BIOLOGICAL AND HISTORICAL FACTORS INFLUENCING GENETIC DIVERSITY IN THE *SCUTELLARIA ANGUSTIFOLIA* COMPLEX (LABIATAE)

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Abstract.—Studies of genetic diversity at isozyme loci were used to examine the phylogenetic distribution of several frequently reported population-genetic parameters in a putatively monophyletic group of plant species, the *Scutellaria angustifolia* complex. The influence of taxon-specific differences in habitat preference, breeding system, degree of endemism, and phylogenetic relatedness was examined. Many characters of reproductive morphology traditionally used in phylogenetic inference vary with breeding system. To the extent that reproductive systems are conservative markers of phylogenetic relationships, one would expect the distribution of genetic variation to be similar in closely related taxa. Results showed that closely related taxa may exhibit very different genetic-diversity statistics and that distantly related taxa may exhibit very similar genetic-diversity statistics. This suggests that complex patterns of evolution of breeding systems and morphological characters have occurred in the ten taxa included in the *Scutellaria angustifolia* complex. Similarity in habitat is not associated with similarity in genetic diversity in this group of species.

Relatively little is known about the genetic structure of entire clades (i.e., monophyletic assemblages of species) and what factors result in differences that are observed in genetic structure among species within a clade. Most studies of genetic structure in plant populations and species have been conducted on single species (Gottlieb, 1974; Hiebert and Hamrick, 1983; Wendel and Parks, 1985; Soltis and Soltis, 1987) or pairs of closely related species for which a particular relationship is postulated: progenitor/derivative (Gottlieb, 1973; Crawford and Smith, 1982*a*; Gottlieb et al., 1985), outcrosser/selfer (Brown and Jain, 1979; Gottlieb, 1984), diploid/polyploid (Crawford and Smith, 1984; Bayer and Crawford, 1986), or sister species (Crawford and Smith, 1982*b*; Layton and Ganders, 1984; Rieseberg and Soltis, 1987). Knowledge of genetic variability in rare or endemic species is important for conservation genetics; consequently, species with restricted distributions have been studied genetically, in some cases in conjunction with more widespread sister species (Schonewald-Cox et al., 1983; Karron, 1987). Many reviews have emphasized breeding systems or ecological determinants in relation to genetic structure of

populations and species (Gottlieb, 1981; Hamrick et al., 1979; Nevo et al., 1984; Loveless and Hamrick, 1984).

The relative importance of variation in habitat type, reproductive biology, extent of geographic distribution, and phylogenetic relatedness to the differences in genetic structure among plant species can be studied best in a monophyletic species group in which variation exists for all of these potential influencing factors. By studying individual species or pairs of sister species, the relative importance of these variables remains obscure. Phylogenetic groups of plant species that have been studied genetically often represent special cases. Species-groups restricted to oceanic islands tend to be genetically homogeneous and little differentiated (Lowrey and Crawford, 1985; Helenurm and Ganders, 1985; Crawford et al., 1987). Mainland species-groups that have been examined electrophoretically have consisted primarily of species that are ecologically and reproductively similar (Crawford and Wilson, 1979; Bruederle and Fairbrothers, 1986; Manos and Fairbrothers, 1987), so that the relative importance of ecology, reproductive biology, and phylogenetic history cannot be interpreted.

This paper presents the results of an electrophoretic study of the genetic diversity and population structure in the *Scutellaria angustifolia* complex, a putatively monophy-

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letic group of ten taxa native to western North America (Table 1). Variation in breeding system, habitat specificity, and degree of endemism among the taxa provides the opportunity to examine the effect of these three factors on the extent and distribution of genetic diversity within and among species of the group. An analysis of phylogenetic relationships within the group (Olmstead, 1989) also enables one to examine the genetic variability among the ten taxa within a phylogenetic context to determine whether similarity in levels of genetic diversity is associated with phylogenetic relatedness.

Plants in the *S. angustifolia* complex are herbaceous perennials occurring in small, widely scattered populations. Taxa in the group have a wide range of habitat specificities (Table 1), from wet streamside habitats to sagebrush desert and chaparral. Geographic distributions vary from taxa that are widespread throughout California or the Great Basin to narrowly restricted taxa in each of the two regions. Variation in corolla size among taxa in the complex is associated with differences in the amount of autogamous seed set (Olmstead, 1988): taxa with small flowers exhibit a high degree of autogamous seed set, whereas the large-flowered taxa exhibit essentially none, suggesting that natural populations of these taxa differ markedly in the degree of selfing and outcrossing. The small isolated nature of the populations in the complex and the lack of any apparent long-distance seed-dispersal mechanism suggest that the taxa in the group are characterized by small effective population sizes with very limited gene flow among populations. All taxa are diploid with $2n = 24$ or $2n = 22$ chromosomes.

MATERIALS AND METHODS

Population Sampling.—Plants sampled for the isozyme studies were collected as rhizomes from a total of 106 populations throughout the distribution of the *Scutellaria angustifolia* complex in western North America (Fig. 1, Appendix) and grown in the greenhouse at the University of Washington. Rhizomes were sampled so as to minimize collecting clonal replicates; 5–20 individuals were sampled from each population, except for populations in which the small population size limited the possible sample size. The large number of populations sampled (relative to most studies of plant genetic diversity) and the relatively small average sample size represent a trade-off designed to make feasible a study of ten taxa composed of small isolated populations throughout a large geographic range. All population samples for each taxon (Table 1) are used in subsequent analyses of population-genetic statistics, except where otherwise noted. Vouchers for all populations are deposited in the herbarium at the University of Washington.

