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Chapter

3

Phoradendron in Mexico and the United States



The generally familiar mistletoes are the leafy *Phoradendron* that typically infest hardwood trees and are placed at doorways for winter celebrations. Several of these mistletoes, however, more resemble the dwarf mistletoes by their apparently leafless stems and presence on conifers; but their large, fleshy berries that are attractive to birds clearly identify them as *Phoradendron*, “the tree thief.” For several reasons, the conifer-infesting *Phoradendron* (the group reviewed here) have not gotten the level of attention from forest managers that the *Arceuthobium* have. *Phoradendron* most typically cause slight damage to junipers in Southwestern woodlands. But these mistletoes include a number of different species, range from Oregon to Mexico, infect a variety of hosts, and provide an interesting model of host–parasite interactions.

Along with the other mistletoes, the taxonomy, biology, physiology, and ecology of the *Phoradendron* are reviewed by Gill and Hawksworth (1961) and Kuijt (1969a). Foresters have long been interested in the *Phoradendron* on incense cedar (Meinecke 1912).

Picture guidebooks are available by Walters (1978) for the Southwest and by Scharpf and Hawksworth (1993) for the Pacific States. General summaries of information including control are provided by Hawksworth and Scharpf (1981), Hernandez (1991), and Vega (1976). The taxonomy of the *Phoradendron* on conifers was first monographed by Trelease (1916) and then revised by Wiens (1964). Confusion over the position and ranking of several taxa (Hawksworth 1979) and recent evidence from molecular systematics (Ashworth 2000) suggest the group requires another taxonomic monograph.

Life History and Biology

The *Phoradendron* have a typical mistletoe life cycle characterized by bird dispersal of sticky seeds, internal parasitism of a woody host, and aerial shoots for flower and fruit production. *Phoradendron* biology, reproduction, and parasitism have received intense study from ecological and evolutionary perspectives.

Life Cycle

The most detailed but still comprehensive study and review of a *Phoradendron* life cycle is that by Felix (1970a) for the mistletoe on *Abies concolor*. A number of bird species feed on the mistletoe fruits and disperse seeds by excreting or regurgitating them. The most important birds for effective dispersal include cedar waxwings, euphonias, silky flycatcher, bluebirds, thrushes, robins, and solitaires (see Sutton 1951, Gill 1990). Seeds pass quickly, and because birds perch in trees, seeds are deposited at suitable sites for infection (often the top or warm side of a potential host, commonly one already infected). Germinating seeds produce a radicle, holdfast, and penetrate the host branch usually near a needle (Ruhland and Calvin 2001). The endophytic system consists of longitudinal strands and sinkers (Calvin and others 1991, Felix 1970a). Once aerial shoots are produced, the *Phoradendron* does photosynthesize, but it is a parasite (see below) not a simple epiphyte. Plants are either male or female. Although Dawson and others (1990a) report a male-bias and provide hypotheses why there might be such a bias, Daugherty and Mathiasen (1999) find the sex ratio is one to one. Flower production and reproduction is typical, except that natural hybridization occurs but rarely (Wiens and Dedecker 1972). Fruits are produced several years after infection; older plants produce more and larger fruits (Dawson and Ehleringer 1991, Dawson and others 1990a, 1990b). Although the shapes of shoots and leaves of *Phoradendron* might mimic their host, the biology behind the appearance is unclear (Atsatt 1993b). Endophytic systems are

perennial, but plants of all ages are subject to mortality by extreme low temperatures (Wagener 1957).

Host–Parasite Physiology

The physiology of *Phoradendron* is generally reviewed by Fisher (1983), Knutson (1983), and Kolb (2002) as typical for most mistletoes (but different from that of the dwarf mistletoes). Many details of the nitrogen, carbon, and water relations of the “xylem-tapping” *Phoradendron juniperinum* are elucidated in a series of recent ecophysiology studies (Ehleringer and others 1986, Marshall and Ehleringer 1990, Marshall and others 1993, 1994). The mistletoes do fix some carbon but get much from their host; mistletoes transpire a lot of water (all from their host); and they get a lot of nitrogen from the host, as the inevitable consequence of the physiological relation (Marshall and others 1994). Lei (1997) concludes that heavy mistletoe infection increases host-plant water stress and reduces vigor, viability, and reproductive success of the host in favor of the mistletoe. McHenry (1934) reports that *Phoradendron* at the Grand Canyon kills juniper. Hawksworth and Wiens (1966) indicate that junipers may also form witches’ broom in response to infection.

Host–Parasite Ecology

Numerous authors have studied the effects of *Phoradendron* parasitism on population dynamics and interactions with other species. Hreha and Weber (1979) compare pinyon dwarf mistletoe (*Arceuthobium divaricatum*) and juniper mistletoe (*Phoradendron juniperinum*) at the South Rim of the Grand Canyon, reporting more infection in bigger (older) trees, a lack of infestation in recently burned (young) areas, and general stability in the populations. They consider the pinyon dwarf mistletoe the more detrimental because it more readily kills its host. Juniper mistletoe often has a patchy distribution, with some trees heavily infested. Gregg (1991) concludes the critical difference between infested and uninfested sites is the need for a dependable moisture supply to maintain the high demand of infected trees. Moisture stress in firs infected by *Phoradendron* is associated with reduced resistance and increased successful attack by the fir engraver (Felix 1970a, Ferrell 1974). Gehring and Whitham (1992) report that on droughty sites, juniper severely infested by mistletoe have lower rates of beneficial mycorrhiza infection, and female junipers are more seriously affected than male junipers. Another three-way, conditional interaction is described by van Ommeren and Whitham (2002) for juniper, mistletoe, and their avian dispersers. Although mistletoe has a negative impact on the health of infected

trees, mistletoe provides a more dependable food source than juniper for the shared avian dispersers of each species' seeds. By considering dispersal and reproductive success in the interaction model, they conclude that the net effect of mistletoe parasitism, depending on populations, shifts between favoring the mistletoe to favoring the juniper.

