MORPHOLOGICAL EVIDENCE FOR CONTINUED SPECIES RECOGNITION AMONG WHITE PINE DWARF MISTLETOES (VISCACEAE): *ARCEUTHOBIUM APACHECUM*, *A. BLUMERI, A. CALIFORNICUM*, *A. CYANOCARPUM*, AND *A. MONTICOLA*

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ABSTRACT

Field identification of dwarf mistletoes (*Arceuthobium*; Viscaceae) often is complicated due to their reduced morphology and sexual dimorphism, requiring the integration of not only morphologic measurements, but also, geographic, host, and/or phenological data. Difficulties in species determination have plagued the taxonomic classification of closely-related *Arceuthobium*, and, hence, their recognition as distinct species has also been questioned. Troubles in the classification of *Arceuthobium* are typified by five taxas in section *Campylopoda*, ser. *Campylopoda*—*A. apachecum*, *A. blumeri*, *A. californicum*, *A. cyanocarpum*, and *A. monticola*—that infect white pines (*Pinus*; subg. *Strobus*) as principal hosts. Each of the aforementioned taxa recently were circumscribed in synonymy with or reduced to subspecies of *A. campylopodum*; we contend that they deserve separate species recognition. To support our position, we conducted morphological analysis for these six taxa using univariate and multivariate statistical approaches. Results demonstrated that *Arceuthobium apachecum*, *A. blumeri*, *A. californicum*, *A. cynanocarpum*, and *A. monticola* can be determined readily to species using morphological data without consideration of geographic location or host specificity. Moreover, all but two of 20 morphological characters across female and male plants of the white pine dwarf mistletoes were significantly different when compared to *A. campylopodum*. Female and male plants of the latter species were also easily segregated from each of the white pine dwarf mistletoes in the combined analysis of only three characters. Thus, the white pine dwarf mistletoes are well-differentiated morphologically, and therefore, should be considered distinct species.

KEY WORDS: dwarf mistletoes, morphology, *Pinus flexilis, Pinus lambertiana, Pinus monticola, Pinus strobiformis*.

RESUMEN

La identificación en campo de los muérdagos enanos (*Arceuthobium*; Viscaceae) es a menudo complicada debido a su morfología reducida y dimorfismo sexual, por lo que se requiere una integración no solo de medidas morfológicas, sino también, de datos geográficos, hospedador, y/o fenológicos. Las dificultades en la determinación de especies han plagado la clasificación taxonómica de *Arceuthobium* muy relacionados, y en consecuencia, su reconocimiento como especies distintas se ha cuestionado también. Los problemas en la clasificación de *Arceuthobium* están tipificados por cinco taxa en la sección *Campylopoda*, ser. *Campylopoda*—*A. apachecum*, *A. blumeri*, *A. californicum*, *A. cyanocarpum*, y *A. monticola*—que infectan a los pinos blancos (*Pinus*; subg. *Strobus*) como huéspedes principales. Cada uno de los taxa mencionados se circunscribieron recientemente en sinonimia con, o reducidos a subespecies de *A. campylopodum*; nosotros sostenemos que deben reconocerse como especies separadas. Para apoyar nuestra posición, llevamos a cabo un análisis morfológico de estos seis taxa usando enfoques estadísticos univariados y multivariados. Los resultados demuestran que *Arceuthobium apachecum*, *A. blumeri*, *A. californicum*, *A. cynanocarpum*, y *A. monticola* se pueden determinar fácilmente como especies usando datos morfológicos sin consideración de la localización geográfica o la especifidad del huésped. Más aún, todos excepto dos de 20 caracteres morfológicos en plantas femeninas y masculinas de los muérdagos sobre pinos blancos fueron diferentes significativamente cuando se compararon con *A. campylopodum*. Las plantas femeninas y masculinas de la última especie también se separaron fácilmente en cada muérdago enano en el análisis combinado de solo tres caracteres. Así, los muérdagos enanos de los pinos blancos están bien diferenciados morfológicamente, y por ello, deben ser considerados como especies distintas.

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Angiospermous plants in the genus *Arceuthobium* M. Bieb. (Viscaceae)—the dwarf mistletoes—are aerial, obligate parasites of members in the family Pinaceae throughout North America, particularly in coniferous forests of the western United States and northern Mexico (Hawksworth & Wiens, 1996). Severe dwarf mistletoe infection is associated with growth loss, premature mortality, reduced seed and cone development, and attack by insects and pathogens (Geils & Hawksworth 2002; Parker et al. 2006; Kenaley et al. 2006, 2008). Dwarf mistletoes are, therefore, considered important ecological agents influencing forest composition, ecosystem services (e.g., wildlife habitat), and overall productivity (Drummond 1982; Hawksworth & Shaw 1984; Hawksworth 1991; Geils & Hawksworth 2002). Although their ecological role as serious pathogens in coniferous forests of western North America has long been recognized, particularly on commercially important timber species, the classification of the dwarf mistletoes in section *Campylopoda* Hawksw. & Wiens, series *Campylopoda* continues to be one of the most controversial and contested taxonomic questions in *Arceuthobium* (Hawksworth & Wiens 1972, 1984, 1996; Nickrent 2012; Mathiasen & Kenaley 2015a, 2015b; Reif et al. 2015; Kuijt 2016; Mathiasen & Kenaley 2016). Five dwarf mistletoes in ser. *Campylopoda* that parasitize white pines (*Pinus*: subg. *Strobus* (Lemmon) A.E. Murray; Price et al. 1998) as principal hosts in the western U.S. and/or northern Mexico include *A. apachecum* Hawksw. & Wiens (Apache dwarf mistletoe), *A. blumeri* A. Nelson (Blumer's dwarf mistletoe), *A. californicum* Hawksw. & Wiens (sugar pine dwarf mistletoe), *A. cyanocarpum* (A. Nelson ex Rydb.) J.M. Coult. & A. Nelson (limber pine dwarf mistletoe), and *A. monticola* Hawksw., Wiens & Nickrent (western white pine dwarf mistletoe). Hawksworth and Wiens (1972, 1996) maintained that these parasites of white pines can be delimited to species from western dwarf mistletoe (*A. campylopodum* Engelm.)—a principal parasite of ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson) and Jeffrey pine (*P. jeffreyi* Grev. & Balf.)—via differences among taxonomically informative characters including male and female plant morphology, host specificities, and phenology. However, for the treatment of *Arceuthobium* in the second edition of *The Jepson manual: vascular plants of California* (TJM2), Kuijt (2012) circumscribed *A. californicum*, *A. cyanocarpum*, and *A. monticola* as well as six additional *Arceuthobium* spp. in synonymy with *A. campylopodum*. The classification proposed by Kuijt (2012) is a radical departure from the original treatment of Californian dwarf mistletoes in the first edition of *The Jepson manual: higher plants of California* (TJM1) provided by Hawksworth and Wiens (1993), effectively ignoring more than one century of field and laboratory studies of *Arceuthobium* in California and elsewhere in North America (Mathiasen & Kenaley 2016). However, Kuijt (2016) recognized the taxonomic challenges of taxa in ser. *Campylopoda* taxa, asserting that additional investigations into host specificities and population variation are needed to further justify the recognition of these taxa at the specific or subspecific level.

George Engelmann first described *A. campylopodum* in 1850 based on a specimen collected from ponderosa pine, likely from northeastern Washington State (Gray 1850; Gill 1935; Hawksworth & Wiens 1996). In 1906, Aven Nelson described *A. cyanocarpum* (as *Razoumofskya cyanocarpa*) in Rydberg (1906) and Coulter and Nelson (1909) used the latter combination which has been conserved to present day (Reif et al. 2015). Likewise, Nelson described *A. blumeri*, in honorarium to J. C. Blumer, on southwestern white pine (*Pinus strobiformis* Engelm.) in the Huachuca Mountains in extreme southern Arizona (Nelson 1913). Over a half-century later, Hawksworth and Wiens (1970) described two additional white pine dwarf mistletoes: *A. apachecum* on southwestern white pine collected in the Santa Catalina Mountains near Mt. Lemmon in southeastern Arizona and *A. californicum* infecting sugar pine (*Pinus lambertiana* Douglas) in the vicinity of Fish Camp, CA in the central Sierra Nevada Mountains. Even though they are not sympatric, *A. apachecum* commonly has been misidentified to *A. blumeri* since, as noted previously, both species infect southwestern white pine in southern Arizona (Mathiasen 1982). Moreover, Hawksworth and Wiens (1972) later revised the host range of *A. californicum* to include western white pine (*Pinus monticola* Douglas ex D. Don) as a secondary host of *A. californicum* and Brewer spruce (*Picea breweriana* S. Watson) as an occasional host. Mathiasen and Hawksworth (1988) later reported the frequency of infection and tree mortality associated with *A. californicum* sensu lato parasitizing sugar pine and western white pine in northern CA and southwestern Oregon; they observed that the frequency of infection and incidence of mortality for western white pine was much greater than what had been

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previously reported. Thereafter, Nickrent and Butler (1990) clearly demonstrated the dwarf mistletoe populations on western white pine in southwestern Oregon and northwestern California were genetically divergent from *A. californicum* and *A. campylopodum* via allozymic analyses. With additional molecular data and field studies, Hawksworth, Wiens, and Nickrent (1992) formally recognized the dwarf mistletoe on western white pine in the Klamath Ranges as a distinct species, *A. monticola*, segregating it from *A. californicum*.

Although Hawksworth and Wiens (1996), as well as Hawksworth et al. (2002), maintained that the morphological and physiological differences between those six dwarf mistletoes clearly supported their classification as species, molecular phylogenetic analyses using nuclear ribosomal DNA (full-length, internal transcribed spacer [ITS] region) and chloroplast *trn T-L-F* sequences indicated these species may be conspecific (Nickrent et al. 2004). More recently, Nickrent (2012) favored his aforementioned phylogenetic study despite contradictory evidence (Nickrent & Bulter 1990) and, regardless, recombined all dwarf mistletoes parasitizing white pines as principal hosts as subspecies of *A. campylopodum*. Nickrent (op. cit.) suggested that taxa in ser. *Campylopoda* represent ecotypes (Clausen et al. 1940) of a variable species delimited by principal host(s) (i.e., environment[s]) and recombined seven additional species of dwarf mistletoe under *A. campylopodum*, for which he recognized a total of 13 subspecies. Because of Nickrent's treatment and Kuijt's (2012) grouping of white pine-infecting dwarf mistletoes in California under *A. campylopodum*, we collected additional morphological data from throughout the geographic ranges of these dwarf mistletoes and then combined univariate and multivariate analyses to obtain a more robust statistical comparison of the morphological characteristics among these dwarf mistletoes. The primary aim of our work was to determine if male and female plants of each white pine dwarf mistletoe—*A. apachecum*, *A. blumeri*, *A. californicum*, *A. cyanocarpum*, and *A. monticola*—can be delimited from *A. campylopodum* and interspecifically among each other regardless of host specificity utilizing only morphological and phenological characters. Recent studies have conducted morphologic analyses of *A. apachecum*, *A. blumeri*, and *A. cyanocarpum* (Reif et al. 2015) as well as *A. monticola* (Mathiasen & Daugherty 2009); however, to the best of our knowledge, no study to date has assessed concomitantly the interspecific morphological discontinuities among these five white pine dwarf mistletoes and their morphologic dissimilarity/similarity to *A. campylopodum*.

METHODS

Morphology and Phenology

We sampled 60 populations of *Arceuthobium campylopodum* throughout its geographic range consisting of 30 populations on ponderosa pine and 30 populations on Jeffrey pine (Fig. 1; Mathiasen & Kenaley 2015). Morphological data collected by Reif et al. (2015) were used for *A. apachecum*, *A. blumeri*, and *A. cyanocarpum* (Fig. 2 and Fig. 3) whereas data collected by Mathiasen and Daugherty (2009) were used for *A. monticola* (Fig. 4). Additional morphological measurements were made in 2012 for *A. apachecum* from near Carnero Lake, Arizona (RLM 1293) and for *A. cyanocarpum* from Lee Canyon in the Spring Mountains, Nevada (RLM 1294). New measurements were also completed in 2013 for *A. cyanocarpum* from Green Creek Canyon on the east side of the Sierra Nevada Mountains (RLM 1322). In addition, 14 populations of *A. californicum* were sampled from throughout its geographic range in California in 2009-2011 specifically for this study (Fig. 4). Voucher specimens consisting of the mistletoe with host material were deposited at the Deaver Herbarium, Northern Arizona University, Flagstaff (ASC), or the University of Arizona Herbarium, Tucson (ARIZ). Voucher and specific population data, including GPS coordinates, were electronically archived via the Southwest Environmental Information Network (SEINet: http://swbiodiversity.org/seinet/).

