1995

Population Structuring and Patterns of Morphological Variation in Californian Styrax (Styracaceae)

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POPULATION STRUCTURING AND PATTERNS OF MORPHOLOGICAL VARIATION IN CALIFORNIAN *STYRAX* (STYRACACEAE)

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ABSTRACT

Recent studies of genetic variation within and among populations and phylogenetic estimates have provided evidence bearing on the evolutionary history and taxonomy of *Styrax* in California (*S. redivivus*). In this paper, data from these studies are further analyzed and integrated with new data from morphology to gain insight into the nature and taxonomic significance of character variation within this species. Six morphological characters thought to be important in the delimitation of infraspecific taxa within *S. redivivus* were measured on 52 herbarium specimens and analyzed with Pearson correlations and multivariate methods. Five characters are significantly associated with latitude and three characters are significantly multiply correlated with latitude. Permutation tests show a significant association between isozyme allelic variation and latitude. Principal components analysis of the morphological data does not reveal distinct clusters. The distribution of character variation shows that most characters vary along continuous latitudinal clines, and no character exhibits an evident gap in character states. Although principal coordinates and neighbor-joining analyses of the isozyme data, and discriminant function analysis of the morphological data suggest the presence of two groups within *S. redivivus,* the sum of evidence does not support the delimitation of infraspecific taxa. A taxonomic treatment of *S. redivivus,* a distribution map of historical Californian collections, and a key distinguishing *S. redivivus* from related taxa are presented. The species status of *S. redivivus* is justified, and implications of the data for conservation are discussed.

Key words: California, conservation, isozymes, multivariate statistics, *Styrax officinalis, Styrax redivivus,* taxonomy.

INTRODUCTION

The genus *Styrax* (Styracaceae) comprises about 120 species of trees and shrubs distributed in eastern and southeastern Asia, the New World, and the Mediterranean region. It is characterized by a 3-locular, superior ovary, usually twice the number of stamens as petals, a campanulate, white, usually 5-parted corolla with petals connate at the base, and a linear style. Leaf arrangement is alternate, and the vesture consists of stellate hairs or scales. *Styrax* is currently divided into Sect. *Foveolaria* (Ruiz & Pav.) Perkins, 3- to 5-ovulate (two species, Cuba and Peru), and Sect. *Styrax,* 16- to 24-ovulate (remaining species). Perkins (1907) maintained two series within Sect. *Styrax:* Ser. *Imbricatae* Gürke (about 30 species) and Ser. *Valvatae* Gürke (about 90 species), delimited on the basis of floral aestivation type. Some species of Sect. *Valvatae* are variable for aestivation (sometimes even within the same individual), suggesting that the two series are not monophyletic (Steenis 1932).

In far western North America, *Styrax* is represented by a single species from Ser. *Imbricatae* occurring from Shasta County to San Diego County, California

(Fig. 1). Californian *Styrax* was originally described by Torrey (1851) as representing a new genus with one species, *Darlingtonia rediviva.* Torrey (1853), upon obtaining good flowering specimens of the plant, transferred the species to the genus *Styrax* as *S. californicum,* and applied the name *Darlingtonia* to the genus of pitcher plants, whence it has been conserved. Wheeler (1945) realized Torrey's mistake as to the correct species name and made the combination *S. rediviva* (Torr.). Howard (1974) recommended that *Styrax* be treated as neuter, but Nicolson and Steyskal (1976) have provided a detailed argument for the use of the masculine gender. Following their opinion, I have used the masculine ending for *Styrax* specific epithets here and elsewhere (e.g., Fritsch 1996).

From the time of Perkins's (1907) worldwide treatment of *Styrax,* the Californian entity has generally been regarded as conspecific with *S. officinalis* L. from the Mediterranean region (southern Greece to Turkey, south to Israel). Perkins (1907) could find no basis upon which to distinguish Californian and Mediterranean material, and subsumed *S. californicum* (= *S. redivivus*) under *S. officinalis.* Subsequent workers (e.g., Rehder 1915; Munz and Johnston 1924; Copeland 1938; Gonsoulin 1974; Thorne 1978; Murray 1982; Shevock 1993) have treated the Californian ma-

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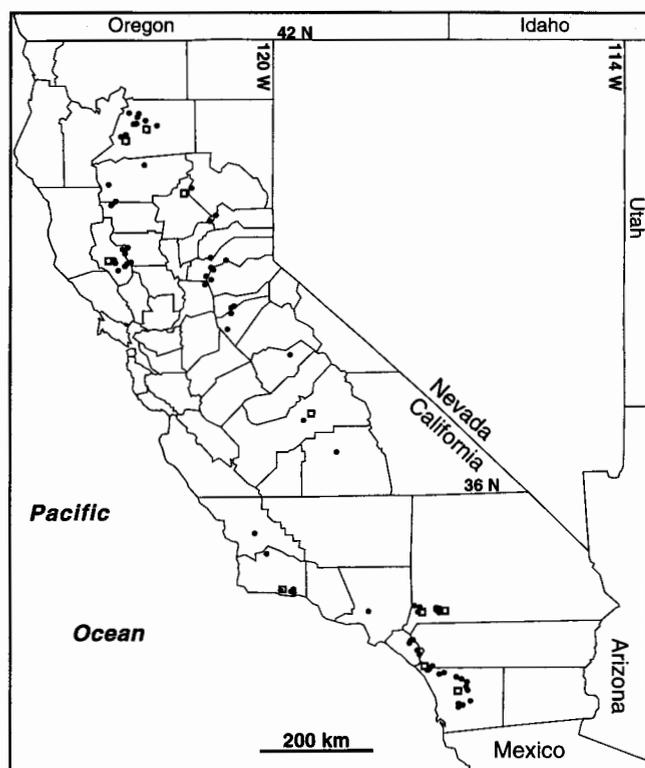
Fig. 1.   Distribution of *Styrax* in California (*S. redivivus*). Open squares are populations sampled for isozyme variation.

terial as one or two infraspecific taxa of *S. officinalis*. As such, *S. officinalis* constitutes a remarkable intercontinental disjunction, and has played a role in phytogeographic models of Tertiary Laurasia (e.g., Axelrod 1975; Raven and Axelrod 1978). Nonetheless, Thorne (1978) doubted whether Californian and Mediterranean populations are conspecific and stressed the need for a thorough biosystematic study of the group. Californian *Styrax* reportedly differs from the Mediterranean entity in a number of characters: rusty brown versus tawny- to white-stellate stalked trichomes on new twigs, petioles, and abaxial leaf surfaces, fewer-flowered racemes, larger flowers, thickened pedicels, a longer staminal tube, a more compressed style, and more pronounced stigma lobes (Rehder 1915; Munz and Johnston 1924; Gonsoulin 1974). Gonsoulin (1974) considered these differences to be minor and inconstant.

Opinion has differed regarding the utility of recognizing infraspecific taxa within Californian *Styrax* and what rank these should be given. Gonsoulin's (1974) treatment followed Eastwood (1906) and Munz and Johnston (1924) in delimiting two varieties (*S. officinalis* var. *fulvescens* (Eastw.) Munz & I.M.Johnston and *S. o.* var. *californicus* (Torr.) Munz & I.M.Johnston). Thorne (1978) treated the varieties as subspecies. Variety *fulvescens* reportedly differs from var. *californicus* in having suborbicular or ovate-orbicular versus broadly ovate laminae, broader and cordate at the base; heavily pubescent versus glabrous or puberulent abaxial leaf surfaces and calices; and a general prevalence of rufous hairs, especially on the calyx (Eastwood 1906; Gonsoulin 1974). Variety *californicus* occurs in northern California, reportedly extending from Siskiyou Co. southwestward to Lake and Alameda counties and from Yuba Co. south to Fresno Co.; var. *fulvescens* is mainly southern Californian, reportedly extending from Mendocino and Lake counties, east to Yuba Co., south in the Sierra Nevada to Fresno Co., and San Luis Obispo Co. south to San Diego Co. (Gonsoulin 1974). In contrast, Shevock (1993) combined all material under a single variety (*S. officinalis* var. *redivivus* [Torr.] R.A.Howard ["H. Howard"]), citing as evidence variable hair density and color throughout California.

Recent studies of genetic variation within and among populations of Californian *Styrax* (here designated *S. redivivus*) using isozymes (Fritsch 1996), and phylogenetic analysis of the genus (Fritsch 1994) have provided insight into the evolutionary history and taxonomy of this group. In this paper, data from these studies are further analyzed and integrated with new data from morphology to gain a deeper understanding of the nature and taxonomic significance of character variation within Californian *Styrax*. A taxonomic treatment of *S. redivivus*, a distribution map of historical Californian collections, and a key distinguishing *S. redivivus* from related taxa are presented. Implications of the data for conservation are discussed.

MATERIALS AND METHODS

Distribution Mapping

The specimens cited in Appendix 1 were used to create the distribution map of *S. redivivus* (Fig. 1). Specimens from the following herbaria were examined: CAS, DS, DUKE, F, GH, JEPS, MO, NY, POM, RSA, SD, and UC. Because populations of *S. redivivus* are usually local, it was considered useful to arrange specimens by locality, each locality representing a separate population. It was sometimes difficult to determine which collections constituted a population from one locality due to imprecise specimen label information. In such cases, the specimen with the more general information was excluded from the distribution map (Appendix 1). No doubt some independent collections that I have combined into a single locality will, upon further study, constitute separate populations, and vice versa.

