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## A Morphometric Analysis of *Arceuthobium campylopodum* and *Arceuthobium divaricatum* (Viscaceae)

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A MORPHOMETRIC ANALYSIS OF *ARCEUTHOBIMUM CAMPYLOPODUM* AND  
*ARCEUTHOBIMUM DIVARICATUM* (VISCACEAE)

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ABSTRACT

Although the classification of pinyon dwarf mistletoe (*Arceuthobium divaricatum*, Viscaceae) has not been controversial to any extent since Engelmann described it in 1878, a recent taxonomic treatment has included this species in western dwarf mistletoe (*A. campylopodum*). While pinyon dwarf mistletoe is only known to parasitize pinyon pines (*Pinus* subsection *Cembroides*), western dwarf mistletoe as it has been known since the late 1800s is a principal parasite of *Pinus ponderosa* and *P. jeffreyi* and has never been observed parasitizing pinyon pines. With reservations about the recent classification of pinyon dwarf mistletoe and its treatment under *A. campylopodum*, we undertook this study to examine in detail the morphological characteristics of pinyon dwarf mistletoe and compare them with those of western dwarf mistletoe. Pinyon and western dwarf mistletoe populations were sampled throughout most of their geographic ranges and morphological traits including plant, flower, fruit, and seed dimensions were measured. Thereafter, we compared morphological characteristics between *A. campylopodum* and *A. divaricatum* using univariate and multivariate statistics to determine significant differences among morphologies of both male and female plants. Our analyses clearly demonstrated that pinyon and western dwarf mistletoe are morphologically distinct as originally proposed by G. Engelmann in the late 19<sup>th</sup> century. Furthermore, the host affinities of the two taxa clearly distinguish them from each other. Therefore, we recommend that *A. campylopodum* and *A. divaricatum* continue to be classified as separate species. Morphological differences between these species are summarized and a key is provided for use in their field identification.

Key words: *Arceuthobium*, dwarf mistletoes, morphological characters, multivariate analyses, *Pinus*

INTRODUCTION

The dwarf mistletoes (*Arceuthobium* spp., Viscaceae) are among the most damaging parasites of commercially valuable conifers in the western United States and Canada (Hawskworth et al. 2002). Severely infected trees suffer reduced growth and premature mortality and are often predisposed to attack by insects. Two widespread and abundant dwarf mistletoes found in the western United States are *A. campylopodum* Engelm. (western dwarf mistletoe) and *A. divaricatum* Engelm. (pinyon dwarf mistletoe) (Hawskworth and Wiens 1972, 1996). Western dwarf mistletoe parasitizes several species of pines including *Pinus ponderosa* Douglas ex Lawson & C. Lawson (ponderosa pine), *P. jeffreyi* Grev. & Balf. (Jeffrey pine), *P. coulteri* D. Don (Coulter pine), and *P. attenuata* Lemmon (knobcone pine), but has never been reported parasitizing pinyon pines (*Pinus* subsection *Cembroides*) present in the West (Hawskworth and Wiens 1972, 1996). In contrast, pinyon dwarf mistletoe exclusively parasitizes pinyons, primarily *P. edulis* Engelm. (Colorado pinyon) and *P. monophylla* Torrey & Frém. (singleleaf pinyon). It has also been reported to infect *P. quadrifolia* Parlat. ex Sudw. (Parry pinyon), *P. cembroides*

Zucc. (Mexican pinyon), *P. discolor* D.K. Bailey & Hawksw. (border pinyon), *P. californiarum* D.K. Bailey (California singleleaf pinyon), and *P. californiarum* subsp. *fallax* (Little) D.K. Bailey (Arizona singleleaf pinyon). However, pinyon dwarf mistletoe only parasitizes these latter five pinyons in a few locations (Hawskworth and Wiens 1996). Major differences in the host affinities of these dwarf mistletoes based on field observations has led to the claim that *P. jeffreyi* is immune to infection by *A. divaricatum* and that *P. monophylla* is immune to infection by *A. campylopodum* (Hawskworth and Wiens 1996).

*Arceuthobium* has long been considered a taxonomically difficult genus because of the morphological and phenological similarities among taxa (Gill 1935; Hawskworth and Wiens 1972, 1996; Hawskworth et al. 2002). Morphological reduction and similarity and sexual dimorphism hamper identification of *Arceuthobium* taxa in the field and have resulted in major differences in taxonomic treatments. However, little disagreement regarding the classification of *A. divaricatum* at the specific level has been presented in the literature since the late 1800s when it was first described by George Engelmann (Engelmann 1878). In the first monograph of *Arceuthobium* in the United States, Gill (1935) classified *A. divaricatum* as a host form of *A. campylopodum* that exclusively parasitized pinyons and hence, under this system, any dwarf mistletoe found on a pinyon was classified as *A. campylopodum* (Engelm.) forma *divaricatum* (Engelm.) Gill. The host-form system proposed by Gill worked well for pinyon dwarf

mistletoe because no other dwarf mistletoes in the United States infect pinyons. However, this system did not work well in high elevation mixed conifer forests where other host forms of *A. campylopodum* were sympatric and, to varying degrees, parasitized more than one host. For example, Gill's host-form system classified all dwarf mistletoes parasitizing a true fir (*Abies* Mill.) as *A. campylopodum* Engelm. forma *abietinum* (Engelm.) Gill, even if the dwarf mistletoe also parasitized hemlock (*Tsuga* [Endl.] Carrière) in the same locality. Gill's treatment required that the mistletoe on hemlock be classified as *A. campylopodum* Engelm. forma *tsugensis* (Rosendahl) Gill, even though the mistletoe on the true fir and the mistletoe on the hemlock were morphologically identical; they were the same mistletoe. Gill's host-form system lacked the recognition that a dwarf mistletoe could cross-infect more than one host species at the same location, which resulted in classifying the same dwarf mistletoe as different forma due solely to the fact that it was on a different tree species.

The inadequacies of Gill's (1935) classification system soon became obvious, and in their first monograph of *Arceuthobium*, Hawksworth and Wiens (1972) classified all of Gill's host forms of *A. campylopodum* as species, including *A. divaricatum*, based on differences in morphology, phenology, chemistry, and host specificity. In their revised monograph for *Arceuthobium*, Hawksworth and Wiens (1996) maintained *A. divaricatum* as a separate species from *A. campylopodum*, based on their distinctive morphologies and host specificities. Maintaining *A. divaricatum* and *A. campylopodum* as separate species was further supported by isozyme (Nickrent 1986) and molecular analyses using nrDNA ITS and chloroplast *trn-L* sequences (Nickrent et al. 1994, 2004).

Despite the seemingly overwhelming evidence in the literature related to the classification of *Arceuthobium divaricatum* as a separate species from *A. campylopodum*, Kuijt included *A. divaricatum* under *A. campylopodum* in the revised Jepson Manual (Baldwin et al. 2012). The use of the revised Jepson Manual by many natural scientists in California has resulted in at least three problems: (1) populations of *A. divaricatum* are being identified as *A. campylopodum*, (2) herbarium specimens of *A. divaricatum* are being annotated as representing *A. campylopodum*, and (3) populations of *A. divaricatum* are appearing on maps as locations for *A. campylopodum*. An example of this third problem can be seen in the CALFLORA map for *A. campylopodum* (<http://www.calflora.org/>). By classifying *A. divaricatum* and 10 other taxa recognized by Hawksworth and Wiens (1996) as separate species under only one species, *A. campylopodum*, the utility of such maps for locating dwarf mistletoe populations by botanists and foresters working in California is greatly diminished (Mathiasen and Kenaley 2015a).

Because of the confusion created by the recent inclusion of *Arceuthobium divaricatum* under *A. campylopodum*, we undertook this study to further compare the morphological characteristics of these dwarf mistletoes. We sampled male and female plants, flowers, fruits, and seeds for these dwarf mistletoes on their respective pine hosts throughout most of their geographic ranges. We then applied both univariate and multivariate statistical analyses to compare the morphological characteristics of plants, flowers, fruits, and seeds from the sampled populations.

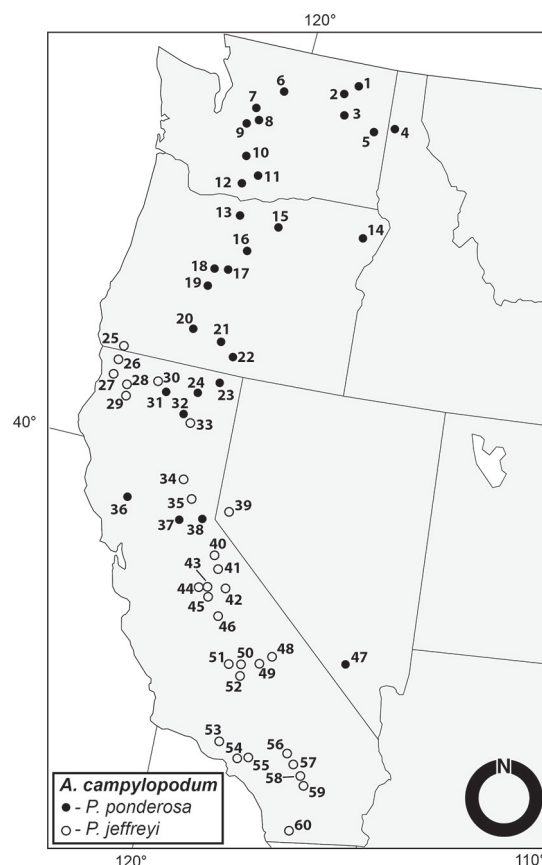


Fig. 1. Approximate locations of collection sites for *Arceuthobium campylopodum* in California, Idaho, Nevada, Oregon, and Washington. Filled circles represent locations where plants were collected from *Pinus ponderosa*. Open circles represent locations where plants were collected from *P. jeffreyi*. Numbers correspond to locations in Appendix 1 (map reproduced with permission by the California Botanical Society (Madroño 62: 6).

