

THE GENUS *PHYSALIS* (SOLANACEAE) IN THE
SOUTHEASTERN UNITED STATES

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ABSTRACT. Keys and descriptions are presented for the 16 species of *Physalis* (Solanaceae) commonly found growing without cultivation in the southeastern United States, as well as for two cultivated species that sometimes escape and persist in disturbed habitats. The study was initiated as part of the Southeast Flora Project, and will ultimately be incorporated into the treatment of the genus for the *Flora of North America*.

Key Words: *Physalis*, Solanaceae, southeastern United States, floristics

The treatment of *Physalis* (Solanaceae) for the southeastern United States was written originally in the early 1980s as a contribution to the Southeast Flora Project, based at the University of North Carolina in Chapel Hill. The ultimate goal of the project was the publication of a revised and updated *Vascular Flora of the Southeastern United States*. In the mid-1980s, the Flora North America Project (FNA) was launched, and many state and regional flora projects were put aside in anticipation of a larger, more comprehensive *Flora of North America*. Although several volumes of this work have been published to date, the volume in which the Solanaceae is to be included will not be in print for several years.

More than a decade ago, the Solanaceae editor for the Southeast Flora Project encouraged me to publish my keys and descriptions of southeastern *Physalis* in order to make the treatment widely available. Since the first draft of this treatment was prepared, I have examined and annotated many additional specimens as part of my research for the Flora North America Project. In addition, some questions pertaining to issues of nomenclature have been resolved. The draft of the original document had been circulated to colleagues in the southeastern U.S., and some of their suggestions have been incorporated, as well. It is my hope that this publication will elicit constructive feedback on the utility of the work for systematists, ecologists, and field biologists, as well as encouraging research on some of the taxa that remain problematic.

For the purpose of the Southeast Flora Project, the southeastern U.S. was defined as encompassing the forested region west to the prairie and north to the terminal moraines. Thus, the region includes Delaware, Maryland, Virginia, North Carolina, South Carolina, Georgia, Florida, Alabama, Mississippi, Louisiana, Arkansas, Tennessee, Kentucky, and West Virginia, with notation of presence in the adjacent states of Texas, Oklahoma, Missouri, Illinois, Indiana, Ohio, Pennsylvania, and New Jersey (from the *Revised Contributors' Guide for the Vascular Flora of the Southeastern United States*, January 1981). As described by the editorial board in the goals of the project, the treatment presented here includes keys, descriptions, habitat and distributional data, and pertinent synonymy for all species of *Physalis* growing without cultivation in the southeastern U.S. It is based entirely on herbarium material borrowed from AUA, CLEMS, DUKE, FLAS, FSU, GA, KNK, LSU, MARY, MEM, MISS, MUR, NCSC, NCU, NLU, PH, SMU, TENN, UARK, UNA, USCH, USF, VPI, and WVA during the early 1980s, specimens borrowed from additional herbaria as part of FNA, and new collections and field observations of the author.

Two non-native species have been included in the key, and full descriptions have been provided. Because the members of *Physalis* are "weedy" and tend to occur in disturbed habitats, it may be difficult for the collector to determine whether a plant is native or not. Both *P. alkekengi* (Chinese Lantern Plant) and *P. philadelphica* (Tomatillo) were represented in herbaria in low numbers, however collection label data indicated that the plants were established and persisting in thickets, fence rows, and along streambanks as well as more obviously cultivated ground such as yards and edges of cultivated fields. Another species, *P. peruviana* L. (Cape Gooseberry) was not included because it was seen only from garden collections and apparently either does not escape or does not persist outside of cultivation. *Physalis peruviana* would be most easy to confuse with *P. heterophylla* except that, in the former species, plants do not become decumbent nor are they glandular, the pedicels are shorter (6–8 mm vs. 9–20 mm in flower; 13–15 mm vs. 20–30 mm in fruit), the anthers are usually blue or blue-tinged, and the filaments are slender.

Two additional species were not included in the key because only a few collections were seen that were weeds in cultivated fields or weeds persisting in previously cultivated ground. The first, *Physalis acutifolia* (Miers) Sandwith, is native to the southwestern U.S. and looks most similar to *P. angulata*. Vegetatively, it can not be distinguished from the narrowest-leaved representatives of that species, even in the field. *Physalis acutifolia* is distinctive in having flowering pedicels 15–40 mm long, a widely flaring corolla limb, and a slightly smaller fruiting calyx that is

nearly filled by the mature berry. *Physalis acutifolia* was seen as only a few collections from a previously cultivated area in Mississippi. The second species, *P. lagascae* Roem. & Schult., is native to the Neotropics. Several collections were seen from Louisiana and Mississippi that were weeds in sugarcane fields or associated areas. *Physalis lagascae* is an annual; the main stem is often decumbent and the lower branches trail along the ground; the leaves are small (2–4 cm long, 0.5–2 cm wide), sparsely pubescent to glabrate, ovate, with entire or irregularly dentate margins; the flowers are small (calyx 3–4 mm long; corolla 4–7 mm long) and have short pedicels (2–5 mm long); the fruiting calyx is small (1–2 cm long, 1–2 cm wide), 10-angled, rounded at base, with a short pedicel (3–6 mm long).

Some *Physalis* species are geographically wide-ranging and have a high degree of morphological variation. For *P. heterophylla* and *P. pubescens*, this variation has been recognized taxonomically (e.g., Small 1933; Waterfall 1958); those varieties have not been recognized here because they could not be correlated with environmental or geographic factors. More detailed study may result in a better understanding of the basis of variation in these taxa. Comprehensive studies of some other taxa, involving a combination of field, herbarium, and laboratory analyses, have resulted in increased insight and revised taxonomy (Hinton 1970, 1976; Sullivan 1985). Because floral morphology is fairly uniform in the genus, where related taxa occur in close proximity hybridization may occur (Hinton 1975; Sullivan 1984, 1985).

In the following treatment, all descriptions have been generated from herbarium specimens and field work. Physiographic provinces are given as follows: Coastal Plain (including Atlantic C.P., Gulf C.P., and Mississippi Embayment), Piedmont (including Piedmont Plateau and Interior Low Plateau) and Mountains (including Blue Ridge, Ridge and Valley, Cumberland Plateau, Allegheny Plateau, Ozarks, and Ouachitas), as outlined in the *Revised Contributors' Guide for the Vascular Flora of the Southeastern United States*, January 1981 (their designations follow Fenneman 1938).

