

A MORPHOMETRIC ANALYSIS OF DWARF MISTLETOES IN THE
ARCEUTHOBIMUM CAMPYLOPODUM–*OCCIDENTALE* COMPLEX (VISCACEAE)

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ABSTRACT

The classification of the dwarf mistletoes comprising the *Arceuthobium campylopodum-occidentale* complex continues to be one of the most difficult taxonomic problems associated with this important group of parasitic flowering plants. The complex consists of four taxa: *A. campylopodum* Engelman, *A. occidentale* Engelman, *A. littorum* Hawksworth, Wiens & Nickrent, and *A. siskiyouense* Hawksworth, Wiens & Nickrent; all of which are morphologically similar, flower and disperse seed in the fall, and parasitize hard pines. We collected morphological measurements for these four taxa from throughout their geographic ranges and used non-parametric and multivariate statistical analyses to compare morphological differences among them. Our analyses demonstrated that male plants of *A. littorum* and *A. siskiyouense* can be delimited morphologically; therefore, we recommend that both taxa continue to be recognized as species. Although, our results indicated that *A. occidentale* is very similar morphologically to *A. campylopodum*, it can be distinguished from the latter species using morphological characters, particularly for female plants. Furthermore, because *A. occidentale* flowers and disperses seed nearly one month later than *A. campylopodum*, we recommend it continue to be treated at the species level pending additional study. Comparative morphological and phenological differences between and among the species studied herein are summarized and can be used for field/ laboratory diagnosis of these taxa.

Key Words: dwarf mistletoes, morphological characters, multivariate analyses, *Pinus attenuata*, *Pinus jeffreyi*, *Pinus muricata*, *Pinus ponderosa*, *Pinus sabiniana*.

Dwarf mistletoes (*Arceuthobium* spp., Viscaceae) are obligate, parasitic flowering plants that are considered to be a taxonomically difficult genus. Because of their parasitic habit they have undergone extreme morphological reduction, which has resulted in many taxa being morphologically similar (Gill 1935, Hawksworth and Wiens 1996). Dwarf mistletoes are dioecious plants and sexual dimorphism between the sexes is pronounced for some species and less so for others (Hawksworth and Wiens 1972, 1996). Because there are often morphological differences between male and female plants, taxonomic descriptions often include morphological data for each sex. Furthermore, because the dwarf mistletoes are obligate parasites of many economically important members of the Pinaceae in the western United States, Canada, and México and are relatively host specific parasites, their host affinities are considered to be an important consideration for their taxonomic classification (Hawksworth and Wiens 1972, 1996; Mathiasen and Daugherty 2007, 2009a, b, 2013).

The classification of the dwarf mistletoes closely allied with *Arceuthobium campylopodum* Engelman has continued to be one of the most difficult taxonomic problems associated with this important group of parasitic flowering plants (Hawksworth and Wiens 1972, 1996; Nickrent et

al. 2004). These dwarf mistletoes parasitize closely related hard pines (Pinaceae) in *Pinus* subsect. *Attenuatae* Burgh, *Pinus* subsect. *Ponderosae* Loudon, and *Pinus* subsect. *Sabinianae* Loudon (Hawksworth and Wiens 1996; Price et al. 1998). However, the susceptibility of affected pines varies considerably depending on the population(s) of dwarf mistletoes parasitizing them (Hawksworth and Wiens 1996). In addition, these dwarf mistletoes are morphologically similar, flower and disperse seed in the fall, and are sometimes sympatric.

Engelmann first described *Arceuthobium campylopodum* in 1850 based on a specimen collected on ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson), likely from northeastern Washington (Gray 1850; Gill 1935; Hawksworth and Wiens 1996). Then in 1878, Engelmann described *A. occidentale* Engelman, a species very similar to *A. campylopodum*, based on a specimen collected on gray pine (*Pinus sabiniana* Douglas ex D. Don) in the southern Sierra Nevada Mountains, California (Kern County) (Wheeler 1878). In their first monograph of *Arceuthobium*, Hawksworth and Wiens (1972) recognized *A. occidentale* as a valid species and listed its principal hosts as gray pine, Monterey pine (*P. radiata* D. Don), and Bishop pine (*P. muricata* D. Don). They maintained that *A.*

occidentale could be differentiated readily from *A. campylopodum* based on phenology, morphology, geographic distribution, and host preference (Hawksworth and Wiens 1972, see pp. 112–114). They also concluded that *A. campylopodum* was a principal parasite of ponderosa pine and Jeffrey pine (*P. jeffreyi* Greville & Balfour) and only occasionally parasitized gray pine.

Following additional studies of the dwarf mistletoe populations parasitizing knobcone pine (*P. attenuata* Lemmon) in northern California and southwestern Oregon, Hawksworth et al. (1992) described *A. siskiyouense* Hawksworth, Wiens & Nickrent as a separate species from *A. campylopodum* based on host range, morphology, phenology, and other physiological discontinuities. They also segregated *A. littorum* Hawksworth, Wiens & Nickrent from *A. occidentale*, basing their classification of *A. littorum* on similar criteria used to separate *A. siskiyouense* from *A. campylopodum*. The delineation of *A. siskiyouense* from *A. campylopodum* and *A. littorum* from *A. occidentale* was also supported by electrophoretic analyses of several isozymes (Nickrent and Butler 1990, 1991). Therefore, in the most recent monograph for *Arceuthobium* worldwide, Hawksworth and Wiens (1996) maintained the classification of what they termed the *Arceuthobium campylopodum-occidentale* complex as four distinct species: 1) *A. campylopodum*, which was primarily a parasite of ponderosa and Jeffrey pines distributed from northern Washington to Baja California, México; 2) *A. occidentale*, which was primarily a parasite of gray pine in the foothills surrounding the Central Valley, California; 3) *A. littorum*, which was a parasite of Monterey and Bishop pines in coastal California; and, 4) *A. siskiyouense*, which was primarily a parasite of knobcone pine in northern California and southwestern Oregon.

Although Hawksworth and Wiens (1996), as well as Hawksworth et al. (2002), indicated that the morphological and physiological differences between the taxa in the *Arceuthobium campylopodum-occidentale* complex clearly supported their classification as species, molecular phylogenetic analyses using nuclear ribosomal internal transcribed spacer (ITS) and chloroplast *trn T-L-F* sequences have suggested these species may be conspecific (Nickrent et al. 2004). Nickrent (2012) subsequently recombined *A. occidentale*, *A. littorum*, and *A. siskiyouense* as subspecies of *A. campylopodum* because of their overlapping host ranges, similar ITS and chloroplast DNA sequences, and morphological similarities. However, Mathiasen and Daugherty (2009a) compared additional morphological data collected for *A. siskiyouense* and compared their results with the data for *A. campylopodum* reported in Hawksworth and Wiens (1996). They concluded that *A. siskiyouense* should not be treated as a

subspecies of *A. campylopodum* as was later proposed by Nickrent (2012). Likewise, Mathiasen and Daugherty (2013) reported additional morphological measurements for *A. occidentale* and *A. littorum* and concluded that the morphological differences between these taxa also supported their classification as distinct species.

Although the morphological data presented here for *Arceuthobium siskiyouense*, *A. littorum*, and *A. occidentale* have been previously reported (Mathiasen and Daugherty 2009a, 2013), additional morphological data was needed for *A. campylopodum* before all four species could be compared using the same morphometric analysis. Because a detailed analysis comparing these four species using both non-parametric univariate and multivariate statistical techniques had not been completed, we undertook this study. This more robust statistical examination of morphological characters for the *A. campylopodum-occidentale* complex has been recommended (Nickrent et al. 2004; Mathiasen and Daugherty 2009a; Nickrent 2012). Furthermore, the need for a detailed morphometric analysis of this complex was justified because of the recent treatment by J. Kuijt (Baldwin et al. 2012) in which *A. siskiyouense*, *A. littorum*, and *A. occidentale* were circumscribed under *A. campylopodum*. Because this highly conservative treatment of the *A. campylopodum-occidentale* complex appears to ignore the morphological and host range differences reported in the scientific literature cited above, a more stringent morphometric analysis of the complex was clearly needed.

METHODS

Sampling and Measurements

Previously, the senior author collected morphological data for *Arceuthobium siskiyouense* from its pine hosts (*Pinus attenuata*, *P. jeffreyi*, and *P. contorta* Douglas ex Loudon) for 15 populations in northwestern California and southwestern Oregon (Fig. 1) (Mathiasen and Daugherty 2009a). In addition, the senior author sampled eight populations of *A. littorum* along the Pacific Coast of California and 28 populations of *A. occidentale* throughout most of its distribution (Fig. 2) (Mathiasen and Daugherty 2013). Morphological measurements were made from plants of *A. littorum* from five and three locations where it parasitized Bishop and Monterey pine, respectively. All of the morphological measurements made for *A. occidentale* were from locations where it parasitized gray pine. From August 2009 to September 2012, we sampled 60 populations of *A. campylopodum* throughout most of its geographic range specifically for this study. This sample consisted of 30 populations on ponderosa pine and 30 populations on Jeffrey

