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SYSTEMATIC STUDIES IN PHYSALIS (SOLANACEAE)

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PREFACE

This dissertation consists of four manuscripts that have been organized according to the format specified for publication in the American Journal of Botany (chapters 1 and 3), Systematic Botany (chapter 2), and the Vascular Flora of the Southeastern United States (chapter 4). The tables and figures are numbered independently in each chapter.

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POLLINATION BIOLOGY OF PHYSALIS VISCOSA

VAR. CINERASCENS (SOLANACEAE)

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ABSTRACT

Physalis viscosa var. cinerascens is a self-incompatible, herbaceous perennial which occurs in disturbed or open habitats in the south-central United States and eastern Mexico. The plants are low-growing and the pendant blossoms are often obscured by the foliage. In Oklahoma the species blooms from April through October. The flowers are yellow with dark purple or brown maculations in the center and a mat of white hairs in the throat. Nectar is produced in small quantities at the base of the ovary and pollen is present in copious amounts. The pollinators are solitary bees which visit the flowers for nectar and pollen. Perdita halictoides is the primary pollinator and is oligolectic on Physalis.

Physalis is an American genus of about 90 species. Generic boundaries are clearly marked by the pendant flowers and inflated fruiting calyx which encloses the berry. The corolla also exhibits an uncommon color combination for the family -- the limb in all but two or three species is yellow, typically with a darker color in the center, and a mat of white hairs in the throat (Fig. 1). The pendant blossoms are often obscured by the foliage and many of the flowers hang just above the ground. In addition, the blossoms have no detectable odor. Consequently, it is difficult to envision how pollinator attraction, and hence pollination, might be accomplished. Pendant flowers are uncommon but distributed among a wide variety of families of dicots and monocots (e.g., Erythronium, Aquilegia, Dodecatheon). Most, however, have brightly colored floral parts and/or are borne on erect stems above the foliage.

Specific boundaries in Physalis are poorly defined, with intergrading forms often uniting species (Rydberg, 1896; Menzel, 1951, 1957, 1960; Waterfall, 1958, 1967; Hinton, 1975, 1970). Presumably these forms result from hybridization. Interspecific hybrids can also be obtained experimentally (Menzel, 1951, 1957; Hinton, 1975, 1976; the latter reported seed set only) and a hybrid origin has been hypothesized for several species (Menzel, 1957, 1960; Waterfall, 1958).

The pollination biology of Physalis is of considerable interest because of the floral features which are relatively uniform throughout the genus, but singular in the family. Thus it seems reasonable to assume that this floral syndrome was significant in the origin and

evolution of the genus. A study of the reproductive biology of the genus may shed light on the selection or stochastic processes involved in the evolution of Physalis. Such a study will also aid in understanding the isolating mechanisms in Physalis, which apparently are poorly formed. As an initial step in studying the reproductive biology of Physalis I conducted an investigation of the pollination biology of P. viscosa L. var. cinerascens (Dunal) Waterfall, which has flowers that are typical for the genus.

MATERIALS AND METHODS--Physalis viscosa var. cinerascens occurs in Oklahoma, Texas, and adjoining states south to Yucatan. It is a low-growing, perennial herb that occurs primarily in disturbed or open habitats such as roadsides, along railroad tracks, or in open fields. During the summers of 1981 and 1982 field studies were conducted on two populations of P. viscosa var. cinerascens in Cleveland County, Oklahoma (Table 1). Limited observations were also made on three additional populations in Oklahoma in 1981 and one in Louisiana in 1982. Sympatric species of Physalis were also observed. Voucher specimens of plants are deposited in OKL. Insects are deposited in the USDA Bee Biology and Systematics Lab in Logan, Utah.

Phenological studies consisted of daily observations of 103 flowers during the months of June and July, 1981. Fruit set was determined for 70 of the 103 which completed flowering (i.e., to wilting of the corolla) without being damaged by grasshoppers. An additional 91

flowers were marked and fruit set determined in 1982.

Stigma receptivity was determined on greenhouse-grown plants using PEROXTESMO KO peroxidase test papers (Machery-Nagel Co., Carle Place, New York). Receptive stigmas cause a color change in the paper from white to bright blue. Tests were performed on stigmas of unopened flowers, open unpollinated flowers, and on open flowers which had been hand-pollinated. For the latter class, several flowers in the same stage of development were hand-pollinated and then tested for stigma receptivity at two-hour intervals until the corollas wilted.

Pollen viability was estimated by staining pollen grains with aniline blue-lactophenol (Hauser and Morrison, 1964). Five flowers were sampled from each of the five Oklahoma populations. One anther from each flower was macerated on a glass slide in the stain, and 300 randomly selected grains were scored for stainability.

The number of pollen grains per flower was determined using a technique modified from that described by Sullivan (1983). All anthers from a sample flower were macerated with 0.5 ml of a lactic acid and glycerine (3:1) solution. The suspension was mixed for 90 sec using a Vortex Genie Mixer. Four counts of one sample from each of the five populations were made using a hemocytometer. The number of pollen grains per flower was calculated by multiplying the number of grains counted by the dilution factor. The number of ovules per flower was determined by crushing a pistil on a glass slide in aniline blue-lactophenol. This was done for three pistils from each of three populations and the mean value calculated.

In order to determine the breeding system, I artificially self-pollinated ($n = 39$) and cross-pollinated ($n = 61$) greenhouse-grown plants on the first morning after anthesis. To exclude insects the flowers were closed with masking tape after pollination. Twenty reciprocal crosses were performed in the greenhouse between P. viscosa var. cinerascens and each of the three other Physalis species that were growing at the two main study sites (Table 1): P. pumila Nuttall (Fig. 2), P. heterophylla Nees (Fig. 3), and P. longifolia Nuttall (Fig. 4).

Over 50 hours were spent collecting and observing anthophilous visitors during June and July, 1981 and 1982. Pollen loads were examined by brushing the insects with small pieces of glycerine jelly (Beattie, 1971). The percentage of Physalis pollen carried by the insects was determined by counting 100 randomly selected grains on each slide.

A series of photographs of the flowers was taken using filters transmitting red (Soligor 25 AIR), yellow (Vivitar 8 K 2), blue (Vivitar 80 C), ultraviolet (Tiffen 8), and visible light (Tiffen UV haze) and Kodak Pan-X film. Photographs were taken with both sky, the natural background for these flowers, and vegetation as backgrounds. In the latter series a gray scale (Kevan et al., 1973) was used for comparison of reflectance. The photographs were used to interpret reflectance, transmittance, and color of the corolla in terms of the color vision of bees (Kevan et al., 1973; Kevan, 1978).

RESULTS--Floral biology--The flowering period of P. viscosa var. cinerascens commences in late April or early May in Oklahoma and continues into October. Each flower lasts from 1-3 days (mean = 1.9 days). The corolla opens each morning of anthesis about 0900 hr CDT and closes at sunset. The corolla of open flowers is reflexed and the stigma and tips of the anthers are slightly exserted. The stigma is receptive from the time the corolla unfolds on the first day until it wilts. Anther dehiscence occurs when the filament has attained its maximum length. Usually, one or more of the anthers dehisce as the corolla unfolds. Dehiscence begins at the apex and proceeds basipetally. Pollen is shed over the 1-3 day period that the flower is open with one or more anthers shedding each day.

Pollen viability is high in four of the five Oklahoma populations studied (range = 85-98%, n = 5 from each population). The exception is the SE Norman population which produced little or no viable pollen (range = 0-0.02%, n = 8). Pollen is produced in copious quantities in P. viscosa var. cinerascens (mean = 1,600,500 grains/flower). The pollen-ovule ratio is 13,172.84 (SE = 3666.67). None of the 39 self-pollinations set fruit, although three of these flowers initiated seed production before aborting. Viable seed was produced from 50 of the 61 cross-pollinations (86%). Another three developing fruits were damaged by lepidopteran larvae. The 8 flowers which were unsuccessfully cross-pollinated all wilted and fell within a few days after pollination. Unmanipulated flowers did not set fruit in the greenhouse. Thus, apomixis does not occur in the populations studied.

Nectar is produced at the base of the ovary. The mat of white hairs in the throat of the corolla holds the nectar near the ovary. There is no discernable scent associated with the flowers.

Reflectance photography revealed that high percentages of yellow, blue, and red wavelengths (comparable to the gray scale chips reflecting 99.5, 98, and 99%, respectively) are reflected by the limb of the corolla (Sullivan, 1984). Ultraviolet light (comparable to the chip reflecting 88%) is reflected by the mat of hairs in the corolla throat and the anthers and pollen (Fig. 5). Little or no visible or UV light is reflected from the five maculations in the throat. With skylight behind the flower there is much less UV reflectance from the center of the corolla, but UV light is transmitted through the main veins of each of the five corolla lobes (Fig. 6). Thus, the flowers appear as a target-pattern to insect visitors. I interpret the yellow limb of the corolla as bee yellow-orange, the throat maculations as bee black, the center of the flower (the hairs, anthers, and pollen) as bee white-yellow, and the main veins of the corolla lobes as a luminescent bee white (Kevan, 1978).

Intrafloral ecology--Fruit set in open-pollinated blossoms of P. viscosa var. cinerascens varied between 1981-82 and among populations. Despite the low pollen viability in the SE Norman population these plants set fruit. Since apomixis did not occur in plants transplanted to the greenhouse from this population, it is assumed that these fruits are the result of pollinations with pollen from other plants in the

vicinity or that some plants in the population are pollen fertile. If, as seems likely, the former is true, then pollen is effectively carried some distance to other populations by pollinators. In 1981, fruit set in the S Norman and SE Norman populations was 13% (n = 30) and 35% (n = 40), respectively, whereas in 1982, fruit set was considerably higher in both populations, 32% (n = 53) at the former site and 58% (n = 38) at the latter. However, the percentage of fruits containing seeds was much lower than this in all cases. In 1982 only 11% of the fruits at the S Norman site and 16% of those at SE Norman contained seeds. The other expanded ovaries had all been damaged by lepidopteran larvae and presumably the ovules or seeds were destroyed. The percentage of expanded ovaries is considered to reflect more accurately pollinator efficiency, however, because it is most likely that lepidopterans oviposit in calyx bases of flowers which have been fertilized and consequently are enlarged (B.A. Drummond III, Illinois State University, pers. comm.). Based on this assumption the combined fruit set for the populations studied in 1981 and 1982 was still only 34% (n = 162). Thus pollinator and/or pollination efficiency is relatively low.

Insects were collected on Physalis as follows: (1) Physalis viscosa var. cinerascens: Augochlorella striata, 7 ♀, 5 ♂; Colletes latitarsis, 5 ♀; Dialictus tegularis, 1 ♀; Perdita halictoides, 19 ♀, 5 ♂; (2) Physalis heterophylla: Perdita halictoides, 6 ♀, 1 ♂; (3) Physalis pumila: Augochlorella striata, 1 ♀; (4) Physalis longifolia: Augochlorella striata, 1 ♀; Perdita halictoides, 21 ♀, 2 ♂. Pollinator frequency is constant but low, with no peak seasonal or diurnal period. With one exception, all visitors fly just above the ground and among the

foliage such that they approach the flowers from below, grasp the stamens with their forelegs, and swing their abdomen up over the stamens and pistil. Thus, pollen from the flower is deposited on the venter of the insect and that on the insect can effectively be deposited on the stigma. All of the visitors observed, therefore, are effective pollinators. They then probe the throat of the corolla for nectar. Most of the visitors collected pollen.

The most frequent visitor of P. viscosa var. cinerascens was Perdita halictoides Smith (Hymenoptera:Andrenidae). This species has also been recorded on P. viscosa (most likely var. elliottii) in Florida and is thought to be oligolectic on Physalis (Eickwort, 1977). Females form pellets of Physalis nectar and pollen which they carry on their scopae. After landing on a flower, females scrape pollen from the anthers with both forelegs, rear upright, and pack the pollen on their scopae with the middle legs. The bee then walks around the rim of the corolla or pivots on the upright stamens, and inserts her proboscis into the throat of the corolla. She then sits upright on the corolla on a tripod formed by her hind legs and abdominal apex and passes nectar from her mouthparts to the pollen pellets via her fore- and middle-legs. This behavioral pattern has previously been described by Eickwort (1977) for Perdita octomaculata on Solidago. Perdita usually forages on several flowers in a small patch of stems before leaving the population.

Augochlorella striata (Provancher) (Hymenoptera:Halictidae) was a frequent visitor to P. viscosa var. cinerascens. Female Augochlorella collected pollen during their visits. Halictids are typically

polylectic (G.C. Eickwort, pers. comm.), and only one-third of the Augochlorella collected carried more than 60% Physalis pollen.

Colletes latitarsis Robertson (Hymenoptera:Colletidae) was an infrequent visitor in the populations studied. Visits to the flowers by this bee are very brief. During a visit the bees rapidly scrape pollen from the anthers and place it onto their scopae. Then, they either leave the population of Physalis or they land on a nearby leaf, groom loose pollen from their head and place it onto their scopae, and resume their visit in the same population. Even after grooming, a considerable amount of pollen remained on the ventral surface of the bee. The loose pollen carried by Colletes was pure Physalis.

Only one Dialictus tegularis (Robertson) (Hymenoptera:Halictidae) was observed on Physalis and it carried no Physalis pollen. Dialictus exhibited the same nectar-foraging behavior as Augochlorella.

Augochlorella, Colletes, and Dialictus also forage on other taxa, in particular Solanum rostratum (Bowers, 1975), which often occurs in the same areas as P. viscosa var. cinerascens. Augochlorella, Colletes, and Perdita were also collected on other species of Physalis which occurred at the S Norman and SE Norman study sites (Table 1). During their visits to these plants the insects exhibited the same foraging behavior as observed on P. viscosa var. cinerascens.

Hybridization studies--All but one of the 20 artificial hybridizations attempted between P. viscosa var. cinerascens and P.

longifolia aborted after the calyx had expanded, but without any development of ovary or seed. For about half of the P. viscosa var. cinerascens X P. pumila (n = 20) and X P. heterophylla (n = 20) crosses, the flowers wilted and fell within a few days without development of the ovary or calyx. Fertilization most likely did not occur in these cases. The other half of the crosses resulted in small fruits with a few aborted seeds. Thus, hybrid plants were not obtained in any interspecific cross.

DISCUSSION--Physalis viscosa var. cinerascens is obligately xenogamous and dependent on solitary bees for pollination. Plants transplanted to the greenhouse and self-pollinated did not produce fruit, whereas cross-pollinations using the same plants resulted in high fruit set. Unmanipulated flowers on greenhouse plants did not set fruit, therefore it seems unlikely that the plants are apomictic. Based on Cruden's (1977) correlation of pollen-ovule ratio and breeding system, P. viscosa var. cinerascens far exceeds the range of expectation for a xenogamous reproductive system. The excess provides abundant food for insect visitors, and probably is an adaptive adjustment for pollinator frequency and/or efficiency.

High seed set is not necessary for reproduction in this species, however, because it has such a successful means of vegetative proliferation. The perennial Physalis species have a prolific system of rhizomes. Each rhizome may extend for several feet before sending up an

above-ground stem, making distinction between plants (genets) in the field difficult. It may also be a factor contributing to the low fruit set in the field, because these plants are self-incompatible. Clusters of flowering stems might be more attractive to potential pollinators, but would also increase the chances for geitonogamous pollinations. In fact, all of the pollinators observed visited more than one flower per cluster of stems during a visit.

Perdita, Colletes, and Augochlorella forage the flowers of P. viscosa var. cinerascens for nectar and pollen. These solitary bees were also collected visiting flowers of other Physalis species at the main study sites, and elsewhere (Stephen, 1954; Eickwort, 1977; Sullivan, 1984). During a visit pollen is deposited on the venter of the insect, which also comes into contact with the stigma of the flower. Thus, all of these insects can successfully transfer pollen from one flower to another.

Floral features are relatively uniform throughout Physalis. The Physalis species growing at the main study sites show few differences in flower size and coloration, which may be associated with a lack of recognition by pollinators. In addition, the blooming periods of these species are almost coincident. Physalis pumila begins blooming approximately 2-3 weeks before the other three species, but all four species then bloom throughout the summer. The major differences between these species are in the distinctiveness and color intensity of the throat maculations (Fig. 1-4). In the populations studied, visitor inconstancy among Physalis would result in the loss of a portion of

pollen and ovules each generation to abortive hybridizations. The proportion would be dependent on insect fidelity and pollen competition. Indeed, the fruit set of open-pollinated P. viscosa var. cinerascens was only 34% compared with the 86% fruit-set obtained in artificial cross-pollinations in the greenhouse. However, this might also result from low incidence of visitors or geitonogamous pollinations.

In the populations I studied, internal barriers prevent the occurrence of interspecific hybridization, although observations of P. viscosa var. cinerascens, P. pumila, P. heterophylla, and P. longifolia reveal that a uniform pollination syndrome is shared by these members of the genus. In areas where cross-compatible Physalis species occur within pollinating distance, inconstancy of pollinators may explain, in part, the blurring of taxonomic boundaries. Hybridization has been implicated in the origin of several species of Physalis in North America (Menzel, 1957, 1960; Waterfall, 1958) and the existence of a hybrid population has been documented in North Carolina (Hinton, 1975).

Pollination has been investigated extensively in the genus Solanum (Hardin, et al, 1972; Bowers, 1975; Buchmann, et al, 1977; Whalen, 1978; Symon, 1979; inter alia) however, the pollination syndromes of species in those genera most closely related to Physalis (e.g., Chamaesaracha, Quincula, Margaranthus) are, as yet, unstudied. Clearly, the distinctive floral features of Physalis (in particular, the pendant blossoms) are part of a specialized pollination syndrome which must have been an important factor in the origin and diversification of the genus. Presumably the switch to pendulous flowers led to a discrete pollination

system. Knowledge of the reproductive biology of those genera which are closely related to Physalis, combined with a better understanding of the phylogenetic relationships of these genera is needed to elucidate further the reproductive and evolutionary significance of the floral features in these taxa.

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Table 1. Study populations of *Physalis viscosa* var. *cinerascens*

Locality	Sympatric species
<hr/>	
SE Norman, Cleveland Co., OK	<u>P. pumila</u> , <u>P. longifolia</u>
S Norman, Cleveland Co., OK	<u>P. heterophylla</u> , <u>P. longifolia</u>
Hopeton, Woods Co., OK	none
Cora, Woods Co., OK	<u>P. (<i>Quincula</i>) lobata</u>
downtown Norman, Cleveland Co., OK	none
Minden, Webster Par., LA	none

Figure 1-6. Flowers of Physalis species included in this study. 1. P. viscosa var. cinerascens with grass as a background and a gray-scale for comparison. Flower 1.9 cm in diameter. 2. P. pumila. Flower 1.9 cm in diameter. 3. P. heterophylla. Flower 2.1 cm in diameter. 4. P. longifolia Flower 1.8 cm in diameter. 5. P. viscosa var. cinerascens with grass as a background. Photographed using a filter which transmits ultraviolet light. 6. P. viscosa var. cinerascens photographed with the sky as a background and using a UV-transmitting filter.



SYSTEMATICS OF THE PHYSALIS VISCOSA
COMPLEX (SOLANACEAE)

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ABSTRACT. A phenetic analysis based on morphological features of the Physalis viscosa complex revealed four major clusters of OTUs, each previously recognized at the species level. Crossing studies are generally consistent with taxonomic inferences based on the phenetic analysis, although two of the species groups are interfertile. Flavonoid profiles also show congruence with the other analyses. Based on the data from all analyses, the Physalis viscosa complex is revised to consist of four species in North America. Physalis cinerascens and P. mollis, previously considered conspecific, are now recognized as distinct species. Physalis cinerascens, with two varieties, is geographically widespread from the south-central United States to Yucatan. Physalis mollis occurs in eastern Texas and adjacent states,

and has one glandular variety in the southernmost portion of its range. Natural hybridization apparently does not occur between P. cinerascens and P. mollis, and only rarely occurs between the varieties within each species. The remaining taxa, found in coastal habitats in the southeastern United States, are treated here as two species: P. angustifolia from along the Gulf Coast; and P. walteri from the southern Atlantic Coast. Although there are high levels of interpopulational variation in both P. angustifolia and P. walteri, no discrete infraspecific taxa are recognized. Hybridization may have occurred between these two species in Florida, resulting in some blurring of species boundaries; however, the two are distinct in the remainder of their ranges.

Physalis L. is an American genus of about 90 species, characterized by pendant flowers and by an inflated fruiting calyx that encloses the berry. Physalis was divided into 3 sections, Physalis (as Euphysalis), Microphysalis, and Megista by Rydberg in 1896. He further divided section Physalis into 9 species groups (interpreted here as series): Pubescentes, Leptophyllae, Angulatae, Philadelphicae, Lanceolatae, Heterophyllae, Stellatae, Versicolores, and Crassifoliae. In his treatment of Physalis for the Manual of the Southeastern Flora (pp. 1107-12; Small 1933) Rydberg, without comment, changed the names of 2 of his 9 series: Leptophyllae became Carpenterianae, and Stellatae became Viscosae. The latter names are superfluous and, therefore, are illegitimate.

Series Stellatae, Rydberg (1896), is composed of herbaceous perennials with predominantly branched trichomes, and occurs from the southeastern and south-central United States to Argentina. Rydberg included 6 species the series -- P. angustifolia, P. fuscomaculata, P. mollis, (including var. cinerascens and var. parvifolia), P. viscosa (including var. maritima = P. walteri of Nuttall), P. elliotii, and P. fendleri. He noted that the species "intergrade more or less", thus distinguishing between them is often difficult.

