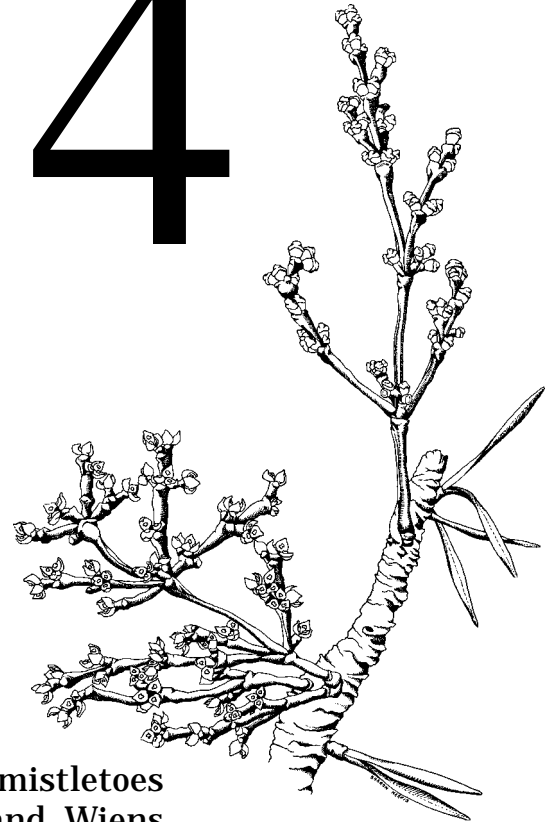


F. G. Hawksworth
D. Wiens
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Chapter

4

Arceuthobium in North America



The biology, pathology, and systematics of dwarf mistletoes are recently and well reviewed in Hawksworth and Wiens (1996). That monograph forms the basis for the text in this and chapter 5 and should be consulted for more information (for example, references, photographs, and distribution maps). In addition to extracting the information that would be most relevant to forest managers and arborists, we here include new references on hosts, distributions, and ecology. The synonymy in this chapter is neither formal nor complete; rather, we provide additional names used in previous, significant literature (such as Gill 1935, Hawksworth and Wiens 1972, Kuijt 1955).

General Life Cycle _____

The life cycle of dwarf mistletoe is distinctive because of two features—obligate parasitism (shared with all mistletoes) and hydrostatically controlled, explosive dispersal (with one exception). The details of cytology, anatomy, embryology, genetics, and evolution that underlie these features are described by Hawksworth and Wiens (1996) and Kuijt (1960a, 1960b, 1969a).

Especially for dwarf mistletoes with their reduced morphologies, differences in reproductive phenology and host specificity are taxonomically decisive (Hawksworth and Wiens 1996). The life histories of several dwarf mistletoes are well studied (Gilbert 1984, 1988, Hawksworth 1961, 1965, Scharpf and Parmeter 1982, Strand and Roth 1976).

Life History

Dwarf mistletoe life history comprises four stages: dispersal, establishment, incubation, and reproduction (fig. 4-1). Dispersal begins when a mature fruit discharges its seed into ballistic flight. Establishment includes the time from the seed lodging at a safe-site until the parasitic relationship is initiated. Several years of incubation pass while an extensive, endophytic system develops under the host's bark. The reproductive stage continues with repeated, intermittent production of aerial shoots and flowers and continued expansion of the endophytic system. Reproduction ends with the death of the mistletoe plant; this usually does not occur until the host itself dies. Various physical and biological factors affect the temporal and spatial unfolding of these processes into population consequences and afford an opportunity for management intervention.

Dispersal—Mistletoe dispersal is effected by the hydrostatic contraction of a mature fruit that propels a single, small seed upon ballistic flight to either a location where a host may be inoculated (safe-site) or

elsewhere. Unlike other mistletoes that are primarily dispersed by birds consuming mature fruits and defecating viable seeds, the dwarf mistletoes rely almost exclusively on this ballistic mechanism. Birds and mammals are important, however, for the rare, long-distance dissemination of seeds to new infection centers (Nicholls and others 1984). The exception is *Arceuthobium verticilliflorum*, which is found in widely spaced pine forests of Mexico. This species has nonexplosive fruits twice the size of other dwarf mistletoes and is predominately dispersed by birds.

The special morphological and anatomical features that facilitate dispersal include the supporting structure for the fruit (pedicel) and characteristic, sticky, viscin cells (Wilson and Calvin 1996, Hawksworth and Wiens 1996). When the fruit matures, the pedicel elongates and water pressure increases. With separation of the fruit from the pedicel, the seed is ejected at nearly 24 m per second (Hinds and Hawksworth 1965) and tumbles in a short ballistic flight until it lands upon and sticks to a surface. The shape of the ballistic trajectory is influenced by height above the ground, pedicel–fruit orientation, seed shape and weight, discharge velocity, and gravity (Hawksworth 1961). Dwarf mistletoe seeds have a mass of 2 to 3 mg; wind affects the flight, but seeds fall to their destination within seconds. Although maximum horizontal displacement may reach 16 m, 10 m is a more typical, free-flight distance (see Escudero and Cibrián 1985). Most seeds are displaced horizontally only 2 to 4 m and deposited lower in the crown; some seeds, however, are shot

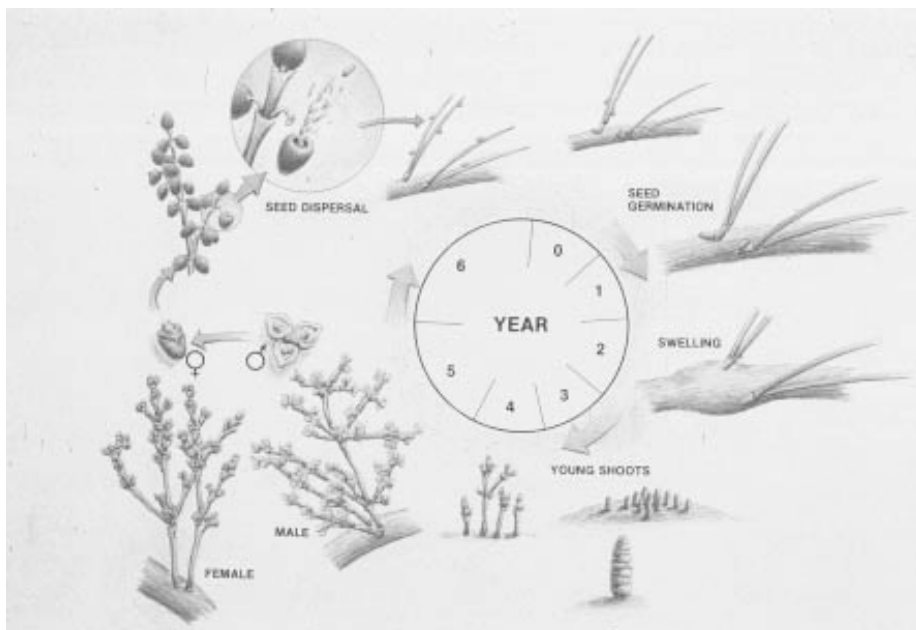


Figure 4-1—Generalized life cycle of a typical dwarf mistletoe. Illustration courtesy of W. R. Jacobi.

higher into the crown to effect vertical spread (Hawksworth and Geils 1985, Richardson and van der Kamp 1972, Shaw and Hennon 1991, Wicker and Hawksworth 1991). Because of variation in crown density, foliage display, and mistletoe position, the rate of seed interception within any tree crown is highly variable. Only about 40 percent of seeds are intercepted by any tree crown; 60 to 80 percent of seeds are retained in the crown from which they originated (reinfection); of those that escape, 90 percent may be intercepted by an adjoining tree (contagion) (Hawksworth 1965, Smith 1985).

After their ballistic flight, seeds continue to move by gravity or rarely by birds and mammals (Nicholls and others 1984). The viscin coating helps the seed adhere to any surface it strikes, including host foliage. After the initial interception, this viscin imbibes water, swells, loosens, and permits the seed to slide down the needle (see Hawksworth and Wiens 1996 for illustrations). If the needle points upward, the seed lodges on a twig at the base of a needle (a good safesite); otherwise, the seed slides off and relocates in the crown or falls to the ground. Most infections, but not all, occur on young branch wood (Sproule 1996a). Although only a few seeds reach safesites (less than 10 percent, according to Hawksworth 1965), large numbers of seeds are produced on heavily infected trees (Hawksworth 1965, Smith 1977, Wicker 1967a). Although it seems inefficient, for short range spread and intensification this dispersal mechanism is effective enough for dwarf mistletoes to have persisted since the Miocene, adapted to nearly a hundred host species, and spread throughout the conifer forests of North America.

Establishment—The physical process of dispersal brings the mistletoe seed within millimeters of establishing a new infection; biological growth completes the establishment phase. Although the embryo of some tropical species begins growth soon after dispersal, most temperate mistletoes do not resume growth (germinate) until the following spring when light, moisture, and temperature are suitable (Gill and Hawksworth 1961, Lamont 1983, Scharpf 1970, Wicker 1974).

Genetic factors, predation, and environmental conditions reduce the number of viable seeds; field germination varies from 7 to 90 percent (Hawksworth and Wiens 1996). The chlorophyllous endosperm helps maintain the embryo and permits growth of the hypocotyl (see Deeks and others 2001). If the germinating seed rests on a host shoot with thin bark and its growth encounters a needle base, it then develops an external holdfast structure and penetration wedge that grows into the host cortex (Scharpf and Parmeter 1967). From the penetration wedge, fine strings of mistletoe tissue — the endophytic system — ramifies throughout

the host cortex and eventually becomes embedded in xylem as “sinkers” (Cibrián and others 1980, Calvin and Wilson 1996, Hunt and others 1996). With the establishment of the endophytic system, the parasitic nutritional relation is initiated. Although little is known about the mechanisms of host resistance (see chapter 7), a high degree of host specificity and inherited variation in susceptibility suggest that physiological compatibility is required for an infection to become established (Kolb 2002).

Incubation—The endophytic system expands within the cortex and becomes embedded in the xylem for a number of years before aerial shoots are produced (incubation period). The endophytic system both encircles the infected branch and grows along it. The nature of distal–proximal growth depends upon the dwarf mistletoe species and point of origin. When a species such as *Arceuthobium douglasii* infects the host’s apical meristem, a systemic infection is established whereby the growth of the endophytic system keeps up with the growth of the host shoot. In other cases, growth of the endophytic system is limited, and a localized (nonsystemic) infection establishes. In nonsystemic infections, the infected branch develops a distinct fusiform swelling (except by a few host species). The incubation period extends from 2 to 12 years depending on mistletoe species and environmental conditions (Hawksworth and Wiens 1996). Typically, incubation periods range from 3 to 4 years.

Even after aerial shoots are produced, the endophytic system continues to grow (Calvin and Wilson 1996). Pathological effects of the mistletoe infection become evident as infected branches develop persistent witches’ brooms, and the upper crown thins and dies. Although a single, systemic infection can eventually develop into a large witches’ broom, most severe pathological effects result from multiple infections. Rarely, the endophytic system grows into the bole and establishes a main stem infection that persists as long as the host lives. Branch infections usually occur in the lower crown. These parasitized branches do not readily self-prune but are subject to breakage (especially large brooms in brittle hosts) and consumption by fire (brooms tend to be low and are highly flammable). Infections in the upper crown are lost as crown-dieback in severely diseased trees progresses.

Reproduction—Dwarf mistletoes are dioecious plants that only reproduce from seeds borne on shoots (see Gilbert 1988). Although dwarf mistletoe shoots have chlorophyll, they have no photosynthetic significance. Their function is primarily reproductive and secondarily in water regulation and synthesis of growth compounds (Wilson and Calvin 1996). Shoots range in size from several millimeters to 0.5 m, but most species are 2 to 10 cm tall. Generally, 1 to 2 years elapse

from shoot appearance to the initial flowering. Several flower crops (range one to five) are usually produced, and shoots many be retained for 2 to 7 years. Meiosis may occur either immediately before flower production (direct flowering) or approximately 5 to 8 months before anthesis (indirect flowering). Most species exhibit definite annual flowering periods, but a few tropical species appear to flower continuously throughout the year. The sex ratio for most species is about 50:50 (Mathiasen and others 1998, Mathiasen and Shaw 1998, Wiens and others 1996). Pollen is either dispersed by wind or insects, and because of the clustered distribution of mistletoes, pollen is seldom limiting. Although fruit maturation in some tropical species occurs in as little as 4 to 5 months, most species require about 1 year (to 19 months) from flowering to seed dispersal. The number of fruits per infection is controlled by variation in the size of the endophytic system, host-parasite physiology, activity by pathogens and insects, and weather. Strand and Roth (1976) observe that the number of seeds produced by *Arceuthobium campylopodum* is related to plant age, but the coefficient of variation usually exceeds 100 percent (even greater than 200 percent). Wicker (1967a) estimates the number of mistletoe seeds produced on trees infected by *A. campylopodum* range from 800 to 2.2 million per year. Escudero and Cibrián (1985) report that *Arceuthobium globosum* produces more than 7.3 million seeds per hectare.

As parasites, dwarf mistletoes inhabit a relatively safe and constant environment and live for many decades. Because they rely upon a host for nutrition and because reproductive success does not require annual seed production, dwarf mistletoes can persist for years without producing aerial shoots (latent infections). Although little is known of the physiological mechanisms that regulate flowering, shoot production is apparently suppressed in the low light (Shaw and Weiss 2000) and in the nutrition environment of shaded lower crowns (Kolb 2002). Opening the canopy (removing trees) commonly results in a proliferation of mistletoe shoots on the residual trees (see chapter 8).

Spread and Intensification

Because ballistic dispersal and parasitism are important attributes of life history, these features are critical factors in determining population characteristics and dynamics (Bloomberg and Smith 1982, Hawksworth and Scharpf 1984, Parmeter 1978, Smith 1977). Ballistic dispersal is effective for short-range dissemination only, and parasitism requires a living host. Consequently, mistletoe plants are clustered within trees, and infected trees occur in patches (Robinson and others 2002). The spatial dynamics of mistletoe populations operate across a range of scales—the tree, neighborhood, stand, and landscape. Because

mistletoes are clustered, infestations are usually described on the bases of incidence (percent of trees infected), severity (relative abundance), area distribution (extent), and spatial patterns (contagion). Successful reproduction leads to spread (Dixon and Hawksworth 1979) and intensification (Geils and Mathiasen 1990). In this context, spread refers to an increase in number of infected trees and the extent of an infestation (including the special case of vertical spread); intensification is increase in the abundance of mistletoe in an infested population. Stand development and management often generate grouping of trees whereby mistletoe disperses readily within groups but infrequently between groups. Even in stands with random or uniform patterns of tree distribution, the abundance of dwarf mistletoe plants often displays spatial autocorrelation. Spread and intensification, of course, are limited (Trummer and others 1998). Infected trees and the dwarf mistletoes they sustain eventually die from fire, insects, disease, or cutting, leading to fragmentation or local extinction of the dwarf mistletoe population.

Rating systems—There are numerous dwarf mistletoe rating systems for describing host susceptibility, mistletoe abundance, and witches' broom abundance (Hawksworth and Wiens 1972, Hawksworth 1977, Tinnin 1998). Each rating system provides a quantitative reference scale for indicating the population status of a mistletoe infestation and its potential for spread and intensification. New systems focus on potential use by wildlife (Parker 2001), fire ecology (Maffei 2002), and adaptations for woodland trees.

The host susceptibility system developed by Hawksworth and Wiens (1972) classifies candidate host species by the percentage expected to become infected where suitably exposed to an inoculum source. The classification is based on either direct field observations or general field experience. The system is meant to reflect the potential physiological susceptibility to infection and parasite development, not the distributional commonness or rarity of the host-pathogen combination. Species with greater than 90 percent infection where exposed to a mistletoe seed source are described as principal hosts; infestations on a principal host population are self-sustaining. Secondary, occasional, and rare hosts exhibit infection levels of 90 to 50 percent, 50 to 5 percent, or less than 5 percent, respectively. Infestations in populations of occasional or rare hosts usually occur where an infected principal host is present. Some species are recognized as hosts either by artificial inoculation or by natural infection of individuals planted beyond their normal range (extralimital hosts). Incompatible hosts are those species in which the dwarf mistletoe is able to establish a parasitic, nutritional relation but not to form aerial shoots. The physiological requirements necessary for

parasitism are satisfied for only a few host and mistletoe combinations; most species are immune.

