New Combinations for *Arceuthobium aureum* (Viscaceae) in Mexico and Central America

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ABSTRACT. Morphological and molecular analyses of *Arceuthobium aureum* Hawksworth & Wiens and *A. globosum* Hawksworth & Wiens (Viscaceae) demonstrated that these taxa are closely related but can be distinguished based on a few morphological differences, phenology, and host ranges. Therefore, the taxa previously treated under *A. aureum* are recombined under *A. globosum*: *A. globosum* subsp. *aureum* (Hawksworth & Wiens) Mathiasen and *A. globosum* subsp. *petersonii* (Hawksworth & Wiens) Mathiasen.

Key words: *Arceuthobium*, Central America, dwarf mistletoe, Mexico, Viscaceae.

Hawksworth and Wiens described *Arceuthobium globosum* Hawksworth & Wiens (Viscaceae) in 1965 from northern Mexico, but mentioned that this species was widely distributed in Mexico and also occurred in Guatemala and Belize (Hawksworth & Wiens, 1965). In their first monograph of the genus *Arceuthobium* M. Bieberstein (Hawksworth & Wiens, 1972), they emphasized that *A. globosum* was highly variable, and that further field research was needed to determine whether this observed variation warranted finer segregation of this species. They later subdivided *A. globosum* into five taxa as follows (Hawksworth & Wiens, 1977, 1996; Wiens & Shaw, 1994): *A. globosum* subsp. *globosum*, *A. globosum* subsp. *grandicaule* Hawksworth & Wiens, *A. aureum* Hawksworth & Wiens subsp. *aureum*, *A. aureum* subsp. *petersonii* Hawksworth & Wiens, and *A. hawksworthii* Wiens & C. G. Shaw bis. These taxa were primarily distinguished from each other by the size of dominant male or female plants, plant color, host range, geographic distribution, phenology, and their tendency to initiate or not initiate the formation of witches' brooms on their pine hosts.

The taxonomic affinities of the *Arceuthobium globosum* complex have been further substantiated through the molecular work of D. L. Nickrent and his coworkers (Nickrent et al., 1994, 2004). The molecular evidence uncovered so far has shown that *A. globosum* and *A. aureum* cannot be differentiated using ITS DNA or chloroplast *trnL* DNA sequences. Furthermore, Nickrent et al. (2004) demonstrated that *A. hawksworthii* is more closely related to *A. hondurense* Hawksworth & Wiens than to *A. aureum*. After additional morphological measurements and observations of the phenology and host ranges of *A. hawksworthii* and *A. hondurense*, Mathiasen (2007) proposed a new combination for *A. hawksworthii*: *A. hondurense* subsp. *hawksworthii* (Wiens & C. G. Shaw bis) Mathiasen.

Because the *Arceuthobium globosum* group is widespread in Mexico and Central America and represents several of the most economically damaging dwarf mistletoes in these regions (Hawksworth & Wiens, 1972, 1996), I began detailed field studies of the morphology, phenology, geographic distribution, and host range of this important group of dwarf mistletoes in 1998. The molecular and morphological data and observations of phenology support a reclassification of *A. aureum*, and its subspecies, as subspecies of *A. globosum*. These data also support the current classification of the populations of *A. globosum* in central Mexico at the subspecific level (subsp. *grandicaule*). This subspecies extends through southern Mexico and Guatemala into Honduras, and its distribution overlaps with *A. aureum* in southern Mexico (Hawksworth & Wiens, 1996; Melgar et al., 2001; Mathiasen et al., 2003) (Fig. 1). In addition, subspecies *grandicaule* parasitizes some of the same hosts as *A. aureum* (Hawksworth & Wiens, 1996). The distribution of *A. globosum* subsp. *globosum* is confined to northwestern Mexico and does not overlap with subspecies *grandicaule* or *A. aureum*; furthermore, only one of the hosts parasitized by *A. globosum* subsp. *globosum* occurs within the geographic range of *A. globosum* subsp. *grandicaule*, and none occur within the range of *A. aureum* (Hawksworth & Wiens, 1996).

1. **Arceuthobium globosum** Hawksworth & Wiens, Brittonia 17: 223. 1965. TYPE: Mexico. Durango: 1.5 mi. E of El Salto on Hwy. 40, on *Pinus cooperi*, 22 Mar. 1963, *D. Wiens & F. G. Hawksworth 3314* (holotype, COLO; isotypes, MEXU, MO, US). Figure 1, locality 17.

The original collection citation for the type specimen was erroneously published as *F. G. Hawksworth & D. Wiens 3414*, Brittonia 17: 225. 1965.

