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XIMENIACEAE Horaninow

• Hog Plum Family

Daniel L. Nickrent

Shrubs or trees, root parasites, evergreen, synoecious. **Leaves** alternate, simple; stipules absent; petiole present; blade margins entire; venation pinnate. **Inflorescences** axillary or at ends of short shoots (brachyblasts), umbels, subumbellate cymes, or fascicles [flowers solitary]. **Flowers** bisexual [functionally unisexual]; perianth and androecium hypogynous; hypanthium absent; sepals 4(–5), distinct, valvate; petals 4(–5), distinct, adaxial surface hairy [not hairy]; nectary present [absent]; stamens 4(–5) or 8 in 2 whorls, distinct, free; anthers dehiscing by longitudinal slits; pistil 1, [2–]4-carpellate, ovary superior, [2–]4-locular proximally, 1-locular distally, placentation free-central, pendulous; ovule 1 per locule, anatropous; style 1; stigma 1. **Fruits** drupes. **Seeds** 1 per locule.

Genera 4, species 13 (1 in the flora): nearly worldwide.

The genera in Ximeniaceae other than *Ximenia* are monospecific. The association of these four genera was first recognized by L. van den Oever (1984) following wood anatomical studies. This clade was also recovered in a cladistic analysis of 80 micro- and macromorphologic characters (V. Malécot et al. 2004). Members of Ximeniaceae share several anatomical features as well as umbellate inflorescences, 4-merous flowers, stamens in two whorls, and lipid-rich fruits. A clade containing three of the four genera was strongly supported in the molecular phylogenetic analysis by Malécot and D. L. Nickrent (2008), and this group was recognized as a family by Nickrent et al. (2010).

1. XIMENIA Linnaeus, Sp. Pl. 2: 1193. 1753; Gen. Pl. ed. 5, 500. 1754 • Hog plum

[For Francisco Ximenes de Luna, 17th century Franciscan monk and botanist]

Shrubs or small trees, long shoots vegetative, short shoots fertile, arising from leaf axils of long shoots, each paired with a thorn. **Stems** glabrous. **Leaves** densely fascicled on short shoots, subcoriaceous, surfaces glabrous or puberulent. **Inflorescences:** bracts 0 or 2–4 at pedicel bases.

Pedicels present. **Flowers:** sepals minute, not accrescent in fruit; petals glabrous or puberulent abaxially, densely hairy adaxially; ovary elongate-conic or lanceoloid. **Drupes** yellow, orange, pink, or red, ellipsoid, oblong-ovoid, or globose. $x = 12$.

Species 10 (1 in the flora): Florida, Mexico, West Indies, Central America, South America, Asia, Africa, Indian Ocean Islands, Pacific Islands, Australia; subtropical and tropical regions.

Fruits of *Ximenia americana* and *X. caffra* Sonder are eaten either raw or cooked. In India, oil from the seeds of *X. americana* is used as a ghee substitute and the wood is used in place of sandalwood (see R. A. DeFilipps 1968 for other economic applications). Anticancer compounds known as ribosome-inactivating proteins have been found in *X. americana* (C. Voss et al. 2006). Long chain acetylenic acids in that species showed potential pesticidal activity (M. O. Fatope et al. 2000).

SELECTED REFERENCE DeFilipps, R. A. 1968. A Revision of *Ximenia* [Plum.] L. (Olacaceae). Ph.D. dissertation. Southern Illinois University, Carbondale.

1. Ximenia americana Linnaeus, Sp. Pl. 2: 1193. 1753 • Hog or Spanish or spiny plum, tallow wood [F]

Varieties 3 (1 in the flora): Florida, Mexico, West Indies, Central America, South America, Asia, Africa, Indian Ocean Islands, Pacific Islands, Australia.

1a. Ximenia americana Linnaeus var. **americana** [F]

Shrubs or small trees to 12 m. **Leaves:** blade elliptic, lanceolate, ovate, obovate, or orbiculate, 1.3–10 cm, apex retuse, obtuse, or acute, with or without 0.5–1 mm mucro; venation eucamptodromous. **Inflorescences** 2–10-flowered; peduncles 1–15 mm. **Pedicels** 4–12 mm. **Flowers:** sepals 0.5–4 mm, ciliate; petals yellow, pale yellow, yellowish green, or white, 4.5–12 mm, recurved at maturity; stamen filaments 2.5–6 mm; anthers 1.5–4.5 mm; style 2.5–5.5 mm. **Drupes** 1–3.5 × 1.1–3 cm. **Seeds** 1.5–2.5 × 1.1–2 cm. $2n = 24$.

Flowering Apr–May(–Nov); fruiting year-round. Pinelands, hammock margins, coastal scrub, coastal sand dunes; 0–30 m; Fla.; Mexico; West Indies; Central America; South America; Asia; Africa; Indian Ocean Islands; Pacific Islands; Australia.

R. A. DeFilipps (1968, 1969) recognized three varieties of *Ximenia americana*, with the pantropical var. *americana* occurring in peninsular Florida. The other varieties occur in Argentina (var. *argentinensis* DeFilipps) and Africa (var. *microphylla* Welwitsch ex Oliver). From greenhouse pot studies, DeFilipps (1969b) determined that *X. americana* is able to exist without a host, thus it should be considered a facultative hemiparasite. The flowers are fragrant and presumably insect pollinated. The anthers dehisce before the flower bud opens and the adaxial hairs on the petals may serve to present the pollen (P. B. Tomlinson 1980). Variety *americana* shows different growth forms on different substrates; plants on sandy coastal areas are sprawling shrubs with orbiculate, fleshy leaves, whereas plants in forests and scrublands are trees with oblong to oblanceolate, thin leaves.

Ximenia inermis Linnaeus, an illegitimate and superfluous name, pertains here.

SCHOEPFIACEAE Blume

• Whitewood Family

Daniel L. Nickrent

Shrubs or trees [perennial herbs], root parasites, evergreen, synoecious; glabrous [hairy]. **Leaves** alternate [2 in fascicle], simple; stipules absent; petiole present; blade margins entire; venation pinnate. **Inflorescences** axillary [terminal], cymes [thyrses, spikes, umbels] or flowers solitary. **Flowers** bisexual, heterostylous; perianth and androecium epigynous; epicalyx present; hypanthium completely adnate to ovary; sepals unknown number [0], connate into cuplike rim; petals [3–]4–5[–6], connate, post-staminal hairs present [absent]; nectary present; stamens [3–]4–5 [–6], opposite petals, distinct, adnate to corolla tube; anthers dehiscing by longitudinal slits; pistil 1, 2–3-carpellate, ovary inferior, 2–3-locular proximally, 1-locular distally, placentation free-central, ovules 3 per ovary, anatropous; style 1; stigma 1. **Fruits** drupes [nutlike achenes]. **Seeds** 1 per fruit.

Genera 3, species 50 (1 in the flora): Florida, Mexico, West Indies, Central America, South America, Asia.

Although *Schoepfia* is often classified in Olacaceae R. Brown, its placement has been dubious for over two centuries. Early molecular phylogenetic studies showed that this genus is more closely related to Loranthaceae Jussieu and Misodendraceae J. Agardh than to Olacaceae (D. L. Nickrent and V. Malécot 2001). Later work (J. P. Der and Nickrent 2008) confirmed this result and also showed the association with *Arjona* Commerson ex Cavanilles and *Quinchamalium* Molina from Andean South America, in agreement with P. van Tieghem (1896). The cupular bracts (epicalyx) subtending the flowers may be a synapomorphy between *Schoepfia* and *Quinchamalium*. These three genera form Schoepfiaceae in the classification of Santalales by Nickrent et al. (2010).

The homology of the reduced calyx in Schoepfiaceae and other Santalales, which often is referred to as a calyculus, has been controversial. D. L. Nickrent et al. (2010) and J. Kuijt (2013) argued that this structure is sepalar in origin, and that interpretation is followed here. The corolla in Schoepfiaceae and many other Santalales bears post-staminal hairs, which arise as a tuft opposite each anther and become attached to the anther by secretions.

1. SCHOEPFIA Schreber, Gen. Pl. 1: 129. 1789 • Whitewood [For Johann David Schoepf, 1752–1800, German physician and botanist]

Shrubs or trees, branching sympodial on distal shoots, glabrous [hairy]. **Leaves:** blade subcoriaceous, surfaces glabrous. **Inflorescences:** peduncle base with persistent imbricate bracts. **Pedicels** absent [present]. **Flowers** sweetly fragrant; epicalyx 3-lobed; nectary annular, fleshy, covering ovary distally; corolla cylindric, subcampanulate, or urceolate, lobes reflexed; filaments short, arising proximal to post-staminal hairs. **Drupes** subtended by persistent epicalyx, with remains of nectary and corolla at apex. $x = 12$.

Species 25 (1 in the flora): Florida, Mexico, West Indies, Central America, South America, Asia.

Twenty species of *Schoepfia* are Neotropical (H. Sleumer 1984) and are classified in sect. *Schoepfia*; five species are in sects. *Schoepfiopsis* (Miers) Engler and *Alloschoepfia* Sleumer of Asia (Sleumer 1935; K. R. Robertson 1982).

1. Schoepfia schreberi J. F. Gmelin, Syst. Nat. 1: 376. 1791 [F]

Schoepfia chrysophylloides (A. Richard) Planchon

Shrubs or trees, 1.3–7(–9) m; bark whitish, corky, fissured; branches striate, olive green to whitish, slender. **Leaf blades** lanceolate, ovate, or elliptic, 4–8 × 2–4 cm, brittle, base cuneate-attenuate to obtuse, apex acuminate, both surfaces shiny, ± tuberculate; venation brochidodromous, midrib sunken on both surfaces, lateral veins 4–6 pairs. **Inflorescences** 1–2 per axil, each a 2–3-flowered cyme or solitary flower; peduncle 1–4 mm. **Flowers** of two forms, pin and thrum; calyx rim entire or slightly lobed, 1 mm; corolla tube yellow or orange and lobes pink to red, urceolate to cylindric, 4.5 mm (pin flowers), cylindric to campanulate, (3.5–)4(–5) mm (thrum flowers); ovary 2-locular in 4-merous flowers, 3-locular in 5-merous flowers; stigma 2–3-lobed, at or distal to included anthers (pin flowers) or proximal to exserted anthers (thrum flowers). **Drupes** pink, orange, or red, subovoid to ellipsoid, (7–)10–13 × (6–)7–8 mm, with persistent rim of corolla at apex.

Flowering Oct–Mar; fruiting Oct–Mar, soon after flowering. Pinelands, coppices, hammocks, limestone and sand substrates; 0–10 m; Fla.; West Indies; n South America.

The species concept used here follows the broad view of H. Sleumer (1984), who considered many of the named variants of *Schoepfia schreberi* to be synonyms. Although they display variable vegetative morphology, flower and fruit morphology appears relatively constant. The floral biology of *S. schreberi* requires investigation. Sleumer indicated that anthers in pin flowers lack pollen; however, P. B. Tomlinson (1980) stated that the heterostylous condition is apparently efficient, given that trees of both forms set fruit. Root parasitism of ten host species was documented by C. R. Werth et al. (1979).

COMANDRACEAE Nickrent & Der

• Bastard Toadflax Family

Daniel L. Nickrent

Herbs or subshrubs, perennial, root parasites, deciduous, synoecious or andromonoecious; glabrous. **Stems** horizontal rhizomes bearing erect fertile shoots. **Leaves** alternate, simple; stipules absent; petiole present or absent; blade margins entire; venation pinnate. **Inflorescences** unisexual or bisexual, axillary cymules or terminal thyrses. **Flowers** bisexual or unisexual; perianth and androecium epigynous; hypanthium completely adnate to ovary or adnate to ovary proximally, free distally; sepals 0; petals (4–)5(–7), usually connate basally, sometimes distinct, valvate, post-staminal hairs present; nectary present; stamens (4–)5(–7), opposite petals, distinct, free; anthers dehiscing by longitudinal slits; pistil 1, 1-carpellate, ovary inferior, 1-locular, placentation free-central, pendulous; ovules 2–4 per locule, anatropous; style 1; stigma 1. **Fruits** pseudodrupes (mesocarp hard, exocarp leathery or fleshy). **Seeds** 1 per fruit.

Genera 2, species 2 (2 in the flora): North America, Mexico, Eurasia.

Comandraceae have not been recognized at the family rank in past classifications, although *Comandra* was placed in its own invalidly published tribe Comandreae by P. van Tieghem (1896). *Comandra* and *Geocaulon* have a suite of generalized morphological features that can be found in many other genera of Santalaceae in the broad sense. Despite this, *Comandra* has a number of distinctive embryological features (M. Ram 1957; B. M. Johri and S. P. Bhatnagar 1960). A molecular phylogenetic analysis recovered a strongly supported *Comandra* and *Geocaulon* clade, which was recognized as a family by D. L. Nickrent et al. (2010). That clade was placed in a polytomy with other Santalaceae in the broad sense in that study. *Comandra* and *Geocaulon* are clearly closely related as revealed by molecular studies; however, M. L. Fernald (1928e) made a good case for maintaining them as separate genera. They differ in a number of features involving the rhizome, plant sex, hypanthium, disc shape, style length, and fruit type.

1. Inflorescences terminal thyrses; flowers bisexual; hypanthia free distally, funnel-shaped; nectaries lining hypanthium; styles filiform; pseudodrupe exocarps leathery . . . . . 1. *Comandra*, p. 409
1. Inflorescences axillary cymules; flowers bisexual and staminate (plants andromonoecious); hypanthia completely adnate to ovaries; nectaries nearly flat; styles short-conic; pseudodrupe exocarps fleshy . . . . . 2. *Geocaulon*, p. 411

1. COMANDRA Nuttall, Gen. N. Amer. Pl. 1: 157. 1818 • Bastard toadflax [Greek *kome*, hair, and *andros*, male, alluding to petal hairs that attach to anthers]

Herbs or subshrubs, perennial, synoecious. **Rhizomes** somewhat woody, white to beige or blue (then drying blackish), cortex corky or papery, loose exfoliating. **Leaves:** petiole short or absent. **Inflorescences** terminal, paniclelike or corymblike thyrses; cymules 3–5-flowered; prophyllar bracteole subtending each flower persistent. **Pedicels** present. **Flowers** bisexual, campanulate; hypanthium adnate to ovary proximally, free distally, funnel-shaped; petals (4–)5(–7), white, yellowing with age, ovate or oblong to lanceolate, reflexed upon maturation; nectary lining hypanthium, lobes small, alternating with filaments; styles filiform; stigmas capitate. **Pseudodrupes** usually multiple, petals persistent, forming neck at apex; exocarp leathery.

Species 1: North America, n Mexico, s Europe (Balkan peninsula); temperate regions.

Circumscription of species within *Comandra* has varied, as have opinions about whether *Geocaulon* is distinct. C. L. Hitchcock and A. Cronquist (1973) considered *Geocaulon* as a species of *Comandra*, whereas M. L. Fernald (1950) recognized separate genera. The treatment here follows the most comprehensive study of *Comandra* to date (M. A. Piehl 1965), which recognized a single variable species with four subspecies.

SELECTED REFERENCE Piehl, M. A. 1965. The natural history and taxonomy of *Comandra* (Santalaceae). Mem. Torrey Bot. Club 22(1): 1–97.

1. Comandra umbellata (Linnaeus) Nuttall, Gen. N. Amer. Pl. 1: 157. 1818 [F]

Thesium umbellatum Linnaeus, Sp. Pl. 1: 208. 1753

Leaf blades light green to grayish or bluish green, lanceolate, elliptic, or ovate, 0.7–5.3 cm, apex obtuse, acute, or acuminate. **Flowers:** hypanthium base not dilated.

Subspecies 4 (3 in the flora): North America, n Mexico, s Europe (Balkan peninsula).

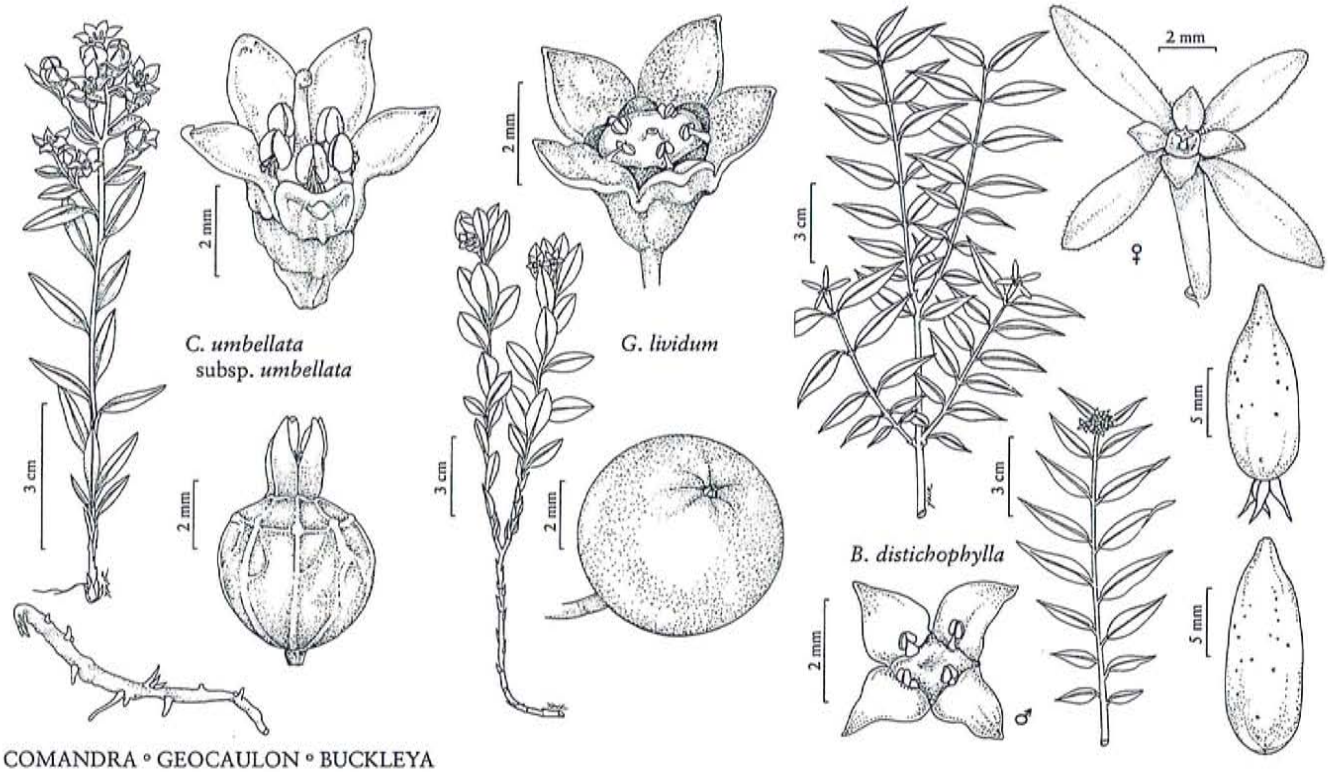
Comandra umbellata is likely the most widespread Santalales species, occurring throughout the United States, southern Canada, and northern Mexico as well as in the Balkan peninsula, where subsp. *elegans* (Rochel ex Reichenbach) Piehl occurs. *Comandra umbellata* is the alternate host for comandra blister rust (*Cronartium comandrae*), which damages pines in North America.

