slopes. Northern Greenland, Ellesmere Island, Axel Heiberg Island, Prince Patrick Island, and Melville Island. Figure 38.

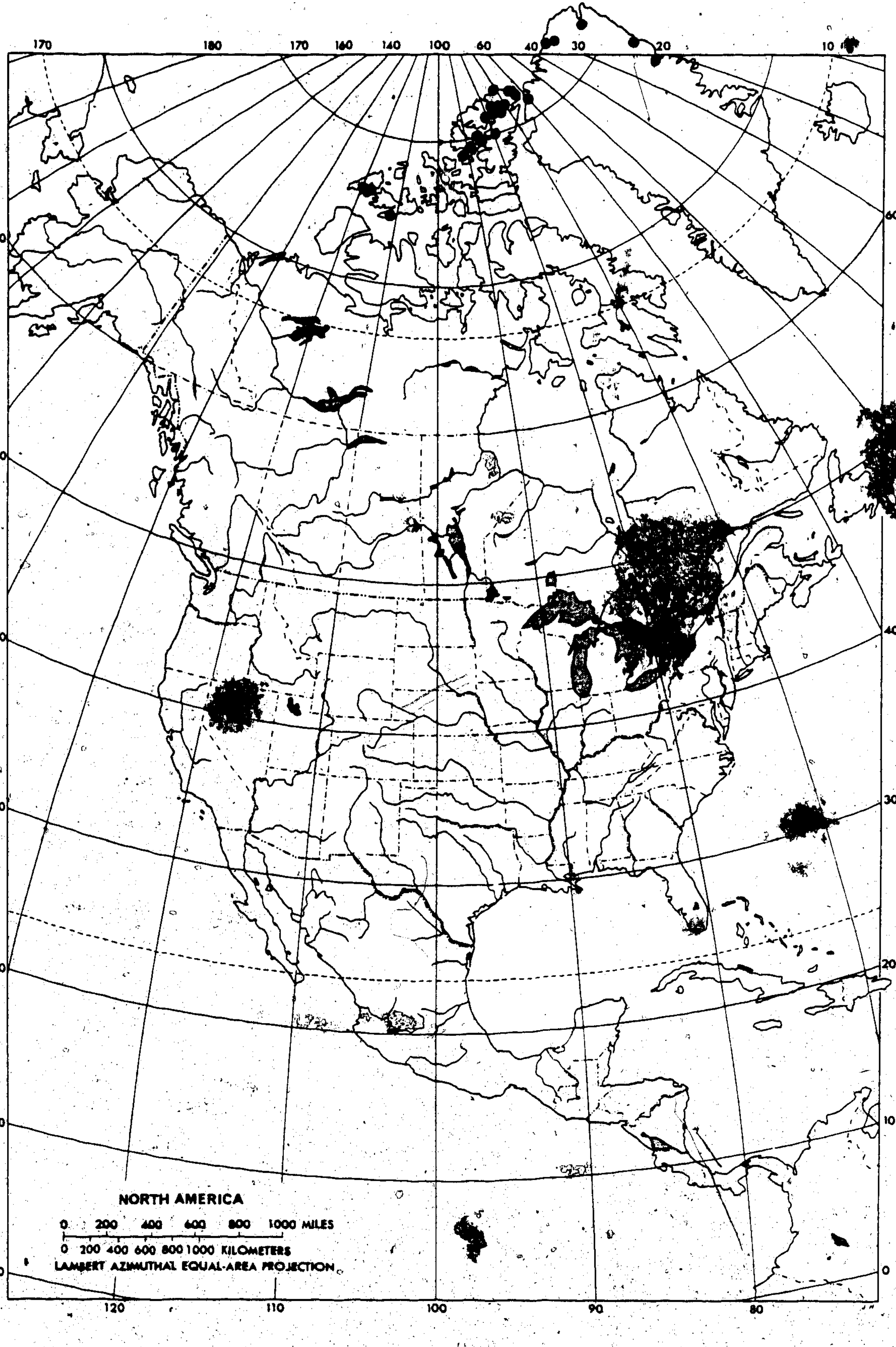
N=14, 2n=28.

Type: Greenland, Gunnar Andersson Valley, 11 July 1917, *Th. Wulff s.n.*

Braya thorild-wulffii Ostf. var. *thorild-wulffii* is a very distinctive North American high arctic endemic. It is somewhat surprising that it has at times [illegible] given only subspecific (Hultén, 1970) or varietal (Boivin, 1967) status under *B. purpurascens*. It differs from other members of the *B. glabella* species group in the decumbent, usually very robust, scapes, in the ovoid, densely pubescent silicles with very short styles, and in the ploidy level. *Braya thorild-wulffii* is the only known tetraploid member of the otherwise octoploid *B. glabella* complex (*B. pilosa* may be an exception — it may be diploid).

Representative specimens: **CANADA: NORTHWEST TERRITORIES:** Ellesmere Island, Hazen Camp, Lake Hazen, *W.J. Maher 176* (DAO), *D.B.O. Savile 4412* (DAO), *D.B.O. Savile 4456* (DAO), *D.B.O. Savile 4470* (DAO), *D.B.O. Savile 4574* (DAO, ALTA), *D.B.O. Savile 4740* (DAO), *D.B.O. Savile 4764B* (DAO); Ellesmere Island, Eureka, *J.G. Harris 1725* (ALTA), *P.F. Bruggemann 912* (DAO), *Beschel 11151* (CAN); Ellesmere Island, head of Tanquary Fjord, *G.R. Brassard 1966* (CAN); Ellesmere Island, south shore of Hawkins Lake, *P.F. Bruggemann 223* (DAO); Ellesmere Island, sandy shore, Caledonian Bay, *I. Waterston W194C/72* (CAN); Ellesmere Island, Cape Sheridan, *J.P. Kelsall 46* (CAN); Ellesmere Island, Ravine Bay, *S.D. MacDonald 34* (CAN); Ellesmere Island, Parr Inlet, *S.D. MacDonald 33* (CAN); Axel Heiberg Island, Thompson Valley, SE of Striae Hill, *Beschel 11071* (CAN); Axel Heiberg Island, Diana Lake at head of Mokka Fjord, *A.E. Porsild 18674* (CAN); Prince Patrick Island, Mould Bay, *S.D. MacDonald 115* (CAN), *P.F. Bruggemann 526* (DAO); Melville Island, Winter Harbour area, *M. Kuc s.n.* (CAN); **GREENLAND:** Heilprin Land, Brønlund Fjord, *K. Holmen 6628* (DAO), *B. Fredskild 265* (DAO, CAN), *B. Fredskild 282* (DAO, CAN); Lilli Snends(?), 76° 45′ N lat. along eastern coast, *A.*

Figure 38. Distribution of *Braya thorild-wulffii* var. *thorild-wulffii*.


NORTH AMERICA
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
170
180
170
160
140
100
60
40
30
20
10
60
50
40
30
20
10
0
120
110
100
90
80

Lundager 80763 (CAN); Skaerfjord, Haard Fegdejord(?), *T. Sørensen s.n.* (CAN); Polaris Bay, near mouth of river, 81° 36′ N 61° 26′ W, *J.M. Powell 423* (CAN).

Braya sect. **Sisymbriastrum** Turcz., Bull. Soc. nat. Mosc. XV. 2. P. 280. (1842)

Plants perennial or rarely biennial; stems leafy and often branched; leaves pinnatifid, dentate, or occasionally entire; fruit a silique, linear, terete or slightly compressed parallel to the septum, torulose (only rarely not torulose), 12 - 33 times longer than broad; septum epidermal cell wall thickenings very thick and irregular; seeds uniseriate.

Type species: *Braya humilis* (C.A. Mey.) Robins.

Braya sect. *Sisymbriastrum* is comprised exclusively of the members of the *B. humilis* species complex as discussed previously in this work. In North America the section includes a single species with four varieties.

Though Turczaninow (1842) did not designate a type species for the section — nor did he list representative specimens — it is clear from his diagnosis, "caule folioso...", "...foliis pinnatifidis...", and "siliquarum forma cum *Eubraya* convenit." that only the members of the *B. humilis* group would fit here. Exactly how Turczaninow envisioned his sect. *Sisymbriastrum*, however, is unclear; he listed no representative specimens, and he continued to place *B. humilis* in the genus *Sisymbrium*. Most authors today agree that *S. humile* C.A. Mey. is indeed a *Braya*, and Turczaninow's sect. *Sisymbriastrum* seems tailor-made for this species group. Since Turczaninow did not designate a type species for the section, I have chosen *B. humilis*, the oldest legitimate epithet in the section, to serve as the type species.

Braya humilis (C.A. Meyer) Robins. in Gray & Wats., Synopt. Fl. N. Am. I. 1., p. 141 (1895)

Plants perennial or rarely biennial from a taproot; caudex simple, becoming branched with age; stems 1 to many, strict, ascending or rarely prostrate, foliose, 3 - 33 cm tall, sparingly to densely pubescent with simple, bifurcate or trifurcate hairs, often purple or purple-tinged; basal leaves narrowly or broadly oblanceolate, obtuse, entire, sinuate-dentate or shallowly pinnatifid, petiolate to cuneate, 3 - 55 mm long, (0.4) 0.8 - 9.0 mm wide, ciliate, especially at the base, glabrescent to densely pubescent with simple, bifurcate and trifurcate hairs, green to deep purple; cauline leaves 3 - 10, generally like the basal leaves but usually reduced upwards; inflorescence dense and subcapitate in flower, densely compact or more often greatly elongated in fruit; sepals 1.5 - 3.1 (3.6) mm long, 0.6 - 1.8 mm wide, obtuse, glabrescent to moderately pubescent with forked or rarely simple hairs, green or purple-tinged, caducous or somewhat persistent; petals 2.5 - 6.9 (7.5) mm long, (0.7) 0.9 - 4.0 (4.2) wide, white or rose-purple (often purple-tinged at base only); fruiting pedicels spreading to erect, (1.0) 1.5 - 7.0 (8.0) mm long; siliques linear, subcylindrical or slightly compressed parallel to the septum, very torulose to not at all torulose, curved or straight, (7.5) [illegible] mm long, 0.6 - 1.2 (2.0) mm broad, glabrescent to densely pubescent with simple or branched hairs, green to dark purple; style 0.2 - 1.4 (1.7) mm long; slender to broad; stigma narrow or capitate, bilobed to entire; seeds 0.7 - 1.3 mm long, 0.3 - 0.75 mm wide, uniseriate.

Braya humilis is an extremely polymorphic species of wide distribution. The great diversity in the species is apparently caused and maintained by polyploidy and inbreeding of isolated populations. Geographically separate populations often look very different, but they generally grade into one another through a series of morphological intermediates. As has been discussed previously, it is impossible to subdivide the complex into consistently recognizable species; it seems most prudent to recognize a single highly variable species. Most of the variation of *B. humilis* is included in the variety *humilis*, and only the most distinctive morphological forms have been segregated out as three additional varieties of the species.

Key to the North American varieties of *B. humilis*

1a. Siliques 1.2 - 1.8 mm wide, not torulose; stems simple, becoming prostrate in fruit; plants of northern Ellesmere Island .... var. *ellesmerensis*

1b. Siliques 0.6 - 1.1 (1.3) mm wide, usually more or less torulose; stems simple or branched, ascending to erect; plants of various distribution 2

2a. Flowers small, average petal length less than 5 mm; most flowers developing normal siliques; leaves often dentate or pinnatifid; plants of wide distribution in North America .... var. *humilis*

2b. Flowers larger, average petal-length greater than 5 mm; most or many flowers not developing normal siliques, aborting; leaves seldom dentate or pinnatifid, entire; plants of the Rocky Mountains and Mackenzie Mountains of northwestern North America 3

3a. Leaves and stems glabrescent to moderately pubescent; plants of river banks, flood plains and occasionally moraines, in the southern Rocky Mountains of Alberta and British Columbia .... var. *maccallae*

3b. Leaves and stems densely pubescent; plants of alpine scree slopes, glacial moraines and occasionally gravel bars, in the Rocky Mountains of Alberta and British Columbia and the Mackenzie Mountains of Northwest Territories .... var. *porsildii*

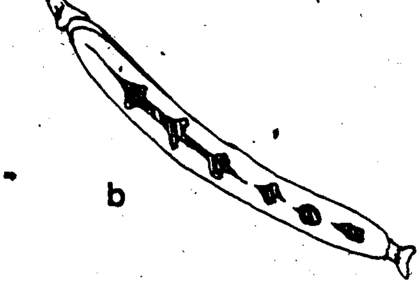
Var. **ellesmerensis** J.G. Harris *var. nov.* Figure 39.

Plantae similis var. *humili* sed differt in caulibus prostratis et siliquis latioribus.

Stems ascending, becoming prostrate in fruit, simple, 3 - 16 cm tall, moderately pubescent with bifurcate and simple hairs, purple or purple-tinged; basal leaves oblanceolate, petiolate or merely cuneate at the base, pinnatifid to entire; 7 - 45 mm long, 1.5 - 6 mm wide,

Figure 39. Illustration of *Braya humilis* var. *ellesmerensis*; a. entire plant (natural size); b. silique with valve removed (x 4).


a
MDK


b

moderately pubescent with simple and bifurcate hairs, green to purple-tinged; cauline leaves 3 - 4; sepals (1.9) 2.5 - 4.2 mm long, (1.1) 1.3 - 2.2 mm wide, pubescent with long simple and bifurcate hairs, green or purple-tinged; petals (3.0) 4.0 - 5.6 mm long, (1.3) 2.0 - 3.3 (3.8) mm wide, distinctly and abruptly divided into claw and broad blade, white or purple-tinged; siliques 9 - 25 mm long, (1.0) 1.2 - 1.8 (2.0) mm wide, straight or curved, not at all or only weakly torulose, fairly densely to moderately pubescent with simple and bifurcate hairs; septum often fenestrate with circular perforations at regular intervals longitudinally or with a narrow, elliptical, longitudinal split at the base or both; style 0.3 - 1.0 mm long, stout; stigma capitate and broadly bilobed or less often not capitate and only indistinctly bilobed; seeds 0.9 - 1.1 mm long, 0.5 - 0.7 mm wide.

Sand, clay, and gravel slopes and plains. Known only from the type locality and nearby areas on northern Ellesmere Island. Figure 40.

2n=42.

Type: Canada, Northwest Territories, Ellesmere Island, "Hazen Camp, 81° 49' N 71° 21' W", "level delta plain, 1 1/2 mi. WSW of Camp", 28 July 1962, *D.B.O. Savile 4763*, DAO 278278! (holotype) Figure 41, DAO 278277!

Braya humilis var. *ellesmerensis* is a fairly distinctive endemic of northern Ellesmere Island. The variety differs from other varieties of *B. humilis* in the greater silique width, in the prostrate habit of the fruiting stems, and in the fenestrate septum.

The plant is very robust and this, along with the prostrate habit and often broad, bilobed stigmas, is very reminiscent of the general appearance of *Braya thorild-wulffii* and *B. glabella* var. *prostrata*, also of the high arctic. In fact, all three of these taxa were collected from the same location on Ellesmere Island as three consecutive collection numbers by Savile (4763, 4764A, 4764B DAO). This is very curious, because prostrate and decumbent stems are very unusual in both *B. humilis* and *B. glabella*; it seems an unlikely coincidence that these three different taxa, all with prostrate to decumbent stems, would be found in the same isolated

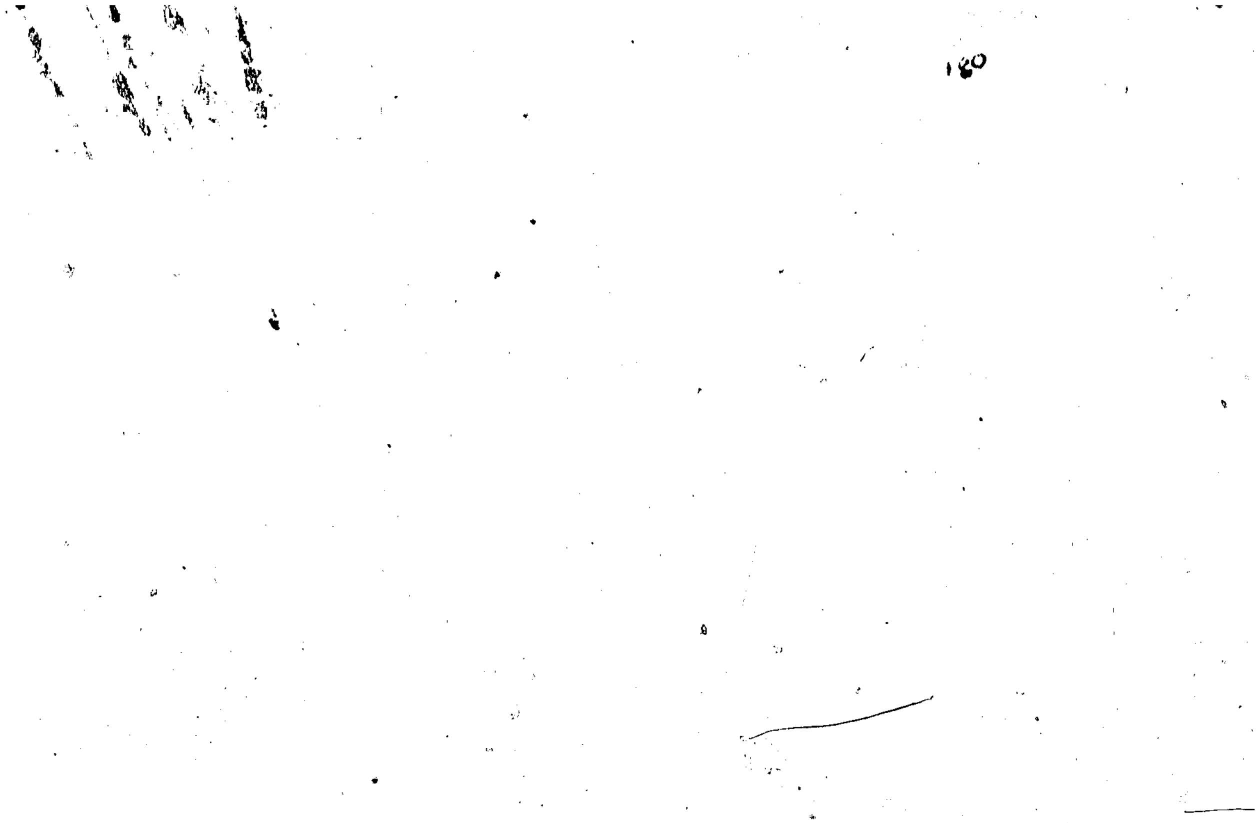


Figure 40. Distribution of *Braya humilis* var. *ellesmerensis*.

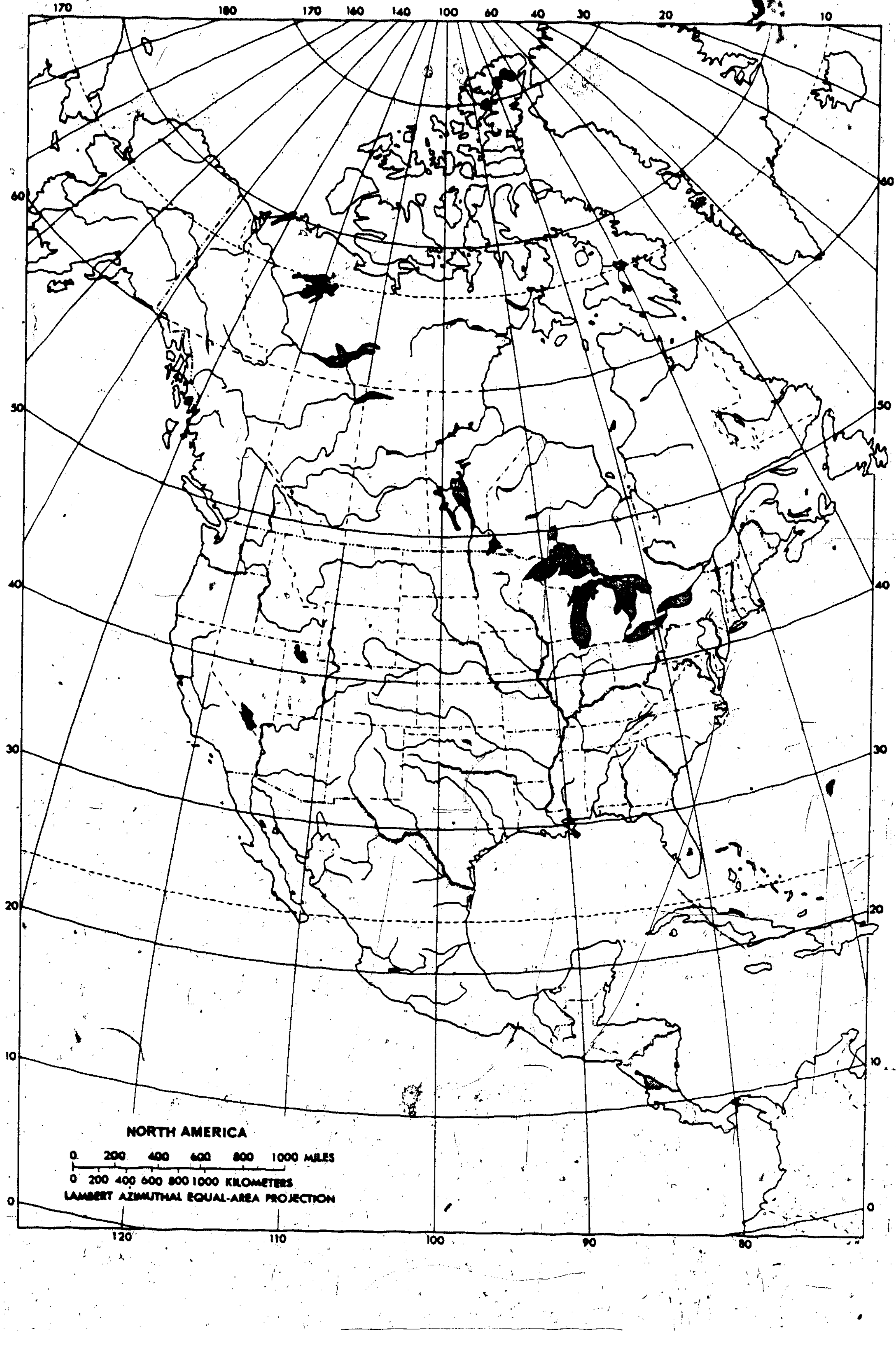

170
180
170
160
140
100
60
40
30
20
10
60
60
50
50
40
40
30
30
20
20
10
10
0
0
120
110
100
90
80
NORTH AMERICA
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

Figure 41. Type specimen of *Braya humilis* (C.A. Mey.) Robins. var. *ellesmerensis* Harris.

2

Braya [illegible] var. ellesmerensis [illegible]

HOLOTYPE

[illegible] J. G. Harris [illegible] August 198[illegible]

Annotated by [illegible]
Department of Agriculture Ottawa

PLANTS OF FRANKLIN DISTR
NORTHWEST TERRITORIES CANADA
ELLESMERE ISLAND
Hazen Camp 81°49'N [illegible]

Braya humilis (C.A. Mey.) [illegible]

Occasional, prostrate on [illegible]
delta plain, [illegible] WSW of [illegible]

No. 4763 D.B.O. Savile [illegible]

PLANT RESEARCH INSTITUTE
DEPARTMENT OF AGRICULTURE OTTAWA

location just by chance. It appears that gene flow of some kind has, or is, taking place between the taxa. It is interesting to note that chromosome counts have been made for all three of Savile's collections (Mulligan, 1965) and they all have a different ploidy level. *Braya thorild-wulffii* was found to be 2n=28, *B. humilis* var. *ellesmerensis* 2n=42, and *B. glabella* var. *prostrata* 2n=56.

Perhaps gene flow has taken place through introgression between *B. humilis* and a hypothetical hexaploid hybrid of *B. thorild-wulffii* and *B. glabella* var. *prostrata*. It is not uncommon to find plants that seem to fall somewhere between typical *B. thorild-wulffii* and *B. glabella* var. *prostrata*. It is possible that chromosome counts of these intermediates may reveal hexaploid, hybrid individuals. It may also be the case, that these postulated hexaploid hybrids are ill-adapted and not persisting.

Representative specimens: CANADA: NORTHWEST TERRITORIES: Ellesmere Island, Fosheim Peninsula, *P.F. Bruggemann 831* (DAO); Ellesmere Island, Hazen Camp, 81° 49' N 71° 21' W, 3/4 mi. N of Camp, *D.B.O. Savile 4411* (DAO); Ellesmere Island, head of Tanquary Fjord, *G.R. Brassard 1338, 1453* (CAN).

Var. **humilis** Figure 42.