Morphology

To assess patterns of morphological variation within *S. redivivus*, six characters were measured on herbar-
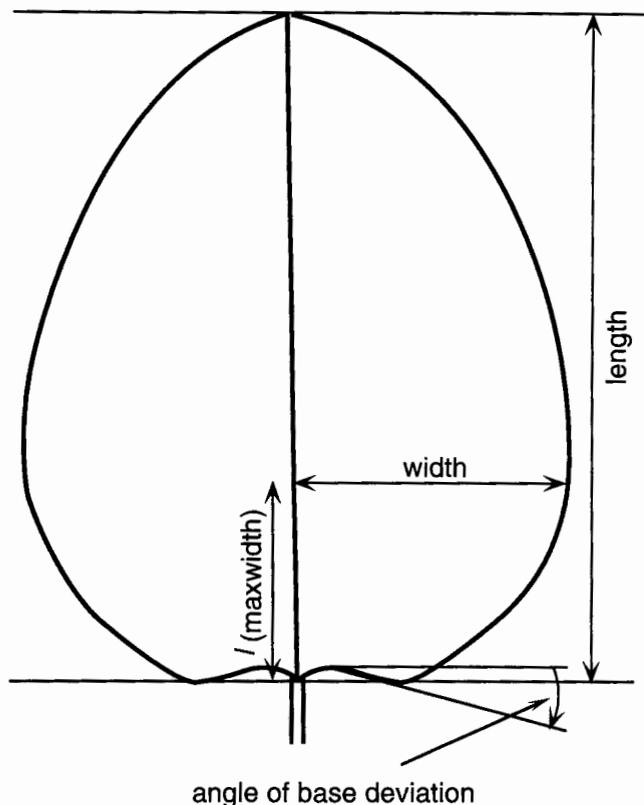
Fig. 2. Diagrammatic representation of some of the leaf parameters measured on herbarium specimens of *Styrax redivivus*. $l_{(maxwidth)}$ = the distance from the base of the lamina to the point of maximum width. Values of the angle of base deviation are positive if the angle is toward the leaf apex (a cuneate base) and negative if the angle is toward the leaf base (a cordate base).

ium specimens: maximum leaf width (= WIDTH), deviation from longitudinal symmetry (a measure of leaf shape; = SHAPE), hair density on the abaxial lamina surface (= LF HAIR), arm length of the longest stellate hairs on the abaxial lamina surface (= ARMLENGTH), calyx hair thickness (= CALYX HAIR), and leaf base angle (= LF BASE). The characters WIDTH, SHAPE, LF HAIR, CALYX HAIR, and LF BASE reportedly distinguish the varieties of *S. redivivus*. The only other character reported for this purpose, the presence of rufous calyx hairs, was excluded from the analysis after preliminary observations revealed the obvious sporadic nature of this character throughout California. This agrees with Shevock (1993). The character ARMLENGTH, although not reported as a distinguishing character, was included after preliminary observations suggested that hair length might be consistently greater in southern Californian populations than those in northern California. WIDTH equals the distance from the margin to the midrib at the point of maximum lamina width (mm; Fig. 2). SHAPE equals $(l_{(maxwidth)}-l/2)/l$, where $l_{(maxwidth)}$ is the distance from the base of the lamina to the point of maximum width (mm) and l is the maximum length

of the lamina (mm; Fig. 2). LF HAIR equals the number of stellate hair bases occurring within approximately 0.14 mm², estimated at 60×. ARMLENGTH (μm) was measured at 60× and excluded hairs of the vein surface, which are sometimes but not always longer than those on the lamina surface. CALYX HAIR was measured by scoring the thickness of the tomentum from 0 to 4, with 0 the thinnest. LF BASE was measured as the angular deviation from a flat (truncate) leaf base (excluding any attenuate portion often present just above the petiole; Fig. 2).

Leaves on one herbarium specimen from each of 52 of the 83 localities (Appendix 1) were used for measurements. These localities spanned the geographical range of *S. redivivus*. Measurements were taken on two leaves per individual and averaged, and were standardized by using only material at or just after anthesis and measuring the two largest terminal leaves from fertile shoots on each individual. The use of flowering material facilitated the measurement of calyx pubescence, which often becomes more difficult to assess in the fruiting stage.

Isozymes

Twenty individuals per population from ten populations sampled across the geographical range of *S. redivivus* were used for isozyme analysis (Appendix 1; Fig. 1). For details regarding collection methods, enzymes surveyed, protein extraction, electrophoresis, staining protocols, and interpretation of isozyme banding patterns, see Fritsch (1996).

Data Analysis

Standard genetic identity (*I*) and distance (*D*) were calculated from allele frequencies of 24 isozyme loci (Fritsch 1996) for all pairwise population comparisons using the methods of Nei (1972, 1978) as implemented with the program GENESTAT Version 2.1 (by P. Lewis and R. Whitkus; Whitkus 1988; Table 1). The distance values were used as input for a permutation test employing Mantel's *Z* statistic (Mantel 1967) to test concordance between matrices derived from geographic distance and Nei's genetic distance. Matrices compared were 1) genetic distance versus geographic distance and 2) genetic distance versus latitude. Conventional correlation tests are not appropriate in these cases because the entries in each matrix are not independent; the *Z* statistic tests the strength of association of paired elements in the two matrices by comparison to a null distribution produced by permutation (Dietz 1983). Permutation tests employing Kendall's K_C statistic and Spearman's *R* statistic were also performed because *Z* is highly dependent on the specific distance measure used (Dietz 1983). These three statistics together cover a wide range of sampling distributions;

Table 1. Nei's genetic identity (above) and distance (below) values among populations of *Styrax redivivus*.

	1	2	3	4	5	6	7	8	9	10
1 Shasta 1	—	0.996	0.955	0.956	0.885	0.901	0.891	0.895	0.846	0.846
2 Shasta 2	0.004	—	0.959	0.961	0.901	0.918	0.909	0.914	0.866	0.870
3 Butte	0.046	0.042	—	0.971	0.892	0.900	0.910	0.909	0.861	0.859
4 Lake	0.045	0.040	0.030	—	0.925	0.905	0.951	0.954	0.902	0.909
5 Fresno	0.122	0.104	0.115	0.078	—	0.916	0.933	0.939	0.921	0.927
6 Santa Barbara	0.105	0.085	0.105	0.100	0.087	—	0.911	0.943	0.957	0.960
7 San Bernardino 1	0.115	0.096	0.095	0.050	0.069	0.094	—	0.982	0.952	0.952
8 San Bernardino 2	0.111	0.090	0.095	0.047	0.063	0.058	0.019	—	0.972	0.980
9 San Diego 1	0.167	0.144	0.149	0.103	0.083	0.044	0.049	0.029	—	0.984
10 San Diego 2	0.167	0.139	0.152	0.095	0.076	0.041	0.050	0.020	0.016	—

thus, their combined use provided a robust test of matrix association. Four thousand iterations were used for each analysis, and significance was tested at the 0.05 level. All three test statistics were calculated using a computer program by E. J. Dietz (1983).

Principal coordinates analysis (PCO), as implemented with NTSYS-pc version 1.8 by F. J. Rohlf (Applied Biostatistics Inc., 1993) was used to ordinate genetic differences among populations of *S. redivivus*. Input consisted of allele frequencies of polymorphic loci. The data were converted to a Nei's genetic distance (Nei 1972) matrix using the SIMGEND command and double-centered using the DCENTER subroutine; eigenvalues were calculated using the EIGEN command; and graphs projecting the populations onto the first two principal coordinates were constructed using the MXPLOT command. To estimate the overall degree of genetic relationship among the populations, the neighbor-joining algorithm (Saitou and Nei 1987) was implemented with the NEIGHBOR81 program in the computer package PHYLIP (PHYLogeny Inference Package by J. Felsenstein, 1989). Input consisted of Nei's genetic distance (Nei 1972; Table 1) for all pairwise comparisons. Analyses were conducted both including and excluding isozyme data from four populations of a species complex from Texas and northeastern Mexico comprising *S. platanifolius* Engelm. ex Torr., *S. texanus* Cory, and *S. youngiae* Cory (the *S. platanifolius* group [= the *S. texanus* group of Fritsch 1996]; complete data set available upon request; for data summary see Fritsch 1996). This group occurs in western Texas and northeastern Mexico and is in all likelihood the closest relative of *S. redivivus* (Fritsch 1994, 1996). Data from the *S. platanifolius* group was included to root the neighbor-joining tree. Bootstraps were performed with the programs SEQBOOT, GENDIST, NEIGHBOR, and CONDENSE, as directed in PHYLIP.

The morphological characters were tested for associations with latitude using Pearson's correlation test, as implemented by the computer program SYSTAT version 5.2 (SYSTAT, Inc., 1992). A multiple Pearson correlation tested for associations among the characters and latitude. All correlations were tested for significance at the 0.05 level. A principal components analysis (PCA) using all characters except WIDTH was performed to ordinate morphological differences among individuals. The character WIDTH was excluded from all analyses because initial results showed that it was variable throughout the range of *S. redivivus* (Fig. 5).

On the basis of morphological variation associated with latitude (see Results), the individuals were partitioned into two groups roughly corresponding to northern and southern individuals. These two groups were subjected to further analyses. Pearson correlations of each character versus latitude were performed to compare patterns of variation within the northern and southern groups. The correlation coefficient from the northern group was compared to that of the southern group for each character, as in Zar (1974; tests performed manually). In addition, multiple Pearson correlations were conducted separately for the northern and southern groups.

The individuals were also partitioned into two groups with the Kmeans clustering algorithm (Hartigan 1975) using SYSTAT. This method finds the best way to divide individuals into a specified number of groups so that they are separated as well as possible. Because only two infraspecific taxa have been proposed within *S. redivivus,* I specified two groups for the algorithm.

To test for group distinctness, canonical discriminant analysis was used to calculate pairwise Mahalanobis distances among both sets of groups (one set from geography, the other from the Kmeans algorithm) using all characters except WIDTH (significance tested at the 0.05 level). In this procedure, the proportion of individuals misclassified by the discriminant function reflects its ability to distinguish among groups.