1. Leaf blades thin, green, not glaucous; pseudodrupes 4–6 mm; rhizome cortices white to beige; Canada, c, e United States. . . . . 1a. *Comandra umbellata* subsp. *umbellata*
1. Leaf blades thin or thick, becoming ± succulent, green to grayish or bluish green, glaucous; pseudodrupes 5–9 mm; rhizome cortices blue, drying blackish; w North America. [2. Shifted to left margin.—Ed.]
2. Leaf blade lateral veins obscure on abaxial surface; proximal part of aerial stems not overwintering; herbs 5–33 cm. . . . . 1b. *Comandra umbellata* subsp. *pallida*
2. Leaf blade lateral veins apparent on abaxial surface; proximal part of aerial stems overwintering; subshrubs 15–40 cm . . . . . 1c. *Comandra umbellata* subsp. *californica*

1a. Comandra umbellata (Linnaeus) Nuttall subsp. **umbellata** [E] [F]

Comandra richardsiana Fernald

Herbs or subshrubs 7–40 cm. **Rhizomes:** cortex white to beige. **Aerial stems** usually branched, sometimes much-branched at base; proximal portions overwintering or not. **Leaves:** blade green, paler abaxially, not glaucous, lanceolate, oblanceolate, elliptic, or ovate, 0.7–5(–7.6) cm, thin, soft, base attenuate to acute, margins often slightly revolute, apex obtuse, sometimes apiculate; midrib and lateral veins conspicuous, protruding on abaxial surface. **Pedicels** 0–1.4 mm. **Flowers** funnel-shaped to almost rotate; petals lanceolate, lanceolate-oblong, or ovate, 2–3 mm; anthers 0.5 mm. **Pseudodrupes** dark to light brown, sometimes red-tinged, not glaucous, subglobose to globose, 4–6 mm, smooth. $2n = 28$.



COMANDRA ◦ GEOCAULON ◦ BUCKLEYA

Flowering Mar–Aug. Swamps and bogs, rich mesic sites, dry, sandy or rocky soils, savannas, early successional forests; 0–700 m; Alta., B.C., Man., N.B., Nfld. and Labr., N.S., Ont., P.E.I., Que., Sask.; Ala., Ark., Conn., Del., D.C., Ga., Ill., Ind., Iowa, Kans., Ky., Maine, Md., Mass., Mich., Minn., Miss., Mo., Nebr., N.H., N.J., N.Y., N.C., N.Dak., Ohio, Okla., Pa., R.I., S.C., S.Dak., Tenn., Vt., Va., W.Va., Wis.

As discussed by M. A. Piehl (1965), subsp. *umbellata* exhibits a wide range of morphological variation, which has prompted various authors to name numerous species and subspecies. A common example is *Comandra richardsiana*, which according to M. L. Fernald (1950) represents a western and northern extreme form with a corymbose inflorescence with cymule branches ascending versus a paniculate inflorescence with cymule branches divergent. Intermediate forms between subsp. *umbellata* and subsp. *pallida* are reported from Alberta, British Columbia, Manitoba, Saskatchewan, Kansas, Minnesota, Missouri, Nebraska, North Dakota, and South Dakota.

1b. Comandra umbellata (Linnaeus) Nuttall subsp. **pallida** (A. de Candolle) Piehl, Mem. Torrey Bot. Club 22(1): 70. 1965

Comandra pallida A. de Candolle in A. P. de Candolle and A. L. P. P. de Candolle, Prodr. 14: 636. 1857; *C. umbellata* var. *pallida* (A. de Candolle) M. E. Jones

Herbs, 5–33 cm. **Rhizomes:** cortex blue, drying blackish. **Aerial stems** often much branched; proximal portions not overwintering. **Leaves:** blade green to grayish green, glaucous, linear to lanceolate, elliptic, or ovate, 0.9–4.2 cm, thick, firm, becoming ± succulent, base attenuate to cuneate, margins not revolute, apex attenuate to acute, often mucronulate or apiculate; midrib obscure or sometimes conspicuous or protruding on abaxial surface, lateral veins obscure. **Pedicels** 0–1.6 mm. **Flowers** funnel-shaped to rotate; petals oblong to lanceolate-oblong, 2.5–5 mm; anthers 0.7 mm. **Pseudodrupes** purplish brown to red, glaucous, subglobose to ovate, 5.5–9 mm, slightly roughened. $2n = 52$.

Flowering Mar–Jul. Open areas, sandy and rocky slopes, sagebrush communities, coniferous and deciduous forests, deserts; 150–2800 m; Alta., B.C., Man., N.W.T., Sask., Yukon; Ariz., Colo., Idaho, Kans., Mont., Nebr., Nev., N.Mex., N.Dak., Okla., Oreg., S.Dak., Tex., Utah, Wash., Wyo.; Mexico (Chihuahua, Coahuila).

As with the other subspecies, subsp. *pallida* is morphologically variable, this likely related to its diverse ecological habitats. Clinal variation and intergradation with the other subspecies that flank its eastern and western boundaries may also play a role (M. A. Piehl 1965). Intermediates between subsp. *pallida* and subsp. *californica* occur in Arizona, New Mexico, Nevada, Oregon, and Washington. Ecotypic variation apparently has a genetic component, as demonstrated by common garden experiments with seeds and vegetative propagules (Piehl). One extreme but widespread form is highly branched basally and has dimorphic leaves, with the proximal blades linear and the distal blades lanceolate or elliptic.

1c. **Comandra umbellata** (Linnaeus) Nuttall subsp. **californica** (Eastwood ex Rydberg) Piehl, Mem. Torrey Bot. Club 22(1): 65. 1965 E

Comandra californica Eastwood ex Rydberg, Fl. Rocky Mts. ed. 2, 1138. 1923; *C. umbellata* var. *californica* (Eastwood ex Rydberg) C. L. Hitchcock

Subshrubs, 15–40 cm. **Rhizomes:** cortex blue, drying blackish. **Aerial stems** often much branched; proximal portions overwintering. **Leaves:** blade light green to bluish or grayish green, slightly paler abaxially, glaucous, broadly elliptic, ovate, lanceolate, or linear, 1.7–5.3 cm, thin, becoming ± succulent, base acute to attenuate, margins rarely revolute, apex acute, often apiculate; midrib and lateral veins apparent and somewhat protruding on abaxial surface. **Pedicels** 0–2.5 mm. **Flowers** funnel-shaped to rotate; petals lanceolate, lanceolate-oblong, or ovate, 2–3.5 mm; anthers 0.6 mm. **Pseudodrupes** brown, not glaucous, subglobose, 5–7.5 mm, smooth.

Flowering Mar–Jul. Dry places, mountains, foothills, open conifer forests, oak woodlands, chaparral margins; 300–3000 m; B.C.; Ariz., Calif., Nev., N.Mex., Oreg., Wash.

Subspecies *californica* is frequent in the Sierra Nevada of California and east of the Cascade range in Oregon and Washington; it is found also on Vancouver Island in British Columbia. In Arizona, this subspecies is restricted to high elevations such as the Santa Catalina Mountains. Intergradation with subsp. *pallida* occurs over wide areas of Arizona, Nevada, New Mexico, Oregon, and Washington.

2. GEOCAULON Fernald, Rhodora 30: 23. 1928 • Northern comandra, false toadflax [Greek *ge*, earth, and *kaulos*, stalk, alluding to slightly subterranean and stemlike rhizome] E

Herbs, perennial, andromonoecious. **Rhizomes** not woody, reddish to dark brown, cortex smooth, not exfoliating. **Leaves:** petiole short. **Inflorescences** axillary (appearing terminal in early developmental stages but occupying middle axils with continued growth of main axis), cymules; cymules mostly 3-flowered; prophyllar bracteole subtending each flower caducous. **Pedicels** present. **Flowers** bisexual and staminate (central flower, or rarely 2 flowers, of dichasium usually bisexual, sometimes staminate, laterals staminate), campanulate to turbinate; hypanthium completely adnate to ovary; petals (4–)5, greenish to bronze (bisexual and unisexual flowers often differing in color), triangular or ovate; nectary nearly flat, lobes prominent, alternating with filaments; styles short-conic; stigmas slightly lobed. **Pseudodrupes** usually solitary; petal remains vestigial at apex; exocarp fleshy.

Species 1: North America.

Geocaulon is one of only two genera named by M. L. Fernald (the other being *Alcoceria*, Euphorbiaceae, now treated as a synonym of *Dalembertia* Baillon). Fernald stated that many features of *Geocaulon* are similar to *Nestronia* (Santalaceae); however, molecular data clearly indicate that *Geocaulon* is sister to *Comandra*.

1. **Geocaulon lividum** (Richardson) Fernald, Rhodora 30: 23. 1928 E F

Comandra livida Richardson in J. Franklin, Narr. Journey Polar Sea, 734. 1823

Stems: rhizomes 1.5–3 mm; aerial shoots 0.7–3 dm. **Leaf blades** elliptic, oblong, or obovate, 1.5–5 × 0.5–1 cm, apex obtuse to rounded, thin, flaccid, surfaces green, grayish green, or purplish. **Inflorescences:** peduncles 5 mm, expanding to 1.5 cm in fruit. **Pedicels** 1 mm. **Flowers** 4 mm diam.; filaments 0.5 mm; styles 0.3 mm. **Pseudodrupes** yellowish orange to scarlet, 6–10 mm. **Seeds** oily, fleshy. $2n = 52$.

Flowering late May–early Aug. Damp humus, *Sphagnum* bogs, wet coniferous forests; 70–2100 m; St. Pierre and Miquelon; Alta., B.C., Man., N.B., Nfld. and Labr., N.W.T., N.S., Nunavut, Ont., Que., Sask., Yukon; Alaska, Idaho, Maine, Mich., Minn., Mont., N.H., N.Y., Vt., Wash., Wis.

Although *Geocaulon lividum* is considered secure across its full range, in parts of the eastern United States it is of special concern (Maine), threatened (New Hampshire), or endangered (New York, Wisconsin).

Fernald described the sexual condition as androdioecious, but F. H. Smith and E. C. Smith (1943) stated that the central flowers of each cymule are pistillate and the laterals staminate, thus the species would be monoecious. Here it is considered andromonoecious, with the central flower (rarely two flowers) bisexual and the lateral staminate (and dropping after anthesis), or sometimes all the flowers staminate.

THESIACEAE Vest
• Thesium Family

Daniel L. Nickrent

Herbs or shrubs, perennial [annual], root parasites, deciduous, synoecious or dioecious. **Leaves** opposite, subopposite, or alternate, simple; stipules absent; petiole present or absent; blade margins entire or minutely serrulate; venation pinnate. **Inflorescences** unisexual or bisexual, terminal or axillary, cymes (sometimes umbel-like) or thyrses, or flowers solitary. **Flowers** bisexual or unisexual; perianth and androecium epigynous; hypanthium completely adnate to ovary, adnate to ovary proximally but free distally, or absent; sepals 0 or 4, distinct, valvate; petals 4–5, distinct [connate], valvate, post-staminal hairs present or absent; nectary present [absent]; stamens 4–5, opposite petals, distinct, free [adnate to petal bases]; anthers dehiscing by longitudinal slits; pistil 1, 3–4-carpellate, ovary inferior, 1-locular, placentation free-central, pendulous; ovules 2–4 per locule, anatropous; style 1; stigma 1. **Fruits** pseudodrupes (mesocarp hard, exocarp leathery or fleshy). **Seeds** 1 per fruit.

Genera 4, species ca. 370 (2 genera, 2 species in the flora): nearly worldwide.

The assemblage of genera comprising Thesiaceae received strong support from molecular phylogenetic analyses (J. P. Der and D. L. Nickrent 2008; Nickrent and M. A. García 2015). *Buckleya* is sister to the remaining genera, which are either endemic to or have their center of diversity in Africa. Because *Buckleya* occurs in eastern North America and Asia, the ancestor to the remaining genera apparently migrated to Africa prior to diversification.

1. Shrubs; leaves opposite or subopposite; flowers unisexual . . . . . 1. *Buckleya*, p. 413
1. Perennial herbs; leaves alternate; flowers bisexual . . . . . 2. *Thesium*, p. 415

1. BUCKLEYA Torrey, Amer. J. Sci. Arts 45: 170. 1843, name conserved • [For Samuel Botsford Buckley, 1809–1884, American botanist]

Shrubs, dioecious. **Stems** hairy. **Leaves** opposite or subopposite, distichous to decussate. **Inflorescences:** staminate 1–3[–5] dichasia, pistillate flowers solitary, subtended by 2 pairs of decussate, deciduous bracts. **Pedicels:** staminate present, pistillate absent. **Flowers** unisexual.

Staminate flowers: hypanthium absent; sepals 0; petals 4, post-staminal hairs absent; nectary squarish; stamens 4. **Pistillate flowers:** hypanthium completely adnate to ovary; sepals 4; petals 4; nectary squarish; ovules 3–4 per locule; stigma 4-lobed. **Pseudodrupes:** exocarp fleshy; pedicels not enlarging or becoming fleshy; sepals accrescent, deciduous [persistent], petals deciduous. $x = 15$.

Species 5 (1 in the flora): e United States, e Asia (China, Japan).

The morphologic nature of the two floral whorls appearing at the fruit apex has received various interpretations. R. K. F. Pilger (1935) referred to the outer whorl as bracts and suggested that they are prophylls from two aborted side flowers of a dichasium. A simpler explanation, followed here, is that the outer whorl represents sepals and the inner whorl petals (F. H. Smith and E. C. Smith 1943; J. P. Der and D. L. Nickrent 2008).

Buckleya is disjunct between eastern North America and Asia. Based on morphologic features such as the deciduous sepals, W. N. Carvell and W. H. Eshbaugh (1982) proposed that *B. distichophylla* is most closely related to *B. graebneriana* Diels of China, a hypothesis supported by the molecular phylogenetic analysis of Li J. H. et al. (2001).

SELECTED REFERENCES Carvell, W. N. and W. H. Eshbaugh. 1982. A systematic study of the genus *Buckleya* (Santalaceae). Castanea 47: 17–37. Li, J. H., D. E. Boufford, and M. J. Donoghue. 2001. Phylogenetics of *Buckleya* (Santalaceae) based on ITS sequences of nuclear ribosomal DNA. Rhodora 103: 137–150.

1. **Buckleya distichophylla** (Nuttall) Torrey, Amer. J. Sci. Arts 45: 170. 1843 • Buckleya, pirate-bush E F

Borya distichophylla Nuttall, Gen. N. Amer. Pl. 2: 232. 1818; *Nestronia distichophylla* (Nuttall) Kuntze

Shrubs rhizomatous, to 3–4 m. **Bark** light brown, smooth, with white lenticels. **Stems** green, terete to slightly 4-angled when young, puberulent; growth sympodial, terminal bud sometimes aborting giving false appearance of dichotomous branching. **Leaves:** petiole short or absent; blade lanceolate or ovate-lanceolate, to elliptic near base of branchlet, 1.2–9 × 0.3–2.9 cm distally, progressively smaller proximally, thin, base cuneate, margins entire, apex attenuate, surfaces puberulent especially on margins and midvein. **Inflorescences** terminal. **Pedicels:** staminate 1–4.2 mm. **Staminate flowers:** petals greenish, 1.2–2.5 × 1.1–2 mm, puberulent; nectary 1–1.8 mm diam. **Pistillate flowers:** sepals greenish, narrowly elliptic to lanceolate, 3–17 × 1–3 mm, apex acuminate, puberulent, venation conspicuously pinnate-reticulate; petals greenish, triangular, 1.3–3 × 1–22 mm, puberulent; ovary narrowly conic, 3.4–15 mm, puberulent; styles 0.7–1.6 mm. **Pseudodrupes** ellipsoid to obovoid, 0.9–3 × 0.4–1.7 cm, puberulent, with small whitish lenticels. $2n = 30$.

Flowering Apr–May, Aug. Dry rocky or shaly outcrops and river bluffs; 500–1000 m; N.C., Tenn., Va.

Buckleya distichophylla is an uncommon shrub in the southern Appalachian Blue Ridge Mountains and adjacent Ridge and Valley region; the reason for its rarity is not understood. One hypothesis is that the plants require both direct sunlight and hemlock (*Tsuga canadensis*) hosts, a rare combination of conditions (A. E. Radford et al. 1968). But other explanations are called for, because *Buckleya* is found in stands lacking hemlock (W. N. Carvell and W. H. Eshbaugh 1982). Moreover, pot-grown plants showed seedling parasitism of 19 different tree species (L. J. Musselman and W. F. J. Mann 1979b); these authors suggested that *Buckleya* requires a distinctive habitat where hemlock happens to be dominant.

Buckleya distichophylla is in the Center for Plant Conservation's National Collection of Endangered Plants. It is not federally listed, but three states (North Carolina, Tennessee, Virginia) list it as threatened or endangered.

2. THESIUM Linnaeus, Sp. Pl. 1: 207. 1753; Gen. Pl. ed. 5, 97. 1754 • [Greek *thes*, laboring servant, alluding to simple appearance] I

Herbs [**shrubs**], perennial [annual], synoecious [dioecious]. **Stems** erect, hairy [glabrous]. **Leaves** alternate [opposite]. **Inflorescences** racemelike [spikelike] thyrses; flowers subtended by bract and 2 bracteoles [bract absent]. **Pedicels** absent [present]. **Flowers** bisexual [unisexual]; hypanthium adnate to ovary proximally, free distally; sepals 0 [present as small lobes or glands]; petals (4–)5, post-staminal hairs present; nectary lining hypanthium; stamens (4–)5; ovules 2–3 per locule; stigma capitate. **Pseudodrupes:** exocarp leathery; pedicel enlarging and becoming fleshy; hypanthium and petals persistent. $x = 6–9$.

Species ca. 365 (1 in the flora): introduced; nearly worldwide.

Thesium is closely related to the South African endemic *Osyridocarpos* A. de Candolle (J. P. Der and D. L. Nickrent 2008). For this reason and because Africa contains the highest species diversity, this region can be assumed to be the center of origin for *Thesium*.