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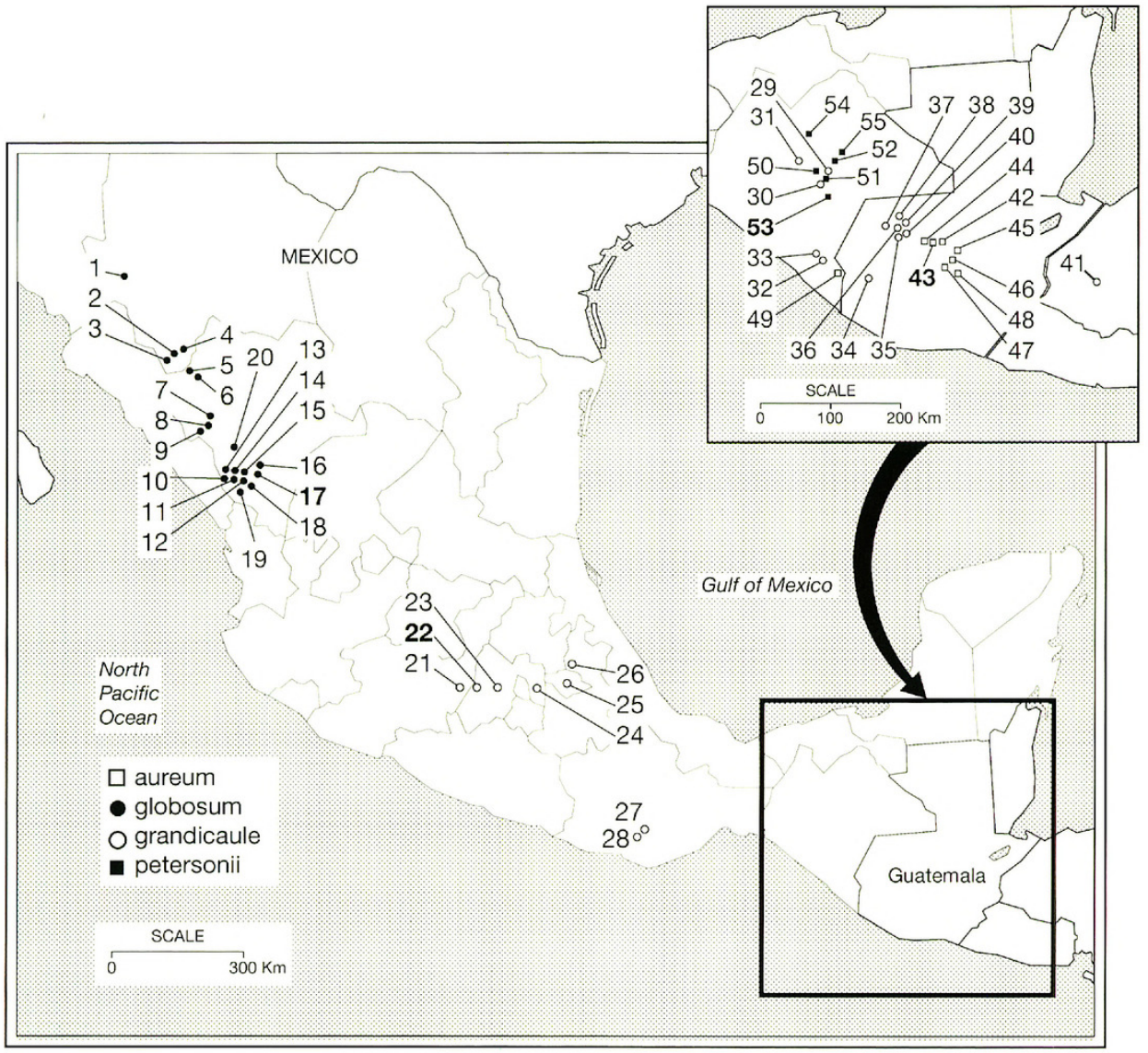

