

A MORPHOLOGICAL COMPARISON OF *ARCEUTHOBIUM ABIETINUM* AND
A. CAMPYLOPODUM (VISCACEAE) AND NOMENCLATURAL
CHANGES FOR *A. ABIETINUM*

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ABSTRACT

Fir dwarf mistletoe (*Arceuthobium abietinum*, Viscaceae) parasitizes true firs (*Abies* spp.) in the Pacific Northwest through California, the Southwest, and into northern Mexico. At present, fir dwarf mistletoe consists of two special forms (*formae speciales*, f. sp.) and one subspecies that are morphologically similar, but exhibit a high degree of host specificity. However, *A. abietinum* has been treated as a subspecies of *A. campylopodum* or conspecific with it in some taxonomic treatments. Therefore, we undertook this study to compare the morphologies of these dwarf mistletoes; collecting morphological data from nearly 100 *A. abietinum* and 60 *A. campylopodum* populations collected across most of their geographic ranges and analyzing these data using univariate and multivariate statistical tests. Our results demonstrated that the special forms and subspecies of *A. abietinum* are morphologically distinct from *A. campylopodum*, thereby, supporting the continued recognition of *A. abietinum* as a separate species. Furthermore, our analysis found significant differences for several of the characters we examined between the special forms of *A. abietinum*. Therefore, we recombined the special forms as subspecies: *A. abietinum* subsp. *abietinum* (formerly f. sp. *concoloris*) and *A. abietinum* subsp. **magnificae** (formerly f. sp. *magnificae*). The previously described *A. abietinum* subsp. *wiensii* was morphologically distinct from subsp. *abietinum* and subsp. *magnificae*. The distinctiveness of these taxa was supported by their host affinities as well.

KEY WORDS: *Abies*, *Arceuthobium*, discriminant function analysis, dwarf mistletoes, subspecies

RESUMEN

El muérdago enano del oyamel (*Arceuthobium abietinum*, Viscaceae) parasita a los oyameles o abetos (*Abies* spp.) en la región occidental, desde California hasta el norte de México. Hasta ahora, el muérdago enano del oyamel consiste de dos formas especiales (*formae speciales*, f. sp.) y una subspecie que son morfológicamente similares, pero presentan un alto grado de especificidad de hospedador. Sin embargo, *A. abietinum* ha sido tratado como subspecie de *A. campylopodum* o como conspecifico con éste en algunos tratamientos taxonómicos. En este estudio se comparan las morfologías de esos muérdagos enanos. Se recabaron datos morfológicos de casi 100 poblaciones de *A. abietinum* y 60 de *A. campylopodum* con materiales colectados en la mayor parte de área de distribución y los datos se analizaron usando pruebas estadísticas univariadas y multivariadas. Nuestros resultados demuestran que las dos formas especiales y la subspecie de *A. abietinum* son morfológicamente diferentes de *A. campylopodum*, lo que justifica que *A. abietinum* siga considerándose como especie separada. Adicionalmente, nuestro análisis encontró diferencias significativas para algunos de los caracteres examinados entre las formas especiales de *A. abietinum*. Por esta razón, recombinaamos esas formas a nivel de subspecie: *A. abietinum* subsp. *abietinum* (previamente f. sp. *concoloris*) and *A. abietinum* subsp. **magnificae** (previamente f. sp. *magnificae*). *Arceuthobium abietinum* subsp. *wiensii*, previamente descrita, difiere también morfológicamente de las otras dos subspecies. La diferencia entre esos taxa es corroborada además por sus preferencias de hospedador.

PALABRAS CLAVE: *Abies*, *Arceuthobium*, análisis de función discriminante, muérdagos enanos, subspecies

INTRODUCTION

Fir dwarf mistletoe (*Arceuthobium abietinum* (Engelm.) Engelm. ex Munz) is a common plant parasite of true firs (*Abies* spp.) from southern Washington through Oregon and California into southern Nevada, southern Utah, Arizona, and northern Mexico (Hawksworth & Wiens 1996). At present, fir dwarf mistletoe is classified as two special forms (*formae speciales*, f. sp.) and one subspecies based on host relationships and several morphological differences. White fir dwarf mistletoe (*A. abietinum* (Engelm.) Engelm. ex Munz f. sp. *concoloris* Hawksw. & Wiens) parasitizes grand fir (*Abies grandis* (Douglas ex D. Don) Lindley) and the hybrid populations of *Abies concolor* (Gordon & Glend.) Lindley ex Hildebr.) × *A. grandis* (Ott 2014; Meyers 2015) in the Cascade Ranges, Klamath-Siskiyou Mountains, and Coast Ranges of Oregon and California. It is common on

Sierra white fir (*Abies lowiana* (Gordon) A. Murray bis) in the Sierra Nevada and San Bernardino Mountains in California (Hawksworth & Wiens 1972, 1996). *Arceuthobium abietinum* f. sp. *concoloris* also occurs in widely isolated populations on Rocky Mountain white fir (*Abies concolor*) in southern Nevada, southern Utah, and Arizona. In northern Mexico, white fir dwarf mistletoe parasitizes Durango fir (*Abies durangensis* Martínez) in widely scattered populations in Chihuahua and Durango (Hawksworth & Wiens 1996; Quiñonez et al. 2013; Quiñonez 2016). Red fir dwarf mistletoe (*A. abietinum* (Engelm.) Engelm. ex Munz f. sp. *magnificae* Hawksw. & Wiens) parasitizes red fir (*Abies magnifica* A. Murray bis), its only host, in the southern Cascade Ranges (near Mount Shasta and Mount Lassen) through the Sierra Nevada Mountains to as far south as the Greenhorn Mountains (Kern County). The other taxon—*Arceuthobium abietinum* (Engelm.) Engelm. ex Munz subsp. *wiensii* Mathiasen & C. Daugherty (Wiens' dwarf mistletoe)—is a principal parasite of red fir and Brewer spruce (*Picea breweriana* S. Watson) in the Klamath-Siskiyou Mountains (Mathiasen & Daugherty 2009).

The classification of the true fir hosts of *Arceuthobium abietinum* in the Pacific Northwest and California has long been debated (e.g. Sudworth 1908; Liu 1971; Hunt 1993; Xiang et al. 2018). Several investigations recently have added to the discussion of true fir taxonomy in these regions. Ott (2014) investigated grand fir and Rocky Mountain white fir populations in the West using chloroplast and mitochondrial DNA sequences to determine maternal and paternal lineages. Based on his findings, Ott classified many fir populations in Oregon and northern California as interspecific hybrids, *A. grandis* × *A. concolor* (Ott 2014; Meyers 2015). Here, we have treated the true fir populations in southern Washington and northern to central Oregon as *A. grandis* and those in southern Oregon and northern California as *A. concolor* × *A. grandis* following Ott (2014) and Meyers (2015). Although the white fir populations in California are often classified as a variety of white fir (*Abies concolor* (Gordon & Glend.) Lindley ex Hildebr.) var. *lowiana* (Gordon) Lemmon) (Hickman 1993), the classification proposed by Hunt (1993) treating these populations as a species (*A. lowiana*) is followed here. Meyers (2015) treated the red fir populations in southern Oregon sometimes referred to as Shasta red fir (*A. magnifica* A. Murray bis var. *shastensis* Lemmon or *A. shastensis* Lemmon) as a hybrid of red fir and noble fir (*A. procera* Rehder), *A. magnifica* × *A. procera* based on a molecular study by Oline (2008). However, we grouped all of the populations of Shasta red fir in northern California and southern Oregon under red fir. Furthermore, the red fir populations in the southern Sierra Nevada Mountains (south of Kings Canyon) with extended bracts on their female cones have now been described as a separate variety: *Abies magnifica* A. Murray bis var. *critchfieldii* Lanner (Lanner 2010). These populations are also grouped herein with red fir.

Since *Arceuthobium abietinum* has been treated as a subspecies of *A. campylopodum* Engelm. (Nickrent 2012, 2016) or conspecifically with *A. campylopodum* (Kuijt 2012), we undertook this study to compare the morphological data we collected for *A. abietinum* and *A. campylopodum* from throughout most of their geographic ranges using both univariate and multivariate statistical tests. We began intensive morphological studies of fir dwarf mistletoe populations throughout its geographic distribution in 2012. This involved collecting additional morphological data from the Southwest, California, Oregon, and Washington, and incorporating these new data into that which had been obtained previously for *A. abietinum* by Mathiasen and Daugherty (2009) and Mathiasen (2011). Morphometric analyses of female and male plants across the four taxa under study confirmed the morphological distinctness of *A. abietinum* from *A. campylopodum*. Therefore, the two special forms—*concoloris* and *magnificae*—as well as subsp. *wiensii* presently ascribed to *A. abietinum* should not be subsumed taxonomically under *A. campylopodum*. Moreover, significant differences among several morphological characters of the special forms of *A. abietinum* support and, hence, justify recombining the special forms as subspecies of *A. abietinum*.

MATERIALS AND METHODS

Plant Material

We sampled 66 populations of *Arceuthobium abietinum* f. sp. *concoloris* and 25 populations of *A. abietinum* f. sp. *magnificae* from throughout most of their geographic ranges (Figs. 1 and 2). Morphological data that had been previously collected for *A. abietinum* (Mathiasen & Daugherty 2009; Mathiasen 2011) were supplemented with additional data collected from 2012 to 2018. The data used for *A. abietinum* subsp. *wiensii* was from seven