RESULTS

Permutation tests showed a significant correlation between genetic and geographic distance matrices (Z
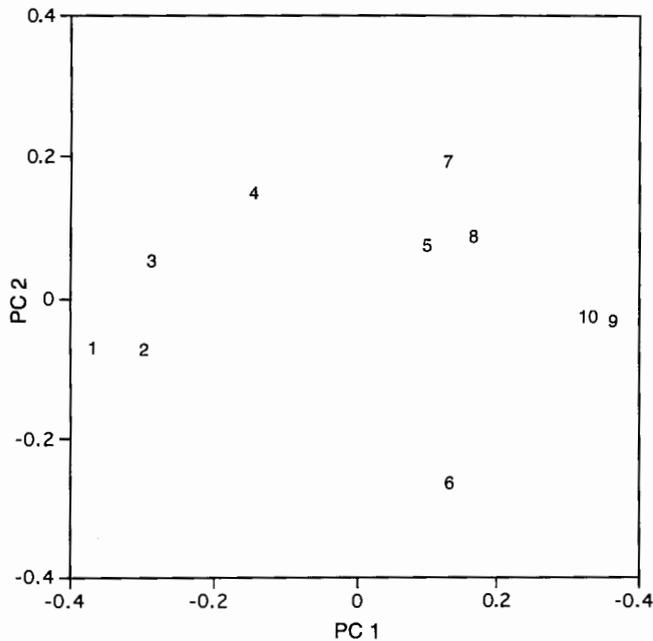
Fig. 3. Principal coordinates analysis of allele frequencies from ten populations of *Styrax redivivus*. The first two axes account for 58.7% and 16.9% of the total variation, respectively. 1 = Shasta 1; 2 = Shasta 2; 3 = Butte; 4 = Lake; 5 = Fresno; 6 = Santa Barbara; 7 = San Bernardino 1; 8 = San Bernardino 2; 9 = San Diego 1; 10 = San Diego 2.

Fig. 4. Neighbor-joining tree of ten populations of *Styrax redivivus* based on isozyme variation. Numerals on each branch result from 1000 bootstraps and indicate the percentage of times the group above the branch occurred among the trees. The tree is unrooted. See Appendix 1 for population localities.

= 2179.7, R = 30178.5, K_C = 218, P < 0.00001 for all) and between genetic and latitudinal matrices (Z = 96.7, R = 30155.3, K_C = 228, P < 0.00001 for all).

The PCO analysis of isozyme allele frequencies showed that populations are ordered with respect to latitude along the first principal coordinate, and suggested two clusters (1–4, 5–10; Fig. 3). In the neighbor-joining analysis that excluded populations of the *S. platanifolius* group, the longest branch observed was that connecting the most northerly population samples (Shasta 1, Shasta 2, Butte, and Lake) to the rest; the bootstrap corresponding to this branch was relatively high (76%; Fig. 4). In the neighbor-joining analysis that included populations of the *S. platanifolius* group, two groups were formed when the tree was rooted with one of the *S. platanifolius* populations, one comprising populations Shasta 1, Shasta 2, Butte, and Lake, the other comprising Fresno, San Bernardino 1, San Bernardino 2, San Diego 1, San Diego 2, and Santa Barbara (tree not shown).

Five of the six characters (SHAPE, LF HAIR, ARMLENGTH, CALYX HAIR, and LF BASE) showed a significant association with latitude (Fig. 5B–F; Table 2A). The character WIDTH was variable throughout the range of *S. redivivus* (Fig. 5A), and therefore was excluded from all subsequent analyses. The five characters were tested for multiple correlation with latitude. When all five characters were included, associations between LF BASE and all other charac-
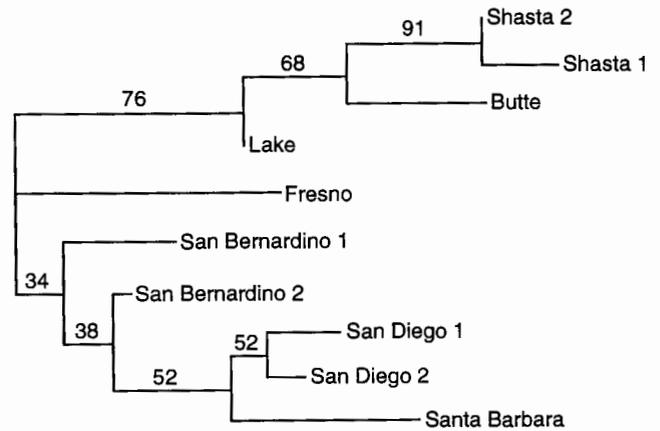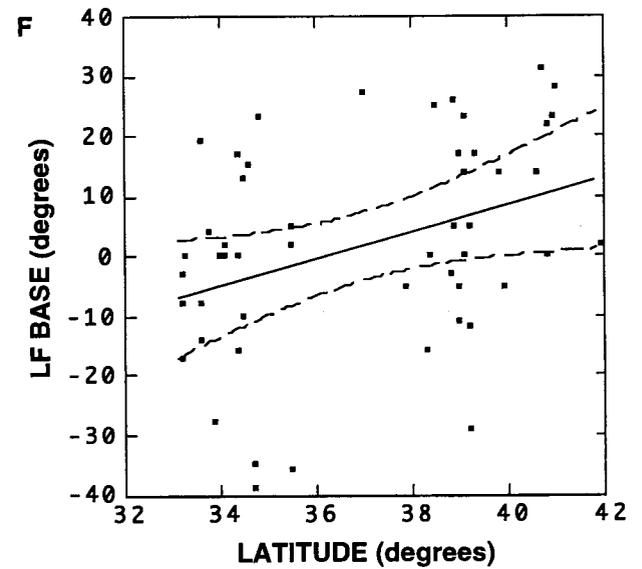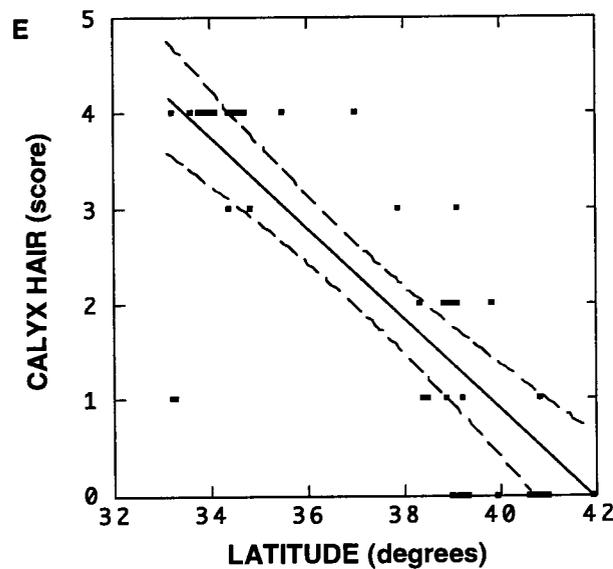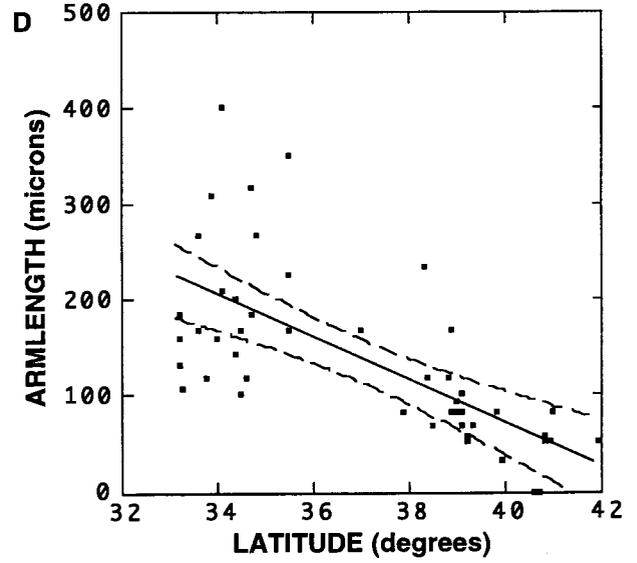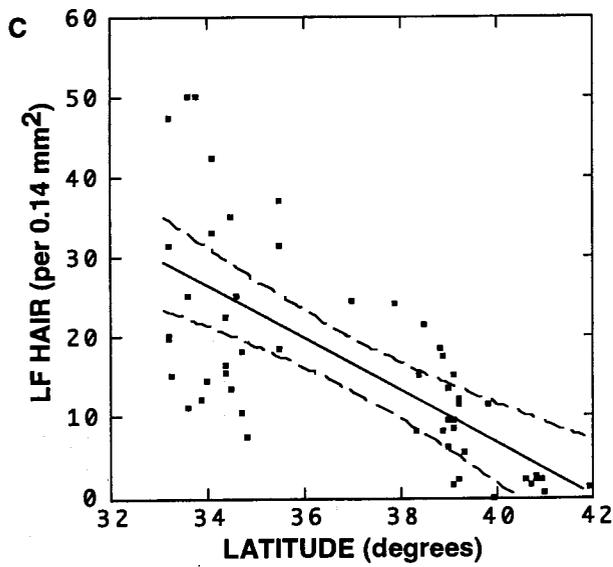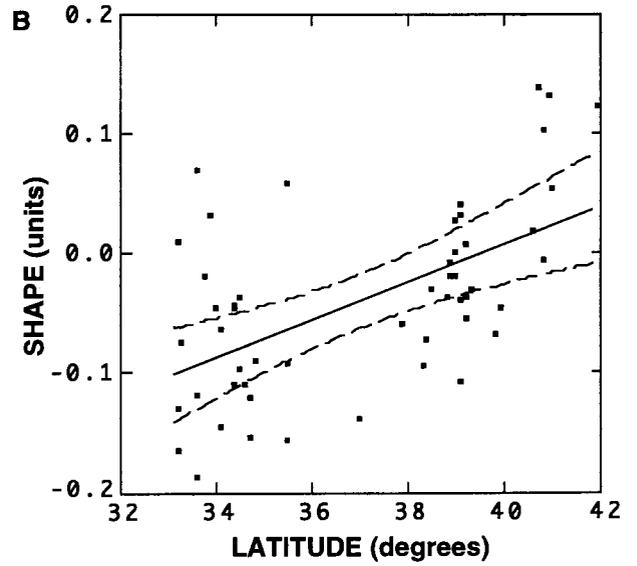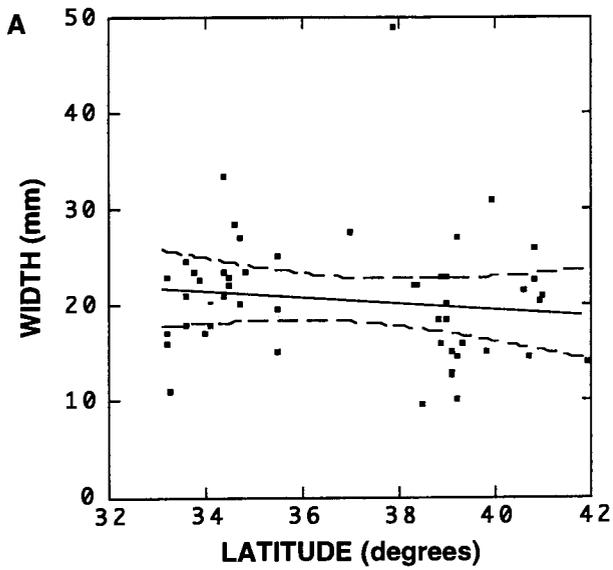
ters except SHAPE were not significant; all other associations were significant except for that between SHAPE and ARMLENGTH, and SHAPE and LF HAIR (Table 2B). When SHAPE was removed from the analysis, all associations were significant except for all associations with LF BASE (not shown); when LF BASE was removed from the analysis, all associations were significant except for those between SHAPE and LF HAIR, and SHAPE and ARM-LENGTH (not shown). When both of these characters were excluded from the analysis, all associations were significant (Table 2C). The characters in Table 2C comprise the only combination of more than two characters and latitude that showed significant associations for all pairwise comparisons.