Menzel (1951, 1957) experimentally demonstrated that genetic isolation barriers are incomplete between some of the species Rydberg recognized. However, her crossing studies were limited in both the number of taxa used and the number of crosses performed. She obtained fertile hybrids between P. viscosa (from the southeastern U. S. coast)

and P. mollis (1951), and among P. viscosa (U. S. populations), P. elliotii, and P. angustifolia (1957). She obtained seeds, which proved to be inviable, from crosses between the members of series Stellatae and members of both series Lanceolatae and Heterophyllae. She also discovered that the karyotypes of the species in the series are similar in total length and short arm to total length ratio, and that the morphology of seedlings and mature plants intergraded to some extent. Based on this information she inferred that the members of Physalis series Stellatae are genetically closely related, and suggested that they be treated as a single polytypic species (1951). After a more detailed study of the morphology and hybridization capability among the Florida members of the series, she suggested that P. elliotii and P. viscosa var. maritima might represent a large scale hybrid swarm (1957).

In 1958 Waterfall revised the North American species of Physalis based on macromorphological features. He did not divide Physalis into subgenera and sections, because of his uncertainty about the circumscription of the genus (i.e., whether Chamaesaracha and Margaranthus are congeneric with Physalis or not). As a result of Waterfall's analysis, all the members of P. series Stellatae except for P. angustifolia and P. fendleri were combined into one large, polymorphic species, P. viscosa. Waterfall divided P. viscosa into three subspecies, two of which he further divided into varieties and forms: (1) ssp. viscosa; (2) ssp. mollis var. mollis and var. cinerascens; and (3) ssp. maritima var. maritima f. maritima, var. maritima f. latifolia, var. elliotii f. elliotii, var. elliotii f. glabra, and var. spathulaefolia. Physalis fuscomaculata was submerged

in the typical subspecies and P. fendleri was considered a synonym of a species in another section of the genus. In addition, Waterfall recognized a new species, P. variovestita. He reported an intergradation of morphological forms between P. variovestita and P. viscosa ssp. mollis and postulated that this was due to gene exchange between the two species. Waterfall and Rydberg agreed in interpreting the typical form of P. viscosa as a South American taxon. In 1967 Waterfall recognized two additional varieties of P. viscosa from Mexico: var. sinuatodentata and var. yucatanensis. He noted that both are "weakly differentiated" from P. viscosa var. cinerascens.

This study treats only the North American members of P. viscosa (Waterfall 1958, 1967): P. viscosa ssp. maritima (excluding var. maritima f. latifolia, which is defined on the basis of a continuous character -- leaf size), and ssp. mollis and the closely related P. angustifolia and P. variovestita. Until subgeneric classification of Physalis has been more thoroughly investigated, it seems preferable to refer to the group of species under investigation as the P. viscosa species complex.

The purposes of this study are: (1) to investigate the potential for hybridization, its occurrence in natural populations, and its possible role in speciation within the Physalis viscosa complex; (2) to investigate the range of morphological variability in the complex and its correlation with flavonoid chemistry and isolation barriers; and (3) to provide a revised classification of the complex based on information obtained during this study.

MATERIALS AND METHODS

Field work was conducted in the southeastern and south-central United States during the summers of 1981-2 and in Mexico during October 1982. Materials for morphological, flavonoid, and breeding analyses were collected from 92 populations. Voucher specimens are deposited in OKL. In addition, 6500 specimens from the following herbaria were examined: AUA, CHAPA, CLEMS, DUKE, F, FLAS, FSU, GA, GH, HAL, KSC, LL, LSU, MARY, MEM, MEXU, MICH, MISS, MO, MONTU, MUR, NCSC, NCU, NLU, NY, OKL, OKLA, PENN, PH, SMU, TENN, TEX, UARK, UC, UNA, US, USCH, USF, VPI, WIS, and WVA. Approximately 3500 of these were collections of members of the Physalis viscosa complex and the remainder were representatives of other species in the genus. For convenience, taxa will be identified in the following sections of this paper by specific or subspecific epithet (e.g., P. viscosa var. elliottii f. glabra = GLABRA; P. viscosa var. elliottii f. elliottii = ELLIOTTII). In addition, populations identified by Waterfall's criteria as intergrades between P. variovestita and P. viscosa ssp. mollis will be referred to as INTERGRADE(S).

Phenetic analysis. Seventy collections were chosen as OTUs (Operational Taxonomic Units) to represent the geographic range and morphological variability of the members of the P. viscosa complex (table 1). Fourteen vegetative and 19 floral characters were scored or measured from each sheet, and from these measurements 8 ratios were calculated (table 2). The basic data matrix may be obtained from the

author. The characters chosen have traditionally been used to distinguish taxa in Physalis, or were determined in a preliminary analysis to exhibit intertaxon variation. Because both discrete and continuous characters were used, the measure of phenetic similarity selected was the General Similarity Coefficient of Gower (1971). The program used was written locally for the University of Oklahoma IBM 3081 computer (GOWER; written by Phillips and Hough). The OTUs were clustered using the unweighted pair group method using arithmetic averages (UPGMA using NTSYS; Sneath and Sokal 1973; Rohlf, et al 1979). The OTUs were also clustered using the Similarity Graph Clustering program of Estabrook (SIMGRA; 1966), which illustrates all connections between OTUs at different levels of similarity. For each UPGMA phenogram the cophenetic correlation coefficient was calculated to measure the agreement between the values represented in each phenogram and those in the original resemblance matrix, and a minimum spanning network was constructed (using NTSYS) to determine the nearest neighbor of each OTU (Sneath and Sokal 1973). A character analysis program (CHARANAL; Duncan and Estabrook 1976) was used to determine the taxonomically significant information content of each character.

Flavonoid analysis. Foliar flavonoids were extracted overnight in 80% methanol, concentrated by flash evaporation, and separated by two-dimensional paper chromatography in butanol:acetic acid:water (3:1:1) and 15% acetic acid. Flavonoids were identified using ultraviolet spectroscopy, acid and enzyme hydrolyses, and chromatography (Mabry, Markham and Thomas 1970). Separate spot patterns were obtained from 2-10 populations of each taxon in the complex (table 1).

Experimental analysis. The plants used for breeding studies were collected from 53 populations in the United States and Mexico (table 1), and grown from either seeds or rhizomes in the greenhouse at the University of Oklahoma. These plants represented 10 taxa in the P. viscosa complex and 4 other species in the genus. Reciprocal cross-pollinations were performed for all possible pair-wise combinations within the complex, excluding SINUATODENTATA and YUCATANENSIS which did not bloom until late in the study. The latter two taxa were crossed only with VARIOESTITA, MOLLIS, SPATHULAEFOLIA, CINERASCENS, and each other. Reciprocal crosses involving other species were: CINERASCENS X P. hederacefolia; CINERASCENS X P. heterophylla; CINERASCENS X P. longifolia; MOLLIS X P. hederacefolia; MOLLIS X P. heterophylla; VARIOESTITA X P. hederacefolia; VARIOESTITA X P. heterophylla; and all taxa of the P. viscosa complex with P. pumila. For each pair of taxa at least 10 crosses were performed and, for most pairs, 20 or more crosses were accomplished. In addition, at least 10 reciprocal crosses were made between populations within each taxon to estimate intrataxon compatibility. To test for self-compatibility, 10 self-pollinations were made on plants of each taxon, except for SINUATODENTATA and YUCATANENSIS. In all cases, flowers were pollinated on the first morning of anthesis and closed with masking tape to exclude pollinators. Plants from 1-5 representative crosses for each successful hybrid combination were grown in the greenhouse for subsequent study. Pollen viability of parents and hybrids was estimated by staining grains with aniline blue-lactophenol (Hauser and Morrison 1964). One anther from each plant was macerated on a glass slide in the stain, and 300 randomly

selected grains were scored for stainability. For hybrid plants, sibling and back-crosses were made when possible.

RESULTS

Phenetic analysis. The phenogram generated for 70 populations of the members of the Physalis viscosa complex (fig. 1) shows four major clusters: (1) VARIOVESTITA, MOLLIS, and INTERGRADES; (2) CINERASCENS, SINUATODENTATA, YUCATANENSIS, and SPATHULAEFOLIA; (3) MARITIMA and ELLIOTTII; and (4) GLABRA and ANGUSTIFOLIA. The cophenetic correlation coefficient is 0.847, indicating that there was only moderate distortion of the original similarity matrix in the production of the phenogram. The minimum spanning network, which illustrates linking of nearest neighbors, is shown in fig. 2.

The VARIOVESTITA OTUs cluster with the MOLLIS and INTERGRADE OTUs at a high phenon level (0.91). The VARIOVESTITA OTUs link closest to one another in the minimum spanning network and connect with the MOLLIS and INTERGRADE OTUs at a similarity of 0.92. Character analysis indicates that the presence of glandular hairs on VARIOVESTITA results in the slight distinction from the MOLLIS and INTERGRADE OTUs, which do not have glandular hairs. The INTERGRADE OTUs cluster with both the MOLLIS and VARIOVESTITA OTUs and hence do not form a discrete group. In the minimum spanning network two INTERGRADE OTUs do connect VARIOVESTITA and MOLLIS, but the third INTERGRADE OTU links only with a MOLLIS OTU.

CINERASCENS clusters with the OTUs representing SINUATODENTATA and YUCATANENSIS at a phenon level of 0.843, indicating only slight differences in overall morphology. The SPATHULAEFOLIA OTUs join the rest of this cluster at a phenon level of 0.814. Character analysis shows that SPATHULAEFOLIA differs from the other members of this cluster in having leaves with entire margins, while the other members of this cluster have leaves with dentate or undulate margins. On the minimum spanning network these taxa link at high similarity levels; YUCATANENSIS links to CINERASCENS at a similarity of 0.927, and to SPATHULAEFOLIA at a similarity of 0.926. SINUATODENTATA links only to YUCATANENSIS, with a similarity of 0.914. The CINERASCENS-SPATHULAEFOLIA-SINUATODENTATA-YUCATANENSIS cluster then joins the VARIOESTITA-MOLLIS cluster at a phenon level of 0.748. On the minimum spanning network the members of these two clusters join by a linkage of CINERASCENS to MOLLIS at a similarity of 0.911. Although the members of these two clusters are very similar, the CHARANAL program shows that there is a consistent difference between the two groups in the corolla throat maculations. The maculations of MOLLIS and VARIOESTITA are indistinct and range from very pale brown to dark brown in MOLLIS to dark purple-black in VARIOESTITA, while those of CINERASCENS, SPATHULAEFOLIA, SINUATODENTATA, and YUCATANENSIS are sharply distinct in outline, and are uniformly dark purple-black.

MARITIMA and ELLIOTTII are intermixed in the third cluster, so that no clear line can be drawn between the two taxa. On the minimum spanning network, however, they appear as distinct groups of OTUs linked at a similarity level of 0.377. The character analysis shows only

slight differences between these two taxa, primarily in leaf length-to-width ratio and in color of the maculations in the corolla throat. The MARITIMA-ELLIOTTII cluster is quite distinct from the first two clusters, joining them at a phenon level of 0.693. On the minimum spanning network, MARITIMA links to SPATHULAEFOLIA at a similarity of 0.855. MARITIMA and ELLIOTTII differ from the members of the first two clusters (except SPATHULAEFOLIA, which has similar leaf morphology) in having some populations with ocher or green maculations in the corolla throat, leaves with entire margins, and higher ratios of leaf length-to-width and leaf blade length-to-petiole length.

GLABRA and ANGUSTIFOLIA cluster at a phenon level of 0.816. The two taxa link on the minimum spanning network at a similarity of 0.914. The character analysis program identifies the GLABRA-ANGUSTIFOLIA cluster primarily by the glabrous stems, leaves, and calyces in these taxa. This last cluster joins the first three at a phenon level of 0.59. On the minimum spanning network, GLABRA links with ELLIOTTII at a similarity level of 0.821.

The same linkage patterns of OTUs can be seen in representative similarity levels obtained using SIMGRA. In addition, this clustering method illustrates the number of connections among taxa in each cluster. At a similarity level higher than 0.921 (fig. 3) the OTUs representing CINERASCENS are already highly interconnected, and have started to connect with the YUCATANENSIS and SPATHULAEFOLIA OTUs. Also, the MOLLIS and INTERGRADE OTUs have formed a network-type linkage. At this same level the MARITIMA, ELLIOTTII, and GLABRA OTUs are single-member

clusters.

At a similarity level greater than 0.905 (fig. 4) the CINERASCENS OTUs have formed a single large, interconnected cluster. The OTUs representing YUCATANENSIS form their own cluster, which has two connections with the CINERASCENS cluster, and which is also connected with the SINUATODENTATA and SPATHULAEFOLIA OTUs. The MOLLIS and INTERGRADE OTUs are highly interconnected, and are linked to the larger CINERASCENS cluster. Also, the VARIOESTITA OTUs have linked to the MOLLIS-INTERGRADE cluster by this level of similarity. The remaining cluster seen at this level consists of 5 of the 7 ANGUSTIFOLIA OTUs and one GLABRA OTU.

The remaining similarity levels (fig. 5-8) show an increasing number of internal connections in the CINERASCENS and MOLLIS clusters, as well as a number of additional connections between the two. These figures also illustrate the gradual addition of GLABRA and ANGUSTIFOLIA OTUs to the existing ANGUSTIFOLIA cluster, and the increase in number of interconnections in that cluster. Also, the MARITIMA and ELLIOTTII OTUs gradually come together in a network-type linkage (fig. 7). This network collapses into an interconnected cluster which links to the large CINERASCENS cluster at a similarity level of 0.855 (not pictured). Finally, the ANGUSTIFOLIA-GLABRA cluster joins the linkage by connecting to the MARITIMA-ELLIOTTII cluster at a similarity level of 0.821 (fig. 8). Even then, OTU 34 (MARITIMA) remains outside the MARITIMA-ELLIOTTII cluster with only 2 linkages to members of that cluster.

Flavonoid analysis. A composite chromatogram and taxonomic distribution of foliar flavonoids of the Physalis viscosa complex are shown in fig. 9. All of the compounds identified to date are kaempferol, myricetin, and quercitin glycosides (fig. 9). Only VARIOVESTITA, SINUATODENTATA, and SPATHULAEFOLIA can be distinguished by their flavonoid profiles, although CINERASCENS and GLABRA each have a distinctive flavonoid race. VARIOVESTITA is the only taxon which exhibits a compound unique to the complex, spot 4.

Breeding studies. Most of the taxa within the Physalis viscosa complex were intercompatible at low levels with at least 10% of the crossing attempts resulting in the production of viable seed (fig. 10). Three groupings of taxa exhibit internal cross-compatibility levels of 40% or greater: (1) MOLLIS, INTERGRADES, and VARIOVESTITA; (2) CINERASCENS, SINUATODENTATA, SPATHULAEFOLIA, and YUCATANENSIS; and (3) MARITIMA, ELLIOTTII, GLABRA, and ANGUSTIFOLIA.

Except for SPATHULAEFOLIA X GLABRA, less than 40% of the crossing attempts between members of different breeding groups set fruit. In addition, all intergroup crosses that produced fruit yielded less than 50 seeds per fruit (intragroup crosses averaged approximately 90 seeds per fruit). Viable seeds resulting from intergroup crosses produced plants that were stunted and generally had lower pollen viability than intra-group hybrids.

As previously noted, morphological differences among MOLLIS, VARIOVESTITA, and the INTERGRADES are primarily in pubescence. Crosses

between MOLLIS and the INTERGRADES produced hybrid plants that resembled the INTERGRADES in pubescence and had high pollen viability (greater than 85%). Crosses between VARIOVESTITA (which is uniformly glandular) and either MOLLIS or the INTERGRADES (which are not glandular) resulted in plants with intermixed glandular and non-glandular hairs. The pollen viability in these hybrids varied from less than 10% to 100%.

Similarly, CINERASCENS differs in morphology from SINUATODENTATA and YUCATANENSIS primarily in pubescence features. Crosses between CINERASCENS and either SINUATODENTATA or YUCATANENSIS produced hybrid plants with the fasciculate hair-type, characteristic of the latter two taxa. Hybrids between CINERASCENS and SPATHULAEFOLIA resemble SPATHULAEFOLIA in habit and are intermediate in leaf morphology. The pollen viability in these hybrids is high (greater than 90%). All but one of the back-crosses with SPATHULAEFOLIA and CINERASCENS ($n = 8$) produced fruit, however all of the fruits from these back-crosses had fewer than 50 seeds per fruit.

Crosses within the third breeding group produced hybrids which varied in morphology to include all of the variation seen in leaf size and shape, density and distribution of trichomes, and corolla throat color seen in wild parental populations. ANGUSTIFOLIA and GLABRA are glabrous plants with narrow leaves, and hybrids between them were uniformly glabrous except for occasional branched hairs on the leaf margins. The leaf morphology of these hybrids varied from short and narrow (similar to some populations of ANGUSTIFOLIA) to long and broad (similar to some populations of MARITIMA). ELLIOTTII and MARITIMA are pubescent plants

with broadly ovate to broadly lanceolate leaves. Crosses between ELLIOTTII and MARITIMA produced plants with sparse to dense pubescence and narrowly to broadly ovate leaves. When either of the glabrous taxa (ANGUSTIFOLIA and GLABRA) were crossed with the pubescent ones (MARITIMA and ELLIOTTII), the resulting hybrids had leaf shapes that varied from ANGUSTIFOLIA-like to MARITIMA-like. The majority of these hybrids were uniformly pubescent, although the density of trichomes varied from sparse to dense. Only one of the glabrous X pubescent hybrids (ANGUSTIFOLIA X ELLIOTTII) was glabrous except for sparse hairs along the leaf margins. Crosses between any two of the parent taxa result in hybrids with high pollen viability (greater than 80%). All but one of the back-crosses and crosses between siblings (n = 9) resulted in fruits with 60 or more seeds.

Crosses involving the members of the *P. viscosa* complex and other species of the genus, with the exception of *P. pumila*, failed to produce viable seed. For most of these crosses the flowers wilted and fell within a few days after pollination. Presumably fertilization did not occur in these instances. In a few instances however (1 MOLLIS X *P. hederæfolia* and 9 CINERASCENS X *P. heterophylla*), small fruits were produced with a few aborted seeds. All but a few of the crosses between the members of the *P. viscosa* complex and *P. pumila* were abortive; however half of the crosses between *P. pumila* and MOLLIS resulted in fruits with a small number of viable seeds. The hybrid plants obtained from these crosses had high pollen viability (greater than 90%), but were stunted and did not resemble any plants found in wild populations.

Morphology of transplants. The INTERGRADE and VARIOVESTITA populations transplanted to the greenhouse did not exhibit any appreciable change in overall morphology from that exhibited in the field. However, three of the four transplanted MOLLIS populations exhibited long, unbranched trichomes on new shoots. Thus, these greenhouse plants were identical to INTERGRADE populations in nature.

Except for one population, greenhouse transplants of CINERASCENS exhibited plasticity only in the size of leaves or flowers. The exception was a population with orbicular leaves and entire margins that produced ovate leaves with undulate margins in the greenhouse. Populations of SPATHULAEFOLIA that had spatulate leaves in nature had distinct petioles in the greenhouse. Populations of SINUATODENTATA and YUCATANENSIS had rounded to attenuate leaf bases in the field, but plants in the greenhouse exhibited more truncate bases with distinct petioles.

Populations of ELLIOTTII from the northern Gulf Coast of Florida developed wider leaves when transplanted to the greenhouse. Thus, they could not be distinguished from populations of MARITIMA, according to Waterfall's criteria for distinguishing between these taxa. Populations of ELLIOTTII from the southern portion of Florida did not exhibit any change in leaf morphology. GLABRA populations exhibited only small change in leaf width, becoming slightly more narrow in the greenhouse. Transplants of ANGUSTIFOLIA and MARITIMA did not exhibit appreciable morphological plasticity.

DISCUSSION

These results clearly illustrate that the members of the P. viscosa complex are a closely related assemblage, as suggested by Rydberg (1896), Menzel (1951, 1957), and Waterfall (1958, 1967). However, my studies reveal a previously undocumented pattern of relationships among the members of the complex. Based on the phenetic analysis, four groups of taxa are apparent: (1) MOLLIS, VARIOESTITA, and the INTERGRADES; (2) CINERASCENS, SINUATODENTATA, SPATHULAEFOLIA, and YUCATANENSIS; (3) MARITIMA and ELLIOTTII; and (4) ANGUSTIFOLIA and GLABRA. Hybridization studies, analysis of hybrids, and comparative flavonoid analysis are generally consistent with the phenetic grouping and so the taxa will be treated in these four groups for the following discussion.

(1) MOLLIS, VARIOESTITA, and the INTERGRADES--These three taxa are remarkably similar in overall morphology, and are characterized by tomentose leaves that are broadly ovate with coarsely dentate margins, and indistinct, brown maculations in the corolla throat. Waterfall (1958) distinguished between MOLLIS and VARIOESTITA primarily by the presence of 2-4 mm long, articulated, branched or unbranched hairs on the latter and their absence on the former. Inexplicably, he failed to mention that the type specimen of VARIOESTITA is an abundantly glandular plant. Waterfall postulated that VARIOESTITA had hybridized with MOLLIS and/or CINERASCENS in southern Texas, and that "intergrading forms" could be found in an area radiating northward in that state. Although he realized that VARIOESTITA is also distinctive in exhibiting

dark purple-black spots in the corolla throat, he used only the long hairs to identify what he called "intergrades". The phenetic analysis demonstrates that the variation noted by Waterfall is not discrete, but that it is within the range of variation found in MOLLIS.

CINERASCENS could not have served as a parent of the INTERGRADES because it is not cross-compatible with MOLLIS, VARIOESTITA, nor any of the populations treated as INTERGRADES. In addition, CINERASCENS is distinct, if only slightly so, from these three in morphology and chemistry. Thus, CINERASCENS is eliminated as a possible parent in any theory concerning hybridization in this group of taxa. However, MOLLIS, VARIOESTITA, and the INTERGRADES are all intercompatible. Hybrids between VARIOESTITA and either MOLLIS or the INTERGRADES have glandular hairs intermixed with non-glandular hairs. In this respect, they do not resemble any of the parental plants, nor any of the herbarium specimens examined.

