MONTANA STATE UNIVERSITY

Biosystematic studies of species of Delphinium occurring in Montana
by Paul Thompson Sawyer

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree
MASTER OF SCIENCE in Botany
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Abstract:
The 11 species of Delphinium occurring' in or expected to be in Montana, Delphinium ajacis, D. andersonii, D. bicolor, D. brownii, D. burkei, D. depauperatum, D. geyeri, D. glaucescens, D. nelsoni, D. nuttallianum and D. occidentale, were studied. Herbarium specimens from Montana State University (Bozeman) and the University of Montana (Missoula) were examined and annotated. The 11 species are grouped into 3 complexes, based upon morphological similarities or dissimilarities. Descriptions and distributions maps of the 11 species are provided, along with a key separating the species.

Delphinium andersonii and D. nelsoni should not be treated as varieties of D. nuttallianum; they are more closely related to D. bicolor than to D. nuttallianum.

Pollen grain and guard cell lengths were determined for 10 species. Pollen grain lengths suggest that D. andersonii might be a polyploid.

Three species, Delphinium bicolor, D. geyeri and D. occidentale, were investigated with serological and electrophoretic techniques. Serological studies did not prove to be reliable or satisfactory. Electrophoretic techniques are useful and could be used in further taxonomic investigations of Delphinium.

BIOSYSTEMATIC STUDIES OF SPECIES OF DELPHINIUM OCCURRING IN MONTANA

by

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ABSTRACT

The 11 species of Delphinium occurring in or expected to be in Montana, Delphinium ajacis, D. andersonii, D. bicolor, D. brownii, D. burkei, D. depauperatum, D. geyeri, D. glaucescens, D. nelsoni, D. nuttallianum and D. occidentale, were studied. Herbarium specimens from Montana State University (Bozeman) and the University of Montana (Missoula) were examined and annotated. The 11 species are grouped into 3 complexes, based upon morphological similarities or dissimilarities. Descriptions and distributions maps of the 11 species are provided, along with a key separating the species.

Delphinium andersonii and D. nelsoni should not be treated as varieties of D. nuttallianum; they are more closely related to D. bicolor than to D. nuttallianum.

Pollen grain and guard cell lengths were determined for 10 species. Pollen grain lengths suggest that D. andersonii might be a polyploid.

Three species, Delphinium bicolor, D. geyeri and D. occidentale, were investigated with serological and electrophoretic techniques. Serological studies did not prove to be reliable or satisfactory. Electrophoretic techniques are useful and could be used in further taxonomic investigations of Delphinium.

INTRODUCTION

Delphinium L., larkspur, is a large genus distributed principally in the Northern Hemisphere, with many closely-related species in western North America. For economic reasons, *Delphinium* has been and continues to be studied. Several species contain poisonous alkaloids capable of causing death to livestock (Kingsbury, 1964). Certain species are used horticulturally (Bailey, 1949). Therefore, it is important that there be means available for easy recognition of the species and subspecies of *Delphinium*. Such means would, in addition, be of intrinsic value to systematists, as basic information regarding this taxon.

There are 11 species of *Delphinium* present in Montana. There have been no completely satisfactory systematic treatments of the genus in the recent floras of western North America. Using present means, for example, it has been nearly impossible to readily separate *D. bicolor* Nutt., *D. nuttallianum*, Pritz., *D. andersonii* Gray and *D. nelsoni* Greene. It is thought that relatively recent isolation of local populations coupled with a history of interspecific hybridization (Epling and Lewis, 1952) have led to the morphological similarities that make species recognition difficult.

The objectives of this study were:

1. to assign the *Delphinium* specimens of the Montana State University Herbarium to their proper species and
2. to construct a usable key for the identification of taxa of the genus *Delphinium* in Montana.

In addition to morphological studies, certain biochemical systematic methods, phytoserology and electrophoresis, were used to aid in species identification.

REVIEW OF LITERATURE

Taxonomy

The genus Delphinium has been studied by numerous workers. Some of the early workers were De Candolle (1824), Sprengel (1825), Engler and Prantl (1891) and Huth (1892 and 1895). Their work is largely of historical interest and of little value to present day workers dealing with western North American larkspurs as they had but few specimens from isolated parts of western North America to study. Gray (1887) described 5 new species, mostly western North American, of Delphinium including D. andersonii. He failed to give detailed descriptions of these species and his key is confusing, but his study contributes some information towards understanding the Delphinium bicolor, D. andersonii, D. nuttallianum, D. nelsoni complex. Rydberg (1900, 1902 and 1912) described several new species of Delphinium, including D. brownii Rydb. and D. glaucescens Rydb. Currently many of Rydberg's species are thought to represent intraspecific categories rather than specific ranks. Wilde (1931) investigated the larkspurs of horticultural interest. His introduction reviews the status of the genus at the time of his publication.

The most recent comprehensive treatments of western North American species of Delphinium have been those reported by Ewan (1945) in which he investigated all species in North America, and by Hitchcock et al. (1964). Ewan's conclusions are based largely on herbarium specimens, but are secondarily supported by field and plot studies in some cases. He lists 79 species of Delphinium in North America which he places in 13 series designed to show evolutionary lines of development. The Montana species

are placed in the following series:

IV TUBERIFORM SERIES
D. nuttallianum Pritz.
D. depauperatum Nutt.

V LIGNIFASCICULATE SERIES
D. bicolor Nutt.
D. nelsoni Greene

VII ELATOPSOID SERIES
D. glaucescens Rydb.
D. occidentale (Wats.) Wats.
D. brownii Rydb.

XIII SPICIFORM SERIES
D. burkei Greene
D. geyeri Greene
D. andersonii Gray

Ewan states that Delphinium has very few reliable characteristics which can be used to distinguish one species of Delphinium from another. Lewis and Epling (1954) reached a similar conclusion concerning California delphiniums. The most reliable characters are leaf blade appearance, corolla color, petal shape, pubescence of the follicle and seed morphology. Lewis and Epling (1954) caution that herbarium studies without field evidence can cause an investigator to arrive at false conclusions. Lewis (1947) presented evidence that environmental differences can change the expression of the leaf appearance. It has also been noted by Lewis and Epling (1954) that certain field characters such as flower color and sepal form can be obscured or lost in herbarium specimens.

Hitchcock's et al. (1964) study includes the species of Delphinium of northwestern United States and is based on herbarium specimens and field observations. Hitchcock differs from Ewan in interpretation of the

D. bicolor, D. nuttallianum complex. It would appear that D. nelsoni Green, D. bicolor f. helleri (Rydb.) Ewan, and D. bicolor f. macallae Ewan in Ewan's treatment are equivalent to Hitchcock's D. nuttallianum var. nuttallianum. Delphinium nuttallianum var. pilosum C. L. Hitchc. has fibrous roots and is probably the same as Ewan's D. bicolor f. montanense (Rydb.) Ewan. Hitchcock places more emphasis on the deep sinus of the lower petals to separate D. nuttallianum from D. bicolor than does Ewan.

Cytogenetics

The basic chromosome number of Delphinium is 8; the usual diploid number is 16 (Tjebbes, 1928, Mehlquist, Blodgett and Brusica, 1943, Lewis et al., 1951, Lewis and Epling, 1954, Ornduff, 1957, Ewan, 1945 and Hitchcock et al., 1964). Lewis et al. (1951) report 3 exceptions: the 2n number of D. variegatum, D. hanseni and D. gypsophilum being either 16 or 32. The tetraploids appear to be autotetraploids. Chromosome numbers determined for those species present in Montana are D. nelsoni, n=8, (Wiens and Halleck, 1962), D. nuttallianum and D. andersonii, n=8, (Lewis et al., 1951), D. bicolor f. helleri (Rydb.) Ewan, n=8, (Ornduff, 1957) and D. ajacis, n=8, (Tebbes, 1928). Idiograms constructed for several species of Delphinium reveal that the karyotypes are nearly, if not, indistinguishable from one another (Lewis et al., 1951, Mehlquist et al., 1943).

It has been reported by Stone (1961, 1963) and Whitehead (1963) that pollen grain and stomate size are useful in separating diploids and tetraploids of the same genus. However, Lewis and Epling (1954) state

that neither pollen grains or stomate size are useful in separating the diploid and tetraploid races of D. gypsophilum.

Evolution

Ewan (1936) proposed that the genus Delphinium of western North America has undergone prolonged isolation resulting in numerous species which can be grouped into series characterized by similar morphological characters and distribution patterns. Ewan (1945) concluded that one reason closely related Delphinium species were hard to distinguish was due to narrow endemism and highly localized ranges. Epling and Lewis (1952) reached the same conclusions based on field studies carried out over an extended period of time. With respect to the species of Delphinium that they studied, they suggested that:

1. the plants were cross pollinating but self compatible,
2. the plants tolerated severe environmental conditions by remaining dormant over a period lasting up to at least 10 years,
3. individual plants of a colony tolerated different environmental conditions,
4. environmental fluctuations resulted in progeny which were more adapted to that particular type of environmental fluctuation,
5. there was more ecotypic variation at the margins of a colony than at its center, and
6. seed dispersal was probably no greater than 0.2 of a mile.

Lewis and Epling (1952) theorize that the above combination of characteristics is a possible mechanism for separation and isolation of ecotypes

within a colony thus resulting in new colonies, forms or species.

Numerous workers, Mehlquist *et al.* (1943), Ewan (1945), Epling and Lewis (1952) and Hitchcock *et al.* (1964) report that some *Delphinium* spp. hybridize. Epling and Lewis (1952) indicate that hybrids have resulted from interspecific rather than intraspecific hybridization even if diploid and tetraploid members of the same species are present in the same colony. It is thus easy to visualize intergrading variations among species of *Delphinium*.

Hybrids reported to occur in Montana are:

D. bicolor Nutt.	x	*D. nelsoni* Green (Ewan, 1945)
D. andersonii Gray	x	*D. bicolor* Nutt. (Ewan, 1945)
D. burkei Greene	x	*D. bicolor* Nutt. (Ewan, 1945)
	and	
D. andersonii Gray	x	*D. glaucescens* Rydb. (Hitchcock *et al.*, 1964)

Finally, Ewan (1945) suggested that one of the 3 primary distribution centers of *Delphinium* occurs in the Bitter Root Range of the central Rocky Mountains.

Phytoserology

Serological techniques have been used by several investigators to indicate differences between different taxa (Creel 1964, Johnson and Fairbrothers, 1965, Fairbrothers, 1966, and Gell, Hawkes and Wright, 1960, and to identify hybrids (Collins, 1965). Hammond (1955) used serological methods to study generic relationships, including *Delphinium*, in the family Ranunculaceae. Lester, Alston and Turner (1965) used serological techniques to study the genus *Baptisia*. They concluded that serology

couldn't distinguish specific differences within the genus but is useful in defining the genus Baptisia. Since 1960 gel-diffusion techniques (Ouchterlony, 1948 and Creel, Ericson and Schulz-Schaeffer, 1965) have largely replaced the photoreflectrometric method developed by Boyden and DeFalco (1943) in phytoserology.

Electrophoresis

Disc-gel electrophoresis is a new technique developed by Ornstein (1964) and Davis (1964) that can be used to advantage by the biosystematist as pointed out by Boulter, Thurman and Turner (1966). In disc-gel electrophoresis proteins move differentially through the polyacrylamide gel forming bands because of the different electrical charges and molecule sizes of the proteins. The bands formed in the gel at the end of the trial can be compared with bands formed by similar trials using material from other species (Vaughan et al., 1965, and Fox, Thurman and Boulter, 1964).

