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THE CLASSIFICATION OF CALIFORNIA VISCACEAE: AN ALTERNATIVE PERSPECTIVE

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ABSTRACT

The classification of Viscaceae in the second edition of the Jepson Manual (TJM2) differs radically from that in the first edition of the Jepson Manual (TJM1). The number of species of *Arceuthobium* M. Bieb. was reduced from 12 in TJM1 to three in TJM2, and for *Phoradendron* Nutt. reduced from seven species to four. The TJM2 treatment is conservative in regards to these taxa, and disregards many morphological, phenological, and other physiological discontinuities (e.g., host preferences) among the Viscaceae of California that have been consistently reported in the scientific literature since the 1960s. The species accepted in TJM2 have widespread geographical distributions containing distinct lineages, some of which we consider different species, and other lineages that may be considered cryptic taxa. These taxa are distinct enough, based on differences in morphology, phenology, host specificity, and geographic isolation, to warrant classification as species or subspecies. The taxonomic recognition of these taxa is of critical importance to resource managers that are responsible for mitigating economic impacts of these parasitic plants, or documenting and protecting rare mistletoes. We present an alternative treatment for the Viscaceae, which recognizes both the cryptic and distinct mistletoes in California. We provide a brief history of the taxonomic classification of mistletoes in California and why we believe the treatment proposed herein is a far better representation of the mistletoe diversity in the state. Keys and descriptions are provided for the identification of mistletoes in the field that use both morphological characters and host-mistletoe relationships.

Key Words: *Arceuthobium*, hosts, mistletoes, *Phoradendron*, Pinaceae, taxonomy, *Viscum*.

Two native genera of Viscaceae, *Arceuthobium* M. Bieb. and *Phoradendron* Nutt. occur in California, as well as the introduced species *Viscum album* L. The classification of Viscaceae in the second edition of The Jepson Manual (TJM2) (Kuijt 2012) recognized four species and two subspecies in *Phoradendron* and three species in *Arceuthobium,* and the introduced species of *Viscum* L. In the first edition of The Jepson Manual (TJM1) (Hawksworth and Wiens 1993), seven species were recognized in *Phoradendron*, 12 species and two subspecies in *Arceuthobium*, and one species in *Viscum*. A comparison of these treatments indicates that they represent diverse perspectives for classification of Viscaceae in California.

Mistletoes are parasitic angiosperms and some populations are associated with economic losses to commercially valuable timber species or nut crops. Forest managers and agricultural enterprises are interested in mistletoe classification, management, and potential negative impacts on tree growth and longevity or nut production. While several mistletoes are common and abundant on their host trees, others are rare species that are of special concern to conservationists.

Since the treatment of Viscaceae in TJM2 is the most recently published classification for this family in California, many scientists may be attempting to identify mistletoes using keys and descriptions that are inadequate for accurate identification of mistletoes occurring in the state. A short summary of the historical classification of Viscaceae in California, as well as an alternative treatment, which we consider an improved taxonomic system for mistletoes in the state, are provided. This treatment is practical and useful to botanists and other resource managers because it considers differences in ecology, morphology, phenology, host affinities, and geography among mistletoe populations in California.

PAST AND RECENT CLASSIFICATIONS OF CALIFORNIA VISCACEAE

Arceuthobium

Arceuthobium has long been considered a taxonomically difficult genus because of the morphological and phenological similarities among taxa (Gill 1935; Kuijt 1955; Hawksworth and Wiens 1972, 1996; Hawksworth et al. 2002).

Morphological reduction and similarity have contributed to problems identifying *Arceuthobium* taxa in the field and major differences in taxonomic treatments. However, because many of the dwarf mistletoes we recognize as species and subspecies are host specific, knowing the geographic location and correct host identification, allows taxa of *Arceuthobium* to be easily determined for most populations in California (see below, Identification of Viscaceae in California: Field Key to *Arceuthobium* species and Appendix 1; the key and Appendix 1 are primarily for field use and will not work well for herbarium collections, particularly if the location and/or host are not indicated on labels).

Engelmann, considered the "father" of *Arceuthobium* classification in North America, described most species of *Arceuthobium* that are known from the United States (Engelmann 1880). The validity of Engelmann's species has been justified on the basis of discontinuities in geography (ecosystem affinity), ecophysiology (host preference), morphometrics, and qualitative morphology. Where some of the species recognized by Engelmann co-occur, they flower at different seasons of the year and thus are also reproductively isolated. The recent classification of the family in TJM2 (Kuijt 2012) placed into synonymy about half of the taxa described by Engelmann (1880).

The first monographic treatment of *Arceuthobium* for the United States recognized three species for California: *A. americanum* Engelm., *A. douglasii* Engelm., and *A. campylopodum* Engelm. (Gill 1935). Gill (1935) also treated eight taxa as "host forms" of *A. campylopodum*, including seven from California that were recognized by Engelmann (1880). Gill's host-form system classified all dwarf mistletoes parasitizing a true fir (*Abies* Mill.) as *A. campylopodum* Engelm. forma *abietinum* (Engelm.) Gill, even if the dwarf mistletoe also parasitized hemlock (*Tsuga* [Endl.] Carrière) in the same locality. Gill's treatment required that the mistletoe on hemlock be classified as *A. campylopodum* Engelm. forma *tsugensis* (Rosendahl) Gill, even though the mistletoe on the true fir and the mistletoe on the hemlock were morphologically identical. Gill's host-form system lacked the recognition that a dwarf mistletoe could cross-infect more than one host species at the same location, which resulted in assigning different names for the same dwarf mistletoe based on each host relationship.

Hawksworth and Wiens (1972) published a monograph of *Arceuthobium*, which became the authoritative publication on the biology and taxonomy of the genus, where they recognized nine species and two special forms (formae speciales) of *A. abietinum* Engelm. ex Munz in California (Table 1). Hawksworth and Wiens used morphology (shoot size and color, flower, and fruit characters), phenology (time of meiosis, flowering, and seed dispersal), palynology (pollen characters), chemical constituents (anthocyanins and flavonoids), cytology (chromosome characters), and host preferences and reactions (hosts and host response to infection) in support of their treatment.

Hawksworth and Wiens (1993) contributed the treatment *Arceuthobium* in TJM1, which recognized 14 taxa in California. This treatment was consistent with the later revised monograph of *Arceuthobium* (Hawksworth and Wiens 1996), which recognized 42 New and Old World species, four of which had two subspecies each, one race of *A. tsugense* (Rosendahl) G. N. Jones, and two formae speciales of *A. abietinum*. The revised monograph provided systematic and descriptive information for each taxon as well as detailed information on the biology, anatomy, physiology, ecological relationships, pathology, and management of dwarf mistletoes. This work also included several new species described for California, including *A. littorum* Hawksw., Wiens & Nickrent, *A. monticola* Hawksw., Wiens & Nickrent, and *A. siskiyouense* Hawksw., Wiens, & Nickrent (Hawksworth et al. 1992; Hawksworth and Wiens 1996) (Table 1).

Phoradendron

The first monograph of *Phoradendron* was published by Trelease (1916), wherein nine taxa were recognized in California. Wiens (1964) published a revision of the species of *Phoradendron* lacking cataphylls (acataphyllous), and recognized seven taxa in California. The latter work served as the backbone for the treatment of *Phoradendron* contributed by Hawksworth and Wiens (1993) in TJM1, that recognized *P. californicum* Nutt., *P. juniperinum* A. Gray, *P. densum* Trel., *P. libocedri* (Engelm.) Howell, *P. macrophyllum* (Engelm.) Cockerell, *P. pauciflorum* Torrey, and *P. villosum* (Nutt.) Nutt. Wiens and Hawksworth (2002) studied *Phoradendron* sect. *Pauciflorae* Engl., and recognized *P. densum*, *P. libocedri*, and *P. pauciflorum* as valid species commonly found in California. Thereafter, Kuijt (2003) published a monograph for *Phoradendron* recognizing four species in the state (*P. bolleanum* [Seem.] Eichler, *P. californicum*, *P. juniperinum*, and *P. serotinum* [Raf.] M. C. Johnston [with two subspecies]). The treatment for *Phoradendron* in TJM2 (Kuijt 2012) followed the 2003 classification, except that *P. serotinum* was treated as *P. leucarpum* (Raf.) Rev. & M. C. Johnston in the electronic on-line version (i.e., Jepson eFlora) based on the nomenclature proposed by Abbott and Thompson (2011).

TABLE 1. Comparison of the classifications for the California Viscaceae proposed here and by Kuijt (2012). Note that 12 taxa of *Arceuthobium* recognized here are synonymized under *A. campylopodum* by Kuijt. [1] Taxa described for California in Hawksworth and Wiens (1972) and recognized by Hawksworth and Wiens (1993, 1996). [2] Taxon described for California in Mathiasen and Daugherty (2009a). [3] Taxa described for California in Hawksworth et al. (1992) and recognized in Hawksworth and Wiens (1993, 1996). [4] Recognized as a species in Wiens and Hawksworth (2002) and as *P. bolleanum* subsp. *densum* in Wiens (1964). [5] Recognized as a species in Wiens and Hawksworth (2002) and as *P. juniperinum* subsp. *libocedri* in Wiens (1964). [6] Recognized as *P. tomentosum* subsp. *macrophyllum* in Wiens (1964). [7] Recognized as a species in Wiens and Hawksworth (2002) and as *P. bolleanum* subsp. *pauciflorum* in Wiens (1964).

	Mathiasen and Kenaley (2016)	Kuijt 2012 (TJM2)
Arceuthobium	*A. abietinum* formae speciales *concoloris*[1]	*A. campylopodum*
	A. abietinum formae speciales *magnificae*[1]	*A. campylopodum*
	A. abietinum subsp. *wiensii*[2]	*A. campylopodum*
	A. americanum[1]	*A. americanum*
	A. californicum[1]	*A. campylopodum*
	A. campylopodum[1]	*A. campylopodum*
	A. cyanocarpum[1]	*A. campylopodum*
	A. divaricatum[1]	*A. campylopodum*
	A. douglasii[1]	*A. douglasii*
	A. littorum[3]	*A. campylopodum*
	A. monticola[3]	*A. campylopodum*
	A. occidentale[1]	*A. campylopodum*
	A. siskiyouense[3]	*A. campylopodum*
	A. tsugense subsp. *tsugense*[1]	*A. campylopodum*
	A. tsugense subsp. *mertensianae*[3]	*A. campylopodum*
Phoradendron	*P. californicum*	*P. californicum*
	P. densum[4]	*P. bolleanum*
	P. juniperinum	*P. juniperinum*
	P. libocedri[5]	*P. juniperinum*
	P. macrophyllum[6]	*P. serotinum* subsp. *macrophyllum*
	P. pauciflorum[7]	*P. bolleanum*
	P. villosum	*P. serotinum* subsp. *tomentosum*
Viscum	*V. album*	*V. album*

Viscum

The European mistletoe (*Viscum album*) was intentionally established on fruit trees by the horticulturist Luther Burbank in Sebastopol, California in the early 1900s for the commercial Christmas ornament industry (Scharpf and Hawksworth 1976; Hawksworth and Scharpf 1986). It is now common in the farmland and communities surrounding Sebastopol (Hawksworth et al. 1991). This is the only example of an introduced mistletoe in the United States, and included in both editions of the Jepson Manual (Hawksworth and Wiens 1993; Kuijt 2012).

PROBLEMS RELATED TO THE CLASSIFICATION OF CALIFORNIA VISCACEAE

The conservative interpretation of Viscaceae in TJM2 facilitates identification of the species recognized. However, it ignores cryptic and distinct taxa present in California, which results in an underrepresentation of the state's mistletoe biodiversity. Some mistletoe species circumscribed in TJM2 have extensive geographical distributions that transcend widely differing ecosystems and habitats. For example, the treatment of *Arceuthobium campylopodum* in TJM2 includes 11 taxa as synonyms (previously recognized as separate taxa in TJM1), and infects Pinaceae from southeastern Alaska to northern Baja California, then eastward through the Intermountain and Rocky Mountain states, and southward to western Texas (Kuijt 2012). Only two other species are recognized in TJM2, *A. americanum* and *A. douglasii*, which infect *Pinus contorta* Loudon and *Pseudotsuga menziesii* (Mirbel) Franco, respectively. Remarkably, no *Arceuthobium* described since 1880 is accepted in the TJM2 treatment of Viscaceae, which is essentially the same classification found in the *Manual of the Flowering Plants of California* (Jepson 1925). In contrast, we recognize 12 species of *Arceuthobium* in California here: the three species recognized in TJM2 and nine species that were reduced to synonymy under *A. campylopodum* (Table 1).

A study utilizing sequences of the nuclear ribosomal DNA (nrDNA; internal transcribed spacer [ITS] region) and those of non-coding chloroplast DNA (cpDNA), *trnT-L-F* by Nickrent et al. (2004) was cited in TJM2 as supporting evidence for reclassifying all species in *Arceuthobium* ser. *Campylopoda* found in California to synonymy under *A. campylopodum.* Although Nickrent et al. (2004) maintained *A. divaricatum* Engelm. as distinct from *A. campylopodum*, it was merged under *A. campylopodum* in TJM2.

Arceuthobium divaricatum is morphologically, physiologically, and genetically distinct from *A. campylopodum* (Hawksworth and Wiens 1972, 1996; Nickrent et al. 2004; Reif et al. 2015). Additional molecular analyses using DNA markers with improved phylogenetic resolution and greater genomic coverage are needed in order to better assess genetic differences and phylogenetic relationships as well as population and species boundaries we recognize among *Arceuthobium* ser. *Campylopoda* in California. To date, only two studies have examined the phylogenetic relationships among some (Nickrent et al. 1994) or all *Arceuthecium* spp. (Nickrent et al. 2004) we recognize in California.