Figure 1. Approximate locations of populations sampled for *Arceuthobium globosum* subsp. *globosum*, (closed circles), *A. globosum* subsp. *grandicaule* (open circles), *A. globosum* subsp. *aureum* (open squares), and *A. globosum* subsp. *petersonii* (dark squares) in Mexico and Central America. Bold numbers represent type localities. *Arceuthobium globosum* subsp. *globosum*: MEXICO. Chihuahua: —1. Ejido Calaveras. —2. Ejido Penito. —3. Cerro Mohinora. —4. El Ocote. Durango: —5. Cocono. —6. 20 km NW of Guanaceví. —7. 15.5 km SW of Altares. —8. 21 km SW of Altares. —9. 40 km SW of Altares. —10. 53 km W of El Salto. —11. 31.5 km W of El Salto. —12. 30 km W of El Salto. —13. 34 km W of El Salto. —14. 22 km W of El Salto. —15. Km post 136 on Mexico Rte. 40. —16. 3.2 km E of El Salto. —**17**. 2.4 km E of El Salto. —18. Ejido El Vriantana. —19. 43 km S of El Salto. —20. 15 km S of San Miguel de las Cruces. *Arceuthobium globosum* subsp. *grandicaule*: MEXICO. Michoacán: —21. 2 km E of San José de la Cumbre. México: —**22**. 35 km E of Zitácuaro. —23. Nevada de Toluca. —24. Llano Grande. Tlaxcala: —25. La Malinche. Puebla: —26. 35 km N of Apizaco. Oaxaca: —27. 35 km S of Miahuatlán. —28. 8 km NW of Suchixtepec. Chiapas: —29. Airport Rd. near San Cristóbal de las Casas. —30. 1.4 km E of jct. of Mexico Rte. 186 and 190 on Rte. 186. —31. 20 km W of San Cristóbal de las Casas. —32. 2.7 km N of La Paz de Rosario. —33. Canada. GUATEMALA. Department San Marcos: —34. Volcán Tajumulco. Department Huehuetenango: —35. 41 km N of Chiantla. —36. 30 km N of Chemal. —37. 5.3 km S of Todos Santos. —38. 21 km N of Santa Eulalia. —39. 18.7 km S of San Juan Ixcoy. —40. 16 km E of Chemal. HONDURAS. —41. Department Lempira: Celaque National Park. *Arceuthobium globosum* subsp. *aureum*: GUATEMALA. Department Alta Verapaz: —42. 3.5 km W of San Cristóbal Verapaz. —**43**. 5 km W of San Cristóbal Verapaz. —44. 8 km W of San Cristóbal Verapaz. —45. 3.3 km E of CA-14 on rd. to Chalisco. Department Baja Verapaz: —46. 5.4 km N of La Cumbre. —47. 1.8 km W of La Cumbre. —48. 1 km S of La Cumbre. MEXICO. Chiapas: —49. El Rosario. *Arceuthobium globosum* subsp. *petersonii*: MEXICO. Chiapas: —50. 0.5 km E of the jct. of Mexico Rte. 186 and 190. —51. 12 km SE of San Cristóbal de las Casas. —52. 18 km E of Rte. 190. —**53**. 52 km SE of San Cristóbal de las Casas. —54. Puebla Nueva. —55. 11 km W of Oxchuc.

1a. Arceuthobium globosum subsp. **globosum**.

Specimens examined. All citations based on *Pinus cooperi* C. E. Blanco, except as noted. MEXICO. **Chihuahua:** 5.5 km S of Calaveras, on *P. durangensis*, 2004 (♂), *Mathiasen 0401* (ASC) (Fig. 1, locality 1); SAGARPA Station, on *P. durangensis*, 2004 (♂), *Mathiasen 0402* (ASC) (Fig. 1, locality 4); 5 km SW of Penito, on *P. durangensis*, 2004 (♂), *Mathiasen 0403* (ASC) (Fig. 1, locality 2); Cerro Mohinora, on *P. durangensis*, 2004 (♂), *Mathiasen 0407* (ASC) (Fig. 1, locality 3). **Durango:** Km post 153 on Mexico Rte. 40, 2003 (♂), *Mathiasen 0301* (ASC), 2005 (♀), *Mathiasen 0541* (ASC) (Fig. 1, locality 10); Km post 136 on Mexico Rte. 40, 2003 (♂), *Mathiasen 0302* (ASC) (Fig. 1, locality 15); 2.4 km E of El Salto on Mexico Rte. 40, 2003 (♂), *Mathiasen 0303* (ASC), 2005 (♀), *Mathiasen 0542* (ASC) (Fig. 1, locality 17); 0.8 km W of Cocono, 2003 (♂), *Mathiasen 0306* (ASC) (Fig. 1, locality 5); 20 km NW of Guanaceví, 2003 (♂), *Mathiasen 0308* (ASC) (Fig. 1, locality 6); 15 km SW of Altares, on *P. durangensis*, 2003 (♂), *Mathiasen 0315* (ASC), 2005 (♀), *Mathiasen 0538* (ASC) (Fig. 1, locality 7), 2003 (♀), *Mathiasen 0316* (ASC); 40 km SW of Altares on rd. to Banome, on *P. durangensis*, 2003 (♂), *Mathiasen 0318* (ASC) (Fig. 1, locality 9); 22 km W of El Salto on Mexico Rte. 40, 2003 (♂), *Mathiasen 0321* (ASC) (Fig. 1, locality 14); 34 km W of El Salto on Mexico Rte. 40, 2003 (♂), *Mathiasen 0323* (ASC) (Fig. 1, locality 13); 30 km W of El Salto on Mexico Rte. 40, 2005 (♀), *Mathiasen 0537* (ASC) (Fig. 1, locality 12); 21.3 km SW of Altares on rd. to Banome, 2005 (♀), *Mathiasen 0539* (ASC) (Fig. 1, locality 8); Ejido El Vriantana, on *P. durangensis*, 2005 (♀), *Mathiasen 0540* (ASC) (Fig. 1, locality 18); 3.2 km E of El Salto on Mexico Rte. 40, 1999 (♂), *Mathiasen 9966* (ASC) (Fig. 1, locality 16); 31.5 km W of El Salto on Mexico Rte. 40, 1999 (♂), *Mathiasen 9969* (ASC) (Fig. 1, locality 11); 43 km S of El Salto on rd. to Pueblo Nuevo, 2007 (♀), *Mathiasen 0711* (ASC) (Fig. 1, locality 19); 15 km S of San Miguel de las Cruces, 2007 (♀), *Mathiasen 0721* (ASC) (Fig. 1, locality 20).

