Systematic Studies of *Eschscholzia* (Papaveraceae).

II. Seed Coat Microsculpturing

CURTIS CLARK AND JUDITH A. JERNSTEDT¹

Abstract. Scanning electron microscope examination of seeds of all thirteen species of *Eschscholzia*, a genus of western North America, reveals distinguishing features which can be used to separate species, provides evidence of seed flotation as an adaptation to runoff dispersal in some species, and provides additional data toward the resolution of taxonomic and evolutionary problems in the genus. Seed surfaces generally consist of ridges or tubercles of radially elongate cells surrounding facets of tabular cells. Surface features of the mature seed are a function of the collapse of these cells during desiccation.

The study of seed coat microsculpturing with the scanning electron microscope has provided taxonomic, evolutionary, and ecological insights in a number of groups. In many cases it has been possible to interpret seed dormancy (Gutterman & Heydecker, 1973), to separate tribes (Whiffin & Tomb, 1972), genera (Mulligan & Bailey, 1976), sections, and even species (Chuang & Heckard, 1972; Ehler, 1976; Hill, 1976; Seavey et al., 1977), and to postulate evolutionary relationships (Chuang & Heckard, 1972; Hill, 1976; Seavey et al., 1977; Whiffin & Tomb, 1972) on the basis of seed coat characteristics.

These techniques can be applied profitably to *Eschscholzia*, a genus of 13 species of western North America. In contrast to seeds of the large genus *Papaver*, which are exceedingly uniform (Tomb, 1974; but see Gunn & Seldin, 1976), those of *Eschscholzia* are elaborately sculptured and quite diverse. Seed characters have been used to distinguish species (e.g., *E. glyptosperma*, *E. lobbii*) in the past (Greene, 1885, 1905; Jepson, 1922; Munz, 1959).

Seeds of *E. californica* were first examined anatomically by Godfrin (1880), who looked only at mature seeds. Brandza (1891) included this species in his broad study of seed integuments. The first detailed study of the ontogeny of the seed coat was undertaken by Meunier (1891). Shaw (1904) studied the histology of seed coats of *E. californica* and certain other Papaveraceae. Sachar and Mohan Ram (1958) and Röder (1958) also examined the seed coat of *E. californica*, the former concurring with previous investigators, the latter differing somewhat, perhaps through inadequacy of observation.

Gunn and Seldin (1976) included twelve species (eleven by our reckoning) of *Eschscholzia* in their light-microscopic study of papaveraceous seeds. They provide a key which separates nine of the species; it includes embryo and color characters, as well as external morphological charac-

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¹ Botany, University of California, Davis, CA 95616.

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ters. As far as we can determine, the first and only previous scanning electron micrograph of an *E. californica* seed, by F. D. Hess, is published in a general botany text (Weier et al., 1974).

Although the seed coats are diverse and seed characters have been used taxonomically in the past, there has never been a comparative study at the scanning electron microscopic level of all the species in the genus. We have examined well over 500 seeds of 69 populations in an attempt to characterize the surface microsculpturing of all thirteen species, and to discover features by which the species may be distinguished and identified.

**Materials and Methods**

Seeds taken from living plants were removed from fully or nearly dry capsules, the criterion being the shrinking by desiccation of the intercostal regions of the fruit. Fully dry capsules are evanescent, springing open and scattering seeds at the slightest misdirected touch.

Seeds from herbarium collections (all specimens examined are at BARC, CAS, and UC, as indicated by the sample number; see Appendix) were taken from packets only, seeds in undehisced fruits mounted on the sheets being immature. Seeds were selected that appeared fully developed and undamaged.

Seeds were attached to aluminum stubs with silver conductive paint and layered with gold in a vacuum evaporator or in a sputter coater. Specimens were observed with a Cambridge Stereoscan S4 scanning electron microscope, and photographed with Kodak 4127 film or Polaroid P/N 55 film. Figures 2–29 show SEM photographs of whole seed mounts and seed coat surfaces of the species examined.

