

Genetic Relationships in *Arceuthobium monticola* and *A. siskiyouense* (Viscaceae): New Dwarf Mistletoe Species from California and Oregon*

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Key Word Index—*Arceuthobium siskiyouense*; *A. monticola*; Viscaceae; electrophoresis; allozymes.

Abstract—Genetic relationships among eight populations of two new species of *Arceuthobium* from the Klamath and Siskiyou Mountains of northwestern California and southwestern Oregon were determined. The principal host of *A. siskiyouense* is *Pinus attenuata* (knobcone pine) whereas *A. monticola* is parasitic primarily on *P. monticola* (western white pine). *Arceuthobium siskiyouense* is most closely related to *A. campylopodum* and *A. littorum* whereas *A. monticola* is related to *A. californicum*. The genetic distinctiveness of both of these species (from *A. campylopodum* and *A. californicum*, respectively) is supported by results of an electrophoretic analysis of isozymes. Genetic distances for within-species comparisons were below 0.26 (mean 0.24) in contrast to between-species distances which were greater than 0.28 (mean 0.33). UPGMA cluster analysis from genetic distances resulted in five groups corresponding to the five mistletoe species. These two new dwarf mistletoe species augment the growing list of plant species endemic to the Siskiyou Mountain region. These results also highlight the utility of isozyme electrophoresis in establishing genetically coherent groups, thus aiding the process of species circumscription within *Arceuthobium*.

Introduction

Floristic investigations of southwestern Oregon and northwestern California have revealed a highly diverse and endemic flora. Smith and Sawyer [1] state that “the region may be viewed as the last major frontier along the Pacific Coast to be studied in detail”. This area centers around the Klamath Mountain Range and is encompassed within the California floristic province [2] and the North Coast floristic region [3]. The Klamath-Siskiyou region supports many arcto-Tertiary relicts, such as *Picea breweriana*, and is known for its high diversity of conifers [2].

Since the publication of the monograph of *Arceuthobium* [4], several new species have been identified and species boundaries in existing taxa redefined [5–7]. More recently, species concepts within the genus have been augmented with genetic data derived from isozyme analyses [8]. In an isozyme analysis of section *Campylopoda* [9], electrophoretic data confirmed the genetic distinctiveness of a segregate of *A. occidentale* (*A. littorum*) parasitic on bishop and Monterey pine. Likewise, populations of *A. tsugense* parasitic on *Tsuga mertensiana*/*Pinus monticola* vs *Tsuga heterophylla* were shown to be genetically distinct [10]. Allozyme divergence in these taxa appears to be correlated with the geographic distribution of the host species, hence these taxa are recognized as subspecies of *A. tsugense* [11]. Herein we focus on the parasites of knobcone pine (*Pinus attenuata*) and western white pine (*P. monticola*) in northwestern California and southwestern Oregon.

Parasites of knobcone pine

Knobcone pine (*Pinus attenuata*) is a member of the closed-cone group (subsect.

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Oocarpae Little and Critchfield) which ranges from the Oregon Cascades to an isolated population in Baja California [12]. This species is abundant in the Siskiyou Mountains of southwestern Oregon, often occurring on rocky and/or serpentine substrates. Further south in California, this pine has a patchy distribution, possibly related to its fire-adapted, successional nature. *Arceuthobium campylopodum* is reported to occur on *P. attenuata* in five California counties (Del Norte, Lake, San Bernardino, Santa Clara and Siskiyou) and two Oregon counties (Curry and Josephine) [4].

In 1986, several dwarf mistletoe individuals that had previously been introduced onto knobcone pine near Camino, California (via seeds collected by R. Scharpf from near Gasquet, California) were analysed electrophoretically. This preliminary study, based upon only 20 individuals, showed that these plants were genetically distinct from typical *A. campylopodum* [13]. Since the seeds may have been collected from only one parent, genetic distance estimates could have been biased owing to the small sample size. Additional collections from the original populations were required to test this result further.

