Status of Dwarf Mistletoes in Central America

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Introduction

Although the dwarf mistletoes (*Arceuthobium* spp., Viscaceae) are widespread and common parasites of Pinaceae in the United States and Mexico, only five species are known from Central America: *Arceuthobium aureum* ssp. *aureum*, *A. globosum* ssp. *grandicaule*, *A. guatemalense*, *A. hawksworthii* and *A. hondurense*. Some of these taxa are considered to be among the rarest dwarf mistletoes in the Western Hemisphere. Another species, *A. nigrum*, has been reported from western Guatemala and Chiapas. As discussed below, we now have morphological and molecular evidence that show a close relationship between the Chiapan population with *A. hondurense* from Honduras.

Little is known regarding the distribution, host range, ecology, and phenology of the Central American *Arceuthobium* taxa (Hawksworth and Wiens 1996). In an effort to fill this gap, field work was conducted in Belize, Guatemala, Honduras, western El Salvador, and Chiapas, Mexico. As a result of this work, we have extended the distribution of some Central American dwarf mistletoe taxa and found that others may now be even less common than reported by Hawksworth and Wiens (1970, 1972, 1977, 1984, 1996). We have also learned more about the host range of these mistletoes and a little more about their phenology. The following summarizes our findings.

Golden Dwarf Mistletoe (*Arceuthobium aureum* Hawksw & Wiens ssp. *aureum* Hawksw. & Wiens)

This dwarf mistletoe occurs in central Guatemala. It seems to be most common in the pine forests west and south of Coban. Hawksworth and Wiens (1977, 1996) reported that golden dwarf mistletoe primarily parastizes *Pinus montezumae* Lamb. and *P.*

pseudostrobus Lindl. and rarely occurs on *P. oaxacana* Mirov. Although we looked for these dwarf mistletoe - host combinations in Guatemala, we did not discover it. The only host we found golden dwarf mistletoe parasitizing was *Pinus maximinoi* H. E. Moore (Mathiasen et al. 1999b). This mistletoe has not been previously reported to induce witches' brooms on its hosts (Hawksworth and Wiens 1977, 1996), however, our work indicates that it commonly causes witches' brooms on *P. maximinoi* (Mathiasen et. al. 1999b). Although Hawksworth and Wiens (1996) (see pages 46 and 56) suggested that *P. oocarpa* Schiede might be a principal host of the golden dwarf mistletoe, we have yet to document this combination. We have observed large trees of *Pinus oocarpa* growing next to severely infected *P. maximinoi* near La Cumbre, and none of the *P. oocarpa* were infected (Mathiasen et al. 1999b). In addition, our observations in pine stands infected with the golden dwarf mistletoe near Chilasco indicate this mistletoe does not infect *P. tecunumanii* (Schw.) Equiliz et Perry, a species closely related to *P. oocarpa* (Perry 1991, Farjon and Styles 1997).

A dwarf mistletoe recently collected from near the summit of Montana de Celaque in western Honduras by Dr. Jose Melgar could be golden dwarf mistletoe based on his morphological measurements and photographs. Because Dr. Melgar collected the mistletoe from *Pinus ayacahuite* Ehren., his discovery would not only be the first report of golden dwarf mistletoe from Honduras, but also the first report of this mistletoe on Mexican white pine. We plan to visit Montana de Celaque in November, 2000 and cooperate with Dr. Melgar to confirm the identity of the dwarf mistletoe.

Golden dwarf mistletoe was first reported to have continuous flowering from February through May (Hawksworth and Wiens 1977). Hawksworth and Wiens (1996) later modified this range to be continuous flowering and seed dispersal throughout the year, or at least during the dry season (November - May). Observations made in early May 1999 found no flowering individuals, whereas flowering plants were seen in March 2000. While we have not observed seed dispersal in this species in March or May, female plants did have fruits at various stages of development in both months. These additional observations show that more information is needed on the phenology, distribution, and host range of this dwarf mistletoe species.

