GEOGRAPHIC VARIATION AND TAXONOMY OF NORTH AMERICAN SPECIES OF MIRABILIS, SECTION OXYBAPHOIDES (NYCTAGINACEAE)

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ABSTRACT

A revision of Mirabilis section Oxybaphoides, Nyctaginaceae, in western North America is presented. Mirabilis oligantha (Standl.) J.F. Macbride, M. oxybaphoides (A. Gray) A. Gray, and M. tenuiloba S. Wats. remain as traditionally classified. Mirabilis bigelovii A. Gray, M. californica A. Gray ex Torr., M. laevis (Benth.) Curran, and M. retorsa Heller are combined as a single species, M. laevis, and recognized as varieties, i.e., M. laevis var. villosa (Kellogg) Spellenb. (comb. nov.), M. laevis var. crassifolia (Choisy) Spellenb. (comb. nov.), M. laevis var. laevis, and M. laevis var. retorsa (Heller) Jepson, respectively. Distribution maps are presented for each species, those for the varieties within the M. laevis complex also indicating geographic distribution of characters. The inspection of these maps was of importance in making taxonomic decisions. Lists of important collections are provided. Chromosome numbers are reported for the first time for M. laevis var. villosa (2n = 30), M. laevis var. retorsa (2n = 31–33) and M. oxybaphoides (2n = 30).

RESUMEN

Se presenta una revisión de Mirabilis, sección Oxybaphoides, Nyctaginaceae, en el oeste de Norteamérica. Mirabilis oligantha (Standl.) J.F. Macbride, M. oxybaphoides (A. Gray) A. Gray, y M. tenuiloba S. Wats. permanecen tal como se clasificaban tradicionalmente. Mirabilis bigelovii A. Gray, M. californica A. Gray ex Torr., M. laevis (Benth.) Curran, y M. retorsa Heller se combinan como una única especie. M. laevis, y reconocidas como variedades, i.e., M. laevis var. villosa (Kellogg) Spellenb. (comb. nov.), M. laevis var. crassifolia (Choisy) Spellenb. (comb. nov.), M. laevis var. laevis, y M. laevis var. retorsa (Heller) Jepson, respectivamente. Se presentan mapas de distribución de todas las especies, y de las variedades en el complejo M. laevis indicando también la distribución geográfica de los caracteres. El estudio de estos mapas fue muy importante para tomar las decisiones taxonómicas. Se ofrecen listas de colecciones importantes. Se citan por primera vez números cromosómicos de M. laevis var. villosa (2n = 30), M. laevis var. retorsa (2n = 31–33) y M. oxybaphoides (2n = 30).

INTRODUCTION

Mirabilis L. is primarily a New World genus comprising 45-60 species distributed from southern Canada to southern South America, with one native to southern Asia (Bogle 1974; Heimerl 1934; Le Duc 1995). Species have been suspected of hybridization (Shinners 1951). In addition, some are known to be autogamous and even cleistogamous (Cruden 1973). Stamens and style curl tightly together in flowers of the species treated here, as in other arid-land Mirabilis in

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southwestern North America, probably effecting self-pollination as observed in *Boerhavia* (Chaturvedi 1989; Spellenberg 2001), species in other *Mirabilis* sections (Cruden 1973; Hernández 1990), and several other genera (Spellenberg & Delson 1977). Coupling hybridization with autogamy may produce individually rather uniform populations, but geographically complex variation patterns (Stebbins 1957).

Such complexes provided fertile ground for the description of numerous entities under taxonomic traditions of early in the 20th century, in which, because of locally uniform populations but widespread variation across a geographic region, taxonomic decisions may be subjective and perhaps utilitarian, following a philosophy expressed by Lewis (1963). Here, for example, more than 40 synonyms apply to our concept of *Mirabilis laevis* (Benth.) Curran and varieties. The taxonomic problems associated with *Mirabilis* were commented upon by Shinners (1951, p. 173) (“*Mirabilis* is surely one of the most troublesome of Southwestern genera, in nomenclature and taxonomy both.”) and by Standley (1931a, p. 73) after several decades of study in the family (“I know of few groups of plants [Neea, Torrubia, *Mirabilis*] in which specific differences are so unstable and so baffling[,] ... no single character seems to be constant.”) Turner (1993), conversely, in a rather refreshing approach to the taxonomy of the genus, noted that if emphasis on vegetative variation were minimized, and fruit characteristics were emphasized instead, the genus in Texas was taxonomically tractable.

*Mirabilis* was divided into six sections by Heimerl (1934; translated in part and reviewed in Le Duc 1995), one of which, *Oxybaphoides* A. Gray, was characterized by slightly accrescent involucres and fruits that are comparatively small and unornamented (Fig. 1). Heimerl included in it the North American species *M. oxybaphoides* (A. Gray) A. Gray, *M. californica* A. Gray (and close allies), a number of South American species, and one southern Asian species.

*Mirabilis oxybaphoides* has presented little taxonomic controversy at the species level since its description by Gray (1853) in the genus *Quamoclitidion*. It is sufficiently distinct from other species of *Mirabilis* (as the genus is now generally construed) that it formed the monotypic genus *Allioniella* of Rydberg (1902). This classification was followed by Standley (1909, 1918) in several treatments of the family, but he was apparently unaware of its presence in Mexico, as it was not included in his treatment of the family for that nation (Standley 1911).

The remaining taxa of the section in North America were placed in a new genus *Hesperonia* by Standley (1909), who emphasized differences of fruit form, shape of the perianth, and number of flowers in the involucre. Standley recognized eight species and several subspecies, emphasizing shape, color, size of the fruit, and vegetative characters such as plant size, leaf size and shape, and characters of vestiture. Jepson (1914) treated this as subgenus *Hesperonia* (Standl.) Jepson, including *M. californica* and *M. tenutloha* S. Wats., noting also
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Fig. 1. Variation in fruits of Nyctaginaceae, section Oxybaphoides, in North America. Fruits are grouped by taxon (Mirabilis laevis, M. oligantha, M. oxybaphoides, M. tenuiloba). Those above the line "laevis" refer to varieties within M. laevis. Fruit above letter N is 7.5 mm long. Each letter refers to a fruit from a different collection. Collections, fully cited in Appendix 2 are identified by asterisk (*) following herbarium of deposition, are: A, Brandegee s.n.; B, Palmer 886; C, Blakley 5657; D, Spellenberg 12336; E, Spellenberg 12335; F, Spellenberg 5444; G, Spellenberg 2982; H, Spellenberg 10206; I, Spellenberg 12332; J, Barneby 18303; K, Spellenberg 12342; L, Spellenberg 12329; M, Eastwood 18313; N, Wiggins & Wiggins 15940; O, Gentry & Fax 11731; P, Moran 23808; Q, Johnston & Muller 603; R, Waterfall 12142; S, Columbus 637; T, Correll & Johnston 24516; U, Powell & B. L. Turner 1708; V, Wiggins & Wiggins 15863; W, Brandegee s.n.

that M. laevis and M. cedrosensis (Standl.) Jepson were closely related if not the same as M. californica. Standley (1931b), upon completing studies of South American Nyctaginaceae, noted that characteristics used to distinguish North American genera allied to Mirabilis did not do so and also chose to unite all in an inclusive Mirabilis, a classification followed by most botanists since then. Of those taxa early placed in Hesperonia as they are recognized here, M. oligantha (Standl.) J.F. Macbride remains poorly known, M. tenuiloba has presented very few problems, but M. laevis has been a source of a plethora of names as taxonomists have attempted to deal with the variation presented by populations in the complex. The high points of these taxonomic meanderings are discussed under each of the taxa below.

Recently Le Duc (1993) described Mirabilis russellii Le Duc from the west coast of Mexico, placing the new species in the section Oxybaphoides because of its suffrutescent nature, campanulate perianth, and mucilaginous anthocarp (when wet). It rests very poorly in this section primarily because of general habit and anthocarp morphology. The single immature anthocarp available to us on the paratype at NMC generally resembles anthocarps of several other Mexican Mirabilis such as M. sanguinea Heimerl, M. hintoniorum Le Duc, and M. urbanii Heimerl, as figured
in Le Duc’s (1995) plate II. For the present treatment of section Oxybaphoides we exclude the species and suggest it lies more comfortably in section Mirabilis.

In this paper we examine the geographic variation and taxonomy of the most complex species in the section in North America, Mirabilis laevis, and we provide a key, descriptions, and distribution maps for the other three species in the section Oxybaphoides in the United States and Mexico. Mirabilis laevis and its component taxa have a tortuous taxonomic history that has resulted in many names published at the specific and infraspecific levels (Rodriguez 1992), based on differing generic, specific, and infraspecific concepts in the group. Generic concepts emphasized primarily the importance of the number of flowers per involucre, the shape of the fruit, and the degree of accrescence of the involucre. Specific or varietal decisions have primarily emphasized fruit shape and surface patterns, color of perianth, and nature of pubescence of foliage and stems.

MATERIALS AND METHODS

For this study more than 3000 herbarium specimens were examined from A, ARIZ, ASU, BRY, CAS, DS, GH, K, MO, NMC, NY, POM, RM, RSA, SD, UC, US, and UTC (abbreviations from Holmgren et al. 1990). From these specimens, 256 from the M. laevis complex were selected that had information about perianth color, possessed ripe fruits and at least midstem leaves, and had adequate data regarding place and date of collection. These specimens represent the morphological variation and geographic range of the taxa. They supplied data for morphological characteristics plotted in Figures 2 and 3 and described in treatments of taxa. Taxonomic decisions were made after study of specimens and the inspection of maps generated by plotting morphological characteristics geographically. Types or microfiches of types for basionyms were seen insofar as possible. From this information taxa were delineated that seemed to have some morphological, ecological and geographical reality. Those that showed considerable intergradation were recognized at the varietal level. The order of taxa in the treatment is based on perceived habitat specialization and reduction in number of fruits as generally compared to other Mirabilis.

We have separated detailed discussions of variation based on study of specimens in the Mirabilis laevis complex from the main taxonomic treatment and have included that in Appendix 1. Appendix 2 consists of standard citations of representative and/or cited specimens, including those that voucher chromosome counts.

Le Duc (1995) provides a key to the sections of Mirabilis.

