



## Systematics of the *Physalis viscosa* Complex (Solanaceae)

Janet R. Sullivan

*Systematic Botany*, Vol. 10, No. 4 (Oct. - Dec., 1985), 426-444.

Stable URL:

<http://links.jstor.org/sici?sici=0363-6445%28198510%2F12%2910%3A4%3C426%3ASOTPVC%3E2.0.CO%3B2-X>

*Systematic Botany* is currently published by American Society of Plant Taxonomists.

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/aspt.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

---

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

## Systematics of the *Physalis viscosa* Complex (Solanaceae)

JANET R. SULLIVAN

Department of Botany and Microbiology, University of Oklahoma,  
Norman, Oklahoma 73019

**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 species from two of the 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 Yucatán. *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 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. Indistinct species boundaries in peninsular Florida suggest that hybridization may have occurred between these two species in this region. However, the two are distinct in the remainder of their ranges.

*Physalis* L. is an American genus of about 90 species, characterized by pendent flowers and by an inflated fruiting calyx that encloses the berry. Rydberg (1896) recognized three sections in the genus: *Physalis* (as *Euphysalis*), *Microphysalis*, and *Megista*. Within section *Physalis* he recognized nine 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* (Small 1933; pp. 1107-1112) Rydberg, without comment, changed the names of two of his nine series: *Leptophyllae* became *Carpenterianae*, and *Stellatae* became *Viscosae*. The latter names are superfluous and, therefore, 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 six species in 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” such that distinguishing between them is often difficult.

Menzel (1951, 1957) experimentally demonstrated that genetic isolation barriers are in-

complete 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 widespread hybrid swarm (1957).

In 1958 Waterfall revised the North American species of *Physalis* based on macromorphological features. He did not recognize subgenera and sections in *Physalis*, 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 *Physalis* series *Stellatae* except for *P. angustifolia* and *P. fendleri* were combined into one large, polymorphic species, *P. viscosa*. Waterfall recognized three subspecies of *P. viscosa* and their inclusive varieties and forms: 1) subsp. *viscosa*; 2) subsp. *mollis* var. *mollis* and var. *cinerascens*; and 3) subsp. *maritima* var. *maritima* f. *maritima*, var. *maritima* f. *latifolia*, var. *elliottii* f. *elliottii*, var. *elliottii* f. *glabra*, and var. *spathulaefolia* (table 1). *Physalis fuscomaculata* was treated as a synonym of 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* subsp. *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* (table 1). 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* subsp. *maritima* (excluding var. *maritima* f. *latifolia*, which is defined on the basis of a continuous character—leaf size), and subsp. *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 1981–1982 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 according to Waterfall's (1958, 1967) classification (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* subsp. *mollis* will be referred to as INTERGRADE(S). A summary of Waterfall's classification of the *P. viscosa* complex is given in table 1.

*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 2). Fourteen vegetative and 19 floral characters were scored or measured from each sheet, and from these measurements 8 ratios were calculated (table 3). Different combinations of trichome types were coded as separate characters so that the variability in this feature could be reflected in the analysis. For example, CINERASCENS has only dendritic hairs (ABB for characters 22, 23, and 25, respectively), while VARIOVESTITA and some populations of MOLLIS are intermixed dendritic and simple (ABA). This manner of character coding may have resulted in weighting of the dendritic trichomes, characteristic of the *P. viscosa* complex, when OTUs without dendritic trichomes (non-*P. viscosa* complex) were included in the analysis. The basic data matrix may be obtained from the author. The characters chosen have been used traditionally to distinguish taxa in *Physalis*, or were determined in a preliminary analysis to exhibit intertaxon variation.

TABLE 1. Comparison of classifications.

Waterfall 1958, 1967	Sullivan 1984
<i>P. angustifolia</i>	<i>P. angustifolia</i> (incl. <i>P. viscosa</i> var. <i>elliottii</i> f. <i>glabra</i> )
<i>P. variovestita</i>	<i>P. mollis</i>
<i>P. viscosa</i>	var. <i>mollis</i>
subsp. <i>mollis</i>	var. <i>variovestita</i>
var. <i>mollis</i>	<i>P. cinerascens</i>
var. <i>cinerascens</i>	var. <i>cinerascens</i>
var. <i>sinuatodentata</i>	(incl. <i>P. viscosa</i> var. <i>sinuatodentata</i> and
var. <i>yucatanensis</i>	var. <i>yucatanensis</i> )
	var. <i>spathulaefolia</i>
subsp. <i>maritima</i>	<i>P. walteri</i>
var. <i>maritima</i>	(incl. <i>P. viscosa</i> var. <i>maritima</i> and var. <i>elliottii</i>
forma <i>maritima</i>	f. <i>elliottii</i> )
forma <i>latifolia</i>	
var. <i>elliottii</i>	
forma <i>elliottii</i>	
forma <i>glabra</i>	
var. <i>spathulaefolia</i>	
subsp. <i>viscosa</i>	<i>P. viscosa</i> (restricted to South America and not treated in this study)

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 also were 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 employed to determine the correlation between each character used in the phenetic analysis and the re-

vised classification scheme. Characters were considered to be significant in delimiting a group of OTUs if that character had a high correlation with the classification ( $\text{Distance (I, J)} = 0.3$  or lower) or if the character had a moderately high correlation ( $\text{D (I, J)} = 0.3\text{--}0.69$ ) and a skewed character state distribution among OTUs.

*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. Separate spot patterns were obtained from 2–10 populations of each taxon in the complex (table 2). Flavonoids were identified using ultraviolet spectroscopy, acid and enzyme hydrolyses, and chromatography (Mabry et al. 1970).

*Experimental analysis.* The plants used for breeding studies were collected from 53 populations in the United States and Mexico (table 2), and grown from either seeds or rhizomes in the greenhouse at the University of Oklahoma. The plants represented ten taxa in the *P. viscosa* complex and four 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 VARIOVESTITA, MOLLIS, SPATHULAEFOLIA, CINERASCENS, and each other. Reciprocal crosses involving other species were: CINERASCENS  $\times$  *P. hederiaefolia*; CINERASCENS  $\times$  *P. heterophylla*; CINERASCENS  $\times$  *P. longifolia*; MOLLIS  $\times$  *P. hederiaefolia*; MOLLIS  $\times$  *P. heterophylla*; VARIOVESTITA  $\times$  *P. hederiaefolia*; VARIOVESTITA  $\times$  *P. heterophylla*; and all taxa of the *P. viscosa* complex with *P. pumila*. For each pair of taxa at least ten crosses were performed and, for most pairs, 20 or more crosses were accomplished. In addition, at least ten reciprocal crosses were made between populations within each taxon to estimate intrataxon compatibility. To test for self-compatibility, ten 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

TABLE 2. Voucher collections used in analyses. A = population used for phenetic analyses, followed by OTU number; B = population used for breeding studies; C = population used for chemical studies.