1b. Arceuthobium globosum subsp. **aureum** (Hawksworth & Wiens) Mathiasen, comb. nov. Basionym: *Arceuthobium aureum* Hawksworth & Wiens, Brittonia 29: 414. 1977. TYPE: Guatemala. Alta Verapaz: 5 km W of San Cristóbal Verapaz on Rte. 7W, 1600 m, 7 Feb. 1975, *F. G. Hawksworth, D. Wiens & G. Player 1596* (holotype, US; isotypes, ENCB, INIF, MEXU, MO, UT). Figure 1, locality 43.

Plants 8–31 cm in height (mean ca. 15 cm); basal diam. of dominant plants 3–13 mm (mean ca. 5 mm); third internode length 10–30 mm (mean ca. 17 mm), 2–7 mm (mean ca. 3 mm) wide; staminate and pistillate plants primarily yellow (golden). Staminate flowers 3- and 4-partite, mean diam. of 3-partite flowers 2.2 mm, mean diam. of 4-partite flowers 2.9 mm. Mature fruit length 3.6–4.6 mm (mean 4.1 mm), 2.3–3 mm wide (mean 2.7 mm); seeds 2.1–2.8 (mean 2.4) mm long, 1–1.3 (mean 1.2) mm wide.

Phenology. Anthesis occurs from mid-February through June with no evident peak. Seed dispersal occurs from August to early October, with no clear peak period of dispersal. Anthesis is continuous during the dry season in Guatemala (March–June).

Specimens examined. All citations based on *Pinus maximinoi* H. E. Moore. GUATEMALA. **Alta Verapaz:** 3.5 km W of San Cristóbal Verapaz on Rte. 7W, 1999 (♂ & ♀), *Mathiasen 9919* (ASC) (Fig. 1, locality 42); 3.3 km E of CA-14 on rd. to Chalisco, 2006 (♂ & ♀), *Mathiasen 0622* (ASC) (Fig. 1, locality 45); 5 km W of San Cristóbal Verapaz on Rte. 7W, 2006 (♂ & ♀), *Mathiasen 0623* (ASC) (Fig. 1, locality 43); 8 km W of San Cristóbal Verapaz on Rte. 7W, 2000 (♂ & ♀), *Mathiasen 0006* (ASC) (Fig. 1, locality 44). **Baja Verapaz:** 1 km S of La Cumbre on Rte. CA-14, 1999 (♂ & ♀), *Mathiasen 9916* (ASC), 2006 (♂ & ♀), *Mathiasen 0621* (ASC) (Fig. 1, locality 48); 5.4 km N of La Cumbre on Rte. CA-14, 1999 (♂ & ♀), *Mathiasen 9917* (ASC) (Fig. 1, locality 46); 1.8 km W of La Cumbre on rd. to Soloma, 2000 (♂ & ♀), *Mathiasen 0005* (ASC) (Fig. 1, locality 47). MEXICO. **Chiapas:** Km 43 on Mexico Rte. 200 near Motozintla, 2002 (♂ & ♀), *Mathiasen 0203* (ASC) (Fig. 1, locality 49).

1c. Arceuthobium globosum subsp. **petersonii** (Hawksworth & Wiens) Mathiasen, comb. nov. Basionym: *Arceuthobium aureum* Hawksworth & Wiens subsp. *petersonii* Hawksworth & Wiens, Brittonia 29: 415. 1977. TYPE: Mexico. Chiapas: near Km 136 on Panamerican Hwy., 52 km SE of San Cristóbal de las Casas, on *Pinus pseudostrobus*, 2250 m, 8 Feb. 1975, *F. G. Hawksworth, D. Wiens & G. Player 1598* (holotype, US; isotypes, ENCB, INIF, MEXU, MO, UT). Figure 1, locality 53.

Plants 18–46 cm in height (mean ca. 30 cm); basal diam. of dominant plants 4–23 mm (mean ca. 10 mm); third internode length 9–38 mm (mean ca. 24 mm), 3–16 mm (mean ca. 6 mm) wide; staminate and pistillate plants yellow-brown. Staminate flowers 3- and 4-partite, mean diam. of 3-partite flowers 2.2 mm, mean diam. of 4-partite flowers 3 mm. Mature fruit length 4.5–5.7 mm (mean 5.1 mm), 2.9–4 mm wide (mean 3.4 mm); seeds 2.4–3.2 (mean 2.9) mm long and 1.2–1.6 (mean 1.4) mm wide.

Phenology. Anthesis occurs from mid-August through early October with a peak in mid-September. Seed dispersal occurs from mid-August to early October with a peak in mid-September.

