



Systematic studies of non-fistulose *Delphinium* taxa common to Montana
by Paul Thompson Sawyer

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree
DOCTOR OF PHILOSOPHY in Botany
Montana State University
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Abstract:

About 1,800 herbarium specimens representing five different taxa, *Delphinium* *bicolor* var. *bicolor*, *D. bicolor* var. *pilosum*, *D. menziesii* var. *nuttallianum*, *D. menziesii* var. *utahense* and *D. depauperatum* have been examined. Species descriptions for these five taxa are provided along with a key which separates the species of *Delphinium* growing in Montana.

Chromatograms of leaf extracts from 37 populations representing the five taxa mentioned above have been made and interpreted.

Evidence from the chromatographic study indicates that the populations called *D. nuttallianum* var. *pilosum* by Hitchcock (1964) and *D. andersonii* by Sawyer (1967) are members of the species *D. bicolor*. Based on morphological and habitat differences this taxon is called *D. bicolor* var. *pilosum*.

The chromatographic patterns for the three species of *Delphinium* mentioned above indicate a close relationship of these species but each one has a unique and distinct pattern. Chromatographic evidence of a *D. bicolor* x *D. menziesii* var. *utahense* hybrid is presented but *D. bicolor* is retained as a separate species because it is believed that this taxon is evolving throughout the major extent of its range isolated from the other delphiniums.

Two taxa within the species *D. menziesii*, *D. menziesii* var. *nuttallianum* and *D. menziesii* var. *utahense* are given varietal rankings based on morphological and chromatographic evidence.

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TAXA COMMON TO MONTANA

by

PAUL THOMPSON SAWYER

A thesis submitted to the Graduate Faculty in partial
fulfillment of the requirements for the degree


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ABSTRACT

About 1,800 herbarium specimens representing five different taxa, Delphinium bicolor var. bicolor, D. bicolor var. pilosum, D. menziesii var. nuttallianum, D. menziesii var. utahense and D. depauperatum have been examined. Species descriptions for these five taxa are provided along with a key which separates the species of Delphinium growing in Montana.

Chromatograms of leaf extracts from 37 populations representing the five taxa mentioned above have been made and interpreted. Evidence from the chromatographic study indicates that the populations called D. nuttallianum var. pilosum by Hitchcock (1964) and D. andersonii by Sawyer (1967) are members of the species D. bicolor. Based on morphological and habitat differences this taxon is called D. bicolor var. pilosum.

The chromatographic patterns for the three species of Delphinium mentioned above indicate a close relationship of these species but each one has a unique and distinct pattern. Chromatographic evidence of a D. bicolor x D. menziesii var. utahense hybrid is presented but D. bicolor is retained as a separate species because it is believed that this taxon is evolving throughout the major extent of its range isolated from the other delphiniums.

Two taxa within the species D. menziesii, D. menziesii var. nuttallianum and D. menziesii var. utahense are given varietal rankings based on morphological and chromatographic evidence.

INTRODUCTION

Many morphological studies including those of Ewan (1945), Taylor (1960), Hitchcock (1964), Sawyer (1967) and Sutherland (1967) have led to various interpretations of certain taxa within the genus Delphinium. With the exception of preliminary breeding and transplant data provided by Sutherland (1967) there are no other systematic data supporting these interpretations. Five non-fistulose taxa of questionable status occur in Montana. Hence it seemed that investigations other than those of a morphological nature could be undertaken profitably to provide evidence which may lead to a better understanding of their relationships.

Paper chromatographic studies involving flavonoid compounds have been used by taxonomists to investigate the following relationships: (1) interspecific hybrid populations such as those of Baptisia (Alston and Turner, 1963), Asplenium (Smith and Levin, 1963) and Vernonia (Hunter, 1967); (2) separation of species as in the case of Dicentra (Fahselt and Ownbey, 1968); (3) distinguishing diploid and tetraploid species of Tragopogon (Brehm and Ownbey, 1965); and (4) following the introgressing populations of Iris (Carter and Brehm, 1969). Although Sutherland (1967) reported that he was unable to separate species of Delphinium using Alston and Turner's (1963) paper chromatographic techniques he indicated that it might be useful within a species. Sutherland (1967) included four of the five non-fistulose taxa of

delphiniums commonly occurring in Montana within the species, D. menziesii. Therefore it seemed appropriate to investigate these taxa chromatographically.

The objectives of this study were twofold: (1) to investigate the relationships of those taxa previously called D. andersonii, D. bicolor, D. depauperatum, D. nelsoni and D. nuttallianum (Sawyer, 1967), using Alston and Turner's (1963) paper chromatographic techniques; and (2) to correlate these findings with morphological data gained from examination of specimens from herbaria located in the northwestern United States.

REVIEW OF LITERATURE

Classification

The early contributors to our knowledge of North American larkspurs include Gray (1887), Huth (1892, 1895), Rydberg (1900, 1902, 1912), Davis (1900) and Wilde (1931). In his publication, Gray appealed for more field observations and collections of North American delphiniums. The paper was intended to serve as a guide until the genus could be treated more completely and included a key to 20 species of which D. bicolor, D. menziesii and D. pauciflorum var. depauperatum are of interest to this study. Huth's (1892) publication is significant because he reported that the delphiniums of northwestern United States often intergrade morphologically and consist of locally isolated populations. He assigned subspecific rankings within three species, two of which are D. bicolor and D. tricornis. In 1895 Huth published a world monograph of Delphinium in which all known taxa of the Pacific northwest were considered as five species, often as subspecies, forms or varieties. He recognized the polymorphic nature of these species and conceded that his treatment consisted of convenient groups which did not necessarily agree with the species of other taxonomists. On the other hand, Rydberg (1900, 1902, 1912) designated new species whenever slight morphological differences existed between populations. Presently most of his species, except D. brownii and D. glaucescens, have been lost in the synonymy. Wilde's (1931) work

horticulturally oriented publication on the genus listed all known scientific names of Delphinium and reviewed the literature published prior to that time.

Ewan's (1945) synopsis of North American delphiniums continues to be the most comprehensive single treatment concerning the Delphinium species of this continent. It has served as the foundation of all later systematic treatments of Delphinium species of the northwestern United States. His study was based on examination of more than 4,000 herbarium sheets which represent those species occurring on the North American continent. Some field observations supplemented Ewan's herbarium data. Ewan, like such other students of the genus as Lewis and Epling (1954, 1959), Taylor (1960), Hitchcock (1964), Sawyer (1967) and Sutherland (1967), concluded that many of the taxa are highly localized, cannot be distinguished by any one constant morphological characteristic, and are subject to hybridization. Because Ewan's taxonomic interpretations were primarily based on morphological studies many of his 79 recognized species have been or will be accorded varietal status. Frequent intergrading populations caused Ewan to prepare regional keys for the taxa he recognized. However, identification still remains difficult.

The recent statewide studies made by Taylor (1960) in Wyoming and Sawyer (1967) in Montana and the northwest regional studies of

Hitchcock (1964) and Sutherland (1967) have resulted in varying conclusions about certain members of the "low larkspur" group. These interpretations are summarized in Table I. The populations referred to by Sawyer (1967) as D. andersonii, for convenience only, have caused Sutherland (1967) and Sawyer much uncertainty. Both investigators suggested that these populations are very closely related to D. bicolor. On the other hand, Hitchcock (1964) gave these populations varietal status in the species D. nuttallianum. Other taxa causing taxonomic disagreement are those referred to as D. nelsoni and D. nuttallianum by Ewan (1945), Taylor (1960) and Sawyer (1967). Sawyer had a broader interpretation of D. nelsoni than Ewan or Taylor and did not recognize the occurrence of D. nuttallianum in Wyoming, referring to all Wyoming populations considered to be D. nuttallianum by Ewan and Taylor as D. nelsoni. On the other hand, Hitchcock (1964) and Sutherland (1967) included all populations of Ewan's D. nuttallianum, D. nelsoni and certain subspecies of D. bicolor as members of the same taxon; D. nuttallianum in the case of Hitchcock and D. menziesii ssp. utahense in the case of Sutherland. The populations called D. nuttallianum by Sawyer (1967) appear to be equivalent to Hitchcock's (1964) D. nuttallianum var. fulvum and Sutherland's (1967) D. menziesii ssp. utahense var. hitchcockii.

Table I. Names reported in the literature for five Delphinium taxa. Names appearing on the same horizontal line apply to the same taxon.

Names used in this thesis	Ewan (1945)	Taylor (1960)	Sawyer (1967)	Hitchcock (1964)	Sutherland (1967)
<u>D. bicolor</u> var. <u>bicolor</u>	<u>D. bicolor</u> Nutt.	<u>D. bicolor</u>	<u>D. bicolor</u>	<u>D. bicolor</u>	<u>D. menziesii</u> ssp. <u>bicolor</u> (Nutt.) Sutherland
<u>D. bicolor</u> var. <u>pilosum</u>	-----	-----	<u>D. andersonii</u> Gray	<u>D. nuttallianum</u> var. <u>pilosum</u> Hitchcock	<u>D. menziesii</u> ssp. <u>bicolor</u> uncertain
<u>D. menziesii</u> var. <u>utahense</u>	<u>D. nelsoni</u> Greene	<u>D. nelsoni</u> <u>D. nuttallianum</u> in part	<u>D. nelsoni</u>	<u>D. nuttallianum</u> var. <u>nuttallianum</u>	<u>D. menziesii</u> ssp. <u>utahense</u> var. <u>utahense</u> (Wats.) Sutherland
<u>D. menziesii</u> var. <u>nuttallianum</u>	<u>D. nuttallianum</u> Pritz.	<u>D. nuttallianum</u>	<u>D. nuttallianum</u>	<u>D. nuttallianum</u> var. <u>fulvum</u> Hitchcock	<u>D. menziesii</u> ssp. <u>utahense</u> var. <u>hitchcockii</u> Sutherland
<u>D. depauperatum</u>	<u>D. depauperatum</u> Nutt. <u>D. burkei</u> Greene	<u>D. burkei</u> ssp. <u>distichiflorum</u> (Hook.) Ewan	<u>D. depauperatum</u> <u>D. burkei</u>	<u>D. depauperatum</u> <u>D. burkei</u>	<u>D. depauperatum</u>

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Cytogenetics

The chromosomes of certain California delphiniums have been studied by Lewis et al. (1951). Their results correlated well with earlier data reported by Tjebbes (1927), Lawrence (1936) and Gregory (1941). The karyotypes of all species studied are nearly indistinguishable and the meiotic configurations of these species are very similar. Lewis and Epling (1959) reported meiotic irregularities such as micronuclei, reciprocal translocations and paracentric inversions in D. hesperium. Chromosome counts have been reported by various workers including Tjebbes (1927), Lewis et al. (1951), Ornduff (1957) and Sutherland (1967). All counts reveal that the base chromosome number within the genus is $x = 8$, with most diploids being $2n = 16$. Three species, D. variegatum, D. hanseni and D. gypsophilum, have been reported by Lewis et al. (1951) to have tetraploid races where $2n = 32$ in addition to the normal diploid where $2n = 16$. Lewis and Epling (1959) could not distinguish morphologically the diploid race of D. gypsophilum from the tetraploid race. Because of the uniformity of karyotypes and chromosome numbers, cytogenetic studies of Delphinium have not been widely pursued by taxonomists.

Evolution

Perhaps the studies of Epling and Lewis (1952) and Lewis and Epling (1959) contribute the most towards understanding evolutionary

development of Delphinium species. Epling and Lewis (1952) presented evidence that individual members of the same colony respond differently to habitat stresses, depending on the genotypes of the individuals. A plant responds to a favorable environment by producing an annual above-ground stem which flowers and sets seeds. If the environment is not favorable to the plant it may respond in several ways: (1) it produces a rosette of leaves without a cauline stem, (2) the flowering stem dies before setting seeds, or (3) the root remains dormant. Thus, the size of the visible colony and the genotypes of the seed-producing members vary from year to year. The environment is the mechanism by which genotypes are selected for a particular set of growing conditions. In the same twelve year study the authors observed a mixed colony of D. parryi and D. hesperium. In only one year (1952) did both species flower. During 1952 a few intermediate individuals were observed and hybridization took place. There was a notable lack of hybrid swarms in this area and in other mixed populations. Generally the hybrids responded to different environmental conditions than their parents and thus remained isolated from them.

Lewis and Epling (1959) proposed that D. gypsophilum, ($2n = 16$) is intermediate in habitat and morphology between D. hesperium and D. recurvatum and has evolved on the diploid level from a series of crosses and backcrosses between D. hesperium and D. recurvatum. The

newly derived taxon remains isolated from its progenitors because of a habitat preference which differs from that of its ancestors. From a series of crosses involving D. hesperium, D. recurvatum and the resulting progeny Lewis and Epling (1959) have obtained individual plants which resemble D. gypsophilum. It seems that two factors account for some of the confusion in interpretation of certain species of Delphinium. They are: (1) similar genomes allowing for frequent hybridization of Delphinium species (Lewis and Epling, 1959 and Sutherland, 1967) and (2) the isolating mechanism of differential habitat preference proposed by Epling and Lewis (1952).

Species Concepts Applied to Delphinium

With the information of Epling and Lewis at hand it now becomes a question of how students of the genus Delphinium wish to interpret the various taxa. Two schools of thought have developed. One follows that of Lewis and Epling (1959) indicated by the following quotation:

"Opinion may be less than unanimous that this process results in speciation, inasmuch as final barriers seem seldom to have arisen in Delphinium. By this criterion, Delphinium would appear to be a long continued anastomosing phylad within which species are approached but seldom realized. Nevertheless, well integrated and independent lines of evolution are formed that may persist for long periods without distintegration even though they may frequently be in contact and interfertile. We regard them as species."

The other school of thought is followed by Hitchcock (1964) and is supported by Sutherland (1967). Their species concept holds that different species must be reproductively isolated. Thus, Sutherland (1967) combined D. bicolor, D. menziesii, D. nelsoni, D. nuttallianum and other taxa into one species, D. menziesii.

MATERIALS AND METHODS

Herbarium Study

A total of 1,796 herbarium sheets of Delphinium from herbaria of Brigham Young University (BRY), the University of Idaho (ID), Montana State University (MONT), Oregon State University (OSC), Washington State University (WS), Utah State University (UTC) and the Plant Research Institute, Ottawa, Canada (DAO) have been examined. Measurements of the specimens examined were omitted from this study because they were included in reports by Hitchcock (1964), Sawyer (1967) and Sutherland (1967). The type specimen of D. nuttallianum var. pilosum C. L. Hitch. (Hitchcock & Muhlick 21274, 7 miles east of Tendoy, Lemhi Co., Idaho, along the Lemhi Pass road) and the isotype of D. nuttallianum var. fulvum C. L. Hitchc. (Hitchcock & Muhlick 20862, about 2 miles east of Plains, Sanders Co., Montana) have been examined.

Chromatographic Study

Plants from 37 populations representing D. bicolor var. bicolor, D. bicolor var. pilosum, D. depauperatum, D. menziesii var. nuttallianum and D. menziesii var. utahense (Table II) were collected and used in chromatographic studies following the procedures of Alston and Turner (1963), with certain modifications. Leaves from many individuals within each population were oven dried at 52°C. A 1 g sample of leaf material was powdered and covered with 3.5 ml of a 1 per cent hydrochloric acid solution in methanol (v/v) and allowed to remain at

Table II. Delphinium material used in the chromatographic study.

Sawyer collection #	Location	Collection date
<u>D. bicolor</u> var. <u>bicolor</u> (<u>D. bicolor</u> *)		
528	Base of Hyalite Canyon, near Bozeman, Gallatin Co., Montana.	6/15/68
530	Bridger Bowl, North of Bozeman, Gallatin Co., Montana.	6/20/68
545	Squaw Creek, Southwest of Bozeman, Gallatin Co., Montana.	5/23/69
536	Gravelly Range, near Crockett Lake, Madison Co., Montana.	7/ 7/68
538	King's Hill, Southeast of Great Falls, Cascade Co., Montana.	7/15/68
539	Hellroaring Creek, Beartooth Plateau, Southwest of Red Lodge, Carbon Co., Montana.	7/20/68
552	Lake St. Mary, Glacier Nat. Park, Glacier Co., Montana.	5/31/69
556	East Glacier, Glacier Co., Montana.	6/ 1/69
(1)**	Mission Range, East of St. Ignatius, Lake Co., Montana.	6/ 1/69
(2)**	Ajax Mountain, Beaverhead Co., Montana	7/ 4/69
567	Southwest of Swamp Lake, Crazy Mountains, near Big Timber, Sweetgrass Co., Montana	8/ 9/69
533	Geode Creek, Yellowstone Nat. Park, Wyoming.	7/ 2/68
<u>D. bicolor</u> var. <u>pilosum</u> (<u>D. andersonii</u> *)		
522	Livingston, Park Co., Montana.	5/15/68
523	Beartrap area of Madison River, East of Norris, Madison Co., Montana.	6/12/68
546	Beartrap area of Madison River, East of Norris, Madison Co., Montana.	5/25/69
547	North of Harrison, Madison Co., Montana.	5/25/69
525	South of Cameron, Madison Co., Montana.	6/12/68
524	Clark Canyon Reservoir, South of Dillon, Beaverhead Co., Montana.	6/12/68
529	West of Three Forks, Broadwater Co., Montana.	6/18/68
548	West of Three Forks, Broadwater Co., Montana.	5/25/69
(3)**	East of Tendoy, Lemhi Co., Idaho.	5/29/69

Table II. (Continued)

Sawyer collection #	Location	Collection date
<u>D. menziesii</u> var. <u>utahense</u> (<u>D. nelsoni</u> *)		
541	Cooke City, Park Co., Montana.	7/12/68
(4)**	Red Rock Lake Refuge, Beaverhead Co., Montana.	6/ 9/69
531	Pacific Creek, Grand Teton Nat. Park, Wyo.	6/30/68
532	Rt. 89, 1.6 miles south of southern border of Yellowstone Nat. Park, Wyoming.	6/30/68
534	Lower Geyser Basin, Yellowstone Nat. Park, Wyoming.	7/ 2/68
540	Clay Butte, Beartooth Plateau, Park Co., Wyoming.	7/12/68
<u>D. menziesii</u> var. <u>nuttallianum</u> (<u>D. nuttallianum</u> *)		
526	Roosville, at the Canadian border, Lincoln Co., Montana.	6/14/68
527	North of Plains, Sanders Co., Montana.	6/15/68
550	North of Plains, Sanders Co., Montana.	5/30/69
549	DeBorgia, Mineral Co., Montana.	5/30/69
551	Lake St. Mary, Glacier Nat. Park, Glacier Co., Montana.	5/31/69
553	Lake St. Mary, Glacier Nat. Park, Glacier Co., Montana.	5/31/69
543	Avalanche Lake, Glacier Nat. Park, Flathead Co., Montana.	7/26/68
554	Anaconda Creek, Glacier Nat. Park, Flathead Co., Montana.	5/31/69
555	Pole Bridge, Glacier Nat. Forest, Flathead Co., Montana.	5/31/69
<u>D. depauperatum</u> (<u>D. depauperatum</u> *)		
537	Grant, Beaverhead Co., Montana.	7/ 7/68

* Names used by Sawyer (1967)

- (1)** collected by L. Bahl's
 (2)** collected by D. Harpster
 (3)** collected by W. E. Booth # 69107
 (4)** collected by R. Dorn # 846

room temperature in the dark for 24 hours. Each chromatogram was prepared for descending, two dimensional chromatography by spotting Whatman 3mm chromatography paper (46 x 57 cm) with 0.05 ml of the extract and placing the paper in a chromatography cabinet. The chromatograms remained in the first solvent system, n-butanol:acetic acid:water (4:1:5 v/v), for approximately 14 hours. They were then dried and placed in the second solvent system, acetic acid:water (15:85 v/v), for approximately 5 hours. The dried chromatograms were inspected in daylight, and then sprayed with a 20 per cent solution of sodium carbonate after which they were inspected in UV light. Rf values, i.e., the distance the solvent moved down the paper divided into the distance each compound moved down the paper, were determined for each spot.