Examination of the raw data matrix (not shown) showed no clear break in character-state variation for any of the six characters with respect to latitude, and no two characters showed obvious correlated gaps in variation. This is reflected in the PCA with morphological characters, in which distinct clusters of individuals were not evident (Fig. 6). However, PCA was consistent with isozyme data and Pearson correlations in detecting a strong latitudinal trend, with southern individuals tending toward positive scores and northern negative on factor 1.

The distribution of individuals in the scatter plots of three morphological characters versus latitude (SHAPE, LF HAIR, and ARMLENGTH; Fig. 5B–D) suggested a pattern of strong clinal variation among northern individuals, but not among southern individuals. Individuals were partitioned into two groups (1–24, 25–52) on the basis of this distinction and the two groups were analyzed for character correlations separately. None of the Pearson correlations of each character versus latitude in the southern group were sig-

nificant; all correlations in the northern group were significant except for that between WIDTH and LF BASE (Table 3A). Multiple correlation excluding WIDTH and LF BASE showed nonsignificant associations in all pairwise associations between characters for southern individuals (Table 3B). For northern individuals, all pairwise associations were significant except for that between LF HAIR and ARMLENGTH (Table 3C). The correlation coefficients for SHAPE, LF HAIR, ARMLENGTH, and CALYX HAIR were significantly different between the northern and southern groups (Table 3A).

Mahalanobis distances among the southern and northern groups (Fig. 6) as calculated from the canonical discriminant analysis with the five characters were significant (all P [univariate and multivariate] ≤ 0.01). The two groups were identified correctly 92% and 86% of the time, respectively, on the basis of the discriminant function (Table 4A). The groups constructed with Kmeans were similar but not identical in composition to those delimited on the basis of geographic location (Fig. 6). The Kmeans algorithm grouped individuals 25, 26, 27, and 37 (see Appendix 1) with the southern individuals, and grouped individual 4 with the northern individuals. The two groups delimited through Kmeans were also significant (all $P \leq 0.011$). These two groups were identified 96% (group A) and 100% (group B) of the time (Table 4B).

DISCUSSION

Field Observations

During collecting trips for isozyme analysis made in 1993, I informally assessed the regional abundance of *S. redivivus*. In most cases, the precise collection locality had to be rediscovered in order to obtain samples—surrounding areas appeared not to harbor the plant, at least in easily accessible places. Regions in which the plant appeared to be so common that precise locality information was not necessary were the Santa Ynez Mountains near San Marcos Pass (Santa Barbara Co.), the Redding area (Shasta Co.), and Palomar Mountain (San Diego Co.). I have been informed (S. Boyd, Rancho Santa Ana Botanic Garden, pers. comm.) that it is also abundant in the Agua Tibia Wilderness, San Diego Co.

Taxonomic Implications of Patterns of Variation within Styrax redivivus

Several patterns elicited by this study provide circumstantial evidence for the delimitation of two infra-

specific taxa within *S. redivivus*: 1) correlations and permutation tests indicate the association of several morphological characters and genetic variation with geography and, more specifically, latitude; 2) at least SHAPE and LF HAIR have a genetic basis, as is evident from a common garden study at Rancho Santa Ana Botanic Garden in southern California (pers. obs.); it is likely that all the observed phenotypes associated with latitude are heritable; 3) the neighbor-joining trees and the PCO analysis resulting from the isozyme data set suggest the presence of two groups, one northern and one southern; 4) significant differences in the strength of association of four characters (SHAPE, LF HAIR, ARMLENGTH, AND CALYX HAIR) with latitude exist between northern and southern individuals, suggesting that different evolutionary processes have taken place in the two groups; and 5) when two groups are delimited through the Kmeans algorithm, Mahalanobis distances are significant and the discriminant function derived from five morphological characters performs extremely well in predicting group membership.

Nonetheless, there are problems with accepting infraspecific taxa on the basis of these criteria. Points (1) and (2) say nothing about gaps or significant differences between groups, which are needed to justify circumscription. Point (3) shows two groups, but little confidence can be afforded to these data for circumscription, because of the low number of population samples.

Point (4) clarifies the distribution of variation from north to south. The characters SHAPE, LF HAIR, and ARMLENGTH show strongly clinal variation in the northern individuals, but not in the southern individuals. However, overall association with latitude for these characters is maintained, despite great overlap between southern and northern individuals, because the southern individuals possess the extremes of variation (Fig. 6). The strongly clinal variation seen among the northern populations might be a result of dispersed introgression of genes from southern populations. In this regard, some Californian plant species have expanded their ranges northward from southern refugia in response to a warmer, dryer climate during the Xerothermic (Raven and Axelrod 1978), and this might have happened in southern populations of *S. redivivus*. Evidence of secondary contact would provide an argument for the delimitation of taxa. However, in the absence of additional molecular variation patterns (i.e., chloroplast and nuclear ribosomal DNA) it remains

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Fig. 5. Scatter plots of the six morphological characters analyzed in this study versus latitude. Solid line = linear regression line; dotted lines = 95% confidence limits. For explanation of character abbreviations, see text.

Table 2. Pearson correlation coefficients (*r*) and Bonferroni probabilities (*P*) for morphological characters of *Styrax redivivus* versus latitude. *N* = 52 in all cases. For explanation of character abbreviations, see text. Values above the diagonal in multiple correlation tables show *P*; values below the diagonal show *r*. (A), single Pearson correlations between each character and latitude; (B), multiple Pearson correlation between SHAPE, LF HAIR, ARMLENGTH, CALYX HAIR, LF BASE, and LATITUDE; (C), multiple Pearson correlation between LF HAIR, ARMLENGTH, CALYX HAIR, and LATITUDE.

A

Character	*r*	*P*
WIDTH	−0.135	0.340
SHAPE	0.567	<0.001
LF HAIR	−0.693	<0.001
ARMLENGTH	−0.687	<0.001
CALYX HAIR	−0.815	<0.001
LF BASE	0.365	0.008

B

Character	SHAPE	LF HAIR	ARMLENGTH	CALYX HAIR	LF BASE	LATITUDE
SHAPE	—	0.592	0.191	0.001	0.028	<0.001
LF HAIR	−0.287	—	<0.001	<0.001	1.000	<0.001
ARMLENGTH	−0.343	0.561	—	<0.001	0.137	<0.001
CALYX HAIR	−0.535	0.684	0.721	—	0.268	<0.001
LF BASE	0.422	−0.164	−0.358	−0.327	—	0.118
LATITUDE	0.567	−0.693	−0.687	−0.815	0.365	—

C

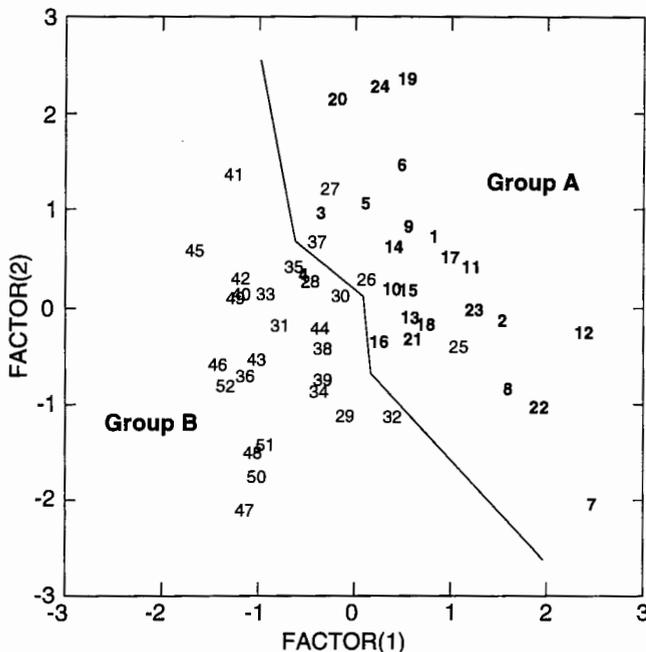| Character	LF HAIR	ARMLENGTH	CALYX HAIR	LATITUDE
LF HAIR	—	<0.001	<0.001	<0.001
ARMLENGTH	0.561	—	<0.001	<0.001
CALYX HAIR	−0.684	0.721	—	<0.001
LATITUDE	−0.693	−0.687	−0.815	—

Fig. 6. Principal components analysis using five morphological characters. The first two axes account for 56.3% and 19.6% of the total variation, respectively. Individuals are numbered from 1 to 52 in order of increasing latitude. Boldface numerals are southern individuals. The line delimits the two groups constructed by the Kmeans algorithm (see text).

unclear whether the clinal trends in northern populations are the result of primary or secondary contact.