PHYSALIS L., GROUND CHERRY

Annual or rhizomatous perennial herbs. Stems erect or weakly decumbent; branched; glabrous to densely pubescent. Leaves simple, alternate or falsely opposite. Leaf blade lanceolate to broadly ovate; glabrous to densely pubescent; apex acuminate to blunt; margins entire to dentate; base unequal, truncate-cordate to rounded-attenuate; petiolate or sessile. Flowers perfect; radially symmetrical; in all but one species

solitary in leaf axils; pedicellate; pendant. Calyx campanulate; enlarged and inflated in fruit, becoming reticulate-membranous and bladder-like, completely enclosing the berry; lobes 5, connivent, scarcely enlarged in fruit. Corolla 5-angulate or obscurely 5-lobed; yellow or white, often with 5 darker spots or smudges in the throat; campanulate-rotate; plicate in bud. Stamens 5; yellow, blue, or tinged blue or purple; inserted near the base of the corolla tube; anther sacs opening longitudinally. Ovary 2-celled; style elongate, slender; stigma minute. Fruit an edible, juicy berry; green, orange, or purple; in all but one species enclosed within the inflated fruiting calyx. Seeds numerous; light brown; reniform, flattened; surface finely pitted; ca. 2 mm long.

About 75 species worldwide, primarily in the Neotropics. Species boundaries are sometimes poorly defined. Some specimens are difficult to determine from preserved material, and field knowledge of the plants is essential. Several species are cultivated for ornament or food; garden escapes can persist for several years.

KEY TO SPECIES OF *PHYSALIS* IN THE SOUTHEASTERN U.S.

1. Flowers 2 or more per leaf axil; berries with spherical seed-like bodies among the flattened, reniform seeds 1. *P. carpenteri*
1. Flowers solitary in leaf axils; berries with flattened, reniform seeds only (2)
 2. Fruiting calyx red, retaining color on drying; corolla white 2. *P. alkekengi*
 2. Fruiting calyx green or orange, drying brown; corolla yellow, often with 5 large spots or smudges in throat (3)
 3. Anthers strongly coiled after dehiscence, blue; corolla throat tinged blue; berry the size of a cherry tomato or slightly larger, pale green or purple-streaked 3. *P. philadelphica*
 3. Anthers not coiled after dehiscence, yellow, blue, or purple; corolla throat purple, brown, green, or ochre; berry small and orange, yellowish or green (4)
 4. Leaves glabrous or nearly so (5)
 5. Flowering calyx typically 6 mm or more long; perennial from deeply buried rhizome (6)
 6. Pedicel glabrous or rarely sparsely pubescent with dendroid-stelliform hairs; leaves sessile, blade narrowly spatulate to linear-lanceolate 4. *P. angustifolia*
 6. Pedicel sparsely pubescent with unbranched, antrorse hairs; leaves petiolate, blade broadly

- ovate to broadly lanceolate
 5. *P. longifolia*
5. Flowering calyx typically 6 mm or less long; annual
 from taproot (7)
7. Corolla throat with 5 large, dark purple-black spots
 or smudges, visible through the dried, pressed
 tissue; fruiting calyx sharply 5-angled (8)
8. Leaf margin entire or dentate with fewer than 8
 teeth per side; fruiting pedicel 15 mm or less
 long 6. *P. pubescens*
8. Leaf margin dentate with 8 or more teeth per
 side; fruiting pedicel mostly 15 mm or more
 long 7. *P. cordata*
7. Corolla throat yellow or only tinged purple; fruiting
 calyx 10-angled (9)
9. Calyx and young stems with glandular hairs;
 flowering pedicel 4–7 mm long; fruiting
 pedicel 5–10 mm long
 8. *P. missouriensis*
9. Calyx and young stems glabrous or sparsely
 pubescent with non-glandular hairs; flower-
 ing pedicel 7–17 mm long; fruiting pedicel
 15–30 mm long 9. *P. angulata*
4. Leaves pubescent (10)
10. Hairs forked, 2–3 branched, or dendroid-stelliform, in
 some species intermixed with simple hairs
 (11)
11. Calyx hispid; hairs stiff, 2–3 branched intermixed
 with unbranched, at least some of which are as
 long as 1–1.5 mm long 10. *P. pumila*
11. Calyx tomentose or sparsely pubescent; hairs soft,
 branching 3 or more times, less than 1 mm
 long, sometimes intermixed with soft, 2–4 mm
 long, branched or unbranched hairs (12)
12. Flowering calyx and abaxial leaf surface white-
 tomentose, hairs obscuring plant surface or
 nearly so; hairs branched, 1 mm or less long,
 in some populations intermixed with 2–4
 mm long, branched or unbranched hairs on
 the stem and calyx 11. *P. mollis*

12. Flowering calyx and abaxial leaf surface sparsely to densely pubescent, hairs not obscuring plant surface; hairs branched, 1 mm or less long only (13)
13. Anthers 1.5× or more longer than the mature filaments; fruiting pedicel mostly 1.5× or more longer than the fruiting calyx; leaf margin dentate, sinuate, or entire 12. *P. cinerascens*
13. Anthers equal to or shorter than the elongated filaments; fruiting pedicel mostly equal to or shorter than the fruiting calyx; leaf margin entire 13. *P. walteri*
10. Hairs all unbranched (14)
14. Flowering calyx typically 6 mm long or less; annual from taproot (15)
15. Corolla throat with 5 large, dark, purple-black spots or smudges, visible through pressed, dried tissue; fruiting calyx sharply 5-angled (16)
16. Stems glabrous or sparsely pubescent with appressed, non-glandular hairs; fruiting calyx glabrous 7. *P. cordata*
16. Stems densely viscid-pubescent with divergent hairs to almost glabrous; fruiting calyx pubescent (17)
17. Leaf blades gray-green, drying orange or with orange patches, margins dentate; pubescence 0.5–1 mm on stems, glands sessile or short-stalked 14. *P. grisea*
17. Leaf blades green, drying green, margins entire to dentate; pubescence less than 0.5 mm, glandular or not 6. *P. pubescens*
15. Corolla throat yellow or only tinged purple; fruiting calyx 10-angled (18)
18. Calyx and young stems sparsely to densely pubescent with intermixed glandular and non-glandular hairs; flowering