*P. angustifolia*. U.S.A. **Alabama**: Baldwin Co., *Sullivan & Laue* 1164 (OKL), A-58, B, C. **Florida**: Bay Co., *Sullivan & Laue* 1167 (OKL), A-52; Franklin Co., *Sullivan & Laue* 1169 (OKL), A-53, C; *Sullivan & Laue* 1170 (OKL), B; Gulf Co., *Sullivan & Laue* 1168 (OKL), A-57, C; Walton Co., *Sullivan & Laue* 1166 (OKL), A-54, C. **Mississippi**: Hancock Co., *Sullivan & Laue* 1152 (OKL), A-56, B, C; Jackson Co., *Sullivan & Laue* 1162 (OKL), A-55, B, C.

*P. hederacea*. U.S.A. **Texas**: Val Verde Co., *Sullivan & Laue* 1300 (OKL), B.

*P. heterophylla*. U.S.A. **Oklahoma**: Cleveland Co., *Sullivan* 1040 (OKL), B.

*P. longifolia*. U.S.A. **Oklahoma**: Cleveland Co., *Sullivan* 1037 (OKL), B.

*P. pumila*. U.S.A. **Oklahoma**: Cleveland Co., *Sullivan* 1036 (OKL), B.

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

*P. variovestita* "intergrades". U.S.A. **Texas**: De Witt Co., *Sullivan et al.* 1123 (OKL), B, C; Ellis Co., *Shinners* 14158 (SMU), A-100; Harris Co., *Sullivan & Laue* 1000 (OKL), B, C; *Sullivan & 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*. U.S.A. **Louisiana**: Bossier Par., *Sullivan & Laue* 1130 (OKL), C; Webster Par., *Sullivan & 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; Bee Co., *Correll* 29304 (LL), A-28; Dallas Co., *Lundell & Lundell* 9232 (MICH), A-29; Hardeman Co., *Correll & Johnston* 16835 (LL), C; Jeff Davis Co., *Sullivan & Laue* 1277 (OKL), B; Lubbock Co., *Derbow* 8 (OKLA), C; Robertson Co., *Sullivan & 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 & 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. **Hildago**: *Pringle* 13130 (MICH), A-30. **Queretaro**: *Barkley et al.* 748 (MICH), A-14.

*P. viscosa* var. *elliottii* f. *elliottii*. U.S.A. **Florida**:

TABLE 2. Continued.

Broward Co., *Sullivan & Laue* 1211 (OKL), B, C; Dade Co., *Sullivan & Laue* 1209 (OKL), B, C; *Sullivan & Laue* 1210 (OKL), A-41, B, C; Hendry Co., *Sullivan & Laue* 1199 (OKL), A-44, B; Hernando Co., *Sullivan & Laue* 1205 (OKL), A-43, B, C; *Sullivan & Laue* 1208 (OKL), B, C; Pasco Co., *Sullivan & Laue* 1032 (OKL), A-42, B; Sarasota Co., *Sullivan & Laue* 1188 (OKL), A-45, C.

*P. viscosa* var. *elliottii* f. *glabra*. U.S.A. **Florida**: Charlotte Co., *Sullivan & Laue* 1190, 1191 (OKL), A-49 & 50, B, C; Collier Co., *Sullivan & Laue* 1207 (OKL), A-48, B, C; Lee Co., *Sullivan & Laue* 1198 (OKL), A-47; Manatee Co., *Sullivan & Laue* 1186 (OKL), B, C; Pinellas Co., *Sullivan & Laue* 1185 (OKL), A-51, C.

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

*P. viscosa* var. *mollis*. U.S.A. **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 & Laue* 1128 (OKL), B, C; *Sullivan & Laue* 1129 (OKL), A-4, B, C. **Oklahoma**: Marshall Co., *Sullivan & Laue* 1039 (OKL), A-5, B; *Sullivan & Laue* 1045 (OKL), A-5, B, C; Pawnee Co., *Waterfall* 12360 (OKLA), A-8, C. **Texas**: Hildago Co., *Lundell & Lundell* 9837 (OKLA), C; Robertson Co., *Sullivan & Starbuck* 1226 (OKL), A-3, B, C; Tarrant Co., *Lundell & Lundell* 12894 (TEX), A-9.

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

*P. viscosa* var. *spathulaefolia*. U.S.A. **Louisiana**: Cameron Par., *Sullivan & Laue* 1006 (OKL), C; *Sullivan & 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 & Laue* 1003 (OKL), A-64, B, C; Kenedy Co., *Lundell & 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. **Yucatán**: *Sullivan & Laue* 1249, 1256 (OKL), A-69 & 71, C; *Sullivan & Laue* 1257, 1258 (OKL), A-70 & 68, B, C.

TABLE 3. Characters used in phenetic analyses of the *Physalis viscosa* complex. <sup>a</sup> Measured a representative elongated filament and its attached anther. <sup>b</sup> This trichome feature was coded as separate characters so that different combinations of trichome types could be reflected for the members of the *P. viscosa* complex.

---

1. Leaf length from apex to base of blade on shortest side (mm). 2. Ratio of leaf length to width (at widest point). 3. Ratio of leaf length to petiole length. 4. Flowering calyx length (mm). 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 (mm). 9. Ratio of fruiting pedicel length to fruiting calyx length. 10. Ratio of fruiting calyx length to width. 11. Length of corolla at maturity (mm). 12. Corolla width at mouth (mm). 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.<sup>a</sup> 17. Total anther length (mm). 18. Anther color blue or tinged blue/purple or tinged purple/yellow. 19. Leaf margin dentate/entire. 20. Leaf base attenuate/truncate/deltoid/cordate. 21. Leaf apex acuminate/acute/obtusely/acute and obtuse. 22. Trichomes predominantly dendritic/not.<sup>b</sup> 23. Trichomes predominantly forked/not.<sup>b</sup> 24. Trichomes predominantly glandular/not. 25. Trichomes predominantly simple/not.<sup>b</sup> 26. Trichomes multicellular/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 (mm). 33. Filaments tinged blue/tinged purple/yellow.