Large-stemmed Dwarf Mistletoe (*Arceuthobium globosum* Hawksw. & Wiens ssp. *grandicaule* Hawksw. & Wiens)

In Central America this dwarf mistletoe only occurs in western Guatemala. Although it is common in the highlands of central Mexico and has been reported as far south as Oaxaca, it has not been discovered in Chiapas. Therefore, the Mexican and Guatemalan populations of this dwarf mistletoe species are separated by ca. 500 km. The Guatemalan populations of the large-stemmed dwarf mistletoe have plants that are predominantly brownish-green, flower from early March into June, and are even larger than the plants found in central Mexico. The Mexican populations have green plants and flower from January to May. Therefore, we plan to conduct additional morphological studies of both populations in the future. Perhaps these widely separated populations are sufficiently

distinct to warrant taxonomic recognition. It is questionable whether analysis of ITS rDNA sequences will provide sufficient numbers of changes (nucleotide substitutions) to differentiate these populations because both subspecies of *A. globosum* and *A. aureum* are genetically very similar.

To date we have only found the large-stemmed dwarf mistletoe parasitizing *Pinus rudis* Endl. and *P. pseudostrobus* in Guatemala. It is most common on *P. rudis* in the Sierra de los Cuchumatanes north of Huehuetenango, but it has also been reported from other high elevation locations including the slopes of the highest volcano in Central America, Volcan Tajumulco at an elevation of just over 3660 m (12,000 feet).

The plants of this dwarf mistletoe are the largest of any *Arceuthobium*. We found male plants measuring over 80 cm in height and female plants over 65 cm. They often occur in large clusters of plants that are greater than a meter in diameter. It commonly occurs on the main stems of infected trees.

Guatemalan Dwarf Mistletoe (*Arceuthobium guatemalense* Hawksw. & Wiens)

The Guatemalan dwarf mistletoe is only known to parasitize Mexican white pine (*Pinus ayacahuite*) and is one of the rarest species of *Arceuthobium*. It commonly forms large witches' brooms and systemic infections. The species was originally described by Hawksworth and Wiens (1970) from an area in the Sierra de los Cuchumatanes about 10 km south of San Juan Ixcoy, Guatemala. Our observations in this area indicate that the white pines have been extensively harvested, and the few white pines remaining are not infected with this mistletoe. Our attempts to locate this dwarf mistletoe at several other locations where it had been collected previously (Hawkworth and Wiens 1996) were also unsuccessful owing to timber harvesting. Although Hawksworth and Wiens (1996) commented that this dwarf mistletoe is quite common around Santa Eulalia, this is no longer the case. We found only two small mistletoe populations near Santa Eulalia where, as above, most of the white pines had been harvested. White pine is a valuable tree in Guatemala and has a number of commercial uses including hand-made furniture.

We have only found one new location for this dwarf mistletoe in Guatemala: 12 km north of Ixchiguan in Department San Marcos. Therefore, it appears that this dwarf mistletoe is being extierpated from the pine forests of Guatemala. Because the Guatemalan dwarf mistletoe is only known outside of Guatemala from a few locations in Chiapas and Oaxaca, Mexico, it is certainly one of the rarest dwarf mistletoes in the Western Hemisphere. We were unable to collect this mistletoe in Chiapas because the previous collection sites are now part of a military base south of San Cristobal de las Casas. We plan to visit the Oaxacan sites in December 2000.

The flowering period of the Guatemalan dwarf mistletoe has been reported to be in August and early September (Hawksworth and Wiens 1972, 1996). However, we found it near peak flowering in May in the Sierra de los Cuchumatanes near Todos Santos, Guatemala. It had just started flowering in May at the population north of Ixchiguan.

Therefore, this species may have two distinct flowering periods (spring and late summer) or populations may flower at different times throughout the year. More information on the flowering and seed dispersal periods for this dwarf mistletoe is needed.

Hawksworth's Dwarf Mistletoe (*Arceuthobium hawksworthii* Wiens & C. G. Shaw III)

Specimens of Hawksworth's dwarf mistletoe have been collected from Belize since 1959, but this taxon was not described until 1994 (Wiens and Shaw 1994). It was previously considered to represent a disjunct population of *Arceuthobium globosum* Hawksw. & Wiens (Hawksworth and Wiens 1972) and later was classified as the golden dwarf mistletoe (Hawksworth and Wiens 1977). However, a detailed analysis of the Belize populations by Wiens and Shaw (1994) indicated these populations are distinct from the golden dwarf mistletoe populations found in central Guatemala.

