NEW SUBSPECIES OF FIR DWARF MISTLETOE (*ARCEUTHOBIUM ABIETINUM:* VISCACEAE) FROM THE WESTERN UNITED STATES AND NORTHERN MEXICO

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ABSTRACT

Two new subspecies of fir dwarf mistletoe (*Arceuthobium abietinum,* Viscaceae) are described herein: **Arceuthobium abietinum** subsp. **mathiasenii** (Mathiasen's dwarf mistletoe) and **Arceuthobium abietinum** subsp. **grandae** (grand fir dwarf mistletoe). The former dwarf mistletoe—Mathiasen's dwarf mistletoe—parasitizes Rocky Mountain white fir in Nevada, Utah, and Arizona and Durango fir in northern Mexico; whereas, grand fir dwarf mistletoe parasitizes grand fir as well grand fir × white fir hybrids in California, Oregon, and Washington. The recognition of these subspecies and, hence, their classification is based on morphological discontinuities and host range differences when compared to white fir dwarf mistletoe (*Arceuthobium abietinum* subsp. *abietinum*), red fir dwarf mistletoe (*A. abietinum* subsp. *magnificae*), and Wiens' dwarf mistletoe (*A. abietinum* subsp. *wiensii*). The combined analyses of plant height, third internode length and width, fruit dimensions, staminate spike and petal dimensions, and anther distance to tip, contributed most to the discrimination of subspp. *grandae* and *mathiasenii* from subspp. *abietinum* and *magnificae*. The flowers of Mathiasen's dwarf mistletoe were larger than all of the other taxa classified under *A. abietinum*. The shoot color of Mathiasen's dwarf mistletoe was frequently blue-green, brown, yellow-brown, or red-brown, and plants were often highly glaucous, while the shoot color of the other subspecies were typically yellow-green or yellow, except for Wiens' dwarf mistletoe whose shoots are often green-brown or red-brown. Differences in host specificity and geographic distribution also distinguish the new subspecies from the other taxa of *A. abietinum*.

Key Words: *Abies concolor, Abies durangensis, Abies grandis, Abies lowiana, Abies magnifica*

RESUMEN

Se describen aquí dos nuevas subespecies de muérdago enano de oyamel (*Arceuthobium abietinum,* Viscaceae): **Arceuthobium abietinum** subsp. **mathiasenii** (muérdago enano de Mathiasen) y **Arceuthobium abietinum** subsp. **grandae** (muérdago enano del abeto grande). El primero, parasita al abeto blanco de las Montañas Rocosas en Nevada, Utah y Arizona, así como al oyamel de Durango en el norte de México; mientras que el segundo parasita al abeto grande en Oregón y Washington. El reconocimiento de estas subespecies y su clasificación se basa en discontinuidades morfológicas y diferencias en la distribución de sus hospedadores en comparación con las del muérdago enano del abeto blanco (*Arceuthobium abietinum* subsp. *abietinum*), el muérdago enano del abeto rojo (*A. abietinum* subsp. *magnificae*), y el muérdago enano de Wiens (*A. abietinum* subsp. *wiensii*). Entre los caracteres distintivos de estos muérdagos están la mayor altura de las plantas masculinas de ambas subespecies en relación a las del muérdago de Wiens, y las flores del muérdago de Mathiasen claramente mayores que las de todos los otros taxa clasificados bajo *A. abietinum*. El color de las ramas del muérdago de Mathiasen es frecuentemente azul-verde, marrón, amarillo-marrón, o rojo-marrón, y las plantas son frecuentemente muy glaucas, mientras que las ramas de las otras subespecies son típicamente amarillo-verdosas o amarillas, excepto para el muérdago de Wiens, cuyas ramas son frecuentemente verde-marrón o rojo-marrón. Adicionalmente, las nuevas subespecies difieren de los otros taxa de *A. abietinum* en su especificidad al hospedero y su distribución geográfica.

Palabras clave: *Abies concolor, Abies durangensis, Abies grandis, Abies lowiana, Abies magnifica*

INTRODUCTION

Fir dwarf mistletoe (*Arceuthobium abietinum* (Engelm.) Engelm. ex Munz) is a common plant parasite of true firs (*Abies* Mill., Pinaceae) from southern Washington through Oregon and California into southern Nevada, southern Utah, Arizona, and northern Mexico (Hawksworth & Wiens 1996). Presently, fir dwarf mistletoe is subdivided into three subspecies based on host relationships and several morphological differences (Mathiasen & Kenaley 2019). White fir dwarf mistletoe (*A. abietinum* (Engelm.) Engelm. ex Munz subsp. *abietinum*) parasitizes grand fir (*Abies grandis* (Douglas ex D. Don) Lindley) and the hybrid populations of *Abies concolor*

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(Gordon & Glend.) Lindley ex Hildebr.) × *A. grandis* (Ott 2014; Ott et al. 2015; Meyers 2015) in the Cascade Ranges, Klamath-Siskiyou Mountains, and Coast Ranges of Oregon and California (Fig. 1). *Arceuthobium abietinum* subsp. *abietinum* is also commonly encountered parasitizing Sierra white fir (*Abies lowiana* (Gordon) A. Murray bis) across the Sierra Nevada and San Bernardino Mountains in California (Hawksworth & Wiens 1996; Mathiasen & Kenaley 2019). However, outside of California, white fir dwarf mistletoe is found in widely isolated populations on Rocky Mountain white fir (*Abies concolor*) in northern Nevada, southern Utah, and Arizona. Likewise, in northern Mexico, *A. abietinum* subsp. *abietinum* has been collected and characterized on Durango fir (*Abies durangensis* Martínez) in widely scattered populations in coniferous forests of Chihuahua and Durango (Hawksworth & Wiens 1996; Quiñonez et al. 2013; Quiñonez 2016). A second subspecies—*A. abietinum* subsp. *magnificae* Mathiasen & Kenaley (red fir dwarf mistletoe)—parasitizes only red fir (*Abies magnifica* A. Murray bis) and is found in the southern Cascade Ranges (near Mount Shasta and Mount Lassen) through the Sierra Nevada Mountains to as far south as Kern County, CA (Fig. 2) (Parmeter & Scharpf 1963; Scharpf & Parmeter 1967; Hawksworth & Wiens 1996; Mathiasen 2011, 2019; Mathiasen & Kenaley 2019). Formerly, these subspecies were classified as special forms (i.e., forma speciales) by Hawksworth and Wiens (1970, 1972, 1996) and Mathiasen (2011, 2019); however, based on morphological differences and host-specificities, Mathiasen and Kenaley (2019) recombined *A. abietinum* f. sp. *concoloris* and f. sp. *magnificae* to *A. abietinum* subsp. *abietinum* and subsp. *magnificae*, respectively. The third subspecies—*Arceuthobium abietinum* 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 (Fig. 3) (Mathiasen & Daugherty 2009).

Recent treatments of *Arceuthobium* and the genus' most taxonomically controversial section *Campylopoda* by Nickrent (2012, 2016) relegated *A. abietinum* sensu lato and 11 other *Arceuthobium* spp. to subspecies under *A. campylopodum* Engelm. (Western dwarf mistletoe) based primarily on phylogenetic analyses of nuclear ribosomal and plastid DNA sequence data (Nickrent et al. 2004). The classification proposed by Nickrent (2012, 2016) is not followed herein; rather, the taxonomic treatment of Hawksworth and Wiens (1996) for *A. abietinum* and revised by Mathiasen and Kenaley (2019) is adopted as this classification system—and the botanical and phytopathoglogical studies upon which it is based—distinguishes *A. abietinum* from *A. campylopodum* by assessing morphological and host range differences (Parmeter & Scharpf 1963; Scharpf & Parmeter 1967; Hawksworth & Wiens 1996; Mathiasen 2019).

Owing to geographic isolation, genetic barriers, and/or hybridization, the true firs throughout western North America are morphologically and genetically diverse (Liu 1971; Critchfield 1988; Farjon 2010; Ott et al. 2015; Xiang et al. 2018). This is particularly the case in the Pacific Northwest and California (Sudworth 1908; Hunt 1993; Ott 2014), wherein, true fir populations and, hence, hosts of *A. abietinum* intergrade yielding morphological intermediates. The geographic delineation and taxonomic treatment of these true fir populations has recently received attention (Ott 2014; Meyer 2015). Integrating microsatellite and morphometric analyses, Ott (2014) investigated maternal and paternal lineages of grand fir and Rocky Mountain white fir populations throughout the western U.S.; delimiting a zone of interspecific hybridization consisting of *A. grandis* × *A. concolor* in the Siskiyou Mountains of northern California and the southern Cascade Mountains. This hybrid zone was similarly located to the transitional zone described by Lacaze and Tomassone (1967), who characterized morphological intermediates of *A. grandis* and *A. concolor* at 43°–44° N in central Oregon. Likewise, examining fir populations across the Oregon Cascades, Daniels (1969) observed that the morphology within the *A. grandis*-*A. concolor* complex was strongly influenced by latitude; whereby northern populations resembled *A. grandis*; whereas, more southerly populations acquired morphologies true to Sierra white fir, *Abies concolor* var. *lowiana* (Gordon). Ott (2014) also designated populations of *A. concolor* throughout the Warner and Sierra Nevada Mountains as *A. concolor* var. *lowiana*. Thus, herein, hosts of *A. abietinum* in southern Oregon and northern California were identified as *A. concolor* × *A. grandis* following Ott (2014) and adopted by Meyers (2015); whereas true-fir hosts in southern Washington and northern to central Oregon were determined as *A. grandis*. Although many botanists ascribe to the treatment of Sierra white fir populations as a variety of *A.*