---

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 ELIOTTII; 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 figure 2. Only those characters considered to have a significant correlation with the classification (see Materials and Methods) are discussed below. The complete listing of correlation values obtained from the character analysis may be obtained from the author.

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 spathulate leaves with entire margins, while the other members of this cluster have ovate to orbicular 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-SPATHULAE-

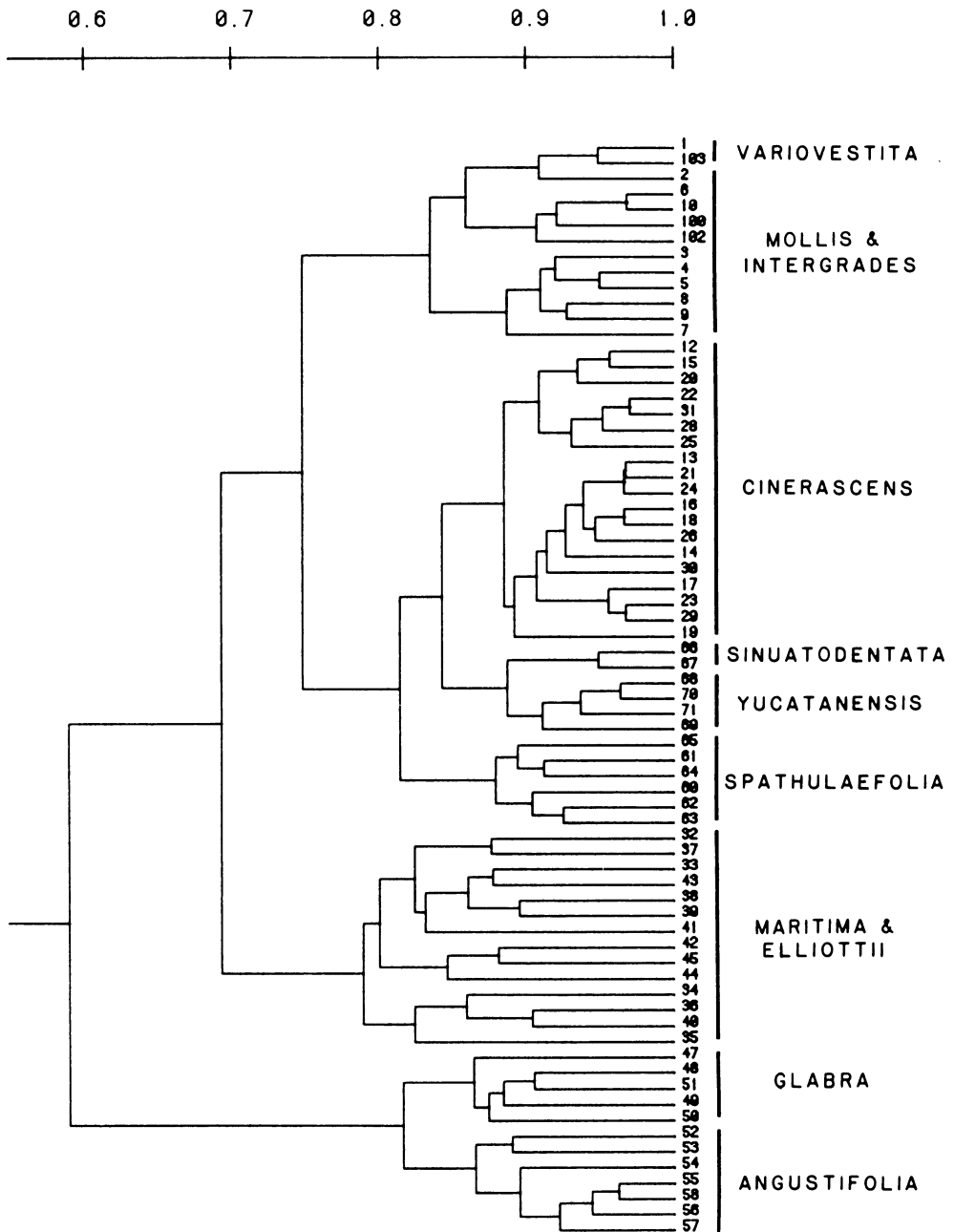


FIG. 1. Phenogram generated using the General Similarity Coefficient of Gower and the UPGMA algorithm for OTUs representing the members of the *Physalis viscosa* complex. The cophenetic correlation coefficient = 0.847.

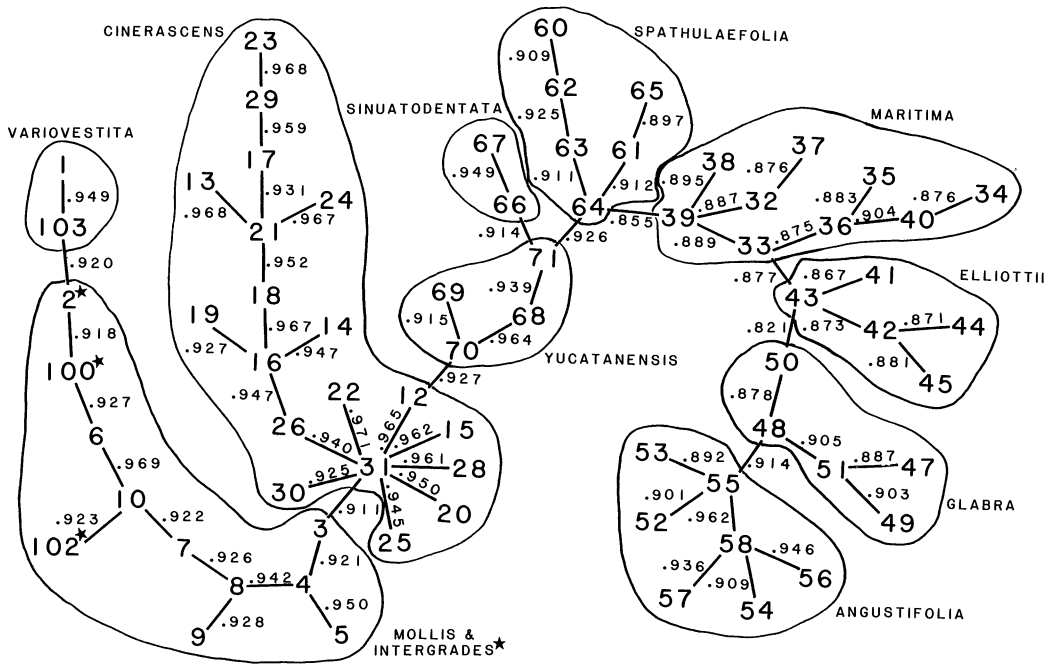


FIG. 2. Minimum spanning network generated using the General Similarity Coefficient of Gower and the UPGMA algorithm for OTUs representing the members of the *Physalis viscosa* complex. The similarity value between each connected pair of OTUs is given on the minimum spanning network.