For each mistletoe population, 10-20 male and 10-20 female infections were randomly collected and the dominant (largest) shoot from each infection was used for morphological measurements. We chose to collect the dominant plant from each infection to standardize measurements across populations and taxa. Morphologic characters measured were those most commonly used for the taxonomic classification of *Arceuthobium* (Hawksworth & Wiens 1996), including: 1) plant height, basal diameter, length and width of the third internode, and shoot (plant) color; 2) mature fruit length, width, and color; 3) seed length, width, and color; 4) sta-

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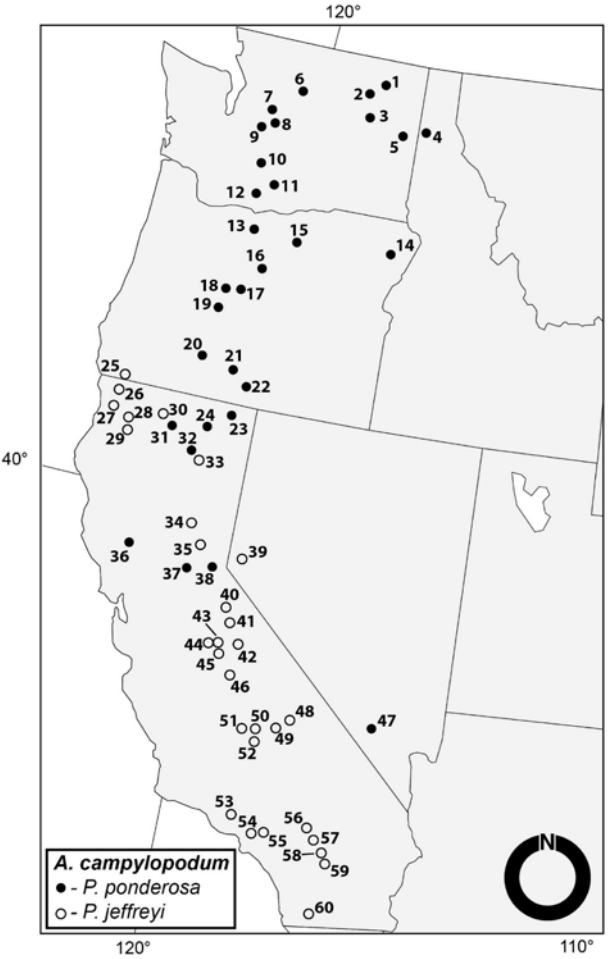

Fig. 1. Approximate location of collection sites for *Arceuthobium campylopodum*. Solid circles present locations where plants were collected from *Pinus ponderosa*. Open circles represent locations where plants were collected from *P. jeffreyi*. **1**—4.5 km N of Gifford on St. Rte. 25; **2**—20 km S of Fruitland on St. Rte. 25; **3**—2 km NW of Nespelem on St. Rte. 155; **4**—2.3 km N of Coeur d'Alene on Fernan Lake rd.; **5**—16 km S of Spokane on St. Rte. 195; **6**—2.5 km W of St. Rte. 153 on Squaw Creek rd.; **7**—Lake Wenatchee on Chiwawa River Loop rd.; **8**—2.6 km W of Squilchuck St. Park on road to Mission Ridge Ski Area; **9**—0.8 km W of St. Rte. 97 on St. Rte 970; **10**—17.6 km E of White Pass on St. Rte. 12; **11**—2 km N of Satus Pass on St. Rte. 97; **12**—3 km S of Trout Lake on St. Rte. 141; **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; **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; **25**—6 km S of Takilma on Greyback rd.; **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 Lake on Pillsbury Lk. rd.; **37**—7.7 km N of Pollock Pines on forest rd. 4; **38**—at entrance to Sugar Pine State Park, west shore of Lk. Tahoe; **39**—Bowers Mansion St. Park, near pool area; **40**—1 km N of Markleeville on St. Rte. 89; **41**—Silver Creek Campground on St. Rte. 4; **42**—Column of the Giants on St. Rte. 108; **43**—Pinecrest Transfer Station 0.5 km W of Pinecrest on St. Rte. 108; **44**—1 km W of Long Barn on St. Rte. 108; **45**—8.5 km E of Crane Flat on St. Rte. 120; **46**—2 km W of Big Creek on rd. to Shaver Lk.; **47**—4.1 km W of Ranger Station at Old Ski Tow Historic Site, Kyle Canyon; **48**—8.5 km W of Sherman Pass on forest rd. 22S05; **49**—2.2 km S of Troy Mdws. Campground, Sequoia Nat. For.; **50**—5.8 km N of rd. to Johnsonville on Western Divide Highway; **51**—Pine Flat, Sequoia Nat. For.; **52**—Tiger Flat, Sequoia Nat. For.; **53**—6.2 km S of St. Rte. 33 on rd. to Mt. Reyes; **54**—1.4 km W of Cloud Burst on St. Rte. 2; **55**—1 km W of Big Pines on St. Rte. 2; **56**—2.4 km N of Fawnskin on forest rd. 2N71; **57**—1.9 km from St. Rte. 38 on rd. to Jenks Lk.; **58**—near Ranger Station in Idylwild; **59**—1.1 km S of the S Fork San Jacinto River Bridge on St. Rte. 74; **60**—0.5 km S of Horse Heaven Campground on Sunrise Highway.

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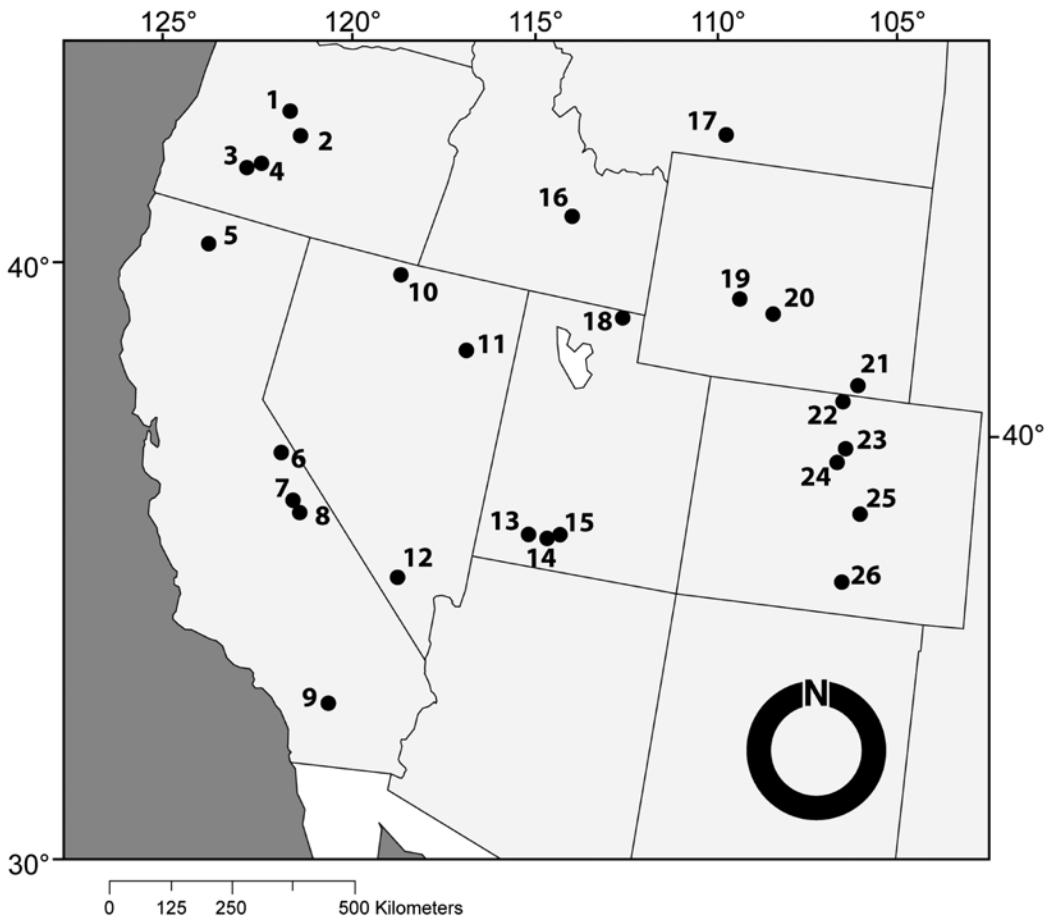

Fig. 2. Approximate location of collection sites for *Arceuthobium cyanocarpum*. Collections from locations 1–3 from *Pinus albicaulis*; collections from locations 4–5 from *Pinus monticola*; collections from locations 6–26 from *Pinus flexilis*. Numbers correspond to the following locations: Oregon; **1**—1 km NW of Little Three Creek Lake; **2**—4.5 km SE of East Lake on forest rd. 21; **3**—Wizard Island, Crater Lake National Park; **4**—Wineglass Overlook on East Rim rd., Crater Lake National Park; **5**—2 km N of Park Creek Divide on forest rd. 17; **6**—Dechambeau Creek; 3 km SE of Lundy Lake; **7**—1 km N of Lake Sabrina rd. on North Lake rd.; **8**—4 km W of Glacier Lodge in North Fork of Big Pine Creek; **9**—N slope of Tahquitz Peak; Nevada; **10**—3.2 km S of Windy Gap, Santa Rosa Range; **11**—10 km S of St. Rte. 227 in Lamoille Canyon, Ruby Mountains; **12**—Lee Canyon Loop trail, Spring Creek Mountains; Utah; **13**—Escalante Summit on St. Rte. 14; **14**—10.5 km W of the East Fork of the Sevier River on Skunk Creek rd.; **15**—0.3 km W of Bryce Point, Bryce Canyon National Park; Idaho; **16**—Craters of the Moon National Monument; Montana; **17**—9.5 km W of Nye and 1.2 km E of Picket Pin Creek; Wyoming; **18**—1.5 km NW of Tony Grove Lake; **19**—5 km NE of South Pass City; **20**—14 km S of Jeffrey City; **21**—16 km E of Laramie on Porcupine Hill rd.; Colorado; **22**—Owl Springs on Cherokee Park rd.; **23**—8.5 km N of Nederland on St. Rte. 72; **24**—2.4 km N of Fall River rd. on Hamlin Gulch rd.; **25**—13.8 km N of Garden of the Gods Park on Rampart Range rd.; **26**—0.5 km E of Rough/Maestas Mountain saddle near La Veta Pass.

minate spikes length and width; 5) staminate flower diameters for three- and four-merous flowers; 6) length and width of staminate flower petals; and, 7) anther diameter and distance to the petal tip (hereafter, referred to anther distance to tip). Plants were consistently measured within 12-h and rarely later than 24-h after collection. Only plants that were still attached to their host's branch and fully turgid were measured. Infections on the main stem/trunk of trees were not collected as removal of such plants is often considerably injurious to the host tree and parasite.