MATERIALS AND METHODS

Morphological Taxonomy

Nearly 300 herbarium sheets obtained from the herbaria at the University of Montana and Montana State University of *Delphinium* species occurring in Montana were studied. Special attention was paid to those characteristics which appear to be useful in identifying the species. Measurements were made to determine stem height and diameter, lengths of petioles, pedicels, sepal spurs and follicles, and to determine the dimensions of the leaf blades, ultimate leaf segments, flowers, sepals and petals. The stems, leaves and inflorescences were observed under magnification to note the types of surface coverings. Particular note and measurements were made of the extent of notching of the lower petal lobes.

Pollen Grain and Guard Cell Size Studies

The sizes of pollen grains and guard cells from each species of *Delphinium* expected to be found in Montana were measured. Pollen grains were obtained from flowers of herbarium specimens of *Delphinium ajacis*, *D. andersonii*, *D. bicolor*, *D. burkei*, *D. depauperatum*, *D. glaucescens*, *D. geyeri*, *D. nelsoni*, 2 forms of *D. nuttallianum* and *D. occidentale*. The pollen grains were mounted on micro slides in water just before they were to be measured. The long axis of the pollen grain was measured using a calibrated ocular micrometer at a magnification of 500 diameters. Ten pollen grains were measured for each sample. Pollen grains from 10 plants of each species were measured except for 4 species. There were 8 replications of *D. burkei*, 7 replications of *D. depauperatum* and

D. geyeri and 6 replications of D. ajacis.

The data were analyzed statistically using the completely random design, one way classification, analysis of variance with unequal replications (Steel and Torrie, 1960). Duncan's New Multiple Range Test (Steel and Torrie, 1960) having 7 replications was used to determine which of the 11 species differed. Another method used to determine which of the 11 species differed was that of computing 95 per cent confidence intervals for the means of each species using Student's t (Steel and Torrie, 1960).

The guard cell sizes for the same 10 species of Delphinium measured in the pollen grain size study were determined. Dried leaves of herbarium specimens were soaked in water and detergent for 15 minutes and the lower epidermis was then peeled from the leaf and mounted in water on a micro slide. The long axis of the longer guard cell of each stomate was measured using a calibrated ocular micrometer at a magnification of 430 diameters. Ten measurements were made from each leaf. One leaf from each of 6 plants of each species was used for measurements.

The same statistical methods used in analyzing the pollen grain data were used to analyze the guard cell data except there was an equal number of replications, 6, in the analysis of variance.

Serological Studies

Mature leaves from many flowering Delphinium sp. plants were picked in the field. As soon as possible the leaves were brought to the laboratory and washed in running tap water for at least 1 hour. The petioles were clipped from the blades and the blades were blotted dry. The leaves were squeezed using a Carver Extractor (Creel, 1964). About 6 ml of

extracted crude sap was placed in vials and frozen at -20 C immediately after extraction. Caution was taken to exclude from squeezing dried leaves or leaves appearing to be diseased. In the first trial, sap from D. bicolor, D. andersonii and D. occidentale was obtained. Sap from 2 populations each of D. bicolor and D. occidentale and from 1 population of D. geyeri was obtained for the second trial.

Purification of the crude sap for injection into rabbits, injection schedules, bleeding methods and gel-diffusion techniques followed the procedures described by Creel (1964) and Creel et al. (1965) for the first trial. One rabbit was used for each antiserum. Antisera were built for D. bicolor, D. andersonii and D. occidentale.

For the second trial crude sap to be used as antigen material was purified using ammonium sulfate saturation procedures (Colowick and Kaplan, 1955). The crude extract was thawed and centrifuged for 10 minutes at 20,000 xg. 0.243 g of ammonium sulfate and 0.1 ml of 1 per cent protamine sulfate for each ml of supernatant were added to the supernatant. This procedure was carried out in a cold room at about 2 C. After 1/2 hour of stirring in the cold room the suspension was again centrifuged at 10,000 xg for 5 minutes. This time the precipitate was taken up in 2 ml of 2.5 per cent sodium chloride solution buffered at pH 7.0. The buffer contained 0.19 g of monobasic potassium phosphate and 0.75 g of dibasic sodium phosphate with enough water added to make 1 liter of buffer (Johnson and Fairbrothers, 1965). This suspension was dialized overnight in the cold room against the phosphate buffer previously described. The partly purified protein solution consisted of protein

insoluble between the 40-60 per cent saturation point of ammonium sulfate. After dialysing, the amount of protein in the solution was determined using the technique of Lowry et al. (1951). The remainder of the solution was diluted with the buffer so that it contained 1 mg of protein per ml of solution. This material was injected into the rabbit as the antigen source. Antisera were built against antigens from Delphinium bicolor, D. geyeri and D. occidentale using 1 rabbit for each antiserum. The rabbits were injected with 1 mg of protein plus an equal volume of Freund's Complete Adjuvant, subcutaneously in the left and right lumbar regions and in back of the front shoulders. At each injection equal amounts of material were injected into each of the locations. Injections were given weekly for 5 weeks. Two weeks after the last injection the rabbits were bled totally by heart puncture.

Serological tests were made using the modified Ouchterlony techniques of Creel (1964) and Creel et al. (1965). Petri dishes were dipped in a 1 per cent (w/v) solution of Formvar in chloroform. Six ml of 1 per cent # 2 ionager were pipetted into petri dishes 5 cm in diameter. After standing several hours, wells were cut in the gel using a cork borer and a template designed after a pattern used by Johnson and Fairbrothers (1965). The pattern consists of a center well for the antiserum and 4 antigen wells spaced equally apart and 5 mm from the periphery of the antiserum well. All wells are 5 mm in diameter. The antigen was prepared by centrifuging the thawed crude sap for 10 minutes at 20,000 xg. The wells were filled with the appropriate antigen and antiserum using micropipettes and allowed to stand at room temperature for 48 hours. Afterward the serological

plates were washed in water and 0.9 per cent saline solution and the gels were placed on glass slides. The gels were then dried at room temperature and stained with a 0.5 per cent solution of amino schwartz. (Jutila, 1966).

Electrophoresis Studies

Amonium sulfate precipitated proteins from leaf extracts of Delphinium bicolor, D. geyeri and D. occidentale were compared by the use of electrophoresis. The leaf extracts were purified by the techniques described in the second trial of the serological methods section. Lowry's technique (Lowry et al., 1951) was used to determine the amount of protein in the solution. The disc-gels were prepared according to the directions of Davis (1964) except the small pore solution was made with 1.52 parts of working solution A, 3.05 parts of working solution C and 0.88 parts of water. The gel had a pH of 8.4. Fifty micrograms of protein were used for each electrophoresis tube. Eight samples, 4 treatments with 2 replications, were electrophoresised 30 minutes at 5 ma per tube. After electrophoresing the gels were stained in 0.5 per cent amino schwarz in 9:1 methanol, acetic acid for 1 hour and then destained in 7 per cent acetic acid using 8.5 ma per tube for 6 hours. After destaining the banding in the gels was analyzed with a Joyce Chromoscan Densitometer.

RESULTS

Morphological Taxonomy

There are 7 species of Delphinium known to be native in Montana. They are D. andersonii, D. bicolor, D. burkei, D. glaucescens, D. nelsoni, D. nuttallianum and D. occidentale. There are 3 species, D. brownii, D. depauperatum and D. geyeri found in states bordering Montana that may be present in Montana. D. ajacis is a cultivated species existing as an escape in Montana.

Single distinctive characteristics that separate one species of Delphinium from another rarely exist. Those characteristics which are measurable do not usually make suitable key characters because the dimensions of a given character often overlap from species to species. Separation of the Montana delphiniums is based primarily on the root systems, the degree of notching of the lower petal blades, the shapes of the inflorescences, the heights and diameters of the stems, the amounts of leaf blade dissection and the types of stem-coverings.

There are 3 types of root systems. They are the globose cluster typified by D. nuttallianum (Figure 4A and B), the fleshy to tubular fascicle represented by D. bicolor (Figure 3C), and the extensive, woody caudex exemplified by D. andersonii (Figure 2A). The stems of delphiniums are fistulose as in D. occidentale (Figure 1A) or non-fistulose as are those of D. nuttallianum (Figure 4B). The stems can be glabrous, pubescent or glaucous. Some species of Delphinium have spreading hairs, and others have appressed hairs. D. depauperatum has hairs which are basally swollen. The leaf blade may be finely dissected so that the ultimate segments are

numerous and not over 2 mm wide as is illustrated by D. geyeri (Figure 6A). The leaf blade of D. nelsoni (Figure 3A), for example, is several times dissected but not as extensively dissected as the leaf blade of D. geyeri. D. occidentale (Figure 1A) is an example of a species having a cuneate leaf blade with 5-7 broad lobes that are only slightly dissected.

The inflorescence is primarily one of 2 types. It can be spikelike with the flowers borne tight to the rachis so that the inflorescence is about the same diameter throughout its entire length (Figure 1A) as illustrated by D. occidentale. The other type of inflorescence is typified by D. bicolor (Figure 3C). The flowers are borne on spreading pedicels with the pedicels at the bottom of the inflorescence being longer and more spreading than those at the tip of the inflorescence. The notching at the tip of the lower petal can be 1/4 to 1/2 the length of the blade (Figure 3B) or very shallow to erose (Figure 3D).

Table I gives a summary of the characters measured. The key and the species descriptions indicate the final results of the morphological study. Dots on the maps indicate those counties of Montana which have Delphinium specimens represented in the herbaria at the University of Montana or Montana State University.

Table I Measurements from herbarium specimens of various characters of Delphinium species occurring or expected to occur in Montana.

	Stem height	Lower petiole length	Flower number	Flower length	Lower pedicel length	Sepal spur length	Lower sepal length	Notch length	Follicle length	Seed length
	cm	cm		mm	mm	mm	mm	mm	mm	mm
D. occidentale	100-300	4-20	20-90	< 25	< 15	10	10-15	< 2	12-20	1.5-3.0
D. brownii										
D. glaucescens	20-90	10-20	15-50	< 25	10-15	8-12	12	0-3	15	1.5
D. geyeri	25-70	6-12	10-30	< 25	10-20	10-15	10-15	0-3	15	2.0-3.5
D. andersonii	25-60	6-15	10-30	20-30	20-30	15-20	10-15	2-4	14-25	2.5
D. bicolor	10-50	2-10	5-20	20-30	10-80	15-20	12-17	< 2	10-17	2.0-2.5
D. nelsoni	15-30	2-10	5-20	20-30	10-40	12-20	12-17	> 2	10-15	2.0-2.5
D. nuttallianum	10-50	2-12	1-8	< 30	5-40	10-25	8-15	> 2	10-15	1.0-1.5
D. depauperatum	15-75	3-10	2-15	< 30	< 15	8-15	9-15	2	15-20	2.0-2.5
D. burkei	25-70	4-10	10-20	< 25	< 10	10-15	8-12	3	10-15	1.5

Key to the species of *Delphinium* in Montana

A Plants annual; 1-carpellate. — *D. ajacis*

A Plants perennial; 3-carpellate.

B Inflorescence spikelike, appearing as an elongate narrow (usually less than 4 cm wide) cylinder; sepals cupped, not flaring.

C Plants mostly over 1 m tall; major segments of all leaves cuneate.

D Follicles pubescent over entire exposed surfaces. — *D. occidentale*

D Follicles pubescent only along the sutures; rare, if occurring at all in Montana. — *D. brownii*

@ Plants less than 1 m tall; only the major segments of the basal leaves, if any, cuneate.

