A COMPARATIVE STUDY OF THE LUPINUS PARVIFLORUS COMPLEX

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by

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The undersigned, appointed by the Dean of the Graduate Faculty, have examined a thesis entitled

A COMPARATIVE STUDY OF THE LUPINUS PARVIFLORUS COMPLEX

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and hereby certify that in their opinion it is worthy of acceptance.

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CHAPTER I

INTRODUCTION

The taxonomic history of the genus Lupinus began with Linnaeus who adopted Tournefort's term. Even a cursory look at the subsequent history of the genus brings to the forefront the diversity of opinions that have been expressed among those taxonomists who have investigated the various taxa of lupines. It should be noted, however, that these early taxonomists were forced to attempt an understanding of the genus by making observations on the morphology alone. However, even in more recent years a divergence of opinion has been expressed in spite of the rather widespread acceptance of the "biological species" concept and broader understanding of the processes of speciation. It was an awareness of the confusion in the genus that suggested an integrated approach, making use of as many of the modern tools of taxonomic research as possible, be taken to investigate a small group of lupines.

The small flowered, perennial lupines of the mountainous areas surrounding the Great Basin of the western United States were delimited as a suitable group of taxa to work on. Investigations

proceeded on these taxa in three areas. A preliminary field survey of the principal pollinators and their behavioral characteristics was made in an attempt to find the correlation, if any, between flower size and the size of the pollinators. Ultimately a quantification of the gene flow, actual and/or potential, will be necessary before the origin of variability within the genus can be understood.

In a second area of investigation, a survey of the alkaloid spectra of the Lupinus parviflorus complex and allied taxa was made. The set of non-morphological characters available in the alkaloids of each taxon represented another group of characters from which relationships between taxa could be evaluated. The alkaloids present in each of the taxa were examined with the aid of thin layer chromatographic techniques.

Finally, in spite of the fact that alkaloids provide an additional set of descriptors for analysis of these small flowered lupine taxa, morphology remains the most practical way of evaluating genetic relationships between such taxa. Modern techniques of computer aided numerical analysis were employed to evaluate the characters traditionally used to describe lupines. Once the characters were evaluated, those that are most efficient at describing the taxa can be used to construct a model based on the overall phenetic similarity of the taxa. Such phenetic models serve

as a useful context for relating other types of data such as those attained from field studies, distributional patterns, chromosome counts, chemotaxonomic studies, etc.

The integrated results of the pollinator study, the chemotaxonomic analysis of the alkaloids and the taximetric analysis of the morphology were used to interpret the relationships of the Lupinus parviflorus complex and allied taxa. The relationships between these taxa are presented in the taxonomic treatment, along with descriptions, distribution maps and illustrations of representative specimens of each taxon.

CHAPTER II

REVIEW OF THE TAXONOMIC AND FLORISTIC TREATMENT OF THE *LUPINUS PARVIFLORUS* COMPLEX AND ALLIED TAXA

Historical Treatment

The complexity of the variation and evolution in *Lupinus* has been reflected in the long and frequently confused treatment of the genus in monographs and floras. Historical reviews of the genus have been provided by Phillips (1955) and more recently by Dziekanowski (1971) and Fleak (1971). Dziekanowski added substantially to the pre-Linnaean review of the knowledge of lupines. The genus *Lupinus* begins with Linnaeus (1753) although origin of the name was with Tournefort.

The *Lupinus parviflorus* complex is composed of small flowered perennial lupines which are related to the *L. argenteus* and *L. caudatus* complexes of larger flowered taxa.

The first small flowered perennials of this complex were recognized by Nuttall who described *L. holosericeus* in Torrey and Gray (1838-1840) and *L. parviflorus* in Hooker and Arnott (1965 reprint). Much confusion has resulted from Nuttall's description of

the "sand bars on the Wahlamet (Willamette ?) River" in Oregon as the type locality of L. holosericeus. No plants resembling Nuttall's type for this species can be found growing in that area today.

C. P. Smith (1927) considered the type locality likely to have been in central Idaho where material can be found which is virtually identical with Nuttall's specimens. The "Old Oregon Trail," over which Nuttall traveled (McKelvey, 1955) passed through central Idaho and it is likely that Nuttall collected L. holosericeus there, before entering the present day state of Oregon.

Watson's (1873) monographic revision of the extratropical North American species included only one additional species of the taxa treated here, Lupinus meionanthus Gray, among the 56 species and 15 varieties listed. Greene (1892, 1900 and 1901) described several lupines of his own collection from Colorado and adjacent areas including Lupinus floribundus, L. ingratus, L. leptostachyus and L. myrianthus. Lupinus hillii was also described by Greene (1912) from a collection of R. R. Hill made in northwestern Arizona.

C. P. Smith added five additional names to the small flowered perennials considered in this study. He did so in his own publication, Species Lupinorum, between 1939 and 1952.

Phillips (1955) produced a monographic treatment of the lupines of North America, exclusive of the southwestern United States and Mexico. Unlike C. P. Smith, who was preoccupied with naming minor variants, Phillips reduced all the lupines found in the area which his work circumscribed to only 16 species. Phillips treated Lupinus parviflorus as a subspecies of L. argenteus. He reduced L. myrianthus to synonomy of L. argenteus ssp. argenteus and L. leptostachyus to L. argenteus ssp. parviflorus. In this work L. myrianthus and L. leptostachyus are considered to represent the same taxon with L. myrianthus the older of these two Greene names. Phillips considered L. meionanthus to be very closely related to L. holosericeus although to the present author's knowledge, he published no name changes in regard to these two taxa.

A summary of the various treatments of the Lupinus parviflorus complex by authors of floristic manuals has been presented in Table 2-1. These treatments are generally not as thorough as those presented by monographers for any single group of lupines, but they do reflect the attitude of the authors toward investigations, both monographic and floristic, of earlier taxonomists who have dealt with the genus.

TABLE 2-1. TREATMENT OF VARIOUS TAXA OF THE LUPINUS PARVIFLORUS COMPLEX AND SMALL FLOWERED ALLIES BY AUTHORS OF FLORISTIC MANUALS.

Authors	Areas Covered	Taxa Treated*
Wooton & Standley 1915	New Mexico	L. ingratus
Rydberg 1922	Rocky Mountains	Sect. Parviflori: L. parviflorus, L. floribundus, L. leptostachyus Sect. Foliosi: L. ingratus Sect. Monticolae: L. roseolus
Jepson 1925	California	L. meionanthus
Peck 1941	Oregon	L. holosericeus
Tidestrom & Kittell 1941	Arizona & New Mexico	L. parviflorus (L. ingratus) L. hillii
C. P. Smith in Abrams 1944	Pacific States	Sect. Calcarati: L. holosericeus, L. meionanthus
Kearney & Peebles 1951	Arizona	L. osterhautianus, L. hillii (L. ingratus var. arizonicus)
Davis 1952	Idaho	L. holosericeus, L. evermannii L. parviflorus

TABLE 2-1 (continued)

Authors	Areas Covered	Taxa Treated*
Harrington 1954	Colorado	L. parviflorus (L. floribundus)
Dunn 1956	Nevada	L. evermannii, L. holosericeus (L. lacuum-trinitatum) L. parviflorus
Munz & Keck 1959	California	L. meionanthus
Hitchcock et al. 1961	Pacific Northwest	L. argenteus var. parviflorus (L. myrianthus, L. floribundus, L. leptostachyus), L. argenteus var. argenteus (L. evermannii, L. roseolus, L. sparhawkianus, L. summae, L. lacuum-trinitatum), L. holosericeus (L. multicincinnus)
Dunn in Welsh et al. 1964	Utah	L. parviflorus
Dunn & Gillett 1966	Canada & Alaska	L. parviflorus (L. allimicranthus)

*Taxa treated as snyonyms are placed in parenthesis following the taxon under which they are included.

Taxonomic Procedures

In this study, numerous herbarium specimens were borrowed from the major herbaria of the United States, for which the author is very grateful. These herbaria are listed below, using the abbreviations in Index Herbariorum as compiled by Lanjouw and Stafleu (1964). These abbreviations are used to make reference to the herbaria in the taxonomic citations of Chapter VI.

ASU: Arizona State University, Tempe, Arizona

BM: British Museum, London, Great Britain

BRY: Brigham Young University, Provo, Utah

COLO: University of Colorado, Boulder, Colorado

DS: Dudley Herbarium, Stanford University, Stanford, California

DS-Sm: Smith Herbarium, Stanford University, Stanford, California

GH: Gray Herbarium, Harvard University, Cambridge, Massachusetts

IDS: Idaho State College, Pocatello, Idaho

IND: Indiana University, Bloomington, Indiana

ISC: Iowa State University, Ames, Iowa

MO: Missouri Botanical Garden, St. Louis, Missouri

MONT: Montana State College, Bozeman, Montana

ND-G: Green Herbarium, University of Notre Dame, Notre Dame, Indiana

NY: New York Botanical Garden, New York, New York

OSC: Oregon State University, Corvallis, Oregon

PH: Academy of Natural Sciences, Philadelphia, Pennsylvania

POM: Pomona College, Claremont, California

RM: Rocky Mountain Herbarium, University of Wyoming, Laramie, Wyoming

RSA: Rancho Santa Ana Botanic Garden, Claremont, California

UC: University of California, Berkeley, California

UNM: University of New Mexico, Alberquerque, New Mexico

UMO: University of Missouri, Columbia, Missouri

US: National Museum, Smithsonian Institution, Washington, D. C.

USFS: Forest Service Herbarium, Washington, D. C.

WIS: University of Wisconsin, Madison, Wisconsin

WS: State College of Washington, Pullman, Washington

WTU: University of Washington, Seattle, Washington

The specimens borrowed from these herbaria were observed and measured for pertinent information, becoming the basis for the descriptive portion of this work. Maps were made on the basis of these borrowed specimens. Each specimen was annotated, to reflect the conclusion of the experimental and morphological investigations.

The procedures used in the description of the taxa follows those most commonly employed for publication in scientific journals. The following abbreviations are used in the descriptions and/or citations:

Ave(s)	= Avenue(s)	mm	= millimeter
btn	= between	Mt(s)	= Mountain (s)
ca	= approximate	Natl	= National
campgrd	= campground	N	= North
cm	= centimeter	NW	= North West
Co	= County	Pk	= Peak, Park
Cr	= Creek	Pt	= Point
dm	= decimeter	R	= River
E	= East	Rd	= Road
Exp	= Experiment	S	= South
ft	= feet	SE	= South East
Hwy	= Highway	SW	= South West
Jct	= Junction	Sta	= Station
L/W	= length/width	Tr	= Trail
mi	= mile	W	= West

Measurements of floral and vegetative characters used in the descriptions are discussed in Chapter V, where a detailed taximetric analysis of the taxa and characters is presented.

CHAPTER III

POLLINATORS OF THE *LUPINUS PARVIFLORUS* COMPLEX AND OTHER *LUPINUS* SPECIES

Introduction

One of the most interesting patterns of variation in the genus *Lupinus* can be observed in the variable flower size. Flowers of the *Lupinus parviflorus* complex and allied taxa range in size from 5 to 9 mm long. Morphologically related taxa of the *L. argenteus* - *L. caudatus* complexes have flowers 8-15 mm long. Parallel segregations of small and large flowered species can be found between allied taxa in other sections of the genus. However, no previous effort has been made to account for the apparently unrelated development of this large and small flowered dichotomy that has been repeated more than once in the genus. The possibility of the interaction of pollinator size and flower size is of particular interest in an attempt to account for the evolution of this flower size variability in *Lupinus*. This potential for the flower size variability acting as a restriction to gene flow must be compared to the actual pollination mechanism of the lupine flowers and the behavioral characteristics of their pollinators.

Review of Literature

Floral morphology has frequently been related to the pollination patterns in many species of plants. Highly modified floral structures have functioned as isolating mechanisms in the evolution of species in many plant families (Baker, 1953, 1959, 1966; Grant, 1949, 1957; Mayr, 1957 and Stebbins, 1950). Plant species which have become dependent on a single or restricted number of pollinators have been shown to exist in the Asclepiadaceae (Macior, 1965 and Woodson, 1954), the Orchidaceae (Allen, 1950 and 1955), and the Scrophulariaceae (Macior, 1969a, b and Sprague, 1962) to cite but a few examples. In plant species exhibiting less highly modified floral structures, there is considerably less chance of pollinator specificity acting to reduce gene flow between species (Grant, 1949).

Floral colors have also influenced the development of pollinator specificity. Blue flowered species within a single genus are frequently pollinated by Bombus species while red flowered species of the same genus are favored by humming birds (Faegre and Pijl, 1966). Free and Butler (1959) discuss experiments which determined that bees react to blue, green and yellow colors while exhibiting no ability to distinguish between red and grey.

The constancy of bees to the flowers of a single species of plant is dependent on many factors. Some of these are: (1) the relative availability of competing plant species with regard to proximity of the plants to the bee colony and abundance of flowers, (2) the relative adaptiveness of the pollinating species to the flowers of the competing plant species and (3) the degree of phenological separation of the competing plant species. The constancy has been measured in two ways, by direct observation of the pollinators visiting the flowers, and by analysis of the corbicular pollen loads for the constituent plant species represented by the pollen. Macior (1970) for example, used the heterogeneity of corbicular pollen loads as a measure of interspecific competition of the plant species for pollinators.

Grant (1950) stated that bees show the highest degree of constancy when single flights are considered. Comparisons of multiple flights were influenced by the factors described above, but colonies and individual bees frequently work the flowers of a single species over many foraging trips until the pollen or nectar in that species is exhausted. Phenological sequences of floral production can be re-inforced by this tendency of bees to continue working a single species of flowers until it is depleted (Macior, 1964,

1965 and 1968a, b). Macior (1970) attributes the large number of taxa in the genus Pedicularis in part to the interaction of these plants with the form and behavior of the pollinators.

In the lupines considered in this study, there is much less variation in floral morphology than in a genus such as Pedicularis. Except for the overall range in size of the flower and difference in the shape of the keel, the flowers of these lupines are relatively similar from species to species. Variation in other morphological features as well as color differences undoubtedly play a role in the pollination ecology of other species in the genus, but are of improbable consequence in segregating pollinators of the group of species considered in this study. Phenological isolation of some species does occur, but rarely is it complete and frequently there is considerable overlap in the flowering period of sympatric species. Among these latter species there is considerable potential for gene flow.

This potential for gene flow, however, must be measured in terms of the pollination biology of each species. Dunn (1956) described the floral mechanisms for pollination in the Lupinus group Micranthii. The same basic mechanism functions in the perennial lupines of this study as were described for larger flowered L. nanus of the group

Micranthii. The keel envelopes the five large anthers which surround the stigma and upper portions of the style. The large stamens are subtended by five smaller and shorter stamens which prevent the pollen from the larger stamens from being forced to the base of the keel. Although the stigma is surrounded by pollen, it is protected by a fringe of long hairs which prevent unaided pollination. Pollination is achieved by pressure exerted by the weight or landing force of the visiting insects on the upper margin of the keel, forcing the pollen trapped in the acumen down into the hairs protecting the stigma and onto the stigmatic surface. Bees are also capable of exerting force on the keel by bracing their heads on the banner petal and pushing downward with their legs.

Although beetles, flies and thrips are known to visit lupine flowers, it has generally been observed that these insects are not effective in the pollination of lupines. They are known to eat the pollen of lupines in situ, usually gaining access to the pollen by entering the keel at the base, or simply eating pollen spilled by bees (Dunn, 1956).

Several genera of Hymenoptera are known to visit lupines. Dunn (1956), citing his own observations and those of Knuth, lists the following genera of bees as having visited various North American

and European lupines: Andrena, Anthidium, Apis, Bombus, Megachile and Osmia. Macior (1971) reported several species of Bombus on Lupinus argenteus of the Colorado front range. All insects foraging on Lupinus apparently do so for the pollen. There has been no evidence of nectaries in any of the lupine species, although those species with a well developed spur might deserve closer investigation in this regard.

Dunn (1956) reported that the smaller (8-12 mm) flowered species of the Lupinus group Micranthii that required insect aid in pollination are visited by Apis. Flowers larger than 14 mm were reported as doubtfully pollinated by Apis, and probably required aid from a larger bee such as Bombus species. More exact estimates of the effectiveness of different pollinators in the self and cross-pollination of Lupinus flowers has been investigated by Horovitz and Thorp (1970). In their experiments, screen cages were used to confine single species of bees with the plants they were to pollinate.

Recent field studies of pollinators have taken advantage of advances in high speed cinematography and stereophotography (Macior 1964, 1965 and 1970). The use of these photographic systems allows the investigator to record in detail the exact manner in which pollination is achieved. Details are frequently observed that cannot be caught by the unaided eye.

Once a pollinator has removed pollen from a flower, the probabilities of transferal of the pollen to another species of plant vary widely. Ehrlich and Raven (1969) have reviewed the problems of assessing gene flow in plants as effected by insect pollinators. Most reports indicate that plants pollinated by bees are effectively isolated by a distance of only 50-100 feet.

Methods and Materials

Investigations of the pollination ecology of the lupine pollinators in this study are limited to an attempt to measure the correlation of flower size with the size of the pollinators. The constancy of the pollinators was measured by the heterogeneity of the corbicular pollen loads.

Collection of lupine pollinators were made at every opportunity on several field collecting trips in the Western United States from June 1968 to August 1971. Although many populations of lupines were sampled for morphological analysis of the plants themselves, frequently there were no pollinators available to collect. The lack of pollinators in these instances can probably be attributed to: (1) the absence of proper pollinators in the general area, (2) the time of day the lupine populations were sampled did not coincide with the

visitation habits of the pollinators, (3) the pollinators had not begun to use the lupines as a source of food, or (4) the visitation frequency of the pollinators was too low to be sampled in a short period.

For those lupine populations that had active pollinators present, the pollinators as well as the plants on which they were working were collected. The insects were killed in a standard killing jar, using ethyl acetate. They were then stored separately, with care being taken to record the plant species they were found working. All pollinators that had a load of pollen on their corbiculae were wrapped separately in tissue paper to insure that each insect would not be separated from the pollen it had collected.

Determination of the pollinators was done by Robbin W. Thorp, Assistant Apiculturist, Department of Entomology, University of California-Davis. The specimens are deposited in the Entomology Museum of the University of Missouri-Columbia.

The length of the pollinator was taken as the best single measure of the overall size. Measurements of the pollinator lengths were taken from the front of the head to the tip of the abdomen, after the specimens were mounted on pins. The specimens were mounted and allowed to dry in an inverted position with the abdomen held parallel to the long axis of the body. This was done to increase the

uniformity of abdominal positions from specimen to specimen, thus minimizing the error in measuring the overall lengths of the insects.

Corbicular pollen loads were removed from the insects and stored in glacial acetic acid. Each pollen sample was acetolyzed by use of the following modification of the basic acetolysis procedure described by Erdtmann (1943):

1. Each sample of pollen in glacial acetic acid was centrifuged and the acid decanted.
2. The pollen was acetolyzed using 1 ml of a solution consisting of one part concentrated sulphuric acid and nine parts acetic anhydride, at 100^{o}C for one minute.
3. The sample was centrifuged and the pollen cleared with a chlorination solution of one part sodium chlorinate, one part concentrated HCl and 100 parts glacial acetic acid.
4. The sample was then washed twice in cellosolve and stained with Safranin 0, and stored in vials.

Slides of each sample of pollen were prepared and examined for the presence of lupine pollen and the pollen of other species. No attempt was made to identify the foreign pollen. Percentages of each type foreign pollen were tabulated from the first 200 grains counted from randomly selected microscopic fields of the slide.

Results and Discussion

Tabulation of the eight taxa of Lupinus and the pollinators found on each taxon is presented in Table 3-1. Most of the pollinators have been determined as belonging to the male or worker castes. Only two queens were recorded. Bombus occidentalis and B. bifarius were found to be the most frequently encountered pollinators among the ten species of Bombus collected on lupine flowers. Only one species of pollinators was collected on Lupinus x alpestris. All the other lupine taxa were visited by multiple species of Bombus. Megachile sp. were infrequently encountered on several lupine taxa but were considered relatively unimportant pollinators of lupines. The low numbers of pollinators sampled requires that this study be treated as only an initial survey of the pollinators of these taxa. It is quite probable that this list is incomplete. Furthermore, no evidence is available to determine the relative effectiveness of each species of Bombus as pollinators of the Lupinus taxa on which they were collected.

TABLE 3-1. POLLINATORS OF BOMBUS SP. ON LUPINUS

Bombus sp.*	Lupinus Taxa							
	parviflorus	myrianthus	argenteus	x alpestris	caudatus	sericeus	leucophyllus	erectus
occidentalis	3W, (3)	3W	1M		1M, 2W	4W,(6)	3W	3W, (1)
bifarius	1W	8W, (2)			3W, (2)	4W,(7)	2W, (1)	4W, (2)
rosnesenskii				1W, (2)				1W
balteatus			1M, 1W					
rufocinctus		1Q, 1W	4W, (2)		1W		1W, (1)	
huntii						1W		
fervidus						1W		
sylvicola		1W, (1)	1W			1W	1W	
flavifrons			1W				1W	
nevadensis		3M			1W	1Q		

*Castes of the pollinators are designated by the following symbols: Q = queens; M = males, W = workers and numbers in parenthesis indicate specimens of undetermined castes.

A comparison of the length of the pollinators and the length of the flowers on which they were collected is summarized in Figure 3-1. It is immediately apparent that large species of Bombus can be found on both large and small species of Lupinus, as can small Bombus species. Again, it is not known whether or not all the pollinators are equally effective at pollinating large and small flowered lupines. However, pollen was collected from flowers by all of the insects examined. In order for the insects to collect the pollen, it is highly probable that the flowers were at least self pollinated. In flowers where there is some degree of self sterility, it might be expected that some pollinators are more effective at carrying out cross pollination than others.

From Table 3-2 it can be seen that the pollen loads of the Bombus pollinators were frequently found to be heterogeneous. Twenty-seven and one-half percent of all pollen loads had at least one percent foreign pollen. From these figures, it can be seen that a substantial competition exists between plant species for pollinators. However, before such a study can be statistically sound, much more field work involving careful scrutiny of localized populations must be made.

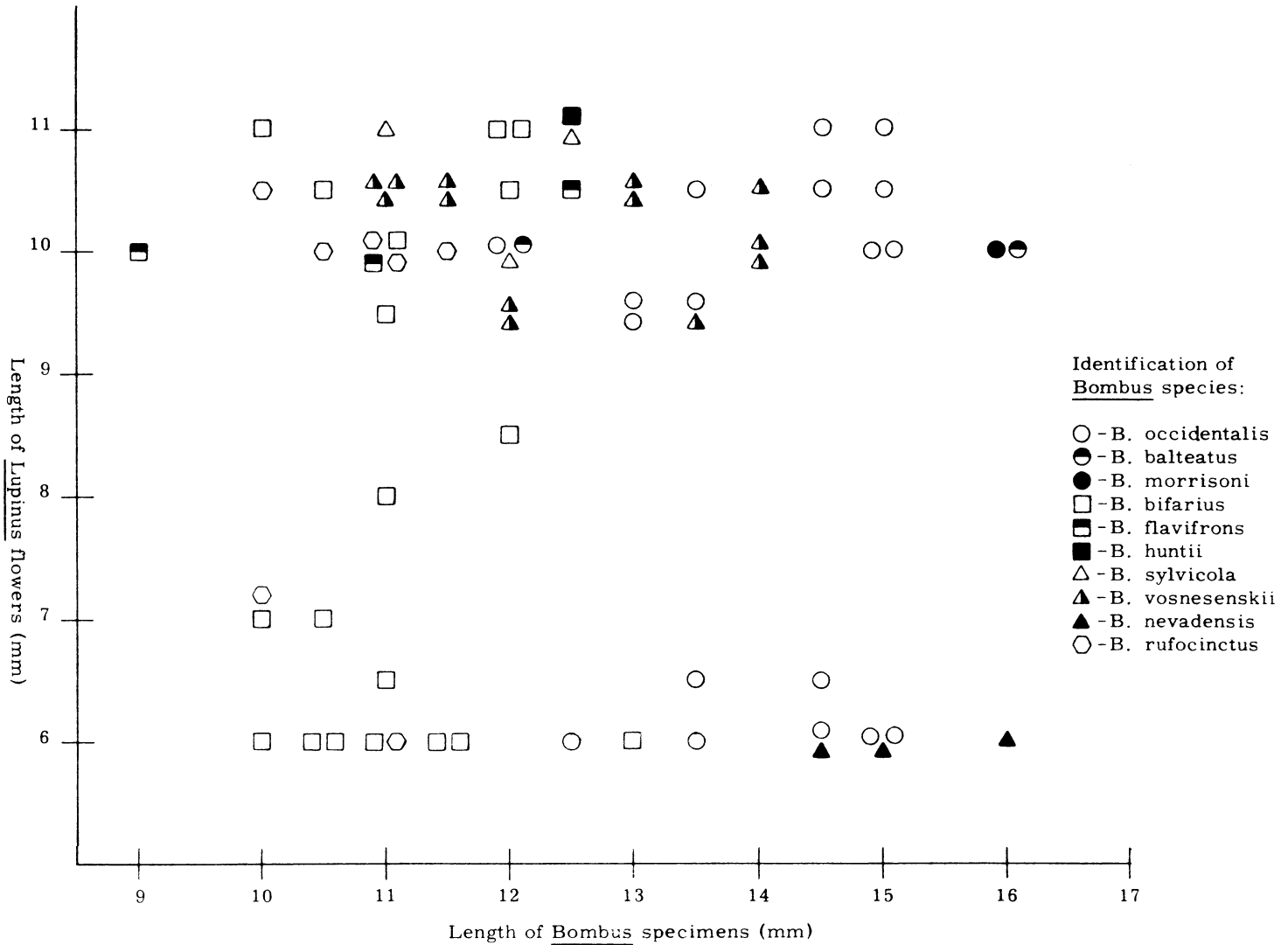


Figure 3-1. A comparison of Lupinus flower lengths with the lengths of their pollinators (Bombus sp.)

TABLE 3-2. POLLEN LOAD ANALYSIS OF *LUPINUS* POLLINATORS

Lupinus sp.	*Bombus* sp.	Pollen Load Constituents: *Lupinus* only	Pollen Load Constituents: *Lupinus* & others*
erectus	occidentalis	4	2
	bifarius	2	1
leucophyllus	occidentalis	1	0
	bifarius	1	1
	rufocinctus	1	1
	flavifrons	1	1
sericeus	occidentalis	8	1
	bifarius	4	2
	nevadensis	1	0
	sylvicola	1	0
	huntii	1	0
caudatus ssp. agrophyllus	occidentalis	1	1
	bifarius	0	1
	nevadensis	1	0
argenteus ssp. spathulatus	flavifrons	1	0
	sylvicola	1	0
x alpestris	rosnesenskii	1	0
	morrisoni	0	1
parviflorus ssp. myrianthus	occidentalis	1	0
	bifarius	8	2
	rufocinctus	2	0
	nevadensis	1	0
	sylvicola	1	0
parviflorus ssp. parviflorus	occidentalis	2	2
	bifarius	0	1
	Totals	45	17
	% of Total	72.5	27.5

*Foreign pollen constituting at least 1% of total.

Conclusions

The occurrence of large and small pollinators on both large and small flowered lupine species suggests that pollinator size may have little or no influence on the selective maintenance of small and large flowered lupines. The heterogeneity of the pollen loads frequently encountered on Lupinus pollinators suggests that lupines are often under considerable competition with other plants for pollinators. Perhaps a hypothesis accounting for the survival advantages of lupines which have a low pollinator specificity and are frequently under strong competition for pollinators of any species, is best made in terms of these legumes being pollinator opportunists.

CHAPTER IV

CHEMOTAXONOMY OF THE *LUPINUS PARVIFLORUS* AND *L. ARGENTEUS* - *L. CAUDATUS* COMPLEXES

Introduction

An application of chemotaxonomic techniques to the *Lupinus parviflorus* complex was made to supplement the phenetic analysis presented in Chapter V. It was recognized that a better evaluation of the relationships between the taxa under study could be gained by comparing the phenetic affinities described by the taximetric analysis with the relationships determined from non-morphological data. The well developed techniques for analysis of lupine alkaloids by use of paper and thin layer chromatography made such a comparison feasible.

Review of Literature

An adequate review of the history of chromatography and the application of chromatographic techniques to the alkaloids of *Lupinus* has been provided by Fleak (1971). The identification and resolution of lupin alkaloids was further reviewed and discussed by Cho and Martin (1971), who also developed the sequential use of thin layer

chromatography (TLC), gas-liquid chromatography (GLC) and the mass spectrometer to identify 22 lupin alkaloids. By using several combinations of substrates and solvents systems for TLC alone, Cho and Martin (1971) were able to resolve most of the 22 lupin alkaloids. However, they did not indicate the exact concentrations of the solvents used in each solvent system to produce the R_f values which were in turn used to identify each of the 22 compounds. Since R_f values can be altered by even a slight change in the solvent system, those values reported by Cho and Martin (1971) are virtually impossible to reproduce except in those instances where precise definitions of the solvent systems are discussed.

The application of chromatographic techniques to the identification of plant components and their subsequent use in solving taxonomic problems has been discussed in Chemotaxonomy and Serotaxonomy, the proceedings of a symposium edited by Hawkes (1968). Harborne stated (in Hawkes, 1968) that the comparison of secondary chemical constituents of plants can be made in three ways: (a) qualitatively, (b) quantitatively, and (c) biosynthetically, where one compound is replaced by another. The first of these approaches is by far the most common, undoubtedly because of the ease at which qualitative or presence-absence data are acquired. However, as

with quantitative data, no relationships are established between the compounds being used to describe the affinities between the taxa. The danger in describing the similarities between taxa based on quantitative or qualitative data is that all compounds are assigned an equal relationship with one another. This, of course, is an obvious distortion. Biosynthesis of secondary compounds is normally a complex sequence of reactions, with each enzymatic change in the sequence resulting in a modification of previously produced compounds. Caution must be exercised, therefore, when interpreting the similarities between taxa for data which do not take into account the biosynthetic relationships of the chemical compounds.

Methods and Materials

The methods employed in the chromatographic analysis of the lupine alkaloids were similar to those employed by Fleak (1971), with the following exceptions. Most of the taxa being investigated in this study produced few fruits on the specimens available for examination. Because of this, it was impossible to obtain seed samples of even a small portion of the taxa. Although it had been previously reported that vegetation samples produced an incomplete and unreliable spectrum of alkaloids compared to the results obtained from seeds (Fleak, 1971), a test of leaf materials (described below)

produced the same set of alkaloids when compared to seeds from the same specimens. Therefore, it was decided that a more complete sample available from leaves would compensate any advantages gained by the use of seeds.

Preparation of the seeds for extracting the alkaloids was similar to the process described by Fleak (1971) with the exception of using paper coin envelopes as containers in which the seeds were crushed. Fleak used aluminum foil for this purpose.

The number of leaves necessary to get adequate spotting of the TLC plates depended on the size of the leaves sampled. Enough material was ground up to produce 1-2 cm^3 of loosely packed dry material. One or two leaflets were sufficient in the case of the larger leaved taxa, while those with smaller leaves necessitated using as many as two-three leaves. Care was taken to sample both young and old leaflets to reduce the possibility of selectively sampling the alkaloids present in the specimen. Leaves were ground up either by using a Wiley Mill or by vigorously crushing them in a small paper envelope. Both methods produced identical results although using the Wiley Mill produced finer particles. The advantage of using the paper envelopes included reduction of the possibility of contamination and speed in preparation of samples.

Once the leaves were properly ground, they were thoroughly wetted with 30% KOH in a test tube. Enough chloroform was added to the treated leaves to completely submerge the particles. After allowing extraction to continue for 12-24 hours at $4^{o}C$, additional chloroform was added (if necessary) to just float the leaf particles off the bottom of the tube. Then the mixture was thoroughly agitated and allowed to settle before sampling.

The chloroform layer containing dissolved alkaloids at the bottom of the test tube was sampled directly with a 50 µl syringe. Approximately 50 µl of the solution was necessary to get an adequate concentration of the alkaloids. Care was taken to clean the needle before applying the chloroform - alkaloid solution to the TLC plates. Failure to do so often resulted in contamination of the plates with fats, oils or other substances adhering to the needle from the upper layer of digested leaves in the test tube. These contaminates produced the effect of inhibiting the flow of the most rapidly moving alkaloids on the thin layer plates, resulting in a bifurcation of the uppermost spots.

The TLC plates (20 x 20 cm) were coated with an adsorbent of Silca Gel G, .25 mm thick. Both commercially prepared and self-prepared plates were used. The pre-coated plates (produced by E. M. Laboratories, Inc.) were found to have the advantage of greater

uniformity in the thickness of the adsorbent and a more durable binding agent. The more uniform coat of adsorbent resulted in greater uniformity in the flow of the solvent up the plate. The durability of the adsorbent coating increased the ease of handling the plates without fear of destruction.