Based on the transplant studies, the occurrence of long articulated hairs (found on VARIOESTITA and the INTERGRADES) is under environmental control. Plants which did not have these long hairs in the field (and so were identified as MOLLIS) exhibited this hair type on the new shoots once transplanted to the greenhouse. In addition, this hair type was found on herbarium specimens examined from throughout the range of MOLLIS, not just in an area radiating from southern Texas as would be expected if their occurrence was the result of hybridization between VARIOESTITA and MOLLIS.

The phenetic and flavonoid analyses also indicate that these three taxa are closely related. However, they also show that the INTERGRADES are not intermediate between VARIOESTITA and MOLLIS, but rather that they fall within the morphological and chemical range of MOLLIS. In addition, my data illustrate that MOLLIS is sufficiently distinct from the other members of the complex to warrant its recognition as a species. VARIOESTITA is similar to Physalis mollis Nuttall in morphology and flavonoid chemistry, and the two produce fertile hybrids. However, VARIOESTITA is morphologically recognizable because of the combination of abundant glandular hairs which are short-dendritic and long articulated, and the dark, indistinct spots in the corolla throat. VARIOESTITA occurs only in south Texas, within the range of P. mollis. The two also do not appear to hybridize, based on a survey of herbarium specimens. Therefore, VARIOESTITA should be recognized as a variety of P. mollis.

Menzel (1960) provided evidence that P. variovestita, as defined by Waterfall (1958), is of hybrid origin. Menzel had located a population in Brazos County, Texas, where P. mollis and P. macrophysa had apparently hybridized to produce plants that resembled P. variovestita. Unfortunately, her collections of the suspected hybrids and parents have been lost, and neither she nor I have been able to relocate the population. In addition, I have not been able to obtain material of P. macrophysa for artificial hybridization studies. Whether the Brazos Co. population was the result of an isolated hybridization event that subsequently ended in extinction, or whether it was the parent population of the now-restricted VARIOESTITA is presently unknown.

(2) CINERASCENS, SINUATODENTATA, SPATHULAEFOLIA, and YUCATANENSIS--These taxa form a distinct group based on all of the analyses and are characterized by dark, distinct maculations in the corolla throat and anthers that are 1.5 X or more longer than the mature filaments. CINERASCENS is geographically widespread and highly variable, particularly in leaf morphology. In addition, two flavonoid races were identified for this taxon. However, the variation in morphology and chemistry is either continuous or is found throughout the range of the taxon. Therefore, subgroups could not be recognized within CINERASCENS. Both SINUATODENTATA and YUCATANENSIS fall within the range of variation found in CINERASCENS and are not recognizably distinct, even using Waterfall's (1958) criterion of trichome morphology, which he admitted was weak. In fact, the "fasciculate" hairs which characterize SINUATODENTATA and YUCATANENSIS are abundant on the lectotype of P. viscosa var. cinerascens, which was designated by Waterfall (1958). Therefore, these three taxa should be combined into Physalis cinerascens (Dunal) Hitchcock.

Unexpectedly, all analyses indicate a close relationship between P. cinerascens and SPATHULAEFOLIA. Previous authors have allied the latter taxon only with MARITIMA and ELLIOTTII (Rydberg 1896; Menzel 1951; Waterfall 1958), presumably based on leaf shape and habitat. SPATHULAEFOLIA is compatible with MARITIMA and ELLIOTTII only at low levels (less than 20% crossing success), has a different flavonoid profile, and differs in overall morphology, however. SPATHULAEFOLIA falls within the range of morphological and chemical variability of P. cinerascens and is cross-compatible at a level of approximately 50%.

However, because *SPATHULAEFOLIA* is recognizable by its flavonoid chemistry, morphology, and geographic range, and because it apparently hybridizes with *P. cinerascens* only rarely in nature, it deserves varietal status.

(3) MARITIMA and ELLIOTTII--These two taxa have long been a source of confusion to taxonomists, as can be discerned by the various annotations on herbarium sheets. To add to the problem, these taxa were interpreted differently by Rydberg (1896) and Waterfall (1958), the two authorities on the genus. Rydberg distinguished between these two taxa on the basis of trichome density (i.e., *MARITIMA* being densely pubescent and *ELLIOTTII* comprising the more sparsely pubescent forms), whereas Waterfall considered leaf shape to be the important distinguishing characteristic (i.e., *MARITIMA* having leaves that are less than two times longer than broad and *ELLIOTTII* having leaves much longer than broad). Each of these taxa encompasses a great deal of variation by either interpretation, however. Part of this variation is environmentally controlled, as revealed by the transplant studies. Thus, the leaf length to width ratio used by Waterfall (1958) to distinguish between *MARITIMA* and *ELLIOTTII* is, to some extent, environmentally controlled. In fact, some populations I identified as *ELLIOTTII* in the field exhibit a *MARITIMA*-type leaf morphology in the greenhouse. All populations which met Waterfall's criteria for identification as *ELLIOTTII* were chemically identical to *MARITIMA*. In addition, these taxa were completely interfertile and not distinct in overall morphology. Thus, I cannot justify taxonomic distinction between these taxa, even at the level of variety. The two should

therefore be combined under Physalis walteri Nuttall, a name which has priority over either P. maritima or P. elliottii at the species level.

(4) ANGUSTIFOLIA and GLABRA--These two taxa cluster separately from the other members of the P. viscosa complex based on the absence of trichomes on the stems, leaves, and flowering calyx. In addition, the two taxa are highly interfertile and have identical flavonoid profiles, except for the occurrence of compound 7 in some populations of GLABRA. Thus, the two taxa should be treated as a single species, P. angustifolia Nuttall. Although variation can be found in size of flowers and leaves, the variation is continuous and so no infraspecific taxa are recognized.

Although P. walteri and P. angustifolia are distinct based on the results of the phenetic analysis, this treatment reflects only absolute presence or absence of trichomes, and not the range of variability found in density. Moreover, P. walteri and P. angustifolia are not distinct chemically, are completely interfertile, and intermediates between the two can be found where their ranges overlap in Florida. The intermediates occur in the peninsular region of Florida, and are represented by different character combinations in different areas on the peninsula (i.e., populations in and around Dade County have narrow, pubescent leaves while plants can be found in the Tampa area with broad, glabrous leaves). While P. walteri and P. angustifolia both occur in peninsular Florida, they occupy discrete ranges outside of this region of the state (P. angustifolia along the Gulf Coast from Florida to Louisiana, and P. walteri along the Atlantic Coast from Florida to

southern Virginia). The two are morphologically distinct in the non-overlapping portions of their ranges, and so should be maintained as distinct species.

After an initial study of the morphological variation, interbreeding capabilities, and hybrids of *P. viscosa* var. *maritima*, *P. elliottii*, and *P. angustifolia*, Menzel (1957) was still unsure of the nature of the variability seen in these taxa, and their evolutionary history. She suggested that the diversity of morphology in these taxa might be the result of a past hybridization event between *P. viscosa* and *P. angustifolia*, with subsequent establishment and divergence of hybrids. I found a high degree of cross-compatibility between any two populations of *P. walteri* and *P. angustifolia*. Hybrids between these species exhibit high pollen viability, and a range of morphological variability which encompasses all the forms found in natural populations. It is likely that *P. walteri* and *P. angustifolia* have hybridized one or more times, and that the hybrids have backcrossed and/or interbred among themselves to produce the variation seen in Florida today. Cross-pollination is highly probable because solitary bees in the genera *Perdita*, *Colletes*, and *Augochlorella* apparently do not distinguish among *Physalis* species, even species with considerable differences in the size and color of the maculations in the corolla throat (Sullivan 1984a, b). It is also likely that fertile hybrids could become established on the frequently-disturbed sand dunes of peninsular Florida.

The classification resulting from these analyses differs substantially from the classifications of either Rydberg (1896) or

Waterfall (1958, 1967). This apparently results because vegetative characteristics predominated their concept of taxa in Physalis. Certainly, this must have been the reason for including such otherwise distinct taxa as P. mollis and P. cinerascens in the same species (Rydberg 1896) or in the same subspecies (Waterfall 1958), or the inclusion of SPATHULAEFOLIA in the same species (Rydberg 1896) or subspecies (Waterfall 1958) as P. walteri. In both of these examples, taxa with similar leaf morphology were grouped, and the considerable differences in floral features overlooked. Such was not the case when all of the members of the complex were included in an unweighted phenetic analysis of overall morphology, and this information combined with hybridization studies and comparative flavonoid analysis.

The relationships of the members of the P. viscosa complex to other species in the genus warrant further study. Menzel (1951) suggested that the species in this complex be combined with the species in series Heterophyllae and Lanceolatae. Comparative morphological studies show that P. heterophylla (classified by Rydberg in series Heterophyllae), P. pumila, and P. virginiana (both classified by Rydberg in series Lanceolatae), are very similar in overall morphology to P. mollis (Sullivan 1984). Although all the non-P. viscosa complex species link distantly from the members of the complex and at one end of the minimum spanning network, P. virginiana and P. mollis are more similar in overall morphology than the latter is to P. cinerascens. However, comparative analysis of flavonoid constituents does not show congruent patterns (Sullivan 1984). Foliar flavonoid patterns for both P. heterophylla and P. pumila are identical to one chemical race of P.

angustifolia, which is quite distinct in overall morphology. Other than this the only chemical similarity among the species studied is in the presence of flavonoid compound 3, which appeared in 5 of the 8 species surveyed outside of the P. viscosa complex. Except for limited crossing success between P. pumila and P. mollis, no successful hybridizations could be made between members of the P. viscosa complex and other species of Physalis. Even based on the combined results from these analyses, it is difficult to assess the relationships of the species in the P. viscosa complex to other species in the genus at this time.

TAXONOMIC TREATMENT

PHYSALIS VISCOSA COMPLEX

Rhizomatous perennial herbs. Stems and leaves glabrous to tomentose with 1 mm or less long, branched or stellate hairs, in one species sometimes intermixed with 2-4 mm long, branched or unbranched hairs. Flowers solitary in leaf axils. Fruiting calyces 10-angled or -ribbed, concave at base. Corollas yellow, often with 5 darker maculations in the throat. Stamens yellow, rarely tinged purple. Pedicels equal to or exceeding calyces in flower and fruit. Berry orange, 0.5-1.5 cm in diameter.

KEY TO NORTH AMERICAN MEMBERS

Leaves glabrous except for occasional, sparse pubescence on

margins.1. P. angustifolia.

Leaves pubescent.

Flowering calyces and abaxial leaf surfaces tomentose such that the plant surface is obscured; pubescence of branched hairs, less than 1 mm long, in some populations intermixed with 2-4 mm long, jointed, branched or unbranched hairs.

Pubescence non-glandular; corollas with pale brown to dark brown maculations in throat. 2a. P. mollis var. mollis.

Pubescence glandular; corollas with deep purple-black maculations in throat. 2b. P. mollis var. variovestita.

Flowering calyces and leaves sparsely to densely pubescent but not such that the plant surface is obscured; pubescence of branched hairs, less than 1 mm long, only.

Anthers equal to or shorter than the mature filaments; fruiting pedicels mostly as long as the fruiting calyces. 3. P. walteri.

Anthers 1.5 X or more longer than the mature filaments; fruiting pedicels mostly 1.5 X or more longer than the fruiting calyces.

Leaf margins dentate, sinuate, or undulate; corollas reflexed when fully open . . . 4a. P. cinerascens var. cinerascens.

Leaf margins entire; corollas not reflexed when fully open. 4b. P. cinerascens var. spathulaefolia.

1. *PHYSALIS ANGUSTIFOLIA* Nuttall, Journ. Acad. Nat. Sci. Phila. 7:113.

1834. TYPE: west Florida, N.A. Ware s.n. (PH!).--P. viscosa L. ssp.

maritima (M.A. Curtis) Waterfall var. elliottii (Kunze) Waterfall
forma glabra Waterfall, Rhodora 60:135. 1958 (TYPE: Florida, Lee
Co., Sanibel Island, May 1901, S.M. Tracy 7608, NY!; ISOTYPES: NY!,
GH!).

Plants from deeply-buried rhizomes, often also with slender, shallow
rhizomes. Stems 1.5-6 dm tall, the stems and lower branches erect or
spreading along the ground and ascending. Stems and leaves glabrous or,
rarely, leaf margins sparsely pubescent with short, branched hairs, 1 mm
or less long. Leaf blades narrowly spatulate to linear-lanceolate;
3-10 (12) cm long, 0.2-1.5 (2) cm wide; apex obtuse to acute; margins
entire; base tapering to stem; sessile. Flowering calyces 5-9 (10) mm
long; glabrous except for the margins, or occasionally sparsely covered
with short, branched hairs, 1 mm or less long; lobes (1) 1.5-3.5 mm
long. Corollas (8) 11-15 (16) mm long; ocher to green indistinct
maculations in throat, main vein of corolla lobes typically purple or
red. Anthers 2.5-3.5 mm long; filaments 1/2 to as wide as anthers.
Flowering pedicels 11-24 (32) mm long. Fruiting calyces typically
orange at maturity; (1.5) 2-3 (4) cm long, 1.5-2.5 cm in diam.; pedicels
15-35 (42) mm long. (n=12). Flowering throughout the year in areas
without frost. Gulf dunes and disturbed areas in sand. Southern
Alabama, Louisiana, and Mississippi, and along the Gulf coast of
Florida.

This species hybridizes with P. walteri in peninsular Florida, and
populations can be found in this state which exhibit intermediate
characteristics.

Representative specimens. ALABAMA. Baldwin Co.: Mobile Point, Fort Morgan, 15 Jun 1982, Sullivan and Laue 1164 (OKL). Mobile Co.: Dauphin Island, 15 Jul 1969, Kral 35596 (NCU). FLORIDA. Bay Co.: public beach west of Laguna Beach, 16 Jun 1982, Sullivan and Laue 1167 (OKL). Dade Co.: Big Bend, west of Tamiami Trail, 1 Apr 1930, Moldenke 852 (DUKE). Collier Co.: vicinity of Sunniland, 1 May 1965, Lakela 28536 (USF). Escambia Co.: Santa Rosa Island, 6.5 mi. west of Casino, 14 Jun 1964, McDaniel 4735 (FSU). Franklin Co.: dunes near west end of Dog Island, 23 Nov 1963, Ward 3817 (FLAS). Gulf Co.: Port St. Joe, 22 May 1955, Menzel and Menzel 55-5, (FSU). Lee Co.: Sanibel Island, 16 Oct 1969, Radford and Leonard 45694 (NCU). Monroe Co.: Big Pine Key, 8 Feb 1977, Correll and Popenoe 48088 (NCU). Okaloosa Co.: Santa Rosa Island, just over bridge from Destin, 31 Jul 1964, McDaniel 4969 (FSU). Wakulla Co.: Mashes Island, 24 Apr 1955, Godfrey 53210 (DUKE, FLAS, FSU, SMU, USF). Walton Co.: dunes 1/2 mi. from Bay Co. line, 27 Apr 1967, Ward 6202 (FLAS). LOUISIANA. Jefferson Par.: north end of Grand Isle, 16 Apr 1981, Vincent and Landrie 4002 (NLU). St. Bernard Par.: n end of Chandeleur Island near lighthouse, 18 May 1960, Lemaire 617 (FSU). MISSISSIPPI. Harrison Co.: Ship Island, 15 Jun 1952, Demaree 21911 (DUKE, SMU). Jackson Co.: Horn Island, 29 Jul 1955, Godfrey and Channel 53711 (DUKE, FSU, NCU).

2. PHYSALIS MOLLIS Nuttall.

Plants from stout, deeply-buried rhizomes, often also with slender, shallow rhizomes. Stems 1.5-5 dm tall, the stems and branches erect.

Stems and leaves tomentose with branched hairs, 1 mm or less long, occasionally also with 2-4 mm long, jointed, branched or unbranched hairs. Leaf blades broadly ovate; 2.5-7 cm long, 1.5-6 (7) cm wide; apex acute; margins coarsely dentate or irregular to almost entire; base truncate to slightly cordate or slightly attenuate; petioles $1/3-4/5$ blade length. Flowering calyces 6-10 (12) mm long; tomentose with branched hairs, 1 mm or less long, occasionally also with 2-4 mm long, jointed hairs; lobes 2.5-5.5 mm long. Corollas 9.5-15 (17) mm long; pale brown to dark brown or purple-black, indistinct maculations in throat. Anthers 3-4 mm long; filaments about $1/2$ as wide as the anthers. Flowering pedicels 10-25 (35) mm long. Fruiting calyces green; 2.5-4 (-5) cm long, 1.5-3 (3.5) cm in diam.; pedicels 20-40 (52) mm long. ($\bar{n} = 12$). Flowers March to October.

2a. *PHYSALIS MOLLIS* Nuttall var. *MOLLIS*, Trans. Am. Phil. Soc.

5(n.s.):194. 1837. TYPE: Arkansas, Nuttall s.n. (HOLOTYPE: not known; ISOTYPES: NY!, PH!).--P. viscosa L. ssp. mollis (Nutt.)
Waterfall var. mollis, Rhodora 60:135-6. 1958.

Plants with non-glandular, branched hairs, 1 mm or less long; some populations also exhibit 2-4 mm long, jointed, branched or unbranched, non-glandular hairs. Corollas with pale brown to dark brown maculations in throat. Fruiting calyces 1.5-3 cm in diam. Disturbed areas in sandy soil. Southeastern Oklahoma, eastern $1/2$ Texas, southwestern Arkansas, and western Louisiana.

Representative specimens. ARKANSAS. Franklin Co.: Ozark, 22 Sep 1964, Demaree 51450 (OKLA). Jefferson Co.: Arkansas River side of Slack

Water Harbor area, Pine Bluff, 14 May 1972, Locke 528 (UARK). Pope Co.: Arkansas River bottoms, Holla Bend National Wildlife Refuge, 22 May 1968, Tucker 7089 (NCU). Stone Co.: vicinity of Little Rock, foot of Fort Roots near Big Rock, 3 May 1939, Merrill 1861 (OKLA). LOUISIANA. Caddo Par.: 2.5 mi. south of Ida, 27 Aug 1966, Thieret 24493 (DUKE). OKLAHOMA. Bryan Co.: U.S. Denison Dam Reservation, north side of Lake Texoma, 18 Jun 1951, Cory 58821 (OKLA). Marshall Co.: Island no. 2, Lake Texoma, 10 Jul 1954, Goodman 5923 (OKLA). TEXAS. Atascosa Co.: 9 mi. NE of Pleasanton, 10 Apr 1955, Shinners 19699 (SMU). Denton Co.: post oak belt about 1 mi. south of Argyle, 23 May 1946, Whitehouse 15780 (MICH, SMU). Harris Co.: Hwy 59 about 0.4 mi. south of bridge over San Jacinto River, 3 July 1956, Traverse 158 (SMU). Llano Co.: 5 mi. east of Llano on Hwy 29, 5 May 1947, Whitehouse 18515 (SMU). McLennan Co.: 2 mi. SSE of Robinson, 4 May 1949, Cory 55660 (SMU). Medina Co.: 2 mi. SW of Devine, 1 May 1954, Johnston, Tharp, and Turner 3401 (SMU, TEX). Parker Co.: 1.5 mi. SE of Springtown, 5 Jun 1949, Shinners 11385 (SMU). Smith Co.: 7 mi. N of Tyler, 8 May 1948, Shinners 10023 (SMU). Victoria Co.: 6.5 mi. west of Victoria, 29 Mar 1949, Cory 55114 (SMU).

2b. *PHYSALIS MOLLIS* Nuttall var. *VARIOVESTITA* (Waterfall) Sullivan, comb. et stat. nov.--TYPE: Texas, Aransas Co., Rockport, back of Rockport Tourist Cottages, April 1947, E. Whitehouse 18179 (MICH!).--P. variovestita Waterfall, Rhodora 60:137. 1958.

Plants with glandular, branched hairs, 1 mm or less long; also with 2-4 mm long, jointed, branched or unbranched, glandular hairs. Corollas with deep purple-black maculations in throat. Fruiting calyces 2.5-3.5

cm in diam. Disturbed areas in sand. Extreme southern counties of Texas, and along the coast north to Aransas Co.

Representative specimens. TEXAS: Brooks Co.: Hwy 285, 14 mi. from Falfurrias, 10 Nov 1962, Solis 51 (TEX). Hidalgo Co.: McAllen, 10 Aug 1937, Cameron 269 (TEX). Kenedy Co.: SE part of Saltillo Pasture, Norias vision of King Ranch, 27 Sep 1953, Johnston 53256.19 (TEX); Yturria Ranch, along railroad, 6 May 1940, (LL, MICH, SMU); King Ranch, near Norias, 15 Mar 1942, Lundell and Lundell 10730 (LL). Willacy Co.: Yturria Station on Hwy 96, 10 Mar 1937, Runyon 4833 (TEX); Yturria, near the station, 11 May 1941, Runyon 2656 (TEX).

3. *PHYSALIS WALTERI* Nuttall, Journ. Acad. Nat. Sci. Phila. 7:112.

1834.--TYPE: South Carolina, Nuttall s.n. (PH!).--P. elliottii Kunze, Linnaea 20:33. 1847. (TYPE: Florida, ad ostium fluv. St. Marks, June 1843, Rugel, s.n., NY!).--P. maritima M.A. Curtis, Amer. Journ. Sci. ser. 2. 1:407. 1849. (TYPE: North Carolina, seacoast, M.A. Curtis s.n., GH!; probable ISOTYPE: NY!).--P. viscosa L. var. maritima (Curtis) Rydberg, Mem. Torr. Bot. Club 4:357. 1896.--P. viscosa L. ssp. maritima (M.A. Curtis) Waterfall var. maritima forma maritima, Rhodora 60:134. 1958.--P. viscosa L. ssp. maritima (M.A. Curtis) Waterfall forma latifolia Waterfall, Rhodora 60:134. 1958. (TYPE: Florida, north part of Jupiter Island, April 1923, Small, Mosier, and DeWinkler 10892 NY!; ISOTYPE: GH!).--P. viscosa L. ssp. maritima (M.A. Curtis) Waterfall var. elliottii (Kunze) Waterfall forma elliottii, Rhodora 60:134-5.

