

Systematic Studies of *Eschscholzia* (Papaveraceae). I. The Origin and Affinities of *E. mexicana*

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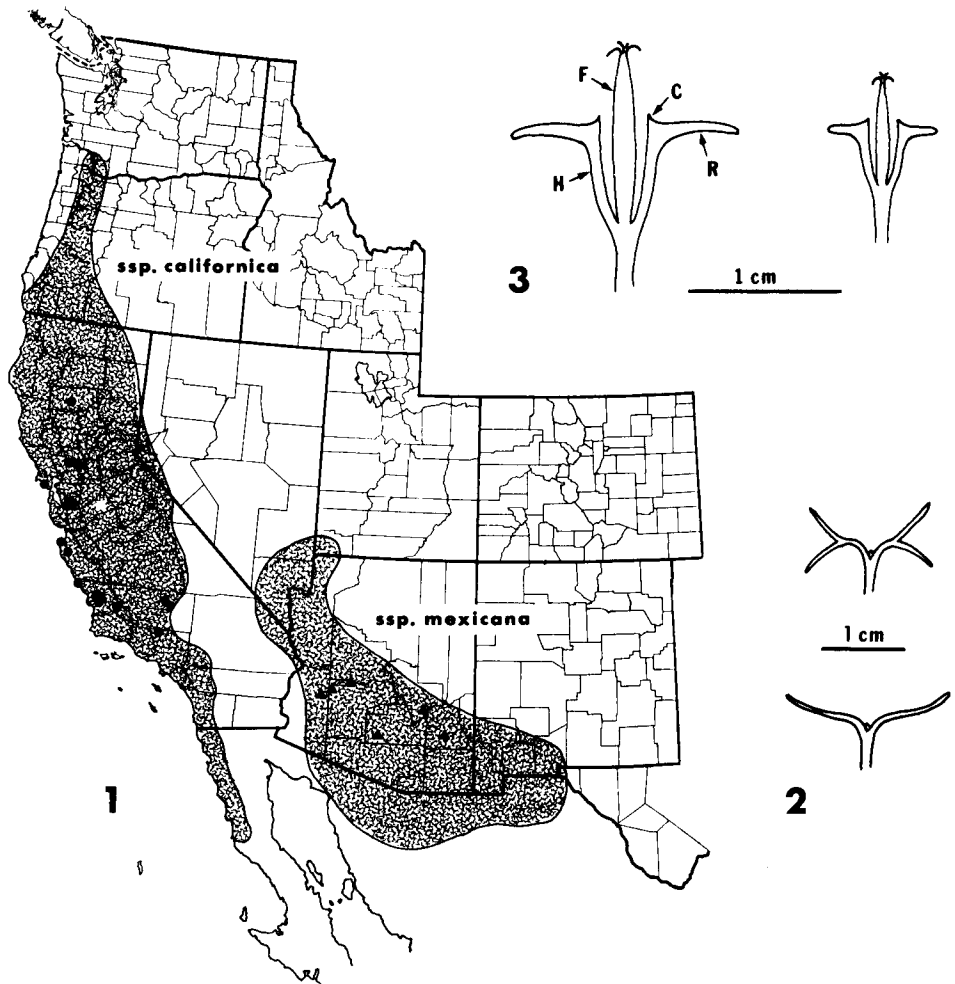
Abstract. *Eschscholzia mexicana* Greene differs from *E. californica* Chamisso only by its entire (versus bifid) cotyledons and its consistent obligately annual growth form. Although the taxa are allopatric in the field, artificial hybrids are easily formed, and are fertile even in F₂ and backcross generations. *Eschscholzia mexicana* is best regarded as a subspecies of *E. californica*, which had extended its range into the Sonoran Desert region during glacial times and has subsequently been isolated by increasing warmth and dryness in the intervening regions.

As generally treated, *Eschscholzia mexicana* is an annual species of the Sonoran Desert, ranging from extreme eastern California east to the Organ Mts. of New Mexico and the Franklin Mts. of western Texas, north into southwestern Utah, and south into northern Sonora and northwestern Chihuahua (Fig. 1). Plants of this species more closely resemble *E. californica*, the common perennial species of the Pacific states (Fig. 1), than any other *Eschscholzia*, and the two species have been thought to be closely related.