The two solvent systems were employed. The system used by Fleak (1971) of chloroform:methanol:diethylamine (15:3:1) proved less satisfactory at uniformly separating the alkaloids than the chloroform:methanol:concentrated ammonia (95:4:1) as suggested by Cho and Martin (1971). However, it was found that a change in the concentration of the components of the latter solvent system resulting from evaporation during more than two runs, substantially altered the R_f values of the individual alkaloids. It was necessary, therefore, to renew the solvent solution frequently. Developing time for the chloroform:methanol:concentrated ammonia ranged from 75-85 minutes.

The plates were allowed to develop 15 cm rather than 10 cm, in order to achieve greater separation of the spots. Both iodoplatinate and Dragendorff reagents were used to stain the alkaloids. Size, color, and shape were diagnostic characters used where similar R_f

values made it difficult to differentiate between spots. The chromatographs were preserved by tracing the spots on paper and by use of color photographs.

The results of the chromatographs are presented in a composite diagram which combines the tracings of all the sample chromatographs for each of the taxa. Those alkaloids that occur consistently in the samples are differentiated from those which appear only sporadically. No attempt is made to identify the spots on the chromatographs, with the exception of sparteine for which a standard was available.

Differentiation of the remaining alkaloids was by the combined use of R_f value, color, and shape of the individual spots. The R_f values described in the composite chromatographic diagram are mean values. The number of samples analyzed for each taxon depended on the availability of the material. This was restricted to one or two specimens in the case of Lupinus roseolus, L. depressus, L. hillii var. osterhautianus and L. parviflorus ssp. floribundus.

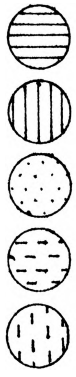
A comparison of the similarity between the taxa based on the presence or absence of alkaloids, is presented in the form of a similarity matrix. The similarity coefficient for each pair of taxa is derived by the following formula:

$$S_{a,b} = \frac{M_{a,b}}{N_{a,b}}$$

where M is the number of alkaloids common to a and b, and N is the total number of comparisons or different alkaloids found in either a or b. N can be found by subtracting M from the sum of the number of alkaloids in a and b.

Results and Discussion

The results of all the chromatographs are summarized in a composite diagram in Figure 4-1. Alkaloids occurring in less than 50% of the samples are indicated by broken lines; those occurring in more than 50% of the samples are shown by use of solid lines. The taxa are indicated by the first four letters of the subspecific or varietal epithet. R_f values can be determined by extension of the scale on the left. The following shading of the spots are used to indicate the colors of the spots as produced when the TLC plates were developed with the iodoplatinate reagent:



Combinations of colors are indicated by combining the shading types.

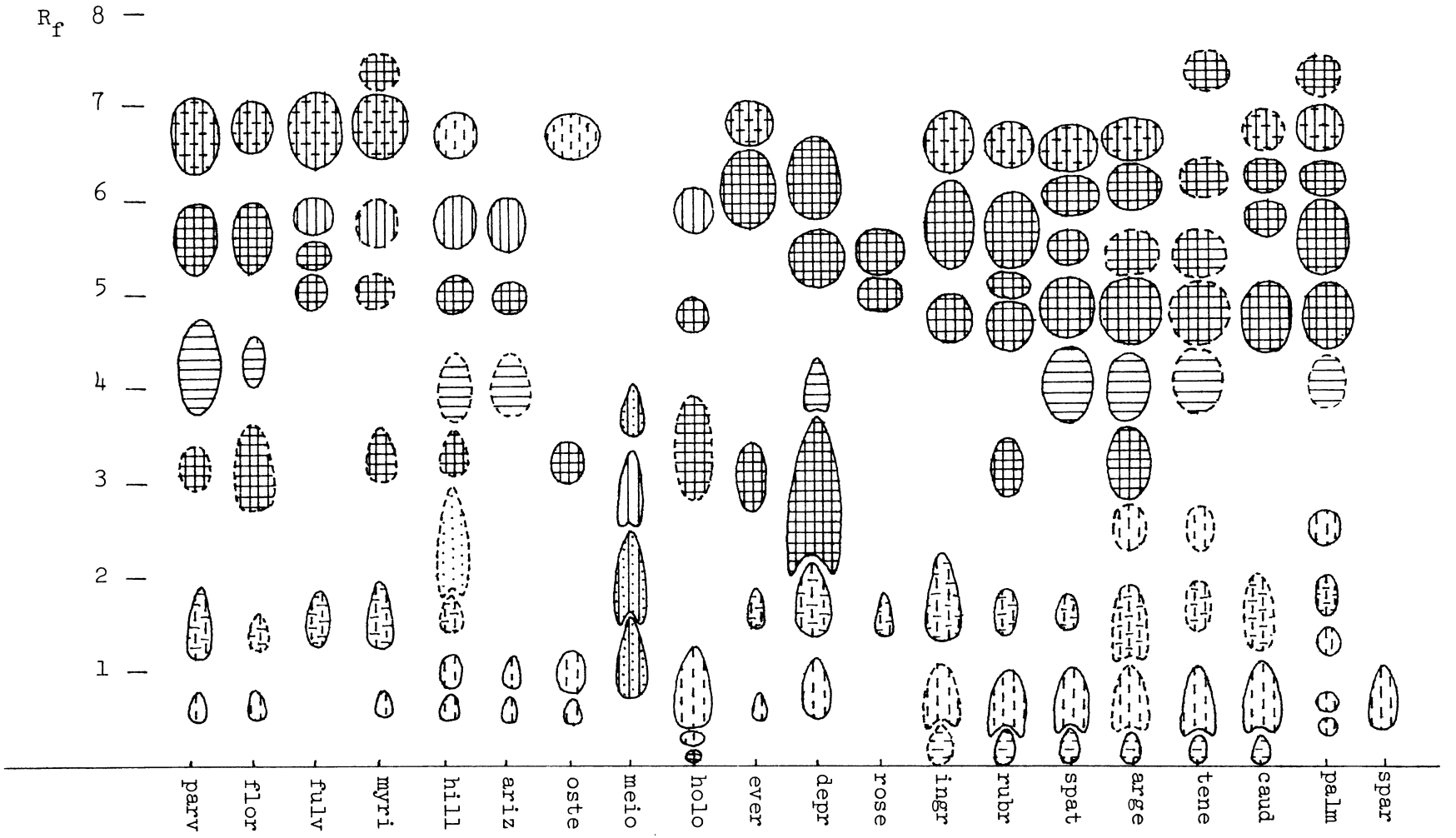


Figure 4-1. Composite diagram of the alkaloid chromatographs of the Lupinus parviflorus and L argenteus - L. caudatus complexes. Solid lines indicate < 50% occurrence in samples tested, broken lines indicate > 50%.

The R_f values of each of the 26 different alkaloids recognized are listed in Table 4-1, along with the color and shape of each. Subtle differences in the shapes were frequently used to differentiate the spots, although only the major differences are described in Table 4-1.

The similarity of the taxa based on a presence-absence comparison of alkaloids is summarized in Table 4-2. As in Figure 4-1. denotation of each taxon is made by abbreviating to the first four letters of the subspecific or varietal epithet. All alkaloids are treated as being present in 100% of the samples for the purpose of computing the similarity matrix.

Lupinus meionanthus is the only taxon which shares no alkaloids with the other taxa. This is particularly interesting in view of the close morphological similarity between this species and L. holosericeus. The latter species has very few alkaloids in common with those of other taxa except ssp. myrianthus (S = .44) with which it has virtually no morphological similarity. Other taxa which are relatively unique in their alkaloidal description (at least with respect to this study) include L. evermannii and L. roseolus. The small number of samples available for analysis of these two species limits the value of recognizing relationships with other taxa, as concluded from these data.

TABLE 4-1

DESCRIPTION OF 26 ALKALOIDS FOUND IN THE *LUPINUS PARVIFLORUS* AND *L. ARGENTEUS* - *L. CAUDATUS* COMPLEXES*

	R_f	Color	Shape
1.	.742	yellow-brown	round
2.	.679	green-brown	round
3.	.663	blue-grey	round
4.	.625	orange-brown	round
5.	.587	dark brown	round
6.	.541	orange-brown	round
7.	.532	orange-brown	round
8.	.505	yellow-brown	round
9.	.483	orange-brown	round
10.	.411	orange-yellow	round
11.	.395	orange	elongate
12.	.385	grey-brown	elongate
13.	.320	orange-brown	round
14.	.308	yellow-brown	round
15.	.290	light beige-brown	elongate
16.	.287	orange-brown	elongate
17.	.242	light blue	round
18.	.239	grey-white	elongate
19.	.200	grey-beige	elongate
20.	.163	blue-green	round
21.	.100	grey-brown	elongate
22.	.100	violet	round
23.	.065	deep blue	elongate
24.	.040	blue	round
25.	.020	green	elongate
26.	.010	orange-brown	round

*R_f values determined from chromatographs developed with chloroform:methanol:ammonia (95:4:1), stained with Dragendorff and Iodoplatinate Reagents.

TABLE 4-2. SIMILARITY MATRIX OF THE LUPINUS PARVIFLORUS AND L. ARGENTEUS - L. CAUDATUS COMPLEXES BASED ON PRESENCE - ABSENCE OF ALKALOIDS

	parv	flor	fulv	myri	hill	ariz	oste	meio	holo	ever	depr	rose	ingr	rubr	spat	arge	tene	caud	palm
parv	1.00																		
flor	1.00	1.00																	
fulv	.37	.37	1.00																
myri	.62	.62	.50	1.00															
hill	.36	.36	.27	.45	1.00														
ariz	.22	.22	.25	.33	.55	1.00													
oste	.25	.25	.00	.22	.44	.28	1.00												
meio	.00	.00	.00	.00	.00	.00	.00	1.00											
holo	.33	.33	.22	.44	.36	.37	.25	.00	1.00										
ever	.37	.37	.25	.33	.33	.11	.12	.00	.10	1.00									
depr	.20	.20	.22	.18	.15	.10	.11	.00	.09	.37	1.00								
rose	.28	.28	.60	.25	.20	.14	.00	.00	.12	.14	.12	1.00							
ingr	.50	.50	.22	.30	.15	.10	.11	.00	.20	.37	.20	.12	1.00						
rubr	.45	.45	.30	.36	.21	.18	.09	.00	.27	.44	.14	.22	.75	1.00					
spat	.27	.27	.44	.25	.21	.18	.09	.00	.33	.44	.40	.22	.45	.45	1.00				
arge	.23	.23	.25	.21	.19	.15	.07	.00	.14	.50	.33	.18	.45	.50	.80	1.00			
tene	.15	.15	.16	.23	.20	.33	.08	.00	.15	.33	.44	.20	.36	.28	.70	.72	1.00		
caud	.36	.36	.20	.33	.14	.09	.10	.00	.18	.50	.30	.11	.86	.67	.67	.54	.45	1.00	
palm	.31	.31	.28	.28	.25	.23	.15	.00	.13	.33	.21	.08	.41	.35	.46	.50	.54	.50	1.00

Relatively close similarity can be found within the intraspecific taxa of Lupinus parviflorus, the intraspecific taxa of L. hillii and within the L. argenteus - L. caudatus complex, paralleling the morphological continuities within and between these groups. It is also interesting to note that the closest similarity of the L. parviflorus complex to the L. argenteus - L. caudatus complex is through L. argenteus ssp. rubricaulis and L. argenteus ssp. ingratus.

The morphological affinities between these two groups of taxa is also through these latter two subspecies of L. argenteus as described by the phenetic analysis in Chapter V. Intraspecific variability in the alkaloid similarity values of L. parviflorus, L. hillii and the interspecific variability of the L. argenteus - L. caudatus complex lends no reliable clues to the taxonomic hierarchies of these groups.

The low similarity values expressed throughout most of the similarity matrix (Table 4-2) may be the result of including alkaloids in the description of each taxon that occur infrequently. The sporadic occurrence of a few alkaloids in some of the taxa may be a function of: (1) random fixation of genes resulting in production of different alkaloids within a taxon, (2) environmental influences on the production of alkaloids resulting in different alkaloids being produced from genetically similar populations or (3) selective

pressure favoring particular alkaloid combinations. There is little evidence to support any of these possibilities although Cranmer and Turner (1967) report that it is unlikely that insect predators are selected against by different combinations of alkaloids. Their hypothesis is that alkaloids are deterrents to predation only on a quantitative basis. Much more experimental evidence is needed, however, before further comments can be made on the sources of variability in lupine alkaloids.

Summary

The occurrence of different alkaloids in the Lupinus parviflorus and L. argenteus - L. caudatus complexes provided data useful to the understanding of the relationships between these complexes. Variability of the alkaloids within each complex was too great to form any conclusions about the intra-group relationships.

Of particular importance to the present study is the clarification of the relationship between Lupinus meionanthus and the morphologically similar L. holosericeus. The complete alkaloidal dissimilarity of L. meionanthus with all of the other small flowered taxa with which it was compared suggests that its inclusion with this group on the basis of its small flowers is artificial.

The ultimate realization of the potential information in the distribution of alkaloids in the taxa of Lupinus will depend on an understanding of the biosynthesis of these compounds, and a knowledge of their role in the biology of the genus.

CHAPTER V

TAXIMETRIC MODEL OF THE LUPINUS PARVIFLORUS COMPLEX AND ALLIED SPECIES

Introduction

One of the greatest problems preventing systematists from making more progress in comprehending taxonomically difficult groups of organisms is the tremendous quantity of complex morphological and other types of data that must be correlated before a thorough system of classification can be devised. Early taxonomists have been able to grasp the relationship in many smaller groups of plants and to some extent more complex groups. However, more often than not these same taxonomists have had to reduce their intuitive understanding to a descriptive system relying on a fragmentary portion of the descriptive features of the groups they treated. The invention of the computer and subsequent development of sophisticated mathematical systems of analysis built upon ideas proposed by early taxonomists has opened up a new area in taxonomic research. The application of these techniques to the Lupinus parviflorus complex was regarded as perhaps the best way to gain an understanding of the tremendous morphological complexity in the group.

Review of Literature

There were very few early taxonomists who recognized the advantages of correlating all features of the organisms they studied. Sokal and Sneath (1963) have reviewed the early contributions of Adanson, Vicq-d'Azur and Whewell who felt that the taxonomist's greatest problems arose from his attempts to weigh characters by placing more value on some characters than on others. These early taxonomists were restricted in their attempt to correlate the many features of the organisms they were working with, by the lack of adequate mathematical models and technical facilities to manipulate large quantities of data. Later methods developed by taxonomists such as Anderson (1949) employed techniques for correlation of larger numbers of characters by use of various matching coefficients, but were also limited by not having the computer available to extend the usefulness of these techniques.

Sokal and Sneath (1963), in addition to providing a thorough review of numerical taxonomic literature to that date, pressed for recognition of three concepts they felt were basic to the development of modern numerical taxonomy. These were the acceptance of unweighted characters, the use of as many characters as possible, and the necessity of using "modern" clustering techniques for the hierarchical recognition of taxa. Of these, the use of unweighted

characters has probably been the most serious restriction as viewed by most traditional taxonomists (Constance, 1964; Kalkman, 1966; Rollins, 1965 and Ross, 1964).

In spite of the sometimes irrational reaction to the ideas presented by Sokal and Sneath (1963), computer aided taxonomic procedures have become more and more commonly used in the past decade. All areas of taxonomy have felt the impact of the computer as an aid in manipulating and storing data. Programs have been devised to aid in the identification of specimens both directly (e.g. Boughey et al., 1968; Goodall, 1968; Morse, 1971) and by use of dichotomous keys (Hall, 1970; Pankhurst, 1970 and Morse, 1968 and 1971). Data storage banks employing computer aided information retrieval systems are being developed and used for individual herbaria (Crovello and MacDonald, 1970) and entire taxonomic data networks such as the Flora North America Program (Shelter, 1971). Distribution mapping and biogeographical analysis are also areas being aided by the computer (Pauken and Metter, 1972; Peters, 1968 and Soper, 1966).

Numerical taxonomic procedures have been applied to many groups of organisms with varying success (Arp and Rogers, 1970; Hawksworth et al., 1968; Heiser et al., 1965; Irwin and Rogers, 1967 and Soule, 1967). For a more complete listing of applications of

numerical taxonomy not included in Sokal and Sneath (1963) see Gilmartin (1967).

Many of the procedural parameters of numerical taxonomy such as sample size, character size, and character weighing have been investigated (Crovello, 1968 a, b, c, e and 1969; and Heiser, et al., 1965). Estabrook (1967) developed a system of character analysis which is based on an information theory model. This analysis system attempts to aid the taxonomist in deciding which characters should be used to describe the set of objects and how best to describe the properties of the characters themselves. Crovello (1968a) found that the addition and subtraction of objects from a numerical analysis did alter the arrangement of the objects, but that this alteration was non-random and had its greatest effect on those groups to which the added or subtracted objects had their greatest affinity.

Character choice and character weighing have been recognized as the least objective area of numerical taxonomy (Gilmartin, 1967). There is considerable philosophical disagreement over the advisability of using weighed vs. non-weighed characters. Crovello (1968d) follows the argument of Sokal and Sneath (1963) in rejecting prior weighing of characters. Others feel that to whatever degree taxonomy as a discipline has been a success, this success can be at least partially attributable to the taxonomist's tacit understanding of

the value of characters as applied to specific groups (Rogers and Tanimoto, 1960; Wirth et al., 1966). The fact that taxonomy has been a success as a foundation for other biological disciplines (Davidson, 1967) and that numerical taxonomic classifications have led to very little change, except in restricted instances, of previous taxonomic classifications, leads to the conclusion that methods employed by the classical taxonomists are quite justifiable. The value of numerical taxonomy becomes one of refinement and of allowing the taxonomist to ask questions which in the past were prohibitively difficult to answer (Gilmartin, 1967).

Application of numerical taxonomy to systematics encourages a dynamic approach to taxonomy in which the similarity models supply a useful context for further comparisons (Constance, 1964; Ornduff and Crovello, 1968). Some of the different types of models are the phenogram or more commonly termed the dendrogram (Sokal and Sneath, 1963), the three dimensional scattergram (Tyron, 1958) and the subgraph (Wirth et al., 1966).

Perhaps the greatest criticism of numerical taxonomy comes from the evolutionists who point out that numerical taxonomy relies on phenetics as a measure of gene flow or interfertility (Sokal and

Crovello, 1970). Others point out that classical taxonomy is frequently guilty of the same assumptions (Ehrlich, 1961; Ehrlich and Holm, 1962 and Ehrlich and Raven, 1969).

Review of Mathematical Models Applied to Analysis of the *Lupinus parviflorus* Complex

The programs used in this study were those developed by Rogers *et al.* (Rogers and Tanimoto, 1960; Estabrook and Rogers, 1966; Rogers and Fleming, 1964 and Wirth *et al.*, 1966). They were chosen on the following basis: (1) those programs more closely follow the general patterns of classical taxonomic analysis, (2) the determination of characters and attributes to be used is not dependent on large numbers of characters, (3) the characters can be weighed according to the taxonomist's view of their importance, allowing greater flexibility and input on the part of the taxonomist without sacrificing the computer's ability to manipulate the data, (4) the use of non-numerical data is easily assimilated into the program, and (5) the subgraph is perhaps the easiest graphic representation of the complex affinities between taxa to comprehend. Coupled with the information theory model for character analysis developed by Estabrook (1967), the graph cluster analysis aids the taxonomist in developing a phenotypic classification of the taxa under study.

The graph cluster analysis can be divided into the following phases as defined by Rogers and Fleming (1964):

1. Selection of material to be modeled (these can be groups of organisms, ecological samples, etc.).
2. Selection of descriptions or characters to partition the objects (in addition to morphological characters, cytological, distributional, ecological, or any other type of descriptor can be used).
3. Measuring and recording of each attribute of each character for all objects.
4. Transferral of these attribute values to coded values on computer cards.
5. Graph cluster analysis of the data resulting in clustering of the objects which are presented in the form of skyline plots and subraphs (Wirth et al., 1966).

The procedure for graph cluster analysis begins with the formation of a similarity matrix which is the result of comparing the attribute values of each character for every pair of objects. This is summarized in the following formula:

$$S_{ij} = \frac{M_{ij}}{N_{ij}}$$

where M is the number of matches between two objects and N is the number of characters being compared. When a character is absent from one or both of the objects being compared, that character does not contribute to the value of the similarity.

The pair-wise comparison gives no indication of how objects are joined into clusters. In order to do this the overall similarity or continuity of the system must be developed. This is done by first converting the similarity ratios into distance functions:

$$d_{ij} = - \log_2 S_{ij}$$

(d = distance) giving a relative value for the "space" between objects. Objects that are similar have a distance between them that approaches 0; those that are dissimilar have a distance value close to 1. The distances expressed by this formula define a semimetric space in which object A may be half related to B and B half related to C, without there being any relationship between A and C. In a geometric sense, the sum of two sides of a triangle are not necessarily greater than the third side in semimetric space, as it does in metric space (Rogers and Fleming, 1964).

Once the objects are arranged in a multidimensional space as described in a distance matrix (formed by finding the distances between each pair of objects), the centroid or center most object is found. This can be done by using the following formula:

$$T = \frac{H}{R}$$

where T is any object, H is the sum of the distances from the object in question to all other objects, and R is the number of times the object has at least one character in common with each other object. T values are found for each object with the lowest T value determined to be the centroid.

The central object then becomes the focal point for the initiation of clusters. The addition of objects to the central object proceeds by the sequential addition of those objects closest to the central object and the cluster expands until further addition of objects results in a large increase in the entropy or inhomogeneity of the cluster (see Rogers and Fleming, 1964 for further explanation of the measures of entropy). At this point, the object with the highest T value rank (lowest actual T value) among the remaining objects not yet clustered, initiates a new cluster. The clustering of objects continues until all objects are joined.

A related but more simplified system of cluster formation is defined by Wirth et al. (1966). In this system, clusters are defined as a collection of objects at a fixed similarity value in which every object in the cluster is less similar to the objects outside the cluster than the fixed similarity value. Acceptable clusters cannot be further subdivided into smaller clusters at the fixed value of similarity. The number of possible partitions or fixed similarity values that can be defined is at most equal to the number of specimens.

The computer starts clustering the objects by searching for the finest partition, the one with the highest fixed similarity value, which is usually the case where all objects are disjoint unless there are two or more identical objects. Lower partitions are then searched for linking objects. This process continues until all objects are clustered.

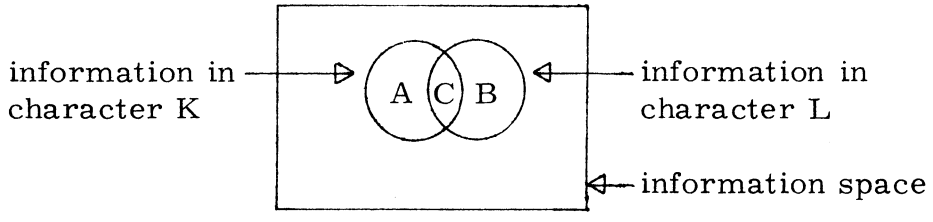
The internal continuity of a cluster is defined by the number of connections that are formed between pairs of objects, relative to the total possible number of connections or paired objects (Wirth et al., 1966). This ratio can be expressed by:

$$\frac{\text{(Total number of existing connections minus necessary connections)}}{\text{(Total possible connections minus necessary connections)}}$$

The minimum number of connections is equal to N - 1, where N is the number of objects in the cluster.

The relative isolation of a cluster can be determined by subtracting from the highest similarity value at which a cluster is formed, the similarity value at which additional objects join the cluster. This numerical value is termed the "moat". It can be thought of as the space surrounding a cluster and separating it from the closest objects (Wirth, et al., 1966). The moat and the connectedness values of a cluster can be useful to a taxonomist in determining the taxonomic value of a cluster.

The analysis of the characters employed in the study followed the procedures outlined by Estabrook (1967). The same computer data deck was used as for the graph cluster analysis. The information theory model for the character analysis can best be explained by use of the heuristic concept of information space. The information space is defined as the totality of information generated by all the characters and their attributes as used in the description of a set of objects.



In the diagram above (from Estabrook, 1967), it can be seen that A is the information held exclusively by K, B is the information held exclusively by L, and C is the information shared by K and L. If both A and B are small and C is correspondingly large, K and L are highly correlated. This could mean that K and L measure the same feature of the objects in different ways and are redundant, or it could be as a result of K and L representing different measures of biologically related phenomena. If both A and B are large and C is nearly empty, K and L are not correlated and contribute to the classification in different ways. If B is nearly empty, but A is not, this indicates that K contains the information in L and represents a refinement of character L. For a detailed mathematical discussion of these concepts see Estabrook (1967).

By determining the amount of information contained in each character, the degree of information shared between characters, and the amount of confusion present in each character, a choice of those characters which most efficiently describe the objects can be made. With this set of descriptors, a more accurate model can be constructed to test the phenotypic affinities between objects.

Materials and Methods

The taximetric analysis was run using the facilities of the University of Colorado at Boulder. The computer programs were supplied by Dr. D. J. Rogers and Mr. W. Reid of the same institution. The following procedure indicates the steps in which the data were gathered and analyzed.

1. Specimens were chosen for analysis as representative of the variability present in the taxa under consideration. Specimens from the Lupinus parviflorus complex and related taxa were supplemented by samples from the L. argenteus and L. caudatus complexes (see Table 5-1). The latter two large flowered complexes were thought to have the closest morphological affinity with the L. parviflorus complex.

2. A list of 63 characters and 271 attributes was compiled, drawing on several floristic keys, descriptions, and the author's experience in handling these taxa (see Table 5-2). The characters were numbered serially. The attributes were numbered sequentially beginning with one for each character. The sequence of attributes is particularly important for those states that were treated as having a well ordered relationship (see Table 5-2). For example, there are five character states or attributes for the character height. These

TABLE 5-1. LIST OF SPECIMENS USED IN TAXIMETRICS STUDY

L. parviflorus

1) Hitchcock 22915 (RM)
2) Christ 16295 (NY)
3) Nelson 6562 (RM)
4) Nelson 6609 (RM)
5) Payson 4382 (RM)
6) Solheim 4909 (RM)
7) Rydberg & Bessey 440 (NY)
8) Baker 9298 (WTU)
9) Owenby 1131 (RM)

L. floribundus

10) Greene July 20, 1889 (NY)
11) Greene July 27, 1873 (GH)

L. myrianthus

12) Weber 7876 (COLO)
13) Weber 9325 (COLO)
14) Rollins 1338 (MO)
15) B. H. Smith 79 (NY)
16) Dunn 14625 (UMO)
17) Lucas 198 (UC)
18) C. P. Smith 3867 (POM)
19) Dunn 14542 (UMO)
20) Downey 61-52a (UMO)
21) Dunn 14569 (UMO)

L. fulvomaculatus

22) Payson 139 (COLO)
23) Payson 547 (WS)
24) Payson & Payson 3904 (MO)
25) W. Hess 444 (COLO)
26) Maguire & Maguire 20430 (RM)
27) Harmon 1191 (UMO)

TABLE 5-1 (continued)

L. ingratus

28) C. P. Smith 3921 (RM)
29) C. P. Smith 4055 (RM)
30) Wolf 2943 (RSA)
31) Nelson 11656 (RM)
32) Goddard 868 (UC)
33) Castetter & Dittmer 3398B (UMO)
34) Eggleston 18686 (NY)
35) Baker 438 (POM)

L. depressus

36) Piper July 19, 1902 (NY)
37) Christ 16900 (NY)
38) Christ 17064 (NY)
39) Christ 17011 (NY)
40) Wilson 271 (MO)

L. meionanthus

41) Baker 1325 (RM)
42) Constance 2455 (UC)
43) C. P. Smith 3812 (RM)
44) Heller 7084 (RM)
45) Howell 18600 (WTU)
46) Heller 9773 (RM)
47) Heller 9971 (RM)

L. holosericeus

48) Cronquist & Holmgren 8808 (WS)
49) Hitchcock & Muhlick 22631 (WS)
50) Cusick 3491 (WS)
51) Pyrah 506 (ISU)
52) Maguire & Holmgren 22671 (UC)
53) Munz 14537 (POM)
54) Davis 4228 (WS)
55) Hitchcock 15527 (WS)
56) Hitchcock & Muhlick 10319 (WS)

TABLE 5-1 (continued)

57) Hitchcock & Muhlick 21988 (UC)
58) MacBride & Payson 3832 (UC)
59) Hitchcock 15554 (WS)
60) Thompson 13647 (WS)
61) Hitchcock 22697 (WS)

L. evermannii

62) Hitchcock 9668 (RM)
63) Hitchcock 14102 (WS)
64) Evermann 533 (GH)
65) Harmon 1481 (UMO)
66) MacBride 3655 (UC)
67) Harmon 580B (UMO)
68) Hitchcock 14082 (COLO)

L. hillii

69) C. P. Smith 4089 (US)
70) Eastwood & Howell 6431 (US)
71) Kearney & Peebles 12192 (US)
72) Wooton July 12, 1892 (US)
73) Collom 217 (US)
74) Peebles 9483 (US)
75) Peebles & E. G. Smith 13283 (US)
76) Shreve 4818 (US)
77) R. R. Hill June 29, 1911 (US)

L. palmeri

78) Cox, Dunn & Harmon 454 #2 (UMO)
79) L. Hess 843 (UMO)
80) Cox, Dunn & Harmon 274a (UMO)
81) Spellman & Harmon 903a (UMO)
82) Jones August 28, 1903 (UMO)

TABLE 5-1 (continued)

L. caudatus ssp. *caudatus*

83) L. Hess 814 (UMO)
84) Dunn 14432 (UMO)
85) Cox, Dunn & Harmon 454 #1 (UMO)
86) Gallian & Dunn 481 (UMO)
87) Gallian & Dunn 511 (UMO)

L. caudatus ssp. *argophyllus*

88) Dunn 6546 (UMO)
89) Downey 6151 (UMO)

L. caudatus X *L. argenteus* var. *tenellus*

90) Dziekanowski 1038 (UMO)

L. caudatus X *L. palmeri*

91) Dunn 13677 (UMO)

L. caudatus X (?)

92) Isely 10042 (UMO)

L. argenteus ssp. *argenteus*

93) Bracelin 500 (UMO)
94) C. P. Smith 4027 (UMO)
95) Cox, Dunn & Harmon 738 (UMO)

L. argenteus ssp. *argenteus* var. *tenellus*

96) Dunn 12314 (UMO)
97) Dunn 11804 (UMO)
98) Castetter 8216 (UMO)
99) Downey 60-18b (UMO)

TABLE 5-1 (continued)

L. argenteus ssp. rubricaulis

100) Dunn 15929 (UMO)
101) Harmon, Cox & Dunn 956 (UMO)
102) Cox, Dunn & Harmon 675 (UMO)
103) L. Hess 1079 (UMO)

L. argenteus ssp. spathulatus

104) Isely 9796 (UMO)
105) Dunn 15051 (UMO)
106) L. Hess 835 (UMO)
107) L. Hess 860 (UMO)

L. ingratus var. arizonicus

108) Eggleston 15664 (US)

L. roseolus

109) Tweedy 270 (NY)

TABLE 5-2. LIST OF CHARACTERS AND ATTRIBUTES

1. Habit[bc]
   1) caespitose
   2) decumbent
   3) erect

2. Height of plant (cm)[ab]
   1) 1 - 20
   2) 21 - 40
   3) 41 - 60
   4) 61 - 80
   5) 81 - 100

3. Diameter of stem (mm)[a]
   1) 0.1 - 0.9
   2) 1.0 - 1.9
   3) 2.0 - 2.9
   4) 3.0 - 3.9
   5) 4.0 - 4.9
   6) 5.0 - 5.9

4. Position of branching
   1) caudex only
   2) lower and upper halves only
   3) caudex and upper half
   4) caudex and lower half
   5) caudex, lower and upper half

5. Stem vesture[bc]
   1) puberulent
   2) strigose
   3) canescent
   4) sericeous
   5) short villous with scattered long hispid hairs
   6) hispidulose

TABLE 5-2 (continued)

---

6. Number of elongated internodes[a]
   1) 0 - 3
   2) 4 - 7
   3) 8 - 11
   4) 12 - 15

7. Presence of leaves at anthesis[a]
   1) basal
   2) basal and cauline
   3) cauline

8. Stipule shape[a]
   1) setaceous
   2) triangular
   3) lanceolate
   4) subulate

9. Stipule length (mm)[a]
   1) 2.1 - 4.0
   2) 4.1 - 6.0
   3) 6.1 - 8.0
   4) 8.1 - 10.0

10. Distance stipule connate to petiole (mm)
   1) 0 - 1.0
   2) 1.1 - 2.0
   3) 2.1 - 3.0
   4) 3.1 - 4.0

11. Length of basal petiole (cm)[ab]
   1) 1.0 - 2.9
   2) 3.0 - 3.9
   3) 4.0 - 4.9
   4) 5.0 - 5.9
   5) 6.0 - 6.9
   6) 7.0 - 7.9
   7) 8.0 - 8.9
   8) 9.0 +

TABLE 5-2 (continued)

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12. Length of mid-cauline petiole (cm)[ab]
    1) 1.2 - 2.9
    2) 2.3 - 3.9
    3) 3.4 - 4.9
    4) 4.5 - 5.9
    5) 5.6 - 6.9