To examine the anatomy of the seed integuments, we preserved mature and immature seeds in 50% FAA, dehydrated them in an ethanol/tert-butanol series, embedded them in paraffin, sectioned at 10 μm, and stained in safranin, fast green, and crystal violet. Figure 1 shows seed coat anatomy.

**General Architecture of the Seed Coat**

*Gross Morphology.*—The seed develops from an anatropous ovule with a conspicuous vascularized raphe. At maturity no distinct abscission zone forms between the raphe and funiculus, the separation occurring by tearing of the dried tissues. The micropyle is situated on a raised protuberance (Fig. 29); this corresponds to the “nipple” of *Eschscholzia* described by Gunn and Seldin (1976), but not necessarily to the nipples of other genera.

*Inner Integument.*—Meunier (1891) described three layers in the inner integument of *E. californica*. We have not carried out further examinations.
Outer Integument.—Meunier described three regions, an inner layer composed of large cells with numerous crystals of calcium oxalate, a middle region of several layers of parenchyma, which becomes greatly flattened radially during the final stages of maturation, and an upper epidermal layer of cells which are radially elongated to a greater or lesser extent, and which possess a cuticle. Our examination of sectioned immature seeds and of cracked mature seeds with the SEM did not show as much detail as Meunier observed. The middle region seems to be almost totally obliterated in mature seeds. All the species we examined seem to follow the same pattern (with variations, such as a multiple outer layer in E. glyptosperma). The general pattern is evident in Figure 1.

Surface Features.—In gross aspect the surface consists of facets formed of tabular cells surrounded by ridges formed of radially elongate cells (Fig. 1). Four species deviate from this pattern—E. glyptosperma has a multiple outer layer of isodiamicratic cells, E. palmeri and E. elegans have raised tubercles in place of ridges, and E. lobbii has greatly elevated tubercles which are somewhat coalesced into ridges.

The crests of the ridges can be serrate, as in E. hypocoides (Fig. 17), but in most species are more uniform in outline (Fig. 3). The radial walls of the ridge cells are usually contiguous (Fig. 5), but are discrete (Fig. 9) in a few species.

We have classified the facet cells into four shapes: concave (Fig. 7), jugiform (Fig. 9; Latin iugum, “yoke,” we considered the term “bageloid,” but rejected it for lack of classical antecedents), foveate (Fig. 19), and polygonal (Fig. 21). They can also appear intermediate between types, or indistinct (appearing “acelullar” at low magnifications). Stomata with guard cells appear on the facets and sometimes the ridges, and are present on all species (Jernstedt & Clark, 1979; a stoma can be seen in the
lower right side of Fig. 19). They are anomocytic, although the shape and arrangement of adjacent cells may be affected. In some species the outer walls of both facet and ridge cells are covered with minute papillae.

Although a body of terminology already exists for the description of seed coats (Murley, 1951; and especially Gunn & Seldin, 1976), the terms are used at the light microscopic level, and do not adequately describe the cellular nature of the seed coat. As an example, Gunn and Seldin use the term “reticulation.” In *Eschscholzia*, it refers to the patterns formed by the multicellular ridges surrounding the multicellular facets. In *Papaver*, it refers to the reticulate appearance of the radial walls of individual epidermal cells. In both cases “reticulate” describes the total aspect of the seed coat, but not the individual cells. We have tried to use terminology which would specifically describe the cells.

**Distinguishing Features of the Species**

We had originally intended to provide a key to the species since with a few exceptions, they can be distinguished solely on the basis of seed coat characters. However, the key we produced was neither short nor easy to use (faults which are all too common for dichotomous keys in general), because it tried to take into account the low percentage of aberrant seeds present in any species, and to present verbally complex differences as “either/or” generalities. A random-access key was found to be equally impractical, since some species have many character-states for characters which are lacking altogether in others.

