A NEW SUBSPECIES AND A NEW COMBINATION IN
ESCHSCHOLZIA MINUTIFLORA (PAPAVERACEAE)

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ABSTRACT

Diploid (n=6) poppies from the El Paso and Rand mountains of the northwestern Mojave Desert, previously referred to *Eschscholzia parishii*, are morphologically distinct from that species, with shorter, broader terminal lobes of the leaves, more oblong seeds without micropapillae, and slightly smaller corollas. In all characters but flower size the plants agree with the hexaploid *E. minutiflora* and tetraploid *E. covillei*. We believe that these plants, not *E. parishii*, represent the diploids in the series. Since the three taxa cannot be consistently distinguished by morphology, and there is no compelling reason to recognize autopolyploid levels as separate species, we describe the new diploid as *Eschscholzia minutiflora* subsp. *twisselmannii* and provide for the tetraploid the new status *E. minutiflora* subsp. *covillei*.

RESUMEN

Amapolas diploides (n=6) de las montañas El Paso y Rand del noroeste del desierto de Mojave, previamente consideradas como *Eschscholzia parishii*, son distintas morfológicamente de esa especie. Estas plantas poseen hojas con segmentos terminales más cortos y anchos, semillas más oblongas y sin micropapilas, y corolas un poco más pequeñas. En todas las características, excepto en el tamaño de las flores, las plantas se parecen más a la hexaploide *E. minutiflora* y a la tetraploide *E. covillei*. Creemos que estas plantas, y no *E. parishii*, representan las diploides en la serie. Debido a que los tres taxones no pueden reconocerse por morfología consistentemente, y no hay una razón obligada a reconocer niveles autopoliploides como especies separadas, nosotros describimos el nuevo diploide como *Eschscholzia minutiflora* subsp. *twisselmannii* y para el tetraploide proveemos el nuevo estado *E. minutiflora* subsp. *covillei*.

An affinity between *Eschscholzia parishii* E. Greene and *E. minutiflora* S. Wats. has been widely accepted since Jepson (1922) reduced the former to a variety of the latter. Lewis and Snow (1951) contended that *E. parishii* should be regarded as a separate species, since it was sympatric with *E. minutiflora* over the entire range of the former, was always morphologically distinguishable from *E. minutiflora* in areas of sympathy, never hybridized with *E. minutiflora*, and had a different chromosome number (n=6, versus n=18 in *E. minutiflora*). Nevertheless, they suggested that it was the diploid progenitor of *E. minutiflora*.

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In 1961, Mosquin applied the name *Eschscholzia covillei* E. Greene to tetraploid plants \( n=12 \) previously referred to *E. minutiflora*, and strongly implied (although never explicitly stated) that the three species formed a polyploid series. He showed differences in flower size and stamen number as well as chromosome number, and pointed out that the two taxa could readily be distinguished when they grew in mixed stands. Clark (1978, 1979, and unpublished) formed greenhouse hybrids of moderate fertility between *E. covillei* and *E. minutiflora*, but was unable to cross either with *E. parishii*. Clark and Jernstedt (1978) suggested, on the basis of seed coat differences as well as hybridization, that *E. parishii* did not represent the diploid progenitor of either *E. minutiflora* or *E. covillei*.

Mosquin (1961) and Twisselmann (1967) both commented on the distinctiveness of *E. parishii* of the Rand and El Paso mountains in northeastern Kern Co. and northwestern San Bernardino Co., California. These populations are further north (120 km) and further west (125 km) than any other populations of *E. parishii*. Our investigations show that these are in fact morphologically distinct from *E. parishii*, and we believe they represent the diploid member of the *E. minutiflora* polyploid series. We have also found that morphological differences do not consistently distinguish the different ploidy levels, and so provide a taxonomic realignment at the subspecific level.

**RESULTS AND DISCUSSION**

*Status of the tetraploid.* *Eschscholzia minutiflora* subsp. *minutiflora* varies greatly in its morphology (in 1905, Greene recognized six other species that can safely be synonymized with it—Clark, 1979), and subsp. *covillei* falls within this variation in all but three traits: flower size, stamen number, and number of pollen colpae. Mosquin also included bud length and stamen length, but those are correlated with flower size in all members of the genus, and thus all three constitute a single character. The number of colpae, which seems to relate to the chromosome number, shows some overlap, as does petal length. The stamen number shows considerable overlap (Mosquin 1961). In mixed stands, the taxa are generally discontinuous morphologically, but large-flowered subsp. *minutiflora* cannot be reliably distinguished from small-flowered subsp. *covillei* when specimens are taken from different populations.

Again in mixed stands, subsp. *covillei* flowers consistently earlier than subsp. *minutiflora*; differences in flowering times have been observed in other polyploid series as well (Clark 1975). However, the overlap in flowering season is almost complete, and subsp. *minutiflora* from the south end of its range will often flower much earlier than subsp. *covillei*, which occurs further north (Table 1).
### Table 1. Comparison of *Eschscholzia minutiflora* subsp. *twisselmannii* with *E. minutiflora* subsp. *minutiflora* subsp. *covillei*, and *E. parishii*. *Measurements of Mosquin (1961); his ranges, based on examination of a number of herbarium collections, slightly exceed what we have observed in the field.*