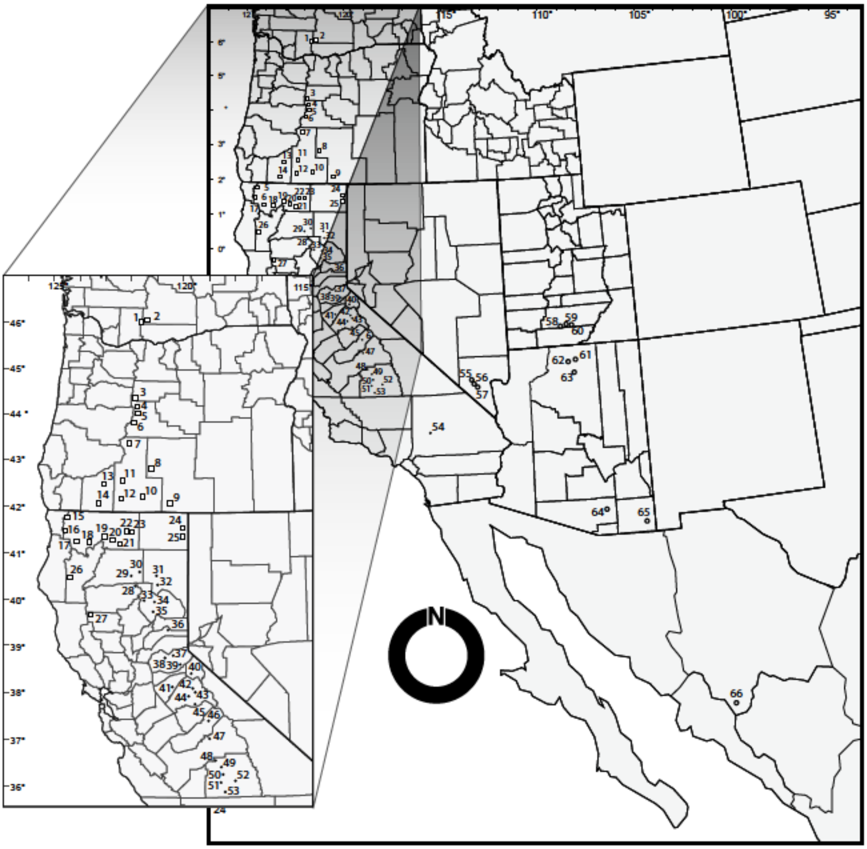

Fig. 1. Approximate locations of populations sampled for *Arceuthobium abietinum* subsp. *grandae* (open squares), *A. abietinum* subsp. *abietinum* (closed circles), and *A. abietinum* subsp. *mathiasenii* (open circles). Modified from Mathiasen and Kenaley (2019). **U.S.A. Washington: 1**—0.5 km E 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 Hamner 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 County 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 Sprs. 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 Sprs. 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. 6S07, **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. 21S50, **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 National Park, 62—Bright Angel Point North Rim Grand Canyon National 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.

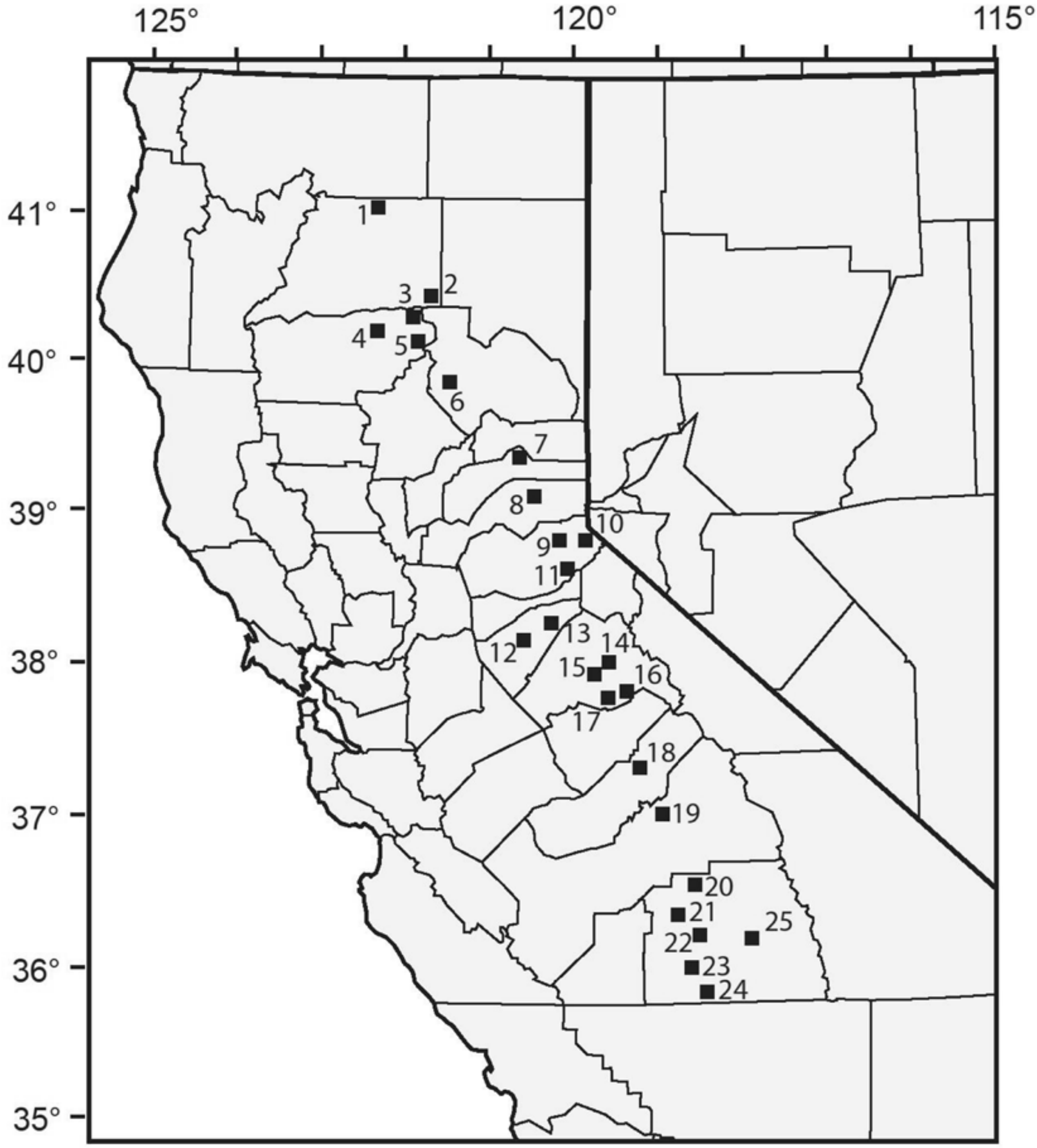

Fig. 2. Approximate locations (black squares) of populations sampled for *A. abietinum* subsp. *magnificae*. **California: 1**—12.2 km S of St. Rte. 89 on forest rd. 39N06, **2**—16 km N of S entrance to Lassen Nat. Park on St. Rte. 89, **3**—2.3 km N of St. Rte. 36 on St. Rte. 89, **4**—2.5 km S of Colby Mtn. Lookout on forest rd. 27N36, **5**—Humboldt Summit, **6**—3 km E of Grizzly Summit on Oroville-Quincy Hyw., **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 Hyw., **24**—Sunday Peak Trailhead on forest rd. 28S16, **25**—Jct. of Sherman Pass Rd. and forest rd. 22S20.

