Arceuthobium microcarpum (Viscaceae): morphological evidence for continued species recognition and discrimination from *Arceuthobium campylopodum*

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ABSTRACT

Western spruce dwarf mistletoe (*Arceuthobium microcarpum*, Viscaceae) parasitizes Engelmann spruce (*Picea engelmannii*) and blue spruce (*P. pungens*) in Arizona and New Mexico. In Arizona, a subspecies (*A. microcarpum* subsp. *aristatae*) also parasitizes Rocky Mountain bristlecone pine (*Pinus aristata*). Although *A. microcarpum* was first segregated from western dwarf mistletoe (*A. campylopodum*) by Engelmann in 1878, its taxonomic classification has undergone several recombinations; the most recent making it a subspecies of *A. campylopodum*. Because the morphologies of *A. campylopodum* and the subspecies of *A. microcarpum* have not been compared using multivariate statistical analyses, we undertook this study. We used morphological data available from our previous taxonomic investigations of these taxa as well as additional data collected for *A. microcarpum* in 2017. Statistical comparisons provided herein demonstrated that *A. microcarpum* can be reliably segregated from *A. campylopodum* using plant heights, plant basal diameters, flower diameters, and fruit and seed dimensions. We were also able to distinguish between the subspecies of *A. microcarpum*, but as expected the differences were not as great as those between *A. campylopodum* and both subspecies of *A. microcarpum*. Furthermore, the host affinities of these taxa clearly distinguished them from each other. Therefore, we recommend that *A. microcarpum* continue to be recognized as a distinct species from *A. campylopodum* and that the subspecies currently recognized under *A. microcarpum* be maintained. Morphological differences between these dwarf mistletoes were summarized. Published on-line www.phytologia.org *Phytologia 100(1): 71-90 (Mar 16, 2018).* ISSN 030319430.
KEY WORDS: dwarf mistletoes, morphological characters, multivariate analyses, *Picea*, *Pinus*.

Western spruce dwarf mistletoe (*Arceuthobium microcarpum* (Engelmann) Hawksworth & Wiens (Viscaceae) is a parasite of Engelmann spruce (*Picea engelmannii* Parry ex Engelmann) and blue spruce (*P. pungens* Engelmann) in Arizona and New Mexico (Mathiasen and Hawksworth 1980, Hawksworth and Wiens 1996). Although it is only locally abundant in the White Mountains, Arizona, it is associated with increased mortality of both of its principal hosts there (Mathiasen et al. 1986). Populations of *A. microcarpum* that severely infect Rocky Mountain bristlecone pine (*Pinus aristata* Engelmann) on the San Francisco Peaks near Flagstaff, Arizona have been classified as *A. microcarpum* (Engelmann) Hawksworth & Wiens subsp. *aristatae* Scott & Mathiasen based on morphological and host range differences with other populations of *A. microcarpum* (Scott and Mathiasen 2009).

Arceuthobium microcarpum was initially segregated from *A. campylopodum* by Engelmann in 1878 as a variant of *A. douglasii* Engelmann based on a collection by Gilbert from Engelmann spruce

near Sierra Blanca in the White Mountains, Arizona (Apache County). In 1915, it was reclassified as *Razoumofskya microcarpa* (Engelmann) Wooton & Standley (Hawksworth and Wiens 1996). In the first monograph of *Arceuthobium* in the United States, Gill (1935) classified it as the host-form of *A. campylopodum* that parasitized spruces (*Picea* spp.): *A. campylopodum* Engelmann forma *microcarpum* (Engelmann) Gill. This classification was used until Hawksworth and Wiens (1970) recombined Gill's forma *microcarpum* as *A. microcarpum*. Hawksworth and Wiens (1972, 1996) maintained the classification of *A. microcarpum* as a species and this treatment has been followed in most, if not all, studies of this dwarf mistletoe since 1972 (e.g. Acciavatti and Weiss 1974; Crawford and Hawksworth 1979; Hawksworth and Mathiasen 1980; Martin and Hutchins 1980; Mathiasen et al. 1986; Lynch 2004; Scott and Mathiasen 2009).

The taxonomic classification of *Arceuthobium microcarpum* recently became a topic of debate primarily because of molecular data (Nickrent et al. 2004). The molecular markers examined thus far indicated *A. microcarpum* is closely related to *A. campylopodum*, and therefore, its segregation from *A. campylopodum* as a distinct species has been questioned (Nickrent 1996; Nickrent et al. 2004). Based on molecular data and the morphological similarities between species in section *Campylopoda* Hawksworth & Wiens, series *Campylopoda*, Nickrent (2012, 2016) recombined *A. microcarpum* as a subspecies of *A. campylopodum*. Because of these recent treatments of *A. microcarpum* as a subsp. of *A. campylopodum* and because the morphologies of *A. campylopodum* and the subspecies of *A. microcarpum* have not been directly compared, we undertook this study using morphological data we had available from previous studies of these taxa (Mathiasen 1977; Mathiasen and Hawksworth 1980; Scott and Mathiasen 2009; Mathiasen and Kenaley 2015). In addition, we collected additional morphological data for *A. microcarpum* subsp. *microcarpum* in 2017. Our objective was to compare the morphologies of these taxa to determine if the classification of the subspecies of *A. microcarpum* or the classification of *A. microcarpum* as a subspecies of *A. campylopodum* were supported by more robust multivariate statistical analyses than have been used in previous studies by Mathiasen and Hawksworth (1980) and Scott and Mathiasen (2009).

MATERIALS AND METHODS

We collected morphological data for *Arceuthobium campylopodum* from 60 populations (30 each from *Pinus ponderosa* Douglas ex Lawson & C. Lawson and *P. jeffreyi* Greville & Balfour) from throughout most of its geographic range (Mathiasen and Kenaley 2015) (Figure 1). Mathiasen and Hawksworth (1980) sampled 26 populations of *A. microcarpum* subsp. *microcarpum* from throughout its geographic distribution in Arizona and from the Mogollon Mountains, New Mexico from 1975-1976 (and see Appendix A in Mathiasen 1977). Additional morphological data for *A. microcarpum* were collected in 2006-2007 from 12 populations in Arizona by Scott and Mathiasen (2009); six of those populations were from the White Mountains, Arizona, two were from the North Rim Grand Canyon, and four were from either the San Francisco Peaks or nearby Kendrick Peak, Arizona (Figure 2). In 2017, additional morphological data were collected for *A. microcarpum* subsp. *microcarpum* from the White Mountains (6 populations), the Pinaleno Mountains (two populations), the Mogollon Mountains (one population), and the North Rim Grand Canyon (one population) (Figure 2). Five of the 10 populations sampled in 2017 were the same as those sampled in 2006-2007. Because the 2011 Wallow Fire destroyed several *A. microcarpum* subsp. *microcarpum* populations in the White Mountains, not all of the same populations sampled in 2006-2007 could be sampled in 2017. Large wildfires have also burned in the Mogollon and Pinaleno Mountains in recent years; hence, populations of subsp. *microcarpum* were only sampled in a few locations in those areas. Furthermore, we only used the morphological data collected by Scott and Mathiasen (2009) for subsp. *aristatae* because the 2010 Schultz Fire drastically reduced the extent of the subsp. *aristatae* population on Schultz Peak, therefore, no additional morphological measurements were completed for this subspecies. Voucher specimens for *A. campylopodum* (Mathiasen and Kenaley 2015) and *A. microcarpum* (Scott and Mathiasen 2009) consisting of the mistletoe with host material were

deposited at the Deaver Herbarium, Northern Arizona University, Flagstaff (ASC), or the University of Arizona Herbarium, Tucson (ARIZ). Voucher and specific population data, including GPS coordinates, for the 2009 and 2015 studies have been archived electronically in SEINet (Southwest Environmental Information Network 2017: http://swbiodiversity.org/portal/index.php). Voucher specimens for the subsp. *microcarpum* populations sampled in 2017 were deposited at the Rancho Santa Ana Botanical Gardens (RSA).

In 1975 and 2006-2007, the following morphological characters for male plants were measured for the subspecies of *Arceuthobium microcarpum*: dominant plant height, dominant plant basal diameter, flower diameter, anther diameter, petal lobe length and width, and distance from the outer edge of the anther to the tip of the petal lobe. The following morphological characters were measured for female plants: dominant plant height, dominant plant basal diameter, length and width of both fruits and seeds. The color of plants, fruits, and seeds were also recorded. Measurements in 1975 were completed with a stereoscope microscope fitted with a micrometer and all other morphological characters were measured using a 10x hand lens with a micrometer (Bausch & Lomb, Bridgewater, NJ) to the nearest 0.1 mm. Male plants were collected during the peak of anthesis and female plants were collected when fruits were mature. Over 20 male or female plants were collected for each population and morphological measurements were completed using ten randomly selected plants for each population sampled. For some populations, more than 10 staminate flowers or fruits/seeds were measured (20). Sample sizes for most morphological characters measured varied between the two species sampled because of the number of populations sampled and the number of plants, staminate flowers, and fruits/seeds measured per population also varied.