Basionym: *Sisymbrium humile* C.A. Meyer in Ledeb., Ic. pl. ross. II., p. 16. (1830)

B. humilis ssp. *arctica* (Böch.) Rollins, Rhod. 55:115. (1953)

B. humilis ssp. *arctica* f. *biloba* Böcher, Medd. Grønl. *124*, 7:23. (1956)

B. humilis ssp. *richardsonii* (Rydb.) Hult., Ark. f. Bot. 7, 1, p. 66. (1968)

B. humilis ssp. *ventosa* Rollins, Rhod. 55:114. (1953)

B. humilis var. *abbei* (Böch.) Boivin, Phytolog. 16:299. (1968)

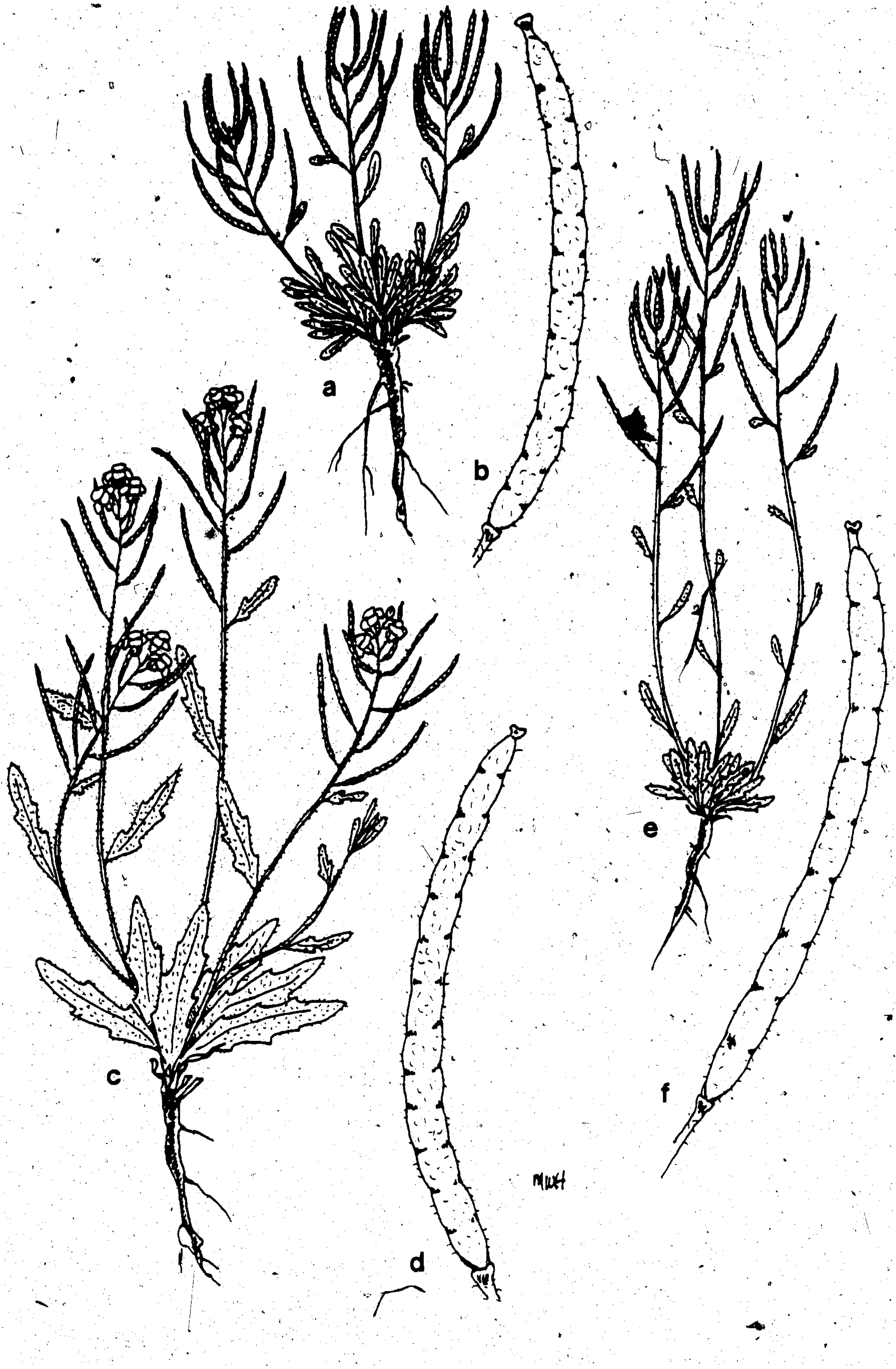
B. humilis var. *americana* (Hook.) Boivin, Pytolog. 16:300. (1968)

B. humilis var. *arctica* (Böch.) Boivin, Phytolog. 18:285. (1969)

B. humilis var. *interior* (Böch.) Boivin, Phytolog. 16:300. (1968)

B. humilis var. *laurentiana* (Böch.) Boivin, Phytolog. 16:300. (1968)

Figure 42. Illustration of *Braya humilis* var. *humilis*; a., c., and e. entire plants (natural size); b., d., and f. siliques (x 4.5).


a
b
c
d
e
f
MWH

B. humilis var. *leiocarpa* (Trautv.) Fern., Rhod. 39:276. (1937)

B. humilis var. *novae-angliae* (Rydb.) Fern., Rhod. 20:201. (1918)

B. humilis var. *ventosa* (Roll.) Boivin, Phytolog. 16:300. (1968)

B. novae-angliae (Rydb.) Sør., Medd. Grønl. *136*, 8:22. (1954)

B. novae-angliae ssp. *abbei* Böcher, Medd. Grønl. *124*, 7:21. (1956)

B. novae-angliae ssp. *ventosa* (Roll.) Böcher, Medd. Grønl. *124*, 7:21. (1956)

B. novae-angliae var. *interior* Böcher, Medd. Grønl. *124*, 7:20. (1956)

B. novae-angliae var. *interior* f. *capitata* Böcher, Medd. Grønl. *124*, 7:20. (1956)

B. novae-angliae var. *laurentiana* Böcher, Medd. Grnl. *124*, 7:19. (1956)

B. americana (Hook.) Fern., Rhod. 28:203. (1926) in part

B. richardsonii (Rydb.) Fern., Rhod. 20:203. (1918)

B. intermedia Sørensen, Medd. Grønl. *136*, 8:15. (1954)

Torularia humilis (C.A. Mey.) Schulz, Pflanzenr. IV, 105, p. 223. (1924)

T. humilis ssp. *arctica* Böcher, Medd. Grønl. *147*, 7:29. (1950)

Pilosella novae-angliae Rydb., Torreya 7:158 (1907)

P. richardsonii Rydb., Torreya 7:159. (1907)

Arabidopsis novae-angliae (Rydb.) Britton in Britton & Brown, Ill. Fl. 2. ed. II., p. 176. (1913)

Plants with most of the variation of the species; stems ascending to erect, branched or simple; petals 2.5 - 4.9 (7.5) mm long, (0.7) 0.9 - 2.3 mm wide; flowers usually developing normal siliques.

Sandy, gravelly soil along streams and rivers, lake shores, roadsides, moraines, and solifluction soils. Widely distributed in northern North America from Alaska east to Great Bear Lake, south through the Rocky Mountains to southern Alberta and British Columbia (with isolated occurrences in Colorado), north through the western Canadian Arctic Archipelago in isolated locations to northern Ellesmere Island; isolated populations in western and eastern Greenland, Hudson Bay, Newfoundland, Anticosti Island, Vermont, and the north shore of Lake Superior. Figure 43.

N=14, 21, 28, 35; 2n=28, 42, 56, 70.

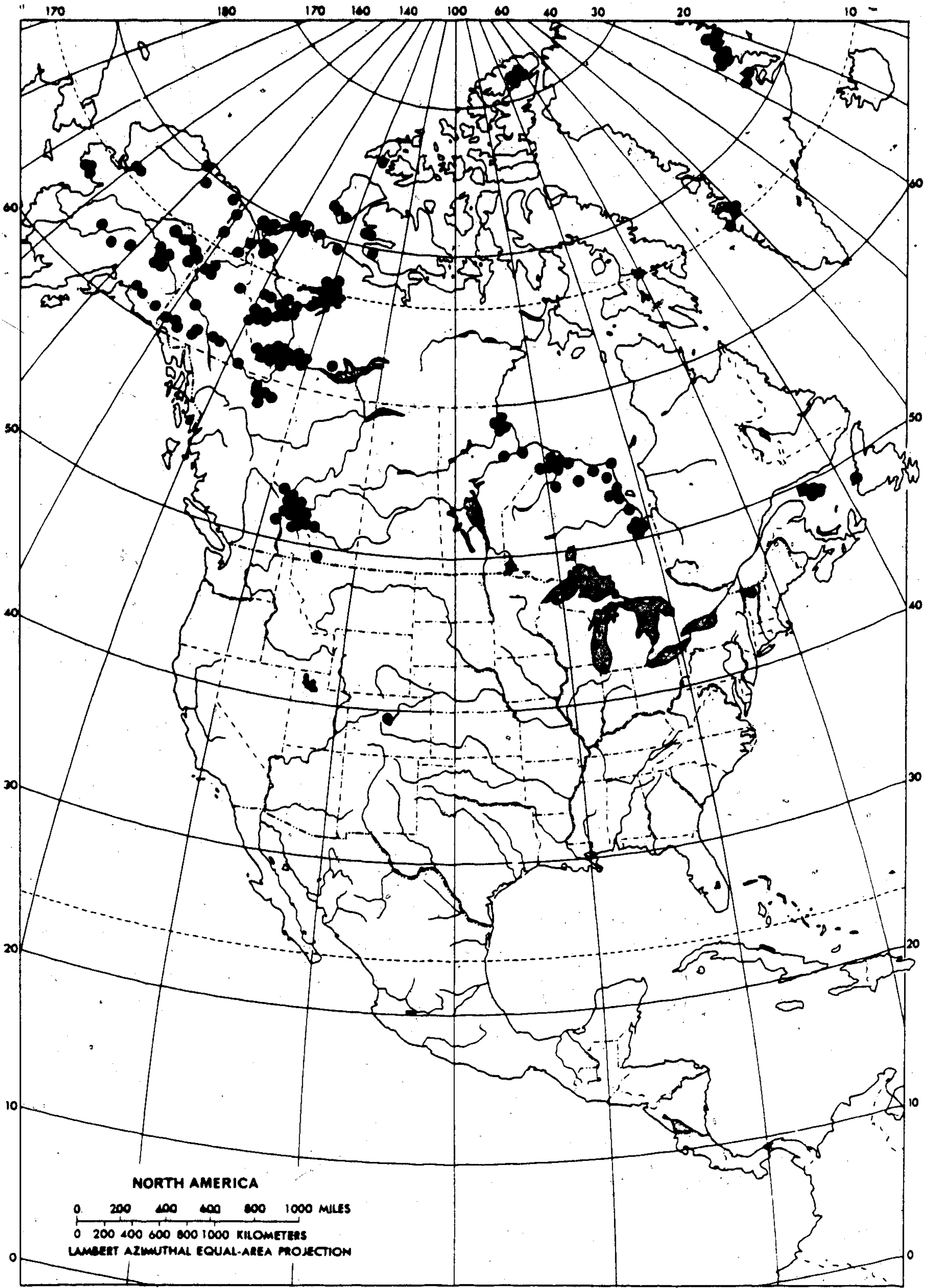
Type: Altai Mountains of Central Asia, 18[illegible] *Bunge 1033*, LE (holotype) Figure 44, ALTA-photo!

The long list of synonyms of *Braya humilis* var. *humilis* attests to the taxonomic confusion which has prevailed in this taxon throughout the last 150 years. Various epithets have been proposed for many of the morphological forms of the species across North America, and the confusion caused by this abundance of names for only slightly-different populations has been compounded by numerous transfers and changes of rank.

I have already discussed Abbe's (1948) six numbered races of *Braya humilis* in eastern North America, and I will not go into the subject again in detail. Suffice it to say that I agree with Abbe that these six morphological forms do not warrant taxonomic recognition. The differences between the forms are slight and somewhat overlapping, and very similar forms can be found in western *B. humilis* populations. In fact, in a common garden, several populations from the Rocky Mountains were essentially identical to naturally occurring populations from eastern North America. Only the Newfoundland and East Greenland races, the two most distinctive of Abbe's six races, perhaps require some additional discussion.

Race 4, from Newfoundland, is composed of very short, dwarfed plants which look markedly different from most other populations of *Braya humilis*. Böcher (1956) considered the Newfoundland race to be a subspecies of *B. novae-angliae* and named it subsp. *abbei*, after E.C. Abbe. Boivin (1968) later transferred the epithet to *B. humilis* as a variety of that species. These Newfoundland plants are known only from dry limestone ledges of Table Mountain, near Port à Port Bay. Fruiting attributes are similar to other eastern *B. humilis* populations, and it seems likely that the dwarfed habit may be just a phenotypic response to its exposed environment. Common garden studies would be useful in determining unequivocably

Figure 43. Distribution of *Braya humilis* var. *humilis* in North America.


170
180
170
160
140
100
60
40
30
20
10
60
50
40
30
20
10
0
NORTH AMERICA
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
120
110
100
90
80

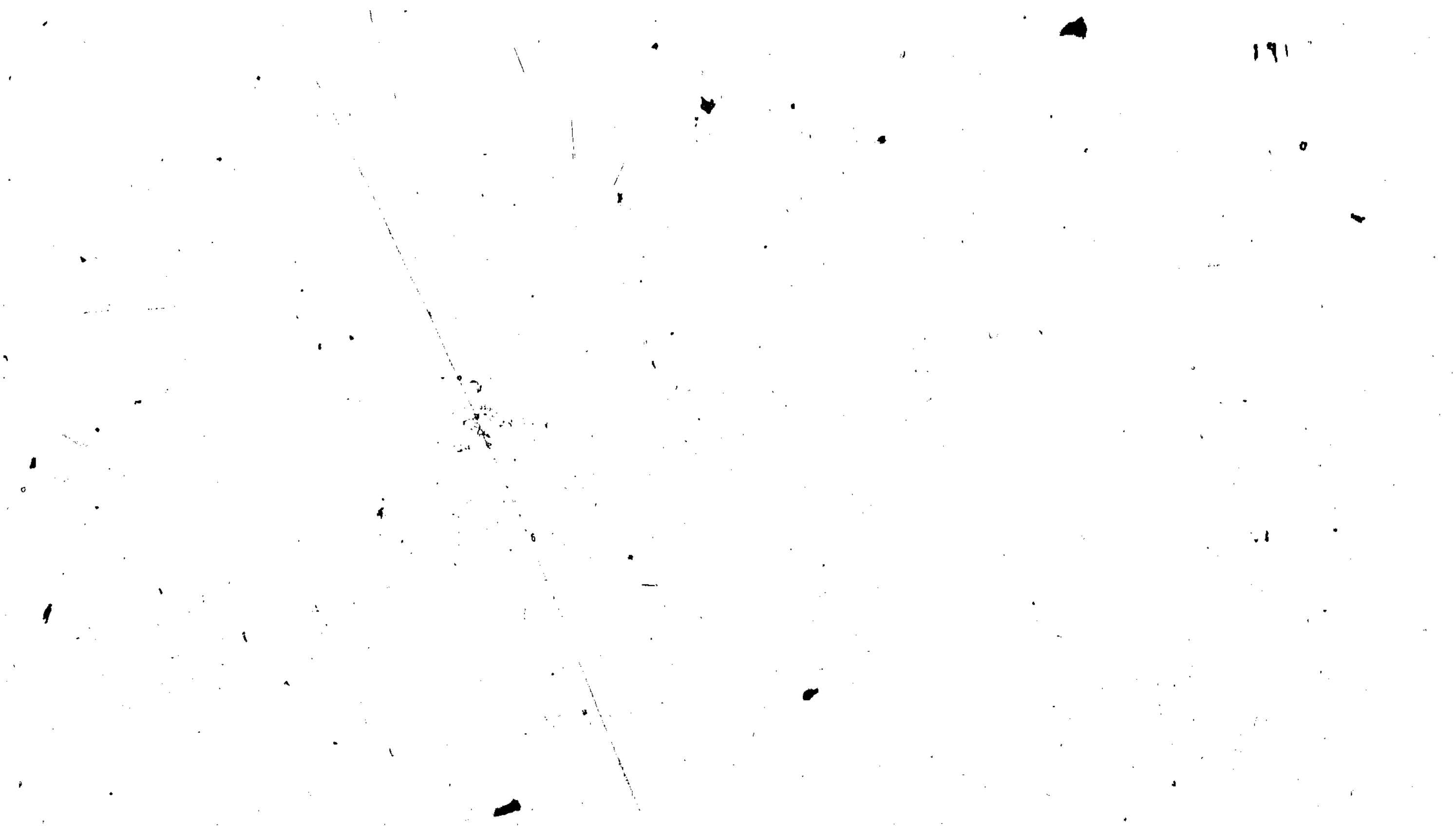


Figure 44. Type specimen of *Braya humilis* (C.A. Mey.) Robins. var. *humilis*.

1033 Altai
In subsalsis siccis ad fluvium
[illegible], [illegible], [illegible] legit
[illegible] Ledebour, ad fluvium [illegible]
[illegible] Bunge.
[illegible] floret Junio Julio,
[illegible]

N Ikonnikov Galitzky
[illegible]
[illegible]
[illegible]

the correct status of this population. For the time being, I have chosen to take a broad view of *B. humilis*, one that allows the submergence of the Newfoundland race within the variable var. *humilis*.

Abbe's (1948) Race 6, from East Greenland, differs from other eastern North American populations of *Braya humilis* in the shorter styles, the bilobed stigmas, the usually simple stems, and in the somewhat broader and more spreading siliques. Böcher (1950) chose to recognize the East Greenland material as a separate subspecies of *Torularia humilis*, subsp. *arctica*. Rollins (1953) transferred the taxon to *Braya*, and Boivin (1969) changed the rank from subspecies to variety, as *B. humilis* var. *arctica*.

As envisioned by Böcher (1956), *B. humilis* subsp. *arctica* ranges from East Greenland through the Canadian Arctic Archipelago to the Mackenzie Delta area. It is true that most *B. humilis* populations within this region display most of the attributes mentioned above and are readily separable from other eastern North American populations. The problem lies more in distinguishing this high arctic material from western North American and Asian plants.

Böcher (1956) maintains that *Braya humilis* subsp. *arctica* differs from Asian *B. humilis* in the size of the flowers, siliques, styles, and pedicels, and in the shape of the stigma. A comparison of East Greenland and Asian *B. humilis* collections, however, indicates that the differences in these attributes do not hold up reliably; there is a tremendous overlap in all of them. I can see no justification for maintaining the East Greenland-Canadian Arctic Islands populations as distinct from typical Asian *B. humilis*.

Also in East Greenland, is another morphological form, the decaploid *Braya intermedia*. Sørensen (1954) thought it likely that *B. intermedia* arose as a hybrid between *B. purpurascens* (*glabella*) (2n=56) and *B. linearis* or *B. humilis* (both 2n=42), and perhaps this is the case. Sørensen listed several attributes that supposedly distinguish *B. intermedia* from *B. linearis* and *B. humilis*, the most important of which are the broader, more torulose siliques, the widened torus, the elongated style, and the chromosome number (2n=70). As a type specimen, Sørensen chose a plant with very short, broad siliques that look quite different from those in most *B. humilis* populations. The specimens listed as paratypes, however, have siliques very similar to those in many *B. humilis* plants from the area. This, coupled with the variability in torus width and style length, make it nearly impossible to reliably separate *B. intermedia*, as envisioned by Sørensen, from neighboring hexaploid *B. humilis* populations. It should also be noted that siliques essentially identical to those on Sørensen's type specimen are occasionally found on Alberta *B. humilis* plants (Porsild & Breitung 16086, 16028, 14713 CAN). These plants also have a high percentage of aborted ovules; perhaps they are also decaploid.

Despite the unique chromosome number and the somewhat unusual silique shape, *Braya intermedia* is not consistently distinguishable from *B. humilis* var. *humilis*, and the two names are considered here to be synonyms. The earliest name, *B. humilis* var. *humilis*, is, therefore, the valid name of the taxon.

In the continental Northwest Territories, Yukon, and Alaska, the high arctic form of *Braya humilis* grades into a larger, more branched, and generally more densely pubescent morphological form which extends south through Alberta and British Columbia. Rydberg (1907) separated this western North American material from typical Asian *B. humilis* as *Pilosella richardsonii* (*B. richardsonii* (Rydb.) Fern.) on the basis of the thicker leaves, the short, dense pubescence, and the thicker, more torulose siliques. Rydberg apparently had very few collections to examine or he would have seen that these purported differences are completely unreliable in separating Asian and North American *B. humilis*; these attributes are entirely overlapping and extremely variable. In fact, these northwestern North American *B. humilis* populations are, as has been noted by Rollins (1953), more similar to Asian plants than are those from other areas of North America. There is little question that *B. richardsonii* must be placed into synonymy under *B. humilis* var. *humilis*.

The differences between the northwestern North American and East Greenland-Canadian Arctic Islands forms of *Braya humilis* also are not reliable enough to allow taxonomic separation. Many of the continental plants are not at all densely pubescent, scarcely or not at all branched, and quite small; while many of the high arctic plants can be quite pubescent, very branched (e.g., the type specimen of *Torularia humilis* ssp. *arctica* from East Greenland), and quite tall. Cody and Porsild (1980) have noted that high arctic plants have more spreading siliques than do the continental plants, and, indeed, this is a general trend, but it is not nearly universal enough to reliably distinguish specimens from the two regions.

In the Mackenzie Mountains and Rocky Mountains *Braya humilis* populations are at their most diverse. The plants there run the gamut of morphological extremes of the attributes used to characterize *B. humilis* forms in other areas. This is probably due to the somewhat more continuous distribution of the species in these areas, and to the presence of three different chromosome numbers, 2n=28, 2n=42, and 2n=56. There seems to be no tenable alternative to including most of these morphological forms within *B. humilis* var. *humilis*.

Rollins (1953) erected *Braya humilis* subsp. *ventosa* for the isolated populations of the species from central Colorado; he felt that the Colorado plants differed from the eastern North American forms about as much as did those of Böcher's (1950) subsp. *arctica*. The Colorado plants *do* look different than the eastern plants, but they are identical to plants from some Alberta populations. Some other Alberta populations, in turn, are very similar to the eastern plants.

Common garden studies indicate that the low stature and ascending stems of Colorado plants, and some Alberta plants, is environmentally controlled (these plants are all generally from similar habitats on alpine scree slopes). When cultivated in the greenhouse they are much more erect, with longer styles, and they appear very much like plants growing along rivers and streams in Alberta, British Columbia, eastern Canada, and Vermont. There appears to be no reason to maintain subsp. *ventosa* as distinct from *Braya humilis* var. *humilis*.

From the North American center of diversity in the Rocky Mountains and Mackenzie Mountains, *Braya humilis* seems to radiate out segments of the species diversity in various directions. Large, multi-branched, short-styled forms range north through the Mackenzie River Valley to Inuvik, and west through the Yukon to central Alaska. These forms gradually give way to smaller, less branched forms with spreading siliques that range from the Mackenzie Mountains north through the Canadian Arctic Archipelago to eastern Greenland, and west along the Arctic coast to the Seward Peninsula in Alaska. Erect, long-styled forms with slender siliques from the Rockies are disjunct to eastern continental North America and western Greenland.

Seen in this light, with the East and West Greenland populations of *Braya humilis* connecting back to the bank of diversity in western Canada along separate morphological pathways, it is not surprising that the East Greenland populations are somewhat different from the West Greenland and eastern North American populations.

Representative specimens: **CANADA: ALBERTA:** Jasper Natl. Park, roadside ditch, *E.H. Moss 4997* (ALTA, CAN, DAO), *E.H. Moss 4601* (ALTA, CAN, DAO); Jasper Natl. Park, rocky river fan, *S. Scott s.n.* (DAO); Jasper Natl. Park, Sunwapta, *Mrs. C. Schaffer 855, 856* (PH); Jasper Natl. Park, Athabasca, *Mrs. C. Schaffer 854* (PH); Jasper Natl. Park, Devona Wardens Cabin, *P.W. Stringer 536* (ALTA); Jasper Natl. Park, Jasper Lake, *P.W. Stringer 537* (ALTA); Jasper Natl. Park, Fiddle Creek, Athabasca River, *W. Spreadbough 19252* (CAN); Jasper Natl. Park, Talbot Lake area, *J. Cuddeford s.n.* (DAO); Jasper Natl. Park, upper Athabasca River, *J. Cuddeford s.n.* (DAO); Jasper Natl. Park, below Morro Peak along Athabasca River, *J.A. Calder & K.W. Spicer 33838* (DAO 278303, 278302); Jasper Natl. Park, Vine Creek, between Grassy Ridge and De Smet Range, *L.R. Hettinger 57, 68, 313* (ALTA); 6 mi. E of Jasper Natl. Park boundary on David Thompson Hwy., *M.G. Dumais & K. Anderson 2878* (ALTA); 13 mi. E of Jasper Natl. Park boundary on David Thompson Hwy., *M.G. Dumais & K. Anderson 2242* (ALTA); Jasper Natl. Park, Athabasca Valley, S spur of De Smet Range, *A.E. Porsild 21287, 21288* (CAN); Jasper Natl. Park, base of Mt. Grenoch above Devona Road, *A.E. Porsild 20886* (CAN); Jasper Natl. Park, near mouth of Willow Creek, *R. Boonstra & L.N. Carbyn 71* (ALTA); Kinky Lake, ca. 5 mi. E of Jasper Natl. Park gate, *M.G. Dumais 6264* (ALTA); Jasper Natl. Park, near "Kiefer's Kozy Kabins" camp, *G.H. Turner 5206* (ALTA); Jasper Natl. Park, Sunwapta River, Columbia Icefield, *F.J. Hermann 12723* (ALTA); Jasper Natl. Park, Sunwapta River ca. 16 km due SE of Sunwapta Falls, *J.G. Harris & M. Harris 1566* (ALTA); Jasper Natl. Park, 1 mi. N of Athabasca Glacier, *I. Corns s.n.* (DAO); Jasper Natl. Park, Athabasca Glacier near Sunwapta Lake, *J.G. Harris & M. Harris 1568* (ALTA); Jasper Natl. Park, Columbia Icefield, ca. 60 mi. SE of Jasper, *H.J. Scoggan 16433* (CAN); Jasper Natl. Park, Columbia Icefields, terminal moraines, *A.E. Porsild & A.J. Breitung 16334* (CAN); Entrance, Alta, at Jasper Natl. Park gate, *G. Pegg 2078* (DAO); Jasper Natl. Park, Jasper Lake, *D.D. Sharp A164, A213, A193, B112* (ALTA); Jasper Natl. Park, near E gate, *J. Mclean s.n.* (DAO); Jasper Natl. Park, head of Sunwapta Valley, *S. Brown 1372* (PH); Jasper Natl. Park, Mistaya River, 44 miles S of Jasper, *A.E. Porsild 21312* (CAN); Banff Natl. Park, upper drainage of North Saskatchewan River, *A.E. Porsild & A.J. Breitung 14713* (CAN); Banff Natl. Park, North Saskatchewan River, near junc. with Howse River, *A.E. Porsild & A.J. Breitung 16086* (CAN); Banff Natl. Park, junct. of North Saskatchewan and Alexandra Rivers, *A.E. Porsild & A.J. Breitung 16028* (CAN); Banff Natl. Park, North Saskatchewan River N of Saskatchewan Crossing, *B. Boivin 5157* (DAO); Banff Natl. Park, Saskatchewan River above Bear Creek, *S. Brown 911* (PH); Banff Natl. Park, junct. North Fork of West Branch