## MATERIALS AND METHODS

### Morphological Measurements

Morphological data for *A. campylopodum* from 60 populations, 30 each from *Pinus ponderosa* and *P. jeffreyi*, (Mathiasen and Kenaley 2015a; Fig. 1 and Appendix 1) was augmented by morphological data collected for *A. divaricatum* from 60 populations distributed through most of its geographic range in 2014–2015 (Fig. 2 and Appendix 2). Most of these populations were from locations where *A. divaricatum* was parasitizing *Pinus edulis* (30 populations), but we also sampled 23 populations of *A. divaricatum* on *P. monophylla*, and seven populations on *P. californiarum* subsp. *fallax* (Fig. 2). Because we were only able to sample one population of *A. divaricatum* parasitizing *P. californiarum* subsp. *californiarum* in southern California, one population parasitizing *P. cembroides* in western Texas, and two populations of *A. divaricatum* on *P. discolor* in New Mexico, we have not included morphological measurements for plants from those hosts in our results. Voucher specimens for *A. campylopodum* and *A. divaricatum* consisting of the mistletoe with host material were deposited at the University of Arizona Herbarium, Tucson (ARIZ), the Herbarium of Rancho Santa Ana Botanical Garden, Claremont, CA (RSA), or the Deaver

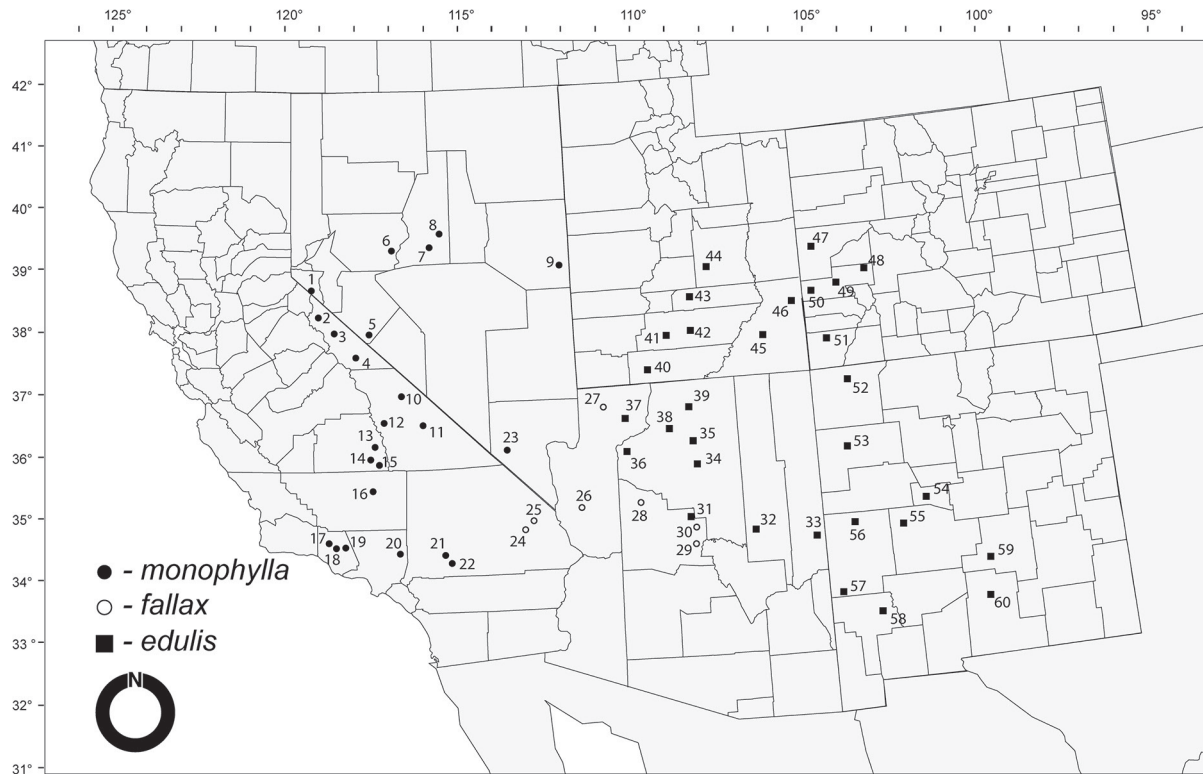


Fig. 2. Approximate locations of collection sites for *Arceuthobium divaricatum* in Arizona, California, Colorado, Nevada, New Mexico, and Utah. Filled circles represent locations where plants were collected from *Pinus monophylla*. Open circles represent locations where plants were collected from *P. californiarum* subsp. *fallax*. Filled squares represent locations where plants were collected from *P. edulis*. Numbers correspond to locations in Appendix 2.

Herbarium, Northern Arizona University, Flagstaff (ASC). Voucher and specific population data, including collection numbers, collection dates, and GPS coordinates, have been archived electronically in SEINet (Southwest Environmental Information Network: (<http://swbiodiversity.org/portall/index.php>) or the Consortium of California Herbaria (<http://lucjeps.berkeley.edu/consortium>).

For each mistletoe population, 10 male and 10 female plants were randomly collected and the dominant plant (largest plant) of each sex was used for morphological measurements. The dwarf mistletoe plant characters measured were those used by Hawksworth and Wiens (1996) for their taxonomic classification of *Arceuthobium*. These included: (1) height, basal diameter, third internode length and width, and color of male and female plants; (2) mature fruit length, width, and color from female plants; (3) seed length, width and color; (4) length and width of mature staminate spikes; (5) staminate flower diameters for 3- and 4-merous flowers (4-merous flowers were rarely observed for *A. divaricatum*); (6) length and width of staminate flower petals; and (7) anther diameter and anther distance from the petal tip.

Plants typically were measured within 12 h, but no later than 24 h after collection. Only plants attached to their host's branch and fully turgid were measured. Quantitative measurements were made using a digital caliper (Mitutoyo America Corp., Aurora, IL) and a 7X hand lens equipped with a micrometer (Bausch & Lomb, Bridgewater, NJ). The basal diameter of plants was measured at the point where the plant was attached to the host branch. The width and length of the third internode above the

base of plants was included in our morphological analyses because these characters have been frequently reported for dwarf mistletoes and provide information on the relative size and thickness of male and female plants (Hawksworth and Wiens 1972, 1996; Mathiasen and Daugherty 2007, 2009a, 2009b, 2013; Mathiasen and Kenaley 2015a, 2015b). The length of the third internode was determined by measuring from the top of the second internode above the base of a plant to the top of the third internode, locations which are easily observed (see Fig. 2.1 and 2.3 in Hawksworth and Wiens 1996). The width of the third internode was measured at its midpoint. Staminate spike and flower measurements were made during the peak of anthesis. Likewise, fruit and seed measurements were made during the peak of seed dispersal.

#### Statistical Analyses

We assessed whether mean values for morphological characters differed significantly between the two dwarf mistletoes and between comparable characters from plants parasitizing *Pinus edulis*, *P. monophylla*, and *P. californiarum* subsp. *fallax* using one-way analysis of variance (ANOVA) and, when appropriate, a posthoc Tukey's Honestly Significant Difference (HSD) Test ( $\alpha = 0.05$ ) (Zimmerman 2004). Quadratic discriminant function analyses (DFA) were also performed separately to assess whether female or male plants of *A. campylopodum* and *A. divaricatum* can be delimited to species according to morphological characters (predicted versus actual; Quinn and Keough 2002; Fig. 3). Discriminant function analyses for female and male plants were conducted