Measurements were made using a digital caliper (Mitutoyo America Corp., Aurora, IL) and a 7x magnifier equipped with a micrometer (Bausch & Lomb, Bridgewater, NJ). The basal diameter of plants was measured at

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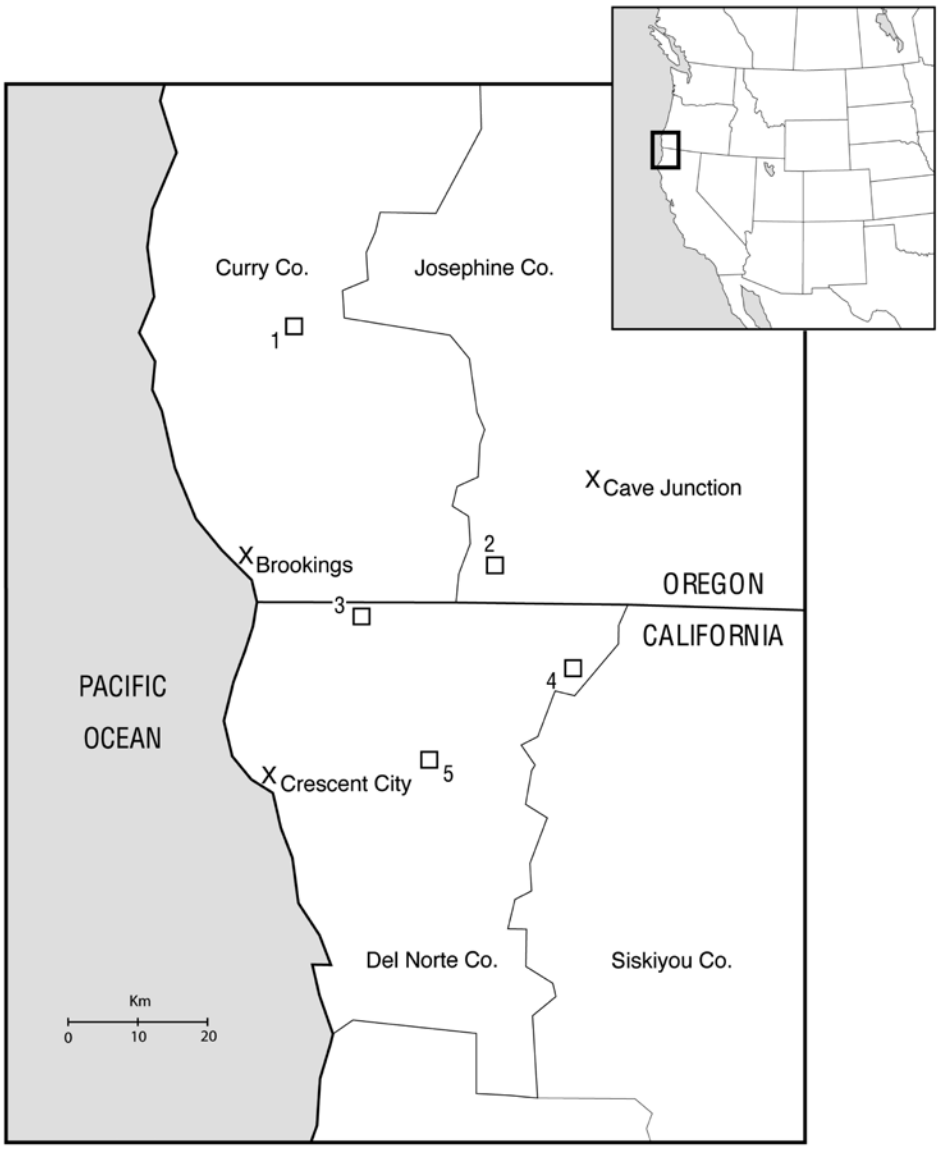

Fig. 3. Approximate location of collection sites for *Arceuthobium monticola* in California and Oregon. All collections from *Pinus monticola*. Numbers correspond to the following locations: 1—0.5 km NE of Snowcamp Mountain Lookout; 2—11 km SW of O'Brien on Oregon Mountain rd.; 3—End of forest rd. 305 at Sourdough Junction; 4—Black Butte trailhead on forest rd. 053; 5—1 km NE of Ship Mountain on forest rd. 16N02.

the point where the plant was attached to the host branch to the nearest 0.1 mm. 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 and provide relative information on plant size and, most importantly, plant thickness (Hawksworth & Wiens 1972, 1996; Mathiasen & Daugherty 2007, 2009, 2013; Mathiasen & Kenaley 2015a, 2015b; Mathiasen et al. 2016). However, we were conscious of Kuijt's (1969) study which demonstrated that plants of *Arceuthobium americanum* Nutt. ex Engelm.—and probably other large dwarf mistletoes—have intercalary meristems that permit continued elon-

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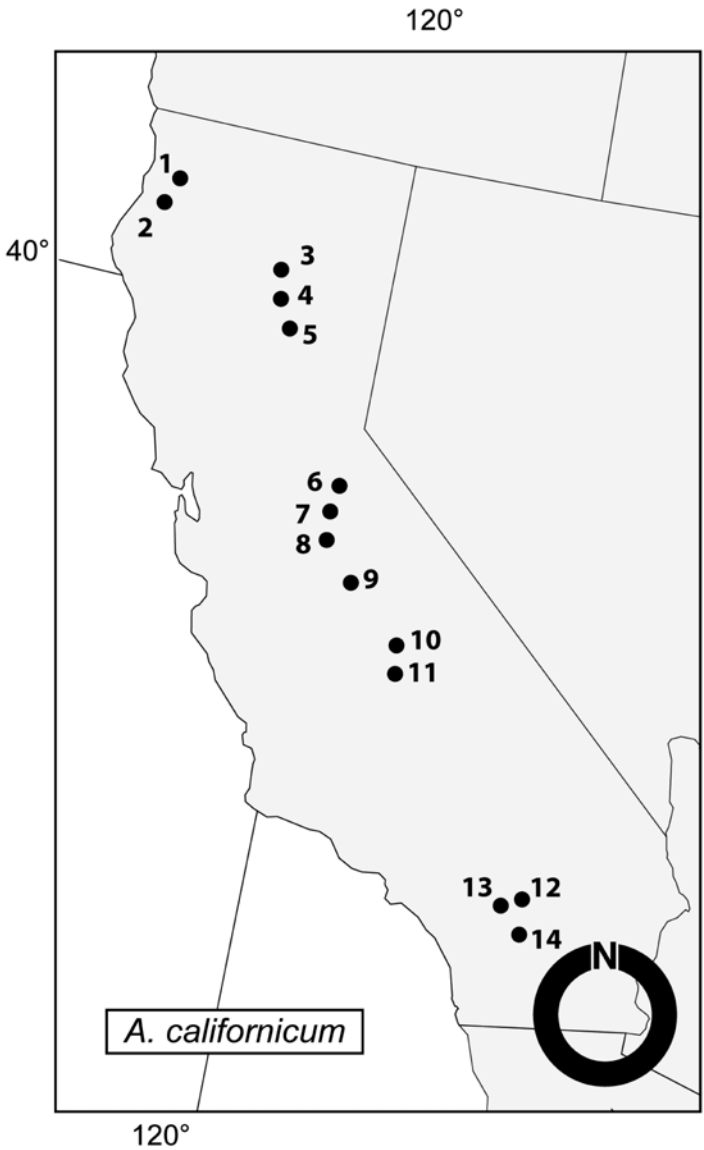

Fig. 4. Approximate location of collection sites for *Arceuthobium californicum* in California. All collections from *Pinus lambertiana*. Numbers correspond to the following locations: **1**—17 km W of St. Rte. 96 on Dillon Mountain rd.; **2**—15 km NW of St. Rte. 96 on Gasquet-Orleans rd.; **3**—Mineral Summit on St. Rte. 76; **4**—1 km S of Colby Mountain Lookout on forest rd. 27N36; **5**—1 km N of Bucks Lake rd on Silver Lake rd.; **6**—5 km N of St. Rte 108 on Beardsley Dam rd.; **7**—12 km W of jct. of forest rd. 17 and forest rd. 14 on forest rd. 14; **8**—8 km NW of Crane Flat Campground on St. Route 120; **9**—5 km N of St. Rte. 168 on Huntington Lake rd.; **10**—2.5 km N of Johnsondale rd. on Western Divide Hiway; **11**—1 km N of Tiger Flat on forest rd. 24S15; **12**—Barton Flats on St. Rte 38; **13**—2 km E of Angeles Oaks on St. Rte. 38; **14**—11 km N of Idylwild on St. Rte. 243.

gation of the third internode over several years. Thus, to avoid such variation among plants/taxa, we standardized the measurement of the third internode by measuring dominant plants at approximately the same time annually (male and female plants in July–August or August–September respectively) and determined the length and width with a digital caliper to the nearest 0.1 mm. The length of the third internode was determined by measuring between the apical most portion of the second and third internodes distal to the base of a plant—

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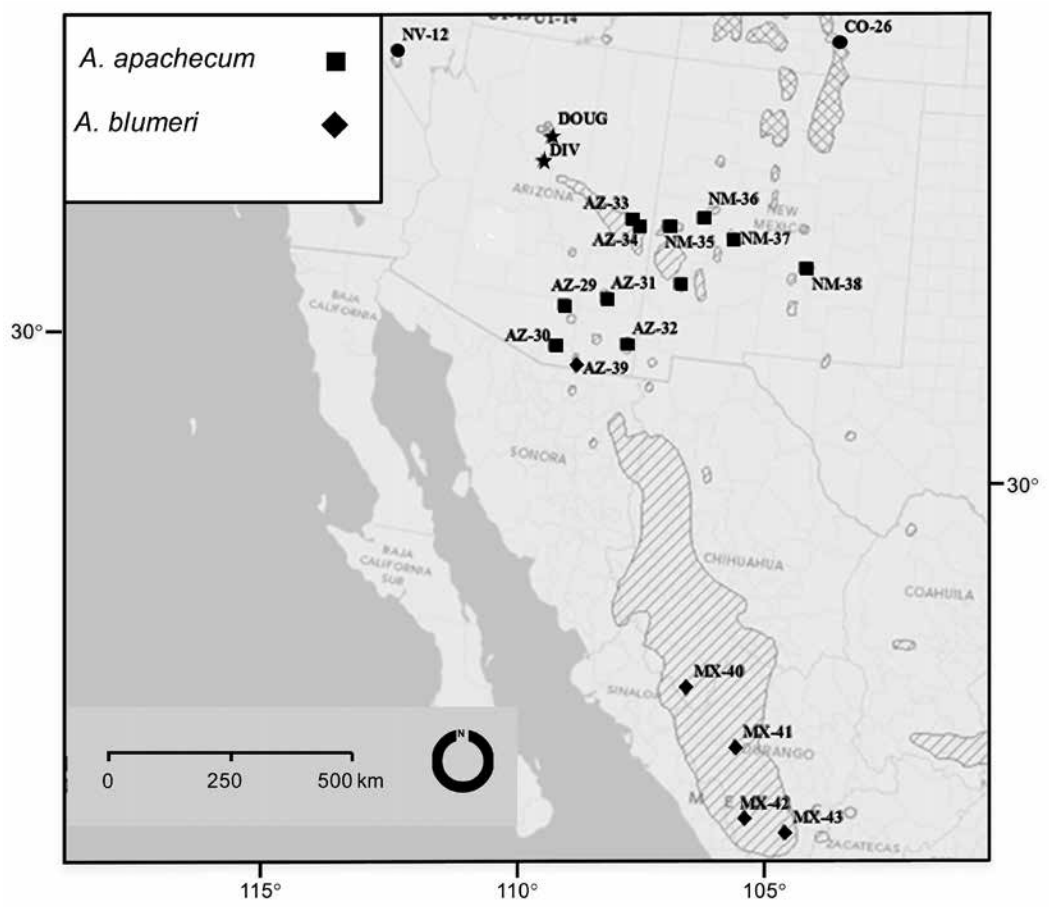

Fig. 5. Geographic location of collection sites for *Arceuthobium apachecum* (solid squares) and *Arceuthobium blumeri* (solid diamonds) in the southwestern United States and northern Mexico—a modification of Fig. 1 (map) appearing in Reif et al. (2015). Outlined areas with diagonal lines represent the distribution of *Pinus strobiformis* (principal host) of the aforementioned white pine dwarf mistletoes across the region. Stars and solid circles denote the collection location of outgroup taxa, *A. douglasii* (DOUG) and *A. divaricatum* (DIV), and *A. cyanocarpum* utilized in the genetic analyses performed by Reif et al. (2015). Cross-thatched areas indicate the geographic distribution of the principal host of *A. cyanocarpum*, *Pinus flexilis*.

locations (i.e. morphological "landmarks") along the plant length that are easily observed (see Figs. 2.1, 2.3, and 2.9 in Hawksworth & Wiens 1996). The width of the third internode was measured across its widest axis. Staminate spike and flower measurements were made during the peak of anthesis (June to August) and, likewise, fruit and seed measurements were made during peak seed dispersal (August to September). 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 species 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 white pine dwarf mistletoes and *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. Dunnett's tests were also executed sepa-