Saskatchewan River, S. *Brown 1006* (CAN); Banff Natl. Park, "The Loop", *W.C. McCalla 3825* (ALTA); Banff Natl. Park, on road around the Loop, *Hanson 22318* (CAN); Banff Natl. Park, roadway, Lower Park, *N.B. Lanson s.n.* (DAO); roadside E of Banff Natl. Park, *D. Puellet (Pelluet?) 264* (ALTA, CAN); Bow River Valley, E of Banff Natl. Park, S. Brown 81 (PH); Banff Natl. Park, Bow River Valley, S slope of Mt. Cascade, *A.E. Porsild & A.J. Breitung 12389* (CAN); Banff Natl. Park, Lake Louise, moraines and alpine slopes near Victoria Glacier, *A.E. Porsild & A.J. Breitung 15703* (CAN); Banff Natl. Park, rocky ground, Lake Louise, *W.C. McCalla 2273* (ALTA); Banff Natl. Park, Molar Creek, *P. Achuff PA7029* (DAO); Banff Natl. Park, Mistaya Creek near Mt. Patterson, *A.E. Porsild & A.J. Breitung 16228* (CAN); Banff Natl. Park, head of Bow Lake, *J.G. Harris 1638* (ALTA); Banff Natl. Park, Bath Creek, ca. 5 km E of Kicking Horse Pass, *J.G. Harris 1640* (ALTA); Banff Natl. Park, Ball Pass S of Shadow Lake, *A.E. Porsild & A.J. Breitung 15467* (CAN); Banff Natl. Park, Parker Ridge, *J.G. Harris 1743* (ALTA); Banff Natl. Park, slopes of Mt. Saskatchewan, *A.E. Porsild & A.J. Breitung 16059* (CAN); Banff Natl. Park, head of Chaba Lake, *S. Brown 1213* (PH); Banff Natl. Park, Saskatchewan River Crossing, *J.A. Calder 23935* (DAO), *I. Corns IC7039* (DAO); Calgary, Elbow River Valley, *G.H. Turner 3775* (ALTA), *M.O. Malte & W.R. Watson 16* (CAN), *W.C. McCalla 8650* (ALTA), *Macoun 18174* (CAN), *W.C. McCalla 7389* (ALTA); White Goat Wilderness, *P. Lee 160* (ALTA); Escarpment Creek, 51° 51′ N 116° 17′ W, *P. McIsaac & B. Hamrell 969* (ALTA); Silver City, *Macoun 2085* (CAN); Waterton Lake, *Macoun 10327* (CAN); Windy Point, [illegible] mi. W of Nordegg on the David Thompson Hwy., *M.G. Dumais & K. Anderson 2960* (ALTA), *M.G. Dumais 4759* (ALTA, DAO); Lac des Arcs, S bank of the river, W of Kananaskis, *M. Dumais 7073* (ALTA); 6 mi. S of Kananaskis Forest Experiment Station, *A.E. Porsild & J. Lid 19273* (CAN); Kananaskis, *J. Macoun s.n.* (DAO); North Saskatchewan River, 48 mi. SW of Nordegg, *E.H. Moss 11004* (DAO); Lower Rock Creek Valley area, near E boundary of Willmore Wilderness Park, *G. Brown 64* (ALTA); Clearwater Forest Reserve, Saskatchewan Crossing, *A.E. Porsild 20494* (CAN), *A.E. Porsild 20493* (CAN); Clearwater Forest Reserve, Mt. Shunda N of Nordegg, *A.E. Porsild 20703* (CAN); Brazeau Natl. Forest Reserve, mouth of Whitehorse Creek, *A.E. Porsild 20826* (CAN); Prospect Mtn., 10 mi. SW of Cadomin, *P. Mortimer 356* (ALTA); Cardinal River, ca. 19 km due SSE of Cadomin, *J.G. Harris 1554* (ALTA); 10 mi. N of Grizzly Creek along road N of the Kananaskis Lakes, *T. Mosquin & M.H. Benn 5213* (DAO); Ram Mtn., between North Ram and North Saskatchewan Rivers, SW of Nordegg, *M. Dumais 7694* (ALTA); **BRITISH COLUMBIA:** Yoho Natl. Park, *A.E. Porsild 18350* (CAN); Yoho Natl. Park, Kicking Horse Valley, *S. Brown 212* (CAN, PH); Yoho Natl. Park, Kicking Horse River near Chancellor Pk. Campground, *J.G. Harris 1627* (ALTA); Yoho Natl. Park, S side of Kicking Horse Creek, *J.G. Packer 1969-38* (ALTA); mountains at Kicking Horse Lake, *J. Macoun 2083* (CAN); Yoho Natl. Park, Kicking Horse River 1 mi. W of Field, *W.C. McCalla 7538* (ALTA); Yoho Natl. Park, Mt. Stephen at Field, *J.A. Calder & D.B.O. Savile 12084* (DAO); Yoho Natl. Park, Kicking Horse River opp. Mt. Stephen, *W.C. McCalla 7540* (ALTA), *W.C. McCalla 9565* (ALTA); Yoho Natl. Park, Field, B.C., *E.M. Farr s.n.* (PH); Yoho Natl. Park, 10 mi. S of Field on Hwy. 1, *R.L. Taylor & L.C. Sherk 4938* (DAO); Yoho Natl. Park, Kicking Horse River below Wapta Falls, *W.C. McCalla 7485* (ALTA); Yoho Natl. Park, flats at head of Emerald Lake, *W.C. McCalla 7031* (ALTA); Yoho Natl. Park, Yoho River near Takakkaw Falls, *J.G. Harris 1630* (ALTA); Kootenay Natl. Park, Vermilion River near the Paint Pots, *J.G. Harris 1641, 1642* (ALTA); Kootenay Natl. Park, Vermilion River ca. 14 km above Kootenay Crossing, *J.G. Harris 1643* (ALTA); Kootenay Natl. Park, Marble Canyon, *R.G.H. Cormack s.n.* (ALTA); Kootenay Natl. Park, Ochre Bend Trail, *K. Seel 55* (DAO); One mi. NE of junct. of Martin and Blaeberry Creeks, *R.L. Taylor & D.H. Ferguson 1840A* (DAO); Kootenay River at Canal Flats, *R.L. Taylor & D.H. Ferguson 3899* (DAO); Columbia Valley, flats of the Columbia River, Golden, B.C., *A.E. Porsild & A.J. Breitung 16536* (CAN); Junct. of Waitabit Creek and Columbia River, *R.L. Taylor & D.H. Ferguson 1746* (DAO); Mt. Kinbasket, Big Bend Hwy., *J.W. Eastham 16017* (DAO); Base of Kinbasket Mtn. on NE side of Kinbasket Lake along Big Bend Hwy., *J.A. Calder & D.B.O. Savile 11979* (DAO); Middle channel of Kinbasket River, Kinbasket Lake, *R.L. Taylor & D.H. Ferguson 770* (DAO); Kinbasket, Big Bend Hwy., *J.W. Eastham 16307* (ALTA, DAO); Kechika River, 20 miles N of Sifton Pass, *N.C. Stewart 13191* (CAN); Muncho Lake Prov. Park, Alaska Hwy. km 700, *J.G. Harris 1551* (ALTA), *W.J. Cody & K.W. Spicer 16332* (DAO); Alaska Hwy., Trout River N of Muncho Lake Prov. Park at mile 482, *J.A. Calder & J.M. Gillett 25561* (DAO); Muncho Lake Prov. Park, N of Muncho Lake, *A.E. Porsild 22347* (CAN); Muncho Lake Prov. Park, E side of Muncho Lake, *J.A. Calder & J.M. Gillett 25590* (DAO); Racing River, at mile 418.8 Alaska Hwy., N of Racing River Bridge, *S.L. Welsh & G. Moore 7345* (BRY); Racing River at mile 418 Alaska Hwy., *J.A. Calder & J.M. Gillett 24672* (DAO); Racing River at mile 416 Alaska Hwy., *J.A. Calder & J.M. Gillett 25463* (DAO); Tetsa River, mile 379 Alaska Hwy., *S.L. Welsh & G. Moore 7300* (BRY); Alaska Hwy., mile 437, *T.M.C. Taylor, A.F. Szczawinski, & M. Bell 274* (CAN, DAO); **MANITOBA**: Churchill area, *E. Beckett 26a* (CAN), *J.M. Gillett 2242* (MT, DAO), *W.B. Schofield & H.A. Crum 6586* (CAN), *D.K. Brown 741* (DAO, CAN), *W.G. Dore 10006* (DAO), *10143* (DAO, CAN), *P.Q. MacKinnon 22* (DAO), *H.J. Scoggan 13894* (CAN), *H.M. Raup 1967* (CAN); York Factory, *H.J. Scoggan 6176* (CAN); Limestone River near Gillam, *W.B. Schofield 1102* (DAO); **NEWFOUNDLAND:** Region of Port à Port Bay, Table Mountain, *M.L. Fernald & H. St. John 10837* (PH, MT, DAO-photo); **NORTHWEST TERRITORIES:** Nahanni Natl. Park, Direction Mtn., *B.J.J. Meuleman M5011* (DAO); Nahanni Natl. Park, Nahanni Plateau, *G.W. Scotter 23596; 23562* (DAO); Nahanni Natl. Park, confluence of Flat and South Nahanni Rivers, *A.L. Cairns 1206* (DAO), *G.W. Scotter 24175, 24176* (DAO); Nahanni Natl. Park, vicinity of Virginia Falls, *G.W. Scotter 23628, 24192, 22799* (DAO), *S. Talbot T 6028-19* (DAO); Nahanni Natl. Park, Deadman Valley area, *H.M. Kershaw 771* (ALTA), *H.M. Kershaw 96* (DAO), *A.H. Marsh 6575, 6000, 4896, 6217, 4988* (DAO), *G.W. Scotter 23523, 23340, 23375, 23392, 12361, 12919, 12267, 12261, 12921, 12440, 23512, 12802, 12947, 12790, 22740* (DAO); Mackenzie Mountains, near confluence of N. Nahanni and Mackenzie Rivers, *A.E. Porsild 16635* (CAN), *V.C. Wynne-Edwards 8477, 8478, 8479* (CAN); Mackenzie Mountains, Canada Tungsten Mine area, *W.J. Cody & K.W. Spicer 16371* (DAO), *K.W. Spicer 1597, 1662* (DAO); Nahanni Range, W end of Little Doctor Lake, *W.J. Cody & K.W. Spicer 12128* (DAO); Nahanni Range, W end of Cli Lake, *W.J. Cody & K.W. Spicer 12303, 12259* (DAO); Mackenzie Mountains, Carcajou Lake, *W.J. Cody & F.M. Brigham 20519* (DAO); Mackenzie Mountains, Florence Lake, *W.J. Cody & F.M. Brigham 20980* (DAO); Mackenzie Mountains, Mirror Lake, *W.J. Cody & F.M. Brigham 20414* (DAO); Mackenzie Mountains, Tern Lake, *W.J. Cody & G.W. Scotter 19518* (DAO); Carcajou River, mi. 23E Canol Rd., *W.J. Cody & R.L. Gutteridge 7774* (DAO); Mackenzie Mountains, Keele River area, *W.J. Cody 20049* (DAO), *E. Kvale & K. Haggard 265* (DAO), *W.J. Cody & G.W. Scotter 19356, 19205, 19370, 19166, 19268* (DAO); Mackenzie Mountains, Twitya River ca. 2 mi W of Deca Creek, *W.J. Cody & G.W. Scotter 19456* (DAO), *W.J. Cody 19995* (DAO); Mackenzie Mountains, June Lake area, *W.J. Cody 17112, 17108, 17235* (DAO); Fort Simpson area, *W.J. Cody & J.M. Matte 8799* (MT, DAO, ALTA), *W.J. Cody & J.M. Matte 8030, 8087, 9334, 9039, 8154* (DAO), *H.M. Raup & J.H. Soper 9918* (ALTA, CAN), *G. Lawson s.n.* (CAN), *V.C. Wynne-Edwards 8601* (CAN), *J.G. Harris 1657* (ALTA); Liard River at Mackenzie Hwy. crossing, *J.G. Harris 1659* (ALTA); Mackenzie Hwy., Trout River, *J.G. Harris 1670* (ALTA); Mackenzie River, 10 mi above Sans Sault Rapids, *A.E. Porsild 16722* (CAN); Mackenzie River-Yellowknife Hwy., mi. 39, *J.W. Thieret 9100* (DAO); Great Bear River, Mt. Charles, *A.E. & R.T. Porsild 3294* (MT, CAN); NW shore of Great Bear Lake, between Jones Point and Fort Rae, *R. Bedford 1925* (CAN); Great Bear Lake, N shore of McTavish Arm, *A.E. & R.T. Porsild 5177* (CAN); Great Bear Lake, mouth of Haldane River, *A.E. & R.T. Porsild 5039* (CAN); Mackenzie River, Bear Rock, *A.E. & R.T. Porsild 3383* (CAN), *A.E. Porsild 16710* (MT, CAN); Norman Wells area, *J.K. Rigby 40* (BRY, DAO), *W.J. Cody & R.L. Gutteridge 7339* (DAO), *7329* (ALTA, DAO), *W.J. Cody 2808, 13166* (DAO), *2815* (DAO, MT); Mackenzie River Delta at Inuvik, *J.G. Harris 1432* (ALTA); Mackenzie River Delta, Jackfish Creek, *J.D. Lambert s.n.* (DAO); Mackenzie River Delta, Campbell Lake, *A.E. & R.T. Porsild 1991, 1925* (CAN), *W.J. Cody & F. Kehoe 12692, 12715, 12723, 12732* (DAO); Liverpool Bay, Nicholson Island, *A.E. & R.T. Porsild 2890* (CAN), *A.E. Porsild 16780* (CAN); Tuktoyaktuk Penin., *C.D. Larsen & W.H. Owen 74-4201* (DAO); N side or Richards Island, Mackenzie Delta, *W.J. Cody & D.H. Ferguson 10007* (DAO), *A.E. & R.T. Porsild 2228, 2234, 2235* (CAN), *A.E. Porsild 16826, 16827* (CAN); DEW line site, Pin 1, Clinton Point, *J.A. Parmelee 3208* (DAO); Cape Dalhousie, *A.E. & R.T. Porsild 2761* (CAN); Atkinson Point, *A.E. & R.T. Porsild 2622* (CAN); Cape Parry Penin., near the Horton River, *G.W. Scotter & S. Zoltai 25853* (DAO); West Cache Creek, *S.L. Welsh & J.K. Rigby 12064* (BRY); Ellesmere Island, Hazen Camp, Lake Hazen, *W.J. Maher 36* (DAO), *C.R. Harrington s.n.* (ALTA), *P. Kevan s.n.* (ALTA), *D.B.O. Savile 4669, 4455* (DAO), *4544* (DAO, ALTA); Eglinton Island, *M. Kuc s.n.* (CAN); Banks Island, Masik River, *M. Kuc s.n.* (CAN); Banks Island, De Salis Bay, *A.E. Porsild 17624* (CAN); Banks Island, Sachs Harbour, *A.E. Porsild 17517* (CAN); Victoria Island, vicinity of Holman Island trading post, *A.E. Porsild 17291* (ALTA, CAN), *17292* (CAN); Victoria Island, Wollaston Land, *D. Jenness 411* (CAN); **ONTARIO:** junct. of Fawn and Poplar Rivers, *D.R. Moir 893* (CAN, MT); 32 mi from mouth of Black Duck River, *D.R. Moir 1931* (MT); Fort Severn, *I. Hustich 1435* (CAN); junct. of Fawn River and Mink Creek, *D.R. Moir 743* (CAN); Winisk and Shamattawa River junct., *W.K.W. Baldwin 7890* (CAN); Severn River, opp. mouth of Beaver River, *D.R. Moir 244* (CAN); Severn River, Hudson Bay, *J. Macoun 2087* (CAN); Lake River, James Bay, *A. Dutilly & E. LePage 16782* (DAO); Albany, James Bay, *A. Dutilly & E. LePage 15941* (DAO); Winisk River, Hudson Bay, *A. Dutilly & J. Frenette 40063* (MT); Attawapiskat River, junct. with Muketei River, *A.E. Porsild, W.K.W. Baldwin, H. Sjors & G. Sjors 19980* (CAN); down river from Atik Island, *W.K.W. Baldwin 7600* (CAN); Polar Bear Prov. Park, Cape Henrietta Maria, *H.G. Lumsden 3021* (CAN); 60 miles up Kapiscon River, *W.J. Wilson 54009* (CAN); mouth of Ekman River, *D.B. Dowling 34555* (CAN); Moose Factory, James Bay, *W. Baldwin, I. Hustich, J. Kucyniak & R. Tuomikoski 718* (MT, CAN); *A.E. Porsild 4636* (CAN); Moose River, Moosonee, James Bay, *A. Dutilly & E. LePage 15441* (CAN, DAO, MT); Moose and Abitibi Rivers, *A. Dutilly & E. LePage 36534* (MT, DAO, CAN); **QUEBEC: Anticosti Island:** Galiote River, *F.F. Marie-Victorin & Rolland-Germain 24846* (PH, MT, CAN); Jupiter River, *J. Macoun (335113)2086* (CAN), *F.F. Marie-Victorin & Rolland-Germain 24845* (MT), *F.F. Marie-Victorin & Rolland-Germain 24847* (MT), *F.F. Marie-Victorin & Rolland-Germain 24848* (PH, MT), *F.F. Marie-Victorin & Rolland-Germain 24849* (MT, CAN, PH); Chicotte River, *F.F. Marie-Victorin & Rolland-Germain 24850, 27202* (MT, CAN); Brick River, *F.F. Marie-Victorin & Rolland-Germain 27203* (MT, PH); Riviere des Caps, *F.F. Marie-Victorin & Rolland-Germain 27208* (MT); McKane River, *F.F. Marie-Victorin & Rolland-Germain 27263* (MT, CAN); **YUKON:** Yukon River above Rink Rapids, *J. Macoun 58380* (CAN); Cassiar Mtns., 60° 12′ N 130° 28′ W, *W.H. Poole 115* (DAO); Ingersoll Islands, *M.W. Gorman 993* (CAN); Bonnet Plume River, 65° 01′ N 134° 05′ W, *P. Vernon s.n.* (DAO); near Porter Creek, Whitehorse area, *J.M. Gillett 3547* (DAO); Porter Creek, 3 miles N of Whitehorse, *J.M. Gillett 3487* (MT, DAO); McIntyre Creek 3 miles N of Whitehorse, *J.M. Gillett 3469* (DAO); Rose-Lapie River Pass, Canol Rd. mile 116, *A.E. Porsild & A.J. Breitung 10062* (CAN); Rose-Lapie River Pass, Canol Rd. mile 118, *A.E. Porsild & A.J. Breitung 10138* (CAN); Rose-Lapie River Pass, Canol Rd. mile 105, *A.E. Porsild & A.J. Breitung 10899* (CAN); Near conflux of Dezadeash, Kaskawulsh & Alsek Rivers, 12 mi. SW of Haines Junction, *A.M. Pearson 126* (CAN); St. Elias Mtns., Kaskawulsh River Valley, *A.M. Pearson 67-28A* (CAN); St. Elias Mtns., Steele Glacier and vic., *D.F. Murray & B.M. Murray 1406* (CAN); Alaska Hwy. mi. 1133, ca. 0.4 km W of Donjek River bridge, *G.W. Douglas 10300* (BRY); Vicinity of Mackintosh (Alaska Hwy. mi. 1022), ca. 8 mi. W of Mackintosh, *W.B. Schofield & H.A. Crum 7551* (CAN); Kluane Lake at mi. 1070 Alaska Hwy., *S.L. Welsh & G. Moore 7884* (BRY); south end of Kluane Lake at mi. 1054 Alaska Hwy., *S.L. Welsh & G. Moore 7848* (BRY); Slims River Valley, ca. 2 km W of Slims River, *G.W. Douglas & G.G. Douglas 8475* (BRY, DAO); mountains above Vulcan Creek, S end of Kluane Lake, *W.B.*

Schofield & H.A. Crum 8210 (CAN); S end of Kluane Lake, *M.P. Porsild & R.T. Porsild 13* (CAN); Ogilvie Mtns., Dempster Hwy., km 160, *J.G. Harris 1470* (ALTA); Windy Pass, Dempster Hwy., km 155, *J.G. Harris 1409* (ALTA); Dempster Hwy., Engineer Creek' Campground at km 194, *J.G. Harris 1413* (ALTA); Ogilvie Mtns., 65° 30′ N 137° 05′ W, *L.H. Green 12* (DAO); Ogilvie Mtns., Dempster Hwy. mi. 83, *R.T. Porsild 1514, 1701* (CAN); Ogilvie Mtns., Dempster Hwy. mi. 110, *A.E. Porsild & R.T. Porsild 23632* (CAN); Ogilvie Mtns., Dempster Hwy. mi. 148, *R.T. Porsild 2018* (CAN); Richardson Mtns., Rock River, Dempster Hwy. km 438.6, *J.G. Harris 1465* (ALTA); Firth River at junct. with Muskeg Creek, *S.L. Welsh & J.K. Rigby 10565* (BRY); Rampart House on the Alaska-Yukon border, *J.E.H. Martin 100* (DAO); **GREENLAND: East Greenland:** head of Franz Joseph Fjord, *Seidenfaden 523.b* (CAN); Gauss Penin., Western Parallel Valley, *G. Wängsjö s.n.* (DAO); Vibeke Sø, Ole Rømers Land, *F.H. Schwarzenbach 511m* (C); Krumme Langsø, Ole Rømers Land, *F.H. Schwarzenbach 1253* (C); Charcots Land, 71° 54′ N 29° 00′ W, *K. Holmen & S. Lægaard 613* (C); west side of Loch Fynes Bünd Fjældmark, *G. Seidenfaden 196* (C); Hinks Land, Nordvestfjord, Scoresby Sund, *G. Halliday 127/71* (CAN); Ella Island, Cape Oswald, *T. Sørensen 3556b, 3575c, 4223, 3562a, 3575e* (C); Musk-ox Fjord, *G. Seidenfaden 292.b* (MT), *332* (C), *J. Vaage s.n.* (CAN); Ymer Island, Blomsterbugten, *G. Seidenfaden 401* (MT); Ymer Island, Carl Jacobsen Bugt, *T. Sørensen 3060a* (C); Clavering Island, Granatelv., *T. Sørensen 4231* (CAN); Clavering Island, Green Valley, *T. Sørensen 799* (CAN); **West Greenland:** Sondre Stromfjord area, *T.W. Böcher 489* (DAO), *A.E. Porsild 8646* (CAN), *D.C. Nutt 325* (CAN), *H.G. Vevers 197* (DAO); Itivdleg Fjord, Quiqua, *M.P. & A.E. Porsild s.n.* (MT); **U.S.A.: ALASKA:** Delta Junction area, *M. Williams 2483* (BRY), *W.J. Cody & T.J.M. Webster 5481* (DAO, M), *J.G. Harris 1388* (ALTA), *W.J. Cody & T.J.M. Webster 5634* (DAO), *W.J. Cody & T.J.M. Webster 6013* (DAO); near Farewell Lake, 62° 32′ N 153° 37′ W, *W.H. Drury, Jr. 2540* (CAN); McGrath region, *W.H. Drury, Jr. 2231* (CAN); Circle airfield, *L.A. Spetzman 5023* (CAN); S bank of Yukon River at Circle, *S.L. Welsh & G. Moore 8466* (BRY); Anvil Hill, Nome, *E. LePage 23861* (DAO); Pump Station #3, Alyeska Pipeline Haul Road, *B. Welsh et al. 1199* (BRY); Colville River, ca. 13 mi S of Arctic River, *K.J. Stone 738* (BRY); Upper Sheenjek Valley, 8 mi N of Ambresvajun Lake (Last Lake), *A.R. Batten & C.G. Batten 75-236* (DAO); White Mtns., *O. Gjaerevoll 503* (CAN); George Parks Hwy., 5.5 km N of Denali Natl. Park turnoff, *J.G. Harris 1232* (ALTA); Alaska Range, Richardson's Hwy. between Summit and McCarty, *A.E. Porsild & R.T. Porsild 422* (CAN); Seward Peninsula, Anvil Mt., ca. 7 km NNE of Nome, *J.G. Harris 1331* (ALTA), *S.L. Welsh 5948* (BRY), *M. Williams 1544, 1544a* (BRY); Seward Peninsula, south coast near Bluff, *A.E. Porsild & R.T. Porsild 1238* (CAN); Onion Portage, 2 mi up Ambler River from village of Ambler, *C. Schweger & B. Schweger 93-46* (ALTA); North end of Walker Lake, S slope of Brooks Range, *G. Smith 2471* (CAN); Eagle Bluff, ca. 1 mi NW of Eagle, *S.L. Welsh & G. Moore 8633* (BRY), *A.R. Batten & J.C. Dawe 78-240* (DAO); Taylor Hwy., Jack Wade area, Forty Mile River, *M. Williams 2145* (BRY); Bank of the Yukon River at Eagle, *J.G. Harris 1393* (ALTA); Along Copper River, ca. 0.5 km above confluence with Chitina River, *J.G. Harris 1168* (ALTA); near head of Chitina River, *H.M. Laing 90* (CAN); along road to McCarthy, ca. 10 km from Copper River Bridge, *J.G. Harris 1174* (ALTA), *D. Taylor & J. Taylor 1* (ALTA); Tanana River near Johnson River, *L.A. Spetzman 561* (CAN); Richardson Hwy. near Salchaket Lake, *W.J. Cody & T.J.M. Webster 5876* (DAO); **COLORADO:** slope of North Star Mountain, W of Hoosier Pass, *R.C. Rollins & W.A. Weber 51288* (GH), *B.C. Johnston 2371* (ALTA), *H.D. Ripley & R.C. Barneby 10393* (GH), *R.C. Rollins, W.A. Weber & C. Livingston 5153* (GH), *A.E. Porsild & W.A. Weber 23099* (CAN), *W.A. Weber 8753* (M), *E. Hultén & W.A. Weber s.n.* (DAO); **VERMONT:** Willoughby Cliffs of Mt. Pisgah, SE tip of Willoughby Lake, *J.G. Harris 1742* (ALTA), *C.G. Pringle s.n.* (PH), *F.H. Horsford s.n.* (PH), *W.W. Eggleston & A.J. Grout s.n.* (PH), *G.G. Kennedy s.n.* (PH), *W.W. Eggleston 205* (PH), *C.H. Knowlton s.n.* (PH).

Var. **maccallae** J.G. Harris *var. nov.* Figure 45.

Differt a var. *ellesmerensi* et var. *humili* petalis grandioribus et siliquis saepe abortivis.

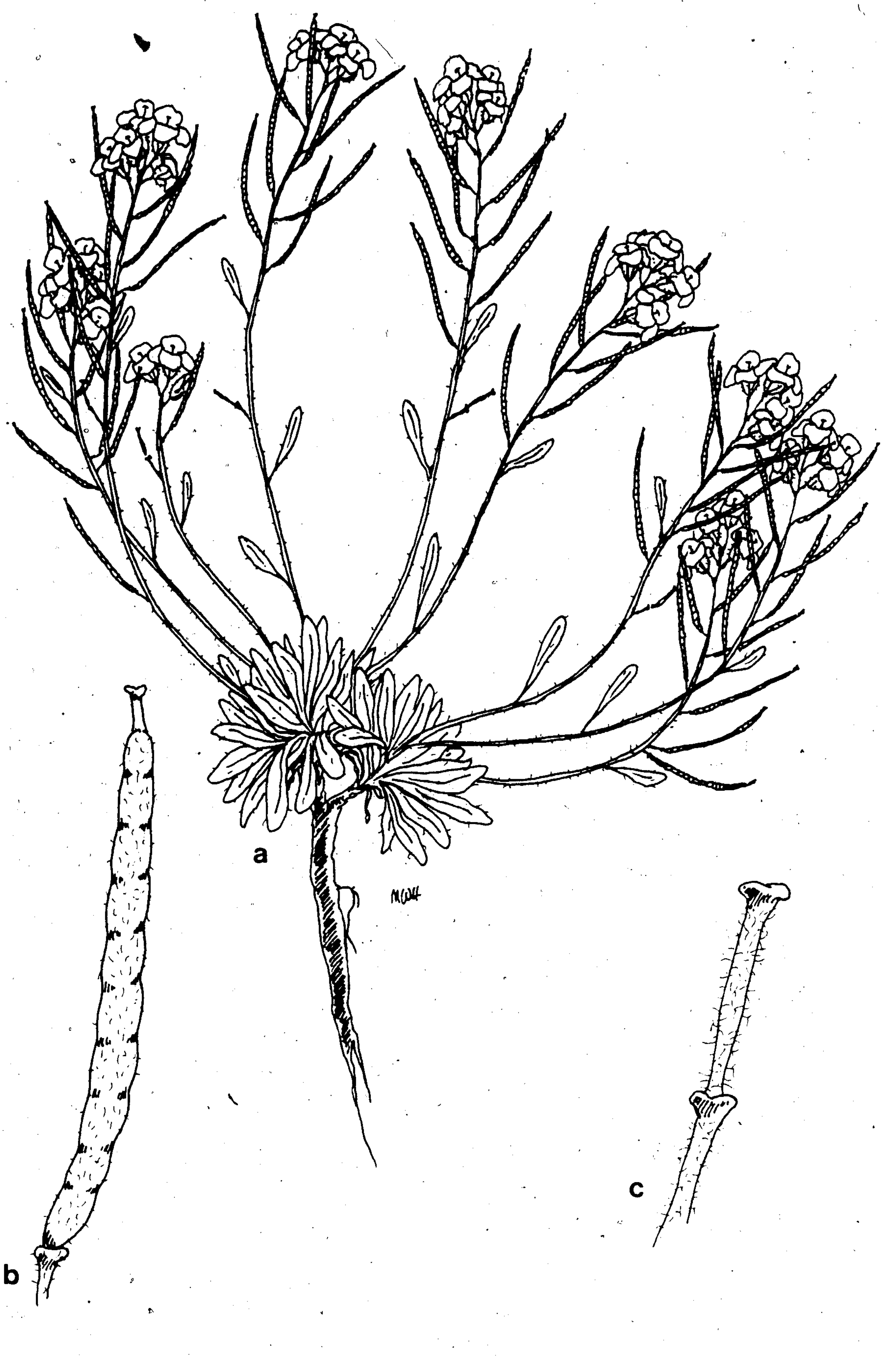
Stems ascending to erect, simple or sometimes branched, 4 - 23 cm tall, moderately pubescent with bifurcate and simple hairs; basal leaves from a pronounced rosette, oblanceolate, rounded or narrowly obtuse, sessile with a cuneate base to distinctly petiolate, entire or occasionally sinuate-dentate, 5 - 50 mm long, 1 - 7 mm wide, glabrescent to moderately pubescent with bifurcate and simple hairs; cauline leaves 3 - 5 (7), often much reduced, often arising from very near the stem base and giving an almost scapose appearance; sepals 2.3 - 3.6 mm long, 1.2 - 1.8 (2.0) mm wide, sparingly to moderately pubescent with long bifurcate and simple hairs, green to lightly purple-tinged; petals (4.4) 4.9 - 6.7 (7.2) mm long, (2.1) 2.3 - 4.0 (4.2) mm wide, usually distinctly and abruptly divided into a narrow claw and broad blade, white or the claw occasionally purple-tinged; siliques more or less torulose, often aborted and undeveloped, when fully developed 9 - 24 mm long, 0.7 - 1.2 mm wide, moderately to densely pubescent with bifurcate and simple hairs; style (0.4) 0.7 - 1.3 (1.5) mm long, fairly stout; stigma not at all capitate to moderately capitate, entire to bilobed; seeds 0.9 - 1.3 mm long, 0.45 - 0.65 mm wide.