TAXONOMY

Herbaceous to suffrutescent or shrubby perennials; root (of North American taxa; others unknown) long, cylindrical, cordlike; stems erect to decumbent or prostrate, densely to sparsely leafy. Leaves more or less evenly distributed, basal leaves larger, petiolate, distal leaves smaller, short-petiolate or sessile, margins plane. Inflorescences axillary and terminal in open or congested, few- or repeatedly-branched cymes; involucres bell-shaped, slightly accrescent, with 1 or 3 flowers inserted at base. Perianth broadly funnelform, abruptly flared from narrow tube, deeply 5-lobed; stamens 3-5. Fruit ellipsoid or obovoid, base not or slightly constricted, apex rounded, truncate, or somewhat nipple-like, surface with 0 or 5-10 indefinite or prominent lines, often somewhat furrowed, smooth or very slightly rugose, usually glabrous, mucilaginous when wetted.

A poorly understood section of about 10–20 species, North America, South America, southern Asia. Heimerl (1934) suggested there were about 23 species in the section, but considerable redefinition and consolidation of taxa in North America has reduced that number. Diversity is greatest in South America (Heimerl 1934).

**KEY TO NORTH AMERICAN MIRABILIS, SECTION OXYBAPHOIDES**

1. Involucres 3-flowered. 1. M. oxybaphoides

1. Involucres 1-flowered (very rarely 2 flowers).

2. Fruits 6–8 mm long; perianth white, 15–18 mm long above the constriction. 4. M. oligantha

2. Fruits 2.5–5.5 mm long; perianth white, pink, or magenta, 7–15 mm long above the constriction.

3. Involucr in flower 7–10 mm long, the lobes narrowly lanceolate, at the base 1/4–1/3 as wide as long; perianth white or pale pink; leaf blades commonly 4–6 cm long, ascending. 3. M. tenuiloba

3. Involucr in flower 3–6 mm long, the lobes triangular to lanceolate, at the base 1/3 to equally as wide as long; perianth white, pink, or magenta; leaf blades commonly 1–3.5 cm long, spreading or ascending. 2. M. laevis


**Oxybaphus** *wrightii* Hemsl., Biol. Centr. Amer. 3:3. 1882. Type: NORTH MEXICO: Chiricahau Mountains, Wright (HOLOTYPE K). Hemsley sites only general locality
and collector, without number or date. Gray (1853) cites Wright I721 (GH), from Guadalupe Pass in the "Chiricahua Mountains," the collection probably seen by Hemsley. If from the present day Guadalupe Pass, the collection originated in the Peloncillo Mountains in New Mexico.


Plants usually loosely clump-forming, herbaceous basally, the stems often intertwined and clambering through other vegetation. Stems ascending, spreading or decumbent, 0.2–1.2 m long, repeatedly branched, green throughout, puberulent in lines or throughout, glandular or not, the pubescence denser distally. Leaves thin or slightly fleshy; petioles up to 3.5 cm long on basal leaves, becoming progressively shorter distally, the distal leaves sub sessile or on petioles to 4 mm long; blades of the basal and midstem leaves broadly deltoid or ovate, 1.5–8.0 cm long, 1.0–7.5 cm wide, glabrous or puberulent, and then often glandular, the base cordate, the apex usually acuminate or acute, sometimes rounded; distal leaves from broadly deltoid to lanceolate, 5–15 mm long, 3–10 mm wide, the base cordate or rounded. Inflorescence loosely and narrowly cymose or narrowly thyrsoid. Involucres solitary or loosely clustered at the ends of branches, or solitary in forks of branches or axils of leaves, on slender peduncles up to 17 mm long, glandular-puberulent, widely bowl-shaped in fruit, much broader than deep, 5–9 mm long, the 5 bracts united by their margins 1/3–1/2 their length, the lobes approximately equal, broadly triangular, 4–6 mm long, about as wide at the base, the apices acute. Perianth campanulate, purplish pink, pale pink, or occasionally white, sparsely viscid-puberulent externally, 5–9 mm long, about as wide, strongly constricted above the indurcate base. Fruits 3 per involucre, olive or dark brown and black-mottled or evenly black, broadly obovoid to nearly spherical, ca. 2.5–3.5 mm long, the width ca. 70–90% of the length, smooth or very slightly rugulose, sometimes faintly marked with 5 shallow grooves (Fig. 1). 2n = 30 (Spellenberg & Soreng 5858).

Distribution (Fig. 4).—Southern Nevada, southern Utah, and southern Colorado, south through Arizona, New Mexico, and western Texas to northern Chihuahua, western Coahuila, and western Nuevo León, in open woods, on banks in woodland, among brush or boulders, usually where somewhat moist, 1500–2600 m. Flowering (June–)August–October.

The species is readily recognized by the distinctive shape of the leaves. At the apex of the petiole the base of the blade is broadly cuneate within the sinus of the overall cordate base; the curve at each side of the base of the blade reversing in a sinuate manner before joining the petiole. The apex of the blade is usually acuminate. Very glandular-pubescent plants and glabrate plants may occur in the same population (Spellenberg et al. 9681). Plants may be sufficiently viscid to "catch little birds" (label data, Vestal & Vestal 56). Leaf shape is consis-
tent throughout the range except in Nuevo León, where leaves on some plants are cordate-truncate at the base, rounded at the tip. On these plants the stems are little-branched and apparently ascending.

Plants were used by Native Americans to help heal “broken or bent” bones (label data, Vestal & Vestal 408).


*Plants* few-stemmed and clambering through other vegetation to many stemmed and forming clumps as wide or wider than tall; stems from the previous year often present and skeletal-white. *Stems* herbaceous or suffrutescent or clearly woody basally, 0.15–0.8 m long, erect or decumbent, repeatedly branched and appearing more or less dichotomous, glabrous, glabrate, puberulent, more or less scabrous, or viscid-villous, when pubescent, the pubescence denser distally, hairs spreading or retrorse; internodes 0.5–11.5 cm long. *Leaves* more or less fleshy, pubescent like the stem; *petioles* 1–22 mm on basal leaves, becoming progressively shorter distally, 0–4 mm long on distal leaves; *blades* of the basal and midstem leaves ovate, deltoid-ovate, ovate-rhombic, or subreniform, 1–4(-5.5) cm long, 0.5–3.5(-5) cm wide, the base cordate, truncate, or broadly obtuse, apex acute (occasionally attenuate), obtuse, or rounded, distal leaves lanceolate, lance-ovate, or ovate-rhombic, 5–17(-23) mm long, 3–11(-26) mm wide, the base cordate, truncate, or rounded. *Inflorescences* cymose or, in western races, more or less thyrsoid by partial suppression of one of the pair of axes. *Involucres* clustered and nearly sessile at the ends of branches, or solitary in forks of branches or axes of leaves, on peduncles 3–12 mm long, campanulate, 3–7 mm long in flower, enlarging about 1.5 × in fruit, the peduncles elongating slightly and deflected; lobes of involucre 5, 1/3 as long to equalling the length of the tubular portion, slightly unequal, narrowly to broadly triangular or triangular-lanceolate, the base 1/3 to equal to the height. *Perianth* widely flared from a narrow constriction atop the indurate base, white, white with magenta veins, pink, lavender, or magenta, sparingly puberulent externally, 10–16 mm long, in full anthesis usually slightly wider. *Fruits* 1 (rarely 2) per involucre, gray or dark brown to almost black, ovoid, obvoid, or almost spherical, 3–5.5 mm long, 3–4 mm wide, glabrous, almost smooth to moderately rugose, often faintly mottled with darker brown or black, with or without 10 paler, diffuse longitudinal lines, becoming mucilaginous when wetted (Fig. 1).

**Distribution** (Figs. 2, 3).—United States from central California and eastern Oregon southward through southwestern Utah and central Arizona, south to Mexico in west-central Sonora and west-central Baja California Sur.
MIRABILIS LAEVIS

- var. CRASSIFOLIA
- var. RETRORSA
- var. VILLOSA

flower
- white
- pink
- purple

involucre lobes
- = or > than tube
- < than tube

pubescence on stems and inflorescence
- < hairs conical or coarse
- = hairs long, often viscid
- > hairs slender, usually short, reflexed

Fig. 2. Distribution of *Mirabilis laevis* varieties in western United States. Varieties as recognized in this treatment are indicated by open or closed circles or squares, and characters of specimen from that site are indicated by symbols attached to circle or square (as indicated in legend in inset). Map simplified from Rodriguez (1992).

We recognize four intergrading varieties based on morphological differences that serve to help delineate more or less distinct geographic races. For the past century authors have wrestled with the variation presented by these plants, some taking a rather conservative view and placing most forms in an inclusive *Mirabilis laevis*, others splitting variants as species or infraspecific taxa. Even on one of the syntypes (NY) of *Mirabilis californica*, the first of the variants to
be split from *M. laevis*, the epithet "leavis Benth." appears on the collecting label along with "*Oxybaphus glabrifolius* Vahl." Curran (1888), in transferring *Mirabilis laevis* from *Oxybaphus* noted that plants recently brought from Magdalena Bay were "nearly but not quite glabrous, the inequality of the involucral lobes variable and often not greater than is found in our Californian
forms." Wiggins (1964) placed all forms in the complex south of about 27° N in Baja California Sur into *M. laevis*, apparently ignoring populations to the north except for *Mirabilis californica* var. *cedrosensis*, which he noted to occur from San Clemente Island, California, southward on the west side of Baja California to the Vizcaino Desert area (ca. 27° N). In that work Wiggins noted the inland specimens of *M. laevis* to be "quite viscid-puberulent to short-villous and often have the coarser and almost retrorse scabrous hairs on the upper stems that occur in forms of *M. californica*.

What was previously considered *Mirabilis californica* now comprises *M. laevis* var. *crassifolia*, which usually has an inflorescence with a more or less well defined central axis and shorter lateral branches, the entire shape being irregularly conical. We are terming this inflorescence form "thyroid." This contrasts to the much more openly and symmetrically forked inflorescences of many of the inland populations. We call these "cymose." The distinctions are not sharp.