For each population of *Arceuthobium campylopodum*, 10–20 male and 10–20 female infections (infected branches) were collected separately and the dominant plant (largest plant) from each infection was used for morphological measurements. The following morphological characters were measured: 1) height, basal diameter, third internode length and width, and color of male and female plants; 2) mature fruit length, width, and color; 3) seed length, width and color; 4) length and width of staminate spikes; 5) staminate flower diameters for 3- and 4-merous flowers; 6) length and width of staminate flower petals; and 7) anther diameter and anther distance from the petal tip. Plant heights were measured to the nearest 0.1 cm and all other measurements were made to the nearest 0.1 mm. Plants were usually measured within 12-h, but no later than 24-h after collection. Only plants that were still attached to their host's branch and fully turgid were measured. 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. Staminate spike and flower measurements were made during the peak of anthesis and fruit and seed measurements were made during the peak of seed dispersal.

Statistical Analyses

One-way analysis of variance (1-way ANOVA) was performed to examine the variance in each of the male and female morphological characters between *Arceuthobium microcarpum* and *A. campylopodum* ($\alpha = 0.05$). Mean differences among morphologic characters of female and male plants across taxa were assessed using a post-hoc Tukey's honestly significant difference (HSD; $\alpha = 0.05$) test. Dunnett's tests were also executed separately to determine whether means for each female and male morphologic character were significantly different when comparing each of the subspecies of *A. microcarpum* individually to *A. campylopodum*.

Morphological differences across six female and seven male characters among taxa – *Arceuthobium campylopodum*, *A. microcarpum* subsp. *aristatae*, and *A. microcarpum* subsp. *microcarpum* – were tested simultaneously and separately by sex using multivariate analysis of variance

(MANOVA). Standard and forward-stepwise quadratic discriminant function analyses (DFA) were also performed to determine whether female and male plants could be segregated by taxonomic affiliation (i.e., field diagnosis vs. predicted taxonomic membership) utilizing either female or male plant morphology (Quinn and Keough 2002). Because previous molecular phylogenetic analyses suggested that *A. microcarpum* and *A. campylopodum* may be conspecific (i.e., the same species differing only by principal host; Nickrent et al. 2004), DFAs for female and male plants were performed separately using complete morphological records for each taxon and setting the prior probability to 0.3333 per taxon rather than according to field diagnosis and, hence, sample size. Standardized correlation coefficients (SCC) for female and male morphologies were calculated as part of the standard DFA to determine the overall contribution of each morphologic character to the discriminant function; thereby, providing the principal female or male character(s) separating the dwarf mistletoes. Thereafter, the standard DFAs were validated by resampling separately the original (complete) data set for female and male plants; selecting at random 50 complete records per taxon and re-executing the DFA using a full-model (i.e., 6 female or 7 male characters simultaneously). Forward-stepwise DFA was executed separately for female and male plants to assess the combinations of female and male morphologies resulting in the highest precision (%, predicted/field determined) in taxonomic membership, and hence, maximize differences among taxa. Only the diameter of 3-merous male flowers was included in the DFAs because few 4-merous flowers were measured for *A. microcarpum*. One-way and multivariate analyses of variances, multiple comparisons of mean differences, and DFAs were computed in JMP Pro v13.0 (SAS Institute, Cary, North Carolina, USA). Ninety-five percent (95%) confidence intervals (α= 0.05) were also calculated in lieu of standard deviations and errors.

RESULTS

The means for every morphological character measured were significantly larger for *Arceuthobium campylopodum* than for either of the subspecies of *A. microcarpum*; this was demonstrated by ANOVA and corresponding Tukey's HSD and Dunnett's tests (Table 1). The principal characters found to differentiate between *A. campylopodum* and *A. microcarpum* and its subspecies *aristatae* are summarized in Table 2. Another striking dissimilarity between *A. campylopodum* and the subspecies of *A. microcarpum* was that the latter taxa often formed 2-merous staminate flowers; this was observed many times while measuring male flowers in 1975, 2007, and 2017. In addition, staminate flowers with five petals were also observed for *A. microcarpum*, although rarely and, interestingly, one male plant was found that produced only 5-merous flowers with ten mature, open flowers. Unlike *A. microcarpum*, staminate flowers of *A. campylopodum* with only two or five petals were never observed; it consistently formed only 3- and 4-merous flowers in approximately equal proportions.

In contrast to the large morphological differences between *Arceuthobium campylopodum* and the subspecies of *A. microcarpum*, the subspecies were morphologically similar (Table 1). The mean heights of both male and female plants were significantly different as were the mean basal diameters. Mean diameters of 3- and 4-merous flowers were not significantly different, but sample sizes for 4-merous staminate flowers were relatively small. The mean length and width of petals, anther diameters, and the distance to the tip of petals were also not significantly different for the subspecies. However, mean fruit length and width were significantly different as was seed width; mean seed length was not significantly different between the subspecies.

Multivariate analysis of variance (MANOVA) of complete records for female and male plants of *Arceuthobium campylopodum*, *A. microcarpum* subsp. *aristatae,* and *A. microcarpum* subsp. *microcarpum* revealed significant differences in the overall morphology among taxa for female (Wilks' λ= 0.0928, Approximant $F_{12, 1786}$= 339.7, $P < 0.0001$; Pillai's Trace= 1.05, Approximant $F_{12, 1788}$= 166.2, $P < 0.0001$) and male plants (Wilks' λ= 0.1975, Approximant $F_{14, 1488}$= 132.9, $P < 0.0001$; Pillai's Trace= 0.9373, Approximant $F_{14, 2020}$= 93.9, $P < 0.0001$). Standard DFA utilizing six female and seven male

morphological characters (i.e., full-models) resulted in the correct classification (%, predicted/field diagnosed) of 96.1% and 89.1% of female and male plants, respectively (Table 3; Figure 3). Female plants of *A. campylopodum* determined a priori via field diagnosis were assigned correctly to *A. campylopodum* 100% of the time, whereas ≤ 1% of female *A. microcarpum* subsp. *aristatae* (0.9%) and subsp. *microcarpum* (1.0%) were classified to *A. campylopodum* when considering complete morphologic data (Table 4). Moreover, the taxonomic membership for female plants of *A. microcarpum* subsp. *aristatae* (96.3%) and *microcarpum* (90.1%) was predicted correctly ≥ 90.1% of the time. The first and second canonical (c1 and c2) explained 97.6% and 2.4% of the variation among female plants, respectively (Table 5; Figure 3); wherein, fruit length ($SCC_{c1, c2}$= 0.62, -0.05), plant height ($SCC_{c1, c2}$= 0.20, -1.0), seed length ($SCC_{c1, c2}$= 0.45, 0.01), and basal diameter ($SCC_{c1, c2}$= 0.30, 0.27) contributed most to the separation of *A. campylopodum* and the subspecies of *A. microcarpum*. Fruit ($SCC_{c1, c2}$= 0.11, 0.20*)* and seed width ($SCC_{c1, c2}$= 0.06, 0.34) contributed least to the discrimination of taxa. Standard DFA of female plant morphology was also supported by the stepwise DFA of female plant parts (Table 3), indicating that ≥ 88.2% of *A. campylopodum* (100%), *A. microcarpum* subsp. *aristatae* (98.1%), and *A. microcarpum* subsp. *microcarpum* (88.2%) were classified correctly to taxonomic membership when considering only fruit length, plant height, seed length, and basal diameter. Further examination of the female stepwise DFA results also revealed that *A. campylopodum* (99.2%) and the subspecies of *A. microcarpum* (98.1%, 84.7%) could be effectively delineated morphologically using only two of the four aforementioned female characters – fruit length and plant height. Resampling the female dataset (50 randomly-selected, complete records per taxon) and executing a full-model DFA also yielded nearly identical results (Table 5; Figure 3); classifying correctly 98.0% (147/150) of female plants and readily delimiting *A. campylopodum* from *A. microcarpum* sensu lato. Likewise, as with utilizing complete records, the female DFA with resampled data segregated clearly *A. microcarpum* subsp. *aristatae* and subsp. *microcarpum* (Figure 3). Means and associated 95% confidence intervals for morphological characters of female plants by predicted species according to full-model DFA are presented in Table 6.