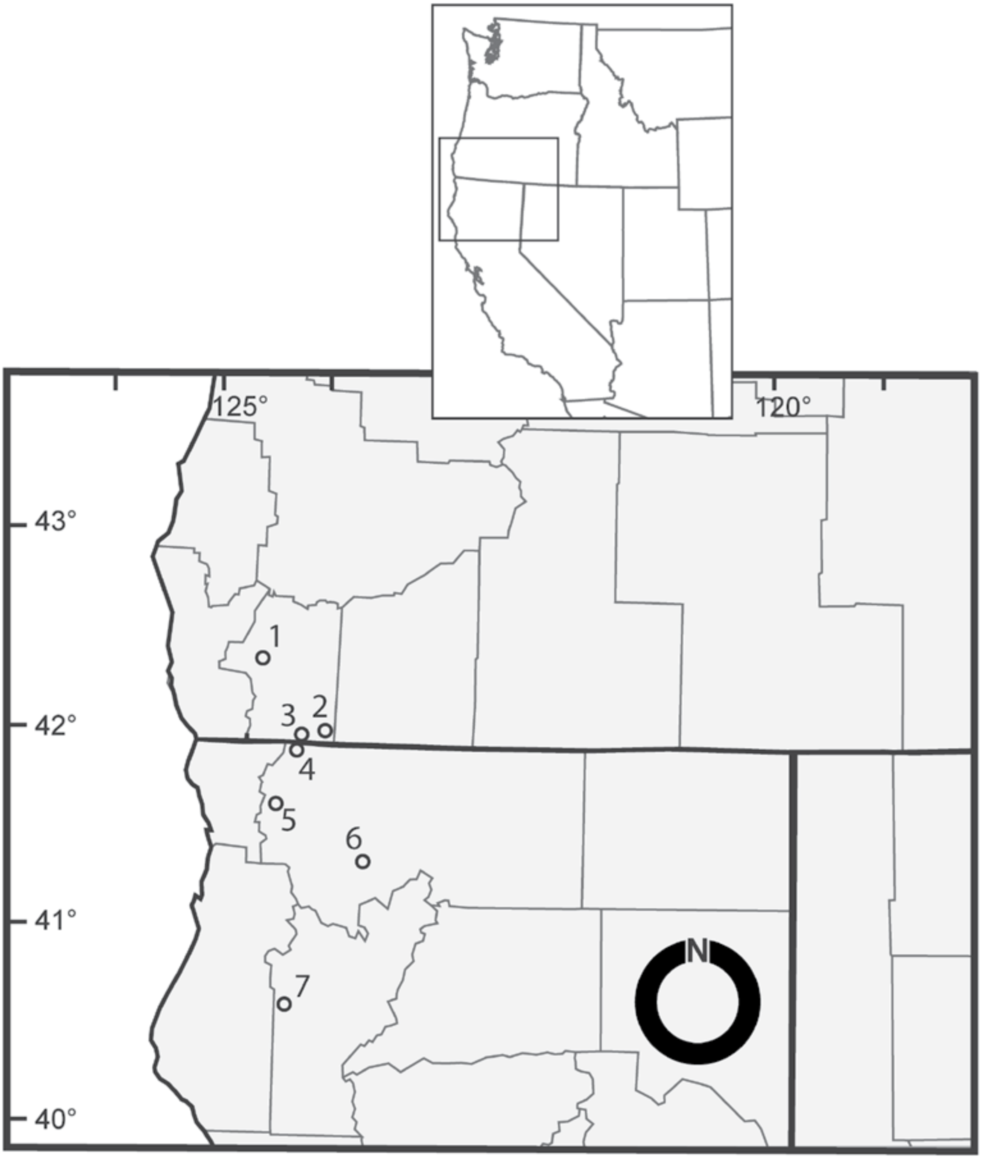

Fig. 3. Approximate locations of populations sampled for *Arceuthobium abietinum* subsp. *wiensii*. Modified from Mathiasen and Daugherty (2009). Oregon: 1—Flat Top Mtn., 2—Steve Fork Cr., 3—Althouse Mtn.; California: 4—Bolan Mtn., 5—Baldy Mtn., 18 km west of Indian Cr. on Doolittle Cr. Rd., 6—Etna Summit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

concolor (e.g., Hickman 1993), the classification of Hunt (1993) for these variant populations of white fir in California and Nevada is followed here, recognizing these populations as *A. lowiana.*

As with the grand fir-white fir complex, Oline (2008) estimated chloroplast haplotype frequencies based on *rbcL* and *trnD* sequences for red fir and noble fir (*Abies procera* Rehder) in the southern Cascades as well as Klamath–Siskiyou and Sierra Nevada Mountains, demonstrating that a broad zone of hybridization between red fir and noble fir occurs within southern Oregon and northern California. Thereafter, Meyers (2015) treated the red fir populations in southern Oregon—commonly referred to as Shasta red fir (*A. magnifica* A. Murray var. *shastensis* Lemmon or *A. shastensis* Lemmon)—as interspecific hybrids, *A. magnifica* × *A. procera*. Moreover, Lanner (2010) recently described *Abies magnifica* var. *critchfieldii* Lanner (Critchfield red fir) to recognize red fir populations in the extreme southern Sierra Nevada Mountains (south of Kings Canyon) with smaller female cones and extended bracts. In the present work, populations of Shasta red fir in northern California and southern Oregon as well as Critchfield red fir in the southernmost distribution of *A. magnifica* were treated as red fir sensu lato.

Analyses of morphological data collected during 2012–2018 from throughout the geographic range of white fir dwarf mistletoe (*Arceuthobium abietinum* subsp. *abietinum*) revealed that plants infecting *Abies concolor* in the Southwest and northern Mexico were noticeably smaller and possessed a different color than plants found on white fir in California. Likewise, regardless of plant sex, *A. abietinum* subsp. *abietinum* sensu lato on grand fir and grand fir-white fir hybrids of the Pacific Northwest and northern California were noticeably smaller when compared to white fir dwarf mistletoe infecting Sierra white fir throughout the Sierra Nevada Mountains. Therefore, a more detailed analysis of the morphological characters of the populations of white fir dwarf mistletoe parasitizing Rocky Mountain white fir, Sierra white fir, and the grand fir-white fir complex was warranted. Subsequent morphometric analyses presented herein supported the description of two new subspecies of fir dwarf mistletoe based on significant differences between several morphological characters, host preferences, and geographic distributions.

NOMENCLATURAL CHANGES

Arceuthobium abietinum (Engelm.) Engelm. ex Munz subsp. **mathiasenii** Kenaley, **subsp. nov.** Type: UTAH. Kane Co.: Pink Cliffs, 4 km SW of Crawford Pass on forest road 203, Dixie National Forest, elev. 2740 m, Lat. 37°26'22"N, Long. 112°18'51"W, parasitic on *Abies concolor,* 26 Jul 2018, *R.L. Mathiasen 1510* (holotype: RSA; isotypes: ARIZ, US).

Arceuthobium abietinum Engelm. ex Munz f. sp. *concoloris* Hawksw. & Wiens, pro parte, Brittonia 22:265–269. 1970.

Plantae 3.1–17.2 cm altae; surculi prinicipales basi 1.9–5.7 (2.9) mm diam.; internodis tertiis 5.6–21.6 mm longis, 2.2 mm latis; fructus maturi 4.7 mm longi, 3.0 mm latis; anthesis mense Jul–Aug; fructus maturitas Sep–Oct. In *Abies concolor*, *Abies durangensis*, et *Picea mexicana* parasiticae.

Plants 3.1–17.2 cm in height (mean 9.5 cm female; mean 9.3 cm male); basal diameter of dominant plants 1.9–5.7 mm (mean 2.9 mm); third internode length 5.6–21.6 mm (mean 13.1 mm female; mean 12.6 mm male) and 2.2 mm wide; staminate plants primarily yellow-brown or red-brown, but may be blue-green or yellow-green; some plants are highly glaucous; pistillate plants primarily red-brown, green-brown, or blue-green, but some rarely yellow-brown; some plants are highly glaucous; staminate flowers 3 or 4-partite, flower diameter of 3-partite flowers 2.1–3.6 mm (mean 3.1 mm), flower diameter of 4-partite flowers 3.0–5.2 mm (mean 4.1 mm); mature fruit length 3.7–5.7 mm (mean 4.7 mm) and 2.2–3.8 mm wide (mean 3.0 mm). Seeds 1.8–3.0 mm long (mean 2.4 mm) and 0.9–1.5 mm wide (mean 1.2 mm).

Etymology.—*Arceuthobium abietinum* subsp. *mathiasenii* is named in honor of Dr. Robert L. Mathiasen, recognizing his nearly 50 years of exemplary scientific research and education on the taxonomy and systematics of dwarf mistletoes throughout western North America.

Common name.—Mathiasen's dwarf mistletoe

Phenology.—Anthesis is from early-July to mid-August, but the peak period of flowering is usually in early-August. Seeds are dispersed from late-August to late-September with a peak in early-September.

Habit.—Parasitic principally on *Abies concolor* in the United States and *Abies durangensis* in México; occasionally parasitic on *Picea mexicana* Martínez; rarely parasitic on *Pinus strobiformis* Engelm. Host susceptibility classification used here and below is based on the system described in Hawksworth and Wiens (1996).

Distribution.—Mathiasen's dwarf mistletoe occurs in small, disjunct populations in southwestern Nevada (Spring and Sheep mountains), southern Utah (Pink Cliffs and Navajo Lake), northern Arizona (North and South Rim Grand Canyon), southern Arizona (Santa Catalina and Chiricahua mountains), and in the Sierra Madre Occidental of Mexico; near Yahuirachi and on Cerro Mohinora, Chihuahua and near Tamazula and on Cerro Gordo, Durango (Fig. 1). Elevation range is from ca. 2080 m in the Chiricahua Mountains, Arizona to as high as 3060 m on Cerro Mohinora, Chihuahua, Mexico.

Arceuthobium abietinum (Engelm.) Engelm. ex Munz subsp. **grandae** Kenaley, **subsp. nov.** Type: OREGON. Deschutes Co.: Cascade Range, 1.6 km NW of State Route 242 on forest road 1030, Deschutes National Forest, elev. 1370 m, Lat. 44°19'04"N, Long. 121°44'44"W, parasitic on *Abies grandis,* 11 Aug 2019, *R.L. Mathiasen 1550* (holotype: RSA; isotypes: ARIZ, OSC, US).

Arceuthobium abietinum Engelm. ex Munz f. sp. *concoloris* Hawksw. & Wiens, pro parte, Brittonia 22:265–269. 1970.

Plantae 5.2–18.8 cm altae; surculi prinicipales basi 1.7–6.8 (3.0) mm diam.; internodis tertiis 7.0–46.2 mm longis, 2.0 mm latis; fructus maturi 3.2–6.2 (4.7) mm longi, 2.2–4.0 (3.0) mm latis; anthesis mense Jul–Aug; fructus maturitas nuper Aug–Oct. In *Abies grandis* et *Abies grandis* × *Abies concolor* parasiticae.

Plants 5.2–18.8 cm in height (mean 11.5 cm female; mean 11.3 cm male); basal diameter of dominant plants 1.7–6.8 mm (mean 3.0 mm); third internode length 7.0–46.2 mm (mean 15.1 mm female; mean 13.6 mm male) and 2.0 mm wide; staminate plants primarily yellow-green or yellow; pistillate plants primarily green-brown; staminate flowers 3 or 4-partite, flower diameter of 3-partite flowers 2.1–3.7 mm (mean 2.7 mm), flower diameter of 4-partite flowers 2.7–4.8 mm (mean 3.7 mm); mature fruit length 3.2–6.2 mm (mean 4.7 mm) and 2.2–4.0 mm wide (mean 3.0 mm). Seeds 1.7–3.4 mm long (mean 2.5 mm) and 0.8–1.6 mm wide (mean 1.1 mm).

