

**KEYS TO THE FLORA OF FLORIDA: 19,  
PHYSALIS (SOLANACEAE)**

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**ABSTRACT**

*Physalis* (Solanaceae) is represented in Florida by 13 species. Of these, 8 are native and 5 are believed introduced. Though some are rare, none is considered endangered. Two species (*P. arenicola*, *P. walteri*) are each formed of two varieties. ***Physalis walteri* var. *glabra*** is recognized as a new combination. *Physalis pubescens* var. *integrifolia* is here assigned specific rank, as ***Physalis integrifolia***, a new combination. *Physalis grisea*, *P. integrifolia*, *P. lanceifolia* and *P. turbinata* are newly reported for Florida. Two species reported for Florida are excluded. An amplified key is given to the Florida taxa.

**KEY WORDS:** *Physalis*, Solanaceae, Florida flora.

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The North American flora hardly contains a more difficult genus for its size than *Physalis*. -- Asa Gray, Proc. American Academy 10: 62. 1874.

The cautionary warning of Asa Gray has not deflected American scholars from efforts to understand the genus *Physalis* (Solanaceae) in North America. From the limited materials then available, Gray (1874) recognized 17 species. Per Axel Rydberg took up the task (Mem. Torrey Bot. Club 4: 297-374. 1896), with regional treatments contributed to J. K. Small's *Flora* (1903) and *Manual* (1933). A detailed, lifelong study by U. T. Waterfall (Rhodora 60: 107-114, 128-142, 152-173. 1958; *ibid.* 69: 82-120, 203-239, 319-329. 1967) documented 93 species and numerous varieties. In the 1940s, Margaret Y. Menzel began an extensive series of greenhouse crossing experiments (Proc. Amer. Philos. Soc. 95: 132-183. 1951; Yearb.

Amer. Philos. Soc. 1957: 262-266. 1957). In 1984, Janet R. Sullivan drafted a floristic review of the southeastern species (*Rhodora* 106: 305-326. 2004). The Florida species have been addressed by two highly useful guides: Andre F. Clewell (1985), who reported 8 species in the Florida panhandle; and Richard P. Wunderlin & Bruce F. Hansen (2003), who recognized 9 species from throughout the state.

The present synopsis treats 13 species of *Physalis* from within the state. The increase over the numbers reported by Clewell and Wunderlin & Hansen is caused, not by new introductions, but by variations that have long been known elsewhere (Mexico, mostly) and previously overlooked in Florida, now treated at specific rank.

The Florida species of *Physalis* are best understood when partitioned into sections (not necessarily nomenclaturally valid), as recognized by Menzel (1951). The "Carpenterianae" consists of a single species, the coastal plain endemic, *P. carpenteri*. This is separated morphologically by a unique clustering of flowers (rather than single) at each node, a condition described by Sullivan (2004) as perhaps representing a "telescoped axillary branch." Its habitat is similarly unique in that it seems restricted to small sites of disturbed soil, often on the loose materials pushed out from burrows of the gopher tortoise (*Gopherus polyphemus*). It has been suggested (Erdman West, pers. comm., 1962) that the tortoise would encounter, and surely feed upon, the fruits of this plant, then deposit its seeds on suitable loose soil surrounding the burrow. The food-source relationship of the tortoise with the Gopher Apple (*Licania michauxii*) has been documented (Castanea 64: 263-265. 1999), an alliance not yet shown with *P. carpenteri*. But the historic range of the gopher tortoise closely corresponds to the known range of the *Physalis*, permitting a long co-adaptation and perhaps co-evolution of these two rare species.

The "Viscosae" in Florida consists of at least two quite distinct, largely coastal species, with a probable hybrid intermediate in both morphology and range (Waterfall, 1958: 134-135; Menzel, 1951: 174). Species of this group have been carefully analyzed (Sullivan, Syst. Bot. 10: 426-444. 1985) and are now well understood. All are

sparsely to densely pubescent with stellate or radially branched hairs. *Physalis angustifolia*, with narrow, glabrous leaves, is quite frequent along the panhandle coastal dunes, then is disjunct to shores of the southernmost peninsula and keys. *Physalis walteri*, with broad, densely pubescent leaves, is more widespread, locally common from coastal Virginia into peninsular Florida.

The geographic distance between the two areas of *Physalis angustifolia* is almost precisely occupied by plants obviously related to these two species, an apparent hybrid, but with broad, glabrous leaves. Sullivan (1985: 439) found plants from these populations to be interfertile with similar flavonoid profiles. She followed Rydberg (1897) in weighing pubescence above leaf shape (rather than Waterfall, 1958), and thus placed the intermediate with *P. angustifolia* (rather than with *P. maritima*). Because of the nearly identical flavonoid profiles, Sullivan chose to leave the intermediate taxon unnamed.