1958.

Plants from stout and usually deeply-buried rhizomes. Stems 0.5-4 dm tall, the stems and lower branches erect or spreading along the ground and ascending. Stems and leaves sparsely to densely covered with branched hairs, 1 mm or less long. Leaf blades broadly elliptic or ovate to ovate-lanceolate; (2.5) 3.5-9 (13) cm long, (1) 1.5-5 (7) cm wide; apex obtuse or acute; margins entire or rarely undulate; base rounded to attenuate; petioles 1/6-1/2 blade length. Flowering calyces (5) 6-9 (11) mm long; densely to sparsely covered with branched hairs, 1 mm or less long; lobes 1.5-4 (5) mm long. Corollas (9) 11-15 (18) mm long; dark to pale brown, ocher, or green distinct or indistinct maculations in throat, the main veins of the corolla lobes sometimes purple or red. Anthers 2.5-3.5 mm long; filaments as wide as anthers. Flowering pedicels 9-25 (35) mm long. Fruiting calyces green; 2-3.5 (4) cm long, 1.5-2.5 cm in diam.; pedicels 15-40 (45) mm long. (n=12). Flowering throughout the year in areas without frost. Beach dunes and disturbed areas in sand. Chiefly Atlantic Coast of Florida, Georgia, North Carolina, South Carolina, and Virginia, but also inland in Florida and Georgia, and sporadically in coastal Alabama and Mississippi.

This species hybridizes with P. angustifolia in peninsular Florida, and populations can be found in this state which exhibit intermediate characteristics such as broadly ovate, glabrous leaves.

Representative specimens. FLORIDA. Brevard Co.: Indiatlantic Beach, 8 Jun 1957, Menzel and Menzel 57-189 (FSU). Dixie Co.: flatwoods, 1 mi. north of Horseshoe, 14 May 1942, West and Arnold s.n. (FLAS). Glades

Co.: rt. 721, south of the Brighton Indian Reservation, 22 Jun 1982, Sullivan and Laue 1203 (OKL). Lake Co.: pinelands east of Eustis, 7 May 1918, Small 8644 (NY). Nassau Co.: Amelia Beach dunes, 18 Jun 1982, Sullivan and Laue 1183 (OKL). Palm Beach Co.: Ocean Ridge, Boynton Beach, 11 Jun 1957, Menzel and Menzel 57-222 (FSU). St. Johns Co.: sandy banks bordering salt marshes, San Sebastian River, St. Augustine, 22 May 1964, Godfrey 63963 (NCU). St. Lucie Co.: dunes of Atlantic Ocean near Fort Pierce, 29 Jul 1962, Lake1a 25240 (GH). Volusia Co.: behind dunes along Atlantic Coast south of New Smyrna Beach, 14 Oct 1976, Duncan and Duncan 30306 (DUKE, NCSC). GEORGIA. Glynn Co.: sandy ridge at edge of beach across Jekyll Island, 11 Jun 1951, Duncan 12549 (GA). McIntosh Co.: airstrip on Sapelo Island, 16 Apr 1954, Duncan 17714 (MICH, NCSC, NCU). NORTH CAROLINA. Brunswick Co.: sea strand and brackish marshes in the vicinity of Long Beach, 23 May 1973, Almeda, Primack, and Wyatt 1885 (DUKE, GA). Carteret Co.: Shackleford Bank along the north side of the island between High Hill and Whale Creek, 15 Aug 1970, Wilbur 12694 (DUKE). Dare Co.: back of first dune on beach, 2 mi. north of rt. 158, north of Kitty Hawk, 11 Jun 1949, Fox and Godfrey 2313, (NCSC, PH). Pender Co.: inner margin of beach, near salt marsh, 1 mi. north of New Topsail Beach, 1 Jul 1950, Fox and Boyce 3741 (GH, NY, UARK). SOUTH CAROLINA. Beaufort Co.: sand dunes, Hunting Island State Park, 3 Apr 1956, Ahles and Bell 10403 (NCU). Charleston Co.: sandy roadside east of Charleston, 20 May 1957, Ahles 25792 (NCU). Horry Co.: beach dunes, Myrtle Beach, 25 May 1957, Bell 7680 (NCU). VIRGINIA. Princess Anne Co.: sand dunes on Cape Henry, Virginia Beach, 15 Sep 1969, Straley 502 (VPI).

4. *PHYSALIS CINERASCENS* (Dunal) Hitchcock.

Plants from stout, deeply-buried rhizomes. Stems 0.5-5 dm tall, erect, the lower branches typically spreading along the ground and ascending. Stems and leaves sparsely to densely covered with branched hairs, 1 mm or less long. Leaf blades orbicular, ovate, or spatulate; 1.5-8 (9) cm long, 1-6 (8) cm wide; apex acute or obtuse; margins coarsely dentate, sinuate, undulate, or entire; base truncate to attenuate; petioles 1/5 to as long as blades. Flowering calyces (3.5) 5-9 (11) mm long; sparsely to densely covered with branched hairs, 1 mm or less long; lobes 1.5-4.5 mm long. Corollas (7) 9-16 mm long; dark purple-black, distinct maculations in throat, these sometimes bisected by yellow main veins of the corolla. Anthers 2-5 mm long; filaments 1/2 to as wide as the anthers. Flowering pedicels 10-33 mm long. Fruiting calyces green; 1.5-3.5 (4.5) cm long, 1-3.5 cm in diam.; pedicels 15-60 mm long. (\bar{n} = 12). Flowering all year in areas without frost.

4a. *PHYSALIS CINERASCENS* (Dunal) Hitchcock var. *CINERASCENS*, Spring

Flora of Manhattan 32. 1894.--LECTOTYPE: circa Matamoros urbem, April 1831, Berlandier 2316 (GH!; ISOLECTOTYPES: F!, NY!).--P. viscosa L. var. sinuatodentata Schlecht., Linnaea 19:309. 1846. (TYPE: Mexico, C. Ehrenberg s.n., HAL!).--P. pensylvanica L. var. cinerascens Dunal, DC Podr. 13(1):435. 1852.--P. curassavica L. var. sinuatodentata (Schlecht.) Dunal, DC Podr. 13(1):438. 1852.--P. mollis Nutt. var. cinerascens (Dunal) Gray, Proc. Amer. Acad. Arts and Sci. 10:66. 1875.--P. mollis Nutt. var. parvifolia Rydb., Mem. Torr. Bot. Club 4:355. 1896.--P. saltillensis Fernald,

Proc. Amer. Acad. Arts and Sci. 35:568-9. 1900. (TYPE: Mexico, Coahuila, plants collected at Saltillo and vicinity, 1898, E. Palmer 332, US!; ISOTYPE: MICH!).--P. viscosa L. ssp. mollis (Nutt.) Waterfall var. cinerascens (Dunal) Waterfall, Rhodora 60:136. 1958.--P. viscosa L. var. yucatanensis Waterfall, Rhodora 69:104. 1967, (TYPE: Mexico, Yucatan, Chichankanab, G.F. Gaumer 1798, F!; ISOTYPES: NY!, US!).

Leaves orbicular to broadly ovate; 1-6 (8) cm wide; base truncate to rounded or slightly attenuate; margins dentate, sinuate, or undulate. Corolla limbs reflexed when fully open. Filaments approximately 1/2 as wide as anthers. Fruiting calyces 1.5-3 (3.5) cm long, 1-2 cm in diam.; pedicels 15-60 mm long. Disturbed habitats. Chiefly in Oklahoma, Texas, eastern New Mexico, southern Kansas, southwestern Missouri, western Arkansas, western Louisiana, eastern Mexico s to Yucatan. Also found sporadically in the southeastern U. S.

Representative specimens. LOUISIANA. Webstaer Par.: Minden, 12 Jun 1982, Sullivan and Laue 1131 (OKL). NEW MEXICO. Lea Co.: 21 mi. west of Hobbs, 19 Aug 1947, Waterfall 7836 (NY). OKLAHOMA. Grady Co.: prairie NE of Bradley, 12 Jul 1963, Pearce 929 (OKLA). Payne Co.: prairie 1 mi. north of Stillwater, 6 Aug 1968, Waterfall 17316 (OKLA). Pushmataha Co.: valley of Kiamichi River, SE of Tuskahoma, 23 May 1966, Means 2461 (OKLA). Woods Co.: sandy soil near river, Freedom, 1 Jun 1913, Stevens 726 (OKLA). TEXAS. Bee Co.: rt. 181, 5 mi. south of Beeville, 16 Apr 1964, Correll 29304 (LL, SMU, UC). Brewster Co.: Pena Blanca, about 5 mi. south of Marathon, 24 Jul 1952, Warnock 10881 (LL, SMU). Childress

Co.: Hwy 256, about 8 mi. east of Memphis, 13 Jun 1973, Higgins 7247 (NY). Garza Co.: 3 mi. south of Post, 22 Jun 1963, Rowell and Waterfall 8650 (OKLA). Harris Co.: 15 mi. SW of Houston, 17 Apr 1965, Rios and Cavazos 112 (LL). Maverick Co.: near Elm Creek, 30 mi. NE of Eagle Pass, 2 May 1954, Tharp, Turner, and Johnston 3604 (DUKE, SMU, TEX). Palo Pinto Co.: north city limits of Straw, 6 May 1951, Shinners 13211 (SMU). Rains Co.: 3.8 mi. SE of Point, 27 Jul 1953, Shinners 15578 (OKLA, SMU). Starr Co.: below Falcon Dam, 17 Mar 1962, McCart et al 7870 (OKLA, TEX). Tom Green Co.: west of San Angelo, 7 Jun 1969, Grimes 276 (SMU, TENN). Travis Co.: Pecan Springs, 17 May 1940, Lundell and Lundell 8946 (LL, MICH). MEXICO. Coahuila: about 20 mi. east of Saltillo, open sandy slopes, 27 May 1951, McVaugh 12319 (MICH). Hidalgo: valley near Dublin, 2 Jul 1901, Pringle 9416 (MICH, NY). Yucatan: near station, Dzitas, Chichen Itza, 29 Jun 1932, Steere 1647 (MICH).

4b. *PHYSALIS CINERASCENS* (Dunal) Hitchcock var. *SPATHULAEFOLIA* (Torr.)

Sullivan, comb. nov.--TYPE: Texas, Rio Bravo, Seabeach, March 1853, Schott 30. (NY!; ISOTYPE: F!).--*P. lanceolata* Michx. var. *spathulaefolia* Torr. in Emory, Rep. U.S. and Mexican Bound. Surv. 2, part 1:153. 1859.--*P. viscosa* L. var. *spathulaefolia* (Torr.) A. Gray, Proc. Amer. Arts and Sci. 10:67. 1874.--*P. viscosa* L. ssp. *maritima* (M.A. Curtis) Waterfall var. *spathulaefolia* (Torr.) A. Gray, Rhodora 60:135. 1958.

Leaves broadly ovate to spatulate; 1-4 cm wide; bases attenuate; margins entire. Corolla limbs not reflexed when fully open. Filaments 1/2 to as wide as anthers. Fruiting calyces 2.5-3.5 (4.5) cm long,

(1.5) 2-3.5 cm in diam.; pedicels 25-60 mm long. Gulf dunes and disturbed habitats near the coast in sand. Western Louisiana, Texas, and northern Tamaulipas.

Representative specimens. LOUISIANA. Cameron Par.: about 2 mi. east of Holly Beach, 7 Jul 1962, Thieret 8816 (NCU). TEXAS. Aransas Co.: Rockport, 25 April 1947, Whitehouse 18292 (SMU). Brazoria Co.: 4 mi. SE of Freeport, 21 Nov 1945, Cory 51057 (NY, MICH, SMU). Cameron Co.: Del Mar Beach, 12 Mar 1942, Lundell and Lundell 10703 (MICH, SMU, TEX). Chambers Co.: Old railroad 6 mi north of High Island, Winnie, 31 Oct 1970, Demaree 63225 (OKLA). Galveston Co.: Texas City, 6 Apr 1950, Turner 1798 (SMU). Jefferson Co.: 13 mi. west of Sabine Pass, 18 Nov 1945, Cory 50972 (NY, MICH, SMU). Kenedy Co.: Norias Division of King Ranch, littoral zone along Laguna Madre, 23 Sep 1958, Lundell and Correll 15149 (LL). Kleberg Co.: sand dunes near Mifflin, 3 Oct 1952, Correll 14838 (LL). Nueces Co.: Mustang Island, 9 Mar 1982, Sullivan et al 1127 (OKL). San Patricio Co.: high banks of Aransas River, Mare Trap Pasture, Welder Wildlife Refuge, 29 Sep 1956, Rowell 5213 (SMU). Willacy Co.: 4 mi. west of Redfish Bay on south edge of Norias erg, 9 Mar 1954, Johnston 54169 (TEX). MEXICO. Tamaulipas: vicinity of LaBarra, 8 km east of Tampico, 1-8 Feb 1910, Palmer 298 (NY).

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Table 1. Voucher collections used in analyses. A = populations used for phenetic analyses, followed by OTU number; B = populations used for breeding studies; C = populations used for chemical studies.

P. angustifolia. ALABAMA: Baldwin Co., Sullivan and Laue 1164 (OKL), A-58, B, C. FLORIDA: Bay Co., Sullivan and Laue 1167 (OKL), A-52.; Franklin Co., Sullivan and Laue 1169 (OKL), A-53, C; Sullivan and Laue 1170 (OKL), B; Gulf Co., Sullivan and Laue 1168 (OKL), A-57, C; Walton Co., Sullivan and Laue 1166 (OKL), A-54, C. MISSISSIPPI: Hancock Co., Sullivan and Laue 1152 (OKL), A-56, B, C; Jackson Co., Sullivan and Laue 1162 (OKL), A-55, B, C.

P. hederifolia. TEXAS: Val Verde Co., Sullivan and Laue 1300 (OKL), B.

P. heterophylla. OKLAHOMA: Cleveland Co., Sullivan 1040 (OKL), B.

P. longifolia. OKLAHOMA: Cleveland Co., Sullivan 1037 (OKL), B.

P. pumila. OKLAHOMA: Cleveland Co., Sullivan 1036 (OKL), B.

P. variovestita. TEXAS: Aransas Co., Sullivan et al. 1125 (OKL), B, C; Whitehouse 18179 (MICH), A-1; Kenedy Co., Lundell and Lundell 8715 (SMU), A-103; Lundell and Lundell 10730 (LL), C.

P. variovestita "intergrades". TEXAS: De Witt Co., Sullivan et al. 1123 (OKL), B, C; Ellis Co., Shinners 14158 (SMU), A-100; Harris Co., Sullivan and Laue 1000 (OKL), B, C; Sullivan and Laue 1002 (OKL), B; Medina Co., Johnston et al. 3401 (TEX), A-2, C; Victoria Co., Cory 55114 (SMU), A-102.

P. viscosa var. cinerascens. LOUISIANA: Bossier Par., Sullivan and Laue 1130 (OKL), C; Webster Par., Sullivan and Laue 1131 (OKL), A-18,

C. NEW MEXICO: Lea Co., Demaree 60672 (OKLA), A-26; Miller 1938 (FLAS), C. OKLAHOMA: Cleveland Co., Sullivan 1041 (OKL), A-16, B, C; Sullivan 1044 (OKL), B; Greer Co., Barber 854 (OKLA), A-20; Pushmataha Co., Means 2461 (OKLA), A-25; Woods Co., Sullivan et al. 1068 (OKL), A-17, C. TEXAS: Bandera Co., Smith 503 (LL), A-23, C; Bee Co., Correll 29304 (LL), A-28; Dallas Co., Lundell and Lundell 9232 (MICH), A-29; Hardeman Co., Correll and Johnston 16835 (LL), C; Jeff Davis Co., Sullivan and Laue 1277 (OKL), B; Lubbock Co., Derbow 8 (OKLA), C; Robertson Co., Sullivan and Starbuck 1229 (OKL), C; Taylor Co., Mahler 1314 (OKLA), A-19; Uvalde Co., Cory 44514 (TEX), A-31; Val Verde Co., Correll and Flyr 38411 (LL), A-24; Sullivan and Laue 1303, 1304 (OKL), B; Walker Co., Correll 31981 (LL), A-21; Webb Co., Sanchez 92 (TEX), A-22. MEXICO: Chiapas, Matuda 239 (MICH), A-15; Chihuahua Palmer 240 (MICH), A-12; Coahuila, McVaugh 12319 (MICH), A-13; Hidalgo, Pringle 13130 (MICH), A-30; Queretaro, Barklev et al. 748 (MICH), A-14.

P. viscosa var. elliottii f. elliottii. FLORIDA: Broward Co., Sullivan and Laue 1211 (OKL), B, C; Dade Co., Sullivan and Laue 1209 (OKL), B, C; Sullivan and Laue 1210 (OKL), A-41, B, C; Hendry Co., Sullivan and Laue 1199 (OKL), A-44, B; Hernando Co., Sullivan and Laue 1025 (OKL), A-43, B, C; Sullivan and Laue 1028 (OKL), B, C; Pasco Co., Sullivan and Laue 1032 (OKL), A-42, B; Sarasota Co., Sullivan and Laue 1188 (OKL), A-45, C.

P. viscosa var. elliottii f. glabra. FLORIDA: Charlotte Co., Sullivan and Laue 1190, 1191 (OKL), A-49 & 50, B, C; Collier Co., Sullivan and Laue 1207 (OKL), A-48, B, C; Lee Co., Sullivan and Laue 1198 (OKL), A-47; Manatee Co., Sullivan and Laue 1186 (OKL), B, C;

Pinellas Co., Sullivan and Laue 1185 (OKL), A-51, C.

P. viscosa var. maritima. FLORIDA: Dixie Co., Sullivan and Laue 1010 (OKL), A-33, B, C; Glades Co., Sullivan and Laue 1203 (OKL), A-35, B, C; Lake Co., Sullivan and Laue 1034 (OKL), B; Levy Co., Sullivan and Laue 1021, 1023 (OKL), B; Nassau Co., Sullivan and Laue 1183 (OKL), C; St. Johns Co., Sullivan and Laue 1217 (OKL), A-32, B, C; St. Lucie Co., Sullivan and Laue 1214 (OKL), A-36, B; Sullivan and Laue 1215 (OKL), B, C; Volusia Co., Sullivan and Laue 1216 (OKL), A-37, C. GEORGIA: Chatham Co., Sullivan and Laue 1218 (OKL), A-40, B, C; Glynn Co., Sullivan and Laue 1179 (OKL), A-34, C. NORTH CAROLINA: Carteret Co., Sullivan and Laue 1223 (OKL), A-39, B, C; Sullivan and Laue 1224 (OKL), B; Pender Co., Sullivan and Laue 1221 (OKL), A-38, B, C.

P. viscosa var. mollis. ARKANSAS: Franklin Co., Davis 615 (UARK), C; Demaree 51450 (OKLA), A-7; Jefferson Co., Locke 528 (UARK), A-10; Stone Co., Palmer 1861 (OKLA), A-6. LOUISIANA: Caddo Par., Sullivan and Laue 1128 (OKL), B, C; Sullivan and Laue 1129 (OKL), A-4, B, C. OKLAHOMA: Marshall Co., Sullivan and Laue 1039 (OKL), A-5, B; Sullivan and Laue 1045 (OKL), A-5, B, C; Pawnee Co., Waterfall 12360 (OKLA), A-8, C. TEXAS: Hildago Co., Lundell and Lundell 9837 (OKLA), C; Robertson Co., Sullivan and Starbuck 1226 (OKL), A-3, B, C; Tarrant Co., Lundell and Lundell 12894 (TEX), A-9.

P. viscosa var. sinuatodentata. MEXICO: Veracruz, Sullivan and Laue 1234, 1235 (OKL), A-67 & 66, B, C.

P. viscosa var. spathulaefolia. LOUISIANA: Cameron Par., Sullivan and Laue 1006 (OKL), C; Sullivan and Laue 1007 (OKL), A-65, B, C; Vermillion Par., Killmer 36 (NLU), C. TEXAS: Aransas Co., Sullivan et

al. 1124 (OKL), B; Sullivan et al. 1126 (OKL), B, C; Whitehouse 18292 (SMU), A-62; Brazoria Co., Fleetwood 10221 (SMU), C; Cameron Co., Crow 81 (NLU), C; Chambers Co., Sullivan and Laue 1003 (OKL), A-64, B, C; Kenedy Co., Lundell and Lundell 8714 (LL), A-60, C; Nueces Co. Sullivan et al. 1127 (OKL), A-63, C; Willacy Co. Runyon 1811 (TEX), A-61, C.

P. viscosa var. yucatanensis. MEXICO: Yucatan, Sullivan and Laue 1249, 1256 (OKL), A-69 & 71, C; Sullivan and Laue 1257, 1258 (OKL), A-70 & 68, B, C.

Table 2. Characters used in phenetic analyses of the Physalis
viscosa complex.

