A COMPARISON OF NORTH AND SOUTH AMERICAN *LUPINUS* GROUP *MICROCARPI* (LEGUMINOSAE)

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ABSTRACT

Lupinus group *Microcarpi* occurs disjunctly in North and South America, primarily in central California and Chile. This study addresses the question of whether the disjunct representatives, variously referred to *L. microcarpus, L. densiflorus, L. ruber* or *L. subvexus,* are distinct. Data for vegetative and floral features were taken from South American specimens and were compared to those from population samples from California. The analyses show that some South American plants are smaller, but in all features have a range of variation within that of California plants. Affinities of the South American specimens were assessed by multigroup discriminant analysis and an a posteriori classification procedure whereby each one was assigned to a population sample from California. The South American specimens were assigned to a few California populations identified as *L. densiflorus, L. subvexus* and *L. ruber,* or intermediates between them. Neither floral nor vegetative features can be used to distinguish the South American representatives of group *Microcarpi* from some North American representatives.

RESUMEN

Lupinus del grupo *Microcarpi* ocurre descontinuadamente en América del Norte y del Sur, principalmente en California Central y en Chile. Este estudio se dirige a tratar de resolver la pregunta que si las especies llamadas *L. microcarpus, L. densiflorus, L. ruber* y *L. subvexus* son distintas. Los datos de las características vegetativas y florales fueron tomados de ejemplares sudamericanos y comparados con ejemplares obtenidos de poblaciones en California. El análisis de los datos indica que algunas de las plantas sudamericanas son más pequeñas que las de California, pero en todas las otras características, el rango de varación está dentro del que se obtiene de los ejemplares obtenidos en California. Las afinidades de los ejemplares sudamericanos fueron valorados por medio de un análisis discriminativo multigrupo y un método de clasificación de posterioridad en el cual cada uno de los ejemplares sudamericanos fueron asignados a una muestra de la población de California. Los ejemplares sudamericanos se asignaron a unas poblaciones californianas identificadas como *L. densiflorus, L. ruber* y *L. subvexus* o especies intermedias. Las características vegetativas y florales no se pueden usar para distinguir entre las especies obtenidas en América del Sur y aquellas obtenidas en California.

The informal group *Microcarpi* is easily delimited from the various assemblages of *Lupinus* summarized by Charles Piper Smith (1944). It is a group of annuals with sessile perfoliate cotyledons, ovoid two-seeded fruits and verticillate flowers. Members of the group occur disjunctly in North and South America, primarily in central California and Chile.

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In a series of papers Smith (1917, 1918a,b, 1919) treated the *Microcarpi* as consisting of five species including 35 new or newly combined varieties. The group has not been studied in its entirety since. Authors of regional floras have treated it only in part, and their various interpretations largely have resulted in a more confusing taxonomy. No two subsequent treatments are in complete agreement as to the disposition of the taxa or the names to be used for them. The disagreement centers around a fundamental taxonomic question: are populations from North and South America distinct?

In this paper I compare morphological data obtained from herbarium specimens from South America with those obtained from population samples from California. The aim of the comparison is to document the range of morphological variation in the disjunct representatives, and to determine if the South American plants are morphologically distinct from their North American counterparts. I also compare distributional and ecological information obtained from the specimens and from my collection data.

Historical Perspective

Smith's (1917, 1918a,b, 1919) group *Microcarpi* included *L. microcarpus* Sims, described from plants grown from seed originally collected in Chile, and *L. densiflorus* Benth., described from plants grown from seed collected by Douglas in California. Smith also recognized *L. subvexus* C. P. Smith, *L. horizontalis* Heller and *L. luteolus* Kell. Three of these (*L. microcarpus, L. densiflorus* and *L. subvexus*) were described as occurring in both North and South America. These three and *L. horizontalis,* of California desert habitats (Smith 1918a), form a problematical complex. The fifth species, *L. luteolus,* was described as occurring in California and Oregon. It can be separated from the complex by several features (Smith 1919a), and has been treated as a distinct species by subsequent authors.

Jepson (1936) commented on the close resemblance of North and South American specimens. He wrote (p. 278), "In certain cases, if the labels were removed, it would seem impossible, on the basis of the material itself, to say whether a given sheet were Californian or Chilean." Jepson placed all California representatives of the complex into *L. microcarpus.* He considered a portion of the California material, including *L. subvexus,* to be typical of the species. He recognized three additional varieties, *L. m.* var. *densiflorus* Jeps., *L. m.* var. *horizontalis* Jeps., and *L. m.* var. *ruber* (Heller) C. P. Smith (=*L. ruber* Heller).