In previous taxonomic treatments, collections of the knobcone pine dwarf mistletoe were included in *A. campylopodum* [4, 6]. A situation near Gasquet, Del Norte County, California, was described where a dwarf mistletoe (then presumed to be *A. campylopodum*) was common on *Pinus attenuata* but rare on associated *P. ponderosa* [4]. Observations of the plants from these northern counties revealed morphological features and host preferences that differed from typical *A. campylopodum*. Further studies have demonstrated that the knobcone pine dwarf mistletoe is a distinct, although closely related species, which has been named *Arceuthobium siskiyouense* Hawksworth, Wiens and Nickrent [11]. *Arceuthobium siskiyouense* differs from *A. campylopodum* in its shorter, more slender shoots, smaller fruits, later flower period, absence of nonsystemic witches' broom formation and different host preferences. In marked contrast to *A. campylopodum*, which has a vast range from northern Idaho and northern Washington to Baja California, *A. siskiyouense* is restricted to the Klamath Mountains of southwestern Oregon (Curry and Josephine Counties) and the Siskiyou Mountains in Del Norte and Siskiyou Counties in northwestern California (Fig. 1).

Parasites of western white pine

Western white pine (*Pinus monticola*) is an important timber species in the western U.S. and ranges from southern British Columbia to the south central Sierra Nevada and westwards to western Montana. It can be found from near sea level in the north to elevations over 2800 m in the southern portion of its range. Western white pine is common in the Klamath Mountains and may occur as low as 150 m in elevation on serpentine soils in Del Norte County [12].

The parasites of sugar pine (*Pinus lambertiana*) and western white pine were previously placed within *A. californicum* [4]. Western white pine was listed as a secondary host for *A. californicum* by Hawksworth and Wiens [4], based on their own and previous collections made in Del Norte County, California and Curry and Josephine Counties, Oregon. The principal host for *A. californicum* is sugar pine, hence the northern California and southern Oregon populations on western white pine were considered range disjunctions for this mistletoe. Mathiasen and Hawksworth [14] examined the percentage of infection and mortality at two sites (Oregon Mt., Josephine County, Oregon and Black Butte, Del Norte County, California) where both *P. lambertiana* and *P. monticola* were parasitized. At both sites, the intensity of infection and per cent mortality of *P. monticola* was greater than that on *P. lambertiana*. This host preference difference between the northern and southern populations of *A. californicum* suggested that two biologically distinct entities may exist.

Pinus monticola is also listed as a secondary host for *Arceuthobium tsugense* [4],