1. Thesium ramosum Hayne, J. Bot. (Schrader) 1800(1): 30, plate 7 [left]. 1800 F I W

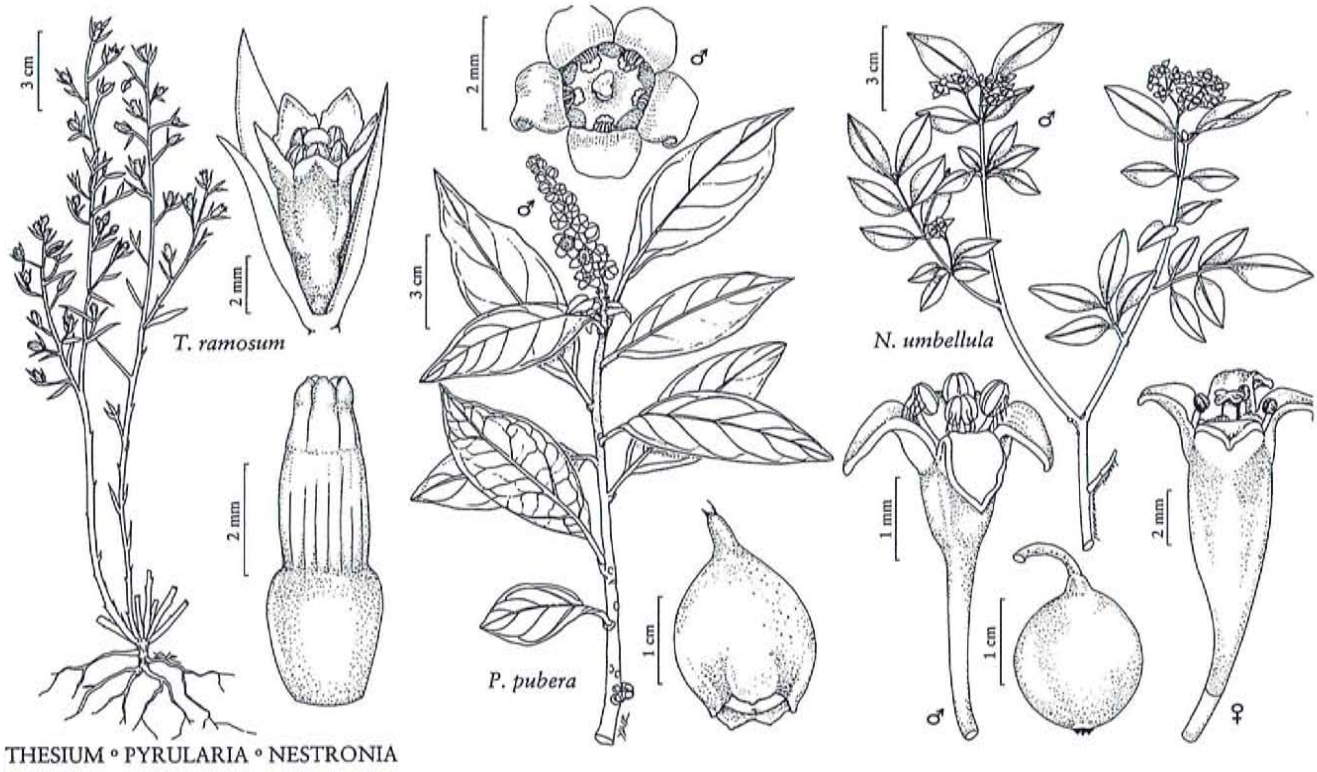
Herbs 15–40(–70) cm. **Stems:** caudex relatively unbranched, to 15 mm diam.; aerial stems 20–100+, to 2 mm diam. **Leaves:** blade scalelike proximally, linear to falcate distally, 30–45 (–91) × 1–3 mm; margins minutely serrulate; midvein prominent, lateral veins less prominent or absent. **Inflorescences** 10–20 cm; bract lanceolate, 1.2–3 times flower length; bracteoles linear, 0.5–1 times flower length. **Flowers** bell- or funnel-shaped, 3–4 mm; hypanthium 1 mm; petals white with green central adaxial stripe, 1–1.3 mm, margins with small lobes; stamens 1.5 mm, exserted; style plus stigma 1.5 mm. **Pseudodrupes** brown, 2–3 mm, longitudinally striate, glabrous; swollen pedicel reddish brown or amber, 1.5–2 mm; persistent perianth remnants 1–2 mm.

Flowering summer. Riparian areas, dry, rocky slopes, roadsides, pastureland, open fields; 400–1800 m; introduced; Alta.; Idaho, Mont., N.Dak.; Eurasia.

The native range of *Thesium ramosum* is in temperate Eurasia from the Balkans to Siberia (R. Hendrych 1964; A. G. Miller 1982). The species was first reported in North America in 1943 from Towner County, North Dakota. An herbarium specimen collected in 1993 (at RM) documents its occurrence in Teton County, Idaho. Later it was recorded also from Madison and Teton counties, Montana (L. J. Musselman and S. C. Haynes 1996), and in 2001 discovered near Calgary, Alberta, where it is well established in and around Fish Creek Provincial Park (I. D. MacDonald, pers. comm.). The historical data suggest that this species has potential for significant range expansion within North America. The diversity of hosts recorded for the Montana population indicates that it is a host generalist.

The North American plants were originally reported to be *Thesium linophyllon* (T. Van Bruggen 1986), but L. J. Musselman and S. C. Haynes (1996) determined that they are either *T. arvense* Horvátovszky or *T. longifolium* Turczaninow. A DNA sequence from the Montana population was identical to that of *T. ramosum* from Eurasia (M. García, pers. comm.). The North American populations differ from the Eurasian ones in bract size, persistent perianth remnant length relative to the pseudodrupe length, and fleshy pedicel color, but the significance of these features in this polymorphic taxon is not clear.

Thesium ramosum is called *T. arvense* in many European and North American publications, all following the recommendation of R. Hendrych (1961). That name, as pointed out by W. Gutermann (2009), is a superfluous new one for a Linnaean species and is therefore illegitimate.


3 cm
2 mm
T. ramosum
2 mm
THESIUM ◦ PYRULARIA ◦ NESTRONIA
2 mm
♂
3 cm
♂
P. pubera
1 cm
3 cm
♂
N. umbellula
1 mm
♂
1 cm
2 mm
♀

CERVANTESIACEAE Nickrent & Der

• Buffalo Nut Family

Daniel L. Nickrent

Shrubs [trees], root parasites, deciduous, dioecious [synoecious, polygamous, trioecious]. **Leaves** alternate, simple; stipules absent; petiole present; blade margins entire [spinose]; venation pinnate. **Inflorescences** unisexual, terminal or axillary, racemes [spikes, cymes, panicles]. **Flowers** unisexual [bisexual]; perianth and androecium perigynous or epigynous; hypanthium completely adnate to ovary; sepals 0; petals (4–)5(–6), distinct, post-staminal hairs present; nectary present; stamens (4–)5(–6), opposite petals, distinct, adnate to petal base; anthers dehiscing by longitudinal slits; staminodes present in pistillate flowers; pistil 1, carpel number unknown; ovary ½ inferior (staminate flowers) or almost superior (pistillate flowers), becoming inferior during fruit development, 1-locular, placentation free-central, pendulous; ovules 2–3 per locule, anatropous; style 1; stigma 1; pistillode present in staminate flowers. **Fruits** pseudodrupes (mesocarp hard). **Seeds** 1 per fruit.

Genera 8, species 20 (1 in the flora): e, se United States, South America, Asia, Africa.

Cervantesiaceae show a trend from bisexual to fully unisexual flowers, with intermediate stages seen by the presence of staminodes and pistillodes, as well as trioecy in *Scleropyrum* Arnott. Carpel number in Cervantesiaceae is unclear, and the necessary anatomical studies have not been done. The fruits in this family (the largest in Santalales) have a hard or crustaceous mesocarp. Because the mesocarp is hard, not the endocarp, these are considered pseudodrupes, not true drupes. In *Jodina* Hooker & Arnott ex Meisner, the endocarp is apparently consumed during endosperm development (S. P. Bhatnagar and G. Sabharwal 1969); this interpretation is extended to other members of the family.

The affinity of the eight genera of Cervantesiaceae, first noted by H. U. Stauffer (1957, 1961), was confirmed using molecular phylogenetic methods (J. P. Der and D. L. Nickrent 2008; Z. S. Rogers et al. 2008). The segregation of Cervantesiaceae from Santalaceae in the broad sense follows the classification of Nickrent et al. (2010). *Pyrularia* is the only genus in the family with species occurring in both the Old and New Worlds.

1. PYRULARIA Michaux, Fl. Bor.-Amer. 2. 231. 1803 • Buffalo or oil nut [Genus *Pyrus* and Latin *-aria*, connecting, alluding to pear-shaped fruit]

Shrubs [trees], dioecious [polygamous]. **Leaf blades** herbaceous; venation brochidodromous, conspicuous. **Pedicels** present. **Flowers:** petals recurved [spreading]; nectary prolonged into scales between filament bases; styles long and cylindric (staminate flowers) or short and conic (pistillate flowers); stigma capitate, 2–3-lobed. **Pseudodrupes** crowned with expanded disc surrounded by swollen petal bases.

Species 2 (1 in the flora): e, se United States, Asia.

The sexual condition in *Pyrularia* is not clear, which is reflected in varied descriptions. The genus has been called dioecious (M. L. Fernald 1950), subdioecious (H. A. Gleason and A. Cronquist 1991), and polygamous (Xia N. H. and M. G. Gilbert 2003). The anthers and filaments in *P. pubera* are smaller on pistillate flowers, do not contain pollen, and are considered staminodes. Thus, at least this species is functionally dioecious. The polygamous condition reported for the Chinese species *P. edulis* (Wallich) A. de Candolle requires further investigation.

1. Pyrularia pubera Michaux, Fl. Bor.-Amer. 2: 233. 1803

E F

Shrubs rhizomatous, much branched, to 4 m; young growth minutely pilosulous. **Petioles** (5–)10(–19) mm. **Leaf blades** ovate-oblong, obovate, or elliptic, (4.2–)10(–21) × (2–)4(–8) cm, base acute to rounded, apex acute to acuminate, surfaces puberulent when young. **Inflorescences:** staminate terminal on axillary branches, erect, 3–8 cm, 15+-flowered; pistillate terminal or axillary, to 9-flowered; bracts caducous, pilose. **Staminate flowers** green, turbinate, 4 mm diam.; pistillode stigma above anthers. **Pistillate flowers** green, turbinate, 5–6 mm diam.; stigma at same height as staminode anthers. **Pseudodrupes** yellowish, pyriform or subglobose, 2–3 × 1–2 cm; exocarp splitting irregularly when mature, releasing mesocarp/seed. $2n = 38$.

Flowering May–Jul; fruiting Sep–Oct. Rich forests; 200–1400 m; Ala., Ga., Ky., N.Y., N.C., Pa., S.C., Tenn., Va., W.Va.

Pyrularia pubera can be locally abundant in the Blue Ridge Mountains and Appalachian Plateau, often forming dense stands in second-growth forests. The species is apparently a host generalist (D. J. Leopold and R. N. Muller 1983) and has been reported to parasitize planted fir trees (*Abies fraseri*) in Virginia (L. J. Musselman and S. C. Haynes 1996). The seeds are very high in oil. Cytotoxic and antimicrobial peptides called thionins are present in *P. pubera* (L. P. Vernon et al. 1985).

SANTALACEAE R. Brown
• Sandalwood Family

Daniel L. Nickrent

Shrubs or trees, root parasites [stem parasites], evergreen or deciduous, synoecious or dioecious [monoecious, andromonoecious]. **Leaves** opposite [alternate, whorled], simple; stipules absent; petiole present; blade margins entire; venation pinnate. **Inflorescences** unisexual or bisexual, axillary or terminal, thyrses or umbels [spikes, racemes, cymes, panicles, fascicles], or flowers solitary. **Flowers** bisexual or unisexual; perianth and androecium perigynous or epigynous; hypanthium adnate to ovary proximally, free distally [completely adnate to ovary]; sepals 0; petals 3–4(–5), distinct, valvate, post-staminal hairs present or absent; nectary present [absent]; stamens 3–4(–5), opposite petals, distinct, free; anthers dehiscing by longitudinal slits; staminodes present in pistillate flowers; pistil 1, 1–3-carpellate, ovary ½ inferior or inferior, 1–3-locular proximally, 1-locular distally, placentation free-central, pendulous; ovules 2–4 per ovary, anatropous; style 1; stigma 1. **Fruits** pseudodrupes (mesocarp hard). **Seeds** 1 per fruit.

Genera 11, species 67 (2 genera, 2 species in the flora): nearly worldwide.

This circumscription of Santalaceae in the strict sense derives from the molecular phylogenetic results of J. P. Der and D. L. Nickrent (2008). That study yielded a strongly supported clade of 11 genera that contains a diverse array of life forms from root parasitic trees and shrubs to aerially parasitic mistletoes, including three genera that previously have been segregated as Eremolepidaceae. *Nestronia*, the only genus of Santalaceae native to North America, is sister to *Colpoon* P. J. Bergius and *Rhoiacarpos* A. de Candolle, both South African endemics. These three genera, as well as *Osyris* Linnaeus, share a number of morphologic features, including habit, epigynous flowers, anther morphology, presence of nectaries, and fruit type; they previously have been classified in Santaleae A. de Candolle (= Osyrideae Reichenbach). Using phylogenetic trees calibrated for time with fossil evidence, it appears that *Nestronia* diverged from its Old World relatives in the Eocene.

SELECTED REFERENCE Der, J. P. and D. L. Nickrent. 2008. A molecular phylogeny of Santalaceae (Santalales). Syst. Bot. 33: 107–116.

1. Rhizomatous shrubs, to 1 m; inflorescences axillary, umbels or flowers solitary; petals white to greenish; se United States north of Florida . . . . . 1. *Nestronia*, p. 420
1. Trees, to 9 m; inflorescences axillary and terminal, thyrses; petals rose to crimson red or maroon; Florida . . . . . 2. *Santalum*, p. 420

1. NESTRONIA Rafinesque, New Fl. 3: 12. 1838 • Leachbrush [Greek *knestron*, name for *Daphne*] E

Darbya A. Gray

Shrubs, deciduous, probably dioecious. **Stems** glabrous. **Leaves:** petiole short. **Inflorescences** axillary, pedunculate umbels (staminate) or flowers solitary (pistillate). **Pedicels** present. **Flowers** unisexual; perianth and androecium epigynous; hypanthium in staminate flowers turbinate or campanulate, in pistillate flowers a short tube; petals 3–4(–5), post-staminal hairs present (staminate flowers) or absent (pistillate flowers); nectary lining hypanthium, wavy or slightly lobed distally; stamens 3–4(–5), in staminate flowers exserted, in pistillate flowers staminodial, ± included; ovary inferior, 3-locular proximally, 1-locular distally; ovules 2–3; styles in pistillate flowers conic; stigmas 3–4-lobed. **Pseudodrupes** spheric, without prominent perianth remnants at apex.

Species 1: se United States.

The sexual condition of *Nestronia* has been reported to be dioecious (A. E. Radford et al. 1968) or polygamodioecious (J. K. Small 1933; R. K. F. Pilger 1935; H. A. Gleason and A. Cronquist 1991). Flowers referred to as pistillate or bisexual possess staminal structures. Flowers from Virginia that have gynoecia were examined and had small anthers that lacked pollen. Therefore, these structures are staminodes, and the species is dioecious. Whether truly bisexual flowers exist in *Nestronia* remains to be determined. The pistillate flowers of *Nestronia* have been cited as an example of a receptacular inferior ovary by F. H. Smith and E. C. Smith (1942), but R. H. Eyde (1975) questioned this interpretation, favoring the more common appendicular inferior ovary.

1. **Nestronia umbellula** Rafinesque, New Fl. 3: 13. 1838 • Conjurer's nut, Indian olive E F

Darbya umbellulata A. Gray; *Nestronia quadriala* (Bentham & Hooker f.) Kuntze; *N. undulata* Rafinesque

Shrubs to 1 m, rhizomatous, forming large colonies. **Stems** forming shoots from crown. **Leaves:** petiole 2–5 mm; blade ovate-lanceolate, 2–7 × 0.7–3.2 cm (mean 4.2 × 1.8 cm), decreasing in size toward base of shoot, base acute, apex acute, abaxial surface glaucous, adaxial surface bright green. **Staminate inflorescences** 3–11-flowered. **Flowers** fragrant, staminate 2–3 mm, pistillate 6–10 mm, petals white to greenish, margins puberulent. **Pseudodrupes** yellowish green, spheric, 1–2 × 0.8–1.8 cm.

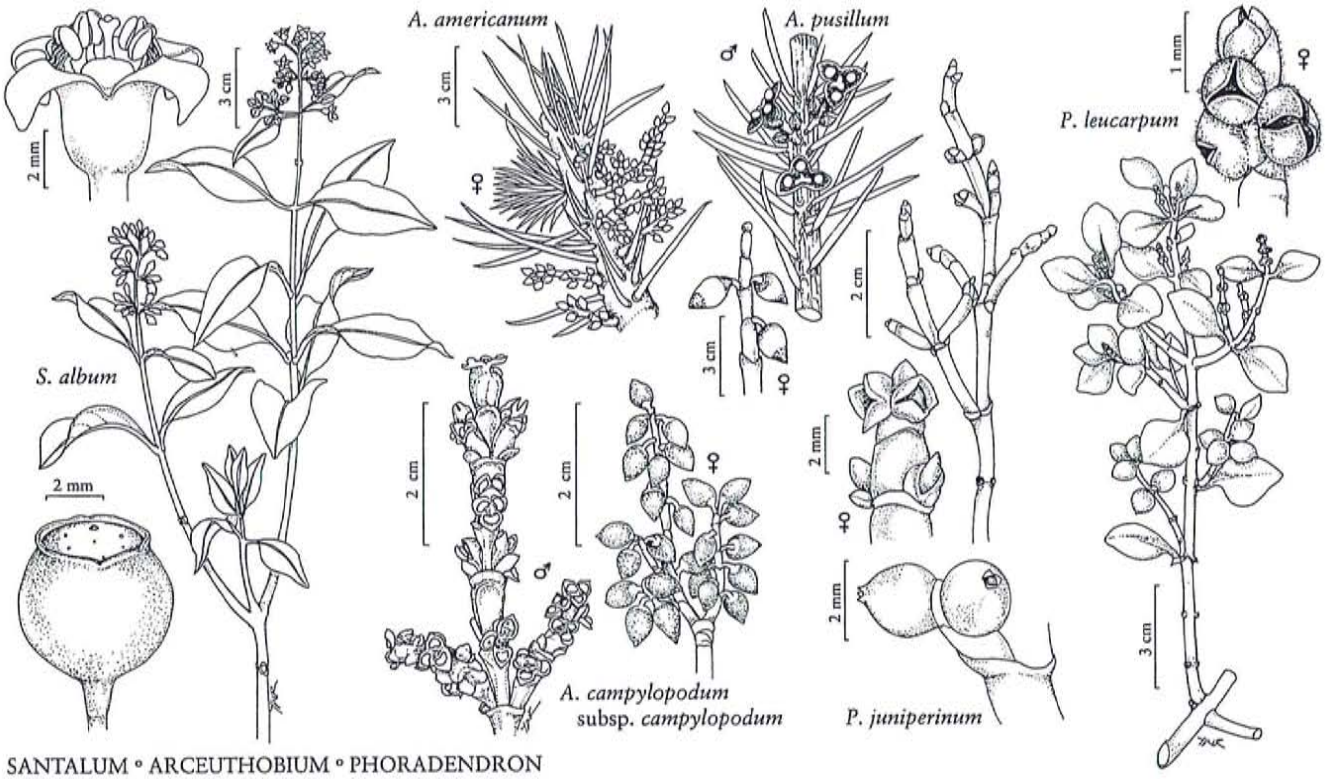
Flowering May–Jun. Moist and dry woodlands and stream banks; 20–500 m; Ala., Ga., Ky., N.C., S.C., Tenn., Va.