But field experience is not content with this null assignment. For a long span of the Florida gulf coast, between Wakulla County in the eastern panhandle to Collier County in the southwest peninsula, a distance of 500 km., plants of the *angustifolia* - *maritima* complex are almost entirely of the intermediate form. These differences, sufficient to be recognized by any school child, merit nomenclatural recognition.

This intermediate form has long been known as *Physalis elliotii*, but Kunze's type for that name seems closer to typical *P. maritima* (Waterfall, 1958: 134). A name that clearly represents the intermediate is Waterfall's ponderous *Physalis viscosa* ssp. *maritima* var. *elliottii* forma *glabra* (1958: 135). Since Sullivan used Waterfall's "*glabra*" as her label (not in a formal nomenclatural sense) for plants of the intermediate form, it is appropriate that Waterfall's terminal epithet be retained. There is no prior varietal epithet for the taxon. The required new combination follows.

*Physalis walteri* Nuttall var. **glabra** (Waterfall) D. B. Ward,  
comb. et stat. nov. Basionym: *Physalis viscosa* L. ssp.

*maritima* (Nutt.) Waterfall var. *elliottii* (Kunze) Waterfall  
forma *glabra* Waterfall, Rhodora 60: 135. 1958.

The "Lanceolatae" in Florida, as elsewhere, are difficult to identify with confidence. Plants believed to be typical *Physalis virginiana* are found occasionally, but its var. *subglabrata*, common northward, and the other varieties recognized by Waterfall (1958: 152-156) seem not to reach the state. *Physalis arenicola* with two poorly distinguished varieties occur throughout the peninsula.

*Physalis heterophylla*, a species assumed by most writers to be a Florida species, was termed by Waterfall (1958: 140) "an extremely variable assemblage." Yet northeastern plants -- the type was from Pennsylvania -- are easily and consistently distinguished from Florida plants bearing that name. Rydberg (1903: 986) recognized that difference, and assigned the name *P. sinuata*. Rydberg's type (NY), a Chapman collection borrowed for this study, was of a plant with broadly ovate leaves and coarse low rounded teeth, well matching plants found in dry pinelands of the upper peninsula. The Florida plants exhibit a feature that has not been mentioned and which understandably disappears upon pressing -- the blades tend to be borne in a vertical plane. Though the distribution and characteristics of the Florida plants are scarcely now better known than by Rydberg, it has seemed prudent to call attention to their differences, by the use of his epithet.

The "Angulatae" in Florida are nearly all the broad-leaved typical *Physalis angulata*, found commonly through the state; its leaves are broadly ovate, coarsely dentate, and its flowers are of moderate size with green or brown centers, and bluish stamens. But in an area of the Everglades centered around Flamingo, plants have been known for many years with lanceolate sinuate-margined leaves, much smaller flowers with yellow centers, and yellow stamens. Authors have struggled with these anomalous plants, from Rydberg (1933: 1109) who noted them as an unnamed form under *P. angulata*, to Sullivan (2004: 318) who remarked on similarities with the western *P. acutifolia* (Miers) Sandw. Their true relationship, however, seems to be with a

Mexican plant, *P. lanceifolia*, not previously recognized to occur in Florida. The differences with *P. angulata* are quite sufficient to retain specific rank, rather than reduced by Waterfall (1967: 219) to *P. angulata* var. *lanceifolia*. Again, the distribution and characteristics of the Florida plants are poorly understood, and it may be found that variations within *P. angulata* are a consequence of introgression with this Mexican relative.

The "Pubescentes" in Florida seem entirely to be introduced. All are annuals, and have migrated readily with cultivation. Five species are present within the state. The near-glabrous *P. cordata* is most readily recognized. But *P. pubescens* and its variants are commonly treated as a complex that is either undivided or composed of inconsequential varieties. Recently, a seeming extreme disjunct -- from Central America to northeastern U.S. -- was resolved by recognition of the northern plant as distinct (M. Martinez, Taxon 42: 103-104. 1993), as *P. grisea*; it is now known in Florida as a weed of cultivated fields. Two other uncommon Florida plants, usually overlooked as *P. pubescens*, are worthy of specific distinction. *Physalis turbinata*, though distinguished largely on its larger size, seems not to overlap *P. pubescens*, and is recognized here, new to the Florida flora. *Physalis integrifolia*, readily identified by its translucent leaves and also new to the Florida flora, requires a transfer from its present varietal status, as follows.

***Physalis integrifolia*** (Dunal) D. B. Ward, comb. et stat. nov.  
Basionym: *Physalis hirsuta* Dunal var. *integrifolia* Dunal in  
DeCandolle, Prodr. 13(1): 445. 1852.