Probably the least ambiguous evidence for the circumscription of two taxa comes from the Kmeans algorithm (Point 5), which separates two groups that perform nearly perfectly in the discriminant analysis. Nonetheless, recognition of these groups would require the placement of one specimen from San Diego Co. (*Reed 10850*) in an otherwise northern group, one specimen from Lake Co. (*L. Benson 124*) in an otherwise southern group, and the ability to distinguish among the taxa in Calaveras Co., where both taxa would occur in close proximity. The two anomalies plus the problem of distinguishing the taxa in clearly intermediate areas does not provide sufficient evidence for recognizing two taxa.

The scatter plots of Fig. 5B–E strongly suggest that the significant associations between the characters SHAPE, LF HAIR, ARMLENGTH, and CALYX HAIR result from truly clinal variation with respect to latitude; poor sampling at intermediate latitudes explains the two apparent clusters of data points in several of the plots. Furthermore, examination of the raw data set reveals no instances of any two characters with gaps occurring among the same individuals. Finally, a clear break in character variation is not exhibited in the PCA analysis; rather, the PCA plot shows continuous distribution of individuals ordered with respect to latitude from one extreme of the plot to the other.

Table 3. Pearson correlation coefficients (*r*) and Bonferroni probabilities (*P*) for morphological characters of *Styrax redivivus* versus latitude, partitioned into southern (individuals 1–24) and northern (individuals 25–52) groups. For explanation of character abbreviations, see text. Values above the diagonal in multiple correlation tables show *P*; values below the diagonal show *r*. (A), single Pearson correlations between each character and latitude; notation at end of row indicates significance level of a test for differences between northern and southern correlation coefficients: *, *P* < 0.005; **, *P* < 0.001; N.S., not significant at level 0.05; (B), multiple Pearson correlation between SHAPE, LF HAIR, ARMLENGTH, CALYX HAIR, and LATITUDE, southern individuals; (C), same as (B), northern individuals.

A

Character	Southern indls. r_1	Southern indls. P_1	Northern indls. r_2	Northern indls. P_2	r_1 vs. r_2
WIDTH	0.279	0.186	−0.213	0.277	N.S.
SHAPE	−0.016	0.941	0.773	<0.001	**
LF HAIR	−0.179	0.402	−0.785	<0.001	*
ARMLENGTH	0.297	0.158	−0.623	<0.001	**
CALYX HAIR	0.353	0.091	−0.691	<0.001	**
LF BASE	−0.057	0.793	0.204	0.297	N.S.

B

Character	SHAPE	LF HAIR	ARM-LENGTH	CALYX HAIR	LATI-TUDE
SHAPE	—	0.858	1.000	1.000	1.000
LF HAIR	0.358	—	1.000	1.000	1.000
ARMLENGTH	0.310	0.135	—	1.000	1.000
CALYX HAIR	0.175	0.252	0.260	—	0.908
LATITUDE	−0.016	−0.179	0.297	0.353	—

C

Character	SHAPE	LF HAIR	ARM-LENGTH	CALYX HAIR	LATI-TUDE
SHAPE	—	0.014	0.017	0.001	<0.001
LF HAIR	−0.573	—	0.055	0.001	<0.001
ARMLENGTH	−0.565	0.510	—	0.004	0.004
CALYX HAIR	−0.658	0.680	0.627	—	<0.001
LATITUDE	0.773	−0.785	−0.623	−0.691	—

These patterns effectively preclude the delimitation of two taxa in *S. redivivus*.

Species Status of Styrax redivivus

Evidence from Fritsch (1996) has provided strong justification for recognizing *S. redivivus* as a distinct species, regardless of whether an isolation (biological; Mayr 1969), phylogenetic (Rosen 1978; Mishler and Donoghue 1982), or taxonomic (Cronquist 1988) species concept is employed. Genetic distances derived from isozyme variation indicate high genetic divergence between Californian and Mediterranean populations (Fritsch 1996). This provides inferential evidence for species status according to the isolation species concept. Divergence time estimates based on genetic distances indicate that *S. redivivus* and *S. officinalis* have probably been separated intercontinentally for at least five million years (Fritsch 1996).

Phylogenetic evidence indicates that the two entities are not sister taxa: the closest relatives of *S. redivivus*

Table 4. Discriminant function analysis. Totals in the last column indicate the number of individuals in each group; totals in the bottom row indicate the number of individuals predicted in each group by the discriminant function. Cells with identical column and row designation indicate the number of individuals classified correctly by the discriminant function; cells with nonidentical column and row designation indicate the number of individuals classified incorrectly by the discriminant function. (A), individuals grouped by latitude (see text); (B), individuals grouped by the Kmeans algorithm.

A Group	South	North	Total
South	22	2	24
North	4	24	28
Total	26	26	52
B Group	A	B	Total
A	26	1	27
B	0	25	25
Total	26	26	52

are the species comprising the *S. platanifolius* group, as inferred from studies of chloroplast and nuclear ribosomal DNA (Fritsch 1994, 1996). The current treatment (i.e., including *S. redivivus* in *S. officinalis* while retaining the Texas-Mexico taxa as different species) is unambiguously inconsistent with the phylogeny. To be consistent with the phylogeny it is justifiable to either 1) include *S. youngiae, S. texanus, S. platanifolius,* and *S. redivivus* in *S. officinalis,* or 2) remove *S. redivivus* from *S. officinalis.* The first circumscription might be justified because Mediterranean *Styrax* is the sister group to the California-Texas-Mexico clade and thus all these taxa (the *S. officinalis* group) comprise a monophyletic group (Fritsch 1994, 1996). However, isozyme genetic divergence between California and Texas-Mexico populations is within the range typical for that between congeneric species rather than within the same species (Fritsch 1996).

Final evidence comes from the elucidation of diagnostic morphological characters from field observations and examination of herbarium specimens, providing justification for the species status of *S. redivivus* under a taxonomic species concept. My field observations show that *S. redivivus* has orange-yellow pollen whereas *S. officinalis* has light yellow pollen. Also, *S. redivivus* has corolla lobes that are reflexed an average of 35° away from the longitudinal plane at anthesis, whereas *S. officinalis* has corolla lobes that are reflexed an average of 80° (*N* = 40 for both species, two populations and 20 plants per population sampled for each species, *P* < 0.001). These two diagnostic characters were only noticed by comparing both groups in the field, which probably explains why they were not detected by previous workers.

Examination of herbarium specimens of *S. officinalis* (F, GH, MO, NY, RSA) provides additional mor-

phological evidence for treating *S. redivivus* as a distinct species. Torrey (1853) reported three characters distinguishing *S. redivivus* from *S. officinalis*: thickened pedicels, a longer staminal tube, and fewer-flowered racemes. The first two characters are clearly diagnostic (see Appendix 2); the third is not diagnostic because of overlap, but on the average the species are different (1–6 flowers in *S. redivivus,* mean = 2.8, 2–6 flowers in *S. officinalis,* mean = 3.8). Munz and Johnston (1924) listed three characters distinguishing *S. redivivus* from *S. officinalis*: dark- versus light-colored stalked stellate hairs on the leaf veins and midrib abaxially, a more compressed style, and a more prominently lobed stigma. Apparently, they either did not see Torrey's (1853) description or they ignored it. All these characters they considered to be minor and inconstant; hence, they treated *S. redivivus* as a variety of *S. officinalis*. Of these three characters, the hair color difference is diagnostic (see Appendix 2); the other two are not at all reliable. The only other character reported to distinguish the two taxa is larger flowers in *S. redivivus* (Rehder 1915; a varietal distinction). This character also cannot be considered diagnostic, although the flowers are generally larger (16–26 mm long in *S. redivivus,* 13–20 mm long in *S. officinalis*). I have discovered two other characters useful in distinguishing the taxa: pedicel length (4–9 mm long in *S. redivivus,* 8–17 mm long in *S. officinalis,* and relative pedicel versus calyx length (pedicel 0.5–1.4 times as long as the calyx in *S. redivivus,* 1.4–3.3 times in *S. officinalis*). These taxa can easily be distinguished from each other and from the taxa of the *S. platanifolius* group with the aid of the key in Appendix 2.

Conservation

Styrax redivivus apparently has a relict distribution: its ancestors were part of a more widely distributed species in the Tertiary (Fritsch 1996). Yet, the current ecological factors that limit the distribution and abundance of this species are poorly known. The species appears to tolerate widely different soil types, shade levels, and moisture regimes, although it seems to prefer clay soils or rocky outcrops, protected ravines or washes, and north- or east-facing slopes. Nevertheless, in many areas seemingly suitable for the plant, it is not present. It appears not to be establishing new populations in any significant number; some populations are senescent (e.g., Auburn, Placer Co.). The only locality where I observed seedlings was Mt. Palomar (San Diego County); they were growing underneath presumably maternal parents. Plants probably resprout after fire; they do not spread vegetatively. Dispersal mechanisms are unknown, and seeds have no structures associated with dispersal via wind or water; therefore, seeds may be dispersed only locally by ei-

ther gravity or ground mammals, or both; if so, the seeds are probably only secondarily preferred (as suggested by one common name for the plant, "bitternut" (Jepson 1925). Seeds may also be water-dispersed downslope. Detailed study of the natural history and ecology (especially seed ecology, demography, and habitat requirements) of *S. redivivus* are needed to provide further insight into the reasons for the species' sporadic distribution, Californian endemism, and role in Madrean-Tethyan vegetation patterns (see Fritsch 1996), and would also facilitate conservation efforts.

