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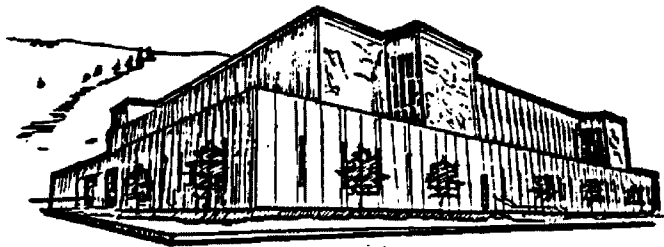
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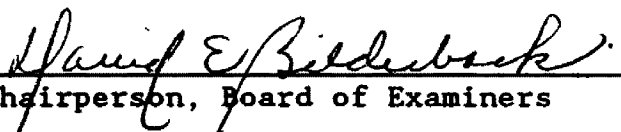


BIOSYSTEMATICS OF *PHLOX KELSEYI* (POLEMONIACEAE)

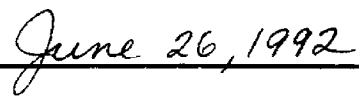
by  
Lisa M. Campbell  
B.A., University of Montana, 1985

Presented in partial fulfillment of the requirements for the degree of  
Master of Arts in Botany  
University of Montana  
1992

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Campbell, Lisa M., M.A., February 1992  
Division of Biological Sciences

Biosystematics of *Phlox kelseyi* (Polemoniaceae) (125 pp.)

Director: David E. Bilderback *DEB*

*Phlox kelseyi* (section *Occidentales*) is endemic to southern Wyoming, west-central Montana and southern Idaho with disjunct populations in Colorado and Nevada. Several infraspecific taxa are recognized: ssp. *kelseyi*, comprised of varieties *kelseyi* and *missoulensis*, and ssp. *salina*. The species is montane; var. *kelseyi* occurs in seasonally wet meadows, var. *missoulensis* inhabits wind swept ridges and ssp. *salina* grows on saline clay flats in Nevada. Many sect. *Occidentales* species exhibit intrapopulational and interpopulational morphological variation such that delimitation of these taxa is difficult. This variability is reflected in the taxonomy of the *P. kelseyi* group. An objective of this study was to identify and characterize the breeding system of *P. kelseyi*. A secondary objective was to circumscribe the taxa based on morphological and cytological information, and the ability to exchange genes.

*Phlox kelseyi* is polymorphic for corolla color. A pilot study conducted on one population indicated that white- and pink-flowered plants are freely interbreeding, while blue-flowered forms are only able to cross among themselves. The population was further examined for the presence of reproductive isolation. Low levels of compatibility were detected among the color morphs; however, the evidence is not sufficient to discount the potential of an ethological reproductive isolating mechanism.

Herbarium specimens were used to assess variation in morphological characters. Most characters are normally and continuously distributed, consistent with the concept of morphological species. Analysis of variance and Chi-square tests were used to determine diagnostic and synthetic characters; only 10 characters were found to be significantly different among the taxa. Morphological patterns were examined by principal component and discriminant analyses. The infraspecific taxa did segregate, although the clusters were not discrete. Dendrograms substantiate the observation that there is a high level of intrapopulational variation relative to interpopulational variation present in this species.

Examination of meiotic and mitotic chromosome material to determine ploidy levels and chromosome number did not yield reliable counts. However, a survey of somatic material indicates that  $2n = 14$  for one population of var. *missoulensis*.

Complete geographical isolation coupled with differences in 10 morphological characters supports recognition of the infraspecific taxa of *Phlox kelseyi* at the level of subspecies.

## ACKNOWLEDGEMENTS

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I wish to thank the numerous people who assisted me during portions of this research. Botany graduate students and others who helped make pollinator exclusion mechanisms: Kathy Ahlenslager, Mark Bjorlie, Frank Dugan, Karen Haagenon, Scott Miles, Denise Mott, Lisa Sapperstein, Lisa Schassburger, Jeff Strachan and Sue Trull. Tom Gnojeck and Jerry Theim provided locality information. Marianne Farr obtained interlibrary loans of critical literature. Dick Lane and David Patterson advised me on statistical computing and methodology, respectively. Nora Leach assisted with mitotic chromosome squashes. Peter Lesica helped on collecting trips. Ruth MacDonald assisted with the 1987 pollination experiments. Jeff Strachan was particularly generous, advising me on many matters and sharing equipment so freely. Finally, I thank my family for their support.

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## Chapter I

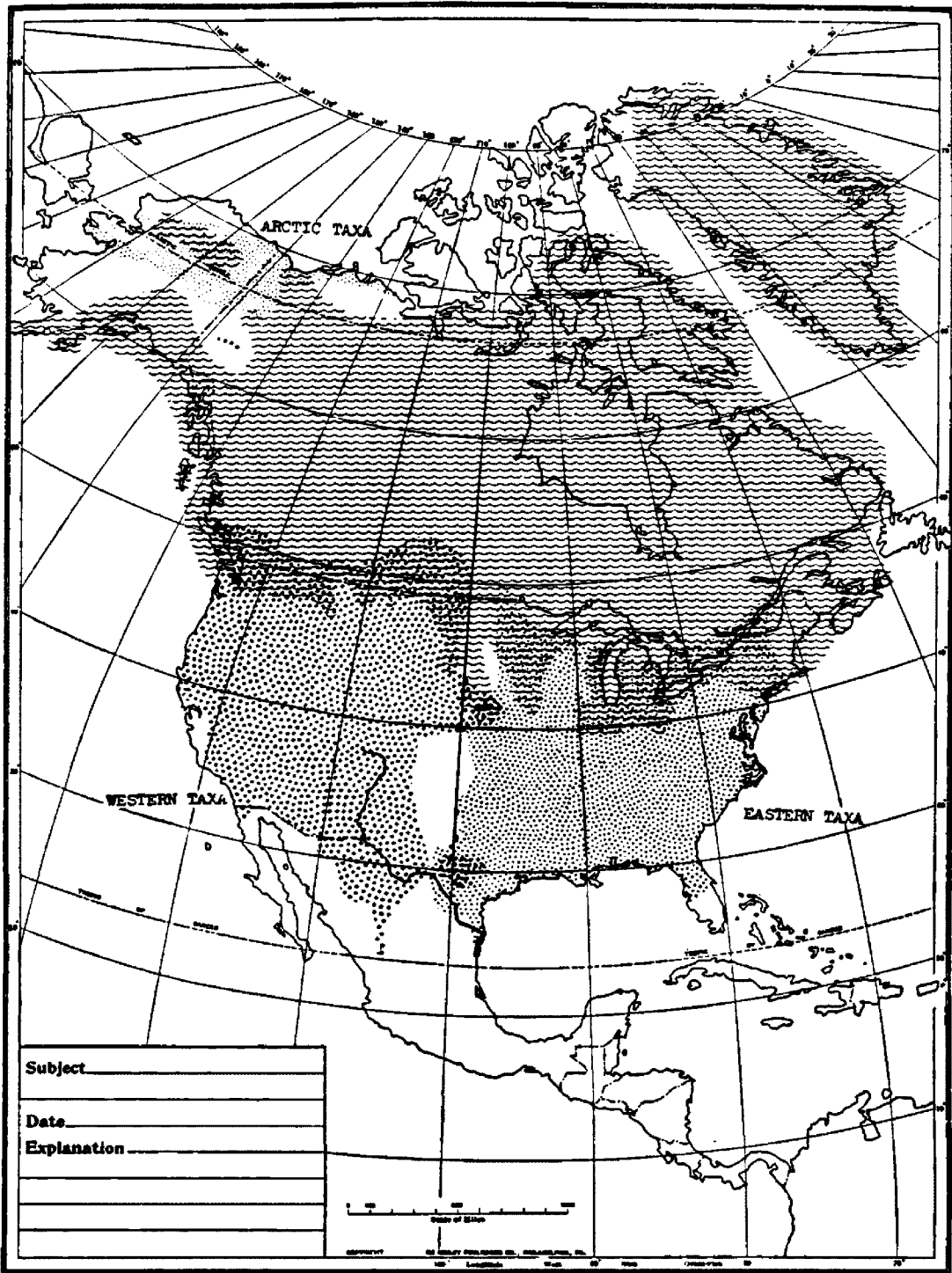
### INTRODUCTION

The genus *Phlox* L. comprises 60 North American and one Eurasian species. Species of *Phlox* are distributed almost continuously throughout the continental United States and range southward to the Tropic of Cancer in Chihuahua, Mexico, and northward to approximately 53 degrees North in Saskatchewan, Canada. The range then becomes discontinuous as *P. hoodii* Richardson and *P. sibirica* L., the Eurasian species, straddle the Arctic circle between 135--175 degrees North longitude (Wherry 1955) (Fig. 1). As this broad distribution suggests, *Phlox* species occupy a variety of habitats.

A member of the Polemoniaceae DC, *Phlox* is in the Asteridae and has the characteristic tubular, pentamerous flowers with epipetalous stamens of this subclass. Polemoniaceous flowers are perfect with the stamens alternate to the corolla lobes. Both the calyx and corolla are partially connate. The two or three carpellate superior ovary forms a capsule. *Phlox* is distinguished by actinomorphic, salverform corollas with the filaments attached at successive levels within the corolla tube. The pistil comprises three carpels; the stigma is three lobed and the ovary has three locules, each producing one axile ovule. *Phlox* leaves are simple and opposite. Most species are perennial herbs, with some acquiring enough woodiness to be considered subshrubs (Grant 1959).

*Phlox* was first described by Linnaeus in Hortus Cliffortianus (1737) based on a collection of *P. glaberrima* L. from Virginia. The first valid publication of *Phlox* appears in Species Plantarum (1753).

Figure 1. Range of the genus *Phlox*. Waved lines indicate the Wisconsin glaciation. (Figure from Wherry 1955, p. 7.)



Using his sexual system, Linnaeus classified *Phlox* in the Pentandria Monogynia in *Genera Plantarum* (1754). *Phlox*, Greek for "flame," describes the brightly colored flowers (Wherry 1955, Cronquist 1959), which make some species of horticultural interest.

Aside from a superfluous nomenclatural change to *Fonna* by Adanson (1763), subsequent taxonomists (de Jussieu, de Candolle and Bentham and Hooker) have maintained the Linnaean concept of *Phlox*. The genus has been treated by Adanson (1763), Bentham (1845), A. Gray (1870), E. E. Nelson (1899), Brand (1907), Wherry (1955) and Grant (1959).

In his monograph, Wherry (1955) reviewed prior treatments and concluded that they do not reflect natural relationships. Wherry (1955) proposed three taxonomic sections based on style length relative to stigma length and over-all plant robustness; these were further split into 18 subsections, 67 species and 84 subspecies. The generic ancestor that Wherry proposed was "...a glandular-pubescent evergreen shrub with ample inflorescences of short-styled flowers" and funnellform corollas. This progenitor presumably "differentiated into short- and long-styled groups in pre-glacial times." Figure 2 depicts Wherry's scheme of evolutionary trends in the sections of *Phlox*. Within sect. *Protophlox* Wherry, evolutionary advancement resulted in reductions of woodiness and number of flowers per inflorescence, constriction of the corolla tube and, in some species complexes, style elongation. Evolutionary trends in sect. *a-phlox* Wherry of reduced woodiness, wider leaves, increased number of nodes and plant height resulted in the robust, long-styled phlox of this group. Also long-styled, sect. *Microphlox* Wherry underwent reduction in plant height, leaf size and

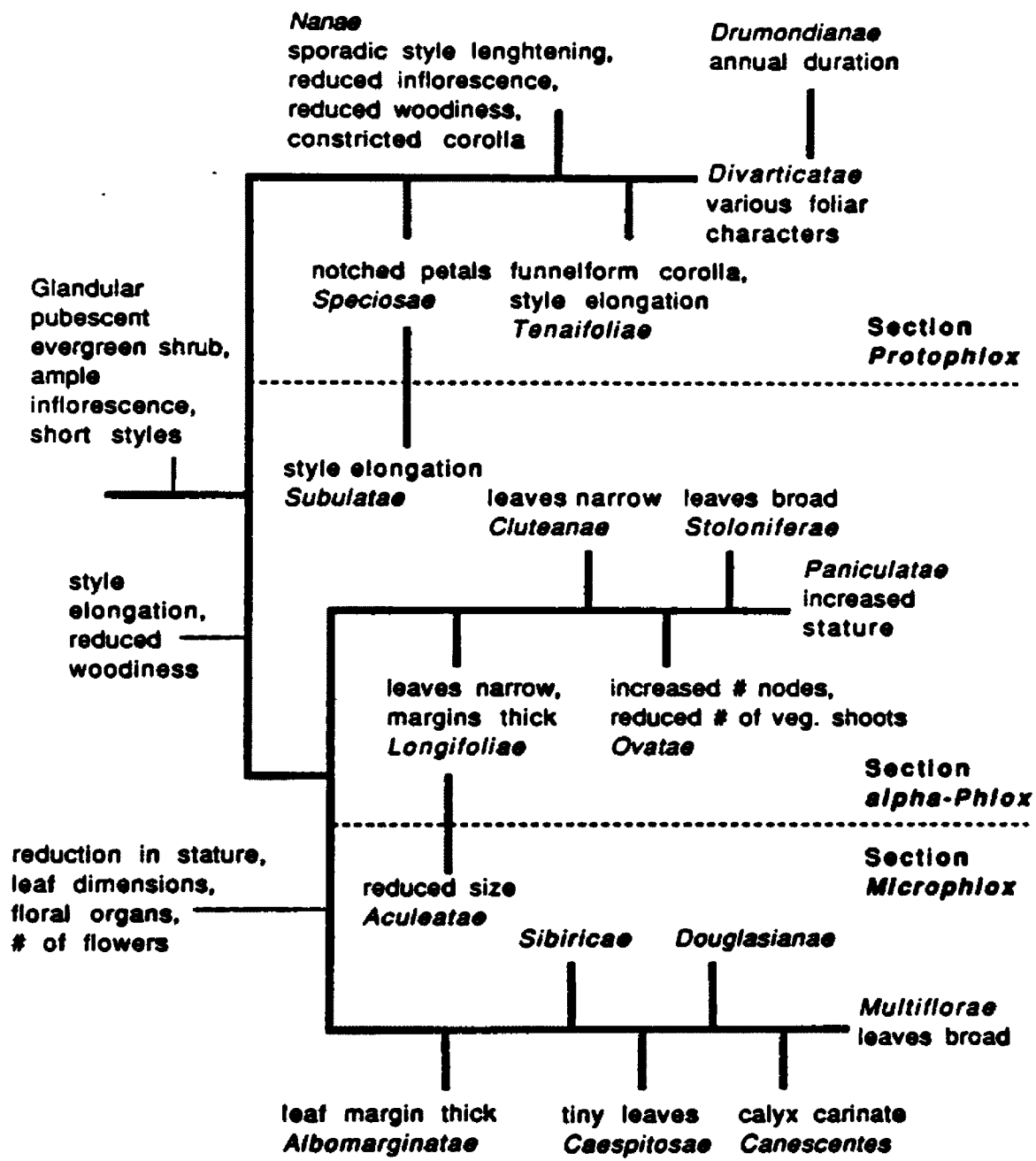


Figure 2. Diagram of phylogenetic relationships for the sections and subsections of *Phlox*; redrawn from Wherry (1955).

flower number, which lead to the robustness in sect. *a-phlox*. Other trends in sect. *Microphlox* include thickening of the leaf margins and carinate intercostal calyx membranes.

#### INFRAGENERIC CLASSIFICATION

Grant's (1959) monograph of the Polemoniaceae grouped *Phlox* species into Wherry's sections, conserved some older section names, and refined the section definitions with a suite of vegetative and reproductive characters (Table 1).

In Grant's classification, sections *Phlox* (= sect. *a-phlox* of Wherry) and *Divaricatae* Peter (= sect. *Protophlox* of Wherry) comprise tall plants (25--125 cm) with deciduous, large to medium leaves (10--85 mm long); showy, paniculate or cymose inflorescences; and large seeds. Section *Occidentales* A. Gray (= sect. *Microphlox* of Wherry) are shorter, often caespitose plants (3--15 cm tall), with evergreen, medium-sized, narrow leaves (3--20 mm long x 1--5 mm wide). Flowers are terminal and borne singly or in cymes with up to three flowers which, due to the bushy habit of the plant, has the same visual effect as a showy inflorescence. Relative to corolla length, sect. *Occidentales* species have short stamens and styles; the stigmatic region is less than five-eighths of the style and seeds are medium to small (Grant 1959).

Wherry (1955) recognized that the genus segregates into eastern and western taxa, the distribution of which correlates well with the extension of the Wisconsinan ice sheet (Fig. 1). Sections *Phlox* and *Divaricatae* have both eastern and western representatives; the southern ranging species are in sect. *Divaricatae*. Section *Occidentales*



Table 1. Comparison of the Sections of *Phlox* (Grant 1959).

Section	Duration	Habit	Leaves	Inflorescence	Stamens	Style and Stigma	Seeds
<i>Phlox</i>	perennial	herbs, or rarely woody at base	deciduous, large to medium-sized	flowers mostly numerous in cymes or panicles	long, equalling corolla or exerted	style long, stigma short	large
<i>Divaricatae</i>	perennial or annual	herbs, or woody at base	deciduous, large to medium-sized	flowers mostly numerous in cymes or panicles	short, included	style short stigma long	large
<i>Occidentales</i>	perennial	subshrubs, often cespitose	evergreen, medium-sized to needle-like	flowers solitary or few, terminal on branches	short, included	style short, stigma short	medium-sized or small

comprises only western and Eurasian taxa.

#### CHARACTERISTICS OF SECTION *OCCIDENTALES*

The taxonomic boundaries in section *Occidentales* are not clearly defined because variation exists in both floral and vegetative characters (Wherry 1955, Cronquist 1959, 1984) (Fig. 3). Within-population variation is often as great as the variation observed between populations, making unequivocal delimitation of taxa difficult. Wherry (1955) noted that in populations, "There is marked variation, and individuals believed to represent one species may seemingly intergrade with those belonging to other species." Cronquist (1959) believed that the taxa are real but lack complete morphological distinction. Conspecific populations and the ability for phloxes to naturally hybridize further confuses the taxonomy (Anderson et al. 1952, Levin 1963, 1975). This variation and difference in interpretation of its significance is reflected in modern treatments of the section. Wherry (1955) described seven subsections comprising 26 species and 47 subspecies; Grant recognized 23 species with no infraspecific taxa. To the other extreme, Jepson in *The Flora of California* (1929), treated sect. *Occidentales* as one species composed of 3 varieties (after Cronquist 1959). Figure 3 diagrammatically represents ranges of variation for selected diagnostic characters among the sect. *Occidentales* species that occur in the distributional range of *P. kelseyi*. For many species, the range of characteristics overlaps, rendering them not truly diagnostic.

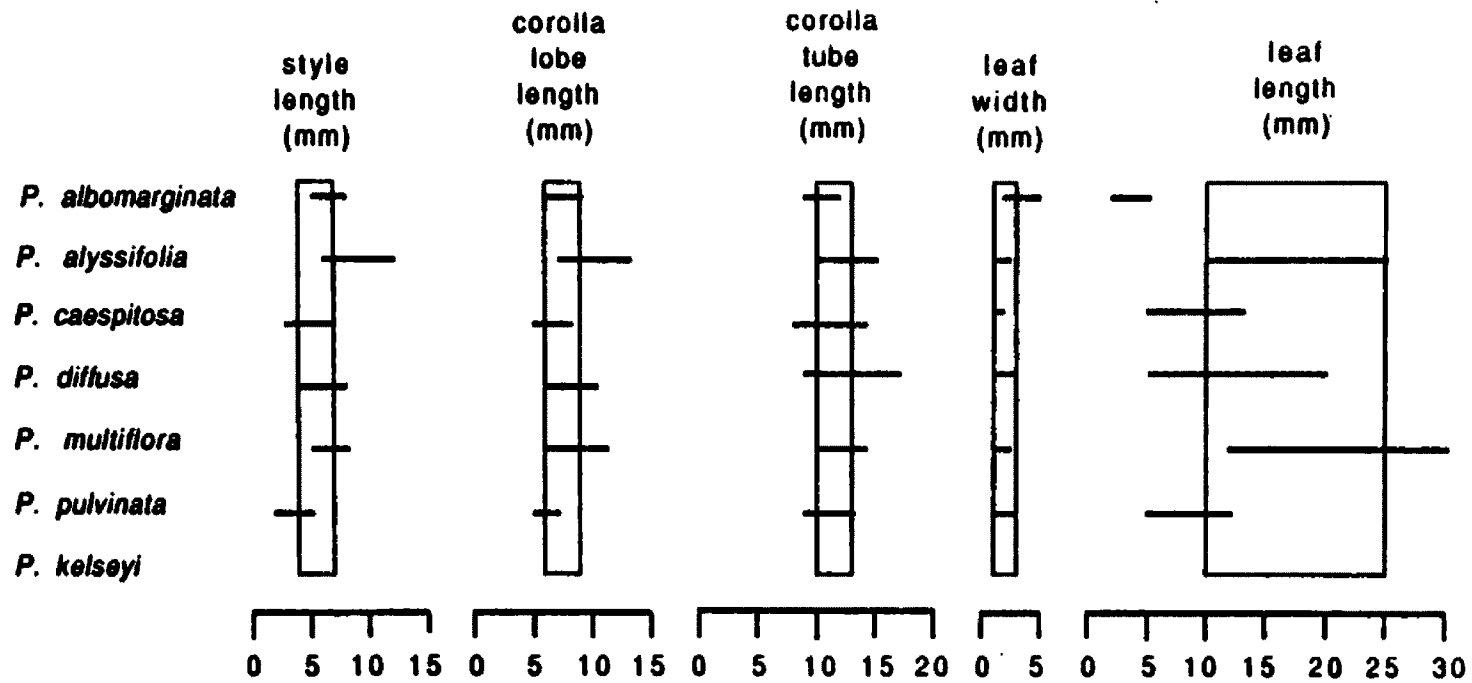


Figure 3. Comparison of *Phlox kelseyi* to selected species of section *Occidentalis* based on measurements from Cronquist (1959). Vertical rectangle is the range for *P. kelseyi*.