This summary of the Florida species of *Physalis* has taken an inordinate span of time. Soon after receiving U. T. Waterfall's 1958 synopsis of the species north of Mexico -- and then quite without field knowledge of my own -- I spread out the FLAS materials with the expectation I could quickly sort the jumble of erratically identified Florida specimens. Though many sheets fell into place, a number resisted assignment. I was cheered on by my mentor and beloved friend, Erdman West (FLAS), who had collected many of the puzzling

specimens and was frustrated in being unable to name them. I was pushed to gather more field data by Margaret Y. Menzel (FSU) who was then winding down her extensive greenhouse crossing experiments. Dr. Waterfall resolved some of my questions by his detailed 1967 report of the Mexican and West Indian species; in 1970, after much correspondence, I visited him in his attic herbarium in Stillwater and received further generous help. In the 1980s Patricia K. Holmgren (NY) loaned me a series of critical early Florida specimens. Janet R. Sullivan entered the field with her analysis of the *Physalis viscosa* allies, then with her synopsis of the southeastern species. Milo Pyne, then a student in North Carolina, corresponded regarding my interests and his careful (but yet unpublished) documentation of the Carolina species. In 2007 Jimi Sadle, botanist of the Everglades National Park, came upon plants of *Physalis lanceifolia* and stimulated me to completion and publication of these observations. I am grateful to all these folks.

**PHYSALIS L.**      Ground Cherries<sup>1</sup>

1. Flowers several in each upper leaf axil; corolla yellow to greenish-yellow with green or brownish blotches in throat; fruiting calyx nearly globose, small (to 1 cm. dia.), scarcely larger than enclosed berry; leaf blades broadly ovate, at least some strongly unequal at base (one side extending along petiole 5-10 mm. further than the other); plants erect, to 1.5 m. tall, from perennial vertical taproot. Moist to dry hammocks, usually on disturbed and exposed mineral soil (gopher mounds, tree throws). Panhandle and north Florida (s. to Dixie, Alachua counties); rare. Summer.

**CARPENTER'S GROUND CHERRY.**

***Physalis carpentieri* Ridd. ex Rydb.**

1. Flowers solitary in leaf axils; fruiting calyx conspicuously inflated, larger than enclosed berry; leaf blades approximately symmetrical (each side extending equally along petiole).
2. Plants pubescent at least in part with hairs stellate (radially branched, with 3-4 arms), either abundantly covering foliage or, if leaves glabrous, restricted to tips and edges of sepals; perennial, from deeply buried rhizomes.

3. Leaves linear, 10-20 times longer than wide, glabrous; plants erect. Vegetated dunes and sandy roadsides, always near the coast. Panhandle (Escambia to Wakulla County), disjunct to south peninsula (Collier to Dade County, and Florida Keys); frequent. All year.

**Physalis angustifolia** Nutt.

3. Leaves ovate, elliptic, obovate, or spatulate, 2-10 times longer than wide, stellate pubescent (except var. *glabra*); plants erect to many-stemmed and sprawling. Sandy soils, dunes. All year.

**Physalis walteri** Nutt.

- a. Leaves stellate pubescent. Coasts and interior of the peninsula, disjunct and perhaps adventive in panhandle (Jackson, Wakulla counties); frequent. [*Physalis elliotii* Kunze; *Physalis maritima* Curtis; *Physalis viscosa* L. ssp. *maritima* (Curtis) Waterfall] A variant with leaves 5-7 cm. broad, occurring along the lower east coast (St. Lucie southward), has been called forma *latifolia* Waterfall. var. **walteri**
  - a. Leaves glabrous. West coast of peninsula (Levy to Monroe County), inland (Hendry County); infrequent. [*Physalis elliotii*, misapplied.] Clearly an intergrade with *P. angustifolia* in leaf pubescence and shape. var. **glabra** (Waterfall) D. B. Ward
  2. Plants glabrous or pubescent, but if pubescent, with simple hairs; stellate hairs lacking or few and inconspicuous; annual or perennial.
  4. Perennial, from slender horizontal rhizomes (often deeply buried and broken off in collecting); anthers yellow, 2.5-5.0 mm. long.
  5. Pedicels and upper stems with retrorse, stiff, short hairs; leaves narrowly ovate, sinuately toothed. Sandy roadsides, disturbed pinelands. Panhandle (Leon, Lafayette counties); rare. Spring.
- Physalis virginiana** Mill.
5. Pedicels and upper stems with spreading soft lax hairs (some long, to 3-5 mm.).
  6. Foliage and stems abundantly viscid-pubescent (often encrusted with adhering sand); leaf blades borne in

vertical plane, broadly ovate with wavy margins; rhizomes cord-like (2-3 mm. dia.), often deeply buried. Sandy pinelands. Upper peninsula; infrequent. Spring. [*Physalis heterophylla* Nees var. *villosa* Waterfall] **Physalis sinuata** Rydb. in Small

- 6. Foliage and stems not viscid or sparingly so; leaf blades borne in horizontal plane, narrowly ovate with even margins; rhizomes slender (1.5 mm.), commonly shallow. Waste areas, sandy fields. Peninsula (Suwannee R. southward); frequent. Spring.

