

## The Hybrid Nature of *Encelia laciniata* (Compositae: Heliantheae) and Control of Population Composition by Post-dispersal Selection

DONALD W. KYHOS

Department of Botany, University of California, Davis, California 95616

CURTIS CLARK

Department of Biological Sciences, California State Polytechnic University,  
Pomona, California 91768

WILLIAM C. THOMPSON

Department of Botany, University of California, Davis, California 95616

**ABSTRACT.** Experimental studies show that the type and most collections of *Encelia laciniata* are F<sub>1</sub> hybrids between *E. ventorum* and *E. palmeri*. Other collections referred to *E. laciniata* are hybrids between *E. ventorum* and *E. asperifolia*. Only where the parental species occur together can one find *E. laciniata* and then it is strictly confined to zones of intermediate habitat or disturbance. Progeny tests show that lack of pollinator fidelity results in many backcross and other recombinant embryos, but these are expressed as mature plants only in direct proportion to the severity of habitat disturbance and are absent altogether from undisturbed sites. Hybrids and their derivatives largely displace the parent species in areas of extreme disturbance. Only extremely intense to absolute post-dispersal selection can account for these phenomena.

*Encelia laciniata* Vasey & Rose (1889) has been uncritically accepted as a valid species since it was originally described (Blake 1913; Shreve and Wiggins 1964; Wiggins 1980). However, plants of this taxon are in most respects strikingly intermediate between *E. palmeri* Vasey & Rose and *E. ventorum* T. S. Brandeg. Moreover, herbarium records show that *E. laciniata* occurs only in areas where *E. palmeri* and *E. ventorum* are sympatric.

These facts suggest that *E. laciniata* is a hybrid, and field observations reinforce this view. *Encelia laciniata* typically occurs as comparatively infrequent, scattered individuals where *E. palmeri* and *E. ventorum* are either in intimate contact or close together. Furthermore, *E. laciniata* is found in obviously disturbed sites or in habitats that appear intermediate between those of *E. ventorum* and *E. palmeri*. Such patterns are characteristic of hybrids in many plant groups.

Although these facts are suggestive, they do not prove that *E. laciniata* is a hybrid. Possibly it is a self-maintaining entity of hybrid origin, such as an allopolyploid or a stabilized diploid species comparable to *Delphinium gypsophilum* (Lewis and Epling 1959). To resolve this problem we made experimental hybrids, conducted progeny tests, and examined the chromosomes of all the taxa. This work revealed the somewhat complex

hybridity of the plants identified for the past 90 years as *E. laciniata*. Whereas the type specimen of *E. laciniata* (lectotype: F!, here designated; isotypes: GH!, US!) and most plants that have been referred to that species are apparently the hybrid product of *E. ventorum* and *E. palmeri*, we have also shown that plants identified as *E. laciniata* at one locality are in fact hybrids between *E. ventorum* and a third species, *E. asperifolia* (S. F. Blake) Clark & Kyhos.

These studies have, in addition, provided insights into the selective forces operating within these natural *Encelia* populations.

#### MATERIALS AND METHODS

We studied plants at 16 localities and made a total of 27 collections (table 1), mainly of fruits but occasionally of seedlings or older plants of moderate size. Because the fruits of all three species germinated with some difficulty, the embryos were routinely dissected from all enclosing layers and placed in Petri dishes on filter paper moistened with a dilute solution of Bordeaux or Benomyl fungicides. Treated thus, essentially all germinated, generally within 36 hours. Plants from 13 representative collections were grown in the greenhouse in a UC-type potting mix (Baker 1957).

Experimental hybrids were produced by gently brushing capitula together or by transferring pollen from one capitulum to the receptive stigmas of the other. This and other studies have shown no evidence of self-compatibility in any North American *Encelia* species.

To examine trichome morphology, we preserved leaves in FAA (9 ethanol : 9 water : 1 formalin solution : 1 glacial acetic acid, v/v); these were dehydrated in an ethanol-water series, transferred to amyl acetate or left in absolute ethanol, dried in a critical-point drier using carbon dioxide, plated with gold or gold-palladium in a sputter coater, and viewed with a Cambridge Stereoscan S2.

