1-1-1995

The rare, serpentine endemic *Streptanthus morrisonii* (Brassicaceae) species complex, revisited using isozyme analysis

Rebecca W. Dolan
Butler University, rdolan@butler.edu

Systematic Botany (1995), 20(3): pp. 338–346

The Rare, Serpentine Endemic *Streptanthus morrisonii* (Brassicaceae) Species Complex, Revisited Using Isozyme Analysis

REBECCA W. DOLAN

Department of Biological Sciences,
Butler University, 4600 Sunset Avenue,
Indianapolis, Indiana 46208

ABSTRACT. The *Streptanthus morrisonii* (Brassicaceae) complex is a group of six narrowly-distributed obligate serpentine endemic taxa whose habitat is threatened by geothermal development. Isozyme analysis of this little-studied complex supports the delineation of two species, *S. morrisonii* and *S. brachiatus*, but is at odds with the treatment of two subspecies based on morphology. These results may be influenced by small sample sizes but genetic studies of other *Streptanthus* taxa have shown patterns of relatedness that often transgress subspecies boundaries based on morphology. The present study further shows that members of the *S. morrisonii* complex share high genetic identity values (mean = 0.87) and are not genetically depauperate (mean value for percent of loci polymorphic = 37%, average number of alleles per locus = 1.48, and average heterozygosity per locus = 0.137). Preservation of their serpentine outcrop habitat is essential to the survival of these plants.

The *Streptanthus morrisonii* F. W. Hoffman complex is a group of very narrowly distributed obligate serpentine endemics. These plants have been little studied or collected. Their habitat is remote, several taxa are known from only single populations and the plants are difficult to distinguish based on morphological traits. They have, however, received recent attention because their habitat is threatened by geothermal energy procurement and mining activities. This study was undertaken to determine whether biochemical genetic data from isozyme analysis support the classification based on morphology.

The *Streptanthus morrisonii* complex comprises two species: *S. morrisonii*, with three described subspecies, and *S. brachiatus* F. W. Hoffman, with two subspecies. The complex was originally placed in the subgen. *Euclisia* Nutt. ex Torrey & A. Gray, based on the co-occurrence of zygomorphic flowers, nonbracteate inflorescences, and one or two pairs of stamens with connate or partially connate filaments (Hoffman 1952). Hoffman also noted a biennial (i.e, monocarpic perennial) life history for these plants, and the presence of glabrous, glaucous cabbage-like rosette leaves not found in other taxa in the subgenus. This distinction led Kruckeberg and Morrison (1983) to place the complex in a new section, *Biennes* Kruckeberg & Morrison.

Related taxa in subgen. *Euclisia* include the more widely distributed annual serpentine endemic *S. glandulosus* Hook., *S. breweri* Gray, *S. tortuosus* Kell., *S. polygaloides* Gray, *S. niger* Greene, and *S. insignis* Jepson species complexes (Morrison 1941). Hoffman (1952) thought the *S. morrisonii* complex most closely related to *S. breweri*.

Streptanthus morrisonii has four recognized subspecies. *Streptanthus morrisonii* subsp. *morrisonii* grows on serpentine outcrops and adjacent serpentine chaparral in north central Sonoma County. This subspecies, the most widely distributed taxon in the complex, grows in the large serpentine area known as "The Cedars" (Fig. 1; Tables 1, 2). *Streptanthus morrisonii* subsp. *hirtiflorus* F. W. Hoffman, a highly restricted taxon known from a single 100 m^2 area of outcrop and totaling only several hundred plants, is found within the range of *S. morrisonii* subsp. *morrisonii*. Disjunct to the east of The Cedars is *S. morrisonii* subsp. *elatus* F. W. Hoffman, on the Lake-Napa county line (Fig. 1). This taxon is restricted to several closely spaced outcrops. A fourth subspecies, *S. morrisonii* subsp. *kruckebergii* Dolan & LaPré occurs in extreme eastern Lake-Napa County line near Knoxville and has recently been reported from Mendocino County (L. Vorobik, pers. comm.).

Streptanthus brachiatus subsp. *brachiatus* is a morphologically uniform taxon that has been collected only from the immediate vicinity of Socrates Mine in the Mayacmas Mountains of northern Sonoma County (Fig. 1; Tables 1, 2). The habitat has been severely altered by past mining. Plants occur primarily on open outcrop surfaces but are also found scattered in adjacent

chaparral. *Streptanthus brachiatus* subsp. *hoffmanii* Dolan & LaPré is a more morphologically heterogeneous taxon that occurs on scattered outcrops within several thousand meters to the southeast. Calyx color in this subspecies is yellow or purple, with plants ranging in habit from short and much-branched to tall and remotely branched.