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rately to determine whether means for each female and male morphologic character were significantly different when comparing each of the five white pine dwarf mistletoes individually to *A. campylopodum*. Multivariate analysis of variance (MANOVA) was also performed separately for female and male plants across taxa to control for experiment error (family-wise Type I error; Rancher 2002) and, by plant sex, to determine whether differences existed between the combined morphologies for the white pine dwarf mistletoes and western dwarf mistletoe. A second suite of multivariate analyses – standard and forward-stepwise quadratic discriminant function analyses (DFA)—were performed as well to determine whether female or male plants of *A. apachecum*, *A. blumeri*, *A. californicum*, *A. campylopodum*, *A. cyanocarpum*, and *A. monticola* can be delimited to species membership by the joint examination of morphological characters (Quinn & Keough 2002). Discriminant function analyses classification compared actual species membership defined a priori via field determination to predicted species membership according to only female or male morphologies. The diameter of male flowers was not included in the DFAs as we couldn't control for interspecific differences among the ratio of 3- and 4-lobed staminate flowers. Because previous molecular phylogenetic analyses suggested that all six taxa may be conspecific (i.e., the same species differing only by principal host; Nickrent et al. 2004), DFAs for female and male plants were performed separately using equal prior probabilities for each species (0.1667) rather than proportional to their occurrences in the data set(s) and, hence, by our field determination. Standardized correlation coefficients for morphological characters were calculated to assess the overall contribution of each morphologic character to the discriminant function, which provided the principal morphologies separating the dwarf mistletoes. Stepwise DFA was also utilized to examine systematically the smallest number of morphological characteristics, female or male, resulting in the highest precision in species classification (%, predicted/field determined). To further validate the DFA, we resampled separately the original (complete) data set for female and male plants; selecting at random 25 complete records per species and re-executing the DFA using a full-model (i.e., 8 female or 10 male characters simultaneously). One-way and multivariate analyses of variances, multiple comparisons of mean differences, and DFAs were computed in JMP Pro v12.0.1 (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 AND DISCUSSION

Collectively, our statistical analyses—ANOVA, MANOVA, and DFA—clearly demonstrated that *Arceuthobium apachecum*, *A. blumeri*, *A. californicum*, *A. cynanocarpum*, and *A. monticola* can be determined readily to species using morphological data without consideration of geographic location, host specificity, and/or phenological data (Tables 1-5, 7; Fig. 6). Among these parasites, *A. cyanocarpum* was the most readily distinguished from the other white pine-infecting dwarf mistletoes, including *A. apachecum*—a distinct, yet, genetically closely-related species to *A. cynanocarpum* (Reif et al. 2015). Likewise, *A. californicum* and *A. monticola*—two taxa once considered conspecific (Hawksworth & Wiens 1972)—are indeed similar across four morphologic characters; however, they can be determined to species regardless of host data via measurement of multiple, female and male morphologies. The latter result further supports the allozymic analyses of *A. californicum* and *A. monticola* reported by Nickrent and Butler (1990) as well as the separation of these taxa at the specific level (Hawksworth et al. 1992). Moreover, our analyses also clearly demonstrated that *A. apachecum*, *A. blumeri*, *A. californicum*, *A. cyanocarpum*, and *A. monticola* are morphologically distinct from *A. campylopodum* (Tables 1, 3, 5, 7; Fig. 6) and can be readily separated statistically (≥82.8% field determined plants) from the latter white pine mistletoes using as few as three female or male characters (Table 3). Across all morphological characters for each of the five white pine dwarf mistletoes, only female and/or male plant height(s) for *A. blumeri* and *A. californicum* were not significantly different when compared statistically to *A. campylopodum*. Minus female and male plant height, staminate spike width, and anther distance to tip, the dimensions for all morphological characters—female or male—were significantly larger for *A. campylopodum* than those of the white pine dwarf mistletoes. Phenological data including time of flowering and seed dispersal, however, separated only *A. californicum* from the other white pine dwarf mistletoes and *A. campylopodum* (Fig. 7). In contrast, the comparisons

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TABLE 1. Morphological comparison of male and female plants for *Arceuthobium apachecum*, *A. blumeri*, *A. californicum*, *A. campylopodum*, *A. cyanocarpum*, and *A. monticola*. Data are listed as **mean** (95% confidence interval, α= 0.05) [N= measurements]. Means followed by different capital letters in the same row were significantly different according to a Tukey's honestly significant difference (HSD) test (α= 0.05). Likewise, by row, darkened/bolded cells (text) indicate a significant difference in mean measurement compared to *A. campylopodum* (control) using a Dunnett's test. Plant heights are in cm whereas all other measurements are 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).

Character[a]	*Arceuthobium apachecum*	*Arceuthobium blumeri*	*Arceuthobium californicum*	*Arceuthobium campylopodum*	*Arceuthobium yanocarpum*	*Arceuthobium monticola*
PH						
Female	**5.1 C (±0.2) [215]**	**10.0** A (±0.6) [130]	**9.9** A (±0.4) [100]	**10.4** A (±0.2) [600]	**3.6 B (±0.1) [258]**	**8.5 D (±0.5) [50]**
Male	**3.7 C (±0.2) [240]**	**9.8** A (±0.6) [130]	**8.1 B (±0.4) [120]**	**9.7** A (±0.2) [600]	**2.8 D (±0.1) [273]**	**7.8 B (±0.5) [50]**
BD						
Female	**2.1 C (±0.1) [215]**	**2.8 B (±0.1) [130]**	**3.0 B (±0.1) [100]**	**3.4** A (±0.1) [600]	**2.0 C (±0.1) [258]**	**2.9 B (±0.1) [50]**
Male	**1.9 C (±0.1) [240]**	**2.7 B (±0.1) [130]**	**2.7 B (±0.1) [120]**	**3.2** A (±0.0) [600]	**1.8 C (±0.0) [273]**	**2.8 B (±0.1) [50]**
LTI						
Female	**8.2 C (±0.3) [215]**	**11.3 B (±0.6) [130]**	**11.5 B (±0.5) [100]**	**13.0** A (±0.2) [600]	**6.5 D (±0.2) [258]**	**11.5 B (±1.0) [50]**
Male	**5.9 C (±0.3) [240]**	**10.9 B (±0.6) [130]**	**10.1 B (±0.5) [120]**	**11.9** A (±0.2) [600]	**5.2 D (±0.2) [273]**	**9.9 B (±0.8) [50]**
WTI						
Female	**1.6 C (±0.0) [215]**	**2.0 B (±0.0) [130]**	**1.9 B (±0.0) [100]**	**2.5** A (±0.0) [600]	**1.5 D (±0.0) [258]**	**1.7 C (±0.1) [50]**
Male	**1.6 D (±0.0) [240]**	**2.1 B (±0.0) [130]**	**1.7 C (±0.0) [120]**	**2.5** A (±0.0) [600]	**1.5 D (±0.0) [273]**	**1.7 C (±0.1) [50]**
SSL	**9.3 C (±0.3) [275]**	**13.7 A (±0.6) [230]**	**8.7 C (±0.3) [200]**	**12.7** B (±0.3) [760]	**5.8 D (±0.2) [294]**	**8.6 C (±0.4) [100]**
SSW	**2.6 BC (±0.1) [275]**	**2.6 B (±0.0) [230]**	**1.8 D (±0.0) [200]**	**3.0** A (±0.0) [760]	**2.5 C (±0.1) [294]**	**1.4 E (±0.0) [100]**
FD						
3-merous	**2.7 C (±0.1) [150]**	**3.0 B (±0.0) [120]**	**2.6 D (±0.1) [100]**	**3.1** A (±0.0) [399]	**2.6 D (±0.0) [221]**	**2.5 D (±0.1) [50]**
4-merous	**2.1 D (±0.1) [133]**	**4.1 B (±0.1) [120]**	**3.5 C (±0.1) [100]**	**4.2** A (±0.0) [361]	**2.8 E (±0.0) [172]**	**3.6 C (±0.1) [50]**
PL	**1.3 C (±0.0) [283]**	**1.5 B (±0.0) [240]**	**1.2 E (±0.0) [200]**	**1.6** A (±0.0) [760]	**1.3 D (±0.0) [393]**	**1.3 DE (±0.0) [100]**
PW	**1.2 B (±0.0) [283]**	**1.2 BC (±0.0) [240]**	**1.1 D (±0.0) [200]**	**1.4** A (±0.0) [760]	**1.1 CD (±0.0) [393]**	**1.1 D (±0.0) [100]**
AD	**0.5 C (±0.0) [283]**	**0.7 A (±0.0) [240]**	**0.5 C (±0.0) [200]**	**0.6** B (±0.0) [760]	**0.5 D (±0.0) [393]**	**0.5 C (±0.0) [100]**
ADT	**0.5 B (±0.0) [283]**	**0.5 B (±0.0) [240]**	**0.4 D (±0.0) [100]**	**0.6** A (±0.0) [910]	**0.5 C (±0.0) [353]**	**0.4 CD (±0.0) [50]**
FL	**4.1 D (±0.1) [205]**	**4.7 C (±0.1) [180]**	**5.1 B (±0.1) [100]**	**5.4** A (±0.0) [480]	**3.5 E (±0.1) [218]**	**4.7 C (±0.1) [50]**
FW	**2.9 C (±0.0) [205]**	**2.8 C (±0.0) [180]**	**3.1 B (±0.1) [100]**	**3.7** A (±0.0) [480]	**2.4 D (±0.0) [218]**	**3.0 BC (±0.1) [50]**
SL	**2.1 E (±0.0) [205]**	**2.2 D (±0.0) [180]**	**2.7 B (±0.1) [100]**	**3.5 A** (±0.0) [480]	**1.9 F (±0.0) [208]**	**2.5 C (±0.1) [50]**
SW	**1.1 C (±0.0) [205]**	**1.1 C (±0.0) [180]**	**1.2 B (±0.0) [100]**	**1.5 A** (±0.0) [480]	**1.1 D (±0.0) [208]**	**1.1 BC (±0.0) [50]**

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TABLE 2. One-way analysis of variance (ANOVA) testing by morphologic character for male and female plants of *Arceuthobium apachecum*, *A. blumeri*, *A. californicum*, *A. campylopodum*, *A. cynanocarpum*, and *A. monticola*.

Character	Sum of Squares			Mean Square			
	Taxa	Error	Total	Taxa	Error	F-ratio	P-value
Plant height							
Female	11049.0	7084.6	18133.6	2209.8	5.3	$F_{5,1347}$= 420.2	<.0001
Male	12880.1	8587.8	21467.9	2576.0	6.1	$F_{5,1407}$= 422.0	<.0001
Basal diameter							
Female	490.9	502.2	993.1	98.2	0.4	$F_{5,1347}$= 263.3	<.0001
Male	506.4	378.4	884.9	101.3	0.3	$F_{5,1407}$= 376.5502	<.0001
Length of third internode							
Female	9271.6	10588.2	19859.8	1854.3	7.9	$F_{5,1347}$= 236.0	<.0001
Male	12134.8	11163.8	23298.6	2427.0	7.9	$F_{5,1407}$= 305.9	<.0001
Width of third internode							
Female	232.7	117.2	349.9	46.5	0.1	$F_{5,1347}$= 534.7	<.0001
Male	249.1	117.2	366.3	49.8	0.1	$F_{5,1407}$= 597.8	<.0001
Staminate spike length	13917.1	25387.3	39304.3	2783.4	13.7	$F_{5,1853}$= 203.1597	<.0001
Staminate spike width	423.7	418.6	842.2	84.7	0.2	$F_{5,1853}$= 75.0897	<.0001
Flower diameter							
3-merous	67.7	116.5	184.2	13.5	0.1	$F_{5,1034}$= 120.1876	<.0001
4-merous	304.2	213.6	517.7	60.8	0.2	$F_{5,930}$= 264.892	<.0001
Petal length	38.2	79.4	117.5	7.6	0.0	$F_{5,1970}$= 189.462	<.0001
Petal width	30.8	66.2	97.0	6.2	0.0	$F_{5,1970}$= 183.2353	<.0001
Anther diameter	10.4	23.8	34.2	2.1	0.0	$F_{5,1970}$= 171.7942	<.0001
Anther distance to tip	5.4	34.2	39.5	1.1	0.0	$F_{5,1930}$= 60.5106	<.0001
Fruit length	684.3	262.2	946.5	136.9	0.2	$F_{5,1227}$= 640.4223	<.0001
Fruit width	268.6	151.3	419.9	53.7	0.1	$F_{5,1227}$= 435.6552	<.0001
Seed length	525.7	156.5	682.1	105.1	0.1	$F_{5,1217}$= 817.7832	<.0001
Seed width	38.9	28.6	67.4	7.8	0.0	$F_{5,1217}$= 331.3608	<.0001

of host specificity supported the separation of the white pine dwarf mistletoes from *A. campylopodum* as well as provide additional taxonomically informative characters for their field identification and species determination. Therefore, our morphometric analyses do not support the classification of the white pine dwarf mistletoe studied here under *A. campylopodum* as treated by Kuijt (2012) nor do they support their classification as subspecies of *A. campylopodum* as proposed by Nickrent (2012).