Martin (1941) felt that *E. mexicana* was "not a very convincing species, but hardly to be merged entirely with any of the others of our region [Nevada]." Cook (1962) speaks of "the very closely related [to *E. californica*] or identical species, *Eschscholzia mexicana* . . ." and suggests (1961) that the annual form of *E. californica* extends from Alameda Co., California, to Texas and Sonora. Lyman Benson has also suggested that *E. mexicana* is perhaps not specifically distinct from *E. californica* (pers. comm., 1976).

Historically, the maintenance of *E. mexicana* as a species distinct from *E. californica* is almost an accidental result of botanical regionalism. E. L. Greene, the author of *E. mexicana*, certainly believed that it was distinct from *E. californica*, but he also felt that four more species of the Sonoran Desert and 62 species (mainly of his own description) of Baja California, California, Oregon, and Nevada were also distinct from either *E. californica* or *E. mexicana* (1905), all of which have been subsequently submerged within one or the other of these two species. Furthermore, Greene did not even distinguish between a "mexicana" group and a "californica" group. Since the time of Greene, various botanists have placed all 66 other names in synonymy with either *E. mexicana* or *E. californica*. Arizona botanists have placed Arizona species in synonymy with *E. mexicana* (the earliest epithet from their region) and California botanists have placed California species in synonymy with *E. californica*.

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FIGS. 1-3. 1. Native distribution of *Eschscholzia californica*. Circles (*ssp. californica*) and triangles (*ssp. mexicana*) represent populations used in this study. 2. Seedling of subsp. *californica* (above), with bifid cotyledons; seedling of *ssp. mexicana* (below). 3. Cross-sectional view of receptacle and young fruit of *E. californica*. Left, subsp. *californica*, showing the maximum development of the hypanthium rim (R), the body of the hypanthium (H), the fruit (F), and the point of attachment of the corolla and stamens (C), which abscise shortly after pollination. Right, *ssp. mexicana*, showing the less-developed rim typical of most populations of this subspecies and some of *ssp. californica*.

(the oldest epithet from this region). Only a few taxonomists, such as Martin (1941) in Nevada, have been forced to compare the taxa and distinguish between them.

The characters used by Martin to separate the taxa are the perennial nature of *E. californica*, its bifid cotyledons (Fig. 2), and its widely flaring hypanthium rim (Fig. 3), as contrasted with the annual habit, entire cotyledons, and somewhat narrower hypanthium rim of *E. mexicana*. Cook

(1962) found that width of the hypanthium rim was not an especially useful character in *E. californica*, varying with the season and the position of the flower in the inflorescence.

Believing that further study would better elucidate the biological relationships between the taxa, and consequently allow a more precise taxonomic treatment, I investigated the constancy of key characters, examined seed coat microsculpturing, observed both species in their natural habitats, and formed artificial hybrids, to test interfertility and inheritance of characters.

MATERIALS AND METHODS

I obtained living plants for this study at 22 localities in California and Arizona (Appendix 1) by transplanting seedlings or adult plants from the field, and by germinating field-collected seed. Plants transplanted best as seedlings; transplantation of adults is generally successful only with the longer-lived perennials. Seeds were germinated in plastic Petri plates on filter paper moistened with a 500 ppm solution of gibberellic acid (after the method of Cook, 1961), or, in the case of some California populations, directly in the potting mix with the application of distilled water.

Cultivation.—Plants were grown in a UC-type potting mix (Baker, 1957) in plastic pots. Greenhouse temperatures sometimes exceeded 40°C but were never lower than 5°C.

Experimental Hybridization.—Since *E. californica* exhibits a low frequency of self-pollination (Cook, 1962), it was necessary to emasculate flowers intended as carpellate parents in artificial cross-pollinations by removing the undehisced stamens with forceps shortly after opening of the protandrous flowers. Plants having all flowers either emasculated or removed were placed in groups to avoid the possibility of flowers brushing together or of wind pollination. This procedure was successful, since emasculated flowers which were not subsequently pollinated set no fruit.