THE *PHLOX KELSEYI* COMPLEX

*Phlox kelseyi* Britton occurs in montane regions from southern Idaho to west-central Montana and south to Wyoming with disjunct populations reported from Park County, Colorado and Nevada (Fig. 4). *Phlox kelseyi* is a caespitose, woody-based perennial that fits the "subshrub" description. A suite of characters defines *P. kelseyi*: leaves long and narrow (11--13 mm long x 1.5 mm wide); leaves tipped with a sharp mucro; leaf margins slightly thickened, with varying amounts of cilia that may be gland-tipped; intercostal calyx membranes flat; corolla 17.6--18.8 mm long, of which approximately three-fifths is fused; styles 5.3--6.0 mm long (Fig. 5). *Phlox kelseyi* is polymorphic for corolla color, exhibiting white, pink, or a range of blue-violet hues.

*Phlox kelseyi* includes the following taxa:

- ssp. *kelseyi*
  - var. *kelseyi*
  - var. *missoulensis*
- ssp. *salina*

Subspecies *salina* has been reported only from disjunct populations in Colorado and two counties in Nevada. As its subspecific epithet suggests, ssp. *salina* occurs on highly alkaline or "saline" soils. East of the Continental Divide, subspecies *kelseyi* occurs sporadically from Teton to Beaverhead counties, Montana and in Albany County, Wyoming. West of the Divide, populations occur in Missoula and Granite counties, Montana and in Lemhi and Caribou counties, Idaho. Variety *kelseyi* occurs on hummocks in seasonally wet alkaline meadows, hence its common names "alkali" or "marsh phlox". Variety *missoulensis* (Wherry) Cronq.

**Figure 4. The distribution of *Phlox kelseyi*.**

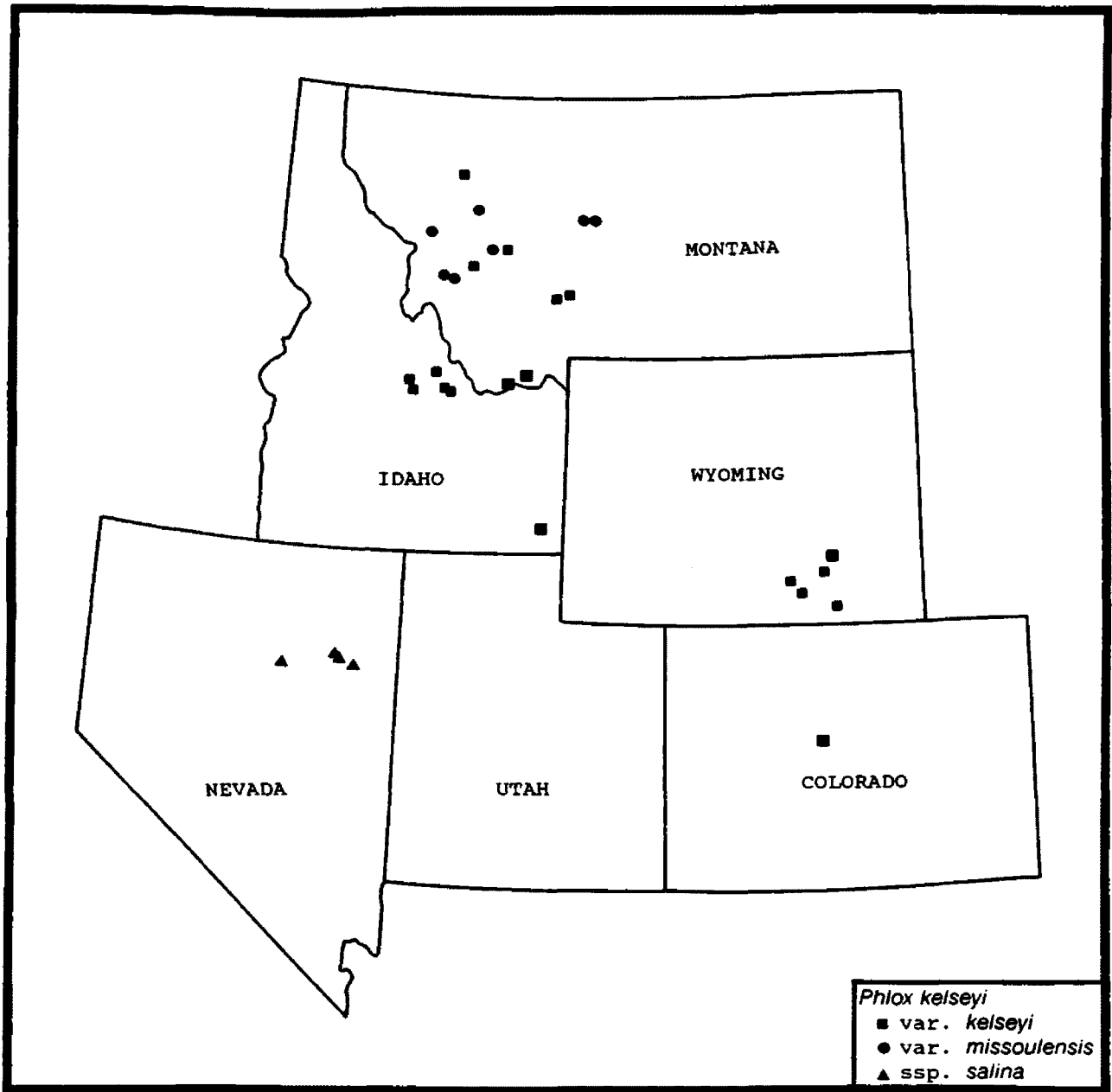
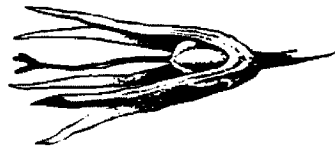
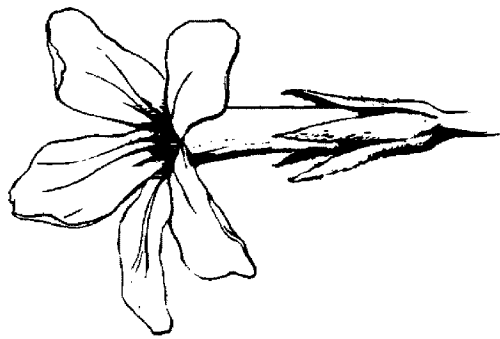


Figure 5. A typical *Phlox kelseyi* flower. Bar equals 6 mm. (Drawing by R. Petty.)





is endemic to Montana where it is known from seven localities. This variety occurs on wind-blasted mountain ridges and passes that are typically water-stressed for a portion of their growing season.

Some of the morphological variation in *P. kelseyi* undoubtedly results from the extremely different habitats in which the infraspecific taxa grow. Variety *kelseyi* forms spreading clumps, while var. *missoulensis*, with its condensed internodes, forms alpine-like cushion plants. In general habit and vegetative and floral morphology, ssp. *salina* resembles a diminutive var. *kelseyi*. No sympatric populations of any of the taxa are known; the closest populations of the varieties *kelseyi* and *missoulensis* occur in Lewis & Clark County, Montana, separated by 32 air kilometers.

*Phlox kelseyi* has had various taxonomic interpretations (Table 2). Wherry (1941) recognized three morphs of *P. kelseyi* based on vegetative differences, which, due to geographical separation, he placed into subspecies. *Phlox kelseyi* ssp. *glandulosa* Wherry, the common form, differed from ssp. *genuina* in having glandular trichomes. In his subsequent monograph, Wherry (1955), recognized the glandular form as a variant of no taxonomic rank. Wherry distinguished ssp. *variabilis* (Brand) Wherry from the other subspecies by its firm leaves and alpine habitat. Wherry described ssp. *variabilis* as, "varying in glandularity, and grading into *P. caespitosa*." Later, Wherry (1955) reverted this entity to specific rank.

First named in 1944, *Phlox missoulensis* Wherry was based on a 1939 collection from Missoula County, Montana. Morphologically, this phlox

Table 2. Modern taxonomic treatments of *Phlox kelseyi* Britton

WHERRY (1941)	WHERRY (1944)	WHERRY (1955)	GRANT (1959)	CRONQUIST (1959)
<i>Phlox kelseyi</i> Britt ssp. <i>genuina</i> (nomen novum)		Sect. <i>Microphlox</i> (Brand) Wherry Subsect. <i>Sibiricae</i> Wherry <i>P. kelseyi</i> Britt ssp. <i>-kelseyi</i>  variant of <i>-kelseyi</i>	Sect. <i>Occidentales</i> A. Gray  <i>P. kelseyi</i>	<i>P. kelseyi</i>  var. <i>kelseyi</i>
ssp. <i>glandulosa</i> (new subspecies)		ssp. <i>salina</i> (Jones) Wherry		var. <i>salina</i>
ssp. <i>variabilis</i> (Brand) (status novus)	<i>P. variabilis</i> Brand  <i>missoulensis</i> Wherry (species novus)	Subsect. <i>Douglasianae</i> Wherry <i>P. missoulensis</i> Wherry	<i>P. missoulensis</i>	var. <i>missoulensis</i>

has been most closely allied to *P. caespitosa* Nutt. (= *P. douglasii* Hook.), but differs from the latter species in having longer, wider leaves (Fig. 3) and longer sepals. Wherry placed *P. kelseyi* in subsection *Sibiricae* Wherry, which is characterized by inconspicuous leaf and sepal midribs and thin leaf margins (Fig. 2). Subsection *Douglasianae* Wherry, which encompasses *P. missoulensis*, is characterized by conspicuous midribs, narrow intercostal membranes and glandular trichomes. It is interesting to note that while Wherry interpreted these taxa as fairly distant taxonomically, he did include a population of what is now recognized as *P. kelseyi* var. *missoulensis* within the range of *P. kelseyi* (1955). This population is located on a mountain pass in Meagher County, Montana, not var. *kelseyi* habitat and otherwise out of the range of var. *kelseyi*. Cronquist (1959) reduced all three taxa to varietal level by distinguishing habitat and vegetative differences; he characterized var. *kelseyi* as "succulent" whereas var. *missoulensis* has "firmer herbage." Cronquist (1959) recognized the potential to confuse var. *missoulensis* and *P. pulvinata* (Wherry) Cronq., also in sect. *Occidentales*, because of overlapping characteristics and similar habitats.

Thus far, the infraspecific taxa of *Phlox kelseyi* have been delimited by habitat differences and morphological surveys of limited extent. Wherry (1955) analyzed only 25 specimens of *P. kelseyi* and ten specimens of *P. missoulensis*. The amount of morphological intergradation within and between *Phlox* taxa indicates that other information in addition to an extensive morphological survey is needed to elucidate taxa. Wherry (1955) noted, "the more fully the plants have been

evident it has become that the morphological data in themselves are inadequate to decide... which deserve species and which deserve infraspecific status."

#### THE SPECIES CONCEPT

The nature of a species has fascinated biologists since John Locke's time (Levin 1979). Inherent in the modern species concept is the capacity for gene exchange; populations of a single species are able to exchange genes, while populations of different species are unable to exchange genes as measured by production of fertile offspring (Stace 1980, Grant 1981). Since plant species do not always conform to this concept (see Stebbins 1950, Grant 1981 for reviews of plant hybridization) biologists continue to debate: what is a plant species? Conventionally, the notion of a "good" plant species is one in which genetic communality is reflected by a discrete morphology (Stace 1980). Stace (1980) defines an "ideal" species as having "...no sharp discontinuities of phenotype within its spectrum of variation, and does not merge with other species." However, similar morphology may belie reproductive barriers (Stebbins 1950) and not all morphologically similar groups are freely interbreeding, resulting in what Stebbins (1950) terms "cryptic species." Often this phenomenon is associated with a change in ploidy level (Stebbins 1950, Stace 1980) such as that observed in the *Crepis neglecta-fuliginosa* complex, which results in infertile hybrids (Babcock 1947 in Stebbins 1950). Some morphologically distinct *Orphrys* species are able to interbreed when a change in pollinator behavior breaks down the reproductive isolating mechanism

(Faegri et al. 1979, Grant 1981).

That species should be practical units that plant taxonomists can use, has met general agreement. But the criteria that should be used to delimit plant species remain a matter of contention. Darwin (1859 in Grant 1981), being among the earliest skeptics of the species concept as applied to plants recognized, "Certainly no clear line of demarcation has yet been drawn between species and subspecies...I look at the term species as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other..."

While Grant (1981) also regarded species as biological units or groups of organisms that are interbreeding and reproductively isolated from other such groups, he recognized four types of species:

1) taxonomic species are morphological clusters that are functional for identification and classification; 2) micro-, or agamospecies; 3) successional species; and 4) biosystematic species, or ecospecies.

In reviewing the literature about the theory of plant species, Levin (1979) concluded that species are "utilitarian mental constraints" that are inconsistent in their basis and that plant species erroneously convey natural groups that are genetically and evolutionarily linked. Three tenets are implied by the term "species": 1) species are separate breeding groups; 2) species represent a point of departure from those organisms with which they share a common ancestry and hence, a common gene pool (Dobzhansky in Levin 1979); and 3) evolution occurs at the species level (Mayr in Levin 1979). Levin (1979) contended that the significance of observed morphological variation and the processes responsible for these differences are questionable and may not reflect

the genetic differences implicit by specific rank.

The biological definition of a species--freely interbreeding organisms--holds well for members of the animal kingdom in which hybridization events are rare and usually result in sterile offspring. Successful natural and artificial plant hybridization is well documented (Levin 1963, 1967, 1983), and estimates indicate that natural interspecific hybridizations are not uncommon (Stace 1980). The degree of  $F_1$  fertility ranges from sterility to complete fertility and all possible intermediate conditions. Introgression or back-crossing of hybrids with parental genomes can further confuse the genealogy. Some hybrid swarms result in a group of organisms exhibiting one large morphological continuum uniting the original two taxa (Stace 1980).

#### GENE FLOW IN PLANT POPULATIONS

How can plant populations, the members of which are non-migratory, interbreed? Genetic exchange may occur between plant populations via pollen and seed dispersal (Levin 1981). Erlich and Raven (1969) consider gene flow to have taken place only when new alleles or allele combinations have been incorporated into a genome. They hypothesize that the physical distance over which gene flow occurs is minimal. Most studies on plant gene flow have concentrated at the population or neighborhood level and substantiate minimal gene flow predictions in entomophilous pollination systems (Levin and Kerster 1968, Price and Waser 1979, Schaal 1980). Such studies report that pollen dispersal is greater than would be expected by observing pollinator behavior alone, but that gene flow distances are nevertheless small. In a small (ca. 5

m<sup>2</sup>) experimental population of *Lupinus texensis* Hook., Schaal (1980) found no gene flow between plants at the edges of the population. Explosive seed dispersal, such as that exhibited by *Phlox*, has been shown to distribute seeds only moderate distances (averages up to 1.12 m and maximum distance of 4 m) from the parent plant (Levin and Kerster 1968, Price and Waser 1979, Schaal 1980), indicating that interpopulational seed spread from such plants would be dependent on post dehiscence dispersal by animals. For *Phlox kelseyi*, with small isolated populations, interpopulational and perhaps intrapopulational gene flow may be contingent on the breeding system. Various levels of self-compatibility are present in the genus *Phlox*; Levin (1978) reports self-compatibility in *P. roemariana* Scheele, some self-incompatibility in *P. drummondii* Hook. and complete self-incompatibility in *P. cuspidata* Scheele.

#### POLLINATION SYNDROMES IN *PHLOX*

Attempts to understand and quantify gene flow within and between angiosperm populations has led to an increase in pollination studies. Early pollination biology studies yielded descriptive accounts and led to an understanding of floral function. Interpretation of plant and animal morphology and life history strategies revealed the coevolution of flowering plants and their insect pollinators, resulting in predictive pollination syndromes (Faegri et al. 1979, Baker 1983).

Probably the most exhaustive work testing pollination syndrome hypotheses is Grant's *Flower Pollination in the Phlox Family* (1965). Grant and Grant (1965) found ten pollination syndromes in the

Polemoniaceae, including self-pollination and cross-pollination by bats and a range of specialized insects with long mouth parts. Most species have more than one pollination syndrome and some, such as *Polemonium viscosum* Nutt., exhibit "pollination races." Incorporating phylogenies from his monograph, Grant presented an evolutionary sequence of the pollination syndromes in the Polemoniaceae (Grant and Grant 1965). For the North American taxa, he believed that bee pollination is the most primitive condition; butterfly pollination and autogamy are intermediate; and hawkmoth and moth syndromes are the most advanced. Grant found convergent evolution for similar syndromes in different tribes of the family.

Floral features of *Phlox* such as tubular, anthocyanic corollas, nectar production and moderate amounts of pollen are indicative of pollination by specialized insects (Faegri et al. 1979). Tubular corollas with nectar secreted at the base function to exclude insects with mouthparts out of the range of the length of the tube. Faegri et al. (1979) classify tubular flowers with a rim, such as the corolla lobes in *Phlox*, as "trumpet" flowers. The rim facilitates insects alighting; insects visiting flowers without a rim structure must be able to hover in front of the flower.

Knuth (1909) described the pollination syndrome of *Phlox paniculata* L., which has a slightly bent corolla tube corresponding to the proboscis of its hawk-moth pollinator. Of the known insect pollination syndromes for *Phlox*, Lepidopterians are the most prevalent (Grant and Grant 1965; Levin 1969, 1970a, 1970b; Shaw et al. 1986) but bees, long-tongued flies and moths are also pollinators (Grant and Grant



1965, Tepedilo 1979). Thrips have also been reported as *Phlox* pollinators, but substantiating documentation is lacking (Faegri et al. 1979, Veer 1980).

*Phlox kelseyi* is polymorphic for corolla color and exhibits white-, blue-, and pink-flowered forms. Ford (1940 in Kay 1982), defines a color polymorphism as variation occurring within a population at a frequency greater than can be explained by mutation. Insects can distinguish between colors and exhibit preference for certain colors (Kevan 1978). This preference has resulted in constancy for particular color morphs in *Raphanus sativus* L. (Staton 1987), *Ipomoea purpurea* (L.) Roth (Epperson et al. 1986), *P. drummondii* (Levin et al. 1984), *Cirsium arvense* (L.) Scop. and *Succisa pratensis* Moench (Kay 1982). Kay (1982) found Hymenopteran constancy to be adaptable to local conditions while Lepidopteran and Syrphid flies exhibited "discrimination which may involve innate or fixed colour preferences." Pollinator preference and ensuing assortative mating may thus maintain populational polymorphisms. Levin (1970a) found pollinator preference for corolla color to be a barrier of hybridization in conspecific populations of *P. pilosa* L. and *P. glaberrima* L. Kay (1978) summarizes the scenarios in which disassortative as well as assortative pollination could maintain polymorphisms.

In a pilot study of controlled breeding system experiments on a population of *P. kelseyi* var. *missoulensis*, I found varying levels of compatibility among three colormorphs. While white-, and pink-flowered plants appeared to be freely interbreeding, the blue-flowered plants were only able to cross among themselves.

## STATEMENT OF THE PROBLEM AND STUDY OBJECTIVES

*Phlox kelseyi* comprises two subspecies; ssp. *kelseyi* has two varieties. The spatially confined populations are usually separated by large distances, resulting in a sporadic distribution. Often, the morphological variation observed within a population is as great as that between populations and populations exhibit varying degrees of corolla color polymorphism. While the genus as a whole has been studied, there has been no comprehensive systematic study of *P. kelseyi*. To gain better understanding of this morphologically variable shrubby phlox, I included the following objectives in my study:

1. Elucidate diagnostic and synthetic characters.

Methods:

- a. examine and quantify vegetative and floral characters from herbarium specimens;
  - b. treat these data statistically to determine those characters that have significantly different means among the taxa.
2. Distinguish morphological patterns among the populations.

Methods:

- a. perform principal component analysis in order to examine patterns based on overall morphological similarities.
  - b. perform discriminant analysis in order to determine the degree of separation among the taxa based on morphological dissimilarities among the populations.
3. Determine chromosome numbers, ploidy level and pairing behavior.

Method:

- a. Perform standard stain and squash techniques on meiotic and/or mitotic material.
4. Identify and characterize the breeding systems of *Phlox kelseyi* and the potential for gene exchange within and between the varieties.

Methods:

- a. Perform controlled crosses that test for levels of outcrossing, self-pollination and self-compatibility;
- b. test for crossability within and between the color morphs within a variety as well as intervarietally.
5. Circumscribe the taxa in an appropriate classification based on morphological and cytological information and the ability to exchange genes.

Method:

- a. Synthesize data and other information collected from morphology, cytology and breeding system studies.

## SIGNIFICANCE OF RESEARCH

1. To my knowledge, this research is the first comprehensive examination of *Phlox* taxa in sect. *Occidentales* and is the first attempt to apply the biological concept of a species in this group of morphologically variable phloxes. Very little is known about perennial plant breeding systems.

2. This research examined the breeding system and compatibility levels within and between infraspecific taxa. Relatively few species of

flowering plants have been examined at this level; for those that have been studied surprisingly complex patterns have emerged.

3. This research has examined the potential of detecting reproductive isolating mechanisms in *P. kelseyi*.

## Chapter II

### MATERIALS AND METHODS

#### A. MORPHOLOGICAL STUDIES

Most populations throughout the range of *Phlox kelseyi* were visited and collections made during the spring and summer of 1986 and 1987, with the exception of the Colorado population. Specimens, including types, were examined from the following seventeen herbaria:

Academy of Natural Sciences (Philadelphia)	(PH)
Booth Herbarium, Montana State University	(MONT)
Gray Herbarium	(GH)
Herbarium of Pomona College	(POM)
Intermountain Herbarium	(UTC)
Marion Owenby Herbarium, Washington State University	(WS)
Missouri Botanical Garden	(MO)
New York Botanical Garden	(NY)
Rancho Santa Ana Botanical Garden	(RSA)
Rocky Mountain Herbarium	(RM)
United States National Herbarium	(US)
University of California, Berkeley	(UC)
University of Colorado Museum	(COLO)
University of Idaho Herbarium	(ID)
University of Montana Herbarium	(MONTU)
University of Washington	(WTU)
Willard Sherman Turrell Herbarium, Miami University	(MU)

Seventy-seven herbarium specimens identified as *Phlox kelseyi* were acquired to assess morphological characters. Specimens were selected to represent the distributional range and morphological variation of *Phlox kelseyi*. After confirming identification, the exsiccatae comprised 45 var. *kelseyi*, 19 var. *missoulensis* and four ssp. *salina* specimens (Table 3). The number of populations and specimens examined is indicative of the relative abundance of each taxon.