13. Flower length (mm)[abc]
    1) 5.0 - 5.9
    2) 6.0 - 6.9
    3) 7.0 - 7.9
    4) 8.0 - 8.9
    5) 9.0 - 9.9
    6) 10.0 - 10.9
    7) 11.0 +

14. Number of leaflets in majority of leaves
    1) 6
    2) 7
    3) 8
    4) 9
    5) 10 - 11

15. Length of longest leaflet (cm)[abc]
    1) 1.1 - 2.0
    2) 2.1 - 3.0
    3) 3.1 - 4.0
    4) 4.1 - 5.0
    5) 5.1 - 6.0
    6) 6.1 +

16. Length of shortest leaflet of same leaf (cm)[a]
    1) 1.1 - 2.0
    2) 2.1 - 3.0
    3) 3.1 - 4.0
    4) 4.1 - 5.0

TABLE 5-2 (continued)

17. Width of longest leaflet (cm)[abc]
    1) 2.1 - 4.0
    2) 4.1 - 6.0
    3) 6.1 - 8.0
    4) 8.1 +

18. Length/width ratio of longest leaflet[ab]
    1) 2 - 4
    2) 4 - 6
    3) 6 - 8
    4) 8 - 10

19. Leaflet shape[a]
    1) eliptic
    2) oblanceolate
    3) spathulate

20. Leaflet apex shape[a]
    1) acute
    2) obtuse
    3) truncate

21. Folding of leaflet[ab]
    1) flat
    2) semi-conduplicate
    3) conduplicate

22. Leaflet vesture above[bc]
    1) glabrous
    2) puberulent
    3) finely strigose
    4) villose
    5) sericeous
    6) hispidulose
    7) coarsely strigose

TABLE 5-2 (continued)

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23. Leaflet vesture below[bc]
    1) pilose
    2) puberulent
    3) finely strigose
    4) villose
    5) sericeous
    6) hispidulose
    7) coarsely strigose

24. Peduncle length (cm)[ab]
    1) 0 - 2.0
    2) 2.1 - 4.0
    3) 4.1 - 6.0
    4) 6.1 - 8.0

25. Raceme length (cm)[ab]
    1) 1.0 - 3.0
    2) 3.1 - 6.0
    3) 6.1 - 9.0
    4) 9.1 - 12.0
    5) 12.1 - 15.0
    6) 15.1 +

26. Bract shape[a]
    1) setaceous
    2) triangular
    3) lanceolate
    4) subulate

27. Bract length (cm)[ab]
    1) 0 - 3.0
    2) 3.1 - 6.0
    3) 6.1 - 9.0
    4) 9.1 - 12.0

28. Bract persistence
    1) caducous
    2) tardily deciduous

TABLE 5-2 (continued)

29. Floral arrangement
    1) verticillate
    2) subverticillate
    3) scattered

30. Flower color
    1) dark blue
    2) blue
    3) light blue
    4) cream
    5) rose-pink

31. Color of eye-spot
    1) white
    2) yellow

32. Color of eye-spot on drying
    1) dark
    2) light

33. Pedicle length (mm)[ab]
    1) 1.1 - 2.0
    2) 2.1 - 3.0
    3) 3.1 - 4.0
    4) 4.1 - 5.0
    5) 5.1 - 6.0

34. Calyx base shape[abc]
    1) obtuse
    2) truncate
    3) gibbous
    4) spurred

35. Calyx length upper lobe (mm)[ab]
    1) 3.0 - 3.9
    2) 4.0 - 4.9
    3) 5.0 - 5.9
    4) 6.0 - 6.9
    5) 7.0 - 7.9

TABLE 5-2 (continued)

36. Calyx length lower lobe (mm)[abc]
    1) 3.0 - 3.9
    2) 4.0 - 4.9
    3) 5.0 - 5.9
    4) 6.0 - 6.9
    5) 7.0 - 7.9
    6) 8.0 - 8.9

37. Calyx vesture[a]
    1) villous
    2) sericeous
    3) pilose

38. Depth of notch in upper lobe of calyx[a]
    1) 0
    2) 0.1 - 1.0
    3) 1.1 - 2.0
    4) 2.1 - 3.0

39. Bracteoles
    1) present
    2) absent

40. Attachment of bracteoles
    1) angle of calyx lobes
    2) base of calyx
    3) midway between angle and base of calyx

41. Banner shape
    1) eliptic
    2) orbicular
    3) suborbicular

42. Banner length (mm)[abc]
    1) 5.1 - 6.0
    2) 6.1 - 7.0
    3) 7.1 - 8.0
    4) 8.1 - 9.0
    5) 9.1 - 10.0
    6) 10.1 - 11.0

TABLE 5-2 (continued)

43. Banner width (mm)[ab]
    1) 5.1 - 6.0
    2) 6.1 - 7.0
    3) 7.1 - 8.0
    4) 8.1 - 9.0
    5) 9.1 - 10.0
    6) 10.1 - 11.0

44. Banner reflexed/appressed ratio[ab]
    1) 1.0 - 0.9
    2) 0.9 - 0.8
    3) 0.8 - 0.7
    4) 0.7 - 0.6
    5) 0.6 - 0.5
    6) 0.5 - 0.4

45. Banner length/width ratio[a]
    1) 0.70 - 0.79
    2) 0.80 - 0.89
    3) 0.90 - 0.99
    4) 1.00 - 1.09
    5) 1.10 - 1.19
    6) 1.20 +

46. Banner vesture[bc]
    1) glabrous
    2) few scattered hairs
    3) densely hairy

47. Banner angle (^{o})[abc]
    1) 110 - 119
    2) 120 - 129
    3) 130 - 139
    4) 140 - 149
    5) 150 - 159

TABLE 5-2 (continued)

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48. Wing length (mm)[ab]
    1) 5.0 - 5.9
    2) 6.0 - 6.9
    3) 7.0 - 7.9
    4) 8.0 - 8.9
    5) 9.0 - 9.9
    6) 10.0 - 10.9
    7) 11.0 +

49. Wing width (mm)[ab]
    1) 2.0 - 2.9
    2) 3.0 - 3.9
    3) 4.0 - 4.9
    4) 5.0 +

50. Wing vesture[b]
    1) glabrous
    2) scattered pubescence

51. Length of wing claw (mm)[a]
    1) 1.0 - 1.9
    2) 2.0 - 2.9
    3) 3.0 - 3.9

52. Width of keel at widest point (mm)[abc]
    1) 2.0 - 2.9
    2) 3.0 - 3.9
    3) 4.0 - 4.9

53. Length of keel from base of claw to tip of acumen (mm)[abc]
    1) 4.0 - 4.9
    2) 5.0 - 5.9
    3) 6.0 - 6.9
    4) 7.0 - 7.9
    5) 8.0 - 8.9
    6) 9.0 - 9.9
    7) 10.0 - 10.9

TABLE 5-2 (continued)

54. Angle of keel (°)[abc]
    1) 60 - 69
    2) 70 - 79
    3) 80 - 89
    4) 90 - 99
    5) 100 - 110

55. Vesture of keel[b]
    1) lateral hairs present
    2) lateral hairs absent

56. Ciliation of keel on upper suture
    1) entire length
    2) above middle only
    3) absent

57. Pod length (cm)[a]
    1) 1.0 - 1.9
    2) 2.0 - 2.9
    3) 3.0 - 3.9

58. Pod width (mm)[a]
    1) 4.0 - 4.9
    2) 5.0 - 5.9
    3) 6.0 - 6.9
    4) 7.0 - 7.9
    5) 8.0 - 8.9

59. Pod vesture
    1) villous
    2) sericeous

60. Number of ovules[a]
    1) 3
    2) 4
    3) 5

TABLE 5-2 (continued)

61. Number of seeds[a]
    1) 1 - 2
    2) 2 - 3
    3) 3 - 4

62. Diameter of seeds (widest measurement in mm)[a]
    1) 1.0 - 1.9
    2) 2.0 - 2.9
    3) 3.0 - 3.9
    4) 4.0 - 4.9
    5) 5.0 - 5.9

63. Color of seeds
    1) solid cream
    2) solid light brown
    3) solid dark brown
    4) speckles on light background
    5) speckles on dark background

[a]Characters whose attributes were considered to be well ordered.
[b]31 characters used in character analysis and first graph cluster analysis.
[c]15 characters used in second graph cluster analysis.

attributes are well ordered to reflect the fact that a plant with a height of 10 cm is more similar to a plant 30 cm tall than a 10 cm tall plant is to a plant 50 cm tall (Estabrook and Rogers, 1966).

The sum of the attributes for each character include the total range in variability of all the objects being measured. Usually the range of variability for each character could be separated into distinct states. In characters that were continuous, the attribute divisions were chosen subjectively, with an attempt to minimize the number of attributes while maximizing the information content of each character, i.e., its ability to classify the objects (specimens) under consideration. The number of attributes each character possesses determines its relative capacity to group or separate objects. The greater the number of attributes, the greater the ability of the character to separate objects becomes.

3. Vegetative measurements were taken directly from herbarium specimens. Floral measurements were taken from dissected flowers which were first boiled and then mounted in plastic on a glass slide as described by Dunn (1954).

The descriptions of most of the measurements for the characters are self evident. However, the following characters require special attention to avoid multiple interpretations of the manner in which they

are made: floral length, banner length, banner width, banner angle, banner reflex/appressed ratio (r/a ratio), keel length, keel width, and keel angle. A description of these characters is provided in Figure 5-1. Measurements taken from unmounted flowers can be expected to give different values, especially on those parts that are highly three dimensional in the living condition. Flattening the flowers on a slide should increase the repeatability of the measurements.

Measurements from all specimens were recorded in a loose leaf notebook. These were then converted to the corresponding attribute number for each character value. Transferral of the attribute value to computer cards was made for each character. Characters which were absent from the specimen were assigned an attribute value of zero.

4. A dendrogram using the similarity measure described by Estabrook and Rogers (1966) was prepared by the computer on specimens 1-107, using 63 characters. The dendrogram was examined for the degree of cluster formation which is an indication of the adequacy of the characters and attributes employed to describe the variability in the objects.

5. Thirty-one of the 63 characters thought to contain the greatest amount of information (see Table 5-2) were subjectively selected from the list of 63 for an analysis to determine the amount of

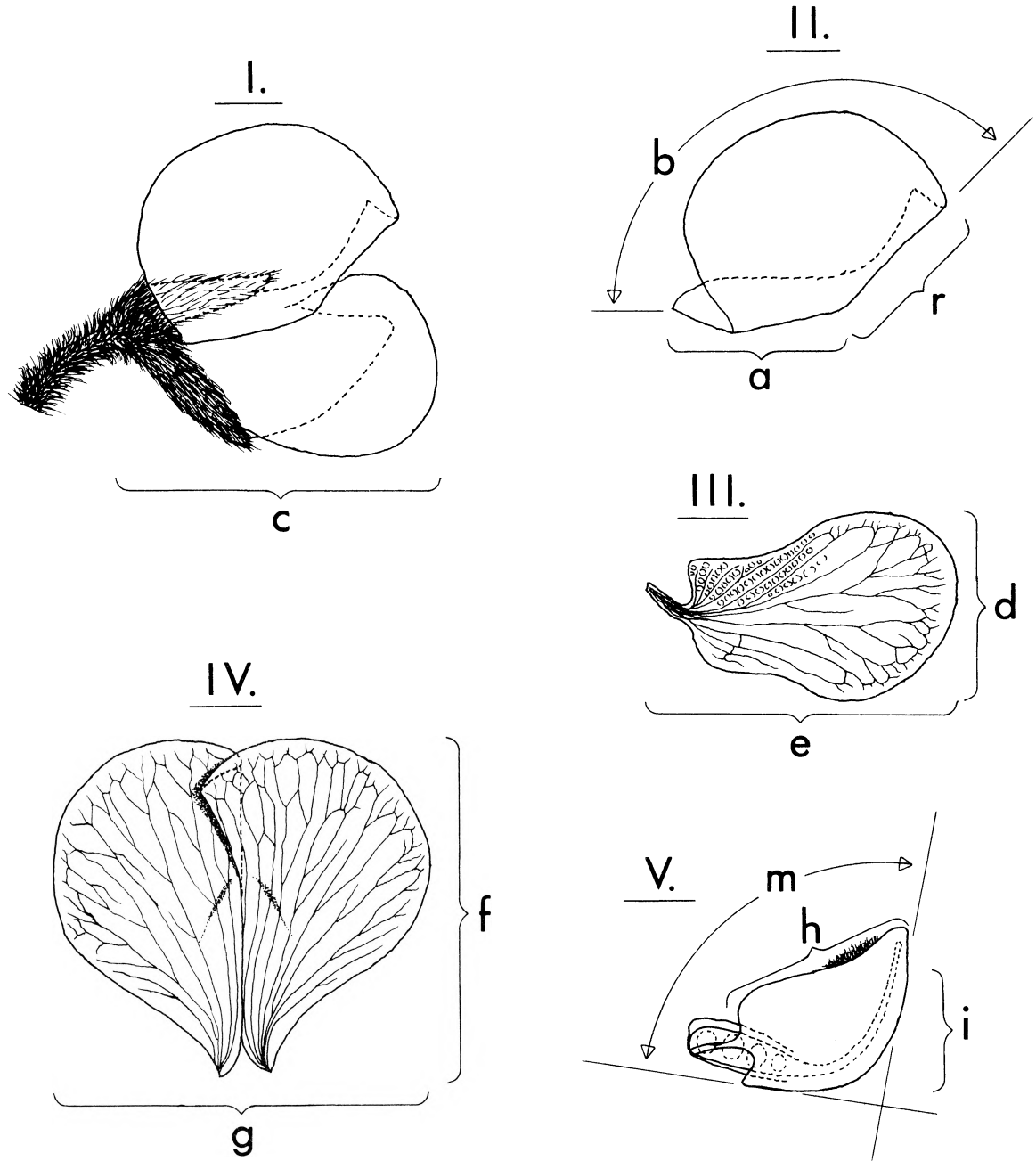


Figure 5-1. Description of selected floral measurements. Diagrams represent: I. whole flower, c = floral length; II. folded banner, b = banner angle, a = appressed portion, r = reflexed portion (r/a = reflexed/appressed ratio); III. wing, d = width, e = length; IV. flattened banner, f = length, g = width; V. keel with reproductive structures, h = length, i = width, m = keel angle.

information each character shared with other characters and relative information contained by each character. The character analysis employs the information theory model developed by Estabrook (1967).

6. Fifteen characters were selected on the basis of this analysis in an attempt to minimize the redundancy among characters employed while retaining sufficient information to segregate the variability present in the objects (see Table 5-2).

7. Two graph cluster analysis were computed as described by Wirth, Estabrook and Rogers (1966). In the first analysis, 54 objects were analyzed using 31 characters (see Table 5-2). In the second analysis, the same set of objects were analyzed with the exception of the omission of object number 12. Fifteen characters were employed (see Table 5-2).

Results of the graph cluster analysis are presented in two forms: (1) the skyline plot and (2) the subgraph. The skyline plot is prepared by the computer and shows the formation of clusters, the degree of similarity at which clusters join, and the "moat" or distinctness of each cluster as indicated by the range in similarity over which a cluster remains unchanged. The skyline plot does not indicate the steps by which clusters were formed or the relationship between clusters. Subgraphs are drawn to show the connections that are

formed between clusters. In addition, internal connections which are a measure of the continuity of a cluster are described by the subgraphs.

Results

The identification of the objects in the dendrogram (Figure 5-2) reflects the original concept of the taxa in the case of the small flowered Lupinus parviflorus complex and follows the monographic treatment of Hess (1969) for the L. caudatus - L. argenteus complex. The presence of well defined groups in the dendrogram is an indication that the choice of characters and designation of attributes is sufficient to describe the objects being analyzed. The distribution of the objects within the groups is mostly consistent with the predetermined treatment of the taxa, as reflected by the fact that most of the groups defined by the dendrogram consist of a single taxon. However, confusion is present in the distribution of L. argenteus var. tenellus, L. palmeri, and to some extent L. fulvomaculatus. The subspecies of L. caudatus are not clearly separated by this treatment. Clustering of L. meionanthus with L. holosericeus is in a stepwise fashion suggestive of a clinal relationship as also in L. myrianthus and L. ingratus.

There are five large clusters defined by the dendrogram. From left to right they are: L. myrianthus - L. ingratus cluster, L. hillii cluster; L. argenteus (ssp. spathulatus and ssp. rubricaulis) - L. parviflorus cluster; the L. depressus - L. evermannii cluster and the L. caudatus - L. holosericeus - L. meionanthus cluster. Lupinus argenteus was split with ssp. spathulatus and ssp. rubricaulis associated closer to L. parviflorus and L. argenteus ssp. argenteus closer to L. caudatus ssp. caudatus and L. caudatus ssp. argophyllus.

Relationships between clusters cannot be deduced from the dendrogram since the linear ordering of objects within clusters is arbitrary. The arrangement of objects above any given verticle axis can be rotated 360^{o}. The definition of the clusters in the dendrogram do, however, provide a source for comparison in further analysis of the 63 characters and their ability to more efficiently describe these clusters.

A survey of the 63 characters indicated that 32 of these characters probably contribute very little to the description of the clusters. A comparison of the clusters formed by the graph cluster analysis of 54 objects using the remaining 31 characters and the placement of the objects in the dendrogram is discussed under analysis of the skyline plots.

Table 5-3 compares the fraction of information shared between each pair of the 31 characters. Those characters which share .30 or more of their information with one or more characters are arranged in Figure 5-3 to show the amount of information shared between these characters in .10 unit intervals. Characters that share less than .30 of their information contribute relatively little to the redundancy in the set of descriptors.

The sum of the fractions of information each character shares with each other character is a measure of the amount of information contained in each character. This sum of fractional information shared is made by adding all the comparisons between each character and all other characters in Table 5-3. These sums are listed in Table 5-4 for each character. Those characters which are highest in total information shared are either the most redundant of characters, or contain the most information for describing the biological relationship between characters. The best character for efficient description of a set of objects are those that share a high proportion of their information with other characters, but contribute little to confusion to the description of the objects, i.e., have a low degree of entropy (Table 5-4). Characters which share little information with other characters contribute little to the classification based on other characters. If such characters are of marginal

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	29	30	31		Characters
	.67	.66	.44	.10	.22	.34	.29	.04	.23	.62	.56	.08	.55	.03	.23	.19	.14	.15	.27	.13	.13	.28	.08	.26	.15	.03	.10	.30	.14	.18	1	Habit
		.40	.21	.06	.12	.26	.12	.06	.16	.36	.36	.08	.30	.03	.09	.09	.02	.07	.07	.13	.09	.14	.05	.14	.09	.04	.03	.13	.11	.16	2	Height
			.28	.07	.16	.29	.14	.04	.34	.56	.51	.06	.19	.11	.08	.14	.08	.10	.11	.15	.16	.28	.05	.13	.10	.09	.04	.17	.16	.08	3	Stem Vesture
				.16	.24	.19	.11	.07	.05	.18	.20	.10	.15	.12	.17	.10	.12	.19	.24	.19	.21	.08	.14	.21	.11	.02	.04	.23	.15	.09	4	Basal Petiole Length
					.11	.05	.02	.03	.01	.09	.08	.04	.07	.03	.08	.09	.10	.09	.08	.04	.05	.04	.03	.07	.06	.04	.02	.10	.04	.01	5	Mid-Cauline Petiole Length
						.10	.05	.05	.05	.11	.12	.07	.13	.04	.09	.23	.24	.22	.44	.31	.10	.06	.05	.48	.21	.01	.07	.49	.09	.06	6	Flower Length
							.23	.04	.13	.25	.25	.07	.18	.04	.09	.05	.07	.10	.06	.10	.12	.07	.03	.10	.08	.02	.03	.13	.13	.05	7	Leaflet Length
								.08	.29	.14	.11	.07	.14	.06	.05	.05	.03	.07	.04	.08	.10	.08	.02	.06	.07	.04	.02	.06	.05	.01	8	Leaflet Width
									.09	.11	.12	.05	.09	.02	.09	.04	.06	.08	.06	.13	.08	.09	.04	.06	.03	.02	.01	.10	.05	.04	9	Leaflet L/W
										.33	.33	.01	.10	.12	.04	.10	.04	.08	.06	.10	.11	.23	.03	.06	.06	.13	.01	.08	.11	.07	10	Leaflet Folding
											.89	.09	.18	.08	.08	.11	.11	.14	.13	.14	.15	.19	.09	.17	.09	.07	.05	.17	.15	.19	11	Leaflet Vesture Above
												.06	.18	.07	.11	.11	.11	.12	.12	.14	.17	.18	.09	.16	.09	.07	.04	.17	.15	.17	12	Leaflet Vesture Below
													.15	.04	.07	.09	.08	.08	.08	.10	.05	.03	.06	.12	.07	.01	.04	.08	.06	.01	13	Peduncle Length
														.02	.05	.07	.05	.08	.09	.11	.07	.09	.07	.12	.06	.02	.03	.14	.05	.02	14	Raceme Length
															.04	.05	.09	.15	.06	.14	.11	.07	.09	.11	.13	.02	.02	.10	.09	.01	15	Bract Length
																.04	.04	.05	.10	.07	.10	.01	.04	.15	.07	.02	.01	.09	.11	.01	16	Pedicel Length
																	.16	.21	.38	.17	.11	.21	.04	.27	.08	.03	.05	.40	.15	.01	17	Calyx Base Shape
																		.62	.28	.22	.12	.05	.06	.27	.15	.03	.06	.29	.10	.03	18	Calyx Upper Lobe Length
																			.23	.19	.12	.05	.04	.25	.12	.04	.06	.23	.09	.01	19	Calyx Lower Lobe Length
																				.32	.11	.09	.05	.44	.18	.01	.06	.50	.09	.01	20	Banner Length
																					.13	.04	.08	.28	.24	.01	.05	.25	.08	.01	21	Banner Width
																						.05	.07	.11	.05	.02	.02	.12	.10	.05	22	Banner r/a
																							.02	.09	.07	.16	.04	.11	.15	.01	23	Banner Vesture
																								.08	.05	.01	.01	.08	.02	.01	24	Banner Angle
																									.23	.01	.07	.43	.11	.02	25	Wing Length
																										.01	.11	.29	.05	.05	26	Wing Width
																											.03	.09	.14	.01	27	Wing Vesture
																												.20	.09	.01	28	Keel Width
																													.08	.02	29	Keel Length
																														.03	30	Keel Angle
																															31	Keel Ciliation

TABLE 5-3. MATRIX OF THE FRACTION OF INFORMATION SHARED BETWEEN EACH PAIR OF 31 CHARACTERS.

TABLE 5-4. COMPARISON OF 31 CHARACTERS FOR INFORMATION SHARED AND ENTROPY

	Character	Sum of fractions of information shared	Entropy
1.	Habit	7.59	.64
2.	Height	4.64	2.07
3.	Stem vesture	5.73	2.27
4.	Basal petiole length	4.79	2.94
5.	Mid-Cauline petiole length	1.86	2.05
6.	Flower length	4.72	2.46
7.	Leaflet length	3.65	2.35
8.	Leaflet width	2.61	1.91
9.	Leaflet L/W ratio	1.87	1.46
10.	Leaflet folding	3.55	1.54
11.	Leaflet vesture above	6.02	1.95
12.	Leaflet vesture below	5.84	1.99
13.	Peduncle length	2.00	1.64
14.	Raceme length	3.55	2.51
15.	Bract length	2.09	1.05
16.	Pedicel length	2.20	1.90
17.	Calyx base shape	3.82	1.68
18.	Calyx upper lobe length	3.83	1.88
19.	Calyx lower lobe length	4.03	2.09
20.	Banner length	4.76	2.34
21.	Banner width	4.13	2.38
22.	Banner r/a ratio	2.98	2.23
23.	Banner vesture	3.06	1.29
24.	Banner angle	1.58	1.91
25.	Wing length	5.06	2.52
26.	Wing width	3.15	1.55
27.	Wing vesture	1.25	.50
28.	Keel width	1.42	.87
29.	Keel length	5.63	2.52
30.	Keel angle	2.92	1.99
31.	Keel ciliation	1.43	1.00

interest they can be discarded. However, if a character shares little information, but has a low level of entropy, it may be functional in describing a small set of the objects. Their inclusion with a small set of selected characters would be valuable on this basis.

Figure 5-3 indicates the presence of three groups of characters that are highly correlated among the 17 characters which share the most information. The group of vegetative characters (1, 2, 3, 4, 7, 10, 12, 14) can be divided into two groups of characters which may be biologically related. Characters 1, 2, 4, 7, and 14 are size functions of the vegetative portions of the plant. Characters 3, 11, and 12 are measures of pubescence which may be biologically related to the leaflet folding, character 10, on the basis of being similarly influenced by environmental stresses. A harsh environment selecting for greater pubescence may also select for a folded leaflet.

From the characters in Figure 5-3 the following were selected to be used in an attempt to describe the objects more efficiently by reducing the redundancy in the set of descriptors: 1, 3, 6, 7, 11, 12, 19, 20 and 29 (see Table 5-4). Six additional characters: 8, 17, 23, 24, 28 and 30 (see Table 5-4) were added to provide descriptors thought to be functional in the description of small groups of objects, such as L. depressus, and for analysis of the apparent confusion that exists between closely related taxa. An example of the latter is provided by

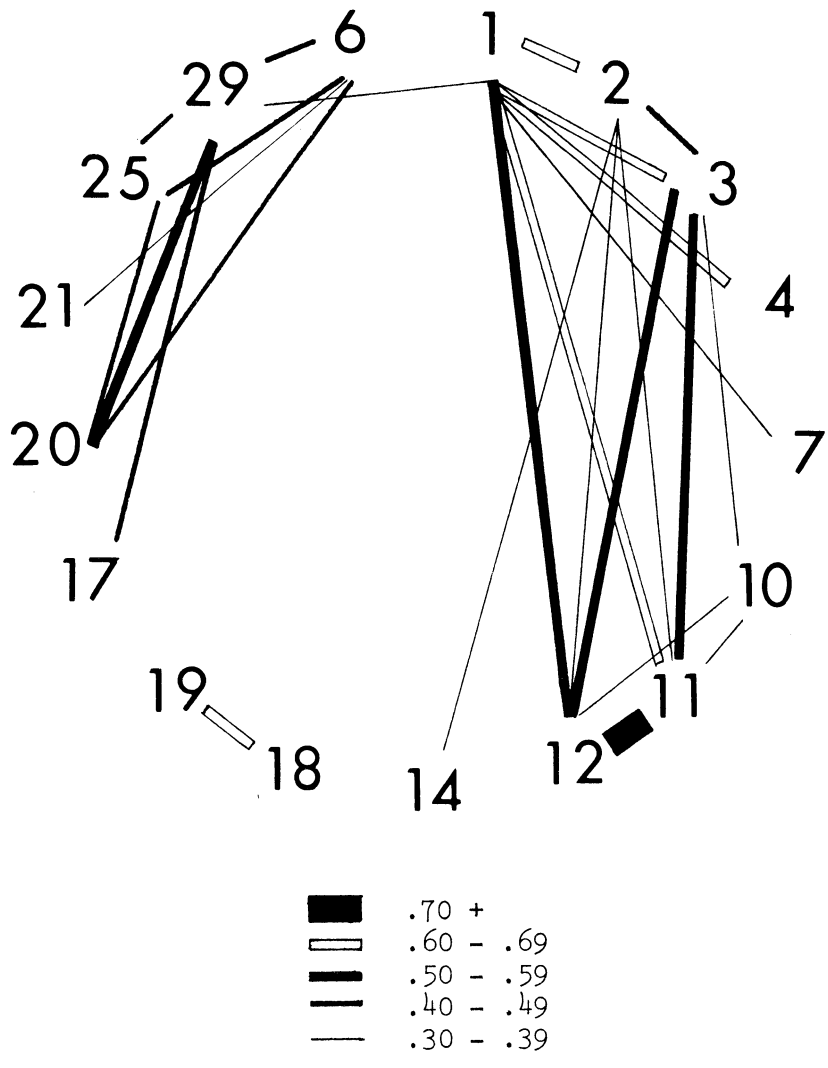


Figure 5-3. Fraction of information between characters sharing greater than .30 of their information (see Table 5-2 for description of characters).

character 17, calyx base shape, which was thought to have been functional in describing Lupinus caudatus and L. holosericeus. The only consistent morphologically difference between L. meionanthus and L. holosericeus is the presence of pubescence on the back of the banner in the latter, providing the reason for including character 23 in the analysis. The leaflet width (8), banner angle (24), keel width (28) and keel angle (30) were thought to have been functional in relating L. myrianthus to L. fulvomaculatus and L. ingratus. These characters would not otherwise have been included on the basis of a high sum of fractional information shared or low entropy (Table 5-4).

Results of the graph cluster analysis are presented for analysis of 54 objects representing all taxa included in the study. In the first analysis 31 characters are used as listed in Table 5-4. In the second analysis 15 characters selected from the character analysis are used to determine the effectiveness of reducing the number of characters in a description of the objects. Presentation of the results make use of the skyline plot and subgraph in each case.

The skyline plot for the analysis of 54 objects described by 31 characters is presented in Figure 5-4. The similarity value at which two or more objects join to form a cluster can be determined by the horizontal lines which join the objects. These lines, when extended to the left, intercept the similarity scale or C value scale,

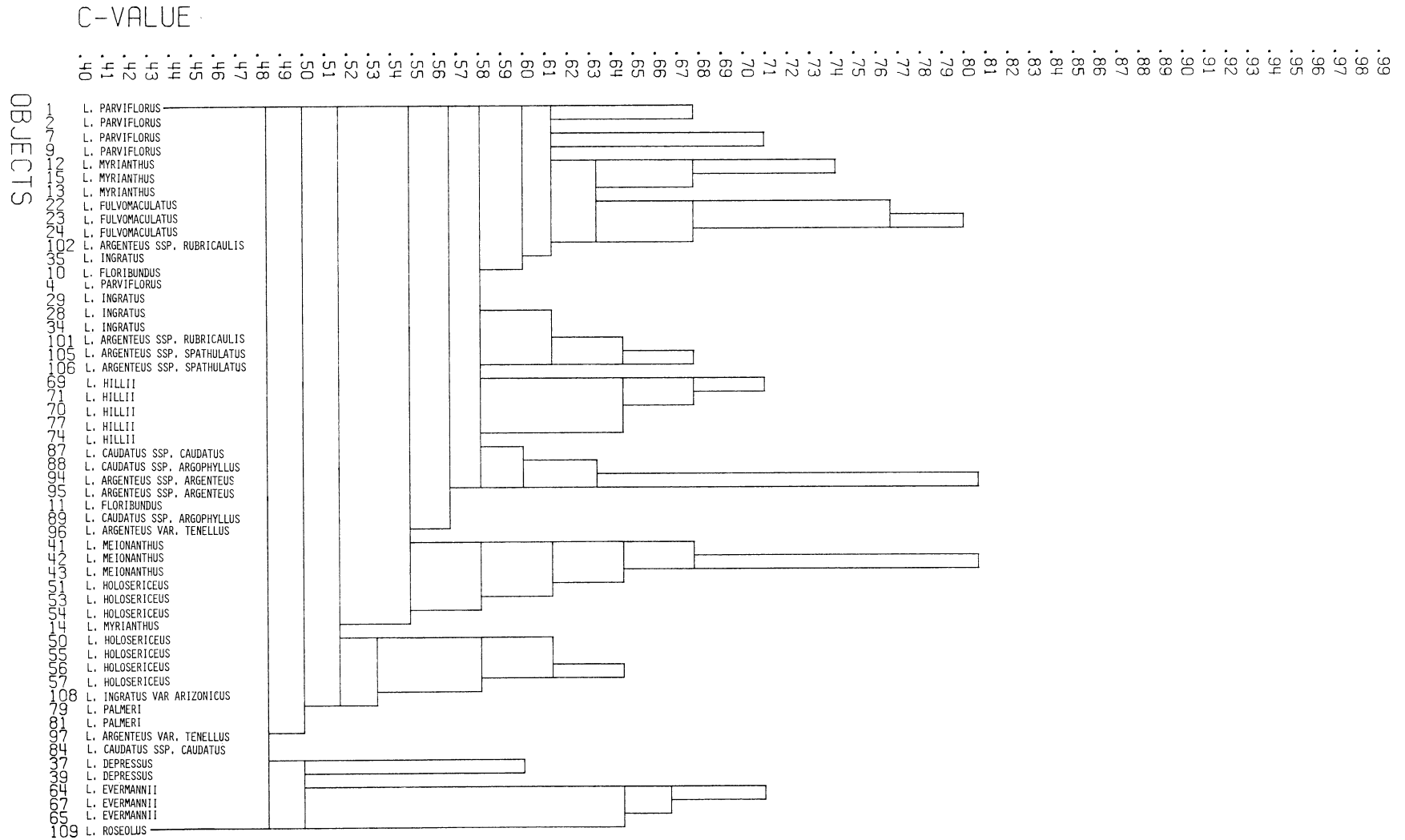


Figure 5-4. Skyline plot of 54 representative specimens of the Lupinus parviflorus and L. argenteus - L. caudatus complexes as described by 31 characters.

giving the highest degree of similarity at which the cluster exists. The exclusiveness of a cluster is a measure of the difference between the similarity value at which a cluster first forms and the similarity value at the point of acquisition of additional members. This exclusiveness is termed the "moat" by Wirth et al. (1966).