Electrophoretic Analysis.—Starch-gel electrophoresis was performed using young leaves and stem apexes. The extraction buffer was 0.1 M tris-HCl, pH 7.5, 0.001 M EDTA, 0.01 M KCl, 0.01 M MgCl, 8% (wt./vol.) PVP 40,000, with 0.1% (vol./vol.) 2-mercaptoethanol added just before beginning the extraction (Soltis et al., 1983). Filter-paper wicks were soaked in the extracts and inserted into 12.5% starch gels. Three buffer systems were used to resolve nine enzyme systems. Aspartate amino transferase (AAT), fluorescent esterase (FE), phosphoglucose isomerase (PGI), and triose phosphate isomerase (TPI) were resolved using a lithium–borate buffer system: gel buffer = 0.004 M LiOH, 0.029 M boric acid, 0.033 M tris, and 0.005 M citric acid, pH 8.0; electrode buffer = 0.039 M LiOH and 0.263 M boric acid, pH 8.0 (modification of number 8 of Soltis et al. [1983]). Aconitase (ACN), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), phosphoglucose isomerase (PGI), and phosphoglucomutase (PGM) were resolved on a continuous histidine–citric-acid buffer system: gel buffer = 0.009 M L-histidine, 0.002 M citric acid, pH 6.0; electrode buffer = 0.065 M L-histidine, 0.016 M citric acid, pH 6.0 (number 9 of Soltis et al. [1983]). Shikimate dehydrogenase (SkDH) was resolved on a discontinuous buffer system: gel buffer = 0.02 M histidine–HCl, pH 7.0; electrode buffer = 0.4 M citric acid, trisodium salt, pH 7.0 (number 1 of Soltis et al. [1983]). Gels were stained according to the procedures of Soltis et al. (1983). For each enzyme, gene loci and isozymes were labelled 1, 2, 3, etc., and for each locus, alleles and allozymes were labeled a, b, c, etc., begin-
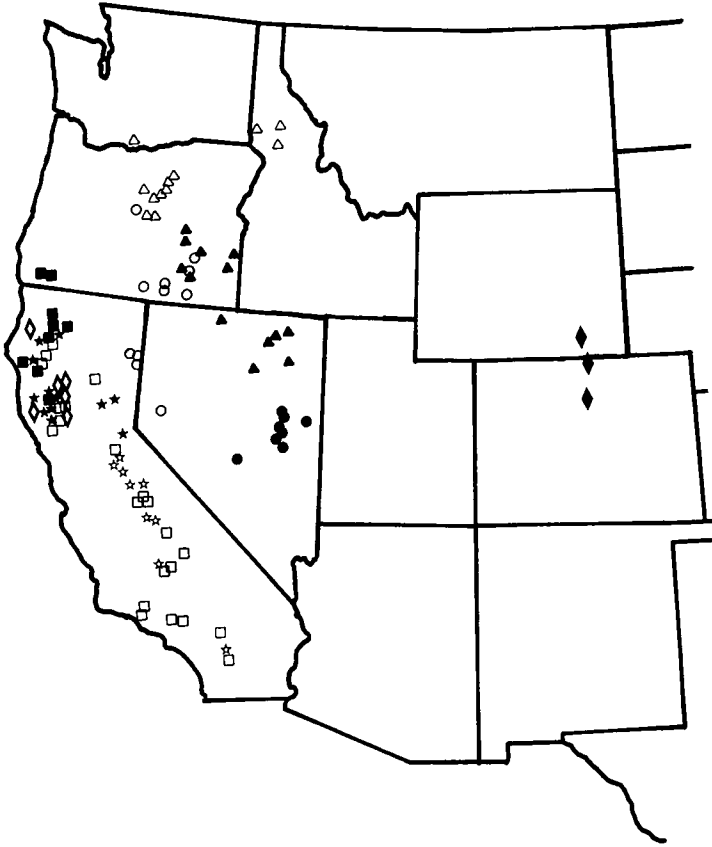
Fig. 1. Distribution of the 106 populations sampled for the electrophoretic analysis of the *Scutellaria angustifolia* complex. For locality information, see Appendix. Symbols: △ = *S. angustifolia angustifolia*, ▲ = *S. angustifolia micrantha*, ■ = *S. antirrhinoides*, ☆ = *S. bolanderi*, ◆ = *S. brittonii*, ★ = *S. californica*, ○ = *S. nana*, ● = *S. sapphirina*, □ = *S. siphocampyloides*, ◇ = *S. tuberosa*.

ning with the most-anodally migrating bands.

Data Analysis.—Data consisted of allozyme genotypes for each individual for all loci sampled. Genetic-variability statistics including allele frequency, number of alleles per locus, percentage of polymorphic loci, percentage heterozygosity, hierarchical F statistics for the apportionment of genetic diversity (Nei, 1973), and genetic identity (Nei, 1978) were calculated using BIO-SYS-1 (Swofford and Selander, 1981). The effective number of alleles (n_e) was calculated following Kimura and Crow (1964):

$$n_e = \frac{1}{\sum\limits_{i=1}^{n} \hat{p}^2}$$

where n is the number of alleles detected

and p is the allele frequency. Wright's (1951) fixation index, F, is a function of observed and expected heterozygosities: $F = (H_e - H_o)/H_e$. F was calculated only for populations with sample sizes of eight or greater and with two or more polymorphic loci. Within-population statistics and hierarchical F statistics were calculated only for population samples with five or more individuals.

RESULTS

Nine enzymes encoded by 18 gene loci provided consistently interpretable results for all populations (Table 2). Several additional loci were not included because they could not be resolved uniformly in all populations (*Fe-2*, *Lap-1*, and *Pgi-1*) or could not be interpreted readily due to overlap-

TABLE 1. Number of populations sampled, distribution, habitat, and breeding system for each of the ten taxa in the *Scutellaria angustifolia* complex.

Taxon	Number of populations sampled	Distribution	Habitat	Breeding system
S. angustifolia Pursh ssp. *angustifolia*	12	eastern WA, OR, and adjacent ID	ponderosa pine woodland; basalt derived substrate	long-flowered; outcrossing
S. angustifolia Pursh ssp. *micrantha* Olmstead	13	northern Great Basin (OR, NV, and ID)	pinyon/juniper, sagebrush; basalt substrate	short-flowered; selfing
S. antirrhinoides Benth.	9	northern CA and adjacent OR	openings in mixed conifer woodlands; various substrates	short-flowered; selfing
S. bolanderi Gray	10	CA; Sierra Nevada foothills; southern CA mountains	pine/oak woodlands; streamside gravel	short-flowered; some selfing
S. brittonii Porter	3	Rocky Mt. front range (WY, CO, and NM)	ponderosa pine woodland; granite substrate	long-flowered; outcrossing
S. californica Gray	12	CA; North Coast Range; northern Sierra Nevada	mixed conifer/oak woodland; various substrates	short-flowered (white); outcrossing
S. nana Gray	11	northern Great Basin (CA, NV, OR, and ID)	sagebrush desert; basalt substrate	short-flowered (white); outcrossing
S. sapphirina (Barneby) Olmstead	8	central Nevada	sagebrush desert; on and off basalt	short-flowered; selfing
S. siphocampyloides Vatke	22	CA; Sierra foothills and Coast ranges	mixed conifer and oak woodlands; various substrates	long-flowered; outcrossing
S. tuberosa Benth.	6	Coast ranges of CA and southern OR	chaparral	short-flowered; some selfing

ping banding patterns between isozymes (*6Pgd-1* and *6Pgd-2*). Apparent duplicate gene loci were observed for the dimeric enzymes IDH (*Idh-1* and *Idh-2*) and MDH (*Mdh-1* and *Mdh-2*). For IDH, the minimum electrophoretic pattern consisted of three bands, whereas for MDH, a consistent pattern of three or more bands was observed for a pair of polymorphic loci; the other MDH loci varied independently. All other enzymes exhibit numbers of loci typically reported for genetically diploid plants (Gottlieb, 1981, 1982).

Allelic Diversity Among Loci. — All 18 isozyme loci were polymorphic in one or more species, when the 99% criterion was applied (Gottlieb, 1981). In all, 97 alleles were detected, with the number of alleles per locus ranging from two alleles for *Mdh-5* to 13 alleles for *Pgi-2* (mean of 5.4 alleles detected

per locus). The number of taxa for which a given locus is polymorphic ranges from one taxon for *Mdh-5* and *Tpi-2* to nine taxa for *Pgi-2* (mean of 4.7 taxa polymorphic per locus). Three of the 18 loci examined (*Mdh-5, Pgm-2,* and *Tpi-2*) have the same allele present at highest frequency in all ten taxa, while two loci (*Pgi-2* and *Skdh*) have as many as six different alleles predominating in different taxa.