The only other work in which North American members of the complex are treated as *L. microcarpus* is that of Hitchcock et al. (1961). They recognized *L. m.* var. *scopulorum* C. P. Smith from

Vancouver Island and adjacent islands of Washington, and *L. m.* var. *microcarpus* for all other populations from Washington to Baja California, and South America.

Munz's (1959) treatment of the California complex is diametrically opposed to Jepson's. Munz recognized *L. horizontalis, L. ruber, L. subvexus* with four varieties, and *L. densiflorus* with six varieties. From this treatment it might be concluded that the name, *L. microcarpus,* does not apply to North American plants.

Dunn and Gillett (1966) stated that *L. microcarpus* is a southern hemisphere relative of the *L. densiflorus* complex of the northern hemisphere. They concluded that North American taxa could not be interpreted as *L. microcarpus* because its original description referred to blue flowers and torulose pods, but did not refer to keel ciliation.

In a recent dissertation Planchuelo (1978) placed all Argentinean specimens of the group into *L. microcarpus.* She treated the Argentinean taxa described by Smith (1943) as synonyms, but did not study the Chilean taxa described by Smith (1918a,b, 1940).

To avoid confusion in the following discussion, I refer to North American representatives as the *L. densiflorus* complex, and follow Munz's (1959) treatment. *Lupinus luteolus* is excluded from the study.

Methods and Materials

To document geographic distribution of South American members of group *Microcarpi,* I examined approximately 125 collections from BM, CAS, DS, GH, K, MO, RSA, UC and US. Collection data for those used in the analyses are given in Table 1. A total of 74 specimens for 56 collections were measured, and are identified by numbers as given in Table 1. The South American specimens include representatives of the nine taxa recognized by Smith (1918a,b, 1940, 1943) as occurring in Chile and Argentina. Six collections are type specimens.

To document distribution and variation of North American taxa, I collected extensively in California and consulted herbarium specimens from outside the state. The 41 samples used here (Table 2) are part of a larger study of the *L. densiflorus* complex in California. Each sample consisted of 20 plants, so data from 820 specimens form the data base. Most of the samples are from San Luis Obispo Co., near the center of the range of the complex and where all four species (*L. densiflorus, L. ruber, L. subvexus, L. horizontalis*) are known to occur (Munz 1959, Hoover 1970). The populations are from localities along west to east climatic gradients characterized by decreasing winter rainfall and increasing summer temperatures. Although the majority of populations can be identified as belonging

TABLE 1. COLLECTION DATA FOR SOUTH AMERICAN SPECIMENS OF *Lupinus*. Numbers in parentheses represent identification numbers for purposes of analysis. An asterisk (*) designates specimens for which data for all variables were obtained and included in the diagnosis.