Inclusion of each object number in the clusters of the graph can be made by extending a line parallel to the verticle axis of the graph from the number to the highest horizontal line above it. The first major cluster is complex, including a number of smaller clusters, and consists of objects 1, 2, 7, 9, 12, 15, 13, 22, 23, 24, 102, 35 and 10 (listed sequentially as they appear in Figure 5-4). All of these objects except numbers 102 and 35 belong to the L. parviflorus complex of small flowered perennials of the Rocky Mountains. Objects 102 and 35 are Lupinus argenteus ssp. rubricaulis and L. ingratus respectively. Additional members of these latter two taxa make up the next small cluster (numbers 29, 28, 34, 101, 105 and 106). The third cluster is composed solely of L. hillii (numbers 69, 71, 70, 77 and 74). The fourth cluster consists of L. argenteus and L. caudatus. The grouping of L. meionanthus and L. holosericeus in the fifth and sixth clusters is similar to the clustering of these objects in the dendrogram (Figure 5-2). Lupinus

depressus (numbers 37 and 39) form a small distinct cluster which unite only at a very low similarity value with L. evermannii (numbers 64, 67 and 65) and L. roseolus (number 109).

The composition of the clusters in the 15 character graph cluster analysis, as presented by the skyline plot in Figure 5-5, is basically similar to the cluster composition in the 31 character analysis. The higher similarity values in Figure 5-5 are reflective of the fact that an increase in the efficiency in a set of characters, made possible by selection of characters with the highest information content and lowest entropy, increases the probability that two similar objects will have the same attribute values for each character.

Figure 5-6 presents the same clustering analysis as presented in the skyline plots (Figures 5-4 and 5-5), in a different form. The subgraphs in Figure 5-6 define the relationship between clusters, the position of connections that form between clusters, and the internal continuity of clusters for both the 31 and 15 character analyses.

Formation of the clusters in subgraphs I and II is very similar. Objects representing Lupinus parviflorus and allied taxa cluster early in the graph development. This primary cluster is joined by smaller clusters of L. argenteus ssp. rubricaulis, L. argenteus ssp.

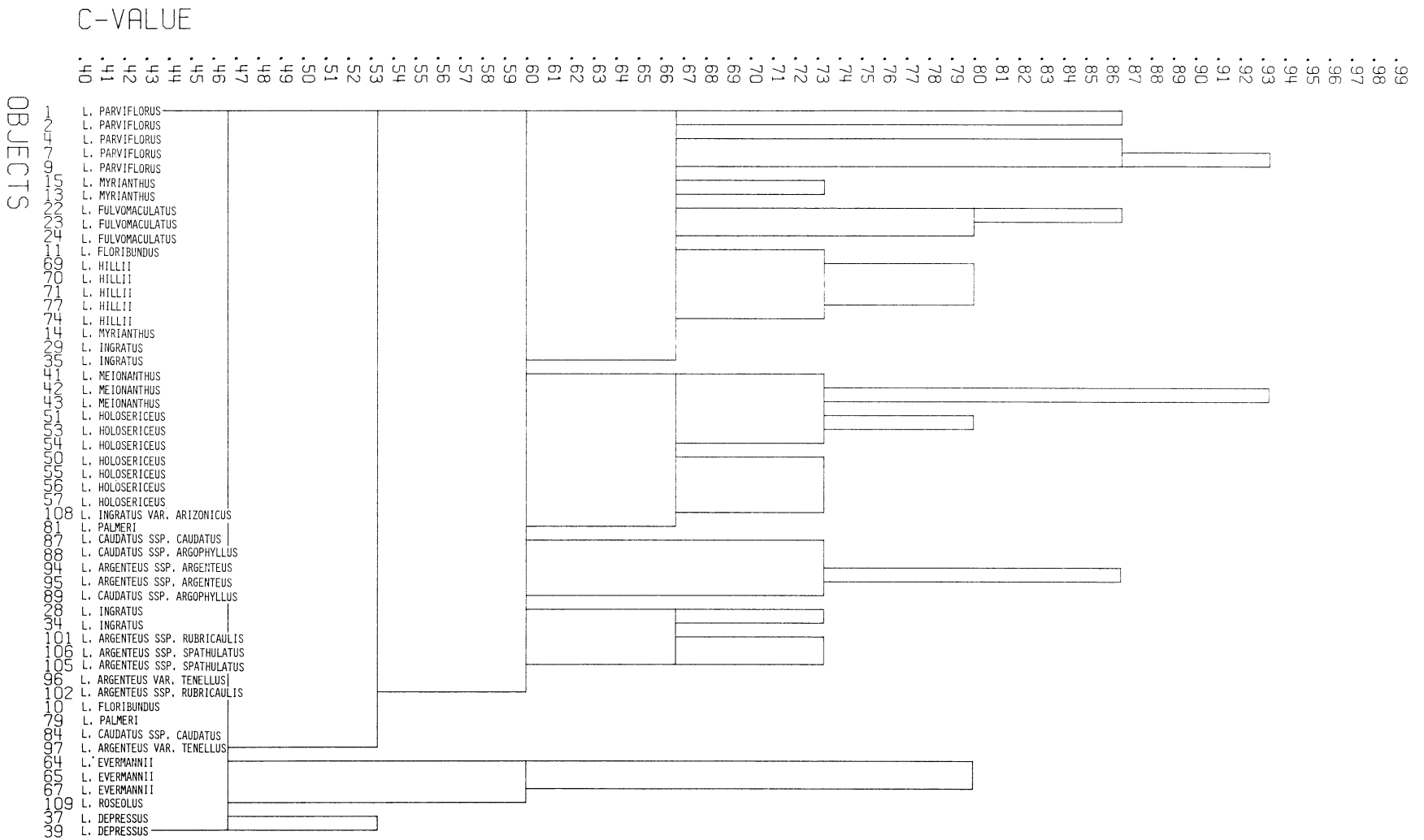


Figure 5-5. Skyline plot of 53 representative specimens of the Lupinus parviflorus and L. argenteus - L. caudatus complexes as described by 15 characters.

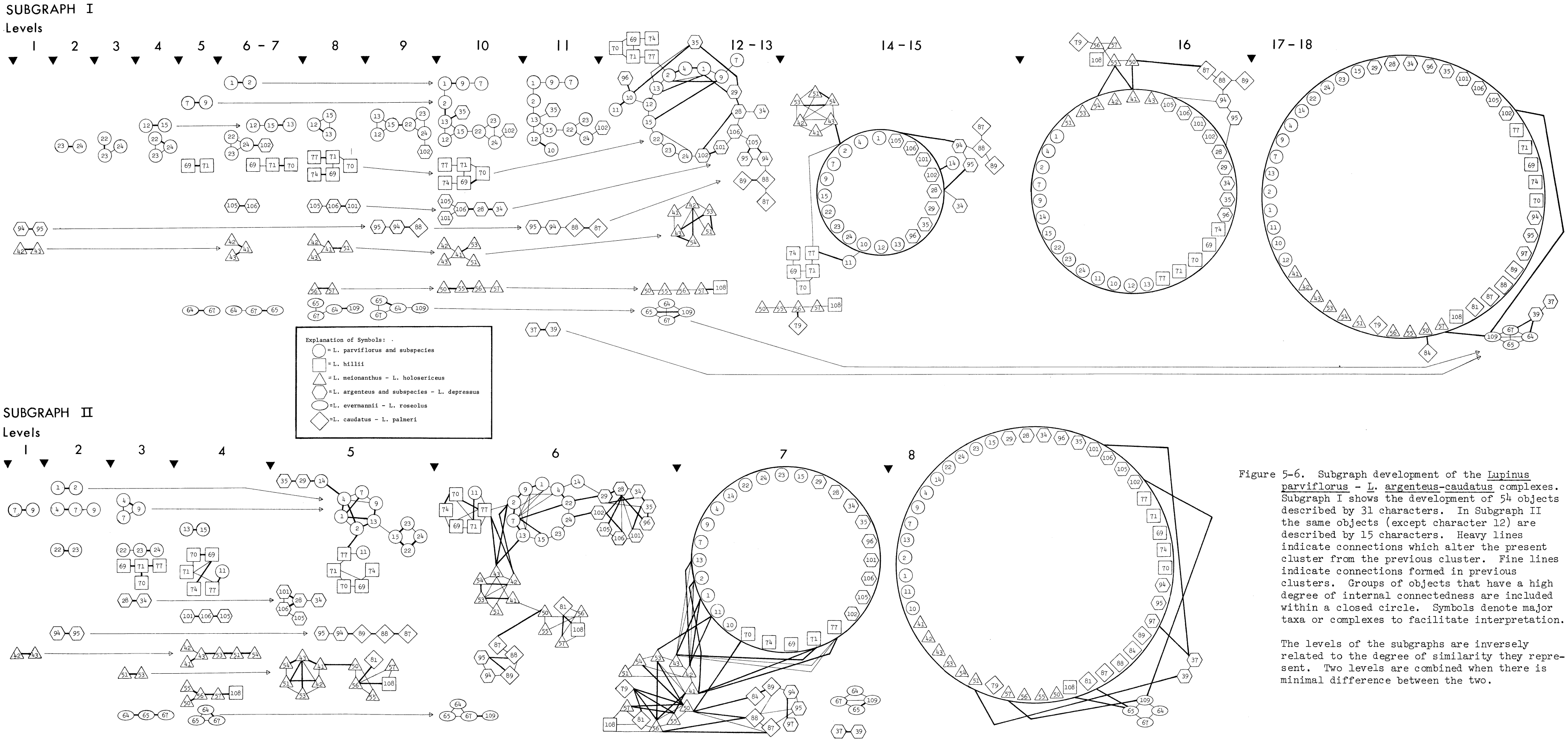


Figure 5-6. Subgraph development of the Lupinus parviflorus - L. argenteus-caudatus complexes. Subgraph I shows the development of 54 objects described by 31 characters. In Subgraph II the same objects (except character 12) are described by 15 characters. Heavy lines indicate connections which alter the present cluster from the previous cluster. Fine lines indicate connections formed in previous clusters. Groups of objects that have a high degree of internal connectedness are included within a closed circle. Symbols denote major taxa or complexes to facilitate interpretation.

The levels of the subgraphs are inversely related to the degree of similarity they represent. Two levels are combined when there is minimal difference between the two.

spathulatus, L. ingratus and L. hillii. Lupinus holosericeus and L. meionanthus form small clusters which connect with the larger L. parviflorus cluster at a low similarity.

In both subgraphs the same three L. holosericeus specimens form a cluster with L. meionanthus indicating confusion in the morphology of these two taxa. Lupinus argenteus ssp. argenteus and L. argenteus ssp. tenellus are grouped with the L. caudatus subspecies. Lupinus palmeri exhibits the same inconsistency of affinity in the subgraphs as was evident in the dendrogram.

Lupinus evermannii collections form an early cluster with the L. roseolus specimens and remain independent until the last clustering stage. Lupinus depressus collections form a cluster at a later level, but also remain independent until the last stage of clustering. In subgraph I the two small distinct clusters form connections between themselves at the same level that they join the main cluster. In subgraph II they remain independent.

Lupinus floribundus is morphologically intermediate in position to L. hillii and L. myrianthus. This is particularly evident in subgraph I where in level 14-15, objects 10 and 11 form part of the connecting bridge between L. parviflorus and L. hillii clusters. In

subgraph II, L. floribundus (number 11) is linked at an early stage to L. hillii which, together with object number 10, join the L. parviflorus cluster at level 7.

Discussion and Conclusions

The attempt to describe the morphological variability of the Lupinus parviflorus complex and related taxa, as efficiently and precisely as possible, required analysis of as much of the variability present in these taxa as could be reasonably manipulated by the computer. Analysis of this variability demanded that no prior assumptions be made regarding the relative ability of each of the characters to describe the set of objects being described. For this reason, all 63 morphological characters were used in the first description of the objects.

The dendrogram produced by the analysis of 107 specimens, using the 63 characters, becomes a basis of comparison for analysis of the effect of reducing the number of descriptors (characters). Because the clusters described in the dendrogram remained essentially unaltered through the reduction of the number of characters, it is probable that the final set of 15 characters contains most of the information necessary to describe the taxa being analyzed. It is unlikely that the reduction in the set of objects from 107 to 54 could have

altered the definition of the clusters, since the 54 objects represented roughly equal portions of each of the clusters defined by the dendrogram.

The 15 characters chosen to describe the objects in the last cluster analysis are not necessarily the best characters. It is possible that some of the confusion present in those characters not used for the description of the subgraphs could be filtered out by a better definition of their character states. The group of highly correlated characters (Figure 5-3) describes four different sets of descriptors:

1. Vegetative lengths (leaflet, stem, habit and petioles),
2. Vegetative vesture (stem and leaflet surfaces) and leaflet folding,
3. Calyx lengths (upper and lower lobes), and
4. Petal lengths (banner length, banner width, keel length) and calyx base shape.

The vegetative characters, though highly correlated, probably represent different measures of highly related biological phenomena. The two groups of floral characters are relatively independent, sharing less than 30% of their information between any two characters, one from each group. It is somewhat of a puzzle why the calyx base shape should be highly correlated with petal measurements, specifi-

cally 40% correlated to keel length. It must be emphasized that the correlation of characters presented in this study does not necessarily hold for any smaller or larger set of taxa. It should also be noted that the correlation of characters can be affected both genetically and environmentally. Neither possibility has been tested in this study.

The development of the dendrogram and subgraphs indicates a lack of continuity among the small flowered lupines when considered as a group. When treated with the Lupinus argenteus - L. caudatus complex, portions of the small flowered lupines demonstrate affinities to either the L. argenteus or L. caudatus portion of this complex. Lupinus parviflorus and its subspecies (as treated in Chapter VI on the taxonomy of the small flowered lupines) L. parviflorus ssp. parviflorus, L. parviflorus ssp. myrianthus, and L. parviflorus ssp. floribundus have a close affinity with L. argenteus ssp. rubricaulis and L. argenteus ssp. spathulatus and L. argenteus ssp. ingratus. Lupinus hillii is linked to L. parviflorus ssp. parviflorus and L. parviflorus ssp. myrianthus. Lupinus parviflorus ssp. floribundus is morphologically very similar to L. hillii as is shown by the early linkage of object 11 to the L. hillii cluster in subgraph I (Figure 5-6). Lupinus parviflorus ssp. floribundus is known only from a few old collections made in the type locality. Any treatment of this taxon must be considered tentative until new collections are made.

Lupinus holosericeus and L. meionanthus are very similar taxa that have an affinity for L. caudatus ssp. caudatus and L. caudatus ssp. argophyllus. Lupinus meionanthus also forms connections with L. parviflorus ssp. parviflorus and L. hillii. The relationship between L. meionanthus - L. holosericeus and L. caudatus is probably heavily influenced by the pubescence of the vegetation and also the pubescence on the back of the banner in L. holosericeus and even more densely so in L. caudatus. In addition, the flower size ranges almost continuously from the smallest in L. meionanthus to the largest in L. caudatus, with L. holosericeus intermediate. The affinity between L. meionanthus and L. parviflorus - L. hillii is probably superficially dependent on the similarly small flower sizes.

The affinity between the Lupinus parviflorus and L. caudatus is probably through L. argenteus ssp. argenteus and L. argenteus ssp. argenteus var. tenellus. Lupinus argenteus ssp. spathulatus and L. argenteus ssp. rubricaulis form the links between L. parviflorus and L. argenteus ssp. argenteus.

The confusion that exists in L. palmeri, L. argenteus ssp. argenteus var. tenellus, and L. caudatus hybrids may be due to one or both of the following causes:

(1) The characters and character states were not adequate to describe the proper affinities of these objects,

(2) The objects may not represent a natural taxon.

Lupinus argenteus ssp. argenteus var. tenellus has been described as a natural hybrid and as in the L. caudatus hybrids, were scattered in the dendrogram and subgraphs because they represent intermediates to natural taxa. Lupinus palmeri has not been described as a hybrid and the parameters of this species should be re-examined to see if a new definition of the species is required or better descriptors should be provided for a taximetric analysis.

The models provided in this taximetric analysis should not be looked upon as providing the final solutions to the taxonomy of the taxa under study, but as a working context for further analysis of all kinds.

CHAPTER VI

TAXONOMY

A. THE LUPINUS PARVIFLORUS COMPLEX AND ALLIED SPECIES.

Plants perennial, erect or decumbent; stems 1 - 11 dm tall, solitary or more commonly several arising from a woody caudex, variously pubescent to glabrate; basal leaves present or absent at anthesis; cauline leaves few to many; leaflets 6-12 linear-elliptic to broadly oblanceolate, apices acute to obtuse or emarginate, largest 1.0-6.8 cm long, 2.5-16.0 mm wide, variously pubescent to glabrous on upper surface; flowers in densely to sparsely flowered racemes; calyces bilabiate, obtuse to gibbous, lips entire or shallowly toothed, upper-lip of two fused sepals, lower-lip of 3 fused sepals; flowers light to dark blue or cream (rose tinged in L. roseolus Rydb.), 5.5-10.0 mm long; banners variously pubescent, reflexed above the midpoint, reflexed/appressed ratio (r/a) of 0.39-0.76, 5.5-9.0 mm long, 5.0-9.0 mm wide; wings glabrous, clawed, 5.8-10.2 mm long, 3-5 mm wide, fused distally; keels ciliate or glabrous on the upper margin, glabrous laterally, apices short and blunt or elongate-arcuate, reflexed at 65 - 108°; ovules 3-5; seeds variously colored.

The small flowered perennial lupine species treated here include a diverse group of plants. They are believed to represent multiple derivations from the large flowered Lupinus argenteus - L. caudatus complex. In addition, L. meionanthus, originally included because of its apparent affinity with L. holosericeus, has subsequently been shown to be at most only distantly related to L. holosericeus.

B. KEY TO THE LUPINUS PARVIFLORUS COMPLEX AND ALLIED SPECIES.

1. Leaflets strigose to densely sericeous above . . . . . (2)

    2. Plants decumbent spreading, forming large mats: flowers 8.5-10.2 mm long; keel glabrous . . . . 6. L. depressus

    2. Plants erect, not forming mats; flowers less than 8.5 mm long; keel ciliate on upper margin.

        3. Stem vesture of variable length with both long appressed to spreading hispidulose and short dense strigose hairs; plants of Arizona and New Mexico . . . . . (4)

            4. Flowers 5.2-7.0 mm long; stems appressed to ascending pubescent; banner glabrous or with few scattered hairs . . . . . 2. L. hillii var. hillii

            4. Flowers 7.0-8.2 mm long; stems and banners various.

                5. Stems appressed to ascending pubescent; banner glabrous . 2a. L. hillii var. arizonicus

                5. Stems spreading hispidulose; banner pubescent dorsally 2b. L. hillii var. osterhautianus

3. Stem vesture of uniform length, plants not from Arizona or New Mexico.

6. Banners densely pubescent dorsally; leaves silky sericeous 4. L. holosericeus

6. Banners glabrous or at most with sparsely scattered hairs.

7. Flowers 5.0-6.8 mm long; foliage silky sericeous; plants of Sierra Nevada Mts. 3. L. meionanthus

7. Flowers 7.0-8.0 mm long; foliage spreading or appressed canescent; plants of central Idaho 5. L. evermannii

1. Leaflets glabrous above (sparsely strigose in L. parviflorus ssp. floribundus and L. roseolus) . . . . . (8)

8. Keels elongate, arcuate, glabrous; flowers mostly cream, tinged with blue or rose . . . . . (9)

9. Plants less than 20 cm tall; flowers rose tinged . . . . . 7. L. roseolus

9. Plants greater than 25 cm tall; flowers cream (occasionally with blue tinge) . . . . . 8. L. argenteus ssp. ingratus

8. Keels short blunt; ciliate near acumen; flowers blue (10)

10. Leaflets sparsely strigose above, at least on lower leaves; stems strigose with few long hispidulose hairs . . . . . 1c. L. parviflorus ssp. floribundus

10. Leaflets glabrous above; stem vesture puberulent.

11. Leaflets narrowly oblanceolate to oblanceolate . . . . . 1a. L. parviflorus ssp. myrianthus var. myrianthus

11. Leaflets broadly oblanceolate

12. Eyespot light brown on drying; plants of Wyoming, Montana and Idaho . . . . 1. L. parviflorus ssp. parviflorus

12. Eyespot dark brown on drying; plants of SW Colorado and adjacent Utah . . . . 1b. L. parviflorus ssp. myrianthus var. fulvomcaulatus

1. Lupinus parviflorus (ssp. parviflorus) Nutt., Hook. and Arn. Bot. Beechy Voy. 336. 1840.

   Type: "Columbia Plains," Nuttall (PH; Isotype GH; photo UC, UMO).

Synonymy: L. allimicranthus C. P. Smith, Sm. Spec. Lup. 318. 1942.

Type: IDAHO, Fremont Co., Warm River Dugway, R. J. Davis June 13, 1930 (IDS; photo UMO).

L. argenteus ssp. parviflorus (Nutt.) Phillips (pro parte), Wash. State Coll. Res. Studies 23: 190. 1955.

L. argenteus var. parviflorus (Nutt.) C. L. Hitchc. Vasc. Pls. Pacific N. W. 3: 302. 1961.

Common name: Lodge-pole Lupine.

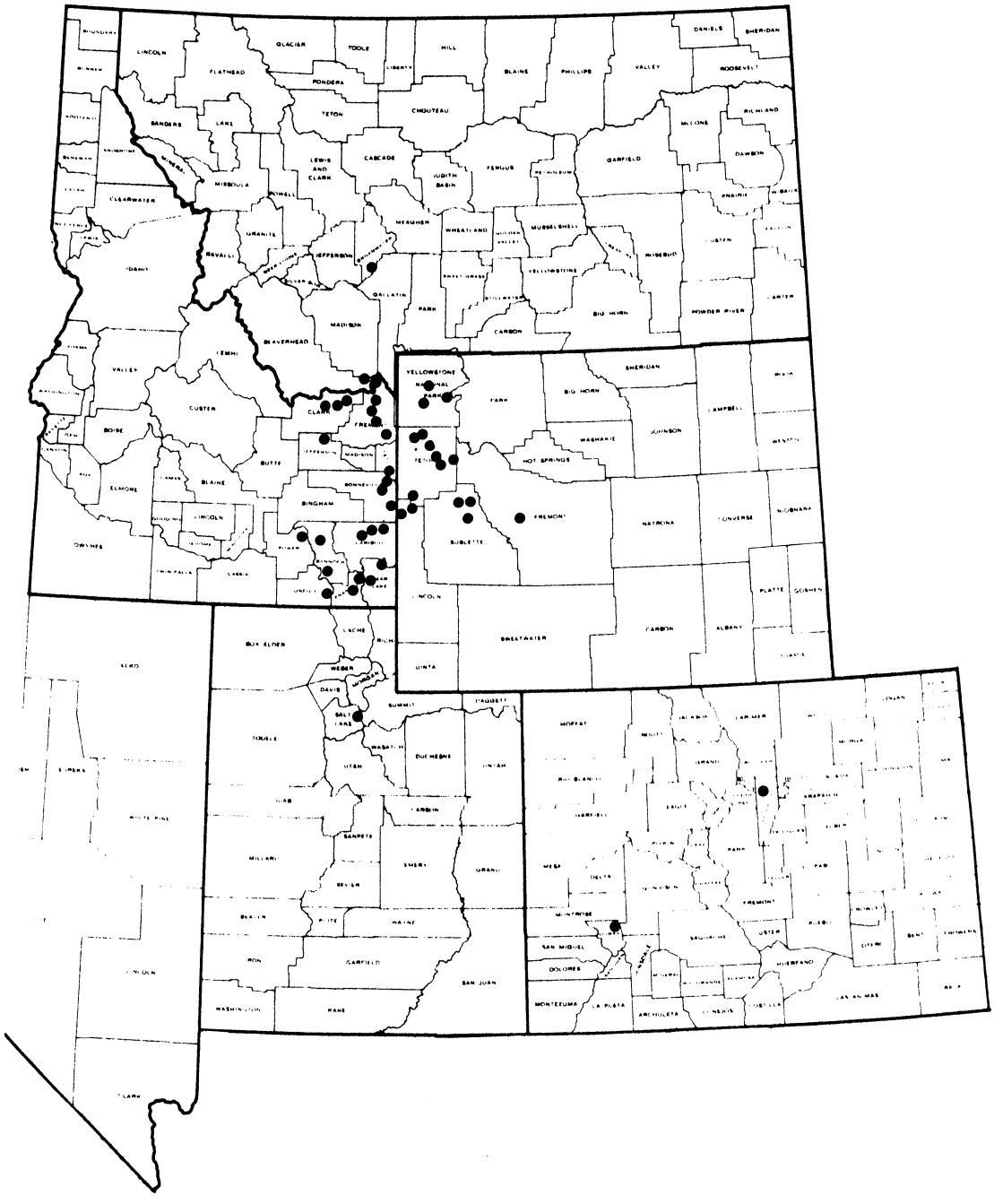
Plants erect; stems 1 to several from a woody caudex, 2.0-7.0 dm tall, mostly 2-4 mm in diameter, minutely appressed pubescent, glabrate below in age, sparsely branching above; lower leaves fallen or withered at anthesis; petioles short, mostly 2-4 cm long; stipules setaceous to narrowly triangular, 3-5 mm long basally connate about 1 mm to petiole; leaflets 7-9, largest 2.5-6.0 mm long, 5-16 mm wide, L/W ratio 2.8-5.3, glabrous above, minutely puberulent below, broadly oblanceolate to obovate, rounded or mucronulate; peduncles 1-6 cm long; racemes 3.5-20.0 cm long,

subverticillate, verticils 7-10 mm distant; bracts 2.5-6.0 mm long, 1 mm wide, narrowly lanceolate; pedicels 1.8-4.5 mm long, villous; flowers blue, 6-8 mm long; calyces villous, upper-lips obtuse, 2.8-4.0 mm long, minutely notched, lower-lips 3.2-5.0 mm long, entire; bracteoles about 1 mm, attached to the apex of the angle between calyx lobes; banner glabrous, 5.5-7.5 mm long, 6.5-9.0 mm wide, suborbicular, r/a ratio 0.5, banner angle 125-136°; wings 6.0-8.0 mm long, 3.0-4.5 mm wide, claw 0.8-1.5 mm long; keels 5.5-6.0 mm long, 2.5-3.0 mm wide, ciliate near acumen, angle of keels 70-80°; ovules 3-4; pods 2.0-2.5 cm long, 6.0-7.5 mm wide, villous; seeds 2-3, mottled from light grey to grey-brown with darker flecks, 4 mm x 3 mm x 1.5 mm.

Lupinus parviflorus ssp. parviflorus is commonly found in damp woods of lodgepole pine, spruce or fir, but occasionally in drier sites of sagebrush grassland. It occurs mostly between 5,500 and 8,500 feet in elevation. The distribution of L. parviflorus ssp. parviflorus is limited to western Wyoming, eastern Idaho, southeastern Montana, and scattered into northern Colorado and northeastern Utah. Flowering begins in mid-June and continues until mid-September.

Morphologically this subspecies blends into L. parviflorus ssp. myrianthus and L. parviflorus ssp. myrianthus var. fulvomaculatus especially in central Colorado and central Utah. However, these intermediates may represent only environmental modifications of the latter two southern taxa which normally have narrower leaves and a dark eyespot, especially in var. fulvomaculatus, where it is particularly evident on drying.

Figure 6-1. A typical specimen of Lupinus parviflorus ssp. parviflorus.



Map 1. Distribution of Lupinus parviflorus ssp. parviflorus

Distribution of Lupinus parviflorus ssp. parviflorus (Map 1).

Partial citation: COLORADO: JEFFERSON CO.: Evergreen, C. P. Smith 4030 (RM - intermediate to L. parviflorus ssp. myrianthus). OURAY CO.: Colona, Mts E, Payson 2339 (MO, RM, UC - intermediate to L. parviflorus ssp. myrianthus var. fulvomaculatus).

IDAHO: BANNCOCK CO.: Garden Cr, S. 3, T. 95, R. 35E, Lingenfelter 741 (COLO, NY, RSA, UC, WIS, WTU); Pocatello, 11 mi SW, Christ and Christ 18548 (NY); Scout Mtn, T. 8S, R. 35, S. 34, Baker 9591 (WTU); Summit Ranger Sta, 2 mi W, T. 12S, R. 36E, S. 31, Baker 9328 (WTU). BEAR LAKE CO.: Liberty, 6 mi W, Christ 16179 (NY); Georgetown, 11 mi NE, Christ and Christ 18845 (NY). BONNEVILLE CO.: Swan Valley, 27 mi SE, Christ and Christ 18927 (NY); Big Hole Mts, Victor 9 mi SW, Hitchcock and Muhlick 22915 (RM); 14 mi NE, Christ 16310 (NY). CARIBOU CO.: Davis Cr Trail, Blackfoot Tr Rd, Harmon 1405 (UMO); Mill Canyon Campground, Caribou Natl Forest, Harmon 1404 (UMO); Soda Springs, 49 mi NE on Diamond Cr, Christ 16140 (NY); 44 mi NE, Christ 16144 (NY); Blackfoot R Rd, 25 mi E on Lander Tr Rd, Harmon 1407 (UMO). CLARK CO.: Killgore, near; W Fork Camas Cr, Rust 777 (US); Christ 2953 (NY); 4 mi E, Christ 15494 (NY); Pass, Taylor and Odell Cr, Schmautz, Wallstein and Conner 195

(US); Spencer, 3 mi above Beaver Cr, Cronquist 1301 (IDS, MO); Beaver Canyon, Shear 5054 (US). FRANKLIN CO.: Liberty, 14 mi W, Christ 16186 (NY); Strawberry Cr Ranger Sta, 2 mi W, Baker 9298 (WTU). FREMONT CO.: Henry Lake, wooded hillside SW of, Payson and Payson 2035 (MO, RM); Henry's Fork of Snake R, N of Ashton, Cronquist 1649 (MO); Last Chance, 2 mi S, Harmon 1455 (UMO); Ashton, 10 mi N, Cronquist 1533 (MO, WTU); N, Christ 5487 (NY); 8 mi N, Maguire and Maguire 1261 (RM); Drummond, 2 mi SW, Christ 16295 (NY); Macks Inn, 25 mi S, Christ 15482 (NY); Island Park, near, Henderson 4836 (GH, OSC, WS). ONEIDA CO.: Preston, head Worm Cr Valley, C. P. Smith 2177 (UMO). TETON CO.: Victor, hills SE, Payson and Payson 2166 (NY, RM); Victor, Merrill 374 (US); Merrill and Wilcox 1022 (GH, NY, RM, US); Moose Cr, Christ 5240 (NY); 5 mi SW, Christ 16312 (NY).

MONTANA: GALLATIN CO.: Forks of the Madison, Rydberg and Bessey 4440 (GH, NY, US). BEAVERHEAD CO.: Red Rock Pass, Hitchcock 23877 (COLO, RM). MADISON CO.: Beaver Cr, Schmautz 138 (US).

UTAH: SALT LAKE CO.: Wasatch Mts, Upper Mill Cr Canyon, Downey 15 (UMO).

WYOMING: BIG HORN CO.: Powder R, Goodding 330 (COLO, RM). FREMONT CO.: Jct Hwy 789 and 28, Gillett and Taylor 11584 (UMO); Sublett Pass, above Brooks Lake, Harmon 1430 (UMO); Wind R, 10 mi W, Costello and Rollins 2059 (MO); Jct Brooks Lake Rd and Hwy 26-287, 3 mi N, Harmon 1413 (UMO). LINCOLN CO.: Alpine, on Snake R near Idaho boundary, Payson and Armstrong 3498 (COLO, RM); Hoback Jct, 5 mi S, Harmon 561 (UMO). SUBLETTE CO.: New Fork Lakes, A. Nelson 10129 (RM); Kendall, Payson and Payson 2945 (MO, NY, POM, UC, US); lower end, Payson et al. 4382 (GH, MO, RM, WS); Green R Lakes, Owenby 1131 (MO, RM, WS). TETON CO.: Camp Davis, Hoback R, Wehmeyer 5019 (GH, NY), Loveland 5019 (MO); Hoback Jct, 5 mi S, Harmon 562, 561 (UMO); Jackson Lake, Cantelow July 10, 1942 (US), Gleason 197 (WS); campground at N end, Dunn 12300 (UMO); Jct rd to Yellowstone near Ranger Sta, Dunn 9270 (UMO); 15 mi N, Dunn 9271 (UMO); Oxbow Bend, Buffalo Fork R, Harmon 555 (UMO); Summit, 7 mi W, Dunn 9265 (UMO); Turpin Ranch Rd, 1/2 mi E, Dunn 9265 (NY); Black Rock Meadows, Williams 1609 (MO); Teton Wilderness Area, S. 36, R. 112W, T. 8N, Venrick 369 (MO); Moran, Nelson and Nelson 1069 (MO, NY); Togwotee Pass, Brenckle 39-240 (MO); Jackson Hole Wildlife Pk, Reed and Reed 1288 (RM); Near Swan Lake, Solheim and Solheim 4909 (RM); Buffalo Fork Jct, 16 mi

E, Harmon 1445 (UMO); Jct Two Ocean Lake Rd and Hwy 89-287, Harmon 1442 (UMO); Moran Jct, 13.9 mi N, Cox, Dunn, Harmon 704 (UMO); Teton Forest Res, Brandegee July and Aug 1897 (US); Wind R Lake and Hwy 287, 2 mi N, Cox, Dunn and Harmon 706 (UMO); Entrance Grand Teton Natl Pk, 4 mi S, Harmon 550 (UMO). YELLOWSTONE NATL. PK.: Letterman Aug 5, 1885 (MO); Hwy A, halfway between Yellowstone Lake and Lewis Lake, Dunn 12298 (UMO); Sylvan Pass Rd, F. H. Smith 151 (WS); Yellowstone Lake, Nelson and Nelson 6562, 6609 (RM).