Chromosome studies were made using the conventional acetocarmine squash technique. The percentage of viable pollen, after staining with cotton blue in lactophenol, was estimated by counts of at least 300 grains per sample.

Herbarium specimens were examined at CAS, DAV, DS, SD, and UC.

#### OBSERVATIONS AND RESULTS

*Parent species.* *Encelia ventorum* is a common dune plant of the west-central coast of Baja California (fig. 1; Johnson 1977). It is one of the most unusual species in its linear-dissected leaves (fig. 2), larger stature, paucity of flowers, pubescence consisting primarily of glands (fig. 3B), and habitat, which is unique within the genus.

The larger plants stabilize the dunes: as sand collects at the base, adventitious roots from the buried stems and continued apical growth keep the plant from being totally buried. At one locality along the shore of

TABLE 1. Localities of study collections; all locations are in Baja California, Mexico. All collections were made in 1978. Vouchers are at DAV; population numbers are in italics.

---



---

*Encelia asperifolia*

*106*, ca. 17 km N of Millers Landing, 29 Mar 1978; *117*, rd. to Scammons Lagoon, near S edge of Lagoon, 29 Mar; *129*, near Rosarito, 12 May; *132*, Millers Landing, 12 May; *137*, near Cataviñá, 29 May.

*E. laciniata*

*105*, Guerrero Negro, ca. 150 m E of the junction of the main rd. with the dirt rd. to the old wharf, 28 Mar; *113*, Millers Landing, 12 May; *120*, adjacent to Bahía Asunción, 8 May; *122* and *125*, 19.2 km SE of Bahía Asunción, 7 May; *138*, Guerrero Negro, ca. 150 m E of the junction of the main rd. with the dirt rd. to the old wharf, 11 May.

*E. palmeri*

*102*, 63 km N of Santa Rosalía, 27 Mar; *103*, 136 km NW of Santa Rosalía on Méx. hwy 1, 27 Mar; *112*, rd. S to Punta Abrejos, 26.2 km SW of Méx. hwy 1, 7 May; *116*, Guerrero Negro, ca. 150 m E of the junction of the main rd. with the dirt rd. to the old wharf, 11 May; *118*, Méx. hwy 1, 24 km S of Guerrero Negro, 7 May; *119*, 37.3 km W of San José de Castro, 8 May; *126*, rd. to Punta Abrejos, 6.1 km SW of Méx. hwy 1, 27 May; *128*, 19.2 km SE of Bahía Asunción, 7 May.

*E. ventorum*

*100*, rd. to Scammons Lagoon, S edge of Lagoon, 29 Mar; *101*, 7.2 km N of Guerrero Negro, 29 Mar; *114*, Millers Landing, 12 May; *124*, 19.2 km SE of Bahía Asunción, 7 May; *131*, rd. to Scammons Lagoon, S edge of Lagoon, 29 Mar; *136*, Guerrero Negro, ca. 150 m E of the junction of the main rd. with the dirt rd. to the old wharf, 11 May.

*E. asperifolia* × *E. ventorum* hybrids

*121* and *135*, Millers Landing, 12 May.

---

Bahía Asunción, a single plant on an elevated shell terrace had accumulated a mound of sand (and plant) about 2 m high and 5 m in diameter (fig. 3A).

In contrast to the sand-gathering capacity of the adult plants, the seedlings have been found growing on the ripple faces of dunes without trapping any sand at all. We suspect that the divided leaves (in contrast to the broad leaves in other species) may be responsible in part for the low wind resistance of seedlings, but this will require experimental verification.

The leaves of both seedlings and larger plants in the greenhouse trap water droplets from a "fogger" watering nozzle; these droplets coalesce and run down the leaves, eventually dropping to the ground at the base of the plants. With the pubescent broad-leaved species (e.g., *E. palmeri*), the droplets remain in place until they are much larger and then generally drop directly to the ground at the perimeter of the canopy. Because the habitat of *E. ventorum* is often foggy in summer, the leaf shape may also help trap this moisture and make it more readily available to the plant.