Without collection data (1 GH*). Argentina, Chubut: Pampette s. of Lago Colhué Huapi, *Riggs 56* (type of *L. verticillatus* C. P. Smith, 2 GH*). Neuquen: Chos Malal y Agrio, 600–1200 m, *Comber 188* (type of *L. comberanus* C. P. Smith, 3 K*). Río Negro: Vicinity of General Roca, 250–360 m, *Fischer 280* (type of *L. fischerianus* C. P. Smith, 4 BM, GH*, K). Chile, without collection data (5 BM*); without locality, *Cuming s.n.* (6 BM*); *Cuming 567* (7 BM); *Cruckshanks 135* (8 K*); 1832, *Bridges s.n.* (9 K*); 1864–65, *Reed s.n.* (10a,b K* 2 sheets); Feb 1888, *Philippi s.n.* (11 K*). Province undetermined, Andes, *Reynolds s.n.* (12 GH*); Salto de Conchalí, Nov 1883, *Philippi s.n.* (13 BM*); San Pedro Nolasco, collector unknown (14 BM*); Cordillero de Curico, *Ruíz P. s.n.* (15 GH*). Aconcagua: Uspallata Pass, Juncal, 2300 m, *Buchtien 1180* (16a BM*, 16b GH*). Antofagasta: Taltal, 600 m, *Werderman 856* (17a BM*, 17b DS*, 17c GH*, 17d K*, 17e UC*); ca. 10 km e. of Taltal, 75 m, *Worth and Morrison 15807* (18 UC). Arauco: Arauco, *Pennell 1297* (19 GH*). Atacama: Cerro Campaña, 15 Nov 1884, *Philippi and Borchers s.n.* (20 BM); Río Sancarrón below Rucas, ca. 3200 m, *Johnston 6204* (21a GH*, 21b K*). Biobío: Pailahueque, *Pirion 203* (22 GH*). Cautín: Between Temuco and Río Quepe, Dec 1905, collector unknown (23 BM*); Temuco, *Elliott 218* (24 BM*). Colchagua: San Fernando near Tinguiririca Bridge, *Montero 15* (25 GH*). Coquimbo: Baños del Toro, 3500 m, *Werdermann 197* (26a BM*, 26b CAS*, 26c GH*, 26d UC*); Coquimbo, July–Aug 1856, *Harvey s.n.* (27 GH*, K); 14 km e. of Nueva Elqui, 3200 m, *Wagenknecht 18122* (28 GH*, UC). Concepción: Concepción, *Reed s.n.* (type of *L. densiflorus* var. *reedii* C. P. Smith, 29 GH*); Concepción, *Elliott 78* (30 BM*); Concepción, Nov 1926, *Günther and Buchtien s.n.* (31 BM*); Lota, 7 Nov 1868, *Cunningham s.n.* (32 K*); Lota, 20 Dec 1902, *Elwes s.n.* (33 K*). O'Higgins: Rancagua, *Bertero s.n.* (34 K*); Cachapual, Rancagua, *Bertero 393* (35 GH*); Cachapual, Rancagua, *Bertero 393 et 1116* (36a BM*, 36b GH*). Santiago: Bath of Colina, 1825, *Macrae s.n.* (type of *L. densiflorus* var. *barbatissimus* C. P. Smith, 37 GH*, K); Colina, 1825, *Macrae s.n.* (38 K*); 3 km n. of El Tabo, 20 m, 30 Nov 1970, *Simon s.n.* (39 DS*, RSA); Río Teso Romeral, *Biere 57* (40 GH*). Talca: Talca, Nov 1925, *Gunckel s.n.* (41 GH*). Valparaíso: Valparaíso, *Cuming 567* (42a BM*, 42b K*); Valparaíso, 1844, *Bridges s.n.* (43 BM*); rd from Valparaíso to Quillota, *Bridges s.n.* (type of *L. densiflorus* var. *decumbens* C. P. Smith, 44 K*); Valparaíso, *Cumming s.n.* (45 K*); Valparaíso, *Robinson s.n.* (46 K*); Valparaíso, *Mathews 363* (47a BM*, 47b GH*, 47c K*); Valparaíso, 1914, *Calvert s.n.* (48 BM); ca. 4 km from Valparaíso on rd to Quebrada Verde, 290 m, *Morrison 16713* (49a GH*, 49b K*, UC); Renaca ca. 18 km from Valparaíso, 10 m, *Morrison 16847* (50 GH*, K, UC); between Viña del Mar and Concón, 60 m, *Landeman 193* (51a BM*, 51b K*); Viña del Mar a Concón, *Pirion 268* (52 GH*); Concón, collector unknown (53 BM*); 21 m wege nach Concón, Nov 1928, *Günther and Buchtien s.n.* (54a CAS*, 54b DS*); 6.2 km n. of Puchuncavia, 30 m, *Simon 134* (55 CAS*, RSA); Limache, Camino al Paugal, *Looser 135* (56 GH*).

to one of the four species of Munz and Hoover, several are morphologically intermediate and cannot be identified with certainty.

Morphological data consisted of seven vegetative and 12 floral variables. Leaf measurements were taken from the largest leaf of the specimen, and floral measurements from flowers at anthesis. Seventeen quantitative variables are listed in Table 3. The other two

TABLE 2. COLLECTION DATA FOR CALIFORNIA POPULATION SAMPLES OF THE *Lupinus densiflorus* COMPLEX. Collection numbers are those of the author.