Determining taxonomic membership via DFA across seven male plant characters was less precise when compared to the DFA utilizing female morphologies; resulting in 89.1% of all complete male records being assigned correctly to their taxonomic identity (Table 3). However, the first and second canonical discriminant functions for the full-model DFA of male plant morphology explained 93.6% and 6.4%, respectively, of the variation among *Arceuthobium campylopodum*, *A. microcarpum* subsp. *aristatae*, and *A. microcarpum* subsp. *microcarpum*. The seven percent (7%) reduction in the total correct classification between female and male standard DFAs was in large part due to the misclassification of male *A. microcarpum* to their subspecific membership (Table 4). Field-determined male plants of *A. campylopodum* were consistently and correctly classified to *A. campylopodum* (97.3%), whereas, 10.6% of male *A. microcarpum* subsp. *microcarpum* were incorrectly assigned to subsp. *aristatae* and, conversely, 20.6% of male *A. microcarpum* subsp. *aristatae* were predicted to subsp. *microcarpum* rather than subsp. *aristatae* (Table 4). The two subspecies of *A. microcarpum*, however, were only predicted to *A. campylopodum* ≤ 2.7% of the time and, thus, male plants of *A. microcarpum* sensu lato were readily segregated morphologically from male *A. campylopodum*. Based on standardized correlation coefficients (SCC) for the first and second canonicals (c1 and c2), male characters contributing most to predicting taxonomic membership were basal diameter ($SCC_{c1, c2}$= 0.72, 0.63), diameter of 3-merous flowers ($SCC_{c1, c2}$= 0.63, 0.08), and plant height ($SCC_{c1, c2}$= 0.03, -1.2). In fact, limiting the male DFA model to only basal diameter, 3-merous flower diameter, and plant height resulted in the correct classification of 95.0% and 89.4% of male *A. campylopodum* and *A. microcarpum* subsp. *aristatae*, respectively (Table 3). However, executing a full-model DFA – incorporating petal length ($SCC_{c1, c2}$= -0.15, 0.17), anther distance to tip ($SCC_{c1, c2}$= 0.06, 0.01), and anther diameter ($SCC_{c1, c2}$= 0.05, -0.01) – was necessary to maximize morphological differences among taxa, particularly between subspecies of *A. microcarpum* (Table 3). Discriminant function analysis using a random sample of male records (resampled dataset) successfully validated the full-model DFA with complete records: effectively separating *A. campylopodum* and *A. microcarpum* sensu lato, yet, providing limited support to the separation of *A. microcarpu*m subsp.

aristatae and subsp. *microcarpum* (Figure 3). Multivariate means and 95% confidence ellipses for male plants of the subspecies of *A. microcarpum* were discrete in ordination space for DFAs executed with either the complete or resampled dataset, however, as evident by the overlapping 50% contour ellipses, multiple specimens of male *A. microcarpum* subsp. *microcarpum* shared morphologies consistent with those predicted for subsp. *aristatae* (Table 6; Figure 3).

DISCUSSION

Classifying *Arceuthobium microcarpum* as the same species or as a subspecies of *A. campylopodum* is not supported by our analyses of the morphological characters we measured for these taxa. Both of these species can be reliably identified by differences in their plant heights, basal diameters, flower diameters, and fruit length and width (Table 2). All of the morphological characters measured were significantly larger for *A. campylopodum* than those of *A. microcarpum*; *A. microcarpum* and its subspecies *aristatae* form much smaller and thinner plants. Multivariate analysis of variance as well as standard and stepwise DFAs of female and male plant characters demonstrated that *A. campylopodum* and *A. microcarpum* are morphologically distinct and can be effectively predicted to taxonomic membership using as few as two female (fruit length and plant height) and three male characters (basal diameter, 3-merous flower diameter, and plant height).

Another morphological difference between *Arceuthobium campylopodum* and *A. microcarpum* is the number of petals formed on staminate flowers; *A. campylopodum* consistently forms 3- and 4-merous flowers in approximately equal frequencies, but *A. microcarpum* consistently forms predominantly 3-merous flowers and only occasionally forms 4-merous flowers. In addition, *A. microcarpum* will occasionally form 2-merous and rarely 5-merous flowers, whereas, 2- and 5-merous flowers have not been reported previously for *A. campylopodum* (Hawksworth and Wiens 1996; Mathiasen and Kenaley 2015).

Although the morphologies of the subspecies of *Arceuthobium microcarpum* were similar, there were a few significant univariate differences between them (Table 2) and, using multivariate approaches, female plants between the two subspecies were readily delimited to taxonomic membership (i.e., actual vs. predicted; Tables 3 and 4). However, male plants of subsp. *microcarpum* (20.6%) were often misclassified to subsp. *aristatae* (Table 4; Figure 3) and the predicted male morphologies between subspecies were nearly identical – differing only by basal diameter and plant height (Table 6). Collectively, female and male plants of subsp. *aristatae* are much smaller than those of subsp. *microcarpum*. In addition, the fruits are smaller for subsp. *aristatae* when compared to those of subsp. *microcarpum*.

Peak anthesis for subsp. *aristatae* occurred one to two weeks earlier on the San Francisco Peaks than for subsp. *microcarpum* in the White Mountains in 2006 and 2007 (Scott and Mathiasen 2009). Furthermore, seed dispersal of subsp. *aristatae* also starts and ends one to two weeks earlier on the San Francisco Peaks than seed dispersal of subsp. *microcarpum* in the White Mountains. Observations of phenology in 1975 also found that subsp. *aristatae* flowers and disperses seed earlier than subsp. *microcarpum* (Mathiasen & Hawksworth 1980).

The host range of *Arceuthobium microcarpum* subsp. *microcarpum* is quite distinct from *A. campylopodum*; its principal hosts are Engelmann and blue spruce and it rarely infects corkbark fir (*Abies lasiocarpa* (Hooker) Nuttall var. *arizonica* (Merriam) Lemmon). Rocky Mountain ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson var. *scopulorum* Engelmann) is immune to infection by *A. microcarpum* (Hawksworth and Wiens 1996). The principal hosts of *A. campylopodum* are ponderosa and Jeffrey pines and it has never been reported to infect any species of spruce (Hawksworth and Wiens 1996). Even though *A. microcarpum* subsp. *aristatae* parasitizes bristlecone pine as its principal host and

rarely parasitizes southwestern white pine (*P. strobiformis* Engelmann) (Mathiasen and Hawksworth 1980), these white pines are in subgenus *Strobus* Lemmon and are not closely related to ponderosa or Jeffrey pines which are hard pines in subgenus *Pinus* L. Therefore, the host affinities of *A. campylopodum* and *A. microcarpum* are distinct and support their classification as separate species. Quantitative data on the susceptibility of Engelmann spruce to *A. microcarpum* subsp. *aristatae* demonstrated that it is much less susceptible (an occasional host) than bristlecone pine (Mathiasen and Hawksworth 1980, Scott and Mathiasen 2009). This major difference in the susceptibility of Engelmann spruce between the subspecies of *A. microcarpum* was further support for the classification of the populations parasitizing bristlecone pine in northern Arizona at the subspecific level.

Although the flowering periods of *Arceuthobium microcarpum* and *A. campylopodum* overlap in August and early September (Mathiasen and Hawksworth 1980; Hawksworth and Wiens 1996; Scott and Mathiasen 2009), these taxa are geographically isolated by approximately 300 km. Hence, cross pollination and hybridization is precluded by their geographic isolation, but it is unknown how long populations of these mistletoes have been separated. However, it is unlikely their distributions have overlapped even in the Pleistocene because *A. microcarpum* is not found in the spruce-fir forests north of Arizona in Nevada, Utah, or Colorado. Although southwestern dwarf mistletoe (*A. vaginatum* (Wildenow) Presl subsp. *cryptopodum* (Engelmann) Hawksworth & Wiens, the common parasite of Rocky Mountain ponderosa pine in the Southwest, is frequently sympatric with *A. microcarpum*, *A. vaginatum* flowers in the spring (April-May), not in the late summer. Therefore, the dwarf mistletoes that are principal parasites of ponderosa pine in the United States (*A. campylopodum* and *A. vaginatum*) are either geographically isolated from *A. microcarpum* or prevented from crossing with it by differences in flowering periods.

Additional evidence that *Arceuthobium microcarpum* warrants separation from *A. campylopodum* at the species level was presented by Crawford and Hawksworth (1979). Their analyses of the flavonoid chemistry of *Arceuthobium* found that *A. microcarpum* had the most distinctive flavonoid profile consisting of six compounds; while *A. campylopodum* contained only two of the flavonoid compounds detected. Crawford and Hawksworth (1979), therefore, maintained the unique flavonoid profile of *A. microcarpum* strongly supported its classification as a separate species.