Although the ITS and cpDNA regions are utilized routinely for resolving plant taxonomic issues due to their easy amplification and the availability of universal primers for both gene regions (Zimmer and Wen 2013), their phylogenetic resolving power remains poor or weak among some closely-related plants, including *Arceuthobium* spp. (Nickrent et al. 1994, 2004; Baldwin et al. 1995; Taberlet et al. 2007; Starr et al. 2009; Shaw et al. 2014). Current evidence suggests that morphology and/or ecological differences between closely-related plants may have evolved faster than commonly examined, "rapidly" evolving gene regions, such as ITS (Baldwin 2000; Álvarez and Wendel 2003; Feliner and Rosselló 2007). Thus, morphological and, in the case of dwarf mistletoes, host affinities may provide better fine-scale characters for recognizing evolutionary lineages than DNA data. Given these considerations, Reif et al. (2015) utilized amplified fragment length polymorphisms (AFLPs) and multivariate analyses of morphological data to examine the population genetics among *A. cyanocarpum* (A. Nelson ex Rydberg) Coulter & Nelson and two species not present in California, *A. blumeri* A. Nelson and *A. apachecum* Hawksw. & Wiens. Using this integrated approach, Reif and colleagues demonstrated that these taxa are distinct and should be recognized at the specific rank. Future research using AFLPs or advanced genotyping methods (e.g., genotyping-by-sequencing, see Elshire et al. 2011) should be conducted to examine genetic differences between population boundaries of *A. campylopodum* and its California relatives in order to estimate accurately the level(s) of inter- and intraspecific genetic differentiation among them.

The same problems related to grouping morphologically and physiologically distinct dwarf mistletoes under one species are also apparent for *Phoradendron* in TJM2. For example, two leafy conifer-infecting species, *P. densum* and *P. pauciflorum*, which were recognized by Wiens and Hawksworth (2002), are synonymized with *P. bolleanum* in TJM2. The latter species was described from the Sierra Madre Occidental of Mexico (Seeman 1856). Wiens and Hawksworth (2002) studied *P. bolleanum* as far south as the Sierra Madre del Sur in tropical Mexico, and conducted field studies of *P. densum* and *P. pauciflorum* throughout California. They concluded that the latter species can be differentiated from *P. bolleanum* using morphology, phenology, and host affinities in California. This is supported by Ashworth (2000a, b) who used ribosomal DNA sequences (ITS and domains D1 and D8 of the 26S rRNA gene) to investigate relationships among *Phoradendron* taxa and found that *P. densum* and *P. pauciflorum* each possess a unique indel that distinguished these two species from *P. bolleanum*. Therefore, we concur with Wiens and Hawksworth (2002) and treat *P. densum* and *P. pauciflorum* as separate species.

Additionally, in TJM2, *Phoradendron serotinum* (=*P. leucarpum*; Reveal and Johnston 1989, Abbot and Thompson 2011) is recognized as a species, comprised of two subspecies: *P. serotinum* subsp. *macrophyllum* (Engelm.) Kuijt and subsp. *tomentosum* (DC) Kuijt. These taxa are not only morphologically distinct, but are usually restricted to different hosts and flower at different seasons of the year (summer versus winter) and are thus reproductively isolated (Wiens 1964). Therefore, we consider *P. macrophyllum* (*P. serotinum* subsp. *macrophyllum* in TJM2) and *P. villosum* (*P. serotinum* subsp. *tomentosum* in TJM2) as distinct species from *P. serotinum*. This conclusion is partially supported by sequence data (Ashworth 2000a, b) where *P. macrophyllum* and *P. villosum* were well segregated from each other based on the ITS sequence and indel data, but *P. macrophyllum* was not segregated from *P. serotinum*. We also classify *P. libocedri* as distinct from *P. juniperinum* based on morphology and host specialization, but this is not supported by ribosomal DNA data (Ashworth 2000a, b). Similar to our suggestions for further study of *Arceuthobium*, we suggest that molecular work utilizing more variable loci with greater genomic coverage should be undertaken to investigate phylogenetic and taxonomic relationships among closely related species of *Phoradendron*.

Pre-zygotic isolating mechanisms separate the California species of *Phoradendron* and include spatial or geographic isolation (restriction to specific ecosystems), ecophysiological isolation through habitat specialization (host specificity), and reproductive isolation where the flowering times of co-occurring (sympatric) species are partitioned over different seasons of the year (Wiens 1962, 1964). Hybridization is rare, worldwide, in both Loranthaceae and Viscaceae (Hawksworth and Wiens 1996; Polhill and Wiens 1998). In California, only two instances of

TABLE 2. Morphological measurements for *Arceuthobium campylopodum* and *A. cyanocarpum*. Data are listed as **mean**, (SD), n. Means 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 ($\alpha = 0.05$). Data for *A. campylopodum* taken from Mathiasen and Kenaley (2015a) and for *A. cyanocarpum* taken from Reif et al. (2015). Plant heights are in cm and all other measurements in mm.

Character	*Arceuthobium campylopodum*	*Arceuthobium cyanocarpum*	P
Plant Height			
Female	**10.4** A (2.7) 600	**3.6** B (1.9) 258	<0.0001
Male	**9.7** A (3.0) 600	**2.8** B (1.8) 273	<0.0001
Basal Diameter			
Female	**3.4** A (0.7) 600	**2.0** B (0.4) 258	<0.0001
Male	**3.2** A (0.6) 600	**1.8** B (0.4) 273	<0.0001
Length of Third Internode			
Female	**13.0** A (3.1) 600	**2.0** B (0.4) 258	<0.0001
Male	**12.0** A (3.3) 600	**5.2** B (1.6) 273	<0.0001
Width of Third Internode			
Female	**2.5** A (0.4) 600	**1.5** B (0.2) 258	<0.0001
Male	**2.5** A (0.4) 600	**1.5** B (0.2) 273	<0.0001
Staminate Spike Length	**12.0** A (4.7) 760	**5.8** B (1.8) 294	<0.0001
Staminate Spike Width	**3.0** A (0.3) 760	**2.5** B (0.8) 294	<0.0001
Flower Diameter			
3-merous	**3.1** A (0.4) 400	**2.6** B (0.3) 220	<0.0001
4-merous	**4.2** A (0.5) 360	**2.8** B (0.5) 172	<0.0001
Petal Length	**1.6** A (0.2) 760	**1.3** B (0.2) 393	<0.0001
Petal Width	**1.4** A (0.2) 760	**1.1** B (0.2) 393	<0.0001
Anther Diameter	**0.6** A (0.1) 760	**0.5** B (0.2) 393	<0.0001
Anther Distance from Tip	**0.6** A (0.1) 760	**0.5** B (0.1) 253	<0.0001
Fruit Length	**5.4** A (0.5) 480	**3.5** B (0.4) 218	<0.0001
Fruit Width	**3.7** A (0.4) 480	**2.4** B (0.3) 218	<0.0001
Seed Length	**3.5** A (0.4) 480	**1.9** B (0.2) 208	<0.0001
Seed Width	**1.5** A (0.4) 480	**1.1** B (0.1) 208	<0.0001
Principal Hosts in California	*Pinus ponderosa, P. jeffreyi*	*Pinus flexilis, P. albicaulis*	

natural hybridization are known, both between *Phoradendron densum* and *P. juniperinum* (Wiens 1961; Vasek 1966). However, species integrity is not compromised because the hybrids are sterile (Wiens and DeDecker 1972). Therefore, the apparent lack of hybridization or sterility when rare hybrids occur in *Phoradendron* lends further support to the integrity of the species we contend are morphologically, genetically, and physiologically distinct.

We realize that morphological reduction and similarities in the inflorescences and flowers of both *Phoradendron* and *Arceuthobium* makes the circumscription of taxa challenging. Because of these traits, the Viscaceae in California (and elsewhere) require detailed studies and observations in nature to fully understand and quantify differences in their morphology, phenology, geography, and host specificity. A study of herbarium specimens alone may not be adequate, particularly if the aim is to quantify accurately the minute characters and landscape-scale patterns that define cryptic plants such as some taxa of *Arceuthobium* and *Phoradendron*. For these reasons, the Viscaceae of California require field study to clearly understand their ecological and taxonomic relationships (Wiens 1964; Hawksworth et al. 1992; Hawksworth and Wiens 1996; Wiens and Hawksworth 2002; Mathiasen and Kenaley 2015a).

Even with careful study, the overlap of some gross morphological characters (e.g., plant height and leaf size) may impede easy identification of some species. In such cases, differences among variable quantitative characteristics may be resolved by univariate and/or multivariate statistics (Quinn and Keough 2002) resulting in the identification of characters to assist with identification (Mathiasen and Kenaley 2015a, b; Reif et al. 2015). For example, Table 2 compares the morphological characteristics of two very distinctive dwarf mistletoes that occur in California, *Arceuthobium campylopodum* and *A. cyanocarpum*. Each morphological character measured is significantly different between the two species, demonstrating clear morphological differences. Furthermore, their host affinities in California are also quite distinct (Table 2; Figs. 1 and 2): *A. campylopodum* is a principal parasite of *Pinus ponderosa* Lawson and *P. jeffreyi* Grev. & Balf., whereas *A. cyanocarpum* is a principal parasite of *P. flexilis* James and *P. albicaulis* Engelm. (Hawksworth and Wiens 1996). Therefore, placing *A. cyanocarpum* in synonymy under *A. campylopodum* as proposed in TJM2 is not warranted; these two taxa are among the

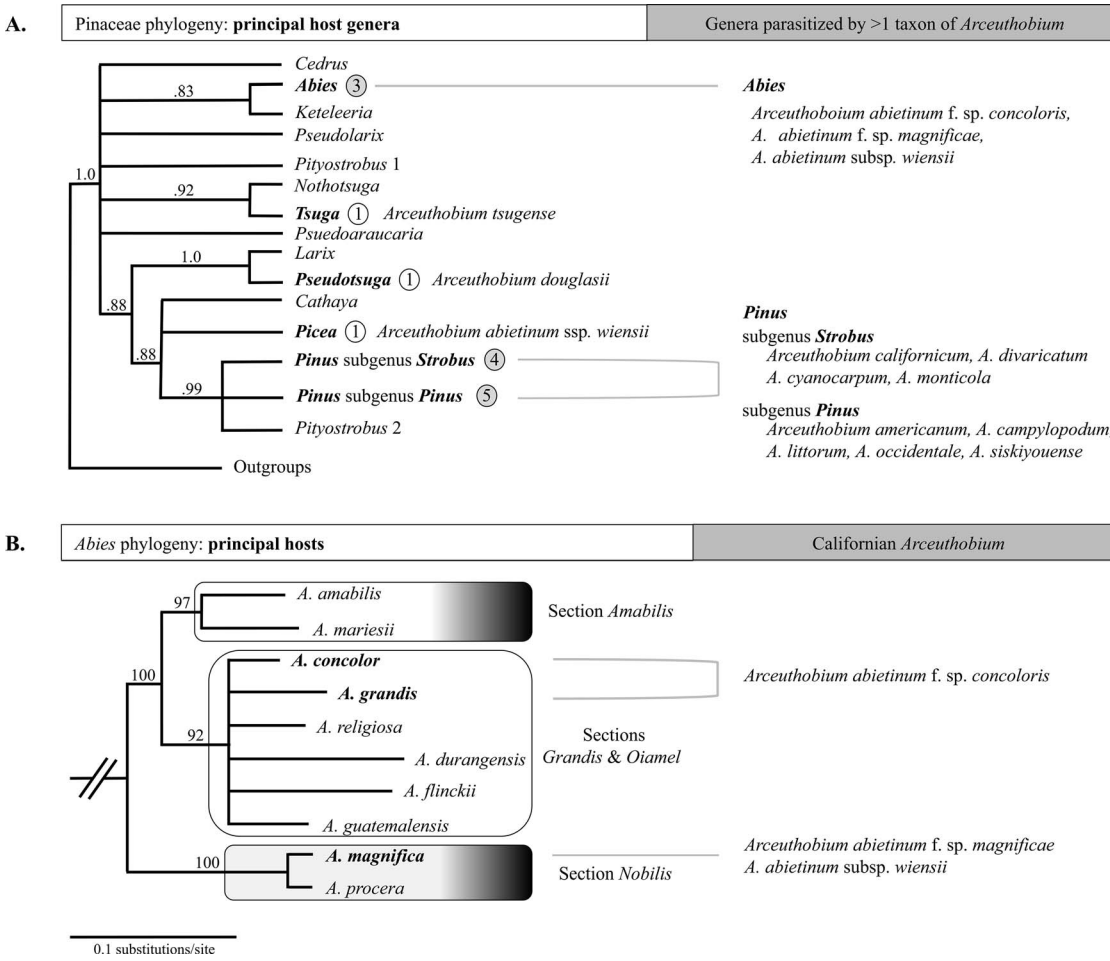

FIG. 1. Host-dwarf mistletoe relationships in California: principal host phylogenies and parasitizing taxa in the genus *Arceuthobium*. (A) Consensus tree comparing genera in the Pinaceae using combined, chloroplast DNA sequences (*matK* and *rbcL*) and morphological data (modification of Fig. 1F from Gernandt et al. 2008). The number of host-dwarf mistletoe combinations per genus/subgenus (circles) and corresponding *Arceuthobium* are provided. Principal host(s) of California *Arceuthobium* (bold) includes four separate genera (*Abies, Tsuga, Pseudotsuga,* and *Picea*) and two subgenera of *Pinus* (subg. *Pinus* and subg. *Strobus*). Numbers above branches represent Bayesian posterior probabilities after 5.0×10^7 generation (burn-in = 20%, total sample = 2.0×10^4 trees); branches with <0.80 support were collapsed. (B) Maximum likelihood analysis using the internal transcribed spacer (ITS) region of true firs (*Abies*) parasitized by taxa in *Arceuthobium* (modification of Fig. 3 from Xiang et al. 2009). Branch support was estimated using parsimony bootstrap analysis (1000 pseudo-replicates). Note that the principal host for the formae speciales of *A. abietinum* in California consists of two, phylogenetically distinct fir species, whereas, the principal host for *A. abietinum* ssp. *wiensii* includes *Abies magnifica* and *Picea breweriana* in Fig. 1A.

most morphologically and physiologically distinct species in ser. *Campylopoda* (Table 2; Figs. 3 and 4). Likewise, determining and recognizing taxa below the specific rank—the questions of subspecies—can also be facilitated by detailed morphologic analyses either alone or in combination with host affinity data.