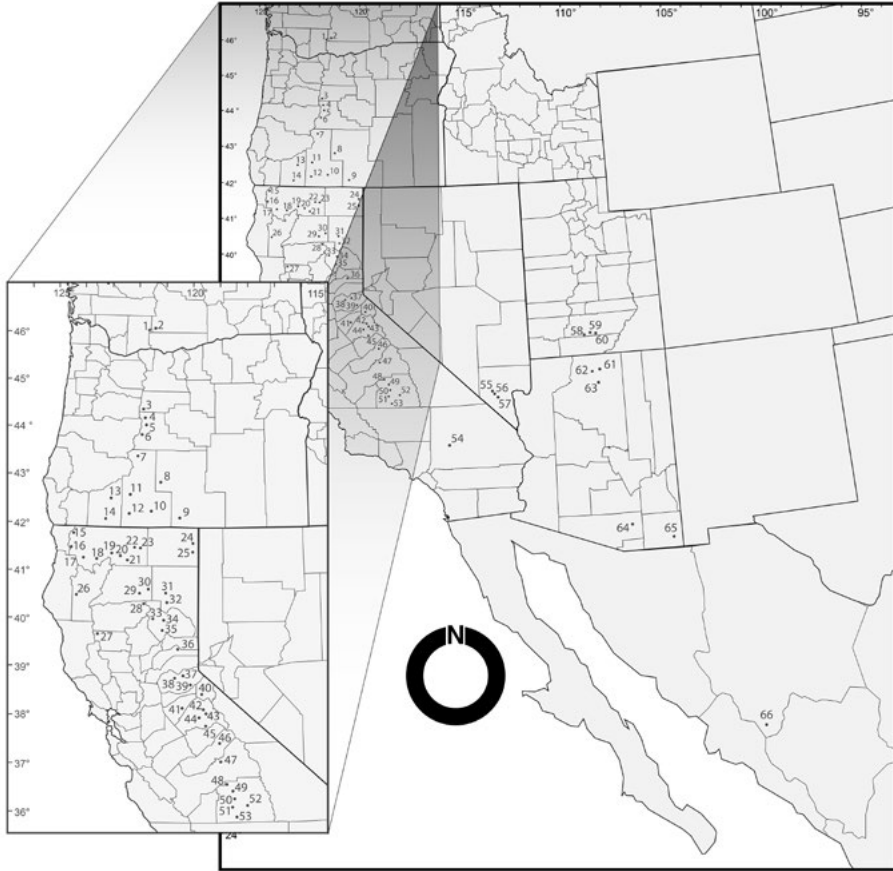


FIG. 1. Approximate locations (black circles) of populations sampled for *Arceuthobium abietinum* f. sp. *concoloris*—recombined herein to *A. abietinum* subsp. *abietinum*. USA. Washington: 1—0.5 km E of Trout Lk. Big Tree on forest rd. 8020, 2—11 km NE of Trout Lk. on Bird Cr. Mdws. rd.; Oregon: 3—E end of Suttle Lk., 0.2 km from St. Rte. 20, 4—12 km W of Sisters on St. Rte. 242, 5—17 km S of Sisters on forest rd. 16, 6—2.6 km W of Swampy Lk. on Mt. Bachelor Highway, 7—SE side of Hammer Butte on rd. to summit, 8—20 km SW of Silver Lk., 6 km W of forest rd. 27 on forest rd. 041, 9—3.7 km N of St. Rte. 140 on Cottonwood Mdws. Rd., 10—2 km N of Bly Pass on St. Rte. 140, 11—0.1 km S of boundary of Crater Lk. Nat. Park on St. Rte. 62, 12—12 km W of Klamath Co. line on St. Rte. 66, 13—1 km E of entrance to Stewart St. Park on St. Rte. 62, 14—3 km SW of Mt. Ashland on forest rd. 40S15; California: 15—At jct. of Grayback rd. and Kelly Lk. Rd., 16—Rock Creek Butte on forest rd. 01, 17—Yellow Jacket Ridge ca. 8 km NW of Little North Fork Campground, 18—3 km N of Eaton Lk., 19—10 km W of Stewart Hot Spgs. on forest rd. 17, 20—1 km W of trailhead to Black Butte, 21—6 km W of McCloud on St. Rte. 89 at jct. to Mt. Shasta Ski Park, 22—21 km N of forest rd. 13 on forest rd. 19, 23—4 km S of Stevens Pass on forest rd. 06, 24—Stough Lk. Campground, 25—3 km W of Patterson Guard Station on forest rd. 64, 26—8 km N of St. Rte. 36 on forest rd. 01 to South Fork Mountain, 27—3 km W of Alder Spgs. on forest rd. 07, 28—1 km W of Mineral Summit on St. Rte. 72, 29—11 km W of N entrance to Lassen Nat. Park on St. Rte. 44, 30—17 km SW of Old Station St. Rte. 44, 31—13 km SE of Westwood Jct. on St. Rte. 44, 32—1 km W of Fredonyer Pass on St. Rte. 36, 33—1.6 km E of Humboldt Summit on forest rd. 302, 34—1 km S of St. Rte. 36 on St. Rte. 89, 35—6 km W of Meadow Valley on high rd. to Bucks Lk., 36—W shore of Jackson Mdws. Res. on forest rd. 07, 37—3 km W of forest rd. 03 on forest rd. 11N58, 38—7 km N of Sly Park on rd. 05, 39—19 km S of US 50 on Silverfork Road, 40—Silver Cr. Campground on St. Rte. 4, 41—11 km E of Dorrington on St. Rte. 4, 42—Lower parking area of Dodge Ridge Ski Park, 43—5 km S of Aspen Mdws. on forest rd. 3N09, 44—11 km N of forest rd. 14 on forest rd. 31, 45—9 km E of Crane Flat on St. Rte. 120, 46—11 km E of Fish Camp on forest rd. 6507, 47—NW side of Huntington Lk., 48—2 km SE of St. Rte. 180 on forest rd. 14S29, 49—1.5 km W of Atwell Campground on Mineral King Rd., 50—0.2 km N of Quaking Aspen Campground on forest rd. 21550, 51—Parker Pass on Western Divide Highway, 52—7 km W of Sherman Pass on St. Rte. 41, 53—1 km S of Tiger Flat on rd. 25S16, 54—8 km E of Angeles Oaks on St. Rte. 38; Nevada: 55—Upper bristlecone pine trail, Las Vegas Ski Area, 56—Mahogany Flat Campground on St. Rte. 158, 57—Echo trailhead in Kyle Canyon; Utah: 58—4 km SE of Navajo Lk. on rd. 53, 59—4 km W of forest rd. 092 on forest rd. 203, 60—2 km S of Crawford Pass on rd. 92; Arizona: 61—3 km S of jct. to Point Imperial on Cape Royal Road, North Rim Grand Canyon Natl. Park, 62—Bright Angel Point, North Rim Grand Canyon Natl. Park, 63—Grandview Point South, Rim Grand Canyon Nat. Park, 64—Ridge above Marshall Gulch, Santa Catalina Mtns., 65—3 km E of Turkey Cr. in Mormon Can., Chiricahua Mtns.; Mexico. Chihuahua: 66—on main rd. 5 km below summit of Cerro Mohinora.

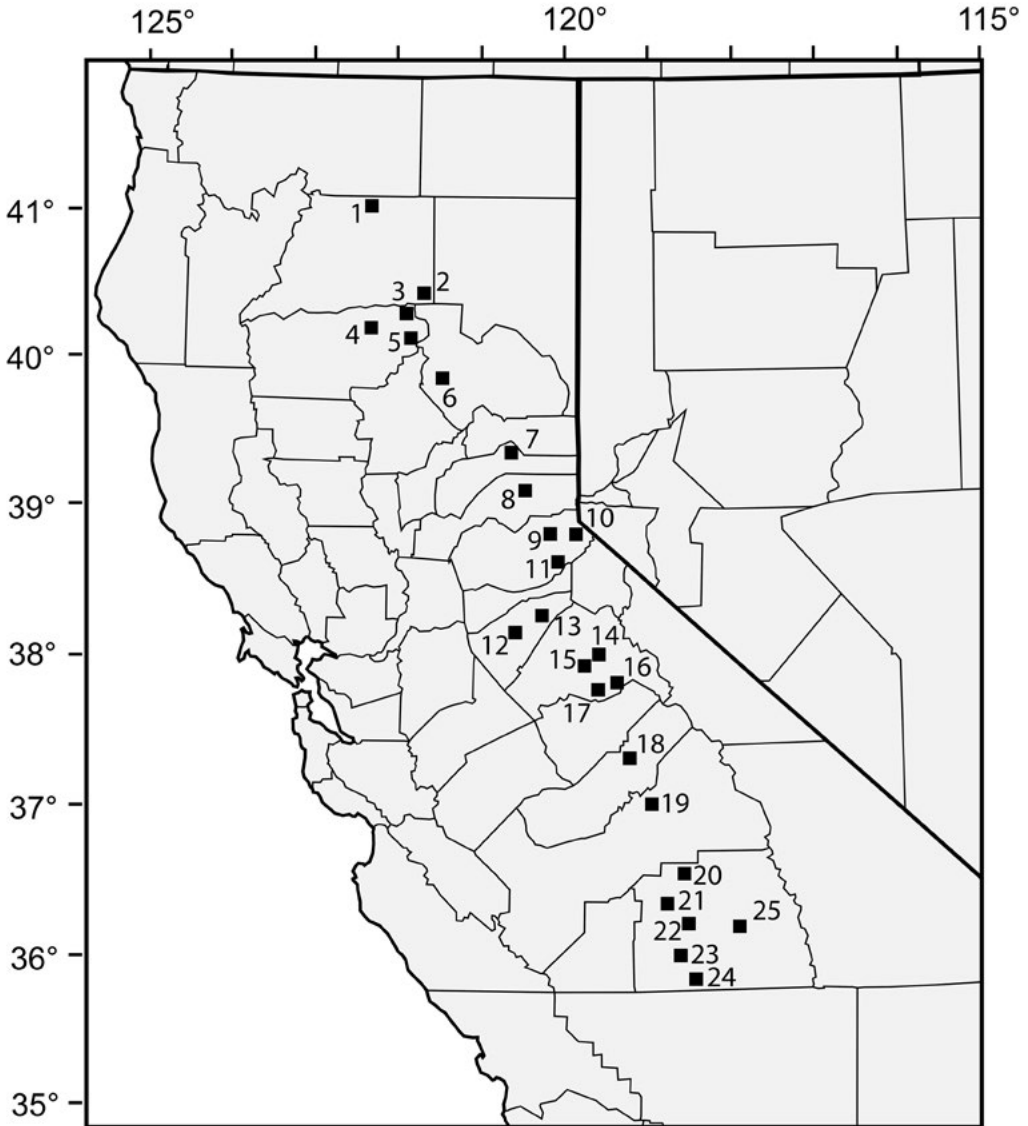


Fig. 2. Approximate locations (black squares) of populations sampled for *Arceuthobium abietinum* f. sp. *magnifica*—recombined herein to *A. abietinum* subsp. *magnifica*. California: 1—12.2 km S of St. Rte. 89 on forest rd. 39N06, 2—16 km N of S entrance to Lassen Nat. Park on St. Rte. 89, 3—2.3 km N of St. Rte. 36 on St. Rte. 89, 4—2.5 km S of Colby Mtn. Lookout on forest rd. 27N36, 5—Humboldt Summit, 6—3 km E of Grizzly Summit on Oroville-Quincy Hwy., 7—W shore of Jackson Mdws. Res. on forest rd. 07, 8—1 km S of Ice Lk. on Soda Sprs. Rd., 9—Lyons Cr. on Wright's Lk. Road, 10—Echo Summit on US 50, 11—1.8 km NE of forest rd. 5 on Silverfork Rd., 12—12.5 km E of Dorrington on St. Rte. 4, 13—W end of Lk. Alpine on St. Rte. 4, 14—1 km W of Dodge Ridge Ski Area on forest rd. 4N36, 15—5 km S of Aspen Mdws. on forest rd. 4N33, 16—Porcupine Cr. on St. Rte. 120, 17—16.5 km E of Crane Flat on St. Rte. 120, 18—10 km E of Fish Camp on forest rd. 6S07, 19—2 km E of dam on Huntington Lk., 20—2.5 km E of St. Rte. 180 on forest rd. 14S18, 21—Mineral King at Cold Sprs. Campground, 22—Summit Trailhead at N end of forest rd. 21S50, 23—Peppermint Cr. on Western Divide Hwy., 24—Sunday Peak Trailhead on forest rd. 28S16, 25—Jct. of Sherman Pass Rd. and forest rd. 22S20.

