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Origin of *Opuntia curvospina* (Cactaceae)

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ABSTRACT. *Opuntia curvospina* ($n = 22$) is intermediate in morphology and in ploidy level between *O. chlorotica* ($n = 11$) and *O. phaeacantha* ($n = 33$) and exhibits frequent meiotic aberrations and reduced pollen stainability. These data support the interpretation of *O. curvospina* as a species of hybrid origin between *O. chlorotica* and *O. phaeacantha*. *Opuntia martiniana* (L. Benson) Parfitt is superficially similar to *O. curvospina*, is also tetraploid ($n = 22$), but is distinguished by its style shape and other characters.

Opuntia curvospina was described by Griffiths (1916) based on specimens from the hilly desert region between Searchlight, Nevada, and Nipton, California. It was subsequently reduced to synonymy, first with *O. chlorotica* Engelm. & Bigel. (Britton and Rose 1919) and more recently with *O. phaeacantha* Engelm. var. *major* Engelm. (Benson 1969a, b). Recent chromosome studies have directed attention to reevaluating the relationships of these taxa (Pinkava and McLeod 1971; Pinkava et al. 1973, 1977; Parfitt 1978; Pinkava and Parfitt unpubl.), suggesting a hybrid origin for *O. curvospina* (Pinkava et al. 1973; McLeod 1973). This paper presents further data from additional chromosome studies, morphological and distributional studies, flavonoid chemistry, and pollination ecology that support the suggested hybrid origin of *O. curvospina*.

I have assumed that dry-fruited prickly-pears (series *Polyacanthae* and *Basilares*) cannot produce fleshy-fruited offspring (series *Opuntiae*), therefore only the latter were studied in the region of *O. curvospina*. Nearby *O. phaeacantha* var. *phaeacantha* and *O. macrorrhiza* are limited to higher elevations and are excluded from biosystematic considerations, but the former is included in the key for convenience in comparing the varieties of *O. phaeacantha*. *Opuntia martiniana* [*O. littoralis* (Engelm.) Cockerell var. *martiniana* (L. Benson) L. Benson] was included in the study because of its morphological and geographical similarities to *O. curvospina*. The California populations of *O. curvospina* were studied only from herbarium specimens.

MATERIALS AND METHODS

A complete set of voucher specimens is deposited in ASU, an incomplete set in OSH. Vegetative portions of each voucher were killed and fixed for at least 24 hr in FAA (ethanol-glacial acetic acid-formalin, 85:10:5, v/v/v) before pressing. Flower parts were pressed as usual. Morphological characters and measurements were determined from herbarium specimens whenever possible. Areole distribution on the stem is

expressed as the number of areoles on one segment face and margin, as visible on a segment mounted on an herbarium sheet. The number of areoles on the ovary includes those on all surfaces, except on the apical rim where they often coalesce. Habit was noted in the field.

Buds for meiotic chromosome determinations were fixed in modified Carnoy's solution (chloroform-ethanol-glacial acetic acid, 6:3:1, v/v/v). Anthers were stained in iron-acetocarmine and squashed according to the method of Beeks (1955). Pollen was obtained from herbarium specimens up to ten years old and stained in aniline-blue-lactophenol for 24 hr (Maneval 1936) to determine approximate fertility.

Flavonoids were extracted from the flowers and identified by standard methods and the modifications of Clark and Parfitt (1980).

RESULTS AND DISCUSSION

Morphology. *Opuntia chlorotica* is a tall plant with a conspicuous trunk and ascending branches. The stems and ovaries bear numerous areoles with translucent yellow glochids and spines. Although sometimes absent, the spines are usually numerous, up to ten per areole.

Opuntia phaeacantha is a lower, spreading plant that lacks a definite trunk and has the lower branches resting on the ground. The stems and especially the ovaries bear very few areoles. Spines are fewer per areole (up to six), opaque, mostly brown in var. *major* and usually all chalky white in var. *discata*.

Opuntia curvospina is morphologically intermediate between *O. chlorotica* and *O. phaeacantha* (table 1). It has a conspicuous trunk and ascending branches but is intermediate in height. Areoles are numerous but fewer than in *O. chlorotica*. Spines are numerous, translucent yellow in the apical half and reddish brown in the basal half. Because of the reduced plant height and especially the brown spine coloration, *O. phaeacantha* var. *major* seems a more likely parent than var. *discata*.