1a. Lupinus parviflorus ssp. myrianthus comb. nov.

Basionym: Lupinus myrianthus Greene, Pitt. 4:134, 1900.

Type: COLORADO, meadows about Gunnison, E. L. Greene Sept. 1, 1896.

Synonymy: Lupinus leptostachyus Greene, Pl. Baker. 3:36. 1901.

Isotypes: COLORADO, Sapinero, Gunnison watershed, Baker 182 (GH, MO, NY, UC, US; photo UMO).

Plants perennial, erect, 1 to several stems from a woody caudex, branching in upper 2/3 of stem; stems 4-10 dm tall, 2-6 mm in diameter, minutely puberulent except for occasional sparsely strigose pubescence in axils of leaves; leaves mostly cauline, basal leaves usually absent by anthesis; petioles 2-5 cm long; stipules 5-8 mm long, basally connate for 2-3 mm, narrowly triangular; leaflets 6-9, oblanceolate to linear-elliptic, acute to occasionally obtuse on lower most leaves, largest 2-5 cm long,4-8 mm wide, glabrous above, sparsely to densely strigulose below; peduncles 1.5-4.5 cm long; racemes 10-20 cm long, densely subverticillate; bracts lanceolate, 3.5-5.0 mm long, caducous; pedicels 2-3 mm long; flowers light blue, 6-8 mm long; calyces villous, upper-lips obtuse at base, 3.0-4.5 mm long, lower-lips 3.5-5.0 mm long, bracteoles minute, attached in angle of upper and lower calyx lobes;

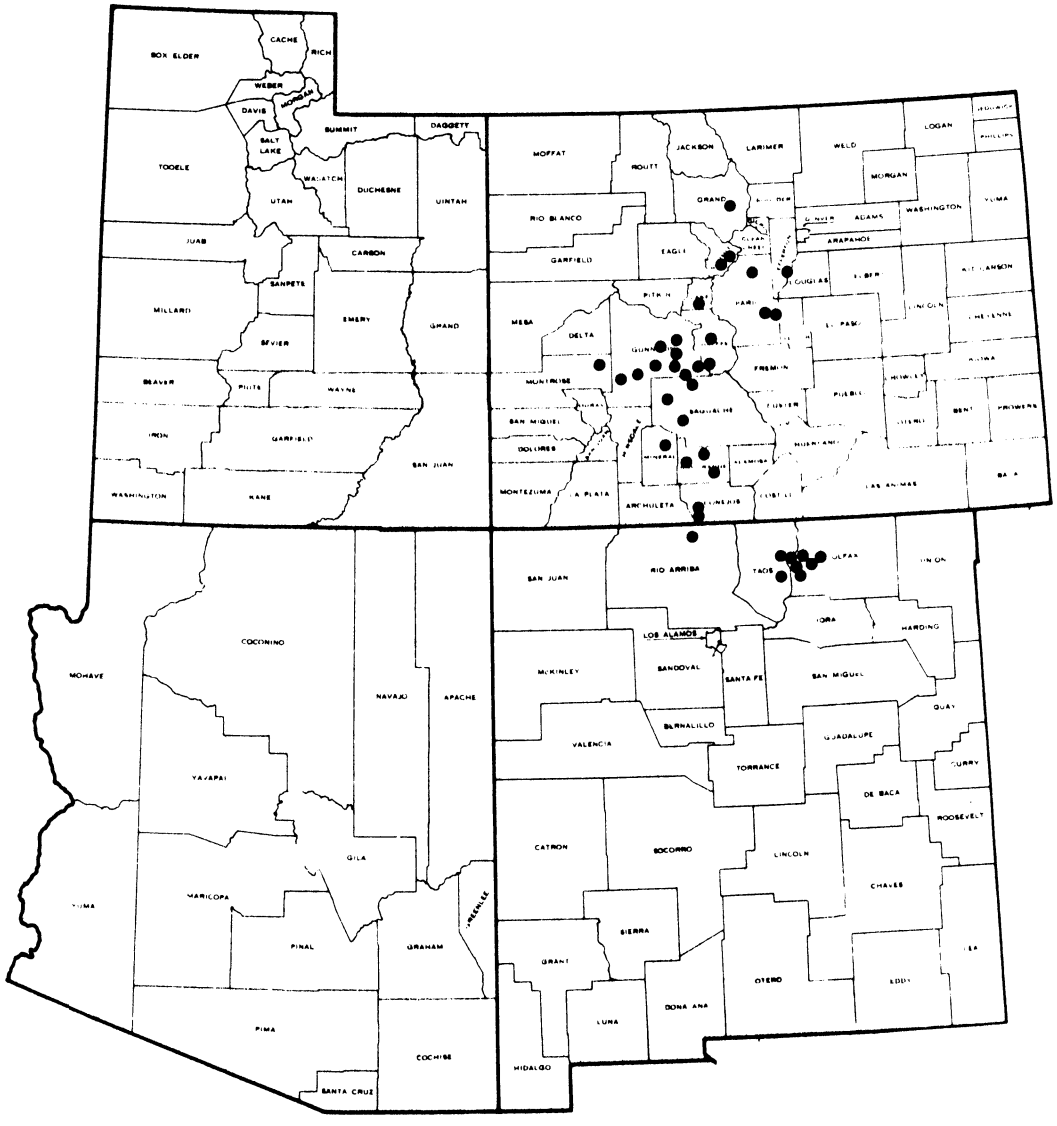
banners orbicular, glabrous, 6.0-7.5 mm long, 6-8 mm wide, r/a ratio of 0.5-0.7, banner angles 115-135°, with white eye spot drying light brown; wings glabrous, 6.5-8.0 mm long, 3.5-5.0 mm wide, claws 1.0-1.5 mm long; keels glabrous laterally, with dense ciliation near acumen or absent, 2.2-3.0 mm at widest point, angle of keels 65-88°; ovules 3-5; pods 1.5-2.2 cm long, 5-6 mm wide, villous; seeds 2-4, 3.0-3.5 mm long, 1.5 mm thick, finely mottled brown or grey.

Lupinus parviflorus ssp. myrianthus is found throughout the west central part of Colorado, southward into northern New Mexico. The form represented by this subspecies is most typical in the region around the Gunnison Valley where it ranges from 6,800 to 8,500 feet in elevation. It is frequently growing in sagebrush, but prefers areas with ample water, e.g. along irrigation ditches, drainage ditches, along small streams, etc. Flowering occurs from late June to early September. The long flowering period is the result of the frequently numerous secondary and tertiary inflorescences which are produced sequentially.

In the northern part of its range, L. parviflorus ssp. myrianthus merges with L. parviflorus ssp. parviflorus making identification between the two difficult. However, the hiatus formed by the drier valleys of northern Colorado and southern Wyoming is a

substantial isolating barrier between the two subspecies. Lupinus leptostachyus Greene is virtually identical with L. parviflorus ssp. myrianthus. To the south, L. parviflorus ssp. myrianthus intergrades in most morphological features with L. argenteus ssp. ingratus. Occasional hybrids have also been seen between adjacent colonies of L. caudatus ssp. argophyllus and L. parviflorus ssp. myrianthus.

Figure 6-2. A typical specimen of Lupinus parviflorus ssp. myrianthus.



Map 2. Distribution of Lupinus parviflorus ssp. myrianthus

Distribution of Lupinus parviflorus ssp. myrianthus (Map 2).

Partial citation: COLORADO: CHAFFEE CO.: Little Cochetopa Cr, C. P. Smith 3901 (POM - intermediate to L. argenteus ssp. ingratus); Salida, Bear Cr Ranger Sta, Johnston 637 (GH). CONEJOS CO.: Conejos Campgrd, 4 mi NW of Cumbres Pass Rd, Weber 7876 (COLO); Elk Cr Camp, off Hwy 17, Hess and Dunn 917 (UMO). GRAND CO.: Granby, Ripley and Barneby 10492 (NY). GUNNISON CO.: Almont, 5 mi N, Dunn 14584 (UMO); 2 mi N, Dunn 14817 (UMO); Dziekanowski 652 (UMO); 6.1 mi N. Fleak 301 (UMO); 3.8 mi E, Howard 64-68 (UMO); 4 mi W, Kane 554 (WIS); Cimmaron, 5 mi E, Dunn 14569 (UMO); Doyleville, 1 mi E, Dunn 14225 (UMO); 1.3 mi E, Dunn 15008 (UMO); Dziekanowski 682 (UMO); Golden Camp Rd, 3 mi S of airport, B. Dwyer 30 (UMO); Gothic, 12.8 mi SE, Harper 342 (MO); Gunnison, Baker 448 (MO, NY, POM, WS, US); Clemens 6/30/1913 (POM); Eggleston 14209 (GH, US); C. P. Smith 3871 (POM); 4.5 mi NE, Hamann 88 (UMO); 8 mi N, Hess 866 (UMO); 6 mi E, Vader 423 (UMO); Natl Forest, 6 mi W of Hwy 114, Dunn 14534 (UMO); Jack's Cabin, Baker 617 (GH, MO, NY, POM, RM, US), Harmon 588, 650, 653, 1598 (UMO); C. P. Smith 3880 (POM); Jack's Cabin cut-off, 3 mi NE, Dunn 15183 (UMO); Jct US 50 and Colo 114, 4 mi N, Harmon 690 (UMO); Mt Carbon, vicinity of, Eggleston 7759, 5696, 5743 (US); Monarch Pass, 7.8 mi W on US 50,

Dziekanowski and Fleak 865 (UMO); Ohio Creek, Eggleston 14215 (GH, US); Ohio Cr Rd, 4 mi N of Colo 135, Havens 114 (UMO); Parlin, E side, Dunn 14265 (UMO); 7 mi E, Kannis 95 (UMO); B. H. Smith 79 (NY); Pitkin, Clokey 3023 (GH, NY, RM, UC, US); Underwood and Selby 414 (NY); Prosser Cr, Cochetopa Hills, Rollins 1336, 1338 (GH, MO, NY); Roaring Judy Fish Hatchery on Colo 135, vicinity, Hess 741 (UMO); Rocky Mtn Biological Sta, Pinnick 5572 (IND); Sapinero, Greene 182 (US); Ripley and Barneby 7160 (NY); C. P. Smith 3867 (POM); Weber 9325 (COLO); 11 mi W, Harmon, 598 (UMO); Sargents, 2.7 mi E, Harmon 906 (UMO); Taylor R Rd, 1 mi SW of Jack's Cabin cut-off, Harmon 586 (UMO). JEFFERSON CO.: Platte Canyon, Eastwood 7/1886 (COLO). LAKE CO.: Lake Cr, C. P. Smith 3917 (POM, UMO - intermediate to L. argenteus ssp. ingratus); Lower Lake, C. P. Smith 3918 (POM, UMO - intermediate to L. argenteus ssp. ingratus); Twin Lakes, Clokey 3578, 3579 (MO, NY, POM, RM - intermediate to L. argenteus ssp. ingratus); C. P. Smith 3920 (POM - intermediate to L. argenteus ssp. ingratus). MINERAL CO.: Wagon Wheel Gap Exp Sta Rd, Murdoch 4750 (MO, UC, US). MONTROSE CO.: Gunnison R, Ramaley 16129 (COLO). PARK CO.: Clokey 3291 (GH, RM - intermediate to L. argenteus var. ingratus); Lake George, 6 mi W, Harmon 673 (UMO), Hess 879 (UMO); Wilkerson Pass, 3 mi

E, Dunn 14891 (UMO). RIO GRANDE CO.: Del Norte, Ramaley 16225 (COLO); Rock Cr Canyon, near Monte Vista, Ramaley 15601 (COLO); South Fork, 1 mi below, Eggleston 20535 (GH, NY); Hapeman 8/23/1918 (RM); Ramaley 17012 (COLO). SAGUACHE CO.: Hwy 114, 2-3 mi from, Dunn 14542 (UMO); Jct Hwy 114 and 50, Dunn and Willey 14551 (UMO); Sargent, Cochetopa Forest, C. P. Smith 3896 (POM - intermediate to L. argenteus ssp. ingratus); Long Branch R. S., C. P. Smith 3894 (POM - intermediate to L. argenteus ssp. ingratus); Stone Cellar R.S., 3 mi N, Weber 5785 (COLO). SUMMIT CO.: Breckenridge, Crandall 4130 (RM - intermediate to L. argenteus ssp. ingratus); Dillon, Eggleston 11954 (US); Loveland Pass, 16.1 mi S, Gillett and Taylor 11494 (UMO).

NEW MEXICO: COLFAX CO.: Aqua Fria, Rd to Aqua Fria Mt, Gordon 429 (UMO); Eagle Nest, Harmon 628 (UMO); Eagle Nest Hill, Lucas 198 (MO, RM, RSA, UC); Eagle Nest Lake, Castetter 1569 (RM); Elizabethtown, 1/2 mi N, Bacigalupi 598 (GH, UC, WTU); St. John, July-Sept. 1896 (UMO); Red River Pass, 5 mi E, Downey 61-52a, 61-52b (RSA, UMO); 4-1/2 mi E, Harmon 629 (UMO); Ute Pk, vicinity, Standley 14250 (GH, US). RIO ARRIBA CO.:

Chama, Earle 7/18/1898 (NY). TAOS CO.: Rio Fernandez de Taos Canyon, Eggleston 19134 (US); Turkey Mt, Harris 54 (US); Webber's Cattle Camp, Rio Fernandez de Taos Canyon, Eggleston 19280 (US).

1b. Lupinus parviflorus ssp. myrianthus var. fulvomaculatus comb. nov.

Basionym: Lupinus fulvomaculatus Payson, Bot. Gaz. 60:376. 1915. Type: COLORADO, Tabeguache Basin, Payson 547 (Isotypes COLO, GH, MO).

Plants perennial, erect, 1 to several stems from a woody caudex, branching from upper half of stems; stems 4-10 dm tall, 2.5-6.0 mm in diameter, minutely puberulent becoming glabrate; leaves mostly cauline; basal petioles when present 6.5-11.0 cm long, cauline petioles 2.8-6.4 cm long; stipules 5.5-9.0 mm long, basally connate for 1/3 - 2/3 their length, triangular; leaflets 7-8, oblanceolate to lance-elliptic, apex acute to obtuse, largest 2.5-6.8 cm long, 4.1-12.0 mm wide, flat, glabrous above, strigulose below; peduncles 2.3-6.4 cm long; racemes (7.5) 12-25 cm long, densely subverticillate to verticillate; bracts triangular to lanceolate 3.8-6.0 mm long, caducous; pedicels 2.1-3.2 mm long; flowers light blue, 7-8 mm long; calyces villous, upper-lips obtuse at base, 3.1-5.0 mm long, minutely notched, lower-lips 4.0-6.5 mm long, entire, bracteoles minute, attached at the lateral sinus; banners orbicular, 6.0-8.0 mm long, 6.0-8.0 mm wide, L/W ratio 1.0-1.25, r/a ratio 4.8-5.5, banner angle 121-142°, glabrous, with conspicuous dark brown eyespot in center; wings glabrous, 7.5-9.0

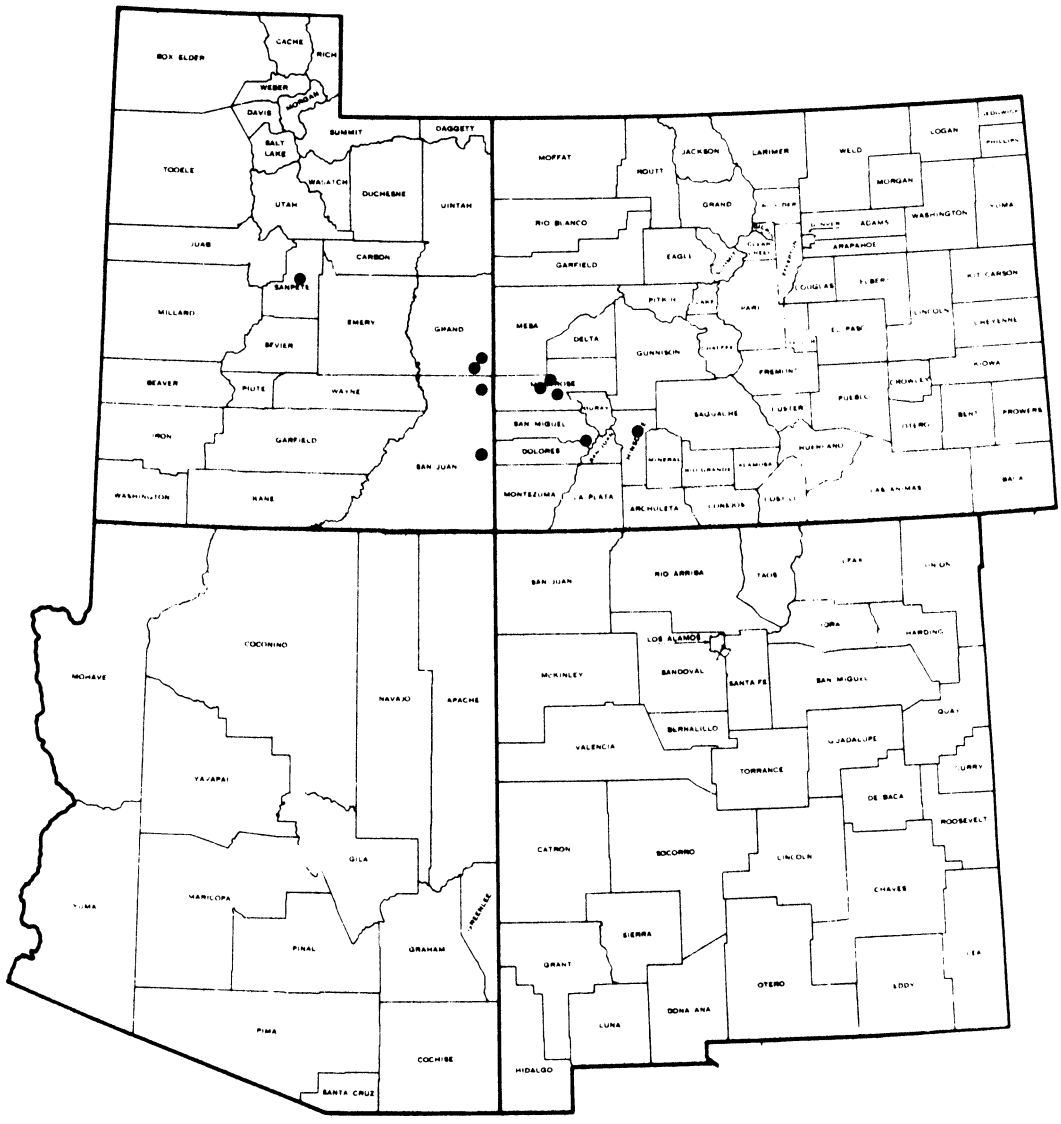
mm long, 4.0-4.9 mm wide, claws 1.1-2.0 mm long; keels glabrous laterally, with dense ciliation near acumen, dark blue at apex, 2.5-3.0 mm wide, 5.8-6.7 mm long, angle of keels 69-89°; ovules 3-5; pods 2.5-3.0 cm long, 0.7-0.9 mm wide, villous; seeds 3-5, 3.5 mm x 2.8 x 1.5 mm thick, finely mottled.

Found scattered through the higher elevations of southwestern Colorado and southeastern Utah between 7,500 and 9,500 feet, at mostly higher elevations than L. parviflorus ssp. myrianthus var. myrianthus. Lupinus parviflorus ssp. myrianthus var. fulvomaculatus is somewhat variable in its vegetative morphology, ranging from the broad leaflets of L. parviflorus ssp. parviflorus to narrow leaflets of L. parviflorus ssp. myrianthus var. myrianthus. The variable size of the leaflets and general vigor of the plants may be affected by environmental conditions to a large degree. The flowers of var. fulvomaculatus, however, have a larger mean size than either ssp. parviflorus or ssp. myrianthus and are characterized by a very dark eye spot which is particularly prominent on drying.

In addition, experimental results of the chromatography indicate that L. parviflorus ssp. myrianthus varieties consistently differ from L. parviflorus ssp. parviflorus with regard to at least

two alkaloids. It can also be seen from the graph cluster analysis that each of the three taxa formed clusters among themselves before joining together in a single cluster.

Figure 6-3. A typical specimen of Lupinus parviflorus ssp. myrianthus var. fulvomaculatus.



Map 3. Distribution of Lupinus parviflorus ssp. myrianthus var. fulvomaculatus

Distribution of Lupinus parviflorus ssp. myrianthus var. fulvomaculatus (Map 3).

Partial citation: COLORADO: HINSDALE CO.: Henson Canyon, Lake City, C. P. Smith 3861 (POM, RM). MONTROSE CO.: Tabeguache Basin, Payson 139 (COLO, GH); Payson 547 (COLO, GH, MO, WS); Uncompahgre Divide, Payson and Payson 3904 (GH, MO, RM). SAN MIGUEL CO.: Lizard Head Pass, 11.1 mi N, Harmon 1191 (UMO).

UTAH: GRAND CO.: Oowah Lake, La Sal Mts, Wiens and Arnow 4145 (MO); Warner Ranger Sta, La Sal Mts, Flowers June 25, 1948 (BRY); Maguire and Maguire 20429 (UC, WS); 20430 (RM); Sharsmith 4431 (IDS, ISC, NY, RM, UC, US, WIS, WS); Maguire et al. 20431 (GH). SAN JAUN CO.: Moab, 15 mi SE, Oowah Lake Campgrd, Hess 444 (COLO); Montezuma Canyon, E of Monticello, Rydberg and Garrett 9707, 9706 (NY, RM, US). SANPETE CO.: Ephraim, plateau NW, Tidestrom 1410 (NY).

1c. Lupinus parviflorus ssp. floribundus comb. nov.

Basionym: Lupinus floribundus Greene, Proc. Acad. Phil. 1892: 364. 1893.

Lectotype: COLORADO, "middle and upper Bear Creek, west of Denver," Greene 1873, 1875 and 1889.

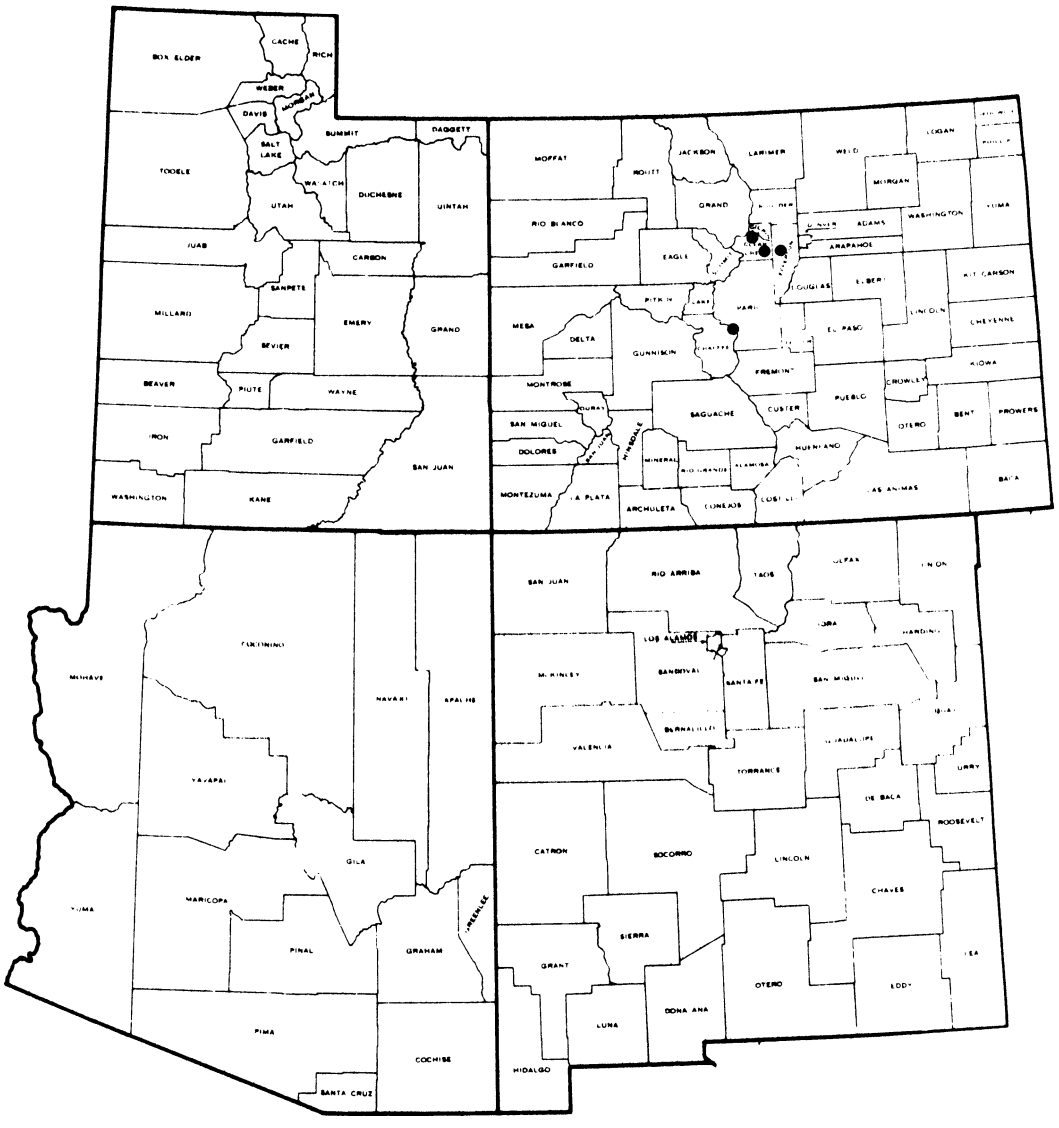
(Lectotype designated herein, ND-G; Isotype NY; Paratypes GH, ND-G).

Plants erect; stems perennial, 1 to few from a woody caudex, branching in upper portions, minutely puberulent, interspersed with scattered hispidulose hairs; leaves cauline at anthesis; cauline petioles 2.5-3.7 cm long; stipules 5.0-7.0 mm long, setaceous, basally connate 1-2 mm; leaflets 7-10 (12), oblanceolate to broadly oblanceolate, apex acute or obtuse, largest 1.4-2.7 cm long, 4-7 mm wide, L/W ratio 3.5-5.3, semiconduplicate, finely to coarsely strigose above and below except occasionally glabrous above on upper leaves; peduncles 1.7-4.6 cm long; raceme 9.7-12.1 cm long, densely subverticillate; bracts 2.5-2.8 mm long, lanceolate, caducous; calyces villous, upper-lips truncate above, 3.0 mm long, minutely notched, lower-lips 3.8-4.5 mm long, entire, bracteoles minute, attached in sinus of angle between lobes of calyx; banners orbicular, glabrous, 5.8 mm long, 6.1 mm wide, L/W ratio 95, r/a ratio 0.5, angle of banner 102-116^{o}; wings glabrous, 6.5 mm

long, 3.5-3.8 mm wide, claws 1 mm long; keels glabrous laterally, densely ciliate on upper margin near acumen, 2.0-2.5 mm wide, 5.0-6.1 mm long, angle of keel 70-88°; ovules 3-4; pods 1.5 cm long, 4.5 mm wide, villous; seeds 1-3, cream color.

This subspecies is known only from the mountains in the vicinity of the type locality of Bear Creek which runs from Mt. Evans east and slightly north to Denver. It was reported to have been growing under ponderosa pines. However, this entire area is currently being highly developed, making the existence of living specimens of this taxon questionable. No recent collections of L. parviflorus ssp. floribundus have been found among the specimens borrowed.

Figure 6-4. Photograph of the lectotype of Lupinus floribundus, a typical specimen of Lupinus parviflorus ssp. floribundus.



Map 4. Distribution of Lupinus parviflorus ssp. floribundus

Distribution of Lupinus parviflorus ssp. floribundus (Map 4).

Partial citation: COLORADO: CLEAR CREEK CO.: Brookvale, Churchill, June 19, 1918 (MO); Indian Pk, near Brookvale, Churchill June 17, 1918 (MO - intermediate to L. argenteus ssp. ingratus). CLEAR CREEK AND JEFFERSON CO.S: Bear Cr, Greene July 27, 1873 (ND-G, GH); Upper Bear Cr, Greene July 29, 1889 (ND-G, NY). JEFFERSON CO.: Evergreen, C. P. Smith 4030 (US). PARK CO.: Trout Cr Pass, Isely 6584 (UMO - intermediate to L. argenteus ssp. ingratus).

2. Lupinus hillii (var. hillii) Greene. Leaflets Bot. Obs. & Crit. 2: 236. 1912.

Holotype: ARIZONA, Coconino Forest Reservation, "common in open thinly grassy groves of yellow pine." R. R. Hill, 29 June, 1911 (US).

Synonymy: Lupinus marcusianus C. P. Smith, Sm. Spec. Lup. 137. 1940.

Holotype: ARIZONA, Grand Canyon Bright Angel, M. E. Jones, July 22, 1920 (DS-Sm, Isotype POM).

Plants perennial; stems erect, 1 to several, branching from a woody caudex and upper portions, 2.0-2.5 dm tall, 2.0-3.5 mm in diameter at base, covered with short dense villous pubescence interspersed with fewer long white hirsute hairs; leaves mostly cauline; basal petioles when present 5-8 cm long, mid-cauline petioles 3.0-4.5 cm long; stipules 4.5-7.0 mm long, basally connate to petiole 1.5-3.0 mm, triangular; leaflets 7-10 (12), narrowly oblanceolate to lance-elliptic, acute or obtuse, largest 1.0-3.7 cm long, 4-9 mm wide, L/W ratio 3.5-5.5, moderately to densely silky strigose on both surfaces; peduncles 1.2-5.0 cm long; racemes 3.5-11.0 cm long, subverticillate to verticillate; bracts 4.0-7.0 mm long, lanceolate to triangular, caducous; pedicels 1.5-3.0 mm long; flowers light to dark blue, 6-7 mm long; calyx base obtuse

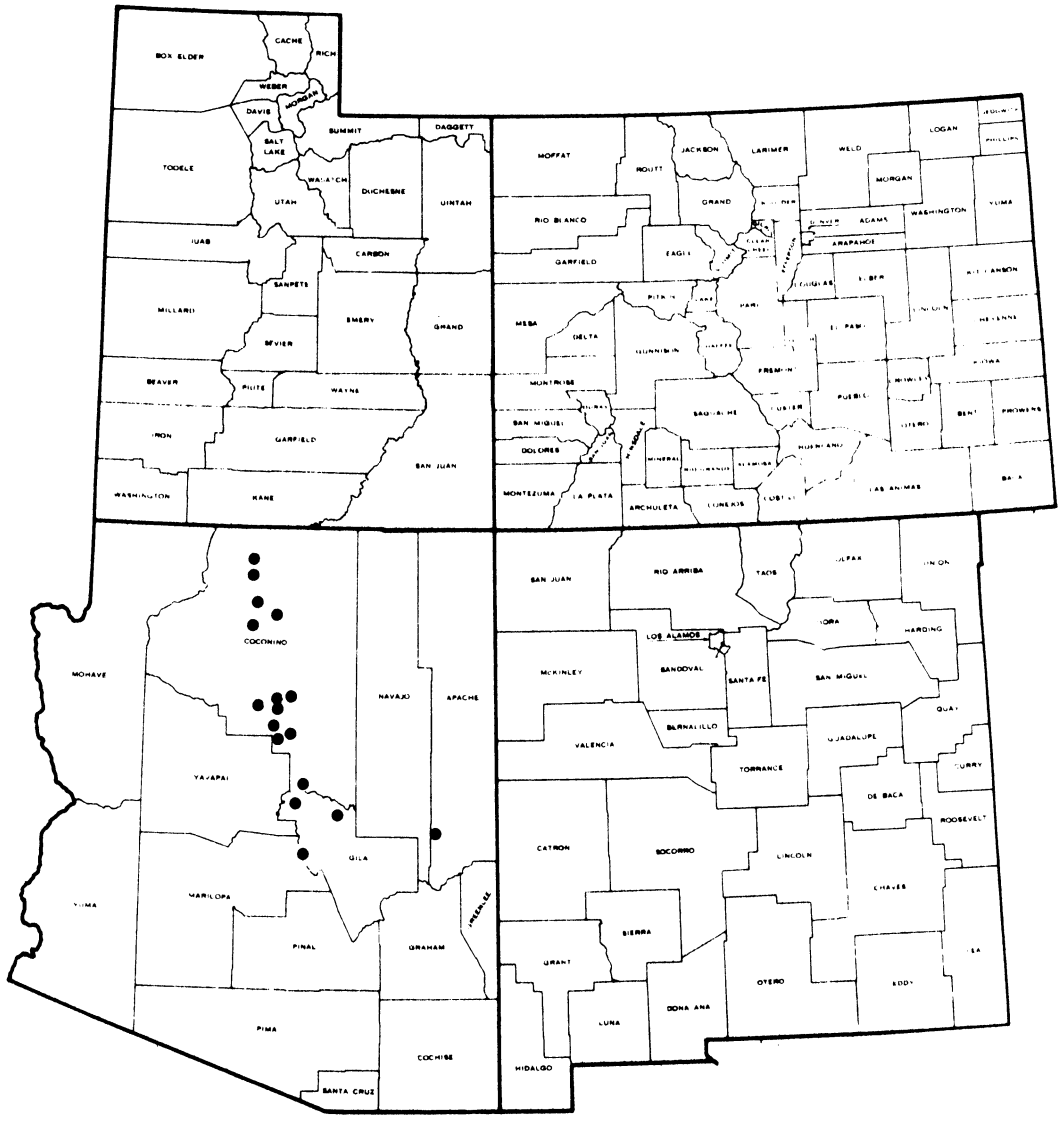
above, upper-lips 3.5-5.0 mm long, minutely notched, lower-lips 4.5-6.0 mm long, villous, bracteoles minute, attached in angle of lobes of calyx; banners orbicular or occasionally suborbicular, glabrous, 5.8-7.0 mm long, 6.5-7.4 mm wide, L/W ratio 0.78-1.07, r/a ratio 0.52-0.76, banner angle 114-132°; wings glabrous, 6.5-7.5 mm long, 3.5-4.2 mm wide, claws 1.0-1.2 mm long; keels glabrous laterally, densely ciliate on upper margin near acumen, 2-3 mm wide, 5.0-6.2 mm long, keel angle 71-83°; ovules 3-4; pods 2.0-2.3 cm long, 6-8 mm wide; silky villous; seeds 2-4, 5 mm x 4.4 mm x 2 mm, mottled on dark background.