Hawksworth's dwarf mistletoe is one of the rarest dwarf mistletoes because so far it is known only from a small area in the Mountain Pine Ridge region of western Belize. However, Wiens and Shaw (1994) speculated that this dwarf mistletoe might occur in eastern Guatemala in a disjunct population of its principal host, *Pinus caribaea* var. *hondurensis* (Senecl.) Barr. & Golf., that occurs in the vicinity of Poptun (Perry 1991).

Several excursions to Belize were made to observe flowering, seed dispersal, host range and distribution of Hawksworth's dwarf mistletoe. One trip to eastern Guatemala was made in an attempt to locate this species near Poptun. A summary of our findings, taken from Mathiasen et. al. (1999a), is presented below.

Distribution

Hawksworth's dwarf mistletoe is common in the Mountain Pine Ridge east of Augustine, particularly along the Baldy Beacon, Hidden Valley Falls, Brunton Trail, Orchid Hill and Granite Cairn Roads. We observed populations of Hawksworth's dwarf mistletoe at an elevation of 520 m at several locations, but the mistletoe is most common above 600 m. The reasons for the lower elevation limitation are unclear, because its pine hosts are continuously distributed throughout the Mountain Pine Ridge at elevations below 500 m. In addition, as was reported by Wiens and Shaw (1994), we did not observe Hawksworth's dwarf mistletoe in the lower elevation *Pinus caribaea* var. *hondurensis* forests closer to the coast of Belize.

Our surveys now provide adequate information to estimate the distribution of this rare dwarf mistletoe in the Mountain Pine Ridge. Apparently it only occurs in an area of approximately 250 sq. km (Figure 1). Because the highlands of the Mountain Pine Ridge are geologically distinct and have evidently been isolated from other highland regions of Central America for several thousand years (Bateson 1972, Bateson and Hall 1977, Means 1997), Hawksworth's dwarf mistletoe has been separated from other dwarf mistletoe populations long enough to have evolved into a distinct taxon, endemic to the Mountain Pine Ridge. Molecular phylogenetic analyses of nuclear ribosomal ITS

sequences (Nickrent 1996) support the treatment of Hawksworth's dwarf mistletoe as a separate species.

In March 1998 we surveyed the pine populations near Poptun, Guatemala. These pine populations are typical *Pinus caribaea* var. *hondurensis* as reported by Perry (1991). We estimate the overall forest area dominated by pine near Poptun to be restricted to about 300 square km, so the majority of the pine forest (elevation 500 to 700 m) in this area was surveyed. Hawksworth's dwarf mistletoe was not observed in these forests, and we believe it does not occur there. Therefore, it is doubtful that Hawksworth's dwarf mistletoe occurs in Guatemala.

Host Range

We examined host material collected from several pines at different elevations in the Mountain Pine Ridge in an attempt to clarify the identity of the hosts parasitized by Hawksworth's dwarf mistletoe (Wiens and Shaw 1994). For dwarf mistletoe-infected pines, specimens with needles and mature female cones were collected and forwarded to J. P. Perry, Jr. for confirmation of our tentative field identifications. Additionally, a sample was taken from a putative hybrid (*Pinus caribaea* var *hondurensis* X *Pinus oocarpa* var. *ochoterenai*). In all cases our identification of the host agreed with those of Mr. Perry, except that he felt the putative hybrid was best classified as *P. oocarpa* var. *ochoterenai*. Our field observations from the Mountain Pine Ridge confirm that *P. caribaea* var *hondurensis* is the principal host of Hawksworth's dwarf mistletoe in this area. In many areas this pine is severely infected and tree mortality is common in severely infested pine stands.