Similar to *O. curvospina* is *O. martiniana*. It is a smaller plant also with a trunk and ascending branches. However, areoles tend to be fewer than in *O. phaeacantha*. While the colors of the spines are similar to *O. curvospina*, they are pale or dull by comparison. Flower characters set apart *O. martiniana* from the other taxa. Its style is swollen at or above the middle, abruptly narrowed above, and tapered below (fig. 1). In other prickly-pears of the southwestern United States and the adjacent region of Mexico, most of whose styles were examined, the style tapers gradually upward from a swollen base (fig. 1). Also, the ovary of *O. martiniana* is more slender than in the other species studied.

The shape of the spines in cross-section has been given great importance by Benson (1969a, b, c). However, some specimens of *O. martiniana* from the type locality have spines flattened, instead of round as described by Benson (1969a, b). Some specimens of *O. phaeacantha* have spines that are round in cross-section, not flattened. Usually the spines of *O. martiniana* are not strongly flattened and the spines of the other species are.

TABLE 1. Morphological characters of *Opuntia curvospina* and related species.

Character	<i>O. chlorotica</i>	<i>O. curvospina</i>	<i>O. martiniana</i>	<i>O. phaeacantha</i> var. <i>major</i>	<i>O. phaeacantha</i> var. <i>diversa</i>
Habit	Trunk 20-30 cm, branches ascending	Trunk 10-15 cm, branches ascending	Trunk 10-20 cm, branches ascending	Trunk absent, branches spreading	Trunk absent, branches spreading
Plant height (m)	1.5-2.5	0.5-1.5	ca. 0.6	0.1-1.0	0.5-1.5
Stem segment length/width (cm)	11-20/11-17	13-22/12-19	9-16/9-15	12-22/10-14	18-33/12-21
Areoles/segment face	(66-)73-130	(45-)50-71	26-48(-55)	31-50	38-54(-65)
Ovary areoles	34-54	(16-)18-32	8-11(-18)	6-18	8-18
Spines in upper areoles	(0-)1-10	3-10	3-8	1-4	1-6
Style shape	Tapering upward	Tapering upward	Tapering downward	Tapering upward	Tapering upward
Spine direction	Mostly reflexed	Reflexed- spreading	Mostly spreading	Spreading or some deflexed	Appressed to appressed- spreading
Spine color	Translucent yellow	Bright red-brown, apex trans- lucent yellow	Pale yellow, base dull red-brown	Brown or apical 1/3 white	White or basal 1/3 brown
Ovary apex width (cm); pressed at anthesis	2-2.5	2-2.5	1.5	1.5-2.5	2-3

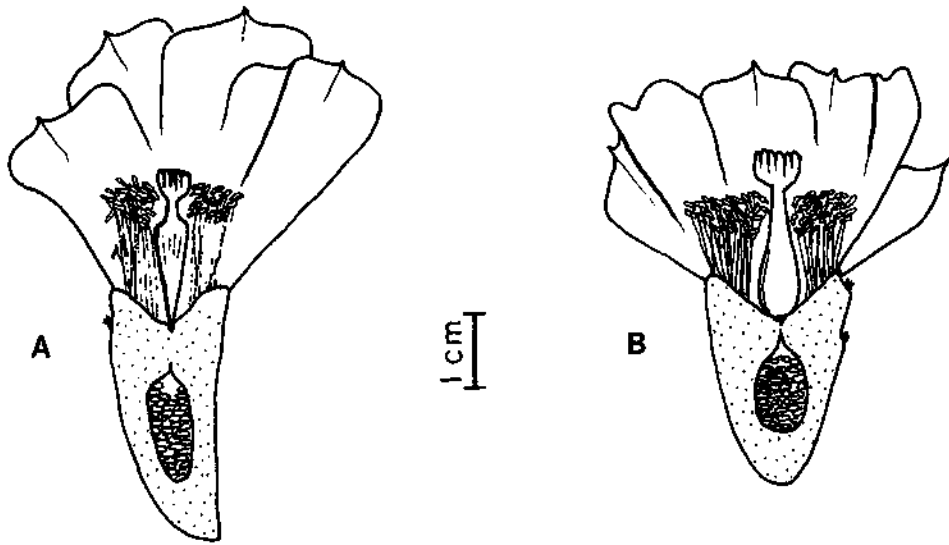


FIG. 1. Longitudinal sections of flowers of two species of *Opuntia*. A. *O. martiniana*. B. *O. phaeacantha* var. *major*.