- pedicel 4–7 mm long; fruiting pedicel 5–10 mm long 8. *P. missouriensis*
18. Calyx and young stems glabrous or only sparsely pubescent with non-glandular hairs; flowering pedicel 7–17 mm long; fruiting pedicel 15–30 mm long
 9. *P. angulata*
14. Flowering calyx typically 6 mm long or more; perennial from deeply buried rhizome . . . (19)
19. Leaf blade broadly ovate to sub-orbicular; base rounded truncate, or sub-cordate; plants glandular or non-glandular (20)
20. Stems densely villous, hairs divergent, 1–2 mm long, often intermixed with shorter glandular hairs; rhizomes stout and deeply buried 15. *P. heterophylla*
20. Stems glabrous to villous, hairs appressed, shorter than 1 mm, sometimes intermixed with 1–2 mm long, divergent hairs or shorter glandular hairs; rhizomes slender and typically shallow
 16. *P. arenicola*
19. Leaf blade narrowly ovate to broadly lanceolate or oblanceolate; base attenuate (21)
21. Pedicel and flowering calyx glabrous or sparsely pubescent; hairs less than 0.5 mm long, antrorse 5. *P. longifolia*
21. Pedicel and flowering calyx densely pubescent with divergent hairs that are 1–1.5 mm long, intermixed with antrorse or retrorse hairs that are less than 0.5 mm long (22)
22. Leaves oblanceolate with entire margins; pedicel and flowering calyx with both divergent and antrorse hairs
 17. *P. lanceolata*
22. Leaves ovate to broadly lanceolate with dentate margins; pedicel and flowering calyx with both divergent and retrorse hairs 18. *P. virginiana*

1. *Physalis carpenteri* Riddell ex Rydb.

Perennial, 6–10 dm tall, from a stout rhizome. Stems erect, branching frequently, the branches divergent; pubescent with simple, jointed hairs of varying lengths. Leaf blades ovate to ovate-lanceolate; 5–10 (–14) cm long, 3–6 (–9) cm wide; puberulous; apex acuminate; margins entire or rarely coarsely and irregularly dentate; base truncate to rounded; petiole 1/4–1/2 blade length. Flowers 2 or more in leaf axils. Flowering calyx 4.5–7.5 mm long, sparsely pubescent; lobes 1.5–3.5 mm long, typically unequal; pedicel 5–10 mm long. Corolla pale yellow, with 5 pale brown or green smudges in throat; 8–12 mm long. Anthers yellow, 1.5–2.5 mm long; filament less than 1/2 as wide as anther. Fruiting calyx green, only slightly inflated, 10-angled, base rounded; 1–2 cm long, 1–2 cm in diameter; pedicel 5–15 mm long. Spherical, seed-like bodies interspersed with the seeds. ($n = 12$) Flowering mid-June to early September.

This species is found in moist sand or clay soils, in hardwood and mixed pine-hardwood forests, near rivers, and disturbed habitats such as roadsides and waste areas in the Coastal Plain Province. Specimens were seen from Florida, Louisiana, and Mississippi.

Physalis carpenteri is very different from the other members of the genus in having clustered flowers, apparently due to the presence of a telescoped axillary branch (Waterfall 1958). In a recent infrageneric study based on morphology and chloroplast DNA, Martínez (1999) showed *P. carpenteri* to be part of a monophyletic *Physalis*. One sheet examined notes the species to be an annual, but the large underground portion of the specimens examined appears similar to the rhizomes of perennial taxa. Many specimens include only the upper branches, and despite attempts to re-locate populations documented by herbarium specimens, I have not seen this species in the field.

2. *Physalis alkekengi* L. (Chinese Lantern Plant)

Perennial, 3–9 dm tall, from a stout rhizome. Stems erect, usually unbranched; glabrous or sparsely hairy with simple, short, divergent hairs. Leaf blades broadly ovate; 6–11 cm long, 4–8.5 cm wide; glabrous to sparsely pubescent; apex acute; margins entire or irregularly dentate; base truncate to subcordate; petiole 1/10–2/5 blade length. Flowers solitary in leaf axils. Flowering calyx 4–7 mm long, tomentose with long, simple hairs; lobes 2–3.5 mm long; pedicel 9–13 mm long. Corolla white, without darker spots or smudges in the throat; 10–15 mm long. Anthers yellow, 2.5–3 mm long; filaments less than 1/2 as wide as anthers. Fruiting calyx reddish or bright red, 10-angled, base sunken; 3–5.5 cm long, 2.5–4.5 cm in diameter; pedicel 20–40 mm long. ($n = 12$) Flowering in June.

This species is a native of Europe that is often grown for its ornamental fruiting calyx and then locally spread from cultivation. In my New Hampshire garden, *Physalis alkekengi* spreads aggressively by vegetative means and no viable seeds have been produced. However, habitats mentioned on collection labels were fence rows, thickets, vacant lots, roadsides, and streambanks, more likely indications of reproduction by seed. Only about 12 specimens were seen, mostly from northern states of the region such as Maryland, Tennessee, Virginia, and West Virginia [one specimen from adjacent Pennsylvania].

3. *Physalis philadelphica* Lam. (Tomatillo)

Annual, 1.5–10 dm tall, from a slender taproot. Stems erect, branching, the upper branches divergent; glabrous to sparsely hairy with simple, short, appressed hairs. Leaf blades ovate to ovate-lanceolate; 2–7 cm long, 2–4 cm wide; glabrous or sparsely hairy; apex acuminate; margins dentate to entire; base rounded to attenuate; petiole 1/2 to as long as blade. Flowers solitary in leaf axils. Flowering calyx 5–7 (–10) mm long, sparsely vestite to glabrous; lobes 2–4 mm long; pedicel 3–6 mm long. Corolla yellow, with 5 blue-tinged spots or smudges in throat; 7–15 mm long. Anthers blue, strongly twisted after dehiscence, 3 mm long; filaments about 1/2 as wide as anthers. Fruiting calyx green, nearly filled or often burst by the viscid pale green to purplish or purple-streaked berry, 10-angled, sunken at base; 2–3 cm long, 2–3 cm in diameter; pedicel 3–8 (–11) mm long. ($n = 12$) Flowering all year in areas without frost.

