

## REVISION OF PHYSALIS SECTION *EPETEIORHIZA* (SOLANACEAE)

MAHINDA MARTÍNEZ\*

### RESUMEN

El género *Physalis* incluye alrededor de 90 especies que se han agrupado tentativamente en cuatro subgéneros. En esta revisión se trata a las especies de la sección *Epeteiorhiza*, del subgénero *Rydbergis* caracterizadas por su hábito herbáceo, vestiduras de pelos simples, glandulares o ausente, flores solitarias, corola rotada amarilla y cálices del fruto redondeados hasta fuertemente 5-angulados. Se reconoce 14 especies que se distribuyen desde el sur de Canadá hasta Sudamérica. Se incluye la altitud, tipo de vegetación, época de floración, nombres comunes y uso. Algunas especies como *P. pubescens* y *P. cordata* se han establecido en los trópicos del Viejo Mundo.

Palabras clave: sistemática, *Physalis* sect. *Epeteiorhiza*.

### ABSTRACT

The genus *Physalis* includes about 90 species which are tentatively grouped into four subgenera. Morphology is used to revise sect. *Epeteiorhiza*, subgenus *Rydbergis*. The species in this section are defined by their herbaceous habit, either glabrous or with vestiture of simple or glandular hairs, solitary flowers, with rotate yellow corollas and terete to strongly 5-angled fruiting calyces. Fourteen species ranging from Canada to South America are recognized by this study. Data of their altitudinal distribution, vegetation type, flowering, common names and uses are included. Some species, such as *P. pubescens* and *P. cordata* have become established in the Old World tropics.

Key words: systematics, *Physalis* sect. *Epeteiorhiza*.

\*Escuela de Biología, Universidad Autónoma de Querétaro. Cerro de las Campanas s/n, Col. Centro, Querétaro, Querétaro. México.

## INTRODUCTION

The genus *Physalis*, with about 90 species, is among the largest genera in subfamily Solanoideae, surpassed only by *Lycianthes* and *Solanum*. Estimation of the number of species within the genus vary enormously, from 75 (D'Arcy, 1991) to 120 (Hendrych, 1989) probably because the species are similar morphologically, and collections with good field notes, as well as experimental work, are lacking. In addition, most of the early type materials is either inaccessible or lost. To date, the only comprehensive work on the genus is still Waterfall's (1958, 1967). A revision of the genus *Physalis*, although needed, seems unlikely in the near future because of the problems previously mentioned, and its complicated nomenclature.

The genus is easily recognized by its accrescent fruiting calyx that envelops the berry. Other genera (*Chamaesaracha*, *Leucophysalis*, *Deprea*, *Larnax*) share this character but differ in corolla shape, habit, or details of the inflorescence (see Estrada and Martínez, in press, for a key to the genera). *Physalis* had been considered a cosmopolitan genus, but workers (D'Arcy, 1991, Nee, 1991) agree that the genus is native to America. Species collected in the Old World tropics are almost certainly post-Colombian introductions, with the exception of *P. alkekengi* which is the only native species to the Old World (D'Arcy, 1991; Nee, 1991). The center of diversity of *Physalis* is Mexico with over 70 species, most of them endemic. The United States and Central America also have several endemic species; a few also occur in South America.

Several species have been under cultivation for a long time. Some are grown for their juicy berries, such as *P. philadelphica* Lam., in Mexico known as "tomate verde" or "tomate de cáscara", *P. peruviana* L. ("uchuba") from the Andes, and *P. grisea* (Waterf.) M. Martínez from the Eastern United States (Nee, 1991). *Physalis alkekengi* L. ("Chinese lantern") is used as an ornamental and a medicinal.

The four species have been introduced and established elsewhere. Other species such as *P. chenopodiifolia* Lam., *P. coztomatl* Moc. et Sessé ex Dunal, and *P. pubescens* L. are gathered from their wild populations for edible fresh fruits or for medicinal purposes. However, most of the species have restricted habitats, and many are known only from the type material or from a few additional collections.

The delimitation of sect. *Epeteiorhiza* is based mostly on cladistic analysis of restriction enzymes fragments of chloroplast DNA, as well as hair morphology based on scanning electron microscopy (Martínez, 1993). The species treatment is based on gross morphology of herbarium specimens and field data.

## TAXONOMIC HISTORY

*Physalis* was established by Linnaeus in 1753 with nine species subdivided into two groups. G. Don (1837) named the sections proposed by Nees von Esenbeck (1831) applying *Physalodendron* to the woody species, *Eurostorhiza* to the perennial, rhizomatous species, *Epeteiorhiza* to the annual species, and *Anomalae* to the species

with tubular corollas noting that they might belong to another genus. Dunal (1852) recognized only sect. *Eurostorhiza* and sect. *Epeteiorhiza* referring the species of sect. *Anomalae* and sect. *Physalodendron* to the genus *Withania*. Rydberg (1896) did not recognize these infrageneric categories and established the sections *Physalis* (as *Euphysalis*), *Microphysalis*, and *Megista*, further subdividing sect. *Physalis* into seven species groups that were later raised by Menzel (1951) to the rank of sections (see Martínez, in press, for a discussion on the nomenclature of the subdivisions). The characters used to subdivide the genus since Linnaeus (1753) are habit (shrubby, annuals or perennials), flower arrangement (solitary or aggregated), morphology of the flower bud, shape of the fruiting calyx, and pubescence.

As currently circumscribed, *Physalis* includes *Quincula* and *Margaranthus* (Martínez, 1993; Axelius, 1995), but excludes *P. amphitrica* and *P. calidaria*, which were transferred to the new genus *Tzeltalia* (Estrada and Martínez, in press). The genus is considered by Martínez (in press) as divided into four subgenera (*Physalis*, *Physalodendron*, *Quincula*, and *Rydbergis*). *Rydbergis* includes the majority of species and is subdivided into nine sections defined by habit, pubescence, hair morphology, and fruiting calyces.

#### GENERAL MORPHOLOGY OF THE GENUS *PHYSALIS*

*Habit.* Life form can be of three kinds: 1) annual (e.g., *P. missouriensis*); 2) rhizomatous perennial geophytes (e.g., *P. cinerascens*), and 3) shrubby or arborescent perennials (e.g., *P. cozcomatl* and *P. arborescens*). In tropical regions, the annual habit is not always absolute, and some plants may continue to persist for extended periods or produce new growth from the aerial parts, appearing somewhat woody at the base. However, these plants usually do not survive for more than two years.

*Physalis* species are mostly erect, varying in size from a few centimeters up to 2 m high (e.g., *P. nicandroides*). Some species such as *P. hederifolia* are prostrate, and only two species, *P. gracilis* and *P. longicaulis*, have repent stems that root at the nodes. Plants can either branch profusely (*P. crassifolia*) or maintain a single stem, (*P. melanocystis*). Stems of *Physalis* are usually terete, but in some species they are angled, as in *P. angulata*.

The species of sect. *Epeteiorhiza* are annual or non-rhizomatous perennial herbs, with perenating ligneous stems. All the species are erect and have terete stems.

*Leaves.* The leaves of *Physalis* can be sessile or petiolate, and the base of the blade is frequently oblique. Blades have entire, toothed, or serrate margins, and the shape varies from reniform to ovate and from linear to lanceolate. Leaves are alternate, but frequently geminate, these of similar shape but unequal in size, the smaller leaves about half the size or less than the larger. The size and shape of leaves show considerable infra-specific variation. Ordinary epidermal cells are polygonal in outline and lack surface sculpturing (Fig. 1a). Bessis and Guyot (1979) studied

stomatal characters of 56 species in 45 genera of the Solanaceae. They found stomata to be informative at the tribal and genus levels. In *Physalis*, stomata are confined to the lower leaf surface and are described as meso-perigenous anisocytic; a few perigenous anomocytic stomata are also present, a feature common to all species in the family (Bessis and Guyot, 1979). Neither the ordinary epidermal cells nor the stomata provide useful information at the specific level.

In sect. *Epeteiorhiza*, leaves are petiolated, with an elliptic, oblong, ovate, rhombic or deltate shape. Leaves are always alternate when mature, but at the top of the stem they are geminate.

*Vestiture.* Morphological differences in hair types proved diagnostic. Hairs have been used in several taxonomic studies in the Solanaceae, especially in *Solanum* (Seithe, 1979; Seithe and Anderson, 1982), where they have been useful at the level of series and species. In *Physalis*, hairs were used, along with other characters to group species (Rydberg, 1896). For example, species with branching hairs made up his *Stellatae* group. Seithe and Sullivan (1990) investigated the hair morphology of ten species of *Physalis*. They found two classes of hairs: 1) long, branched and unbranched hairs with or without glandular tips (Figs. 1 a; b); and 2) short hairs tipped with multicellular glands (Fig. 1 a). Both types of hairs developed from one epidermal cell. No variability was found in the second hair class, but the first was further subdivided into six types: gland-tipped unbranched, glandless unbranched, gland-tipped branched, glandless branched, stelliform, and dendroid-stelliform. Hairs on other organs of the plant were similar to those of the upper leaf surface and frequently, two or more kinds of hairs are intermixed.

When analyzed with the scanning electron microscope (SEM), *Physalis* presented two different hair surfaces: smooth and rugose (nomenclature of Barthlott, 1990). For example, members of section *Stellatae* (*P. cinerascens* and *P. pumila*) had branching hairs with a rugose secondary surface that contrasted with the smooth surface of the short multicellular glandular hairs (type-2, Fig. 1a).

Simple glandular hairs with a smooth surface were found in ten of the 14 species of section *Epeteiorhiza* (Fig. 1b). Only *Physalis minuta*, *P. cordata* and *P. grisea* have simple hairs that lack glands. Except for *P. porrecta*, which was glabrous, members of section *Epeteiorhiza* had short multicellular glandular hairs (type 2 of Seithe and Sullivan, Fig. 1a). However, simple multicellular glandular hairs were also present in members of other sections, e.g., *P. greenmanii* and *P. coztomatl* of section *Coztomatae*, and *P. lagascae* of section *Angulatae*.

*Flowers.* They are axillary and solitary except in *P. arborescens*, *P. melanocystis*, *P. aggregata* and *P. carpentieri*, where the flowers are aggregated into fascicles of two to five flowers. Flowers are usually pendulous, although a few species have flowers with a lateral orientation. Erect flowers are absent in the genus. In sect. *Epeteiorhiza*, the flowers are pedicellate, pendulous, and solitary in the leaf axis.

Corolla shape is usually rotate to campanulate (Fig. 2 a), either apically 5-angled, or 5-lobed (as in *P. alkekengi*). Tubular corollas with an open limb are rare, occurring

only in *P. glutinosa* and *P. campanula*. Urceolate corollas are present only in *P. solanaceous* (Fig. 2 b), whereas all members of sect. *Epeteiorhiza* have rotate corollas.

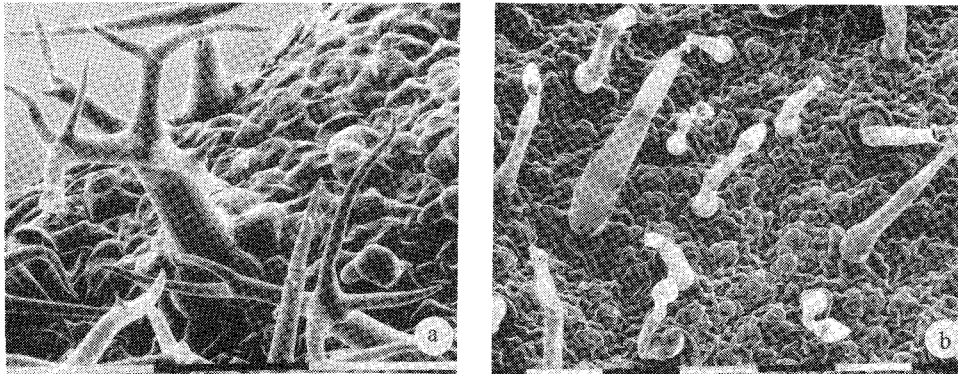


Fig. 1. Hair morphology of *Physalis*; a) long hairs (branching) and short hairs (glandular) from the abaxial surface of the leaves of *P. cinerascens* (A. Salinas F3917, TEX); b) long hairs, glandular, from the leaves of *P. ignota* (Britton and Wilson 5767, NY). Barr equals 0.1 mm.

Corolla color in most species varies from yellow to greenish or whitish, either maculated or not. Only *P. solanaceous* has purple corollas, whereas *P. alkekengi* has white corollas. Maculae can be a single, solid blotch (Fig. 2 c), or composed of several aggregated smaller dots (Fig. 2 d). The color of maculations varies from greenish, dull brown to dark blue or purple; the apex varies from obtuse to acute or acuminate (Fig. 2 c, d). The vast majority of species in *Physalis* have a mat of white hairs in the throat of the corolla, near the maculations. Sullivan (1986) suggested that such pubescence retains nectar which is produced in microquantities. Because most species of *Physalis* are bee pollinated (Sullivan, 1986), corolla color in the ultraviolet range can be distinctive. Sullivan (1986) studied the ultra violet light patterns of *P. cinerascens*, a dark-maculated species. She deduced that the yellow limb of the corolla is seen by the bee as yellow-orange, the throat maculations as black, hairs, anthers, pollen as white-yellow, and the veins as luminescent-white. Color and shape of the maculations show little variation within species, making them very useful characters.

In sect. *Epeteiorhiza*, petals are yellow, cream yellow or whitish, either immaculated or with maculations. The color of the maculation can be greenish or light brown, therefore only slightly contrasting from the rest of the corolla, or strongly contrasting as dark blue or purple. All the maculations are solid, either confluent at the base, or separated.

Anthers in *Physalis* dehisce longitudinally and are basifixed. Color of anthers and filaments varies from green to yellow to blue-tinged, blue or purple. The color is taxonomically provisionally useful, because some intraspecific variation occurs. In *P. philadelphica* the anthers twist after dehiscence, in all other species the anther remain straight. Anther shape varies from sagittate, oblong or linear. The flowers

usually have one mature stamen when they first unfold; the remainder matures over several days. Pollen is shed over a 1-3 day period with one or more anthers shedding each day (Sullivan, 1986).

Anthers in sect. *Epeteiorhiza* are always oblong, but color differs from yellow, green, yellow with blue lines, or blue.

*Fruits.* The fruit of *Physalis* is a two-carpellate berry with either juicy or rather dry pericarp. The color of mature berries varies from green to yellow to orange or purple. Berries are sometimes produced on a gynophore. Seeds are usually abundant (ca. 50 seeds per fruit), but the number of seeds within fruits diminishes as the flowering season progresses, often to only five or six.

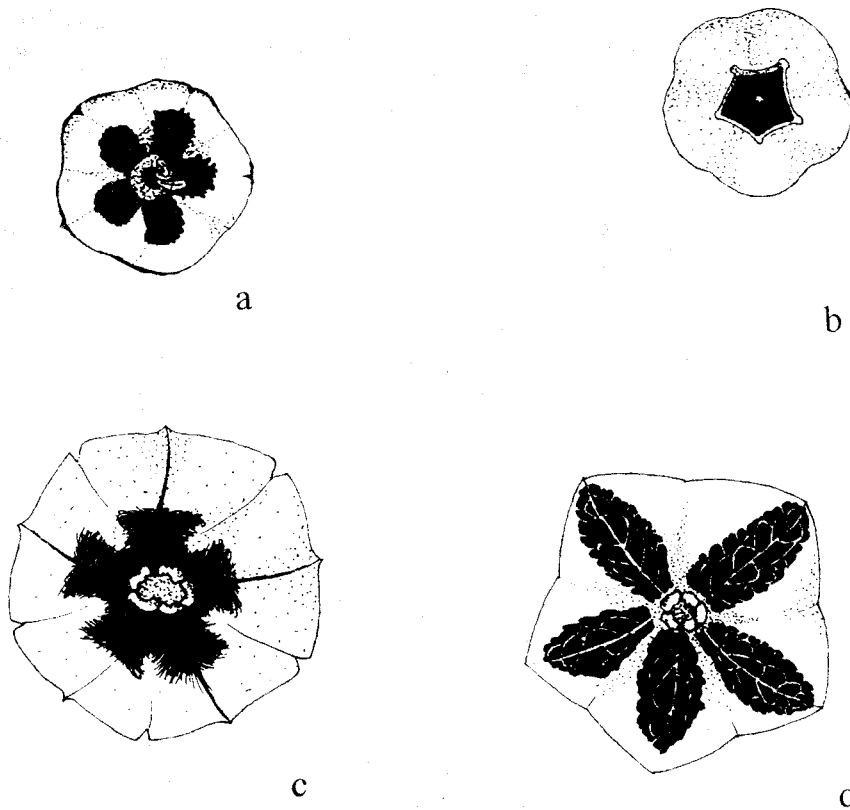


Fig. 2. Corolla shape and maculations in *Physalis*: a) rotund corolla of *P. pubescens* L.; b) urceolate corolla of *P. solanaceus* (Schltdl.) Axelius; c) solid maculation with obtuse apex of *P. gracilis* Miers; d) aggregated dots with acuminate apex of *P. coztomatl* Moc. et Sessé ex Dunal.

The berry is loosely enclosed by the accrescent, bladder-like calyx (Fig. 5). The shape of the fruiting calyx can be either strongly 5-angled (Fig. 3 a) or 10-angled = "terete" (Fig. 3 b). Fresh fruiting calyces are usually green, turning light brown or yellow at maturity (bright orange in *P. alkekengi*, almost black in *P. arborescens* and *P. melanocystis*). The shape of fruiting calyces has been used to subdivide the genus, but cladistic analysis based on chloroplast DNA indicates that some 5-angled fruiting species like *P. pubescens* may be more closely related to terete fruiting species (*P. missouriensis*) than to other 5-angled species as *P. pruinosa* (Martínez, 1993).

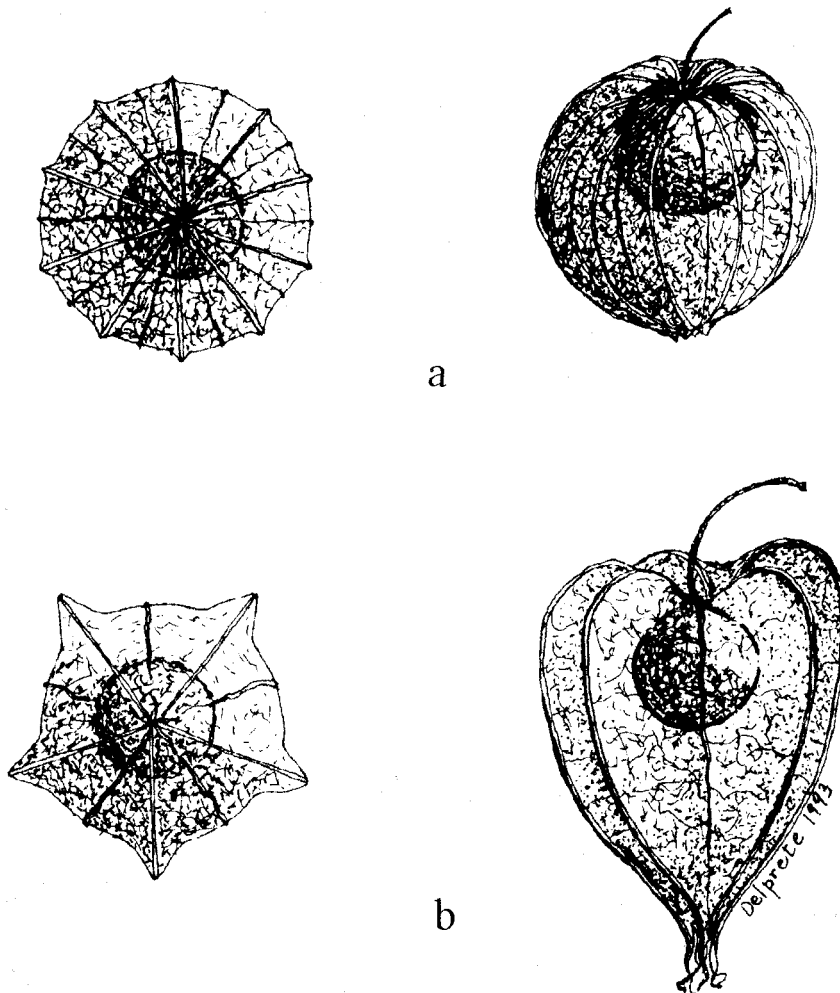


Fig. 3. Accrescent calyx in *Physalis* in frontal and lateral view, respectively: a) terete calyx of *P. gracilis* Miers; b) 5-angled calyx of *P. cordata* Mill.

Most members of sect. *Epeteiorhiza* have invaginated, strongly 5-angled fruiting calyces. Only *P. leptophylla* and *P. missouriensis* have slightly 5-angled to almost terete calyces, which are only slightly invaginated.

*Seeds.* Seed morphology has been used to subdivide the family Solanaceae into sub-families, it has been used to a limited extent at lower taxonomic levels (Bahadur and Farooqui, 1986). Seeds in *Physalis* vary in color from light yellow to brown, except for *P. parvianthera* that has black seeds. They vary in size from 0.6-3.0 mm in length. All species have reniform seeds, except for the oblique-triangular seeds of *P. parvianthera*. The seeds have a thick periclinal wall described in untreated seeds as foveolate (Waterfall, 1958) (Fig. 4 a). If the wall is removed by enzyme etching (Lester and Durrands, 1984), the seeds display an array of provisionally useful patterns (Fig. 4 b). All species of *Physalis* investigated so far (Axelius, 1992, Martínez, 1993), with the exception of *P. peruviana*, have shallow testa cells with undulate anticlinal walls and holes through the thickening at the bottom. The holes are part of a layer of a tube-network that occurs beneath the outer epidermis (Axelius, 1992). Overall cell size varies from 0.07 mm in *P. carpentieri* to 0.2 mm in *P. rydbergii*. Cells vary from as long as wide, to twice as long as wide, excepting only *P. rydbergii*, in which cells are up to four times longer than wide. All species of *Physalis* have low anticlinal walls, of which the bottom holes vary from round to oblong. In sect. *Epeteiorhiza*, seeds are either golden (i.e., bright yellow), or brown with sizes from 1.5 mm to 2.5 mm.

*Chromosomes.* Chromosome numbers in *Physalis* have a base of  $x = 12$ , as the rest of the tribe Solaneae, except for *P. lobata*, which has  $n = 11$ . Menzel (1951) found that *P. angulata* and *P. peruviana* are tetraploid ( $2n = 48$ ), and the rest of the 20 species she studied were uniformly diploid with  $2n = 24$ . Seven species investigated later (Averett and Powell, 1972; Martínez, 1993) had the same chromosome number. The members of sect. *Epeteiorhiza* that have been investigated for chromosome numbers (*P. cordata*, *P. ignota*, *P. patula*, and *P. pubescens*) all have  $2n = 24$ .