Although mistletoe abundance could be quantified by number of plants, biomass, or other indicators, mistletoe severity is usually described by a relative index for the amount of host crown affected, the dwarf mistletoe rating, DMR (Hawksworth 1977). By this system (fig. 6-1), the live host crown is divided into thirds; each third is rated as 0 if no live branches are apparently infected, 1 if not more than half of the branches are infected, or 2 if more than half of the branches are infected. The system allows a description of mistletoe distribution within crown thirds, or by summing values for crown thirds, abundance for the tree as a whole (DMR), or by averaging tree ratings, severity for a group or stand of trees. If tree ratings (0 to 6) are averaged over all susceptible trees in a stand, the result is stand-DMR; if tree ratings are averaged over infected trees only (1 to 6), the result is stand-DMI (Geils and Mathiasen 1990). The distinction is useful because of the computational identity among DMR, DMI, and the fraction of trees infected (incidence):

$$\text{DMR} = \text{DMI} \times (\text{incidence}).$$

DMR is a good single index of mistletoe severity; but DMI and incidence may be preferred to illustrate separately the severity of infection upon infected trees and relative abundance of infected trees in the population.

Although the DMR system applies well to many important hosts such as spruce, larch, and yellow and white pines, it is less practical for other hosts (Dooling 1978, Shaw and others 2000). In many hemlock and fir stands, the upper crown where much of the mistletoe would be found is obscured by height and foliage. The low, round, compact form of pinyons and general distribution of mistletoe throughout the crown make division into crown thirds impractical. In Douglas-fir, individual branches are difficult to count, but systemic witches' brooms are obvious. Tinnin (1998) suggests a variation to the DMR system, BVR for broom-forming hosts; in his system broom volume substitutes (in part) for number of infected branches in rating a crown third. Other variations are possible, but to avoid confusion, these other variations should not be referred to as DMR.

Spread and intensification are both strongly influenced by the same factors and are really just alternative views of the same basic life history processes—dispersal, establishment, incubation, and reproduction. Intensification of an infected host can occur from auto-infection, allo-infection, or both. The initial infection of a previously uninfected host (both spread and intensification) can only result from allo-infection. Dispersal is primarily affected by the physical configuration of the seed's environment—tree and crown density,

vertical crown distribution (structure), and stand species composition. Establishment, incubation, and reproduction are determined by weather, genetic, and other biological factors, some of which are nearly fixed such as host susceptibility. Other factors such as host height growth and predation are extremely variable and difficult to predict. In most cases, the most valuable piece of information for predicting dwarf mistletoe behavior and response to management is knowledge of the mistletoe species. Although all dwarf mistletoes share a common genus morphology, most taxa are readily identifiable when size, branching pattern, color, and brooming response are considered together. Furthermore, most species can be determined based on host and distribution.

Description of Genus

Arceuthobium Dwarf mistletoe

Arceuthobium M. Bieb. Flora Taurico-Caucasica 3(IV) Supplement, p. 629, 1819. Nom. Cons. 2091
= *Razoumofskyia* Hoffman.

Herbs or shrubs from 0.5 cm to approximately 70 cm high (see fig. 4-2 and 4-3); parasitic on Pinaceae and Cupressaceae; plants glabrous, variously colored from greenish yellow to orange, reddish, or black; dioecious; stems with variant (anomalous) patterns of secondary growth; leaves reduced to minute, opposed, connate scales; internodes angled (at least when young); flowers generally decussate or rarely whorled on young shoots, 2 to 4 mm across; staminate flowers with a central nectary, perianth segments usually three to four (rarely two and up to seven) bearing a sessile, one-chambered, circular anther on each perianth segment; pollen spherical with six alternating spiny and smooth sections; pistillate flower manifestly epigynous with one style, perianth segments persistent, adnate to ovary, two-merous; ovary one-chambered; fruit an ovoid berry, one-seeded, mucilaginous and bicolored (distal and basal portions of different shades), explosive at maturity (one exception); seeds without true integuments, usually 3 to 5 mm long, ovate-lanceolate, containing one (rarely two) distal, cylindrical embryo, with copious endosperm.

A genus of 42 species in two subgenera. Subgenus *Arceuthobium* is characterized by verticillate (whorled) branching and occurring mostly in the Old World represented in North America by three species (*A. abietis-religiosae*, *A. americanum*, and *A. verticilliflorum*). Subgenus *Vaginata* occurs only in the New World and characterized by flabellate (fan-like) branching. Thirty-six taxa are described for North America (table 4-1). Type species: *Arceuthobium oxycedri* (DC.) M. Bieb.

Table 4-1—Dwarf mistletoes of Canada, Mexico, and the United States.

<i>Arceuthobium</i> taxon	Canada	United States	Mexico
<i>A. abietinum</i> f. sp. <i>concoloris</i>	-	X	X
<i>A. abietinum</i> f. sp. <i>magnificae</i>	-	X	-
<i>A. abietis-religiosae</i>	-	-	X
<i>A. americanum</i>	X	X	-
<i>A. apacheum</i>	-	X	X
<i>A. aureum</i> subsp. <i>peteronii</i>	-	-	X
<i>A. blumeri</i>	-	X	X
<i>A. californicum</i>	-	X	-
<i>A. campylopodum</i>	-	X	X
<i>A. cyanocarpum</i>	-	X	-
<i>A. divaricatum</i>	-	X	X
<i>A. douglasii</i>	X	X	X
<i>A. durangense</i>	-	-	X
<i>A. gillii</i>	-	X	X
<i>A. globosum</i> subsp. <i>globosum</i>	-	-	X
<i>A. globosum</i> subsp. <i>grandicaule</i>	-	-	X
<i>A. guatemalense</i>	-	-	X
<i>A. hondurensis</i>	-	-	X
<i>A. laricis</i>	X	X	-
<i>A. littorum</i>	-	X	-
<i>A. microcarpum</i>	-	X	-
<i>A. monticola</i>	-	X	-
<i>A. nigrum</i>	-	-	X
<i>A. oaxacanum</i>	-	-	X
<i>A. occidentale</i>	-	X	-
<i>A. pendens</i>	-	-	X
<i>A. pusillum</i>	X	X	-
<i>A. rubrum</i>	-	-	X
<i>A. siskiyouense</i>	-	X	-
<i>A. strictum</i>	-	-	X
<i>A. tsugense</i> subsp. <i>tsugense</i>	X	X	-
<i>A. tsugense</i> subsp. <i>mertensianae</i>	X	X	-
<i>A. vaginatum</i> subsp. <i>vaginatum</i>	-	-	X
<i>A. vaginatum</i> subsp. <i>cryptopodum</i>	-	X	X
<i>A. verticilliflorum</i>	-	-	X
<i>A. yecorensis</i>	-	-	X
Total number of taxa	6	21	23

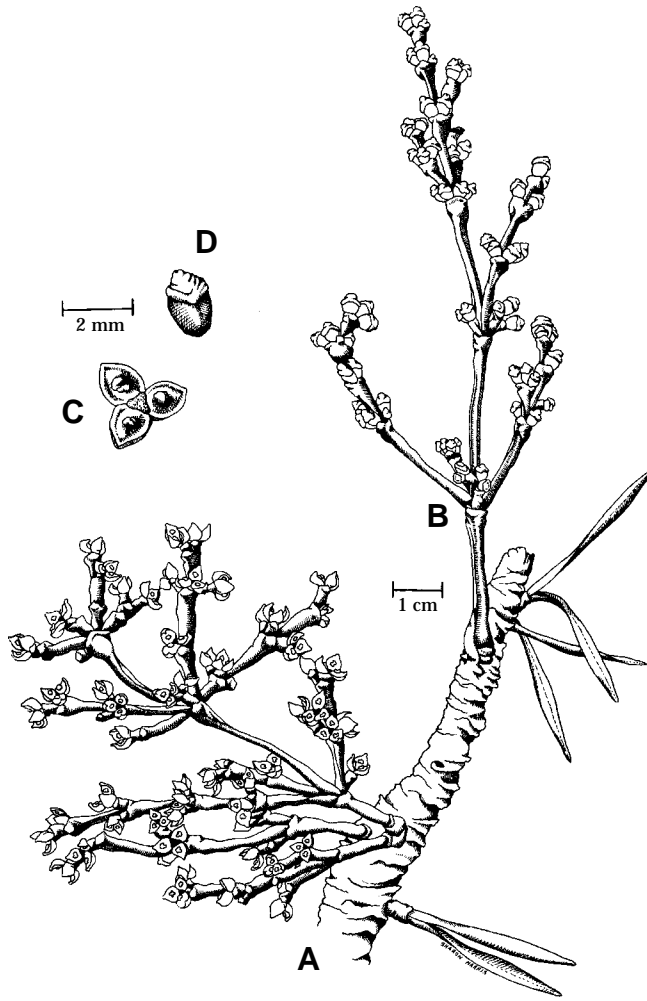


Figure 4-2—*Arceuthobium americanum* in spring, **A** staminate plant with verticillate (whorled) branching, **B** pistillate plant, **C** staminate flower, **D** pistillate flower. Illustration from Hawksworth and Wiens (1972).

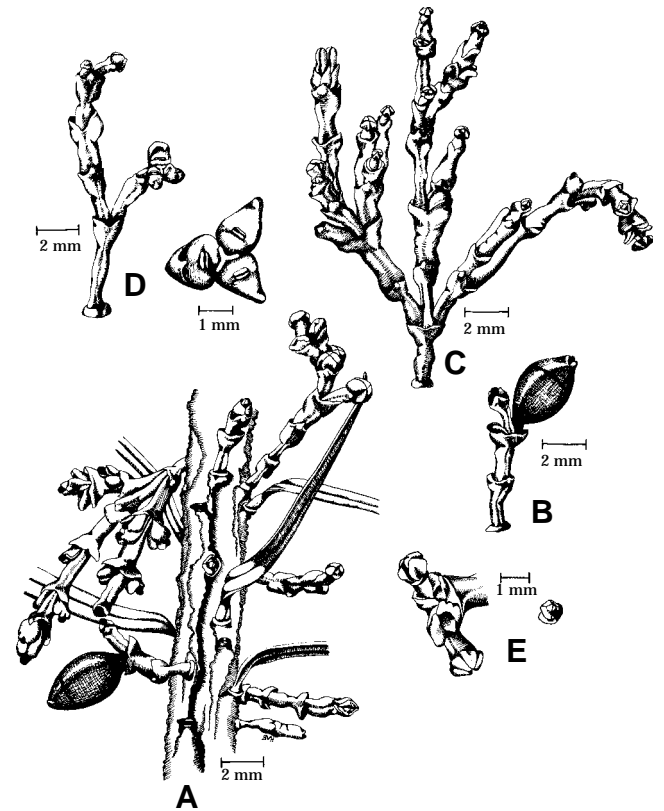


Figure 4-3—*Arceuthobium douglasii* in spring, **A** pistillate plant (left) and staminate plant (right), **B** detail of mature fruit, **C** staminate shoot, **D** staminate shoot with open mature buds (left) and detail of open flower (right), **E** staminate shoots with closed buds. Illustration from Hawksworth and Wiens (1972).

Key to North American Species of *Arceuthobium*

- 1. Distributed in Mexico 2
- 2. Parasites of fir or Douglas-fir 3
 - 3. Shoots 1–3 cm high; parasites of Douglas-fir 11. *A. douglasii*
 - 3. Shoots more than 5 cm high; parasites of fir 4
 - 4. Shoots less than 10 cm high, not verticillate, greenish; Chihuahua 1. *A. abietinum*
 - 4. Shoots 10–20 cm high, some verticillate, yellow; Central Mexico 2. *A. abietis-religiosae*
- 2. Parasites of pine 5
 - 5. Baja California 6
 - 6. Shoots olive–green, about 1–2 mm diameter; parasites of pinyon 10. *A. divaricatum*
 - 6. Shoots yellowish, about 2–4 mm diameter; parasites of *Pinus jeffreyi* or *P. coulteri* 8. *A. campylopodum*

5. Mainland Mexico 7
7. Parasites of pinyon or white pine 8
8. Parasites of pinyon 24. *A. pendens*
8. Parasites of white pine 9
9. Shoots greenish purple to purple; parasites of *Pinus ayacahuite* var. *ayacahuite*; southern Mexico 15. *A. guatemalense*
9. Shoots yellow or gray; parasites of *Pinus strobiformis* or *P. ayacahuite* var. *brachyptera*; northern Mexico 10
10. Shoots yellowish, usually less than 4 cm high; northern Coahuila 4. *A. apacheicum*
10. Shoots gray, usually more than 6 cm high; Chihuahua, Durango, or Nuevo León 6. *A. blumeri*
7. Parasites of yellow pine 11
11. Shoots dark, usually some shade of black, reddish (or dull brown when dried) 12
12. Male and female plants similarly branched (little sexual dimorphism); fruits not glaucous 13
13. Shoots usually more than 10 cm high and more than 1 cm diameter at base; fruits 4–5 mm long, not shiny 30a. *A. vaginatum* subsp. *vaginatum*
13. Shoots usually less than 10 cm high and less than 1 cm diameter at base; fruits about 3 mm long, shiny 26. *A. rubrum*
12. Male and female plants dissimilarly branched (sexually dimorphic); fruits markedly glaucous 21. *A. nigrum*
11. Shoots yellow, brown, gray, or red 14
14. Staminate flowers verticillate on deciduous spikes; mature fruits more than 10 mm long 31. *A. verticilliflorum*
14. Staminate flowers not verticillate on deciduous spikes; mature fruits less than 6 mm long 15
15. Plants of northern Mexico 16
16. Male and female plants dissimilarly branched (sexually dimorphic) 17
17. Male plants essentially non-branched and female plants densely branched 28. *A. strictum*
17. Male plants with very open branches and female plants densely branched 13. *A. gillii*
16. Male and female plants similarly branched (little sexual dimorphism) 18
18. Shoots yellow or yellow–brown 19
19. Shoots bright yellow, in globose clusters, usually more than 10 cm high 14a. *A. globosum* subsp. *globosum*
19. Shoots yellow or brown, not in globose clusters, usually less than 10 cm high 32. *A. yecoreense*
18. Shoots some shade of orange 20
20. Shoots dark–orange, usually more than 20 cm high; mature fruit 7 mm long; Durango or southward 12. *A. durangense*
20. Shoots yellow–orange, usually less than 20 cm high; mature fruit 5 mm long; Chihuahua, Sonora, or Coahuila 30b. *A. vaginatum* subsp. *cryptopodium*
15. Plants of southern Mexico (Chiapas and Oaxaca) 21
21. Shoots glaucous, olive-brown to gray green; parasite of *P. oocarpa* or *P. maximinoi* 16. *A. hondurensense*
21. Shoots not glaucous; reddish, dark green, yellow, or orange 22
22. Shoots reddish; Oaxaca 22. *A. oaxacanum*
22. Shoots dark greenish yellow or orange; Oaxaca or Chiapas 23
23. Shoots yellow, often over 2 cm in diameter at base; elevations above 2,700 m 14b. *A. globosum* subsp. *grandicaule*
23. Shoots yellow–orange, usually less than 2 cm in diameter; elevations below 2,400 m 5. *A. aureum* subsp. *petersonii*

1. Distributed in the United States or Canada	24
24. Parasites principally of pine	25
25. Parasites of pinyon or white pine.....	26
26. Parasites of pinyon	10. <i>A. divaricatum</i>
26. Parasites of white pine	27
27. Parasites of <i>Pinus strobiformis</i>	28
28. Shoots usually less than 4 cm high, yellow; southern Arizona or southern New Mexico	4. <i>A. apachecum</i>
28. Shoots usually more than 6 cm high, gray; Huachuca Mountains of Arizona	6. <i>A. blumeri</i>
27. Parasites of white pines other than <i>Pinus strobiformis</i>	29
29. Parasites of <i>Pinus aristata</i> ; Arizona	19. <i>A. microcarpum</i>
29. Parasites of pines other than <i>Pinus aristata</i> or if parasite of <i>Pinus aristata</i> then not Arizona	30
30. Shoots usually less than 6 cm high, densely clustered around the host branch; parasites of <i>Pinus flexilis</i> , <i>P. albicaulis</i> , <i>P. aristata</i> , or <i>P. longaeva</i>	9. <i>A. cyanocarpum</i>
30. Shoots usually more than 6 cm high, not densely clustered around the host branch; parasites of <i>Pinus monticola</i> or <i>P. lambertiana</i>	31
31. Shoots dark brown; parasites of <i>Pinus monticola</i> ; southwestern Oregon or northeastern California	20. <i>A. monticola</i>
31. Shoots yellow to green; parasites of <i>Pinus lambertiana</i> ; California	8. <i>A. californicum</i>
25. Parasites of yellow pine	32
32. Shoot branches verticillate; parasites principally of <i>Pinus contorta</i> or <i>P. banksiana</i>	3. <i>A. americanum</i>
32. Shoot branches flabellate; parasites principally of pines other than <i>Pinus contorta</i> and <i>P. banksiana</i>	33
33. Arizona, Utah, or eastward	34
34. Fruits glaucous; male plants much more openly branched than female plants; parasites of <i>Pinus leiophylla</i> var. <i>chihuahuana</i>	13. <i>A. gillii</i>
34. Fruits glabrous; male and female plants branch in similar manner; parasites of <i>Pinus ponderosa</i> var. <i>scopulorum</i> , <i>P. arizonica</i> , and <i>P. engelmannii</i> ; north to Colorado	30b. <i>A. vaginatum</i> subsp. <i>cryptopodum</i>
33. Pacific Coast States, Nevada, Idaho, or British Columbia	35
35. Coastal areas (within 10 km of the Pacific Ocean)	36
36. Shoots usually less than 10 cm high; staminate flowers mostly 3-merous; parasites of <i>Pinus contorta</i> var. <i>contorta</i> ; Orcas Island, Washington or British Columbia	29a. <i>A. tsugense</i> subsp. <i>tsugense</i>
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Several other keys and floristic treatments of the dwarf mistletoes are available. Scharpf and Hawksworth (1993) provide photographs and field descriptions for the mistletoe from Washington, Oregon, and California. Unger (1992) provides a similar, general coverage for Canada. Numerous but brief and partial descriptions describe the dwarf mistletoes of Mexico (Cházaro and Olivae 1987a, Hawksworth 1987, Hawksworth and Cibrián 1985, Najera and others 1987, Rodriguez 1983). Recent taxonomic notes include Hawksworth and Wiens (1965, 1977, 1989) and Hawksworth and others (1992b). Because the taxonomy of dwarf mistletoes has changed considerably in the past few decades, especially for some regions (Mexico) and some groups (*campylopodum*, *globosum*, *vaginatum*), care is required when reading the literature to relate the information presented to the proper taxa. Host and distribution information is ultimately derived from specimen collections and field observations. When the name applied to a specimen changes, the information also refers to a different taxa;

published information goes out of date and may be associated with the wrong mistletoe.