Considering the analyses of the morphological data we present here for *Arceuthobium microcarpum* and *A. campylopodum* and the major discontinuities in the host affinities of these taxa, we maintain that it is more consistent with other specific classifications of dwarf mistletoes to continue classifying these taxa as species (Hawksworth and Wiens 1996). Our morphological analyses has demonstrated that these species are readily separated using several characters and field observations of their host affinities also demonstrated that they are genetically distinct in that they parasitize taxonomically distinct members of the Pinaceae as their principal hosts (Table 2). Our analyses also supported the continued classification of the mistletoe populations on spruce in Arizona and New Mexico as a separate subspecies of *A. microcarpum* than the populations that parasitize bristlecone pine in northern Arizona (subsp. *aristatae*).

Classifying *Arceuthobium microcarpum* populations as a subspecies of *A. campylopodum* as proposed by Nickrent (2012, 2016) is clearly not supported by this study. Nickrent's rationale for his treatment was based on his molecular findings (Nickrent 1996, Nickrent et al. 2004) and his conclusion that the species recognized by Hawksworth and Wiens (1996) in ser. *Campylopoda* represented ecotypes of *A. campylopodum*, including *A. microcarpum*. Ecotypes are considered to be an experimental category and their adaptive characteristics have to be empirically proven (Davis and Heywood 1965). Moreover, in the broadest sense and in the absence of experimental testing, ecotypes historically have been defined as intraspecies populations that are interfertile and possess multiple adaptive morphological and/or physiological traits that are quantifiable in nature (Turrill 1946). With the advent of molecular and

genomic tools over the last four decades, the latter definition of ecotype has been amended to include not only intraspecific populations distinguishable by adaptive phenotypic and/or physiological variation for sustained life and reproduction in a particular environment but also allele frequencies across polymorphic loci (Lowry 2012). However, Nickrent (2012) did not provide any experimental evidence – morphological, physiological, or genetic – that substantiated his contention that species in ser. *Campylopoda* should be considered ecotypes. He pointed to the fact that there was no definitive data available on the interfertility of the taxa in the series, but did not discuss that ecotypes are usually proven to be interfertile to some degree by experimental crossings (Clausen et al. 1940, 1948; Davis and Heywood 1965). In addition, Nickrent (2012) did not provide data supporting his supposition that seeds from female plants growing on susceptible hosts die when placed on non-susceptible hosts. Nickrent (2012) also speculated that there appeared to be a correlation with plant height of the taxa in ser. *Campylopoda* with elevation; larger plants occurred at lower elevations and smaller at high elevations. However, he failed to provide any experimental evidence that supported this assertion as well. Based on his definition of ecotypes in *Arceuthobium*, Nickrent (2012) recombined nearly all of the species in ser. *Campylopoda* as subspecies of *A*. *campylopodum* and he followed this classification in his treatment for *Arceuthobium* in the Flora of North America (Nickrent 2016). The application of Nickrent's (2012, 2016) treatment of *A*. *microcarpum* as a subspecies of *A*. *campylopodum* precludes the recognition of *A*. *microcarpum* subsp. *aristatae*. Evidently, Nickrent (2012) was not aware of the description of subsp. *aristatae* by Scott and Mathiasen (2009) because it was not listed under his nomenclatural summary for his recombination *A*. *campylopodum* subsp. *microcarpum* (Engelmann) Nickrent (Nickrent 2012, pg. 10). Therefore, Nickrent (2012) did not consider all of the available morphological and physiological data that had been published for *A*. *microcarpum* and only used Hawksworth and Wiens (1996) as the source of his data. Here, we have provided further evidence that *A*. *microcarpum* is morphologically distinct from *A*. *campylopodum*. Furthermore, our results do not support the Nickrent (2012, 2016) treatment which ignores the existence of subsp. *aristatae* parasitizing bristlecone pine in northern Arizona.

Without having described and named *Arceuthobium microcarpum* subsp. *aristatae*, this rare dwarf mistletoe cannot be protected. From the conservation biology perspective, it is prudent to name plants that can be demonstrated to be genetically, morphologically, and/or physiologically different, even if the differences are cryptic, than to group them as one species (Baldwin 2000). Grouping them together gives the sometimes incorrect impression that a species which actually consists of many genetically different, but morphologically similar populations, are widespread and abundant when in reality they consist of many different species or infraspecific taxa with very limited distributions that deserve recognition from a conservation biology/biodiversity perspective (Baldwin 2000, Simpson 2010). Following the classification of most of the taxa in ser. *Campylopoda* as subspecies of *A*. *campylopodum* as proposed by Nickrent (2012, 2016) prevents the recognition and possibly the conservation of many populations of *Arceuthobium* in the western United States with similar morphologies, but different host affinities, including subsp. *aristatae* (Mathiasen and Kenaley 2015, 2016, 2017).

The recent increases in both size and frequency of high-severity fires across the entire western United States has been especially evident across Arizona (Westerling et al. 2006; Westerling 2016), affecting a large area of the geographic distribution for both subspecies of *Arceuthobium microcarpum*. Due to the parasitic habit of dwarf mistletoes and the high probability for low survival of host trees in high-severity wildfires, these fires can greatly reduce dwarf mistletoe populations (Alexander and Hawksworth 1975; Harrington and Hawksworth 1990; Shaw and Agne 2017). Therefore, the distribution of *A*. *microcarpum* subsp. *aristatae* needs to be evaluated to determine the impacts that several wildfires have had on its populations on Kendrick and Schultz Peaks. In 2000, the Pumpkin Fire burned throughout much of the Kendrick Peak Wilderness Area as did the Boundary Fire in 2017. In 2010, the Schultz Fire burned in a mosaic across Schultz Peak. According to Monitoring Trends in Burn Severity wildfire data (Eidenshink et al. 2007) for the Shultz Fire, approximately one-third of the entire *Arceuthobium microcarpum* subsp. a*ristatae* population burned as high-severity, thus killing many of the dwarf

mistletoe-infected bristlecone pines on Schultz Peak (J. M. Scott unpublished). So far, no field assessment of the mortality of bristlecone pine has been completed on Schultz Peak and this is clearly needed because bristlecone pine is considered a protected species in Arizona under the Arizona Native Plant Law (ANPL) due to its rarity in the state (McDougal 1975). Not only is bristlecone pine rare in Arizona, but the dwarf mistletoe parasitizing it may also be threatened due to the recent fires and may need to be considered for protection under the ANPL. However, it should be emphasized again that the Flora of North America does not recognize subspecies *aristatae* (Nickrent 2016) and therefore, if followed prevents subsp. *aristatae* for consideration for possible protection under the ANPL. Based on our findings, *A. microcarpum* subsp. *aristatae* is morphologically distinct from subsp. *microcarpum* and should be considered as another rare plant present on the San Francisco Peaks that may be in need of protection (McDougal 1975; Rominger and Paulik 1983; Scott and Mathiasen 2009).

While the recent classifications of many previously described species of *Arceuthobium* into subspecies (Nickrent 2012, 2016) is an attempt that appears to be the simplification of species distinctions based primarily on molecular data, the practicality of doing this, in terms of recognition and the possible protection of currently described subspecies such as subsp. *aristatae*, is highly questionable. If the goal of plant systematics/taxonomy is to better understand the relationships among populations of *Arceuthobium* based on their morphology, phenology, and physiological (host affinity) differences, then obscuring these distinctions rather than recognizing them, diminishes rather than furthers our understanding of these ecologically and economically important parasitic plants. This study's results and those of related investigations (Mathiasen and Kenaley 2015, 2016, 2017) move this understanding forward.

ACKNOWLEDGEMENTS

We gratefully acknowledge the assistance with data collection by Dr. Carolyn M. Daugherty.

LITERATURE CITED

Acciavatti, R. E., and M. J. Weiss. 1974. Evaluation of dwarf mistletoe on Engelmann spruce, Fort Apache Indian Reservation, Arizona. Plant Disease Reporter 58: 418-419.

Alexander, M. E., and F. G. Hawksworth. 1975. Wildland fires and dwarf mistletoes: a literature review of ecology and prescribed burning. General Technical Report RM-14, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO.

Baldwin, B. G. 2000. Roles of modern plant systematics in discovery and conservation of fine-scale biodiversity. Madroño 47: 219-229.

Clausen, J., D. D. Keck, and W. M. Hiesey. 1940. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Carnegie Institute of Washington Publications No. 520.