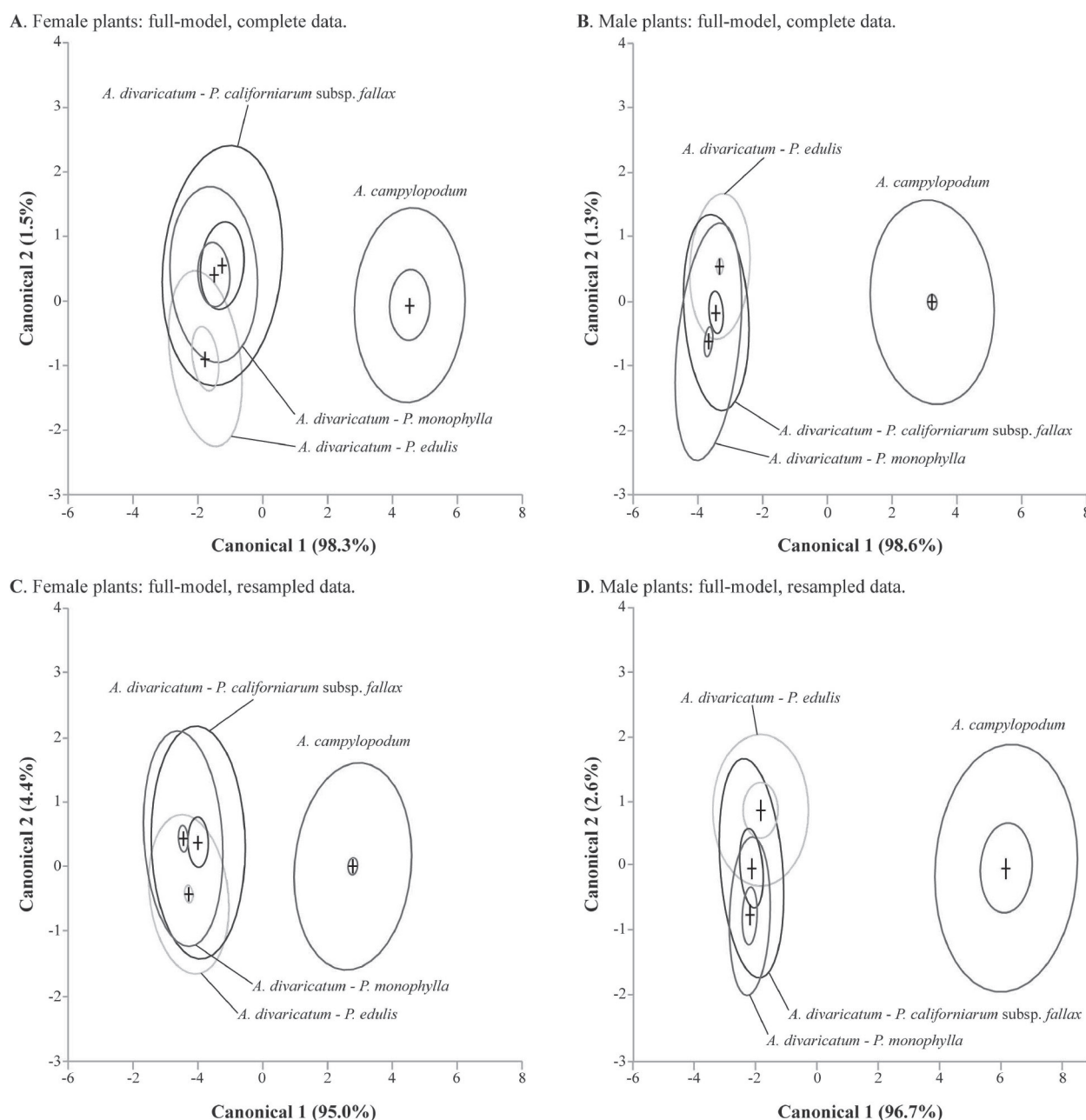


Fig. 3. Canonical plots for discriminant function analyses (DFA) of *Arceuthobium campylopodum* and, according to host, *A. divaricatum* based on morphological characteristics of female (A, C) and male plants (B, D). Multivariate means (cross-hairs) were calculated using complete data for each species by sex (A, B), whereas, to further validate the DFA, means were also calculated using resampled data (25 complete records/species) of female (C) and male plants (D), respectively. For each species (A–D), the inner ellipse is a 95% confidence limit for the mean, and the outer ellipse is a normal contour where approximately 50% of plants for each species reside. Correct classification percentages for male and female plants by DFA (complete and resampled) are presented in Table 6.

on two separate datasets: (1) complete records for *A. campylopodum* as well as *A. divaricatum* partitioned by host (i.e., *P. edulis*, *P. monophylla*, and *P. californiarum* subsp. *fallax*), and (2) complete records for *A. campylopodum* and, collectively, *A. divaricatum* across all three hosts combined. Actual host or species membership was defined a priori via field diagnosis and, although previous molecular analyses supported the separation of *A. campylopodum* and *A. divaricatum* at the specific level (Nickrent 1986; Nickrent et al. 2004), female and male DFAs were executed using equal

prior probabilities for each host-dwarf mistletoe combination (25%, partitioned dataset) or species (50%, combined dataset) rather than proportional to their actual host and/or species membership. Discriminant function analyses were parameterized to include equal prior probabilities in order to remove experimental bias (i.e., a priori identification) from the posthoc classification (% predicted/actual) of dwarf mistletoes by host-dwarf mistletoe combination and species membership. For comparisons of species membership, standardized correlation coefficients for morphological characters were also calculated

Table 1. Morphological measurements for *Arceuthobium campylopodum* collected from *Pinus jeffreyi* and *P. ponderosa* and for *A. divaricatum* collected from *P. edulis*, *P. monophylla*, and *P. californiarum* subsp. *fallax*. Data are listed as mean, (SD), range, [n]. Means followed by different capital letters in the same row were significantly different using ANOVA ( $\alpha = 0.05$ ). Lower case letters in brackets designate sample sizes already listed in the same column. Plant heights are in cm and all other measurements in mm.

Character	<i>Arceuthobium campylopodum</i>	<i>Arceuthobium divaricatum</i>
Plant height		
Female	10.4 A (2.7) 3.9–25.4 [600a]	10.9 B (2.7) 5.2–22.7 [600a]
Male	9.7 A (3.0) 3.6–21.6 [a]	11.7 B (3.3) 5.7–30.4 [a]
Basal diameter		
Female	3.4 A (0.7) 1.7–6.9 [a]	2.6 B (0.5) 1.3–5.0 [a]
Male	3.2 A (0.6) 1.8–6.8 [a]	2.6 B (0.5) 1.6–4.9 [a]
Length of third internode		
Female	13.0 A (3.1) 5.7–29.3 [a]	11.6 B (2.6) 5.8–21.9 [a]
Male	12.0 A (3.3) 4.2–23.2 [a]	11.7 A (2.6) 5.5–21.8 [a]
Width of third internode		
Female	2.5 A (0.4) 1.6–2.7 [a]	1.9 B (0.3) 1.2–3.2 [a]
Male	2.5 A (0.4) 1.4–2.6 [a]	1.9 B (0.3) 1.2–3.1 [a]
Staminate spike length	12.7 A (4.8) 3.7–41.0 [760b]	9.5 B (3.1) 3.2–31.8 [580b]
Staminate spike width	3.0 A (0.3) 2.3–4.2 [b]	1.7 B (0.1) 1.1–2.3 [b]
Flower diameter		
3-merous	3.1 A (0.4) 3.1–4.5 [400]	2.2 B (0.3) 1.4–3.2 [b]
4-merous	4.2 A (0.5) 3.0–6.2 [360]	3.1 B (0.3) 2.2–4.1 [50]
Petal lobe length	1.6 A (0.2) 0.9–2.4 [b]	1.1 B (0.1) 0.7–1.6 [b]
Petal lobe width	1.4 A (0.2) 0.7–2.4 [b]	1.0 B (0.1) 0.6–1.5 [b]
Anther diameter	0.6 A (0.1) 0.4–1.2 [b]	0.4 B (0.1) 0.3–0.7 [b]
Anther distance from tip	0.6 A (0.1) 0.2–1.1 [b]	0.4 B (0.1) 0.2–0.8 [b]
Fruit length	5.4 A (0.5) 4.0–7.2 [480c]	4.4 B (0.3) 3.2–5.3 [590c]
Fruit width	3.7 A (0.4) 2.6–5.6 [c]	2.6 B (0.2) 1.9–3.5 [c]
Seed length	3.5 A (0.4) 2.3–4.7 [c]	2.2 B (0.3) 1.6–3.1 [c]
Seed width	1.5 A (0.2) 1.0–2.0 [c]	1.1 B (0.1) 0.8–1.3 [c]

to determine the overall contribution of each character to the discriminant function. Likewise, when appropriate, stepwise DFA was utilized to examine systematically the smallest number of morphological characteristics, female or male, resulting in the highest percentage in correct classification (% predicted/actual). To further validate the DFAs, we resampled separately the partitioned and collective data for female and male plants; selecting at random 25 complete records per host-dwarf mistletoe combination or species and re-executed the DFA to include all female or male morphological characters simultaneously (full-model) with each plant receiving equal prior probabilities. Analysis of variance tests and DFAs were computed in JMP Pro 12 (SAS Institute, Cary, North Carolina).

## RESULTS

### Morphological Differences

The mean heights of female and male plants of *Arceuthobium campylopodum* were significantly smaller than those of *A. divaricatum* (Table 1). However, even though the mean heights of male plants varied by 2 cm, the mean height of female plants only varied by 0.5 cm. The mean length of the third internode of female plants was significantly different between taxa, but the mean length of the third internode of male plants was not significantly different. Male and female plants of *A. divaricatum* were more slender than those of *A. campylopodum* with both the mean basal diameter and mean width of the third internode for both sexes being significantly smaller for *A. divaricatum* (Table 1).

The staminate spikes of *Arceuthobium campylopodum* were significantly longer on average and the width of staminate spikes was significantly wider than for *A. divaricatum*; the mean width of staminate spikes of *A. divaricatum* being nearly half as wide as those of *A. campylopodum*. A major difference between *A. campylopodum* and *A. divaricatum* was that the latter species predominantly produced 3-merous staminate flowers whose mean diameter (2.2 mm) was significantly smaller than that of the 3-merous flowers of *A. campylopodum* (3.1 mm; Table 1). The mean diameter of 4-merous flowers was also significantly smaller for *A. divaricatum*, but 4-merous flowers were only occasionally observed and measured for populations of *A. divaricatum*; only eight populations were observed with a few 4-merous flowers. The smaller size of the staminate flowers of *A. divaricatum* was a result of its significantly smaller mean petal length and width. Mean anther diameter (0.4 mm) and the distance of anthers from the tips of petals also were both significantly smaller for *A. divaricatum* than *A. campylopodum* (Table 1). Similarly, mean fruit length was much larger for *A. campylopodum* (5.4 mm) than for *A. divaricatum* (4.4 mm), as was the mean width of fruits. Mean seed length and width were also significantly different between the two species (Table 1).

Plant color is not usually an informative character for distinguishing between dwarf mistletoes. However, the color of plants of *A. divaricatum* was distinctly different from those of *A. campylopodum*, the former being consistently brown or dark brown to green-brown compared to the latter which ranged from yellow, yellow-brown, or light brown (Fig. 4–5). Sometimes male plants of *A. divaricatum* were red-brown, yellow-





Fig. 4–5. Color variation between *Arceuthobium campylopodum* and *A. divaricatum*.—4. Female plants of *A. campylopodum* with nearly mature fruits in July. Note that plants are yellow-brown.—5. Female plants of *A. divaricatum* with nearly mature fruits in August. Note that plants are brown-green.