Lupinus hillii var. hillii can be found growing in a variety of habitats from dry pinyon pine ridges to the open grassy floor of mature ponderosa pine forests and even in subalpine meadows. It grows from 6,000 to 9,000 feet, but more frequently from 7,000 to 7,500 feet. Flowering is from mid-June to early September, depending on the vigor of the plant which effects its ability to produce secondary racemes. Seasonal development is effected by the timing of precipitation . Elevation must also strongly influence the length of the flowering season in these plants.

Distribution of L. hillii var. hillii is from the area of Jacob Lake and the northern rim of the Grand Canyon southward to Flagstaff and along the Mogollon Rim.

Lupinus hillii var. hillii apparently forms intermediates with L. palmeri and possibly with L. sitgreavsii which may accoun for the variability found in L. hillii var. osterhautianus and L. hillii var. arizonicus. Other combinations of characters not encompassed by these latter two varieties occur too infrequently to warrant varietal recognition.

Figure 6-5. A typical specimen of Lupinus hillii var. hillii.



Map 5. Distribution of Lupinus hillii var. hillii

Distribution of Lupinus hillii var. hillii (Map 5).

Partial citation: ARIZONA: COCONINO CO.: Buckskin Mts, Jones 6052 (US); Cape Royal, 5 mi N, Grand Canyon Natl Pk, Moore 40, (US); Double Springs, Mormon Lake, Van Winkle 79 (UMO); Flagstaff, Demaree 42711, 42771, 42840, 42783 (ASU, UMO); Jones 4068 (POM, NY, RM, UMO, US); Kearney and Peebles 12192 (US); Lemmon, Aug 1884 and 1889 (GH, US); 1 mi S, C. P. Smith 4092 (RM); 2 mi N, Harmon 621 (UMO); 23 mi SW, Gaines 1209 (WS); city reservoir, C. P. Smith 4074, 4088 (RM, UMO); Flagstaff, Navajo Ordnance Depot, Schallert Aug 2, 1943 (MO, RM); Fort Valley, Rimo Bacigalupi 527 (GH); Grand Canyon, Collum 1939 (ASU); Fleak 395 (UMO); McCleary July 1954 (ASU); 3 mi N of north rim, Downey 61-62a (RSA, UMO); Dziekanowski 1082 (ASU, UMO); north rim, Eastwood and Howell 917 (UC, RSA); Harmon 616 (UMO); Jacob Lake, Mead 965 (US); 3 mi S, Harmon 615 (UMO); 15 mi S, Parker, McClintock and Robbins 6216 (UC); 16 mi S, Dunn 14409 (UMO); 18 mi S, Downey 61-65 (UMO); on road to W. P. Lodge, Collom 850 (US); Kaibab Plateau, Dunn 14443, 14444 (UMO); Mogollon Rim, Collom 217 (US); Mormon Lake, Benson 9690 (POM); Collom 610, July 1939 (ASU, US); Munds Pk, 21 mi S of Flagstaff, C. P. Smith 4089 (US); Pine, 13 mi N, Shreve 8929 (COLO); Pt Final, Grand Canyon Natl Pk, Halvorson 252 (ASU); Schultz Pass

Canyon, 2 mi N of Flagstaff, Downey 61-59, 61-59a (UMO); West Fork Canyon of Oak Cr Canyon, Demaree 44072 (UMO); Willow Spring, Palmer 500, June 10-20, 1890 (GH). GILA CO.: Pine, near, Peebles 9483 (US); Wildcat Springs, Tonto Rim, Jaeger July 11 & 12, 1927 (POM); Young, 18 mi on rd to Payson, Peebles and E. G. Smith 13283 (US). NAVAJO CO.: Indian Ave, E of Pine Top, Deaver 6366 (ASU).

2a. Lupinus hillii var. arizonicus comb. nov.

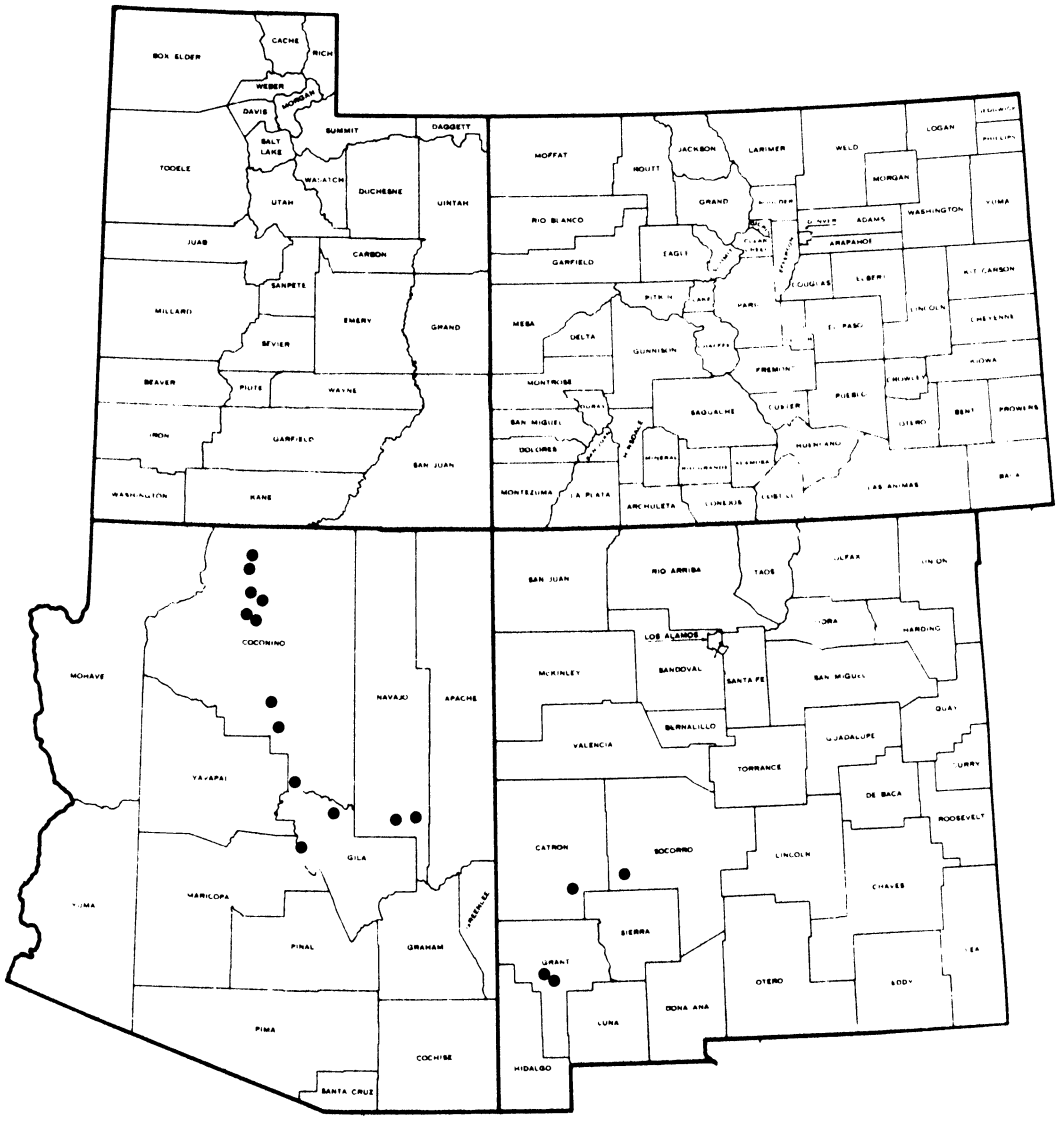
Basionym: Lupinus ingratus var. arizonicus C. P. Smith, Sm. Spec. Lup., 128. 1939.

Holotype: ARIZONA, Grand Canyon, Eggleston 15664 (DS-Sm; Isotypes GH, US).

Lupinus hillii var. arizonicus is similar to L. hillii var. osterhautianus in flower size and shape but differs in having appressed or ascending hairs on the stem, and is pubescent dorsally on the banner.

Lupinus hillii var. arizonicus occurs sympatrically with L. hillii var. hillii in the northern part of its range, but extends further south and east along the Mogollon Rim than either var. hillii or var. osterhautianus.

Figure 6-6. A typical specimen of Lupinus hillii var. arizonicus.



Map 6. Distribution of Lupinus hillii var. arizonicus

Distribution of Lupinus hillii var. arizonicus (Map 6).

Partial citation: ARIZONA: COCONINO CO.: Bright Angel, Colorado R, Tidestrom 2337 (RM, UC); Flatstaff, Adams Sept. (UMO); Grand Canyon, Eggleston 15680 (US); A.E. Hitchcock 42 (US); MacDougal June 26, 1898 (NY); near 6 mi well, Wooton July 12, 1892 (US); Grand Canyon, entrance to Natl Pk, on north rim, Ferris 10236 (UC); Interstate 70, ca. 2-3 mi E on dirt rd to Mormon Lake, Harmon 623 (UMO); Jct of Arizona 64 and US 180, 2.5 mi E, Spellman and Harmon 903 (UMO); Jacob Lake, near, Eastwood and Howell 6431 (US); 2.2 mi SW, Moore, Pinkava, Lehto 6893 (ASU); 3 mi SW, Moore, Pinkava, Lehto 7001 (ASU); 10 mi S, Munz 17011 (POM); Jacob Lake, Kaibab Plateau, Eastwood and Thomas 6390 (US); Long Jim Canyon, Collom Aug 7, 1939 (US); Mormon Lake, Deaver 6019 (ASU); North Rim entrance to Grand Canyon Natl Pk, Halvorson 133 (ASU); Pine, 13 mi N, Shreve 8923 (UC); Walhala Plateau, fire Rd E-6, Halvorson 258 (ASU). GILA CO.: Christopher Mt Range Rd, just off US 160, Harmon 624 (UMO); Tonto Fish Hatchery, 2 mi S, Lehto 994 (ASU). NAVAJO CO.: Linden, 3.3 mi W, Pinkava, Keil and Lehto 14434 (ASU); Showlow, Parker and McClintock 6818 (RM, RSA); Showlow Lake, Sutherland 34 (ASU).

NEW MEXICO: CATRON CO.: Evans Brothers Range, Beaverhead, Datil Forest, Eggleston 20356 (US); Indian Cr, Dunn 7718 (UMO). GRANT CO.: Big Burros Ranger Sta, Gila Forest, Eggleston 17258 (US); Tyron, canyon above, Eggleston 19964 (US). SOCORRO CO.: Little Cr, Gila Forest, Eggleston 16948 (US).

2b. Lupinus hillii var. osterhautianus comb. nov.

Basionym: Lupinus osterhautianus C. P. Smith, Sm. Spec. Lup. 130. 1940.

Holotype: ARIZONA, near Grand Canyon, Geo. E. Osterhaut 6971 (DS).

Lupinus hillii var. osterhautianus differs from L. hillii var. hillii in having a spot of hair on the back of the banner and more elongated keel of L. palmeri while retaining the basically small flower of L. hillii. Other features characteristic of var. osterhautianus are more dense spreading hispidulose hairs on the stem, flowers 6.8-8.0 mm long; banner 6.8-8.0 mm long, 7.0-8.9 mm wide; wings 6.8-8.0 mm long; 3.9-4.9 mm wide; keel 2.0-3.0 mm wide, 6.0-7.1 mm long, sparsely ciliate to glabrous.

Lupinus hillii var. osterhautianus is found growing sympatrically with L. hillii var. hillii.

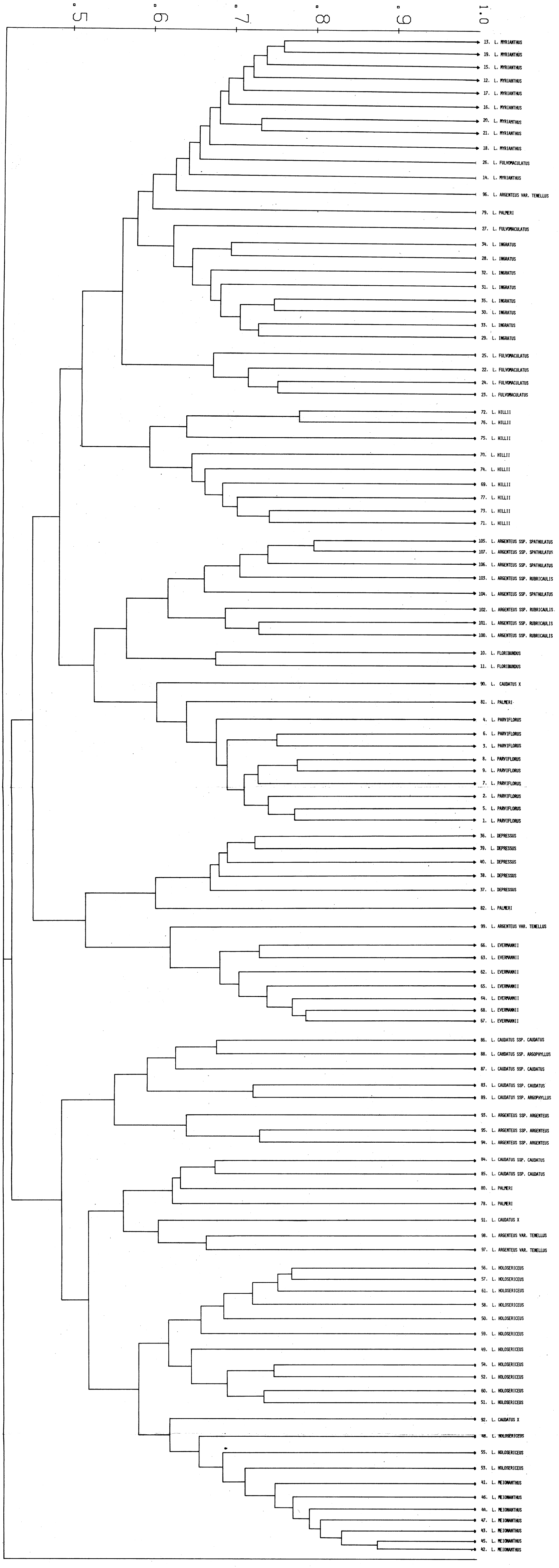
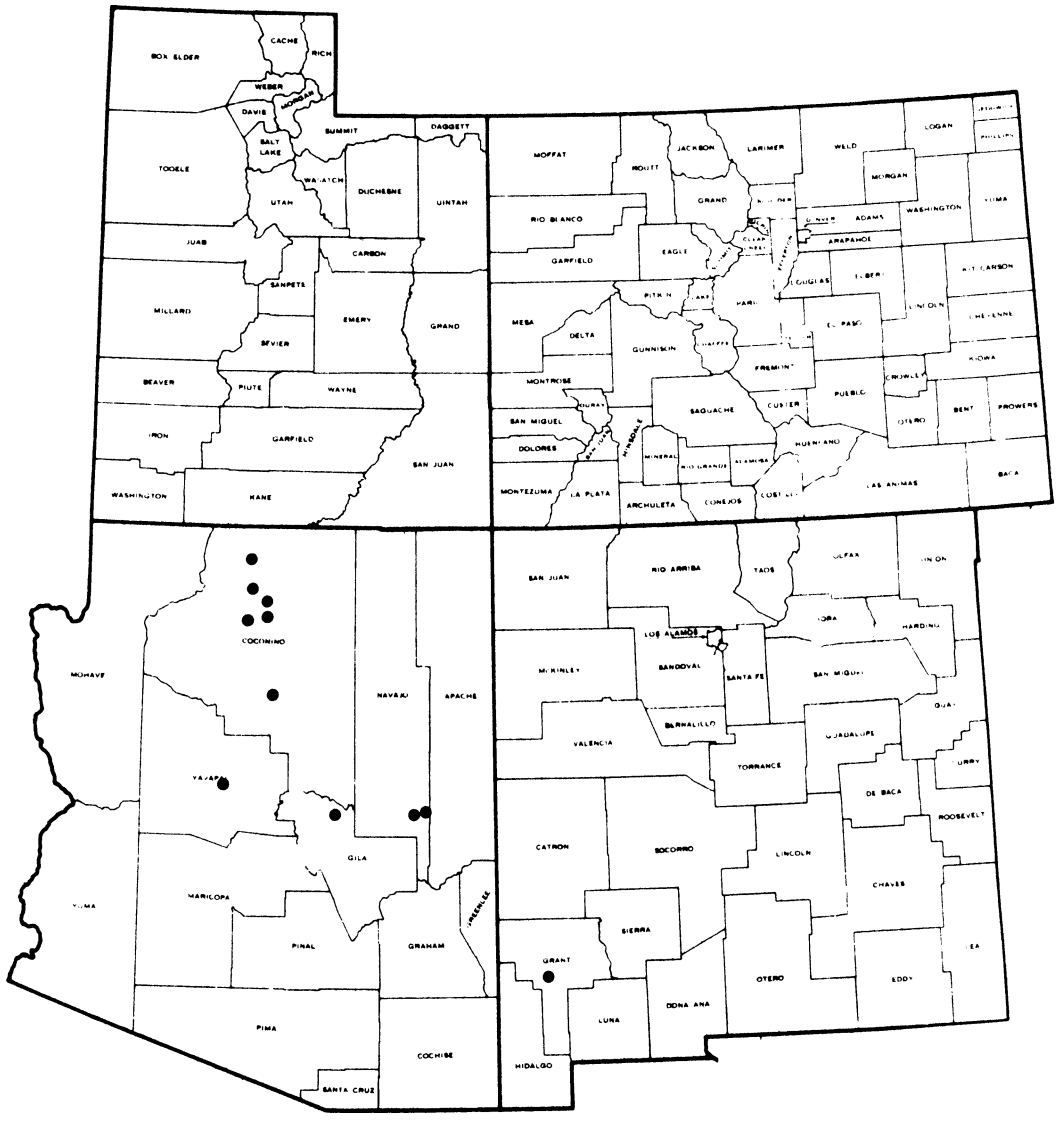


Figure 5-2. Dendrogram of selected specimens of the Lupinus parviflorus and L. argenteus - L. caudatus complexes.

Figure 6-7. A typical specimen of Lupinus hillii var. osterhautianus.



Map 7. Distribution of Lupinus hillii var. osterhautianus

Distribution of Lupinus hillii var. osterhautianus (Map 7).

Partial citation: ARIZONA: COCONINO CO.: Cape Royal, 1-1/2 mi N, Halvorson 170 (ASU); 4 mi N, Halvorson 211 (ASU); btn Desert View and Grand Canyon, Dunn 12648 (UMO); Grand Canyon, Beckwith 94 (NY), A. S. Hitchcock July 1, 1916 (US); Jones July 9, 1925 (POM); north rim, Eastwood and Howell 7016 (US); Horton Cr, Halvorson, May 19, 1963 (ASU); Jacob Lake, Kearney and Peebles 13672 (US); Oak Cr Canyon, Jaeger July 12, 1927 (POM); Wicklund 97 (ASU); Woods 86 (ASU); Sedona, Demaree 41222 (UMO); 12 mi N, Nickerson and Edwards May 6, 1961 (ASU). GILA CO.: Horton Cr, Lehto 761 (ASU); Red Lake, 16 mi NE of Young, Johnson 164 (ASU). MOHAVE CO.: Kingman, Manship 26 (UMO). NAVAJO CO.: Showlow, 10 mi E, Ferris 10085 (UC). PIMA CO.: Mt Lemon, Buehler Oct 12, 1940 (ASU). YAVAPAI CO.: Lynx Lake, Pinkava 2348 (ASU).

NEW MEXICO: GRANT CO.: Big Burros Ranger Sta, Gila Forest, Eggleston 17258 (NY).

3. Lupinus meionanthus A. Gray, Proc. Amer. Acad. 6:522. 1865. Lectotype: NEVADA, near Carson City, C. L. Anderson, 1864 (GH; Isotypes NY, UC, US).

Plants perennial, erect or ascending, 2-7 dm high; stems 2-3 (4) mm in diameter, branching from a woody caudex, with a few short flowering branches above, densely sericeous with fine appressed hairs; leaves evenly distributed over stems; basal petioles variable 1.5-4.0 cm long, cauline petioles 2.5-4.0 cm long; stipules 4-6 mm, basally connate for 1-2 mm; leaflets 6-9, oblanceolate to linear-oblanceolate, largest (1.2) 2.0-3.5 cm long, (2.5) 5.5-6.0 mm wide, L/W ratio 4.0-5.5, densely sericeous on both sides; peduncles 1.5-3.0 cm long; racemes 5-15 cm long, densely or occasionally loosely verticilately flowered; pedicels 2-3 mm long; bracts pubescent, early deciduous, 2.0-4.5 mm long; flowers 5.5-6.8 mm long; lips of calyces sericeous, connate 1 mm from base, upper-lip 3.5-4.0 mm long, lower-lip 4.0-5.0 mm long both shallowly and irregularly toothed; petals dull blue or lilac; banner with yellow center, glabrous, orbicular, 5-6 mm long, 5.0-5.8 mm wide, L/W ratio 1.0-1.2, banner angles 125-135°, r/a ratio 0.5; keels ciliate near acumen, 2.2-4.0 mm wide, angle of keels 82-90°, tip of keels blunt; legumes 1.5-2.5 cm long, 5-6 mm wide, sericeous; seeds 1-4, 3.0 mm x 2.5 mm x 1.5 mm, commonly light beige.

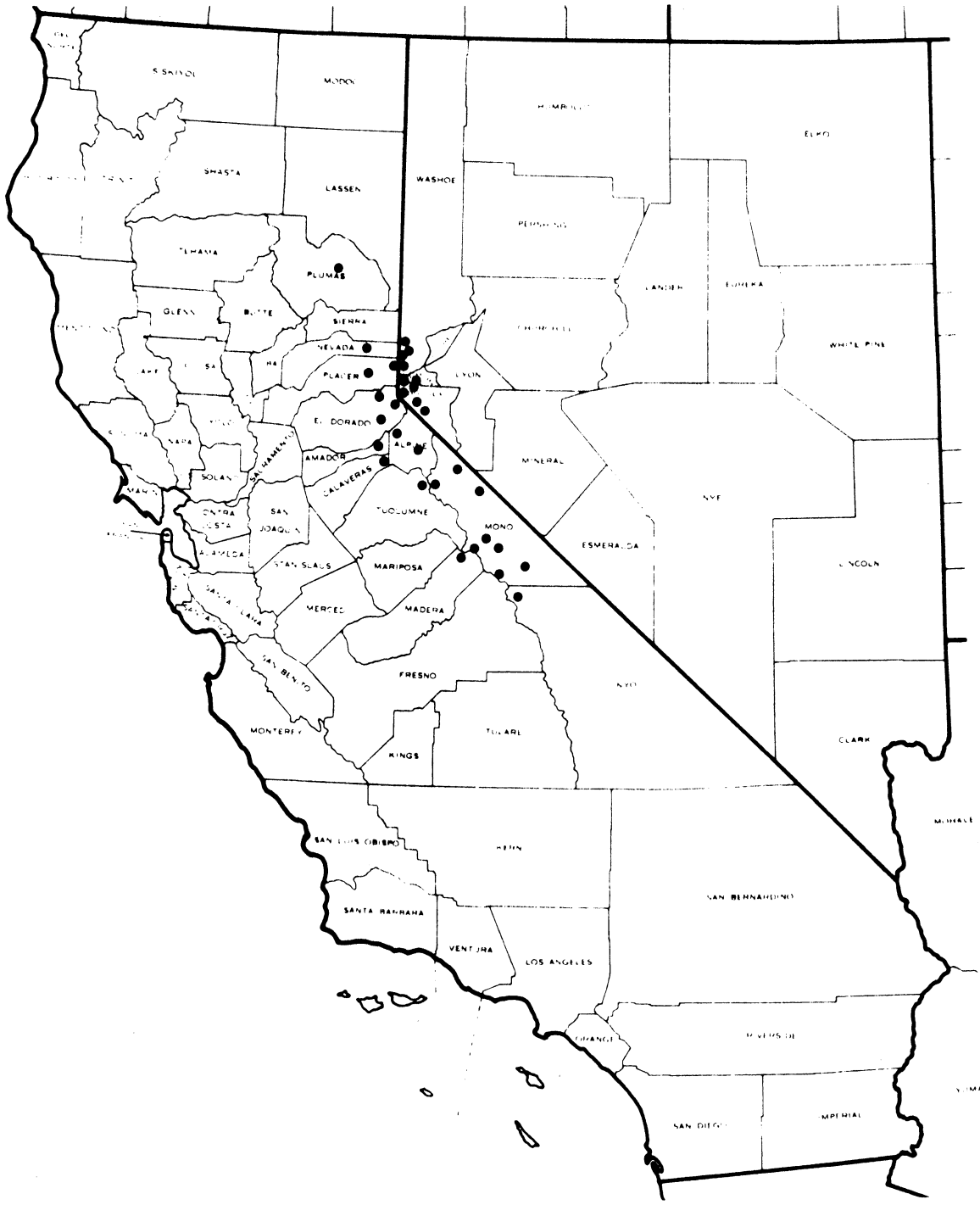
Lupinus meionanthus is found growing 5,000-9,800 feet in dry sites from sage brush scrub to subalpine zones just above timber line. An endemic, this species is restricted to the Sierra Nevada Mountains from Madera and Mono Counties to Plumas and Modoc Counties in California and the extreme western counties of Nevada, in the vicinity of Lake Tahoe. Flowering is from mid-June to late September.

The original description of L. meionanthus provided no designation of a type specimen. The species was described from plants collected by Dr. C. L. Anderson from near Carson City, Nevada with no collection dates cited. However, new species representing several genera were described from Anderson's collections near Carson City in 1862 and 1864. The lectotype designated here is from Anderson's collections in 1864 and marked "n. sp." (new species), from the Gray Herbarium (GH), the specimen from New York (NY) is designated an isotype.

Lupinus meionanthus is very similar to L. holosericeus as is evident in the graph cluster analysis. Phillips (1955) considered L. meionanthus to be closely related to L. holosericeus. However, the glabrous banner easily separates L. meionanthus from L. holosericeus which is sparsely to densely hairy on the back of the banner. In addition, the complete difference in alkaloidal content of

of L. meionanthus and L. holosericeus suggests that the morphological similarity between these species is superficial. The two species have probably been genetically isolated for a long period, if indeed they were ever part of the same genetic pool. Their present distributions are substantially separated.

Figure 6-8. A typical specimen of Lupinus meionanthus.



Map 8. Distribution of Lupinus meionanthus

Distribution of Lupinus meionanthus (Map 8).

Partial citation: CALIFORNIA: ALPINE CO.: Highland Lakes, Howden 53 (UC); 1/4 mi E, Albertus 306 (UC); Red Peak, Hoover 4189 (NY, UC, US); Woods Lake, plateau NW of, Peirson 12101 (RSA). AMADOR CO.: Carson Spur, Hansen 743 (MO); Silver Fork of American R, Calif. 88, Bacigalupi and Whisler 6030 (RM, UC, WTU). CALAVERAS CO.: Mokelumne Pk, 2-1/2 mi S, 4-1/10 mi E, Rutler 28 (UC). EL DORADO CO.: Al Tahoe, Lake Tahoe, Robbins 2036 (UC); Altahre, Truchu R fan, Kimber 143 (WIS); Bijou, Eastwood and Howell 8361 (NY); Cup Lake, Ralston Peak, SE slope, Evans 7/21/1918 (UC); Lake Tahoe, Beach 1268 (UC); Pyramid Peak, Hall et al. 4737 (GH, UC); State Line, Pierson 6180 (RSA). FRESNO CO.: Virginia Lakes, Leach 3256 (OSC). INYO CO.: Crooked Cr, shoulders of Campito Mt, Buckalew 13 (RSA). MADERA CO.: Agnews Tr, Peirson 541 (RSA); Minaret Summit, Raven 3492, 3140 (NY, RSA, UC); Rose 42105 (GH, MO, WS); Summit, range E of Minarets, Congdon 8/19/1899 (UC). MONO CO.: Crowley Lake, 8 mi E, Rose 68143 (COLO); Deep Cr, hill N, Alexander and Kellogg 4029 (NY, RM, UC, WTU); Hot Cr rd, 1 mi E of US 395, Ferris et al. 11067 (GH, UC, WTU); Mono Craters, Shaft Rd No. 1, S, Lorraine 8/6/1938 (GH, RSA, UC, WS); Potato Peak, N slope, Alexander and Kellogg 4524 (UC, US); Potato Mtn, Bridgeport

Cemetary, C. B. Hardham 5124 (UMO); Pumice Valley, 7-1/2 mi S of Leevining, Wolf 5369 (GH, COLO, RSA, WTU); Sonora Pass, Crampton 5655 (UC); Eastwood and Howell 7493 (UC, US); Muller 1108 (UMO); Rose 40748, 42203 (GH, MO, NY, UC, WTU); Rowntree 1932, 7/16/1935 (COLO, POM); .2 mi E, Constance 2455 (GH, NY, RM, UC, WTU); Sweetwater Canyon, Alexander and Kellogg 3948 (UC, WS); Sweetwater Cr, head, Munz 21181 (RSA, WS); N fork, Munz 21256 (RSA, WS); Virginia Lakes, Hoffman 8/10/1933 (GH); Peirson 11216 (RSA); Wheeler Pk, 1 mi SE, Graham 142 (RSA, UC). NEVADA CO.: Castle Pk, Heller 7084 (GH, MO, NY, POM, UC, UMO); Howell 18600 (WTU); Mt Stanford - Castle Pk, Sonne 7/17/1892, 8/4/1895 and 7/1897 (MO, NY, POM, UC); Wiskey Cr, Peirson 19750 (RSA). PLACER CO.: Granite, Wilson 77 (UC); Mt Lincoln, Howell 18674 (US). PLUMAS CO.: Charlies Valley, Sawyer 165 (UC); Genesee Valley, near Genesee, Heller and Kennedy 8864 (GH, MO, NY, POM, US, WTU); Red Clover Cr, canyon of, Hall et al. 4449 (GH, UC). TUOLUMNE CO.: Burst Rock, B. Bolt 444 (UC); Sonora Pass, J. C. Downey 28A (UMO); top, Ramsey 2503 (POM); Rowntree 9/13/1929 (WS); Wolf 6133 (RSA, WTU, WS); 4.9 mi NW, Harmon 807 (UMO); 2-1/2 mi NW, Peterson 500A (UC).

4. Lupinus holosericeus Nutt in T. & G. Fl. N. Am. 1:380. 1840. Holotype: "Islands and gravelly banks of the Wahlamet," Nuttall (BM; Isotype NY).

Synonymy: Lupinus minearanus C. P. Smith, Sm. Spec. Lup. 565. 1946. Holotype: IDAHO: Camas Co., Sawtooth Forest, J. E. Minear 19 (USFS).