I transferred pollen to emasculated flowers with an artist's paint brush, or more successfully, with my index finger, either instrument being immersed between crosses in 70–95% ethanol to kill residual pollen.

A total of 13 different intraspecific F_1 crosses, 16 interspecific F_1 's, 4 F_2 's, and 8 backcrosses were generated, and more than 150 hybrid individuals were examined.

Estimates of Fertility.—Fertility of hybrids can often provide an assessment of the degree of relationship of the parental taxa. I estimated fertility using both pollen stainability and regularity of pairing at first meiotic metaphase.

Pollen was removed from the flowers and stained in cotton blue (Radford et al., 1974). I counted the percentage of well-stained and otherwise normal grains in a sample of at least 250 grains for parental plants and

500 grains for hybrids. Multiple values from a single hybrid or parental population were averaged.

Flower buds for meiotic analysis were fixed in absolute ethanol and acetic acid (3:1, v/v) for 24 hours or longer and stored in 70% ethanol at -5°C . Anthers were squashed in iron-free acetocarmine and viewed with phase optics.

Comparison of Seed Coat Microsculpturing.—Seeds to be examined with the scanning electron microscope were removed dry from seed collections, affixed to the specimen stub with silver conductive paint, shadowed with gold in a vacuum evaporator, and viewed with a Cambridge Stereoscan S4 scanning electron microscope.

Vouchers of field collections and many hybrids are at DAV.

RESULTS

Comparison of the Taxa

Of the three characters used by Martin (1941) to separate the taxa, width of the hypanthium rim is least useful. Although many *E. californica* plants have wide rims, others have rims essentially obsolete, so that variation within *E. californica* encompasses that of *E. mexicana*.

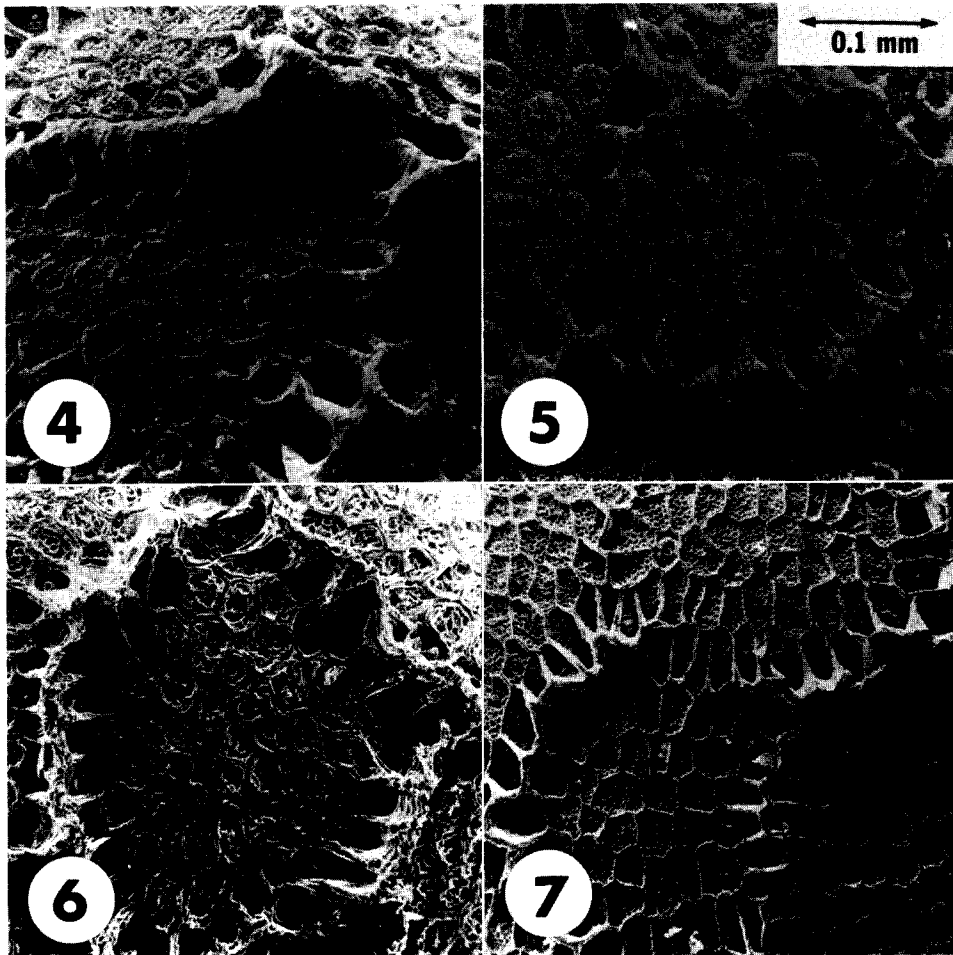
Cotyledons.—Martin's examination of twenty-five embryos of *E. mexicana* and my examination of hundreds of seedlings of both taxa suggest that the cotyledon character is constant. Nevertheless, Curran (1888) reported seedlings of *E. californica* from San Francisco each with either two bifid, two entire, one entire and one bifid, or even trifid and tetrafid cotyledons. Cook (1961) reported five populations out of 41 with a few plants having entire cotyledons, and a single greenhouse-grown plant from population 504 in this study had two entire cotyledons.