Table 2. Morphological measurements for *Arceuthobium divaricatum* from *Pinus edulis*, *P. monophylla*, and *P. californiarum* subsp. *fallax*. Data are listed as mean, (SD) [n]. Means followed by different capital letters in the same row were significantly different using ANOVA followed by a Tukey's Post Hoc HSD test ( $\alpha = 0.05$ ). Lower case letters in brackets designate sample sizes already listed in the same column. Plant heights are in cm and all other measurements in mm.

Character	<i>Pinus edulis</i>	<i>Pinus monophylla</i>	<i>Pinus californiarum</i> subsp. <i>fallax</i>
Plant height			
Female	10.1 A (2.2) [300a]	11.8 B (2.9) [230a]	11.5 B (2.9) [70a]
Male	10.6 A (2.3) [a]	13.0 B (3.8) [a]	12.2 B (3.6) [a]
Basal diameter			
Female	2.6 A (0.5) [a]	2.6 A (0.5) [a]	2.6 A (0.4) [a]
Male	2.5 A (0.5) [a]	2.4 A (0.5) [a]	2.4 A (0.5) [a]
Length of third internode			
Female	11.3 A (2.5) [a]	11.9 B (2.6) [a]	11.6 AB (2.8) [a]
Male	11.5 A (2.4) [a]	12.0 A (2.7) [a]	11.4 A (2.6) [a]
Width of third internode			
Female	1.9 A (0.3) [a]	1.9 A (0.3) [a]	2.0 B (0.3) [a]
Male	1.9 A (0.3) [a]	2.0 A (0.3) [a]	1.9 A (0.3) [a]
Staminate spike length	9.5 A (3.3) [280b]	9.3 A (2.8) [a]	9.7 A (3.3) [a]
Staminate spike width	1.7 A (0.1) [b]	1.7 A (0.1) [a]	1.7 A (0.1) [a]
Flower diameter			
3-merous	2.2 A (0.2) [b]	2.2 A (0.2) [a]	2.2 A (0.2) [a]
Petal lobe length	1.1 A (0.2) [b]	1.0 A (0.2) [a]	1.1 A (0.2) [a]
Petal lobe width	1.0 A (0.1) [b]	1.0 A (0.1) [a]	1.0 A (0.1) [a]
Anther diameter	0.4 A (0.1) [b]	0.4 A (0.1) [a]	0.4 A (0.1) [a]
Anther distance from tip	0.4 A (0.1) [b]	0.3 B (0.1) [a]	0.4 A (0.1) [a]
Fruit length	4.4 A (0.4) [290c]	4.3 A (0.3) [a]	4.4 A (0.3) [a]
Fruit width	2.6 A (0.3) [c]	2.6 B (0.2) [a]	2.7 A (0.2) [a]
Seed length	2.1 A (0.2) [c]	2.2 B (0.3) [a]	2.3 C (0.3) [a]
Seed width	1.1 A (0.1) [c]	1.1 A (0.1) [a]	1.0 A (0.1) [a]

brown or even yellow-green; very few female plants of *A. divaricatum* were these colors.

Because *Arceuthobium divaricatum* parasitizes several different pinyons, we compared the morphological characteristics of male and female plants from three of its pinyon hosts (Table 2). The heights of male and female plants collected from *Pinus monophylla* and *P. californiarum* subsp. *fallax* were significantly larger than those collected from *P. edulis*. Although female and male plants collected from *P. californiarum* subsp. *fallax* were shorter on average than those collected from *P. monophylla*, the means were not significantly different. No other significant differences were detected among the morphological characters measured for plants, flowers, or fruits from the different pinyon hosts. The mean seed length found in the three pinyon hosts was significantly different but only by 0.1 mm, and the mean width of seeds was not significantly different (Table 2). Because the mean heights of male and female plants collected from *P. monophylla* and *P. californiarum* subsp. *fallax* were not significantly different, we combined morphological measurements for plants, flowers, fruits, and seeds from those hosts and compared them to measurements for these characters from only *P. edulis* (Table 3). Again, only the mean heights of female and male plants and mean seed lengths were significantly different. We then compared characters measured from *P. edulis* and pooled measurements from *P. monophylla* and *P. californiarum* subsp. *fallax* with those of *A. campylopodum* (Table 4). The mean heights of female plants from *P. edulis* were not significantly different to those of *A. campylopodum*, but the mean values for all other characters (except third internode length of male plants) of *A. divaricatum* were significantly different from those of *A. campylopodum*.

Although *Arceuthobium campylopodum* and *A. divaricatum* have been reported to flower at approximately the same time (late August to late September), we observed that *A. divaricatum* started flowering in early August, at least two weeks earlier than *A. campylopodum*. Flowering periods of *A. campylopodum* and *A. divaricatum* did overlap in mid to late August; however, these dwarf mistletoes were not found in the same stands and the difference in the start of flowering we observed in California may have been related to the lower elevations where we made our observations for *A. divaricatum*. Seed dispersal of these species occurs from late August to late September, but some populations of *A. divaricatum* at the lowest elevations of its geographic range disperse seed into late October; elevation and its influence on climate may be the primary reason why *A. divaricatum* disperses seed later in the fall than *A. campylopodum* in California.

#### Discriminant Function Analyses

Because some variation in male and female morphologies in *Arceuthobium divaricatum* was evident among the three pinyon hosts, DFA was conducted first on separate female and male plant datasets consisting of measurements of morphological characters from *A. campylopodum* as well as *A. divaricatum* partitioned according to host. Results from these analyses indicated significant differences for the eight female morphological characters of *A. campylopodum* and, partitioned by host, *A. divaricatum* (Wilks'  $\lambda = 0.1201$ , Approx.  $F_{24,3043} = 136.48$ ,  $P < 0.0001$ ; Pillai's Trace = 0.9702, Approx.  $F_{24,3153} = 62.80$ ,  $P < 0.0001$ ). Likewise, significant differences were also found among the 10 male plant characteristics examined for *A. divaricatum* by host and *A. campylopodum* (Wilks'  $\lambda = 0.0702$ ,



Table 3. Morphological measurements for *Arceuthobium divaricatum* from *Pinus edulis* and from *P. monophylla* and *P. californiarum* subsp. *fallax* combined. Data are listed as mean, (SD), range, [n]. Means followed by different capital letters in the same row were significantly different using ANOVA ( $\alpha = 0.05$ ). Lower case letters in brackets designate sample sizes already listed in the same column. Plant heights are in cm and all other measurements in mm.

Character	<i>Arceuthobium divaricatum</i> on <i>Pinus edulis</i>	<i>Arceuthobium divaricatum</i> on <i>Pinus monophylla</i> and <i>P. californiarum</i> subsp. <i>fallax</i>
Plant height		
Female	10.1 A (2.2) 5.2–16.8 [300a]	11.8 B (2.9) 6.3–22.7 [300a]
Male	10.6 A (2.3) 5.7–20.4 [a]	12.8 B (3.8) 5.9–30.4 [a]
Basal diameter		
Female	2.6 A (0.5) 1.7–5.0 [a]	2.6 A (0.5) 1.3–4.4 [a]
Male	2.5 A (0.5) 1.6–4.9 [a]	2.4 A (0.5) 1.6–4.2 [a]
Length of third internode		
Female	11.3 A (2.5) 5.8–20.6 [a]	11.8 A (2.6) 6.9–21.9 [a]
Male	11.5 A (2.4) 5.5–20.1 [a]	11.9 A (2.7) 6.0–21.8 [a]
Width of third internode		
Female	1.9 A (0.3) 1.3–3.0 [a]	1.9 A (0.3) 1.2–3.2 [a]
Male	1.9 A (0.3) 1.2–3.0 [a]	1.9 A (0.3) 1.3–3.1 [a]
Staminate spike length	9.5 A (3.3) 4.1–31.8 [280b]	9.4 A (2.9) 3.2–21.4 [a]
Staminate spike width	1.7 A (0.1) 1.1–2.3 [b]	1.7 A (0.1) 1.3–2.0 [a]
Flower diameter 3-merous	2.2 A (0.3) 1.4–3.1 [b]	2.2 A (0.3) 1.4–3.2 [a]
Petal lobe length	1.1 A (0.2) 0.7–1.6 [b]	1.1 A (0.2) 0.7–1.6 [a]
Petal lobe width	1.0 A (0.1) 0.6–1.4 [b]	1.0 A (0.1) 0.6–1.5 [a]
Anther diameter	0.4 A (0.1) 0.3–0.7 [b]	0.4 A (0.1) 0.3–0.6 [a]
Anther distance from tip	0.4 A (0.1) 0.2–0.7 [b]	0.4 A (0.2) 0.2–0.8 [a]
Mean fruit length	4.4 A (0.4) 3.2–5.3 [290c]	4.4 A (0.3) 3.4–5.1 [a]
Mean fruit width	2.6 A (0.3) 1.9–3.5 [c]	2.6 A (0.2) 1.9–3.2 [a]
Seed length	2.1 A (0.2) 1.6–2.8 [c]	2.2 B (0.3) 1.6–3.1 [a]
Seed width	1.1 A (0.1) 0.8–1.3 [c]	1.1 A (0.1) 0.8–1.3 [a]

Table 4. Comparison of morphological measurements for *Arceuthobium divaricatum* and *A. campylopodum*: *A. divaricatum* data is from *Pinus monophylla* and *P. californiarum* subsp. *fallax* combined, and *P. edulis* alone. Data are listed as mean, (SD) [n]. Means followed by different capital letters in the same row were significantly different using ANOVA followed by a Tukey's Post Hoc HSD test ( $\alpha = 0.05$ ). Lower case letters in brackets designate sample sizes already listed in the same column. Plant heights are in cm and all other measurements in mm.

