AN ABSTRACT OF THE THESIS OF

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Title: A SYSTEMATIC STUDY OF LATHYRUS VESTITUS NUTT. EX T. & G. (FABACEAE) AND ALLIED SPECIES OF THE PACIFIC COAST

Abstract approved: Redacted for Privacy

Kenton L. Chambers

Eight species of Lathyrus (Fabaceae, Faboideae) endemic to the Pacific Coast of North America were the subject of a systematic investigation. Taxa studied included Lathyrus vestitus Nutt. ex T. & G., L. laetiflorus Greene, L. jepsonii Greene, L. splendens Kellogg, L. polyphyllus Nutt. ex T. & G., L. holochlorus (Piper) C. L. Hitchcock, L. delnorticus C. L. Hitchcock and L. sulphureus Brewer.

Taximetric studies, including hierarchical and non-hierarchical cluster analyses followed by discriminant analyses, revealed the existence of one new species. Lathyrus holochlorus, L. delnorticus, L. sulphureus, L. polyphyllus, L. jepsonii and L. splendens were found to be morphologically distinct while extensive morphological intergradation was found between L. vestitus and L. laetiflorus. Principal Components analysis was used to document two clinal trends within the L. vestitus-laetiflorus complex. Flower size increases and floral shape changes from north to south along the Pacific Coast; pubescence increases clinally from north to south and from the coast inland.

The anatomy of stems and leaflets was examined by tissue clearing methods. Vascular anatomy of nodes and internodes was found to conform to patterns described previously for European species of Lathyrus. Epidermal cell shape and stomatal frequency on leaflets varies greatly within species and these data were not useful for taxonomic distinctions.

The diploid chromosome number for all species studied was found to be 2n = 14; only small differences in karyotypes could be noted.

Preliminary studies of breeding systems in Lathyrus vestitus, L. polyphyllus and L. holochlorus revealed these perennial herbaceous species to be self-incompatible, obligate outcrossers dependent primarily upon large bees for pollination.

The new species, named Lathyrus glandulosus, is described; plants referable to L. vestitus and L. laetiflorus are reorganized into five subspecies under the former name. A key and descriptions for all species of Lathyrus, native and introduced, found west of the Sierra-Cascade Crest in Washington, Oregon and California is presented.

A Systematic Study of *Lathyrus vestitus* Nutt. ex T. & G. (Fabaceae) and allied species of the Pacific Coast

by

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Typed by the Author

Steven Leo Broich

To Jolene
and Ann
and Doug

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A SYSTEMATIC STUDY OF *LATHYRUS VESTITUS* NUTT. ex T. & G. (FABACEAE) AND ALLIED SPECIES OF THE PACIFIC COAST

I. INTRODUCTION

Lathyrus L. is a genus of approximatly 150 species of temperate papilionoid legumes (Fabaceae, Faboideae). It is a member of the tribe Vicieae (Adans.) DC. which also includes *Vicia* (ca. 140 species), *Lens* Mill. (5 species, including the domesticated lentil), *Pisum* L. (2 species, including the domesticated pea) and *Vavilovia* A. Fedorov (monotypic) (Kupicha 1977, 1981). No clear distinction exists between *Lathyrus* and *Vicia*; transitional species, found in *Lathyrus* sect. *Orobus* (Bassler 1973) and *Vicia* sect. *Vicilla* (Kupicha 1976), can be separated only on the basis of certain arbitrary characteristics (Kupicha 1981). The center of diversity for both *Lathyrus* and *Vicia* is in the Mediterranean and Irano-turanian region (Kupicha 1981).

A complete subgeneric taxonomy of *Lathyrus* has never been published. European species were organized into sections by Acherson and Graebner (1910) and variations on this scheme have been used since then (Fedchenko 1948; Davis 1970; Czfranova 1971). None of these schemes take into account North and South American or East African species. Research to clarify the infrageneric structure of *Lathyrus* is now in progress (Kupicha, personal communication).

The earliest complete treatment of *Lathyrus* in North America was that of Torrey and Gray (1838). Watson (1876) listed 13 species native to North America while 18 years later White (1894) numbered the native species at 33. C. L. Hitchcock (1952) published the most recent complete revision of *Lathyrus* in North America. Except for the description of one new species (Barneby and Reveal 1971) and

a revision of Utah species for a flora (Welsh 1965, 1978) there has been no taxonomic study of North American Lathyrus species in the last 30 years.

The present investigation examined the systematic relationships among eight species of Lathyrus endemic to the Pacific Coast of North America. Taxa studied included L. delnorticus C. L. Hitchcock, L. holochlorus (Piper) C. L. Hitchcock, L. laetiflorus Greene, L. polyphyllus Nutt. ex T. & G., L. splendens Kellogg, L. sulphureus Brewer ex Gray and L. vestitus Nutt. ex T. & G.

Reported here are studies designed (1) to make a detailed examination of the morphological diversity within this group, (2) to place this morphological variability within an ecological, geographic and historical context and (3) to examine karyotype relationships among these species. The purpose of this investigation was twofold: to expand our knowledge of evolutionary patterns within the North American species of Lathyrus and to produce a classification which works efficiently for the identification of Pacific Coast Lathyrus species.

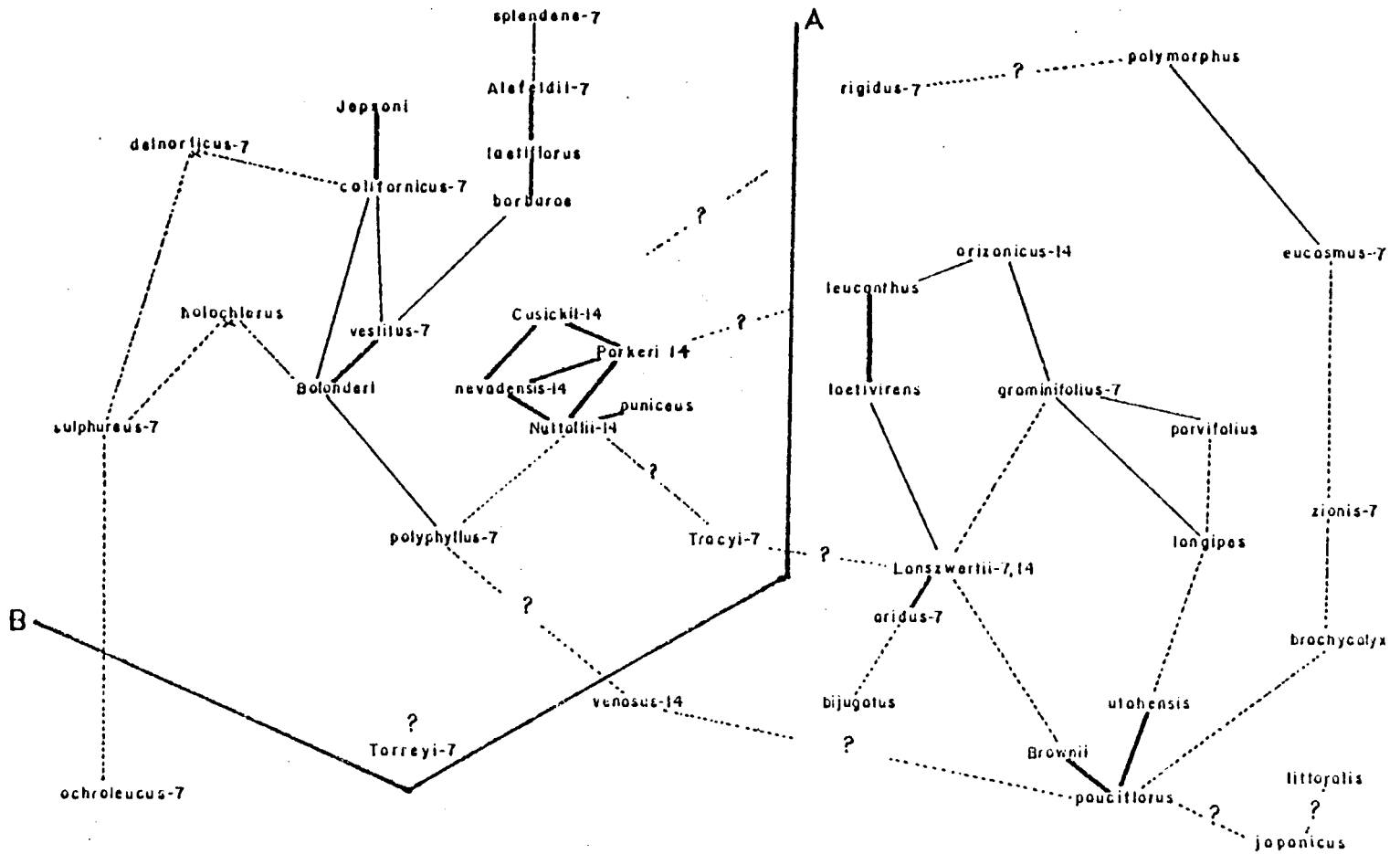
II. TAXONOMIC HISTORY

Hitchcock (1952) summarized his concepts of species relationships among North American Lathyrus in a diagram reproduced as Figure 1. Taxa to the right and below line AB (added by the present author) occur east of the Sierra-Cascade crest, except for L. littoralis and L. japonicus, which are distinct coastal species, L. lanszwertii ssp. aridus and L. pauciflorus ssp. brownii. The latter two subspecies occur in northeastern California. Species to the left and above line AB are endemic to the Pacific Coast with the exception of L. nevadensis ssp. cusickii and ssp. lanceolatus (i.e. vars. parkeri and puniceus), which occur in the mountains of northeastern Oregon and adjacent Idaho. Members of the L. nevadensis complex form a rather distinct group of Pacific Coast plants as do populations referable to L. torreyi. L. tracyi, although endemic to the Klamath Mountain region of northwestern California, is actually closer to L. lanszwertii in morphology (Hitchcock 1952). The remaining species to the left and above line AB in Figure 1 were the subject of this investigation.

The earliest descriptions of species in this group are those of Thomas Nuttall in Torrey and Gray's flora of North America (1838). From his travels along the Pacific Coast Nuttall described L. polyphyllus, L. vestitus and L. strictus. Numerous additional forms in this group were described in the latter half of the 19th century. These included L. sulphureus Brewer (1867), L. splendens Kellogg (1876), L. californicus Watson (1885), L. bolanderi Watson (1885), L. jepsonii Greene (1890), L. violaceus Greene (1893), L. laetiflorus Greene (1893), L. puberulus White ex Greene (1894), L. watsonii White (1894), L. alefeldii White (1894), L. quercetorum Heller (1907), L. ochropetalus Piper (1918) and L. ochropetalus ssp. holochlorus Piper (1918).

Bradshaw (1925) first called attention to the nature of the

Figure 1. Relationships among the North American taxa of Lathyrus as presented by C. L. Hitchcock (1952).



variability within the L. vestitus group. He noted that in L. bolanderi (=L. vestitus),

> "the variation is so great that scores of forms might be described, but I cannot see the value of it at present. Further investigation will be necessary to determine their importance, which being done should be included in a detailed monograph. Accordingly no attempt has been made to name these numerous and perhaps inconstant variations, as, for example, the prostrate form with narrow leaflets and small stipules; the dwarfed erect form with dilated stipules and densly puberulent herbage; the form with broad, thin glabrous leaflets and minute stipules; and the form with coriaceous leaflets and small stipules." (Bradshaw 1925: pp. 233-234)

Under the name L. bolanderi Watson, Bradshaw submerged Greene's species L. violaceus and L. puberulus, White's L. violaceus barbarae and Heller's L. quercetorum. He also noted that Piper's L. ochropetalus "may prove to be only a northern form of L. bolanderi" and recognized White's L. alefeldii as a subspecies of L. laetiflorus Greene.

Bradshaw did not use Nuttall's name L. vestitus for the L. bolanderi group because the Nuttall specimen is labeled "Columbia plains toward the sea", and Bradshaw remarked "what the original L. vestitus was...no botanist has been able to determine. It apparently has never been collected by anyone since that time" (Bradshaw 1925: p. 252).

Jepson (1936) continued to use L. bolanderi Watson. He delimited four varieties under the name: var. violaceus (Greene) Jepson, var. quercetorum (Heller) Jepson, var. barbarae (White) Jepson and var. tracyi (Bradshaw) Jepson based on L. tracyi Bradshaw (1925). While Bradshaw saw L. laetiflorus and L. splendens as "a very distinct group of American species" (p. 260), Jepson (1936) noted that "the two groups, Lathyrus bolanderi Wats. and L. laetiflorus Greene, have been somewhat indefinitely distinguished". He delineated the differences between these two species groups and concluded that "the ranges of the two groups overlap in this region (Monterey, San Luis Obispo and Santa Barbara Counties) and the racial strains perhaps hybridize" (Jepson 1936: p. 390).

For the L. vestitus complex Abrams (1944) used L. bolanderi Watson for glabrous plants and L. vestitus Nutt. ex T. & G. for pubescent plants. Also, he did not accept Bradshaw's merger of L. laetiflorus and L. alefeldii.

Of Nuttall's name L. vestitus, Hitchcock (1952) wrote:

> "Considerable doubt has existed concerning the correct name for this species. Nuttall's type cannot be matched by anything that grows in the vicinity of the Columbia River, the supposed type locality. There can be no reasonable doubt, however, that his plant actually was collected in California as it can be matched perfectly by plants from the Bay region and nearly as well by plants from Monterey..." (Hitchcock 1952: p. 17).

Hitchcock made a much broader interpretation of L. vestitus. He included both glabrous (L. bolanderi Watson and L. ochropetalus Piper) and pubescent (L. violaceus Greene, L. puberulus White ex Greene and L. quercetorum Heller) plants into the vestitus group. He also united the pubescent L. watsonii White and the glabrous L. jepsonii Greene under the latter name and described four subspecies in the L. laetiflorus Greene group of southern California. Of this trio of species Hitchcock concluded that "differences between laetiflorus, jepsoni, and vestitus are almost nebulous" (p. 21).

Hitchcock (1952) also gave specific status to Piper's L. ochropetalus ssp. holochlorus and described a new species within the group: L. delnorticus C. L. Hitchcock.

At the present time, then, native species of Lathyrus endemic to the Pacific Coast number eight and seem to be centered around L. vestitus (with four subspecies) and L. laetiflorus (also with four subspecies).

III. MATERIALS AND METHODS

Data for this study were collected from herbarium specimens and the author's field collections and observations. Approximatly 2500 herbarium specimens from the following institutions were examined: The Jepson Herbarium (JEPS), the University of California (UC), the Dudley Herbarium of Stanford University (DS), the California Academy of Sciences (CAS), the University of Washington (WTU), Humboldt State University (HSU), the herbarium at Rancho Santa Ana Botanical Garden (RSA), Pomona College (POM), Oregon State University (OSC) and the M. E. Peck Herbarium of Willamette University (WILLU). Additional loans of type specimens were obtained from the Gray Herbarium at Harvard University (GH), the New York Botanical Garden (NY) and the British Museum (Natural History) (BM).

Field trips throughout western Oregon and the coast ranges of California were made in June of 1979, 1980 and 1981. In addition to the author's dried plant collections, samples of flowers, stems, nodes and leaflets were preserved in FAA or 70% ethanol. Seed collections were made during July of 1979 and 1981; most attempts to transplant living plants from the wild to greenhouse pots failed. To date, no living specimens, obtained from seed, have flowered under greenhouse conditions.

Taximetric Studies. Phenetic relationships among herbarium specimens were studied by the analysis of two data matricies, herein refered to as LATH and LATHTWO.

The matrix LATH consisted of data collected on 35 traits (Table 1) recorded from 114 herbarium specimens (listed in Appendix A). Trait selections were based on a survey of the literature, the examination of herbarium collections and two years of field work. Measurements on traits 3-9 and 14-17 were taken on 3-5 units per specimen; means of these measurements were used in subsequent analyses. One recently opened flower per specimen was softened (Pohl, 1954) for 5-8 minutes, dissected under a binocular microscope

Table 1. Traits included in (1) LATH and (2) LATHTWO.

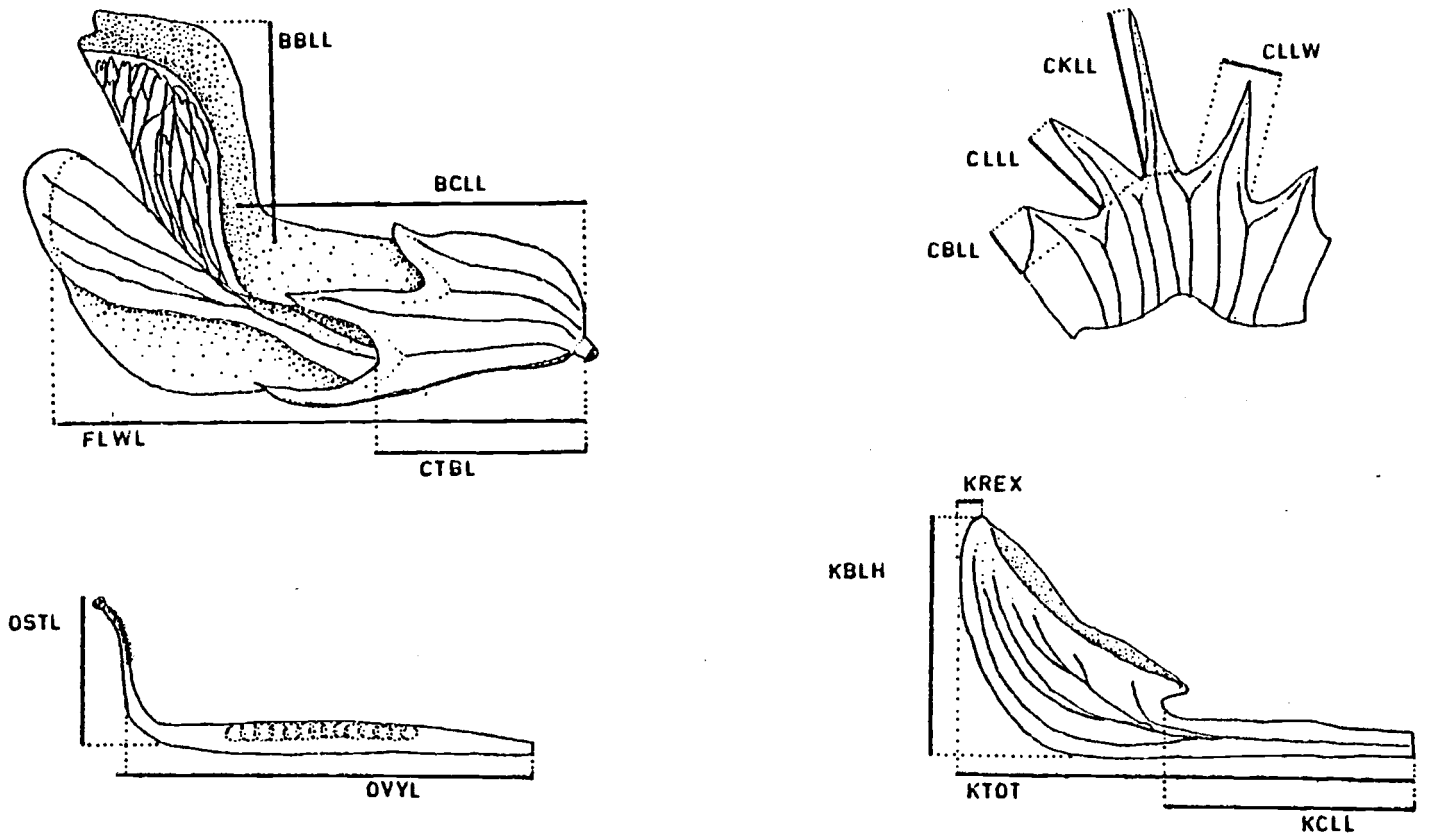
ACRONYM	MATRIX		TRAIT DESCRIPTION
1. NLBR	1		number of lateral branches on the specimen
2. STEM	1		stem winging; 0=round, 1=angled, 2=winged
3. INTL	1		mean internode length between flowering nodes to the nearest mm
4. RACL	1		mean rachis length to uppermost leaflet to nearest mm
5. NOLV	1	2	modal number of leaflets on leaves at flowering nodes
6. LVTL	1	2	mean length of lowermost leaflet at flowering node to nearest mm
7. LVTW	1	2	mean width of lowermost leaflet at a flowering node to nearest mm
8. LVLW	1		leaflet length/width ratio
9. LVTD	1		leaflet density; RACL/NOLV
10. ADPC	1	2	adaxial leaflet pubescence-curly*1
11. ADPG	1		adaxial leaflet pubescence-glandular*1
12. ABPC	1	2	abaxial leaflet pubescence-curly*1
13. ABPG	1		abaxial leaflet pubescence-glandular*1
14. INFL	1		inflorescence length; mean length of inflorescences with 50% or more open flowers
15. NOFL	1		mean number of flowers per inflorescence
16. FLWD	1		mean number of flowers per cm from lowest flower to uppermost flower
17. FLWL	1	2	flower length; see figure 2
18. CTBL	1	2	calyx tube length; see figure 2
19. CLLL	1	2	calyx lateral lobe length; see figure 2
20. CLLW	1	2	calyx lateral lobe width; see figure 2
21. CLLS	1	2	calyx lateral lobe shape; 0=deltoid, 1=linear, 2=flared

Table 1 continued

ACRONYM	MATRIX		TRAIT DESCRIPTION
22. CKLL	1		calyx keel lobe length; see figure 2
23. CBLL	1		calyx banner lobe length; see figure 2
24. CAPC	1	2	calyx pubescence-curly*1
25. CAPG	1	2	calyx pubescence-glandular*1
26. BBLL	1	2	banner blade length; see figure 2
27. BCLL	1	2	banner claw length; see figure 2
28. KTOT	1		keel total length; see figure 2
29. KBLH	1	2	keel blade height; see figure 2
30. KREX	1	2	keel blade tip reflex; see figure 2
31. KCLL	1		keel claw length; see figure 2
32. OVYL	1		ovary length; see figure 2
33. OSTL	1	2	ovary style length; see figure 2
34. OVPC	1	2	ovary pubescence-curly*1
35. OVPG	1	2	ovary pubescence-glandular*1
36. PEDL		2	pedicel length
37. BREX		2	banner reflex; 1=vertical, 2=reflexed against calyx
38. KBLL		2	keel blade length; see figure 2

*1 Pubescence traits in LATH were scored 0=glabrous to sparse, 1= medium to dense. Pubescence traits in LATHTWO were scored 0= glabrous, 1=sparse to medium, 2=dense.

Figure 2. Diagramatic representation of flower measurements included in LATH and LATHTWO.



and pressed in newsprint until dry; flower measurements (Figure 2) were made on dried flowers.

Herbarium specimens included in LATH were selected to cover the geographic range and morphological variability of each taxon. LATH included 32 specimens of L. vestitus, 13 L. jepsonii, 11 L. laetiflorus, 11 L. sulphureus, 10 L. delnorticus, 13 L. holochlorus and 12 L. polyphyllus. Three additional specimens, at first considered to be L. polyphyllus, proved upon initial cluster analysis to be quite distinct; nine additional specimens of this phenotype were located, measured and included in LATH. The final dimensions of the matrix LATH were 114 X 35.

Phenetic relationships among these 114 specimens were examined by a divisive, non-hierarchical clustering algorithm known as CLUSB (provided by C. D. McIntire, Department of Botany and Plant Pathology, Oregon State University) and by three agglomerative, hierarchical algorithms: (1) single linkage, (2) complete linkage and (3) unweighted pair group mean (UWPGM, see Pimentel 1979). The latter three algorithms are part of a computer program known as CLUSTER (provided by J. A. Keniston, Marine Science Center, Oregon State University). The Canberra metric was used as a measure of distance in the agglomerative, hierarchical cluster analyses.

Following cluster analysis the taxa hypothesized to exist in LATH were tested by Stepwise Discriminant Analysis using BMDP7M of the Biomedical Computer Programs, P-series (1979, University of California, Los Angeles).

The analysis of LATH suggested that a more extensive survey of the variability within the L. vestitus and L. laetiflorus complex would be necessary. Two hundred herbarium specimens of this group and an additional 12 specimens of L. splendens were selected and coded for 22 traits (see Table 1). Specimens included in this matrix, called LATHTWO, are listed in Appendix B. The final dimensions of the matrix LATHTWO were 212 X 22.

Flower measurements for LATHTWO were made directly from herbarium specimens without dissection.

The analysis of LATHTWO included clustering by CLUSB, Stepwise Discriminant Analysis (BMDP7M) and a principal components analysis of the data using the Statistical Interactive Programming Package (SIPS) of the Department of Statistics, Oregon State University.

All computer computations were carried out on the Cyber-NOS System of the Milam Computer Center, Oregon State University.

Anatomical Studies. The vascular anatomy of nodes and internodes was studied in reference to the presence and absence of stem wingedness. Nodes including 1-2 cm of internode on each side were fixed in FAA, cleared in sodium hydroxide and chloral hydrate, bleached in Chlorox, dehydrated, stained with Safranin O and stored in xylene (Brady et al. 1964). Cross sections of internodes fixed in FAA were made with a razor blade and mounted in Hoyer's mounting medium (Anderson 1954).

Leaflet anatomy was studied from dried leaflets rehydrated in boiling water and mounted in Hoyer's. An additional series was made by first clearing the rehydrated leaflets in a solution of 50 ml dH_2O:20 ml glycerine:100 gm chloral hydrate.

Karyotype Studies. The number and morphology of mitotic chromosomes of each taxon were studied from root tip smears. In addition to the author's collections, seeds of L. jepsonii ssp. jepsonii were obtained from W. Roderick (Tilden Park Botanical Garden Berkeley, CA), seeds of L. vestitus and L. laetiflorus ssp. barbarae were obtained from Mary Allcott (Santa Barbara Botanic Garden, Santa Barbara, CA) and seeds of L. vestitus from Monterey County, California were obtained from Dr. J. R. Griffin (Hastings Natural History Reservation, Carmel Valley, CA).

Seeds were scarified with a razor blade and stored in rolls of damp germination paper (Dillard Paper Co., Doraville, GA) in a refrigerator at ca. 5°C for 1-2 months. Five to six of these rolls were then placed in a vertical position in a glass jar containing 100 ml tap water, covered with a clear plastic bag and placed in a growth chamber on a cycle of 18 hours light at 22°C and 6 hours dark at 18°C. One or two weeks after germination, the seedlings were

transplanted to the greenhouse in a soil mixture of equal parts sand, peat and soil.

Root tips were pretreated with saturated aqueous para-dichloral benzene at 10-15°C for four hours, fixed in 95% ethanol:glacial acetic acid (3:1), hydrolized in 1N HCl for 20 minutes at 60°C, stained in Fuelgens stain (Darlington and La Cour 1975) and stored in 70% ethanol in a refrigerator (ca. 5°C).

Stained root tips were squashed in 45% acetic acid and examined on a trinocular Zeiss Phase-contrast microscope. All photographs were made at 1000X (oil emersion) using an Exakta (Ihagee, Dresden, Germany) camera body and Kodak technical pan film (2415). Slides were not made permanent.

Pollen morphology and stainability were examined by mounting pollen grains from herbarium specimens in aniline blue/lactophenol; after ca. 24 hours or more, plump blue-staining grains were scored as fertile.

Studies of Reproductive Biology. Studies of floral ontogeny and morphology were made on flowers fixed in FAA, washed in 50% ethanol and, usually, dried in newsprint.

The pollination biology of populations of L. vestitus, L. holochlorus and L. polyphyllus was studied in the vicinity of Corvallis, Oregon. Three or four inflorescences in a colony were bagged with netting (1.0 mm^2 mesh) prior to flowering and observed throughout the flowering season. Styles of dried, abscised flowers from bagged inflorescences were rehydrated in boiling water, hydrolyzed in 1N HCl (20 min. at 60°C), stained with acidified aniline blue/Safranin O (Nair and Narasimhan 1963), mounted Hoyer's and examined for evidence of self-pollination.

Reciprocal hand pollinations were also made among individuals of these three species growing in McDonald State Forest, Benton County, Oregon. One or two flowers per inflorescence were emasculated prior to anthesis and cross pollinated with pollen found in the keel of the male parent. All other flowers on the inflorescence were removed. Because the petals were also removed in this procedure,

no bags were used to exclude pollinators.

Ecological Studies. Ecological and geographic relationships among the taxa were studied in the field and by a review of the literature concerning the existing vegetation and vegetational history of the Pacific Coast.

In the field, particular attention was paid to ecological and morphological relationships among sympatric taxa.

Herbarium collections were used to map the distribution of taxa and morphological variation within taxa in relation to physiographic features and vegetation types.

IV. RESULTS

Taximetric Studies

Cluster Analysis of LATH

Cluster analysis was used here to examine the distribution of the analysed specimens in p-dimensional hyperspace, where p equaled the number of traits scored on each specimen. CLUSB is a devisive, polythetic, non-hierarchical clustering algorithm (Williams 1971) which minimizes within-cluster sums-of-squares at each step. Groups formed are phenotypically as homogeneous as possible. Clustering by CLUSB is somewhat analogous to an analysis of chemical structure by mass spectroscopy. The original single cluster is broken into groups and the internal composition of these groups at each step gives information about the array of specimens in hyperspace.

Five CLUSB analyses were made on all or parts of LATH. The overall conclusions of these analyses are as follows.

(1) The group of three specimens notable for dense glandular leaflet pubescence consistently separated first in the division process. These specimens are not referable to any described species in Lathyrus, and the phenotype was provisionally given the name "L. glandulosus". Nine additional specimens with this phenotype were located, measured, and added to LATH for further analysis.

(2) Specimens referable to the named species L. holochlorus, L. delnorticus and L. sulphureus remained in a single cluster beyond the first 10 divisions. In a separate analysis using data from these three taxa only, the specimens clustered along specific lines. These three species seem to form a separate unit of similar but internally homogeneous entities.

(3) Specimens of L. polyphyllus consistently clustered together, indicating another internally homogeneous, morphologically distinct entity.

(4) Three specimens, originally entered as L. laetiflorus (11V, and 12V) or L. jepsonii (22V), consistently clustered with specimens

of L. vestitus. Reexamination of these specimens revealed they had been misidentified and indeed, were referable to L. vestitus. The specimens were reassigned to L. vestitus for discriminant analysis.

(5) The remaining specimens of L. jepsonii and L. laetiflorus consistently clustered together at early stages and then separated along specific lines except that 4J and 6J often clustered with specimens of L. laetiflorus while 4L and 5L often clustered with specimens of L. jepsonii. Flowers of L. jepsonii and L. laetiflorus are very similar in size and shape. The two species are allopatric and differ primarily in that the former has markedly winged stems. Stem wingedness was not sufficient to separate completely the two groups in this polythetic clustering analysis.

(6) Specimens referable to L. vestitus represented the morphologically most diverse group in LATH, often breaking up into four or five separate clusters. Cluster membership was inconsistant from one analysis to the next and some specimens tended to move back and forth between clusters at successive divisions of a single analysis. This suggests the presence of a continuum of variability within L. vestitus.

The results of the hierarchical, agglomerative clustering analyses are displayed in Figures 3-8. The program CLUSTER had a maximum capacity of 75 cases (specimens). Therefore, the matrix LATH was split into two parts; data for specimens of L. delnorticus, L. holochlorus, L. sulphureus, L. polyphyllus and "L. glandulosus" (n=12) were assembled into a matrix called LATHA. LATHB consisted of data for L. vestitus, L. laetiflorus and L. jepsonii.

Dendrograms of the LATHA analyses (Figures 3-5) reveal the existence of five separate groups corresponding to the five species included in the matrix. A close phenetic relationship among specimens of L. holochlorus, L. sulphureus and L. delnorticus is evident: specimen 6S (L. sulphureus) clustered with specimens of L. holochlorus, while specimen 8S and often 10S clustered with L. delnorticus. Specimens of L. polyphyllus and "L. glandulosus" consistently clustered into two distinct groups.

Figure 3.

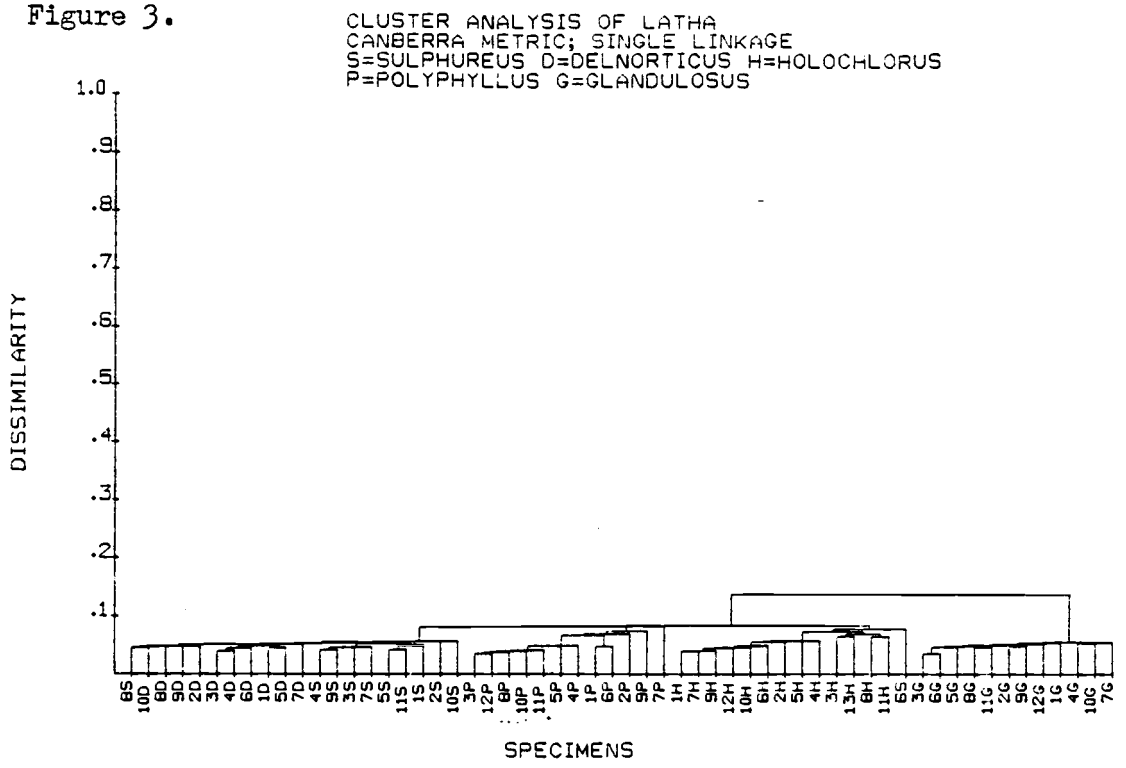


Figure 4.

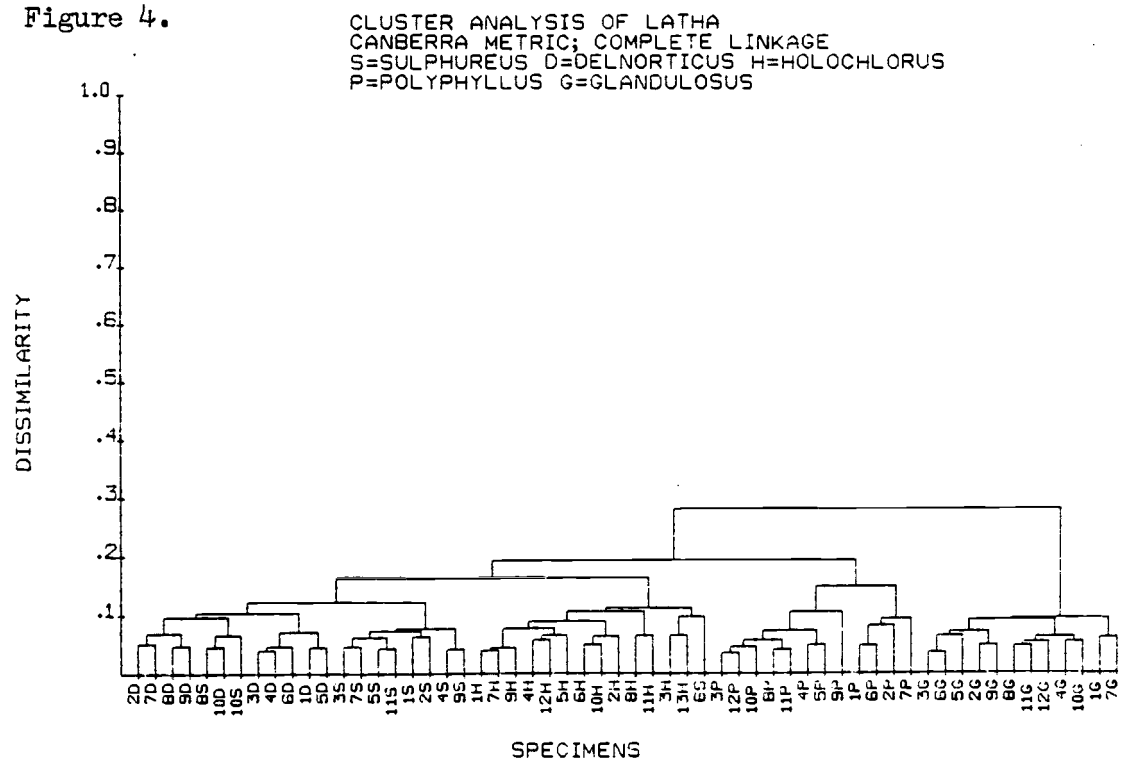


Figure 5.

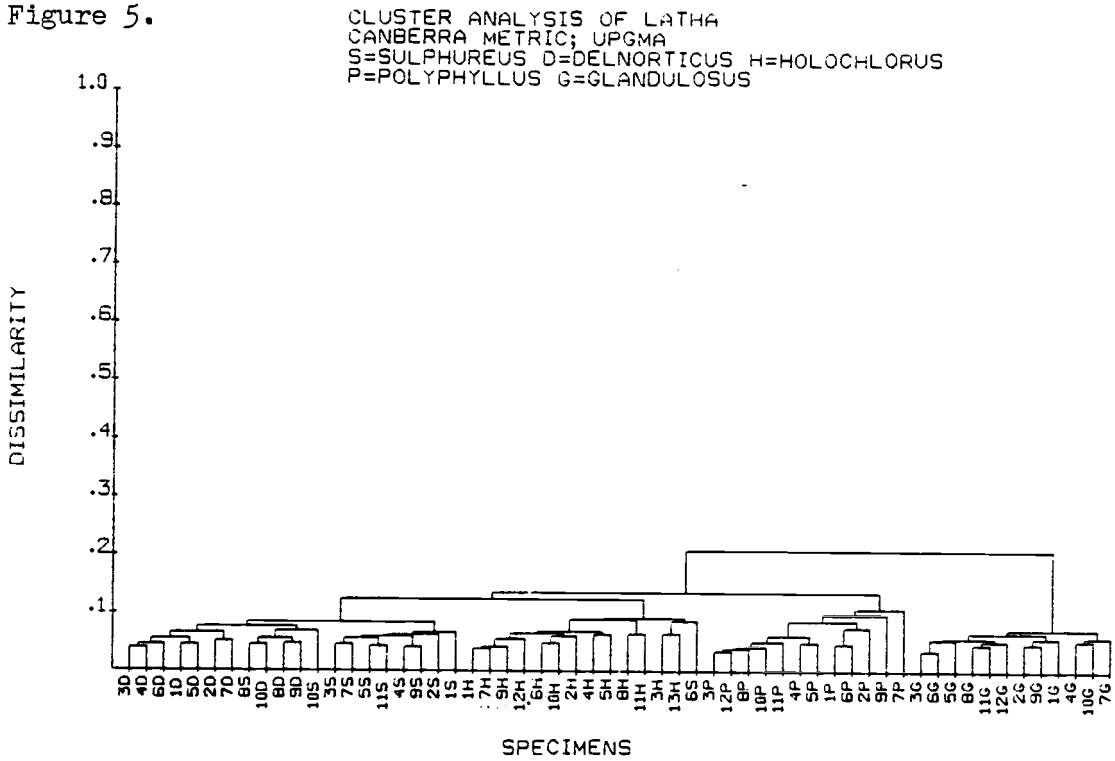


Figure 6.

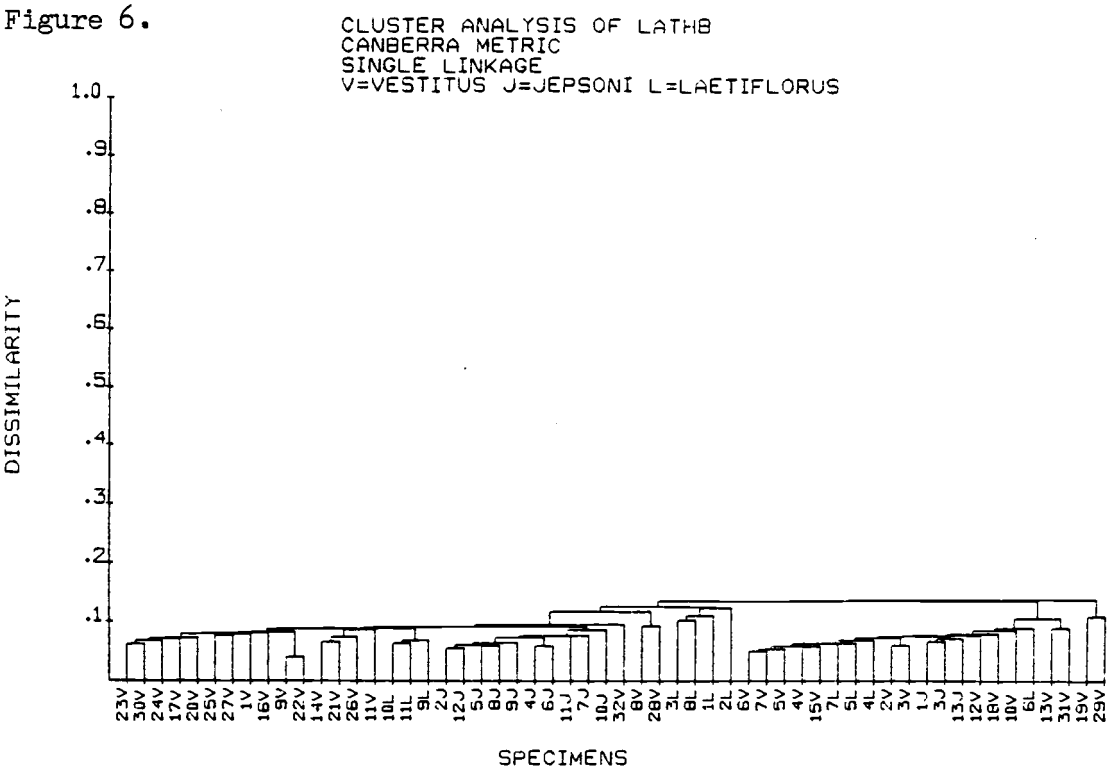


Figure 7.