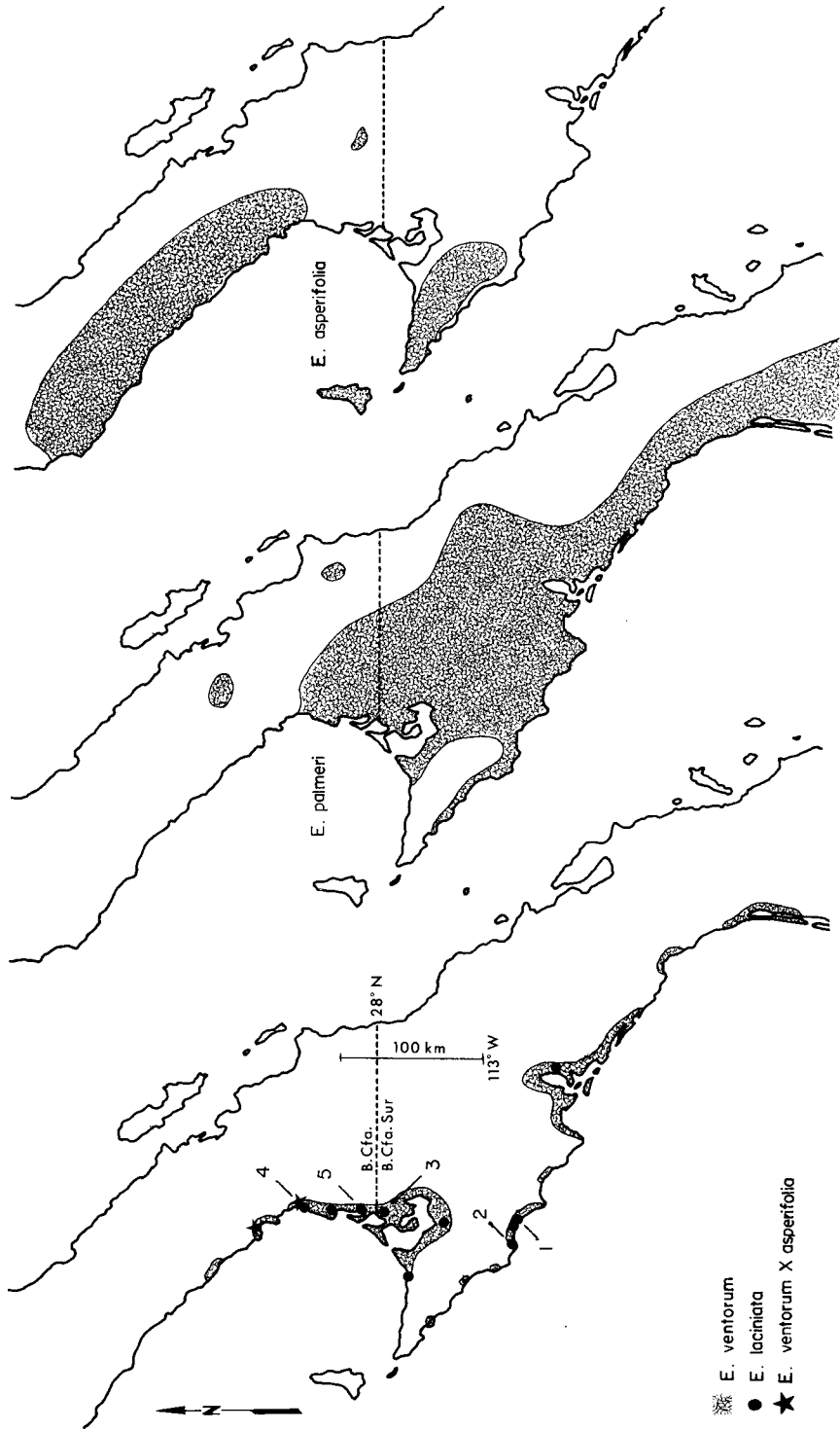


FIG. 1. Distribution of *Encelia* species in central Baja California. Numbers 1-5 mark study sites described in text.

