

SOLANACEAE POTATO FAMILY

PART TWO: KEY TO THE GENERA AND SOLANUM L.

Scott T. Bates, Frank Farruggia, Edward Gilbert,
Raul Gutierrez, Darin Jenke, Elizabeth Makings, Erin Manton,
Douglas Newton, and Leslie R. Landrum
School of Life Sciences
Arizona State University
Tempe, AZ 85287-4501

Annual and perennial herbs or shrubs (sometimes trees or vines elsewhere); unarmed or armed, the surfaces glabrous to variously hairy. LEAVES simple to variously compound, alternate, sub-opposite or fascicled. INFLORESCENCES uniflorous, panicles, umbels, racemes, or complex cymes. FLOWERS pedicellate, ebracteate, 4–5(–6)-merous, actinomorphic to zygomorphic; calyx synsepalous, deeply lobed to unlobed; corolla sympetalous; stamens usually the same number as corolla lobes, the filaments adnate to corolla tube between lobes, the anthers free, adherent, or connivent, basifixed or dorsifixed, ovate to lanceolate-linear, opening longitudinally or by terminal slits or pores; perigynous nectary often present; pistil syncarpous, usually bicarpellate and bilocular; stigma capitate to bilobed; style 1, terminal; ovary superior, usually bicarpellate and bilocular, the placentation axile, the ovules numerous, campylotropous. FRUITS capsules or berries; seeds many, mostly wingless and reniform-flattened, less often winged and prismatic. —Ca. 90 genera and 3000–4000 spp. worldwide, especially in C. and S. Amer. (Nee 2004).

1. Fruit a spiny capsule; flower (3.8–)5–26 cm long *Datura*
- 1' Fruit a berry or capsule without spines; flowers 0.5–7 cm long 2
2. Woody shrubs or trees 3
3. Flowers to 3–4.5 cm long; fruits capsules; petioles > 1.5 cm long; leaves 4–17 cm long *Nicotiana glauca*
- 3' Flowers 0.5–2.5 cm long; fruits berries; petioles < 1.5 cm long; leaves 1–5 cm long 4
4. Twigs often ending in thorns; flowers normally solitary in leaf axils; corolla white, greenish, to purple, rarely over 15 mm wide; anthers longitudinally dehiscent *Lycium*
- 4' Twigs unarmed; flowers normally in umbels or racemes; corolla deep blue to lavender; 15–30 mm wide; anthers terminally dehiscent *Solanum xanti*
- 2' Herbaceous or suffrutescent herbs 5
5. Corolla salverform, funnelform, or urceolate (mostly longer than wide) 6
6. Corolla notably zygomorphic; stamens 4 *Browallia*
- 6' Corolla actinomorphic or nearly so; stamens 5 7
7. Corolla urceolate 8
8. Calyx inflated in fruit; corolla purple *Margaranthus*
- 8' Calyx not inflated in fruit; corolla greenish to cream-white ... *Salpichroa*

- 7' Corolla salverform to funnelform9
 9. Leaves > 2 cm wide; flowers > 1.5 cm long; generally erect ... *Nicotiana*
 9' Leaves < 2 cm wide; flowers < 1 cm long; generally decumbent
 *Calibrachoa*
- 5' Corolla rotate to broadly campanulate (mostly wider than long) 10
 10. Calyx inflated in fruit, covering entire fruit, similar in appearance to a
 'Chinese lantern' 11
 11. Corolla yellow to cream-colored *Physalis*
 11' Corolla purple *Quincula*
- 10' Calyx sometimes accrescent, but not inflated in fruit 12
 12. Fruits capsules *Browallia*
 12' Fruits berries 13
 13. Stamens dehiscent by short, terminal slits or pores *Solanum*
 13' Stamens dehiscent longitudinally 14
 14. Leaves compound; anthers connivent *Solanum lycopersicum*
 14' Leaves simple; anthers free 15
 15. Calyx lobes about as long as tube; leaves mostly > 3 cm wide;
 inflorescence umbel-like, with 5 or more flowers *Jaltomata*
 15' Calyx lobes much shorter than tube; leaves < 2.5 cm wide;
 inflorescence simple, with 1–2 flowers 16
 16. Leaves ovate-lanceolate, mostly 1 cm or more wide; corolla
 without tomentose pads on inner surface *Capsicum*
 16' Leaves narrowly linear to elliptic, less than 0.5 cm wide;
 corolla with tomentose pads on inner surface alternating with
 stamens *Chamaesaracha*

Solanum L. Nightshade

Annual or perennial herbs and shrubs in ours, some armed with prickles, the surfaces often hairy, the hairs simple, branched, or stellate, sometimes glandular. LEAVES petiolate, simple, to pinnately compound, the margins entire, dentate to deeply lobed. INFLORESCENCES mostly borne between nodes, often lateral (opposite a leaf on stem), uniflorous to complex cymes. FLOWERS (4–)5-merous, actinomorphic to zygomorphic; calyx sometimes accrescent in fruit; corolla rotate to broadly campanulate; stamens sometimes unequal; anthers basifixed, oblong to lanceolate-linear, opening by terminal slits or pores; filaments shorter than anthers; stigma capitate. FRUITS berries, remaining fleshy or becoming dry; seeds wingless, lenticular to flattened-reniform. —18 spp. in AZ, ca. 1400 spp. worldwide, especially in S. Amer. (Bohs 2001).

Known as “the deadly nightshades” due to high concentrations of alkaloids in the vegetative and reproductive structures of some species. The genus contains important agricultural crops such as tomato (*S. lycopersicum*), potato (*S. tuberosum*), eggplant (*S. melongena*), and many regionally cultivated species. *Solanum* has also been used medicinally worldwide, for example, in the American Southwest a preparation of *S. elaeagnifolium* was used in treating ear, nose, and throat ailments, as well as eye infections and toothaches (Rea 1997).