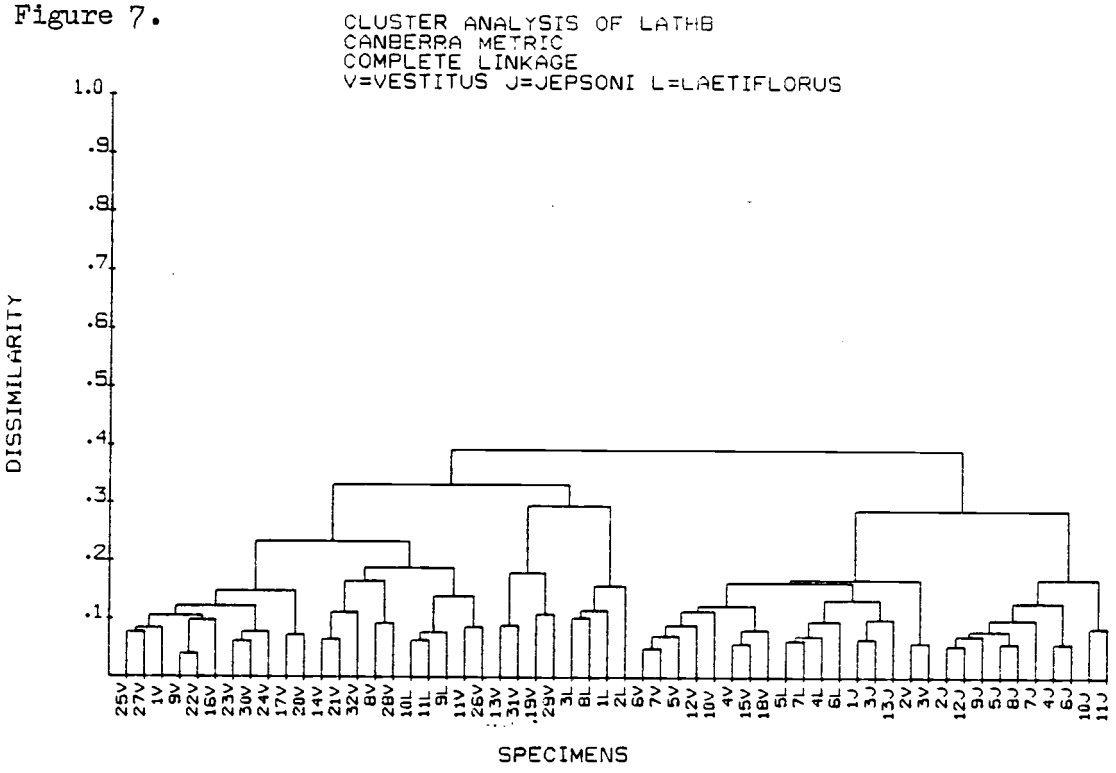
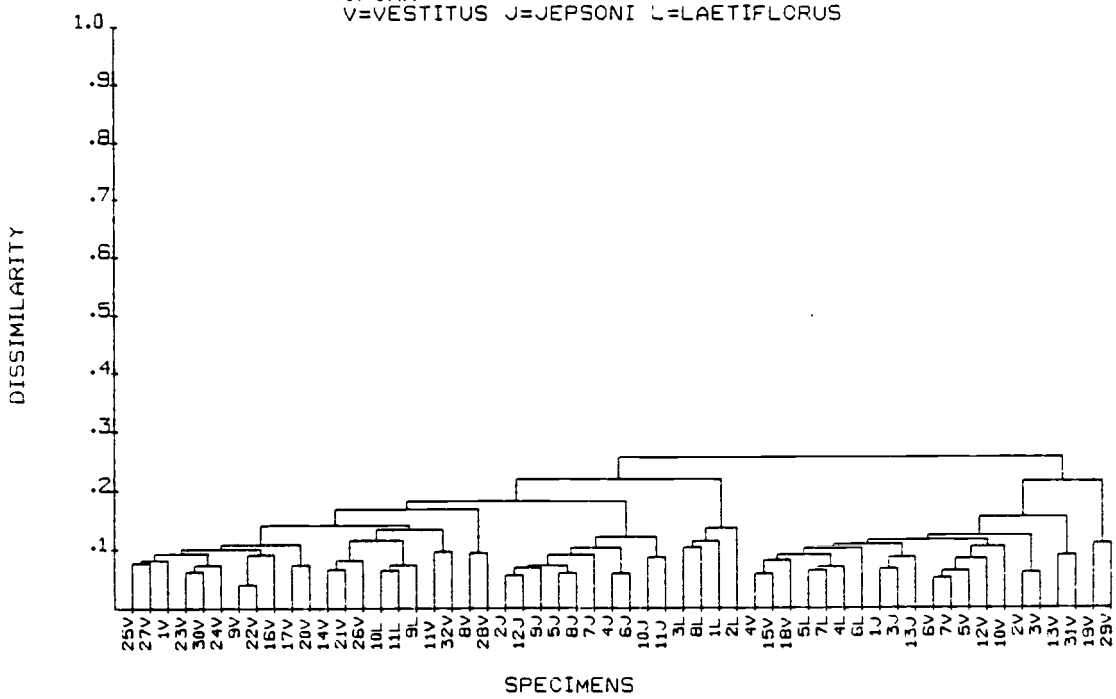


Figure 8.



Figures 6-8 display dendrograms of the analyses of LATHB. At first glance, the relationships among these three species appear complex. There are no cases, however, of cross-species matches in the initial pairs formed. In general, small groups of intraspecific clusters were formed and then united into heterogeneous mixtures. Ten specimens of L. jepsonii (2J-12J) consistently clustered into a single unit. The remaining three specimens of jepsonii (1J, 3J and 13J) consistently clustered together and then joined to a heterogeneous mixture of glabrous L. laetiflorus (4L-7L) and glabrous L. vestitus (4V-7V, 10V, 12V, 15V and 18V). Four specimens of laetiflorus (1L-3L and 8L) consistently clustered together and then were joined at a fairly high disimilarity (ca. 0.2 in the UPGMA dengrogram; ca. 0.3 in the complete linkage analysis) to a large cluster consisting of pubescent L. laetiflorus (9L-11L) and the remaining (pubescent) vestitus (1V, 8V, 16V, 17V, 20V-32V). It appears that pubescent traits played an important role throughout these analyses.

The overall conclusion of the cluster analyses is that seven phenotypic entities corresponding to species delineated by Hitchcock (1952) exist in LATH. One additional undescribed phenotype is also present.

Discriminant Analysis of LATH

"Discriminant analysis" is actually a generic term used to cover a collection of statistical procedures (Pimentel 1979). The stepwise discriminant analysis program BMDP7M provides (1) a univariate analysis of each trait, (2) a "stepped" selection procedure which selects variables on the basis of their "discrimination power", (3) a multivariate analysis of variance at each step to test for significant differences among group mean vectors, (4) a direct and jackknifed classification of all individuals, (5) the jackknifed Mahalanobis D^2 distance of each case from all group mean vectors and the a posteriori probability of the membership of each case to each group and (6) the ordination of all cases in the first two dimensions of canonical space. The information provided by the program can also be used to calculate the Mahalanobis D^2 distance between group mean vectors.

Given the nature of data in LATH and the assumptions underlying multivariate analysis of variance (Pimentel 1979), probabilistic interpretations given by the program were accepted cautiously. Discriminant analysis was used here as a set of "indication procedures" (Tukey 1962) rather than a hypothesis testing procedure.

Table 2 displays means and standard deviations for each trait within each group. Table 3 lists the initial F-values (variance among groups/variance within groups) for each trait. The stepwise algorithm admits traits into the model one at a time on the basis of the greatest F-ratio, recalculates all F-ratios with the error remaining in the current model and then selects the next trait on the basis of the recalculated F-values. If two traits are highly correlated, one will be admitted to the model while the F-ratio of the other trait will drop to non-significance. BMDP7M is iterative until F-ratios of all unselected traits are less than 4.00.

Traits selected in the stepwise discriminant analysis of LATH are indicated in Table 3. Traits which showed the highest power of discrimination among these taxa were stem wingedness, ovary style length, presence or absence of glandular pubescence on the ovary, flower density, calyx lateral lobe shape and number of lateral branches. The direct classification rate (i.e. classifications made with functions calculated with data from all specimens) was 99.1%. The jackknifed classification rate, where each individual is removed from the analysis and then classified by functions calculated with the remaining specimen data, was 96.5%.

Diagonal elements in Table 4 are the mean D^2 distances of each specimen from the mean vector of the species to which it is assigned. This number gives a relative estimate of variability within each taxon based on the traits selected by the program. L. laetiflorus (40.6) and L. vestitus (28.5) are the most variable entities within LATH. L. jepsonii (18.1) and L. holochlorus (17.4) are a distant third and fourth; the remaining taxa are internally much more homogeneous.

Off-diagonal elements of Table 4 are D^2 distances between pairs

Table 2. Means and standard deviations for all metric traits for the taxa in LATH.

TRAIT	VESTITUS $\bar{X}$	VESTITUS s	LAETIFLORUS $\bar{X}$	LAETIFLORUS s	JEPSONII $\bar{X}$	JEPSONII s	POLYPHYLLUS $\bar{X}$	POLYPHYLLUS s
INTL (cm)	5.1	2.1	6.0	1.6	5.9	1.7	5.0	1.3
RACL (cm)	8.4	2.6	7.5	1.3	10.4	2.1	14.4	2.5
INFL (cm)	11.5	3.8	13.0	4.7	13.4	3.1	11.8	2.1
KBLH (mm)	8.2	0.8	10.6	1.0	9.4	1.0	7.1	0.4
KTOT (mm)	12.9	1.1	14.4	1.9	13.0	1.5	11.9	0.5
OVYL (mm)	11.3	1.3	13.0	1.9	12.3	1.2	11.4	0.6
LVLW (cm)	3.4	1.8	4.2	4.5	3.5	0.9	2.3	0.6
NOLV	10.2	1.6	9.3	1.2	10.7	1.1	12.6	1.3
NOFL	12.1	3.7	8.7	1.1	11.6	2.7	9.7	1.4
FLWL (mm)	15.0	1.1	16.8	2.1	15.9	1.1	15.9	1.0
LVTL (cm)	3.1	0.8	3.0	0.4	4.1	0.6	4.0	0.9
LVTW (cm)	1.1	0.6	1.1	0.5	1.2	0.3	1.8	0.6
LVTD	1.3	0.5	1.3	0.3	1.1	0.2	0.9	0.1
FLWD	2.7	1.0	1.7	0.5	2.3	0.5	0.7	0.7
CTBL (mm)	4.1	0.5	4.3	0.4	4.5	0.5	0.5	0.5
CLLL (mm)	5.1	1.2	3.4	0.6	3.6	1.1	0.6	0.6
CLLW (mm)	1.7	0.4	1.4	0.3	1.4	0.3	0.3	0.3
CKLL (mm)	5.6	1.5	4.2	0.9	4.2	1.6	0.8	0.8
CBLL (mm)	1.4	0.6	1.3	0.4	0.9	0.3	0.4	0.4
BCLL (mm)	0.9	0.1	0.9	0.1	0.9	0.1	1.0	0.0
BBLL (mm)	1.0	0.1	1.4	0.2	1.1	0.2	1.0	0.0
KCLL (mm)	6.8	0.6	5.9	0.9	7.1	0.7	7.5	0.6
KREX (mm)	1.0	0.7	1.0	0.8	2.1	1.0	0.3	0.4
OSTL (mm)	5.9	0.7	7.9	1.0	7.4	0.5	4.8	0.2
CLLS	1.9	0.4	0.4	0.5	0.7	0.9	0.3	0.6
STEM	0.9	0.9	1.0	0.0	2.0	0.0	1.0	0.0
NLBR	0.3	0.3	0.4	1.4	3.6	3.6	0.1	3.6
n	32		11		13		12	

Table 2 continued

TRAIT	SULPHUREUS $\bar{X}$	SULPHUREUS s	DELNORTICUS $\bar{X}$	DELNORTICUS s	HOLOCHLORUS $\bar{X}$	HOLOCHLORUS s	GLANDULOSUS $\bar{X}$	GLANDULOSUS s
INTL (cm)	5.9	1.6	5.7	1.3	4.8	0.8	6.1	1.1
RACL (cm)	10.6	1.7	10.7	2.1	8.1	1.3	15.3	1.9
INFL (cm)	10.9	3.3	8.9	0.9	8.0	2.1	14.8	3.8
KBLH (mm)	5.5	0.5	5.8	0.5	7.4	0.8	6.4	0.4
KTOT (mm)	10.1	1.0	9.2	0.7	11.2	0.9	9.6	0.8
OVYL (mm)	9.5	0.8	8.0	0.7	10.2	1.2	7.7	1.2
LVLW	2.4	0.8	3.5	0.8	2.0	0.3	3.1	0.6
NOLV	9.1	0.9	11.1	1.3	8.8	0.8	15.1	2.0
NOFL	12.9	3.4	10.2	1.5	10.5	2.3	8.9	1.6
FLWL (mm)	11.9	0.7	10.9	1.1	13.1	0.8	11.7	1.1
LVTL (cm)	3.7	0.7	3.7	0.5	3.4	0.5	4.4	0.5
LVTW (cm)	1.5	0.4	1.1	0.2	1.7	0.4	1.4	0.3
LVTD	0.9	0.1	1.0	0.2	1.1	0.2	1.0	0.1
FLWD	3.5	0.5	3.8	0.6	5.0	1.0	1.4	0.4
CTBL (mm)	3.9	0.4	3.7	0.4	3.8	0.3	3.5	0.3
CLLL (mm)	3.4	0.9	4.0	0.8	3.3	0.7	4.0	0.7
CLLW (mm)	0.9	0.2	1.0	0.2	1.3	0.3	1.0	0.2
CKLL (mm)	4.7	0.7	5.1	1.1	4.0	0.8	4.6	1.1
CBLL (mm)	0.7	0.1	1.2	0.3	1.7	0.5	1.6	0.4
BCLL (mm)	0.8	0.1	0.7	0.1	0.8	0.1	0.8	0.1
BBLL (mm)	0.5	0.0	0.7	0.1	0.8	0.1	0.8	0.1
KCLL (mm)	6.7	0.4	5.4	0.5	7.2	0.8	5.9	0.6
KREX (mm)	2.4	0.4	1.7	0.3	1.9	0.7	1.7	0.5
OSTL (mm)	4.2	0.4	4.1	0.4	5.1	0.5	4.5	0.3
CLLS	2.0	0.0	1.5	0.5	0.8	0.9	0.8	0.4
STEM	1.0	0.0	2.0	0.0	1.0	0.0	2.0	0.0
NLBR	0.1	3.3	0.0	.0.	2.5	0.4	0.0	0.0
n	11		10		13		12	

Table 3. Initial F values and the traits selected in the stepwise discriminant analysis of LATH, LATHA (without L. glandulosus) and LATHB.

	ANALYSIS OF LATH		ANALYSIS OF LATHA		ANALYSIS OF LATHB	
TRAIT	INITIAL F	TRAITS SELECTED	INITIAL F	TRAITS SELECTED	INITIAL F	TRAITS SELECTED
INTL	1.35		1.92		1.22	
RACL	24.11		21.09		5.36	
INFL	5.60		6.68		1.43	
KBLH	69.06	X	30.08	X	32.48	X
KTOT	35.11		42.74		5.61	
OVYL	29.59		26.38		6.52	
LVLW	2.11		10.51		0.41	
NOLV	29.43	X	36.06	X	3.10	
NOFL	4.35		4.33		4.84	
FLWL	44.47		66.22		7.68	
LVTL	7.40		2.06		10.52	
LVTW	5.25		4.93		0.36	
LVTD	5.49		5.50		2.30	X
FLWD	31.74	X	28.61	X	6.04	
CTBL	14.06		22.86		3.40	
CLLL	9.83		1.90		14.14	
CLLW	14.86	X	10.51		4.62	
CKLL	4.38		3.40		6.89	
CBLL	8.11		14.20		7.03	
BCLL	13.70		29.57	X	0.43	
BBLL	51.02		71.12	X	28.88	
KCLL	14.45	X	24.44		3.86	
KREX	15.41	X	40.03	X	9.37	
OSTL	72.91	X	14.38		39.71	
CLLS	19.48	X	15.24		35.41	X
ADPC	12.71	x	0.00		3.16	
ADPG	0.00		0.00		0.00	
ABPC	13.07		0.00		0.92	
ABPG	0.00		0.00		0.00	
CAPC	13.96	x	0.00		0.83	
CAPG	16.04	x	0.00		1.84	
OVPC	11.83		0.00		6.04	
OVPG	28.42	x	0.00		14.60	
STEM	118.54	X	114.89	X	91.26	X
NLBR	21.98	X	44.17	X	0.90	
	$F^{7}_{107,0.05}=2.12$		$F^{3}_{42,0.05}=2.84$		$F^{2}_{52,0.05}=3.18$	

Table 4. Mean Mahalanobis D^2 values within taxa (diagonal elements) and D^2 distances between taxa from the stepwise discriminant analysis of LATH. Traits used for these calculations are those indicated in Table 3, column 3.

	GLANDULOSUS	POLYPHYLLUS	HOLOCHLORUS	DELNORTICUS	SULPHUREUS	JEPSONII	LAETIFLORUS	VESTITUS
VESTITUS	190.2	57.1	71.3	139.4	84.0	103.1	70.1	28.5
LAETIFLORUS	492.9	136.4	126.0	320.9	296.4	109.8	40.6	
JEPSONII	309.3	156.7	121.8	154.8	225.9	18.1		
SULPHUREUS	331.6	146.6	128.2	179.7	4.2			
DELNORTICUS	173.6	222.6	193.0	5.2				
HOLOCHLORUS	368.7	122.6	17.4					
POLYPHYLLUS	270.8	9.2						
GLANDULOSUS	7.2							

of mean species vectors. The closest species pairs are L. vestitus with L. polyphyllus (57.1), vestitus with L. laetiflorus (70.2) and vestitus with L. holochlorus (71.3). All other species pairs are over 100 D^2 units apart. The closeness of L. vestitus to L. polyphyllus is surprising; at no time in the CLUSB analyses did specimens of these two species cluster together beyond the first few divisions. Since these D^2 values are calculated with a subset of the traits used in the CLUSB analyses of LATH, perhaps the array of species in hyperspace differs somewhat.

The ordination of specimens of LATH in the first two dimensions of discriminant (canonical) space is given in Figure 9. These two axes account for 63.7% of the total variation in the model. Specimens referable to "L. glandulosus" are quite distant from the remaining groups. Taxa which appear to overlap in the first two dimensions are usually well separated in the third and forth dimensions (see caption, Figure 9).

Additional discriminant analyses were run of LATHA (without "L. glandulosus" specimens) and LATHB. Ordinations in discriminant space resulting from these analyses are displayed in Figures 10 and 11, respectively.

Eight traits were selected in the stepwise discriminant analysis of LATHA (see Table 3). The direct classification rate was 100% correct; the jackknifed rate was 97.8%. Specimen 9S appears to be intermediate between L. sulpureus and L. delnorticus but an extensive examination of herbarium collections suggested no intergradation between these two species.

Four traits, indicated in Table 3, were selected in a stepwise discriminant analysis of LATHB. The direct classification rate was 98.2% correct; the jackknifed rate was 96.4%. This ordination (Figure 11) accounts for 100% of the variation in the model (since there were only three groups in the analysis) and suggests that L. laetiflorus and L. vestitus intergrade.

Figure 9. The ordination of specimens in LATH by scores of the first two canonical variables (CV) resulting from stepwise discriminant analysis.

Symbol	Species	group means CV1	CV2	CV3
D	delnorticus	-5.4	-2.3	-2.4
G	glandulosus	-9.2	1.2	2.8
H	holochlorus	2.2	-1.7	-3.3
J	jepsonii	0.4	-5.7	1.3
L	laetiflorus	4.6	-2.7	2.0
P	polyphyllus	0.8	1.2	0.6
S	sulphureus	-0.9	2.5	-5.2
V	vestitus	2.5	2.9	1.3
cumulative % of variance		41.7%	63.7%	80.3%

functions for the canonical variables

CV1 = -5.59 + (0.66)(KBLH) - (0.17)(NOLV) + (0.32)(FLWD) + (0.69)(CLLW) + (0.56)(KCLL) - (0.59)(KREX) + (0.42)(OSTL) + (0.33)(CLLS) - (0.96)(ADPC) + (3.12)(CAPC) - (0.70)(CAPG) - (2.31)(OVPG) - (3.92)(STEM) + (0.22)(NLBR)

CV2 = 13.27 - (0.5)(KBLH) - (0.18)(NOLV) - (0.65)(FLWD) + (0.47)(CLLW) + (0.20)(KCLL) - (0.95)(KREX) - (0.62)(OSTL) + (0.50)(CLLS) + (3.10)(ADPC) - (4.04)(CAPC) + (0.85)(CAPG) + (2.57)(OVPG) - (3.88)(STEM) - (0.68)(NLBR)

Figure 9.

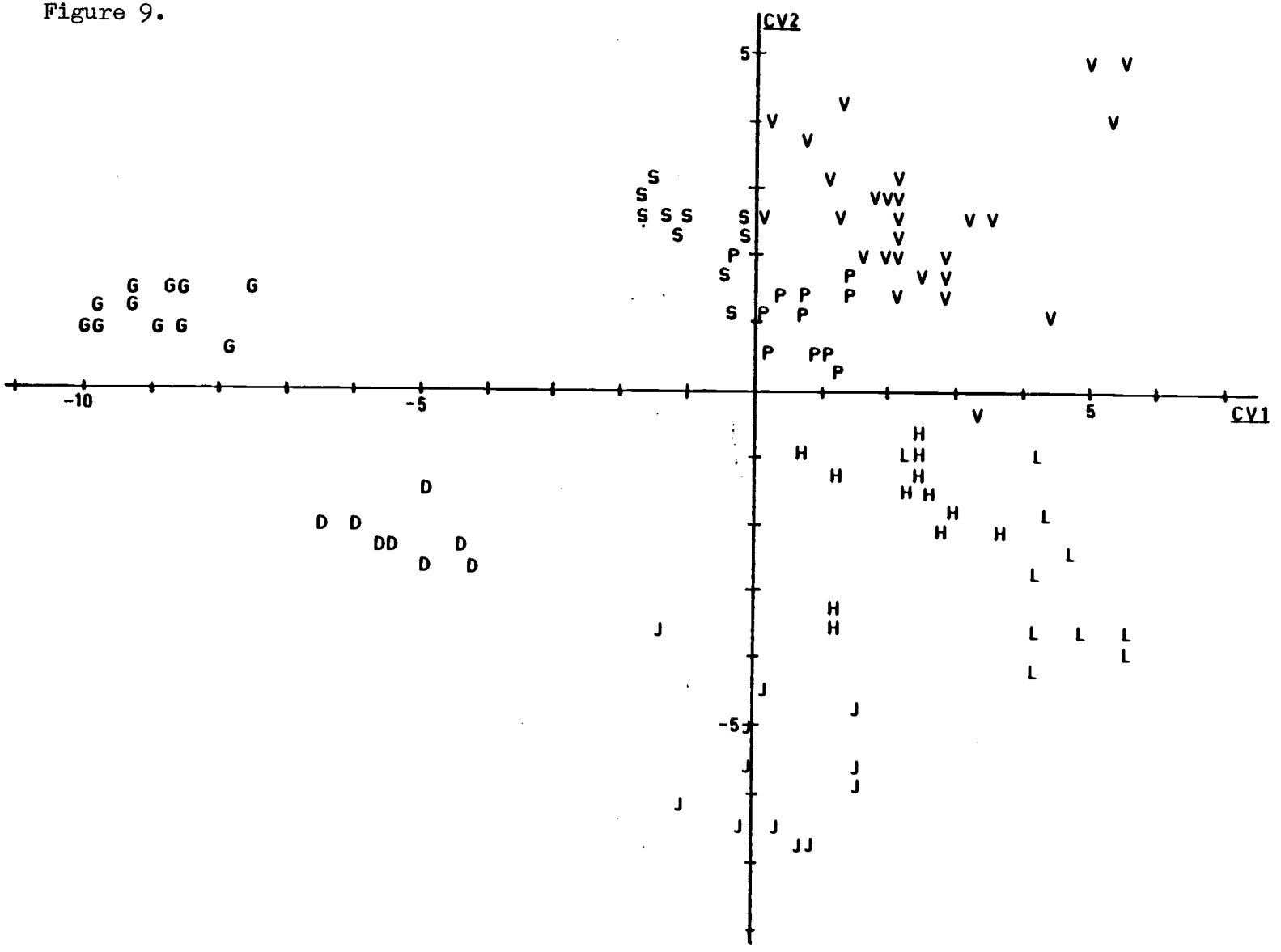


Figure 10. Ordination of specimens of LATHA (minus those of L. glandulosus) by scores of the first two canonical variables (CV) resulting from stepwise discriminant analysis.

symbol	species	group means CV1	CV2	CV3
D	delnorticus	6.7	-1.8	-2.4
H	holochlorus	-4.0	2.1	-3.3
P	polyphyllus	-2.5	-5.1	2.3
S	sulphureus	1.4	4.8	3.6
cumulative % of variance		41.3%	77.8%	100.0%

functions for the canonical variables

CV1 = 6.18 - (1.0)(KBLH) + (0.01)(NOLV) - (0.41)(FLWD) - (5.5)(BCLL) - (1.44)(BBLL) + (0.42)(KREX) + (5.83) (STEM) + (0.22)(NLBR)

CV2 = 9.93 - (0.19)(KBLH) - (0.56)(NOLV) = (0.08)(FLWD) + (4.72)(BCLL) - (10.00)(BBLL) + (1.83)(KREX) - (1.91) (STEM) + (0.22)(NLBR)

Figure 11. Ordination of specimens of LATHB by scores of the first two canonical variablies (CV) resulting from stepwise discriminant analysis.

symbol	species	group means CV1	CV2
J	jepsonii	-3.9	0.9
L	laetiflorus	-0.5	-2.6
V	vestitus	1.8	0.5
cumulative % of variance		75.8%	100.0%

functions for the canonical variables

CV1 = 6.44 - (0.21)(KBLH) - (0.88)(LVTD) + (0.92)(CLLS) - (4.02)(STEM)

CV2 = 2.32 - (0.87)(KBLH) + (1.12)(LVTD) + (0.89)(CLLS) + (2.49)(STEM)

Figure 10.

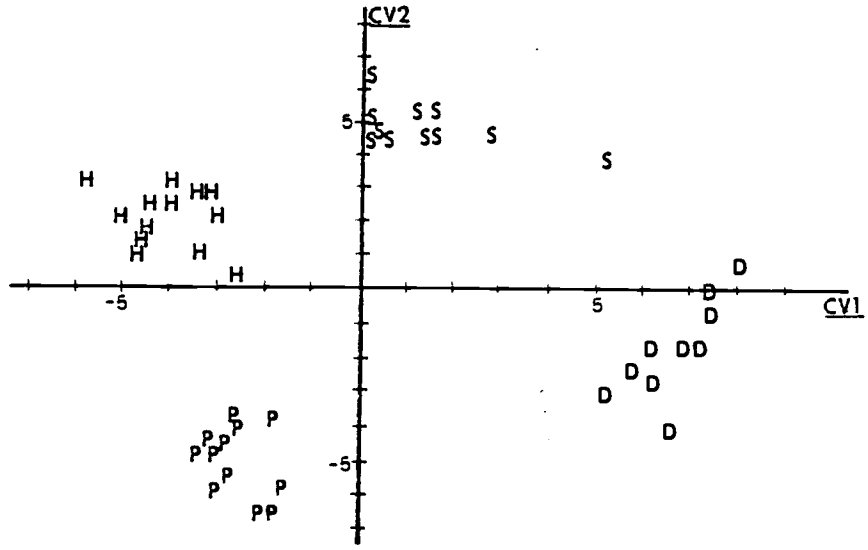
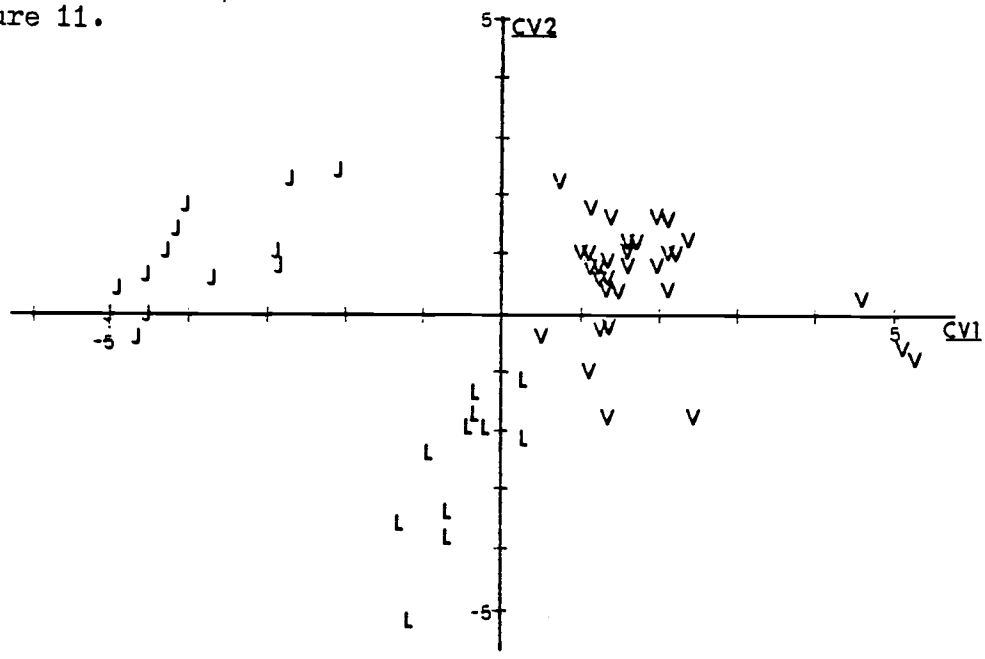


Figure 11.



Analysis of LATHTWO

On the basis of the discriminant analysis of LATHB, the high variability within L. laetiflorus in comparison the the number of specimens examined (n=11, in LATH) and a subsequent reexamination of herbarium specimens, intergradation between L. vestitus and L. laetiflorus appeared to be extensive and required more careful examination. The matrix LATHTWO was assembled for this study.

A CLUSB analysis of data in LATHTWO suggested that five somewhat distinct geographical groups exist in this complex. From north to south these groups consist of (1) glabrous, relatively small flowered specimens from Oregon and Coastal California, (2) pubescent, relatively small flowered specimens from the coastal mountains of Mendocino and Lake Counties to Santa Barbara County, California, (3) glabrous specimens with medium sized flowers from Ventura and western Los Angeles Counties, California, (4) pubescent specimens with medium sized flowers from eastern Los Angeles County and the San Bernardino Mountains and (5) mostly glabrous large flowered specimens from areas south of San Bernardino County, California. Groups (1) and (2) are referable to L. vestitus; groups (3), (4) and (5) are referable to L. laetiflorus.

A stepwise discriminant analysis was performed on the groups determined in the CLUSB analysis; resulting data are contained in Table 5. Twelve traits were selected by the program: leaflet length, leaflet width, flower length, style length, lateral calyx lobe width, lateral calyx lobe shape, adaxial leaflet surface pubescence, calyx pubescence (both curly and glandular) and banner blade reflex. The direct classification rate was 96% correct, the jackknifed classification rate was 93% correct.

Variation within these groups (diagonal elements, Table 6) is rather uniform. Group (4) is the most variable while group (2) which contained the most specimens and covers the greatest geographical area, is least variable. D^2 distances between pairs of groups (off-diagonal elements, Table 6) are positively correlated, for the most part, with geographic distance with the exception of the

Table 5. Means and standard deviations for the groups hypothesized to exist in LATHTWO.

TRAIT	(1) BOLANDERI $\bar{X}$	s	(2) VESTITUS $\bar{X}$	s	(3) LAEVICARPUS $\bar{X}$	s	(4) BARBARAE $\bar{X}$	s	(5) ALEFELDII $\bar{X}$	s
LVTL (cm)	35.0	8.1	26.7	5.5	29.7	5.0	31.8	9.5	27.5	5.1
LVTW (cm)	13.5	5.6	9.8	3.5	10.5	3.4	8.9	3.9	11.6	4.5
NOLV	9.4	1.5	10.0	1.3	9.1	1.1	8.7	0.8	8.4	1.2
FLWL (mm)	14.7	1.0	15.2	0.9	15.8	0.8	15.8	1.2	18.5	1.4
BCLL (mm)	8.9	1.0	8.6	0.8	8.4	0.8	8.2	0.7	8.1	0.6
BBLL (mm)	9.7	0.9	9.6	1.0	10.8	1.0	11.4	1.9	13.2	1.6
KBLL (mm)	7.3	1.0	8.0	0.6	8.2	0.8	8.9	0.9	10.9	1.4
KBLH (mm)	8.1	0.8	8.8	0.8	9.9	0.9	10.6	1.0	12.2	1.2
OSTL (mm)	5.8	0.6	6.3	0.8	7.3	0.8	8.3	0.6	9.0	0.6
CTBL (mm)	4.3	0.6	4.2	0.5	4.2	0.6	4.5	0.5	4.5	0.5
CLLL (mm)	5.6	0.8	4.5	0.9	3.9	0.6	3.7	0.7	3.2	0.8
CLLW (mm)	2.0	0.0	1.8	0.4	1.5	0.5	1.4	0.5	1.6	0.5
KREX (mm)	1.2	0.9	1.4	0.7	1.3	0.7	1.4	0.7	1.5	1.2
CLLS	2.0	0.0	1.9	0.3	1.3	0.8	0.5	0.6	0.2	0.5
ADPC	0.1	0.4	1.7	0.6	0.1	0.2	0.9	0.9	0.1	0.3
ABPC	0.2	0.4	1.8	0.4	0.2	0.4	1.2	0.8	0.7	0.7
CAPC	0.1	0.3	1.4	0.6	0.9	0.3	1.2	0.5	1.3	0.6
CAPG	0.1	0.3	0.3	0.4	0.0	0.0	0.1	0.3	0.2	0.4
OVPC	0.3	0.6	1.7	0.6	0.1	0.3	1.7	0.5	0.4	0.6
OVPG	1.3	0.8	1.9	0.3	0.4	0.7	1.3	0.9	1.2	0.9
PEDL (mm)	3.8	0.7	4.6	0.8	1.3	1.3	6.1	1.4	7.4	1.4
BREX	1.0	0.0	1.0	0.0	0.4	0.4	1.2	0.4	1.9	0.3
n	21		67		33		31		48	

Table 6. Mean Mahalanobis D^2 values within taxa (diagonal elements) and D^2 distances between taxa derived from the stepwise discriminant analysis of LATHTWO. Traits used to calculate these data include LVTL, LVTW, FLWL, OSTL, CLLW, CLLS, ADPC, CAPC, OVPC, OVPG AND BREX.

	ALEFELDII	BARBARAE	LAEVICARPUS	VESTITUS	BOLANDERI
BOLANDERI	70.0	23.5	17.6	46.7	11.4
VESTITUS	59.6	22.4	31.3	10.0	
LAEVICARPUS	31.4	22.4	12.8		
BARBARAE	28.4	18.8			
ALEFELDII	14.1				

apparent phenetic relationships between groups (1) and (3). The close relationships between these two groups is probably due to the great similarity in pubescence traits.

Figure 12 displays the ordination of these five groups in the first two dimensions of canonical space. The first axis appears to be related to flower size and shape with flower size increasing from left to right. The second axis is primarily related to pubescence differences; glabrous plants received more negative scores.

An additional discriminant analysis of LATHTWO, including data for 12 specimens of L. splendens was run. Lathyrus splendens is a species endemic to southern San Diego County, California, and is seemingly related to southern forms of L. laetiflorus. The ordination in canonical space, displayed in Figure 13, adequately summarizes the results of this analysis. Even when large flowered specimens of group (5) (L. laetiflorus ssp. alefeldii) are treated as a separate entity, they remain clustered with specimens of the L. vestitus/laetiflorus complex and quite distinct from specimens of L. splendens.

Variation within the L. vestitus/laetiflorus complex could also be considered clinal. Flower size appears to increase and flower shape changes from north to south; pubescence density appears to increase from north to south and inland from the coast. Cluster analysis "assumes" discrete groups exist and proceeds to arrange specimens into clusters regardless of validity (Pimentel 1979). An alternative approach to the analysis of variation in LATHTWO is ordination by Principal Components; the numerical results of such an analysis on the correlation matrix derived from LATHTWO are given in Table 7.

The first principal component accounts for 31.8% of the variation in LATHTWO. It is clearly related to size and shape of flowers. This component contains 77.3% of the variance in keel blade height, 76.9% of the variance in ovary style length, 66.9% of the variance in calyx lateral lobe length and 65.2% of the variance in flower length. The data indicate that size of flowers is inversely related to the shape of the lateral calyx lobe.

Figure 12. Ordination of specimens in LATHTWO by scores of the first two canonical variables (CV) resulting from stepwise discriminant analysis. Stars indicate specimens found to have less than 70% stainable pollen.

group	symbol	taxon	group means CV1	CV2	CV3
(1)	♦	ssp. bolanderi	-2.5	-3.2	0.6
(2)	□	ssp. vestitus	-3.0	1.2	0.6
(3)	△	ssp. laevicarpus	0.6	-2.6	-0.9
(4)	●	ssp. barbarae	0.6	1.5	-2.2
(5)	○	ssp. alefeldii	4.5	0.5	0.9
cumulative % of variance			65.2%	88.7%	97.9%

functions for canonical variables

CV1 = -7.59 - (0.02)(LVTL) - (0.02)(LVTW) + (0.42)(FLWL) - (0.28)(BCLL) + (0.63)(OSTL) - (0.26)(CLLW) - (0.87)(CLLS) - (0.67)(ADPC) + 0.01)(CAPC) - (0.36)(OVPC) - (0.04)(OVPG) + (1.40)(BREX)

CV2 = -2.39 - (0.02)(LVTL) - (0.06)(LVTW) + (0.30)(FLWL) - (0.45)(BCLL) + (0.10)(OSTL) - (0.24)(CLLW) - (0.44)(CLLS) + (0.68)(ADPC) + (0.88)(CAPC) + (0.86)(OVPC) + (0.48)(OVPG) - (0.20)(BREX)

Figure 12.

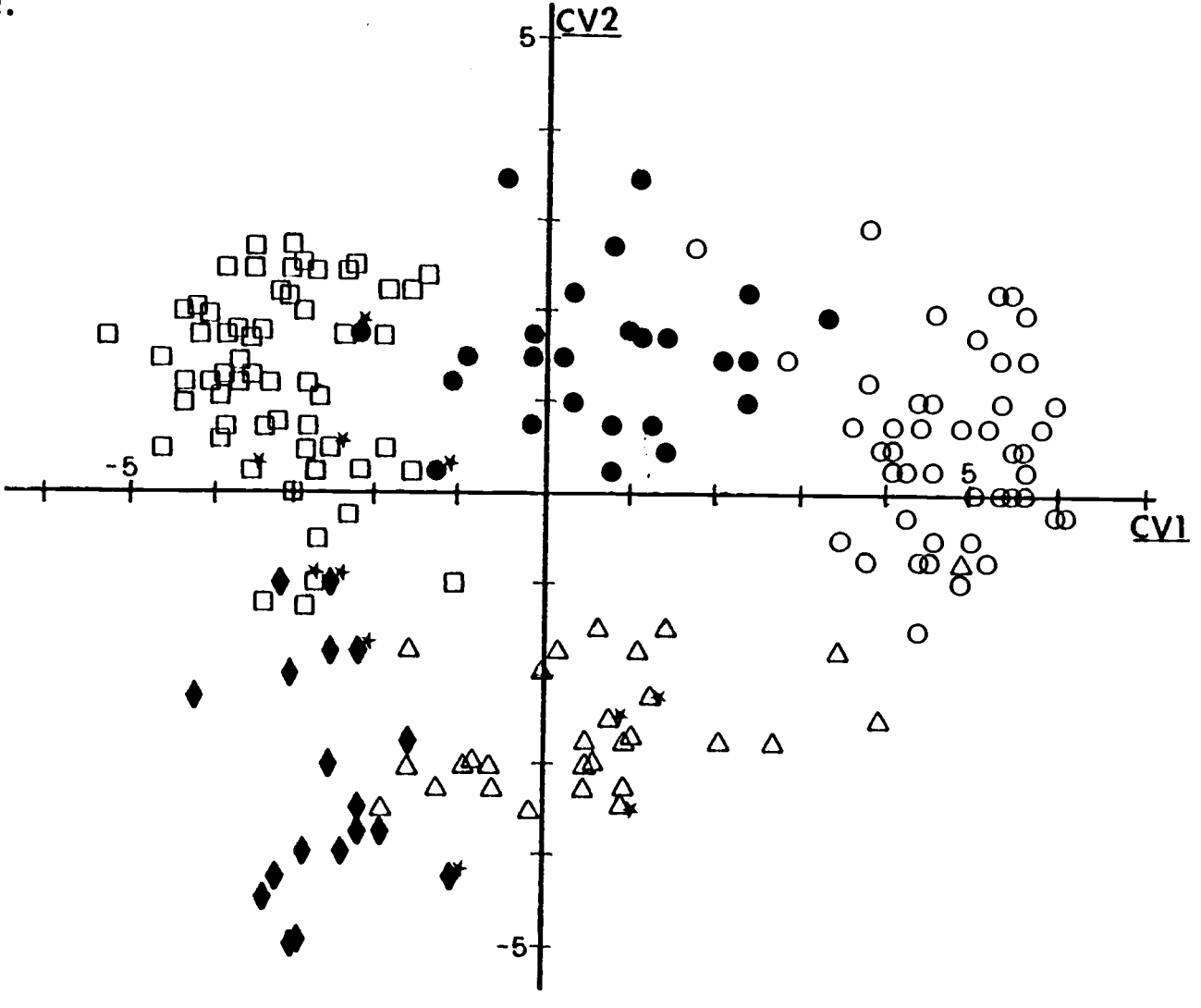


Figure 13. Ordination of specimens in LATHTWO and an additional 12 specimens of L. splendens by scores of the first two canonical cariables (CV) resulting from stepwise discriminant analysis.

group	symbol	taxon	group means CV1	CV2	CV3
(1)	♦	ssp. bolanderi	2.8	2.4	-1.4
(2)	□	ssp. vestitus	3.6	-1.7	-0.3
(3)	△	ssp. laevicarpus	0.4	2.6	-0.8
(4)	●	ssp. barbarae	0.5	-0.9	0.5
(5)	○	ssp. alefeldii	-3.4	0.5	1.9
	⌂	L. splendens	-13.3	-2.0	-2.9
cumulative % of variance			74.7%	87.3%	94.3%

CV1 = 11.83 + (0.02)(LVTL) - (0.14)(FLWL) - (0.24)(BBLL) - (0.30)(KBLL) - (0.61)(OSTL) + (0.07)(CLLL) + (0.44)(CLLS) + (0.52)(ADPC) + (0.14)(CAPC) + (0.47)(OVPC) - (0.10)(OVPG) - (1.03)(BREX)

CV2 = 6.16 + (0.20)(LVTL) - (0.10)(FLWL) - (0.02)(BBLL) - (0.16)(KBLL) - (0.19)(OSTL) + (0.03)(CLLL) - (0.07)(CLLS) - (0.87)(ADPC) - (0.68)(CAPC) - (0.74)(OVPC) - (0.55)(OVPG) + (0.64)(BREX)

Figure 13.