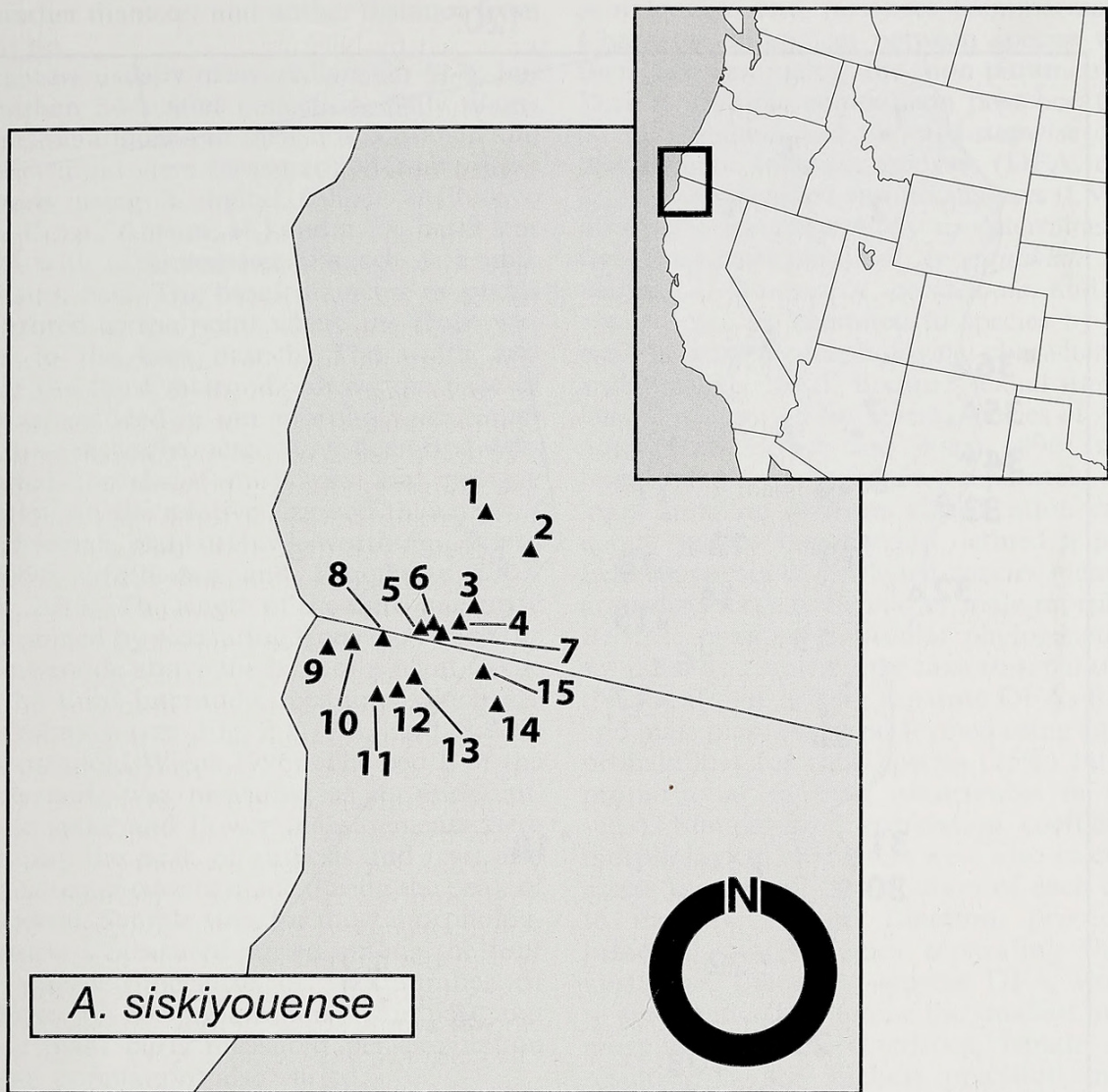


FIG. 1. Approximate location of collection sites in California and Oregon for *A. siskiyouense* (modified from Mathiasen and Daugherty 2009). Collections by R. L. Mathiasen (RLM); vouchers deposited at the Deaver Herbarium, Northern Arizona University, Flagstaff (ASC) or the University of Arizona Herbarium, Tucson (ARIZ). Numbers correspond to the following locations: 1 - Chrome Ridge, RLM 9877, ARIZ; 2 - Lookout Gap, RLM 0528, ASC; 3 - Rock Creek on Oregon Mountain Road, RLM 0859, ARIZ; 4 - Type locality for *A. siskiyouense* on Oregon Mountain Road, RLM 0863, ARIZ; 5 - 3 km southwest of Bain Station, RLM 9849, ASC; 6 - Bain Station, RLM 9848, ASC; 7 - Oregon Mountain, RLM 9843, ASC; 8 - Smith River Bridge, RLM 0510, ASC; 9 - High Divide, RLM 0504, ASC; 10 - Pine Flat Mountain, RLM 0513, ASC; 11 - Old Gasquet Toll Road, near Danger Point, RLM 0521, ASC; 12 - Old Gasquet Toll Road near Elevenmile Creek, RLM 9868, ASC; 13 - Old Gasquet Toll Road near Twelvemile Creek, RLM 0523, ASC; 14 - Bear Gulch, RLM 9886, ASC; 15 - 5 km north of Black Butte, RLM 9882, ASC.

pine (Fig. 3). 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 information and specific population data, including GPS coordinates, have been archived electronically in the Southwest Environmental Information Network (SEINet 2014). Detailed voucher data and a map for each collection location can be retrieved with SEINet using the collection number and herbarium listed for each location in Figures 1–3.

For each mistletoe population, 10–20 male and 10–20 female infections were collected separately

and the dominant plant (largest plant) from each infection was used for morphological measurements. The dwarf mistletoe plant characters measured were those used by Hawksworth and Wiens (1996) for the taxonomic classification of *Arceuthobium* taxa. The following morphological characters were measured: 1) height, basal diameter, third internode length and width, and color of male and female plants; 2) mature fruit length, width, and color; 3) seed length, width and color; 4) length and width of staminate spikes; 5) staminate flower diameters for 3- and 4-merous flowers (5-merous for *A. littorum*); 6) length and width of staminate flower petals;

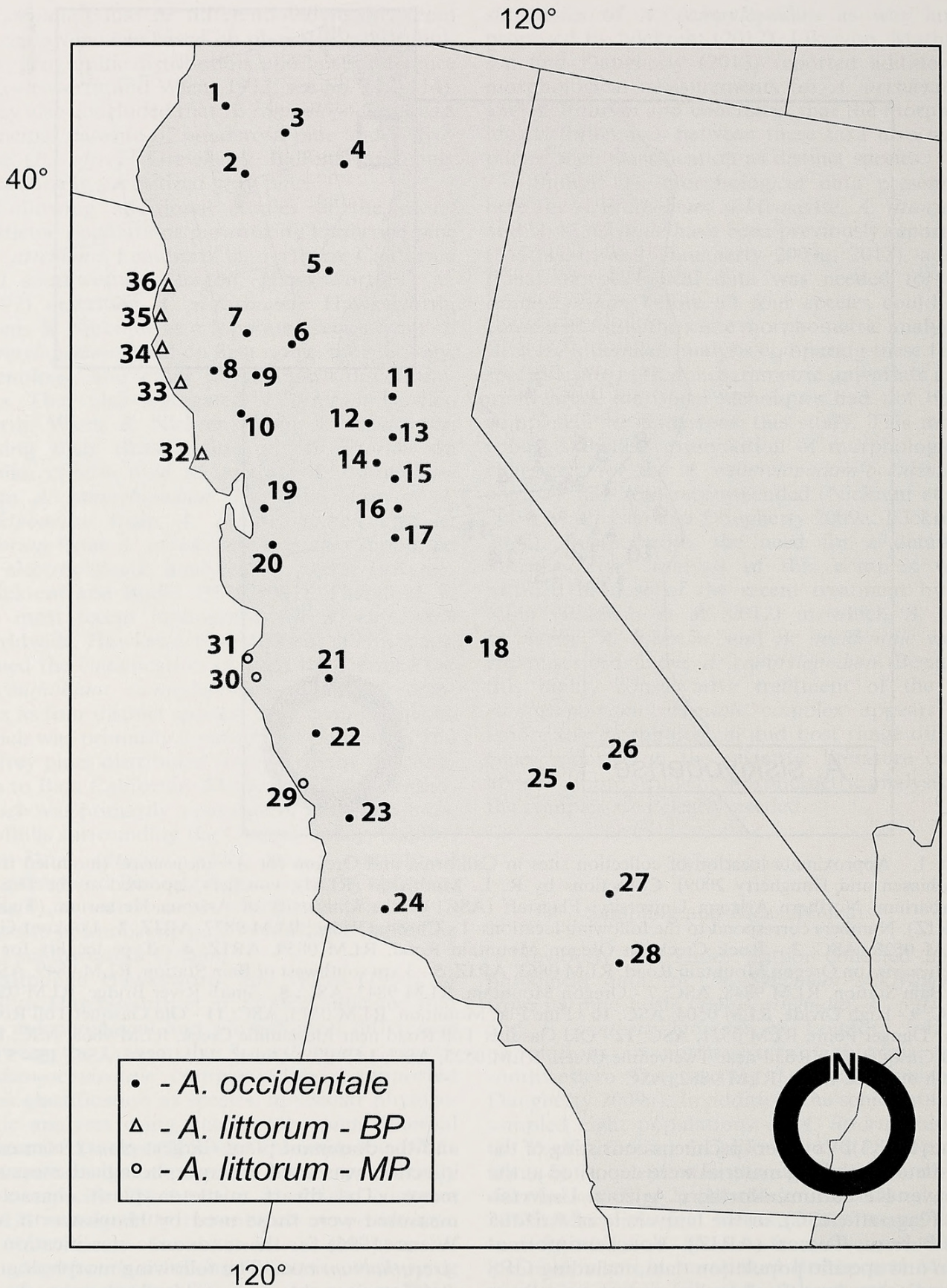


FIG. 2. Approximate location of collection sites for *Arceuthobium occidentale* and *A. littorum* in California from Mathiasen and Daugherty (2013). Dark circles represent locations where *A. occidentale* was collected and measured on *Pinus sabiniana*. Open circles represent locations where *A. littorum* was collected and measured on *Pinus radiata* (MP). Open triangles represent locations where *A. littorum* was collected and measured on *Pinus muricata* (BP). Collections by R. L. Mathiasen (RLM); vouchers deposited at the University of Arizona Herbarium, Tucson (ARIZ). Numbers correspond to the following locations: 1- 2 km S of St. Rte. 299 on Burnt Ranch School rd., RLM 1281, ARIZ; 2 - Beegum Creek on St. Rte. 36, RLM 1229, ARIZ; 3 - 1 km S of St. Rte. 299 on Carr

and 7) anther diameter and anther distance from the petal tip.

Plants were usually measured within 12-h, but no later than 24-h after collection. Only plants that were still attached to their host's branch and were fully turgid were measured. Measurements were made using a digital caliper (Mitutoyo America Corp., Aurora, IL) and a 7× hand lens equipped with a micrometer (Bausch & Lomb, Bridgewater, NJ). The basal diameter of plants was measured at the point where the plant was attached to the host branch. The width and length of the third internode above the base of plants was included in our morphological analyses because these characters have been frequently reported for dwarf mistletoes and provide information on the relative size and thickness of male and female plants (Hawksworth and Wiens 1972, 1996; Mathiasen and Daugherty 2007, 2009a, b, 2013). The length of the third internode was determined by measuring from the top of the second internode above the base of a plant to the top of the third internode, locations which are easily observed (see Fig. 2.1, 2.3, and 2.9 in Hawksworth and Wiens 1996). The width of the third internode was measured at its midpoint. Staminate spike and flower measurements were made during the peak of anthesis and fruit and seed measurements were made during the peak of seed dispersal. Sample sizes for most morphological characters measured varied among the four species sampled because of the number of populations (8–60 populations) sampled and plants or plant parts measured per population (10–20 per population) also varied.