The effective number of alleles provides a measure of allelic evenness and equals the observed number of alleles only when all alleles are present in equal frequencies. Fourteen of 18 loci in the *S. angustifolia* complex have an effective number of alleles less than two, indicating that most of the allelic diversity at these loci is in the form of alleles at low frequency, with one allele predominating in most populations. Four

TABLE 2. Allele frequencies for ten taxa of *Scutellaria*. Taxon abbreviations: ANG = *S. angustifolia angustifolia*, MIC = *S. a. micrantha*, ANT = *S. antirrhinoides*, BOL = *S. bolanderi*, BRI = *S. brittonii*, CAL = *S. californica*, NAN = *S. nana*, SAP = *S. sapphirina*, SIP = *S. siphocampyloides*, and TUB = *S. tuberosa* (see Table 1).

| | | Allele frequency | | | | | | | | | | |
| | | Taxon | | | | | | | | | | Mean of all pop- |
Locus	Allele	ANG	MIC	ANT	BOL	BRI	CAL	NAN	SAP	SIP	TUB	ulations
Aat-1	a	0.260	—	—	1.000	—	—	—	—	—	—	0.124
	b	—	—	—	—	—	—	—	1.000	—	—	0.075
	c	0.677	0.962	—	—	—	0.222	1.000	—	0.042	1.000	0.389
	d	0.063	0.038	1.000	—	1.000	0.778	—	—	0.958	—	0.412
Aat-2	a	—	—	0.004	—	—	—	—	—	0.065	—	0.014
	b	—	—	—	—	0.146	—	—	—	—	—	0.004
	c	0.844	1.000	0.977	—	0.854	1.000	0.733	—	0.935	—	0.709
	d	0.156	—	0.019	—	—	—	0.267	1.000	—	1.000	0.179
	e	—	—	—	1.000	—	—	—	—	—	—	0.094
Acn-1	a	0.975	1.000	0.834	0.008	—	0.008	—	—	—	—	0.305
	b	0.025	—	0.166	0.992	1.000	0.964	0.997	1.000	1.000	1.000	0.691
	c	—	—	—	—	—	0.028	0.003	—	—	—	0.004
Acn-2	a	0.237	—	—	—	—	0.101	—	—	—	0.584	0.071
	b	0.763	0.619	1.000	—	1.000	0.893	0.939	1.000	1.000	0.416	0.781
	c	—	—	—	1.000	—	0.006	0.061	—	—	—	0.101
	d	—	0.381	—	—	—	—	—	—	—	—	0.047
Fe-1	a	—	—	—	—	—	0.177	—	—	0.028	—	0.026
	b	0.926	0.919	0.944	1.000	—	0.813	0.444	1.000	0.732	—	0.757
	c	0.074	0.004	0.056	—	1.000	0.010	0.494	—	0.240	1.000	0.201
	d	—	0.077	—	—	—	—	0.062	—	—	—	0.016
Idh-1	a	—	0.019	—	—	—	—	—	—	0.018	—	0.006
	b	0.969	0.981	1.000	1.000	1.000	0.994	1.000	1.000	0.955	—	0.928
	c	0.031	—	—	—	—	—	—	—	0.027	—	0.009
	d	—	—	—	—	—	0.006	—	—	—	1.000	0.057
Idh-2	a	—	—	—	—	—	—	0.042	—	—	—	0.004
	b	—	0.019	—	—	—	—	—	—	—	—	0.002
	c	0.969	0.981	0.994	1.000	1.000	0.979	0.958	1.000	0.955	—	0.921
	d	0.031	—	—	—	—	0.021	—	—	0.045	—	0.015
	e	—	—	—	—	—	—	—	—	—	1.000	0.057
	f	—	—	0.006	—	—	—	—	—	—	—	0.001
Mdh-1	a	0.679	0.661	0.022	—	—	—	—	—	—	—	0.160
	b	—	—	—	—	0.281	—	—	—	—	—	0.008
	c	0.321	0.339	0.619	1.000	0.719	0.912	0.357	—	0.992	—	0.591
	d	—	—	—	—	—	—	—	0.125	—	—	0.009
	e	—	—	0.359	—	—	0.083	0.643	0.875	0.008	—	0.174
	f	—	—	—	—	—	—	—	—	—	1.000	0.057
	g	—	—	—	—	—	0.005	—	—	—	—	0.001
Mdh-2	a	—	—	—	—	0.281	—	—	—	—	—	0.008
	b	1.000	1.000	1.000	0.900	0.719	1.000	0.997	0.973	1.000	—	0.924
	c	—	—	—	—	—	—	—	—	—	1.000	0.057
	d	—	—	—	—	—	—	0.003	0.027	—	—	0.002
	e	—	—	—	0.100	—	—	—	—	—	—	0.009
Mdh-3	a	—	0.057	—	—	—	0.005	—	—	—	—	0.007
	b	1.000	0.866	1.000	0.950	1.000	0.995	0.977	0.977	1.000	—	0.918
	c	—	—	—	—	—	—	—	—	—	1.000	0.057
	d	—	—	—	—	—	—	0.023	0.023	—	—	0.004
	e	—	—	—	0.050	—	—	—	—	—	—	0.005
	f	—	0.077	—	—	—	—	—	—	—	—	0.009
Mdh-4	a	—	—	—	—	—	0.057	—	—	0.023	—	0.011
	b	1.000	1.000	1.000	—	1.000	0.943	1.000	1.000	0.977	—	0.838
	c	—	—	—	1.000	—	—	—	—	—	1.000	0.151

TABLE 2. Continued.