Clausen, J., D. D. Keck, and W. M. Hiesey. 1948. Experimental studies on the nature of species. III. Environmental responses of climatic races of *Achillea*. Carnegie Institute of Washington Publications No. 581.

Crawford, D. J., and F. G. Hawksworth. 1979. Flavonoid chemistry of *Arceuthobium* (Viscaceae). Brittonia 31: 212-216.

Davis, P. H., and V. H. Heywood. 1965. Principles of Angiosperm Taxonomy. D. Van Nostrand Company, Inc. Princeton, NJ.

Eidenshink, J., B. Schwind, K. Brewer, Z. Zhu, B. Quayle, and S. Howard. 2007. A. project for monitoring trends in burn severity. Fire Ecology (Special Issue) 3: 3-21.

Gill, L. S. 1935. *Arceuthobium* in the United States. Connecticut Academy of Arts and Science Transactions 32: 111-245.

Harrington, M. G., and F. G. Hawskworth. 1990. Interactions of fire and dwarf mistletoe on mortality of southwestern ponderosa pine. In Effects of fire management on southwestern natural resources; proceedings of the symposium. J. S. Krammes, technical coordinator, General Technical Report RM-191, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO. Pp. 234-240.

Hawksworth, F. G., and D. Wiens. 1970. New taxa and nomenclatural changes in *Arceuthobium* (Viscaceae). Brittonia 22: 265-269.

Hawksworth, F. G., and D. Wiens. 1972. Biology and classification of dwarf mistletoes (*Arceuthobium*). Agriculture Handbook 401, USDA Forest Service, Washington, DC.

Hawksworth, F. G., and D. Wiens. 1996. Dwarf mistletoes: biology, pathology, and systematics. Agriculture Handbook 709, USDA Forest Service, Washington, DC.

Lowry, D. B. 2012. Ecotypes and the controversy over stages in the formation of new species. Biological Journal of the Linnean Society 106: 241-257.

Lynch, A. M. 2004. Fate and characteristics of *Picea* damaged by *Elatobium abietinum* (Walker) (Homoptera:Aphididae) in the White Mountains of Arizona. Western North American Naturalist 64: 7-17.

Martin, W. C., and C. R. Hutchins. 1980. A flora of New Mexico. Vaduz, Lichtenstein: J. Cramer.

Mathiasen, R. L. 1977. The taxonomy and epidemiology of dwarf mistletoes parasitizing white pines in Arizona. Ph.D. dissertation. University of Arizona, Tucson.

Mathiasen, R. L., and F. G. Hawksworth. 1980. Taxonomy and effects of dwarf mistletoe on bristlecone pine on the San Francisco Peaks, Arizona. Research Paper RM-224, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO.

Mathiasen, R. L., F. G. Hawksworth, and C. B. Edminster. 1986. Effects of dwarf mistletoe on spruce in the White Mountains, Arizona. Great Basin Naturalist 46: 685-689.

Mathiasen, R. L., and S. C. Kenaley. 2015. A morphometric analysis of dwarf mistletoes in the *Arceuthobium campylopodum-occidentale* complex (Viscaceae). Madroño 62: 1-20.

Mathiasen, R. L., and S. C. Kenaley. 2016. The classification of California Viscaceae: an alternative perspective. Madroño 63: 8-33.

Mathiasen, R. L., and S. C. Kenaley. 2017. *Arceuthobium tsugense* (Viscaceae): four subspecies with contrasting morphologies and host distributions. Journal of the Botanical Research Institute of Texas 11: 363-390.

McDougal, W. B. 1975. The problem of endangered plant species in northern Arizona. Plateau 47: 8-10.

Nickrent, D. L. 1996. Molecular systematics. *In* Hawksworth, F. G., and D. Wiens. Dwarf mistletoes: biology, pathology, and systematics. Agriculture Handbook 709, USDA Forest Service, Washington, DC. Pp. 155-172.

Nickrent, D. L. 2012. Justification for subspecies in *Arceuthobium campylopodum* (Viscaceae). Phytoneuron 51: 1-11.

Nickrent, D. L. 2016. Viscaceae Batch – Christmas Mistletoe Family. *In* Flora of North America. Volume 12. Flora of North America Editorial Committee (editors). Oxford University Press, New York, NY. Pp. 422-440.

Nickrent, D. L., M. A. García, M. P. Martín, and R. L. Mathiasen. 2004. A phylogeny of all species of *Arceuthobium* (Viscaceae) using nuclear and chloroplast DNA sequences. American Journal of Botany 91: 125-138.

Quinn, G. P., and M. J. Keough. 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, UK.

Rominger, J. M., and L. A. Paulik. 1983. A floristic inventory of the plant communities of the San Francisco Peaks Research Natural Area. USDA Forest Service General Technical Report RM-96, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO.

Scott, J. S., and R. L. Mathiasen. 2009. Bristlecone pine dwarf mistletoe: *Arceuthobium microcarpum* subsp. *aristatae* (Viscaceae), a new subspecies of western spruce dwarf mistletoe from northern Arizona. Journal of the Botanical Research Institute of Texas 3: 13-22.

Simpson, M. G. 2010. Plant systematics. Academic Press, Cambridge, MA.
Shaw, D. C., and M. C. Agne. 2017. Fire and dwarf mistletoe (Viscaceae: *Arceuthobium* species) in western North America: contrasting *Arceuthobium tsugense* and *Arceuthobium americanum*. Botany 95: 231-246.
Southwest Environmental Information Network. 2015. Available on-line at http://swbiodiversity.org/portal/index.php. (accessed 15 January 2018).
Turrill, W. B. 1946. The ecotype concept. New Phytologist 45: 34-43.
Westerling, A. L. 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Philosophical Transactions of the Royal Society 371: 20150178.
Westerling, A.L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western US forest wildfire activity. Science 313: 940-943.

Table 1. Morphological measurements for *Arceuthobium campylopodum*, *A. microcarpum* subsp. *microcarpum*, and *A. microcarpum* subsp. *aristatae*. Data are listed as mean, (SD), [n]. Means followed by different capital letters in the same row were significantly different using a one-way analysis of variance (ANOVA) followed by a Tukey's honestly significant difference post hoc test (α = 0.05). Mean measurements for *A. microcarpum* subsp. *aristatae* and subsp. *microcarpum* significantly different to *A. campylopodum* when compared via a Dunnett's test are in bold type (α = 0.05; *P*< 0.0001). Lower case letters in the brackets designate sample sizes already listed in the same column. Plant heights are in cm and all other measurements are in mm. ---------- indicates no data were collected.

Character(s)	***Arceuthobium campylopodum***	***Arceuthobium microcarpum* subsp. *aristatae***	***Arceuthobium microcarpum* subsp. *microcarpum***
Plant height			
Female	10.4 A (2.7) [600a]	**3.6** C (2.2) [177]	**6.9** B (1.3) [473]
Male	9.7 A (3.0) [a]	**2.7** C (2.0) [152]	**6.0** B (1.3) [383]
Basal diameter			
Female	3.4 A (0.7) [a]	**1.8** C (0.8) [167]	**2.0** B (0.6) [433]
Male	3.2 A (0.6) [a]	**1.8** B (0.5) [121]	**1.9** B (0.5) [257]
Third internode length			
Female	13.0 A (3.1) [a]	----------	**11.4** B (2.8) [120a]
Male	12.0 A (3.3) [a]	----------	**9.8** B (2.5) [100b]
Third Internode Width			
Female	2.5 A (0.4) [a]	----------	**1.7** B (0.2) [a]
Male	2.5 A (0.4) [a]	----------	**1.7** B (0.2) [b]
Flower Diameter	3.1 A (0.4) [400]	**2.4** B (0.5) [257]	**2.4** B (0.3) [355]
3-merous			
4-merous	4.2 A (0.5) [360]	**3.2** B (0.3) [30]	**3.2** B (0.7) [50]
Petal lobe length	1.6 A (0.2) [760b]	**1.3** B (0.2) [94a]	**1.3** B (0.2) [261c]
Petal lobe width	1.4 A (0.2) [b]	**1.1** B (0.2) [a]	**1.1** B (0.2) [c]
Anther diameter	0.6 A (0.1) [b]	**0.5** B (0.1) [a]	**0.5** B (0.1) [c]
Anther distance to tip	0.6 A (0.1) [b]	**0.5** B (0.1) [a]	**0.5** B (0.1) [c]
Fruit length	5.4 A (0.5) [480c]	**3.3** C (0.5) [281b]	**3.5** B (0.6) [530d]
Fruit width	3.7 A (0.4) [c]	**2.1** C (0.4) [b]	**2.2** B (0.4) [d]
Seed length	3.5 A (0.4) [c]	**2.4** B (0.3) [107c]	**2.4** B (0.3) [314e]
Seed width	1.5 A (0.2) [c]	**1.1** C (0.2) [c]	**1.1** B (0.1) [e]

Table 2. Summary of the principal characters separating *Arceuthobium campylopodum*, *A*. *microcarpum* subsp. *microcarpum*, and *A*. *microcarpum* subsp. *aristatae*. Data for morphological characters are means; plant heights in cm and all other measurements in mm. Numbers and hosts in bold type represent key morphological or physiological differences between the taxa. Host susceptibility classification based on information in Mathiasen and Hawksworth (1980), Hawksworth and Wiens (1996), and Scott and Mathiasen (2009).