Voucher specimens representing the chromatographed populations have been deposited in the herbarium at Montana State University.

TAXA DESCRIPTIONS AND KEYS

Description of the Genus Delphinium L.

Delphinium L. Sp. Pl. 530. 1753, Gen. Pl. ed. 5. 236. 1754

Annual or perennial; from a fibrous, tuberous or globose root system; stems erect, fistulose to non-fistulose, dying back to below ground level each year; leaves alternate, cauline, orbicular to reniform, 3-5 palmately lobed, each lobe being either broadly cuneate or several times dichotomously dissected; inflorescence a raceme, in many cases additional racemes arise from the axils of bracts or leaves; flowers complete, zygomorphic, hypogynous, calyx of 5 separate, petaloid sepals, the topmost having an ovate blade and a proximal portion forming an elongated spur; the remaining 4 grouped into 2 lateral sepals and 2 lower sepals, each group being unlike yet the individual sepals being elliptical, obovate or oblanceolate; corolla of 4, separate, dimorphic petals, divided into 2 groups of 2 petals each, the top two being cartilaginous, waxy and spurred at the rear, the spurs serving as nectar cups and projecting into the sepal spur; the lower 2 petals clawed about 1/2 their lengths with the bearded blades being oval to orbicular, often bifid at the apices; stamens separate, included, protandrous, with basifixed anthers borne on filaments dilated for about 1/2 of the filament length; carpels 1-3,

separate, developing into many-seeded follicles with persisting styles.

The native delphiniums of Montana and the West are perennial and normally have three carpels.

Key to the Species of Delphinium in Montana

- A Plants annual; carpel 1; cultivated species including D. ajacis
- A Plants perennial; carpels 3
 - B. Plants mostly over 1-1.5 m tall; major segments of all leaves cuneate
 - C Follicles pubescent over entire exposed surfaces D. occidentale
 - C Follicles pubescent only along the sutures; rare, if occurring at all in Montana D. brownii
 - B Plants less than 1.5 m tall; only the major segments of the basal leaves, if any, cuneate
 - D Inflorescence spike-like, appearing as an elongate, narrow (usually less than 4 cm wide) cylinder; sepals cupped, not flaring
 - E Stems fistulose; glaucous, appearing reddish throughout; flower color a dull, rust purple; root system extensive, fibrous D. glaucescens
 - E Stem neither fistulose nor glaucous, green in color, at least for the upper half; root system shallow and tuberous D. depauperatum

- D Inflorescence spreading, open, usually wider at the base than the top, often over 4 cm wide; sepals flaring
- F Plants densely pubescent, having a grayish cast; roots forming an extensive, woody caudex; the ultimate leaf segments not over 1 mm wide; rare, if occurring at all in Montana D. geyeri
- F Plants not grayish and if densely pubescent the root system is not extensive; ultimate leaf segments over 1 mm wide
- G Root system globose or slightly tuberous; lateral petals notched 1/2 the length of the blade
- H Lateral petals ochre in color, ~~tending to be longer~~ than wide D. menziesii var. nuttallianum
- H Lateral petals blue, nearly as wide as long D. menziesii var. utahense
- G Root system fibrous; lower petals may or may not be deeply notched
- I Lower petals notched over 1/4 of their length; leaf blades displayed at the same height; flowers blue D. bicolor var. pilosum
- I Lower petals not notched over 1/4 of their length; leaf blades displayed at various heights; flowers purple D. bicolor var. bicolor

Species Descriptions

Delphinium bicolor Nutt. Jour. Acad. Phila. 7:10. 1834.

Synonymy listed under varieties

Perennial; stems non-fistulose, up to 8 dm tall, usually 2-4 dm, single or several, stoutly attached to a fibrous, often extensive root system; stems green, reddish at base; pubescence of villous, spreading, often basally swollen, pustular hairs, sometimes crisped to short stubble-like hairs; leaves alternate, usually near the base of the stem, usually 3-8 per stem; blades orbicular to reniform, each of the 3-5 main lobes dichotomously dissected 3-4 times, borne on petioles 2-12 cm long, glabrous to pubescent; inflorescence a raceme with 3-30 flowers, usually 8-12; axillary racemes often present; pedicels 2-10 cm long, spreading; flowers purple to blue; sepal spur stout, curved down at tip; sepals large, broadly elliptical, flaring; upper petals white with purple veins or white with blue tips; lower petal blades the same color as the sepals, orbicular to elliptical, 8-10 mm long, not notched to deeply dissected, the gap a slit.

Plants belonging to this species are divided into two varieties, D. bicolor var. bicolor and D. bicolor var. pilosum. These two varieties are described on following pages and can be easily identified by the following criteria; variety pilosum has a deep, extensive root system, with 4-10 leaves, all displayed at about the same height

on the stem, blue flowers and elliptical, deeply notched lower petals; whereas variety bicolor has a shallow root system, 3-6 leaves, purple flowers and orbicular lower petals which are only slightly, if at all, notched.

Delphinium bicolor Nutt. Jour. Acad. Phila. 7:10. 1834, based on Wyeth, dry hills near Flat-headoor Sallish Rivers, probably western Montana.

Delphinium bicolor var. montanense Rydb. Mem. N. Y. Bot. Gard. 1:157. 1900, based on the lectotype F. W. Traphagen, Deer Lodge, Powell Co., Montana 1888. Plectrornis bicolor montanense (Rydb.) Lunell, Amer. Midl. Natur. 4:362. 1916. Delphinium bicolor f. montanense (Rydb.) Ewan, Univ. Colo. Stud, Ser. D. 2:123. 1945.

Delphinium menziesii subsp. bicolor (Nutt.) D. Sutherland, Ph.D. Thesis, University of Washington, Seattle 1967. (proposed by Sutherland but not published.)

Perennial; stem non-fistulose, 2-8 dm tall, usually 2.5-4 dm, usually single, stoutly attached to a fibrous root system which may be extensive; stem green or straw colored, reddish at base; pubescence commonly spreading, the hairs often pustular and basally swollen, more dense towards the top, often glabrous at base; leaves alternate, near base, displayed at different levels, 2-8 per stem, commonly 3-4; blades orbicular, highly dissected; petioles 2-10 cm long, pubescence if present sparse, similar to stem; inflorescence a raceme, with 3-10 flowers, usually 5-10; axillary racemes occasionally present, pubescence like that of stem, usually more dense; pedicels 1.5-10 cm long,

commonly 2.5 cm, spreading; flowers purple, showy, large; sepal spur stout, curved down at tip; sepals 10-20 mm long, elliptical, flaring to reflexed; upper petals white with purple veins; lower petal blades purple, orbicular, usually over 10 mm long, not dissected to slightly bifid for less than 1/4 of blade length. (Figures 1 and 9A)

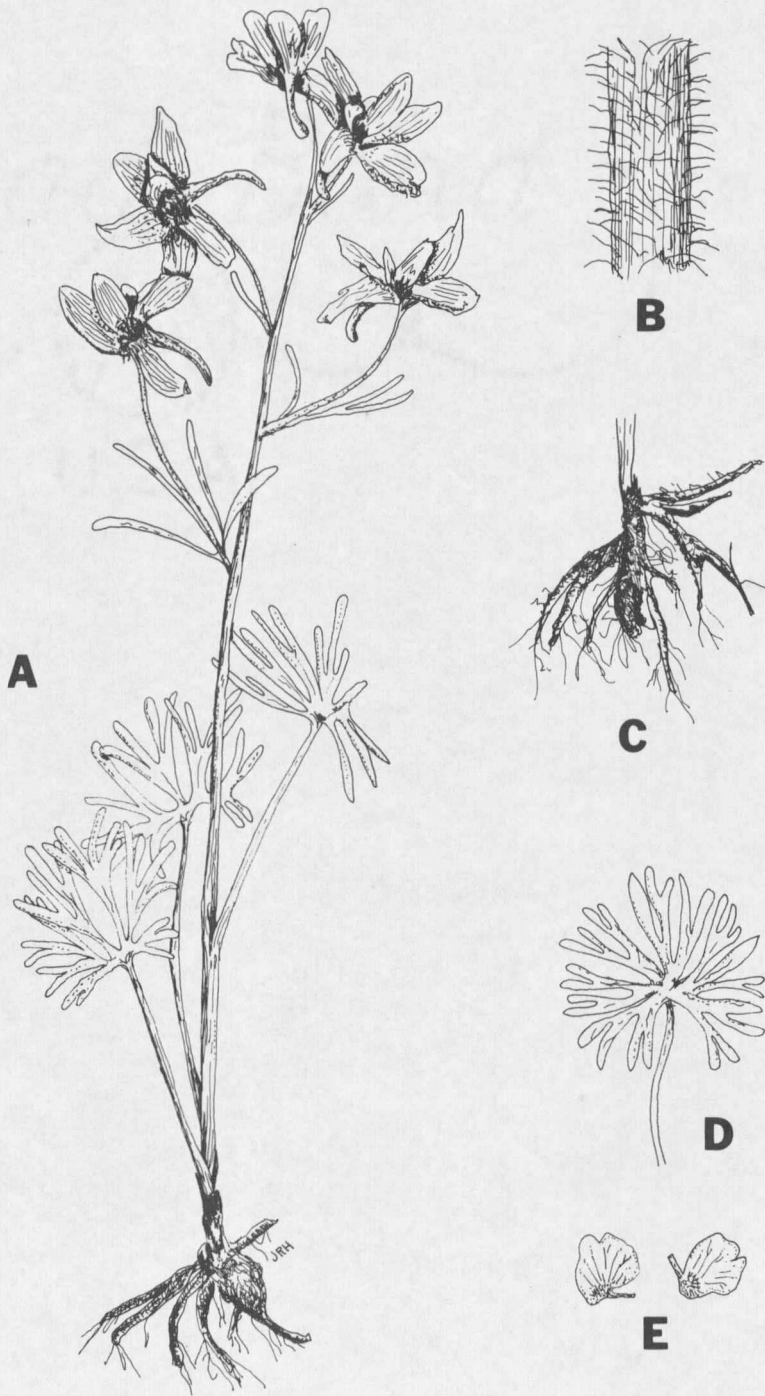
Delphinium bicolor var. bicolor flowers throughout May and early June at low elevations and may flower as late as August at high elevations. It grows along roadsides, ditches and in moist to mesic meadows. This taxon is the most common larkspur in Montana and ranges from North Dakota and South Dakota to northern Wyoming, eastern Washington, central Oregon, and into Canada. (Figure 6A)

In Montana the characters of D. bicolor var. bicolor are relatively stable, even in the area where its range overlaps with that of D. menziesii var. utahense along the border of Montana, Idaho and Wyoming from the Red Rock Refuge area to Cooke City and Red Lodge. Two characters, the pubescence of the stem and the lobing of the lower petals, vary throughout the state. Individual D. bicolor var. bicolor plants do not always have the spreading hairs typical of that variety nor are the lower petals always shallowly bifid. Individual plants, often occurring in colonies with plants having all the typical "bicolor" features, have deeply bifid lower petals. Nevertheless, these individuals have the typical fibrous root system, the

Figure 1. Delphinium bicolor var. bicolor.

- A A typical D. bicolor var. bicolor plant. Note the spreading inflorescence and flaring sepals. The sepals and lower petals are purple. X 2/3
- B Spreading hairs typical of D. bicolor. The hairs may be basally swollen and pustular. X 10
- C Typical fibrous root system of D. bicolor var. bicolor. Note that the stem is strongly attached to the root. X 2/3
- D A typical leaf. Note that the 4-5 major lobes have been dichotomously dissected 3-4 times. X 2/3
- E Typical lower petals. The large, orbicular blade has a very shallow notch at the tip. X 2/3

Drawing by J. R. Hodgson.



large roundish lower petals, and the gap of the blade is only a slit rather than being a wide v-shaped gap. These plants are unmistakably D. bicolor var. bicolor.

Representative collections: MONTANA: Miller 69, Walker Flats, 5 m. n.w. of Bozeman, Gallatin Co.; Sawyer 567, s.w. of Swamp Lake, Crazy Mt., Sweetgrass Co.; Bahls, Mission Mts., 5 m. e. of St. Ignatius, Lake Co.; Sawyer 530, Bridger Bowl, 20 m. n. of Bozeman, Gallatin Co.; Sawyer 539, Hellroaring Ck., Beartooth Mts., 10 m. s. of Red Lodge, Carbon Co.; Sawyer 545, Squaw Ck., Gallatin Canyon, Gallatin Co.; Sawyer 556, E. Glacier, Glacier Co.; Roessner, White Sulphur Springs, Meagher Co.; Arthun 48, 1/4 m. w. of Roscoe, Carbon Co.; Booth 5515, Harlowton, Wheatland Co.; Booth 59266a, 2 m. w. of Glendive, Dawson Co.; Eyde, 4 m. e. of Wisdom, Beaverhead Co.; Scharff, 21 m. s. of Reed Point, Stillwater Co.; Cotner, Elk Ck., Wilsall, Park Co.; Hughes, Missoula, Missoula Co.; Booth, Plentywood, Sheridan Co.; Mussehl and Zapatka 3, Judith Mt., Hilger, Fergus Co.; Sawyer 536, Gravelly Range, Call Road, Madison Co.; Sawyer 552, Lake St. Mary, Glacier Nat. Park, Glacier Co.; Sawyer 528, mouth of Hyalite Canyon, Gallatin Co.; Sawyer 538, King's Hill Pass, 45 m. s.e. of Great Falls, Cascade Co.; Harpster, e.e. side of Ajax Mt., Beaverhead Co.; Trask, 5 m. n.e. of Deer Lodge, Powell Co.; Taylor, 20 m. e. of Wolf Ck., Lewis and Clark Co.; Booth 54115, 10 m. s. of Boulder, Jefferson Co.; Chalmers 122, 4 m. s. of Choteau, Teton Co.; Booth 6053, n. of Geyer, Highwood Mt., Judith Basin Co.; IDAHO: Hitchcock and Muhlick 21254, 13.2 m. e. of Tendoy, Lemhi Co.; WYOMING: Sawyer 533, Geode Ck., Yellowstone Nat. Park; Metcalf and Yager, Big Horn Mts., Big Horn Co.

Exceptions can be found in the Lemhi Pass-Salmon area along the Idaho-Montana border. Here plants with "bicolor-like" flowers and variable pubescence maintain a D. menziesii var. utahense root and habit, as well as deeply notched lower petals. The two taxa have undoubtedly exchanged genes in this area. Collections representing these kinds of populations include: IDAHO: Hitchcock and Muhlick 21254, top of

Lemhi Pass on the Montana-Idaho border, 13.2 m. e. of Tendoy; Cronquist 174-36, base of Long Tom Mts., near the Salmon River; Hitchcock and Muhlick 14151, 3 m. from the head of Panther Ck., Lemhi Co.; Preece and Turner 2346, 35 m. n. of Salmon on highway 93; Hitchcock and Muhlick 14215, w. slope of Quartzite Mt., Lemhi Co.; MONTANA: Hitchcock and Muhlick 12650, 1/4 m. below Ajax Mill, Beaverhead Co.

In 1969 Mrs. Darlene Harpster collected delphiniums on the east side of Ajax Mountain near Jackson, Montana. Some of these plants, although being similar to D. bicolor, possessed D. menziesii var. utahense traits, including the deeply lobed petals. The roots were not present on the specimens examined. She commented that, on the same date, the year before larkspur plants from the same area were more numerous, more robust and had larger flowers.