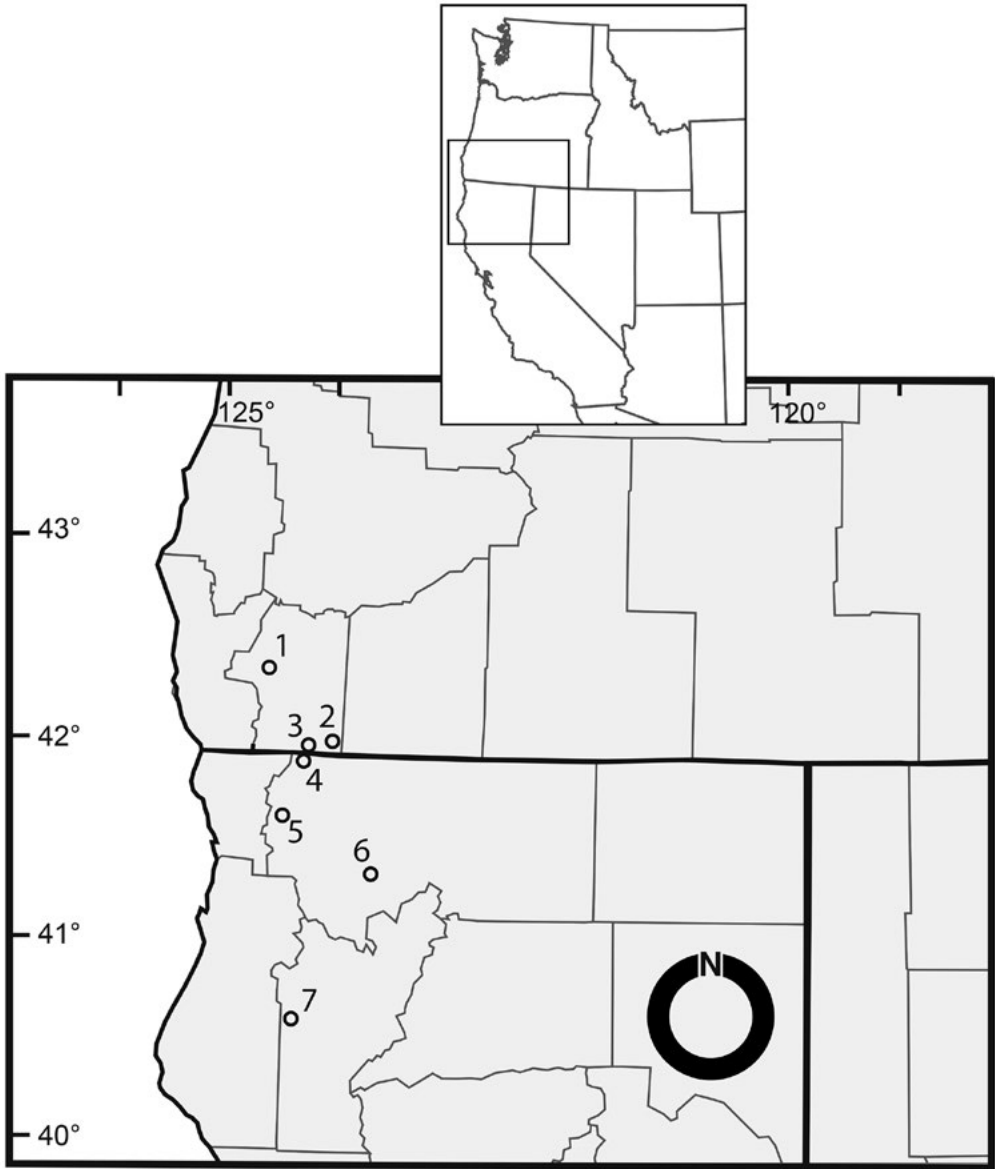


FIG. 3. Approximate locations of populations sampled for *Arceuthobium abietinum* subsp. *wiensii*. Modified from Mathiasen and Daugherty (2009). Oregon: 1—Flat Top Mtn., 2—Steve Fork Cr., 3—Althouse Mtn.; California: 4—Bolan Mtn., 5—Baldy Mtn., 18 km west of Indian Cr. on Doolittle Cr. Rd., 6—Etna Summit on rd. to Sawyers Bar, 7—South Fork Mtn., 20 km north of Rte. 36.

populations (Fig. 3) sampled by Mathiasen and Daugherty (2009). We also used data from 60 populations of *A. campylopodum* collected by Mathiasen and Kenaley (2015a, 2015b) (Fig. 4). Some populations were sampled in multiple years after 2014.

From each dwarf mistletoe population sampled, 20 to 60 infections were collected and the dominant shoot from each infection was used for morphological measurements. The dwarf mistletoe plant characters measured were those used by Hawksworth and Wiens (1996) for taxonomic classification of *Arceuthobium*.

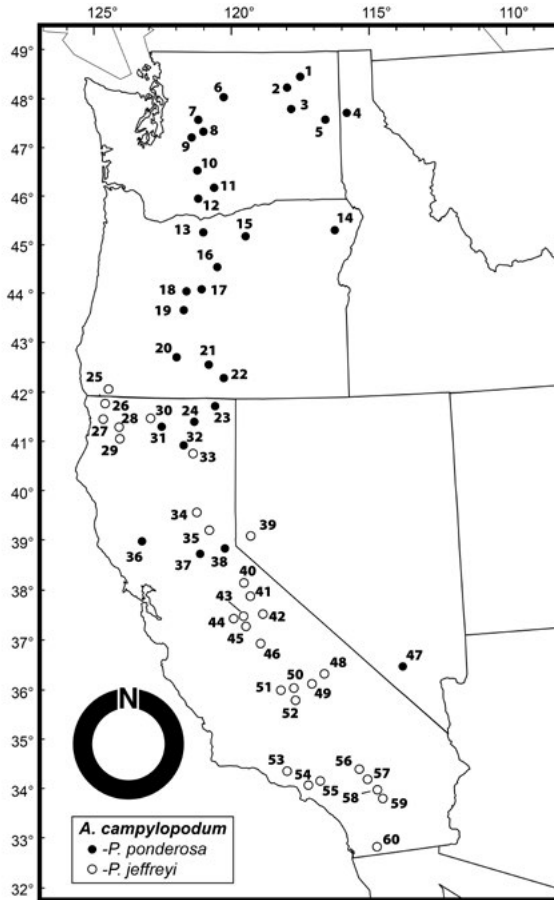


FIG. 4. Approximate locations of collection site for *Arceuthobium campylopodum*. Solid circles present locations where plants were collected from *Pinus ponderosa*. Open circles represent locations where plants were collected from *P. jeffreyi*. From Mathiasen and Kenaley (2015b). **Washington:** 1—4.5 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 Cr. 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 Lk. on St. Rte. 141; **Idaho:** 4—2.3 km N of Coeur d'Alene, Idaho on Fernan Lk. 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—4.8 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 Lk. 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, 39—Bowers Mansion St. Park, above swim. pool area, 40—1 km N of Markleeville on St. Rte. 89, 41—Silver Cr. 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 Cr. on rd. to Shaver Lk., 48—8.5 km W of Sherman Pass on forest rd. 22505, 49—2.2 km S of Troy Mdws. Campground, Sequoia Nat. For., 50—5.8 km N of rd. to Johnsonville on Western Divide Hwy., 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 USDA Ranger Station in Idlywild, 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 Hwy.; **Nevada:** 47—4.1 km W of USDA Ranger Station at Old Ski Tow Historic Site, Kyle Canyon.

The following morphological characters were measured: height, basal diameter, third internode length and width, and color of the tallest male and female shoot from each infection collected; mature fruit length, width, and color; seed length and width; staminate spike length and width; staminate flower diameter; number, length and width of staminate petals; and 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 & Wiens 1972, 1996; Mathiasen & Daugherty 2007, 2009, 2013; Mathiasen & Kenaley 2015a, 2015b). The length of the third internode was determined by measuring from the top of the second internode above the base of the plant to the top of the third internode, locations which are easily observed (see Figs. 2.1, 2.3, and 2.9 in Hawksworth & 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 (July to August) and, likewise, fruit and seed measurements were made during peak seed dispersal (late August to early October). Measurements of staminate spike lengths and widths, flower dimensions, and fruit/seed dimensions were made to the nearest 0.1 mm. Sample sizes for morphological characters measured varied among the four taxa examined herein because of the number of populations sampled and the number of plants measured per population also varied.

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 separately across the intraspecific taxa of *A. abietinum* and were also compared with those of *A. campylopodum*. 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. In addition, we ran a Dunnett's test ($\alpha=0.05$) with *A. campylopodum* as the control.

Following univariate analyses, multivariate analysis of variance (MANOVA) was used to test morphological differences among the intraspecific taxa of *Arceuthobium abietinum* as well as *A. campylopodum*, incorporating simultaneously eight female characters and, in a separate MANOVA, ten male characters. Separate MANOVA by plant sex were executed to minimize experimental error (family-wise Type I error; Rancher 2002). To do so, the univariate data set was modified to comprise only complete records for female and male plants. Following MANOVAs, standard quadratic discriminant function analyses (DFA) was performed by plant sex to determine whether female or male plants could be delimited by taxonomic affiliation (i.e., field diagnosis vs. predicted taxonomic membership) utilizing either female or male plant morphologies, respectively (Quinn & Keough 2002). Standardized correlation coefficients (SCC) for female and male morphologies were calculated as part of the standard DFAs 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. The standard DFAs for female and male plants were then validated by resampling separately the complete records for female and male plants; selecting at random 50 complete records per taxon and re-executing the DFA using a full-model (i.e., 8 female or 10 male characters simultaneously). Thereafter, forward-stepwise DFA was executed separately for female and male plants to identify the combinations of female and male morphologies resulting in the highest precision (% predicted/field determined) in taxon membership, maximizing differences among taxa. As noted previously, *A. abietinum*, and its recognized special forms and subspecies, were recently reclassified as subspecies of *A. campylopodum*; therefore, standard and stepwise-DFAs were executed using the equal prior probability option (0.25) rather than specifying the prior probability according to taxon proportion within female or male datasets (i.e., field diagnosed plants). One-way and multivariate analyses of variances, and multiple comparisons of mean differences as well as DFAs were computed

in JMP Pro 14.0 (SAS Institute, Cary, North Carolina, USA). Ninety-five percent (95%) confidence intervals ($\alpha=0.05$) were also calculated in lieu of standard deviations and errors.

RESULTS

Univariate Analyses

Although both male and female plants of *Arceuthobium abietinum* f. sp. *concoloris* and f. sp. *magnificae* were morphologically similar as reported by Hawksworth and Wiens (1972, 1996) and Mathiasen (2011), sampling from several additional populations of both special forms found significant differences among several morphological characters (Tables 1 and 2). Male and female plant heights and basal diameters for f. sp. *concoloris* were significantly smaller than those of f. sp. *magnificae*. On average, both male and female plants of *A. campylopodum* were significantly smaller than f. sp. *concoloris* and f. sp. *magnificae*, but larger than subsp. *wiensii*.

The basal diameter of female plants was significantly larger for *A. campylopodum* than f. sp. *concoloris* and subsp. *wiensii* (Tables 1 and 2). The basal diameter of female plants for f. sp. *magnificae* was significantly larger than that of *A. campylopodum*. The basal diameters of male plants were significantly different between f. sp. *concoloris* and *magnificae*, but not between subsp. *wiensii* and *A. campylopodum*.