Description of Species _____

1. *Arceuthobium abietinum*

Fir Dwarf Mistletoe

Arceuthobium abietinum Engelm. ex Munz, Manual Southern California Botany: 114, 1935.

=*A. campylopodum* f. *abietinum*.

Description. Mean shoot height 8 (maximum 22) cm. Shoots yellow green to yellow, branches flabellate. Basal diameter of dominant shoots 1.5 to 6.0 (mean 2) mm. Third internode 4 to 23 (mean 14) mm long, 1.5 to 4.0 mm (mean 2) mm wide; length/width ratio is 7:1 to 9:1. Staminate flowers 2.5 mm across; perianth three-merous, sometimes four-merous, apex acute; same color as shoots; segments 1.2 mm long, 1.0 mm wide. Mature fruit 4 by 2 mm; proximal portion 2.5 mm long. Seeds 2.8 by 1.2 mm.

Key to the Formae Speciales

1. Parasitic principally on *Abies concolor* or *A. grandis*; known in two areas in Chihuahua on *A. durangensis*. The primary distribution is from southern Washington southward through the Cascade and southern Coast Ranges in Oregon, and the North Coast and Cascade Ranges, Sierra Nevada to southern California. Isolated populations occur in southern Utah, northern and southern Arizona, and Chihuahua
 1a. *A. abietinum* f. sp. *concoloris*.
1. Parasitic principally on *Abies magnifica* from southwestern Oregon (Josephine) to the southern Sierra Nevada, California 1b. *A. abietinum* f. sp. *magnifica*.

Phenology. Meiosis in July. Anthesis usually August and September. Fruits mature in September or October of the year following pollination; maturation period averages 13 to 14 months. Seeds germinate from February through June.

Hosts. Fir.

Discussion. Parmeter and Scharpf (1963) first report that the dwarf mistletoe on *Abies concolor* does not infect associated *A. magnifica*, and conversely, the parasite of *A. magnifica* does not parasitize associated *A. concolor*. We are unable, however, to find any morphological, phenological, or chemical differences useful to distinguish between the two mistletoes. Because the host affinities of these two dwarf mistletoes are distinct and they are of considerable importance in forestry, we treat them as *formae speciales*. Branch death or “flagging” by the fungus *Cytospora abietis* is one of the most conspicuous field symptoms for infection by this dwarf mistletoe (Scharpf 1969a). The biology, pathology, and management of fir dwarf mistletoe are discussed by Filip and others (2000), Scharpf (1969b), and Scharpf and Parmeter (1967, 1982).

Hunt (1993) reorganizes the taxonomy of *Abies* and recognizes several combinations not previously used in the dwarf mistletoe literature. In his treatment, *Abies lasiocarpa* refers to west-side populations in the Pacific Northwest and British Columbia and *A. bifolia* to east-side and Rocky Mountain populations. Status of the corkbark fir (= *Abies lasiocarpa* var. *arizonica*) in the Southwest is left as uncertain. *Abies lowiana* is recognized as species rather than subspecies.

1a. *Arceuthobium abietinum*

White Fir Dwarf Mistletoe

Arceuthobium abietinum Engelm. ex Munz f. sp. *concoloris* Hawksw. & Wiens, Brittonia 22:267, 1970.

Hosts. The principal hosts of this dwarf mistletoe are *Abies concolor*, *A. grandis*, *A. durangensis*, and *A. lowiana*. *Abies concolor* (Nevada, Utah, and Arizona) and *A. lowiana* (California) are about equally susceptible, although the dwarf mistletoe is more widely distributed on the latter. The rare *Picea breweriana* in Oregon is associated with infected *Abies concolor* and is heavily infected by *Arceuthobium abietinum*. On the

North Rim of Grand Canyon, Arizona, *Abies bifolia* (usually referred to *Abies lasiocarpa* var. *arizonica*) is occasionally parasitized where this tree grows in association with infected *A. concolor*. *Abies amabilis* is a rare host of this dwarf mistletoe at Crater Lake, Oregon. *Pinus ayacahuite* var. *brachyptera*, *P. contorta* var. *murrayana*, *P. lambertiana*, and *P. monticola* are rare hosts.

Distribution. United States (Washington, Oregon, California, Nevada, Utah, and Arizona), and Mexico (Chihuahua). *Arceuthobium abietinum* f. sp. *concoloris* is widely distributed from southern Washington (Skamania, Wenatchee, and Klickitat) south through the Cascade Range and Sierra Nevada to the San Bernardino Mountains, California. A single, relict population is known in the Willamette Valley, Oregon. It also occurs along the coast ranges from Mendocino, California, to Curry, Oregon. Isolated populations are known in Nevada (Spring, Sheep, and Groom Mountains) and Utah (Kane). The parasite is known in Arizona from the Grand Canyon, the Chiricahua Mountains (Cochise), and the Santa Catalina Mountains (Pima). This dwarf mistletoe is reported on *Abies durangensis* from in two localities in Chihuahua 1,000 km south of Arizona. *Arceuthobium abietinum* f. sp. *concoloris* occurs from near sea level along the coast of northern California and southern Oregon to over 2,650 m in the Spring Mountains of southern Nevada.

Discussion. In the Northwest, two other species of *Arceuthobium* occur on fir: (1) *Arceuthobium tsugense* on *Abies amabilis*, *A. grandis*, and *A. lasiocarpa* and (2) *Arceuthobium laricis* on *Abies grandis* and *A. lasiocarpa*. However, insofar as we are aware, neither of these dwarf mistletoes is sympatric with *Arceuthobium abietinum*. *Arceuthobium tsugense* and *A. laricis* rarely infect pure stands of fir, but they may parasitize fir secondarily in stands where the principal hosts of these dwarf mistletoes are parasitized (for example, hemlock by *A. tsugense* and larch by *A. laricis*). *Arceuthobium tsugense* differs from *A. abietinum* by shorter (7 cm), green to purple shoots compared with the longer (10 cm), yellowish shoots of *A. abietinum*. *Arceuthobium*

laricis is readily distinguished from *A. abietinum* by shorter, darker shoots (4 cm versus 10 cm) and shorter (in summer) staminate spikes (2 to 3 mm versus 5 to 7 mm). 1b.

Arceuthobium abietinum

Red Fir Dwarf Mistletoe

Arceuthobium abietinum Engelm. ex Munz f. sp. *magnificae* Hawksw. & Wiens, Brittonia 22:268, 1970.

Hosts. *Abies magnifica*.

Distribution. United States (Oregon and California). *Arceuthobium abietinum* f. sp. *magnificae* is distributed from Josephine, Oregon, to Kern, California, in the southern Sierra Nevada. Guyon and Munson (1991) record it within 3 km of the Nevada border. Elevational range is 1,500 to 2,400 m.

Discussion. *Arceuthobium abietinum* f. sp. *magnificae* is a common and serious disease agent of the *Abies magnifica* forests of the Sierra Nevada (Scharpf 1969b).

2. Arceuthobium abietis-religiosae

Mexican Fir Dwarf Mistletoe

Arceuthobium abietis-religiosae Heil, Zentralblatt f. r Bakteriologie Abteilung 2:28, 1923 [and see Hawksworth and Wiens, Brittonia 17:231, 1965].

Description. Mean shoot height 10 (maximum 16) cm. Shoots olive green, older shoots typically with black variegations, occasionally with verticillate branching. Basal diameter of dominant shoots 2 to 10 (mean 4) mm. Third internode 8 to 24 (mean 15.4 ± 5.3) mm long, 1 to 4 (mean 2.8) mm wide, length/width ratio 5.5:1. Staminate buds two to four per node. Staminate flowers 2 mm long, 2.4 mm across; perianth mostly three-merous, sometimes four-merous; apex obtuse-acute; same color as shoots on outer surface, reddish on inner surface distal to anther; segments 1.2 mm long, 0.9 mm wide. Pistillate flowers 1.0 mm long, 0.5 mm across. Mature fruit 3.5 by 2 mm; proximal portion 2.5 mm long. Seeds 2.2 by 1.0 mm.

Phenology. Meiosis in September. Anthesis poorly known but apparently flowering in March to April and September to October. Fruits probably mature in October or November.

Hosts. Known only on fir. *Abies religiosa* (including var. *emarginata*) is by far the most common host, but also this dwarf mistletoe also parasitizes *A. vejarii* and probably other Mexican firs.

Distribution. Mexico (Distrito Federal, Hidalgo, Jalisco, Mexico, Michoacán, Nuevo León, Puebla, Tamaulipas, Tlaxcala). This dwarf mistletoe is common in the *Abies religiosa* forests of Central Mexico and Sierra Madre Oriental (Hernandez and others 1992, Madrigal 1967). Elevational range is 2,500 to 3,350 m.

Discussion. This distinctive Mexican dwarf mistletoe is characterized by its large shoots, occasional

verticillate branching, and exclusive parasitism of fir. With the exception of the rare occurrence of *Arceuthobium abietinum* in Chihuahua, this is the only dwarf mistletoe that parasitizes fir in Mexico.

3. Arceuthobium americanum

Lodgepole Pine Dwarf Mistletoe

Arceuthobium americanum Nutt. ex Engelm. in Gray, Boston Journal Natural History 6:214, 1850.

Description. Mean shoot height 5 to 9 (maximum 30) cm. Shoots yellowish to olive green, with verticillate branching (fig. 4-2). Basal diameter of dominant shoots 1 to 3 (mean 1.5) mm. Third internode 6 to 23 (mean 12 ± 3.0) mm long, 1 to 2 (mean 1.2) mm wide (20 collections), length/width ratio 10.1:1. Staminate flowers borne on pedicel-like segments, 2 mm long, 2.2 mm across; perianth mostly three-merous, sometimes four-merous; same color as the shoots; segments 1.1 mm long, 1.0 mm wide. Pistillate flowers verticillate; 1.5 mm long, 1.0 mm across; two-merous. Mature fruit 3.5 to 4.5 (mean 4) mm long, 1.5 to 2.5 (mean 2) mm wide; proximal portion about 2.5 mm long. Seeds 2.4 by 1.1 mm.

Phenology. Meiosis in August. Anthesis usually from early April to early June, with extremes from late March to late June. Fruits mature in late August or September of the year following pollination; maturation period averages 16 months. Germination begins in May in Colorado.

Hosts. The principal hosts are *Pinus contorta* var. *latifolia*, var. *murrayana*, and *P. banksiana*; all are about equally susceptible. *Pinus contorta* var. *contorta* is infected in southern coastal British Columbia (Smith and Wass 1979). *Pinus ponderosa* var. *scopulorum* is frequently parasitized in Colorado, Utah, and Wyoming, usually where this tree is associated with infected *P. contorta* but also in pure stands of *Pinus ponderosa*. *Pinus ponderosa* var. *ponderosa*, however, is less susceptible and only occasionally infected. Other occasional hosts include *P. albicaulis*, *P. flexilis*, and *P. jeffreyi*. Rare, artificially inoculated, or extra-limital hosts are *Abies lasiocarpa* (Mathiasen and others 1996a), *Picea engelmannii*, *P. glauca* (incompatible), *P. pungens*, *P. mariana* (incompatible), *Pinus aristata*, *P. mugo*, *P. sylvestris*, and *Pseudotsuga menziesii* (incompatible).

Distribution. Canada (British Columbia, Alberta, Saskatchewan, Manitoba, and Ontario) and the United States (Washington, Idaho, Montana, Oregon, California, Utah, Wyoming, Colorado, and possibly Nevada). *Arceuthobium americanum* has the most extensive distribution of any North American dwarf mistletoe. The distribution of *Arceuthobium americanum* is centered on the range of its principal host, *Pinus contorta*, and rarely occurs within the distribution of *Pinus contorta* var. *contorta* (shore pine). *Arceuthobium americanum* occurs in outlying populations of *Pinus*

contorta var. *latifolia* in Southeastern Alberta and in north central Montana (Phillips, Hill, and Liberty). *Arceuthobium americanum* distribution maps include Alberta, British Columbia, Manitoba, Saskatchewan, Montana, Utah, Colorado, and California (see Brandt and others 1998, Hawksworth and Wiens 1996, Muir 2002). This dwarf mistletoe varies in elevation from 200 m near Lake Athabasca in northern Alberta and Saskatchewan to 3,350 m in central Colorado.

Discussion. *Arceuthobium americanum* induces characteristic systemic witches' brooms on *Pinus contorta* and produces the same type of broom on *P. ponderosa*. The witches' brooms formed on *Picea engelmannii*, however, are nonsystemic (Hawksworth and Graham 1963a). Kuijt (1960a) notes that *A. americanum* cannot perpetuate itself over time on *Pinus jeffreyi* or *P. ponderosa* var. *ponderosa* in California. In northern Colorado and southern Wyoming, however, the parasite is aggressive in pure stands of *P. ponderosa* var. *scopulorum* outside the range of *A. vaginatum* subsp. *cryptopodum*, which is the typical parasite on *P. ponderosa* in the Rocky Mountains. Hawksworth and Johnson (1989a) provide a synopsis of the biology and management of this mistletoe in the Rocky Mountains. Other general and silvicultural information is given by Baranyay (1970), Hawksworth and Dooling (1984), van der Kamp and Hawksworth (1985), and Van Sickle and Wegwitz (1978).

4. *Arceuthobium apacheum* Apache Dwarf Mistletoe

Arceuthobium apacheum Hawksw. & Wiens, Brittonia 22:266, 1970.

=*A. campylopodum* f. *blumeri*

Description. Mean shoot height 3 to 4 (maximum 9) cm. Shoots yellow, green, or reddish, branches flabellate and densely clustered. Basal diameter of dominant shoots 1 to 2 (mean 1.8) mm. Third internode 5 to 10 (mean 7.2 ± 2.0) mm long, 1 to 2 (mean 1.5) mm wide, length/width ratio 4.8:1. Flowers axillary. Staminate flowers 2.7 mm across; perianth three- to four-merous; same color as shoots; segments 1.3 mm long, 0.9 mm wide. Mature fruit 4 by 2.5 mm; proximal portion 2.5 mm long. Seeds 2.8 by 1.2 mm.

Phenology. Meiosis in July. Anthesis from late July to mid-September, peak in mid-August. Fruits mature from mid-August to mid-October, peak in September; maturation period averages about 13 months.

Host. Known only naturally on *Pinus strobiformis*, but successfully inoculated by Mathiasen (1978) on *Pinus flexilis*.

Distribution. United States (Arizona, New Mexico) and Mexico (Coahuila). This dwarf mistletoe has a limited distribution in southern Arizona and central New Mexico, with an outlier in the Sierra del Carmen in northern Coahuila. In Arizona, it occurs in the

White, Pinaleno, Santa Catalina, Santa Rita, and Chiricahua Mountains and in New Mexico in the Mangas, San Mateo, Magdalena, and Capitan Mountains. Elevational range is 2,000 to 3,000 m.