E Leaves all of one form (finely dissected); stem glaucous, somewhat fistulose and often reddish; flower color dull; root system topped by a woody caudex. — *D. glaucescens*

E Leaves dimorphic, the lower leaves with broad cuneate segments, the upper leaves finely dissected; stems rarely glaucous, fistulose or reddish; flowers bright; roots forming a small fleshy cluster; rare in Montana. — *D. burkei*

B Inflorescence not as above but open, often being wider at the base than the top, often over 4 cm wide; sepals usually flaring but if cupped the root system is not extensive.

F Plants densely pubescent, having a grayish cast; roots and 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 but if densely pubescent the root system is not extensive; ultimate leaf segments over 1 mm wide.

G Plants with a root system topped with a woody caudex; leaf blades all displayed at about the same height; lower petals notched over 1/3 of their length. D. andersonii

G Plants without a woody caudex; leaf blades spaced at different heights on the stem; if the root system is somewhat extensive the lower petals will be notched less than 1/4 of their length.

H Root system forming a globose cluster; sepal spur nearly straight and slender.

I Sepals cupped; inflorescence somewhat spikelike; stem hairs spreading; rare in Montana. D. depauperatum

I Sepals flaring; inflorescence not spikelike; stem hairs appressed downward. D. nuttallianum

J Stems weak, often procumbent; growing in moist alpine environments. High Mountain Form

J Stems sturdy, upright; growing in dry environments Low Land Form

H Root system fibrous or fleshy; sepal spurs curved and stout.

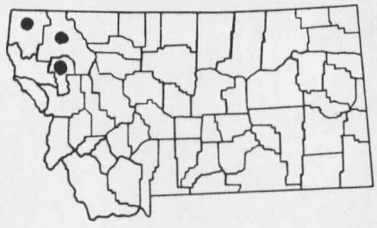
K Lower petals notched less than 1/4 the length of the blade; stem hairs spreading at right angles to the stem. D. bicolor

K Lower petals notched over 1/4 the length of the blade; stem hairs spreading to appressed. D. nelsoni

Delphinium ajacis L. "Rocket Larkspur"

Delphinium ajacis L., Sp. Pl. 531. 1753.
Delphinium ajacis f. alba Cheney., Rhodora. 27:142. 1925.
For full synonymy of D. ajacis see Huth., 1895 375.

Annual plants, 30-70 cm tall, arising from slender tap roots; stems single, green, slender, the upper part of the stem pubescent; leaves cauline, borne on short petioles; blade finely dissected, the ultimate segments 1 mm wide; inflorescence often branched, with 5-15 loosely arranged flowers borne on ascending pedicels 5-10 mm long; flowers purplish blue; sepals flaring, spur 12-20 mm long, slender and straight; lateral and lower sepals about equal, 10 mm long; petals pale to purplish blue; lower petals not notched; follicle 1, about 5-8 mm long.



Delphinium ajacis is an escape from cultivation and flowers in July and August. (Figure 6B)

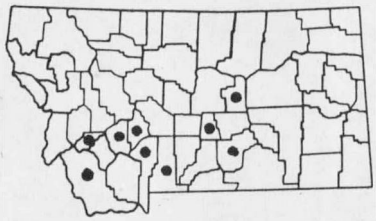
Representative collections: Bachert 308, Whitefish, Flathead Co.; Blankenship 474, St. Ignatius, Lake Co.

Delphinium andersonii Rydb. "Anderson's Larkspur"

Delphinium andersonii Gray, Bot. Gaz. 12:53. 1887, based on C. L. Anderson 172, near Carson City, Nev. 1865.
Delphinium tricorne var. andersonii Huth, Helios 10(Abh.): 37. 1892.
Delphinium cognatum Greene, Pitt. 3:14. 1896.
Delphinium bicolor var. cognatum Davis, Minn. Bot. Stud. 2:438. 1900.
Delphinium zylorrhizum Rydb., Bull. Torrey Club 39:321. 1912
Delphinium megacarpum Nels. & Macbr., Bot. Gaz. 55:373. 1913.
Delphinastrum andersonii Nieuwl., Am. Midl. Nat. 3:172. 1914.
Delphinium andersonii ssp. cognatum Davids., ex Ewan, U. Colo. Stud. Ser. D 2:195. 1945.
Delphinium andersonii var. cognatum R. J. Davis. Madrono 11:144.1951.

Delphinium nuttallianum var. pilosum C. L. Hitchc., Vas. Pl. of the Pac. NW. Hitchcock, Cronquist, Ownbey, Thompson. 17:359. pa 2. 1964.

Perennial plants, 25-60 cm tall, arising from an extensive woody, caudex; stems 1-several, straw-colored, non-fistulose, smooth and hard, glabrous to pubescent with appressed hairs; leaves borne on petioles 6-15 cm long, the lower petioles longer than the upper ones, such that the blades are displayed at 1 level; blades finely dissected, waxy beneath, the ultimate segments 1-2 mm wide; inflorescence simple to compound below with 10 or more loosely arranged flowers borne on straight ascending pedicels, the lower pedicels being 20-30 mm long; flowers purplish blue, large, over 25 mm long; sepals flaring, spur 15-20 mm long; lateral and lower sepals somewhat unequal, 13-15 mm long; upper petals yellowish with bluish tips; lower petals large, blue, notched more than 1/3 the length of the blade; follicles pubescent when young, becoming glabrous at maturity, 15-20 mm long.



Delphinium andersonii flowers in late June and July. It occurs in dry sandy locales and grows in colonies. D. andersonii appears to be closely related to D. bicolor. The habitat, flowering period, colonizing habit, deeply notched lower petals and more extensive roots distinguish it from D. bicolor (Figure 2A). These plants have been called D. nuttallianum var. pilosum by Hitchcock et al. (1964).

A colony of this species in Beaverhead County (Figure 2B, Booth # 65163) has bigger flowers and appressed stem hairs not characteristic

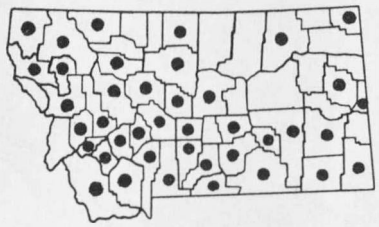
of other D. andersonii colonies.

Representative collections: Booth 65163, 10 miles S. of Brenner, Beaverhead Co.; Blankenship 6/1/1901, Lombard, Broadwater Co.; Blankenship 5/18/1906, Anaconda, Deer Lodge Co.; Booth 65176, 5 m. W. of Three Forks, Gallatin Co.; Blankenship 656, Logan, Gallatin Co.; Booth 604, 8 m. S. E. of Billings, Yellowstone Co.; Hawkins 136, White Beaver Cr.; Booth 6/17/1957, 8 m. N. E. of Ryegate, Golden Valley Co.

Delphinium bicolor, Nutt. "Low Larkspur"

Delphinium bicolor Nutt., Journal Acad. Phila. 7:10. 1834, based on Wyeth, dry hills near Flat-Head or Sailish Rivers, probably western Montana.
Delphinium bicolor var. montanease Rydb., Mem. N. Y. Bot. Gard. 1:157. 1900.
Plectrornis bicolor montanense Lunell, Am. Midl. Nat. 4:362. 1916.
Delphinium bicolor f. montanense Ewan, U. Colo. Stud. Ser. D 2:123. 1945.

Perennial plants, 15-50 cm tall but most commonly 20-36 cm, arising from a fleshy to fibrous root, which can be extensive; stems usually single, non-fistulose, green to straw-colored, pubescent with spreading hairs at least on the upper half of the stem; leaves few, lowest blades orbicular, borne on petioles 2-10 cm long; blades finely dissected, the ultimate segments usually 2 mm wide; inflorescences simple, loose with 5-20 flowers borne on ascending pedicels 1-8 cm long; flowers deep purple, large, usually over 25 mm long; sepals flaring, spur 15-20 mm long, stout, the lower sepals longer than the lateral sepals, usually 15 mm long; upper petals colorless with purple veins; lower petals large, 8-10 mm long with a shallow notch less than 1/4 the blade length; follicles 10-17 mm long.



Delphinium bicolor flowers in May and June. It grows in moist

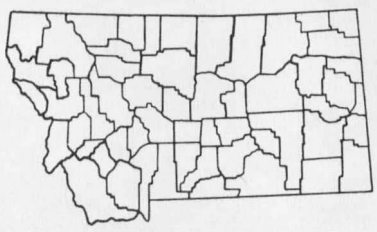
Mountain meadows, fields and roadside ditches. It is the most common delphinium of low stature in Montana. D. bicolor is variable and is closely related to D. nelsoni, D. andersonii and D. nuttallianum. D. bicolor can be separated from D. nuttallianum by its non-globose root, shallowly notched lower petals and spreading stem hairs. The shallowly notched lower petals are the only constant characteristic separating D. bicolor from D. nelsoni. Besides the notching difference in the lower petal, D. andersonii has a more extensive root system, later flowering date, colonizing habit and occurs in a drier habitat. (Figure 3C)

Representative collections: Syblon 524, Roundup, Musselshell Co.; Hendrickson 24, Hamilton, Ravalli Co.; Sawyer 468, Hyalite Canyon, Gallatin Co.; Gilroy 14, Missoula, Missoula Co.; Booth 59266a, Glendive, Dawson Co.; Booth 5515, Harlowton, Wheatland Co.; Booth 592902, Plentywood, Sheridan Co.; Mussehl & Zapatka 3, Hilger, Fergus Co.; Hitchcock 1545, 5 m. E. of Perma, Sanders Co.; Ryerson 504, Norris, Madison Co.; Miller 60, 2 m. E. of Stanford, Judith Basin Co.; Booth 52121, 15 m. N. of Helena, Lewis & Clark Co.; Booth 59223, 15 m. N. W. Broadus, Powder River Co.; Booth 4/22/1962, 4 m W. of Deer Lodge, Powell Co.; Hunter 5/11/1959, Culbertson, Roosevelt Co.; Baker 5/24/1959, 3 m. N. of Reed Point; Dolan 45, 30 m. S. of Havre, Hill Co.; Torgerson 32, Billings, Yellowstone Co.; Sawyer 469, Gravelly Range.

Delphinium brownii Rydb. "Brown's Larkspur"

Delphinium brownii Rydb., Bull. Torr. Bot. Club. 29:148. 1902, based on A. Brown 13 VIII, Banff, Alberta 1893.
Delphinium canmorense Rydb., Fl. Rocky Mts. ed. 1. 312 1061 1917.

Perennial plants, 1-3 m tall, from an extensive woody caudex; stem fistulose and somewhat glaucous; leaves cauline, borne on long petioles with cuneate blade; inflorescence spikelike with many small blue flowers; sepals cupped, 9-11 mm long;



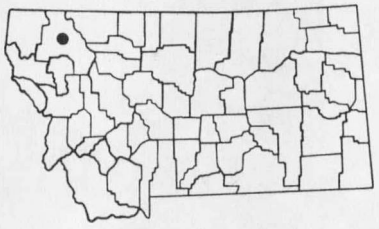
follicles 12-14 mm long, pubescent along the sutures of the follicles.

Delphinium brownii has not been found in Montana, but could be expected in the northcentral part of this state. It is found in Alberta, Saskatchewan and Alaska where it grows in stands of aspen and willow. It is referred to by Budd (1952) as D. scopulorum Gray and by Hulten (1944) and Moss (1959) as D. glaucum S. Wats.