We finally settled on the method used by Peterson (1947), which is certainly more suited to rapid identification of birds than the dichotomous keys of Blair et al. (1968). We feel that one picture is worth a dozen key-couplets; with distinguishing features pointed out by “field marks” in the captions, the plates (Figs. 2–27) should provide a reasonably rapid and accurate means of identifying species. Since commonly used contemporary keys (Munz, 1959, 1968) are barely adequate to distinguish the species using a combination of floral and vegetative characters, our contribution will certainly be of some use.

Four species can be immediately distinguished from the rest by their major deviations from the basic plan: *E. glyptosperma* (Figs. 6, 7) with sunken stomata on an undulating surface; *E. lobbii* (Figs. 26, 27) with elongated tubercules, and *E. elegans* (Figs. 22, 23) and *E. palmeri* (Figs. 24, 25) with lower tubercules. Of the remaining nine, *E. californica* (Figs. 2, 3) can be taken as a basis for comparison, with other species deviating from it to a greater or lesser degree. The seed of *E. californica* is globose or only slightly elongate, and has low ridges with uniform crests which undergo an abrupt transition to the facets, these comprising a variety of cell shapes. Papillae are present. Seeds of the other eight species may be presumed to have these characteristics, unless indicated otherwise in the captions.
Table 1. Colors of *Eschscholzia* seeds.

<table>
<thead>
<tr>
<th>Species</th>
<th>Light brown</th>
<th>Medium brown</th>
<th>Dark brown</th>
<th>Ridges lighter than facets*</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. californica</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>O</td>
</tr>
<tr>
<td><em>E. caespitosa</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>S</td>
</tr>
<tr>
<td><em>E. glyptosperma</em></td>
<td>+</td>
<td>+</td>
<td>NA</td>
<td></td>
</tr>
<tr>
<td><em>E. parishii</em></td>
<td>+</td>
<td>+</td>
<td></td>
<td>S</td>
</tr>
<tr>
<td><em>E. coovillei</em></td>
<td>+</td>
<td>+</td>
<td></td>
<td>N</td>
</tr>
<tr>
<td><em>E. minutiflora</em></td>
<td>+</td>
<td>+</td>
<td></td>
<td>N</td>
</tr>
<tr>
<td><em>E. lemmoneii</em></td>
<td>+</td>
<td>+</td>
<td></td>
<td>O</td>
</tr>
<tr>
<td><em>E. hyphcoideus</em></td>
<td>+</td>
<td>+</td>
<td></td>
<td>O</td>
</tr>
<tr>
<td><em>E. rhombipetala</em></td>
<td></td>
<td>+</td>
<td></td>
<td>N</td>
</tr>
<tr>
<td><em>E. ramosa</em></td>
<td>+</td>
<td></td>
<td></td>
<td>S</td>
</tr>
<tr>
<td><em>E. elegans</em></td>
<td>inadequate data</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>E. palmeri</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>NA</td>
</tr>
<tr>
<td><em>E. lobbi</em></td>
<td>+</td>
<td></td>
<td></td>
<td>NA</td>
</tr>
</tbody>
</table>

* O = often; S = seldom; N = never; NA = not applicable.

Gunn and Seldin (1976) used seed color as a distinguishing feature, and while this character is not readily apparent in gold-plated seeds prepared for the SEM, it does seem useful for distinguishing seeds which cannot be separated otherwise. Seed color may be uniform over the entire surface, or facets may be darker than ridges. Slightly immature dry seeds are usually darker than fully mature seeds. It appears that cells of the outer layer may be either air-filled or filled with cell breakdown products. The former are refractive and light-colored, and the latter are translucent and allow the dark color of the basal layer of the outer integument to show through. Seed colors are summarized in Table 1.

With a light microscope such as a stereo dissecting scope, one can see about as much detail as is observable in the whole-seed SEM photos. Although positive identification may not always be possible, the distinguishing features of facet cell shape, ridge serration, ridge-to-facet transition, and color, as well as seed shape and general form of the reticulation, are generally visible at higher magnifications.