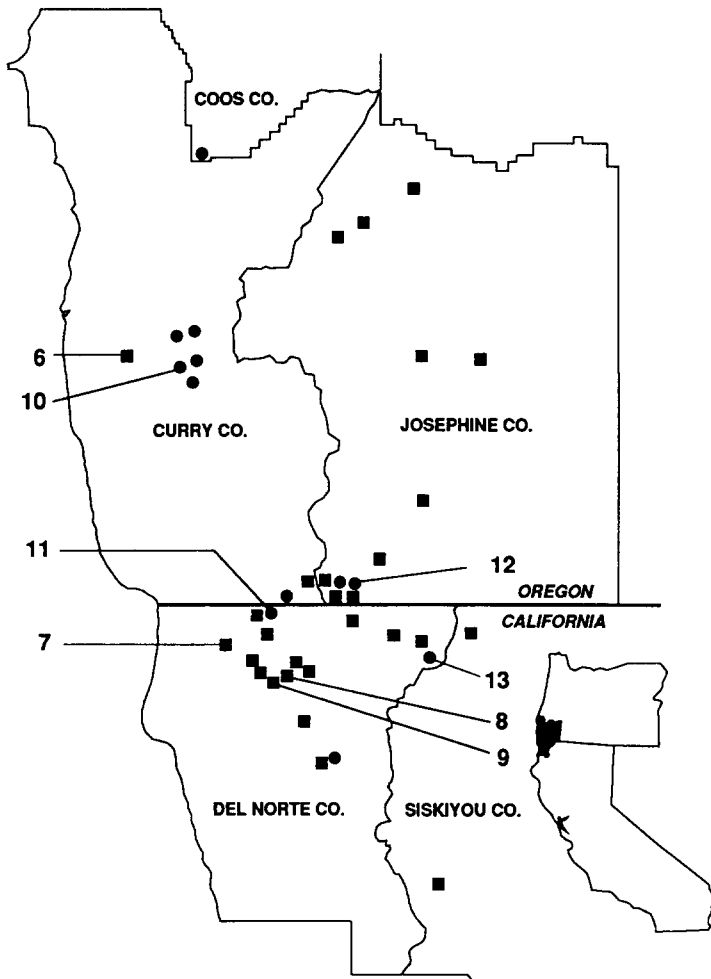


FIG. 1. DISTRIBUTION OF *ARCEUTHOBIMUM SISKIYOUENSE* (BOXES) AND *A. MONTICOLA* (DOTS) IN CALIFORNIA AND OREGON. Populations sampled for the isozyme analysis are numbered. See Materials and Methods for the key to population numbers.

although this host may be as susceptible to this parasite as the principal host (hemlock) in some stands [10]. Three other dwarf mistletoe species, *A. cyanocarpum*, *A. abietinum*, and *A. laricis* (all members of section *Campylopoda*), may, on occasion, also parasitize this pine. Despite the frequency of parasitism by several dwarf mistletoes and unlike nearly all other western U.S. *Pinus* species, *P. monticola* has previously not been considered a principal host for any dwarf mistletoe species.

Field and laboratory studies of the mistletoes from southwestern Oregon and northwestern California indicate that they are best treated as a distinct species, *Arceuthobium monticola* [11]. The western white pine dwarf mistletoe is endemic to the Klamath mountains of southwestern Oregon (Coos, Curry and Josephine Counties) and the Siskiyou Mountains of Del Norte County in adjacent northwestern California (Fig. 1). *Arceuthobium monticola* differs from *A. californicum* by the presence of darker shoot color, later flowering and seed dispersal periods, and its relative abundance on *Pinus monticola* vs *P. lambertiana*. This species is apparently not sympatric with *A. californicum*, whose range extends north only to Shasta County and southeastern Siskiyou County (near Bartle) in the Sierra Nevada.

The high level of endemism present in the Siskiyou Mountains and the apparent morphological discontinuities between the two new species and related members of Section *Campylopoda* prompted the biosystematic investigation. The purpose of this study was to sample populations of these newly named dwarf mistletoe species for use in a comparative isozyme analysis. Specifically, our aim was to determine genetic distances between the parasites from northern California and southwestern Oregon found on *P. attenuata* and the more widespread *Arceuthobium campylopodum*. Similarly, we wish to use genetic distance data to measure affinities between *A. monticola* and *A. californicum*.

Materials and Methods

Collection localities. Shoot material for isozyme analysis was obtained from four populations each of *Arceuthobium monticola* and *A. siskiyouense* during the summer of 1988 in Del Norte County, California and Curry and Josephine Counties, Oregon (Fig. 1). One population of *A. californicum* (Castella, 5) was also collected in 1988 (Nickrent 2710, 3.0 miles east of Castella, Shasta County, California) to allow a comparison to be made with *A. monticola*. In the present study, allozymic comparisons were also made with selected *A. campylopodum* s.l. and *A. littorum* populations. Details on these populations and dwarf mistletoe sampling methods have been described [9]. Voucher specimens from all populations were deposited at FPF and ILL. Unless otherwise noted, all populations of *Arceuthobium monticola* were parasitic on *Pinus monticola* and all populations of *A. siskiyouense* were parasitic upon *P. attenuata*. Population names and numbers are given in parentheses following each locality description.

Arceuthobium siskiyouense. Curry County, Oregon: Forest Highway (FH) 1703, 4.6 miles north of junction with F.H. 100, Nickrent and Wiens 2702 (Red Flat, 6). Del Norte County, California: on *P. attenuata* and *P. jeffreyi*, five air miles ESE of Smith River, T. 18N, R 1 E, Secs. 3 and 4, Nickrent and Wiens 2703 (Smith River, 7); 4.0 miles east of Gasquet, Nickrent and Wiens 2706 (Danger Pt., 8); on *P. jeffreyi*, east of Gasquet at the beginning of F.H. 314, Nickrent and Wiens 2707 (Gasquet, 9).