The *Phoradendron* also exhibit a curious phenomenon whereby a mistletoe is parasitized by another mistletoe of the same or different species (Hawksworth and Wiens 1966, Wiens and Calvin 1987). Although several of the conifer-infecting *Phoradendron* may be infected by other *Phoradendron* mistletoes (Felix 1970b), the occurrence is too rare to effect a significant biological control.

Description of Genus

Phoradendron Mistletoe, injerto

Shrubby parasite of trees and other woody plants (fig. 3-1), woody at base, glabrous or hairy; shoots cylindrical, green or less often reddish, 20 cm in

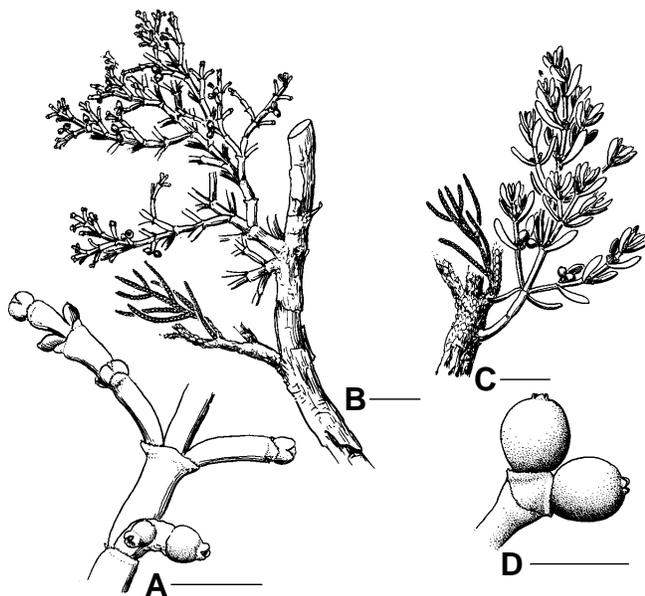


Figure 3-1—*Phoradendron* (all scales represent 5 mm). **A**, *P. juniperinum* on host; **B**, *P. juniperinum* with young fruit; **C**, *P. densum* on host; **D**, young fruits of *P. densum*. Adapted from Hitchcock and others (1964), p. 99, drawing by J.R. Janish. Our **C** and **D** originally labeled as *P. bolleanum* in figure, but accompanying text suggests figure represents *P. bolleanum* var. *densum* (Torr.) Fosberg, which we recognize as *P. densum*.

height, nodes constricted, lacking epicortical roots; phyllotaxy opposite or decussate; inflorescence a spike; perianth generally three-parted and persistent; anthers small, sessile and bilocular; fruit a berry, 3 to 6 mm, single color of white, pink, or reddish. A genus of about 200 species in temperate and tropical America. Type species: *Phoradendron californicum* Nuttall.

The genus *Phoradendron*, the largest genus of mistletoes, is in serious need of definitive taxonomic study. Trelease (1916) is the first monographic study of the genus, but Wiens (1964) revises many of Trelease's taxa that occur on conifers (see table 3-1). This taxonomy is further reconsidered by Hawksworth and Wiens (1993a, 1993b) for the flora of California, Nevada, and Arizona. Other floristic treatments with keys and illustrations include Hitchcock and others (1964) for the Pacific Northwest, McMinn (1939) for California, Standley (1920) for Mexico, and Wiggins (1980) for Baja California. Kuijt (1996) questions the significance and interpretation of many of the traditional morphological features used for the taxonomy of *Phoradendron*. Ashworth (2000) provides much insight to the relations among these mistletoes using techniques of molecular systematics.

Most of the taxa of *Phoradendron* that parasitize conifers are in the section *Pauciflorae* as described by Wiens (1964). Ashworth (2000) reports that these taxa (see table 3-1), delimited by morphological features, also form a single, related cluster based on molecular features. *Phoradendron rhipsalinum* is also a parasite of conifers but is apparently more closely related to a number of *Phoradendron* that typically infect hardwoods. A few other *Phoradendron* reportedly occur on conifers, but these are either rare cases or possibly misidentifications. Usual conifer host genera are *Abies*, *Calocedrus*, *Cupressus*, *Juniperus*, *Taxodium* (table 3-2). Martínez (1948) illustrates *Phoradendron velutinum* on *Pinus leiophylla* in Pueblo, but this is a rare host for a mistletoe with a wide host range, and we know of no other reports on pines.

In 1990, Wiens and Hawksworth drafted a further revision of *Phoradendron* section *Pauciflorae* that has never been completed and published (copy on file at Flagstaff Laboratory, Rocky Mountain Research Station). In that draft, they proposed recognizing seven new species on American conifers and raising to specific rank a previously submerged taxon not now generally accepted at that level. Although we do not describe any new species in this publication, we do suggest here that there may be differences in some populations that warrant recognition at the specific level. We leave it to other taxonomists using morphological and molecular techniques to judge these opinions. Specimens for these "ined" taxa are assembled for deposition at the U.S. National Herbarium.

Table 3-1—Taxonomic history of *Phoradendron* that parasitize conifers.