**Systematic Considerations**

Seeds of related species possess similar microsculpturing. The seeds of the two subspecies of *E. californica* (ssp. *californica* and ssp. *mexicana*)

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* Figs. 2–7. SEM views of the seeds of *Eschscholzia* species. Characters in *italics* correspond to the arrows in the figures. Features in **bold face** represent typical examples of the facet cell and ridge types discussed in the text. 2. *E. californica* (504); facet (F) and ridge (R). 3. *E. californica* (489); ridge crest uniform, abrupt transition between ridge and facet (right); papillae present (center); facet cells never foveate. 4. *E. caespitosa* (571). 5. *E. caespitosa* (580); contiguous walls of the ridge cells (square); differs from *E. californica* by its more elongate shape, somewhat thinner ridges, and lack of papillae. 6. *E. glyptosperma* (544). 7. *E. glyptosperma* (539); facet cells concave only (circle); stomata located in prominent *pits* (center right); papillae present (below); no definite ridges or facets.
(Greene) C. Clark) are almost indistinguishable. Seeds of tetraploid *E. covillei* and its hexaploid relative *E. minutiflora* (Figs. 12, 13) are not clearly separable.

Greater differences in microsculpturing can correspond to lesser degrees of relationship. *Eschscholzia lemmontii* (Figs. 14, 15) and *E. hypecoides* (Fig. 16) form experimental hybrids of moderate fertility (Clark, unpubl. data), and are morphologically similar, yet distinct, as are their seeds. *Eschscholzia caespitosa* and *E. californica* are morphologically somewhat similar, but are not known to hybridize in the field or experimentally, and are ecologically separated. Their seeds are easily distinguished by the lack of papillae on the former. *Eschscholzia glyptosperma* (Fig. 7) is most likely an aneuploid derivative of *E. parishii* (Clark, unpubl.), but the conspicuous difference in seed coat morphology is in agreement with other data indicating a substantial amount of divergence between the taxa.

*Eschscholzia parishii* (*n* = 6) has been considered to form with *E. covillei* (*n* = 12) and *E. minutiflora* (*n* = 18) a polyploid series (Lewis & Snow, 1951; Mosquin, 1961). Yet its seed coat microsculpturing (Figs. 8, 9) is somewhat unlike that of the two polyploids, which corresponds with other data suggesting that the extant *E. parishii* may differ from the diploid ancestor (Clark, unpubl.).

The annual, island species *E. ramosa* (Figs. 20, 21) (*n* = 12) and *E. elgans* (*n* = 18) also seem to represent part of a polyploid series (Ernst, 1958; Raven, 1963). Their seeds, however, are strikingly dissimilar (Greene, 1905, clearly recognized the distinctions). The seeds of *E. elgans* most closely resemble those of *E. palmeri*, a perennial island species. The seeds which most closely resemble *E. ramosa* are those of *E. caespitosa*, a widespread mainland annual. We have not observed living specimens of any of the island species, and few herbarium collections were available to us, but we believe that further research may call for a reassessment of the relationships among these species.

*Eschscholzia rhombipetala* has always been an enigmatic species. Less than a dozen collections seem to exist, and to our knowledge the species has not been recollected in recent years. Our attempts to locate the plants in the field have been singularly fruitless.

At various times we believed *E. rhombipetala* to be a diminutive *E. caespitosa*, a wayfaring *E. minutiflora*, a depauperate *E. californica*, or a
taxonomic dumping ground for depauperate specimens of a number of species. Certainly some of the specimens labeled *E. rhombipetala* fall in that latter category. However, a number of specimens, including the holotype, have seen features as well as other features in common, and we are now convinced that the species exists (Peter Raven supported this in a conversation in June 1978, saying that he had seen the species in the field in 1949, and that it was very distinctive).

Seeds of *E. rhombipetala* (Figs. 18, 19) have many similarities to those of *E. lemmontii*, especially the frequency of foveate facet cells. The plants also resemble *E. lemmontii* somewhat, having a similar inflated hypanthium, and leaves mostly basal. Flowers of *E. rhombipetala* are much smaller, and its geographic range is more to the north, into the driest parts of the California inner south Coast Ranges. Ernst (1964) mentioned that pollen of *E. rhombipetala* had more colpae than did a number of other *Eschscholzia* species, and noted that the polyploid *E. minutiflora* did also. *Eschscholzia minutiflora* also has small flowers, and both this and the pollen character are a likely result of its polyploidy. Therefore, we predict that *E. rhombipetala* will prove to be a polyploid derivative of *E. lemmontii*, having adaptions which enable it to survive in a harsher environment.