-
1. Leaf length from apex to base of blade on shortest side. 2. Ratio of leaf length to width (at widest point). 3. Ratio of leaf length to petiole length. 4. Flowering calyx length. 5. Ratio of flowering calyx length to pedicel length. 6. Ratio of length of calyx teeth to total flowering calyx length. 7. Ratio of flowering calyx teeth length to width at base. 8. Fruiting calyx length. 9. Ratio of fruiting pedicel length to fruiting calyx length. 10. Ratio of fruiting calyx length to width. 11. Length of corolla at maturity. 12. Corolla width at mouth. 13. Spots in corolla throat sharply defined/not. 14. Corolla spot color dark purple-black/brown/ocher/green/blue. 15. Stigma shape truncate/clavate/capitate. 16. Ratio of anther length to filament length. 17. Total anther length. 18. Anther color blue or tinged blue/purple or tinged purple/yellow. 19. Leaf margin dentate/entire. 20. Leaf base attenuate/rounded/deltoid/cordate. 21. Leaf apex acuminate/acute/obtuse/acute and obtuse. 22. Trichomes predominantly dendritic/not. 23. Trichomes predominantly forked/not. 24. Trichomes predominantly glandular/not. 25. Trichomes predominantly simple/not. 26. Trichomes jointed/not. 27. Stems and leaves pubescent/glabrous. 28. Calyx completely covered with trichomes/trichomes on margin only. 29. Abaxial corolla surface covered with trichomes/ trichomes on margin only/glabrous. 30. Annual/perennial. 31. Stem angled/terete. 32. Style length. 33. Filaments tinged blue/tinged purple/yellow.
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Fig. 1. Phenogram generated using the General Similarity Coefficient of Gower and the UPGMA algorithm for OTUs representing the members of the Phvsalis viscosa complex. The cophenetic correlation coefficient = 0.847.

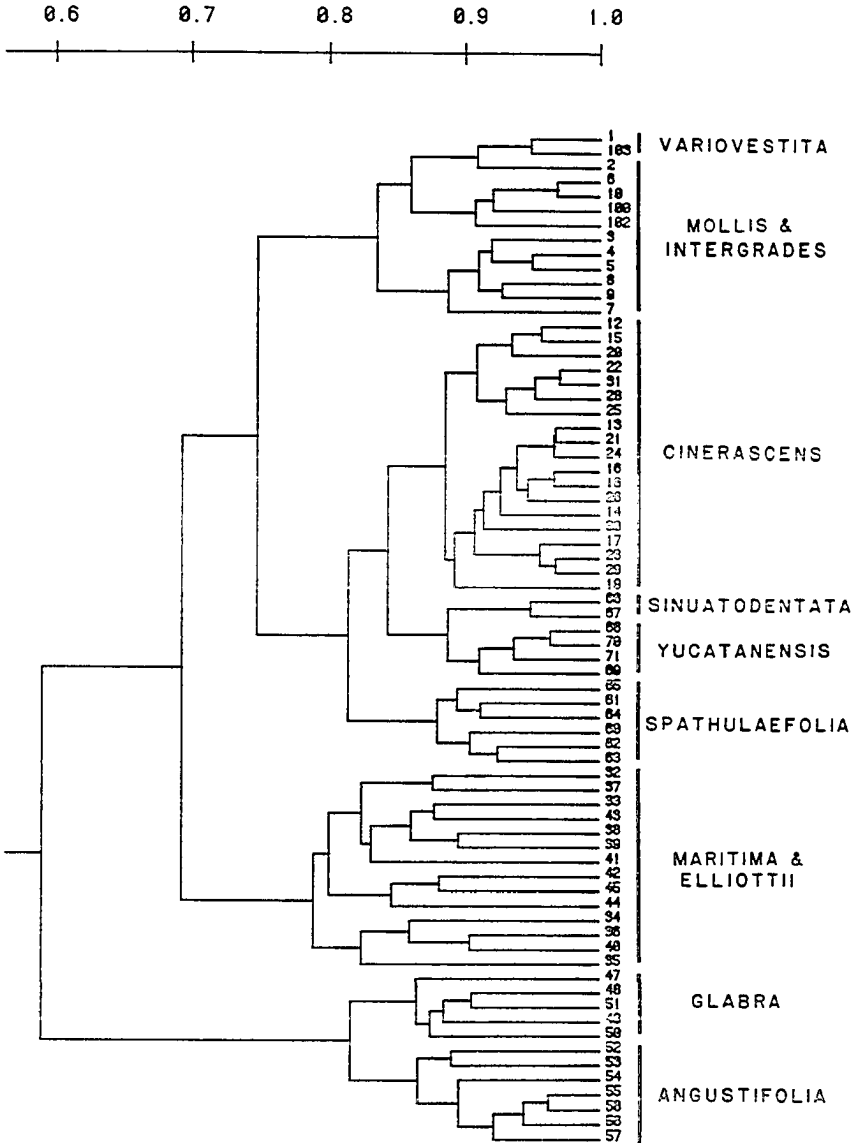


Fig. 2. Minimum spanning network generated using the General Similarity Coefficient of Gower and the UPGMA algorithm for OTUs representing the members of the Physalis viscosa complex. The similarity value between each connected pair of OTUs is given on the minimum spanning network.

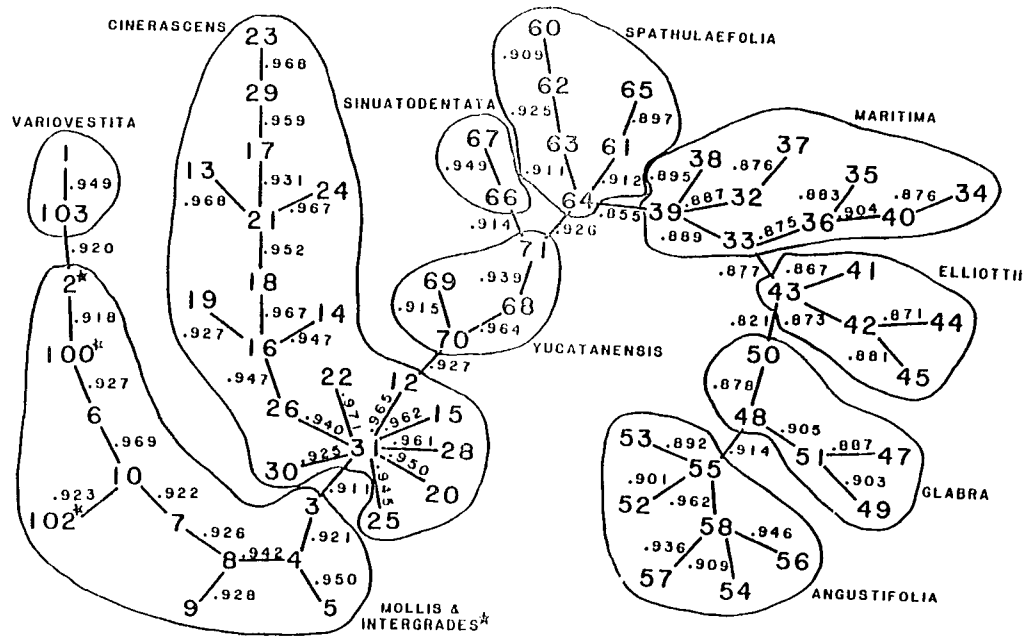


Fig. 3-6. Representative levels of the Similarity Graph Cluster Analysis (Estabrook 1966) of the members of the Physalis viscosa complex. Clusters contain OTUs that have three or more connections to other members of that cluster. Fractions indicate the numbers of actual connections within and between clusters over the number of possible connections. Single-member clusters (OTUs that are not connected to any other OTU) and similarity values for each level illustrated are listed on the left of each figure.

Fig. 7-8. Representative levels of the Similarity Graph Cluster Analysis (Estabrook 1966) of the members of the Physalis viscosa complex. Clusters contain OTUs that have three or more connections to other members of that cluster. Fractions indicate the numbers of actual connections within and between clusters over the number of possible connections. Single-member clusters (OTUs that are not connected to any other OTU) and similarity values for each level illustrated are listed on the left of each figure.

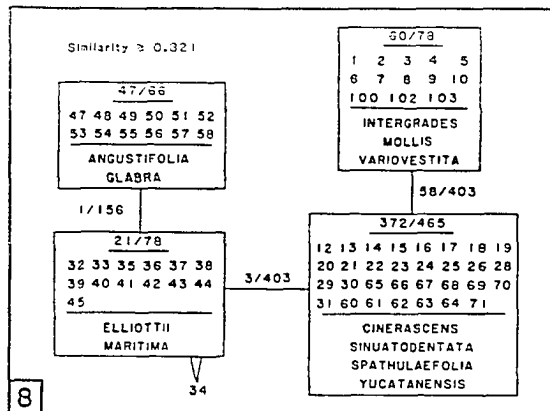
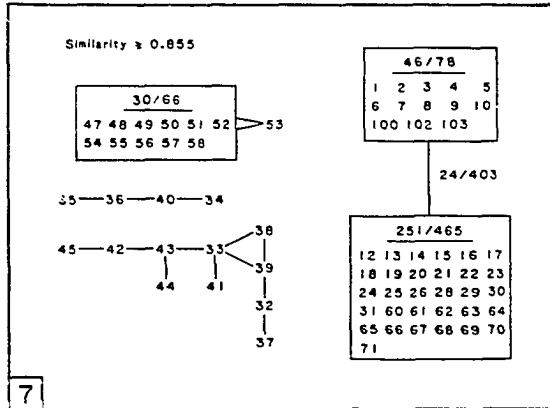
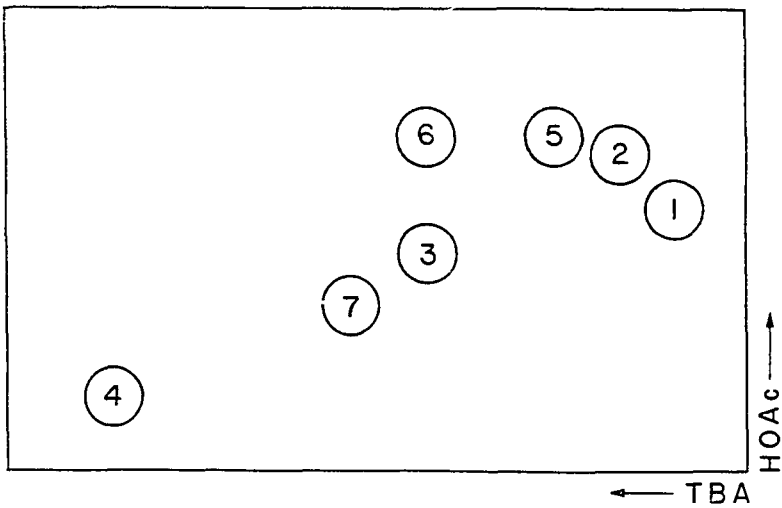
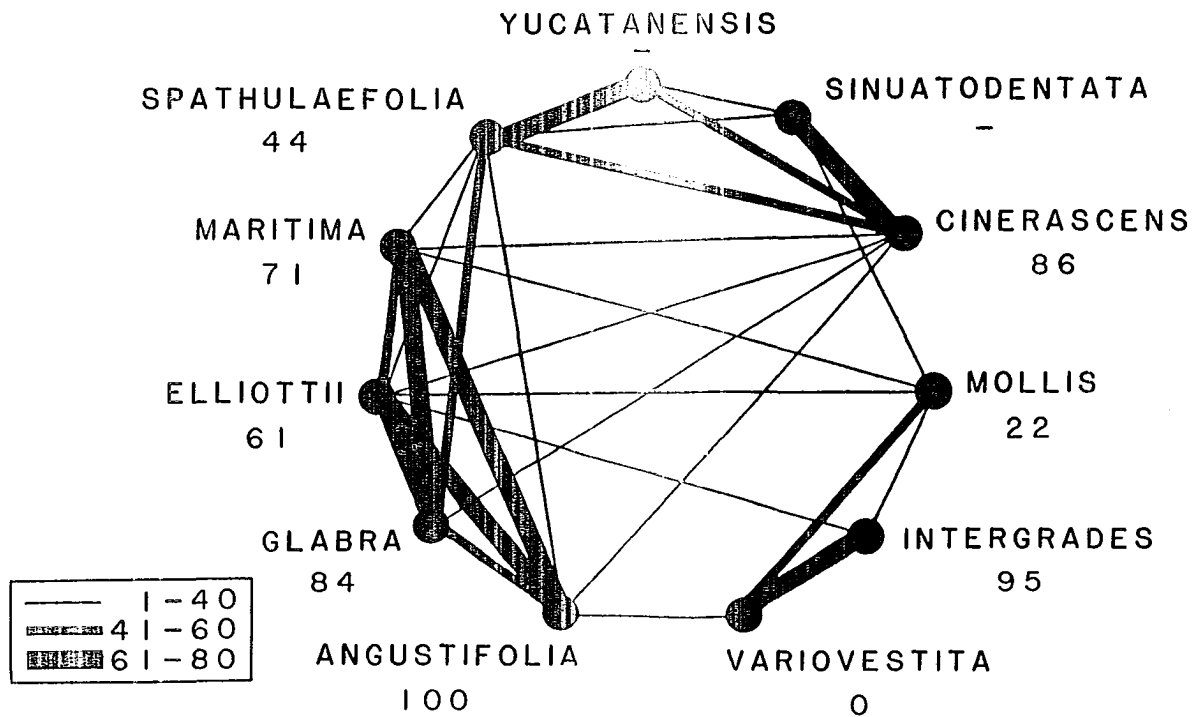


Fig. 9. Composite chromatogram and taxonomic distribution of foliar flavonoids of the Physalis viscosa complex. Compounds are as follows: (1) myricetin 3-O-glucoarabinoside; (2) kaempferol 7-galactosyl-3-O-arabinoside; (3) myricetin 3-O-glycoside; (4) not identified; (5) not identified; (6) quercetin 3-O-glucoside or -diglucoside; (7) not identified.



Taxon	n	1	2	3	4	5	6	7
MOLLIS	7	●	●	●				
INTERGRADES	3	●	●	●				
VARIOVESTITA	2	●	●	●	●			
CINERASCENS	6	●	●	●			●	
"	3	●	●			●		
SINUATODENTATA	2					●		
YUCATANENSIS	4	●	●			●		
SPATHULAEFOLIA	9						●	
MARITIMA	6						●	●
"	4			●				
ELLIOTTII	2						●	●
"	4			●				
GLABRA	3			●				
"	2			●				●
ANGUSTIFOLIA	6			●				

Fig. 10. Hybridization among the members of the Physalis viscosa complex. Lines between taxa represent the percent of attempted crosses that produced viable seed. Numbers below each taxon indicate percent of intra-taxon crosses that produced viable seed.



PALYNOLOGY AND SYSTEMATICS OF
PHYSALIS AND QUINCULA (SOLANACEAE)

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ABSTRACT

Pollen of Physalis and the segregate genus Quincula was examined using light and scanning electron microscopy to determine the congruence of palynological characteristics with other comparative data. The pollen morphology within Physalis is relatively uniform, parallelling the great similarity among species in other features. Physalis has small grains that are subprolate in equatorial view and triangular with convex sides to round in polar view. Quincula lobata has larger grains, that are oblate in equatorial view and triangular with straight sides in polar view. Pollen morphology and size support the recognition of Quincula as a genus distinct from Physalis.

Palynological investigations in the Solanaceae have been conducted at all levels in the taxonomic hierarchy, from broadly-based surveys of genera and their tribal relationships (Basak, 1967; Murry and Eshbaugh, 1971; Gentry, 1979, in press) to more comprehensive studies of species relationships and infraspecific taxa (Romanov, 1965; Anderson and Gensel, 1976; Gbile and Sowunmi, 1979; Gentry, 1979). Few of these authors have utilized scanning electron microscopy (SEM) in their analyses, although SEM and transmission electron microscopy (TEM) have recently been used by Gentry (1979, in press) to determine relationships of genera in the Solanaceae and closely-related families.

Although Murry and Eshbaugh (1971) agreed with Erdtman (1952) and Basak (1967) that the pollen morphology in the Solanaceae is "remarkably homogeneous", they found that many genera and species in the tribe Solaninae (of which Physalis is a member) could be differentiated by combining morphological and statistical information.

In a study utilizing both SEM and light microscopy (LM), Anderson and Gensel (1976) found that differences in size and exine ornamentation served to distinguish species and series in Solanum section Basarthrum. Gbile and Sowunmi (1979) determined that differences observed with LM in the size and shape of pollen grains and in the exine pattern were sufficient to distinguish species, subspecies, and varieties of some Nigerian members of the genus Solanum. Thus, morphological features and size of pollen may be useful in systematic studies on the generic level and, possibly, on the specific and subspecific levels in the Solanaceae.

Physalis is a large American genus composed of about 90 species. In recent years, Physalis has been the focus of several systematic investigations (Menzel, 1951, 1957, 1960; Waterfall, 1958, 1967; Hinton, 1970, 1975, 1976; Hudson, 1983; Sullivan, 1984) in order to better understand patterns of karyology, hybridization, morphology, and chemistry within the genus. However, little is known about the variation in palynological features of Physalis, and their value in systematic analyses of the genus. Murry and Eshbaugh (1971) examined pollen of 4 species of Physalis as part of their LM analysis of palynology of the Solaninae, but their purpose was not to determine the significance of pollen features within genera. They characterized Physalis pollen as subprolate in equatorial view, semi-angular in polar view, with reticulate sculpturing, an ectexine which is thicker than the endexine, a small to intermediate polar area (Polar Area Index; Faegri and Iverson, 1964), and a somewhat inconspicuous vestibulum. They also found statistically significant differences in both polar and equatorial diameters among the four Physalis species they analyzed. The purpose of this study is to investigate the utility of palynology in systematic studies in Physalis by comparing information on exine features and size of pollen with the most recent taxonomic treatment of the Physalis viscosa complex (Sullivan, 1984), and with Rydberg's (1896) subgeneric treatment of the genus.

MATERIALS AND METHODS--Pollen was examined from 17 species and infraspecific taxa of Physalis (10 representatives of the P. viscosa complex and 7 from other series of the subgenus Physalis), and from the

closely-related, monotypic Quincula. Pollen samples were obtained from unopened anthers of greenhouse-grown plants or from herbarium specimens. Vouchers are located in DUKE, FSU, MEXU, OKL, and USF (Sullivan, 1984). Samples were taken from 1-3 populations of each taxon to represent different portions of the taxon's geographic range. Pollen was acetolyzed according to the procedure given in Erdtman (1969) and filtered through a fine wire mesh. A small portion of one sample population of each taxon was critical-point-dried using a Pelco Model H Critical Point Drying Unit and mounted on an aluminum stub for scanning electron microscopy. The stubs were coated with gold and stored in a dessicator until they were examined with an ETEC Autoscan. The remainder of each acetolyzed pollen sample was mounted on a glass slide in glycerine jelly. Measurements were made from grains mounted in glycerine jelly. For all collections, 20 measurements were made of the polar diameter (P) and of the equatorial diameter (E), and the P/E ratio was calculated.

RESULTS--Pollen of all the species examined is similar in overall size, shape, and exine ornamentation, although some differences among species can be seen in these features (Fig. 1-9). The pollen of Quincula lobata is much larger than any of the other species examined, and does not overlap in size with the other species (Fig. 1). Quincula is oblate in equatorial view (Fig. 10), and triangular with straight sides in polar view (Fig. 11). In addition, Quincula has a very small apocolpium (distance between colpi 0.1 diameter of grain in polar view) relative to the other species examined (Fig. 11). In contrast, pollen of Physalis

is subprolate (Fig. 2), and convex-triangular (Fig. 3, 5) to circular (Fig. 4). Also, Physalis species have larger apocolpia (distance between colpi 0.2-0.4 diameter of grain in polar view; Fig. 3-5).

Physalis, Fig. 1-9--Pollen tricolporate. Equatorial view subprolate; 14.3-26 μ . Polar view sub-circular to triangular with slightly convex sides; ectexine protruding in the region of the endoaperture; 18.2-31.2 μ . P/E ratio 1.1-1.4. Colpus extending almost the entire length of the grain; membrane psilate (Fig. 6) to crustate (Fig. 7); endoaperture lalongate. Exine ornamentation of minute, rounded (Fig. 8) or sharp spinules of varying degrees of density; spinules may be interspersed with minute, irregularly-shaped granules (Fig. 9).

Distinguishing features of each species examined are listed below by series.

(a) Series Pubescentes--P. pubescens. Ektexine protrusions over the endoapertures rounded and extending over the colpi (Fig. 3-4). Colpus membrane granulate. Exine ornamentation of only slightly-raised, rounded spinules, interspersed with small, irregularly-shaped granules.

(b) Series Angulatae--P. angulata. Ektexine protrusions over the endoapertures rounded and extending over the colpi. Colpus membrane granulate. Exine ornamentation of sharp-pointed spinules.

(c) Series Leptophyllae--P. carpenteri. Ektexine protrusions over the endoapertures rounded and extending partially over the colpi. Colpus membrane sparsely granulate. Exine ornamentation of sharp-pointed spinules.

(d) Series Heterophyllae--P. heterophylla. Ektexine protrusions over the endoapertures angular and not extending over the colpi (Fig. 5). Colpus membrane sparsely granulate. Exine ornamentation of only slightly-raised, rounded spinules.

(e) Series Lanceolatae--P. pumila. Ektexine protrusions over the endoapertures rounded and extending over the colpi. Colpus membrane granulate. Exine ornamentation of rounded spinules.

P. longifolia. Ektexine protrusions over the endoapertures rounded and extending over the colpi. Colpus membrane crustate. Exine ornamentation of rounded spinules.

(f) Series Philadelphicae--P. ixocarpa. Ektexine protrusions over the endoapertures angular and not extending over the colpi. Colpus membrane psilate. Exine ornamentation of only slightly-raised, rounded spinules.

(g) Series Stellatae--P. cinerascens. Ektexine protrusions over the endoapertures rounded and extending partially over colpi. Colpus membrane granulate to crustate. Exine ornamentation of rounded spinules.

P. mollis. Ektexine protrusions over the endoapertures rounded and extending partially over colpi. Colpus membrane granulate. Exine ornamentation of rounded spinules.

P. angustifolia. Ektexine protrusions over the endoapertures angular and not extending over colpi. Colpus membrane granulate. Exine

ornamentation of rounded spinules.

P. walteri. Ektexine protrusions over the endoapertures rounded and extending partially over colpi. Colpus membrane granulate. Exine ornamentation of rounded spinules.