Hawksworth and Wiens (1996) considered subspecies in *Arceuthobium* to be "geographically restricted populations of dwarf mistletoes that were distinguished by a few relatively small but consistent variations." While morphological characters used to separate subspecies and species of *Arceuthobium* often overlap, statistical analyses have demonstrated that some character means among subspecies are consistent and significantly different, regardless of the host (Wass and Mathiasen 2003; Mathiasen and Daugherty 2007; 2009a, Scott and Mathiasen 2009). Although Hawksworth and Wiens (1996) maintained that subspecies of *Arceuthobium* were geographically separate, field studies have now demonstrated that the geographic distributions of subspecies sometimes overlap. Thus, the key element of the subspecies concept in *Arceuthobium* is the relatively small but consistent

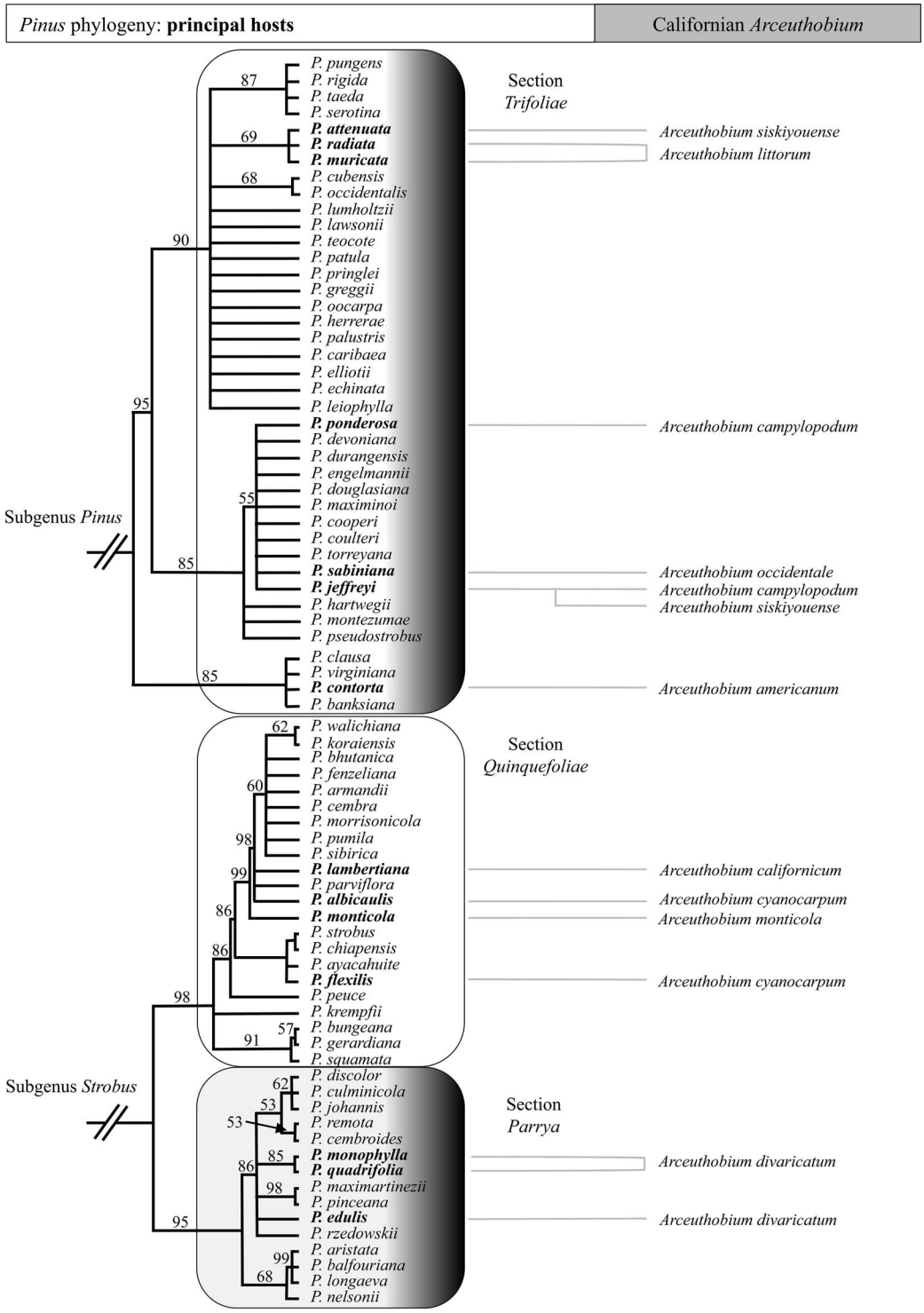

FIG. 2. Phylogeny of the genus *Pinus* (subg. *Pinus* and subg. *Strobus*) based on maximum parsimony analysis combining two chloroplast DNA gene regions (*matK* and *rbcL*; modification of Fig. 2 from Gernandt et al. 2005). Branch support was estimated via 500 bootstrap replicates. Note that, in California, 14 species of *Pinus* (bold) are recognized as principal hosts of a total of nine species of *Arceuthobium*. All host-dwarf mistletoe combinations are unique as no single-species of *Pinus* serves as a principal host to more than one species of *Arceuthobium*. Five species of *Arceuthobium* (*A. americanum*, *A. californicum*, *A. monticola*, *A. occidentale* and *A. siskiyouense*)

FIG. 3. Female plants of *Arceuthobium campylopodum* on *Pinus ponderosa* in late August with mature fruits. The largest plants are approximately 12 cm in length and the fruits are approximately 5 × 3 mm.

FIG. 4. Female plants of *Arceuthobium cyanocarpum* on *Pinus flexilis* in late August with mature fruits. The largest plants are approximately 4 cm in length and the fruits are approximately 3.5 × 2.5 mm.

differences among taxa. In addition, host affinities are critical in the classification of subspecies in *Arceuthobium* because differences in host preferences reflect corresponding and underlying genetic differentiation between taxa. Based on our analyses of morphological characters and knowledge of host affinities, we recognize three subspecies of *Arceuthobium* in California: two under *A. tsugense* (Hawksworth et al. 1992; Mathiasen and Daugherty 2007) and one under *A. abietinum* (Mathiasen and Daugherty 2009a). We have also continued the use of special forms under *Arceuthobium abietinum* proposed by Hawksworth and Wiens (1972, 1996), because we have observed that the populations of *A. abietinum* in the Cascade Ranges and Sierra Nevada parasitizing *Abies concolor* (Gordon & Glend.) Lindley do not infect *A. magnifica* Andr. Murray, and vice versa.

Field studies of species with extensive geographical distributions sometimes reveal the presence of evolutionarily autonomous cryptic taxa. The discovery and naming of cryptic lineages has been a common pathway for achieving greater understanding of species complexes and provides foundational knowledge for future experimental studies and surveys for plant biodiversity (Frankham et al. 2012). We, therefore, agree with Baldwin (2000) that cryptic taxa should be given taxonomic recognition as species, or at least subspecies, even though identification may be more difficult (see also the Philosophy section of TJM2, pp. 1–2). As Baldwin (2000) emphasized, the cryptic differences between plant groups, such as characters associated with ecophysiology (e.g., host affinities for mistletoes, our addition), are more important to their survival and evolution than differences humans can observe visually. This concept definitely applies to the California Viscaceae.

THE IMPORTANCE OF HOST SPECIALIZATION IN CLASSIFYING THE CALIFORNIA VISCACEAE

Host-mistletoe relationships evident in California, and elsewhere, have evolved over thousands of years and remain one of the most important components in any taxonomic treatment of mistletoes, particularly *Arceuthobium*. Principal host-dwarf mistletoe combinations also provide insight into the evolution of the group. Yet the genetic and physiological mechanisms mediating host-specialization in mistletoes and the contribution of host preference to group speciation remain poorly understood. Host specialization is particularly important to forest resource managers and conservationists who are interested in either decreasing or increasing the abundance of these parasitic plants on the landscape. Any taxonomic treatment of this ecologically and economically important family that ignores host affinities of these relatively host-specific parasites is not representative of the genetic differences

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principally and separately parasitize only one species of *Pinus* in California. Three species of *Arceuthobium* (*A. campylopodum*, *A. cyanocarpum*, and *A. littorum*) are reported to parasitize principally and separately two closely related species of *Pinus*. Only *A. divaricatum* parasitizes more than two species of *Pinus* (pinyons) as principal hosts in California.

mistletoes have evolved over millennia (Hawksworth 1987, Hawksworth and Wiens 1996; Mathiasen 1996; Mathiasen and Kenaley 2015a, b).

The taxa we recognize herein are not only morphologically and/or phenologically distinguishable; their host affinities—particularly, principal host(s)—set them apart from each other (Figs. 1 and 2). For example, the treatment in TJM2 suggests that *Arceuthobium campylopodum* in California infects all Pinaceae genera except *Pseudotsuga* (Fig. 1A). However, years of field observations by botanists and foresters have demonstrated clearly that populations of *A. campylopodum* parasitizing *Pinus ponderosa* and *P. jeffreyi* in California do not parasitize *Abies concolor*, *A. grandis* (Douglas) Lindley (Fig. 1B), *Pinus monticola* Douglas, or *Pinus monophylla* Torrey & Frém. where these trees co-occur (Fig. 2; Hawksworth and Wiens 1996). However, secondary and occasional hosts of *A. campylopodum* include pines in section *Trifoliae* such as *Pinus attenuata* Lemmon and *P. coulteri* D. Don. *Arceuthobium campylopodum* also occasionally infects *P. contorta* and *P. sabiniana* Douglas (Hawksworth and Wiens 1996). While two additional taxa of *Arceuthobium* (*A. occidentale* and *A. siskiyouense*) also commonly infect *P. sabiniana* and *P. attenuata*, these dwarf mistletoes are differentiated from *A. campylopodum* by morphological differences and/or flowering period (Mathiasen and Kenaley 2015a). Furthermore, several dwarf mistletoes (not recognized as distinct species in TJM2) never infect the principal hosts of *A. campylopodum* (*P. ponderosa* and *P. jeffreyi*) in California including: *A. abietinum*, *A. californicum*, *A. cyanocarpum*, *A. divaricatum*, *A. monticola*, and probably *A. tsugense* (Hawksworth and Wiens 1996). Therefore, classifying all of these dwarf mistletoes under *A. campylopodum* completely ignores the host preferences and underlying genetic differences these species have evolved and negates the ability of foresters and conservationists to consider these important parasite-host relationships when managing dwarf mistletoes in California. Placing all of the these species of *Arceuthobium* into synonymy with *A. campylopodum* also results in unrealistic distribution maps for dwarf mistletoes in California as illustrated by the CALFLORA map for *A. campylopodum* (http://www.calflora.org/) which actually represents the distribution of *A. campylopodum* and 10 other taxa we recognize as valid species or subspecies.

To further illustrate problems arising when species diversity is not recognized, consider the conservation of a cryptic species of dwarf mistletoe in the Klamath Ranges: *Arceuthobium abietinum* Engelm. ex Munz subsp. *wiensii* Mathiasen & C. Daugherty. If populations of this dwarf mistletoe were classified as *A. campylopodum*, its host affinities would encompass most of the conifers found in the Klamath Ranges. However, this dwarf mistletoe only parasitizes *Picea breweriana* S. Watson, *Abies magnifica*, occasionally *A. concolor*, and rarely *Pinus monticola* in that region (Mathiasen and Daugherty 2009a). Therefore, in order to insure the survival of this host-specific parasitic plant, these hosts must be preserved where populations of this rare mistletoe exist. If this dwarf mistletoe's hosts were eliminated from the area by wildfire or logging activities and immune conifers were selected for recruitment or replanting following the disturbance(s), the dwarf mistletoe would probably not survive and could become extinct. Knowledge of this rare dwarf mistletoe's preferred habitat (host relationships) is critical to its preservation just as for any rare plant species. Failing to name and recognize the existence of this cryptic dwarf mistletoe lineage, as well as disregarding its ecological adaptations to certain habitats (hosts) would contribute to its potential loss. This is one example, or consequence, of how classifying the majority of the dwarf mistletoes in California as *A. campylopodum* could adversely affect their management and/or preservation.

There are additional examples of *Arceuthobium* populations in California with similar morphologies, yet they possess clear ecophysiological differences as demonstrated by their principal host preferences (Figs. 1B and 2). Probably the best example is illustrated by the populations of *Arceuthobium abietinum* parasitizing *Abies concolor* and *A. magnifica* in the Sierra Nevada. Both greenhouse studies and field observations have repeatedly supported the hypothesis that there are two morphologically similar, yet physiologically distinct populations: one that infects only *A. concolor* and not *A. magnifica*, and one that infects only *A. magnifica* and not *A. concolor* (Parmeter and Scharpf 1963; Scharpf and Parmeter 1967; Hawksworth and Wiens 1972, 1996). Because these populations are morphologically almost identical, while demonstrating a proven affinity for either *A. concolor* or *A. magnifica*, but not both, they were not given formal taxonomic status by Hawksworth and Wiens (1972, 1996) but were designated as special forms of *A. abietinum*. The morphological similarity of these populations has also been demonstrated by Mathiasen (2011). The circumscription of *A. abietinum* under *A. campylopodum* compromises the management of these populations for conservation purposes or for timber management decisions. As treated herein, *A. campylopodum* is a parasite of hard pines and not true firs and *A. abietinum* is primarily a parasite of true firs and causes considerable economic damage in forests of the Sierra Nevada (Scharpf and

Parmeter 1967; Hawksworth and Wiens 1996). This, in and of itself, is a valid reason for not applying the treatment for *Arceuthobium* in TJM2.

In *Phoradendron,* host affinities are also indicative of genetic differences among taxa. This is best typified by *P. libocedri* and *P. pauciflorum*. Each of these species parasitizes only one host; *Calocedrus decurrens* (Torrey) Florin and *Abies concolor*, respectively. These mistletoes are also morphologically distinct from other *Phoradendron* species (Wiens 1964; Wiens and Hawksworth 2002) although they are placed in synonymy under *P. juniperinum* and *P. bolleanum*, respectively, in TJM2.

Host preferences also delimit *P. juniperinum* and *P. densum* in California. As appropriately indicated by its specific epithet, *P. juniperinum* only parasitizes *Juniperus* throughout its geographic range. *Phoradendron densum*, however, occurs on *Juniperus* and several species of *Cupressus* in California and the Southwest (Wiens 1964; Wiens and Hawksworth 2002). The morphological differences between *P. juniperinum* and *P. densum* distinguish these taxa and host preferences and phenology further contribute to characterize *P. densum* as separate from *P. bolleanum* (Wiens 1964; Wiens and Hawksworth 2002), a species that was synonymized with *P. bolleanum* in TJM2. Finally, while both *P. villosum* and *P. macrophyllum* clearly have relatively large host ranges, *P. villosum* is primarily a parasite of *Quercus* in California and throughout its geographic distribution, while *P. macrophyllum* parasitizes a wide range of hardwood trees, but only rarely occurs on *Quercus* (Wiens 1964).