Discussion. The exclusive occurrence of two dwarf mistletoes species, *Arceuthobium apacheum* and *A. blumeri*, on a single host species, *Pinus strobiformis*, is unique in *Arceuthobium*. Geographically consistent morphological and broom differences indicate that separate taxonomic status is warranted (Mathiasen 1982). Although they are not sympatric, they approach 60 km of each other in southern Arizona. *Arceuthobium apacheum*, but not *A. blumeri*, frequently induces witches' broom formation.

5. *Arceuthobium aureum* subsp. *petersonii* Peterson's Dwarf Mistletoe

Arceuthobium aureum Hawksw. & Wiens subsp. *petersonii* Hawksw. & Wiens, Brittonia 29:415, 1977. =*A. globosum*

Description. Shoots 14 to 40 (mean 24) cm tall, golden to yellow-brown, branches flabellate. Basal diameter of dominant shoots 14 to 35 (mean 23) mm. Third internode 14 to 35 (mean 23) mm long and 2.5 to 8 (mean 5) mm wide.

Phenology. Anthesis in September. Fruits mature June and July; maturation period of 9 to 10 months, which is several months less than is common for many dwarf mistletoes.

Hosts. *Pinus michoacana*, *P. montezumae*, *P. oaxacana*, *P. oocarpa*, *P. patula*, and *P. pseudostrobus* are the principal and only hosts. *Pinus michoacana* is somewhat less susceptible and is infected only when it grows in association with the other principal hosts.

Distribution. Mexico (Oaxaca, Chiapas). This dwarf mistletoe is common between San Cristóbal de las Casas and Teopisabout (Chiapas). Its distribution in Oaxaca is poorly known by a few collections from Miahuátlán to Suchixtepec. Elevational range is 2,200 to 2,450 m.

Discussion. The taxon recognized here as *Arceuthobium aureum* had been in the *Arceuthobium globosum* complex (Hawksworth and Wiens 1972, 1977). *Arceuthobium aureum* includes two subspecies, but only subspecies *petersonii* is found in Mexico. This subspecies is characterized by tall, slender, brown to golden shoots, long fruits (5 mm), long pedicels (4 mm), and tendency to form witches' brooms.

6. *Arceuthobium blumeri* Blumer's Dwarf Mistletoe

Arceuthobium blumeri A. Nels., Botanical Gazette 56:65, 1913.

=*A. campylopodum* var. *cryptopodum*

=*A. campylopodum* f. *blumeri*.

Description. Mean shoot height 6 to 7 (maximum 18) cm, gray to straw or light green, branches flabellate.

Basal diameter of dominant shoots 1 to 3 (mean 2.1) mm. Third internode 5 to 14 (mean 9.1 \pm 2.5) mm long, 1 to 2 (mean 1.6) mm wide, length/width ratio 5.5:1. Staminate flowers 2.5 mm long, 2.5 to 3.0 mm across; perianth three- to six-merous (mostly three- or four-merous), segments 1.3 mm long, 1.0 mm wide, apex acute. Mature fruit 4 by 2.5 mm, proximal portion 2.5 mm long. Seeds 2.7 by 1.0 mm.

Phenology. Meiosis in July. Anthesis from mid-July to late-August, with a peak in early August (Mathiasen 1982). Fruits mature from late August to early October, with a peak in mid-September; maturation period averages 13 to 14 months.

Hosts. *Pinus strobiformis* and *P. ayacahuite* var. *brachyptera*. The host affinities of *Arceuthobium blumeri* are not clear because of the taxonomic confusion surrounding the white pine complex of *Pinus flexilis-strobiformis-ayacahuite* (Equiluz 1991, Hawksworth 1991, Perry 1991). Most host populations of this dwarf mistletoe are best referred to *P. ayacahuite* var. *brachyptera* in the Sierra Madre Occidental and *P. strobiformis* var. *potosiensis* on Cerro Potosí (Nuevo León). *Pinus flexilis* can be infected by inoculation (Mathiasen 1978).

Distribution. United States (Arizona) and Mexico (Sonora, Chihuahua, Durango, Nuevo León, and Coahuila). This dwarf mistletoe extends southward from the Huachuca Mountains in southern Arizona through the Sierra Madre Occidental in Chihuahua and Sonora to southern Durango. In the Sierra Madre Oriental, it is known only from Cerro Potosi (Nuevo León) and San Antonio de las Alazanas (Coahuila), but it probably occurs elsewhere over this extensive distribution (Cibrián and others 1980). Elevational range is 2,150 to 3,250 m.

Discussion. The parasitism of *Arceuthobium blumeri* and *A. apacheum* on *Pinus strobiformis* is discussed under *A. apacheum*. Distinctive features of *Arceuthobium blumeri* include its gray-colored shoots, four- to six-merous staminate flowers, and rare formation of witches' brooms.

7. *Arceuthobium californicum*

Sugar Pine Dwarf Mistletoe

Arceuthobium californicum Hawksw. & Wiens, Brittonia 22:266, 1970.

=*A. campylopodum* f. *cryptopodum*

=*A. campylopodum* f. *blumeri*.

Description. Mean shoot height 8 cm (maximum 12) cm, greenish to bright yellow, turning brown at base of older shoots, branches flabellate. Basal diameter of dominant shoots 1.5 to 4.0 (mean 2) mm. Third internode 6 to 16 (mean 10.5 \pm 2.9) mm long, 1 to 2 (mean 1.5) mm wide, length/width ratio 7.0:1. Flowers axillary. Staminate flowers 3.3 mm across; perianth three- or four-merous, segments 1.5 mm long, 1.1 mm

wide. Mature fruit 4 by 2.5 mm; proximal portion 2.0 mm long. Seeds 3.2 by 1.2 mm.

Phenology. Meiosis in July. Anthesis usually in mid-July to mid-August, with extremes from early July to late August. Fruits mature from mid-September to mid-October, with extremes from late August to early November; maturation period averages 13 to 14 months.

Hosts. The only principal host is *Pinus lambertiana*. In association with infected *P. lambertiana*, *P. monticola* is secondarily parasitized (Mathiasen and Hawksworth 1988). Infected *P. lambertiana* produce large, compact witches' brooms.

Distribution. United States (California). This species is distributed from Mount Shasta southward through the North Coast Range, and through the Cascade Range south to Lake County and the west side of the Sierra Nevada to the Cuayamaca Mountains (San Diego). Elevational range is 600 to 2,000 m.

Discussion. *Arceuthobium californicum* is common in many areas and a serious pathogen of *Pinus lambertiana* (Scharpf and Hawksworth 1968).

8. *Arceuthobium campylopodum*

Western Dwarf Mistletoe

Arceuthobium campylopodum Engelm. in Gray, Boston Journal Natural History 6:214, 1850.

=*A. campylopodum* f. *typicum*.

Description. Mean shoot height 8 (maximum 13) cm, olive green to yellow, branches flabellate. Staminate plants brownish, and pistillate plants greenish. Basal diameter of dominant shoots 1.5 to 5.0 (mean 3) mm. Third internode 7 to 22 (mean 11.3 \pm 3.8) mm long, 1.5 to 2.5 (mean 2.0) mm wide, length/width ratio 5.6:1. Staminate flowers 3.0 mm across; perianth three-merous (occasionally four-merous), segments 1.4 mm long, 1.0 mm wide. Mature fruit 5.0 by 3.0 mm.

Phenology. Meiosis in July. Peak anthesis usually from mid-August to early October, with extremes from early August to late October. Fruits usually mature from early September to mid-November, with extremes from late August to late November; maturation period averages 13 months.

Hosts. The principal and most commonly infected hosts are *Pinus ponderosa* var. *ponderosa* and *P. jeffreyi*. *Pinus jeffreyi* is somewhat more susceptible than *P. ponderosa*, but both species incur considerable damage. Other trees frequently infected, particularly when associated with the above hosts, are *Pinus attenuata* and *P. coulteri*. In the Spring Mountains, Nevada, *P. ponderosa* var. *scopulorum* is a common and seriously damaged host, but this is the only known area where *Arceuthobium campylopodum* occurs naturally within the range of *scopulorum*. Occasional hosts for *A. campylopodum* are *P. contorta* var. *latifolia*, var. *murrayana*, and *P. sabiniana*. *Pinus lambertiana* is a

rare host. Hosts by artificial inoculation are *Abies concolor*, *A. grandis*, *Picea abies*, *Pinus sylvestris*, *P. mugo*, *P. resinosa*, and *Larix occidentalis*. Although *Abies concolor*, *A. grandis*, and *Larix occidentalis* are commonly associated with *Pinus ponderosa* infected by *A. campylopodum*, they are not known to be naturally infected. *Pinus washoensis* is expected to be susceptible, but we know of no collections or reports on this species.

Distribution. United States (Washington, Idaho, Oregon, California, and Nevada) and Mexico (Baja California Norte). *Arceuthobium campylopodum* occurs from northern Washington and eastern Idaho, south through Oregon and California (but not the southern Coast Range) to the Sierra Juárez and Sierra de San Pedro Mártir (Baja California Norte). The distribution of this and other taxa in California is discussed by Kuijt (1960a). In Nevada, it occurs near Lake Tahoe and in the Spring Mountains (Clark). *Arceuthobium campylopodum* is distributed by elevation from 30 m along the Columbia River, near Hood River, Oregon, to 2,500 m in the Spring Mountains, Nevada.

Discussion. *Arceuthobium campylopodum* is a serious pathogen of *Pinus jeffreyi* and *P. ponderosa*. Our observations suggest that host damage is more severe in the southern or drier parts of the distribution. The most severely infested stands are in the California Laguna Mountains and on the east-side of the Sierra-Cascade forests. The biology, ecology, and management of this mistletoe are discussed by Kimmey and Mielke (1959), Schmitt (1996), and Stand and Roth (1976). The serious mortality caused by this mistletoe to pine in Oregon is described by Roth (2001).

9. *Arceuthobium cyanocarpum* Limber Pine Dwarf Mistletoe

Arceuthobium cyanocarpum (A. Nels. ex Rydb.) A. Nels., New Manual of Botany of the Central Rocky Mountains, p. 146, 1909.
= *A. campylopodum* f. *cyanocarpum*.

Description. Mean shoot height 3 (maximum 7) cm, yellow-green, branches flabellate, densely clustered. Basal diameter of dominant shoots 1 to 2 (mean 1.4) mm. Third internode 2 to 14 (mean 5.2 ± 2.0) mm long, 1.0 to 1.5 (mean 1.1) mm wide; length/width ratio 4.7:1. Staminate flowers 3.0 mm across; perianth three-merous (rarely four-merous), same color as shoots; segments 1.4 mm long, 1.0 mm wide, apex acute. Mature fruit 3.5 by 2.0 mm; proximal portion 2.0 mm long. Seeds 2.0 by 0.9 mm.

Phenology. Meiosis in July. Peak anthesis from mid-July to early September, with extremes from early July to mid-September. Fruits mature from mid-August to late September; maturation averages 12 months. Seed germination mostly in June.

Hosts. *Pinus flexilis* is the most common host of this dwarf mistletoe throughout its extensive geographical

range. *Pinus albicaulis*, *P. aristata*, and *P. longaeva* are also principal hosts even though they are not common within the range of *Arceuthobium cyanocarpum*. *Pinus albicaulis* is infected in western Wyoming, northern Nevada, central Oregon, and northern California. Infection of *P. aristata* is known from La Veta Pass, Colorado, in association with infected *P. flexilis*. *Pinus longaeva* is parasitized in many areas of Utah and Nevada. In northern California, *Pinus monticola* is a secondary host; and *Pinus balfouriana* is an occasional host (Mathiasen and Daughtery 2001). *Tsuga mertensiana* in central Oregon is another secondary host; and other occasional or rare hosts include *Picea engelmannii* (doubtful), *P. contorta* var. *latifolia*, and *P. ponderosa* var. *scopulorum*. *Pinus strobus* and *P. strobiformis* are susceptible to infection by artificial inoculation (Hawksworth and Wiens 1972).

Distribution. United States (Idaho, Montana, Oregon, California, Nevada, Utah, Wyoming, and Colorado). This dwarf mistletoe occurs from southern Montana and northern Wyoming south to southern Colorado and west to Oregon and California where it occurs on the east side of the Sierra Nevada, in the Panamint Mountains (Death Valley National Monument), and in the San Bernardino to San Jacinto Mountains (southern California). Distribution maps for *Arceuthobium cyanocarpum* are available for Colorado and Nevada (see Hawksworth and Wiens 1996). Elevational range is 1,600 m in southern Montana to nearly 3,050 m in central Colorado.

Discussion. This dwarf mistletoe, which characteristically infects *Pinus flexilis* and associated high-altitude white pines, is easily recognized by small, densely clustered shoots and common branch flagging. Witches' brooms are typically small and compact, and infection is usually throughout the entire crown. *Arceuthobium cyanocarpum* causes heavy mortality in *Pinus flexilis* in the Rocky Mountains and in *P. albicaulis* on Mount Shasta, California (Mathiasen and Hawksworth 1988).

10. *Arceuthobium divaricatum* Pinyon Dwarf Mistletoe

Arceuthobium divaricatum Engelm. in U.S. Geographical Survey West of 100th Meridian (Wheeler Report) 6:253, 1878.

= *A. campylopodum* f. *divaricatum*.

Description. Mean shoot height 8 (maximum 3) cm, olive green to brown, branches flabellate. Basal diameter of dominant shoots 1.5 to 4.0 (mean 2) mm. Third internode 6 to 15 (mean 9.8 ± 2.4) mm long, 1 to 2 (mean 1.6) mm wide, length/width ratio 6.1:1. Staminate flowers 2.5 mm across; perianth three-merous; segments 1.1 mm long, 0.9 mm wide. Mature fruit 3.5 by 2.0 mm; proximal portion 2.0 mm long. Seeds 2.0 by 0.9 mm.

Phenology. Meiosis in July. Peak anthesis usually from early August to late September. Fruits usually mature from early September to late October in the year following pollination; maturation period averages 13 months.

Hosts. *Arceuthobium divaricatum* is restricted to pinyon. The most common principal hosts are *Pinus edulis* (Arizona, Colorado, New Mexico, Texas, and Utah) and *P. monophylla* (California, Nevada). A second set of pinyons including *P. californiarum*, *P. cembroides*, *P. discolor*, and *P. quadrifolia* are also classed as principal hosts even though the mistletoe is not common in their distributions. Infestations occur locally on *P. californiarum* in the Mojave Desert Ranges of New York Mountains, Providence Mountains, Joshua Tree National Monument (subsp. *californiarum*), and Southwest mountains of Zion National Park, Black Hole, and central Arizona (subsp. *fallax*). *Pinus cembroides* is parasitized only in the Davis Mountains, Texas. *Pinus discolor* is parasitized only at Fort Bayard and the Mule Mountains, New Mexico. *Pinus quadrifolia* is parasitized in the Sierra Juárez and Sierra San Pedro Mártir of Baja California and Laguna Mountains, California.

Distribution. United States (California, Nevada, Utah, Colorado, Arizona, New Mexico, and Texas) and Mexico (Baja California Norte). *Arceuthobium divaricatum* occurs in eastern and southern California (the White and Inyo Mountains, the Mount Pinos area, the San Bernardino Mountains, and the Mojave Desert Ranges), the southern three-fourths of Nevada and Utah, western Colorado, Arizona (except far southwest), New Mexico (except far northeast), and south to the Davis Mountains (western Texas). In Mexico, it is known only in northern Baja California. The northernmost population of which we are aware is in the Pilot Range (Box Elder, Utah). Kuijt (1960a) identifies several the scattered populations of this parasite in California; its distribution is probably more common than indicated by collections. *Arceuthobium divaricatum* and *Phoradendron juniperinum* commonly infest the two dominant species respectively of pinyon-juniper woodlands of the Southwestern United States, especially at the Grand Canyon (Hreha and Weber 1979). Distribution maps are published for Colorado, Utah, and New Mexico (see Hawksworth and Wiens 1996). Elevational range is from 1,200 m near Sedona, Arizona to 3,000 m in the San Mateo Mountains of New Mexico.

Discussion. The witches' brooms induced by this dwarf mistletoe are often poorly developed and not conspicuous because of the stunted habit of even healthy trees. Our observations suggest that witches' brooms are more consistent in *Pinus edulis* than in *P. monophylla*. Shoots of the mistletoe are often long, slender, and spreading, especially the staminate plants

that also tend to have relatively few flowers per shoot. *Arceuthobium divaricatum* is the only dwarf mistletoe of pinyon in the United States. Mathiasen and others (2002a) summarize information on this mistletoe.