Statistical Analyses

We assessed whether values for morphological characters differed between and among species using Welch's *t* tests to accommodate unequal

sample sizes and variances (Zimmerman 2004). Character differences between species were further assessed using the non-parametric Steel-Dwass, multiple comparison post hoc test ($\alpha = 0.05$). Standard and forward-stepwise quadratic discriminant function analyses (DFA, otherwise known as canonical variate analyses [CVA]) were also performed separately to determine whether female or male plants of *Arceuthobium campylopodum*, *A. littorum*, *A. occidentale*, and *A. siskiyouense* can be delimited to species by the joint examination of morphological characters (Quinn and Keough 2002). Because sexual dimorphism has been reported for several species of *Arceuthobium* (Hawksworth and Wiens 1996), male and female plants were examined separately. Discriminant function analyses classification compared actual species membership defined a priori via field diagnosis to predicted species memberships according to only female or male morphologies. Because previous molecular phylogenetic analyses failed to resolve these taxa to separate species (Nickrent et al. 2004), separate DFAs for female and male plants were performed using equal prior probabilities for each species (25%) rather than proportional to their occurrences in the data set(s). Standardized correlation coefficients for morphological characters were also calculated to assess the overall contribution of each character to the discriminant function, providing the principal morphologies separating the dwarf mistletoes. Likewise, stepwise DFA was utilized to systematically examine the smallest number of morphological characteristics, female or male, resulting in the highest precision in species classification (% actual/predicted). To further validate the DFA, we separately resampled the original (complete) data set for female and male plants; selecting at random 50 complete records per species and re-executing the DFA using a full-model (i.e., all morphological characteristics

Powerhouse rd., RLM 1227, ARIZ; 4 - 29 km E. of Redding on St. Rte. 44 at Black Butte rd., RLM 1226, ARIZ; 5 - 14 km NE of St. Rte. 99 on St. Rte. 70, RLM 1230, ARIZ; 6 - 0.5 km E of Colusa County line on St. Rte. 20, RLM 1231, ARIZ; 7 - 3 km from St. Rte. 20 on County Rd. M-12, RLM 1232, ARIZ; 8 - 3 km S of Covelo on St. Rte. 162, RLM 1283, ARIZ; 9 - Entrance to Langtry Winery, RLM 1239, ARIZ; 10 - Butts Canyon, RLM 1238, ARIZ; 11 - 1 km S of Auburn on St. Rte. 49, RLM 1240, ARIZ; 12 - Beales Pt. Campground on Folsom Lake, RLM 1264, ARIZ; 13 - 4 km N of Placerville on St. Rte. 49, RLM 1241, ARIZ; 14 - 6 km S of St. Rte. 16 on St. Rte. 124, RLM 1243, ARIZ; 15 - Columbia Airport rd., RLM 1245, ARIZ; 16 - 11 km S of Angels Camp on St. Rte. 4, RLM 1244, ARIZ; 17 - N side of Roberts Memorial Bridge on St. Rte. 120, RLM 1246, ARIZ; 18 - 0.2 km SW of Prather on Auberry Rd., RLM 1251, ARIZ; 19 - 3 km N of entrance gate to Mount Diablo State Park, RLM 1263, ARIZ; 20 - 19 km E of San Jose on Mount Hamilton rd., RLM 1262, ARIZ; 21 - 5 km W of visitors center in Pinnacles Nat. Mon., RLM 1261, ARIZ; 22 - 10 km E of Jolon on Nacimiento-Fergusson rd., RLM 1258, ARIZ; 23 - 5 km SE of St. Rte. 58 on Pozo rd., RLM 1302, ARIZ; 24 - 13 km E of Los Olivos on Figueroa Mt. rd., RLM 1291, ARIZ; 25 - 13 km E of Glenville on St. Rte. 155, RLM 1250, ARIZ; 26 - 3 km S of Kernville, RLM 1249, ARIZ; 27 - 1 km SW of St. Rte. 58 on Hart Flat rd., RLM 1265, ARIZ; 28 - 1 km S of Lake Hughes on Lake Hughes rd., RLM 1247, ARIZ; 29 - 1 km N of Cambria on Santa Rosa Cemetery rd., RLM 1257, ARIZ; 30 - 0.5 km E of St. Rte. 1 on Fern Canyon rd., RLM 1259, ARIZ; 31 - Pacific Grove, 0.5 km E of Stevenson Dr. on Forest Lake rd., RLM 1260, ARIZ; 32 - 3 km NW of Inverness, Pt. Reyes Nat. Seashore, RLM 1287, ARIZ; 33 - 0.5 km E of St. Rte. 1 on Kruse-Rhododendron rd., RLM 1236, ARIZ; 34 - 7 km E of Pt. Arena on Eureka Hill rd., RLM 1235, ARIZ; 35 - 4 km E of Albion River on Little River rd., RLM 1285, ARIZ; 36 - 4 km E of Fort Bragg on St. Rte 20, RLM 1233, ARIZ.

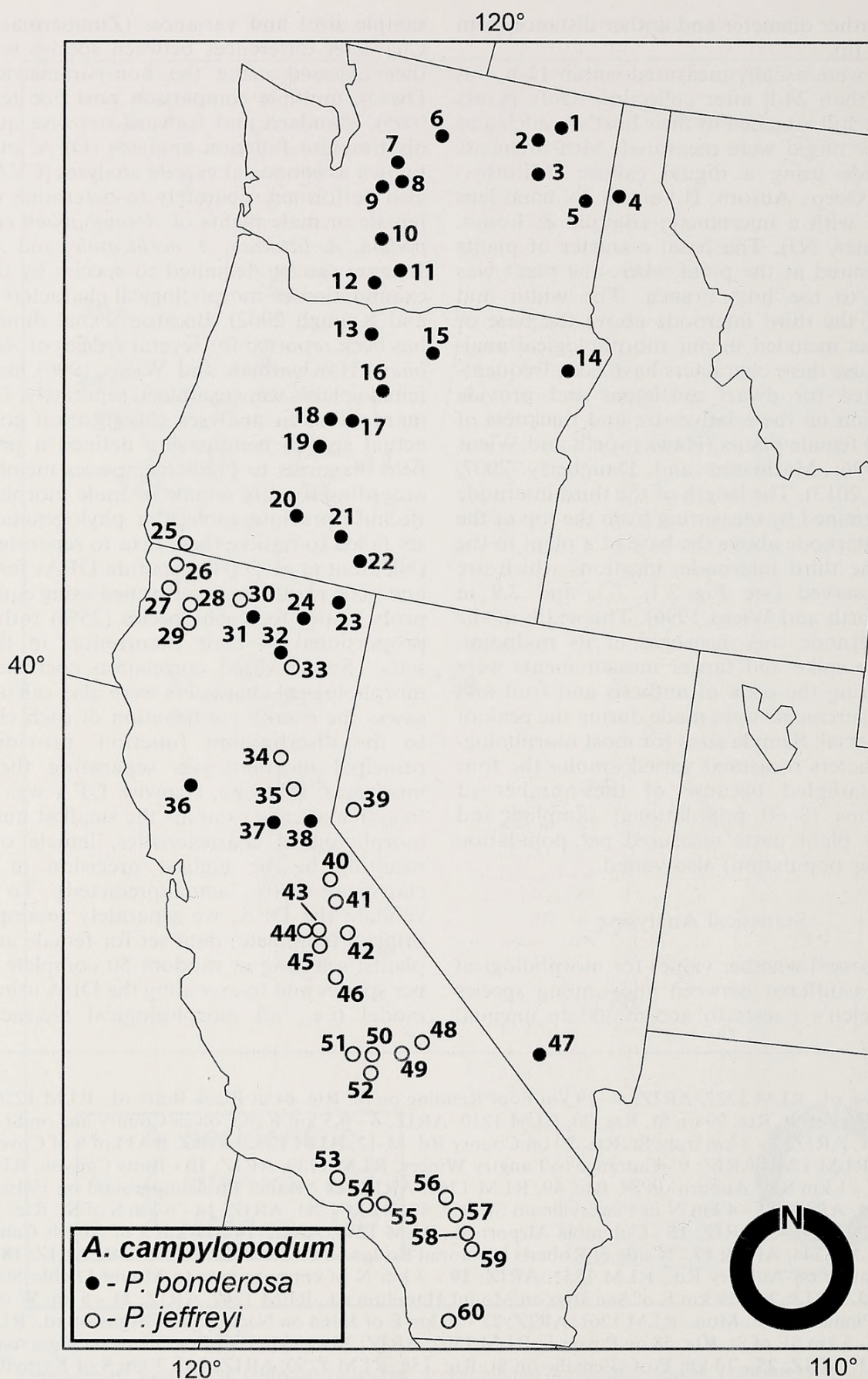


FIG. 3. Approximate locations of collection site for *Arceuthobium campylopodum*. Closed circles present locations where plants were collected from *Pinus ponderosa*. Open circles represent locations where plants were collected from *P. jeffreyi*. Collections by R. L. Mathiasen (RLM); vouchers deposited at the Deaver Herbarium, Northern Arizona University, Flagstaff (ASC) or the University of Arizona Herbarium, Tucson (ARIZ). Numbers correspond to the following locations: 1 - 4.5 km N of Gifford on St. Rte. 25, RLM 1202, ARIZ; 2 - 20 km S of Fruitland on St. Rte. 25, RLM 1204, ARIZ; 3 - 2 km NW of Nespelem on St. Rte. 155, RLM 1205, ARIZ;

simultaneously; and with equal prior probabilities). Non-parametric tests and DFAs were computed in JMP Pro 10 (SAS Institute, Cary, NC).

RESULTS

The mean heights of female plants for all four taxa were similar, but female plants of *A. siskiyouense* were significantly smaller than the other species (Table 1, Appendix 1). Mean plant heights for male plants were also similar, but those of *Arceuthobium littorum* were significantly larger than *A. campylopodum* and *A. siskiyouense*; whereas, those of *A. siskiyouense* were significantly smaller than the other taxa. The mean for the basal diameters of male and female plants ranged from 3.0–3.9 mm across all four species. However, the mean diameters for female plants of *A. occidentale* and *A. siskiyouense* were significantly smaller compared to the other two species. The mean basal diameter of male plants of *A. littorum* was significantly larger when compared separately to the other three species, while the basal diameters of *A. occidentale* and *A. siskiyouense* were significantly smaller. The length

of the third internodes of female plants for *A. occidentale* was significantly smaller than *A. campylopodum*, *A. littorum*, and *A. siskiyouense* (Table 1). However, for male plants, length of the third internode was largest and significantly greater for *A. littorum* when compared to the other species examined. Although the mean width of the third internode for male and female plants only varied from 2.0–2.7 mm, significant differences were evident between and across species with male and female plants of *A. littorum* possessing the widest third internodes followed by male and female plants of *A. campylopodum*, *A. occidentale*, and *A. siskiyouense*, respectively. The mean width of the third internode and the mean basal diameter of plants was smaller for *A. siskiyouense* and *A. occidentale* than the other two species, thereby, indicating plants of the former species are consistently more slender in appearance than those of *A. campylopodum* or *A. littorum*.

The staminate spikes of *Arceuthobium littorum* were significantly longer on average than any of the other three species, but staminate spikes of *A. occidentale* were also significantly longer than those of *A. campylopodum* and *A. siskiyouense*.

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

TABLE 1. MORPHOLOGICAL MEASUREMENTS FOR *ARCEUTHOBIMUM CAMPYLOPODUM*, *A. OCCIDENTALE*, *A. LITTORUM*, AND *A. SISKIYOUENSE*. Data are listed as mean, (SD) [n]. Means are presented in bolded typeface, those followed by different capital letters in the same row were significantly different using Welch's t tests and the nonparametric Steel-Dwass, multiple comparison post hoc test ($\alpha = 0.05$). Lower case letters in brackets designate sample sizes already listed in the same column. Plant heights are in cm and all other measurements in mm.