Quincula lobata, Fig. 1, 10-11--Pollen tricolporate. Equatorial view oblate; 27.3-33.8 μ . Polar view triangular with straight sides; ektexine protruding in the region of the endoaperture; 31.2-33.8 μ . P/E ratio 1.1. Colpus extending almost the entire length of the grain; membrane sparsely granulate. Endoaperture lalongate. Exine ornamentation of minute spinules.

DISCUSSION--Pollen morphology in Physalis is highly uniform and there is a great amount of overlap among species in size of grains. This is not surprising, in view of the great similarity among Physalis species in other floral characteristics (Rydberg, 1896; Menzel, 1951, 1957; Hinton, 1970, 1975, 1976; Hudson, 1983; Sullivan, 1984, in press) and in pollination syndromes (Sullivan, 1984, in press). Despite the relative uniformity in shape and exine ornamentation, the majority of the representatives from 7 of the 9 series in Physalis section Physalis (Rydberg, 1896; as Euphysalis) can be distinguished by a combination of differences in shape of the ektexine protrusion in the region of the endoaperture, size of the apocolpium, and exine ornamentation pattern.

All of the species examined have protruding ektexine in the region of the endoaperture. However, in P. angustifolia, P. heterophylla, and P.

ixocarpa the protrusions are angular in polar view and do not extend over the colpi, while in the remaining species the protrusions are rounded and extend at least partially over the colpi and pores. Size of the apocolpium is variable in the genus, from 0.2-0.4 grain diameter in polar view. Considerable variability occurs within species in this feature, as well. None of the species examined exhibited as small an apocolpium as Q. lobata (0.1 grain diameter in polar view). There are also slight differences among species in exine ornamentation. The minute spinules found on all of the species examined are rounded on most taxa, but are sharp on P. angulata and P. carpenteri. The spinules are almost absent on P. heterophylla, such that the exine of this species appears only slightly roughened. This condition is approached in both P. ixocarpa and P. pubescens, which both exhibit more widely-spaced spinules that are only slightly raised. In addition, P. pubescens and P. cinerascens exhibit minute, irregularly-shaped granules interspersed with the spinules. The occurrence of the granules is uniform in P. pubescens, and irregular in P. cinerascens. The colpus membranes exhibited different degrees of granule density, from almost entirely smooth (psilate) in P. ixocarpa, to densely incrustated with granules (crustate) in P. longifolia and one population of P. cinerascens.

Although each of the species examined is somewhat distinctive in possessing a particular combination of characters, the morphological and size variation does not corroborate species relationships based on other analyses. In addition, there is considerable variation within species, at least those in the P. viscosa complex (series Stellatae), such that the ability to discriminate among species based on pollen features is

questionable. The uniformity of pollen in this genus is consistent with the high degree of similarity among Physalis species in other floral features.

In contrast to the pollen of Physalis, that of Quincula is oblate in equatorial view and triangular with straight sides in polar view. Quincula also has a much smaller apocolpium than Physalis, such that its colpi almost join at the poles. In addition, pollen of Q. lobata is much larger than that of any of the Physalis species examined. Thus, Quincula is distinctive in both size and shape of its pollen grains.

This study substantiates the contention of Menzel (1950) and Averett (1979) that Quincula be considered distinct from Physalis. Quincula lobata was retained by Waterfall (1958) as a species of Physalis, although it also differs from the members of Physalis in base chromosome number as well as in morphology of the flowers, fruits, seeds, leaves, and trichomes (Rydberg, 1896; Menzel, 1950; Averett, 1979; Averett and Powell, 1972). The distinctions between Physalis and Quincula pollen are also consistent with the findings of Murry and Eshbaugh (1971), that genera within the Solaninae can be distinguished by a combination of morphological and statistical features.

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Fig. 1. Size range and sample mean in polar and equatorial diameter, and P/E ratio for Physalis and Quincula. Three populations (20 pollen grains from each in polar and in equatorial view) were measured for each species or variety except for the following: P. angustifolia, 6 populations; P. cinerascens var. cinerascens, 9; P. longifolia, 1; P. mollis var. mollis, 5; P. mollis var. variovestita, 1; P. pubescens, 1; P. walteri, 7.

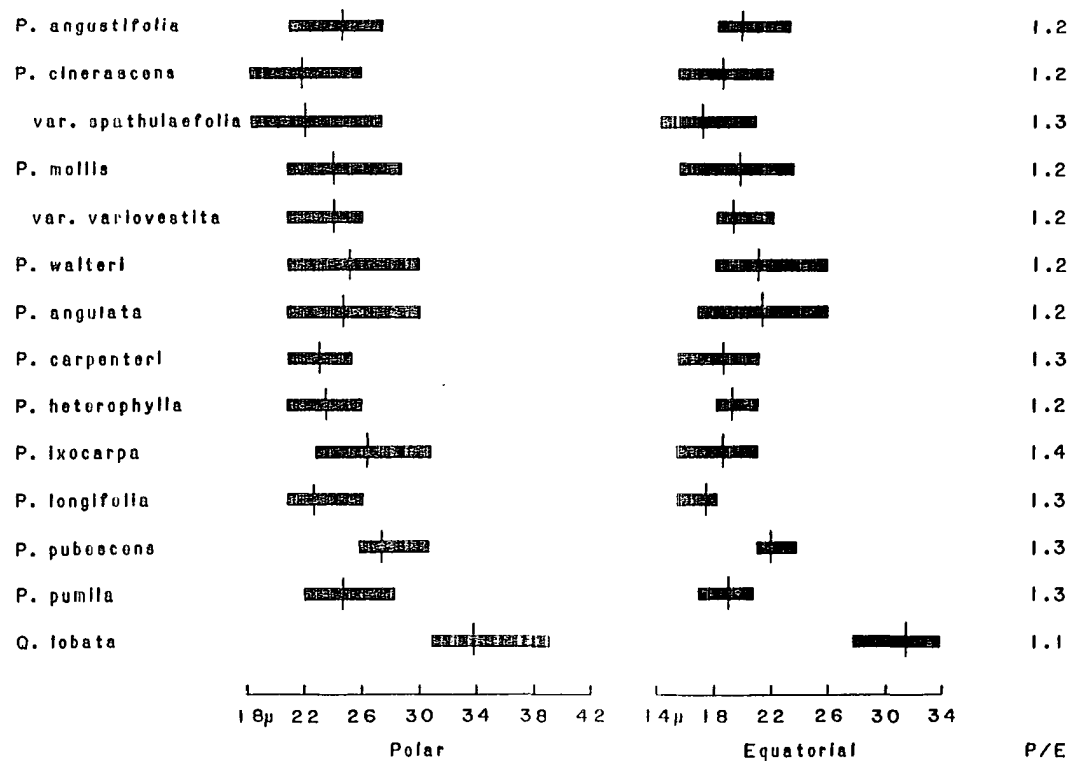


Fig. 2-7. SEM of Physalis pollen. 2. P. carpenteri, illustrating subprolate shape in equatorial view. X 4,200. 3. P. cinerascens, illustrating rounded ectexine protrusions extending over the colpi and large apocolpium. X 4,160. 4. P. walteri, illustrating round shape in polar view. X 3,675. 5. P. heterophylla, illustrating triangular shape with convex sides in polar view and angular ectexine protrusions not extending over the colpi. X 3,600. 6. P. ixocarpa, high magnification of the colpus illustrating psilate membrane. X 7,000. 7. P. cinerascens, high magnification of the colpus illustrating crustate membrane. X 6,000.

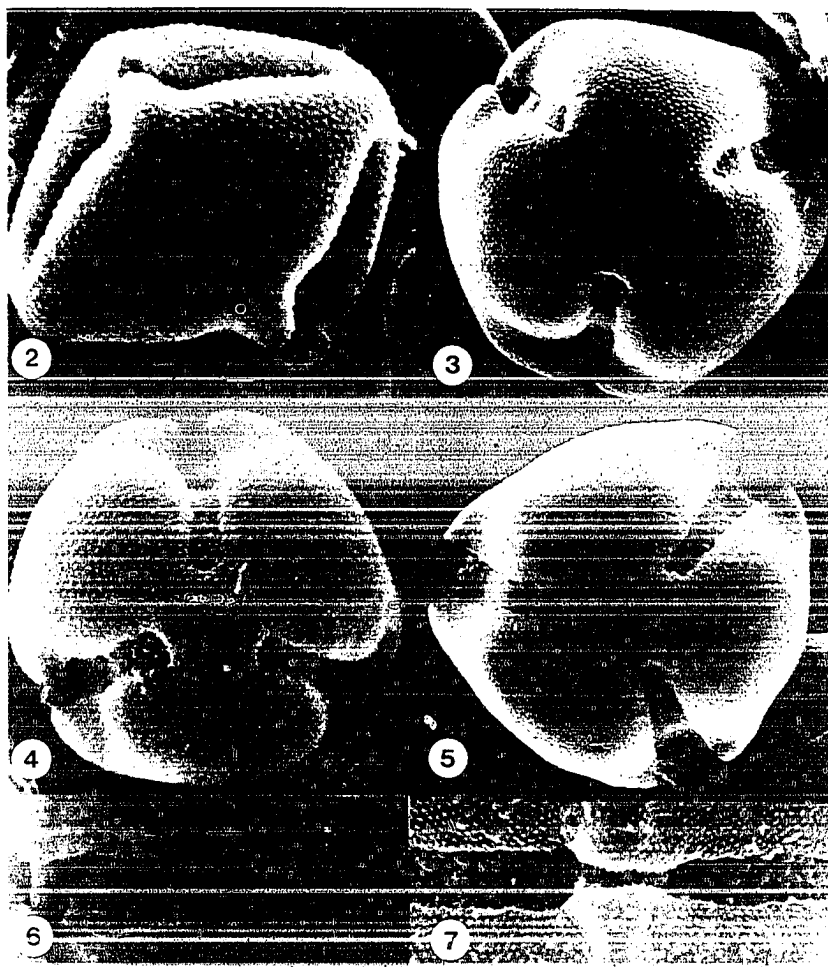
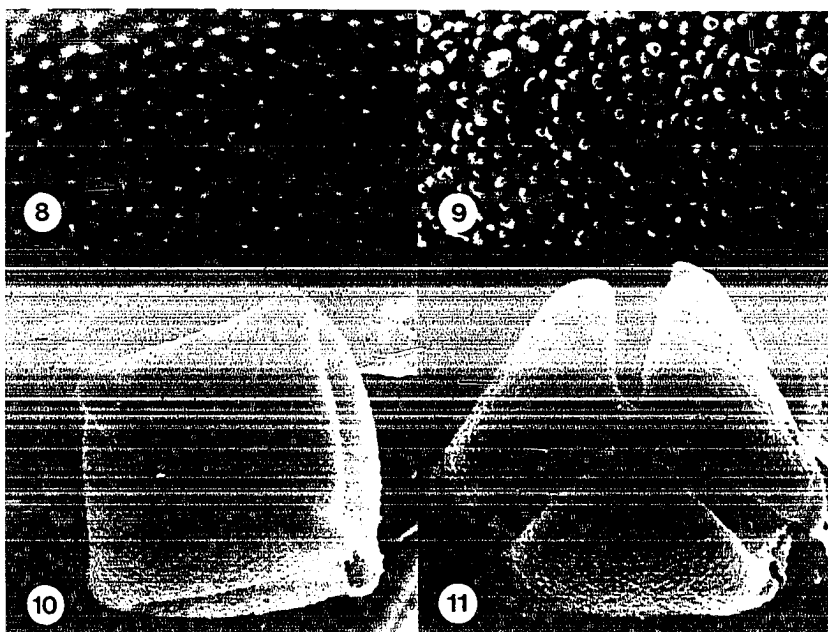


Fig. 8-11. SEM of Physalis and Quincula pollen. 8. P. cinerascens, high magnification of exine with rounded spinules. X 15,000. 9. P. pubescens, high magnification of exine with rounded spinules interspersed with irregularly-shaped granules. X 15,000. 10. Q. lobata, illustrating oblate shape in equatorial view. X 2,000. 11. Q. lobata, illustrating triangular shape with straight sides in polar view and small apocolpium, such that colpi almost touch at pole. X 2,000.



PHYSALIS L., Ground Cherry

Contributed by Janet R. Sullivan

Annual or rhizomatous perennial herbs; stems erect or weakly decumbent, branched, glabrous to densely pubescent. Leaves simple, alternate or falsely opposite, blades lanceolate to broadly ovate, glabrous to densely pubescent, apex acuminate to blunt, margins entire to dentate, base unequal, truncate-cordate to rounded or attenuate; petiolate or sessile. Flowers radially symmetrical; solitary or several in leaf axils; pedicellate; pendulous. Calyx campanulate, enlarged and inflated in fruit, becoming reticulate-membranous and bladder-like, completely enclosing the berry; lobes 5, connivent, scarcely enlarged in fruit; corolla 5-angulate or obscurely 5-lobed, yellow or white, often with 5 darker maculations in the throat, campanulate-rotate, plicate in bud; stamens 5, yellow, blue, or tinged blue or purple, erect, inserted near the base of the corolla tube, anther-sacs opening longitudinally; stigma minute, ovary 2-celled. Fruit an edible juicy berry, green, orange, or purple, invested by inflated calyx. Seeds numerous, reniform, flattened, ca. 2 mm long, finely-pitted.

About 90 species worldwide, primarily in the Neotropics. Species boundaries are often poorly defined, and recent monographs disagree with respect to circumscription of species. This genus is in need of modern systematic study.

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- 1 Flowers 2 or more per leaf axil; berries with spherical seed-like bodies among the flattened, reniform seeds..... 1. P. carpenteri.
- 1 Flowers solitary in leaf axils; berries with flattened, reniform seeds only.
- 2 Fruiting calyces red, retaining their color on drying; corollas white..... 2. P. alkekengi.
- 2 Fruiting calyces green or orange, drying brown; corollas yellow, often with maculations in throat.

- 3 Anthers strongly coiled after dehiscence, blue; corolla throat tinged blue; berries purple..... 3. P. ixocarpa.
- 3 Anthers not coiled after dehiscence, yellow, blue, or purple; corolla throat purple, brown, green or ocher; berries orange, yellowish, or green.
- 4 Leaves glabrous or nearly so.
- 5 Flowering calyces typically 6 mm or more long; perennials from rhizomes.
- 6 Pedicels glabrous or rarely sparsely pubescent with branched hairs; leaves sessile, blades narrowly spatulate to linear-lanceolate..... 4. P. angustifolia.
- 6 Pedicels sparsely pubescent with unbranched hairs; leaves petiolate, blades broadly ovate to broadly lanceolate..... 5. P. longifolia.
- 5 Flowering calyces typically 6 mm or less long; annuals from taproots.
- 7 Corolla throat with 5 large, dark, purple-black maculations, visible through back of dried, pressed flowers; fruiting calyces sharply 5-angled.
- 8 Leaf margins entire or dentate with fewer than 10 teeth per side; fruiting pedicels 15 mm or less long..... 6. P. pubescens.

8 Leaf margins dentate with 10 or more teeth per side;
 fruiting pedicels mostly 15 mm or more
 long..... 7. P. cordata.

7 Corolla throat yellow or only tinged dark purple; fruiting
 calyces 10-angled.

9 Calyces and young stems with glandular
 hairs..... 8. P. missouriensis.

9 Calyces and young stems glabrous or sparsely pubescent
 with non-glandular hairs.

10 Flowering pedicels 2-5 mm long; fruiting pedicels 3-6
 mm long..... 9. P. lagascae.

10 Flowering pedicels 7-17 mm long; fruiting pedicels
 15-30 mm long..... 10. P. angulata.

4 Leaves pubescent.

11 Trichomes 2 or more branched or stellate, in some species
 intermixed with simple hairs.

12 Calyces hispid, hairs stiff, 2-3 branched and unbranched,
 of varying lengths, at least some of which are as long
 as 1-1.5 mm long..... 11. P. pumila.

12 Calyces tomentose to sparsely pubescent, hairs soft,
 branching 3 or more times, less than 1 mm long,
 sometimes intermixed with soft, 2-4 mm long, branched

or unbranched hairs.

13 Flowering calyces and leaf undersurfaces tomentose, hairs obscuring plant surface; hairs branched, 1 mm or less long, in some populations intermixed with 2-4 mm long, branched or unbranched hairs on the stems and calyces..... 12. P. mollis.

13 Flowering calyces and leaf undersurfaces sparsely to densely pubescent, hairs not obscuring plant surface; hairs branched, 1 mm or less long only.

14 Anthers 1.5 X or more longer than the mature filaments; fruiting pedicels mostly 1.5 X or more longer than the fruiting calyces; leaf margins dentate, sinuate, or entire..... 13. P. cinerascens.

14 Anthers equalling or shorter than the elongated filaments; fruiting pedicels mostly equal to or shorter than the fruiting calyces; leaf margins entire only..... 14. P. walteri.

11 Trichomes all unbranched.

15 Flowering calyces typically 6 mm or less long; annuals from taproots.

16 Corolla throat with 5 large, dark, purple-black maculations, visible through back of pressed, dried

- corollas; fruiting calyces sharply 5-angled.
- 17 Fruiting calyces glabrous; plants glabrous or
sparsely pubescent with appressed, non-glandular
hairs..... 7. P. cordata.
- 17 Fruiting calyces pubescent; plants densely viscid-
pubescent with divergent hairs to almost
glabrous.
- 18 Leaf blades gray-green, drying orange or with
orange patches; leaf margins
dentate..... 15. P. pruinosa.
- 18 Leaf blades green, drying green; leaf margins
entire to dentate... 6. P. pubescens.
- 16 Corolla throat yellow or only tinged purple; fruiting
calyces 10-angled.
- 19 Calyces and young stems sparsely to densely
pubescent with intermixed glandular and non-
glandular hairs..... 8. P. missouriensis.
- 19 Calyces and young stems glabrous or only sparsely
pubescent with non-glandular hairs.
- 20 Flowering pedicels 2-5 mm long; fruiting
pedicels 3-6 mm
long..... 9. P. lagascae.

- 20 Flowering pedicels 7-17 mm long; fruiting
pedicels 15-30 mm
long..... 10. P. angulata.
- 15 Flowering calyces typically 6 mm or more long; perennials
from rhizomes.
- 21 Leaf blades broadly ovate to suborbicular; leaf bases
rounded, truncate, or subcordate.
- 22 Flowering pedicels 6-8 mm long; plants never
viscid..... 16. P. peruviana.
- 22 Flowering pedicels 9-20 mm long; plants viscid or
non-viscid.
- 23 Stems densely villous, hairs divergent, 1-2 mm
long, intermixed with shorter glandular hairs;
rhizomes stout and deeply-
buried..... 17. P. heterophylla.
- 23 Stems glabrous to villous, hairs appressed,
shorter than 1 mm, sometimes intermixed with
1-2 mm long, divergent hairs or shorter
glandular hairs; rhizomes slender and
typically shallow.. 18. P. arenicola.
- 21 Leaf blades narrowly ovate to broadly lanceolate or
oblanceolate; leaf bases attenuate.

24 Pedicels and flowering calyces glabrous or sparsely
pubescent; hairs less than 0.5 mm long,
antrorse..... 5. P. longifolia.

24 Pedicels and flowering calyces densely pubescent
with divergent hairs, 1-1.5 mm long, intermixed
with antrorse or retrorse hairs, less than 0.5 mm
long.

25 Leaves oblanceolate with entire margins;
pedicels and flowering calyces with both
divergent and antrorse
hairs..... 19. P. lanceolata.

25 Leaves ovate to broadly lanceolate with dentate
margins; hairs on the pedicels and flowering
calyces with both divergent and retrorse
hairs..... 20. P. virginiana.

1. *P. carpenteri* Riddell ex Rydberg. Perennial, 6-10 dm tall,
from a stout rhizome; stems erect, branching frequently, branches
divergent, pubescent with simple jointed hairs of varying lengths. Leaf
blades ovate to ovate-lanceolate, 5-10 (14) cm long, 3-6 (9) cm wide,
puberulous, apices acuminate, margins entire or rarely coarsely and
irregularly dentate, bases truncate to rounded; petioles 1/4-1/2 blade
length. Flowers 2 or more in leaf axils. Flowering calyces 4.5-7.5 mm

long, sparsely pubescent, lobes 1.5-3.5 mm long, typically unequal; corollas pale yellow with pale brown or green, indistinct maculations in throat, 8-12 mm long; anthers yellow, 1.5-2.5 mm long, filaments less than 1/2 as wide as anthers; pedicels 5-10 mm long. Fruiting calyces green, 10-angled and only slightly inflated, 1-2 cm long, 1-2 cm in diam., convex at bases, pedicels 5-15 mm long. Spherical, seed-like bodies interspersed with the seeds. (n=12) Summer. Disturbed habitats; cp. Fla, La, and Miss.

2. *P. alkekengi* L. CHINESE LANTERN PLANT. Perennial, 3-9 dm tall, from a stout rhizome; stems erect, usually unbranched, glabrous or sparsely hairy with simple, short, divergent hairs. Leaf blades broadly ovate, 6-11 cm long, 4-8.5 cm wide, glabrous to sparsely pubescent, apices acute, margins entire or irregularly dentate, bases truncate to subcordate; petioles 1/10-2/5 blade length. Flowers solitary in leaf axils. Flowering calyces 4-7 mm long, tomentose with long simple hairs, lobes 2-3.5 mm long; corollas white without darker maculations in throat, 10-15 mm long; anthers yellow, 2.5-3 mm long, filaments less than 1/2 as wide as anthers; pedicels 9-13 mm long. Fruiting calyces reddish or bright red, 10-angled, 3-5.5 cm long, 2.5-4.5 cm in diam., deeply concave at bases, pedicels 20-40 mm long. (n=12) Summer. Native of Europe. Often grown for its ornamental fruiting calyx and locally spread from cultivation.