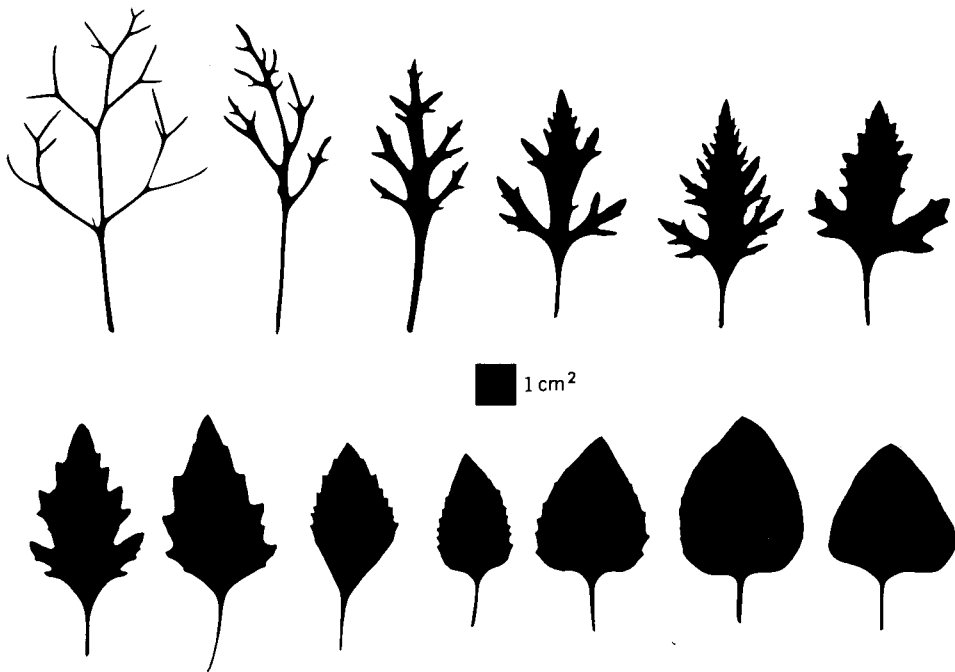


FIG. 2. Range of variation of leaf silhouettes in *Encelia* hybrids at site 3; upper left = *E. ventorum*; upper right = typical *E. laciniata*; lower right = *E. palmeri*.

Whereas most species of *Encelia* flower profusely but only after rainy spells, *E. ventorum* flowers sparsely but over an extended period. Prolonged flowering is probably related to the habitat. The Pacific coastal dunes are a much less severely dry environment than most *Encelia* habitats. The sand retains water at some depth throughout the year, and coastal fog is common in summer. Thus, reproductive effort can be spread over a longer time. Also, the individual plants, by their size, appear to be longer-lived than most plants of other *Encelia* species.

*Encelia palmeri* is a common shrub of the lowlands of the Llano Vizcaíno and as far north as Millers Landing and the road to Bahía de los Ángeles. It extends south along the west side of the mountains all the way to the Cape. In the central part of the peninsula it is conspicuously absent only from the Sierra Vizcaíno and the mountains along the Gulf of California (fig. 1). Plants in favorable sites may approach 2 m in height, but most are less than a meter. The heads are borne on long peduncles in a diffuse panicle. The entire or slightly sinuate leaves are ovate, deltoid, or sometimes cordate (fig. 2). The pubescence is of long multicellular hairs and smaller moniliform hairs (fig. 3C).