11. *Arceuthobium douglasii* Douglas-fir Dwarf Mistletoe

Arceuthobium douglasii Engelm. in U.S. Geographical Survey West of 100th Meridian (Wheeler Report) 6:253, 1878.

Description. Mean shoot height 2 (maximum 8) cm, olive green, branches flabellate (fig. 4-3). Basal diameter of dominant shoots 1.0 to 1.5 (mean 1) mm. Third internode 2 to 6 (mean 3.6 ± 1.2) mm long, 1.0 mm wide, length/width ratio 3.6:1. Flowers usually axillary in pairs, occasionally borne on pedicel-like segments. Staminate flowers 2.0 mm long, 2.3 mm across; perianth mostly three-merous (occasionally four- or two-merous); segments rounded at the apex, without a keel, inner surface reddish to purple, lower surface same color as shoots, about 1.0 mm long, 1.0 mm wide. Pistillate flowers 1.5 mm long, 1.5 mm across. Mature fruit olive-green 3.5 to 4.5 (mean 4) mm long, 1.5 to 2.0 mm wide, obovate; proximal portion 2.5 mm long. Seeds 2.4 by 1.1 mm.

Phenology. Staminate meiosis in September, pistillate meiosis in April. Peak anthesis is usually in April or May, but with marked latitudinal variation—March in Mexico, late April to early May in Arizona and New Mexico, late May in Colorado, Utah, and Oregon, and early to mid-June in Washington, northern Idaho, and Montana. Fruit maturity is more uniform throughout the distribution, however, usually from late August to late September; maturation period averages 17 to 18 months. The seeds germinate in March.

Hosts. The principal and only commonly infected host is *Pseudotsuga menziesii*. Both var. *menziesii* (Washington, Oregon, and California) and var. *glauca* (from British Columbia through the Rocky Mountains to Central Mexico) are parasitized, although it is much more common on var. *glauca*. Where associated with infected *Pseudotsuga menziesii*, *Abies amabilis* is occasionally infected. Rare hosts are *Abies concolor*, *A. grandis*, *Picea pungens*, and *P. engelmannii*. Mathiasen (1999) reports that the two taxa *Abies lasiocarpa*, a secondary host (66 percent infected), and *Abies bifolia*, an occasional host (15 percent infected) differed significantly in susceptibility to *Arceuthobium douglasii* on plots where the principal host was over 90 percent infected.

Distribution. Canada (British Columbia), United States (Washington, Idaho, Montana, Oregon, California, Nevada, Utah, Colorado, Arizona, New Mexico, and Texas) and Mexico (Chihuahua, Durango, Coahuila, and Nuevo León). *Arceuthobium douglasii*

has the greatest latitudinal range (3,000 km) of any species in the genus. This dwarf mistletoe is common in eastern Washington, eastern Oregon, Idaho, western Montana, Idaho, Utah, Colorado, and New Mexico. It is rare in Nevada (Wheeler Peak), Wyoming (Teton), and Texas (Guadalupe Mountains). Marshall and Filip (1999) relate the occurrence of this mistletoe to stand and ecological relations in Oregon. The distribution of the dwarf mistletoe in Mexico is poorly known, and it is probably more widespread than suggested by a few available records from Chihuahua, Coahuila, Durango, and Nuevo León. Distribution maps of *Arceuthobium douglasii* are published for British Columbia, Montana, Utah, Colorado, New Mexico, and California (see Hawksworth and Wiens 1996). The altitudinal range of this dwarf mistletoe is correlated with latitude; it occurs as low as 300 m near Lytton (British Columbia) and as high as 3,250 m on Cerro Potosí (Nuevo León).

Discussion. This dwarf mistletoe is the smallest in Western North America, but its typically systemic mode of infection produces large witches' brooms and causes severe growth loss and mortality in *Pseudotsuga menziesii* (Tinnin and others 1999). Brooms provide special wildlife habitat for foraging, resting, and nesting (see chapter 5). Hadfield and others (2000) and Schmitt (1997) discuss the biology, ecology, and management of this mistletoe.

12. *Arceuthobium durangense* Durangan Dwarf Mistletoe

Arceuthobium durangense (Hawksw. & Wiens) Hawksw. & Wiens, *Phytologia* 66:7, 1989.
=*A. vaginatum* subsp. *durangense*.

Description. Mean shoot height 20 to 30 (50) cm, bright orange; older shoots becoming pendulous. Basal diameter of dominant shoots 4 to 8 (mean 6) mm. Third internode 9 to 22 (mean 17.9 ± 4.1) mm long, 3.5 to 6.0 (mean 4.5) mm wide, length/width ratio 3.3:1. Internodes often slightly swollen at base. Staminate flowers 2.5 mm long, 2.5 mm across, segments 1 mm long, 1 mm wide. Mature fruit 7 by 3.5 mm; bluish; proximal portion 4 mm long. Seeds 4 by 1.5 mm.

Phenology. Time of meiosis unknown (probably February). Anthesis usually in April. Fruits mature from mid-July to September of the year following pollination; maturation period averages 15 to 18 months.

Hosts. *Pinus douglasiana*, *P. durangensis*, *P. michoacana*, *P. montezumae*, and *P. pseudostrobus* are the principal hosts. *Pinus herrerae* is occasionally parasitized when it occurs near infected principal hosts. The host status of *Pinus oocarpa* needs confirmation.

Distribution. Mexico (Durango, Sinaloa, and Jalisco). This rather local dwarf mistletoe occurs on the western escarpment of the Sierra Madre Occidental (Durango,

Sinaloa, and perhaps Nayarit) and in the Sierra de Quilla (Jalisco). Elevational range is 1,450 to 2,750 m.

Discussion. Although previously referred to as a subspecies of *Arceuthobium vaginatum*, we now recognize this dwarf mistletoe as a distinct species. *Arceuthobium durangense* is not sympatric with *A. vaginatum* and differs by its larger, bright orange shoots, distinct branching pattern, and larger fruit.

13. *Arceuthobium gillii* Chihuahua Pine Dwarf Mistletoe

Arceuthobium gillii Hawksw. & Wiens, *Brittonia* 16:22, 1964.

=*A. vaginatum* subsp. *cryptopodum*.

Description. Mean shoot height 8 to 15 (maximum 25) cm, greenish-brown, branches flabellate. Basal diameter of dominant shoots 2.5 to 8.0 (mean 4) mm. Third internode 5 to 18 (mean 10.7 ± 3.4) mm long, 2.0 to 4.5 (mean 2.8) mm wide, length/width ratio 3.8:1. Staminate flowers 3.5 mm long, 2.5 to 4.0 (mean 3.2) mm across. Pistillate flowers 1.5 mm long, 1 mm across. Mature fruit 4 to 5 mm long, 2 to 3 mm wide, the proximal portion of fruit conspicuously glaucous. Seeds 3.1 by 1.4 mm.

Phenology. Meiosis in September. Anthesis usually in March and April. Fruits mature in October of the year following pollination; maturation period averages 19 months, the longest in the genus. Seed germination begins in April.

Hosts. The principal and only commonly infected hosts are *Pinus leiophylla* var. *chihuahuana*, *P. lumholtzii*, and *P. herrerae*. Although *Pinus leiophylla* var. *leiophylla* is a principal host, it is not common within the range of *Arceuthobium gillii*. In western Chihuahua, this dwarf mistletoe rarely parasitizes *Pinus arizonica* var. *arizonica* and *P. cooperi*.

Distribution. United States (Arizona and New Mexico) and Mexico (Chihuahua, Durango, Sinaloa, and Sonora). This dwarf mistletoe occurs in southeastern Arizona (Santa Catalina, Rincon, Santa Rita, Huachuca, and Chiricahua Mountains) and the Animas Mountains in southwestern New Mexico. It is most common in western Chihuahua, but it is also distributed in adjacent northern and eastern Sonora, northern Durango, and northeastern Sinaloa. Elevational range is from 1,700 m in southern Arizona to 2,650 m in southern Chihuahua.

Discussion. This dwarf mistletoe has long been confused with *Arceuthobium vaginatum* subsp. *cryptopodum*, but it differs in host preference, phenology, and its conspicuously glaucous fruits. These two dwarf mistletoes are usually separated by at least 300 m of elevation in Arizona and New Mexico. Where they co-occur in central Chihuahua, there is no evidence of hybridization. A characteristic feature of *Arceuthobium gillii* is its strong sexual dimorphism—staminate plants

tall and openly branched and pistillate plants small and densely branched. This dwarf mistletoe causes open, nonsystemic witches' brooms and serious mortality in *Pinus leiophylla* var. *chihuahuana* and *P. lumholtzii*.

14. *Arceuthobium globosum*

Arceuthobium globosum Hawksw. & Wiens, Brittonia 17:223, 1965.

Description. Shoot height 20 to 50 (maximum 70) cm, yellow to greenish, branches flabellate. Basal diameter of dominant shoots 3 to 48 mm. Third internode 4 to 37 mm long, 2 to 24 mm wide. Staminate flowers about 3.5 to 5.0 mm long, 3.0 to 3.5 mm across; perianth three- or four-merous; same color as shoots; segments 1.3 mm long, 1.0 mm wide. Pistillate flowers 1.5 mm long, 1.5 mm across. Mature fruit 5 to 7 mm long, 3 to 4 mm wide; proximal portion 3.5 mm long, with pedicels 4.0 to 5.0 mm long. Seeds 5 by 2 mm.

Hosts. Common on yellow pine.

Discussion. Hawksworth and Wiens (1972) note considerable variation within collections determined as *Arceuthobium globosum*. Subsequent studies by Hawksworth and Wiens (1977) and Wiens and Shaw (1994) have resulted in the segregation of *Arceuthobium globosum* (*sensu lato*) into five taxa:

- *Arceuthobium aureum* subsp. *aureum* (Guatemala)
- *Arceuthobium aureum* subsp. *petersonii* (Southern Mexico)
- *Arceuthobium globosum* subsp. *globosum* (Northwestern Mexico)
- *Arceuthobium globosum* subsp. *grandicaule* (Central Mexico and Central America)
- *Arceuthobium hawksworthii* (Central America)

14a. *Arceuthobium globosum* subsp. *globosum* Rounded Dwarf Mistletoe

Description. Shoots 15 to 20 (maximum 50) cm high, bright yellow, branches flabellate. Basal diameter of dominant shoots 3 to 10 (mean 7) mm. Third

internode 19 mm long, 4 mm wide. Staminate flowers 4 mm wide. Mature fruit 5 by 2.5 mm. Seeds 4 by 2 mm.

Phenology. Anthesis usually March and April. Fruits mature June and July; maturation period averages 15 to 16 months.

Hosts. The principal hosts are *Pinus cooperi*, *P. durangensis*, and *P. engelmannii*. *Pinus arizonica* is occasionally parasitized; *Pinus teocote* is a rare host.

Distribution. Mexico (Sonora, Chihuahua, Durango, and Jalisco). This subspecies is widely distributed in the pine forests of the Sierra Madre Occidental from northwestern Chihuahua and adjacent Sonora, through Durango to northern Jalisco. Elevational range is 2,300 to 2,800 m.

Discussion. This dwarf mistletoe is characterized by its bright yellow, globose clusters, and absence of witches' broom formation.

14b. *Arceuthobium globosum* subsp. *grandicaule* Large-Stemmed Dwarf Mistletoe

Arceuthobium globosum Hawksw. & Wiens subsp. *grandicaule* Hawksw. & Wiens, Brittonia 29:413, 1977.

Description. Shoots 18 to 50 (maximum 70, mean 25) cm tall, yellow green, typically dark at the base of older shoots, branches flabellate. Basal diameter of dominant shoots 10 to 48 (mean 17) mm. Third internode 14 to 37 (mean 27) mm long, 3 to 20 (mean 7) mm wide. Staminate flowers 5 mm wide, four-merous. Mature fruits 6 to 7 mm long, 3.5 mm wide. Seeds 5 by 3 mm.

Phenology. Meiosis in December. Anthesis from January through May, with peak March and April. Fruits maturing July through October; maturation period averages 16 to 18 months. Seed dispersal from early July to early November, with a peak from mid-August to mid-September (Escudero and Cibrián 1985).

Hosts. This subspecies has one of the broadest host ranges of any dwarf mistletoe. It infects at least 12 species of Mexican pines, all of which appear to be about equally susceptible (but see Valdivia 1964): *Pinus douglasiana*, *P. durangensis*, *P. hartwegii*, *P.*

Key to the Subspecies of *Arceuthobium globosum*

1. Plants yellowish; shoots usually 15 to 20 (maximum 50) cm tall, less than 1 cm diameter at the base; witches' brooms not formed; shoots usually only on the host branches; northern Mexico 14a. *A. globosum* subsp. *globosum*
1. Plants greenish to yellow-green, typically dark at the base of older shoots; shoots usually 25 to 40 (maximum 70) cm tall, greater than 1 cm diameter at the base; witches' brooms usually induced; shoots on branches, but also frequently on the lower main trunks; central and southern Mexico to the highlands of western Guatemala 14b. *A. globosum* subsp. *grandicaule*.

lawsonii, *P. maximinoi*, *P. michoacana*, *P. montezumae*, *P. patula*, *P. pringlei*, *P. pseudoarceuthobium*, *P. rudis*, and *P. teocote*.

Distribution. Mexico (Jalisco, Michoacán, Mexico, Hidalgo, Distrito Federal, Guerrero, Puebla, Tlaxcala, Veracruz, and Oaxaca), Guatemala, and Honduras. *Arceuthobium globosum* subsp. *grandicaule* is the most abundant dwarf mistletoe in Central Mexico, common in western Guatemala, and recently reported in Honduras (Melgar and others 2001). Elevational range is 2,450 to 4,000 m (Hernandez and others 1992).

Discussion. This subspecies has large shoots reaching a height of 70 cm and with a basal diameter of 5 cm. Valdivia (1964) reports *Arceuthobium globosum* is present on nearly 40 percent of 400,000 ha of pine forest in northeastern Michoacán. Vázquez (1994a) discusses the importance and sampling method for this mistletoe.

15. *Arceuthobium guatemalense* Guatemalan Dwarf Mistletoe

Arceuthobium guatemalense Hawksw. & Wiens, Brittonia 22:267, 1970.

Description. Mean shoot height 1 to 3 cm on systemic witches' brooms, but shoots on nonsystemic infections up to 7 cm high; living shoots greenish to purple, yellow to brown when dried, branches flabellate. Basal diameter of dominant shoots 2.0 to 2.5 mm. Third internode 8 to 15 (mean 11.4 ± 2.8) mm long, 1.5 to 2.0 (mean 1.7) mm wide; length/width ratio 6.7:1. Staminate flowers 2 mm across; perianth two- or three-merous, segments 0.9 mm long, 0.7 mm wide. Mature fruit 3.5 to 4.0 mm long, 1.5 to 2.0 mm wide; distal portion 1.2 mm long; dark green, glabrous, with a slightly swollen ring at the base of the fruit where it joins the pedicel. Seeds 2.0 by 0.8 mm.

Phenology. Time of meiosis unknown. Anthesis apparently in August and early September. Fruits mature in September; maturation period about 12 to 13 months. Seed germination in September.

Hosts. Known only on *Pinus ayacahuite* var. *ayacahuite*.

Distribution. Mexico (Oaxaca and Chiapas) and Guatemala. This distinctive species is known only from the high mountains of Western Guatemala and Southern Mexico. Elevational range is poorly known; our collections are from 2,450 to 3,100 m.

Discussion. The consistent formation of systemic witches' brooms is a distinctive characteristic of this species; brooms sometimes measure 3 to 5 m across. An unusual feature of these witches' brooms is that the shoots of the dwarf mistletoe are consistently formed on 1-year-old host shoots and, in some cases, on the current year's growth. This species causes extensive

damage and considerable mortality to *Pinus ayacahuite*.

16. *Arceuthobium hondurensis* Honduran Dwarf Mistletoe

Arceuthobium hondurensis Hawksworth & Wiens, Brittonia 22: 267, 1970.

=*Arceuthobium nigrum*

Description. Mean shoot height ca. 14 (max. 21) cm, olive brown to grayish green, markedly glaucous; branches flabellate. Basal diameter of dominant shoots 3 to 9 (mean 5) mm; nodes of older shoots swollen; lateral branches of staminate plants at nearly right angles to the axis of the main shoot; third internode 7 to 12 (mean 9.1 ± 1.5) mm long, 2.5 to 4.0 (mean 3.2) mm wide; length/width ratio 6.1:1. Staminate flowers approximately 2.5 mm across; inner surface reddish, lower surface the same color as the shoots; perianth usually three-merous (sometimes two- or four-merous), segments approximately 1.2 mm long, 0.8 mm wide; nectary with two large and one small lobe. Pistillate flowers with stigmas exerted approximately 0.5 mm, with copious stigmatic exudate at anthesis. Mature fruit 5.5 by 3.0 mm, greenish glaucous; proximal portion approximately 4.0 mm long. Seeds approximately 3.1 by 1.5 mm. n = 14.