Because of its local distribution and apparently poor establishment capacity, *S. redivivus* should be monitored for possible population decline. The species is still common enough to forego state or federal listing, but many, especially low-elevation, populations are threatened by overgrazing, dam building, and urbanization. I have not directly observed browsing by grazing animals, but I have seen the heavily grazed slopes at Kings River (Pine Flat Reservoir, Fresno Co.) that were nearly devoid of the plants except for rocky areas inaccessible to livestock. The related species *S. texanus* has declined dramatically through the effects of exotic grazing mammals in Texas (Cory 1943; Cox 1987) and *S. officinalis* serves as forage for grazing mammals in the Mediterranean region (Le Houérou 1981; pers. obs.). Because *S. redivivus* prefers water courses along foothill woodland slopes, reservoir creation has played a role in its decline. The establishment of Pine Flat Reservoir on the Kings River is known to have reduced the abundance of *S. redivivus* in the area, as is evident by collections from now inundated areas. At Folsom (Sacramento Co.) and Silver Rapids (Calaveras Co.), inundation has no doubt contributed to local decline or extirpation. Urbanization also appears to have contributed to the probable elimination of the Folsom population, as well as populations near Clear Lake, Lake Co. *Styrax redivivus* must have at one time been abundant at Clear Lake, judging from the numerous collections made, but now appears to be restricted; I only found one small population after several hours of searching along the western lake perimeter.

It is hoped that this report will increase awareness of the uncommon nature of *S. redivivus* enough so that vouchers will be made when the plant is encountered, especially at localities not listed here or at localities where the species is thought to be extirpated.

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APPENDIX 1: Specimens Cited

1. Specimens used in morphological studies and distribution mapping. Acronyms in boldface represent specimens used for morphological analyses. Boldface numerals in brackets correspond to the individuals in Fig. 6. Boldface localities are those sampled for isozyme analysis; names in brackets after these localities are abbreviations used in the text. Localities at which *Styrax redivivus* is thought to have been extirpated are underlined. The total number of localities is 83.

Amador Co.—Glencoe, *Belshaw 2379* (**RSA[29]**, UC); Mt. Zion, *Nordstrom 840* (UC).

Butte Co.—**Pulga/Feather River Canyon/Feather River Highway [Butte]**, *Balls 22509* (RSA, SD), *Fritsch 1353* (**RSA[45]**), *Howell 49700* (NY), 15 May 1923 *Pattee s.n.* (CAS), *Shevock 1783* (RSA), *Williams 84–23–2* (NY).

Calaveras Co.—Golden Gate Hill/Gwin Mine/Mokelumne Hill/Mokelumne River, 17 May 1854 *Bigelow s.n.* and *Bigelow s.n.* (GH, NY), *Blaisdell s.n.* (**A[28]**, CAS), *Hansen 227* (A, DS, NY), *Jepson 1819* (JEPS), *Roseberry 225* (UC); Silver Rapids, *Stanford 300* (GH, **POM[27]**).

Colusa Co.—Between Walker Ridge Road and Leesville, *Heller 13111* (A, DS, F, **NY[43]**), *Shock 68* (RSA), *Smith 9039* (POM); Near Lake Co. line, *Hoover 4988* (UC).

El Dorado Co.—near Auburn/Cool, *Davidson 100* (JEPS), *Wythe s.n.* (JEPS); Road to Pilot Hill/Sweetwater/Sweetwater Creek, 1907 *K. Brandegee s.n.* (NY), *McNeal 2026* (NY), *Robbins 1934* (CAS, **GH[32]**, UC), *Russell 113* (CAS).

Fresno Co.—**Kings River [Fresno]**, 10 May 1953 *Buckalew s.n.* (GH, UC), *Crawford JMC-25* (UC), *Fritsch 1355* (RSA), 2 May 1923 *Graves s.n.* (JEPS), *Lindner 89* (RSA), *Quibell 1565* (DUKE, POM), *Quibell 1927* (CAS, NY, **RSA[25]**, UC), *Quick 46–14* (CAS, GH), *Shevock 8682* (CAS); Near Piedra, *Heckard 7686,* (JEPS), 13 May 1919 *Kelley s.n.* (JEPS), *Shevock 7058* (CAS), *Wetherell 236* (DS).

Glenn Co.—11 mi NE of Alder Springs, *Munz 13335* (**RSA[44]**); Mud Flat, *Heller 11535* (CAS, DS, F, GH, NY, UC).

Lake Co.—E of Clear Lake, *Eastwood & Howell 5640* (A, CAS, F, UC), *Simmtacchi 264* (RSA, UC); **W of Clear Lake [Lake]**, 24 Apr 1931 *C. Benson s.n.* (POM), 12 May 1932 *C. Benson s.n.* (**POM[38]**), *L. Benson 124* (**POM[37]**), *L. Benson 343* (POM),

30 May 1917 *Bentley s.n.* (DS), 1 May 1924 *Blankinship s.n.* (MO), 13 May 1925 *Blankinship s.n.* (RSA), 9 May 1926 *Blankinship s.n.* (CAS), *Carter 353* (UC), *Fritsch 1354* (RSA), 28 Apr 1940 *Hastings s.n.* (UC), *Howell 15589* (A, CAS, POM), 13 Jun 1917 *Platt s.n.* (JEPS), *Thorne 46798* (RSA); Near Hough Springs, *Abrams 6273* (A, DS, NY), *Breedlove 5180* (DUKE[42]), *Wolf 2115* (RSA, SD); Lower Lake, 11 May 1901 *Bowman s.n.* (A[35]); Near Siegler Meadows, *Cantelow 2233* [8 May 1938] (CAS, RSA[34]), *Cuff 133* (UC), *Neuns 165* (UC); E of Stanton, *Bacigalupi 3187* (JEPS, NY[41], UC), *Cronemiller 50672* (CAS), *Jepson 8983* (JEPS), *Kildale 5007* (DS); Walker Ridge off Hwy. 20, *Wheeler 264* (CAS); 31.5 mi W of Williams, *Clausen 1027* (DS, POM[36], UC).

Los Angeles Co.—Glendale Hills, *Payne 2980* (RSA[17]).

Mariposa Co.—Yosemite Valley, 27 Apr 1895 *Perkins s.n.* (RSA[26]).

Nevada Co.—Combie Dam, *Josephson 37* (UC).

Orange Co.—San Juan Canyon, *Moran 27196* (SD), *Spring 34* (UC); Santiago Coal Mine, *Lewis 380* (UC); Sierra Peak to Black Star Canyon, *Boyd 6205* (RSA[11]), *Harvey 85* (RSA), *Hutt 373* (DUKE), *Lathrop 6185* (RSA), *Thorne 32849* (RSA), *Wolf 4441* (RSA); Trabuco Canyon, *Balls & Everett 22842* (RSA), 30 May 1903 *Bradshaw s.n.* (POM), *Moran 22599* (RSA, SD, UC), *Peirson 3493* (DS, JEPS, POM[9]), 14 Jun 1940 *Pequegnat s.n.* (POM), *Smith 5453* (F).

Placer Co.—Auburn, *Ames s.n.* (F), *Carter 1485* (A, NY, UC), *Crum 2043* (UC), *Dunn s.n.* (CAS), *Fritsch 1383* (RSA[33]), *Jepson 18581a* (JEPS); 6 mi N of Colfax, *Hitchcock 6391* (NY[40]); Foresthill, *James 119* (JEPS), 15 May 1939 *Jump s.n.* (A[39], CAS, UC), *Smith 2540* (UC); Newcastle/8 mi N of Folsom, *Howe 1815* (SD), Apr–May 1904 *Mackie s.n.* (POM[31]), *Wolf 8609* (GH, MO, NY, RSA), *Wolf 9283* (RSA).

Plumas Co.—Feather River Canyon, *Cantelow 3612* (CAS).

Riverside Co.—Temecula, 2 May 1938 *Stubblefield s.n.* (NY, RSA[8]); Tin Mine Canyon, *Olmsted 401* (RSA[12]).

Sacramento Co.—Folsom, 30 Apr 1939 *Copeland s.n.* (A, CAS, DS, F, NY, POM, UC), *Copeland 621* [= 23 Apr 1928] (DS, POM[30]), *Copeland 1614* (DS, GH, UC), Apr 1916 *Cravens s.n.* (DS), *Nordstrom 79* (UC).