While the mean length of the third internode was significantly smaller for f. sp. *concoloris* versus f. sp. *magnificae*, the mean widths of the third internodes of male and female plants were not significantly different (Tables 1 and 2). The mean lengths and widths of third internodes of f. sp. *magnificae* were significantly larger than those of f. sp. *concoloris* and subsp. *wiensii*. The color of male and female plants of the two special forms was yellow-green, green, or green-brown, while those of subsp. *wiensii* were green, green-brown, or reddish. Plants of *A. campylopodum* were yellow, yellow-brown, or sometimes green.

The mean diameter of 3-merous staminate flowers of *Arceuthobium abietinum* f. sp. *concoloris* was significantly larger than f. sp. *magnificae* (Tables 1 and 2). Hawksworth and Wiens (1972, 1996) reported that staminate flower diameter of *A. abietinum* (for both special forms) was 2.5 mm, so this must have been for 3-merous flowers because we found that 3-merous flower diameters averaged 2.9 and 2.6 mm for f. sp. *concoloris* and *magnificae*, respectively. The mean diameter of 4-merous staminate flowers for these two taxa was 3.8 mm. Hawksworth and Wiens did not report flower diameters for 4-merous flowers, but Mathiasen (2011) reported that 4-merous flowers averaged 3.7 mm in diameter.

Fruits and seeds of *Arceuthobium abietinum* f. sp. *concoloris* were approximately the same dimensions as f. sp. *magnificae* (Tables 1 and 2). However, the mean length of fruits of subsp. *wiensii* (4.2 mm) was significantly smaller than the mean length of fruits of f. sp. *concoloris*, f. sp. *magnificae*, and *A. campylopodum*. The mean widths of fruits of all taxa of *A. abietinum* were not significantly different, but, when mean fruit width of the latter taxa were compared separately and directly to *A. campylopodum*, they were significantly smaller than *A. campylopodum*. Likewise, mean seed dimensions among *A. abietinum* taxa were similar; however, as with mean fruit length, the mean seed length and width for f. sp. *concoloris* and f. sp. *magnificae* as well as subsp. *wiensii* were significantly smaller than those of *A. campylopodum*. Morphological characteristics and host specificities delimiting *A. abietinum* f. sp. *concoloris*, f. sp. *magnificae*, subsp. *wiensii*, and *A. campylopodum* are summarized in Table 3.

Multivariate Analyses

Separate multivariate analysis of variance (MANOVA) tests for female and male morphologies indicated that there were significant differences among the taxa of *A. abietinum* and *A. campylopodum* across 8 female (Wilks' Lambda approx. $F_{24, 5456.1} = 153.1, P < 0.001$; Pillai's Trace approx. $F_{24, 5649} = 104.1, P < 0.001$; Hotelling-Lawley approx. $F_{24, 4068.3} = 221.2, P < 0.001$) and 10 male morphological characters (Wilks' Lambda approx. $F_{30, 5604} = 150.4, P < 0.001$; Pillai's Trace approx. $F_{30, 5733} = 96.2, P < 0.001$; Hotelling-Lawley approx. $F_{30, 4355.4} = 234.1, P < 0.001$). Standard DFA of female and male morphologies (8 female and 10 male characteristics, respectively) correctly classified a total of 67.2% (1271/1892) female and 78.4% male plants (1507/1922) to the correct taxon when utilizing equal prior probabilities rather than probabilities proportional to their field diagnosis (Table 4). Means with associated 95% confidence intervals for female and male characters by predicted taxon

TABLE 1. Morphological measurements for *Arceuthobium abietinum* f. sp. *concoloris*, f. sp. *magnificae*, subsp. *wiensii*, and *A. campylopodum*. Data are listed as mean, (SD) [n]. Means followed by different capital letters in the same row were significantly different using analysis of variance (ANOVA) and a Tukey's HSD Post Hoc test ($\alpha=0.05$). Likewise, by row, underlined means were significantly different from the means for *A. campylopodum* (control) using a Dunnett's 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. In the present work, *A. abietinum* f. sp. *concoloris* was recombined to subsp. *abietinum* and *A. abietinum* f. sp. *magnificae* was recombined to subsp. *magnificae*.

Character	<i>concoloris</i>	<i>magnificae</i>	<i>wiensii</i>	<i>campylopodum</i>
Plant Height				
Female	11.3 A (3)[1040a]	12.2 B (3.0)[350a]	9.5 C (2.3)[230a]	10.4 D (2.7)[600a]
Male	11.0 A (3.0)[830b]	11.9 B (2.7)[330b]	8.9 C (2.3)[160b]	9.7 D (3.0)[a]
Basal Diameter				
Female	3.2 A (0.8)[a]	3.6 B (0.8)[a]	3.2 A (0.7)[a]	3.4 C (0.7)[a]
Male	3.0 A (0.7)[b]	3.3 B (0.7)[b]	3.1 AC (0.6)[b]	3.2 C (0.6)[a]
Length of Third Internode				
Female	14.8 A (4.0)[a]	16.2 B (3.9)[a]	14.7 A (3.6)[a]	13.0 C (3.1)[a]
Male	14.0 A (3.7)[b]	15.4 B (3.7)[b]	13.5 A (3.2)[b]	12.0 C (3.3)[a]
Width of Third Internode				
Female	2.2 A (0.4)[a]	2.3 B (0.4)[a]	1.9 C (0.3)[a]	2.5 D (0.4)[a]
Male	2.2 A (0.4)[b]	2.2 A (0.4)[b]	1.9 B (0.3)[b]	2.5 C (0.4)[a]
Staminate Spike Length	10.5 A (2.8)[1320]	9.4 B (3.0)[600c]	8.7 C (2.5)[290c]	12.7 D (4.8)[760c]
Staminate Spike Width	2.1 A (0.3)[1320]	2.0 B (0.3)[c]	1.5 C (0.2)[c]	3.0 D (0.3)[c]
Flower Diameter				
3-merous	2.9 A (0.4)[780c]	2.6 B (0.3)[330d]	2.4 C (0.2)[140d]	3.1 D (0.4)[400d]
4-merous	3.8 A (0.4)[c]	3.8 A (0.4)[d]	3.2 B (0.2)[d]	4.2 C (0.5)[360]
Petal Length	1.4 A (0.2)[1560d]	1.4 A (0.2)[660]	1.2 B (0.2)[280e]	1.6 C (0.2)[760e]
Petal Width	1.2 A (0.2)[d]	1.2 B (0.2)[c]	1.0 C (0.1)[e]	1.4 D (0.2)[e]
Anther Diameter	0.6 A (0.1)[d]	0.6 A (0.1)[c]	0.5 B (0.1)[e]	0.6 C (0.1)[e] ^a
Anther Distance from Tip	0.6 A (0.2)[d] ^a	0.5 B (0.1)[c]	0.6 AC (0.1)[e]	0.6 C (0.2)[e] ^a
Fruit Length	4.7 A (0.5)[910e]	4.7 A (0.5)[370e]	4.2 B (0.4)[150f]	5.4 C (0.5)[480f]
Fruit Width	3.0 A (0.3)[f]	3.0 A (0.4)[e]	3.0 A (0.3)[f]	3.7 B (0.3)[f]
Seed Length	2.5 A (0.3)[f]	2.5 A (0.3)[e]	2.4 A (0.2)[f]	3.5 B (0.4)[f]
Seed Width	1.2 A (0.1)[f]	1.2 AB (0.2)[e]	1.1 B (0.1)[f]	1.5 C (0.2)[f]

^a—Means were significantly different because of rounding to the nearest 0.1. See Table 2 for *P*-values.

membership are presented in Table 5. Although the overall correct classification of female plants was lower when compared to male plants, full-model standard DFA of female plants correctly identified and delimited female plants of *A. campylopodum* 94.6% of the time (Table 6). When considering multiple female morphologies, *A. campylopodum* was rarely assigned ($\leq 3.1\%$) to *A. abietinum* f. sp. *concoloris*, f. sp. *magnificae*, or subsp. *wiensii*. Similarly, female plants of *A. abietinum* subsp. *wiensii* were classified correctly 82.0% of the time; whereas, 56.3% of female *A. abietinum* f. sp. *concoloris* and 51.7% of female *A. abietinum* f. sp. *magnificae* were correctly predicted to their taxon membership (Table 6). Consequentially, the misclassification of female plants (i.e., those assigned to a taxon unlike its field determination) was largely attributable to morphological comparisons between f. sp. *concoloris* and f. sp. *magnificae* (Table 6), as 21.4% of female f. sp. *concoloris* were assigned to female f. sp. *magnificae* and 25.4% of female f. sp. *magnificae* were classified to female f. sp. *concoloris*. Female plants of f. sp. *concoloris* and f. sp. *magnificae* were occasionally misclassified to subsp. *wiensii* 16.3% and 18.0% of the time, respectively. Inspection of the standard DFA canonical details and multivariate means for complete records of female plants among *A. abietinum* f. sp. *concoloris*, f. sp. *magnificae*, subsp. *wiensii* and *A. campylopodum* (Table 7—Female complete; Fig. 5A) indicated that the first two discriminant functions (canonicals) explained a total of 98.8% of the variation among the complete records for female plants (N= 1892; Table 8). Furthermore, the multivariate means as well as 95% confidence ellipses for *A. abietinum* f. sp. *concoloris*, f. sp. *magnificae*, and subsp. *wiensii* were discretely different and non-overlapping in dimensional space. Moreover, utilizing complete records and standard DFA, female plants of *A. abietinum* taxa were clearly segregated from *A. campylopodum* (Fig. 5A). Likewise, for DFA using resampled female plants (N= 50 complete

TABLE 2. *P*-values for morphological measurements for *Arceuthobium campylopodum*, *A. abietinum* f. sp. *concoloris*, *A. abietinum* f. sp. *magnifica*, and *A. abietinum* subsp. *wiensii* using analysis of variance (ANOVA) followed by a Tukey's HSD Post Hoc test ($\alpha = 0.05$). Plant heights are in cm and all other measurements in mm. Comparisons are for *A. campylopodum* and *A. abietinum* f. sp. *concoloris* (C-A); *A. campylopodum* and *A. abietinum* f. sp. *magnifica* (C-M); *A. campylopodum* and *A. abietinum* subsp. *wiensii* (C-W); *A. abietinum* f. sp. *concoloris* and *magnifica* (A-M); *A. abietinum* f. sp. *concoloris* and subsp. *wiensii* (A-W); and *A. abietinum* f. sp. *magnifica* and subsp. *wiensii* (M-W). Note herein, *A. abietinum* f. sp. *concoloris* was recombined to *A. abietinum* subsp. *abietinum* and, likewise, f. sp. *magnifica* was recombined to *A. abietinum* subsp. *magnifica*.