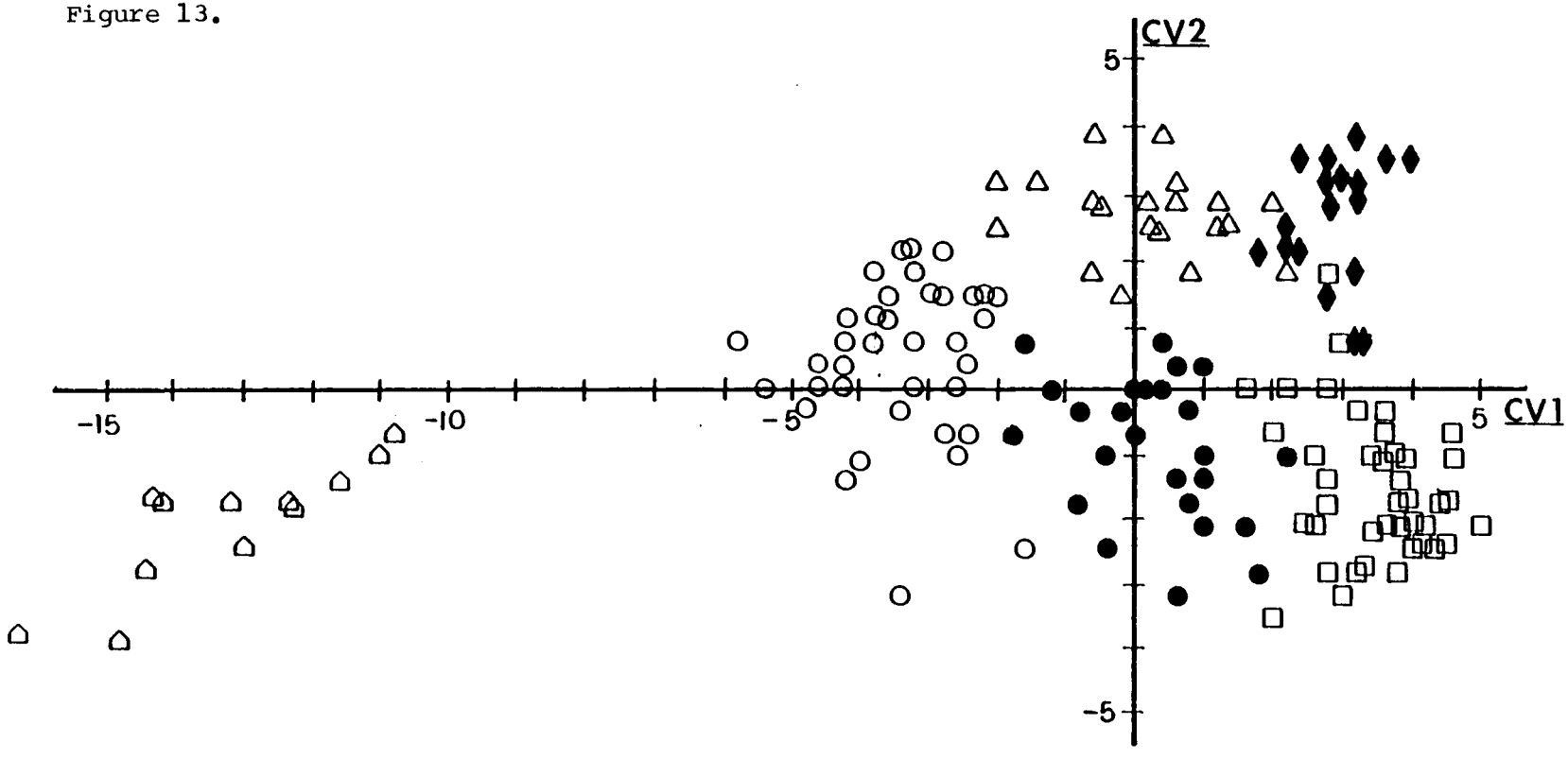


Table 7. Data for the first three eigenvectors resulting from a principal components analysis of the correlation matrix from LATHTWO. Given are the eigenvectors (v), the correlations between the principal component scores and the original scores (r) and the percent variability (%s) of each trait accounted for by the vector.

	VECTOR 1			VECTOR 2			VECTOR 3		
TRAIT	v	r	%s	v	r	%s	v	r	%s
LVTL	-.005	-.014	0.0	-.223	-.386	14.9	.262	.331	11.0
LVTW	-.052	-.139	1.9	-.106	-.184	3.4	.380	.481	23.2
NOLV	.193	.512	26.1	.062	.108	1.2	.149	.189	3.6
FLWL	-.305	-.808	65.2	.082	.143	2.0	.169	.214	4.6
BCLL	.098	.259	6.7	-.027	-.047	0.2	.174	.221	4.8
BBLL	-.296	-.785	61.4	.074	.128	1.6	.093	.118	1.4
KBLL	-.293	-.777	60.2	.149	.259	6.7	.122	.115	2.4
KBLH	-.332	-.878	77.3	.120	.209	4.3	.116	.147	2.2
OSTL	-.328	-.867	75.9	.118	.204	4.2	-.004	-.005	0.0
CTBL	-.084	-.221	5.0	.023	.039	0.2	.485	.614	37.7
CLLL	.230	.609	37.1	-.131	-.227	5.2	.439	.555	30.9
CLLW	.082	.217	4.7	.047	.082	0.7	.321	.406	16.5
KREX	-.050	-.131	1.8	.087	.151	2.3	.307	.388	15.2
CLLS	.309	.818	66.9	-.075	-.131	1.7	.159	.202	4.0
ADPC	.216	.573	32.7	.388	.673	45.2	.043	.055	0.3
ABPC	.152	.403	16.2	.464	.805	64.7	.046	.058	0.3
CAPC	-.033	-.088	0.8	.479	.830	69.0	.070	.089	0.8
CAPG	.045	.119	1.4	.150	.261	6.8	.062	.078	0.6
OVPC	.170	.449	20.3	.394	.682	46.6	-.014	-.017	0.0
OVPG	.146	.388	14.9	.238	.412	17.0	-.070	-.089	0.8
PEDL	-.300	-.793	63.1	.081	.140	2.0	-.010	-.013	0.0
BREX	-.297	-.787	61.8	.047	.082	0.7	-.000	.000	0.0
eigenvalue		7.010			3.005			1.603	
% total variance		31.8%			13.7%			7.3%	
cumulative %		------			45.5%			52.7%	

The second component accounts for 13.7% of the variation in LATHTWO and is dominated by pubescence scores for leaflets, the calyx and the ovary. The third component accounts for 7.3% of the variation in LATHTWO and primarily relates to variability in calyx tube length and lateral calyx lobe length. The remaining 47% of the variation in LATHTWO is distributed rather evenly throughout the remaining 19 components; eigenvector loadings were difficult to interpret.

Figures 14-17 display the geographic distribution of principal component scores (rounded to the nearest whole number and scaled to be greater than 0.0) for individual specimens. The geographic trend in scores for the first principal component (Figures 14-15) relating to flower size and shape is broadly clinal. Small flowered specimens (scores = 7-9) are most often collected in central coastal California; to the south, size and shape change gradually reaching scores of 0-2 (large flowers) in San Diego County. No distinct boundaries appear in this clinal trend.

Geographic variation in scores for the second component (Figures 16 and 17) is more discontinuous. One "boundary" appears to be present in western Ventura County (Figure 17). Specimens collected in the Santa Ynez and San Rafael Mountains are typically pubescent (scores = 4-7) but in the Ojai Valley and to the northeast, most collections are glabrous (scores = 1-3). This corresponds to the traditional boundary between plants referable to L. vestitus (found to the north) and those referable to L. laetiflorus (found to the south) and it becomes apparent that the separation of these two "species" in Santa Barbara, Ventura and Los Angeles Counties depends primarily on presence or absence of pubescence. In other parts of the ranges of both L. vestitus and L. laetiflorus, as well as in L. jepsonii, presence or absence of pubescence is accorded only subspecific importance. Although the extreme phenotypes in the L. vestitus/laetiflorus complex are quite distinct, they can be connected by a series of intermediate forms; this analysis documents the continuous nature of this intergradation.

Figure 14. Geographic distribution of scores of the first principal component in central California.

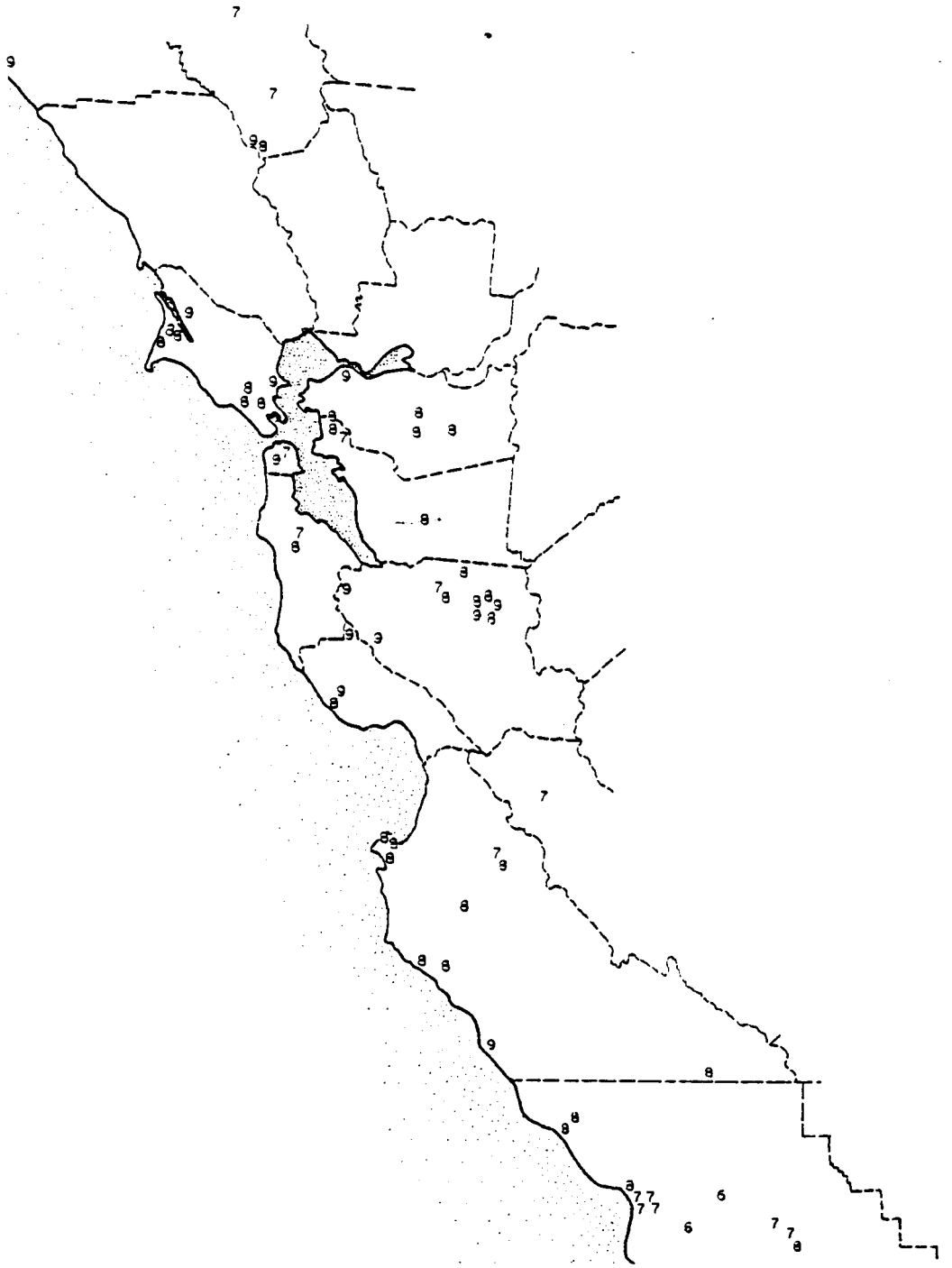


Figure 15. Geographic distribution of scores of the first principal component in southern California.

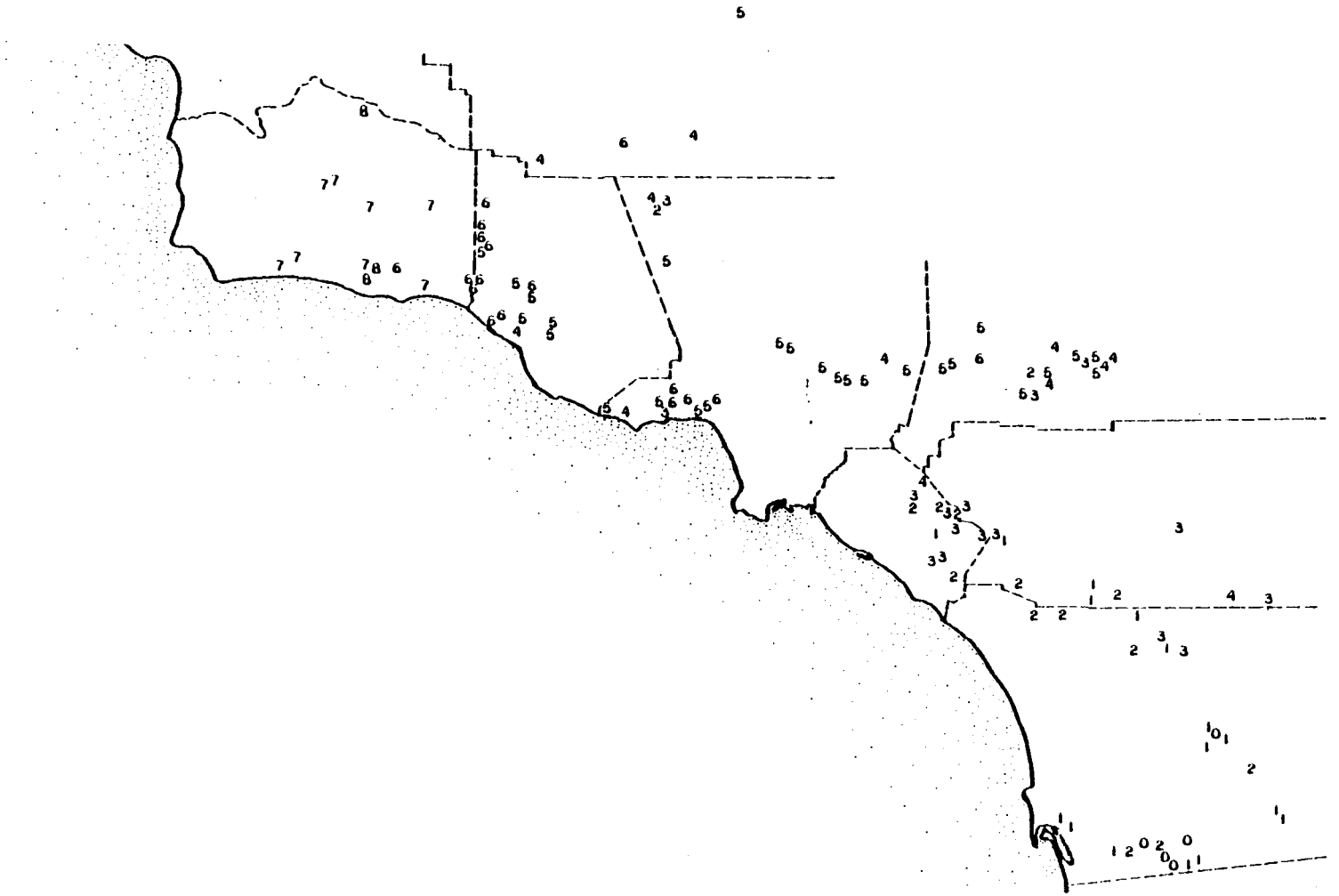


Figure 16. Geographic distribution of scores of the second principal component in central California.

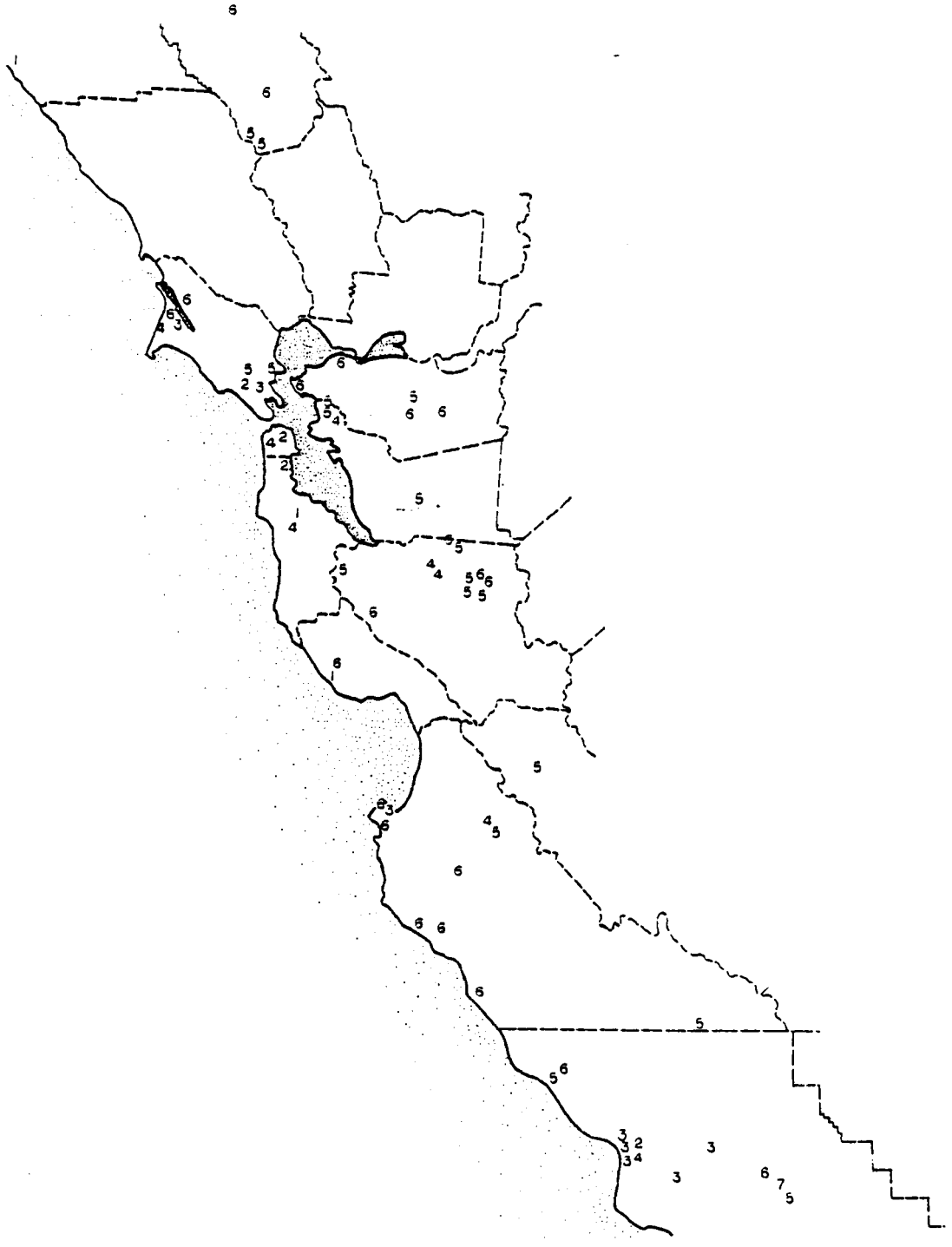
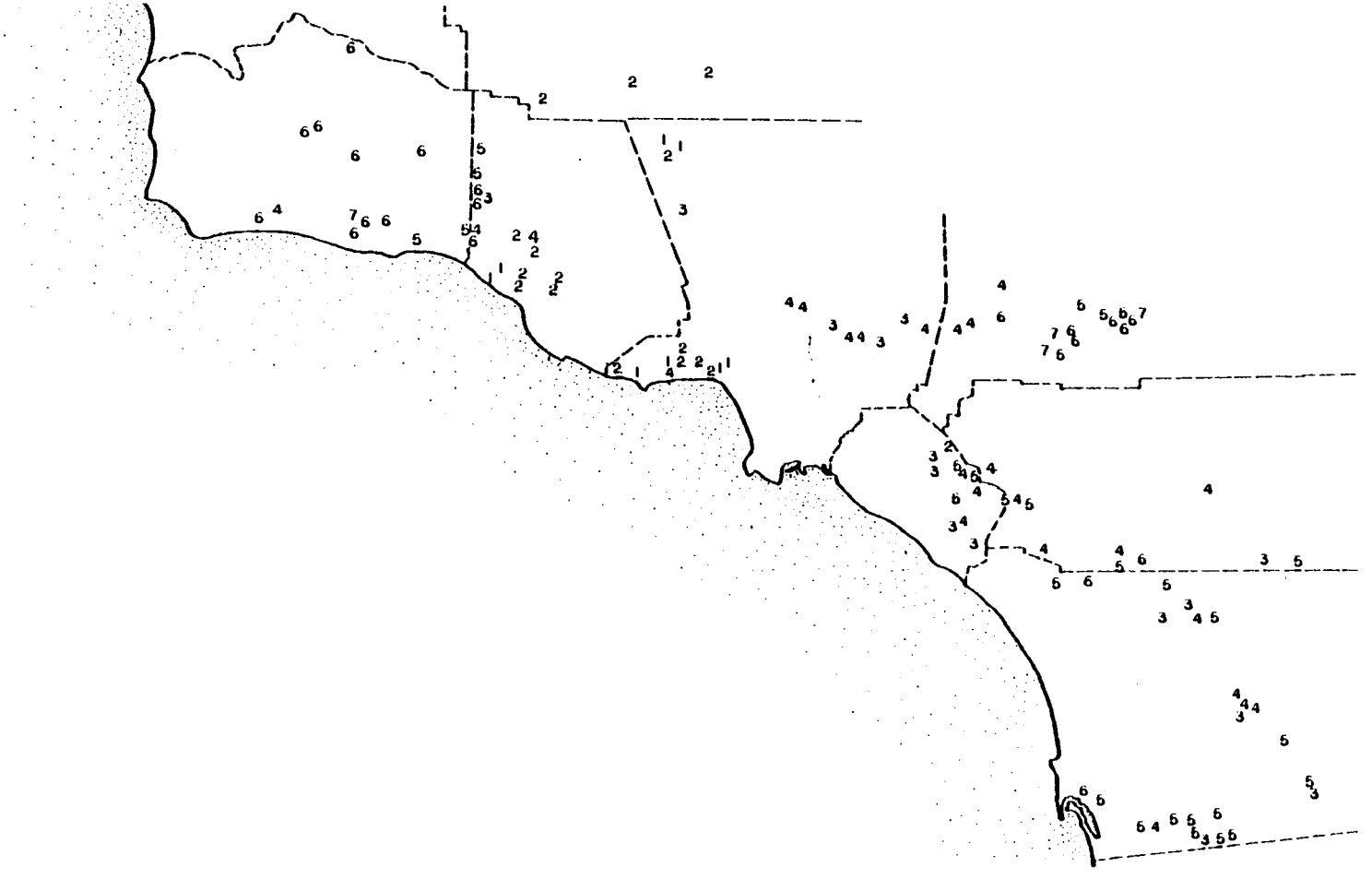


Figure 17. Geographic distribution of scores of the second principal component in southern California



Conclusions from the Taximetric Studies

These phenetic studies suggest that L. holochlorus, L. delnorticus, L. polyphyllus, L. jepsonii, L. sulphureus and L. splendens are morphologically distinct. An undescribed species, herein called L. glandulosus, is also quite distinct morphologically. Specimens referable to L. vestitus and L. laetiflorus display a remarkable amount of morphological variability but intergrade and probably should be treated taxonomically as part of one polymorphic species complex. A nomenclatural revision of this complex as one species will be given in a later section; for the purposes of the following discussion, however, names need to be introduced. The correct names, at the subspecific level, for groups (1) to (5) are: (1) ssp. bolanderi, (2) ssp. vestitus, (3) ssp. laevicarpus, (4) ssp. barbarae and (5) ssp. alefeldii. These names are used in Figures 12 and 13 and in Tables 5 and 6.

Anatomical Studies

Stem Anatomy

The stem anatomy of the Vicieae has been reviewed by Kupicha (1975). Members of the tribe are unique in having two vascular bundles in the cortex of the stem. These bundles typically arise from the main stelic system on opposite sides of a node, pass through the internode within the cortex of the stem and then fuse to the lateral leaf traces. All species of Lathyrus examined here display this type, called "complete replacement" by Kupicha (1975).

In some species there is a proliferation of cortical cells and the concomitant branching of the cortical vascular bundles to form a thin "wing" structure on opposing sides of the stem. Of the species studied here, L. delnorticus, L. glandulosus and L. jepsonii have "winged stems. The "wings" of L. jepsonii are most prominent, often being greater than 2 mm in width. Given the universal presence of cortical vascular bundles in Lathyrus, all species tend to have angular to narrowly "winged" stems. While the presence of winged stems is diagnostic for these three species, it is necessary for a person

to have some experience with the range of variability within both winged and nonwinged species if they are to use this character to full advantage for identification of specimens. At the present time it is impossible to estimate the amount of phenotypic plasticity of stem wingedness. In general, however, specimens of L. jepsonii collected along waterways often seem to be more prominantly winged, while dry conditions may render stem wings narrower.

Leaflet Anatomy

Stomata are common on abaxial leaflet surfaces; stomatal frequency on adaxial surfaces varies from zero to fairly frequent. Leaflets of the same species collected from different habitats exhibited marked differences, those from dryer sites tending to be thicker and more coriacous, and to have fewer adaxial stomata.

Crystals, similar to those pictured by Fahn (1974: Fig. 112, p. 254) were observed in the vascular bundle sheath cells of all species. Apparently these crystals are soluble in the clearing solution used and were found only in rehydrated leaflets mounted directly in Hoyer's medium. Previous studies of Lathyrus leaflets have used epidermal peels, and the presence of these crystals has gone unreported.

Trichome types occuring on leaflet epidermis of Vicieae have been reviewed by Shah and Kothari (1973) and Kupicha (1977). Of the types illustrated by Kupicha (1977) the stalked glandular trichome (her Fig. 5A) and the unicellular trichome (her Fig. 5C) are common on native Lathyrus species at greatly differing densities.

A few glandular trichomes are present somewhere on all species studied; they occur densely on the abaxial leaflet surface and other vegetative surfaces of L. glandulosus, making this species quite distinctive. Glandular trichomes also occur at high densities on the ovaries of L. glandulosus and some forms of L. vestitus.

Hooked or straight unicellular trichomes (herein referred to as "curly" pubescence) are also very sparsely present on at least some surfaces of all species. Dense curly pubescence occurs on leaflets of L. jepsonii ssp. californicus, L. vestitus ssp. vestitus , L. vestitus ssp. barbarae, L. sulphureus var. argillaceus and some

forms of L. vestitus ssp. alefeldii. Of the specimens in LATHTWO, 21% were found to be glabrous on upper leaflet surfaces but pubescent below. This suggests that presence or absence of pubescence on leaflet surfaces is controlled by several genes that can be "unlinked".

Adaxial stomata are absent on all glabrous forms of L. vestitus but are present on leaflets covered with curly pubescence. Adaxial stomata are fairly common on both glabrous and pubescent specimens of L. jepsonii.

Leaflets of L. sulphureus, L. jepsonii and L. delnorticus seem to be unusually impervious to rehydration with boiling water; perhaps this is due to a thicker cuticle than on other species.

Several authors (Senn 1938; Bassler 1973; Simola 1967) consider stomatal frequency and epidermal cell wall shape as taxonomically important in Lathyrus. In the series of four or more leaflets examined from each of the species studied here, epidermal cell morphology and stomatal frequency were both found to be quite variable within species and even within single leaflets, so much so that specific distinctions are difficult to make.

Karyotype Studies

The karyotype may be defined as "the phenotypic appearance of the somatic chromosomes in contrast to their genic content", (Jackson 1971: p. 238). Phenotypic differences among karyotypes can include (1) differences in number, (2) differences in absolute size of chromosomes, (3) differences in centromere position, (4) differences in relative chromosome size and (5) differences in number and(or) position of satellites (Stebbins 1971).

A summary of chromosome counts for Lathyrus endemic to North America is given in Table 8. Of the counts included in this table, those of Cobb (1950) and Sands (unpublished) were summarized by Hitchcock (1952). Hitchcock's report was apparently overlooked by the standard chromosome number compendia and therefore data for most North American species have not been included in the summaries of

Table 8. A summary of literature concerning chromosome counts for species of Lathyrus endemic to North America.

species	n	2n	citation
arizonicus Britt.	14		Cobb (1950)
		28	Sands (unpublished)*1
brachycalyx Rydb.		14	Sands (unpublished)
delnorticus C. L. Hitchcock		14	Sands (unpublished
graminifolius (Wats.) White	7		Cobb (1950)
jepsonii Greene	7		Cobb (1950)
		14	Sands (unpublished)
laetiflorus Greene			
ssp. laetiflorus	7		Raven et al. (1965)
ssp. alefeldii (White) Bradshaw	7		Cobb (1950)
		14	Sands (unpublished)
lanszwertii Kell.			
ssp. lanszwertii	14		Cobb (1950)
ssp. aridus (Piper) Bradshaw	7		Cobb (1950)
		14	Sands (unpublished)
nevadensis (Wats.)			
ssp. lanceolatus (Howell) C. L. Hitchcock	14		Cobb (1950)
		28	Sands (unpublished)
ochroleucus Hook.		14	Senn (1938) Ledingham (1957)
polyphyllus Nutt. ex T. & G.		14	Sands (unpublished)
rigidus White		14	Sands (unpublished)
splendens Kell.	7		Cobb (1950)
		14	Sands (unpublished)
sulphureus Brew. ex Gray	7		Cobb (1950)
		14	Sands (unpublished)
torreyi Gray	7		Cobb (1950)
		14	Sands (unpublished)
tracyi Bradshaw	7		Cobb (1950)

Table 8. continued

species	n	2n	citation
venosus Muhl.	14		Senn (1938)
		28	Senn (1938)
			Ledingham (1957)
vestitus Nutt. ex T. & G. ssp. bolanderi (Wats.) C. L. Hitchcock	7		Cobb (1950)
		14	Sands (unpublished)
zionis C. L. Hitchcock		14	Sands (unpublished

*1 The counts of Stanley M. Sands, Botany Department, University of Washington, were made in 1949 and listed by Cobb (1950)

Lathyrus so far published (Fedorov 1969; Kupicha 1977).

Polyploid taxa are rare in Lathyrus. Intraspecific polyploidy (2n=14 and 28) is known from two old world species, one circumboreal species and one new world species (L. lanszwertii Kell.) All reported tetraploid species (L. venosus Muhl., L. nevadensis Wats. and L. arizonicus Britt.) are endemic to North America. Polyploidy has not been reported in the species studied here.

The diploid chromosome number for all species examined in the present study was found to be 14. Reported here are first counts for L. holochlorus, L. glandulosus, L. jepsonii ssp. jepsonii and several pubescent collections of L. vestitus. Additional counts for L. delnorticus, L. jepsonii ssp. californicus, L. polyphyllus, L. sulphureus and L. vesitus ssp. bolanderi agree with those previously reported. Table 9 presents a summary of counts made in the present study.

Karyotypes of all species studied are symetrical and fall into classes 1A and 1B outlined by Stebbins (1971). The chromosome complements of these species are similar to one another (Figures 19 and 20). There is less than a 25% difference in measured total chromosome length among all species studied; L. jepsonii seems to have the longest complement (ca. 46 micrometers) while L. polyphyllus the shortest complement (ca. 36 micrometers). The ratio of longest to shortest

Table 9. A catalogue of chromosome counts made in the present study. All accessions listed below were found to have a diploid number of 14.

seed lot	species	origin
	L. delnorticus C. L. Hitchcock	
139		DEL NORTE CO., CA: Panther Flat Campground, Six Rivers National Forest. R3E T16N Sec. 22. FV: 642, 761. GV: 1271.*1
143		DEL NORTE CO., CA: along French Hills Road, 0.3 mi. from Jct. with Hwy #199. R1E T17N Secs. 24-25. FV: 654, 753. GV: 1273.
	L. holochlorus (Piper) C. L. Hitchcock	
126		BENTON CO., OR: Oak Creek Road in fence row. T11S R5W Sec. 19.
131		LINN CO., OR: along Hwy #99E opposite Linn-Benton Comm. Coll. R4W T11S Sec. 36. FV: 630.
	L. glandulosus sp. nov.	
178		HUMBOLDT CO., CA: 0.4 mi. E of the Freshwater-Kneeland Road on the road to Maple Creek. FV: 772, 1149.
180		HUMBOLDT CO., CA: ca. 4 mi. S of the Kneeland School on the road to Bridgeville. FV: 777, 1153.
	L. jepsonii Greene ssp. *jepsonii*	
107		CONTRA COSTA CO., CA: Brown's Island near the town of Pittsburg. Received from W. Roderick, Tilden Park Botanical Garden, Berkeley, CA. GV: 1278.
	L. jepsonii Greene ssp. *californicus* (Wats.) C. L. Hitchcock	
185		TRINITY CO., CA: 0.8 mi. E of Dinsmore's on Hwy #36. R5E T30N Sec. 3. FV: 1166.
	L. polyphyllus Nutt. ex T. & G.	
123		LINN CO., OR: along Peoria Road. R4W T12S Sec. 8. FV: 615. GV: 1275.
124		BENTON CO., OR: MacDonald's State Forest, ca. 300 yds from the Oak Creek Entrance. R5W T11S Sec. 19. FV: 1103.

Table 9. continued.

L. polyphyllus (continued)

135 BENTON CO., OR: along Peterson Road. R6W T12S Sec. 35. FV: 603, 715. GV: 1274.

173 SISKIYOU CO., CA: 2.4 mi. N of Happy Camp on road to Takilma, OR. FV: 1182.

L. sulphureus Brewer ex Gray

176 JOSEPHINE CO., OR: 0.5 mi. S of Waldo on FS 40S03. R8W T40S Sec. 28. FV: 1131.

L. vestitus Nutt. ex T. & G. ssp. bolanderi (Wats.) C. L. Hitchcock

141 DEL NORTE CO., CA: Panther Flat Campground, Six Rivers National Forest. R3E T17N Sec. 22. FV: 643, 759. GV: 1272.

L. vestitus Nutt. ex T. & G. ssp vestitus

154 SANTA BARBARA CO., CA: seed received from Mary Allcott, Santa Barbara Botanic Garden, Santa Barbara, CA. Garden seed, exact origin unknown. GV: 1276.

157 VENTURA CO., CA: ca. 40 mi. S of Ventucopa, CA on Hwy #53. Los Padres National Forest. FV: 808.

158 MONTEREY CO., CA: south slope of Junipero Serra Peak, Los Padres National Forest. R5E T21S Sec. 4. seed received from J. R. Griffin, Hastings Natural History Reservation, Carmel Valley, CA. GV: 1277.

159 MONTEREY CO., CA: along Arnold Road, Hastings Reservation. seed received from J. R. Griffin.

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*1 All specimens cited above are those of the author's and have been deposited at Oregon State University Herbarium (OSC). Field Vouchers (FV) indicate herbarium specimens of individuals from the same population from which seeds were later collected or herbarium specimens of the plant from which seed were taken. Greenhouse vouchers (GV) are herbarium specimens of Greenhouse grown plants from which root tips were collected.

Figure 18. Chromosomes of Pacific Coast Lathyrus. A. L. glandulosus Broich (Broich 1149); B. L. holochlorus (Piper) C. L. Hitchc. (Broich 630); C. L. sulphureus Brewer ex Gray (Broich 1131); D. L. jepsonii Greene ssp. jepsonii (Broich 1278); E. L. jepsonii Greene ssp. californicus (Wats.) C. L. Hitchc. (Broich 1166).

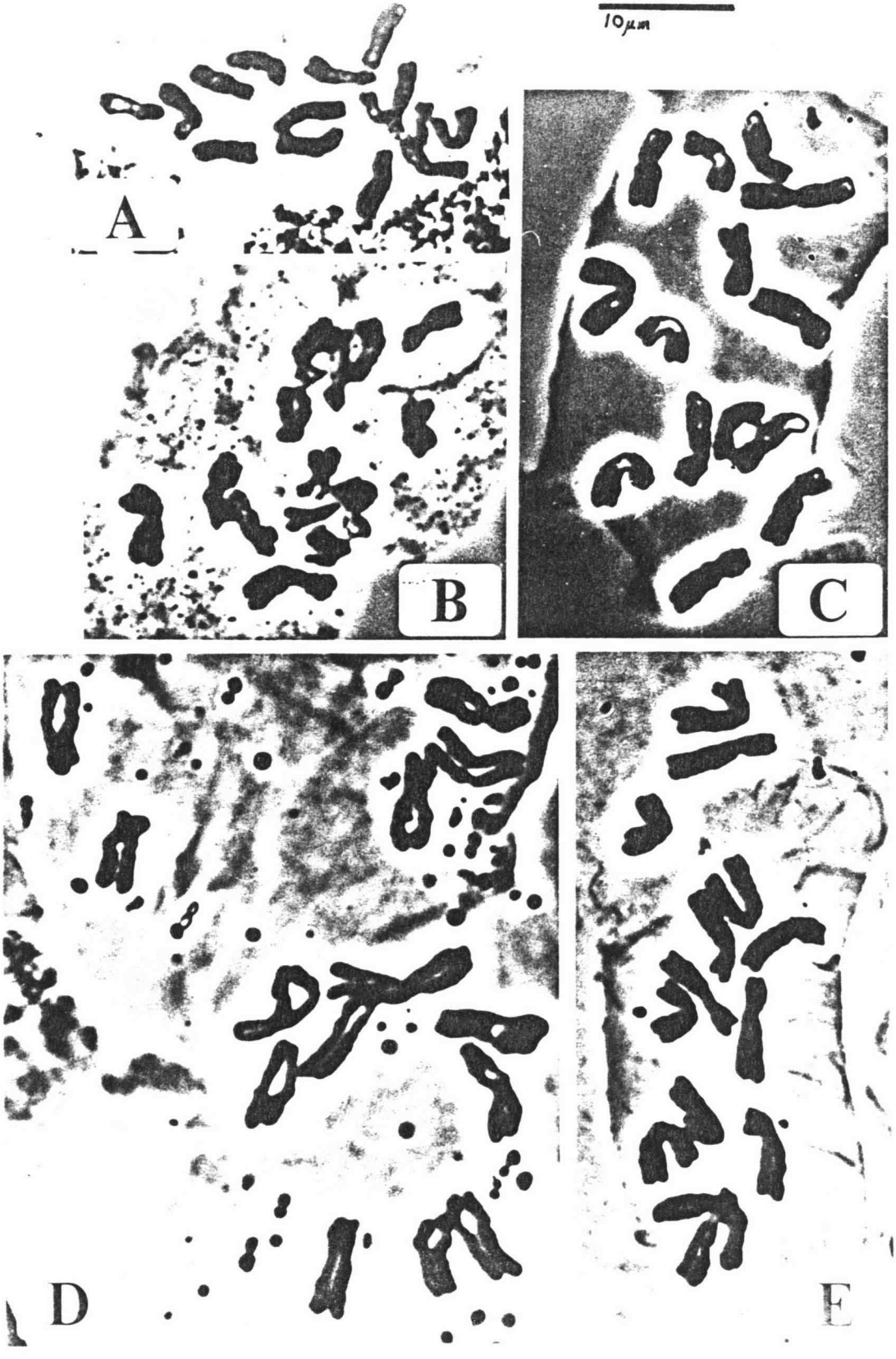

10μm
A
B
C
D
E

Figure 19. Chromosomes of Pacific Coast Lathyrus. A. L. polyphyllus Nutt. ex T. & G. (Broich 1103); B. L. vestitus Nutt. ex T. & G. ssp. vestitus (Santa Barbara County, California) (Broich 1267); C. L. delnorticus C. L. Hitchc. Broich 654, 753, 1273); D. L. vestitus Nutt. ex T. & G. ssp. vestitus (Monterey County, California) (no voucher); E., F. L. vestitus Nutt. ex T. & G. ssp. bolanderi (Wats.) C. L. Hitchc. (Del Norte County, California) (Broich 643, 759, 1272), photographs at two focal planes.


10μm
A
B
C
D
E
F

chromosome ranged from 1.4 to 1.7. Each genome seems to consist of 3-4 metacentric chromosomes of decreasing length ranging from 7.1 to 5.5 micrometers and 4-3 submetacentric chromosomes also decreasing in length from ca. 7.0 to 5.0 micrometers. These chromosome lengths are greater than those reported for annual European species of Lathyrus (Rees and Hazarika 1967).

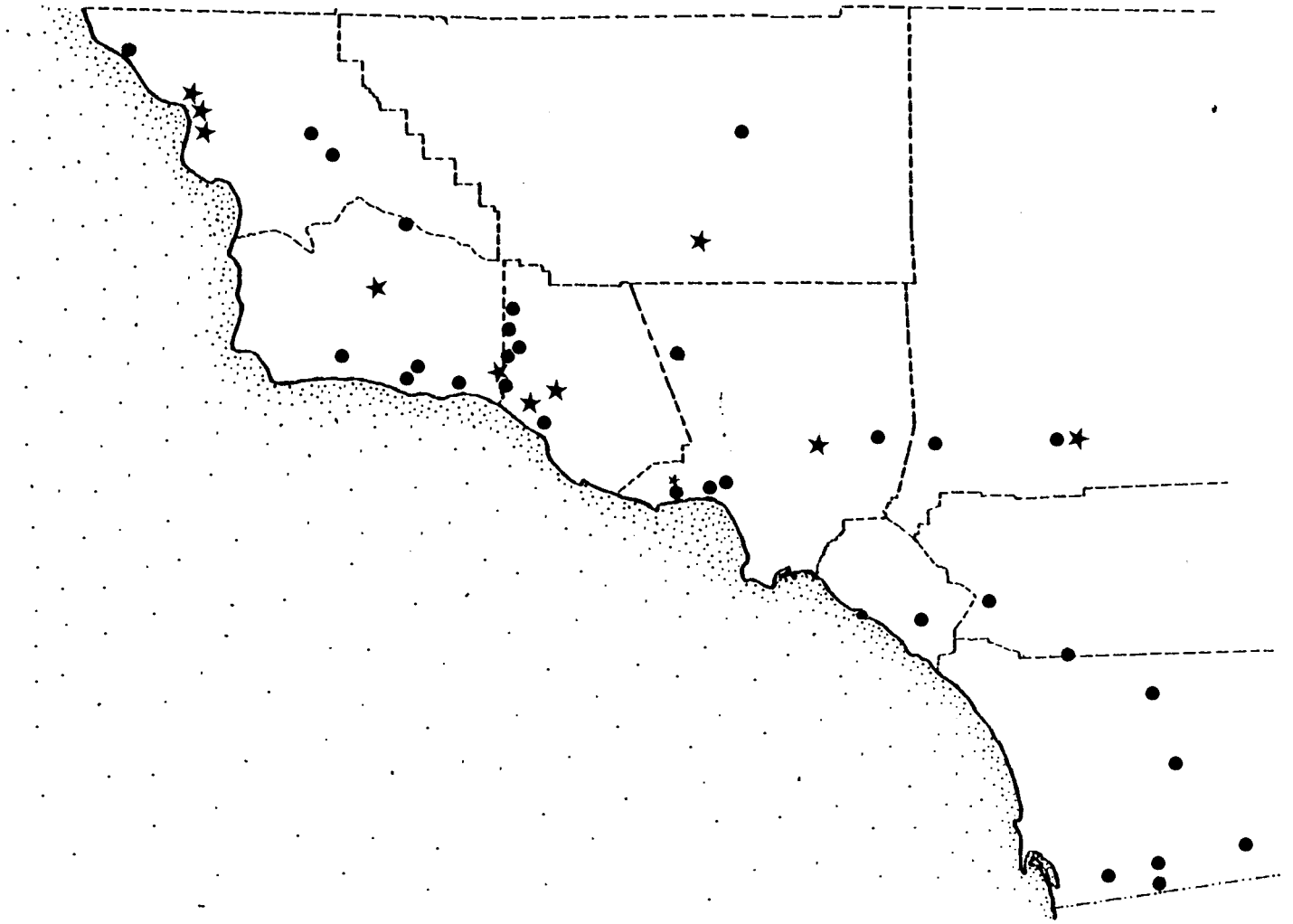
On the average 5-10 good metaphase plates were observed per root tip prepared but in most cases only 1-4 good photographs at 1000X were available for careful numerical analysis of each species. Differences in degree of contraction were observed on slides and also among the photographs taken; photographs exhibiting maximally contracted chromosomes were used for measurement. Given this small sample and the karyotype similarity among the species studied, interspecific differences could not be detected over the possible sources of error involved in karyotype measurements (Bentzer et al. 1971).

There have been two reports of meiotic irregularities in L. laetiflorus. Cobb (1950) described "chromatid-like" bridges, lagging chromosomes and "complements in second anaphase stage...deficient for one or more chromosomes". Raven et al. (1965) reported a bridge and fragment at meiotic anaphase I.