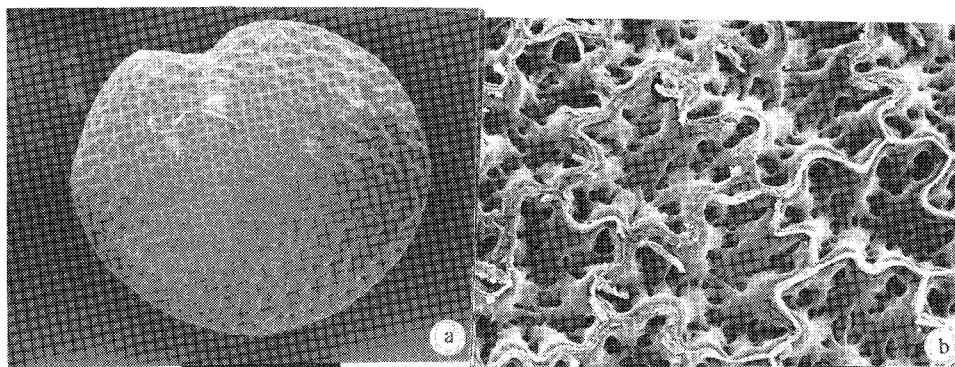


Fig. 4. Seeds of *Physalis*: a) untreated seed of *P. nicandroides* Schltld. (L. Hernández 2488, TEX), bar equals 1 mm; b) same seed after treatment, bar equals 0.1 mm.



## TAXONOMY

*Physalis* L., Sp. Pl. 1753.- Type: *Physalis alkekengi* L.

*Alkekengi* Tourn., Adans. Fam. Pl. 2:218. 1763.

*Herschella* Bowdich, Excurs. Mader. 159. 1825.

*Quincula* Raf., Atlantic J. 1:145. 1832.-Type *Quincula lobata* (Torrey) Raf.

[=*Physalis lobata* Torrey]

*Alicabon* Raf., Sylva Tell. 56. 1838.

*Margaranthus* Schltld., In. Sem. Hort. Halensis 8. 1838.-Type *Margaranthus solanaceus* Schltld.

*Megista* Tourn., Ann. Soc. Linn. 17:115. 1869.

Annual or perennial herbs, forming rhizomes in some species, less frequently shrubs; vestiture composed of vesicles, or of simple, branching or glandular trichomes, frequently a mixture of two types of trichomes. Leaves petiolate, alternate, frequently paired; blades linear, oblong, elliptic or ovate, margins entire, toothed or lobed. Flowers pedicellate, solitary, or seldomly aggregated in axillary fascicles of 3-5 flowers; flowering calyces campanulate or seldom tubular-campanulate, 5-lobed; flowering buds plicate; corollas subrotate to campanulate-rotate or campanulate, seldom tubular-campanulate or urceolate, mostly yellow, but a few species with purple or white petals, if yellow, maculated with 5 strongly contrasting or dull maculations that can be solid or composed of several separate dots, or maculations wanting; corolla tube glabrous or pubescent at the insertion of filaments; filaments filiform or flattened; stamens 5, anthers dehiscing longitudinally, oblong, linear-oblong or sagittate, green, yellow, blue, blue-tinged or purple; style filiform, stigma capitate, truncate or clavate. Fruit a berry, green, purple, orange, yellow or brown at maturity, loosely and completely enveloped by the accrescent calyces; fruiting calyces reticulate, 5- or 10-angled, invaginated at the base or not; seeds several to many, laterally compressed, testa foveolate, seldom tuberculate.

KEY TO THE SUBGENERA OF *PHYSALIS*

1. Corolla lobed
  2. Corolla rotate, distinctly lobed, immaculate, pollen microspinulate, fruit a thin walled berry, chromosomes  $x = 12$ , one with a conspicuous satellite, plants herbaceous, native to the Old World. .... Subgen. *Physalis*
  2. Corolla rotate, distinctly lobbed, maculated, pollen granular, fruit a thick walled juicy berry, chromosomes without a conspicuous satellite, plants distinctly ligneous, native to the New World. .... Subgen. *Physalodendron*
1. Corolla not lobed.
  3. Corolla rotate, purple, immaculate, pollen microspinulate, fruit a dry berry, chromosomes  $x = 11$ , plants native to the deserts of North America. .... Subgen. *Quincula*
  3. Corolla rotate, campanulate or urceolate but not distinctly lobed, mostly maculated, pollen granular, fruit a thick walled berry, chromosomes  $x = 12$  without a satellite, plants native to the New World. .... Subgen. *Rydbergis*

KEY TO THE SECTIONS OF SUBGENUS *RYDBERGIS*

1. Flowers aggregated into fascicles, corky bodies among the seeds. .... Sect. *Carpenteriae*
1. Flowers solitary, fruits without corky bodies among the seeds.
  2. Corolla maculations composed mostly of separated spots, plants mostly of high elevations (>1,500 m). .... Sect. *Coztomatae*
  2. Corolla maculations solid, plants mostly of lower elevations.
    3. Corolla tubular campanulate. .... Sect. *Campanulatae*
    3. Corolla mostly rotate, seldom urceolate, never tubular campanulate.
      4. Plants perennial through rhizomes, with simple or branching hairs.
        5. Plants mostly covered with branching hairs. .... Sect. *Stellatae*
        5. Plants mostly covered with simple hairs, or a few branching hairs present.
          6. Plants covered with simple hairs with a smooth surface, hairs not aggregated. .... Sect. *Lanceolatae*
          6. Plants covered with hairs aggregated into tufts, or hairs with a rugose surface.
            7. Plants with hairs in tufts, corolla immaculate, restricted to Tehuacán. .... Sect. *Tehuacanensis*
            7. Plants with solitary hairs, corolla maculated, plants restricted to other dry areas of Mexico. .... Sect. *Rydbergis*
  4. Plants annual or perennial through a ligneous base, seldomly forming rhizomes, but if so, then the plants glabrous
    8. Fruiting calyces terete, plants glabrous or with simple hairs..... Sect. *Angulatae*
    8. Fruiting calyces mostly 5-angled, if almost terete, then the plants densely pubescent. .... Sect. *Epeteiorhiza*

*Physalis* subg. *Rydbergis* Hendrych, *Acta Univ. Carol.-Biol.* 33:1-42. 1989. Sect. *Epeteiorhiza* G. Don, *Gen. Syst.* IV:449. 1837. Lectotype: *Physalis pubescens* L.  
*Physalis* sp. group *Pubescentes* Rydb., *Mem. Torrey Bot. Club* 4:332. 1896.  
*Physalis* sp. group *Leptophyllae* Rydb., *Mem. Torrey Bot. Club* 4:328. 1896.

Annual or perennial herbs, but if perennials, not forming rhizomes; vestiture commonly composed of simple or 1-4 celled glandular hairs or a mixture of both, the secondary surfaces smooth, glands dark brown or transparent. Leaves alternate and paired, one leaf always much smaller (less than one half) than the other; blades varying from oblong to lanceolate or ovate, base oblique, margin entire, undulate, dentate or crenate. Flowers pedicellate, solitary in the leaf axils; flowering calyces campanulate, the lobes deltoid, triangular, lanceolate or acuminate; corolla rotate-campanulate, yellow to greenish-cream, 0.3-2.0 cm in diameter; petals maculate with five strongly contrasting purple spots, or maculations dull brown or greenish, seldomly wanting; corolla tube glabrous or pubescent within at insertion of filaments; filaments flattened, blue, purple, or green; anthers oblong, yellow, green, blue-tinged or blue; style filiform, stigma capitate. Fruit a spherical or ellipsoid berry, glutinous or not, green, yellow or dark brown at maturity; fruiting calyces mostly 5-angled, seldom terete, invaginated basally or not; seeds golden or dark brown, more than 50 per fruit, testa foveolate.

The species of sect. *Epeteiorhiza* are native to America, ranging from southern Canada to Northern Argentina and the West Indies. The weedy *Physalis pubescens* has become established in the Old World, and *P. cordata* has been collected infrequently in China and India from open areas of lowland habitat. A few species are part of the native vegetation of oak or tropical montane forest.

KEY TO THE SPECIES OF SECT. *EPETEIORHIZA*

1. Mature stems glabrous to minutely puberulous
  2. Flowers 0.5-0.6 cm wide; flowering calyces with deltate lobes; fruiting calyces 1.5-2.0 cm long. .... **7. *P. minuta***
  2. Flowers 0.8-2.0 cm wide; flowering calyces with lanceolate lobes; fruiting calyces 3.0-5.5 cm long.
    3. Flowering calyces villous, the lobes 2.5 mm wide; plants of high (>1,500 m) elevations. .... **12. *P. porrecta***
    3. Flowering calyces glabrous to minutely puberulous, the lobes 0.8-1.0 mm wide; plants of low elevations. .... **2. *P. cordata***
1. Mature stems villous, velutinous, sericeous or tomentose.
  4. Calyx lobes deltate; fruiting calyces 10-angled, not invaginated at the base.
    5. Petals with 5 purple maculations. .... **6. *P. leptophylla***
    5. Petals immaculate. .... **8. *P. missouriensis***
  4. Calyx lobes narrowly triangular, lanceolate or acuminate; fruiting calyces strongly 5-angled, invaginated at the base.
    6. Petals with strongly contrasting purple or dark blue maculations; fruiting calyces 1.5-2.0 (3.0) cm wide.
      7. Fruiting calyces 1.5 cm wide or less, plants restricted to Chiapas and Guatemala. .... **1. *P. angustiphysa***
      7. Fruiting calyces 2.0 cm wide or more.
        8. Fruiting calyces deeply invaginated; corolla maculations not merging at the base.
          9. Leaf margins dentate; plants of north and central Mexico  
..... **11. *P. patula***
          9. Leaf margins crenate; plants restricted to the Rocky Mountains, USA  
..... **9. *P. neomexicana***
        8. Fruiting calyces not deeply invaginated; corolla maculations merging at the base.
          10. Pubescence without glandular hairs; anthers yellow; plants odorless or nearly so. .... **3. *P. grisea***
          10. Pubescence glandular; anthers mostly blue or purple; plants with strong odor. .... **14. *P. pubescens***
    6. Petals with weakly contrasting greenish or brown maculations, or maculations absent; fruiting calyces (2.5) 3-4.5 cm wide.
      11. Fruiting calyces tomentose throughout, hairs not glandular. .... **4. *P. ignota***
      11. Fruiting calyces glandular-pubescent at least on the veins.
        12. Fruiting calyces 1.5-3.0 cm long. .... **11. *P. patula***
        12. Fruiting calyces 3.0-5.5 cm long.

13. Fruiting pedicel much thickened, 1.1-2.0 mm in diameter.  
 .....10. *P. nicandroides*
13. Fruiting pedicel not thickened, 0.5 mm in diameter:  
 14. Anthers yellow, fruit glutinous..... 13. *P. pruinosa*  
 14. Anthers blue or blue-tinged, fruit not glutinous .....5. *P. latiphysa*

1. *Physalis angustiphysa* Waterf., Rhodora 69:228. 1967. Type: Guatemala: Huehuetenango, La Sierra (Tujimach) across river from San Juan Atitlán, 8 Sep 1952, *Steyermark 51977* (Holotype: **US!**; Isotype: **F!**)

Perennial herbs 20-100 cm high. Stems densely villous with multicellular glandular hairs up to 2 mm long. Leaves villous, 5-14 cm long; petioles 1.5-5.0 cm long, blades ovate to deltate, densely villous throughout, 3-10 cm long, 3.5-7.0 cm wide, apex acute, base cordate, margin coarsely dentate to almost entire. Flowering peduncles 4.5-9.0 mm long; flowering calyces villous with triangular lobes 2.5-3.5 mm long, 1.5-2.0 mm wide; corollas yellow, 1.1-1.5 cm in diameter, the petals with 5 separate strongly contrasting maculations, pubescent within; filaments and anthers blue or blue-tinged, anthers 2.5-2.8 mm long. Fruiting peduncles 4.5-9.0 mm long; fruiting calyces 5-angled, 2-3 cm long, ca. 1.5 cm wide, villous throughout. Mature berry spherical, ca. 1.5 cm in diameter, containing numerous golden foveolate seeds ca. 2 mm in diameter.

**Distribution** (Fig. 5). Restricted to Mexico and Guatemala, 800-2900 m in oak or tropical montane forest.

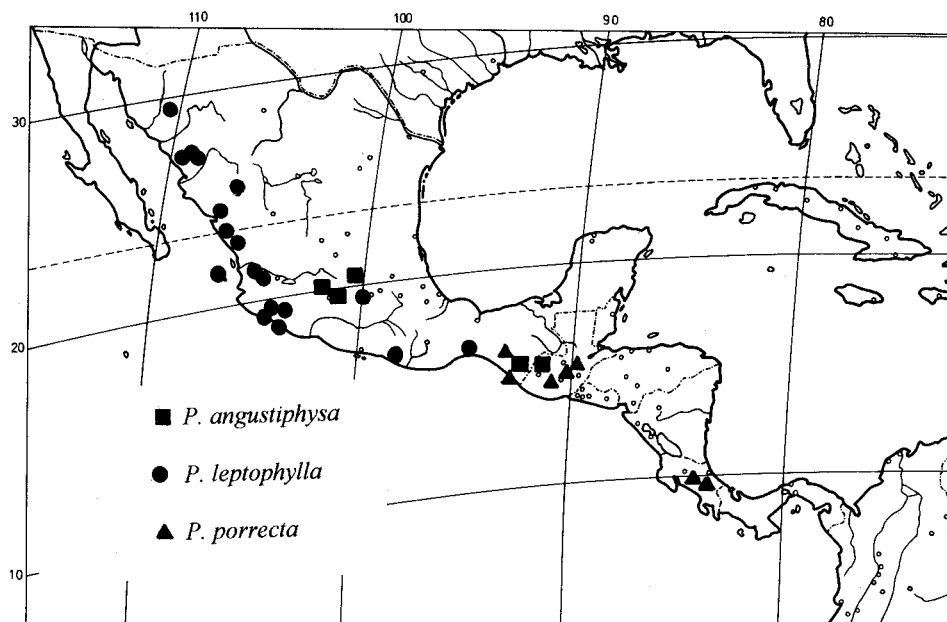


Fig. 5. Distribution of *P. angustiphysa*, *P. leptophylla*, and *P. porrecta*.

**Flowering.** July-January.

**Common names.** "Chush-gutz", "tomate-zope" (Guatemala), "chichol-antivo" (tzotzil), "miltomate" (Mexico).

**Uses.** Reported as medicinal from Chiapas.

**Observations.** *Physalis angustiphysa* seems to be closely related to *P. pubescens* L., from which it is readily distinguished by its perennial habit, very narrow fruiting calyces (not exceeding 1.5 cm wide), and a very dense vestiture.

**Representative specimens examined.** GUATEMALA HUEHUETENANGO: between Puente Negro and Los Alisos on way to Aguacatán, 16 Sep 1971, *Molina 26548* (F). MEXICO: CHIAPAS: Mpio. Ocozocoautla de Espinosa, head of the Río de la Venta at Chorreadero near Derna, 24 Aug 1974, *Breedlove 36559* (CAS, MEXU, NY). GUANAJUATO: 4 km al E de Tierras Negras, municipio de Pénjamo, 17 Nov 1991, *J. Rzedowski 51282* (IEB, QMEX). MICHOACÁN: Zitácuaro-Coyota, 25 Aug 1938, *Hinton 13156* (F, NY, US); Cerro La Alberca, municipio de Villa Jiménez, 20 Nov 1991, *E. Pérez y E. García 2590* (IEB, QMEX); 5 km al N de Atécuaro, municipio de Morelia, 21 Jul 1992, *J. Rzedowski 51555* (IEB, QMEX).

2. *Physalis cordata* Mill., Gard. Dict. 8:14. 1768. Type: Mexico: Veracruz, without further locality, 1730, *Houstoun s.n.* Holotype: BM, Sloane collection. Photoholotype BH!

*Physalis clarionensis* Waterf., *Rhodora* 69:326. 1967. Type: Mexico: Colima: Clarion Island, Mar-Jun 1897, *Anthony 411*. Holotype: UC. Isotypes: CAS! NY!

*Physalis galapagoensis* Waterf., *Rhodora* 70:408. 1968. Type: Ecuador: Galapagos Islands, Isla Santa Cruz, vicinity of Charles Darwin Research Station, Academy Bay, 15 Feb 1964, *Wiggins 18724*. Holotype: DS. Isotype: OKL. Neither the holotype nor the isotype has been located; however, examination of the 13 additional collections cited by Waterfall leaves little doubt as to the taxon concerned, and its name relegated to synonymy herein.

Annual herb 25-200 cm high. Stems glabrous to minutely puberulous. Leaves glabrous, 5-20 cm long; petioles 2.5-6.0 cm long; blades ovate to deltate, glabrous or sometimes puberulent, 3.5-11.0 cm long, 3-8 cm wide, apex acute to acuminate, base cordate, sometimes oblique only up to 5 mm off, margins dentate to almost entire. Flowering peduncles 3.5-8.0 mm long; flowering calyces glabrous to puberulent, with lanceolate lobes, 2-5 mm long, 0.8-1.0 mm wide; corollas yellow, 0.8-2.0 cm in diameter; petals with 5 dark brown to purple maculations, pubescent within; filaments brown, anthers yellow, blue-tinged or blue, up to 3 mm long. Fruiting peduncles 1.5-2.4 cm long; fruiting calyces strongly 5-angled, 3.0-4.5 cm long, 1.2-3.0 cm wide, always longer than wider, glabrous throughout to minutely puberulous. Mature berry ellipsoid, ca. 1.5 cm long, 1.0 cm wide, yellow, containing numerous brown foveolate seeds ca. 1.5 mm in diameter.

**Distribution** (Figs. 6, 7). From southern USA. and throughout the Mexican and Central American lowlands to Brazil in South America and the West Indies. Introduced to Asia. The plant is a weed of lowland habitats, mostly occurring from 0 to 100 m, in sandy or clay soils. In the greenhouse, the species is selfing and very sensitive to drought.

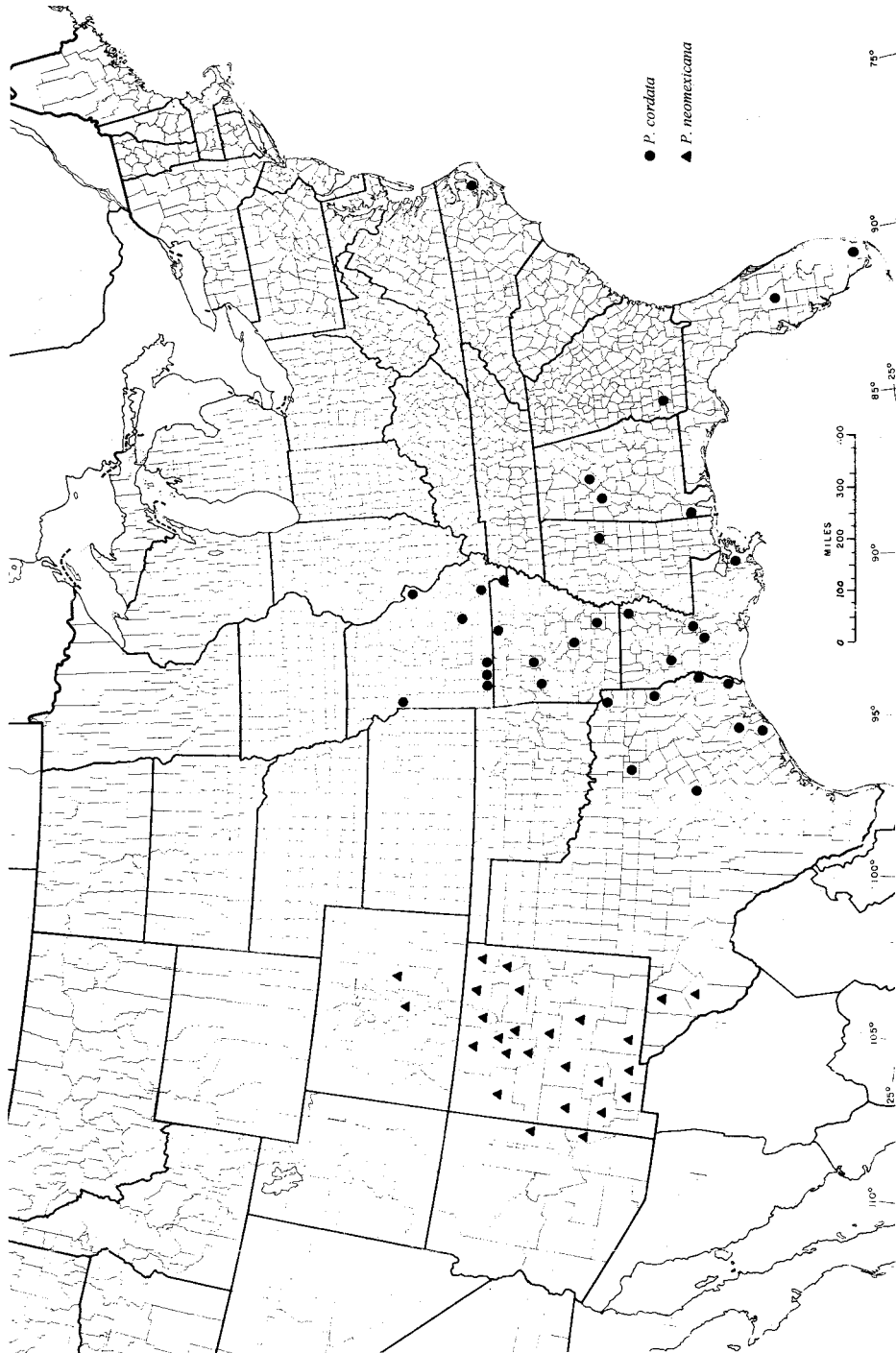


Fig. 6. Distribution of *P. cordata* in the United States and *P. neomexicana*.