**KEY THE VARIETIES OF MIRABILIS LAEVIS**

1. Plants glabrous or with a few hairs in distal parts; lobes of involucre lanceolate, width of base 1/2–2/3 times the height of lobe; perianth probably magenta.  
2a. *M. laevis* var. *laevis*  

1. Plants pubescent, rarely glabrate; lobes of involucre lanceolate to triangular, width of base 1/2–1 times height of lobe; perianth white, pink or magenta.  
2. Perianth pink or magenta, rarely white; width of lobe of involucre at base often 1/2–2/3 times height of lobe; plants pubescent, the pubescence usually not notably viscid nor retrorse (but hairs often stout and recurved along the coast); inflorescence commonly narrow and more or less thyroid.  
2b. *M. laevis* var. *crassifolia*  

2. Perianth white, rarely pale pink; width lobe of involucre at base 2/3–1 times height of lobe; plants commonly notably viscid-pubescent or sparsely short-pubescent with retrorse hairs; inflorescences broad, cymose.  
3. Plants viscid-pubescent, hairs spreading, ascending or sometimes retrorse.  
2c. *M. laevis* var. *villosa*  

2d. *M. laevis* var. *retrorsa*

**2a. Mirabilis laevis** (Benth.) Curran var. *laevis*.  

*Stems* glabrous. *Leaves* glabrous adaxially, with a few short straight hairs abaxially; *blades* of the basal and midstem leaves ovate or deltoid-ovate, 3–4 cm long, 2–3 cm wide, apex acute; distal leaves lanceolate, lance-ovate, or rhombic-ovate, 7–14 mm long, 2–5 mm wide. *Inflorescence* narrowly thyrsoid-like, with a long main axis and shorter side branches bearing near their tips involucres borne singly or in small clusters. *Involucres* 7–10 mm long, sparsely short viscid-villous, the bracts united 1/3–1/2 their length, the lobes lanceolate or ovate-lanceolate, acute. *Perianth* magenta. *Fruit* almost spherical, 4.5 mm long, 4 mm wide (Fig. 1).

*Distribution* (Fig. 3).—Apparently restricted to the vicinity of Magdalena
Bay, Baja California Sur, Mexico; habitat not recorded, 0-50? m. Flowering late winter and spring.


Mirabilis californica A. Gray ex Torr. in W. H. Emory, Rep. U.S. Mex. Bound. 2(1):169, 173, plate 48. 1859. Oxybaphus californicus (A. Gray) Hook. in Bentham & Hook. f., Gen. Pl. 3:4. 1880. Hesperonia californica (A. Gray) Standl., Contr. U.S. Natl. Herb. 12:364. 1909. TYPE: NOVA CALIFORNIA: San Diego, sand hills, 1850, C.C. Parry s.n. (LECTOTYPE, here designated: NY!). In proposing the name, Gray states that M. californica came from “dry hills, San Diego, California,” and then indicates the collectors “Parry, Thurber.” On a sheet from the Torrey Herbarium at NY are three specimens. One, at the top, collected in Los Angeles by Mr. Rich is of no further concern. At the bottom of the sheet are two portions of plants associated with a single label, indicating the plants were collected by C.C. Parry on “sand hills” in San Diego in 1850. Because the statement on the label most closely matches the habitat described, and the specimen at the lower right of the sheet clearly is the source of the illustration for plate 48 (mistyped as plate 46 in the original description), we are selecting the material at the bottom of the sheet as the lectotype. SYNTYPES: San Diego, Wood Valley, May 1852, Thurber 569 (2 specimens, GH); Bigelow, Whipple Expedition, on the Colorado, 1853–54 (GH!, NY!) [which represents the var. villosa (Kellogg) Spellenberg, as delimited herein], Bigelow, 21 Mar 1954 (GH!). At the time of publication Gray questioned whether Oxybaphus laevis Benth. might be the same as his new species, noting that the species is “commonly more or less pubescent, and rarely glabrata.” Torrey (U.S. Rep. Expl. Miss. Pacific 4:131. 1857) assigned Bigelow specimens incorrectly to Oxybaphus glabriofoliis Vahl. Gray, in the protologue of M. californica, cites Torrey's listing, correcting the placement of these specimens. Gray later, in the protologue of M. bigelowii alludes to the Bigelow specimens and indicates that this new taxon occurs “perhaps in California on the Colorado.”


Mirabilis laevis var. cordifolia Dunkle, Bull. S. Calif. Acad. Sci. 40:108. 1941. TYPE: CALIFORNIA: San Clemente Island, Chinetti Canyon, 3 Apr 1939, Dunkle 7234 (HOLOTYPE: RSA #350685; ISOTYPE RSA #464676). Both specimens at RSA have been transferred from LAM; of the two the holotype has a hand written label with the word “type.” Dunkle (1941) noted two variants in the same population, his new var. cordifolia intermixed with var. cedrosensis.
Stems often glabrous basally, viscid-pubescent or more or less scabrous distally. Leaves puberulent, viscid-villous, or more or less scabrous, sometimes becoming glabrate with age (or occasionally glabrous); blades of the basal and midstem leaves ovate-rhombic, subreniform, or deltoid-ovate, 1–4.5 cm long, 0.4–3.5 cm wide, the apex obtuse or acute, occasionally rounded; distal leaves lanceolate, lance-ovate, or ovate-rhombic, 5–14 mm long, 2–7 mm wide. Inflorescence often rather thyrsoid-like after the first few dichotomous branches, the branches short, the involucres in clusters along a main axis. Involucres 5–9 mm long, densely short viscid-villous or sometimes slightly scabrid, the bracts united 1/3–2/3 their length, the lobes ovate or ovate-oblong, obtuse or acute. Perianth pink, lavender, magenta, occasionally white. Fruit ovoid, 3–5 mm long, 2.7–3.7 mm wide, dark to pale gray-brown and mottled with dark gray-brown, tan, or red-brown, sometimes faintly and irregularly pale-striped (Fig. 1).

Distribution (Figs. 2, 3).—West-central California south along the coast, on the Channel Islands, and in the Coast Ranges to the Viscaino Desert, Baja California Sur and the coastal islands, Mexico; coastal bluffs, road banks, coastal scrub, grasslands, chaparral, oak woodland, often on rocky outcrops, 0–1830 m. Flowering most of the year, most vigorously in spring.

A particularly difficult area with regard to variation is around the southern end of the Sierra Nevada in California, where three of the varieties are in contact. Howell 38179, from the Lake Isabella region in Kern Co., illustrates very well the problematic classification of some specimens. It was first left unidentified in Mirabilis, then sometime later placed in an inclusive M. laevis; 9 years later was identified as M. retorsa; 21 years later as M. bigelovii var. bigelovii, and shortly later placed in a variable var. crassifolia. The specimen combines the spreading leaves and (light) villous pubescence of var. bigelovii, the pointed leaves and rather long involucre lobes of var. crassifolia, and some retrorse hairs similar to var. retorsa. Flower color was not given by the collector and is not evident from the specimen, but as judged from Spellenberg’s collections from this area, flowers were probably white. Nearby, from the entrance to Kern River Canyon, comes Howell 38142, a late-season collection showing thyrsoid inflorescences of var. crassifolia, and fairly pointed leaves, but in other respects is the var. villosa; a similar, later collection (Howell 38675) from the same area notes “calyx rose.” For plants from the lower reaches of the Kern River Canyon, Spellenberg’s observations note flowers only pink to rose, yet if these plants were collected eastward they easily would be placed in more consistently white-flowered var. villosa. Twisselmann 8391, from the same area, is more or less villous and has blunt leaves, in these respects similar to the var. villosa, but it has a more or less accrescent involucre with proportionately longer lobes, more reminiscent of var. crassifolia. Also seemingly intergradient to var. villosa is Bedell 74–5 and Twisselmann 198, both from the north end of the Temblor Range in western Kern Co.; they have
thick fleshy leaves that are blunt, short involucre lobes, but thyrsoid inflorescences; Twisselmann notes that flowers are “purple.”

Mirabilis laevis var. crassifolia may also intergrade with M. oligantha in Baja California Sur (Moran 18723).

Much has been made of features of pubescence over the taxonomic history of this group. Even within var. crassifolia there is considerable variation. Near the coast, and particularly on the islands of northwestern Mexico, hairs are stout and conical, distinguishing Hesperonia cedrosensis and subsequent synonyms. This pubescence type is thoroughly intergradient to finer but still conical-based hairs common within the var. crassifolia. Fruit characteristics, such as those used to distinguish H. heimerliti, also an island population, seem to be completely inconsistent from population to population. Other specimen-based discussion focuses individually on characteristics that have been used to distinguish species in this complex and is found in Appendix 1.

The label on a specimen collected in Baja California (Moran 12832) notes the indigenous name and use “Yerba del Empacho-bueno para el estomacho.” The vernacular name is repeated on Moran 23821 from Baja California Sur.

2c. Mirabilis laevis var. villosa (Kellogg) Spellenb., comb. nov. Mirabilis californica var. villosa Kellogg. Proc. Calif. Acad. Sci. 3:10. 1863. TYPE: CALIFORNIA. MONO CO.: Calif. Hwy. 182 10 m from Nevada border, Devil’s Gate, canyon of East Walker River, Spellenberg 12326, 12 Jun 1996 (NEOTYPE, here designated: NMC: ISONEOTYPES !!) BYU, CAS, F, K, MEXU, MO, NY, RM, RSA, UC, US). Kellogg (1863) provides brief but clear description of a plant that matches the classic concept of Mirabilis bigelovii except that he notes his var. villosa to have a “pink perigonium” (rather than white). He notes the taxon to come “from the interior-Devil’s Gate and Carson River...” but he cites no documenting specimens. We found no specimens that were seen by Kellogg, all perhaps having been destroyed in the 1906 San Francisco fire. During field work involving this complex Spellenberg could not find Mirabilis at the well known “Devil’s Gate” along U.S. Hwy. 395 north of Bridgeport, Mono Co., Calif., nor were plants to be found along the upper portions of the West Walker River along this highway. In either place habitat seems incorrect. They do occur, however, at a lesser known “Devil’s Gate” along the East Walker River (Delorme Mapping 1990) northeast of Bridgeport, and this is presumed to be Kellogg’s Devil’s Gate. Plants from this site form the neotype series.

Mirabilis bigelovii A. Gray, Proc. Amer. Acad. 21:413. 1886. Hesperonia bigelovii (A. Gray) Standl. N. Amer. Fl. 21:235. 1918. TYPE: Grand Canyon, May 1885, A. Gray s.n. (HOLOTYPE: GH!). Gray cites his own collection in the protologue, indicating also that the type comes from “below Peach Spring” where the species is “common.” The holotype has penned in Gray’s hand on a printed label “Grand Canon” and “Mirabilis bigelovii n. sp.,” but does not mention Peach Spring. In the protologue Gray alludes to Bigelow specimens, as discussed herein in the nomenclatural section under Mirabilis californica.