3. *P. ixocarpa* Brotero ex Hornemann. TOMATILLO. Annual, 1.5-10 dm tall, from a slender taproot; stems erect, branching, the upper branches divergent, glabrous to sparsely hairy with simple, short,

appressed hairs. Leaf blades ovate to ovate-lanceolate, 2-7 cm long, 2-4 cm wide, glabrous or sparsely hairy, apices acuminate, margins dentate to entire, bases rounded to attenuate; petioles 1/2 to as long as blades. Flowers solitary in leaf axils. Flowering calyces 5-7 mm long, sparsely vestite to glabrous, lobes 2-4 mm long; corollas yellow with blue-tinged maculations in throat, 7-15 mm long; anthers blue, strongly twisted after dehiscence, 3 mm long, filaments about 1/2 as wide as anthers; pedicels 3-6 mm long. Fruiting calyces green, 10-angled, 2-3 cm long, 2-3 cm in diam., concave at bases, nearly filled or often burst by viscid purplish berry, pedicels 3-8 mm long. (n=12) All year. Introduced from the southwest and Mexico; cultivated, escaped and frequently established in waste places.

4. *P. angustifolia* Nuttall. Perennial, 1.5-6 dm tall, from a deeply-buried rhizome, often also with slender, shallow rhizomes; stems and lower branches erect or spreading along the ground and ascending, glabrous. Leaf blades narrowly spatulate to linear-lanceolate, 3-10 (12) cm long, 0.2-1.5 (2) cm wide, glabrous or with sparse, branched hairs on the margins, apices obtuse to acute, margins entire, bases tapering to stem; sessile. Flowers solitary in leaf axils. Flowering calyces 5-9 (10) mm long, glabrous except for the margins or, occasionally, entire calyx sparsely pubescent, lobes (1) 1.5-3.5 mm long; corollas yellow with ocher to green indistinct maculations in throat, the main vein of each corolla lobe often purple or red, (8) 11-15 (16) mm long; anthers yellow, 2.5-3.5 mm long, filaments 1/2 to as wide as anthers; pedicels 11-24 (32) mm long. Fruiting calyces typically orange when ripe but drying brown, 10-angled, (1.5) 2-3 (4) cm

long, 1.5-2.5 cm in
long. (n=12) All y
Ala, Fla, La, Miss.

This species hybr
populations can be
characteristics.

5. *P. longifolia*
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broadly lanceolate,
sparsely strigose wi
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rounded; petioles 1/
Flowering calyces (5
antrorse hairs, lobes
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tinged blue, 2-4 mm
pedicels 5-20 mm long
1.5-3 cm in diam., co
mm long. (n=12) Late

Leaf blades lanceolat
Leaf blades broadly o
blue.....

long, 1.5-2.5 cm in diam., concave at bases, pedicels 15-35 (42) mm
long. (n=12) All year. Beach dunes and disturbed areas in sand; GC.
Ala, Fla, La, Miss. Incl. *P. elliottii* Kunze--S, in part.

This species hybridizes with *P. walteri* in peninsular Florida, and
populations can be found in this state that exhibit intermediate
characteristics.

5. *P. longifolia* Nuttall. Perennial, 2-6 dm tall, from a stout,
deeply-buried rhizome; erect, branching frequently on upper portions of
plant, glabrous to sparsely hairy with short simple, antrorse hairs, 0.5
mm or less long. Leaf blades broadly ovate to ovate-lanceolate or
broadly lanceolate, 2.5-10 (13) cm long, 1-6 (7) cm wide, glabrous or
sparsely strigose with short antrorse hairs, apices acute, margins
entire to coarsely dentate with only a few teeth, bases truncate to
rounded; petioles 1/5-2/5 blade length. Flowers solitary in leaf axils.
Flowering calyces (5) 7-12 (15) mm long, sparsely strigose with short
antrorse hairs, lobes 3-6 mm long; corollas yellow with purple-brown
indistinct maculations in throat, 10-20 mm long; anthers yellow or
tinged blue, 2-4 mm long, filaments as wide as or wider than anthers;
pedicels 5-20 mm long. Fruiting calyces green, 10-angled, 2-4 cm long,
1.5-3 cm in diam., convex or slightly concave at bases, pedicels 15-35
mm long. (n=12) Late spring through fall.

Leaf blades lanceolate; anthers yellow..... 5a. var. *longifolia*

Leaf blades broadly ovate or ovate-lanceolate; anthers tinged

blue..... 5b. var. *subglabrata*

5a. var. *longifolia*. Leaf blades 2.5-7.5 cm long, 0.5-2.5 cm wide. Corollas 9-13 mm long; pedicels 5-14 mm long. Disturbed habitats; cp. and mts. Ark. {Tex, Okla, and Mo}.

5b. var. *subglabrata* (Mack. & Bush) Cronquist. Leaf blades 3.5-10 cm long, 2-6 cm wide. Corollas 10-18 mm long; pedicels 8-18 mm long. Disturbed habitats; all prov. SE except Fla. {Okla, Mo, Ill, Ind, Ohio, Pa, and NJ}. *P. subglabrata* Mack. & Bush--S,F; *P. virginiana* var. *subglabrata* (Mack. & Bush) Waterfall--R.

6. *P. pubescens* L. Annual, 0.5-8 dm tall, from a slender taproot; stems erect, branching frequently, branches divergent, glabrous to villous with simple, jointed glandular hairs of varying lengths, all shorter than 0.5 mm long. Leaf blades broadly ovate to orbicular, 2.5-8 cm long, 2-7 cm wide, villous with glandular hairs to almost glabrous, apex acute to short-acuminate, margins coarsely dentate with only a few teeth (less than 10 per side) or entire, bases rounded; petioles from 1/5 to as long as blades. Flowers solitary in leaf axils. Flowering calyces 3-6 mm long, villous to almost glabrous, lobes 1-3.5 mm long; corollas yellow with large dark purple-brown distinct maculations in throat, 6-11 mm long; anthers blue or rarely only tinged blue, 1-2 mm long, filaments as wide as anthers; pedicels 3.5-9 mm long. Fruiting calyces green, sharply 5-angled, 2-3 cm long, 1.5-2.5 cm in diam., concave at bases, pedicels 6-15 mm long. (n=12) All year. Disturbed habitats; all prov. SE. {ALL}. Incl. *P. floridana* Rydb.; *P. turbinata* Medic.--S; *P. barbadensis* Jacq.--S, F; *P. pubescens* var. *glabra* (Michx.) Waterfall, in part--R; *P. pubescens* var. *integrifolia*

(Dunal) Waterfall--G.

7. *P. cordata* Miller. Annual, 1.5-5 dm tall, from a slender taproot; stems erect, branching frequently, glabrous or sparsely hairy with simple, appressed hairs, less than 0.5 mm long. Leaf blades broadly ovate to orbicular, 4.5-8.5 cm long, 3.5-7.5 cm wide, glabrous except for sparse hairs on veins, apices acuminate, margins coarsely dentate with 10 or more teeth per side, bases rounded to truncate or cordate; petioles $2/3$ to as long as blades. Flowers solitary in leaf axils. Flowering calyces 3.5-6.5 mm long, glabrous or very sparsely hairy, lobes 2-4.5 mm long; corollas yellow with large purple-brown distinct maculations in throat, 6.5-9.5 mm long; anthers blue or blue-tinged, 1.5-2.5 mm long, filaments as wide as anthers; pedicels (4.5) 6-11 mm long. Fruiting calyces green, sharply 5-angled, (2.5) 3-4 cm long, 2-3 cm in diam., glabrous, concave at bases, pedicels (10) 15-35 mm long. Late summer to fall. Disturbed habitats, usually in sand; chiefly cp. Ala, Ark, Fla, Ga, La, Miss, NC, SC, and Tenn. {Tex and Okla}. *P. pubescens* var. *glabra* (Michx.) Waterfall--R, in part.

8. *P. missouriensis* Mackenzie & Bush. Annual, 1.5-5.5 dm tall, from a slender taproot; stems erect, branching frequently, sparsely to densely pubescent with simple, jointed, glandular and non-glandular hairs, less than 0.5 mm long. Leaf blades broadly ovate to orbicular, 2.5-5.5 cm long, 1.5-5 cm wide, sparsely glandular-pubescent, apices acute, margins irregularly and shallowly dentate, bases rounded or sometimes truncate; petioles $2/5$ to as long as blades. Flowers solitary in leaf axils. Flowering calyces 2.5-4 mm long, densely glandular

pubescent, lobes 1-2 mm long; corollas yellow, without darker maculations in throat, 5-7 mm long; anthers yellow, 1-1.5 mm long, filaments less than 1/2 as wide as anthers; pedicels 4-7 mm long. Fruiting calyces green, 10-angled, 1-2 cm long, 1-2 cm in diam., densely glandular-hairy, convex or only slightly concave at bases, pedicels 5-10 mm long. Summer. Rocky ledges; mts. Ark. {Mo and Okla}.

9. *P. lagascae* Roemer and Schultes. Annuals, 1-9 dm tall, from a slender taproot; stems erect or decumbent, branching frequently, lower branches trailing along the ground, sparsely covered with simple jointed hairs up to 2-4 mm long. Leaf blades ovate, 2-4 cm long, 0.5-1 cm wide, sparsely pubescent to glabrate, apices acute, margins entire to irregularly dentate or sinuate, bases rounded to somewhat cordate; petioles 1/4 to as long as blades. Flowers solitary in leaf axils. Flowering calyces 3-4 mm long, glabrous to sparsely pubescent with simple, jointed hairs, lobes 1-1.5 mm long; corollas yellow, tinged dark purple-brown in throat or without maculations, 5-7 mm long; anthers tinged blue or violet, 1-1.5 mm long, filaments as wide as anthers; pedicels 2-5 mm long. Fruiting calyces green, 10-angled, 1-2 cm long, 1-2 cm in diam., convex at bases, pedicels 3-6 mm long. All year. Introduced from Neotropics; only collections seen were weeds of sugarcane fields in La.

10. *P. angulata* L. Annual, 1-20 dm tall, from a large taproot; stems erect, branching frequently, glabrous or sparsely hairy with simple, jointed hairs, 0.5 mm or less long. Leaf blades elliptic to linear-lanceolate, 3-10 (14) cm long, 1-8 cm wide, glabrous to sparsely

hairy, apices acuminate, margins deeply and coarsely irregularly dentate with acuminate teeth, bases rounded to attenuate; petioles $1/3$ - $2/3$ blade length. Flowers solitary in leaf axils. Flowering calyces 3-5 mm long, sparsely hairy or glabrous except for margins, lobes 1-3 mm long; corollas yellow without throat maculations or only rarely tinged purple, 6-10 mm long; anthers blue or blue-tinged, 1-3 mm long, filaments less than $1/2$ as wide as anthers; pedicels 7-17 (22) mm long. Fruiting calyces green, 10-angled, 2-4 cm long, 1.5-2.5 cm in diam., only slightly concave at bases, pedicels 15-30 mm long. (n=12, 24) All year. Disturbed habitats; chiefly cp. and pied. SE except Del, Md, and WVa. {Tex, Okla, Mo, and Ill}. Incl. P. angulata var. pendula Rydb.--F. Some plants in s. Fla. have linear to lanceolate, sinuate leaf blades and small corollas (4-5 mm long).

11. *P. pumila* Nuttall. Perennial, 1.5-4 dm tall, from a stout deeply-buried rhizome; stems erect, branching infrequently at upper nodes, branches ascending, hispid, hairs jointed, 0.5-2 mm long, simple and/or 2-3 branched. Leaf blades ovate to ovate-lanceolate, 3-8 (10) cm long, 2-5 cm wide, hispid, apices acute, margins entire to undulate, rarely sinuate-dentate, bases attenuate; petioles $1/10$ - $2/5$ blade length. Flowers solitary in leaf axils. Flowering calyces 6-12 mm long, hispid, lobes (2.5) 3-5 (6) mm long; corollas yellow with pale brown or green in throat without distinct maculations, 11-16 mm long; anthers yellow, 2-3 mm long, filaments as wide as the anthers; pedicels (7) 14-30 mm long. Fruiting calyces green, 10-angled, 2.5-3.5 (4) cm long, 1.5-3 cm in diam., concave at bases, pedicels 25-55 mm long. (n=12) Early spring through fall. Disturbed habitats; cp. and mts. Ark and La. {Tex, Okla,

and Mo}.

12. *P. mollis* Nuttall. Perennial, 1.5-5 dm tall, from a stout, deeply-buried rhizome, often also with slender, shallow rhizomes; stems erect, branching occasionally, branches ascending, tomentose with branched hairs, less than 1 mm long, obscuring plant surface, occasionally also with 2-4 mm long, jointed, branched or unbranched hairs at lower nodes. Leaf blades ovate, 2.5-7 cm long, 1.5-6 (7) cm wide, tomentose, apices acute, margins coarsely dentate or irregular to almost entire, bases truncate; petioles 1/3-4/5 blade length. Flowers solitary in leaf axils. Flowering calyces 6-10 (12) mm long, tomentose with short, branched hairs, occasionally also with long, jointed hairs, lobes 2.5-5.5 mm long; corollas yellow with pale brown to dark brown indistinct maculations in throat, 9.5-15 (17) mm long; anthers yellow or rarely with a blue or purple tinge, 3-4 mm long, filaments about 1/2 as wide as the anthers; pedicels 10-25 (35) mm long. Fruiting calyces green, 10-angled, 2.5-4 (-5) cm long, 1.5-3 cm in diam., concave at bases, pedicels 20-40 (52) mm long. (n=12) Late winter through fall. Disturbed habitats; cp. and mts. Ark and La. {Tex and Okla}.

13. *P. cinerascens* (Dunal) Hitchc. Perennial, 0.5-5 dm tall, from a large, deeply-buried rhizome; stems and lower branches erect or spreading along the ground and ascending, sparsely to moderately densely pubescent with branched hairs, 1 mm or less long. Leaf blades ovate to spatulate, 1.5-8 (9) cm long, 1-6 (8) cm wide, sparsely to moderately densely pubescent, apices acute or obtuse, margins coarsely dentate, sinuate, or undulate or entire, bases truncate to attenuate; petioles

1/5 to as long as blades. Flowers solitary in leaf axils. Flowering calyces (3.5) 5-9 mm long, pubescent, lobes 1.5-4 mm long; corollas yellow with dark purple-black, distinct maculations in throat, these sometimes bisected by yellow main veins of the corolla, (8) 9-16 mm long; anthers yellow or rarely with a purple tinge, 2-5 mm long, filaments 1/2 to as wide as the anthers; pedicels 10-33 mm long. Fruiting calyces green, 10-angled, 1.5-3.5 (4.5) cm long, 1-3.5 cm in diam., concave at bases, pedicels 15-60 mm long. (n=12) All year in areas without frost.

Leaf bases truncate to slightly attenuate, margins dentate, sinuate, or entire; corolla limbs reflexed when fully

open..... 13a. var. cinerascens

Leaf bases attenuate, margins entire; corolla limbs not reflexed when

fully open..... 13b. var. spathulaefolia

13a. var. cinerascens. Fruiting calyces 1.5-3 cm long, 1-2 cm in diam., pedicels 15-60 mm long. Disturbed habitats; chiefly cp. Ark and La. {Tex and Okla}. Occasionally introduced elsewhere in SE.

13b. var. spathulaefolia (Torr.) Sullivan. Fruiting calyces 2.5-4.5 cm long, (1.5) 2-3.5 cm in diam., pedicels 25-60 mm long. Gulf dunes and disturbed habitats near the coast in sand; GC. La. {Tex}.

14. P. walteri Nuttall. Perennial, 0.5-4 dm tall, from a stout and usually deeply-buried rhizome; stems and lower branches erect or spreading along the ground and ascending, sparsely to moderately densely

covered with branched hairs, 1 mm or less long. Leaf blades elliptic or ovate to ovate-lanceolate, (2.5) 3.5-11 (13) cm long, 1.5-5 (7) cm wide, sparsely to moderately densely pubescent, apices obtuse or acute, margins entire or rarely undulate, bases rounded to attenuate; petioles 1/6-1/2 blade length. Flowers solitary in leaf axils. Flowering calyces (5) 6-9 (11) mm long, pubescent, lobes 1.5-4 (5) mm long; corollas yellow with dark to pale brown, ocher, or green distinct or indistinct maculations in throat, the main veins of the corolla lobes sometimes purple or red, (9) 11-15 (18) mm long; anthers yellow or infrequently tinged purple, 2.5-3.5 mm long, filaments as wide as anthers; pedicels 9-25 (35) mm long. Fruiting calyces green, 10-angled, 2-3.5 cm long, 1.5-2.5 cm in diam., concave at base, pedicels 15-35 (45) mm long. (n=12) All year. Beach dunes and disturbed areas in sand; cp. Ala, Fla, Ga, Miss, NC, SC, and Va. P. viscosa L.--G, S; P. elliotii Kunze, in part--S; P. maritima M.A. Curtis--F; P. viscosa var. maritima (M.A. Curtis) Rydb.--G; P. viscosa ssp. maritima (M.A. Curtis) Waterfall--R.

This species hybridizes with P. angustifolia in Florida, and populations can be found in that state that exhibit intermediate characteristics.

15. P. pruinosa L. Annual, 3-6 dm tall, from a large taproot; stems erect, branching frequently, the branches spreading, villous with simple, jointed hairs, 0.5-1 mm long. Leaf blades broadly ovate, 3.5-11 cm long, 2.5-10 cm wide, gray-green, drying orange or with orange patches, pubescence of short, simple hairs (0.5 mm long) intermixed with

stalked and sessile glands (much shorter than 0.5 mm long), apices acute, margins coarsely dentate, bases broadly rounded to slightly cordate; petioles $2/5-4/5$ blade length. Flowers solitary in leaf axils. Flowering calyces 3-5 mm long, short-pubescent, lobes 1.5-2.5 mm long; corollas yellow with large dark purple-brown distinct maculations in throat, 5-8 mm long; anthers blue or tinged blue, 1-2 mm long, filaments $1/2$ as wide as the anthers; pedicels 4-6 mm long. Fruiting calyces green, sharply 5-angled, 2-3.5 cm long, 1.5-2.5 cm in diam., concave at bases, pedicels 5-12 mm long. (n=12) Summer through fall. Disturbed habitats; chiefly mts. and pied. NC, SC, Tenn, and WVa. {Pa}. Frequently cultivated and escaped elsewhere in SE. P. pubescens var. grisea Waterfall--G, R.

16. *P. peruviana* L. Perennial, 3-10 dm tall, from a large, deeply-buried rhizome; stems erect, branching frequently, villous with simple, jointed hairs up to 1 mm long. Leaf blades ovate, 5-10 cm long, 4-7 cm wide, villous, apices acuminate, margins entire or with few irregular teeth, bases truncate to cordate; petioles $1/5-1/2$ blade length. Flowers solitary in leaf axils. Flowering calyces 8-9 mm long, villous, lobes 4-5 mm long; corollas yellow with dark blue-tinged maculations in throat, 10-14 mm long; anthers blue or tinged blue, 3.5-4 mm long, filaments $1/2$ as wide as the anthers; pedicel 6-8 mm long. Fruiting calyces green, 10-angled, 3-4 cm long, 2.5-3 cm in diam., concave at bases, pedicels 13-15 mm long. (n=12, 24) Native of South America. Escaped from cultivation and established in waste places.