Although sometimes reported as specific to pines, *Nestronia* parasitizes a wide variety of host plants (D. D. Horn and R. Kral 1984). The species is apparently adapted to early successional habitats, thus natural disturbance may favor its spread and establishment (L. J. Musselman 1982; G. Libby and C. Bloom 1998).

Nestronia umbellula is listed as threatened, endangered, or of conservation concern by each state in which it occurs except Alabama, which does not provide regulatory protection to plants.

2. SANTALUM Linnaeus, Sp. Pl. 2: 349. 1753; Gen. Pl. ed. 5, 165. 1754 • Sandalwood [Greek *santalon*, derived from Sanskrit *chandana*, fragrant] I

Trees [shrubs], evergreen, synoecious. **Stems** glabrous. **Leaves:** petiole well developed. **Inflorescences** axillary and terminal, thyrses [cymes, racemes, umbels]. **Pedicels** present. **Flowers** bisexual; perianth and androecium perigynous [epigynous]; hypanthium campanulate [very short, funnelform, cylindric]; petals 4, post-staminal hairs present; nectary lining hypanthium, lobed distally; stamens 4, with hairs at filament base; ovary ½ inferior to almost superior [inferior], 1-locular; ovules 2–4; styles long, cylindric [short]; stigmas 3-lobed. **Pseudodrupes** rimmed by circular collar (scar or perianth remnants) at apex. $x = 10$.



Species 15 (1 in the flora): introduced, Florida; Asia (Indonesia), Pacific Islands (Papua New Guinea), Australia; introduced also elsewhere in Asia (India).

1. Santalum album Linnaeus, Sp. Pl. 2: 349. 1753 F I

Trees 4–9 m, upright or clambering, sprawling among other vegetation; branches slightly angular-striate. **Leaves:** petiole 2-ribbed, 1–1.8 cm; blade ovate to lanceolate-elliptic, 3.5–6 × 1.1–2.3 cm, apex obtuse or acute, adaxial surface shiny, darker green than abaxial surface; venation brochidodromous. **Inflorescences:** peduncles 4–11 mm. **Pedicels** to 1 mm. **Flowers** 3–4 mm; petals turning rose to crimson red or maroon through maturation, reflexed, triangular, 2 mm, post-staminal hairs white, long, coarse; nectary lobes reddish, ovate, prominent; stamens situated between nectary lobes; filaments longer than anther, positioning anthers above nectary lobes at height of stigma; styles 2 mm. **Pseudodrupes** nearly spheric, 7 × 8 mm, borne on short peduncle, often 1 per dichasium; epicarp dark red to black, mesocarp smooth. **Seeds** spheric. $2n = 20$.

Flowering Jul–Dec; fruiting Jul–Dec. Overgrown pine rocklands; 0 m; introduced; Fla.; Asia (Indonesia); introduced also elsewhere in Asia (India), Australia.

Santalum album has long been cultivated for its fragrant wood, and its oil is used in incense, perfume, cosmetics, and medicines (L. Hamilton and C. E. Conrad 1990).

Santalum album was introduced into cultivation after 1920 at the USDA Chapman Field Subtropical Horticulture Research Station in Miami-Dade County, Florida. The first collections documenting its escape from cultivation were made in 1989 and 1991 at that location. Later collections indicate that the species is common along the edges of a pine rockland remnant, thus indicating that a small colony had become established. An additional plant was also seen at the Deering Estate at Cutler (a county preserve) near Chapman Field (R. P. Wunderlin, pers. comm.). Given that flowers and fruits are present on vouchered specimens, *S. album* appears to be reproducing and spreading via its bird-dispersed fruits and seeds. This introduction demonstrates that sandalwood is not host specific, as none of its North American hosts in Florida are found within its natural range.

Santalum album is exceptional in the genus by having the ovary often appearing nearly superior. The ovaries in the remaining species of *Santalum* are half inferior or more.

VISCACEAE Batsch

• Christmas Mistletoe Family

Daniel L. Nickrent

Herbs, subshrubs, or shrubs, perennial, aerially parasitic on branches of angiosperms and gymnosperms, evergreen, dioecious or monoecious; roots present as haustorial endophytes. **Stems** erect or pendulous, brittle, nodes articulated. **Leaves** opposite [whorled], simple; stipules absent; petiole present or absent; blade brittle, fleshy, or scalelike, margins entire; venation pinnate or parallel [palmate]. **Inflorescences** unisexual or bisexual, axillary or terminal, spikelike thyrses or cymes [fascicles]. **Flowers** unisexual, radially symmetric or ± asymmetric; perianth epigynous; hypanthium absent (staminate flowers) or completely adnate to ovary (pistillate flowers); sepals 0; petals (2–)3–4(–6), usually distinct, sometimes connate basally, valvate, post-staminal hairs absent; nectary present or absent (staminate flowers), absent or not well defined (pistillate flowers); stamens (2–)3–4(–6), opposite petals, distinct, adnate to petals; anthers dehiscing by transverse slits or pores; pistil 1, 2[–3]-carpellate, ovary inferior, 0–1-locular, embryo sacs arising from placental nucellar complex; no true integumented ovules formed; style 0 or 1, very short; stigma 1, undifferentiated or 2[–3]-lobed [capitate]. **Fruits** berries (explosively dehiscent in *Arceuthobium*). **Seeds** 1 per fruit, viscin sticky or mucilaginous.

Genera 7, species ca. 575 (3 genera, 15 species in the flora): nearly worldwide.

To people in the northern hemisphere, the word mistletoe most often calls to mind a branch parasite in Viscaceae. In Europe, the Christmas mistletoe is typically *Viscum album*, whereas in North America, it is more often a species of *Phoradendron*. Mistletoe is associated historically with ancient Teutonic myths and Druidic rituals, but vestiges of these associations survive today as Yuletide kissing, a custom that dates to sixteenth-century England. Viscaceae represent just one of five clades that contain mistletoes, the others being Misodendraceae J. Agardh, Loranthaceae Jussieu, Santalaceae, and Amphorogynaceae Nickrent & Der (R. L. Mathiasen et al. 2008; D. L. Nickrent et al. 2010). Thus, the term mistletoe describes both a habit (an aerial parasite) and a taxonomic association (a member of Santalâles). Early twentieth-century works (for example, A. Engler and K. Krause 1935) often treated Viscaceae as a subfamily of Loranthaceae, and indeed this practice persists today in some floras, herbaria, and popular treatments. But molecular phylogenetic work has greatly clarified relationships among the five mistletoe clades, showing that they originated independently at different time periods

(J. P. Der and Nickrent 2008; R. Vidal-Russell and Nickrent 2008). Thus, the mainly tropical family Loranthaceae, whose members often have large, bird-pollinated flowers, is only distantly related to Viscaceae with small, insect-pollinated flowers.

In North America, *Arceuthobium* and *Phoradendron* are native, and *Viscum* was introduced purposely and is now naturalized. By far, *Arceuthobium* is the most economically significant viscaceous mistletoe. In 1982, timber losses caused by species of *Arceuthobium* for western North America were estimated as 130 million cubic meters (D. B. Drummond 1982; F. G. Hawksworth and D. Wiens 1996). Although these losses are severe, particularly in areas managed for timber production, species of *Arceuthobium* also play important ecological roles in natural forest ecosystems, for example its witches' brooms provide nesting habitat for the northern spotted owl (R. Everett et al. 1997). Native trees as well as cultivated fruit and nut trees can be negatively impacted by *Phoradendron* in North America, Mexico, and Central and South America, but the extent of damage has not been quantified. In addition to its use as a Christmas holiday novelty, *Viscum* is also being explored for a variety of medicinal uses including treatments for some forms of cancer (A. Bussing 2000).

Viscaceae have been shown by molecular phylogenetic studies to be sister to Amphorogynaceae Der & Nickrent (previously a tribe of Santalaceae), which includes root and stem parasites (J. P. Der and D. L. Nickrent 2008; Su H. J. et al. 2015). Resolution of some relationships among the genera of Viscaceae had been seen from molecular studies conducted over a decade ago, but only recently has a clear picture emerged. *Viscum* and *Notothixos* Oliver are sister to the remaining genera, which include a clade consisting of *Korthalsella* Tieghem and *Ginalloa* Korthals and another of *Phoradendron/Dendrophthora* and *Arceuthobium*. From a biogeographic perspective, *Arceuthobium* is interesting because it is the only mistletoe to occur naturally in both the Old and New Worlds. A hypothesis by F. G. Hawksworth and D. Wiens (1972) is that *Arceuthobium* evolved in Asia and, following a trans-Beringian migration, underwent a massive radiation in the New World. Chloroplast spacer sequences show, however, that the New World species are most similar to *Phoradendron*, whereas the Old World species have accumulated numerous deletions (Nickrent and M. A. García 2009). The most parsimonious hypothesis is that both *Arceuthobium* and *Phoradendron* first evolved in the New World, possibly in the Mexican highlands, where both genera are today quite diverse, and *Arceuthobium* then colonized the Old World.

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1. Leaves scalelike; anthers 1-locular; berries on recurved pedicels, 2-colored, explosively dehiscent; seeds sticky when fruit dehisces; endosperm globose to pyriform . . . . . 1. *Arceuthobium*, p. 424
1. Leaves well developed or scalelike; anthers 2-locular or multilocular; berries sessile, 1-colored, not explosively dehiscent; seeds mucilaginous when removed from fruit; endosperm ± flattened.
   2. Inflorescences spikelike thyrses, with intercalary meristems; flowers borne in cavities or grooves; anthers 2-locular; ovaries 1-locular; embryos oriented longitudinally . . . 2. *Phoradendron*, p. 434
   2. Inflorescences dichasial cymes, without intercalary meristems; flowers not borne in cavities or grooves; anthers multilocular; ovaries 0-locular; embryos oriented transversely . . . . . 3. *Viscum*, p. 439

1. ARCEUTHOBIUM M. Bieberstein, Fl. Taur.-Caucas. 3: 629. 1819, name conserved

• Dwarf mistletoe [Greek *arceuthos*, juniper, and *bios*, life, alluding to *A. oxycedri*, which parasitizes that host]

Herbs or subshrubs, dioecious; parasitic on branches of Pinaceae [Cupressaceae], infections localized, nonsystemic, or systemic, sometimes inducing witches' brooms. **Stems** multiple; primary branching fanlike, secondary branching fanlike or whorled. **Leaves** scalelike, connate. **Inflorescences** axillary or terminal, spikelike thyrses; flowers borne singly or in cymes in axils of subtending scales, not in cavities or grooves. **Staminate flowers:** petals 3–4(–6), triangular, distinct, radially symmetric or slightly asymmetric; stamens 3–4(–6); anthers 1-locular, dehiscing by transverse slits; nectary (= central cushion) present. **Pistillate flowers:** petals 2(–3), deltate, connate basally; ovary 1-locular; style very short to absent; stigma 2-lobed, secreting pollination droplet. **Berries** borne on recurved pedicels (when mature), explosively dehiscent from pedicellar end, 2-colored, smooth, glaucous, petal remnants not persisting. **Seeds** sticky when fruit dehisces, mucilaginous later after imbibing water; endosperm globose to pyriform; embryo oriented longitudinally. $x = 14$.

Species 29 (7 in the flora): North America, Mexico, West Indies, Central America, Eurasia, Africa, Atlantic Islands.

Species of *Arceuthobium* have received much attention because of their negative impact on commercially important conifers and also because of their fascinating life history. Most mistletoes rely on birds to disperse their seeds, but in all but one species of *Arceuthobium* (*A. verticilliflorum* Engelmann from Durango, Mexico), seeds are dispersed by explosive dehiscence. Another feature considered an evolutionary advancement is reduced photosynthesis accompanying greater dependence on host carbon. *Arceuthobium* can be considered on the brink of becoming a holoparasite (D. L. Nickrent and M. A. García 2009). It can form three basic types of infections on the host. The first, called a localized infection, is present as the mistletoe shoots emerge from an often swollen host branch at the original site of seedling penetration. In some species, the infections remain localized, but in many species they later develop into witches' brooms, with the parasite inducing prolific branching of the host distal to the point of infection. With nonsystemic witches' brooms, the mistletoe endophyte remains localized, whereas with systemic witches' brooms, the parasite endophyte occurs within the broom, sometimes existing adjacent to and dividing in synchrony with the host apical meristem (J. Kuijt 1960).

Arceuthobium has long been considered a taxonomically difficult group, mainly owing to losses and reductions in morphologic features used for classification. L. S. Gill (1935) was the first to propose a comprehensive treatment of the genus in the United States. In their classification, F. G. Hawksworth and D. Wiens (1972) utilized many of the same features as Gill, such as branching pattern, but did not agree with his host-form concept. Host specificity in *Arceuthobium* ranges from specialists (only one host known) to generalists that parasitize over a dozen species. Hawksworth and Wiens and D. L. Nickrent (1996) strongly advocated that mistletoe morphologic integrity was maintained irrespective of host being parasitized and recognized 28 and 42 species, respectively.

A classification of *Arceuthobium*, revised from D. L. Nickrent (1996), was given by Nickrent et al. (2004), who recognized 26 species in two subgenera and 11 sections. That system is followed here, considering only subg. *Vaginata* Hawksworth & Wiens because all North American *Arceuthobium* reside there. This classification differs most from F. G. Hawksworth and D. Wiens (1972) with regard to sect. *Campylopoda* Hawksworth & Wiens, whereas the latter authors recognized 13 species in this section, Nickrent et al. recognized only two.

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1. Secondary branching whorled; staminate pedicels present; lateral staminate flowers subglobose in bud; flowering (Mar–)Apr–Jun; principal hosts *Pinus banksiana* and *P. contorta* . . . . . 1. *Arceuthobium americanum*
1. Secondary branching fanlike; staminate pedicels absent (present in *A. douglasii*); lateral staminate flowers lenticular or subglobose in bud; flowering Feb–Dec; hosts various Pinaceae.
   2. Flowering Jul–Dec.
      3. Parasites of pinyon pines (principally *Pinus edulis* and *P. monophylla*) . . . . . 6. *Arceuthobium divaricatum*
      3. Parasites of other Pinaceae (*Abies*, *Picea*, *Pinus*, *Larix*, and *Tsuga*) . . . . . 7. *Arceuthobium campylopodum*
   2. Flowering Feb–Jun(–Jul).
      4. Lateral staminate flowers subglobose in bud; plants forming systemic witches' brooms; principal host *Pseudotsuga menziesii* . . . . . 2. *Arceuthobium douglasii*
      4. Lateral staminate flowers lenticular in bud; plants forming localized infections or systemic or nonsystemic witches' brooms; principle hosts *Picea* and *Pinus*.
         5. Secondary branches (1–)3 cm, rarely seen; plants forming systemic witches' brooms; principal host *Picea*; e North America . . . . . 3. *Arceuthobium pusillum*
         5. Secondary branches 8–20(–27) cm; plants forming localized infections or nonsystemic witches' brooms; principal host *Pinus*; w North America.
            6. Staminate and pistillate plants dimorphic; principal host *Pinus leiophylla* var. *chihuahua*; Arizona, New Mexico . . . . . 4. *Arceuthobium gillii*
            6. Staminate and pistillate plants not dimorphic; principal hosts primarily *Pinus ponderosa*, sometimes *P. durangensis*, and *P. engelmannii*; w United States . . . . . 5. *Arceuthobium vaginatum*

1. Arceuthobium americanum Nuttall ex Engelmann, Boston J. Nat. Hist. 6. 214. 1850 • Lodgepole pine dwarf mistletoe E F

Razoumofskya americana (Nuttall ex Engelmann) Kuntze

Plants usually forming systemic witches' brooms, sometimes nonsystemic witches' brooms in secondary hosts. **Stems** yellowish to olive green; secondary branching whorled, branches 5–9(–30) cm, third internode 6–23 × 1–2 mm, dominant shoot 1–3 mm diam. at base. **Staminate pedicels** present. **Staminate flowers** radially symmetric, subglobose in bud, 2.2 mm diam.; petals 3(–4), same color as stems. **Berries** proximally olive green, distally yellowish to reddish brown, 3.5–4.5 × 1.5–2.5 mm. **Seeds** ellipsoid, 2.4 × 1.1 mm, endosperm green. $2n = 28$.

Flowering (Mar–)Apr–Jun; fruiting Aug–Sep. Coniferous forests, especially jack or lodgepole pine; 200–3400 m; Alta., B.C., Man., Ont., Sask.; Calif., Colo., Idaho, Mont., Nev., Oreg., Utah, Wash., Wyo.

Meiosis occurs in August, with fruits maturing 16 months after pollination; seeds germinate in May.

The principal hosts of *Arceuthobium americanum* are *Pinus contorta* var. *latifolia* in western North America, *P. contorta* var. *murrayana* in the Sierra Nevada and Cascade ranges of the western United States, and *P. banksiana* in western Canada. A study utilizing AFLPs (C. A. Jerome and B. A. Ford 2002) documented that the parasite exists as three genetic races that correspond to these host species. *Arceuthobium americanum* has the most extensive geographic range of any species of the genus and can utilize other species as secondary hosts, including *P. albicaulis*, *P. flexilis*, *P. jeffreyi*, and *P. ponderosa*, as well as a number of rare hosts. Although young infections may be localized, *A. americanum* eventually forms massive systemic

witches' brooms. Interestingly, when parasitizing some secondary hosts, the brooms may become nonsystemic, possibly indicating partial breakdown of coordinated developmental pathways.