Character	***Arceuthobium campylopodum***	***Arceuthobium microcarpum* subsp. *aristatae***	***Arceuthobium microcarpum* subsp. *microcarpum***
Plant height			
Female	**10.4**	**3.6**	**6.8**
Male	**9.7**	**2.7**	**5.9**
Basal diameter			
Female	**3.4**	**1.8**	**2**
Male	**3.2**	**1.8**	**1.9**
Flower diameter			
3-merous	**3.1**	2.4	2.4
Fruit length	**5.4**	3.3	3.4
Fruit width	**3.7**	2.1	2.2
Host Susceptibility			
Principal	***Pinus jeffreyi*** ***P. ponderosa***	***Pinus aristata***	***Picea engelmannii*** ***Picea pungens***
Secondary	*P. attenuata* *P. coulteri*	None	None
Occasional	*P. contorta* var. *murrayana* and var. *latifolia* *P. sabinianna*	***Picea engelmannii***	None
Rare		*Pinus strobiformis,* *Abies lasiocarpa* var. *arizonica*	*Abies lasiocarpa* var. *arizonica*

Table 3. Predicted taxonomic membership according to forward, stepwise discriminant function analyses (DFA) for the morphological classification of female (n= 6 characters) and male plants (n= 7 characters) using complete data. Anther diameter (AD); anther distance from tip (ADT); basal diameter (BA); fruit length (FL); fruit width (FW); petal length (PL); petal width (PW); plant height (PH); 3-merous flower diameter (3-FD). Sample size (n; female, male plants): *Arceuthobium campylopodum* (480, 402), *A. microcarpum* (314, 247), and subsp. *aristatae* (107, 94).

Stepwise DFA (step [character])	**Classified correctly to taxon membership** (%, [N predicted/ N field determined])			
	Total	*A. campylopodum*	*A. microcarpum* subsp. *aristatae*	*A. microcarpum* subsp. *microcarpum*
Female				
1. [FL]	84.2 [759/901]	98.8 [474/480]	23.4 [25/107]	82.8 [260/314]
2 [*], [PH]	94.0 [847/901]	99.2 [476/480]	98.1 [105/107]	84.7 [266/314]
3 [*], [*], [SL]	95.3 [859/901]	100.0 [480/480]	98.1 [105/107]	84.7 [274/314]
4 [*], [*], [*], [BD]	95.7 [862/901]	100.0 [480/480]	98.1 [105/107]	88.2 [277/314]
5 [*], [*], [*], [*], [SW]	96.0 [865/901]	100.0 [480/480]	98.1 [105/107]	89.2 [280/314]
6 [*], [*], [*], [*], [*],[FW]	96.1 [866/901]	100.0 [480/480]	96.3 [103/107]	90.1 [283/314]
Male				
1 [BD]	65.3 [492/753]	91.5 [368/402]	80.9 [76/94]	18.7 [48/257]
2 [*], [3-FD]	71.8 [541/753]	95.3 [383/402]	58.5 [55/94]	40.1 [103/257]
3 [*, [*], [PH]	86.6 [652/753]	95.0 [382/402]	89.4 [84/94]	72.4 [186/257]
4 [*], [*], [*], [PW]	87.5 [659/753]	95.8 [385/402]	89.4 [84/94]	73.9 [190/257]
5 [*], [*], [*], [*], [PL]	88.0 [663/753]	96.0 [386/402]	89.4 [84/94]	75.1 [193/257]
6 [*], [*], [*], [*], [*], [ADT]	88.6 [667/753]	96.8 [389/402]	89.4 [84/94]	75.5 [194/257]
7 [*], [*], [*], [*], [*], [*], [AD]	89.1 [671/753]	97.3 [391/402]	88.3 [83/94]	76.7 [197/257]

Table 4. Quadratic discriminant function (DFA) using complete morphological records and equal prior probability per taxon (0.333): assignment of field diagnosed female and male plants of *Arceuthobium campylopodum*, *A. microcarpum* subsp. *aristatae*, and *A. microcarpum* subsp. *microcarpum* to predicted taxonomic membership based on 6 female and 7 male characters (full-model for each sex).

Plant sex / *Arceuthobium* taxon (Total N = field determined plants)	**Assigned species membership according to DFA (%) [N= field determined plants]**		
	A. campylopodum	*A. microcarpum* subsp. *aristatae*	*A. microcarpum* subsp. *microcarpum*
Female			
A. campylopodum (480)	**100.0 [480]**	0.0 [0]	0.0 [0]
A. microcarpum subsp. *aristatae* (107)	1.0 [3]	**96.3 [103]**	2.8 [3]
A. microcarpum subsp. *microcarpum* (314)	0.9 [1]	8.9 [28]	**90.1 [283]**
Male			
A. campylopodum (402)	**97.3 [391]**	2.2 [9]	0.5 [2]
A. microcarpum subsp. *microcarpum* (257)	2.7 [7]	**88.3 [83]**	10.6 [10]
A. microcarpum subsp. *aristatae* (94)	1.1 [1]	20.6 [53]	**76.7 [197]**

Table 5. Canonical statistics: quadratic discriminant function analysis (DFA) of female (n= 6 morphological characters) and male plants (n= 7 morphological characters) using complete data or randomly selected records (n= 50 complete records/taxon) for *Arceuthobium campylopodum*, *A. microcarpum* subsp. *aristatae* and *A. microcarpum* subsp. *microcarpum*.

Canonical	**Eigenvalue**	**Percentage**	**Cumulative percentage**	**Canonical correlation**	**Likelihood Ratio**	**Approx. F**	***P*-value**
Female - Complete							
1	7.99	97.6	97.6	0.9427	0.0928	$F_{12, 1786}$= 339.68	<.0001
2	0.20	2.4	100.0	0.4074	0.8340	$F_{5, 894}$= 35.60	<.0001
Female - Resampled							
1	11.42	93.4	93.4	0.9589	0.0446	$F_{12, 284}$= 88.38	<.0001
2	0.80	6.6	100.0	0.6677	0.5542	$F_{5, 143}$= 23.00	<.0001
Male - Complete							
1	3.17	93.6	93.6	0.8717	0.1975	$F_{14, 1488}$= 132.88	<.0001
2	0.22	6.4	100.0	0.4212	0.8226	$F_{6, 745}$= 26.78	<.0001
Male - Resampled							
1	4.10	88.4	88.4	0.8966	0.1275	$F_{14, 282}$= 36.28	<.0001
2	0.54	11.6	100.0	0.5914	0.6502	$F_{6, 142}$= 12.73	<.0001

Table 6. Quadratic discriminant function analyses (DFA) of male and female plants using complete data for *Arceuthobium campylopodum*, *A. microcarpum* subsp. *aristatae*, and *A. microcarpum* subsp. *microcarpum*. Comparison of morphological characters (means) according to predicted classification to taxonomic membership. Ninety-five percent confidence intervals (±) were computed for comparison of mean differences. Mean plant heights in cm and all other measurements in mm.