Univariate Morphologic Analyses

As noted previously, *Arceuthobium cyanocarpum* was most dissimilar morphologically compared to the other four white pine dwarf mistletoes—particularly for female plants (Table 1). A total of 12 of the 20 morphological characters across female (7⁄8) and male (5⁄12) plants of *A. cyanocarpum* were significantly different when compared simultaneously to *A. apachecum*, *A. blumeri*, *A. californicum*, and *A. monticola*. For female plants, the basal diameter of *A. cyanocarpum* (mean= 2.0 mm) was the lone morphologic character with similarity to one or more of the other white pine dwarf mistletoes, differing from *A. apachecum* by only 0.1 mm. Likewise, for male *A. cyanocarpum*, the mean basal diameter and width of the third internode as well as staminate spike width were not significantly different when compared to *A. apachecum* as well as the latter species and *A. blumeri*, respectively. The mean diameter of 3-merous flowers, petal length and width, and anther distance to tip for *A. cyanocarpum* also were not significantly different from the means of those characters for both *A. californicum* and *A. monticola*. However, the mean dimensions of female and male plants of *A. cyanocarpum* were consistently and, more often than not, significantly smaller in comparison to the other white pine parasites and *A. campylopodum* with the lone exception being mean staminate spike width. The mean width of staminate spikes for *A. cyanocarpum* was much larger than those for *A. californicum* and *A. monticola* (Table 1). The maximum plant height we measured for *A. cyanocarpum* (6.7 cm) was similar to that reported by Hawksworth and Wiens (7 cm; Hawksworth & Wiens 1996). Our results clearly demonstrated that *A. cyanocarpum* is well dif-

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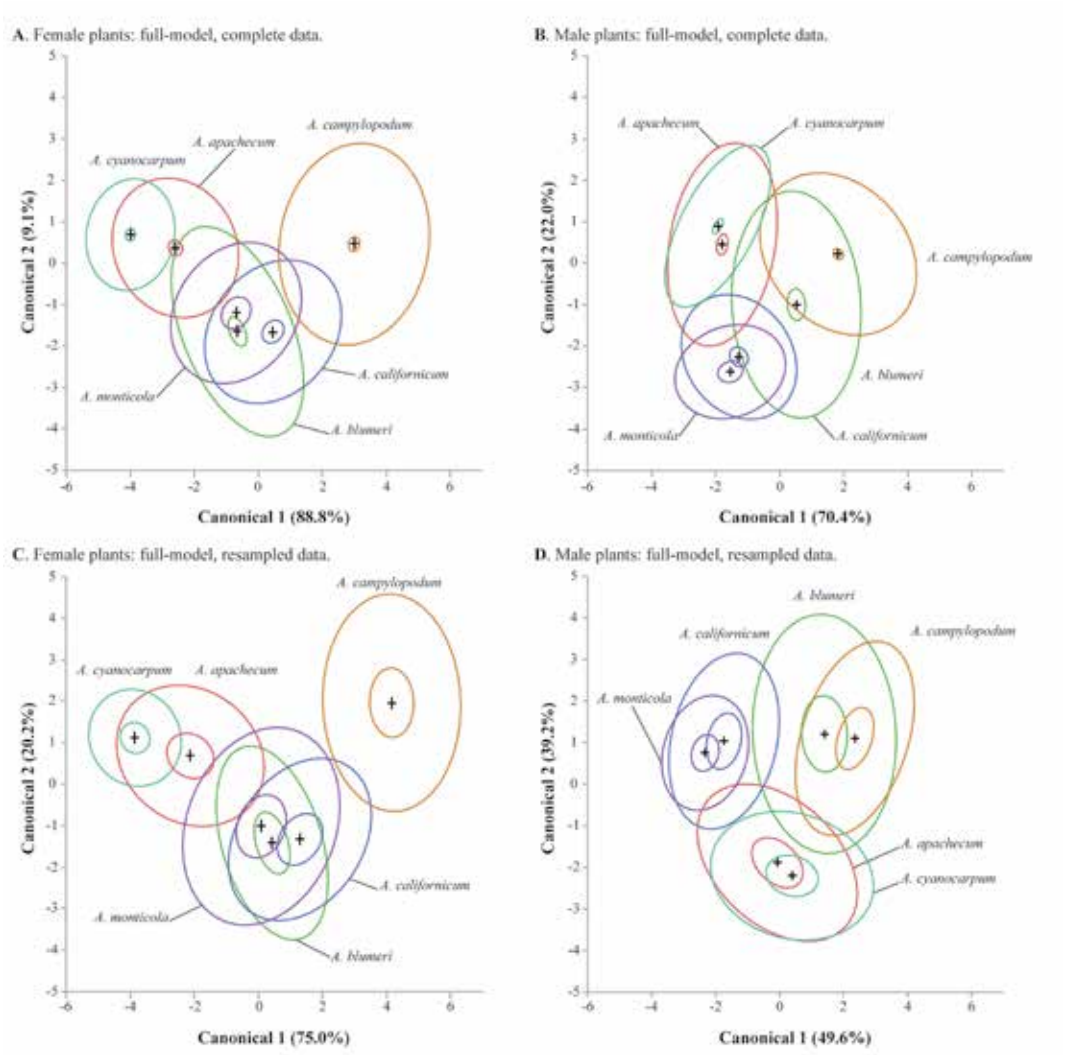

Fig. 6. Canonical plots for discriminant functions analyses (DFA) of female (A, C; N= 8 characters) and male morphologies (B, D; N= 10 characters) for *Arceuthobium apachecum*, *A. blumeri*, *A. californicum*, *A. campylopodum*, *A. cyanocarpum*, and *A. monticola*. Separate DFAs were executed for female and male plants using complete (A, B) and resampled datasets (C,D). The latter analyses utilizing resampled data (25 complete records/species) were performed to validate DFAs using complete data. Across all analyses (A–D), a multivariate mean (crosshair) as well as 95% confidence (inner) and 50% normal contour (outer) ellipses were computed for each species.

ferentiated from *A. campylopodum* and classifying it under the latter species (Kuijt 2012) or as a subspecies (Nickrent 2012) is unwarranted.

Although sharing several morphological similarities with *Arceuthobium cyanocarpum*, *A. apachecum* was also readily distinguishable from all white pine dwarf mistletoes and *A. campylopodum* with significantly different mean measurements for eight of the 20 morphologic characters examined (Table 1). These characters included plant height, 3- and 4-merous flower diameter, fruit and petal length, and seed length. The mean basal diameter for female and male plants of *A. apachecum* was also significantly different when compared to *A. blumeri, A. californicum*, *A. campylopodum*, and *A. monticola*, whereas, for female plants, the mean width of the third internode of *A. apachecum* differed significantly in comparison to all dwarf mistletoes examined except

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TABLE 3. Forward, stepwise discriminant function analysis (DFA): classification of female and male plants of the white pine dwarf mistletoes and western dwarf mistletoe (*Arceuthobium campylopodum*) to correct species membership following the sequential addition of morphological characters most-to-least 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).

	Correct species membership (%, [N predicted/ N field determined])						
Stepwise DFA (step [character[a]])	Total	*A. apachecum*	*A. blumeri*	*A. californicum*	*A. campylopodum*	*A. cyanocarpum*	*A. monticola*
Female							
1. [FL]	53.5 [628/1173]	57.6 [118/205]	0.0 [0/130]	54.0 [54/100]	57.5 [276/480]	78.4 [163/208]	34.0 [17/50]
2 [*], [SL]	66.2 [777/1173]	47.8 [98/205]	60.8 [79/130]	30.0 [30/100]	78.8 [378/480]	83.2 [173/208]	38.0 [19/50]
3 [*], [*], [WTI]	74.0 [868/1173]	54.1 [111/205]	65.4 [85/130]	37.0 [37/100]	90.8 [436/480]	84.6 [176/208]	46.0 [23/50]
4 [*], [*], [*], [PH]	76.7 [900/1173]	58.0 [119/205]	61.5 [80/130]	45.0 [45/100]	91.0 [437/480]	89.9 [187/208]	62.0 [31/50]
5 [*], [*], [*], [*], [FW]	79.2 [929/1173]	62.9 [129/205]	63.8 [83/130]	55.0 [55/100]	91.7 [440/480]	90.4 [188/208]	68.0 [34/50]
6 [*], [*], [*], [*], [*],[SW]	80.6 [946/1173]	63.9 [131/205]	66.9 [87/130]	55.0 [55/100]	93.3 [448/480]	91.3 [190/208]	70.0 [35/50]
7 [*], [*], [*], [*], [*],[*], [LTI]	81.2 [952/1173]	66.3 [136/205]	68.5 [89/130]	61.0 [61/100]	92.9 [446/480]	88.9 [185/208]	70.0 [35/50]
8 [*], [*], [*], [*], [*],[*], [*], [BD]	83.2 [976/1173]	70.2 [144/205]	73.8 [96/130]	68.0 [68/100]	92.9 [446/480]	87.0 [181/208]	82.0 [41/50]
Male							
1 [WTI]	49.7 [692/1393]	12.9 [31/240]	49.2 [64/130]	41.0 [41/100]	65.0 [390/600]	60.8 [166/273]	0.0 [0/50]
2 [*], [SSW]	60.4 [842/1393]	27.9 [67/240]	57.7 [75/130]	81.0 [81/100]	77.2 [463/600]	40.7 [111/273]	90.0 [45/50]
3 [*, [*], [PH]	69.9 [974/1393]	20.8 [50/240]	61.5 [80/130]	80.0 [80/100]	81.3 [488/600]	83.5 [228/273]	96.0 [48/50]
4 [*], [*], [*], [ADT]	73.2 [1020/1393]	45.4 [109/240]	66.9 [87/130]	80.0 [80/100]	81.7 [490/600]	75.5 [206/273]	96.0 [48/50]
5 [*], [*], [*], [*], [BD]	76.0 [1058/1393]	52.1 [125/240]	71.5 [93/130]	84.0 [84/100]	82.8 [497/600]	77.7 [212/273]	94.0 [47/50]
6 [*], [*], [*], [*], [*], [AD]	79.3 [1105/1393]	60.8 [146/240]	71.5 [93/130]	84.0 [84/100]	85.8 [515/600]	80.6 [220/273]	94.0 [47/50]
7 [*], [*], [*], [*], [*], [*], [PL]	81.2 [1131/1393]	59.6 [143/240]	75.4 [98/130]	86.0 [86/100]	89.2 [535/600]	81.7 [223/273]	92.0 [46/50]
8 [*], [*], [*], [*], [*], [*], [*], [PW]	82.2 [1145/1393]	65.8 [158/240]	80.0 [104/130]	86.0 [86/100]	88.5 [531/600]	80.6 [220/273]	92.0 [46/50]
9 [*], [*], [*], [*], [*], [*], [*], [*], [SSL]	84.1 [1172/1393]	70.4 [169/240]	80.8 [105/130]	89.0 [89/100]	88.5 [531/600]	84.6 [231/273]	94.0 [47/50]
10 [*], [*], [*], [*], [*], [*], [*], [*], [*], [LTI]	84.1 [1171/1393]	71.7 [172/240]	80.8 [105/130]	90.0 [90/100]	88.5 [531/600]	82.8 [226/273]	94.0 [47/50]