Sandy, gravelly river banks and flood plains. Occasionally moving onto glacial moraines and slopes. Endemic to the southern Rocky Mountains of Alberta and British Columbia. Figure 46.

N=14, 2n=28.

Type: Canada, British Columbia, Yoho National Park, "flats of Kicking Horse River, opp. Mt. Stephen and east of Field, B.C.", 24 June 1943, *W.C. McCalla 7539*, ALTA! (holotype). Figure 47.

Figure 45. Illustration of *Braya humilis* var. *maccallae*; a. entire plant (natural size); b. silique (x 7); c. aborted silique (x 10).


a
b
c

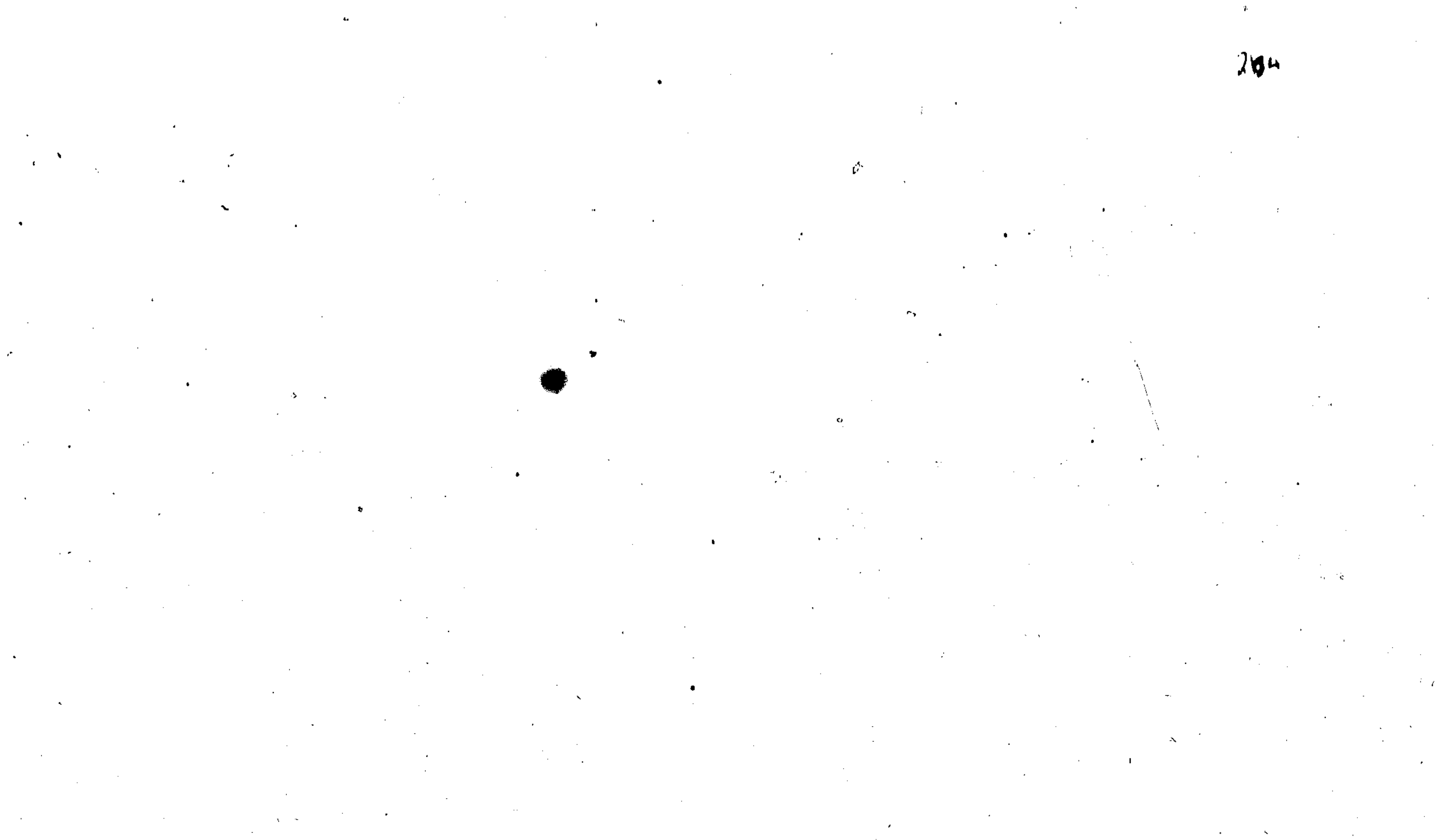


Figure 46. Distribution of *Braya humilis* var. *maccallae*.

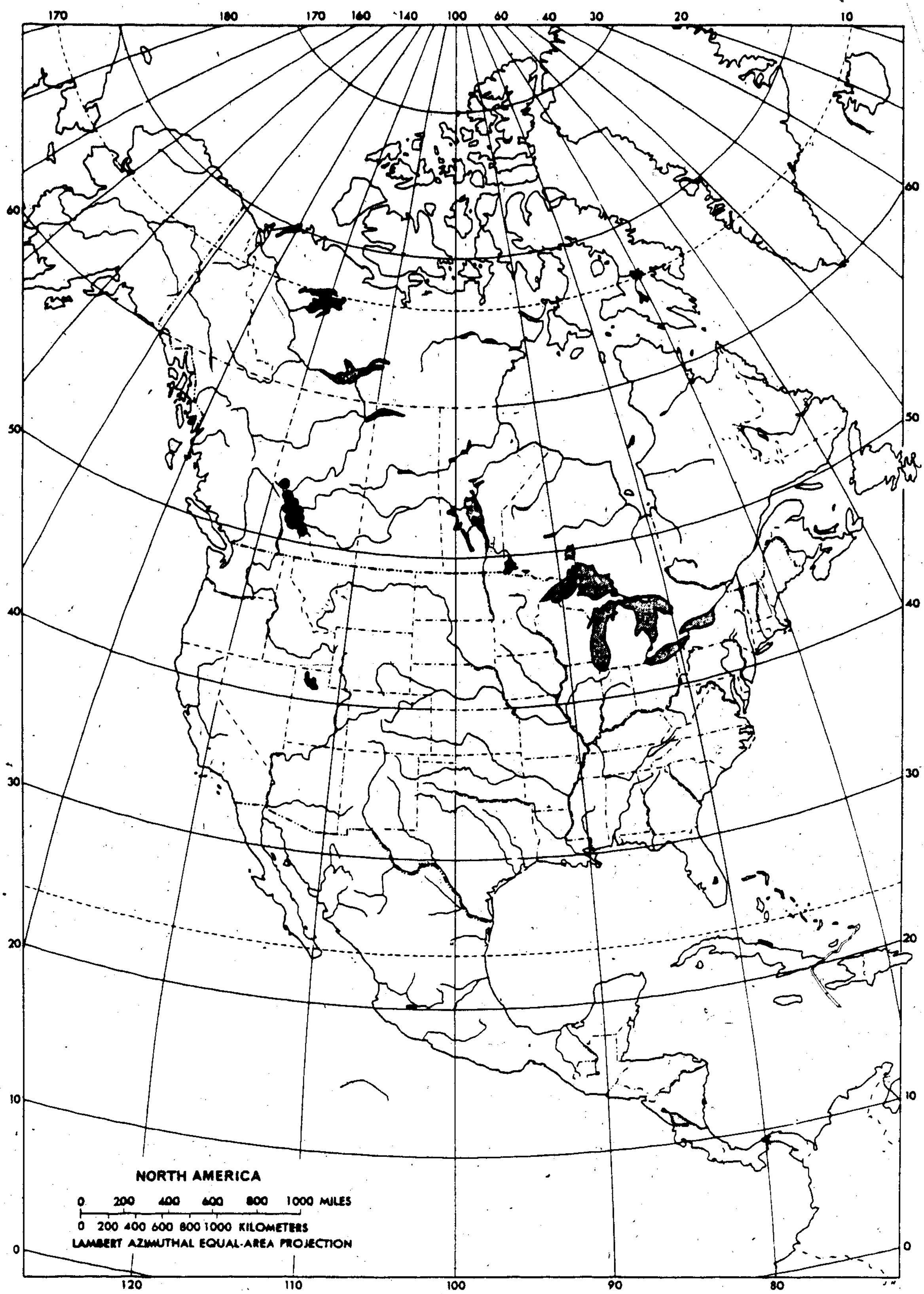

NORTH AMERICA
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
170
180
170
160
140
100
60
40
30
20
10
60
50
40
30
20
10
0
120
110
100
90
80

Figure 47. Type specimen of *Braya humilis* (C.A. Mey.) Robins. var. *maccallae* Harris.

[illegible]

BERNARD BOIVIN 1971
Ministère de l'Agriculture, Ottawa

HERBARIUM OF W. C. McCALLA

PLANTS OF WESTERN CANADA
COLLECTED BY W. C. McCALLA

[illegible]

Braya humilis var. mccallae var. nov.
HOLOTYPE
DETERMINED J. G. Harris   Date August 1984

Braya humilis var. *maccallae* differs from other *B. humilis* varieties in the mostly entire leaves in a dense basal rosette (the cauline leaves are much reduced and arise from near the base of the stem, giving an almost scapose appearance to the plant), the exceptionally large flowers, and the high percentage of aborted siliques. Variety *maccallae* is superficially very similar to var. *porsildii*, differing only in the glabrescent to moderate leaf and stem pubescence, and in habitat preference (var. *maccallae* prefers floodplains and gravel bars, while var. *porsildii* prefers alpine slopes and moraines). The esterase isozyme profiles of var. *maccallae*, however, are much more complex than those of var. *porsildii*, suggesting that the two varieties are not as closely related as might otherwise be expected.

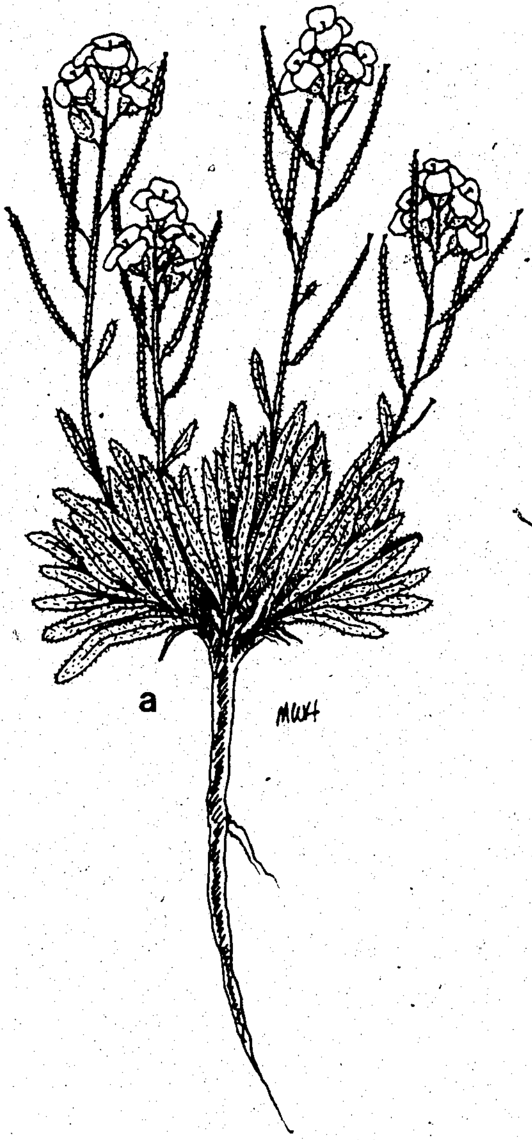
Boivin first recognized that the taxon was distinct, and proposed, but never actually published, the name *Braya humilis* var. *maccallae*. The name honors W.C. McCalla, collector of several representative specimens of the variety, including the type specimen.

Representative specimens: **CANADA: ALBERTA:** Banff Natl. Park, flats at junct. of No. Fork and West Br. Saskatchewan River, *S. Brown 1004* (GH, PH), *1006* (PH); Banff Natl. Park, on bank below the L. Louise - Jasper Road, mile 50, *W.C. McCalla 7076* (ALTA); Jasper Natl. Park, Sunwapta River near Beauty Ck., *I. Corns s.n.* (DAO); Jasper Natl. Park, Sunwapta River, about mile 50, *E.H. Moss 4852* (CAN); Jasper Natl. Park, along Sunwapta River between Jasper and Banff, *A. Löve & D. Löve 6629* (DAO); Jasper Natl. Park, 10 miles NW of the Columbia Glacier, *T. Mosquin & L. Mosquin 4691* (DAO); Jasper Natl. Park, below Morro Peak along Athabaska River, *J.A. Calder & K.W. Spicer 33838* (DAO); **BRITISH COLUMBIA:** Yoho Natl. Park, Kicking Horse River, ca. 2 km above Field, *J.G. Harris 1634* (ALTA); Yoho National Park, sandy flats of Kicking Horse River opp. Mt. Stephen and east of Field, *W.C. McCalla 9566* (ALTA); on old gravel bar in Kicking Horse River, 3 miles E. of west Yoho Natl. Park gate, *R.L. Taylor & D.H. Ferguson 2427* (DAO); Wapta Moraine, Yoho Valley, *E.M. Farr s.n.* (PH); Yoho Natl. Park, near Mt. Stephen Bung. Camp, *W.C. McCalla 7009* (ALTA); Yoho Natl. Park, alluvial plain at the head of Emerald Lake, *J.G. Harris 1629* (ALTA), *W.C. McCalla 7452* (ALTA), *7030* (ALTA); Yoho Natl. Park, Emerald Lake, *S. Brown 328* (PH), *C. Schäffer s.n.* (PH), *J. Macoun 16* (PH); Kootenay Natl. Park, Lake McArthur, *F.K. Butters & E.W.D. Holway 153* (GH).

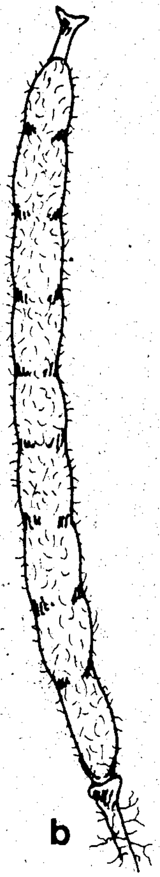
Var. **porsildii** J.G. Harris *var. nov.* Figure 48.

Brayae humili var. *maccallae* aemulans, differt caulibus et foliis dense pubescentibus.

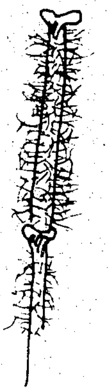
Figure 48. Illustration of *Braya humilis* var. *porsildii*; a. entire plant (natural size); b. silique (x 7); c. aborted silique (x 7.5).



a



b



c

Stems ascending to erect (rarely decumbent), simple or occasionally branched, 3 - 17 (25) cm tall, densely pubescent with bifurcate and simple hairs; basal leaves in a dense rosette, oblanceolate, rounded or narrowly obtuse, distinctly petiolate or merely cuneate at the base, usually entire but at times weakly sinuate-dentate, 3 - 30 mm long, 1 - 5 mm wide, densely pubescent with bifurcate and simple hairs; cauline leaves 3 - 5; sepals (2.0) 2.3 - 3.7 mm long, (1.1) 1.3 - 1.8 mm wide, pubescent with bifurcate and simple hairs; petals 4.4 - 6.9 mm long, (1.9) 2.3 - 4.2 mm wide, distinctly and abruptly divided into claw and broad blade, white; siliques more or less torulose, often aborted and undeveloped, when fully developed (8) 9 - 25 mm long, 0.8 - 1.2 mm wide, densely pubescent with bifurcate and simple hairs; style 0.7 - 1.3 (1.5) mm long, fairly broad; stigma not at all capitate to moderately capitate, entire to bilobed; seeds 1.0 - 1.3 mm long, 0.45 - 0.68 mm wide.

Dry alpine scree slopes, glacial moraines, and gravel bars, often on limestone gravels and soils. Rocky Mountains of Alberta and British Columbia from Banff north to the Mackenzie Mountains of Northwest Territories to about 65° north latitude. Figure 49.

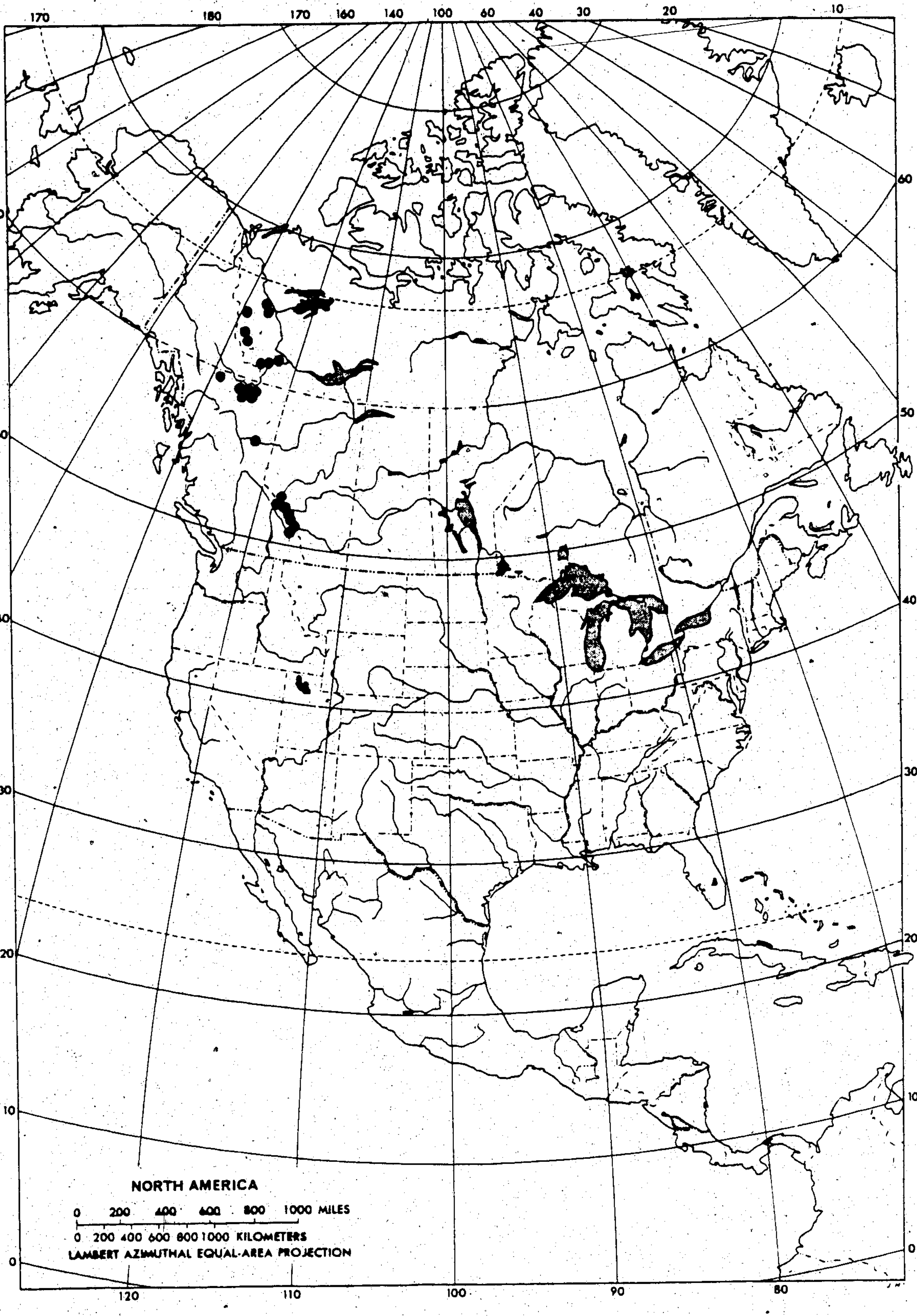
$2n=28$.

Type: Canada, Alberta, Jasper National Park, "Lateral moraines of Athabaska Glacier", 28 July 1946, *A.E. Porsild & A.J. Breitung 16335*, CAN! (holotype). Figure 50.

Braya humilis var. *porsildii* is distinguished from other varieties of the species by the very densely pubescent, entire leaves, the very large flowers, and the high percentage of aborted siliques. The distinctive morphology and unique esterase isozyme banding patterns of these plants support the segregation of this taxon as a distinct variety.

The simple enzyme profiles, low chromosome number ($2n=28$), and self-incompatibility suggest that var. *porsildii* may be the most primitive North American variety of *Braya humilis*. This variety, or an ancestor of it, may have given rise to the other *B. humilis* varieties.

Figure 49. Distribution of *Braya humilis* var. *porsildii*.


NORTH AMERICA
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
170
180
170
160
140
100
60
40
30
20
10
60
50
40
30
20
10
0
120
110
100
90
80

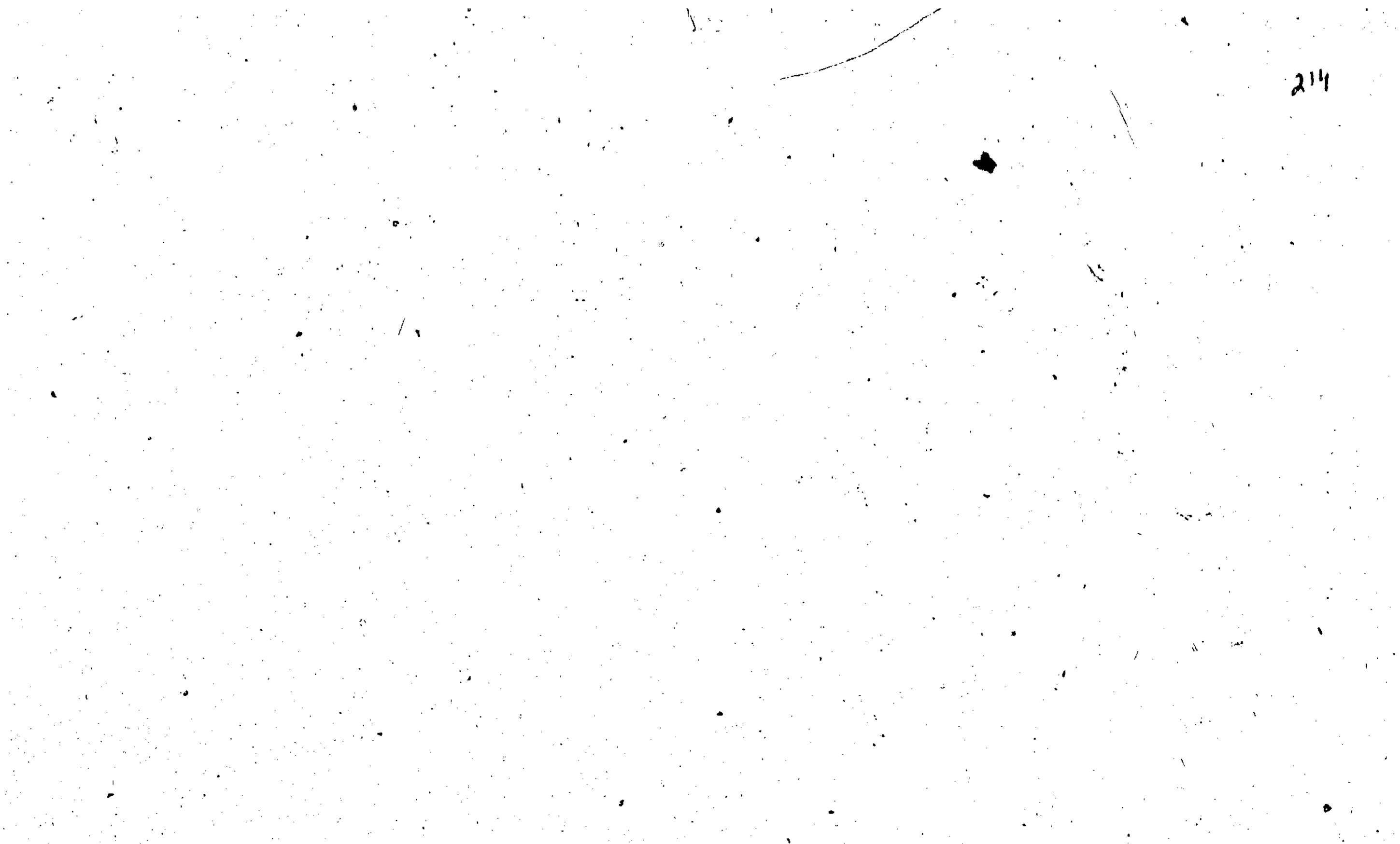


Figure 50. Type specimen of *Braya humilis* (C.A. Mey.) Robins. var. *porsildii* Harris.

Braya humilis var. *porsildii* var. nov

HOLOTYPE

DETERMINED J. G. Harris Date August 1974

NATIONAL HERBARIUM OF CANADA
FLORA OF JASPER NATIONAL PARK,
ALBERTA.

No.

(specimen photographed J.2694)

A. E. Porsild and A. J. Breitung 1946

Rocky Mt. Flora

The taxon was first recognized as unique by Porsild, who proposed the name *Braya vestita* on several herbarium sheets. The name was never published however; and, because the epithet *vestita* has already been proposed as a variety of *B. bartlettiana* (Hultén, 1970), I have named the variety , instead, in honor of its discoverer, A.E. Porsild, in recognition of his invaluable contributions to our understanding of northern plants.

Representative specimens: **CANADA: ALBERTA:** Jasper Natl. Park, vicinity of Athabasca Glacier, *A.E. Porsild & A.J. Breitung 14495* (CAN); Jasper Natl. Park, Columbia Icefield, ca. 60 miles SE of Jasper, *H.J. Scoggan 16439* (CAN); Jasper Natl. Park, *H.M. Laing 291* (CAN); Jasper Natl. Park, Columbia Icefields area, *S. Kojima s.n.* (DAO); Jasper Natl. Park, shoulder of Athabasca Mt., *E.H. Moss 4928* (ALTA, CAN); Jasper House, Rocky Mountains, *Burke s.n.* (GH); Banff Natl. Park, North Saskatchewan River at Saskatchewan Glacier, *B. Boivin 5083* (DAO); Banff Natl. Park, ridge between Mt. Athabaska and Saskatchewan Glacier, near mile 114 on Banff-Jasper Hwy., *A.E. Porsild & A.J. Breitung 14586, 14554* (CAN); Banff Natl. Park, Parker Ridge, *A. Harmon s.n.* (ALTA-photo); Banff Natl. Park, Lake Louise, moraines and alpine slopes near Victoria Glacier, *A.E. Porsild & A.J. Breitung 15704* (CAN); Banff Natl. Park, Nigel Pass, *I. Corns s.n.* (DAO); Banff Natl. Park, terminal moraines of Victoria Glacier above Lake Louise, *J.G. Harris 1639* (ALTA); Banff Natl. Park, alpine slopes of Mt. Saskatchewan, *A.E. Porsild & A.J. Breitung 16060* (CAN). **BRITISH COLUMBIA:** vicinity of Summit Pass, Rocky Mts., *H.M. Raup & D.S. Correll 10564* (CAN); Alaska Hwy., North Tetsa River east of Summit at mile 380, *J.A. Calder & I. Kukkonen 27395* (DAO); Stone Mountain Prov. Park, Summit Lake, *J.G. Harris 1553* (ALTA); just SW of Good Hope Road at mile 66 on Cassiar Road, *J.A. Calder & J.M. Gillett 24769* (DAO); north of Muncho Lake at mile 474 Alaska Hwy., *J.A. Calder & J.M. Gillett 25544* (DAO); along Toad River at Mile 432 Alaska Hwy., *J.A. Calder & J.M. Gillett 25343* (DAO); Graham River, *Mrs. J.N. Henry 501* (PH); below Mt. St. George at Mile 393 Alaska Hwy, west of Summit, *J.A. Calder & J.M. Gillett 26575* (DAO); Prospector's Valley, *F.K. Butters & E.W.D. Holway 139* (GH); **NORTHWEST TERRITORIES:** Mackenzie Mts., 64° 47′ N 129° 37′ W, *E. Kvale & K. Haggard 227, 235* (DAO); Nahanni Natl. Park, 61° 16′ N 124° 12′ W, *S. Talbot T 6077-16* (DAO); Mackenzie Mts., 62° 24′ N 127° 14′ W, *E.R. Rowlands 9* (DAO); Nahanni Natl. Park, South Nahanni River, Deadman Valley, Prairie Creek fan, *H.M. Kershaw 99* (DAO); Liard River between Nahanni Butte and Simpson, *C.H. Crickmay 51* (CAN); Carcajou Range: Carcajou Lake, *W.J. Cody & F.M. Brigham 20540, 20954* (DAO); Mackenzie Mts., 62° 55′ N 126° 38′ W, *E. Kvale & K. Haggard 14, 62* (DAO); Carcajou Lake, Little Keele River, *P.M. Youngman & G. Tessier 725* (CAN).