Conclusions

The California species of *Arceuthobium* constitute a particularly critical example of the value of giving taxonomic recognition to morphologically and physiologically differentiated populations because they are amongst the most economically and ecologically important plant pathogens of North American conifers (Hawksworth and Wiens 1996; Mathiasen 1996; Hawksworth et al. 2002; Mathiasen et al. 2008). If botanists, ecologists, conservationists, wildlife biologists, and especially foresters, are to make intelligent decisions regarding the preservation of mistletoe populations or sustainable harvesting of commercially valuable forest trees infected by mistletoes, they require the most current, specific, and definitive data available that are attendant to a species name. We submit that this treatment of California Viscaceae is of far greater practical value for resource managers and conservationists than that found in TJM2, and especially useful for identification of populations in the field.

In regions where the flora is relatively well known, the plant systematics community will once again have to confront the problem of how to define species and subspecies if cryptic plant lineages, as well as rare and endangered species, are to be protected and hence preserved. This is now a matter of critical environmental concern and natural scientists should embrace the classification of the California Viscaceae we propose as well as practical classifications for other plant groups as recommended by Baldwin (2000).

Lastly, we do not believe that the treatment of the California Viscaceae in TJM2, which is essentially a classification used before the year 1878, reflects, nor advances, the totality of knowledge presently available for the designation of species in this family. We, therefore, provide the following alternative treatment for the California Viscaceae which closely follows the treatment presented by Hawksworth and Wiens (1993), but improves upon their taxonomic keys, considers relevant literature published since then, and updates the classification of some taxa based on the discovery of an additional cryptic mistletoe in northern California.

Identification of Viscaceae in California

Mistletoe Family

Here we recognize Viscaceae (sensu Der and Nickrent 2008) as the family containing all of the mistletoes in California. Mistletoes are obligate parasitic plants of woody gymnosperms and angiosperms. They are dioecious or monoecious (dioecious in California), perennial, evergreen shrubs. Their stems are brittle with many branches and their leaves are simple, entire, opposite, four-ranked, with a blade or sometimes with scale-like leaves. Inflorescences are spikes or open cymes that are typically axillary, but sometimes terminal. The plants have bracts that are opposite, four-ranked, and scale-like, with each pair fused. Flowers are unisexual, radial, 2–5 mm wide and have perianth parts typically in one series. Staminate flowers have 3–4 (2–7) parts with anthers typically sessile, opposite, and borne on the perianth segments. Pistillate flowers have 2–4 perianth parts, an inferior ovary with one chamber, and an unbranched style with a relatively obscure stigma. The fruit is a berry containing mucilaginous viscin and typically has one seed, sometimes two. Viscaceous mistletoe seeds are dispersed by a variety of birds (*Phoradendron*) or explosively ejected from the fruit (*Arceuthobium*).

Because the following treatment for Viscaceae most resembles that found in TJM1 (Hawksworth and Wiens 1993), we have followed the treatments for the Cupressaceae (Bartel 1993) and Pinaceae (Griffin 1993) presented in TJM1.

FIELD KEY TO VISCACEAE GENERA IN CALIFORNIA

1. Stems generally <20 cm, may be angled, at least when young; leaves <1 mm, scale-like; fruits bicolored berries, explosive, somewhat compressed-spheric; pedicel recurved when mature; parasitic only on members of the Pinaceae in California . . . . . *Arceuthobium*
1′. Stems >20 cm, rounded; leaves 5−80 mm, or scale-like and ≤1 mm; fruits one colored berries, not explosive, spheric; pedicel not recurved when mature; parasitic on angiosperms and gymnosperms
   2. Perianth parts generally 3; inflorescence many flowered, open or interrupted spikes; flowers sunken into axis; berry diameter 3−6 mm; leaf (blade and pedicel) usually 5−50 mm long or scale-like, <1 mm; anthers 2 chambered; parasitic on angiosperms, occasionally on gymnosperms . . . . . *Phoradendron*
   2′. Perianth parts generally 4; inflorescence few-flowered, dense cymes; flowers not sunken into axis; berry diameter 6−10 mm; leaf (blade and pedicel) usually 50−70 mm long; anthers several chambered; parasitic on angiosperms . . . . . *Viscum*

ARCEUTHOBIUM MARSCHALL VON BIEBERSTEIN

Dwarf mistletoe

These mistletoes are dioecious herbs or shrubs from 0.4–90 cm tall. Plants are glabrous and vary in color from green, greenish-yellow to yellow-brown, orange, purple, reddish, or black. Their leaves are reduced to minute, opposite, connate scales. Staminate flowers are generally decussate or rarely verticillate, and 2−5(-6) mm across, with a central nectary. Male flowers have (2-)3–4(-7) petals, each with a sessile, uniloculate, circular anther. Pollen grains are spherical with 6-alternating spiny and smooth sections. Pistillate flowers are epigynous with 1 style and 2 persistent petals that are adnate to the ovary, which has one chamber. Fruits are a bicolored, ovoid berry with one seed (rarely 2), enveloped in viscin, and recurved and explosive at maturity. Seeds lack true integuments and are usually 2−5(-6) mm long and 1−3(-4) mm wide, ovate-lanceolate with 1 (rarely 2) distal embryo.

Dwarf mistletoes are obligate parasites of trees in the Pinaceae in North America; elsewhere in the Old World there are species that parasitize trees in the Cupressaceae. Because they are widespread and common parasites, reduce the growth of their host trees, and are associated with premature mortality, they are considered to be among the most serious and economically important forest pathogens in the United States. However, they are also recognized as important for many wildlife species because they provide food and habitat. Nearly all dwarf mistletoes induce the formation of dense masses of branches on infected trees called "witches' brooms," which not only aid in observing dwarf mistletoes, but serve as nesting, resting, and hiding sites for many species of birds and mammals.

Because species of *Arceuthobium* recognized here are relatively host specific, the following key facilitates identification of dwarf mistletoes by using known host preferences in California (Hawksworth and Wiens 1996). However, this then requires correct identification of the host(s) parasitized by the dwarf mistletoe under investigation.

More detailed botanical descriptions and nomenclature for each species or subspecies can be found in the reference(s) listed at the end of the Diagnostic Characters for each taxon. The full citations for the references are listed in the Literature Cited. Because upon drying, mistletoe plants often change color and the fruits can shrink significantly (25–30%), the following keys are primarily for field use and will not work as well for dried, herbarium collections.

FIELD KEY TO *ARCEUTHOBIUM* SPECIES IN CALIFORNIA

1. Parasites principally of *Pinus*
   2. Parasites of *Pinus* subg. *Strobus* (D. Don) Lemmon with 1–5 needles per fascicle, one fibrovascular bundle per leaf (Haploxylon or soft pines)
      3. Parasite of *Pinus monophylla* (1 needle per fascicle), *P. edulis* (2 needles per fascicle), and *P. quadrifolia* ([3]4[5] needles per fascicle) . . . . . 8. *A. divaricatum*
      3′. Parasites of *Pinus* subg. *Strobus* with 5 needles per fascicle (white pines) or *Picea breweriana* with 1 needle
         4. Shoots usually less than 4 cm, yellow-green, densely clustered around the host branch, parasite of *Pinus albicaulis*, *P. flexilis*, *P. monticola*, and occasionally *P. balfouriana* . . . . . 7. *A. cyanocarpum*
         4′. Shoots usually more than 4 cm, dark brown or yellow-green, not densely clustered around the host branch, parasites of *Pinus lambertiana*, *Pinus monticola, or Picea breweriana*
            5. Shoots dark brown, parasite of *Pinus monticola* and *Picea breweriana* in northwestern California . . . . . 11. *A. monticola*
            5′. Shoots yellow to green, parasite of *Pinus lambertiana* . . . . . 5. *A. californicum*

2′. Parasites of *Pinus* subg. *Pinus* with 2–3 needles per fascicle, two fibrovascular bundles per leaf (Diploxylon or hard pines)
6. Plants branching in whorls; parasite principally of *Pinus contorta* . . . . . 4. *A. americanum*
6′. Plants (at least some) branching flabellately; parasites principally of pines other than *Pinus contorta*
7. Plants green to dark green; not glaucous at base; 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; parasite of *Pinus muricata* and *P. radiata* along the Pacific Coast . . . . . 10. *A. littorum*
7′. Plants reddish-brown, yellow, yellow-brown, olive-green, or straw; occasionally glaucous at base; basal diameter of female plants usually less than 3.5 mm; staminate spike length usually less than 15 mm; diameter of 3-merous and 4-merous flowers about 3 mm and 4 mm, respectively; 5-merous flowers rare; anther diameter about 0.6 mm; parasitic on *Pinus attenuata*, *P. coulteri*, *P. jeffreyi*, *P. ponderosa*, or *P. sabiniana*
8. Plants dark brown or reddish brown, plants usually less than 10 cm; third internode widths usually less than 2 mm; staminate spike widths usually less than 2.5 mm; parasite of *Pinus attenuata* and *P. jeffreyi* in the Klamath Ranges . . . . . 13. *A. siskiyouense*
8′. Plants yellow or brown or straw; plants usually greater than 10 cm; third internode widths usually greater than 2 mm; staminate spike widths usually greater than 2.5 mm; parasitic on *Pinus coulteri, P. jeffreyi, P. ponderosa*, or *P. sabiniana*
9. Plants primarily yellow or yellow-brown; third internode widths about 2.5 mm; fruits lightly glaucous; anthesis from late August to late September; parasite of *Pinus attenuata, P. coulteri, P. jeffreyi,* and *P. ponderosa* . . . . . 6. *A. campylopodum*
9′. Plants yellow-brown or straw; third internode widths about 2.2 mm; fruits highly glaucous; anthesis from early October to December; parasitic primarily on *Pinus sabiniana* in the foothills surrounding the Great Central Valley, in the southern Sierra Nevada (Kern and Tulare counties), and on the north slope of the Transverse Ranges . . . . . 12. *A. occidentale*

1′. Parasites principally of *Abies, Picea*, *Pseudotsuga*, or *Tsuga*
10. Parasites of *Pseudotsuga* or *Tsuga*
11. Shoots usually less than 3 cm long; flowering from April to May; parasite of *Pseudotsuga* . . . . . 9. *A. douglasii*
11′. Shoots usually more than 3 cm long; flowering from August to September; parasites of *Tsuga*
12. Plants less than 5 cm; often green-brown; basal diameter of male and female plants 2 mm; mature fruits about 4 mm long and 3 mm wide; parasite of *Tsuga mertensiana* and occasionally *P. monticola* . . . . . 15. *A. tsugense* subsp. *mertensianae*
12′. Plants usually more than 5 cm, green or yellow-green; basal diameter of male and female plants >2 mm; mature fruits about 4.5 mm long and 3 mm wide; parasite of *Tsuga heterophylla* near the coast of northern California . . . . . 14. *A. tsugense* subsp. *tsugense*

10′. Parasites of *Abies* or *Picea*
13. Plants usually less than 10 cm, usually reddish brown; parasite of *Abies magnifica* and *Picea breweriana* in the Klamath Ranges, occasionally on *Abies concolor* . . . . . 3. *A. abietinum* subsp. *wiensii*
13′. Plants usually more than 10 cm, yellow-green to green-brown; parasites of *Abies concolor*, *A. grandis*, or *A. magnifica*
14. Plants frequently green-brown; parasite of *Abies magnifica* in the Sierra Nevada. . . . . 2. *A. abietinum* f. sp. *magnificae*
14′. Plants frequently yellow-green; parasite of *Abies concolor* and *A. grandis* . . . . . 1. *A. abietinum* f. sp. *concoloris*

Identification of *Arceuthobium* in California

The following section provides information needed to identify the taxa of *Arceuthobium* we classify as species, subspecies, or special forms in California. This section includes scientific names, most commonly infected hosts, distribution, a brief diagnostic description, and references to literature that provide more detailed descriptions for each taxon.

1. *Arceuthobium abietinum* Engelmann ex Munz formae speciales *concoloris* Hawksworth & Wiens

White fir dwarf mistletoe

Hosts: The most commonly infected host of this dwarf mistletoe in California is *Abies concolor*. In far northern California, *A. grandis* is a principal host. In most instances when dwarf mistletoe is collected on *A. concolor* in California it should be identified as *A. abietinum* f. sp.

concoloris. This dwarf mistletoe will also infect *Pinus lambertiana* and infection appears to be more common than reported in the literature. However, when dwarf mistletoe is observed on *P. lambertiana* in California, it will usually be *Arceuthobium californicum* (see number 5 below).

Distribution: *Arceuthobium abietinum* f. sp. *concoloris* is common from the San Bernardino Mountains north through the Sierra Nevada and Cascade Ranges into Oregon and southern Washington. It is also common in the Klamath Ranges. It occurs in scattered populations in the North Coast Ranges.

In the Sierra Nevada there are populations of *A. abietinum* that only infect *Abies concolor* and populations that only infect *A. magnifica*, but plants of these populations are morphologically nearly identical. Because it has been demonstrated by many observations in mixed-conifer forests that the dwarf mistletoe on *A. concolor* will not infect *A. magnifica* and vice versa, these populations have been classified as special forms (formae speciales; f. sp.) This designation has no formal taxonomic status and should not be confused with subspecies (subsp.).

Diagnostic Characters: **Plants** 5–24 cm tall (mean 12), yellow or yellow-green, rarely green-brown. **Basal diameter** of dominant plants 2–6.2 mm (mean 3.6). **Staminate flowers** 3- or 4-merous, 3-merous flowers 2.1–3.5 mm in diameter (mean 2.7), 4-merous flowers 2.7–4.8 mm in diameter (mean 3.7). **Petals** 0.9–2 mm long (mean 1.4), 0.8–1.6 mm wide (mean 1.2), apex acute, same color as plants. **Anther** diameter 0.2–0.9 mm (mean 0.6). **Fruits** 3.3–6.1 mm long (mean 4.8) and 2.2–3.8 mm wide (mean 3.1), light green and lightly glaucous. **Seeds** 1.9–3.2 mm long (mean 2.5) and 0.8–1.6 mm wide (mean 1.2). **Anthesis** occurs from late June to mid October with peak flowering from mid July to late September. **Seed dispersal** starts in early September and ends in early November, but peak dispersal is from mid September to mid October. See Hawksworth and Wiens (1996, p. 179) and Mathiasen (2011) for additional descriptions of this species.