Character	<i>Arceuthobium campylopodum</i>	<i>Arceuthobium occidentale</i>	<i>Arceuthobium littorum</i>	<i>Arceuthobium siskiyouense</i>
Plant Height				
Female	10.4 A (2.7) [600a]	10.6 A (3.0) [280a]	10.3 A (2.6) [100a]	9.1 B (1.9) [280a]
Male	9.7 A (3.0) [a]	10.1 AB (2.9) [a]	10.5 B (3.0) [a]	8.2 C (1.8) [210b]
Basal Diameter				
Female	3.4 A (0.7) [a]	3.2 B (0.6) [a]	3.9 C (0.9) [a]	3.0 D (0.6) [a]
Male	3.2 A (0.6) [a]	3.0 B (0.7) [a]	3.5 C (0.7) [a]	3.1 B (0.5) [b]
Length of Third Internode				
Female	13.0 A (3.1) [a]	12.0 B (3.0) [a]	13.7 A (3.7) [a]	13.4 A (3.5) [a]
Male	12.0 A (3.3) [a]	11.7 A (3.1) [a]	13.5 B (3.1) [a]	12.2 A (3.3) [b]
Width of Third Internode				
Female	2.5 A (0.4) [a]	2.2 B (0.4) [a]	2.6 C (0.3) [a]	2.0 D (0.3) [a]
Male	2.5 A (0.4) [a]	2.2 B (0.4) [a]	2.7 C (0.3) [a]	2.1 D (0.3) [b]
Staminate Spike Length	12.7 A (4.7) [760b]	13.9 B (4.7) [200b]	20.6 C (10.5)[a]	11.8 A (2.9) [300c]
Staminate Spike Width	3.0 A (0.3) [b]	2.9 B (0.3) [b]	3.4 C (0.4) [a]	2.0 D (0.2) [c]
Flower Diameter				
3-merous	3.1 A (0.4) [400]	3.0 B (0.3) [185c]	3.5 C (0.6) [50]	3.2 A (0.3) [150d]
4-merous	4.2 A (0.5) [360]	4.1 A (0.6) [c]	5.2 B (0.8) [135]	4.5 C (0.5) [d]
5-merous	None observed	Only one 5-merous flower observed	5.7 (0.5) [20]	None observed
Petal Length	1.6 A (0.2) [b]	1.5 B (0.2) [370d]	1.9 C (0.3) [205b]	1.5 B (0.2) [c]
Petal Width	1.4 A (0.2) [b]	1.3 B (0.2) [d]	1.6 C (0.3) [b]	1.5 D (0.2) [c]
Anther Diameter	0.6 A (0.1) [b]	0.6 A (0.1) [d]	0.9 B (0.2) [b]	0.8 B (0.2) [c]
Anther Distance from Tip	0.6 A (0.1) [b]	0.6 A (0.1) [d]	0.9 B (0.2) [b]	0.8 C (0.1) [c]
Fruit Length	5.4 A (0.5) [480d]	5.2 B (0.6) [220e]	5.4 A (0.5) [a]	5.2 B (0.6) [190d]
Fruit Width	3.7 A (0.4) [d]	3.3 B (0.5) [e]	3.6 A (0.3) [a]	3.4 B (0.4) [e]
Seed Length	3.5 A (0.4) [d]	3.5 A (0.3) [e]	3.4 A (0.3) [a]	3.1 B (0.4) [e]
Seed Width	1.5 A (0.4) [d]	1.3 B (0.2) [e]	1.3 B (0.2) [a]	1.3 B (0.2) [e]

Staminate spikes of *A. littorum* were often unbranched and were sometimes approximately six cm in length. Moreover, male plants of *A. littorum* emerging from infected branches occasionally did not branch and were almost five cm in height. The mean width of staminate spikes was also much larger for *A. littorum* and smallest for *A. siskiyouense* when all four species were compared simultaneously; the mean width of staminate spikes was significantly different across species (Table 1).

The mean diameter of 3-merous flowers was much larger for *Arceuthobium littorum* and similar for the other three species (Table 1, Appendix 1). The mean diameter of 4-merous flowers was similar for *A. campylopodum* and *A. occidentale*, largest for *A. littorum*, and *A. siskiyouense* was intermediate among the other species. Petal lobe dimensions were similar across all four taxa, but the mean length of petal lobes was greatest for *A. littorum* (Table 1). Similarly, the mean width of petal lobes only varied by 0.1–0.3 mm between the species, but was significantly different. Mean anther diameter for *A. littorum* was significantly greater than *A. campylopodum*

and *A. occidentale*, but not *A. siskiyouense*. Although smaller than *A. littorum*, the mean anther diameter of *A. siskiyouense* was also significantly greater than the anther diameters of *A. campylopodum* and *A. occidentale*. However, the mean anther diameters for the latter two taxa – *A. campylopodum* and *A. occidentale* – were identical.

Mean fruit length only varied from 5.2–5.4 mm, but was significantly different for *Arceuthobium littorum* and *A. campylopodum* than *A. occidentale* (Table 1); mean seed width followed a similar pattern. The mean length of seeds was significantly less for *A. siskiyouense* and mean seed width greatest for *A. campylopodum*, but mean seed width was not significantly different among the four taxa.

Plant color of *A. littorum* was dark green to dark greenish-brown and distinctly different from those of the other three species. Plants of *Arceuthobium siskiyouense* were dark brown to reddish-brown whereas those of *A. occidentale* consistently were yellow to yellow-green or straw in color and typically highly glaucous, giving them a bluish tinge. Plants of *A. campylopodum*

TABLE 2. MORPHOLOGICAL MEASUREMENTS FOR *ARCEUTHOBIUM CAMPYLOPODUM* ON *PINUS PONDEROSA* AND *P. JEFFREYI*. Data are listed as mean, (SD) (range) [n]. Means are presented in bold typeface. No significant differences between means were found using Welch's t tests and the nonparametric Steel-Dwass, multiple comparison post hoc test ($\alpha = 0.05$). Lower case letters in brackets designate sample sizes already listed in the same column. Plant heights are in cm and all other measurements in mm.

Character		<i>Pinus ponderosa</i>	<i>Pinus jeffreyi</i>
Plant Height	Female	10.5 (2.6) (4.6–22.3) [300a]	10.3 (2.8) (7.4–25.4)[300a]
	Male	9.7 (2.5) (3.6–19.5) [a]	9.7 (3.4) (3.9–21.6) [a]
Basal Diameter	Female	3.4 (0.7) (1.7–6.9) [a]	3.4 (0.7) (1.9–6.6) [a]
	Male	3.2 (0.6) (2.2–5.7) [a]	3.2 (0.7) (1.8–6.8) [a]
Length of Third Internode	Female	13.1 (2.5) (5.7–21.0) [a]	12.9 (3.6) (6.5–29.3) [a]
	Male	12.0 (3.2) (4.2–19.5) [a]	11.9 (3.4) (6.4–23.2) [a]
Width of Third Internode	Female	2.5 (0.3) (1.6–3.7) [a]	2.5 (0.4) (1.6–3.6) [a]
	Male	2.5 (0.3) (1.6–3.6) [a]	2.4 (0.4) (1.4–3.6) [a]
Staminate Spike Length		12.4 (4.7) (4.3–36.1) [300b]	12.8 (4.7) (3.7–41.0) [500b]
Staminate Spike Width		3.2 (0.2) (2.5–4.2) [b]	3.0 (0.2) (2.3–3.5) [b]
Mean Flower Diameter	3-merous	3.2 (0.4) (2.1–4.0) [140]	3.1 (0.4) (2.2–4.5) [260]
	4-merous	4.3 (0.5) (3.1–5.6) [160]	4.1 (0.5) (3.0–5.3) [240]
Petal Length		1.6 (0.2) (1.0–2.4) [b]	1.5 (0.2) (0.9–2.3) [b]
Petal Width		1.4 (0.2) (0.8–2.0) [b]	1.4 (0.2) (0.7–2.1) [b]
Anther Diameter		0.6 (0.1) (0.4–1.1) [b]	0.6 (0.1) (0.4–1.2) [b]
Anther Distance from Tip		0.6 (0.1) (0.2–1.1) [b]	0.6 (0.1) (0.2–1.1) [b]
Mean Fruit Length		5.4 (0.5) (4.0–7.2) [210d]	5.4 (0.5) (4.2–7.0) [290c]
Mean Fruit Width		3.7 (0.5) (2.6–5.6) [d]	3.6 (0.4) (2.8–4.9) [c]
Seed Length		3.5 (0.4) (2.5–4.7) [d]	3.4 (0.5) (2.3–4.6) [c]
Seed Width		1.5 (0.2) (1.1–2.0) [d]	1.5 (0.2) (1.0–2.0) [c]

were yellow, yellow-brown, or olive green and, if glaucous, this was found primarily near the base of older plants.

Comparing morphological measurements for male and female plants of *Arceuthobium campylopodum* collected from *Pinus ponderosa* and *P. jeffreyi*, we found no significant differences among any of the mean values calculated (Table 2). Although measurements for most of the morphological characters varied slightly between plants collected from the two hosts, the standard deviations for many of the characters we examined were similar. It is, however, noteworthy that we collected and measured female plants over 25 cm in height from *P. jeffreyi* in western Nevada (near Bowers Mansion) and over 20 cm from *P. ponderosa* in northern California (near Pollock Pines) (Fig. 3: sites 39 and 37, respectively).

The principal characteristics separating the four species are summarized in Table 3 and a key for identifying them in the field is provided below.

Discriminant Function Analyses

Means and associated 95% confidence intervals for morphological characters of female and

male plants across predicted species according to full-model discriminant function analyses (DFA) are presented in Table 4. Discriminant function analyses of eight and 10 female and male morphological characters, respectively, demonstrated clear interspecific separation of *Arceuthobium littorum* and *A. siskiyouense* as well as the latter two species from *A. campylopodum* and *A. occidentale*. For DFA of female plant morphology, results indicated significant differences existed among eight morphologically informative characters for *A. campylopodum*, *A. littorum*, *A. occidentale*, and *A. siskiyouense* (Wilks' $\lambda = 0.3393$, Approximant $F_{24,2845.8} = 53.54$, $P < 0.0001$; Pillai's Trace = 0.88, Approximant $F_{24,2949} = 51.28$, $P < 0.0001$); classifying 75.0% (744/992) of the specimens to the correct species. The first two canonicals (discriminant functions) explained 86.3% of the total variation (Table 5; Fig. 4A) with *A. littorum*, *A. occidentale*, and *A. siskiyouense* correctly classified (predicted/actual) to species 99.0% (99/100), 72.7% (160/220), and 80.0% (152/190) of the time, respectively. Standardized correlation coefficients, indicating the relative importance of individual female morphological characters in defining the discriminant functions (canonicals), are listed in Table 6. Width of the third internode, seed length and

TABLE 3. SUMMARY OF THE PRINCIPAL CHARACTERS SEPARATING *ARCEUTHOBium CAMPYLOPODUM*, *A. OCCIDENTALE*, *A. LITTORUM*, AND *A. SISKIYOUENSE*. Data for morphological characters are means; plant heights in cm and all other measurements in mm. Numbers in bold face type represent key morphological or phenological differences between the taxa. Host susceptibility classification based on information in Hawksworth and Wiens (1996) and Mathiasen and Daugherty (2009a).