Locus	Allele	Allele frequency										Mean of all populations
		Taxon										
		ANG	MIC	ANT	BOL	BRI	CAL	NAN	SAP	SIP	TUB	
Mdh-5	a	1.000	1.000	1.000	1.000	1.000	1.000	0.979	1.000	1.000	1.000	0.998
	b	—	—	—	—	—	—	0.021	—	—	—	0.002
Pgi-2	a	—	—	—	0.900	—	—	—	—	—	—	0.085
	b	—	0.013	—	—	—	0.051	—	—	0.124	—	0.033
	c	0.096	—	0.734	0.100	—	0.754	—	—	0.800	—	0.334
	d	—	—	—	—	—	—	0.064	—	—	—	0.007
	e	—	—	0.012	—	—	0.108	—	—	0.011	—	0.015
	f	0.820	0.820	0.125	—	—	0.087	0.642	0.008	0.053	—	0.292
	g	0.042	0.167	0.074	—	—	—	0.271	0.992	—	—	0.134
	h	0.042	—	—	—	—	—	0.023	—	—	—	0.007
	i	—	—	—	—	—	—	—	—	0.008	—	0.002
	j	—	—	0.055	—	—	—	—	—	—	1.000	0.061
	k	—	—	—	—	0.665	—	—	—	0.004	—	0.020
	l	—	—	—	—	0.019	—	—	—	—	—	0.001
	m	—	—	—	—	0.316	—	—	—	—	—	0.009
Pgm-1	a	—	—	—	—	0.307	—	0.010	—	—	1.000	0.066
	b	—	—	0.701	—	—	0.008	—	—	—	—	0.060
	c	1.000	1.000	0.287	1.000	0.693	0.624	0.955	—	0.972	—	0.746
	d	—	—	—	—	—	0.087	0.035	1.000	—	—	0.089
	e	—	—	0.012	—	—	0.204	—	—	0.028	—	0.030
	f	—	—	—	—	—	0.060	—	—	—	—	0.007
	g	—	—	—	—	—	0.017	—	—	—	—	0.002
Pgm-2	a	0.025	—	—	—	—	0.010	—	—	—	—	0.004
	b	0.010	0.003	0.006	—	—	0.007	0.123	0.076	0.021	—	0.026
	c	0.923	0.976	0.905	1.000	1.000	0.973	0.849	0.924	0.914	0.897	0.932
	d	—	—	—	—	—	—	—	—	—	0.028	0.002
	e	—	0.021	—	—	—	—	—	—	—	—	0.003
	f	0.042	—	—	—	—	0.010	0.028	—	0.065	0.075	0.026
	g	—	—	0.089	—	—	—	—	—	—	—	0.007
Skdh	a	—	—	0.022	—	—	0.015	—	—	—	—	0.004
	b	—	—	0.846	—	—	0.418	—	—	0.700	—	0.264
	c	0.016	—	0.091	—	—	0.518	—	—	0.099	—	0.089
	d	0.984	0.981	0.041	—	—	—	—	—	0.201	—	0.277
	e	—	0.019	—	—	—	0.049	0.096	—	—	1.000	0.074
	f	—	—	—	—	1.000	—	—	1.000	—	—	0.104
	g	—	—	—	1.000	—	—	0.904	—	—	—	0.188
Tpi-1	a	—	—	—	—	—	—	0.045	—	0.045	—	0.014
	b	—	—	—	0.300	—	—	—	—	—	—	0.028
	c	—	—	—	—	—	—	—	—	—	1.000	0.057
	d	1.000	1.000	0.995	0.700	0.907	0.579	0.934	0.966	0.947	—	0.844
	e	—	—	0.005	—	—	0.421	0.021	0.034	—	—	0.053
	f	—	—	—	—	0.093	—	—	—	—	—	0.002
	g	—	—	—	—	—	—	—	—	0.008	—	0.002
Tpi-2	a	1.000	1.000	0.970	1.000	1.000	1.000	1.000	1.000	0.998	1.000	0.997
	b	—	—	—	—	—	—	—	—	0.002	—	0.001
	c	—	—	0.030	—	—	—	—	—	—	—	0.002
Number of unique alleles:			0	4	3	5	7	3	3	2	3	6

TABLE 3. Summary of genetic variability in ten taxa of *Scutellaria*: total number of alleles per taxon (A_t), mean number of alleles per locus (A), mean number of alleles per polymorphic locus (A_p), effective number of alleles (n_e), percentage of loci polymorphic per taxon (P_S; 99% criterion), mean percentage of loci polymorphic per population (P_p; 99% criterion), observed heterozygosity (H_o), expected heterozygosity (H_e), Wright's fixation index (F), with the number of populations for which F is calculated (N) and the standard deviation of F.

| | | | | | | | | | Wright's fixation index | | |
Taxon	A_t	A	A_p	n_e	P_s	P_p	H_o	H_e	F	N	SD
S. angustifolia	34	1.89	2.45	1.20	61.11	18.06	0.088	0.078	0.018	5	0.465
S. a. micrantha	32	1.78	2.40	1.16	55.56	6.81	0.022	0.029	0.631	4	0.380
S. antirrhinoides	38	2.11	2.90	1.21	55.56	19.84	0.067	0.073	0.319	6	0.299
S. bolanderi	23	1.28	2.00	1.07	22.22	8.35	0.030	0.023	—	0	—
S. brittonii	25	1.39	2.17	1.19	33.33	20.37	0.064	0.094	0.042	3	0.552
S. californica	46	2.56	3.17	1.33	66.67	31.94	0.114	0.125	0.071	8	0.164
S. nana	38	2.11	2.50	1.27	66.67	31.73	0.106	0.123	0.138	6	0.237
S. sapphirina	24	1.33	2.00	1.04	27.78	7.80	0.020	0.021	0.035	4	0.368
S. siphocampyloides	40	2.22	2.82	1.16	61.11	11.12	0.046	0.043	−0.024	7	0.148
S. tuberosa	21	1.17	2.50	1.07	11.11	7.43	0.052	0.031	−0.330	2	0.330
Overall:	32.1	1.78	2.79	1.17	46.11	17.01	0.064	0.067	0.119	45	

loci (*Aat-1, Mdh-1, Pgi-2,* and *Skdh*) have effective numbers of alleles ranging from 2.45 to 4.85, indicating a broader distribution of genetic diversity.

Genetic Variability Among Taxa.—The total number of alleles detected per taxon (A_t) ranges from 21 (1.17 alleles per locus) in *S. tuberosa* to 46 (2.56 alleles per locus) in *S. californica.* The mean number of alleles per polymorphic locus ranges from the minimum possible of 2.0 for *S. bolanderi* and *S. sapphirina* to 3.17 for *S. californica.* The mean effective number of alleles per locus for each taxon ranges from 1.04 for *S. sapphirina* and 1.07 in *S. tuberosa* and *S. bolanderi* to 1.33 in *S. californica* (Table 3). The mean percentage of loci polymorphic per population (P_p) for the entire group is 17.0 (Table 3). The range of mean values for P_p for individual taxa varies from 6.81% for *S. angustifolia micrantha* to 31.94% for *S. californica.* The mean percentage of loci polymorphic at the species or subspecies level (P_s) for all taxa is 46.1, with values for individual taxa ranging from 11% for *S. tuberosa* to 67% for *S. californica* and *S. nana* (Table 3). The mean observed heterozygosity (H_o) for all populations is 0.064. Mean values for taxa in the complex vary more than fivefold from 0.020 for *S. sapphirina* to 0.114 for *S. californica.* Mean expected heterozygosity estimates (H_e) vary similarly from 0.021 for *S. sapphirina* to 0.125 for *S. californica.*

Comparing values of Wright's fixation index (F) between populations or taxa provides a relative measure of the degree of inbreeding that may result from differences in breeding system or from population subdivision. A value of zero signifies random mating. The mean F value for all populations considered is 0.119. Values of F for taxa in the *S. angustifolia* complex range from −0.330 for *S. tuberosa* to 0.631 for *S. angustifolia micrantha* (Table 3). Since the error resulting from the sampling of clonally related individuals within a population sample is likely to lower the estimate of H_e relative to H_o, many F values reported here are likely to underestimate true values of F. Therefore, negative values of F probably do not represent selection favoring heterozygotes or the result of negative assortative mating. Positive values of F may result from partial selfing and from substructuring of the population due to nonrandom dispersal of seeds and pollen (Levin and Kerster, 1974) and subsequent increases in consanguineous matings or from matings between genetically identical clonal replicates.