In an effort to determine the frequency and geographic distribution of such irregularities, pollen stainability was assessed in a sample of 50 herbarium specimens collected in or south of Monterey County, California and included in the matrix LATHTWO. Of this sample, 12 specimens (24%) had 70% or less stainable pollen. The geographical distribution of these specimens does not seem significant (see Figure 21) but many of these specimens appear to be "intermediate" between the groups identified in the cluster analysis of LATHTWO. Starred specimens in Figure 12 indicate collections with 70% or less stainable pollen.

These data suggest that morphological differentiation among southern California populations of this complex is being accompanied by chromosomal divergence. However, until such time that an intensive program of experimental hybridization among a large collection of plants collected in southern California can be undertaken, the

Figure 20. Geographic distribution of fertile and semi-sterile herbarium specimens sampled from the LATHTWO collection. Stars indicate locations of semi-sterile specimens.



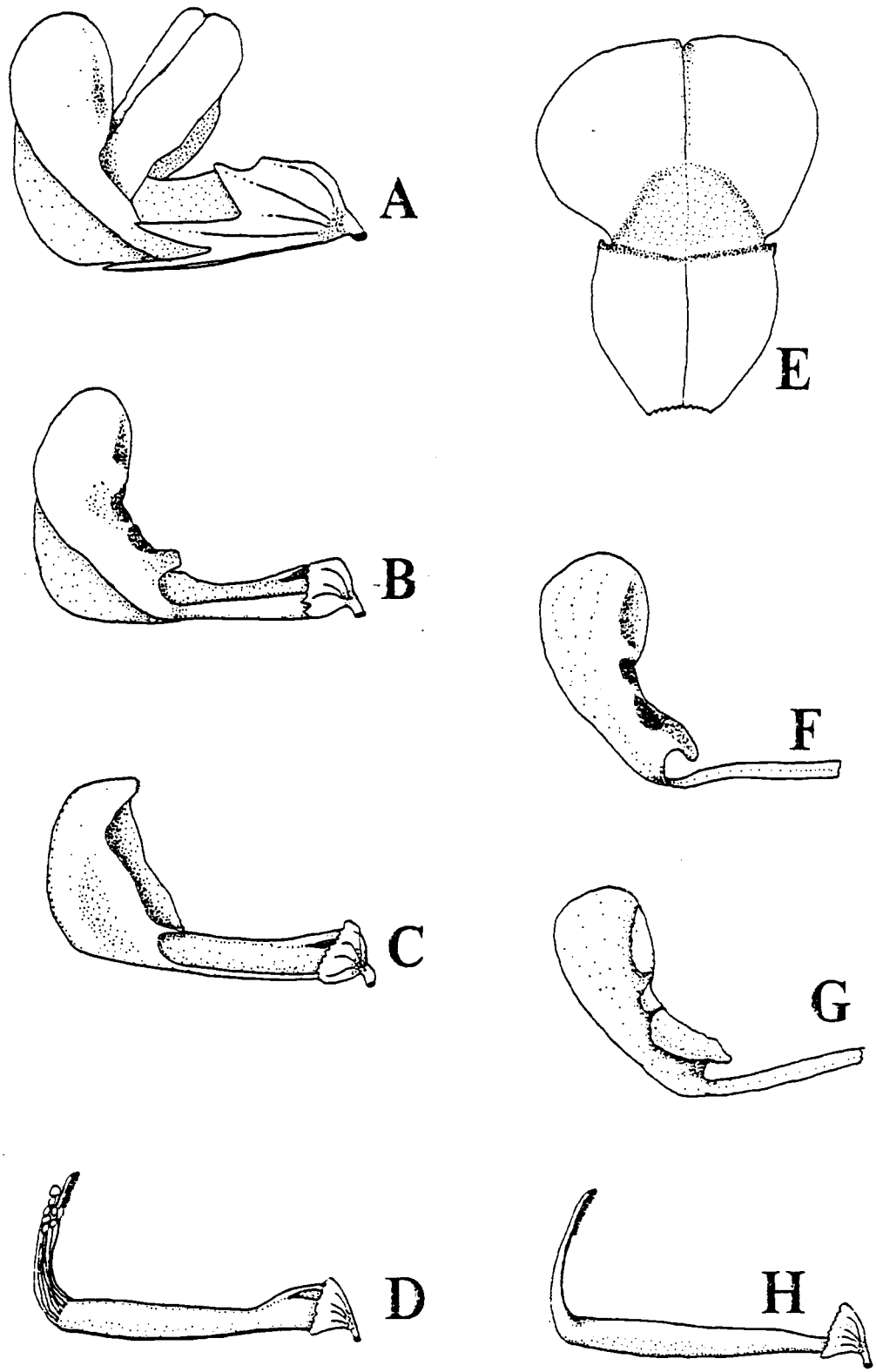
significance and extent of this divergence is difficult to assess. Regretably, seeds of southern California populations of the L. vestitus complex were unavailable for karyotype analysis.

Reproductive Biology

The floral display of Pacific Coast Lathyrus species consists of a series of axillary racemes of 6-20 flowers maturing acropetally over a period of a week or more. Flower density ranges from 0.6 to 6.8 flowers per cm; L. sulphureus (3.5 ± 0.5), L. delnorticus (3.8 ± 0.6) and L. holochlorus (5.0 ± 1.0) are notable for greater flower densities. Casual observation suggests that there are more flowers per inflorescence open at any one time on these species than others studied here.

Flowers of all Lathyrus species are bilaterally symetrical and consist of a five-lobed tubular calyx, five separate polymorphic petals, 10 stamens and a simple pistil (Figure 21). The corolla consists of a banner petal, two wing petals and two keel petals. Each petal, in turn, consists of a basal claw and a terminal petaloid blade. The banner claw is 5-12 mm wide and envelopes the claws of the other four petals, the staminal column and the pistil; claws of the remaining petals are 1-2 mm wide and as long as the calyx tube. The banner blade is cordate to orbicular in shape, 10-14 mm wide, 8-16 mm long, and is typically reflexed 90° from the floral axis. Wing petal blades are elliptic, 0.6-1.0 mm long and 0.3-0.6 mm wide. The inner dorsal margins of the wing petal blades bear 1-2 proximal "sockets" and a distal fold. These structures fit into a pocket formed by a fold in the dorsal margin of each keel petal. The ventral keel petal margins are connate and form a structure shaped like a prow of a boat in which the androecium and gynoecium are borne. The androecium consists of ten stamens basically united into a staminal tube with free filaments distally each bearing an anther. The stamen in the dorsal position is usually only weakly fused into place in the staminal tube and is arched away from the tube at the base to form

Figure 21. A dissection of a flower of L. delnorticus Hitchcock illustrating the typical floral morphology of Pacific Coast Lathyrus: A. entire flower; B. flower with banner and calyx lobes removed; C. flower with banner and wing petals and calyx lobes removed; D. flower with calyx lobes and corolla removed; E. banner petal, front view; F. outside surface of wing petal; G. inside surface of wing petal showing "sockets"; H. the gynoceium. The line in the upper right hand corner is 10 mm long.


A
B
C
D
E
F
G
H

two holes through which insects can gain access to the nectar secreted into the staminal tube. Nectaries of Lathyrus species are the concave annular type (Fahn 1974) and occur in the receptacle between the base of the staminal column and the ovary. The pistil contains 10-20 ovules; the style is bent 90° to the floral axis and bears a dorsal row of hairs below the stigma.

In all Lathyrus species studied here, two upper lobes of the calyx are 1-2 mm in length and subtend the banner petal (hence, "banner lobes"), the two lateral lobes vary from 3-7 mm in length while the lower calyx lobe is 3-8 mm long and subtends the keel petals (hence, "keel lobe"). The keel lobe is always approximately equal to or greater than the lateral lobes in length and is usually narrower than the lateral lobes.

Figure 21, a dissection of a flower of L. delnorticus, illustrates the typical morphology described above.

The calyx tube length, the length of all petal claws, banner blade length, ovary length and flower lengths are usually correlated. All petal blade lengths are correlated and keel blade height and style length are also correlated. Differences in size and exceptions to these correlations take on taxonomic importance.

In L. glandulosus, unlike all other species studied, the wing petal blades extend beyond the keel 2-4 mm. In this respect, flowers of L. glandulosus resemble those of L. pauciflorus, an eastern Oregon and Washington species which occurs occasionally in the Klamath Mountains and the Sierran foothills.

In L. vestitus ssp. alefeldii and L. splendens the banner blade is longer than the banner claw and is reflexed almost 180° to lie parallel to the floral axis. This condition is most extreme in the latter species.

The banner blade of L. sulphureus is shorter and narrower than the banner claw and this combination of traits gives the entire flower a distinctive "stubby" appearance unique to this species. In addition, the style of L. sulphureus is distally rotated 90°, another feature unique to L. sulphureus.

Corolla color varies considerably among these species. Petals of L. delnorticus, L. holochlorus and L. sulphureus are cream to white in color with rose colored veins in the banner blade. Petals of L. polyphyllus and L. glandulosus are purple with the banner usually a darker shade than the wings or keel. Petals of L. vestitus ssp. alefeldii and L. spendens are wine red. The corollas of L. jepsonii and the remaining subspecies of L. vestitus range from purple through various shades of lavender and pink to almost white.

Flower color varies widely in L. vestitus and L. jepsonii and also varies somewhat with age in other species making this trait difficult to use in keys.

Pacific coast Lathyrus species are protandrous; anthesis occurs a day or so before the banner blade folds into the vertical position (i.e., the flower "opens"). Pollen is shed into the keel below the stigma. The wing petals are traditionally considered to be a "landing platform" for insects in search of pollen and(or) nectar (Faegri and van der Pijl 1979). As the insect lands the entire wing/keel apparatus is depressed downward so that the stigma is pushed through the dorsal (free) keel petal margins and into the thorax and abdomen of the insect. Pollen grains are also "brushed" out of the keel by the stylar hairs located on the dorsal surface below the stigma. Pollination, therefore, is sternotribic as in most papilionaceous flowers (Faegri and van der Pijl 1979). Pollinators are mostly large, strong bees of the genera Bombus, Synhalonia and Osmia and also butterflies (Moldenke 1976). Bees of these genera are strong fliers and cover considerable distances while foraging (Moldenke, personal communication); neighborhood sizes may be rather large.

Stigmas from abscised flowers collected from bagged inflorescenses of L. holochlorus, L. polyphyllus and L. vestitus ssp. bolanderi growing in the Corvallis area were all found to bear pollen grains. At least one pollen grain had germinated and penetrated the stigmatic tissue on a style of L. holochlorus. However, no seed were set on flowers of bagged inflorescences and seed-set is absent in many small colonies of seemingly one clone.

These observations suggest that native Lathyrus are obligatorily out-crossed species with a genetic incompatibility system a conclusion also reached by Moldenke (1976). The fact that pollen can germinate occasionally on the stigma of the same flower suggests a gametophytic/sporophytic recognition system (Heslop-Harrison 1975) as studied extensively in Trifolium (Townsend 1971); however, much further research will be necessary to confirm this hypothesis for Lathyrus.

Seeds of the species studied here are mottled olive-yellow and black or are completely black in color when mature, and they range in weight from 10 to 100 mgs (Table 10). Seeds of L. jepsonii ssp. jepsonii are heavier and larger than other taxa including L. jepsonii ssp. californicus. Seed weight in L. vestitus increases from north to south (Table 10). Variation in seed size is considerable among individuals within one population and among population of one species; data collected so far are difficult to generalize.

Seed reproduction in Pacific Coast Lathyrus is limited by the availability of compatible pollen and also by seed predation by "pea weevils" of the family Bruchidae. The female weevil lays eggs in or on the developing fruits, and larvae feed on embryos and the developing seeds (Janzen 1969). When collecting Lathyrus seed it is common to find 3-5 flat, empty pods on an inflorescence or to find externally well developed seed which are hollow and contain a mature bruchid beetle. In many populations examined, few good seed were found.

The reviews of Johnson (1975) and Levin (1973) suggest that the presence of trichomes on ovaries might be a defense mechanism against beetle predation, but observations made thus far cannot substantiate this hypothesis for these Lathyrus. Investigations into the adaptive nature of ovary pubescence in Lathyrus will have to assess several factors simultaneously: local levels of ovipositing beetle populations, spatial relationships among Lathyrus individuals and the availability of compatible pollen, seed size, number of seed produced per individual and dispersal ability (Janzen 1969).

Table 10. Mean seed weight in mg, standard deviations and ranges for seed collections of Pacific Coast Lathyrus species.

TAXON	SEED LOT	LOCATION	$\bar{X}$	s	RANGE	SAMPLE SIZE
delnorticus						
	139	Del Norte Co., CA	29.9	3.9	24-36	12
	142	Del Norte Co., CA	32.6	2.9	29-38	12
	175	Josephine Co., OR	25.1	3.2	21-28	12
glandulosus						
	178	Humboldt Co., CA	26.7	5.9	18-30	12
	179	Humboldt Co., CA	21.9	3.6	13-28	19
	180	Humboldt Co., CA	22.6	4.3	13-30	16
holochlorus						
	127	Linn Co., OR	45.9	4.2	37-54	30
	132	Linn Co., OR	40.9	5.4	31-49	30
jepsonii ssp. jepsonii						
	107	Contra Costa Co., CA	104.6	7.0	92-119	12
jepsonii ssp. californicus						
	185	Humboldt Co., CA	54.8	11.6	36-70	12
	186	Humboldt Co., CA	51.9	7.9	40-59	10
polyphyllus						
	123	Linn Co., OR	38.3	6.5	33-52	12
	133	Linn Co., OR	36.6	4.2	30-50	30
	137	Benton Co., OR	41.7	5.1	28-42	30
	173	Siskiyou Co., CA	44.6	7.9	30-53	12
splendens						
	Wolf 2126 (RSA)	San Diego Co., CA	65.3	9.1	60-80	15
sulphureus						
	176	Josephine Co., OR	30.2	3.6	25-31	12
vestitus ssp. bolanderi						
	191	Benton Co., OR	14.1	2.5	10-20	12
	144	Del Norte Co., CA	28.7	3.0	25-32	12
	188	Del Norte Co., CA	18.8	3.8	14-26	15
	187	Humboldt Co., CA	18.6	4.3	13-28	12
vestitus ssp. vestitus						
	158	Monterey Co., CA	33.0	6.3	21-39	12
	160	Monterey Co., CA	30.9	9.8	16-45	10
	161	Monterey Co., CA	35.0	6.6	31-49	15
	154	Santa Barbara Co., CA	54.0	6.4	48-69	12
	155	Santa Barbara Co., CA	45.5	4.2	37-52	12
	157	Ventura Co., CA	45.9	6.6	37-54	15
vestitus ssp. alefeldii						
	Wolf 10925 (RSA)	San Diego Co., CA	46.3	8.3	33-61	15

Persistence by rhizomes appears to be an important survival strategy for Lathyrus along the Pacific Coast.

Ecology and Distribution

All forms studied herein are endemic to the area west of the crests of the Cascade Range and the Sierra Nevada in Washington, Oregon and California and in the coastal mountains of southern California. The climate of this region is characterized by mild moist winters and warm dry summers. Annual precipitation decreases from north to south and from the coast inland. These climatic trends are superimposed on great topographic and edaphic diversity, and the resulting vegetation is quite complex. In broad terms, the region consists of two floristic areas: the Pacific Northwest Coast and the California Floristic Province. The northern boundary of the California Floristic Province is from Coos Bay, Oregon, "southeasterly to the divide between the Umpqua and the Rogue Rivers and thence continues on southeasterly, up the arm of the Rogue River Valley in which Ashland is situated, to the Oregon California line" (Howell 1957: p. 135). The vegetation of Oregon and Washington has been described by Franklin and Dyrness (1973); that of California by Major and Barbour (1977). Statewide classifications of California vegetation have been given by Munz and Keck (1949) and Kuchler (1977). Significant reviews of Pacific Coast vegetational history have been written by Detling (1968), Wolf (1969), Whitaker (1961), Axelrod (1959, 1966, 1981) and Raven and Axelrod (1978).

Most native species of Lathyrus which occur along the Pacific Coast can be found in the Klamath Mountains of northwestern California and adjacent Oregon. Lathyrus is considered to be Arcto-Tertiary in origin (Bassler 1966; Raven and Axelrod 1978), and the Klamath Mountains are known to be a center of endemism for relics of the Arcto-Tertiary Geoflora (Stebbins and Major 1965). Whittaker (1961) has written that the Klamath region can be,

> "regarded primarily not as a center of origin for forests of other parts of the west, but as a center toward which meso-

> phytic forests of the past have shrunk, and as a center of accumulation of species of varied evolutionary history in diverse habitats of ancient land surfaces " (Whittaker 1961: p. 17).

Raven and Axelrod (1978) conclude that in the Klamath Mountains,

> "the precipitation season is longer than elsewhere in California, there is more summer rain, winters are not excessively cold, temperatures are more moderate in the summer and drought stress is lower here than in the Sierra and southward where the forests are not so diverse" (Raven and Axelrod 1978 P. 14).

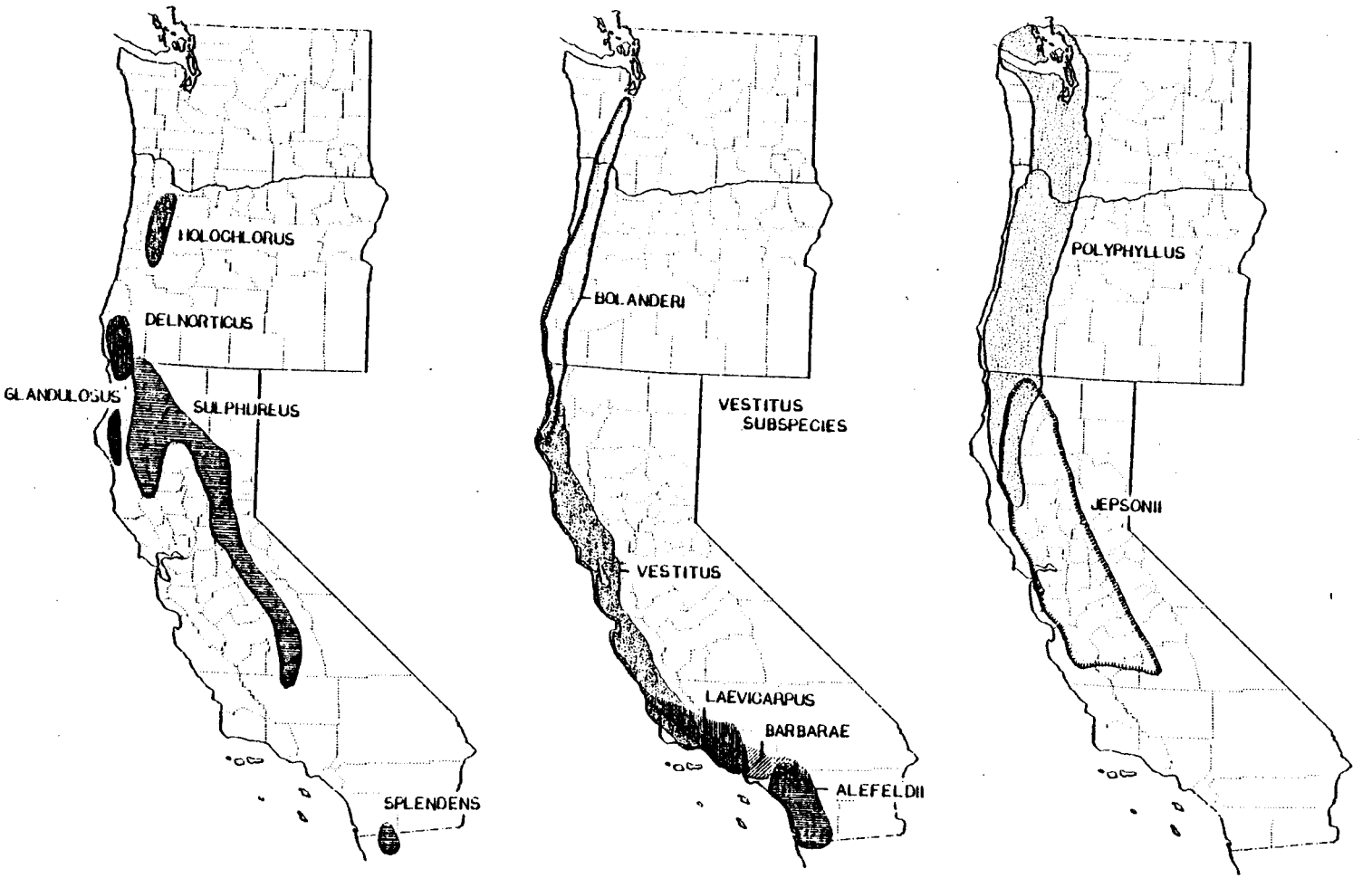
North of the Klamath region the landscape is dominated by mesic temperature forests unique in the world for nearly total dominance by coniferous species (Franklin and Dyrness 1973). The replacement of the dominant deciduous tree species of the Arcto-Tertiary Geoflora by coniferous species is thought to be the result of the change to relatively mild, wet winters and dry summers in contrast to the wet, hot summers and cold winters in which eastern deciduous forests are found. Fewer species of Lathyrus are found north of the Klamath Mountains.

South of the Klamaths the climate is increasingly drier and warmer. Central California is ecotonal between a flora derived from the Arcto-Tertiary Geoflora and species which evolved as part of the Madro-Tertiary Geoflora in southwestern North America (Axelrod 1958). In this area Arcto-Tertiary genera have "radiated extensively in California, producing clusters of species. This radiation has generally occured in the drier, bordering vegetation of Madrean derivation" (Raven and Axelrod 1978: p. 16).

Four of the species studied here are rather restricted in distribution (Figure 22). Lathyrus holochlorus is found only in Quercus woodlands and grasslands of the Willamette Valley in Oregon. Lathyrus delnorticus is restricted to serpentine slopes in the Klamath Mountains of southwest Oregon and adjacent California while L. glandulosus is found in mixed evergreen forests and oak woodlands upland from the coastal redwood forests of Humboldt and northern Mendocino Counties in California. Lathyrus splendens is found in chaparral in extreme southern San Diego County, California and adjacent Mexico.

Figure 22. The geographic distribution of Pacific Coast Lathyrus species allied to L. vestitus Nutt. ex T. & G.

Figure 22.


HOLOCHLORUS
DELNORTICUS
GLANDULOSUS
SULPHUREUS
SPLENDENS
BOLANDERI
VESTITUS
SUBSPECIES
VESTITUS
LAEVICARPUS
BARBARAE
ALEFELDII
POLYPHYLLUS
JEPSONII

Lathyrus polyphyllus (Figure 22) is a common understory component of the temperate coniferous forests west of the Cascade Crest in Washington and Oregon. It also occurs in the Willamette Valley, the valleys of southwestern Oregon and in the mixed evergreen forests of northern California. Farther south and in the inner northern California Coast Ranges it is restricted to higher elevations; the most southern collection of L. polyphyllus is from fir-pine forests above Clear Lake in Lake County, California.

Lathyrus sulphureus (Figure 22) is found in foothill oak-digger pine woodlands of the inner North Coast Ranges of California and in the western foothills of the Sierra Nevada. It is not found in the Coast Ranges south of San Francisco Bay but occurs as far south as the Greenhorn Mountains in Kern County on the eastern side of the San Joaquin Valley. The southern limit of L. sulphureus in the California Coast Ranges is in northern Lake County.

The distribution of L. jepsonii (Figure 22) is similar to that of L. sulphureus; it occurs in the inner North Coast Ranges and the foothills of the Sierra Nevada. Unlike L. sulphureus, L. jepsonii is also found in the Coast Ranges south of San Francisco Bay and is (or was) common in riparian communities of the Sacramento and San Joaquin Valleys. Lathyrus jepsonii ssp. jepsonii is confined to the freshwater (Tule) marshes of the San Francisco Bay region; the pubescent ssp. californicus is widespread and has been collected from Shasta to Tulare Counties.

Populations referable to the L. vestitus/laetiflorus complex occur from Puget Sound to Baja California (Figure 22) and are found in many plant communities. Subspecies bolanderi is a common element in the temperature coniferous forests of the Washington and Oregon Coast Ranges; in northern California and farther south is is restricted to the coast. Subspecies vestitus is found from Del Norte County south to Santa Barbara County in California. It occurs in a variety of habitats: coastal redwood forests, northern and southern oak woodlands and in Chaparral. In southern California subspecies of L. vestitus (formerly referable to L. laetiflorus) replace one

another north to south (Figures 22 and 23). Subspecies laevicarpus is most common in Ventura and western Los Angeles Counties (including the Santa Monica Mountains); ssp. barbarae is most often collected in the San Gabriel and San Bernardino Mountains of eastern Los Angeles and San Bernardino Counties. Subspecies alefeldii occurs to the south in Orange, Riverside and San Diego Counties.

Site sympatry is common between L. vestitus and L. polyphyllus in Oregon and northern California where they co-occur in forest openings and along road cuts. Site sympatry was also observed between L. vestitus and L. delnorticus and between vestitus and L. glandulosus. At most of these sites "open habitat" existed for colonization by hybrids (Anderson 1949); hybrids or hybrid swarms, however, were never observed.

Experimental hybridizations made among L. polyphyllus, L. holochlorus and L. vestitus in the Corvallis area all failed to set seed. It was impossible to determine whether this was due to pre- or post-fertilization genetic barriers (Levin 1971) or simply to failure in the hybridization techniques used.

Lathyrus sulphureus and L. jepsonii are sympatric throughout most of their ranges but no evidence of morphological intergradation could be found in herbarium collections. Subspecies of L. vestitus s. l. are parapatric to one another and morphological intergradation at boundaries between subspecies is often extensive.

Finally, L. jepsonii and L. vestitus are parapatric from northern Mendocino and Lake Counties to southern Monterey and San Benito Counties in California (Figure 24). Although the majority of specimens collected within this area are easily assignable to one or the other species, a number of collections appear to be intermediate between them. Phenological data, displayed in Figure 25, suggest that in the area of sympatry, L. vestitus flowers for a much longer time and usually reaches peak flowering somewhat earlier than L. jepsonii. There are also ecological differences: L. vestitus is more common in woodlands and in Chaparral while L. jepsonii is more often collected in grasslands and along watercourses.

Hitchcock (1952) reported that experimental hybridization was

Figure 23. Geographic distribution of L. vestitus Nutt. ex T. & G. in southern California.

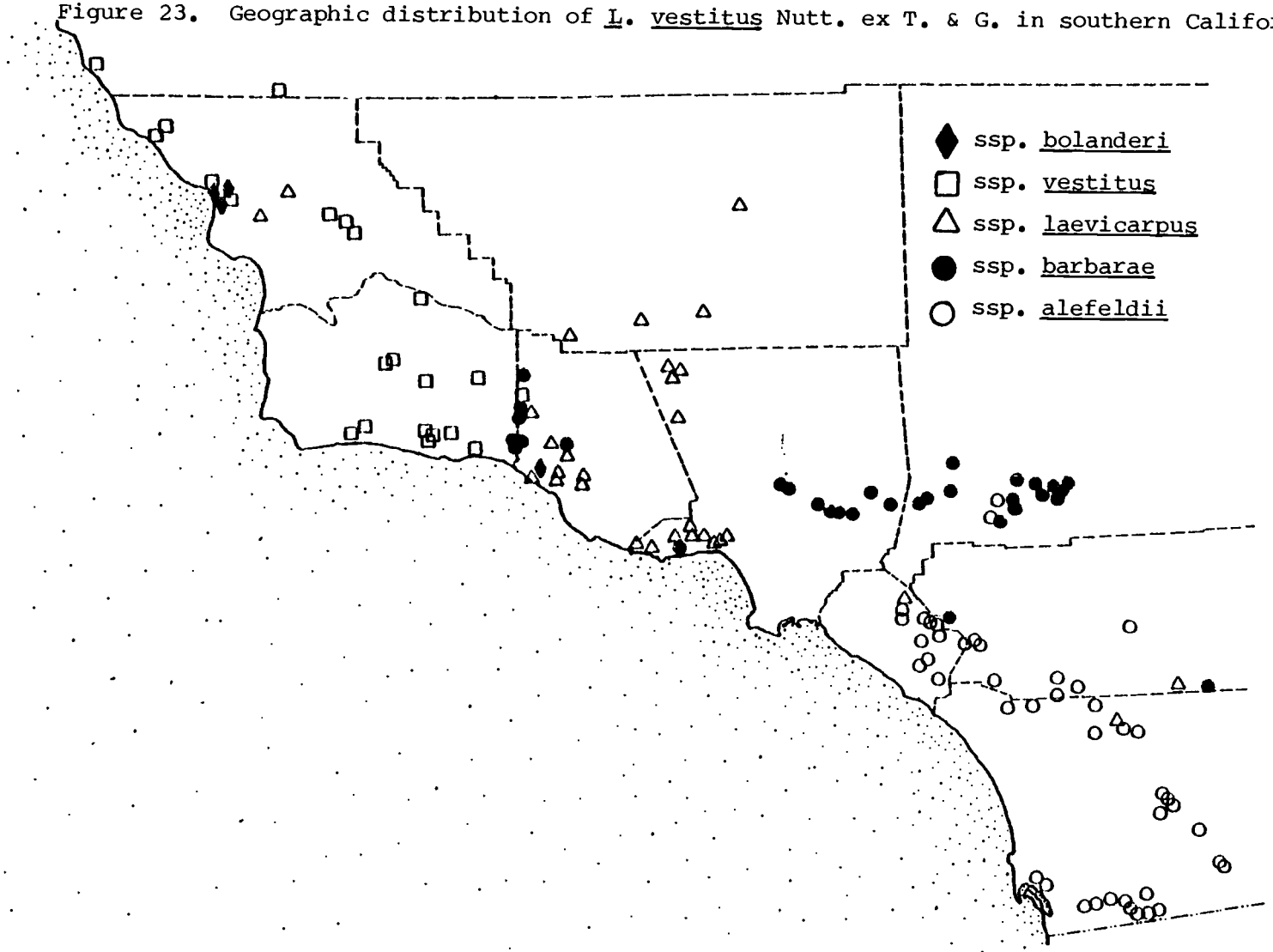


Figure 24. Geographic distribution of Lathyrus vestitus Nutt. ex T. & G., L. jepsonii Greene and possible hybrid collections in central California.

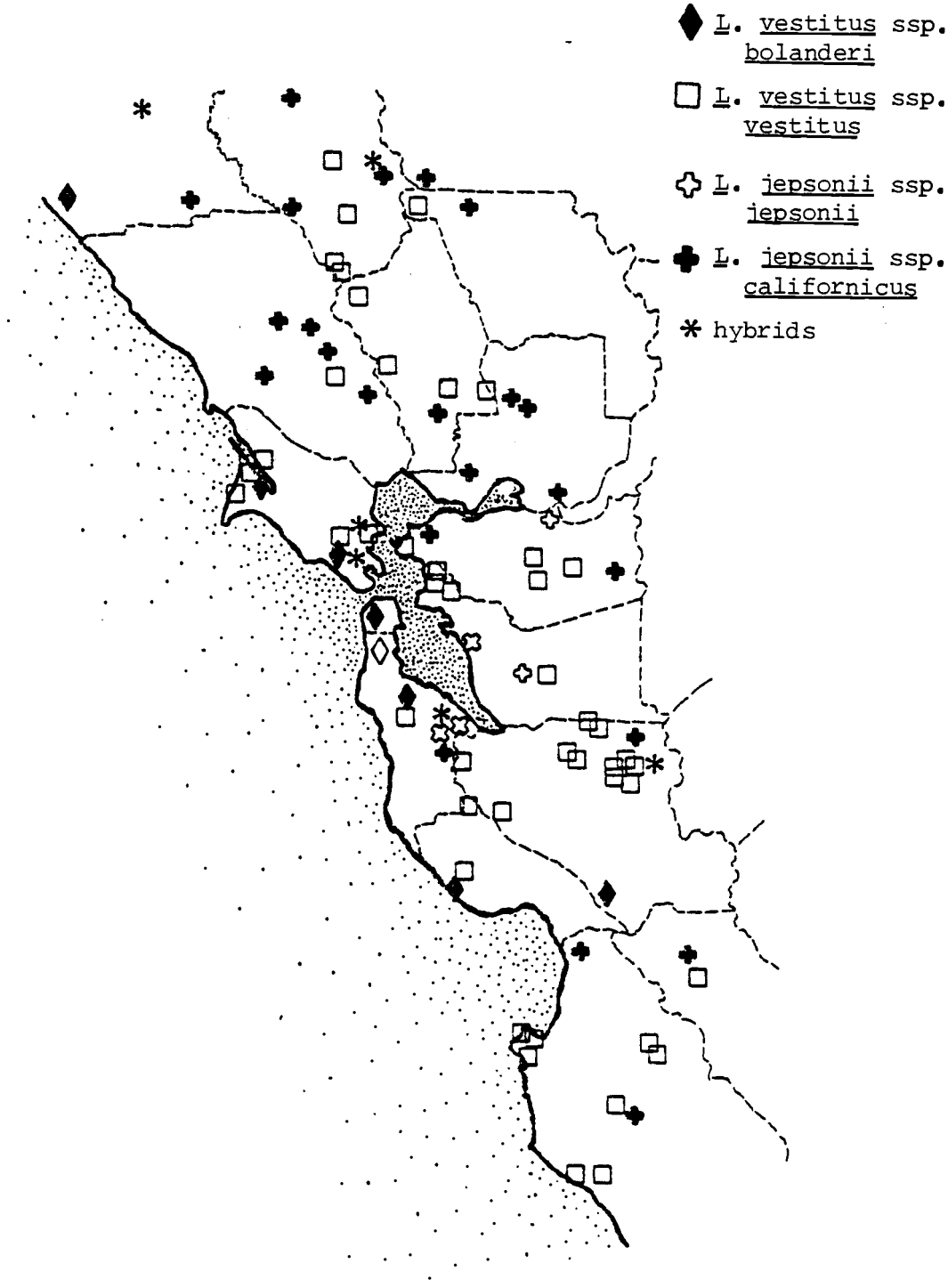
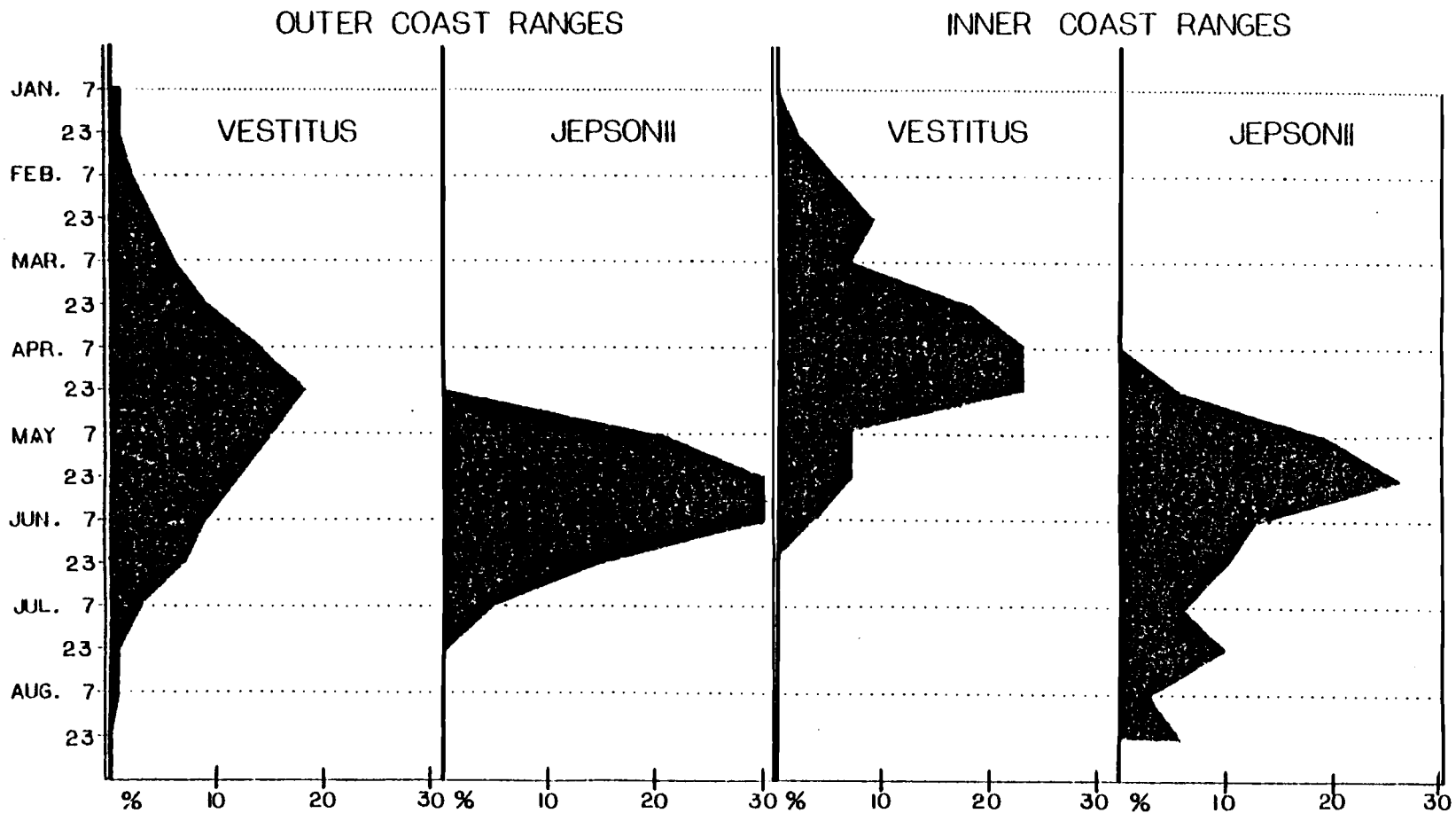


Figure 25. Phenological comparison of L. vestitus and L. jepsonii in the areas in which they are sympatric. Data are expressed in percent of the total number of specimens collected in the area. The "Outer Coast Ranges" include areas in Mendocino, Sonoma, Marin, San Francisco, San Mateo, Santa Cruz, western Santa Clara and Monterey Counties; 139 specimens of L. vestitus and 20 specimens of L. jepsonii were recorded there. The "Inner Coast Ranges" include areas in Lake, Napa, eastern Sonoma, Yolo, Solano, Contra Costa, Alameda, eastern Santa Clara and San Benito Counties; 57 specimens of L. vestitus and 31 specimens of L. jepsonii were recorded in these counties.

Figure 25.


OUTER COAST RANGES
INNER COAST RANGES
VESTITUS
JEPSONII
VESTITUS
JEPSONII
JAN. 7
23
FEB. 7
23
MAR. 7
23
APR. 7
23
MAY 7
23
JUN. 7
23
JUL. 7
23
AUG. 7
23
% 10 20 30 % 10 20 30 % 10 20 30 % 10 20 30

successful between L. jepsonii and L. vestitus and living F_1 plants were obtained. However, data on the fertility of the hybrids were not given and voucher specimens of hybrid plants have not been found. The genetic origin of any given herbarium specimen is difficult to determine. Documentation of introgressive hybridization depends a great deal on ecological characteristics of hybrid plants and their putative parents (Anderson 1949), but herbarium specimen labels rarely give the kind of data needed. Data on pollen fertility would be difficult to interpret in the absence of vouchered experimental hybrids. Given the variability within L. vestitus and the paucity of macroscopic characteristics with which to separate vestitus from jepsonii it is difficult to decide whether the various intermediate collections represent hybrids, phenotypic convergence or relic genotypes from an ancestral gene pool which gave rise to both species.

V. EVOLUTIONARY RELATIONSHIPS

The species of Lathyrus studied here form an apparently natural alliance of diploid, self-incompatible perennial herbs endemic to the Pacific Coast of North America. The pattern of morphological and karyotypic variability among these species is similar to that found in other perennial herbaceous and woody diploid species complexes of California (Raven and Axelrod 1978; Grant 1981). Relationships among California species of Delphinium provide a parallel example. Like Lathyrus, Delphinium is a genus of relatively large-flowered, bee pollinated perennial forest herbs of Arcto-Tertiary origin (Epling and Lewis 1952). Polyploidy is also rare in Delphinium and karyotype differences among species are small (Lewis et al 1951). Existing data suggest that morphologically different forms in both Lathyrus (Hitchcock 1952) and Delphinium (Epling and Lewis 1959) are interfertile. Evolutionary divergence in both genera has taken place at the diploid level in areas of California now dominated by vegetation of Madro-Tertiary origin.

In such groups interfertile entities remain morphologically distinct by geographic isolation and by "genetic coherence" which permits "two genetically compatible but distinct ecological forms to exist in adjacent but ecologically distinct habitats without losing their identity" (Nobs 1963: p. 79). If environmental conditions allow for the survival of hybrids, morphological distinctions become blurred, sometimes only locally and sometimes on a regional scale (Anderson 1949; Muller 1952). Cycles of hybridization, recombination and isolation under changing climatic conditions and in areas of great edaphic and topographic diversity have been responsible for much morphological confusion in some groups and for recent and sometimes rapid speciation. Other well documented examples of this have been given by Beeks (1962) for Mimulus sect. Diplacus and by Lenz (1958, 1959) for species of Iris series Californicae.

Within the group of Lathyrus studied here there seem to be four distinct subgroups: 1) L. glandulosus, 2) L. polyphyllus, 3) L.

holochlorus, L. delnorticus and L. sulphureus and 4) L. jepsonii, L. vestitus sensu lato and L. splendens.

1) Vegetatively, L. glandulosus most resembles L. polyphyllus but has winged stems as in L. delnorticus and L. jepsonii. In floral characteristics it most resembles L. pauciflorus, although quantitative data are lacking. In pubescence it is unlike any native Lathyrus described.

Hitchcock (1952) cited and annotated several collections of L. glandulosus as possible hybrids between L. polyphyllus and L. jepsonii ssp. californicus, but this hypothesis is difficult to support. Neither of the putative parental species are notable for glandular pubescence, the ovaries of both are entirely glabrous and the flowers of L. glandulosus are smaller than both. Taximetric studies reported here indicate that specimens referable to L. glandulosus are definably different from all other species of Lathyrus growing along the Pacific Coast, and there seems to be adequate evidence to justify the specific status of this taxon. Its present distribution in Humboldt and northern Mendocino Counties suggests that it is a paleoendemic, perhaps formerly more widespread, but now restricted to the southern Klamath area. The unique combinations of traits of L. glandulosus probably have their orign, therefore, in an ancestral gene pool rather than from later hybridization between extant species.

2) Lathyrus polyphyllus, along with L. nevadensis and L. vestitus ssp. bolanderi, is characteristic of the temperate coniferous forests of the Coast Ranges in Washington and Oregon. It reaches its southern limit in California in northern Lake County, and in northern California it is restricted to coastal forests or higher elevation fir forests. Vegetatively, it can be confused with L. vestitus ssp. bolanderi but floral characteristics of the two species are different. Lathyrus polyphyllus and L. vestitus ssp. bolanderi often grow together but I have never observed what I would consider hybrids between these two taxa. Lathyrus polyphyllus is a distinct, relatively homogeneous, widespread species whose closest relatives seem to lie among the other Pacific Coast species studied here.

3) Hitchcock (1952) considered L. delnorticus and L. holochlorus to be of hybrid origin: L. delnorticus as a cross between L. sulphureus and L. jepsonii ssp. californicus, and L. holochlorus as a cross between L. sulphureus and L. vestitus, probably ssp. bolanderi. Preliminary results of an experimental hybridization program reported by Hitchcock (1952) indicated interfertility between the supposed parental species and, in the later case, flowering F_1 hybrids were produced which were "classifiable as L. holochlorus as that plant is keyed and described in this paper" (Hitchcock 1952: p. 32). No further reports of this work were ever published and herbarium specimens of hybrid plants have not been found in the WTU collection. Attempts to intercross L. holochlorus and L. vestitus ssp. bolanderi growing in the vicinity of Corvallis, Oregon, have failed thus far.