2. **Arceuthobium douglasii** Engelmann in J. T. Rothrock, Rep. U.S. Geogr. Surv., Wheeler, 253. 1879 • Douglas-fir dwarf mistletoe

Razoumofskya douglasii (Engelmann) Kuntze

Plants forming systemic witches' brooms. **Stems** yellowish green, olive green, orange-brown, or maroon; secondary branching fanlike, branches 2(–8) cm, third internode 2–6 × 1 mm, dominant shoot 1–1.5 mm diam. at base. **Staminate pedicels** present. **Staminate flowers** radially symmetric, subglobose in bud, 2.3 mm diam.; petals (2–)3(–4), reddish or purple. **Berries** proximally olive green to purplish, distally yellow, brownish orange, or maroon, 3.5–4.5 × 1.5–2 mm. **Seeds** ellipsoid, 2.4 × 1.1 mm, endosperm bright green. $2n = 28$.

Flowering (Mar–)Apr–May(–Jun); fruiting Aug–Sep (–Oct). Coniferous forests with Douglas fir; 300–3300 m; B.C.; Ariz., Calif., Colo., Idaho, Mont., Nev., N.Mex., Oreg., Tex., Utah, Wash., Wyo.; Mexico (Chihuahua, Coahuila, Durango, Nuevo León).

Staminate meiosis occurs in September, pistillate in April, with fruits maturing 17 to 18 months after pollination; seeds germinate in March.

Arceuthobium douglasii has the widest latitudinal distribution of any North American dwarf mistletoe. Its principal host is *Pseudotsuga menziesii*, but it is occasionally found also on *Abies amabilis*, *A. concolor*, *A. grandis*, *A. lasiocarpa*, *Picea engelmannii*, and *P. pungens*. Plants of *Arceuthobium douglasii* induce massive systemic witches' brooms that severely affect host growth and may eventually result in host mortality. Section *Minuta* Hawksworth & Wiens was erected to accommodate the two diminutive North American dwarf mistletoes, *A. douglasii* and *A. pusillum*. Isozymes and later DNA analyses showed that these two species are not closely related, thus their small shoot size and spring flowering evolved in parallel.

3. **Arceuthobium pusillum** Peck, Trans. Albany Inst. 7: 191. 1872 • Eastern dwarf mistletoe [E] [F]

Plants forming systemic witches' brooms. **Stems** green, orange, red, maroon, or brown; secondary branching (rarely seen) fanlike, branches 1(–3) cm, third internode 1–1.9 × 0.5–1.5 mm; dominant shoot 1 mm diam. at base; pistillate stems usually longer than staminate. **Staminate pedicels** absent. **Staminate flowers** radially symmetric, 1 terminating stem or 3 in dichasium, terminal subglobose in bud, lateral lenticular in bud, 1.7–2.2 mm diam.; petals (2–)3(–4), red to maroon. **Berries** proximally green, distally yellowish to reddish brown, 3 × 1.3–1.8 mm. **Seeds** pyriform to elliptic, 1.4–1.8 × 1–1.4 mm, endosperm bright green. $2n = 28$.

Flowering (Mar–)Apr–May(–Jun); fruiting Sep–Oct. Spruce forests within 500 m of coast and inland bogs, often within 2 km of lakes and rivers; 0–800 m; Man., N.B., Nfld. and Labr. (Nfld.), N.S., Ont., P.E.I., Que., Sask.; Conn., Maine, Mass., Mich., Minn., N.H., N.J., N.Y., Pa., R.I., Vt., Wis.

Staminate meiosis occurs in September, pistillate meiosis in May, with fruits maturing five months after pollination; seeds germinate in May to June.

In 1858, Thoreau wrote about the witches' brooms of Eastern dwarf mistletoe, over a decade before the species was actually described. Lucy B. Millington of Warrensburg, New York, recognized the mistletoe in 1871 and related her discovery via correspondence with C. H. Peck, who named the species in the following year (B. S. Smith 1992). The species was later found to be widespread in spruce forests throughout the Great Lakes states.

Arceuthobium minutum Engelmann, which pertains here, was published in 1871 but without a description, hence it is invalid.

Arceuthobium pusillum forms massive systemic witches' brooms that severely affect the vigor of its principal host, *Picea mariana* (black spruce). White spruce (*P. glauca*) and red spruce (*P. rubens*) are less commonly infected. Occasional to rare hosts include *Abies balsamea*, *Larix laricina*, *Pinus banksiana*, *Pinus resinosa*, and *Pinus strobus*. Molecular phylogenetic work revealed that *Arceuthobium pusillum* is most closely related to *A. bicarinatum* Urban of Hispaniola (D. L. Nickrent et al. 2004). Given that these two species differ greatly in size, this result demonstrates the dramatic morphologic changes that ancestors of *A. pusillum* underwent, possibly as adaptations to cold climates.

4. Arceuthobium gillii Hawksworth & Wiens, Brittonia 16: 55, figs. 1A, 2A. 1964 • Chihuahua pine dwarf mistletoe

Plants forming nonsystemic witches' brooms; staminate and pistillate plants dimorphic: staminate taller with open divaricate branching, pistillate shorter with dense branching. **Stems** olive green, greenish brown, greenish yellow, or orange; secondary branching fanlike, branches 8–15(–25) cm, third internode 5–18 × 2–4.5 mm, dominant shoot 2.5–8 mm diam. at base. **Staminate pedicels** absent. **Staminate flowers** slightly asymmetric, (proximal petal deflexed at anthesis), lenticular in bud, 2.5–4 mm diam.; petals 3, same color as stem abaxially, tawny reddish brown adaxially. **Berries** proximally olive green and conspicuously glaucous with bluish hue, distally greenish or yellowish brown, 4–5 × 2–3 mm. **Seeds** pyriform to ellipsoid, 3–4 × 2–3 mm, endosperm dark olive green. $2n = 28$.

Flowering Feb–Apr; fruiting Oct. Coniferous and mixed forests with Chihuahua pine; 1700–2700 m; Ariz., N.Mex.; Mexico (Chihuahua, Durango, Sinaloa, Sonora).

Meiosis occurs in September, with fruits maturing 19 to 20 months after pollination; seeds germinate in April.

In the flora area, *Arceuthobium gillii* is found in the Chiricahua, Huachuca, Santa Catalina, and Santa Rita mountains of Arizona, and the Animas Mountains of New Mexico; its principal host is *Pinus leiophylla* var. *chihuahua*. Subspecies *nigrum* Hawksworth & Wiens, which occurs in the Sierra Madre Occidental and Oriental of Mexico, was subsequently elevated to species rank as *A. nigrum* (Hawksworth & Wiens) Hawksworth & Wiens. The two species are apparently allopatric but occur in the same mountain range in northern Durango, Mexico. Both form nonsystemic witches' brooms on members of *Pinus* subsect. *Leiophylla* Loudon and are closely related as shown by molecular analyses (D. L. Nickrent et al. 2004).

5. Arceuthobium vaginatum (Humboldt & Bonpland ex Willdenow) J. Presl in F. Berchtold and J. S. Presl, Prir. Rostlin 2: 28. 1825

Viscum vaginatum Humboldt & Bonpland ex Willdenow, Sp. Pl. 4: 740. 1806

Subspecies 2 (1 in the flora): sw, wc United States, n Mexico.

5a. Arceuthobium vaginatum (Humboldt & Bonpland ex Willdenow) J. Presl subsp. **cryptopodum** (Engelmann) Hawksworth & Wiens, Brittonia 17: 230. 1965 • Southwestern dwarf mistletoe

Arceuthobium cryptopodum Engelmann, Boston J. Nat. Hist. 6: 214. 1850

Plants forming nonsystemic witches' brooms; staminate and pistillate plants not dimorphic. **Stems** green, yellow, orange, reddish brown, or dark purple; secondary branching fanlike, branches 10–20(–27) cm, third internode 4–16 × 2–4.5 mm, dominant shoot 2–10 mm diam. at base. **Staminate pedicels** absent. **Staminate flowers** radially symmetric, lenticular in bud, 2.5–3 mm diam.; petals 3–4(–6), green, greenish yellow, or light pink, sometimes differing abaxially and adaxially. **Berries** proximally olive green, distally brown, 4.5–5.5 × 2–3 mm. **Seeds** pyriform to ellipsoid, 2.8 × 1.8 mm, endosperm green or green and maroon. $2n = 28$.

Flowering (Apr–)May–Jun(–Jul); fruiting Jul–Aug (–Sep). Coniferous forests with ponderosa pine; 1700–3000 m; Ariz., Colo., N.Mex., Tex., Utah; Mexico (Chihuahua, Coahuila, Sonora).

Meiosis occurs in March to April, with fruits maturing 14 to 15 months after pollination; seeds germinate in August to September immediately after dispersal.

Subspecies *cryptopodum* occurs in the southwestern United States and northern Mexico, whereas subsp. *vaginatum* occurs in the Sierra Madre Occidental and Sierra Madre Oriental of Mexico. The two subspecies are sympatric in central Chihuahua, where some morphologically intermediate populations occur. The Mexican subspecies is often deeply pigmented (dark brown to black), has larger shoots and staminate flowers, and flowers in May and June.

Subspecies *cryptopodum* can be found parasitizing its most common principal host, *Pinus ponderosa* var. *scopulorum*, in nearly every location where this tree occurs. It forms nonsystemic witches' brooms that can be massive, increasing the longevity of the supporting branch, which would normally self-prune. This subspecies also parasitizes other principal hosts such as *P. durangensis* Roezl ex Gordon, *P. engelmannii* and *P. ponderosa* var. *arizonica*, as well as secondary and occasional hosts such as *P. aristata*, *P. contorta*, and *P. cooperi* C. E. Blanco. The parasite can be damaging to its host in some portions of its range, such as the Front Range of the Rocky Mountains in Colorado and south-central New Mexico.

6. **Arceuthobium divaricatum** Engelmann in J. T. Rothrock, Rep. U.S. Geogr. Surv., Wheeler, 253. 1879 • Pinyon dwarf mistletoe

Razoumofskya divaricata (Engelmann) Coville

Plants usually forming localized infections only, sometimes forming small nonsystemic witches' brooms. **Stems** olive green, orange, or reddish brown, glaucous; secondary branching fanlike, branches 8(–13) cm, slender, third internode 6–15 × 1–2 mm, dominant shoot 1.5–4 mm diam. at base. **Staminate pedicels** absent. **Staminate flowers** radially symmetric, lenticular in bud, 2.5 mm diam.; petals 3, light yellowish green. **Berries** proximally olive or grayish to bluish green, distally olive green to brown, glaucous, 3.5 × 2 mm. **Seeds** ellipsoid, 2 × 0.9 mm, endosperm bright green. $2n = 28$.

Flowering Aug–Sep; fruiting Sep–Oct. Pinyon-juniper woodlands; 1200–3000 m; Ariz., Calif., Colo., Nev., N.Mex., Tex., Utah; Mexico (Baja California).

Meiosis occurs in July, with fruits maturing 13 months after pollination.

Arceuthobium divaricatum is parasitic only on pinyon pines. Its principal hosts are *Pinus edulis* and *P. monophylla*, but it can also parasitize *P. cembroides*, and *P. quadrifolia*. Most infections are localized; however, over time small witches' brooms can form that are cryptic given the shrubby habit of the host tree. Pinyon dwarf mistletoe was classified in sect. *Campylopoda* (F. G. Hawksworth and D. Wiens 1972), as was another parasite of pinyons from Mexico, *A. pendens* (Hawksworth and Wiens 1980). Isozyme data first showed that these species are not part of sect. *Campylopoda* (D. L. Nickrent 1996), and this was later confirmed with DNA evidence (Nickrent et al. 2004). Moreover, the two pinyon dwarf mistletoes are not closely related to each other; *A. divaricatum* is close to *A. douglasii*, and *A. pendens* is sister to *A. guatemalense* Hawksworth & Wiens of Mexico and Guatemala.

7. **Arceuthobium campylopodum** Engelmann, Boston J. Nat. Hist. 6: 214. 1850 • Western dwarf mistletoe [F]

Razoumofskya campylopoda (Engelmann) Kuntze

Plants forming localized infections only or nonsystemic witches' brooms. **Stems** yellow, yellowish green, green, olive green, brown, light tan, orange, red, maroon, or purple; secondary branching fanlike, branches 3–10(–22) cm, third internode 2–15(–23) × 1–3.5(–5) mm, dominant shoot 1–6 mm diam. at base. **Staminate pedicels** absent. **Staminate flowers** slightly asymmetric (distal lateral petals keeled and hooded, proximal petal not keeled, deflexed at anthesis), lenticular in bud, 2.3–3.3 mm diam.; petals 3–4(–6), yellowish green. **Berries** proximally yellowish green or olive green, distally yellow, orange, or brown, 3–5 × 2–3 mm. **Seeds** pyriform to ellipsoid, 3.3–5.5 × 2.3–4 mm, endosperm bright green. $2n = 28$.

Subspecies 13 (13 in the flora): w North America, n Mexico.

Arceuthobium campylopodum is here considered a wide ranging and polymorphic species that parasitizes a number of hosts in Pinaceae throughout western North America and northern Mexico. Earlier taxonomic concepts, such as those of L. S. Gill (1935) and J. Kuijt (1955), recognized several forms of *A. campylopodum* that usually corresponded with principal host species. F. G. Hawksworth and D. Wiens (1972, 1996) elevated those forms to species, stating that morphologic integrity is maintained even when parasitizing nonprincipal hosts. Despite this claim, most of the characters they used to differentiate species were quantitative with continuous variation. The absence of hybridization was also given as evidence for separate species status; however, all species have the same chromosome number and very similar morphology, thus it is not clear how a hybrid would be recognized should it occur. Examination of dwarf mistletoe specimens without information on location and host can often result in an ambiguous identification.

During the 1980s and 1990s, biosystematic studies were conducted using isozyme electrophoresis, particularly within sect. *Campylopoda*. Results of these studies, summarized by D. L. Nickrent (1996), in some cases provided evidence for populational genetic divergence but in other cases did not. Following those studies, phylogenetic analyses of chloroplast *trn*L-F and nuclear rDNA ITS sequences were applied to species level questions (Nickrent et al. 1994, 2004). All members of sect. *Campylopoda* had essentially identical DNA sequences in these regions, in contrast with species in other sections, which showed greater genetic distances.

All taxa within sect. *Campylopoda* were examined with respect to their morphology, host associations, levels of sympatry, and genetic relationships (D. L. Nickrent 2012). That study concluded that all taxa of sect. *Campylopoda*, recognized as species by F. G. Hawksworth and D. Wiens (1996), are best viewed as ecotypes of a single variable species, *Arceuthobium campylopodum*. Two factors were used to justify describing the variants at the rank of subspecies: less than 20% of the time are the 13 subspecies sympatric with one another (they are generally geographically and ecologically isolated), and subspecies have already been described in *A. vaginatum*. For a complete list of synonyms for each subspecies, see Nickrent.

A morphometric study using discriminant function analysis was conducted by R. L. Mathiasen and S. C. Kenaley (2015) on four taxa within sect. *Campylopoda*: *Arceuthobium campylopodum* subspp. *campylopodum*, *littorum*, *occidentale*, and *siskiyouense*. With the exception of male plants of the last subspecies, this analysis showed that the 95% confidence intervals overlapped, indicating potential misclassification of the taxa assigned *a priori* to species. Differences in multivariate means indicate that some differentiation has occurred among these four taxa. An additional three taxa of sect. *Campylopdoda* that parasitize white pines were examined by B. P. Reif et al. (2015) using amplified fragment length polymorphisms: *A. campylopodum* subspp. *apachecum*, *blumeri*, and *cyanocarpum*. Support was low for genetic differentiation between the first two subspecies, whereas greater differentiation was seen between these and the third, in agreement with D. L. Nickrent et al. (2004). These two studies examined seven of the 13 taxa in sect. *Campylododa*, hence more work is needed simultaneously treating the entire complex. Although these authors argued that their results support classification at the species level, their results could also be viewed as evidence for early stages of genetic differentiation among widespread populations, thus equally supporting classification at the subspecific rank.

SELECTED REFERENCES Mathiasen, R. L. and S. C. Kenaley. 2015. A morphometric analysis of dwarf mistletoes in the *Arceuthobium campylopodum-occidentale* complex (Viscaceae). Madroño 62: 1–20. Nickrent, D. L. 2012. Justification for subspecies in *Arceuthobium campylopodum* (Viscaceae). Phytoneuron 2012-51: 1–11. Reif, B. P. et al. 2015. Genetic structure and morphological differentiation of three western North American dwarf mistletoes (*Arceuthobium*: Viscaceae). Syst. Bot. 40: 191–207.

1. Stems 3–5(–11) cm; principal hosts *Larix*, *Picea*, *Pinus albicaulis*, *P. aristata*, *P. flexilis*, *P. longaeva*, *P. strobiformis*, and *Tsuga*; plants forming witches' brooms; usually occurring at 1000–3000 m.
   2. Stems 3(–9) cm; principal host *Pinus*.
      3. Third internodes 5–7.2(–10) mm; staminate flowers 2.7 mm diam.; principal host *Pinus strobiformis*; Arizona, New Mexico . . . . . 7c. *Arceuthobium campylopodum* subsp. *apachecum*
      3. Third internodes 2–5.2(–14) mm; staminate flowers 3 mm diam.; principal hosts *Pinus albicaulis*, *P. aristata*, *P. flexilis*, and *P. longaeva*; widely distributed in w United States but not Arizona . . . . . 7f. *Arceuthobium campylopodum* subsp. *cyanocarpum*
   2. Stems 4–5(–11) cm; principal hosts *Larix*, *Picea*, and *Tsuga*.
      4. Staminate flowers 2.7 mm diam.; principal hosts *Larix* and *Tsuga*; British Columbia, nw United States. . . . . 7g. *Arceuthobium campylopodum* subsp. *laricis*
      4. Staminate flowers 2.3 mm diam.; principal host *Picea*; Arizona, New Mexico. . . . . 7i. *Arceuthobium campylopodum* subsp. *microcarpum*
1. Stems 5–12(–22) cm; principal hosts *Abies*, *Pinus attenuata*, *P. contorta*, *P. jeffreyi*, *P. lambertiana*, *P. monticola*, *P. muricata*, *P. ponderosa*, *P. radiata*, *P. sabiniana*, *P. strobiformis*, and *Tsuga*; plants forming localized infections only or forming witches' brooms; usually occurring at 0–2500 m.
   5. Principal hosts *Abies*, *Pinus contorta*, and *Tsuga*.
      6. Stems 8(–22) cm; third internodes 4–14 (–23) cm; principal hosts *Abies concolor* and *A. magnifica*; Arizona, California, Nevada, Oregon, Utah, Washington. . . . . 7b. *Arceuthobium campylopodum* subsp. *abietinum*
      6. Stems 5–7(–13) cm; third internodes 4–9 (–16) cm; principal hosts *Abies*, *Pinus*, and *Tsuga*; British Columbia to California . . . . . 7m. *Arceuthobium campylopodum* subsp. *tsugense*
   5. Principal host *Pinus* (subsp. *siskiyouense* rarely on *P. contorta*).
      7. Principal host *Pinus strobiformis*; plants usually forming localized infections only; Arizona. . . . . 7d. *Arceuthobium campylopodum* subsp. *blumeri*
      7. Principal hosts other than *Pinus strobiformis*; plants forming localized infections only or forming witches' brooms; California, Idaho, Oregon, Washington.
         8. Principal hosts *Pinus* subg. *Strobus* (white and soft pines).
            9. Shoots yellow or green; plants forming witches' brooms; principal host *Pinus lambertiana*; California . . . . . 7e. *Arceuthobium campylopodum* subsp. *californicum*
            9. Shoots olive green or brown; plants forming localized infections only; principal host *Pinus monticola*; nw California, sw Oregon . . . . . 7j. *Arceuthobium campylopodum* subsp. *monticola*
         8. Principal hosts *Pinus* subg. *Pinus*.