Genetic Differentiation.—Genetic-diversity analysis by means of hierarchical F statistics can be used to assess genetic differentiation among a complex of species descended from a common ancestor (Wright, 1965, 1978; Nei, 1973). For the analysis of the *S. angustifolia* complex, three hierarchical categories were defined: popu-

TABLE 4. Summary of genetic diversity (Nei, 1973) and differentiation at all loci among taxa in the *Scutellaria angustifolia* complex: total genetic diversity (H_t), population-level genetic diversity (H_p), population differentiation (D_{ps}), species-level (or subspecies-level) genetic diversity (H_s), species differentiation (D_{st}), and apportionment of genetic diversity within populations (H_p/H_t), among populations within taxa (D_{ps}/H_t), and among taxa (D_{st}/H_t).

| | | | | | | Proportion of genetic diversity | | |
| | | | | | | Within populations | Among populations within taxa | Among taxa |
Locus	H_t	H_p	D_{ps}	H_s	D_{st}			
Aat-1	0.6018	0.0327	0.0766	0.1093	0.4925	0.054	0.128	0.818
Aat-2	0.4139	0.0816	0.0721	0.1537	0.2602	0.197	0.174	0.629
Acn-1	0.4359	0.0247	0.0325	0.0572	0.3787	0.057	0.074	0.869
Acn-2	0.2863	0.0596	0.1207	0.1803	0.1060	0.208	0.422	0.370
Fe-1	0.4256	0.1200	0.1387	0.2587	0.1669	0.282	0.326	0.392
Idh-1	0.1476	0.0257	0.0337	0.0594	0.0882	0.174	0.229	0.597
Idh-2	0.1682	0.0319	0.0515	0.0834	0.0848	0.190	0.306	0.504
Mdh-1	0.5943	0.1116	0.1411	0.2527	0.3415	0.188	0.237	0.575
Mdh-2	0.1596	0.0253	0.0239	0.0492	0.1104	0.159	0.149	0.692
Mdh-3	0.1682	0.0329	0.0446	0.0775	0.0908	0.195	0.265	0.540
Mdh-4	0.1585	0.0052	0.0011	0.0063	0.1522	0.033	0.007	0.960
Mdh-5	0.0077	0.0061	0.0016	0.0077	0.0000	0.802	0.198	0.000
Pgi-2	0.7665	0.2064	0.1766	0.3830	0.3835	0.269	0.231	0.500
Pgm-1	0.4586	0.0895	0.0892	0.1787	0.2800	0.195	0.195	0.610
Pgm-2	0.1493	0.1088	0.0405	0.1493	0.0000	0.729	0.271	0.000
Skdh	0.7850	0.1002	0.1388	0.2390	0.5460	0.128	0.176	0.696
Tpi-1	0.2450	0.0678	0.0677	0.1355	0.1145	0.271	0.271	0.458
Tpi-2	0.0106	0.0084	0.0022	0.0106	0.0000	0.798	0.202	0.000
Overall (across loci):	0.3326	0.0632	0.0695	0.1327	0.1999	0.190	0.209	0.601

lation, species (or subspecies), and total clade. The amount of genetic diversity within each category in ascending order in the hierarchy is represented by H_p, H_s, and H_t. The results of the genetic-diversity analysis are shown for each locus separately and for all 18 loci combined (Table 4). Single-locus estimates of total genetic diversity range from 0.008 for *Mdh-5* to 0.785 for *Skdh*, with a mean for all loci of 0.333. The sampled loci exhibit a range of levels of differentiation among taxa. Averaging all 18 loci, 60.1% of the total genetic diversity is the result of differentiation among the ten taxa in the *S. angustifolia* complex, 20.9% is the result of differentiation among populations within species or subspecies, and the remaining 19.0% represents the portion of total diversity that exists as variation among individuals within populations.

Hierarchical F statistics also were calculated for each taxon individually (Table 5). Values of H_t range from 0.027 for *S. sapphirina*, indicating that it is the most genetically homogeneous taxon, to 0.181 for *S. californica*, with a mean value for all ten

taxa of 0.111. Differentiation among populations within a species is designated G_{pt} (F_{st} of Wright [1965]). Estimates of population differentiation range from 18.7% for *S. tuberosa* to 75.5% for *S. angustifolia micrantha* with a mean of 42.1% for all ten taxa (Table 5).

Genetic Identity.—Within each taxon, mean genetic identities, shown on the diagonal in Table 6, range from 0.907 for *S. californica* to 0.983 for *S. tuberosa*, with a mean for all ten taxa of 0.941. Interspecific genetic identities within the *S. angustifolia* complex also are similar to those reported from other studies, but with a somewhat lower average identity. Genetic similarities between taxa range from 0.203 to 0.911 (for the two subspecies of *S. angustifolia*), with a mean genetic identity for all pairwise species comparisons of 0.617 compared to 0.67 reported by Gottlieb (1981) for congeneric genetic identities.

DISCUSSION

Substantial variation in the extent and distribution of genetic variability exists

TABLE 5. Summary of genetic diversity (Nei, 1973) and differentiation for ten taxa of the *S. angustifolia* complex: total genetic diversity (H_t), population-level genetic diversity (H_p), and apportionment of genetic diversity within populations (H_p/H_t) and among populations (G_{pt}).

Taxon	H_t	H_p	H_p/H_t	G_{pt}
S. angustifolia angustifolia	0.1306	0.0798	0.611	0.389
S. a. micrantha	0.1072	0.0263	0.245	0.755
S. antirrhinoides	0.1377	0.0724	0.526	0.474
S. bolanderi	0.0812	0.0227	0.280	0.720
S. brittonii	0.1170	0.0927	0.792	0.208
S. californica	0.1813	0.1291	0.712	0.288
S. nana	0.1745	0.1174	0.673	0.327
S. sapphirina	0.0271	0.0209	0.770	0.230
S. siphocampyloides	0.1134	0.0422	0.372	0.628
S. tuberosa	0.0373	0.0303	0.813	0.187
Mean:	0.1107	0.0634	0.579	0.421

among species in the *Scutellaria angustifolia* complex. This variation in genetic variability in a clade that exhibits a diversity of habitats, breeding systems, and distributional ranges provides the opportunity to examine the relative importance of these taxon-specific characteristics (Table 1) to the extent and distribution of genetic diversity in plant species. The fact that these species have a well-understood phylogenetic history based on isozyme and morphological data (Olmstead, 1989) makes this an exceptional opportunity, because the relative importance of phylogenetic relatedness also can be considered (see Felsenstein, 1985).

Breeding System and Genetic Diversity.— High levels of heterozygosity and polymorphism and low levels of population differentiation (G_{pt}) have been associated with predominantly outbreeding plant species, whereas total genetic diversity (H_t) is not substantially correlated with breeding system (Gottlieb, 1981; Loveless and Hamrick, 1984). This generally is true in the *S. angustifolia* complex; however, the direct comparison of heterozygosity, polymorphism, and population differentiation for assessing breeding systems is restricted in its application by the interaction of factors that influence genetic structure in populations. The effect of such interactions can be illustrated by examples from *Scutellaria*.