Character	C-A	C-M	C-W	A-M	A-W	M-W
Plant Height						
Female	<i>P</i> < 0.0001	<i>P</i> = 0.0007	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001
Male	<i>P</i> < 0.001	<i>P</i> = 0.0216	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001
Basal Diameter						
Female	<i>P</i> < 0.0001	<i>P</i> = 0.0076	<i>P</i> = 0.0166	<i>P</i> < 0.0001	<i>P</i> = 0.9996	<i>P</i> < 0.0001
Male	<i>P</i> < 0.0001	<i>P</i> = 0.5194	<i>P</i> = 0.0155	<i>P</i> < 0.0001	<i>P</i> = 0.0710	<i>P</i> = 0.0041
Length Third Internode						
Female	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> = 0.9498	<i>P</i> < 0.0001
Male	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> = 0.4620	<i>P</i> < 0.0001
Width Third Internode						
Female	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> = 0.0004	<i>P</i> < 0.0001	<i>P</i> < 0.0001
Male	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> = 0.7017	<i>P</i> < 0.0001	<i>P</i> < 0.0001
Staminate Spike Length	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> = 0.0309
Staminate Spike Width	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001
Flower Diameter						
3-merous	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001
4-merous	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> = 0.3644	<i>P</i> < 0.0001	<i>P</i> < 0.0001
Petal Length	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> = 0.7343	<i>P</i> < 0.0001	<i>P</i> < 0.0001
Petal Width	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001
Anther Diameter	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> = 0.9810	<i>P</i> < 0.0001	<i>P</i> < 0.0001
Anther Distance to Tip	<i>P</i> = 0.0379	<i>P</i> = 0.6669	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> = 0.9329	<i>P</i> < 0.0001
Fruit Length	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.1000	<i>P</i> = 0.2116	<i>P</i> < 0.0001	<i>P</i> < 0.0001
Fruit Width	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> = 0.4085	<i>P</i> = 0.8364	<i>P</i> = 0.2985
Seed Length	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> = 0.4925	<i>P</i> = 0.8036	<i>P</i> = 0.3133
Seed Width	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> < 0.0001	<i>P</i> = 0.4966	<i>P</i> = 0.0019	<i>P</i> = 0.0814

records per taxon; Fig. 5C), the multivariate means and confidence ellipses were not associated with *A. campylopodum* in multidimensional space. However, given the reduced sample size, the confidence ellipses for *A. abietinum* f. sp. *concoloris* and f. sp. *magnifica* demonstrated considerable overlap when the female dataset was validated using 50 complete records per taxon (Fig. 5C).

The female morphological characteristic contributing most to the prediction of taxon membership using full-model DFA, particularly for *Arceuthobium campylopodum* and *A. abietinum* subsp. *wiensii*, was seed length followed by fruit length, fruit width, width of the third internode, plant height, and length of the third internode (Tables 4 and 8). Utilizing these six female plant morphologies alone in the DFA resulted in an overall correct classification of 94.4% of female *A. campylopodum* and 80.0% of female *A. abietinum* subsp. *wiensii*. Moreover, >90% of female *A. campylopodum* were correctly assigned using only four morphological characters—seed length, fruit length and width, and width of the third internode. Conversely, the addition of all 8 female characters to include basal diameter and seed width was necessary to maximize differences between female *A. abietinum* f. sp. *concoloris* and f. sp. *magnifica*. Multivariate analyses of female morphologies were consistent with the univariate comparisons, whereby multiple comparison procedures for seed length, fruit dimensions, width of the third internode, plant height, and length of the third internode were significantly different between or among two or more of the four taxa examined.

As reported with DFA for female plants, the first two canonicals determined using standard DFA of male plant morphologies (N= 10 characters) combined to explain the majority of variation (98.2%) among the complete records of male plants (N= 1992; Table 7). The multivariate means and 95% confidence ellipses by male

TABLE 3. Summary of the principal characters separating *Arceuthobium abietinum* f. sp. *concoloris*, f. sp. *magnifica*, subsp. *wiensii*, and *A. campylopodum*. Data for morphological characters are means; plant heights in cm and all other measurements in mm. In the present work, *A. abietinum* f. sp. *concoloris* was recombined to subsp. *abietinum* and *A. abietinum* f. sp. *magnifica* was recombined to subsp. *magnifica*.

Character	<i>concoloris</i>	<i>magnifica</i>	<i>wiensii</i>	<i>campylopodum</i>
Plant Height				
Female	11.3	12.2	9.5	10.4
Male	11.0	11.9	8.9	9.7
Plant Color	Yellow, yellow-green green, green-brown	Yellow, yellow- red-brown, red	Brown-green, brown, yellow	Yellow-brown,
Width of Third Internode				
Female	2.3	2.3	1.9	2.5
Male	2.2	2.2	1.9	2.5
Staminate Spike Width	2.1	2.0	1.5	3.0
Flower Diameter				
3-merous	2.9	2.6	2.4	3.1
4-merous	3.8	3.8	3.2	4.2
Fruit Length	4.7	4.7	4.2	5.4
Fruit Width	3.0	3.1	3.0	3.7
Principal Hosts^a	<i>Abies grandis</i> ; <i>A. grandis</i> × <i>A. concolor</i> ; <i>A. lowiana</i> ; <i>A. concolor</i> ; <i>A. durangensis</i>	<i>Abies magnifica</i> ^b	<i>Abies magnifica</i> ; <i>Picea breweriana</i>	<i>Pinus ponderosa</i> ; <i>P. jeffreyi</i>
Secondary Hosts	None	None	None	<i>Pinus coulteri</i> ; <i>P. attenuata</i>
Occasional Hosts	<i>Abies lasiocarpa</i>	None	<i>Abies grandis</i> × <i>concolor</i> ^c	<i>Pinus contorta</i> var. <i>murrayana</i>
Rare Hosts	<i>Abies amabilis</i> ; <i>Pinus contorta</i> var. <i>murrayana</i> ; <i>P. lambertiana</i> ; <i>P. monticola</i>	None	<i>Pinus monticola</i>	<i>Pinus lambertiana</i> ^d

^a Host susceptibility classification based on information in Hawksworth and Wiens (1996) and Mathiasen and Daugherty (2009).

^b Includes *Abies magnifica* var. *critchfieldii* (Lanner 2010).

^c Reported originally as *Abies lowiana* (Mathiasen & Daugherty 2009).

^d The report of *Arceuthobium campylopodum* parasitizing *Pinus lambertiana* is unconfirmed and probably based on parasitism by *A. abietinum* subsp. *abietinum* on *P. lambertiana* (Mathiasen & Kenaley 2017).

taxon were also discretely different and non-overlapping in multidimensional space (Fig. 5B). Standard DFA of male morphologies utilizing complete data and equal prior probabilities across taxa also increased the precision of correctly classified *Arceuthobium campylopodum* (95.2%; Table 6). Moreover, the precision of assigning *A. abietinum* f. sp. *concoloris* and subsp. *wiensii* correctly increased $\geq 11.7\%$ when utilizing complete data for male plants when compared to complete data for female plants, resulting in the correct classification of 72.1% and 93.7% male f. sp. *concoloris* and subsp. *wiensii*, respectively. Likewise, an increase in the percentage of correct classification was also observed for *A. abietinum* f. sp. *magnifica* (56.4%) when executing standard DFA on male plant characters across taxa (Table 6). Male plants of the latter taxon were most often misclassified (33.0%) to *A. abietinum* f. sp. *concoloris* and were rarely assigned to either subsp. *wiensii* (6.7%) or *A. campylopodum* (3.9%). Similarly, using standard DFA, male *A. abietinum* f. sp. *concoloris* were often misclassified to f. sp. *magnifica* (20.2%) and rarely to subsp. *wiensii* (3.6%). No plants of *A. abietinum* f. sp. *concoloris*, however, were assigned taxon membership to *A. campylopodum*. Among the 10 male characters, staminate spike width, plant height, basal diameter, width of the third internode, and, petal length provided the most discriminatory power, segregating male plants of *A. abietinum* f. sp. *concoloris* and subsp. *wiensii* as well as *A. campylopodum* (Tables 4 and 8). Including only these five male characters within the male DFA model resulted in >70% correct classification of *A. abietinum* f. sp. *concoloris* (70.1%), subsp. *wiensii* (90.0%), and *A. campylopodum* (96.2%). The full-suite of male characteristics to include the addition of anther diameter and distance to tip, length of the

TABLE 4. Forward, stepwise discriminant function analysis (DFA): classification of female and male plants of *Arceuthobium abietinum* f. sp. *concoloris*, f. sp. *magnifica*, subsp. *wiensii*, and *A. campylopodum* to taxon membership via the sequential addition of morphological characters most correlated to the discriminant function. a.—Plant height (PH), basal diameter (BD), length and width of third internode (LTI, WTI), staminate spike length and width (SSL, SSW), flower diameter (FD), petal length and width (PL, PW), anther diameter (AD), anther distance to tip (ADP), fruit length and width (FL, FW), and seed length and width (SL, SW).

Stepwise DFA (step [character ^a])	Total	Correct taxon membership (% [N predicted/ N field determined])			
		<i>Arceuthobium campylopodum</i>	<i>Arceuthobium abietinum concoloris</i>	<i>magnifica</i>	<i>wiensii</i>
Female					
1 [SL]	36.5 [690/1892]	86.5 [415/480]	10.7 [98/912]	16.9 [59/350]	78.7 [118/150]
2 [*], [FL]	55.2 [1044/1892]	89.8 [431/480]	46.9 [428/912]	20.3 [71/350]	76.0 [114/150]
3 [*], [*], [FW]	58.2 [1102/1892]	89.0 [427/480]	49.3 [450/912]	33.1 [116/350]	72.7 [109/150]
4 [*], [*], [*], [WTI]	58.9 [1114/1892]	91.0 [437/480]	45.2 [412/912]	43.1 [151/350]	76.0 [114/150]
5 [*], [*], [*], [*], [PH]	59.9 [1134/1892]	92.5 [444/480]	44.8 [409/912]	46.3 [162/350]	79.3 [119/150]
6 [*], [*], [*], [*], [*], [LTI]	62.5 [1183/1892]	94.4 [453/480]	48.2 [440/912]	48.6 [170/350]	80.0 [120/150]
7 [*], [*], [*], [*], [*], [*], [BD]	65.7 [1243/1892]	95.0 [456/480]	53.6 [489/912]	50.0 [175/350]	82.0 [123/150]
8 [*], [*], [*], [*], [*], [*], [*], [SW]	67.2 [1271/1892]	94.6 [454/480]	56.2 [513/912]	51.7 [181/350]	82.0 [123/150]
Male					
1 [SSW]	64.4 [1238/1922]	96.5 [579/600]	54.3 [452/822]	22.4 [74/330]	83.1 [133/160]
2 [*], [PH]	66.0 [1268/1922]	95.7 [574/600]	51.0 [424/822]	40.9 [135/330]	84.4 [135/160]
3 [*], [*], [BD]	70.0 [1345/1922]	95.3 [572/600]	60.3 [502/822]	40.3 [133/330]	86.2 [138/160]
4 [*], [*], [*], [WTI]	73.0 [1403/1922]	96.0 [576/600]	67.5 [562/822]	37.9 [125/330]	87.5 [140/160]
5 [*], [*], [*], [*], [PLL]	75.4 [1450/1922]	96.0 [576/600]	70.4 [586/822]	44.8 [148/330]	87.5 [140/160]
6 [*], [*], [*], [*], [*], [ADT]	75.9 [1459/1922]	96.2 [577/600]	71.0 [591/822]	44.5 [147/330]	90.0 [144/160]
7 [*], [*], [*], [*], [*], [*], [LTI]	76.6 [1472/1922]	95.7 [574/600]	71.7 [597/822]	48.2 [159/330]	88.7 [142/160]
8 [*], [*], [*], [*], [*], [*], [PLW]	78.2 [1503/1922]	96.3 [578/600]	72.4 [602/822]	52.7 [174/330]	93.1 [149/160]
9 [*], [*], [*], [*], [*], [*], [*], [AD]	78.3 [1505/1922]	95.5 [573/600]	72.1 [600/822]	55.1 [182/330]	93.7 [150/160]
10 [*], [*], [*], [*], [*], [*], [*], [*], [SSL]	78.4 [1507/1922]	95.2 [571/600]	72.1 [600/822]	56.4 [186/330]	93.7 [150/160]

TABLE 5. Means and 95% confidence intervals for morphological characters according to predicted species membership based on full-model, quadratic discriminant function analysis for female and male plants. For comparison, means and confidence intervals for field diagnosed taxa are provided (\pm), statistically identical to predicted plants (—). Plant height is in cm whereas all other mean measurements by character are in mm. In the present work, *Arceuthobium abietinum* f. sp. *concoloris* was recombined to subsp. *abietinum* and *A. abietinum* f. sp. *magnifica* was recombined to subsp. *magnifica*.