Literature Cited

Abbe, E.C. 1948. *Braya* in boreal Eastern America. Rhodora 50:1-15.

Al-Shehbaz, I.A. 1973. The biosystematics of the genus *Thelypodium* (Cruciferae). Contrib. Gray Herb. No. 204:3-148.

Al-Shehbaz, I.A. 1977. Protogyny in the Cruciferae. Syst. Bot. 2:327-333.

Babbel, G.R. and R.K. Selander 1974. Genetic variablity in edaphically restricted and widespread plant species. Evolution 28:619-630.

Bateman, A.J. 1955. Self-incompatibility systems in Angiosperms III. Cruciferae. Heredity 9:53-68.

Benson, L. 1959. Plant taxonomy. Ronald Press, New York.

Bessey, C.E. 1915. Phylogenetic taxonomy of flowering plants. Ann. Mo. Bot. Garden 2:109-164.

Böcher, T.W. 1950. Contributions to the flora and plant geography of West Greenland II. Medd. om Grønl. *147*, No. 7, 1-39.

Böcher, T.W. 1956. Further studies in *Braya humilis* and allied species. Medd. om Grønl. *124*, No. 7, 1-29.

Böcher, T.W. 1966. Experimental and cytological studies on plant species. IX. Some arctic and montane Crucifers. Biol. Skrifter Dan. Vid. Selsk. 14 (7):1-74.

Böcher, T.W. 1973. Interspecific hybridization in *Braya* (Cruciferae). Ann. Bot. Fennici 10:57-65.

Böcher, T.W. and K. Larsen. 1950. Chromosome numbers of some arctic or boreal flowering plants. Medd. om Grønl. *147*, No. 6, 1-32.

Boivin, B. 1967. Énumération des Plantes du Canada VIII. Natur. Can. 94:625-655.

Boivin, B. 1968. Flora of the prairie provinces. Phytologia 16:219-339.

Boivin, B. 1969. Flora of the prairie provinces. Phytologia 17:58-292.

Brassard, G.R. 1971. Endemism in the flora of the Canadian High Arctic. Natur. Can. 98:159-166.

Britton, N.L. 1913. *In* Britton, N.L. and A. Brown. An illustrated flora of the northern United States, Canada and the British possessions. Vol. I[illegible]735 pp. Charles Scribner's Sons, New York.

Brown, R. 1823. *Chloris Melvilliana.* W. Clowes, London.

Brown, R. 1824. *In* A supplement to the appendix of Captain Parry's voyage for the discovery of a North-West Passage, in the years 1819-1820. No. XI. *In* Parry, W.E. Journal of a voyage for the discovery of a northwest passage from the Atlantic to the Pacific; performed in the years 1819-1820 in H.M.S. Hecla and Griper. J. Murray, London.

Bunge, A. 1841. *In* Ledebour, C.F. Flora Rossica sive enumeratio plantarum. Vol. I. Stuttgart.

Canada Dept. of Energy, Mines and Resources. 1983. Principal mineral areas of Canada. Map 900A, 33 rd. ed.

Carmichael, J.W. 1983. The TAXMAP classification program. Univ. of Alberta Computing Services [pamphlet] 21 p.

Cody, W.J. 1971. A phytogeographical study of the floras of the continental Northwest Territories and Yukon. Natur. Can. 98:145-158.

Cody, W.M. and A.E. Porsild. 1980. Vascular plants of the continental Northwest Territories. Natl. Museum of Canada, Ottowa.

Coulthart, M.B. 1979. A comparative electrophoretic study of an allopolyploid complex in *Brassica*. M.Sc. Thesis, University of Alberta, Edmonton.

Coulthart, M.B. and K.E. Denford. 1982. Isozyme studies in *Brassica*. I. Electrophoretic techniques for leaf enzymes and comparison of *B. napus, B. campestris* and *B. oleracea* using phosphoglucomutase. Can. J. of Plant Sci. 62:621-630.

Cronquist, A. 1968. The evolution and classification of flowering plants. Houghton Mifflin, Boston.

Cronquist, A. 1981. An integrated system of classification of flowering plants. Columbia Univ. Press, New York.

Denford, K.E. 1970. A study of the seed proteins of certain *Brassica* species using electrophoretic and seriological techniques. Ph.D. Thesis, University of London, U.K.

Ettlinger, M.G. and A. Kjaer. 1968. Sulfur compounds in plants. *In* Mabry, T.J., R.E. Alston and V.C. Runeckles, eds., Recent advances in phytochemistry. Appleton-Century-Crofts, New York.

Ettlinger, M.G. and C.P. Thompson. 1962. Studies of mustard oil glucosides (II), AD no. 290747, Office of Technical Services, U.S. Dept. of Commerce, Washington, D.C.

Favarger, C. 1961. Sur l'emploi des nombres de chromosomes en géographie botanique historique. Ber. Geobot. Inst. Rübel 32:119-146.

Fernald, M.L. 1918. Some North American representatives of *Braya humilis*. Rhodora 20:201-203.

Fernald, M.L. 1925. Persistence of plants in unglaciated areas of boreal America. Mem. Am. Acad. Arts Sci. 15:237-342.

Fernald, M.L. 1926. Two summers of botanizing in Newfoundland. Rhodora 28:202-204.

Fernald, M.L. 1937. No title. Rhodora 39:276.

Fernald, M.L. 1950. Gray's manual of botany. ed. 8. 1632 pp. D. Van Nostrand Co., New York.

Gaiser, L.O. 1953. *In* Rollins, R.C. *Braya* in Colorado. Rhodora 55:110-111.

Gams, H. 1933. Das alter der alpinen Endemismus. Ber. Schweitz. Bot. Ges. 42:467.

Gelert, O. 1898. Notes on arctic plants. Bot. Tidskr., Vol. 21.

Geltung, P. 1934. Studies on the vascular plants of East Greenland between Franz Joseph Fjord and Dove Bay (Lat. 73°15′ - 76°20′ N.). Medd. om Grønl. *101*, No. 2, 57-62.

Gleason, H.A. 1952. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. Vol. 2. 655 pp. Lancaster Press, Lancaster, Penn.

Gottlieb, L.D. 1977. Electrophoretic evidence and plant systematics. Ann. Missouri Bot. Gard. 64:161-180.

Handel-Mazzetti, H. von 1941. Das Alpenbreitschötchen. *Braya alpina* Stb. u. Hoppe un seine arktischen Vorfahren. Jahrb. des Ver. z. Schutze der Alpenpflanzen und -Tiere. 15. Jahrgang pp. 44-48.

Hauser, L.A. and T.J. Crovello. 1982. Numerical analysis of generic relationships in *Thelypodieae* (Brassicaceae). Syst. Bot. 7:249-268.

Hayek, A. von 1911. Entwurf eines Cruciferen-Systems auf phylogenetischer Grundlage. Beiheft. Bot. Centralbl. XXVII. Abt. 1. Heft.2.

Hedge, I.C. 1976. A systematic and geographical survey of the old world Cruciferae. *In* Vaughan, J.G., A.J. MacLeod and B.M.G. Jones, eds., The biology and chemistry of the Cruciferae. Academic Press, London.

Hegi, G. 1958. Illustrierte Flora von Mittel-Europa. Band IV, Part 1. C. Hanser, München.

Holmen, K. 1952. Cytological studies in the flora of Pearyland, North Greenland. Medd. om Grønl. *128*, No. 5, 1-40.

Hooker, J.D. 1862. *In* Bentham, G. and J.D. Hooker, Genera plantarum vol. 1, pp. 57-102. Reeve & Co., London.

Hooker, W.J. 1830. Flora Boreali-Americana. Vol. I. H.G. Bohn, London.

Hultén, E. 1937. Outline of the history of arctic and boreal biota during the Quaternary period. 168 pp.

Hultén, E. 1958. The amphi-Atlantic plants and their phytogeographical connections. Kungl. Svenska Vetenskapsakademiens Handlingar. Fjärde Serien. Band 7, No. 1. Almqvist & Wiksell, Stockholm.

Hultén, E. 1968. Comments on the flora of Alaska and Yukon. Ark. f. Bot. 7:1-147.

Hultén, E. 1970. The circumpolar plants. II. Kungl. Svenska Vetenskapsakademiens

Handlingar. Fjärde Serien. Band 13, No. 1. Almqvist & Wiksell, Stockholm.

Ives, J.D. 1963. Field problems in determining the maximum extent of Pleistocene glaciation along the eastern Canadian seabord — A geographer's point of view. *In:* Löve, A. and D. Löve (Eds.). North Atlantic Biota and their history. pp. 337-354. Pergamon Press, New York.

Janchen, E. 1942. Das system der Cruciferen. Oesterr. Bot. Z. 91:1-28.

Johnson, A.W. and J.G. Packer. 1967. Distribution, ecology, and cytology of the Ogotoruk Creek flora and the history of Beringia, pp. 245-265 *In* Hopkins, D.M. (ed.) The Bering land bridge. Stanford Univ. Press, Stanford. 495 pp.

Johnson, T.F. 1971. *In* Rollins, R.C. 1971. Protogyny in the Cruciferae. Contrib. Gray Herb. No. 201:3-6.

Johnston, B.C. 1984. Status report: *Braya humilis* (C.A. Mey.) Robins. ssp. *ventosa* Rollins, U.S. Dept. of Agriculture, Forest Service, Region 2. Lakewood, Colorado. Unpublished report, 17 pp. + Appendices.

Jordal, L.H. 1952. Some new entities in the flora of the Brooks Range region, Alaska. Rhodora 54:36-38.

Jørgensen, C.A., Th. Sørensen and M. Westergaard. 1958. The flowering plants of Greenland; a taxonomical and cytological survey. Biol. Skr. Dan. Vid. Selsk. *9*, No. 4, 72-74.

Jørgensen, C.A. and M. Westergaard. 1954. *In* Sørensen, Th. New species of *Hierocloë, Calamagrostis*, and *Braya*. Medd. om Grønl. *136*, No. 8, 1-24.

Kerner, A. 1895. The natural history of plants. Vol 2. (English translation by F.W. Oliver.) New York.

Kjaer, A. 1960. Naturally derived isothiocyanates (mustard oils) and their parent glucosides. Fortschr. Chem. Org. Naturst. 18:122-176.

Kjaer, A. 1963. The distribution of sulfur compounds. *In* Swain, T., ed., Chemical plant taxonomy, Chap. 16. Academic Press, London.

Kjaer, A. and S.E. Hansen. 1958. Isothiocyanates XXXI. The distribution of mustard oil glucosides in some *Arabis* species. A chemotaxonomic approach. Botan. Tidsskr. 54:374-378.

Krause, E.H.L. 1902. *In* Sturm, A. Flora von Deutchland.

Lewis, D. 1947. Competition and dominance of incompatibility alleles in diploid pollen. Heredity 1:85-108.

Manton, I. 1932. Introduction to the general cytology of the Cruciferae. Ann. Botany 46:509-566.

Marie-Victorin, Fr. 1938. Phytogeographical problems in eastern Canada. Am. Midl. Nat. 19:489-558.

Meyer, C.A. 1830. *In* Ledebour, C.F. Icones plantarum novarum vel imperfecte cognitarum floram Rossicam, imprimis Altaicam, illustrantes. I. Deubner, London.

Meyer, C.A. 1831. *In* Ledebour, C.F. Flora Altaica. Berlin.

Morisset, P. 1971. Endemism in the vascular plants of the Gulf of St. Lawrence region. Natur. Can. 98:167-177.

Mosquin, T. 1971. Evolutionary aspects of endemism. Natur. Can. 98:121-130.

Mulligan, G.A. 1965. Chromosome numbers of the family Cruciferae. II. Can. J. Bot. 43:657-668.

Murray, D.F. 1983. *in sched.*, Mouth of River Mackenzie, Richardson s.n., National Herbarium of Canada (CAN) 64149, Ottawa.

Nevo, E. 1978. Genetic variation in natural populations: patterns and theory. Theor. Pop. Biol. 13:121-177.

Ornduff, R. 1969. Reproductive biology in relation to systematics. Taxon 18:121-133.

Ostenfeld, C.H. 1923. Critical notes on the taxonomy and nomenclature of some flowering plants from northern Greenland. Medd. om Grønl. *64*, No. 5, 176-178.

Ostenfeld, C.H. 1926. The flora of Greenland and its origin. Kgl. Danske Vid. Selsk. Biol. Medd. VI. 3.

Packer, J.G. 1963. The taxonomy of some North American species of *Chrysoplenium* L. section *Alternifolia* Franchet. Can. J. Bot. 41:85-103.

Packer, J.G. 1971. Endemism in the flora of western Canada. Natur. Can. 98:131-144.

Packer, J.G. 1974. Differentiation and dispersal in alpine floras. Arctic and Alpine Research 6:117-128.

Packer, J.G. and D.H. Vitt. 1974. Mountain Park: a plant refugium in the Canadian Rocky Mountains. Can. J. Bot. 52:1393-1409.

Pandey, K.K. 1956. Incompatibility in autotetraploid *Trifolium pratense*. Genetics 41:353-366.

Payson, E.B. 1923. A monographic study of *Thelypodium* and its immediate allies. Ann. Missouri Bot. Gard. 9:233-324.

Petrovsky, V.V. 1975. *In* Korobkov, A.A., V.V. Petrovsky, T.V. Plieva, O.V. Rebristaja, N.N. Taraskina, A.I. Tolmatchev, and B.A. Jurtzev. Flora arctica URSS VII. Papaveraceae-Cruciferae. pp. 179. Leningrad.

Porsild, A.E. 1943. Materials for a flora of the continental Northwest Territories of Canada. Sargentia IV:44-47.

Porsild, A.E. 1955. The vascular plants of the Western Canadian Arctic Archipelago. Bull. 135, Natl. Museum of Canada, Ottawa

Prantl, K. 1891. *In* Engler, A. and K. Prantl. Die natürlichen Pflanzenfamilien. vol. 3, pt. 2. W. Engelmann, Leipzig.

Prest, V.K. 1969. Retreat of Wisconsin and recent ice in North America. Geological Survey of Canada, Dept. of Energy, Mines and Resources, Map 1257-A.

Raup, H.M. 1934. Botany of Peace and Liard River regions. Contrib. Arn. Arboretum VI:166-168.

Richardson, J. 1823. *In* Franklin, J. Narrative of a journey to the shores of the Polar Sea in the years 1819,20,21, and 22. Botanical Appendix. J. Murray, London.

Richardson, J. 1830. *In* Hooker, W.J. Flora Boreali-Americana. Vol. I. H.G. Bohn, London.

Robinson, B.L. 1895. *In* Gray, A. and S. Watson. Synoptical flora of North America. Vol. I, Part I. New York.

Rodman, J.E. 1974. Systematics and evolution of the genus *Cakile* (Cruciferae). Contrib. Gray Herb. No. 205:3-146.

Rodman, J.E. 1980. Population variation and hybridization in sea-rockets (*Cakile*, Cruciferae): seed glucosinolate characters. Amer. J. Bot. 67:1145-1159.

Rollins, R.C. 1939. The cruciferous genus *Stanleya*. Lloydia 2:109-127.

Rollins, R.C. 1941. A monographic study of *Arabis* in western North America. Rhodora 43:289-325.

Rollins, R.C. 1942. A tentative revision of the genus *Romanschulzia*. Contr. Dudley Herb. 3:217-226.

Rollins, R.C. 1953. *Braya* in Colorado. Rhodora 55:109-116.

Rollins, R.C. 1956. Some new primitive Mexican Cruciferae. Rhodora 58:148-157.

Rollins, R.C. 1958. The genetic evaluation of a taxonomic character in *Dithyrea* (Cruciferae). Rhodora 60:145-152.

Rollins, R.C. 1959. The genus *Synthlipsis* (Cruciferae). Rhodora 61:253-264.

Rollins, R.C. 1971. Protogyny in the Cruciferae and notes on *Arabis* and *Caulanthus*. Contrib. Gray Herb. No. 201, 1-10.

Rollins, R.C. 1982a. A new species of the Asiatic genus *Stroganowia* (Cruciferae) from North America and its biogeographic implications. Syst. Bot. 7:214-220.

Rollins, R.C. 1982b. *Thelypodiopsis* and *Schoenocrambe* (Cruciferae). Contrib. Gray Herb. No. 212 pp. 71-102.

Rouy, G. 1899. Illustr. Plantarum Europæ rariorum. XI. p. 84.

Rydberg, P.A. 1907. The genus *Pilosella* in North America. Torreya 7:157-162.

Schulz, O.E. 1924. Cruciferae-Sisymbrieae. *In* Engler, A. Das Pflanzenreich IV. 105. Heft 86.

Schulz, O.E. 1936. Cruciferae. *In* Die natürlichen Pflanzenfamilien. Engler, A. & H. Harms, eds., ed. 2., Vol. 17b, pp. 227 - 658. Duncker & Humblot, Berlin.

Scoggan, H.J. 1978. The flora of Canada. Part 3. Natl. Museums of Canada, Ottawa.

Seidenfaden, G. 1930. Botanical investigations during the Danish East Greenland Expedition 1929. Medd. om Grønl. *74*, No. 1, 365-382.

Seidenfaden, G. 1931. Moving soil and vegetation in East Greenland. Medd. om Grønl. *87*, No. 2, 1-21.

Solbrig, O.T. 1972. Breeding system and genetic evolution in *Leavenworthia*. Evolution 26:155-160.

Soltis, D.E. 1982. Allozymic variability in *Sullivantia* (Saxifragaceae). Syst. Bot. 7:26-34.

Sørensen, Th. 1954. New species of *Hierocloë, Calamagrostis,* and *Braya*. Medd. om Grønl. *136*, No. 8, 1-24.

Stafleu, F.A. (ed.) 1978. International code of botanical nomenclature. Regnum veget. Vol. 97.

Stebbins, G.L. 1942. The genetic approach to problems of rare and endemic species. Madroño 6:241-258.

Stebbins, G.L. 1950. Variation and evolution in plants. Columbia Univ. Press, New York.

Stebbins, G.L. 1957. Self fertilization and population variability in the higher plants. Amer. Natur. 91:337-354.

Sternberg, C. and D.H. Hoppe. 1815. *Braya*, eine neue Pflanzengattung. Denkschr. Kgl. Bot. Gesellsch. Regensburg I. 1:65-76.

Takhtajan, A. 1969. Flowering plants: Origin and dispersal. Oliver & Boyd, Edinburgh.

Tijo, J.H. and A. Levan. 1950. The use of oxyquinoline in chromosome analysis. An. Estac. Exp. Aula Die Cons. Super. Invest. Cient. 2:21-64.

Turczaninow, N. 1842. Bulletin de la Soc. Imp. des Nat. de Moscou XV. 2.

Vasil'chenko, I.T. 1939. *In* Komarov, V.L. Flora of the U.S.S.R. Vol. VIII. (English translation, 1970), Jerusalem.

Vaughan, J.G. and K.E. Denford. 1968. An acrylamide gel electrophoretic study of the seed proteins of *Brassica* and *Sinapis* species, with special reference to their taxonomic value. J. Exp. Bot. 19:724-732.

Vaughan, J.G., J.R. Phelan and K.E. Denford. 1976. Seed studies in the Cruciferae. *In* Vaughan, J.G., A.J. MacLeod and B.M.G. Jones, eds., The biology and chemistry of the Cruciferae. Academic Press, London.

Vaughan, J.G., A. Waite, D. Boulter and S. Waiters. 1966. Comparative studies of the seed proteins of *Brassica campestris, Brassica oleracea*, and *Brassica nigra*. J. Exp. Bot. 17:332-343.

Vaughan, J.G. and A. Waite. 1967a. Comparative electrophoretic studies of certain species of *Brassica* and *Sinapis*. J. Exp. Bot. 18:100-109.

Vaughan, J.G. and A. Waite. 1967b. Comparative electrophoretic studies of the seed proteins of certain amphidiploid species of *Brassica*. J. Exp. Bot. 18:269-276.

Vaughan, J.G. and J.M. Whitehouse. 1971. Seed structure and the taxonomy of the Cruciferae. J. Linn Soc., Bot. 64:383-409.

Watson, S. 1878. Bibliographic index to North American botany. Part I. pp. 51-52. Smithsonian Institution, Washington.

Westergaard, M. 1948. *In* Löve, A. and D. Löve. Chromosomes of northern plant species. Iceland Univ. Inst. Appl. Sci. Dept. Agr. Rept. B, 3:1-131.

Wolf, S.J., J.G. Packer, and K.E. Denford. 1979. The taxonomy of *Minuartia rossii* (Caryophyllaceae). Can. J. Bot. 57:1673-1686.

Appendix 1. Collections used for enzyme analyses

Braya fernaldii

CANADA: NEWFOUNDLAND: Pistolet Bay, Burnt Cape, 51° 34′ N 55° 45′ W, dry limestone gravel barrens, 12 August 1982, *J. Harris 1733a* (ALTA); Straits of Belle Isle, Cape Norman, 51° 37′ N 55° 54′ W, limestone gravel barrens, 12 August 1982, *J. Harris 1736* (ALTA).

Braya glabella var. *glabella*

CANADA: ALBERTA: Cardinal River, ca. 19 km due SSE of Cadomin, gravel river bank, 22 August 1981, *J. Harris 1555* (ALTA); Jasper Natl. Park, Athabasca Glacier, margin of small pond on terminal moraines, 25 August 1981, *J. Harris & M. Harris 1569* (ALTA); U.S.A.: ALASKA: Prudhoe Bay, ca. 1 mi ENE of Deadhorse Airport, gravelly bluffs, marginal Sagavanirktok River, 5 August 1981, *S. Welsh 20769 [C]* (BRY); Seward Peninsula, Anvil Mtn., 7 km NNE of Nome, scree slopes, 9 July 1981, *J. Harris 1332* (ALTA); Seward Peninsula, Anvil Mtn., 7 km NNE of Nome, disturbed roadside gravel, 9 July 1981, *J. Harris 1330* (ALTA); Seward Peninsula, Kigluaik Mts., mile 49 on Nome-Taylor Hwy., 65° 00′ N 164° 38′ W, talus slope, 14 July 1981, *J. Harris 1371* (ALTA); Seward Peninsula, Teller Rd., Nome, near mile 18, Cleveland Creek, limestone knoll, 9 August 1974, *M. Williams 3271, A. Strutz 2027* (BRY).

Braya glabella var. *purpurascens*

CANADA: NORTHWEST TERRITORIES: Ellesmere Island, Alexandra Fjord, 78° 53′ N 75° 55′ W, barren soil on solifluction lobes on steep hillside, 24 July 1982, *J. Harris & O. Kukal 1720* (ALTA); Ellesmere Island, Alexandra Fjord, sandy gravel bars along river, 24 July 1982, *J. Harris 1724* (ALTA); Ellesmere Island, Grise Fjord, 76° 25′ N 82° 55′ W, gravelly soil near airstrip, 18 July 1982, *J. Harris 1691* (ALTA); Devon Island, Truelove Lowland, 75° 33′ N 84° 40′ W, moist gravelly soil, 22 July 1982, *J. Harris 1719* (ALTA); Baffin Island, 71° 59′ N 79° 14′ W, July 1982, *G. Scotter 67295* (CAFB); U.S.A.: ALASKA: Prudhoe Bay, ca. 1 mi ENE of Deadhorse Airport, gravelly bluffs, marginal Sagavanirktok River, 5 August 1981, *S. Welsh 20769 [A, B]*[14] (BRY); Prudhoe Bay, adjacent to the Crazy Horse Motel, disturbed tundra community with some reseeded grasses, 6 August 1981, *B. Welsh 1233* (BRY); Prudhoe Bay, abandoned airstrip near pump station #1, gravel-covered tundra, disturbed community, 6 August 1981, *B. Welsh et al. 1246a, 1247b* (BRY); Prudhoe Bay, 22 July 1978, *A. Strutz & J. Shelton 2240* (BRY); SVALBARD: Kongsfiord, Ny-Alesund, 14 August 1981, *O. Rønning s.n.* (ALTA).

Braya longii

CANADA: NEWFOUNDLAND: Straits of Belle Isle, between Point Savage and Sandy Cove, 51° 21′ N 56° 41′ W, moist soil in gravel limestone barrens, 11 August 1982, *J. Harris 1727* (ALTA).

Braya thorild-wulffi var. *thorild-wulffii*

CANADA: NORTHWEST TERRITORIES: Ellesmere Island, Eureka, 80° 00′ N 85° 48′ W, dry clay barrens, 27 July 1982, *J. Harris 1725* (ALTA).

---

[14] This collection is composed of three individuals somewhat intermediate to var. *purpurascens* and var. *glabella*. Enzymes from each of these three individuals were examined separately as A, B, and C.

Braya linearis

GREENLAND: Sondre Stromfjord, ca. 2.5 km E of airfield along river, wet alkaline clay soil at edge of small ponds on old river bank terrace, 13 August 1983, *J. Harris 1790* (ALTA).