Delphinium burkei Greene "Burke's Larkspur"

Delphinium burkei Greene, Erythea 2:183. 1894, based on J. Burke from Snake River, Ida. 1844.
Delphinium simplex Dougl., ex Hook. Fl. Bor. Am. 1:25. 1829.
Delphinium simplex var. distichiflorum Hook., Lond. Journ. Bot. 6:67. 1847.
Delphinium distichum Geyer, ex Hook. op. cit. 68 as a synonym.
Delphinium azureum ssp. distichum Huth, Engl. Bot. Jahrb. 20:344. 1895.
Delphinium azureum ssp. simplex Huth, Engl. Bot. Jahrb. 20:344. 1895.
Delphinastrum distichum Nieuwl., Am. Midl. Nat. 3:172. 1914.
Delphinium strictum var. distichiflorum St. John, Fl. S. E. Wash. 2 ed. 153. 1937.
Delphinium burkei ssp. distichiflorum Ewan, U. Colo. Stud. Ser. D. 2:172. 1945.

Perennial plants, 25-70 cm tall, arising from a small fleshy cluster of roots; stems single, greenish, non-fistulose, with at least the upper part of the stem pubescent with appressed hairs; leaves strongly dimorphic, lowest leaves cuneate, not finely dissected and borne on petioles 4-10 cm long, the upper cauline leaves finely dissected, the ultimate segments linear, not over 1-2 mm wide, borne on very short petioles; blades slightly pubescent; inflorescence simple



except the lower most portion, spikelike, forming a narrow cylinder of 10-20 flowers borne on strongly ascending pedicels less than 10 mm long; flowers dark blue, small, less than 25 mm long; sepals cupped, spur 10-15 mm long, narrow and straight; lateral and lower sepals about the same size, less than 12 mm long; upper petals colorless except the bluish tips; lower petals the same color as sepals, and deeply notched to at least 2/5 of the blade; follicles pubescent, 10-15 mm long at maturity.

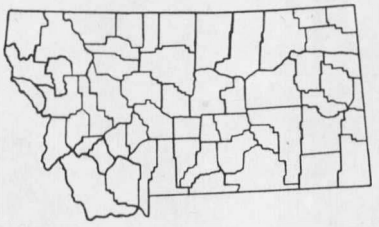
Delphinium burkei flowers from late May to early July. It is found in sagebrush plains, seepage areas and sandy stream banks. D. burkei has been rarely collected in northwest Montana. D. burkei is closely related to D. depauperatum and can be separated from it by the strongly dimorphic leaves. (Figure 5C)

Representative collections: Hitchcock & Muhlich 21588, Status Pass, Yakima Co. Wash.; Hitchcock & Muhlich 20888, 5 m. S. W. of Teanaway Jct. Kittitas Co. Wash.; Oswald 1257, Willow Flats, Teton Co., Wyo.; Harvey 7/30/52, Glacier Nat. Park.

Delphinium depauperatum Nutt. "Slim Larkspur"

Delphinium depauperatum Nutt., T. & G. Fl. N. Am. 1:33. 1833, based on T. Nuttall 1834, from the Blue Mts. N. E. Ore.
Delphinium pauciflorum var. depauperatum Gray, Bot. Gaz. 12:54. 1887.
Delphinium tricorne var. depauperatum Huth, Helios 10(Abh.);37. 1892.
Delphinium diversifolium Greene, Pitt. 3:93. 1896.
Delphinium scopulorum var. diversifolium Davis, Min. Bot. Stud. 2:449. 1900.
Delphinium diversicolor Rydb., Bull. Torrey Club 29:149. 1902.
Delphinium cyanoreios Piper, Contr. U. S. Nat. Herb. 16:202. 1913.
Delphinium diversifolium ssp. harneyense Ewan. U. Colo. Stud. Ser. D. 2:163. 1945.
Delphinium cyanoreios f. wallowense Ewan. U. Colo. Study Ser. D. 2:163. 1945.
Delphinium cyanoreios f. idahoense Ewan, U. Colo. Study Ser. D. 2:164. 1945.

Perennial plants, 15-75 cm tall, arising from a small globose clump of fleshy roots; stems single, greenish to reddish, weak, non-fistulose, pubescent at least on the upper half of the stem with spreading, basally swollen hairs; leaves cauline, the lowest ones long petioled, (3-10 cm), less finely dissected than the upper leaves which are borne on short petioles, finely dissected, the ultimate segments linear; inflorescence simple, somewhat spikelike, with the 2-15 flowers borne on ascending pedicels less than 15 mm long; rachis and pedicels densely pubescent with spreading, basally swollen hairs; flowers purplish, less than 30 mm long; sepals slightly cupped, spur 12-20 mm long, narrow and straight; lateral and lower sepals about the same size, less than 15 mm long; upper petals white with purple veins; lower petals same color as the sepals, notched at least 1/2 the length of the blade; follicles pubescent, 15-20 mm long at maturity.



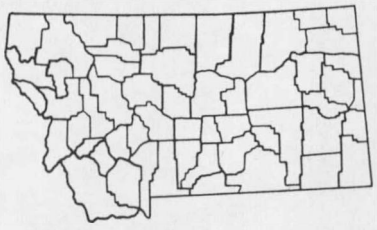
Delphinium depauperatum flowers from early June through July. It grows in sandy sage brush plains or dry meadowland. D. depauperatum is rarely if at all present in Montana, but might be expected to occur in the northwestern part of the state. It is closely related to D. burkei and D. nuttallianum. (Figure 5A).

Representative collections: Hitchcock & Muhlich 20837, 3 m. N. of Cascade, Valley Co., Idaho; Hitchcock & Muhlich 21356, 10 m. N of Ketchum, Blaine Co. Idaho; Hitchcock & Muhlich 20835, 21 m. W. of Lowman, Boise Co., Idaho; Hitchcock & Muhlich 20908, 1/2 m. S. W. of King Mt., Harney Co., Ore.

Delphinium geyeri Greene "Geyer's Larkspur"

Delphinium geyeri Greene, Erythea 2:189. 1894, based on C. Geyer 163 from slopes of undulating plains between Kansas and Platte Rivers. Delphinium viscidum Rydb., Bull. Torr. Bot. Club. 39:322. 1912. Delphinium geyeri f. viscidum (Rydb.) Ewan, U. Colo. Stud. Ser. D 2:177. 1945.

Perennial plants, 25-70 cm tall, but usually 40-50 cm tall, arising from a long, woody caudex; stems 1-several, greenish-gray, non-fistulose, covered with a grayish appressed pubescence; leaves cauline, borne on long petioles, the lower ones being 6-12 cm long; blades dissected into narrow, linear ultimate segments less than 2 mm wide, densely pubescent with grayish appressed hairs on both surfaces; inflorescence simple except the lower most portion, more or less spikelike, 10-30 flowers borne on strongly ascending pedicels 1-2 cm long; flowers grayish blue, 25 mm or less long; sepals flaring, spur 10-15 mm long, stout and nearly straight, lateral and lower sepals about the same size, 10-15 mm long; upper petals white with bluish tips; lower petals same color as sepals, deeply notched to scarcely notched even within flowers of the same plant; young follicles pubescent, 15 mm long at maturity.



Delphinium geyeri flowers in June and July. It is found in moist to dry rangeland, commonly growing in colonies. D. geyeri is common in Wyoming but there are no Montana specimens in the Montana State University or University of Montana herbaria. D. geyeri is readily distinguished from other species of Delphinium treated in this investigation by the combination of root, stem leaf and inflorescence characters as well as its grayish-green

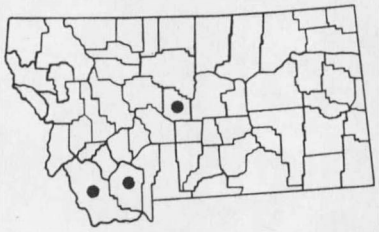
cast. The flaring sepals serve to separate D. geyeri from other species with spikelike inflorescences. (Figure 6A)

Representative collections: Booth 66021, Thermopolis, Wyo.; E. Nelson 3354, Laramie Hills, Wyo.; Gverton 408x, Cheyenne, Wyo.; Metcalf & Yager 7/3/1950, 10 m. E. of Cody, Wyo.; Ehlers 7/13/1922, Golden, Jefferson Co., Colo.; Ownbey 1385, Veta Pass, Costilla Co., Colo.; A. Nelson 9769, Mt. Bass, Hot Sulphur Springs, Colo.

Delphinium glaucescens Rydb. "Glaucous Larkspur"

Delphinium glaucescens Rydb., Mem. N. Y. Bot. Gard. 1:155. 1900, based on Rydberg and Bessey 4078, Electric Peak, Yellowstone Park. Delphinium glaucescens var. multicaule Rydb., Mem. N. Y. Bot. Gard. 1:156. 1900.

Perennial plants, 20-90 cm tall but usually 40-60 cm tall, arising from a tough, woody caudex; stems 1-several, glaucous, straw to reddish colored, fistulose, glabrous to sparsely pubescent; leaves borne on long petioles, the lower petioles being the longest (10-20 cm) so that the blades are displayed at about the same level, blades may be finely dissected, but usually the ultimate segments of the lower leaves are 5 mm or more wide, sparsely pubescent on both surfaces; inflorescence simple except the lower most portion, spikelike with 15-50 somewhat loosely arranged flowers borne on strongly ascending, pubescent pedicels 10-15 mm long; flowers dull blue, small, less than 25 mm long; sepals cupped, spur 8-12 mm long, short and stout, curving downward at the tips; lateral and lower sepals about the same size, less than 12 mm long; upper petals white with purple veins; lower petals small, of the same color as the sepals and deeply notched to scarcely notched even within flowers of the same plant; young



follicle pubescent, becoming glabrous at maturity.

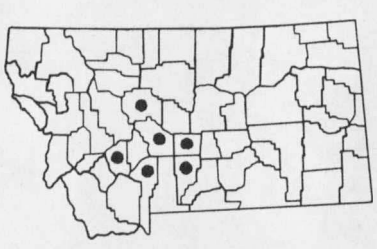
Delphinium glaucescens flowers from late June to early August. It is found in moist open parks, mountain talus slopes, dry sandy meadows and open sagebrush areas, in southwestern Montana. It is more closely related to D. occidentale than to any other Delphinium included in this study. (Figure 1B)

Representative collections: Bessey & Rydberg 4078, Electric Peak, Mont.; Rydberg & Bessey 4071, Cedar Mt, Mont.; Jamison 7/27/51, Vigilante Exp. Stat., Madison Co.; Hitchcock 15801, 12 m. S of Dillon, Beaverhead Co.; Hitchcock 20919, Gravelly Range, Madison Co.; Hitchcock 20920, 2.5 m. E. of Ruby River, Madison Co.; Wolstad GRW-11, 3 m. E. of Staudemyers, Beaverhead Co.; Jones 7/14/1908, Lima; Hitchcock & Muhlich 21128, Manns Lake, Harney Co., Ore.

Delphinium nelsoni Greene "Nelson's Larkspur"

Delphinium nelsoni Greene, Pitt. 3:92. 1896, based on A. Nelson 48, from mouth of Telephone Canyon, Wyo.
Delphinium menziesii sensu. Gray, Acad. Nat. Sci. Phila. 15:57. 1863.
Delphinium bicolor var. nelsoni (Greene) Davis, Op. cit. 438. 1900.
Delphinium dumetorum Greene, Pl. Bakerianae 3:4. 1901.
Delphinastrum nelsoni (Greene) Nieuwl., Am. Midl. Nat. 3L172. 1914.
Delphinium nelsoni f. Dunetorum (Greene) Ewan, U. Colo. Stud. Ser. D 2:129. 1945.