Character	<i>Arceuthobium campylopodum</i>	<i>Arceuthobium occidentale</i>	<i>Arceuthobium littorum</i>	<i>Arceuthobium siskiyouense</i>
Plant Height				
	Female	10.4	10.6	10.3
	Male	9.7	10.1	10.5
Plant Color	Olive-green, yellow	Yellow, yellow-green, straw	Brown-green, dark green, yellow-brown	Dark brown, brown-green, red-brown
Plants Glaucous	Occasionally	Highly glaucous	Occasionally	Seldom
Basal Diameter				
	Female	3.4	3.2	3
	Male	3.2	3	3
Width of Third Internode				
	Female	2.5	2.2	2
	Male	2.5	2.2	2.1
Staminate Spike Length	12.7	13.9	20.6	11.8
Staminate Spike Width	3.1	2.9	3.4	2
Flower Diameter				
	3-merous	3.1	3	3.2
	4-merous	4.2	4.1	4.5
	5-merous	None observed	Rarely formed	None observed
Peak Anthesis	August-September	October-November	September	August-September
Peak Seed Dispersal	September-October	November-December	September-October	September-October
Fruit Color	Light green	Light green	Dark green to red	Light green
Fruits Glaucous	Lightly glaucous	Highly glaucous	Lightly glaucous	Lightly glaucous
Sympatric taxa	<i>A. occidentale</i> , <i>A. siskiyouense</i>	<i>A. campylopodum</i>	Not sympatric	<i>A. campylopodum</i>
Principal Hosts	<i>Pinus ponderosa</i> , <i>P. jeffreyi</i>	<i>P. sabiniana</i>	<i>P. muricata</i> , <i>P. radiata</i>	<i>P. attenuata</i> , <i>P. jeffreyi</i>
Secondary Hosts	<i>P. attenuata</i> , <i>P. coulteri</i>	<i>P. attenuata</i> , <i>P. coulteri</i>	None	None
Occasional Hosts	<i>P. contorta</i> , <i>P. sabiniana</i>	<i>P. jeffreyi</i> , <i>P. ponderosa</i>	<i>P. contorta</i>	<i>P. contorta</i> , <i>P. ponderosa</i>

TABLE 4. QUADRATIC DISCRIMINANT FUNCTION ANALYSES (DFA) OF MALE AND FEMALE PLANTS. Comparison of morphological characters (means) across predicted classification to species. Ninety-five percent confidence intervals (\pm) were computed for comparison of mean differences.

Character(s)		<i>Arceuthobium campylopodum</i>	<i>Arceuthobium occidentale</i>	<i>Arceuthobium littorum</i>	<i>Arceuthobium siskiyouense</i>
Female					
Plant height (PH)		10.4 (\pm 0.28)	10.4 (\pm 0.37)	9.9 (\pm 0.45)	9.0 (\pm 0.22)
Basal Diameter (BD)		3.5 (\pm 0.07)	3.1 (\pm 0.07)	3.8 (\pm 0.16)	2.9 (\pm 0.07)
Length of Third Internode (LTI)		13.2 (\pm 0.30)	11.7 (\pm 0.33)	13.1 (\pm 0.63)	13.1 (\pm 0.42)
Width of Third Internode (WTI)		2.5 (\pm 0.03)	2.2 (\pm 0.04)	2.5 (\pm 0.06)	1.9 (\pm 0.03)
Fruit Length (FL)		5.5 (\pm 0.05)	5.2 (\pm 0.07)	5.4 (\pm 0.09)	5.2 (\pm 0.05)
Fruit Width (FW)		3.7 (\pm 0.04)	3.3 (\pm 0.05)	3.6 (\pm 0.06)	3.4 (\pm 0.04)
Seed Length (SL)		3.5 (\pm 0.05)	3.5 (\pm 0.04)	3.4 (\pm 0.06)	3.1 (\pm 0.06)
Seed Width (SW)		1.5 (\pm 0.02)	1.3 (\pm 0.02)	1.3 (\pm 0.03)	1.3 (\pm 0.02)
Male					
Plant height (PH)		9.9 (\pm 0.29)	9.2 (\pm 0.22)	10.4 (\pm 0.59)	8.2 (\pm 0.24)
Basal Diameter (BD)		3.3 (\pm 0.06)	2.9 (\pm 0.05)	3.5 (\pm 0.12)	3.1 (\pm 0.06)
Length of Third Internode (LTI)		12.2 (\pm 0.31)	11.1 (\pm 0.30)	13.3 (\pm 0.57)	12.3 (\pm 0.45)
Width of Third Internode (WTI)		2.5 (\pm 0.03)	2.2 (\pm 0.04)	2.7 (\pm 0.06)	2.1 (\pm 0.03)
Petal Length (PL)		1.6 (\pm 0.02)	1.5 (\pm 0.02)	1.9 (\pm 0.06)	1.5 (\pm 0.03)
Petal Width (PW)		1.4 (\pm 0.02)	1.2 (\pm 0.02)	1.5 (\pm 0.05)	1.4 (\pm 0.03)
Anther Diameter (AD)		0.6 (\pm 0.01)	0.6 (\pm 0.01)	0.9 (\pm 0.04)	0.8 (\pm 0.02)
Anther Distance from Tip (ADT)		0.6 (\pm 0.01)	0.5 (\pm 0.01)	0.9 (\pm 0.04)	0.7 (\pm 0.02)
Staminate Spike Length (SSL)		13.0 (\pm 0.46)	13.4 (\pm 0.54)	19.9 (\pm 1.95)	11.6 (\pm 0.38)
Staminate Spike Width (SSW)		3.0 (\pm 0.03)	2.9 (\pm 0.03)	3.4 (\pm 0.06)	2.0 (\pm 0.03)

width, and basal diameter were most strongly correlated with the first two canonicals and hence contributed most to defining species membership when only female plants were considered. In contrast, *A. campylopodum* was only classified correctly 69.1% (333/482) of the time, and was most often misclassified to *A. occidentale* (14.3%, 69/482) followed by *A. siskiyouense* (12.7%, 61/482) and, rarely, *A. littorum* (3.9%, 19/482; Table 7). Similarly, *A. occidentale* was classified incorrectly as *A. campylopodum* (11.8%, 26/220), *A. siskiyouense* (12.3%, 27/220), and, rarely, *A. littorum* (3.2%, 19/220), whereas, *A. siskiyouense* identified a priori was only misclassified to *A. campylopodum* (8.4%, 16/190) and *A. occidentale* (11.6%, 22/190). Using width of the third internode alone, female plants of *A. siskiyouense* were classified correctly (predicted/actual) 85.3% (162/190) of the time; readily delineating *A. siskiyouense* from *A. campylopodum*, *A. littorum*,

and *A. occidentale* (Table 7). Moreover, with the addition of morphological characters (predictor variables) such as seed width and length, basal diameter, fruit width, plant height, and length of the third internode – the seven most correlated characters – to the discriminant function (Table 7), the precision of classification and, hence, delineation of *A. littorum* improved to 98.0% while the correct classification of *A. siskiyouense*, *A. occidentale*, and *A. campylopodum* was 79%, 73.2%, and 69.1%, respectively. Although female plants of *A. campylopodum* consistently were misclassified \leq 38.0% of the time across the stepwise DFA analyses when 4–8 morphological characters were considered (Table 7), the multivariate means of all four taxa did not intersect in ordination space when analyses were executed using all eight morphological characters (full-model) with either the complete or resampled data set (Fig. 4A and C).

TABLE 5. CANONICAL STATISTICS: QUADRATIC DISCRIMINANT FUNCTION ANALYSIS (DFA) FOR FEMALE (N = 8 MORPHOLOGICAL CHARACTERS) AND MALE PLANTS (N = 10 MORPHOLOGICAL CHARACTERS) OF *ARCEUTHOBIUM CAMPYLOPODUM*, *A. LITTORUM*, *A. OCCIDENTALE* AND *A. SISKIYOUENSE*.

Canonical	Eigenvalue	Percent	Cumulative Percent	Canonical Correlation	Likelihood Ratio	Approximant F	P-value
Female							
1	0.71	52.89	52.89	0.65	0.34	F _{23, 2846} = 53.54	<0.0001
2	0.45	33.43	86.32	0.56	0.58	F _{14, 1964} = 43.66	<0.0001
3	0.19	13.69	100	0.4	0.84	F _{6, 983} = 30.27	<0.0001
Male							
1	3.49	81.53	81.53	0.88	0.12	F _{30, 3221} = 115.62	<0.0001
2	0.61	14.26	95.79	0.62	0.53	F _{18, 2196} = 46.23	<0.0001
3	0.18	4.21	100	0.39	0.85	F _{8, 1099} = 24.77	<0.0001