Phylogenetic history can influence species-level polymorphism and total genetic variability. The two subspecies of *Scutellaria angustifolia* exhibit contrasting breeding systems; subspecies *angustifolia* is large-flowered and outcrossing, while subspecies *micrantha* is small-flowered and largely selfing. These taxa have similar values for H_t, but the large-flowered subspecies has levels of heterozygosity four times greater (0.088 vs. 0.022) than the small-flowered subspecies and retains more than three times the genetic diversity in the average population (H_p) than does its small-flowered relative (0.080 vs. 0.026). Polymorphism at the population level also is higher in subspecies *angustifolia* (18.1% vs. 6.8%), as predicted, whereas polymorphism at the taxon level (P_s) is not substantially different between the two taxa (61.1% vs. 55.6%). The comparison of taxon-level polymorphism between these two subspecies differs from the expectation of greater polymorphism in the more outcrossing subspecies (Gottlieb, 1981) but can be explained readily. From the phylogenetic analysis of the group (Olmstead, 1989), it can be inferred that the large-flowered subspecies is derived from the small-flowered subspecies (unlike the more common occurrence of small-flowered selfers derived from large-flowered outcrossers). Populations of the small-flowered subspecies *micrantha* each retain less genetic variability than a typical population of the large-flowered subspecies *angustifolia*, but the cumulative polymorphism (P_s) and total genetic diversity (H_t) are similar in the two subspecies.

Differences in the extent of geographic distribution may cause conclusions about breeding systems that are based on levels of heterozygosity and polymorphism to be

TABLE 6. Mean genetic identities (Nei, 1978) within taxa (along diagonal) and between taxa of the *Scutellaria angustifolia* complex.

	Taxon									
Taxon	1	2	3	4	5	6	7	8	9	10
1) *S. angustifolia angustifolia*	0.927									
2) *S. a. micrantha*	0.911	0.911								
3) *S. antirrhinoides*	0.762	0.737	0.923							
4) *S. bolanderi*	0.579	0.547	0.553	0.968						
5) *S. brittonii*	0.667	0.641	0.736	0.568	0.958					
6) *S. californica*	0.727	0.704	0.832	0.630	0.758	0.907				
7) *S. nana*	0.769	0.759	0.706	0.649	0.756	0.766	0.925			
8) *S. sapphirina*	0.615	0.586	0.650	0.531	0.674	0.662	0.711	0.981		
9) *S. siphocampyloides*	0.740	0.712	0.849	0.637	0.819	0.893	0.770	0.648	0.925	
10) *S. tuberosa*	0.246	0.234	0.203	0.278	0.333	0.271	0.356	0.297	0.260	0.983

misleading. *Scutellaria nana* is a widespread, relatively common species throughout the Great Basin, whereas *S. sapphirina* is a narrowly restricted species consisting of isolated populations in the mountains of eastern Nevada. Levels of heterozygosity and polymorphism are much higher in *S. nana* than in its sister species, *S. sapphirina*. Also, there is less differentiation among populations of *S. nana* than among those of *S. sapphirina*, thus suggesting that there is more inbreeding in *S. sapphirina*. However, greater total genetic diversity and polymorphism are commonly associated with greater geographic distribution (Loveless and Hamrick, 1984; Karron, 1987); consequently, a direct comparison of these values will not provide a valid assessment of breeding systems in two species with such large differences in distribution. The phylogenetic analysis of the group (Olmstead, 1989) implies that *S. sapphirina* may be the progenitor of *S. nana*. This suggests that the greater differentiation among populations of *S. sapphirina* could be the result of a long history of population isolation, whereas the lesser differentiation among populations of the widespread *S. nana* may reflect recent colonization of its present range.

The highest values for Wright's fixation index are found in the two small, blue-flowered taxa, *S. antirrhinoides* of northern California and *S. angustifolia micrantha* of eastern Oregon and adjacent Nevada and Idaho. In California, *S. antirrhinoides* has a large-flowered sister taxon, *S. siphocampyloides,* and in eastern Oregon, *S. angus-* *tifolia micrantha* has a large-flowered sister taxon, *S. a. angustifolia*. In each region, the small-flowered taxon exhibits a much higher *F* value than the large-flowered taxon (0.319 vs. −0.024 in California and 0.631 vs. 0.018 in eastern Oregon). This suggests that there are differences in breeding system between members of each pair of taxa, with the small-flowered taxon exhibiting a substantial amount of inbreeding and the large-flowered taxon mating essentially at random. Greenhouse studies are consistent with this hypothesis: the small-flowered plants exhibit a greater amount of autogamous seed production in an insect-free greenhouse than do the large-flowered plants (Olmstead, 1988).

Two species, *S. californica* and *S. nana,* exhibit levels of total diversity (H_t), population-level diversity (H_p), heterozygosity, and polymorphism that are very similar to each other and substantially higher than any of the other species in the group (Tables 3, 5); yet these two species are very dissimilar morphologically, ecologically, and geographically. Both species have small flowers that are similar in size to other less genetically variable species in the group. The similarity in genetic variability between these two species may be coincidental; however, they share white flowers, a character of potential significance to reproductive biology (blue flowers are typical of most other species in the group). It is possible that an insect pollinator common to these two white-flowered species may result in greater outbreeding than for the blue-flowered species (ad-

ditional data on pollinators for these species are needed to test this hypothesis). Alternatively, shared flower color may be coincidental, and the similarity in genetic variability between these species may reflect present or historical factors related to population size or life history traits.

Geographic Distribution and Genetic Diversity.—The generality of restricted genetic variability in species with narrow distributions (Hamrick et al., 1979; Karron, 1987) is consistent with the evidence from the *S. angustifolia* complex. The taxa with the most restricted ranges have the highest intraspecific genetic identities (Table 6), and three of these (*S. bolanderi, S. sapphirina,* and *S. tuberosa*) have the lowest estimates of total genetic diversity (H_t) in the group.

Sampling design is particularly important when the question of interest involves the relationship between geographic distribution and genetic variability. In this study of ten taxa, estimated values for three parameters of genetic variability that are often used for comparison between species (mean number of alleles per locus, the mean number of alleles per polymorphic locus, and the percentage of polymorphic loci per species) (Hamrick et al., 1979; Gottlieb, 1981; Hamrick, 1983; Vogelmann and Gastony, 1987; Karron, 1987) exhibit positive correlations with the number of populations sampled, although only one of the three correlations is significant at the $P < 0.05$ level (mean number of alleles per locus, $r = 0.612$, $P < 0.1$; mean number of alleles per polymorphic locus, $r = 0.444$, $P < 0.01$; percentage of polymorphic loci per species, $r = 0.624$, $P < 0.1$). These results are consistent with statistical sampling theory (Larsen and Marx, 1981), which predicts that, as the number of samples increases, a greater portion of the total variability will be encountered. This suggests that the use of these genetic-variability estimates should be limited to comparisons between species for which a similar number of populations have been sampled (Crawford et al., 1984).