Etymology.—*Arceuthobium abietinum* subsp. *grandae* is named according to its principal host, *Abies grandis*, within much of its geographic distribution in Oregon and Washington. The feminine ending *-is* of the host's specific epithet (i.e., *grandis*) was changed to the plural feminine ending *-ae* in order to maintain convention among previously classified subspecies of *Arceuthobium* (Hawksworth et al. 1992; Wass & Mathiasen 2003; Mathiasen & Daugherty 2007, 2009; Scott & Mathiasen 2009; Mathiasen & Kenaley 2019).

Common name.—Grand fir dwarf mistletoe.

Phenology.—Anthesis is from late-July to late-August, but the peak period of flowering is usually from early-August to mid-August. Seeds are dispersed from late-August into early-October with a peak in mid-September.

Habit.—Parasitic principally on *Abies grandis* and *A. grandis* × *A. concolor* hybrids. Rarely parasitic on *Picea engelmannii* Parry ex Engelm. and *Pinus lambertiana* Douglas. Host susceptibility classification used here and below is based on the system described in Hawksworth and Wiens (1996).

Distribution.—This dwarf mistletoe occurs from southern Washington (Klickitat, Skamania, and Yakima counties) through the Cascade and Siskiyou mountains in Oregon to the Klamath and southern Cascade Mountains (near Mount Shasta) of northern California. The southern limit of its distribution in the Cascade Mountains is in the vicinity of Mount Shasta (Siskiyou and Shasta counties). It occurs in the Warner Mountains in northeastern California and along the coast of California (Humboldt and Mendocino counties). In the Coast Ranges of western California, it is found as far south as Colusa County near Snow Mountain.

MATERIALS AND METHODS

Plant material

A total of 12 populations of *Arceuthobium abietinum* subsp. *mathiasenii* were sampled from within its geographic range (Fig. 1). From each population, 20 to 40 infections were collected and the dominant shoot from each infection was used for morphological measurements. In order to make a comparison with the morphological characters of *Arceuthobium abietinum* subsp. *abietinum*, data for the latter subspecies from 27 populations—collected and reported by Mathiasen and Kenaley (2019)—were used from the Sierra Nevada Mountains and southern Cascade Ranges (Fig. 1). Likewise, 27 populations of *A. abietinum* subsp. *grandae* were sampled across the geographic range of *A. grandis* and *A. grandis* × *A. concolor* in the southern Cascade Mountains north of Mount Lassen, in the Coast Ranges of California, from the Klamath-Siskiyou Mountain Region, into central Oregon and southern Washington (Mathiasen & Kenaley 2019) (Fig. 1). Morphological data for *A. abietinum* subsp. *magnificae* were from Mathiasen (2011) and Mathiasen and Kenaley (2019) and for *A. abietinum* subsp. *wiensii* from Mathiasen and Daugherty (2009). Plant characters measured herein were those utilized by Hawksworth and Wiens (1996) for taxonomic classification of *Arceuthobium*: height (PH), basal diameter (BD), length and width of third internode (LTI, WTI), color of the tallest male and female shoot per infection collected; mature fruit length (FL), width (FW), and color; seed length (SL) and width (SW);

staminate flower diameter (FD), petal number (merosity), petal length (PL) and width (PW); staminate spike length (SSL) and width (SSW); and, anther diameter (AD) and distance from the petal tip (i.e., anther distance to tip, ADP).

Measurements were made using a digital caliper (Mitutoyo America Corp., Aurora, IL) and a 7× magnifier equipped with a micrometer (Bausch & Lomb, Bridgewater, NJ). Basal diameter of plants to the nearest 0.1 mm was measured at the point of plant attachment to the host branch. The length and width of the third internode distal to the base of plants were also included in our morphological analyses because these characters frequently have been reported for male and female plants of dwarf mistletoes, providing relative information on plant size and, most importantly, plant thickness (Hawksworth & Wiens 1972, 1996; Mathiasen & Daugherty 2007, 2009; Mathiasen & Kenaley 2015, 2019; Kenaley et al. 2016; Mathiasen et al. 2016). 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 most morphological characters measured varied among the five 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 *Arceuthobium abietinum*. Mean differences among morphological characters across taxa by plant sex were assessed using a post-hoc Tukey's honestly significant difference (HSD; $\alpha= 0.05$) test. In addition, a Dunnett's test ($\alpha= 0.05$) was executed with female or male plants of *A. abietinum* subsp. *abietinum* as the control.

Following univariate analyses, multivariate analysis of variance (MANOVA) was used to test morphological differences among the intraspecific taxa of *Arceuthobium abietinum*, incorporating simultaneously eight female characters and, in a separate MANOVA, ten male characters. MANOVA tests were executed by plant sex to minimize experimental error (family-wise Type I error; Rancher 2002). Thus, female and male univariate data sets were modified separately to comprise only complete records for female and male plants. Following MANOVAs, standard quadratic discriminant function analysis (DFA) was performed by plant sex to determine whether female or male plants could be delimited by subspecies (i.e., taxonomic affiliation, comparison of field diagnosis vs. predicted taxonomic membership) utilizing either female or male plant morphologies, respectively (Quinn & Keough 2002). Standardized correlation coefficients for female and male morphologies were calculated to assess the overall contribution of each morphologic character to the discriminant function by plant sex, providing principal female or male character(s) separating subspecies of *A. abietinum*. Thereafter, DFA of female and male plant parts were validated individually by selecting at random 50 complete records per subspecies and re-executing the DFA using a full-model (i.e., 8 female or 10 male characters simultaneously). Forward-stepwise DFA was also 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 subspecies membership. 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 ($\alpha= 0.05$) and standard deviations were also calculated for comparing the variance in morphologies among taxa of *A. abietinum*.

RESULTS AND DISCUSSION

The statistical analyses—ANOVA, MANOVA, and DFA—presented herein clearly demonstrated that *Arceuthobium abietinum* subsp. *mathiasenii* and subsp. *grandae* can be determined readily among the subspecies *abietinum*, subsp. *magnificae*, and subsp. *wiensii* using morphological data without consideration of geographic location, host specificity, and/or phenological data (Tables 1–8; Fig. 4). Plants of *A. abietinum* subsp. *abietinum* and subsp. *magnificae* were morphologically similar as reported by Hawksworth and Wiens (1972,

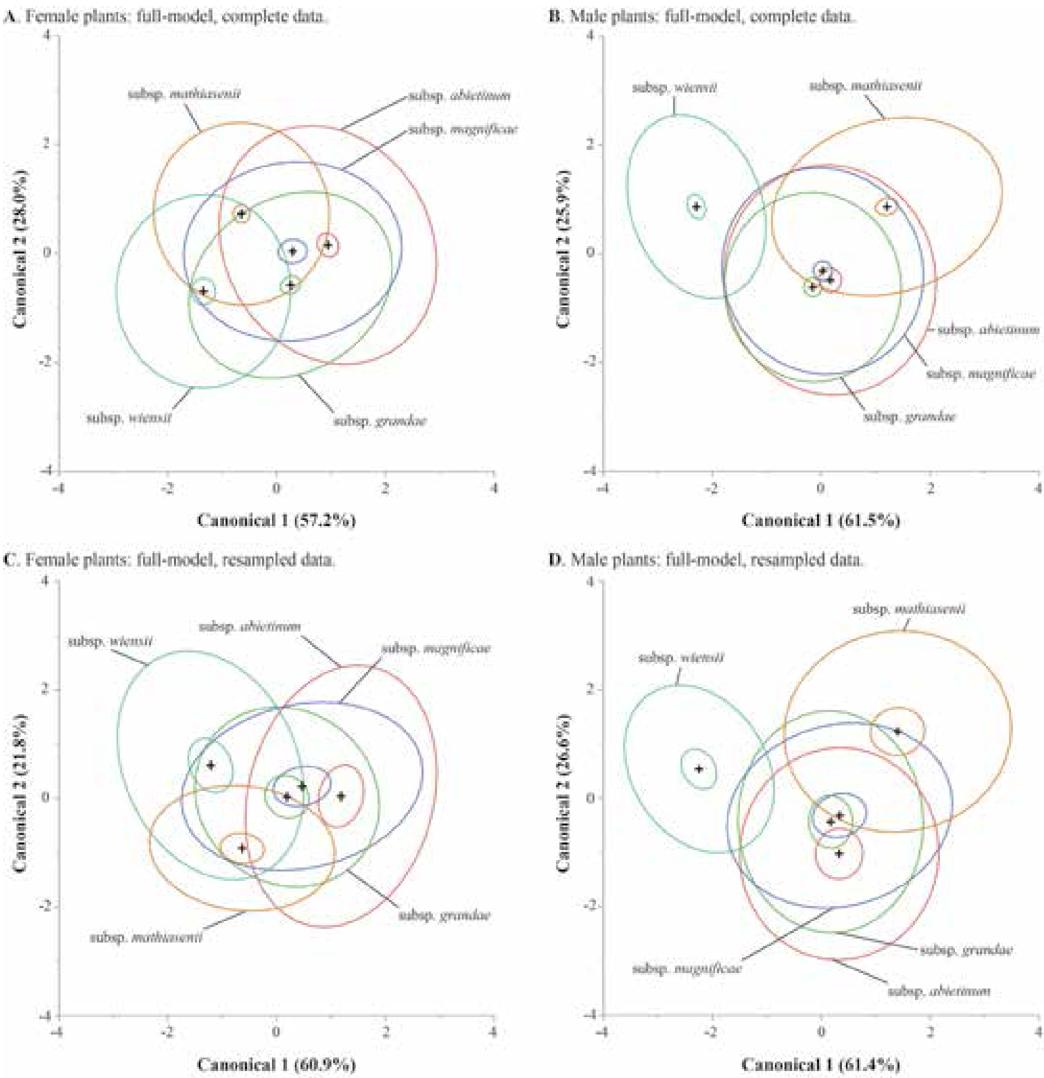

Fig. 4. Canonical plots for standard discriminant function analyses (DFA) of *Arceuthobium abietinum* subsp. *abietinum*, subsp. *grandae*, subsp. *magnificae*, subsp. *mathiasenii*, and subsp. *wiensii* based on morphological characteristics of female (A, C) and male plants (B, D). Multivariate means (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 subspecies (A–D), the inner ellipse corresponds to a 95% confidence limit for the mean, and the outer ellipse represents a normal 50% contour illustrating the approximate area wherein 50% of plants for each taxon reside.