Braya humilis var. *humilis*

CANADA: ALBERTA: Banff Natl. Park, head of Bow Lake, sandy gravelly soil, 27 June 1982, *J. Harris 1638* (ALTA); Banff Natl. Park, Parker Ridge, soil patches in rocky alpine tundra, 27 August 1982, *J. Harris 1743* (ALTA); Banff Natl. Park, Bath Creek, ca. 5 km E of Kicking Horse Pass, sandy area on gravel bar, 29 June 1982, *J. Harris 1640* (ALTA); Cardinal River, ca. 19 km due SSE of Cadomin, gravel river bank, 22 August 1981, *J. Harris 1554* (ALTA); Jasper Natl. Park, Sunwapta River, ca. 16 km due SE of Sunwapta Falls, rocky gravel bar, 25 August 1981, *J. Harris & M. Harris 1566* (ALTA); Jasper Natl. Park, Athabasca Glacier, glacial till near Sunwapta Lake, 25 August 1981, *J. Harris & M. Harris 1568* (ALTA); Ram Mtn., W of Rocky Mountain House on Strachan Rd. between North Ram and North Saskatchewan Rivers, SW of Nordegg, scree slopes below tower, 3 August 1974, *M. Dumais 7694* (ALTA); **BRITISH COLUMBIA:** Kootenay Natl. Park, Vermilion River near the Paint Pots, on gravel bar, 29 June 1982, *J. Harris 1641* (ALTA); Kootenay Natl. Park, Vermilion River, ca. 14 km above Kootenay Crossing, sandy soil on gravel bar, 29 June 1982, *J. Harris 1643* (ALTA); Muncho Lake Prov. Park, km 700 on Alaska Hwy., scree slope near timberline, 15 August 1981, *J. Harris 1551* (ALTA); **YUKON:** Windy Pass, km 155 on Dempster Hwy., disturbed area along roadside, 28 July 1981, *J. Harris 1409* (ALTA); Richardson Mtns., Rock River at km 438.6 on Dempster Hwy., rocky, sandy soil along stream bank, 2 August 1981, *J. Harris 1465* (ALTA); Ogilvie Mtns., km 160 on Dempster Hwy., gravelly flood plain along road, 4 August 1981, *J. Harris 1470* (ALTA); mile 1133 Alaska Hwy., ca. 0.4 km W of Donjek River bridge, dry roadside, 25 July 1977, *G. Douglas & V. Tait 10300* (BRY); **NORTHWEST TERRITORIES:** Mackenzie River Delta at Inuvik, sandy soil, 31 July 1981, *J. Harris 1432* (ALTA); along the Mackenzie River, ca. 5 km below the confluence with the Liard River, Fort Simpson, barren sandy areas of steep river banks, 11 July 1982, *J. Harris 1657* (ALTA); along the Liard River at the [illegible]enzie Hwy. crossing, steep sandy river bank, 12 July 1982, *J. Harris 1659* (ALTA); N[illegible]n Wells, west edge of airport, SW of fuel area, spruce woods, 14 July 1974, *J. Rigby 40* (BRY); **U.S.A.: ALASKA:** along the Copper River ca. 0.5 km above confluence with the Chitina River, ca. 3 km E of Chitina, gravel river bank, 19 June 1981, *J. Harris 1168* (ALTA); 5.5 km N of Denali Natl. Park turnoff on George Parks Hwy., gravel roadside, 26 June 1981, *J. Harris 1232* (ALTA); Seward Peninsula, Anvil Mtn., 7 km NNE of Nome, scree slopes, 9 July 1981, *J. Harris 1331* (ALTA); Tanana River ca. 2 km NW of Delta Junction, sandy, rocky soil, 21 July 1981, *J. Harris 1388* (ALTA); ca. 10 km from Copper River bridge on road to McCarthy, overlook along roadside over Chitina River, sandy soil, 7 July 1982, *D. Taylor & J. Taylor 1* (ALTA); **COLORADO:** between Hoosier Pass and North Star Mtn., rocky slope, 28 July 1981, *B. Johnston 2371* (ALTA); **VERMONT:** Willoughby Cliffs of Mt. Pisgah, along the SE tip of Willoughby Lake, talus slopes and rubble, 18 August 1982, *J. Harris 1742* (ALTA).

Braya humilis var. *mccallae*

CANADA: BRITISH COLUMBIA: Yoho Natl. Park, Kicking Horse River ca. 2 km above Field, sandy soil on gravel flood plain, 26 June 1982, *J. Harris 1634* (ALTA).

Braya humilis var. *porsildii*

CANADA: ALBERTA: Banff Natl. Park, terminal moraines of Victoria Glacier above Lake Louise, sandy, gravelly soil, 28 June 1982, *J. Harris 1639* (ALTA); **BRITISH COLUMBIA:** Stone Mtn. Prov. Park, alpine scree slopes above Summit Lake, 16 August 1981, *J. Harris*

1553 (ALTA).

Appendix 2. Collections used for TAXMAP morphological analysis

OTU 1: Alaska, Prudhoe Bay, *A. Strutz & J. Shelton 2240* (BRY).
OTU 2: Alaska, Prudhoe Bay, *B. Welsh et al. 1233* (BRY).
OTU 3: Alaska, Prudhoe Bay, *B. Welsh et al. 1247b* (BRY).
OTU 4: Alaska, Seward Penin., Cleveland Creek, *A. Strutz 2027* (BRY).
OTU 5: Alaska, Prudhoe Bay, *B. Welsh et al. 1246a* (BRY).
OTU 6: Alaska, Seward Penin., Cleveland Creek, *M. Williams 3271* (BRY).
OTU 7: Alaska, Prudhoe Bay, *S. Welsh 20769(a)* (BRY).
OTU 8: Alaska, Prudhoe Bay, *S. Welsh 20769(b)* (BRY).
OTU 9: Alaska, Prudhoe Bay, *S. Welsh 20769(c)* (BRY).
OTU 10: Newfoundland, Cape Norman, *J. Harris 1736* (ALTA).
OTU 11: Newfoundland, Burnt Cape, Pistolet Bay, *J. Harris 1733(a).(ALTA).*
OTU 12: Newfoundland, Burnt Cape, Pistolet Bay, *J. Harris 1733(b).(ALTA).*
OTU 13: Newfoundland, between Savage Point and Sandy Cove, *J. Harris 1727* (ALTA).
OTU 14: Ellesmere Island, Eureka, *J. Harris 1725* (ALTA).
OTU 15: Banks Island, Bernard River, *Maher & MacLean cat. no. 139* (CAN).
OTU 16: Ellesmere Island, Alexandra Fjord, *J. Harris 1724* (ALTA).
OTU 17: Ellesmere Island, Alexandra Fjord, *J. Harris 1720* (ALTA).
OTU 18: Devon Island, Truelove Lowland, *J. Harris 1719* (ALTA).
OTU 19: Ellesmere Island, Grise Fjord, *J. Harris 1691* (ALTA).
OTU 20: Ellesmere Island, Hazen Camp, *D.B.O. Savile 4764A* (DAO).
OTU 21: Northwest Territories, Arctic Sea Coast, *J. Richardson s.n.* (K).
OTU 22: Alberta, Jasper Natl. Park, Columbia Glacier, *J. & M. Harris 1569* (ALTA).
OTU 23: Alberta, Cardinal River, *J. Harris 1555* (ALTA).
OTU 24: Alaska, Seward Penin., Kigluaik Mtns., *J. Harris 1371* (ALTA).
OTU 25: Alaska, Seward Penin., Anvil Mtn., *J. Harris 1330* (ALTA).
OTU 26: Alaska, Seward Penin., Anvil Mtn., *J. Harris 1332* (ALTA).
OTU 27: Northwest Territories, *A.E. Porsild 30205* (CAN).
OTU 28: Northwest Territories, Clinton Point, *J.A. Parmelee 3206* (DAO).
OTU 29: Cornwallis Island, near Resolute, *J. Harris 1726* (ALTA).
OTU 30: Ellesmere Island, Alexandra Fjord, *J. Harris & O. Kukal 1723* (ALTA).
OTU 31: Newfoundland, Straits of Belle Isle, Savage Point, *M. Fernald & B. Long 28426* (CAN).
OTU 32: Baffin Island, Frobisher Bay, *H. Senn & J. Calder 3898* (DAO).
OTU 33: Newfoundland, Straits of Belle Isle, Yankee Point, *M. Fernald et al. 28427* (PH).
OTU 34: Greenland, *Meehan 10*
OTU 35: Yukon Territory, Richardson Mtns., *J. Calder 33952* (DAO).
OTU 36: Northwest Territories, Tuktoyaktuk Penin., *C. Larsen & W. Owen 74-4261* (DAO).
OTU 37: Northwest Territories, Mackenzie Mountains, near June Lake, *W. Cody 17106* (DAO).
OTU 38: Alaska, Bullen, *G. Argus & W. Chunys 5798* (CAN).
OTU 39: Greenland, *M. Porsild s.n.* (CAN).
OTU 40: Southampton Island, Southampton, *M. Malte 120677* (CAN).
OTU 41: Northwest Territories, Mackenzie Mountains, near June Lake, *W. Cody 17452* (DAO).
OTU 42: Northwest Territories, Cape Parry, *J. Parmelee 3004* (DAO).
OTU 43: Northwest Territories, Mackenzie Mountains, near O'Grady Lake, *W. Cody 16953* (DAO).
OTU 44: Northwest Territories, Mackenzie Mountains, near June Lake, *W. Cody 17238* (DAO).
OTU 45: Northwest Territories, Mackenzie Mountains, near Little Divide Lake, *W. Cody*

16653 (DAO).

OTU 46: Quebec, Hudson Bay, Richmond Gulf, *E. & L. Abbe 3819* (DAO).

OTU 47: Newfoundland, Straits of Belle Isle, Sandy Cove, *M. Fernald et al. 26723* (PH).

OTU 48: Northwest Territories, Mackenzie Mountains, Mirror Lake, *W. Cody & F. Brigham 20413* (DAO).

OTU 49: Northwest Territories, Great Bear Lake, *A. & R. Porsild 4698* (CAN).

OTU 50: Newfoundland, Pistolet Bay, Cape Norman, *K. Weigand & B. Long 28440* (GH).

OTU 51: Alaska, Prudhoe Bay, *G. Halliday A220/75* (BM).

OTU 52: Northwest Territories, N end of Richards Island, *A. Porsild 16828* (CAN).

OTU 53: Alaska, Cape Beaufort, *E. Hultén s.n.* (BRY).

OTU 54: Svalbard,

OTU 55: Greenland, Sondre Stromfjord, *J. Harris 1790* (ALTA).

OTU 56: Colorado, Hoosier Pass, *B. Johnston 2371* (ALTA).

OTU 57: Alberta, Ram Mtn., *M. Dumais 7694* (ALTA).

OTU 58: Alaska, along Copper River at confluence with Chitina River, *J. Harris 1168* (ALTA).

OTU 59: Alaska, Chitina River, *D. & J. Taylor 1* (ALTA).

OTU 60: Alaska, G. Parks Hwy. near Denali Natl. Park turnoff, *J. Harris 1232* (ALTA).

OTU 61: Alaska, Seward Penin., Anvil Mtn., *J. Harris 1331* (ALTA).

OTU 62: Alaska, Delta Junc., *J. Harris 1388* (ALTA).

OTU 63: Yukon, Dempster Hwy., km 155, *J. Harris 1409* (ALTA).

OTU 64: Northwest Territories, near Inuvik, *J. Harris 1432* (ALTA).

OTU 65: Yukon, Richardson Mtns., Rock River, *J. Harris 1465* (ALTA).

OTU 66: Yukon, Ogilvie Mtns., Dempster Hwy., km 160, *J. Harris 1470* (ALTA).

OTU 67: British Columbia, Muncho Lake Prov. Park, *J. Harris 1551* (ALTA).

OTU 68: British Columbia, Summit Lake, *J. Harris 1553* (ALTA).

OTU 69: Alberta, Cardinal River, *J. Harris 1554* (ALTA).

OTU 70: Alberta, Jasper Natl. Park, Sunwapta River, *J. & M. Harris 1566* (ALTA).

OTU 71: Alberta, Jasper Natl. Park, Athabasca Glacier, *J. & M. Harris 1568* (ALTA).

OTU 72: British Columbia, Yoho Natl. Park, Kicking Horse River near Field, *J. Harris 1634* (ALTA).

OTU 73: Alberta, Banff Natl. Park, head of Bow Lake, *J. Harris 1638* (ALTA).

OTU 74: Alberta, Banff Natl. Park, Bath Creek, *J. Harris 1640* (ALTA).

OTU 75: British Columbia, Kootenay Natl. Park, Paint Pots, *J. Harris 1642* (ALTA).

OTU 76: British Columbia, Kootenay Natl. Park, Vermilion River, *J. Harris 1643* (ALTA).

OTU 77: Northwest Territories, Fort Simpson, *J. Harris 1657* (ALTA).

OTU 78: Northwest Territories, Liard River, *J. Harris 1659* (ALTA).

OTU 79: Vermont, Mt. Pisgah, *J. Harris 1742* (ALTA).

OTU 80: Alberta, Banff Natl. Park, Parker Ridge, *J. Harris 1743* (ALTA).

OTU 81: Yukon, Alaska Hwy., mi 1133, *G. Douglas 10300* (BRY).

OTU 82: Northwest Territories, Norman Wells, *J. Rigby 40* (BRY).

OTU 83: Alberta, Banff Natl. Park, Victoria Glacier, *J. Harris 1639* (ALTA).

OTU 84: Greenland, Ole Rømers Land, *F. Schwarzenbach 1253* (C).

OTU 85: Alberta, Banff Natl. Park, The Loop, *W. McCalla 2272* (ALTA).

OTU 86: Alberta, Banff Natl. Park, Mt. Saskatchewan, *A. Porsild & A. Breitung 16060* (CAN).

OTU 87: British Columbia, Yoho Natl. Park, Kicking Horse River E of Field, *W. McCalla 7539* (ALTA).

OTU 88: Alaska, Eagle Bluff, *S. Welsh & G. Moore 8633* (BRY).

OTU 89: Alaska, Yukon River at Eagle, *J. Harris 1393* (ALTA).

OTU 90: Yukon, S end of Kluane Lake, *S. Welsh & G. Moore 7848* (BRY).

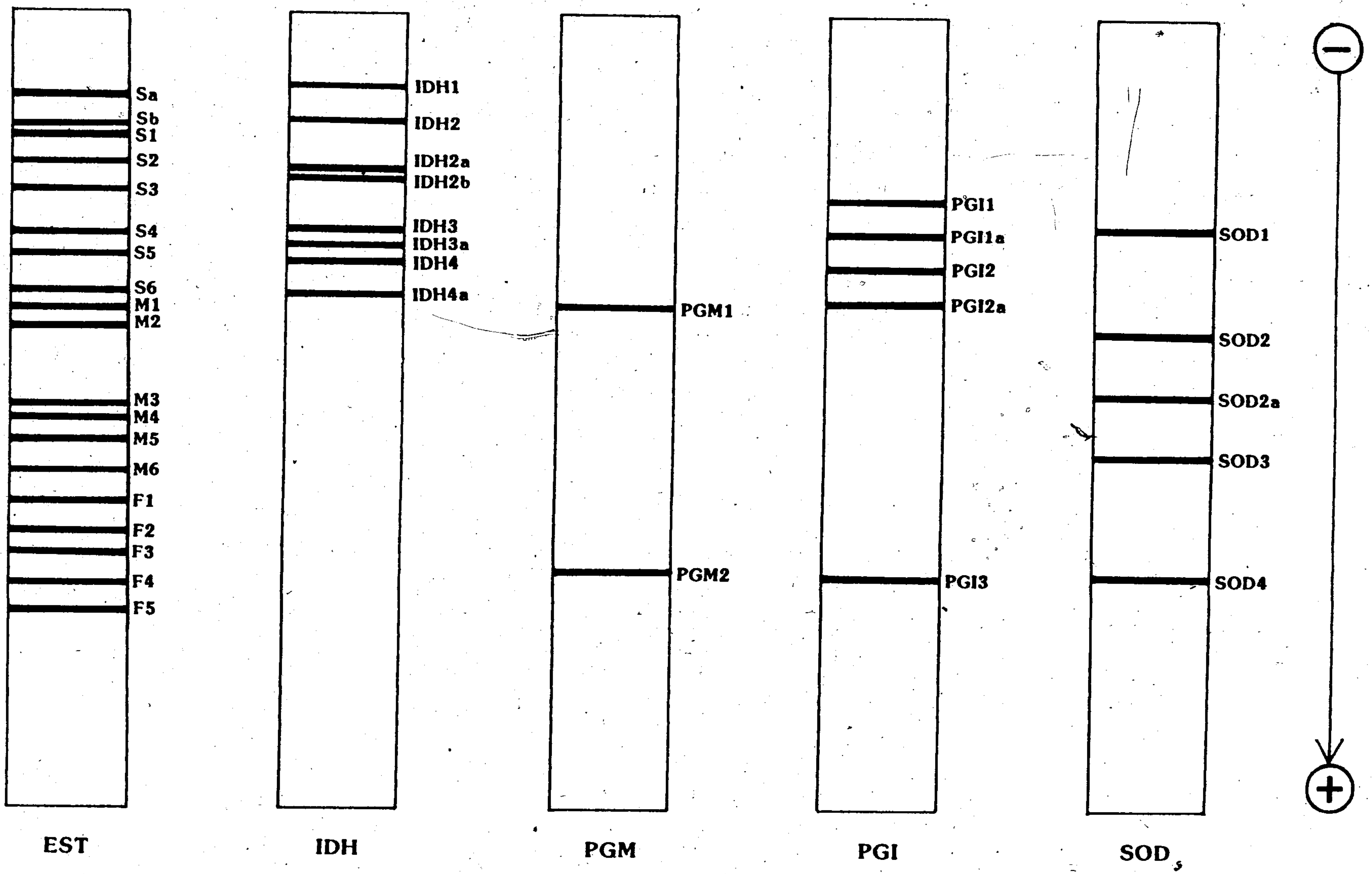
OTU 91: Alaska, near Prudhoe Bay, *B. Welsh 1199* (BRY).

OTU 92: Greenland, Sondre Stromfjord, *T. Böcher 489* (DAO).

OTU 93: Greenland, Musk-Ox Fjord, *G. Seidenfaden 292b* (MT).

OTU 94: Ontario, Hudson Bay, Winisk River, *A. Dutilly & J. Frenette 40063* (MT).
OTU 95: Ontario, James Bay, Moose River, *A. Dutilly & E. LePage 15441* (CAN).
OTU 96: Quebec, Anticosti Island, Jupiter River, *Marie-Victorin & Rolland-Germain 24849* (MT).
OTU 97: Manitoba, Churchill, *J. Gillett 2242* (MT).
OTU 98: Vermont, Willoughby Cliffs of Mt. Pisgah, *C. Pringle s.n.* (PH).
OTU 99: Alaska, Seward Penin., Anvil Mtn., *E. LePage 23861* (CAN).
OTU 100: Newfoundland, Port à Port Bay, Table Mtn., *M. Fernald & H. St. John 10837* (MT).
OTU 101: Asia, Barguzinsky Mtns., Barguzinsky River, *V. Siplivinsky 5020* (LE).
OTU 102: Asia, Altai Region, *V. Vereshehagin 372* (LE).
OTU 103: Ellesmere Island, Hazen Camp, *D. Savile 4763* (DAO).

Appendix 3. Diagram of banding patterns in electrophoretic gels.



Appendix 4. Data matrix for numerical analysis of morphological attributes.

RAW ATTRIBUTE VALUES BY OTU

		OTU'S									
	ATTRIBUTES	1	2	3	4	5	6	7	8	9	10
1	silique length	6.10	6.20	7.10	8.40	6.00	9.30	6.90	7.30	8.50	5.70
2	silique width	1.80	2.40	2.10	1.30	1.70	1.50	2.40	2.10	1.70	1.10
3	silique width/length	0.30	0.38	0.29	0.16	0.29	0.16	0.34	0.29	0.20	0.18
4	style length	0.82	0.67	0.83	1.20	0.93	1.19	0.78	0.68	1.50	0.72
5	style width	0.40	0.48	0.38	0.36	0.43	0.36	0.38	0.45	0.33	0.31
6	style width/length	0.49	0.72	0.46	0.30	0.46	0.30	0.49	0.66	0.22	0.43
7	style shape	3.00	3.00	3.00	2.00	3.00	1.50	3.00	3.00	2.00	1.00
8	stigma shape	4.00	3.50	4.00	3.00	4.00	2.00	4.00	4.00	3.00	1.50
9	stigma breadth	3.00	3.00	4.00	2.00	3.00	1.00	3.00	4.00	2.00	3.00
10	silique pub. type	3.00	3.00	3.00	1.00	5.00	3.00	3.00	4.00	0.0	3.00
11	silique pub. degree	4.00	3.00	3.00	2.00	2.00	3.00	5.00	3.00	0.0	5.00
12	fruiting pedicel length	3.20	3.10	2.70	3.40	2.90	3.80	1.90	3.30	4.40	1.70
13	inflorescence length	4.30	3.80	2.70	4.70	2.00	4.30	8.90	3.60	5.10	2.10
14	inflorescence density	53.20	57.90	83.20	59.00	88.60	56.50	31.30	77.40	51.20	98.90
15	seed row number	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	1.00
16	seed length	1.00	1.10	1.10	1.50	1.10	1.20	1.10	1.00	1.20	1.10
17	seed width	0.51	0.63	0.60	0.71	0.68	0.59	0.56	0.54	0.59	0.49
18	seed width/length	0.52	0.59	0.53	0.48	0.59	0.48	0.52	0.53	0.50	0.44
19	petal length	2.80	3.30	3.20	3.40	3.70	4.30	2.80	2.75	4.20	3.50
20	petal width	1.50	1.60	1.50	1.50	1.50	1.60	1.40	1.10	1.30	1.10
21	petal width/length	0.54	0.48	0.47	0.44	0.41	0.37	0.50	0.40	0.31	0.31
22	sepal length	2.10	2.40	-99.00	2.60	2.60	2.80	2.20	2.60	2.90	2.30
23	sepal width	1.40	1.30	-99.00	1.20	1.30	1.20	1.20	1.40	1.30	1.30
24	sepal width/length	0.67	0.54	-99.00	0.46	0.50	0.43	0.55	0.54	0.45	0.57
25	sepal pub. type	2.00	1.00	-99.00	1.00	1.00	1.00	1.00	1.00	0.0	1.00
26	sepal pub. degree	3.00	1.00	-99.00	2.00	2.00	4.00	3.00	2.00	0.0	2.00
27	plant height	8.30	7.60	4.90	9.30	6.70	10.80	12.80	8.00	9.20	4.90
28	stem leafyness	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
29	stem branching	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.00	0.0	0.0
30	stem rosettes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.00	0.0
31	stem number/plant	3.00	8.30	1.50	6.00	1.80	5.00	3.00	14.00	7.00	1.50
32	stem pub. type	4.00	2.00	4.00	4.00	4.00	3.00	4.00	3.00	3.00	5.00
33	stem pub. degree	4.00	4.00	5.00	3.00	3.00	4.00	5.00	5.00	3.00	5.00
34	basal leaf length	1.50	2.00	1.00	3.40	3.00	2.90	2.50	2.20	2.00	1.00
35	basal leaf width	1.50	1.80	1.40	1.50	1.80	1.10	1.80	1.80	1.20	0.90
36	basal leaf width/length	0.10	0.09	0.14	0.05	0.06	0.04	0.07	0.08	0.06	0.09
37	leaf pub. type	2.00	2.00	2.00	2.00	1.00	3.00	2.00	4.00	1.00	2.00
38	leaf pub. degree	2.00	2.00	2.00	4.00	2.00	5.00	2.00	2.00	1.00	4.00
39	basal leaf margin	1.00	1.00	1.00	0.0	1.00	0.0	0.0	0.0	0.0	0.0
40	stem habit	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
41	septum margin base	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.00
42	siliques aborted	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

	ATTRIBUTES	11	12	13	14	15	16	17	18	19	20
1	silique length	5.20	3.80	7.40	6.30	7.00	6.30	5.80	7.00	6.50	8.90
2	silique width	0.90	1.00	1.20	4.10	4.50	2.00	2.00	2.60	1.90	3.10
3	silique width/length	0.18	0.26	0.17	0.65	0.64	0.32	0.34	0.37	0.29	0.35
4	style length	0.97	0.65	0.86	0.66	0.45	0.96	0.67	0.74	0.57	1.50
5	style width	0.36	0.32	0.40	0.75	0.50	0.40	0.43	0.49	0.42	0.60
6	style width/length	0.37	0.49	0.47	1.14	1.10	0.42	0.64	0.66	0.74	0.40
7	style shape	2.00	1.00	1.00	2.00	2.00	2.00	2.00	3.00	3.00	3.00
8	stigma shape	3.00	3.00	3.00	3.00	2.00	2.00	3.00	3.00	4.00	2.00
9	stigma breadth	3.00	3.00	3.00	1.00	1.00	2.00	3.00	3.00	3.50	2.10
10	silique pub. type	5.00	5.00	0.0	3.00	0.0	0.0	0.0	3.00	3.00	1.00
11	silique pub. degree	7.00	2.00	0.0	7.00	0.0	0.0	0.0	5.00	5.00	4.00
12	fruiting pedicel length	1.70	1.20	2.90	2.20	3.50	2.80	2.30	2.80	2.50	4.00
13	inflorescence length	2.90	0.80	4.80	4.20	3.40	2.40	1.90	2.40	2.00	7.70
14	inflorescence density	84.50	100.00	41.00	65.20	71.00	91.00	99.10	97.10	98.20	46.00
15	seed row number	1.50	2.00	1.50	2.00	2.00	2.00	2.00	2.00	2.00	2.00
16	seed length	1.10	1.00	1.20	1.40	1.70	1.20	1.10	1.20	1.30	1.50
17	seed width	0.55	0.62	0.69	0.73	0.90	0.53	0.52	0.63	0.58	0.83
18	seed width/length	0.51	0.59	0.56	0.53	0.53	0.44	0.47	0.52	0.46	0.55
19	petal length	-99.00	-99.00	4.20	2.70	-99.00	4.10	3.30	3.90	3.30	4.20
20	petal width	-99.00	-99.00	1.90	1.10	-99.00	2.60	2.10	2.50	2.00	2.90
21	petal width/length	-99.00	-99.00	0.45	0.41	-99.00	0.63	0.64	0.64	0.61	0.69
22	sepal length	2.10	1.60	3.10	2.70	3.40	2.80	2.30	2.70	2.40	3.40
23	sepal width	1.30	0.91	1.50	1.60	2.00	1.70	1.50	1.60	1.30	1.80
24	sepal width/length	0.62	0.57	0.48	0.59	0.59	0.61	0.65	0.59	0.54	0.53
25	sepal pub. type	-99.00	0.0	1.00	1.00	0.0	0.0	0.0	1.00	1.00	1.00
26	sepal pub. degree	-99.00	0.0	1.00	5.00	0.0	0.0	0.0	1.00	1.00	1.00
27	plant height	5.30	1.70	10.20	6.90	7.30	5.20	3.80	4.70	3.50	11.50
28	stem leafyness	1.00	1.00	1.00	0.0	0.0	1.00	1.00	1.00	1.00	0.0
29	stem branching	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
30	stem rosettes	0.0	0.0	1.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0
31	stem number/plant	2.00	1.00	5.00	1.70	1.70	2.70	1.20	4.70	2.70	3.00
32	stem pub. type	5.00	5.00	3.00	3.00	1.00	4.00	5.00	5.00	5.00	2.00
33	stem pub. degree	5.00	3.00	3.00	5.00	1.00	3.00	3.00	4.00	4.00	4.00
34	basal leaf length	1.20	0.35	3.30	1.30	1.50	1.50	1.00	1.20	1.30	2.60
35	basal leaf width	1.10	0.70	1.70	1.40	3.00	1.90	1.60	1.40	1.60	4.50
36	basal leaf width/length	0.09	0.20	0.05	0.11	0.20	0.13	0.16	0.12	0.12	0.17
37	leaf pub. type	3.00	0.0	1.00	1.00	1.00	1.00	3.00	1.00	1.00	2.00
38	leaf pub. degree	3.00	0.0	1.00	4.00	1.00	2.00	2.00	2.00	2.00	1.00
39	basal leaf margin	0.0	0.0	0.0	0.0	0.0	2.00	1.00	1.00	1.00	1.00
40	stem habit	2.00	2.00	2.00	1.00	1.00	2.00	2.00	2.00	2.00	1.00
41	septum margin base	1.00	1.00	1.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0
42	siliques aborted	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