San Bernardino Co.—Arrowhead Highlands/Lake Arrowhead, 29 Apr 1934 *Edge s.n.* (RSA), 14 May 1938 *Gluechert s.n.* (RSA[23]); Cajon Canyon, *Thorne 39466* (MO); **City Creek [San Bernardino 2]**, May 1949 *Harris s.n.* (CAS), *Henrickson 2482* (RSA), *Howell 1248* (RSA), *Johnson 1439* (RSA), *Johnston 2857* (POM), *Johnston 2935* (DS, POM[14]), *McMinn 1560* (UC), *Peirson 5198* (RSA), *Stark 1504* (DS, RSA, UC), *Thorne 51890* (NY, RSA); Devil Canyon, *Wheeler 4101* (CAS, RSA), 18 May 1904 *Wilder s.n.* (POM[15]); **Devore Station/Glenn Helen Ranch/Glenn Helen Road/Sycamore Flat/Lytle Creek [San Bernardino 1]**, *Abrams 13967* (GH, DS), *Craig 992* (A), *Crow 265* (RSA), *Hall 888* (UC), *Howell 23436* (CAS), 15 Apr 1932 *Jaeger s.n.* (DS, POM), *Munz 11058* (POM[13]), *Peirson 8750* (RSA), *Swinney 2729* (RSA), *Thorne 39465* (DS, GH, NY, RSA, SD), *Wheeler 1943* (DS, RSA, UC), *Wiegand & Wiegand 1663* (GH), *Wolf 10299* (DS, NY, RSA); San Sevaine Canyon, *Ewan 10982* (CAS, GH, MO), *Ewan 10986* (CAS, GH), 11 Jul 1935 *Johnston s.n.* (POM); Sheep Creek Canyon, 22 May 1929 *Kusche s.n.* (RSA[18]); Upper Warm Springs Canyon, *Sanders 14177* (RSA); Waterman Canyon, *Bacigalupi 5872* (JEPS), *Balls 14411* (RSA), *Emery 168* (CAS), *Hilend 215* (RSA), *Jepson 5551* (JEPS, RSA), 7 May 1926 *Jones s.n.* (A, CAS, DS, NY[16], UC), 30 Jun 1926 *Jones s.n.* (A, CAS, DS, GH, NY, UC), *Lewis 158* (UC), *Munz 2228* (DS), *Parish 11389* (POM, UC), *Peirson 851* (RSA), *Shaw 14* (DS).

San Diego Co.—Barona Valley, *Beauchamp 1717* (SD), *Gander 3991* (SD); Black Mt., *Ertter 6161* (RSA[2], UC); Castro Canyon, *Gander 4321* (SD); De Luz, *Gander 8214* (SD); **Devil Canyon [San Diego 1]**, *Boyd 7593* (CAS, RSA[10]); El Cajon Mt., *Gander 2211* (SD), *Moran 15882* (RSA[3], SD); Foster, *Reed 10850* (POM[4]), *Smith 5249* (F, MO); Lake Henshaw, *Gander 2895* (SD), *Gander 3727* (SD), 14 Aug 1947 *Gastil s.n.* (SD), *Tilforth 2116* (RSA); Mesa Grande, *Ferguson 65* (JEPS, SD), *Gander 200* (SD, UC), 27 May 1945 *Huey s.n.* (SD), 20 Oct 1907 *Merriam s.n.* (CAS), *Spencer 1147* (CAS, GH, NY, POM[1]), *Spencer 1596* (A); Middle Cuyamaca Peak; *Moran 11945* (DS, SD); **Mt. Palomar [San Diego 2]**, *Dunkle 5286* (RSA[6]), *Gander 230* (SD), *Howe 881* (SD), 27 Jul 1926 *Jones s.n.* (CAS, DS, RSA), *Meyer 495* (JEPS), Jun 1926 *Nichols s.n.* (SD), *Purer 6680* (SD), 18 May 1929 *Salmons s.n.* (DS, F, GH, NY, POM, SD, UC), Jun 1930 no collector (SD 3675); Rainbow/Pala, *Fiker 3488* (NY, UC), *Gander 3776* (SD), *Gander 8190* (SD), *Gray 1927* (JEPS), 19 Apr 1941 *Hood s.n.* (NY[7]), *Jensen 141* (UC), *Jones 28257* (POM), *Reed 5830* (NY), 3 Apr 1931 *Rowntree s.n.* (CAS); San Luis Rey River, *Mason 3138* (DS, UC), *Munz 10353* (A, POM[5], UC); Santa Margarita Mts.: Camp Pendleton, *Beauchamp 1887* (SD); Warner Springs, 1913 *Buttle s.n.* (CAS), 11 Oct 1858 *Hayes s.n.* (NY).

San Luis Obispo Co.—Colwell Ranch, *Lee 635* (RSA[24], UC).

Santa Barbara Co.—Highway 166/Los Padres Park, 8 May 1965 *Wallace s.n.* (RSA[22]); La Combre Peak, *Mason 456* (GH[21], UC); Mission Canyon, 27 May 1909 *Eastwood s.n.* (CAS); Painted Cave, *Eastwood 33* (A, F, MO, NY[19], UC), *Wiggins 8508* (A, DS), *Wolf 2302* (CAS, DS, POM, RSA, UC); Rattlesnake Canyon, *McMinn 1093a* (DS), 20 Aug 1954 *Pollard s.n.* (CAS); **San Marcos Pass Area [Santa Barbara]**, *Embree 352* (UC), *Fritsch 1356* (RSA), *Hall 7-H* (JEPS), *Heckard 6735* (JEPS), 10 May 1952 *Pollard s.n.* (RSA[20]), 24 Jun 1953 *Pollard s.n.* (CAS), *True 966* (UC).

Shasta Co.—Cedar and Cow Creek, 30 Apr 1900 *Baker s.n.* (UC), 1 May 1900 *Baker s.n.* (DS), *Johannsen 122* (UC), 5 Sep 1907 *Merriam s.n.* (CAS); Delta/La Moine/Pollock, *Applegate 5749* (CAS, RSA), *Eastwood & Howell 1804* (A, CAS), *Jepson 6177* (JEPS, NY), *Jepson 6184* (JEPS), *McVaugh 6238* (UC), 9 Oct 1919 *Merriam s.n.* (CAS), *Rose 34238* (DS, F, NY, POM[51]), *Wolf 11475* (RSA); **Ingot [Shasta 1]**, Jun 12 1923 *Bettiel s.n.* (CAS), *Fritsch 1352* (RSA), *Hitchcock 6486* (CAS, RSA[48]); Kennet [now McCloud River Arm of Shasta Reservoir], Jun 1912 *Conubse s.n.* [?; = "Baird" (CAS)], *Eastwood 1455a* (A, CAS, GH), 16 May 1913 *Smith s.n.* (A[49], CAS), Jul 1912 *Smith s.n.* (CAS), *Smith 168* (CAS); McCloud Bridge, *Webster 7771* (DUKE[50]); Minnesota, *Johannsen 149* (UC), *Josephson 11* (UC); Pit River/ Pit River Bridge, *Brown 273* (F, NY[52]), *Heller 13498* (DS, F, NY), *Jones 29078* (DS, POM, UC), *Lorenzen s.n.* (JEPS), *Mason 5876* (GH, UC), *McMinn 2493* (UC); 20 mi N of Redding, *Grant 7976* (UC); **near Shasta [Shasta 2]**, *Bacigalupi 7035* (JEPS), 18 Aug 1899 *Dudley s.n.* (DS), *Everett & Balls 23922* (RSA), *Fritsch 1351* (RSA), *Munz 13192* (RSA[46]); Shasta-Trinity National Forest: Sierra Pacific Industries land, *Kierstead 89–76* (UC); Whiskeytown area, *Balls 18665* (NY, RSA), *Balls 20724* (NY, RSA), *Howell 29185* (CAS, NY), *Josephson 24* (UC), *Rose 54029* (NY, RSA), *Saufferer 141* (NY); *Smith & Sawyer 8710* (RSA[47]).

Sierra Co.—Cedar Glen [= Cedar Grove?], 25 May 1920 *Jones s.n.*

Tehama Co.—SW of Paskenta, *Crampton 7773* (CAS, UC), *Everett & Balls 20314* (RSA), *Mallory 78* (JEPS); Paynes Creek, *Oswald 4566* (UC); [S?] Yolla Bolly Mts. ["Yolo Bolo Mt."], 20 Sep 1892 *Brandegee s.n.* (UC).

Tulare Co.—Kaweah, *Hopping 1901* (JEPS).

Yuba Co.—Strawberry Valley, *Burks 38* (UC).

2. Specimens excluded from the distribution map because locality information was either too general or obscure.

Amador Co.—*Hansen 1891* (UC). **Butte Co.**—May 1879 *Bidwell s.n.* (GH, NY); Durham, 3 May 1932 *Morrison s.n.* (CAS); Ridge