1996), Mathiasen (2011), and Mathiasen and Kenaley (2019). Although several morphological characters were similar between *A. abietinum* subsp. *abietinum* and *A. abietinum* subsp. *mathiasenii*, there were several consistent morphological differences (Tables 1 & 2). Moreover, across female and male plants, a total of 18 of 20 morphological characters (6/8 female, 12/12 male) of Mathiasen's dwarf mistletoe were significantly different when compared to subsp. *abietinum*. Likewise, *A. abietinum* subsp. *mathiasenii* was also morphologically distinct from subspp. *grandae*, *magnificae*, and/or *wiensii* when comparing female or male plant characteristics either individually (univariate analyses; Tables 1 & 2) or simultaneously (multivariate analyses; Tables 4–6; Fig. 4). Multivariate analysis of variance (MANOVA) of female and male morphologies revealed significant differences

Table 1. Comparison of means across morphological characteristics among *Arceuthobium abietinum* subspecies *abietinum*, *grandae*, *magnificae*, *mathiasenii*, and *wiensii*. 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 (α= 0.05). Likewise, by row, means underlined were significantly different when compared individually to *A. abietinum* subsp. *abietinum* (control) using a Dunnett's test (α= 0.05). Plant heights are in cm and all other measurements in mm. 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).

		Arceuthobium abietinum subsp.				
Character[a]		*abietinum*	*grandae*	*magnificae*	*mathiasenii*	*wiensii*
PH						
	Female	**13.2** A (3.2) [290]	**11.5** C (2.6) [390]	**12.2** B (3.0) [350]	**9.5** D (2.3) [360]	**9.5** D (2.3) [230]
	Male	**12.7** A (3.1) [250]	**11.3** B (2.8) [280]	**11.9** B (2.7) [330]	**9.3** C (2.2) [300]	**8.9** C (2.3) [160]
BD						
	Female	**3.6** A (0.9) [290]	**3.1** BC (0.8) [390]	**3.6** A (0.8) [350]	**3.0** C (0.6) [360]	**3.2** B (0.7) [230]
	Male	**3.3** A (0.8) [250]	**2.9** C (0.6) [280]	**3.3** A (070) [330]	**2.8** C (0.5) [300]	**3.1** B (0.6) [160]
LTI						
	Female	**16.7** A (4.4) [290]	**15.1** B (3.6) [390]	**16.2** A (3.8) [350]	**13.1** C (3.3) [360]	**14.7** B (3.6) [230]
	Male	**16.0** A (3.8) [250]	**13.6** B (3.3) [280]	**15.4** A (3.7) [330]	**12.6** C (3.3) [300]	**13.5** BC (3.2) 160]
WTI						
	Female	**2.4** A (0.4) [290]	**2.0** D (0.3) [390]	**2.2** B (0.4) [350]	**2.2** C (0.3) [360]	**1.9** E (0.3) [230]
	Male	**2.4** A (0.4) [250]	**2.0** C (0.3) [280]	**2.2** B (0.4) [330]	**2.2** B (0.3) [300]	**1.9** D (0.3) [160]
SSL		**10.4** B (2.8) [390]	**9.9** B (2.3) [520]	**9.4** C (3.0) [600]	**11.3** A (3.2) [410]	**8.7** D (2.5) [290]
SSW		**2.1** B (0.3) [390]	**2.0** D (0.3) [520]	**2.0** C (0.3) [600]	**2.4** A (0.3) [410]	**1.5** E (0.3) [290]
FD						
	3-merous	**2.8** B (0.3) [280]	**2.7** C (0.3) [250]	**2.6** C (0.3) [330]	**3.1** A (0.4) [250]	**2.4** D (0.2) [140]
	4-merous	**3.7** B (0.4) [280]	**3.7** B (0.4) [250]	**3.8** B (0.5) [330]	**4.1** A (0.4) [250]	**3.2** C (0.2) [140]
PL		**1.4** C (0.2) [510]	**1.4** C (0.2) [550]	**1.4** B (0.2) [660]	**1.5** A (0.2) [500]	**1.2** D (0.2) 280]
PW		**1.2** B (0.2) [510]	**1.2** B (0.2) [550]	**1.2** B (0.2) [660]	**1.4** A (0.2) [500]	**1.0** C (0.1) [280]
AD		**0.5** C (0.1) [510]	**0.5** C (0.1) [550]	**0.6** B (0.1) [660]	**0.6** A (0.1) [500]	**0.5** D (0.1) [280]
ADT		**0.6** B (0.2) [510]	**0.5** D (0.1) [550]	**0.5** C (0.1) [660]	**0.7** A (0.2) [500]	**0.6** B (0.1) [280]
FL		**4.9** A (0.5) [320]	**4.7** B (0.5) [290]	**4.7** B (0.5) [370]	**4.7** B (0.4) [300]	**4.2** C (0.4) [150]
FW		**3.0** A (0.3) [320]	**3.0** A (0.3) [290]	**3.0** A (0.4) [370]	**3.0** A (0.3) [300]	**3.0** A (0.3) [150]
SL		**2.5** A (0.3) [320]	**2.5** B (0.3) [290]	**2.5** AB (0.3) [370]	**2.4** C (0.2) [300]	**2.4** BC (0.2) [150]
SW		**1.2** A (0.1) [320]	**1.1** B (0.1) [290]	**1.2** AB (0.2) [370]	**1.2** A (0.1) [300]	**1.1** B (0.1) [150]

among the infraspecific taxa of *A. abietinum* across eight female (Wilks' Lambda approx. $F_{32, 4353.2}$= 35.3, P< 0.0001; Pilllai's Trace approx. $F_{32, 4732}$= 32.7, P< 0.0001; Hotelling-Lawley approx. $F_{32, 3075.5}$= 37.4, P< 0.001) and 10 male morphological characters (Wilks' Lambda approx. $F_{40, 4961.6}$= 47.0, P< 0.0001; Pilllai's Trace approx. $F_{40, 5244}$= 41.7, P< 0.0001; Hotelling-Lawley approx. $F_{40, 3650.2}$= 52.1, P< 0.0001). Separate full-model DFAs of female and male morphologies correctly classified female and male plants of *A. abietinum* subsp. *mathiasenii* 63.7% (191/300) and 76.0% (228/300) of the time (Table 6). In addition, the majority of female plants (>50%) diagnosed a priori via field identification as subsp. *mathiasenii* were correctly classified to its predicted taxonomic affiliation utilizing only 5 of 8 female morphologies—height, third internode length and width, and fruit dimensions (Table 4). The classification of Mathiasen's dwarf mistletoe was improved utilizing DFA and a complete suite of male morphologies (i.e., full-model, 10 characteristics, and equal prior probabilities) (Tables 4 & 6); resulting in 76.0% (228/300) of male plants correctly delimited to subsp. *mathiasenii*. The combined analyses of staminate spike width, plant height, and anther distance to tip readily differentiated male plants of subsp. *mathiasenii* (74.0%, 222/300) from each of the other subspecies (Table 4). Multivariate means for female and male plants of Mathiasen's dwarf mistletoe were clearly disjunct in multidimensional space when compared to other subspecies of *A. abietinum* utilizing full-model DFA and either complete or resampled data (50 complete records/species) (Fig. 4). Means with associated 95% confidence intervals for female and male plants predicted to subsp. *mathiasenii* are presented in Table 5.

The female plants of *Arceuthobium abietinum* subsp. *mathiasenii* were significantly smaller than those of subsp. *abietinum*, subsp. *magnificae*, and subsp. *grandae*, but not those of subsp. *wiensii*. The color of plants of

Table 2. *P*-values for morphological comparisons among subspecies of *Arceuthobium abietinum* using analysis of variance (ANOVA) followed by a Tukey's HSD Post Hoc test (α= 0.05). Subspecies-character comparisons less than *P*= 0.05 are in bold type. 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).