The *Streptanthus morrisonii* complex, like other obligate serpentine taxa in the genus (Kruckeberg 1956, 1958), exhibits much local differentiation (Dolan and LaPré 1989). This can make species and subspecies identification difficult. Features of the plants are generally uniform within a given outcrop, but much variation exists between outcrops and it is often difficult to match the features of a particular plant to a described taxon: the existing taxonomy for many *Streptanthus* Nutt. taxa seems inadequate to describe the variation encountered in the field.

Additional factors that make these plants difficult to study include the inaccessibility of some sites (two of the populations described in this paper occur on federal land but had to be reached by helicopter), poor preservation of diagnostic traits on herbarium sheets, and the need to have material from different parts of the life cycle (i.e., rosette leaves that are lost before flowers are present) for identification using published keys.

This study reports data gathered as part of a directed study funded by the Bureau of Land Management to determine the identity of *Streptanthus* species growing on serpentine outcrops in areas that potentially could be developed for geothermal energy production. The work was funded by an unusual cooperative agreement between developers, state regulatory agencies, and the federal government (Dolan 1991). The study area included the only known populations of *S. brachiatus* subsp. *brachiatus* (the Socrate's Mine jewelflower) and *S. morrisonii* subsp. *elatus* (Morrison's jewelflower), both Category 2 Candidates for listing under the Endangered Species Act at the time the study was initiated. This category is reserved for species for which more information is needed before assessment of the need for official protective status can be made.

All known populations of members of the complex were revisited and inventoried. Particular attention was paid to the unusually polymorphic subspecies, *S. brachiatus* subsp. *hoffmanii*, that differs from other subspecies in the section by having variable floral color, plant height, and habit in different portions of the series of outcrops on which it grows. The other five taxa are morphologically uniform for these traits (see Table 1).

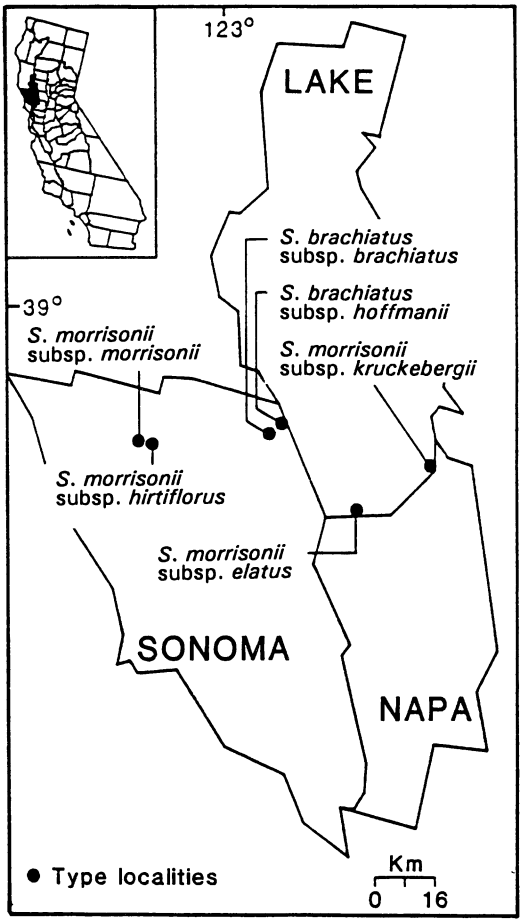

FIG. 1. Map of the type localities of members of the *Streptanthus morrisonii* complex (from Dolan and LaPré 1989).

Isozyme analysis was used to estimate genetic similarity in these apparently closely related yet morphologically distinct and geographically disjunct taxa. Our visits to the collection sites in some cases are apparently the first since they were visited by Hoffman in the 1940's.

MATERIALS AND METHODS

Table 1 summarizes the significant features that distinguish members of the complex. Type localities, geographic ranges, and estimated

TABLE 1. Distinguishing morphological features of the *Streptanthus morrisonii* complex. Abbreviations following taxon names are used in Tables 3–5.

Taxon	Morphological traits				
	Calyx color	Calyx pubescence	Juvenile leaf color	Upper connate filaments	Habit
S. morrisonii subsp. *morrisonii* (SMM)	yellow	most glabrous	uniformly green	with orange vascular traces	tall, remotely branched
S. morrisonii subsp. *hirtiflorus* (SMH)	purple	hirtellous	mottled	with purple vascular traces	intermediate height, variable branching
S. morrisonii subsp. *elatus* (SME)	yellow	variable	heavily mottled with purple-brown	uniformly yellow	tall, remotely branched
S. morrisonii subsp. *kruckebergii* (SMK)	yellow	variable	mottled	uniformly yellow	tall, remotely branched
S. brachiatus subsp. *brachiatus* (SBB)	purple	absent	mottled	with purple vascular traces	short, much branched
S. brachiatus subsp. *hoffmanii* (SBH)	purple or yellow	variable	mottled	with purple vascular traces	short, much branched to intermediate, remotely branched

numbers of individuals for each taxon are presented in Fig. 1 and Table 2. All sites were visited several times throughout 1985-1987. Material used in electrophoresis was collected in the spring and summer of 1986 and 1987 at the type locality for each taxon. Two additional locations were sampled for the polymorphic taxon *S. brachiatus* subsp. *hoffmanii* to encompass the range of morphological variation in this subspecies. Samples of this taxon were collected from: 1) the type locality (flowers purple, plants short and much-branched), designated SBH-1; 2) an outcrop southeast of the type locality (flowers yellow or purple, plants short and much-branched) designated SBH-2, and 3) a site further to the southeast (flowers yellow, plants tall and remotely-branched), designated SBH-3.