<table>
<thead>
<tr>
<th></th>
<th>minutiflora</th>
<th>covillei</th>
<th>twisselmannii</th>
<th>parishii</th>
</tr>
</thead>
<tbody>
<tr>
<td>Petal size</td>
<td>4–10 mm*</td>
<td>7–18 mm*</td>
<td>4–20 mm</td>
<td>8–22 mm*</td>
</tr>
<tr>
<td>Terminal leaf</td>
<td>short, blunt</td>
<td>short, blunt</td>
<td>short, blunt</td>
<td>longer, pointed</td>
</tr>
<tr>
<td>divisions</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Seed shape</td>
<td>oblong</td>
<td>oblong</td>
<td>oblong</td>
<td>spherical</td>
</tr>
<tr>
<td>Seed micropapillae</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>yes</td>
</tr>
<tr>
<td>Jugiform</td>
<td>absent</td>
<td>rare</td>
<td>not seen</td>
<td>common</td>
</tr>
<tr>
<td>ridge cells</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distribution</td>
<td>Sonoran, Colorado, Mojave Deserts, SW Great Basin</td>
<td>Mojave Desert</td>
<td>northwestern Mojave Desert</td>
<td>Colorado, western Sonoran deserts</td>
</tr>
</tbody>
</table>

The taxa hybridize in cultivation. A hybrid between subsp. *minutiflora* (collected northwest of Ocotillo in San Diego Co., California, *Clark 522, DAV*) and subsp. *covillei* (from the Newberry Mountains in San Bernardino Co., California, *Clark 561, DAV*) was of intermediate morphology. Its pollen fertility was 37% (based on a sample of 500 grains). At metaphase I, around 7–11 chromosomes were unpaired univalents. The paired chromosomes did not spread well and were thus impossible to analyze fully, but there appeared to be at least some trivalents. There is no indication that the taxa hybridize in the field.

Subspecies *twisselmannii* shows the same morphological similarities, but experimental hybrids with either subsp. *minutiflora* or subsp. *covillei* have not yet been made.

Both the morphological overlap and ability to hybridize support subspecific status, but the change in status is also supported on evolutionary grounds. Separate species are not generally recognized in autoploid complexes, because the mechanisms that created higher ploidy levels can recur, leading to gene flow between levels (Clark 1975). Even in the absence of gene flow, a lack of morphological divergence is an indication that the ploidy levels still share common evolutionary tendencies.

Thus, the differences between the taxa are not great enough either from the standpoint of morphology or of evolutionary biology to warrant their maintenance as separate species.
Fig. 1. Scanning electron micrographs of the seed of *Eschscholzia minutiflora* subsp. *twisselmannii*. A. ×37. B. ×360.
The new diploid. All three subspecies of *E. minutiflora* somewhat resemble *E. parishii*. However, subs. *twisselmannii* agrees with the other two subspecies, and is clearly dissimilar from *E. parishii*, in leaf shape and three features of the seeds (Table 1, Fig. 1).

Seed coat microsculpturing is useful in many cases for distinguishing *Eschscholzia* species (Clark and Jernstedt 1978). All three subspecies of *E. minutiflora* have somewhat elongate seeds, up to 1.3 times as long as wide. They lack micropapillae on the epidermal cells, and the epidermal cells of both ridges and facets may be concave or foveate, but are almost never jugiform. The seeds of subs. *twisselmannii* cannot be distinguished from those of the other two subspecies.

In contrast, the seeds of *Eschscholzia parishii* are nearly spherical. They always have micropapillae, and jugiform cells are common on both facets and ridges.

The taxa are also distinguished by the terminal leaf divisions. In *E. parishii*, they are pointed and 2–3 times as long as wide. In all three subspecies of *E. minutiflora*, they are blunt and 1–1.5 times as long as wide.

In addition to its morphological similarity, subs. *twisselmannii* is well-placed geographically as the diploid member of the *E. minutiflora* complex. It is sympatric with the tetraploid subs. *covillei*, unlike *E. parishii*, which is completely allopatric (all are sympatric with the widespread subs. *minutiflora*). It has a much more restricted distribution than the tetraploid, and preliminary evidence suggests that it may be substrate-specific to rhyolitic tufts, granitics, and similar rocks.

**Nomenclature**


*Eschscholzia minutiflora* S. Watson, var. *darwinensis* M. E. Jones, Contr. W. Bot. 8:2–3. 1898.—Type: USA, California, Inyo Co., on mesas, Darwin, 1897 (holotype, POM).

Since no name existed for the taxon at the rank of subspecies, either epithet could have been chosen. *Covillei* was chosen because it has been more commonly used in recent years as a result of Mosquin’s (1961) paper. Mosquin felt that both types agreed with the morphology of the tetraploids, but there is no unequivocal evidence that either is in fact tetraploid.
Eschscholzia minutiflora S. Watson subsp. twisselmannii C. Clark & Faull, subsp. nov.—TYPE: USA, California, Kern County, Red Rock Canyon State Park, just E of CA Highway 14 at southern junction with Abbott Rd., on low mounds of eroded pink tuff along a streamcourse, 2 Apr 1988, Clark 642 (holotype, CAS!; isotype, UC!).


Allied to Eschscholzia minutiflora subsp. minutiflora and covillei, differing by its larger flowers. Differing from Eschscholzia parishii by shorter terminal divisions of the leaves and more oblong seeds lacking micropapillae and jugiform cells. Chromosome number n=6.

The subspecies is known with certainty only from the El Paso and Rand mountains of the western Mojave Desert, although large-flow-ered E. minutiflora have been reported from the Death Valley region (DeDecker 1984; listed as E. parishii).

PARATYPES: USA, California, Kern County, 2 mi SE of Searles Station, Lewis and Mosquin 1117 (LA); El Paso Mountains, Mesquite Canyon, 0.6 mi N of Red Rock–Randsburg Rd. at a junction 1.1 mi W of its junction with Garlock Rd., 1 April 1988, Clark 640 (CSPU).

The epithet honors Ernest C. Twisselmann, whose keen observa-tions have been a source of inspiration and a stimulus for pro-ductive work for us and many other California botanists.

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LITERATURE CITED


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