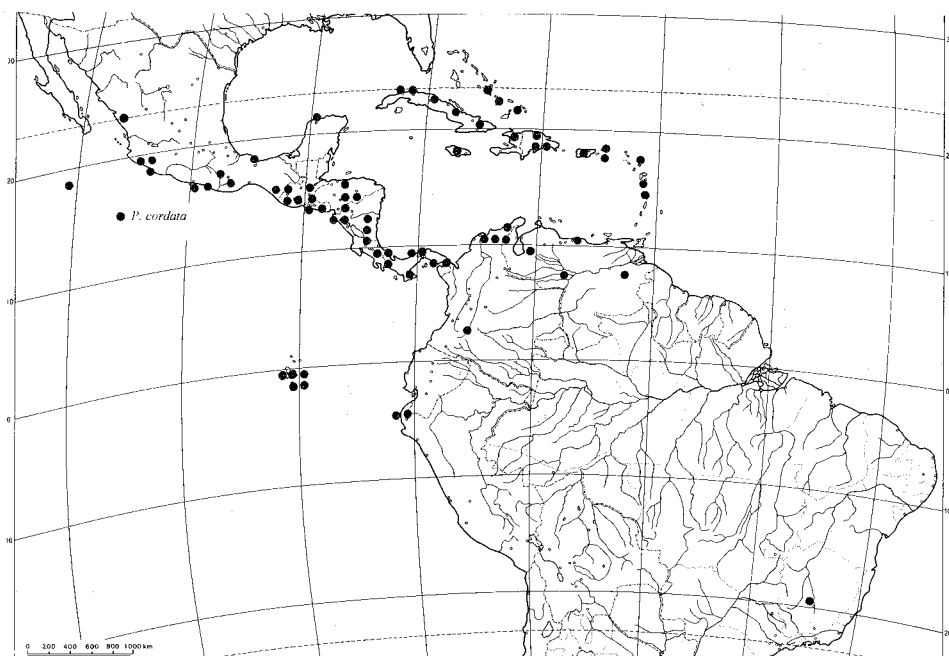


Fig. 7. Distribution of *P. cordata* in Mexico, Central America, South America and the West Indies

**Flowering.** In the USA flowering from July to November. In the rest of its range flowering throughout the year.

**Common names.** “Joapoca” (Brazil); “trepetoropo” (Colombia); “huevito”, “huevo de tortuga”, “miltomate” (El Salvador); “tomatillo” (Guatemala); “chimbomba menuda” (Nicaragua); “ground cherry” (USA).

**Observations.** *Physalis cordata* is probably dispersed by water, which perhaps explains its presence in the Galapagos and Clarion islands. *Physalis clarionensis* is but a depauperated form of *P. cordata*, since both have been collected at the same locality. The species has been collected in China and India where the species is probably adventive.

**Representative specimens examined.** **BAHAMAS:** Caicos Islands, S Caicos, 14-16 Dec 1907, *Wilson 7674* (F, NY). **BERMUDA:** Sandys Par., 18 Jul 1905, *Moore 3443* (CAS). **BRAZIL:** MINAS GERAIS: Alfenas, 1 Mar 1969, *Carauta 821* (US, atypical). PARANÁ: near Porto Byington, 23 Jan 1967, *Lindeman 4386* (NY). **CHINA:** HAINAN: Tan, Kap Shan and vicinity, 12-24 Feb 1933, *Lau 1123* (NY). **COLOMBIA:** DEL VALLE: Samaria, on Río Timba 2 km W of Timba, 13 Apr 1943, *Fosberg 20527* (US). LA GUAJIRA: Clausura Napaipa rumbo a Maicao, 13 Feb 1963, *Saravia 2225* (US). MAGDALENA: corregimiento de Santa Rosa, 18 Jul 1971, *Romero-Castañeda 11.057* (F, NY). **COSTA RICA:** CARIAGO: between Turrialba and Inter-American Inst. of Agr. Sci., 16 Nov 1953, *Heiser 3735* (F). **LIMÓN:** between Río Bananito and Cahuita, 13 Feb 1977,

*Gentry 3747* (OKL). CUBA: HABANA: Río Almendrares to Playa de Mariano, 22-23 Dec 1910, *Wilson 9504* (US). MATANZAS: Ciudad Matanzas, 25 Mar 1903, *Britton 595* (F). ORIENTE: Guantánamo Bay, 17-30 Mar 1909, *Britton 2240* (US). SANTA CLARA: Colonia Limones, Ingenio Soledad near Cienfuegos, 25 Jan 1903, *Pringle 40* (US). DOMINICAN REPUBLIC: MONTE CRISTI: 23 Nov 1971, *Jiménez 5960* (NY). ECUADOR: GALAPAGOS ISLANDS: Santa Cruz Island, Academy Bay, 3 Feb 1964, *Fournier 133* (US). EL SALVADOR: AHUACHAPÁN: vicinity of Ahuachapán, 9-27 Jan 1922, *Standley 20253* (US). LA LIBERTAD: vicinity of La libertad, 13 Apr 1922, *Standley 23237* (US). SANTA ANA: vicinity of Metapán, 29 Jan-1 Feb 1947, *Standley 3314* (F). SAN MIGUEL: vicinity of San Miguel, 24-27 Feb 1922, *Standley 21070* (US). SAN SALVADOR: along the road from San Martín to Laguna de Ilopango, 1 Apr 1922, *Standley 22560* (US). GUATEMALA : BAJA VERAPAZ: Niño Perdido, on San José road, 18 Jun 1977, *Lundell 21133* (F). CHIQUIMULA : 2 km from Esquipulas village, 6 Dec 1969, *Molina 25189* (F, NY, US). ESCUINTLA: near San José, 30-31 Jan 1939, *Standley 63963* (F). IZABAL: Los Amates, 12 Mar 1991, *Martínez & Hernández 1920* (TEX). JUTIAPA: vicinity of Jutiapa, 24 Oct-5 Nov 1940, *Standley 76159* (F). RETALHULEU: Ciudad Retalhuleu, 10 Jan 1907, *Kellerman 6665* (F, US). SAN MARGOS: Río Cabús, near Malacatán, 15 Mar 1939, *Standley 68888* (F). SANTA ROSA: vicinity of Taxiaco, 2 Dec 1940, *Standley 79023* (F). HAITI : vicinity of Jean Rabel, 25 Jan-9 Feb 1929, *Leonard 12695* (NY). HONDURAS : ATLÁNTIDA: bank of Tela river, between Rivas Gordas and Tila, 10 Apr 1970, *Molina 25696* (F). EL PARAÍSO: Río Jamestrán, NW of Chichicaste, 14 Dec 1958, *Molina 8805* (F, MO). MORAZÁN: Quebrada Capa Rosa, above Casa Grande near Zamorano, 13-17 Aug 1947, *Standley 12222* (F). OLANCHO: vicinity of Juticalpa, 5-16 Mar 1949, *Standley 17709* (F). INDIA KARNATAKA: Saem Hosur Taluk, Nov 1932, *Yeshode 447* (NY). MADRAS: Presidency College, 8 Feb 1932, *Janaki 702* (NY). JAMAICA : Spanish Town, 3 Sep, 1908, *Harris 10639* (NY). MEXICO: CAMPECHE: Tuxpeña, 6 Nov 1913, *Lundell 936* (CAS, F, NY, US). CHIAPAS: Esperanza, Escuintla, 13 Apr 1947, *Matuda 16484* (F). COLIMA: 5-10 mi N Tecomán, 25 Dec 1958, *Thompson 341* (TEX). GUERRERO: 16 km N of Acapulco, 22 Jan 1982, *Miller 295* (LL). JALISCO: 4 mi N of Bahía Navidad, 8 Nov 1960, *McVaugh 20843* (MEXU, TEX). OAXACA: vicinity of Cafetal Concordia, 1-15 Apr 1933, *Morton 2556* (US). VERACRUZ: San Andrés Tuxtla, estación de biología U.N.A.M., 19 Sep 1984, *Ibarra 1989* (MEXU). SINALOA: Santa Fe, Dec 1921, *Ortega 4384* (US). YUCATÁN: Izamal, Sep 1913, *Gaumer s.n.* (MEXU). NICARAGUA: BOACO: along hgw. 33 from Río Grande de Matagalpa on road from hgw. 1 to Terrabona, 9 Aug 1978, *Stevens 9892* (MEXU). CHONTALES: Hacienda Veracruz, 8 km S of Cuapa, 21 Sep 1983, *Nee 28300* (NY, TEX). MANAGUA: 16 Jun 1926, *Chaves 98* (US). RIVAS: vicinity of Chichigalpa, 12-18 Jul 1947, *Standley 11153* (F). PANAMA (selected from 11 collections): BOCAS DEL TORO: SE y NE del Campamento Changuinola, 19 Jan 1980, *Correa 3344* (NY). COLÓN: between France Field and Catival, 9 Jan 1924, *Standley 30236* (US). DARIÉN: Chocó village, 24 Jul 1977, *Folsom 4555* (MEXU). LOS SANTOS: Río Tonosí, vicinity of Tonosí, 25 May 1967, *Lewis 1579* (F). PANAMÁ: Piria, 24 Sep 1967, *Duke 14424* (US). PUERTO RICO (selected from 14 collections): MAYAGÜEZ: road from Mayagüez to Joyua, 20 Jun 1901, *Underwood 140* (NY, US). RÍO PIEDRAS: Ciudad Piedras, 5 Dec 1898, *Goll 1005* (US). UNITED STATES OF AMERICA: ALABAMA: Jefferson Co., 16 Sep 1897, *Eggert s.n.* (MO). Mobile Co., 1878, *Mohr s.n.* (MO, NY, US). Tuscaloosa Co., 25-27 Jul 1900 *Pollard 334* (US). ARKANSAS: Drew Co., 16 Oct 1937, *Demaree 16498* (NY). Fulton Co., 18 Sep 1900, *Bush 961* (MO, NY). Hot Springs Co., 2 Oct 1938, *Demaree 18471* (MO, NY). Logan Co., 13 Aug 1937, *Demaree 15743a* (NY). Pope Co., 21 Aug 1939, *Demaree 20185* (MO). FLORIDA: Dade Co., 1 Oct 1983, *Nee 28607* (MO). Polk Co., 3 Sep 1958, *King s.n.* (TEX, US). GEORGIA: Baker Co., 12 Jun 1947, *Thorne 4596* (NY). LOUISIANA: Avoyelles Par., 11 Oct 1985, *Thomas 94090* (MO). Evangeline Par., 1 Nov 1986, *Thomas 98981* (MO, NY).



Natchitoches Par., 2 Oct 1915, *Palmer 8777* (CAS). Orleans Par., 7 Jul 1896, *Joor s.n.* (MO). West Carroll Par., 4 Aug 1903, *Moseley s.n.* (US). MISSOURI: Barry Co., 17 Sep 1896, *Bush 547* (MO, NY). Butler Co., 7 Jul 1893, *Eggert s.n.* (MO, NY). Dunklin Co., 17 Sep 1893, *Bush 98* (MO, NY, OKLA). Jackson Co., 19 Jul 1888, *Bush 49* (MO). Saint Louis Co., Aug 1841, *Englemann s.n.* (MO). Shannon Co., 22 Aug 1907, *Bush 727* (MO). Stone Co., 18 Oct 1913, *Palmer 4697* (US). Taney Co., 25 Aug 1935, *Steyermark 19627* (US). MISSISSIPPI: Oktibbeha Co., 11-17 Aug 1896, *Pollard 1338* (MO, NY, US). NORTH CAROLINA: Hyde Co., 27 Oct 1968, *Leonard 2218* (DUDL, LL, TEX). TEXAS: Bell Co., 25 Oct 1930, *Wolff 2655* (US). Bowie Co., 15 Sep 1898, *Heller 4253* (NY, US). Brazoria Co., 5 Sep 1970, *Fleetwood 9918* (LL). Dallas Co., 10 Sep 1877, *Ward s.n.* (US). Harris Co., 1872, *Hall 503* (NY, US). Newton Co., 23 Jul 1939, *Tharp 42-141* (TEX). Orange Co., 1 Sep 1923, *Tharp 2518* (TEX). Panola Co., 10 Oct 1902, *Revercheron 3239* (MO, NY). VENEZUELA: APURE: NE caserío San Camilo, Río Nulita, 5 Apr 1968, *Steyermark 101875* (US). BOLÍVAR: Piar, Los Aceites, NW de El Manteco, Jul 1978, *Delascio 7399* (NY). DISTRITO FEDERAL: vicinity of Maracao, 31 Aug 1924, *Pittier 11544* (US). ZULIA: Mará, NW slopes of Cerro Negro, 29 May 1980, *Steyermark 122767* (NY).

3. *Physalis grisea* (Waterf.) M. Martínez, Taxon 42:103. 1993. *Physalis pubescens* L. var. *grisea* Waterf., Rhodora 60:167. 1958. Type: USA: Massachusetts, Middlesex Co., Cambridge, rubbish heap, 24 Sep 1884, *Walter Deane s.n.* Holotype: GH! Isotype: NY!

Annual herbs 10-50 cm high. Stems sericeous, non glandular hairs multicellular, 0.5-3.0 mm long. Leaves mostly sericeous, orange-tinged when dry, 10-20 cm long; petioles 5-7 cm long; blades ovate to lanceolate, apex acute to acuminate, base oblique with a difference of 0.5-1.0 cm, margins coarsely dentate. Flowering peduncles 4-6 mm long; flowering calyces with triangular lobes 1.5-2.2 mm long, sericeous; corollas yellow 0.7-1.0 mm in diameter, the petals with 5 dark purple maculations, glabrous within; filaments purple, anthers yellow or sometimes with a faint tinge of blue, 1.1-2.0 mm long. Fruiting peduncles 6-10 mm long; fruiting calyces strongly 5-angled, 2.5-3.0 cm long, 1.0-2.2 cm wide, always longer than wider, sericeous throughout with multicellular hairs. Mature berry spherical, 1.0-1.5 cm in diameter, yellow, containing numerous brown foveolate seeds 1.5-2.0 mm in diameter.

**Distribution** (Fig. 8). From southern Canada throughout the USA. Some specimens are believed to represent introductions; the original natural range was probably the NE USA. The vast majority of collections were made well over 20 years ago, suggesting perhaps that the natural populations are becoming decimated. The plant grows spontaneously in disturbed habitats (cultivated fields and waste areas).

**Flowering.** From May to October.

**Common names.** "Hairy ground cherry", "husk tomato", "shuck tomato", "strawberry tomato", "dwarf cape-goosberry".

**Uses.** The sweet fruit is eaten fresh or in preserves. The species is commonly offered for sale in seed catalogs.

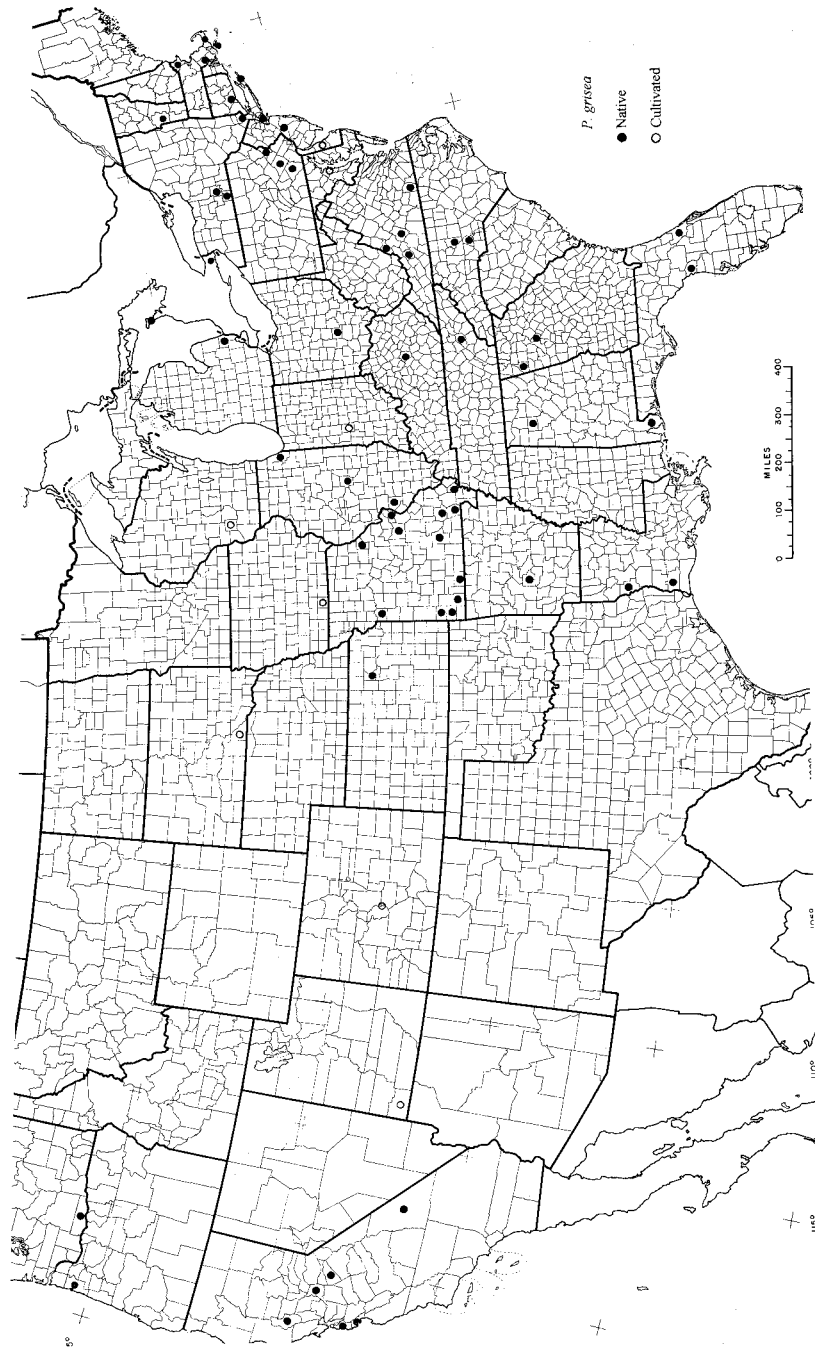


Fig. 8. Distribution of *P. grisea*.

**Observations.** *Physalis grisea* is closely related to *P. pubescens*, from which it is probably derived through human selection. The two are readily distinguished by the color of the anthers (yellow in *P. grisea*, mostly purple in *P. pubescens*), the coarsely dentate leaves, the sweet berry, and the lack of glands in the hairs. In living plants, *P. grisea* does not emit the strong odor of *P. pubescens*.

**Representative specimens examined.** CANADA: ONTARIO: Elgin Co., 18 Aug 1959, *James 3362* (OKLA). Southampton, 20 Aug 1901, *Macoun 54521* (NY). UNITED STATES OF AMERICA: ALABAMA: Baldwin Co., May 1907, *Dukes 118* (NY). Winston Co., 28 Apr 1880, *Mohr s.n.* (US). ARKANSAS: Garland Co., 24 Oct 1968, *Demaree 59643* (OKLA). CALIFORNIA: Calaveras Co., no date, *Blaisdell s.n.* (CAS). Inyo Co., 20 Jun 1931, *Hoffmann 491* (CAS). Marin Co., 30 Aug 1953, *Pollard s.n.* (CAS). Lake Co., 23 Oct 1929, *Blankinship s.n.* (MO). Sacramento Co., 22 Oct 1963, *Miller s.n.* (CAS). Santa Cruz Co., 27 Jul 1959, *Hesse 2727* (CAS). COLORADO (cultivated): College Farm, 20 Aug 1892, *no collector* (NY). CONNECTICUT: New Haven, 1874, *Kleenberg s.n.* (CAS). DELAWARE (cultivated): Kent Co., 3 Sep 1877, *Commons s.n.* (NY). FLORIDA: Citrus Co., 10 Jul 1967, *Montelaro s.n.* (OKLA). Volusia Co., 24 Aug 1911, *Hood s.n.* (MO). GEORGIA: Floyd Co., no date, *Chapman s.n.* (MO). DeKalb Co., 1-6 Aug 1895, *Small s.n.* (F, NY). ILLINOIS: Cook Co., Sep 1938, *Haynie 3521* (F). Macon Co., 29 Sep 1940, *Mills s.n.* (NY). Saint Clair Co., 26 Sep 1959, *Neill 11402* (MO). INDIANA (cultivated): Putnam Co., 9 Aug 1977, *Haurcot s.n.* (NY). IOWA (probably introduced): Decatur Co., 20 Aug 1914, *Anderson s.n.* (MO). KANSAS: Riley Co., Sep 1885, *Kellerman s.n.* (MO). KENTUCKY: Madison Co., 10 Aug 1965, *Grossman 590* (NY). LOUISIANA: Calcasieu Par., 18 Jul 1938, *Correll 9566* (NY). Sabine Par., 9 Jul 1968, *Thieret 30220* (LL). MARYLAND (cultivated from seeds from Idaho): Prince George Co., 30 Sep 1944, *McVaugh 6738* (F). MASSACHUSETTS: Barnstable Co., 5 Sep 1898, *Greenman 382* (MO). Bristol Co., 21 Sep 1959, *Seymour 18488* (CAS, MO). Dukes Co., 22 Sep 1915, *Bidenell 7693* (NY). Essex Co., 1 Aug 1868, *Morong s.n.* (NY). MICHIGAN: St. Clair Co., 25 Aug 1906, *Dodge s.n.* (TEX). MISSOURI: Barry Co., 28 Sep 1898, *Mackenzie s.n.* (OKLA). Buttler Co., 2 Oct 1892, *Dewart s.n.* (MO). Franklin Co., 18 Aug 1933, *Steyermark 8307* (MO). Jackson Co., 25 Oct 1897, *Mackenzie s.n.* (NY). Jasper Co., 6 Oct 1925, *Bush 10402* (NY). New Madrid Co., 2 Sep 1897, *Bush 189* (NY). Newton Co., 29 Oct 1954, *Palmer 59291* (F). Ralls Co., 13 Oct 1933, *Matthew 1265* (MO). Saint Louis Co., 16 Aug 1885, *Kellog s.n.* (MO). Shannon Co., 2 Sep 1918, *Bush 8753* (MO). Taney Co., 24 Sep 1899, *Bush 316* (MO). Wayne Co., 26 Aug 1898, *Trelease s.n.* (MO). NEW JERSEY: 6 Sep 1917, *Hastings s.n.* (NY). NEW YORK: Bronx Co., 12 Sep 1950, *Ahles s.n.* (CAS). Chemung Co., 3 Aug 1898, *Lucy 11098* (NY). Suffolk Co., 6 Oct 1906, *Bicknell 7692* (NY). Tompkins Co., 7 Aug 1934, *Hoisington s.n.* (OKLA). Westchester Co., 3 Nov 1896, *Bicknell 7691* (NY). NORTH CAROLINA: Stanley Co., 24 Sep 1956, *Ahles 19977* (NY). Wake Co., 31 Oct 1948, *Gregory s.n.* (US). OHIO: Pickaway Co., 25 Oct 1966, *Bartaley 3059* (NY). OREGON: Tillamook Co., 10 Sep 1874, *Lloyd s.n.* (NY). PENNSYLVANIA: Berks Co., 7 Oct 1939, *Wilkens 6078* (CAS). Lancaster Co., 27 Aug 1890, *Small s.n.* (OKLA). Southampton Co., 1880, *Raw 65* (MO). SOUTH DAKOTA: Georgy Co., 24 Oct 1948, *White s.n.* (US). TENNESSEE: Knox Co., Jun 1896, *Ruth s.n.* (MO). UTAH (probably introduced): Washington Co., 17 Jun 1934, *Harrison 6247* (MO). VERMONT: Ruthland Co., 17 Sep 1906, *Dutton s.n.* (MO). VIRGINIA: Allegheny Co., 5 Sep 1903, *Steele 216* (NY). Bedford Co., 30 Aug 1872, *Curtiss s.n.* (NY). Brunswick Co., 1942, *Lewis 3630* (VPI). Pulaski Co., 5 Sep 1910, *FSH s.n.* (VPI). WASHINGTON: Klickitat Co., Sep-4 Nov 1874, *Sucksdorf 2285* (NY). WISCONSIN (cultivated): Richland Center, 8 Oct 1977, *Nee 14630* (MO).