Taximetric data reported here indicate a close phenetic similarity among L. delnorticus, L. holochlorus and L. sulphureus, but do not suggest that phenotypes of delnorticus and holochlorus are intermediate between the parental species suggested by Hitchcock. Differences in distribution and ecology among L. vestitus, L. sulphureus and L. holochlorus are such that it is difficult to account for both a hybrid origin and the present ranges of the three species. In the case of L. delnorticus, ecological and geographic data are not so difficult to reconcile, but it could be equally argued that the similarities among delnorticus, L. jepsonii and L. sulphureus are the result of ancestral relationships and not recent hybridization.

It appears to me that L. sulphureus, L. delnorticus and L. holochlorus are vicariant species. They are phenotypically similar but distinct entities with distinct geographic distributions and were probably derived from a common ancestral species group.

4) Relationships among L. vestitus sensu lato, L. jepsonii and L. splendens are complex. Plants formerly referable to L. laetiflorus resemble both L. jepsonii and L. vestitus. They are allopatric with jepsonii and ecologically distinct. On the other hand, L. vestitus and L. laetiflorus overlap geographically and intergrade extensively, and populations of "laetiflorus" appear to be

a morphologically diverse extension of L. vestitus into similar habitats of the Transverse and Peninsular Ranges of southern California. Lathyrus splendens seems to be a distinct derivation of L. vestitus ssp. alefeldii, the southernmost form of the vestitus-laetiflorus complex.

The pattern of floral variation in the L. vestitus-laetiflorus complex is clinal. Flower size increases and flower shape changes from north to south. The most likely factor underlying this pattern is variation in the "pollination environment". Andrew Moldenke (personal communication) notes an almost complete absence of Bombus south of the Santa Ynez and San Rafael mountains in Santa Barbara County. This absence may be an indication of a radically different pollinator guild for Lathyrus in southern California and therefore selection pressure resulting in divergence of floral form in the area.

Plant pubescence is also quite variable. Although there are exceptions, glabrous plants are most often found to the north or near the coast while pubescent individuals grow inland. The discrete nature of this pubescence variation suggests it is probably under relatively simple genetic control. This and the environmental correlations make plant pubescence rather useful for taxonomic distinctions.

To account for the patterns of morphological variability and geographic distribution within this subgroup I propose the following hypothesis: Lathyrus jepsonii and northern forms of L. vestitus first differentiated from an ancestral complex; jepsonii in response to drying conditions which developed west of the Sierra Nevada in response to the uplift of the Coastal Ranges, and vestitus within the California coastal ranges. Pleistocene glacial episodes allowed the southern migration of Arcto-Tertiary forest elements into southern California (Axelrod 1966) and populations of the L. jepsonii-vestitus complex were probably relatively recent migrants to the area. Cycles of glacial and interglacial epochs served alternately to connect and isolate Lathyrus populations in southern California and the result has been rather rapid but incomplete differentiation.

At least three closely related phenotypic groups can be found south of Santa Barbara County, and there is evidence to suggest chromosomal divergence has occurred among these populations. A saltational speciation event (Lewis 1966) may have been the cause of the divergence of L. splendens from the main series of populations of L. vestitus in southern California.

I believe that the most efficient taxonomic treatment of this subgroup is to maintain L. jepsonii and L. splendens as separate species but to treat L. laetiflorus as part of L. vestitus. Lathyrus jepsonii does not occur in the southern end of the San Joaquin Valley or adjacent mountains. To the north, one can separate it from L. vestitus, and the two species seem to exist as separate population systems adapted to differing ecological conditions. Morphological intergradation between L. vestitus and forms referable to L. laetiflorus is so complete that a taxonomic treatment as two species is nearly impossible and probably would be deceptive. The arrangement proposed here, which conforms to what Grant (1981) calls "taxonomic species", will facilitate the identification and further study of L. vestitus as one polymorphic evolving species complex.

VI. THE SPECIES OF LATHYRUS OF THE PACIFIC COAST

Introduction

Given herein is a key and a description for all species of Lathyrus, native and introduced, which occur west of the Sierra-Cascade Crest in Washington, Oregon and California and in the coastal mountains of southern California. For native taxa, this geographic partitioning appears natural; only five of the 16 native speces treated here occur elsewhere in North America. Complete nomenclatural treatments and descriptions are give for those species studied intensively; shorter descriptions are give for the remaining taxa. Data on introduced and additional native species were compiled from Hitchcock (1952), a number of floristic treatments (Jepson 1936; Abrams 1944; Munz and Keck 1959; Peck 1961; Ball 1968; Davis 1970) and from personal observations. Limited numbers of specimens of L. nevadensis, L. pauciflorus and L. tracyi were borrowed from WTU, UC and CAS for examination.

The concept of "species" upon which native taxa in this treatment are based most resembles that of Cronquist's, whereby "species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means" (Cronquist 1978: p. 15). However, the philosophical notion behind the use of this definition is that of Grant's (1981); the units described here are "taxonomic species". Biosystematic data for Pacific Coast Lathyrus are meager. Hitchcock (1952) reported successful interspecific corsses between a number of forms treated here as spearate species. If (or when) additional data from hybridizations become available, I suspect that many species of North American Lathyrus will be found to be interfertile much as in other perennial herbaceous genera of western North America (Grant 1981). Biosystematic information, such as it is now, is included in the descriptions of the various taxa; readers are invited to make their own judgements concerning the nature and extent of "biological species" within Lathyrus in North America.

Following the example of Barneby (1964) the key makes use of geographic boundaries as well as morphological characteristics of the plants. While there is always the danger of unsuspected range extensions creating difficulties with such a key, the geographic extent of native species is reasonably well known and this problem should be minimal. The advantages of such key leads far outweight possible disadvantages.

The following points should be considered when using the key and descriptions given below. 1) Flower length is taken to be the distance from the base of the calyx tube to the distal margin of the keel petals; wing petal blades, when extending beyond the distal keel margin, are not included in this measurement. All flower measurements were made on dried specimens; a shrinkage factor of perhaps 10% should be considered when measuring live specimens. In most cases this comes to 1-2 mm. 2) Rachis lengths and numbers of leaflets are given for leaves subtending inflorescences. 3) Leaflet lengths, widths and length/width (L/W) ratios are given for basal leaflets of leaves subtending inflorescences. 4) A vestiture of soft, unicellular hairs, whether straight, curved or wavy is herein referred to as curly pubescence. 5) Glandular pubescence refers to the presence of trichomes with 2-4 bulbous cells on a short stalk; glandular cells range from clear to dark reddish-brown in color. 6) Pubescence density on ovaries decreases with fruit development. References to ovary pubescence in the key and descriptions concerns this condition during flowering. 7) Stems are considered winged if internode ridges midway between flowering nodes are greater than 1.5-2.0 mm wide; anything less is considered "sharply angled" or simply "angled (reference to "narrowly winged" stems implies wings between 1-2 mm in width) 8) Quantitative measurements given represent the typical range for the taxon; extremes are placed in parentheses. 9) Whenever possible, terminology for vegetation types follows Munz and Keck (1959) for California and Franklin and Dyrness (1973) for Oregon and Washington.

A list of specimens examined is given in Appendix C.

A Key to the species of Lathyrus of the Pacific Coast

1a. Upper cauline leaves with two or fewer leaflets.....Group I

1b. Upper cauline leaves with more than two leaflets.....2

2a. Plants coastal, occurring on sand dunes or in coastal marshes.....Group II

2b. Plants growing inland from the coast; if coastal then not on sand dunes or in coastal marshes.....3

3a. Plants found north of 43° North Latitude (Pacific Northwest Coast).....Group III

3b. Plants found south of 43° North Latitude (California Floristic Province).....4

4a. Plants found in or north of San Luis Obispo County, California.....Group IV

4b. Plants found in or south of Santa Barbara, Ventura and Kern Counties, California.....Group V

Group I: Introduced species

5a. Leaflets lacking.....6

5b. Leaflets present, two.....7

6a. Stipules enlarged, hastate; rachis a branched tendril.....1. L. APHACA

6b. Stipules and tendrils absent; rachis forming a grass-leaf-like phylode.....2. L. NISSOLIA

7a. Flowers yellow.....3. L. PRATENSIS

7b. Flowers purple or red to white but never yellow.....8

8a. Plants annual; flowers 1-4 per raceme.....9

8b. Plants perennial; flowers 4-15 per raceme.....15

9a. Flowers greater than 13 mm long; stems broadly winged.....10

9b. Flowers less than 13 mm long; stems angular to narrowly winged.....11

10a. Leaves and fruits glabrous.....4. L. TINGITANUS

10b. Leaves and fruits pubescent....5. L. ODORATUS

11a. Flowers solitary (rarely 2), peduncle prolonged into a bristle greater than 5 mm long.....12

11b. Flowers 2-4, peduncle not terminated in a bristle 5 mm or more long.....14

12a. Calyx teeth 2-3 times longer than calyx tube; style twisted at anthesis.....6. L. CICERA

12b. Calyx teeth subequal to calyx tube; style not twisted at anthesis.....13

13a. Peduncle much longer than rachis of subtending leaf..... .....7. L. ANGULATUS

13b. Peduncle equal to or shorter than rachis of subtending leaf.... .....8. L. SPHAERICUS

14a. Fruits glabrous.....9. L. PUSILLUS

14b. Fruits pubescent, covered with pustulose-based hairs..... .....10. L. HIRSUTUS

15a. Stems wingless.....11. L. TUBEROSUS

15b. Stems broadly winged.....16

16a. Stipules one-half or less as wide as stem, mostly linear-lanceolate, 1-3 cm long.....12. L. SYLVESTRIS

16b. Stipules greater than one-half width of stem, broadly lanceolate to ovate, 3-5 cm long...13. L. LATIFOLIUS

Group II: Native Coastal Species

17a. Tendrils lacking, rachis prolonged into a flattened bristle; plants densly villous; pods to 3 cm long, 1 cm wide..... .....14. L. LITTORALIS

17b. Tendrils well developed, often branched, usually longer than 1 cm; plants glabrous to sparsely pubescent; pods if 1 cm wide, then 4-5 cm long.....18

18a. Stems narrowly winged; leaflets mostly 4-6, stipules linear to lanceolate, much narrower than leaflets..... .....15. L. PALUSTRIS

18b. Stems merely angled; leaflets 6-12, stipules broad, as large as leaflets.....16. L. JAPONICUS

Group III: Native Species of the Pacific Northwest Coast

19a. Tendrils absent, rachis may be prolonged into a short bristle less than 1 cm long.....20

19b. Tendrils present, greater than 1 cm long, often branched.....21

20a. Flowers 1-2; leaflets (8)10-12(14); ovary pubescent in flower.....17. L. TORREYI

20b. Flowers more than 2 per node; leaflets usually 4-6; ovary glabrous in flower...18a. L. NEVADENSIS ssp. NEVADENSIS

21a. Flowers white.....22

21b. Flowers rose to purple.....23

22a. Lateral calyx lobes linear, not broadened above the base, equal to or shorter than the calyx tube; plant often branched at or just below the flowering nodes.....25. L. HOLOCHLORUS

22b. Lateral calyx lobes broadened considerably above the base, usually longer than the calyx tube; plants almost never branched at or just below the flowering nodes.....22b. L. VESTITUS ssp. BOLANDERI

23a. Leaflets (11)12-14(15), stipules broad, ovate, approaching leaflets in size; raceme usually shorter than rachis of subtending leaf.....28. L. POLYPHYLLUS

23b. Leaflets (4)6-8(10), stipules linear, much smaller than leaflets; raceme usually longer than rachis of subtending leaf.....18b. L. NEVADENSIS ssp. LANCEOLATUS

Group IV: Native Species of the Northern California Floristic Province

24a. Tendrils absent, rachis sometimes prolonged into a bristle less than 1 cm long.....25

24b. Tendrils present, greater than 1 cm long, often branched.....28

25a. Flowers 1-2 per node; leaflets 10-12.....17. L. TORREYI

25b. Flowers more than 2 per node; leaflets usually fewer than 10.....26

26a. Flowers white.....20. L. TRACYI

26b. Flowers pale reddish or bluish to purple, but not white.....27

27a. Flowers less than 12 mm long.....19. L. LANSZWERTII ssp. ARIDUS

27b. Flowers more than 12 mm long.....18a. L. NEVADENSIS ssp. NEVADENSIS

28a. Stems narrowly to broadly winged.....29

28b. Stems angled, not clearly winged.....35

29a. Ovaries sparsely to densely glandular and(or) curly pubescent in flower.....30

29b. Ovaries completely glabrous.....32

30a. Leaflets 13-17, lower leaflet surfaces densely glandular pubescent.....29. L. GLANDULOSUS

30b. Leaflets 6-12, lower leaflet surfaces glabrous to densely curly pubescent but glandular hairs few in number.....31

31a. Leaflets pubescent...22a. L. VESTITUS ssp. VESTITUS

31b. Leaflets glabrous....22b. L. VESTITUS ssp. BOLANDERI

32a. Flowers white, less than 13 mm long.....26. L. DELNORTICUS

32b. Flowers pale pink to purple, greater than 13 mm long.....33

33a. Leaflets pubescent...24b. L. JEPSONII ssp. CALIFORNICUS

33b. Leaflets glabrous.....34

34a. Stems broadly winged; lateral calyx lobes deltoid, shorter than calyx tube.....24a. L. JEPSONII ssp. JEPSONII

34b. Stems only narrowly winged; lateral calyx lobes broadened above the base, equal to or longer than calyx tube.....22b. L. VESTITUS ssp. BOLANDERI

35a. Banner claw wider and longer than banner blade; style twisted at anthesis..27. L. SULPHUREUS

35b. Banner claw equal to or less than banner blade in both length and width; style not twisted at anthesis.....36

36a. Lateral calyx lobes considerably broadened above base, usually longer than calyx tube; ovary sparsely to densely glandular and(or) curly pubescent.....37

36b. Lateral calyx lobes widest at base, deltoid to narrowly lanceolate; ovary glabrous.....38

37a. Leaflets glabrous....22b. L. VESTITUS ssp. BOLANDERI

37b. Leaflets pubescent...22a. L. VESTITUS ssp. VESTITUS

38a. Wing petals 2-4(5) mm longer than keel.....
.....21. L. PAUCIFLORUS ssp. BROWNII

38b. Wing petals subequal to keel.....39

39a. Flowers less than 12 mm long.....40

39b. Flowers more than 12 mm long.....41

40a. Flowers white.....20. L. TRACYI

40b. Flowers pale lavender or rose to purple.....
.....19. L. LANSZWERTII ssp. ARIDUS

41a. Leaflets (11)12-14(15), stipules broad, ovate, approaching leaflets in size, raceme usually shorter than rachis of subtending leaf.....28. L. POLYPHYLLUS

41b. Leaflets (4)6-8(10), stipules linear, much smaller than leaflets; raceme usually longer than rachis of subtending leaf.....18b. L. NEVADENSIS ssp. LANCEOLATUS

Group V: Native Species of the Southern California Coast Ranges

42a. Flowers less than 15 mm long...21. L. PAUCIFLORUS ssp. BROWNII

42b. Flowers greater than 15 mm long.....43

43a. Flowers wine red to dark purplish, usually greater than 17 mm long; banner reflexed to almost 180°, parallel with floral axis.....44

43b. Flowers white to light purple but not red or dark purple, usually less than 17 mm long, banner not so extremely reflexed.....45

44a. Flowers greater than 21 mm long; style longer than 13 mm.....
.....23. L. SPLENDENS

44b. Flowers less than 21 mm long; style less than 13 mm long.....
.....22e. L. VESTITUS ssp. ALEFELDII

45a. Ovary completely glabrous; calyx glabrous with ciliate margins; leaflets glabrous.....
.....22c. L. VESTITUS ssp. LAEVICARPUS

45b. Ovary sparsely to densely glandular and(or) curly pubescent; calyx pubescent; leaflets pubescent or, more rarely glabrous on the upper surface or completely glabrous.....46

46a. Lateral calyx lobes more or less flared above base, usually equal to ro longer than calyx tube; style less than 7.5 mm long.
.....22a. L. VESTITUS ssp. VESTITUS

46b. Lateral calyx lobes more or less deltoid, widest at base, usually equal to or shorter than calyx tube; style greater than 7.5 mm long.....22d. L. VESTITUS ssp. BARBARAE

Descriptions of Taxa

1. LATHYRUS APHACA L.

Glabrous annual; stem angled, 2-6 dm long; leaflets absent, rachis reduced to a tendril, stipules large, lanceolate to ovate, hastate, 1-5 cm long, 0.5-4 cm wide. Flowers usually solitary, 8-10 mm long, calyx lobes much longer than calyx tube, corolla yellow. Legume glabrous, 2-3.5 cm long, 3.8 mm wide. 2n = 14. Native of western Europe; occasional in northern California, Oregon and Washington.

2. LATHYRUS NISSOLIA L.

Glabrous to sparsely pubescent annual; stem, not winged, 1-8 dm long; leaflets absent, rachis forming a linear, grass-like phyllode to 13 cm long, tendrils absent. Racemes 1-2 flowered, flowers 8-11 mm long, calyx lobes shorter than calyx tube, corolla crimson. Legume glabrous or pubescent, 3-6 cm long, 2-4 mm wide. 2n = 14. Native of western Europe; known here from one collection in Washington County, Oregon. Not included in Hitchcock and Cronquist (1973).

3. LATHYRUS PRATENSIS L.

Glabrous or pubescent perennial; stems not winged, 4-10 cm long, usually profusely branched; leaflets 2, linear to elliptic, 1-3(4) cm long, 2-9 mm wide, stipules sagitate, tendrils well developed. Racemes with 3-12 flowers; flowers 9-11 mm long, calyx lobes shorter than calyx tube, corolla yellow. Legumes glabrous or pubescent, 2-4 cm long, 4-7 mm wide. 2n = 14, 28, 42. Common throughout Europe where it is a taxonomically difficult group (Brunsberg 1977); known here from Washington.

4. LATHYRUS TINGITANUS L.

Glabrous annual; stems narrowly winged, 6-12 dm long; leaflets 2, linear-lanceolate to ovate, 2-8 cm long, 4-15 mm wide, tendrils well developed. Racemes with 1-2(3) flowers; flowers 14-16 mm long, calyx lobes shorter than calyx tube, corolla bright purple, wings greatly exceeding keel in length. Legumes glabrous, 6-10 cm long, 8-10 mm wide. 2n = 14. Native to western Mediterranean region; occasional throughout the Pacific Coast area.

5. LATHYRUS ODORATUS L.

Pubescent annual; stems winged, 3-20 dm long; leaflets 2, ovate to elliptic, 2-6 cm long, 7-30 mm wide, tendrils well developed. Racemes with 1-4(5) flowers; flowers greater than 20 mm long, calyx lobes greater than or equal to calyx tube in length, corolla various colors from white to purple. Legumes pubescent, 5-7 cm long, 1-2 cm wide. 2n = 14. Native to the central Mediterranean region; widely cultivated as an ornamental. Escaped but probably not really established along the Pacific Coast.

6. LATHYRUS CICERA L.

Glabrous annual; stems winged, 2-10 dm long; leaflets 2, linear to lanceolate, 1-9 cm long, 1-6 mm wide, tendrils well developed. Flowers solitary, peduncles longer than rachis of subtending leaf, calyx lobes longer than calyx tube, corolla reddish purple, style

twisted at anthesis. Legumes glabrous, 2-4 cm long, 5-10 mm wide with two keels on the dorsal suture. 2n = 14. Southern Europe, often cultivated for fodder; known from San Mateo and Amador Counties in California.

7. LATHYRUS ANGULATUS L.

Glabrous to pubescent annual; stems not winged, 1-5 dm long; leaflets 2, linear to linear-lanceolate, 2-6 cm long, 1-7 mm wide, tendrils well developed. Flowers solitary, peduncle much longer than rachis of subtending leaf, calyx lobes less than or equal to calyx tube in length, corolla pale blue to purple, style not twisted at anthesis. Legumes glabrous, 2.5-5 cm long, 3-4 mm wide, with indistinct reticulate venation. 2n = 14. Mediterranean; occasionally collected in Oregon.

Although included in Peck's manual for Oregon, L. angulatus was apparently overlooked by Hitchcock (1952). It is collected rather frequently in Oregon and is often confused with the following species from which it differs in flower color, peduncle length in relation to the subtending leaf rachis length and in the absence of prominent venation on the fruits.

8. LATHYRUS SPHAERICUS Retz.

Glabrous to pubescent annual; stems not winged, 1-5 dm long; leaflets 2, linear to linear-lanceolate, 2-6 cm long, 1-7 mm wide, tendrils well developed. Flower solitary, peduncles subequal to rachis of subtending leaf, flowers 7-9 mm long, calyx lobes greater than or equal to calyx tube in length, corolla orange-red, style not twisted at anthesis. Legumes glabrous, 3-7 cm long, 4-7 mm wide, with prominent reticulate venation. 2n = 14. Southern Europe; common in Oregon, also reported in Napa County, California. See discussion of L. angulatus L.

9. LATHYRUS PUSILLUS Elliott

Sparsely pubescent annual, stems narrowly to broadly winged,

3-6 dm long; leaflets 2, linear-lanceolate to elliptic, 3-7 cm long, tendrils well developed. Racemes with 2 flowers; flowers 7-9 mm long, calyx lobes longer than calyx tube, corolla bluish. Legumes 3-4 cm long, 2-4 mm wide. 2n = 14. Native of eastern North (?); introduced into Oregon.

Hitchcock (1952) expressed some doubt as to the origin of this species. Lathyrus pusillus represents the only annual North American species having 2 leaflets. In morphology it is similar to several Mediterranean species (including the next), and perhaps it was introduced into eastern North America at the time of European colonization.

10. LATHYRUS HIRSUTUS L.

Sparingly hirsute annual, stems narrowly to broadly winged, 2-10 dm long; leaflets 2, linear to lanceolate, 3-8 cm long, 2-20 mm wide, tendrils well developed. Racemes with 1-3(4) flowers; flowers 7-9 mm long, calyx lobes subequal to calyx tube, corolla red to bluish. Legumes conspicuously hirsute with pustulose-based hairs, 2.5-4 cm long, 5-8 mm wide. 2n = 14. Central and southern Europe; reported in the Willamette Valley of Oregon.

11. LATHYRUS TUBEROSUS L.

Glabrous perennial from rhizomes with small tubers, stems angled, 2-6 dm long; leaflets 2, elliptic to oblong, 2-4 cm long, 5-15 mm wide, tendrils well developed. Racemes with 4-10 flowers; flowers 8-12 mm long, calyx lobes shorter than calyx tube, corolla reddish. Legumes glabrous 2-4 cm long, 4-7 mm wide. 2n = 14. Central Europe; collected occasionally along roadsides in Washington.

12. LATHYRUS SYLVESTRIS L.

Glabrous perennial, stems broadly winged, 6-20 dm long; stipules mostly linear-lanceolate, 1-3 cm long; leaflets 2, lanceolate to elliptic-lanceolate, 5-12 cm long, 0.5-2 cm wide, tendrils well developed. Racemes with 4-9 flowers; flowers ca. 15 mm long, calyx

lobes shorter than calyx tube, corolla reddish. Legumes glabrous, 4-7 cm long, 5-15 mm wide. 2n = 14. Native of central Europe; established in waste places and along roadsides in Washington and Oregon. See discussion of next species with which L. sylvestris can be confused.

13. LATHYRUS LATIFOLIUS L.

Glabrous perennial, stems broadly winged, 8-20 dm long; stipules broadly lanceolate to ovate, 3-5 cm long; leaflets 2, lanceolate-elliptic to obovate-lanceolate, to 15 cm long and 5 cm wide; tendrils well developed. Racemes with 5-15 flowers; flowers 15-20 mm long, calyx lobes shorter than calyx tube, corolla red, pinkish-red to white. Legumes glabrous, 5-11 cm long, 5-10 mm wide. 2n = 14. Native of central and southern Europe, commonly established throughout the Pacific Coast. L. latifolius resembles L. sylvestris; it differs in having broader and longer stipules, larger fruits and somewhat larger flowers.

14. LATHYRUS LITTORALIS (Nutt. ex T. & G.) Endl.

Densely villous perennial from rhizomes; stems 1-6 dm long, angled, prostrate to erect, not scandent, often profusely branched. Leaves 1-3 cm long; tendrils bristle-like, sometimes flattened into a leaflet-like appendage; stipules semi-hastate, ovate to lanceolate, 1-2 cm long, 0.5-1.0 cm wide, usually larger than leaflets; leaflets 4-6, densely villous, narrowly obovate to oblanceolate, 1-2 cm long, 4-8 mm wide, lenght/width ratio 2-3. Racemes much longer than subtending leaf rachis, 4-6 flowered; flowers 13-15 mm long, corolla dark purple; lateral calyx lobes equal to or greater than calyx tube in length, deltoid to narrowly lanceolate; banner claw subequal to banner blade, keel strongly recurved; ovary densely curly pubescent, style 4-5 mm long, flattened, not twisted. Legumes pubescent, 2-3 cm long, 8-10 mm wide, 1-5 seeded. Chromosome number unknown.

Sand dunes along the Pacific Coast from Monterey County, California to Vancouver Island.

Lathyrus littoralis is a very distinctive native species endemic to the Pacific Coast. It appears to have no close relatives in the area.

15. LATHYRUS PALUSTRIS L.

Glabrous to sparsely pubescent perennial from rhizomes; stems 3-10 cm long, angled to narrowly winged, scandent. Leaves (2)4-6(7) cm long; tendrils well developed, unbranched or branched; stipules semi-hastate, narrowly lanceolate to linear, entire, often constricted into two lobes, 5-20(25) mm long, 1-8 mm wide, much smaller than leaflets; leaflets 4-6, glabrous to sparsely pubescent, narrowly elliptic, 2.5-5 cm long, 5-10 mm wide, L/W ratio (2.4)3.5-5.0(7.0). Racemes much longer that subtending leaf rachis, (3)4-5(6) flowered; flowers 12-14 mm long, corolla purple; lateral calyx lobes usually longer than calyx tube; banner claw subequal to banner blade in length; wings exceeding keel 2-4 mm; ovary glabrous to densely glandular or glandular-curly pubescent, style 5-6 mm long, flattened, not twisted. Legumes glabrous to sparsely glandular pubescent, 4-6 cm long, 4-6 mm wide, 5-8 seeded. 2n = 42.

Circumboreal; along the Pacific Coast in brackish sloughs and tidewater marshes from northern California to Alaska.

Vesture varies from glabrous (var. palustris) to densely soft pubescent forms referable to var. pilosus (Cham.) Ledeb. Lathyrus palustris is unique in the genus with an apparently hexaploid chromosome number of 2n = 42.

16. LATHYRUS JAPONICUS Willd.

Glabrous perennial from rhizomes; stems 1-5 dm long, angled to narrowly winged, procumbent. Leaves 6-10 cm long; tendrils longer than 1 cm, branched or unbranched; stipules hastate, ovate, 2-4 cm long, 1.5-2.5 cm wide, entire, equal to leaflets in size; leaflets 6-10, ovate to elliptic, 3-5 cm long. 15-25 mm wide, L/W ratio 1.5-2.5. Racemes equal to or longer than subtending leaf rachis, 4-8 flowered; flowers ca. 15 mm long, corolla reddish-purple to purple;

lateral calyx lobes longer than calyx tube, broadened above the base; banner claw subequal to banner blade in length, winges exceed keel by 4-5 mm; ovary densely curly and glandular pubescent, style 6-7 mm long, flattened, not twisted. Legumes sparsely curly and glandular pubescent, 3-7 cm long, ca. 1 cm wide. 2n = 14.

Circumboreal; found on sand dunes along the Pacific Coast from Del Norte County, California, to Alaska.

Pubescent forms are known but Pacific Coast populations are uniformly glabrous and referable to var. glaber (Ser.) Fernald.

17. LATHYRUS TORREYI Gray

Finely villous perennial from rhizomes; stems 5-30 cm long, not winged, decumbent to erect but not scandent. Leaves (3)4-5(6) cm long; tendrils bristle-like; stipules semi-hastate, linear to lanceolate, entire, often constricted into two lobes, 5-12 mm long, 1-5 mm wide, much smaller than leaflets; leaflets (8)10-12(14), ovate to elliptic, 5-15 mm long, 4-10 mm wide, L/W ratio (1.0)1.2-2.0(2.7). Racemes much shorter than subtending leaf rachis, 1-2 flowered; flowers 8-10 mm long; corolla pale purple; lateral calyx lobes deltoid, shorter than calyx tube; banner blade equal to or longer than banner claw; ovary densely glandular and curly pubescent, style 4-5 mm long, flattened, not twisted. Legumes villous, 1-2 cm long, ca. 5 mm wide. 2n = 14.

Openings in mesic Coast Ranges forests, below 1500 ft.; Santa Cruz County, California, to southwestern Washington.

Lathyrus torreyi has a very distinctive combination of traits and apparently is only distantly related to other species of Lathyrus along the Pacific Coast.

18. LATHYRUS NEVADENSIS Watson

Glabrous to sparsely pubescent perennial from rhizomes; stems 1-8 dm long, not winged, erect to clambering. Leaves 1-7(10) cm long; tendrils absent or bristle-like to well developed and branched; stipules semi-hastate, linear to lanceolate, usually entire, often

constricted into two lobes, 5-15 mm long, 1-5 mm wide, much smaller than leaflets; leaflets 4-8, glabrous to rather densely short-pubescent, ovate-elliptic to broadly lanceolate, (1)2-4(6) cm long, (0.5)1-2(3) cm wide, L/W ratio 2-3. Racemes usually longer than subtending leaf rachis, 2-6 flowered; flowers 12-16 mm long; corolla pale to dark purple; lateral calyx lobes deltoid, much shorter than calyx tube; banner blade equal to or longer than banner claw; wings subequal to keel in length; ovary glabrous, style 4-6(7) mm long, flattened, not twisted. Legumes glabrous, 3-7 cm long, 4-9 mm wide. 2n = 28.

Yellow pine, red fir and mixed evergreen forests of northern California and the temperate coniferous forests to the north; in the Sierra Nevada and Cascade Mountains from Madera County, California, to British Columbia; Coast Ranges from Lake County, California, northward to the Olympic Mountains. Also found in the mountains of northeastern Oregon, adjacent Washington and Idaho.

18a. LATHYRUS NEVADENSIS Wats. ssp. NEVADENSIS

Plants 1-3(4) dm tall; stems erect; leaflets usually 4-6, tendrils short and unbranched to absent. Range as above.

18b. LATHYRUS NEVADENSIS Wats. ssp. LANCEOLATUS (Howell) C. L. Hitchc.

Plants 2.5-5 dm tall; stems mostly scandent; leaflets usually 6-8, tendrils usually well developed and branched. Range as above.

Lathyrus nevadensis represents a morphologically diverse group of tetraploid populations of northwestern North America. It was revised by Hitchcock (1952) who recognized three subspecies, two of which commonly occur along the Pacific Coast. As described above, ssp. nevadensis is shorter, erect, generally smaller all around and lacks tendrils; ssp. lanceolatus is taller, sprawling, generally larger and has well developed tendrils. A continuum of variation exists between these extremes and the subspecies are sympatric throughout the range of the species along the Pacific Coast. A third subspecies, ssp. cusickii (Wats.) C. L. Hitchc., is confined to Northeastern Oregon and adjacent areas.

Hitchcock (1952) also described three varieties of ssp. lanceolatus, distinguishable chiefly on the basis of subtle differences in corolla color. I have chosen not to recognize these varieties; given the variation in L. nevadensis as a whole, a quadrinomial scheme seems unwarranted.

19. LATHYRUS LANSZWERTII Kell. ssp. ARIDUS (Piper) Bradshaw

Finely puberulent perennial from rhizomes; stems 1-8 dm long, angled, erect to clambering, unbranched or branched near the ground. Leaves 2-4 cm long; tendrils bristle-like to well developed; stipules linear to narrowly lanceolate, 5-15(20) mm long, 1-2 mm wide, much smaller than leaflets; leaflets (4)6-8(10), linear to narrowly lanceolate, 3-6(8) cm long, (1.5)2-5(6) mm wide, L/W ratio 10-15. Racemes 2-4(5) flowered, usually shorter than rachis of subtending leaf; flowers 8-11 mm long; corolla pale purple, lavender or rose; lateral calyx lobes deltoid, shorter than calyx tube; banner claw subequal to banner blade in length; wings subequal to keel; ovary glabrous, style 4-5 mm long, flattened, not twisted. Legumes glabrous, 4-6 cm long, 3-6 mm wide. 2n = 14, 28.

Generally east of the Cascades in Washington and Oregon and throughout the Great Basin. Found in the Pacific Coast region on dry slopes and in openings in yellow pine forests of north central California (Siskiyou, Trinity and Shasta Counties) and also, perhaps, in the western Sierra Nevada.

As delimited by Hitchcock (1952), L. lanszwertii consists of two subspecies: ssp. lanszwertii and ssp. aridus. Welsh (1965, 1975) has expanded the concept of lanszwertii to include specimens formerly referable to L. arizonicus, L. leucanthus and L. leucanthus var. laetivirens and has classified Utah populations into three varieties. Comments of Hitchcock (1952) further suggest that L. graminifolius and L. bijugatus are closely allied to L. lanszwertii and, in my experience, most specimens of L. tracyi are barely distinguishable from L. lanszwertii ssp. aridus. The L. lanszwertii complex is badly in need of study. However, most of the taxonomic problems are among populations growing east of the Cascade-Sierra

Crest.

20. LATHYRUS TRACYI Bradshaw

Glabrous or pubescent perennial from rhizomes; stems 1.5-5 dm long, angled, erect to scandent, often branched throughout their entire length. Leaves (0.5)1-6 cm long; tendrils absent to well developed and branched; stipules semi-hastate, linear to narrowly lanceolate, entire, often constricted into two lobes, 6-12 mm long, 1-3(4) mm wide, much smaller than leaflets; leaflets (2)4-6(8), either ovate and (1.5)2-3(4) cm long and 0.5-1.5 cm wide, or linear and (3)4-5(5.5) cm long and 2.5 mm wide. Racemes (3)5-8 flowered, usually longer than rachis of subtending leaf; flowers 9-10 mm long, corolla cream-white with lavender veins in banner; lateral calyx lobes deltoid to narrowly lanceolate, equal to or less than calyx tube; banner claw subequal to banner blade in length; wings subequal to keel in length; ovary glabrous, style 4-5 mm long, flat, not twisted. Legumes glabrous, 2.5-3.5 cm long, 4-7 mm wide. 2n = 14. Dry slopes, mixed evergreen and yellow pine forests of Humboldt, Trinity and Siskiyou Counties of northern California.

Specimens now referable to L. tracyi have strikingly dimorphic leaflets: either they are nearly linear, with L/W ratios in the range of 8-12, or they are ovate with L/W ratios ranging from 1.5 to 2.5. The linear-leafleted forms are distinguishable from L. lanszwertii only on the basis of flower color; other distinctions listed by Hitchcock (1952) such as number of leaflets, narrower stipules and smaller flowers, do not seem to hold up under quantitative analysis. In all probability, L. tracyi is conspecific with L. lanszwertii. However, in lieu of a complete investigation of the L. lanszwertii complex, I hesitate to pass judgement on the disposition of L. tracyi. (see remarks under L. lanszwertii ssp. aridus).

21. LATHYRUS PAUCIFLORUS Fernald ssp. BROWNII (Eastw.) Piper

Glabrous perennial from rhizomes; stems 2-6 dm long, angled, erect to ascending, unbranched or branched near the base of the plant;

leaves 3-6 cm long; tendrils absent to well developed and branched; stipules semi-hastate, narrowly lanceolate to linear, entire to crenate-dentate, sometimes constricted into two acute lobes, 5-15 mm long, 1-5(5) mm wide, much smaller than leaflets; leaflets glabrous (4)6-10, either ovate (1.5-3 cm long, 5-15 mm wide with L/W ratios 2-3) or linear (2.5-3.5 cm long, 3-5 mm wide, L/W ratios 7-12). Racemes 2-5 flowered, quite varied in relationship to length of subtending leaf rachis; flowers 12-14 mm long; corolla white to bluish; lateral calyx lobes deltoid, shorter than calyx tube; banner claw equal to or shorter than banner blade; wings 2-5 mm longer than keel, keel tip strongly recurved; style 4-5 mm long, flattened, not twisted. Legumes glabrous, 3-5 cm long, 4-7 mm wide. Chromosome number unknown.

Dry slopes, yellow pine forests, south central Oregon to the Tehachapi Range in Kern County, California, and in the northern Coast Ranges of California from the Oregon border to the vicinity of Snow Mountain in northeastern Lake County.

Hitchcock (1952) regarded ssp. brownii as "more unique" than other subspecific entities delimited in his revision and felt that it, perhaps, could be accorded specific rank. However, in general habit and floral structure it is referable to the L. pauciflorus complex, most of which is found east of the Cascade-Sierra Crest. This group as a whole is quite polymorphic and is need of further study.

22. LATHYRUS VESTITUS Nutt. ex T. & G., Fl. N. Am. 1:174. 1838.

Glabrous to densely curly pubescent perennial from rhizomes; stems 2-20 dm long, angled to narrowly winged, erect to procumbent or climbing, branched 1-3 times at ground level. Leaves (4)6-9(12) cm long; tendrils well developed, usually branched; stipules semi-hastate, ovate to linear, (0.5)1-2.5(3) cm long, (1)3-10(15) mm wide, dentate to nearly entire, sometimes constricted into two lobes, from subequal to much smaller than leaflets; leaflets (6)8-12(14), glabrous to densely pubescent, linear to ovate, (1.5)2-4(5) cm long, (0.5)1-2.5(3) cm wide, L/W ratios 1-10. Racemes (6)8-15(22)

cm long bearing 8-15(18) flowers at 1-3 flowers per cm; flowers (13) 15-18(21) mm long; corolla deep red-purple to white; calyx tube 3-5 mm long, glabrous to densely pubescent, banner lobes deltoid, 1-2 mm long, lateral lobes deltoid to broadly flared, 1.5-7 mm long, 1-3 mm wide, keel lobes narrowly triangular 3-7 mm long; banner claw 8-12 mm long, 7-10 mm wide, banner blade 8-15 mm long, 8-16 mm wide, reflexed 90-180° in flower; wings subequal to keel, claw 4-5 mm long, blade 8-12 mm long, 4-6 mm wide; keel claw 5-8 mm long, keel blades 7-14 mm long, 7-12 mm in height, tip recurved 0-3 mm; ovary glabrous to densely glandular and(or) curly pubescent, 9-14 mm long in flower, containing 15-20 ovules, style 6-9(10) mm long, flattened, not twisted. Legumes glabrous to sparsely glandular and(or) curly pubescent, 4-6 cm long, 4-7 mm wide. Seeds mottled olive brown or olive green and black to pure black, weighting (10)15-50(70) mgs. 2n = 14.

Found in a wide variety of habitats along the Pacific Coast from the vicinity of Puget Sound to Baja California; not found in the Sierra Nevada and rare in the western Cascade Range.

Populations of L. vestitus in the vicinity of Corvallis, Oregon, are self-incompatible. Hitchcock (1952) reports hybrid seed from the following crosses: L. vestitus ssp. alefeldii (his L. laetiflorus ssp. alefeldii) X L. splendens and L. vestitus ssp. barbarae (his L. laetiflorus ssp. barbarae) X L. jepsonii ssp. californicus. Both Cobb (1950) and Raven et al (1965) report meiotic irregularities in individuals collected in San Diego and Los Angeles Counties, California, respectively. Approximately 20-25% of the individuals collected south of San Luis Obisop County, California, (sample size = 52) were found to have less than 70% stainable pollen.

As delimited here, L. vestitus sensu lato includes all specimens formerly referable to L. laetiflorus Greene and all previously described entities treated by Hitchcock (1952) under these two names. The five subspecies described below represent modal combinations of traits identified by taximetric studies which seem to be relatively distinct geographically. Lathyrus vestitus s.l. represents a widespread, polymorphic species complex currently evolving into a number

of partially distinct entities and, given the range of habitats in which it is found, probably consists of several to many ecotypes.

22a. LATHYRUS VESTITUS ssp. VESTITUS

L. vestitus Nutt. ex T. & G., Fl. N. Am. 1:276. 1838. Type: Columbia Plains, Nuttall (BM!). Orobus vestitus Alef., Bonplandia 9:145. 1861.

L. venosus var. β T. & G., Fl. N. Am. 1:174. 1838. Type: Oregon; Nuttall (not seen).

L. palustris var. ε T. & G., Fl. N. Am. 1:276. 1838. Type: California; Douglas (not seen).

L. vestitus var. multiflorus Torr., Pac. R. R. Rep. 4:76. 1856. Type: California; Marin County, Tomales Bay, 19 April 1853, Bigelow (not seen).

L. violaceus Greene, Erythea 1:105. 1893. Type: grown at Berkeley from seeds from Los Angeles County, Davy s.n. (UC 15387!). L. bolanderi ssp. violaceus (Greene) Bradshaw, Bot. Gaz. 80:252. 1925. L. vestitus ssp. violaceus (Greene) Abrams, Ill. Flora Pac. States 2:626. 1944.

L. puberulus White ex Greene, Man. Bot. San Francisco 85. 1894. Type: California, Napa County, March 1852, Thurber 485 (GH NY). L. vestitus var. puberulus (White ex Greene) Jepson, Fl. W. Mid. Calif. 298. 1901. L. vestitus ssp. puberulus (White ex Greene) C. L. Hitchcock, Univ. Wash. Publ. Biol. 15:18. 1952.

L. quercetorum Heller, Muhlenbergia 2:290. 1907. Type: California; Santa Clara County, Mt. Hamilton, 31 May 1907, Heller 8623 (WTU!). L. bolanderi ssp. quercetorum (Heller) Bradshaw, Bot. Gaz. 80:253. 1925. L. bolanderi var. quercetorum (Heller) Jepson, Fl. Calif. 2:391. 1936.

Leaflets ovate to linear, medium to densely curly pubescent on both surfaces or, less frequently, on the lower surface only; flowers 14–16(17) mm long; lateral calyx lobes considerably broadened above the base, usually longer than the calyx tube; ovary medium to densely glandular and(or) curly pubescent; style less than 7.5 mm long.

Chaparral, northern and southern oak forests; (Humboldt) Mendocino and Lake Counties, California, south to Santa Barbara County.

Lathyrus vestitus ssp. vestitus of Hitchcock (1952) is referable only to plants with more or less erect stems, 1-4 dm in length with shorter internodes than typical specimens within this complex. Nuttall's type collection certainly displays this habit, and although plants with this phenotype are most often collected in hillside grasslands in the San Francisco Bay region, they occur in coastal areas from Monterey Bay to Curry County, Oregon. I concur with Hithcock (1952) concerning the origin of Nuttall's specimen; it could not have come from anywhere near the Columbia River and must have been collected along the coast of central California.

Although extreme examples of this phenotype are striking, taximetric analyses revealed a more or less continuous distribution for internode length, and it is not always easy to assign this name unambiguously sensu Hitchcock. This growth habit may be a phenotypic response to an open environment and high light intensities similar to that documented by transplant studies in Lespedeza (Clewell, 1964: his Figure 1). No doubt there have been genotypic responses to habitat variability among populations of L. vestitus, but considering the great morphological variability within the species as a whole, I hesitate to give this particular phenotype taxonomic recognition. Therefore, the name vestitus at the subspecific level is applied to all pubescent plants originating from central California.

Subspecies vestitus includes linear leafleted forms and a number of specimens with leaflets which are glabrous above but medium to densely pubescent below. The latter phenotype is most often collected in coastal areas from Sonoma County south to San Luis Obispo County.