Electrophoretic Procedures. Single flowering inflorescences of 10 plants per population were collected for electrophoretic analysis. Flowers and buds were wrapped in moist paper towels, placed in plastic bags, and shipped to the lab within 24 hr, where they were processed for horizontal starch gel electrophoresis. Material collected and shipped in this way, and refrigerated upon arrival, remained viable for up to 10 days. Tissue was extracted in a buffer of 25 ml tris pH 8.0, 25 ml distilled water, and 77 mg dithiothreitol. Alcohol dehydrogenase (ADH) and phosphoglucoisomerase (PGI) were run in a variation of the Poulik buffer system (Heywood 1980) at 200 volts for 2.5 hr. Malate dehydrogenase (MDH) and phosphoglucomutase (PGM) were run in a histidine/citrate buffer system (Ellstrand 1984) at 25 ma for 3 hr. Esterase (EST) was run in a lithium borate system (Scandalios 1969) at 200 volts for 3.5 hr. Standard enzyme stains were used (Shaw and Prasad 1970; Soltis et al. 1983), except for ADH, for which the staining solution was buffered with tris at pH 8.5. When more than one putative locus was observed for an enzyme, loci were numbered sequentially, with the least anodally migrating locus designated 1. Enzyme variants for individual loci were assigned sequential letters in the same manner.

Because of the extreme rarity of these plants and uncertainty concerning the abundance of taxa at the start of the study, care was taken to minimize negative impacts of collection and field study. Sample sizes of ten individuals per population used in this study are at the lowest end of recommended sample sizes for genetic studies of rare plants proposed by the Center for Plant Conservation (Falk and Holsinger 1991). Although sample sizes of 25-30 individuals are often used in studies of genetic variation, based on the argument that this number will allow a 95% confidence level of sampling alleles present at frequencies of 5% or greater (Marshall and Brown 1975), questions concerning the significance of rare alleles have led some authors to suggest smaller sample sizes can provide sufficient data for rigorous analysis (see

TABLE 2. Type localities, range, and estimated numbers of individuals for each taxon in the *Streptanthus morrisonii* complex. Specimens for study were collected at type localities unless otherwise noted. Voucher specimens are deposited at UC. Abbreviations used in the text follow taxon names.

Taxon	Estimated number of individuals	Distribution
S. morrisonii subsp. *morrisonii*	10,000	Type locality: serpentine outcrop, head-waters of Big Austin Creek at Layton Chromite Mine, Sonoma county, California. Range: additional sites in "The Cedars," are Red Slide on Bargemann Creek, Devil Creek, Gilliam Creek (all the preceding are tributaries of East Austin Creek and located in the same serpentine area, scattered across eight sections).
S. morrisonii subsp. *hirtiflorus*	100–200	Type locality: headwaters of East Austin Creek, a short distance above Dorrs' Cabin, Sonoma county, California. Found only at this site, in an area of 100 m^2.
S. morrisonii subsp. *elatus*	1000–2000	Type locality: serpentine outcrop on low saddle, 0.25 mi west of White's Point, Table Mountain Road, ca. 5 mi east of Mountain Mill House, Napa-Lake county line, California. Known only from this location.
S. morrisonii subsp. *kruckebergii*	100,000	Type locality: Dunnigan Hill in Knoxville Recreation Area on the Lake-Napa county line in the region of Knoxville. Range: scattered adjacent outcrops of approximately 120 acres on a 900–1000 acre watershed.
S. brachiatus subsp. *brachiatus*	1000	Type locality: exposed Serpentine Ridge near Socrates Mine (now believed to have been incorrectly identified by Hoffman as Contact Mine), east of Pine Flat, Sonoma county, California, on the Sonoma-Lake county line. Only known location for taxon.
S. brachiatus subsp. *hoffmanii*	4000	Type locality: Serpentine outcrop on Bear Rd ¼ mi S of three-way junction with Ridge Road and Davis Road on the Lake-Sonoma county line.

Brown and Briggs 1991; Falk 1991). However, a caveat to all conclusions based on genetic data is that they are based on a small number of loci and individuals. For the extremely rare *Streptanthus morrisonii* subsp. *hirtiflorus*, only two plants were tested. As a result, this taxon was not included in any analyses.