4. *Physalis ignota* Britton, Mem. Torrey Bot. Club 16:100. 1920. Type: Cuba: Santa Clara, Rio Arimao, 22 Mar 1910, *Britton & Wilson 5767*. Holotype: NY!  
*Physalis pentagona* S.F. Blake, Contr. U.S. Natl. Herb. 24:20. 1922. Type: Guatemala: Izabal, Los Amates, 9 May 1919, *Blake 7313*. Holotype: us!

Annual herbs, 30-500 cm high, densely covered with short multicellular glandular grey hairs throughout. Leaves tomentose, 7-19 cm long; petioles 1.5-8.0 cm long; blades mostly elliptic (rarely ovate), 5.5-11.5 cm long, 3-9 cm wide, apex acuminate, base oblique (rarely cordate), margin entire to rarely dentate. Flowering peduncles 3.5-6.0 mm long; flowering calyces with triangular lobes, 2-3 mm long, 0.6-1.1 mm wide; corollas yellow or greenish-cream, 6-11 mm in diameter, immaculate, pubescent within; filaments green or purple, anthers green or blue-tinged, 1.6-2.5 mm long. Fruiting peduncles 10-17 mm long. Fruiting calyces strongly 5-angled, 2-5 cm long, 2-4 cm wide, tomentose throughout. Mature berry spherical, ca. 1 cm in diameter, containing numerous seeds ca. 1.5 mm in diameter.

**Distribution** (Fig. 9). From Chiapas (Mexico) throughout Central America and the West Indies. The plant occurs from sea level up to 1500 m in sandy soils, usually associated with rivers or streams. The species is sympatric with *P. pubescens* and *P. gracilis*.

**Flowering.** Throughout the year.

**Common names.** "Huevo de tortuga", "miltomate" (El Salvador); "soplón", "miltomate" (Guatemala); "tomatillo", "vejiga de perro", "farolito" (Honduras); "popa", "popita" (Nicaragua).

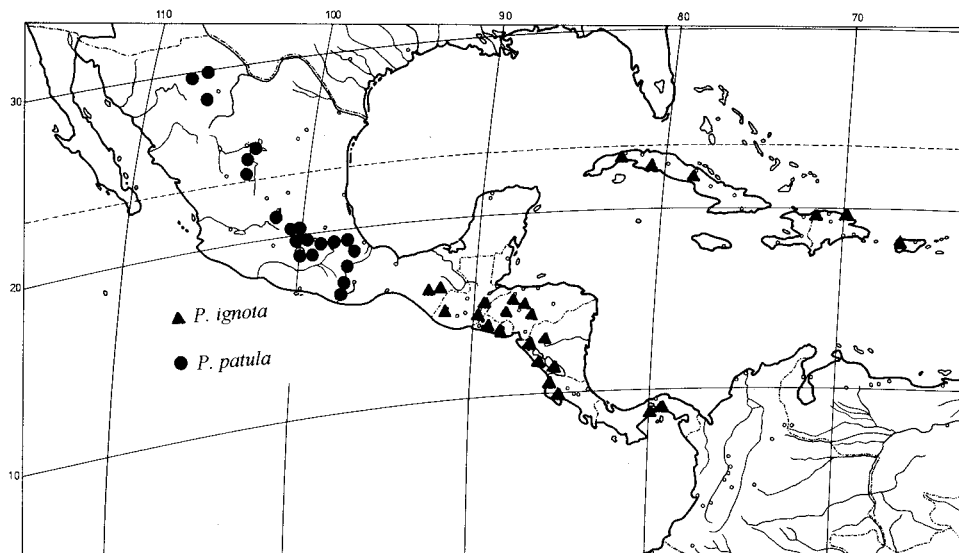


Fig. 9. Distribution of *P. ignota* and *P. patula*.

**Observations.** *Physalis ignota* is readily distinguished from the other species in the section by its very small corolla and large fruiting calyces which are densely tomentose. *Physalis ignota* is adapted to wet areas. Nevertheless, it is probably closely related to *P. pruinosa* and *P. nicandroides*, both adapted to dry habitats, sharing with them the large, deeply invaginated fruiting calyces and the corollas without strongly contrasting maculations.

**Representative specimens examined.** COSTA RICA : GUANACASTE: Santa Rosa, Aug 1971, *Callaway 202* (US). CUBA: CAMAGÜEY: near railroad station, 31 Mar 1909, *Schafer 1127* (NY). HABANA: near Playa de Mariano, 28 Nov 1916, *León 6864* (NY). SANTA CLARA: Limones, Soledad, 23 Aug 1927, *Jack 6264* (F, NY, US). DOMINICAN REPUBLIC: Nigua, 30 Oct 1971, *Liogier 18228* (US). EL SALVADOR: SAN MIGUEL: vicinity of San Miguel, 24-27 Feb 1922, *Standley 21092* (NY, US). SANTA ANA: vicinity of Metapán, 29 Jan-1 Feb 1947, *Standley 3316* (F). SAN SALVADOR: vicinity of San Salvador, 30 Mar-24 Apr 1922, *Standley 23156* (NY, US). SAN VICENTE: vicinity of San Vicente, 2-11 Mar 1922, *Standley 21166* (US). GUATEMALA : BAJA VERAPAZ: La Cumbre, km 132 to Salamá, 30 Sep 1972, *Molina 27720* (F). CHIQUIMULA: between Ramírez and Cumbre de Chiquimula, between Chiquimula and Zacapa, 15 Oct 1940, *Standley 74568* (F). IZABAL: Los Amates, 12 Mar 1991, *Martínez & Hernández 1918* (TEX). JUTIAPA: vicinity of Jutiapa, 24 Oct-5 Nov 1940, *Standley 75722* (F). SAN MARCOS: near Ayutla, 14-15 Mar 1939, *Standley 68808* (F). ZACAPAN: vicinity of Zacapa, 7-16 Oct 1940, *Standley 73609* (F). HONDURAS: COMAYAGUA: Comayagua Valley, 4 Sep 1968, *Molina 22676* (F, NY). CORTÉS: carretera a Chamelecón, 27 Mar 1963, *Molina 11626* (F, NY). EL PARAÍSO: near Limonal, 6 Jan 1951, *Standley 28159* (F). MORAZÁN: along rd. from El Zamorano toward Chagüite, 9 Jul 1949, *Standley 21004* (F). SANTA BÁRBARA: between Llamas and Gualala, 23 Aug 1968, *Molina 22056* (F, NY). VALLE: Amapala, 11 Sep 1945, *Rodríguez 3398* (F). MEXICO: CHIAPAS: Cintalapa, at Las Cruces on rd. to La Ciénega, 18 Sep 1981, *Breedlove 52891* (CAS, NY). NICARAGUA: ESTELÍ: vicinity of Guava, 20 km from Estelí town, 5 Nov 1968, *Molina 23116* (NY). LEÓN: along hgw. 12 ca. 4 km SE of intersection with hgw. 52, 8 Aug 1978, *Stevens 9781* (MEXU). MANAGUA: hgw. 10 bridge along Río Montelimar, 28 Jul 1978, *Stevens 9523* (MEXU). MASAYA: Parque Nacional Volcán, 26 Aug 1978, *Neill 4625* (MEXU). RIVAS: above Begüe, Isla Ometepe, 14 Sep 1983, *Nee 28017* (TEX). PANAMA: PANAMÁ: vicinity of San Carlos, 5 Dec 1938, *Allen 1136* (NY, US). PUERTO RICO: Ensenada, 11 Dec 1985, *Liogier 35745* (NY).

5. *Physalis latiphysa* Waterf., *Rhodora* 60:169. 1958. Type: USA: Arizona, Pima Co., Rondstadt Ranch east of Baboquivari Mountains, 23 Sep 1939, *Kearney & Peebles 14425*. Holotype: ARIZ!

Annual herbs 30-45 cm high. Stems densely glandular-pubescent, hairs multicellular. Leaves sericeous, 5.5-16.0 cm long; petioles 2.5-7.5 cm long; blades ovate, sericeous, 3.0-8.5 cm long, 1.5-7.0 cm wide, apex acuminate, base truncate, seldomly oblique up to 3 mm off, margin entire to seldomly dentate with up to 4 teeth per side. Flowering peduncles 4-11 mm long; flowering calyces glandular-pubescent with acuminate lobes, 2.2-2.5 mm long, 1.0-1.5 mm wide; corollas cream-yellow 3.5-4.0 mm in diameter, petals with 5 separate dark blue maculations within;

filaments pubescent, blue; anthers blue or blue-tinged, ca. 1 mm long. Fruiting peduncles 1.8-2.0 cm long; fruiting calyces strongly 5-angled, 3-4 cm long, 2.5-3.5 cm wide, frequently as long as wide, glandular-pubescent throughout. Mature berry spherical, 1.3-2.0 cm in diameter, not glutinous, containing numerous brown foveolate seeds ca. 2.5 mm in diameter.

**Distribution**(Fig. 10). From southern Arizona, known from only one collection in Sonora, Guanajuato and Michoacán (Mexico).

**Flowering.** July-September.

**Observations.** *Physalis latiphysa* is closely related to *P. pruinosa* from which it differs in possessing shorter flowering pedicels and blue anthers. These characters place it also close to *P. nicandroides*, but *P. latiphysa* has longer hairs, thinner fruiting peduncles, and papery (not leathery) fruiting calyces. From both, *P. latiphysa* differs in having a non-glutinous fruit.

**Specimens examined.** MEXICO:GUANAJUATO: 4 km al N de Uriangato, municipio de Uriangato, 16 Oct 1992, *J. Rzedowski 51820* (IEB, QMEX). MICHOACÁN: 7 km al E de Villa Jiménez, sobre el camino a Copándaro, 5 Oct 1986, *J. Rzedowski 40745* (IEB, QMEX). SONORA: between Tepapa and Batuc, 28 Sep 1934, *Wiggins 7503* (CAS). UNITED STATES OF AMERICA ARIZONA: Cochise Co., 21 Aug 1981, *Van Devender s.n.* (ARIZ). Pima Co., 31 Aug 1940, *Kearney 14932* (ARIZ, US). Santa Cruz Co., 30 Aug 1931, *Harrison 8158* (ARIZ).

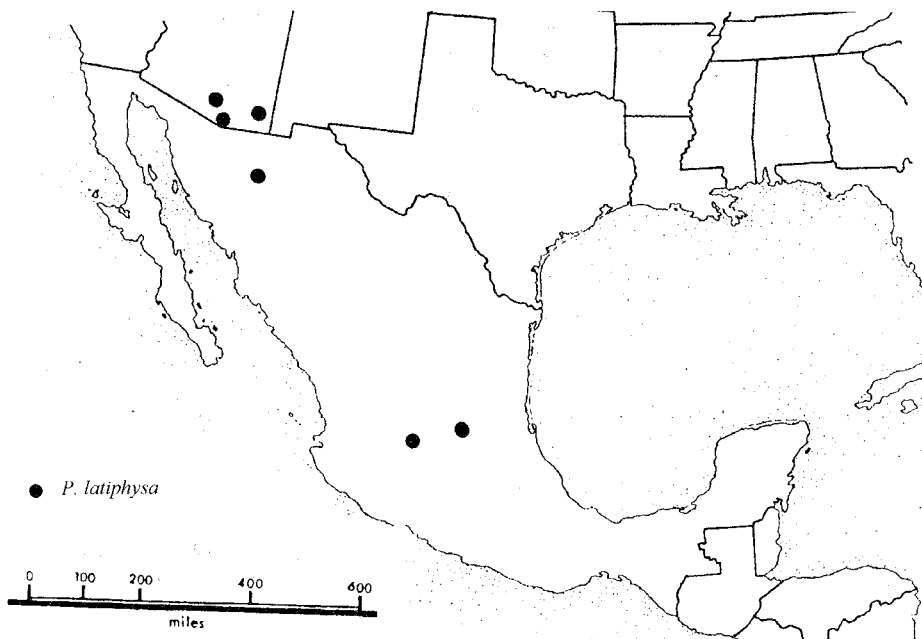


Fig. 10. Distribution of *P. latiphysa*.

6. *Physalis leptophylla* B. L. Rob et Greenm., Proc. Amer. Acad. Arts 29:389. 1894. Type: Mexico, Sinaloa near Mazatlan, Jan 1889, *W.G. Wright 1252*. Lectotype: **GH!** (Fig. 11).

Annual herbs 15-100 cm high, profusely branched. Stems villous with multicellular glandular hairs up to 2 mm long. Leaves villous 7.5-15.0 cm long; blades ovate to elliptic, villous especially along the veins, 4-10 cm long, 2.5-6.0 cm wide, apex acuminate, base cordate, sometimes oblique up to 4 mm off, margin entire. Flowering peduncles 2.5-3.0 mm long; flowering calyces villous with deltate lobes 1.0-1.5 mm long, 1.0-1.5 mm wide; corollas pale yellow, 0.7-11.0 mm in diameter, the petals with 5 separate purple maculations, glabrous within; filaments brown; anthers blue or blue-tinged, rarely yellow, 1.5-2.0 mm long. Fruiting peduncles 2.5-3.0 mm long; fruiting calyces slightly 5-angled to terete, only slightly invaginated, 1.5-2.5 cm long, 0.9-1.8 cm wide, always longer than wide, villous throughout. Mature berry ca. 1 cm in diameter, containing numerous golden foveolate seeds ca. 1 mm in diameter.

**Distribution** (Fig. 5). Restricted to Mexico in the Pacific lowlands. The plant is a weed of dry habitats growing in disturbed habitats of tropical forest and scrubland, sea level to 600 m. Although not frequently collected, the plant is reported as abundant where encountered.

**Flowering.** Throughout the year.

**Common names.** "Tomate", "tomatillo", "tomate del monte", "shiquipiltzi".

**Uses.** The ripe fruits are cooked in Sonora.

**Observations.** *Physalis leptophylla* is sympatric with *P. pruinosa* and several mixed collections have been noted (i.e. *Gentry 4771 NY*, *Lott 1455 F, MEXU, MO*). The former is readily distinguished from the latter by the shape of the calyx lobes (obtuse in *P. leptophylla*, acuminate in *P. pruinosa*) and the length of the peduncles that in *P. leptophylla* never exceed 0.3 cm, whereas *P. pruinosa* has 1.7-3.0 cm long peduncles.

*Physalis leptophylla* is probably closest to *P. missouriensis* and *P. pubescens*. From the former species it differs in the presence of corolla maculations and leaf shape and from the later it differs in the shape of calyx lobes (obtuse vs. triangular) and fruiting calyces (almost terete in *P. leptophylla*). Rydberg (1896) included this species in his series *Leptophyllae*, which I do not recognize as valid based on cpDNA and epidermal SEM evidence (Martínez, 1993).

**Representative specimens examined:** MEXICO: COLIMA: Vicinity of Manzanillo, 2 Dec 1925, *Ferris 6134 (CAS)*. DURANGO: 10 mi N of Tamazula, 18 Dec 1939, *Gentry 5270 (CAS, NY)*. MÉXICO: Temascaltepec, at Bejucos, 13 Nov 1933, *Hinton 5204 (US)*. GUERRERO: terrenos frente a gasolinería Revolcadero, Mpio. Puerto Marqués, 15 Sep 1981, *López-Forment 1411 (MEXU)*. JALISCO: estación de Biología Chamela, 20 Nov 1974, *Pérez 1100 (F, MEXU)*. NAYARIT: María Madre, Tres Marías Islands, between penal colony and W side of Island, 24 Oct 1925, *Ferris 5717 (CAS, US)*. OAXACA: Arroyo del Mármol, ladera W del cerro Guiengola, 18 Km NW de Tehuantepec, 3 Sep 1986, *Torres 406 (MEXU, MO)*. SINALOA: Mpio. Elota, 5.7 mi N of jct with road to La Cruz on México 15, 28 Jan 1962, *Breedlove 1549 (CAS)*. SONORA: Alamos, 28 Oct 1939, *Gentry 4771 (CAS, F, NY, US)*.

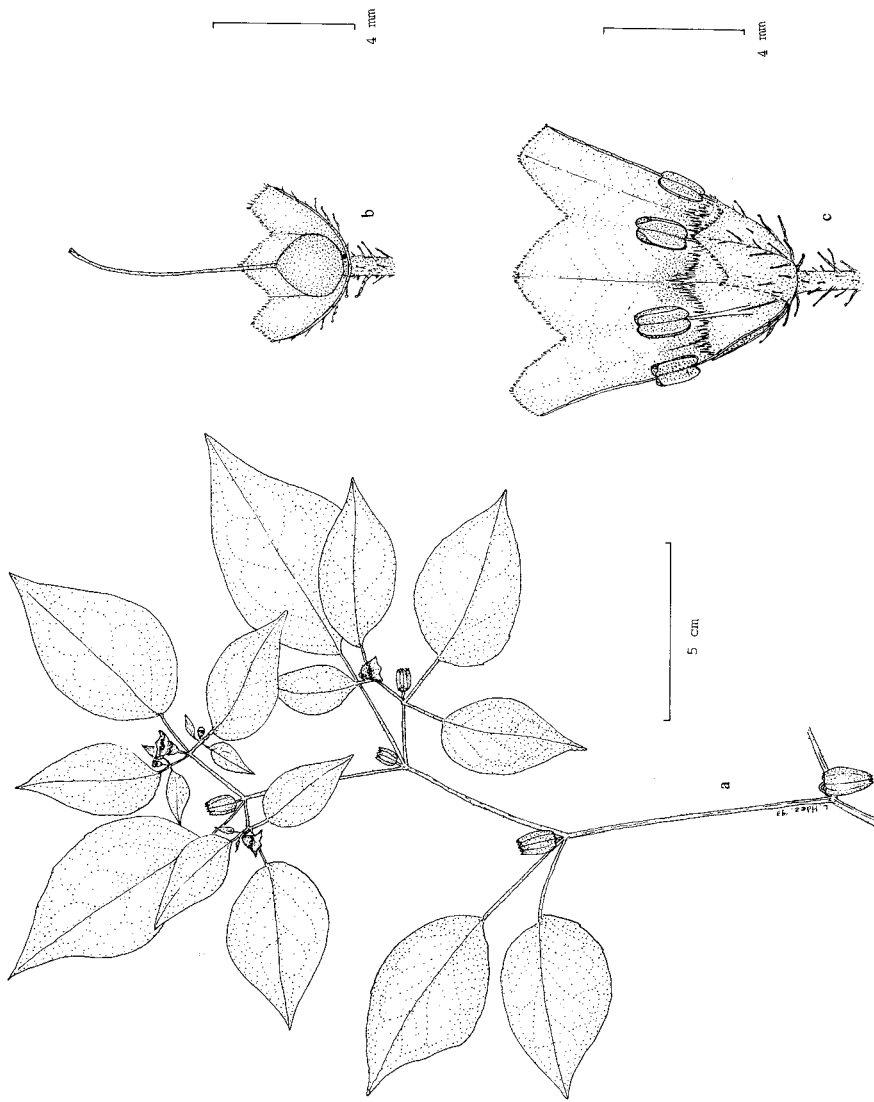


Fig. 11. *P. leptophylla* B. L. Rob et Greenm.: a) branch with flowers and fruits; b) detail of the ovary and style; c) detail of the corolla.



7. *Physalis minuta* Griggs, *Torrey* 3:138. 1903. Type: Mexico: Guerrero, Acapulco, winter of 1894-1895, *Palmer 304*. Holotype: US! A voucher with the same collection number is on deposit at NY!, but the plant is a specimen of *P. philadelphica*.

*Physalis mimulus* Waterf., *Rhodora* 69:211. 1967. Type: Mexico: Colima, Socorro Island, Mar 1889, *Townsend s.n.* Holotype: US!

Annual herbs 15-40 cm high. Stems strigose, becoming glabrate with age. Leaves strigose, 3.5-9.9 cm long; petioles 2.0-5.5 cm long, blades lanceolate, ovate to broadly ovate, becoming glabrate with age, 1.5-4.0 cm long, 0.5-2.5 cm wide, the apices acute, bases obtuse, oblique up to 5 mm off, margins entire to undulate. Flowering peduncles 3.5-5.5 mm long, flowering calyces strigose with deltate lobes 1.0-1.5 mm long, 0.5-1.0 mm wide; corollas yellow, 5-6 mm in diameter, petals immaculate or with 5 separate purple maculations, glabrous within; filaments purple, anthers yellow, 1.0-1.5 mm long. Fruiting peduncles 5-8 mm long; fruiting calyces strongly 5-angled, invaginated, 1.5-2.0 cm long, 1.0-1.5 cm wide, strigose. Mature berry ellipsoid, ca. 0.8 cm long, 0.6 cm wide, containing numerous golden foveolate seeds ca 1.5 mm in diameter.

**Distribution** (Fig. 12). Mexico and Central America in sandy soils along the Pacific Coast.

**Flowering.** Throughout the year.

**Uses.** Palmer reported in the label of his specimen 304 (US) that the species was sold in Acapulco's market throughout the year, but most probably he was referring to *P. philadelphica*, the common "tomatillo."

**Observations.** *Physalis minuta* is closely related to *P. cordata* from which it differs in its smaller size, mostly immaculate corollas and long petioles. *Physalis mimulus* appears to be a depauperate form of *P. minuta* from Socorro Island.

**Representative specimens examined:** COSTA RICA: GUANACASTE: Playa del Coco, 1 mi S of entrance along beach, 12 Oct 1975, *Durkee 75-100* (F, MO). PUNTARENAS: Isla San Lucas, Golfo de Nicoya, 21 Oct 1984, *Grayum 4274* (MO). MEXICO: COLIMA: Puente Palo Verde II between Cuyutlán and Armería, 9 Nov 1991, *Sanders 11914* (TEX). JALISCO: Mpio. La Huerta, Rancho Cuixmala, 13 Sep 1911, *Sanders 11173* (TEX). NAYARIT: about 7.7 mi N of Santa Cruz, 9 Sep 1973, *Stevens 2022* (MO). NICARAGUA: CARAZO: estación de biología Chacocenter, 9 Nov 1984, *Grijalva 4150* (MO). CHINANDEGA: Corinto, 19 Jul 1947, *Standley 11555* (F). LEÓN: Las Peñitas al SE de Poneloya, 1 Jul 1982, *Sandino 3200* (MO). MANAGUA: ca. 1.9 km W of Montelimar, 31 Aug 1977, *Stevens 3609* (MO). RIVAS: 2.6 km NW of entrance of San Martín on rd to Río Escalante, 3 Aug 1978, *Stevens 9740* (MO). PANAMA: LOS SANTOS: beach at Montagre, 23 Dec 1966, *Burch 1205* (F, NY).