22b. LATHYRUS VESTITUS ssp. BOLANDERI (Watson) C. L. Hitchcock, Univ. Wash. Publ. Biol. 15:19. 1952.

L. bolanderi Watson, Proc. Am. Acad. 20:363. 1885. Type: California; Oakland, thickets, creek banks, April-May, 1865,

Bolander 337 (holotype GH!, isotype NY).

L. peckii Piper, Proc. Biol. Soc. Wash. 31:190. 1918. Type: Oregon; Curry County, Harbor, 31 July 1913, M. E. Peck 4008 (not seen).

L. ochropetalus Piper, Proc. Biol. Soc. Wash. 31:189. 1918. Type: Washington; Seattle, June 1891, C. V. Piper 482 (holotype US, isotypes WTU! WSC NY). L. vestitus ochropetalus (Piper) C. L. Hitchcock, Univ. Wash. Publ. Biol. 15:19. 1952.

L. polyphyllus var. insedundus Jepson, Man. Fl. Pl. Calif. 582. 1925. Type: California; Marin County, Olema, 28 March 1897, Jepson 13644 (JEPS!).

Leaflets ovate to linear, glabrous; flowers (13)14-16 mm long; lateral calyx lobes broadened considerably above the base and longer than the calyx tube; ovary glabrous to sparsely glandular pubescent, style less than 7.0 mm long.

Openings in mixed evergreen and temperate coniferous forests; western Cascades and Coast Ranges of Washington and Oregon and in Del Norte and Humboldt Counties in California; south along the California coast to San Luis Obisop County.

Hitchcock's (9152) ssp. ochropetalus and ssp. bolanderi are distinguishable only on the basis of flower color; the former is said to have ochroleucous to creamy white flowers, the latter purplish flowers. White-flowered specimens are found from Curry and Josephine Counties, Oregon, northward. To the south most flowers have bluish to purplish tints of some sort, usually shades of lavender or rose. Morphologically the two subspecies are indistinguishable. I have chosen here to treat as one taxon all glabrous specimens of Washington, Oregon and coastal California; ssp. bolanderi intergrades with ssp. laevicarpus in Ventura County, California. (see also L. polyphullus and L. holochlorus for a discussion of differences among these three taxa.)

22c. LATHYRUS VESTITUS ssp. LAEVICARPUS Broich, ssp. nov.

Planta foliolis et ovariis omnino glabris; floribus 14-17 mm longis; lobis calycis lateralibus tubo brevioribus longioribusve;

stylo plerumque longiore quam 7.0 mm.

Leaflets ovate to linear, completely glabrous; flowers 14-17 mm long; calyx glabrous with ciliate margins, lateral lobes deltoid to broadened above the base, shorter than to longer than the calyx tube; ovary completely glabrous, style usually more than 7.0 mm long.

Chaparral and southern oak forests; Ventura, western Los Angeles, and southwestern Kern Counties, California. Type: California; Ventura County, Ojai-Saticoy Highway #150 about 10 miles east of Saticoy, 2 June 1952, C. L. Hitchcock 19573 (holotype WTU!, isotypes RSA! WS!).

When taximetric studies of this complex revealed a significant number of completely glabrous specimens with medium sized flowers originating from the region delimited above, it was assumed that Hitchcock's ssp. glaber (under L. laetiflorus) provided an available epithet for this group. However, the type of that taxon proves to have densely pubescent ovaries and is referable to the next subspecies. Therefore, it is necessary to describe a new entity. Subspecies laevicarpus intergrades with ssp. bolanderi to the north and ssp. barbarae to the south.

22d. LATHYRUS VESTITUS ssp. BARBARAE (White) Broich, comb. nov.

L. violaceus var. barbarae White, Bull. Torrey Bot. Club 21:452. 1894. Type: California; Santa Barbara, Wheelock in 1893 (NY!). L. strictus var. barbarae (White) Jepson, Man. Fl. Pl. Calif. 584. 1925. L. laetiflorus ssp. barbarae (White) C. L. Hitchcock, Univ. Wash. Publ. Biol. 15:22. 1952.

L. venosus var. grandiflorus Torr., Pac. R. R. Report 4:77. 1856 Type: California; Cocomungo, Bigelow in 1853-54.(not seen).

L. laetiflorus Greene, Erythea 1:105. 1893. Type: California; seeds from Los Angeles County, cultivated at Berkeley, May 1903 (holotype UC 15337!, isotype DS 118490!).

L. strictus var. thacherae Jepson, Man. Fl. Pl. Calif. 584. 1925. Type: California; Ventura County, Ojai Valley, 12 May 1916, Thacher 22 (JEPS!).

L. laetiflorus ssp. glaber C. L. Hitchcock. Univ. Wash. Publ. Biol. 15:22. 1952. (pro parte, including type). Type:

Mexico, Lower California, Ensenada, 10 April 1882, M. E. Jones (holotype UC!, isotype GH).

Leaflets ovate to linear, glabrous to densely curly pubescent; flowers (14)15–18 mm long; calyx pubescent, lateral lobes deltoid to narrowly lanceolate, usually shortern than calyx tube; overy densely glandular and(or) curly pubescent; style greater than 7.5 mm long.

Chaparral and southern oak forests of eastern Los Angeles, San Bernardino, Riverside and Orange Counties, California.

Leaflet pubescence varies greatly within this subspecies: there are plants with completely glabrous leaflets, plants with leaflets that are glabrous above and pubescent below and plants with densely pubescent leaflets. Pubescence varies clinally; plants from the Santa Monica and San Gabriel Mountains tend to be glabrous to subglabrous while specimens collected in the San Bernardino Mountains are densely pubescent. Despite this variability, taximetric studies indicate that this group is morphologically coherent.

Glabrous leafleted forms can be confused with ssp. laevicarpus; however, ssp. barbarae consistently has pubescent ovaries. Pubescent forms intergrade with ssp. vestitus and can be separated from that taxon only on the somewhat arbitrary basis of the morphology of lateral calyx lobes and length of the style.

22e. LATHYRUS VESTITUS ssp. ALEFELDII (White) Broich, comb. nov.

L. alefeldii White, Bull. Torrey Bot. Club 21:449. 1894. Type: California; San Diego, May 1852, Thurber 574 (holotype NY, isotype GH!). L. strictus var. alefeldii (White) Jepson, Man. Fl. Pl. Calif. 584. 1925. L. laetiflorus var. alefeldii (White) Jepson, Fl. Calif. 2:391. 1936. L. laetiflorus ssp. alefeldii (White) C. L. Hitchcock, Univ. Wash. Publ. Biol. 15:23. 1952.

L. strictus Nutt. ex T. & G., Fl. N. Am. 1:176. 1838, not Graver, 1784. Type: St. Diego, California, Nuttall (not seen).

Orobus californicus Alef., Bonplandia 9:146. 1861, not L. californicus Douglas.

Leaflets ovate to linear, subglabrous to glabrous; flowers 16–20

(21) mm long; calyx pubescent, lateral lobes deltoid, shorter than calyx tube; ovaries glabrous to densely glandular pubescent, style 7-10 mm long.

Chaparral, San Diego, Orange and Riverside Counties south into Baja California and on Santa Catalina Island.

Plants referable to ssp. alefeldii have large, wine-red flowers with greatly reflexed banners. In shape, these flowers resemble those of L. splendens but they are smaller and there is now overlap in floral size between these two taxa. Morphological intergradation between ssp. alefeldii and both ssp. laevicarpus and ssp. barbarae is extensive.

23. LATHYRUS SPLENDENS Kell., Proc. Cal. Acad. Sci. 7:90. 1876.
Type: Southern California, J. M. Hutchings in May 1876. (CAS)

Glabrous to sparsely pubescent perennial from rhizomes; stems 4-30 dm long, angled, scandent on shrubs. Leaves (4)5-8 cm long; tendrils well developed, usually branched; stipules semi-hastate, lanceolate to linear, 10-20 mm long, 2-8 mm wide, usually dentate, sometimes constricted into two lobes, much smaller than leaflets; leaflets 6-10, usually glabrous above and moderately pubescent below, ovate to lanceolate or linear, 2-4 cm long, 3-15 mm wide, L/W ratio 2-4.5 or 8-9. Racemes 4-16 cm long bearing (4) 6-10 flowers. Flowers 25-30 mm long; corolla deep wine red; calyx tube 5-6 mm long, usually medium curly pubescent, banner lobes deltoid, lateral lobes deltoid to narrowly lanceolate, equal to or less than calyx tube in length, 3-5 mm long, 1-2 mm wide, keel lobe 4-7 mm long; banner claw 8-9 mm long, ca. 1 mm wide, banner blade 20-26 mm long, ca. 20 mm wide, reflexed 180° in flower; wings subequal to keel, claw 5-6 mm long, blade 17-20 mm long, 8-10 mm wide; keel claw 6-8 mm long, keel blade 10-15 mm long, 16-21 mm high; ovary 14-17 mm long in flower, style 14-20 mm long, flattened, not twisted. Legumes sparsely glandular pubescent, 5-8 cm long, 5-9 mm wide. Seeds black, weighing 45-75 mgs. $2n = 14$.

Chaparral, extreme south central San Diego County, California, and adjacent Mexico.

Hitchcock (1952) has reported hybrid seed from crosses of L. splendens by L. jepsonii ssp. californicus and by L. vestitus ssp. alefeldii (his L. laetiflorus ssp. alefeldii).

A number of authors (Bradshaw 1925; Jepson 1936; Hitchcock 1952) have commented on the apparent close relationship of L. splendens with what is referred to here as L. vestitus ssp. alefeldii. Taximetric studies reveal no morphological intergradation in floral size but resemblances are striking; these two taxa might be considered a parent-offspring species pair and, perhaps, an example of sympatric speciation worthy of an evolutionary study to determine the factors involved in their origin.

24. LATHYRUS JEPSONII Greene, Pittonia 2:158. 1890.

Glabrous or pubescent perennial from rhizomes; stems 4-25 dm long, broadly winged, scandent, usually branched 1-3 times near ground level; leaves 9-12 cm long; tendrils well developed, branched; stipules semi-hastate, narrowly lanceolate to linear, 10-20(30) mm long, 2-6 mm wide, dentate or constricted into two lobes, much smaller than leaflets; leaflets glabrous or pubescent, 9-12, narrowly ovate to lanceolate, 3-6 cm long, 0.5-2.0 cm wide, L/W ratio 3-5. Racemes 8-15(19) cm long bearing 6-14(17) flowers at 1.5-3 per cm; flowers (13)15-17 mm long, corolla pale pink to rose purple; clayx tube 3.5-5 mm long, banner lobes deltoid, 0.5-1.5 mm long, lateral lobes deltoid to lanceolate and broadened above the base, 1.5-4(5) mm long, 1-2 mm wide, keel lobe linear triangular, 3-5 mm long; banner claw 8-13 mm long, 8-10 mm wide, banner blade 8-13 mm long, 12-17 mm wide, erect in flower; wings subequal to keel, claw 6-8 mm long, blade 8-10 mm long, 4-6 mm wide; keel claw ca. 4 mm long, keel blades 6-7 mm long, 8-10 mm high, tip recurved 1-3 mm; ovary completely glabrous, 10-15 mm long in flower, containing 14-16 ovules, style 1-8.5 mm long, flattened, not twisted. Legumes glabrous, 5-9 cm long,6-9 mm wide. Seeds black weighing 50-110 mg. 2n = 14.

Grasslands, marshes and along forest streams; inner Coast Ranges, the Central Valley and the foothills of the Sierra Nevada from Monterey, San Benito and Tulare Counties northward to Siskiyou County,

California.

Lathyrus jepsonii has been reported to be interfertile with L. sulphureus, L. vestitus ssp. bolanderi, L. vestitus ssp. barbarae (=L. laetiflorus ssp. barbarae) and L. splendens (Hitchcock 1952).

Lathyrus jepsonii appears to be closely related to the L. vestitus complex. It can be distinguished from members of that group by its broadly winged stems, light green, lanceolate leaflets, usually deltoid lateral calyx lobes and glabrous ovaries. It is ecologically distinct from L. vestitus and, for the most part, has a different geographic distribution. The ranges of these two species overlap in the central California Coast Range from northern Lake and Mendocino Counties to Monterey and San Benito Counties. A few collections from this area appear to be intermediate between these two species; intermediate collections have narrowly winged stems, light green leaflets, long lanceolate, sometimes flared, lateral calyx lobes and pubescent ovaries. When ovaries are pubescent, these plants will be identified as L. vestitus in the key given above. Intergradation between L. jepsonii and L. vestitus does not appear extensive and most specimens present no problem in identification. However, it is quite possible that localized introgressive hybridization takes place between these two taxa where their ranges overlap.

24a. LATHYRUS JEPSONII ssp. JEPSONII

L. jepsonii Greene, Pittonia 2:158. 1890. Type: California; Solano County, Teal Station, Suisum Marshes, 6 October 1890, Jepson (holotype UC, isotype NY).

Leaflets glabrous to subglabrous.

Collected primarily in the Suisun Marshes above San Pablo Bay and at the southern end of San Francisco Bay. A few glabrous collections have come from Tulare, Fresno and San Joaquin Counties.

Hitchcock (1952) seemed to apply the epithet ssp. jepsonii only to plants collected in the Suisun Marshes and cites glabrous specimens collected elsewhere as "glabrous variants in the area where the hairy form usually occurs and can as well be called ssp. jepsonii as

californicus" (p. 20). These specimens were annotated by Hitchcock as ssp. californicus. To be consistent, all glabrous L. jepsonii, regardless of origin, should be referred to subspecies jepsonii.

Lathyrus jepsonii ssp. jepsonii is relatively rare and, given the extent of human disturbance in the San Francisco Bay region, probably should be considered in danger of extinction.

24b. LATHYRUS JEPSONII ssp. CALIFORNICUS (Watson) C. L. Hitchcock, Univ. Wash. Publ. Biol. 15:18. 1952.

L. venosus var. californicus Watson, Proc. Am. Acad. 11:133. 1876. Lectotype (designated by C. L. Hitchcock): California; Sonoma County, E. Samuels 45 (GH). L. californicus (Watson) Watson, Proc. Am. Acad. 20:363. 1885, not L. californicus Douglas, 1828.

L. watsonii White, Bull. Torrey Bot. Club 21:447. 1894. Type: California; Monterey and Sonoma Counties, J. Torrey in 1865 (GH NY).

Leaflets medium to densely curly pubescent.

Occurs throughout the range of the species.

Subspecies californicus is a widespread pubescent form of L. jepsonii occurring along stream banks and in oak-pine forests from Shasta to Tulare Counties in California.

25. LATHYRUS HOLOCHLORUS (Piper) C. L. Hitchcock, Univ. Wash. Publ. Biol. 15:31-32. 1952.

L. ochropetalus ssp. holochlorus Piper, Proc. Biol. Soc. Wash. 31:190. 1918. Type: Oregon, Benton County, hills south of Corvallis, May 1916, Gilbert 115 (holotype WS, isotype OSC!).

Glabrous perennial from rhizomes; stems 3-10 dm long, angled to narrowly winged, scandent, often branched at or just below the flowering nodes. Leaves 6-10 cm long; tendrils well developed, branched; stipules semi-sagittate, lanceolate to linear, 10-20mm long, 1-8 mm wide, dentate or occasionally constricted into two lobes, usually much smaller than leaflets; leaflets glabrous, 8-10(12), ovate to lanceolate,

25–45 mm long, 15–25 mm wide, L/W ratio 1.5–2.5. Racemes 5–10(15) cm long bearing 7–14(16) flowers at 3.5–5.5 per cm; flowers 12–14(15) mm long, corolla cream white with lavender to rose colored veins in banner; calyx tube 3.5–4.5 mm long, banner lobes deltoid, ca. 1 mm long, lateral lobes narrowly lanceolate, subequal to calyx tube, 3–5 mm long, 1–2 mm wide, keel lobe linear, 3–5 mm long; banner claw 7–10 mm long, 5–8 mm wide, banner blade 7–9 mm long, 10–13 mm wide, erect in flower; wings subequal to keel, claws 8–10 mm long, blade 8–9 mm long, 3–4 mm wide; keel claws 7–8 mm long, keel blades 5–6 mm long, 6–8 mm high, tip recurved 0–3 mm; ovary glabrous, 9–11 mm long in flower, containing 12–14(18) ovules, style 5–6 mm long, flattened, not twisted. Legumes glabrous, 3–5 cm long, 4–7 mm wide. Seeds greenish-tan or reddish-tan mottled with black, weighing 40–60 mg. 2n = 14.

Roadside fencerows, grasslands and oak woodlands in the Willamette Valley of Oregon, from Lane County north to the vicinity of Portland.

In pollination experiments, bagged inflorescences failed to set seed despite abundant pollen loads on the stigma from anthers of the same flower. All attempted crosses between L. holochlorus, L. vestitus and L. polyphyllus to date have failed.

Lathyrus holochlorus is sometimes confused with white-flowered forms of L. vestitus ssp. bolanderi. It differs in having somewhat smaller flowers with shorter, lanceolate lateral calyx lobes, more dense, secund racemes and often lateral branches at or just below the flowering nodes. Lathyrus vestitus ssp. bolanderi is confined to openings in Coast Range forests west of the Willamette Valley, and sympatry between these two species has not been observed.

In agricultural areas of the Willamette Valley, L. holochlorus is found in roadside fencerows, frequently with Symphoricarpos albus, Rosa spp. and Rubus spp. It is most often collected west of the Willamette River in Benton, Polk and Yamhill Counties. Several small populations, observed for 2–4 years, have consistently failed to set seed despite the presence of pollinators. This is probably because each colony represents one self-incompatible clone.

26. LATHYRUS DELNORTICUS C. L. Hitchcock, Univ. Wash. Publ. Biol. 15:30. 1952. Type: California; Del Norte County, 0.2 mi. below bridge over Myrtle Creek on Hwy 199, 8 June 1949, C. L. Hitchcock 19100 (holotype WTU!, isotypes DS! UC!).

Glabrous perennial from rhizomes; stems 2-8 dm long, winged, erect to ascending, unbranched or branched at ground level. Leaves 9-12(16) cm long; tendrils well developed, branched; stipules semi-hastate, lanceolate to narrowly lanceolate, 10-30 mm long, 3-15 mm wide, wide, entire to dentate, sometimes nearly as large as terminal leaflets; leaflets glabrous, (8)9-12(14), lanceolate, 30-50 mm long, 5-15 mm wide, L/W ratio 3-5. Racemes 7-10 cm long bearing 8-12 flowers at 3-5 per cm; flowers 9-12 mm long, corolla white with lavender veins in banner blade; calyx tube 3.5-4.5 mm long, glabrous, banner lobes deltoid, 1-2 mm long, lateral lobes lanceolate, usually subequal or longer than calyx tube, 3-5 mm long, 0.5-1.0 mm wide, keel lobe linear, 5-6 mm long; banner claw 6-9 mm long, 5-7 mm wide, banner blade 6-9 mm long, 9-14 mm wide, erect in flower; wings subequal to keel, claws 4-6 mm long, blades 5-7 mm long, 3-4 mm wide; keel claws 6-7 mm long, keel blade 4-6 mm long 5-7 mm high, tip recurved 1-2 mm; ovary glabrous, 7-9 mm long in flower, containing 9-12(16) ovules, style 4-5 mm long, flattened, not twisted. Legumes glabrous, 3-4 cm long, 3-5 mm wide. Seeds greenish-tan to reddish-tan mottled with black, weighing 25-35 mg. 2n = 14.

Serpentine areas along rivers and creeks in the Siskiyou Mountains; Josephine and Curry Counties in Oregon and Del Norte and western Siskiyou Counties in California. It is not known to occur north of the Rogue River, east of the Illinois River Valley or south of the South Fork Smith River.

The adaptation of L. delnorticus to serpentine soils is unique among Pacific Coast Lathyrus.

27. LATHYRUS SULPHUREUS Brewer ex Gray, Proc. Am. Acad. 7:399. 1867.

Glabrous or pubescent perennial from rhizomes; stems 5-15 dm long, angled, clambering, branched only at ground level. Leaves 9-12(13) cm long; tendrils well developed, branched; stipules semi-sagitate,

ovate to lanceolate,(10)15-25 mm long, 4-10 mm wide, dentate, sometimes nearly as large as terminal leaflets; leaflets glabrous or more rarely pubescent, 7-11, ovate-elliptic to narrowly elliptic, 25-50 mm long, 10-20 mm wide, L/W ratio 1-3(4). Racemes 7-10(14) cm long bearing (6)9-15(20) flowers at 3-5 per cm; flowers 11-13 mm long, corolla yellow to cream white; calyx tube 3.5-4.5 mm long, banner lobes deltoid, 0.5-1.0 mm long, lateral lobes lanceolate to flared above the base, usually shorter than the calyx tube, 2-4 mm long,0.5-1.5 mm wide, keel lobe linear, 4-6 mm long; banner claw 8-10 mm long, 8-12 mm wide, banner 5-6 mm long, 7-10 mm wide, erect in flower; wings subequal to keel, claws 6-7 mm long, blades 4-6 mm long, 3-4 mm wide; keel claws 6-8 mm long, keel blade 4-6 mm long, 5-6 mm high, tip strongly recurved; ovary glabrous, 8-10 mm long in flower, containing 11-13 ovules, style 4-5 mm long, twisted 90° at time of anthesis. Legumes glabrous, 4-7 cm long, 4-6 mm wide. Seeds dark brown to black, slightly mottled with tan, weighing 20-40 mg. 2n = 14.

Forests of oak and pine in the Inner Coast Ranges of northern California, from Lake County north to the Oregon Border, and in the foothills of the Sierra Nevada from the Greenhourn Mountains of Kern County north to Siskiyou County.

Hitchcock (1952) reported successful crosses between L. sulphureus, L. vestitus ssp. bolanderi and L. jepsonii ssp. californicus.

Lathyrus sulphureus is unique among Pacific Coast Lathyrus in that the banner claw is longer and wider than the banner blade. This gives the flower a "stubby" appearance. It is also unique among North American species in that the style is twisted 90° at the time of anthesis. Lathyrus sulphureus is morphologically relatively homogeneous and lacks the linear-leafleted forms common in other western species, but it is divisible into two varieties on the basis of pubescence.

27a. LATHYRUS SULPHUREUS var. SULPHUREUS

L. sulphureus Brewer ex Gray, Proc. Am. Acad. 7:399. 1867.

Type: California; Granes Flat, Brewer 1623 (holotype GH,

isotype UC!).

L. ochroleucus var. pedunculis Torr., Pac. R. R. Rep. 4:77. 1857. Type: California; Murphy's, Begelow (not seen).

Rattan in 1886, specimen marked "a" (not seen).

Leaflets glabrous.

Variety sulphureus is the common form of L. sulphureus, occurring throughout the range cited above.

27b. LATHYRUS SULPHUREUS var. ARGILLACEUS Jepson, F. Calif. 2:293. 1936. Type: California; Tehama County, Rosewood, 1899, Jepson 13635 (JEPS!).

Leaflets densely curly pubescent.

The pubescent var. argillaceus represents an apparently rare form which needs further study. In the more than 45 years since its description by Jepson there are still no more than the five specimens seen by Hitchcock (1952) in California herbaria. These five collections are from rather widely separated sites, from Shasta and Tehama Counties in the north to Placer County further south. In 1980 I collected several sterile, pubescent specimens in Nevada County which are probably referable to this taxon, but I did not have time to search the northwestern Sierra Nevada foothills for additional material. Therefore, it is difficult to judge the geographical extent of populations referable to this variety.

28. LATHYRUS POLYPHYLLUS Nutt. ex T. & G., Fl. N. Am. 274. 1938. Type: Columbia woods, Nuttall (holotype PH, isotype NY).

L. ecirrhosus Heller, Muhlenbergia 1:54. 1904. Type: California; Lake County, Heller 5944 (NY, DS).

Glabrous perennial from rhizomes; stems 4-8 dm long, angled, erect or scandent usually unbranched, sometimes branched at ground level. Leaves 11-16(20) cm long; tendrils well developed, branched; stipules semi-hastate, ovate to lanceolate, 20-30(40) mm long, (5)10-20 mm wide, dentate, approaching leaflets in size; leaflets glabrous, 11-15, ovate to lanceolate, 30-50(60) mm long, 10-30 mm wide, L/W

ratio 1.5-3(4). Racemes 9-14(16) cm long, bearing 8-12 flowers at 1.5-2.5 per cm; flowers 15-18 mm long, corolla banner dark purple, keel and wings lighter, calyx tube 4.5-5.5(6.0) mm long, banner lobes deltoid, 1-2 mm long, lateral lobes deltoid to narrowly lanceolate, usually shorter than calyx tube, 3-4 mm long, ca. 1 mm wide, keel lobe linear, 3-6 mm long; banner claw 10-14 mm long, 6-9 mm wide, banner blade 7-10 mm long, 15-15 mm wide, suberect to erect in flower; wings subequal to keel in length, claws 7-9 mm long, blades 8-10 mm long, 4-5 mm wide; keel claws 7-9 mm long, blades 5-7 mm long, 6.5-7.5 mm high, tip usually not recurved; ovary glabrous, 10-12 mm long in flower, containing 12-15(18) ovules, style 4-6 mm long, flattened, not twisted. Legumes glabrous, 4-7 cm long, 4-9 mm wide. Seeds mottled black and tan, weighing 30-50 mg. $2n = 14$.

Temperate coniferous forests from Vancouver Island south in the Coast Ranges and western Cascades of Washington and Oregon; and in mixed evergreen and coniferous montaine forests of northwestern California to northern Lake County.

In pollination experiments, bagged inflorescences failed to set seed despite self pollination. All attempted crosses of L. polyphyllus to L. holochlorus and L. vestitus ssp. bolanderi have failed to date.

Lathyrus polyphyllus is probably the most common species of Lathyrus in the coniferous forests of western Washington and Oregon. In southwestern Oregon and adjacent California it can be confused with purplish-flowered forms of L. vestitus ssp. bolanderi; in this particular region differences between these two taxa are subtle. Lathyrus polyphyllus typically has darker purple banners, more leaflets, deltoid to narrowly lanceolate lateral calyx lobes which are equal to or less than the calyx tube in length, and completely glabrous ovaries. Lathyrus vestitus ssp. bolanderi has lighter lavender or rose-colored flowers, fewer leaflets, lateral calyx lobes broadened above the base and equal to or longer than the calyx tube, and usually a few (sometimes submicroscopic) glandular hairs on the ovary. One could perhaps consider this phenotypic similarity an

outcome of introgression; but I have never seen what I would consider hybrids or introgressed populations, and attempts to cross these two taxa have failed thus far.

29. LATHYRUS GLANDULOSUS Broich, sp. nov.

Type: California; Humboldt County, 5.3 mi. northeast of the Freshwater-Kneeland road on the road to Maple Creek, T4N R2E ca. Sec. 2, 9 June 1981, Broich 1146 (holotype OSC, isotypes WTU, ISC, HSU).

Planta perennis, rhizomatos, dense glandulosa pubescens; caulibus 3-6 dm altis, anguste vel late alatis, erectis vel scandentibus; foliolis 14-18, inferne dense glandulosis pubescentibus, ovatis ad lanceolatis, 3-5 cm longis, 1-2 cm latis; racemis (5)7-11(14)-floris, foliis brevioribus; floribus 10-12(14) mm longis, vexillo purpureo, alis et carina albis; ovariis dense glandulosis pubescentibus; stylo 4-5 mm longis, complanato, non torti; leguminibus 3-5 cm longis, 6-8 mm latis, parce glandulosis pubescentibus.

Densely glandular pubescent perennial from rhizomes; stems 3-6 dm long, narrowly to widely winged, erect to clambering, unbranched or branched at ground level. Leaves 14-18 cm long; tendrils well developed, branched; stipules semi-hastate, narrowly lanceolate to linear, 10-20 mm long, 1-5 mm wide, usually constricted into two acute lobes, much smaller than leaflets; leaflets sparsely curly and densely glandular pubescent below, 14-18, ovate to lanceolate, 3-5 cm long, 1-2 cm wide, L/W ratio 2-4. Racemes 10-16(20) cm long, shorter than the rachis of the subtending leaf, with (5)7-11(14) flowers at 1-2 per cm; flowers 10-12(14) mm long, banner purple, wings and keel lighter; calyx tube 3-4 mm long, banner lobes deltoid, 1-2 mm long, lateral lobes narrowly lanceolate, subequal to or longer than calyx tube, 3-5 mm long, ca. 1 mm wide, keel lobe linear, 4-6 mm long; banner claw 7-10 mm long, 5-7 mm wide, banner blade 7-10 mm long, 11-14 mm wide, erect in flower; wings 1-3 mm longer than keel, claws 5-7 mm long, blade 7-10 mm long, 4-6 mm wide; keel claws 5-7 mm long, keel blades 4-5 mm long, 6-7 mm high, tip strongly recurved; ovary densely glandular pubescent, 6-10 mm long in flower, containing 10-14

ovules, style 4-5 mm long, flattened, not twisted. Legumes sparsely glandular pubescent, 3-5 mm long, 6-8 mm wide. Seeds mottled green or tan and black, weighing 15-30 mg. 2n = 14.

Roadsides and oak woodlands upland from the redwood forests of Humboldt and northern Mendocino Counties in California.

The earliest collections I have seen of this species were those of J. P. Tracy. In herbaria these specimens often have been left unnamed or have been labeled L. polyphyllus, a species to which they are vegetatively similar. However, taximetric studies indicate that specimens referable to L. glandulosus, as described here, are phenotypically different from all other Pacific Coast taxa and there is adequate evidence to justify the specific status of these populations.

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APPENDICES

Introduction

The three appendices that follow contain citations for (A) the specimens included in the matrix LATH, (B) the specimens included in the matrix LATHTWO and (C) additional specimens examined. Type specimens listed in the taxonomic section as examined are not included here. Herbarium abbreviations follow Holmgren and Keuken (1974); in appendices A and B the herbarium citation lists first, the specimen measured, followed by a slash, and then duplicates if they exist. For example: (DS/ UC WTU) indicates that the DS specimen was measured, duplicates from UC and WTU were examined.

Additional abbreviations are as follows:

CA: California
ca: approximately
CO: County
CG: Campground
Cr: Creek

E: east
Hwy: highway number
jct: junction
km: kilometres
mi: miles

Mt: Mount ...
N: north, also: NE: northeast; NW: northwest
Natl For: National Forest
OR: Oregon
R: range

Rd: an officially named road
rd: an unofficially named road
S: south, also: SE: southeast; SW: southwest
S (followed by a number): section number
sn: sine numero (without number)
T: township
W: west
w/: with
WA: Washington

Appendix A: The Specimens in LATH

OTU Lathyrus delnorticus C. L. Hitchcock

1D Josephine Co., OR: 3 mi W of Gasquet Trail Marker on the O'brien-Sourdough Camp rd, 21 June 1950, Kruckeberg 1865 (WTU/ UC)

2D Josephine Co., OR: ca 5 mi sw of O'brien, 9 July 1949, Hitchcock 19103 (CAS/ DS UC OSC WTU)

3D Del Norte Co., CA: Panther Flat CG, Six Rivers Natl For, 4 June 1979, Broich 642 (OSC)

4D Del Norte Co., CA: along French Hills RD 0.4 mi from jct w/ Hwy 199, 6 June 1979, Broich 654 (OSC)

5D Del Norte Co., CA: Grassy Flat CG, Six Rivers Natl For, 18 May 1980, Broich 752 (OSC)

6D Del Norte Co., CA: along French Hills Rd 0.5 mi from jct w/ Hwy 199, 18 May 1980, Broich 753 (OSC)

7D Del Norte Co., CA: 0.2 mi below Myrtle Cr bridge on Hwy 199, 4 June 1979, Broich 639 (OSC)

8D Del Norte Co., CA: Ceder Cr Flat, 28 May 1938, Van Deventer 243 (JEPS)

9D Del Norte Co., CA: Shelley Cr, 2 July 1936, Eastwood and Howell 3678 (UC/CAS)

10D Curry Co., OR: 0.5 mi downstream from bridge over the Chetco River on Forest Service Rd 3917, 9 June 1980 Broich 735 and Rogers-Rochna (OSC)

Lathyrus glandulosus Broich sp. nov.

1G Humboldt Co., CA: along Maple Creek Rd, 0.5 mi from jct w/ Kneeland-Bridgeville rd, 20 May 1980, Broich 772 (OSC)

2G Humboldt Co., CA: 26 mi N of Bridgeville on rd to Kneeland, 20 May 1980, Broich 777 (OSC)

3G Humboldt Co., CA: Kneeland Prairie, 10 June 1906, Tracy 2474 (UC)

4G Humboldt Co., CA: on rd to Maple Creek 5.3 mi NE of jct w/ Kneeland-Bridgeville rd, 9 June 1981, Broich 1146 (OSC)

5G Humboldt Co., CA: on rd to Maple Creek 7.2 mi NE of jct w/ Kneeland-Bridgeville rd, 9 June 1981, Broich 1147 (OSC)

6G Humboldt Co., CA: on rd to Maple Creek 0.7 mi NE of jct w/ Kneeland-Bridgeville rd, 9 June 1981, Broich 1148 (OSC)

7G Humboldt Co., CA: on rd to Maple Creek 1.0 mi NE of jct w/ Kneeland-Bridgeville rd, 9 June 1981, Broich 1149 (OSC)

OTU Lathyrus glandulosus Broich sp. nov. continued

8G Humboldt Co., CA: 4.9 mi S of the Kneeland School on rd to Bridgeville, 9 June 1981, Broich 1154 (OSC)

9G Mendocino Co., CA; ca 9 mi S of Legget on rd to coast, 21 May 1980, Broich 784 (OSC)

10G Mendocino Co., CA: S Fork of Eel River opposite Rd Mt, 10 mi S of Humboldt Co line, 28 April 1933, Tracy 12074 (UC)

11G Humboldt Co., CA: Cameron Hill, Kneeland, 19 May 1946, Tracy 17530 (UC)

12G Humboldt Co., CA: along "Lord Ellis Rd", W of Summit between N Fork of Mad River and Redwood Cr, 15 June 1946, Tracy 17571 (UC)

Lathyrus holochlorus (Piper) C. L. Hitchcock

1H Linn Co., OR: lakes and ponds near Orleans, 3 mi E of Corvallis, 11 May 1918, Lawrence 1459 (DS)

2H Benton Co., OR: moist meadows S of Corvallis, 5 May 1923, G.H., A.F. and L.F. sn (DS 150788)

3H Lane Co., OR: ca 10 mi S of Cottage Grove, 30 May 1951, Hitchcock 19345 (WTU/ UC)

4H Yamhill Co., OR: 7 mi S of McMinnville, 29 May 1951, Hitchcock 19296 (WTU/ UC)

5H Polk Co., OR: 2 mi S of Willamina on Hwy 22, 29 May 1951, Hitchcock 19303 (UC/ WTU)

6H Lane Co., OR: 2.8 mi N of Lorane, 5 June 1980, Broich 852 (OSC)

7H Linn Co., OR: 4 mi E of Crabtree, 29 April 1980, Broich 701 (OSC)

8H Linn Co., OR: ca 2 mi N of Tangent on Hwy 99W, 24 May 1979, Broich 630 (OSC)

9H Linn Co., OR: Freeway Lakes County Park, T11S R3W S25, 16 May 1979, Broich 617 (OSC)

10H Benton Co., OR: along Eureka Rd, T13S R5W S35, 10 May 1979, Broich 602 (OSC)

11H Polk Co., OR: 1 mi S of Monmouth on Hwy 99W, 0.2 mi E on Stapleton Rd, T8S R4W S31, 8 May 1980, Broich 733 (OSC)

12H Yamhill Co., OR: ca 5 mi S of Lafayette on rd to Hopewell, 8 May 1980, Broich 729 (OSC)

13H Yamhill Co., OR: 5 mi E of Yamhill on Hwy 240, T3S R3W S7, 8 May 1980, Broich 728 (OSC)

OTU Lathyrus jepsonii Greene

1J Solano Co., CA: Suisun Marsh, 6 July 1913, Eastwood 3445 (CAS)

2J Humboldt Co., CA: vicinity of Garberville, 30 May 1927, Tracy 8091 (WTU)

3J Mendocino Co., CA: near Handley's, 3 May 1903, McMurphy 134 (DS)

4J Mendocino Co., CA: ca 4 mi S of Laytonville on Hwy 101, 7 June 1949, Hitchcock 19079 (WTU/ UC)

5J Trinity Co., CA: 0.2 mi W of bridge over S Fork Trinity River near Hwy 299, 8 June 1949, Hitchcock 19089 (WTU/ UC)

6J Marin Co., CA: Fairfax Hills, 18 May 1947, Howell 23174 (CAS)

7J Butte Co., CA: Chico-Hamilton rd 6 mi from Chico, 1 May 1914, Heller 11345 (CAS/ WTU DS OSC)

8J Butte Co., CA: 1 mi N of Durham, 14 May 1937, Wolf 8670 (CAS/ WTU)

9J Siskiyou Co., CA: Cantaro, 23 May 1923, Eastwood 11937 (CAS)

10J Monterey Co., CA: Big Cr, Frances Simes Hastings Natural History Reservation, 29 May 1945, Linsdale 299 (CAS)

11J San Benito Co., CA: Tres Pinos, 14 May 1918, Eastwood 6891 (UC/ CAS)

12J San Benito Co., CA: on Coalinga Rd, 11 mi N of Clear Creek Rd, 10 May 1965, Hesse 3284 (DS)

13J Alameda Co., CA: road by Kaiser Plant, Niles Canyon, 7 May 1968, Wetzel 352 (DS)

Lathyrus laetiflorus Greene (for reclassifications, refer to listings in Appendix B)

1L San Diego Co., CA: head of Otay Lake, T18S R1E S4, 5 March 1938, Wieslander 729 (UC)

2L San Diego Co., CA: slopes along Jamul River Valley, upper Otay Lakes RD 5.4 mi W of jct w/ Hwy 94, 17 March 1962, Bacigalupi 8280 with Heckard and Hutchison (JEPS)

3L San Diego Co., CA: Warner's Hot Springs, 1913, Buttle sn (CAS 65275)

4L Kern Co., CA: Studhorse Canyon, 26 May 1964, Twisselmann 9528 (CAS/ RSA)

5L Kern Co., CA: s.8 mi SE of mouth of Pastoria Cr, T10N R18W S32, 26 April 1935, Nordstrom 492 (UC)

6L Riverside Co., CA: San Juan Mts, San Juan Canyon, Hwy 74, 27 May 1941, Winblad sn (CAS 296649)

OTU Lathyrus laetiflorus Greene continued

7L Los Angeles Co., CA: summit of Liebre Mt, 2 June 1959, Twisselmann 5318 (CAS)

8L Los Angeles Co., CA: Santa Catalina Island, 6 February 1964, Thorne and Everett 33303 (UC)

9L San Bernardino Co., CA: 1.5 mi E of Seven Oaks, San Bernardino Natl For, 4 June 1949, Hitchcock 19060 (WTU/ UC CAS RSA DS)

10L San Bernardino Co., CA: Camp Ro-Ki-Li, Barton Flats, San Bernardino Mts, 28 May 1947, Munz 11928 (WTU/ DS RSA)

11L Santa Barbara Co., CA: Camino Cielo near Brush Peak, Santa Ynez Mts, 16 May 1956, Pollard sn (CAS 411689)

Lathyrus polyphyllus Nutt. ex T. & G.

1P Linn Co., OR: intersection of Tangent Drive and Peoria Rd, T12S R4W S8, 15 May 1979, Broich 615b (OSC)

2P Benton Co., OR: along Peterson Rd, T12S R6W S35, 16 May 1979, Broich 621 (OSC)

3P Yamhill Co., OR: on Peavine Rd, 0.2 mi E of jct w/ Gopher Valley Rd, T4S R6W S11, 8 May 1980, Broich 724 (OSC)

4P Linn Co., OR: near Hwy 20 3 mi E of Cascadia, T13S R3E S25, 20 May 1979, Broich 626 (OSC)

5P Humboldt Co., CA: near Kneeland School, 20 May 1980, Broich 773 (OSC)

6P Lake Co., CA: Deer Valley CG, Mendocino Natl For, 22 May 1980, Broich 794 (OSC)

7P Josephine Co., OR: hillside, S side of Wolf Cr, Wolf Creek Park, T33S R6W S21, 17 May 1980, Broich 736 (OSC)

8P Josephine Co., OR: 10 mi E Cave Junction on rd to Oregon Caves Natl Monument, 18 May 1980, Broich 743 (OSC)

9P Josephine Co., CA: 0.5 mi S of O'brien on Hwy 199, 18 May 1980, Broich 749 (OSC)

10P Lincoln Co., OR: ca 5 mi E of Benton Co line on Hwy 34, 4 June 1980, Broich 840 (OSC)

11P Benton Co., OR: ca 3 mi W of Wren along Hwy 20, 4 June 1980, Broich 846, OSC)

12P Lane Co., OR: Lane County Park W of Lorane on Siuslaw River rd, 5 June 1980, Broich 854 (OSC)

OTU

Lathyrus sulphureus Brewer ex Gray

1S Glenn Co., CA: W of Bennett Spring on the Newville-Covelo rd, 16 June 1915, Heller 11994 (CAS/ DS OSC WTU)

2S Josephine Co., OR: Waldo junction, 18 May 1930, Kildale 9638 (DS)

3S Calaveras Co., CA: Angels Camp, 11 April 1923, Eastwood 11621 (CAS)

4S Mariposa Co., CA: Wawona, T4S R21E S28, Augustine 146 (UC)

5S Madera Co., CA: North Fork S.R.E. Plots, North Fork, 26 April 1934, Bacigalupi 2313 (DS/ UC)

6S Tuolumne Co., CA: Ackerson Meadow near Mather, 22 June 1930, Heusi and Walker 180 (DS)

7S Fresno Co., CA: Pine Ridge, 15-25 June 1900, Hall and Chandler 287 (UC)

8S Amador Co., CA: May 1893, Hansen 12 (CAS/ DS)

9S Tulare Co., CA: Balch Park, 7 June 1937, Winblad sn (CAS 247586)

10S Lake Co., CA: near top of Elk Mt, 1 June 1965, Ackley sn (CAS 453895)

11S Butte Co., CA: Paradise, May 1898, Bruce 2446 (DS)

Lathyrus vestitus Nutt. ex T. & G.