Data were amassed from specimen labels and from 47 morphological characters (Table 4) assessed for each specimen. Eighteen vegetative and twenty nine floral characters were selected such that all above-ground features of the plants were examined. Fruit and seed characters were not recorded because these structures were not present on the majority of the herbarium specimens. Some of the 47 characters had been used in previous taxonomic treatments; others were selected based on the variation observed during field studies.

#### 1. Continuous character distribution

To determine whether parametric tests, which assume a normal distribution, could be employed in the statistical analysis of continuous character variation, the distribution of each morphological character was examined several ways. Histograms were inspected to assess the continuance and normality of the character distributions. Frequency tables and histograms of the infraspecific taxa were compared to those for the species as a whole to determine the contribution of each taxon to the variation present in *Phlox kelseyi*.

Table 3. Number of specimens and populations examined for morphological analyses.

	Number of Populations	Number of Specimens
<i>var. kelseyi</i>		
Lewis & Clark Co., MT	2	3
Madison Co., MT	3	5
Beaverhead Co., MT	3	5
Deerlodge Co., MT	2	2
Gallatin Co., MT	2	2
Teton Co., MT	3	8
Custer Co., ID	3	4
Caribou Co., ID	1	2
Lemhi Co., ID	2	3
Albany Co., WY	4	7
Fremont Co., WY	1	1
Uinta Co., WY	1	1
Park Co., CO	1	2
	-----	-----
Total	28	45
<i>var. missoulensis</i>		
Lewis & Clark Co., MT	1	2
Granite Co., MT	3	4
Judith Basin Co., MT	1	1
Meagher Co., MT	3	4
Missoula Co., MT	1	4
Park Co., MT	1	2
Powell Co., MT	2	2
	-----	-----
Total	12	19
<i>ssp. salina</i>		
White Pine Co., NV	2	3
Eureka Co., NV	1	1
	-----	-----
Total	3	4

Total number of populations = 43  
 Total number of individuals = 68

Table 4. Morphological characters examined.

VEGETATIVE CHARACTERS

Habit  
 Plant height  
 Leaf length  
 Leaf width  
 Leaf length:width  
 Leaf shape  
 Leaf pubescence  
 Leaf pubescence glands  
 Mucro presence  
 Mucro length  
 Leaf margin  
 Leaf margin cilia  
 Margin cilia glands  
 Ciliate portion of leaf margins  
 Internode length--midplant  
 Internode length--lower plant  
 Stem pubescence  
 Stem pubescence glands

REPRODUCTIVE CHARACTERS

Number of flowers per stem  
 Pedicel presence  
 Pedicel length  
 Corolla length  
 Corolla tube length  
 Corolla lobe length  
 Corolla lobe width  
 Corolla lobe length:width  
 Portion of corolla fused  
 Corolla:calyx length  
 Calyx length  
 Calyx tube length  
 Calyx lobe length  
 Portion of calyx fused  
 Calyx margins  
 Calyx pubescence  
 Calyx pubescence glands  
 Number of anthers exposed  
 Anther length  
 Placement of lowest anther (from corolla base)  
 Placement of upper anther (from corolla base)  
 Pistil length  
 Ovary length  
 Style length  
 Stigma length  
 Stigma:style  
 Style:pistil  
 Corolla tube:pistil  
 Pollen diameter



## 2. Univariate statistical analysis

Univariate statistical analyses were utilized to determine character means, ranges and variance to discern morphological patterns. Analysis of variance (ANOVA) was used to determine whether the taxa represented the same statistical population with the same mean by comparing the variability within taxa to variability between taxa (Sokal and Rohlf 1981). More specifically, ANOVA was used to test the null hypothesis that there is no difference in the true population means of the infraspecific taxa for each of the continuous characters. A multiple comparison test (least-significant difference) (Nie et al. 1986) was used for pair-wise comparison of the character means to isolate the combinations of infraspecific taxa that are significantly different for each qualitative character. These tests assume that the variance is the same for each group. Since variance is hard to assess for a sample of four, it was assumed that the variance was the same for all of the infraspecific taxa. Because this assumption of equal variance may have been violated, it was also desired to examine the data using nonparametric tests.

Since the sample sizes of the taxa varied from 45 to four specimens, the taxa were compared using the nonparametric Kruskal-Wallis one-way analysis of variance test (Sokal and Rohlf 1981). This test uses ranks to compare the taxa and is used to test the same hypothesis as ANOVA: that the infraspecific taxa have the same mean (location) and represent the same statistical population, or taxon (Sokal and Rohlf 1981).

Discrete variables were summarized in contingency tables listing

frequency and percent of occurrence within a taxon for each of the different character states. To determine if a character state frequency is significantly different than can be expected by chance alone, a Chi-square test for independence was used to compare the observed to the expected cell frequency. This test also was applied to the null hypothesis that the infraspecific taxa are from the same taxon (Bhattacharyya et al. 1977).

### 3. Multivariate statistical analysis

Multivariate statistical approaches reduce the dimensionality of data sets and were used to assess morphological patterns among the taxa by grouping the individual specimens. Morphological similarities among the individuals were evaluated by computing squared Euclidean distances. Distance measures were then used to cluster the individuals using two hierarchical techniques: the average linkage between groups method (UPGMA) and single linkage (nearest neighbor) method.

A member of a pair of highly correlated characters is eliminated from phenetic analyses so as not to give disproportionate statistical weight to any character (Jardine et al. 1971). Also, perhaps more importantly, one in a pair of highly correlated characters is eliminated in an attempt to reduce over emphasizing of any particular gene or gene sequence that might be producing a pleiotropic effect (Sneath and Sokal 1979). For example, if a measurement taken from the same organ from the upper, middle and lower regions of the plant is found to be highly correlated, two of the measurements may be eliminated since, given the modular nature of plant growth, it is likely that they are controlled by

the same gene or genes. Because in this data set the number of variables is large relative to the number of individuals, it was desired to reduce the number of variables for principal component analysis (PCA) and discriminant analysis (Jolliffe 1972).

Characters (variables) were clustered based on correlation using the average linkage between groups method (R-technique of Sneath and Sokal 1973). Based on visual inspection of a distance plot of the clusters, I selected the seventh cluster stage (coefficient = .455) to define the clusters because at this stage discrete clusters were formed (Table 5). Depending on the size of the cluster, one or two characters with low correlations were selected to be used for further analyses.

*PRINCIPAL COMPONENT ANALYSIS*-- Principal component analysis (PCA) decreases a three dimensional data matrix to fewer dimensions which enables two dimensional plotting of the individuals. As a multi-dimensional plot, the characters and the individuals' value for the characters (measurements) would occupy many axes with the individuals plotted around them in space (Radford 1986). New variables, or principal components, are computed from the original variables (Radford et al. 1974, Sokal and Rohlf 1981), and are oriented such that each one lies perpendicular to the previous one. The first component is the linear combination of the variables that has the largest variance; successive components describe decreasingly less. Eigenvalues are interpreted as the variance of the new component (Sokal and Rohlf 1981). Components with eigenvalues greater than one were retained for analysis. Since the first few components describe the most variation, the individuals were plotted on the first three components to observe

Table 5. Morphological characters selected from cluster analysis (coefficient = 0.455) for multivariate analyses.

VEGETATIVE CHARACTERS

Leaf length  
Leaf length:width  
Internode length-- midplant

REPRODUCTIVE CHARACTERS

Corolla tube length  
Corolla lobe length:width  
Calyx length  
Anther length  
Pistil length  
Pollen diameter

patterns among the taxa. Principal component analysis was used solely to observe patterns among the individuals and not for interpretation of the components.

*DISCRIMINANT ANALYSIS*-- Discriminant analysis is used when the variability of individual characters is such that the taxa overlap making it difficult to distinguish groups (Radford et al. 1974). New linear combinations of the variables are computed that maximize the variation between the taxa while minimizing the within taxon variation, thus optimally separating the individuals (Sokal and Rohlf 1981). Discriminant analysis was performed on the same characters used in principal component analysis. The first discriminant function (new variable) has the greatest between:within taxa variability; this ratio decreases with successive functions (Sokal and Rohlf 1981). The distribution of *Phlox kelseyi* specimens and taxon centroids (means) was plotted on the first two functions. Discriminant functions are predictive variables that can also be used to classify unknown individuals (Sokal and Rohlf 1969, Radford et al. 1974). The specimens examined were classified into the three infraspecific taxa.

## B. CYTOLOGICAL STUDIES

### 1. Meiotic Chromosome Examination.

Flower buds were collected in the early spring from three populations of variety *kelseyi* and two of var. *missoulensis* (APPENDIX A). The Nevada populations of ssp. *salina* were visited too late in the growing season to collect pollen mother cells. Preparation of plant material and slides was after Radford et al. (1974). Buds were fixed in

the field in 3:1 (v:v) ethyl alcohol-propionic acid solution.

The following day, the material was rinsed in a series of alcohol concentrations and stored in 70% ethyl alcohol in a freezer.

Slides of anthers were prepared with propionic-carmin stain, and thumb pressure was applied to spread the cells apart. The material was scanned with a standard light microscope; cells were further examined under phase contrast.

## 2. Mitotic Chromosome Examination

Seedling root tips from one population each of var. *kelseyi* and ssp. *salina* and from two populations of var. *missoulensis* served as the source of somatic cells for mitotic chromosome analysis (APPENDIX A). Several germination regimes were employed in an attempt to ensure some success. Mitosis was arrested in approximately four-day-old radicles using 8-hydroxyquinoline (Radford et al. 1974). The material was then fixed under suction in 3:1 (v:v) ethyl alcohol and stored under refrigeration in 70% alcohol.

The procedure outlined in Dyer (1979) was followed to prepare slides from the root tips. The material was heated for approximately 20 minutes at 60 degrees C in 1 N hydrochloric acid to loosen the cells, stained with orcein and macerated. Slides were examined using a standard light microscope and phase contrast illumination.

## C. BREEDING SYSTEM STUDIES

Breeding system studies were conducted on Waterworks Hill, Missoula Co., Montana (T 13N R 19W Sec 15). Waterworks Hill is a moderate elevation ridgeline (1220 m) rising approximately 170 m from

the valley floor. The hill, part of the Belt Series (Habeck 1984), is composed of Precambrian sedimentary rocks (Alt et al. 1972) and was covered by Glacial Lake Missoula. During the Pleistocene Epoch, the lake left behind the sediments that characterize this site. The ridge is oriented NNW-SSE (Habeck 1984) and is located at the mouth of Hellgate Canyon such that it experiences almost constant wind blast. These winds contribute to the shallow, gravelly soils (Habeck 1984) and negligible snow pack. Despite the relatively low elevation, Waterworks Hill supports a community of alpine-like cushion plants.

With the exception of a test for apomixis performed in 1985, breeding system studies comprised the same tests each year (Table 6), with only slight modifications in experimental technique. The number of flowers and plants treated in 1986 was increased to sample more of the population and so that the data could be statistically analyzed. Plants were randomly selected from those having a minimum number of flower buds to facilitate the experiments. Each treated plant was tagged with an identifying number and the color of the flowers was recorded. Individual flowers were tagged along the pedicel with nylon fish line color coded for the treatment.

Plants examined for outcrossing were only tagged. For all other treatments, the plants were placed in mesh or mesh and wire exclosures to exclude potential pollinators. To test for self-pollination, young flower buds were tagged. *Phlox kelseyi* is protandrous; within a flower the anthers mature successivly such that pollen is still being presented when the stigma is receptive. Therefore, in all other treatments involving controlled pollinations, the flowers were first emasculated by

Table 6. Breeding system experimental design. Sample sizes for crosses performed on *Phlox kelseyi* var. *missoulensis* (Missoula, MT population). The number of flowers treated on the total number of plants for 1985 and in ( ), for 1986 experiments.

Ovule Parent

	Blue	Pink	White
Outcrossing	25 fls/5 pls (25 fls/5 pls)	25 fls/5 pls (25 fls/5 pls)	25 fls/5 pls (25 fls/5 pls)
Self -pollination	25 fls/5 pls (25 fls/5 pls)	25 fls/5 pls (25 fls/5 pls)	25 fls/5 pls (25 fls/5 pls)
Self -compatibility	7 fls/2 pls (25 fls/5 pls)	7 fls/2 pls (25 fls/5 pls)	7 fls/5 pls (25 fls/5 pls)
Apomixis*	2 fls/1 pl	2 fls/1 pl	2 fls/1 pl
P			
O Blue	5 fls/2 pls (10 fls/5 pls)	5 fls/2 pls (10 fls/5 pls)	5 fls/2 pls (10 fls/5 pls)
L White	5 fls/2 pls (15 fls/5 pls)	5 fls/2 pls (10 fls/5 pls)	5 fls/2 pls (15 fls/5 pls)
L Pink	5 fls/2 pls (15 fls/5 pls)	5 fls/2 pls (15 fls/5 pls)	5 fls/2 pls (10 fls/5 pls)
E			
N			

\* This treatment was performed only in 1985



removing the anthers using fine forceps while the corolla was still enfolded. To save time, in 1987 the entire corolla was removed to emasculate the flowers. Stigmatic surfaces were examined under magnification to ensure that no pollen grains were present before a treatment was performed.

Flowers examined for apomixis were emasculated and exclosed. Self-compatibility was examined by pollinating emasculated flowers with pollen from the same plant. For reciprocal crosses among the color morphs, mates were chosen such that they were not nearest neighbors but fell within ten meters of each other to best mimic pollinator foraging behavior (Handel 1983). Anthers were transported through the community in glass dishes; pollination was effected by rubbing an anther across the stigmatic surface using fine forceps. Seeds were retrieved when the fruits were mature, prior to dehiscence.

## Chapter III

### RESULTS AND DISCUSSION

The principal questions that I sought to answer via statistical analysis of morphological characteristic variation were:

1. Are character distributions indicative of discrete groups within the *Phlox kelseyi* complex; that is, are there significant differences among the taxa for morphological characters?

2. If groups are present, what taxonomic category (e.g., species, subspecies or variety) best describes the morphological variation present?

#### A. ANALYSIS OF QUANTITATIVE CHARACTERS

Descriptive statistics for the quantitative characters examined are summarized in Table 7, and the data are presented in APPENDIX B. Although the sample size is small, subspecies *salina* does consistently represent minimal values of the morphological measurements. Morphological characteristics of the species as a whole as well as the three infraspecific taxa are continuous. Characteristics for the species and the varieties *kelseyi* and *missoulensis* are normally distributed; normality cannot be assessed for ssp. *salina* because of its small sample size. However, slight multi-modality is exhibited for several characters: leaf length, leaf width, leaf length:width, midplant internode length, lower plant internode length, pedicel length and corolla length, thus data for these characters cluster around different means for one or more of the taxa.

Table 7. Summary statistics for morphological characters of *Phlox kelseyi* and its infraspecific taxa. F probability values are from oneway ANOVA and H significance statistic values are from Kruskal-Wallis test. Pairs with significantly different means ( $P < 0.05$ ) are indicated (+,\*) next to the means. (*P. kelseyi* (species)  $n = 68$ , var. *kelseyi*  $n = 45$ , var. *missoulensis*  $n = 19$ , ssp. *salina*  $n = 4$ .)

	MEAN	SD	MIN	MAX	F PROB	H SIG
<u>HEIGHT (cm)</u>						
SP	6.79	1.76	3.5	12.0	.1076	.0436
<i>v. kelseyi</i>	7.01	1.53	3.5	11.0		
<i>v. missoulensis</i>	6.63	2.16	4.0	12.0		
ssp. <i>salina</i>	5.12	1.31	4.0	6.5		
<u>LEAF LENGTH (mm)</u>						
SP	12.32	4.86	3.5	25.0	.0069*	.0059**
<i>v. kelseyi</i>	12.6 +	4.84	5.0	25.0		
<i>v. missoulensis</i>	13.18	4.2	8.0	24.0		
ssp. <i>salina</i>	5.12+	1.43	3.5	7.0		
<u>LEAF WIDTH (mm)</u>						
SP	1.55	0.47	0.75	3.0	.0007*	.0007**
<i>v. kelseyi</i>	1.69+	0.44	1.0	3.0		
<i>v. missoulensis</i>	1.3	0.4	0.75	2.0		
ssp. <i>salina</i>	1.06+	0.31	0.75	1.5		
<u>LEAF LENGTH:WIDTH</u>						
SP	8.53	3.48	3.0	18.0	.0037*	.0039**
<i>v. kelseyi</i>	7.99	3.35	3.0	16.7		
<i>v. missoulensis</i>	10.48*	3.02	6.0	18.0		
ssp. <i>salina</i>	5.27*	2.78	3.3	9.3		
<u>MIDPLANT INTERNODE (mm)</u>						
SP	4.03	3.39	0.5	12.0	.0008*	.0003**
<i>v. kelseyi</i>	5.1 +	3.61	1.0	12.0		
<i>v. missoulensis</i>	2.07	1.51	0.5	5.0		
ssp. <i>salina</i>	1.37+	1.10	0.5	3.0		
<u>LOWERPL INTERNODE (mm)</u>						
SP	3.68	3.30	0.5	15.0	.0107*	.0005**
<i>v. kelseyi</i>	4.48+	3.54	0.5	15.0		
<i>v. missoulensis</i>	2.39	2.13	0.5	9.0		
ssp. <i>salina</i>	0.75+	0.28	0.5	1.0		
<u>PEDICEL LENGTH (mm)</u>						
SP	3.33	2.11	0.25	9.0	.0468*	.0167
<i>v. kelseyi</i>	3.65+	2.01	0.25	9.0		
<i>v. missoulensis</i>	3.03	2.28	0.25	9.0		
ssp. <i>salina</i>	1.06+	0.59	0.25	1.5		
<u>COROLLA LENGTH (mm)</u>						
SP	18.42	2.45	11.5	26.2	.0252*	.0918
<i>v. kelseyi</i>	18.58+	2.12	14.0	26.2		
<i>v. missoulensis</i>	18.69 *	2.12	14.0	26.0		
ssp. <i>salina</i>	15.25+*	3.22	11.5	19.0		

<u>COROLLA TUBE LENGTH (mm)</u>						
SP	11.15	2.0	7.25	20.0	.1213	.1341
<i>v. kelseyi</i>	11.03	1.72	7.25	17.0		
<i>v. missoulensis</i>	11.76	2.52	8.5	20.0		
<i>ssp. salina</i>	9.62	1.65	7.5	11.5		
<u>COROLLA LOBE LENGTH (mm)</u>						
SP	7.34	1.24	4.0	10.0	.6664	.8394
<i>v. kelseyi</i>	7.3 +	1.1	5.0	9.0		
<i>v. missoulensis</i>	7.53 *	1.25	6.0	10.0		
<i>ssp. salina</i>	7.0 +*	2.58	4.0	10.0		
<u>COROLLA LOBE WIDTH (mm)</u>						
SP	5.65	0.97	3.0	8.0	.0038*	.0643
<i>v. kelseyi</i>	5.72	0.92	3.0	8.0		
<i>v. missoulensis</i>	5.8	0.78	4.25	7.25		
<i>ssp. salina</i>	4.12	1.31	3.0	6.0		
<u>LOBE LENGTH:WIDTH</u>						
SP	1.31	0.22	0.88	1.88	.7929	.5685
<i>v. kelseyi</i>	1.31	0.24	0.88	1.88		
<i>v. missoulensis</i>	1.3	0.17	1.0	1.67		
<i>ssp. salina</i>	1.38	0.09	1.3	1.5		
<u>PORTION FUSED</u>						
SP	1.63	0.24	0.5	2.38	.6596	.3043
<i>v. kelseyi</i>	1.65	0.24	0.5	2.38		
<i>v. missoulensis</i>	0.49	0.07	0.36	0.64		
<i>ssp. salina</i>	1.57	0.21	1.43	1.9		
<u>COROLLA:CALYX LENGTH (mm)</u>						
SP	3.09	1.59	0	7.25	.6925	.7426
<i>v. kelseyi</i>	3.2	1.71	0	7.25		
<i>v. missoulensis</i>	2.82	1.30	0.5	6.0		
<i>ssp. salina</i>	3.06	1.56	1.0	4.5		
<u>CALYX LENGTH (mm)</u>						
SP	8.49	1.44	6.0	14.0	.6294	.4140
<i>v. kelseyi</i>	8.48	1.56	6.0	14.0		
<i>v. missoulensis</i>	8.64	1.22	7.0	11.0		
<i>ssp. salina</i>	7.87	0.85	7.0	9.0		
<u>CALYX TUBE LENGTH (mm)</u>						
SP	4.32	0.63	3.0	6.0	.3795	.3820
<i>v. kelseyi</i>	4.40	0.67	3.0	6.0		
<i>v. missoulensis</i>	4.18	0.44	3.5	5.0		
<i>ssp. salina</i>	4.12	0.85	3.0	5.0		
<u>CALYX LOBE LENGTH (mm)</u>						
SP	4.15	1.31	2.0	8.0	.4426	.2957
<i>v. kelseyi</i>	4.05	1.40	2.0	8.0		
<i>v. missoulensis</i>	4.46	1.19	2.5	7.0		
<i>ssp. salina</i>	3.75	0.5	3.0	4.0		
<u>PORTION CALYX FUSED</u>						
SP	0.51	0.08	0.33	0.71	.3420	.3437
<i>v. kelseyi</i>	0.52	0.09	0.33	0.71		
<i>v. missoulensis</i>	0.49	0.07	0.36	0.64		
<i>ssp. salina</i>	0.53	0.08	0.43	0.64		