Sex / Character	Taxa classified via discriminant function analysis [field diagnosed]			
	<i>Arceuthobium campylopodum</i>	<i>concoloris</i>	<i>Arceuthobium abietinum magnifica</i>	<i>wiensii</i>
Female				
Plant height (PH)	10.3 \pm 0.2 [—]	11.1 \pm 0.2 [11.5 \pm 0.2]	13.5 \pm 0.0 [12.2 \pm 0.3]	9.6 \pm 0.2 [9.6 \pm 0.4]
Basal diameter (BA)	3.3 \pm 0.1 [3.4 \pm 0.1]	3.0 \pm 0.0 [3.2 \pm 0.1]	3.9 \pm 0.1 [3.6 \pm 0.1]	3.2 \pm 0.1 [3.3 \pm 0.1]
Length of third internode (LTI)	13.1 \pm 0.3 [13.0 \pm 0.3]	14.3 \pm 0.3 [15.0 \pm 0.3]	17.4 \pm 0.4 [16.2 \pm 0.4]	14.6 \pm 0.4 [15.0 \pm 0.6]
Width of third internode (WTI)	2.4 \pm 0.0 [2.5 \pm 0.0]	2.1 \pm 0.0 [2.2 \pm 0.0]	2.4 \pm 0.0 [2.3 \pm 0.0]	2.0 \pm 0.0 [—]
Fruit length (FL)	5.4 \pm 0.0 [—]	4.9 \pm 0.0 [4.7 \pm 0.0]	4.7 \pm 0.0 [4.7 \pm 0.1]	4.3 \pm 0.0 [4.2 \pm 0.1]
Fruit width (FW)	3.6 \pm 0.0 [3.7 \pm 0.0]	3.0 \pm 0.0 [—]	3.0 \pm 0.0 [—]	3.0 \pm 0.0 [—]
Seed length (SL)	3.4 \pm 0.0 [3.5 \pm 0.0]	2.4 \pm 0.0 [—]	2.5 \pm 0.0 [—]	2.4 \pm 0.0 [—]
Seed width (SW)	1.5 \pm 0.0 [—]	1.2 \pm 0.0 [—]	1.1 \pm 0.0 [—]	1.1 \pm 0.0 [—]
Male				
Plant height (PH)	9.6 \pm 0.2 [9.7 \pm 0.2]	10.7 \pm 0.2 [11.0 \pm 0.2]	12.6 \pm 0.3 [11.9 \pm 0.3]	9.0 \pm 0.3 [8.9 \pm 0.4]
Basal diameter (BA)	3.2 \pm 0.1 [3.2 \pm 0.0]	2.9 \pm 0.2 [3.0 \pm 0.0]	3.6 \pm 0.1 [3.3 \pm 0.1]	3.1 \pm 0.1 [—]
Length of third internode (LTI)	11.9 \pm 0.3 [11.9 \pm 0.3]	13.5 \pm 0.2 [14.0 \pm 0.3]	16.5 \pm 0.4 [15.4 \pm 0.4]	13.6 \pm 0.4 [131.5 \pm 0.5]
Width of third internode (WTI)	2.4 \pm 0.0 [2.5 \pm 0.0]	2.2 \pm 0.0 [—]	2.3 \pm 0.0 [2.2 \pm 0.0]	1.9 \pm 0.0 [—]
Petal length (PL)	1.5 \pm 0.0 [—]	1.4 \pm 0.0 [—]	1.4 \pm 0.0 [1.2 \pm 0.0]	1.2 \pm 0.0 [—]
Petal width (PW)	1.4 \pm 0.0 [—]	1.2 \pm 0.0 [—]	1.2 \pm 0.0 [—]	1.0 \pm 0.0 [—]
Anther diameter (AD)	0.6 \pm 0.0 [—]	0.5 \pm 0.0 [—]	0.6 \pm 0.0 [—]	0.5 \pm 0.0 [—]
Anther distance from tip (ADT)	0.6 \pm 0.0 [—]	0.5 \pm 0.0 [—]	0.6 \pm 0.0 [0.5 \pm 0.0]	0.5 \pm 0.0 [0.6 \pm 0.0]
Staminate spike length (SSL)	13.0 \pm 0.4 [12.9 \pm 0.4]	9.8 \pm 0.2 [9.9 \pm 0.2]	9.9 \pm 0.3 [9.7 \pm 0.3]	8.7 \pm 0.4 [8.8 \pm 0.4]
Staminate spike width (SSW)	3.0 \pm 0.0 [—]	2.0 \pm 0.0 [—]	2.1 \pm 0.0 [—]	1.5 \pm 0.0 [—]

TABLE 6. Standard discriminant function (DFA): assignment of field diagnosed female and male plants of *Arceuthobium abietinum* f. sp. *concoloris*, f. sp. *magnificae*, subsp. *wiensii*, and *A. campylopodum* utilizing 8 female and 10 male characters (full-model per plant sex) as well as equal prior probability per taxon (0.25). In the present work, *A. abietinum* f. sp. *concoloris* was reclassified to subsp. *abietinum* and *A. abietinum* f. sp. *magnificae* was reclassified to subsp. *magnificae*.

Plant sex / <i>Arceuthobium</i> taxon Sex / Character	Taxa classified (%) [N= field determined plants] via full-model DFA			
	<i>A. campylopodum</i>	<i>Arceuthobium abietinum</i>		
		<i>concoloris</i>	<i>magnificae</i>	<i>wiensii</i>
Female—8 morphological characters				
<i>A. campylopodum</i> (480)	94.6 [454]	2.1 [10]	3.1 [15]	0.2 [1]
<i>A. abietinum</i> f. sp. <i>concoloris</i> (912)	3.3 [30]	56.3 [513]	24.1 [220]	16.3 [149]
<i>A. abietinum</i> f. sp. <i>magnificae</i> (350)	4.9 [17]	25.4 [89]	51.7 [181]	18.0 [63]
<i>A. abietinum</i> subsp. <i>wiensii</i> (150)	0.0 [0]	8.7 [13]	9.3 [14]	82.0 [123]
Male—10 morphological characters				
<i>A. campylopodum</i> (600)	95.2 [751]	2.8 [17]	2.0 [12]	0.0 [0]
<i>A. abietinum</i> f. sp. <i>concoloris</i> (832)	4.1 [34]	72.1 [600]	20.2 [168]	3.6 [30]
<i>A. abietinum</i> f. sp. <i>magnificae</i> (330)	3.9 [13]	33.0 [109]	56.4 [186]	6.7 [22]
<i>A. abietinum</i> subsp. <i>wiensii</i> (160)	0.0 [0]	4.4 [7]	1.9 [3]	93.7 [150]

TABLE 7. Canonical statistics for standard discriminant function analyses (DFA) of female and male plants of *Arceuthobium abietinum* f. sp. *concoloris*, f. sp. *magnificae*, subsp. *wiensii* and *A. campylopodum*. DFAs were executed using a full-model (N= 8 female or 10 male characters) and equal prior probabilities (0.25). Canonical details according to plant sex are subdivided by analyses performed on the complete and randomized resampled (50 complete records/taxon) datasets.

Canonical	Eigenvalue	Percentage	Cumulative percentage	Canonical correlation	Likelihood Ratio	Approximant F	P-value
Female—Complete							
1	2.59	91.8	91.8	0.8494	0.2246	$F_{24, 5456.1} = 153.09$	<.0001
2	0.20	7.1	98.8	0.4081	0.8067	$F_{14, 3764} = 30.48$	<.0001
3	0.03	1.2	100.0	0.1790	0.9680	$F_{6, 1883} = 10.38$	<.0001
Female—Resampled							
1	2.86	82.4	82.4	0.8607	0.1576	$F_{24, 548.8} = 20.37$	<.0001
2	0.55	15.9	98.2	0.5957	0.6079	$F_{14, 380} = 7.70$	<.0001
3	0.06	1.8	100.0	0.2401	0.9423	$F_{6, 191} = 1.95$	<.0751
Male—Complete							
1	3.41	92.7	92.7	0.8794	0.1766	$F_{30, 5604} = 150.41$	<.0001
2	0.20	5.5	98.2	0.4106	0.7790	$F_{18, 3820} = 28.22$	<.0001
3	0.07	1.8	100.0	0.2510	0.9370	$F_{8, 1911} = 16.06$	<.0001
Male—Resampled							
1	4.84	89.7	89.7	0.9104	0.1062	$F_{30, 549.6} = 21.01$	<.0001
2	0.41	7.6	97.3	0.5391	0.6203	$F_{18, 376} = 5.63$	<.0001
3	0.14	2.7	100.0	0.3543	0.8745	$F_{8, 189} = 3.39$	<.0001

third internode, petal width, and staminate spike width were necessary to maximize the correct classification of male *A. abietinum* f. sp. *magnificae*. Validation of the male DFA via resampling 50 male complete records clearly separated *A. abietinum* taxa from *A. campylopodum*, as well as subsp. *wiensii* from f. sp. *concoloris* and f. sp. *magnificae* (Fig. 5D). Re-executing the full-model DFA on resampled male plants also revealed that the multivariate means of *A. abietinum* f. sp. *concoloris* and f. sp. *magnificae* were different in dimensional space, yet, the 95% confidence ellipses overlapped. The latter result was largely due to male *A. abietinum* f. sp. *magnificae* identified a priori in the field being misclassified to f. sp. *concoloris*.