We were unable to find locations with sufficient numbers of *Pinus oocarpa* var. *ochoterenai* growing near severely infected *P. caribaea* var. *hondurensis* to gather quantitative data on the comparative susceptibility of these hosts to Hawksworth's dwarf mistletoe. However, based on our observations at several locations where *P. caribaea* var. *hondurensis* and *P. oocarpa* var. *ochoterenai* were both parasitized by this dwarf mistletoe, we believe the latter pine is less susceptible. In some areas where many *P. caribaea* var. *hondurensis* were severely infected and where many dead pines of this species had evidence of past mistletoe infection (witches' brooms), infection of large (> 10 m in height) *P. oocarpa* var. *ochoterenai* was much less severe and less frequent. In addition, we observed infection of small *P. caribaea* var. *hondurensis* (less than 2 m in height) under larger individuals of this species but small *P. oocarpa* var. *ochoterenai* growing in the same areas were not infected. Therefore, we have tentatively classified *P. oocarpa* var. *ochoterenai* as a secondary host using the host susceptibility classification system of Hawksworth and Wiens (1972, 1996).

The taxonomic status of the *Pinus oocarpa* populations in the Mountain Pine Ridge is still in question and some investigators consider these populations to be more representative of *P. tecunumanii* (Farjon and Styles 1997). Others consider these populations to represent *P. oocarpa* var. *ochoterenai* (Hunt 1962, Perry 1991). We have chosen to follow the classification of Perry (1991) for these pine populations.

Plant Measurements

Measurements from fresh specimens of male and female plants of Hawksworth's dwarf mistletoe were made, thus augmenting the small amount of data available for this species. Plant height (nearest 0.1 cm), width of shoot bases (nearest 0.1 mm), third internode length (nearest 1.0 mm), and third internode width (nearest 0.1 mm) were measured on the dominant shoots from 150 infections of each sex (300 total plants). Means, standard deviations, maximums, and minimums for these four morphological characters are presented below:

	Female				Male			
	Mean	S. Dev.	Max.	Min.	Mean	S. Dev.	Max.	Min.
Height (cm)	15.6	3.4	27.8	9.6	15.7	3.8	32.8	7.8
Base (mm)	3.8	0.8	6.9	2.1	3.5	0.9	7.8	2.3
Third Internode Length (mm)	12.2	2.3	19.0	7.0	11.8	2.6	21.0	6.0
Width (mm)	2.7	0.5	4.5	1.9	2.5	0.5	4.4	1.7

The largest plants found were males (approximately 33 cm), heights which slightly exceeded the maximum value (30 cm) reported by Wiens and Shaw (1994); otherwise, these sizes and ranges are consistent with those reported by Wiens and Shaw. It is interesting to note that based on our measurements of 300 Hawksworth's dwarf mistletoe plants [the largest set of plant measurements completed for a single dwarf mistletoe species of which we are aware (see Hawksworth and Wiens 1996)], male and female plants do not differ significantly in these four morphological characters. So while this species definitely displays a distinctive sexual dimorphism (Wiens and Shaw 1994), male and female size is approximately the same.

Phenology

Male plants of Hawksworth's dwarf mistletoe were still flowering on March 5, 1998 at elevations over 800 m in the Mountain Pine Ridge area. As was reported by Wiens and Shaw (1994), male flowers had perianths that were predominantly 3-merous and rarely 4-merous, but we did not observe male flowers with the vivid red color inside the perianth lobes described by Wiens and Shaw. The male flowers we observed were the same color on the inside as on the outside - a shade of yellowish-brown that is slightly darker than the staminate spike shoot color. Female flowers were in an early stage of fruit development on many plants and no mature fruits were observed on this date (early March). Wiens and Shaw (1994) speculated that Hawksworth's dwarf mistletoe disperses its seed in June. However, our observations in early June 1998 indicated that fruits were immature. Additional observations from August 18-20, 1998 revealed only a few fruits nearing maturity. At this time, no seeds were being dispersed and attempts to manually expel seeds were unsuccessful. Incipient seed dispersal was observed in early

October 1999. Anthesis was not occurring in June 1998, August 1998, or October 1999. Wiens and Shaw (1994) speculated that Hawksworth's dwarf mistletoe has multiple flowering and seed dispersal periods. However, this taxon appears to have only one period of anthesis annually (mid January through early March) and one annual seed dispersal period that we estimate is from mid October through November. Therefore, fruit maturation only requires 7 - 8 months. We plan to visit Belize again in early November 2000 to document seed dispersal of Hawksworth's dwarf mistletoe.