The monotypic genus *Hunnemannia* Sweet is found in central Mexico from Nuevo León to Oaxaca. It is clearly related to *Eschscholzia*, having similar flowers, fruits, and foliage. Distinguishing features are the petalate stigma and separate sepals of *Hunnemannia* (*Eschscholzia* has linear stigmas and a calyptriform calyx). The single species, *Hunnemannia fumariifolia*, has been included in *Eschscholzia* by some authors (Baillon, 1874), but Ernst (1962) maintained it as a separate genus.

Seeds of *Hunnemannia* (Fig. 28) are quite unlike those of *Eschscholzia*. There are no distinct ridges and facets, some of the walls of the isodiametric surface cells being slightly elongated radially, forming rough sinusities on the surface. Stomata are absent, and the seeds are substantially larger than those of any of the *Eschscholzia* species. Seed coat morphology clearly confirms the distinctness of the genus *Hunnemannia*.

**Adaptive Features of the Seed Coat**

The capsules of *Eschscholzia* are explosively xerochastic. This mechanism of seed dispersal has been recognized for a number of years (Cham-

Figs. 14–19. Italicics and bold face as in Figs. 2–7. 14. *E. lemmontii* (554); seed larger and somewhat more elongate than *E. covillei*. 15. *E. lemmontii* (554); ridge crests serrate, ridges merging with facets less gradually than in *E. covillei*; facet cells foveate (left of center), jugiform, or polygonal; papillae usually absent. 16. *E. hypoeoides* (553); seed more elongate than *E. lemmontii*. 17. *E. hypoeoides* (553); ridges high, abrupt transition to facets, crests very serrate; facet cells jugiform, concave, or often indistinct, but never foveate; papillae absent. 18. *E. rhombipetala* (CAS-3); ridges low, straight, transition to facets very abrupt, crests generally uniform. 19. *E. rhombipetala* (CAS-3); facet cells almost exclusively foveate (circle); papillae present or absent.
isko, 1820; Smith, 1902; Jepson, 1922). This explosive dehiscence, however, provides only short-distance dispersal. Features of the seed coat provide a plausible mechanism for dispersal over longer distances.

The outer cells of the integument, especially those comprising the ridges or tubercles, are air-filled in the dry mature seed. This, along with entrapment of air bubbles by the irregular outer surface, confers a low specific gravity to the seeds, which, in conjunction with surface tension, allows the seeds to float. Mature dry seeds of *E. californica*, *E. caespitosa*, *E. glyptosperma*, *E. parishii*, *E. covillei*, *E. minutiflora*, *E. lemmonei*, *E. hype- coides*, and *E. lobbii* (all the species of which there were sufficient seeds available for experimentation) float when dropped on the surface of water, and when water is poured on top of them in a vial.

Seeds of *E. parishii*, its polyploid relatives *E. covillei* and *E. minutiflora*, and the related *E. glyptosperma* were placed in vials and water was added. Initially, nearly all the seeds of each species floated. The vials were shaken briefly and the seeds allowed to settle. Approximately 90% of the *E. glyptosperma* seeds remained floating. Only one-fourth of the *E. parishii* seeds remained floating, as did about half of the *E. covillei* and *E. minutiflora* seeds. This suggests increasing adaptation in the group for run-off dispersal. These species inhabit desert regions, and are commonly found growing along seasonally dry watercourses (this is especially true of *E. glyptosperma*, the species with the most buoyant seeds). During the rainy season, flood waters would pick up seeds which had fallen in the channel. These would be deposited wherever the velocity of the current was reduced, e.g., along the banks and at obstructions in the channel. In fact, plants of these species are usually found growing in precisely those locations.