Perennial plants, 15-30 cm tall, arising from a fleshy to fibrous root; stem single, green to straw-colored, non-fistulose, pubescent with spreading or appressed hairs; leaves few, the lowest ones orbicular in outline and borne on petioles 2-10 cm long, the blades finely dissected, but the ultimate segments usually 2 mm wide; inflorescence simple, loose, 5-20 flowers borne on pedicels 1-4 cm long, the lowest pedicels spreading; flowers purple to blue; sepals flaring, spur 12-20 mm long, stout, lower



sepals longer than the lateral sepals; upper petals colorless with purple veins; lower petals purple, notched over 1/4 the length of the blade; follicles 10-15 mm long.

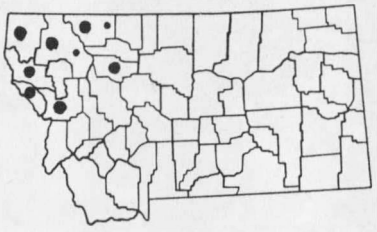
Delphinium nelsoni flowers in May and June. It occurs in moist mountain meadows and roadsides, in the southcentral counties of Montana. It is more common in Wyoming. D. nelsoni is very closely related to D. bicolor which it resembles except for the more deeply notched lower petals. (Figure 3A)

Representative collections: Booth 6/3/1959, 10 m. W. of Great Falls, Cascade Co.; Booth 6/5/1959, 2 m. S. of White Sulphur Springs, Meagher Co.; Cotner 6/20/1939, Horse Shoe Hills, Gallatin Co.; Booth 6/10/1959, 3 m. N. of Whitehall, Jefferson Co.; Bell 6/18/1956, Harlowton, Wheatland Co.; Oswald 1042, Teton Co., Wyo.; Hill 389, Laramie Hills, Wyoming.

Delphinium nuttallianum Pritz. "Nuttall's Larkspur"

Delphinium pauciflorum Nutt., T. & G. Fl. N. Am. 1:33. 1838, based on T. Nuttall from Blue Mts. N. E. Ore.
Delphinium nuttallianum Pritz., ex Walpers. Rep. 2:744. 1843.
Delphinium helleri Rydb., Bull. Torrey Club. 39:321. 1912.
Delphinastrum nuttallianum Nieuwl., Am. Midl. Nat. 3:172. 1914.
Delphinium bicolor f. helleri Ewan, U. Color. Stud. Ser. D. 2:121. 1945.

Perennial plants, 10-50 cm tall, arising from a globose cluster of fleshy roots; stem usually single, green to straw-colored, weak, non-fistulose, glabrous to pubescent, the hairs appressed; lower cauline leaves borne on long petioles, (2-12), ultimate segments lobed, numerous and over 2 mm wide; the upper leaves borne on short petioles, the ultimate segments being linear and few in number, 3-5; inflorescence simple,



loose, with 1-8 flowers, borne on bow-shaped ascending pedicels 1/2-4 cm long; rachis and pedicels may have basally swollen hairs; flowers blue, less than 30 mm long; sepals flaring, spur 10-25 mm long, slender, straight to curved at the tips; lateral and lower sepals about the same size, less than 15 mm long; upper petals colorless; lower petals varying from colorless with purple veins to the same color as the sepals, notched more than 1/4 the length of the blade; follicles 10-15 mm long at maturity.

Delphinium nuttallianum flowers from late June through August. It is found in moist mountain meadows near streams or in dry sagebrush plains. There seem to be 2 forms, small weak-stemmed plants found in moist mountain meadows of Glacier National Park indicated on the map by small dots and more robust plants of dry sage brush plains indicated on the map by large dots. (Figure 4A and B)

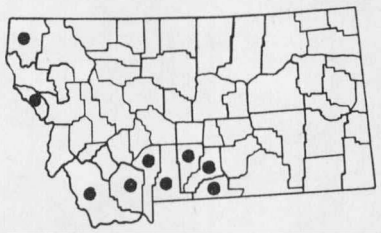
Delphinium nuttallianum is closely related to D. burkei, D. bicolor and D. nelsoni. D. nuttallianum can be distinguished from D. burkei by its more flaring sepals, and its more spreading inflorscence. The globose roots, appressed hairs and the deeply divided lower petals separated D. nuttallianum from D. bicolor. The globose roots separate D. nuttallianum from D. nelsoni.

Representative collections: High Mountain Form; Sawyer 482, near Sperry Chalet, Glacier Nat. Park; Sawyer 466, near Avalanche Lake, Glacier Nat. Park; Unbach 816, Little St. Mary's Lakes, Glacier Nat. Park; Harvey 6486, Logan Pass, Glacier Nat. Park; Roeder 268, Old Faithful, Yellowstone Nat. Park. Low Land Form: Booth 6312, 8 m. N. W. of Missoula, Missoula Co.; Hitchcock 2242, 4 m. E. of Thompson Falls, Sanders Co.; Schmautx JES-319, Libby Ranger Sta., Lincoln Co.; Booth 6/14/1952, 3 m. W. of E. gate, Glacier Nat. Park; Booth 63193, Bynum, Teton Co.; Harvey 4914, Big Prairie, Glacier Nat. Park.

Delphinium occidentale (Wats.) Wats. "Tall Larkspur"

Delphinium elatum var. occidentale Wats., Bot. King. Exp. 11. 1871, S. Watson 38, Wasatch Mts., Utah.
Delphinium occidentale Wats., Bot. Calif. 2:428. 1880.
Delphinium occidentale var. reticulatum A. Nels., Bull. Torrey Club. 27:261. 1900.
Delphinium cucullatum A. Nels., Bull. Torrey Club. 27:262. 1900.
Delphinium multiflorum Rydb., Bull. Torrey Club. 29:147. 1902.
Delphinium reticulatum Rydb., Bull. Torrey Club. 33:140. 1906.
Delphinium abietorum Tidestr., Proc. Biol. Soc, Wash. 27:61. 1914.
Delphinastrum occidentale Nieuwl., Am. Midl. Nat. 3:172. 1914.
Delphinium scopulorum ssp. occidentale Abrams, III Fl. Pac. St. 2:187. 1944.
Delphinium occidentale ssp. cucullatum Ewan, U. Colo, Stud. Ser. D. 2:138. 1945.
Delphinium occidentale var. cucullatum R. J. Davis, Madrono. 11:144. 1951.
Delphinium occidentale var. griseum St. John, Leafl. West. Bot. 9:96. 1960.

Perennial plants, 1-3 m tall, arising from a large woody caudex; stems 1-several, green to yellowish, fistulose, glabrous below the inflorescence and slightly glaucous; leaves all cauline, borne on petioles 4-20 cm long; blades 6-12 cm wide, divided into 5-7 major cuneate lobes; inflorescence simple except lowermost portion, spikelike, cylindraceous, over 20 cm long with 20-100 flowers borne on ascending pedicels less than 15 mm long; flowers blue to white with bluish streaks, small, less than 25 mm long; sepals cupped, spur 10 mm long, stout, lateral and lower sepals about the same length, 10-15 mm long; upper petals bluish or white with bluish tips, lower petals blue, shallowly notched; mature follicles 12-20 mm long, pubescent throughout. (Figure 1A)



Delphinium occidentale flowers in July and August and occurs in moist mountain or montane meadows. D. occidentale has been split into several species, subspecies and varieties by several authors. It is closely related to D. brownii but can be separated from it by its completely pubescent follicles.

Representative collections: Blankenship 8/19/1896, Bridger Cr. Basin, Gallatin Co.; Hitchcock & Muhlich 13405, 1 m. S. of Independence, Stillwater Co.; Booth 3807, Livingston, Park Co.; Sawyer 480, Bear Canyon, Gallatin Co.; Sawyer 478, Hyalite Canyon, Gallatin Co.; Booth 61672, Bull Lake, Lincoln Co.; Hitchcock 1652, 1 m. E. of Boulder River, Sweetgrass Co.; Booth 52422, Red Rock Pass, Beaverhead Co.; Booth 3807, Livingston, Park Co.; Booth 6056, Highwood Mountains, Judith Basin Co.; Jones 8/29/1902, Bridger Mts., Gallatin Co.

Pollen Grain and Guard Cell Size Studies

Significant differences in the pollen grain lengths of the 10 Delphinium species are indicated by analysis of variance at the 5 per cent level of significance. Duncan's New Multiple Range Test at the 5 per cent level of significance and the 95 per cent confidence intervals (Figure 7) give evidence that there are no significant differences between the pollen grain lengths of D. occidentale, both forms of D. nuttallianum and D. depauperatum. Similarly there are no significant differences between D. geyeri, D. nelsoni, D. bicolor and D. glaucescens. D. burkei is intermediate between the 2 groups. D. andersonii and D. ajacis have the longest pollen grains, and they differ from each other and all other species.

Guard cell sizes of the 10 Delphinium species differ significantly according to analysis of variance at the 5 per cent level of significance.

FIGURE I

A *Delphinium occidentale*. The identifying characters are the woody caudex; fistulose stem; 5-7 cuneate segments per leaf; spikelike inflorescence and cupped sepals.

B *Delphinium glaucescens*. The identifying characters are the woody caudex; fistulose stem, finely dissected leaf blade and spikelike inflorescence. The sepals of this specimen appear more flaring than sepals of this species normally are.



A

HERBARIUM OF MONTANA STATE COLLEGE
FLORA OF MONTANA

Paul L. Sawyer



B

FLORA OF OREGON

21128 Delphinium andersonii Gray

HARNEY CO: open sagebrush desert 23 miles s. of Folly Farm, near Nanna Lake, T 31 S, R 37 E, in sandy soil
plants mostly many (fistulose) stemmed from a large mass of fibrous (woody) roots; spur shorter than the deep blue, well spread, nearly equal sepals; lower petals small, bifid about half length of the blade; size of plant could be partially due to the extremely favorable growing conditions
C. Leo Hitchcock

May 28, 1957

FIGURE 2

A *Delphinium andersonii*. The woody caudex; leaf blades displayed at the same level; open inflorescence and flowers with large, flaring sepals are noticeable identifying characters of *D. andersonii*.

B Representative specimen of the *Delphinium andersonii* colony from Beaverhead County. Members of this colony have flowers which are larger than the normal *D. andersonii* flower.