The geographic distribution of the sampled populations may be another confounding factor. Populations sampled from a narrowly restricted species may be much closer geographically and could be genetically more homogeneous due to gene flow or historical

reasons than are widely scattered populations of a widespread species (Karron et al., 1988). Similarly, the degree of genetic differentiation among populations within a species (F_{ST} of Wright [1965]), another estimate frequently used for species comparisons (Hamrick, 1983; Loveless and Hamrick, 1984), was found to exhibit a significant positive correlation with the number of populations sampled ($r = 0.849$, $P < 0.05$) for nine taxa in *Scutellaria* (omitting *S. bolanderi,* for which the two population samples represent two subspecific taxa). It is unclear to what extent this correlation is a function of the number of populations sampled or whether it is the result of the close proximity of the small number of populations sampled for narrowly restricted species or of other unrelated variables.

Considering two estimates of genetic variability that are not correlated with number of populations sampled in this study, the most narrowly restricted species (*S. bolanderi, S. sapphirina,* and *S. tuberosa*) exhibit the lowest values of H_t and H_p (Table 5). These results suggest that, in the *S. angustifolia* complex, restriction in geographic range is associated with reduced levels of genetic variability and that this reduced variability is not simply a reflection of the close proximity of the sampled populations.

Knowledge of breeding system and geographic range does not always allow one to predict levels of genetic diversity. *Scutellaria siphocampyloides* is a widespread, large-flowered, primarily outcrossing species that is characterized by unexpectedly low levels of total genetic diversity and heterozygosity and a relatively high degree of differentiation among populations. A very low value for Wright's fixation index and lack of autogamous seed set in greenhouse-grown plants (Olmstead, 1988) indicate that this taxon is highly outcrossing relative to other taxa in the group. An explanation for the apparently anomalous data observed for *S. siphocampyloides* may lie in the history of the population dynamics within that taxon. A combination of factors including greater clonal reproduction, smaller average natural population sizes, and frequent occurrences of population extirpation and recolonization among small isolated populations could keep the level of observed genetic di-

versity low, relative to the expected level for a species exhibiting the life-history characteristics of *S. siphocampyloides.*

Habitat Specificity and Genetic Diversity.—Conifer woodlands are the preferred habitats of four taxa, while three taxa inhabit sagebrush desert (Table 1). Within each of these two contrasting habitat types, taxa exhibit widely divergent estimates for almost every genetic-diversity parameter measured, suggesting that shared habitat preference does not imply an adaptive value for any particular level of genetic diversity measured. If the extent and distribution of genetic variability can be considered a consequence of environment and life-history strategy, one may expect species with similar habitat specificities to exhibit similar levels of genetic diversity. However, the results of this study are consistent with the studies reviewed by Hamrick et al. (1979), who found no significant difference associated with habitat type for three commonly reported estimates of genetic diversity.

Genetic Differentiation Within and Among Species.—Hierarchical F statistics and genetic identity provide complementary insight into the genetic structure of a species. Hierarchical F statistics estimate the degree to which the total genetic variability of a species can be accounted for within populations and between populations, whereas genetic identity (Nei, 1978) estimates the degree of genetic similarity between individual populations. The relatively high levels of G_{pt} exhibited by most species of the *S. angustifolia* complex, compared to most other studies (Hamrick, 1983; Loveless and Hamrick, 1984; Wendel and Parks, 1985), may represent a combination of factors including a substantial amount of selfing in many populations and the effect of genetic drift on the small, widely-scattered populations that characterize most species of *Scutellaria.*

Genetic identities among conspecific populations in a wide variety of flowering plants generally range from 0.90 to 1.00, averaging about 0.95 (Gottlieb, 1981; Crawford, 1983); this reflects closely the variation observed in the *S. angustifolia* complex (mean $I = 0.941$). Genetic identities within and among species and subspecies of *Scutellaria* (mean intertaxon $I =$

0.617) are typical of continental species groups (Crawford, 1983). The average value for congeneric genetic identities reported by Gottlieb ($I = 0.67$) is probably inflated to a certain degree, because many previous studies have examined congeneric species that were believed in advance to be closely related species-pairs. It should be noted that this group of ten closely related taxa represents only a small part of the diversity within *Scutellaria,* which is world-wide in distribution, and that the average genetic identities among taxa within the entire genus would be much lower, probably below the level of resolution obtainable by isozyme electrophoresis, due to the confounding effects of convergent and identical electromorphs. The danger of drawing general conclusions regarding the genetic similarity of congeneric species is brought into focus when the present study is contrasted with studies such as those of the Hawaiian species of *Tetramolopium* (Lowrey and Crawford, 1985) and *Bidens* (Helenurm and Ganders, 1985). In these studies, the genetic similarity among all populations within each group (seven species of *Tetramolopium* and 15 species of *Bidens*) shows no greater differentiation than that found among populations within most single species of *Scutellaria.*

Whereas genetic identity and other measures of genetic similarity or distance have been used frequently to express the genetic relationship among a group of species, the use of hierarchical F statistics to assess the genetic structure of species groups has been uncommon (Bruederle and Fairbrothers, 1986). Therefore, no comparable body of information on the apportionment of total genetic diversity into within-species and among-species components during the course of phylogenetic radiations in plants is available. Three studies in which hierarchical F statistics have been used to assess genetic structure in an entire clade of plants are available for comparison. Differentiation between species accounts for 5.3% of the total genetic diversity in a clade of eight taxa in *Sedum* (M. F. Denton and Olmstead, unpubl.), 51.6% in a clade of four taxa in *Carex* (Bruederle and Fairbrothers, 1986), and 62.5% in this study of ten taxa in *Scutellaria.* It is evident from this small number
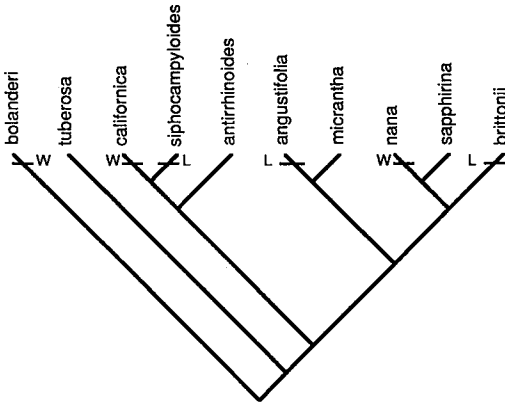
FIG. 2. Reconstruction of the phylogeny of the *Scutellaria angustifolia* complex showing the evolution of long flowers (L) and white corolla color (W).

of studies that considerable variation exists in the genetic structure of plant species-groups and that more such studies are needed before generalizations can be made.

Phylogenetic Relationship and Genetic Diversity.—The effect of phylogenetic relationship on the extent and distribution of genetic variation in related plant species has not been examined previously within the context of genetic-diversity statistics. To the extent that characters of reproductive morphology are conservative indicators of phylogenetic relatedness as well as of population genetic structure through their relationship to breeding systems, one may expect that closely related species would exhibit similar genetic-diversity statistics. In a study of genetic divergence among six species of *Layia,* estimates of heterozygosity, polymorphism, and the number of alleles per polymorphic locus indicated that the most closely related species also have the most similar estimates of genetic variability (Warwick and Gottlieb, 1985). In contrast, close phylogenetic relationship is not correlated with similarity in observed levels of genetic diversity in the *S. angustifolia* complex.