Hesperonia glutinosa subsp. gracilis Standl., Contr. U.S. Natl. Herb. 12:365. 1909. H. limosa subsp. gracilis (Standl.) Standl., Muhlenbergia 5:104. 1909. Type: ARIZONA: Sabino Canyon, 1892, J.S. Tourney 471k (HOLOTYPE: US). PARATYPES: ARIZONA: without locality, 1876, Palmer 644 (US!). ARIZONA: Tempe, 6 Apr 1896, J.S. Tourney s.n. (UC - 2 sheets). CALIFORNIA: Colton, Feb 1881, G.R. Vasey s.n. (US! - 3 sheets, 2 apparently seen by Standley, 1 possibly not). NEW MEXICO: without locality, G.R. Vasey s.n., 1881 (US?) [as Standley notes in the discussion of this paratype, the location is probably incorrect; Standley knew of no collections from New Mexico, and none have been seen in the present study. Ewan and Ewan (1981) indicate that Vasey was in central and northern New Mexico, well away from nearest known populations in Arizona, and that specimens were apparently sent back to Washington unlabelled, increasing the possibility of error. To Spellenberg, the New Mexico paratype appears very similar to Vasey paratypes from Colton, California, particularly US #22631].

Stems moderately to densely villous or viscid-villous, often with wavy hairs, or puberulent with ± retrorse hairs, the pubescence denser and increasingly viscid distally. Leaves ± fleshy, viscid-villous; blades of the basal and midstem leaves reniform-ovate, broadly deltoid-ovate, or suborbicular, 0.5-4 cm long, 1-3.7 mm wide. Inflorescence usually cymose, the branches ± equal throughout; involucres 5-7 mm long, the bracts united ca. 2/3 their length, the lobes ovate-triangular or ovate-oblong, obtuse or acute. PERIANTH white or pale pink, occasionally (especially in far western part of range) deep pink or purple. Fruit ellipsoid to obovoid or almost spherical, 4-6 mm long, 2.5-4 mm wide, gray-brown, dark charcoal-brown, or olive, often dark-mottled, often faintly marked with 10 paler longitudinal lines (Fig. 3). 2n = 30 [Spellenberg 5444].
Distribution (Figs. 2, 3).—Southeastern Oregon through Nevada, southwestern Utah, southern California (primarily southeastern, but extending west as far as eastern San Luis Obispo Co.), western Arizona to Baja California and northwestern Sonora; roadbanks, slopes, open desert, often among brush or in open woodland, 35–2200 m. Flowering most of the year, most vigorously in spring.

In California the var. villosa (as M. bigelowii), has been considered to be from east of the Sierra Nevada and the Transverse Range. Nevertheless, around the San Joaquin Valley some plants of the var. crassifolia approach the var. villosa (e.g., Ewan 10309; Hoover 3170; Raven et al 9240, Twisselmann 8377) or cannot be excluded from it as here defined (e.g., Bacigalupi et al. 5205; Eastwood & Howell 5839; Ferris & Bacigalupi 10350; Keck 2158).

A vernacular name in Baja California recorded for this species is “Yerba de la Vieja” (Moran 23774).

From the type locality to the north plants are sporadic along the East Walker River and along the West Walker River where it exits from the Sierra Nevada and piñon pine vegetation into the Great Basin and its shrub association (Spellenberg 12331, 12332). Other plants in the region have much shorter, sparser pubescence and are more readily referable to the var. retrorsa (Spellenberg 12327, 12329, 12333). No obvious habitat differences were detected between the two pubescence phases. Collection 12333 had flowers closed in mid-morning that were very slightly pinkish. Otherwise, all plants seen in flower had white perianths.

In discussing M. aspera on the Colorado and Mojave deserts, Parish (1907) notes intergradation along edges of range with M. californica, and places the former into the latter as a subspecies. Intergradation is particularly evident in perianth color—those plants from the zone of contact having pink (rather than red-purple or white) perianths. To the west, in the var. crassifolia, perianth color is usually red-violet, but white-flowered plants are known. To the east the var. villosa usually has a white perianth, occasionally with a pale pink tube, or rarely entirely pale pink. The pattern probably results from selection pressure of primarily diurnal pollinators in the west and nocturnal pollinators in the drier deserts to the east (Baker [1961] discusses various pollinators in Mirabilis froebelii (Behr) Greene, a species with red-violet flowers).

The pivotal nature of the var. villosa in the Mirabilis leavis complex is indicated by its extensive synonymy. As indicated by the discussion of variation as seen in various specimens (Appendix I), the variety is variable and often intergrades with var. crassifolia and the var. retrorsa. In southeastern California and Baja California it is sometimes distinguished with difficulty from M. tenuiloba.

Stems glabrous or with a few retrorse hairs below, sparsely to densely retrorse-puberulent distally, when densely pubescent, then often also ± viscid. Leaves ± fleshy, puberulent with retrorse hairs; blades of the basal and midstem leaves reniform-ovate, broadly deltoid ovate, or suborbicular, occasional orbicular-reniform, 0.5–3.5 cm long, 1–3.4 cm wide. Inflorescence usually cymose, the branches ± equal throughout; involucres 5–7 mm long, the bracts united ca. 2/3 their length, the lobes ovate-triangular or ovate-oblong, obtuse or acute. Perianth white or occasionally white tinged with pink at the base, rarely entirely pale pink. Fruit ellipsoid to obovoid or ± spherical, 3.5–5 mm long, 2.6–4 mm wide, occasionally slightly wider than long, gray-brown, dark charcoal-brown, or olive, occasionally dark-mottled, often faintly marked with 10 paler longitudinal lines (Fig. 1). 2n = 31–33 II (Strother 1256).

Distribution (Figs. 2, 3).—Southeastern Oregon, western and southern Nevada, southwestern Utah, northwestern Arizona, southern California, and northern Baja California; arid open areas among desert brush or in open woodland, often on banks, 60–2000 m. Flowering in spring, occasionally in winter, less frequently at other times.

In general, plants of the var. retrorsa are smaller, with smaller leaves, and apparently are more compact, providing more of a forking, repeating “wishbone” aspect (Bagley 2098, Clemens and Jonson 1690, Clokey & Templeton 5725, Munz 16449), than most of those of var. villosa. Nevertheless, open sprawling plants with stems 3.5–4 dm long, with leaves 2+ cm long, and inflorescences ± thrystone-like (Peirson 7180), resemble in aspect either the var. crassfolia or the var. villosa. Local environmental factors may also affect the phenotype; e.g., Munz & Keck 4754 is a lanky plant with broad thin leaves. It is said to come from “among rocks along canyon” and may be a shade form. Plants indistinguishable from the tighter, smaller, northern forms of this variety occur as far south as the mountains of southern California (Peirson 9846) and Baja California (Moran 14842).

The variety retrorsa may co-occur with the var. villosa (see two specimens at DUD, Train s.n., 30 Apr 1937, both from Darwin Falls Canyon; also Duran 3455 [retrorsa] and Mooney et al. 132 [villosa], both from Silver Canyon in the White Mountains). Munz noted his collections I3036 (var. retrorsa) to be not glutinous, I3037 (var. villosa) from the same site to be glutinous. The Duran 3455 specimen cited immediately above has long internodes and spreading rounded leaves more typical of var. villosa, but has very short, mostly retrorse hairs; in respect to habit and pubescence it is intermediate between the two varieties. Mixed collections of the two are represented by M. & E. Epling s.n. and
Maguire & Holmgren 25193. The two also occur in close vicinity on the east side of the Sierra Juárez in northern Baja California (Thorne, Boyd, et al. 61758 = var. retrorsa; Thorne et al. 57784 = var. villosa).

As discussed for the var. crassifolia, Kern Co., California, is also an area of particular difficulty concerning the var. retrorsa. Numerous collections suggest intergradation with the var. villosa; e.g., very dense pubescence, clearly retrorse, is present in Eastwood 3200; on Hall and Chandler 6882, a similar plant from the same general region, the collectors note that the flowers are pure white and the plants are viscid. Further indicating the difficulty of satisfactorily classifying material from this area, two specimens collected very near one another a week apart in the same year each represent a different variety; Voegelin 67 is nearest the var. crassifolia, whereas Cole and Voegelin 120 is clearly var. retrorsa. Another pair of specimens from the same vicinity, in Red Rock Canyon (vicinity of Red Rock Canyon State Park) are the var. retrorsa (Abrams 11877) and a fairly lightly pubescent phase of the var. villosa (Munz 1246). Howell 37115, in its fairly dense but downward-flexed pubescence, approaches the var. villosa, and in its pointed leaves the var. crassifolia (flowers on the specimen appear to have been white). In this region of contact between the three varieties, ± typical plants of the var. retrorsa occur (Howell 38667).


Plants forming leafy clumps 0.3-1 m or more in diameter, usually with many stems, herbaceous or somewhat suffrutescence basally. Stems ascending 0.2-1 m long, with few to many ascending branches, pale green or white at base, green distally, puberulent in lines or throughout, usually glandular-viscid, the pubescence denser distally. Leaves slightly fleshy; petioles to 2.2(-5) cm long on basal leaves, becoming progressively shorter distally, the distal leaves sessile or on petioles to 4 mm long and gradually intergrading to the bracts of the inflorescence; blades of basal and midstem leaves broadly deltoid or ovate, the largest often wider than long, 2-5(-8) cm long, 1.7-7.0(-12) cm wide, glabrate to glandular villous, the base rounded to cordate, the apex usually acute, sometimes rounded; distal leaves from broadly deltoid to lanceolate, often acuminate, 1-2 cm long, 7-15 mm wide, the base cordate or rounded. Inflorescence usually narrowly thyrsoid. Involucres densely clustered among distal leaves or bracts near ends of branches, on peduncles 0-2 mm long, glandular-pubescent, narrowly campanulate, deeper than broad, 7-16 mm long, the 5 bracts united by margins 1/3-1/2 their length, the lobes approximately equal, narrowly lance-oblong, 1/5-1/4 as wide at the base, the apices acute or attenuate. Perianth cam-
panulate, white (rarely pink), sparsely viscid-puberulent externally, 13–18 mm long, about as wide, strongly constricted above the indurate base. Fruits 1 per involucre, dull reddish brown to almost black, rarely with 10 inconspicuous and very slightly paler lines, broadly ovoid to nearly spherical, 4–6 mm long, the width 60–85% of the length, smooth or very slightly rugulose, sometimes faintly marked with very shallow grooves (Fig. 1).

Distribution (Fig. 4).—Southern California, southwestern Arizona, and northwestern Sonora, south to Baja California Sur, on slopes, canyon sides, cliffs, and among rocks, or in gravel or sand in semi-arid and arid areas, 0–400(–900) m. Flowering late winter and spring, occasionally other times.