	ATTRIBUTES	21	22	23	24	25	26	27	28	29	30
1	silique length	4.50	9.90	6.90	5.20	7.10	6.50	6.80	6.40	5.90	5.90
2	silique width	3.00	1.60	1.40	1.20	1.40	1.40	1.60	1.90	1.80	2.30
3	silique width/length	0.67	0.16	0.21	0.23	0.20	0.22	0.23	0.29	0.30	0.39
4	style length	1.70	1.10	0.88	0.72	0.88	0.97	1.05	0.69	0.56	0.76
5	style width	0.40	0.31	0.43	0.28	0.36	0.28	0.42	0.43	0.47	0.47
6	style width/length	0.24	0.28	0.49	0.39	0.41	0.29	0.40	0.62	0.84	0.62
7	style shape	2.00	1.00	2.00	1.00	1.50	1.00	2.00	3.00	3.00	2.00
8	stigma shape	3.00	2.00	3.00	1.50	1.50	2.00	4.00	3.50	4.00	1.50
9	stigma breadth	4.00	2.00	2.00	2.00	2.00	1.50	3.00	3.50	3.00	2.00
10	silique pub. type	3.00	5.00	6.00	1.00	3.00	3.00	5.00	5.00	3.00	0.0
11	silique pub. degree	6.00	4.00	4.00	3.50	1.00	1.00	6.00	3.00	5.00	0.0
12	fruiting pedicel length	4.00	3.20	3.10	2.10	2.50	3.10	2.70	3.10	2.20	3.00
13	inflorescence length	3.50	3.50	3.40	1.50	3.00	2.10	6.40	5.00	2.00	2.70
14	inflorescence density	65.00	84.00	79.50	97.40	79.30	91.70	45.90	54.30	93.80	83.80
15	seed row number	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
16	seed length	0.80	1.40	1.30	1.10	1.20	1.10	1.00	1.10	1.00	1.10
17	seed width	0.50	0.66	0.69	0.62	0.67	0.63	0.58	0.55	0.66	0.63
18	seed width/length	0.63	0.47	0.52	0.55	0.56	0.57	0.57	0.48	0.64	0.57
19	petal length	5.60	3.10	-99.00	2.60	2.80	2.90	2.40	3.40	3.40	3.70
20	petal width	3.60	1.30	-99.00	1.20	1.30	1.40	1.10	1.70	2.00	2.30
21	petal width/length	0.64	0.42	-99.00	0.46	0.46	0.48	0.46	0.50	0.59	0.62
22	sepal length	3.10	2.80	-99.00	2.00	1.90	2.00	2.20	2.40	2.60	2.70
23	sepal width	1.80	1.50	-99.00	0.83	1.00	1.00	1.20	1.40	1.50	1.80
24	sepal width/length	0.58	0.54	-99.00	0.42	0.53	0.50	0.55	0.58	0.58	0.67
25	sepal pub. type	3.00	1.00	-99.00	1.00	1.00	0.0	3.00	1.00	1.00	0.0
26	sepal pub. degree	4.00	3.00	-99.00	3.00	1.00	0.0	5.00	3.00	1.00	0.0
27	plant height	7.50	6.80	7.30	4.70	6.30	5.50	12.50	12.10	5.20	7.80
28	stem leafyness	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
29	stem branching	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.00	0.0	0.0
30	stem rosettes	0.0	0.0	0.0	1.00	1.00	0.0	0.0	2.00	2.00	0.0
31	stem number/plant	3.00	3.00	3.20	1.40	2.10	1.40	2.30	8.80	7.20	2.50
32	stem pub. type	2.00	6.00	6.00	3.00	4.00	4.00	5.00	3.00	3.00	5.00
33	stem pub. degree	4.00	4.00	4.00	3.00	3.00	3.00	4.00	4.00	4.00	2.00
34	basal leaf length	1.50	1.90	1.70	1.10	1.50	1.20	1.80	2.00	1.70	1.70
35	basal leaf width	1.50	1.10	1.50	0.80	1.30	1.20	1.37	1.57	1.42	1.96
36	basal leaf width/length	0.10	0.06	0.09	0.07	0.09	0.10	0.08	0.08	0.08	0.11
37	leaf pub. type	1.00	3.00	2.00	2.00	3.00	3.00	3.00	2.00	3.00	1.00
38	leaf pub. degree	5.00	3.00	2.00	2.00	4.00	3.00	4.00	2.00	2.00	2.00
39	basal leaf margin	0.0	0.0	0.0	1.00	1.00	1.00	3.00	1.00	2.00	2.00
40	stem habit	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
41	septum margin base	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
42	siliques aborted	1.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

	ATTRIBUTES	31	32	33	34	35	36	37	38	39	40
1	silique length	5.40	7.00	5.20	6.90	6.40	6.20	8.00	8.40	7.40	10.70
2	silique width	1.10	2.00	1.30	1.70	1.80	1.70	1.70	2.50	2.00	1.80
3	silique width/length	0.21	0.29	0.24	0.24	0.28	0.27	0.21	0.30	0.26	0.17
4	style length	0.73	0.61	0.61	0.63	0.78	0.69	1.09	0.94	0.67	1.04
5	style width	0.45	0.48	0.39	0.31	0.34	0.36	0.42	0.56	0.38	0.38
6	style width/length	0.62	0.79	0.64	0.49	0.44	0.52	0.39	0.60	0.57	0.37
7	style shape	2.00	3.00	2.00	3.00	2.00	3.00	1.50	3.00	2.50	2.00
8	stigma shape	3.00	2.00	1.50	2.00	2.00	3.00	2.00	3.00	3.00	3.00
9	stigma breadth	1.50	1.00	1.00	1.00	1.00	3.00	3.50	3.00	2.00	2.00
10	silique pub. type	1.00	1.00	0.0	5.00	1.00	4.00	1.00	1.00	5.00	5.00
11	silique pub. degree	2.00	5.00	0.0	3.00	2.00	5.00	1.00	5.00	5.00	4.00
12	fruiting pedicel length	2.80	3.30	2.00	3.00	2.80	2.30	3.10	3.10	2.70	3.10
13	inflorescence length	2.50	3.60	1.40	1.90	3.30	3.10	3.80	7.10	4.30	8.40
14	inflorescence density	84.70	81.50	98.00	95.30	64.20	70.40	85.30	51.30	60.90	57.30
15	seed row number	1.00	2.00	1.50	2.00	2.00	2.00	2.00	2.00	2.00	2.00
16	seed length	1.30	1.20	1.20	1.30	-99.00	1.20	1.50	1.10	1.00	1.30
17	seed width	0.75	0.57	0.69	0.66	-99.00	0.58	0.73	0.62	0.46	0.66
18	seed width/length	0.60	0.47	0.56	0.50	-99.00	0.50	0.47	0.54	0.47	0.52
19	petal length	3.90	3.80	3.10	-99.00	3.30	3.30	4.10	3.20	2.80	-99.00
20	petal width	1.90	2.20	1.80	-99.00	1.90	1.40	2.00	1.70	1.50	-99.00
21	petal width/length	0.49	0.58	0.58	-99.00	0.58	0.42	0.49	0.53	0.54	-99.00
22	sepal length	2.50	2.70	2.30	2.40	2.10	2.50	3.00	2.80	2.30	-99.00
23	sepal width	1.50	1.60	1.40	1.30	1.40	1.40	1.40	1.40	1.20	-99.00
24	sepal width/length	0.60	0.59	0.61	0.54	0.67	0.56	0.47	0.50	0.52	-99.00
25	sepal pub. type	1.00	1.00	0.0	0.0	0.0	1.00	1.00	1.00	1.00	-99.00
26	sepal pub. degree	1.00	2.00	0.0	0.0	0.0	1.00	3.00	4.00	2.00	-99.00
27	plant height	7.50	9.10	5.60	6.30	6.00	7.70	9.20	11.10	8.20	15.40
28	stem leafyness	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
29	stem branching	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
30	stem rosettes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.00
31	stem number/plant	6.00	2.20	1.00	4.00	2.20	2.30	1.80	2.30	4.50	1.80
32	stem pub. type	3.00	4.00	3.00	6.00	3.00	4.00	3.00	2.00	4.00	5.00
33	stem pub. degree	3.00	3.00	3.00	3.00	2.00	4.00	3.00	5.00	3.00	3.00
34	basal leaf length	1.90	2.10	1.40	1.30	0.80	1.20	2.20	3.00	2.00	3.10
35	basal leaf width	1.06	1.96	1.44	1.53	1.27	1.48	1.83	2.30	1.22	1.62
36	basal leaf width/length	0.06	0.09	0.11	0.12	0.17	0.12	0.09	0.08	0.06	0.05
37	leaf pub. type	1.00	1.00	1.00	3.00	1.00	3.00	3.00	1.00	2.00	1.00
38	leaf pub. degree	2.00	4.00	1.00	4.00	1.00	5.00	2.00	4.00	2.00	1.00
39	basal leaf margin	0.0	1.00	0.0	0.0	0.0	3.00	1.00	1.00	1.00	0.0
40	stem habit	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
41	septum margin base	1.00	0.0	1.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0
42	siliques aborted	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

	ATTRIBUTES	41	42	43	44	45	46	47	48	49	50
1	silique length	12.20	6.00	6.00	10.10	6.10	6.60	5.10	9.00	7.90	5.00
2	silique width	1.70	1.90	1.40	1.50	1.30	1.60	1.20	1.10	1.30	1.30
3	silique width/length	0.14	0.32	0.23	0.15	0.21	0.24	0.24	0.12	0.17	0.26
4	style length	0.90	0.59	0.54	1.00	1.03	0.75	0.77	1.61	0.68	0.78
5	style width	0.34	0.42	0.29	0.31	0.31	0.41	0.41	0.41	0.31	0.35
6	style width/length	0.38	0.71	0.54	0.31	0.30	0.55	0.53	0.25	0.46	0.45
7	style shape	2.00	3.00	2.00	2.00	2.00	2.00	2.00	1.00	2.00	2.00
8	stigma shape	3.50	3.00	1.50	2.50	4.00	3.00	3.00	1.50	2.00	3.00
9	stigma breadth	3.00	3.00	1.00	1.00	3.00	3.00	1.00	1.00	1.00	3.00
10	silique pub. type	3.00	2.00	3.00	0.0	0.0	1.00	0.0	0.0	5.00	3.00
11	silique pub. degree	2.00	3.00	5.00	0.0	0.0	5.00	0.0	0.0	5.00	5.00
12	fruiting pedicel length	3.80	2.70	2.40	7.50	3.60	2.20	2.30	2.40	2.60	1.70
13	inflorescence length	6.30	3.40	1.40	5.60	4.30	3.50	1.50	3.60	5.20	1.90
14	inflorescence density	64.00	69.70	100.00	50.00	50.00	79.00	98.40	75.00	54.60	100.00
15	seed row number	2.00	2.00	2.00	2.00	2.00	2.00	1.50	1.50	2.00	1.50
16	seed length	1.30	0.90	1.20	1.10	-99.00	1.20	1.20	-99.00	1.10	1.20
17	seed width	0.73	0.48	0.56	0.59	-99.00	0.59	0.76	-99.00	0.55	0.64
18	seed width/length	0.58	0.53	0.47	0.51	[illegible]	0.49	0.61	-99.00	0.49	0.52
19	petal length	-99.00	4.40	2.70	-99.00	[illegible]	2.90	3.70	2.90	3.00	3.00
20	petal width	-99.00	2.30	1.40	-99.00	[illegible]	1.10	1.90	1.20	1.10	1.00
21	petal width/length	-99.00	0.52	0.52	-99.00	[illegible]	0.38	0.51	0.41	0.37	0.33
22	sepal length	-99.00	2.50	2.30	-99.00	[illegible]	2.20	3.10	2.40	2.10	2.20
23	sepal width	-99.00	1.70	1.10	-99.00	-99.00	1.10	1.50	1.10	1.10	1.10
24	sepal width/length	-99.00	0.68	0.48	-99.00	-99.00	0.50	0.48	0.46	0.52	0.50
25	sepal pub. type	-99.00	0.0	1.00	0.0	-99.00	1.00	0.0	0.0	2.00	0.0
26	sepal pub. degree	-99.00	0.0	1.00	0.0	-99.00	2.00	0.0	0.0	3.00	0.0
27	plant height	13.30	7.90	9.20	10.10	13.30	8.10	6.50	14.30	15.30	4.50
28	stem leafyness	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
29	stem branching	1.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.00	0.0
30	stem rosettes	2.00	1.00	0.0	1.00	2.00	0.0	0.0	2.00	2.00	0.0
31	stem number/plant	3.00	12.30	3.00	1.00	1.00	1.60	2.80	1.00	1.80	1.70
32	stem pub. type	5.00	4.00	5.00	3.00	1.00	2.00	3.00	4.00	6.00	5.00
33	stem pub. degree	3.00	4.00	4.00	2.00	1.00	5.00	3.00	3.00	3.00	3.00
34	basal leaf length	3.00	2.10	3.30	5.20	3.20	2.60	1.50	2.30	2.80	1.00
35	basal leaf width	1.64	1.94	1.07	2.38	1.35	1.41	1.24	0.61	0.84	0.82
36	basal leaf width/length	0.06	0.09	0.03	0.05	0.04	0.05	0.08	0.03	0.03	0.08
37	leaf pub. type	4.00	1.00	3.00	1.00	1.00	2.00	1.00	1.00	3.00	2.00
38	leaf pub. degree	2.00	2.00	2.00	1.00	2.00	4.00	2.00	2.00	3.00	2.00
39	basal leaf margin	3.00	1.00	0.0	2.00	2.00	1.00	0.0	1.00	4.00	0.0
40	stem habit	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
41	septum margin base	0.0	0.0	0.0	0.0	0.0	0.0	1.00	0.0	0.0	1.00
42	siliques aborted	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

	ATTRIBUTES	51	52	53	54	55	56	57	58	59	60
1	silique length	6.90	7.70	8.30	6.00	9.60	13.60	14.30	20.10	19.30	16.10
2	silique width	1.10	1.50	1.20	2.00	1.10	0.98	0.86	0.89	0.93	0.68
3	silique width/length	0.16	0.20	0.15	0.33	0.11	0.07	0.06	0.04	0.05	0.04
4	style length	1.11	0.84	0.96	0.85	0.45	0.89	0.77	0.48	0.47	0.83
5	style width	0.34	0.36	0.24	0.41	0.36	0.38	0.37	0.35	0.53	0.33
6	style width/length	0.31	0.43	0.25	0.48	0.80	0.43	0.48	0.73	1.10	0.40
7	style shape	2.00	2.00	2.00	3.00	2.00	1.00	1.00	1.00	1.00	1.00
8	stigma shape	2.00	3.00	3.50	4.00	2.50	1.50	1.00	1.50	1.00	1.50
9	stigma breadth	2.00	3.00	2.00	4.00	1.50	1.00	1.00	1.50	1.00	1.00
10	silique pub. type	1.00	5.00	1.00	1.00	3.00	5.00	5.00	2.00	2.00	5.00
11	silique pub. degree	2.00	6.00	2.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00
12	fruiting pedicel length	3.70	3.60	3.40	2.00	3.50	2.80	2.20	4.10	3.60	3.70
13	inflorescence length	7.00	6.70	4.10	2.60	4.20	3.20	3.10	4.60	11.10	7.50
14	inflorescence density	64.00	53.00	73.00	85.20	76.50	53.30	88.00	56.60	16.80	42.90
15	seed row number	2.00	2.00	2.00	2.00	1.00	1.00	1.00	1.00	1.00	1.00
16	seed length	-99.00	1.10	1.30	1.00	0.89	0.95	0.98	1.10	0.93	1.00
17	seed width	-99.00	0.57	0.64	0.52	0.51	0.54	0.51	0.61	0.54	0.45
18	seed width/length	[illegible]	0.52	0.48	0.53	0.57	0.57	0.52	0.55	0.58	0.45
19	petal length	4.10	3.20	-99.00	3.50	3.10	3.30	3.00	3.60	3.90	3.90
20	petal width	1.60	1.40	-99.00	1.60	1.20	1.20	1.10	1.80	1.70	1.50
21	petal width/length	0.39	0.44	-99.00	0.46	0.39	0.36	0.37	0.50	0.44	0.38
22	sepal length	2.80	2.50	-99.00	2.30	2.60	2.40	2.10	2.20	2.20	2.40
23	sepal width	1.30	1.20	-99.00	1.20	1.40	1.20	0.80	1.00	1.10	1.00
24	sepal width/length	0.46	0.48	-99.00	0.52	0.54	0.50	0.37	0.45	0.50	0.42
25	sepal pub. type	1.00	1.00	-99.00	1.00	2.00	4.00	5.00	1.00	2.00	4.00
26	sepal pub. degree	2.00	4.00	-99.00	1.00	4.00	4.00	4.00	4.00	4.00	5.00
27	plant height	13.80	8.30	8.00	6.00	12.60	7.40	6.60	8.70	23.00	11.10
28	stem leafyness	1.00	1.00	1.00	1.00	3.00	4.00	4.00	4.00	5.00	3.00
29	stem branching	0.0	0.0	0.0	0.0	2.00	2.00	2.00	2.00	5.00	2.00
30	stem rosettes	2.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
31	stem number/plant	3.20	1.00	2.30	12.00	6.90	12.50	5.00	4.70	10.60	8.80
32	stem pub. type	5.00	3.00	2.00	1.00	6.00	6.00	6.00	2.00	1.00	5.00
33	stem pub. degree	3.00	5.00	2.00	5.00	4.00	5.00	4.00	3.00	5.00	4.00
34	basal leaf length	3.80	1.60	2.20	1.60	2.30	1.60	2.00	2.10	4.00	1.60
35	basal leaf width	1.38	1.30	0.63	1.60	0.88	2.00	1.90	3.30	5.80	1.60
36	basal leaf width/length	0.04	0.08	0.03	0.10	0.04	0.13	0.09	0.16	0.15	0.10
37	leaf pub. type	1.00	3.00	1.00	1.00	3.00	6.00	4.00	1.00	1.00	4.00
38	leaf pub. degree	2.00	4.00	1.00	1.00	2.00	3.00	2.00	5.00	3.00	4.00
39	basal leaf margin	3.00	3.00	0.0	1.00	2.00	2.00	2.00	4.00	2.00	1.00
40	stem habit	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
41	septum margin base	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
42	siliques aborted	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

	ATTRIBUTES	61	62	63	64	65	66	67	68	69	70
1	silique length	12.80	15.30	15.10	14.60	13.60	10.80	9.60	11.40	12.50	12.60
2	silique width	0.75	0.81	0.83	0.73	0.78	0.86	0.75	0.86	1.00	0.87
3	silique width/length	0.06	0.05	0.05	0.05	0.06	0.08	0.08	0.08	0.08	0.07
4	style length	0.72	0.40	0.93	0.44	0.50	0.58	0.69	0.86	0.79	0.71
5	style width	0.31	0.41	0.39	0.41	0.41	0.35	0.44	0.37	0.40	0.36
6	style width/length	0.43	1.00	0.42	0.93	0.82	0.60	0.64	0.43	0.51	0.51
7	style shape	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
8	stigma shape	1.00	2.50	3.00	2.00	2.00	3.00	2.00	2.50	2.00	1.50
9	stigma breadth	1.00	2.00	3.00	1.00	2.00	3.00	1.00	2.00	1.00	2.00
10	silique pub. type	5.00	5.00	5.00	4.00	5.00	5.00	3.00	3.00	6.00	4.00
11	silique pub. degree	5.00	6.00	6.00	5.00	5.00	5.00	6.00	6.00	5.00	4.00
12	fruiting pedicel length	3.20	2.00	4.80	3.50	3.50	2.80	3.90	3.90	3.10	2.40
13	inflorescence length	4.30	3.30	4.30	12.10	5.30	3.50	3.10	2.70	3.80	3.60
14	inflorescence density	64.80	61.60	46.40	15.60	49.10	58.10	74.40	75.80	73.50	64.00
15	seed row number	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
16	seed length	0.86	1.10	0.94	0.87	0.97	0.87	1.00	1.10	0.94	0.97
17	seed width	0.47	0.55	0.50	0.50	0.53	0.52	0.54	0.47	0.56	0.55
18	seed width/length	0.55	0.50	0.53	0.57	0.55	0.60	0.55	0.55	0.60	0.57
19	petal length	-99.00	3.70	3.10	3.80	-99.00	3.70	4.20	6.10	3.80	3.60
20	petal width	-99.00	1.70	1.40	1.90	-99.00	1.60	2.10	3.30	1.70	1.20
21	petal width/length	-99.00	0.46	0.45	0.50	-99.00	0.43	0.50	0.54	0.45	0.33
22	sepal length	-99.00	2.30	1.80	2.20	-99.00	2.50	2.10	2.90	2.20	2.00
23	sepal width	-99.00	2.20	0.89	1.10	-99.00	1.00	1.00	1.30	1.10	1.00
24	sepal width/length	-99.00	0.52	0.49	0.50	-99.00	0.40	0.48	0.45	0.50	0.50
25	sepal pub. type	5.00	5.00	5.00	4.00	4.00	5.00	3.00	4.00	4.00	5.00
26	sepal pub. degree	5.00	5.00	5.00	3.00	5.00	3.00	3.00	5.00	2.00	2.00
27	plant height	8.60	8.80	6.90	21.50	9.40	9.00	8.30	5.60	7.00	9.90
28	stem leafyness	3.00	5.00	3.00	6.00	3.00	3.00	4.00	3.00	3.00	3.00
29	stem branching	1.00	3.00	0.0	5.00	1.00	1.00	0.0	0.0	2.00	1.00
30	stem rosettes	0.0	0.0	0.0	1.00	0.0	0.0	0.0	0.0	0.0	0.0
31	stem number/plant	1.60	10.60	2.30	20.30	1.70	1.40	1.40	1.70	4.00	4.70
32	stem pub. type	5.00	6.00	5.00	5.00	4.00	5.00	4.00	4.00	5.00	5.00
33	stem pub. degree	4.00	4.00	4.00	4.00	4.00	3.00	4.00	5.00	4.00	4.00
34	basal leaf length	0.86	1.20	0.68	3.00	0.70	0.49	0.80	0.90	0.92	0.53
35	basal leaf width	1.60	1.80	0.93	3.10	1.40	1.00	1.30	1.90	1.50	1.20
36	basal leaf width/length	0.19	0.15	0.14	0.10	0.20	0.20	0.16	0.21	0.16	0.23
37	leaf pub. type	3.00	6.00	6.00	6.00	3.00	6.00	4.00	4.00	6.00	4.00
38	leaf pub. degree	3.00	5.00	5.00	3.00	4.00	4.00	6.00	6.00	4.00	2.00
39	basal leaf margin	2.00	1.00	1.00	1.00	3.00	2.00	1.00	1.00	2.00	2.00
40	stem habit	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
41	septum margin base	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
42	siliques aborted	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.00	0.0	0.0

	ATTRIBUTES	71	72	73	74	75	76	77	78	79	80
1	silique length	14.40	15.90	14.00	12.00	15.30	12.10	19.90	19.70	16.50	13.30
2	silique width	0.97	0.83	0.95	0.87	0.73	0.91	0.80	0.78	0.73	1.10
3	silique width/length	0.07	0.05	0.07	0.07	0.05	0.08	0.04	0.04	0.04	0.08
4	style length	0.82	0.91	1.40	0.77	1.00	0.90	0.46	0.39	0.84	0.75
5	style width	0.39	0.43	0.30	0.24	0.24	0.35	0.56	0.45	0.22	0.39
6	style width/length	0.48	0.47	0.21	0.31	0.24	0.39	1.20	1.20	0.26	0.52
7	style shape	1.50	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
8	stigma shape	2.50	1.50	2.50	2.50	2.00	2.50	2.50	2.50	1.00	1.50
9	stigma breadth	3.00	1.00	2.00	2.00	2.00	2.00	2.00	2.00	1.00	2.00
10	silique pub. type	3.00	4.00	-99.00	5.00	5.00	5.00	4.00	4.00	4.00	4.00
11	silique pub. degree	4.00	6.00	-99.00	5.00	5.00	5.00	4.00	4.00	2.00	4.00
12	fruiting pedicel length	3.50	5.00	3.20	2.90	3.50	3.30	2.90	3.60	4.70	2.80
13	inflorescence length	3.70	6.10	3.00	4.60	4.60	4.90	11.60	9.90	7.60	3.20
14	inflorescence density	78.60	39.50	87.00	68.40	81.90	63.70	23.60	27.70	46.70	88.30
15	seed row number	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
16	seed length	1.10	1.10	0.95	0.85	0.90	1.00	0.84	0.83	0.89	1.00
17	seed width	0.55	0.51	0.50	0.48	0.51	0.50	0.43	0.43	0.48	0.63
18	seed width/length	0.50	0.46	0.53	0.56	0.57	0.50	0.51	0.52	0.54	0.63
19	petal length	-99.00	5.50	4.40	4.10	3.90	3.80	3.80	3.80	3.20	-99.00
20	petal width	-99.00	3.30	1.70	1.80	2.00	2.00	1.70	1.50	1.10	-99.00
21	petal width/length	-99.00	0.60	0.39	0.44	0.51	0.53	0.45	0.39	0.34	-99.00
22	sepal length	-99.00	2.90	2.40	2.60	2.40	2.40	2.40	2.40	2.20	-99.00
23	sepal width	-99.00	1.50	1.10	1.40	1.30	1.30	1.20	1.00	1.00	-99.00
24	sepal width/length	-99.00	0.52	0.46	0.54	0.54	0.54	0.50	0.42	0.45	-99.00
25	sepal pub. type	-99.00	3.00	4.00	4.00	4.00	3.00	3.00	3.00	3.00	-99.00
26	sepal pub. degree	-99.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	1.50	-99.00
27	plant height	8.70	9.00	5.00	6.30	9.10	10.30	17.70	16.00	12.60	6.10
28	stem leafyness	3.00	4.00	4.00	5.00	3.00	4.00	6.00	6.00	3.00	3.00
29	stem branching	1.00	1.00	1.00	1.00	0.0	1.00	5.00	5.00	2.00	0.0
30	stem rosettes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.00	0.0
31	stem number/plant	4.60	1.80	4.60	3.60	2.90	3.30	19.30	6.40	4.60	1.70
32	stem pub. type	4.00	6.00	6.00	6.00	5.00	6.00	5.00	6.00	5.00	5.00
33	stem pub. degree	3.00	4.00	4.00	4.00	3.00	3.00	3.00	4.00	3.00	3.00
34	basal leaf length	0.97	1.90	0.96	0.91	1.20	1.30	3.30	3.80	3.70	1.06
35	basal leaf width	1.40	3.00	1.40	1.30	1.90	1.70	2.90	3.90	3.30	1.50
36	basal leaf width/length	0.14	0.16	0.15	0.14	0.16	0.13	0.09	0.10	0.09	0.14
37	leaf pub. type	4.00	6.00	4.00	4.00	5.00	4.00	4.00	6.00	4.00	4.00
38	leaf pub. degree	2.00	5.00	2.00	3.00	2.00	2.00	2.00	2.00	2.00	4.00
39	basal leaf margin	2.00	2.00	1.00	1.00	2.00	2.00	1.00	1.00	5.00	2.00
40	stem habit	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
41	septum margin base	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
42	siliques aborted	0.0	1.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