Kern Co.: 1.0 mi n. of Reyes Sta., *1134*; Crocker Cyn., 2.9 mi e. of San Luis Obispo Co. line, *1154*; Gypsum Mine Rd., 1.0 mi e. of Simmler–Bitterwater Rd., *1186*. Monterey Co.: county rd G19, 1 mi w. of US 101, n. of Bradley, *1179*. San Luis Obispo Co.: CA 166, 3.1 mi w. of Sierra Madre Rd., *1133*; county rd 285, 0.9 mi se. of CA 58, *1137*; Hurricane Rd., 0.9 mi ne. of county rd 285, *1138*; base of Crocker Grade at county rd 285, *1139*; *1140*; slope w. of San Juan R. at CA 58, *1141*; Shell Cr. Rd. at CA 58, *1142*; Atascadero–Creston Rd., 1.9 mi e. of Templeton Rd., *1143*; Huerhuero–LaPanza Rd., 0.2 mi nw. of CA 58, *1144*; CA 41, 0.7 mi e. of Cripple Cr. Rd., *1145*; El Camino Real, Santa Margarita, 0.3 mi e. of US 101, *1146*; Pozo Rd., 0.3 mi e. of CA 58, *1147*; Pozo Rd., 0.7 mi w. of Salinas R. Bridge, *1148*; CA 166, 11.9 mi e. of US 101, *1149*; CA 166, 3.2 mi e. of Sierra Madre Rd., *1150*; Hi Mt. Rd., 8.8 mi ne. of Lopez Lake Rd., *1151*; Klau Mine Rd. just e. of Cypress Mt. Rd., *1152*; county rd 285, 6.9 mi s. of CA 58, *1153*; Elkhorn Trail Rd., 4.8 mi se. of Hurricane Rd., *1155*; *1156*; county rd 285, 2.3 mi n. of Coachoro Camp Rd., *1157*; *1158*; Avenales Ranch Rd., 3.3 mi e. of American Cyn. Rd., *1160*; Avenales Ranch Rd., 0.3 mi nw. of Avenales Guard Sta., *1161*; Avenales Ranch Rd., 2.0 mi se. of Avenales Guard Sta., *1162*; *1163*; USFS Rd., 2.1 mi e. of Los Machos Cr., *1171*; *1172*; Thirty-Five Cyn. Rd., 2.7 mi s. of Branch Mt. Rd., *1173*; Cable Corral Rd. at CA 166, *1174*; Almond Spring Ranch, Adelaida–Nacimiento Rd., *1175*; Nacimiento Rd., 1.4 mi e. Chimney Rock Rd., *1176*; Nacimiento Lake Rd., 0.6 mi n. of Nacimiento Dam, *1177*; Wellsona Rd. at River Rd., *1180*; El Pomar Rd., 0.1 mi s. of Vaquero Drive, *1181*; Eagle Ranch, 0.3 mi s. of Santa Barbara Rd. n. of Santa Margarita, *1182*; Camatti Cyn. Rd., 1.2 mi s. of Gillis Cyn. Rd., *1185*.

were appraisals of wing and keel ciliation. Wing ciliation was recorded as either of three states: 0, absent; 1, present above; 2, present above and below. Keel ciliation was recorded as either of two states: 0, absent below; 1, present below. I selected the 19 variables to summarize size and shape of vegetative and floral structures, and to include features used in previous treatments.

Some taxonomic or field characters are not easily assessed for numerical analyses and were excluded for this reason. Smith (1918b et seq.), Munz (1959) and Hoover (1970) distinguished *L. densiflorus* as having spreading or arching racemes with secund flowers and fruits. This feature is related to the degree of branching on any one plant, and where the plants are growing. Often flowers on primary racemes do not become secund. Plants otherwise identifiable as *L. subvexus* or *L. horizontalis* may develop secund flowers and fruits. The feature is neither consistent within populations, nor unique to those identifiable by other features as *L. densiflorus*. Furthermore, it is extremely difficult to assess in pressed specimens if fruits are not present. *Lupinus horizontalis, L. ruber* and *L. subvexus* have been described as having ascending, erect or suberect flowers and fruits. Erectness is related to flower size; small flowers are ascending to erect whereas larger ones are suberect to spreading. The original figure of *L. microcarpus* showed ascending flowers, but the South

TABLE 3. RANGE AND MEAN VALUES FOR SOUTH AMERICAN AND CALIFORNIAN SPECIMENS OF *Lupinus* GROUP *Microcarpi*. All measures are in mm. n = number of specimens.

Variable	n	South American		Californian	
		Range	Mean	Range	Mean
Leaflet number	72	6–11	8.3	5–12	9.3
Leaflet width	71	2.0–12.0	5.1	2.0–12.5	6.9
Leaflet length	71	8.0–40.0	21.7	9.5–59.5	29.6
Petiole length	71	13.0–120.0	61.0	15.0–221.0	106.5
Peduncle length	72	15.0–150.0	65.7	19.0–320.0	140.1
Length between verticils 1 and 2	72	7.0–40.0	17.8	8.0–50.5	22.4
Bract length	72	2.5–8.5	5.0	3.5–12.5	6.3
Pedicel length	73	0.5–3.5	1.4	0.5–5.0	1.7
Upper calyx lobe length	73	2.2–5.0	3.7	1.1–7.8	4.0
Lower calyx lobe length	73	5.4–10.0	7.5	5.2–10.7	7.9
Banner length, base to flexion	74	4.5–8.0	5.8	4.2–10.6	6.8
Banner length, flexion to apex	74	4.5–8.2	5.7	3.7–9.7	6.5
Banner width, flexion to margin	74	1.4–3.5	2.5	1.3–6.2	3.5
Wing width	74	2.7–5.3	3.9	2.2–7.8	4.9
Wing length	74	9.0–14.4	11.7	8.8–17.7	13.6
Keel length	73	9.2–14.0	11.7	8.4–17.7	12.9
Keel width	73	0.9–1.5	1.1	0.9–2.9	1.7

American specimens exhibit as much variation in this feature as California plants.