<u>ANTHER LENGTH (mm)</u>							
SP	1.59	0.35	1.0	2.5	.8376	.7864	
<i>v. kelseyi</i>	1.61	0.34	1.0	2.5			
<i>v. missoulensis</i>	1.56	0.36	1.0	2.5			
<i>ssp. salina</i>	1.62	0.47	1.0	2.0			
<u>LOWER ANTHER PLACEMENT</u>							
<u>FROM RECEPTICLE (mm)</u>							
SP	10.26	1.7	5.0	15.0	.3100	.2100	
<i>v. kelseyi</i>	6.93	1.67	2.0	13.0			
<i>v. missoulensis</i>	6.97	1.03	5.0	9.0			
<i>ssp. salina</i>	5.75	1.32	4.0	7.0			
<u>UPPER ANTHER PLACEMENT (mm)</u>							
SP	6.87	1.51	2.0	13.0	.0832	.0912	
<i>v. kelseyi</i>	10.41	1.63	5.0	15.0			
<i>v. missoulensis</i>	10.31	1.70	7.0	14.0			
<i>ssp. salina</i>	8.43	1.85	6.0	10.0			
<u>PISTIL LENGTH (mm)</u>							
SP	8.24	1.3	5.0	12.25	.1632	.0937	
<i>v. kelseyi</i>	8.45	1.42	5.0	12.25			
<i>v. missoulensis</i>	7.89	1.01	5.5	10.25			
<i>ssp. salina</i>	7.52	0.33	7.25	8.00			
<u>OVARY LENGTH (mm)</u>							
SP	1.48	0.28	1.0	2.0	.8934	.8387	
<i>v. kelseyi</i>	1.47	0.31	1.0	2.0			
<i>v. missoulensis</i>	1.51	0.25	1.0	2.0			
<i>ssp. salina</i>	1.5	0.0	1.5	1.5			
<u>STYLE LENGTH (mm)</u>							
SP	5.75	1.19	3.0	9.0	.0786	.0443	
<i>v. kelseyi</i>	5.97	1.28	3.0	9.0			
<i>v. missoulensis</i>	5.34	0.91	3.0	7.25			
<i>ssp. salina</i>	5.09	0.12	5.0	5.25			
<u>STIGMA LENGTH (mm)</u>							
SP	1.05	0.25	0.5	2.0	.9079	.6102	
<i>v. kelseyi</i>	1.05	0.25	0.5	2.0			
<i>v. missoulensis</i>	1.07	0.23	0.75	1.75			
<i>ssp. salina</i>	1.03	0.32	0.75	1.5			
<u>STIGMA:STYLE</u>							
SP	0.18	0.09	0.08	0.9	.9912	.0806	
<i>v. kelseyi</i>	0.16	0.11	0.08	0.9			
<i>v. missoulensis</i>	0.17	0.33	0.12	0.26			
<i>ssp. salina</i>	0.17	0.04	0.13	0.23			
<u>STYLE:PISTIL</u>							
SP	0.82	0.06	0.58	0.95	.9693	.5115	
<i>v. kelseyi</i>	0.82	0.07	0.73	0.93			
<i>v. missoulensis</i>	0.81	0.05	0.68	0.95			
<i>ssp. salina</i>	0.81	0.01	0.8	0.83			
<u>PISTIL:COROLLA</u>							
SP	1.36	0.26	0.78	2.6	.3748	.1265	
<i>v. kelseyi</i>	1.34	0.28	0.78	2.6			
<i>v. missoulensis</i>	1.43	0.18	1.10	1.75			
<i>ssp. salina</i>	1.28	0.24	1.0	1.59			

POLLEN DIAMETER ( $\mu\text{m}$ )

SP	39.85	3.89	32.67	51.45	.6352	.5326
<i>v. kelseyi</i>	40.0	4.14	32.67	51.45		
<i>v. missoulensis</i>	39.88	3.61	33.69	45.82		
<i>ssp. salina</i>	38.05	1.59	36.68	40.25		

The continuous frequency distribution of the morphological characteristics suggests that the infraspecific taxa represent a single statistical population and provides no evidence to reject the hypothesis that the three taxa comprise a single morphological species.

To address the question of discrete groups within the *Phlox kelseyi* complex, analysis of variance (ANOVA) and Kruskal-Wallis test were performed for each of the continuous characters to determine if there are diagnostic characters that differentiate the infraspecific taxa. One-way analysis of variance detected significant differences ( $P < .05$ ) in the means for eight characters (Table 7). Sokal and Rohlf (1981) recommend a significance level of 1% for Kruskal-Wallis analysis of variance when the sample sizes are uneven. Using this conservative criterion, Kruskal-Wallis analysis found significant differences ( $P < .01$ ) in the means of five characters, each of which was also found to be different by ANOVA (Table 7).

The three characters found to be different by ANOVA that have high significance values for the Kruskal-Wallis H statistic are pedicel length, corolla length and corolla lobe width. In the case of the character corolla length, the discrepancy between the two tests may be explained by an outlying *ssp. salina* value for this character. For these three characters I accept the null hypothesis and conclude that there is not a significant difference among the three taxa.

Pair-wise comparisons of the taxa found no differences between the varieties *kelseyi* and *missoulensis* (Table 7). For the five significantly different characters as revealed by both ANOVA and Kruskal-Wallis test (leaf length, leaf width, leaf length:width, and mid-

and lowerplant internodes), *ssp. salina* differs from *var. kelseyi* with respect to four characters and differs from *var. missoulensis* with respect to one character. Subspecies *salina* is different from both varieties in leaf length. This analysis agrees with the observations of Wherry (1942) and Cronquist (1984) that *ssp. salina* has shorter and narrower leaves than *var. kelseyi*. In summary, ANOVA and Kruskal-Wallis test show that *ssp. salina* differs from the other two taxa in eight of the 32 continuous characters, and that for these characters no difference exists between varieties *kelseyi* and *missoulensis*. Taxonomically, this type of difference is described at the infraspecific level.

#### B. ANALYSIS OF QUALITATIVE CHARACTERS

The contingency tables used to analyze the 18 qualitative characters are presented in APPENDIX C. Pubescence and glandularity varies among the taxa, and is even variable within some populations (Table 8). However, variety *missoulensis* tends to be a more pubescent form whereas subspecies *salina* is mostly glabrous, having only pubescent calyces. Calyces are commonly a pubescent structure for the species as a whole with 87% of the specimens exhibiting this feature. Trichomes of *var. missoulensis* tend to be gland-tipped which is an atypical character for *ssp. salina*.

The Chi-square test of independence was used to identify diagnostic characters in the *Phlox kelseyi* complex. Significant differences ( $p < .05$ ) were found in six of the 18 characters including leaf pubescence, leaf margin cilia glands and calyx glands (Table 8).



Table 8. Significantly different ( $P < 0.05$ ) discrete characters of the *Phlox kelseyi* infraspecific taxa. Table includes frequencies and, in parentheses, the percent occurrence in each taxon. (var. *kelseyi* (Pkk)  $n = 45$ , var. *missoulensis* (Pkm)  $n = 19$ , ssp. *salina* (Pks)  $n = 4$ .)

	<u>Pkk</u>	<u>Pkm</u>	<u>Pks</u>
<u>HABIT</u> ( $P < 0.0001$ )			
Cushion	7 (15.6)	13 (68.4)	2 (50)
Cushion-Decumbent	4 ( 8.9)	5 (26.3)	2 (50)
Decumbent	38 (75.6)	1 ( 5.3)	0
<u>LEAF PUBESCENCE</u> ( $P = 0.0061$ )			
Absent	39 (86.7)	10 (52.6)	4 (100)
Present	6 (13.3)	9 (47.4)	0
<u>LEAF MARGIN CILIA GLANDS</u> ( $P = 0.0354$ )			
Absent	38 (84.4)	11 (57.9)	4 (100)
Present	7 (15.6)	8 (42.11)	0
<u>CILIATE PORTION OF LEAF</u> ( $P = 0.0072$ )			
< .50	5 (77.8)	8 (42.1)	4 (100)
> .50	10 (22.2)	11 (57.9)	0
<u>NUMBER OF ANTHERS EXPOSED</u> ( $P = 0.0069$ )			
0	10 (22.2)	9 (47.4)	4 (100)
1-2	16 (35.6)	9 (47.4)	0
3-5	19 (42.2)	1 ( 5.3)	0
<u>CALYX GLANDS</u> ( $P = 0.550$ )			
Absent	15 (33.3)	3 (15.3)	3 (75)
Present	30 (66.7)	16 (84.2)	1 (25)

Leaf pubescence and leaf margin cilia glands are more commonly present in variety *missoulensis* than the other two taxa. Calyx trichome glands are common in the two varieties, and were only sparsely present on one specimen of ssp. *salina*.

Presence of leaf margin cilia is a consistent character for variety *missoulensis* and subspecies *salina*, but is not present on all var. *kelseyi* plants (Table 8). The portion of the margin that is ciliate is significantly different ( $p < .0000$ ) between the taxa. Characteristically, less than half of the leaf margin is ciliate in ssp. *salina*, while greater than half is ciliate in var. *missoulensis*. The portion that is ciliate is highly variable in var. *kelseyi*.

There is a difference in habit among the taxa; variety *kelseyi* has a decumbent habit, var. *missoulensis* is characterized by a cushion habit. Subspecies *salina* exhibits both cushion forms and more relaxed, prostrate plants depending on the site; in wetter conditions the stems are more condensed.

The species has linear to lanceolate leaves. Although a Chi-square test of independence does not indicate a significant difference in leaf shape, analysis of variance detects a difference ( $p < .0037$ ) in leaf dimension between the taxa (Table 8). As indicated by leaf length:width ratio, variety *missoulensis* has narrower leaves ( $x = 1.3$  mm); 63% of the specimens have linear or linear-lanceolate leaves while lanceolate leaves occur on 46% of var. *kelseyi* ( $x$  width = 1.68 mm) and 100% of ssp. *salina* plants ( $x$  width = 1.06 mm).

*Phlox kelseyi* stamens are attached at successive levels along the corolla tube, maturing at different rates. Anthers produce yellow-

orange pollen that, to the human eye, contrasts with the corolla color contributing to the flowers' attractiveness. Typically, zero to two anthers are exposed from the corolla, and are exerted in only one population of var. *kelseyi*.

To summarize, distinct groups are present in the *Phlox kelseyi* complex that can be distinguished by ten diagnostic characters (Table 9).

*CLUSTER ANALYSIS*-- Cluster analysis was used to assess the nature of the groups in the *Phlox kelseyi* complex. The dendrogram (APPENDIX D) produced by the unweighted average linkage between groups method based on the characters in Table 5 did not cluster the infraspecific taxa into unambiguous groups. However, of the three taxa, subspecies *salina* does separate with three of the four specimens forming a discrete cluster. Members of varieties *kelseyi* and *missoulensis* are intermixed in most of the clusters. For both varieties a pair of members from a population often cluster together, but then are separated by large distances from other members of the same population. A dendrogram produced by the nearest neighbor method (APPENDIX D) also was examined for the ordering of population members since the average linkage method was not satisfactory. This method arranged members of the same taxon more discretely, but members of the same population were separated.

That the infraspecific taxa did not separate well by cluster analysis may be due to several reasons. First, the characters analyzed may be too highly correlated for distance techniques (Radford et al. 1974). The separation of members of the same populations indicates that there is as much variability within individual populations as between

Table 9. Salient morphological characters in *Phlox kelseyi* (measurements in mm).

Character	var. <i>kelseyi</i>	var. <i>missoulensis</i>	ssp. <i>salina</i>
Leaf length	5.0--25.0 x = 12.6	8.0--24.0 x = 13.18	3.50--7.0 x = 5.12
Leaf width	1.0--3.0 x = 1.69	0.75--1.5 x = 1.3	0.75--1.5 x = 1.06
Leaf l:w	3.3--16.7 x = 7.99	6.0--18.0 x = 10.48	3.3--9.3 x = 5.27
Midplant Internode	1.0--12.0 x = 5.1	0.5--5.0 x = 2.07	0.5--3.0 x = 1.37
Lower Plant Internode	0.5--15.0 x = 4.48	0.5--9.0 x = 2.39	0.5--1.0 x = 0.75
Habit	decumbent (76%)	cushion (68%)	cushion (50%) cush/decum (50%)
Leaf pubescence	absent (86%)	present (47%)	absent (100%)
Margin cilia glands	absent (84%)	present (42%)	absent (100%)
Ciliate portion of margin	> 1/2 (41%)	> 1/2 (95%)	< 1/2 (100%)
Calyx glands	present (67%)	present (84%)	absent (75%)

the populations for the characters examined. The cluster analysis indicates a distinction at a level that might be expected of infraspecific taxa.

*PRINCIPAL COMPONENT ANALYSIS*-- Figure 6 is a plot of the individuals on the first two principal components derived from the nine characters in Table 5. The taxa overlap in their distribution, but there is some segregation into groups; however, the groups are not discrete. Variety *missoulensis* forms two groups but is interspersed with members of var. *kelseyi*. The subspecies *salina* individuals cluster together well. The degree of morphological variation of the taxa shown on the principal component plot may be due in part to the varying sample sizes. Variety *kelseyi* shows the most morphological variation, but does not express the full range of the species. Subspecies *salina* represents one end of the continuum of the species, and shows morphological similarity to one of the var. *missoulensis* groups.

The two variety *missoulensis* and three var. *kelseyi* specimens near the subspecies *salina* cluster are those that are classified as ssp. *salina* by discriminant analysis (discussed below). I have identified the two outliers from the var. *missoulensis* region (indicated by arrows) as *Phlox pulvinata* (Wherry) Cronq.

*DISCRIMINANT ANALYSIS*-- Discriminant analysis utilizing the characters in Table 5 has a 75% accuracy rate of confirming the identity of the specimens (Table 10). Since a 33% accuracy rate is expected from chance alone the solution may appear mediocre; however, discriminant analysis using the diagnostic characters was no better and in

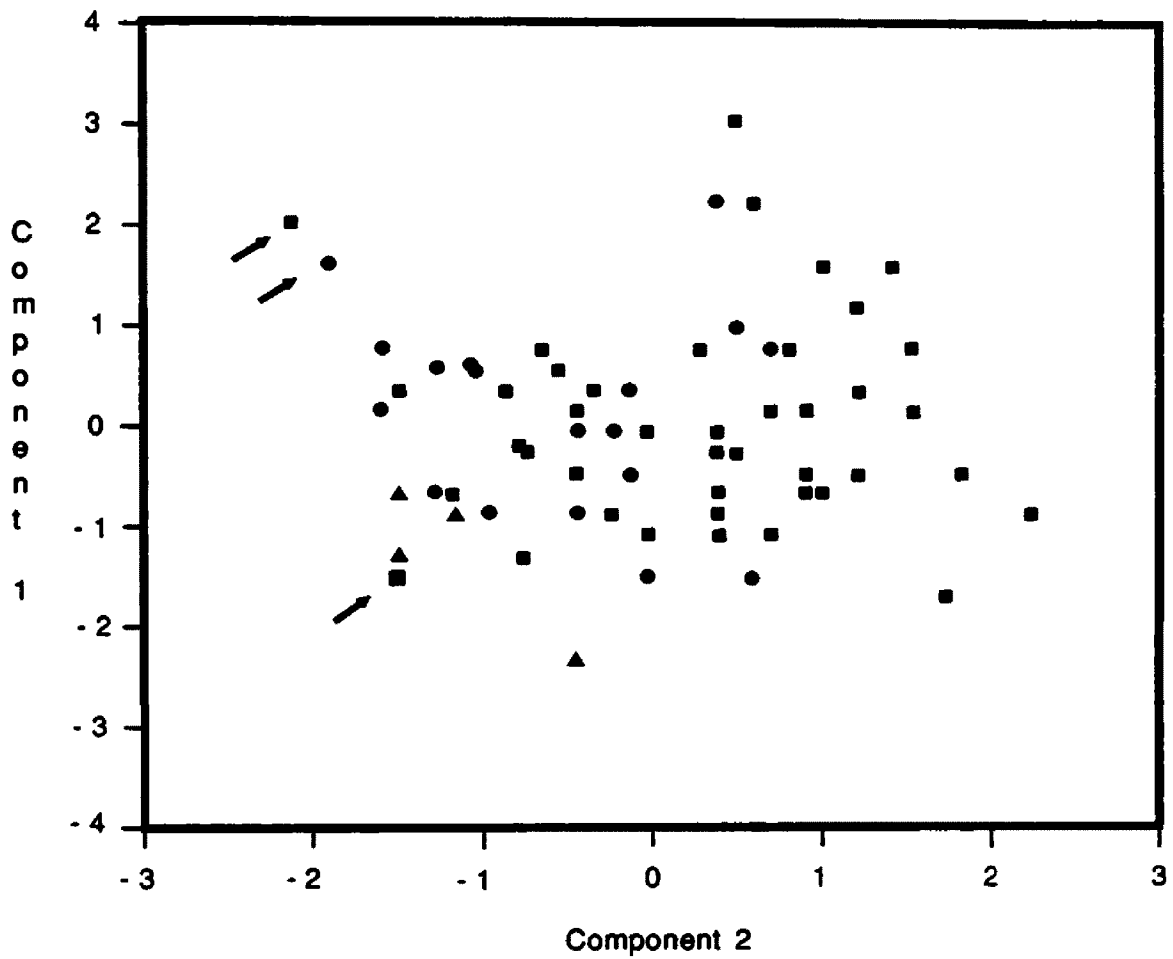


Fig. 6. Projections of *Phlox kelseyi* specimens onto the first two principal components. The first component explains 28% of total character variance, the second component 17%. ( ■ *P. kelseyi* var. *kelseyi*; ● *P. kelseyi* var. *missoulensis*; ▲ *P. kelseyi* ssp. *salina*.)

Table 10. Predicted taxon membership from discriminant analysis for *Phlox kelseyi* specimens examined. (*Phlox kelseyi* var. *kelseyi* (Pkk), *P. kelseyi* var. *missoulensis* (Pkm), *P. kelseyi* ssp. *salina* (Pks)).

Actual taxon	<i>n</i>	Predicted Taxon		
		Pkk	Pkm	Pks
<i>var. kelseyi</i>	45	31 68.9%	11 24.4%	3 6.7%
<i>var. missoulensis</i>	19	0 0.0%	16 84.2%	3 15.8%
<i>ssp. salina</i>	4	0 0.0%	0 0.0%	4 100.0%

discriminant analysis using all 29 continuous characters, the accuracy rate was only increased to 85%. Variety *kelseyi*, with the largest sample size and the morphological range of the species for most characters, had some individuals classified in each of the other two taxa. Sixteen percent of the var. *missoulensis* specimens were classified as ssp. *salina*. These two taxa are smaller, more condensed plants with narrower leaves and shorter styles than var. *kelseyi*. Both discriminant and principal component analysis detected a greater morphological similarity between var. *missoulensis* and ssp. *salina* than var. *kelseyi* and ssp. *salina*.

This method of multivariate analysis produces the most distinction among the *Phlox kelseyi* taxa since it maximized differences between the taxa. The individuals plotted on the first two functions form overlapping groups (Fig. 7). As with principal component analysis, the relative amount of variability shown by each taxon may be partially due to sample size. Variety *kelseyi* specimens are the most widely distributed across the functions. The specimen clustering with ssp. *salina* was the outlier in principal component analysis, that I have identified as *Phlox pulvinata*.

Of the ten diagnostic characters for *Phlox kelseyi*, calyx trichome glands is the only constant floral character and since floral characters are expected to be under more selective pressure for consistency (Grant 1981), these findings are compatible with the concept of a morphological species. My examination of morphological characters agrees with Cronquist's (1959) inclusion of var. *missoulensis* into the species *P. kelseyi*. Analysis of morphological characters substantiates Wherry's



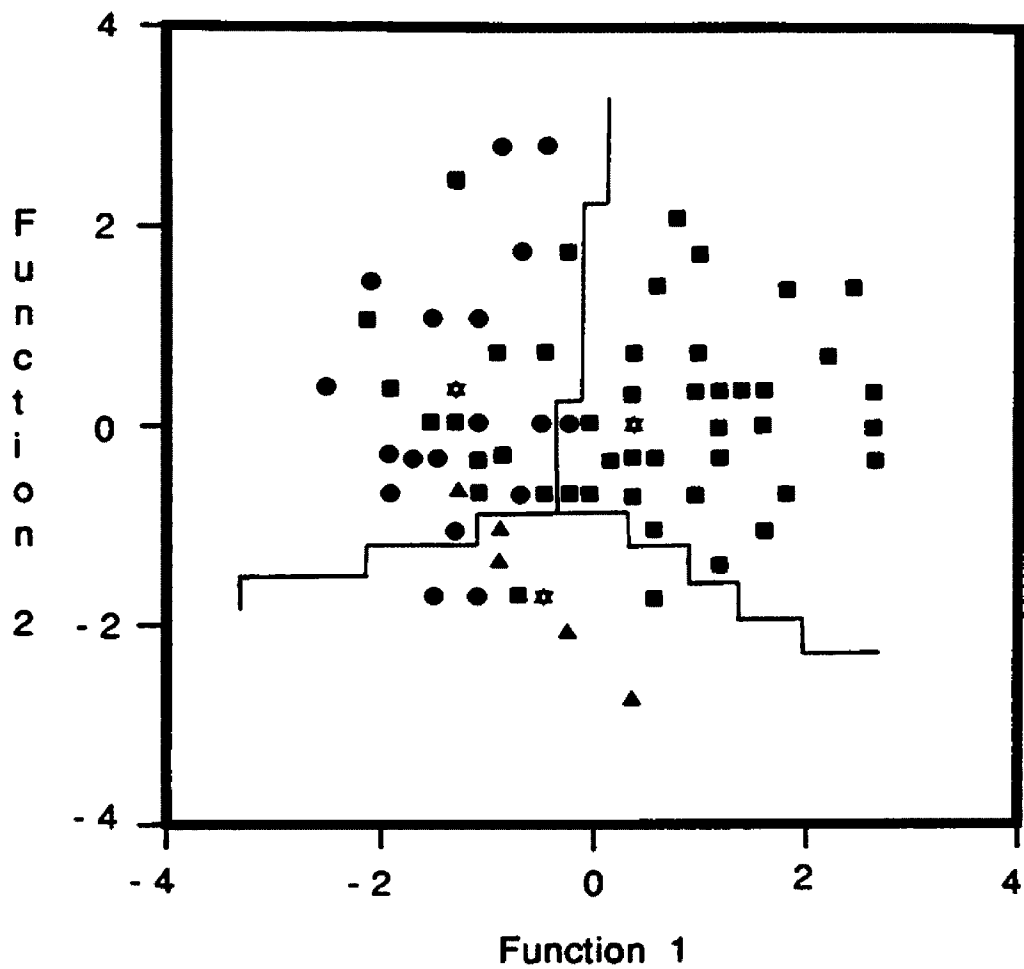


Fig. 7. *Phlox kelseyi* specimens and taxon centroids (☆) plotted on the first two discriminant functions. Taxon regions are delineated. ( ■ *P. kelseyi* var. *kelseyi*; ● *P. kelseyi* var. *missoulensis*; ▲ *P. kelseyi* ssp. *salina*.)

description (1955) of the variation present in these taxa and isolates more specifically how that variation is distributed among the taxa. Wherry described these taxa as having mucronate leaves with thickened leaf margins having varying amounts of cilia that may be gland tipped. These characters were found consistently in *P. kelseyi*; glandularity is almost absent in ssp. *salina* and is most common in var. *missoulensis*. Variety *missoulensis* was described by Wherry (1955) as having glandular-pilose leaves; however, my survey found pubescence on about half of the specimens examined, and only one quarter were glandular. Glandularity was found to be variable in var. *kelseyi*; Wherry (1941) split *P. kelseyi* into subspecies based on this feature, but later reverted ssp. *glandulosa* to a variant of ssp. *kelseyi* (Wherry 1955). As the most comprehensive survey of *P. kelseyi*, this morphological analysis has refined the character descriptions for the infraspecific taxa, particularly those of ssp. *salina* since my interpretation of this taxon is more exclusive.