Near the White Bird-Pollock area of Idaho, populations have "bicolor" flowers except that the large lower petals have variable lobing, some of them being deeply notched and with spreading hairs. However, these plants have the "utahense" habit and shallow globose to tuberous root systems. These plants must possess various combinations of D. bicolor var. bicolor and D. menziesii var. utahense genes, which makes it difficult to assign them to either parental taxon with certainty. Typical specimens representing these populations are:

J. H. Christ 12531, Heaven's Gate, Seven Devils Mountains, Idaho; Hitchcock and Muhlick 20840, 8 m. n. of White Bird, Idaho.

The latter collection was examined on four different herbarium sheets distributed to various herbaria and although the specimens possessed the same general characteristics, there was much variability in the lobing of the lateral petals and in the pubescence.

Larkspur specimens from the central area of Oregon around John Day, Dayville, Mitchell and Prineville closely resemble D. bicolor var. bicolor except for the deep lobing of the large roundish lower petal. One would assign these specimens to D. bicolor var. bicolor without much hesitation but an occasional specimen with the habit and root characteristic of D. menziesii var. utahense occurs from the same area. Specimens representing the aberrant "bicolor" populations include:

OREGON: Cronquist 6390, 12 m. s. of Canyon City; Cronquist 6918, 10 m. w. of Mitchell; Cronquist 6367, 11 m. s. of Ukiah; Hitchcock and Muhlick 20781, 20 m. e. of Prineville; Hitchcock and Muhlick 20788, 30 m. w. of Dayville.

Members of the bicolor variety may also cross with D. menziesii var. nuttallianum in the Moscow, Idaho-Pullman, Washington area. Here the plants retain the "nuttallianum" habit, root and pustular hairs but possess a variance of flower traits, some of which typify D. bicolor. (Figure 9C) Specimens representing this mixture are:

WASHINGTON: Hitchcock and Muhlick 23491, Asotin Co.; Hitchcock and Muhlick 20851, Anatone, Asotin Co.; Baker 13936, 2 m. s. of Asotin, Asotin Co.

Delphinium bicolor var. pilosum (C. L. Hitchc.) P. T. Sawyer comb. nov.

Delphinium nuttallianum var. pilosum Hitchcock, Vas. Pl. Pac. Northwest. Hitchcock, Cronquist, Ownbey, Thompson 2:359. 1964, based on C. L. Hitchcock and C. V. Muhlick 21274, 7 miles east of Tendoy, Lemhi Co., Idaho, 7/1/1957, the holotype.

Perennial; stems non-fistulose, 2-8 dm high, commonly 3-4 dm., single or several, stoutly attached to an extensive fibrous root system; stems green or tan, reddish towards base; pubescence short, stubble-like, gland-tipped or spreading often with swollen base, glabrous towards base; leaves alternate, displayed at nearly the same height as a result of unequal petiole lengths, 5-12 per stem, commonly 6-8; blades orbicular, 3-5 main lobes 3-4 times dichotomously dissected; petioles as much as 12 cm long; inflorescence a raceme with 10-30 flowers, usually 10-16; axillary racemes often present; pedicels 1-5 cm long, spreading; flowers blue, large, showy; sepal spur stout, curved down at tip; sepals 10-20 mm long, elliptical, flaring; upper petals white with blue tips; lower petal blade blue, elliptical, usually less than 10 mm long, notched at least 1/3 its length.

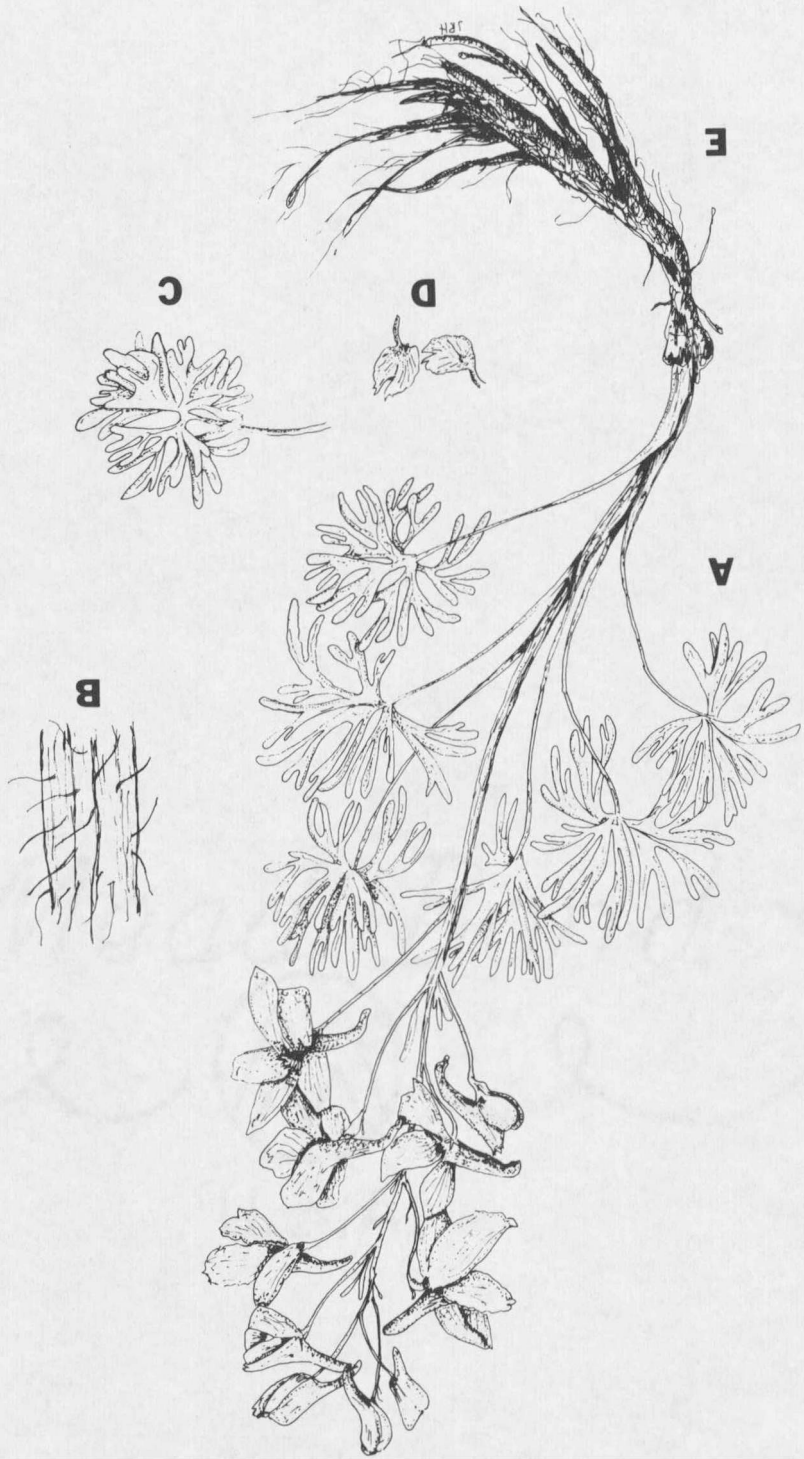
(Figures 2, 10 and 11)

Delphinium bicolor var. pilosum tends to flower later than the bicolor variety. Variety pilosum begins to flower in mid-May and continues to flower through June and into July. It grows in dry sandy, calcareous soils and is commonly found along the river terraces

Figure 2. Delphinium bicolor var. pilosum.

- A Typical D. bicolor var. pilosum plant. Note that the several leaves are displayed at nearly the same height of the stem. The blue flowers are large with flaring sepals. The inflorescence is spreading. X 3/5
- B Typical spreading hairs of the stem. The hairs may be basally spreading or not. X 15
- C Typical leaf. X 3/5
- D Typical lower petals. Note the elliptical shape and the deep lobing. X 3/5
- E The typical extensive fibrous root system. X 3/5

Drawing by J. R. Hodgson.



of the Jefferson, Madison, Missouri and Yellowstone Rivers. Delphinium bicolor var. pilosum has a very limited range being most common in Montana but extending over Lemhi Pass into Idaho, its type locality. It is rarely found in Oregon (Figure 6C).

Delphinium bicolor var. pilosum seems to be morphologically and ecologically distinct from variety bicolor in Montana with the exception of the populations growing along the river terraces of the Madison River near Norris, Montana. Here the two taxa grow together with intermediate forms appearing interspersed among D. bicolor var. bicolor and D. bicolor var. pilosum. The intermediate individuals have the deep purple flowers typical of the bicolor variety but retain the habit, extensive roots and deeply notched lower petals of the pilosum variety. Delphinium bicolor var. pilosum around Tendoy, Idaho retains the important "pilosum" features but tends to have purplish sepals.

Representative specimens: MONTANA: Sawyer 524, 4.5 m. w. of Clark Canyon reservoir, Beaverhead Co.; Sawyer 547, 3.7 m. n. of Harrison, Madison Co.; Sawyer 523, Madison Bridge, 5 m. n. of Norris, Madison Co.; Sawyer 519, Livingston, Park Co.; Sawyer 525, 19 m. s. of Ennis, Madison Co.; Sawyer 548, w. of Three Forks, Broadwater Co.; Sawyer 522, Livingston, Park Co.; Sawyer 503, 3.9 m. w. of Clark Canyon Reservoir, Beaverhead Co.; Booth 65163, 10 m. s. of Brenner, Beaverhead Co.; Booth 604, 8. m. s. e. of Billings, Yellowstone Co.; Booth, 3 m. n. of Whitehall, Jefferson Co.; Booth, 10 m. w. of Great Falls, Cascade Co.; Hartung 26, 1/2 m. e. of Joliet, Carbon Co.; Davidse and Collotzi 652, Airport, Billings, Yellowstone Co.; Suksdorf 257, 258, Jackrabbit Gulch, 9 m. n.w. of Wilsall, Park Co.; Witt,

between Livingston and Bozeman Pass, Park Co.; IDAHO:
Hitchcock and Muhlick 21271, 10 m. e. of Tendoy, Lemhi Pass,
 Lemhi Co.; Hitchcock and Muhlick 21274, 7 m. e. of Tendoy, Lemhi
 Co.; Tassey and Hugie, 8 m. w. of Grasmere, Owyhee Co.;
Spellenberg 1709, 8 m. s.w. of highway 281 near Arco, Butte Co.;
OREGON: Cronquist 8145, 22 m. s. of Juntura, Malheur Co.

Delphinium depauperatum Nutt., in T. & G. Fl. N. Amer. 1:33. 1838.

Delphinium pauciflorum var. depauperatum Gray, Bot. Gaz. 12:54.
 1887. Delphinium tricornis var. depauperatum, Huth, Helios 10
 (Abh.) 37. 1892, based on Nuttall, 1834, Blue Mts. Columbia
 N.E. Ore.

Delphinium burkei Greene, Erythea 2:183. 1894, based on Burke,
 "Snake Country" July 11, 1844-46.

Delphinium diversifolium Greene, Pitt. 3:93. 1896. Delphinium
scopulorum var. diversifolium (Greene) K. C. Davis, Minn. Bot
 Stud. 2:449. 1900, based on Greene, "near the station, Holborn,
 Elko Co., Nev., July 15, 1896.

Delphinium diversicolor Rydb., Bull. Torrey Bot. Club 29:149.
 1902, based on Tweedy 34, Rattlesnake Creek, Beaverhead Co.,
 Mont., June, 1887.

Delphinium cyanoreios Piper, Contr. U.S. Nat. Herb. 16:202.
 1913, based on Colville 2444, near Sled Creek R. S., Wallowa
 Co., Oreg., June 25, 1907.

Delphinium diversifolium ssp. harneyense Ewan, Univ. Colo. Stud.
 Ser. D. 2:115. 1945. Delphinium diversifolium var. harneyense
 (Ewan) R. J. Davis, Madroño 11:144. 1951, based on Cusick 1982,
 "Streambanks of Steens Mountains," Harney Co., Ore., 1898.

Delphinium cyanoreios f. wallowense Ewan, Univ. Colo. Stud. Ser.
 D. 2:163. 1945, based on Cusick 3325, Cliff Creek, Wallowa Mts.,
 Ore., Aug. 21, 1908.

Delphinium cyanoreios f. idahoense Ewan, Univ. Colo. Stud. Ser.
 D. 2:164. 1945, based on L. Constance 1938, summit of White
 Bird Grade, Idaho Co., Ida., July 3, 1937.

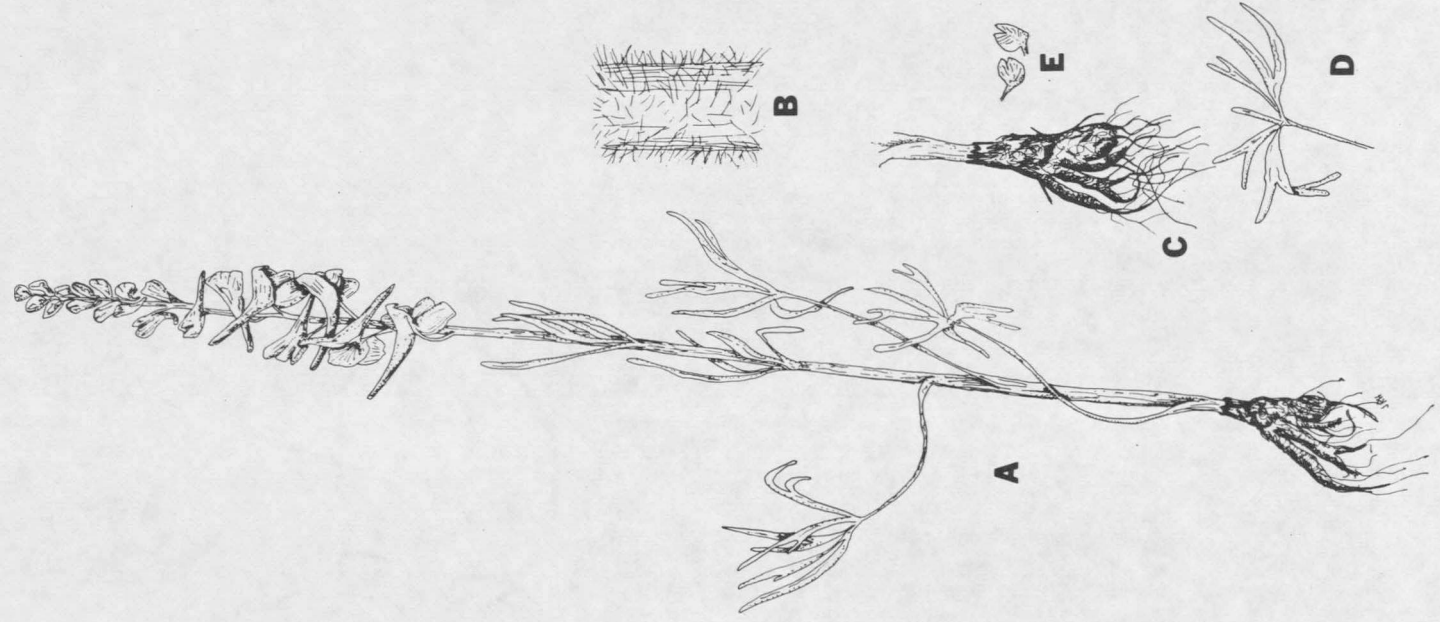
Perennial; stems non-fistulose, 2-8 dm high, usually 5-6 dm, usually single but sometimes 2-3, stoutly attached to a tuberous to shallow fibrous root system; stems green to straw-colored, sometimes reddish at base; pubescence usually spreading, pustular and basally swollen but sometimes crisped, usually more dense towards top, base becoming glabrous with age; leaves alternate, dispersed along stem, 3-12 per stem, usually 4-7; blades, lower ones often cuneate, upper ones finely dissected, ultimate segments linear, not all plants have dimorphic leaves, glabrous to densely hairs, sometimes crisped; petioles 2.5-12 cm long, usually 5 cm; inflorescence a cylindrical, spike-like raceme with 4-40 flowers, usually 10-12, pubescence spreading to crisped, often dense; axillary racemes often present; pedicels 0.6-2.5 cm long, usually 1.3 cm, appressed and curved upward; flowers blue; sepal spur slender, straight, extending across the rachis; sepals elliptical, cupped forward; upper petals white, often with blue veins; lower petals usually blue, may be ochre, dark blue veins visible, elliptical, less than 10 mm long, deeply bifid with a wide "v" notch. (Figures 3 and 14)

Delphinium depauperatum usually flowers from late June until early August but plants growing on relatively dry sites flower in late May. This species grows in wet areas such as stream banks, irrigation ditches and poorly drained areas of meadows and sage brush

Figure 3. Delphinium depauperatum.

- A Typical D. depauperatum plants. Note the cylindrical inflorescence caused by the appressed pedicels. The sepal spur is straight and the sepals are cupped forward. Oftentimes the leaves may be of two shapes; the lower blades having broad lobes and the upper blades being highly dissected. Flowers are blue. X 1/2
- B Typical spreading hairs. There may also be basally swollen pustular hairs. X 15
- C Typical shallow tuberous root system. X 1/2
- D The leaf blade. X 1/2
- E Typical lower petals. X 1/2

Drawing by J. R. Hodgson.



communities. Delphinium depauperatum occurs from western Montana, northwest Wyoming, and northern Nevada, throughout Idaho, into southeastern Washington, central and eastern Oregon to northern California. (Figure 6D)

Sutherland (1967) suggests that this species is highly polymorphic, perhaps as a result of habitat variance. Plants growing at the eastern extreme of its range, particularly those in Montana, seem to be uniform and generally lack the large cuneate basal leaves found in the more western populations. The tuberous root system, non-fistulose stem, the spike-like inflorescence, cupped sepals and straight spur along with the moist habitat are distinctive features of D. depauperatum, which make it easily distinguished from other low larkspurs in Montana.

Sutherland (1967) indicates that gene exchange takes place between D. menziesii and D. depauperatum in the tri-corner area of Oregon, Washington and Idaho. To date there is no evidence indicating D. depauperatum x D. menziesii var. utahense hybrids are in Montana. Since the ranges of these two species overlap hybrids could occur, but it seems likely that the flowering time and habitat differences of the two species would isolate them.