Trelease (1916)	Wiens (1964)	Accepted here
<i>P. bolleanum</i> Eichler <i>P. tequilense</i> n. sp.	<i>P. bolleanum</i> subsp. <i>bolleanum</i>	<i>P. bolleanum</i> (Seem.) Eichl.
<i>P. capitellatum</i> Torrey n. sp.	<i>P. capitellatum</i> Torr. ex Trel.	<i>P. capitellatum</i> Torr. ex Trel. ^a
<i>P. densum</i> Torrey n. sp. <i>P. guadalupense</i> n. sp. ^c <i>P. saltillense</i> n. sp.	<i>P. bolleanum</i> subsp. <i>densum</i> (Torr.) Wiens, comb. nov.	<i>P. densum</i> Torr. ex Trel. ^{a,b} <i>P. saltillense</i> Trel. ^d
<i>P. juniperinum</i> Engelm. <i>P. ligatum</i> n. sp.	<i>P. juniperinum</i> subsp. <i>juniperinum</i>	<i>P. juniperinum</i> Engelm. ex A. Gray ^{a,b}
<i>P. libocedri</i> Howell	<i>P. juniperinum</i> subsp. <i>libocedri</i> (Engelm.) Wiens, comb. nov.	<i>P. libocedri</i> (Engelm.) T.J. Howell ^b
<i>P. longifolium</i> Eichler	<i>P. longifolium</i> Eichler ex Trel.	<i>P. longifolium</i> Eichler ex Trel.
<i>P. minutifolium</i> Urban	<i>P. minutifolium</i> Urban	<i>P. minutifolium</i> Urban
<i>P. pauciflorum</i> Torrey	<i>P. bolleanum</i> subsp. <i>pauciflorum</i> (Torr.) Wiens, comb. nov.	<i>P. pauciflorum</i> Torr. ^{a,b} <i>P. rhipsalinum</i> Rzed. ^e

^aName used in Hawksworth and Wiens (1993a).

^bName used in Hawksworth and Wiens (1993b).

^cWiens (1964) indicates this taxon probably now extinct.

^dReferred to by Hawksworth and Cibrián (1985) as *P. densum* subsp. *saltillense* (Trel.) Wiens.

^eTaxon first recognized in 1972.

Description of Species

1. *Phoradendron bolleanum*

Bollean Mistletoe

Phoradendron bolleanum (Seem.) Eichl., Mart. Fl. Bras, v. II. 134.

Description. Plants 20 to 30 cm high, reddish; internodes 10 to 20 mm long; leaves spatulately linear-elliptical, 8 to 22 mm long and 1 to 4 mm wide, sessile, apex acute reddish, densely hairy; mature fruit is about 4 mm diameter, white to straw-colored (Trelease

1916, Cházaro and Oliva 1987b with illustration). This mistletoe is usually characterized by its bright reddish to brown color; however, some all-green populations have been found in central Chihuahua (Hawksworth and Cibrián 1985).

Hosts. Usual hosts are *Juniperus* and *Arbutus*. This is the only *Phoradendron* on *Arbutus* (*A. arizonica* and *A. xalapensis*); the closely related *Arctostaphylos* (*A. pungens*) is also rarely infected. Vega (1976) lists the hosts of "*Phoradendron bolleanum*" as not only *Juniperus* and *Arbutus* (*A. unedo*) but also *Quercus*,

Table 3-2—Host range and distribution of *Phoradendron* on conifers.

<i>Phoradendron</i>	Principal hosts	Mexico	United States
<i>P. bolleanum</i>	<i>Juniperus</i> , <i>Arbutus</i>	X	-
<i>P. capitellatum</i>	<i>Juniperus</i>	X	-
<i>P. densum</i>	<i>Juniperus</i> , <i>Cupressus</i>	X	X
<i>P. juniperinum</i>	<i>Juniperus</i> , <i>Cupressus</i>	X	X
<i>P. libocedri</i>	<i>Calocedrus</i>	X	X
<i>P. longifolium</i>	<i>Quercus</i> , <i>Pinus</i>	X	-
<i>P. minutifolium</i>	<i>Juniperus</i>	X	-
<i>P. pauciflorum</i>	<i>Abies</i>	X	X
<i>P. rhipsalinum</i>	<i>Taxodium</i> , <i>Quercus</i>	X	-
<i>P. saltillense</i>	<i>Juniperus</i> , <i>Cupressus</i>	X	-
	Total number of species	10	4

Pinus, and *Abies*. Given that he lists the distribution for this mistletoe to include Baja California, we suspect he is including *P. pauciflorum* and other *Phoradendron* under this name. *Cupressus benthami* is an unusual host in the pine-cypress woodlands of Veracruz (Cházaro 1989a).

Distribution. Mexico (Chihuahua, Durango, Hidalgo, Jalisco, Nayarit, Querétaro, Sonora, Sinaloa, Veracruz, and Zacatecas). Common in Sierra Madre Occidental, and Zacatecas to central Chihuahua (Hawksworth and Cibrián 1985). Cházaro (1989a) records *Phoradendron bolleanum* on *Cupressus* (*C. benthami*) in Veracruz. This is the most widespread *Phoradendron* on conifers in Mexico. Known elevational range is from 1,900 to 2,500 m. The mistletoe on junipers in eastern New Mexico, western Texas, and northern Coahuila are considered another taxa.