Cytology. Chromosome numbers obtained in this study from preparations of microsporogenesis are consistent with previously published reports (table 2). In most of the taxa studied, meiosis is regular. Multivalents commonly occur in polyploids, but they do not appear to affect normal meiotic processes.

The diploid, *O. chlorotica*, appears to be highly fertile. Meiosis was consistently regular and pollen stainability was 86(74–97)% in five sam-

TABLE 2. Chromosome numbers of *Opuntia curvospina* and related species.

<i>O. chlorotica</i> :	$2n = 22$ (Stockwell 1935), $n = 11$ (Pinkava and McLeod 1971; Reveal and Styer 1973; Pinkava et al. 1977; Parfitt 1978; Pinkava and Parfitt unpubl.).
<i>O. curvospina</i> :	$n = 22$ (Pinkava et al. 1973, 1977; Parfitt 1978; Pinkava and Parfitt unpubl.).
<i>O. littoralis</i> :	$2n = 66$ (Philbrick 1963).
var. <i>vaseyi</i> :	$n = 33$ (Pinkava et al. 1973).
<i>O. martiniana</i> :	$2n = 44$, $n = 22$ (Pinkava and Parfitt unpubl.).
<i>O. phaeacantha</i> :	$2n = 66$ (Stockwell 1935; Yuasa et al. 1973), $2n = 44$ (Yuasa et al. 1973).
var. <i>discata</i> :	$2n = 66$ (Yuasa et al. 1973; Weedon and Powell 1978; Grant and Grant 1979), $n = 33$ (Pinkava and McLeod 1971; Pinkava et al. 1973, 1977). $2n = 66 + 1$ (Pinkava et al. 1973). $2n = 44$ (Grant and Grant 1979).
var. <i>major</i> :	$2n = 66$ (Weedon and Powell 1978; Grant and Grant 1979), $n = 33$ (Pinkava and McLeod 1971; Pinkava et al. 1973, 1977; McLeod 1975; Parfitt 1978; Pinkava and Parfitt unpubl.). $2n = 44$ (Grant and Grant 1979).

ples. Minor meiotic aberrations were detected in the hexaploid *O. phaeacantha*. As with other *Opuntia* polyploids (Pinkava and McLeod 1971), multivalents involving two or more pairs of chromosomes were present among the bivalents. An aneuploid number, $2n = 33_{II} + 1_1$, has been reported for *O. phaeacantha* var. *discata* with the comment that the specimen approaches var. *major* in some characters (Pinkava et al. 1973). Pollen stainability from 15 samples of *O. phaeacantha* was 86(58–99)% with 2.5(0–5)% micropollen.

Unlike either putative parent species, *O. curvospina* consistently has a tetraploid number in meiotic material (table 2). At metaphase I, the most frequently seen arrangement was four bivalents and nine quadrivalents. Occasionally more than four bivalents were seen, perhaps resulting from quadrivalents broken by excessive squash pressure during the preparation of the slide.

The first inversion bridges and fragments reported for the Cactaceae were found in two plants of *O. curvospina* (Pinkava et al. 1973). In the present study, an additional specimen was found with the fragment and bridge. The fragment and lagging chromosomes seen in late anaphase I and telophase I of many *O. curvospina* indicate this aberration to be apparently established in this taxon. Inversions, commonly found in interspecific hybrids (Magoon et al. 1958), are very uncommon in "good" species (Brown 1972).

In addition to the acentric fragment, as many as four laggards were aggregated into a micronucleus that formed a third spindle in telophase II. The laggards, fragments, and aggregates of these remained separate from the main nuclei. This resulted in the formation of micropollen that varied greatly in number and size. Pollen stainability of *O. curvospina* was 62(15–83)% in eleven samples, lower than in the other species studied. This was correlated with 8(1–26)% micropollen and the great number of normal-sized pollen grains with a reduced chromosome complement. Some tetrads appeared to be normal.

If *O. curvospina* were indeed conspecific with either *O. chlorotica* (Britton and Rose 1919) or *O. phaeacantha* var. *major* (Benson 1969a, b), it would be reasonable to expect one of these to have the same chromosome number (Brown 1972) as *O. curvospina*. If it were an autopolyploid derivative, *O. curvospina* would not be expected to differ significantly from the diploid parent except in size (Pinkava et al. 1977; Pinkava and McGill 1979; Pinkava and Parfitt unpublished). The tetraploid number coupled with frequent meiotic aberrations and reduced pollen fertility (Magoon et al. 1958) implicate *O. curvospina* as a hybrid between diploid and hexaploid parents such as *O. chlorotica* and *O. phaeacantha* respectively.