1V Mendocino Co., CA: along Hwy 20 4 mi E of jct w/ Hwy 101, 7 June 1949, Hitchcock 19074 (WTU)

2V Humboldt Co., CA: 2 mi W of Blue Lake on Hwy 299, 8 June 1949, Hitchcock 19096 (WTU/ UC)

3V Humboldt Co., CA: 0.5 mi S of Weott on Hwy 101, 7 June 1949, Hitchcock 19082 (WTU/ UC)

4V Douglas Co., OR: 10 mi E of Remote, 31 May 1951, Hitchcock 19368 (DS)

5V Del Norte Co., CA: Waldo-Crescent City rd, 4 May 1907, Eastwood 190 (CAS)

6V Coos Co., OR: Middle Fork of Coquille River, T29S R12W S26, 21 April 1940, Detling 4080 (UC/ OSC)

7V Coos Co., OR: W end of Eden Valley, Powers-Glendale Pass rd, 1 July 1953, Hitchcock 19935 (WTU)

8V Lake Co., CA: 6 mi up grade on W side of Bartlet Mt, 6 May 1928, Abrams 12425 (DS)

9V Lake Co., CA: 5 mi N of Middleton on Hwy 29, 4 May 1963, Lloyd 2588 (JEPS)

pg. 128 not used

OTU Lathyrus vestitus Nutt. ex T. & T. continued

10V San Luis Obispo Co., CA: Cambria, 1 March 1947, Hoover 6631 (DS/ RSA CAS UC)

11V Ventura Co., CA: Foster Park on N slope of Red Mt, 22 April 1971, Pollard sn (CAS 547841)

12V Mendocino Co., CA: Mendocino City, 21-24 June 1922, Abrams and Bacigalupi 8183A (DS)

13V Mendocino Co., CA: near Point Arena, 11 July 1938, Eastwood and Howell 6251 (CAS/ WTU)

14V Napa Co., CA: Mt St. Helena grade 2 mi below Hawkins Mt Camp, 25 February 1928, Woly 1491 (DS)

15V Mendocino Co., CA: 5 mi NE of Rockport, 3 July 1953, Hitchcock 19968 (WTU)

16V Santa Cruz Co., CA: ca 1 mi toward Saratoga summit from jct of Hwy 9 w/ Big Basin Rd, 7 March 1953, Thomas 2837 (DS)

17V Santa Cruz Co., CA: 1 mi W of Bonny Doon, 17 March 1955, Hesse 1443 (CAS)

18V Santa Cruz Co., CA: 3 mi from coast on Bonny Doon rd, 18 April 1955, Hesse 1515 (CAS)

19V Marin Co., CA: E side of Redwood Canyon, Mt Tamalpais, 14-15 April 1906, McMurphy sn (DS 670340)

20V Marin Co., CA: Bolinas Ridge, 1 April 1944, Howell 19366 (CAS/ WTU)

21V Marin Co., CA: Pt. Reyes Peninsula 6 mi from tip, 6 June 1950, Hitchcock 19256 (WTU/ UC)

22V Napa Co., CA: summit of St. Helena grade, 3 May 1928, Abrams 12239 (DS)

23V Monterey Co., CA: on coast 20-25 mi N of San Simeon, 31 March 1961, Kirby 1291 (CAS)

24V Monterey Co., CA: N Fork of Big Sur River, Santa Lucia Mts, 11 May 1920, Abrams 7396 (DS)

25V Monterey Co., CA: upper Carmel Valley ca 2 mi NE of Jamesburg, 19 May 1942, Durham sn (DS 302992)

26V San Benito Co., CA: along Tres Pinos Cr 1 mi SE of Emmet School, 26 April 1970, Wiggins and Ferris 9345 (CAS / DS WTU)

27V Alameda Co., CA: Niles Canyon Rd between Mission Blvd and Palomares Rd, 15 April 1969, Wetzel 755 (DS)

28V Santa Clara Co., CA: foothills W of Los Gatos, 4 April 1904, Heller 7283 (DS)

29V Mendocino Co., CA: outskirts of Ft Bragg, 0.5 mi N of Puddingstone Cr, 6 May 1950, Ferris 12202 (WTU/ UC)

OTU Lathyrus vestitus Nutt. ex T. & G. continued

30V Monterey Co., CA: along Big Sur Hwy, 27 March 1955, Howitt 78 (CAS)

31V San Luis Obispo Co., CA: Poly Canyon (Brizziolari Cr of maps), 11 February, Hoover 6616 (DS/CAS)

32V San Mateo Co., CA: Reservoir Hill, San Bruno Mt, 14 March 1965, McClintock sn (CAS 529070)

Appendix B: The Specimens of LATHTWO

The four digit number preceding each citation is a number (OTU) assigned for computer coding. Specimens are cited by subspecies and by state and county of origin (north to south) within subspecies.

Lathyrus vestitus Nutt. ex T. & G. ssp. bolanderi (Wats.) Hitchcock

OREGON. DOUGLAS CO.: 0320-as 4V in LATH.

COOS CO.: 0520-as 6V in LATH; 0620-as 7V in LATH.

CALIFORNIA. DEL NORTE CO.: 0420-as 5V in LATH.

HUMBOLDT CO.: 0120-as 2V in LATH; 0220-as 3V in LATH.

MENDOCINO CO.: 0118-as 12V in LATH; 0218-as 13V in LATH; 0318-as 15V in LATH; 0418-as 29V in LATH.

MARIN CO.: 0417-Manzanita, 11 April 1948, Rose 48040 (WTU); 0817- 1 mi E of Inverness, 24 April 1963, Lloyd 238 (JEPS); 1017- Mt Tamalpias, February 1895, Eastwood sn (UC 15377).

SAN MATEO CO.: 0614-SE slope of San Bruno Hills, ca 1 mi N of Brisbane, 30 April 1942, Rollins 3012 (DS/ WTU); 0714-back of San Mateo on Half Moon Bay Rd, 28 May 1907, Heller 8583 (WTU/ DS).

SAN FRANCISCO CO.: grassy slopes of McLaren Park, 30 March 1956, Raven 8908 (CAS).

SANTA CRUZ CO.: 0314-as 18V in LATH.

Lathyrus vestitus Nutt. ex T. & G. ssp. vestitus

CALIFORNIA. MENDOCINO CO.: 0119-as 1V in LATH.

LAKE CO.: 0219-as 8V in LATH; 0319-as 9V in LATH.

NAPA CO.: 0419-as 14V in LATH; 0519-as 22V in LATH.

MARIN CO.: 0117-as 19V in LATH; 0217-as 20V in LATH; 0317-as 21V in LATH; 0517-Inverness Ridge, 9 July 1944, Howell 19699 (WTU/ CAS); 0617-near San Rafael, 18 January 1925, Howell 730 (CAS); 0717-Ross Valley, 23 March 1896, Jepson 13627 (JEPS); 0917- 1 mi SE of Fairfax, T1N R6W, 2 April 1935, Yates 5054 (UC).

CONTRA COSTA CO.: 0516-open grassy cliff near Pt Richmond, 17 Airil 1937, Robbins 120 (UC); 0616-along Morgan Territory Rd E of Mt Diablo, 7 mi N of jct w/ Manning Rd, 15 April 1971, Heckard 2472 (JEPS); 0716-upper Marsh Cr, SE of Mt Diablo, 4 April 1931, Mason sn (JEPS 55365); 0816-Mt Diablo, 30 May 1915, Eastwood sn (CAS 65459); 0916-Crockett-Martinez rd above Carquinez Straits, 18 April 1962, Sharsmith 4945 (UC).

ALAMEDA CO.: 0116-as 27V in LATH; 0216-Oakland Hills, 1891, Michener and Bioletti sn (WTU 94123); 0316-Berkeley, 22 February 1899, Chandler 206 (UC); 0416-Berkeley, 23 April 1892, Jepson 13630 (JEPS); 1016-hills near Berkeley, 21 January 1900, Tracy 474 (UC).

SAN FRANCISCO CO.: 0914-W slopes of Mt Sutro, N of Laguna Honda, 30 April 1957, Rubtzoff 3244 (CAS).

SAN MATEO CO.: 0514-as 32V in LATH.

SANTA CRUZ CO.: 0114-as 16V in LATH; 0214-as 17V in LATH.

SANTA CLARA CO.: 0414-as 28V in LATH; 1014-foothills E side of Santa Cruz Mts, 5 mi S of Palo Alto, Panorama Trail, 30 April 1974, Martineau 50 (DS); 0215-back of Alum Rock Park, 27 April 1907, Heller 8480 (DS/ WTU); 0315-E slope of Sugarloaf Mt, 25 April 1936, Sharsmith 3638 (UC/ DS); 0415- 2 mi NNE of Mt Isabel, T7S R3E S1, 13 May 1938, Graham 411 (UC); 0515-N side of Mt Hamilton near Kincaid, 25 February 1934, Sharsmith 559 (DS/ UC); 0615-E slopes of Mt Hamilton near summit, 10 March 1934 Sharsmith 606a (DS/ UC); 0715-Mt Day in the Mt Hamilton Range, 29 April 1908, Heller 8926 (WTU/ DS); 0815-Alum Rock Park, 26 April 1907, Pendleton 666 (JEPS); 0915-Mt Hamilton, 31 May 1907, Heller 8623 (UC/ DS); 1015-S end of Oak Ridge on W side of Mt Hamilton Range, 21

April 1933, Ferris and Bacigalupi 8279 (DS).

SAN BENITO CO.: 0115-as 26V in LATH.

MONTEREY CO.: 0113-as 23V in LATH; 0213-as 24V in LATH; 0313-as 25V in LATH; 0413-as 30V in LATH; 0513-along Carmel-Pacific Grove Hwy, 28 March 1955, Howitt 90 (CAS); 0613-pine woods 2 mi W of Monterey, 5 March 1908, Jepson 2995 (JEPS); 0713-E (Parkfield) slope of Hog Canyon Rd, 30 April 1970, Twisselmann 16446 (CAS); 0813-Johnson Brothers Ranch, Chualar Canyon, 6-9 April 1942, Grinell 1157 (UC); 0913- 17-mi drive, 25 April 1917, McGuire sn (CAS 65461); 1013-ca 2 mi up Chualar Canyon on E side of Salinas Valley near Chualar, 3 March 1963, Howitt 1418 (CAS).

SAN LUIS OBISPO CO.: 0111-as 10V in LATH; 0611- 6 mi N of Moro Bay, 16 April 1929, Wiggins 3641 (WTU/ DS); 0811- between Pine Mt and Rock Butte, N of Cambria, 18 May 1961, Hardham 7110 (RSA); 0112-Martinez Canyon, La Panza Quadrangle T30S R17E S21, 29 April 1937, Peterson 773 (UC); 0212- 4 mi NE of Pozo, T3S R15E S12, 19 April 1937 Hendrix 42 (UC); 0312-Sycamore Cr, W slope of La Panza Range, 20 April 1947, Hoover 6996 (CAS); 0512-Crestan, 29 June 1927, Feudge 1690 (POM).

SANTA BARBARA CO.: 0412- 2.5 mi SW of Spanish Ranch, 20 March 1936, French 762 (UC/ RSA); 0109-as 11L in LATH; 0209-Mojoqui Falls S of Salvang, 24 February 1935, Schreiber 1637 (UC); 0309-S base of San Marcos Pass, 7 mi below summit, 19 May 1954, Munz 19432 (RSA); 0409-lower Cold Spring Canyon, 17 April 1965, Pollard sn (CAS 526850); 0509-San Marcos Pass, 11 November 1931, Ewan 5327 (DS/ WTU POM); 0609-Kineran Canyon, San Marcos Pass, 1 May 1954, Pollard sn (CAS 389376); 0709-S side of Gaviota Pass, 26 March 1925, Munz 9308 (POM); 0110- at saddle on Big Pine Mt, San Rafael Mts, 27 June 1963, Blakley 6037 (RSA); 0210- 1.25 mi NW of McKinley Mt, T7N R28W S6, 19 May 1936, Paterson 190 (UC); 0310- 0.5 mi NE of Zaca Peak on Azca Ridge, San Rafael Mts, 16 April 1961, Blakley 4035 (RSA); 0410- SE of Zaca Lake, 10 April 1955, Pollard sn (CAS 398959).

Lathyrus vestitus Nutt. ex T. & G. ssp. laevicarpus Broich ssp. nov.

KERN CO.: 0108-as 4L in LATH; 0208-as 5L in LATH; 0308-as 7L in LATH; 0708-Black Bob Canyon, San Emigdio Range, 3 June 1963, Twisselmann 8356 (CAS/RSA); 0808-Rowen, Techachapi Mts, 14 April 1916, Jepson 6744 (JEPS).

VENTURA CO.: 0107-as 11V in LATH; 0307-Ojai-Saticoy Hwy (150) ca 10 mi E of Saticoy, 2 June 1952, Hitchcock 19573 (WTU/ RSA); 0407-Saticoy, 17 April 1916, Eastwood 5094 (CAS); 0507-coastal canyon 11 mi S of Magu Point, 23 April 1944, Gould 2326 (CAS/ UC); 0607, 0907-Hall Canyon 2 mi E of Ventura, 29 March 1932, Wolf 2921 (WTU DS/ RSA); 1007-Senior Canyon, T5N R23W S28, 19 March 1934, Sowder 242 (UC).

LOS ANGELES CO.: 0508-Oakgrove Canyon, Liebre Mts, 19-21 June 1908, Abrams and McGregor 393 (DS/ POM); 0608-Liebre CG, Angeles Natl For, 2 July 1963, Griesel and Miller sn (RSA 165705/ DS 511438); 0206-Malibou Rd, Santa Monica Mts, 11 May 1935, Purer 6561 (DS); 0306-Santa Monica Canyon, April 1901, Abrams 1469 (DS); 0406-Santa Monica Mts, 3 April 1901, Abrams 1303 (POM); 0506-Mandeville Canyon, Santa Monica Mts, March 1929, Clokey and Templeton 4463 (UC/ POM); 0806-along Mulhalland Drive, 0.5 mi E of Beverly Glen Boulevard, 3 May 1959, Raven 14071 (RSA/ CAS); 0906-Gopango Canyon, Santa Monica Mts, 17 May 1920, Munz and Harwood 3986 (POM).

Lathyrus vestitus Nutt. ex T. & G. ssp. barbarae (White) Broich comb. nov.

LOS ANGELES CO.: 0408- 6.5 mi SE of Whitaker Peak, T5N R17W S15, 7 January 1935, Gifford 407 (RSA/ UC); 0106-Pacoima Canyon, Santa Monica Mts, 19 April 1919, Peirson 374 (RSA); 1006-Mulholland Drive 1 mi E of Laurel Pass, 3 May 1959, Raven 14100 (RSA/ CAS); 0105-Wilson and Sierra Madre wall, April 1901, Abrams 1495 (POM/ DA); 0205-Tujunga Canyon, E end of San Gabriel Mts, 9 October 1921, Pierson sn (RSA 90453); 0305-first canyon E of Rubio Canyon, S base of San Gabriel Mts, 11 March 1919, Peirson 104 (RSA/ JEPS); 0405-hills W of Arroyo Seco, near Pasadena, 25 April 1920, Peirson 1926 (RSA); 0505-Tujunga Canyon, W end of San Gabriel Mts, 16 May

1920, Peirson 2137 (RSA/ JEPS); 0605-Big Santa Anita Trail, S base of San Gabriel Mts, 2 May 1921, Peirson 4691 (RSA); 0705-forks of the San Gabriel River, 23 April 1925, Peirson 5796 (RSA); 0805-upper portion of Evey Canyon, San Gabriel Mts, 25 June 1967, Thorne and Thorne 37103 (DS).

SAN BERNARDINO CO.:0104,0804- 1.5 mi E of Seven Oaks, San Bernardino Mts, 4 June 1949, Hitchcock 19060 (WTU CAS/ DS); 0204, 0304-Camp Ro-Ki-Li, Barton Flats, San Bernardino Mts, Munz 11928 (WTU RSA/ DS); 0404-Canyon Diablo, vicinity of San Bernardino, 27 April 1902, Parish 4715 (DS); 0504-Fredalba Park, 3 June 1902, Parish 4963 (DS); 0604, 0704-Mill Cr Canyon, ca 7 mi N of Menton, San Bernardino Natl For, 4 June 1949, Hitchcock 19058 (WTU CAS/ DS RSA UC); 0904-Fredalba Park, San Bernardino Mts, July 1905, Grout sn (POM 29610); 1104-Arrowhead Canyon, 7 May 1919, Spencer 1101 (POM/ CAS); 1204-near San Bernardino, May 1894, Parish sn (RSA 102273); 0905-Stoddard Canyon, Angeles Natl For, 2 April 1971, Gibson 1782 (RSA); 1005-Lytle Creek Canyon, 1 May 1952, Taylor sn (RSA 79247); 1105-Cajon Pass, spring 1924, Jones sn (POM 29628).

RIVERSIDE CO.: 1503-Santa Rosa Mts, 30 May 1937, Ramsey and Ramsey 1325 (POM).

Lathyrus vestitus Nutt. ex T. & G. ssp. alefeldii (White) Broich comb. nov.

SAN BERNARDINO CO.: 1004-N of Fontana, 23 March 1938, Ramsey and Ramsey 2561 (POM).

ORANGE CO.: 0302-base of West Ladd Truck Trail, mouth of Baker Canyon, Santa Ana Mts, 10 February 1935, Everett 6292 (RSA/ WTU CAS); 0502, 1202- 0.5 mi above Trabuco Oaks, Trabuco Canyon, W slope of Santa Ana Mts, 6 March 1931, Wolf 1835 (RSA POM/ UC); 0602-Sierra Canyon, Santa Ana Mts, 24 April 1920, Munz and Harwood 3776 (POM); 0702-Silverado Canyon, Santa Ana Mts, 11 April 1925, Peirson 5731 (RSA); 0902-Silverado Canyon, 10 April 1925, Peirson sn (JEPS 55289); 1002-lookout at top of Elsinore Mt, 4 June 1944, Cooper 1374 (RSA); 1102- 12.2 mi E of San Juan Capistrano on Hwy 74, 6 March 1962, Breedlove 1787 (DS); 1302, 1402-Santiago Peak Trail,

June 1901, Abrams 1813 (POM DS); 1502, 1602-Santiago Dam W base of Santa Ana Mts, 8 March 1932, Wolf 2699 (WTU RSA).

RIVERSIDE CO.: 0303-Van Deventer's, Santa Rosa Mts, 24 May 1901, Jepson 1423 (JEPS); 0403-Augustine Ranch, Palomar, 31 May 1901, Jepson 1564 (JEPS); 0503-Temecula Cr, 7 June 1913, Hall 9435 (DS); 0603- 0.4 mi W of Dripping Springs, 23 April 1959, Raven 14016 (RSA); 1203-Temecula Canyon, 21 March 1925, Jaeger sn (POM 48270); 0102- 8 mi W of Murrieta, 4 April 1965, Lathrop 5627 (RSA); 0202-Lake Elsinore, 15 May 1938, Winblad sn (CAS 282333); 0402-Santa Ana Mts above San Juan Hot Springs, 24 April 1937, Eastwood and Howell 3910 (CAS); 0802-Leach Canyon, Elsinore Region, 28 April 1922, Peirson 2946 (RSA).

SAN DEIGO CO.: 0103-as 3L in LATH; 0703- 4 mi S of Temecula, 12 April 1940, Hitchcock 6009 (WTU); 0803- 1 mi N of turn off to Palomar Mt on Henshaw Dam-Pala Hwy, 4 June 1949, Hitchcock 19056 (WTU); 0903-N end of Laguna Mts, 24 June 1924, Munz 3849 (POM); 1003-Pala Grade, 21 March 1925, Jaeger sn (POM 48701); 1303-Crest of ridge, Palomar Mt, 22 June 1924, Munz 8216 (POM); 1403- 3 mi N of Henshaw Dam, 4 June 1949, Hitchcock 19055 (UC); 0100, 0500-Pine Hills, ca 6 mi S of Julian on Hwy 79, 4 June 1949, Hitchcock 19054 (WTU RSA); 0200, 0600, 0700-along Hwy 80 2 mi SE of Pine Valley, 3 June 1949, Hitchcock 19052 (RSA WTU); 0300-Cuyamaca Lake, 27 June 1923, Munz and Harwood 7246 (POM); 0400-near summit of Monument Peak Laguna Mts, 27 June 1924, Peirson 4882 (RSA); 0101-as 1L in LATH; 0201-as 2L in LATH; 0301, 0901-readside ca 12 mi E of Dulzura on Hwy 94, 3 June 1949, Hitchcock 19047 (RSA WTU/ UC); 0401-between Barrett Dam and Cottonwood Cr, 10 May 1924, Munz and McNeil 7980 (POM); 0501-Mt Otay, 26 June 1935, Gander 223 (UC); 0601-just W of Miramar Naval Air Station, Miramar Rd, 3 April 1961, Hughes 393 (POM); 0701-Harper Ranch near Cuyamaca Lake, 23 June 1932, Epling, Darsie, Knox and Robison sn (DS 224859); 0801-near Hwy 94 ca 17 mi E of Dulzura, 3 June 1949, Hitchcock 19049 (RSA); 1001-vicinity of San Diego, 1897, Wright 104 (JEPS); 1101-Witch Cr, 19 April 1925, Hill sn (POM 98166); 1201-Barrett, 21 April 1949, Rose 49091 (WTU);

1301-Dulzura, 2 May 1930, Rowntree sn (CAS 296465); Moro Hills, near Fallbrook, 24 April 1903, Abrams 3310 (POM).

Intermediate Specimens. The following specimens are cited as intermediate between the subspecies of L. vestitus, either because they were identified as such by discriminant analysis, or because they cannot be assigned to subspecies using the key given in the taxonomic section. They can be considered as examples of intergradation between the subspecies.

ssp. bolanderi (Wats.) Hitchcock intermediate to ssp. vestitus

SAN LUIS OBISPO CO.: 0211-as 31V in LATH; 0311- 6 mi E of Moro Bay on rd to Atascadero, 16 April 1929, Ferris 7683 (UC/ DS); 0411-on coast, 6 mi N of Moro Bay, 16 April 1929, Wolf 3629 (RSA); 0511-grassy flat on Morro Cr, 25 March 1925, Munz 9212 (UC); 0911-1 mi N of San Luis Obispo, 16 March 1940, Miossi 204 (UC).

ssp. vestitus intermediate to ssp. barbarae (White) Broich comb. nov.

VENTURA CO.: 0809-Murietta Canyon, Ojai District, 5 May 1960, Pollard sn (CAS 479032); 0909-Ocean View Trail near Divide Peak, Santa Ynez Mts, 11 June 1957, Pollard sn (CAS 479025); 1009-near Divide Peak, Santa Ynez Mts, 16 June 1948, Pollard sn (CAS 343916); 0510-Wheeler's Canyon, 4 February 1945, Pollard sn (CAS 330661); 0610-Lakes Ridge, Ventrua River basin, 12 June 1949, Pollard sn (CAS 352054); 0710-Lakes Ridge above Maricopa Rd on Matilija-Sespe divide, 22 June 1955, Pollard sn (CAS 479026); 0810-Upper Matilija Canyon, 15 March 1947, Pollard sn (CAS 336784); 1010-Maricopa Rd, 10 February 1945, Pollard sn (CAS 330822).

ssp. barbarae (White) Broich comb. nov. intermediate to ssp. laevicarpus Broich ssp. nov.

VENTURA CO.: 0207-Fairview Rd near Rancho Rinconada, Ojai Valley, 5 April 1968, Pollard sn (CAS 540972); 0707-Sulphur Mt Rd, 27 January 1945, Pollard sn (CAS 330658); 0807-Pratt Canyon, 18 February 1945, Pollard sn (CAS 330659).

LOS ANGELES CO.: 0606, 0706- 1 mi NE of entrance to Stokes Canyon, Santa Monica Mts, 2 June 1959, Everett and Balls 23835 (UC WTU/ RSA).

ssp. laevicarpus Broich ssp. nov. intermediate to ssp. alefeldii (White) Broich comb. nov.

RIVERSIDE CO.: 0203-Pipe Cr, Hemet Valley, Jan Jacinto Mts, 24 June 1922, Munz 5803 (POM).

Lathyrus splendens Kellogg

SAN DIEGO CO.: 01SP- 5 mi W of Campo, 14 March 1931, Munz 11953 (POM); 02SP-Potrero grade at 2250 ft, 12 May 1925, Peirson 5817 (RSA); 03SP-jct of Campo Rd w/ Hwy 80, Manzanita, 17 May 1945, Whitaker sn (RSA 55097); 04SP-Campo, Barrett Rd, 23 April 1939, Ramsey and Ramsey 416 (POM); 05SP-Barrett, 31 March 1932, Epling and Robison sn (RSA 11386); 06SP-summit above Jacumba, 10 May 1924, Munz and McNeil 8061 (POM); 07SP- 2 mi W of Boulevard, 8 April 1940, Hitchcock 5996 (RSA); 08SP-Tecate Mt, 10 May 1924, Munz and McNeil 7989 (POM); 09SP-halfway between Dulzura and Cottonwood, 12 April 1935, Youngberg 45 (POM); 10SP-Potrero grade, Tacate Mt, 10 May 1924, Munz and McNeil 8015 (POM); 11SP- 2 mi N of Tecate, T18 S R3 or 4W, 26 April 1964, Cronquist 9891 (RSA); 12SP-Tecate, 10 May 1924, Munz and McNeil 7998 (POM).

Appendix C: Additional Specimens Examined

Lathyrus delnorticus C. L. Hitchcock

OREGON. COOS CO.: E slope of Iron Mt along Rock Cr at Smith Claim, 30 May 1947, Baker 4243 (OSC); E slope of Iron Mt along Rock Cr at Smith Claim, 9 August 1946, Baker 3026 (OSC).

CURRY CO.: along Rd 368, 9.9 mi from jct of Hunter Cr Rd w/ Hwy 101 S of Gold Beach, T37S R14W S24, 11 July 1981, Chambers 4854 (OSC); 23 mi up Pistol River Rd, 30 June 1951, Hitchcock 19523 (WTU); base of Green Craggie (or Big Craggies) 5 mi E of Snow Camp Mt and Windy Valley, Siskiyou Natl For, 8 July 1973,

Denton 3103 (WTU); ca 0.5 mi NW of Frog Lake, on Siskiyou Natl For boundary T36S R13W S19 SW¼, 27 June 1981, Nelson 49 (OSC); Quosatana Cr Rd, T36S R13W S28, 22 June 1981, Nelson 46 (OSC); on bank of Nancy Cr at confluence w/ Illinois River, T35S R11W S20, 19 June 1981, Nelson 41 (OSC); Snow Camp Lookout, T37S R12W S30 NW¼ of SW¼, 10 July 1981, Nelson 62 (OSC).

JOSEPHINE CO.: Pearsoll Peak ca 11 mi W of Selma, 18 June 1930, Leach 2935 (OSC); E side of Pearsoll Peak, T38S R10W S1, 22 July 1964, Waring 445 (OSC); Oak Flat Rd W of Selma 1.7 km W of Store Gulch, T37S R9W S33, 15 July 1968, White and Lillico 68 (OSC); ca 3 mi SW of O'brien, 2 July 1952, Hitchcock 19948 (OSC WTU); 15.7-17 mi W of Selma on Illinois River Rd, 20 June 1973, Denton 2440 (OSC HSU); 2.2 mi W of Gasquet Trail on O'brien-Sourdough Rd, 21 June 1950, Kruckeberg 1857 (WTU UC); 3 mi W of O'brien on Banks of Wiskey Cr, 25 June 1950, Kruckeberg 1962 (UC); Takilma, T40S R5E S26, 22 June 1958, Van Deventer sn (HSU 62386); 2 mi S of Takilma, 26 June 1918, Peck 8019 (WILLU); near California state line on Grant Grants Pass-Crescent City Rd, 4 August 1913, Peck 7844 (WILLU); same 1 July 1918, Peck 8082 (WILLU); near bridge over Illinois River on Eight Dollar Mt Rd, T38S R8W S19, 7 June 1981, Broich 1129 (OSC); 2.0 mi SW of O'brien along Whisky Cr, T41S R9W S4, 8 June 1981, Broich 1134 (OSC); 2.2 mi E of Takilma Jct on FS rd 4007, T40S R6E S31, 11 June 1981, Broich 1187 (OSC); 4.9 mi S of FS rd 4007 on rd through Takilma, T41S R5E S15, 11 June 1981, Broich 1188 (OSC). CALIFORNIA. DELNORTE CO.: near Douglas Park 9 mi E of Cresent City on Grants Pass Rd, 4 July 1926, Kildale 2283 (DS); 0.5 mi W of "Darlingtonia Cottages" along Smith River and Why 199, 8 July 1949, Hitchcock 19101 (WTU UC CAS); along Smith River 0.5 mi below Patrick's Cr, 24 July 1927, Wolf 868 (DS); lower slopes of French Hill near Gasquet, 29 June 1942, Parks and Tracy 17207 (UC WTU); Patrick's Cr on Crescent City-Grant's Pass Rd, 1 July 1922, Abrams and Bacigalupi 8575 (DS); grade between Van and Gordon Mt, 23 June 1952, Munz 17710 (WTU); Gordon Mt, 29 June 1930 Kildale 9881 (DS); Douglas Park on Smith River, 24 June 1936, Thompson 12916 (WTU);

Gasquet to Patricks, 1 July 1922, Abrams and Bacigalupi 8529 (DS); Del Norte Co, May 1936, Van Deventer sn (CAS 284703); Douglas Park, 5 June 1928, Thompson 4502 (DS); near Gasquet, 3 July 1936, Eastwood and Howell 3764 (CAS); Shelley Cr below Monumental, 13 June 1936, Parks and Tracy 15212 (UC); S bank of Smith River 2.7 mi NE of Gasquet on Hwy 199, 8 June 1962, Breedlove 3143 (DS); near Gasquet, 1 June 1935, Parks and Tracy 11237 (UC); Stoney Cr bog near Gasquet, T17N R2E S16, 13 May 1973, Smith 6753 (HSU); base of Crazy Peak on Hwy 196, 28 June 1973, Denton 2870 (HSU OSC); Darlingtonia, August 1943, Parks 24253 (HSU); near Boundry Trail close to Klamath, 26 June 1979, Overton and Butler 6696 (HSU); Gasquet, 16 May 1979, Clifton and Overton 2567 (HSU); near Gasquet, 16 May 1979, Clifton and Overton 2571 (HSU); Crescent Quadrangle T17N R1E S12, 25 May 1978, Renner 587 (HSU); old Gasquet Toll Rd, T17N R2E S21, 19 June 1975, Barker 921 (HSU); Monumental 6.3 mi N of Patrick's Cr jct, 2 July 1975, Barker 1079b (HSU); Red Mt, T13N R2E S11, 12, 13, 14, 7 July 1964, Van Deventer sn (HSU 61784); Cedar Cr N of Gasquet, 28 May 1938, Van Deventer sn (HSU 61584); High Plateau Rd at forks, T18 N R2E S26,27,33,34,35, 9 July 1963, Van Deventer sn (HSU 60994); French Hill Rd, 8.7 mi from Hwy 199, 14 July 1978, Nelson 4186 (HSU); French Hill Rd 2.4 mi from Hwy 199, T17N R2E S29, 14 June 1978, Nelson 4172 (HSU); Panther Flat CG off Hwy 199, T17N R3E S22, 3 June 1979, Broich 638, 644, 761 (19 May 1980) (OSC); 0.2 mi W of Myrtle Cr bridge on Hwy 199, 12 June 1981, Broich 1190 (OSC).

SISKIYOU CO.: Clear Cr Trail N of Trout Camp, T17N R5E S29, 4 July 1980, Renner 1425 (HSU); Bell Echo, T17N R5E S15, 8 July 1960, Van Deventer sn (HSU 60784); along Clear Cr Trail between West Fork and Preston Cr, T16N R5E, 19 June 1977, Sawyer and Cope 2946 (HSU); Youngs Valley, T17N R5E S9, 10, 16 August 1957, Van Deventer sn (HSU 62307).

Lathyrus glandulosus Broich sp. nov.

CALIFORNIA. HUMBOLDT CO.: 2 mi E of Korbel on Korbel-Maple Cr Rd, 23 April 1960, Winter sn (HSU 15267); headwaters of Bear Cr along

Cow Cr fire trait, 8 June 1934, Constance 837 (HSU JEPS); Kneeland Prairie, 10 June 1906, Tracy 2474 (UC); Kneeland Prairie, 26 June 1912, Tracy 3855 (UC); Kneeland Prairie, 24 August 1930, Tracy 9170 (UC); valley of S Yager Cr near "Redwood House", 26 July 1942, Tracy 17298 (UC WTU); near the Dan McBride place SE end of Kneeland, 23 June 1946, Tracy 17595 (UC); Fickle Hill, 7 August 1948, Tracy 18085 (UC); Fickle Hill, 20 June 1949, Tracy 19313 (UC); 3 mi E of Kneeland on Butter Valley Rd, 29 June 1950, Tracy 18934 (UC); 1.2 mi SE of Blue Lake on rd to Maple Cr, 9 June 1981, Broich 1141 (OSC); 2.7 mi S of Kneeland School on rd to Bridgeville, 9 June 1981, Broich 1153 (OSC); Eureka, April 1913, Hutchinson sn (CAS sn).

Lathyrus holochlorus (Piper) C. L. Hitchcock

OREGON. CLACKAMAS CO.: Eagle Cr, 25 May 1925, Suksdorf 3325 (CAS WTU).

YANMILL CO.: 4 mi SW of Newberg on Hwy99W, 29 May 1951, Hitchcock 19289 (CAS WTU UC DS); 10 mi SW of McMinnville, 29 May 1951, Hitchcock 19297 (UC WTU); 13 mi S of Newberg on Hwy 99W, 30 May 1964, Hitchcock 23705 (UC WTU HSU); near McMinnville, 12 April 1926, Gorman 7534 (UC); 2 mi W of Amity on rd to Bellevue, T5S R5W S25, 8 May 1980, Broich 717 (OSC); 4 mi W of Amity on rd to Bellevue, T5S R5W S26, 8 May 1980, Broich 718 (OSC); 6 mi W of Amity on rd to Bellevue, T5S R5W S27, 8 May 1980, Broich 719 (OSC); 0.7 mi E of Bellevue on rd to Amity, 8 May 1980, Broich 720 (OSC); 3 mi NW of Bellevue on Gopher Valley Rd, T5S R6W S14, 8 May 1980, Broich 721 (OSC); 4 mi NW of Bellevue on Gopher Valley Rd, T5S R6W S11, 8 May 1980, Broich 722 (OSC); jct of Gopher Valley Rd and Dupee Valley Rd, T4S R6W S36, 8 May 1980, Broich 723 (OSC); 2 mi W of Carlton on rd to Nastucca Reservoir, T3S R4W S20, 8 May 1980, Broich 725 (OSC).

MARION CO.: Salem, May 1911, Peck 1961 (WILLU); Salem, 7 May 1910, Peck 1327 (WILLU); Salem, no date, Reynolds sn (WILLU 8966); Pacific Hwy near Woodburn, 9 May 1927, Gabrielson and Ingram 59470 (OSC).

POLK CO.: 8 mi W of Salem along Hwy 22, 29 May 1951, Hitchcock 19308 (WTU); 5 mi N of Pedee along Hwy 223, 30 May 1951, Hitchcock 19320 (UC); Rickreal, 4 June 1933, Fleischman sn (OSC 30140); 16 mi N of Wren on Hwy 223, T9S R6W S22, 3 May 1980, Broich 206 (OSC).

LINN CO.: 3 mi E of Corvallis near Orleans, 11 May 1918, Standley 1459 (OSC); 5 mi E of Corvallis, 30 April 1939, Lammi sn (OSC 62770); roadside 1 mi E of Corvallis, 12 April 1947, Baker 3650 (OSC); 3.3 mi E of Corvallis on Hwy 34 near jct w/ Orleans Avenue, 9 May 1978, Halse 1751 (OSC).

BENTON CO.: near S College Farm, 14 April 1915, Yates sn (OSC 16380); open woods W of Corvallis, 4 May 1916, Friedman 571 (OSC); Scott's Hill, Corvallis, 26 May 1925, Patty sn (OSC 19956); Mary's River bridge, 12 April 1916, Greene sn (OSC 16187); Brook Lane, 3 May 1916, Gilkey 28 (OSC); 3 mi S of Corvallis, 11 April 1926, Scullen 44 (OSC); vicinity of Oak Cr, Corvallis, 28 April 1926, Mallery sn (OSC 41985); near Corvallis, 27 May 1892, Storms sn (OSC 16318); military reservation, 15 May 1930, Raof sn (OSC 41972); Corvallis, 1 May 1915, Cronemilles 240 (OSC); Corvallis, 15 May 1914, Gilbert 570 (OSC); along Oak Cr, SW of Corvallis, 4 May 1916, Gilbert 569, (OSC); NW of Corvallis, 6 May 1916, Gilbert 568 (OSC); Corvallis, 26 April 1925, Severance and Stason 2402 (UC); 1 mi W of Corvallis, 24 April 1926, Belden sn (UC 864587); 1 mi S of Marys River bridge on S Philomath Rd, T12S R6W S24, 5 May 1980, Broich 716 (OSC); along Oak Cr in pasture of OSU Farm, T11S R5W S33, 20 May 1981, Broich 1065 (OSC); along Oak Cr at 30th St., T12S R5W S3, 20 May 1981, Broich 1066 (OSC); along Rock Cr Rd into Corvallis Watershed, T12S R6W S29, 30, 21 May 1981, Broich 1072 (OSC); 0.1 mi N of Oak Cr Laboratory, McDonald Forest, T11S R5W S8, 30 May 1981, Broich 1102 (OSC); along Oak Cr Rd 0.3 mi S of entrance to McDonald Forest, T11S R5W S19, 20 May 1982, Broich 1297 (OSC).

LANE CO.: along the Lorane Hwy S of city limits of Eugene 3 May 1924, Constance sn (UC 576711); 5 mi N of Lorane, 30 May 1951, Hitchcock 19377 (WTU UC).

pg. 142 not used

DOUGLAS CO.: hillsides near Looking Glass, Roseburg Quadrangle, 29 April 1914, Cusick 3924 (WTU).

Lathyrus jepsonii Greene ssp. jepsonii

CALIFORNIA. NAPA CO.: Suisun Marsh, 6 October 1923, Mason 772 (UC); Draw Bridge, 15 August 1892, Bioletti sn (UC 15334); tidal marsh in Napa River, August 1892, Bioletti sn (DS 118489).

SOLANO CO.: Suisun Marshes: 15 October 1905, Kudley sn (DS 34291); 21 September 1904, Heller sn (WTU 85328); 25 August 1927, Heller 14462 (UC WTU); 6 July 1913, Eastwood 3445 (UC CAS); 28 August 1938, Howell 14592 (WTU CAS DS); 28 August 1938, Rose 38240 (WTU UC); 12 July 1945, Mason 12650 (DS UC); 11 May 1959, Crampton 5203 (UC CAS); Suisun: 28 August 1920, V. Jones sn (CAS 65337); 6 June 1903, Baker 3226 (UC CAS DS); Grissly Island on Montezuma Slough: 23 July 1940, Alexander and Kellogg 1871 (WTU UC); 18 September 1943, Alexander and Kellogg 3527 (UC); 28 May 1981, Broich 839 (OSC); along Hwy between Vacaville and Elmira, 12 May 1928, Heller 14542 (WTU).

CONTRA COSTA CO.: Marsh Cr Canyon, 24 May 1930, Stanford 1515 (CAS); San Leandro, 21 June 1915, Eastwood 4729 (CAS); "Botany Cove", Brown's Island, 5 September 1978, Knight et al. 3227 (CAS).

ALAMEDA CO.: rd by Kaiser Plant, Niles Canyon, 7 May 1968, Wetzel 352 (DS).

SAN JOAQUIN CO.: Rough and Ready Island, Stockton, 1903, Berg sn (DS 34285).

SANTA CLARA CO.: Stanford University, March 1900, Atkinson sn (DS 34333); Los Buellu Hills, 10 May 1909, Smith sn (WTU 254538); foothills near Stanford University, 16 May 1902, Baker 849 (CAS); near Stanford University, 1894, Tompkins sn (DS 62824); rd by P.O. to Laguinata, Stanford University, 20 May 1902, Dudley sn (DS 18594); rd to Cooley's Landing between Cavanaugh's and corner of Coleman tract, 5 June 1906, Dudley sn (DS 104213); field between University P.O. and Lake Lagunita, Stanford University, 6 June 1906, Dudley sn (DS62820); Stanford University, May 1901, Abrams

1641 (DS); San Francisquito Cr, Stanford University, 14 May 1901, Dudley sn (DS 111955); Rose Hill, 19 May 1896, Dudley sn (DS 104198).

SAN MATEO CO.: rd from Bay to Menlo, 12 May 1897, Dudley sn (DS 104205).

SAN BENITO CO.: Bitterwater, no date, McCoy sn (UC 15394).

FRESNO CO.: Big Creek region, July 1915, McDonald sn (CAS 65518).

TULARE CO.: entrance to Tule Indian Reservation, 21 May 1933, Winblad sn (UC 864421).

Lathyrus jepsonii Greene ssp. californicus (Wats.) C. L. Hitchcock CALIFORNIA. SISKIYOU CO.: Sisson, 21 July 1912, Eastwood 1279 (CAS); Soda Cr, 30 July 1921, Eastwood 10998 (CAS): Horse Cr and Klamath R River, 18 June 1945, Rose 45137 (CAS); by Sacramento River, 3 August 1905, Dudley sn (DS 34301); Stony Cr near trail from Trinity Alps Resort to Grant's Peak, 4 August 1926, Baker 214-'26 (DS); Shackleford Cr, 6 July 1910, Butler 1644 (DS CAS); Carville, 15 June 1931, Van Dyke sn (CAS 189650); bench along Sacramento River near Shasta Retreat, 9 June 1928, Heller 14500 (DS); near Castle Craggs, 26 July 1921, Campbell sn (CAS 65521); 8.6 mi S of Happy Camp on Hwy 96, 11 June 1981, Broich 1181 (OSC).

HUMBOLDT CO.: near Dinsmore's, 23 June 1937, Eastwood and Howell 4769 (CAS); Burr Valley on NW slope of Buck Mt, 17 June 1936, Tracy 14964 (UC); Dinsmore's along Van Duzen River, 1 July 1942, Tracy 17361 (UC); McKeown Ranch N of Dinsmore's, T2N R5E S 28, 33, 34, 17 June 1972, Anderson, Nelson and Dowty 5702A (HSU); 2.6 mi W of Dinsmore's on Hwy 36, 10 June 1981, Broich 1166 (OSC).

TRINITY CO.: Coffee Cr Canyon near Battle Cr, 27 July 1937, Howell 13593 (CAS); Red Mt Trail at cr crossing N of Trinity Alps Resort, Pollard sn (CAS 385855); Morris Meadow, Stuart Fork of Trinity River, 24 August 1948, Alexander and Kellogg 5550 (DS); Brushy Flat near Ruth, 29 June 1941, Tracy 16962 (UC); Weaverville,

9 July 1880, Kleeberger sn (CAS 65504); rd between Callahan and Trinity Center, Roundtree sn (CAS 296464); 0.2 mi E of Mad River, 10 June 1981, Broich 1167 (OSC).

TEHAMA CO.: 0.5 mi S of Brown Camp, Yolla Bolly Mts, 14 July 1971, Keeler-Wolf 268 (JEPS).

SHASTA CO.: Goose Valley, 19 June-11 July 1912, Eastwood 839 (CAS); Redding, 24 May 1913, Smith 238 (CAS); Hatchet Cr E of Round Mt, 18 July 1930, Benson 2211 (DS).

PLUMAS CO.: near Snake Lake, Quincy, 7 July 1950, Weatherby 1464 (CAS DS); headwaters of Clear Cr, Plumas Natl For, 4 July 1934, Quick 1332 (CAS).

MENDOCINO CO.: Sherwood Valley, 17 June 1899, Dudley sn (DS 64876); Potter Valley, 19 May 1925, Eastwood 12727, 12728 (CAS); near Yorkville, 20 June 1937, Eastwood and Howell 4574 (CAS); S city limits of Willetts along Hwy 101, 7 June 1949, Hitchcock 19077 (WTU UC CAS DS OSC); 15 mi N of Covelo on rd to Alderpoint, 4 July 1953, Hitchcock 20017 (WTU); E of Round Valley, June 1882, Rattan sn (DS 16742); Round Valley, 1 June 1925, Kelly sn (CAS 128622); 7.6 mi W of Hwy 101 on Hwy 128, 22 May 1980, Broich 791 (OSC).

LAKE CO.: 18 mi E of Clear Lake on Hwy 20 to Williams, 6 June 1949, Hitchcock 19071 (WTU DS UC CAS OSC); 5 mi W of Clear Lake on Hwy 20, 7 June 1949, Hitchcock 19073 (WTU DS CAS UC); between Cobb Mt and Adams Springs on the Binkley Ranch, 5 July 1933, Jussel 372 (CAS); Thistle Springs, Mt Sanhedrin, 27 July 1902, Heller sn (CAS 186265); foothills S of Mt Sanhedrin, midway between Potter Valley and Hullville, 19 July 1902, Heller 5903 (DS); Bachelor Valley Rd 1.5 mi from Hwy 20 W of Witter Springs P.O., 16 April 1978, Alcasas 33 (HSU).