Discussion. My field observations and plant measurements of three *Arceuthobium globosum* populations near San Miguel Suchixtepec, Oaxaca, Mexico, indicate these populations are representative of subspecies *grandicaule* and not subspecies *petersonii*. Male plants of these populations were not flowering in September 2006, which is further evidence that these populations are not subspecies *petersonii*. Therefore, further fieldwork is needed in Oaxaca to determine if

subspecies *petersonii* occurs there as reported by Hawksworth and Wiens (1977, 1996).

Specimens examined. All citations based on *Pinus pseudostrobus* Lindley, except as noted. MEXICO. **Chiapas:** 0.5 km E of jct. of Mexico Rte. 186 & 190 on Rte. 186, 2002 (♂ & ♀), *Mathiasen 0201* (ASC) (Fig. 1, locality 50); 52 km SE of San Cristóbal de las Casas (at Km 136) on Rte. 190, 2000 (♂ & ♀), *Mathiasen 0008* (ASC), 2002 (♂ & ♀), *Mathiasen 0212* (ASC), 2005 (♂ & ♀), *Mathiasen 0573* (ASC), 2006 (♂ & ♀), *Mathiasen 0638* (ASC) (Fig. 1, locality 53); 2.1 km N of Puebla Nueva, on *P. maximinoi*, 2002 (♂ & ♀), *Mathiasen 0208* (ASC) (Fig. 1, locality 54); 11 km W of Oxchuc on Mexico Rte. 186, 2000 (♂ & ♀), *Mathiasen 0018* (ASC) (Fig. 1, locality 55); 12 km SE of San Cristóbal de las Casas, 2006 (♂ & ♀), *Mathiasen 0639* (ASC) (Fig. 1, locality 51); 18 km E of Rte. 190 on Rte. 186, on *P. montezumae* A. B. Lambert, 2006 (♂ & ♀), *Mathiasen 0640* (ASC) (Fig, 1, locality 52).

1d. Arceuthobium globosum subsp. **grandicaule** Hawksworth & Wiens, Brittonia 29: 413. 1977. TYPE: Mexico. México: Km 59 on Hwy. 15, 35 km E of Zitácuaro, 2600 m, on *Pinus montezumae*, 13 Feb. 1975, *F. G. Hawksworth & G. Player 1607* (holotype, US; isotypes, ENCB, FPF, INIF, MEXU, MO, UT). Figure 1, locality 22.

Specimens examined. All citations based on *Pinus pseudostrobus*, except as noted. GUATEMALA. **Huehuetenango:** 30 km N of Chemal on rd. to Soloma, on *P. hartwegii*, 1999 (♂), *Mathiasen 9921* (ASC) (Fig. 1, locality 36); 5.3 km S of Todos Santos, 1999 (♂), *Mathiasen 9922* (ASC) (Fig. 1, locality 37); 41 km N of Chiantla on rd. to Soloma, on *P. hartwegii*, 1999 (♂), *Mathiasen 9925* (ASC) (Fig. 1, locality 35); 21 km N of Santa Eulalia on rd. to Barillas, on *P. hartwegii*, 1999 (♂), *Mathiasen 9929* (ASC) (Fig. 1, locality 38); 18.7 km S of San Juan Ixcoy on rd. to Soloma, on *P. hartwegii*, 1999 (♂), *Mathiasen 9930* (ASC) (Fig. 1, locality 39); 16 km E of Barillas rd. near Chemal, on *P. hartwegii*, 2000 (♂), *Mathiasen 0005* (ASC) (Fig. 1, locality 40). **San Marcos:** ca. 5 km W of Villa Nueva on Volcán Tajumulco, on *P. hartwegii*, 1999 (♂), *Mathiasen 9927* (ASC) (Fig. 1, locality 34). HONDURAS. **Lempira:** summit of Cerro Las Minas, Celaque Natl. Park, on *P. hartwegii*, 2000 (♂), *Mathiasen 0054* (ASC) (Fig. 1, locality 41). MEXICO. **Chiapas:** 1.4 km E of jct. of Rte. 186 & 190 on Rte. 186, 2000 (♀), *Mathiasen 0022* (ASC) (Fig. 1, locality 30); 2.7 km N of La Paz de Rosario, 2002 (♀), *Mathiasen 0204* (ASC) (Fig. 1, locality 32); 0.2 km N of Canada, 2002 (♀), *Mathiasen 0207* (ASC) (Fig. 1, locality 33); 20 km W of San Cristóbal de las Casas on Mexico Rte. 190, 2002 (♀), *Mathiasen 0211* (ASC) (Fig. 1, locality 31); 1.1 km W of Mexico Rte. 186 on airport rd., 2002 (♀), *Mathiasen 0214* (ASC) (Fig. 1, locality 29). **México:** 35 km E of Zitácuaro on Mexico Rte. 59, on *P. montezumae*, 1998 (♀), *Mathiasen 98142* (ASC) (Fig. 1, locality 22); 1.5 km S of Railes on rd. to Nevada de Toluca, on *P. hartwegii*, 1998 (♀), *Mathiasen 98144* (ASC) (Fig. 1, locality 23); 4 km S of Llano Grande, on *P. hartwegii*, 2001 (♂), *Mathiasen 0114* (ASC), 2005 (♀), *Mathiasen 0550* (ASC) (Fig. 1, locality 24). **Michoacán:** 26 km E of Morelia on Mexico Rte. 15, 1998 (♀), *Mathiasen 98143* (ASC) (Fig. 1, locality 21). **Oaxaca:** 35 km S of Miahuatlán on Mexico Rte. 175, 2006 (♀), *Mathiasen 0645* (ASC) (Fig. 1, locality 27); 8 km NW of San Miguel Suchixtepec on Mexico Rte. 175, 2006 (♀), *Mathiasen 0644* (ASC) (Fig. 1, locality 28). **Puebla:** 35 km N of Apizaco, on *P. hartwegii*, 2005 (♀), *Mathiasen 0549* (ASC) (Fig. 1, locality 26). **Tlaxcala:** La Malinche, on *P. hartwegii*, 2001 (♂), *Mathiasen 0115* (ASC), 2005 (♀), *Mathiasen 0548* (ASC) (Fig. 1, locality 25).