Plants of *O. martiniana* from the type locality are also tetraploid (table 2). Quadrivalents and most other aberrations common to *O. curvospina* were not seen. However, random separation (24/20, 23/21) and lagging chromosomes (22/21/1, 21/16/7, 20/18/6) at anaphase I appeared respon-

sible for a somewhat lowered pollen stainability of 80(68–86)% and 2(0.5–5)% micropollen in four samples. Although *O. martiniana* has the same chromosome number as *O. curvospina*, its meiotic behavior and morphology set it apart from the hybrid. Although treated as a variety of the hexaploid *O. littoralis* by Benson (1969a, b), *O. martiniana* probably has very different origins from that coastal species. The report of *O. martiniana* crossing with *O. phaeacantha* (Benson 1969a) has not been substantiated.

Grant and Grant (1979) reported both tetraploid and hexaploid numbers from *O. phaeacantha* vars. *major* and *discata* in Texas but did not explain the origins of, or the reproductive interactions between, plants of the different ploidy levels. Chromosome numbers in some individuals determined by Grant and Grant (1979) were both tetraploid and hexaploid. These numbers, like the tetraploid *O. phaeacantha* reported by Yuasa et al. (1973), were determined from root tip material. Weedon and Powell (1978) have shown that a single root tip can yield ploidy levels of $4n$, $5n$, and $7n$.

Pollination ecology. The week of 7–14 Jun 1978 represented a span of time when *O. chlorotica* and *O. phaeacantha* flowered together in the Cerbat Mountains of northwestern Arizona. During this week, *O. phaeacantha* was producing its last flowers of the season; many plants had already finished flowering. At this same time, the first flowers of *O. chlorotica* were beginning to open; many plants of this species did not begin flowering until later in the week. Thus, the putative parent species had the opportunity to hybridize if they shared a common pollen vector. However, the phenological overlap was slight and possibly absent in other years or in other areas. This may help to explain why *O. curvospina* does not always occur where the putative parents are found together. Interestingly, *O. curvospina* was at the peak of its flowering during the time of overlap between the other two species.

As may be expected for a genus where hybridization is common, the known pollen vectors for *Opuntia* are not at all species-specific. Insects visiting the flowers of *O. chlorotica* and *O. phaeacantha*, apparently all of the same few species (Parfitt and Pickett 1980), were also visitors to *O. curvospina*.

Chemistry. All of the taxa studied, plus *O. littoralis* var. *littoralis*, produced the same set of flavonoid glycosides (Clark and Parfitt 1980). These chemical data cannot be used to support or refute the conclusions regarding interspecific relationships arrived at through other studies. Flower flavonoids in *Opuntia* are of limited diversity and are therefore of little value in distinguishing most species. Different groups of species may have different sets of flavonoids, but within a group there may be no interspecific variation in flavonoid composition. The identical flavonoid patterns of the species studied do support placing them together in series *Opuntiae* (Benson 1969a, b, c). Preliminary results on *O. basilaris*

(series *Basilares*), *O. erinacea* (series *Polyacanthae*), and *O. acanthocarpa* (subgenus *Cylindropuntia*, series *Echinocarpaceae*) indicate that their arrays of flavonoids are different from each other and from series *Opuntiae*.

Conclusions. Evidence from this study suggests that *O. curvospina* originated from the hybridization of *O. chlorotica* and *O. phaeacantha*. The varieties of *O. phaeacantha* intergrade to the extent that intermediates are often more common than the varieties themselves. Therefore it is not apparent whether var. *major*, var. *discata*, or an intermediate was involved in the parentage of *O. curvospina*. Because of *O. curvospina*'s reduced size and brown spine coloration, var. *major* tends to be the more likely parent.

Although *O. martiniana* is similar in morphology and chromosome number to *O. curvospina*, there are significant differences that set them apart. The distinguishing characters are mainly style shape and meiotic behavior, but usually areole density and the size and shape of the ovary are also useful. Although gross morphology indicates a close relationship to *O. curvospina*, the parentage is not apparent. Its style shape cannot be explained by gene flow from any extant species. It seems unlikely that the tetraploid, *O. martiniana*, and the hexaploid, *O. littoralis*, share similar origins as implied by the taxonomy of Benson (1969a, b). The former is known from a single mountain range in northwestern Arizona; *O. littoralis* s. str. occurs only on the coastal plain of southern California. *Opuntia martiniana* is, therefore, recognized as a species in the following taxonomy.