above Enterprise, *Heller 11891* (A, CAS, DS, F, NY, UC); Road to Goldbank Mine, *Ahart 2369* (CAS). **Calaveras Co.**—Calaveras River, Apr 1850 *Gibbes s.n.* (NY). **El Dorado Co.**—Grade near Auburn, Apr 1914 no collector (SD 6100); Feather River, *Bille s.n.* (JEPS), *Monnet 655* (CAS); Knoll Spring Ridge, *Douthitt 33144* (CAS). **Lake Co.**—Between Leesville and Hough Spring, *Abrams 12577* (DS, NY). **Los Angeles Co.[?]**—Los Angeles, *Nevin 1429* (GH). **"Mendocino Co.?"**—*Vasey s.n.* (GH) [doubtfully from there, considering that there are no other collections from Mendocino County and the locality information is questionable]. **Orange Co.**—S of Corona, 23 Apr 1966 *Roos s.n.* (RSA); Mountains E of San Juan Capistrano, *Roos 2326* (POM). **Placer Co.**—Rattlesnake Bend, Jun 1920 *King s.n.* **Plumas Co.**—1875 *Ames s.n.* (GH); 1875 *Austin s.n.* (NY). **San Bernardino Co.**—Baruco Canyon, 17 May 1938 *Winblad s.n.* (A); San Bernardino, San Bernardino Mts., Jul 1904 *Allen s.n.* (UC), 13 Apr 1922 *Clemens s.n.* (A, CAS), *Cummings 197* (GH, NY), 21 Sep 1880 *Engelmann & Sargent s.n.* (A), May 1878 *Lemmon s.n.* (F), *S.B. and/or S.B. and W.F. Parish 307* and various dates (A, CAS, DS, F, JEPS, MO, NY, RSA, UC), *Vasey 361* (DS), *Wright 808* (DS), *Wright 216* (GH), 11 May 1926 no collector (RSA 390746), no collector (RSA 297955, F 313554); San Bernardino Mts. [and McCloud River; mixed collections], no collector [Lemmon?] (UC 367205), *Lemmon s.n.* (F, POM). **San Diego Co.**—Smith Mountain, 3 Jul 1896 *McClatchie s.n.* (NY). **Santa Barbara Co.**—Santa Barbara, *Bolander [& Kellock] s.n.* (GH, NY); Between Santa Maria and Santa Barbara, 30 Apr 1939 *Stubblefield s.n.* (RSA); Santa Ynez Mts., 1888 [1889?] *Brandegee s.n.* (A, F, GH), *Dunn 6814* (22 May 1891; NY, POM, UC), *Howe s.n.* (SD), Jul 1907 *Marshall s.n.* ["Fremont's Pass"] (DS, UC), 20 Apr 1956 *Pollard s.n.* [Slippery Rock Ridge] (RSA). **Shasta Co.**—(San Bernardino Mts.) and McCloud River [mixed collections], no collector [Lemmon?] (UC 367205), *Lemmon s.n.* (F, RSA); McCloud River, *Scupham 150* (NY); Redding, 16 Apr 1923 *Bettiel s.n.* (CAS), 3 May 1911 *Blankinship s.n.* (JEPS), May 1923 *Boyd s.n.* (CAS), 16 Apr 1938 *Rose s.n.* (CAS), 1 May 1928 *Rose s.n.* (CAS); Sacramento River, 1838–1842 *Wilkes s.n.* (NY); Squaw Creek Ranger Station, Jun 1916 *Drew s.n.* (DS); Upper Sacramento, 1845–1847 *Fremont s.n.* (GH, NY), *Hulse s.n.* (NY), 9 Sep 1882 *Pringle s.n.* (A, F, GH, NY), Aug 1912 *Smith s.n.* (POM); Ydalpom, *McAllister 9* (CAS). **Southern California**—*Parry & Lemmon 226* (GH, F, NY), *Lemmon s.n.* (F). **California**—*King 272* (CAS), *Lemmon s.n.* (A, POM), *LeRoy s.n.* (NY), *Lobb 345* (F, NY). **California**—near U.S. Fishery, *Lemmon s.n.* (GH). **No locality**—State survey, no collector, 4512 (UC), 1903 *Rattan s.n.* (DS).

3. Collections cited by Gonsoulin (1974) but no elements seen by me and therefore not mapped.

Cited as *S. officinalis* var. *californica*:

El Dorado Co.—Natoma Ditch, 14 May 1907 *Brandegee s.n.* (PH). **Fresno Co.**—Mill Creek, *Bacigalupi 7686* (FSU). **Lake Co.**—Soda Bay, 9 Aug 1931 *Schulthers s.n.* (UC).

Cited as *S. officinalis* var. *fulvescens*:

Fresno Co.—Trimmer, *Clark 46–14* (GH). **San Bernardino Co.**—San Bernardino Mts., *Clark 15916* (SMU). **San Diego Co.**—Fall Brook, May 1883 *Parry s.n.* (MO).

4. Additional notes.

Bracelin 1235 and *2586* [Alameda Co.] (various herbaria) are unquestionably from a cultivated specimen of *S. officinalis* L.; *Kelee* [Alameda Co.] (UC) is presumed cultivated, and therefore was not mapped.

APPENDIX 2: Key to the *Styrax officinalis* Group and Taxonomic Treatment of *Styrax redivivus*

1. Stalked stellate hairs on vegetative parts (one or more of the following: abaxial surface of at least some leaves, especially along the veins; petioles; at base of new shoots) absent, or if present then the stellate portion usually white or tawny; free portion of stamen tube 0–0.5 mm long; pedicels 8–17 mm long, usually the same width throughout; corolla lobes widely spreading; pollen pale yellow . . . . *S. officinalis*
1. Stalked stellate hairs on vegetative parts (as above) golden yellow to dark brown; free portion of stamen tube 1–7 mm long; pedicels 4–9 mm long, becoming widened from the base to the apex; corolla lobes moderately spreading; pollen orange-yellow
   2. Larger undehisced capsules 7–10 mm long; larger seeds 6–9.5 mm long; mature capsule pubescence canescent; pedicel 1.3–2.3 times as long as the calyx; calices 3–5(–6) × 4.5–5.5 mm; leaf margins often coarsely lobed or irregularly undulate . . . . *S. platanifolius* group
   2. Larger undehisced capsules 11–15 mm long; larger seeds 9.5–12 mm long; mature capsule pubescence tawny or fulvous; pedicel 0.5–1.4 times as long as the calyx; calices 4–7 × 5–7 mm; leaf margins never lobed . . . . *S. redivivus*

STYRAX REDIVIVUS (Torr.) L.C.Wheeler, *Bull. S. Calif. Acad. Sci.* **44**: 94. 1946. *Darlingtonia rediviva* Torr., *Proc. Amer. Assoc. Adv. Sci.* **4**: 191. 1851. *Styrax californicum* Torr., *Smithsonian Contr. Knowl.* **6**: 4. 1853. *Styrax officinalis* L. var. *californicus* (Torr.) Rehder, *Mitt. Deutsch. Dendrol. Ges.* **24**: 226. 1915. *Styrax officinalis* L. var. *californicus* (Torr.) Munz & I.M.Johnston, *Bull. Torrey Bot. Club* **51**: 298. 1924. *Styrax officinale* L. var. *rediviva* (Torr.) R.A.Howard, *Sida* **5**: 337. 1974. *Styrax officinale* L. subsp. *redivivum* (Torr.) Thorne, *Aliso* **9**: 195. *Styrax officinalis* L. subsp. *californica* (Torr.) E.Murray, *Kalmia* **12**: 25. 1982.—TYPE: U.S.A. California: Shasta Co., Upper Sacramento (vicinity of Sacramento and Pitt rivers [Gonsoulin 1974]), 1845–1847 *Fremont s.n.* (holotype: NY!; isotype: GH!).

Styrax californica Torr. var. *fulvescens* Eastw., *Bot. Gaz.* (*Crawfordsville*) **41**: 286. 1906. *Styrax officinalis* L. var. *fulvescens* (Eastw.) Munz & I.M. Johnston, *Bull. Torrey Bot. Club* **51**: 297. 1924. *Styrax officinalis* subsp. *fulvescens* (Eastw.) R.M.Beauch., *Aliso* **9**: 194. 1978. *Styrax officinalis* subsp. *fulvescens* (Eastw.) E.Murray, *Kalmia* **12**: 25. 1982.—TYPE: U.S.A. California: Santa Barbara Co., Painted Cave Ranch, Santa Ynez Mountains, 17 May 1904 *Eastwood s.n.* (holotype: CAS, destroyed; lectotype, selected here, U.S.A. California: Santa Barbara Co., Santa Ynez Mountains, 1888 *T.S. Brandegee s.n.* [1889 according to Ewan 1942], GH!; isolectotypes, A!, F!).

No isotypes of 17 May 1904 *Eastwood s.n.* are known to exist. A duplicate of 1888 *T.S. Brandegee s.n.* apparently does not occur at Brandegee's herbarium, UC, which otherwise would have been designated as the lectotype.

Deciduous shrub multistemmed from the base, to 4 m. Young twigs green, white-stellate pubescent, often toward the base with scattered, golden, rusty brown, or dark-brown, stalked stellate hairs; outer layer of older twigs often exfoliating into long strips. Petiole 3–14 mm long. Lowest pair of leaves on each shoot often subopposite and smaller than the rest. Lamina chartaceous, 3.0–7.5(–11.7) × 2.5–6.5(–8.8) cm, broadly elliptic, ovate, obovate, or orbicular, secondary veins (6–)7–8(–9); apex rounded, broadly cuspidate, obtuse, or broadly acute; base truncate, rounded, cordate or broadly cuneate, usually also slightly attenuate; adaxially glabrous to soft-stellate-pubescent; abaxially nearly glabrous to densely and thickly grayish-green stellate-tomentose, with scattered, golden, rusty brown, or dark-brown stellate hairs especially prevalent on veins and

the lowest pair of leaves on each shoot, the stellate portion often deciduous from the dark-orange base; margin entire. Inflorescences racemose, false-terminal, often contracted and thus appearing um-bellate, 2–5 cm long, 1–6-flowered (mean = 3). Pedicels 4–9 mm long, becoming widened from the base to the apex. Pedicels 0.5–1.4 times as long as the calyx. Calyx 4–7 × 5–7 (mean length = 5.7) mm, campanulate, grayish green stellate-pubescent, sometimes with additional larger rufous hairs, margin and/or teeth frequently glandular; calyx teeth 6–9, irregularly distributed, to 0.8 mm long, narrow-deltoid to linear, the calyx margin truncate between the teeth. Corolla white, 16–26 mm long, petals connate up to the calyx mar-gin; corolla lobes 5–7(–8–10), typically 6, imbricate in bud, 10–21 × 4–7 mm, overlapping, spreading, thin, elliptic, the outer surface stellate-pubescent. Free portion of the stamen tube 2–7 mm long; distinct portion of filament 2–9 mm long, straight, margins parallel, ventrally planar and white-stellate-pubescent, becoming glabrous to-ward the apex, the hairs with arms to 0.4 mm long; anthers 4–6 mm long, the connective not or only slightly prolonged beyond the non-tapered anther sacs; pollen orange-yellow. Ovary densely stellate-pubescent; style pubescent at base only to nearly throughout; stigma 0.3–0.7 mm in diameter. Capsule 11–15 × 10–12 mm (broader when 2–3-seeded), globose, 3-valve-dehiscent, hard walled, tawny- or ful-vous-stellate-pubescent at least when mature, shallowly rugose after dehiscence. Seeds 9.5–12 mm long. Seed coat glabrous.