[10. Shifted to left margin.—Ed.]

10. Plants usually forming witches' brooms.
    11. Third internodes 7–11(–22) × 1.5–2(–2.5) mm; staminate flowers: petals 3(–4); principal hosts *Pinus jeffreyi* and *P. ponderosa*; California, Idaho, Oregon, Washington . . . . . 7a. *Arceuthobium campylopodum* subsp. *campylopodum*
    11. Third internodes 10–15(–20) × 2–3.5(–5) mm; staminate flowers: petals 4; principal hosts *Pinus muricata* and *P. radiata*; coastal California . . . . . 7h. *Arceuthobium campylopodum* subsp. *littorum*
10. Plants usually forming localized infections only.
    12. Stems yellow or orange; principal host *Pinus sabiniana*; flowering Sep–Nov(–Dec); California (surrounding central valley and in Coast Ranges) . . . 7k. *Arceuthobium campylopodum* subsp. *occidentale*
    12. Stems brown; principal host *Pinus attenuata*; flowering Aug–Sep; nw California, sw Oregon . . . . . 7l. *Arceuthobium campylopodum* subsp. *siskiyouense*

7a. Arceuthobium campylopodum Engelmann subsp. campylopodum F

Plants usually forming witches' brooms. **Stems** yellow, green, olive green, orange, or brown, 8(–13) cm; third internode 7–11(–22) × 1.5–2(–2.5) mm, dominant shoot 1.5–5 mm diam. at base. **Staminate flowers** 3 mm diam.; petals 3(–4). **Berries** 5 × 3 mm.

Flowering Aug–Oct; fruiting Sep–Nov. Coniferous forests with ponderosa or Jeffrey pine; 30–2500 m; Calif., Idaho, Oreg., Wash.; Mexico (Baja California).

Meiosis occurs in July, with fruits maturing 13 months after pollination.

The distribution of subsp. *campylopodum* overlays a subset of the range of its principal host, *Pinus ponderosa*. The treatment of the host species by R. Kral (1993) recognized three varieties, two of which (*P. ponderosa* var. *ponderosa* and var. *scopulorum*) intergrade in Idaho, Montana, and Washington. With this taxonomic concept, the hosts of subsp. *campylopodum* would include *P. ponderosa* subsp. *scopulorum*. In contrast, The Gymnosperm Database (http://www.conifers.org/pi/Pinus_ponderosa.php) uses a modification of the classification by F. Lauria (1991), which suggests that *P. ponderosa* is composed of four subspecies: subspp. *ponderosa*, *benthamiana* (Hartweg) Silba, *brachyptera* (Hartweg) Silba, and *scopulorum*. Based on the geographical limits of these four subspecies, it appears that *Arceuthobium campylopodum* subsp. *campylopodum* is restricted to the *P. ponderosa* subspp. *ponderosa* and *benthamiana*. In addition to *P. ponderosa*, *P. jeffreyi* is another principal host. Both are heavily parasitized, thus this mistletoe is considered a major pathogen of these commercially important trees (F. G. Hawksworth and D. Wiens 1996). Secondary to rare hosts include *P. attenuata*, *P. contorta*, *P. coulteri*, *P. lambertiana*, and *P. sabiniana*.

7b. Arceuthobium campylopodum Engelmann subsp. abietinum (Engelmann) Nickrent, Phytoneuron 2012-51: 9. 2012 • Fir dwarf mistletoe

Arceuthobium douglasii Engelmann var. *abietinum* Engelmann in W. H. Brewer et al., Bot. California 2: 106. 1880; *Razoumofskya abietina* (Engelmann) Abrams

Plants forming witches' brooms. **Stems** yellow, green, olive green, orange, brown, or red, 8(–22) cm; third internode 4–14(–23) × 1.5–2(–4) mm, dominant shoot 1.5–6 mm diam. at base. **Staminate flowers** 2.5 mm diam.; petals 3(–4). **Fruits** 4 × 2 mm.

Flowering Jul–Aug(–Sep); fruiting Sep–Oct. Coniferous forests generally with fir; 0–2700 m; Ariz., Calif., Nev., Oreg., Utah, Wash.; Mexico (Chihuahua).

Meiosis occurs in July, with fruits maturing 13 to 14 months after pollination.

Subspecies *abietinum* includes forma speciales *concoloris* Hawksworth & Wiens, which parasitizes *Abies concolor* (white fir), and forma speciales *magnificae* Hawksworth & Wiens, which parasitizes *A. magnifica* (red fir). These forms were based upon inoculation studies showing that seeds of one form apparently will not infect the other's host species and vice versa (J. R. Parmeter and R. F. Scharpf 1963). Morphologically the two forms are extremely similar, with the former having a greater mean shoot height (10 versus 6 cm). The white fir dwarf mistletoe occurs throughout the above geographical range, whereas red fir dwarf mistletoe is restricted to California and southwestern Oregon. In addition to the above two species of fir, *Abies durangensis* Martínez and *A. grandis* are principal hosts; secondary to rare hosts include *A. lasiocarpa*, *Picea breweriana*, *Pinus ayacahuite* C. Ehrenberg ex Schlechtendal, *Pinus contorta*, *Pinus lambertiana*, and *Pinus monticola*.

7c. **Arceuthobium campylopodum** Engelmann subsp. **apachecum** (Hawksworth & Wiens) Nickrent, Phytoneuron 2012-51: 10. 2012 • Apache dwarf mistletoe

Arceuthobium apachecum Hawksworth & Wiens, Brittonia 22: 266. 1970

Plants forming witches' brooms. **Stems** yellow, green, or red, 3.5(–9) cm; third internode 5–7.2(–10) × 1–1.5(–2) mm, dominant shoot 1–2 mm diam. at base. **Staminate flowers** 2.7 mm diam.; petals 3–4(–5). **Fruits** 4 × 2.5 mm.

Flowering Jul–Sep; fruiting Aug–Oct. Coniferous forests with southwestern white pine; 2000–3000 m; Ariz., N.Mex.; Mexico (Chihuahua).

Meiosis occurs in July, with fruits maturing 13 months after pollination.

Subspecies *apachecum* is known only from a portion of the range of its only host tree, *Pinus strobiformis*. Subspecies *blumeri* also utilizes this host, but the two taxa are not sympatric.

7d. **Arceuthobium campylopodum** Engelmann subsp. **blumeri** (A. Nelson) Nickrent, Phytoneuron 2012-51: 9. 2012 • Blumer's dwarf mistletoe

Arceuthobium blumeri A. Nelson, Bot. Gaz. 56: 65. 1913

Plants usually forming localized infections only, rarely forming witches' brooms. **Stems** yellow, light green, or light tan, 6.5 (–18) cm; third internode 5–9.1(–14) × 1–1.6(–2) mm, dominant shoot 1–3 mm diam. at base. **Staminate flowers** 2.5–3 mm diam.; petals 3–4(–6). **Fruits** 4 × 2.5 mm.

Flowering Jul–Aug; fruiting Aug–Oct. Coniferous forests with southwestern white pine; 2100–3300 m; Ariz.; Mexico (Chihuahua, Durango, Nuevo León).

Meiosis occurs in July, with fruits maturing 13 to 14 months after pollination.

In addition to *Pinus strobiformis*, *P. ayacahuite* in Mexico is a principal host for subsp. *blumeri*. In the flora area, this subspecies occurs only in the Huachuca Mountains, but it is more widely distributed in the Sierra Madre Occidental of Chihuahua and Durango and is disjunct in the Sierra Madre Oriental on Cerro Potosí in Nuevo León. The molecular phylogenetic study by D. L. Nickrent et al. (2004) showed subsp. *blumeri* to be sister to the other members of sect. *Campylopoda*. Given that Mexico is likely the center of origin for *Arceuthobium* (Nickrent and M. A. García 2009), it is likely that subsp. *blumeri* represents an early diverging member of this species.

7e. **Arceuthobium campylopodum** Engelmann subsp. **californicum** (Hawksworth & Wiens) Nickrent, Phytoneuron 2012-51: 10. 2012 • Sugar pine dwarf mistletoe E

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

Plants forming witches' brooms. **Stems** bright yellow or green, 6–8(–14) cm; third internode 6–10.5(–16) × 1–1.5(–2) mm, dominant shoot 1.5–4 mm diam. at base. **Staminate flowers** 3.3 mm diam.; petals 3–4. **Fruits** 4 × 2.5 mm.

Flowering Jul–Aug; fruiting Sep–Oct. Coniferous forests with sugar pine or western white pine; 600–2000 m; Calif.

Meiosis occurs in July, with fruits maturing 13 to14 months after pollination.

As the common name implies, subsp. *californicum* is parasitic primarily on *Pinus lambertiana*, secondarily on *P. monticola*. It is found from the Peninsular Ranges of San Diego County through the Sierra Nevada to the Cascade Range of Siskiyou County, as well as some locations in the Klamath Mountains. In some locations it is sympatric with subsp. *campylopodum*, and rarely both taxa can be found on the same host. It induces large witches' brooms on sugar pine and is considered a serious pathogen of that species.

7f. **Arceuthobium campylopodum** Engelmann subsp. **cyanocarpum** (A. Nelson ex Rydberg) Nickrent, Phytoneuron 2012-51: 9. 2012 • Limber pine dwarf mistletoe E

Razoumofskya cyanocarpa A. Nelson ex Rydberg, Fl. Colorado, 100. 1906; *Arceuthobium cyanocarpum* (A. Nelson ex Rydberg) J. M. Coulter & A. Nelson

Plants forming witches' brooms. **Stems** yellow, green, olive green, or brown, 3(–7) cm; third internode 2–5.2(–14) × 1–1.1(–1.5) mm, dominant shoot 1–2 mm diam. at base. **Staminate flowers** 3 mm diam.; petals 3(–4). **Fruits** 3.5 × 2.5 mm.

Flowering Jul–Sep; fruiting Aug–Sep. Coniferous forests; 1600–3100 m; Calif., Colo., Idaho, Mont., Nev., Oreg., Utah, Wyo.

Meiosis occurs in July, with fruits maturing 12 months after pollination.

Subspecies *cyanocarpum* is widely distributed at high elevations in the western United States from the Rocky Mountains to the Sierra Nevada of California. Its most common host is *Pinus flexilis*; however, *P. albicaulis*,

P. aristata, and *P. longaeva* are also listed as principal hosts, owing to their high incidence of infection. Additional secondary to rare hosts include *Picea engelmannii*, *Pinus balfouriana*, *Pinus contorta*, *Pinus monticola*, *Pinus ponderosa*, and *Tsuga mertensiana*. This mistletoe is a significant pathogen in many locations, sometimes resulting in massive host tree mortality.

7g. **Arceuthobium campylopodum** Engelmann subsp. **laricis** (M. E. Jones) Nickrent, Phytoneuron 2012-51: 9. 2012 • Larch dwarf mistletoe E

Arceuthobium douglasii Engelmann var. *laricis* M. E. Jones, Biol. Ser. Bull. State Univ. Montana. 15: 25. 1910; *A. laricis* (M. E. Jones) H. St. John; *Razoumofskya laricis* (M. E. Jones) Piper

Plants forming witches' brooms. **Stems** green, olive green, maroon, or purple, 4(–6) cm; third internode 5–8(–14) × 1–1.3(–2.5) mm, dominant shoot 1.5–3 mm diam. at base. **Staminate flowers** 2.7 mm diam.; petals 3(–4). **Fruits** 3.5 × 2.5 mm.

Flowering Jul–Aug; fruiting (Aug–)Sep(–Oct). Coniferous forests, especially with western larch or mountain hemlock; 600–2300 m; B.C.; Idaho, Mont., Oreg., Wash.

Meiosis occurs in June, with fruits maturing 13 to 14 months after pollination.

Larix occidentalis and *Tsuga mertensiana* are the principal hosts for subsp. *laricis*; secondary to rare hosts include *Abies grandis*, *A. lasiocarpa*, *Picea engelmannii*, *Pinus albicaulis*, *Pinus contorta*, *Pinus monticola*, and *Pinus ponderosa*. This dwarf mistletoe is a major pathogen on larch in Idaho and Montana.

7h. **Arceuthobium campylopodum** Engelmann subsp. **littorum** (Hawksworth, Wiens & Nickrent) Nickrent, Phytoneuron 2012-51: 10. 2012 • Coastal dwarf mistletoe E

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

Plants usually forming witches' brooms. **Stems** olive green or brown, 8–12(–20) cm; third internode 10–15(–20) × 2–3.5(–5) mm, dominant shoot 2–5 mm diam. at base. **Staminate flowers** 3 mm diam.; petals 4. **Fruits** 4–5 × 3 mm.

Flowering Aug–Sep; fruiting Sep–Oct. Closed-cone pine forests; 0–300 m; Calif.

Meiosis occurs in July, with fruits maturing 14 months after pollination.

Subspecies *littorum* parasitizes *Pinus muricata* and *P. radiata*, and occasionally *P. contorta* in Alameda, Mendocino, and Monterey counties. It has the largest shoots among the 13 subspecies of *Arceuthobium campylopodum*.

7i. **Arceuthobium campylopodum** Engelmann subsp. **microcarpum** (Engelmann) Nickrent, Phytoneuron 2012-51: 10. 2012 • Western spruce dwarf mistletoe E

Arceuthobium douglasii Engelmann var. *microcarpum* Engelmann in J. T. Rothrock, Rep. U.S. Geogr. Surv., Wheeler, 253. 1879; *A. microcarpum* (Engelmann) Hawksworth & Wiens

Plants forming witches' brooms. **Stems** yellowish green, green, orange, red, maroon, or purple, 5(–11) cm; third internode 5–9.3(–16) × 1–1.5(–2) mm, dominant shoot 1.5–3 mm diam. at base. **Staminate flowers** 2.3 mm diam.; petals 3(–4). **Fruits** 3.5 × 2 mm.

Flowering (Jul–)Aug–Sep; fruiting (Aug–)Sep(–Oct). Coniferous forests, especially with blue or Engelmann spruce; 2400–3200 m; Ariz., N.Mex.

Meiosis occurs in July, with fruits maturing 12 to 13 months after pollination.

Subspecies *microcarpum* is a serious pathogen on its principal hosts, *Picea engelmannii* and *P. pungens*, as well as on *Pinus aristata* in northern Arizona. Rare hosts include *Abies lasiocarpa* and *Pinus strobiformis*. Interestingly, this mistletoe is not found in the central Rocky Mountains where its principal hosts are most abundant.

7j. **Arceuthobium campylopodum** Engelmann subsp. **monticola** (Hawksworth, Wiens & Nickrent) Nickrent, Phytoneuron 2012-51: 10. 2012 • Western white pine dwarf mistletoe E

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

Plants forming localized infections only. **Stems** olive green or brown, 5–7(–10) cm; third internode 8–12(–15) × 1.5–1.7(–2) mm, dominant shoot 2–4 mm diam. at base. **Staminate flowers** 3 mm diam.; petals 3. **Fruits** 4–4.5 × 2–2.5 mm.

Flowering Jul–Aug; fruiting Oct–Nov. Coniferous forests, especially western white pine; 700–1900 m; Calif., Oreg.

Meiosis likely occurs in July, with fruits maturing 15 months after pollination.

The principal host of subsp. *monticola* is *Pinus monticola*; secondary to rare hosts include *Picea breweriana*, *Pinus jeffreyi*, and *Pinus lambertiana*. It is endemic to the Klamath and Siskiyou Mountains.

7k. **Arceuthobium campylopodum** Engelmann subsp. **occidentale** (Engelmann) Nickrent, Phytoneuron 2012-51: 10. 2012 • Digger pine dwarf mistletoe E

Arceuthobium occidentale Engelmann in J. T. Rothrock, Rep. U.S. Geogr. Surv., Wheeler, 254, 375. 1879

Plants usually forming localized infections only. **Stems** yellow or orange, 8(–17) cm; third internode 7–12.7(–18) × 1.5–1.8 (–3.5) mm, dominant shoot 1.5–5 mm diam. at base. **Staminate flowers** 3 mm diam.; petals 3–4. **Fruits** 4.5 × 3 mm.

Flowering Sep–Nov(–Dec); fruiting (Sep–)Oct–Jan (–Feb). Coniferous and mixed forests, especially digger pine; 30–1200 m; Calif.

Meiosis occurs in August, with fruits maturing 13 months after pollination.

Pinus sabiniana is the principal host of subsp. *occidentale*; secondary hosts include *P. attenuata*, *P. coulteri*, *P. jeffreyi*, and *P. ponderosa*, as well as some exotic species of pines. Subspecies *occidentale* occurs in the foothills surrounding the Central Valley and in the Coast Ranges.

7l. **Arceuthobium campylopodum** Engelmann subsp. **siskiyouense** (Hawksworth, Wiens & Nickrent) Nickrent, Phytoneuron 2012-51: 10. 2012 • Knobcone pine dwarf mistletoe E

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

Plants forming witches' brooms. **Stems** brown, 6–8(–10) cm; third internode 8–9(–15) × 2 mm, dominant shoot 2–2.5 mm diam. at base. **Staminate flowers** 3 mm diam.; petals 3–4. **Fruits** 4 × 2.5 mm.