1. Plants armed with prickles 2
2. Leaves unlobed or shallowly lobed 3
3. Larger leaves wider than 3.5 cm, the margins lobed; seeds reddish brown
..... *S. carolinense*
- 3' Larger leaves not wider than 3.5 cm, the margins repand-undulate; seeds tan to
brownish black 4
4. Shrubs to 2.5 m tall; prickles stout, from a thickened base; fruits erect; known
only from Organ Pipe Cactus National Monument (Pima County)
..... *S. hindsianum*
- 4' Rhizomatous herbs to 1 m tall; prickles thin and delicate; fruit pendulous;
distributed throughout the state *S. elaeagnifolium*
- 2' Leaves variously pinnatifid to pinnatisect 5
5. Cauline hairs non-glandular, mostly stellate; corolla yellow *S. rostratum*
- 5' Cauline hairs glandular, mostly simple; corolla violet to blue or yellow 6
6. Leaves with rounded ultimate lobes; corolla violet to blue; anthers of two sizes;
seeds minutely pitted *S. heterodoxum*
- 6' Leaves with acute ultimate lobes; corolla yellow; anthers of three sizes; seeds
radially ridged *S. lumholtzianum*
- 1' Plants unarmed, without prickles 7
7. Leaves compound 8
8. Anthers adherent; corolla yellow (drying white); leaflets toothed or lobed; fruit
mostly greater than 1.5 cm in diameter, yellow-green to red at maturity; herbage
glandular-pubescent *S. lycopersicum*
- 8' Anthers free; corolla white to purple; leaflets entire; fruit mostly less than 1.5 cm
in diameter, green at maturity; herbage glabrous to densely hairy with occasional
glandular hairs 9
9. Corolla usually white, 2.8–3.5 cm in diameter; leaflets usually 2–3 times
longer than wide; herbage glabrous to sparsely pilose *S. jamesii*
- 9' Corolla usually purple or rarely white tinged with purple, around 1.8–3.3 cm
in diameter; leaflets usually less than 2 times longer than wide; herbage sparsely
to copiously pilose *S. stoloniferum*
- 7' Leaves simple (sometimes lobed) 10
10. Herbage with stellate hairs; leaves coriaceous, the underside densely
pubescent 11
11. Shrubs to 2.5 m tall; fruit erect; known only from Organ Pipe Cactus
National Monument (Pima County) *S. hindsianum*
- 11' Rhizomatous herbs to 1 m tall; fruit pendulous; distributed throughout the
state *S. elaeagnifolium*
- 10' Herbage lacking stellate hairs; leaves subcoriaceous to membranaceous, the
underside glabrous to hirsute, or densely villous 12
12. Corolla deep blue to lavender; shrub or subshrub *S. xanti*
- 12' Corolla white (sometimes lightly tinged blue); herbs or sometimes
subshrubs 13
13. Leaves deeply lobed *S. triflorum*
- 13' Leaves unlobed or shallowly lobed 14
14. Inflorescence 1–2-flowered; fruit white *S. adscendens*
- 14' Inflorescence cymose to paniculate, usually with 2 or more flowers;
fruits red, purplish, black, green or brown 15

15. Herbage villous, with some multicellular and some glandular hairs; calyx enlarged in fruit, covering lower half of fruit base; mature fruit in fresh material yellowish red to dark brown *S. physalifolium*
 15' Herbage glabrous to strigose, the hairs all unicellular and non-glandular; calyx not enlarged in fruit; mature fruit in fresh material black to purplish, rarely green 16
 16. Anthers greater than 2 mm long; corolla greater than 3 mm long *S. douglasii*
 16' Anthers less than 1.5 mm long; corolla less than 2.5 mm long *S. americanum*

Solanum adscendens Sendtn. (ascending). Sonoita nightshade. —Annual herbs 10–40 cm tall, taller than wide, without tubers or stolons, unarmed, with some branches divergent, pubescent to hirsute. LEAVES alternate and sub-opposite, simple, lanceolate to ovate, 1–5 cm long, 1–2.2 cm wide, ca. 2 times as long as wide, the margin entire, the blade membranous; apex acute; base rounded to attenuate; petiole 3–20 mm long. INFLORESCENCES usually solitary flowers (rarely 2-flowered). FLOWERS actinomorphic; peduncle 6–15 mm long, narrowing at base, strongly deflexed; calyx 3–4 mm long, campanulate, more densely pubescent than leaves, the lobes longer than the tube, linear to oblong; corolla to 10 mm wide, rotate, white, drying yellow; stamens equal; anthers to 3 mm long, not adherent; filaments ca. 1/3 as long as anthers; style straight, about equal to stamens. FRUITS 5–8 mm in diam., milk-white, descending, not enclosed by the calyx; seeds 2.5–3 mm long, many, yellow-brown, lustrous, reniform. [*S. deflexum* Greenm.]. —In shade of shrubs along washes and hillsides, usually in sandy soils; pine-oak woodlands: Cochise, Pima, Pinal, Santa Cruz cos. (Fig. 1A); 1000–1700 m (3500–5600 ft); Aug–Sep; AZ to s Mex.; C. Amer.

Solanum americanum Mill. (of America). American black nightshade. —Annual or short-lived perennial herbs, sometimes turning woody with age, usually greater than 1 m tall, without tubers or stolons, unarmed; herbage glabrous to pubescent to variously strigose; stems terete to angled, sometimes with small, antrorsely curved teeth on the angles. LEAVES alternate or sub-opposite, simple, ovate to lance-elliptic, 2–9 cm long, 1–5 cm wide; margin entire to coarsely-toothed; base sub-truncate to attenuate; apex broadly acute to acuminate; petiole (1–)2–6(–8) cm long. INFLORESCENCES umbel-like racemes, lateral, borne between nodes or sometimes at nodes opposite leaves, (1–)3–8(–12)-flowered; peduncle 8–30 mm long. FLOWERS actinomorphic (Fig. 3A); pedicel 2–12 mm long; calyx 0.5–2 mm long, the lobes broadly lanceolate to rounded, about equal to or 1/2 as long as the tube; corolla rotate-stellate to reflexed, white or white tinged with purple, 2–6 mm in diameter; style included to 1 mm longer than anthers, pubescent \pm half its length; stamens \pm equal, (0.5–)1–1.5(–2) mm long; anthers connivent; filaments 1/2 or less as long as anthers, 1 mm long or less. FRUITS subglobose, 4–8 mm wide, green, orange-brown or blackish at maturity, not enclosed in the calyx; sclerotic granules 0–5; seeds orbicular, minutely pitted, 1–1.3 mm wide. —Agricultural areas, waste places and riparian areas: La Paz, Maricopa,

Mohave, Pima, Yavapai cos. (Fig. 1B); 50–1800 m (200–6000 ft); throughout the year; s. and w. U.S.; Mex; probably native to Eurasia.

Solanum americanum, *S. douglasii*, and *S. physalifolium* belong to the “*Solanum nigrum*” complex (also known as the “black nightshades”), a cosmopolitan group of about 30 species with a center of diversity in the New World tropics. They have been used by humans medicinally, for food and fodder, or as dyes, and reports of their use date back to the earliest records in written history (Edmonds 1985, Edmonds & Chweya 1997, Dehmer 2001, PBI *Solanum* Project 2009). Species related to black nightshades are also troublesome agricultural weeds and frequently hosts to destructive animals and diseases of crops. They are known to contain toxic levels of alkaloids, varying with climate, season and soil type (Ogg et al. 1981, Schilling & Andersen 1990).

The black nightshades are taxonomically challenging due to a variety of biological, environmental, and historical factors including polyploidy, their autogamous habit, ability to hybridize, phenotypic plasticity, and widespread geography (Stebbins & Paddock 1949, Schilling & Heiser 1979, Edmonds & Chweya 1997). Nomenclatural problems have also added to the confusion. Species related to *S. nigrum* have been reclassified innumerable times and there is extensive synonymy with over 300 published names (Ogg et al. 1981, Dehmer 2001, Knapp 2001).

The complex also has few consistent diagnostic morphological characters. Almost all authors acknowledge the difficulty assigning species names to dried specimens as well as the inconvenient necessity of large numbers of characters needed to differentiate taxa at the specific level (e.g., Soria & Heiser 1961, Heiser et al. 1979).

The nomenclature used here is tentative as the taxonomy is complicated and beyond the scope of this treatment. Arizona taxa may include more and/or different species than we recognize (e.g., Schilling 1981, Manoko et al. 2007). Variable and closely related forms in this group may represent “species in the making” and taxonomic subdivisions will certainly change over time.