2. *Arceuthobium abietinum* Engelmann ex Munz formae speciales *magnificae* Hawksworth & Wiens

Red fir dwarf mistletoe

Arceuthobium abietinum f. sp. *magnificae* is one of the principal disease agents of *Abies magnifica* in the Sierra Nevada. A canker-causing fungus, *Cytospora abietis* Sacc, often infects branches infected by this mistletoe. A symptom known as "flagging" is common on dwarf mistletoe-infected *A. magnifica* due to a combination of dwarf mistletoe and *Cytospora* killing the branch distal to the point of infection. As branches die, needles turn red and then brown, and the infected branches can be easily observed. "Flagged" branches on *A. magnifica* make it relatively easy to observe dwarf mistletoe-infected trees in the Sierra Nevada.

Hosts: The only host of this dwarf mistletoe is *Abies magnifica*.

Distribution: *Arceuthobium abietinum* f. sp. *magnificae* occurs from near Mount Lassen (Shasta and Lassen Counties) to as far south as the southern Greenhorn Mountains (Kern County) east to the *A. magnifica* forests near Sherman Pass (Tulare County). Any dwarf mistletoe found on *A. magnifica* in this geographic area is *A. abietinum* f. sp. *magnificae*. This dwarf mistletoe is not known to cross infect any other hosts thus far. *Arceuthobium abietinum* subsp. *wiensii* can also be found on *Abies magnifica* in the Klamath Ranges (see number 3 below).

Diagnostic Characters: **Plants** 6–22 cm tall (mean 12), yellow, yellow-green, or green-brown. **Basal diameter** of dominant plants 2.1–7.6 mm (mean 3.6). **Staminate flowers** 3 or 4-merous, 3-merous flowers 2.2–3.7 mm in diameter (mean 2.6), 4-merous flowers 2.6–5 mm in diameter (mean 3.6). **Petals** 0.9–2 mm long (mean 1.5), 0.8–1.7 mm wide (mean 1.2), apex acute, same color as plants. **Anther** diameter 0.3–0.9 mm (mean 0.6). **Fruits** 3.4–5.9 mm long (mean 4.7) and 2.2–3.9 mm wide (mean 3.1), light green and lightly glaucous. **Seeds** 1.8–3.3 mm long (mean 2.5) and 0.8–1.6 mm wide (mean 1.2). **Anthesis** peaks from early August to mid September. **Seed dispersal** peaks from early September to late October. See Hawksworth and Wiens (1996, p. 182) and Mathiasen (2011) for additional descriptions of this species.

3. *Arceuthobium abietinum* Engelmann ex Munz subsp. *wiensii* Mathiasen & C. Daugherty

Wiens' dwarf mistletoe

This dwarf mistletoe could have also been commonly referred to as Brewer spruce dwarf mistletoe because one of its principal hosts is *Picea breweriana*. However, it also severely parasitizes *Abies magnifica* and occasionally infects *A. concolor*, so its host range alone demonstrates that it is distinct from both *Arceuthobium abietinum* f. sp. *concoloris* and *A. abietinum* f. sp. *magnificae*. Given its limited geographic range and infection of *Picea breweriana* and *Abies magnifica*, this dwarf mistletoe is relatively easy to identify.

Hosts: *Arceuthobium abietinum* subsp. *wiensii* severely infects *Picea breweriana* and *Abies magnifica*. These hosts are about equally susceptible and in some populations of this dwarf mistletoe where *P. breweriana* is absent, *A. magnifica* is severely infected. *Arceuthobium abietinum* subsp. *wiensii*

will occasionally infect *Abies concolor*. In southern Oregon, it is sometimes observed on *Pinus monticola*, so it likely could be found infecting this host in northern California.

Distribution: *Arceuthobium abietinum* subsp. *wiensii* is common on *Abies magnifica* and occasionally infects *A. concolor* on Baldy Mountain (near Happy Camp), near Etna Summit, and on South Fork Mountain (near Mad River) in northern California. We presently know of only one location in California where this rare dwarf mistletoe occurs on *Picea breweriana*; near Baldy Mountain. Many severely infected *P. breweriana* are present on the east slopes of Baldy Mountain as well as many dead spruce killed by the mistletoe. This dwarf mistletoe also severely parasitizes *P. breweriana* at a few other locations in southern Oregon, so it is probable that it occurs on this host at other locations in northern California.

The geographic range of A. *abietinum* subsp. *wiensii* does not overlap with that of *A. abietinum* f. sp. *magnificae* and there is a distinct gap in the distribution of these dwarf mistletoes. We have been unable to locate any dwarf mistletoe infection of *Abies magnifica* near Mt. Shasta or west of there around Mt. Eddy, although this tree is common in those areas.

Diagnostic Characters: **Plants** 4–16 cm tall (mean 9), staminate plants green-brown, but may be red-brown, pistillate plants green-brown, but some red-brown or rarely yellow-brown. **Basal diameter** of dominant plants 1.8–5.8 mm (mean 3.2). **Staminate flowers** 3 or 4-merous, 3-merous flowers 2–2.9 mm in diameter (mean 2.4), 4-merous flowers 2.6–3.8 mm in diameter (mean 3.2). **Petals** 0.8–2. mm long (mean 1.2), 0.7–1.4 mm wide (mean 1), apex acute, same color as plants. **Anther** diameter 0.4–0.7 mm (mean 0.5). **Fruits** 3.1–5.0 mm long (mean 4.2) and 2.2–3.5 mm wide (mean 3), light green and lightly glaucous. **Seeds** 1.9–2.9 mm long (mean 2.4) and 0.9–1.5 mm wide (mean 1.1). **Anthesis** from early July through late August with the peaks in late July to early August. **Seed dispersal** occurs from early September to mid October with peaks in late September to early October. See Mathiasen and Daugherty (2009a) for another description of this species.

4. *Arceuthobium americanum* Engelmann

Lodgepole pine dwarf mistletoe

Arceuthobium americanum can easily be identified by its nearly exclusive parasitism of *Pinus contorta*, verticillate branching and attachment of fruits, slender plants, and spring flowering period (early April to early June).

Hosts: *Pinus contorta* subsp. *murryana* (Grev. & Balf.) Critchf. is the principal host in California. This dwarf mistletoe occasionally parasitizes *P. ponderosa* and *P. jeffreyi* when these pines are growing near infected *P. contorta* in California.

Distribution: This common dwarf mistletoe occurs from the San Bernardino Mountains north through the Sierra Nevada and Cascade Ranges to north-central and northeastern California. It is common throughout much of the geographic distribution of *P. contorta*.

Diagnostic Characters: **Plants** 5–9 cm tall (maximum 30), yellow or olive-green with verticillate branching. **Basal diameter** of dominant plants 1–3 mm (mean 1.5). **Staminate flowers** produced on pedicel-like segments, mostly 3-merous, but occasionally 4-merous, 3-merous flowers 2 mm in diameter. **Petals** approximately 1.1 mm long and 1 mm wide, same color as plants. Mean **anther** diameter 0.6 mm. **Fruits** verticillate, 3.5–4.5 mm long (mean 4) and 1.5–2.5 mm wide (mean 2). **Seeds** 2.4 × 1.1 mm. **Anthesis** is from late March to late June with peak flowering from early April to early June. **Seeds** are dispersed from late August to late September. See Hawksworth and Wiens (1996, p. 184) for a more detailed description of this species.

5. *Arceuthobium californicum* Hawksworth & Wiens

Sugar pine dwarf mistletoe

This dwarf mistletoe is only found in California and can be easily identified by its slender, green to yellowish-green plants, late spring to summer flowering period (mid June to late July), and by its exclusive parasitism of *Pinus lambertiana*. The only other dwarf mistletoe occasionally found on *P. lambertiana* in California, which could be confused with *Arceuthobium californicum*, is *A. abietinum* f. sp. *concoloris* (see number 1 above). Its thicker plants can distinguish the latter dwarf mistletoe and relatively poor shoot production on *P. lambertiana*. In addition, at locations where *A. abietinum* f. sp. *concoloris* occurs on *P. lambertiana*, infection of *Abies concolor* will be common and severe, while infection of the *P. lambertiana* in the stand will be obviously uncommon. In rare situations, both dwarf mistletoes may be present in an area, and in those cases, the two dwarf mistletoes maintain their preference for their principal hosts. Although both *A. cyanocarpum* and *A. campylopodum* have been reported infecting *P. lambertiana*, these crossover infections are extremely rare.

Hosts: The only confirmed host of this dwarf mistletoe is *P. lambertiana*. The report of *Arceuthobium californicum* on *Pinus monticola* is based on infection by *A. cyanocarpum* on this tree near Castle Lake southwest of Mount Shasta (Siskiyou County).

Distribution: *Arceuthobium californicum* occurs from the Klamath Ranges (near Dillon Moun-

tain, northwest of Orleans, Siskiyou County) south through the North Coast Ranges to near Clear Lake (Lake County). It is also occurs in the southern Cascade Ranges from near Mount Lassen and then along the west side of the Sierra Nevada to as far south as the Kern River Drainage. It is also found in the San Bernardino, San Jacinto, and Cuyamaca Mountains of southern California.

Diagnostic Characters: **Plants** 6–15 cm tall (mean 10), greenish to bright yellow, turning brown at base of older shoots, flabellately branched. **Basal diameter** of dominant shoots 1.5–4.0 mm (mean 2.8). Flowers axillary. **Staminate spike** length 4.1–14.8 mm (mean 8.7), 1.1–2.1 mm wide (mean 1.8). **Staminate flowers** 3 or 4-merous, 3-merous flowers 1.9–3.4 mm in diameter (mean 2.6), 4-merous flowers 2.5–4.2 mm in diameter (mean 3.6). **Petals** 0.8–1.9 mm long (mean 1.2), 0.7–1.5 mm wide (mean 1.1), apex acute, same color as plants. **Anther** diameter 0.3–0.7 mm (mean 0.5). **Fruits** 4.3–6.0 mm long (mean 5.1) and 2.5–3.8 mm wide (mean 3.1), light green and lightly glaucous. **Seeds** 2.0–4.3 mm long (mean 2.7) and 0.8–1.6 mm wide (mean 1.2). **Anthesis** starts in mid June and ends in late August with peak flowering from late June to mid July. **Seed dispersal** occurs from mid September to mid October. See Hawksworth and Wiens (1996, p. 197) for another description of this species.

6. *Arceuthobium campylopodum* Engelmann

Western dwarf mistletoe

Its relatively thick, yellow, yellow-brown, or green shoots and parasitism of *Pinus ponderosa* and *P. jeffreyi* most easily identify *Arceuthobium campylopodum*. It typically induces the formation of large witches' brooms on infected trees, which often have swollen and resinous branches. It can be confused with *A. siskiyouense* in the Klamath Ranges where these mistletoes may co-occur and both infect *P. jeffreyi* and *P. attenuata*. However, *A. siskiyouense* is more slender and typically has reddish brown shoots (see number 13 below). *Arceuthobium campylopodum* is also common on *P. coulteri* and *P. attenuata*.

Arceuthobium campylopodum can also be confused with *A. occidentale* (see number 12 below). The primary distinction between *A. occidentale* and *A. campylopodum* is that the former species primarily parasitizes *Pinus sabiniana* in the foothills around the Great Central Valley and in the Coast Ranges. Female plants of *A. occidentale* also tend to be more tightly clumped together and the fruits are often very glaucous (bluish), so female plants are most useful for identifying these dwarf mistletoes from each other. Furthermore, *A. occidentale* consistently flowers later in the year (October to November) than *A. campylopodum* (August to September).

Hosts: *Pinus ponderosa* and *P. jeffreyi* are the principal hosts in California. *Arceuthobium campylopodum* also infects *P. attenuata*, *P. coulteri*, and *P. contorta* subsp. *murrayana*, but usually when these trees are associated with severely-infected *P. ponderosa* or *P. jeffreyi*. Throughout most of California the dwarf mistletoe likely found on *P. ponderosa*, *P. jeffreyi*, *P. coulteri*, or *P. attenuata* will be *A. campylopodum*. Only in the Klamath Ranges, where *A. siskiyouense* also occurs, will there be populations of two different dwarf mistletoes on *P. jeffreyi* and *P. attenuata*. These dwarf mistletoes can co-occur so they must be identified using the differences in their morphological characteristics in those situations. *Arceuthobium campylopodum* occasionally infects *P. sabiniana* on the western slopes of the Sierra Nevada, but again this usually occurs in locations where there is also severe infection on *P. ponderosa* or *P. jeffreyi*.

Distribution: *Arceuthobium campylopodum* is the most widely distributed dwarf mistletoe in California. It is common on *P. ponderosa* and *P. jeffreyi* from the Laguna Mountains (San Diego County) north through the Transverse Ranges, then through the Sierra Nevada and Cascade Ranges into the Modoc Plateau and Klamath Ranges. It is also common in the northern part—but not the southern part—of the Coast Ranges.

Diagnostic Characters: **Plants** 4–25 cm tall (mean 10), yellow, yellow-brown or olive-green. **Basal diameter** of dominant plants 1.7–6.9 mm (mean 3.3). **Staminate spike** length 3.7–41 mm (mean 12.7), 2.3–4.2 mm wide (mean 3). **Staminate flowers** 3 or 4-merous, 3-merous flowers 2–4.5 mm in diameter (mean 3.1), 4-merous flowers 3–5.6 mm in diameter (mean 4.2). **Petals** 0.7–2.4 mm long (mean 1.6), 0.7–2.4 mm wide (mean 1.4), same color as plants. **Anther** diameter 0.4–1.2 mm (mean 0.6). **Fruits** 4–7.2 mm long (mean 5.4) and 2.6–5.6 mm wide (mean 3.7), light green and lightly glaucous. **Seeds** 2.3–4.7 mm long (mean 3.5) and 1–2 mm wide (mean 1.5). **Anthesis** occurs from early August to late September (early October in some years) with peak flowering from mid August to mid September. **Seed dispersal** primarily occurs between early September and early October. See Hawksworth and Wiens (1996, p. 199) and Mathiasen and Kenaley (2015a) for additional descriptions of this species.