Discussion. *Phoradendron bolleanum* is a widespread and diverse mistletoe with a complicated taxonomic history. We are attempting here to include only reports of *P. bolleanum* subsp. *bolleanum* and populations resembling the type on juniper from the Sierra Madre Occidental and parasitizing both *Juniperus* and *Arbutus*. We describe other taxa under *P. densum* and *P. pauciflorum*.

Phoradendron bolleanum is unusual for mistletoes of section *Pauciflorae sensu* Wiens (1964) in that it commonly parasitizes both gymnosperms and angiosperms (Hawksworth and Wiens 1966). Trelease (1916) questions whether one species of mistletoe would occur on such unrelated host genera; and without experimental evidence, the question is still open. However, no morphological grounds for a taxonomic separation of the populations on the two hosts have been found. Although infections of *Juniperus* and *Arbutus* frequently occur together, we have seen many situations from Chihuahua to Jalisco where only one host is infected, even though the other is present. For example, *P. bolleanum* has been found in Jalisco on *Arbutus* only, even though *Juniperus* occurs in the same areas (M. Cházaro B., personal communication). This suggests that there may be two host races of the mistletoe, one primarily parasitic on *Juniperus* and one on *Arbutus*. The areas where both types of hosts are infected may represent instances of sympatry of the two races. Carefully controlled, crossinfection experiments are needed to determine the status of the host populations of this mistletoe.

Various authors have attempted to sort out the systematic relations among taxa of *Phoradendron bolleanum* complex. Wiens (1964) revised the previous work by Trelease and Fosberg but later revised himself in floral treatments for Texas (Wiens 1970), Arizona (Hawksworth and Wiens 1993a), and California (Hawksworth and Wiens 1993b). Further changes by Hawksworth and Wiens are contemplated in an

uncompleted draft. Ashworth (2000) identifies several sister groups for taxa of the complex: *P. bolleanum* subsp. *bolleanum* groups with *P. minutifolium*, *P. densum* and *P. pauciflorum* (both previously considered as subspecies of *P. bolleanum*) group together.

2. *Phoradendron capitellatum*

Hairy Mistletoe

Phoradendron capitellatum Torr. ex Trel., Genus *Phoradendron* 25, pl 17, 1916.

=*Phoradendron bolleanum* var. *capitellatum* (Torr. ex Trel.) Kerney & Peebles

Description. Plants 30 to 80 cm tall, yellow-green; internodes 5 to 15 mm long, pendulous with age; leaves 6 to 14 mm long and 2 to 3 mm wide, densely hairy with stellate trichomes; flowers December to February; mature fruit is about 3 mm in diameter, pinkish-white (Hawksworth and Scharpf 1981 with color picture and 1993a).

Hosts. Known hosts are *Juniperus deppeana*, *J. pinchotii*, *J. monosperma*, and *J. osteosperma*. It usually occurs at elevations below *Phoradendron juniperinum*, but the two species are sometimes sympatric and rarely even on the same host tree.

Distribution. United States (Arizona, New Mexico) and Mexico (Chihuahua, Sonora). This mistletoe has a restricted distribution and is known only in central and southeastern Arizona (nine counties), southwestern New Mexico (Grant, Hidalgo, Luna), northeastern Sonora, and northwestern Chihuahua (Hawksworth and Cibrián 1985). Hawksworth and Scharpf (1981) map its distribution in the United States and into Mexico. Known elevational range is 800 to 1,700 m.

Discussion. This highly distinctive parasite of junipers is characterized by its small, densely stellate-pubescent leaves. It is the only leafy mistletoe known to occur on junipers in Arizona and is poorly known. Ashworth (2000) finds that *Phoradendron capitellatum* is the most divergent taxa within the *Pauciflorae*, although there is some support for a sister group with *P. juniperinum*.

3. *Phoradendron densum*

Dense mistletoe

Phoradendron densum Torr. ex Trel., Genus *Phoradendron* 27, 1916.

=*Phoradendron bolleanum* var. *densum* (Torr. ex Trel.) Fosberg,

=*Phoradendron bolleanum* subsp. *densum* (Torr. ex Trel.) Wiens

Description. Plants 10 to 30 cm high, green (fig. 3-1); internodes 6 to 17 mm long; leaves 10 to 20 mm long and 2 to 4 mm wide, glabrous, sessile, apex obtuse; mature fruit is about 4 mm in diameter, white to straw-colored. (Hawksworth and Scharpf 1981 with color photo, Hitchcock and others 1964 with illustration).

Hosts. *Cupressus arizonica*, *C. bakeri*, *C. goveniana*, *C. macnabiana*, *C. macrocarpa* (rare), *C. sargentii*, *Juniperus californica*, *J. monosperma*, *J. occidentalis*, *J. osteosperma*, *J. pinchotii*. The mistletoe is reported on *Pinus monophylla* at Mt. Pinos (Ventura, California) by McMinn (1939), but this has not been confirmed.

Distribution. United States (Arizona, California, Oregon) and Mexico (Baja California). The mistletoe ranges from southern Oregon (Klamath and Jackson) throughout California to the lower elevations of the Sierra San Pedro Mártir in Baja California, Mexico, and with outlying populations in central Arizona on *Cupressus* (Coconino, Yavapai, Maricopa, and Gila). Trelease (1916) reports *Phoradendron densum* from Sonora, and the Forest Pathology Herbarium-Fort Collins, CO, holds collections as well from Coahuila and Nuevo Leon, although these collections may more properly belong under *Phoradendron saltillense*.