Our approach in this treatment was to determine if it was possible to recognize discreet entities based on herbarium material from Arizona specimens. It appears there are three. The vegetative characters of *S. physalifolium* easily distinguish it from the other two. The differences between “*S. americanum*” and “*S. douglasii*”, however, were more subtle. Past authors have used a variety of taxonomic characters in identification keys for the *Solanum nigrum* complex (e.g., habit, vestiture, inflorescence, corolla length, degree of style exertion, calyx in fruit, berry surface, seed size, number of sclerotic granules/fruit, pollen grain diameter, stomatal aperture length, chromosome numbers). We found overlap with almost all observable field characters and many of the others impractical when sorting out any reliable differences between them. However, anther length and to a lesser degree, corolla size, turned out to be consistent, albeit limited characters, for a useful separation of “*S. americanum*” and “*S. douglasii*”. Although there are occasionally intermediates between the small-anthered “*S. americanum*” and larger-anthered “*S. douglasii*,” the boundaries were too vague to delineate a third taxon.

Solanum carolinense L. (from Carolina). Carolina horse-nettle, ball-nettle. —Perennial herbs, rhizomatous, without tubers, to 1 m tall, armed with prickles to 7 mm long, the surface covered with sessile stellate hairs throughout. LEAVES alternate, simple, ovate, to 12 cm long and 8 cm wide; margin with 2–4 lobes on each side; blade subcoriaceous, the lower surface densely covered with stellate hairs, with prickles along the main veins; petiole to 3 cm long; base cuneate to truncate; apex acute. INFLORESCENCES panicles, 4–10-flowered; peduncles to 5 cm long. FLOWERS zygomorphic (Fig. 3H); pedicels 7–15 mm long; calyx to 1 cm long, the lobes 1–2 times longer than the tube, equal, narrowly deltoid, acuminate; corolla campanulate, purple in ours, to 3 cm in diam., with stellate hairs along the midveins of the outer surfaces of the corolla lobes; stamens equal, to 12 mm long, the anthers 5 times as long as the filaments, not adherent; style exceeding the anthers by 2–10 mm; stigma subcapitate, to 1 mm wide. FRUITS to 2 cm in diam., not invested in the calyx, green with pale green to greenish grey markings when immature, yellow when mature, pendant; seeds lenticular, reddish brown, shiny, minutely pitted. —Known from only one site in Arizona along Queen Creek (W.S. Radcliff *s.n.*, ASU): Maricopa Co. (Fig. 1C); ca. 500 m (1500 ft); May; throughout the U.S.; e Can.

Solanum douglasii Dunal (for David Douglas). Greenspot nightshade. —Annual or short-lived perennial herbs, sometimes turning woody with age, usually less than 1 m tall, without tubers or stolons, unarmed; herbage glabrous to pubescent to variously strigose; stems terete to angled, sometimes with small, antrorsely curved teeth on the angles. LEAVES alternate or sub-opposite, simple, 2–9 cm long, 1–5 cm wide, ovate to lance-elliptic; margin entire to coarsely-toothed; base truncate to attenuate; apex broadly acute to acuminate; petiole (1–)2–6(–8) cm long. INFLORESCENCES umbel-like racemes, lateral, borne between nodes or sometimes at nodes opposite leaves, (1–)3–8(–12)-flowered; peduncle 8–30 mm long. FLOWERS actinomorphic (Fig. 3B); pedicel 2–12 mm long; calyx 1.5–2.5 mm long, the lobes lanceolate to rounded, about as long as to 1/4 the length of the tube; corolla rotate-stellate to reflexed, white or white tinged with purple, sometimes gland-dotted, sometimes with basal brownish star, 8–25 mm in diam.; style as long as stamens or up to 3 mm longer, pubescent \pm half its length; stamens of \pm equal length, (2.5–)3–4(–4.5) mm long; anthers connivent; filaments 1/5 or less as long as anthers, usually much less than 1 mm long. FRUITS subglobose, 6–12 mm wide, green, orange-brown or blackish at maturity, not enclosed in the calyx; sclerotic granules 0–5; seeds orbicular, minutely pitted, 1–1.6 mm wide. —Agricultural weeds also found in waste places and riparian areas: All cos. except Apache (Fig. 1D); 50–2500 m (~200–8000 ft); throughout the year; s. U.S. from AL to CA; Mex.; probably native to N. Amer.

Solanum elaeagnifolium Cav. (leaves like *Elaeagnus*). Silverleaf nightshade. —Perennial herbs, rhizomatous, without tubers, to 1 m tall, sparsely to copiously armed with prickles, these to 5 mm long, thin, delicate; surfaces covered with stellate hairs throughout. LEAVES alternate, simple, linear to oblong-lanceolate, to 10 cm long and 2.5 cm wide, the margin entire, sinuate-repand or

shallowly lobed; blade coriaceous, the lower surface densely covered with stellate hairs; petiole to 5 cm long; base attenuate, oblique, or rounded; apex acute. INFLORESCENCES panicles, 5–8-flowered; peduncles to 15 mm long. FLOWERS zygomorphic (Fig. 3C); pedicels to 2 cm long; calyx to 1 cm long, the lobes 1/2 as long to as long as the tube, unequal, linear; corolla rotate, purple or sometimes white, to 3.5 cm in diam., having stellate hairs along the midveins of the outer surfaces of the corolla lobes; stamens equal, to 13 mm long, the anthers 4 times as long as the filaments, not adherant; style exceeding the anthers by 2–10 mm; stigma clavate, to 1 mm wide. FRUITS to 1.5 cm in diam., not invested in the calyx, green with pale green to greenish grey markings when immature, yellow when mature, pendant; seeds lenticular, pale to dark brown, shiny and minutely pitted. —Disturbed areas: all cos. (Fig. 1E); below 1200 m (4000 ft); Mar–Oct; s and w U.S.; Mex.

Solanum heterodoxum Dunal (Greek: *heteródoxos*, of another opinion). Melon-leaf nightshade. —Annual herbs, taprooted, without tubers or stolons, 30–70 cm tall, pubescent, densely armed with prickles 2–9 mm long; hairs 0.2–0.8 mm long, simple over most of the plant, frequently gland-tipped. LEAVES alternate, deeply dissected, bipinnatifid to compound, broadly ovate to obovate or deltoid, 4–11 cm long, with irregular-stellate trichomes on the lower surface, and simple, gland-tipped trichomes on the upper and lower surface, the stellate trichomes with 2–5 rays, the main veins armed with scattered prickles; petioles 2–7 cm long, armed with prickles; base of leaf or leaflets variable, acute to cordate; apices of ultimate lobes rounded to obtuse. INFLORESCENCES 4–10 cm long, raceme-like monochasial cymes, 5–9-flowered; peduncles 1–5 cm long. FLOWERS somewhat zygomorphic, perfect or having nonfunctional stigmas and abortive ovules in the terminal portions of the inflorescence; pedicel 0.5–2 cm long; calyx campanulate, the tube 1.5–2.2 mm long, the lobes deltoid, 2–5 mm long; corollas stellate-pentagonal, 1–1.7 cm wide, loosely folded between the lobes, violet to blue; stamens unequal; anthers oblong, of two sizes, the lowermost extended anther 3.5–5 mm long, purple-tinged, incurved at the tip, the upper shorter anthers 2–4 mm long and yellow; filaments ca. 1/5 as long as the anthers; styles slender, extending out beyond the anthers; stigmas 0.3–0.6 mm across. FRUITS spherical, 0.9–1.2 cm in diam., tightly invested by the densely armed, burr-like accrescent tube of the calyx; seeds dark brown, 2.5–2.9 mm long, lenticular to broadly ovate, minutely pitted. [*Solanum mullus* Hort. Monsp. ex Dunal, *S. virginianum* Pav. ex Dunal]. —Silty, sandy, or gravelly soils of dunes, streambeds, washes, and open hillsides: Cochise, Graham, Maricopa, Santa Cruz, Yavapai cos. (Fig. 1F); 590–1650 m (1950–5400 ft.); Jun–Oct; NM; n and c Mex.