Arceuthobium monticola. Curry County, Oregon: Snow Camp Mt., Nickrent and Wiens 2701 (Snow Camp Mt., 10). Josephine County, Oregon: 7.6 miles southwest of O'Brien on Oregon Mt. Rd., Nickrent and Wiens 2708 (O'Brien, 12). Del Norte County, California: three miles east of Smith River bridge, 10 air miles north of Gasquet, Nickrent and Wiens 2705 (Smith River, 11); near Black Butte, three miles east of Sanger Peak, Nickrent and Wiens 2709 (Black Butte, 13).

Isozyme methods. Seven polymorphic enzyme systems representing nine loci were resolved in *A. siskiyouense* and *A. monticola*: *ADH-1*, *ADH-2*, *G-6-PDH*, *IDH*, *MDH-3*, *MDH-4*, *PGI*, *PGM* and *6-PGDH*. The gel buffers and staining schedules cited in Nickrent and Butler [9] were followed in this study. The computer program BIOSYS-1 [15] was used to calculate gene diversity statistics, genetic distances, and construct UPGMA [16] dendrograms. Chord distances [17] were used for UPGMA phenogram construction.

Results

Allelic diversity

All loci examined among the eight populations of dwarf mistletoes on *Pinus attenuata* and *P. monticola* were polymorphic. The table of allele frequencies can be obtained from the first author upon request. Several alleles, such as *ADH-1*⁸⁷, *MDH-3*¹⁰⁹, and *6-PGD*⁵⁷, are unique to *A. siskiyouense*. Likewise, *IDH*¹¹¹, *6-PGD*³⁰ and *6-PGD*⁵⁷ are found only in *A. monticola*. *ADH-2*¹²⁴ is found solely in the two new species, whereas the *PGM*⁶⁵ and *G-6-PDH*⁸² alleles found in other section *Campylopoda* taxa are absent in these species. The *PGM*⁶⁵ allele appears to be restricted to *A. campylopodum* and *A. occidentale* and absent from *A. littorum*, *A. monticola*, and *A. siskiyouense*. The *6-PGD*¹⁶⁴ allele appears to be unique to *A. californicum*. The two predominant alleles at the *MDH-3* locus (*MDH-3*⁸⁰ and *MDH-3*¹⁰⁰) showed marked frequency differences between *A. campylopodum* s.l., *A. littorum*, *A. siskiyouense*, *A. monticola* and *A. californicum* (Fig. 2). *Arceuthobium siskiyouense*, like *A. campylopodum*, has the *MDH-3*¹⁰⁰ allele in high frequency. *Arceuthobium monticola* differs in that these two alleles are present in nearly equal frequencies, which is most similar to *A. californicum*.

Genetic variability

Genetic variability among the four populations of *A. siskiyouense* and *A. monticola* is compared with the values for four populations of *A. campylopodum* (s.l.) and *A.*

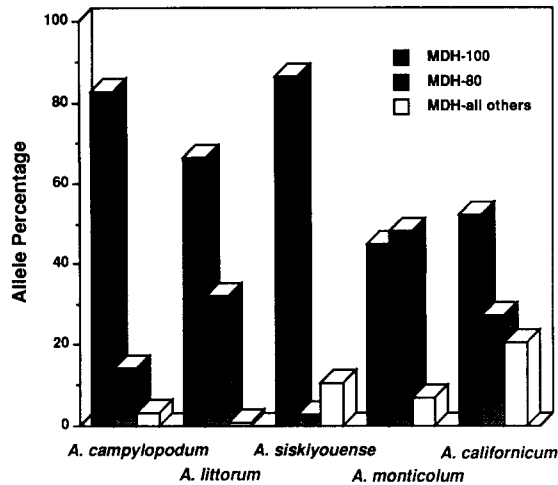


FIG. 2. ALLELE PERCENTAGES FOR *MDH-3* IN FIVE SPECIES OF *ARCEUTHOBIUM*.

littorum [9] in Table 1. *Arceuthobium campylopodum* showed a higher mean number of alleles per locus (A) than either *A. siskiyouense*, *A. monticola*, or *A. littorum*. The latter three taxa have more limited geographic distributions than the former which indicates that a relationship exists between allelic diversity and geographic range. The mean percentage of polymorphic loci (P) for all species is similar (Table 1). Observed (direct count) heterozygosity (H_o) was higher in *A. monticola* and *A. siskiyouense* than in *A. campylopodum* and *A. littorum*.