Character	<i>Arceuthobium divaricatum</i> from <i>Pinus edulis</i>	<i>Arceuthobium divaricatum</i> from <i>Pinus monophylla</i> and <i>P. californiarum</i> subsp. <i>fallax</i>	<i>Arceuthobium campylopodum</i>
Plant height			
Female	10.1 A (2.2) [300a]	11.8 B (2.9) [230a]	10.4 A (2.7) [600a]
Male	10.6 A (2.3) [a]	12.8 B (3.8) [a]	9.7 C (3.0) [a]
Basal diameter			
Female	2.6 A (0.5) [a]	2.6 A (0.5) [a]	3.4 B (0.7) [a]
Male	2.5 A (0.5) [a]	2.4 A (0.5) [a]	3.2 B (0.6) [a]
Length of third internode			
Female	11.3 A (2.5) [a]	11.8 B (2.6) [a]	13.0 B (3.1) [a]
Male	11.5 A (2.4) [a]	11.9 A (2.7) [a]	11.9 A (3.3) [a]
Width of third internode			
Female	1.9 A (0.3) [a]	1.9 A (0.3) [a]	2.5 B (0.4) [a]
Male	1.9 A (0.3) [a]	1.9 A (0.3) [a]	2.5 B (0.4) [a]
Staminate spike length	9.5 A (3.3) [280b]	9.4 A (2.9) [a]	12.7 B (4.8) [760b]
Staminate spike width	1.7 A (0.1) [b]	1.7 A (0.1) [a]	3.0 B (0.3) [b]
Flower diameter 3-merous	2.2 A (0.2) [b]	2.2 A (0.2) [a]	3.1 B (0.4) [400c]
Petal lobe length	1.1 A (0.2) [b]	1.1 A (0.2) [a]	1.6 B (0.2) [c]
Petal lobe width	1.0 A (0.1) [b]	1.0 A (0.2) [a]	1.4 B (0.2) [c]
Anther diameter	0.4 A (0.1) [b]	0.4 A (0.1) [a]	0.6 B (0.1) [c]
Anther distance from tip	0.4 A (0.1) [b]	0.4 B (0.1) [a]	0.6 C (0.1) [c]
Mean fruit length	4.4 A (0.4) [290c]	4.4 A (0.3) [a]	5.4 B (0.5) [480d]
Mean fruit width	2.6 A (0.3) [c]	2.6 B (0.2) [a]	3.7 B (0.4) [d]
Seed length	2.1 A (0.2) [c]	2.2 B (0.3) [a]	3.5 C (0.4) [d]
Seed width	1.1 A (0.1) [c]	1.1 A (0.1) [a]	1.5 B (0.2) [d]

Table 5. Summary of the principal characters separating *Arceuthobium campylopodum* and *A. divaricatum*. Data for morphological characters are means; plant heights in cm and all other measurements in mm. Numbers in bold represent key morphological differences between the taxa.

Character	<i>Arceuthobium campylopodum</i>	<i>Arceuthobium divaricatum</i>
Plant height		
Female	10.4	10.9
Male	9.7	11.7
Plant color	Yellow, yellow-brown	Olive-green, green, dark brown
Basal diameter		
Female	3.4	2.6
Male	3.2	2.6
Width of third internode		
Female	2.5	1.9
Male	2.5	1.9
Staminate spike width	3	1.7
Flower diameter		
3-merous	3.1	2.2
4-merous	4.2	3.1
Petal length	1.6	1.1
Petal width	1.4	1
Fruit length	5.4	4.4
Fruit width	3.7	2.6
Seed length	3.5	2.2
Seed width	1.5	1.1
Host(s) <sup>a</sup>		
Principal	<i>Pinus jeffreyi</i> ; <i>P. ponderosa</i> var. <i>ponderosa</i>	<i>Pinus californiarum</i> subsp. <i>fallax</i> ; <i>P. cembroides</i> ; <i>P. discolor</i> ; <i>P. edulis</i> ; <i>P. monophylla</i> ; <i>P. quadrifolia</i>
Secondary	<i>P. attenuata</i> ; <i>P. coulteri</i>	None
Occasional	<i>P. contorta</i> var. <i>murrayana</i> and var. <i>latifolia</i> ; <i>P. sabiniana</i>	None
Rare	<i>P. lambertiana</i>	None
Immune	<i>P. monophylla</i>	<i>P. jeffreyi</i> ; <i>P. ponderosa</i> var. <i>scopulorum</i>

<sup>a</sup> Host susceptibility classification based on information in Hawksworth and Wiens (1996) from their field observations only.

Approx.  $F_{30,3367.3} = 165.16$ ,  $P < 0.0001$ ; Pillai's Trace = 1.0581, Approx.  $F_{30,3447} = 62.61$ ,  $P < 0.0001$ ). The first two discriminant functions (canonicals) for the DFA of female and male plants accounted for  $\geq 98.3\%$  and  $\leq 1.3\%$  of the total variation (Fig. 3), whereas the third discriminant function for female and male plants accounted for  $\leq 0.22$  of the total variation. Female and male plants of *A. campylopodum* were readily distinguished morphologically from *A. divaricatum* on all three pinyons because 100% (600/600) and 99.8% (479/480) of male and female plants diagnosed a priori as *A. campylopodum* were predicted correctly (% predicted/actual) to this species using 8 and 10 morphological characters, respectively (Table 6). However, samples of female or male plants of *A. divaricatum* from the various pinyon hosts, analyzed as above, were indistinguishable (Table 6; Fig. 3).

Female plants of *A. divaricatum* collected from *P. edulis* were often misclassified to *P. monophylla* (18.6%) and *P. californiarum* subsp. *fallax* (12.4%). Likewise, *A. divaricatum* on *P. monophylla* and *P. californiarum* subsp. *fallax* were consistently and incorrectly classified  $\geq 34.1\%$  of the time as parasitizing *P. edulis*.

A similar pattern in misclassification was also apparent for predicting host trees of *A. divaricatum* according to morphological characteristics of male plants, where the host tree was predicted correctly only 72.9%, 57.1%, and 62.9% of the time for male plants infecting *P. edulis*, *P. monophylla*, and *P. californiarum* subsp. *fallax*, respectively (Table 6). Although the precision in classification of *A. divaricatum* to its pinyon host increased markedly following DFAs on a randomized resample of female and male plants, the female plants of *A. divaricatum* on *P. monophylla* and *P. californiarum* subsp. *fallax* were, again, frequently misclassified and placed correctly to host only 68% of the time. Thus, morphological measurements for male and female plants on all pinyon hosts were combined (combined datasets) to further assess species membership between *A. divaricatum* and *A. campylopodum* as well as identify the morphological characters contributing most to interspecific separation.

Means and associated 95% confidence intervals for morphological characters of female and male plants across predicted species according to full-model DFA are presented in Table 7. Discriminant function analysis using separately eight female and 10 male morphological characters (full-model) clearly demonstrated separation of *Arceuthobium campylopodum* and *A. divaricatum*;  $\geq 98.3\%$  of female and male plants identified via field diagnosis as *A. divaricatum* or *A. campylopodum* were predicted correctly to species (Table 8). For DFA of female plants, results indicated significant differences between multivariate means for *A. campylopodum* and *A. divaricatum* (Wilks'  $\lambda = 0.1353$ , Exact  $F_{8,1051} = 839.06$ ,  $P < 0.0001$ ; Hotelling-Lawley Trace = 6.3868, Exact  $F_{8,1051} = 839.06$ ,  $P < 0.0001$ ; Pillai's Trace = 0.8646, Exact  $F_{8,1051} = 839.06$ ,  $P < 0.0001$ ). The discriminant function accounted for 100% of the total variation as only one dimension is possible when assigning two groups. Female plants of *Arceuthobium divaricatum* were correctly classified (predicted/actual) to species 98.3% (570/580) of the time, and hence the percentage of female *A. divaricatum* assigned to *A. campylopodum* was only 1.7% (10/580). Similarly, 100% of female *A. campylopodum* were classified correctly when considering all eight female morphological characters. Examination of the standardized correlation coefficients (scc) indicated that seed length (scc = 1.63), width of the third internode (scc = 1.48), and fruit width (scc = 0.85) were most strongly correlated with the discriminant function, thereby contributing most to defining species membership for female plants. Using these three characters alone, female plants of *A. campylopodum* and *A. divaricatum* were classified correctly to species 100% (480/480) and 97.9% (568/580) of the time, respectively. Moreover, with the addition of plant height, fruit length, and length of the third internode as predictor variables, the percentage of female *A. divaricatum* predicted correctly to species increased slightly to 98.6% (572/580)—the highest correct classification percentage achieved for female *A. divaricatum* by either the full-model or stepwise-DFA (Table 8).

Table 6. Discriminant function analyses (DFAs) of female and male plants using complete records and resampled data for *Arceuthobium campylopodum* and, partitioned by pinyon host, *A. divaricatum*. Data are presented as: correct classification (count [N]), % [predicted/actual].