Whalen (1979) cites three varieties of *S. heterodoxum* as occurring in the United States and Mexico. *S. h.* var. *setigeroides*, with stems densely covered in needle-like prickles and pentagonal corollas with broadly deltoid lobes, is probably the only variety in AZ.

Solanum hindsianum Benth. (for Richard Brinsley Hinds). Hinds' nightshade, Tomatillo espinoso. —Shrubs to 2.5 m tall, without tubers or rhizomes, unarmed to sparsely armed with stout prickles to 10 mm long, the young growth covered with stellate hairs. LEAVES alternate, simple, oblong-lanceolate to ovate, to 6.5 cm long and 4.5 cm wide; blade coriaceous, lower surface densely tomentose, the hairs stellate; margin entire to undulate; petiole to 2.5 cm long; base rounded, truncate or oblique; apex acute to rounded. INFLORESCENCES racemes, with fewer than 5 flowers; peduncles to 3 cm long. FLOWERS actinomorphic; pedicel to 1.5 cm long; calyx to 2 cm long, the lobes 2–3 times longer than the tube, unequal, linear to narrowly deltoid; corolla rotate, purple in ours, to 5.5 cm in diam., having stellate hairs along the midveins of the outer surfaces of the corolla lobes; stamens unequal, to 13 mm long, the anthers 3–4 times as long as the filaments, not adherent; style equal to or exceeding the anthers by 1–8 mm; stigma capitate, to 1 mm wide. FRUITS to 2 cm in diam., not invested in the calyx, green with pale green to greenish grey markings when immature, dark brown when mature, erect; seeds lenticular, dark brown, shiny, minutely pitted. —Rocky hillside, often among boulders: known only from Organ Pipe Cactus National Monument, Pima Co. (Fig. 2A); 500–600 m (1500–1800 ft); Mar; Son., Baja C., Mex.

Solanum jamesii Torr. (for Edwin James). Wild potato. —Perennial herbs, 10–30(–50) cm tall, glabrous to pilose and somewhat glandular, with rhizomes bearing tubers, these about (5–)10–15(–20) mm in diam.. LEAVES alternate, pinnately compound, 7–15 cm long, 4–9 cm wide, upper surface glabrous or nearly so, the lower surface with short glandular hairs; leaflets (5–)7–9(–13), linear-elliptic to lanceolate, usually 2–3 times longer than wide, the lowermost leaflets much reduced; small interstitial leaflets rarely interposed between the larger leaflets; leaflet base oblique, often decurrent on rachis; leaflet apex acute; most distal lateral leaflets (1.7–)2.5–5(–6) cm long, 0.5–1.5(–2) cm wide; terminal leaflet usually only slightly larger than laterals, (2.5–)3–6.5 long, (0.6–)1–2(–2.5) wide; petioles to 3 cm long. INFLORESCENCES paniculate cymes, lateral or pseudoterminal on leafy branches, few to several-flowered, ebracteate; peduncle 1–6 cm long. FLOWERS actinomorphic (Fig. 3F); pedicels 1–3 cm long, articulate near mid-point; calyx up to 8 mm long; lobes 1–3 times longer than tube, irregular, triangular-ovate, acuminate to caudate; corolla rotate-stellate, white, 2–3.5 cm in diam.; lobes ca. 2 times as long as tube, ovate-lanceolate to triangular-lanceolate, subobtuse to subacuminate, pubescent distally especially along margins; stamens equal, 5–7 mm long; anthers 3–5 times longer than filaments; style usually exceeding stamens by 4–6 mm. FRUITS ca. 1 cm in diam., not enclosed by calyx, green throughout; seeds ovate, green-white, ca. 2 mm long. [*S. j.* var. *heterotrichium* Bitter, *S. j.* var. *sinclairii* Bitter & Correvon, *S. j.* subsp. *septentrionale* Bitter]. —Grasslands, juniper-pinyon woodlands, scrub deserts, oak thickets, coniferous and deciduous forests: Apache, Cochise, Coconino, Greenlee, Gila, Mohave, Navajo, Pima, Santa Cruz cos. (Fig. 2B); 1500–2600 m (5000–8500 ft); mid-Jul–early Oct; CO, TX, UT; n Mex.

A close relative to the cultivated potato; tubers have been reportedly used as a food source by some Native American tribes. This plant is highly variable and has been separated into several varieties by some authors. This treatment considers the complex to be a single variable species.

Solanum pinnatisectum Dun. occurs on some Arizona species lists due to a 1951 Donovan S. Correll annotation of an ARIZ (32189) specimen collected by Leslie Goodding (#277) in the Huachuca Mountains. This specimen was determined as *S. jamesii* by Spooner, Rodriguez, and van den Berg in 2001.

Solanum lumholtzianum Bartlett (for Carl S. Lumholtz). Lumholtz nightshade, Sonoran nightshade, Mala Mujer. —Annual herbs, taprooted, without tubers or stolons, 20–70 cm tall, pubescent, armed with prickles 4–9 mm long; hairs up to 0.7 mm long, simple over most of the plant, frequently gland-tipped. LEAVES alternate, deeply dissected, bipinnatifid to tripinnatifid or compound, broadly ovate, 5–13 cm long, with stellate trichomes and simple, gland-tipped trichomes on the upper and lower surface, the stellate trichomes with 4–5 rays, the main veins armed with scattered prickles; petioles 2.5–7 cm long, armed with prickles; base of leaf or leaflets variable, acute to subcordate; apices of ultimate lobes obtuse to acute. INFLORESCENCES 3–8 cm long, raceme-like monochasial cymes, 6–10-flowered, peduncles 0.5–3 cm long. FLOWERS somewhat zygomorphic, perfect or having nonfunctional stigmas and abortive ovules in the terminal portions of the inflorescence; pedicel 0.5–1.5 cm long; calyx campanulate, the tube 1.8–2.2 mm long, the lobes linear-lanceolate, 5–12 mm long; corollas stellate, 1.3–1.8 cm wide, yellow; stamens unequal; anthers oblong, of three sizes, the lowermost extended anther 6.5–8.6 mm long, occasionally purple-tinged, incurved at the tip, the two adjacent shorter anthers 5.6–7.5 mm long, also terminally incurved, the uppermost shortest pair 4.5–6 mm long; filaments ca. 1/4 as long as the anthers; styles slender, extending out beyond the anthers; stigmas to 0.5 mm across. FRUITS broadly ovoid, 1.1–1.4 cm in diam., tightly invested by the densely armed accrescent tube of the calyx; seeds dark brown, 3–3.5 mm long, broadly ovate to suborbicular, radially ridged. —Sandy or gravelly soils of washes, stream-banks, hillsides, or occasionally roadsides: Pima, Santa Cruz cos. (Fig. 2C); 1020–1400 m (3350–4550 ft); Jul–Oct; s AZ; n Mex.