Perennation.—Though plants of *E. californica* are generally capable of perennating (Clark, unpublished), I have been unable to induce any plants of *E. mexicana* to perennate under greenhouse conditions, and there is no evidence that any ever perennate in the field.

Stamen Number.—Cook (1961, 1962) believed that stamen number could be a useful character for distinguishing races of *E. californica*. I have counted as few as 13 stamens and as many as 47 in *E. californica*, whereas in *E. mexicana* there are generally 20–25.

Seed Germination.—Seeds of some populations of *E. californica* germinate with no special treatment, whereas others (e.g., 521, 536) show less than 10% germination even with gibberellic acid and cold treatment. Most populations of *E. mexicana* have a low germination rate, but never lower than these *E. californica* populations.

Seed Coat Microsculpturing.—Both taxa are more variable than most other *Eschscholzia* species, and there are no characters which clearly sep-



FIGS. 4-7. Scanning electron micrographs of the seed surface of *E. californica*. 4. Ssp. *californica* (446). 5. Ssp. *californica* (ASL). 6. Ssp. *mexicana* (515). 7. Ssp. *mexicana* (510).

arate them. In contrast, seed coat characters can be used to distinguish easily between other species in the genus which are presumed to be closely related. The structure of the seed coat is described by Clark and Jernstedt (this volume, pp. 386-402) but comparative photographs of *E. californica* and *E. mexicana* are presented here (Figs. 4-7).

Habitat and Climatic Preferences.—Although the two taxa are morphologically quite similar, they show definite differences in the environments they inhabit. *Eschscholzia californica* occupies a wide variety of habitats, from coastal dunes and open slopes in redwood forests to arid plains and valleys and even desert margins, but it is found in full desert environments only at the extreme southern end of its range in northern Baja