FOLIA - SINUATODENTATA - YUCATANENSIS cluster then joins the VARIOVESTITA-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 VARIOVESTITA are indistinct in outline and range from very pale brown to dark brown in MOLLIS, while those of CINERASCENS, SPATHULAEFOLIA, SINUATODENTATA, and YUCATANENSIS are sharply distinct in outline, and are uniformly dark purple-black.

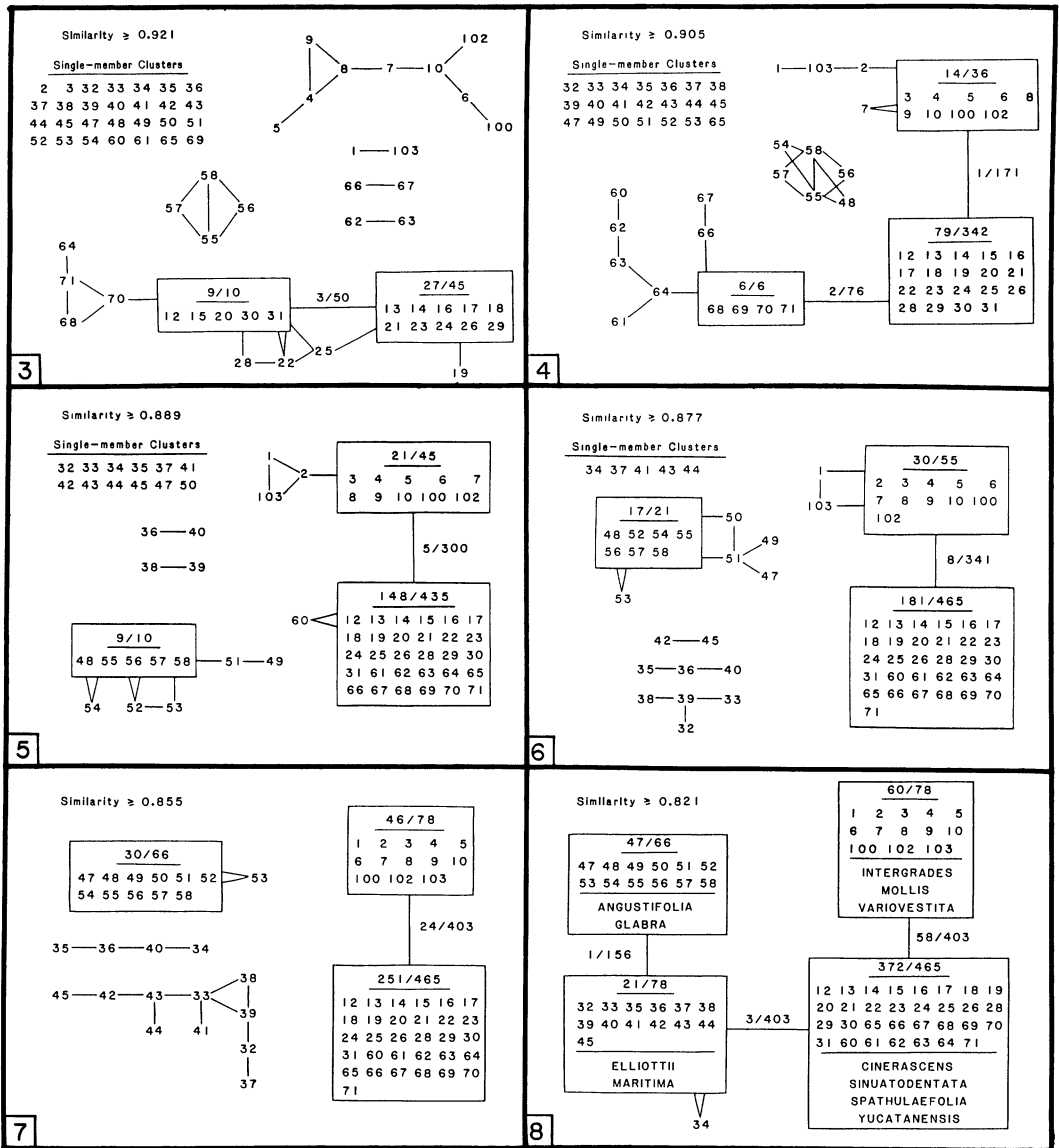
MARITIMA and ELLIOTTII are intermixed in the third cluster, so that no clear line can be drawn between the two taxa. On the minimum spanning network, however, they appear as distinct groups of OTUs linked at a similarity level of 0.877. The character analysis shows only slight differences between these two taxa, pri-

marily 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 calyxes 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 pattern of OTUs can be





FIGS. 3-8. 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.

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 connected also with the SINUATODENTATA and SPATHULAEFOLIA OTUs. The MOLLIS and INTERGRADE OTUs are highly interconnected, and are linked to the larger CINERASCENS cluster. Also, the VARIOVESTITA 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 (figs. 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 that 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 two 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 figure 9. All of the compounds identified to date are kaempferol, myricetin, and quercetin 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 that exhibits a compound unique to the complex, spot 4.

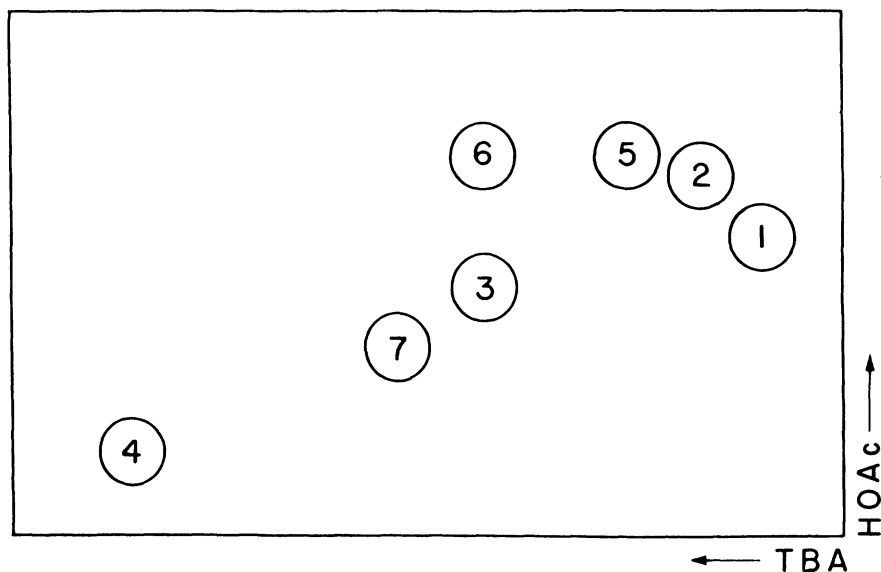
*Breeding studies.* Most of the taxa within the *Physalis viscosa* complex were intercompatible