Solanum lycopersicum L. (Greek: *lycos*, wolf; *persikon*, peach). Tomato (derived from Nahuatl word *tomatl*). —Annual to perennial herbs without tubers or stolons; stems 1–3 m long, decumbent with age, fleshy, unarmed, pubescent with unicellular and uniseriate multicellular hairs, sticky-glandular, aromatic. LEAVES alternate, irregularly pinnately compound to pinnatifid, (10–)20–40 cm long, (3–)7–10 cm wide, with hairs like those on stem; primary lateral leaflets 3–4(–5) pairs, 2–5 cm long, 0.8–2.5 cm wide, ovate to elliptic; base oblique, truncate to cordate; apex acute-attenuate; margin dentate-crenate to shallowly lobed, more so near base; terminal leaflet usually larger than laterals, 3–6 cm long, 1.5–3 cm wide; small interstitial leaflets common; petiole 1.2–6 cm long. INFLORESCENCES few-flowered racemes, to 10 cm long, ebractate, rarely branched; peduncle 1.5–5 cm. FLOWERS actinomorphic, more than 5-merous in some cultivars; pedicels 1–1.2 cm long; calyx 0.5–1.2 cm long, with tube minute, the lobes linear; corolla 0.7–2.5 cm long, 1–2 cm in diam., pentagonal, yellow; lobes 2–4 times as long as tube, narrowly lanceolate, reflexed, sparsely pubescent on tips and margins; anthers connivent in a staminal column 0.6–0.8 cm long, this narrowly cone-shaped,

tapered and sterile at tip; filaments minute to 0.5 mm long; style 0.6–1 cm long, usually not exceeding in staminal column. FRUITS 1.5–2.5(–12) cm wide, yellow-green, orange to red; seeds 2.5–3.3 mm long, obovate, pale brown, narrowly winged at apex. [*Lycopersicon esculentum* Mill., *Lycopersicon lycopersicum* (L.) Karst. ex Farw., *Lycopersicon pyriforme* Dunal]. —Waste areas, abandoned fields, roadsides, riverbeds; typically collected near populated areas, no persistent populations occur in Arizona: Coconino, Maricopa, Yavapai cos. (Fig. 2D); 300–2100 m (1000–7000 ft); Apr–Sep; native to S. Amer., cultivated worldwide.

This species displays enormous variation in fruit shape and size. A small-fruited variety, called “*S. l. var. cerasiforme*” by some authors, have been suggested to be ancestral to the cultivated form, though recent work has shown this variety to be a mixture of wild and cultivated forms (Nesbitt & Tanksley 2002).

Solanum physalifolium Rusby (leaves of *Physalis*). Hairy nightshade. —Annual or short-lived perennial herb to 70 cm tall, without tubers or stolons, unarmed; herbage moderately to densely villous, with gland-tipped hairs, some multicellular; stems terete to angled. LEAVES alternate to sub-opposite, simple, lance-ovate to lance-elliptic, 2–6 cm long, 1–3 cm wide; margin entire to coarsely toothed; base truncate to attenuate; apex rounded to acuminate. INFLORESCENCES umbel-like racemes, lateral, borne between nodes or sometimes at nodes opposite leaves, (2–)4–8(–12)-flowered; peduncle 5–30 mm long. FLOWERS actinomorphic; pedicel 2–15 mm long; calyx 1–3 mm long, the lobes lanceolate to rounded, reaching about 1/4 to 2/3 the length of the tube; corolla actinomorphic, rotate to weakly campanulate (this sometimes not obvious in dried specimens), white or white tinged with purple, with basal brownish star, 3–6 mm in diam., with broadly triangular lobes; style as long as stamens or up to 1 mm longer, pubescent \pm half its length; stamens of \pm equal length, 1.5–2(–2.5) mm long; anthers connivent; filaments less than 1 mm long. FRUITS orbicular, 6–9 mm wide, dark green to purple to brownish-green, at least lower half of mature fruit covered with enlarged calyx; sclerotic granules 0–5; seeds 1–2 mm wide, orbicular, orange-brown in dried specimens. [*S. sarrachoides* Sendtn. and *S. villosum* (L.) Mill. have been misapplied]. —Infrequent in disturbed areas: Coconino, Maricopa, Navajo, Yavapai cos. (Fig. 2E); 900–2100 m (~3000–7000 ft); Jun–Oct; throughout N. Amer. excluding se states; introduced from S. Amer.

Solanum rostratum Dunal (beaked). Buffalobur nightshade. —Annual herbs, to 70 cm tall, without tubers or stolons, abundantly armed on herbage and calyx with straight, straw-colored prickles, these sometimes more than 1 cm long on fruiting calyces; copiously stellate-pubescent throughout (also with occasional simple hairs), the cauline stellae sessile or sometimes on a stalk up to 1 mm long. LEAVES alternate, (bi-)pinnatifid to pinnatisect near the base, the lobes irregular in shape with rounded or obtuse apices; blades elliptic to broadly ovate in outline, to ca. 12 cm long, submembranous to subcoriaceous, stellate-pubescent on both surfaces, prickly along principal veins, the veins impressed above; petioles to ca. 8 cm long, usually ca. 2/3 the length of the blade. INFLORESCENSES raceme-like monochasial cymes, to ca. 15 cm long; peduncles 1–4 cm long. FLOWERS

somewhat zygomorphic (Fig. 3D); pedicel to ca. 1 cm long; calyx 5–12 mm long, the lobes usually at least 2 times as long as the tube (sometimes much longer); corolla rotate, yellow, 15–25 mm in diam., stellate-pubescent on the outer surface, loosely folded between the lobes, the two lower lobes somewhat larger and curving outward; stamens unequal; anthers ca. 2 times longer than filaments, the lowermost anther greater than 1 cm long, red-purple tinged, curved, the 4 uppermost anthers 6–8 mm long, yellow, straight; style curved, equal to or exceeding the long anther. FRUITS 9–12 mm in diam., erect, closely invested by the densely prickly, accrescent tube of the calyx; seeds flattened, ovoid, dark brown, alveolate. [*Androcera rostrata* (Dunal) Rydb.]. —A common weed of overgrazed pastures and roadsides: all cos. except La Paz, Yuma (Fig. 2F); 250–2250 m (800–7400 ft); Jun–Sep; all states except FL; throughout Mex. and s Can.