Sex / Character(s)		***Arceuthobium campylopodum***	***Arceuthobium microcarpum* subsp. *aristatae***	***Arceuthobium microcarpum* subsp. *microcarpum***
Female				
	Plant height (PH)	10.3 (±0.2)	3.0 (±0.1)	6.7 (±0.2)
	Basal diameter (BD)	3.4 (±0.2)	1.6 (±0.1)	2.0 (±0.1)
	Fruit length (FL)	5.4 (±0..0)	3.2 (±0.1)	3.3 (±0.1)
	Fruit width (FW)	3.7 (±0.0)	2.1 (±0.1)	2.2 (±0.0)
	Seed length (SL)	3.5 (±0.0)	2.4 (±0.0)	2.4 (±0.0)
	Seed width (SW)	1.5 (±0.0)	1.1 (±0.0)	1.1 (±0.0)
Male				
	Plant height (PH)	9.5 (±0.3)	3.0 (±0.2)	7.0 (±0.3)
	Basal diameter (BA)	3.2 (±0.1)	1.8 (±0.1)	2.0 (±0.1)
	Flower diameter (3-lobed, 3-FD)	3.1 (±0.0)	2.4 (±0.1)	2.3 (±0.0)
	Petal length (PL)	1.5 (±0.0)	1.3 (±0.0)	1.3 (±0..0)
	Petal width (PW)	1.4 (±0.0)	1.1 (±0.0)	1.1 (±0.0)
	Anther diameter (AD)	0.6 (±0.0)	0.5 (±0.0)	0.5 (±0.0)
	Anther distance from tip (ADT)	0.6 (±0.0)	0.5 (±0.0)	0.5 (±0.0)

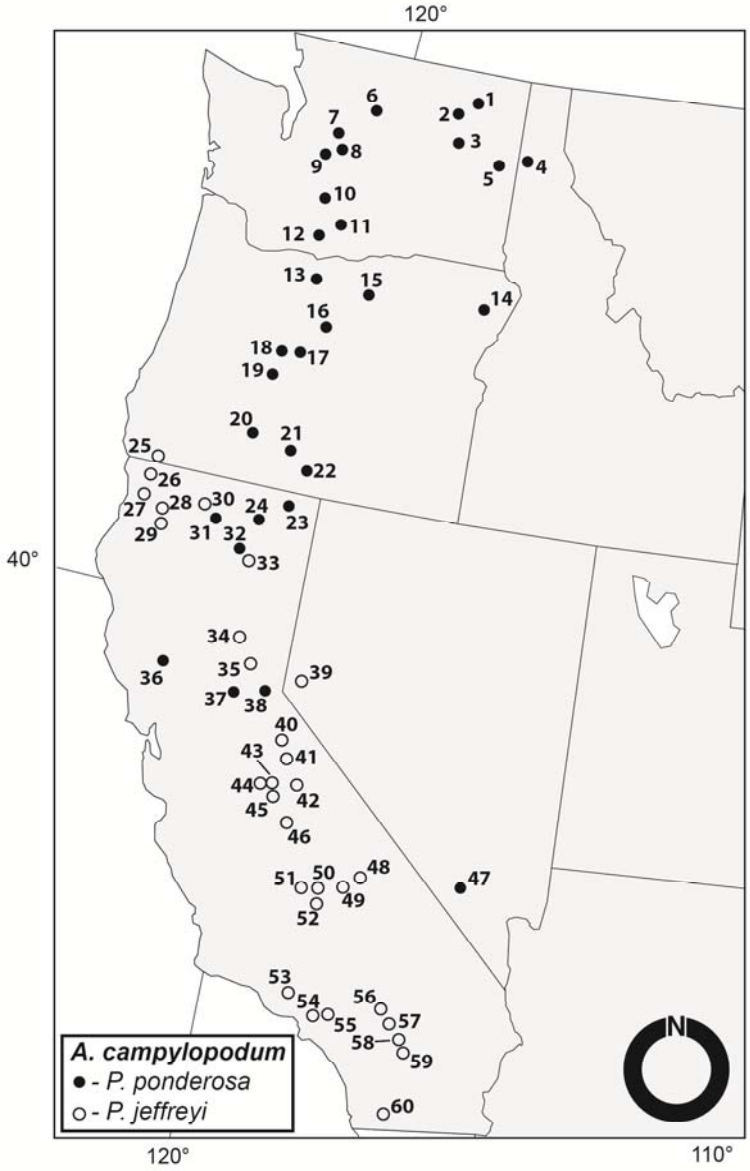

Figure 1. Approximate locations of collection sites for *Arceuthobium campylopodum* in Washington, Idaho, Oregon, California, and Nevada. Closed circles present locations where plants were collected from *Pinus ponderosa*. Open circles represent locations where plants were collected from *P. jeffreyi*. Numbers correspond to the following locations: **Washington**: **1**- 4.5 km N of Gifford on St. Rte. 25, **2** - 20 km S of Fruitland on St. Rte. 25, **3** - 2 km NW of Nespelem on St. Rte. 155, **5** - 16 km S of Spokane on St. Rte. 195, **6** - 2.5 km W of St. Rte. 153 on Squaw Creek rd., **7** - Lake Wenatchee on Chiwawa River Loop rd., **8** - 2.6 km W of Squilchuck St. Park on road to Mission Ridge Ski Area, **9** - 0.8 km W of St. Rte. 97 on St. Rte 970, **10** - 17.6 km E of White Pass on St. Rte. 12, **11** - 2 km N of Satus Pass on St. Rte. 97, **12** - 3 km S of Trout Lake on St. Rte. 141; **Idaho**: **4** - 2.3 km N of Coeur d'Alene on Fernan Lake rd.; **Oregon**: **13** - 6.4 km W of Friend on forest rd. 27, **14** - 6.4 km S of Joseph on E shore of Wallowa Lk., **15** - 9.4 km on Sheep Cr. rd from forest rd. 51, Wallowa-Whitman Nat. For., **16** - 1.8 km E of Ochoco Summit on St. Rte. 26, **17** - 12.2 km W of St. Rte. 97 on St. Rte. 138, **18** - 15.2 km S of Sisters on forest rd. 16, **19** - 1 km from forest rd. 44 on forest rd. 4410, Pringle Falls Exp. For., **20** - Fort Klamath Cemetery on St. Rte. 62, **21** - 3 km W of Quartz Mtn. Pass on St. Rte. 140, **22** - Warner Mtn. Ski Hill on St. Rte. 26, **25** - 6 km S of Takilma on Greyback rd.; **California**: **23** - 3.4 km W of County rd. 48 on forest rd. 73, west shore of Goose Lk., **24** - 16 km N of Adin on St. Rte. 299/139, **26** - 1 km S of forest rd. 17N26 on forest rd. 17N11, Klamath Nat. For., **27** - 6.2 km W of St. Rte. 96 on Dillon Mtn. rd., **28** - 9.6 km S of Callahan on St. Rte. 3, **29** - 10 km E of St. Rte 3 on forest rd. 17, Shasta-Trinity Nat. For., **30** - 2.4 km W of Stewart Hot Springs on forest rd. 17, **31** - 2 km N of St. Rte. 89 on Mt. Shasta Ski Park rd., **32** - 0.1 km S of St. Rte. 299 on St. Rte. 89, **33** - 2 km S of Old Station on St. Rte. 44, **34** - 2 km W of St. Rte. 44 on forest rd. 101, **35** - 14.4 km W of Susanville on St. Rte. 36, **36** - 19.5 km N of Upper Lake on Pillsbury Lk. rd., **37** - 7.7 km N of Pollock Pines on forest rd. 4, **38** - at entrance to Sugar Pine State Park, west shore of Lk. Tahoe, **40** - 1 km N of Markleeville on St. Rte. 89, **41** - Silver Creek Campground on St. Rte. 4, **42** - Column of the Giants on St. Rte. 108, **43** - Pinecrest Transfer Station 0.5 km W of Pinecrest on St. Rte. 108, **44** - 1 km W of Long Barn on St. Rte. 108, **45** - 8.5 km E of Crane Flat on St. Rte. 120, **46** - 2 km W of Big Creek on rd. to Shaver Lk., **48** - 8.5 km W of Sherman Pass on forest rd. 22S05, **49** - 2.2 km S of Troy Mdws. Campground, Sequoia Nat. For., **50** - 5.8 km N of rd. to Johnsonville on Western Divide Highway, **51** - Pine Flat, Sequoia Nat. For., **52** - Tiger Flat, Sequoia Nat. For., **53** - 6.2 km S of St. Rte. 33 on rd. to Mt. Reyes, **54** - 1.4 km W of Cloud Burst on St. Rte. 2, **55** - 1 km W of Big Pines on St. Rte. 2, **56** - 2.4 km N of Fawnskin on forest rd. 2N71, **57** - 1.9 km from St. Rte. 38 on rd. to Jenks Lk., **58** - near Ranger Station in Idylwild, **59** - 1.1 km S of the S Fork San Jacinto River Bridge on St. Rte. 74, **60** - 0.5 km S of Horse Heaven Campground on Sunrise Highway; **Nevada**: **39** - Bowers Mansion St. Park, **47** - 4.1 km W of Ranger Station at Old Ski Tow Historic Site, Kyle Canyon.