Flower color in *L. densiflorus* varies from white to yellow, to pink and rose, and to lavender and purple. Often the amount of pink or purple varies in the wing and banner petals so that overall flower color is not easily described. Yellow and white flowers are generally restricted to populations of *L. densiflorus,* but all degrees of pink to purple are found in other members of the complex. Yellow, pink, and purple are generally intensified in dried specimens, but retention of original color is related to duration and method of drying. Sometimes flowers fade to a straw color on drying. The South American specimens do not appear to have flower colors different from California plants. Although the original description of *L. microcarpus* referred to blue flowers, all subsequent authors have described them as rose or lavender. I have not seen any specimen of the group that appears to have blue flowers typical of other lupine species.

Data analyses included a tabulation of minimum, maximum, and mean values for each variable. All variables could not be measured from some South American specimens, so the mean values were based on a varying number of observations (n) as given in Table 3. In addition, multigroup discriminant analysis and diagnosis were carried out as described in BIOSTAT II (Pimentel and Smith 1985). With these methods discriminant analysis is first performed on pop-

ulation samples, and then each individual of uncertain affinity is assigned to a population of the discriminant analysis by an a posteriori Geisser classification procedure. In this study discriminant analysis was performed on the samples from California, and the diagnosis on the South American specimens. Each South American specimen was assigned to a population sample from California. Because missing data are not allowed for these analyses, four South American collections (numbers 7, 18, 20 and 48) were excluded and the diagnosis was performed on 69 of the specimens indicated in Table 1. For these analyses the data were log transformed.

Results

Geographic distribution. All South American specimens I examined are from Argentina and Chile. Smith's (1941) report of *L. microcarpus* from Peru was based on *Weberbauer 148* (Dpto. Lima, inter Matucana et Chanpothio, 26 Dec 1901, B) a specimen presumably destroyed.

Chilean plants occur along the coast from Taltal (25°26′S, Prov. Antofagasta) to Valdivia (39°49′S, Prov. Valdivia), and inland from Río Sancarrón (29°33′S, Prov. Atacama) to Temuco (38°44′S, Prov. Cautín). Approximately one-third of the specimens I examined were collected before 1900, many from areas near ports. Precise locality and habitat data are often scanty but are sufficient for the following ecological characterization. The Chilean plants grow in sandy soils, rocky places and grasslands from the coast to the Andes at elevations from near sea level to 600 m. A few specimens were collected along the western slope of the Andes at reported elevations of 2300 to 3500 m.

Argentinean plants occur from latitude 33°S in Prov. Mendoza to latitude 46°S near the southern border of Prov. Chubut. They grow in the same kinds of habitats as in Chile, but are regarded as rare and introduced (Planchuelo 1978).

In North America members of the *L. densiflorus* complex occur near the coast from San Diego Co. (32°N) to Humboldt Co., California (40–41°N), and disjunctly near Victoria, British Columbia (48°N). Inland localities extend from Sierra de Juarez, Baja California Norte (31°N) to central Washington (45°N). Within this range they are most abundant in California between latitudes 34°N and 38°N, from the coast eastward to the Sierra Nevada foothills. In central California these lupines grow primarily in sandy soils of valleys and low hills at elevations from near sea level to 1500 m. They are most abundant in roadside and intermittent streamside habitats, but also occur in grasslands and desert washes. They do not occur at elevations above 1550 m, nor east of the Sierra Nevada.

These distribution records, my field observations, and informa-

TABLE 4. ACTUAL AND PERCENTAGE OCCURRENCE OF WING AND KEEL CILIATION STATES IN SOUTH AMERICAN AND CALIFORNIAN SPECIMENS OF *Lupinus* GROUP *Microcarpi.*

	South American		Californian	
	n	%	n	%
Wing ciliation:				
0, absent	21	28	175	21
1, present above	46	67	539	66
2, present above and below	2	5	105	13
Keel ciliation:				
0, absent below	67	90	542	66
1, present below	7	10	277	34