KEY TO *OPUNTIA CURVOSPINA* AND ALLIES

- Spines reflexed, translucent yellow, becoming dull brown, then black with age; fruit areoles 34–54, excluding the apical rim; stem areoles 73–110 (66–130) per segment face, including the margin 1. *O. chlorotica*
- Spines (all or some of them) spreading, not all yellow: white, brown, white and brown, or brown and yellow, the latter becoming dull brown, then black with age; fruit areoles 6–32; stem areoles 26–71 per segment face.
- Shrub 0.1–1.5 m tall; spines white, brown, or brown and white, or opaque-yellow and brown; fruit areoles 8–18; style with a rounded swelling below the middle 2. *O. phaeacantha*
- Spines present in all areoles or nearly so, chalky-white or sometimes brown in the basal one-eighth 2a. var. *discata*
- Spines usually absent from the lower one-fourth or more of the segment, brown or sometimes whitish in the apical one-half.
- Stems trailing; spines 3–9 above, absent from the lower one-fourth or less of the segment 2b. var. *phaeacantha*
- Stems clumped, suberect; spines usually 1–3 above, absent from the lower one-half or more of the segment 2c. var. *major*
- Arborescent, 0.5–1.5 m tall; spines translucent yellow with brown bases, becoming dull brown, then black with age; fruit areoles (16–)18–32 or, if fewer, the style with a truncate swelling above the middle.
- Style thickest below the middle, the swollen portion lanceolate to elliptic-lanceolate in outline; ovary at anthesis stout, 2–2.5 cm in diameter at the apex; spines yellow, the basal one-half or more of most spines reddish brown 3. *O. curvospina*

Style thickest at or above the middle, the swollen portion oblanceolate in outline and nearly truncate at the apex; ovary at anthesis slender, ca. 1.5 cm in diameter at the apex; spines yellow, the basal one-third or less of at least some spines dull brown 4. *O. martiniana*

1. *OPUNTIA CHLOROTICA* Engelm. & Bigel. in Engelm., Proc. Amer. Acad. Arts 3:91. 1856.—LECTOTYPE (fide Benson 1970 in herb. MO): United States, Bill Williams Mt., 2 Jan 1853, *Bigelow s.n.* (MO, photograph: ASU!).

Distribution: Rocky hills and, occasionally, flats in desert grassland, oak or juniper-pinyon woodland, and open chaparral; 900–1500 m; S California, S Nevada, Arizona, SW New Mexico, and in Baja California Norte and Sonora.

2. *OPUNTIA PHAEACANTHA* Engelm. in Gray, Mem. Amer. Acad. Arts 4:51. 1849.—LECTOTYPE (fide Benson 1970 in herb. MO): United States, Santa Fe, Nov 1846, *Fendler 8* (MO, photograph: ASU!).

The typical variety and var. *major* are very similar, the types of both being from the vicinity of Santa Fe, New Mexico. Pending further bio-systematic data, the two are maintained. Although considered as synonymous with *O. littoralis* var. *martiniana* by Benson (1969a, b), *O. charlestonensis* Clokey appears to be an unusual population of *O. phaeacantha*. It has the characteristic style shape of the latter and spines were described as being white, not yellow. However, further studies may indicate it deserves varietal status within *O. phaeacantha*. For synonymy of the following varieties, see Benson (1969a, b, c).

- 2a. *OPUNTIA PHAEACANTHA* Engelm. in Gray var. *PHAEACANTHA*.

Distribution: Arid grassland, juniper-pinyon woodland, interior chaparral, and open ponderosa pine forest; 1350–2400 m; Arizona, S Utah, S Colorado, New Mexico, and W Texas.

- 2b. *OPUNTIA PHAEACANTHA* Engelm. in Gray var. *MAJOR* Engelm., Proc. Amer. Acad. Arts 3:293. 1856.—LECTOTYPE (fide Benson 1970 in herb. MO): New Mexico, 4 miles E of Santa Fe on S side of rocky butte, 22 Dec 1846, *Fendler s.n.* (MO, photograph: ASU!).