Flowering Aug–Sep; fruiting Sep–Oct. Coniferous forests, especially closed-cone pine forests with knobcone pine; 400–1200 m; Calif., Oreg.

Meiosis likely occurs in July, with fruits maturing 13 months after pollination.

The principal host of subsp. *siskiyouense* is *Pinus attenuata*; rare hosts include *P. contorta*, *P. jeffreyi*, and *P. ponderosa*. Subspecies *siskiyouense* is endemic to the Klamath and Siskiyou mountains.

7m. **Arceuthobium campylopodum** Engelmann subsp. **tsugense** (Rosendahl) Nickrent, Phytoneuron 2012-51: 10. 2012 • Hemlock dwarf mistletoe E

Razoumofskya tsugensis Rosendahl, Minnesota Bot. Stud. 3: 272, plates 27, 28. 1903; *Arceuthobium tsugense* (Rosendahl) G. N. Jones; *A. tsugense* subsp. *amabilae* Mathiasen & C. M. Daugherty; *A. tsugense* subsp. *contortae* Wass & Mathiasen; *A. tsugense* subsp. *mertensianae* Hawksworth & Nickrent

Plants forming witches' brooms. **Stems** yellow, green, olive green, or purple, 5–7(–13) cm; third internode 4–9.2(–16) × 1–1.5(–2) mm, dominant shoot 1.5–4 mm diam. at base. **Staminate flowers** 2.8 mm diam.; petals 3–4. **Fruits** 3 × 3 mm.

Flowering Jul–Sep(–Oct); fruiting (Aug–)Sep–Nov. Coniferous forests; 0–2500 m; B.C.; Alaska, Calif., Idaho, Oreg., Wash.

Meiosis occurs in July, with fruits maturing 12 to 13 months after pollination.

Subspecies *tsugense* has the broadest host range among all subspecies of *Arceuthobium campylopodum*. F. G. Hawksworth and D. Wiens (1996) considered subsp. *tsugense* to be a distinct species with two subspecies, subspp. *tsugense* and *mertensianae*. Two additional subspecies have been named in *A. tsugense*: subsp. *amabilae* and subsp. *contortae*. Although the authors of these subspecies presented evidence of quantitative character variation and differences in phenology and host preferences, all variants are here considered host races of subsp. *tsugense* (and could be treated taxonomically as forms if so desired). The principal hosts of subsp. *tsugense* are *Abies amabilis*, *A. lasiocarpa*, *A. procera*, *Pinus contorta*, *Tsuga heterophylla*, and *T. mertensiana*. Secondary to rare hosts include *A. grandis*, *Picea breweriana*, *Picea engelmannii*, *Picea sitchensis*, *Pinus albicaulis*, *Pinus monticola*, and *Pseudotsuga menziesii*.

2. PHORADENDRON Nuttall, J. Acad. Nat. Sci. Philadelphia, n.s. 1: 185. 1848

• Mistletoe [Greek *phor*, thief, and *dendron*, tree, alluding to parasitism]

Subshrubs, evergreen, monoecious or dioecious; hemiparasitic on branches of woody angiosperms and gymnosperms, infections localized [systemic]. **Stems** single or multiple; branching percurrent (branches with single main axis) [pseudodichotomous]. **Leaves** scalelike or well developed. **Inflorescences** axillary or terminal, unisexual (bisexual in *P. rubrum*), spikelike thyrses with intercalary meristems; flowers borne in cavities or grooves. **Staminate flowers:** petals (2–)3(–4), triangular, distinct; stamens (2–)3(–4); anthers 2-locular, dehiscing by transverse slits; nectary absent. **Pistillate flowers:** petals (2–)3(–4), triangular, distinct; ovary 1-locular; style short; stigma undifferentiated [2-lobed]. **Berries** sessile, not explosively dehiscent, 1-colored, smooth or puberulent, petal remnants persisting at apex. **Seeds** mucilaginous when removed from fruit, endosperm flattened, ovate to elliptical in broadest outline; embryo oriented longitudinally. $x = 14$.

Species ca. 244 (7 in the flora): United States, Mexico, West Indies, Central America, South America.

Although not particularly diverse in the United States, *Phoradendron* underwent a massive radiation in Mexico, Central America, and South America. The first modern taxonomic treatment of the genus was by W. Trelease (1916), who named 240 species. More recently, J. Kuijt (2003) produced a monograph that included 234 species, but the similarity in number belies the fact that only 18 of the names accepted by Trelease were retained.

Phoradendron is closely related to *Dendrophthora* Eichler (a genus of 125 species), separated from it only by the presence of 2-locular versus 1-locular anthers. Whether these two genera are monophyletic remains to be tested using molecular methods (V. E. T. M. Ashworth 2000). Together *Phoradendron* and *Dendrophthora* are important components of mesic and arid environments in the New World, particularly because their fruits provide food for various bird species that disperse their seeds.

In the key and descriptions that follow, basal phyllotaxy refers to the orientation of the basal pair of leaves or cataphylls on a lateral branch. When those leaves or cataphylls are in the same plane as the main and lateral branch, basal phyllotaxy is median; when they are at right angles to that plane, it is transverse. Flower seriation refers to the arrangement of flowers on fertile internodes (J. Kuijt 2003). Different seriation may occur in staminate and pistillate inflorescences of the same species (for example in *Phoradendron californicum*). Flowers typically are arranged in one or more columns above each bract, and each set of columns is topped by a single median flower. Each fertile internode has two sets of flower columns, one above each of the opposite bracts. When two columns of flowers occur above the bract, the condition is called biseriate. When three columns of flowers occur, the condition is triseriate. Uniseriate and multiseriate conditions exist, but only outside the flora area. When only three flowers occur above each bract, seriation cannot always be determined (for example in *P. juniperinum*).

SELECTED REFERENCES Ashworth, V. E. T. M. 2000. Phylogenetic relationships in Phoradendreae (Viscaceae) inferred from three regions of the nuclear ribosomal cistron. I. Major lineages and paraphyly of *Phoradendron*. Syst. Bot. 25: 349–370. Ashworth, V. E. T. M. 2000b. Phylogenetic relationships in Phoradendreae (Viscaceae) inferred from three regions of the nuclear ribosomal cistron. II. The North American species of *Phoradendron*. Aliso 19: 41–53. Kuijt, J. 2003. Monograph of *Phoradendron* (Viscaceae). Syst. Bot. Monogr. 66. Trelease, W. 1916. The Genus *Phoradendron*: A Monographic Revision. Urbana. Wiens, D. 1964. Revision of the acataphyllous species of *Phoradendron*. Brittonia 16: 11–54.

1. Leaves scalelike.
   2. Stems green to olive green, glabrous; inflorescence fertile internodes usually 1; parasitic on gymnosperms, frequently *Calocedrus* and *Juniperus* . . . . . 1. *Phoradendron juniperinum*
   2. Stems grayish green to reddish green (in full sun), densely hairy (hairs silvery white, closely appressed), becoming glabrate; inflorescence fertile internodes (1–)2–4(–6); parasitic on angiosperms, frequently *Prosopis*, *Senegalia*, or *Vachellia* . . . . 2. *Phoradendron californicum*
1. Leaves well developed.
   3. Basal phyllotaxy median.
      4. Stems densely stellate-hairy; plants dioecious; Arizona, New Mexico, Texas . . . . . 3. *Phoradendron capitellatum*
      4. Stems glabrous; plants monoecious; Florida . . . . . 4. *Phoradendron rubrum*
   3. Basal phyllotaxy transverse.
      5. Staminate and pistillate inflorescences 3–6 mm; pistillate inflorescence fertile internodes each 2-flowered; parasitic on *Abies*, *Cupressus*, and *Juniperus* . . . . . 5. *Phoradendron bolleanum*
      5. Staminate and pistillate inflorescences 10–80 mm; pistillate inflorescence fertile internodes each (4–)6–11(–24)-flowered; parasitic on angiosperms.
         6. Flowering Oct–Mar; stem internodes 8–59 mm; berries glabrous. . . . 6. *Phoradendron leucarpum*
         6. Flowering Jul–Sep; stem internodes 1.5–3.8 mm; berries puberulent below petals . . . . . 7. *Phoradendron villosum*

1. Phoradendron juniperinum A. Gray, Mem. Amer. Acad. Arts, n. s. 4: 58. 1849 • Juniper or incense cedar mistletoe F

Phoradendron juniperinum subsp. *libocedri* (Engelmann) Wiens; *P. juniperinum* var. *libocedri* Engelmann; *P. juniperinum* var. *ligatum* (Trelease) Fosberg; *P. libocedri* (Engelmann) Howell; *P. ligatum* Trelease

Subshrubs erect, 1–2(–2.5) dm, dioecious. **Stems** green to olive green, glabrous; internodes terete, 5–20 × 1.5–2.5 mm. **Leaves** green to olive green, scalelike; blade triangular, 2 mm, apex acute; basal phyllotaxy transverse. **Staminate inflorescences** 3–5 mm; peduncle with 1 internode, 3 mm; fertile internode usually 1, 6-flowered, seriation unknown, flowers 3 (2 proximal, 1 distal) per bract. **Pistillate inflorescences** 3–5 mm; peduncle with 1 internode, 2 mm; fertile internode 1, 2-flowered, flowers 1 per bract. **Flowers:** petals 3–4, 0.5–1 mm. **Berries** white or pinkish, globose to ellipsoid-globose, 4–5 × 3 mm, glabrous. $2n = 28$.

Flowering summer–early fall. Forests or woodlands with juniper or incense cedar; 800–2900 m; Ariz., Calif., Colo., Idaho, Nev., N.Mex., Oreg., Tex., Utah; Mexico (Baja California, Chihuahua, Coahuila, Sonora).

Phoradendron juniperinum is often classified as having two subspecies, subspp. *juniperinum* and *libocedri*. Subspecies *juniperinum* is found throughout the species' range as globose infections on various species of *Juniperus*. The larger, pendent parasites of *Calocedrus* from California have been recognized as subsp. *libocedri*. J. Kuijt (2003) argued that this habit could be a host response because intermediate morphologies are known; the two taxa are not recognized here.

2. Phoradendron californicum Nuttall, J. Acad. Nat. Sci. Philadelphia, n. s. 1: 185. 1848 • Mesquite mistletoe

Phoradendron californicum var. *distans* Trelease; *P. californicum* var. *leucocarpum* (Trelease ex Munz & I. M. Johnston) Jepson

Subshrubs pendent, 1–5(–20) dm, dioecious. **Stems** grayish green to reddish green (in full sun), densely hairy, hairs silvery white, closely appressed, becoming glabrate; internodes terete, 10–20(–30) × 1–1.7(–2.5) mm. **Leaves** grayish green, scalelike; blade triangular, 1.5–3 mm, apex acute; basal phyllotaxy transverse or median. **Staminate inflorescence** 5–25 mm, peduncle with 1(–2) internodes, each 0.5–3 mm; fertile internodes (1–)2–3(–5), each 6–14-flowered, biseriate, flowers 1–3 per column. **Pistillate inflorescences** 5–10 mm, elongating in fruit; peduncle with 1(–2) internodes, each 0.5–3 mm; fertile internodes (1–)2–4(–6), each 2-flowered, flowers 1 per bract. **Flowers:** petals 3(–4), 1–2 mm. **Berries** white, translucent yellowish, pinkish, orange-red, or maroon, globose, 3–6 × 3–6 mm, glabrous. $2n = 28$.

Flowering late fall–winter. Desert scrub or washes with mesquite or acacia; 0–1800 m; Ariz., Calif., Nev., Utah; Mexico (Baja California, Baja California Sur, Sinaloa, Sonora).

Phoradendron californicum, like *P. juniperinum*, bears only scalelike leaves, but this character has evolved independently in the two species (V. E. T. M. Ashworth 2000). *Phoradendron californicum* differs by its different hosts (legumes versus conifers) and

inflorescences with more than one fertile internode. Molecular data indicate that *P. californicum* is not part of the acataphyllous Boreales group in the sense of W. Trelease (1916) but allied with cataphyllous tropical species (Ashworth). Varieties and host races have been proposed, but these are not recognized in the most recent monograph of the genus (J. Kuijt 2003). In addition to its primary hosts, *Prosopis*, *Senegalia*, and *Vachellia*, *Phoradendron californicum* has also been recorded from a number of other hosts including *Condalia*, *Dalea*, *Ebenopsis*, *Havardia*, *Larrea*, *Olneya*, *Parkinsonia*, and sometimes is hyperparasitic on *Psittacanthus*.

3. **Phoradendron capitellatum** Torrey ex Trelease, Phoradendron, 25, plate 17. 1916 • Downy mistletoe

Phoradendron bolleanum (Seemann) Eichler var. *capitellatum* (Torrey ex Trelease) Kearney & Peebles

Subshrubs erect but pendulous with age, 3–6 dm, dioecious. **Stems** green, densely hairy, hairs stellate, fine, white; internodes terete, 5–15 × 1–2 mm. **Leaves** green, well developed; petiole indistinct; blade narrowly elliptic to spatulate or oblanceolate, 8–15 × 1–3 mm, fleshy, base cuneate, apex rounded or acute; basal phyllotaxy median. **Staminate inflorescences** 3–5 mm; peduncle with 1 internode, 0.5–2.5 mm; fertile internodes 1–2, each 6-flowered, seriation unknown, flowers 3 (2 proximal, 1 distal) per bract. **Pistillate inflorescences** 3–5 mm; peduncle with 1 internode, 0.5–2.5 mm; fertile internodes 1–2, each 2-flowered, flowers 1 per bract, deeply embedded in axis. **Flowers:** petals 3, 1 mm. **Berries** pinkish white, globose, 3.5 × 3.5 mm, glabrous. $2n = 28$.

Flowering winter. Juniper-pinyon woodlands; 1000–2000 m; Ariz., N.Mex., Tex.; Mexico (Chihuahua, Sonora).

Phoradendron capitellatum is parasitic exclusively on *Juniperus* (for example, *J. monosperma*, *J. osteosperma*, and *J. pinchotii*). This species has sometimes been classified as a subspecies of *P. bolleanum*; however, it differs in flowering time, basal phyllotaxy, stellate pubescence, and inflorescences sometimes with more than one fertile internode. These two species, along with *P. juniperinum*, were supported as monophyletic using molecular data, although relationships among them were not fully resolved (V. E. T. M. Ashworth 2000). These parasites of conifers were all classified in sect. *Pauciflorae* Engler in the sense of D. Wiens (1964).

4. **Phoradendron rubrum** (Linnaeus) Grisebach, Fl. Brit. W.I., 314. 1860 • Narrow-leaved mistletoe

Viscum rubrum Linnaeus, Sp. Pl. 2: 1023. 1753

Subshrubs erect, 3.5–5 dm, monoecious. **Stems** green, glabrous; internodes quadrangular proximally, flattened distally, keeled proximally to nodes, 20–30 × 3(–7) mm. **Leaves** dull green, well developed; petiole (3–)5(–8) mm; blade obovate, elliptic, oblanceolate, or oblong-lanceolate, (40–)50.5(–90) × 20–40 mm, thin, base cuneate, apex rounded; basal phyllotaxy median. **Inflorescences** bisexual, staminate flowers few, irregularly placed among pistillate, to 25 mm; peduncle with 1(–2) internodes, each 3 mm; fertile internodes 3, each 6–18-flowered, biseriate, flowers 1–4 per column. **Flowers:** petals 3, 1 mm. **Berries** lemon yellow or orange [pink, red], ovoid to globose, 4 × 3 mm, glabrous.

Flowering year-round. Hammocks with West Indian mahogany; 0–500 m; Fla.; West Indies.

Phoradendron rubrum is a mainly Caribbean species that has been recorded in the flora area only from Key Largo, Monroe County. Its primary host is *Swietenia mahagoni*, but it has been found also on *Byrsonima*, *Guapira*, *Mangifera*, and *Pisonia*.

5. **Phoradendron bolleanum** (Seemann) Eichler in C. F. P. von Martius et al., Fl. Bras. 5(2): 134m. 1868 • Bollean mistletoe

Viscum bolleanum Seemann, Bot. Voy. Herald, 295, plate 63. 1856; *Phoradendron bolleanum* subsp. *densum* (Torrey ex Trelease) Wiens; *P. bolleanum* var. *densum* (Torrey ex Trelease) Fosberg; *P. bolleanum* subsp. *pauciflorum* (Torrey) Wiens; *P. densum* Torrey ex Trelease; *P. hawksworthii* Wiens; *P. pauciflorum* Torrey

Subshrubs erect, forming globose clumps, to 10 dm, dioecious. **Stems** green, brown, reddish brown, or orange, glabrous or slightly puberulent, hairs simple; internodes terete, to 2 cm. **Leaves** green, well developed, glabrous or slightly puberulent, hairs simple; petiole very short or absent; blade terete to narrowly oblong or oblanceolate, 7–35 × 1–10 mm, thin, base slightly tapered, apex acute-apiculate to rounded; basal phyllotaxy transverse. **Staminate inflorescences** 3–6 mm, glabrous or slightly puberulent, hairs simple; peduncle with 1 internode, 1–2 mm; fertile internode usually 1, 6–20-flowered, triseriate, flowers 1–3 per column or not in columns. **Pistillate inflorescences** 3–6 mm, elongating

in fruit, glabrous or slightly puberulent, hairs simple; peduncle with 1 internode, 1.5–3 mm; fertile internodes 1(–2), each 2-flowered, flowers 1 per bract. **Flowers:** petals 3–4, 1–2 mm. **Berries** white to pink, ovoid, 3.5–5 × 3.5–5 mm, glabrous. $2n = 28$.

Flowering May–Aug. Coniferous forests; 300–3000 m; Ariz., Calif., N.Mex., Oreg., Tex.; Mexico; Central America (Guatemala).

This treatment follows J. Kuijt (2003), who considered *Phoradendron bolleanum* to be a widespread and variable species complex. The three main taxa that often have been recognized as species are *P. bolleanum* in the narrow sense, *P. densum*, and *P. pauciflorum*. *Phoradendron bolleanum* in the narrow sense has small, narrow leaves and frequently parasitizes *Juniperus* as well as *Arbutus*. The *P. pauciflorum* variant has broad leaves and mostly parasitizes *Abies concolor*. The *P. densum* variant tends to have leaves that are intermediate between those of the other two variants; it ranges from Oregon to Mexico and parasitizes *Cupressus* and *Juniperus*. Molecular analyses indicate that *P. bolleanum* is not monophyletic unless *P. minutifolium* Urban is synonymized with the other variants. Hybrids between *P. bolleanum* and *P. juniperinum* produce plants closely resembling *P. minutifolium* (D. Wiens and M. DeDecker 1972). As pointed out by Kuijt, molecular studies will be required to determine species boundaries within this complex.