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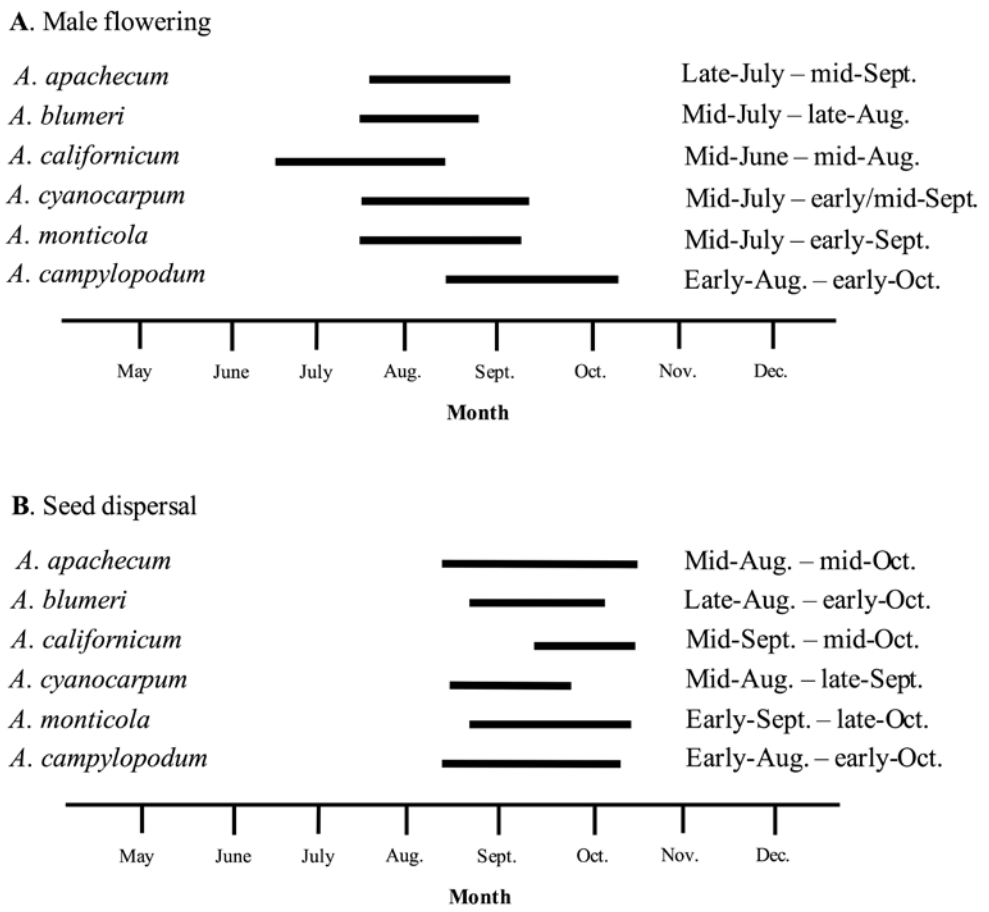

Fig. 7. Phenology of male flowering (anthesis; A) and seed dispersal from female plants (B) by species: *Arceuthobium apachecum*, *A. blumeri*, *A. californicum*, *A. cyanocarpum*, *A. monticola*, and *A. campylopodum*.

A. monticola. Similarly, mean staminate spike length and anther diameter for *A. apachecum* were similar to *A. californicum* and *A. monticola*; yet; the latter two characters consistently segregated *A. apachecum* from *A. blumeri*, *A. campylopodum*, and *A. cyanocarpum*. When utilized separately, the examination of anther distance to tip and seed width provided clear mean pairwise differences when *A. apachecum* was compared to *A. campylopodum* and *A. cyanocarpum*, and to *A. californicum*, *A. campylopodum*, and *A. cyanocarpum*, respectively (Table 1). Collectively, these results indicate that *A. apachecum* is more closely-related morphologically to *A. cyanocarpum* than to *A. blumeri* with which it shares a principal host (i.e., *Pinus strobiformis*) in the Southwest (Mathiasen 1982; Hawksworth & Wiens 1996). Moreover, *A. apachecum* is unequivocally distinct morphologically among the white pine dwarf mistletoes and to western dwarf mistletoe and, hence, our findings do not support the circumscription of *A. apachecum* under *A. campylopodum* (Kuijt 2012) or its reclassification to a subspecies of *A. campylopodum* (Nickrent 2012).

Mean female and male morphologies of *Arceuthobium blumeri* were rarely insignificant statistically when compared to *A. campylopodum*—similar in only female and male plant height (Table 1). Although mean measurements for female and male characters of *A. blumeri* often overlapped with those of other white pine dwarf mistletoes, particularly *A. californicum* and *A. monticola* (Table 1), Blumer's dwarf mistletoe was morphologically distinct across six of the 20 characters examined, including width of the third internode (female and

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male), staminate spike length, male flower diameter (3-merous and 4-merous), and anther diameter as well as petal and seed length. The mean basal diameter for female and male plants of *A. blumeri*, however, was similar in dimension to those of *A. californicum* and *A. monticola*, while seed width was also nearly identical to that of *A. monticola* and *A. apachecum*. As previously noted above, *A. blumeri* and *A. apachecum* also shared similar mean measurements for petal, staminate spike, and seed width as well as anther distance to tip. Thus, female and male plants of *A. blumeri* are similar in size to *A. campylopodum*; however, they are more compact and slender in comparison to the latter dwarf mistletoe. Morphologic differences presented for *A. blumeri* support the phylogenetic position of this taxon. Although it shares a common distant ancestor with *A. campylopodum*, *A. blumeri* appears to be monophyletic and, hence phylogenetically distinct from *A. campylopodum* as well as other taxa in ser. *Campylopoda* including *A. apachecum*, *A. californicum*, *A. cyanocarpum*, and *A. monticola* (Nickrent et al. 2004). Our morphologic analyses for *A. blumeri* also provided added support to the amplified fragment length polymorphism (AFLP) analysis conducted by Reif et al. (2015), where populations of *A. blumeri* were more similar genetically to *A. apachecum* than *A. cyanocarpum*. Further molecular analyses (e.g., AFLP or genotyping-by-sequencing [Elshire et al. 2011]) comparing the population genetics of *A. blumeri* to those of *A. californicum* and *A. monticola* as well as other taxa in ser. *Campylopoda* are lacking and, hence, should be addressed to provide new insight(s) into their genetic similarities and evolutionary histories.

Arceuthobium californicum and *A. monticola* were once considered conspecific, separable by only geography and principal host until electrophoretic analyses provided a clear delineation between these taxa (Hawksworth & Wiens 1972; Nickrent & Butler 1990). The close relationship between these two white pine parasites was also evident in our morphological analyses as only the mean female plants height and width of the third internode of female plants as well as mean staminate spike width differed significantly between *A. californicum* and *A. monticola*. Thus, although plant color of *A. californicum* (green to yellow) differs from that of *A. monticola* (dark brown to red brown to green-brown; Mathiasen & Daugherty 2009), these two dwarf mistletoes are morphologically very similar. The classification of *Arceuthobium monticola* as a subspecies of *A. californicum*, however, should not be considered given the morphological, physiological, and genetic differences between them and their apparent geographic isolation (Fig. 4 and 5; Nickrent & Butler 1990; Hawksworth et al. 1992; Hawksworth & Wiens 1996). It is also important to note that we measured plants that were much larger for both of these species (maximum height 14.9 and 13.4 cm, respectively) than were reported previously by Hawksworth and Wiens (1996) (12 and 7 cm, respectively). However, Hawksworth et al. (1992) noted the maximum height of plants for *A. monticola* was 10 cm and it is unclear why this statistic was not also reported in Hawksworth and Wiens (1996). Moreover, previous descriptions for flowers of *A. monticola* (Hawksworth et al. 1992) indicated that it only formed 3-merous flowers. Mathiasen and Daugherty (2009), from which our *A. monticola* dataset is based—also reported 3-merous flowers were usually more numerous on plants. However, they found 4-merous flowers were also formed, and this character varied as *A. monticola* produced both 3- and 4-merous flowers (rarely 5-merous flowers) and a few male plants had predominantly 4-merous flowers (Mathiasen & Daugherty 2009). In contrast, we found that *A. californicum* produced flowers in approximately equal ratios of 3 and 4-merous flowers. Similarly, *A. apachecum* usually produced 3- and 4-merous (rarely 5-merous) flowers. Four-lobed and occasionally 3- and 5-lobed male flowers, and rarely 6-merous, were observed for *A. blumeri* whereas *A. cyanocarpum* flowers were almost exclusively 3- and rarely 4-merous.

Multivariate morphologic analysis

Separate multivariate analysis of variance (MANOVA) for female and male plant morphologies supported the univariate analyses presented above, indicating significant differences were present among eight female and 10 male plant characters of *A. apachecum*, *A. blumeri*, *A. californicum*, *A. campylopodum*, *A. cyanocarpum*, and *A. monticola* (Table 4). Likewise, discriminant function analyses for female and male plant characters also complemented and supported our univariate statistics (Tables 3, 5, 7; Fig. 6). Means and associated 95% confidence intervals for morphological characters of female and male plants by predicted species according to DFA utilizing a full-model, equal prior probabilities, and complete data are presented in Table 5. For female plants, DFA executed using eight morphological characters (full-model) and complete records effectively classified 83.4%

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Table 4. Multivariate analysis of variance (MANOVA) test statistics based on separate and complete datasets for morphologic measurements of female and male plants (N= 8 and 10 characters, respectively) for *Arceuthobium apachecum*, *A. blumeri*, *A. californicum*, *A. campylopodum*, *A. cynanocarpum*, and *A. monticola*.

Plant sex	Test	Value	Approximant F	P-value
Female				
	Wilks' Lambda	0.0525	$F_{40, 5059.1}$= 122.2	<.0001
	Pillai's Trace	1.5070	$F_{40, 5820.0}$= 62.8	<.0001
	Hotelling-Lawley	8.7976	$F_{40, 3466.0}$= 254.8	<.0001
	Roy's Max Root	7.8075	$F_{8, 1164.0}$= 1136.0	<.0001
Male				
	Wilks' Lambda	0.0981	$F_{50, 6288.0}$= 83.5	<.0001
	Pillai's Trace	1.4976	$F_{50, 6910.0}$= 59.1	<.0001
	Hotelling-Lawley	4.1962	$F_{50, 4462.2}$= 115.5	<.0001
	Roy's Max Root	2.9559	$F_{10, 1382.0}$= 408.5	<.0001

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

Sex / character(s)	*Arceuthobium apachecum*	*Arceuthobium blumeri*	*Arceuthobium californicum*	*Arceuthobium campylopodum*	*Arceuthobium cyanocarpum*	*Arceuthobium monticola*
Female						
Plant height (PH)	5.2 (±0.2)	10.2 (±0.6)	9.7 (±0.3)	10.4 (±0.3)	3.5 (±0.1)	8.3 (±0.3)
Basal diameter (BA)	2.1 (±0.1)	2.8 (±0.1)	2.9 (±0.1)	3.4 (±0.1)	2.0 (±0.1)	2.9 (±0.1)
Length of third internode (LTI)	8.5 (±0.3)	11.4 (±0.6)	11.5 (±0.4)	13.1 (±0.3)	6.2 (±0.2)	11.6 (±0.8)
Width of third internode (WTI)	1.6 (±0.0)	2.0 (±0.1)	1.9 (±0.0)	2.5 (±0.0)	1.5 (±0.0)	1.7 (±0.1)
Fruit length (FL)	4.1 (±0.1)	4.7 (±0.1)	5.2 (±0.1)	5.4 (±0.0)	3.4 (±0.0)	4.7 (±0.1)
Fruit width (FW)	2.9 (±0.1)	2.8 (±0.1)	3.2 (±0.0)	3.7 (±0.0)	2.4 (±0.0)	3.0 (±0.1)
Seed length (SL)	2.1 (±0.0)	2.2 (±0.0)	2.8 (±0.1)	3.5 (±0.0)	1.9 (±0.0)	2.5 (±0.1)
Seed width (SW)	1.1 (±0.1)	1.1 (±0.0)	1.2 (±0.0)	1.5 (±0.0)	1.0 (±0.0)	1.1 (±0.0)
Male						
Plant height (PH)	3.6 (±0.2)	9.8 (±0.5)	8.0 (±0.5)	9.7 (±0.3)	2.8 (±0.1)	7.7 (±0.5)
Basal diameter (BA)	1.9 (±0.1)	2.7 (±0.1)	2.7 (±0.1)	3.3 (±0.1)	1.8 (±0.0)	2.8 (±0.1)
Length of third internode (LTI)	5.8 (±0.3)	10.9 (±0.5)	9.8 (±0.5)	12.1 (±0.3)	5.0 (±0.2)	10.0 (±0.6)
Width of third internode (WTI)	1.6 (±0.0)	2.1 (±0.0)	1.7 (±0.0)	2.5 (±0.0)	1.5 (±0.0)	1.7 (±0.1)
Petal length (PL)	1.3 (±0.0)	1.5 (±0.0)	1.2 (±0.0)	1.6 (±0.0)	1.5 (±0.0)	1.2 (±0.0)
Petal width (PW)	1.2 (±0.0)	1.2 (±0.0)	1.1 (±0.0)	1.4 (±0.0)	1.3 (±0.0)	1.1 (±0.0)
Anther diameter (AD)	0.5 (±0.0)	0.7 (±0.0)	0.5 (±0.0)	0.6 (±0.0)	0.6 (±0.0)	0.5 (±0.0)
Anther distance from tip (ADT)	0.5 (±0.0)	0.5 (±0.0)	0.4 (±0.0)	0.6 (±0.0)	0.6 (±0.0)	0.4 (±0.0)
Staminate spike length (SSL)	9.2 (±0.3)	13.4 (±0.6)	8.7 (±0.4)	12.9 (±0.4)	9.4 (±0.5)	8.8 (±0.5)
Staminate spike width (SSW)	2.7 (±0.1)	2.8 (±0.1)	1.8 (±0.0)	3.0 (±0.0)	2.6 (±0.1)	1.4 (±0.0)