Morphology. Twenty populations of subspecies *globosum* were measured from northern Mexico; 13 populations of subspecies *grandicaule* were measured from central and southern Mexico, seven from Guatemala, and one from Honduras; seven populations of subspecies *aureum* were measured from Guatemala and one from southern Mexico; and six populations of subspecies *petersonii* were measured from Chiapas, Mexico (Fig. 1). These populations included the type locality for each taxon as well as several populations not previously sampled by Hawksworth and Wiens (1965, 1977, 1996). For each population, 10 or 20 male and 10 or 20 female plants were collected and the largest shoot from each collection was used for morphological measurements. Plant measurements were made within 24 hours of collection.

The dwarf mistletoe characters measured were those used by Hawksworth and Wiens (1996) for taxonomic classification: (1) height, basal diameter, third internode length and width, and color of the tallest male and female shoot from each infection collected; (2) mature fruit length, width, and color; (3) seed length, width, and color; (4) staminate flower diameter for flowers with three perianth lobes and four perianth lobes, respectively; (5) number, color of the adaxial surface, and length and width of staminate perianth lobes; (6) anther distance from the perianth lobe tip; and (7) anther diameter. At least 100 measurements were made for mature fruits and staminate flowers. In addition, the width of the terminal staminate spike was measured because this character distinguishes *Arceuthobium globosum* from *A. aureum* (Hawksworth & Wiens, 1977).

The principal morphological differences between the subspecies of *Arceuthobium globosum* were plant dimensions, plant color, staminate flower diameter, and staminate spike width (Table 1, Appendices A and B; appendices available online at http://www.for.nau.edu/SOFArchive/Faculty/RLMathiasen/080529-01.pdf). Both male and female plants of subspecies *grandicaule* were the largest of the subspecies and those of subspecies *aureum* were the smallest. Plants of subspecies *globosum* and *petersonii* were intermediate in height, basal diameter width, and third internode dimensions. The primary morphological characteristics distinguishing subspecies *grandicaule* from the other subspecies were its very large plants and shoot color. It

Table 1. Principal morphological and physiological differences between the subspecies of *Arceuthobium globosum*. Measures are expressed as mean (range) values.

Characters	*A. globosum* subsp. *globosum*	*A. globosum* subsp. *grandicaule*	*A. globosum* subsp. *aureum*	*A. globosum* subsp. *petersonii*
Plant height (cm)				
Male plants				
Mean	21 (11–42)	45 (17–93)	15 (8–31)	32 (19–46)
Female plants				
Mean	20 (8–45)	38 (17–66)	14 (8–22)	27 (18–46)
Basal diameter (mm)				
Male plants				
Mean	11 (5–32)	16 (6–37)	5 (3–13)	10 (4–23)
Female plants				
Mean	13 (4–26)	18 (6–40)	6 (3–13)	13 (7–20)
Width of terminal staminate spike (mean, mm)	1.9	2.0	1.2	1.1
Mean staminate flower diameter (mm)				
3 lobes/flower	3.1	3.1	2.2	2.2
4 lobes/flower	4.2	4.2	2.9	3.0
Mean fruit length (mm)	6.7	7.0	4.1	5.1
Mean fruit width (mm)	4.1	4.1	2.7	3.4
Plant color	yellow	yellow-green	yellow (golden)	yellow-brown
Witches' brooms formed	rarely	frequently	frequently	frequently
Peak flowering	March–April	March–April	February–June	September
Peak seed dispersal	June–July	mid-August–mid-September	August–October	September
Distribution	northwest Mexico	central and southern Mexico, Guatemala, and Honduras	Chiapas, Mexico, and Guatemala	Chiapas, Mexico

consistently had male and female plants larger than 40 cm in length, the basal diameter of plants was typically greater than 1.5 cm, and its third internode dimensions were much larger than the other subspecies (Appendices A and B). While the color of male and female plants varied and overlapped to some extent, plants of subspecies *grandicaule* were yellow-green, plants of subspecies *globosum* and *aureum* were usually yellow (golden), and those of subspecies *petersonii* were yellow-brown. However, many male plants of subspecies *grandicaule* in Guatemala were also yellow-brown, but the large size, basal diameters, third internode dimensions, and staminate spike widths of the Guatemalan plants were characteristic of subspecies *grandicaule*. Furthermore, male plants in these populations flowered in March, not September.