Solanum stoloniferum Schtdl. (bearing stolons). Fendler's wild potato. —Perennial herbs, 10–15(–50) cm tall, pilose throughout, with stolons and tubers; tubers round to ellipsoid, white to purple, up to 3 cm long. LEAVES alternate, pinnately compound, usually about 7.5–22 cm long, 3.5–8 cm wide, more or less pubescent on upper and lower surfaces; leaflets (3–)5–7(–9), mostly less than 2 times longer than wide, with younger leaflets sometimes purple beneath; most distal lateral leaflets (1.5–)2.5–6.5 cm long, (0.5–)1.5–2.7(–3.5) cm wide, ovate to elliptic, with apex acute to acuminate, with base cuneate to rounded-oblique, often decurrent on rachis; terminal leaflet usually much larger than laterals, (1.8–)3.5–7.5(–10) cm long, (1.5–)2.5–4.5(–7) cm wide, elliptic to obovate, with apex acute to acuminate, with base cuneate; small interstitial leaflets sometimes present between the larger ones; petioles 1.5–4 cm long. INFLORESCENCES racemose or paniculate cymes, lateral or pseudoterminal, 3–26-flowered, ebracteate, usually densely pilose and sometimes sparsely glandular; peduncles 3.4–10 cm long. FLOWERS actinomorphic (Fig. 3G); pedicels 1–3.5 cm long; calyx 4–7(–30) mm long, with lobes 1–2 times as long as tube, ovate-lanceolate to triangular-lanceolate, acute to long-attenuate; corolla pentagonal-rotate, blue, purple or white and purple-tinged, ca. 1.8–3.3 cm in diam., with lobes 1.5–4 mm long, edges of corolla flat; stamens equal, 3–6 mm long; anthers 2–4 times longer than filaments; style as long as stamens, or exceeding them by up to 4 mm. FRUITS 0.9–1.7 cm in diam., not invested in calyx, white to deep green, sometimes with darker green stripes and white spots; seeds ovate in outline, green-white, ca. 2 mm long. [*Solanum fendleri* A. Gray]. —Open coniferous forest: Apache, Cochise, s Coconino, Gila, Graham, Greenlee, Pima, Pinal, Santa Cruz cos. (Fig. 2G); 1950–2750 m (6500–9000 ft), occasionally lower; late Jul–early Oct; NM, TX, s to Oax., Mex.

One of the most common, widespread, and polymorphic species of the wild potatoes. Arizona populations tend to be of shorter stature and have fewer interstitial leaflets than in the southern part of its range. Tubers have been reportedly used as a food source by some Native American tribes.

Solanum triflorum Nutt. (three flowers). Cutleaf nightshade. —Annual herbs, 10–50 cm tall, unarmed, without tubers or stolons, sparsely to densely appressed pubescent; stems divergent, spreading to decumbent. LEAVES simple, alternate, oblong to ovate, deeply pinnatifid, 2–5 cm long, 1–2 cm wide, ca. 2 times as long as wide, with individual lobes lanceolate, the blade submembranous; petiole 5–20 mm long; apex acute; base cuneate. INFLORESCENCES umbels with (1–)2–3(–6)-flowered; peduncle 5–15 mm long. FLOWERS actinomorphic (Fig. 3E); pedicel up to 5 mm long; calyx 2.5–5 mm long, campanulate, the lobes longer than tube, linear, acute; corolla white, drying yellow, up to 8 mm wide; stamens equal; anthers 2.5–3 mm long, not adherent, straight; filaments about as long as anthers; style about as long as stamens. FRUITS 9–14 mm in diam., green, ascending, not enclosed by calyx; seeds 2.5–3 mm in diam., many, sub-orbicular, flat, yellow-brown. —Roadsides, washes, sandy soil, dry scrub lands, juniper woodlands: Apache, Cochise, Coconino, Gila, Maricopa, Mohave, Navajo, Pinal, Yavapai cos. (Fig. 2H); 600–2600 m (2000–8500 ft); May–Sep; c U.S.; native to S. Amer.

In times of food shortage the Indians of west central NM boiled the berries, ground them with chili and salt, and ate them as a condiment with mush or bread (Ebeling 1986).

Solanum xanti A. Gray (for L. I. Xantus). Purple nightshade. —Subshrub, woody at base, 40–90 cm tall, unarmed, without tubers or stolons, puberulent to soft-pilose mainly on stems and veins of leaves. LEAVES simple, elliptic, ovate or lanceolate, 1–5 cm long, 0.5–2 cm wide, ca. 2 times as long as wide, submembranous, the margin entire or rarely with occasional teeth; apex acute to rounded; base rounded to oblique; petiole 5–15 mm long. INFLORESCENCES an umbel-like panicle with up to 6 flowers; peduncle 5–2 mm long. FLOWERS actinomorphic (Fig. 3I); pedicel 5–15 mm long; calyx up to 7 mm long and wide, campanulate, the lobes deltoid, shorter than the tube; corolla deep blue to lavender, 15–30 mm wide; stamens equal; anthers 4–5 mm long, not adherent, opening by a short slit; filaments up to 1/3 as long as the anthers; style longer than the stamens. FRUITS 10–15 mm in diam., green, not enclosed by the calyx; seeds 1.5–2 mm in diam., numerous, yellowish brown, reniform. —Rocky bajada slopes in chaparral: Coconino, Gila, Graham, Greenlee, Maricopa, Mohave, Navajo, Pima, Santa Cruz, Yavapai cos. (Fig. 2I); 1000–2100 m (3000–7000 ft); Apr–Nov; AZ, CA; Baja C., Mex.

Native Americans of the central valley of California ate the berries raw (Ebeling, 1986).

ACKNOWLEDGMENTS

We thank Sandra Knapp for her informal input in this treatment and the identification of *S. physalifolium* material from photos. The curators and staff at ARIZ, ASU, and DES made specimens available for study. Max Licher kindly provided some images in Figure 3.