Multivariate analyses were not able to discern complete distinction in the three groups present in the *Phlox kelseyi* complex. The morphological overlap of these taxa is of a magnitude indicative of infraspecific taxa. Among the most distinctive characters of the taxa are their ranges and habitats, features not included in multivariate analyses. Since the populations lack zones of overlap, these taxa have the attributes of the taxonomic rank of subspecies. Taxonomic conclusions are presented in Chapter IV.

### C. CYTOLOGICAL STUDY

Chromosome analysis serves a dual purpose in a systematic study. Characteristics of the karyology, such as chromosome number, size, location of the centromere and presence of fragments, add to the body of phenetic data, and pairing behavior may indicate hybridizations and/or reproductive incompatibilities (Stace 1980). Several surveys of *Phlox* chromosomes (Flory 1934, Meyer 1944 and Grant 1959) have documented chromosome numbers for twenty-nine species of *Phlox*. Flory (1934) first reported the base chromosome number for the genus as  $X = 7$ . Multiple ploidy levels occur in a few species; the greater levels often involve a horticultural variety (Grant 1959). Of the sixty species of *Phlox*, twenty-five diploids ( $2n = 14$ ) (Flory 1934, Meyer 1944), one triploid ( $3n = 21$ ) (Meyer 1944) and four tetraploids ( $2n = 28$ ) (Meyer 1944) have been reported. Six aneuploids ( $14 + 1$ ) are reported in *Phlox*, and Meyer (1944) found chromosome fragments in 20% of the plants examined. Our knowledge of *Phlox* karyology is hindered by questionable source material as commercial and horticultural plants have been reported and not all wild plants were from documented populations (Grant 1959).

Chromosome numbers are known for four section *Occidentales* species of which two are tetraploids. The chromosome number of *Phlox kelseyi* has never been reported. The late stages of prophase II and metaphase are when chromosomes are usually most easily counted in angiosperm species (Radford et al. 1974). My examination of chromosome material did not yield reliable counts for any of the taxa; pro- and telophase were the most commonly observed stages of meiosis, when the chromosomes are too congested to accurately identify individuals. Frequently,

pollen mother cells in all stages of meiosis were present in the same bud suggesting that the time frame in which meiosis occurs is brief. Within a *P. kelseyi* population flowering is relatively synchronous making the collection time of meiotic material critical. Since most floral buds were collected in the afternoon, it appears that meiosis may be occurring in the early AM, as is the case with other polemoniaceous flowers (D. Wilken, pers. comm.). A survey of mitotic material did indicate that, for the Missoula, MT population of var. *missoulensis*,  $2n = 14$ .

#### D. BREEDING SYSTEM STUDIES

In 1985 I conducted a pilot study investigating the breeding system of one population of *Phlox kelseyi* var. *missoulensis*. This population, located on Waterworks Hill, Missoula, is polymorphic for corolla color, exhibiting blue-, pink-, and white-flowered plants. Treatments (Table 6) included tests for self-compatibility, self-pollination, apomixis, and all combinations of crosses between the color morphs. All crosses performed were reciprocal crosses; each plant served as the pollen parent as well as the ovulate parent. Seed set was used to measure the success of a cross; most *Phlox* flowers are capable of producing a maximum of three seeds per capsule. Plants were also examined for levels of natural outcrossing.

From this study I concluded that the population is self-compatible and naturally self-pollinating (Table 11). Differences in the level of outcrossing and self-pollination indicated that these plants are pollinated by other means, most probably a long-tongued insect. No

Table 11. Mean seed set per flower (max. = 3) from 1985 breeding system treatments. Numbers in parentheses are number of flowers/number of plants.

		<u>Ovule Parent</u>		
		Blue	Pink	White
Outcrossing		1.29 (25/5)	2.18 (25/5)	1.48 (25/5)
Self -pollination		0.6 (25/5)	0.714 (25/5)	0.33 (25/5)
Self -compatibility		0 (7/2)	0.70 (7/2)	0.80 (7/2)
Apomixis		0 (2/1)	0 (2/1)	0 (2/1)
P	Blue	1.275 (5/2)	0 (5/2)	0 (5/2)
L	Pink	0 (5/2)	1.986 (5/2)	0.17 (5/2)
L	White	0 (5/2)	2.086 (5/2)	2.27 (5/2)
E				
N				

apomixis was detected, and it is not known to occur in the genus (Grant 1965).

Experimental cross pollinations between the color morphs indicated that the pink- and the white-flowered plants are freely interbreeding, but that the blue-flowered plants are only able to cross among themselves. The amount of natural seed set varied among the morphs; the pink-flowered plants exhibited considerably higher rates of outcrossing. Using outcrossing rates to represent base reproductive efforts, the level of self-pollination among the color morphs varied; the blue-flowered forms exhibited 45%, the pink forms 33% and white forms 22% of their base seed set from self pollination. If the blue-flowered forms are only successfully cross-pollinated by others blue-flowered plants, then they would be compatible with less of the population than the white and pink forms and may be compensating for this by increasing the amount of self-pollination. A reproductive barrier could be maintained by insects pollinating disassortatively between the color morphs.

To substantiate the potential sympatric reproductive isolating mechanism in the Waterworks Hill population, I increased the sample sizes (Table 6) for the breeding system treatments in 1986. The actual number of flowers retrieved (Table 12) from these experiments differs due to several factors: experimental error in the design of enclosure cages, loss to livestock and a late spring hail storm that destroyed the self-pollination treatment.

Table 12. Mean seed set per flower (max. = 3) from 1986 breeding system treatments. Numbers in parentheses are number of flowers/number of plants.

		<u>Ovule Parent</u>		
		Blue	Pink	White
Outcrossing		0.90 (10/2)	0 (5/1)	1.08 (3/13)
Self -pollination		0	0	0
Self -compatibility		0.181 (11/3)	0.125 (13/3)	0 (17/4)
P	Blue	0.625 (8/2)	0.143 (14/4)	0.444 (18/6)
L	Pink	0.1875 (16/5)	0.478 (23/9)	0.571 (7/3)
L	White	0 (14/3)	0.777 (9/3)	0 (8/4)
E				
N				

Again in 1986 the amount of natural seed set differed among the color morphs. The data obtained from the pink-flowered plants are insufficient for comparisons (only from one plant); however, the blue-flowered plants again exhibited much lower seed set from outcrossing than the white-flowered forms.

Intercolor crosses detected some potential for gene exchange among the morphs. Seeds were produced in two of the six white-flowered plants that were crossed with blue-flower pollen; however, the crosses were not successful when the blue forms served as the ovulate plant. Crosses between pink and blue forms resulted in low levels of seed set in both combinations of crosses, but crosses were successful in only one plant.

Even if a reproductive isolating mechanism is present in the population, low levels of compatibility among the color morphs may occur for several reasons. If this is an incipient barrier, it may not be present throughout the population. Grant (1981) states that "Partial reproductive isolation is commonly present between races of the same species" and that reproductive isolating mechanisms are frequently a combination of barriers occurring at several stages in reproduction. The low crossabilities among the color morphs from experimental pollinations doesn't present enough evidence to discount the possibility that a reproductive isolating mechanism is present especially if the mechanism is primarily ethological.

Lacking conclusive evidence about the potential for gene exchange among the color morphs in this population of variety *missoulensis*, I repeated the experiments on the Waterworks Hill population in 1987. Since breeding system experiments are so time intensive and *P. kelseyi*



has a short flowering period, only one field population could be examined per year; however, I also performed intervarietal crosses on nursery transplants. Using different enclosure mechanisms, I performed tests for outcrossing, self-compatibility, self-pollination and the color crosses. Western Montana experienced unusually high temperatures and drought conditions during the *Phlox kelseyi* blooming period in 1987. Corollas withered prematurely, and pollen became limited as it would desiccate within a day. Nursery transplant encountered the same heat induced problems. In these experimental populations as well as others observed throughout Montana, fruit abortion rates were extremely high that year, making it impossible to accurately determine whether an experimental cross was unsuccessful due to an incompatibility mechanism or due to the climatic conditions.

*POLLINATOR ACTIVITY IN PHLOX KELSEYI*-- For three consecutive years, I visited the Waterworks Hill population consistently throughout the *Phlox kelseyi* blooming period at all times of daylight and during evening dusk. While insects were observed on *Phlox* plants and thrips were frequently present, none were seen pollinating flowers or exhibiting any constancy behavior that would indicate that they are *Phlox* pollinators. During most of the day this site has high winds and subsequently low ambient temperatures; while hymenopterans were observed visiting other species, lepidopteran activity is usually low but may increase in the late afternoon when the wind frequently subsides. This population lacks the characteristic perfumey smell associated with many *Phlox* species, indicating low nectar production. Seed set indicates that the population is receiving pollinator service, but my observations

and the relatively low seed production in the blue- and the white-flowered plants implies that the population may be pollinator limited.

## Chapter IV

### TAXONOMIC CONCLUSIONS

*Phlox kelseyi* comprises three infraspecific taxa with few morphological differences. The most distinctive character of the taxa are their discrete ranges and unique habitats. Du Rietz (1930 in Stace 1980) defines subspecies as "regional facies of a species" and varieties as "local facies of a species," with some ecological or genetic differences, but distributed such that gene exchange may occur. Lacking zones of distributional overlap, the infraspecific taxa of *P. kelseyi* represent geographic demes and thus, are better described as subspecies. The following taxonomic treatment reflects this opinion by elevating the varieties *kelseyi* and *missoulensis* to subspecific rank.

### TAXONOMIC TREATMENT

#### *Phlox* L.

*Phlox* L., Hort. Cliff. 1737. --TYPE: *P. paniculata* L. Refer to Grant (1959) for a description of the genus.

#### *Phlox* sect. *Occidentales* A. Gray

*Phlox* sect. *Occidentales* A. Gray, Proc. Amer. Acad. Arts. 8:252. 1870. --LECTOTYPE: *P. caespitosa* Nutt. Lectotypified by Grant, Natural History of the *Phlox* Family. p. 119. 1959.

#### *Phlox kelseyi* Britton

*Phlox kelseyi* Britton, Bull. Torrey Bot. Club. 19:225. --TYPE: MONTANA. LEWIS & CLARK CO.: Helena, Fairgrounds, May 1891, *F. D. Kelsey* s. n. HOLOTYPE: NY! --*Fonna kelseyi* Nieuwl. & Lunel, Amer. Midl. Naturalist 4:512. 1916.

Perennial subshrubs to 12.5 cm tall; stems mostly glabrous, some with glandular trichomes. Leaves sessile; linear to lanceolate, 3.5--25 mm long, 0.75--4 mm wide, some pubescent above, infrequently glandular, sharply mucronate, margin ciliate for 1/4 to the entire length. Inflorescence a 1--3 flowered cyme; terminal; pedicel 0.25--9 mm long. Calyx 6--14 mm long, vestiture mostly dense with long, frequently glandular trichomes, sepals fused for 1/3 to 4/5 their length; corolla blue, pink, or white, 11.5--26 mm long, petals fused for 1/2 to 3/4 their length, lobes 4--11 mm long and 3--8 mm wide, length:width 0.8--2; anthers 1--2.5 mm long, filaments inserted at successive levels along corolla tube; pistil 5--15 mm long, stigma 0.5--2 mm long, papillate; style 2.25--13 mm long, ovary 1--2 mm long; pedicel 0.25--9 mm. Fruit 5--6 mm long, a septicidical capsule, ovate, glabrous.

KEY TO THE INFRASPECIFIC TAXA OF *PHLOX KELSEYI*

- A. Leaves 0.75--2 mm wide.
- B. Leaf length:width 5.5--18;  
 mountain ridges, MT .....1. ssp. *missoulensis*
- BB. Leaf length:width 3.5--9.5; alkaline  
 clay flats, NV .....2. ssp. *salina*
- AA. Leaves 1--4 mm wide; seasonally wet  
 montane meadows, CO, WY, MT, ID.....3. ssp. *kelseyi*

1. *Phlox kelseyi* ssp. *missoulensis* (Wherry) L. M. Campbell

*Phlox kelseyi* ssp. *missoulensis* (Wherry) L. M. Campbell *stat. et comb. nov.* --TYPE: *P. missoulensis* Wherry, Notul. Nat. Acad. Nat. Sci. Philadelphia. 146:7. 1944. MONTANA. MISSOULA CO.: Missoula, gravely outcrop on ridge of Waterworks Hill, elev. 3500 ft, 28 Apr

1939, M. J. Reed 8. HOLOTYPE: PH! --*P. k. var. missoulensis* (Wherry) Cronq., Fl. Pacific Northwest. p. 132. 1959.

Cushion forming subshrubs, 4--12 cm tall; internodes mostly condensed, 0.5--9 mm long. Leaves linear to lanceolate, 5--24 mm long, 0.75--2 mm wide, length:width 5--18, some pubescent above, few with glandular trichomes, margins ciliate for 1/2--3/4 their length, some with glandular cilia. Pedicels 0.25--9 mm long. Gravelly slopes to the fringes of adjacent open grasslands. Distribution: Montana: Meagher, Granite, Lewis & Clark and Missoula Counties, elev. 1200--2600 m, April--June.

Representative Specimens: MONTANA. MEAGHER CO.: King's Hill, switchback, 4 Jul 1948, F. Rose 4082 (MONTU); GRANITE CO.: Foothills of the Sapphire Range, in triangle between Rock Creek and Skalkaho roads, off Hwy 38, E of road to ranch, elev. 5000 ft, only pink and blue flowers, 23 May 1973, K. H. Lackschewitz 3502 (MO, MONTU); LEWIS & CLARK CO.: Summit of MacDonald Pass, corollas clear white, 29 Jun 1945, C. L. Hitchcock and C. V. Muhlick 11745 (MO, NY, UTC).

Excluded populations: MONTANA. LAKE CO.: McDonald Peak, Mission Mountains. Three collections from this population were examined; each specimen had been determined as a different species. These plants have shorter leaves and styles than ssp. *missoulensis* and occur at slightly higher elevations; I have identified them as *Phlox pulvinata* Cronq.

2. *Phlox kelseyi* ssp. *salina* (M. E. Jones) Wherry

*Phlox kelseyi* ssp. *salina* (M. E. Jones) Wherry, Notul. Nat. Acad. Sci. Philadelphia 113:5. 1942. --TYPE: NEVADA. WHITE PINE CO.: Cherry Creek, 21 May 1906., M. E. Jones s. n. HOLOTYPE: POM! -- *P.*

*doulgasii* var. *salina* M. E. Jones, Contr. W. Bot. 13:3. 1910.

Cushion forming perennials, 4--6.5 cm tall; internodes 0.5--5 mm long. Leaves lanceolate, 3.5--7 mm long, 0.75--1.5 mm wide, glabrous, margins ciliate for  $< 1/2$  their length. Pedicels 0.25--1.5 mm. Alkaline clay flats, elev. ca. 1850 m. Distribution: Nevada, May--June.

Representative specimens: **NEVADA. WHITE PINE CO.**: Monte Neva Hot Springs, alkaline clay flats, elev. 5900 ft, 15 Jun 1944, *H. D. Ripley and R. C. Barneby 6279* (NY); **ERUREKA CO.**: Monitor Valley, Hot Springs Hill, elev. 6120 ft, 21 May 1981, *A. Theim & M. Williams 6473* (NY).

Excluded populations: **COLORADO. PARK CO.**: Antero Junction. Wherry described ssp. *salina* as a diminutive form of ssp. *kelseyi* and stated that the two subspecies integrate. In his monograph, Wherry (1955) presented a less exclusive circumscription of this subspecies than is currently accepted, by including Idaho populations of *Phlox kelseyi*. While the Nevada populations hold together well taxonomically, the putative population from Colorado poses problems. The original collection (1949) was annotated by Wherry as an intermediate of ssp. *salina* and *kelseyi*; however, the nearest populations of these taxa are ca. 360 and 160 miles, respectively, away from the Colorado populations. To my knowledge, only one subsequent collection has been made (*W. A. Weber 17766*). There are several differences in the two collections; one has longer, narrower leaves, a shorter style, all five anthers exposed from the corolla tube, and a pollen diameter of 51.45  $\mu\text{m}$ , while the other specimen has only one anther exposed, and a pollen diameter of 45.53  $\mu\text{m}$ . Not having personally visited the population, it is difficult to assign these specimens to a taxon. From my inspection of the

herbarium material and the results of my principal components analysis, I would identify these plants as ssp. *kelseyi*. Field examination of the population may discount my conclusion and reveal that it belongs to another species of *Phlox*.

### 3. *Phlox kelseyi* ssp. *kelseyi* Wherry

*Phlox kelseyi* ssp. *genuina* Wherry, Notul. Nat. Acad. Philadelphia 87:8. 1941 --TYPE: MONTANA. LEWIS & CLARK CO.: Helena, Fairgrounds, May 1891, *F. D. Kelsey s. n.* HOLOTYPE: NY!

*Phlox kelseyi* ssp. *glandulosa* Wherry, Notul. Nat. Acad. Philadelphia 87:8. 1941. --TYPE: IDAHO. CARIBOU CO.: Bear River, 2 mi W of Soda Springs, 30 May 1939, *R. J. Davis 827.* HOLOTYPE: PH!

Decumbent subshrubs, 3.5--12.5 cm tall; stems sparsely pubescent or not, internodes 0.5--15 mm long. Leaves lanceolate or linear-lanceolate, 3.5--25 mm long, 1--4 mm wide, length:width 2.5--16.5, mostly glabrous above, margins ciliate for  $> 1/2$  their length. Pedicels 0.25--9 mm long. Seasonally wet, hummocky meadows, elev. 1400-2800 m. Distribution: Colorado, Wyoming, Montana and Idaho, May--July.

Representative specimens: WYOMING. ALBANY CO.: Red Buttes, 10 Jun 1903, *A. Nelson 9217* (MO, NY, RM); MONTANA. TETON CO.: Pine Butte Swamp, T 24N R 7W S 18 Q SE, in moist meadow, elev. 4700 ft, 7 Jun 1982, *K. Lackschewitz and P. Lesica 10008* (MONTU); GALLATIN CO.: Manhattan, 9 Jun 1901, *E. W. Scheuber s. n.* (US); BEAVERHEAD CO.: South of Red Rocks Lake, alkaline swamp, elev. 5600 ft, 28 Jun 1937, *F. W. Pennell 20590* (GH, PH, RMS, UCSB); IDAHO. CUSTER CO.: Thousand Springs, T 9N R 21E S 3 QS NE, 22 Jun 1983, *D. Henderson 6606* (NY, RMS); CARIBOU CO.: Bear River, 2 mi W of Soda Springs, seepy flats, 8 Jul 1949, *J. H. Christ*

18583 (ID, NY, WS).



## SUMMARY

As with many *Phlox* species, *Phlox kelseyi* (section *Occidentales*), is a morphologically variable complex of populations, in which some characteristics, such as leaf width and leaf, corolla and pistil lengths, integrate with other *Phlox* taxa. Currently, three infraspecific taxa comprise *P. kelseyi*; the taxonomic treatment of these and other taxa considered to be *P. kelseyi* has varied. An attempt to elucidate the biosystematic relationships in this group included morphological, cytological and breeding system investigations.

Previous morphological surveys of the *Phlox kelseyi* group were based on a small number of specimens. My research expanded earlier works (Wherry 1935, Grant 1959) by examining a greater number of characters on more populations. Characters were statistically analyzed to determine whether they are synthetic or diagnostic. Multivariate approaches were used to examine patterns in the populations based on their morphological similarities and differences.

Breeding system studies were designed to examine the potential for gene flow within and between populations of the two taxa native to Montana. Based on indications from a pilot study that a reproductive barrier was present, my study emphasized testing for crossabilities among the color morphs in one population of ssp. *missoulensis*. Several factors contributed to reducing the original scope of the breeding system studies and no information was gained about the potential for gene flow between the taxa; however, certain trends were found in the one intensively studied population. All of the color morphs are self-

compatible and self-pollinate at different rates. Low levels of crossability between a few of the blue-flowered plants and the other two morphs suggest that a reproductive barrier may be present in the population. Both mitotic and meiotic cells were examined to determine ploidy levels and chromosome number. While no documentable counts were obtained, examination of mitotic cells indicates that  $2n = 14$  in one population of *ssp. missoulensis*.