Representative Collections: MONTANA: Sawyer 537, 2 m. n. of Grant, Beaverhead Co.; Hitchcock and Muhlick 14942, 1/2 m. e. of Odell Lake, Beaverhead Co.; Harvey 5108, Camas Ck. Valley, Glacier

Nat. Park, Flathead Co., IDAHO: Hitchcock and Muhlick 13986, 10 m. s. of McCall, Valley Co.; Hitchcock and Muhlick 14099, 15 m. w. of Cape Horn near Elk Ck. Ranger Station, Valley Co.; Hitchcock and Muhlick 21356, 10 m. n. of Ketchum, Blaine Co.; Hitchcock and Muhlick 20820, 18 m. s. of Idaho City, Boise Co.; Hitchcock and Muhlick 20835, 21 m. w. of Lowman, Boise Co.; WYOMING: Oswald 1257, 1/2 m. n.w. of Biological Station, Grand Teton Nat. Park; OREGON: Hitchcock and Muhlick 20708, 1/2 m. s.w. of King Mt., Harney Co.; Hitchcock and Muhlick 20911, 6 m. s. of Allison Guard Stat., Harney Co.; Keil 1118, Umatilla, Umatilla Co.; Cronquist 8765, head of McCoy Ck., w. of Steens Mts. Harney Co.; WASHINGTON: Hitchcock and Muhlick 21588, 10 m. n. of Satus Pass, Yakima Co.; Hitchcock and Muhlick 21816, 17 m. s. of Asotin, Asotin Co.; Hitchcock and Muhlick 20888, 5 m. n.e. of Teanaway Jct., Kittitas Co.

Delphinium menziesii DC. Syst. Veg. 1:355. 1818.

Delphinium tricorne (var.) menziesii Huth, Helios 10 (Abh.); 37. 1892. Delphinium tricorne ssp. menziesii Huth, Engl. Bot. Jahrb. 20: 343. 1895. Delphinastrum menziesii Nieuwl. Amer. Midl.Natur. 3:172. 1914, based on Menzies, "New Georgia".

A narrow interpretation of D. menziesii (Hitchcock, 1964) confines this species to certain delphiniums growing along the west coast of Canada and the United States south to northern California. However, Sutherland's (1967) much broader interpretation combined many species of the northwest into one species, D. menziesii, representing a tremendously variable, wide ranging taxon with numerous subspecies and several varieties. Following Sutherland's system in part, the two taxa occurring in Montana are considered in this thesis to be different varieties of D. menziesii. Sutherland (1967) treated these two taxa as different varieties of D. menziesii ssp. utahense. Considering these two varieties to represent a small part of a

variable whole, no species description will be presented for D. menziesii, but descriptions of two varieties, D. menziesii var. nuttallianum and D. menziesii var. utahense follow on subsequent pages.

Delphinium menziesii var. nuttallianum P. T. Sawyer comb. nov.
Delphinium nuttallianum var. fulvum C. L. Hitchcock, Vas. Pl. Pac. Northwest. Hitchcock, Cronquist, Ownbey, Thompson 2: 359. 1964. Delphinium menziesii ssp. utahense var. hitchcockii D. Sutherland, Ph.D. Thesis, 1967. Univ. of Washington, Seattle, (proposed by Sutherland but not published) based on Hitchcock and Muhlick 20862, 2 miles east of Plains, Sanders Co., Mont.

Perennial; stem non-fistulose, 2-9 dm tall, commonly 5 dm, usually single, weakly attached to a globose root system; stems green above, reddish at base; pubescent at top, glabrous or sparsely pubescent at base, usually crisped but sometimes of spreading hairs with pustular swollen bases or both; leaves alternate, along stem, 2-10 per stem, usually 4-7; blades much dissected, ultimate segments long and linear; petioles 5-18 cm long; pubescence like that of stem; inflorescence a raceme with 2-25 flowers, commonly 8-10; axillary racemes sometimes present; pedicels 1.5-10 cm long; usually 2.5 cm, uniformly curved giving the inflorescence a more or less uniform width; flowers blue, showy, not as large as those of D. bicolor; sepal spur stout to slender, curved at tip; sepals narrowly elliptical, slightly cupped forward to spreading; upper petals blue with white

fringes and blue veins; lower petal blades usually ochre but sometimes blue, elliptical to oval, not over 10 mm long, deeply bifid with a wide "v" notch. (Figures 4 and 12)

Delphinium menziesii var. nuttallianum flowers from May through June and into August at high elevations. It grows in mesic to dry situations such as hillsides, roadsides and meadows. Depauperate plants with weak stems, few leaves and few flowers but with "nuttallianum" features grow in moist to wet sites at high elevations (Figure 12A). This taxon has a limited range, (Figure 6C) extending from northwest Montana across northern Idaho to the northeast corner of Oregon, the southeast corner of Washington and into southeastern British Columbia.

Delphinium menziesii var. nuttallianum has relatively uniform populations throughout its range, although the lower petal color of some plants is blue instead of the normal ochre. The exception to this statement occurs in the populations of the Moscow, Idaho-Spokane, Washington area. These plants possess traits characteristic of D. bicolor and D. menziesii var. utahense and are apparently the result of frequent gene exchanges of these taxa. (Figure 13C)

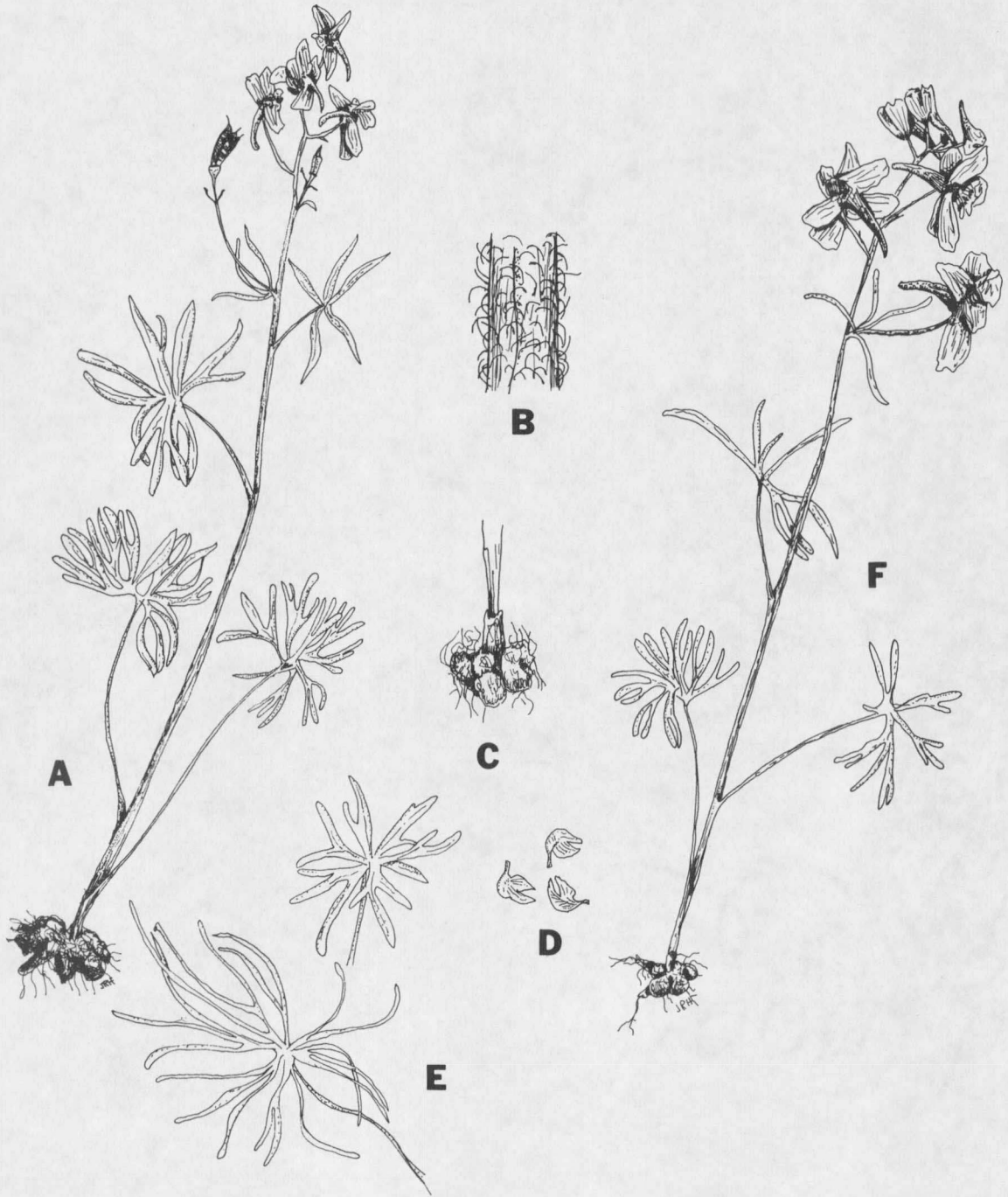
Some specimens having intergrading traits are:

WASHINGTON: Marion and Ruth Ownbey 2044, 2 m. s. of Pullman, Whitman Co.; H. T. Rogers 289, 9 m. s. of Grand coulee Dam, Grant Co.; H. T. Rogers 339, 10 m. n. of the Kettle River,

Figure 4. Delphinium menziesii var. nuttallianum.

- A, F Typical D. menziesii var. nuttallianum plants. Note the linear segments of the upper leaves and the spindly habit. The inflorescence is spreading. The sepals are flaring to slightly cupped forward. Flowers are blue. X 3/5
- B Crisped hairs typical of this taxon. Most are curved downward. Some are basally swollen and pustular. X 10
- C Typical shallow globose root system with a weak attachment to the stem. X 3/5
- D Typical elliptical, deeply lobed lower petals. X 3/5
- E A finely dissected lower leaf blade often associated with this taxon.
- A Represents the "high mountain form" and has smaller flowers and a more depauperate appearance than the "lowland form" seen in F. The plant represented by F is not as tall or robust as most. X 3/5

Drawing by J. R. Hodgson.



Ferry Co.; Gleason 159, Spokane River, 9 m. from Spokane, Spokane Co.

Representative Collections: MONTANA: Sawyer 482, 1/2 m. from Sperry Chalet, Glacier Nat. Park, Flathead Co.; Creel, Hidden Lake, 2 m. from Logan Pass, Glacier Nat. Park; Metcalf, near DeBorgia, Mineral Co.; Sawyer 543, w. of Avalanche Lake, Glacier Nat. Park, Flathead Co.; Sawyer 466, e. end of Avalanche Lake, Glacier Nat. Park Flathead Co.; Umbach 366, Mary Baker Lake, Glacier Nat. Park, Glacier Co.; Umbach 816, Little St. Mary's Lake, Glacier Nat. Park Glacier Co.; Booth 6312, 8 m. n.w. of Missoula, Missoula Co.; Sawyer 526, Roosville, Lincoln Co.; Sawyer 527, 5.3 m. e. of Plains, Sanders Co.; Sawyer 551, 11.3 m. w. of the e. boundary of Glacier Nat. Park, Going to the Sun Road, Glacier Co.; Sawyer 555, .3 m. s. of the Pole Bridge, Flathead Nat. For., Flathead Co.; Sawyer 553, 4.5 m. w. of the border of Glacier Nat. Park, Going to the Sun Road, Glacier Co.; Blankenship, Thompson Falls, Sanders Co.; Schmautz JES 319, Libby Ranger Stat., Lincoln, Lincoln Co.; Hitchcock and Muhlick 20862, 2 m. e. of Plains, Sanders Co.; Hitchcock and Muhlick 20855, DeBorgia, Mineral Co.; Hitchcock and Muhlick 2242, 4 m. ee. of Thompson Falls, Sanders Co.; IDAHO: Hitchcock and Muhlick 20868, 2 m. s. of Cusick, Pend Oreille Co.; Hitchcock and Muhlick 20865, 2 m. w. of Clark Fork, Bonner Co.; Hitchcock and Muhlick 20866, 5 m. e. of Newport, Bonner Co.; Hitchcock and Muhlick 20852, 5 m. s. of Tensed, Benewah Co.

Delphinium menziesii var. utahense (Wats.) P. T. Sawyer comb. nov.
Delphinium menziesii var. utahense Wats., Bot. King. Exp. 12. 1871. Delphinium nelsonii ssp. utahense Ewan, Uni. Colo. Stud. Ser. D 2:130. 1945, based on Watson 42, Wasatch Mts., Utah.

Delphinium pauciflorum Nutt., T. & G. Fl N. Amer. 1:33. 1838.
Delphinium nuttallianum Pritz. ex. Walpers, Rep. 2:744. 1843.
Delphinium menziesii var. pauciflorum Huth, Engl. Bot. Jahrb. 20:445. 1895.

Delphinastrum nuttallianum Nieuwl. Amer. Midl. Natur. 3:172. 1814, based on Nuttall, "Blue Mts. of Columbia" northeast Ore.

Delphinium pauciflorum var. nevadense Gray, Syn Fl. N. Amer. 1:50. 1895. Delphinium sonnei Greene, Pittonia 3:246. 1897. Delphinium pauciflorum var. sonnei Smiley, Univ. Cal. Publ. Bot. 9:190. 1921, based on the lectotype of Ewan, N. H. Bolander, "Cisco Sierras," 1873.

Delphinium nelsonii Greene, Pitt. 3:92. 1896. Delphinium, bicolor var. nelsonii K. C. Davis, Minn. Bot. Stud. 2:439. 1900. Delphinastrum nelsonii Nieuwl., Amer. Midl. Natur. 3:172. 1914, based on Nelson 48, Mouth of Telephone Canyon, Wyo. May 23, 1894

Delphinium dumetorum Greene, Pl. Baker. 3:4. 1901. Delphinium nelsonii f. dumetorum Ewan, Univ. Colo. Stud. Ser. D 2:129. 1945, based on C. F. Baker 35, Cimarron, Delta Co., Color., 6/6/1901.

Delphinium leonardii Rydb., Bull. Torr. Bot. Club 39:320. 1912, based on Leonard 205, Garfield, Utah, 5/30/1884.

Delphinium helleri Rydb., Bull. Torrey Bot. Club 39:321. 1912. Delphinium bicolor f. helleri Ewan, Univ. Colo. Stud. Ser. D 2:121. 1945, based on Heller and Heller 2951, Lewiston, Nez Perce Co., Idaho, 4/24/1896.

Delphinium pinetorum Tidestrom, Proc. Biol. Soc, Wash. 26: 121, 1913. Delphinium nelsonii f. pinetorum Ewan, Univ. Colo. Stud. Ser. D 2:130. 1945, based on Tidestrom 2375, Kaibab Plateau, Coconino Co., Ariz.

Delphinium menziesii var. fulvum A. Nels. & Macbr., Bot. Gaz. 61:30. 1916. Nomen subnudum by Ewan (1945, p 211).

Delphinium venenosum A. Nels., Univ. Wyo. Publ. Sci. Bot. 1:126, 1926, based on Beath, headwaters of LaBarge Creek and of Gray's River, Lincoln Co., Wyo.

Delphinium bicolor f. mccallae Ewan, Univ. Colo. Stud. Ser. D 2:122. 1945, based on McCalla 2759, Lillooet, B. C., May 27, 1921.

Delphinium linepetalum f. viscidum Ewan, Univ. Colo. Ser. D. 2:127. 1945, based on Thompson 6010, 10 miles north of Entiat, Chelan Co., Wash., Apr. 18, 1931.