7. *Arceuthobium cyanocarpum* (A. Nelson ex Rydberg) Coulter & Nelson
Limber pine dwarf mistletoe

This dwarf mistletoe is identified by its parasitism of *Pinus flexilis* and *P. albicaulis*, small yellow-green plants that are densely clus-

tered around infected branches, and fruits that are usually highly glaucous (bluish).

Hosts: *Pinus flexilis* is the only host of this dwarf mistletoe on the east side of the Sierra Nevada and in southern California. On Mount Shasta, Black Butte, and near Mount Eddy it is found on *P. albicaulis*, but there it also commonly infects *Pinus monticola* and occasionally *P. balfouriana* Grev. & Balf. subsp. *balfouriana*. It has not been reported to infect the *P. balfouriana* subsp. *austrina* Mastrogiuseppe & Mastrogiuseppe populations in the southern Sierra Nevada. In Nevada and Utah, *P. longaeva* D. K. Bailey is also a common host, so this dwarf mistletoe may infect *P. longaeva* in California, but it has not yet been reported on this host.

Distribution: In California, *Arceuthobium cyanocarpum* only occurs on Mount Shasta, south and west of Mount Eddy, in a few scattered, isolated populations on the east side of the southern Sierra Nevada, and in a few locations in the San Bernardino and San Jacinto Mountains. However, it is widely distributed through the Rocky Mountains as far north as central Oregon and western Montana and east through southern Idaho, Nevada, Utah, and Colorado.

Diagnostic Characters: **Plants** 1–5 cm tall (mean 3), yellow, yellow-green, to rarely reddish. **Basal diameter** of dominant plants 1–3.5 mm (mean 1.9). **Staminate flowers** 3 or 4-merous, 3-merous flowers 1.9–3.5 mm in diameter (mean 2.6), 4-merous flowers 1.8–3.8 mm in diameter (mean 2.8). **Petals** 0.8–2 mm long (mean 1.3), 0.7–1.7 mm wide (mean 1.1), same color as plants. **Anther** diameter 0.2–0.7 mm (mean 0.5). **Fruits** 2.5–4.5 mm long (mean 3.5) and 1.7–3.2 mm wide (mean 2.4), light green and lightly to highly glaucous. **Seeds** 1.3–2.5 mm long (mean 1.9) and 0.8–1.5 mm wide (mean 1.1). **Anthesis** starts in early July and ends in mid September, but peak anthesis is between mid July and late August. **Seed dispersal** occurs from mid August to late September. See Hawksworth and Wiens (1996, p. 201) for another description of this species.

8. *Arceuthobium divaricatum* Engelmann

Pinyon dwarf mistletoe

Arceuthobium divaricatum is easily identified because it is the only dwarf mistletoe found on pinyon pines in California and elsewhere in the United States.

Hosts: The most commonly infected pinyon pine in California is *Pinus monophylla*. *Arceuthobium divaricatum* has been reported to infect *P. quadrifolia* Parl. in the Laguna Mountains, California. It also infects *P. edulis* Engelm. in the New York and Clark Mountains, San Bernardino County. All other conifers are considered to be immune to infection by this dwarf mistletoe. If the classification of several pinyon pine populations in southern California as *Pinus californiarum* D. K. Bailey subsp. *californiarum* and *P. californiarum* subsp. *fallax* (Little) D. K. Bailey is recognized, then note that these pinyon pines have also been reported as hosts of this dwarf mistletoe.

Distribution: *Arceuthobium divaricatum* occurs exclusively on pinyon pines and is locally abundant in scattered populations in the Transverse Ranges and several of the Desert Mountains of the Mojave Desert in San Bernardino and Inyo Counties. It also occurs in the eastern and southern Sierra Nevada, White Mountains, and Inyo Mountains.

Diagnostic Characters: **Plants** 5–30 cm tall (mean 11), green, brown-green, or brown. **Basal diameter** of dominant plants 1.3–5 mm (mean 2.5). **Staminate spike** length 3.2–31 mm (mean 9.1), 1.1–2.3 mm wide (mean 1.7). **Staminate flowers** 3-merous, occasionally 4-merous, 3-merous flowers 1.4–3.1 mm in diameter (mean 2.2). **Petals** 0.7–1.6 mm long (mean 1.1), 0.6–1.3 mm wide (mean 1.0), same color as plants. **Anther** diameter 0.3–0.6 (mean 0.4). **Fruits** green, lightly glaucous, 3.2–5.1 long (mean 4.3), 1.9–3.5 mm wide (mean 2.6). **Seeds** 1.6–3.1 mm long (mean 2.1), 0.8–1.3 mm wide (mean 1.1). **Anthesis** is from early August to early October, with peak flowering from late August to mid September. **Seed dispersal** is from early September to early November with a peak from mid September to mid October. See Hawksworth and Wiens (1996, p. 204) for another description of this species. This reference also discusses infection of *Pinus californiarum* by *Arceuthobium divaricatum* (pp. 204−205).

9. *Arceuthobium douglasii* Engelmann

Douglas-fir dwarf mistletoe

Arceuthobium douglasii can easily be identified by its nearly exclusive parasitism of *Pseudotsuga menziesii*, small plants that often occur along infected branches after the second or third internode, its reddish to purple flowers, and its spring flowering period (April to early June). *Arceuthobium douglasii* induces the formation of large, round witches' brooms on infected trees. It is often difficult to find shoots on infected branches, particularly in dense forests where little light reaches the lower canopy.

Hosts: *Pseudotsuga menziesii* is the principal host throughout this mistletoe's geographic range.

Distribution: *Arceuthobium douglasii* has the greatest latitudinal range of any dwarf mistletoe, but in California it has only been found in the southern Cascade Ranges near Mount Lassen

and Mount Shasta, in the North Coast Ranges, and in the Klamath Ranges.

Diagnostic Characters: **Plants** 0.5–3 cm tall, mostly less than 2 cm, olive-green, secondary branches rare. **Basal diameter** of dominant plants 1–1.5 mm (mean 1). **Staminate flowers** usually axillary in pairs, occasionally borne on pedicel-like segments, mostly 3-merous, but rarely 2- or 4-merous, 3-merous flowers 2.3 mm in diameter. **Petals** approximately 1 mm long and 1 mm wide, apex rounded, inner surface of petals reddish to purple, lower surface same color as plants. Mean **anther** diameter 0.4 mm. **Fruits** olive green, 3.5–4.5 mm long (mean 4) and 1.5–2 mm wide (mean 1.7). **Seeds** 2.4 × 1.1 mm. **Anthesis** peaks from early April to late May, but can start as early as late March and extend to mid June. **Seed dispersal** occurs from late August to late September. See Hawksworth and Wiens (1996, p. 207) for a more detailed description of this species.

10. *Arceuthobium littorum* Hawksworth, Wiens, & Nickrent

Coastal dwarf mistletoe

Arceuthobium littorum is one of the least common dwarf mistletoes in the United States. It is only known from a few, isolated populations along the Pacific Coast of California from near Fort Bragg south to Cambria. This dwarf mistletoe was previously classified as *A. occidentale* (see number 12 below) and some investigators group this mistletoe under *A. campylopodum*; but, we consider it to be sufficiently differentiated by its plant color, male flower size, and its parasitism of *Pinus muricata* D. Don and *P. radiata* D. Don to be treated as a separate species. This dwarf mistletoe commonly forms male flowers with five petals, and rarely with six petals, which is not a characteristic of other dwarf mistletoes found in California.

Hosts: The principal hosts of this dwarf mistletoe are *Pinus muricata* and *P. radiata*. *Pinus muricata* is the principal host in the North Coast populations (north of San Francisco), while *P. radiata* is the host in the Central Coast populations. The rare *Pinus contorta* subsp. *bolanderi* (Parl.) Critchf. is also infected in areas where it is associated with severe infection on *P. muricata*.

Distribution: This dwarf mistletoe occurs in widely scattered populations along the North and Central Coasts from east of Fort Bragg (Mendocino County) to Cambria (San Luis Obispo County). Although only a few populations are known, it probably occurs in many additional areas, which have not been discovered yet; many of these areas are on private property near the coast. This is the dwarf mistletoe found on *Pinus radiata* in Carmel and Monterrey.

Diagnostic Characters: **Plants** 5–19 cm tall (mean 10), dark green to green-brown. **Basal diameter** of dominant plants 2.6–7 mm (mean 3.7). **Staminate spike** length 6.1–55.9 mm (mean 20.6), 2.1–4.2 mm wide (mean 3.4). **Staminate flowers** 3-, 4-, or 5-merous, rarely 6-merous, 3-merous flowers 2.4–4.8 mm in diameter (mean 3.5), 4-merous flowers 3.4–6.9 mm in diameter (mean 5.2), 5-merous flowers 4.4−6.9 mm in diameter (mean 5.7). **Petals** 1.0–2.8 mm long (mean 1.9), 0.8–2.5 mm wide (mean 1.6), same color as plants. **Anther** diameter 0.4–1.5 mm (mean 0.9). **Fruits** 4–6.4 mm long (mean 5.4) and 2.9–4.4 mm wide (mean 3.6), dark green to reddish, not glaucous. **Seeds** 2.5–4.2 mm long (mean 3.4) and 1–1.6 mm wide (mean 1.3). **Anthesis** starts in late August, peaks in mid to late September, and ends by mid October. **Seed dispersal** starts in early September, peaks in late September and early October, and is completed by early November. However, there are reports of seed dispersal lasting into December. See Hawksworth et al. (1992), Hawksworth and Wiens (1996, p. 224), Mathiasen and Daugherty (2013), and Mathiasen and Kenaley (2015a) for additional descriptions of this species.

11. *Arceuthobium monticola* Hawksworth, Wiens, & Nickrent

Western white pine dwarf mistletoe

Arceuthobium monticola can be distinguished from *A. cyanocarpum* and *A. californicum* by it brown shoots and nearly exclusive parasitism of *Pinus monticola* in the Klamath Ranges.

Hosts: *Pinus monticola* is the principal host in California and *P. lambertiana* is rarely infected. However, in northern California this dwarf mistletoe severely parasitizes *Picea breweriana* as well, but only in a few locations (e.g., near Black Butte in western Siskiyou County).

Distribution: This dwarf mistletoe is rare in the Klamath Ranges of Del Norte and Siskiyou Counties. Although it also occurs in southern Oregon, the 2002 Biscuit Fire that burned approximately 500,000 acres on the Siskiyou National Forest destroyed several populations. Because of its rarity in northern California and southern Oregon, *A. monticola* should be considered for conservation status.

Diagnostic Characters: **Plants** 4–13 cm tall (mean 8), usually dark brown, but some staminate plants may be yellow. **Basal diameter** of dominant plants 2–3.8 mm (mean 2.9). **Staminate spike** length 5–14.2 mm (mean 8.6), 1.1–1.8 mm wide (mean 1.4). **Staminate flowers** 3 or 4-merous, 3-merous flowers 2–3.1 mm in diameter (mean 2.5), 4-merous flowers 3–4.6 mm in diameter (mean 3.6). **Petals** 0.8–1.7 mm long (mean 1.3), 0.7–1.3 mm wide (mean 1.1), same color as plants. **Anther** diameter 0.4–0.8 mm (mean 0.5).

Fruits 4–5.6 mm long (mean 4.7) and 2.4–3.5 mm wide (mean 3), light green and lightly glaucous. **Seeds** 1.8–3.2 mm long (mean 2.5) and 0.9–1.4 mm wide (mean 1.2). **Anthesis** begins in mid-July, peaks in early- to mid-August, and continues into early-September. **Seed dispersal** starts in early September, peaks in late September, and is finished by late October. See Hawksworth et al. (1992), Hawksworth and Wiens (1996, p. 228), and Mathiasen and Daugherty (2009b) for additional descriptions of this species.

12. *Arceuthobium occidentale* Engelmann

Gray pine dwarf mistletoe

Arceuthobium occidentale is similar in appearance to *A. campylopodum*. The primary distinction between *A. occidentale* and *A. campylopodum* is that the former species primarily parasitizes *Pinus sabiniana* in the foothills of the Sierra Nevada around the Great Central Valley and in the Coast Ranges of California. Female plants of *A. occidentale* also tend to be more tightly clumped together and the fruits are often very glaucous (bluish), so female plants are most useful for identifying these dwarf mistletoes from each other. Furthermore, *A. occidentale* consistently flowers in the fall (October to November) and *A. campylopodum* flowers in the late summer (August to September).

Hosts: *Pinus sabiniana* is the most commonly infected host, but both *P. coulteri* and *P. attenuata* are infected when growing near severely infected *P. sabiniana*. In addition, both *P. ponderosa* and *P. jeffreyi* are infected by *A. occidentale* in areas where these hosts are outside the range of their principal parasite, *A. campylopodum*, and they are growing among severely infected *P. sabiniana*. Furthermore, in some areas along the west side of the Sierra Nevada at the lower elevational range of *P. ponderosa*, *A. occidentale* will cause severe infection on *P. ponderosa* in the absence of *P. sabiniana*. This is one of the reasons some classifications group *A. occidentale* and *A. campylopodum* as the same species; their similar morphological characteristics are another reason. *Arceuthobium occidentale* has also been found infecting planted *P. radiata* growing near infected *P. sabiniana* on Mount Hamilton, California. But as far as is known, *A. occidentale* does not occur within the natural range of *P. radiata*. If dwarf mistletoe is observed on *P. radiata* it is most likely *A. littorum* (see number 10 above).

Distribution: This dwarf mistletoe is relatively common on *P. sabiniana* throughout the foothills surrounding the Great Central Valley and near the Kern River in the southern Sierra Nevada. It also is common in the Coast Ranges from near Mount Pinos in Ventura County to as far north as eastern Mendocino County. Although it occurs near the Central Coast in Monterrey and San Luis Obispo Counties, its range does not overlap with the *Pinus muricata* and *P. radiata* populations found there.