My comprehensive morphological investigation demonstrates, through the distribution of characters, that the taxa should be included in a morphological species and supports others' treatments (Wherry 1955, Grant 1959, Cronquist 1959) in detecting three infraspecific entities. Due to inconclusive results in portions of this research, my taxonomic treatment rests on morphometrics and field observations. Since the taxa have few morphological differences and distinct geographic distributions, I have treated them as subspecies.

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## APPENDIX A

### POPULATIONS SAMPLED IN CYTOLOGICAL STUDIES

#### Meiotic studies:

*Phlox kelseyi* ssp. *kelseyi*. MONTANA. Beaverhead Co.: Snowline, ca. 8.5 mi N of Monida Pass (Montana/Idaho), T 14S R 7W Sec 20.

*Phlox kelseyi* ssp. *kelseyi*. MONTANA. Deer Lodge Co.: Warm Springs, ca. 15 air mi from Butte, 1 mi E of Hwy 90, T 5N R 9W Sec 18, near settling ponds.

*Phlox kelseyi* ssp. *kelseyi*. MONTANA. Teton Co.: Pine Butte Swamp, ca. 45 air mi from Great Falls, T 24N R 8W.

*Phlox kelseyi* ssp. *missoulensis*. MONTANA. Granite Co.: Emerine Gulch, ca. 50 air mi from Missoula, 11 mi W on secondary road off Hwy 10A, T 6N R 16W Sec 35.

*Phlox kelseyi* ssp. *missoulensis*. MONTANA. Missoula Co.: Missoula, Waterworks Hill, elev. 3300-3500 ft.

#### Mitotic studies:

*Phlox kelseyi* ssp. *kelseyi*. MONTANA. Teton Co.: Pine Butte Swamp, ca. 45 air mi from Great Falls, T 24N R 8W.

*Phlox kelseyi* ssp. *missoulensis*. MONTANA. Granite Co.: Emerine Gulch, ca. 50 air mi from Missoula, 11 mi W on secondary road off Hwy 10A, T 6N R 16W Sec 35.

*Phlox kelseyi* ssp. *kelseyi*. MONTANA. Missoula Co.: Missoula, Waterworks Hill, elev. 3300-3500 ft.

*Phlox kelseyi* ssp. *salina*. NEVADA. White Pine Co.: Monte Neva Hot Springs, 90 air mi SE of Elko, W of Hwy 93, T 21N R 64E.



APPENDIX B

MORPHOLOGICAL DATA

*Phlox kelseyi* ssp. *kelseyi* (Pkk)  
*P. kelseyi* ssp. *missoulensis* (Pkm)  
*P. kelseyi* ssp. *salina* (Pks)

SPECIES	HEIGHT	HABIT	LEAF LENGTH	LEAF WIDTH	LF LEN WIDTH RATIO
-----	-----	-----	-----	-----	-----
PKM	4.5	C	10.00	1.25	8.00
	6.5	C	10.00	1.00	10.00
	7.5	C	14.00	1.00	14.00
	6.0	C	11.00	1.00	11.00
	6.0	C	13.50	1.50	9.00
	4.5	C	10.00	1.50	6.70
	6.0	C	9.00	1.50	6.00
	11.0	CD	12.00	1.00	12.00
	6.5	CD	22.00	2.00	11.00
	4.5	C	13.00	1.75	7.43
	6.0	C	15.00	2.00	7.50
	5.5	CD	24.00	2.00	12.00
	6.5	CD	18.00	1.00	18.00
	6.0	C	12.00	1.50	8.00
	4.0	C	12.00	1.00	12.00
	6.0	C	11.00	1.00	11.00
	7.0	D	8.00	.75	10.67
12.0	C	15.00	1.00	15.00	
10.0	CD	11.00	1.10	10.00	
PKS	4.0	C	5.00	1.50	3.30
	4.0	C	3.50	1.00	3.50
	6.0	CD	7.00	.75	9.30
	6.5	CD	5.00	1.00	5.00

SPECIES	HEIGHT	HABIT	LEAF LENGTH	LEAF WIDTH	LF LEN WIDTH RATIO
-----	-----	-----	-----	-----	-----
PKK	10.0	D	25.00	2.00	12.50
	5.0	D	9.00	2.00	4.50
	7.0	D	13.00	2.00	6.50
	5.5	C	5.00	1.25	4.00
	6.0	CD	13.00	1.25	10.40
	8.0	D	13.00	1.01	12.87
	6.0	C	7.50	1.50	5.00
	6.0	C	15.00	1.25	12.00
	7.0	D	16.00	1.50	10.70
	7.5	D	10.00	1.00	10.00
	7.5	D	20.00	2.00	10.00
	7.5	D	14.00	2.00	7.00
	8.0	D	14.00	1.50	9.33
	8.5	D	12.00	1.75	6.86
	8.0	D	13.00	2.00	6.50
	11.0	D	10.00	1.25	8.00
	8.0	D	20.00	1.75	11.40
	7.0	D	11.00	1.00	11.00
	3.5	D	9.00	2.50	3.60
	8.0	D	10.00	3.00	3.33
	5.0	D	8.00	2.25	3.56
	7.0	D	14.00	1.75	8.00
	6.0	D	11.00	2.00	5.50
	6.0	D	10.00	2.00	5.00
	9.0	D	15.00	1.00	15.00
	7.5	C	6.00	2.00	3.00
	6.0	D	5.00	1.50	3.33
	6.5	C	5.50	1.50	3.67
	6.5	C	16.00	2.00	8.00
	8.0	D	20.00	2.00	10.00
	6.5	D	10.00	1.20	10.00
	6.0	D	9.00	2.00	4.50
	6.0	CD	11.00	1.25	8.80
	5.0	C	8.00	2.00	4.00
	7.0	D	15.00	1.50	10.00
	6.0	D	11.00	2.00	5.50
	6.5	CD	6.00	1.00	6.00
	10.0	D	13.00	2.00	6.50
	6.0	D	16.00	2.00	8.00
	6.0	D	19.00	2.00	9.50
	7.5	D	13.00	2.00	6.50
	5.5	CD	11.00	1.50	7.33
	7.0	D	13.00	1.33	9.74
	7.0	D	10.00	1.25	12.50
	11.0	D	25.00	1.50	16.70

SPECIES	HEIGHT	HABIT	LEAF LENGTH	LEAF WIDTH	LF LEN WIDTH RATIO
-----	-----	-----	-----	-----	-----
PKM	4.5	C	10.00	1.25	8.00
	6.5	C	10.00	1.00	10.00
	7.5	C	14.00	1.00	14.00
	6.0	C	11.00	1.00	11.00
	6.0	C	13.50	1.50	9.00
	4.5	C	10.00	1.50	6.70
	6.0	C	9.00	1.50	6.00
	11.0	CD	12.00	1.00	12.00
	6.5	CD	22.00	2.00	11.00
	4.5	C	13.00	1.75	7.43
	6.0	C	15.00	2.00	7.50
	5.5	CD	24.00	2.00	12.00
	6.5	CD	18.00	1.00	18.00
	PKM	6.0	C	12.00	1.50
4.0		C	12.00	1.00	12.00
6.0		C	11.00	1.00	11.00
7.0		D	8.00	.75	10.67
12.0		C	15.00	1.00	15.00
10.0		CD	11.00	1.10	10.00
PKS	4.0	C	5.00	1.50	3.30
	4.0	C	3.50	1.00	3.50
	6.0	CD	7.00	.75	9.30
	6.5	CD	5.00	1.00	5.00

SPECIES	LEAF SHAPE	MUCRO	MUCRO LEN	LF PUBESCENCE	LF GLANDS
-----	-----	-----	-----	-----	-----
PKK	LAN	P	3	A	A
	LAN	P	2	A	A
	LAN	P	3	A	A
	LAN	P	2	A	A
	LINLAN	P	3	P	A
	LINLAN	P	2	P	A
	LAN	P	2	A	A
	LIN	P	2	P	P
	LINLAN	P	2	A	A
	LINLAN	P	3	A	A
	LIN	P	5	A	A
	LINLAN	P	4	A	A
	LINLAN	P	1	A	A
	LINLAN	P	3	A	A
	LINLAN	P	2	A	A
	LIN	P	2	A	A
	LIN	P	2	A	A
	LANLIN	P	3	P	P
	LAN	P	3	A	A
	OBLENS	P	2	P	A
	LAN	P	2	A	A
	LINLAN	P	2	A	A
	LAN	P	2	A	A
	LINLAN	P	2	A	A
	LINLAN	P	1	A	A
	LAN	P	2	A	A
	LAN	P	2	A	A
	LAN	P	2	A	A
	LAN	P	4	P	P
	LAN	P	1	A	A
	LAN	P	2	A	A
	LAN	P	2	A	A
	LAN	P	2	A	A
	LAN	P	2	A	A
	LAN	P	3	A	A
	LIN	P	3	A	A
	LAN	P	2	A	A
	LINLAN	P	2	A	A
	LAN	P	3	A	A
	ENS	P	2	A	A
	LIN	P	2	A	A
	LINLAN	P	2	A	A
	LAN	P	2	A	A
	LIN	P	1	A	A
	LIN	P	3	A	A
	LINLAN	P	1	A	A

SPECIES	LEAF SHAPE	MUCRO	MUCRO LEN	LF PURESCENCE	LF GLANDS	
-----	-----	-----	-----	-----	-----	
PKM	LIN	P	2	A	A	
	LIN	P	3	P	P	
	LIN	P	2	A	A	
	LINLAN	P	3	A	A	
	LAN	P	3	A	A	
	LAN	P	1	P	A	
	LIN	P	3	A	A	
	LIN	P	4	A	A	
	LANLIN	P	2	P	P	
	LAN	P	2	P	A	
	LIN	P	2	A	A	
	LIN	P	1	A	A	
	PKM	LAN	P	2	P	A
		LINLAN	P	3	P	P
LINLAN		P	2	P	A	
LIN		P	3	A	A	
LIN		P	3	P	P	
LAN		P	2	P	P	
LANLIN		P	2	A	A	
PKS	LAN	P	2	A	A	
	LAN	P	1	A	A	
	LAN	P	2	A	A	
	LAN	P	1	A	A	

SPECIES	MARGIN	MARGINAL CILIA	CILIA GLANDS	CILIATE PORTION
-----	-----	-----	-----	-----
PKK	T	P	A	3
	T	P	A	4
	T	P	A	4
	T	A	A	0
	T	P	A	3
	T	P	A	5
	T	P	A	4
	T	P	A	5
	T	A	A	0
	T	P	A	6
	T	P	A	3
	T	A	A	0
	T	A	A	0
	T	A	A	0
	T	P	A	2
	T	P	P	4
	T	P	P	3
	T	P	P	6
	WT	P	A	4
	WT	P	A	5
	WT	P	P	4
	WT	P	P	6
	WT	P	A	6
	T	P	A	6
	WT	P	A	2
	WT	P	A	4
	T	P	P	4
	T	P	P	4
	T	P	P	3
	T	P	A	3
	T	P	A	4
	WT	P	A	4
	T	P	A	4
	T	P	A	0
	T	P	A	5
	T	P	A	3
	T	P	A	4
	T	P	A	7
	T	P	A	6
	T	P	A	6
	T	P	A	6
	T	P	A	6
	WT	P	A	5
	T	P	A	0
	T	P	A	3
	T	A	A	0

SPECIES	MARGIN	MARGINAL CILIA	CILIA GLANDS	CILIATE PORTION
-----	-----	-----	-----	-----
PKM	T	P	A	4
	T	P	P	6
	C	A	A	0
	T	P	A	4
	T	P	A	6
	T	P	A	6
	T	P	P	6
	T	P	A	5
	T	P	P	6
	T	P	A	5
	T	P	A	4
	T	P	P	7
	T	P	A	6
	T	P	P	7
	T	P	A	6
	T	P	P	5
	T	P	P	7
T	P	P	7	
T	P	A	5	
PKS	T	P	A	1
	WT	P	A	3
	T	P	A	2
	T	P	A	2

SPECIES	INTERNODE MIDPL	INTERNODE LOWERPL	STEM PUBESCENCE	STEM GLANDS
-----	-----	-----	-----	-----
PKK	7.00	3.00	A	A
	4.00	3.40	A	A
	12.00	10.00	A	A
	1.00	.50	A	A
	1.50	3.00	A	A
	3.00	1.00	A	A
	5.00	3.00	A	A
	1.00	2.00	A	A
	12.00	4.00	A	A
	8.00	4.00	A	A
	12.00	8.00	A	A
	11.00	1.50	A	A
	4.00	12.00	A	A
	5.00	6.00	A	A
	10.00	10.00	A	A
	4.00	3.00	P	P
	10.00	14.00	P	P
	10.00	8.00	P	P
	3.50	1.50	A	A
	2.00	6.00	P	A
	3.00	2.00	P	A
	8.50	7.50	P	P
	5.00	4.00	P	P
	7.00	7.00	P	P
	2.00	1.00	A	A
	2.00	1.50	A	A
	1.50	1.50	A	A
	1.50	1.00	A	A
	2.00	1.00	A	A
	1.00	3.00	A	A
	1.50	3.00	P	P
	4.50	1.50	P	P
	4.00	3.00	A	A
	1.00	2.00	A	A
	3.00	3.00	A	A
	2.00	3.00	A	A
	2.00	2.00	A	A
	4.00	8.00	A	A
	8.00	4.00	P	A
	8.00	6.00	P	A
	10.00	15.00	P	A
	4.00	5.00	A	A
	4.00	7.00	A	A
	2.00	1.00	A	A
	12.00	5.00	P	A



SPECIES	INTERNODE MIDPL	INTERNODE LOWERPL	STEM PUBESCENCE	STEM GLANDS
-----	-----	-----	-----	-----
PKM	.50	.75	A	A
	.50	1.00	A	A
	1.00	1.50	A	A
	1.00	2.00	A	A
	3.00	1.00	A	A
	1.00	2.00	A	A
	5.00	5.00	A	A
	5.00	3.00	A	A
	.50	1.00	A	A
	2.00	1.00	A	A
	3.50	6.00	P	P
	2.00	9.00	P	P
	3.00	2.00	A	A
	3.00	1.50	A	A
	1.00	2.00	A	A
	2.00	1.25	A	A
	4.00	.50	P	P
	.50	3.00	A	A
	1.00	2.00	A	A
	PKS	1.00	1.00	A
.50		.50	A	A
3.00		1.00	A	A
1.00		.50	A	A

SPECIES	FLS PER STEM	PEDICEL	PEDICEL LEN
-----	-----	-----	-----
PKK	4	P	3.00
	1	P	2.00
	5	P	6.00
	1	P	1.00
	1	P	1.50
	1	P	1.25
	1	P	3.00
	1	P	3.00
	1	P	5.00
	1	P	5.00
	4	P	4.00
	1	P	7.00
	4	P	4.00
	1	P	5.00
	1	P	5.00
	4	P	3.00
	1	P	1.00
	1	P	5.00
	1	P	3.00
	6	P	5.00
	4	P	3.00
	1	P	6.00
	4	P	6.00
	4	P	5.00
	1	P	8.50
	1	P	1.50
	1	P	.50
	1	P	3.00
	1	P	2.00
	1	P	2.00
	3	P	4.00
	1	P	.50
	1	P	3.00
	4	A	4.00
	1	P	3.00
	1	P	4.00
	1	P	.25
	1	P	5.00
	2	P	4.00
	2	P	4.00
	1	P	9.00
	1	P	3.00
	1	P	2.00
	4	P	2.50
	1	P	6.00

SPECIES	FLS PER STEM	PEDICEL	PEDICEL LEN
-----	-----	-----	-----
PKM	1	P	.50
	1	P	.50
	4	P	2.00
	1	P	5.50
	1	P	2.00
	1	P	2.00
	1	P	2.00
	1	P	3.00
	3	P	9.00
	4	P	.25
	1	P	3.00
	1	P	7.00
	4	P	5.00
	1	P	1.00
	1	P	3.00
	1	P	1.50
	1	P	4.00
	1	P	3.50
	1	P	3.00
PKS	1	P	1.00
	1	P	.25
	4	P	1.50
	1	P	1.50

SPECIES	COROLLA LEN	COROLLA TUBE LEN	COROLLA LOBE LEN	LOBE WIDTH
PKK	18.00	10.50	6.00	5.00
	17.00	8.50	7.00	5.00
	20.00	12.00	9.00	5.00
	17.25	7.25	5.00	5.00
	17.25	11.00	7.00	5.50
	18.00	10.00	8.00	6.00
	18.00	11.00	7.00	5.00
	20.00	17.00	9.00	5.00
	20.00	11.00	9.00	6.25
	21.50	14.00	7.50	5.25
	21.00	12.00	9.00	7.00
	21.00	11.50	9.00	7.00
	20.00	13.00	7.00	6.00
	17.25	10.25	7.00	5.00
	18.00	10.00	8.00	5.00
	20.00	11.00	9.00	7.00
	23.00	13.00	9.00	6.00
	18.00	10.00	8.00	5.00
	14.00	8.00	6.00	6.00
	19.00	10.00	8.00	7.00
	19.00	11.50	7.00	7.00
	18.00	11.00	8.00	7.00
	19.00	11.00	8.00	7.00
	18.00	12.00	6.00	5.50
	17.00	10.00	7.00	6.00
	20.00	11.00	9.00	6.00
	16.00	10.00	6.00	5.25
	19.00	11.00	8.50	6.00
	19.00	11.50	8.00	4.25
	16.50	11.00	6.00	6.00
	17.00	10.00	7.00	8.00
	17.00	10.00	7.00	8.00
	17.00	10.00	7.00	5.00
	14.00	9.00	5.00	3.00
	20.00	13.00	6.50	6.00
	19.00	12.00	6.50	6.00
	19.00	8.00	7.00	5.00
	18.50	12.25	6.00	5.00
	17.00	11.00	7.00	5.00
	18.00	12.00	6.00	6.00
	26.20	14.00	8.00	5.50
	21.00	13.00	7.00	6.00

SPECIES	COROLLA LEN	COROLLA TURE LEN	COROLLA LOBE LEN	LORE WIDTH
-----	-----	-----	-----	-----
<b>PKM</b>	19.00	11.00	8.00	6.00
	18.00	10.00	8.00	6.00
	19.00	12.00	7.00	6.00
	18.50	11.00	7.00	6.00
	20.00	12.00	8.00	6.00
	19.00	12.00	7.00	7.00
	15.25	10.00	6.00	5.00
	20.00	12.50	7.50	5.50
	24.00	14.00	10.00	7.25
	14.25	9.00	6.00	6.00
	21.00	13.50	7.00	6.00
	20.00	11.00	9.00	6.00
	20.00	13.00	8.00	5.00
	20.25	11.00	9.00	7.00
	15.00	9.00	6.00	4.50
	15.00	8.50	6.25	4.25
	16.00	20.00	6.50	5.50
	18.00	11.00	7.00	5.25
	23.00	13.00	10.00	6.00
<b>PKS</b>	11.50	7.50	4.00	3.00
	14.00	9.50	10.00	3.50
	16.50	11.50	6.00	4.00
	19.00	10.00	8.00	6.00

SPECIES	LOBE LEN : WIDTH	PORTION OF COROLLA FUSED	AMT COROLLA TUBE EXCEEDS CALYX	CALYX LEN
-----	-----	-----	-----	-----
PKK	1.20	1.71	2.00	9.00
	1.40	.50	.50	8.00
	1.80	1.67	2.50	10.00
	1.45	1.57	4.00	7.00
	1.27	1.57	6.00	8.00
	1.30	1.80	4.00	7.00
	1.40	1.64	0.00	12.00
	1.80	1.18	2.00	12.00
	1.44	1.82	1.00	10.00
	1.43	1.54	6.00	9.00
	1.29	1.75	3.50	14.00
	1.29	1.83	3.00	9.00
	1.17	1.54	4.00	8.00
	1.40	1.68	1.50	8.00
	1.60	1.80	3.25	7.00
	1.29	1.82	4.00	9.00
	1.50	1.77	4.00	11.00
	1.60	1.80	2.00	8.00
	1.00	1.75	1.00	7.00
	1.14	1.90	5.00	8.00
	1.07	1.65	3.50	8.00
	1.08	1.70	2.25	8.50
	1.20	1.70	3.00	9.00
	1.17	1.64	3.00	8.00
	.93	1.70	2.00	8.00
	1.00	1.64	3.50	7.00
	1.30	1.73	6.00	6.00
	1.09	1.50	7.25	8.00
	1.17	1.70	3.00	8.00
	1.50	1.82	2.50	9.00
	1.14	1.60	1.05	8.00
	1.42	1.73	3.00	9.00
	1.88	1.65	4.25	3.00
	1.00	1.50	2.00	9.00
	.88	1.70	2.00	7.50
	1.40	1.70	2.75	7.00
	1.67	1.53	3.00	7.00
	1.17	1.54	4.00	9.00
	1.08	1.58	3.00	9.00
	1.40	2.38	0.00	9.00
	1.20	1.51	7.00	7.00
	1.40	1.55	5.00	6.00
	1.00	1.50	3.00	10.00
	1.45	1.87	6.00	7.00
	1.20	1.60	3.00	9.00

SPECIES	LOBE LEN : WIDTH	PORTION OF COROLLA FUSED	AMT COROLLA TUBE EXCEEDS CALYX	CALYX LEN
-----	-----	-----	-----	-----
PKM	1.33	1.64	3.00	7.00
	1.67	1.77	6.00	8.00
	1.33	1.73	3.50	9.50
	1.33	1.80	1.00	9.00
	1.17	1.58	2.00	10.00
	1.17	1.68	2.00	9.50
	1.33	1.67	4.00	8.00
	1.00	1.58	3.25	9.00
	1.20	1.53	3.00	7.25
	1.36	1.60	4.00	8.00
	1.38	1.71	4.50	10.50
	1.00	1.58	1.50	7.00
	1.17	1.55	3.00	11.00
	1.50	1.80	3.00	8.00
	1.60	1.54	3.50	10.00
	1.30	.54	2.00	9.25
	1.30	1.67	2.00	7.00
	1.47	1.76	.50	8.25
1.18	1.65	2.00	8.00	
PKS	1.33	1.50	1.00	7.50
	1.42	1.47	2.75	9.00
	1.50	1.43	4.50	7.00
	1.30	1.90	4.00	8.00