The population in the Sierra San Pedro Mártir infects *Juniperus californica* but not *Cupressus*, which occurs at higher elevations (Hawksworth and Wiens 1966). The reciprocal situation occurs in Arizona; the mistletoe infects cypress but not junipers, even though junipers are widely distributed and abundant in the State. Hawksworth and Scharpf (1981) provide a distribution for Oregon, California, and Arizona. Known elevational range is 200 to 2,300 m.

Discussion. Ashworth (2000) illustrates the close systematic relationships among the taxa of section *Pauciflorae* sensu Wiens. Her work, however, also brings out the taxonomic difficulty among *Phoradendron bolleanum*, *P. densum*, and the various taxa at one time or other considered subspecies of these (see table 3-1). For the reviewer (such as here), the problem is determining to which taxa various reports of hosts and distribution refer. Based on their descriptions and distributions, Hawksworth and Wiens (1993a, 1993b) restrict their interpretation of *P. densum* to include only certain populations from Oregon to Baja California on juniper and cypress and from central Arizona on cypress. Many of the mistletoes on either cypress or

juniper from the Sierra Madre Oriental are now referred to *Phoradendron saltillense*. From eastern New Mexico, western Texas, and northern Coahuila (Wiens 1964), it is now referred to Hawksworth's mistletoe (see below). Several other populations usually referred to either *P. bolleanum* or to *P. densum* also have differences in morphology, life history, hosts, and distribution, so that they may warrant recognition at the specific level. Considering the difficulty of classifying these mistletoes using traditional criteria, molecular techniques (for example, Ashworth 2000) should be considered.

The population of *Phoradendron* on various junipers in western Texas, southern New Mexico, and Coahuila has been referred to as *Phoradendron bolleanum* subsp. *hawksworthii* (Wiens 1970) and *Phoradendron hawksworthii* (Hawksworth 1979, Hawksworth and Cibrián 1985, Hawksworth and Scharpf 1981). Although the name *Phoradendron hawksworthii* Wiens is accepted by the PLANTS database (USDA, NRCS 2001), it is not yet a validly published name and remains "ined." The Hawksworth's mistletoe plants are about 10 to 25 cm tall, dark green, with internodes 6 to 12 mm long. Leaves are 6 to 25 mm long, 2 to 2.5 mm wide and slightly hairy. The mature fruit is white and about 4 mm in diameter. The hosts are *Juniperus ashei*, *J. deppeana*, *J. flaccida*, *J. monosperma*, and *J. pinchotii*. This mistletoe is common throughout western Texas (Brewster, Culbertson, Edwards, Hudspeth, Presido, Terrell, Val Verde) and occurs in southern New Mexico (Dona Ana, Lincoln, Otero, Socorro?) and northern Coahuila (Sierra del al Encantada). [Note: the population collected from northwest of Carrizozo, NM, in 1969 could not be relocated and may be extinct.] The Hawksworth's mistletoe resembles *P. saltillense* but is distinguished by several features (table 3-3). Hawksworth's mistletoe is not sympatric with *P. capitellatum*, which also occurs on junipers in southern New Mexico. Hawksworth's mistletoe, however, is sympatric with *P. juniperinum* and may even infect

Table 3-3—Comparison of Hawksworth's mistletoe and *Phoradendron saltillense*.

Character	Hawksworth's mistletoe ^a	<i>Phoradendron saltillense</i>
leaf width	narrow, 2 mm or less	wide, more than 3 mm
leaf transection	upper surface flattened, lower rounded	dorsoventrally flattened
tip of mature leaf	abrupt, with point 0.2–0.3 mm or with the scar of such a point	never developing a point
internode length ^b	short, 6–12 mm, mean 9 mm	long, 6–17 mm, mean 11 mm
segments per staminate inflorescence	usually only one segment	typically two segments

^a*Phoradendron densum* populations in western Texas and southern New Mexico.

^bInternode length is correlated with total plant size.

the same tree; but Hawksworth's mistletoe usually extends to lower elevations than the distribution of *P. juniperinum*. Both *P. juniperinum* and Hawksworth's mistletoe appear to induce a witches' broom formation on its host (Hawksworth and Wiens 1966, D. Conklin, personal communication).

4. *Phoradendron juniperinum*

Juniper mistletoe

Phoradendron juniperinum Engelm. ex A. Gray, Mem. Am. Acad. N. S. iv. 59, 1849.

Description. Plants 20 to 40 cm tall, globose, green to yellow-green, glabrous; internodes 5 to 10 mm long; leaves reduced to minute scales; mature fruit is about 4 mm in diameter, pinkish-white colored (Hawksworth and Wiens 1993a, 1993b, Hichcock and others 1964 with illustration).

Hosts. Common hosts are *Juniperus californica*, *J. deppeana*, *J. pinchotii*, *J. flaccida*, *J. monosperma*, *J. occidentalis*, *J. osteosperma*, and *J. scopulorum*. *Cupressus arizonica* is commonly parasitized in central Chihuahua, but this tree is rarely infected in Texas (Hawksworth and Cibrián 1985), Arizona (Hawksworth and Wiens 1966), and New Mexico (Linnane 1987). Other rare hosts are *C. bakeri* in California (Hawksworth and Wiens 1966), *Chamaebatiara millefolium* (Rosaceae) in Arizona (Hawksworth 1952), and *Pinus monophylla* (Hawksworth 1979). Vega (1976) adds *Juniperus mexicanus* as a host.