No formal genetic analyses were conducted to document the pattern of inheritance of putative alleles. Allelic assignments were based on the observed pattern of populational variation, the known subunit structure of the enzymes, the cellular compartmentalization generally observed for plant enzymes (Kephart 1990), and consultation with other labs.

RESULTS

Highly resolved banding patterns characteristic of diploids were obtained for five enzyme systems encoded for by nine putative loci. A total of 20 apparent alleles were detected. Malate dehydrogenase and phosphoglucoisomerase were monomorphic for two putative loci each for all populations studied. Figure 2 illustrates schematic banding patterns for variable loci; allele frequencies are presented in Table 3.

There is an apparent gene duplication for phosphoglucomutase resulting in three PGM loci instead of the expected number of two for diploid plants (Kephart 1990) in all taxa except the most eastern, *Streptanthus morrisonii* subsp. *kruckebergii*. The presence or absence of variation at the PGM3 locus distinguishes the other subspecies of *Streptanthus morrisonii* from *S. brachiatus*, with *S. morrisonii* being monomorphic. *Streptanthus morrisonii* subsp. *kruckebergii* has a high-frequency, taxon-specific allele at the PGM3 locus (*Pgm3a*).

Values for pairwise comparisons of Nei's unbiased genetic identity [corrected for small sample size (Nei 1978)] for all populations are presented in Table 4. The mean genetic identity for pairwise comparisons of all sites is 0.874. *Streptanthus morrisonii* subsp. *elatus* and subsp. *morrisonii* have a genetic identity of 0.927. Both

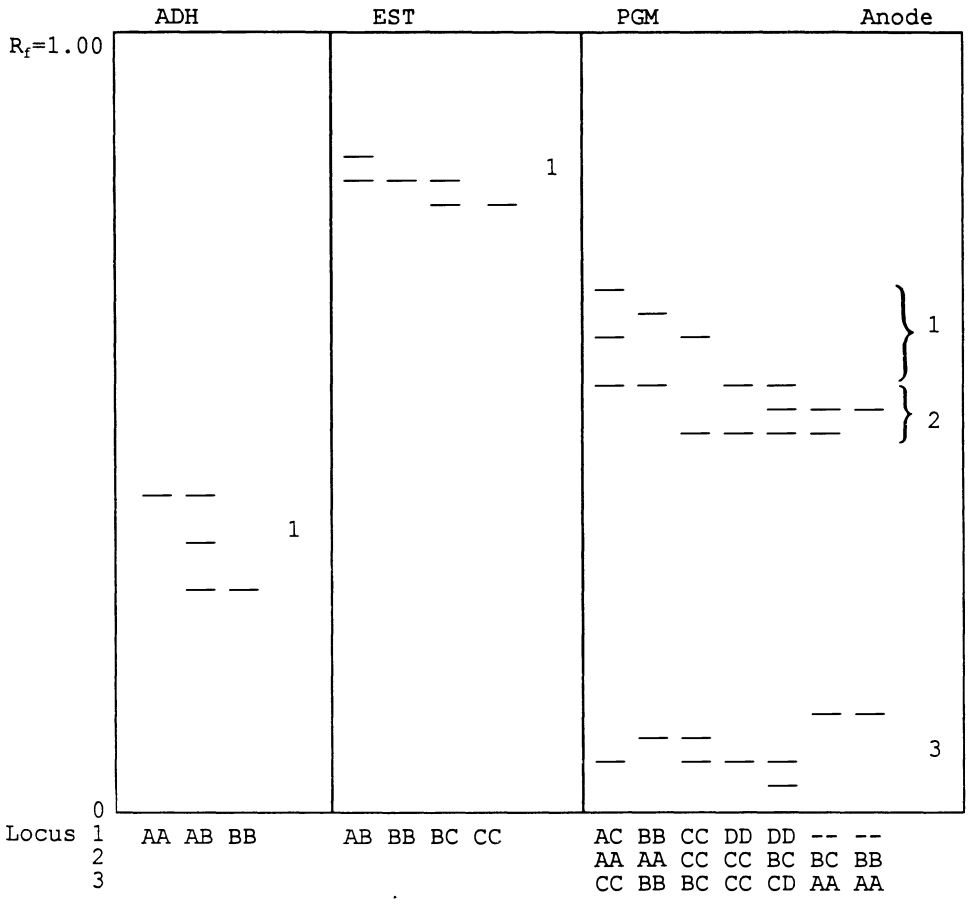

FIG. 2. Schematic diagram of representative banding patterns in the polymorphic enzyme systems studied in the *Streptanthus morrisonii* complex. Capital letter designations at bottom of Fig. are presumed genotypes for banding patterns in each lane. The slowest band of PGM1 (D) comigrates with the fastest band (A) of PGM2.

are less similar to *S. brachiatus* (0.831 and 0.886 respectively). Table 4 further reveals a high similarity between the subspecies of *S. brachiatus* and between the morphologically distinct subsamples of *S. morrisonii* subsp. *hoffmanii*. In fact, the three subsamples have an average genetic identity value of 0.934. *Streptanthus morrisonii* subsp. *kruckebergii* is the most dissimilar of all studied, averaging a genetic identity of 0.726 with the other two subspecies of *S. morrisonii*, and perhaps surprisingly, 0.833 with the samples of *S. brachiatus*.