SPECIES	CALYX TUBE LEN	CALYX LOBE LEN	PORTION OF CALYX FUSED	CALYX MARGIN
-----	-----	-----	-----	-----
PKK	4.00	5.00	.44	H
	3.00	5.00	.38	T
	5.00	5.00	.50	T
	4.00	3.00	.57	T
	4.00	4.00	.50	T
	4.00	3.00	.57	T
	5.00	7.00	.42	O
	4.00	8.00	.33	O
	5.00	5.00	.50	T
	5.00	4.00	.55	T
	6.00	8.00	.43	T
	6.00	3.00	.67	W
	4.00	4.00	.50	O
	4.00	4.00	.50	T
	4.00	3.00	.60	O
	5.00	4.00	.55	T
	5.00	6.00	.45	T
	4.00	4.00	.50	T
	5.00	2.00	.71	O
	5.00	3.00	.63	O
	5.00	3.00	.63	O
	4.00	4.50	.47	O
	4.00	5.00	.44	T
	4.50	3.50	.56	T
	5.00	3.00	.63	W
	4.00	3.00	.57	T
	3.00	3.00	.50	T
	5.00	3.00	.63	O
	3.00	5.00	.38	T
	4.00	5.00	.44	T
	4.00	4.00	.50	T
	4.00	5.00	.44	T
	4.00	4.00	.50	O
	5.00	3.00	.55	T
	5.00	2.00	.67	W
	4.00	3.00	.57	O
	5.00	2.00	.71	T
	5.00	4.00	.55	O
	4.00	5.00	.44	O
	4.00	5.00	.44	W
	4.00	3.00	.57	O
	4.00	2.00	.67	T
	5.00	5.00	.50	H
	4.00	3.00	.57	T
	4.50	4.50	.50	O



SPECIES	CALYX TUBE LEN	CALYX LOBE LEN	PORTION OF CALYX FUSED	CALYX MARGIN
-----	-----	-----	-----	-----
PKM	5.00	3.00	.63	T
	3.50	6.00	.37	O
	4.00	5.00	.44	O
	4.00	6.00	.40	T
	5.00	4.50	.53	O
	4.00	4.00	.50	T
	4.00	5.00	.44	TW
	4.00	3.25	.55	TW
	4.00	4.00	.55	T
	5.00	5.50	.47	T
	4.50	2.50	.64	T
	4.00	7.00	.36	O
	4.00	4.00	.50	T
	4.50	5.50	.45	T
	4.50	5.00	.49	T
	3.50	3.50	.50	T
	4.00	4.00	.48	H
	4.00	4.00	.50	T
	4.00	3.00	.57	T
	PKS	4.50	3.00	.64
5.00		4.00	.55	T
3.00		4.00	.43	T
4.00		4.00	.50	T

SPECIES	CALYX PUBESCENCE	CALYX GLANDS	ANTHERS EXPOSED	ANTHER LEN
-----	-----	-----	-----	-----
PKK	P	A	7	1.50
	P	A	0	1.50
	P	A	1	1.50
	A	A	2	1.50
	P	P	2	1.75
	P	P	2	1.25
	P	P	0	1.50
	P	P	1	1.50
	A	A	6	1.00
	P	A	2	1.75
	P	A	6	2.00
	A	A	7	2.25
	A	A	0	1.25
	P	P	0	1.25
	P	A	6	1.50
	P	P	6	2.00
	P	P	1	1.50
	P	P	1	1.50
	P	P	5	2.10
	P	P	7	1.20
	P	P	3	2.25
	P	P	4	2.00
	P	P	6	2.00
	P	P	6	2.00
	P	P	7	2.00
	P	P	1	1.25
	P	P	6	1.50
	P	P	6	1.50
	P	P	0	1.25
	P	P	1	1.50
	P	P	6	1.50
	P	P	4	1.50
	A	A	6	2.00
	P	P	1	2.00
	P	P	5	1.50
	P	A	1	1.25
	A	A	0	1.75
	P	P	0	1.00
	P	P	2	1.50
	P	P	1	1.90
	P	P	0	1.50
	P	P	1	1.25
	A	A	0	2.25
	A	A	1	2.00
	P	P	0	1.33

SPECIES	CALYX PUBESCENCE	CALYX GLANDS	ANTHERS EXPOSED	ANTHER LEN
-----	-----	-----	-----	-----
PKM	P	P	2	1.50
	P	P	0	1.25
	A	A	6	2.10
	P	P	1	1.25
	P	P	0	2.00
	P	P	0	1.50
	P	P	0	1.50
	P	P	0	1.50
	P	A	0	1.30
	P	P	1	1.25
	P	P	0	1.75
	P	P	0	2.50
	P	P	1	1.50
	P	A	1	1.01
	P	P	1	1.50
	P	P	2	1.50
	P	P	2	2.00
	P	P	0	1.25
	P	P	1	1.50
	PKS	P	A	0
P		A	0	1.50
P		A	0	1.00
P		P	0	2.00

SPECIES	LOWER ANTHOR	UPPER ANTHOR	PISTIL LEN
-----	-----	-----	-----
PKK	7.00	10.00	7.25
	6.00	9.00	7.00
	7.00	11.00	9.00
	6.00	9.50	8.53
	6.00	10.00	7.50
	6.50	10.00	7.50
	6.00	9.50	8.00
	7.00	10.50	6.50
	7.00	11.00	11.00
	8.00	13.00	9.75
	4.00	11.00	8.00
	6.00	11.00	8.75
	6.50	11.00	8.00
	6.50	8.75	7.25
	6.50	11.00	7.00
	7.50	10.00	9.00
	7.00	12.00	9.50
	13.00	15.00	9.50
	6.00	8.00	10.25
	3.00	5.00	8.20
	7.50	12.00	12.25
	7.00	9.00	9.25
	7.00	11.00	10.50
	7.00	10.00	7.25
	7.00	9.00	8.00
	8.00	10.00	8.00
	8.00	11.00	7.00
	6.50	11.75	8.25
	5.75	9.00	7.50
	8.00	10.00	9.00
	6.50	9.00	9.50
	7.75	11.00	9.00
	11.00	13.00	8.50
	8.00	10.00	10.00
	8.00	10.50	5.50
	7.00	10.00	8.00
	2.00	7.00	5.00
	6.75	11.00	7.25
	7.00	12.00	8.50
	7.00	11.00	8.00
	9.00	11.00	11.00
	6.50	10.00	8.00
	6.50	10.00	8.50
	8.00	13.00	10.50
	7.00	11.00	8.50

SPECIES	LOWER ANTHER	UPPER ANTHER	PISTIL LEN
-----	-----	-----	-----
PKM	8.00	10.25	7.50
	7.00	10.00	8.25
	6.00	10.20	7.00
	8.00	12.00	7.50
	6.50	10.00	7.75
	5.00	9.00	7.25
	7.00	9.00	8.25
	7.75	11.75	8.00
	5.50	7.00	5.50
	8.25	12.00	8.25
	7.00	11.00	8.50
	8.00	12.00	10.25
	6.00	10.00	10.00
	7.00	8.00	7.33
	5.75	8.00	7.50
6.75	14.00	8.00	
7.00	10.00	7.50	
9.00	11.75	8.00	
7.00	10.00	7.75	
PKS	4.00	6.00	7.50
	5.50	8.00	7.36
	7.00	10.00	7.25
	6.50	9.75	8.00

SPECIES	OVARY LEN	STYLE LEN	STIGMA LEN	STIGMATIC PORTION
-----	-----	-----	-----	-----
PKK	1.50	5.00	1.25	.20
	1.00	5.00	1.00	.17
	1.25	6.75	1.00	.13
	1.46	5.59	1.13	.16
	1.50	5.00	1.00	.17
	1.50	5.00	1.00	.17
	1.75	5.25	1.00	.16
	1.50	4.50	1.00	.18
	2.00	7.25	1.75	.19
	1.50	7.25	1.00	.12
	1.50	5.50	2.00	.15
	1.50	6.25	1.00	.14
	1.50	5.50	1.00	.15
	1.50	4.75	1.00	.17
	1.00	5.25	.75	.13
	2.00	6.00	1.00	.14
	1.50	4.75	.75	.14
	1.00	7.50	1.00	.12
	1.75	8.00	1.25	.90
	2.00	4.20	1.25	.23
	2.00	9.00	1.25	.12
	1.00	7.00	1.25	.15
	2.00	7.75	1.25	.15
	1.00	5.50	1.00	.15
	1.75	5.50	.75	.12
	2.00	6.00	1.00	.14
	2.00	4.00	1.00	.20
	1.50	5.75	1.00	.15
	1.25	5.00	1.25	.20
	1.50	6.50	1.00	.13
	1.50	7.00	1.00	.13
	1.50	6.50	1.00	.13
	1.50	6.00	1.00	.14
	1.50	8.50	.75	.08
	1.50	3.00	1.00	.25
	1.50	6.00	1.00	.14
	1.00	3.50	.50	.13
	1.50	5.50	.75	.12
	1.50	6.50	.75	.10
	1.50	6.00	1.00	.14
	1.50	7.50	1.25	.14
	1.00	6.25	.80	.11
	1.00	6.00	1.50	.20
	1.20	8.00	1.10	.12
	1.00	6.50	1.10	.14

SPECIES	OVARY LEN	STYLE LEN	STIGMA LEN	STIGMATIC PORTION
-----	-----	-----	-----	-----
PKM	1.50	5.00	1.00	.17
	1.50	5.50	1.25	.19
	1.50	4.50	1.20	.21
	1.25	4.50	1.20	.18
	1.25	5.75	.75	.12
	1.25	5.25	.75	.13
	1.50	6.00	1.00	.14
	1.75	5.25	1.00	.16
	1.75	3.00	.75	.20
	1.50	5.50	1.25	.19
	1.75	5.50	1.25	.19
	1.75	7.25	1.25	.15
	2.00	7.00	1.00	.13
	1.00	5.33	1.01	.16
	1.25	6.00	1.10	.15
	1.25	5.00	1.75	.26
	1.50	5.00	1.00	.17
	1.75	5.25	1.00	.16
	1.75	5.00	1.00	.17
	PKS	1.50	5.25	.75
1.50		5.13	.88	.15
1.50		5.00	1.00	.17
1.50		5.00	1.50	.23

SPECIES	STYLE : PISTIL	COROLLA TUBE : PISTIL	POLLEN DIAMETER (UM)
-----	-----	-----	-----
PKK	.81	1.35	39.30
	.60	1.21	39.74
	.86	1.33	38.47
	.81	1.54	36.99
	.80	1.50	40.92
	.80	1.33	38.88
	.78	1.38	34.55
	.85	2.60	37.98
	.82	1.00	37.85
	.85	1.44	39.69
	.81	1.50	44.84
	.88	1.30	34.79
	.81	1.63	39.08
	.79	1.40	40.18
	.86	1.43	36.26
	.78	1.22	47.04
	.58	1.37	38.69
	.89	1.05	42.39
	.90	.78	46.55
	.66	1.22	48.34
	.84	.94	45.33
	.89	1.08	38.96
	.81	1.00	36.75
	.90	1.52	37.49
	.78	1.25	32.67
	.88	1.38	45.80
	.71	1.57	42.83
	.82	1.45	36.90
	.83	1.33	46.35
	.83	1.22	38.85
	.84	1.05	39.80
	.83	1.22	37.73
	.82	1.35	41.65
	.93	1.10	44.53
	.73	1.36	51.45
	.88	1.25	37.98
	.80	1.80	32.77
	.86	1.79	38.38
	.85	1.41	38.47
	.88	1.00	41.65
	.79	1.11	34.84
	.88	1.38	38.54
	.88	1.41	42.08
	.89	1.33	35.64
	.89	1.53	40.18



SPECIES	STYLE : PISTIL	COROLLA TUBE : PISTIL	POLLEN DIAMETER (UM)
-----	-----	-----	-----
PKM	.77	1.42	45.82
	.80	1.33	44.78
	.82	1.45	40.97
	.82	1.57	40.13
	.89	1.60	37.50
	.84	1.55	36.75
	.83	1.38	36.75
	.85	1.52	34.00
	.78	1.75	40.80
	.68	1.64	38.33
	.82	1.64	36.75
	.79	1.29	37.40
	.83	1.27	44.22
	.80	1.10	40.43
	.86	1.23	43.12
	.95	1.13	33.69
	.84	1.25	45.02
	.80	1.47	41.16
.78	1.63	40.28	
PKS	.80	1.00	37.10
	.82	1.30	36.68
	.83	1.59	40.25
	.81	1.25	38.17

## APPENDIX C

CONTINGENCY TABLES FOR DISCRETE MORPHOLOGICAL CHARACTERS

Mucro: absent (A), present (P).

MUCRO	COUNT EXP VAL COL PCT STD RES	SP			ROW TOTAL
		PKK	PKM	PKS	
P	45 45.0 100.0% .0	19 19.0 100.0% .0	4 4.0 100.0% .0	68 100.0%	
COLUMN TOTAL	45 66.2%	19 27.9%	4 5.9%	68 100.0%	

Habit: caespitose (C), casepitose-decumbent (CD), decumbent (D).

HBT	COUNT EXP VAL COL PCT STD RES	SP			ROW TOTAL		
		PKK	PKM	PKS			
		C	7 14.6 15.6% -2.0	13 6.1 68.4% 2.8		2 1.3 50.0% .5	22 32.4%
		CD	4 7.3 8.9% -1.2	5 3.1 26.3% 1.1		2 .6 50.0% 1.7	11 16.2%
D	34 23.2 75.6% 2.3	1 9.8 5.3% -2.8	0 2.1 .0% -1.4	35 51.5%			
COLUMN TOTAL		45 66.2%	19 27.9%	4 5.9%	68 100.0%		

CHI-SQUARE	D.F.	SIGNIFICANCE	MIN E.F.
32.47525	4	0.0000	0.647

Leaf shape: ensiform (ENS), lanceolate (LAN), lanceolate-linear (LANLIN), obensiform (OBLENS).

SHP	COUNT	SP			ROW TOTAL
		EXP VAL	COL PCT	STD RES	
		PKK	PKM	PKS	
ENS	1	0	0	1	1
	.7	.3	.1	1.5%	
	2.2%	.0%	.0%		
	.4	-.5	-.2		
LAN	20	5	4	29	29
	19.2	8.1	1.7	42.6%	
	44.4%	26.3%	100.0%		
	.2	-1.1	1.8		
LANLIN	1	2	0	3	3
	2.0	.8	.2	4.4%	
	2.2%	10.5%	.0%		
	-.7	1.3	-.4		
LIN	8	9	0	17	17
	11.3	4.8	1.0	25.0%	
	17.8%	47.4%	.0%		
	-1.0	2.0	-1.0		
LINLAN	14	3	0	17	17
	11.3	4.8	1.0	25.0%	
	31.1%	15.8%	.0%		
	.8	-.8	-1.0		
OBLENS	1	0	0	1	1
	.7	.3	.1	1.5%	
	2.2%	.0%	.0%		
	.4	-.5	-.2		
COLUMN TOTAL	45	19	4	68	68
	66.2%	27.9%	5.9%	100.0%	

CHI-SQUARE

D. F.

SIGNIFICANCE

MIN E. F.

15.66386

10

0.1097

0.059

Leaf pubescence: absent (A), present (P).

LFPUB	COUNT	SP			ROW TOTAL
		EXP VAL	COL PCT	STD RES	
		PKK	PKM	PKS	
A	39	10	4	53	
	35.1	14.8	3.1	77.9%	
	86.7%	52.6%	100.0%		
	.7	-1.2	.5		
P	6	9	0	15	
	9.9	4.2	.9	22.1%	
	13.3%	47.4%	.0%		
	-1.2	2.3	-.9		
COLUMN TOTAL	45	19	4	68	
	66.2%	27.9%	5.9%	100.0%	

<u>CHI-SQUARE</u>	<u>D.F.</u>	<u>SIGNIFICANCE</u>	<u>MIN E.F.</u>
10.25383	2	0.0061	3.852

Leaf pubescence glands: absent (A), present (P).

LFGL	COUNT	SP			ROW TOTAL
		PKK	PKM	PKS	
A	42	14	4	60	
	39.7	16.8	3.5	88.2%	
	93.3%	73.7%	100.0%		
	.4	-.7	.3		
P	3	5	3	8	
	5.3	2.2	.5	11.8%	
	6.7%	26.3%	.0%		
	-1.0	1.8	-.7		
COLUMN TOTAL	45	19	4	68	
	66.2%	27.9%	5.9%	100.0%	

CHI-SQUARE	D. F.	SIGNIFICANCE	MIN E. F.
5.53544	2	0.0628	0.471

Leaf margin: same as lamina(0), thickened (T), white & thickened (WT).

MRG	SP			ROW TOTAL	
	COUNT	PKK	PKM		PKS
	EXP VAL				
	COL PCT				
STD RES					
0	0	1	0	1	
	.7	.3	.1	1.5%	
	.0%	5.3%	.0%		
	-.8	1.4	-.2		
T	36	18	3	57	
	37.7	15.9	3.4	83.5%	
	80.0%	94.7%	75.0%		
	-.3	.5	-.2		
WT	9	0	1	10	
	6.6	2.8	.6	14.7%	
	20.0%	.0%	25.0%		
	.9	-1.7	.5		
COLUMN TOTAL	45	19	4	68	
	66.2%	27.9%	5.9%	100.0%	

<u>CHI-SQUARE</u>	<u>D.F.</u>	<u>SIGNIFICANCE</u>	<u>MIN E.F.</u>
6.90454	4	0.1410	0.059

Leaf margin cilia: absent (A), present (P).

MRGCL	COUNT	SP			ROW TOTAL
		EXP VAL	COL PCT	STD RES	
		PKK	PKM	PKS	
A	8	1	0		9
	6.0	2.5	.5		13.2%
	17.8%	5.3%	.0%		
	.8	-1.0	-.7		
P	37	18	4		59
	39.0	16.5	3.5		36.8%
	82.2%	94.7%	100.0%		
	-.3	.4	.3		
COLUMN TOTAL	45	19	4		68
	66.2%	27.9%	5.9%		100.0%

<u>CHI-SQUARE</u>	<u>D.F.</u>	<u>SIGNIFICANCE</u>	<u>MIN E.F.</u>
2.47029	2	0.2908	0.529



Leaf margin cilia glands: absent (A), present (P).

MRG GL	COUNT	SP			ROW TOTAL
		EXP VAL	COL PCT	STD RES	
		PKK	PKM	PKS	
A	38	11	4	53	
	35.1	14.8	3.1	77.9%	
	84.4%	57.9%	100.0%		
	.5	-1.0	.5		
P	7	8	0	15	
	9.9	4.2	.9	22.1%	
	15.6%	42.1%	.0%		
	-2.9	1.9	-2.9		
COLUMN TOTAL	45	19	4	68	
	66.2%	27.9%	5.9%	100.0%	

<u>CHI-SQUARE</u>	<u>D.F.</u>	<u>SIGNIFICANCE</u>	<u>MIN E.F.</u>
6.68000	2	0.0354	0.832

Ciliate portion of leaf margin (percent, from the leaf base).

CIL	COUNT	SP			ROW TOTAL
		EXP VAL	COL PCT	STD RES	
		PKK	PKM	PKS	
< .50	1	35	8	4	47
		31.1	13.1	2.8	69.1%
		77.8%	42.1%	100.0%	
		.7	-1.4	.7	
> .50	2	10	11	0	21
		13.9	5.9	1.2	30.9%
		22.2%	57.9%	.0%	
		-1.0	2.1	-1.1	
	COLUMN TOTAL	45	19	4	68
		66.2%	27.9%	5.9%	100.0%

<u>CHI-SQUARE</u>	<u>D. F.</u>	<u>SIGNIFICANCE</u>	<u>MIN E. F.</u>
9.86336	2	0.0072	1.235

Stem pubescence: absent (A), present (P).

STPUB	SP			ROW TOTAL
	COUNT			
	EXP VAL			
	COL PCT			
STD RES	PKK	PKM	PKS	
A	31	16	4	51
	33.8	14.3	3.0	75.0%
	68.9%	84.2%	100.0%	
	-.5	.5	.6	
P	14	3	0	17
	11.3	4.8	1.0	25.0%
	31.1%	15.8%	.0%	
	.8	-.8	-1.0	
COLUMN TOTAL	45	19	4	68
	66.2%	27.9%	5.9%	100.0%

<u>CHI-SQUARE</u>	<u>D.F.</u>	<u>SIGNIFICANCE</u>	<u>MIN E.F.</u>
3.08928	2	0.2134	1.000

Stem pubescence glands: absent (A), present (P).

STGLS	COUNT EXP VAL COL PCT STD RES	SP			ROW TOTAL		
		PKK	PKM	PKS			
		A	37 37.7 82.2% -.1	16 15.9 34.2% .0		4 3.4 100.0% .4	57 83.8%
		P	8 7.3 17.8% .3	3 3.1 15.8% .0		0 .6 .0% -.8	11 16.2%
COLUMN TOTAL	45 66.2%	19 27.9%	4 5.9%	68 100.0%			

CHI-SQUARE	D.F.	SIGNIFICANCE	MIN E.F.
0.85912	2	0.6508	0.647

Calyx pubescence: absent (A), present (P).

PUB	SP			ROW TOTAL
	COUNT	EXP VAL	COL PCT	
	STD RES	PKK	PKM	PKS
A	8	1	0	9
	6.0	2.5	.5	13.2%
	17.8%	5.3%	.0%	
	.8	-1.0	-.7	
P	37	18	4	59
	39.0	16.5	3.5	86.8%
	82.2%	94.7%	100.0%	
	-.3	.4	.3	
COLUMN TOTAL	45	19	4	68
	66.2%	27.9%	5.9%	100.0%

<u>CHI-SQUARE</u>	<u>D.F.</u>	<u>SIGNIFICANCE</u>	<u>MIN E.F.</u>
2.47029	2	0.2908	0.529

Calyx pubescence glands: absent (A), present (P).