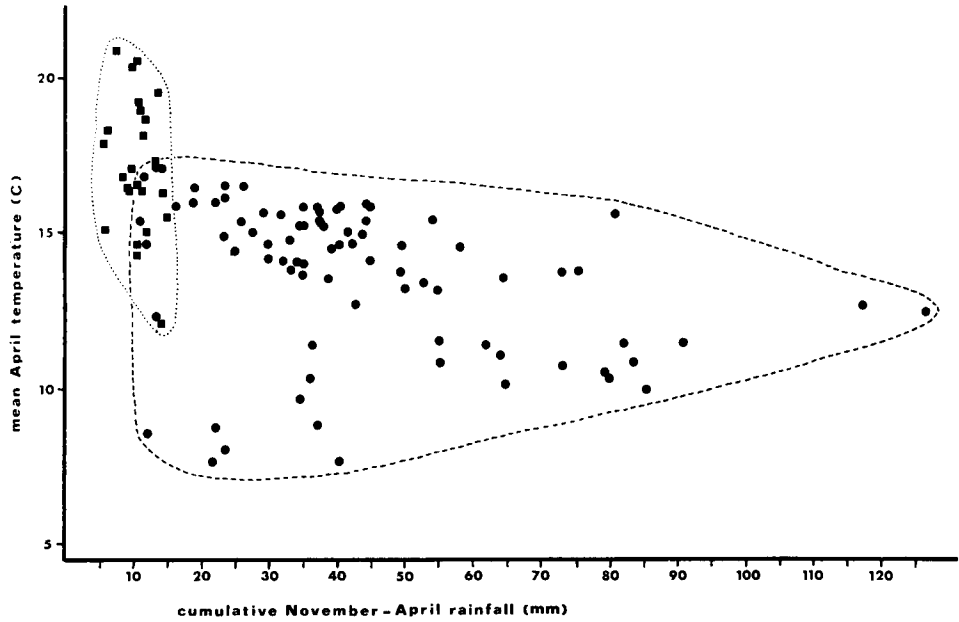


FIG. 8. Climatic tolerances of the subspecies of *E. californica*. Circles, ssp. *californica*; squares, ssp. *mexicana*. Data from Wernstedt (1972).

California. *Eschscholzia mexicana*, on the other hand, grows primarily in deserts. Thus there would seem to be a climatic separation between the two taxa.

To determine the nature and extent of these climatic differences, I plotted cumulative November–April precipitation against mean April temperature for a number of localities where the plants grow (Fig. 8).

Cumulative November–April precipitation is a more relevant measure than cumulative annual precipitation, since spring-flowering annual *E. mexicana* derives no benefit from summer convective storms that account for much of the precipitation of the Sonoran and Chihuahuan deserts, and summer precipitation is negligible over most of the range of *E. californica*. Mean April temperature provides a crude measure of temperature during the flowering season.

Examination of Fig. 8 shows that the two taxa overlap somewhat. The *E. californica* stations involved in the overlap are in the dry eastern part of the south Coast Ranges and along the desert margin. Here the plants are unable to perennate under natural conditions, enduring for their entire lives conditions much like those which affect *E. mexicana*.

Formation and Analysis of Hybrids

Hybridization is generally uncommon in *Eschscholzia*. Field hybrids are virtually unknown. Artificial hybridization of *E. parishii* and *E. glypto-*

sperma produces few viable seeds, and the resulting plants are highly infertile. *Eschscholzia lemmonii* × *hypocoides* hybrids, although freely produced, have reduced fertility. A total of over forty attempts to hybridize *E. californica* with either *E. parishii*, *E. glyptosperma*, *E. caespitosa*, *E. lemmonii*, *E. hypocoides*, and *E. lobbii* were unsuccessful (Clark, unpublished data).

In direct contrast is the artificial hybridization of *E. californica* with *E. mexicana*. Hybrid seed is formed with no great difficulty, failures being due to technical problems, rather than any biological incompatibility. The seed germinates more readily than seed of *E. mexicana*, around 40–80% in a one-month period. Hybrid plants are vigorous in container culture.

Fertility.—Pollen fertility of parental and hybrid plants is presented in Appendix 2. It is apparent that pollen fertility is slightly depressed in the interspecific F_1 's (ca. 73%), even in comparison to the intraspecific F_1 's (ca. 96%), but that fertility is regained in the F_2 's (94.5%) and backcrosses (ca. 82%). These values for pollen fertility are much higher than those of *E. glyptosperma* × *parishii* crosses (ca. 0%), *E. californica* × *minutiflora* crosses (ca. 20%), *E. caespitosa* × *minutiflora* crosses (ca. 2%), *E. lemmonii* × *hypocoides* crosses (ca. 50%), and even some intraspecific crosses in *E. parishii* (ca. 0%) (Clark, unpublished data).

In order to determine whether the high pollen fertility is indeed an indication of normal meiosis, meiosis was examined in the hybrids 1KM, 6KM, 7KM, 9KM, and 11KM (Appendix 2), and was found in all cases to be regular, yielding six bivalents in the microsporocytes at I metaphase and microspores with six chromosomes each.