Even in cases where populations are not found in channeled terrain, flotation dispersal can be an important factor. Infrequent but intense desert rainstorms can cause a phenomenon called *sheet flooding* (Shreve & Wiggins, 1964), where floodwaters move as a sheet over unchanneled, often gently sloping terrain. Flotation would enable the seeds to be transported over long distances.

Other species are often found along intermittent stream courses in xeric parts of their ranges, e.g., *E. californica* in the inner south Coast Ranges. Runoff would seem to be an important means of seed dispersal for these populations as well. In contrast, suitable habitats for plants of mesic regions are well-drained uplands, and though runoff dispersal might aid down-slope movement, it would ultimately bring seeds to inhospitable areas.

Figs. 20–25. Italicized and bold face characters as in Figs. 2–7. 20. *E. ramosa* (UC-21); seeds smaller than those of *E. caespitosa*, with narrower ridges. 21. *E. ramosa* (UC-21); ridges (below) low, narrow, transition to facets abrupt, crests uniform; facet cells polygonal (circle) or rarely jugiform; papillae absent. 22, 23. *E. elegans* (UC-19); tubercles indistinct. 24, 25. *E. palmeri* (BARC-1); tubercles low, distinct.
Figs. 26–29. 26. *E. lobbii* (SMP); tubercles very elongated, coalescing into ridges. 27. *E. lobbii* (CRB). 28. Seed of *Hunnemannia fumariifolia*. 29. Region of the micropyle on a seed of *E. californica* (473); the raphe (R) terminates in torn tissues where it had been attached to the funiculus; above that is the micropylar nipple (M).

**Conclusions**

SEM examination of seed coat microsculpturing is an exceedingly useful tool in the study of *Eschscholzia*. The seeds of all species examined exhibit distinctive morphology, enabling them, for the most part, to be distinguished solely on the basis of seed characters. Similarities and differences in seed coats correspond in some cases with current concepts of the taxonomy of the genus, but in other instances suggest the need for alternate interpretations.

We have observed features of the seed coat which clearly have value for seed dispersal: *E. glyptosperma*, which grows along seasonal water-
courses in the desert, has a seed coat well adapted for flotation, and thus runoff dispersal. Since seeds of other species of the genus are able to float through a combination of buoyancy and surface tension, runoff dispersal is a likely possibility for others as well.

A knowledge of seed coat microsculpturing also provides the possibility of identifying specimens when other information is lacking or contradictory, for assessing relationships of variant populations, and for gaining a better understanding of evolution and adaptation in the genus.

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**LITERATURE CITED**


APPENDIX

Specimens examined. Letter in parentheses refers to source of seeds: field-grown plants (F), greenhouse-grown plants (G), and herbarium collections (H). Collection numbers of Clark (vouchers at DAV) were used when available for identifying SEM stubs; in other cases the stub identification (used in Figs. 2–27) is in brackets. Seed collections have no whole-plant vouchers.

_E. californica_ Chaminso

_ssp. californica_

CALIFORNIA. Alameda Co.: SE of Livermore, _Clark 492_ (G); Kern Co.: Kernville, _Clark 535_ (G); Los Angeles Co.: E of Gorman, _Clark 446_ (G); Marin Co.: Coast near Muir Woods, _Clark 504_ (F); Monterey Co.: Arroyo Seco, _Clark 508_ (G): Asilomar beach, _seed collection [ASL]_ (F); San Luis Obispo Co.: E of Santa Margarita, _Clark 500_ (F); Tehama Co.: S of Proberta, _Clark 502_ (F); Yolo Co.: W of Winters, _Clark 489_ (F); Winters, _Clark 473_ (G).

_ssp. mexicana_ (Greene) C. Clark

ARIZONA. Gila Co.: W of Peridot, _Clark 515_ (G); Maricopa Co.: W of Wickenburg, _Clark 511_ (G); Pinal Co.: S of Casa Grande, _Clark 518_ (G); Yuma Co.: WSW of Aguila, _Clark 510_ (G); ESE of Salome, _Clark 519_ (F).