BUTTE CO.: Sacramento Valley 1 mi N of Durham, 12 June 1937, Wolf 8786 (DS); 8 mi from Bangor on Oroville rd, 9 May 1953, Raven 5426 (CAS); Berry Canyon near Clear Cr, 8 May 1902, Heller and Brown 5489 (DS);near Clear Cr, 15-30 April 1897, Brown 213 (DS); De Sabla, June 1917, Edwards sn (DS 81569); Durham, 1 May 1932, Morrison sn (CAS 196271).

SIERRA CO.: Cedar Glen, 25 May 1920, Jones sn (CAS 65512).

PLACER CO.: Emigrant Gap, July 1882, Jones 3573 (UC CAS DS).

SONOMA CO.: Bennett Valley SE of Santa Rosa, 7 June 1902, Heller 5659 (DS); Santa Rosa Cr E of Santa Rosa, 11 June 1902, Heller 5692 (DS); 2 mi N of Windsor, 19 May 1936, Eastwood and Howell 2523 (CAS WTU); near Mark West Springs, 15 May 1938, Eastwood and Howell 5506 (CAS WTU); Guerueville, 16 June 1877, Rattan sn (DS 17634).

NAPA CO.: Draw Bridge, 15 August 1892, Bioletti sn (UC 15334); Napa River 1 mi N of Napa, 29 May 1952, Raven 4092 (CAS).

YOLO CO.: Buckeye Cr on Goodin Ranch, 25 June 1916, Stinchfield 332 (DS); 1 mi N of Saxon Station, 9 May 1960, Crampton 5510 (UC); 2 mi E of Winters on Hwy 128, 20 May 1961, Dumford 1041 (OSC).

SOLANO CO.: along rd between Suisun and Cordelia, 16 May 1940, Heller 15652 (DS WTU); along Hwy between Vacaville and Elmira, 12 May 1928, Heller 14542 (WTU); Elmira rd 1 mi E of Vacaville, 29 April 1915, Jepson 6269 (WTU); Jewett Ranch at Vacaville, 8 May 1924, Jepson 10,400 (WTU); Elmira, 6 May 1903, Baker 2922 (CAS).

SACRAMENTO CO.: along Hwy 160 on Sherman Island, 28 May 1981, Broich 838 (OSC).

EL DORADO CO.: Pyramid Peak, 1900, Atkinson sn (DS 34536).

CONTRA COSTA CO.: Alhambra Valley, 22 May 1887, Rattan sn (CAS 414271, DS 79905, DS 17641); Marsh Cr Canyon, 24 May 1930, Stanford 1515 (CAS).

SAN JOAQUIN CO.: Rough and Ready Island 1903, Berg sn (UC 61035, DS 34285); Middle River bridge over San Joaquin River, on Byron-Stockton Hwy, 26 June 1943, Alexander and Kellogg 3454 (UC); Lathrop bridge on San Joaquin River, 20 July 1933, Howell 11446 (DS CAS OSC).

CALAVERAS CO.: Mokelumne Hill, 1899, Bluisdell sn (CAS 65523).

SAN MATEO CO.: Lake Searsville, 26 May 1930, Benson 2137 (WTU).

SANTA CLARA CO.: E slope of Seeboy Ridge in Mt Hamilton Range, 26 May 1935, Sharsmith 3215 (DS).

TOULUMNE CO.: Twain Harte, 26 June 1952, Hitchcock 19627 (WTU).

MONTEREY CO.: Castroville, May-June 1901, Burtt-Davy 7546 (DS); Priest Valley, 1938, Dudley sn (CAS 261799); SW part of Monterey Co, May 1937, Dudley sn (CAS 254642).

SAN BENITO CO.: ravine above New Idria, 31 May 1899, Dudley sn (DS 13105); between the Pinnacles and Paicines, 3 May 1937, Eastwood and Howell 4238 (CAS).

MERCED CO.: Merced River botton at Snelling Bridge, 10 May 1925, Howell 1035 (CAS); Pacheco Pass, 23 March 1925, Abrams 10737 (DS).

MARIPOSA CO.: Blockman's Ranch, 28 April 1915, Eastwood 4359 (CAS).

FRESNO CO.: San Joaquin River bottom ca N of Fruit Avenue, 10 May 1953, Quibell 2149 (WTU); confluence of N and S Forks of Kings River, 5 March 1923, Duncan sn (DS 130857).

Lathyrus polyphyllus Nutt. ex T. & G.

WASHINGTON. CALLAM CO.: Squim, 1915, Grant sn (UC 212332); Lake Crescent, 23 July 1930, Parks and Parks 0671 (UC); base of Mt Angeles, 4 July 1908, Flett 3357 (UC); Olympic Mts, August 1900, Elmer 2535 (DS); along Elwah River, vicinity of Altare Public Camp, Olympic Mts, 22 June 1940, Wiggins 9421 (DS); Elwah River, 1 July 1933, G. N. Jones 3999 (CAS WTU).

KING CO.: Seattle: 15 May 1929, Benson 1663 (DS); 5 May ?, Furry sn (WTU 11298); 11 May 1949, Hitchcock 18971 (DS WTU CAS UC) UC); 14 June 1902, M. E. Jones sn (DS 153545): 10 June 1888, C. V. Piper sn (WTU 11060, 11061); 8 May 1889, Piper sn (WTU 11081); June 1892, Piper sn (WTU 11074); 4 June 1933, Thompson 8963 (UC WTU DS); 1 June 1935, Thompson 11570 (UC WTU CAS DS); 25 April 1933, G. N.

Jones 4313 (WTU); Three Tree Point, Puget Sound, 10 May 1929, Benson 1620 (DS WTU); Mercer Island, 29 June 1920, Eastwood 9956 (CAS); Lake Washington, 21 May 1908, Haberkorn sn (WTU 272602).

PIERCE CO.: Tacoma, 19 June 1920, Eastwood 9642 (CAS); Nisqually Prairie, 29 May 1937, Eyerdam sn (UC 583867); N side of Regents Park in Tacoma, 10 June 1946, Johansen sn (UC 755842); ¼ mi E of 84th St S in Tacoma, 10 June 1946, Johansen sn (WTU 116207).

THURSTON CO.: 15 mi N of Olympia, 20 July 1937, Eyerdam 1712 (WTU).

LEWIS CO.: upper valley of the Nesqually, 1 June-20 July 1895, Allen 132 (DS UC).

COWLITZ CO.: 3 mi S of Kalama, 8 May 1940, Gould 1114 (UC).

SKAMANIA CO.: on Dog Cr near Cooks, 12 May 1924, Suksdorf 11670 (UC WTU CAS); Wind River Nursery, Gifford Pinchot Natl For, 18 June 1928, Eringer sn (OSC 31333, 31664).

KLICKITAT CO.: Big White Salmon River near Bingen, 19 June 1886, Suksdorf sn (WTU 196446); W Klickitat Co, 19 May 1891, Suksdorf 2021 (WTU UC); Bingen, 7 July 1927, Suksdorf 12315 (WTU).

OREGON. COLUMBIA CO.: hillside near Clatskanie, 15 May 1927, Thompson 2464 (WTU).

WASHINGTON CO.: open woods near Forest Grove, 1 April 1926, Thompson 641 (WTU); woods near Tonquin, 10 May 1927, Thompson 2369 (WTU DS).

MULTNOMAH CO.: Portland, 20 May-26 June 1883, Henderson sn (DS 118498); N shore Lake Oswego, 1 mi N of Oswego, 29 May 1951, Hitchcock 19279 (WTU); Rocky Butte, 24 May 1903, Sheldon S.12032 (DS OSC); Portland, 15 May 1888, Henderson 130 (OSC).

HOOD RIVER CO.: 10 mi S of Hood River, 3 June 1951, Hitchcock 19423 (WTU UC); Dry Dr Falls, Cascade Locks, 10 June 1937, Gustafson 176 (OSC).

MARION CO.: Salem: 24 April 1915, Nelson 69 (DS); no date, Reynolds sn (WILLU 8967); 14 May 1910, Peck 5239 (WILLU); Silver Cr Falls, 8 July 1912, Peck 5240 (WILLU).

POLK CO.: 1 mi above Rickreal Cr Rd on Burma Rd, T18S R6W S4, 13 June 1954, Clarkson 77 (OSC).

BENTON CO.: E slope of Mary's Peak, 6 June 1948, Baker 5411 (WTU OSC); Mary's Peak, 21 April 1915, Owens sn (OSC 6460); Oregon State Agricultural Experiment Station, Legume Nursery, 3 June 1913, Schoth 28823 (OSC); Mary's Peak Rd, 6 May 1951, Heuston sn (OSC 112889); 3 mi S of Corvallis, 11 April 1926, Scullen 42 (OSC); 0.1 mi S of Bull Run Cr, T12S R6W S35, 5 May 1980, Broich 715 (OSC); Rock Cr Rd into Corvallis Watershed, T12S R6W S29, 30, 21 May 1981, Broich 1073 (OSC); along Rd 6020 in McDonald Forest, T11S R5W S7, 25 May 1981, Broich 1100 (OSC); along rd 600 in McDonald Forest, T11S R5W S8, 2 June 1981, Broich 1120 (OSC).

LINN CO.: 10 mi E of Sweet Home on Hwy 20, 9 June 1949, Hitchcock 19110 (WTU); upper S Santiam Hwy, 18 May 1946, Storm sn (OSC 80101).

LANE CO.: 1 mi S of Crow, 30 May 1951, Hitchcock 19334 (WTU); along Rd 15026 into Unit 7B of H. J. Andrews Exp For, T15S R5E S23, 23 June 1966, Franklin and Dyrness 54 (OSC).

DOUGLAS CO.: Castle Rock Trail, T16S R5E S4, 3 June 1938, Detling 2837 (UC); 5 mi N of Kellogg, 31 May 1951, Hitchcock 19350 (UC WTU CAS); 2 mi E of Camas Valley, 31 May 1951, Hitchcock 19361 (WTU); coast mountains near Roseburg, 23 June 1887, Howell sn (DS 96083, OSC 5971, 154321); Silver Butte, T31S R6W S?, 26 May 1949, Detling 6373 (OSC); 8 km W of Elkton, T22S R8W S33, Sundberg 996 (OSC); near Reston, 9 July 1916, Peck 5228 (WILLU); Rogue-Umpqua divide 20 mi W of Crater Lake, 1 August 1916, Peck 5225 (WILLU).

COOS CO.: 20 mi N of Agness, 31 May 1951, Hitchcock 19373 (WTU UC); 65 mi W of Grants Pass on rd to Agness, 1 June 1951, Hitchcock 19378 (WTU UC).

CURRY CO.: Rogue River Canyon 5 mi N of Illahe, 26 April 1947, Baker 3690 (UC CAS OSC WILLU); 10 mi N of Agness, 1 July 1951, Hitchcock 19929 (WTU); Bear Camp Picnic area, T34S R10W S11, 11 July 1981, Nelson 68 (OSC); on Lobster Cr Rd 11.8 mi N of Bridge over Rogue River, T34S R13W S35, 28 June 1981, Nelson 51 (OSC).

JOSEPHINE CO.: Oregon Caves, 20 June 1935, Applegate 9654, 9676 (DS); Lake Mt Trail, SE of Oregon Caves, 6 August 1936, Applegate 10756 (DS); Noname Cr SW of Oregon Caves, 12 July 1937, Applegate 11146 (DS); Siskiyou Natl For on Rd 3941 5 mi E of jct w/ Rd 3942, ca 20 mi E of Cave Junction, 22 June 1973, Denton 2546 (WTU); Siskiyou Natl For on Rd 3916 4.4 mi S of jct w/ Rd 4031, ca 30 mi E and S of Cave Junction, 25 June 1973, Denton 2701 (WTU); ca 20 mi SW of Grants Pass on Hwy 199, 9 June 1949, Hitchcock 19106 (WTU); 20 mi N of Galice on rd to Agness, 1 June 1051, Hitchcock 19387 (WTU); ca 20 mi S of Applegate on Applegate-Ruch Loop Rd, 2 June 1951, Hitchcock 19400 (WTU UC); roadside from California line to Waldo on Happy Camp-Waldo rd, 9 July 1948, Hoffman 2562 (UC); flat N of summit on rd from Takilma to Happy Camp, 8 June 1972, Howell and True 48851 (CAS); Oregon Caves on trail up Lake Mt, 7 July 1928, Kildale 5653 (DS); Oregon Caves, 25 May 1939, Meola 155 (WTU UC); near Peavine Lookout, T34S R8W S21, 26 July 1937, Priebe sn (OSC 35927); upper Little Sixmile Cr, Illinois River Valley, T38S R9W S2, 10 May 1969, White and Lillico 165 (OSC); Union Cr, 21 June 1928, Sipe sn (OSC 36529); around Squaw Lake, T41S R3W S11, 2 July 1963, Waring 160 (OSC); 1 mi E of Oregon Caves, 15 July 1918, Peck 8239 (WILLU); 8,7 mi W of Wolf Creek on Grave Cr Rd, T33S R7W S34, 2 May 1981, Broich 1030 (OSC).

JACKSON CO.: Ashland Cr, Siskiyou Mts, 6 June 1895, Applegate 143 (DS); Antelope Cr, 3 June 1898, Applegate 2361 (DS); mouth of Willow Cr, 6 June 1898, Applegate 2413 (DS); Jenny Cr region near Pinehurst, 9 June 1925, Applegate 4368 (DS WILLU); near Russel's Resort on Hwy 99, 18 June 1938, Baker 9038 (CAS); Ashland, 20 April 1934, Eastwood and Howell 1721 (CAS); ca 22 mi from Applegate on Applegate-Ruch Loop Rd, 2 June 1951, Hitchcock 19401 (WTU UC); 2 mi E of Green Spring Summit, Klamath Junction and Klamath Falls Hwy, 2 June 1951, Hitchcock 19410 (WTU UC); Low Sap Trail of Whiskey Peak, 28 June 1931, Peck 16480 (WILLU); N slope of Mt Ashland, 19 July 1913, Peck 5241 (WILLU).

KLAMATH CO.: summit of Green Springs Mt between Ash-

land and Klamath Falls, 24 June 1927, Gilkey sn (OSC 90081).
CALIFORNIA. SISKIYOU CO.: along Indian Cr Rd,16.7 mi NW of Happy Camp, 10 June 1962, Breedlove 3298 (DS); along Takilma-Happy Camp Rd, 6 July 1939, Hitchcock and Martin 5209 (DS WTU UC); near Black Bear Summit S of Sawyer's Bar on ridge rd to Cecilville, 17 June 1958, Quick 58-33 (CAS); on Takilma-Happy Camp Rd near State Line, 16 June 1951, Tracy 19469 (WTU UC); along Specimen Cr, Sawyers Bar Quad, T41N R11W S31, 29 May 1976, Sawyer and Stillman 2745 (HSU); T13N R6E S10, 1 July 1975, Whiteley 121 (HSU).

HUMBOLDT CO.: Little Bear Harbor, 1866, Bolander 6508 (UC); near Dinsmore's, 23 June 1937, Eastwood and Howell 4776 (CAS); ca 10 mi W of Willow Cr near Hwy 299, 8 June 1949, Hitchcock 19090 (UC WTU); 3 mi W of Willow Cr near Hwy 299, 8 June 1949, Hitchcock 19094 (UC WTU); Trinity Summit, 1 July 1901, Manning 61½ (UC); between Le Perron Flat and Whiteys Peak on trail, E of Orleans, 14 June 1949, Thomas 909 (DS); valley of the Van Duzen River oppisite Buck Mt, 27 June-30July 1908, Tracy 2731 (UC); Bald Mt, 22 June 1923, Tracy 6344 (UC); Kneeland in woods near schoolhouse, 24 May 1931, Tracy 9455 (UC); near Corral Prairie, 20 July 1932, Tracy 10735 (UC); near Corral Prairie, 22 July 1935, Tracy 14126 (UC); Trinity Summit, on ridge 2 mi E of Grove's Prairie, 8 August 1936, Tracy 15128 (UC); near Green Point, W of Redwood Cr on Trinity Hwy, 15 July 1946, Tracy 17570 (UC); near Harris, 31 May 1948, Tracy 18008 (UC); Willow Cr canyon along Trinity Hwy, 11 July 1948, Tracy 18074 (UC); 1½ mi N of Forest Service Public Camp on Trinity Summit Rd, 18 August 1948, Tracy 18118 (UC); Kinsey Ridge E of headwaters of Redwood Cr, 11 August 1949, Tracy 18474 (UC); near Grissly Camp on Little Hors Linto Cr (Trinity Summit), 2 July 1950, Tracy 18975 (UC); slopes below Mill Cr, Hoopa Quadrangle T9N R6E S33, 23 June 1979, Sawyer and Ericksen 3392 (HSU); McKeown Ranch N of Dinsmore, T2N R5E S28, 29, 33, 34, 30 May 1976, Nelson and Nelson 2626 (HSU); 16.7 mi N of Bridgeville on rd to Kneeland, 20 May 1980, Broich 778 (OSC).

TRINITY CO.: summit of South Fork Mt, 17 July 1926, Baker 56 (DS); South Fork Mt, 2 mi N on Blake Lookout Rd, 7 June

1939, Cantelow 2642 (CAS); South Fork Mt 2 mi N on Blake Lookout Rd, 8 June 1940, Cantelow sn (CAS 363843); Hettinshaw Valley-Zenia, 1 mi S of Panther Cr, 20 June 1937, Wolf 8946 (WTU CAS); Brown's Canyon Campground, T1S R6E S5, 23 May 1976, Nelson and Nelson 2508 (HSU); along rd 6E42, T1S R6E S19, 10 June 1976, Nelson 2688 (HSU).

MENDOCINO CO.: Idol House, 12 May 1901, Chandler 1075 (UC); on Bell Springs Rd 4.2 mi E of Hwy 101, T23N R15W S8, 1 May 1977, Sweet 19 (HSU).

LAKE CO.: Dashiell's, Mt Sanhedrin, 23 May 1925, Eastwood 12927 (CAS); Elk Mt, 21 July-16 August 1905, Tracy 2328 (UC).

Lathyrus splendens Kellogg

CALIFORNIA. SAN DIEGO CO.: near Campo, 26 May 1903, Abrams 3605 (POM); grown at Rancho Santa Ana Botanic Garden from seed collected 2 mi E of Dulzura, 24 February 1954, Balls 18823 (RSA); Walker's Ranch, Jacumba, 26 June 1885, Cleveland sn (RSA 15976); N of Campo, 28 April 1949, Fleming 13395 (RSA); burn at Dulzura, 22 May 1941, Gander 9446 (RSA); Potrero Grade, 2 June 1913, Hall 9410 (POM); 5 mi E of Dulzura on Hwy 94, 3 June 1949, Hitchcock 19046 (RSA); ca 17 mi E of Dulzura on Hwy 94, 3 June 1949, Hitchcock 19050 (RSA); near Campo, March 1918, McGregor 2081 (DS); San Diego Co, 16 February 1929, Parks 0373 (POM); E of Campo, 11 June 1937, Roos 199 (POM); near Campo, 28 April 1918, Spencer 721 (POM); Dulzura, 3 May 1938, Wieslander 728 (RSA); 5 mi W of Campo, 15 March 1931, Wolf 1912 (RSA); 1½ mi above Dulzura, 19 February 1926, Wiggins 1788 (OSC).

MEXICO. BAJA CALIFORNIA NORTE: 5 mi E of Tecate, 13 May 1948, Wiggins 11793 (OSC); Sierra Juarez 6 km SE of Japa, 26 May 1979, Moran 27372 (RSA).

Lathyrus sulphureus Brewer ex Gray

OREGON. JOSEPHINE CO.: Waldo, 3 July 1948, Ripley and Barneby 9596 (CAS); ca 1 mi S of Waldo Rd on FS 40S03, 8 June 1981, Broich 1131 (OSC).

CALIFORNIA. SISKIYOU CO.: Klamath River near Yreka, 8 May 1909, Quigley 707 (JEPS UC).

TRINITY CO.: E Weaver Cr, 20 May 1914, Yates 324 (UC); ca 12 mi SE of Alderpoint on rd to Covello, 4 July 1954, Hitchcock 20031 (WTU); on trail to Red Mt, T26N R12W S16-21, 9 June 1978, Sawyer and Nelson 3178 (HSU); above Deer Lick Springs Rd along Readings Cr, 3 mi from jct w/ Hwy 3, T2N R9W S6, 12 May 1979, York 272 (HSU); 8.2 mi NE of Hayfork on Hwy 3, 10 June 1981, Broich 1175 (OSC).

SHASTA CO.: Redding, 19 March 1936, Rose 157 (JEPS); Kennet, 2 May 1913, Smith 160 (CAS); Ydalpour, 29 April 1918, McAllister and McAllister 22 (CAS); rd to Deer Lick Springs, 0.2 mi from jct w/ Hwy 36, T29N R10W S10, 6 May 1978, Smith, Sawyer and Nelson 9821 (HSU).

TEHAMA CO.: Log Spring Ridge between Log Spring and Government Flat, 9 July 1941, Eastwood and Howell 9736 (CAS); Red Bluff, June 1917, Wiekes sn (CAS 65470).

PLUMAS CO.: NW of Greenville, 16 June 1943, Ripley and Barneby 5777 (WTU CAS); Auburn, May 1892, Ames sn (UC 212331); Greenville, 17 June 1920, Clemens sn (CAS 65478); 5 mi SW of Greenville on rd to Quincy, 28 May 1950, Hitchcock 19229 (UC CAS); Willow Cr, 24 June 1912, Hall 9267 (UC); near Quincy, 13 June 1913, Heller 10833 (DS UC); Forest Lodge, Greenville, 11 June 1927, Eastwood 14458 (CAS); between Taylorville and Crescent Mills, 12 July 1907, Heller and Kennedy 8826 (DS CAS); WPRR, Marston, 2 July 1914, C.P. Smith 2908 (CAS).

MENDOCINO CO.: along Poonburry Rd between Dos Rios and Covelo, 6.3 mi E of Dos Rios, 28 May 1949, Wiggins 12142 (UC DS WTU); E of Round Valley, June 1884, Rattan sn (DS 17643).

LAKE CO.: Dashiell's, Mt Sanhedrin, 28 May 1925, Eastwood 12776 (CAS); foot of Mt Sanhedrin, June 1917, Reynolds sn (CAS 65480); Elk Mt Rd to Pillsburry Lake, 17 June 1941, Baker 9953 (UC); near Snow Mt, 24 June 1891, Brandegee sn (UC 81778).

BUTTE CO.: Brush Cr, 1907, Couger sn (UC 127751); 3 mi above Centerville, 10 April 1915, Heller 11846 (UC DS CAS OSC);

Brush Cr Ranger Station E of Oroville, 19 May 1939, Cantelow 2438 (CAS); near Durham, April 1935, Brown sn (DS 246414); Durham, 8 May 1932, Morrison sn (CAS 196269); 5 mi below Magalia on Oroville Rd, 18 May 1937, Wolf 8730 (CAS); Berry Canyon (near Clear Cr), 7 May 1902, Heller and Brown 5485 (DS).

SUTTER CO.: 1.5 mi N and 3.5 mi W of Union School, T16N R2E S19, 30 March 1934, Sindel 42 (UC); western base of Marysville Buttes, 22 April 1926, Ferris 6389 (DS); N side of Marysville Buttes, 6 May 1914, Heller 11370a (UC DS CAS WTU OSC).

SIERRA CO.: S Fork of Uba River along Downieville Rd, 28 April 1926, Smith 1744 (CAS).

NEVADA CO.: head of S fork of Wolf Cr, 7 June 1916, Hall and Essig 10166 (UC DS CAS); Nevada City, 20-22 June 1912, Eastwood 540 (CAS); N slopes of Harmony Ridge, 5 mi N of Seven Mile House, 25 June 1969, Rose 69059 (HSU OSC); 2 mi E of Grass Valley on Hwy 20, 24 May 1980, Broich 803 (OSC); along Brunswick Rd, 0.5 mi SE of Glenbrook, 24 May 1980, Broich 804 (OSC).

PLACER CO.: Blue Canyon, 25 June 1908, Walker 1291 (UC); ca 1 mi W of Baxter, 7 May 1940, Hitchcock 6320 (WTU); ca 1 mi N of Baxter, 7 May 1940, Hitchcock 6344 (UC DS WTU).

SACRAMENTO CO.: Folsom, no date, Brandegee sn (UC 1395462).

EL DORADO CO.: Placerville, May 1907, Brandegee sn (UC 1395460); above N Fork of Webber Cr, ca 3 mi E of Camino, 5 June 1943, Robbins 1130 (UC); meadow near Webber Cr, 1 mi S of Placerville, 13 April 1924, Benson 33 (DS); along Hwy 50 5 mi E of Placerville, 6 June 1949, Hitchcock 19065 (CAS DS WTU UC OSC); 30 mi E of Placerville along Hwy 50, 6 June 1949, Hitchcock 19066 (WTU UC); near Camino, 1913, Brandegee sn (UC 1395463).

AMADOR CO.: 1891, Hanson sn (UC 15354); between Sutter Cr and Daffodil Hill along Gopher Gulch Rd near Rancheria Cr, 28 April 1962, Hutchinson 2390 (JEPS); 3.6 mi NW of Pine Grove, T7N R12E S18, 7 June 1936, Nordstrom 826 (UC); Cosumnes River, 23 April 1946, Lenz sn (HSU 02131).

CALAVERAS CO.: Mokelumne Hill, no date, Blaisdell sn (CAS 65472); near Angels, 18-30 May 1895, Davy 1447 (UC); Murphy's Camp, 18-30 May 1895, Davy 1512 (UC); San Antonio Cr between Murphy's and sheep ranch, 18-20 May 1895, Davy 1572 (UC); San Andreas, 23 April 1941, Eastwood and Howell 8698 (CAS); Gavin Mine, 17 May 1902, Jepson 1781a (JEPS); Hwy 4, 24 May 1956, Pawed 73 (DS); 1 mi NE of Jesus Maria, T5N R12E S14, 23 July 1936, Bleshaw 2525 (UC); 5.8 mi N of San Andreas on rd to Mokelumne Hill, 23 May 1933, Wolf 4904 (CAS WTU).

TUOLUMNE CO.: Mather, 4 July 1925, Mason 2143 (UC WTU); 3 mi above Tuolumne Meadows, 20 March 1936, Mason 11021 (UC); 5 mi E of Columbia toward Italian Bar, T2N R15E, 15 April 1936, Belshaw 1858 (UC); Columbia, 29 April 1916, Grant 677 (JEPS); Yankee Hill, Columbia, 14 May 1916, Grant 765 (JEPS); 2.5 mi NE of Tuolumne City, 30 March 1963, Lloyd 2283 (JEPS); 0.5 mi W of P.O. at Twain Harte, 10 June 1944, Alexander and Kellogg 3672 (UC); Soulsbyville, April 1934, Herick sn (CAS 254643); 1 mi W of Keystone, 1 April 1923, Abrams 10038 (DS); along Phoenix Lake Rd 2.8 mi NE of HWY 108 between Twain Harte and Sonora, T2N R15E S22, 29 May 1971, Wiggins 21361 (DS OSC); hills near French Flat, 11-16 April 1919, Ferris 1584 (DS UC CAS).

MARIPOSA CO.: Hazel Green to Yosemite, July 1896, Jepson 13625 (JEPS); Alder Cr Trail, Yosemite Park, 1 July 1911, Jepson 4316 (JEPS); Big Meadow Rd near Big Meadow, T3S R20E S3, 26 May 1936, Hawbecker sn (UC 128978); 1.5 mi S of Miami, T5S R20E S36, 6 June 1935, Schlobohm 147 (UC); Wowona, 1 July 1923, Howell 99 (UC); above Water Ditch, Mariposa, 17 May 1903, Congdon sn (DS 388682, UC 137194); Benton Hills, 20 April 1883, Congdon sn (DS 118494, UC M 041063); Futruanelt, 13 May 1984, Congdon sn (DS 34261); Yosemite Valley, 4-12 July 1901, Grant sn (UC 168909); near Wowney's Cabin, Dogtown, 5 mi E of Coulterville, 12 May 1941, Miller sn (UC 1329663); Eightmile (Wawona)Rd, 28 June 1911, Hall 8985 (UC); near Cave Cr, 8 June 1911, Hall 8886 (UC);

MADERA CO.: Coarsegold, 14 May 1932, Benson 3584 (DS);

slopes below Kennedy Table on rd from Hildreth to Hideaway Ranch ca 5 mi E of O'Neals, 29 April 1961, Bacigalupi 7667 (JEPS); Fresno Flats, 10 May 1928, Jepson 12856 (JEPS); at Coarsegold on Raymond Rd, 19 May 1941, Ferris and Bacigalupi 10391 (DS).

FRESNO CO.: Pinehurst, 3 June 1921, Newlon 205 (JEPS); Pine Ridge, 15-25 June 1900, Hall and Chandler 82 (UC); North Fork, 1911, Noddin sn (JEPS 55320); 1.5 mi NW of Big Cr on Stump Springs Rd, T8S R25E S20, Sierra Natl For, 23 July 1956, Fisher 55 (UC); above Dunlap on Miramonte Rd, 9 May 1941, Coburn 256 (UC); jct of N and S Forks of King's River, 30 March 1923, Duncan sn (DS 125715); Rush Cr Mill, 1895, McCarchel sn (CAS 65482).

TULARE CO.: S Fork of Tule River on main rd above Pat's Camp, 9 May 1968, Twisselmann 14181 (CAS); Mineral King Rd, 3.1 mi above Hammond, 1 June 1968, Twisselmann 14237 (CAS); N Fork of Tule River, 8 May 1969, Twisselmann 15267 (CAS); Colony Spring, August 1900, Dudley 3334 (DS); Coffee Pot Camp, Sequoia Natl For in vicinity of Homer's Hose, 11 July 1897, Dudley 1767 (DS); 47 Maple Canyon, Colony Rd, 27 Jay 1901, Hopping sn (JEPS 55308); Cedar Cr, N Fork of Keweah River in Sequoia Park, 21 June 1900, Jepson 616a (JEPS).

KERN CO.: high hill above head of Lumreau Cr, 12 June 1965, Farnsworth 576 (CAS); 2.1 mi S of Summit Camp, 27 June 1952, Hitchcock 19635 (WTU); S of Summit Camp, Greenhorn Mts, 9 July 1933, Peirson 10689 (JEPS UC); Old Kernville Rd 3.9 mi E of Greenhorn Pass, 21 June 1957, Twisselmann 3726 (CAS); N end of Piute Mt, 22 June 1962, Twisselmann 7360 (CAS); just above Alta Sierra Lodge, Greenhorn Mt Park, 9 July 1963, Twisselmann 8605 (CAS); above Shirley Meadows, 9 July 1963, Twisselmann 8633 (CAS); Shirley Meadows, 29 July 1965, Twisselmann 11376 (CAS); 4.25 mi E of Poso Mine on slope of Badger Canyon, May 1943, Smith 803 (JEPS); Eugene Grade, 0.75 mi below top, 16 July 1963, Smith 1195 (JEPS WTU).

Lathyrus sulphureus Brewer ex Gray var. argillaceus Jepson

CALIFORNIA. TEHAMA CO.: Crane Cr, 25 April 1899, Jepson 13634 (JEPS).

SHASTA CO.: Redding, 3 May 1911, Blankinship sn (JEPS 697); Pit River, 19 April 1914, McMurphy sn (DS 10058).

Lathyrus vestitus Nutt ex T. & G.

More than 1300 specimens referable to the L. vestitus complex were examined in this study. The following list includes a representative sample intended to fill the distributional gaps left by the citations listed in Appendices A and B.

Lathyrus vestitus ssp. bolanderi (Wats.) C. L. Hitchcock

WASHINGTON. KING CO.: Seattle: 3 June 1888, Piper sn (WTU 11083); June 1892, Piper sn (WTU 11080); July 1892, Piper sn (WTU 34516); 1892, Shumway sn (WTU 112745); 15 July 1930, Thompson 5206 (DS WTU).

THURSTON CO.: Olympia, 24 May-23 August 1892, Henderson sn (WTU 11374, 11376).

OREGON. WASHINGTON CO.: near Forest Grove, 15 April 1926, Thompson 807 (WTU); Scroggins Cr Valley near Gaston, 21 May 1927, Thompson 2494a (WTU).

MARION CO.: Woodburn, 4 June 1882, Howell sn (OSC 5978).

BENTON CO.: along rd 6020 in McDonald Forest, T11S R5W S7, 25 May 1981, Broich 1087, 1099 (30 May 1981)(OSC); along rd 600 in McDonald Forest, T11S R5W S8, 2 June 1981, Broich 1121 (OSC).

LANE CO.: 3 mi from Lowell, 7 April 1934, Henderson sn (CAS 212924).

DOUGLAS CO.: Glendale, 19 June 1902, M. E. Jones sn (DS 153546); 2 mi S of Myrtle Cr, 13 April 1934, Eastwood and Howell 1473 (CAS); near summit between Looking Glass Cr and Coquille River, 13 May 1924, Abrams and Benson 10525 (DS); Umpqua Valley, Rosebrug Quadrangle, 20 June 1914, Cusick 4159 (WTU OSC DS); ca 5 mi N of Kellogg, 31 May 1951, Hitchcock 19349 (UC CAS DS WTU); 2 mi E of Camas Valley, 31 May 1951, Hitchcock 19362 (WTU); near Ten-mile, 27 June 1939, Peck 20284 (WILLU); 3 mi S of Dillard, 13 July 1945, Peck 23731 (WILLU); ca 8 mi E of Reedsport on Hwy 38, 12 June 1981, Broich 1196 (OSC).

COOS CO.: Empire Rd, Marshfield, 14 July 1911, Haydon 33 (CAS); open bluffs at Bandon, 20 June 1936, Thompson 12793 (WTU); 4 mi S of Charleston, 17 July 1926, Scullen 87 (OSC); Eden Ridge above S Fork of Coquille River, 28 May 1926, Ingram 1988 (OSC); Brewster Canyon, 10 July 1916, Peck 5229 (WILLU).

CURRY CO.: mouth of Tate Cr along Rogue River, 27 April 1947, Baker 3814 (UC); beach dunes 2 mi NW of Port Orford, 1 July 1951, Hitchcock 19526 (WTU); seaward face of shore bluff, The Heads, Port Orford, 22 June 1919, Peck 8459 (WILLU); Port Orford, 28 July 1919, Peck 8967 (WILLU); The Heads, Port Orford, 18 June 1926, Peck 14670 (WILLU); Brookings, May 1915, Thompson 206 (DS); 10 mi N of Gold Beach, 4 June 1928, Thompson 4478 (DS).

JOSEPHINE CO.: ca 18 mi S of Roseburn on Grants Pass Rd, 9 June 1949, Hitchcock 19108 (UC); 8,7 mi W of Wolf Cr on the Grave Cr Rd, 2 May 1981, Broich 1029 (OSC); 2.5 mi E of the Takilma Jct on O'brien-Happy Camp rd, 11 June 1981, Broich 1186 (OSC); Wolf Cr Park W of Wolf Cr, hill S side of Cr, 17 May 1981, Broich 737 (OSC); 0.5 mi S of O'brien along Hwy 199, 18 May 1981, Broich 750 (OSC).

CALIFORNIA. DEL NORTE CO.: Mill Cr, 27 June-1 July 1922, Abrams 8468b (DS); Smith River, 8 April 1902, Goddard 328 (UC); ca 6 mi NW of Gasquet on cut off to Hwy 101, 8 June 1949, Hitchcock 19099 (UC); ½ mi W of "Darlingtonia Cottages" along Smith River and Hwy 199, 8 July 1949, Hitchcock 19102 (UC WTU); 5 mi S of Crescent City, T15N R1W, July 1937, Nordstrom 1433 (UC); grassy slopes facing ocean south of mouth of Klamath River, 12 May 1929, Tracy 8587 (UC).

HUMBOLDT CO.: near Harris, 22 June 1937, Eastwood and Howell 4719 (CAS); Bull Springs to Harris, 8 June 1899, Davy and Blasdale 5358 (UC); Humboldt Bay, May 1901, Chandler 1201 (DS UC); bluff N of Big Lagoon, 25027 June 1922, Abrams and Bacigalupi 8296 (DS); Willow Cr, 16 June 1918, Abrams sn (DS 90208); between Eureka and Orick, 27 June 1941, Winblad sn (CAS 296656); Bear River Ridge 7 mi S of Ferndale, 8 June 1950, Tracy 18728 (UC); 2 mi E of Kneeland on Butter Valley Rd, 4 July 1949, Tracy 18327 (UC); S Fork of

Eel River between Miranda and Redway, 24 April 1932, Tracy 9815 (UC); Dinsmore's Ranch, valley of the Van Duzen River opposite Buck Mt, 26 June 1913, Tracy 4352 (UC).

Lathyrus vestitus ssp. vestitus

OREGON. CURRY CO.: Brookings, 17 May 1924, Abrams and Benson 10710 (DS); 1 mi S of Harbor, 8 June 1949, Hitchcock 19095 (UC); city lot in Brookings, 8 June 1949, Hitchcock 19097 (UC WTU CAS); Brookings, 7 July 1939, Peck 20436, 20443 (WILLU).

CALIFORNIA. DEL NORTE CO.: ca 1.0 mi off Hwy 199 on Patrick's Cr Rd, 19 May 1980, Broich 763, 764 (OSC); clearing in Cedar Rustic CG, Six Rivers Natl For, 8 June 1981, Broich 1138 (OSC).

HUMBOLDT CO.: near South Bay, 25-27 June 1922, Abrams and Bacigalupi 8245 (DS); near Hydesville, 11 May 1912, Tracy and Babcock 3610 (UC); valley of the Van Duzen River opposite Buck Mt, 3 August 1912, Tracy 3971 (UC WTU); 1.9 mi N of Bridgeville on rd to Kneeland, 20 May 1980, Broich 782, 783 (OSC).

MENDOCINO CO.: S Mill Cr Canyon near Ukiah, 28 April 1918, Abrams 6941 (DS); along Hwy 101 ca 4 mi S of Willets, 7 June 1949, Hitchcock 19075 (WTU UC); near Comptche, 23-29 June 1906, Walker 253 (UC); 6.5 mi W of Orr's Hot Springs, 23 May 1936, Eastwood and Howell 2725 (CAS); near Greenwood, 29 June 1922, Eastwood 11488 (UC CAS); Ridgewood summit on Redwood Hwy, 1 April 1928, Kildale 4380 (DS); Fort Bragg, 12 July 1931, M. E. Jones sn (UC 479111).

LAKE CO.: Dashiells, Mt Sanhedrin, 22 May 1925, Eastwood 12777 (CAS); Sawmill Flat, Bartlett Mt, 19 June 1945, Howell 21023 (CAS); Allen's Springs, 20 June 1882, Cleveland 49 (UC); Cobb Mt, 31 March 1931, Jussel 58 (CAS); Jordan Park on rd to Lower Lake, 1 May 1932, Jussel sn (CAS 195322); 2 mi E of Oat Hill Mine, 3 June 1933, Wiggins 6732 (DS UC).

SONOMA CO.: near Sonoma, 18 April 1862, Brewer 966 (UC); hills E of Santa Rosa, 10 March 1902, Heller and Brown 5026 (DS); Bodega Bay, 11 April 1902, Heller and Brown 5254 (DS); near

Guerneville on rd from Edendale to Vacation Beach, 18 May 1953, Rubtzoff 1411 (CAS); S slopes of Fitch Mt, near Healdsburg, 3 June 1952, Rubtzoff 1155 (CAS); Granite Hills, 2 mi E of Santa Rosa, 11 March 1902, Heller 5026 (WTU).

NAPA CO.: Howell Mt grade to New Eden, no date, Jepson 531 (JEPS); Howell Mt, Napa Range, 6 April 1924, Jepson 10316 (JEPS WTU); Mt St. Helena at Toll House, 27 April 1924, Jepson 10370 (JEPS); Howell Mt below New Eden, 26-27 November 1896, Jepson 13631 (JEPS); 0.5 mi S of Calistoga, 29 March 1953, Raven 5205 (CAS); Soda Cr E of Chiles Valley, 19 April 1953, Raven and Stebbins 5322 (CAS); Sulphur Springs Canyon just N of the Resort, 22 January 1954, Raven 6386 (CAS); 5 mi S of Calistoga, 12 April 1924, Heller 13839 (DS); St. Helena grade, 3 May 1928, Abrams 12218 (DS); summit St. Helena grade, 3 May 1928, Abrams 12239 (DS); 1½ mi NE of Calistoga, 25 March 1928, Wiggins 2884 (UC DS).

YOLO CO.: Cache Cr canyon 4 mi N of Rumsey, 7 May 1938, Crum 1984 (UC).

SOLANO CO.: near Vacaville, 28 April 1902, Heller and Brown 5396 (DS); Tolenas Spring, 23 March 1898, Sitchell sn (UC 15329).

SAN FRANCISCO CO.: top of ridge E of Ocean View, 20 March 1897, Dudley sn (DS 104202); Mission Hills, 1 May 1897, Dudley sn (DS 111949); N slope of Bay View Hills, 10 June 1956, Howell 31528 (CAS); Presidio, 23 May 1895, Tidestrom sn (JEPS 55358); slopes above Laguna Honda, 2 May 1954, Raven 6823 (CAS); San Miguel Hills, 16 March 1957, Rubtzoff 3114 (CAS).

SAN MATEO CO.: Woodside, 9 March 1895, Applegate 140 (DS); King's Mt, 10 May 1902, Baker 801 (UC); San Bruno Hills, 6 April 1903, Baker 1893 (CAS); Lake Pilarcitos, 20 April 1895, Davy 1054 (UC); San Mateo, May 1903, Elmer 4745 (DS CAS UC); San Bruno Hills, 20 April 1907, Heller 8454 (DS WTU); Kings Mt, 29 May 1935, Rose 35191 (CAS); 0.75 mi above Woodside on Kings Mt Rd, April 1925, Wiggins 1661 (DS); Alpine Cr Rd, 14 April 1928, Wiggins 2910 (DS); 2 mi N of Langley Hill, NE of La Honda, 8 May 1935, Yates 5203 (UC).

SANTA CRUZ CO.: Capitola, 13 October 1902, Abrams 3049 (DS); Laurel, 29 June 1914, C. P. Smith 2891 (CAS); 2 mi W of Boulder Cr, 8 May 1935, Yates 5186 (UC); Soquel Valley 1 mi S of Mountain School, 30 March 1950, Thomas 1392 (DS); rd from Bielawski Lookout Station into region between Deer Cr and Kings Cr, 11 April 1950, Thomas 1519 (DS); ca 4 mi below Saratoga Summit, 23 April 1950, Thomas 1627 (DS); Bear Cr Rd ca 2 mi from summit, 28 January 1951, Thomas 1516 (DS); near summit of Hwy 17, 23 May 1953, Thomas 3173 (DS).

For citations of ssp. laevicarpus Broich ssp. nov., ssp. barbarae (White) Broich comb. nov. and ssp. alefeldii (White) Broich comb. nov. see Appendix B.

Lathyrus vestitus ssp. bolanderi (Wats.) C. L. Hitchcock intermediate to L. jepsonii ssp. jepsonii

CALIFORNIA. SANTA CLARA CO.: Isabel Cr, Mt. Hamilton Range, 19 May 1923, Bacigalupi sn (DS 147946).

Lathyrus vestitus ssp. vestitus intermediate to L. jepsonii ssp. californicus (Wats.) C. L. Hitchcock

CALIFORNIA. MARIN CO.: Fairfax Hills, 18 May 1947, Howell 23174 (WTU); Novato, 20 May 1945, Leschke sn (CAS 344520).

MENDOCINO CO.: ca 12 mi S of Laytonville on Hwy 101, 7 June 1949, Hitchcock 19078 (WTU UC).

LAKE CO.: 5 mi W of Clear Lake on Hwy 20, 7 June 1949, Hitchock 19073 (CAS DS).