of field determined specimens to correct species (Table 3). The first two discriminant functions (canonicals; Table 6) explained 97.8% of the total variation across female dwarf mistletoes; correctly classifying all female plants to species (predicted/field determined) ≥70.2% of the time, whereas, 92.9% of female *A. campylopodum* were assigned correctly to species membership and was most often misclassified to *A. californicum* (5.8%; Table 7). In addition to female *A. campylopodum*, female *A. cyanocarpum* (87.0%) and *A. monticola* (82.0%) identified *a priori* via field determination were also classified consistently and correctly to species. The latter two white pine dwarf mistletoes—*A. cyanocarpum* and *A. monticola*—were occasionally assigned incorrectly to *A. apachecum* (12.0%) and *A. californicum* (8.0%), respectively, and rarely predicted to *A. blumeri* and *A. campylopodum* (Table 7). As with the univariate analyses for female plants, female DFAs had less resolving power in delineating *A. apachecum* (70.2%), *A. blumeri* (73.8%), and *A. californicum* (68.0%). Female plants of *A. apachecum* were commonly misclassified to *A. cyanocarpum* (19.5%) and to a lesser percentage, *A. blumeri* (7.3%), and assigned rarely (1.5%) to *A. californicum* and *A. monticola*. In contrast, field determined female plants of *A. blumeri* were predicted occasionally to *A. apachecum* (6.2%) and *A. californicum* (11.5%). Likewise, female *A.*

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TABLE 6. Canonical statistics: quadratic discriminant function analyses (DFA) of female and male plants of *A. apachecum*, *A. blumeri*, *A. californicum*, *A. campylopodum*, *A. cyanocarpum*, and *A. monticola* executed using a full-model (N= 8 female and 10 male characters) and equal prior probabilities (0.1667). Canonical details by plant sex are subdivided according to analyses performed on the complete and randomized resampled (25 complete records/species) datasets. a—Cum. (Cumulative), Can. (Canonical), and Like. (Likelihood).

Canonical	Eigenvalue	Percent	Cum. percent[a]	Can. correlation[a]	Like. ratio[a]	Approximant F	P-value
Female - Complete							
1	7.81	88.7	88.7	0.94	0.05	$F_{40, 5091.1}$= 122.18	<.0001
2	0.80	9.1	97.8	0.67	0.46	$F_{28, 4187.5}$= 35.66	<.0001
3	0.12	1.4	99.2	0.33	0.83	$F_{18, 3287.1}$= 12.36	<.0001
4	0.06	0.7	99.9	0.24	0.93	$F_{10, 2326.0}$= 8.58	<.0001
5	0.01	0.1	100.0	0.11	0.99	$F_{4,1164.0}$= 3.25	0.0117
Female - Resampled							
1	6.60	74.6	74.6	0.93	0.03	$F_{40, 600.0}$= 18.94	<.0001
2	1.51	17.1	91.7	0.78	0.22	$F_{28, 499.0}$= 9.43	<.0001
3	0.56	6.3	98.0	0.60	0.54	$F_{18, 396.6}$= 5.27	<.0001
4	0.15	1.7	99.7	0.36	0.85	$F_{10, 280.0}$= 2.41	0.0092
5	0.03	0.3	100.0	0.16	0.97	$F_{4, 141}$= 0.95	0.4389
Male - Complete							
1	2.96	70.4	70.4	0.86	0.10	$F_{50, 6288.0}$= 83.46	<.0001
2	0.92	22.0	92.4	0.69	0.39	$F_{36, 5169.5}$= 41.25	<.0001
3	0.22	5.2	97.7	0.42	0.75	$F_{24, 4003.0}$= 17.69	<.0001
4	0.09	2.1	99.8	0.29	0.91	$F_{14, 2762.0}$= 9.48	<.0001
5	0.01	0.2	100.0	0.09	0.99	$F_{6, 1382.0}$= 1.93	0.0723
Male - Resampled							
1	2.79	49.6	49.6	0.86	0.05	$F_{50, 619.1}$= 11.74	<.0001
2	2.21	39.2	88.8	0.83	0.18	$F_{36, 511.4}$= 8.20	<.0001
3	0.45	8.0	96.8	0.56	0.58	$F_{24, 397.9}$= 3.41	<.0001
4	0.13	2.4	99.2	0.34	0.84	$F_{14, 276.0}$= 1.74	0.0473
5	0.04	0.8	100.0	0.21	0.96	$F_{6, 139.0}$= 1.04	0.4049

TABLE 7. Classification matrices: field determination by predicted species membership for female and male plants of *Arceuthobium apachecum*, *A. blumeri*, *A. californicum*, *A. campylopodum*, *A. cyanocarpum*, and *A. monticola* based on quadratic discriminant function analyses. Separate analyses were executed per sex using complete morphological records, a full-model (N= 8 female and 10 male morphologic characters), and equal prior probabilities (0.1667).

Plant Sex / Field determination			Predicted species membership (%, [N= field determined plants])			
(N= plants)	*A. apachecum*	*A. blumeri*	*A. californicum*	*A. campylopodum*	*A. cyanocarpum*	*A. monticola*
Female						
A. apachecum (205)	**70.2 [144]**	7.3 [15]	1.5 [3]	0.0 [0]	19.5 [40]	1.5 [3]
A. blumeri (130)	6.2 [8]	**73.8 [96]**	11.5 [15]	0.0 [0]	0.8 [1]	7.7 [10]
A. californicum (100)	1.0 [1]	11.0 [11]	**68.0 [68]**	4.0 [4]	0.0 [0]	16.0 [16]
A. campylopodum (480)	0.0 [0]	0.2 [1]	5.8 [28]	**92.9 [446]**	0.0 [0]	1.0 [5]
A. cyanocarpum (208)	12.0 [25]	0.5 [1]	0.0 [0]	0.0 [0]	**87.0 [181]**	0.5 [1]
A. monticola (50)	2.0 [1]	4.0 [2]	8.0 [4]	4.0 [2]	0.0 [0]	**82.0 [41]**
Male						
A. apachecum	**71.7 [172]**	4.2 [10]	6.7 [16.0]	2.1 [5]	15.4 [37]	0.0 [0]
A. blumeri	5.4 [7]	**80.8 [105]**	6.2 [8.0]	7.7 [10]	0.0 [0]	0.0 [0]
*A. californicum (*100)	1.0 [1]	1.0 [1]	**90. 0 [90]**	0.0 [0]	0.0 [0]	8.0 [8]
A. campylopodum	2.7 [16]	8.3 [50]	0.0 [0]	**88.5 [531]**	0.5 [3]	0.0 [0]
A. cyanocarpum	0.1 [38]	1.1 [3]	0.4 [1]	1.8 [5]	**82.8 [226]**	0.0 [0]
A. monticola	0.0 [0]	2.0 [1]	4.0 [2]	0.0 [0]	0.0 [0]	**94.0 [47]**

californicum were most frequently misclassified to *A. monticola* (16.0%) followed by *A. blumeri* (11.0%), and rarely to *A. campylopodum* and *A. apachecum*. Female plants of *A. californicum*, however, were not assigned to *A. cyanocarpum*. Moreover, step-wise DFA for female plants (Table 3) clearly demonstrated that *A. campylopodum* could be clearly delimited correctly to species >90.8% of the time using as few as three characters—fruit

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TABLE 8. Quadratic discriminant function analysis (DFA) of female and male morphologies (N= 8 and 10 male characters, respectively) of *Arceuthobium apachecum*, *A. blumeri*, *A. californicum*, *A. campylopodum*, *A. cyanocarpum*, and *A. monticola*: 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. 5	Can. 1	Can. 2	Can. 3	Can. 4	Can. 5
Plant height	0.20	-0.86	0.48	-0.18	-0.42	0.31	-0.50	-0.50	-0.23	0.99
Basal diameter	0.01	-0.07	-0.57	-0.41	0.36	0.06	-0.33	0.58	0.43	0.08
Length of third internode	-0.02	0.22	-0.42	0.48	1.05	0.08	-0.02	0.11	0.07	-0.42
Width of third internode	0.50	0.49	0.83	-0.05	-0.21	0.67	0.45	-0.05	-0.20	-0.67
Fruit length	0.49	-0.84	-0.09	0.18	-0.2					
Fruit width	-0.03	0.77	-0.15	0.67	-0.18					
Seed length	0.66	0.12	-0.55	-0.67	-0.22					
Seed width	-0.02	0.27	0.53	0.24	0.36					
Petal length						-0.04	0.18	-0.68	0.73	-0.03
Petal width						0.15	0.16	1.05	-0.12	0.56
Anther dimeter						0.03	-0.33	-0.41	0.04	-0.37
Anther distance to tip						0.12	0.33	-0.05	0.55	0.13
Staminate spike length						0.09	-0.26	-0.26	0.04	-0.21
Staminate spike width						0.29	0.65	-0.16	-0.57	0.33

length, seed length, and width of the third internode. Similarly, the percentage of correct classification for female *A. cyanocarpum* was improved to a maximum of 91.3% using a reduced model consisting of the six most correlated morphologic characters to the discriminant function (Table 3); these characters included fruit length and width, seed length and width, width of the third internode, and plant height. Standardized correlation coefficients—indicating the contribution of individual female morphologies (predictor variables) to the discriminant function—calculated using a full-model (i.e , all 8 female characters) and complete records for each dwarf mistletoe are summarized in Table 8. Although female plants of *A. apachecum*, *A. blumeri,* and *A. californicum* were most often misclassified to *A. cyanocarpum*, *A. californicum*, and *A. blumeri*, respectively, the multivariate means and associated 95% confidence ellipses across these comparisons did not intersect in multidimensional space when DFA was executed using all eight female characters and complete data (Fig. 6). Multivariate means among *A. apachecum* versus *A. cyanocarpum* and *A. blumeri* vs. *A. californicum* were also separated in multidimensional space for female DFA utilizing a full-model and resampled data (25 complete records/species). Ninety-five percent confidence ellipses for *A. apachecum* and *A. cyanocarpum* did not overlap as well, while some overlap was evident between *A. blumeri* and *A. californicum*. Collectively, full-model DFAs using either complete or resampled data readily distinguished female white pine dwarf mistletoes from *A. campylopodum* and each other.