*Encelia palmeri* generally inhabits flat areas with well-developed soil; plants are seldom found in rocky areas and are especially common in

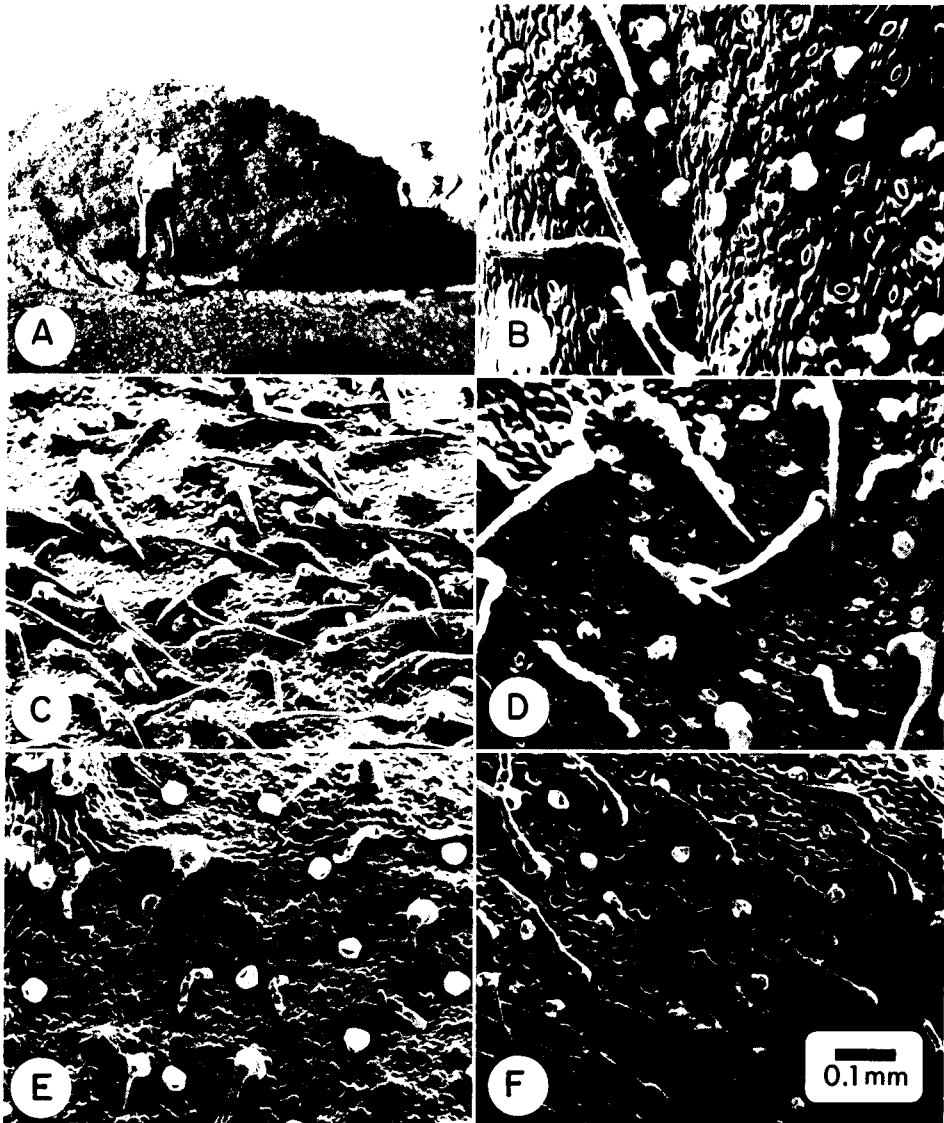


FIG. 3. Habit and leaf trichomes of *Encelia*. A. *E. ventorum* at site 1. B–F. Scanning electron micrographs; all same magnification. B. *E. ventorum* (131), primarily glands with hairs along midveins. C. *E. palmeri* (126), no glands, many long multicellular, and moniliform hairs. D. *E. laciniata* (138), many glands plus scattering of long and moniliform hairs. E. *E. asperifolia* (132), glands, multicellular hairs with stout bases, and moniliform hairs. F. *E. ventorum* × *asperifolia* (135, natural hybrid), glands, more slender multicellular hairs, and moniliform hairs.

sandy soils. It may rarely extend onto backdunes but is generally restricted to areas off dunes.