	Total (N)	<i>Arceuthobium campylopodum</i>	<i>Arceuthobium divaricatum</i>		
			<i>Pinus edulis</i>	<i>Pinus californiarum</i> subsp. <i>fallax</i>	<i>Pinus monophylla</i>
Complete – Female					
<i>A. campylopodum</i>	480	479, 99.8%	0, 0.0%	1, 0.2%	0, 0.0%
<i>A. divaricatum</i>					
<i>P. edulis</i>	290	3, 1.0%	197, 67.9%	36, 12.4%	54, 18.6%
<i>P. californiarum</i> subsp. <i>fallax</i>	70	0, 0.0%	29, 41.4%	32, 45.7%	9, 12.9%
<i>P. monophylla</i>	220	2, 0.9%	75, 34.1%	35, 15.9%	108, 49.1%
Resample – Female					
<i>A. campylopodum</i>	25	25, 100%	0, 0.0%	0, 0.0%	0, 0.0%
<i>A. divaricatum</i>					
<i>P. edulis</i>	25	0, 0.0%	23, 92.0%	0, 0.0%	2, 8.0%
<i>P. californiarum</i> subsp. <i>fallax</i>	25	0, 0.0%	7, 28.0%	17, 68.0%	1, 4.0%
<i>P. monophylla</i>	25	0, 0.0%	4, 16.0%	4, 16.0%	17, 68.0%
Complete – Male					
<i>A. campylopodum</i>	600	600, 100%	0, 0.0%	0, 0.0%	0, 0.0%
<i>A. divaricatum</i>					
<i>P. edulis</i>	280	1, 0.4%	204, 72.9%	44, 15.7%	31, 11.1%
<i>P. californiarum</i> subsp. <i>fallax</i>	70	0, 0.0%	16, 22.9%	44, 62.9%	10, 14.3%
<i>P. monophylla</i>	210	0, 0.0%	46, 21.9%	44, 21.0%	120, 57.1%
Resample – Male					
<i>A. campylopodum</i>	25	25, 100%	0, 0.0%	0, 0.0%	0, 0.0%
<i>A. divaricatum</i>					
<i>P. edulis</i>	25	0, 0.0%	23, 92.0%	2, 8.0%	0, 0.0%
<i>P. californiarum</i> subsp. <i>fallax</i>	25	0, 0.0%	2, 8.0%	21, 84.0%	2, 8.0%
<i>P. monophylla</i>	25	0, 0.0%	4, 16.0%	2, 8.0%	22, 88.0%

Significant differences among 10 male morphological characters of *Arceuthobium campylopodum* and *A. divaricatum* were also revealed by DFA (Wilks'  $\lambda = 0.0824$ , Exact  $F_{10,1149} = 1279.59$ ,  $P < 0.0001$ ; Hotelling-Lawley Trace = 11.1366, Exact  $F_{10,1149} = 1279.59$ ,  $P < 0.0001$ ; Pillai's Trace = 0.9176, Exact  $F_{10,1149} = 1279.59$ ,  $P < 0.0001$ ), classifying correctly 100% (600/600) and 99.8% (559/560) of male plants identified a priori to *A. campylopodum* and *A. divaricatum*, respectively. Staminate spike width (scc = 0.97) was most strongly correlated to the discriminant function and, using this morphological character alone (i.e., minus all other male plant measurements), resulted in the total correct classification to species of 99.8% (1158/1160) across all male plants—100% (600/600) *A. campylopodum* and 99.6% (558/560) *A. divaricatum* (Table 8). Therefore, although univariate statistics presented herein demonstrated significant differences between *A. campylopodum* and *A. divaricatum* across 9 of 10 male characters used in the full-model DFA, utilizing the other eight male characters (e.g., plant height, basal diameter, staminate spike length, anther measurements, etc.) within the DFA model were unnecessary to delimit male plants to species since DFA using only staminate spike width correctly predicted species membership for all but two male plants of *A. divaricatum* (Table 8).

#### DISCUSSION

Classifying *Arceuthobium campylopodum* and *A. divaricatum* as conspecific or the latter species as a subspecies of *A. campylopodum* is not supported by our analyses of the morphological characters for these taxa as both species can

Table 7. Discriminant function analyses (DFA) of male and female plants: comparison of morphological characters by predicted classification to *A. campylopodum* and *A. divaricatum* using complete data per taxon. Ninety-five percent confidence intervals ( $\pm$ ) were computed for comparison of mean differences. Combined analysis of plants on *Pinus edulis*, *P. monophylla*, and *P. californiarum* subsp. *fallax*.

Character by plant sex	Comparison between species (predicted)	
	<i>Arceuthobium campylopodum</i>	<i>Arceuthobium divaricatum</i>
Female		
Plant height (PH)	10.3 ( $\pm 0.24$ )	10.9 ( $\pm 0.22$ )
Basal diameter (BA)	3.4 ( $\pm 0.06$ )	2.6 ( $\pm 0.04$ )
Length of third internode (LTI)	13.1 ( $\pm 0.27$ )	11.5 ( $\pm 0.21$ )
Width of third internode (WTI)	2.5 ( $\pm 0.03$ )	1.9 ( $\pm 0.02$ )
Fruit length (FL)	5.4 ( $\pm 0.04$ )	4.4 ( $\pm 0.03$ )
Fruit width (FW)	3.7 ( $\pm 0.04$ )	2.6 ( $\pm 0.02$ )
Seed length (SL)	3.5 ( $\pm 0.04$ )	2.2 ( $\pm 0.02$ )
Seed width (SW)	1.5 ( $\pm 0.02$ )	1.1 ( $\pm 0.01$ )
Male		
Plant height (PH)	9.7 ( $\pm 0.24$ )	11.7 ( $\pm 0.28$ )
Basal diameter (BA)	3.2 ( $\pm 0.05$ )	2.5 ( $\pm 0.04$ )
Length of third internode (LTI)	11.9 ( $\pm 0.26$ )	11.7 ( $\pm 0.21$ )
Width of third internode (WTI)	2.5 ( $\pm 0.03$ )	1.9 ( $\pm 0.02$ )
Petal length (PL)	1.5 ( $\pm 0.02$ )	1.1 ( $\pm 0.01$ )
Petal width (PW)	1.4 ( $\pm 0.02$ )	1.0 ( $\pm 0.01$ )
Anther diameter (AD)	0.6 ( $\pm 0.01$ )	0.4 ( $\pm 0.01$ )
Anther distance from tip (ADT)	0.6 ( $\pm 0.01$ )	0.4 ( $\pm 0.01$ )
Staminate spike length (SSL)	12.9 ( $\pm 0.40$ )	9.5 ( $\pm 0.26$ )
Staminate spike width (SSW)	3.0 ( $\pm 0.02$ )	1.7 ( $\pm 0.01$ )



Table 8. Forward-stepwise discriminant function analysis (DFA) for female and male plants of *Arceuthobium campylopodum* and *A. divaricatum*: correct classification counts (N = predicted/actual) and percentages (%; predicted/actual) with the sequential addition of morphological characters (steps) most-to-least correlated to the discriminant function. Anther diameter (AD); anther distance to tip (ADT); basal diameter (BD); fruit length (FL); fruit width (FW); length of third internode (LTI); plant height (PH); petal length (PL); petal width (PW); seed length (SL); staminate spike length (SSL); staminate spike width (SSW); seed width (SW); and width of the third internode (WTI).

Stepwise DFA by plant sex (step: morphological character[s])	Correct classification to species				
	Total (%)	<i>Arceuthobium campylopodum</i>		<i>Arceuthobium divaricatum</i> <sup>a</sup>	
		Count	%	Count	%
Female					
1: SL	95.5	451/480	94.0	561/580	96.7
2: SL, FW	98.4	478/480	99.6	565/580	97.4
3: SL, FW, WTI	98.9	480/480	100.0	568/580	97.9
4: SL, FW, WTI, PH	99.0	479/480	99.8	570/580	98.3
5: SL, FW, WTI, PH, FL	99.1	479/480	99.8	571/580	98.4
6: SL, FW, WTI, PH, FL, LTI	99.2	480/480	100.0	572/580	98.6
7: SL, FW, WTI, PH, FL, LTI, BD	99.2	480/480	100.0	571/580	98.4
8 (Full-model): SL, FW, WTI, PH, FL, LTI, BD, SW	99.1	480/480	100.0	570/580	98.3
Male					
1: SSW,	99.8	600/600	100.0	558/560	99.6
2: SSW, WTI	99.9	600/600	100.0	559/560	99.8
3: SSW, WTI, SSL	99.9	600/600	100.0	559/560	99.8
4: SSW, WTI, SSL, PH	99.9	600/600	100.0	559/560	99.8
5: SSW, WTI, SSL, PH, LTI	99.9	600/600	100.0	559/560	99.8
6: SSW, WTI, SSL, PH, LTI, PW	99.9	600/600	100.0	559/560	99.8
7: SSW, WTI, SSL, PH, LTI, PW, BD	99.9	600/600	100.0	559/560	99.8
8: SSW, WTI, SSL, PH, LTI, PW, BD, ADT	99.9	600/600	100.0	559/560	99.8
9: SSW, WTI, SSL, PH, LTI, PW, BD, ADT, AD	99.9	600/600	100.0	559/560	99.8
10 (Full-model): SSW, WTI, SSL, PH, LTI, PW, BD, ADT, AD, PL	99.9	600/600	100.0	559/560	99.8

<sup>a</sup> Combined data for plants collected on *Pinus edulis*, *P. monophylla*, and *P. californiarum* subsp. *fallax*.

be identified easily by differences in one or more morphological characters as well as their host affinities (Tables 5, 7, and 8; Fig. 3). For example, the basal diameter, width of the third internode, and the width of mature staminate spikes were significantly smaller for plants of *A. divaricatum* than those of *A. campylopodum*; overall, male and female plants of *A. divaricatum* were much more slender when compared to plants of *A. campylopodum*. This characteristic is easily discernible when male or female plants of *A. divaricatum* and *A. campylopodum* are placed side-by-side for visual comparisons (Fig. 4–5). However, plant size alone does not easily distinguish these species even though the mean heights of male and female plants were significantly different (Table 1). Other characters that distinguished *A. divaricatum* from *A. campylopodum* were its much smaller 3-merous flowers, rare formation of 4-merous flowers, and smaller fruits and seeds (Tables 7 and 8). Furthermore, although plant color is a qualitative character, *A. divaricatum* can usually be distinguished using plant color as its female plants are typically brown or green-brown while those of *A. campylopodum* typically are yellow, yellow-brown, or light brown (Fig. 4–5). Again, these color differences can be easily observed when recently collected plants are compared side-by-side; upon drying these color differences are more difficult to observe.