Delphinium andersoni Gray
P.E. Sawyer 10/19/66
HERBARIUM OF MONTANA STATE COLLEGE
FLORA OF MONTANA
Delphinium nuttallianum Pritz.
Three Forks, Gallatin County, Montana,
about 5 miles west; range grassland, sandy
soil, dry. June 20, 1965
W.E.Booth # 65179 Sap expressed for serologi-
cal work

A


Delphinium andersoni Gray P.E. Sawyer 10/18/66
HERBARIUM OF MONTANA STATE COLLEGE
FLORA OF MONTANA
Delphinium
About 10 miles south of Brenner, Montana
Beaverhead County, Montana; about 6000
Ft. elevation; dry shortgrass rangeland,
lower north slope; loose soil, sandy-loam.
One patch of about ½ acre seen in this area.
Sap expressed for seralogical work.
June 20, 1965 W.E.Booth # 65163

B

FIGURE 3

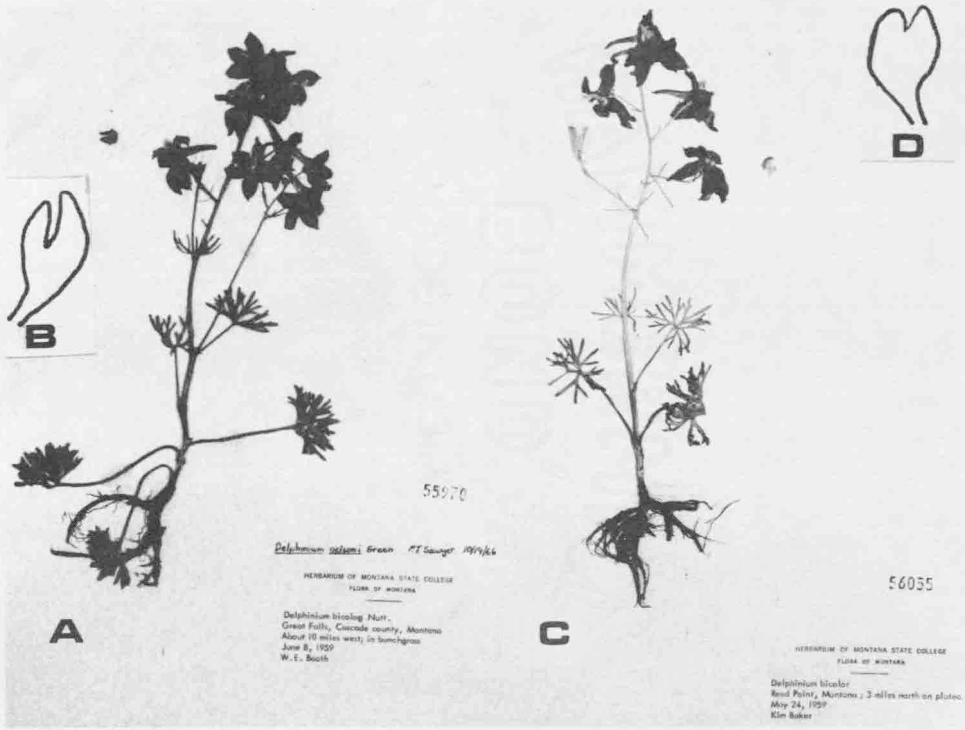
A *Delphinium nelsoni*. The shallow fasciculate root system; few finely dissected leaves; open inflorescence and large flaring sepals are readily visible identifying characters. *D. nelsoni* differs from *D. bicolor* by its deeply divided lower petals.

B Drawing of a deeply divided lower petal of *D. nelsoni*.

C *Delphinium bicolor*. This species is characterized by the shallow fasciculate root system; few leaves; open inflorescence and flowers with large flaring sepals. The stout sepal spur and the lower sepals which are longer than the lateral sepals are also visible.

D Drawing of a shallowly divided lower petal of *D. bicolor*.

E *Delphinium bicolor*. The root system, several stems per plant and leaves of these specimens resemble those of *D. andersonii*, but the flowers are typical of *D. bicolor*. These specimens suggest a close relationship between *D. andersonii* and *D. bicolor*.


B
55970
Delphinium nelsoni Green MT Sanger 19/9/46
HERBARIUM OF MONTANA STATE COLLEGE
FLORA OF MONTANA
Delphinium bicolog Nutt.
Great Falls, Cascade county, Montana
About 10 miles west; in bunchgrass
June 8, 1959
W.E. Booth
A
C
56035
HERBARIUM OF MONTANA STATE COLLEGE
FLORA OF MONTANA
Delphinium bicolor
Reed Point, Montana ; 3 miles north on plateau
May 24, 1959
Kim Baker
D


E

FIGURE 4

A High mountain form of Delphinium nuttallianum. This species is characterized by a globose cluster of roots, weak stems, finely dissected basal leaves, upper leaves with 3-7 entire ultimate segments; few flowered, open inflorescence and flaring sepals.

B Low land form of Delphinium nuttallianum. This form has identifying characters very similar to the high mountain form of D. nuttallianum, but it is more robust. The leaves flowers and roots are similar to those in figure 4A.

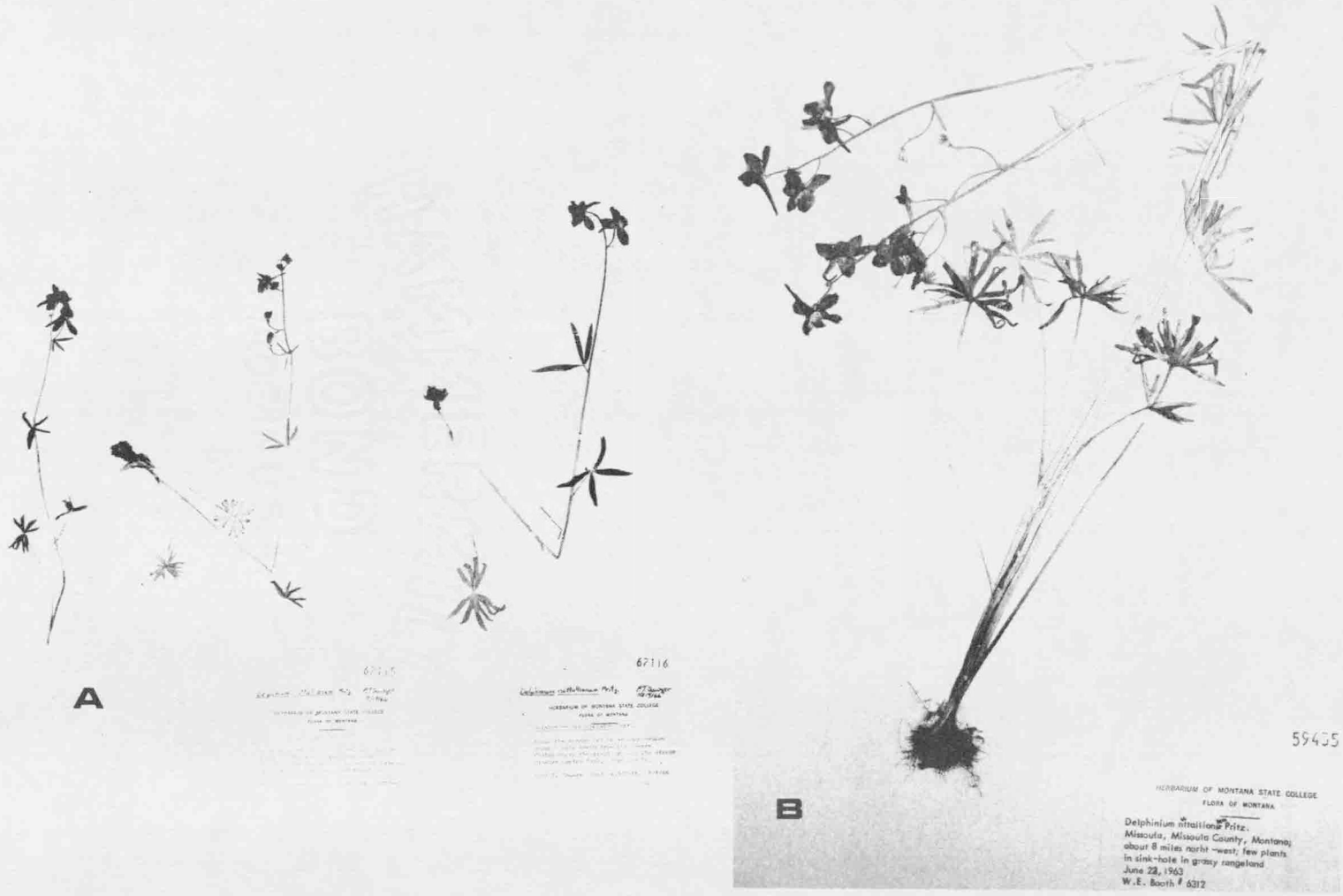
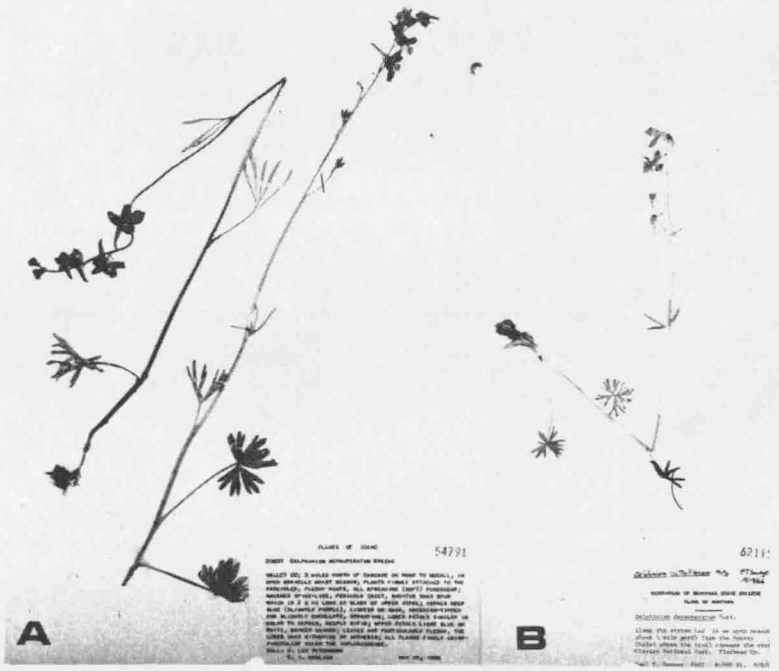

A
67116
B
59435
HERBARIUM OF MONTANA STATE COLLEGE
FLORA OF MONTANA
Delphinium nuttallianum Pritz.
Missoula, Missoula County, Montana;
about 8 miles north-west; few plants
in sink-hole in grassy rangeland
June 22, 1963
W.E. Booth # 6312

FIGURE 5

A *Delphinium depauperatum*. These plants closely resemble *D. nuttallianum*, but have a more spikelike inflorescence and flowers with somewhat cupped sepals. This species is of rare occurrence in Montana.

A *Delphinium nuttallianum*. This species might be confused with *D. depauperatum*, but has an open inflorescence and flowers with flaring sepals.

C *Delphinium burkei*. The shallow globose root system, dimorphic leaves; spikelike inflorescence; cupped sepals and straight, slender sepal spurs are readily visible identifying characters of *D. burkei*.



A

PLANTS OF IDAHO 54791

B

6211

C

565.1

FLORA OF WASHINGTON

20888 Delphinium burkei Greene

KITTITAS CO.: T 20 N, R 16 E, S 32, in heavy adobe soil near highway about 3 miles n.e. of Teanaway Junction, about 4 miles s.w. of Virden. soil now dry but earlier very springy plants associated with Camassia, Erythia, and Poa pratensis; roots small fleshy, fascicled, not at all fibrous close to the ground surface, firmly attached to the (usually) single or 2 or 3 stems, leaves strongly dimorphic, not fleshy, all plants examined (of the several hundred in the colony eglandular, sepals deep bluish-purple a few more nearly blue, others nearly purple, not widely spread, but rather (especially the lower) cupped forward; petals colored about as the sepals, the upper ones whitish-haired, the lower ones deeply bifid; follicles scarcely at all spreading. racemes 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 contact.

C. Leo Hitchcock
C. V. Muhlick June 25, 1956

FIGURE 6

A *Delphinium geyeri*. The extensive woody caudex; several stems per plant; leafy stem; finely dissected leaf blade; somewhat spikelike inflorescence and flaring sepals are identifying characters of *D. geyeri*. This species is rare in Montana.

B *Delphinium ajacis*. This species, an escape from cultivation in Montana, is an annual with a tap root, finely dissected leaves, and 1 carpel.