8. *Physalis missouriensis* Mack. et Bush, *Trans. Acad. Sci. St. Louis* 12:84. 1902. Type: USA: Missouri, Jackson Co., Red Bridge, 18 Sep 1901, *Mackenzie 485*. Holotype: K.K.Mackenzie Herb. (NY, not located); Isotypes: GH!, MICH, WIS.

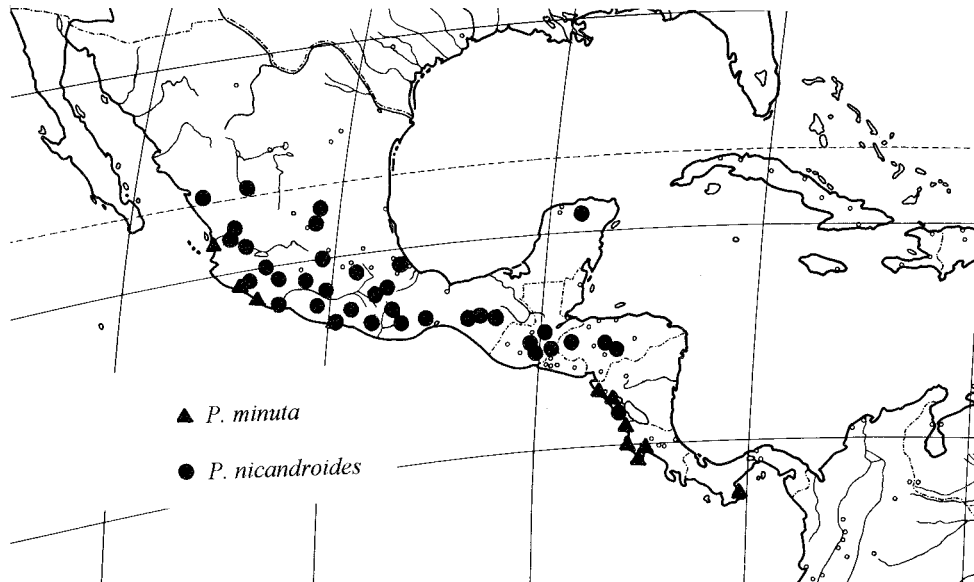


Fig. 12. Distribution of *P. minuta* and *P. nicandroides*.

Annual herbs 15-40 cm high. Stems profusely branching, densely villous with multicellular glandular hairs 0.5-1.2 mm long. Leaves villous, 3.5-9.5 cm long; petioles 1-4 cm long; blades ovate to oblong, villous throughout but sometimes more densely so on the veins, 2.5-5.5 cm long, 2.0-4.5 cm wide, apices acute, bases obtuse to cordate, oblique in some specimens, up to 5 mm off, margins crenate. Flowering peduncles 2.5-6.0 mm long; flowering calyces villous with deltate lobes 1.5-2.5 mm long, 1.4-2.0 mm wide; corollas yellow, 7.0-9.5 mm in diameter, immaculate, pubescent within; filaments and anthers yellow, blue or blue-tinged, 0.8-1.0 mm long. Fruiting peduncles 5.5-9.0 mm long; fruiting calyces slightly 5-angled to terete, only slightly invaginated, 1.5-2.5 cm long, 1.5-2.0 cm wide, longer than wide, villous throughout. Mature berries spherical, 1.0-1.5 cm in diameter, containing numerous golden foveolate seeds ca. 2 mm in diameter.

**Distribution** (Fig. 13). Restricted to the United States in Arkansas, Kansas, Missouri and Oklahoma.

**Flowering.** From June to October.

**Observations.** *Physalis missouriensis* is readily distinguished from other species in the section *Epeteiorhiza* because of its almost terete fruiting calyces and immaculate corollas. Superficially, it resembles *P. angulata*, from which it differs in being densely villous-glandular throughout and having pedicels that do not exceed 1 cm in length.

Rydberg (1896) incorrectly identified this species as *P. lagascae* and considered it to belong to his series *Leptophyllae* because of its almost terete fruiting calyces. However, cpDNA data and SEM studies indicate that it is close to *P. pubescens*.

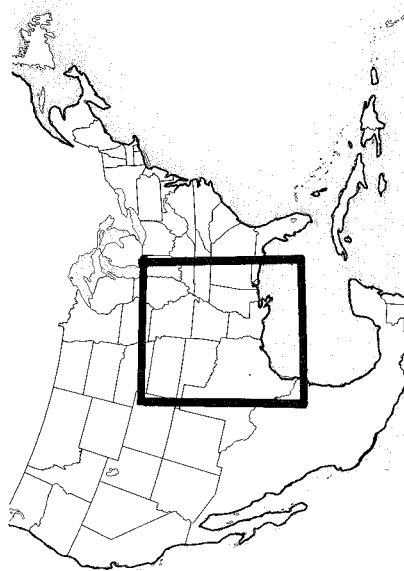
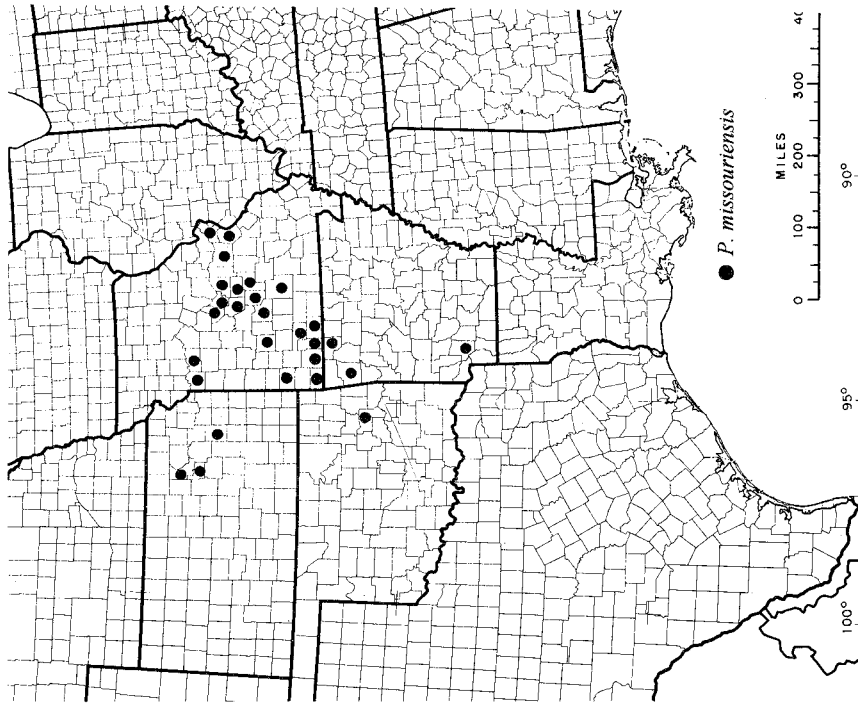


Fig. 13. Distribution of *P. missouriensis*.

**Representative specimens examined.** UNITED STATES OF AMERICA: ARKANSAS: Carroll Co., 23 Oct 1925, *Palmer 29310* (MO). Washington Co., 27 Sep 1930, *Moore 3008* (TEX). KANSAS: Geary Co., 3 Oct 1935, *Gates 18663* (MO). Osage Co., 25 Aug 1989, *McGreggor 40103* (MO). Riley Co., 22 Aug 1895, *Norton 366* (MO, NY). MISSOURI: Barry Co., 7 Sep 1898, *Trelease 1126* (MO). Christian Co., 6 Jul 1937, *Steyermark 22962* (MO). Cole Co., 18 Aug 1937, *Steyermark 24911* (MO). Franklin Co., 4 Aug 1937, *Anderson s.n.* (MO). Jackson Co., 6 Aug 1888, *Bush 1023* (MO). Jasper Co., 10 Jul 1910, *Palmer 2988* (MO). Jefferson Co., Sep 1912, *Gray s.n.* (MO). Lafayette Co., 13 Aug 1937, *Steyermark 24704* (MO). Maries Co., 29 Aug 1937, *Steyermark 25579* (MO). McDonald Co., 4 Jul 1933, *Kellogg s.n.* (MO). Miller Co., 25 Oct 1936, *Steyermark 20660* (MO). Montieau Co., 16 Aug 1937, *Steyermark 24792* (MO). Phelps Co., 22 Oct 1913, *Kellogg 196* (MO). Polk Co., 1 Aug 1937, *Steyermark 24051* (MO). Pulaski Co., 26 Aug 1937, *Steyermark 25397* (MO). St Louis Co., 20 Jul 1896, *Letterman s.n.* (MO). Stone Co., 22 Aug 1935, *Steyermark 19532* (MO). Taney Co., 12 Jun 1898, *Bush 173* (MO). Texas Co., 27 Sep 1990, *Summers 3841* (MO). OKLAHOMA: Muskogee Co., 26 Aug 1927, *Little 2568* (OKL).

**9. *Physalis neomexicana*** Rydb., Mem. Torrey Bot. Club 4: 325. 1896. *Physalis foetens* Poir. var. *neomexicana* (Rydb.) Waterf., Rhodora 60: 168. 1958. *Physalis subulata* Rydb. var. *neomexicana* (Rydb.) Waterf. ex Kartesz et Gandhi, Phytologia 72:89. 1992. Type USA: New Mexico [Santa Fe; cf. Gray 1849], 1847, *Fendler 678*. Lectotype: **GH!** Isolectotype: **GH!**

Annual herbs 10-50 cm high. Stems angulate and blue tinged at least at the top, densely covered with multicellular glandular hairs up to 1.5 mm long. Leaves 2.5-9.5 cm long, glandular-pubescent with multicellular hairs; petioles 0.5-3.5 cm long; blades ovate, 2.0-6.5 cm long, 1-5 cm wide, apex acute, base truncate, if oblique, only 3 mm off, margins crenate. Flowering peduncles 3.0-4.5 mm long; flowering calyces with acuminate lobes 2.0-3.5 mm long; corollas yellow, 0.8-1.3 cm in diameter, the petals with 5 separate dark blue maculations, pubescent within at insertion of filaments; filaments and anthers blue or blue-tinged, anthers 0.9-1.2 mm long. Fruiting peduncles 0.8-1.0 cm long; fruiting calyces strongly 5-angled, densely glandular-pubescent, 2-3 cm long, 2.0-2.5 cm wide, frequently as long as wide. Mature berry spherical, 1-2 cm in diameter containing numerous brown foveolate seeds 2.0-2.5 mm in diameter.

**Distribution** (Fig. 6). Restricted to the USA. in the Rocky Mountains in the states of Colorado, New Mexico, Arizona and Texas. The plant grows from 1500 to 2500 m in disturbed pinyon-juniper forest or disturbed short grassland.

**Flowering.** From June to September.

**Common names.** "Ground cherry", "tomate del campo".

**Observations.** When describing *P. neomexicana*, Rydberg included a flowering specimen from California (*Orcutt s.n.*, 1883 US) which has triangular calyx lobes, yellow anthers and long (3 cm) peduncles which I think does not belong to this species. The exclusion leaves *P. neomexicana* as a species endemic to the Rocky Mountains.

*Physalis neomexicana* and *P. patula* (formerly called *P. foetens*) are closely related, but they have distinct morphological characters and different distributions. Therefore, I treat them as different species.

**Representative specimens examined.** UNITED STATES OF AMERICA: ARIZONA: Apache Co., 2 Sep 1966, *Barr 66-111* (ARIZ). Greenlee Co., 14 Aug 1974, *Pinkava P12431* (NY). COLORADO: Fremont Co., 18 Aug 1952, *Waterfall 10886* (OKLA). El Paso Co., 19 Jul 1872, *Redfield 545* (MO). NEW MEXICO: Bernardillo Co., 21 Sep 1975, *Tierney 2* (ALBU). Catron Co., 9 Sep 1987, *Shelton 125* (NY). Colfax Co., 27 Aug 1916, *Standley 13869* (NY). Dona Ana Co., 10 Sep 1899, *Wootton s.n.* (US). Grant Co., 1 Aug 1911, *Holzinger s.n.* (US). Hardin Co., 23 Sep 1907, *Hansen s.n.* (ALBU). Lincoln Co., May-Jun 1898, *Skehan 60* (CAS, F, NY, US). Los Alamos Co., 4 Sep 1979, *Tierney 59* (ALBU). Luna Co., 2 Sep 1978, *Davis 473* (MO). McKinley Co., 28 Aug 1936, *Gardner s.n.* (ALBU). Otero Co., 17 Aug 1952, *Casteller 5526* (ALBU). Rio Arriba Co., 28 Aug 1946, *Parker 6449* (CAS). Sandoval Co., 12 Aug 1957, *Yarnell 84* (ALBU). Santa Fe Co., 27 Sep 1964, *Bobisud 44* (ALBU). San Miguel Co., 21 Aug 1974, *Higgins 9099* (NY). Socorro Co., 8 Aug 1903, *Metcalfe 425* (NY). Taos Co., 25 Aug 1965, *Martin 6022* (ALBU). Torrance Co., 31 Aug 1946, *Parker 6529* (CAS, NY). Union Co., 19 Jun 1911, *Standley 6197* (US). TEXAS: Culberson Co., 3 Sep 1954, *Warnock 11991* (OKLA). Jeff Davis Co., 26 Jul 1986, *Worthington 14337* (NY).

**10. *Physalis nicandroides*** Schldl., *Linnaea* 19:311. 1846. Type: Mexico: [Hidalgo] Atotonilco el Grande, Sep 1837, *Ehrenberg 760* (HAL). Lectotype, selected here: HAL. Photolectotype: MEXU!

Annual herbs, 40-300 cm high. Stem unbranched, densely glandular-pubescent. Leaves glandular-tomentose, 7-19 cm long; petioles 2.5-5.0 cm long; blades of the growing season ovate to oblong, 4.5-14.0 cm long, 3-11 cm wide. Blades of the dry season associated with mature fruits oblong to elliptic, 3.5-4.0 cm long, 2-3 cm wide. Both kind of leaves with acute apex, base oblique up to 1 cm off, margin dentate to almost entire. Flowering peduncles ca. 6 mm long, flowering calyces glandular-pubescent with acuminate lobes 1.5-4.5 mm long, 0.5-0.8 mm wide; corollas pale yellow or whitish, 5-6 mm in diameter, glandular-pubescent outside, villous within, the petals with 5 greenish not strongly contrasting maculations; filaments dark blue or purple, anthers greenish, blue-tinged or blue, 1.4-2.0 mm long. Fruiting peduncles much thickened, 1.1-2.0 mm in diameter, 10-14 mm long; fruiting calyces strongly 5-angled with a leathery texture, 3.0-5.0 cm long, 2.0-4.5 cm wide, frequently as long as wide, glandular-pubescent. Mature berry spherical, 1.0-1.5 cm in diameter, glutinous, dark brown, containing numerous dark brown foveolate seeds ca. 2.5 mm in diameter.

**Distribution** (Fig. 12). From Durango throughout Mexico and S to Nicaragua. The plant grows in disturbed habitats of pine-oak forest, thorn forest and scrubland; from sea level up to 1900 m.

**Flowering.** From July to December. Collected with ripe fruits in January and February.

**Common names.** “Miltomate”, “tomate zope” (Guatemala); “tomatillo”, “vejiga de perro” (Honduras); “matapulgas”, “tomate culebra”, “tomate de perro”, “tomatón”, “yucu-quoise” (Mexico).

**Uses.** Reported as a medicinal in Morelos; in Guerrero, the sticky leaves are laid over the floor forming a carpet that acts as an insect trap, especially for fleas; the fruit is occasionally eaten in Morelos (Mexico) and Guatemala.

**Observations.** *Physalis nicandroides* is closely related to *P. pruinosa*, from which it differs in having a thickened peduncle in fruit, colored anthers and hairs of the stem of a uniform size.

**Representative specimens examined.** GUATEMALA: CHIMALTENANGO: near finca La Alameda, 7 Dec 1938, *Standley 59082* (F). CHIQUIMULA: between Ramírez and Cumbre de Chiquimula, 15 Oct 1940, *Standley 74564* (F). GUATEMALA: Guatemala City, 1939, *Aguilar 141* (F). JUTIAPA: vicinity of Jutiapa, 24 Oct-5 Nov 1940, *Standley 75718* (F, US). QUICHE: without locality, 1942, *Aguilar 1118* (F). SANTA ROSA: La Joya de Limón, E of Cuilapa, 25 Nov 1940, *Standley 78317* (F). ZACAPA: near divide on road between Zacapa and Chiquimula, 9 Oct 1940, *Standley 73840* (F). HONDURAS: COMAYAGUA: near El Banco, 29 Sep-5 Oct 1951, *Williams 18335* (F, US). OCOTEPEQUE: vicinity of Ocotepeque town, Marchala river, 30 Aug 1968, *Molina 22497* (F, NY). MORAZÁN: vicinity of Suyapa, Sep-Dec 1948, *Standley 15380* (F). MEXICO: CHIAPAS: Mpio. Berriozábal, flats near Berriozábal, 23 Aug 1981, *Breedlove 52384* (CAS, MEXU). COLIMA: rancho El Jabalí, 20 km NNW of Colima, 6 Jan 1991, *Sanders 10277* (TEX). DURANGO: Ciudad de Durango, 20 Oct 1911, *Patoni 286* (MEXU). GUANAJUATO: Santiago Maravatio, 8 Aug 1987, *Rzedowski 44206* (MEXU). GUERRERO: Mpio. Tlapa, a 8 km N de Tlapa, 16 Nov 1982, *Martínez 2665* (MEXU, TEX). JALISCO: Río Blanco, Jun-Oct 1886, *Palmer 582* (NY). MICHOACÁN: Mpio. Uruapan, 1 km al S de Uruapan camino a Nueva Italia, 15 Nov 1983, *Martínez 5255* (MEXU, NY). MORELOS: 3 km SE de la Joya, entre Cuernavaca y Yautepec, 30 Dec 1990, *Hernández 2488* (TEX). NAVARIT: Mpio. Ixtlán, km 5-6 terracería a Cacalután, 22 Sep 1989, *Téllez 12293* (MEXU, TEX). OAXACA: Valle de Etla, 25 Sep 1895, *Smith 720* (MEXU). PUEBLA: Mpio. Huehuetlán el Chico, ejido Tzicatlán, 6 Nov 1980, *Arreola TZ-570* (MEXU, TEX). SAN LUIS POTOSÍ: 64 mi NE of San Luis Potosí, 20 Aug 1959, *Waterfall 15712* (F, NY). SINALOA: Mpio. Culiacán, Santa María, 1927, *González 6694* (CAS, F, US). VERACRUZ: Mpio. Acultzingo, 5 km ENE of center of Acultzingo, 20 Sep 1986, *Nee 33132* (NY). YUCATÁN: Izamal, without date, *Gaumer 1446* (F, US). NICARAGUA: MASAYA: Parque Nacional Volcán Masaya, 27 Oct 1977, *Neill 2808* (LL).

11. *Physalis patula* Mill., Gard. Dict. 8:12. 1768. Type: Mexico: Veracruz, without further locality, 1731, *Houstoun s.n.* Holotype: **BM**, Sloane collection. Photoholotype: **BH! NY! OS!**

*Physalis foetens* Poir. in Lam., Encycl. Méth. Bot., Suppl. 2:348. 1817. Type: Mexico (?) but reportedly from “Peru”, without further locality, 1803-1804, *Bonpland s.n.* Holotype: **FI**. The holotype was probably mislabeled as to locality, because the species is only known to occur in central Mexico.

*Physalis subulata* Rydb., Bull. Torrey Bot. Club 22:306. 1895. Type: Mexico: Chihuahua, waste grounds, Guerrero, 8 Sep 1887, *Pringle 1344*. Holotype: **GH!** Isotypes **F! MEXU! NY! OKL!**

Annual herbs, 10-150 cm high. Stems angular, densely glandular-pubescent, hairs 0.2-1.0 mm long. Leaves glandular-pubescent, 2.0-11.0 cm long; petioles 0.5-3.4 cm long; blades oblong to narrowly oblong or rhombic, glandular-pubescent, 1.5-7.5 cm long, 0.5-4.0 cm wide, apex acute, base attenuate or oblique up to 1.3 cm off, margin coarsely dentate. Flowering peduncles 2.5-9.0 mm long; flowering calyces glandular-pubescent with acuminate lobes 3-5 mm long, 1.5-2.0 mm wide; corollas yellow, 1.0-2.5 cm in diameter, petals immaculate or with 5 separate brown or blue maculations; filaments and anthers blue, anthers 1.5-2.7 mm long. Fruiting peduncles 7-14 mm long; fruiting calyces strongly 5-angled, 1.5-3.0 cm long, 1.0-3.0 cm wide, frequently as long as wide, glandular-pubescent. Mature berry spherical, 1.0-1.3 cm in diameter, yellow, containing numerous brown foveolate seeds ca. 2mm in diameter. The plant emits a strong offensive odor.

**Distribution** (Fig. 9). Restricted to Mexico, from Chihuahua to Oaxaca. The plant is a weed of dry highland habitats frequently associated with cultivated fields. It occurs from 900-2700 m in clay soil.

**Flowering.** July- December.

**Common names.** "Tomatillo", "hierba del zopilote", "jaltomate hediondo".

**Observations.** I am following Nee (1986) in the application of name *Physalis patula*. Although he later thought the name could be a synonym of *P. angulata* L. (Nee, pers. comm.), there is a description of the holotype at OKL "plant hairy throughout (probably viscid, as the pin-head glandular trichomes are very slender and small)...." which excludes this possibility. Waterfall, in the photograph deposited at OKL, interpreted the hair description as that of the fruiting stage of a mold. He made no reference to the name in his treatments.

*Physalis patula* has corolla which range from immaculate to maculate with five separate brown or blue blotches. The plants from Chihuahua with blue maculations and small corollas can be referred to as *P. subulata*, but the collections of Bye 9827 (UCR) have individuals with both forms, suggesting that they are but variations of the same plant. There are no other characters that correlate with the maculations.

I have not seen the holotype of *P. foetens*, but the collection Bourgeau 352 from Mexico City (BR, F, GH, OKLA! P, US!) was annotated by Poiret with that name, and gives a clear idea as to Poiret's species-concept.