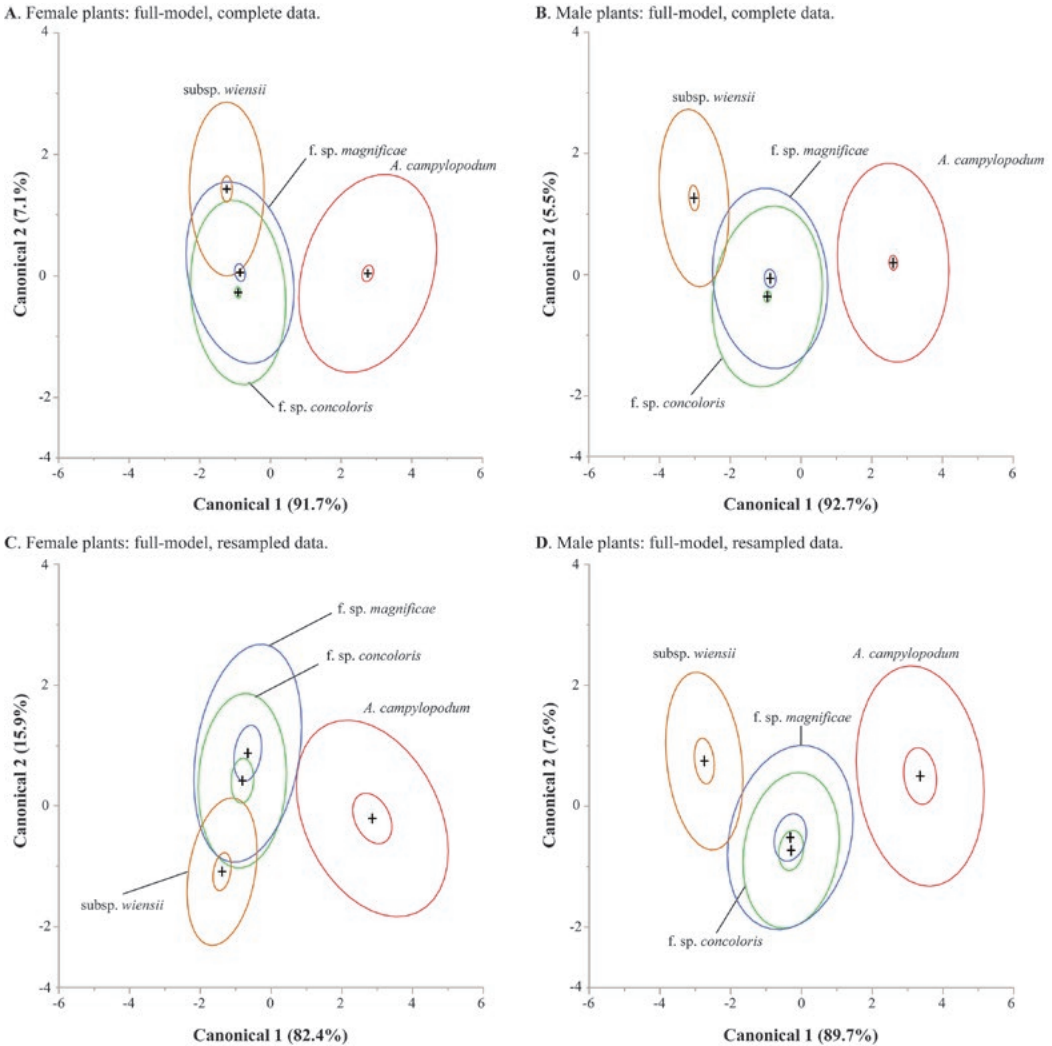


FIG. 5. Canonical plots for standard discriminant function analyses (DFA) of *Arceuthobium abietinum* f. sp. *concoloris*, f. sp. *magnificae*, subsp. *wiensii*, and *A. campylopodum* based on morphological characteristics of female (A, C) and male plants (B, D). Multivariate means (crosshairs) were computed using complete data for each species by sex (A, B). In order 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 corresponds to a 95% confidence limit for the mean, and the outer ellipse represent a normal 50% contour illustrating the approximate area within 50% of plants for each taxon reside. In the present work, *A. abietinum* f. sp. *concoloris* was recombined to subsp. *abietinum* and *A. abietinum* f. sp. *magnificae* was recombined to subsp. *magnificae*.

NOMENCLATRURAL CHANGES

Arceuthobium abietinum (Engelm.) Engelm. ex Munz subsp. **abietinum**, Man. S. Calif. Bot. 114. 1935. *Arceuthobium abietinum* Engelm. in Gray, Proc. Amer. Acad. Arts 8:401. 1872. *Arceuthobium douglasii* Engelm. var. *abietinum* Engelm. in Watson, Botany of California 2:107. 1880. *Arceuthobium occidentale* Engelm. var. *abietinum* Engelm. in Watson, Botany of California 2: 107. 1880. *Razoumofskyia douglasii* (Engelm.) Kuntze var. *abietina* (Engelm.) Howell, Fl. Northwest Amer. 1:609. 1902. *Razoumofskyia douglasii* (Engelm.) Kuntze var. *abietina* (Engelm.) Piper, Contr. U.S. Natl. Herb. 11:223. 1906. *Razoumofskyia abietina* (Engelm.) Tubeuf f. *parvula* Tubeuf, Naturwiss. Z. Fors.-Landw. 17:219. 1919. *Razoumofskyia abietina* (Engelm.) Tubeuf f. *magna* Tubeuf, loc. Cit. 220. *Razoumofskyia abietina* (Engelm.) Abrams, Illust. Fl. Pacific Coast States 1:530. 1923. *Arceuthobium*

TABLE 8. Standard discriminant function analysis (DFA) of female (N= 8 characters) and male morphologies (N= 10 male characters) of *Arceuthobium abietinum* f. sp. *concoloris*, f. sp. *magnificae*, subsp. *wiensii* and *A. campylopodum*: standardized correlation coefficients by canonical (Can.), indicating the individual contribution of each morphologic character to the classification of species membership.

Character	Female			Male		
	Can. 1	Can. 2	Can. 3	Can. 1	Can. 2	Can. 3
PH	-0.13	-0.83	0.22	0.01	-0.80	0.28
BD	-0.12	0.37	0.60	-0.12	0.85	0.69
LTI	-0.22	0.42	0.21	-0.23	0.13	0.47
WTI	0.52	-0.09	0.07	0.37	-0.46	-0.63
FL	0.11	-1.04	-0.03			
FW	0.27	0.75	0.29			
SL	0.79	0.24	0.11			
SW	0.01	-0.22	-0.35			
PL				0.06	-0.72	0.24
PW				0.21	0.11	-0.03
AD				-0.10	0.29	-0.03
ADT				-0.15	0.42	0.15
SSL				-0.01	0.10	-0.20
SSW				0.90	0.09	0.21

campylopodum Engelm. f. *abietinum* (Engelm.) Gill, Trans. Connecticut Acad. Arts Sci. 32:195. 1935. *Arceuthobium abietinum* (Engelm.) Hawksw. & Wiens, Brittonia 22:268. 1970. *Arceuthobium abietinum* (Engelm.) Hawksw. & Wiens forma specialis *concoloris* Hawksw. & Wiens, Brittonia 22:267–268. 1970. *Arceuthobium campylopodum* Engelm. subsp. *abietinum* Nickrent, Phytoneuron 51:9. 2012. TYPE: U.S.A. CALIFORNIA. Sierra Co.: Sierra Valley on *Abies concolor*, Lemmon, 1875 (LECTOTYPE: MO; ISOTYPE: GH).

Plants 3.1–24.5 cm in height (mean ca. 11 cm); basal diameter of dominant plants 1.7–6.8 mm (mean 3.1 mm); third internode length 3.2–37.2 mm (mean 14.3 mm) and 2.2 mm wide; staminate plants primarily yellow-green; pistillate plants primarily yellow-green or green-brown; staminate flowers 3 or 4-partite, diameter of 3-merous flowers 2.0–3.9 mm (mean 2.9 mm); diameter of 4-merous flowers 2.7–5.2 mm (mean 3.8 mm); mature fruit length 3.2–6.2 mm (mean 4.7 mm) and 2.2–4.1 mm wide (mean 3.0 mm). Seeds 1.3–3.4 mm long (mean 2.5 mm) and 0.8–1.6 mm wide (mean 1.2 mm).

Phenology.—Anthesis from early-July through early-September peaking in late-July to early-August; seed dispersal from late-August to late-October with peak dispersal in late-September.

Habit.—Principally parasitic on *Abies concolor*, *A. grandis* (including *A. concolor* × *A. grandis*), *A. lowiana*, and *A. durangensis*. Occasionally parasitic on *Abies lasiocarpa* (Hooker) Nutt. and *Picea mexicana* Martínez. Rarely parasitic on *Pinus lambertiana* Douglas, *Pinus monticola* Douglas ex D. Don, *Pinus strobiformis* Engelm., and *Pinus contorta* Douglas ex Loudon var. *murrayana* (Grev. & Balf.) Engelm. The host susceptibility classification used here is based on the system described in Hawksworth and Wiens (1996).

Distribution.—White fir dwarf mistletoe occurs from southern Washington (Klickitat, Skamania, and Yakima counties) through the central Cascade Ranges and southern Coast Ranges of Oregon into the Klamath and Siskiyou Ranges and southern Cascade Ranges of northern California. It is then distributed through the Sierra Nevada Mountains and northern Coast Ranges of California to as far south as the San Bernardino Mountains (Fig. 1). Disjunct populations of white fir dwarf mistletoe are present in the Spring Creek and Sheep Mountains of southern Nevada, in the White and Pink Cliffs areas of southern Utah, south to the North and South Rims of the Grand Canyon. White fir dwarf mistletoe also occurs in isolated populations in southern Arizona (Santa Catalina and Chiricahua Mountains) and known from two populations each in the States of Chihuahua and Durango, Mexico. Elevation range is from near sea level in the Coast Range of California to as high as 3060 m on Cerro Mohinora in southern Chihuahua, Mexico.

Common name.—white fir dwarf mistletoe

Arceuthobium abietinum (Engelm.) Engelm. ex Munz subsp. **magnificae** Mathiasen & Kenaley, **subsp. nov.**

Arceuthobium abietinum Engelm. ex Munz f. sp. *magnificae* Hawksw. & Wiens, *Brittonia* 22:268. 1970. TYPE: U.S.A. CALIFORNIA. Placer Co.: Echo Summit, near road to summer home unit S of U.S. Hwy. 50, 38.811667°N; 120.028611°W, elev. ca. 2200 m, parasitic on *Abies magnifica*, 7 Sep 2018, R.L. Mathiasen & C.M. Daugherty 1531 (HOLOTYPE: RSA-880268, Barcode 0168201; ISOTYPES: BRIT, UC, US).

Plantae 6–25 (12) cm altae; surculi principales basi 2–8 (3.5 mm diam.); internodis tertiis 8–31 (15) mm longis, 2.2 mm latis; fructus maturi 4.7 mm longi, 3.0 mm latis; anthesis mense Julio–Augusto; fructus maturitas Septembri–Octobri. In *Abies magnifica* parasiticae.

Plants 6.0–25.1 cm in height (mean ca. 12 cm); basal diameter of dominant plants 1.9–7.6 mm (mean 3.5 mm); third internode length 7.6–31.3 mm (mean 15.8 mm) and 2.3 mm wide; staminate plants primarily yellow-green; pistillate plants primarily yellow-green or brown-green; staminate flowers 3 or 4-partite, diameter of 3-merous flowers 2.0–3.7 mm (mean 2.6 mm); diameter of 4-merous flowers 2.6–5.0 mm (mean 3.8 mm); mature fruit length 3.4–5.9 mm (mean 4.7 mm) and 2.2–3.9 mm wide (mean 3.0 mm). Seeds 1.8–3.3 mm long (mean 2.5 mm) and 0.8–1.6 mm wide (mean 1.2 mm).