Genetic distance between species

The chord distances [17] derived from the nine polymorphic loci across 17 populations are shown in Table 2. The lowest value for interpopulational comparisons is between populations 1 and 2 (*A. campylopodum*) and 14 and 15 (*A. littorum*) which both had genetic distances of 0.192. The largest genetic distance between two populations was between 13 (*A. monticola*) and 16 (*A. littorum*). Since genetic identities (similarities) as well as distances are reported in isozyme studies, the genetic identity measure of Nei [18] is also shown in Table 2. Conclusions about genetic affinities do not change based upon distance or similarity estimates.

The means and ranges of distance values between populations of the same species and between populations of different species provide information on the relative distinctiveness of the taxa (Table 3). For all species considered here, the smallest distances are those resulting from within-species comparisons. This is shown by the difference between the highest and lowest intraspecific genetic distance values (excluding *A. californicum* since it is represented by only one population) which ranged from 0.048 to 0.061 (mean 0.054). Populations of *A. siskiyouense* appear to be more differentiated from each other than are populations of *A. monticola*, as shown by their respective genetic distance differences (0.057 and 0.048). The difference between the highest and lowest interspecific genetic distance values ranged from 0.071 to 0.136 (mean of 0.107), i.e. twice the intraspecific value.

Cluster analysis

The UPGMA cluster analysis (Fig. 3) segregated the 17 populations into five groups at or above a genetic distance of 0.275. The first two groups are composed of the four populations of *A. campylopodum* (1–4) and the four populations of *A. littorum* (14–17). The four populations of *A. siskiyouense* (6–9) cluster together and appear to be more

TABLE 1. GENETIC VARIABILITY FOR FIVE SPECIES OF *ARCEUTHOBIMUM*

Species/ population	Host*	Mean sample size/locus	A	P†	Mean heterozygosity	
					H_o	H_e ‡
<i>A. campylopodum</i>						
1–4.§	—	35.4	3.1	92.5	0.256	0.293
<i>A. californicum</i>						
5. Castella	LAM	21.7	2.6	77.8	0.289	0.311
<i>A. siskiyouense</i>						
6. Red Flat	ATT	18.0	2.2	100.0	0.346	0.292
7. Smith River	ATT/JEF	31.8	3.6	100.0	0.384	0.402
8. Danger Point	ATT	16.8	2.6	100.0	0.334	0.448
9. Gasquet	JEF	25.6	2.0	77.8	0.303	0.343
	Means	23.0	2.6	94.4	0.341	0.371
<i>A. monticola</i>						
10. Snow Camp Mt.	MON	34.7	2.1	66.7	0.192	0.220
11. Smith River	MON	27.0	2.8	77.8	0.354	0.365
12. O'Brien	MON	32.6	3.0	100.0	0.292	0.383
13. Black Butte	MON	34.9	2.6	88.9	0.372	0.405
	Means	32.3	2.6	83.3	0.303	0.343
<i>A. littorum</i>						
14–17.¶	—	39.5	2.6	91.3	0.231	0.251

*Host abbreviations: LAM = *Pinus lambertiana*, MON = *P. monticola*, ATT = *P. attenuata*, JEF = *P. jeffreyi*.

†A locus is considered polymorphic if more than one allele was detected.

‡Unbiased estimate [17].

§Mean values from 18 populations of *A. campylopodum* (s.l.) from Nickrent and Butler [9]. Hosts included *P. ponderosa*, *P. jeffreyi*, *P. sabiniana*.

¶Mean values from nine populations of *A. littorum* in Nickrent and Butler [9]. Hosts included *P. radiata*, *P. muricata* and *P. contorta* ssp. *contorta*.

closely related to *A. campylopodum* and *A. littorum* than to *A. monticola* or *A. californicum*. The Danger Point and Gasquet populations of this species cluster together, as would be expected based upon their close geographic proximity. Conversely, the next most similar population is not Smith River but Red Flat which is ca. 70 km (vs 10 km) to the northwest in Curry Country, Oregon.