Sex Ratio

Dwarf mistletoes are dioecious and most species have a 1:1 sex ratio (Hawksworth and Wiens 1996), but some species are reported to have a female-biased sex ratio (Hawksworth and Wiens 1996, Wiens et al. 1996). In May and August 1998 we systematically examined separate infections of Hawksworth's dwarf mistletoe and determined their sex based on flower morphology of mature plants. Twenty *Pinus caribaea* var. *hondurensis* were felled and the sex of mature mistletoe plants determined. Of 1066 infections examined, 522 were male and 544 were female, thus the sex ratio is essentially 1:1 like most species of *Arceuthobium*.

Honduran Dwarf Mistletoe (*Arceuthobium hondurense* Hawksw. & Wiens)

Honduran dwarf mistletoe was described in 1970 from southeast of Tegucigalpa, Honduras on *Pinus oocarpa* (Hawksworth and Wiens 1970). Hawksworth and Wiens (1972, 1996) speculated that this dwarf mistletoe could be so rare in Honduras that it might be in danger of extinction if the extensive harvesting of pine forests continued. Since then, three additional populations of this rare dwarf mistletoe have been discovered (Beatty et al. 1998, Mathiasen et al. 1999b). The four known locations in Honduras are:

1. Cusuco National Park, Cortes - approximately 20 km northwest of San Pedro Sula.
2. Piedra Grande Area, Francisco Morazan - approximately 20 km southeast of Tegucigalpa.
3. Lepaterique Area, Francisco Morazan - approximately 5 km east of Lepaterique.
4. Celaque National Park, Lempira - on main trail to mountain summit from visitor's center.

However, so little is still known about its host range and distribution in Central America that it can still be considered one of the rarest dwarf mistletoes described from the Western Hemisphere. It may also occur in El Salvador in the vicinity of Montecristo (Santa Ana Province) near the borders of Honduras and Guatemala, but this tentative report (Hawksworth and Wiens 1996) needs to be confirmed. Our brief attempt to locate this dwarf mistletoe in the Montecristo area in 1999 failed. However, we agree with Hawksworth and Wiens that should dwarf mistletoe be discovered in the Montecristo area, it most likely would be Honduran dwarf mistletoe because the most common host there is *P. oocarpa*.

Based on our observations of Honduran dwarf mistletoe in Honduras and of black dwarf mistletoe (*Arceuthobium nigrum* Hawksw. & Wiens) in Mexico, we concluded that the

black dwarf mistletoe populations in Chiapas, Mexico, should be classified as Honduran dwarf mistletoe. Our identification was based on morphological characters (plant color and size, male flower perianth lobe color, female flower stigma length) and host range of the dwarf mistletoe in Chiapas and Honduras (parasitism of *P. tecunumanii*). To determine whether these populations were best assigned to *A. nigrum* or *A. hondurense*, plant samples were obtained from Chiapas, Mexico and Honduras. Sequences of nuclear ITS rDNA clearly indicate that the Chiapan plants are very closely related to *A. hondurense* from Honduras, not *A. nigrum* (from Oaxaca, Mexico). These results thus confirm our suspicions based upon morphological characters. Moreover, the geographic range and number of populations of Honduran dwarf mistletoe have been modified dramatically. This also indicates that the report of black dwarf mistletoe in Guatemala (Hawksworth and Wiens 1977) was probably based on an observation of Honduran dwarf mistletoe. Therefore, it now appears that the Honduran dwarf mistletoe is not in danger of extinction as suggested by Hawksworth and Wiens (1996, p. 222).

Host Range

Thus far, Honduran dwarf mistletoe has only been reported to parasitize *Pinus oocarpa* and *P. tecunumanii* (Mathiasen et. al. 1999a, Mathiasen et. al. 2000). Hawksworth and Wiens (1996) recorded the host of Honduran dwarf mistletoe in northwestern Honduras as *P. maximinoi*, but this host classification was tentative and based on information provided to one of us (J. S. Beatty) by Honduran Forestry personnel. Our examination of the pines being parasitized in northwestern Honduras indicates that the host is *P. oocarpa* var. *ochoterenai* (or *P. tecunumanii* depending on which pine expert you follow) and not *P. maximinoi* as reported by Hawksworth and Wiens. Therefore, we conclude that Honduran dwarf mistletoe only parasitizes *P. oocarpa* and *P. tecunumanii* in Honduras (Mathiasen et. al. 1999a, Mathiasen et. al. 2000). Because so little is currently known about the distribution and host range of Honduran dwarf mistletoe, it is likely that once its distribution is better documented in Central America, it may be found parasitizing other species of *Pinus*.