The species is from east of the mountains in southern California and from near the gulf in Baja California and therefore is mostly a desert species. It is known in Arizona only from the Tinajas Altas Mountains in Yuma Co., where it was collected in 1940 by L. Goodding (s.n. 7 Mar 1940), the collection remaining unidentified for more than 50 years. It was rediscovered (Felger & Bryles 92-613) and reported from there by Felger (1993). As noted by Felger, the species was sympatric with M. bigelovii (= M. laevis var. villosa) (Felger & Bryles 92-614). A. and R. Nelson apparently collected M. laevis var. retrorsa (3236, but as M. limosa) in sympatry with M. tenuiloba (3236a), perhaps separating the collections later under the "a" number. The Nelson collection of M. tenuiloba 3236a has leaf tips more rounded than usual for the species, plants are less robust, and involucres in the shorter portion of the range for the species. It may be an introgressed plant. Gander 1301, a robust, more "typical" M. tenuiloba, among a number of other collections, is from the same canyon. Sympathy involving such similar perennial species provides the opportunity for hybridization. Occasional collections such as Moran 8877 have involucres with triangular teeth 3–4 mm long, shorter than the tube, also suggesting intergradation with M. laevis.

MacBride (1918) considered Chandler 5332, from near Escondido in southern California, to be included in his concept of M. tenuiloba var. polypylla, the only record north of Mexico for this entity. That specimen is here considered to be an extreme form of M. laevis var. crassifolia. Other somewhat similar specimens, having at maturity rather large involucres for M. laevis var. crassifolia, are from the Channel Islands (see Blakley 5238, Clokey 4923, Raven 17655).

The southernmost collection in Baja California Sur (Wiggins et al. 258) is much less pubescent that is characteristic of M. tenuiloba. The specimen was originally identified as M. oligantha.


Plants usually dense shrubs or subshrubs. Stems erect, ascending or spreading, 0.3–1.2 m long, repeatedly branched, with a whitish or gray exfoliating bark on older stems, glandular-puberulent, densely so distally, becoming glabrate with age. Leaves slightly fleshy; petioles 1–20 mm long, about 1/5–1/3 the length of the blade, becoming progressively shorter distally; blades of the midstem leaves broadly deltoid-ovate or ovate, about 2–5 cm long, 1.5–3 cm wide, sparsely to densely glandular puberulent, the base subcordate, rounded, or broadly cuneate, the apex acute, obtuse, or sometimes rounded; distal leaves progressively reduced from midstem leaves, from ovate to lanceolate, those among the flowers as small as 5 mm long, 2 mm wide, with a petiole of 1 mm long, the base rounded to cuneate. Inflorescence when well developed widely branching, the main axis
zig-zag, or sometimes comparatively dense and thyrsoid. *Involucres* or solitary in forks of branches or axils of leaves, on slender peduncles 4–15 mm long that are deflexed after anthesis, glandular-puberulent, narrowly urn-shaped in flower, distended by the globose fruit, 7–10 mm long, the 5 bracts united by margins about 1/2 their length, the lobes narrowly triangular or lanceolate, 4–5 mm long, 1/3–1/2 as wide at the base, the apices acute. *Perianth* campanulate, usually white, less often pinkish or lavender, sparsely puberulent externally, especially on the tube, 12–20 mm long, about as wide, strongly constricted above the indurate base. *Fruits* 1 per involucre, dark brown or nearly black, sometimes with 5 faint paler lines, ellipsoid, 6–8 mm long, smooth or slightly rugulose, sometimes faintly marked with 5 shallow grooves (Fig. 1).

**Distribution** (Fig. 4).—Central Baja California and northern Baja California Sur, on dry rocky slopes among desert shrubs and cacti, 50–600 m. Flowering fall to early spring, sometimes later.

*Mirabilis oligantha* is an endemic to the Baja California peninsula. A puzzling series of collections, mostly identified originally as *M. bigelovii*, come from the mountains of northern Baja California Sur, particularly from the vicinity of Picachos de Santa Clara, where *M. oligantha* has been collected (Gentry 7717). These plants may not have been so shrubby and stems may have been sprawling. They have rather sparse foliage, the progressively reduced leaves in the inflorescence characteristic of several *M. oligantha* specimens, and flowers borne singly or in few-flowered clusters. *Involucres* are small for *M. oligantha*, but have long lobes. Flower color noted on labels is white, pink, or lavender: *Mirabilis laevis* var. *crassifolia* occurs in the region, and the plants may represent intergradient forms. Such specimens have been annotated as that variety, with the note that they may be intergradient (Gentry 7697, Moran 18723, Moran & Reveal 19671, 19689).

Standley (1909) distinguished *Hesperonia oligantha* from other species in his key in part by stating that flowers are “purplish red.” He also noted that stamens are “long exserted” in *M. oligantha*. Though the stamens are exserted somewhat in the species, as judged from herbarium specimens, the “long exserted” impression comes from Standley mistaking flowers as *Hesperonia* that actually are from some gamopetalous family, not Nyctaginaceae, attached as fragments to the holotype sheet. These flowers appear to have been dark in color. In 1911 and 1918 Standley did not mention flower color. Wiggins (1964) explicitly noted that *M. tenuiloba* has a white perianth and scarcely exserted stamens, and that *M. oligantha* (including *M. polyphylla*) has a white (or pink?) perianth, but for that species there is no mention of stamens. Of the 15 collections of *M. oligantha* seen, labels of five report the perianth as white or creamy white. One reports “white, slightly pinkish” (Moran 23808) and another “pale lavender” (Gentry & Fox 11731)
APPENDIX I
Specimen-based discussion on characteristics that have been used to distinguish taxa in the Mirabilis laevis complex. Plants vary in many features, and often a collection used to illustrate one point also illustrates others. Specimen citations comprise Appendix 2.

**Mirabilis laevis var. crassifolia**

**Pubescence of var. crassifolia.** — The var. crassifolia is variable with regard to pubescence within populations (Werf 4221 notes “plants conspicuously glandular, others not”), and intergrades with the var. retrorsa and villosa to the east. The var. crassifolia usually has hairs that are noticeably broader at the base, somewhat or considerably coarser than the finer pubescence of the var. villosa or the short retrorse hairs of the var. retrorsa. Intergrades to the more villous var. villosa occur through much of range and are maintained in var. crassifolia primarily because of their relatively acute lower leaves, often comparatively long involucre lobes, and more or less thyroid inflorescences (Daniel 1345; Templeton 11388; Thorne & Tifftor 14356). Such plants are particularly common in the southern California mountains and in Baja California. Others, particularly from interior Baja California, have blunter leaves and slightly finer pubescence than coastal plants, and in this respect begin to approach the var. villosa (Burgess 6095; Carter, Alexander & Kellogg 2522; Moran 18694). These are retained in the var. crassifolia because of generally thyroid inflorescences and magenta or pink flowers. In California, specimen from near the coast in Ventura Co. has most of the characteristics of the var. villosa, i.e., long internodes, rounded leaves, villous pubescence, but has proportionately longer involucre lobes as in the var. crassifolia and flowers that are magenta to lavender (Thompson 1857), plants to the north in Santa Barbara Co., are also similar (Pollard s.n., 30 Sep 1956). Others from this region have more acute leaves and proportionately narrower and longer involucre lobes as in the var. crassifolia (Bourell et al. 2938), contrasting with other plants in the region such as Hoover 7644, which has rounded lower leaves and proportionately short involucre lobes, but which has strongly tapering hairs more consistent with var. crassifolia. Extremely lightly pubescent plants that have pointed leaves and rather long involucre lobes occur on western edge of the California desert (Dunkle 3411).

Standley (1909) established Hesperonia cedrosensis in large part on the conspicuous, conical, recurved hairs, the extreme of this feature resulting in +hispidulous plants as occur on Cedros Island (Henrickson 14453). Plants with such hairs are almost entirely coastal but not necessarily insular (Standley 1918). Plants of the Viscaino region in central Baja California may have pubescence similar to the stout recurved trichomes of plants from Cedros Island (Boyd, Ross & Appleby 8100; Gentry 7391), as do plants along the northern Pacific coast of Baja California, which have notably pointed leaves (Chisaki & Newcomb 525; Epling & Robinson s.n., 15 Feb 1935). Specimens that have stout recurved hairs interspersed with finer hairs occur on the Channel Islands (Brandegee s.n., 25 Aug 1894; Munz 6645) and in the southern part of the range (Wallace 176). Others from the same islands show fewer recurved hairs and have somewhat more glandular puberulence (Moran 6848) or are barely recurved-pubescent at all but are more (Eastwood 6387) or less (Breedlove 2874) viscid-villos. The latter has rounded lower leaves reminiscent of the var. villosa, as do many plants on the Channel Islands, where larger, but not especially recurved, hairs may be mixed with a fine glandular hairs (Raven 17307). A very villous plant from these islands, thus similar to var. villosa, has long involucre lobes characteristic of var. crassifolia (Thorne 37483). Plants with large conical downward-curved hairs may occur inland to the north, as in Fresno Co. (Boolettian s.n., 6 Apr 1951).

Plants of var. crassifolia are not completely distinct from the var. retrorsa. Howell 39241, from Monterrey Co., is an open sprawling plant with pointed leaves as expected in the var. crassifolia, but has short calyx lobes and sparse retrorse hairs more similar to those of the var. retrorsa. Other collections, but from southern California, also well away from the main range of the var. retrorsa, are lightly pubescent and have some retrorse hairs on stem, but have long involucre lobes more characteristic of
the var. crassifolia (Epling & Ellison s.n., 28 Mar 1930). Plants on the west slope of the southern Sierra Nevada approach var. villosa in their more or less villose pubescence, the hairs of which may be somewhat deflexed, and in their blunt leaves (Benson 3214, Hoover 3170), similar combinations of characteristics are found at the southern end of this mountain range where the geographic ranges of the three varieties come into contact (Jepson 6752, Thorne 31702). Along the contact zone of the var. retrorsa with the var. crassifolia in southern California are plants with retrorsa hairs and white flowers, but with pointed leaves and rather long involucral lobes and conical hairs (Kamb 902).

A sparsely pubescent, lanky, very thin-leaved plant (Munz et al. 2672) appears to be an environmentally modified phase, having been collected on a "damp hillside."