Figure 3 is a cluster diagram (generated by the UPGMA method; Sneath and Sokal 1973) that graphically summarizes the overall genetic similarity of populations, using the pairwise genetic identity values. The first branch in the dendrogram separates *S. morrisonii* subsp. *kruckebergii* from the other sites and taxa, indicating that it is the most genetically distinct. The second branch separates the other two *Streptanthus morrisonii* subspecies from *S. brachiatus*. SBH-1 and SBH-2 subsamples of *S. brachiatus* subsp. *hoffmanii* cluster together and more closely to *S. brachiatus* subsp. *brachiatus* than does subsample SBH-3.

Within-population measures of total genetic variation show subspecies of *S. morrisonii* to have levels of variation similar to or lower than the levels reported by Hamrick et al. (1991) in their review of endemic plants (Table 5). The values for *S. morrisonii* taxa may be biased, however, by the small number of plants surveyed. Values for average heterozygosity per locus and per-

TABLE 3. Allele frequencies at polymorphic loci for plants of the *Streptanthus morrisonii* complex ($N = 10$ for all taxa except *S. morrisonii hirtiflorus* where $N = 2$). Complete taxon names are provided in the text and Table 1. Abbreviated taxon names are explained in Table 1. SBH populations 1, 2, and 3 are explained in Materials and Methods.

Locus	Allele	Taxon/Population							
		SMM	SMH	SME	SMK	SBB	SBH-1	SBH-2	SBH-3
Pgm1	*a*	—	—	—	—	0.05	—	—	—
	b	—	—	—	—	0.25	0.30	0.20	0.30
	c	—	—	—	—	0.50	0.10	0.20	0.35
	d	1.00	1.00	1.00	—	0.20	0.60	0.60	0.35
Pgm2	*a*	—	—	—	—	0.40	0.30	0.35	0.10
	b	0.05	—	0.15	0.85	0.35	0.30	0.55	0.85
	c	0.95	—	0.85	0.15	0.25	0.40	0.10	0.05
Pgm3	*a*	—	—	—	0.90	—	—	—	—
	b	—	—	—	—	0.45	0.55	0.70	0.95
	c	0.95	1.00	1.00	0.10	0.55	0.45	0.30	0.05
	d	0.05	—	—	—	—	—	—	—
Est	*a*	—	—	—	0.50	—	—	—	—
	b	0.20	0.50	1.00	0.50	0.80	0.80	0.90	0.45
	c	0.80	0.50	—	—	0.20	0.20	0.10	0.55
Adh	*a*	—	—	—	—	0.05	0.10	0.30	—
	b	1.00	1.00	1.00	1.00	0.95	0.90	0.70	1.00

cent of loci polymorphic for subspecies of *S. brachiatus* are greater than average reported values, but fall within the range previously reported (Hamrick et al. 1979). Average number of alleles per locus are lower than those generally reported for endemic plants.

Numbers of individuals found during field surveys for each taxon/population were comparable to numbers reported by Hoffman (1952) (Table 2), although numbers fluctuate from year to year and place to place within the barrens. Exact numbers are difficult to determine because of the cryptic coloring of the rosette leaves in non-flowering plants.

DISCUSSION

The cluster analysis (Fig. 3) places two subspecies of *Streptanthus morrisonii* (*S. morrisonii* subsp. *morrisonii* and *S. morrisonii* subsp. *elatus*) together, separate from the subspecies of *S. brachiatus* that appear together in a different cluster. This result agrees with findings based on profiles of glucosinolates (mustard oil glucosides) in seeds (Rodman et al. 1981), that showed *S. brachiatus* and *S. morrisonii* to be distinct and detected intraspecific variation in *S. morrisonii*, corresponding to described subspecies.

The cluster diagram further shows two relationships that are at variance with taxonomy based on morphology: the relationship of the two subspecies of *S. brachiatus* to each other and the relationship of *S. morrisonii* subsp. *kruckebergii* to other members of the complex. *Streptanthus brachiatus* subsp. *brachiatus* is placed in the cluster analysis within the range of variation found in *S. brachiatus* subsp. *hoffmanii*, indicating that these two taxa may be a single, morphologically variable taxon.