Plant Measurements

Measurements were made from fresh specimens of male and female plants of Honduran dwarf mistletoe collected in March and August, 1998. Measured characters were the same as for Hawksworth's dwarf mistletoe (above), but only 25 infections of each sex were measured for this species. Means, standard deviations, maximums, and minimums for these four morphological characters are presented below:

	Female				Male			
	Mean	S. Dev.	Max.	Min.	Mean	S. Dev.	Max.	Min.
Height (cm)	13.6	3.0	19.4	9.1	20.2	4.5	32.2	11.5
Base (mm)	4.0	0.6	5.8	2.8	4.4	0.7	6.3	3.6
Third Internode Length (mm)	10.7	2.5	16.0	7.0	14.0	2.3	18.0	8.0
Width (mm)	3.3	0.3	3.9	2.7	3.4	0.5	4.8	2.8

The sizes and ranges of these characters for female plants are nearly identical to those reported for this taxon (both sexes combined) by Hawksworth and Wiens (1972, 1996), but the sizes and ranges for male plants are larger. For instance, the largest plant (s) reported by Hawksworth and Wiens (either sex) was only 21 cm compared to the 32-cm male plant we measured from southeast of Tegucigalpa. However, measurements of the Chiapan populations of Honduran dwarf mistletoe indicate that male plants can exceed 50 cm in height. In addition, our observations of this mistletoe from several locations indicate the color of both male and female plants varies from the olive-brown, grayish green colors reported by Hawksworth and Wiens (1972, 1996) to dark brown (nearly black) and reddish brown.

Phenology

Male plants of Honduran dwarf mistletoe had begun flowering and some fruits on female plants were beginning to disperse seed in late August 1998. Therefore, flowering and seed dispersal of Honduran dwarf mistletoe starts slightly earlier than September, which was reported by Hawksworth and Wiens (1972, 1996) as the period of both flowering and seed dispersal. However, we have also found male plants of Honduran dwarf mistletoe flowering in March and November, so this mistletoe may have two or more flowering periods. It is also possible that different populations flower at different times throughout the year. The inside of male flower perianths of Honduran dwarf mistletoe is bright red as previously reported (Hawksworth and Wiens 1972, 1996), but perianth lobes become the same color as male shoots when dried. Just as for Hawksworth's dwarf mistletoe, male and female plants of Honduran dwarf mistletoe also demonstrate a high degree of sexual dimorphism. Male plants are more open and spreading and female plants are more compact and densely branched.

Sex Ratio

In August 1998 we systematically examined infections on five *Pinus oocarpa* trees and determined the sex of 64 mature mistletoes. On small trees (less than 6 m in height) binoculars were used to score mistletoe sex from the ground. Only one larger tree (10 m in height) with several infections was destructively sampled. The sex ratio of this small sample of mature plants was essentially 1:1 (31 females and 33 males), but a larger sample is needed to confirm this preliminary finding.

Black Dwarf Mistletoe (*Arceuthobium nigrum* Hawksw. & Wiens)

Hawksworth and Wiens (1977) speculated that black dwarf mistletoe occurs in western Guatemala (Department San Marcos) based on a report by Dr. Ed Clark. Unfortunately, Dr. Clark did not collect specimens of the "black" dwarf mistletoe he observed. Although the distribution map in Hawksworth and Wiens (1996) indicates this mistletoe does occur in western Guatemala, their discussion of its distribution (page 229) mentions that it is only a possibility that this species occurs in Guatemala. Our attempts to find black dwarf mistletoe near San Marcos, Guatemala, have not been successful. The pine forests around San Marcos have also been extensively harvested and it will be difficult to find this dwarf mistletoe if it does still occur in that area. As our discussions above indicate, we now know the population of this mistletoe in Chiapas is actually Honduran dwarf mistletoe. Therefore, we believe the "black" dwarf mistletoe seen in Guatemala was probably a population of Honduran dwarf mistletoe. Therefore, the most southern populations of black dwarf mistletoe known are in central Oaxaca, Mexico (Hawksworth and Wiens 1996).