17. *P. heterophylla* Nees. Perennial, 1.5-10 dm tall, from a

stout, deeply-buried rhizome; stems erect to decumbent, branching frequently, branches spreading along the ground and ascending, villous with simple, jointed, divergent hairs 1-2 mm long, often with shorter glandular hairs. Leaf blades broadly ovate to suborbicular, (3) 4-11 (13) cm long, 3-9 (10) cm wide, villous and often glandular, apices acute, margins deeply and irregularly dentate to almost entire, bases truncate to slightly cordate; petioles 1/3-2/3 blade length. Flowers solitary in leaf axils. Flowering calyces 6-12 mm long, villous and often glandular, lobes 3-6 mm long; corollas yellow with large purple-brown indistinct maculations in throat, 10-17 mm long; anthers yellow or infrequently tinged blue, 2.5-4.5 mm long, filaments as wide as anthers and usually conspicuously clavate at apex; pedicels 9-15 (20) mm long. Fruiting calyces green, 10-angled, 2.5-4 cm long, 1.5-3 cm in diam., concave at bases, pedicels 20-30 mm long. (n=12) Late spring through early fall. Disturbed habitats, often in shade; all prov. SE {ALL}. Incl. *P. ambigua* (Gray) Britton; *P. nyctaginea* Dunal; *P. sinuata* Rydb.--S; *P. heterophylla* var. *ambigua* (Gray) Rydb.; *P. heterophylla* var. *clavipes* Fern.; *P. heterophylla* var. *nyctaginea* (Dunal) Rydb.--F

18. *P. arenicola* Kearney. Perennial, 0.5-3 dm tall, from a slender, deeply-buried rhizome, typically also with slender, shallow rhizomes; stems erect, few-branched, glabrous to villous with simple, antrorse hairs, less than 1 mm long, sometimes interspersed with 1-2 mm long, simple, jointed hairs, sometimes viscid. Leaf blades ovate to suborbicular, 1.5-6 (6.5) cm long, 1-5 cm wide, villous with short glandular and long jointed hairs or rarely almost glabrous, apices acute, margins entire to coarsely and irregularly dentate with few

teeth, bases truncate to cordate; petioles $1/4$ - $2/3$ blade length. Flowers solitary in leaf axils. Flowering calyces 6-12 mm long, villous, lobes 2-5 mm long; corollas yellow with pale reddish-brown, indistinct maculations in throat or without maculations, 10-17 mm long; anthers yellow, 2.5-4 mm long, filaments $1/2$ to as wide as anthers; pedicels (8) 11-17 (45) mm long. Fruiting calyces green, 10-angled, 2-3.5 cm long, 1.5-2.5 cm in diam., slightly concave at bases, pedicels 15-30 (35) mm long. (n=12) All year. Disturbed habitats, in sand; cp. Ala, Fla, and Ga. Incl. P. ciliosa Rydb.--S

19. P. lanceolata Michaux. Perennial, 2-4 dm tall, from a large, stout rhizome; stems decumbent, branching infrequently, sparsely pubescent with simple, antrorse hairs, 0.5 mm or less long, or simple, jointed, divergent hairs, 1-1.5 mm long. Leaf blades oblanceolate, 4-10 cm long, 2-6 cm wide, pubescent with short, appressed, and long, divergent hairs, apices acute, margins entire to slightly undulate, bases attenuate; petioles $1/25$ - $1/3$ blade length. Flowers solitary in leaf axils. Flowering calyces 6-10 mm long, hispid with long jointed hairs, lobes 2-5 mm long; corollas yellow with pale brown indistinct maculations in throat, 10-15 mm long; anthers yellow, 2.5-3.5 mm long, filaments $1/2$ as wide as anthers; pedicels 10-20 mm long. Fruiting calyces green, 10-angled, 2-3.5 cm long, 1.5-3 cm in diam., scarcely concave at bases, pedicels 10-30 mm long. (n=12) Spring through summer. Sandhills; cp. and pied. Ga (cp.), NC, and SC (cp.). P. lanceolata Michx., in part--S, F. Southeastern U.S. plants ascribed to this species were considered by Waterfall to be hybrids between P. heterophylla X P. virginiana, but have since been shown by Hinton to be

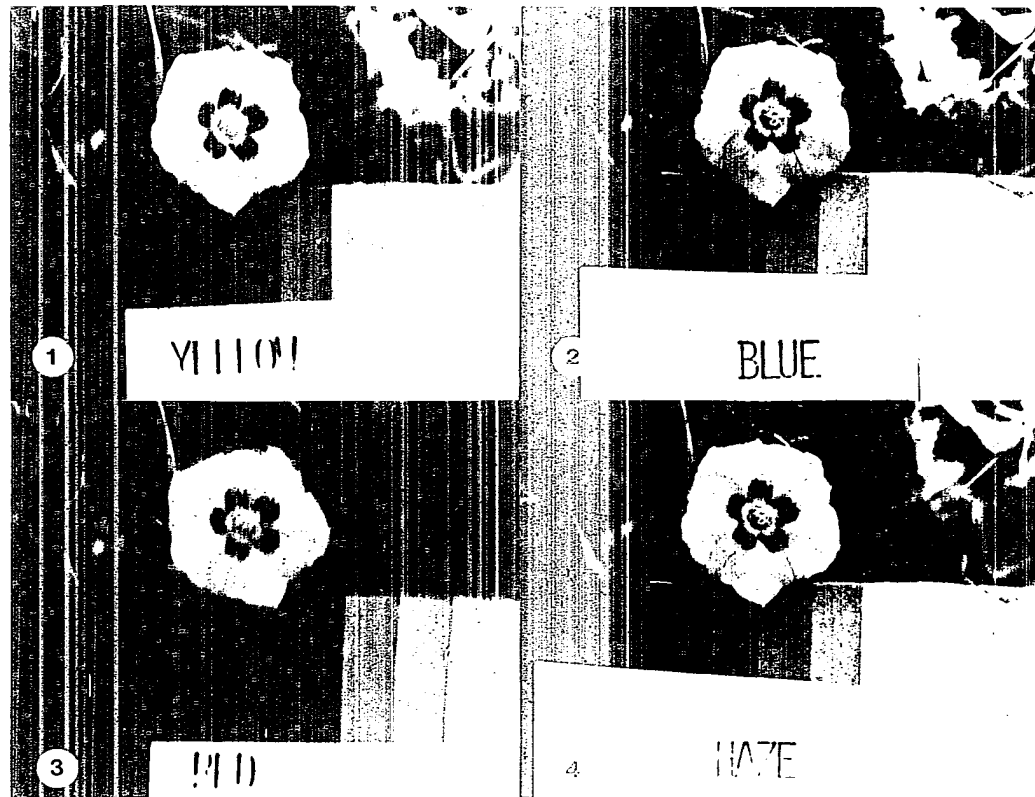
members of a distinct species.

20. *P. virginiana* Miller. Perennial, 1-4 dm tall, from a stout rhizome; erect, branching infrequently, hispid with 1 mm long, jointed, simple, divergent hairs and 0.5 mm or less long, retrorse hairs. Leaf blades ovate to broadly lanceolate, 2-7 (9) cm long, 1-5 (6) cm wide, pubescent with long, jointed and short, retrorse hairs, apices acute, margins coarsely to shallowly dentate or entire, bases truncate to obtuse; petioles 1/5-1/2 blade length. Flowers solitary in leaf axils. Flowering calyces 6-12 (14) mm long, hispid with long jointed and short retrorse hairs, lobes 3-6 mm long; corollas yellow with dark purple-brown indistinct maculation in throat, 10-17 (20) mm long; anthers yellow or sometimes tinged blue, 2-3 mm long, filaments as wide as or wider than anthers; pedicels (6) 9-19 (27) mm long. Fruiting calyces green, 10-angled, 2-4 cm long, 1.5-3 cm in diam., concave at bases, pedicels 15-30 mm long. (n=12) Spring through fall. Disturbed habitats; all. prov. SE. {ALL}. Incl. *P. intermedia* Rydb.; *P. monticola* Mohr.; *P. rigida* Pollard & Ball--S.

APPENDIX A

Color-filter photography of Physalis flowers.

Figure 1. A flower of P. viscosa var. cinerascens photographed with color filters. Gray scale chips in each figure reflect (from left to right) 12.5, 25, 50, 75, 88, 94, 97, 98, 99, 99.5, and 100%. 1. Yellow, Vivitar 8 K 2. 2. Blue, Vivitar 80 C. 3. Red, Soligor 25 AIR. 4. Visible light, Tiffen UV haze.



APPENDIX B

Insect collections.

Table 1. Insects collected on Physalis species. Insect specimens deposited in the collections at the USDA Bee Biology & Systematics Lab in Logan, Utah. Voucher collections of plants in OKL.

P. angustifolia. FLORIDA. Bay Co.: 1 Colletes, June 1982; Lee Co.: 1 unidentified to genus, June 1982.

P. cinerascens. LOUISIANA. Webster Par.: 3 Colletes, June 1982.

P. heterophylla. ARKANSAS. Benton Co.: 1 Augochlorella, 1 Colletes, 8 Perdita, July 1983.

P. longifolia. IOWA. Davis Co.: 1 Colletes, August 1983; Iowa Co.: 2 Augochlorella, 5 Colletes, August 1983; Mahaska Co.: 1 Augochlorella, 2 Colletes, 7 Perdita, August 1983. MISSOURI. Randolph Co.: 1 Augochlorella, August 1983. NEBRASKA. Custer Co.: 1 Colletes, 1 Perdita, August 1983.

P. pubescens. ARKANSAS. Benton Co.: 1 Augochlorella, 1 Perdita, July 1983.

APPENDIX C

Phenetic analysis.

Table 1. Voucher collections of Physalis species other than the members of the P. viscosa complex used in phenetic analyses.

-
- P. angulata. ALABAMA: Marengo Co., Moore 322-69 (NCU), OTU-85.
 ARKANSAS: Saline Co., Demaree 37274 (NCU), OTU-84. GEORGIA:
 Mitchell Co., Bozeman 5134 (NCU), OTU-87. LOUISIANA: Lafayette Par.,
Thieret 10292 (NCU), OTU-86. NORTH CAROLINA: Brunswick Co., Godfrey
10083 (NCU), OTU-83.
- P. heterophylla. IOWA: Story Co., Jeffs s.n. (OKL), OTU-76.
 KENTUCKY: Warren Co., Nicely 3290 (MEM), OTU-74 MISSISSIPPI:
 Claiborne Co., Darwin and Sundell 1582 (NLU), OTU-73. OKLAHOMA: Bryan
 Co., Riggs and Moore s.n. (OKL), OTU-72. SOUTH CAROLINA: Cherokee Co.,
Ahles 26982 (NCU), OTU-75.
- P. pubescens. ARKANSAS: Marion Co., Demaree 30902 (OKL), OTU-91.
 FLORIDA: Levy Co., Cooley et al. 7175 (USF), OTU-90. MISSOURI: Stone
 Co., Redfearn 26924 (NCU), OTU-89. TEXAS: Robertson Co., Sullivan and
Starbuck 1227, (OKL), OTU-92. VIRGINIA: Mecklenberg Co., Ahles and
James 61928 (NCU), OTU-88.
- P. pumila. KANSAS: Douglas Co., Horr E77 (OKL), OTU-97. MISSOURI:
 Jackson Co., Bush 12452A (OKL), OTU-96. OKLAHOMA: Comanche Co., Seneca
s.n. (OKL), OTU-93; Mc Curtain Co., Sears 3588 (OKL), OTU-95; Muskogee

Co., Bebb 4281 (OKL), OTU-98; Pontotoc Co., Robbins 3114 (OKL), OTU-94.

P. virginiana. ARKANSAS: Benton Co., Demaree 6643 (OKL), OTU-80.

MISSISSIPPI: Lafayette Co., Chandler s.n. (OKL), OTU-81. NORTH

DAKOTA: Cass Co., Stevens 261 (OKL), OTU-82. OKLAHOMA: Latimer Co.,

Hammon 68 (OKL), OTU-79. SOUTH CAROLINA: Pickens Co., Ahles 14303

(NCU), OTU-78.

Fig. 1. Phenogram generated using the General Similarity Coefficient of Gower and the UPGMA algorithm for OTUs representing the members of the Physalis viscosa complex and representative OTUs of other species in the genus. The cophenetic correlation coefficient = 0.855.

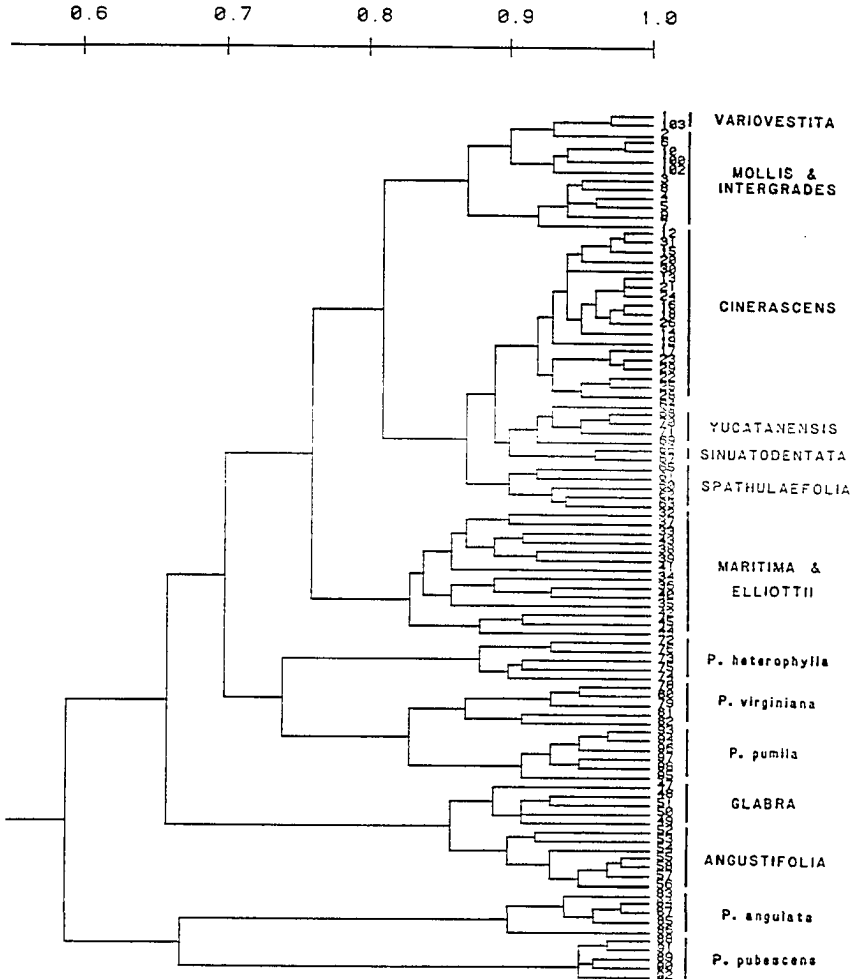
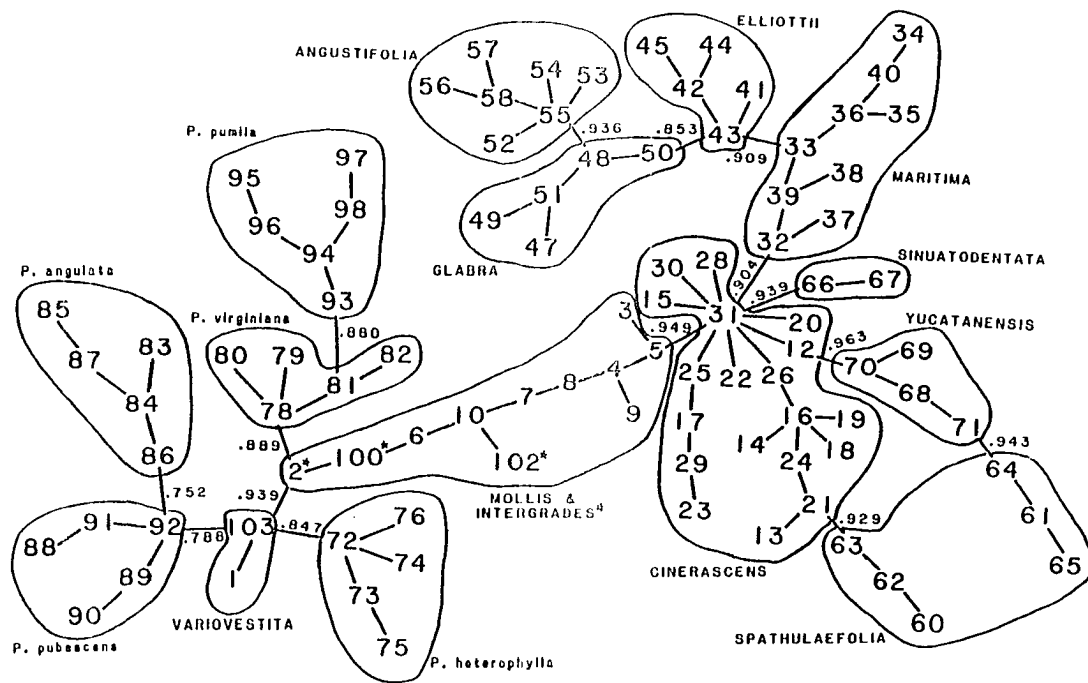


Fig. 2. Minimum spanning network generated using the General Similarity Coefficient of Gower and the UPGMA algorithm. Similarity values are listed on the minimum spanning network for closest OTUs between two groups of taxa.



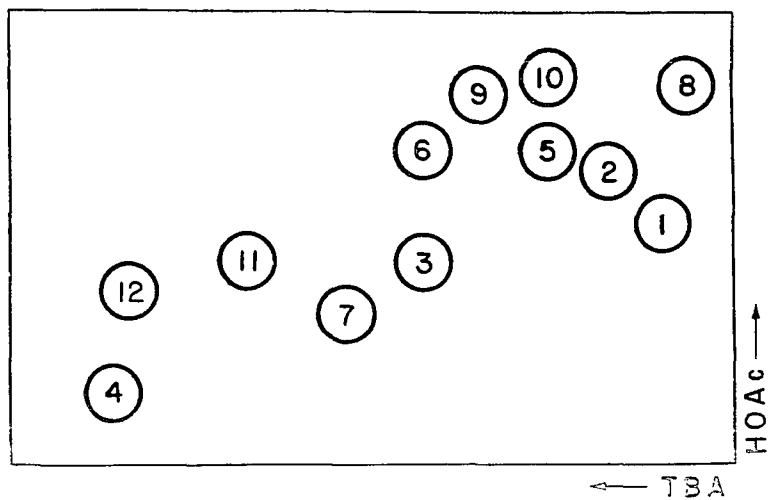
APPENDIX D

Flavonoid analysis.

Table 1. Voucher collections of Physalis species other than the members of the P. viscosa complex used in flavonoid analyses.

-
- P. angulata. MEXICO: Tabasco, Sullivan and Laue 1239 (OKL).
P. hederæfolia. TEXAS: Val Verde Co., Sullivan and Laue 1300, (OKL).
P. heterophylla. OKLAHOMA: Caddo Co., Sullivan et al. 1119, (OKL).
P. ixocarpa. NEW YORK: Tompkins Co., Hoisington 340 (OKL).
P. (Quincula) lobata. OKLAHOMA: Cimarron Co., Sullivan et al. 1102, (OKL).
P. longifolia. OKLAHOMA: Cleveland Co., Sullivan 1037, (OKL).
P. pubescens. TEXAS: Robertson Co., Sullivan and Starbuck 1227, (OKL).
P. pumila. OKLAHOMA: Cleveland Co., Sullivan 1036, (OKL).
-

Figure 1. Flavonoid profiles for species of Physalis other than the members of the P. viscosa complex. Compounds are as follows: (1) myricetin 3-O-glucoarabinoside; (2) kaempferol 7-galactosyl-3-O-arabinoside; (3) myricetin 3-O-glycoside; (4) not identified; (5) not identified; (6) quercetin 3-O-glucoside or -diglucoside; (7), (8), (9), (10), (11), (12) not identified.



Species	1	2	3	4	5	6	7	8	9	10	11	12
<i>P. angulata</i>			⊗									
<i>P. hederaefolia</i>	⊗					⊗					⊗	⊗
<i>P. heterophylla</i>			⊗				⊗					
<i>P. ixocarpa</i>								⊗	⊗	⊗		
<i>P. lobata</i>	⊗	⊗										
<i>P. longifolia</i>			⊗									
<i>P. pubescens</i>			⊗									
<i>P. pumila</i>			⊗				⊗					

APPENDIX E

Pollen analysis vouchers.

Table 1. Specimens followed by an "S" were examined with SEM.

Physalis angulata. OKLAHOMA. Muskogee Co., Little 188 (OKL). TEXAS. McLennan Co., York 46232 (OKL). MEXICO. Tabasco, Sullivan and Laue 1239 (OKL), S.

Physalis angustifolia. ALABAMA. Baldwin Co., Sullivan and Laue 1164 (OKL). FLORIDA. Charlotte Co., Sullivan and Laue 1191 (OKL); Collier Co., Sullivan and Laue 1208 (OKL), S; Franklin Co., Sullivan and Laue 1169 (OKL), S; Lee Co., Sullivan and Laue 1198 (OKL). MISSISSIPPI. Hancock Co., Sullivan and Laue 1152 (OKL).

Physalis carpenteri. FLORIDA. Jackson Co., Mitchell and Ramsey 1100 (USF), S; Liberty Co., Godfrey 71493 (FSU); Wakulla Co., Godfrey 64173 (FSU).

Physalis cinerascens var. cinerascens. LOUISIANA. Webster Par., Sullivan and Laue 1131 (OKL). OKLAHOMA. Cleveland Co., Sullivan 1044 (OKL), S; Woods Co., Sullivan et al. 1068 (OKL). MEXICO. Veracruz, Sullivan and Laue 1234, S, 1235 (OKL); Roe et al. 1290 (MEXU); Yucatan, Sullivan and Laue 1249, 1256, S, 1257 (OKL).

Physalis cinerascens var. spathulaefolia. LOUISIANA. Cameron Par. Sullivan and Laue 1007 (OKL). TEXAS. Aransas Co., Sullivan et al. 1126 (OKL), S; Nueces Co., Sullivan et al. 1127 (OKL).

Physalis heterophylla. COLORADO. Larimer Co., Eskeu 259 (OKL). IOWA.

Story Co., Jefferis s. n. (OKL-77106). OKLAHOMA. Cleveland Co., Sullivan 1040 (OKL), S.

Physalis ixocarpa. NEW YORK. Thompsons Co., Hoisington 340 (OKL), S. VIRGINIA. Arlington Co., Green and Schmitt 3689 (USF). WASHINGTON, D. C. Steele s. n. (DUKE-22985).

Physalis longifolia. OKLAHOMA. Woods Co., Sullivan et al. 1062 (OKL), S.

Physalis mollis var. mollis. LOUISIANA. Caddo Par., Sullivan and Laue 1128 (OKL). OKLAHOMA. Marshall Co., Sullivan and Laue 1045 (OKL). TEXAS. DeWitt Co., Sullivan et al. 1123 (OKL); Harris Co., Sullivan and Laue 1000 (OKL), S; Robertson Co., Sullivan and Starbuck 1226 (OKL), S.

Physalis mollis var. variovestita. TEXAS. Aransas Co., Sullivan et al. 1125 (OKL), S.

Physalis pumila. MISSOURI. Jackson Co., Bush 12452a (OKL). OKLAHOMA. Muskogee Co., Bebb 3902 (OKL); Oklahoma Co., Waterfall 1949 (OKL), S.

Physalis pubescens. TEXAS. Robertson Co., Sullivan and Starbuck 1227 (OKL), S.

Physalis walteri. FLORIDA. Broward Co., Sullivan and Laue 1211 (OKL); Dade Co., Sullivan and Laue 1209, S, 1210 (OKL); Dixie Co., Sullivan and Laue 1010 (OKL); Glades Co., Sullivan and Laue 1203 (OKL), S; Nassau Co., Sullivan and Laue 1183 (OKL); Pasco Co., Sullivan and Laue 1032 (OKL). NORTH CAROLINA. Pender Co., Sullivan and Laue 1221 (OKL).

Quincula lobata. OKLAHOMA. Cimarron Co., Sullivan, et al. 1102 (OKL); Comanche Co., Seneca s. n. (OKL-116429); Woods Co., Sullivan, et al. 1067 (OKL), S.