LITERATURE CITED

- BOHS, L. 2001. A revision of *Solanum* section *Cyphomandropsis* (Solanaceae). *Systematic Botany Monographs* 61: 1–83.
- DEHMER, K.J. 2001. Conclusions on the taxonomy of the *Solanum nigrum* complex by molecular analysis of IPK germplasm accessions. Pp. 85–86. In: R.G. van den Berg, G.W.M. Barendse, G.M van der Weerden and C. Mariani (eds.). *Solanaceae V: Advances in Taxonomy and Utilization*. Nijmegen University Press, Nijmegen.
- EBELING, W. 1986. *Handbook of Indian Foods and Fibers of Arid America*. University of California Press, Berkeley.
- EDMONDS, J.M. 1985. Biosystematics of *Solanum sarrachoides* Sendtner and *S. physalifolium* Rusby (*S. nitidibaccatum* Bitter). *Botanical Journal of the Linnean Society* 92:1–38.
- EDMONDS, J.M. and J.A. CHWEYA. 1997. *The Black Nightshades: Solanum nigrum L. and Related Species*. Institute of Plant Genetics and Crop Plant Research, Gatersleben/International Plant Genetic Resources Institute, Rome.
- HEISER, Jr., C.B., D L. BURTON and E.E. SCHILLING. 1979. Biosystematic and taxometric studies of the *Solanum nigrum* complex in eastern North America. Pp. 523–528. In: J.G. Hawkes, R.N. Lester and A.D. Skelding (eds.). *The Biology and Taxonomy of the Solanaceae*. Academic Press, New York.
- KNAPP, S. 2001. Is morphology dead in *Solanum* taxonomy? Pp. 23–38. In: R.G. van den Berg, G.W.M. Barendse, G.M van der Weerden and C. Mariani (eds.). *Solanaceae V: Advances in Taxonomy and Utilization*. Nijmegen University Press, Nijmegen.
- MANOKO, M.L.K., R.G. VAN DEN BERG, R.M.C. FERON, G.M. VAN DER WEERDEN and C. MARIANI. 2007. AFLP markers support separation of *Solanum nidoflorum* from *Solanum americanum* sensu stricto (Solanaceae). *Plant Systematics Evolution* 267: 1–11.
- NEE, M. 2004. *Solanaceae*. Pp. 355–357. In: N. Smith, S.A. Mori, A. Henderson, D.W. Stevenson and S.V. Heald (eds.). *Flowering Plants of the Neotropics*. New York Botanical Garden, New York.
- NESBITT, T.C. and S.D. TANKSLEY 2002. Comparative sequencing in the genus *Lycopersicon*: implications for the evolution of fruit size in the domestication of cultivated tomatoes. *Genetics* 162: 365–379.
- OGG Jr., A.G., B.S. ROGERS and E.E. SCHILLING. 1981. Characterization of the Black Nightshade (*Solanum nigrum*) and related species in the United States. *Weed Science Society of America Journal* 29: 2732.
- PBI SOLANUM PROJECT. 2009. *Solanaceae Source*. <http://www.nhm.ac.uk/solanaceaesource/> (Accessed 2009 April).

REA, A.M. 1997. *At the Desert's Green Edge: An Ethnobotany of the Gila River Pima*. University of Arizona Press, Tucson.

SCHILLING, E.E. 1981. Systematic of *Solanum* sect. *Solanum* (*Solanaceae*) in North America. *Systematic Botany* 6: 172–185.

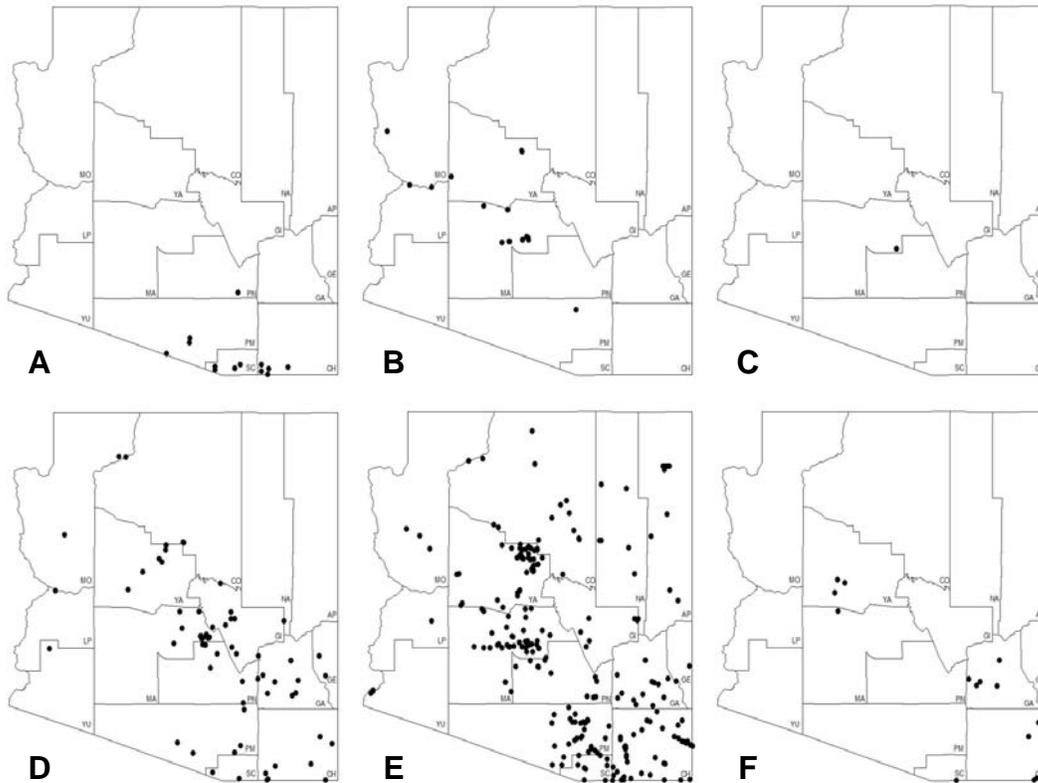
SCHILLING, E.E. and R.N. ANDERSEN. 1990. The black nightshades (*Solanum* section *Solanum*) of the Indian subcontinent. *Botanical Journal of the Linnaean Society* 102: 253–259.

SCHILLING, E.E. and C.B. HEISER, Jr. 1979. Crossing relationships among diploid species of the *Solanum nigrum* complex in North America. *American Journal of Botany* 66: 709–716.

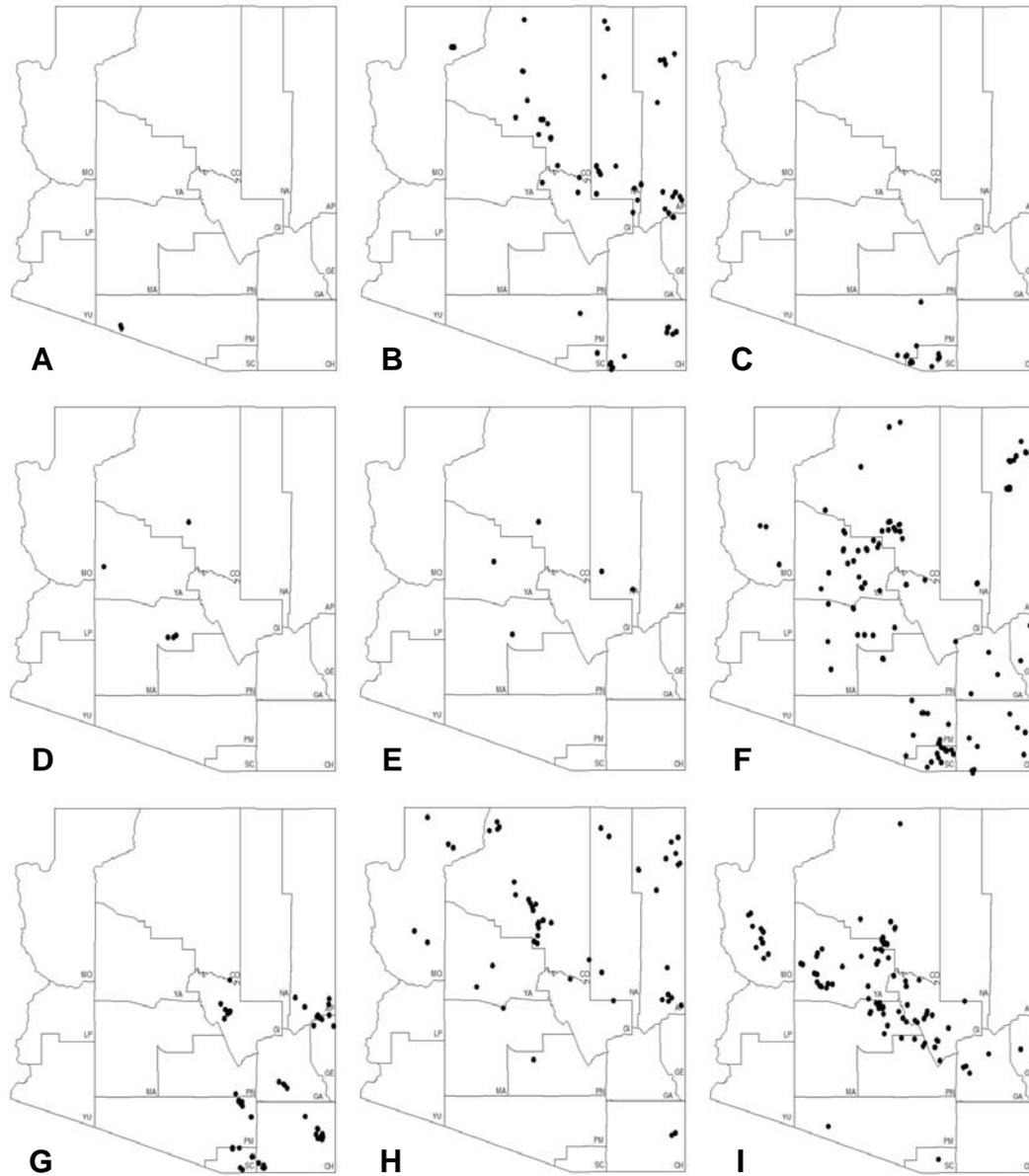
SORIA, J.V. and C.B. HEISER, Jr. 1961. A statistical study of relationships of certain species of the *Solanum nigrum* complex. *Economic Botany* 15: 245–255.