This species has been introduced from the southwest and Mexico. It is cultivated for its fruits, which are commonly used in salsa. The species escapes frequently and becomes established in disturbed sites such as fence rows, edges of cultivated fields, and along roadsides. Only about 10 specimens were seen, mostly from northern states of the region such as Maryland, Tennessee, Virginia, and West Virginia [one specimen from adjacent Illinois].

4. *Physalis angustifolia* Nutt.

Perennial, 1.5–6 dm tall, from a deeply buried rhizome, often also with slender, shallow rhizomes. Stems and lower branches erect or spreading along the ground and ascending; glabrous. Leaf blades narrowly spatulate to linear-lanceolate; 3–10 (–12) cm long, 0.2–1.5 (–2) cm wide; glabrous or with sparse, branched hairs on the margins; apex obtuse to acute; margins entire; base tapering to stem; sessile. Flowers

solitary in leaf axils. Flowering calyx 5–9 (–10) mm long, glabrous except for the margins or, occasionally entire calyx sparsely pubescent with dendroid-stelliform hairs; lobes (1–) 1.5–3.5 mm long; pedicel 11–24 (–32) mm long. Corolla yellow, with 5 ochre to green smudges in throat, the main vein of each corolla lobe often purple to red; (8–) 11–15 (–16) mm long. Anthers yellow, 2.5–3.5 mm long; filaments 1/2 to as wide as anthers. Fruiting calyx typically orange when ripe but drying brown, 10-angled, sunken at base; (1.5–) 2–3 (–4) cm long, 1.5–2.5 cm in diameter; pedicel 15–35 (–42) mm long. ($n = 12$) Flowering all year in areas without frost.

This species is found on beach dunes, edges of pine woods, and disturbed coastal areas in sand in the Gulf Coastal Plain Province. Specimens were seen from Alabama, Florida, Louisiana, and Mississippi.

Physalis angustifolia hybridizes with *P. walteri* in disturbed, sandy habitats of peninsular Florida and populations can be found in the state that exhibit intermediate floral and vegetative characteristics. Waterfall (1958) recognized these intermediates as forms of a broadly defined *P. viscosa* (*P. viscosa* var. *elliottii* f. *elliottii* and f. *glabra*). *Physalis angustifolia* and its relationship to the members of the genus with dendroid-stelliform hairs were examined in detail by Sullivan (1985).

5. *Physalis longifolia* Nutt.

Perennial, 2–6 dm tall, from a stout, deeply buried rhizome. Stems erect, branching frequently on upper portions of plant; glabrous to sparsely hairy with short, simple, antrorse hairs, 0.5 mm or less long. Leaf blades ovate to ovate-lanceolate or broadly lanceolate; 2.5–10 (–13) cm long, 1–6 (–7) cm wide; glabrous or sparsely strigose with short, antrorse hairs; apex acute; margins entire to coarsely dentate with only a few teeth; base truncate to rounded; petiole 1/5–2/5 blade length. Flowers solitary in leaf axils. Flowering calyx (5–) 7–12 (–15) mm long, sparsely strigose with short, antrorse hairs; lobes 3–6 mm long; pedicel 5–20 mm long. Corolla yellow, with 5 purple-brown smudges in throat; 10–20 mm long. Anthers yellow or tinged blue, 2–4 mm long; filaments as wide as or wider than anthers. Fruiting calyx green, 10-angled, rounded or only slightly sunken at base; 2–4 cm long, 1.5–3 cm in diameter; pedicel 15–35 mm long. ($n = 12$) Flowering May through October.

In the past, this species has been aligned with *Physalis virginiana* (Waterfall 1958) and morphological variation has been given taxonomic recognition. More recent assessment has favored the recognition of

P. longifolia as a distinct species. This, as well as the recognition of a morphological and geographically based variant, var. *subglabrata*, is supported by my field observations and survey of herbarium specimens. The typical variety is more common in the central U.S. and has narrower leaves that are slightly more pubescent. Anther color further serves to distinguish the two reliably.

Leaf blades lanceolate; anthers yellow 5a. var. *longifolia*
 Leaf blades ovate to ovate-lanceolate; anthers tinged blue
 5b. var. *subglabrata*

5a. var. *longifolia*

Leaf blades 2.5–7.5 cm long, 0.5–2.5 cm wide. Flowering pedicel 5–14 mm long. Corolla 9–13 mm long. This is a variety typically of the prairie region of the central U.S. In the Southeast, specimens can be found in fields, open woods, sandy areas, and disturbed sites, primarily in the Ozark Plateau and Arkansas Valley. Specimens have been seen from Arkansas and Mississippi [also from adjacent Missouri, Oklahoma, and Texas].

5b. var. *subglabrata* (Mack. & Bush) Cronquist

Leaf blades 3.5–10 cm long, 2–6 cm wide. Flowering pedicel 8–18 mm long. Corolla 10–18 mm long. This variety is found in open woods, fields, river bottoms, and disturbed habitats such as roadsides and cultivated sites in all provinces. Specimens have been seen from all states in the region [also from adjacent Illinois, Indiana, Missouri, New Jersey, Ohio, Oklahoma, and Pennsylvania].

Synonym: *Physalis virginiana* var. *subglabrata* (Mack. & Bush) Waterf. (Radford et al. 1968).

6. *Physalis pubescens* L.

Annual, 0.5–8 dm tall, from a slender taproot. Stems erect, branching frequently, the branches divergent; glabrous to villous with simple, jointed, glandular hairs of varying lengths, all shorter than 0.5 mm long. Leaf blades broadly ovate to orbicular; 2.5–8 cm long, 2–7 cm wide; villous with glandular hairs to almost glabrous; apex acute to short-acuminate; margins coarsely dentate with only a few teeth (fewer than 10 per side) or entire; base rounded; petiole from 1/5 to as long as blade. Flowers solitary in leaf axils. Flowering calyx 3–6 mm long, villous to almost glabrous; lobes 1–3.5 mm long; pedicel 3.5–9 mm long. Corolla yellow, with 5 large, dark purple-brown spots in throat; 6–11 mm long.