Distribution. United States (Oregon, California, Nevada, Utah, western Colorado, Arizona, New Mexico, and western Texas) and Mexico (Baja California, Chihuahua, Durango, Sonora). It occurs in the Chisos Mountains in Big Bend National Park, Texas (Brewster), but is not yet known in adjacent Coahuila, Mexico. A collection in the Forest Pathology Herbarium-Fort Collins, CO, includes a single collection by J.R. Weir (no date) from Oakley, ID (Cassia) with a *Juniperus osteosperma* infected by *Phoradendron juniperinum*. Bunderson and others (1986) attempt to predict the distribution on the mistletoe from environmental site factors. Hawksworth and Scharpf (1981) provide a distribution map. Known elevational range is 1,000 to 2,600 m.

Discussion. The taxon described by Trelease (1916) as *Phoradendron ligatum* for its constricted scales is now included under *P. juniperinum* (Wiens 1964). This distinctive leafless species is the most widespread *Phoradendron* on conifers. *Phoradendron juniperinum* is geographically sympatric with *P. capitellatum* in Arizona, with Hawksworth's mistletoe in New Mexico, and with *P. densum* in California. In fact, natural hybrids of *P. juniperinum* x *P. densum* that appear to be sterile F1 plants have been found in the Inyo and San Bernardino Mountains in California

(Wiens and DeDecker 1972). Vasek (1966) observes that *P. juniperinum* usually does not parasitize *Juniperus californica*, and *P. densum* usually does not parasitize *J. osteosperma*. *Phoradendron juniperinum* forms a sister group with *P. libocedri*, but there is also some evidence in support of another sister group with *P. capitellatum* (Ashworth 2000).

Phoradendron juniperinum is a widespread and common mistletoe on junipers in many of the Western States. It is the subject of numerous studies on eco-physiology (see below). Several curious observations (Hawksworth and Wiens 1966) on *P. juniperinum* include rarely occurring massive witches' brooms and parasitism by *Phoradendron villosum* subsp. *coryae* (normally on oak).

5. *Phoradendron libocedri*

Incense-cedar mistletoe

Phoradendron libocedri (Engelm.) T.J. Howell, Fl. N.W. Amer. 1:608, 1902.

=*Phoradendron juniperinum* Engelm. ex Gray var. *libocedri* Engelm.

=*Phoradendron juniperinum* Engelm. ex Gray subsp. *libocedri* (Engelm.) Wiens

Description. Plants 20 to 80 cm tall, woody only at base, older plants pendulous, green; internodes 10 to 29 mm long; leaves reduced to minute scales; pistillate inflorescences usually with one segment and two flowers (occasionally more); mature fruit 4 mm in diameter, pinkish white to straw colored (Hawksworth and Wiens 1993b).

Hosts. On *Calocedrus decurrens*. There is one collection by Platt and Felix (Dodge Ridge, Tuolumne, CA, 1968) of *Phoradendron libocedri* on *Abies concolor*. They report only a single fir tree was infected in a stand where the mistletoe was common on the associated incense cedar. Weir (5995 from Del Norte CA in 1917) is a *Chamaecyparis lawsoniana* with a single infection of *P. libocedri*; he reports infected incense cedar are nearby.

Distribution. United States (California, Oregon, Nevada) and Mexico (Baja California). The main range of the mistletoe is from southern Oregon (Jackson, Josephine, Klamath) through the Cascade and Sierra Nevada Ranges to southern California. The population in Nevada (Douglas) is near the California border. Isolated known occurrences are in northern Oregon (Jefferson, Warm Springs Indian Reservation) and on San Benito Peak in the South Coast Range in Monterey County, California. It also occurs in the Sierra Juarez and Sierra San Pedro Mártir in Baja California (Wiggins 1980). Although the mistletoe has a wide range, it is not very common (McMinn 1939). Hawksworth and Scharpf (1981) provide a picture of an infested incense cedar and a distribution map. Known elevational range is 400 to 2,500 m.

Discussion. *Phoradendron libocedri* had been considered a subspecies of *P. juniperinum* (Wiens 1964) but is here recognized again at the specific level (Trelease 1916). *Phoradendron libocedri* and *P. juniperinum* are sympatric in the Sierra Nevada, but each remains restricted to its own host; *P. libocedri* has longer internodes and is more pendulous (mimicking its host? see Ashworth 2000). The two taxa, however, do form a very close sister group (Ashworth 2000). Meinecke (1912) describes the swellings and burls caused by *Phoradendron libocedri* and speculates on the age and parasitism of the mistletoe.

6. *Phoradendron longifolium*

Phoradendron longifolium Eichler ex Trel. Genus *Phoradendron* 53, 1916.

Description. Plants becoming generally woody; internodes 15 to 30 mm long; leaves linear, 32 to 84 mm long by 6 to 9 mm wide, apex rounded to acute; fruit 3 to 4 mm diameter, lightly puberulent (Wiens 1964, Bello 1984 with illustration, Bello and Gutierrez 1985).

Hosts. Usually *Quercus* but also *Alnus*, *Pinus pseudostrabus*, *P. michoacana* (Bello Gutierrez 1985).

Distribution. Mexico (Durango, Tamaulipas, Hidalgo, Mexico, Oaxaca).

Discussion. Wiens (1964) places *Phoradendron longifolium* in section *Calyculatae* but admits little material was available for morphological comparisons to other *Phoradendron*. Ashworth (2000) reports *P. longifolium* forms a sister group with *P. galeottii* with which it shares several morphological features, but not time of flowering, which Wiens uses as a taxonomic character. Although *P. longiflorum* occurs in pine woodlands of central Mexico, we have no information on how common or damaging it is.