Character[a]	Comparison of *Arceuthobium abietinum* subsp.									
	abietinum				*grandae*			*magnificae*		*mathiasenii*
	grandae	*magnificae*	*mathiasenii*	*wiensii*	*magnificae*	*mathiasenii*	*wiensii*	*mathiasenii*	*wiensii*	*wiensii*
PH										
Female	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*= 0.0138	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	***P*= 0.9999**
Male	*P*< 0.0001	*P*= 0.0018	*P*< 0.0001	*P*< 0.0001	***P*= 0.0513**	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	***P*= 0.6686**
BD										
Female	*P*< 0.0001	***P*= 0.9236**	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*= 0.6167	***P*= 0.3134**	*P*< 0.0001	*P*< 0.0001	*P*= 0.0165
Male	*P*< 0.0001	***P*= 0.9973**	*P*< 0.0001	*P*= 0.0266	*P*< 0.0001	*P*= 0.9893	*P*= 0.0004	*P*< 0.0001	*P*= 0.0064	*P*< 0.0001
LTI										
Female	*P*< 0.0001	***P*= 0.5392**	*P*< 0.0001	*P*< 0.0001	*P*= 0.0004	*P*< 0.0001	***P*= 0.6875**	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001
Male	*P*< 0.0001	***P*= 0.2672**	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*= 0.0048	***P*= 0.9982**	*P*< 0.0001	*P*< 0.0001	***P*= 0.0631**
WTI										
Female	*P*< 0.0001	*P*= 0.0007	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*= 0.0284	*P*= 0.0110	*P*< 0.0001	*P*< 0.0001
Male	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*= 0.0003	***P*= 0.9479**	*P*< 0.0001	*P*< 0.0001
SSL	***P*= 0.1499**	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*= 0.0087	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*= 0.0066	*P*< 0.0001
SSW	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*= 0.0009	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001
FD										
3-merous	*P*= 0.0433	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	***P*= 0.1153**	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001
4-merous	***P*= 0.9864**	***P*= 0.0619**	*P*< 0.0001	*P*< 0.0001	*P*= 0.0269	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001
PL	***P*= 0.9819**	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001
PW	***P*= 0.0687**	***P*= 0.8751**	*P*< 0.0001	*P*< 0.0001	***P*= 0.3709**	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001
AD	***P*= 0.9720**	*P*= 0.0031	*P*< 0.0001	*P*= 0.0069	*P*= 0.0002	*P*< 0.0001	*P*= 0.0314	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001
ADT	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	***P*= 0.9899**	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001
FL	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	*P*< 0.0001	***P*= 0.9777**	***P*= 0.9994**	*P*< 0.0001	***P*= 0.9223**	*P*< 0.0001	*P*< 0.0001
FW	***P*= 0.8501**	***P*= 0.8252**	***P*= 0.9998**	***P*= 0.8440**	***P*= 0.2288**	***P*= 0.7760**	***P*= 0.9997**	***P*= 0.9062**	***P*= 0.3251**	***P*= 0.7818**
SL	*P*= 0.0326	***P*= 0.2173**	*P*< 0.0001	*P*= 0.0024	***P*= 0.8858**	***P*= 0.0003**	***P*= 0.7060**	*P*< 0.0001	***P*= 0.2300**	***P*= 0.1845**
SW	*P*= 0.0002	***P*= 0.0995**	***P*= 1.000**	*P*< 0.0001	***P*= 0.6328**	***P*= 0.0031**	***P*= 0.6467**	***P*= 0.1152**	***P*= 0.0801**	*P*= 0.0002

Table 3. Summary of the principal characters separating *Arceuthobium abietinum* subspecies *abietinum, grandae, magnificae, mathiasenii*, and *wiensii*. Data for morphological characters are means; plant heights in cm and all other measurements in mm. 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).

Character	*Arceuthobium abietinum* subsp.				
	abietinum	*grandae*	*magnificae*	*mathiasenii*	*wiensii*
Plant Height					
Female	13.2	11.5	12.2	9.5	9.5
Male	12.7	11.3	11.9	9.3	8.9
Plant Color	Yellow, yellow-green	Yellow, yellow-green, green-brown	Yellow, yellow-red-brown, red	Yellow-brown, brown, red	Brown-green, red-brown, red
Width of Third Internode					
Female	2.4	2.0	2.3	2.2	1.9
Male	2.4	2.0	2.2	2.2	1.9
Staminate Spike Width	2.1	2.0	2	3	1.5
Flower Diameter					
3-merous	2.8	2.7	2.6	3.1	2.4
4-merous	3.7	3.7	3.8	4.1	3.2
Fruit Length	4.9	4.7	4.7	4.7	4.2
Fruit Width	3.0	3.0	3.1	3.0	3.0
Principal Hosts[a]	*Abies lowiana*	*Abies grandis*; *A. grandis* × *A. concolor*	*Abies magnifica*[b] *A. durangensis*	*Abies concolor*; *Picea breweriana*	*Abies magnifica;*
Secondary Hosts	None	None	None	None	None
Occasional Hosts	*Abies lasiocarpa*	None	None	*Picea mexicana*	*Abies grandis* × *concolor*[c]
Rare Hosts	*Abies amabilis; Pinus contorta* var. *murrayana; P. lambertiana; P. monticola*	*Picea engelmannii*; *Pinus lambertiana*	None	*Pinus strobiformis*	*Pinus monticola*

subsp. *mathiasenii* was frequently green-brown, red-brown, or blue-green, while the color of plants of subsp. *abietinum* and subsp. *magnificae* were typically yellow-green, or yellow as described by Hawksworth and Wiens (1972, 1996) and Mathiasen and Kenaley (2019). However, occasionally the female plants, and rarely the male plants, of subsp. *magnificae* were green-brown, particularly at the northern end of its geographic range. The bluish-green to reddish-brown color of the plants of subsp. *mathiasenii* is a distinctive character of this dwarf mistletoe, but there was a large amount of variation in the color of both staminate and pistillate plants within and among different populations. However, some plants of subsp. *mathiasenii* were nearly red on the North Rim of the Grand Canyon, a characteristic not observed for plants of subsp. *abietinum*, *grandae*, and *magnificae* (Hawksworth & Wiens 1996; Mathiasen 2011; Table 3). However, red plants have been frequently observed for *A. abietinum* subsp. *wiensii* (Mathiasen & Daugherty 2009).

Staminate flowers of *Arceuthobium abietinum* subsp. *mathiasenii* were significantly larger in size (both 3- and 4-merous flowers) than those of subsp. *abietinum*, subsp. *grandae*, subsp. *magnificae*, and subsp. *wiensii* (Tables 1 & 2). Hawksworth and Wiens (1972, 1996) reported that staminate flower diameters of *A. abietinum* were 2.5 mm, so this must have been for 3-merous flowers because Mathiasen (2011) reported that 3-merous flower diameters averaged 2.7 and 2.6 mm for *A. abietinum* subsp. *abietinum* and subsp. *magnificae*, respectively. The mean diameter of 3-merous staminate flowers for subsp. *mathiasenii* in this study was 3.1 mm. Hawksworth and Wiens did not report flower diameters for 4-merous flowers; however, the mean diameter of 4-merous flowers was also larger for subsp. *mathiasenii* (4.1 mm) than that reported by Mathiasen (2011) for subsp. *abietinum* and subsp. *magnificae* (approximately 3.7 mm). Staminate flowers of subsp. *mathiasenii* are much larger than those of subsp. *wiensii* (Table 1). Likewise, fruit length of *A. abietinum* subsp. *mathiasenii* was greater when compared with subsp. *wiensii*; but, similar to those of subspp. *grandae* and *magnificae*, and slightly

Table 4. Forward, stepwise discriminant function analysis (DFA): classification of female and male plants of *Arceuthobium abietinum* subspecies *abietinum, grandae, magnificae, mathiasenii,* and *wiensii* 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]])	Correct taxon membership (%, [N predicted/ N field determined])					
	Total	*Arceuthobium abietinum* subsp.				
		abietinum	*grandae*	*magnificae*	*mathiasenii*	*wiensii*
Female						
1. [PH]	31.5 [375/1192]	39.7 [115/290]	33.9 [99/292]	0.0 [0/160]	27.0 [81/300]	53.3 [80/150]
2 [*], [WTI]	40.6 [484/1192]	26.9 [78/290]	51.0 [149/292]	30.0 [48/160]	43.0 [129/300]	53.3 [80/150]
3 [*], [*], [FL]	46.1 [550/1192]	43.1 [125/290]	52.4 [153/292]	13.1 [21/160]	53.0 [159/300]	61.3 [92/150]
4 [*], [*], [*], [FW]	46.9 [559/1192]	42.1 [122/290]	52.4 [153/292]	26.9 [43/160]	49.3 [148/300]	62.0 [93/150]
5 [*], [*], [*], [*], [LTI]	50.2 [598/1192]	40.3 [117/290]	54.5 [159/292]	35.6 [57/160]	54.0 [162/300]	68.7 [103/150]
6 [*], [*], [*], [*], [*],[SL]	52.0 [620/1192]	43.1 [125/290]	56.2 [164/292]	37.5 [60/160]	55.7 [167/300]	69.3 [104/150]
7 [*], [*], [*], [*], [*],[*], [SW]	54.9 [655/1192]	43.8 [127/290]	57.5 [168/292]	41.9 [67/160]	63.0 [189/300]	69.3 [104/150]
8 [*], [*], [*], [*], [*],[*], [*], [BD]	56.2 [670/1192]	44.8 [130/290]	58.6 [171/292]	43.8 [70/160]	63.7 [191/300]	72.0 [108/150]
Male						
1 [SSW]	38.6 [510/1322]	14.8 [37/250]	45.0 [127/282]	11.2 [37/330]	58.7 [176/300]	83.1 [133/160]
2 [*], [PH]	46.5 [615/1322]	32.4 [81/250]	35.8 [101/282]	21.8 [72/330]	77.3 [232/300]	80.6 [129/160]
3 [*, [*], [ADT]	49.8 [659/1322]	36.0 [90/250]	48.6 [137/282]	24.2 [80/330]	74.0 [222/300]	81.3 [130/160]
4 [*], [*], [*], [PL]	52.3 [691/1322]	37.2 [93/250]	58.2 [164/282]	25.2 [83/330]	74.0 [222/300]	80.6 [129/160]
5 [*], [*], [*], [*], [BD]	55.4 [733/1322]	36.0 [90/250]	62.8 [177/282]	30.0 [99/330]	77.0 [231/300]	85.0 [136/160]
6 [*], [*], [*], [*], [*], [WTI]	57.6 [761/1322]	44.0 [110/250]	64.9 [183/282]	28.5 [94/330]	78.3 [235/300]	86.9 [139/160]
7 [*], [*], [*], [*], [*], [*], [LTI]	59.8 [791/1322]	46.8 [117/250]	68.4 [193/282]	33.3 [110/330]	78.0 [234/300]	85.6 [137/160]
8 [*], [*], [*], [*], [*], [*], [*], [PW]	60.9 [805/1322]	48.0 [120/250]	67.7 [191/282]	37.0 [122/330]	76.7 [230/300]	88.8 [142/160]
9 [*], [*], [*], [*], [*], [*], [*], [*], [SSL]	62.4 [825/1322]	50.0 [125/250]	68.1 [192/282]	41.5 [137/330]	74.7 [224/300]	91.9 [147/160]
10 [*], [*], [*], [*], [*], [*], [*], [*], [*], [AD]	63.4 [838/1322]	51.2 [128/250]	68.4 [193/282]	42.7 [141/330]	76.0 [228/300]	92.5 [148/160]