Phylogenetic Relationships and Classification of Central American *Arceuthobium*

The previously published molecular phylogeny of *Arceuthobium* based on ITS rDNA sequences included 22 taxa (Nickrent et al. 1994). The affinities of *A. hawksworthii* and *A. aureum* ssp. *aureum* were mentioned in Nickrent (1996, p. 171), although these taxa were not included on the phylogram published in that chapter. In addition to these two taxa, ITS sequences have since been obtained from *A. hondurense*, *A. globosum* ssp. *grandicaule*, and *A. aureum* ssp. *petersonii* (Figure 2). Many of the previously reported relationships (clades) remain, but the addition of the new taxa provided greater resolution. For example, both subspecies of *A. globosum* and *A. aureum* are very closely related and occur on a well-supported clade. As mentioned above, the taxon originally named as *A. nigrum* from Chiapas has an ITS sequence nearly identical to the accession of *A. hondurense* from Honduras. These sequences are most closely related to *A. hawksworthii*. A relationship between *Arceuthobium bicarinatum* Urban, a species that occurs on the island of Hispaniola, and *A. hondurense* had been proposed based upon morphological evidence (Hawksworth and Wiens 1996). ITS data do not support this proposed relationship but indicate that *A. hondurense* is a component of Series *Stricta* along with A. *durangense, A. strictum*, and *A. vaginatum*. Moreover, ITS analyses indicate that *A. bicarinatum* is a component of Series *Pusilla* and is most closely related to *A. pusillum* of eastern North America, a surprising result given their divergent morphologies. Given these genetic data, the classification proposed in Nickrent (1996) must be ammended. It is proposed that *A. hondurense* be moved from Section *Pusilla* into Series *Stricta*. Because Section *Pusilla* emerges as a clade among other Series of Section *Vaginata*, a classification that is more compatible with the molecular data would rename this Section as a Series.

Plant Collections

Specimens of the above dwarf mistletoes collected from our trips to Central America and southern Mexico have been deposited at the Deaver Herbarium, Northern Arizona University, Flagstaff, AZ; the US National Herbarium, Washington, D.C.; the Forestry Herbarium, Ministry of Agriculture, Belmopan, Belize; the Herbario Paul C. Standley, Escuela Agricola Panamericana, Zamorano, Honduras; and the Herbario, Escuela Nacional de Ciencias Forestales, Siguatepeque, Honduras.