The mean diameters of staminate flowers for subspecies *globosum* and *grandicaule* were the same; this was true for both 3- and 4-partite flowers (Table 1). The mean diameters of staminate flowers for subspecies *aureum* and *petersonii* were also the same, but were much smaller than the staminate flowers of subspecies *globosum* and *grandicaule* (Table 1). The mean diameter of staminate flowers was one of the most consistent morphological differences that distinguished subspecies *globosum* and *grandicaule* from subspecies *aureum* and *petersonii*. The mean length and width of fruits of subspecies *globosum* and *grandicaule* were similar, but the fruits of subspecies *petersonii* and *aureum* were consistently smaller. However, the fruits of subspecies *petersonii* were slightly larger than those of subspecies *aureum* (Table 1). Seed dimensions were nearly the same for all four subspecies. Another consistent morphological character that separated subspecies *globosum* and *grandicaule* from subspecies *aureum* and *petersonii* was the width of terminal staminate spikes (Hawksworth & Wiens, 1977). This width was consistently smaller for subspecies *aureum* and *petersonii*; when staminate plants of the four subspecies were compared, this character easily distinguished subspecies *globosum* and *grandicaule* from subspecies *aureum* and *petersonii* (Table 1, Appendix A).

Phenology. Hawksworth and Wiens (1977, 1996) indicated one of the principal physiological differences between the subspecies of *Arceuthobium globosum* was their periods of anthesis and seed dispersal. Therefore, I made additional observations of flowering and seed dispersal from 1999 to 2007. The flowering periods of subspecies *globosum*, *grandicaule*, and *aureum* overlap in the spring (March–May), but subspecies *grandicaule* starts flowering as early as January in central Mexico and subspecies *aureum* continues flowering into June in Guatemala. While the duration of flowering for subspecies

petersonii is still not well established, my observations and those of Hawksworth and Wiens indicate its peak flowering period is consistently in the late summer (September), and not during the spring. Hawksworth and Wiens (1977, 1996) reported that subspecies *aureum* flowers continuously during the dry season (February–May) in Guatemala. My observations of subspecies *aureum* support this, and I found that it flowers well into June. Peak flowering periods for subspecies *globosum* and *grandicaule* are consistently during March. The peak seed dispersal period for subspecies *globosum* is in July (Hawksworth & Wiens, 1996), while the peak seed dispersal for subspecies *grandicaule* is from mid-August to mid-September (Escudero & Cibrián, 1985) in central Mexico. Its peak for seed dispersal in Guatemala is from July to September. Hawksworth and Wiens (1977, 1996) reported that subspecies *petersonii* reached its peak of seed dispersal in June–July, but I found that it peaks in September–October. There is no distinctive peak for seed dispersal of subspecies *aureum* in Guatemala, and female plants were found with some mature fruits whenever observations were made there.

Host susceptibility. *Arceuthobium globosum* subsp. *aureum* is parasitic principally on *Pinus maximinoi* in Guatemala. Although it has been reported to parasitize *P. pseudostrobus*, *P. montezumae*, *P. pseudostrobus* var. *apulcensis* (Lindley) Shaw (*P. oaxacana* Mirov), and *P. oocarpa* Schiede ex Schlechtendal in Guatemala (Hawksworth & Wiens, 1977, 1996), I have not observed it on these hosts there. Furthermore, my observations in Guatemala indicate *P. oocarpa* is not susceptible to infection, and therefore, additional observations and field data are needed to clarify the host range of subspecies *aureum* in Guatemala.

In Chiapas, subspecies *petersonii* is parasitic principally on *Pinus pseudostrobus* and *P. montezumae*. My observations at two sites in Chiapas indicate that subspecies *petersonii* does not infect *P. maximinoi*, but this pine is the principal host of subspecies *aureum* in Guatemala. Although *P. oocarpa*, *P. pseudostrobus* var. *apulcensis* (*P. oaxacana*), and *P. devoniana* Lindley (*P. michoacana* Martínez) have been reported to be principal hosts of subspecies *petersonii* in Chiapas (Hawksworth & Wiens, 1996), they are much less susceptible than *P. pseudostrobus* and *P. montezumae*. However, I do not have enough quantitative data on the susceptibility of these pines to place them into the susceptibility classes used by Hawksworth and Wiens (1996). Hawksworth and Wiens (1996) reported that *P. patula* Schiede ex Schlechtendal & Chamisso was a principal host of subspecies *petersonii*, but I have not observed infection on this host. Further fieldwork is also needed to clarify the host range and host susceptibility of pines to subspecies *petersonii* in Chiapas.