Cotyledons.—*E. californica* × *mexicana* F_1 's had two entire cotyledons, or two bifid cotyledons, or one entire and one bifid (Table 1). Data for F_2 's and backcrosses are also listed (one backcross progeny had one bifid and one trifold cotyledon). I am unable to postulate a simple Mendelian basis for this inheritance. Cotyledons of greenhouse populations of the individual taxa grown from field-collected seed are as invariable as natural populations, yet the complete range of phenotypes present in the F_1 generation suggests incomplete dominance, polygenic inheritance, or substantial heterozygosity in the parental populations.

Stamen number.—In this character the hybrids are almost precisely intermediate between their parents.

Growth Habit.—After flowering, F_1 and most F_2 and backcross plants were able to resume vegetative growth prior to flowering again, and many continued this pattern through several cycles of vegetative and floral growth. This is the manner in which *Eschscholzia* perennates (Clark, unpublished). Parental *E. mexicana* plants are not capable of this growth pattern. Lifespan of the hybrids varied from less than a year for many of the F_1 's and backcrosses to *E. mexicana*, to over two years (and still

TABLE 1. Cotyledon shapes of *E. californica* × *mexicana* hybrids.

Hybrid*	Bifid Bifid	Bifid Entire	Entire Entire	Hybrid*	Bifid Bifid	Bifid Entire	Entire Entire
1KM	2	1	6	13KM	2	0	1
2KM	0	0	1	1MK	1	1	1
3KM	4	0	0	2MK	0	0	3
4KM	3	0	0	1KM × 1KM	2	0	3
5KM	0	0	3	2KM × 2KM	1	2	6
6KM	0	1	4	3KM × 3KM	0	0	1
7KM	0	1	5	5KM × 5KM	0	1	7
8KM	0	0	2	1KM × 511	0	0	1
9KM	1	0	0	5KM × 504	2	1	5
11KM	0	0	1	5KM × 506	4	0	0
12KM	0	0	1	501 × 1KM	2	0	0

* Abbreviations of hybrids given in Appendix 2.

living) for some of the backcrosses to *E. californica*. Behavior of the hybrids is in a sense intermediate to that of the parents, the hybrids being capable of the reversion to vegetative growth necessary to perennate, but incapable of sustaining long-term growth under the rigors of continued container culture throughout several seasons.

CONCLUSIONS

Taxonomy.—Available evidence strongly indicates that *Eschscholzia californica* and *E. mexicana* are best treated as conspecific taxa. In contrast to the other recognized species of *Eschscholzia*, there are no breeding barriers between the taxa. Interspecific F_1 's are only slightly less fertile than intraspecific F_1 's, and fertility is even higher in F_2 's and backcrosses. Meiosis in the hybrids is normal, indicating an absence of any substantial chromosome repatterning or other chromosomal incompatibilities. The hybrids are as vigorous in container culture as their parents. The taxa have the potential to freely exchange genes, with no barriers of infertility or inviability.

Furthermore, the two taxa are morphologically indistinguishable save for the growth form (which is not a clear dichotomy between annuals and perennials) and cotyledon shape (which is also not totally reliable). A number of other characters can be used in concert to help distinguish them, especially since many races of *E. californica* (e.g., coastal forms) are quite distinctive, but there are populations of both taxa which, if collection data are lacking, cannot be "identified" except with the two more or less constant characters above.

Since these taxa are somewhat more distinct and certainly more discrete than the varieties recognized within *E. californica s. str.* (Jepson, 1922; Munz, 1959; these varietal names are perhaps best ignored), I propose that *E. mexicana* be treated as a subspecies of the earlier *E. californica*.

ESCHSCHOLZIA CALIFORNICA Chamisso subsp. **mexicana** (Greene) C. Clark, comb. et stat. nov.