A. Female Plants: Complete Data Set, Full-Model

B. Male Plants: Complete Data Set, Full-Model

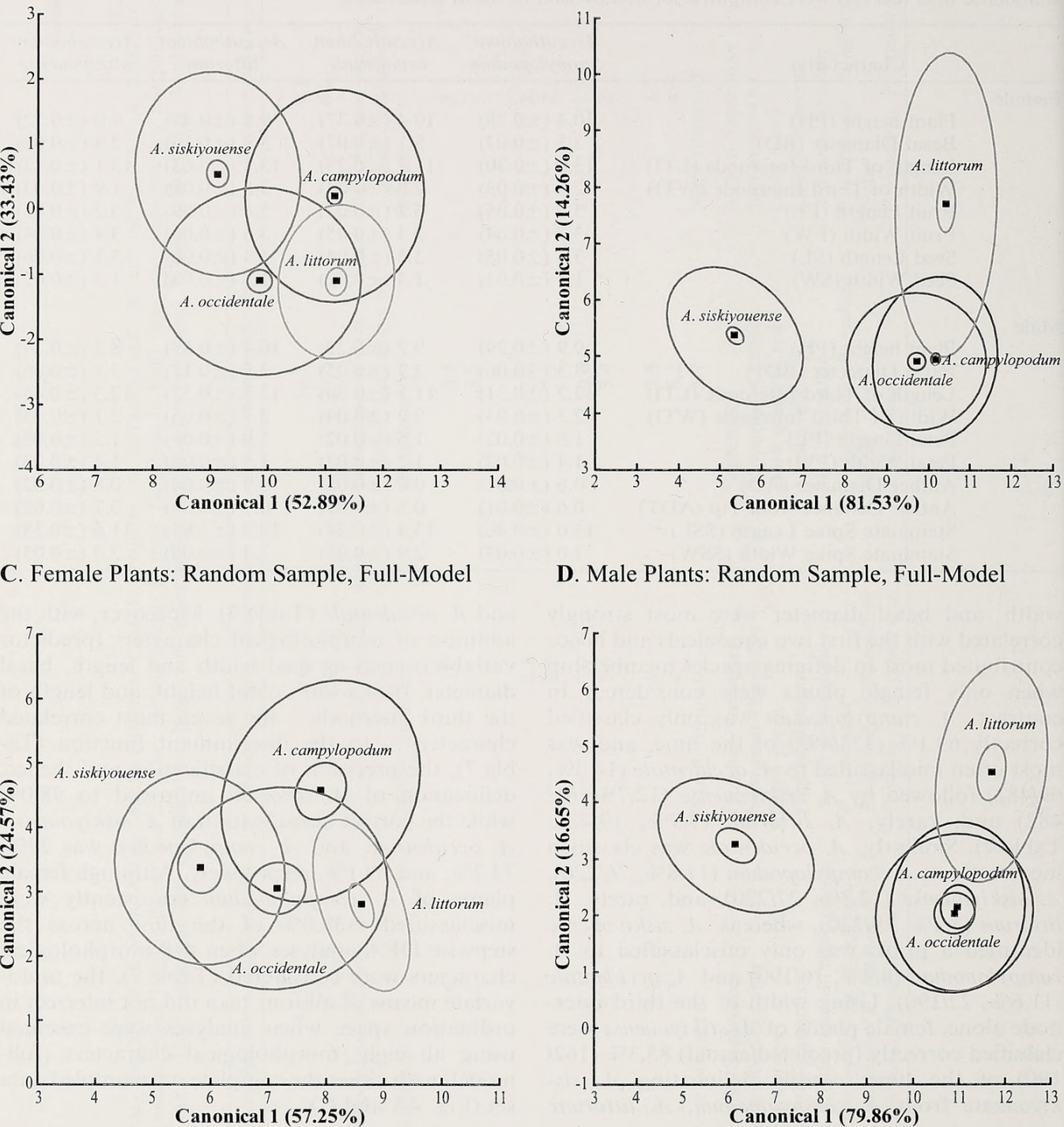


FIG. 4. Canonical plots for discriminant function analyses (DFA) of *Arceuthobium campylopodum*, *A. littorum*, *A. occidentale*, and *A. siskiyouense* based on morphological characteristics of female (A, C) and male plants (B, D) shown in Table 7. Multivariate means (squares) were computed using complete data for each species by sex (A, B), whereas, to further validate the DFA, means were also calculated using a random subset (50 complete records/species) of female (C) and male plants (D), respectively. For each species (A-D), the inner ellipse correspond to a 95% confidence limit for the mean, and the outer ellipse represent a normal 50% contour illustrating the approximate area within which 50% of plants for each species reside.

As with multivariate analyses for female plants, DFA on male plants revealed significant differences among 10 morphological characters of *Arceuthobium campylopodum*, *A. littorum*, *A. occidentale*, and *A. siskiyouense* (Wilks' $\lambda = 0.1170$, Approximant $F_{30,3220.6} = 115.62$, $P < 0.0001$; Pillai's Trace = 1.3100, Approximant $F_{30,3297} = 85.13$, $P < 0.0001$; Table 5). However, unlike the full-model DFA on female plant morphology, the first two axes described greater than 95% (95.8%) of the variation among male plants (Fig. 4B) and five morphological charac-

TABLE 6. QUADRATIC DISCRIMINANT FUNCTION ANALYSIS (DFA) FOR FEMALE (N = 8 MORPHOLOGICAL CHARACTERS) AND MALE PLANTS (N = 10 MORPHOLOGICAL CHARACTERS) OF *ARCEUTHOBIMUM CAMPYLOPODUM*, *A. LITTORUM*, *A. OCCIDENTALE*, AND *A. SISKIYOUENSE*: STANDARDIZED CORRELATION COEFFICIENTS INDICATING THE RELATIVE IMPORTANCE OF A MORPHOLOGICAL CHARACTER(S) IN SPECIES DELINEATION. Plant height (PH); basal diameter (BD); length of third internode (LTI); width of the third internode (WTI); fruit length (FL); fruit width (FW); seed length (SL); seed width (SW); petal length (PL); petal width (PW); anther diameter (AD); anther distance to tip (ADT); staminate spike length (SSL); and, staminate spike width (SSW).

	Female			Male		
	Canonical 1	Canonical 2	Canonical 3	Canonical 1	Canonical 2	Canonical 3
PH	−0.18	−0.32	−1.03	0.26	0.08	−0.36
BD	−0.17	−0.38	0.74	−0.3	−0.03	0.23
LTI	−0.14	0.59	0.71	−0.18	0.07	0.01
WTI	1.09	−0.07	−0.14	0.41	0.15	0.59
FL	−0.09	−0.23	−0.2			
FW	0.36	0.37	0.49			
SL	0.16	−1.06	−0.2			
SW	0.23	1.11	−0.46			
PL				−0.32	0.38	−0.21
PW				0.34	0.25	−0.48
AD				−0.23	0.3	−0.47
ADT				1	0.05	0.06
SSL				−0.16	−0.57	0.87
SSW				−0.35	0.68	0.24

ters – staminate spike length and width, anther diameter and distance to tip, and width of the third internode – contributed most to predicting species membership (Table 6). Using these five morphological characters in the DFA of male plants, total correct classification (predicted/actual) was 74.8% across all four taxa; yet, *A. littorum* (90.0%) and *A. siskiyouense* (99.1%) rarely were misclassified, compared to *A. campylopodum* (66.3%) and *A. occidentale* (67.0%) which were more often incorrectly classified (Table 7). In addition, 24.0% (144/600) of male plants identified in the field as *A. campylopodum* – many collected from known populations of *A. campylopodum* (Hawksworth and Wiens 1996) – were predicted to *A. occidentale* and, likewise, male plants of *A. occidentale* (21.4%, 43/200) sometimes were misclassified as *A. campylopodum*. Species membership for male plants of *A. littorum* and *A. siskiyouense*, however, rarely was predicted ($\leq 2.0\%$) to either *A. campylopodum* (1/100 and 0/210) or *A. occidentale* (2/100 and 1/210) when all 10 of the male plant morphological characters were considered. Furthermore, male plants of *A. littorum* and *A. siskiyouense* were readily distinguishable from one another and separable from *A. campylopodum* and *A. occidentale* when jointly comparing only the dimensions of staminate spikes, anther distance to tip, and the width of the third internode (Table 7). The distinct morphological differences between male plants of *A. littorum* and *A. siskiyouense* as well as their comparisons to male plants of *A. campylopodum* and *A. occidentale* also were maintained when DFA was applied to the reduced, resampled data set (50 complete records/taxon; Fig. 4D).

DISCUSSION

Morphological Comparisons

The most distinct species of the four taxa in the *Arceuthobium campylopodum-occidentale* complex are *A. littorum* and *A. siskiyouense*. *Arceuthobium littorum* can easily be distinguished from the other three taxa by its geographic distribution along the coast of California, plant color, length and width of staminate spikes, width of the third internode on male plants, anther distance to tip, flower diameters, occasional formation of 5-merous and rarely 6-merous flowers, and parasitism of *P. radiata* and *P. muricata* (Mathiasen and Daugherty 2013) (Table 3). In addition, isozyme analyses (Nickrent and Butler 1990) and secondary branching patterns (Mark and Hawksworth 1981; Nickrent and Butler 1990) distinguish it from the other three taxa in the complex. Furthermore, Nickrent and Butler (1991) demonstrated that *A. littorum* could be differentiated genetically from *A. campylopodum* by differences at nine isozyme loci and the presence of a sex-linked *MDH-3* allele in staminate plants.

Although *Arceuthobium siskiyouense* is morphologically similar to *A. campylopodum* (Mathiasen and Daugherty 2009a), the results of our morphological measurements demonstrated that these species can be distinguished using several characters. The most conspicuous morphological difference between these species being plant color, width of the third internode for male and female plants, and the staminate spike width of male plants (Table 3).

Arceuthobium siskiyouense is more difficult to separate from *A. occidentale* based on the

TABLE 7. FORWARD, STEPWISE DISCRIMINANT FUNCTION ANALYSIS (DFA): CLASSIFICATION (%), PREDICTED/ACTUAL) ACROSS SPECIES WITH THE SEQUENTIAL ADDITION OF MORPHOLOGICAL CHARACTERS (STEPS) – MOST-TO-LEAST CORRELATED TO THE DISCRIMINANT FUNCTIONS – FOR FEMALE AND MALE PLANTS. Plant height (PH); basal diameter (BD); length of third internode (LTI); width of the third internode (WTI); petal length (PL); petal width (PW); anther diameter (AD); anther distance to tip (ADT); fruit length (FL); fruit width (FW); seed length (SL); seed width (SW); staminate spike length (SSL); and, staminate spike width (SSW).

Stepwise DFA (Step [Morphological Charactera])		Correct Classification by Species (% [Predicted/Actual])				
		Total	<i>A. campylopodum</i>	<i>A. occidentale</i>	<i>A. littorum</i>	<i>A. siskiyouense</i>
Female						
1 [WTI]		36.5 [362/992]	24.3 [117/482]	8.6 [19/220]	64.0 [64/100]	85.3 [162/190]
2 [WTI, SW]		51.8 [514/992]	52.1 [251/482]	20.9 [46/220]	65.0 [65/100]	80.0 [152/190]
3 (WTI, SW, SL)		59.4 [589/992]	57.1 [275/482]	50.0 [110/220]	67.0 [67/100]	72.1 [137/190]
4 (WTI, SW, SL, BD)		65.5 [650/992]	62.0 [299/482]	57.7 [127/220]	86.0 [86/100]	72.6 [138/190]
5 (WTI, SW, SL, BD, FW)		67.9 [674/992]	64.3 [310/482]	62.7 [138/220]	85.0 [85/100]	74.2 [141/190]
6 [WTI, SW, SL, BD, FW, PH]		72.2 [716/992]	66.8 [322/482]	68.2 [150/220]	97.0 [97/100]	77.4 [147/190]
7 [WTI, SW, SL, BD, FW, PH, LTI]		74.5 [742/992]	69.1 [333/482]	73.2 [161/220]	98.0 [98/100]	79.0 [150/190]
8 [WTI, SW, SL, BD, FW, PH, LTI, FL]		75.0 [744/992]	69.1 [333/482]	72.7 [160/220]	99.0 [99/100]	80.0 [152/190]
Male						
1 [SSW]		47.7 [529/1110]	20.3 [122/600]	66.5 [133/200]	65.0 [65/100]	99.5 [209/210]
2 [SSW, ADT]		55.1 [611/1110]	30.8 [185/600]	72.0 [144/200]	78.0 [78/100]	97.1 [204/210]
3 [SSW, ADT, WTI]		71.7 [796/1110]	61.8 [371/600]	65.0 [130/200]	88.0 [88/100]	98.6 [207/210]
4 [SSW, ADT, WTI, SSL]		73.2 [812/1110]	64.7 [388/600]	64.5 [129/200]	89.0 [89/100]	98.1 [206/210]
5 [SSW, ADT, WTI, SSL, AD]		74.8 [830/1110]	66.3 [398/600]	67.0 [134/200]	90.0 [90/100]	99.1 [208/210]
6 [SSW, ADT, WTI, SSL, AD, PW]		79.1 [878/1110]	72.8 [437/600]	73.0 [146/200]	89.0 [89/100]	98.1 [206/210]
7 [SSW, ADT, WTI, SSL, AD, PW, PL]		78.7 [873/1110]	71.8 [431/600]	72.5 [145/200]	90.0 [90/100]	98.6 [207/210]
8 [SSW, ADT, WTI, SSL, AD, PW, PL, BD]		79.6 [883/1110]	71.0 [426/600]	75.5 [151/200]	97.0 [97/100]	99.5 [209/210]
9 [SSW, ADT, WTI, SSL, AD, PW, PL, BD, PH]		79.8 [886/1110]	71.3 [428/600]	76.0 [152/200]	97.0 [97/100]	99.5 [209/210]
10 [SSW, ADT, WTI, SSL, AD, PW, PL, BD, PH, LTI]		81.3 [902/1110]	73.3 [440/600]	78.0 [156/200]	97.0 [97/100]	99.5 [209/210]