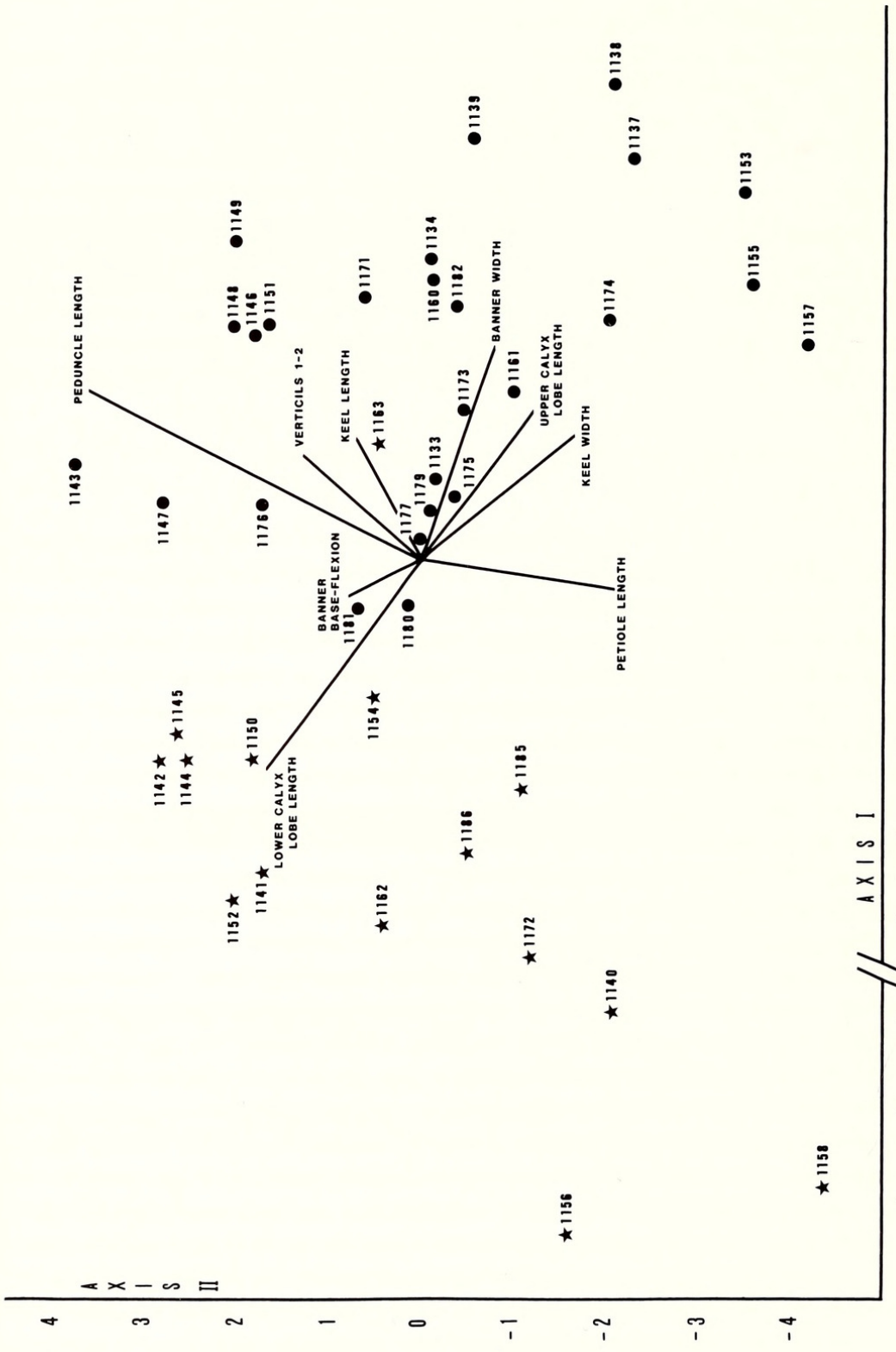
tion from the literature, indicate that plants from both hemispheres occur generally within the same latitudes and elevations, and in similar habitats. Both areas of distribution have Mediterranean climates and are well-known for their disjunct ranges of closely related species (Raven 1963).

Morphological comparisons. Table 3 shows that the South American specimens are often smaller, particularly in vegetative features, than the California specimens. South American specimens have a narrower range of variation than those from California, but generally exhibit a range of variation within that of the California specimens. Minimum values for five vegetative measurements were recorded from South American plants, but all maximum values were from California plants.

For all variables, South American specimens have smaller mean values than California specimens. Differences in mean values are particularly striking for the petiole and peduncle measurements. Differences in the mean values for the floral variables are less apparent. Except for wing and keel petal lengths, the differences between the two groups is ≤ 1 mm.

Results for wing and keel ciliation features are given in Table 4. Fewer South American specimens have cilia present on both margins of the wing and keel petals.