Streptanthus morrisonii subsp. *kruckebergii* is the most genetically distinct taxon studied. Pairwise genetic identity values (Table 4) show greater identity between *S.* morrisonii subsp. *kruckebergii* and *S. brachiatus* than between *S. morrisonii* subsp. *kruckebergii* and other *S. morrisonii* taxa. *Streptanthus morrisonii* subsp. *krucke-*

TABLE 4. Nei's unbiased genetic identity (Nei 1978) values for pairwise comparison of members of the *Streptanthus morrisonii* complex. Abbreviated taxon names are explained in Table 1. SBH populations 1, 2, and 3 are explained in Materials and Methods.

	SMM	SME	SMK	SBB	SBH-1	SBH-2
SME	0.927	—	—	—	—	—
SMK	0.701	0.751	—	—	—	—
SBB	0.831	0.886	0.843	—	—	—
SBH-1	0.883	0.934	0.821	0.989	—	—
SBH-2	0.790	0.869	0.826	0.973	0.993	—
SBH-3	0.686	0.861	0.843	0.944	0.919	0.896

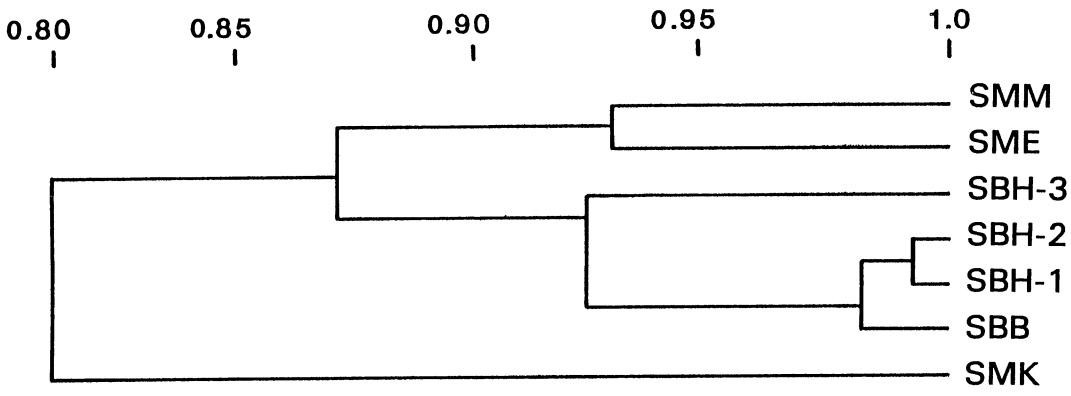

FIG. 3. Cluster diagram based on Nei's (1978) unbiased genetic identity values generated by the UPGMA method (Sneath and Sokol 1973); cophenetic correlation coefficient = 0.88.

bergii also lacks the PGM duplication present in all the other taxa in the species complex.

Gene duplication is likely a conservative trait and has been used to establish lineages in other plant groups (e.g., Gottlieb and Weeden 1979). Mayer et al. (1994) found evidence of gene duplication in nine of 13 enzymes in members of the *S. glandulosus* complex. They attributed this high frequency to ancient polyploidy. The relatively high chromosome number ($n = 14$) in the complex compared to the family as a whole is presented as further evidence. The significance of the duplication to an understanding of phylogeny and relatedness in the *Streptanthus morrisonii* cannot be determined from this limited study, but, taken with the pairwise genetic identity data, it may indicate that *Streptanthus morrisonii* subsp. *kruckebergii* should be recognized as a separate species and that the sect. *Biennes* may not be monophyletic.

Pairwise genetic identity values (Table 4) for all members of the complex except *S. morrisonii* subsp. *kruckebergii* are relatively high [Crawford (1990) reported a mean genetic identity of 0.90 in a review of studies of conspecific populations], indicating little genetic divergence among the taxa, despite the morphological differences present. High genetic identity values have also been reported for members of the *Streptanthus glandulosus* complex (Mayer et al. 1994).

Several factors may account for the discrepancy between taxonomic relationships revealed by the current study and past treatments of the *S. morrisonii* complex based on morphology. The relatively small sample sizes of numbers of individuals tested and loci surveyed in the current study may not be adequate to reflect true relationships in the group. However, non-absolute congruence of morphological and allozyme data have been previously reported for both rare and common plants (for reviews see Hamrick 1989; Crawford 1990). It has been postulated that this lack of congruence is characteristic of species undergoing unusual or rapid evolution (Schaal et al. 1991). In a study of adaptive radiation in Hawaiian Islands' *Bidens* L., Helenurm and Ganders (1985) found relatedness based on isozyme analysis that transgressed subspecific boundaries based on morphology but that was highly correlated with geographic distance between the islands on which different subspecies were found. They

TABLE 5. Estimates of genetic variation in the *Streptanthus morrisonii* complex. Abbreviated taxon names are explained in Table 1.