STEBBINS, L G. and E.F. PADDOCK. 1949. The *Solanum nigrum* complex in Pacific North America. *Madrono* 10: 70–81.

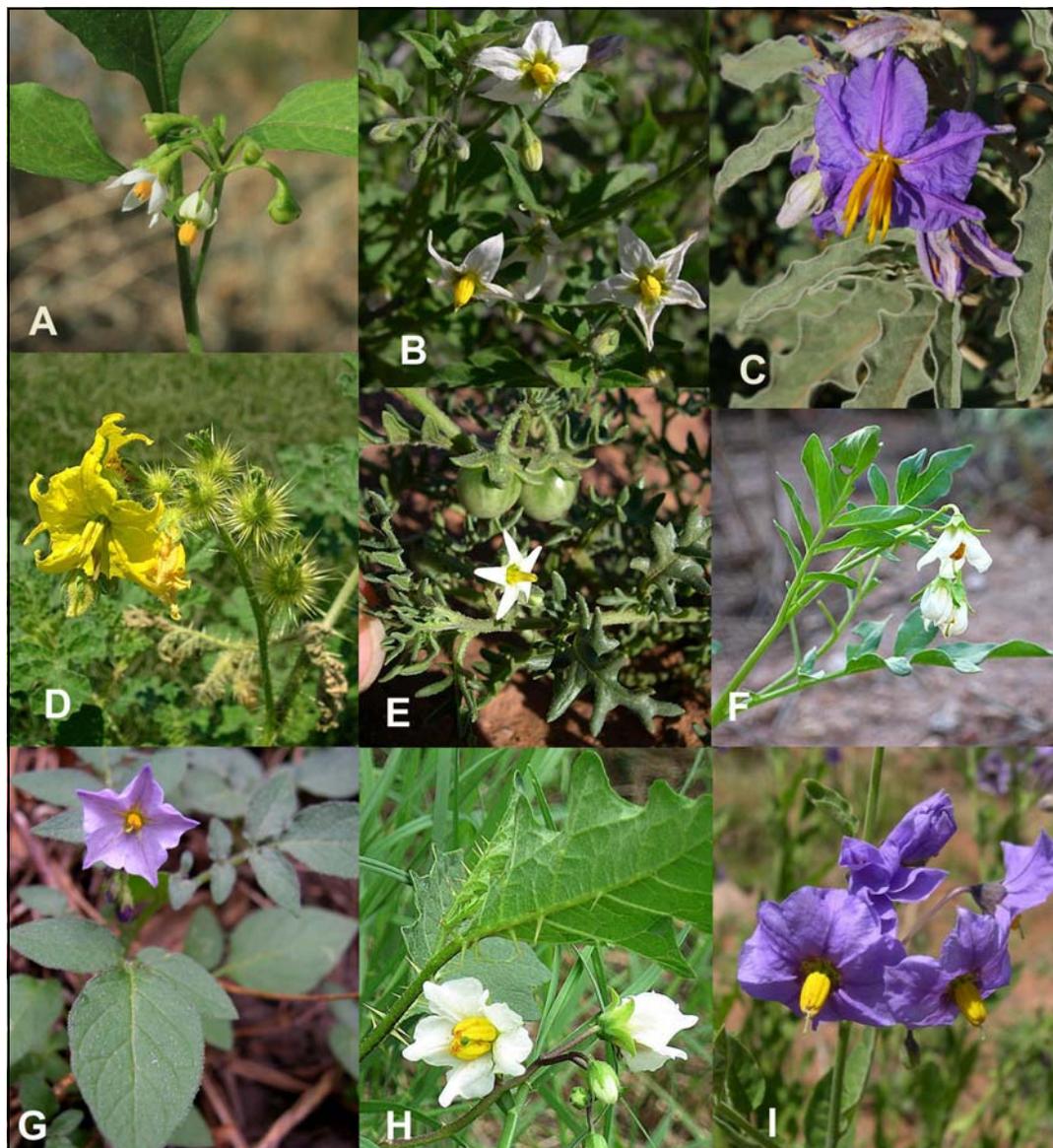
WHALEN, M.D. 1979. Taxonomy of *Solanum* Section *Androceras*. *Gentes Herbarium* 11: 1–465.



Solanaceae Figure 1. Distribution of: (A) *Solanum adscendens*; (B) *Solanum americanum*; (C) *Solanum carolinense*; (D) *Solanum douglasii*; (E) *Solanum elaeagnifolium*; (F) *Solanum heterodoxum*.



Solanaceae Figure 2. Distribution of: (A) *Solanum hindsianum*; (B) *Solanum jamesii*; (C) *Solanum lumholtzianum*; (D) *Solanum lycopersicum*; (E) *Solanum physalifolium*; (F) *Solanum rostratum*; (G) *Solanum stoloniferum*; (H) *Solanum triflorum*; (I) *Solanum xanti*.



Solanaceae Figure 3. *Solanum* species in flower. (A) *Solanum americanum*; (B) *Solanum douglasii*; (C) *Solanum elaeagnifolium*; (D) *Solanum rostratum*; (E) *Solanum triflorum*; (F) *Solanum jamesii*; (G) *Solanum stoloniferum*; (H) *Solanum carolinense*; (I) *Solanum xanti* (Photos B, D, E, G, & I by Max Licher; A, C & F by Elizabeth Makings; and H by Raul Gutierrez).