7. *Phoradendron minutifolium*

Injerto de párraro

Phoradendron minutifolium Urban Bot. Jahrb. Syst 23, Beibl. 57:2, 1897

Description. Plants 30 to 80 cm tall, dull green; internodes 4 to 12 mm long; leaves 3 to 5 mm long and 1 to 1.5 mm wide, resembling scales, glabrous; spike one-jointed; mature fruit is about 4 mm in diameter, pinkish–white colored (Hernandez 1991 with illustration, Trelease 1916).

Hosts. *Juniperus deppeana* (Acosta and others 1992). Other juniper species are probably hosts, but our host collections are only identified as *Juniperus* sp. Depending on how populations in Colima and Jalisco are classified, also on *Cupressus*.

Distribution. Mexico (Chihuahua, Coahuila, Durango, Puebla, Tlaxcala, Veracruz). The mistletoe is most common in Tlaxcala (Hernández 1991) and Veracruz and in the Sierra Madre Occidental in southern Chihuahua and Durango. An apparently extreme

outlier occurs in northern Coahuila in the Sierra del Carmen (across from Big Bend, TX). Depending on how populations on *Cupressus* are classified, also in Colima and Jalisco. Known elevational range is 2,000 to 2,750 m.

Discussion. *Phoradendron minutifolium* in Coahuila is sympatric with *Phoradendron saltillense* on juniper; the two mistletoes sometimes even coinfect the same tree. *Phoradendron minutifolium* and *P. bolleanum* subsp. *bolleanum* form a close sister group (Ashworth 2000).

A population of *Phoradendron* that appears similar to *P. minutifolium* occurs on *Cupressus* in the nearby vicinities of El Sauz and Terrero, Sierra de Mammitlan and Cerro Grande in Colima and Jalisco. Although these mistletoe are referred by the name *Phoradendron olivae* (Cházaro 1990, Cházaro and others 1992), we are unable to confirm that this name has been validly published, but the holotype is reported to be a collection by Wiens, Cházaro, Hawksworth, and Olivo (7051, 1 August 1989) deposited at IBUG (Universidad de Guadalajara). The hosts are variously identified as *Cupressus benthami* and *C. lusitanica*. The plants on *Cupressus* are larger and more open-formed because of longer internodes (15 to 25 mm) and smaller leaves (only 1 to 2 mm long). The mistletoes of *Cupressus* have a distribution far to the west and south of those on *Juniperus*. Additional study of these mistletoes is needed.

8. *Phoradendron pauciflorum*

Fir mistletoe

Phoradendron pauciflorum Torr., Pacif. Rail. Rep. iv. 134.

=*Phoradendron bolleanum* (Seem.) Eichl. var. *pauciflorum* (Torr.) Fosberg

=*Phoradendron bolleanum* (Seem.) Eichl. subsp. *pauciflorum* (Torr.) Wiens

Description. Plants 20 to 40 cm high, green; internodes 10 to 21 mm long; leaves with short petiole, 5 to 30 mm long and 5 to 8 mm wide, glabrous; leaf apex obtuse; mature fruit is about 4 mm wide, pinkish white to straw colored (Hawksworth and Scharpf 1981 with color picture, Hawksworth and Wiens 1993a, 1993b).

Hosts. *Abies concolor* is usually the only host, although autoparasitism has been reported (Felix 1970b). It rarely parasitizes *Cupressus arizonica* var. *montana* in the Sierra San Pedro Mártir, Baja California, Mexico, where this tree is associated with infected *Abies* (Hawksworth and Wiens 1966).

Distribution. United States (Arizona, California) and Mexico (Baja California). This mistletoe is common in the central and southern Sierra Nevada (Calaveras) south to the Sierra San Pedro Mártir in Baja California, Mexico (Wiggins 1980). An extreme disjunct occurs in southern Arizona (Pima) in the

Santa Catalina and Rincon Mountains. Hawksworth and Scharpf (1981) provide a distribution map. Known elevational range is 1,400 to 2,600 m.

Discussion. This species was previously submerged under *Phoradendron bolleanum* (table 3-1) and confused with *P. densum* (Wiens 1964). Felix (1970a) provides a detailed study of the biology of *P. pauciflorum* including information on reproduction and dispersal, shoot growth, endophytic system, branch mortality, mistletoe mortality, effects on host, associated species, and epiparasitism.

A population of an unnamed *Phoradendron* occurs on the rare *Abies durangensis* in Chihuahua, Durango, and Jalisco. This mistletoe on fir is sometimes sympatric with *P. bolleanum*, but has yellow-green, linear leaves with an acuminate apex. The populations include a few widely scattered localities in the Sierra Madre Occidental; all the *A. durangensis* populations that we have visited in Durango are parasitized by this mistletoe.

9. *Phoradendron rhipsalinum*

Phoradendron rhipsalinum Rzed., Cact. Suc. Mex 17:102, 1972.

Description. Plants 2 to 4 m long, pendulous, bright green; leaves 4 to 6 cm long and 4 to 5 mm wide, glabrous; mature fruit yellow-green, 1.5 mm in diameter (Bello 1984 with illustration, and Bello and Gutierrez 1985 with picture and detailed description).

Hosts. *Taxodium distichum* var. *mexicanum*. *Quercus castanea* is also infected (Bello 1984, Bello and Gutierrez 1985).

Distribution. Mexico (Guanajuato, Jalisco, Mexico, Michoacán). Known elevational range is 1,600 to 2,300 m in pine-oak woodlands to subtropical matorral.