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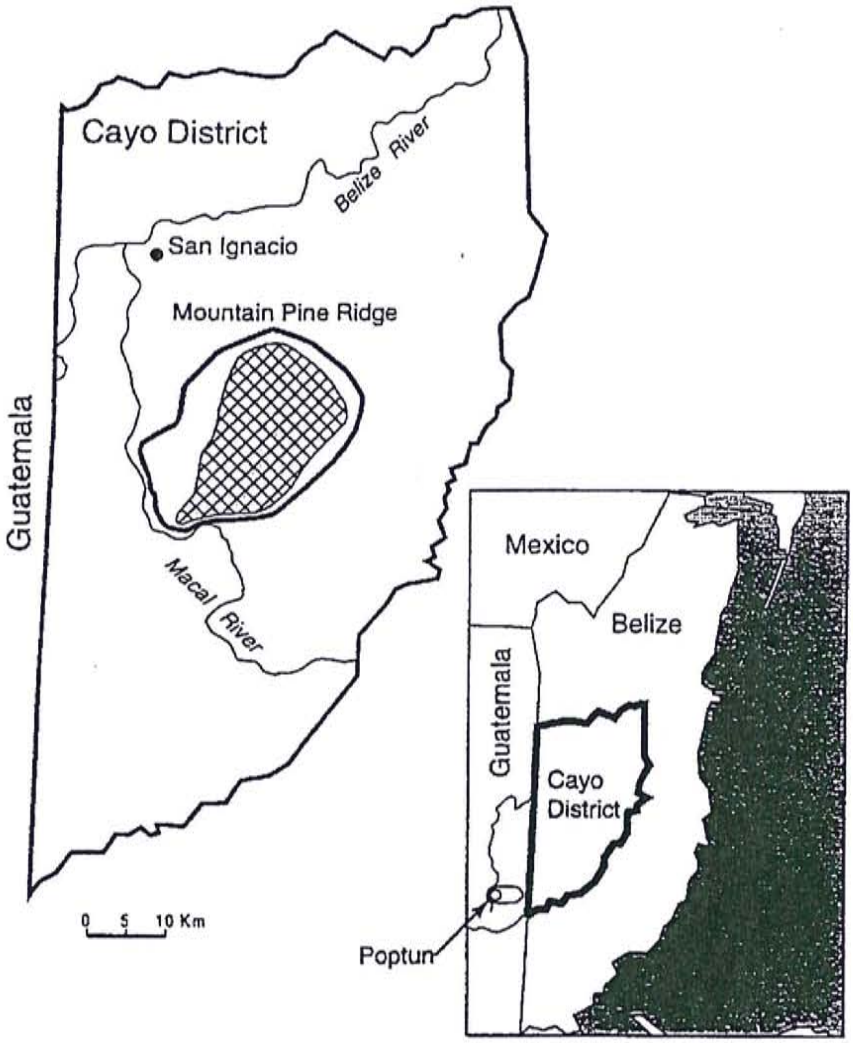

Figure 1. Location of the Mountain Pine Ridge Region (MPR) in Belize and the approximate distribution of *Arceuthobium hawksworthii* within the MPR. The thick line in blow-up represents the MPR and the cross-hatched area represents the distribution of *A. hawksworthii* (approximately 250 sq. km). Approximate area of pine forests surveyed in Guatemala is indicated by dark line around Poptun.

Figure 2. Strict consensus phylogram (of 10 equally parsimonious trees of length 733) derived from an analysis of nuclear ribosomal ITS sequences. Numbers above the branches represent number of nucleotide substitutions, numbers below the branches are bootstrap percentage values (100 replications). Nodes without bootstrap values were present in less than 50% of the replications (i.e. not strongly supported). If Section Pusilla were reduced to a series, then Section Vaginata would be monophyletic, albeit with only 36% bootstrap support. Species abbreviations are as follows:

ABM = A. abietinum (Engelm.) Hawksw. & Wiens f. sp. magnificae Hawksw. & Wiens

ABR = A. abietis-religiosae Heil.

AME = A. americanum Nutt. ex Engelm.

APA = A. apachecum Hawksw. & Wiens

AUR-AUR = A. aureum Hawksw. & Wiens ssp. aureum

AUR-PET = A. aureum ssp. petersonii Hawksw. & Wiens

BIC = A. bicarinatum Urban

CAM = A. campylopodum Engelm.

DIV = A. divaricatum Engelm.

DOU = A. douglasii Engelm.

DUR = A. durangense (Hawksw. & Wiens) comb. nov.]

GIL = A. gillii Hawksw. & Wiens ssp. gillii

GLO-GLO = A. globosum Hawksw. & Wiens ssp. globosum

GLO-GRA = A. globosum ssp. grandicaule Hawksw. & Wiens

GUA = A. guatemalense Hawksw. & Wiens

HON = A. hondurense Hawksw. & Wiens

MIC = A. microcarpum (Engelm.) Hawksw. & Wiens

NIG = A. nigrum (Hawksw. & Wiens) comb. nov.]

OXY = A. oxycedri (DC) M. Bieb.

PEN = A. pendens Hawksw. & Wiens

PUS = A. pusillum Peck

RUB = A. rubrum Hawksw. & Wiens

STR = A. strictum Hawksw. & Wiens

VAV = A. vaginatum (Willd.) Presl. ssp. vaginatum

VAC = A. vaginatum ssp. cryptopodum (Engelm.) Hawksw. & Wiens

VER = A. verticilliflorum Engelm.

Figure 2 (cont.).