Phenology. Meiosis in August or early September. Anthesis and fruit maturity in September; maturation period averages ca. 12 months.

Hosts. The only known hosts are *Pinus oocarpa* var. *oocarpa*, var. *ochoterenia*, and *P. tecunumanii* (Mathiasen and others 1998, 2000a).

Distribution. Honduras, Mexico (Chiapas, Oaxaca), and possibly El Salvador. The distribution of this species is poorly known; only four collections are known from Honduras and three from Mexico (Mathiasen and others 2001, 2002b). Elevational range is poorly known, probably between 1,200 and 1,650 m.

Discussion. Collections from Mexico had been previously confused with *Arceuthobium nigrum* (Mathiasen and others 2001, 2002b). *Arceuthobium hondurensis* and *A. bicarinatum*, a species endemic to Hispaniola, are both rare species threatened by deforestation and are distributed at the southern limits of dwarf mistletoes and pines in the New World.

17. *Arceuthobium laricis* Larch Dwarf Mistletoe

Arceuthobium laricis (Piper) St. John, Flora of Southeast Washington and Adjacent Idaho: 115, 1937.

=*A. campylopodium* f. *laricis*.

Description. Mean shoot height 4 (maximum 6) cm, mostly dark purple, branches flabellate. Basal diameter of dominant shoots 1.5 to 3.0 (mean 2) mm. Third internode 5 to 14 (mean 8.0 to 2.0) mm long, 1.0 to 2.5 (mean 1.3) mm wide, length/width ratio 6.1:1.

Staminate flowers 2.7 mm across; perianth mostly three-merous (sometimes four-merous); segments 1.4 mm long, 1.1 mm wide. Pistillate flowers 1 mm long, 1 mm across. Mature fruit 4.5 by 2.5 mm; proximal portion 2.5 mm long.

Phenology. Meiosis in June. Peak anthesis from mid-July to late August, with extremes from early July to early September. Fruits usually mature in September, with extremes from early August to early October; maturation period averages 13 to 14 months.

Hosts. Mathiasen (1998a) revises the host relations of *Arceuthobium laricis* based on field studies and previous reports (Mathiasen and others 1995a). The principal and commonly infected host is *Larix occidentalis*. *Tsuga mertensiana* and *Pinus contorta* var. *latifolia* are secondary hosts. Occasional hosts are *Abies lasiocarpa* and *P. ponderosa* var. *ponderosa*; but *Abies amabilis* and *Pinus albicaulis* are tentatively classified occasional as well. *Abies grandis*, *Picea engelmannii*, *Pinus monticola*, and *Tsuga heterophylla* are rare hosts. Extra-limital hosts and artificially inoculated hosts include *Larix decidua*, *L. leptolepis*, *Picea abies*, *P. glauca*, *Pinus banksiana*, *P. resinosa*, and *P. sylvestris*. (Hawksworth and Wiens 1996). Although natural population of the high-elevation *Larix lyallii* appear not to be infested, this species may become infected if planted in a suitable environment (Mathiasen and others 1995b).

Distribution. Canada (British Columbia) and the United States (Washington, Oregon, Idaho, and Montana). *Arceuthobium laricis* occurs generally throughout the range of its principal host, *Larix occidentalis*, in southern British Columbia, east of the Cascade Mountains in Washington and northern Oregon, northern and central Idaho, and western Montana. Distribution maps of *Arceuthobium laricis* are published for British Columbia and Montana (see Hawksworth and Wiens 1996). Elevational range is 650 to 2,250 m.

Discussion. *Arceuthobium laricis* has long been recognized as a serious pathogen of *Larix occidentalis* (Weir 1916a). Infection usually results in the formation of heavy but compact brooms. Because larch branches are brittle, larger brooms are readily broken off. Surveys in the Inland Empire (eastern Washington, northern Idaho, and western Montana) show that most larch stands are infested and infection rates are commonly high (Hawksworth and Wiens 1996). Mathiasen (1998b) reports that initial infection of *Larix occidentalis* can be when the plants are quite young; Mathiasen recommends that, to avoid spread, removal of the infected overstory should be done before regeneration is 7 years old or 1 m tall. Other publications of interest to managers include those by Beatty and others (1997), Taylor (1995), Wicker and Hawksworth (1991), and Weir (1961a).

18. *Arceuthobium littorum*

Coastal Dwarf Mistletoe

Arceuthobium littorum Hawksw., Wiens & Nickrent, Novon 2:206, 1992.

=*A. campylopodum* f. *typicum*

=*A. occidentale*

Description. Shoots 8 to 20 (mean 12) cm, brown to yellow-brown, branches flabellate. Basal diameter of dominant shoots 2 to 5 (mean 3.5) mm. Third internode 10 to 20 (mean 15) mm long, 2 to 2.5 (mean 2.2) mm wide, mature fruits 4 to 5 mm long; staminate flowers mostly four-merous.

Phenology. Meiosis occurs in July, flowering begins in August, with peak anthesis probably occurring in September. Seed dispersal probably peaks in September or October.

Hosts. *Pinus radiata* and *P. muricata* are the primary hosts. It occasionally infects Bolander pine (*Pinus contorta*) where this tree is associated with infected *P. muricata*.

Distribution. United States (California: Mendocino, Sonoma, Marin, Monterey, and San Luis Obispo). *Arceuthobium littorum* is restricted to a region within 10 km of the Pacific Ocean from Fort Bragg south to Point Reyes on *Pinus muricata* and along the central coast at Monterey and Cambria on *P. radiata*. It also parasitizes the small population of *P. muricata* associated with infected *P. radiata* at Huckleberry Hill, Monterey, and is established at three locations by transplanting infected *Pinus radiata*—Stanford Arboretum, North Berkeley, and Hillsborough. Elevational range is from sea level to 250 m.

Discussion. Previously, Hawksworth and Wiens (1972) include *Arceuthobium littorum* in *A. occidentale*. A primary feature for distinguishing *A. littorum* from *A. occidentale* is the production of large, nonsystemic witches' brooms.

19. *Arceuthobium microcarpum*

Western Spruce Dwarf Mistletoe

Arceuthobium microcarpum (Engelm.) Hawksw. & Wiens, Brittonia 22:268, 1970.

=*A. campylopodum* f. *microcarpum*.

Description. Mean shoot height 5 (maximum 11) cm, green to purple, branches flabellate. Basal diameter of dominant shoots 1.5 to 3.0 (mean 2) mm. Third internode 5 to 16 (mean 9.3 ± 2.2) mm long, 1 to 2 (mean 1.5) mm wide, length/width ratio 6.2:1. Staminate flowers 2.3 mm across; perianth mostly three-merous (rarely four-merous); segments 1.2 mm long, 1.0 mm wide. Pistillate flowers 1 mm long, 1 mm across. Mature fruit 3.5 by 2.0 mm; proximal portion 2.5 mm long. Seeds 2.4 by 1.0 mm.

Phenology. Meiosis in July. Anthesis in mid-August to early September, with extremes from late July to late September. Fruits mature in September, with

extremes from late August to early October; maturation period averages 12 to 13 months.

Hosts. This dwarf mistletoe is a common and serious pathogen only on *Picea engelmannii* and *P. pungens*. On the San Francisco Peaks of northern Arizona, however, it also parasitizes *Pinus aristata*. *Pinus strobiformis* and *Abies lasiocarpa* var. *arizonica* are rarely infected even where they are associated with infected principal hosts. If populations of a spruce in southern Arizona were determined to be *Picea mexicana* rather than *P. engelmannii* (Taylor and others 1994), this species would be an additional host.

Distribution. United States (Arizona and New Mexico). *Arceuthobium microcarpum* has one of the more restricted distributions in the genus. In Arizona, the parasite occurs on the North Rim of the Grand Canyon, the San Francisco Peaks and nearby Kendrick Peak, White Mountains, and Pinaleno Mountains. In New Mexico, this dwarf mistletoe is present at several locations in the Mogollon Mountains and in the Sacramento Mountains. Elevational range is 2,400 to 3,150 m.

Discussion. This localized species in Arizona and New Mexico is characterized by its near exclusive occurrence on spruce (Hawksworth and Graham 1963a). This species induces small, dense witches' brooms. Heavily infected trees bear hundreds of such witches' brooms. This dwarf mistletoe causes heavy mortality in stands of *Picea pungens* and, to a lesser extent, of *P. engelmannii*.

20. *Arceuthobium monticola*

Western White Pine Dwarf Mistletoe

Arceuthobium monticola Hawksw., Wiens & Nickrent, *Novon* 2:205, 1992.

=*A. campylopodum* f. *blumeri*

=*A. californicum*

Description. Shoots 5 to 10 (mean 7) cm tall, dark brown, branches flabellate. Basal diameter of dominant shoots 2 to 4 (mean 3) mm; third internode 8 to 15 (mean 12) mm long, 1.5 to 2.0 mm wide. Staminate flowers mostly three-merous. Mature fruits 4.0 to 4.5 mm long, 2.0 to 2.5 mm wide.

Phenology. The period of anthesis is poorly known but apparently occurs late July through August. Fruits mature October and November; maturation period averages 15 months.

Hosts. The principal and only commonly infected host is *Pinus monticola*. *Pinus lambertiana* is a secondary host; *Picea breweriana* an occasional host; and *Pinus jeffreyi* a rare host.

Distribution. United States (Oregon, California). *Arceuthobium monticola* is a local endemic in the Klamath Mountains of southwestern Oregon (Coos, Curry, and Josephine) and the Siskiyou Mountains of adjacent northwestern California (Del Norte and possibly Siskiyou). Elevational range is 700 to 1,900 m.

Discussion. Hawksworth and Wiens (1972) include this taxon under *Arceuthobium californicum*; but subsequent field and laboratory studies demonstrate that it is a distinct species and not apparently sympatric with *A. californicum*. *Arceuthobium monticola* differs from *A. californicum* in its much darker shoot color, later flowering and seed dispersal periods, and host preference for *Pinus monticola* rather than *P. lambertiana*.

21. *Arceuthobium nigrum*

Black Dwarf Mistletoe

Arceuthobium nigrum (Hawksw & Wiens) Hawksw. & Wiens, *Phytologia* 66:9, 1989.

=*A. gillii* subsp. *nigrum*.

Description. Mean shoot height 15 to 35 (45) cm, dark brown to black. Basal diameter of dominant shoots 3 to 8 (mean 5) mm. Third internode 5 to 19 (mean 10.8 ± 3.8) mm long, 2.5 to 6.0 (mean 3.7) mm wide (six collections), length/width ratio 2.9:1. Staminate flowers 3 mm long, 3.5 mm across. Mature fruit 6 to 9 (mean 7) mm long, 3.5 mm wide, proximal portion 2 to 3 mm. Seeds 3.5 by 1.3 mm.

Phenology. This dwarf mistletoe is unusual in *Arceuthobium* by having flowering periods in March and April and September and October. Seed dispersal occurs in September, presumably from flowers pollinated the previous year; when the seeds from the March through April pollinations mature is unknown.

Hosts. This dwarf mistletoe is most common on the principal hosts *Pinus leiophylla* vars. *leiophylla*, var. *chihuahuana*, and *P. lumholtzii*. *Pinus lawsonii*, *P. oaxacana*, *P. patula*, *P. teocote* are also highly susceptible and rated as principal hosts. *Pinus montezumae* and *P. pseudostrobus* are occasional hosts. *Pinus arizonica* var. *arizonica* and *P. cooperi* are rare hosts.

Distribution. Mexico (Durango, Zacatecas, Guanajuato, Querétaro, Hidalgo, Michoacán, Mexico, Tlaxcala, Puebla, Veracruz, Oaxaca, Chiapas) and possibly Western Guatemala. This mistletoe is reported from the northeastern slope of Volcán la Malintzi (Malinche), Tlaxcala (Hernandez and others 1992), and is common on pines in Central and Eastern Mexico. Elevational range is 1,800 to 2,800 m.

Discussion. *Arceuthobium nigrum* resembles *A. gillii*. Both species possess markedly glaucous fruits, strong sexual dimorphism (open, divaricate branching in staminate plants versus densely branched in pistillate plants), and parasitize similar hosts. Although *A. nigrum* was previously classed as a subspecies of *A. gillii*, specific status is warranted (Hawksworth and Wiens 1989). *Arceuthobium nigrum* is a larger plant than *A. gillii* and has dark green to black shoots 15 to 35 (maximum 45) cm high, whereas those of *A. gillii* are only 8 to 15 (maximum 25) cm tall, and colored greenish brown. *Arceuthobium nigrum* also has the two flowering periods (March and April, and September and October) compared to only one for

A. gillii (March and April). To our knowledge, these species are not sympatric.

22. *Arceuthobium oaxacanum*

Oaxacan Dwarf Mistletoe

Arceuthobium oaxacanum Hawksw. & Wiens, *Phytologia* 66:7, 1989.

=*A. rubrum*

Description. Shoots 8 to 20 (mean 12) cm tall, pale brown to reddish, branches flabellate. Basal diameter of dominant shoots 2 to 4 (mean 3) mm. Third internode 10 to 17 (mean 12) mm long and 2 to 3 mm wide.

Phenology. Anthesis in July. Fruits mature in August of the following year; maturation period averages 13 months.

Hosts. *Pinus lawsonii*, *P. michoacana*, and *P. pseudostrobus* are principal hosts; all are about equally susceptible. *Pinus oaxacana* is an occasional host.

Distribution. Mexico (Oaxaca). This species is known from only three localities (two south of Miahuatlán and one near Ixtlán). Elevational range is 2,000 to 2,200 m.

Discussion. Hawksworth and Wiens (1989) recognize *Arceuthobium oaxacanum* as a distinct species previously considered an extreme disjunct (about 1,200 km) of *A. rubrum*. In general, *A. oaxacanum* is a larger, lighter colored, more openly branched plant and causes larger witches' brooms than *A. rubrum*. Furthermore, *Arceuthobium oaxacanum* principally parasitizes *Pinus lawsonii*, *P. michoacana*, *P. pseudostrobus*, and occasionally *P. oaxacana*; none of these pines occurs within the range of *A. rubrum*.

23. *Arceuthobium occidentale*

Digger Pine Dwarf Mistletoe

Arceuthobium occidentale Engelm., U.S. Geographical Survey West of 100th Meridian (Wheeler Report) 6:375, 1878.

=*A. campylopodum* f. *typicum*.

Description. Mean shoot height 8 (maximum 17) cm, yellowish, glaucous, branches flabellate. Basal diameter of dominant shoots 1.5 to 5.0 (mean 2) mm. Third internode 7 to 18 (mean 12.7±2.0) mm long, 1.5 to 3.5 (mean 1.8) mm wide, length/width ratio 7.1:1. Staminate flowers 3.0 mm across; perianth three- or four-merous; segments 1.5 mm long, 1.0 mm wide. Mature fruit 4.5 by 3.0 mm; proximal portion 3.0 mm long. Seeds 2.6 by 1.0 mm.

Phenology. Meiosis in August. Peak anthesis from late September to late November, extremes from early September to early December. Most fruits mature from mid-October to mid-January, with extremes from late September to early February; maturation period averages 13 months.

Hosts. *Pinus sabiniana* is the most common and only principal host. *Pinus coulteri* and *P. attenuata* are secondary hosts where they occur with infected *P. sabiniana*. Whether the occasional hosts *Pinus ponderosa* and *P.*

jeffreyi are infected, however, varies by location and association with their principal dwarf mistletoe, *A. campylopodum*. In the California Coast Range (outside the distribution of *Arceuthobium campylopodum*), these pines are commonly infected where they are occur with infected *P. sabiniana*. In the Sierra Nevada (where *A. campylopodum* occurs), they are seldom infected even under infected *P. sabiniana*. Extralimital and hosts by artificial inoculation are *Pinus banksiana*, *P. bungeana*, *P. caribaea*, *P. halepensis*, *P. palustris*, *P. pinea*, *P. radiata*, *P. sylvestris*, *P. thunbergii*, *P. torreyana*, and *P. virginiana*.

Distribution. United States (California). This dwarf mistletoe is a California endemic and commonly occurs on *Pinus sabiniana* throughout the foothills and low mountains surrounding the Central Valley of California and along the Coast Ranges from Mount Pinos (Ventura) north to Mendocino. Elevational range is about 30 to 1,200 m in the southern Sierra Nevada.