_E. caespitosa_ Bentham

CALIFORNIA. Calaveras Co.: Copperopolis, _Davy 1348_ [UC-8] (H); El Dorado Co.: Sweet-
water Creek, 2 Jun 1908, K. Brandegee s.n. [UC-7] (H); Glenn Co.: 10 mi E of Alder Springs, Heller 11440 [UC-12] (H); Kern Co.: Greenhorn Peak, Benson 3642 [UC-11] (H); Lake Co.: Scotts Valley, NW of Lakeport, Tracy 1685 [UC-10] (H); Clear Lake boatworks, Ernst 549 [BARC-3] (H); Los Angeles Co.: Santa Monica Mts., 18 Apr 1981, Epling s.n. [UC-9] (H); Mariposa Co.: N of Bear Valley Clark 571 (F); Mendocino Co.: E of Calpella, Ernst 544 [BARC-2] (H); Monterey Co.: near Big Creek, Santa Lucia Mts., 14 Jun 1909, K. brandegee s.n. [UC-14] (H); Napa Co.: W of Winters, Clark 490 (F,G); Tulare Co.: N of Milo, Clark 579 (F); Tuolumne Co.: S of Mocassin, Clark 570 (F); N of Coulterville, Clark 580 (F).

E. glyptosperma Greene
California, Inyo Co.: E of Tecopa, Clark 532 (G); W of Townes Pass, Clark 533 (G); San Bernardino Co.: S of Amboy in Sheephole Mts., Clark 528 (G); S of Amboy in Sheephole Mts., Clark 539 (F,G); E of Ludlow, Clark 544 (F,G).

E. parishii Greene
United States. California. San Bernardino Co.: S of Joshua Tree, Clark 537 (F); S of Amboy in Sheephole Mts., Clark 542 (F,G); San Diego Co.: S of Borrego, Clark 524 (G); County Road 522 W of Imperial Co. line, Clark 525 (G); México. Baja California: W of Bahía de los Ángeles, Clark 568 (F); Arroyo de Calamajue at Calamajue, Porter 595 [UC-1] (H).

E. cossilieri Greene
California, Inyo Co.: Death Valley, Hole-in-the-Rock Spring, 20 Apr 1985, Epling s.n. [UC-2] (H); San Bernardino Co.: S of Newberry Mts., Clark 561 (F); Newberry Mts., seed collection [NYB] (F,G).

E. minutiflora Watson
California, Inyo Co.: Panamint Valley, Clark 534 (G); Kern Co.: S of Ridgecrest, Clark 543 (F,G); San Bernardino Co.: N of Vidal Junction, Clark 520 (G); Goff, Clark 531 (G); San Diego Co.: S of Borrego, Clark 523 (G).

E. lemmontii Greene
California, Fresno Co.: SW of Coalinga, Clark 556 (F,G); San Luis Obispo Co.: W slope of Temblor Range, Clark 554 (F,G).

E. hypococoides Bentham
California, Fresno Co.: N of Parkfield, Clark 552 (F); Monterey Co.: N of Parkfield, Clark 553 (F,G); Stanislaus Co.: Del Puerto Canyon Rd, Clark 563 (G).

E. rhombipetala Greene
California, Lower San Joaquin Valley, Greene s.n., CAS 2541, Holotype [CAS-3] (H); Contra Costa Co.: Antioch, Jun 1887, KC s.n. [CAS-2] (H); Near Byron Springs, Mar 1888, Greene s.n. [UC-6] (H); San Luis Obispo Co.: La Punta Dist, Howser 7861 [CAS-1, UC-5] (H).

E. ramosa Greene

E. elegans Greene

E. palmeri Rose
México. Baja California: Guadalupe I., Franceschi 21 [UC-15] (H); Guadalupe I., Moran 13797 [UC-16] (H); Guadalupe I., Ernst 271 [BARC-1] (H).
E. lobbii Greene

Hunnemannia fumarifulia Sweet
Commercial seed source: Geo. W. Park Seed Co.