A
62113
Montana State University
FLORA OF MONTANA


B

Duncan's New Multiple Range test at the 5 per cent level of significance and the 95 per cent confidence intervals (Figure 8) denote that D. burkei differs from all the other species of Delphinium studied. The other species of Delphinium studied do not differ statistically from one another.

Serological Studies

Precipitation lines were obtained on the gel-diffusion plates. In some cases there were no apparent differences between species as the same precipitate lines formed between the antiserum specific for a particular species and other species. The precipitate lines on numerous plates were not clear and distinct and could not be accurately interpreted.

Electrophoresis Studies

The number of bands for 3 different trials with 3 different species are given in Table II (below). Trials 1 and 2 were made with partially purified leaf extract. Trial 3 was made with crude leaf extract.

Table II. Numbers of bands obtained by electrophoresis from leaf extracts of Delphinium species.

	Trials		
Species	1	2	3
D. bicolor	7	8	7
D. geyeri	8	6	7
D. occidentale	7	8	9

Not only was the number of bands inconsistent in the first two trials but the patterns of the bands were also inconsistent.

There were no differences in replications within any single trial.

The densigraph and a diagram representing the banding of the disc-gels using crude sap, trial 3, is given in Figure 9.

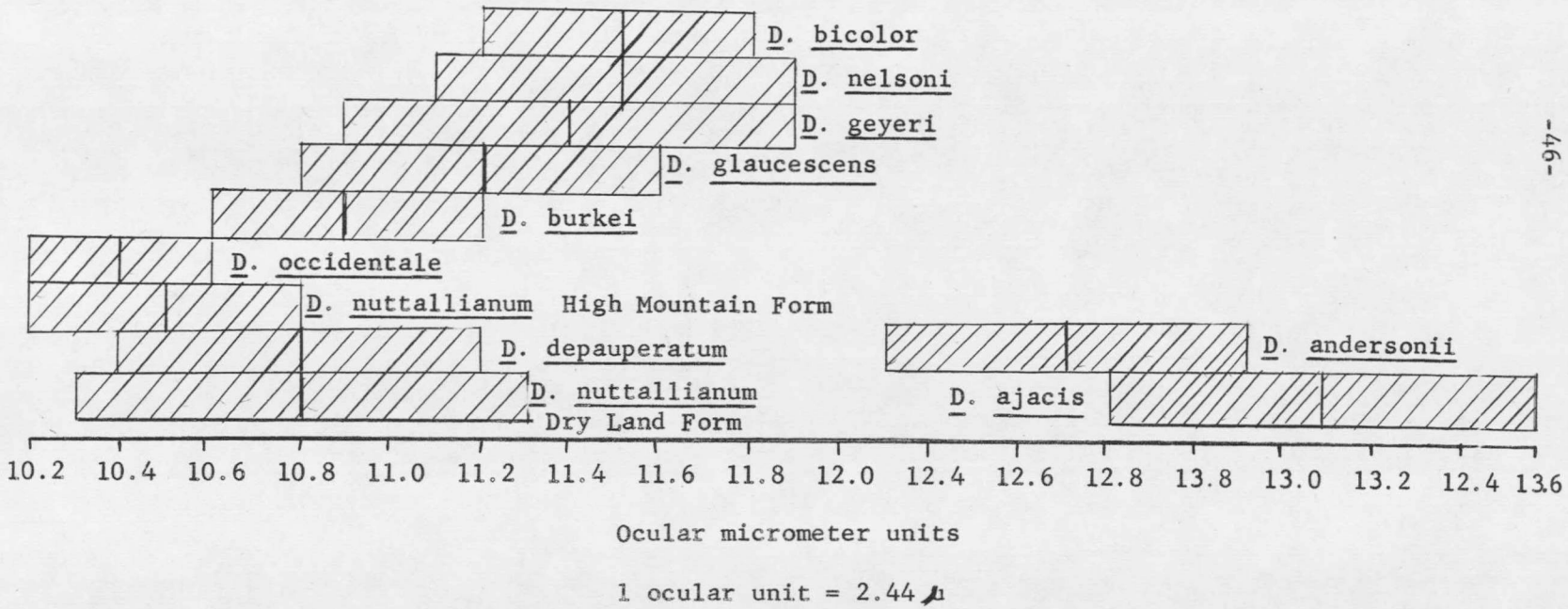


Figure 7 95% confidence intervals based on mean pollen grain lengths of 10 Delphinium species.

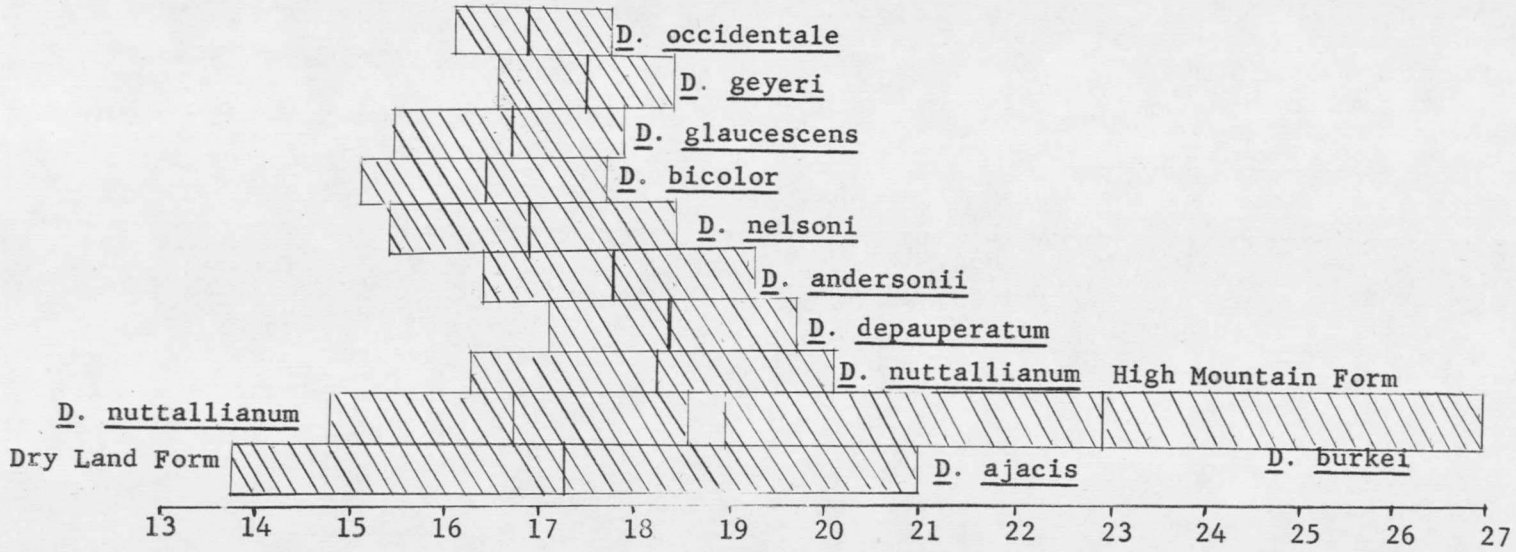


Figure 8 95% confidence intervals based on mean guard cell lengths of 10 Delphinium species.

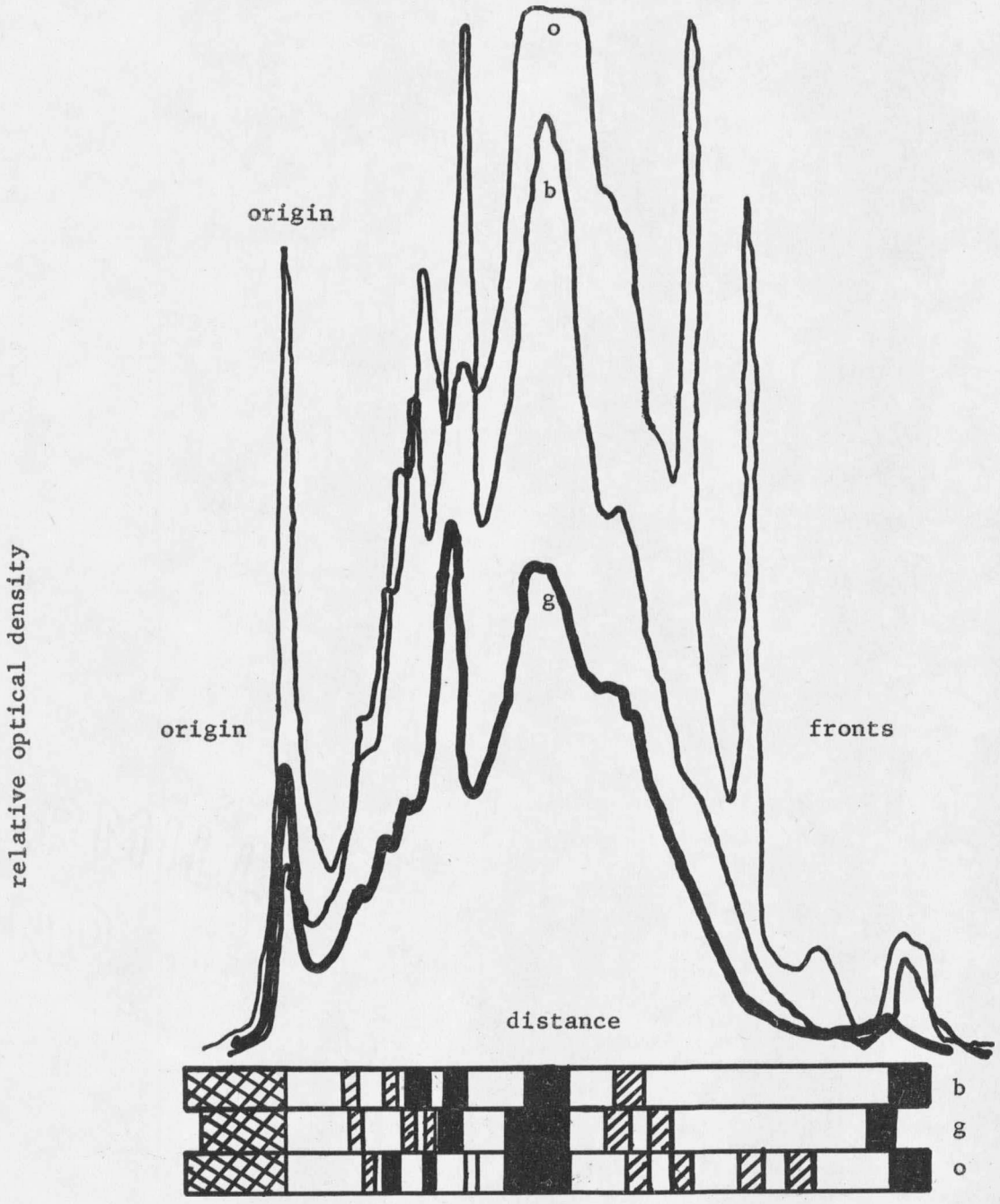


Figure 9 Trial 3. Densigraph of electrophoretic separations of D. bicolor, D. geyeri and D. occidentale, expanded 3:1, coincided with a diagram of the disc-gels expanded 3:1.

b, _____ D. bicolor g, _____ D. geyeri o, _____ D. occidentale

DISCUSSION

Morphological Taxonomy

The Montana delphiniums can be divided into 3 groups or complexes. The bicolor complex includes D. bicolor, D. nelsoni and D. andersonii. The nuttallianum complex includes D. nuttallianum, D. depauperatum and D. burkei. D. nuttallianum although a member of the nuttallianum complex is closely related to the bicolor complex species and serves as a link between the two complexes. The occidental complex includes D. occidentale, D. brownii and D. glaucescens.