**Representative specimens examined.** MEXICO: CHIHUAHUA: Mpio. Batopilas, S side of Barranca de Batopilas, W of La Bufa, 20 Oct 1980, Bye 10035 (UCR). DISTRITO FEDERAL: Tláhuac, vertiente E del Cerro de Santa Catarina, 13 Aug 1968, Rzedowski 26037 (CAS, MEXU, NY). DURANGO: along hgw. 45 N of Durango, 21 Aug 1982, Worthington 8951 (NY). GUANAJUATO: 4-5 km de San Miguel de Allende, 22 Aug 1978, Kishler 350 (MEXU). HIDALGO: Santiago Tepetlatoxco, 20 Oct 1977, Espinosa 394 (MEXU). JALISCO: Potrero La Colorada, 5 km W de la carretera Ojuelos-Lagos, 24 Sep 1983, Alcocer 62 (MEXU). MÉXICO: above Santa Fe, 26 Aug 1900, Pringle 9139 (F, MEXU, US). OAXACA: Río Teposcolula, 500 m al S del poblado, 11 Jul 1981, García 527 (MEXU). PUEBLA: Xochitecatl cerca de Texmelucan, 16 Oct 1970, Boege 1543 (MEXU). QUERÉTARO: 8 mi E of Querétaro, 23 Aug 1961, Waterfall

16547 (F, US). TLAXCALA: Mpio. Hueyotlipan, 7 km al NW de San Siemón Xipetzingo, 11 Aug 1983, *Williams 86* (CAS, F, MEXU). VERACRUZ: Mpio. Perote, outskirts of town on the NE side, 11 Dec 1985, *Nee 32079* (NY, TEX).

12. *Physalis porrecta* Waterf., *Rhodora* 69:237. 1967. Type: Costa Rica: San José, vicinity of El General, Nov 1936, *Skutch 2931*. Holotype: US! Isotypes: GH, NY.

Perennial herbs, 30-100 cm high. Stems velutinous on one side, becoming glabrous with age, hairs sometimes glandular. Leaves velutinous to almost glabrous, 7-16 cm long; petioles velutinous, 2.0-6.5 cm long; blades elliptic to ovate, velutinous, 5-10 cm long, 3-8 cm wide, apex acuminate, base obtuse, margins dentate. Flowering peduncles 5-15 mm long, 1.8-2.0 mm wide; flowering calyces villous, 5 mm long, 2.5 mm wide, reflexed at anthesis; corollas yellow, 1.2-2.0 cm in diameter, petals with 5 brown, not strongly contrasting, maculations, pubescent within at insertion of filaments; filaments brown, anthers yellow, green or blue-tinged, 2.2-2.5 mm long. Fruiting peduncles 1.0-1.5 cm long; fruiting calyces glabrous, reticulated, strongly 5-angled, 3.0-5.5 cm long, 2-3 cm wide; always longer than wider, lobes 1.0-1.5 cm long. Mature berry spherical, ca. 1 cm in diameter.

**Distribution** (Fig. 5). Restricted to southern Mexico, Guatemala and Costa Rica, from 1500-2500 m elevation. The plant seems to form part of the native vegetation growing on volcanic soils.

**Flowering.** Throughout the year.

**Common names.** "Miltomate", "tomatillo" (Guatemala).

**Observations.** When describing *Physalis porrecta*, Waterfall included with this a flowering specimen from the lowlands of Oaxaca, Mexico (*Morton 2556 US*), which I think is best referred to as *P. cordata*. Another lowland specimen cited by Waterfall is one from Chiquimula, Guatemala (*Standley 73738 F*), a densely glandular plant referred here to *P. pruinosa*. These two exclusions leave *P. porrecta* as primarily restricted to highland habitats.

*Physalis porrecta* is closely related to *P. cordata*, from which it differs in possessing a velutinous vestiture, larger reticulated fruiting calyces and having a highland habitat.

**Specimens examined.** COSTA RICA: ALAJUELA: Zarcero, 20 Oct 1937, *Smith A554* (F). CARTAGO: El Muñeco, on the Río Navarro, 6-7 Mar 1926, *Standley 51093* (US). SAN JOSÉ: vicinity of Santa María de Dota, 26 Dec 1925-3 Jan 1926, *Standley 44061* (US). GUATEMALA: BAJA VERAPAZ: Niño Perdido, on San José road, 18 Jun 1977, *Lundell 21133* (F, LL). CHIMALTENANGO: Tres Cruces, 9 mi W of San Miguel Dueñas, 5 Aug 1960, *Beaman 4007* (TEX). Región Positos, above Las Calderas, 16 Dec 1940, *Standley 80199* (F). GUATEMALA: old road to San Lucas, vicinity of San Rafael, 27 Sep 1972, *Molina 27607* (F). Barranco above Dueñas, 21 Jan 1939, *Standley 63252* (F, US). Above Pastores, 23 Dec 1938, *Standley 60860* (F). Barranco above Dueñas, 21 Jan 1939, *Standley 63211* (F, US). QUETZALITENANGO: Región of Azufral, N slope of Volcán Zunil, 3 Feb 1941, *Standley 85731* (F, US). Mountains



above Zunil, 3 Feb 1941, *Standley 85842* (F). Along Río Samalá, near Santa María de Jesús, 25 Jan 1941, *Standley 84688* (F). Volcán Zunil, 7 Aug 1934, *Skutch 970* (US). SAN MARCOS: along Río Tacaná, above San Antonio, 22 Feb 1939, *Standley 66134* (US); slopes of Cerro Tumbador, 15 km W of San Marcos, 15 Dec 1962, *Williams 23063* (F, NY); 5 mi E of San Marcos, 14 Jul 1977, *Croat 41035* (MEXU); 6 mi SW of Tajumulco, 26 Feb 1940, *Steyermark 36596* (F). MEXICO: CHIAPAS: Mpio. Siltepec, ridge above Siltepec on rd to Huixtla, 1 Feb 1982, *Breedlove 58284* (CAS).

**13. *Physalis pruinosa* L.**, Sp. Pl. 184. 1753. Type: "Habitat in America", without further locality, date or collector. Holotype: LINN 247.13. Microfiche IDC 137! Photoholotype NY! (Fig. 14)

*Physalis maxima* Mill., Gard. Dict. 8:15. 1768. Type: Mexico: Veracruz, without further locality, 1730, *Houstoun s.n.* Holotype: BM, Sloane collection. Photoholotypes: BH! OKLA! US!

*Physalis cordifolia* Dunal in DC., Prodr. 13:441. 1852. Type: from a cultivated plant in the Lugduno-Baravo Gardens, 1829, *De la Roche s.n.* Holotype: G-DC. Microfiche IDC 2098!

*Physalis nicandroides* Schlttdl. var. *attenuata* Waterf., *Rhodora* 69:235. 1967. *Nom. invalid.*, no type was designated.

Annual herb 20-140 cm high. Stems pubescent with a mixture of long (2.0-2.5 mm) and short (0.5-1.0 mm) multicellular glandular hairs. Leaves 3.5-16.5 cm long, densely pilose with multicellular glandular hairs; petioles 1.0-6.5 cm long; blades 2.5-12.0 cm long, 2-9 cm wide, ovate to elliptic, pilose, the apices acute to acuminate, base cordate or truncate, sometimes oblique up to 1 cm off, the margins dentate to seldomly entire. Flowering peduncles 1.7-3.0 cm long; flowering calyces long-pilose, with acuminate lobes 2.5-6.0 mm long, 1.0-1.5 mm wide; corollas yellow 1.0-1.5 cm in diameter, the petals with 5 brown weakly contrasting maculations, glabrous or pubescent within; filaments blue, anthers always yellow 2.0-3.5 mm long. Fruiting peduncles not thickened, ca. 0.5 mm in diameter, 3.0-5.5 cm long. Fruiting calyces strongly 5-angled, 3.5-6.0 cm long, 2.5-4.0 cm wide, always longer than wide, glandular-pilose. Mature berry spherical, 1.0-2.5 cm in diameter, dark brown, glutinous containing numerous brown foveolate seeds ca. 2 mm in diameter.

**Distribution** (Fig. 15). From Chihuahua throughout Mexico and Central America (except Panama and El Salvador) south to Argentina. The plant is a weed growing at low elevations (up to 1400 m) in humid montane, oak or, more frequently, dry deciduous forest.

**Flowering.** From July to August in Mexico and Central America, collected with ripe fruits only in January-March. In South America, flowering from January to May.

**Common names.** "Farolito", "vejiga de perro" (Honduras); "miltomate", "tomatillo" (Guatemala); "tumatcho", "chipin sox" (huave) "tomate de culebra", "tomate de hoja", "tomate", "tomatillo", "tomatillo grande" (Mexico).

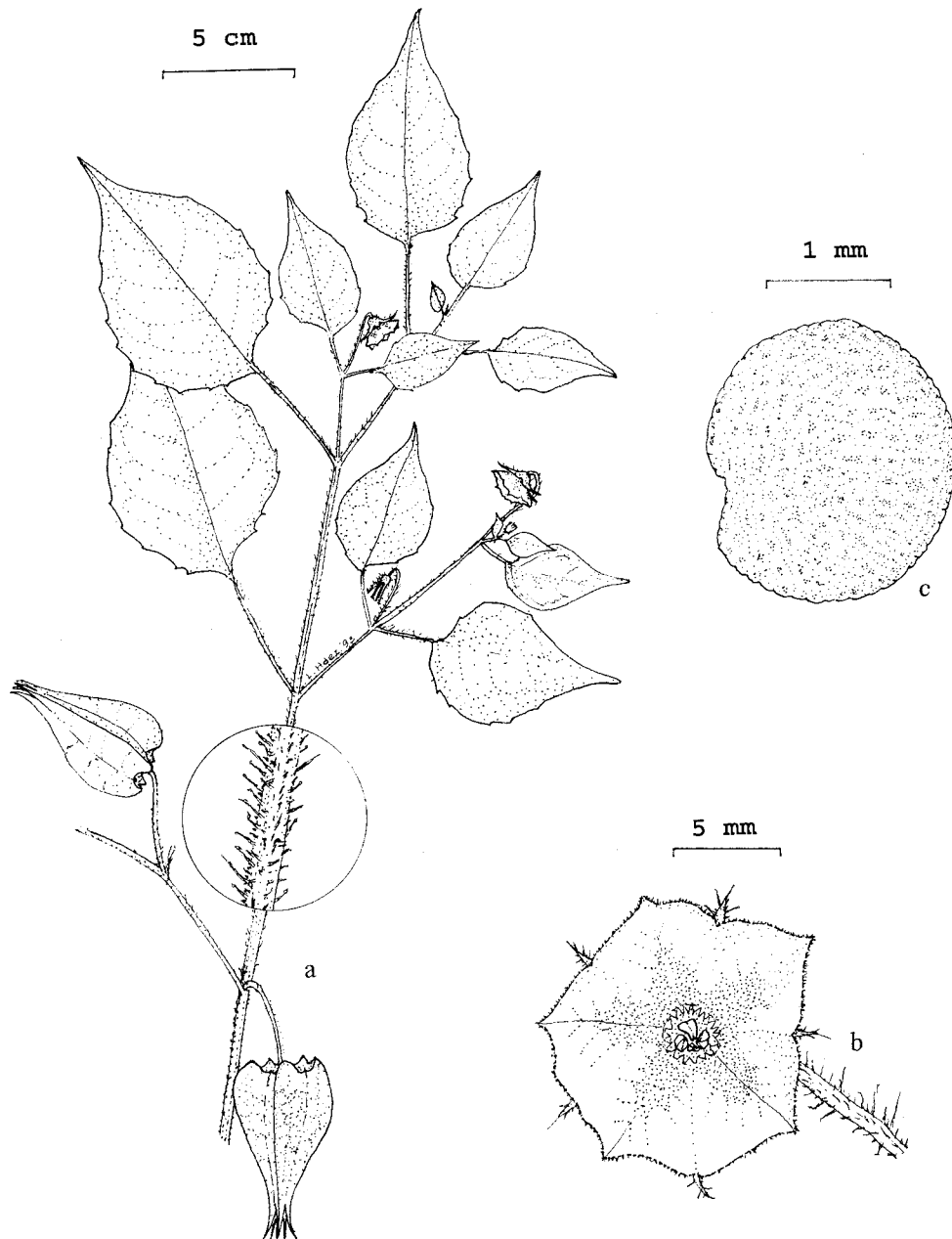


Fig. 14. *P. pruinosa* L.: a) branch with flowers, fruit, and a detail of the pubescence; b) flower; c) untreated seed.

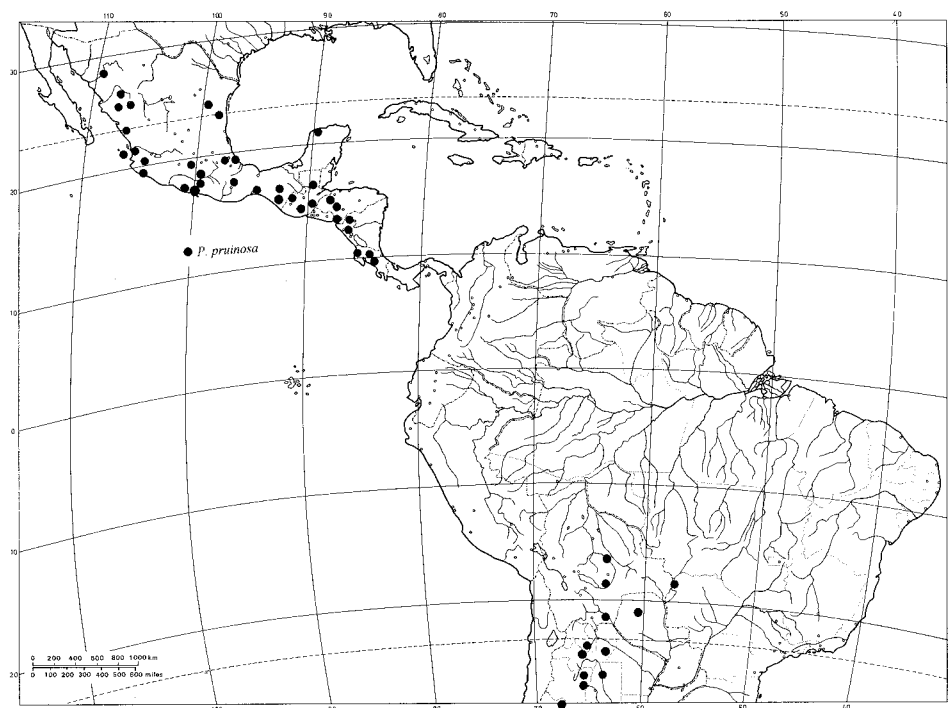


Fig. 15. Distribution of *P. pruinosa*.

**Uses:** The fruit is eaten in Mexico.

**Observations.** *Physalis pruinosa* is readily distinguished by its yellow anthers, long peduncles and a mixture of long and short stem-hairs. At maturity, the stems tend to become glabrous and the species may be confused with *P. nicandroides*. However, *P. pruinosa* does not have thickened fruiting peduncles.

**Representative specimens examined.** ARGENTINA: CATAMARCA: Ambato, La Puerta, 6 Apr 1947, *Muller* 2 (NY). JUJUY: San Pedro Cuesta de las Lajitas, 23 Feb 1961, *Cabrera* 13773 (US). LA RIOJA: Capital, Los Duraznillos al km 33, 19 May 1943, *Alaníz* 115 (F, NY). SALTA: Joaquín V. González, 31 Jan 1945, *Aguilar* 315 (NY). SANTIAGO DEL ESTERO: Guasayán Villa La Calera, 6 Feb 1944, *Pierotti* s.n. (US). TUCUMÁN: Trancas, Río Tipamayo. 17 Apr 1926, *Venturi* 4225 (NY). BOLIVIA: SANTA CRUZ: Caballero, 11 km SW of Comarapa on rd to Chilón, 7 Aug 1987, *Nee* 35564 (NY). TARJA: Cercado, San Luis, 3 Jun 1986, *Bastián* 967 (NY). COSTA RICA: GUANACASTE: Santa Rosa, Sep 1971, *Callaway* 331 (F). SANTA ROSA: Asserí, 27 Nov 1953, *Heiser* 3767 (F). GUATEMALA: CHIMALTENANGO: 10 km S from Godínez, Los Ídolos dridge, 21 Sep 1971, *Molina* 26703 (F). CHIQUIMULA: near divide on rd. From Zacapa to Chiquimula, 9 de Oct 1940, *Standley* 73738 (F). ESCUINTLA: near Las Lajas, 28 Nov 1938, *Standley* 58158 (F). GUATEMALA: Santa Fé, 2 km SW of La Aurora, 25 Sep 1972, *Molina* 27530 (F). HUEHUETENANGO: near El Reposo, 14-18 Dec 1972, *Williams* 41358 (F). JALAPA: 6 mi S

of Miramudo, 5 Dec 1939, *Steyermark 32696* (F). JUTIAPA: Lago Retana, between Ovejero and Progreso, 26 Nov 1939, *Steyermark 31975* (F). PETÉN: Santa Elena, 13 Sep 1966, *Contreras 6090* (CAS, F). HONDURAS: CHOLUTECA: vicinity of Pespire, 18-25 Oct 1950, *Standley 27101* (F). COMAYAGUA: vicinity of Comayagua, 12-23 Mar 1947, *Standley 5956* (F). MORAZÁN: vicinity of Tegucigalpa, 29 Nov 1949, *Standley 24788* (F). VALLE: Amapala, 11 Sep 1945, *Válerio 3376* (F). MÉXICO: CHIAPAS: Mpio. Venustiano Carranza, at Soyatitán, 12 Sep 1966, *Laughlin 1982* (CAS, F). CHIHUAHUA: La Cieneguita, Río Mayo, 10 Sep 1936, *Gentry 2632* (F, MEXU, US). GUERRERO: Mpio. Petatlán, El Camalotillo, 23 Oct 1983, *Martínez 5172* (MEXU). JALISCO: Mpio. Zapotitlán, Rancho El Jabalí, 22 km N of Colima, 22 Sep 1991, *Sanders 11665* (TEX). MÉXICO: Mpio. Temascaltepec, Bejucos, 15 Aug 1935, *Hinton 8174* (NY, US). MICHOACÁN: Rancho Viejo camino Tierra Blanca-Bastán del Cobre, 6 Oct 1981, *Soto 3204* (MEXU). NAYARIT: 12-13 mi S of Las Varas, 20 Sep 1960, *McVaugh 19226* (US). OAXACA: Mpio. Tehuantepec, 15 km SW of Buenos Aires, 13 Sep 1985, *Torres 7346* (MEXU). SINALOA: Mpio. Concordia, 53 km NE of Villa Unión, 1 Oct 1985, *Bartholomew 2518* (CAS). SONORA: San Bernardo and vicinity, Sep 1961, *Argüelles 131* (US). TAMAULIPAS: 19 km al E de la carretera Zaragoza-González, 27 Sep 1984, *Romero 133* (MEXU, UAT). VERACRUZ: Mpio. Coatepec, faldas del cerro Chavarrillo, 7 Sep 1979, *Castillo 865* (F). YUCATÁN: without locality, 1917-1921, *Gaumer 24310* (F). NICARAGUA: ESTELÍ: N slope of Cerro Tomabú, 16 Oct 1979, *Stevens 14941* (MEXU). MANAGUA: vicinity of Managua, 1 Jul 1923, *Maxon 7560* (US). PARAGUAY: Nueva Asunción, ruta Trans-Chaco, 12 Mar 1979, *Schinini 16522* (NY). VENEZUELA: ZULIA: Bolívar entre El Pensador y Las Tres Marías, 22 Jul 1980, *Buntig 9388* (NY).

14. *Physalis pubescens* L., Sp. Pl. 183. 1753. Type: "In India utraque", without further locality, date or collector. Holotype: LINN 247.11. Microfiche IDC 137! (Fig. 16)

*Physalis villosa* Mill., Gard. Dict. 8:13. 1768. Type: Mexico: Veracruz, without further locality, 1730, *Houstoun s.n.* Holotype: BM, Sloane collection. Photoholotype BH!

*Physalis turbinata* Medik., Acad. Theod. Palatina 4: 189. t.2. 1780. Type: if any, not located. Fig. 2 in the original publication might serve as an adequate type.

*Physalis barbadensis* Jacq., Misc. Austriac. 359. t.39. 1781. *Physalis hirsuta* var. *barbadensis* (Jacq.) Dunal, in DC. Prodr. 13:446. 1852. Type: if any, not located. Fig. 39 in the original publication might serve as an adequate type.

*Physalis obscura* Michx. var. *glabra* Michx., Fl. Bor. Amer. 1:149. 1803. *Physalis barbadensis* Jacq. var. *glabra* (Michx.) Fernald, Rhodora 51:82. 1949. *Physalis pubescens* L. var. *glabra* (Michx.) Waterf., Rhodora 60:165. 1958. Type: USA: without further locality or date, collected presumably by Michx. Holotype: P, photoholotype GH!

*Physalis obscura* Michx. var. *viscido-pubescens* Michx., Fl. Bor. Amer. 1:149. 1803. *Physalis viscido-pubescens* (Michx.) Dunal in DC., Prodr. 13:442. 1852. Type: USA: "habitat in Carolina", without date, collected presumably by Michx. Holotype P, photoholotype GH!

*Physalis neesiana* Sendtn. in Martius, Fl. bras. 10:131. 1846. Type: Brazil: Spiritus Sancti, without date, *Menzie 128*. Holotype: M. Fragments of holotype: OKLA!