Anthers blue or rarely only tinged blue, 1–2 mm long; filaments as wide as anthers. Fruiting calyx green, sharply 5-angled, base sunken; 2–3 cm long, 1.5–2.5 cm in diameter; pedicel 6–15 mm long. ($n = 12$) Flowering all year in areas without frost.

This species is found in fields, pastures, hammocks, low woods, edges of swamps, riverbanks, and disturbed habitats such as roadsides and waste ground in all provinces. Specimens have been seen from all states in the region, as well as all adjacent states.

Synonym: *Physalis pubescens* var. *glabra* (Michx.) Waterf., in part (Radford et al. 1968).

In the past, this species has been broadly defined to include *Physalis cordata* and *P. grisea*, and several morphological variants have been recognized (e.g., Gleason and Cronquist 1991; Waterfall 1958). More recent taxonomic opinion favors the recognition of *P. cordata* and *P. grisea* as distinct morphological species. *Physalis pubescens*, as treated here, includes both var. *pubescens* and var. *integrifolia* (Dunal) Waterf. without taxonomic recognition of varieties. In my field observations and survey of herbarium specimens, morphological intergradation was seen in all characteristics and no geographic or habitat distinction could be discerned between them. A systematic study focused on the variation in this and related species may provide insight into the nature of the variation observed.

7. *Physalis cordata* Mill.

Annual, 1.5–5 dm tall, from a slender taproot. Stems erect, branching frequently; glabrous or sparsely hairy with simple, appressed hairs that are less than 0.5 mm long. Leaf blades broadly ovate to orbicular; 4.5–8.5 cm long, 3.5–7.5 cm wide; glabrous except for sparse hairs on veins; apex acuminate; margins coarsely dentate with 10 or more teeth per side; base rounded to truncate or cordate; petiole $2/3$ to as long as blade. Flowers solitary in leaf axils. Flowering calyx 3.5–6.5 mm long, glabrous or very sparsely hairy; lobes 2–4.5 mm long; pedicel (4.5–) 6–11 mm long. Corolla yellow, with 5 large purple-brown spots in throat; 6.5–9.5 mm long. Anthers blue or blue-tinged, 1.5–2.5 mm long; filaments as wide as anthers. Fruiting calyx green, glabrous, sharply 5-angled, sunken at base; (2.5–) 3–4 cm long, 2–3 cm in diameter; pedicel (10–) 15–35 mm long. Flowering July through October.

This species is found primarily in sandy soils, along rivers, in pine woods, and in disturbed habitats such as yards and fields, chiefly in the Coastal Plain Province but also from the Piedmont in Tennessee and Mountain Provinces in Arkansas. Specimens have been seen from

Alabama, Arkansas, Florida, Georgia, Louisiana, Mississippi, North Carolina, South Carolina, and Tennessee [also from adjacent Oklahoma and Texas].

Synonym: *Physalis pubescens* var. *glabra* (Michx.) Waterf., in part (Radford et al. 1968).

Physalis cordata is quite distinctive, morphologically. It can be distinguished from *P. pubescens*, with which it has been considered conspecific, by the large, coarse teeth on its leaf margins and its long fruiting pedicels. Any systematic study of *P. pubescens* should include *P. cordata*, in order to better understand the relationship between these two taxa.

8. *Physalis missouriensis* Mack. & Bush

Annual, 1.5–5.5 dm tall, from a slender taproot. Stems erect, branching frequently; sparsely to densely pubescent with simple, jointed, glandular and non-glandular hairs that are less than 0.5 mm long. Leaf blades broadly ovate to orbicular; 2.5–5.5 cm long, 1.5–5 cm wide; sparsely glandular-pubescent; apex acute; margins irregularly and shallowly dentate; base rounded or sometimes truncate; petiole $\frac{2}{5}$ to as long as blade. Flowers solitary in leaf axils. Flowering calyx 2.5–4 mm long, densely glandular-pubescent; lobes 1–2 mm long; pedicel 4–7 mm long. Corolla yellow, without darker spots or smudges in throat; 5–7 mm long. Anthers yellow, 1–1.5 mm long; filaments less than $\frac{1}{2}$ as wide as anthers. Fruiting calyx green, densely glandular-hairy, 10-angled, rounded or only very slightly sunken at base; 1–2 cm long, 1–2 cm in diameter; pedicel 5–10 mm long. Flowering June through August.

This species is found on rocky bluffs, dolomite ledges, cliffs, and wooded slopes on the Ozark Plateau. Specimens have been seen from Arkansas [also from adjacent Missouri and Oklahoma].

9. *Physalis angulata* L.

Annual, 1–20 dm tall, from a large taproot. Stems erect, branching frequently; glabrous or sparsely hairy with simple, jointed hairs that are 0.5 mm or less long. Leaf blades elliptic to linear-lanceolate; 3–10 (–14) cm long, 1–8 cm wide; glabrous to sparsely hairy; apex acuminate; margins deeply and coarsely irregularly dentate with acuminate teeth; base rounded to attenuate; petiole $\frac{1}{3}$ – $\frac{2}{3}$ blade length. Flowers solitary in leaf axils. Flowering calyx 3–5 mm long; sparsely hairy or glabrous except for margins; lobes 1–3 mm long; pedicel 7–17 (–22) mm long. Corolla yellow, without spots or smudges or only rarely tinged purple in throat; 6–10 mm long. Anthers blue or blue-tinged, 1–3 mm long;

filaments less than 1/2 as wide as anthers. Fruiting calyx green, 10-angled, only slightly sunken at base; 2–4 cm long, 1.5–2.5 cm in diameter; pedicel 15–30 mm long. ($n = 12, 24$) Flowering all year in areas without frost.

This species is found in hardwood and pine woods, woodland borders, sandhills, stream margins, edges of marshy areas, fields, pastures, and waste places, chiefly in the Coastal Plain and Piedmont Provinces. Specimens have been seen from Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, North Carolina, South Carolina, Tennessee, and Virginia [also from adjacent Illinois, Missouri, Oklahoma, and Texas].