The two Oregon populations of *A. monticola* (10 and 12) are shown in the phenogram as being more similar to each other than they are to the two California populations (11 and 13). The cluster composed of *A. californicum* and *A. monticola* joins the remaining populations at a genetic distance of 0.355. Although only one population of *A. californicum* was used, this analysis indicates that these two species are distinct as shown by their connection at a genetic distance of 0.340.

Discussion

Genetic identities for conspecific populations average ca. 0.95 [19]. This level of genetic similarity was seen among populations of *Arceuthobium campylopodum* and *A. occidentale* [9] and was used as evidence supporting their recognition as one taxonomic and biological species. Similarly high intraspecific genetic identities were seen among populations of *A. littorum* [9] and, in the present study, with populations of *A. monticola* and also *A. siskiyouense*. Results from these studies indicate that for section *Campylopoda* of *Arceuthobium*, genetically cohesive groups that can be classified at the species level form at genetic identities [18] of ca. 0.93 or higher or genetic distances [17] of 0.275 or lower. Although no fixed allelic differences have been detected that can unequivocally differentiate the five species considered herein, signifi-

TABLE 2. MATRIX OF GENETIC IDENTITY AND DISTANCE COEFFICIENTS* FOR 17 POPULATIONS OF *ARCEUTHOBIUM*

Population no. and name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1. Paradise	***	0.988	0.956	0.977	0.929	0.939	0.970	0.950	0.933	0.878	0.875	0.869	0.869	0.972	0.972	0.906	0.927
2. Lassen	0.192	***	0.976	0.965	0.940	0.906	0.939	0.948	0.949	0.901	0.897	0.882	0.919	0.943	0.956	0.862	0.902
3. Figueroa	0.245	0.193	***	0.951	0.927	0.882	0.913	0.932	0.920	0.927	0.910	0.913	0.924	0.933	0.955	0.860	0.911
4. Emerald Bay	0.236	0.193	0.217	***	0.895	0.927	0.959	0.940	0.932	0.881	0.867	0.881	0.856	0.934	0.944	0.891	0.897
5. Castella	0.310	0.329	0.325	0.353	***	0.802	0.873	0.855	0.860	0.877	0.917	0.886	0.896	0.890	0.918	0.830	0.872
6. Red Flat	0.261	0.297	0.295	0.310	0.399	***	0.943	0.959	0.919	0.833	0.770	0.823	0.793	0.948	0.917	0.901	0.927
7. Smith River	0.267	0.288	0.300	0.278	0.371	0.273	***	0.967	0.933	0.862	0.880	0.870	0.854	0.952	0.952	0.914	0.917
8. Danger Point	0.321	0.319	0.321	0.332	0.381	0.263	0.287	***	0.982	0.887	0.877	0.875	0.908	0.924	0.931	0.865	0.889
9. Gasquet	0.307	0.284	0.309	0.303	0.377	0.269	0.261	0.230	***	0.901	0.891	0.887	0.925	0.878	0.893	0.825	0.845
10. Snow Camp Mt.	0.340	0.300	0.290	0.332	0.358	0.332	0.341	0.341	0.294	***	0.943	0.986	0.926	0.839	0.864	0.759	0.827
11. Smith River	0.362	0.338	0.346	0.374	0.321	0.404	0.323	0.369	0.331	0.261	***	0.951	0.962	0.823	0.868	0.776	0.816
12. O'Brien	0.355	0.335	0.327	0.338	0.331	0.379	0.300	0.358	0.331	0.235	0.251	***	0.924	0.837	0.869	0.798	0.836
13. Black Butte	0.369	0.319	0.332	0.379	0.347	0.411	0.351	0.333	0.303	0.283	0.238	0.273	***	0.824	0.861	0.736	0.807
14. Ft. Bragg	0.193	0.256	0.274	0.281	0.312	0.261	0.286	0.345	0.332	0.337	0.372	0.352	0.395	***	0.985	0.944	0.973
15. Pt. Arena	0.232	0.268	0.267	0.280	0.312	0.293	0.280	0.322	0.331	0.335	0.352	0.344	0.375	0.192	***	0.948	0.952
16. Gualala	0.272	0.326	0.329	0.313	0.371	0.293	0.307	0.367	0.364	0.392	0.401	0.376	0.443	0.218	0.227	***	0.945
17. Monterey	0.277	0.306	0.302	0.322	0.321	0.305	0.311	0.373	0.373	0.371	0.387	0.377	0.413	0.222	0.253	0.241	***

*Above diagonal: unbiased genetic identity [18]. Below diagonal: chord distance [17].