Taxon	Average heterozygosity per locus	Average number alleles/locus	% loci PM
SMM	0.060	1.33	33.3
SME	0.030	1.11	11.1
SMK	0.109	1.33	33.3
SBB	0.258	1.89	55.6
SBH	0.229	1.74	51.8
Average values for narrowly endemic plants (Hamrick et al. 1991)	0.063	2.48	26.0

proposed that speciation occurred through a stepping-stone process across the islands, that the adaptive radiation of subspecies may be limited to only a few genes controlling morphological and ecological traits, and that genetic differentiation at isozyme loci has not occurred at the same rate. If evolution in the *Streptanthus morrisonii* complex has followed a stepping-stone pattern across available outcrop habitat "islands," it may be significant that this taxon is the most disjunct to the east. However, see Mayer et al. (1994) for a discussion of important caveats when comparing models of speciation on serpentine habitat islands with island archipelagos.

Lack of congruence between morphological and genetic data may be especially characteristic of *Streptanthus*. In studies of subspecies in the *Streptanthus glandulosus* complex, Kruckeberg (1956) determined that relatedness based on interfertility of hybrids was more closely correlated to geographic distance between outcrops of origin than to subspecific designation based on morphology, perhaps a finding similar to that in *Bidens*. More recently, Mayer et al. (1994) and Mayer and Soltis (1994) examined members of the *S. glandulosus* species complex using isozymes and analysis of chloroplast DNA phylogeny. They again identified geographically structured groups that sometimes included neighboring populations of different taxa, with genetic distance between two populations correlated with geographic distance between the populations.

Taxa in the *Streptanthus morrisonii* complex meet the criteria of 'narrow endemics' in the classification scheme of rarity developed by Kruckeberg and Rabinowitz (1985); they are low in numbers and are of limited geographic distribution, restricted to single serpentine outcrops or a limited range of adjacent outcrops. The serpentine outcrop habitat on which they depend is unsuitable for building or agriculture but has historically been mined for mercury, chromite, and other metals. Current short-term threats to outcrop sites include off-road vehicles, gold mining, and development activities related to geothermal energy production. With its small numbers of individuals, *S. morrisonii* subsp. *hirtiflorus* is at risk of extinction through the action of stochastic demographic events. Long-term threats may include conversion of outcrop rock to serpentine-derived soil during the course of succession with subsequent invasion of chaparral vegetation; members of the complex do not grow in dense chaparral.

Several authors have recently called for the preservation of all known populations for some rare plants with limited distributions (Lesica et al. 1988; Hickey et al. 1991). Such a conservation strategy is needed for members of the *Streptanthus morrisonii* complex. Isozyme analysis shows the complex is not genetically depauperate and may be undergoing rapid speciation, worthy features for conservation efforts.

ACKNOWLEDGMENTS. This work was supported by Contract No. YA551-CT4-340080 between the U.S. Department of the Interior, Bureau of Land Management and Tierra Madre Consultants of Riverside, CA. I extend special thanks to Dr. Norm Ellstrand and Janet Clegg for assistance with electrophoresis, to John Hutchinson for lab assistance, and to Holcomb Research Institute, Butler University, for technical support. Dr. Lawrence LaPré, Tierra Madre Consultants, performed most of the field work on this project. Arthur Kruckeberg and Jim Bartel provided helpful comments on early drafts of the manuscript. The Associate Editor and two anonymous reviewers greatly improved the current text.

LITERATURE CITED

BROWN, A. H. D. and J. D. BRIGGS. 1991. Sampling strategies for genetic variation in *Ex Situ* collections of endangered species. Pp. 99–122 in *Genetics and conservation of rare plants*, eds. D. A. Falk and K. E. Holsinger. New York: Oxford Univ. Press.

CRAWFORD, D. J. 1990. *Plant molecular systematics*. New York: John Wiley and Sons.

DOLAN, R. W. 1991. Cooperation between developers, regulators, and the federal government to resolve taxonomic status of rare plants: a case history. Natural Areas Journal 11: 168.

——— and L. F. LAPRÉ. 1989. Taxonomy of *Streptanthus* Sect. *Biennes*, the *Streptanthus morrisonii* complex (Brassicaceae). Madroño 36: 33–40.

ELLSTRAND, N. C. 1984. Multiple paternity within the fruits of the wild radish, *Raphanus sativus*. American Naturalist 123: 819–828.

FALK, D. A. 1991. Joining biological and economic models for conserving plant genetic diversity. Pp. 209–224 in *Genetics and conservation of rare plants*, eds. D. A. Falk and K. E. Holsinger. New York: Oxford Univ. Press.

——— and K. E. HOLSINGER. 1991. *Genetics and conservation of rare plants*. New York: Oxford Univ. Press.

GOTTLIEB L. D. and N. F. WEEDEN. 1979. Gene du-

plication and phylogeny in *Clarkia*. Evolution 33: 1024–1039.