Some plants in southern Florida have linear to lanceolate, sinuate leaf blades and very small flowers (corollas 4–5 mm long). These have been given taxonomic recognition in the past as *Physalis angulata* var. *pendula* Rydb. However, examination of over 1000 herbarium sheets revealed an intergradation of morphology between var. *angulata* and var. *pendula*, and no geographic or habitat distinction between the two. Another species, *P. acutifolia* (Miers) Sandwith, so closely resembles the narrow-leaved populations of *P. angulata* in vegetative characters that they could not be distinguished, even in the field. When in flower, *P. acutifolia* is distinctive in having flowering pedicels 15–40 mm long, a widely flaring corolla limb, and a slightly smaller fruiting calyx that is nearly filled by the mature berry. *Physalis acutifolia* is a species of the southwestern U.S., but specimens were seen from Bolivar County, Mississippi in an area that had been under cultivation previously.

10. *Physalis pumila* Nutt.

Perennial, 1.5–4 dm tall, from a stout deeply buried rhizome. Stems erect, branching infrequently at upper nodes, the branches ascending; hispid with jointed, simple and/or 2–3 branched hairs that are 0.5–2 mm long. Leaf blades ovate to ovate-lanceolate; 3–8 (–10) cm long, 2–5 cm wide; hispid; apex acute; margins entire to undulate, rarely sinuate-dentate; base attenuate; petiole 1/10–2/5 blade length. Flowers solitary in leaf axils. Flowering calyx 6–12 mm long, hispid; lobes (2.5–) 3–5 (–6) mm long; pedicel (7–) 14–30 mm long. Corolla yellow, tinged pale brown or green in throat but without distinct spots or smudges; 11–16 mm long. Anthers yellow, 2–3 mm long; filaments as wide as anthers. Fruiting calyx green, 10-angled, sunken at base; 2.5–3.5 (–4) cm long, 1.5–3 cm in diameter; pedicel 25–55 mm long. ($n = 12$) Flowering early March through September.

This species can be found in dry, rocky soil in prairies, fields, and disturbed habitats. A species chiefly of prairies in the central U.S. In the Southeast specimens have been seen from the Gulf Coastal Plain and Mountain Provinces of western Arkansas and Louisiana [also from adjacent Missouri, Oklahoma, and Texas].

11. *Physalis mollis* Nutt.

Perennial, 1.5–5 dm tall, from a stout, deeply buried rhizome, often also with slender, shallow rhizomes. Stems erect, branching occasionally, the branches ascending; tomentose with dendroid-stelliform hairs that are less than 1 mm long and obscuring the plant surface, occasionally also with 2–4 mm long jointed, dendroid-stelliform or unbranched hairs at lower nodes. Leaf blades ovate; 2.5–7 cm long, 1.5–6 (–7) cm wide; tomentose; apex acute; margins coarsely dentate or irregular to almost entire; base truncate; petiole 1/3–4/5 blade length. Flowers solitary in leaf axils. Flowering calyx 6–10 (–12) mm long, tomentose with short, dendroid-stelliform hairs, occasionally also with long, unbranched, jointed hairs; lobes 2.5–5.5 mm long; pedicel 10–25 (–35) mm long. Corolla yellow, with 5 pale brown to dark brown smudges in throat; 9.5–15 (–17) mm long. Anthers yellow or rarely with a blue or purple tinge, 3–4 mm long; filaments about 1/2 as wide as anthers. Fruiting calyx green, 10-angled, sunken at base; 2.5–4 (–5) cm long, 1.5–3 cm in diameter; pedicel 20–40 (–52) mm long. ($n = 12$) Flowering early March through October.

This species can be found in sandy soil in prairies, along roadsides, and disturbed habitats. Coastal Plain and Mountain Provinces. Specimens have been seen from Arkansas and Louisiana [also from adjacent Oklahoma and Texas]. Relationships among the *Physalis* species with dendroid-stelliform hairs were examined in detail by Sullivan (1985).

12. *Physalis cinerascens* (Dunal) Hitchc.

Perennial, 0.5–5 dm tall, from a large, deeply buried rhizome. Stems and lower branches erect or spreading along the ground and ascending; sparsely to moderately densely pubescent with dendroid-stelliform hairs that are 1 mm or less long. Leaf blades ovate to spatulate; 1.5–8 (–9) cm long, 1–6 (–8) cm wide; sparsely to moderately densely pubescent; apex acute or obtuse; margins coarsely dentate, sinuate, undulate, or entire; base truncate to attenuate; petiole 1/5 to as long as blade. Flowers solitary in leaf axils. Flowering calyx (3.5–) 5–9 mm long, pubescent; lobes 1.5–4 mm long; pedicel 10–33 mm long. Corolla yellow, with 5

dark purple-black spots in throat, these sometimes bisected by the yellow main veins of the corolla; (8–) 9–16 mm long. Anthers yellow or rarely with a purple tinge, 2–5 mm long; filaments 1/2 to as wide as anthers. Fruiting calyx green, 10-angled, sunken at base; 1.5–3.5 (–4.5) cm long, 1–3.5 cm in diameter; pedicel 15–60 mm long. ($n = 12$) Flowering all year in areas without frost.

Leaves ovate; leaf base truncate to slightly attenuate; leaf margins dentate, sinuate, or entire; corolla limb reflexed when fully open 12a. var. *cinerascens*

Leaves spatulate; leaf base attenuate; leaf margins entire; corolla limb not reflexed when fully open 12b. var. *spathulaefolia*

12a. var. *cinerascens*

Fruiting calyx 1.5–3 cm long, 1–2 cm in diameter, fruiting pedicel 15–60 mm long. This variety can be found in prairies, fields, roadsides, and disturbed habitats. Chiefly Coastal Plain. Specimens have been seen from Arkansas and Louisiana [also from adjacent Oklahoma and Texas]. This is a species primarily of the prairies and mountains in the south-central U.S., but occasionally it is found elsewhere in the Southeast. The pollination biology of *Physalis cinerascens* var. *cinerascens* has been described by Sullivan (1984, as *P. viscosa* var. *cinerascens*). The relationship between the two varieties of *P. cinerascens* was examined in detail by Sullivan (1985).