**Flower color of var. crassifolia.**—Usually var. crassifolia has a deep rose or magenta perianth, intergrading through pink along the eastern edge of its range with the mostly white-colored var. villosa (see discussion there). Nevertheless, and contrary to the key for Hesperonia by Standley (1909), within the range of var. crassifolia, sporadic variants with pale or white flowers are fairly frequent. "Flowers vary from purple to white" in populations in the northern part of range (Merced Co., Lyon 932) or "pale white with rose tint along veins" (San Benito Co., Ewan 10309, a plant very closely approaching var. villosa). Toward the southern end of the range plants with white (Gentry 8694, Moran & Reveal 1967, Orcutt 219a, Reed & Reed 7259), almost white (Gray s.n.), white tinged with pink (Moran & Reveal 20006), pure white veined red (Trask s.n.), white to light lavender (Henrickson 8940), or pale lavender (Moran & Reveal 19870) flowers occur; sometimes in mixed populations (Ewan 7041 - white, 7042 - pink, Moran 20414 - pink, 20415 - white). Pale-flowered, white-flowered, or mixed, populations in this region and along the eastern edge of the range are probably a response to selection pressures from nocturnal pollinators in the desert (e.g., Jepson 6073, 8839). Whitish-flowered plants also occur in the coastal scrub of Baja California (Hodgson & Pinkava 3011), white, pink and "red" flowers occur in the same population near the coast in southern California (Hastings s.n., 16 Apr 1941), and plants may occasionally have flowers white with red veins (Trask 193). Trask 14, however, from the same general locality, has magenta flowers. The last two specimens are paratypes of H. cedrosensis.

**Leaf shape of var. crassifolia.**—In an attempt to distinguish species in the complex, authors have reiterated features emphasized by Standley (1918), where leaves of the var. crassifolia (as Hesperonia californica) are said to be "... obtuse or acutish... most of them narrowed to the apex and never rounded" (Standley 1918). Leaves are illustrated with rather round apices in Torrey's (1859) original plate (# 48), which we believe is based upon the lectotype selected by us. At the northernmost known locality in the Coast Ranges, in Alameda Co., plants are much less pubescent than is common in the variety, but in may have either rounded midstem leaves (Havlík 929) or rather pointed leaves (Spellenberg 12335); the latter clearly has the thyrsoid inflorescence characteristic of this variety. Plants with long internodes, spreading + rounded or bluntly acute leaves, lightly glandular-villosous pubescence, and rather cymose inflorescences from the interior coast ranges in San Benito and Merced counties are very close to var. villosa; flower color is not indicated on specimens (Reylik 25, Hoover 4309, Spellenberg 12336).

**Inflorescence of var. crassifolia.**—In their extremes, the differences between the thyrsoid inflorescence of western races and the neatly forked inflorescence of some eastern populations from the desert are notable. From the western edge of the Colorado Desert, where collectors mostly note rose perianths (rarely white - Munz & Everett 16245), plants are open, sprawling, and leafy, the inflorescences thyrse-like as the var. crassifolia. Nearby, on the sandy desert plain are plants more typical of var. retrorsa, less leafy in appearance, with recurved hairs, shorter erect or spreading stems, and an inflorescence that is much less thyrse-like, though it is still not neatly forked (V. & A. Grant 15979).

**Fruits of var. crassifolia.**—Various authors have indicated certain fruit shapes or surface pattern are distinctive for taxa, particularly at the varietal level. Munz & Keck (1968) indicate considerable variation in the fruit of a broadly delineated M. laevis (= var. crassifolia in sense of this paper), indicating
the fruits to be "dark, sometimes mottled or pale-striate, smooth," but provide specific and limited characteristics for the fruit of infraspecific taxa of *M. bigelovii*. Standley (1918) also maintains limited variation for the fruits in his taxa within Hesperonia. In the var. *crassifolia* fruits may be obovoid, broadly ellipsoid or globose, grayish brown, and very faintly dark-mottled (*Eastwood & Howell 2396, Philbrick 868-80, Solbrig 2670*); irregularly and faintly pale-striped and indefinitely dark-mottled (*Rose 63030*); pale gray-tan, mottled faintly with tan (*Wiggins 2054*); grayish brown mottled with red brown (*Spellenberg 10208*); dark charcoal brown, faintly mottled darker (*Youngberg 7*); dark brown, faintly mottled darker and very faintly striped, paler near the apex (*Munz & Harwood 3900*); grayish brown and mottled faintly slightly darker, with faint pale stripes at each end (*Havlík 929*).

**Mirabilis laevis var. retrorsa**

**Pubescence of var. retrorsa.**—Two collections from the Granite Mountains, eastern San Bernardino Co., Calif., indicate intergradation between var. *retrorsa* and var. *villosa*, and perhaps the low significance of pubescence characters in general. Both these plants are similar in general aspect, being small and well branched; *Stein 12* is glabrate, with a few downward-oriented hairs on the stems (a "good" var. *retrorsa*), whereas *Tilford & Tilford 1012* is villous. From the area of contact in southern California intermediate plants occur; *Gould 2248*, from the east base of the Coast Ranges in San Diego Co., has glandular villosity, some hairs downward directed, and white flowers as in var. *villosa*, but hairs with conical villosities and thyrsoid inflorescences similar to var. *crassifolia*.

**Flowers of var. retrorsa.**—Flowers are usually white, but there occasionally are other color forms; white limb and rose throat (*Clemson & Jonson 1690*); rose (*Twisselman 7280*); white and rose-pink at same site (*Hall and Chandler 6882, 6884*, respectively).

**Inflorescence of var. retrorsa.**—The very neatly forked branching characteristic of this variety is illustrated by *Peirson 8900, Holmgren & Holmgren 7697*, and *Twisselman 7280*. Near the area of contact with var. *crassifolia*, plants may have thyrsoid inflorescences (*Benson 3136, M. E. Jones s.n., 25 Apr 1906, Winblad s.n., 2 Feb 1937*); the Jones specimen also has unusually long involucre lobes for the variety.

**Fruits of var. retrorsa.**—Fruit shape and surface pattern are variable; + globose, gray brown, not lined (*Reveal & Reveal 50*); + globose, with 10 pale lines (*Henrickson 18257, Henrickson & Bekey 18288*); + globose, yellowish brown, faintly darker mottled, not lined (*Ferris 7998*); broadly obovoid, dark, with 10 thin pale lines (*Munz & Keck 7862, Peirson 8900*); broadly obovoid, smoky brown, not lined (*Spellenberg et al. 3151*); ellipsoid, brown dark and very faintly mottled, incompletely and faintly 10-lined pale (*Thorne 33848*). One population has plants occasionally with 2 fruits per involucre (*Spellenberg 12342*).

**Leaves of var. retrorsa.**—Leaves are usually obtuse or rounded at the tip. In the zone of intergradation to the var. *crassifolia* in southern California, intermediate plants may have acute leaves (*Henrickson 5537*). A pair of specimens suggest a strong genetic component to leaf shape and size, nature of pubescence, and involucral characteristics. Progeny from a collection with white flowers, small, acute leaves, and the pubescence of var. *retrorsa* from the north end of the Coachella Valley (*Munz and Everett 16245*) has retained these features (flower color not given) when grown in the Rancho Santa Ana Botanic Garden in Claremont (*Balls 19406*). A very acute-leaved phase of open habit is represented by *Henrickson 17348*.

**Mirabilis laevis var. villosa**

**Involucre of var. villosa.**—Ordinarily, the involucral lobes of the var. *villosa* are about 1/2-1/3 the length of the tube. Plants in southwestern Arizona have unusually long involucral lobes, equal to, or even slightly longer than, the tube. These may have resulted from introgression with *M. tenuiloba* (*Reeves & Lehto L20124, Harrison II*). Some plants from the peninsula of Baja California have the dense viscid-villosous pubescence of the var. *villosa* but more or less thyrsoid inflorescences characteristic of var. *crassifolia*, and involucral lobes about as long as the tube (e.g., *Carter 5449, Thorne et al. 62452*).
Flower color of var. villosa.—Flowers are usually white in this variety. All three varieties mix in the Sierra San Pedro Martir of Baja California, where pink- or purple-flowered villous plants occur (Daniel 1414, Moran 24540). Transition from pink to white is seen in specimens where the throat retains pink but the perianth limb is white (M. Baker 4544, Palmer 208). On the west side range of var. villosa a number of collections document color variation in flowers within populations or departure from the usually white perianths of more eastern plants; white or pink perianths (Holmgren & Holmgren 6535), white to lavender (Munz & Hitchcock 12046), deep lavender (Wilken & Werner 7485), or pink (Cooper 2257—a plant intermediate to var. crassifolia in its acute leaves). In southeastern California collections by Hall and Chandler note white (7023) and pink (7024) flowers to occur in the same vicinity.

Pale pink, pink, lavender, or purple flowers are also known from farther east (Graham 3222, Henrickson 14004, Lloyd 2866; Train 1377; Wiggins 9648). In Kern Co., California, characteristics of varieties are variously combined; Twisselmann 8377 and Keck 2158, both from western part of the county are of open habit, have fairly large fruits, rather blunt leaves, and very villous pubescence, similar to “good” var. villosa, but in its “magenta” flowers and thyrsoid inflorescence it is more similar to the var. crassifolia. Eastward in the county, are plants with “rosy-purplish” perianths and lighter pubescence, with a few retrorse hairs, leaves spreading, large and blunt, overall with an aspect like var. villosa, but the lighter pubescence and spreading leaves characteristic also of var. retroversa (Howell 37226).

Leaf shape of var. villosa.—Plants with acute leaf apices occur along or near line of contact with the var. crassifolia in southern California (Peirson 1853; Roos s.n., 26 Mar 1966; Thorne & Tilford 40843; Tilforth & Durley 340). Sonoran plants often have ± acute leaves (Spellenberg 5444; Van Devender & Kearns s.n., 18 Feb 1977). More or less typical plants with rounded leaf apices occur as far west as the Transverse Ranges of California (Gustafson 1025).

Pubescence of var. villosa.—In the mountains of southern California plants often are more sparsely pubescent in basal parts but are notably villous in upper parts (Peirson 5336). Lightly pubescent specimens in southwestern Arizona (Peebles et al. 463) approach the var. retroversa, as do plants from southeastern California with the open habit and large, broad leaves of var. villosa, but with very short pubescence, often sparse on lower parts (Robinson & Lindner 57).

Inflorescences of var. villosa.—The dichotomous inflorescence characteristic of the desert races of M. laevis from east of the Sierra Nevada and the southern California coastal ranges is nicely illustrated by Glocy & Anderson 6603. Thyrsoid-like inflorescences more characteristics of the var. crassifolia occur in var. villosa well away from the range of the former in eastern Mojave Desert (Charlton & Pitzer 1834), or nearer to range of var. crassifolia in the southern California coastal ranges (Holmgren & Holmgren 7539) or in Baja California (Wiggins 20832).