A further difference between these dwarf mistletoes is their host range; the principal and only hosts of *Arceuthobium divaricatum* are pinyons (Table 5). In contrast, *A. campylopodum* primarily parasitizes *Pinus ponderosa* and *P. jeffreyi* with the latter species claimed to be immune to

infection by *A. divaricatum* (Hawksworth and Wiens 1996). It is probable that *P. ponderosa* is also immune to infection by *A. divaricatum*; Hawksworth and Wiens (1996) observed that where *P. ponderosa* was sympatric with infected pinyons, *A. divaricatum* was found infecting only pinyons. Although they refrained from classifying *P. ponderosa* as immune to *A. divaricatum*, Hawksworth and Wiens did suggest *P. ponderosa* var. *scopulorum* Engelm. (Rocky Mountain ponderosa pine) may be immune to *A. divaricatum* in the Southwest.

Because the dwarf mistletoes are extremely important both ecologically and economically, emphasis must be placed on their ecological and pathological roles in forest ecosystems. These two dwarf mistletoes clearly have very different host ranges and hence, their pathological significance in forests of the western United States is also distinct. Any efforts to manage populations of these parasites to mitigate their effects on tree growth and mortality within severely infested stands must consider these differences (Hawksworth and Wiens 1996). Recognition of the host affinities developed by dwarf mistletoes is critical in their classification because we consider differences in host preference(s) to reflect corresponding and underlying genetic and physiological differentiation among dwarf mistletoes.

In addition to our morphological analyses, the separation of *Arceuthobium divaricatum* from *A. campylopodum* is also supported by isozyme and molecular studies. Nickrent (1986, 1996) reported that, based on isozyme analyses, *A. divaricatum* was most closely aligned with and biochemically similar to *A. douglasii* Engelm. (Douglas-fir dwarf

mistletoe), and was clearly distinct from *A. campylopodum*. Both *A. divaricatum* and *A. douglasii* shared 16 alleles across 6 loci and both species were fixed for one isozyme (glutamate dehydrogenase GDH<sup>66</sup>), which was absent in all other species of *Arceuthobium* studied, including *A. campylopodum*. This demonstrated that *A. divaricatum* was genetically distinct from *A. campylopodum*. Furthermore, Nickrent et al. (2004) presented phylogenetic analyses using sequence data of ITS and chloroplast *trn-L* DNA that also demonstrated *A. divaricatum* was most closely related phylogenetically to *A. douglasii*, not *A. campylopodum*. Based on DNA sequence data, Nickrent et al. (2004) placed *A. divaricatum* in a clade with *A. douglasii* in section *Minuta* Hawksw. & Wiens rather than section *Campylopoda* Hawksw. & Wiens, where *A. campylopodum* is presently classified. Most recently, Reif et al. (2015) also demonstrated that *A. divaricatum* was genetically different from three species in section *Campylopoda* (*A. apachecum* Hawksw. & Wiens, *A. blumeri* A. Nelson, and *A. cyanocarpum* (A. Nelson ex Rydberg) Coulter & Nelson) using amplified fragment length polymorphism (AFLP) analyses. Although *A. campylopodum* was not included in their study of dwarf mistletoes of section *Campylopoda* that parasitize white pines (*Pinus* subgenus *Strobus*), *A. divaricatum* and *A. douglasii* were utilized as outgroup taxa and were genetically distinct to the aforementioned white pine dwarf mistletoes presently classified to section *Campylopoda*. Therefore, the circumscription of *A. divaricatum* under *A. campylopodum* (Baldwin et al. 2012) is not justified based on our rigorous morphological analyses, their apparent host affinities based on field observations, and the isozyme and molecular studies reported to date.

It is interesting to note that male and female mean plant heights of *Arceuthobium divaricatum* collected from *Pinus monophylla* and *P. californiarum* subsp. *fallax* were significantly larger on average than those of plants collected from *P. edulis* (Tables 2 and 3). The differences in plant heights may be related to the greater amount of annual precipitation at sites typically colonized by *P. monophylla*—primarily during the late fall, winter, and early spring—compared to that of *P. edulis* (Malusa 1992; Cole et al. 2008). Most notably, *P. monophylla* typically receives more rain on average in May and June (45 mm) than *P. edulis* (34 mm) (Cole et al. 2008). Therefore, the larger plant heights of *A. divaricatum* sampled from *P. monophylla* may have been affected directly by the increased moisture present where this host occurs or indirectly by greater vigor of this host produced by the higher moisture regimes it grows under, particularly during the spring months of May and June. However, plant heights of *A. divaricatum* collected from *P. californiarum* subsp. *fallax* were also larger than those collected from *P. edulis* and these pinyons grow under similar bi-seasonal precipitation patterns where they receive most of their precipitation during the summer (July to September) monsoon season (Malusa 1992; Cole et al. 2008). Therefore, precipitation patterns experienced by the pinyon hosts of *A. divaricatum* alone probably don't account for the greater mean heights of plants collected from *P. monophylla* and *P. californiarum* subsp. *fallax*. Because the mean plant height was the only significantly different morphological character between the populations of *A. divaricatum* on *P. monophylla* and *P. edulis*, we don't

recommend these populations be considered for separate taxonomic recognition as subspecies of *A. divaricatum*. The host-parasite and/or environmental factors contributing to the significant differences between mean plant heights for *A. divaricatum* collected from *P. edulis* and *P. monophylla*/*fallax* remain unclear.

We have not reported morphological measurements for plants of *Arceuthobium divaricatum* collected from *Pinus californiarum* subsp. *californiarum*, *P. discolor*, *P. cembroides*, or *P. quadrifolia*, but we did observe infection on the first three hosts and we measured a few male and female plants collected from *P. discolor* in New Mexico and *P. cembroides* in Texas. Plant, flower, fruit, and seed dimensions measured from *P. discolor* were morphologically similar to those of plants collected from *P. edulis*. Plant dimensions measured from *P. cembroides* were similar to plants from *P. edulis* as well. As reported by Hawksworth and Wiens (1996), infection of *P. californiarum* subsp. *californiarum*, *P. cembroides*, and *P. discolor* was severe where we observed these hosts and we agree that these pinyons should also be classified as principal hosts of *A. divaricatum*, even though they are not common within its geographic range. Although *A. divaricatum* has been reported parasitizing *P. quadrifolia* on the east slope of the Laguna Mountains (San Diego County, CA; Beauchamp 1986), we did not observe infection of this host in the Laguna Mountains where we searched for this host/dwarf mistletoe combination in 2015. While *A. divaricatum* has been collected on *P. quadrifolia* from the Sierra Juárez and reported in the Sierra San Pedro Mártir, Baja California, we were unable to visit these mountains during this study.

While Hawksworth and Wiens (1972, 1996) reported the maximum height of plants of *Arceuthobium divaricatum* as 13 cm, we measured female plants greater than 20 cm and male plants greater than 30 cm in height (Table 1). We found that fruits averaged 4.5 mm in length and 2.6 mm in width whereas Hawksworth and Wiens reported fruits were only 3.5 × 2.0 mm. Furthermore, Hawksworth and Wiens did not report that *A. divaricatum* occasionally formed 4-merous flowers, only 3-merous, and they reported that flowers were larger (2.5 mm) in diameter than the 3-merous flowers we measured (mean = 2.2 mm). Possible reasons for these differences were that we measured many more collections (60) than Hawksworth and Wiens (19) and our measurements were made on fresh material, not dried herbarium specimens. The discrepancy between our diameter measurements for 3-merous flowers, however, is unclear, unless they reported the maximum diameter they observed for flowers. We measured 3-merous flowers as large as 3.2 mm and 4-merous flowers as large as 4.1 mm. Although we don't know the reasons for these differences, it is evident from our morphological measurements that plants, flowers, and fruits of *A. divaricatum* are often much larger than what has been reported previously in the literature.

In light of the morphological data presented herein, previous isozyme and molecular findings, and the major discontinuities in the host affinities for each taxon, we advocate retention of separate species status for *Arceuthobium campylopodum* and *A. divaricatum*.

KEY FOR IDENTIFICATION OF *ARCEUTHOBIMUM CAMPYLOPODUM*  
AND *A. DIVARICATUM*

1. Basal diameters usually >3 mm; width of third internode usually >2 mm; staminate spike width usually >2 mm; staminate flowers 3- and 4-merous and >3 mm across; mature fruits typically >5 mm long and 3 mm wide; seeds about  $3.5 \times 1.5$  mm; primarily parasitic on *Pinus ponderosa* and *P. jeffreyi*; also common on *P. attenuata* and *P. coulteri* ..... *Arceuthobium campylopodum*
- 1'. Basal diameters usually <3 mm; width of third internode usually <2 mm; staminate spike width usually <2 mm; staminate flowers predominantly 3-merous and <3 mm across; mature fruits <5 mm long and 3 mm wide; seeds about  $2.2 \times 1.1$  mm; parasitic on pinyon pines ..... *Arceuthobium divaricatum*

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Appendix 1. Collection locations and voucher specimen numbers for *Arceuthobium campylopodum*. Collections by R. L. Mathiasen (RLM). All vouchers were deposited at the University of Arizona Herbarium, Tucson (ARIZ), except for RLM 0938 (population 46) which was deposited at the Deaver Herbarium, Northern Arizona University, Flagstaff (ASC). Population numbers correspond to locations in Fig. 1.