**Physalis arenicola** Kearney

- a. Pubescence short, fine, more or less glandular.

var. **arenicola**

- a. Pubescence long (1.5-1.0 mm.), non-glandular.

[*Physalis ciliosa* Rydb.]

var. **ciliosa** (Rydb.) Waterfall

- 4. Annual, from much-branched, mostly vertical roots; anthers bluish (rarely yellow), 1.0-2.5 mm. long.

- 7. Blades coarsely dentate, with long-acuminate teeth; fruiting calyx 10-ribbed (the intermediate veins equal in prominence to the midveins of the calyx lobes); corolla dark yellow or greenish in center; plant robust (to 1 m. tall), weedy.

- 8. Leaves ovate to ovate-lanceolate; flowers ±10 mm. dia.; anthers 2.0-2.5 mm. long. Moist shady riverbottoms, thickets, ditchbanks. Throughout; frequent (less so in panhandle). All year. **Physalis angulata** L.

- 8. Leaves lanceolate to linear-lanceolate; flowers ±8 mm. dia.; anthers 1.0-2.0 mm. long. Open tropical hammocks. Southwest peninsula (Monroe County), sometimes northward; infrequent. All year. [*Physalis angulata* Nees var. *lanceifolia* (Nees) Waterfall]

**Physalis lanceifolia** Nees

- 7. Blades variously sub-entire to serrate, teeth rounded to acute; fruiting calyx 5-ribbed (with each rib centered on a calyx lobe midvein); corolla with dark (usually black) center; plants weak-stemmed, often sprawling (to 0.4 m. tall).



9. Plants glabrous (or with a few hairs on the calyx); leaf blades with acute regular teeth. Gardens, disturbed areas, often weedy. Panhandle and north Florida where frequent, to central and south peninsula (Dade) where rare. Summer. [*Physalis pubescens* L. var. *glabra* (Michx.) Waterfall; *Physalis turbinata*, misapplied] \* **Physalis cordata** Mill.
9. Plants pubescent, long-haired or with intermixed long hairs and stalked glands, at least on petioles and stems; leaf blades with irregular blunt teeth (except at times *P. grisea*), or entire.
10. Surface of leaf gray-mealy, only sparingly pubescent, glands absent or not apparent; blades toothed, often sharply so, to the base. Cultivated fields, where weedy. West-central peninsula (Citrus=Inverness); rare. Summer. [*Physalis pruinosa*, misapplied; *Physalis pubescens* L. var. *grisea* Waterfall] \* **Physalis grisea** (Waterfall) M. Martinez
10. Surface of leaf copiously pubescent, at least along veins below, not mealy, stalked glands usually conspicuous.
11. Leaf blade flaccid and translucent, usually with a few teeth, 3-4 on each side, or entire. Mucklands, low fields. Throughout; rare. Summer. [*Physalis pubescens*, misapplied; *Physalis pubescens* L. var. *integrifolia* (Dunal) Waterfall] \* **Physalis integrifolia** (Dunal) D. B. Ward
11. Leaf blade opaque, usually toothed nearly to base with 5-8 teeth on each side.
12. Leaves 2-4 cm. broad; fruiting calyx 20-30 mm. long. Waste areas, cultivated fields, mucklands. Southern peninsula; frequent. All year. [*Physalis floridana* Rydb. in Small] \* **Physalis pubescens** L.
12. Leaves 4-8 cm. broad; fruiting calyx 30-40 mm. long. Cleared fields, pinelands, prairies. South-central peninsula (Lee, Polk, Highlands counties); rare. Spring-summer. [*Physalis*

*barbadensis* Jacq.; *Physalis pubescens*,  
misapplied]

\* ***Physalis turbinata*** Medic.

Excluded names:

***Physalis heterophylla*** Nees

Northern. Reported for Florida (Small, 1933), and for several north Florida counties (Clewell, 1985; Wunderlin, 1998). Spms. so named are apparently all *P. sinuata* or *P. virginiana*.

***Physalis longifolia*** Nutt.

Northern. Reported for Leon Co. (Wunderlin & Hansen, 2003). The several spms. so named (FSU) are better referred to *P. virginiana*.

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<sup>1</sup> This paper is a continuation of a series begun in 1977. The "amplified key" format employed here is designed to present in compact form the basic morphological framework of a conventional dichotomous key, as well as data on habitat, range, and frequency. Amplified keys are being prepared for all genera of the Florida vascular flora; the present series is restricted to genera where a new combination is required or a special situation merits extended discussion.