Phenology.—Anthesis from late-July through mid-September with the peaks in early to late-August; seed dispersal from late-August to late-October with peaks in late-September to early-October.

Habit.—Parasitic only on *Abies magnifica* and its varieties *shastensis* and *critchfieldii*.

Distribution.—Red fir dwarf mistletoe occurs from near Mount Shasta (Siskiyou Co.) to Mount Lassen in the southern Cascade Ranges and through the Sierra Nevada Mountains to as far south as the Greenhorn Mountains (Kern Co., California). Elevation range is from 1500 to 2400 m.

Etymology.—The subspecific epithet refers to the name of the only known host of this dwarf mistletoe—red fir (*Abies magnifica*).

Common name.—red fir dwarf mistletoe.

DISCUSSION

As demonstrated herein using univariate and multivariate statistical approaches, the intraspecific taxa of *Arceuthobium abietinum* can be differentiated morphologically comparing several characters. Furthermore, they can be distinguished with high precision comparing multiple characters simultaneously, particularly when utilizing a complete suite of male plant morphologies (Tables 1, 3, and 5; Fig. 5). Full-model standard DFA utilizing complete data and comparing separately female and male plants consistently separated the multivariate means and associated 95% confidence ellipses of f. sp. *concoloris* and f. sp. *magnificae* as well as subsp. *wiensii* (Fig. 5A & B), whereas the 50% contours among these three taxa demonstrated considerable overlap. The resolution of the full-model DFAs for female and male plants of f. sp. *concoloris* and f. sp. *magnificae* also decreased following DFA validation by plant sex—resampling complete data to include only 50 complete records per taxon by sex (Fig. 5C & D). Multivariate means for f. sp. *concoloris* and f. sp. *magnificae* were different in multidimensional space, yet, their associated 95% confidence ellipses were not discrete. Likewise, stepwise discriminant function analyses for female and male plants consistently separated *A. abietinum* subsp. *wiensii* from the two special forms, whereas, *A. abietinum* f. sp. *concoloris* was readily differentiated from f. sp. *magnificae* using male morphologies. Collectively, the standard and stepwise DFAs demonstrated that subsp. *wiensii* shares morphological similarities with the special forms; however, subsp. *wiensii* is morphologically discrete compared to f. sp. *concoloris* and f. sp. *magnificae* when comparing simultaneously multiple female or male characters (Table 4). A complete suite of male and female morphologies, however, is required to maximize morphological differences between and the taxonomic classification for f. sp. *concoloris* and f. sp. *magnificae*. Yet, between the latter special forms, four female and seven male morphological discontinuities separated *A. abietinum* f. sp. *concoloris* and *A. abietinum* f. sp. *magnificae*, including female and male plant height, basal diameter, staminate spike length and width, petal length, and anther distance to tip (Tables 1 and 5). Because the special forms of *A. abietinum* can be differentiated using these morphological characters, we maintain that it is advisable to classify them as subspecies. Therefore, we recombined *A. abietinum* f. sp. *magnificae* to *A. abietinum* subsp. *magnificae*. Because the original description of *A. abietinum* was based on a collection from white fir, *A. abietinum* f. sp. *concoloris* becomes *A. abietinum* subsp. *abietinum* and not *A. abietinum* subsp. *concoloris*. The nomenclatural changes are hereafter recognized.

Recent treatments of *Arceuthobium* (Nickrent 2012, 2016) classify *A. abietinum*—and, hence, subsp. *abietinum*, subsp. *magnificae*, and subsp. *wiensii*—as a subspecies of *A. campylopodum*. However, as demonstrated here, *A. campylopodum* is quite distinct morphologically from the three subspecies of *A. abietinum*, its plants were thicker and more robust in general and its fruits and seeds were on average much larger (Tables 1 and 2). In addition, the staminate spikes, 3- and 4-merous flowers, and petals of *A. campylopodum* were longer and wider on average than each of the subspecies of *A. abietinum*. The color of male and female plants is different between these taxa; those of *A. campylopodum* are predominantly yellow-brown, brown, or yellow while those of *A. abietinum* are predominantly yellow-green, green, or green-brown. Our analyses of the morphologies of *A. campylopodum* and the subspecies of *A. abietinum* using DFA also demonstrated the distinctiveness of *A. campylopodum* (Fig. 5).

Another important difference between *Arceuthobium campylopodum* and *A. abietinum* is their host affinities. *Arceuthobium campylopodum* almost exclusively parasitizes hard pines (*Pinus* spp.) in subgenus *Diploxylon* (Hawksworth & Wiens 1996; Mathiasen & Kenaley 2015b) (Table 3). In contrast, the subspecies of *A. abietinum* are primarily parasites of true firs (*Abies* spp.) with the exception of subsp. *wiensii* that also parasitizes Brewer spruce as a principal host. Only subsp. *abietinum* is known to rarely parasitize a hard pine: Sierra lodgepole pine (*Pinus contorta* var. *murrayana*), which is also an occasional host of *A. campylopodum* (Hawksworth & Wiens 1996). However, this is the only “overlap” in the host relationships of these dwarf mistletoes. Although subsp. *abietinum* rarely parasitizes white pines in subgenus *Haploxylon*, such as *Pinus lambertiana*, *P. monticola*, and *P. strobiformis*, *A. campylopodum* does not parasitize white pines. The only report of *A. campylopodum* on *P. lambertiana* remains unconfirmed and this report is now thought to be based on infection of *P. lambertiana* by subsp. *abietinum* in Oregon (Mathiasen & Kenaley 2017). Furthermore, one of the principal hosts of *A. campylopodum* (*P. ponderosa* Douglas ex Lawson & C. Lawson) is immune to infection by subsp. *abietinum*. In addition, two of the principal hosts of subsp. *abietinum* (*Abies concolor* and *A. grandis*) are also immune to *A. campylopodum* (Hawksworth & Wiens 1996). The exceptionally distinct host preferences of *A. campylopodum* and *A. abietinum* are indicative of major physiological and genetic differences between them and are further evidence that they deserve taxonomic recognition as separate species (Hawksworth & Wiens 1972, 1996; Mathiasen 2010, 2011, 2019; Mathiasen & Daugherty 2009). The principal host of *Arceuthobium abietinum* subsp. *magnificae* is *Abies magnifica*; it is not known to parasitize any other hosts, including those that are commonly parasitized by subsp. *abietinum* (Mathiasen 2011, 2019). In contrast, *A. abietinum* subsp. *abietinum* parasitizes several conifers, but not *Abies magnifica* (Table 3, Mathiasen 2019).

The geographic range of *Arceuthobium abietinum* subsp. *magnificae* extends from near Mount Shasta (Siskiyou Co.) through the Sierra Nevada Mountains to as far south as the Greenhorn Mountains (Kern Co.). It also occurs east of the Greenhorn Mountains near Sherman Pass. In contrast to the relatively limited distribution of subsp. *magnificae*, subsp. *abietinum* is distributed from southern Washington through the Cascade and Coast Ranges of Oregon, south through the Klamath Geological Province, northern Coast Ranges and Sierra Nevada Mountains of California to the San Bernardino Mountains. It then occurs in widely scattered populations in southern Nevada, southern Utah, Arizona and south into Chihuahua and Durango, Mexico. The reasons why subsp. *abietinum* has such a large geographic distribution, but has only survived in a few, widely isolated populations in Nevada, Utah, Arizona and northern Mexico is unclear, but is probably related to environmental conditions which have limited the occurrence of stand-replacing wildfires where it occurs today. It is possible that additional populations of subsp. *abietinum* will eventually be discovered in the Southwest and northern Mexico where conditions on cool, moist, north-facing aspects have allowed it and its hosts to survive past climatic changes and wildfires.

It is important to note that Mathiasen (2011) only sampled 34 populations of *Arceuthobium abietinum* (17 of subsp. *abietinum* and subsp. *magnificae* each) and these were only from the southern Cascades (near Mt. Lassen, Shasta Co.) south to the Greenhorn Mountains (Kern Co.). His sample for subsp. *abietinum* was from a relatively small part of its geographic range and only from one of its principal hosts, *Abies lowiana*. This current study included a much larger sample size of plants, flowers, and fruits for subsp. *abietinum*. It also included a

much larger sample of the geographic range for subsp. *abietinum* and from all of its principal hosts. The larger sample size of populations from entire range of subsp. *abietinum* and from all of its principal hosts undoubtedly influenced the differences we found between the two subspecies. Although we only sampled eight additional populations of subsp. *magnifica* for this study, the mean values we obtained from our larger sample size were approximately the same as those reported by Mathiasen (2011). Our results only varied by 0.1–0.3 mm for the basal diameter of male plants (3.4 versus 3.5 mm), the length of the third internode of female and male plants (15.7 versus 16.0 mm and 15.5 versus 15.4 mm, respectively), the diameter of 4-merous flowers (3.8 versus 3.6 mm), and the length of petals (1.4 versus 1.5 mm).

Another physiological difference between *Arceuthobium abietinum* subsp. *abietinum* and subsp. *magnifica* is that they have slightly different flowering and seed dispersal periods. Although Hawksworth and Wiens (1996) reported that subsp. *abietinum* and subsp. *magnifica* had similar flowering and seed dispersal periods, their phenograms illustrating flowering and seed dispersal, indicated that subsp. *abietinum* reached its flowering peak about two weeks earlier, around the first of August versus mid-August for subsp. *magnifica*. Seed dispersal reached its peak at about the same time for both subspecies, about the end of September. However, Scharpf and Parmeter (1967) reported that their observations of seed dispersal of both subspecies at the same location indicated subsp. *magnifica* started seed dispersal one week earlier. Mathiasen (2011) also reported that his observations of flowering and seed dispersal in the Sierra Nevada Mountains indicated that both flowering and seed dispersal of the subspecies overlapped, but subsp. *abietinum* did begin flowering and seed dispersal earlier than subsp. *magnifica*. These slight differences in flowering and seed dispersal periods provide additional support for recombining the special forms as subspecies of *A. abietinum*.

Differences in plant size and host range have been the principal characters used to separate subspecies of *Arceuthobium* (Hawksworth & Wiens 1972, 1996; Hawksworth et al. 1992; Wass & Mathiasen 2003; Mathiasen 2007, 2008; Mathiasen & Daugherty 2007, 2009; Scott & Mathiasen 2009) and these are the principal characteristics that distinguish the subspecies of *Arceuthobium abietinum* (Tables 1 and 2). In summary, our analyses of the morphologies of *A. campylopodum* and *A. abietinum* supported the continued recognition of these dwarf mistletoes as separate species. Their host relationships also support this conclusion. Moreover, our analyses of the morphologies of special forms of *A. abietinum* supported their recombination as subspecies, thereby, removing the use of formae speciales for populations of *A. abietinum* which exhibit extreme host specificity and are separated by a few, but significantly different, morphological characters.

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