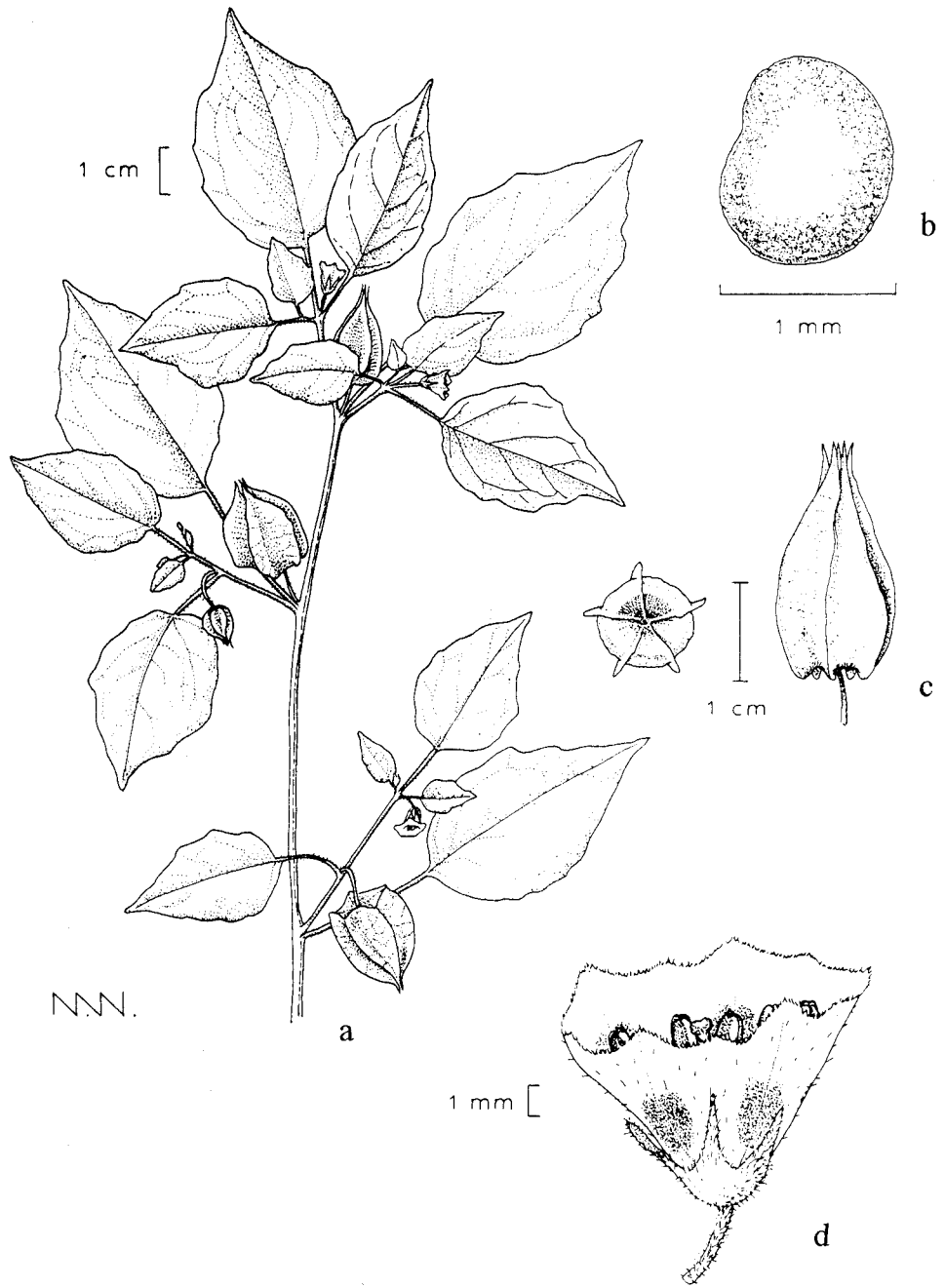


Fig. 16. *P. pubescens* L.: a) branch with flowers and fruits, b) seed; c) frontal and lateral view of the fruiting calyx; d) flower.

*Physalis hirsuta* Dunal var. *integrifolia* Dunal in DC., Prodr. 13:445. 1852. *Physalis pubescens* L. var. *integrifolia* (Dunal) Waterf., Rhodora 60:166.1958. Type: USA Ohio: "In sylvaticis agri Cincinnatianni civ. Ohio", 1837, *Frank 30*. Holotype: **G-DC**. Microfiche IDC 2089!

*Physalis hirsuta* var. *repandodentata* Dunal in DC., Prodr. 13:445. 1852. Type: without locality, date or collector. Holotype **G-DC**. Microfiche IDC 2098!

*Physalis floridana* Rydb. in Small, Fl. Southeastern U.S. 983. 1903. Type: USA Florida: Walton Co.: Summer 1885, *Curtiss s.n.* Holotype: **NY!** Isotypes: **F!**, **NY!**

Annual or biennial herbs 10-150 cm high, sometimes profusely branched. Stems variously pubescent, pilose to glandular-pilose with multicellular hairs up to 3 mm long. Leaves variously pubescent but mostly villous, 3-17 cm long; petioles 1.5-7.0 cm long; blades ovate to deltate, villous especially on the lower surface, mostly 2-10 cm long, 1-7 cm wide, apex acute to acuminate, base obtuse to truncate, if oblique, only up to 3 mm off, margins irregularly dentate to almost entire. Flowering peduncles 2-7 mm long; flowering calyces villous with triangular lobes 1.5-3.0 mm long; corollas yellow, 0.9-1.5 cm in diameter, the petals with 5 dark purple maculations, pubescent within at insertion of filaments; filaments and anthers purple or blue, yellow in a few specimens, anthers up to 2 mm long. Fruiting peduncles 5-10 mm long; fruiting calyces strongly 5-angled, 1.2-3.0 cm long, 1.8-2.5 cm wide, always longer than wide, villous throughout with multicellular hairs. Mature berry spherical, ca. 1 cm in diameter, green-purple to yellow, containing numerous brown foveolate seeds ca. 1.5 mm in diameter.

**Distribution** (Fig. 17, 18). From NE USA along the Atlantic Coastal Region, westwards to California and throughout the Mexican lowlands to Argentina in South America and the West Indies. The plant is a common weed of lowland habitats, mostly occurring from 0 to 900 m (up to 2700 m in Colombia), usually in sandy soils near rivers.

**Flowering.** From June to December in the USA except Florida where it flowers throughout the year, as in the rest of its range (Mexico, Central and South America).

**Common names.** "Sapo de gato" (Belize); "muyaca", "motojobo" (Bolivia); "canapú" (Brazil); "uva de perro", "uchuba", "uvilla" (Colombia); "mutios panga", "tsisin cucuna", "tomate de monte" (Ecuador); "huevo de tortuga", "miltomate", "huevitos", "tomatillo" (El Salvador); "miltomate", "tomatillo" (Guatemala); "batanto" (Haiti); "tomatillo" (Honduras); "cocostomat", "tomatillo", "miltomate", "tomate culebra" (Mexico); "topetón", "hierba de sapo" (Panama); "yutuimas", "bolsa mullaca", "bolsa mullaca blanca" (Peru); "ground cherry", "low hairy ground cherry" (USA); "topotopo" (Venezuela).

**Uses.** The fruit is eaten in Bolivia, Colombia, Ecuador, El Salvador, Mexico and Peru. It has been reported as medicinal in Ecuador (against measles) and in Peru.

**Observations.** Several names have been proposed based upon the variability of leaf shape and vestiture, but these characters are highly variable and taken together or singly do not appear to have any geographical correlations. Because of

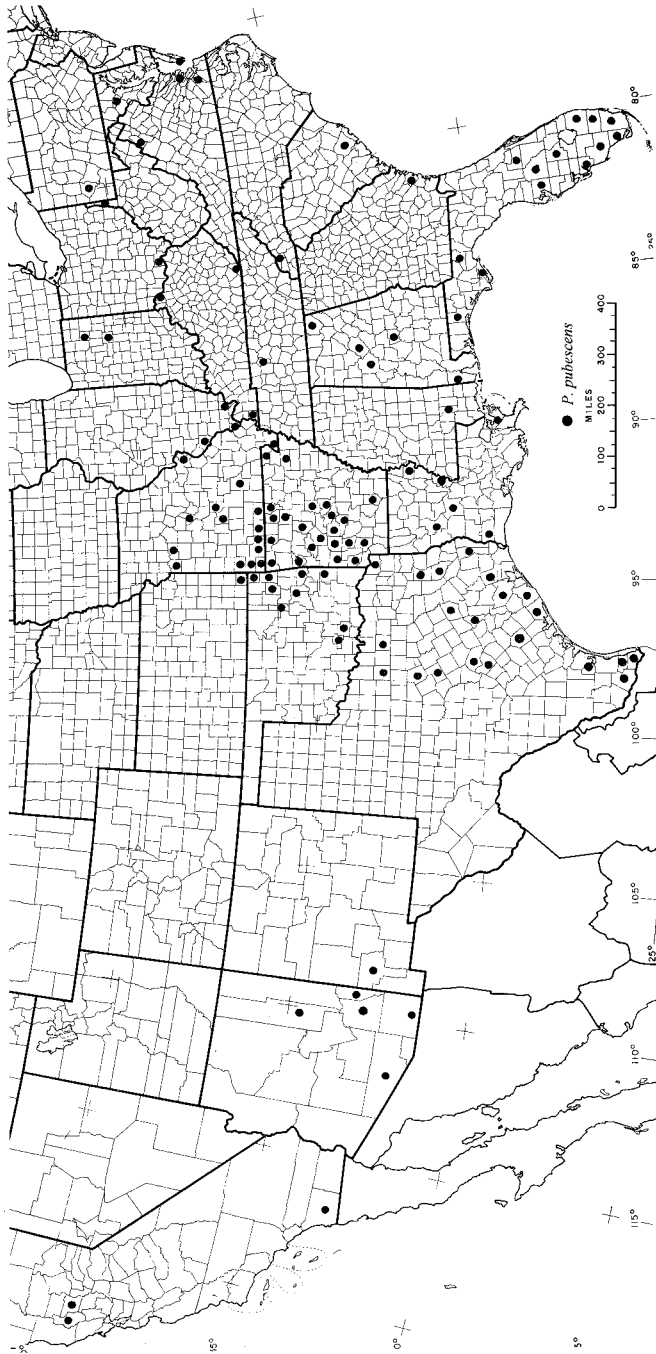


Fig. 17. Distribution of *P. pubescens* in the United States.

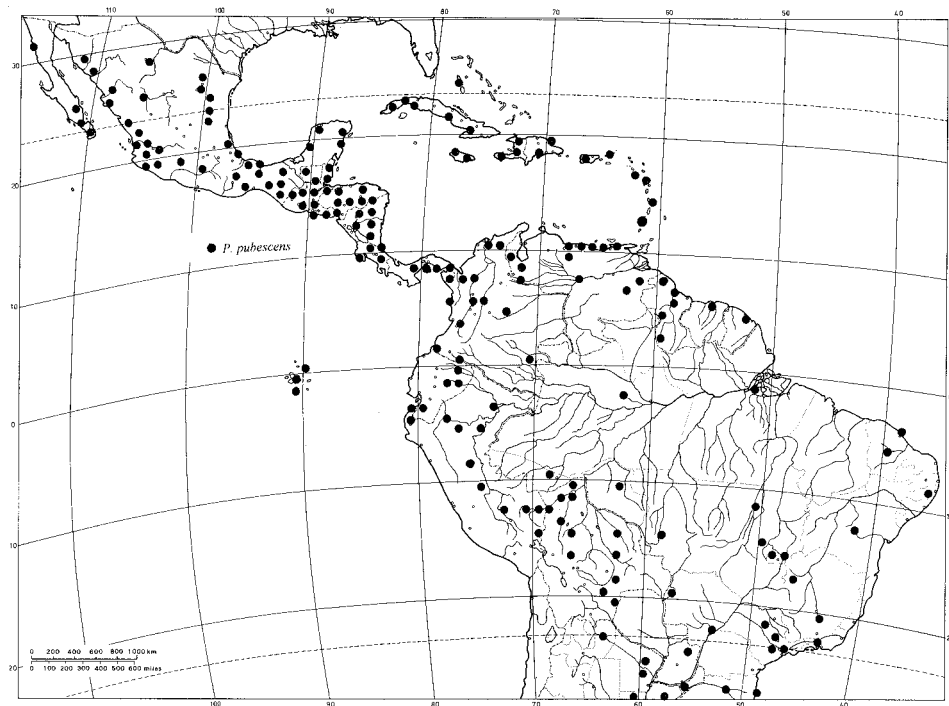


Fig. 18. *P. pubescens* in Mexico, Central America, South America, and the West Indies.

this variation and its behavior in the greenhouse, I have opted to treat the variation as part of a single widespread, rather heteromorphic species.

The characters that distinguish the species are the dark maculate corollas, purple to blue anthers, and the villous, strongly 5-angled fruiting calyces. A few South American collections (marked below) have yellow anthers and can be referred to as *Physalis neesiana*. However, yellow anthers, though rare, are found elsewhere in the range of *Physalis pubescens* (e.g. in Arizona, *Bertelsen 91-080 ARIZ*). Since such specimens do not exhibit any other character that might differentiate them, I cannot recognize *P. neesiana*.

**Representative specimens examined.** ARGENTINA: CHACO: Río Bermejo, 8 km S de Puerto Velázquez, 14 Feb 1986, *Cristóbal 2102 (NY)*. CORRIENTES: Concepción Pueblo, 25 Apr 1944, *Ibarra 327 (NY)*. FORMOSA: Laguna Oca, 5 Sep 1944, *Rojas 12235 (F)*. MISIONES: Posadas "La Granja", 14 Dec 1907, *Ekman 804 (NY)*. SALTA: Orán, campamento Y.P.F. Río Pescado, 3 Mar 1943, *Meyer 5152*, yellow anthers, (F). SANTA FE: Reconquista, Río Paraná, Isla Mascota, 1 Feb 1936, *Job 904 (NY)*. BELIZE: COROZAL: Cerro Maya Ruins, Lowry's Bright, 28 Feb 1983, *Crane 301 (MO)*. ORANGE WALK: 2 mi N of Orange Walk, 19 Aug 1980, *Sutton 112 (MO)*. TOLEDO: Solomon Camp, vicinity of the jct of Richardson Creek and Bladen Ranch, 12 Mar 1987, *Davidse 32049 (MO)*. BOLIVIA: BENI: Cercado, Casabe, 15 m



E Trinidad on road to Ascención de Guarayos, 14 Dec 1988, *Nee 37178* (NY). LA PAZ: Iturralde, Puerto Heath along Río Madre de Dios, 26 Aug 1985, *Nee 31563* (NY). PANDO: Manuripi along Río Madre de Dios, between Trinidadcito and San Miguel, km 50 WSW of Riberalta, 21 Aug 1985, *Nee 31495* (NY). SANTA CRUZ: Provincia Florida, gorge of Río Pirari, ca. 1 km NE of jct. with Río Bermejo, 16 Feb 1988, *Nee 36330* (CAS, NY). BRAZIL: ACRE: Sena Madureira trail to Río Iaco from km 7 road to Sena Madureira to Río Blanco, 1 Oct 1968, *Prance 7725* (F, NY, US). AMAZONAS: Basin of Río Demeñi, vicinity of Totobi, 26 Feb 1969, *Prance 10244* (F). CERA: Quixada, margins of Acude Boa Agua, 12 Sep 1935, *Drouet 2430* (NY). DISTRITO FEDERAL: 25 km NE of Brasilia, 7 Sep 1965, *Irwin 8073a* (NY). GOIAS: 78 km SE of Aragarças, 22 Jun 1966, *Irwin 17592* (NY). MATO GROSSO: Between Xavantina and Garapu, 27 Sep 1964, *Irwin 6974* (NY). MINAS GERAIS: 5 km SE of Paracatu, 6 Feb 1970, *Irwin 26200* (NY). PARA: 1 km EN of Santa Izabel, 10 Jul 1935, *Drouet 2040*, yellow anthers, (F). PARANÁ: Morretes, Estrada de Graciosa, vista Cavalcanti, 1 Jul 1953, *Ghatschbach 3208* (US). PERNAMBUCO: Tapéra, Aug 1929, *Pickel 2041* (US). RIO GRANDE DO SUL: Pelotas, 4 Apr 1955, *Sacco 378* (NY). RONDONIA: 9.5 km SE of Ariquemes, 18 Mar 1987, *Nee 34437*, yellow anthers, (NY). SAO PAULO: Estacao Pilar, 28 Nov 1898, *Edwall 15444* (US). SANTA CATARINA: Sao Miguel d'Oeste, 19 Dec 1964, *Smith 14167* (NY). COLOMBIA: ANTIOQUIA: 13 km E de Bolívar, 13 Jan 1949, *Araque 19031* (US). BOLÍVAR: Tierra Alta, Río Sinu, 7-10 Mar 1918, *Pennell 4669* (F). BOYACA: 100 m NW of Bogotá, 29 May 1932, *Laurance 126* (F). CHOCO: margen izquierda Río Cacarica, 15 Jul 1957, *Romero 6397* (F). NARIÑO: alrededores de Sámaniego, 10 Jan 1952, *Fernández 1160* (NY). META: Villacencio, 11 Nov 1938, *Cuatrecasas 4624* (US). MAGDALENA: Santa Marta near Masinga, 8 Nov 1898, *Smith 1171* (NY). SANTANDER: Boca de Rosario, Río Magdalena, 15 Jan 1918, *Pennell 3899* (NY). VAUPES: Mitu & vicinity, 20 May 1976, *Zarucchi 1609* (US). COSTA RICA (selected from 35 collections): ALAJUELA: Echeverría et San Antonio at San José, 10 Nov 1912, *Brenes s.n.* (NY). CARTAGO: between Turrialba and Tica, 29 Oct 1953, *Heiser 3682a* (F). GUANACASTE: Along Río Higuerón, 29-30 Jun 1977, *Liesner et al. 2727* (MO). HEREDIA: Cerro Chompipe, N of San Rafael, 25-29 Aug 1964, *Lems s.n.* (US). LIMÓN: Refugio Barranca de Colorado, 13 Nov 1988, *Grayum 9036* (MO). PUNTARENAS: Near airport on slopes, 9 Feb 1974, *Liesner 1950* (MO). SAN JOSÉ: Tabarcira, Mora, 22 Apr 1963, *Jiménez 672* (F). CUBA: CAMAGÜEY: Vicinity of la Gloria, 2 Feb 1909, *Shaffer 232* (NY). HABANA: Río Almendreres to Playa de Mariano, 22 Dec 1910, *Wilson 9490* (NY). MATANZAS: near Camasí, 10 Oct 1923, *Bro. Leon 13128*, (NY). ORIENTE: Sierra Maestra prope Dauquiri, 28 Oct 1916, *Eckman 8075* (NY). PINAR DEL RÍO: Laguna Jovero and vicinity, 5-7 Dec 1911, *Sharp 10746* (NY). SANTA CLARA: Trinidad mountains, Santa Clara Sigüanea, 2-5 Mar 1910, *Britton 4959* (F). DOMINICAN REPUBLIC: SANTIAGO: San José, Vallecito, 10 Jan 1930, *Valeur 352* (F, US). LA VEGA: bank of Maimon River, 18 Jan 1946, *Allard 14748* (NY). ECUADOR: el oro: Puyago and vicinity, Aug 1978, *Daly 111* (NY). GALÁPAGOS ISLANDS: Albemarle Island, Iguana Cove, 17 Mar 1906, *Stewart 3392* (CAS). NAPO: vicinity of Coca, 250 m, 10 Mar 1985, *Molau 1590* (NY). PASTAZA: Tarabita, 3 km from turnoff, 23 Dec 1979, *Croat 49678* (NY). EL SALVADOR: AHUACHAPÁN: vicinity of Ahuachapán, 9-27 Jan 1922, *Standley 20243* (US). LA UNIÓN: 13-21 Feb 1922, *Standley 20882* (US). MORAZÁN: 15 km NE of San Miguel, 11 Dec 1941, *Tucker 517* (F). SAN SALVADOR: 20 Dec 1921-4 Jan 1922, *Standley 19669* (US). SAN VICENTE: Vicinity of San Vicente, 7-14 Feb 1947, *Standley & Padilla 3694* (F). FRENCH GUIANA: CAYENNE: 3 Jun 1921, *Broadway 390* (NY, US). GUATEMALA: ALTA VERAPAZ: near town, 2 Apr 1939, *Standley 70261* (F). BAJA VERAPAZ: 6 km from Rabinal to Guatemala, 2 Oct 1972, *Molina & Molina 27781* (F). CHIMALTENANGO: at Tres Cruces, 9 mi W of San

Miguel Dueñas, 5 Aug 1960, *Beaman 4007* (US). CHIQUIMULA: Montaña Nonoja, 11 Nov 1939, *Steyermark 31667* (F). HUEHUETENANGO: between Ixcán & Río Ixcán, 23 Jul 1942, *Steyermark 49330* (F,US). IZABAL: Puerto Méndez, 12 Jun 1970, *Contreras 10024* (MO). JUTIAPA: between Jutiapa and las Tunas, 4 Nov 1940, *Standley 76296* (F). PETÉN: Parque Paraíso, frente a Flores, 17 Mar 1991, *Martínez & Hernández 1922* (TEX). PROGRESO: El Rancho, 24 Mar 1939, *Standley 69050* (F). SAN MARCOS: 1 km SE de Rodeo, 12 Mar 1991, *Martínez & Hernández 1917* (TEX). SANTA ROSA: La Sepultura, W of Chiquimula, 5 Dec 1940, *Standley 79319* (F). ZACAPA: Zacapa, 23 Apr 1939, *Standley 72022* (F). GUYANA: EAST DEMARERA-WEST COAST: Akyma, Demarera River, 9 - 10 Jan 1920, *Hitchcock 17428* (NY, US). MAZARUNI-POTARO: Potaro River, 23 Oct - 3 Nov 1923, *De la Cruz 4427* (NY, US). NORTH WEST: Barima River, 19-22 Mar 1923, *De la Cruz 3422* (F, NY, US). HAITI: L'ARTIBONITE: vicinity of Enney, 22 Jan 1926, *Leonard 8772* (US). DEPARTMENT DU NORD: Vicinity of Marmelade, 18 Dec 1925, *Leonard 8110* (NY). HONDURAS: ATLÁNTIDA: La Fragua, 7 Feb 1928, *Standley 55702* (US). COLÓN: vicinity of Tocoa, 9 Feb 1987, *Croat 64545* (MO). COMAYAGUA: 13-23 Mar 1947, *Standley 5288* (F). COPÁN: Ruins and Santa Rita, 20 Nov 1969, *Molina 24689* (NY). CORTÉS: Vicinity of la Lima, 11-20 Apr 1947, *Standley 7228* (F). EL PARAÍSO: Drainage of Río Yeguaré, 15 Jan 1952, *Molina 5043* (F). GRACIAS A DIOS: Caserío de Rus-Rus, 17-21 Jul 1977, *Nelson 4108* (MO). MORAZÁN: Zamorano, Jan 1945, *Válero 2184* (F). OLANCHO: between Juticalpa and airport, 14 Mar 1949, *Standley 18018* (F). VALLE: Amapala, 11 Sep 1945, *Válero 3375* (F). YORO: Near Progreso, 24 Jan 1928, *Standley 55095* (F). JAMAICA: PORT ANTONIO: 28 Jan-6 Feb 1899, *Millsbaugh 931* (F). MEXICO: BAJA CALIFORNIA SUR: gravel road to Álvaro Obregón, ca. 8 km W of La Paz on rd. to Cabo San Lucas, 5 Mar 1992, *Panero et al. 2855* (TEX). CAMPECHE: 5 km outside of Bolonché which is 68 km SW of Mina, 19 Apr 1973, *Butterwick 295* (LL). CHIAPAS: Chenalhó, NW side of Sierra Santa Cruz, near Colonia of Choro, 10 Jan 1967, *Ton 1859* (MEXU). CHIHUAHUA: southwestern Chihuahua, Aug - Nov 1885, *Palmer 140* (MEXU, US, NY). COLIMA: Rancho el Jabalí, 22 km (airline) from Colima in the SW foothills of the Volcán de Colima, 1 Oct 1991, *Vázquez 1288* (TEX). GUERRERO: Temisco, second barranca E of Temisco, 6 Nov 1937, *Mexia 8760* (CAS, F, NY, US). JALISCO: Guadalajara, Jul-Oct 1886, *Palmer 473* (NY, US). MICHOACÁN: Mpio. Apatzingán, 4 mi W of Apatzingán, 8 Aug 1941, *Leavenworth 1381* (F). NAYARIT: km 10-13 sobre terracería a El Cuarenteño, que empieza a 300 m al W de El Izote, 4 Jan 1986, *Téllez 9538* (MEXU, TEX). NUEVO LEÓN: Horsetail Falls, 30 mi SE of Monterrey, 30 Nov 1958, *Thompson 294* (OKL, TEX). OAXACA: Mpio. Puerto Ángel, Zipolite camino por el río, 9 Feb 1976, *Shapiro 332* (MEXU). PUEBLA: Cuetzalan, Cuauhtapanaloyan, 22 Dec 1980, *Basurto 312* (MEXU). QUINTANA ROO: Mpio. Carrillo Puerto, 100 m al E de Ramonal, 17 Jan 1984, *Durán 756* (MEXU). SINALOA: 30 mi E of Culiacán, 18 Mar 1972, *Breedlove 24449* (CAS). SONORA: Cajón de los Guenijos, 2 Sep 1890, *Lloyd 433* (US). TABASCO: Macuspana, along Arroyo Hular, S of Macuspana, 28 Sep 1944, *Gilly 346* (MO). TAMAULIPAS: vicinity of Ciudad Victoria, 1 Feb-9 Apr 1907, *Palmer 53* (F, MO, NY, US). VERACRUZ: Balsapote, 7 Oct 1968, *Martínez 1772* (MEXU). YUCATÁN: Kancabconot, Jan 1917, *Gaumer 23514* (F, MO, NY, US). NICARAGUA: CHONTALES: ca. 4.5 km S of hgw 7 (from ca 3.6 km E of la Gateada) on rd. to Nueva Guinea, 17 Jul 1977, *Stevens 2776* (LL). ESTELÍ: Estelí River, 5 km from Estelí, 3 Nov 1968, *Molina 22993* (NY). GRANADA: En la isla San Ramón, Isleta la Granada, 11 Aug 1982, *Martínez 1565* (MEXU). RIVAS: Vicinity of Moyogalpa, Isla de Ometepe, 16 Sep 1983, *Nee 28178* (NY). ZELAYA: Río Rama, above rápido Machuca, 16 May 1978, *Stevens 8898* (MEXU). PANAMA: CANAL ZONE: Barro Colorado Island, 25 Jul 1960, *Ebinger 594* (US). COLÓN: 1-2 km from Portobelo hgw up the Río Guanache, 17 Feb