at low levels with at least 10% of the crossing attempts resulting in the production of viable seed (fig. 10). Reciprocal crosses gave approximately the same percent cross-compatibility. The exception was SPATHULAEFOLIA × CINERASCENS, which produced seed only when SPATHULAEFOLIA served as the pollen parent. 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 × 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 stainability (typically lower than 65%;  $\bar{x}$  = 60.75; range = 21–93;  $N$  = 13) than intragroup hybrids (typically 85% or greater).

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. The only hybrid in this group that flowered had a high percentage of stainable pollen (88%). Crosses between VARIOVESTITA (uniformly glandular) and either MOLLIS or the INTERGRADES (not glandular) resulted in plants with intermixed glandular and non-glandular hairs. The pollen stainability in these hybrids varied from 8% to 100% ( $\bar{x}$  = 41.62;  $N$  = 4).

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 stainability in these hybrids is high ( $\bar{x}$  = 94.29; range = 92–97;  $N$  = 2). All but one of the back crosses with SPATHULAEFOLIA



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. 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.

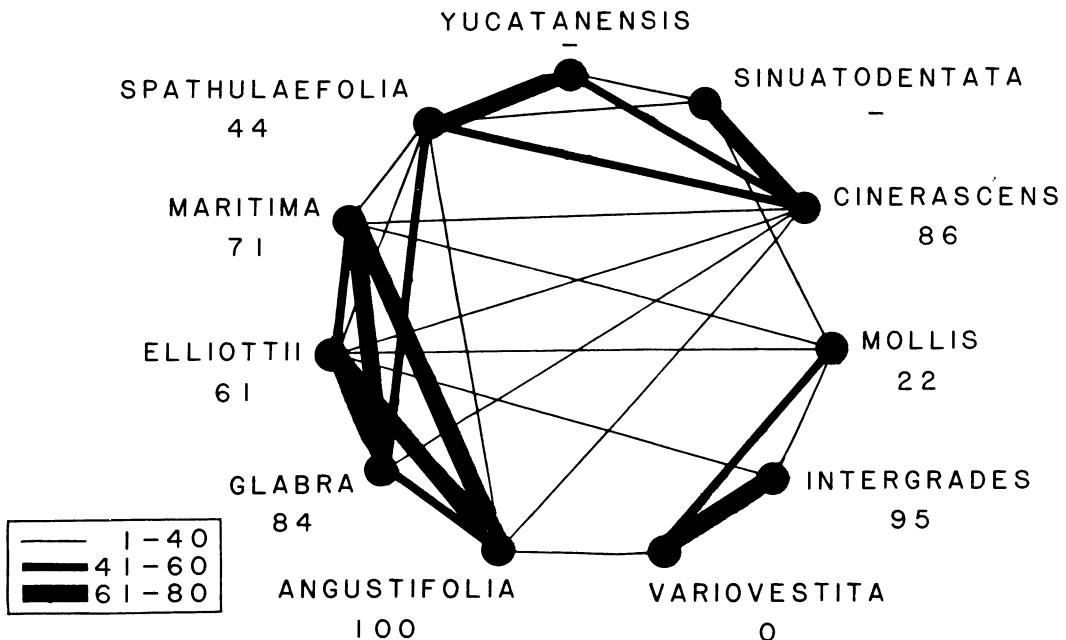


FIG. 10. Hybridization among the members of the *Physalis viscosa* complex. Lines between taxa represent the percent of attempted crosses that produced viable seed. Numbers below each taxon indicate percent of intra-taxon crosses that produced viable seed.

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 that varied in morphology to include all of the variation observed in leaf size and shape, density and distribution of trichomes, and corolla throat color of 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 MA-

RITIMA-like. The majority of these hybrids was uniformly pubescent, although the density of trichomes varied from sparse to dense. Only one of the glabrous  $\times$  pubescent hybrids (ANGUSTIFOLIA  $\times$  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 stainability ( $\bar{x} = 93.29$ ; range = 61-100;  $N = 55$ ). 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 ( $N = 73$ ), 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 cases (1 MOLLIS  $\times$  *P. hederifolia* and 9 CINERASCENS  $\times$  *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* ( $N = 125$ ) were abortive; however, half of the crosses between *P. pumila* and MOLLIS (total  $N = 10$ ) resulted

in fruits with a small number of viable seeds. The only hybrid from this group that flowered had high pollen stainability (97%). All of the *P. pumila* × MOLLIS hybrids 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 nearly entire margins that produced ovate leaves with regularly 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, according to Waterfall's criteria, they could not be distinguished from populations of MARITIMA. 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, VARIOVESTITA, and the IN-

TERGRADES; 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, VARIOVESTITA, 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 VARIOVESTITA 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 VARIOVESTITA is an abundantly glandular plant. Waterfall postulated that VARIOVESTITA 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 VARIOVESTITA also is 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, VARIOVESTITA, 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, VARIOVESTITA, and the INTERGRADES are all intercompatible. Hybrids between VARIOVESTITA 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 VAR-

IOVESTITA and the INTERGRADES) is under environmental control. Plants that 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 VARIOVESTITA 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 VARIOVESTITA 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. VARIOVESTITA is similar to *Physalis mollis* Nuttall in morphology and flavonoid chemistry, and the two produce fertile hybrids. However, VARIOVESTITA is morphologically recognizable because of the combination of abundant glandular hairs that are short-dendritic and long articulated, and the dark, indistinct spots in the corolla throat. VARIOVESTITA 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, VARIOVESTITA 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* apparently had 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 County 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 VARIOVESTITA 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 times 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 (1967) criterion of trichome morphology, which he admitted was weak. In fact, the "fasciculate" hairs that 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) A. S. Hitchcock.