Table 5. Means and 95% confidence intervals for morphological characters according to predicted subspecies membership based on full-model, quadratic discriminant function analysis for female and male plants. Plant height is in cm whereas all other mean measurements by character are in mm.

Sex / Character	Taxa classified via discriminant function analysis *Arceuthobium abietinum* subsp.				
	abietinum	*grandae*	*magnificae*	*mathiasenii*	*wiensii*
Female					
Plant height (PH)	14.7 ± 0.5	11.7 ± 0.2	13.5 ± 0.4	9.1 ± 0.2	9.5 ± 0.3
Basal diameter (BD)	4.1 ± 0.1	3.0 ± 0.1	3.6 ± 0.1	3.0 ± 0.1	3.2 ± 0.1
Length of third internode (LTI)	17.9 ± 0.6	14.6 ± 0.1	18.7 ± 0.4	12.6 ± 0.3	14.9 ± 0.5
Width of third internode (WTI)	2.5 ± 0.1	1.9 ± 0.0	2.5 ± 0.0	2.2 ± 0.0	2.0 ± 0.0
Fruit length (FL)	5.0 ± 0.1	4.7 ± 0.0	4.7 ± 0.1	4.7 ± 0.0	4.2 ± 0.1
Fruit width (FW)	3.0 ± 0.0	3.0 ± 0.0	3.0 ± 0.1	3.0 ± 0.0	2.9 ± 0.0
Seed length (SL)	2.6 ± 0.0	2.5 ± 0.0	2.4 ± 0.0	2.4 ± 0.0	2.4 ± 0.0
Seed width (SW)	1.2 ± 0.0	1.1 ± 0.0	1.1 ± 0.0	1.2 ± 0.0	1.1 ± 0.0
Male					
Plant height (PH)	12.7 ± 0.4	11.3 ± 0.3	11.9 ± 0.3	9.3 ± 0.3	8.9 ± 0.4
Basal diameter (BD)	3.3 ± 0.1	2.9 ± 0.1	3.3 ± 0.1	2.8 ± 0.1	3.1 ± 0.1
Length of third internode (LTI)	16.0 ± 0.5	13.7 ± 0.4	15.4 ± 0.4	12.6 ± 0.4	13.5 ± 0.5
Width of third internode (WTI)	2.4 ± 0.0	2.0 ± 0.0	2.2 ± 0.0	2.2 ± 0.0	1.9 ± 0.0
Petal length (PL)	1.4 ± 0.0	1.4 ± 0.0	1.4 ± 0.0	1.5 ± 0.0	1.2 ± 0.0
Petal width (PW)	1.2 ± 0.0	1.2 ± 0.0	1.2 ± 0.0	1.3 ± 0.0	1.0 ± 0.0
Anther diameter (AD)	0.6 ± 0.0	0.5 ± 0.0	0.6 ± 0.0	0.6 ± 0.0	0.5 ± 0.0
Anther distance from tip (ADT)	0.6 ± 0.0	0.5 ± 0.0	0.5 ± 0.0	0.6 ± 0.0	0.6 ± 0.0
Staminate spike length (SSL)	9.9 ± 0.3	9.9 ± 0.3	9.7 ± 0.3	11.4 ± 0.4	8.8 ± 0.4
Staminate spike width (SSW)	2.0 ± 0.0	1.9 ± 0.0	2.1 ± 0.0	2.4 ± 0.0	1.5 ± 0.0

Table 6. Standard discriminant function (DFA): assignment of field diagnosed female and male plants of *Arceuthobium abietinum* subspecies *abietinum*, *grandae*, *magnificae*, *mathiasenii*, and *wiensii* utilizing 8 female and 10 male characters (full-model per plant sex) as well as equal prior probability per taxon (0.20).

Plant sex / *Arceuthobium* taxon (Total N = field determined plants)	Taxon classification (%) [N= field determined plants] via full-model DFA *Arceuthobium abietinum* subsp.				
	abietinum	*grandae*	*magnificae*	*mathiasenii*	*wiensii*
Female - 8 morphological characters					
A. abietinum					
subsp. *abietinum* (290)	**44.8 [130]**	17.2 [50]	17.2 [50]	16.9 [49]	3.8 [11]
subsp. *grandae* (292)	11.6 [34]	**58.6 [171]**	8.6 [25]	10.3 [30]	11.0 [32]
subsp. *magnificae* (160)	13.8 [22]	13.8 [22]	**43.8 [70]**	18.8 [30]	10 [16]
subsp. *mathiasenii* (300)	4.3 [13]	10.0 [30]	10.7 [32]	**63.7 [191]**	11.3 [34]
subsp. *wiensii* (150)	0.7 [1]	5.3 [8]	6.0 [9]	16.0 [24]	**72.0 [108]**
Male - 10 morphological characters					
subsp. *abietinum* (250)	**51.2 [128]**	18.4 [46]	13.2 [33]	14.0 [35]	3.2 [8]
subsp. *grandae* (282)	11.3 [32]	**68.4 [193]**	9.9 [28]	5.3 [15]	5.0 [14]
subsp. *magnificae* (330)	16.1 [53]	22.4 [74]	**42.7 [141]**	13.6 [45]	5.2 [17]
subsp. *mathiasenii* (300)	5.3 [16]	9.7 [29]	6.3 [19]	**76.0 [228]**	2.7 [8]
subsp. *wiensii* (160)	1.2 [2]	4.4 [7]	1.3 [2]	0.6 [1]	**92.5 [148]**

less when compared to subsp. *abietinum* (Tables 1 & 2). The color of fruits for subsp. *mathiasenii* was green-brown to green, while the color of fruits for both special forms was consistently green. The mean length of seeds of subsp. *mathiasenii* and subsp. *wiensii* were smaller than those of the other subspecies, but were not significantly different.

The principal hosts of *Arceuthobium abietinum* subsp. *mathiasenii* are Rocky Mountain white fir and Durango fir. There have only been four locations reported for this dwarf mistletoe on Durango fir in the Sierra Madre Occidental; two in Chihuahua and two in Durango, Mexico (Hawksworth & Wiens 1996; Quiñonez

Table 7. Canonical statistics for standard discriminant function analyses (DFA) of female and male plants of *Arceuthobium abietinum* subspecies *abietinum, grandae, magnificae, mathiasenii,* and *wiensii*. DFAs were executed using a full-model (N= 8 female or 10 male characters) and equal prior probabilities (0.20). Canonical details according to plant sex are subdivided by analyses performed on the complete and randomized resampled (50 complete records/species) datasets.

Canonical	Eigenvalue	Percentage	Cumulative percentage	Canonical correlation	Likelihood Ratio	Approximant F	P-value
Female - Complete							
1	0.58	57.11	57.11	0.6057	0.4272	$F_{32, 4353.2}$= 35.28	<.0001
2	0.28	28.02	85.14	0.4705	0.6748	$F_{21, 3391.7}$= 23.71	<.0001
3	0.13	12.39	97.53	0.3342	0.8666	$F_{12, 2364}$= 14.62	<.0001
4	0.03	2.47	100.00	0.1563	0.9756	$F_{5, 1883}$= 5.92	<.0001
Female - Resampled							
1	0.72	60.88	60.88	0.6472	0.3815	$F_{32, 879.3}$= 8.20	<.0001
2	0.26	21.84	82.72	0.4532	0.6565	$F_{21, 686.8}$= 5.16	<.0001
3	0.17	14.39	97.11	0.3815	0.8262	$F_{12, 480}$= 4.01	<.0001
4	0.03	2.89	100.00	0.1817	0.9670	$F_{5, 241}$= 1.65	0.1484
Male - Complete							
1	0.98	61.47	61.47	0.7034	0.2960	$F_{40, 4961.6}$= 46.96	<.0001
2	0.41	25.90	87.37	0.5405	0.5859	$F_{27, 3823.6}$= 28.45	<.0001
3	0.16	9.85	97.22	0.3683	0.8277	$F_{16, 2620}$= 16.24	<.0001
4	0.04	2.78	100.00	0.2058	0.9577	$F_{7, 1311}$= 8.28	<.0001
Male - Resampled							
1	1.48	61.42	61.42	0.7725	0.1884	$F_{40, 896.7}$= 12.40	<.0001
2	0.64	26.63	88.05	0.6252	0.4672	$F_{27, 692.8}$= 7.64	<.0001
3	0.21	8.80	96.85	0.4183	0.7669	$F_{16, 476}$= 4.22	<.0001
4	0.08	3.15	100.00	0.2656	0.9295	$F_{7, 239}$= 2.59	0.0136