- Eschscholzia mexicana* Greene, Bull. California Acad. Sci. 1:69. 1885. Type: New Mexico. Plains of the Gila [River], Apr 1880, *Greene s.n.* (Holotype, CAS!; isotype, UC!).
- Eschscholzia douglasii* Hooker & Arnott var. *parvula* A. Gray, Smiths. Contr. Knowl. 5:10 (Pl. Wright. Tex.-Neo-Mex.). 1853. Type: Texas. [El Paso Co.:] Among rocks, on mountains near El Paso, Apr 1852, *Wright 1310* (Lectotype, GH! [here designated]; isotypes, GH!, GH!).
- Eschscholzia parvula* (A. Gray) Cockerell, Bot. Gaz. 26:279. 1898.
- Eschscholzia aliena* Greene, Pittonia 5:260. 1905. Type: Arizona. [Santa Cruz Co.:] Nogales, May 1892, *T. S. Brandegees s.n.* (Holotype, CAS!).
- Eschscholzia jonesii* Greene, Pittonia 5:261. 1905. Type: Arizona. [Mohave Co.:] Hackberry, 24 May 1884, *Jones 4362* (Holotype, US!).
- Eschscholzia arizonica* Greene, Pittonia 5:261. 1905. Type: Arizona. [Yavapai Co.:] Bradshaw Mts., 22 Jun 1892, *Toumey 48-C* (Holotype, US!).

Annual herbs, differing from the typical subspecies by their entire cotyledons, obligately annual growth, and desert habitat.

Evolution.—A notable feature of *E. californica* (including ssp. *mexicana*) is its disjunct distribution. A number of other plant species, both annual and perennial, show similar California-Arizona disjunctions, among these *Platystemon californicus* Bentham, *Quercus chrysolepis* Liebmann, *Q. turbinella* Greene (Munz, 1959), *Clarkia rhomboidea* Douglas, *C. epilobioides* (Nuttall) Nelson & Macbride, *C. purpurea* (Curtis) Nelson & Macbride, *Dryopteris arguta* (Kaulfuss) Watt, *Ribes quercetorum* Greene, *Cercocarpus betuloides* Torrey & Gray, *Lupinus succulentus* Koch, *Rhus ovata* Watson, *Fremontodendron californicum* Coville, *Lonicera interrupta* Bentham, and *Trichostema micranthum* A. Gray (Mosquin, 1964). In the case of *Clarkia rhomboidea*, Mosquin postulates that the environments of the Great Basin during the height of the Wisconsin glaciation were adequate to support the species and that a continuous distribution may have existed across the region at that time.

It is likely that many of the other disjunctions can be accounted for in a similar manner. Full-glacial climates of the North American deserts were cooler and perhaps wetter than at present and woodland vegetation was dominant at much lower elevations than today (Wells & Berger, 1967; Wells & Hunziker, 1976). Examination of post-glacial fossil woodrat middens in the lower elevations of the Mojave Desert shows vegetation dominated by juniper and joshua tree, even as recently as 7800 years b.p. (van Devender, 1977).

Eschscholzia californica ssp. *californica* can be found today growing in juniper-joshua tree woodlands (or what remains of them after clearing) in the western Mojave Desert in the region of Lancaster, California, and further west. During full-glacial times habitats suitable for *E. californica* must have extended across the Mojave and into Arizona. The species likely had a continuous distribution across this region. With the advent of warmer and drier climates toward the end of the glaciation, the species

was eliminated from the lower Mojave. Further east, populations were able to adapt to the drier conditions of the Sonoran Desert; these remain as ssp. *mexicana*.

Having arisen from marginal populations of the variable *E. californica*, and subsequently adapting to a lesser range of environments, ssp. *mexicana* might be expected to be much less variable, and indeed it is. The obligate annuality of the subspecies can be viewed as a response to conditions under which perennation is impossible, and any amount of photosynthate held in reserve to allow perennation could be more advantageously spent on the formation of seeds to insure future generations.

One might also expect that plants of ssp. *mexicana* should most closely resemble those of ssp. *californica* in the far western Mojave. This is not the case. The western Mojave plants have wider hypanthium rims and generally bushier growth.

Perhaps the best explanation for the lack of similarity is that no populations of ssp. *californica* grow in an environment which is precisely identical to that of ssp. *mexicana*. The adaptation of different populations to dissimilar environments has resulted in dissimilarity of appearance.

Eschscholzia californica ssp. *mexicana* thus represents a group of marginal populations of the species which have recently become isolated from the rest of the species by climatic change, and which have adapted in isolation to somewhat different environmental conditions, but have retained the general characteristics and adaptive features of the parent species.