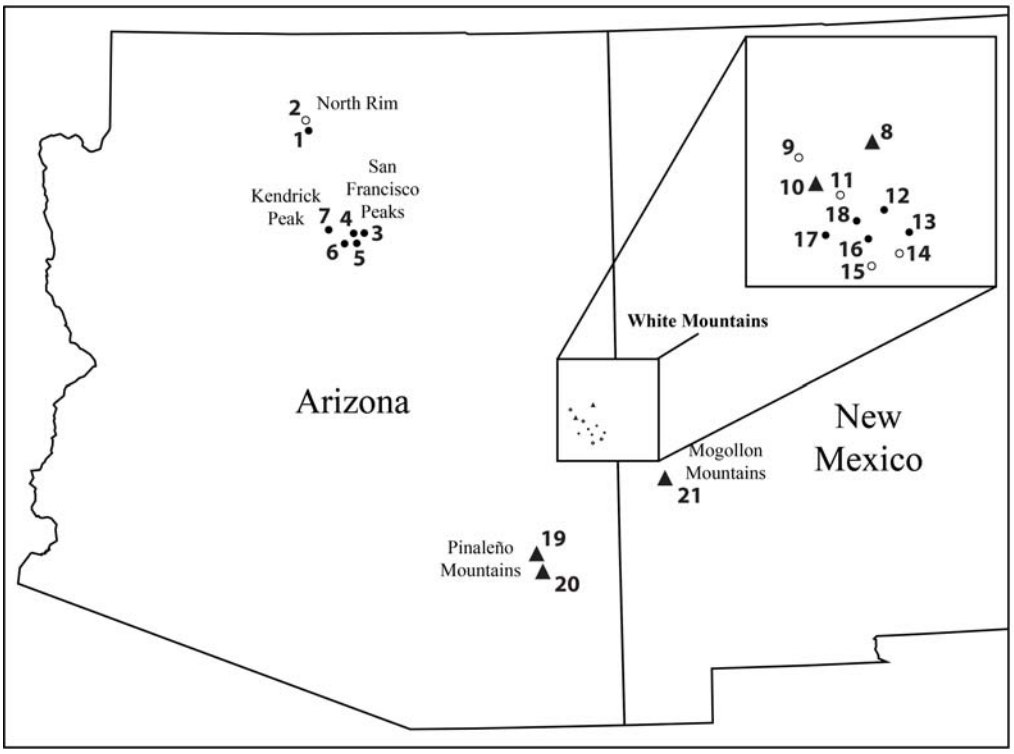

Figure 2. Approximate locations for plant collections of *Arceuthobium microcarpum* in 2007 and 2017. Collection sites for 2007 are indicated by closed circles. Collection sites where plants were sampled in 2007 and 2017 are indicated by open circles. Sites where plants were sampled in 2017 only are indicated by open triangles. Plants were collected from bristlecone pine (BCP), Engelmann spruce (ES), or blue spruce (BS) as indicated in parentheses for each collection site. **Arizona**: **1**- Point Royal Road, North Rim Grand Canyon National Park (BS), **2** - 6 km south of park boundary on State Route 67, North Rim Grand Canyon National Park (BS), **3** - Inner Basin of San Francisco Peaks (ES), **4** - "Secret Meadow" in southeast Inner Basin of San Francisco Peaks (BCP and ES), **5** - Schultz Peak BCP and ES), **6** - Weatherford Trail ca. 1 km south of Doyle Saddle (BCP), **7** - summit of Kendrick Peak (ES), **8** - 1 km W of Greer on forest road 575 (BS), **9** - Lee Valley Reservoir (BS), **10** - Big Lake at junction of forest road 249 and State Route 261 (BS), **11** - 4 km east of Big Lake on forest road 249 (BS), **12** - Williams Valley near forest road 249 (BS), **13** - 6 km S of Alpine near State Route 191 (BS), **14** - 3 km N of Hannagan Meadows near State Route 191 (BS), **15** - Cache Cienega near forest road 26 (ES and BS), **16** - along forest road 72 (ES and BS), **17** - along forest road 402 (ES and BS), **18** - John's Canyon near forest road 405 (BS), **19** - Soldier Creek campground (ES), **20** - Hospital Flat campground (ES); **New Mexico**: **21** - Willow Creek campground.

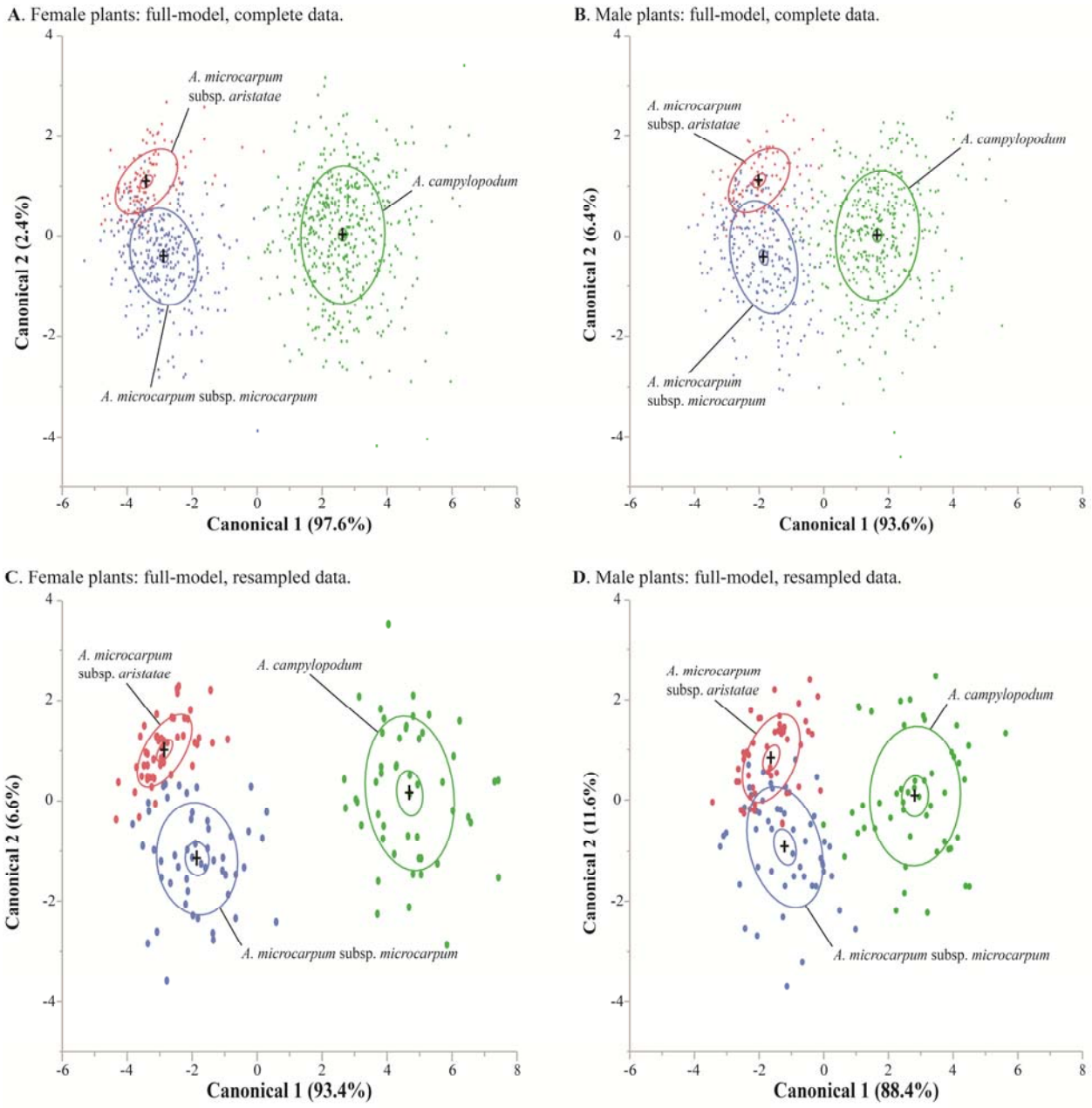

Figure 3. Canonical plots for discriminant function analyses (DFA) of *Arceuthobium campylopodum*, *A. microcarpum* subsp. *microcarpum*, and *A. microcarpum* subsp. *aristatae* based on morphological characteristics of female (A, C) and male plants (B, D) shown in Table 6. Multivariate means (squares) were computed using complete data for each species by sex (A, B), whereas, to further validate the DFA, means were also calculated using a random subset (50 complete records/taxon) of female (C) and male plants (D), respectively. For each taxon (A-D), the inner ellipse correspond to a 95% confidence limit for the mean, and the outer ellipse represent a normal 50% contour illustrating the approximate area within which 50% of plants for each species reside.