GL	COUNT	SP			ROW TOTAL
		EXP VAL	COL PCT	STD RES	
		PKK	PKM	PKS	
A	15	3	3		21
	13.9	5.9	1.2		30.9%
	33.3%	15.8%	75.0%		
	.3	-1.2	1.6		
P	30	16	1		47
	31.1	13.1	2.8		69.1%
	66.7%	84.2%	25.0%		
	-.2	.8	-1.1		
COLUMN TOTAL	45	19	4		68
	66.2%	27.9%	5.9%		100.0%

<u>CHI-SQUARE</u>	<u>D.F.</u>	<u>SIGNIFICANCE</u>	<u>MIN E.F.</u>
5.80174	2	0.0550	1.235

Calyx margin: not distinctive (O), hyline (H), thickened (T), thickened & white (TW), white (W).

CALMRG	COUNT EXP VAL COL PCT STD RES	SP			ROW TOTAL
		PKK	PKM	PKS	
O	15 13.2 33.3% .5	4 5.6 21.1% -.7	1 1.2 25.0% -.2	20 29.4%	
H	2 2.0 4.4% .0	1 .8 5.3% .2	0 .2 .0% -.4	3 4.4%	
T	24 25.8 53.3% -.4	12 10.9 63.2% .3	3 2.3 75.0% .5	39 57.4%	
TW	0 1.3 .0% -1.2	2 .6 10.5% 1.9	0 .1 .0% -.3	2 2.9%	
W	4 2.6 5.9% .8	0 1.1 .0% -1.1	0 .2 .0% -.5	4 5.9%	
COLUMN TOTAL	45 66.2%	19 27.9%	4 5.9%	68 100.0%	

CHI-SQUARE  
-----

8.57890

D. F.  
-----

8

SIGNIFICANCE  
-----

0.3791

MIN E. F.  
-----

0.113

Number of anthers exposed from corolla.

AN	COUNT	SP			ROW TOTAL
		EXP VAL	COL PCT	STD RES	
		PKK	PKM	PKS	
0	10	9	4		23
	15.2	6.4	1.4		33.3%
	22.2%	47.4%	100.0%		
	-1.3	1.0	2.3		
1-2	16	9	0		25
	16.5	7.0	1.5		36.8%
	35.6%	47.4%	.0%		
	-.1	.8	-1.2		
1-2	10	1	0		11
	7.3	3.1	.6		16.2%
	22.2%	5.3%	.0%		
	1.0	-1.2	-.8		
3 -- 5	9	0	0		9
	6.0	2.5	.5		13.2%
	20.0%	.0%	.0%		
	1.2	-1.6	-.7		
COLUMN TOTAL	45	19	4	68	
	66.2%	27.9%	5.9%	100.0%	

CHI-SQUARE	D.F.	SIGNIFICANCE	MIN E.F.
17.73255	6	0.0069	0.529



Number of flowers per stem.

NMFL	COUNT	SP			ROW TOTAL
		EXP VAL	COL PCT	STD RES	
		PKK	PKM	PKS	
1	31	15	3		49
	32.4	13.7	2.9		72.1%
	68.9%	78.9%	75.0%		
	-.3	.4	.1		
2	2	0	0		2
	1.3	.6	.1		2.9%
	4.4%	.0%	.0%		
	.6	-.7	-.3		
3	1	1	0		2
	1.3	.6	.1		2.9%
	2.2%	5.3%	.0%		
	-.3	.6	-.3		
4	9	3	1		13
	8.6	3.6	.8		19.1%
	20.0%	15.8%	25.0%		
	.1	-.3	.3		
5	1	0	0		1
	.7	.3	.1		1.5%
	2.2%	.0%	.0%		
	.4	-.5	-.2		
6	1	0	0		1
	.7	.3	.1		1.5%
	2.2%	.0%	.0%		
	.4	-.5	-.2		
COLUMN TOTAL	45	19	4		68
	66.2%	27.9%	5.9%		100.0%

CHI-SQUARED.F.SIGNIFICANCEMIN E.F.

2.98296

10

0.9818

0.059

Pedicel pubescence: absent (A), present (P)

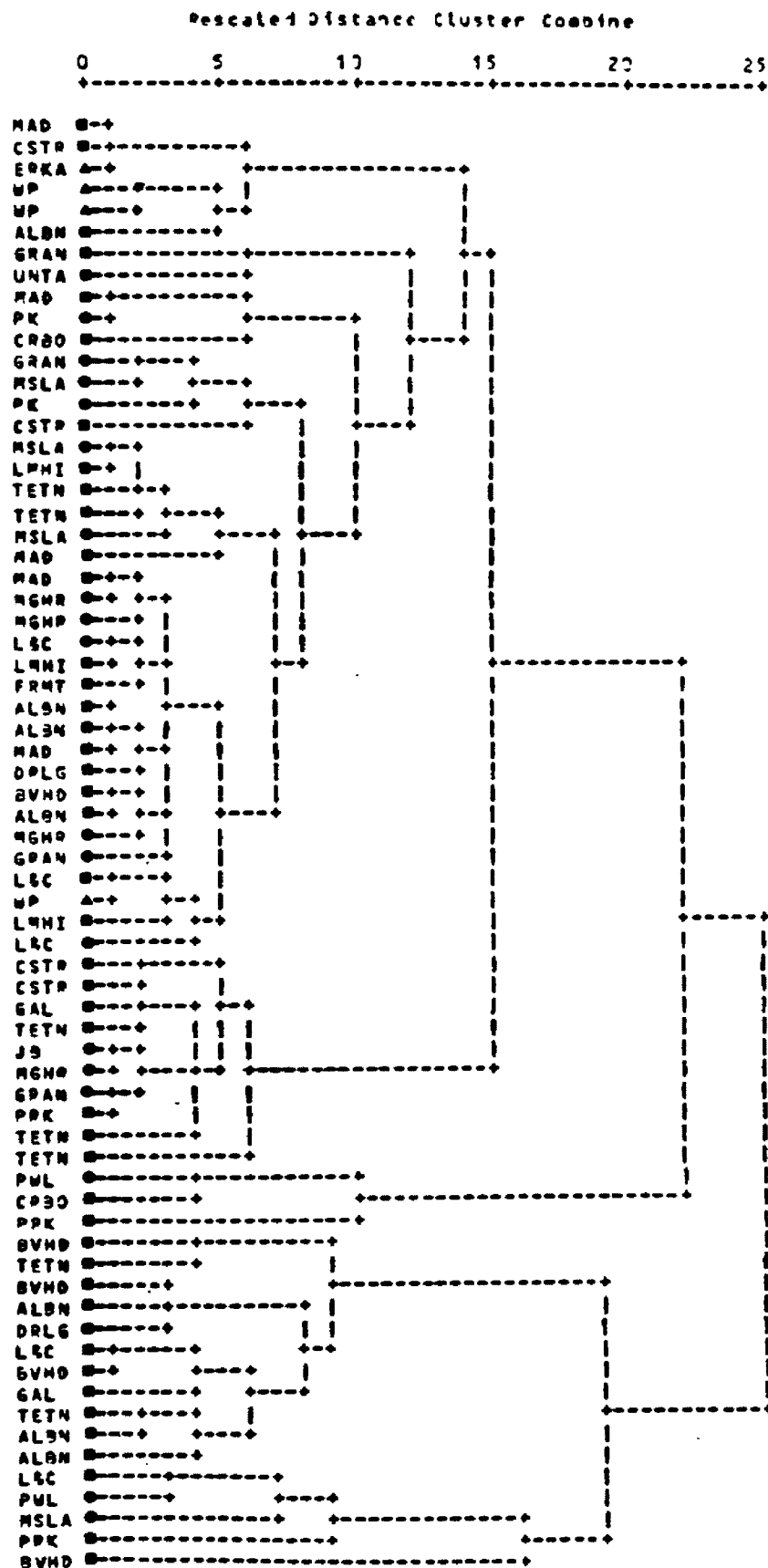
PED	COUNT EXP VAL COL PCT STD RES	SP			ROW TOTAL
		PKK	PKM	PKS	
A	1 .7 2.2% .4	0 .3 .0% -.5	0 .1 .0% -.2	1 1.5%	
P	44 44.3 97.8% -.1	19 18.7 100.0% .1	4 3.9 100.0% .0	67 98.5%	
COLUMN TOTAL	45 66.2%	19 27.9%	4 5.9%	68 100.0%	

CHI-SQUARE	D.F.	SIGNIFICANCE	MIN E.F.
0.51874	2	0.7715	0.059

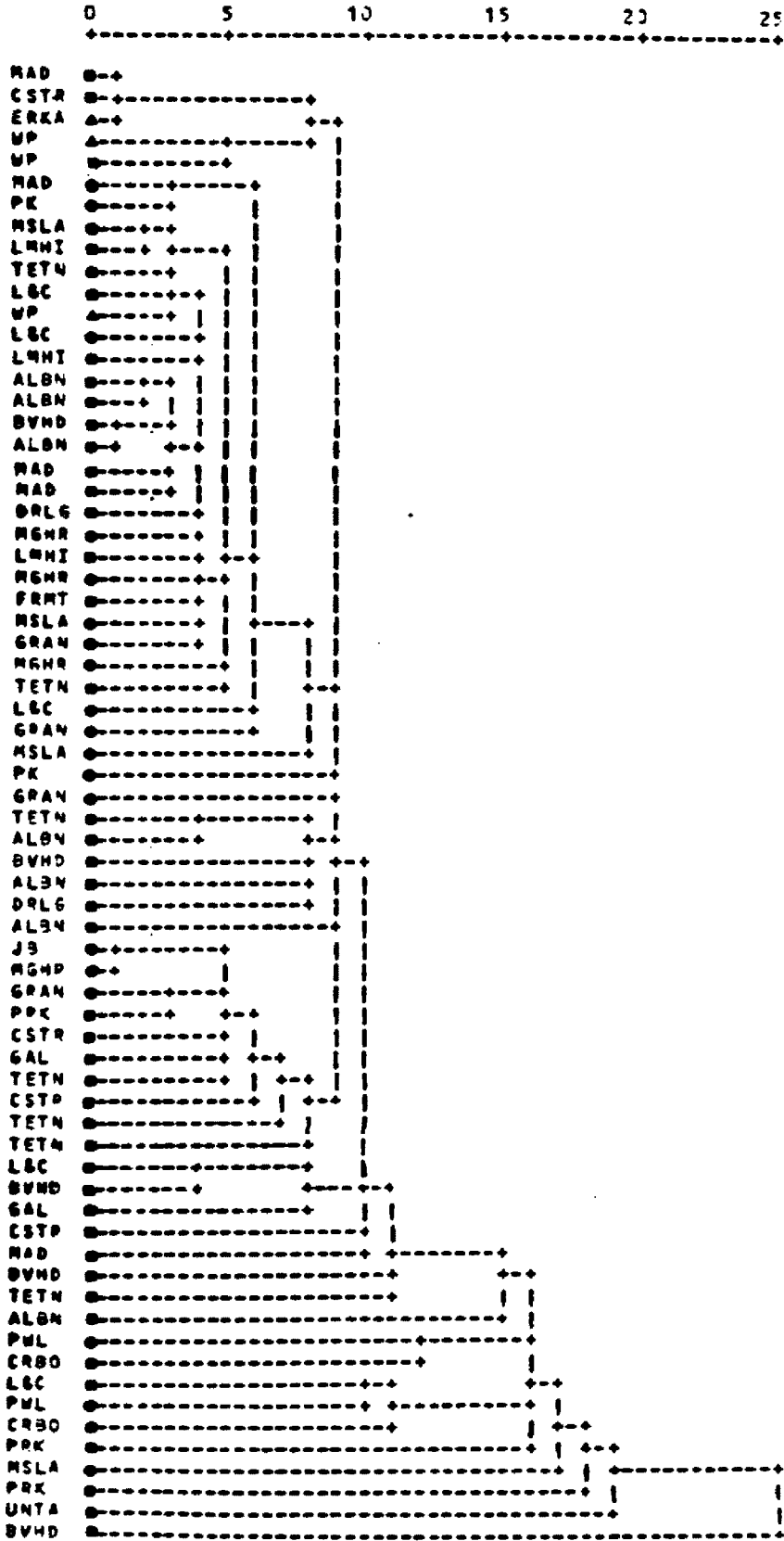
## APPENDIX D

### DENDROGRAMS

Dendrograms of specimens from cluster analysis of squared Euclidean distances. The first figure was produced by the average linkage between groups method (UPGMA). The second figure was produced by the single linkage (nearest neighbor) method. Specimens are indicated as *Phlox kelseyi* ssp. *kelseyi*, *P. kelseyi* ssp. *missoulensis* and *P. kelseyi* ssp. *salina*. Locality abbreviations are as follows: Albany Co., WY (ALBN), Beaverhead Co., MT (BVHD), Carbon Co., ID (CRBO), Custer Co., Idaho (CSTR), Deerlodge Co., MT (DRLG), Eureka Co., NV (ERKA), Fremont Co., WY (FRMT), Gallatin Co., MT (GAL), Granite Co., MT (GRAN), Judith Basin Co., MT (JB), Lemhi Co., ID (LMHI), Lewis & Clark Co., MT (L&C), Madison Co., MT (MAD), Meagher Co., MT, (MGHR), Missoula Co., MT, (MSLA), Park Co., CO (PK), Park Co., MT (PRK), Powell Co., MT (PWL), Teton Co., MT (TETN), Uinta Co., WY (UNTA), White Pine Co., NV (WP),



Rescaled Distance Cluster Combine



## APPENDIX E

EXSICCATAE

*Phlox kelseyi* ssp. *missoulensis*. MONTANA. GRANITE CO.: Rough Fescue Ridge, 7500 ft, 14 Jun 1977, K. Lackschewitz 7320. Foothills of the Sapphire Range, in triangle between Rock Creek and Skalkaho roads, off Hwy 38, E of road to ranch, elev. 5000 ft, 23 May 1973, K. H. Lackschewitz 3502. LEWIS & CLARK CO.: MacDonald Pass, 6000 ft, 25 June 1945, C. L. Hitchcock & C. V. Muhlick 11745. 6235 ft, 22 May 1971, T. J. Watson 1244. 6000 ft, 30 Jun 1976 K. Lackschewitz 6574. 6700 ft, 18 Jul 1976, T. J. Watson 1270. Lewis & Clark Pass, 5700 ft, 16 Jun 1968, K. Lackschewitz 384. 25 Jun 1968, M. Mooar 8618. MEAGHER CO.: Little Belt Mtns, near the pass (King's Hill), 1896, J. H. Flodman 734. King's Hill, 7398 ft, 20 Jul 1946, F. H. Rose 3168. Switchback, 4 Jul 1948, F. H. Rose 4082. King's Hill, 45 mi SSE of Great Falls, 24 Jul 1948, R. F. Daubenmire 48213. MISSOULA CO.: Missoula, 7 May 1897, M. J. Elrod 48. 1916, F. E. Paulson 114. Missoula, Waterworks Hill, 27 Apr 1921, A. N. Steward 383. 15 May 1923, R. J. Kirkwood 1386. Missoula, Umlin Hill, 25 May 1923, J. E. Kirkwood 1386. Waterworks Hill, Apr 1925, A. Maclay 40. 3600 ft, 9 May, 1933, C. L. Hitchcock 1549. 19 Apr 1935, F. H. Rose 37. 23 Apr 1938, J. R. Demorest 7. 27 Apr 1938 R. A. Robinson 4. 3500 ft, 21 Apr 1939, F. H. Rose 701. Gravely outcrop on ridge of Waterworks Hill, elev. 3500 ft, 28 Apr 1939, M. J. Reed 8 [Type]. 25 Apr 1940, F. H. Rose 1067. 13 May 1948, S. L. Glowenke 11290. 13 May 1948, E. T. Wherry s. n. 9 May 1976, P. F. Stickney 3385. 2 May 1977, C. Bara 9. 9 May 1979, J. Beehler 31.

*Phlox kelseyi* ssp. *kelseyi*. COLORADO. PARK CO.: 3.5 mi N of Antero Jct., Antero Reservoir, 9200 ft, 8 June 1949, C. W. Penland & J. B. Hartwell 3840. Antero Junction, 28 May 1986, W. Weber 17766. IDAHO. CARIBOU CO.: Soda Springs, 1889, J. B. s. n. 12 May 1937, J. H. Christ 7142. Bear River, 2 mi W of Soda Springs, 30 May 1939, R. J. Davis 827, [Type of *P. kelseyi* spp. *glandulosa*]. 8 July 1949, J. H. Christ 18583. Travertine area 1 mi W of Soda Springs, W. P. Cottman 17639. CUSTER CO.: 2 mi W of Dickey, 13 Jun 1944, C. L. Hitchcock & C. V. Muhlick 8905. 2 mi E of Dickey, 21 Jun 1947, C. L. Hitchcock 15619. Thousand Springs, 22 June 1983, D. Henderson et al. 6606. LEMHI CO.: Mead Meadow, 5000 ft, 14 Apr 1930, A. M. Cusick 106. 3 mi N of Gilmore, 17 May 1941, R. J. Davis 3124. Along Birch Creek, ca 20 mi E of Gilmore, 25 Jun 1947, C. L. Hitchcock 15765. 10 mi SE of Leadore, 3 Jun 1951, J. H. Christ 51-295A. Birch Creek, 2 mi N of Clark Co. line, 3 Jun 1951, J. H. Christ 51-300. 2 mi S of Lemhi Co. line, 3 Jun 1951 J. H. Christ 51-303A. Birch Creek Valley, along Hwy 28, N of county line, ca 10 mi N of Blue Dome, 4 Jun 1975, D. Henderson, J. Jewell & J. Anderson. Birch Creek drainage between Lemhi Range and Beaverhead Mtns. 38 mi from Dubois, 6600 ft, 25 May 1981, S. Goodrich 15438. MONTANA. BEAVERHEAD CO.: Monida, 16 Jun 1899 A. Nelson 5418. S. of Red Rocks, 5600-5700 ft, 28 Jun 1937, F. W. Pennell 20590. Lima, alpine, 14 Jun 1908, M. E. Jones s. n. Red Rock Lake Refuge, 6600 ft, 11 Jun 1968, R. D. Dorn 318. Road to Lima Reservoir, 6500 ft, K. H. Lackschewitz & J. Pierce 10705. Monida, 10 Jun

1985, *P. Lesica* 3363. **DEERLODGE CO.:** Deer Lodge vicinity, *L. A. Fitch s. n.* Warm Springs, 4800 ft, 21 May 1906, *J. W. Blankenship* 781. Anaconda, 24 Jun 1909, *J. W. Blankenship s. n.* Warm Springs, just E of Hwy. 10, 15 May 1948, *E. T. Wherry s. n.* 23 Jun 1970, *M. Mooar* 12093. 1 mi E of Warm Springs, 4800 ft, 14 Jun 1984, *K. H. Kackschewitz & L. Eichorn* 10725.

**LEWIS & CLARK CO.:** Helena, 1888, *F. D. Kelsey s. n.* Helena, July 1890, *F. D. Kelsey s. n.* Helena, Fairgrounds, May 1891, *F. D. Kelsey s. n.* [Type]. Helena, Jun 1890, *F. W. Anderson s. n.* 5 Sep 1892, *F. D. Kelsey s. n.* 1892, *E. N. Brandegees s. n.* 1894, *F. D. Kelsey s. n.* Without location, *L. A. Fitch s. n.* Helena, 26 May 1899, *E. N. Brandegees s. n.* Vicinity of Helena, *N. L. Britton s. n.* Helena fairgrounds, *S. A. Merritt s. n.* In the fairgrounds N of Helena, 17 May 1948, *E. T. Wherry s. n.*

**GALLATIN CO.:** Manhattan, 9 June 1901, *E. W. Scheuber s. n.* Belgrade, 2 May 1959, *McLees s. n.* Twin Bridges, *L. A. Fitch s. n.*

**TETON CO.:** Pine Butte Swamp, T 24N R 7W S 18E, 7 Jun 1982, *K. Lackschweitz & P. Lesica* 10008. Duhr Fen, 7 Jun 1982, *P. Lesica & K. Lackschweitz* 2004.

**WYOMING. ALBANY CO.:** Cooper Creek, 6 Jun 1898, *E. Nelson* 4336. Sand Creek, 2 Jun 1900, *A. Nelson* 7041. Red Buttes, 10 Jun 1903, *A. Nelson* 9217. Centennial, foothills, Jul 1928, *O. M. Clark* 131. Dutton Creek, 8000 ft, 7 Jun 1958, *C. L. Porter & M. W. Porter* 7456. Medicine Bow, 9500 ft, 2 Jun 1956, *R. K. Gierisch* 1813.

**FREMONT CO.:** Beaver Divide, 6700 ft, 29 May 1952, *N. A. Kissinger K-39*. Beaver Rim, 7000 ft, 2 Jun 1984, *R. Dorn* 4029.

**PLATTE CO.:** Guernsey Reservoir, N of Platte River, 4700 ft, 10 May 1958, *C. L. Porter & M. W. Porter* 7452.

*Phlox kelseyi* ssp. *salina*. **NEVADA. EUREKA CO.:** Monitor Valley, Hot Springs Hill, T 19N R 50E S 5, 6120 ft, 21 May 1981, *A. Tiehm & M. Williams* 6473. 6120 ft, 9 Jun 1982, *M. J. Williams & A. Tiehm* 82-170-5.

**WHITE PINE CO.:** Cherry Creek, 21 May 1906, *M. E. Jones s. n.* [Type]. Cherry Creek, 8 mi SE of Hwy 35, 3.5 mi NW of Hwy 93, 16 Jun 1940, *E. T. Wherry s. n.* Monte Neva Hot Springs, 5900 ft, 15 Jun 1944, *H. D. Ripley & R. C. Barneby* 6279. Spring Valley, Baking Powder Flat, 5700 ft, 17 Jun 1982, *M. Williams & A. Tiehm* 82-153-7. Spring Valley, 5680 ft, 4 Jun 1985, *T. Knight* 1508.