Delphinium menziesii ssp. utahense var. utahense (Wats.)
Sutherland, Ph.D. Thesis 1967. Univ. of Washington, Seattle.
(proposed by Sutherland but not published)

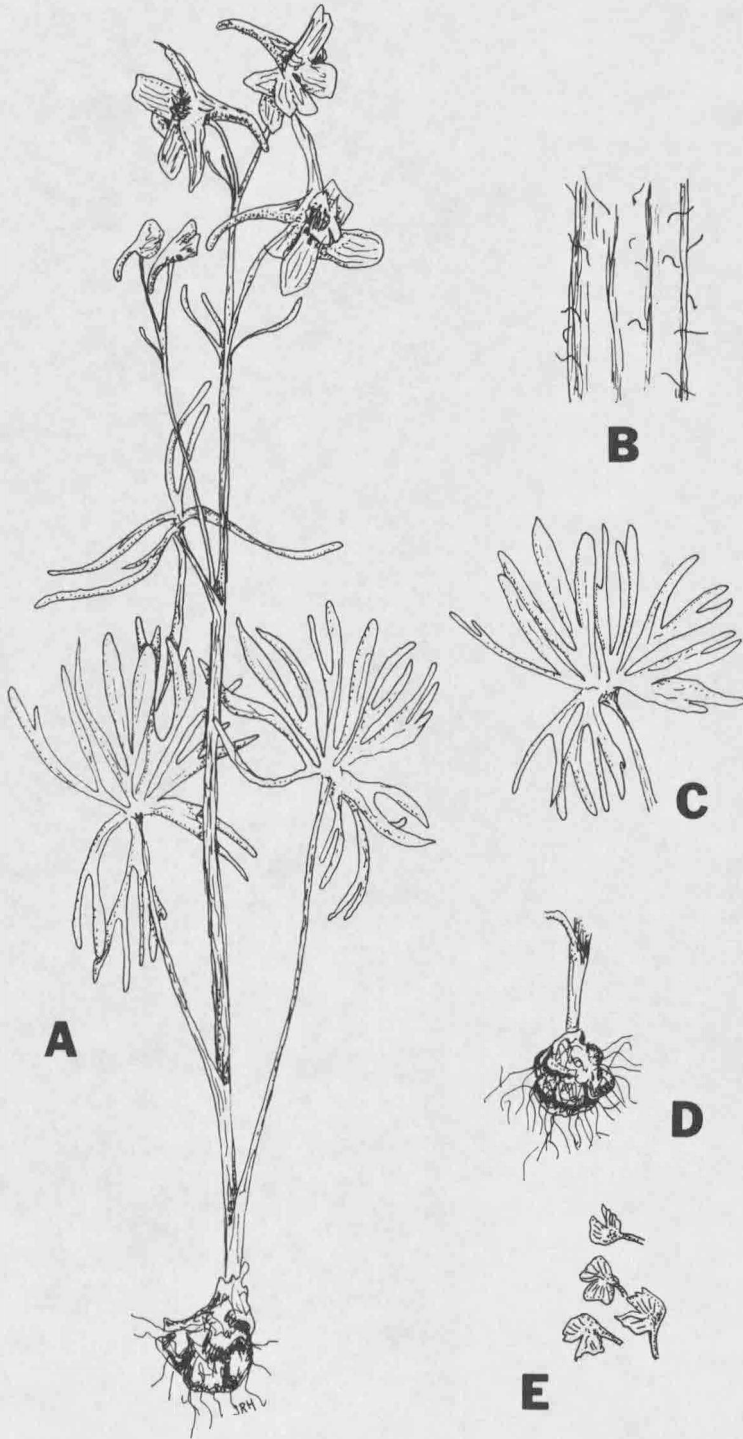
Perennial; stems non-fistulose, 2-9 cm tall, usually 3 cm, usually single, weakly attached to a globose or tuberous root system; stem green, reddish at base, pubescence densely crisped to sparse, often glabrous at base; leaves alternate, towards base of stem, 2-8 per stem, usually 3-4; blades orbicular, 4-5 main lobes dichotomously dissected 3-4 times; petioles 2.5-10 cm long, usually 5 cm, crisped hairs to glabrous; inflorescence a raceme with 3-20 flowers, commonly 6-10; crisped hairs; axillary raceme sometimes present; pedicels 2.5-10 cm long, spreading, often not uniform in length or degree of spreading; flowers usually purple or dark blue, large and showy like those of D. bicolor or smaller; sepal spur stout curved down at tip; sepals 10-20 mm long, elliptical, flaring; upper petals purple to blue with white fringes and blue veins; lower petals purple, oval to elliptical, often as wide as long, usually less than 10 mm long, often less than 8 mm, deeply notched, with a wide "v" gap. (Figures 5 and 13A)

Delphinium menziesii var. utahense flowers from May through July and August at high elevations and grows in mesic to dry meadows and disturbed areas along roads and ditches. This taxon has a vast range including southwestern Canada, Washington, Oregon, Idaho,

Figure 5. Delphinium menziesii var. utahense.

- A Typical D. menziesii var. utahense plant. Note the D. bicolor-like leaves and the spreading inflorescence. The flowers are purple with flaring sepals. An axillary raceme is present. X 3/4
- B Crisped hairs typical of this taxon. The pubescence is often more dense than is shown here. X 15
- C Typical leaf blade. The lobes are usually dichotomously dissected 3-4 times. X 3/4
- D Typical shallow, globose root system. Note the weak attachment of the tapering stem. X 3/4
- E Typical lower petals. Note the small deeply notched blades which are as wide as they are long. The wide "v" shaped gap is typical. X 3/4

Drawing by J. R. Hodgson.



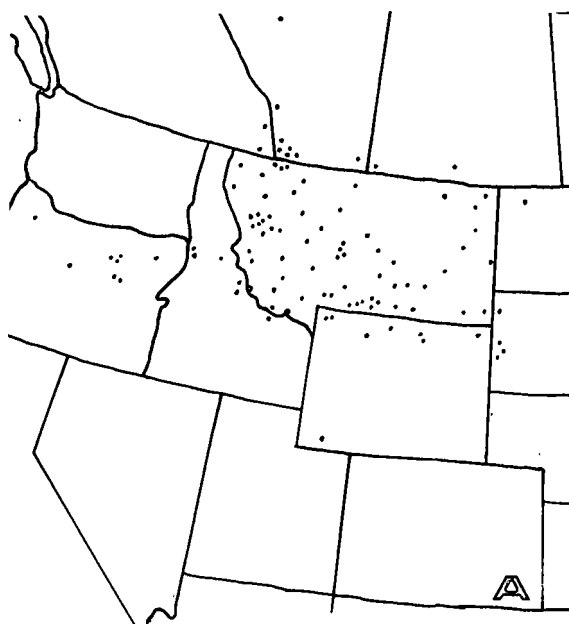
Wyoming, Utah, Colorado and Arizona. In Montana it is found along the southern border from the Big Hole area to the Red Lodge area.

(Figure 6B)

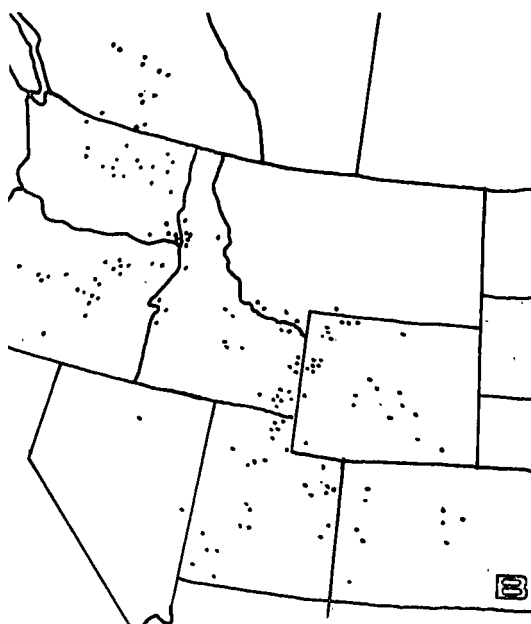
Delphinium menziesii var. utahense seems to be the most stable and distinct in the southern part of its range where such identifying features as the "bicolor" habit, crisped hairs, purple flowers, small oval, deeply notched lower petals and shallow root system remain constant. In parts of Idaho, Oregon and Washington many plants acquire traits similar to those of D. bicolor and D. menziesii var. nuttallianum suggesting hybridization among these taxa. These situations have been discussed in detail earlier in this paper.

Representative Collections: MONTANA: Sawyer 541, 1.7 m. e. of Cooke City, Park Co.; Dorn 846, Red Rock Lake Refuge, Beaverhead Co.; Dorn 391, Red Rock Lake Refuge, Beaverhead Co.; Sawyer 518, 3 m. n.e. of Cooke City, Park Co.; Hitchcock 16926, Black Butte, Gravelly Range, Madison Co.; Witt 1228, 3 m. e. of Cooke City, Park Co.; Hitchcock and Sutherland 23873, Red Rock Pass, Beaverhead Co.; Calvert 136, Odell Ck., Beaverhead Co.; WYOMING: Hill 389, Laramie Hills; Roeder 268, Feather Lake, Yellowstone Nat. Park; Sawyer 540, Clay Butte Fire Tower, Park Co.; Sawyer 531, 7 m. w. of the e. boundary of Grand Teton Nat. Park, Pacific Ck., Teton Co.; Sawyer 534, Lower Geyser Basin, Yellowstone Nat. Park; Smith 1, Mount Washburn, Yellowstone Nat. Park; Martinka, 3 m. n. of Moose, Grand Teton Nat. Park; Buechner W76, Gros Ventre Range; Hitchcock 16684, Lookout Station 3 m. w. of Bear Lake, Park Co.; Williams 1113, Grand Teton Nat. Park; Porter and Rollins 5863, Clay Butte, Park Co.; UTAH: Winklesky 38, Box Elder picnic ground, Brigham City; Harrison 9050, Kaiparowitz Plateau, near the head of Rock Ck., Kane Co.; Livingston 7117, Rock Canyon, Provo; Welsh 209, Dinosaur Nat. Mon.; Stocks 11, Smithfield; Welsh 5235, 7 m. s. of Enterprise; IDAHO: Hitchcock and Muhlich 9531, 11 m. w. of Challis, Custer

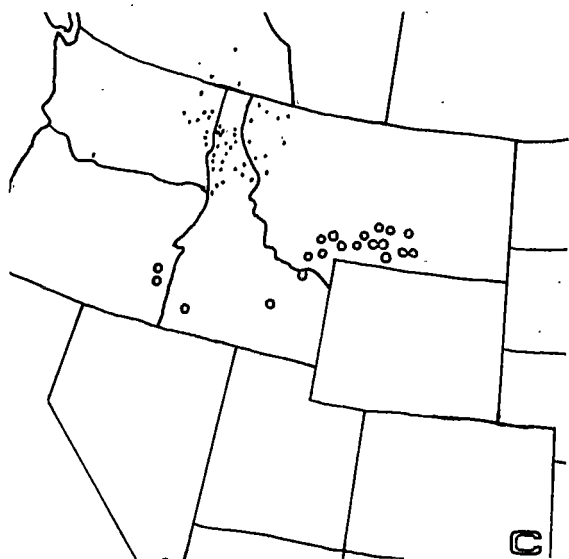
Co.; Hitchcock and Muhlick 20846, 3 m. n. of Winchester, Lewis Co.; Lingenfelter 626, 5 m. s.e. of Pocatello, Bannock Co.; Beck 100, N. Fork of the Clearwater River, Clearwater Co.; Jones 202, Heaven's Gate, Seven Devils Mt.; Cronquist 2434, 9 m. n. of Ketchum, Blaine Co.; Major 10, Caribou Nat. For., Caribou Co.; COLORADO: Booth 46937, 8 m. n. of Crested Butte; A. Nelson 10545, Palmer Lake; A. Nelson 10443, Burango; Baker 216, Cimarron near Gunnison; OREGON: Hitchcock and Muhlick 20794, 10 m. n. of Mt. Vernon, Grant Co.; Hitchcock and Muhlick 20814, 12 m. e. of Pendelton, Umatilla Co.; Hitchcock and Muhlick 13827, 10 m. n.w. of Meacham, Umatilla Co.; Kruckeberg 2464a, 1/2 m. below Hat Point, Sacajawea Camp, Wallowa Co.; WASHINGTON: Hitchcock and Muhlick 20872, 14 m. e. of Republic, Stevens Co.; Hitchcock and Muhlick 20879, 12 m. n.e. of Wenatachee, Douglas Co.; Daubenmire 5432, 6 m. n. of Odessa; Moomaw, Coulee City, Grant Co.



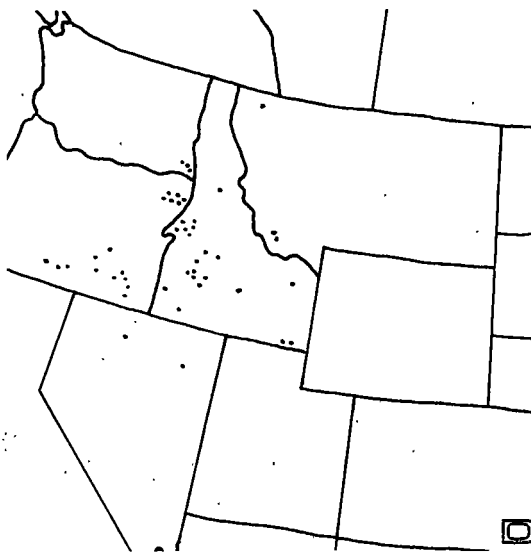
D. bicolor var. bicolor



D. menziesii var. utahense



- D. menziesii var. nuttallianum
- D. bicolor var. pilosum



D. depauperatum

Figure 6. Distribution maps for five taxa of Delphinium occurring in Montana.

RESULTS

Data obtained from the chromatographic studies are summarized in Table III, IV and V and in Figures 7 and 8. Twenty eight spots have been distinguished from the Delphinium material chromatographed. Distinct differences were found in the chromatogram patterns obtained from the three species studied, D. bicolor, D. depauperatum and D. menziesii, as well as minor, but constant differences between the varieties within D. bicolor and D. menziesii. Upon spraying a chromatogram with sodium carbonate and inspecting it in UV light the taxon from which the leaf extract was obtained could be readily recognized. Five of the 28 spots were present in all of the Delphinium material studied. The chromatogram patterns obtained from populations of each taxon were uniform, differing only in the size and color intensity for any one spot. Repeated trails from a single population produced more uniform patterns than those of different populations of the same taxon. Chromatograms from plants collected in the same locale, but during different years, were uniform. All spots except spot 6 consistently appeared if the compounds were present in the leaf extract. The color development of spot 6 was slow and faint. Although this spot is not always present it was observed in a sufficient number of chromatograms to determine its existence as a constituent of certain taxa.

Rf values of a particular spot (some more than others) varied over a range of ± 6 because of differences in the chromatographic

Table III. Characteristics of components obtained by chromatographing leaf extracts from *Delphinium* populations.










Spot #	Rf x 100 range	Appearance of spots with various treatments				Distribution	
		non-sprayed		Na ₂ CO ₃ sprayed			
		Day-light	UV light	Day-light	UV light		
1	94.4-96.2	0-0	G	-	dkG	dkS	b,p,a,t,u,n,d
2	86.0-91.7	88.0-89.7	-	-	-	bB	b,p,a,t,u,n,d
3	70.0-76.1	86.0-88.4	-	-	-	fB	b,p,a,t,u,n,d
4	58.0-61.7	78.0-81.5	vpY	-	vfY	bGY	b,p,a,t,u,n,d
5	41.0-48.9	70.0-78.0	-	-	-	fB	b,p,a,t,u,n,d
6	22.0-24.0	87.0-88.0	-	-	-	slL	b,p,a,t,u,n
7	50.0-55.0	66.0-70.5	-	-	-	fF	b,p,a,t, n,d
8	82.0-85.6	82.0-87.0	-	-	-	GY	p,a,t,u, d
9	21.1-21.5	80.0-82.7	-	dkP UVab	vfYBr	dkP	b,p,a,t, d
10	38.1-39.0	66.2-67.0	pYG	dkP UVab	vbY	vbY	b,p,a,t
11	15.0-21.4	84.5-89.0	-	-	-	fB	b,p,a,t
12	13.0-16.0	73.0-77.2	vfY	dkP UVab	fY	dY	b,p,a,t
13	46.5-53.6	79.0-82.8	-	-	-	fB	b,p,a,t
14	13.0-13.0	83.0-83.5	-	-	fdY	fdY	u,n
15	33.1-37.0	74.0-77.0	-	dkP UVab	vbY	vbYBr	u,n
16	32.5-36.3	79.5-82.3	-	dkP UVab	-	dkP	u,n
17	46.0-49.0	83.0-86.0	-	dkP UVab	vbY	vbY	u,n
18	45.5-47.5	86.8-90.7	-	dkP UVab	-	dkP	u,n
19	28.0	91.8	fGBr	-	fYBr	dkP	d
20	42.8	74.7	-	-	-	OY	d
21	61.7	87.0	-	dkP UVab	vbY	dyYBr	d
22	61.7	92.5	-	dkP UVab	Br	dkP	d
23	91.7	41.8	-	-	-	fF	d
24	89.5	67.6	-	-	-	fPk	a
25	91.7	63.4	-	-	-	fB	a
26	82.9	56.6	-	-	-	fB	a
27	91.7	26.2	-	-	-	fF	a
28	89.4	8.1	-	-	-	fF	t

Color of spots: B=blue, Br=brown, F=flesh color, GY=greenish yellow, L=light, O=orange, P=purple, Pk=pink, S=salmon, UV=ultra violet, Y=yellow, YBr=yellowish-brown, YG=yellowish-green.

Descriptive terms of spots: ab=absorber, b=bright, d=dull, dk=dark, dy=dirty, f=faint, p=pale, sl=slow color development, v=very.

Distribution of spots: b=D. bicolor var. bicolor, p=D. bicolor var. pilosum, a=collection from Ajax Mt., t=collection from Tendoy, u=D. menziesii var. utahense, n=D. menziesii var. nutallianum, d=D. depauperatum.

Figure 7. Diagrammatic chromatograms typical of D. bicolor var. bicolor, D. bicolor var. pilosum, D. menziesii var. utahense and D. menziesii var. nuttallianum.