12b. var. *spathulaefolia* (Torr.) J.R. Sullivan

Fruiting calyx 2.5–4.5 cm long, (1.5–) 2–3.5 cm in diameter, fruiting pedicel 25–60 mm long. This variety is found on Gulf dunes and disturbed habitats near the Gulf Coast in sand. Specimens have been seen from Louisiana [also from adjacent Texas]. In the past, this taxon was considered to be more closely related to *Physalis walteri* (as varieties of *P. viscosa* subsp. *maritima*; Waterfall 1958). Both are taxa of coastal sand dunes and have similar vegetative morphology, which is eye-catching when working primarily with herbarium specimens. Relationships among the taxa with dendroid-stelliform hairs were examined in detail by Sullivan (1985).

13. *Physalis walteri* Nutt.

Perennial, 0.5–4 dm tall, from a stout and usually deeply buried rhizome. Stems and lower branches erect or spreading along the ground and ascending; sparsely to moderately densely covered with dendroid-stelliform hairs that are 1 mm or less long. Leaf blades elliptic or ovate

to ovate-lanceolate; (2.5–) 3.5–11 (–13) cm long, 1.5–5 (–7) cm wide; sparsely to moderately densely pubescent; apex obtuse or acute; margins entire or rarely undulate; base rounded to attenuate; petiole 1/6–1/2 blade length. Flowers solitary in leaf axils. Flowering calyx (5–) 6–9 (–11) mm long, pubescent; lobes 1.5–4 (–5) mm long; pedicel 9–25 (–35) mm long. Corolla yellow, with 5 dark brown to pale brown, ochre, or green spots or smudges in throat, the main veins of the corolla lobes sometimes purple or red; (9–) 11–15 (–18) mm long. Anthers yellow or infrequently tinged purple, 2.5–3.5 mm long; filaments as wide as anthers. Fruiting calyx green, 10-angled, sunken at base; 2–3.5 cm long, 1.5–2.5 cm in diameter; pedicel 15–35 (–45) mm long. ($n = 12$) Flowering all year in areas without frost.

This species is found on beach dunes and in disturbed areas in sand. Coastal Plain. Specimens have been seen from Alabama, Florida, Georgia, Mississippi, North Carolina, South Carolina, and Virginia.

Synonym: *Physalis viscosa* subsp. *maritima* (M.A. Curtis) Waterf. (Radford et al. 1968).

Physalis walteri hybridizes with *P. angustifolia* in disturbed, sandy habitats of peninsular Florida and populations can be found in the state that exhibit intermediate floral and vegetative characteristics. Waterfall (1958) recognized these intermediates as forms of a broadly defined *P. viscosa* (*P. viscosa* var. *elliottii* f. *elliottii* and f. *glabra*). Relationships among the members of the genus with dendroid-stelliform hairs were examined in detail by Sullivan (1985).

14. *Physalis grisea* (Waterf.) M. Martínez

Annual, 3–6 dm tall, from a large taproot. Stems erect, branching frequently, the branches spreading; villous with simple, jointed hairs that are 0.5–1 mm long. Leaf blades broadly ovate; 3.5–11 cm long, 2.5–10 cm wide; gray-green, drying orange or with orange patches; pubescence of short, simple hairs that are ca. 0.5 mm long intermixed with stalked glands that are much shorter than 0.5 mm long and sessile glands; apex acute; margins coarsely dentate; base broadly rounded to slightly cordate; petiole 2/5–4/5 blade length. Flowers solitary in leaf axils. Flowering calyx 3–5 mm long, short-pubescent; lobes 1.5–2.5 mm long; pedicel 4–6 mm long. Corolla yellow, with 5 large, dark purple-brown spots in throat; 5–8 mm long. Anthers blue or tinged blue, 1–2 mm long; filaments 1/2 as wide as anthers. Fruiting calyx green, sharply 5-angled, sunken at base; 2–3.5 cm long, 1.5–2.5 cm in diameter; pedicel 5–12 mm long. ($n = 12$) Flowering June through October.

This species is found in open areas such as meadows, pastures, disturbed woodlands and river bottoms, and cultivated sites. Chiefly Mountain and Piedmont Provinces. Specimens have been seen primarily from North Carolina, South Carolina, Tennessee, and West Virginia, but sporadically elsewhere in the Southeast [also from adjacent Ohio and Pennsylvania].

Synonym: *Physalis pubescens* var. *grisea* Waterf. (Gleason and Cronquist 1991; Radford et al. 1968).

Most specimens of this species were annotated by me as *Physalis pruinosa* L., based on synonymy given in Waterfall (1958). The application of that name has since been clarified by Martínez (1993), who determined that the correct name for our plants is *P. grisea*. *Physalis grisea* can be distinguished from *P. pubescens*, with which it has been considered conspecific, by the often larger leaves that have a distinctive gray-green color and exhibit orange patches on drying. Closer examination of the foliage of *P. grisea* reveals sessile or short-stalked glands as opposed to the glandular hairs of *P. pubescens*. Any systematic study of *P. pubescens* should include *P. grisea*, in order to better understand the relationship between these two taxa.

15. *Physalis heterophylla* Nees

Perennial, 1.5–10 dm tall, from a stout, deeply buried rhizome. Stems erect to decumbent, branching frequently, branches spreading along the ground and ascending; villous with simple, jointed, divergent hairs that are 1–2 mm long, often also with shorter, glandular hairs. Leaf blades broadly ovate to sub-orbicular; (3–) 4–11 (–13) cm long, 3–9 (–10) cm wide; villous and often glandular; apex acute; margins deeply and irregularly dentate to almost entire; base truncate to slightly cordate; petiole 1/3–2/3 blade length. Flowers solitary in leaf axils. Flowering calyx 6–12 mm long, villous and often glandular; lobes 3–6 mm long; pedicel 9–15 (–20) mm long. Corolla yellow, with 5 large purple-brown smudges in throat; 10–17 mm long. Anthers yellow or infrequently tinged blue, 2.5–4.5 mm long; filaments as wide as anthers and usually conspicuously clavate at apex. Fruiting calyx green, 10-angled, sunken at base; 2.5–4 cm long, 1.5–3 cm in diameter; pedicel 20–30 mm long. ($n = 12$) Flowering May through September.