Diagnostic Characters: **Plants** 5–23 cm tall (mean 11), yellow, yellow-brown or dark brown, highly glaucous. **Basal diameter** of dominant plants 1.7–6.4 mm (mean 3.1). **Staminate spike** length 6.2–34 mm (mean 13.9), 2.2–3.9 mm wide (mean 2.9). **Staminate flowers** 3 or 4-merous, 3-merous flowers 2.2–4.1 mm in diameter (mean 3), 4-merous flowers 3–6.2 mm in diameter (mean 4.1). **Petals** 1.1–2.5 mm long (mean 1.5), 0.7–2.2 mm wide (mean 1.3), same color as plants. **Anther** diameter 0.4–1 mm (mean 0.6). **Fruits** 4–6.8 mm long (mean 5.2) and 2.4–4.7 mm wide (mean 3.3), light green and highly glaucous. **Seeds** 2.5–4.3 mm long (mean 3.5) and 1–1.7 mm wide (mean 1.3). **Anthesis** starts in early October, peaks in late October or early November, and finishes in mid December. **Seed dispersal** starts in early October, peaks in late October to early November, and ends in late December. See Hawksworth and Wiens (1996, p. 231), Mathiasen and Daugherty (2013), and Mathiasen and Kenaley (2015a) for additional descriptions of this species.

13. *Arceuthobium siskiyouense* Hawksworth, Wiens, & Nickrent

Knobcone pine dwarf mistletoe

Arceuthobium siskiyouense is most likely to be confused with *A. campylopodum*. However, *Arceuthobium siskiyouense* has more slender, reddish-brown plants than the thicker, yellow, yellow-brown or green plants of *A. campylopodum*. While this character is more difficult to observe, the width of the mature staminate spikes of *A. siskiyouense* are much more slender (mean 2 mm) than those of *A. campylopodum* (mean 3 mm).

Hosts: *Pinus attenuata* and *P. jeffreyi* are the principal hosts of *A. siskiyouense* in far northern California and *P. contorta* subsp. *contorta* is an occasional host.

Distribution: *Arceuthobium siskiyouense* is common in the Klamath Ranges in Del Norte County and western Siskiyou County.

Diagnostic Characters: **Plants** 5–17 cm tall (mean 9), usually reddish-brown, but some staminate plants may be yellow-brown to green-brown. **Basal diameter** of dominant plants 1.8–6.1 mm (mean 3.1). **Staminate spike** length 5.2–19.1 mm (mean 11.8), 1.5–2.6 mm wide (mean 2). **Staminate flowers** 3 or 4-merous, 3-merous flowers 2.5–3.9 mm in diameter (mean 3.2), 4-merous flowers 3.6–5.9 mm in diameter (mean 4.5). **Petals** 1.1–2.0 mm long (mean 1.5), 1–2.1

mm wide (mean 1.5), same color as plants. **Anther** diameter 0.4–1.2 mm (mean 0.8). **Fruits** 3.8–6.1 mm long (mean 5.2) and 2.5–4.3 mm wide (mean 3.4), light green and lightly glaucous. **Seeds** 2–4 mm long (mean 3.1) and 0.8–1.9 mm wide (mean 1.3). **Anthesis** begins in late July, peaks in mid August, and continues into early September. **Seed dispersal** starts in late September, peaks in mid to late October, and is completed by late November. See Hawksworth et al. (1992), Hawksworth and Wiens (1996, p. 241), Mathiasen and Daugherty (2013), and Mathiasen and Kenaley (2015a) for additional descriptions of this species.

14. *Arceuthobium tsugense* (Rosendahl) G. N. Jones subsp. *tsugense*

Western hemlock dwarf mistletoe

This dwarf mistletoe is rarely found in northern California near the Pacific Coast.

Hosts: *Tsuga heterophylla* (Raf.) Sarg. is the only host in California.

Distribution: This dwarf mistletoe is only known from two confirmed locations in California at present; east of Blue Lake on Route 299 (Humboldt County) and east of Mendocino (Mendocino County). However, this mistletoe is a common and damaging parasite of *T. heterophylla* in Oregon, Washington, Alaska, and British Columbia.

Diagnostic Characters: **Plants** 3–16 cm tall (mean 8), green, green-yellow, green-brown, purple. **Basal diameter** of dominant plants 1.3–5.5 mm (mean 2.7). **Staminate flowers** 3 or 4-merous, 3-merous flowers 1.8–4.7 mm in diameter (mean 3.2), 4-merous flowers 2.8–5.9 mm in diameter (mean 3.8). **Petals** 1–2.2 mm long (mean 1.5), 0.8–2.2 mm wide (mean 1.2), same color as plants. **Anther** diameter 0.3–1.3 mm (mean 0.7). **Fruits** 3.3–5.5 mm long (mean 4.4) and 2.2–3.5 mm wide (mean 2.9), light green. **Seeds** 1.8–3.5 mm long (mean 2.6) and 0.8–1.4 mm wide (mean 1.1). **Anthesis** begins in late July, peaks in August, and ends by late September. **Seed dispersal** is from late September to early November. See Hawksworth and Wiens (1996, pp. 243–244) for another description of this species.

15. *Arceuthobium tsugense* (Rosendahl) G. N. Jones subsp. *mertensianae* Hawksworth & Nickrent

Mountain hemlock dwarf mistletoe

This dwarf mistletoe can be identified by its green-brown shoots, which range in size from 2−5 cm and its parasitism of *Tsuga mertensiana* (Bong.) Carrière.

Hosts: *Tsuga mertensiana* is the principal host in California. This mistletoe also occurs on *Pinus monticola*, but usually just when this tree is growing near severely infected *T. mertensiana*. It has also been reported infecting *Picea breweriana* in the Klamath Ranges.

Distribution: This dwarf mistletoe is scattered in locally abundant populations from around Mosquito Lakes (Alpine County), west of Lake Tahoe (Alpine Meadows Ski Area, Placer County), in the vicinity of Gold Lake (Plumas County), in Mount Lassen National Park (Tehama County), and in a few widely scattered locations in the Klamath Ranges (Shasta and Siskiyou counties). It is also found in southern Oregon.

Diagnostic Characters: **Plants** 2–11 cm tall (mean 6), yellow-green, green-brown. **Basal diameter** of dominant plants 1–3.7 mm (mean 2). **Staminate flowers** 3 or 4-merous, 3-merous flowers 1.9−2.9 mm in diameter (mean 2.4), 4-merous flowers 2.4–3.8 mm in diameter (mean 3.1). **Petals** 0.8–1.5 mm long (mean 1.1), 0.7–1.3 mm wide (mean 1), same color as plants. **Anther** diameter 0.3–0.7 mm (mean 0.5). **Fruits** 3.8–4.8 mm long (mean 3.8) and 1.8–3.5 mm wide (mean 2.6), light green and slightly glaucous, often with purplish to reddish tip. **Seeds** 2.2–3.4 mm long (mean 2.8) and 0.8–1.4 mm wide (mean 1.1). **Anthesis** starts in early August, peaks in mid August to mid September, and is completed by early October. **Seed dispersal** occurs from mid August to mid September. See Hawksworth et al. (1992) and Hawksworth and Wiens (1996, pages 243–244 and 249) for additional descriptions of this species.

Phoradendron Nuttall

Mistletoe

These mistletoes are obligate parasites of many woody trees in North America, but in California only three species are not host specific and instead parasitize several woody angiosperms. Four of the seven species of *Phoradendron* in California parasitize conifers in the Pinaceae or Cupressaceae. Although they are parasites, species of *Phoradendron* are not considered to be serious forest pathogens because they primarily absorb water and minerals from their hosts. However, severe infection can stress the host tree, particularly under drought conditions, and in some cases contribute to their premature death. These mistletoes can also reduce fruit production of severely infected trees.

Mistletoes in this genus are evergreen shrubs with stems usually larger than 25 cm. Leaves are opposite and either foliaceous or reduced to connate, deltoid scales. Plants are either glabrous or pubescent. Inflorescences are jointed, axillary,

or rarely terminal spikes. All of the species of *Phoradendron* in California are dioecious. Flowers have a 3-merous (2–4) calyx. Pistillate flowers are epigynous, with 1 style, a capitate stigma, an ovary with one chamber, and a calyx that is adnate to the ovary. *Phoradendron* fruits are a white, pink, or sometimes reddish drupe with one seed and a mucilaginous coating (viscin). The seeds are primarily dispersed by numerous species of birds.

Field Key to *Phoradendron* Species in California

1. Leaves reduced to connate scales
   2. Stems canescent, especially at distal tip, reddish to green; pistillate inflorescence with 2−7 segments; primarily parasitic on leguminous shrubs and trees in desert regions . . 1. *P. californicum*
   2′. Stems glabrous throughout, green to yellow green; pistillate inflorescence with 1−2 segments; parasitic on *Juniperus* or *Calocedrus decurrens* in mountain regions
      3. Parasite of *Juniperus*; internodes usually less than 1 cm long; plants usually remaining erect . . . . . 3. *P. juniperinum*
      3′. Parasite of *Calocedrus decurrens*; internodes usually over 1 cm long; plants often becoming pendulous . . . . . 4. *P. libocedri*
1′. Leaves not reduced to connate scales
   4. Leaf length usually >20 mm; stems usually with hairs; staminate inflorescence with 2−7 segments; pistillate inflorescence with 6–24 flowers; parasites of woody dicots
      5. Primarily a parasite of *Quercus*, but also on other hardwoods; leaves obovate-elliptic, 15−45 mm long, 10−22 mm wide; inflorescences densely stellate; staminate inflorescence with 2−4 segments, usually with 15–45 flowers; pistillate inflorescence usually with 2−3 segments and usually with 7−24 flowers; flowering July-September . . . . . 7. *P. villosum*
      5′. Parasite of woody dicots other than *Quercus*; leaves obovate to elliptic-orbicular, 23−42 mm long, 15−29 mm wide; inflorescences usually glabrous; staminate inflorescence with 2–7 segments, usually with 15–60 flowers; pistillate inflorescence with 2−5 segments and usually with 6–20 flowers; flowering December–March . . . . . 5. *P. macrophyllum*
   4′. Leaf length usually <20 mm; stems glabrous; staminate inflorescence usually with one segment; pistillate inflorescence with 2 flowers; parasites of *Juniperus*, *Cupressus*, or *Abies concolor*
      6. Parasite of *Juniperus* or *Cupressus*; leaves 10−20 mm long and 2−5 mm wide; staminate inflorescence usually with less than 10 flowers . . . . . 2. *P. densum*
      6′. Parasite of *Abies concolor*; leaves usually 5−25 mm long, 5−8 mm wide; staminate inflorescence usually with more than 10 flowers . . . . . 6. *P. pauciflorum*

Identification of *Phoradendron* in California

1. *Phoradendron californicum* Nuttall

Desert mistletoe

Phoradendron californicum is the common mistletoe found on *Prosopis* L. and *Parkinsonia* L. (and other trees and shrubs in the Fabaceae) in the Mojave and Sonora Deserts of the Southwest and northwestern Mexico. Because of its relative host specificity, scale-like leaves, and geographic distribution in desert ecosystems this mistletoe is easily identified.

Hosts: Common on leguminous trees and shrubs, particularly *Prosopis*, *Parkinsonia*, *Acacia*, and *Olneya*.

Distribution: This mistletoe is common in the Mojave Desert of southeastern California; it is found from Inyo County south into Baja California, Mexico. It is also common in the Sonora Desert of Arizona and northern Mexico.

Diagnostic Characters: **Plants** forming large, pendulous clumps, often over a meter in diameter, internodes 13–28 mm long (mean 20), 1–2.5 mm wide (mean 1.7), red to green, whitish canescent to subglabrous. **Leaves** ca. 1 mm long; inflorescence moderately whitish canescent. **Staminate inflorescence** with 1–6 segments (mean 3), individual segments with 4–10 flowers (mean 6). **Anthesis** occurs from December to March. **Pistillate inflorescence** with 1–7 segments (mean 3), individual segments with 2–6 flowers (mean 3). **Fruits** white to red, 3 mm in diameter, essentially glabrous, mature during the winter. See Wiens (1964, p. 31) for another description of this species.

2. *Phoradendron densum* Trelease

Dense mistletoe

Hosts: This mistletoe parasitizes several species of *Juniperus* and *Cupressus*. Known hosts include *Juniperus californica* Carrière, *J. occidentalis* Hooker, *J. osteosperma* (Torrey) Little, *Cupressus arizonica* E. Greene, *C. bakeri* Jepson, *C. forbesii* Jepson, *C. goveniana* Gordon, *C. macnabiana* A. Murray, *C. macrocarpa* Gordon, and *C. sargentii* Jepson.

Distribution: *Phoradendron densum* occurs throughout California on *Juniperus* and *Cupressus*. It displays a very dense habit, hence the common name. It has small (about 14 × 4 mm), oblong, sessile leaves with rounded tips. *Phoradendron densum* should not be confused with the other

common mistletoe on *Juniperus* in California, *P. juniperinum*, because the latter mistletoe has leaves that are reduced to connate scales and appears to be "leafless."

Diagnostic Characters: **Plants** forming dense clumps of branches up to a meter in diameter, but usually about 30–50 cm in height, internodes 6–17 mm long (mean 11), 1.5–2 mm wide (mean 1.7), typically green, glabrous. **Leaves** typically oblanceolate, sessile, 10–20 mm long (mean 14), 2–5 mm wide (mean 3), apex usually obtuse. **Staminate inflorescence** with 1–2 segments, individual segments with 6–13 flowers (mean 8). **Anthesis** approximately from late May to mid August. **Pistillate inflorescence** with 1–2 segments, individual segments with 2 flowers. **Fruits** white to lightly pink, 4 mm in diameter, mature in the winter. See Wiens (1964, p. 29) and Wiens and Hawksworth (2002) for additional descriptions of this species.

3. *Phoradendron juniperinum* A. Gray

Juniper mistletoe

Hosts: This mistletoe only parasitizes *Juniperus* throughout California.

Distribution: *Phoradendron juniperinum* is common on *Juniperus* in California. Its scale-like leaves and pink to white berries that are mature in winter easily identify this mistletoe. Like other species of *Phoradendron* birds disseminate its seeds.