The reason for the lack of correspondence between phylogenetic relatedness and genetic variability among species of *Scutellaria* is evident when one considers the evolution of reproductive characters in the group (Fig. 2). Two characters of reproductive morphology that may have a substan-

tial effect on breeding system (flower color and corolla length) represent multiple cases of parallel evolution within the group. White flower color and long corollas have evolved independently in three separate lineages during the phylogenetic radiation of the group from an ancestor inferred to have short blue flowers (Olmstead, 1989). Many of the observed differences in genetic diversity among species are correlated with flower color and corolla length. White-flowered species, except the narrowly restricted and genetically depauperate *S. bolanderi,* exhibit the highest levels of genetic diversity among the taxa examined. Plants with long corollas generally exhibit higher levels of heterozygosity and polymorphism than the short-flowered plants. Within each of three species-groups within the *S. angustifolia* complex (Fig. 2), there are taxa with divergent values for many genetic-diversity statistics, suggesting that evolution has affected the extent and distribution of genetic variation within species of the *S. angustifolia* complex in many ways.

Conclusions

A combination of factors, biological and historical, influences the extent and distribution of genetic diversity within and among species of the *S. angustifolia* complex. In this clade of ten taxa, 60.1% of the total genetic diversity represents differentiation among species, 20.9% represents differentiation among populations within species, and the remaining 19.0% resides within populations. Too few studies of clade-level genetic structure have been carried out for comparisons to suggest which factors influence the distribution of genetic diversity at this level.

The results of this study suggest the following conclusions regarding the factors that influence genetic diversity in species of the *S. angustifolia* complex. 1) Differences in breeding system account for most of the observed variation in genetic diversity among species and are reflected primarily in the estimates of heterozygosity, population-level polymorphism, inbreeding (Wright's fixation index, F), and population differentiation. 2) The extent of a species' geographic range influences genetic diversity in species

with narrowly restricted distributions, resulting in lower estimated values for total genetic diversity, population-level genetic diversity, and population-level polymorphism. 3) The very different habitat preferences characterizing species in the *S. angustifolia* complex appear to have little or no influence on the extent or distribution of genetic diversity within species occupying different habitats. 4) Phylogenetic relatedness does not imply any similarity in genetic structure among species. It is not clear whether this last conclusion is a general one regarding the phylogenetic significance of genetic diversity; the amount of parallel evolution within the group could make the *S. angustifolia* complex a special case. It appears that genetic-diversity statistics are constrained by the phylogenetic history of species only insofar as the characters affecting reproductive biology are similarly constrained.

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Populations and sample sizes (*N*) of *Scutellaria* surveyed for electrophoretic variation are given in the table below. All collections by R. G. Olmstead. Vouchers deposited at the University of Washington Herbarium.

Taxon	Population	*N*	Collection number(s)
S. angustifolia angustifolia	Anson Wright Park, OR	5	301, 302
	Mitchell Summit, OR	4	315
	Mitchell, OR	8	318
	Antelope, OR	5	499
	Fairview Campground, OR	10	638
	Spray, OR	22	640
	Maury Mts. 1, OR	10	700
	Maury Mts. 2, OR	5	702
	Kendrick, ID	4	551
	Orofino, ID	4	552
	Kamiah, ID	1	553
	Lyle, WA	8	692
S. a. micrantha	Idlewyld Campground, OR	3	333
	Princeton Jct., OR	4	348
	Page Spring, Frenchglen, OR	18	351, 709
	Silvies River, OR	9	636
	Steens Mt., OR	10	715
	Cow Lake, OR	11	729
	Succor Creek, OR	8	733
	Ruby Mts., NV	10	618
	Independence Mts., NV	2	622
	Jack Creek, NV	3	624
	Wild Horse Dam, NV	7	630
	Emigrant Pass, NV	14	631
	Santa Rosa Mts., NV	12	632
S. antirrhinoides	Miranda, CA	9	421
	Van Duzen River, CA	5	429
	Coffee Creek, CA	13	461
	Big Flat, CA	2	465
	Sawyer's Bar, CA	3	472
	Rogue River, OR	11	656
	Rogue River Trail, OR	9	654
	Canyon Creek Trail, CA	14	680
	Snow Mt., CA	11	878
S. bolanderi	Mt. Bullion, CA	3	374
	Groveland, CA	4	386
	Vallecitos, CA	3	390
	Sheep Ranch, CA	4	395
	Toll House, CA	1	569
	Watts Valley Rd., CA	1	570
	Linns Valley, CA	1	821
	Wawona, CA	1	836b
	Idylwild, CA	6	803
S. brittonii	Stateline, hwy. 287, CO	9	641
	Ward, CO	12	642
	Vedawoo, WY	5	645
S. californica	Bartlett Springs, CA	16	371, 668
	Ripstein Camp, CA	4	678
	Canyon Creek, CA	12	454, 682
	Blue Oak Campground, CA	13	534, 673
	Indian Valley, CA	17	666
	Willits, CA	2	542
	Snow Mt., CA	2	870
	Summit Springs, Snow Mt., CA	8	881
	Van Duzen Bridge, CA	5	888
	Whitehall, CA	13	402, 837
	Oregon Creek, CA	9	839
	Yuba River, CA	2	844

APPENDIX.   Continued.

Taxon	Population	N	Collection number(s)
S. nana	Princeton Jct., OR	2	350
	Fields, OR	13	359, 728
	Prineville Reservoir, OR	12	693
	Steens Mt., OR	18	726
	Hart Mt. 1, OR	13	750
	Hart Mt. 2, OR	8	751
	Adel, OR	10	754
	Susanville, CA	2	415
	Rye Patch Rd. 1, CA	2	581
	Rye Patch Rd. 2, CA	3	584
	Fernley, NV	8	588
S. sapphirina	Hunts Canyon Guard Station, NV	8	595
	Little Antelope Summit, NV	10	596
	Cottonwood Creek, NV	1	600
	Ellison Guard Station, NV	1	606
	White River Narrows, NV	1	607
	White River Campground, NV	11	609
	Currant Summit, NV	11	614
	Schell Creek Range, NV	12	615
S. siphocampyloides	Calaveras, CA	4	396
	Butte Meadows, CA	2	418
	Post Creek, CA	12	438, 676
	Peanut, CA	6	447
	Junction City, CA	12	677
	Oakhurst, CA	2	562
	Bass Lake, CA	6	564
	Alder Spring, CA	2	568
	Sequoia National Park, CA	3	571
	Butts Canyon Rd., CA	12	574, 669
	Walker Ridge Rd. 1, CA	10	663
	Walker Ridge Rd. 2, CA	11	665
	Blue Oak Campground, CA	7	671
	Sespe Creek, CA	10	782
	Tule Creek, CA	1	785
	Chilao, CA	12	792
	Horse Flats, CA	4	794
	San Jacinto Mts., CA	8	804
	San Bernardino Mts., CA	10	807
	Kennedy Meadows, CA	8	813
	Greenhorn Summit, CA	3	826
	Wofford Heights	3	828
S. tuberosa	Long Point 1, CA	2	512
	Long Point 2, CA	7	515
	Walker Ridge, CA	21	522, 524
	Cow Mt., CA	3	536
	Willow Creek, CA	1	544
	Forest hwy. 7, Elk Creek, CA	15	660