Discussion. This is one of the most distinctive Mexican mistletoes. Its 4 to 6 cm long "strap-like" leaves make it unusual. It forms huge pendulous masses hanging from the bald-cypress trees that look from a distance like masses of Spanish moss. Ashworth (2000) concludes this mistletoe does not fit with the other parasites of conifers in the section *Pauciflorae* but appears more closely related to *P. brachystachyum* rather than *P. bolleanum* as suggested by Kuijt (1996). It causes severe mortality to bald-cypress, for example in the vicinity of Zamora, Jalisco. Although approximately 120 species of mistletoe occur in Mexico, this is the only species described by a Mexican botanist (Cházaro and others 1992).

10. *Phoradendron saltillense*

Phoradendron saltillense Trel. Genus *Phoradendron* 27, 1916.

= *P. bolleanum* subsp. *densum* (Torr.) Wiens, pro parte.

Description. Plants moderately long and stout; internodes 10 to 20 mm, papillate-hispid; leaves

narrowly oblong, 20 to 30 mm long by 2 to 3 mm wide, sessile, apex acute; spike 50 to 60 mm long, with single joint and pistillate two-flowered (Trelease 1916, Standley 1920).

Hosts. *Cupressus arizonica*, *C. benthami*, *Juniperus deppeana*, *J. flaccida*, *J. monosperma*, and *J. saltillense*.

Distribution. Mexico (Coahuila, Nuevo Leon, San Luis Potosi, Puebla). Known elevational range is 1,850 to 2,850 m. This mistletoe is common the Sierra del Carmen, northern Coahuila, and it may occur in the Chisos Mountains, Texas. Hawksworth and Cibrián (1985) lists *P. densum* subsp. *saltillense* (Trel.) Wiens on *Cupressus arizonica* in Coahuila and on *Juniperus* in the Sierra Madre Oriental from Coahuila to Zacatecas.

Discussion. *Phoradendron saltillense* is first described by Trelase (1916), accepted by Standley (1920), submerged under *Phoradendron bolleanum* subsp. *densum* by Wiens (1964), and recognized here as a validly published name. It is separated from *P. densum* populations in Arizona by more than 1,000 km, but near to Hawksworth's mistletoe in the Sierra del Carmen. It is distinguished from Hawksworth's mistletoe by several morphological features (table 3-3). *Phoradendron saltillense* is sympatric in Nuevo Leon and Coahuila with populations of an unnamed *Phoradendron* that have longer, narrower, thinner leaves and a more open branching habit; these two contrasting mistletoes may even occur in the same tree.

Importance

Although the *Phoradendron* mistletoes that infect conifers are widely distributed in the Western United States and in Mexico on a number of common and valuable hosts, their importance is mostly on a local basis and for special uses. In the United States, *Phoradendron* are most important in California on incense cedar and true fir in certain areas and important broadly across the Southwest (California to Texas) on junipers. In Mexico, *Phoradendron* (all species) are found throughout the Republic, but only recognized as a forest plague on about 4,000 ha in Jalisco, Mexico, and Michoacán (Martinez 1983). Hawksworth and Cibrián (1985), however, add that *Phoradendron* are damaging to junipers in the north (Sierra Madre Occidental, Oriental, and del Carmen). Although *Phoradendron* are a minor issue on a few forest species (see Felix 1970a, Meinecke 1912), they can be a serious concern in some recreation and other high-value sites (Frankel and others 1989, Linnane 1987). These mistletoes have a high nutritional value as animal forage (Urness 1969) and are utilized as such (Cházaro and Oliva 1988b, Gallina 1988). *Phoradendron* mistletoes are also consumed by humans as a stimulating

beverage (Whiting 1950) and as a traditional medicine for childbirth and several ailments (Cházaro and Oliva 1988a, Moore 1979, Whiting 1950). A strong caution, however, is appropriate. Various compounds from *Phoradendron* and other mistletoes are being investigated for their pharmacological potential, but many of these compounds are present in toxic dosages to humans (Turner and Szczawinski 1991). Although it is the more leafy *Phoradendron* mistletoes on hardwoods that are usually harvested commercially for winter-festival greenery, the conifer mistletoe can still be enjoyed for attracting numerous, colorful birds (Sutton 1951).

Management Strategies

Phoradendron mistletoes seldom cause sufficient damage in an area that control is required; but where management objectives indicate that mistletoe control is justified, cultural methods are available. Although there are insects that feed on these mistletoes (Burke 1975) and fungi that caused disease (Horst 2002, Scharpf and Hawksworth 1966), there are no biological control programs for the *Phoradendron*.

Chemical control has been tested using various herbicides (Quick 1963) and ethephon (Adams and others 1993), but none are recommended. We know of no genetic improvement programs to develop conifer resistance to *Phoradendron* mistletoes. Cultural methods are briefly discussed by Frankel and others (1989), Hawksworth and Scharpf (1981), and Hernandez (1991). Operations include regenerating with a nonhost tree, thinning trees to improve vigor and tolerance of the infestation, and sanitation by removing infected trees or branches or removing aerial shoots. Pruning infected branches is often sufficient; where the loss of infected branches cannot be accepted, the aerial shoots can be just knocked off. Removing the shoots does not eliminate the mistletoe infection but does reduce its reproduction and damage. Shoots will reappear after several years. Covering infected branches with tarpaper or creosote has not proven either attractive or effective. Perhaps the best way for discouraging additional bird-dispersal of mistletoe seeds is with branch pruning or shoot removal (since it is often the mistletoe fruits that initially attract the birds). Given the modest damage and slow rate of increase of these mistletoes, these methods are usually sufficient.