Fruits of var. villosa.—Fruits in this variety vary from nearly globose to ellipsoid or obovoid, the surface mottled or striped. Example of variation are: fruits ± globose, grayish, with 10 very faint and indefinite pale lines (Lloyd 2636, Munz 12465, Spellenberg 10206, Turner 62-2); broadly obovoid, indefinitely pale-lined at base (Morefield 4800, Spellenberg 2982); ± globose, 10 faint, pale lines alternating with 10 diffuse darker lines (Parish 3183, Munz 10390); ± globose, very dark and dark-mottled, without lines (J. & L. Roos 4182); ellipsoid or obovoid, gray or brown and black- or dark-mottled (Boyd et al. 2112, Felger & Valenzuela L. 86-180, Higgins 6378, Reeves & Lehto L20124, Roos s.n, Spellenberg 10205); broadly obovoid, unlined, grayish brown (Jepson 5939) or faintly lined (Jepson 5937, same time and place).

APPENDIX 2

Representative and/or cited specimens. Specimens are cited by taxon, and within taxa geographically by country, state, and county, then alphabetically by collector. Those specimens that provided fruit for illustration in Figure 1 are indicated by and an asterisk (*) following herbarium citation.
Mirabilis laevis var. crassifolia

MEXICO. BAJA CALIFORNIA: 21.9 mi E of El Rosario via Hwy. 1, 13 Oct 1981, Burgess et al. 6095 (ARIZ, SD); 0.9 mi N of Rosario, 6 Feb 1953, Chisaki & Newcomb 525 (ARIZ, GH, RM, SD, UC); San Matías Pass of Sierra San Pedro Martir, 20 May 1981, Daniel 1345 (ASU); Cedros Is., ca. 2 mi S of lighthouse on E side, 23 Feb 1977, Davidson 3488 (RSA); 5 mi N of San Quintin, 15 Feb 1935, Epling & Robinson s.n. (ARIZ, GH, NY, RM, UC); Mina Desengaña, ca. 16 mi N of Punta Prieta, 30 Mar 1950, Gentry 8886 (ARIZ); Cedros Is., ca. 1 mi S of village at Cabo Norte, 19 Jan 1975, Henrickson 14453 (NMC); 1 km N of San Vicente, 6 Jan 1984, Hodgson & Pinkava 3011 (ASU); South Todos Santos Is., 7 Apr 1948, Moran 2802 (UC); Sierra San Borja, Rancho Carrizo, 20 Mar 1966, Moran 12832 (SD); San Esteban Is., NE peak, 28 Apr 1962, 112935W, 26 Apr 1966, Moran 13051 (SD); San Martín Is., 21 Apr 1970, Moran 17458 (RSA); 7 mi SE of Laguna Chapala, 18 Oct 1971, Moran 18694 (ARIZ, RSA, SD); Guadalupe Island, south end of island, 30 Mar 1889, Palmer 886 (US*); ca. 23 km NW of parador Cataviña [Santa Ihez], 15 Jun 1980, Reeder & Reeder 7259 (SD); San Martín Island, 3 mi off cinder cone of San Quintin, 21 Feb 1986, Thorne 61594 (RSA); Guadalupe Island, NE Anchorage, 28–29 Mar 1988, Thorne 63015. BAJA CALIFORNIA SUR: NW end of Viscaino Peninsula on road from Bahía Tortugas to Punta Eugenia, 2 May 1993, Boyd, Ross & Appleby 8100 (TEX); 26 km N of San Ignacio, 10 Jan 1948, Carter, Alexander & Kellogg 2522 (ARIZ, UC); 8 mi N of San Juancito, 8 Mar 1939, Gentry 4314 (ARIZ, GH); E bajada of Sierra Calvario, 10–15 Mar 1947, Gentry 7391 (ARIZ, RSA, UC); Picachos de Santa Clara, 5–10 Nov 1974, Gentry 7697 (SD); 2–3 mi E of Punta Eugenia, 13 Mar 1949, Gentry 8694 (ARIZ); between Volcán Tres Virgenes and Cerro Azufre, 27° 29' N, 112° 34' W, 11 Apr 1973, Henrickson 8940 (SD); Rancho la Laguna, Sierra San Francisco, 27° 35' N, 113° 02' W, 23 Nov 1976, Moran 23281 (SD); 6 mi N of San Andrés, Arroyo Calvario, 10 Feb 1973, Moran & Reveal 20006 (SD); Picachos de Santa Clara, 3 Feb 1973, Moran & Reveal 19689 (SD), 19671 (ASU, POM, SD); Cerro Azufre, 27° 30' N, 112° 36' W, 20 Oct 1971, Moran 18723 (SD, UC); Volcán las Tres Virgenes, 27° 29' N, 112° 36' W, 11 Apr 1973, Moran 20414 (SD), 20415 (SD, UC); Arroyo Malarrimo 11 mi S of mouth, 6 Feb 1973, Moran & Reveal 19870 (ASU, SD, UC). U.S.A. CALIFORNIA. Alameda Co.: W-facing slope of Mission Peak, 16 Jun 1980, Hovák 929 (CAS); E side of Fremont on Mission Peak, 16 Jun 1996, Spellenberg 12335 (F, MO, NMC*, NY, RSA, UC, US). Fresno Co.: Owens Mtn., 6 Apr 1951, Boolootian s.n. (JEPS); Owens Mtn., 6 mi SE of Friant Dam, 9 May 1953, Quibell 1890 (RSA). Kern Co.: Greenhorn Mts., Mt. Breckenridge, 3 Apr 1932, Benson 3214 (UC); Oildale - Woody Road, 17 Apr 1938, Hoover 3170 (DS, UC); entrance to Kern River Canyon, 7 Jul 1962, Howell 38142 (CAS); Woofford, 7 Jul 1962, Howell 38179 (CAS); Kern River Canyon, 21 Sep 1962, Howell 38675 (CAS); Caliente, 15 Apr 1916, Jepson 6752 (JEPS); 2.6 mi E of Caliente, 16 May 1963, Thorne 31702 (RSA); Templar Range, Cedar Canyon, 1 Jun 1952, Wittliff 198 (CAS); mouth of Kern Canyon, 11 Jun 1963, Wittliff 8391 (CAS, RSA, UC); 2 mi NE of Weldon, 5 May 1933, Voegelin 67 (UC). Los Angeles Co.: San Clemente Island, 10 Jun 1962, Blakley 5238 (SD); San Clemente Is., 25 Aug 1894, Braddegey s.n. (UC); Santa Monica Mts., Las Flores Canyon, 28 Mar 1930, Epling & Ellison s.n. (MO, RSA, UC); Los Angeles, 16 Apr 1904, Grant 791 (ARIZ, CAS, DS, RSA, UC); Los Angeles, May 1885, Gray s.n. (GH); Pacific Palisades, Temescal Canyon, 16 Apr 1941, Hastings s.n. (NY); Santa Catalina Is., S of Wilson’s Harbor, 2 Mar 1941, Moran 6699 (RSA); San Clemente Is., 2 mi S of Eel Point, 18 Sep 1958, Moran 6848 (DS, RSA, UC) [same site, 9 Mar 1959, Moran 7170 (DS, RSA)]; San Clemente Is., E coast, 9 Apr 1923, Munz 6645 (POM, UC); E of Zuma Beach, 4 Apr 1959, Raven 13964 (RSA); San Clemente Is., S of Eel Point, 11 Apr 1962, Raven 17307 (RSA, SD); San Clemente Is., just N of Guds, 9 May 1962, Raven 17655 (RSA, SD); near isthmus on Santa Catalina Is., Templetom 11388, 25 Feb 1968 (RSA); Santa Barbara Is., Cat Canyon, 28 Apr 1968, Thorne 37483 (RSA, SD); San Gabriel Mts., San Dimas Canyon, 9 Apr 1971, Thorne & Tilford 41536 (RSA); San Clemente Is., May 1903, Trask s.n. (A). Merced Co.: Mine Canyon near Little Panoche Valley, 6 Apr 1940, Hoover 4309 (DS); Mine Creek 1.5 mi N of junction of Merced, Fresno, San Benito cos., 11 Apr 1935, Lyon 932 (UC). Monterey Co.: 6 mi from King City, 10 May 1936, Eastwood & Howell 2396 (CAS, NY, UC); Redwood Gulch, 20 May 1960, Hardham 5795 (RSA); 6 mi N of King City, San Lorenzo Creek, 7 May 1963, Howell 39241 (RSA); 6 mi NE King City, 7 May 1963, J.T. Howell 39241 (RSA); 6 mi NE of King City, 7 May 1963, Rose 63030 (CAS, DS, RSA). Riverside Co.: Whitewater Canyon about 3 mi from mouth, 8 Apr 1932,
Ewan 7041 (POM); San Gorgonio Pass, 25 May 1914, Jepson 6073 (JEPS); Whitewater Wash near Whitewater, 11 Apr 1948, Korb 902 (JEPS); Dry Morongo Wash, 2 May 1952, Munz & Everett 16245 (RSA); San Benito Co.: ca. 6 mi SE of Pancho School, 12 May 1958, Beyllick 25 (RSA); Cherry Hill Sch. W of Llanada, 25 Apr 1937, Ewan 10309 (RSA); 17.6 mi from New Idria on road to Panoche, 6 May 1956, Raven et al. 9240 (RSA); Road 107, 14.5 km SE of junction with Little Panoche Rd, 27 km NW of New Idria, 17 Jun 1996, Spellenberg 12336 (NMC*, NY, UC). San Bernardino Co.: Dry Morongo Creek, 6 Apr 1933, Dunkle 3411 (RSA); Santa Ana River Canyon, 3 May 1919, Munz, Street & Williams 2672 (POM); Hwy. 330 ca. 3 mi E of Highlands, 27 May 1990, Spellenberg 10208 (NMC, NY, UC); Collius Valley, Indian Canyon, 28 Apr 1920, Jepson 8859 (JEPS); Fallbrook, 15 May 1920, Munz & Harwood 3900 (RSA); San Diego, Chollas Valley, 1 Jan 1884, Orcutt 2799 (MO). San Luis Obispo Co.: summit of Cottonwood Pass, 1 May 1949, Hoover 7644 (CAS); Escondido, 5 Jun 1904, Chandler 5332 (DS, GH, UC) (cited in new combination of M. tenutiloba var. polyphylla); 3 mi S of Clemente, 19 Mar 1966, Wallace 176 (SD); Otay Lake, 12 Apr 1981, Werff 4221 (SD); Cuyamaca Mts., 6 mi below Alpine, 20 Mar 1926, Wiggins 2054 (SD); Camp Kearney Mesa, 7 Apr 1935, Youngberg 7 (POM). Santa Barbara Co.: Santa Barbara Island. Cat Canyon, 4 May 1963, Blakley 5657 (US*); toward Figueroa Mtn., 4 Apr 1986, Bourrell, Patterson & Timbrough 2938 (CAS); Santa Cruz Is., 17 May 1962, Breedlove 2874 (DS); Santa Cruz Is., 9 Jun 1930, Clokey 4923 (NY, RSA, UC); Santa Cruz Is., 16–17 Jul 1917, Eastwood 6387 (CAS); Santa Barbara Is., Cat Canyon, 19 Mar 1968, Phibbs 868-80 (RSA); W of Goleta, 20 Sep 1956, Pollard s.n. (CAS);... Ventura Co.: 5 mi S of Fillmore, 2 Apr 1958, Solbrig 2670 (NY); 2 mi E of Point Mugu, 14 Mar 1959, Thompson 1857 (CAS).