Most of the hosts of subspecies *grandicaule* do not occur in the geographic range of subspecies *globosum* and vice versa (Perry, 1991; Farjon & Styles, 1997). Only *Pinus durangensis* Martínez is severely parasitized by both subspecies *globosum* and *grandicaule*. While *P. teocote* Schlechtendal & Chamisso has been reported as a principal host of subspecies *grandicaule*, this pine has only been reported to be rarely infected by subspecies *globosum* (Hawksworth & Wiens, 1996).

Although Hawksworth and Wiens (1977, 1996) noted that subspecies *aureum* did not induce the formation of witches' brooms and that subspecies *petersonii* only did so occasionally, I observed that both of these mistletoes consistently caused the formation of witches' broom on their principal hosts in Guatemala and Chiapas, Mexico. Hawksworth and Wiens (1996) also reported that subspecies *globosum* seldom initiated the formation of witches' brooms on its hosts, but that subspecies *grandicaule* consistently induced brooms. My observations supported that subspecies *grandicaule* consistently induced broom formation. Although subspecies *globosum* usually did not initiate the formation of brooms on its pine hosts, it rarely induced witches' broom formation on *Pinus cooperi* in Durango, Mexico.

Molecular data. Maximum parsimony analysis of nuclear ribosomal ITS sequences and chloroplast *trnL* region sequences demonstrated that subspecies *globosum*, *grandicaule*, *aureum*, and *petersonii* cannot be distinguished from each other using these molecular regions (Nickrent et al., 2004). The close affinity of these taxa is also supported by the small p-distances between the samples of these taxa generated from molecular data using PAUP analysis (Swofford, 2002; Nickrent, unpublished data).

Originally, Hawksworth and Wiens treated all of the populations representing *Arceuthobium globosum* and *A. aureum* under *A. globosum* (Hawksworth & Wiens, 1972). They later segregated these populations based on plant size, color, phenology, and distribution (Hawksworth & Wiens, 1977, 1996). The populations of *A. globosum* currently treated as distinct species by Hawksworth and Wiens have a few consistent morphological differences between them (Table 1), have different flowering and seed dispersal periods, and parasitize different hosts to some degree. However, they have many similar morphological characteristics, have similar ITS and *trnL* region DNA sequences, and are capable of parasitizing some of the same hosts, all of which clearly demonstrate that these mistletoes are closely related. Hawksworth

and Wiens (1996: 146) defined subspecies in *Arceuthobium* as "geographically restricted populations delimited by a few relatively small but consistent variations." Although the distribution of subspecies *grandicaule* overlaps with subspecies *petersonii* around San Cristóbal de las Casas, Chiapas, subspecies *grandicaule* consistently flowers in March and subspecies *petersonii* flowers in September there. Because of the morphological and physiological differences I detected between subspecies *globosum*, *grandicaule*, *aureum*, and *petersonii*, the classification of these populations as subspecies of *A. globosum* is the most consistent classification based on Hawksworth and Wiens' concept of subspecies in *Arceuthobium*. Differences in plant size, phenology, and distribution have been the principal characters used by Hawksworth et al. (1992) and Hawksworth and Wiens (1996) to separate subspecies. Therefore, the classification for *A. aureum* and *A. aureum* subsp. *petersonii* as subspecies of *A. globosum* is more consistent with the taxonomic framework established by Hawksworth and Wiens for *Arceuthobium* than treating *A. aureum* as a distinct species.

Key to the Subspecies of *Arceuthobium globosum* in Mexico and Central America

1a. Plants yellow or green; staminate spike ca. 2 mm wide near apex; staminate flowers 3–4 mm diam.; distributed in northern and central Mexico.
  2a. Plants yellow, forming globose clusters of shoots; plant height usually 15–25 cm, basal diameter of plants ca. 1 cm; witches' brooms rarely formed on host pines; Durango and Chihuahua, Mexico. . *A. globosum* subsp. *globosum*
  2b. Plants yellow-green, base of old plants dark brown; plant height usually 35–50 cm; basal diameter of plants ca. 2 cm; witches' brooms commonly formed on host pines . . . . . *A. globosum* subsp. *grandicaule*

1b. Plants golden to yellow-brown; staminate spike usually ca. 1 mm wide near apex; staminate flowers 2–3 mm diam.; distributed in Chiapas, Mexico, and Guatemala.
  3a. Plants golden to bright yellow; plant height usually 10–20 cm; mature fruits ca. 4 × 2.7 mm; flowering from February to June; parasitic primarily on *Pinus maximinoi*; distributed in central Guatemala, but also known from southern Chiapas, Mexico . . . . . *A. globosum* subsp. *aureum*
  3b. Plants yellow-brown; plant height usually 25–40 cm; mature fruits ca. 5 × 3.4 mm; flowering and seed dispersal in September; parasitic primarily on *Pinus pseudostrobus*; distributed in central Chiapas, Mexico. . . . . *A. globosum* subsp. *petersonii*

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