- | | | | |
|--|--|---|--|
|  | Common to all taxa |  | Present except in <u>D. menziesii</u> var. <u>utahense</u> |
|  | Confined to <u>D. bicolor</u> |  | Absent from <u>D. bicolor</u> var. <u>bicolor</u> & <u>D. menziesii</u> var. <u>nuttallianum</u> |
|  | Confined to <u>D. menziesii</u> |  | Present except in <u>D. menziesii</u> |
|  | Confined to <u>D. depauperatum</u> |  | Confined to the population from Ajax Mountain |
|  | Present except in <u>D. depauperatum</u> | • | Leaf extract deposit |

Scale: BAW 1 cm = 4.6 cm, WA 1 cm = 4.8 cm

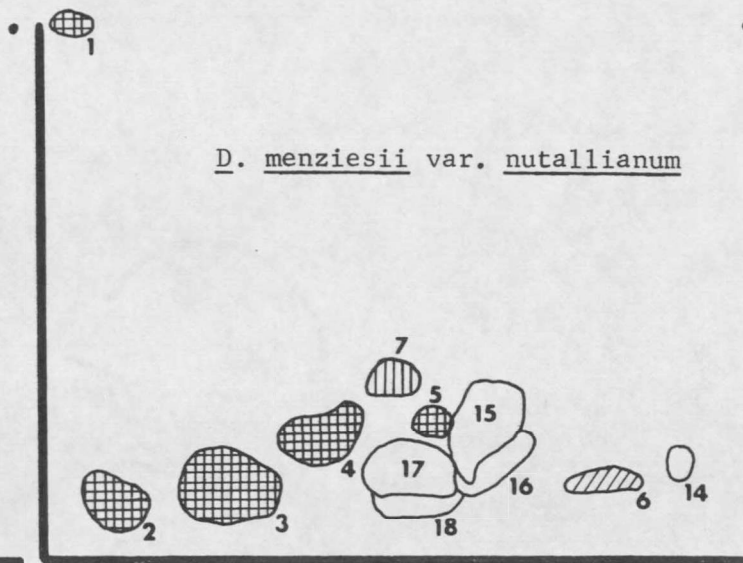
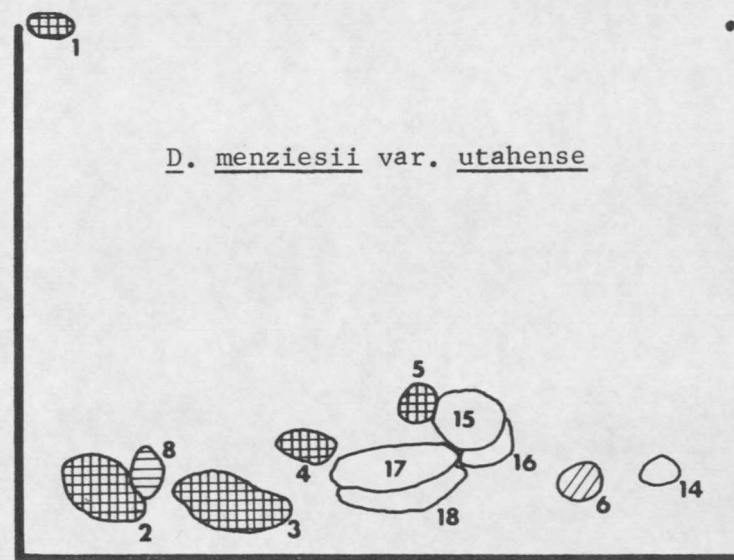
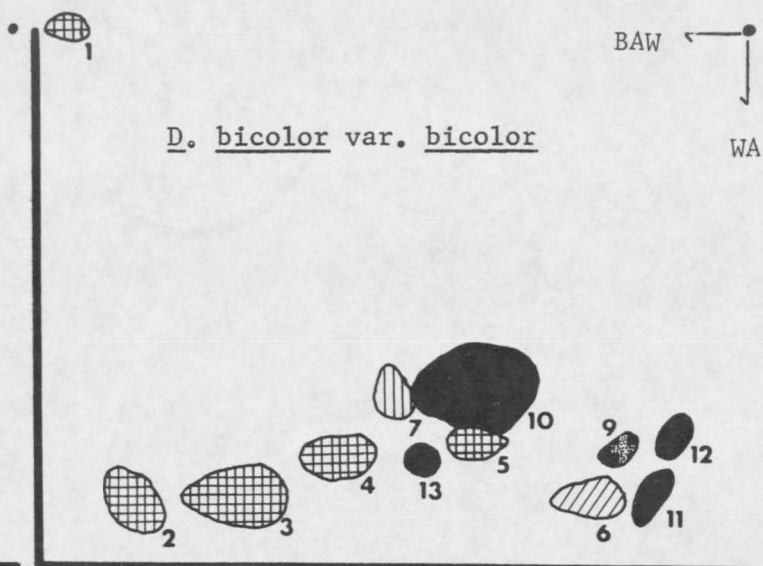
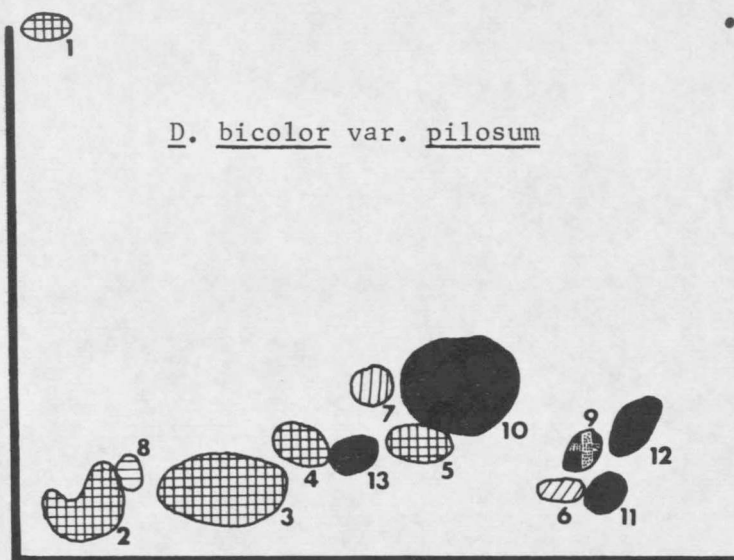









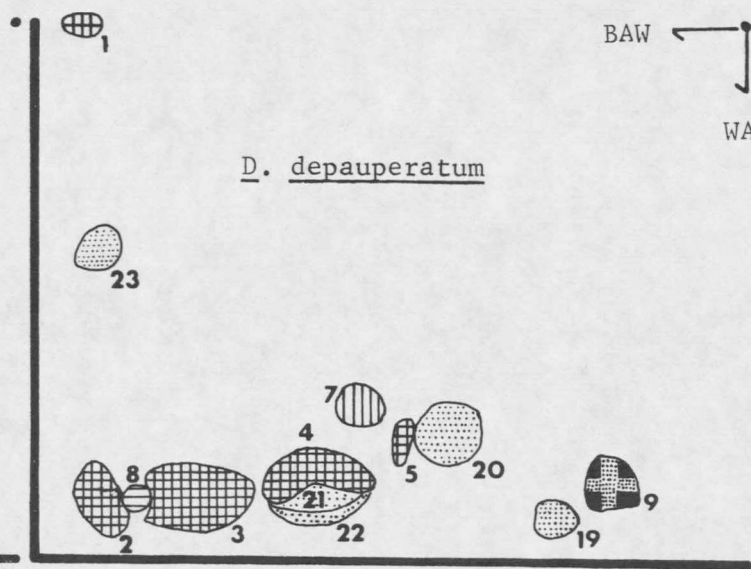
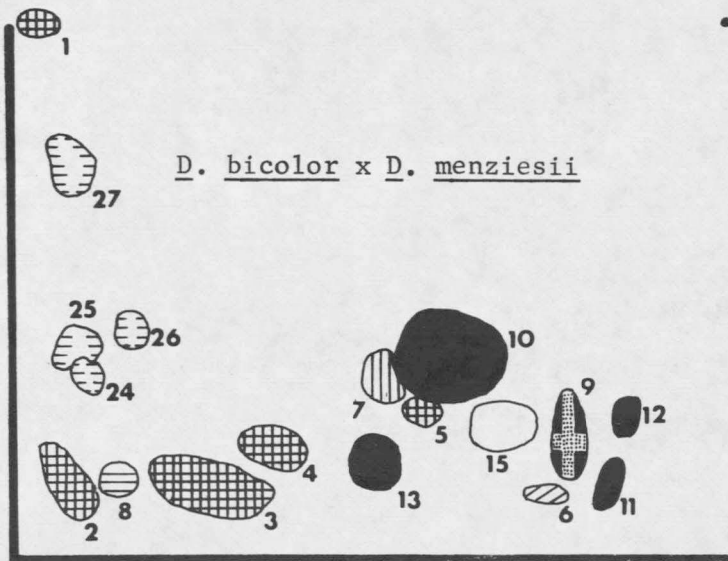


Figure 8. Diagrammatic chromatograms typical of a D. bicolor x D. menziesii population from Ajax Mountain and D. depauperatum.

- | | | | |
|--|--|--|--|
|  | Common to all taxa |  | Present except in <u>D. menziesii</u> var. <u>utahense</u> |
|  | Confined to <u>D. bicolor</u> |  | Absent from <u>D. bicolor</u> var. <u>bicolor</u>
& <u>D. menziesii</u> var. <u>nuttalianum</u> |
|  | Confined to <u>D. menziesii</u> |  | Present except in <u>D. menziesii</u> |
|  | Confined to <u>D. depauperatum</u> |  | Confined to the population from
Ajax Mountain |
|  | Present except in <u>D. depauperatum</u> | • | Leaf extract deposit |

Scale: BAW 1 cm = 4.6 cm, WA 1 cm = 4.8 cm



BAW ↙
WA ↓

Table IV. Distribution of leaf extract components from Delphinium taxa. Compounds were distinguished using a modified paper chromatography technique of Alston and Turner (1963). X indicates the presence of a particular spot on the chromatogram.

Taxon	Spot #																											
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
<u>D. bicolor</u> var. <u>bicolor</u>	x	x	x	x	x	x	x	x		x	x	x	x															
<u>D. bicolor</u> var. <u>pilosum</u>	x	x	x	x	x	x	x	x	x	x		x	x															
<u>D. bicolor</u> var. <u>pilosum</u> *	x	x	x	x	x	x	x	x	x	x		x	x															x
<u>D. bicolor</u> var. <u>pilosum</u>	x	x	x	x	x	x	x	x	x	x		x	x															
<u>D. menziesii</u> var. <u>utahense</u>	x	x	x	x	x	x									x	x												
<u>D. menziesii</u> var. <u>nuttallianum</u>	x	x	x	x	x	x									x	x												
<u>D. depauperatum</u>	x	x	x	x	x																							

* Population from Tendoy, Idaho; type locality. ** Population from Ajax Mt., Mont.

conditions such as, temperature, concentration of the leaf extract and the time the chromatogram remained in the solvent. Rf variations were apparent between taxa, between populations within a taxon and between replications of a population. The Rf values presented in this study were obtained by averaging all trials within a taxon.

Although the spots were not chemically identified, the decision as to whether spots of different chromatograms were the same or not was based on three factors: (1) Rf values; (2) color and appearance of the spot in UV light after being sprayed with sodium carbonate and (3) by loading a chromatogram with leaf extract from two different populations in varying combinations. If the Rf value of similar appearing spots varied by a difference of six or less, they were assumed to be identical. The method of loading a chromatogram with extracts from two different populations proved extremely useful in arriving at decisions concerning whether similar spots with wide ranging Rf values, such as 5, 7, 10, 11, 12, 13, 15, and 17, were the same or not the same. Spots 24 through 27 were found only in the colony collected from Ajax Mountain and are assumed to be either hybrid spots (spots not produced by either parental populations but found in the hybrid) or else they represent compounds which exist in the parents, but which are not concentrated enough to appear on the chromatograms even though they are present. Spot 28 was present only in the populations collected

from Tendoy at the type locality of D. bicolor var. pilosum.

The paired affinity index, a numerical method of expressing relationships of taxa developed by Ellison, Alston and Turner (1962), was obtained by dividing the number of spots possessed in common by the two taxa being compared by the total number of spots of those two taxa and multiplying this value by 100. Two taxa with a higher paired affinity value were assumed to be more closely related than two taxa with a lower value. Paired affinity indices of the six taxa investigated are presented in Table V.

Table V. Paired affinity index values of the chromatographic data for six taxa of Delphinium. A high value between two taxa indicates a closer relationship of those taxa than a lower value.

	<u>D. bicolor</u> var. <u>bicolor</u>	<u>D. bicolor</u> var. <u>pilosum</u>	<u>D. bicolor</u> x <u>D. menziesii</u> *	<u>D. menziesii</u> var. <u>utahense</u>	<u>D. menziesii</u> var. <u>nuttallianum</u>
<u>D. bicolor</u> var. <u>pilosum</u>	92.3	----	----	----	----
<u>D. bicolor</u> x <u>D. menziesii</u> *	66.6	72.2	----	----	----
<u>D. menziesii</u> var. <u>utahense</u>	33.3	38.9	36.4	----	----
<u>D. menziesii</u> var. <u>nuttallianum</u>	41.2	38.9	36.4	84.6	----
<u>D. depauperatum</u>	38.9	44.4	36.4	31.6	31.6

* Population from Ajax Mt., Mont.

DISCUSSION

The non-fistulose larkspurs of Montana are closely related. Their similar morphological appearances, the evidence that these taxa hybridize and an element of likeness in their chromatograms provide ample evidence of their close affinities. The questions to be discussed in this thesis are; how are these taxa related? and, how should they be classified?

The fact that morphologically similar populations have consistently similar chromatograms whereas morphologically different taxa have different chromatograms suggests an answer to the question; how are these taxa related? The five morphologically recognized taxa, D. bicolor var. bicolor, D. bicolor var. pilosum, D. depauperatum, D. menziesii var. nuttallianum and D. menziesii var. utahense, separate into three distinct groups based on chromatographic evidence. Inspection of Figures 7 and 8 and Table IV and V reveals that D. bicolor var. bicolor and D. bicolor var. pilosum form a group of closely related taxa; that D. menziesii var. nuttallianum and D. menziesii var. utahense belong to a second group of closely related taxa; and that D. depauperatum is distinct from either of the other two groups. The chromatograms of these three groups all have several compounds which are unique to each group.

Plants assigned morphologically to the taxa D. bicolor var. bicolor and D. bicolor var. pilosum are the only plants whose

chromatograms possess spots 10, 11, 12, and 13. The chromatograms of these two taxa differ only in that those of the pilosum variety have spot 8 and those of the bicolor variety lack that spot. The taxon referred to as D. andersonii by Sawyer (1967) and D. nuttallianum var. pilosum by Hitchcock (1964) has caused much uncertainty as to how it should be classified. Of this taxon Sutherland (1967) wrote, "Disposition uncertain, perhaps nearest Delphinium menziesii subsp. bicolor". The chromatographic evidence in this thesis suggests that the pilosum variety is very closely related to D. bicolor. Because the chromatograms of D. bicolor var. pilosum are much more similar to those of D. bicolor than to those of D. menziesii, it seems well to assign the "pilosum" taxon to the species D. bicolor. Material collected from the type locality of D. nuttallianum var. pilosum near Tendoy, Idaho chromatographed like all other populations of D. bicolor var. pilosum except for the additional spot 28, which was not found in any other population chromatographed in this study. It should not be suggested that the Tendoy population belongs to a different taxon from other D. bicolor var. pilosum populations as all are within the morphological realm of D. bicolor var. pilosum.

The chromatographic data also clarified the relationship questions concerning D. nuttallianum and D. nelsoni (D. menziesii var. nuttallianum and D. menziesii var. utahense respectively in this

thesis). Among the taxa investigated spots 14, 15, 16, 17, and 18 are unique to these two taxa and the chromatographic differences between the two are very slight (Table IV and V, and Figure 7). Sawyer (1967) previously placed these two taxa in separate species. Now, with new evidence, it seems proper to combine these two taxa into one species. Sutherland (1967) included both in the species, D. menziesii. Because populations of D. menziesii var. menziesii were not chromatographed there is no evidence to support or refute Sutherland's interpretation. For the time being it seems best to accept Sutherland's premise and include D. nelsoni and D. nuttallianum in the species, D. menziesii.

A population of D. nuttallianum (D. menziesii var. nuttallianum in this thesis) from Glacier National Park considered by Sawyer (1967) to represent the high mountain form had chromatograms identical to those of populations considered to be the lowland form of D. nuttallianum. Regardless of differences in the appearance of the two forms, they must be considered as part of the same taxon. The question remains open as to whether the two forms represent different ecotypes. Transplant studies might provide evidence which could answer this question.

It has been pointed out by Sutherland (1967) and again in this thesis that along the southwestern border of Idaho and Montana members of D. bicolor and D. menziesii var. utahense hybridize

producing individuals with traits intermediate to each taxon. The delphinium plants collected by Mrs. Harpster in 1969 from the Ajax Mountain population has many individuals with deeply lobed petals, and although the roots were not present, this population can be considered to contain individuals which are intermediate between D. bicolor and D. menziesii var. utahense. The chromatograms (Figure 8) for this population are intermediate, possessing spots (9, 10, 11, 12, and 13) typical of D. bicolor and others (15, and 8) which are found in the chromatograms of D. menziesii var. utahense. In addition, spots 24, 25, 26, and 27 are present only on the chromatograms of the population from Ajax Mountain. These spots may represent hybrid spots or they may be compounds which are not concentrated enough to show up on the chromatograms of the suspected parental populations.

The second question posed at the beginning of this discussion: How should these taxa be classified? is much more difficult to answer. The question arises: Are all of the taxa investigated, with the exception of D. depauperatum, members of the same species as proposed by Sutherland (1967)? or Do members of the "bicolor group" belong to a different species than those of the "menziesii group"?

A taxonomist employing reproductive isolation to delimit a species must combine D. bicolor and D. menziesii into one species as Sutherland (1967) has done. He combined these taxa and several others into one

species, D. menziesii. There is no question that members of D. bicolor var. bicolor, D. menziesii var. utahense and D. menziesii var. nuttallianum hybridize and produce fertile F₁ generations. Although the experimental evidence presented by Sutherland (1967) indicating that D. bicolor, D. menziesii var. nuttallianum and D. menziesii var. utahense, among others, hybridize producing fertile F₁ generations is scanty and in places lacking, the morphological evidence (Sutherland, 1967 and Sawyer in this study) supports the hypothesis of hybridization between these taxa. Chromatography has now added to this list of evidence.

However, it is not a universally shared point of view among taxonomists that different species must be reproductively isolated, as indicated by the quotation appearing earlier in this thesis from Lewis and Epling (1959). They suggest that taxa can be considered separate species even though they interbreed with the production of fertile offspring, if the two parental taxa remain isolated from the offspring and the three evolve divergently.