Diagnostic Characters: **Plants** forming dense clumps of branches up to 60 cm in diameter, stems woody at their base when mature, glabrous, internodes 5–12 mm long (mean 8), 1.5–2.5 mm wide (mean 1.8), typically green, but some plants appearing yellow-green or almost brown. **Leaves** reduced to scales about 1 mm long, often finely ciliate. **Staminate inflorescence** with 1–2 segments, individual segments with 5–9 flowers (mean 7). **Anthesis** is approximately from July through September. **Pistillate inflorescence** with 1 segment with 2 flowers. **Fruits** pinkish white, 4 mm in diameter, glabrous, mature in the winter. See Wiens (1964, p. 22) for another description of this species.

4. *Phoradendron libocedri* (Engelmann) Howell

Incense cedar mistletoe

Hosts: This mistletoe only parasitizes *Calocedrus decurrens* (Cupressaceae) in California and southern Oregon.

Distribution: *Phoradendron libocedri* is common in California wherever *Calocedrus decurrens* grows. Thus far, it has not been reported to parasitize *Juniperus*. However, *P. libocedri* is easily distinguished from *P. juniperinum* by its longer internodes, pendulous habit, and, as noted, exclusive parasitism of *Calocedrus decurrens*.

Diagnostic Characters: **Plants** forming dense clumps of branches up to 80 cm in diameter, stems woody at their base when mature, glabrous, internodes 8–20 mm long (mean 13), 1–2 mm wide (mean 1.5), typically dark green, often pendulous. **Leaves** reduced to scales about 1 mm long, often finely ciliate. **Staminate inflorescence** with 1–2 segments, individual segments with 5–9 flowers (mean 7). **Anthesis** is approximately from July through September. **Pistillate inflorescence** with 1 segment with 2 flowers. **Fruits** pinkish white, 4 mm in diameter, glabrous, mature in the winter. See Wiens (1964, p. 24) for another description of this species.

5. *Phoradendron macrophyllum* (Engelmann) Cockerell

Big leaf mistletoe

Phoradendron macrophyllum is a common parasite of a wide variety of hardwood trees from central California south to northern Mexico and east across southern Arizona and New Mexico into western Texas. It has large, smooth leaves that may be as long and wide as 50 × 30 mm. This is the common mistletoe on willows and cottonwoods along drainages throughout its wide geographic range. This is the mistletoe on *Juglans* and other hardwoods in the orchards and cities of the Great Central Valley. *Phoradendron macrophyllum* has nearly smooth stems (few, if any hairs) while those of *P. villosum* (number 7 below) —a principal parasite of *Quercus*—have obviously hairy stems.

Hosts: *Phoradendron macrophyllum* is reported to parasitize over 70 species of hardwood trees in over 30 genera. It has one of the largest host ranges of any *Phoradendron* in the United States. Therefore, a large, leafy mistletoe observed on a hardwood in California will most often be *P. macrophyllum*. It is rare on *Quercus* in California; the mistletoe common on *Quercus* throughout California is *P. villosum* (see number 7 below).

Distribution: *Phoradendron macrophyllum* is found from the Great Central Valley of California (Butte County) south in the Coast Ranges and foothills of the Sierra Nevada to southern California and northern Mexico. It then ranges east across the Mojave Desert into central Arizona south of the Mogollon Rim and then across the Sonora Desert into southern New Mexico. It is common along the Rio Grande River in southern New Mexico south into west Texas.

Diagnostic Characters: **Plants** forming dense clumps of branches up to a meter in diameter, stems woody at their base when mature, green, usually glabrous, internodes 22–59 mm long

(mean 36), 1.5–3 mm wide (mean 2.1), typically dark green or yellow-green. **Leaves** obovate, elliptic-orbicular, 23–42 mm long (mean 31), 15–30 mm wide (mean 20). **Staminate inflorescence** with 2–7 segments (mean 4), individual segments with 15–60 flowers (mean 34). **Anthesis** is approximately from December through March. **Pistillate inflorescence** with 2–5 segments (mean 3), each segment with 6–20 flowers (mean 11). **Fruits** distinctly white, 4–5 mm in diameter, glabrous, mature in the winter. See Wiens (1964, p. 41) under *P. tomentosum* subsp. *macrophyllum* for another description of this species.

6. *Phoradendron pauciflorum* Torrey

Fir mistletoe

Phoradendron pauciflorum is a common parasite of *Abies concolor* especially in the Sierra Nevada. It has long, spatula-shaped leaves and is the only *Phoradendron* that occurs on *A. concolor*, so it is easily identified.

Hosts: This mistletoe is only known to parasitize *Abies concolor*.

Distribution: *Phoradendron pauciflorum* occurs from the central Sierra Nevada (Calaveras County) to southern California in the San Bernardino, San Gabriel, San Jacinto, and Laguna Mountains. It also occurs in the Santa Catalina and Rincon Mountains of southern Arizona and the Sierra San Pedro Mártir of Baja California, Mexico.

Diagnostic Characters: **Plants** forming dense clumps up to 70 cm in diameter, stems woody at their base when mature, green, glabrous, internodes 10–21 mm long (mean 15), 1.5–2.5 mm wide (mean 2). **Leaves** subpetiolate, usually oblanceolate, 5–25 mm long (mean 20) and 5–8 mm wide (mean 6), apex acute-obtuse. **Staminate inflorescence** with 1–2 segments, individual segments with 6–14 flowers (mean 10). **Anthesis** is approximately from July through September. **Pistillate inflorescence** with 1 segment with 2 flowers. **Fruits** white, glabrous, 4 mm in diameter, mature in the winter. See Wiens (1964, p. 30) and Wiens and Hawksworth (2002) for additional descriptions of this species.

7. *Phoradendron villosum* (Nuttall) Nuttall

Oak mistletoe

This mistletoe is easily identified by its whitish to yellowish pubescence, its large, fleshy to leathery leaves, and common parasitism of *Quercus*. Some trees have many mistletoe plants and these can easily be observed during the winter when leaves are off the host, but remain on the mistletoe plants. Birds disseminate the mistletoe seeds.

Hosts: This mistletoe is primarily a parasite of *Quercus*, but has also been reported on other hardwood hosts in California.

Distribution: *Phoradendron villosum* is common on *Quercus* in and around the Great Central Valley, in the southern Sierra Nevada, and in the South Coast Ranges. It is also common in Oregon.

Diagnostic Characters: **Plants** up to one meter in diameter; most parts covered with whitish or yellowish pubescence; stems woody at maturity, internodes 15–38 mm long (mean 24), 1–3 mm wide (mean 2.1), typically gray-green or yellow-green. **Leaves** very densely pubescent, obovate-elliptic, often thick and leathery, 15–45 mm long (mean 27), 10–22 mm wide (mean 15). **Inflorescences** densely stellate. **Staminate inflorescence** with 2–4 segments, individual segments usually with 15–45 flowers (mean 29). **Anthesis** occurs from July through September. **Pistillate inflorescence** with 2–3 segments, individual segments usually with 7–24 flowers (mean 13). **Fruits** white to pink, about 3−4 mm in diameter, puberulent just below the calyx, mature in the late fall to winter. See Wiens (1964, p. 44) for another description of this species.

Viscum

European Mistletoe

1. *Viscum album* L.

European Mistletoe

Only *Viscum album* occurs in California, and was purposely introduced to Sebastopol by Luther Burbank around 1900.

Hosts and Distribution: Parasitic on several genera of deciduous trees, including fruit trees, in Sonoma County (vicinity of Sebastopol and Santa Rosa).

Diagnostic Characters: *Viscum album* is a dioecious evergreen shrub with stems that are usually >20 cm tall, round, and green or less often reddish. **Branches** are opposite or sometimes whorled. **Leaves** are usually 5–8 cm long and about 1.5 cm wide, narrow obovate, with a short petiole. The **inflorescence** is a cyme, with few flowers formed on short or sessile peduncles that are subtended by a pair of fused bracts. **Flower parts** are in fours and anthers have several chambers. **Pistillate flower** parts are deciduous. **Fruits** are 6–10 mm in diameter, spheric, and on a short pedicel, white and they mature during the winter.

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APPENDIX 1. Identification of mistletoes in California using common hosts and geographic location.[1]

Host	Location	Mistletoe
Haploxylon Pines (soft pines)[2]		*Arceuthobium*
Pinus albicaulis (Whitebark pine)	Mt. Shasta, Mt. Eddy	*A. cyanocarpum*
Pinus balfouriana[3] (Foxtail pine)	Mt. Eddy	*A. cyanocarpum*
Pinus edulis (Colorado pinyon pine)	Clark and New York Mtns.	*A. divaricatum*
Pinus flexilis (Limber pine)	East side of the Sierra Nevada, San Bernardino, and San Jacinto Mtns.	*A. cyanocarpum*
Pinus lambertiana[4] (Sugar pine)	Near Orleans, south to the North Coast Range, Mt. Lassen south on the west side of the Sierra Nevada to the Cuyamaca Mtns. in San Diego County	*A. californicum*
Pinus monophylla (Singleleaf pinyon pine)	East side of the Sierra Nevada, Mojave Desert Mtns., and Transverse Ranges	*A. divaricatum*
Pinus monticola (Western white pine)	Klamath Ranges	*A. monticola*
	Mt. Shasta, Mt. Eddy	*A. cyanocarpum*
Pinus quadrifolia (Parry pinyon pine)	Laguna Mtns.	*A. divaricatum*
Diploxylon Pines (hard pines)[2]		
Pinus attenuata (Knobcone pine)	Klamath Ranges	*A. siskiyouense*
	All other regions	*A. campylopodum*
Pinus contorta subsp. *murrayana* (Lodgepole pine)	Modoc Plateau south through the Cascade Ranges and Sierra Nevada to the San Bernardino Mtns.	*A. americanum*
Pinus coulteri (Coulter pine)	Transverse and Peninsular Ranges	*A. campylopodum*
Pinus jeffreyi[5] (Jeffrey pine)	Klamath Ranges	*A. siskiyouense*
	North Coast Ranges, Klamath Ranges east and south through the Sierra Nevada, Transverse Ranges, and south to the Laguna Mtns.	*A. campylopodum*
Pinus muricata (Bishop pine)	North Coast north of San Francisco to near Fort Bragg	*A. littorum*
Pinus ponderosa[6] (Ponderosa pine)	North Coast Ranges, Klamath Ranges, east and south through the Sierra Nevada to the Transverse Ranges, and Laguna Mtns.	*A. campylopodum*
Pinus radiata (Monterey pine)	Central Coast south of San Francisco to near Cambria	*A. littorum*
Pinus sabiniana[7] (Gray pine)	Foothills of the Coast Ranges and Sierra Nevada, and the Transverse Ranges (north slope)	*A. occidentale*
Other Common Hosts		
Abies concolor[8] (White fir)	Klamath and Cascade Ranges, Sierra Nevada, and the San Bernardino Mtns.	*A. abietinum* f. sp. *concoloris*
Abies grandis (Grand fir)	Klamath Ranges and the North Coast Ranges	*A. abietinum* f. sp. *concoloris*
Abies magnifica (Red fir)	Sierra Nevada	*A. abietinum* f. sp. *magnificae*
	Klamath Ranges and South Fork Mountain	*A. abietinum* subsp. *wiensii*

Appendix 1. Continued

Host	Location	Mistletoe
Picea breweriana (Brewer spruce)	Klamath Ranges	*A. abietinum* subsp. *wiensii* *A. monticola*
Pseudotsuga menziesii (Douglas fir)	Klamath Ranges, North Coast Ranges, Mt. Shasta, and Mt. Lassen	*A. douglasii*
Tsuga heterophylla (Western hemlock)	North Coast Ranges	*A. tsugense* subsp. *tsugense*
Tsuga mertensiana (Mountain hemlock)	Klamath Ranges, Mt. Shasta, Mt. Lassen, and northern High Sierra Nevada	*A. tsugense* subsp. *mertensianae* *Phoradendron*
Juniperus (Junipers)	East side of the Cascade Ranges, along the east side of the Sierra Nevada to the San Bernardino Mtns. and Desert Mtns.	*P. juniperinum*
Juniperus and *Cupressus* (Junipers and cypresses)	Klamath Ranges and Coast Ranges, west side of the Sierra Nevada, Transverse Ranges, and Desert Mtns.	*P. densum*
Libocedrus decurrens (Incense cedar)	Throughout California	*P. libocedri*
Abies concolor[8] (White fir)	From Calaveras County south through the Sierra Nevada and South Coast Ranges to San Diego County	*P. pauciflorum*
Quercus	Throughout California	*P. villosum*
Leguminous Trees/Shrubs	Mojave and Sonora Desert	*P. californicum*
Hardwoods other than *Quercus*	Central to southern California	*P. macrophyllum* *Viscum*
Hardwoods including *Acer, Betula, Malus, Populus, Prunus, Pyrus,* and *Ulmus*	Sonoma County (Santa Rosa-Sebastopol)	*V. album*

[1] Appendix 1 is not designed for the identification of mistletoes in California using herbarium specimens, unless both the host and geographic location are clearly indicated on the herbarium label.
[2] *Pinus* is subdivided into two subgenera: subgenus *Strobus*, which are also known as haploxylon or soft pines, and subgenus *Pinus*, which are also referred to as diploxylon or hard pines. Haploxylon pines have one vascular bundle per needle while diploxylon pines have two vascular bundles per needle.
[3] In the Mount Eddy area (Siskiyou County) *Pinus balfouriana* is only an occasional host of *Arceuthobium cyanocarpum*.
[4] *Pinus lambertiana* is occasionally infected by *Arceuthobium abietinum* f. sp. *concoloris* in forests where there is also severe infection on *Abies concolor* by this dwarf mistletoe.
[5] In the Klamath Ranges *Arceuthobium siskiyouense* and *A. campylopodum* occasionally occur in the same area and both can infect *Pinus jeffreyi*. At these locations, it is necessary to carefully examine the staminate spikes of male plants; the spikes of *A. siskiyouense* are about 2 mm wide and those of *A. campylopodum* are about 3 mm in width. *Pinus jeffreyi* is occasionally infected by *A. americanum*, but only in areas where there is also severe infection on *Pinus contorta* by this dwarf mistletoe.
[6] *Pinus ponderosa* may be occasionally infected by *Arceuthobium americanum* and *A. occidentale* in the Sierra Nevada.
[7] *Pinus sabiniana* is occasionally infected by *Arceuthobium campylopodum* on the west side of the Sierra Nevada.
[8] Here we classify white fir as *Abies concolor,* which includes *Abies concolor* var. *lowiana* (Gordon) Lemmon.