independent examination of morphological discontinuities, but it can be distinguished from *A. occidentale* by its plant color, smaller mean plant size for male and female plants, smaller basal diameter and third internode widths, and its smaller staminate spike dimensions (Table 3). As demonstrated by standard and stepwise DFA, female and male plants of *A. siskiyouense* can also be delineated from *A. occidentale* and *A. campylopodum* using a single female and male morphological character – width of the third internode and staminate spike width, respectively (Table 7). It is, however, difficult to distinguish *A. siskiyouense* from *A. campylopodum* based on host range because *A. siskiyouense* severely parasitizes both *P. attenuata* and *P. jeffreyi* and its parasitism of *P. ponderosa* remains uncertain (Mathiasen and Daugherty 2009a). Because *A. campylopodum* also severely parasitizes *P. jeffreyi* and *P. attenuata* (Table 3), using infection of these hosts to separate *A. siskiyouense* from *A. campylopodum* remains problematic and not practical for the purpose of field identification.

The separation of *Arceuthobium occidentale* from *A. campylopodum* as distinct species using morphological characters is the most difficult based on our data (Tables 3 and 7; Fig. 4). Populations of these taxa are morphologically similar as our univariate and discriminant function analyses demonstrated. Male plants of *A. campylopodum* were most often misclassified in our DFAs as *A. occidentale* and likewise, incorrectly classified male plants of *A. occidentale* commonly were predicted to *A. campylopodum* and rarely *A. siskiyouense*. Although DFA of female plants using the full-suite of morphological characters provided better resolving power to species/taxon membership than male plants, particularly for *A. occidentale* (Table 7; Fig. 4), nearly 31% of female plants for *A. campylopodum* were classified incorrectly, and as noted previously for male plants, the majority of misclassifications were predicted to *A. occidentale*. However, when all of the morphological characters measured for male and female plants were used, the DFA results demonstrated that both *A. campylopodum* and *A. occidentale* were correctly classified from 69–78% of the time (Table 7). The principal characteristics separating *A. campylopodum* from *A. occidentale* were plant glaucosity and phenology; *A. occidentale* plants were highly glaucous and *A. occidentale* flowered and dispersed seed much later in the fall than *A. campylopodum* (Table 3). In fact, in stands where these dwarf mistletoes are sympatric, the best approach to delineating these taxa is to use their phenological differences. Using timely observations in October or November, one can readily differentiate *A. campylopodum* and *A. occidentale* by determining which plants are flowering and/or dispersing seed (*A. occidentale*) and which have

already completed these processes (*A. campylopodum*).

Our analyses are among the first to compare morphological characters of the same species of dwarf mistletoe collected from different hosts. The only other study of this nature was conducted by Mathiasen and Daugherty (2009a) for *Arceuthobium siskiyouense* when they compared morphological characters for plants collected from two principal hosts and one occasional host. They found little difference in the means and ranges for the majority of the morphological characters examined for plants collected from the principal hosts of *A. siskiyouense*, but plants as well as flower diameters and fruit dimensions measured from the occasional host were slightly smaller on average. Therefore, we expected that *A. campylopodum* collected from *Pinus ponderosa* and *P. jeffreyi* would also demonstrate some morphological variation, possibly resulting in small, yet, significant differences. However, no significant differences were evident for any of the morphological characters measured for male or female plants of *A. campylopodum* on separate principal hosts as many of the means were identical (Table 2). Furthermore, the ranges and standard deviations for the characters we examined were also similar. The largest differences in standard deviation were for measurements of the height of male plants and the length of the third internode for female plants, but the means for these characters were nearly the same. These results and those of Mathiasen and Daugherty (2009a) support the concept emphasized by Hawksworth and Wiens (1972, 1996) that species of dwarf mistletoes maintain their morphological identity when they occur on different hosts.

Host Range Differences

The host range of three of the four taxa in the *Arceuthobium campylopodum-occidentale* complex clearly overlap; only *A. littorum* has distinct (i.e., species-specific) host affinities parasitizing *Pinus radiata* and *P. muricata* along the coast of California. *Arceuthobium siskiyouense* is a primary parasite of *P. attenuata*, but has been reported to severely parasitize *P. jeffreyi* as well (Mathiasen 2009, 2011). Although Hawksworth and Wiens (1996) reported that *A. siskiyouense* only rarely infected *P. ponderosa*, further work on this mistletoe-host relationship is needed because the susceptibility of *P. ponderosa* is based solely on a single population of *A. siskiyouense* near Gasquet, California (Hawksworth and Wiens 1972; Hawksworth et al. 1992). Our observations at the same location could not confirm the susceptibility of *P. ponderosa* to *A. siskiyouense* as we were unable to locate this host-dwarf mistletoe combination there. Species boundaries between *A.*

campylopodum and *A. occidentale* are less clear because their host ranges overlap inasmuch as both *P. attenuata* and *P. coulteri* are highly susceptible to each species and both mistletoes parasitize *P. ponderosa*, *P. jeffreyi*, and *P. sabiniana* to varying degrees. Currently, *P. attenuata* and *P. coulteri* are considered as secondary hosts of both *A. campylopodum* and *A. occidentale*, but our observations at several locations in southern and northern California suggest these pines may be more susceptible to both dwarf mistletoes – possibly warranting the promotion of these pines to principal hosts. Further data are also required on the susceptibility of *P. ponderosa* to *A. occidentale*, which is currently considered to be only an occasional host (Hawskworth and Wiens 1996). However, our observations at several locations along the western slope of the Sierra Nevada Mountains indicated *P. ponderosa* is likely more susceptible to *A. occidentale* than an occasional host. Furthermore, our observations of *A. occidentale* infections on *P. jeffreyi* were not adequate to estimate host susceptibility in this dwarf mistletoe-host combination, but Hawskworth and Wiens (1996) considered *P. jeffreyi* to be an occasional host of *A. occidentale*. The host ranges of *A. campylopodum* and *A. occidentale* clearly overlap and additional research is needed to better quantify the susceptibility of all these hard pines to both mistletoes.

Phenology

The flowering and seed dispersal periods of *Arceuthobium littorum*, *A. siskiyouense*, and *A. campylopodum* overlap; flowering occurs from mid-August to early-October while seed dispersal occurs from mid-September to mid-October (Hawskworth and Wiens 1996; Mathiasen and Daugherty 2009a, 2013). Flowering period and seed dispersal of *A. occidentale*, however, occurs much later in the fall; flowering from mid-October through late November with seed dispersal beginning in early November and generally concluding in December – occasionally ending in early January of some years (Hawskworth and Wiens 1996; Mathiasen and Daugherty 2013). Peak flowering of *A. occidentale*, therefore, does not overlap with that of the other three species and, although populations of *A. occidentale* on *P. sabiniana* and *A. campylopodum* on *P. ponderosa* are rarely sympatric, flowering periods likely preclude gene flow between these dwarf mistletoes. Gene flow between *A. littorum* and the other three taxa certainly is precluded because it is not sympatric with them. However, *A. littorum* does occur within approximately 60 km of *A. occidentale* in Monterey and San Luis Obispo Counties (Mathiasen and Daugherty 2013), yet it is unlikely that pollen can be

transferred effectively over 60 km by insects and/or wind (Hawskworth and Wiens 1996). As noted by Mathiasen and Daugherty (2013), the seed dispersal period for *A. littorum* requires additional study because Peirce (1905) reported previously that this species – classified as *A. occidentale* in his report – dispersed seed as late as December and January in some years.

Taxonomic Classification

Hawskworth and Wiens (1996, p. 146) discussed their classification of subspecies of *Arceuthobium* in some detail. They considered subspecies to be “geographically restricted populations of dwarf mistletoes that were distinguished by a few relatively small but consistent variations.” At that time, they recognized subspecies under four taxa: 1) *A. aureum* Hawskworth & Wiens; 2) *A. globosum* Hawskworth & Wiens; 3) *A. tsugense* (Rosendahl) G. N. Jones; and, 4) *A. vaginatum* (Willdenow) Presl. They also recognized one race under *A. tsugense*. Over the last decade, several new subspecies of *Arceuthobium* have been described. The race Hawskworth and Wiens formerly recognized for populations of *A. tsugense* that parasitize shore pine in Washington and southern British Columbia has been described as a subspecies (Wass and Mathiasen 2003) and another subspecies of *A. tsugense* has been described from Oregon (Mathiasen and Daugherty 2007). *Arceuthobium hawksworthii* Wiens & C. G. Shaw bis has been recombined as a subspecies of *A. hondurense* Hawskworth & Wiens (Mathiasen 2007) and the subspecies of *A. aureum* described by Hawskworth and Wiens (1977, 1996) have been recombined as subspecies of *A. globosum* (Mathiasen 2008). In addition, a dwarf mistletoe that severely parasitizes Brewer’s spruce (*Picea breweriana* S. Watson) in southern Oregon and northern California, has been described as a subspecies of *A. abietinum* (Engelmann) Hawskworth & Wiens (Mathiasen and Daugherty 2009b). Finally, the dwarf mistletoe populations on bristlecone pine (*Pinus aristata* Engelmann) in northern Arizona have been described as a subspecies of *A. microcarpum* (Engelmann) Hawskworth & Wiens (Scott and Mathiasen 2009). Drawing upon these treatments for subspecific classifications, the primary characteristics presently recognized for delineating subspecies in *Arceuthobium* are significant differences in mean plant heights, staminate spike dimensions, and flower dimensions as well as differences in phenology, geographic distribution, and host range. Although the range in the measurements for many morphological characters used to separate subspecies (and often species) of *Arceuthobium* often overlap, statistical analyses have demonstrated that the means for characters

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separating taxa remain consistent and significantly different, regardless of the host. Similarly, although Hawksworth and Wiens (1972, 1996) maintained that subspecies of *Arceuthobium* were usually geographically separate, field studies have now demonstrated that the geographic distributions of most of the currently recognized subspecies overlap, but that the subspecies can be distinguished using host ranges, phenology, and morphological characters (Wass and Mathiasen 2003; Mathiasen 2008; Mathiasen and Daugherty 2007, 2009b; Scott and Mathiasen 2009).