All members of the bicolor complex have open inflorescences, flaring sepals, non-fistulose stems and finely dissected leaves. Both fasciculate and caudex type root systems are represented in the complex and there is a tendency for the root system to be extensive. Also within the complex are species with deeply notched lower petals and shallowly notched lower petals.

The nuttallianum complex is typified by globose root systems, finely dissected leaves, non-fistulose stems and a tendency for the sepals to be cupped and the inflorescences to be spikelike. D. nuttallianum which does not have the cupped sepals and spikelike inflorescence links the bicolor and nuttallianum complexes.

Members of the occidentale complex have extensive root systems, spikelike inflorescences, cupped sepals, cuneate leaves and fistulose stems tending to be glaucous. Figure 10 diagrams this proposed scheme and summarizes the evidence upon which the scheme is based.

These complexes are not too unlike the series proposed by Ewan and shown in the Review of Literature Section on page 3. The exceptions are

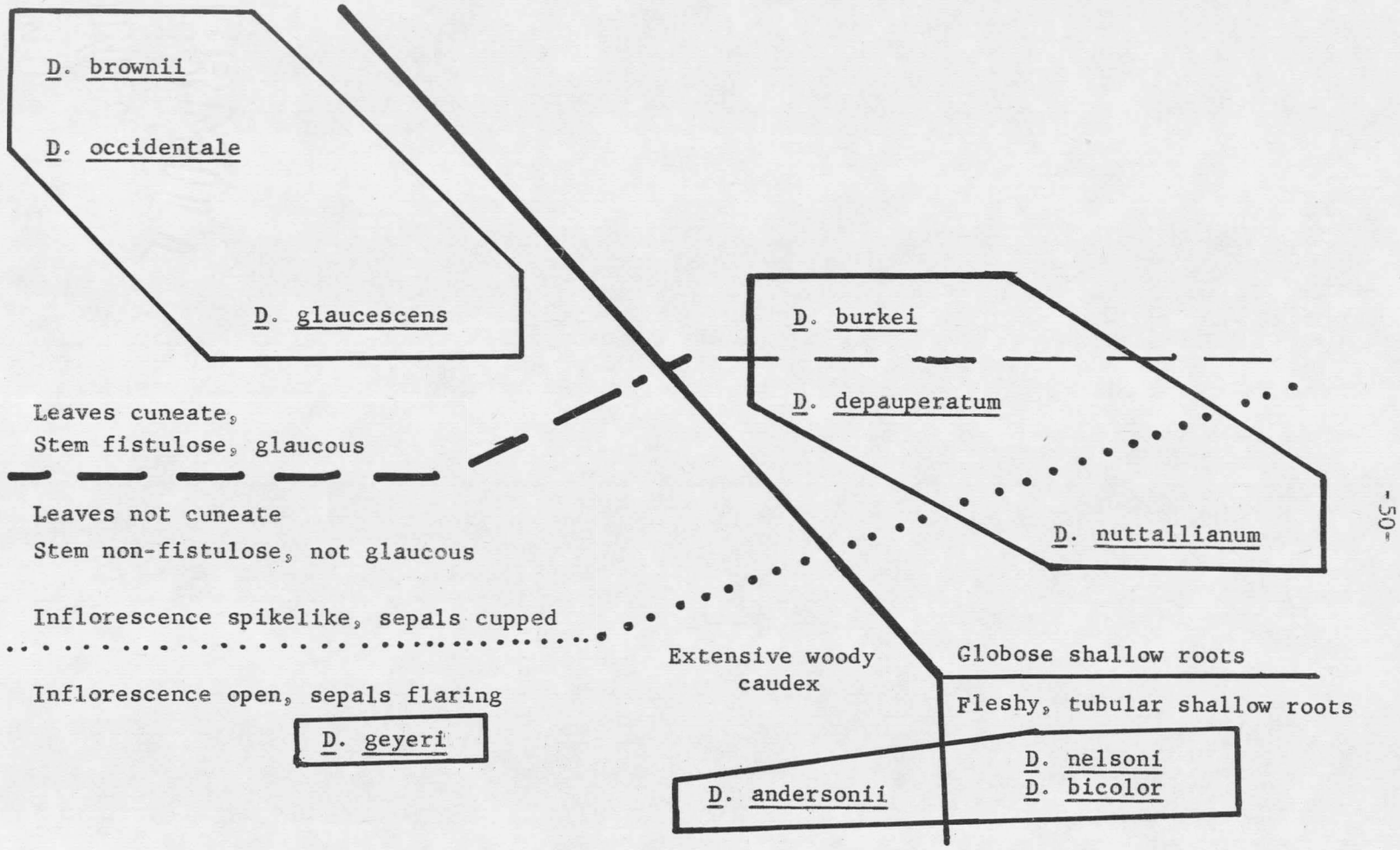


Figure 10 Diagram based on morphological characteristics showing presumed relationships of species associated with the classification of the genus Delphinium in Montana. Heavier lines indicate that the characters are distinctive. Narrower lines indicate that the characters separated by the line tend to intergrade.

D. burkei, here included in the nuttallianum complex, equivalent to Ewan's Tuberiform Series, instead of the Spiciform Series of Ewan, and D. andersonii also included in Ewan's Spiciform Series but now moved to the bicolor complex, the equivalent of the Lignifasciculate Series of Ewan.

Delphinium nelsoni may be a variety of D. bicolor. It differs from D. bicolor only by its deeply notched lower petals. The fasciculate root system of D. nelsoni prevents it from being placed with D. nuttallianum as Hitchcock et al. (1964) has done. There are many similarities between D. bicolor and D. nuttallianum (Figure 3 and 4) but the deeply notched lower petals and the globose root systems provide morphological evidence for giving these plants specific rank. The low land form of D. nuttallianum resembles D. bicolor more closely than the high mountain form. The similarity of flowers and roots is evidence for including the 2 forms as members of the same species. The flower and leaf morphology of D. andersonii is very similar to that of D. bicolor and D. nelsoni (Figure 2 and 3). D. andersonii differs from them by its extensive root system, harder stem, later flowering date, its colony forming habit and its occurrence in a drier habitat. Delphinium andersonii probably evolved from D. bicolor, and can not be considered to be a variety of D. nuttallianum, as Hitchcock et al. (1964) has recommended, because of its extensive root system. Future study may demonstrate that the plants called D. andersonii in this thesis are not equivalent to D. andersonii Gray.

Field investigations need to be made. The limited distributions of both forms of D. nuttallianum, and of D. nelsoni, D. glaucescens and D. andersonii suggest that within the genus Delphinium, ecotypes may have become isolated thus evolving new species or new forms of a given species. It seems probable that the results obtained by Epling and Lewis (1952) from their field studies are applicable to certain species of Delphinium in Montana. Certainly the 2 forms of D. nuttallianum, the colonies of D. andersonii, and the slightly different-appearing colony of the latter in Beaverhead County, as well as D. bicolor and D. nelsoni should be studied in the field with the conclusions of Epling and Lewis in mind.

Pollen Grain and Guard Cell Size

Pollen grain and guard cell size have been used to distinguish ploidy levels as pointed out in the Review of Literature. Based on previous chromosome counts made within the genus Delphinium, also mentioned in the Review of Literature, it is not expected that many, if any, species of Delphinium native to Montana would have a ploidy level higher than the 2x number. It might be expected that the pollen grain length of D. ajacis, a horticultural escape being so unlike the other delphiniums, might differ from the other species of Delphinium. D. andersonii has unusually large flowers. This fact coupled with the different pollen grain length would suggest that D. andersonii might have a higher ploidy level than the 2x number. The strong resemblence of D. andersonii to D. bicolor and D. nelsoni suggests that if it is a polyploid, its genomes could have been derived from either one or both of these species.

The 2 statistically different groups based on pollen grain length, one containing D. occidentale, D. nuttallianum and D. depauperatum, the other containing D. bicolor, D. nelsoni, D. geyeri and D. glaucescens, roughly coincide with the morphological scheme presented in Figure 10. However, this fact may or may not be evidence for the proposed morphological relationships presented in Figure 10.

The guard cell size results are those which could be expected if there is no difference in ploidy level of the investigated species with the exception of D. burkei. There is no other evidence suggesting that D. burkei might be a polyploid and no explanation for the larger guard cell length can be given in this thesis. Guard cell size does not support the concept that D. andersonii might be a polyploid. However, stomate size is not necessarily a sure indicator of polyploidy (Stone, 1961). Statistically there is much less variation in the pollen grain study than in the guard cell study.

The fact that some species differ statistically from others in pollen grain and guard cell length does not mean that these 2 measurements can be used to distinguish species. In both pollen grain and guard cell studies the longest measurement of the species with the shortest mean length overlapped the shortest measurement of the species with the longest mean length.

Serological Studies

Montana species of Delphinium can not be separated using the serological methods followed in this study. The results were inconclusive,

and any results reported would be subject to the interpreters bias. However, the methods used were not varied sufficiently to rule out the possible value of serology as a taxonomic tool in future studies of Delphinium.

Electrophoresis Studies

Based on the results of 3 trials using 3 species of Delphinium it appears that electrophoresis could be a useful tool in separating species and demonstrating relationships in further taxonomic studies in the genus. The banding patterns of D. bicolor, D. geyeri and D. occidentale differ sufficiently so that the 3 species can be identified by electrophoresis. From the preliminary results it appears that D. bicolor and D. geyeri are more closely related to each other than either one is to D. occidentale. Their banding patterns are more similar to each other than to the pattern of D. occidentale.

The inconsistencies encountered between the first and second trials indicate that it is better to use crude, unpurified plant extract in future electrophoresis studies.

SUMMARY

A taxonomic study of 11 species of Delphinium in or expected to be in Montana was carried out using morphological, serological and electrophoretic methods. Examination of herbarium specimens resulted in finding combinations of distinguishing characters useful in separating the 11 species. Descriptions of the 11 species and a key separating the species were written. The 11 species of Delphinium were placed in 3 different complexes based on morphological similarities and dissimilarities. Delphinium nelsoni, D. bicolor and D. andersonii were included in the bicolor complex; D. nuttallianum, D. burkei and D. depauperatum in the nuttallianum complex and D. occidentale, D. brownii and D. glaucescens in the occidentale complex. Delphinium andersonii and D. nelsoni should not be considered varieties of D. nuttallianum as Hitchcock has suggested.

Pollen grain length studies generally supported the author's morphological scheme of grouping the species and suggested that D. andersonii might be a polyploid. Pollen grain length, however, could not be used to identify Montana species of Delphinium. A guard cell length study indicated that all species were statistically alike except D. burkei. Guard cell length could not be used to separate any Montana delphiniums.

Serological studies were unsatisfactory and therefore inconclusive.

Disc-gel electrophoresis might be a useful tool if combined with other methods to further study relationships of species of Delphinium. General disc-gel electrophoresis results indicated that D. geyeri and

D. bicolor are more closely related than either one is to D. occidentale. This finding supported the author's 3-complex scheme.

There was some evidence from the studies to indicate that the confusing speciation within the genus Delphinium in Montana results from isolation of different ecotypes of a once common species, as well as from hybridization and introgression. The high mountain and low land forms of D. nuttallianum may represent 2 different ecotypes of the same species that are becoming isolated from one another.

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Biosystematic studies of
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in Montana

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John Hendrickson
Dianne
Ritter
2 weeks
3 WKS USE

N378
Sa97
cop.2

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