Full-model discriminant function analysis for male plants resulted in a slight improvement in the overall correct classification of taxa to species membership (84.1%) when compared to DFA of female morphologies (Tables 3 and 7), classifying five of six *Arceuthobium* spp. to correct species ≥80.8% of the time with *A. apachecum* (71.7%) being the lone exception (Table 3). The first two canonicals explained 92.4% of the variation across male plants (Table 6). Similar to female DFA, field determined male plants of *A. campylopodum* were also clearly delimited to species utilizing a full-model (88.5%; 10 male characters) or a reduced model (≥81.3%), consisting of only three to eight morphologic characters. However, unlike female DFAs, *A. campylopodum* was most often misclassified to *A. blumeri* (8.3%) rather than *A. californicum* (0.0%; Table 7). *Arceuthobium apachecum* was again frequently misclassified as *A. cyanocarpum* (15.4%); however, their multivariate means did not intersect in multidimensional space for male DFAs using complete data or a random subset of records (25 records/species) (Fig. 6). Full-model DFA with complete data for male plants also effectively distinguished *A. blumeri* (80.8%), *A. californicum* (90.0%), and *A. monticola* (94.0%) from each other as well as when compared separately to *A. apachecum* or *A. cyanocarpum*. Width of the third internode, staminate spike width, and plant height for male plants clearly separated *A. campylopodum* from the five white pine dwarf mistletoes while the

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latter male morphologic characters in combination with anther distance to tip, basal diameter, petal length, and petal width contributed most to defining species membership (Table 8). Thus, male plants of the white pine dwarf mistletoes can also be determined to species using multiple morphologic characters and segregated effectively from *A. campylopodum* in as few as three characters. These results again support our assertion that these white pine dwarf mistletoes should not be grouped under *A. campylopodum* as treated by Kuijt (2012) or as subspecies of this latter taxon as suggested by Nickrent (2012).

Phenology: Flowering Time and Seed Dispersal

Throughout their geographic distributions, we observed consistent periodicities in male flowering (anthesis; Fig. 7A) and seed dispersal (Fig. 7B) from female plants among *Arceuthobium apachecum*, *A. blumeri*, and *A. cyanocarpum* and between *A. californicum* and *A. monticola*. Anthesis began in mid- to early-September for *A. cynanocarpum*—often starting after *A. apachecum* which flowered in mid-July to mid-September. Likewise, although both of the latter species began seed dispersal in mid-August, *A. cyanocarpum* most often terminated seed dispersal in late-September whereas *A. apachecum* continued dispersing seed into mid-October. Slightly different in comparison to *A. apachecum* and *A. cynanocarpum*, *A. blumeri* initiated male flowering in mid-July, continuing into late-August. The periodicity for seed dispersal in *A. blumeri* also differed slightly compared to *A. apachecum* and *A. cyanocarpum*, whereby, female fruits of *A. blumeri* matured in late-August to early-October. These observations for anthesis and seed dispersal of *A. apachecum*, *A. blumeri*, and *A. cyanocarpum* agree with those reported by Hawksworth and Wiens (1996).

Male flowering in *Arceuthobium californicum* began in mid-June and peaked in mid-July to early-August, completing anthesis by mid-August (Fig. 7A). Fruits of *A. californicum* most often matured shortly thereafter from mid-September to mid-October with extremes from late-August to early-November (Fig. 7B). In contrast, Hawksworth and Wiens (1992) reported that *A. monticola*—the white pine dwarf mistletoe most similar morphologically to *A. californicum* (Table 1)—doesn't begin anthesis until mid-July with flowering climaxing in early- to mid-August, and continuing into early-September. They also noted seed dispersal for *A. monticola* started in early-September, peaked in late September, and was finished by late-October, which is similar to *A. californicum*. Our observations of flowering for *A. monticola* generally agreed with those reported by Hawksworth et al. (1992); however, we found the peak and termination of seed dispersal for *A. monticola* occurs in September and October, respectively (Fig. 7B; Mathiasen & Daugherty 2009). We consistently observed that *A. monticola* had completed seed dispersal by late-October and did not extend this aspect of its life cycle into November as reported by Hawksworth et al. (1992). Anthesis of *A. campylopodum* is from mid-August to early-October, with extremes from early-August to late-October (Fig. 7A). Its fruits usually mature and eject seed from early-September to mid-November (Fig. 7B). Therefore, the periodicities for anthesis and seed dispersal overlap across all of the species examined, except that flowering for *A. californicum* initiates earlier in mid-June and ends by early August. This is a key characteristic that distinguishes *A. californicum* from the other five species we studied here.

Principal Hosts: Observations

Across collection sites, we found *Arceuthobium apachecum* and *A. blumeri* exclusively on southwestern white pine (*Pinus strobiformis*)—their only principal host—confirming that both of these white pine dwarf mistletoe are indeed host specific (Mathiasen 1982; Hawksworth & Wiens 1996). Although *A. blumeri* has been reported on Mexican white pine (*P. ayacahuite* Ehrenb.) in northern Mexico (Mathiasen 1982), these white pine populations are now considered to be southwestern white pine (*P. strobiformis*; pers. comm. S. Gonzalez). Likewise, in the present study, we only observed populations of *A. monticola* infecting western white pine (*P. monticola*); however, this white pine dwarf mistletoe is also a principal parasite of Brewer spruce (*Picea breweriana*). Thus far, *A. californicum* has not been confirmed to parasitize western white pine (Mathiasen & Daugherty 2009), although this pine is common in the geographic range of *A. californicum* in the Sierra Nevada Mountains (Griffin & Critchfield 1972). Moreover, we have now collected *A. californicum* from the Klamath Ranges (near Orleans), but its distribution still remains south of that for *A. monticola*, so thus far it does not appear that the geographic ranges of *A. monticola* and *A. californicum* overlap. The principal hosts of *A. cyanocarpum* are limber

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pine (*P. flexilis*) and whitebark pine (*P. albicaulis* Engelm.), Rocky Mountain bristlecone pine (*P. aristata* Engelm ,) and Great Basin bristlecone pine (*P. longaeva* D. K. Bailey; Hawksworth & Wiens 1996; Reif et al. 2015).

Although Hawksworth et al. (1992) and Hawksworth and Wiens (1996) reported that *Arceuthobium californicum* rarely parasitizes western white pine, this is evidently based on one report of this mistletoe-host combination from Castle Lake Campground, west of Shasta City, California (see Hawksworth and Wiens 1996, p. 334). Our field observations at Castle Lake, and our comparison of specimens of *A. californicum* and *A. cyanocarpum*, indicate the dwarf mistletoe infecting western white pine at Castle Lake is *A. cyanocarpum*. Therefore, we believe there are no confirmed reports of *A. californicum* on western white pine at this time. We also observed *A. monticola* infecting sugar pine (*P. lambertiana*) at two locations in northern California, but this pine is clearly a rare host of *A. monticola* at both locations. In contrast, sugar pine is the principal host of *A. californicum* and, commonly, is severely infected in many areas of California where this host-parasite combination occurs (Hawksworth & Wiens 1996). Although *A. cyanocarpum* primarily parasitizes white pines, it has been reported to occasionally parasitize mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) in the Cascade Mountains and rarely parasitize lodgepole pine (*P. contorta* Douglas ex Loudon) and ponderosa pine (*P. ponderosa*) in the Rocky Mountains as well. However, it has only been rarely reported on sugar pine thus far (Mathiasen & Daugherty 2010).

In the present study, we only observed *Arceuthobium campylopodum* on hard pines (subg. *Pinus*) including ponderosa pine, Jeffrey pine (*P. jeffreyi*), knobcone pine (*P. attenuata* Lemmon), Coulter pine (*P. coulteri* D. Don), and gray pine (*P. sabiniana* Douglas ex D. Don). The only reports of *A. campylopodum* parasitizing a white pine are based on rare infection of sugar pine in southern Oregon (Hawksworth & Wiens 1996), but this report has never been confirmed. Western white pine is immune to infection by *A. campylopodum*, but this white pine is the principal host of *A. monticola* and a secondary host of *A. cyanocarpum* in northern California and southern Oregon (Mathiasen & Hawksworth 1988, Hawksworth & Wiens 1996).

CONCLUSIONS

Our morphological analyses of female and male plants of *Arceuthobium apachecum*, *A. blumeri*, *A. californicum*, *A. cyanocarpum*, and *A. monticola* indicated that these mistletoes should be treated as species and not relegated to subspecies of *A. campylopodum* as proposed by Nickrent (2012). Furthermore, it is obvious that these parasites of white pines should not be grouped under *A. campylopodum* as proposed by Kuijt (2012). Although there is considerable overlap in periodicity of male flowering and seed dispersal from female plants, the white pine dwarf mistletoes are morphologically distinguishable from *A. campylopodum* and each other. Flowering time and the principal parasitism of *Pinus lambertiana* clearly separate *A. californicum* from the four other white pine dwarf mistletoes we studied as well as *A. campylopodum*. Furthermore, differences in host affinities and/or geographic distributions among these white pine dwarf mistletoes set them apart from each other.

Reminiscent of his review (Kuijt 1973) of Hawksworth and Wiens' first monograph for *Arceuthobium* (Hawksworth & Wiens 1972), Kuijt (2016) continued to argue that taxa in ser. *Campylopoda* cannot be distinguished using morphological characteristics, particularly the mean length of the third internode. We have clearly demonstrated here and in previous work that these species can be separated consistently using statistically significant differences between the means of several morphological characters of female and male plants (Mathiasen & Daugherty 2009, 2013; Mathiasen & Kenaley 2015a, 2015b; Mathiasen et al. 2016). Thus, we cannot dismiss these morphologic differences among ser. *Campylopoda* taxa as simply statistically significant, yet, trivial differences among populations of a "ringed species" or a hybrid swarm complex as proposed by Kuijt (2016). In his paper, Kuijt (2016) essentially asserted that the dimensions of flowers and fruits of dwarf mistletoes cannot be measured accurately because they are too small; a perspective that contemporary biologists/taxonomists likely will take exception with given the capabilities of present day mensuration equipment and technologies. With minimal training, plant height and length as well as basal diameter can be measured accurately—and with repeatability—to the nearest 0.1 cm or 0.1 mm using a digital caliper, whereas, flowers, fruit, and seed dimensions can also be determined with great precision using a magnifier equipped with a micrometer.

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However, the principal points Kuijt (2016) appears to address are solely argumentative; questioning anyone's "taxonomic judgement" who disagrees with his grouping of all taxa in ser. *Campylopoda* sensu Hawksworth and Wiens (1996) and, specifically, the continued comparison of means and ranges for the third internode length among dwarf mistletoes (Mathiasen & Kenaley 2015a; Nickrent 2012). He is rightfully granted to have his own perspectives on the taxonomic treatment of ser. *Campylopoda* taxa—a perspective that has remained unchanged for over 40 years (Kuijt 1973). We, however, respectively disagree that past taxonomic decisions other than his own—either by us or colleagues—for grouping *Arceuthobium* spp. were based primarily on significant differences between means or overlap in the ranges of the third internode length. Although we do report and compare the means for third internode lengths, we have previously and will continue to place little emphasis on this character; including for the white pine dwarf mistletoes studied here. Likewise, the taxonomic treatments of ser. *Campylopoda* by Hawksworth and Wiens (1972, 1996) or the recent reclassification proposed by Nickrent (2012) were not based solely on interspecific differences, or lack thereof, in the third internode length. Nickrent (2012), however, did indeed reference the overlapping ranges of third internodal lengths reported by Hawksworth and Wiens (1996) in support of his taxonomic recommendations for ser. *Campylopoda* taxa; yet the foundation for his recommendations was clearly based on ITS and *trn T-L-F* DNA sequence data (Nickrent et al. 2004). In the past, we have noted Kuijt's concern regarding the use of third internode length (Mathiasen & Daugherty 2013) and pointed out that the width of the third internode in conjunction with basal diameter can provide informative data for comparing the relative thickness of dwarf mistletoe plants (Mathiasen & Kenaley 2015a). Hence, we will continue to measure third internode lengths and report this information while placing little emphasis on significant differences for reasons cited by Kuijt (1969, 2016).

Finally, it should be clear that although we do conclude that there are taxonomically significant differences among the white pine dwarf mistletoes and *A. campylopodum* based on the morphological characters we measured, we also considered differences in phenology and host specificity. Hence, our taxonomic conclusions on ser. *Campylopoda* taxa are based on a wide range of morphological and physiological characteristics and do not agree with Kuijt's (2012, 2016) superficial treatment of these taxa. We have clearly demonstrated here and in a previous work that these species can be consistently separated using morphological data and univariate as well as multivariate statistical analyses—even without consideration(s) of geographic isolation, host specificities, phenology, and third internode length (Mathiasen & Daugherty 2009, 2013; Mathiasen & Kenaley 2015a, 2015b; Mathiasen et al. 2016).

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