6. **Phoradendron leucarpum** (Rafinesque) Reveal & M. C. Johnston, Taxon 38: 107. 1989 • Oak or American mistletoe F

Viscum leucarpum Rafinesque, Fl. Ludov., 79. 1817; *Phoradendron coloradense* Trelease; *P. eatonii* Trelease; *P. flavens* Grisebach subsp. *macrophyllum* (Engelmann) A. E. Murray; *P. flavens* var. *macrophyllum* Engelmann; *P. flavens* var. *tomentosum* (de Candolle) Engelmann; *P. flavescens* (Pursh) Nuttall ex A. Gray; *P. leucarpum* subsp. *angustifolium* (Kuijt) J. R. Abbott & R. L. Thompson; *P. leucarpum* subsp. *macrophyllum* (Engelmann) J. R. Abbott & R. L. Thompson; *P. leucarpum* subsp. *tomentosum* (de Candolle) J. R. Abbott & R. L. Thompson; *P. longispicum* Trelease; *P. macrotomum* Trelease; *P. serotinum* (Rafinesque) M. C. Johnston; *P. serotinum* subsp. *macrophyllum* (Engelmann) Kuijt; *P. serotinum* var. *macrophyllum* (Engelmann) M. C. Johnston; *P. serotinum* var. *macrotomum* (Trelease) M. C. Johnston; *P. serotinum* subsp. *tomentosum* (de Candolle) Kuijt; *P. tomentosum* (de Candolle) Engelmann ex A. Gray; *P. tomentosum* subsp. *macrophyllum* (Engelmann) Wiens; *P. tomentosum* var. *macrophyllum* (Engelmann) L. D. Benson

Subshrubs erect, 4–10 dm, dioecious. **Stems** green, grayish green, or yellowish green, hairy, hairs simple or stellate, white or yellow, becoming glabrate; internodes terete, 8–59 × 1–3 mm. **Leaves** bright green, yellowish green, or grayish green, well developed, hairy, hairs simple or stellate; petiole 3–8 mm; blade obovate, spatulate, ovate, ovate-elliptic, or nearly orbiculate, 14–48 × 8–30 mm, thin to thick and rigid, base cuneate to obtuse, apex rounded; basal phyllotaxy transverse. **Staminate inflorescences** 10–80 mm, hairy, hairs simple or stellate; peduncle with 1 internode, 2–4 mm; fertile internodes 2–7, each (15–)29–39(–62)-flowered, triseriate, becoming irregular, flowers 1–10 per column. **Pistillate inflorescences** 10–80 mm, hairy, hairs simple or stellate; peduncle with 1 internode, 2–4 mm; fertile internodes 2–6, each (4–)6–11(–20)-flowered, triseriate, flowers 1–3 per column. **Flowers:** petals 3, 1 mm. **Berries** white, oblong to globose, 3–6 × 2–5 mm, glabrous.

Flowering Oct–Mar. Hardwood forests and woodlands; 0–1800 m; Ala., Ariz., Ark., Calif., Del., D.C., Fla., Ga., Ill., Ind., Kans., Ky., La., Md., Miss., Mo., N.J., N.Mex., N.Y., N.C., Ohio, Okla., Oreg., Pa., S.C., Tenn., Tex., Va., W.Va.; Mexico (Chihuahua, Coahuila, Durango, Nuevo León, San Luis Potosí, Sonora, Tamaulipas).

J. Kuijt (2003) used the name *Phoradendron serotinum*, based on the name *Viscum serotinum* Rafinesque (1820), not *P. leucarpum*, which is based on the earlier name by the same author, *V. leucarpum* (1817). A proposal to conserve the later name (D. L. Nickrent et al. 2010b) was not accepted, thus the name *P. leucarpum* has priority.

Phoradendron leucarpum has a convoluted taxonomic history, reflecting not only various species concepts but also complex evolutionary and ecological processes. Among the 234 species of *Phoradendron*, J. Kuijt (2003) recognized subspecies only in *P. leucarpum* (as *P. serotinum*). In addition to the typical subspecies from eastern Texas eastward, they are subsp. *augustifolium* from Mexico, subsp. *macrophyllum* from eastern Texas through New Mexico and Arizona to California and Oregon, and subsp. *tomentosum*, with about the same distribution as subsp. *macrophyllum* but also extending into Mexico. Kuijt noted that in some geographic areas, such as east-central Texas, the putative subspecies show a continuum of morphological intergradation.

A population genetic and morphometric study of this complex was undertaken by A. K. Hawkins (2010). Principal component analyses using the characters that J. Kuijt (2003) considered to be diagnostic of the subspecies, such as leaf size, color, and venation, as well as the type and density of hairs present on young vegetative and reproductive tissues, in addition to host species, did not result in clusters corresponding to the four described subspecies. Moreover, F_{ST} analyses of microsatellites showed significant interpopulational differentiation that did not match the subspecies that

Kuijt recognized. Because morphological and molecular analyses show that subspecies, at least as defined by Kuijt, cannot be differentiated in *Phoradendron leucarpum*, no subspecies are accepted here.

Phoradendron leucarpum is the only species of the genus found east of Texas. It parasitizes over 60 species of native and introduced trees, especially *Acer*, *Fraxinus*, *Juglans*, *Nyssa*, *Platanus*, *Populus*, *Quercus*, *Salix*, and *Ulmus*.

SELECTED REFERENCE Hawkins, A. K. 2010. Subspecific Classification within *Phoradendron serotinum* (Viscaceae): Development of Microsatellite Markers for Assessment of Population Genetic Structure. M.S. thesis. Sam Houston State University.

7. Phoradendron villosum (Nuttall) Nuttall ex Engelmann, Boston J. Nat. Hist. 6: 212. 1850 • Pacific or oak mistletoe

Viscum villosum Nuttall in J. Torrey and A. Gray, Fl. N. Amer. 1: 654. 1840; *Phoradendron flavens* Grisebach var. *villosum* (Nuttall) Engelmann

Subshrubs erect, to 1 dm, dioecious. **Stems** green or olive green, grayish from pubescence, hairy, hairs stellate, becoming hirtellous to glabrate; internodes terete, 1.5–3.8 × 1–3 mm. **Leaves** green or olive green, grayish from pubescence, stellate-hairy; blade obovate-elliptic to orbiculate, 13–45 × 9–22 mm, thin to thick and fleshy, base subtruncate to acute, apex rounded to acute; basal phyllotaxy transverse. **Staminate inflorescences** 10–80 mm, stellate-hairy; peduncle with 1 internode, 2–4 mm; fertile internodes 2–5, each (14–)26(–44)-flowered, triseriate, becoming irregular, flowers 2–7 per column. **Pistillate inflorescences** 10–80 mm, stellate-hairy; peduncle with 1 internode, 2–4 mm; fertile internodes 2–3, each (6–)11(–24)-flowered, triseriate, flowers 1–4 per column. **Flowers:** petals 3–4, 1 mm. **Berries** white to pink, oblong to globose, 3 × 3 mm, puberulent below petals.

Subspecies 3 (2 in the flora): w, sw, sc United States, n Mexico.

Phoradendron villosum was treated by J. Kuijt (2003) as a synonym of *P. serotinum* subsp. *tomentosum* (= *P. leucarpum* in this treatment), but *P. villosum* has a different, non-overlapping flowering time, shorter stem internodes, and hairy berries. In addition, *P. villosum* averages fewer pistillate inflorescence fertile internodes than *P. leucarpum*. Molecular studies by V. E. T. M. Ashworth (2000, 2000b) showed that *P. villosum* did not form part of the strongly supported *P. leucarpum* clade. For these reasons, they are here considered distinct species, as was done by D. Wiens (1964).

Subspecies *flavum* (I. M. Johnston) Wiens, distinguished by its yellow leaf hairs, is found in Coahuila and Durango, Mexico.

1. Hairs on young stems, leaf blades, and inflorescences of one type, uniformly distributed and of similar lengths; pistillate inflorescence internodes each (7–)12(–24)-flowered; California, Oregon . . . . 7a. *Phoradendron villosum* subsp. *villosum*
1. Hairs on young stems, leaf blades, and inflorescences of two types, some in dense clusters, relatively longer, others uniformly distributed, relatively shorter; pistillate inflorescence internodes each (6–)8(–12)-flowered; Arizona, New Mexico, Texas . . . . . 7b. *Phoradendron villosum* subsp. *coryae*

7a. Phoradendron villosum (Nuttall) Nuttall ex Engelmann subsp. **villosum**

Phoradendron villosum var. *rotundifolium* Trelease

Hairs on young stems, leaf blades, and inflorescences of one type, uniformly distributed and of similar lengths. **Staminate inflorescences:** internodes each (15–)29(–45)-flowered. **Pistillate inflorescences:** internodes each (7–)12(–24)-flowered. $2n = 28$.

Flowering Jul–Sep. Oak woodlands; 20–2200 m; Calif., Oreg.; Mexico (Baja California).

Subspecies *villosum* is parasitic mainly on oaks, including *Quercus agrifolia*, *Q. douglasii*, and *Q. lobata* (V. E. Thompson and B. E. Mahall 1983), but can be found on *Aesculus*, *Arctostaphylos*, *Betula*, *Populus*, *Robinia*, and *Salix*. The subspecies is distributed from the Coast Ranges and Willamette Valley of Oregon south through the Sierra Nevada and Coast and Transverse ranges of California into northern Baja California.

7b. Phoradendron villosum (Nuttall) Nuttall ex Engelmann subsp. **coryae** (Trelease) Wiens, Brittonia 16: 45. 1964

Phoradendron coryae Trelease, Phoradendron, 43, plate 44. 1916; *P. villosum* var. *coryae* (Trelease) B. L. Turner

Hairs on young stems, leaf blades, and inflorescences of two types, some in dense clusters, relatively longer, others uniformly distributed, relatively shorter. **Staminate inflorescences:** internodes each (14–)25(–44)-flowered. **Pistillate inflorescences:** internodes each (6–)8(–12)-flowered.

Flowering Jul–Sep. Oak woodlands; 400–2400 m; Ariz., N.Mex., Tex.; Mexico (Chihuahua, Coahuila, Sonora).

In the flora area, subsp. *coryae* is found in Arizona south of the Mogollon Rim, through central New Mexico to the Chisos and Davis mountains of western Texas. Its principal hosts are *Quercus* species.

The molecular study by V. E. T. M. Ashworth (2000b) showed that *Phoradendron villosum* is paraphyletic because *P. scaberrimum* Trelease forms a clade with subsp. *coryae*. All three of these taxa parasitize *Quercus*, and a shared indel supported their phylogenetic relationship.

3. VISCUM Linnaeus, Sp. Pl. 2: 1023. 1753; Gen. Pl. ed. 5, 448. 1754 • Christmas mistletoe [Latin name for mistletoe, alluding to viscid fruits] I

Shrubs [herbs], dioecious [monoecious]; parasitic on branches of woody angiosperms and gymnosperms, infections localized. **Stems** single or multiple; branching pseudodichotomous [percurrent]. **Leaves** well developed [scalelike]. **Inflorescences** axillary or terminal, dichasial cymes. **Staminate flowers:** petals (3–)4(–6), triangular, distinct; stamens (3–)4(–6); anthers multilocular, dehiscing by numerous pores; nectary absent. **Pistillate flowers:** petals (3–)4(–6), triangular, distinct; ovary 0-locular; style absent [short-conic]; stigma poorly differentiated [capitate]. **Berries** sessile in bracteal cup [pedicel present, not recurved], not explosively dehiscent, 1-colored, smooth [warty], scars of petal remnants at apex. **Seeds** mucilaginous when removed from fruit, endosperm slightly flattened, ovate to elliptic in broadest outline; embryo oriented transversely. $x = 14$.

Species ca. 130 (1 in the flora): introduced; Eurasia, Africa, Indian Ocean Islands, Australia.

Viscum is widely distributed in the Old World and is present in North America via purposeful introduction. The genus is most diverse in tropical and southern Africa, where various species form a decreasing aneuploid series (from $x = 14$) (D. Wiens 1975). Higher gametic chromosome numbers are the result of polyploidy, which is relatively uncommon in Viscaceae. Several species of dioecious *Viscum* show translocation heterozygosity that determines plant sexuality and sex ratios in populations (Wiens and B. A. Barlow 1979; A. Aparicio 1993).

SELECTED REFERENCES Bussing, A., ed. 2000. Mistletoe: The genus *Viscum*. Amsterdam. Gill, L. S. 1935. *Arceuthobium* in the United States. Trans. Connecticut Acad. Arts 32: 111–245. Wiens, D. and B. A. Barlow. 1979. Translocation heterozygosity and the origin of dioecy in *Viscum*. Heredity 42: 201–222.

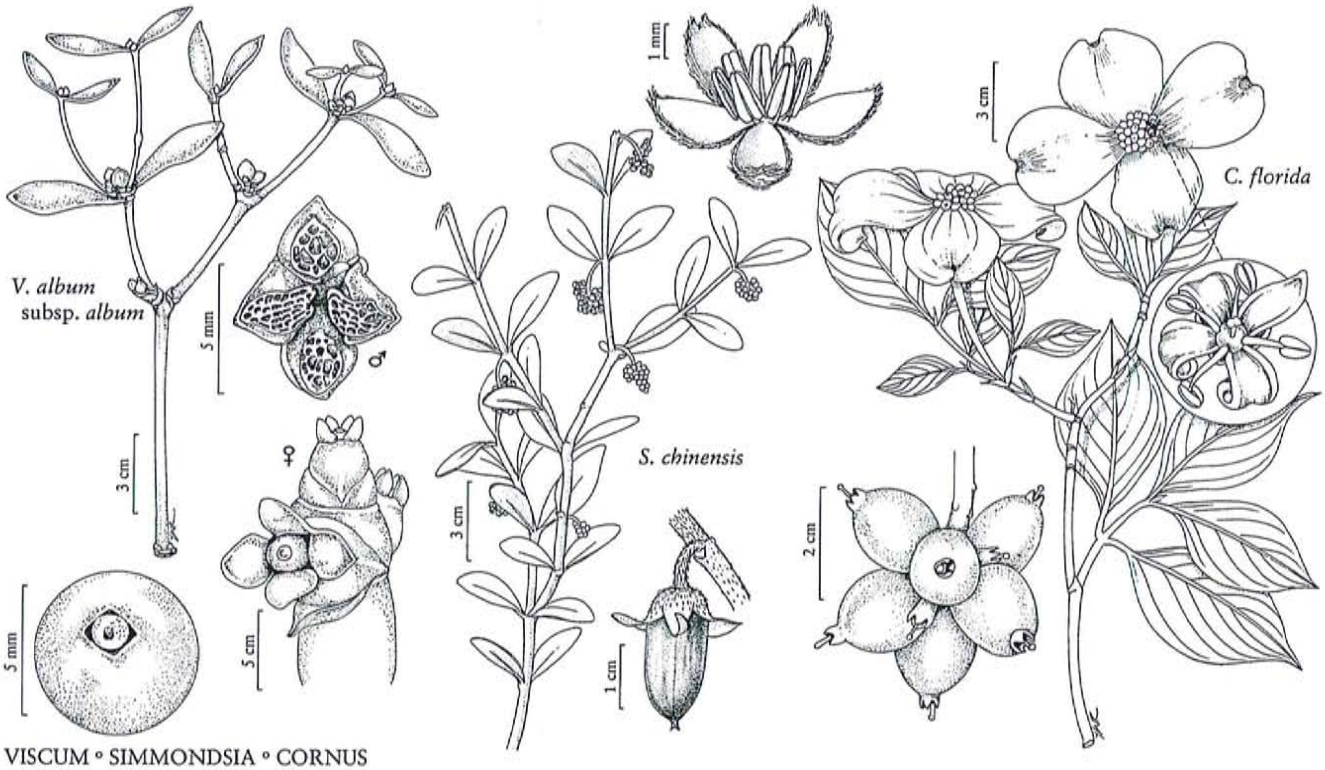
1. Viscum album Linnaeus, Sp. Pl. 2: 1023. 1753 F I W

Subspecies 3 (1 in the flora): introduced; Europe, Asia.

Viscum album is found throughout Europe and western Asia and has been divided into subsp. *album* on woody angiosperms, subsp. *abietis* (Wiesbaur) Abromeit on *Abies*, and subsp. *austriacum* (Wiesbaur) Vollmann on *Picea* and *Pinus* (D. Zuber 2004).

1a. Viscum album Linnaeus subsp. **album** • European mistletoe F I W

Shrubs forming globose infections, to 2 m diam. **Leaves** green to yellowish green; blade oblanceolate or obovate-oblong, 3–8 cm, leathery, base attenuate, apex rounded, surfaces glabrous; venation parallel, veins 3–7. **Staminate inflorescences** simple dichasia, consisting of 3 flowers subtended by 2 bracts fused into cupule. **Pistillate inflorescences** compound dichasia, usually 3-flowered; primary peduncle 4–6 mm; lateral flowers each subtended by 1 bract; terminal flower subtended by 2 bracts at apex of 2 mm secondary peduncle. **Staminate flowers** sessile, 5 mm; petals yellow; anthers white, covering most of petal adaxial surface. **Pistillate flowers** sessile,



VISCUM ◦ SIMMONDSIA ◦ CORNUS

somewhat flattened, 2 mm; stigma cushion-shaped. **Berries** white, globose, 6–10 mm, apex with dark markings representing stigma surrounded by petal scars. $2n = 20$.

Flowering Feb–Apr; fruiting Nov–Dec. Orchards, urban forests; 60–100 m; introduced; B.C.; Calif.; Europe; w Asia.

Subspecies *album* parasitizes many different tree species, but is most often found on *Crataegus*, *Malus*, *Populus*, *Robinia*, and *Tilia*. It was inoculated onto trees in the Sebastopol area, Sonoma County, California, around 1900 by the horticulturalist Luther Burbank, who wished to cultivate it for Christmas decorations (R. F. Scharpf and W. McCartney 1975). Although this source remained localized for several decades, by the 1980s the population had been spread to 114 km² by birds such as cedar waxwings (*Bombycilla cedrorum*) and American robins (*Turdus migratorius*) (F. G. Hawksworth and Scharpf 1986). A survey in 1996 showed the mistletoe infestation occupied 220 km² but remained localized to Sonoma County (Scharpf 2002). In 1988, European mistletoe was found in Victoria, British Columbia, parasitizing *Malus*, but the population had apparently been purposely introduced more than 37 years before (C. E. Dorworth 1989). This naturalized mistletoe is categorized by the California Department of Food and Agriculture as a Noxious Weed List B because it has potential to negatively impact orchard crops. *Viscum album* is being studied extensively because it contains lectins that appear to have anticancer efficacy (A. Bussing 2000).