Table 8. Standard discriminant function analysis (DFA) of female (N= 8 characters) and male morphologies (N= 10 male characters) of *Arceuthobium abietinum* subspecies *abietinum, grandae, magnificae, mathiasenii,* and *wiensii*: 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. 4	Can. 1	Can. 2	Can. 3	Can. 4
PH	0.94	-0.51	-0.61	-0.30	0.08	-0.98	-0.16	0.29
BD	-0.16	-0.24	0.21	0.92	-0.40	0.18	0.51	-0.86
LTI	-0.20	-0.22	0.79	-0.57	-0.18	0.12	0.43	-0.20
WTI	-0.02	0.97	0.59	-0.16	0.46	0.05	0.22	0.94
FL	0.85	0.51	-0.37	0.15				
FW	-0.56	-0.27	0.38	-0.23				
SL	0.28	-0.50	0.25	0.65				
SW	-0.17	0.56	-0.15	-0.15				
PL					0.36	-0.45	-0.10	-0.37
PW					0.30	0.03	-0.18	0.20
AD					-0.03	0.10	-0.06	0.03
ADT					-0.41	0.71	0.57	0.39
SSL					0.05	0.09	-0.21	0.21
SSW					0.71	0.10	0.15	-0.55

2016) (Fig. 1). Mathiasen's dwarf mistletoe occasionally infects Mexican spruce (*Picea mexicana*) on Cerro Mohinora in Chihuahua, Mexico (Mathiasen 2010) and rarely infects what has been identified as Mexican white pine (*Pinus ayacahuite* C. Ehrenb. ex Schltdl.) in northern Chihuahua (Hawksworth & Wiens 1996). However, the white pine populations found in Chihuahua are now recognized as southwestern white pine (*Pinus strobiformis*) (Frankis 2009; Moreno-Letelier & Piñero 2009).

The reddish-brown color of plants of *Arceuthobium abietinum* subsp. *mathiasenii* is similar to that of Wiens' dwarf mistletoe (Mathiasen & Daugherty 2009). Although these subspecies have plants that are closer to each other in size, they differ in several other morphological characteristics, particularly flower diameter and fruit length (Table 1). Wiens' dwarf mistletoe primarily parasitizes Brewer spruce and red fir in southwestern Oregon and northwestern California, while Mathiasen's dwarf mistletoe is a parasite of Rocky Mountain white fir in the southwestern U.S. and Durango fir in northern Mexico. However, both of these subspecies of fir dwarf mistletoe parasitize spruce, white firs, and white pines to some extent (Table 3).

The geographic range of *Arceuthobium abietinum* subsp. *mathiasenii* does not overlap with subspp. *abietinum*, *grandae*, *magnificae*, or *wiensii*. The closest populations of the latter two taxa to subsp. *mathiasenii* are on the southern end of the Sierra Nevada Mountains in Tulare County south of Sequoia National Park, approximately 250 km west of the Spring Mountains, Nevada (Fig. 1). Subspecies *mathiasenii* only occurs in small, isolated populations in Nevada, Utah, Arizona, and northern Mexico although its principal host, Rocky Mountain white fir is common in the mountains of the Southwest. The area with the most populations of subsp. *mathiasenii* is the North Rim of the Grand Canyon. The reasons why subsp. *mathiasenii* has only survived in a few, widely isolated populations are unclear, but is probably related to the environmental conditions present which have limited the occurrence of stand-replacing wildfires at each location. It is possible that additional populations of subsp. *mathiasenii* 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.

Like Mathiasen's dwarf mistletoe, grand fir dwarf mistletoe—*Arceuthobium abietinum* subsp. *grandae*—is morphologically distinct from subspp. *abietinum* and *wiensii,* while, sharing morphological similarities with subsp. *magnificae*, including fruit dimensions and staminate flower diameters (Tables 1–3, 5 & 6; Fig. 4). In addition to clear distinctions in principal host(s), discussed below, *A. abietinum* subsp. *grandae* is delimited readily from subsp. *magnificae* by plant color as female and male plants of subsp. *grandae* typically are green-brown and yellow or yellow-green, respectively; whereas, the shoots of subsp. *magnificae* are yellow-green-brown to red. Morphological analyses executed herein revealed that the grand fir and red fir dwarf mistletoes can be discriminated and determined by direct comparison of female plant height, third internode dimensions, staminate spike length and width as well as anther length and distance to tip (Tables 1–2). Likewise, mean measurements for female and male plants of subsp. *grandae* were significantly different across ≥13 of 20 total characteristics when compared directly to the other subspecies. Standard DFA using complete data for female and male plants supported univariate analyses—correctly classifying 58.6% (171/292) of female plants and 68.4% (193/282) male plants of subspecies *grandae* (Table 6). Stepwise-DFA of female and male plant parts also demonstrated that >52% of field-identified grand fir dwarf mistletoe was predicted to subspecies *grandae* utilizing only four female or male characteristics (Table 4). Female morphology contributing most to the prediction of subspecies of *A. abietinum* were plant height, width of the third internode, and fruit dimensions; whereas, the staminate spike width, plant height, anther distance to the tip, and petal length contributed most to the discriminant function for predicting male plants to subspecies (Table 8). The latter morphologies were also the most statistically important morphologies reported by Mathiasen and Kenaley (2019), justifying subspecies *abietinum* and *magnificae* and the continued recognition of subsp. *wiensii*.

Multivariate means and 95% confidence ellipses for female plants of grand fir dwarf mistletoe were also discretely different and non-overlapping in multidimensional space when compared to other subspecies of *A. abietinum* utilizing a full-model DFA with complete data (Fig. 4A). Although the 95% confidence ellipse for the multivariate mean of female plants for subsp. *grandae* and *magnificae* overlapped when the DFA was executed with resampled data (50 complete records per taxon; Fig. 4C), female plants of grand fir dwarf mistletoe were effectively classified to subsp. *grandae* (60%, 30/50) and were occasionally misclassified to subsp. *abietinum* (12%, 6/50) followed by subspp. *mathiasenii* (10%; 5/50) and *wiensii* (10%; 6/50). Female plants of grand fir dwarf mistletoe were rarely misclassified to subsp. *magnificae* when executing DFA with either complete (8.6%, 25/292) or resampled data (8.0%, 4/50). Similarly, standard DFA with complete male data revealed the multivariate mean for male plants of subsp. *grandae* was discrete when compared to male plants of the other subspecies, while the 95% confidence ellipse overlapped slightly with only subsp. *abietinum* (Fig. 4B). The same DFA, however, only occasionally assigned subsp. *grandae* to subspp. *abietinum* (11.3%, 32/282) and *magnificae* (9.9%, 28/282) or rarely to subsp. *mathiasenii* (5.3%, 15/282) and *wiensii* (5.0%, 14/282) (Table 6). Moreover, validation of the male full-model yielded considerable overlap among the 95% confidence ellipses corresponding to multivariate means of subspp. *grandae*, *abietinum*, and *magnificae*. However, the multivariate means per subspecies were discrete in multidimensional space using resampled data and subsp. *grandae* was only occasionally classified to subsp. *magnificae* (14%, 7/50) and rarely assigned to subsp. *abietinum* (6%; 3/50).

In addition to plant color and morphology, *Arecuthobium abietinum* subsp. *grandae* is easily distinguished from the other infraspecific taxa of *A. abietinum* by its host range (Table 3) and geographic distribution (Fig. 1). *Arceuthobium abietinum* subsp. *grandae* is a principal parasite of grand fir and hybrid intermediates of grand fir and white fir in southern Washington (Klickitat, Skamania, and Yakima counties) through the Oregon Cascades to its southernmost limit in the Cascade Mountains of northern California near Mount Shasta (Siskiyou and Shasta counties). Populations of grand fir dwarf mistletoe also occur in the Warner Mountains (Modoc County) in northeastern California as well as along the coast in northwestern California (Humboldt and Mendocino counties) and south in the Coast Ranges of western California to the vicinity of Snow Mountain in northwestern Colusa County. The geographic distributions of subsp. *grandae* and subsp. *magnificae* do overlap in northern California near Mount Shasta (Figs. 1 & 2) (Hawksworth & Wiens 1996). However, subsp. *magnificae* exclusively parasitizes red fir, whereas, subsp. *grandae* does not (Hawksworth & Wiens 1996). If the *Abies* host is questionable (grand fir vs. red fir), morphological discontinuities, such as differences in female plant height, third internode dimensions as well as staminate spike dimensions separate these two subspecies.

The principal characters for the classification of subspecies in *Arceuthobium* has long been based on differences in plant size, geographic distribution, and host range (Hawksworth & Wiens 1972, 1996; Hawksworth et al. 1992; Wass & Mathiasen 2003; Mathiasen 2007, 2008; Mathiasen & Daugherty 2007, 2009; Scott & Mathiasen 2009; Mathiasen & Kenaley 2017, 2019). These are the principal characteristics that distinguish *Arceuthobium abietinum* subsp. *mathiasenii* from *A. abietinum* subsp. *grandae* as well the latter two taxa when compared to *A. abietinum* subsp. *abietinum*, subsp. *magnificae,* and subsp. *wiensii*.

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