	ATTRIBUTES	81	82	83	84	85	86	87	88	89	90
1	silique length	17.10	18.80	-99.00	15.20	16.60	18.10	17.40	19.60	29.20	21.20
2	silique width	0.79	0.86	-99.00	1.27	0.94	1.10	0.81	0.89	0.78	1.00
3	silique width/length	0.05	0.05	-99.00	0.08	0.06	0.06	0.05	0.05	0.03	0.05
4	style length	0.56	0.45	-99.00	0.69	0.66	0.83	1.10	0.79	0.86	0.64
5	style width	0.30	0.34	-99.00	0.42	0.36	0.55	0.36	0.35	0.47	0.53
6	style width/length	0.54	0.76	-99.00	0.61	0.55	0.66	0.33	0.44	0.55	0.83
7	style shape	1.00	1.00	-99.00	1.00	1.00	1.00	1.00	1.00	1.50	1.00
8	stigma shape	3.00	2.50	-99.00	2.50	1.00	2.00	1.00	1.00	3.00	2.00
9	stigma breadth	3.00	2.00	-99.00	3.00	1.00	2.00	1.50	2.50	2.00	1.00
10	silique pub. type	5.00	5.00	-99.00	5.00	6.00	4.00	2.00	2.00	5.00	3.00
11	silique pub. degree	6.00	3.00	-99.00	4.00	6.00	6.00	4.00	5.00	4.00	5.00
12	fruiting pedicel length	2.90	4.60	-99.00	2.90	4.80	4.70	4.00	4.00	4.10	1.40
13	inflorescence length	6.20	14.50	-99.00	5.20	5.00	6.40	3.50	3.60	8.50	7.40
14	inflorescence density	28.50	29.20	-99.00	59.70	42.20	39.20	[illegible]	5.80	15.40	31.30
15	seed row number	1.00	1.00	1.00	1.00	1.00	1.00	[illegible]	43.30	1.00	1.00
16	seed length	0.94	0.85	-99.00	0.98	-99.00	1.10	[illegible]	1.00	-99.00	0.94
17	seed width	0.50	0.46	-99.00	0.60	-99.00	0.66	[illegible]	1.00	-99.00	0.61
18	seed width/length	0.53	0.54	-99.00	0.61	-99.00	0.60	[illegible]	0.50	-99.00	0.65
19	petal length	3.10	3.60	5.00	4.00	3.70	5.70	6.10	0.50	6.30	3.10
20	petal width	1.40	1.70	2.60	1.40	1.40	2.70	3.40	4.70	3.00	1.30
21	petal width/length	0.45	0.47	0.52	0.35	0.38	0.47	0.56	2.30	0.48	0.42
22	sepal length	2.00	2.30	2.20	2.70	2.20	2.50	2.60	0.49	3.30	1.90
23	sepal width	0.97	1.20	1.30	1.40	1.00	1.30	1.40	2.90	1.20	0.90
24	sepal width/length	0.49	0.52	0.59	0.52	0.45	0.52	0.54	1.40	0.36	0.47
25	sepal pub. type	4.00	4.00	4.00	3.00	4.00	3.00	3.00	0.48	4.00	3.00
26	sepal pub. degree	2.00	3.00	5.00	4.00	6.00	5.00	4.00	3.00	3.00	3.00
27	plant height	16.00	24.40	3.00	11.50	9.40	10.10	10.90	4.00	14.40	12.60
28	stem leafyness	4.00	6.00	3.00	2.50	4.00	3.00	3.00	26.20	7.00	4.00
29	stem branching	3.00	5.00	0.0	0.0	2.00	1.00	1.00	7.00	2.00	2.00
30	stem rosettes	0.0	0.0	0.0	0.0	0.0	0.0	1.00	4.00	0.0	0.0
31	stem number/plant	-99.00	-99.00	2.10	8.00	9.50	10.80	15.00	0.0	1.60	12.00
32	stem pub. type	5.00	5.00	5.00	5.00	5.00	3.00	6.00	1.00	5.00	5.00
33	stem pub. degree	4.00	3.00	5.00	3.00	4.00	5.00	4.00	5.00	4.00	4.00
34	basal leaf length	-99.00	-99.00	0.71	14.00	15.10	17.00	18.30	4.00	33.30	20.20
35	basal leaf width	-99.00	-99.00	1.80	1.30	2.10	2.80	2.90	25.80	3.80	2.40
36	basal leaf width/length	-99.00	-99.00	0.25	0.09	0.14	0.16	0.16	5.00	0.11	0.12
37	leaf pub. type	6.00	4.00	4.00	4.00	4.00	3.00	3.00	0.19	3.00	4.00
38	leaf pub. degree	4.00	2.00	6.00	3.00	4.00	5.00	2.00	4.00	4.00	3.00
39	basal leaf margin	-99.00	-99.00	2.00	3.00	4.00	1.00	2.00	4.00	5.00	1.00
40	stem habit	2.00	2.00	2.00	2.00	2.00	2.00	2.00	4.00	2.00	2.00
41	septum margin base	0.0	0.0	-99.00	0.0	0.0	0.0	0.0	2.00	0.0	0.0
42	siliques aborted	0.0	0.0	-99.00	0.0	0.0	1.00	1.00	0.0	0.0	0.0

	ATTRIBUTES	91	92	93	94	95	96	97	98	99	100
1	silique length	19.30	16.30	16.40	21.00	16.40	20.10	20.00	17.50	17.00	10.00
2	silique width	0.76	0.86	1.10	0.77	0.70	1.00	0.83	0.71	1.10	0.73
3	silique width/length	0.04	0.05	0.07	0.04	0.04	0.05	0.04	0.04	0.06	0.07
4	style length	0.63	0.83	0.70	1.00	1.00	1.05	1.00	0.84	0.59	0.89
5	style width	0.38	0.38	0.54	0.31	0.25	0.48	0.35	0.24	0.55	0.39
6	style width/length	0.60	0.46	0.77	0.31	0.25	0.46	0.35	0.29	0.93	0.44
7	style shape	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.50	1.00
8	stigma shape	2.50	2.00	4.00	2.50	2.00	1.00	3.00	2.00	3.50	3.00
9	stigma breadth	1.50	2.00	3.00	2.00	2.00	1.00	2.00	2.00	3.00	2.00
10	silique pub. type	4.00	5.00	5.00	3.00	5.00	5.00	2.00	3.00	5.00	5.00
11	silique pub. degree	4.00	4.00	4.00	4.00	4.00	3.00	3.00	3.00	4.00	4.00
12	fruiting pedicel length	3.40	2.40	3.30	3.40	3.20	2.60	3.50	3.20	3.90	1.50
13	inflorescence length	5.10	5.50	5.50	5.80	3.80	5.10	5.20	5.80	9.10	1.60
14	inflorescence density	38.30	48.90	62.80	26.20	50.00	52.40	50.50	58.30	16.40	100.00
15	seed row number	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
16	seed length	0.95	1.10	0.83	0.93	-99.00	1.10	0.88	0.86	0.97	-99.00
17	seed width	0.43	0.49	0.53	0.45	-99.00	0.66	0.41	0.45	0.58	-99.00
18	seed width/length	0.45	0.45	0.64	0.48	-99.00	0.60	0.47	0.52	0.60	-99.00
19	petal length	4.00	3.40	-99.00	3.80	4.10	3.90	4.10	3.10	-99.00	3.10
20	petal width	1.40	1.20	-99.00	1.10	1.40	1.60	1.60	0.90	-99.00	1.10
21	petal width/length	0.35	0.35	-99.00	0.29	0.34	0.41	0.39	0.29	-99.00	0.35
22	sepal length	2.30	2.10	-99.00	2.10	2.40	2.30	2.30	1.80	-99.00	1.80
23	sepal width	0.90	1.00	-99.00	0.80	1.00	1.10	1.00	0.70	-99.00	0.70
24	sepal width/length	0.39	0.48	-99.00	0.38	0.42	0.48	0.43	0.39	-99.00	0.39
25	sepal pub. type	3.00	3.00	-99.00	3.00	3.00	3.00	2.00	1.00	-99.00	2.00
26	sepal pub. degree	3.00	2.00	-99.00	3.00	2.00	2.00	2.00	1.00	-99.00	1.00
27	plant height	10.20	16.80	10.10	14.80	20.00	14.30	12.40	10.80	20.10	3.80
28	stem leafyness	4.00	6.00	3.00	7.00	7.00	7.00	5.00	4.00	4.00	3.00
29	stem branching	0.0	3.00	0.0	5.00	4.00	3.00	3.00	2.00	2.00	1.00
30	stem rosettes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.00
31	stem number/plant	8.50	5.00	2.80	5.00	9.00	18.00	3.30	8.00	10.00	2.70
32	stem pub. type	4.00	3.00	4.00	2.00	2.00	4.00	2.00	3.00	5.00	4.00
33	stem pub. degree	4.00	3.00	3.00	4.00	3.00	3.00	3.00	2.00	3.00	3.00
34	basal leaf length	19.60	32.00	11.10	12.50	34.00	26.00	23.80	16.00	32.00	8.70
35	basal leaf width	1.60	2.90	1.20	1.10	2.60	2.40	1.10	1.20	2.70	1.00
36	basal leaf width/length	0.08	0.09	0.11	0.09	0.08	0.09	0.05	0.08	0.08	0.11
37	leaf pub. type	4.00	3.00	3.00	3.00	3.00	3.00	2.00	2.00	4.00	3.00
38	leaf pub. degree	3.00	1.00	4.00	1.00	1.00	1.00	1.00	1.00	2.00	1.00
39	basal leaf margin	2.00	4.00	2.00	1.00	2.00	4.00	3.00	3.00	1.00	0.0
40	stem habit	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
41	septum margin base	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
42	siliques aborted	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

	ATTRIBUTES	101	102	103
1	silique length	10.40	13.80	21.00
2	silique width	0.83	0.92	1.50
3	silique width/length	0.08	0.07	0.07
4	style length	0.69	0.77	0.70
5	style width	0.39	0.42	0.60
6	style width/length	0.57	0.55	0.86
7	style shape	1.00	1.00	1.00
8	stigma shape	2.00	2.00	4.00
9	stigma breadth	1.00	1.00	3.00
10	silique pub. type	3.00	5.00	3.00
11	silique pub. degree	4.00	4.00	4.00
12	fruiting pedicel length	5.20	2.90	4.00
13	inflorescence length	4.80	6.50	7.00
14	inflorescence density	-99.00	30.00	33.00
15	seed row number	1.00	1.00	1.00
16	seed length	-99.00	0.80	0.99
17	seed width	-99.00	0.56	0.66
18	seed width/length	-99.00	0.70	0.67
19	petal length	5.10	3.70	5.10
20	petal width	3.00	1.60	2.40
21	petal width/length	0.59	0.43	0.47
22	sepal length	2.20	2.30	3.50
23	sepal width	1.00	1.10	1.70
24	sepal width/length	0.45	0.48	0.49
25	sepal pub. type	3.00	3.00	3.00
26	sepal pub. degree	4.00	4.00	4.00
27	plant height	13.50	12.90	12.00
28	stem leafyness	6.00	6.00	3.00
29	stem branching	2.00	1.00	1.00
30	stem rosettes	0.0	0.0	0.0
31	stem number/plant	5.80	10.30	8.00
32	stem pub. type	4.00	5.00	4.00
33	stem pub. degree	3.00	3.00	3.00
34	basal leaf length	20.40	17.20	25.00
35	basal leaf width	3.30	3.10	3.00
36	basal leaf width/length	0.16	0.18	0.12
37	leaf pub. type	3.00	4.00	2.00
38	leaf pub. degree	2.00	4.00	4.00
39	basal leaf margin	4.00	4.00	4.00
40	stem habit	2.00	2.00	1.00
41	septum margin base	0.0	0.0	0.0
42	siliques aborted	0.0	0.0	0.0

Appendix 5. Data matrix for numerical analysis of IDH, PGM, PGI and SOD attributes.

RAW ATTRIBUTE VALUES BY OTU

OTU'S

	ATTRIBUTES	1	2	3	4	5	6	7	8	9	10
1	IDH1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2	IDH2	0.0	0.0	0.0	0.0	0.0	0.0	1.00	0.0	0.0	0.0
3	IDH2a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4	IDH2b	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
5	IDH3	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
6	IDH3a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
7	IDH4	2.00	3.00	3.00	1.00	1.00	3.00	1.00	2.00	0.0	2.00
8	IDH4a	0.0	0.0	0.0	0.0	1.00	0.0	1.00	0.0	0.0	0.0
9	SOD1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
10	SOD2	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
11	SOD2a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
12	SOD3	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
13	SOD4	2.00	2.00	2.00	2.00	1.00	2.00	1.00	1.00	2.00	2.00
14	PGM1	3.00	1.00	3.00	3.00	0.0	3.00	3.00	3.00	3.00	3.00
15	PGM2	0.0	3.00	3.00	3.00	3.00	3.00	3.00	0.0	3.00	0.0
16	PGI1	3.00	3.00	2.00	2.00	3.00	2.00	2.00	2.00	2.00	3.00
17	PGI1a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18	PGI2	0.0	1.00	3.00	3.00	0.0	3.00	3.00	3.00	3.00	0.0
19	PGI2a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
20	PGI3	0.0	2.00	2.00	2.00	0.0	0.0	0.0	0.0	2.00	0.0

	ATTRIBUTES	11	12	13	14	15	16	17	18	19	20
1	IDH1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2	IDH2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3	IDH2a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.00	0.0
4	IDH2b	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.00	0.0
5	IDH3	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	0.0	3.00
6	IDH3a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.00
7	IDH4	0.0	1.00	1.00	1.00	3.00	3.00	1.00	0.0	0.0	3.00
8	IDH4a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
9	SOD1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
10	SOD2	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
11	SOD2a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.00	0.0
12	SOD3	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	0.0	2.00
13	SOD4	2.00	2.00	2.00	2.00	0.0	2.00	1.00	2.00	1.00	0.0
14	PGM1	0.0	3.00	3.00	3.00	3.00	3.00	3.00	0.0	0.0	3.00
15	PGM2	3.00	3.00	3.00	3.00	0.0	3.00	0.0	3.00	0.0	0.0
16	PGI1	2.00	1.00	1.00	1.00	3.00	1.00	3.00	0.0	0.0	0.0
17	PGI1a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.00	0.0
18	PGI2	3.00	3.00	3.00	3.00	0.0	3.00	3.00	0.0	0.0	3.00
19	PGI2a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.00	0.0
20	PGI3	2.00	2.00	2.00	2.00	0.0	2.00	0.0	0.0	0.0	0.0

	ATTRIBUTES	21	22	23	24	25	26	27	28	29	30
1	IDH1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2	IDH2	0.0	0.0	0.0	0.0	0.0	0.0	1.00	1.00	0.0	0.0
3	IDH2a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4	IDH2b	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
5	IDH3	3.00	3.00	3.00	3.00	0.0	3.00	3.00	3.00	3.00	3.00
6	IDH3a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
7	IDH4	2.00	2.00	0.0	3.00	0.0	3.00	3.00	3.00	3.00	0.0
8	IDH4a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
9	SOD1	0.0	0.0	0.0	0.0	0.0	0.0	2.00	0.0	0.0	0.0
10	SOD2	2.00	2.00	2.00	0.0	0.0	2.00	2.00	2.00	2.00	2.00
11	SOD2a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
12	SOD3	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
13	SOD4	2.00	1.00	0.0	0.0	0.0	2.00	2.00	0.0	0.0	0.0
14	PGM1	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
15	PGM2	3.00	0.0	0.0	0.0	3.00	3.00	3.00	0.0	0.0	0.0
16	PGI1	2.00	2.00	2.00	3.00	3.00	1.00	2.00	3.00	2.00	2.00
17	PGI1a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18	PGI2	3.00	3.00	3.00	0.0	3.00	3.00	3.00	0.0	3.00	3.00
19	PGI2a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
20	PGI3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

	ATTRIBUTES	31	32	33	34	35	36	37	38	39	40
1	IDH1	1.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2	IDH2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3	IDH2a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4	IDH2b	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
5	IDH3	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
6	IDH3a	0.0	0.0	0.0	1.00	1.00	1.00	0.0	0.0	0.0	0.0
7	IDH4	2.00	2.00	3.00	1.00	1.00	1.00	3.00	3.00	2.00	1.00
8	IDH4a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
9	SOD1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
10	SO[illegible]	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
11	SOD2a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
12	SOD3	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
13	SOD4	2.00	2.00	2.00	0.0	0.0	0.0	0.0	0.0	2.00	0.0
14	PGM1	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
15	PGM2	0.0	3.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
16	PGI1	2.00	1.00	2.00	2.00	2.00	3.00	2.00	2.00	1.00	2.00
17	PGI1a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18	PGI2	3.00	3.00	3.00	3.00	3.00	0.0	3.00	3.00	3.00	3.00
19	PGI2a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
20	PGI3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

	ATTRIBUTES	41	42	43	44	45
1	IDH1	0.0	0.0	0.0	0.0	0.0
2	IDH2	0.0	0.0	0.0	0.0	0.0
3	IDH2a	0.0	0.0	0.0	0.0	0.0
4	IDH2b	0.0	0.0	0.0	0.0	0.0
5	IDH3	3.00	3.00	3.00	3.00	3.00
6	IDH3a	0.0	0.0	0.0	0.0	0.0
7	IDH4	2.00	0.0	3.00	2.00	3.00
8	IDH4a	0.0	0.0	0.0	0.0	0.0
9	SOD1	0.0	0.0	0.0	0.0	0.0
10	SOD2	2.00	0.0	2.00	2.00	2.00
11	SOD2a	0.0	0.0	0.0	0.0	0.0
12	SOD3	2.00	2.00	2.00	2.00	2.00
13	SOD4	1.00	0.0	2.00	2.00	0.0
14	PGM1	3.00	3.00	3.00	3.00	3.00
15	PGM2	0.0	0.0	0.0	0.0	0.0
16	PGI1	2.00	3.00	0.0	2.00	3.00
17	PGI1a	0.0	0.0	0.0	0.0	0.0
18	PGI2	3.00	0.0	3.00	3.00	0.0
19	PGI2a	0.0	0.0	0.0	0.0	0.0
20	PGI3	0.0	0.0	0.0	0.0	0.0

Appendix 6. Data matrix for numerical analysis of /EST attributes.

RAW ATTRIBUTE VALUES BY OTU

OTU'S

ATTRIBUTES		1	2	3	4	5	6	7	8	9	10
1	F5	1.00	3.00	2.00	3.00	3.00	3.00	2.00	3.00	3.00	3.00
2	F4	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	2.00	3.00
3	F1	2.00	2.00	2.00	2.00	2.00	2.00	2.00	1.00	3.00	2.00
4	F3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
5	F2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
6	M6	0.0	0.0	1.00	1.00	1.00	1.00	1.00	2.00	1.00	2.00
7	M5	1.00	1.00	1.00	1.00	1.00	1.00	1.00	2.00	1.00	1.00
8	M4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
9	M3	1.00	1.00	1.00	1.00	2.00	2.00	1.00	1.00	2.00	2.00
10	M2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
11	M1	0.0	0.0	1.00	1.00	0.0	0.0	0.0	0.0	0.0	1.00
12	Sa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
13	Sb	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
14	S1	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
15	S2	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
16	S3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
17	S4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18	S5	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
19	S6	0.0	0.0	1.00	1.00	0.0	0.0	0.0	0.0	0.0	1.00

ATTRIBUTES		11	12	13	14	15	16	17	18	19	20
1	F5	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	0.0	3.00
2	F4	2.00	3.00	0.0	0.0	0.0	3.00	0.0	3.00	3.00	3.00
3	F1	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	1.00	1.00
4	F3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
5	F2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
6	M6	1.00	2.00	2.00	1.00	1.00	1.00	2.00	1.00	3.00	1.00
7	M5	1.00	1.00	2.00	1.00	1.00	1.00	0.0	1.00	1.00	1.00
8	M4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
9	M3	2.00	2.00	3.00	2.00	2.00	2.00	3.00	1.00	1.00	2.00
10	M2	0.0	0.0	0.0	0.0	0.0	0.0	3.00	0.0	0.0	0.0
11	M1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
12	Sa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.00	0.0
13	Sb	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.00	0.0
14	S1	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	0.0	3.00
15	S2	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	0.0	3.00
16	S3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
17	S4	0.0	0.0	0.0	0.0	0.0	0.0	3.00	3.00	0.0	0.0
18	S5	3.00	3.00	3.00	3.00	3.00	3.00	2.00	0.0	0.0	0.0
19	S6	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.0	3.00	0.0

RAW ATTRIBUTE VALUES BY OTU

	ATTRIBUTES	OTU'S									
		21	22	23	24	25	26	27	28	29	30
1	F5	3.00	3.00	3.00	3.00	3.00	3.00	2.00	2.00	2.00	3.00
2	F4	3.00	3.00	0.0	0.0	0.0	0.0	0.0	1.00	0.0	0.0
3	F1	1.00	2.00	2.00	0.0	2.00	1.00	2.00	2.00	1.00	2.00
4	F3	0.0	0.0	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
5	F2	0.0	0.0	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
6	M6	0.0	0.0	1.00	1.00	1.00	1.00	2.00	2.00	0.0	0.0
7	M5	0.0	0.0	2.00	1.00	1.00	1.00	3.00	2.00	0.0	0.0
8	M4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
9	M3	1.00	1.00	3.00	2.00	3.00	2.00	3.00	3.00	2.00	2.00
10	M2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
11	M1	0.0	0.0	1.00	0.0	0.0	0.0	1.00	1.00	0.0	0.0
12	Sa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
13	Sb	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
14	S1	0.0	2.00	3.00	2.00	2.00	2.00	3.00	3.00	2.00	2.00
15	S2	3.00	3.00	0.0	2.00	2.00	0.0	0.0	0.0	0.0	1.00
16	S3	1.00	2.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
17	S4	0.0	0.0	3.00	2.00	2.00	3.00	3.00	3.00	1.00	3.00
18	S5	0.0	0.0	1.00	0.0	0.0	0.0	1.00	1.00	0.0	0.0
19	S6	0.0	0.0	1.00	0.0	0.0	0.0	1.00	1.00	0.0	0.0

RAW ATTRIBUTE VALUES BY OTU

	ATTRIBUTES	OTU'S									
		31	32	33	34	35	36	37	38	39	40
1	F5	3.00	3.00	0.0	3.00	3.00	3.00	3.00	3.00	3.00	3.00
2	F4	0.0	0.0	0.0	0.0	3.00	3.00	3.00	3.00	3.00	3.00
3	F1	2.00	2.00	1.00	2.00	1.00	1.00	1.00	1.00	3.00	3.00
4	F3	0.0	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
5	F2	0.0	0.0	3.00	3.00	0.0	0.0	0.0	0.0	3.00	3.00
6	M6	0.0	0.0	1.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0
7	M5	3.00	0.0	0.0	2.00	1.00	1.00	1.00	1.00	0.0	0.0
8	M4	0.0	0.0	0.0	0.0	2.00	2.00	2.00	2.00	0.0	0.0
9	M3	3.00	3.00	2.00	3.00	2.00	2.00	2.00	2.00	2.00	2.00
10	M2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
11	M1	0.0	1.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
12	Sa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
13	Sb	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
14	S1	2.00	2.00	1.00	0.0	3.00	3.00	3.00	3.00	3.00	3.00
15	S2	2.00	0.0	2.00	3.00	3.00	3.00	3.00	3.00	1.00	1.00
16	S3	2.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
17	S4	2.00	3.00	1.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
18	S5	1.00	1.00	0.0	1.00	1.00	1.00	1.00	1.00	2.00	2.00
19	S6	1.00	1.00	0.0	1.00	1.00	1.00	1.00	1.00	1.00	1.00

RAW ATTRIBUTE VALUES BY OTU

OTU'S

	ATTRIBUTES	41	42	43	44	45	46	47
1	F5	3.00	3.00	3.00	3.00	3.00	2.00	0.0
2	F4	0.0	0.0	2.00	2.00	0.0	2.00	0.0
3	F1	3.00	1.00	2.00	2.00	1.00	2.00	1.00
4	F3	3.00	3.00	3.00	3.00	3.00	3.00	1.00
5	F2	3.00	2.00	2.00	2.00	2.00	1.00	3.00
6	M6	0.0	0.0	2.00	2.00	0.0	1.00	1.00
7	M5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
8	M4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
9	M3	2.00	3.00	2.00	2.00	3.00	3.00	2.00
10	M2	0.0	0.0	0.0	1.00	0.0	0.0	1.00
11	M1	0.0	0.0	1.00	1.00	1.00	1.00	1.00
12	Sa	0.0	0.0	0.0	0.0	0.0	0.0	0.0
13	Sb	0.0	0.0	0.0	0.0	0.0	0.0	0.0
14	S1	3.00	2.00	2.00	3.00	2.00	2.00	2.00
15	S2	1.00	3.00	3.00	2.00	3.00	3.00	3.00
16	S3	3.00	3.00	2.00	2.00	0.0	2.00	2.00
17	S4	3.00	3.00	0.0	0.0	3.00	3.00	0.0
18	S5	2.00	1.00	0.0	0.0	1.00	1.00	0.0
19	S6	1.00	1.00	1.00	0.0	1.00	1.00	1.00

Appendix 7. List of synonyms

Braya linearis Rouy

Braya fernaldii Abbe
B. americana (Hook.) Fern.
B. purpurascens (R. Br.) Bunge var. *fernaldii* (Abbe) Boivin

Braya glabella Richards. var. **glabella**
B. alpina Sternb. & Hoppe var. *glabella* (Richards.) Wats.
B. alpina Sternb. & Hoppe var. *americana* (Hook.) Wats.
B. alpina Sternb. & Hoppe *β americana* Hook.
B. americana (Hook.) Fern.
B. bartlettiana Jordal
B. bartlettiana Jordal var. *vestita* Hult.
B. henryae Raup

Braya glabella Richards. var. **prostrata** Harris

Braya glabella Richards. var. **purpurascens** (R. Br.) Harris
Platypetalum purpurascens R. Br.
P. dubium R. Br.
B. purpurascens (R. Br.) Bunge
B. purpurascens (R. Br.) Bunge var. *dubia* (R. Br.) Schulz
B. arctica Hook.

Braya longii Fern.
B. purpurascens (R. Br.) Bunge var. *longii* (Fern.) Boivin

Braya pilosa Hook.
B. purpurascens (R. Br.) Bunge f. *pilosa* (Hook.) Schulz
B. purpurascens (R. Br.) Bunge subsp. *pilosa* (Hook.) Hult.

Braya thorild-wulffii Ostenf. var. **glabrata** Harris

Braya thorild-wulffii Ostenf. var. **thorild-wulffii**
B. purpurascens (R. Br.) Bunge subsp. *thorild-wulffii* (Ostenf.) Hult.
B. purpurascens (R. Br.) Bunge var. *thorild-wulffii* (Ostenf.) Boivin
B. pilosa Hook. subsp. *thorild-wulffii* (Ostenf.) Petrovsky

Braya humilis (C.A. Mey.) Robins. var. **ellesmerensis** Harris

Braya humilis (C.A. Mey.) Robins. var. **humilis**
Sisymbrium humile C.A. Mey.
B. humilis (C.A. Mey.) Robins. ssp. *arctica* (Böch.) Rollins
B. humilis (C.A. Mey.) Robins. ssp. *arctica* f. *biloba* Böcher
B. humilis (C.A. Mey.) Robins. ssp. *richardsonii* (Rydb.) Hult.
B. humilis (C.A. Mey.) Robins. ssp. *ventosa* Rollins
B. humilis (C.A. Mey.) Robins. var. *abbei* (Böch.) Rollins
B. humilis (C.A. Mey.) Robins. var. *americana* (Hook.) Boivin
B. humilis (C.A. Mey.) Robins. var. *arctica* (Böch.) Boivin
B. humilis (C.A. Mey.) Robins. var. *interior* (Böch.) Boivin
B. humilis (C.A. Mey.) Robins. var. *laurentiana* (Böch.) Boivin
B. humilis (C.A. Mey.) Robins. var. *leiocarpa* (Trautv.) Fern.

B. humilis (C.A. Mey.) Robins. var. *novae-angliae* (Rydb.) Fern.
B. humilis (C.A. Mey.) Robins. var. *ventosa* (Roll.) Boivin
B. novae-angliae (Rydb.) Sør.
B. novae-angliae (Rydb.) Sør. ssp. *abbei* Böcher
B. novae-angliae (Rydb.) Sør. ssp. *ventosa* (Roll.) Böcher
B. novae-angliae (Rydb.) Sør. var. *interior* Böcher
B. novae-angliae (Rydb.) Sør. var. *interior* f. *capitata* Böcher
B. novae-angliae (Rydb.) Sør. var. *laurentiana* Böcher
B. americana (Hook.) Fern. (in part)
B. richardsonii (Rydb.) Fern.
B. intermedia Sør.
Torularia humilis (C.A. Mey.) Schulz
T. humilis (C.A. Mey.) Schulz ssp. *arctica* Böcher
Pilosella novae-angliae Rydb.
P. richardsonii Rydb.
Arabidopsis novae-angliae (Rydb.) Britt.

Braya humilis (C.A. Mey.) Robins. var. **maccallae** Harris

Braya humilis (C.A. Mey.) Robins. var. **porsildii** Harris