Discussion. Even though *Pinus sabiniana* typically occurs in open, savanna-like forests, *Arceuthobium occidentale* is widely distributed in these stands. Isolated, infected trees more than 100 m away from the closest infected trees are sometimes found, which suggests that bird vectors (possibly phainopepla) are involved in long-distance seed transport of this dwarf mistletoe.

24. *Arceuthobium pendens*

Pendent Dwarf Mistletoe

Arceuthobium pendens Hawksw. & Wiens, *Brittonia* 32:348, 1980.

Description. Mean shoot height 15 (maximum 22) cm, light green, branches flabellate. Basal diameter of dominant shoots 1.5 to 3.5 (mean 2) mm. Third internode 12 to 20 (mean 16) mm long, 1 to 2 (mean 1.5) mm wide. Staminate flowers 2.5 mm across, three-merous.

Phenology. Peak anthesis possibly in September. Fruit maturity from June to September (Cházaro and Oliva 1987a).

Hosts. Known only on *Pinus discolor* (San Luis Potosí) and *P. cembroides* subsp. *orizabensis* (Veracruz and Puebla).

Distribution. Mexico (San Luis Potosí, Veracruz, and Puebla). The distribution of this dwarf mistletoe is poorly known (Cházaro and Oliva 1987a) from only Sierra San Miguelito (San Luis Potosí) and Frijol Colorado (Veracruz), and on the nearby Cerro Pizzaro (Puebla). Elevational range is 2,250 to 2,700 m.

Discussion. The species exhibits striking sexual dimorphism—pistillate plants are densely branched and typically less than 8 cm tall, and mature staminate plants are openly branched and pendant, 15 to 20 cm long. A unique feature of this species, at least in one population, is that only the staminate plants appear to induce systemic witches' brooms. This dwarf mistletoe likely occurs in other areas and on other pinyons.

25. *Arceuthobium pusillum*

Eastern Dwarf Mistletoe

Arceuthobium pusillum Peck, Transactions Albany Institute 7:191, 1872.

=*A. minutum*

=*A. abigenium*.

Description. Mean shoot height 1 (maximum 3) cm, green to brown, usually without secondary branching, but flabellate when occurs. Basal diameter of dominant shoots 1.0 mm. Third internode 1 to 4 (mean 1.9 ± 0.8) mm long, 0.5 to 1.5 (mean 1.0) mm wide, length/width ratio 1.9:1, often markedly wider at top than at base. Pistillate shoots often longer than the staminate. Staminate flowers 1.7 to 2.2 (mean 1.8 mm) across; perianth mostly three-merous (sometimes two- or four-merous); segments 0.8 mm long, 0.7 mm wide. Mature fruit 3.0 mm long, 1.25 to 1.75 mm wide (mean 1.5 mm); proximal portion 2.0 mm long. Seeds 2.0 by 0.9 mm.

Phenology. Staminate meiosis in September, pistillate meiosis in May. Anthesis usually in April or May, with extremes from late March to June. Fruits mature in September or early October of the same year as pollination; maturation period averages 5 months, perhaps the shortest in the genus. Seed germination mostly in May and June.

Hosts. *Arceuthobium pusillum* is most common and widely distributed on *Picea mariana*. *Picea glauca* and *P. rubens* appear to be about as susceptible as *P. mariana*, so are also principal hosts, although the dwarf mistletoe is not as common (except in some old-growth stands). *Larix laricina* is an occasional host. *Abies balsamea*, *Pinus banksiana*, *P. resinosa*, and *P. strobus* are rare hosts. *Picea pungens* is an extralimital host.

Distribution. Canada (Saskatchewan, Manitoba, Ontario, Québec, New Brunswick, Nova Scotia, Prince Edward Island, and Newfoundland) and the United States (Minnesota, Wisconsin, Michigan, New York, Pennsylvania, New Jersey, Connecticut, Massachusetts, Vermont, New Hampshire, Rhode Island, and Maine). *Arceuthobium pusillum* occurs in Canada from Hudson Bay, the Cumberland areas in eastern Saskatchewan to southern Manitoba, southern Ontario, Québec, and the Maritime Provinces including Newfoundland. Its northern limits in Ontario and Québec are poorly known. In the United States, it occurs in the northern parts of Minnesota, Wisconsin, and Michigan, northeastern Pennsylvania, extreme northwestern New Jersey, and all of New England. It is rare near the limits of its southern distribution. *Arceuthobium pusillum* occurs on several islands isolated 30 km or more from the nearest known populations of the dwarf mistletoe—Mantinicus and Monhegan Islands off the Maine Coast and Beaver Island in Lake Michigan. The numerous distribution maps published for *Arceuthobium pusillum* are identified by

Hawksworth and Wiens (1996). Elevational ranges from sea level in Maine and the Maritime Provinces to 800 m on Mount Katahdin, Maine.

Discussion. In spite of having the smallest shoots of any North American mistletoe, *Arceuthobium pusillum* is a damaging pathogen of spruce in many parts of its distribution (Singh and Carew 1989). Mortality is severe in *Picea glauca* along the Maine Coast, and the parasite is considered the most serious disease agent of *P. mariana* in the Great Lakes region. Its biology and management are discussed by Ostry and Nicholls (1979). Witches' brooms appear to be mostly of the systemic type. Shoots usually first appear in late summer or autumn as small eruptions in the bark of host branches 2 years old and mature during the third season. They flower the following spring; fruits mature by autumn. Shoots usually fall after flowering (staminate) or fruiting (pistillate), and only rarely do shoots produce a second crop of flowers. This pattern of reproduction is unique among northern temperate species of the genus. Large swellings on the main trunk are commonly induced by *Arceuthobium pusillum* in old-growth *P. rubens* in New England and New York, but such swellings have not been reported on other spruces. *Arceuthobium pusillum* has an interesting literary and historic past in Thoreau's (1858) description of the witches' broom in spruce at Walden Pond and Lucy Millington's later discovery of the mistletoe itself (Smith 1992). *Arceuthobium pusillum* is common in spruce bogs and generally absent from drier upland sites. In Québec, *A. pusillum* is apparently restricted to within 2 km of lakes or rivers. In Maine, it occurs on *P. glauca* only within 300 to 400 m of the coast. *A. pusillum* may require an uninterrupted period of high atmospheric humidity in the spring for normal growth.

26. *Arceuthobium rubrum*

Ruby Dwarf Mistletoe

Arceuthobium rubrum Hawksw. & Wiens, Brittonia 17:233, 1965.

Description. Mean shoot height 10 (maximum 18) cm, dark red, brown to blackish, branches flabellate. Staminate plants usually taller than pistillate plants. Basal diameter of dominant shoots 2 to 3 (mean 2.4) mm. Third internode 4 to 12 (mean 6.9 ± 2.7) mm long, 2 to 3 (mean 2.3) mm wide, length/width ratio 3.4:1. Staminate flowers 1.0 to 1.5 mm across; mostly three-merous; segments 0.6 mm long, 0.6 mm wide. Mature fruit 3.5 by 2.0 mm. Seeds 2.0 by 1.0 mm.

Phenology. Meiosis probably in June. Anthesis usually in July. Fruits mature from mid-July to August of the year following pollination; maturation period averages 12 to 13 months.

Hosts. Principal hosts are *P. cooperi*, *P. durangensis*, *P. engelmannii*, *P. herrerae*, and *Pinus teocote*, all of which appear to be highly susceptible.

Distribution. Mexico (Durango and Sinaloa). This species has a localized distribution in the Sierra Madre Occidental of Western Mexico. Elevational range is 2,250 to 2,900 m.

Discussion. This distinctive, slender, reddish dwarf mistletoe is apparently widespread in the mountains of Durango. As the plants dry, the red color turns to dull brown, and the apical portion of each segment becomes golden yellow. This gives dried specimens a characteristic banded appearance. The shiny fruits, a character shared only with *Arceuthobium oaxacantum*, readily distinguish this species. Another distinctive characteristic of *A. rubrum* is the exceptionally small, scarcely opened staminate flowers. The populations in the Pueblo Altares area in northern Durango, about 150 km north of the populations around El Salto, have taller, darker, and stouter shoots that superficially resemble *Arceuthobium vaginatum* subsp. *vaginatum*.

27. *Arceuthobium siskiyouense*

Knobcone Pine Dwarf Mistletoe

Arceuthobium siskiyouense Hawksw., Wiens & Nickrent, Novon 2:204, 1992.

=*A. campylopodum*

Description. Mean shoot height 8 (maximum 10) cm, dark brown, branches flabellate. Basal diameter of dominant shoots 2.0 to 2.5 mm across. Third internode 8 to 15 (mean 9) mm long, 2 mm wide. Mature fruits 3.6 by 2.1 mm.

Phenology. Peak anthesis in August. Fruits at maturation not observed.

Hosts. *Pinus attenuata* is the principal and only common host of *Arceuthobium siskiyouense*. This dwarf mistletoe rarely parasitizes *P. contorta*, *P. jeffreyi*, and *P. ponderosa* where these trees grow in association with infected *P. attenuata*.

Distribution. United States (California and Oregon). The distribution of *Arceuthobium siskiyouense* is restricted to the Klamath Mountains of southwestern Oregon (Curry and Josephine) and the Siskiyou Mountains in adjacent northwestern California (Del Norte and Siskiyou). Elevational range is 400 to 1,200 m.

Discussion. Hawksworth and Wiens (1972) include this taxon in *Arceuthobium campylopodum*, but subsequent studies demonstrate it a distinct species related to *A. campylopodum*. The two species are sympatric in several areas, and their flowering periods

partially overlap; but each maintains its own host preferences and distinctive morphologies (for example, *A. siskiyouense* does not induce witches' brooms).

28. *Arceuthobium strictum*

Unbranched Dwarf Mistletoe

Arceuthobium strictum Hawksw. & Wiens, Brittonia 17:234, 1965.

Description. Mean shoot height 7 (maximum 13) cm, pistillate shoots generally greenish yellow brown, branches flabellate. Staminate plants brownish, rarely branching. Staminate plants usually taller than pistillate plants. Basal diameter of dominant shoots 2.5 to 4.0 (mean 3.1) mm. Third internode 1 to 8 (mean 3.6 ±2.0) mm long, 1.5 to 3.5 (mean 2.3) mm wide; length/width ratio 1.6:1. Staminate flowers 3 mm across, perianth three-, four-, or five-merous (rarely six or seven-merous), segments 1.5 mm long, 1 mm wide. Mature fruit 4 by 2.5 mm. Seeds 2.5 by 1.0 mm.

Phenology. Meiosis in July. Anthesis late July through October, with peak in September. Fruits mature from mid-September to October of the year following pollination; maturation period averages 13 months.

Hosts. *Pinus leiophylla* var. *chihuahuana* is the principal host. *Pinus teocote* is an occasional host, and *P. engelmannii* is a rare host.

Distribution. Mexico (Durango). This species is known only in the Sierra Madre Occidental south and west of the city of Durango. Elevational range is 2,200 to 2,500 m.

Discussion. The most distinctive feature of this dwarf mistletoe is the lack of branching by staminate plants. The staminate shoots at anthesis become single spikes 6 to 13 cm long with numerous perianth segments (up to seven, more than any other dwarf mistletoe). The pistillate plants, in contrast, exhibit abundant secondary branching. This dwarf mistletoe causes heavy mortality in its principal host, *Pinus leiophylla* var. *chihuahuana*.

29. *Arceuthobium tsugense*

Hemlock Dwarf Mistletoe

Arceuthobium tsugense (Rosendahl) G.N. Jones, University of Washington Publications in Biology 5:139, 1936 (as *A. tsugensis*).

=*A. campylopodum* f. *tsugensis*.

Description. Mean shoot height 5 to 7 (13) (cm), greenish to reddish, darker in winter, branches

Key to the Subspecies

- 1. Parasitic primarily on *Tsuga heterophylla* or *Pinus contorta* var. *contorta*; shoots 3–13 (mean 7) cm high 29a. *A. tsugense* subsp. *tsugense*
- 1. Parasitic primarily on *Tsuga mertensiana*; shoots 3–9 (mean 5) cm high 29b. *A. tsugense* subsp. *mertensianae*

flabellate. Basal diameter of dominant shoots 1.5 to 4.0 (mean 2.0) mm. Third internode 4 to 16 (mean 9.2 \pm 2.5) mm long, 1 to 2 (mean 1.5) mm wide, length/width ratio 6.1:1. Staminate flowers 2.8 mm across; perianth three- or four-merous, segments 1.2 mm long, 1.0 mm wide. Pistillate flowers 1 mm long, 1 mm across. Mature fruit 3 by 2 mm; proximal portion 2.0 mm long.

Hosts. Mathiasen (1994) reviews the host range of the several taxa included here under *Arceuthobium tsugense* based on natural infection and artificial inoculation. His report provides the basis for hosts and susceptibility used here.

Discussion. Hawksworth and Wiens (1972) comment on the unusually broad host range of *Arceuthobium tsugense*, which encompasses not only both western species of hemlock but also several species of fir, spruce, and pine. *Arceuthobium tsugense* is segregated into subspecies *tsugense* and *mertensiana* and subspecies *tsugense* into two physiologically differentiated host races as western hemlock and shore pine (Hawksworth and others 1992b). Additional field studies on distribution, host preference, and phenology are being conducted to resolve continuing taxonomic uncertainty (see Mathiasen 1994). At this time, however, we retain the taxonomy and host relations presented by Hawksworth and Wiens (1996). Hennon and others (2001) provide a general review and management guide for hemlock dwarf mistletoe. The subspecies are similar morphologically, but the shoots are about 30 percent taller in subsp. *tsugense* than in subsp. *mertensiana* (differences statistically significant at $P < 0.01$).

Phenology. Meiosis in July for both subspecies, but the subsequent phenologies of flowering for the subspecies differ. Flowering averages about 1 to 2 weeks earlier in subsp. *tsugense* (peak anthesis in August, extremes from late July to late September) than for subsp. *mertensiana* (peak anthesis from mid-August to mid-September). In contrast to flowering, the seed dispersal for subsp. *tsugense* averages about 2 to 4 weeks later (late September to early November) than for subsp. *mertensiana* (mid-August, rarely to late October).

29a. *Arceuthobium tsugense* subsp. *tsugense* Western Hemlock Dwarf Mistletoe

Description. As the species, but shoots vary from 3 to 13 cm high, mean 7 cm.

Hosts. *Tsuga heterophylla* is the principal and common host; but *A. lasiocarpa* var. *lasiocarpa* is also considered a principal host, as are (tentatively) *Abies amabilis* and *A. procera*. *Abies grandis* and *Pinus contorta* var. *latifolia* are occasional hosts. Rare hosts are *Picea engelmannii*, *P. sitchensis*, *Pinus monticola*, *Pseudotsuga menziesii*, and *Tsuga mertensiana*. The status of *Pinus contorta* var. *contorta* (shore pine) as a

host is discussed below. Extra-limital and hosts by inoculation (for the western hemlock race) are *Larix decidua* (incompatible), *L. occidentalis* (incompatible), *Picea abies*, *P. glauca*, *Pinus contorta* var. *latifolia*, *Pinus ponderosa*, *P. radiata*, *P. sylvestris*, *Pseudotsuga menziesii*, and *Tsuga canadensis*.

Distribution. Canada (British Columbia) and the United States (Alaska, Washington, Oregon, and California). *Arceuthobium tsugense* subsp. *tsugense* is distributed from Haines, Alaska, to Mendocino, California. *Arceuthobium tsugense* subsp. *tsugense* is common in the *Tsuga heterophylla* forests of coastal Alaska, British Columbia, Washington, and Oregon; but rare in northwestern California; and unlikely in northern Idaho. Elevational range is from sea level in Alaska, British Columbia, and Washington to about 1,250 m in Oregon.

Discussion. Many of the lower infections in *Tsuga heterophylla* produce few shoots of the dwarf mistletoe (Shaw and Weiss 2000). Because dwarf mistletoes are sensitive to light, the absence of dwarf mistletoe shoots from the lower infections may be explained by the dense shade in the lower portions of coastal hemlock forests (Smith 1969). In such situations, vigorous shoots are often found only along margins of stands, on young trees in openings, or in higher branches of older trees. Information on the epidemiology of this mistletoe and management of hemlock is available for Alaska (Shaw and Hennon 1991, Trummer and others 1998, and Wittwer 2002) and Canada (Bloomberg and Smith 1982, Edwards 2001, Muir 1993, Smith 1977).