Although the aim of this paper is to determine if the South American representatives are distinct, some understanding of variation and discrimination of the California samples is necessary to clarify the relationships. Figure 1 portrays the results of the discriminant analysis of the California specimens on canonical axes 1 and 2 that respectively represent 47% and 16% of the differences between the samples. Vectors of variables contributing to ordination of the samples indicate that separation on axis 1 is primarily due to floral


PEDUNCLE LENGTH
VERTICILS 1-2
KEEL LENGTH
BANNER WIDTH
UPPER CALYX LOBE LENGTH
KEEL WIDTH
BANNER BASE-FLEXION
LOWER CALYX LOBE LENGTH
PETIOLE LENGTH
1143
1147
1176
1148
1149
1146
1151
1171
1160
1134
1182
1139
1138
1137
1153
1155
1157
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1180
1154
1150
1145
1142
1144
1141
1152
1162
1186
1185
1172
1140
1156
1158
AXIS I
AXIS II

variables, measurements of the calyx, and of the banner and keel petals. Samples on the right side of the graph have longer and wider keel petals, wider banner petals and longer upper calyx lobes than those on the left side of the graph. Separation on axis 2 is mostly due to vegetative features of peduncle, petiole and verticil lengths. Samples on the upper half of the graph are taller, whereas those on the lower half have smaller leaves. Ordination along axis two roughly parallels an east-to-west climatic gradient of arid-to-mesic habitats; samples on the lower half were collected in the most arid habitats.

Clear or tight clusters of the California samples are not detectable in Fig. 1. I initially identified the majority on the right side as *L. densiflorus,* and those on the lower right as *L. horizontalis.* The remote samples on the lower left were initially identified as *L. ruber,* and those on the upper left as *L. subvexus.* Several samples near the middle of the graph were identified as intermediate between *L. densiflorus* and *L. subvexus,* or intermediate between *L. subvexus* and *L. ruber,* and were collected in areas of sympatric distribution (Hoover 1970).

South American specimens were assigned to 15 samples designated by stars in Fig. 1. All except sample *1163* are on the left side of the graph, and are samples that were identified as *L. ruber, L. subvexus* or intermediates between them. Sample *1163* was initially identified as *L. densiflorus.* The 15 samples are from interior localities and more arid habitats than those not involved in the assignments.

Results of probability assignments for the South American specimens are summarized in Table 5. The probabilities ranged from 19% to 97% and averaged 51.4%. For 61 of 69 South American specimens, assignment to a specific California sample was evident; i.e., resemblance to any other sample was remote. Eight South American specimens (17c, 22, 26a, 31, 33, 36b, 38, 51b as identified in Table 1) had close affinities ($\leq$2%) to two different California samples; in each case the two samples were from nearby localities and like habitats. Forty (58%) of the South American specimens were assigned to just three California samples: *1142, 1162* and *1172.*

The California samples show a clinal pattern of geographic variation (Fig. 1), but there is no evidence of a similar pattern among the South American specimens. This could be a reflection of inadequate sampling, although the specimens are from localities that represent the geographic range and ecological zones where they occur

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FIG. 1. Plot of California samples of *Lupinus* group *Microcarpi* on canonical axes 1 and 2. South American specimens were assigned to those designated by stars. Vectors of variables contributing to the ordination are also plotted.

TABLE 5. DIAGNOSIS ASSIGNMENTS OF SOUTH AMERICAN SPECIMENS (S. Am.) TO CALIFORNIA (Calif.) POPULATION SAMPLES OF *Lupinus* GROUP *Microcarpi*. Column I refers to diagnosis based on 19 variables; Column II to that based on 17 variables.