1982, *Knapp 3613* (MEXU). DARIÉN: Village of Mannene, 30 Apr 1968, *Kirbride 1600* (NY). PANAMÁ: Gorgana beach, 7 Aug 1938, *Woodson 1694* (NY). PARAGUAY: ALTO PARANÁ: Puerto Presidente Strossner, 27 Jan 1982, *Casas 5648* (NY). PERÚ: AMAZONAS: Quebrada Wampushik, entsa Charca, 13 Jun 1973, *Kayap 951* (F, LL, NY). CUZCO: Quinecmil, Jun 1949, *Marin 1534* (F). HUANUCO: Río Azul, 30 km de Tingo María, 15 Oct 1957, *Ferreyra 12747* (US). LORETO: Río Macusari, 16 Sep 1968, *McDaniel 10989* (F). MADRE DE DIOS: Parque Nacional Manu, 11 Aug 1984, *Foster 9808* (NY). PASCO: Oxapampa, 5 km up Río Iscozacín, 9 Jul 1968, *Knapp 7800*, yellow anthers, (NY). PIURA: Nomala, Mar 1912, *Weberbauer 5941*, yellow anthers, (F, NY, US). PUNO: Prov. Sandía, Yanacochloa, 14 Feb 1983, Ochoa 15028 (NY, US). SAN MARTÍN: Boquerón Pass, 92 km from Tingo María on hgw to Pucallpa, 16 Dec 1949-5 Jan 1950, *Allard 21707* (F, US). UCAYALI: vecindades de Yurimaguas, Nov 1982, *Ochoa 14888* (F, US). TUMBES: Zarumilla, 4 Jan 1968, *Simpson 557* (F, NY). PUERTO RICO: RÍO PIEDRAS: Ciudad Río Piedras, 4 May 1899, *Heller 1277* (NY). UNITED STATES OF AMERICA: ALABAMA: Autauga Co., 10 Oct 1970, *Kral 41548* (MO). Jackson Co., Jul 1875, *Mohr 4* (US). Jefferson Co., 18 Jun 1899, *Earle s.n.* (NY). Mobile Co., Jul 1896, *Mackenzie s.n.* (US). Tuscaloosa Co., 25-27 Jul 1900, *Pollard 331* (US). ARIZONA: Cochise Co., 14 Sep 1961, *Gooding 241-61* (OKLA). Graham Co., 12 Sep 1981, *Anderson 413* (ARIZ). Greenlee Co., 1 Nov 1880, *Greene 12955* (MO). Navajo Co., 28 Aug 1971, *Boher 1521* (ARIZ). Pima Co., 14 Sep 1991, *Bertelsen 91-8* (ARIZ). ARKANSAS: Baxter Co., 14 Jun 1942, *Demaree 23554* (MO, NY). Benton Co., 16 Oct 1936, *Bush 15804* (MO). Bradley Co., 17 Jun 1986, *Thomas 96987* (MO). Carroll Co., 1 Oct 1935, *Bush 15237* (MO). Clay Co., 25 Aug 1939, *Demaree 20311* (CAS, NY). Craighead Co., 15 Jun 1927, *Demaree 3420* (MO). Crawford Co., 19 Oct 1937, *Palmer 44429* (MO) Faulkner Co., no date, *Demaree 5656* (NY) 29 Oct 1940, *Demaree 21841* (F, NY). Hempstead Co., 22 Oct 1932, *Demaree 9913* (US). Hot Springs Co., 17 Jul 1938 *Demaree 17957* (MO). Logan CO., 30 Jul 1983, *Sullivan 1310* (OKL). Marion Co., 2 Oct 1937, *Palmer 43877* (MO). Pike Co., 29 Sep 1932, *Demaree 9439 A* (US). Polk Co., 19 Aug 1937, *Demaree 15880* (MO). Pulaski Co., 7 Nov 1937, *Demaree 16640* (F, NY). Saline Co., 8 Jul 1955, *Demaree 37274* (OKL). Searcy Co., 9 Sep 1968, *Demaree 59274* (OKLA). Sevier Co., 20 Oct 1932, *Demaree 9913* (NY). Yell Co., 16 Aug 1939, *Demaree 20109* (F, NY). CALIFORNIA: Colusa Co., 12 Jul 1916, *Stinchfield s.n.* (NY). Lake Co., 18 Sep 1945, *Baker 11226* (CAS). San Diego Co., 6 Dec 1918, *Spencer 1014* (CAS). FLORIDA: Collier Co., 20 Jul 1965, *Lakela 29010* (US). Broward Co., 19 Jan 1930, *Moldenke 480* (MO, NY). Dade Co., 23 Feb 1915, *Small 5495* (NY). Franklin Co., 23 Jul 1987, *Anderson 10792* (MO). Highlands Co., 15 Dec 1929, *Moldenke 5417* (NY). Hillsboro Co., 28 Mar 1923, *Churchill 715* (MO). Lee Co., Jul- Aug 1900, *Hitchcock 232* (F, MO, NY, US). Leon Co., 10 Jul 1955, *Godfrey 53608* (NY). Monroe Co., 26 Feb 1951, *Killip 40921* (US). Orange Co., 20 Dec 1899, *Meislahn 141a* (US). Palm Beach Co., 1 May 1918, *Small 8507*, (US). Polk Co., 23 Jun 1931, *McFarlin 5924* (CAS). GEORGIA: McIntosh Co., 18 Jul 1956, *Duncan 20311* (CAS). ILLINOIS: Alexander Co., 18 Sep 1919, *Palmer 16489* (MO). Hardin Co., 27 Oct 1920, *Palmer 19589* (MO). Saint Claire Co., 17 Oct 1965, *Neill 16791* (MO). INDIANA: Grant Co., 4 Sep 1914, *Deam 15287* (NY). Putnam Co., 1 Jul 1928, *Yuncker 1794* (NY). Whitley Co., 27 Sep 1941, *Friesner 16539* (CAS, MO, NY). KANSAS: Cherokee Co., 3 Oct 1970, *McGregor 23672* (NY). KENTUCKY: Bell Co., 10 Aug 1888, *Lloyd s.n.* (NY). Hickman Co., 23 Aug 1923, *McFarland 2223* (NY). Kenton Co., 19 Sep 1942, *Braun 4650* (US). LOUISIANA: Calcasieu Par., 4 Aug 1990, *Martínez & Hernández 1915* (TEX). Concordia Par., 7 Aug 1988, *Thomas 106712* (MO). Madison Par., 27 Jul 1979, *Rich 1306* (NY). Natchitoches Par., 2 Oct 1915, (MO). Orleans Par., 23 Sep 1970, *Rose 10415* (CAS). Rapides Par., Hale s.n. (NY). MARYLAND: Snow Hill, Sep 1863, *Canby s.n.*

(NY). MISSISSIPPI: Forrest Co., 4 Aug 1971, *Rogers 6867B*, (NY). MISSOURI: Barry Co., 10 Oct 1935, *Bush 15252* (MO). Callaway Co., 26 Jul 1956, *Steyermark 8290* (MO). Dunklin Co., 1 Sep 1930, *Kellogg s.n.* (MO). Jackson Co., 6 Sep 1896, *Mackenzie s.n.* (MO, US). Jasper Co., 28 Sep 1937, *Palmer 43814* (MO). Laclede Co., 20 Jul 1934, *Steyermark 13873* (MO). Lafayette Co., 14 Aug 1937, *Steyermark 24738* (MO). McDonald Co., 1 Sep 1913, *Palmer 4065* (MO). Moniteau Co., 16 Aug 1937, *Steyermark 24820* (MO). Nayne Co., 23 Aug 1936, *Steyermark 21139* (MO). Newton Co., 14 Jul 1927, *Palmer 32492* (NY). Ozark Co., 8 Oct 1927, *Palmer 32962* (MO). Phelps Co., 13 Oct 1922, *Kellogg 197* (MO). Shannon Co., 22 Aug 1901, *Bush 726* (MO). Stone Co., 1 Aug 1983, *Sullivan 1318* (OKL). St. Louis Co., 8 Oct 1933, *Gallagher s.n.* (MO). Taney Co., 12 Jun 1898, *Bush 165* (MO). Washington Co., 30 Aug 1989, *Ravell 2527* (MO). NEW MEXICO: Grant Co., 10 Oct 1881, *Rusby 310* (US). NORTH CAROLINA: Swain Co., 15 Sep 1913, *Mooney s.n.* (US). OKLAHOMA: Delaware Co., 16 Sep 1936, *Bush 15814* (MO). Johnston Co., 15 Apr 1916, *Houston 3572 1/2* (NY). LeFlore Co., 28 Oct 1915, *Palmer 9047* (MO). Mayes Co., 29 Jul 1905, *A.V.H. s.n.* (OKL). Murray Co., 22 Jul 1944, *Hopkins 6429* (OKL). Muskogee Co., 5 Sep 1927, *Little 6184* (OKL). Ottawa Co., 29 Aug 1913, *Stevens 2530* (NY). Sequoyah Co., 10 Sep 1957, *Wallis 5527* (OKL). Tulsa Co., 6 Jul 1957, *Clark 392* (OKL). PENNSYLVANIA: Allegheny Co., 28 Aug 1869, *Porter s.n.* (US). SOUTH CAROLINA: Berkley Co., 17 Jul 1939, *Godfrey 622* (NY, US). Kenton Co., 5 Aug 1905, *Bram 15* (US). Scioto Co., 14 Oct 1951, *Bartley 1485* (US). TENNESSEE: Cheatham Co., 31 Aug 1939, *Svenson 10395* (CAS). TEXAS: Calhoun Co., 21 Jul 1973, *Hartman 3688* (TEX). Bell Co., no date, *Wolff 1273* (US). Bowie Co., 12 Jul 1965, *Cornell 31272* (MO, LL). Brazoria Co., 25 Sep 1973, *Fleetwood 10656* (TEX). Brazos Co., 3 Nov 1948, *Moncrief 147b* (TEX). Cameron Co., 4 Oct 1952, *Correll 14856* (US, LL). Denton Co., 30 Jul 1927, *Ruth 1480* (US). DeWitt Co., 3 Aug 1941, *Riedel s.n.* (TEX). Gonzales Co., 20 Oct 1950, *Tharp 51467* (TEX). Harris Co., 6 Oct 1965, *Correll 31889* (LL, MO). Hidalgo Co., 8 Jun 1941, *Runyon 2717* (TEX). Jackson Co., 27 Nov 1939, *Tharp s.n.* (MO). Jasper Co., 27 May 1957, *Correll 16486* (LL). Liberty Co., 22 Sep 1988, *Orzell 8480* (TEX). Matagorda Co., 8 May 1916, *Palmer 9703* (US). McLennan Co., Aug 1946, *Smith 59* (TEX). Nacogdoches Co., 10 Aug 1964, *Waller 236* (TEX). Robertson Co., 17 Jul 1982, *Sullivan 1227* (OKLA). Rusk Co., Jun-Sep, *Vinzent s.n.* (MO). Travis Co., 11 Nov 1929, *Tharp s.n.* (TEX). Willacy Co., 23 Nov 1953, *Johnston 53256.15* (TEX). Williamson Co., 9 Oct 1944, *Wolcott 314* (TEX). VIRGINIA: Henrico Co., 19 Aug 1940, *Fernald 12794* (US). Isle of Wight Co., 8 Sep 1941, *Fernald 13741* (MO, NY, US). James City Co., 30 Jul 1941, *Fernald 13441* (MO, NY). London Co., Aug 1888, *Holms s.n.* (NY). Luray Co., 7 Sep 1901, *Steele 197* (MO, NY, US). Northampton Co., Sep 1878, *Canby s.n.* (NY). WASHINGTON, D.C.: Washington D.C., 1 Sep 1896, *Steele s.n.* (MO). WEST VIRGINIA: Ohio Co., 22 Sep 1878, *Mertz s.n.* (NY). VENEZUELA: ANZOATEGUI: NE of Bergantín, 16 Feb 1945, *Steyermark 61218* (F). ARAGUA: 7 km SE of Colonia Tovar, 24 Mar 1980, *Steyermark 121820*, yellow anthers (NY). BOLÍVAR: Cerro Picacho, N of Las Nieves, 16 Feb 1961, *Steyermark 88958* (NY). CARABOBO: 1.5 km N of the bridge over Río Trincheras, 4 Aug 1982, *Croat 54538*, (NY). DISTRITO FEDERAL: La Florida near Caracas, 25 Feb 1938, *Alston 5214* (NY, US). GUARICO: 39 km SSW of Calabozo on Hato Masaguaral, 7 Jul 1983, *Rondeau 321* (US). MÉRIDA: Río Chama, 31 Aug 1966, *Steyermark 97022* (US). MIRANDA: Los Teques, 15 Feb 1935, *Archer 3056* (US). TACHIRA: carr. vieja Sn. Cristóbal-El Corozo-Río Trincheras, 4 Aug 1982, *Croat 54538*, yellow anthers (NY). ZULIA: Sierra de Perija al SW de Machiques, 24 Aug 1967, *Steyermark 99688* (US).

**DOUBTFUL AND EXCLUDED NAMES**

- Physalis greenei* Vasey et Rose, Contr. U.S. Natl. Herb. 1:18. 1890. *Nomen nudum*, no description was provided.
- Physalis hirsuta* M. Martens et Galeotti, Bull. Acad. Roy. Sci. Bruxelles 12:132. 1845. Based on *Linden 254*, a voucher could not be located at **GENT**. The curators located *Linden 255* (*Physalis coztomatl* Dunal) and *Linden 256* (*P. pubescens*). The description suggests it could be conspecific with *P. pubescens*, but the name could have priority over other names if this is a good species.
- Physalis linkiana* Nees, Linnaea 6:471. 1831. No specimen was cited in the original description. From the description, the plant seems to be close to *Physalis angulata* from which it was said to differ in having longer peduncles. Any possible type at **B** would have been destroyed during World War II.
- Physalis surinamensis* Miq., Symb. Fl. Surinam. Linnaea 17. 1844. No specimen was cited in the original description. The description is of a hirtellous plant from Surinam with immaculate corollas. I have not seen any specimen referable to this name, either at **U** or elsewhere.

**ACKNOWLEDGMENTS**

This revision was part of my PhD. dissertation, partially supported by Conacyt and the B.L. Turner Fund. L. Hernández, J. Saunders and J. Panero tested the key; B.L. Turner and M. Nee reviewed earlier versions; L. Hernández, P. Delprete, and N. Webber provided the illustrations. R. Jones and L. Hernández reviewed the final version. Two anonymous reviewers and Fernando Chiang kindly reviewed the manuscript and their suggestions greatly improved the paper. I am grateful to the curators of the following herbaria for the loan of their specimens: **ALBU**, **ASUF**, **ARIZ**, **CAS**, **ENCB**, **F**, **G**, **IEB**, **MEXU**, **MO**, **NY**, **OKL**, **OKLA**, **TEX-LL**, **UNM**, **US** and **VPI**. The curator at **HAL** kindly provided a photograph of the type of *P. nicandroides*, the curator at **GENT** kindly searched for the type of *P. hirsuta*.

**LITERATURE CITED**

- AXELIUS, B. 1992. Testa patterns in some species of *Physalis* and some other genera in the tribe Solanaceae (Solanaceae). *Plant Science (Elsevier)* 153:488-502.
- AVERETT, J. E. and A.M. POWELL. 1972. Chromosome numbers in *Physalis* and *Solanum*. *Sida* 5: 3-7.
- AXELIUS, B. 1995. A new combination in *Physalis* (Solanaceae). *Phytologia* 79 (1): 10-11.
- BAHADUR, B. and S.M. FAROOQUI. 1986. Seed and seed coat characters in Australian *Nicotiana*. In: W. D'Arcy (ed.) *Solanaceae biology and systematics*. Columbia University Press, New York, pp. 114-137.

- BARTHLOTT, W. 1990. Scanning electron microscopy of the epidermal surface in plants. In: D. Claugher (ed.) *Scanning electron microscopy in taxonomy and functional morphology*. Clarendon Press, Oxford, pp. 69-94.
- BESSIS, J. and M. GUYOT. 1979. An attempt to use stomatal characters in systematic and phylogenetic studies of the Solanaceae. In: J. G. Hawkes *et al.* (eds.). *The biology and taxonomy of the Solanaceae*. Linnean Society Symposium Series 7: 321-326.
- D'ARCY, W.G. 1991. The Solanaceae since 1976, with a review of its biogeography. In: J.G. Hawkes *et al.* (eds.) *Solanaceae II. Taxonomy, chemistry, evolution*. The Royal Botanic Gardens, Kew and the Linnean Society of London, Surrey, pp. 75-137.
- DON, G. 1837. *A general system of gardening and botany. Founded upon Miller's gardener's dictionary* 7: 447-451.
- DUNAL, F. 1852. Solanaceae. In: A. De Candolle (ed.) *Prodromus Systematis Universalis Regni Vegetabilis* 13 (1), pp. 432-453.
- ESTRADA, E. and M. MARTÍNEZ (in press). *Physalis* (Solanaceae) and allied genera: *Tzeltalia*, a new genus from the highlands of southern Mexico and northwestern Guatemala. *Brittonia*.
- HENDRYCH, R. 1989. *Physalis alkekengi*, in Europa und in der Tschechoslowakei besonders. *Acta Universitatis Carolinae. Biologica* 33: 1-42.
- LESTER, R. N. and P. DURRANDS. 1984. Enzyme treatment as an aid in the study of seed surface structures of *Solanum* species *Annals of Botany* 53: 129-131.
- LINNAEUS, C. 1753. *Species Plantarum*. Vol. I. Edition Shokobutsu-Bunken-Kankowka, Tokyo, pp. 182-184.
- MARTÍNEZ, M. 1993. *Systematics of Physalis (Solanaceae) section Epeteiorhiza*. Ph.D. Dissertation University of Texas, Austin, Texas.
- MARTÍNEZ, M. (in press). Infrageneric taxonomy of *Physalis*. In: M. Nee *et al.* (eds.) *Solanaceae IV. Advances in biology and utilization*. The Royal Botanic Gardens, Kew.
- MENZEL, M.Y. 1951. The cytotaxonomy and genetics of *Physalis*. *Proceedings of the American Philosophical Society* 95:132-182.
- NEE, M. 1991. The systematics of the lesser known edible Solanaceae of the New World. In: J.G. Hawkes *et al.* (eds.) *Solanaceae III. Taxonomy chemistry, evolution*. The Royal Botanic Gardens, Kew and the Linnean Society of London, Surrey, pp. 365-368.
- NEES VON ESENBECK, D.C.G. 1831. Versuch einer Vsrtrandigung über die Arten der Gattung *Physalis*. *Linnaea* 6: 431-483.
- RYDBERG, P.A. 1896. The North American species of *Physalis* and related genera. *Memoirs of The Torrey Botanical Club* 4: 297-372.
- SEITHE, A. 1979. Hair types as taxonomic characters in *Solanum*. In: J.G. Hawkes *et al.* (eds.) *The biology and taxonomy of the Solanaceae*. Linnean Society Symposium Series 7: 307-319.
- SEITHE, A. and G. J. ANDERSON. 1982. Hair morphology and the relationships of species in *Solanum* sect. *Basarthrum*. *Plant Systematics and Evolution* 139: 229-256.
- SEITHE, A. and J. R. SULLIVAN. 1990. Hair morphology and systematics of *Physalis*. *Plant Systematics and Evolution* 170: 193-204.
- SULLIVAN, J. R. 1986. Reproductive biology of *Physalis viscosa*. In: W. D'Arcy (ed.) *Solanaceae biology and systematics*. Columbia University Press. New York, pp. 274-283.
- WATERFALL, U.T. 1958. A taxonomic study of *Physalis* in North America north of Mexico. *Rhodora* 60: 107-114; 128-142; 152-173.

WATERFALL, U.T. 1967. *Physalis* in Mexico, Central America and the West Indies. *Rhodora* 69: 82-120; 203-239; 319-329.