Unexpectedly, all analyses indicate a close relationship between *P. cinerascens* and *SPATHULAEFOLIA*. Previous authors have allied the latter taxon with *MARITIMA* and *ELLIOTTII* (Rydberg 1896; Menzel 1951; Waterfall 1958), presumably based on leaf shape and habitat. However, *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. *SPATHULAEFOLIA* falls within the range of morphological and chemical variability of *P. cinerascens* and is cross-compatible at a level of approximately 50%. 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. In addition, the two taxa were interpreted differently by Rydberg (1896) and Waterfall (1958), the authorities on the genus. Rydberg distinguished between these two taxa on the basis of trichome density (i.e., *MARITIMA* as densely pu-

bescent and ELLIOTTII as the more sparsely pubescent forms), whereas Waterfall considered leaf shape to be the important distinguishing characteristic (i.e., MARITIMA with leaves that are less than two times longer than broad and ELLIOTTII with leaves much longer than broad). Each of these taxa encompasses a great deal of variation by either interpretation. 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 MARITIMA-type leaf morphology in the greenhouse. All populations that 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 that has priority over *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 the 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 observed 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 stainability, and a range of morphological variability that 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 the pollinators 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 is probably due to their emphasis on vegetative characteristics in delimiting species in *Physalis*. Thus, such otherwise distinct taxa as *P. mollis* and *P. cinerascens* were included in the same species (Rydberg 1896) or in the same subspecies (Waterfall 1958), and *SPATHULAEFOLIA* was included 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 other features overlooked. Such was not the case when the results from several lines of evidence were used to evaluate relationships among the members of the complex.

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 1984a). Although all the non-*P. viscosa* complex species link 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 patterns congruent with other data (Sullivan 1984a). 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 five of the eight 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 the 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 branched or stellate hairs. Hairs 1 mm or less long, in one species 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 five 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 white-tomentose, the tomentum obscuring the plant surface on younger leaves; pubescence of branched hairs, less than 1 mm long, intermixed in some populations with multicellular, branched or unbranched hairs 2–4 mm long.
- 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.
- Anthers equal to or shorter than the mature filaments; fruiting pedicels mostly as long as the fruiting calyces . . . . . 3. *P. walteri*
- Anthers 1.5 times or more longer than the mature filaments; fruiting pedicels mostly 1.5 times 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. subsp. *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 (holotype: NY!; isotypes: CM!, F!, GH!, NY!, MO! (accession no. 2876291, not no. 2876288), WIS!, not at PENN!).

Plants from deeply-buried rhizomes, often 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, the leaf margins sparsely pubescent with short, branched hairs 1 mm or less long. Leaves sessile. 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. Flowering calyces 5-9(-10) mm long with lobes (1-)1.5-3.5 mm long, glabrous except for the margins, or occasionally sparsely covered with short, branched hairs 1 mm or less long. Corollas (8-)11-15(-16) mm long, with ocher to green indistinct maculations in throat, with main vein of corolla lobes typically purple or red. Anthers 2.5-3.5 mm long; filaments  $\frac{1}{2}$  to as wide as anthers. Flowering pedicels 11-24(-32) mm long. Fruiting calyces (1.5-)2-3(-4) cm long, 1.5-2.5 cm in diam, typically orange at maturity; 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 that exhibit intermediate morphology.

*Representative specimens.* U.S.A. **Alabama:** Baldwin Co., Mobile Point, Fort Morgan, 15 Jun 1982, *Sullivan & Laue* 1164 (OKL); Mobile Co., Dauphin Island, 15 Jul 1969, *Kral* 35596 (NCU). **Florida:** Bay Co., public beach W of Laguna Beach, 16 Jun 1982, *Sullivan & Laue* 1167 (OKL); Dade Co., Big Bend, W 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 W of Casino, 14 Jun 1964, *McDaniel* 4735 (FSU); Franklin Co., dunes near W end of Dog Island, 23 Nov 1963, *Ward* 3817 (FLAS); Gulf Co., Port St. Joe, 22 May 1955, *Menzel & Menzel* 55-5 (FSU); Lee Co., Sanibel Island, 16 Oct 1969, *Radford & Leonard* 45694 (NCU); Monroe Co., Big Pine Key, 8 Feb 1977, *Correll & Popenoe* 48088 (NCU); Okaloosa Co., Santa Rosa Island, just over bridge from Destin, 31 Jul 1964, *McDaniel* 4969 (FSU); Wakulla Co., Mashles Island, 24 Apr 1955, *Godfrey* 53210 (DUKE, FLAS, FSU, SMU, USF); Walton Co., dunes  $\frac{1}{2}$  mi from Bay Co. line, 27 Apr 1967, *Ward* 6202 (FLAS). **Louisiana:** Jefferson Par., N end of Grand Isle, 16 Apr 1981, *Vincent & 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 & Channel* 53711 (DUKE, FSU, NCU).

## 2. PHYSALIS MOLLIS Nuttall.

Plants from stout, deeply-buried rhizomes, often 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 multicellular, branched or unbranched hairs 2-4 mm long. 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  $\frac{1}{3}$ - $\frac{4}{5}$  as long as leaf blade. Flowering calyces 6-10(-12) mm long with lobes 2.5-5.5 mm long, tomentose with branched hairs 1 mm or less long, occasionally also with jointed hairs 2-4 mm long. Corollas 9.5-15(-17) mm long, with pale to dark brown or purple-black, indistinct maculations in throat. Anthers 3-4 mm long; filaments about  $\frac{1}{2}$  as wide as the anthers. Flowering pedicels 10-25(-35) mm long. Fruiting calyces 2.5-4(-5) cm long, 1.5-3(-3.5) cm in diam, green; pedicels 20-40(-52) mm long ( $N = 12$ ). Flowers March to October.

2a. *PHYSALIS MOLLIS* Nuttall var. *MOLLIS*, Trans. Amer. Philos. Soc. 5(n.s.):194. 1837.—TYPE: Arkansas, *Nuttall s.n.* (holotype: not known; isotypes: NY!, PH!).—*P. viscosa* L. subsp. *mollis* (Nutt.) Waterfall var. *mollis*, *Rhodora* 60:135-136. 1958.

Plants with non-glandular, branched hairs 1 mm or less long, some also with multicellular, branched or unbranched, non-glandular hairs 2-4 mm long. 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 half of Texas, southwestern Arkansas, and western Louisiana.