Lupinus lacuum-trinitatum C. P. Smith, Sm. Spec. Lup. 567. 1946. Holotype: IDAHO: Elmore Co., Trinity Lakes, Featherville, 10 mi W, Hitchcock and Muhlick 10332 (DS-Sm; Isotypes GH, IDS, RM, UC).

Lupinus summae C. P. Smith, Sm. Spec. Lup. 572. 1946. Holotype: IDAHO: Owyhee, Silver City road summit, J. H. Christ and W. W. Ward 8077 (herbarium of J. H. Christ; Isotype UC).

Lupinus multicincinnis C. P. Smith, Sm. Spec. Lup. 735. 1952. Holotype: IDAHO: Elmore Co.: Moores Flat, Sawtooth Forest, R. B. Johnson 252 (USFS).

Plants erect, branching basally from a woody caudex and frequently from upper portion of stems, silky sericeous throughout; stems 2.0-4.5 dm high, 2-3 mm in diameter at base; cauline nodes 4-9; basal petioles 3-10 cm long, cauline petioles 2-5 cm long;

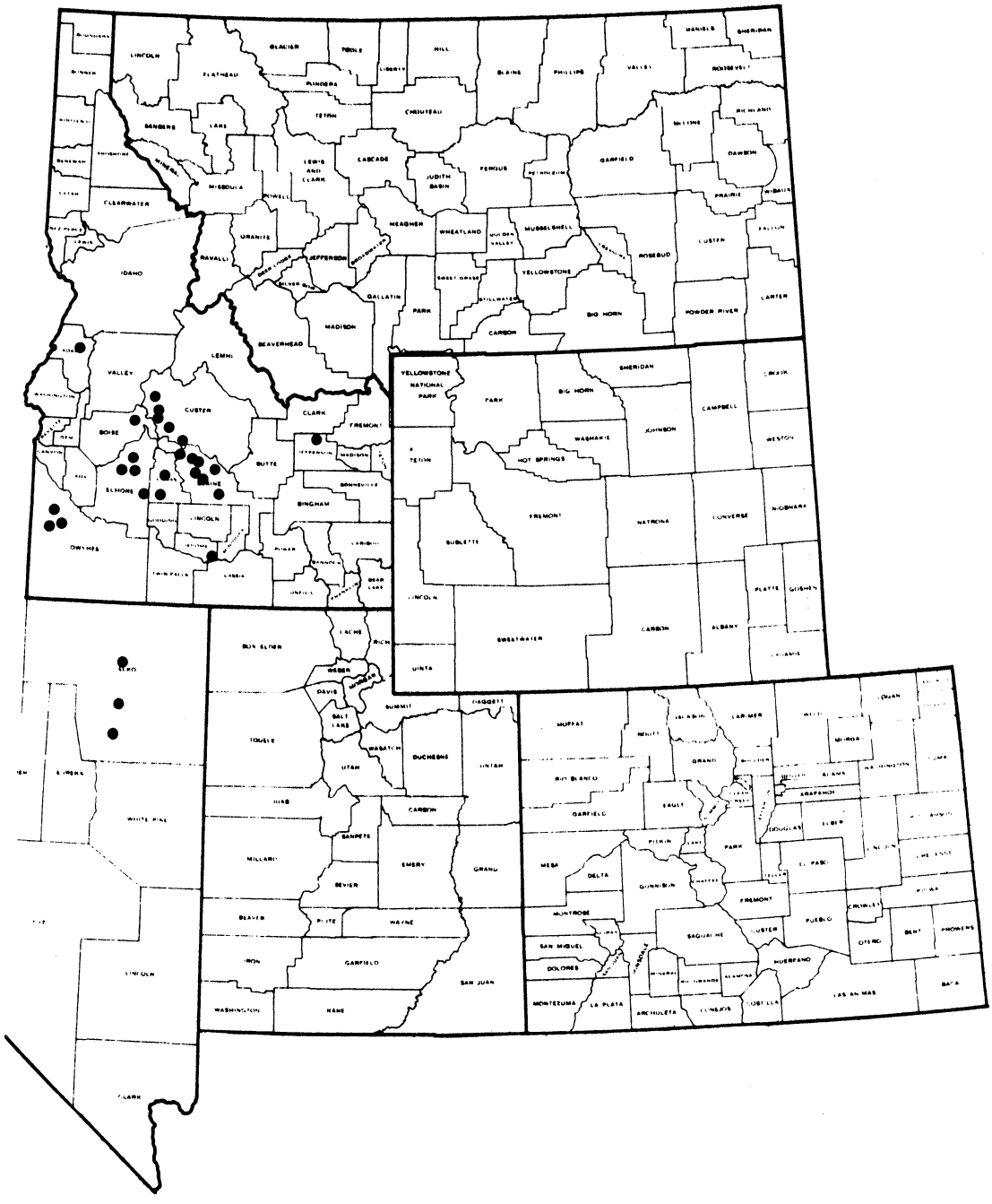
stipules 3.5-7.0 mm, basally connate for 1-2 mm, triangular; leaflets 7-9, densely to sparsely sericeous, linear elliptic, acute, conduplicate, largest 1.5-3.5 cm long, 3-7 mm wide; peduncles 1-6 cm long; racemes 5.5-10.0 (15) cm long, suberticillate or verticillate; bracts 2.5-4.0 mm long, lanceolate to subulate, caducous or occasionally tardily deciduous; pedicels 2-4 mm long; flowers blue to dark blue, 6.5-8.5 mm long; base of calyces truncate to gibbous above, sericeous, upper-lip 3.5-6.0 mm long, minutely notched, lower-lip 4-6 (8) mm long; bracteoles 1 mm or less in length, attached in angle between the calyx lips; banners mostly orbicular, densely pubescent under the calyx, 6.0-8.5 mm long, 6.0-8.5 mm wide, r/a ratio (0.4) 0.5-0.75, banner angles 122-152°, eyespot white to yellowish; wings sparsely pubescent at base or glabrous, 6-9 mm long, 3.0-4.2 mm wide, claws 1-2 mm long; keels ciliate near the acumen sometimes extending the length of the upper margins, laterally glabrous, 2-3 mm wide, 5.5-8.1 mm long, angle of keels 78-97°; ovules 3-5; pods 1.5-2.2 cm long, 5-7 mm wide, sericeous; seeds 1-3.

It has become the common belief that Nuttall's type of L. holosericeus was not collected from the banks of the Whalamet (Willamette ?) Valley of western Oregon as there are no plants which match Nuttall's type presently growing in that region. The

type was probably collected from west central Idaho (Hitchcock, et al., 1961; Smith, 1927). The distribution of the species as understood here is limited to central Idaho and a few locations in Elko Co., Nevada, ranging in elevation from 4,000 to 9,200 feet. It is frequently found in sage grassland, on dry rocky slopes and in lodgepole pine, and less frequently at higher elevations on particularly dry sites. Flowering is from late June at lower elevations and continues until late August.

The confusion in the recognition of Lupinus holosericeus has resulted from Nuttall's attributing the type location to an area where the only extant lupines are very unlike the material represented by the type specimen. In addition, intermediates are frequently found between L. holosericeus and L. caudatus, L. sericeus, and L. leucophyllus.

Figure 6-9. A typical specimen of Lupinus holosericeus.



Map 9. Distribution of Lupinus holosericeus

Distribution of Lupinus holosericeus (Map 9).

Partial citation: IDAHO: ADAMS CO.: New Meadows, Capps 314 (US). BLAINE CO.: Big Camas Prairie, Henderson 3090 (GH); East Fork Wood R, 1 mi up from Gimlet Sta, Christ 16007 (NY); Fisher Cr on US 93, Harmon 583 (UMO); Galena Grade, 2 mi from Stanley, Christ 15790 (NY); Galena Pass, Sawtooth Range, Thompson 13647 (WS, WTU); Hailey, Woods 1911 (RM); Ketchum, 10 mi N, Cronquist 2467 (IDS); Muldoon, 10 mi N, Pyrah 506 (ISC); Obsidian, 2 mi S, Christ 15789 (NY); Picabo, MacBride and Payson 2975 (RM); Redfish Lake, MacBride and Payson 3655 (POM). BOISE CO.: Willow Cr, near divide on Dear Pk Rd, Hitchcock and Muhlick 10050 (GH, IDS, NY, RM, WTU). CAMAS CO.: Dollarhide Summit, Christ 16047 (NY); Fairview, 15 mi E, Hitchcock and Muhlick 22697 (RM, WS, WTU); Soldier, 1/2 mi N, Christ 16058 (NY). CUSTER CO.: Galena Pass, Thompson 13647 (GH, IND, NY); Obsidian, Kruckeberg 4195 (NY, RM); Little Redfish Lake, Cronquist 2711 (IDS); Redfish Lake, 1 mi E, Christ 15778 (NY); Stanley, btn Upper and Lower, Christ 15775 (NY); 15 mi W, Hitchcock and Muhlick 21976 (WTU); 17 mi N, Ellis, July 1921 (UMO). ELMORE CO.: Dixie, 5 mi S, Hitchcock and Muhlick 21988 (NY, UC, WS, WTU); Fairfield, 15 mi W, Hitchcock 15554 (IDS, MO, WS, WTU); Featherville, ca 10 mi W, Hitchcock and Muhlick 10332 (RM, WTU);

Mountain Home, 20 mi NE, Hitchcock 22631 (WTU); Pine, 4 mi SW, Hitchcock 15527 (MO, RM, WS, WTU); ca 4 mi W, Hitchcock and Muhlick 10400 (NY, RM, UC, WS, WTU); 20 mi N, Meyer and Meyer 2297 (MO); Prairie, 2 mi E, Hitchcock 15472 (WS, WTU); Trinity Lakes, Davis 2897 (IDS); 5 mi N, Hitchcock and Muhlick 10319 (GH, NY, RM, UC, WS, WTU). JEFFERSON CO.: Corral, Camas Prairie, MacBride and Payson 3832 (POM, RM, UC). JEROME CO.: Hazelton, 10 mi E, Christ 15423 (NY). OWYHEE CO.: Poison Cr, 1 mi N of summit, Baker 8379 (WTU), Sawpit Summit, Baker 7918 (WTU); Sawpit Cr, 1 mi S of Silver City, Baker 8089 (WTU); Silver City, Davis 4228 (IDS, WS); MacBride 384 (GH, RM); Munz 14537 (POM, UC, WS); summit on rd to, Christ and Ward 8077 (UC); 1/2 mi SE of pass, Maguire and Holmgren 26671 (COLO, GH, NY, UC, WS, WTU); South Mt, Baker 7972, 8023 (WTU); Davis 4568 (NY).

NEVADA: ELKO CO.: Clover Mt Range, near Deeth, Heller 9138, 9241 (POM); Furlong Canyon, Ruby Mts, Train July 10, 1936 (UMO); Lamoille, Downey 31A, 31B (UMO); Pequop Summit, Downey 38 (UMO).

5. Lupinus evermannii Rydb., Bull. Torrey Bot. Club, 30: 225. 1903.

Holotype: IDAHO: near Sawtooth, B. W. Evermann 533 (US; Isotypes MO, NY).

Synonyms: Lupinus sparhawkianus C. P. Smith, Sm. Spec. Lup. 563. 1946.

Holotype: IDAHO: Valley Co., Payette Forest, Martineau and Sparhawk 79 (US).

Plants perennial and densely caespitose, stems erect or ascending, with 2-5 elongated internodes, 1-2 dm high, 1-2 mm in diameter, appressed to somewhat spreading pubescent throughout; basal petioles mostly 4.0-6.5 cm long, cauline petioles 2.0-6.5 cm long; stipules 3-7 mm long, basally connate from 1/5 to 4/5 their length, narrowly triangular to setaceous; leaflets 6-8, oblanceolate to linear oblanceolate, largest 0.5-2.5 mm long, 2.5-6.0 mm wide, acute to obtuse, densely canescent on both surfaces with long appressed to somewhat spreading hairs; peduncles 1.5-2.5 (4.3) cm long; racemes 2-4 (6) cm long, verticillate to subverticillate; pedicels 2.5-4.0 mm long; bracts 3-6 mm long, triangular to lanceolate, caducous; flowers blue, 7-8 mm long; calyces truncate to gibbous above at the base, long villous, upper-lip 3.0-4.5 mm long, minutely notched, lower-lip 4-5 mm long, teeth minute or

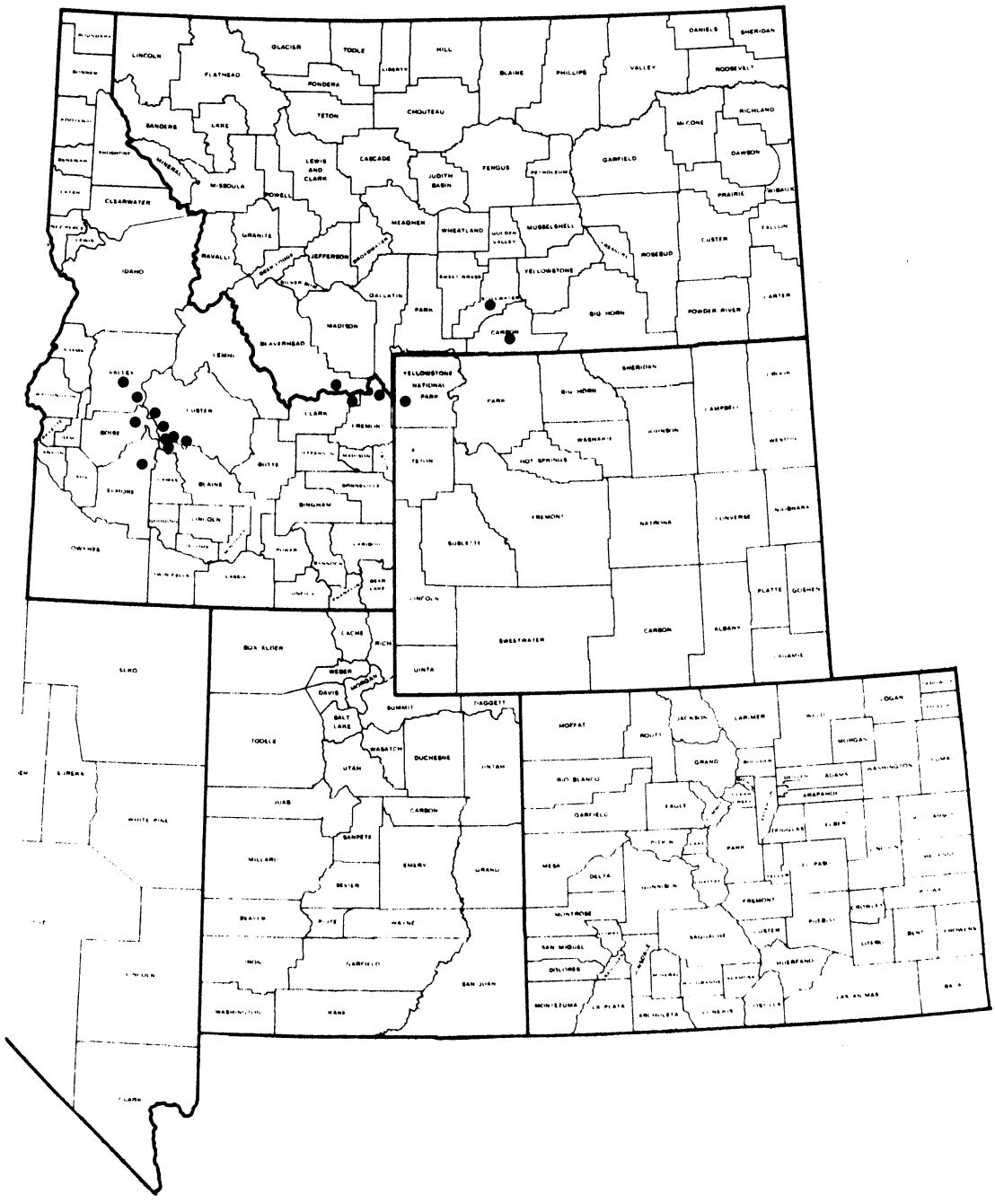
none; bracteoles usually present, minute, attached in angle of calyx lobes; banners orbicular, occasionally with few scattered hairs on back, 7-8 mm long, 7-8 mm wide, L/W ratio 0.88-1.04, r/a ratio 0.52-0.72, banner angles 110-125°; wings glabrous, 7-8 mm long, 3.5-4.6 mm wide, claws 1.0-1.5 mm long; keels glabrous laterally, ciliate near acumen or occasionally the length of the upper margins, 2.1-2.6 mm wide, angle of keels 78-102°, ovules 3-5; legumes 1.4 cm long, 6.0 mm wide, villous; seeds 2-3, 3.5 mm x 3.0 x 1.5 mm, cream colored.

Lupinus evermannii is restricted primarily to west central Idaho. A few populations in eastern Idaho and southwestern Montana have been collected. This species is found in pine woodlands or open gravelly meadows of Artemesia frigida. It is most frequently associated with lodgepole pine but occasionally extends to subalpine meadows in fir and white bark pine. Preferring a dry habitat, this species can be found from 6,500 to 9,200 feet. Flowering is from late June to late August.

Lupinus evermannii is related to Lupinus argenteus and may represent one of the numerous isolated "gene pools" which have been derived from the L. argenteus stock. While the taximetric analysis isolated L. evermannii from the other taxa in the analysis, this was

probably a consequence of an over emphasis on the short stature of L. evermannii. The chromatographic analysis of the alkaloids indicates a number of differences between L. evermannii and L. argenteus. However, the small sample of L. evermannii makes interpretation of these differences difficult.

Figure 6-10. The holotype of Lupinus evermannii.



Map 10. Distribution of Lupinus evermannii

Distribution of Lupinus evermannii (Map 10).

Partial citation: IDAHO: BLAINE CO.: Alturas Lake, Downey 60-30d (UMO); Evermann 458 (US); 1 mi W of US Hwy 93, Harmon 581 (UMO); 2 mi NE, Hitchcock and Muhlick 10561 (GH, NY, RM, UC, WTU); Galena Grade, 2 mi up from Stanley Basin, Christ 15790 (NY); Galena Summit, 9 mi N, Harmon 580 (UMO); Obsidian, 2 mi S, Christ 15789 (NY); Redfish Lake, MacBride and Payson 3655 (GH, RM, UC, US). BOISE CO.: Bull Trout Lake, 35 mi W of Stanley, Cronquist 3666 (GH, IDS, MO). CLARK CO.: Kilgore, 8 mi E, Cronquist and Holmgren 8808 (COLO, UC, WTU, WS). CUSTER CO.: Champion Cr, Fourth of July Cr, ridge btn, Kruckeberg 4537 (NY, WS); Galena Pass, Sawtooth Range, Thompson 13647 (NY); Stanley Lake, 1 mi N, Hitchcock et al. 9668 (GH, NY, RM, UC, US, WS, WTU); 9 mi NW, Harmon 1481 (UMO). ELMORE CO.: Bald Mt, ca 10 mi S of Atlanta, Hitchcock and Muhlick 10252 (WTU). FREMONT CO.: Macks Inn, Christ 15476 (NY); Ponds Lodge, Marr, summer 1940 (POM). VALLEY CO.: Cape Horn Mt, Challis-Boise Natl Forest, Kruckeberg 4182 (NY): Cape Horn, 15 mi W, Hitchcock 14102 (POM, WS, WTU); Gold Fork Lookout, Payette Natl Forest, Thompson 13653 (GH, NY); Landmark, 4 mi S, Hitchcock 14082 (COLO, POM, WS, WTU).

MONTANA: BEAVERHEAD CO.: Odell Mt, Pioneer Mts, Hitchcock 14887 (WTU); Torrey Lake, Pioneer Mts, Hitchcock 15086 (WTU). CARBON CO.: Red Lodge, 20 mi S, Hitchcock and Muhlick 13543 (WTU). STILLWATER CO.: Absarokee, Hawkins, July 20, 1914 (MONT).

WYOMING: YELLOWSTONE NATL PK: Firehole Basin, Oleson 155 (RM); Old Faithful, Davis 4925 (WTU).

6. Lupinus depressus Rydb., Bull. Torrey Bot. Club 30: 225. 1903.

Holotype: IDAHO: "divide between St. Joe and Clearwater Rivers," J. B. Leiberg 1201 (US; Isotypes GH, OSC, UC).

Synonomy: L. argenteus var. depressus (Rydb.) C. L. Hitchc. Vasc. Pls. Pacif. NW. 3:304. 1961.

Plants decumbent, spreading, forming dense mats, 1.0-2.5 dm long, erect; shoots 1-2 mm in diameter, lower spreading portion glabrate, ascending portion appressed to spreading canescent, leaves only on ascending portion of stems; basal petioles short, 1-2 cm long, cauline petioles 2.5-5.5 cm long; basal stipules somewhat inflated and connate to their petioles more than half their length, mid-cauline stipules 5-8 mm long, basally connate for 2-3 mm; leaflets 7-9 mostly narrowly oblanceolate, largest 1.0-2.5 cm long, 3-6 mm wide, L/W ratio 4.0-9.3, densely appressed silvery canescent on both surfaces; peduncles 1.5-4.0 cm, racemes 2-4 cm, somewhat densely flowered; pedicels 4-5 mm long; bracts pubescent, caducous, 3.5-5.0 mm long; flowers 8.5-10.0 mm long; calyx truncate at base, upper-lips 4.5-7.0 mm, irregularly notched from 0.5-3.0 mm deep, lower-lips 5-8 mm long, teeth minute or none, bracteoles usually present, minute; petals blue; banners with white eyespot, glabrous, orbicular, 8.5-9.5 mm long, 8-9 mm wide,

L/W ratio 1.1, r/a ratio 0.6-0.7, banner angle 124-138°; wings glabrous 8.8-10.2 mm long, 4-5 mm wide, claws 1.5-2.0 mm long; keels glabrous, 2.5-2.8 mm wide, 8-9 mm long, angle of keels 82-108°, keel tips elongate; legumes 1.5-2.0 cm long, 6-7 mm wide, densely strigose; seeds 1-2 (3).

Lupinus depressus is restricted to the high (above 7,000 feet) wind swept, rocky alpine ridges of the Clearwater Mtn. Range in northern Idaho. It forms large dense mats which spread out from the central caudex forming a silvery gray cushion over the rocky terrain. Flowering occurs from July to August.

Lupinus depressus, as L. evermannii, has its closest affinity to L. argenteus. The remoteness of the area in which it grows has resulted in relatively few collections being made. These have proven insufficient for the study of relationship between L. depressus and morphologically allied species. Without an adequate survey for intermediates, it is difficult to determine the significance of chromatographic and taximetric studies.

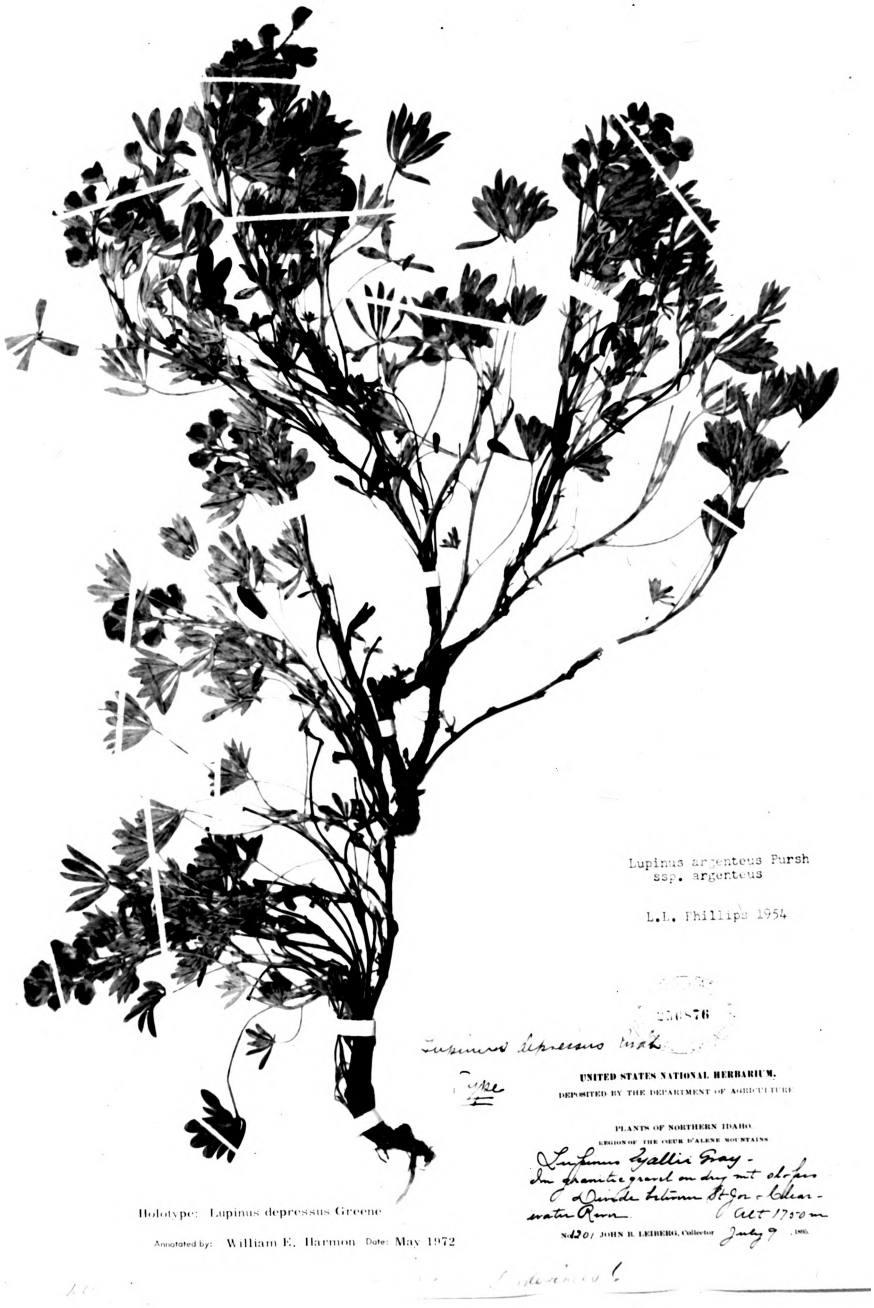
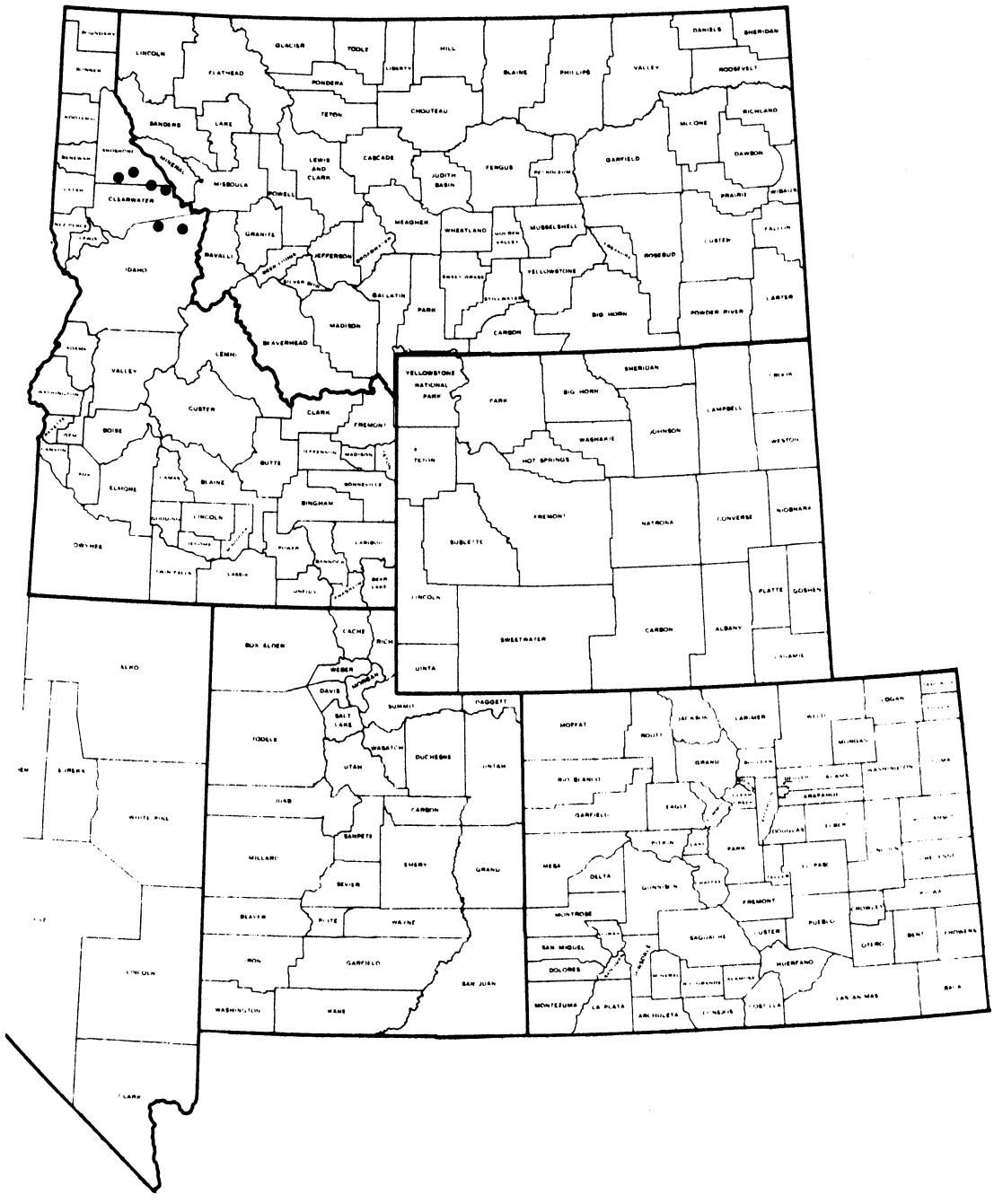


Figure 6-11. The holotype of Lupinus depressus.



Map 11. Distribution of Lupinus depressus

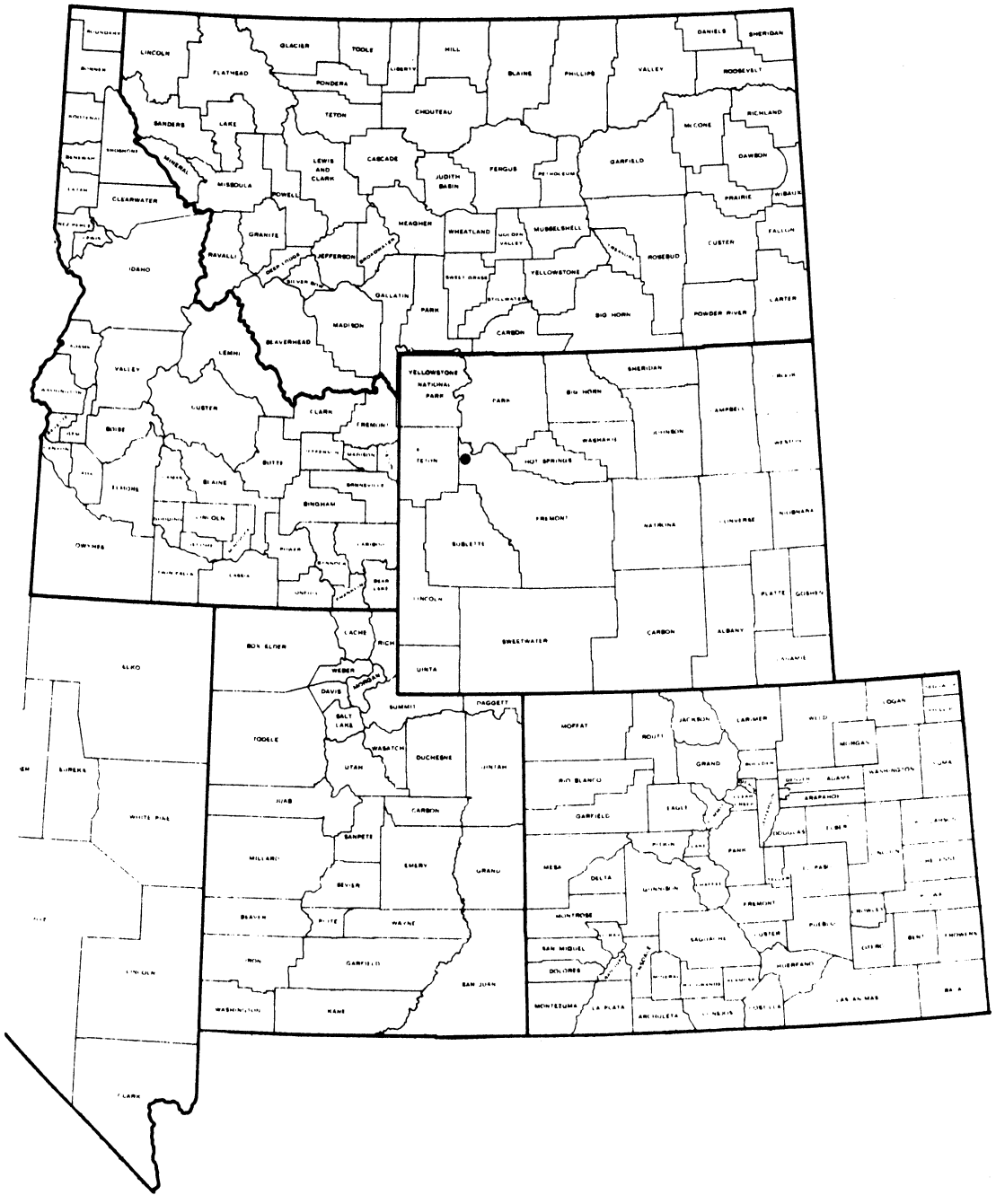
Distribution of Lupinus depressus (Map 11).