Discussion on Western Hemlock Compared to Shore Pine. The taxonomic status of the dwarf mistletoe populations on *Pinus contorta* var. *contorta* is the subject of continued debate (Hawksworth and Wiens 1972, 1996, Hunt and Smith 1978, Smith and Wass 1976, 1979). Dwarf mistletoe population on western hemlock (*Tsuga heterophylla*) and shore pine (*P. contorta* var. *contorta*) are similar morphologically, phenologically, and chemically but appear to have consistent differences in host compatibility. Comparing dwarf mistletoe populations on western hemlock to those on shore pine, respectively, maximum shoot height is about 30 percent greater; fruits are slightly but statistically smaller; anthesis and peak dispersal are later. Flavonoid composition and isozyme patterns are similar. Inoculation of shore pine with dwarf mistletoe seeds from western hemlock produce few infections, but those infections that are successful produce abundant aerial shoots. In contrast, inoculations of western hemlock with dwarf mistletoe seeds from shore pine result in more infections but few produce any shoots. *Tsuga heterophylla* and *Pinus monticola* are considered rare hosts. Other species infected by the shore pine race by artificial inoculation include *Abies amabilis*, *A. grandis*, *Larix occidentalis*,

Picea glauca, *P. engelmannii*, *Pinus contorta* var. *latifolia*, *P. ponderosa*, and *Pseudotsuga menziesii*.

Arceuthobium tsugense subsp. *tsugense* parasitizes *Pinus contorta* var. *contorta* in southwestern British Columbia and the San Juan Islands, Washington. Populations of this dwarf mistletoe are distributed on isolated rocky outcrops along the east coast of Vancouver Island, on the Channel Islands, and the mainland of British Columbia north of Vancouver. Two outlying populations occur 250 km north at Port Clements (Queen Charlotte Islands) and at Terrace (British Columbia mainland). In the United States, populations are known from Orcas and San Juan Islands (Washington). The elevational range is from sea level to 800 m.

29b. *Arceuthobium tsugense* subsp. *mertensianae* Mountain Hemlock Dwarf Mistletoe

Arceuthobium tsugense (Rosendahl) G.N. Jones subsp. *mertensianae* Hawksw & Nickrent, Novon 2:209, 1992.

Description. Shoots are typically shorter (5 cm) than in subsp. *tsugense* (7 cm).

Hosts. The common principal host of *Arceuthobium tsugense* subsp. *mertensianae* is *Tsuga mertensiana*; *T. heterophylla* is only rarely infected, even where this species is closely associated with infected *T. mertensiana*. Other principal hosts are *A. amabilis* and *Abies lasiocarpa*. *Pinus albicaulis* is a secondary host, and *Pinus monticola* is an occasional host. *Picea breweriana* and *Pinus contorta* var. *latifolia*, are rarely infected.

Distribution. Western Canada (southern British Columbia) and Western United States (Washington, Oregon, and California). The distribution of *Arceuthobium tsugense* subsp. *mertensianae* is still poorly known, but it extends from near Vancouver (British Columbia), in the Olympic Mountains, through the Cascade Mountains (Washington and Oregon), and to the central Sierra Nevada (Alpine, California). Hildebrand and others (1997) report on a distribution survey in Washington. Elevational range is 1,200 to 2,500 m.

Discussion. Some populations of *Tsuga mertensiana* such as on Mount Baker and in the Olympic Mountains are exceptionally heavily infected by this dwarf mistletoe.

30. *Arceuthobium vaginatum*

Arceuthobium vaginatum (Willd.) Presl in Berchtold, O PUirozenosti Rostlin aneb Rostinár 2:28, 1825.

Description. Mean shoot height from 20 to 30 (maximum 55 or greater) cm, orange to dark brown, reddish, or black, usually densely branched and erect, but large older plants sometimes become pendulous; branches flabellate; basal diameter of dominant shoots 1 to 3 cm long, 0.2 to 0.4 cm wide. Staminate flower up to 3.5 mm long and up to 3.5 mm across, mostly three-merous (sometimes four-merous), segments up to 2.0 mm long and up to 1.5 mm wide, apex acute to obtuse. Pistillate flower up to 2.5 mm long, up to 1.5 mm across. Fruit 4 to 6 mm long, 2 to 3 mm wide, elliptical to obovate.

Phenology. Anthesis from approximately late March through May.

Hosts. Parasitic on yellow pine.

Discussion. The distributions of the two subspecies overlap in the mountains of central Chihuahua (between latitudes 28° 00' and 28° 30' N) where intermediate characteristics are shown in some populations. Even here, however, there is a tendency to segregate by elevation with subsp. *vaginatum* at lower elevations and subsp. *cryptopodum* at higher elevations. Although the characteristics distinguishing subspecies are greater than those in other species (such as *Arceuthobium tsugense*), this is the only case where we find intermediate populations, therefore we use subspecific rank rather than species rank for this taxon.

30a. *A. vaginatum* subsp. *vaginatum* Mexican Dwarf Mistletoe

Description. Mean shoot height 20 (maximum 55) cm, dark brown to black, rarely reddish. Basal diameter of dominant shoots 4 to 20 (mean 7) mm. Third internode 5 to 30 (mean 17.4 ±6.0) mm long, 2.5 to 8.5 (mean 5.0) mm wide, length/width ratio 2.9: 1. Staminate flower segments 1.6 mm long, 1.1 mm wide. Mature fruit 5.5 by 3.5 mm.

Phenology. Meiosis in February. Anthesis usually March and April. Fruits mature in August of the year following pollination; maturation period averages 16 to 17 months.

Key to the Subspecies

1. Plants dark brown to black, usually over 20 cm tall; staminate flowers usually greater than 3 mm long and wide; anthesis March–April; Sierra Madre Occidental from central Chihuahua southward to the Central Cordillera, and in the Sierra Madre Oriental 30a. *A. vaginatum* subsp. *vaginatum*
1. Plants orange, usually less than 20 cm tall; staminate flowers usually less than 3 mm long and wide; anthesis May–June; Sierra Madre Occidental of central Chihuahua and Sonora and mountains of central Coahuila northward to central Utah and northern Colorado 30b. *A. vaginatum* subsp. *cryptopodum*

Hosts. *Arceuthobium vaginatum* subsp. *vaginatum* has the broadest known host range of any species in the genus. It is collected on 13 species of Mexican pines and undoubtedly occurs on others. It is common on the principal hosts *Pinus arizonica* vars. *arizonica*, var. *stormiae*, *P. cooperi*, *P. durangensis*, *P. engelmannii*, *P. hartwegii*, *P. herrerae*, *P. lawsonii*, *P. montezumae*, *P. patula*, and *P. rudis*. *Pinus teocote* is a secondary host because it was parasitized only when it was associated with an infected principal hosts. It rarely infects *Pinus culminicola* under infested *P. rudis* on Cerro Potosí (Nuevo León).

Distribution. Mexico (Chihuahua, Coahuila, Distrito Federal, Durango, Hidalgo, Jalisco, Mexico, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, Sinaloa, Tamaulipas, Tlaxcala, Veracruz, and Zacatecas). This is the most widely distributed dwarf mistletoe in Mexico, extending from the Sierra Madre Occidental in western Chihuahua south through Durango, Jalisco; into the Central Cordillera of Mexico and Puebla; and occurring in the Sierra Madre Oriental from Coahuila and Nuevo León to Oaxaca. Elevational range is from 2,100 m in Nuevo León to 3,900 m on Nevado de Toluca near Mexico City.

Discussion. The shoots of *Arceuthobium vaginatum* subsp. *vaginatum* exceed 55 cm in height in Central Mexico. The plants exhibit considerable sexual dimorphism and variation. The staminate plants tend to be taller than the pistillate plants, but Vázquez (1991) reports on a population near Texcoco, Mexico, where the pistillate plants were short, erect, and dark, and staminate plants were long, pendulous, and reddish. Plants in some areas of the northern Sierra Madre Oriental are often reddish, but plants just 40 km to the south are again typically black (Hawksworth and Cibrián 1985). The hosts and ecological requirements of *Arceuthobium vaginatum* subsp. *vaginatum* and *A. globosum* are similar; and they frequently sympatric and even occur on the same tree.

30b. *Arceuthobium vaginatum* subsp. *cryptopodum* Southwestern Dwarf Mistletoe

Arceuthobium vaginatum (Willd.) Presl subsp. *cryptopodum* (Engelm.) Hawksw. & Wiens, *Brittonia* 17:230, 1965.

= *A. vaginatum* f. *cryptopodum*.

Description. Mean shoot height 10 cm (maximum 27) cm, usually orange to reddish brown, sometimes dark to near black. Basal diameter of dominant shoots 2 to 10 (mean 4) mm. Third internode 4 to 16 (mean 7.8 ± 3.2) mm long, 2.0 to 4.5 (mean 3.1) mm wide, length/width ratio 2.5:1. Staminate flowers 2.5 to 3.0 (mean 2.7) mm across; perianth segments 1.3 mm long, 1.0 mm wide. Mature fruit 4.5 to 5.5 (mean 5.0) mm long, 2.0 to 3.0 (mean 2.5) mm wide; proximal portion 3.5 mm long. Seeds 2.7 by 1.1 mm.

Phenology. Meiosis in March or April. Anthesis usually in May and June, with extremes from late April to early July. Fruits mature in late July or early August, with extremes from early July to early September. Both anthesis and seed dispersal in Colorado occur 1 to 2 weeks later than in Arizona and New Mexico; maturation period averages 14 to 15 months. Seed germination from August to September, immediately following dispersal.

Hosts. *Pinus ponderosa* var. *scopulorum* is the most common host in Arizona, New Mexico, Colorado, Utah, and Texas. The two races of var. *scopulorum* recognized by Conkle and Critchfield (1988) (Rocky Mountain and Southwestern) appear to be about equally susceptible, but most of the distribution of the Rocky Mountain race is primarily north of that of *Arceuthobium vaginatum* subsp. *cryptopodum*. Other principal hosts include *P. arizonica* var. *arizonica* (Arizona, New Mexico, Chihuahua, and Sonora) and var. *stormiae* (Coahuila), *P. engelmannii* (Arizona, Chihuahua, and Sonora), and *P. durangensis* (Chihuahua and Jalisco). *Pinus cooperi* is a secondary host. Occasional hosts are *Pinus aristata* and *P. contorta* var. *latifolia*. Rare hosts are *Pinus flexilis* and *P. strobiformis*. *Pinus sylvestris* is an extra-limital host.

Distribution. Northern Mexico (Sonora, Chihuahua, and Coahuila) and United States (Utah, Arizona, Colorado, New Mexico, and Texas). *Arceuthobium vaginatum* subsp. *cryptopodum* is widely distributed on *Pinus ponderosa* var. *scopulorum* from central Utah (Sevier and Emery) and northern Colorado (Larimer) to Arizona, New Mexico, western Texas (Guadalupe and Davis Mountains), at least as far south as the Sierra de la Madera (Coahuila) and the Sierra Madre Occidental (Sonora and Chihuahua). *Arceuthobium vaginatum* subsp. *cryptopodum* occurs in nearly every mountain range where *P. ponderosa* var. *scopulorum* grows, including isolated ranges such as the Virgin, Trumbull, and Hualapai Mountains (Arizona), the Ladron, Organ, Guadalupe, and San Andreas Mountains (New Mexico), Navajo Mountain (Utah), and Mesa de Maya (Colorado). *Arceuthobium vaginatum* subsp. *cryptopodum* distribution maps have been published for Colorado, Utah, and New Mexico (see Hawksworth and Wiens 1996). Elevational range is 1,700 to 3,000 m, although it is found primarily between 2,000 and 2,600 m in Arizona and New Mexico.

Discussion. *Arceuthobium vaginatum* subsp. *cryptopodum* is characterized by thick, orange-colored shoots. Populations, however, show various color gradations commonly from yellow to red, greenish in deep shade or on *Pinus contorta* var. *latifolia* or rarely from dark purple such as in the Black Forest of Colorado. This dwarf mistletoe is particularly damaging to *Pinus ponderosa* in the Sacramento Mountains in

south-central New Mexico (Lincoln National Forest and adjacent Mescalero Apache Indian Reservation; Hawksworth and Lusher 1956), central Arizona, and along the Front Range in Colorado. For reasons yet to be explained, the parasite is common but less damaging in southwestern Colorado and southeastern Utah. The witches' brooms induced by *Arceuthobium vaginatum* subsp. *cryptopodum* are similar on all hosts except for *Pinus contorta* var. *latifolia* with small witches' brooms and large branch swellings. Because of the severe damage caused by this mistletoe and the importance of its principal host, there are numerous reports on its biology and management; the most comprehensive study is by Hawksworth (1961) and a general leaflet by Lightle and Weiss (1974).

31. *Arceuthobium verticilliflorum*

Big-Fruited Dwarf Mistletoe

Arceuthobium verticilliflorum Engelm., Botany of California 2:107, 1880.

Description. Mean shoot height 7 (maximum 11) cm, mostly yellow to yellow-green to purplish, without secondary branching, lightly glaucous when young. Basal diameter of dominant shoots 2.5 to 5.0 (mean 3.6) mm. Third internode 2 to 7 (mean 3.0 ± 1.2) mm long, 2.5 to 4.5 (mean 3.2) mm wide, length/width ratio 0.9:1. Staminate flowers 3.5 to 4.5 (mean 4.0) mm across; perianth mostly four-merous (sometimes three-merous); verticillate, with five to 10 flowers per whorl; segments 1.8 mm long, 1.2 mm wide. Mature fruit 15 by 10 mm. Seeds about 11 by 6 mm; embryos 4 by 1 mm.

Phenology. Meiosis September to October. Anthesis usually March and April. Fruits mature in September and October of the year following pollination; maturation period averages 18 to 19 months.

Hosts. This dwarf mistletoe principally parasitizes *Pinus arizonica*, *P. cooperi*, *P. durangensis*, and *P. engelmannii*.

Distribution. Mexico (Durango). Populations occur east of El Salto on the Durango–Mazatlán Highway, in the Sierra Candella, Sierra Huacol, Sierra Guanacevi, and along the road from Santiago Papasquiario to Altares (Cibrián Tovar and others 1980). Elevational range is 2,000 to 2,750 m.

Discussion. Hawksworth and Wiens (1965) report the rediscovery of this unusual species, first described by Engelmann in 1880, from El Salto, Durango. The species is perhaps the most distinctive and primitive in the genus. The staminate shoots are characterized by thick spikes (4 to 6 mm) with verticillate, four-merous flowers; the entire spikes are deciduous after flowering. This is the only dwarf mistletoe in which the pedicels do not elongate and curve downward when the fruits mature. Typically, the pericarp oozes off the top of the seed, and seeds are released but not

explosively discharged. Compared to other dwarf mistletoes, mature fruits are more than twice as large and seeds weight 100 times more (200 to 270 mg). In further contrast, most dwarf mistletoes are found in closed canopy stands as pockets of infested trees with severe infections in the lower crowns; but *Arceuthobium verticilliflorum* is found in open stands with random distributions in trees and crowns. Fruit and seed morphology, ecological distribution, and observation of birds feeding in infected crowns suggest this dwarf mistletoe is dispersed by birds. This dwarf mistletoe causes massive witches' brooms, and the diameter of infected branches is sometimes greater than that of the trunk where the infected branch emerges. Infections on the main trunks of pines sometimes extend up to 3 m in length.

32. *Arceuthobium yecoreense*

Yecoran Dwarf Mistletoe

Arceuthobium yecoreense Hawksw. & Wiens, Phytologia 66:6, 1989.

Description. Mean shoot height 12 (maximum 17) cm, yellow-green to brown, branches flabellate. Basal diameter of dominant shoots 2 to 5 (mean 3) mm. Third internode 10 to 21 (mean 15) mm long, 2 to 4 (mean 2.4) mm wide.

Phenology. Time of anthesis is unknown but suspected to be June. Time of fruit maturity is unknown, but presumed to be September and October.

Hosts. The principal hosts in the Yecora region are *Pinus leiophylla* var. *chihuahuana* and *P. herrerae*. In the Sierra Madre Occidental, it occurs principally on *Pinus durangensis*, *P. herrerae*, *P. lumholtzii*, and *P. leiophylla* var. *chihuahuana*. *Pinus engelmannii* is a secondary host.

Distribution. Mexico (Sonora, Chihuahua, and Durango). The distribution of this dwarf mistletoe is poorly known and only collected from the Yecora region (Sonora and Chihuahua) and about 100 km west of Santiago Papasquiario (Durango). Because it is abundant at two locations separated by more than 400 km, the dwarf mistletoe should be expected in the intervening forest areas as well. Elevational range is 1,600 to 2,500 m.

Discussion. *Arceuthobium yecoreense* is characterized by its slender, greenish–yellow to brownish shoots and early summer flowering period. The plants are morphologically most similar to *A. aureum* subsp. *aureum* of the lowlands of Guatemala. The two populations are similar except that shoots from western Durango have more yellowish and slightly taller shoots. Yecora is the primary pine-producing area of Sonora; the dwarf mistletoe there is both common and damaging.