Mirabilis laevis var. laevis
MEXICO. BAJA CALIFORNIA SUR: Magdalena Bay, 18 Jan 1889, T.S. Brandegee s.n. (GH*); E base San Lazaro Mt., Santa Maria Bay, 30 Mar 1952, Moran 3530; SD; Magdalena Bay, without date, Dr. Sung 28, UC (#101225, mounted on sheet with M. laevis var. crassifolia).

Mirabilis laevis var. retrorsa
MEXICO. BAJA CALIFORNIA: Sierra Juárez, Arroyo el Toruno, 17 Mar 1968, Moran 14842 (ASU, RSA); Cañon de Guadalupe, 32 09 N 115 48 W, 23 Mar 1986, Thorne, Boyd, et al. 61758 (RSA); San Matias Pass, 6.2 mi E of Ejido San Matias, 20 Apr 1985, Thorne and Charrton 60220 (RSA). U.S.A. ARIZONA. Mohave Co.: road from Chloride to the river, 13 May 1931, Eastwood 18313 (CAS*). CALIFORNIA. Inyo Co.: Panamint Range, Emigrant Springs, 6 Apr 1935, Clokey & Templeton 5725 (POM, NY, UC); White Mts., Silver Canyon, 1 Jun 1933, Dutton 3455 (CAS, POM, RSA); Panamint Mts., Surprise Canyon, 13 Jun 1930, Ferris 7988A (DUD, UC); ca. 25 air mi S of Olanche at Little Lake, 8 Jun 1979, Henricksen 18257 (NMC); ca. 25 air mi SSE of Olanche, 12 Jun 1979, Henricksen & Bekey 18288 (NMC, NY); Death Valley, S end, Bradbury Well, 9 Apr 1940, Munz 16449 (POM, UC); Eureka Valley along Big Pine road, 13 May 1962, Reveal & Reveal 50 (NY); ca. 25 mi S of Olanche at Little Lake, 8 Jun 1979, Henricksen 18257 (NMC); Darwin Falls Canyon, 30 Apr 1937, Train s.n. (DUD - 258204); Death Valley Natl. Mon., 25 Mar 1947, Wiggins 11529 (DUD, UC). Kern Co.: Red Rock Canyon, 1 May 1927, Abrams 11877 (POM); butte S of Mojave, 25 Mar 1932, Benson 3136 (POM); 2 mi E of Weldon, 12 May 1933, Cole & Voegelin 120 (UC); Mojave, 12 May 1913, Eastwood 3200 (POM); Mojave - Randsburg region, 0.5 mi W of Big Bend, 1 Jun 1962, Twisselman, 7280 (CAS); near Searsl PO, 8 May 1906, Hall and Chandler 6882, 6884 (UC); California City land development land, 10 Apr 1974, Holmgren & Holmgren 7697 (NMC, RSA); Kernville, 20 May 1962, Howell 37115 (CAS); NE of Lake Isabella, 12 Jul 1962, Howell 38667 (CAS); Red Rock Canyon, 13 May 1930, Peskin 8800 (POM, RSA); Sierra Way on N side of Lake Isabella, 5 km E of junction with Calif. Hwy. 178 at Bella Vista, 19 Jun 1996, Spellenberg 12342 (NMC*, NY); Cache Creek, ca. 0.5 mi W of Big Bend, 1 Jun 1962, Twisselman 7280 (CAS). Los Angeles Co.: Palmdale, May 1925, M. & E. Eping s.n. (MO); Lovejoy Buttes, 17 Apr 1932, Peskin 9846 (RSA). Riverside Co.: cultivated from Munz & Everett 16245, 26 May 1954, Bolls 19406 (RSA); Morongo Valley road ca. 1 mi N of Hwy 60, 7 Apr 1951, V. & A. Grant 15979 (RSA); Indio, 26 Apr 1906, M. E. Jones s.n. (POM); Coachella Valley, 2 Feb

**Mirabilis laevis var. villosa**


Mirabilis oligantha
MEXICO. BAJA CALIFORNIA: Catavina arroyo ca. 5 km N of Santa Ynez, 6 Jun 1974, Carter & Dempster 5865 (NMC); Catavina, 23 Mar 1932, Harvey 501 (US); Catavina Mesa, 22 Apr 1952, Gentry & Fox 11731 (LL*); Catavina, 24 Apr 1954, 114 45’ W, 21 Nov 1976, Moran 23808 (SD*); 1 mi S of Las Arraras, 25 Mar 1960, Wiggins & Wiggins 15940 (ARIZ, TEX*); E of El Marmol on trail to Gulf, 14 Feb 1935, Shreve 6845 (ARIZ); 10.1 mi (by road) N of Bahía San Luis Gonzaga, 6 Oct 1967, Hastings & Turner 67-10 (ARIZ),
SD); Sierra de Volcán 4 mi E of El Marmol, 13 Feb 1935, Wiggins 7571 (UC); Rancho Catavina, 35 mi S of El Marmol, 8 Mar 1930, Wiggins 4406 (UC); San Franciscoquito Wash, 18.7 mi (by Road) SW of Bahía San Luis Gonzaga, 12 Oct 1963, Hasting & Turner 63-158 (ARIZ). BAJA CALIFORNIA SUR: Picachos de Santa Clara, 5–10 Nov 1947, Gentry 7717 (ARIZ).

**Mirabilis oxybaphoides**

**MEXICO. CHIHUAHUA:** Ca. 23 air mi ENE of Villa Ahumada, 12 Sep 1973, Henrickson 12849 (NMC).

Mirabilis tenuiloba
MEXICO. BAJA CALIFORNIA: along trail from Guadalupe Cyn to Laguna Hanson, 32°10'N, 115°42'W, 13 Mar 1988, Clemens & Jonsson 1999 (SD); canyon 3 mi from Bahia de Los Angeles village toward San Borja, 17 Feb 1963, Cowan 2321 (CAS, GH, SD); Cocopa Mts., 22 Apr 1949, Gentry 8712 (ARIZ, RSA, SD); first large canan W of Punta Diablo, 25 Mar 1959, Moran 7251 (DS, SD); 29 mi N of San Luis Gonzaga, 30 oB, 114°40'W , 20 Apr 1960, Moran 8211 (SD); 5 end of North San Lorenzo Island, 24 Mar 1962, Moran 8877 (CAS, SD); ca. 6 km SE of Puerto Refugio, 17 Mar 1977, Moran 23949 (SD); Los Angeles Bay, Dec 1887, Palmer 600 (GH, UC) (paratype of Hesperonia polyphylla); 41.6 mi S of Mexicali, 22 Mar 1970, Powell & Turner 1708 (TEX, US*); Puerto Refugio, Punta Norte de la Isla Angel de la Guarda, 7 Feb 1986, Tenorio L. & Romero de T. 10836 (RSA, TEX); Bahia de los Angeles, 12 Feb 1962, Wiggins & Thomas 238 (US); 3/4 mi S of Puerto Cito, 21 Mar 1963, Wiggins & Wiggins 15863 (ARIZ, DS, GH, TEX, US*); Arroyo la Bocana near Rancho Santa Ynez, 13 Mar 1991, Vandevender et al. 91-410 (ARIZ, NMC).

BAJA CALIFORNIA SUR: San Marcos Island, 23 Apr 1952, Moran 3975 (UC); 29 Mar 1962, Moran 9005 (SD); Carmen Isd., Marquer Bay, 5 Apr 1962, Moran 9199 (RSA, SD, UC); 1 mi S of Mission Los Dolores, 25°05'N, 110°54'W, 4 Dec 1959, Wiggins, Carter, & Ernst 258 (UC); SONORA: Isla San Esteban, N side, 10 Apr 1968, Felger et al. 17573 (ARIZ, RSA, SD, UC); Sierra de Rosario, Gran Desierto, 10 Mar 1973, Felger 20652 (ARIZ, SD). U.S.A. ARIZONA. Yuma Co.: SE side of Tinajas Altas Mts., Borrego Canyon, 16 Jun 1992, Felger & Braya 92-613 (ARIZ, ASU, MO, RSA, TEX, UC); Tinajas Altas Mts., 7 Mar 1940, Goodding s.n. (ASU). CALIFORNIA. Imperial Co.: Colorado Desert, Coyote Wells, Apr 1905, Brandegee s.n. (US*); Coyote Wells, 16 Apr 1983, Jonsson & Clemens 472 (SD); Painted Gorge, 8 Apr 1941, Peirson 13075 (DS, RSA); In-Ko-Pah Mts. along Hwy. 98, 5 Mar 1966, Wallace & Wilkin 110 (RSA).

Riverside Co.: Devil's Canyon above Coral Reef Ranch, 23 Feb 1931, Ewan 4036 (CAS); West Canon, western edge of the Colorado desert, 18 Apr 1907, Parish 6072 (GH, NMC, TEX) (acc. to Parish's note, a toponym); Deep Canyon Wash, 11 Apr 1922, Peirson 2917 (RSA); Deep Canyon drainage, S side lower Pipistrelle Canyon wash, 29 Mar 1973, Zabriskie and Zabriskie 594 (RSA). San Diego Co.: Palm Canyon, Borrego Valley, 17 Mar 1940, Ramsey & Ramsey s.n. (POM); Borrego Desert, canyon toward the Palms, 24 Mar 1939, A. & R. Nelson 3236a (DS); Borrego Palm Canyon, 14 Apr 1936, Gander 1301 (SD).

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