Partial citation: IDAHO: CLEARWATER-SHOSHONE CO'S.: Divide btn St. Joe and Clearwater R, Leiberg 1201 (GH, OSC, UC, US); Indian Henry Ridge, 11 mi NW of Cedars R.S., Christ 17094 (NY); Lolo Trail, Watson 80 (GH); Bitter Root Mts, Piper 4093 (GH). IDAHO CO.: Bald Mt, Lo-Lo-Trail, Piper July 19, 1902 (NY); Indian Lake, Christ 2614 (NY); and Wahoo, Wright 18177 (NY); Indian Graves Pk, on Lo-Lo Trail, Christ 17121 (NY). SHOSHONE CO.: Bearskull Mt, 1/2 mi E, Christ 17011, 17012, 17013, 17015 (NY); Freezeout Ridge, 15 mi E of Clarkia, Christ 16899, 16900 (NY); Freezeout Saddle, Wilson 271 (GH, MO); Red Ires R.S., 14 mi SE, Christ 17064 (NY).

7. Lupinus roseolus Rydb., Bull. Torrey Bot. Club 34:44. 1907. Holotype: WYOMING: Continental Divide, Buffalo Fork, F. Tweedy 270 (NY).

Plants of many short erect stems from a woody caudex; stems 10-13 cm tall, 1.0-1.2 mm in diameter, strigose; cauline petioles 1.5-2.0 cm long, basal petioles 4.0-4.5 cm long; stipules 4-8 mm long, lanceolate, basally connate half their length; leaflets 8, lance-elliptic, acute to obtuse, largest 1.1-1.8 cm long, 2.5-3.2 mm wide, semi-conduplicate, sparsely strigose above to somewhat more densely strigose below; peduncles 1.0-2.5 cm long; racemes 3.5-4.0 cm long, verticillate; bracts 4.5 mm long, lanceolate, caducous; flowers 8.1 mm long, white, tinged with rose; calyces villous, upper-lips truncate above, notched 1 mm, 4.0 mm long, lower-lips 4.1 mm long, entire, bracteoles minute, attached in sinus or angle between calyx lips; banners suborbicular, glabrous, 7.5 mm long, 8.1 mm wide, L/W ratio 0.93, r/a ratio 0.67, angle of banners 130°; wings glabrous, 8.5 mm long, 4.0 mm wide, claws 1.5 mm long; keels glabrous laterally, non-ciliate on upper margins, 2.5 mm wide, 7.5 mm long, angle of keels 81°; ovules 3, seeds unknown.

Figure 6-12. The holotype of Lupinus roseolus.



Map 12. Distribution of Lupinus roseolus

This taxon is known only from the type collection (Map 12). The flower morphology suggests an affinity with L. argenteus although it may bear closer relationship with one of the several subspecies of L. argenteus that are scattered in isolated pockets throughout the northern Rockies. The type collection, made at 10,000 feet in August, was in flower but without fruit.

8. Lupinus argenteus ssp. ingratus comb. nov.

Basionym: Lupinus ingratus Greene, Pitt. 4:133. 1900.

Lectotype: NEW MEXICO: Chama, C. F. Baker 438 (US; Isotypes GH, POM, UC).

Stems erect, 1 to several from a woody caudex, usually branching from upper portions, 4.0-7.5 dm tall, 3-5 mm in diameter at base, minutely puberulent pubescent at base becoming more dense on upper portions of stem; leaves mostly cauline; basal petioles when present, 5-8 cm long, cauline petioles 1.5-4.5 cm long; stipules 5-8 mm long, basally connate about 2 mm to petiole, narrowly triangular; leaflets 7-9, oblanceolate to narrowly elliptic, acute or obtuse, largest 2.2-4.8 cm long, 5.0-8.5 mm wide, L/W ratio 5.0-8.8, glabrous above, sparsely to densely strigulose below; peduncles 2-4 cm long; racemes (7) 10-18 cm long, subverticillate; bracts 3-7 mm long, lanceolate, caducous; pedicels 1.5-3.0 mm long; flowers cream, occasionally tinged at the tips with light blue, 7.5-9.3 mm long; calyces truncate to gibbous above at base, silky pubescent, upper-lips 3.8-5.0 mm long, notched less than 1 mm deep, lower-lips 4.5-6.0 mm long, bracteoles usually present to 1.5 mm long, attached in angle of calyx lips; banners orbicular, glabrous, 6.8-8.0 mm long, 6.8-9.0 mm wide, L/W ratio 0.88 - 1.04, r/a ratio 0.39 - 0.67, banner angle 118-142°; wings

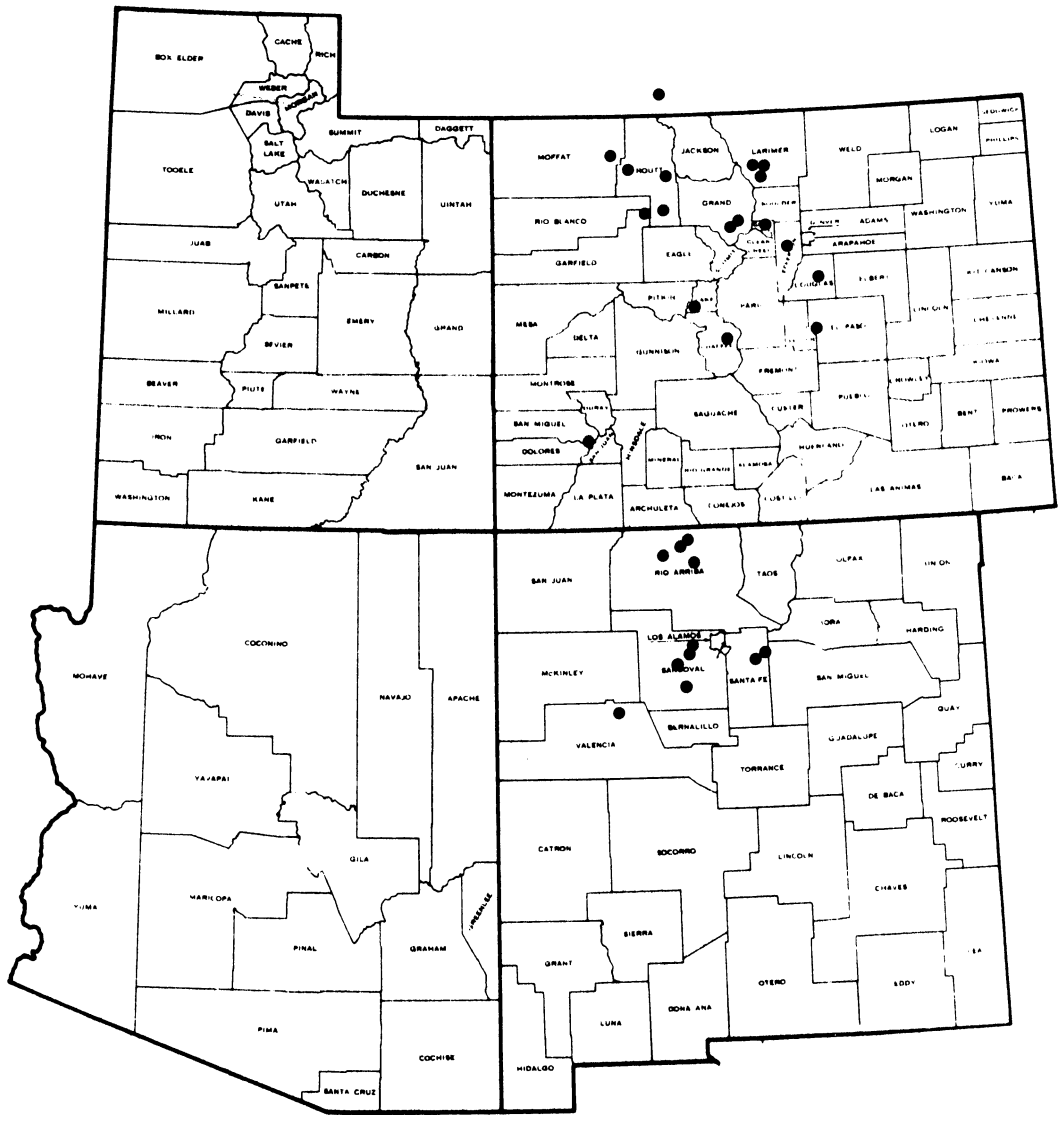
glabrous, 6.0-7.5 mm long, 3-5 mm wide, claws 1.5-2.0 mm long; keels glabrous laterally, without ciliation on upper margins, 2.2-3.9 mm wide, 7.1-9.0 mm long, angle of keels 76-90°; ovules usually 4; pods 2.0-2.5 cm long, 5.5-6.5 mm wide, silky villous; seeds 3-5, cream or grey, occasionally lightly speckled.

Lupinus argenteus ssp. ingratus can be found growing from 7,000 to 11,000 feet in yellow pine forests and dry canyons to grassy meadows in aspen and blue spruce. A few records indicate populations growing in alpine meadows. Flowering is from mid-June to late August. Distribution is from northern New Mexico to northern Colorado.

Lupinus argenteus ssp. ingratus was originally described from a population of small, cream flowered plants in northern New Mexico. This type material represents the center of a cline which combines the floral morphology of Lupinus argenteus with the dwarf flower of Lupinus parviflorus ssp. myrianthus. Intermediates can be found between L. argenteus ssp. ingratus and L. argenteus ssp. rubricaulis as well as between L. argenteus ssp. ingratus and L. parviflorus ssp. myrianthus, making separation of these taxa difficult. However, the floral morphology being basically that of the L. argenteus suggests that L. ingratus Greene be treated as a subspecies of L. argenteus.

In the northern part of its range in Larimer Co., Colorado, specimens of L. argenteus ssp. ingratus frequently have a few strigose hairs scattered on the upper leaf surfaces. The source of this pubescence is not clear. It is interesting to note however, that L. parviflorus ssp. floribundus which has a hairy upper leaf surface also occurs in this region of Colorado. Whether this fact represents "gene flow" between these taxa or if it represents a genetically unrelated occurrence in each case, remains in doubt.

Figure 6-13. A typical specimen of Lupinus argenteus ssp. ingratus.



Map 13. Distribution of Lupinus argenteus ssp. ingratus

Distribution of Lupinus argenteus ssp. ingratus (Map 13).

Partial citation: WYOMING: CARBON CO.: Riverside, 3 mi N, Isely 5187a (ISC).

COLORADO: CHAFFEE CO.: Buena Vista, Harper July 1886 (UC). DOUGLAS CO.: Castle Rock, 3 mi S, Dunn 14219 (UMO). EL PASO CO.: Manitou Springs, Hess 878 (UMO). GARFIELD CO.: Steamboat Springs, Osterhaut 2263 (GH). GILPIN CO.: Rollinsville, Overholts 10150 (MO). GRAND CO.: Hot Sulphur Springs, Engelmann August 1881 (MO); Rocky Mtn Natl Pk, Isely 5247 (ISC). JEFFERSON CO.: Morrison, 2 mi W, Ferchau and Bryant July 28, 1967 (UMO). LAKE CO.: Independence Pass, E, Isely 6577 (UMO). LARIMER CO.: Estes Pk, Isely 5253 (ISC); 3 mi S, Dunn 18292 (UMO); Jct of Tr Ridge Rd and Hidden Valley Rd, Harmon 1382 (UMO); Natl Pk Service yard, Ashton 33-C-1 (RM); Skyland Ranch, Nelson & Nelson 934 (RM); Thompson Cavern, Osterhaut 5516 (RM). MOFFAT CO.: Craig, 10 mi N, Isely 5224 (ISC). PUEBLO CO.: Beulah, Reivitt 28 (UMO). ROUTT CO.: Hayden, 3 mi W, Cox and Dunn 1237 (UMO); Steamboat Springs, Baker 7/12/1894 (POM); Goodding 1599 (GH); Eastwood 1891 (GH); Osterhaut 4968, 2793 (RM); ca 10 mi S, Weber and Maslin 7084 (COLO); 10 mi W, Cox and Dunn 1263 (UMO); Yampa, 2 mi S, Beetle 4908 (ISC). SAN MIGUEL CO.: Lizard Head Pass, 11.1

mi N, Harmon 1191 (UMO).

NEW MEXICO: RIO ARRIBA CO.: Chama, Eastwood Aug 1892 (GH); Earle 20 (NY); C. P. Smith 3922, 3921 (POM, RM); 3 mi S, Wolf 2943 (GH, POM, RSA, UMO); Horse Lake, E, Castetter 6/24/1954 (UNM); Tierra Amarilla, Castetter and Dittmer 3398B (UMO). SANDOVAL CO.: Jimez Springs, Nelson 11656 (RM, UC); Wyman Aug 1934 (GH); 7 mi NE, Bennett 8092 (US); Sulphur Springs, Arseve and Benedict 16542 (US). SANTA FE CO.: Santa Fe, base of mountains above, Fendler 168 (MO); Sante Fe Canon, C. P. Smith 4055 (RM); 9 mi E of Santa Fe, Heller and Heller 3796 (MO, US); Santa Fe Cr, 8 mi E of Santa Fe, Goddard 868 (UC). VALENCIA CO.: La Mosca Pk, Mt Taylor, Castetter July 27, 1952 (UMO); Mt Taylor, San Mateo Mts, Eggleston 18686 (NY).

CHAPTER VII

SUMMARY AND CONCLUSIONS

The problems of investigation in a complex genus such as Lupinus require an integrated approach, making use of as many of the modern tools of taxonomic research as practical. Unidimensional investigations such as those based on morphology alone lead to misinterpretations and multiple conclusions. This was abundantly clear in the review of the historical treatment of L. parviflorus and its allies. The present study attempted to correlate the highly variable morphology of the small flowered perennial lupines of the L. parviflorus complex and allied taxa with a study of their pollination and their alkaloidal chemistry. In addition, a taximetric analysis was made to define as precisely as possible the phenetic affinities among these taxa.

A preliminary survey of the pollinators of several species of lupines suggested that there is little correlation between the size of the flower and the size of the bumblebee visiting it. Bombus species were found to be the most important pollinators of the lupine species observed. Heterogeneity of the corbicular pollen loads of Bombus species on lupines suggests that the lupine species were frequently in strong competition with other plants for pollinators. A hypothesis

viewed lupines as "pollinator opportunists" in which the lupines, frequently found invading disturbed habitats, can take advantage of whatever pollinators are available. It was suggested that further surveys of the pollinators of other groups of lupines and intensive study of localized populations would be useful in determining the degree of "gene flow" between taxa, thus affording a better understanding of the origin of the variability in the genus.

A survey of the alkaloids, using leaf material as a source of alkaloids and separating them with TLC, was made. The alkaloidal spectrum among these same small flowered perennials was very much in agreement with the affinities defined by the phenetic analysis, with one exception. Lupinus meionanthus, considered by some authors to be very closely related to L. holosericeus, was found to have a completely different set of alkaloids not only with L. holosericeus, but with all the other taxa considered in this study. This was taken as an indication that L. meionanthus was not at all closely related to these other taxa.

An alkaloidal comparison of the Lupinus argenteus - L. caudatus complexes with the L. parviflorus complex showed that taxa within each complex were more similar to each other than to the taxa of other complexes. The variability in the results was too great, however, to draw any hierarchial relationships within these complexes

The complexity of the morphological variability has perplexed lupine taxonomists since Linnaeus. Morphology remains, however, the most practical approach to understanding relationships between taxa. For this reason, a taximetric analysis, using the character analysis and graph cluster analysis, was made to get a better understanding of the phenetic interaction of the taxa being studied. As with the chromatographic analysis, the morphologically similar L. argenteus - L. caudatus complexes were included in the taximetric study.

Sixty-three characters were used to describe the taxa of the Lupinus parviflorus complex and related groups. By use of the character analysis, 15 of these characters were chosen as a set of characters which would more efficiently describe the taxa.

Results of the clustering analysis were presented to show not only the relative uniqueness of the taxa, but the relationships between taxa. The cluster analyses were made using 15 characters and a broader spectrum of 31 characters. Results of both were similar, indicating that the 15 character set of descriptors was adequate to describe the variability in the groups.

From the cluster analysis it could be seen that the small flowered taxa considered here have probably been derived from several sources within the genus. The Lupinus caudatus and L. argenteus complexes are the most likely complexes from which these small flowered taxa have been derived, with the possible exception of L. meionanthus. Lupinus parviflorus and its variants are most closely allied to L. argenteus, through L. argenteus ssp. ingratus and L. argenteus ssp. rubricaulis. Lupinus evermannii, L. depressus and L. roseolus are also related to L. argenteus although the exact degree of affinity was not determined because of the lack of sufficient material available to study these taxa. For this reason no name changes were proposed for these taxa. Lupinus ingratus was determined to be sufficiently closely related to L. argenteus to be included as a subspecies of the latter although L. ingratus also forms intermediates with L. parviflorus ssp. myrianthus.

Lupinus holosericeus is most closely allied to L. caudatus. Morphologically L. hillii is most similar to L. parviflorus ssp. floribundus from which it can hardly be distinguished even though these taxa are widely separated geographically. Lupinus hillii var. osterhautianus and L. hillii var. arizonicus blend into L. palmeri and L. caudatus respectively.

The subgraph models of these relationships will serve as useful contexts for further research on these taxa, whether it be with the pollination, morphological, biochemical, or other aspects of their life history. It should be abundantly clear from this study that a reliance on any single source of information can result in incorrect conclusions.

A comparison of all the results of the pollinator study, the chromatographic alkaloid analysis and the taximetric analysis of characters and phenetic relationships were used to formulate a view of the affinities among the taxa being studied. These relationships are presented in a thorough description of each taxon, along with distribution maps and representative illustrations for each. It is believed that such a composite approach will add greater stability to the classification and knowledge of the life history of these taxa.

LITERATURE CITED

Abrams, L. 1944. An illustrated flora of the Pacific States. Vol. II, Stanford University Press, Stanford, California.

Allen, P. A. 1950. Pollination in Coryanthes speciosa. Amer. Orchid Soc. Bull. 19:528-536.

_____. 1955. Pollination in Gongora maculata. Amer. Orchid Soc. Bull. 24:230-234.

Anderson, E. 1949. Introgressive hybridization. John Wiley and Sons, New York.

Arp, G. and D. J. Rogers. 1970. A computer classification of the varieties of Pediocactus simpsonii (Engelm.) B. & R. Cactus and Succulent Journal XLII (1): 40-43.

Baker, H. G. 1953. Dimorphism and Monomorphism in the Plumbaginaceae. III. Correlation of geographical distribution patterns with dimorphism and monomorphism in Limonium. Ann. Bot., N. E. 17:615-627.

_____. 1959. Reproductive methods as factors in Speciation. Cold Spring Harbor Symposium on Quant. Biol. 24:177-191.

_____. 1966. The evolution, functioning and breakdown of heteromorphic incompatibility systems. I. The Plumbaginaceae. Evolution 20:349-368.

Boughey, A. S., K. W. Bridges, and A. G. Ikeda. 1968. An automated biological identification key. Univ. California (Irvine) Mus. Syst. Biol. Res. Ser. No. 2.

Cho, Y. D. and R. O. Martin. 1971. Resolution and unambiguous identification of microgram amounts of 22 lupin alkaloids by sequential use of thin-layer and gas-liquid chromatography and mass spectrometry. Analytical Biochem. 44: 49-57.

Constance, L. 1964. Systematic botany - an unending synthesis. Taxon 13:257-273.

Cranmer, M. F. and B. L. Turner. 1967. Systematic significance of lupine alkaloids, with particular reference to Baptisia (Leguminosae). Evolution 21:508-517.

Crovello, T. J. 1968a. The effect of change of number of OTU's in a numerical taxonomic study. Brittonia 20(4): 346-367.

_____. 1968b. The effect of alteration of technique at two stages in a numerical taxonomic study. Univ. Kans. Sci. Bull. 47(12):761-785.

_____. 1968c. The effect of missing data and of two sources of character values on a phenetic study of the willows of California. Madrono 19(8):301-315.

_____. 1968d. Key communality cluster analysis as a taxonomic tool. Taxon 17(3):241-258.

_____. 1968e. Different concepts of relevance in a numerical taxonomic study. Nature (London) 218(5140):492.

_____. 1969. Effects of change of characters and of number of characters in numerical taxonomy. Amer. Mid. Nat. 81(1):68-86.

_____ and R. D. MacDonald. 1970. Index of EDP-IR projects in systematics. Taxon 19:63-79.

Davidson, R. A. 1967. A cybernetic approach to classification: Preliminaries. Taxon 16(1):1-7.

Davis, R. J. 1952. Flora of Idaho. Wm. C. Brown, Dubuque.

Dunn, D. B. 1954. A method of mounting pressed flowers for study and preservation. Rhodora 56(671):258-260.

_____. 1956a. The breeding systems of Lupinus, group Micranthi. Am. Mid. Nat. 55(2):443-472.

_____. 1956b. Contributions toward a flora of Nevada. Part II - Lupinus. U.S.D.A., Beltsville.

_____ and J. M. Gillett. 1966. The lupines of Canada and Alaska. Queen's Printer, Ottawa.

Dziekanowski, C. T., Jr. 1971. Biosystematics of the Lupinus sparsiflorus complex. Ph. D. Dissertation, University of Missouri, Columbia, Missouri.

Ehrlich, P. R. 1961. Has the biological species concept outlived its usefulness? Systematic Zool. 10:167-176.

_____ and R. W. Holm. 1962. Patterns and Populations. Science 137:652-657.

_____ and P. H. Raven. 1969. Differentiation of Populations. Science 165:1228-1232.

Erdtmann, G. 1943. An introduction to pollen analysis. Chronica Botanica, Waltham, Mass.

Estabrook, G. F. and D. J. Rogers. 1966. A general method of taxonomic description for a computed similarity measure. BioScience 16:789-793.

_____. 1967. An information theory model for character analysis. Taxon 16:86-97.

Faegri, K. and L. van der Pijl. 1966. The principles of pollination ecology. Pergamon, London.

Fleak, L. S. 1971. Biosystematics of the Lupinus sericeus complex. Ph. D. Dissertation. University of Missouri, Columbia, Missouri.

Free, John B. and C. G. Butler. 1959. Bumblebees. Collins, London.

Gilmartin, A. J. 1967. Numerical taxonomy - an eclectic viewpoint. Taxon 16:8-12.

Goodall, D. W. 1968. Identification by computer. BioScience 18: 485-488.

Grant, V. 1949. Pollinating systems as isolating mechanisms in Angiosperms. Evolution 3:82-97.

_____. 1950. The flower constancy of bees. Bot. Rev. 16:379-398.

_____. 1957. The plant species in theory and practice. In Mayr (ed.), The species problem. Amer. Assoc. Advanc. Sci. Publ. No. 50:39.

Greene, E. L. 1892. Ecologae Botanicae, No. 1: 2. Three New Perennial Lupines. Proc. Acad. Nat. Sci. Phil. 1892: 364-365.

_____. 1900. (New Species of Plants.) Pittonia 4:133-134.

_____. 1901. (New Species of Plants.) Pl. Baker. 3:36.

_____. 1912. (New Species of Plants.) Leaflets Bot. Obs. & Crit. 2:236.

Hall, A. V. 1970. A computer-based system for forming identification keys. Taxon 19:12-18.

Harrington, H. D. 1954. Manual of the plants of Colorado. Swallow, Denver.

Hawkes, J. G. (ed.) 1968. Chemotaxonomy and Serotaxonomy. Proceedings of a Symposium held at the Botany Dept., Birmingham University, Academic Press, New York.

Hawksworth, F. G., G. F. Estabrook and D. J. Rogers. 1968. Application of an information theory model for character analysis in the genus Arceuthobium (Viscaceae). Taxon 17(6): 605-619.

Heiser, C. B. Jr., J. Soria and D. Burton. 1965. A numerical taxonomic study of Solanum species and hybrids. Amer. Nat. 99(909):471-488.

Hess, L. W. 1969. The Biosystematics of the Lupinus argenteus complex and allies. Ph. D. Dissertation. University of Missouri, Columbia, Missouri.

Hitchcock, C. L., et al. 1961. Vascular plants of the Pacific Northwest. Univ. Wash. Publ. Biol. 17(2):553-556.

Hooder, W. J. and G. A. W. Arnott. 1965 reprint. The Botany of Capitain Beechy's Voyage. J. Cramer, Weinheim.

Horovitz, A. and R. W. Thorp. 1970. Bees as tools in studies of the reproductive biology of plants. Amer. Mid. Nat. 84(2): 560-563.

Irwin, H. S. and D. J. Rogers. 1967. Monographic studies in Cassia. Mem. N. Y. Bot. Gardn. 16:71-118.

Jackson, R. C. and T. J. Crovello. 1971. A comparison of numerical and biosystematic studies in Haplopappus. Brittonia 23(1):54-70.

Jepson, W. L. 1925. A manual of the flowering plants of California. Assoc. Students Store, Berkeley.

Kalkman, C. 1966. Keeping up with the Jonses. Taxon 15(5): 177-179.

Kearney, T. H. and R. H. Peebles. 1951. Arizona Flora. Univ. of California Press, Los Angeles.

Lanjouw, J. and F. A. Stafleu. 1964. Regnum Vegetabile Vol. 31. Index Herbariorum, Part I. The Herbaria of the World. 5th edition. Kemink, Utrecht.

Linnaeus, C. 1753. Species Plantarum. S. R. Mitis, (publ. in the Polish Electorate of Saxony).

Macior, L. W. 1964. An experimental study of the floral ecology of Dodecatheon meadia. Amer. J. Bot. 51(1):96-109.

_____. 1965. Insect adaptation and behavior in Asclepias pollination. Bull. Torrey Bot. Club 92(2):114-126.

_____. 1966. Foraging behavior of Bombus (Hymenoptera: Apidae) in relation to Aquilegia pollination. Amer. J. Bot. 53(3): 302-309.

_____. 1968a. Pollen foraging behavior of Bombus in relation to pollination of nototribic flowers. Amer. J. Bot. 54(3): 359-364.

_____. 1968b. Bombus (Hymenoptera, Apidae) queen foraging in relation to vernal pollination in Wisconsin. Ecology 49(1): 20-25.

_____. 1969a. Pollination adaption in Pedicularis groenlandica. Amer. J. Bot. 55(8):927-932.

_____. 1969b. Pollination adaption in Pedicularis canadensis. Amer. J. Bot. 55(9):1031-1035.

_____. 1970. The pollination ecology of Pedicularis in Colorado. Amer. J. Bot. 57(6):716-728.

_____. 1971. Personal communication.

Mayr, E. 1957. The Species Problem. Amer. Assoc. Advanc. Sci., Publ. No. 50:39.

McKelvey, S. C. 1955. Botanical exploration of the Trans-Mississippi West, 1790-1850. Arnold Arboretum, Jamaica Plains, Mass.

Morse, L. E. 1968. Construction of identification keys by computer. (Abstract) Amer. J. Bot. 55:737.

_____. 1971. Specimen identification and key construction with time-sharing computers. Taxon 20(2/3):269-282.

Munz, P. A. and D. D. Keck. 1959. A California Flora. Univ. of California Press, Berkeley.

Ornduff, R. and T. J. Crovello. 1968. Numerical Taxonomy of Limnanthaceae. Amer. J. Bot. 55(2):173-182.

Pankhurst, R. J. 1970. A computer program for generating diagnostic keys. Comp. Jour. 13:145-151.

Pauken, R. J. and D. E. Metter, 1971. Geographic presentation of morphologic variation among populations of Ascaphus truei Stenejeger. Systematic Zoology 20(4):434-441.

Peck, M. E. 1941. A manual of the higher plants of Oregon. Binfords and Mort, Portland, pp. 866.

Peters, J. A. 1968. A computer program for calculating degree of resemblance between areas. Syst. Zool. 17:64-69.

Phillips, L. L. 1955. A revision of the perennial species of Lupinus of North America exclusive of southwestern United States and Mexico. Res. Stud. State College of Washington 23:161-201.

Rogers, D. J. and T. T. Tanimoto. 1960. A computer program for classifying plants. Science 132:1115-1118.

_____ and H.S. Fleming. 1964. A computer program for classifying plants. II. A numerical handling of non-numerical data. BioScience 14:15-28.

Rollins, R. C. 1965. On the basis of biological classification. Taxon 14(1):1-5.

Ross, H. H. 1964. Review: Principles of Numerical Taxonomy, by R. R. Sokal and P. H. A. Sneath, W. H. Freman and Co., San Francisco. Syst. Zool. 13(2):106-108.

Rydberg, P. A. 1922, 1954. Flora of the Rocky Mountains and adjacent plains. 2nd ed., New York Botanic Garden, New York.

Shelter, S. G. 1971. (as reported in) Computers in biological systematics, a new university course. J. J. Furlow, L. E. Morse, and J. H. Beaman. Taxon 20(2/3):283-290.

Smith, C. P. 1927. A distributional catalogue of the lupines of Oregon. Contr. Dud. Herb. Standford Univ. 1:7-55.

_____. 1938-1952. Species Lupinorum "Signatures". Privately published.

Sokal, R. R. and T. J. Crovello. 1970. The biological species concept: A critical evaluation. Amer. Natur. 104(93b):127-153.

_____ and P. H. A. Sneath. 1963. Principles of Numerical Taxonomy. W. H. Freeman and Co., San Francisco.

Soper, J. H. 1966. Machine plotting of phytogeographical data. Can. Geogr. 10:15-26.

Soule, M. 1967. Phenetics of natural populations: I. Phenetic relationships of insular populations of the side-blotched lizard. Evolution 21(3):584-591.

Sprague, E. F. 1962. Pollination and evolution in Pedicularis (Scrophulariaceae). Aliso 5:181-209.

Stebbins, G. L. 1950. Variation and Evolution in Plants. Columbia Univ. Press, New York.

Tidestrom, I. and T. Kittell. 1941. A flora of Arizona and New Mexico. The Catholic University of America Press, Washington, D. C.

Torrey, R. and A. Gray. 1838-1840. Flora of North America. Wiley and Putnam, New York.

Tyron, R. C. 1958. Cumulative Communality Cluster Analysis. Educ. & Psych. Measurement 18:3-35.

Watson, S. 1873. Revision of the extra-tropical North American species of the genus Lupinus. Proc. Amer. Acad. Arts & Sci. 8:517-548.

Welsh, S. L., M. Treshow and G. Moore. 1964. Guide to the common Utah plants. Brigham Young Univ. Press, Provo.

Wirth, M., G. F. Estabrook and D. J. Rogers. 1966. A graph theory model for systematic biology, with an example for the Oncidinnae (Orchidaceae). Syst. Zool. 15(1):56-69.

Woodson, R. E. 1954. The North American species of Asclepias L. Ann. Mo. Bot. Gard. 41:1-211.

Wooton, E. O. and P. C. Standley. 1915. Flora of New Mexico. Contr. from the U. S. Nat. Herb., Vol. 19. Washington, D.C.

VITA

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In September of 1960 he entered the University of Missouri-Columbia. He worked his way through undergraduate school as a student worker, and undergraduate teaching assistant and finally as greenhouse foreman for the Botany Department. He graduated with an A. B. in Botany in June, 1966.

In September 1966 he began work on a masters program, completing his thesis in June 1968 on the endemic lupines of the United States which included a study of the geographical development of the genus in the western United States.

Research toward his Ph. D. dissertation was begun in the summer of 1967 at the Rocky Mountain Biological Laboratory, Gothic, Colorado. Field investigations of the small flowered perennial lupines of the Rocky Mountains continued the next two summers at R. M. B. L. and throughout the Rocky Mountains. His formal education and field work were supported, in part, by a National Science Foundation Grant (NSF-GB-5572), by the Edward Palmer Memorial Fellowship and the Gregory Fellowship, teaching assistantships, and grants-in-

aid from the Botany Department and the Graduate School of the University of Missouri.

Professional experience was gained when, during the calendar year of 1970, he acted as a research consultant for the Organization of American States to the Instituto Centro Americano de Investigacion y Tecnologia Industrial (I.C.A.I.T.I.) in Guatemala, C. A. During his tenure in Central America he established a herbarium for I.C.A.I.T.I. from his own collections which were made throughout Central America. He was invited to return to Guatemala in 1971 and again in 1972 to continue his work there.

He is a member of the International Association for Plant Taxonomy, American Society for Plant Taxonomists, Association for Tropical Biology, Missouri Academy of Science, National Geographical Society, National Wildlife Federation and the Smithsonian Institute.

Mr. Harmon married Anne Marie Harer in 1961. They have one daughter, Mary Ellen, born August 28, 1963.

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