In this thesis D. bicolor is retained as a species separate from D. menziesii even though there is evidence that D. bicolor and D. menziesii var. utahense hybridize. Delphinium bicolor is evolving independently without the direct influence of D. menziesii in most of Montana, the major part of its range. It is only on the fringe of

its western range that hybridization with D. menziesii takes place and this seems to have little influence on the "bicolor" populations as a whole. If D. bicolor were to hybridize freely with other species throughout its entire range the species interpretation presented in this thesis would agree with Sutherland's interpretation. However, that does not appear to be the case. Chromatographic evidence does not support the existence of widespread D. bicolor x D. menziesii hybrids in Montana except at Ajax Mountain. Even in Glacier National Park where populations of D. bicolor and D. menziesii var. nuttallianum flowered at the same time within two miles of each other the chromatograms of these two populations were typical for their respective taxa with no evidence of hybrid spots. Chromatograms of Delphinium populations occurring in the Yellowstone Park - Cooke City - Red Lodge area where the ranges of D. bicolor and D. menziesii var. utahense overlap were typical for their respective taxa with no indication of hybridization. In Montana D. bicolor var. bicolor can be readily distinguished from D. menziesii by the fibrous root systems, the spreading hairs and the large non-bifid petals. Because of these distinct morphological characters and the consistent chromatographic pattern of D. bicolor populations, it seems well to follow the species concept of Lewis and Epling and maintain D. bicolor as a separate species.

Because of distinct morphological differences Sutherland (1967) did not combine D. depauperatum with D. menziesii in spite of some evidence that the two taxa may hybridize. The one population of D. depauperatum chromatographed in this study has a unique chromatogram (Figure 8). No other populations studied possessed the spots 19, 20, 21, 22, and 23. It seems justifiable to refer to this taxon as D. depauperatum.

Within the species D. bicolor there are two morphologically distinct taxa. Delphinium bicolor var. pilosum has blue flowers, an extensive root system, 4 to 10 leaves displayed at a nearly uniform height on the stem and deeply bifid lower petals. These robust plants grow on dry sandy calcareous soils. All of these features separate this taxon from D. bicolor var. bicolor which never possesses all of these features. In addition there is a minor but constant difference in the chromatographic patterns of these two varieties. Delphinium bicolor var. pilosum has spot 8 (Figure 7) which D. bicolor var. bicolor lacks. One can best classify the taxon referred to as D. andersonii by Sawyer (1967) and D. nuttallianum var. pilosum by Hitchcock (1964) as a variety of D. bicolor. Therefore it is proposed to refer to this taxon as D. bicolor var. pilosum. The other plants of this species are designated D. bicolor var. bicolor.

Members of D. menziesii which were investigated in this study can be divided into two distinct morphological taxa. D. menziesii var. nuttallianum can be distinguished from D. menziesii var. utahense by its long linear leaf segments, ochre lower petals and a spindly habit. This taxon is confined to northwestern Montana, northern Idaho and the eastern part of Oregon and Washington (Figure 6). Its range overlaps with that of D. menziesii var. utahense along its western edge. The two taxa have few but constant chromatogram differences (Figure 7). Variety nuttallianum has spot 7 but lacks spot 8. Variety utahense has spot 8 but lacks spot 7. Sutherland (1967) refers to these two taxa as different varieties of D. menziesii spp. utahense. Based on the morphological, range and chromatographical differences it seems best to distinguish these two taxa as varieties of D. menziesii. In this thesis the taxon referred to as D. menziesii spp. utahense var. hitchcockii by Sutherland (1967) is designated D. menziesii var. nuttallianum and the taxon referred to by Sutherland (1967) as D. menziesii spp. utahense var. utahense becomes D. menziesii var. utahense.

SUMMARY

There are five different non-fistulose taxa of larkspurs, D. bicolor var. bicolor, D. bicolor var. pilosum, D. depauperatum, D. menziesii var. nuttallianum and D. menziesii var. utahense, which occur commonly in Montana. These five taxa all can be distinguished by morphological characters. Examination of over 1,800 herbarium specimens from the northwestern United States reveals individuals possessing intermediate characters. This suggests that members of these taxa hybridize or introgress occasionally. Delphinium bicolor seems to hybridize much more frequently in central Oregon, parts of Washington and in western Idaho than it does in Montana. Evidence based on morphology and chromatography indicates that D. bicolor and D. menziesii var. utahense hybridize along the west central part of the Montana-Idaho border area near Salmon, Idaho. However in Montana, the major portion of the D. bicolor range, there is little if any, evidence suggesting that D. bicolor hybridizes with other delphiniums. Except for the Delphinium population from Ajax Mountain, D. bicolor and D. menziesii var. utahense remain isolated from one another, even when their ranges overlap. There is no evidence that D. bicolor and D. menziesii var. nuttallianum hybridize in Glacier National Park where the two taxa occur within two miles of each other. It appears that in Montana D. bicolor, D. depauperatum and D. menziesii are evolving along separate lines without the direct gene influence of

each other. Therefore, it seems best not to combine D. bicolor and D. menziesii as Sutherland (1967) has done but rather to follow the philosophy of Lewis and Epline (1959) and maintain the two taxa as separate species.

Chromatographic evidence indicates that there are three distinct groups of low non-fistulose delphiniums in Montana. They are: the "bicolor" group containing D. bicolor var. bicolor and D. bicolor var. pilosum, a taxon previously referred to as D. andersonii by Sawyer (1967) and as D. nuttallianum var. pilosum by Hitchcock (1964); the "menziesii" group containing D. menziesii var. nuttallianum (referred to in the past as D. nuttallianum by Ewan (1945), Taylor (1960) and Sawyer (1967)) and D. menziesii var. utahense (referred to in the past as D. nelsoni by Ewan (1945), Taylor (1960) and Sawyer (1967)); and, the third group which includes the lone member, D. depauperatum. Although the chromatograms of these groups possess five common spots, each group contains four or five unique spots.

The population from Ajax Mountain, which is morphologically most like D. bicolor but like D. menziesii var. utahense in certain characters, is chromatographically intermediate to D. bicolor and D. menziesii. The chromatogram is more like that of D. bicolor than the D. menziesii taxon but in addition it also contains spots not found on the chromatograms of any other taxon. Since no other hybrid

populations were detected by chromatography it is believed that hybridization among D. bicolor and D. menziesii is not widespread in Montana.

Because the two taxa occurring in the "bicolor" group have habitat and morphological differences it was decided to separate the two as varieties. The taxon referred to by Hitchcock (1964) as D. nuttallianum var. pilosum is designated D. bicolor var. pilosum. The other taxon is D. bicolor var. bicolor.

The two taxa within the "menziesii" group are also separated as varieties. Morphological and range differences justify referring to the taxon called D. nuttallianum var. fulvum by Hitchcock (1964) as D. menziesii var. nuttallianum. The more wide ranging taxon referred to in the past as D. nelsoni (Ewan, 1945 and Sawyer, 1967) is D. menziesii var. utahense.

Paper chromatography has been a useful tool in clarifying some of the confusion encountered in the genus Delphinium.

APPENDIX

Figure 9. Plate of D. bicolor var. bicolor.

- A. A typical D. bicolor var. bicolor plant with a fibrous root system, stoutly attached on the stem, spreading inflorescence and flaring sepals.
- B. Typical D. bicolor var. bicolor lower petals. Note the large size and orbicular shape.

Actual size drawing by J. R. Hodgson.

- C. Plants having characteristics of D. bicolor var. bicolor and D. menziesii var. utahense. Note the globose root system which is weakly attached to the stem. These are D. menziesii characters. The flowers are characteristic of D. bicolor except the deeply bifid lower petals which retain the characteristic size and shape of D. bicolor.

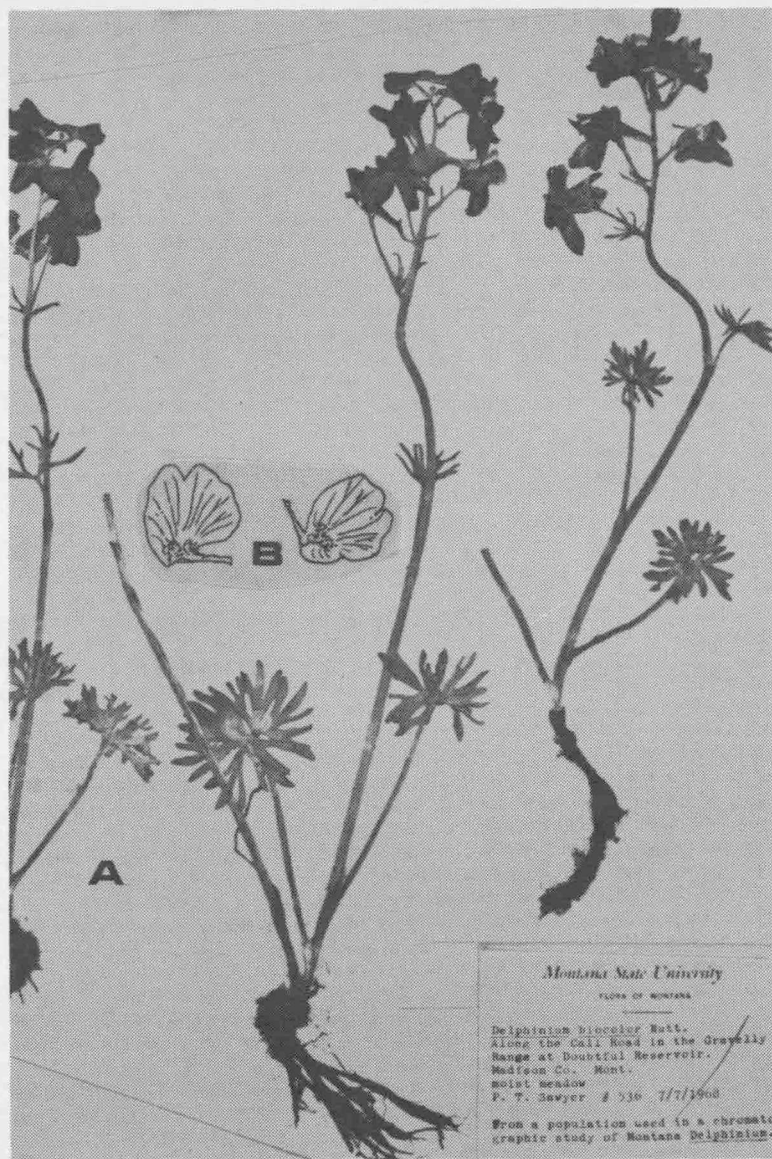


Figure 10. Plate of D. pilosum var. pilosum.

A and C Typical robust plants of D. bicolor var. pilosum with an extensive fibrous root system. Note the numerous stem leaves all displayed at nearly the same level. The flowers are blue and have flared sepals. The inflorescence is spreading.

B Actual size drawing of the lower petals. They are elliptical in shape and are deeply bifid.

Drawing by J. R. Hodgson.

65627
 MONTANA STATE UNIVERSITY
 FLORES OF MONTANA
Delphinium bicolor ssp. *illinoense*
 (L.) F. T. SAWYER
 1.7 miles north of Harrison, Mont.
 on U.S. Rt. 587, Madison Co.
 outcrops of limestone
 outcrops, siltstone, limestone
 present. F. T. Sawyer 5/25/1969
 From a population used in a chromosome
 study of Montana Delphinium.



73

65628
 MONTANA STATE UNIVERSITY
 FLORES OF MONTANA
Delphinium bicolor ssp. *illinoense* (C. L. RICH.) F. T. SAWYER
 4.5 miles west of Clark Canyon Res. Dam
 on Rt. 104 Deerhead Co. Mont.
 DEPT. SANDLOW COLL. OF LIMESTONE
 TACEO.
 F. T. Sawyer & SON 6/12/1969
 From a population used in a chromosome
 study of Montana Delphinium.

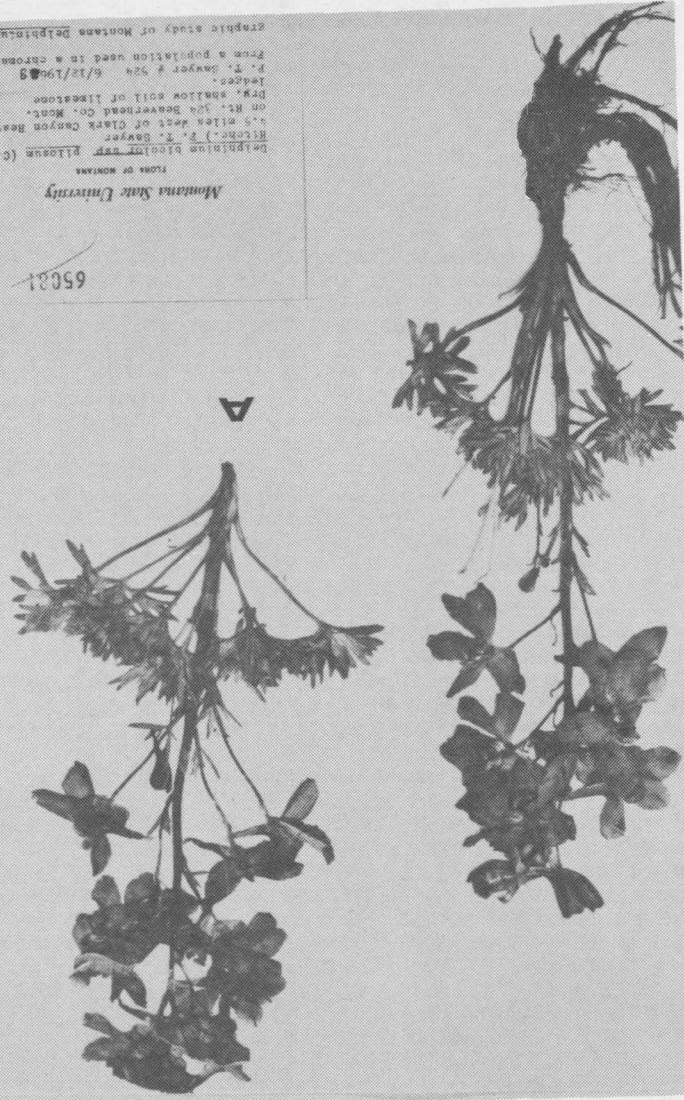
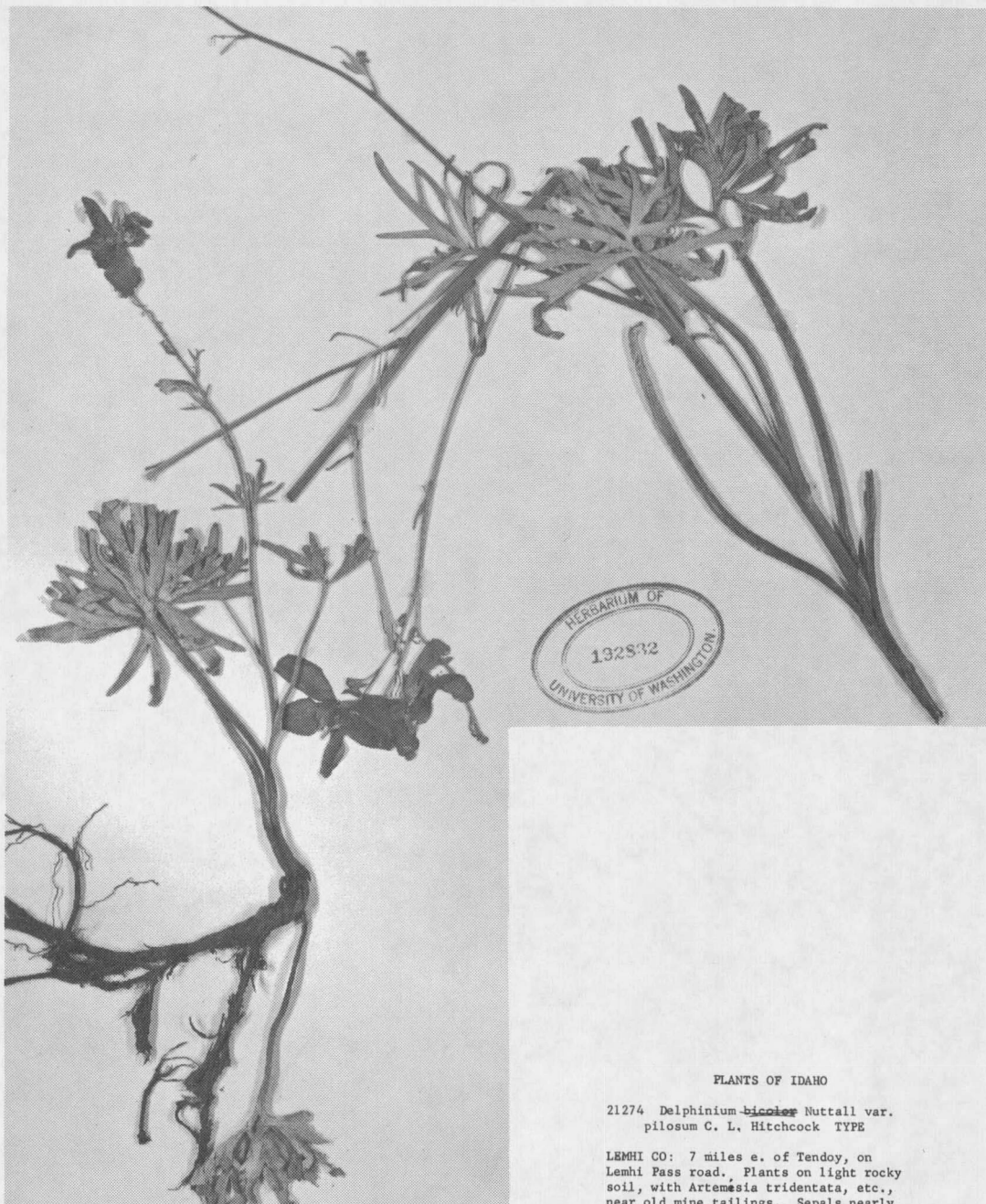


Figure 11.

Holotype of D. nuttallianum var. pilosum from seven miles east of Tendoy, Idaho. In this thesis the taxon is referred to as D. bicolor var. pilosum. These plants have typical D. bicolor var. pilosum features and are not unlike those in Figure 10 A.