*Representative specimens.* U.S.A. **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 S of Ida, 27 Aug 1966, *Thieret* 24493 (DUKE). **Oklahoma:** Bryan Co., U.S. Denison Dam Reservation, N 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 S of Argyle, 23 May 1946, *Whitehouse* 15780 (MICH, SMU); Harris Co., Hwy 59 about 0.4 mi S of bridge over San Jacinto River, 3 Jul 1956, *Traverse* 158 (SMU); Llano Co., 5 mi E 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 et al. 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 W 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, Apr 1947, *E. Whitehouse 18179* (holotype: MICH!).—*P. variovestita* Waterfall, *Rhodora* 60:137. 1958.

Plants with glandular, branched hairs 1 mm or less long, and with multicellular, branched and unbranched, glandular hairs 2–4 mm long. 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.* U.S.A. **Texas:** Brooks Co., Hwy 285, 14 mi from Falfurrias, 10 Nov 1962, *Solis 51* (TEX); Hildago Co., McAllen, 10 Aug 1937, *Cameron 269* (TEX); Kenedy Co., SE part of Saltillo Pasture, Norias Division 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 & Lundell 10730* (LL); Willacy Co., Yturria Station on Hwy 96, 19 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. elliotii* Kunze, *Linnaea* 20:33. 1847.—TYPE: Florida, ad ostium fluv. St. Marks, Jun 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.* (holotype: GH!; probable isotype: NY!).—*P. viscosa* L. var. *maritima* (Curtis) Rydberg, Mem. Torr. Bot. Club 4:357. 1896.—*P. viscosa* L. subsp. *maritima* (M. A. Curtis) Waterfall var. *maritima* forma *maritima*, *Rhodora* 60:134. 1958.—*P. viscosa* L. subsp. *maritima* (M. A. Curtis) Waterfall forma *latifolia* Waterfall, *Rhodora* 60:134. 1958.—TYPE: Florida, north part of Jupiter Island, Apr 1923, *Small, Mosier, and DeWinkler 10892* (holotype: NY!; isotypes: FLAS!, GH!, TENN!).—*P. viscosa* L. subsp. *maritima* (M. A. Curtis) Waterfall

var. *elliotii* (Kunze) Waterfall forma *elliotii*, *Rhodora* 60:134–135. 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  $\frac{1}{6}$ – $\frac{1}{2}$  as long as leaf blade. Flowering calyces (5–)6–9(–11) mm long with lobes 1.5–4(–5) mm long, densely to sparsely covered with branched hairs 1 mm or less long. Corollas (9–)11–15(–18) mm long, with dark to pale brown, ocher, or green distinct or indistinct maculations in throat, with 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 2–3.5(–4) cm long, 1.5–2.5 cm in diam, green. 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 that exhibit intermediate morphology such as broadly ovate, glabrous leaves.

*Representative specimens.* U.S.A. **Florida:** Brevard Co., Indiatlantic Beach, 8 Jun 1957, *Menzel & Menzel 57-189* (FSU); Dixie Co., flatwoods, 1 mi N of Horseshoe, 14 May 1942, *West & Arnold s.n.* (FLAS); Glades Co., rt. 721, S of the Brighton Indian Reservation, 22 Jun 1982, *Sullivan & Laue 1203* (OKL); Lake Co., pine-lands E of Eustis, 7 May 1918, *Small 8644* (NY); Nassau Co., Amelia Beach dunes, 18 Jun 1982, *Sullivan & Laue 1183* (OKL); Palm Beach Co., Ocean Ridge, Boynton Beach, 11 Jun 1957, *Menzel & Menzel 57-222* (FSU); St. Johns Co., sandy banks bordering salt marshes, San Sebastian River, St. Augustine, 2 May 1964, *Godfrey 63963* (NCU); St. Lucie Co., dunes of Atlantic Ocean near Fort Pierce, 29 Jul 1962, *Lakela 25240* (GH); Volusia Co., behind dunes along Atlantic Coast south of New Smyrna Beach, 14 Oct 1976, *Duncan & 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 et al. 1885* (DUKE, GA); Carteret Co., Shackleford Bank along the N 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 N 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 N of New Topsail Beach, 1 Jul 1950, *Fox & Boyce 3741* (GH, NY, UARK). **South Carolina:** Beaufort Co., sand dunes, Hunting Island State Park, 3 Apr 1956, *Ahles & 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) A. S. 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  $\frac{1}{2}$  to as long as leaf blades. Flowering calyces (3.5–)5–9(–11) mm long with lobes 1.5–4.5 mm long, sparsely to densely covered with branched hairs 1 mm or less long. Corollas (7–)9–16 mm long; with dark purple-black, distinct maculations in throat, these sometimes bisected by yellow main veins of the corolla. Anthers 2–5 mm long; filaments  $\frac{1}{2}$  to as wide as the anthers. Flowering pedicels 10–33 mm long. Fruiting calyces 1.5–3.5(–4.5) cm long, 1–3.5 cm in diam, green. Pedicels 15–60 mm long ( $N = 12$ ). Flowering all year in areas without frost.

4a. *PHYSALIS CINERASCENS* (Dunal) A. S. Hitchcock var. *CINERASCENS*, Spring Flora of Manhattan 32. 1894.—LECTOTYPE: circa Matamoros urbem, Apr 1831, *Berlandier 2316* (GH!; isolectotypes: F!, NY!).—*P. viscosa* L. var. *sinuatodentata* Schlecht., *Linnaea* 19:309. 1846.—TYPE: Mexico, C. Ehrenberg s.n. (holotype: HAL!).—*P. pennsylvanica* L. var. *cincerascens* Dunal, DC Prodr. 13(1): 435. 1852.—*P. curassavica* L. var. *sinuatodentata* (Schlecht.) Dunal, DC Prodr. 13(1): 438. 1852.—*P. mollis* Nutt. var. *cincerascens* (Dun-

al) Gray, Proc. Amer. Acad. Arts and Sci. 10:66. 1875.—*P. mollis* Nutt. var. *parvifolia* Rydb., Mem. Torrey Bot. Club 4:355. 1896.—*P. saltillensis* Fernald, Proc. Amer. Acad. Arts and Sci. 35:568–569. 1900.—TYPE: Mexico, Coahuila, plants collected at Saltillo and vicinity, 1898, E. Palmer 332 (holotype: US!; isotype: MICH!).—*P. viscosa* L. subsp. *mollis* (Nutt.) Waterfall var. *cincerascens* (Dunal) Waterfall, Rhodora 60: 136. 1958.—*P. viscosa* L. var. *yucatanensis* Waterfall, Rhodora 69:104. 1967.—TYPE: Mexico, Yucatan, Chichankanab, G. F. Gummer 1798 (holotype: 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 limb reflexed when fully open. Filaments approximately  $\frac{1}{2}$  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 south to Yucatán. Also found sporadically in the southeastern U.S.