	Calif.				Calif.				Calif.		
S. Am.	I	(%)	II	S. Am.	I	(%)	II	S. Am.	I	(%)	II
1	*1162*	(65)		21a	*1158*	(84)	*1156*	39	*1186*	(57)	
2	*1172*	(95)		21b	*1158*	(78)	*1152*	40	*1150*	(46)	
3	*1185*	(29)	*1140*	22	*1163*	(23)		41	*1172*	(36)	*1162*
4	*1172*	(54)		23	*1154*	(33)		42a	*1141*	(19)	
5	*1154*	(48)		24	*1152*	(36)		42b	*1142*	(57)	
6	*1142*	(26)	*1150*	25	*1141*	(54)		43	*1142*	(54)	*1145*
8	*1156*	(38)	*1162*	26a	*1172*	(51)		44	*1162*	(53)	*1141*
9	*1162*	(57)		26b	*1140*	(25)	*1154*	45	*1142*	(56)	*1145*
10a	*1154*	(31)	*1145*	26c	*1162*	(66)		46	*1142*	(49)	*1145*
10b	*1156*	(76)		26d	*1172*	(75)		47a	*1142*	(38)	*1145*
11	*1150*	(65)	*1154*	27	*1162*	(67)	*1141*	47b	*1172*	(63)	*1145*
12	*1162*	(55)		28	*1162*	(76)		47c	*1172*	(85)	
13	*1162*	(97)		29	*1185*	(43)	*1186*	49a	*1172*	(41)	*1141*
14	*1162*	(80)		30	*1142*	(66)		49b	*1172*	(79)	
15	*1162*	(34)		31	*1145*	(23)		50	*1150*	(58)	*1145*
16a	*1162*	(67)		32	*1172*	(69)		51a	*1142*	(42)	*1145*
16b	*1156*	(58)		33	*1141*	(37)		51b	*1185*	(21)	*1141*
17a	*1158*	(44)	*1162*	34	*1142*	(26)	*1143*	52	*1150*	(58)	
17b	*1162*	(35)	*1141*	35	*1172*	(52)	*1145*	53	*1162*	(57)	
17c	*1158*	(46)	*1141*	36a	*1162*	(84)		54a	*1154*	(27)	*1150*
17d	*1172*	(24)	*1141*	36b	*1145*	(23)		54b	*1172*	(48)	*1141*
17e	*1172*	(30)	*1141*	37	*1144*	(38)		55	*1142*	(80)	
19	*1162*	(87)		38	*1145*	(25)		56	*1162*	(80)	*1141*

in South America. Geographical variation among the South American plants would be detected by a differential affinity to the California plants; i.e., specimens would be assigned to populations from similar climatic and ecological zones in California. The South American specimens, however, were identified with a few samples from arid interior localities, the majority to three samples. Comparison of the 15 South American specimens assigned to sample *1172* illustrates that they are from localities of latitudinal and elevational extremes. They include specimen *2* from Prov. Chubut, Argentina at latitude 46°S, specimens *17d* and *17e* from Taltal, Chile at latitude 25°S, specimen *48* from Prov. Valparaiso, Chile at elevation 10 m, and specimens *26a* and *26d* from Prov. Coquimbo, Chile at elevation 3500 m. These results suggest that the South American plants exhibit a more mosaic pattern of variation than the California plants.

As shown in Table 3 South American specimens have shorter peduncles and petioles than California plants. Because these two variables were involved in the discriminant analysis (Fig. 1), assignment of the South American specimens could be influenced by the discrepant values. To test this hypothesis, a second diagnosis

was performed with these variables deleted. Assignment of 36 South American specimens was to the same sample as the previous analysis (Table 5). The assignments were to 14 samples, 13 in common with the previous diagnosis and an additional one (*1143*). There was some variation in the number of South American specimens assigned to the particular California samples, but the overall pattern of assignment did not change. These results show that the widely varying vegetative features do not influence the assignments of the South American specimens.

Discussion and Conclusions

Comparison of the disjunct representatives of *Lupinus* group *Microcarpi* reveals that vegetative structures are smaller in South American plants. As shown by the discrepant values for peduncle length, this size difference is ascribable to plant height. Two explanations can be advanced for the difference; one concerns environment and growing conditions, and the other collecting practices and sampling methodology.

Smith (1918a) pointed out that size and degree of branching of these lupines are a reflection of the plant's environment. Short, unbranched plants are generally found in arid habitats whereas tall, well-branched plants are generally found in more mesic environments. I have observed that plant size at any given locality can vary from year to year depending on relative amount and periodicity of precipitation and temperature extremes. The samples of California populations are from a variety of habitats and were made during favorable years, but collection of individual plants was by random sampling. There is no reason to assume that the South American specimens were collected from less favorable habitats or during less favorable years, but herbarium specimens must be viewed, in an analytical sense, as representing biased samples.

I think the small size of the South American specimens is most likely attributable to past collecting practices. The majority of specimens were collected before 1900, and several during early botanical expeditions to South America. It is reasonable to assume that early collectors were concerned with obtaining as many specimens as possible with limited equipment and facilities, and consequently collected mostly small individuals.

The comparison reveals only slight differences in floral features between North and South American plants. The range of variation observed in South American specimens is within that of the California samples, but the mean values of the South American plants are slightly smaller. The difference in mean values is attributable to relative abundance of large flowered *L. densiflorus* and *L. horizontalis* among the California samples. Fewer South American specimens have cilia present on both margins of the wing and keel petals.

These features are observed more frequently in *L. densiflorus* and *L. horizontalis.*

Although some South American specimens can be readily identified as *L. densiflorus,* the majority are more similar to California populations of *L. subvexus, L. ruber* or intermediates between them. The results clearly demonstrate that South American representatives of group *Microcarpi* are not distinct from some North American representatives. The implications of these results will be addressed in a forthcoming revision of group *Microcarpi.*

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