TABLE 3. MEANS (ABOVE) AND RANGES (BELOW) OF DISTANCE COEFFICIENTS* BETWEEN FIVE *ARCEUTHOBIMUM* SPECIES

<i>Arceuthobium</i> species	No. of populations	1	2	3	4	5
1. <i>A. campylopodum</i>	4	0.213 (0.192–0.245)				
2. <i>A. littorum</i>	4	0.281 (0.193–0.329)	0.225 (0.192–0.253)			
3. <i>A. monticolum</i>	4	0.341 (0.290–0.389)	0.376 (0.335–0.443)	0.257 (0.235–0.283)		
4. <i>A. siskiyouense</i>	4	0.299 (0.261–0.332)	0.321 (0.261–0.373)	0.343 (0.294–0.411)	0.264 (0.230–0.287)	
5. <i>A. californicum</i>	1	0.329 (0.310–0.353)	0.329 (0.312–0.371)	0.339 (0.321–0.358)	0.382 (0.371–0.399)	— —

*Chord distance [17] as in Table 2.

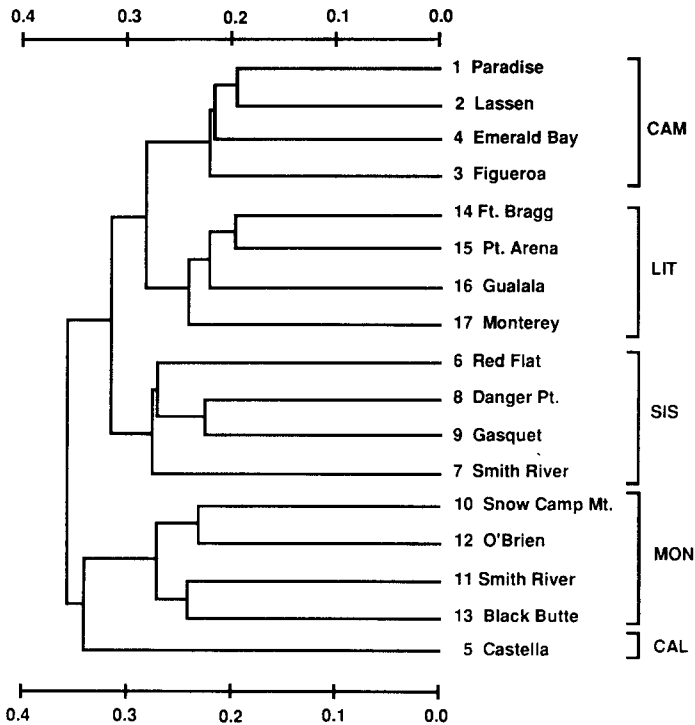


FIG. 3. UPGMA PHENOGRAM FOR 17 *ARCEUTHOBIMUM* POPULATIONS DERIVED FROM THE CHORD DISTANCES [17] GIVEN IN TABLE 2. The cophenetic correlation for this phenogram is 0.827 with a per cent standard deviation of 9.6. Abbreviations for species names are as follows: CAM = *Arceuthobium campylopodum* (s. lat.), LIT = *A. littorum*, SIS = *A. siskiyouense*, MON = *A. monticola*, and CAL = *A. californicum*.

cant allelic frequency differences exist (e.g. for *MDH-3*) that coincide with morphological, phenological and host preference differences.

Admittedly, the determination of species level genetic differences between *Arceuthobium californicum* and *A. monticola* would benefit from the inclusion of more individuals of the former species, especially from populations in the central and southern portion of its range. One analysis of the effect of sample size in electrophoretic studies showed that genetic distance estimates are only slightly affected by sample size and that a single individual may be used for interspecies comparisons [20]. A subsequent study [21] used consensus tree methods to show that UPGMA

dendrogram stability is influenced by several factors including the pattern of genetic differentiation between taxa, levels of heterozygosity among species, and the presence and frequency of unique alleles among taxa. In both sample data sets examined in those studies, consensus index values [22] were at or near 1.0 (indicating identical tree topologies) when greater than 20 individuals per taxon were used. As shown in the present study, the mean sample size per locus for *A. californicum* was greater than 20, therefore it is probable that the UPGMA dendrogram shown in Fig. 3 reflects interspecific relationships. Moreover, it was deemed more beneficial to include the single population in the analysis and derive preliminary results than to exclude the information entirely. Finally, the genetic distance between *A. californicum* and the nearest species (*A. monticola*) is greater than any of the other species pair comparisons examined in this study. We interpret these results as an indication of the genetic distinctiveness of the new species.