This species is found in open hardwood forests, edges of pine woods, fields, roadsides, and disturbed sites, often in shade. This is a widespread species, and is found in all provinces. Specimens have been seen from all states in the region, as well as all adjacent states.

There is some morphological variation in this species, which in the past has been recognized taxonomically (Waterfall 1958). Varieties are not recognized here, since I found morphological intergradation between them and none could be identified reliably. Further study may provide insight into the nature of this variation. In 1975 Hinton reported the occurrence in North Carolina of a population representing a natural hybridization event between *Physalis heterophylla* and *P. virginiana*.

The cultivated *Physalis peruviana* L. (Cape Gooseberry) is similar to *P. heterophylla*. No specimens of this species were seen except for those from gardens, however. *Physalis peruviana* is an erect plant that is not glandular, the pedicels are shorter than those of *P. heterophylla* (6–8 mm in flower; 13–15 mm in fruit), the anthers are blue or blue-tinged, and the filaments are 1/2 as wide as the anthers.

16. *Physalis arenicola* Kearney

Perennial, 0.5–3 dm tall, from a slender, deeply buried rhizome, typically also with slender, shallow rhizomes. Stems erect, few-branched; glabrous to villous with simple, antrorse hairs that are less than 1 mm long, sometimes interspersed with 1–2 mm long, simple, jointed hairs, sometimes viscid. Leaf blades ovate to sub-orbicular; 1.5–6 (–6.5) cm long, 1–5 cm wide; villous with short, glandular and long, jointed hairs or rarely almost glabrous; apex acute; margins entire to coarsely and irregularly dentate with few teeth; base truncate to cordate; petiole 1/4–2/3 blade length. Flowers solitary in leaf axils. Flowering calyx 6–12 mm long, villous; lobes 2–5 mm long; pedicel (8–) 11–17 (–45) mm long. Corolla yellow, with 5 pale reddish-brown smudges in throat or without smudges; 10–17 mm long. Anthers yellow, 2.5–4 mm long; filaments 1/2 to as wide as anthers. Fruiting calyx green, 10-angled, slightly sunken at base; 2–3.5 cm long, 1.5–2.5 cm in diameter; pedicel 15–30 (–35) mm long. ($n = 12$) Flowering all year in areas without frost.

This species is found in sand or sandy soil in woods, hammocks, fields, pastures, and along roadsides. Coastal Plain. Specimens have been seen from Alabama, Florida, and Georgia.

Pressed specimens are sometimes difficult to distinguish from *Physalis heterophylla*. *Physalis heterophylla* is a widespread and morphologically variable species. The presence of slender, cord-like, shallow rhizomes and typically very short pubescence are distinctive for *P. arenicola*.

17. *Physalis lanceolata* Michx.

Perennial, 2–4 dm tall, from a large, stout rhizome. Stems decumbent, branching infrequently; sparsely pubescent with simple,

antrorse hairs that are 0.5 mm or less long, or with simple, jointed, divergent hairs that are 1–1.5 mm long. Leaf blades oblanceolate; 4–10 cm long, 2–6 cm wide; pubescent with short, appressed and long, divergent hairs; apex acute; margins entire to slightly undulate; base attenuate; petiole $1/25$ – $1/3$ blade length. Flowers solitary in leaf axils. Flowering calyx 6–10 mm long, hispid with long, jointed hairs; lobes 2–5 mm long; pedicel 10–20 mm long. Corolla yellow, with 5 pale brown smudges in throat; 10–15 mm long. Anthers yellow, 2.5–3.5 mm long; filaments $1/2$ as wide as anthers. Fruiting calyx green, 10-angled, scarcely sunken at base; 2–3.5 cm long, 1.5–3 cm in diameter; pedicel 10–30 mm long. ($n = 12$) Flowering April through September.

This species is found in sandhills, primarily in the Atlantic Coastal Plain, but also in some Piedmont counties in North Carolina. Specimens have been seen from Georgia, North Carolina, and South Carolina.

Southeastern U.S. plants ascribed to this species were considered by Waterfall (1958) to be hybrids between *Physalis heterophylla* and *P. virginiana*, but have since been shown to be a distinct species (Hinton 1970).

18. *Physalis virginiana* Mill.

Perennial, 1–4 dm tall, from a stout rhizome. Stems erect, branching infrequently; hispid with jointed, simple, divergent hairs that are ca. 1 mm long, and retrorse hairs that are 0.5 mm or less long. Leaf blades ovate to broadly lanceolate; 2–7 (–9) cm long, 1–5 (–6) cm wide; pubescent with long, jointed and short, retrorse hairs; apex acute; margins coarsely to shallowly dentate or entire; base truncate to obtuse; petiole $1/5$ – $1/2$ blade length. Flowers solitary in leaf axils. Flowering calyx 6–12 (–14) mm long, hispid with long, jointed and short, retrorse hairs; lobes 3–6 mm long; pedicel (6–) 9–19 (–27) mm long. Corolla yellow, with 5 dark purple-brown smudges in throat; 10–17 (–20) mm long. Anthers yellow or sometimes tinged blue, 2–3 mm long; filaments as wide as or wider than anthers. Fruiting calyx green, 10-angled, base sunken; 2–4 cm long, 1.5–3 cm in diameter; pedicel 15–30 mm long. ($n = 12$) Flowering April through October.

This species is found in prairies, fields, thickets, open woods, and disturbed habitats such as roadsides, cultivated ground, waste places, and along railroads. This is a species primarily of the Midwest and central plains states, but is found sporadically in the Southeast. Specimens have been seen from all states in the region, as well as all adjacent states.

In the past, *Physalis virginiana* has been treated in a broader sense, including *P. longifolia* (Waterfall 1958), and morphological variation has been given taxonomic recognition. More recent assessment has favored the recognition of *P. longifolia* as a distinct species. In 1975 Hinton reported the occurrence in North Carolina of a population representing a natural hybridization event between *P. virginiana* and *P. heterophylla*.

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