As previously noted, Hawksworth and Wiens (1972, 1996) considered subspecies of *Arceuthobium* to be “geographically restricted populations”, but it has now been demonstrated that most of the subspecies they recognized have relatively extensive geographic ranges. Furthermore, most of the subspecies described by Hawksworth and Wiens reportedly are sympatric with other subspecies of the same taxon (Wass and Mathiasen 2003; Mathiasen and Daugherty 2007; Mathiasen 2008; Mathiasen and Daugherty 2009b; Scott and Mathiasen 2009). Thus, the inclusion and application of geographic restriction within the definition of subspecies in the genus *Arceuthobium* is now inadequate. Therefore, the interpretation of what constitutes “a few relatively small but consistent variations” is left to individuals studying the large number of complex dwarf mistletoe populations with very similar morphological characteristics and that parasitize a diverse range of hosts with varying degrees of infection (i.e., immune to severely infected). As with other groups of morphologically and ecologically similar plants, the dilemma presented is how best to interpret and weigh, collectively and without bias, variations in morphology, phenology, ecological adaptations, and molecular evidence in order to derive a consistent classification concept that is phylogenetically sound and, yet, practically useful to individuals and organizations interested in the classification/identification/management of dwarf mistletoes. Because dwarf mistletoes are extremely important both ecologically and economically, an emphasis must be placed not only on their phylogenetic relationships, but also on their ecological and pathological roles in forest ecosystems. Therefore, recognition of the host affinities developed by dwarf mistletoes – which often are host/mistletoe specific – is critical in their classification as we consider differences in host preference(s) to reflect corresponding and underlying genetic differentiation between populations. Accordingly, dwarf mistletoe taxa that parasitize closely-related hosts and can be delineated statistically across multiple morphological characteristics should be classified at the species level. The number of statistically significant differences between morphological characteristics

can be amended to consider consistent differences – accordant differences demonstrated across populations and geographic distributions – including plant color, number of petals consistently produced in several populations, differences in phenology, and geographic isolation that has prevented gene flow between populations over a substantial period of time as demonstrated for *A. littorum* versus the other species in the *A. campylopodum-occidentale* complex.

Based on our statistical analyses of morphological characteristics of the *Arceuthobium campylopodum-occidentale* complex, we concluded *A. littorum* and *A. siskiyouense* were sufficiently differentiated from *A. campylopodum* and *A. occidentale* to remain classified as species. This conclusion is also supported by other studies of these taxa (Hawksworth and Wiens 1996; Mathiasen and Daugherty 2009a, 2013). We also recommend that *A. occidentale* continue to be classified at the rank of species because it could be separated consistently from *A. campylopodum* by several significantly different characters and our DFA demonstrated that species membership of *A. occidentale* identified a priori in the field could be correctly classified using female or male plant morphology over 70% of the time. It can also be distinguished from *A. campylopodum* by its much later flower and seed dispersal periods which suggests that the opportunity for outcrossing between and/or among populations of these mistletoes likely is limited, if it occurs at all. However, additional multilocus molecular studies (e.g., genotyping via amplified fragment length polymorphism [AFLP] analysis) and studies of the host susceptibility of the hard pines to these dwarf mistletoes should be completed. If additional molecular and field studies can demonstrate that populations of *A. occidentale* can be genetically differentiated from *A. campylopodum* and reveal definitive discontinuities in host preference between these dwarf mistletoes, then the treatment of *A. occidentale* at the specific level could be applied with even greater confidence.

In light of the morphometric analyses presented here, we recommend that the taxa in the *Arceuthobium campylopodum-occidentale* complex continue to be recognized at the specific level by individuals or groups interested in the conservation, management, and/or taxonomy of dwarf mistletoes. We, therefore, urge botanists and other resource specialists involved in the systematics of dwarf mistletoes in California to follow the treatments and use the taxonomic keys proposed for this group of parasitic plants in The Jepson Manual: higher plants of California (Hickman 1993) or the Hawksworth and Wiens (1996) monograph for *Arceuthobium* rather than using the highly conservative treatment of the genus recently presented in the revised Jepson

Manual (Baldwin et al. 2012). The latter treatment groups all taxa in section *Campylopoda* Hawksw. & Wiens, series *Campylopoda* distributed in California under *A. campylopodum*, thereby greatly reducing the number of *Arceuthobium* spp. in the state. Similarly, Nickrent (2012) reclassified all species in series *Campylopoda*, except *A. divaricatum* Engelm., to subspecies of *A. campylopodum*. Both of these treatments completely disregard and fail to integrate the large set of scientific literature available on the morphological, phenological, chemical, and host range differences among the dwarf mistletoes in series *Campylopoda*. As a result, these treatments also obscure the interspecific differences reported here, as well as those repeatedly demonstrated in the extensive historical and contemporary literature related to the morphology, ecology, and pathology of the *A. campylopodum-occidentale* complex. Furthermore, the taxonomic recognition of the taxa in this complex follows the

philosophy outlined by Baldwin (2000) and Baldwin et al. (2012) regarding the need for the classification of natural groups of higher plants, even when the morphological or molecular evidence indicates these taxa are cryptic. As Baldwin (2000) emphasizes, managers involved in biodiversity management and plant conservation need to consider the taxonomic recognition of cryptic taxa because their classification as species or subspecies allows for the protection and, hence, future study of natural groups of plants that may otherwise be ignored. While borderline cases will emerge in circumscribing species, and particularly subspecies – a likely byproduct of the phylogenetic “toolbox” utilized to examine the plant(s) in question, the classification of cryptic taxa is nonetheless needed so that these evolutionarily distinct populations can be conserved. If they are not recognized taxonomically, and thereby remain unnamed, their conservation can clearly be compromised.

KEY TO THE *ARCEUTHOBIMUM CAMPYLOPODUM-occidentale* COMPLEX

A key to the *Arceuthobium campylopodum-occidentale* complex for use in field identification of the species is provided below.

- 1. Plants dark brown or reddish brown, female plants usually less than 10 cm; basal diameters usually 3 mm or less; third internode widths usually 2 mm or less; plants not typically glaucous; staminate spike widths approximately less than 2.5 mm; parasitic on *Pinus attenuata* and *P. jeffreyi* in northwestern California and southwestern Oregon *Arceuthobium siskiyouense*
- 1'. Plants yellow, yellow-brown, olive green, green, dark green, or straw; female plant heights usually greater than 10 cm; basal diameters usually greater than 3 mm; third internode widths usually more than 2 mm; plants often glaucous at their base; staminate spike widths greater than 2.5 mm
 - 2. Plants green to dark green; basal diameter of female plants usually greater than 3.5 mm; staminate spike length usually greater than 15 mm; diameter of 3-merous and 4-merous flowers about 3.5 mm and 5 mm, respectively; 5-merous flowers common; anther diameter about 0.9 mm; parasitic primarily on *Pinus muricata* and *P. radiata* along the Pacific Coast of California *Arceuthobium littorum*
 - 2'. Plants yellow, yellow-brown, olive green, or straw; occasionally glaucous at their base; staminate spike lengths usually less than 15 mm; diameter of 3-merous and 4-merous flowers about 3 and 4 mm, respectively; 5-merous flowers rare; anther diameter about 0.6 mm; parasitic on *Pinus ponderosa*, *P. jeffreyi*, or *P. sabiniana*
 - 3. Plants primarily yellow or yellow-brown; third internode widths about 2.2 mm; fruits lightly glaucous; anthesis from late August to late September; parasitic primarily on *Pinus ponderosa* and *P. jeffreyi* *Arceuthobium campylopodum*
 - 3'. Plants yellow-brown or straw; third internode widths about 2.5 mm; fruits highly glaucous; anthesis from early October to December; parasitic primarily on *Pinus sabiniana* in the foothills surrounding the Central Valley of California. *Arceuthobium occidentale*

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APPENDIX 1

P-VALUES FOR MORPHOLOGICAL MEASUREMENTS FOR *ARCEUTHOBIUM CAMPYLOPODUM*, *A. OCCIDENTALE*, *A. LITTORUM*, AND *A. SISKIYOUENSE* USING THE NONPARAMETRIC STEEL-DWASS, MULTIPLE COMPARISON POST HOC TEST ($\alpha = 0.05$). Plant heights are in cm and all other measurements in mm. Comparisons are for *A. campylopodum* and *A. occidentale* (C-O); *A. campylopodum* and *A. siskiyouense* (C-S); *A. campylopodum* and *A. littorum* (C-L); *A. occidentale* and *A. siskiyouense* (O-S); *A. occidentale* and *A. littorum* (O-L); and *A. siskiyouense* and *A. littorum* (S-L).

Character		C-O	C-S	C-L	O-S	O-L	S-L
Plant Height	Female	P = 0.2316	P < 0.0001	P = 0.0630	P = 0.5966	P < 0.0001	P < 0.0001
	Male	P = 0.9887	P < 0.0001	P = 0.9995	P = 0.9834	P < 0.0001	P < 0.0001
Basal Diameter	Female	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001
	Male	P < 0.0001	P = 0.0494	P < 0.0001	P < 0.0001	P = 0.3329	P < 0.0001
Length Third Internode	Female	P < 0.0001	P = 0.3985	P = 0.3397	P = 0.0003	P < 0.0001	P = 0.9521
	Male	P = 0.9039	P = 0.8573	P < 0.0001	P < 0.0001	P = 0.5421	P = 0.0005
Width Third Internode	Female	P < 0.0001	P < 0.0001	P = 0.0099	P < 0.0001	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
Staminate Spike Length		P = 0.0005	P = 0.4472	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001
Staminate Spike Width		P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001
Flower Diameter	3-merous	P < 0.0001	P = 0.1725	P < 0.0001	P < 0.0001	P < 0.0001	P = 0.0052
	4-merous	P = 0.0121	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001
Petal Length		P = 0.0005	P < 0.0048	P < 0.0001	P < 0.0001	P = 0.9988	P < 0.0001
Petal Width		P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001
Anther Diameter		P = 0.9277	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001
Anther Distance to Tip		P = 0.0001	P = 0.0001	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001
Fruit Length		P = 0.0001	P < 0.0001	P = 0.1000	P = 0.0279	P = 0.4056	P = 0.0005
Fruit Width		P < 0.0001	P < 0.0001	P = 0.9948	P < 0.0001	P = 0.4589	P < 0.0001
Seed Length		P = 0.9759	P < 0.0001	P = 0.4293	P = 0.6079	P < 0.0001	P < 0.0001
Seed Width		P < 0.0001	P < 0.0001	P < 0.0001	P = 0.4767	P = 0.8442	P = 0.2808



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