Delphinium bicolor Subsp. *pilosum* (C.L.Hitchc.) P.T.Sawyer

Paul T. Sawyer
Montana State University May, 1969

PLANTS OF IDAHO

21274 *Delphinium bicolor* Nuttall var.
pilosum C. L. Hitchcock TYPE

LEMHI CO: 7 miles e. of Tendoy, on Lemhi Pass road. Plants on light rocky soil, with *Artemisia tridentata*, etc., near old mine tailings. Sepals nearly equal, widely flared; lower petals, like the sepals, deep blue-purple, fairly deeply bilobed. These plants were growing at a considerably lower level than many specimens of *D. bicolor* that were past flowering.

C. Leo Hitchcock
C. V. Muhlick

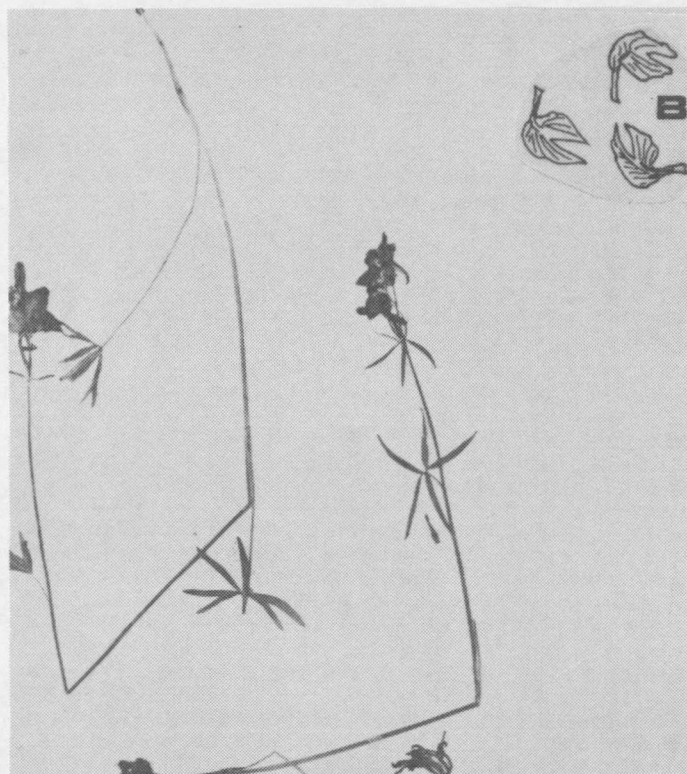
July 1, 1957

Figure 12. Plate of D. menziesii var. nutallianum.

- A A depauperate specimen from the high country of Glacier National Park. Note the globose root system, weakly attached to the stem and the long ultimate leaf segments. The lower petals are ochre.
- B Typical lower petals of D. menziesii var. nutallianum. These lower petals are elliptical with a wide "v" shaped notch. Note that the lower petals tend to be smaller than those of D. bicolor. The typical color of these petals is ochre.

Actual size drawing by J. R. Hodgson.

- C. Typical spindly plants of D. menziesii var. nutallianum. Note the globose root system, the stem tapering at the base, the linear leaf segments and the flaring sepals. The flowers are blue. This represents the lowland form of Sawyer (1967).



A

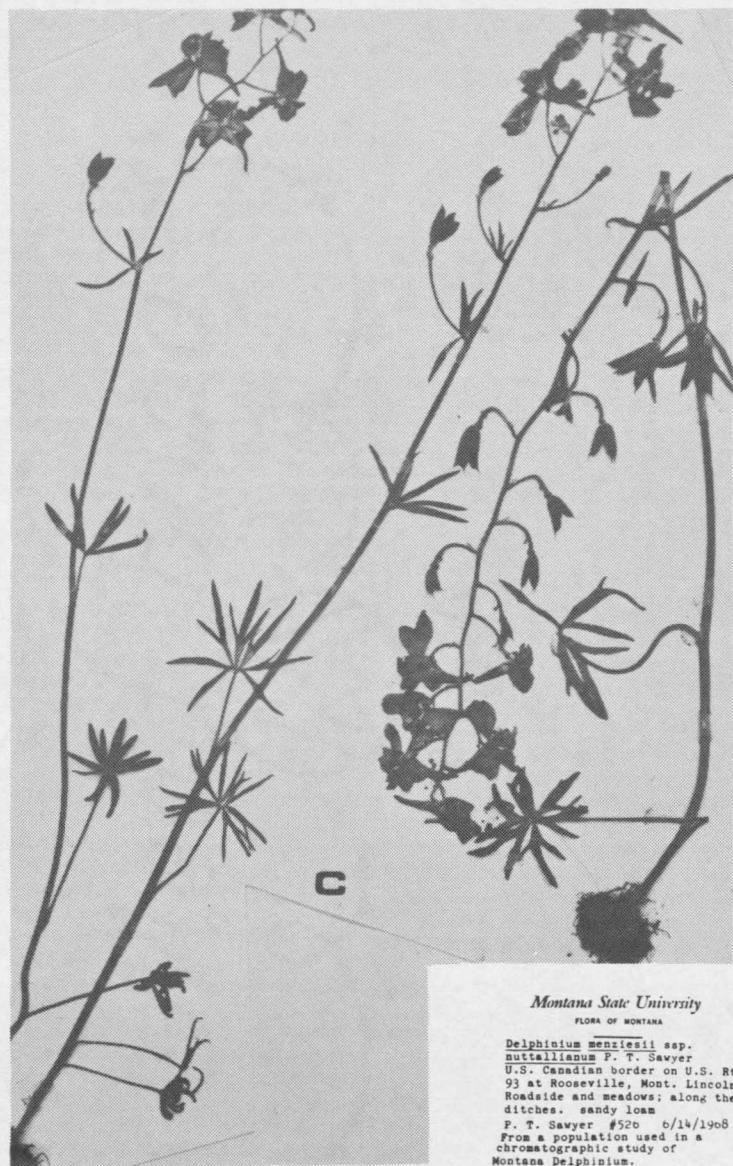
Delphinium menziesii subsp. *nuttallianum* P. T. Sawyer
 (= *nuttallianum* var. *fulvum* C. L. Hitchc.)

Paul T. Sawyer
 Montana State University May, 1969

62114

HERBARIUM OF MONTANA STATE COLLEGE
 FLORA OF MONTANA

DELPHINIUM MENZIESII (P. T. SAWYER) P. T. SAWYER
 (= DELPHINIUM NUTTALLIANUM (C. L. HITCHCOCK) P. T. SAWYER)
 U.S. CANADIAN BORDER ON U.S. RT. 93 AT ROOSEVILLE, MONT. LINCOLN CO.
 ROADSIDE AND MEADOWS; ALONG THE DITCHES. SANDY LOAM
 P. T. SAWYER #520 6/14/1968
 FROM A POPULATION USED IN A CHROMATOGRAPHIC STUDY OF MONTANA DELPHINIUM.



C

Montana State University
 FLORA OF MONTANA

Delphinium menziesii ssp.
nuttallianum P. T. Sawyer
 U.S. Canadian border on U.S. Rt. 93 at Roseville, Mont. Lincoln Co.
 Roadside and meadows; along the ditches. sandy loam
 P. T. Sawyer #520 6/14/1968
 From a population used in a chromatographic study of Montana *Delphinium*.

Figure 13. Plate of D. menziesii var. utahense.

A Typical plants of D. menziesii var. utahense with shallow globose root systems, weakly attached to the stem. The inflorescence is much like that of D. bicolor. The flowers are purple like those of D. bicolor.

B Typical lower petals of D. menziesii var. utahense. Note the small size of the lower petals and the deep, wide gap.

Actual size drawing by J. R. Hodgson.

C Plant having intermediate characteristics of varieties utahense and nuttallianum. The long leaf segments and the habit are typical of the nuttallianum variety of D. menziesii. The flowers and inflorescence are like those of variety utahense.



Montana State University

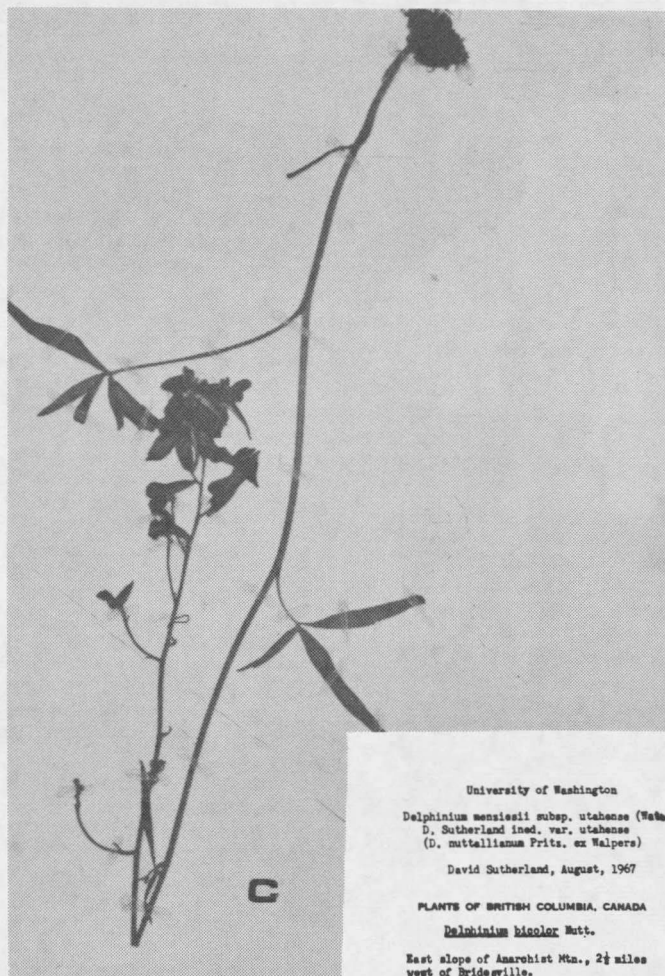
FLORA OF MONTANA

Delphinium menziesii ssp. *utabense* (Wats.)
D. Sutherland

Beaverhead County, Montana: Red Rock
Lake Refuge: T148 R14 S24 SW Sec. 23
Grassland with *Pestuca ovina*, *Cerastium*
arvense Moderate abundance El. 6050'
7/9/1969 H. D. Dorn #840

Vide P. T. Sawyer

From a population used in a chromato-
graphic study of Montana *Delphinium*



University of Washington

Delphinium menziesii subsp. *utabense* (Wats.)
D. Sutherland ined. var. *utabense*
(*D. nuttallianum* Pritz. ex Walpers)

David Sutherland, August, 1967

PLANTS OF BRITISH COLUMBIA, CANADA

Delphinium bicolor Nutt.

East slope of Anacohist Mtn., 2½ miles
west of Bridgewater.

Occasional in shrubby area on steep
hillsides; flowers blue; very large plants
for this species; alt. 3900'.

No. 9568 Coll. J.A. Calder - June 23, 1953
D.B.O. Saville

Delphinium menziesii subsp. *utabense* (Wats.) D. Sutherland
(*D. nuttallianum* Pritz. ex Walpers)

Shows some traits of *D. menziesii* ssp. *nuttallianum*
Paul T. Sawyer
Montana State University May, 1969

DIVISION OF BOTANY, GEORGE HERVEY
DEPARTMENT OF AGRICULTURE, OTTAWA, CANADA

1969-68-85
100-100-10

Figure 14. Plate of D. depauperatum.

A Typical D. depauperatum. Note the tuberous roots and the cylindrical inflorescence. The flowers are appressed to the stem. The sepal spur is straight and the other sepals are cupped forward. The flowers are blue.

B The lower petals of D. depauperatum are small and deeply bifid.

Actual size drawing by J. R. Hodgson.

C Note the dimorphic leaves of this specimen. The lower blades have broad cuneate lobes whereas the upper blades are highly dissected with linear segments. Plants of this type are more common west of Montana. Plants typical of Figure 15 A are typical of the ones occurring in Montana.



Montana State University
 FLORA OF MONTANA
Delphinium sepauperatum Nutt.
 1.2 miles North of the Jet. of Mt.
 574 and road to Bannack near Grant,
 Mont. Beaverhead Co. Very wet ditch
 banks. Standing water.
 P. T. Sawyer # 537 7/7/1968
 From a population used in a chromo-
 graphic study of Montana *Delphinium*.



FLORA OF WASHINGTON
 2088 *Delphinium burkei* Greene
 KILLISNOCK CO. T 20 N, R 14 E, S 30,
 in heavy ashbe soil near highway
 about 3 miles n.e. of Tansaway Junc-
 tion, about 4 miles s.w. of Virden.
 Soil now dry but earlier very springy
 plants associated with *Ceanothus*, *Ger-
 anium*, and *Poa pratensis*; roots small
 fleshy, fascicles, not at all fibrous
 close to the ground surface, firmly
 attached to the (usually) single or
 2 or 3 stems, leaves strongly dimor-
 phic, not fleshy, all plants examined
 (of the several hundred in the colony)
 angulate sepals deep bluish-purple
 a few more nearly blue, others nearly
 purple, not widely spread, but rather
 (especially the lower) cupped for-
 ward; petals colored about as the
 sepals, the upper ones whitish-based,
 the lower ones deeply bifid; follicles
 scarcely at all spreading, saxe-
 cemes spike-like, the pedicels nearly
 erect both in flower and fruit. Here
 there is no indication whatever of
 intermediacy toward *D. multiplex*,
 with which *D. burkei* hybridizes when
 the two cross.

C. Leo Hitchcock
 C. V. McClintock
 June 29, 1956

565.7

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LITERATURE CITED

- Alston, R. E. and B. L. Turner. 1963. Natural hybridization among four species of Baptisia (Leguminosae). *Amer. Jour. Bot.* 50: 159-173.
- Brehm, B. G. and M. Ownbey. 1965. Variation in chromatographic patterns in the Tragopogon dubius-pratensis-porrifolius complex (Compositae). *Amer. Jour. Bot.* 52: 811-818.
- Carter, L. C. and B. G. Brehm. 1969. Chemical and morphological analysis of introgressive hybridization between Iris tenax and I. chrysophylla. *Brittonia* 21: 44-54.
- Davis, K. C. 1900. Native and garden delphiniums of North America. *Minn. Bot. Stud.* 2: 431-457.
- Ellison, W. L., R. E. Alston and B. L. Turner. 1962. Methods of presentation of crude biochemical data for systematic purposes with particular reference to the genus Bahia (Compositae). *Amer. Jour. Bot.* 49: 599-604.
- Epling, C. and H. Lewis. 1952. Increase of the adaptive range of the genus Delphinium. *Evolution* 6: 253-267.
- Ewan, J. 1945. A synopsis of the North American species of Delphinium. *Univ. Colo. Stud. Ser. D* 2: 55-244.
- Fahselt, D. and M. Ownbey. 1968. Chromatographic comparison of Dicentra species and hybrids. *Amer. Jour. Bot.* 55: 334-345.
- Gray, A. 1887. Delphinium, an attempt to distinguish the North American species. *Bot. Gaz.* 12: 49-54.
- Gregory, W. C. 1941. Phylogenetic and cytological studies in the Ranunculaceae Juss. *Am. Phil. Soc. Trans. N.S.* 31: 443-520.
- Hitchcock, C. L. 1964. Delphinium p. 346-366. In Hitchcock, C. L., A. Cronquist, M. Ownbey and J. W. Thompson. 1964. Vascular plants of the Pacific Northwest. Part 2: Salicaceae to Saxifragaceae. Univ. Wash. Press, Seattle.
- Hunter, G. E. 1967. Chromatographic documentation of interspecific hybridization in Vernonia: Compositae. *Amer. Jour. Bot.* 54: 473-477.

- Huth, E. 1892. Die Delphinium-Arten den Vereinigten Staaten von Nord-Amerika. Helios 10 (Abh.): 27-39.
- _____. 1895. Monographie der Gattung Delphinium. Engler Bot. Jahrb. 20: 322-499.
- Lawrence, W. J. C. 1936. The origin of new forms in Delphinium. Genetica 18: 109-115.
- Lewis, H. and C. Epling. 1954. A taxonomic study of Californian delphiniums. Brittonia 8: 1-22.
- _____. 1959. Delphinium gypsophilum, a diploid species of hybrid origin. Evolution 13: 511-525.
- Lewis, H., C. Epling, G. A. L. Mehlquist and C. G. Wyckoff. 1951. Chromosome numbers of Californian delphiniums and their geographical occurrence. Ann. Missouri Bot. Gard. 38: 101-117.
- Ornduff, R. 1957. Documented chromosome numbers of plants. Madrono 14: 111-112.
- Rydberg, P.A. 1900. Catalogue of the flora of Montana and the Yellowstone National Park. N.Y. Bot. Gard. Memoirs 1: 1-492.
- _____. 1902. Studies on the Rocky Mountain flora VII. Bull. Torrey Bot. Club 29: 145-160.
- _____. 1912. Studies on the Rocky Mountain flora XXVII. Bull. Torrey Bot. Club 39: 301-328.
- Sawyer, P. T. 1967. Taxonomic study of Montana delphiniums. Proc. Mont. Acad. Sci. 27: 20-25.
- Smith, D. M. and D. A. Levin. 1963. A chromatographic study of reticulate evolution in the Appalachian Asplenium complex. Amer. Jour. Bot. 50: 952-958.
- Sutherland, D. M. 1967. A taxonomic revision of the low larkspurs of the Pacific Northwest. Ph.D. thesis. Univ. of Washington, Seattle.
- Taylor, R. J. 1960. The genus Delphinium in Wyoming. Univ. of Wyoming Publications Sci. 24: 9-21.

- Tjebbs, K. 1927. The chromosomes of three Delphinium species.
Hereditas 10: 160-164.
- Wilde, E. I. 1931. Studies of the genus Delphinium. Cornell Univ.
Agr. Exp. Sta. Bull. 519: 107 p.

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[REDACTED]
D378 Sawyer, Paul T
Sa97 Systematic studies
cop.2 of non-fistulose
Delphinium taxa
common to Montana

NAME AND ADDRESS

DATE	REMARKS
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