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Appendix 1: Locations of studied populations. Living plants for greenhouse culture were obtained as seeds (S), seedlings (J), or adult plants (A). Collection numbers are those of C. Clark.

Ssp. californica—All locations are in California.

- 446—Los Angeles Co.: E of Gorman (S).
 473—Yolo Co.: Winters (S, A).
 489—Yolo Co.: W of Winters (S, A).
 492—Alameda Co.: SE of Livermore (S, A).
 493—Alameda Co.: SE of Livermore (S, A).
 496—San Luis Obispo Co.: W of Pozo (S, A).
 499—San Luis Obispo Co.: S of Simmler (A).
 500—San Luis Obispo Co.: E of Santa Margarita (S).
 501—San Luis Obispo Co.: NE of Santa Margarita (S).
 502—Tehama Co.: S of Proberta (S).
 504—Marin Co.: Coast W of Muir Woods (S).
 506—San Luis Obispo Co.: NW of San Simeon (A).
 508—Monterey Co.: N of Arroyo Seco Campground (S, A).
 521—Kern Co.: E of Cottonwood Pass (S, A).
 535—Kern Co.: Kernville (J).
 536—Kern Co.: W of Woody (J).
 ASL—Monterey Co.: Asilomar Beach (S).
 RSL—Yolo Co.: Davis (S).

Ssp. mexicana—All locations are in Arizona.

- 510—Yuma Co.: WSW of Aguila (J).
 511—Maricopa Co.: W of Wickenburg (J).
 515—Gila Co.: W of Peridot (J).
 517—Graham Co.: W of Artesia (J).
 518—Pinal Co.: S of Casa Grande (A).
 519—Yuma Co.: ESE of Salome (A).

Appendix 2: Pollen fertility of parental and hybrid samples. Collection number (parents, if hybrid)—**pollen fertility** (number of flowers sampled); e.g., 1 KM (496 × 511)—**76** (5).

Parental californica: 446—**99** (1); 473—**82** (2); 496—**92** (1); 499—**72** (2); 500—**97** (1); 501—**88** (2); 506—**94** (2); 508—**58** (3); 535—**99** (1); RSL—**72** (2).

Parental mexicana: 515—**97** (1); 519—**89** (2).

F₁ californica × *californica*: 1K (500 × RSL)—**78** (2); 2K (500 × 501)—**78** (2); 3K (493 × 499)—**77** (1); 4K (496 × 473)—**59** (1); 5K (496 × 446)—**62** (1); 6K (500 × ASL)—**85** (1); 7K (501 × 473)—**81** (1); 8K (496 × 500)—**94** (1); 9K (501 × 489)—**91** (1); 10K (508 × 473)—**57** (1).

F₁ mexicana × *mexicana*: 2M (517 × 518)—**90** (1); 3M (517 × 515)—**95** (1); 4M (515 × 511)—**75** (1).

*F*₁ *californica* × *mexicana*: 1KM (496 × 511)—**76** (5); 2KM (496 × 515)—**81** (4); 3KM (508 × 511)—**75** (3); 4KM (508 × 518)—**66** (3); 5KM (504 × 518)—**77** (4); 6KM (504 × 511)—**60** (1); 7KM (501 × 511)—**81** (5); 8KM (ASL × 511)—**50** (2); 9KM (500 × 515)—**88** (2); 11KM (500 × 518)—**89** (1); 12KM (492 × 515)—**71** (1); 13KM (506 × 515)—**77** (1).

*F*₁ *mexicana* × *californica*: 1MK (517 × 473)—**90** (2); 2MK (515 × 473)—**70** (2); 4MK (515 × 492)—**56** (1); 5MK (511 × 502)—**58** (1).

*F*₂: 5KM × 5KM—**92** (1); 2KM × 2KM—**93** (1); 1KM × 1KM—**97** (1); 1MK × 1MK—**96** (1).

Backcross to californica: 496 × 1KM—**70** (1); 1MK × 473—**76** (2); 5MK × 504—**55** (1); 1KM × 496—**97** (1); 501 × 1KM—**96** (2); 5KM × 506—**96** (1).

Backcross to mexicana: 1KM × 511—**96** (1); 515 × 2MK—**73** (2).