Population	Location	Specimen number
1	4.5 km N of Gifford on St. Rte. 25	RLM 1202
2	20 km S of Fruitland on St. Rte. 25	RLM 1204
3	2 km NW of Nespelem on St. Rte. 155	RLM 1205
4	2.3 km N of Coeur d'Alene, ID on Fernan Lake Rd.	RLM 1195
5	16 km S of Spokane on St. Rte. 195	RLM 1194
6	2.5 km W of St. Rte. 153 on Squaw Creek Rd.	RLM 1208
7	Lake Wenatchee on Chiwawa River Loop Rd.	RLM 1224
8	2.6 km W of Squilchuck St. Park on Ski Area Rd.	RLM 1209
9	0.8 km W of St. Rte. 97 on St. Rte 970	RLM 1212
10	17.6 km E of White Pass on St. Rte. 12	RLM 1219
11	2 km N of Satus Pass on St. Rte. 97	RLM 1213
12	3 km S of Trout Lake on St. Rte. 141	RLM 1217
13	6.4 km W of Friend on Forest Rd. 27	RLM 1214
14	6.4 km S of Joseph on E shore of Wallowa Lake	RLM 1191
15	9.4 km on Sheep Cr. Rd from Forest Rd. 51	RLM 1188
16	1.8 km E of Ochoco Summit on St. Rte. 26	RLM 1178
17	12.2 km W of St. Rte. 97 on St. Rte. 138	RLM 1171
18	15.2 km S of Sisters on Forest Rd. 16	RLM 1175
19	1 km from Forest Rd. 44 on Forest Rd. 4410	RLM 1173
20	Fort Klamath Cemetery on St. Rte. 62	RLM 1126
21	3 km W of Quartz Mtn. Pass on St. Rte. 140	RLM 1127
22	Warner Mtn. Ski Hill on St. Rte. 26	RLM 1130
23	3.4 km W of County Rd. 48 on Forest Rd. 73	RLM 1131
24	16 km N of Adin on St. Rte. 299/139	RLM 1132
25	6 km S of Takilma on Grayback Rd.	RLM 1167
26	1 km S of Forest Rd. 17N26 on Forest Rd. 17N11	RLM 1166
27	6.2 km W of St. Rte. 96 on Dillon Mtn. Rd.	RLM 1165
28	9.6 km S of Callahan on St. Rte. 3	RLM 1121
29	10 km E of St. Rte 3 on Forest Rd. 17	RLM 1120
30	2.4 km W of Stewart Hot Springs on Forest Rd. 17	RLM 1160
31	2 km N of St. Rte. 89 on Mt. Shasta Ski Park Rd.	RLM 1158
32	0.1 km S of St. Rte. 299 on St. Rte. 89	RLM 1157
33	2 km S of Old Station on St. Rte. 44	RLM 1154
34	2 km W of St. Rte. 44 on Forest Rd. 101	RLM 1153
35	14.4 km W of Susanville on St. Rte. 36	RLM 1032
36	19.5 km N of Upper Lake on Pillsbury Lake Rd.	RLM 0920
37	7.7 km N of Pollock Pines on Forest Rd. 4	RLM 1242
38	Entrance to Sugar Pine State Park	RLM 1147
39	Bowers Mansion St. Park	RLM 1146
40	1 km N of Markleeville on St. Rte. 89	RLM 1133
41	Silver Creek Campground on St. Rte. 4	RLM 1134
42	Column of the Giants on St. Rte. 108	RLM 1145
43	Pinecrest Transfer Station; 0.5 km W of Pinecrest	RLM 1143
44	1 km W of Long Barn on St. Rte. 108	RLM 1142
45	8.5 km E of Crane Flat on St. Rte. 120	RLM 1138
46	2 km W of Big Creek on Shaver Lake Rd.	RLM 0938
47	4.1 km W of Ranger Station on Kyle Canyon Rd.	RLM 1137
48	8.5 km W of Sherman Pass on Forest Rd. 22S05	RLM 1296
49	2.2 km S of Troy Mdws. Campground	RLM 1135
50	5.8 km N of Johnsonville Jct. on W. Divide Highway	RLM 0985
51	Pine Flat, Sequoia Nat. For.	RLM 0980
52	Tiger Flat, Sequoia Nat. For.	RLM 0976
53	6.2 km S of St. Rte. 33 on Mt. Reyes Rd.	RLM 1292
54	1.4 km W of Cloud Burst on St. Rte. 2	RLM 1304
55	1 km W of Big Pines on St. Rte. 2	RLM 1305
56	2.4 km N of Fawnskin on Forest Rd. 2N71	RLM 0986
57	1.9 km from St. Rte. 38 on Jenks Lake Rd.	RLM 0973
58	Forest Service Ranger Station in Idyllwild	RLM 0969
59	1.1 km S of the San Jacinto River on St. Rte. 74	RLM 0967
60	0.5 km S of Horse Heaven Campground	RLM 1306

Appendix 2. Collection locations and voucher specimen numbers for *Arceuthobium divaricatum*. Collections by R. L. Mathiasen (RLM); all vouchers are deposited at the Herbarium of the Rancho Santa Ana Botanical Garden (RSA). Population numbers correspond to locations in Fig. 2.

Population	Location	Specimen number
1	3.8 km W of St. Rte. 395 on Leviathan Mine Rd.	RLM 1390
2	6 km W of St. Rte. 395 on St. Rte. 89	RLM 1389
3	1.7 km S of Camp Antelope Rd. on Burcham Flat Rd.	RLM 1377
4	3.2 km S of Benton Crossing on Chidago Cyn. Rd.	RLM 1378
5	4.5 km S of St. Rte. 6 on Forest Rd. 1N14	RLM 1324 & 1341
6	4.8 km W of Carroll Summit on St. Rte. 772	RLM 1391
7	0.6 km W of Big Creek Campground S of Austin	RLM 1392
8	15 km E of Austin on US 50	RLM 1393
9	Pole Creek Trailhead in Great Basin Nat. Park	RLM 1394
10	1.8 km N of St. Rte. 168 on Bristlecone Pine Rd.	RLM 1340
11	10.4 km S of Trona Jct. in Wildrose Cyn.	RLM 1325 & 1339
12	1.6 km from Nat. For. on Horseshoe Mdw. Rd.	RLM 1388
13	1.6 km W of Kern River on Sherman Pass Rd.	RLM 1379
14	11.2 km W of Chimney Peak Rd. on Long Valley Rd.	RLM 1380
15	0.3 km N of Lamont Peak on Chimney Peak Byway	RLM 1381
16	4.8 km W of Kelso Valley Rd. on Piute Mtn. Rd.	RLM 1387
17	2.2 km N of Lockwood Valley Rd. on Dome Sprs. Rd.	RLM 1386
18	22 km W of Cuddy Valley Rd. on Lockwood Valley Rd.	RLM 1385
19	2.7 km S of Lockwood Valley Rd. on Frazier Mtn. Rd.	RLM 1384
20	3.2 km N of Big Pines Rd. on Mescal Cyn. Rd.	RLM 1383
21	14.4 km S of Lucerne Valley on St. Rte. 18	RLM 1336
22	5.4 km S of St. Rte. 18 on Forest Rd. 3N03	RLM 1382
23	18.4 km W of St. Rte. 95 on Lee Cyn. Rd.	RLM 1326 & 1338
24	Entrance to Caruthers Cyn., New York Mtns.	RLM 1400
25	Entrance to Keystone Cyn., New York Mtns.	RLM 1337 & 1371
26	0.5 km W of Hualapai Mtn. Rd. on DW Ranch Rd.	RLM 1335
27	Little Wolf Hole Pass, Wolf Hole Mtns.	RLM 1353
28	Anvil Rock Rd. exit on I-40	RLM 1397
29	17.6 km S of St. Rte. 260 on Fossil Creek Rd.	RLM 1401
30	1 km S of Bell Rock on St. Rte 179	RLM 1365
31	N slope of Sugarloaf Mtn., Sedona	RLM 1349 & 1355
32	1.6 km N of St. Rte. 260 on Forest Rd. 504 west of Heber	RLM 1334 & 1356
33	3.2 km S of Eager on Forest Rd. 285	RLM 1327 & 1357
34	1 km N of Walnut Cyn. Nat. Monument	RLM 1342
35	4.8 km E of Grand Cyn. Nat. Park on St. Rte. 64	RLM 1348
36	1.6 km E of Grand Cyn. Caverns on St. Rte. 66	RLM 1399
37	11.2 km E of Mt. Trumbull Schoolhouse on Loop Rd.	RLM 1354
38	North Timp Pt. on North Rim Grand Cyn.	RLM 1314 & 1316
39	12.1 km E of Jacob Lake on St. Rte. 89A	RLM 1315
40	4.2 km S of Mt. Carmel Jct. on St. Rte. 89	RLM 1350
41	1.6 km W of Tropic on Bryce Way	RLM 1351
42	5 km S of Boulder on St. Rte. 12	RLM 1352
43	0.3 km N of Forest Rd. 2653 on Forest Rd. 022	RLM 1396
44	1.6 km E of Devil's Cyn. viewpoint on I-70	RLM 1395
45	6 km W of St. Rte. 275 on St. Rte. 95	RLM 1398
46	1.6 km E of La Sal on St. Rte. 46	RLM 1346
47	Colorado Nat. Monument. North Campground	RLM 1366
48	6.4 km N of US 50 on St. Rte. 347	RLM 1367
49	19 km E of St. Rte. 145 on St. Rte. 90	RLM 1368
50	12.8 km W of Bedrock on St. Rte. 90	RLM 1369
51	3.2 km S of St. Rte. 164 on County Rd. 26	RLM 1345
52	17.6 km S of the Colorado St. boundary on St. Rte. 511	RLM 1344
53	0.4 km W of Coolidge on I-40	RLM 1343
54	14.4 km N of St. Rte. 60 on Priest Cyn. Rd.	RLM 1330 & 1360
55	12.8 km W of Magdalena on St. Rte. 60	RLM 1329 & 1359
56	3.2 km W of Pie Town on St. Rte. 60	RLM 1328 & 1358
57	9.6 km E of St. Rte. 180 on Mogollon Rd.	RLM 1333
58	6.4 km N of Fort Bayard on Old Wagon Rd.	RLM 1363
59	1.6 km S of Nogal on St. Rte 37	RLM 1331 & 1361
60	0.3 km E of Forest Rd. 163 above La Luz Cyn.	RLM 1332 & 1362