In the evolutionary diversification of *Arceuthobium*, the host has played a major role in providing potential niches for parasite colonization. With the inclusion now of *A. siskiyouense*, the parasite of knobcone pine and *A. monticola* whose principal host is western white pine, nearly every major conifer species in the Pinaceae has an associated species of dwarf mistletoe. Although morphological differentiation has generally involved quantitative characters and life history features (such as host and flowering times), this electrophoretic study shows that genetically based differentiation has also occurred. Only with information from a variety of different approaches can genetically coherent groups be identified and placed within the taxonomic hierarchy of the genus *Arceuthobium*.

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References

1. Smith, J. P., Jr and Sawyer, J. O., Jr (1988) *Madroño* **35**, 54.
2. Raven, P. R. and Axelrod, D. I. (1978) *Univ. Cal. Publ. Bot.* **72**, 1.
3. Stebbins, G. L. and Major, J. (1965) *Ecol. Monogr.* **35**, 1.
4. Hawksworth, F. G. and Wiens, D. (1972) *Biology and Classification of Dwarf Mistletoe (Arceuthobium)*. U.S.D.A. For. Ser. Agric. Handbook No. 401.
5. Hawksworth, F. G. and Wiens, D. (1980) *Brittonia* **32**, 348.
6. Hawksworth, F. G. and Wiens, D. (1984) *Biology of Dwarf Mistletoes: Proceedings of the Symposium*. (Hawksworth, F. G. and Sharpf, R. F., eds), p. 2. USDA For. Ser. Gen. Tech. Rep. RM-111.
7. Hawksworth, F. G. and Wiens, D. (1989) *Phytologia* **66**, 5.
8. Nickrent, D. L. (1986) *Am. J. Bot.* **73**, 1492.
9. Nickrent, D. L. and Butler, T. L. (1990) *Biochem. Syst. Ecol.* **18**, 253.
10. Nickrent, D. L. and Stell, A. L. (1990) *Biochem. Syst. Ecol.* **18**, 267.
11. Hawksworth, F. G., Wiens, D. and Nickrent, D. L. (1991) *Novon* (submitted).
12. Griffin, J. R. and Critchfield, W. B. (1972) *The Distribution of Forest Trees in California*. Pacific S.W. For. and Range Exp. Sta., Berkeley, California. (Reprinted with supplement in 1976.)
13. Nickrent, D. L. (1987) *Parasitic Plants: Proceedings of the 4th International Symposium on Parasitic Flowering Plants* (Weber, H. C. and Forstreuter, W., eds), p. 597. Phillips Universität, Marburg, F.R.G.
14. Mathiasen, R. L. and Hawksworth, F. G. (1988) *For. Sci.* **34**, 429.
15. Swofford, D. L. and Selander, R. B. (1981) *BIOSYS-1* University of Illinois, Urbana.
16. Sneath, P. H. A. and Sokal, R. R. (1973) *Numerical Taxonomy*. W. H. Freeman, San Francisco.
17. Cavalli-Sforza, L. L. and Edwards, A. W. F. (1967) *Evolution* **21**, 550.
18. Nei, M. (1978) *Genetics* **89**, 583.
19. Crawford, D. J. (1983) *Isozymes in Plant Genetics and Breeding, Part A* (Tanksley, S. O. and Orton, T. J., eds), p. 257. Elsevier, Amsterdam.
20. Gorman, G. C. and Renzi, J., Jr (1979) *Copeia* **1979**, 242–249.
21. Archie, J. W., Simon, C. and Martin, A. (1989) *Evolution* **43**, 678.
22. Rohlf, F. J. (1982) *Mathemat. Biosci.* **59**, 131.