HAMRICK, J. L. 1989. Isozymes and analysis of genetic structure of plant populations. Pp. 87–105 in *Isozymes in plant biology*, eds. D.E. Soltis and P.S. Soltis. Portland, Oregon: Dioscorides Press.

———, M. J. W. GODT, D. A. MURAWSKI, and M. D. LOVELESS. 1991. Correlations between species traits and allozyme diversity: implications for conservation biology. Pp. 76–86 in *Genetics and conservation of rare plants*, eds. D. A. Falk and K. E. Holsinger. New York: Oxford Univ. Press.

———, Y. LINHART, and J. B. MINTON. 1979. Relationships between life history characteristics and electrophoretically detectable genetic variation in plants. Annual Review of Systematics and Ecology 10: 173–200.

HELENURM, K. and F. GANDERS. 1985. Adaptive radiation and genetic differentiation in Hawaiian *Bidens*. Evolution 39: 753–765.

HEYWOOD, J. S. 1980. Genetic correlates of edaphic differentiation and endemism in *Gaillardia*. Ph.D. dissertation, Univiversity of Texas, Austin.

HICKEY, R. J., M. A. VINCENT, and S. I. GUTTMAN. 1991. Genetic variation in running buffalo clover (*Trifolium stoloniferum*, Fabaceae). Conservation Biology 5: 309–316.

HOFFMAN, F. W. 1952. Studies in *Streptanthus*: A new *Streptanthus* complex in California. Madroño 11: 221–233.

KEPHART, S. R. 1990. Starch gel electrophoresis of plant isozymes: a comparative analysis of techniques. American Journal of Botany 77: 693–712.

KRUCKEBERG, A. R. 1956. Variability in fertility of hybrids between isolated populations of the serpentine species, *Streptanthus glandulosus* Hook. Evolution 11: 185–211.

———. 1958. The taxonomy of the species complex *Streptanthus glandulosus* Hook. Madroño 14: 217–227.

——— and J. L. MORRISON. 1983. New *Streptanthus* taxa (Cruciferae) from California. Madroño 30: 230–244.

——— and D. RABINOWITZ. 1985. Biological aspects of endemism in higher plants. Annual Review of Ecology and Systematics 16: 447–479.

LESICA, P., R. F. LEARY, F. W. ALLENDORF, and D. E. BILDERBACK. 1988. Lack of genetic diversity within and among populations of an endangered plant, *Howellia aquatilis*. Conservation Biology 2: 275–282.

MARSHALL D. R. and A. H. D. BROWN. 1975. Optimum sampling strategies in genetic conservation. Pp. 53–80 in *Crop genetic resources for today and tomorrow*, eds. O. H. Frankel and J. G. Hawkes. Cambridge: Cambridge Univ. Press.

MAYER, M. S. and P. S. SOLTIS. 1994. The evolution of serpentine endemics: a chloroplast DNA phylogeny of the *Streptanthus glandulosus* complex (Cruciferae). Systematic Botany: 19: 557–574.

MAYER, M. S., P. S. SOLTIS, and D. E. SOLTIS. 1994. The evolution of the *Streptanthus glandulosus* complex (Cruciferae): genetic divergence and gene flow in serpentine endemics. American Journal of Botany 81: 1288–1299.

MORRISON, J. L. 1941. A monograph of the section *Euclisia* Nutt., of *Streptanthus* Nutt. Ph.D. dissertation, University of California, Berkeley.

NEI, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583–590.

RODMAN, J. E., A. R. KRUCKEBERG, and I. A. AL-SHEHBAZ. 1981. Chemotaxonomic diversity and complexity in seed glucosinolates in *Caulanthus* and *Streptanthus* (Cruciferae). Systematic Botany 6: 197–222.

SCANDALIOS, J. G. 1969. Genetic control of multiple molecular forms of enzymes in plants: a review. Biochemical Genetics 3: 37–79.

SCHAAL, B. A., W. J. LEVERICH, and S. H. ROGSTAD. 1991. Comparison of methods for assessing genetic variation in plant conservation biology. Pp. 123–134 in *Genetics and conservation of rare plants*, eds. D. A. Falk and K. E. Holsinger. New York: Oxford Univ. Press.

SHAW, C. R. and R. PRASAD. 1970. Starch gel electrophoresis of enzymes—a compilation of recipes. Biochemical Genetics 4: 297–320.

SNEATH, P. A. and R. R. SOKAL. 1973. *Numerical taxonomy*. San Francisco: W. H. Freeman and Co.

SOLTIS, D. E., C. H. HAUFLER, D. C. DARROW, and G. J. GASTONY. 1983. Starch gel electrophoresis of ferns: A compilation of grinding buffers, gel and electrode buffers, and staining schedules. American Fern Journal 73: 9–27.