Distribution: Desert scrub, desert grassland, juniper woodland, and open interior chaparral; 900–1350 m; S California, S Nevada, S Utah, Arizona, New Mexico, S Colorado, W Kansas, Oklahoma, Texas, and in Sonora, Chihuahua, and Coahuila.

- 2c. *OPUNTIA PHAEACANTHA* Engelm. in Gray var. *DISCATA* (Griffiths) Benson & Walkington, Ann. Missouri Bot. Gard. 52:265. 1965.—*Opuntia discata* Griffiths, Ann. Rep. Missouri Bot. Gard. 19:266–267, pl. 27. 1908.—*Opuntia engelmannii* Salm-Dyck var. *discata* (Griffiths) C. Z. Nelson, Galesburg (Illinois) Register, 20 Jun 1915.—TYPE: Arizona, “foothills of the Santa Rita Mountains,” Apr 1905, *Griffiths 7790* (US, photograph: ASU!; isotype: POM, photograph: ASU!).

Opuntia superbospina Griffiths, Proc. Biol. Soc. Wash. 29:13. 1916.—*Opuntia phaeacantha* Engelm. var. *superbospina* (Griffiths) L. Benson, J. Cact. Succ. Soc. Amer. 46:79. 1974.—TYPE: Arizona, Mohave Co., "about 15 miles southeast of Kingman," *Griffiths 10574* (type not seen).

Distribution: Desert scrub, desert grassland, and open interior chaparral; 900–1650 m; S California, S Nevada, Arizona, SW Utah, New Mexico, W Texas, and in Sonora, Chihuahua, and Coahuila.

3. *OPUNITA CURVOSPINA* Griffiths, Bull. Torrey Bot. Club 43:88–89. 1916.—TYPE: Nevada, Clark Co., "between Nipton, California, and Searchlight, Nevada," Apr 1912, *Griffiths 10530* (US; photograph: ASU!; isotype: POM; photograph: ASU!).

Distribution: Rocky hills and bajadas in the Mojave Desert, desert grassland, juniper grassland, and open interior chaparral; 1000–1400 m; SE California in San Bernardino County, S Nevada in Clark County, and NW Arizona in Mohave County.

4. *Opuntia martiniana* (L. Benson) Parfitt, comb. nov.—*Opuntia macrocentra* Engelm. var. *martiniana* L. Benson, Cacti Ariz., 2nd ed. 64. 1950.—*Opuntia littoralis* (Engelm.) Cockerell var. *martiniana* (L. Benson) L. Benson in Benson & Walkington, Ann. Missouri Bot. Gard. 52:270. 1965.—TYPE: Arizona, Mohave Co., "Kingman Road (old Hwy 93) on the north side of Hualapai Mountain (foothills)," 30 Mar 1940, *Benson 10169* (POM!).

Distribution: Low rocky hills in juniper grassland, open interior chaparral, and ponderosa pine-chaparral associations in canyons; 1200–1650 m; NW Arizona in the eastern and northern foothills of the Hualapai Mountains. The distribution given here is much reduced in comparison to Benson (1969a, b) because several discordant elements have been excluded in the present treatment.

EXCLUDED NAME

Opuntia mojavensis Engelm. & Bigel. in Engelm., Proc. Amer. Acad. Arts 3:293. 1856.—*Opuntia phaeacantha* Engelm. var. *mojavensis* (Engelm. & Bigel.) Fosberg, Bull. S. Calif. Acad. Sci. 33:103. 1934.—TYPE: California, "on the Mojave, west of the Colorado" (type not seen).

The original description of *O. mojavensis* is too brief for the accurate placement of the name. The number and characteristics of the spines suggest an affinity with *O. curvospina*. However, the prostrate habit and distant areoles indicate an affinity with *O. phaeacantha* var. *major*. This confusion has been expressed in publications (Fosberg 1934, 1942; Armer 1934; Clover and Jotter 1944) and in herbaria where specimens of *O. curvospina* or *O. phaeacantha* were placed under the name *O. mojavensis* or *O. phaeacantha* var. *mojavensis*.

Although Britton and Rose (1919) examined the fragmentary type specimen and reluctantly maintained *O. mojaviensis* as a species, I have been unable to locate the holotype of *O. mojaviensis* at MO, US, NY, or POM. Even with the eventual rediscovery of the type it is doubtful that *O. mojaviensis* will acquire specific or varietal recognition or be accurately placed in the synonymy of an established taxon.

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