REPRESENTATIVE SPECIMENS. U.S.A. **Louisiana:** Webster Par., Minden, 12 Jun 1982, *Sullivan & Laue 1131* (OKL). **New Mexico:** Lea Co., 21 mi W 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 N 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 S of Beeville, 16 Apr 1964, *Correll 29304* (LL, SMU, UC); Brewster Co., Pena Blanca, ca. 5 mi S of Marathon, 24 Jul 1952, *Warnock 10881* (LL, SMU); Childress Co., Hwy 256, ca. 8 mi E of Memphis, 13 Jun 1973, *Higgins 7247* (NY); Garza Co., 3 mi S of Post, 22 Jun 1963, *Rowell & Waterfall 8650* (OKLA); Harris Co., 15 mi SW of Houston, 17 Apr 1965, *Rios & Cavazos 112* (LL); Maverick Co., near Elm Creek, 30 mi NE of Eagle Pass, 2 May 1954, *Tharp et al. 3604* (DUKE, SMU, TEX); Palo Pinto Co., N city limits of Straw, 6 May 1951, *Shimmers 13211* (SMU); Rains Co., 3.8 mi SE of Point, 27 Jul 1953, *Shimmers 15578* (OKLA, SMU); Starr Co., below Falcon Dam, 17 Mar 1962, *McCart et al. 7870* (OKLA, TEX); Tom Green Co., W of San Angelo, 7 Jun 1969, *Grimes 276* (SMU, TENN); Travis Co., Pecan Springs, 17 May 1940, *Lundell & Lundell 8946* (LL, MICH).

MEXICO. **Coahuila:** ca. 20 mi E of Saltillo, open sandy slopes, 27 May 1951, *McVaugh 12319* (MICH). **Hidalgo:** valley near Dublin, 2 Jul 1901, *Pringle 9416*

(MICH, NY). **Yucatán:** near station, Dztas, Chichen Itza, 29 Jun 1932, *Steere 1647* (MICH).

4b. ***Physalis cinerascens*** (Dunal) A. S. Hitchcock var. ***spathulaefolia*** (Torr.) Sullivan, comb. nov.—TYPE: Texas, Rio Bravo, Seabeach, March 1853, *Schott 30* (holotype: NY!; isotype: FI).—*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. Acad. Arts and Sci. 10: 67. 1874.—*P. viscosa* L. subsp. *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 limb not reflexed when fully open. Filaments ½ 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.* U.S.A. **Louisiana:** Cameron Par., about 2 mi E of Holly Beach, 7 Jul 1962, *Thieret 8816* (NCU). **Texas:** Aransas Co., Rockport, 25 Apr 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 & Lundell 10703* (MICH, SMU, TEX); Chambers Co., old railroad 6 mi N of High Island, Winnie, 31 Oct 1970, *Demaree 63225* (OKLA); Galveston Co., Texas City, 6 Apr 1950, *Turner 1798* (SMU); Jefferson Co., 13 mi W 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 & 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 W of Redfish Bay on S edge of Norias erg, 9 Mar 1954, *Johnston 54169* (TEX).

**MEXICO. Tamaulipas:** vicinity of LaBarra, 8 km E of Tampico, 1–8 Feb 1910, *Palmer 298* (NY).

**ACKNOWLEDGMENTS.** This work is part of a doctoral dissertation submitted to the Graduate College of the University of Oklahoma in Norman. I thank J. R. Estes, C. P. Daghlain, R. B. Phillips, G. D. Schnell, J. J. Skvarla, and G. J. Goodman for their constructive comments and discussion during the preparation of this manuscript, D. A. Young for his instruction in flavonoid analysis, and T. M. Laue for his companionship and assistance in the field. I also thank M. Y.

Menzel for sharing her knowledge of and ideas on *Physalis*. I am especially grateful to J. R. Estes for the past four years of guidance, encouragement, and friendship. This work was supported in part by grants from the National Science Foundation (Dissertation Improvement Grant DEB 8205749 to J. R. Estes and the author) and Sigma Xi, and by funds from the George H. M. Lawrence Award from the Hunt Institute for Botanical Documentation.

#### LITERATURE CITED

- DUNCAN, T. and G. F. ESTABROOK. 1976. An operational method for evaluating classifications. *Syst. Bot.* 1:373–382.
- ESTABROOK, G. F. 1966. A mathematical model in graph theory for biological classification. *J. Theor. Biol.* 12:297–310.
- GOWER, J. C. 1971. A general coefficient of similarity and some of its properties. *Biometrics* 27:857–871.
- HAUSER, J. P. and J. H. MORRISON. 1964. The cytochemical reduction of nitro blue tetrazolium as an index of pollen viability. *Amer. J. Bot.* 51:748–752.
- MABRY, T. J., K. R. MARKHAM, and M. B. THOMAS. 1970. *The systematic identification of flavonoids*. New York: Springer-Verlag.
- MENZEL, M. Y. 1951. The cytotaxonomy and genetics of *Physalis*. *Proc. Amer. Philos. Soc.* 95:132–183.
- . 1957. Cytotaxonomic studies of Florida coastal species of *Physalis*. *Yearb. Amer. Philos. Soc.* 1957:262–266.
- . 1960. What is *Physalis variovestita*? *Rhodora* 62:117–121.
- ROHLF, F. J., J. KISHPAUGH, and D. KIRK. 1979. Numerical taxonomic system of multivariate statistical programs. Stony Brook: Tech. Rep. State Univ. New York.
- RYDBERG, P. A. 1896. The North American species of *Physalis* and related genera. *Mem. Torrey Bot. Club* 4:297–374.
- SMALL, J. K. 1933. *Manual of the southeastern flora*. New York: published by the author.
- SNEATH, P. H. A. and R. R. SOKAL. 1973. *Numerical taxonomy*. San Francisco: W. H. Freeman and Co.
- SULLIVAN, J. R. 1984a. Systematic studies in *Physalis* (Solanaceae). Ph.D. dissertation, Univ. Oklahoma, Norman.
- . 1984b. Pollination biology of *Physalis viscosa* var. *cinerascens* (Solanaceae). *Amer. J. Bot.* 71:815–820.
- WATERFALL, U. T. 1958. A taxonomic study of the genus *Physalis* in North America north of Mexico. *Rhodora* 60:107–114, 128–142.
- . 1967. *Physalis* in Mexico, Central America, and the West Indies. *Rhodora* 69:82–120.