*Encelia asperifolia* (S. F. Blake) Clark & Kyhos inhabits areas of topographic relief in the central desert of Baja California from south and

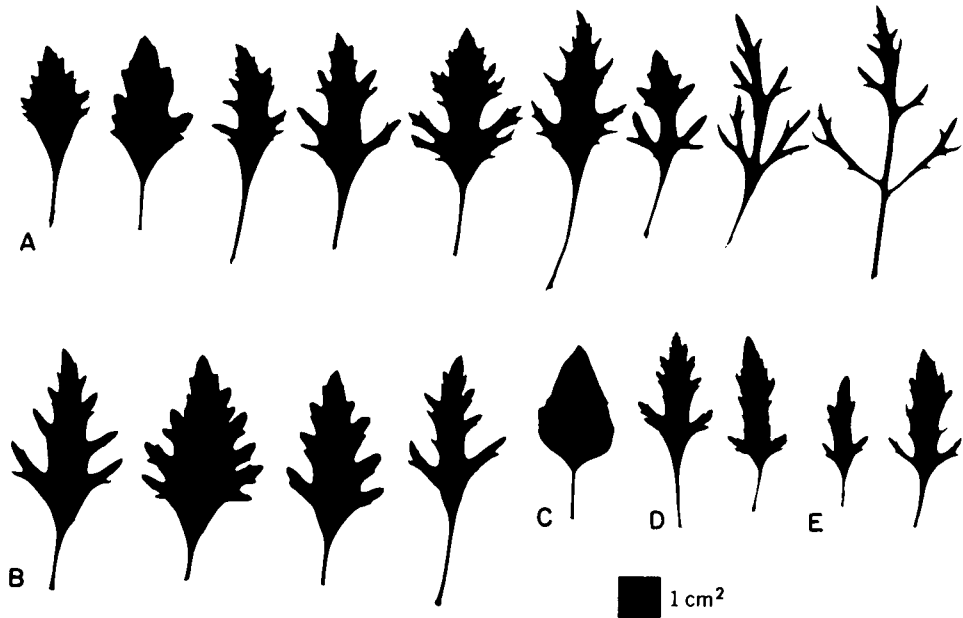


FIG. 4. Leaf silhouettes, *Encelia*. A. Sample of progeny from *E. laciniata* × *laciniata* experimental cross. B. Experimental *E. ventorum* × *palmeri* hybrids (100 × 126). C. *E. asperifolia*. D. Natural *E. ventorum* × *asperifolia* hybrids from site 4. E. Experimental *E. ventorum* × *asperifolia* hybrids (100 × 132).

east of El Rosario south to Millers Landing and farther south in the Sierra Vizcaíno and on Cedros Island (fig. 1). Plants are about a meter tall or less, shrubby, with solitary heads. In contrast to the brown stigmas of *E. ventorum* and *E. palmeri*, *E. asperifolia* has yellow stigmas. The sinuate or entire leaves are generally ovate to almost triangular (fig. 4C). The pubescence is of stout multicellular hairs, moniliform hairs, and glands (fig. 3E).

*Encelia asperifolia* usually grows on rocky, well-drained soils of hillslopes and ravines. Where it occurs with *E. ventorum* at Millers Landing, it grows in silt and clay behind the coastal dunes.

*Natural hybrids.* We critically examined *E. laciniata* and its parental species at five locations in west-central Baja California:

Site 1. On and immediately inland from the sea bluffs, 19.2 km SE of Asunción, a large *E. ventorum* population (124) is limited to dunes capping an elevated shell terrace. *Encelia laciniata* (122 and 125) is entirely confined to the leeward margin of these dunes. Some 100 to 200 m inland on the other side of a backswamp is an extensive population of *E. palmeri* (128). No apparent backcross or other recombinant plants were found.

Site 2. Immediately east of Asunción, several hundred plants of *E. ventorum* and *E. palmeri* occur sympatrically on a deltaic deposit at the

mouth of an arroyo. This sympatry is promoted by an unusual variety of substrates that has resulted from differential deposition in a braided, seasonally wet stream course. *Encelia laciniata* (120) is almost totally confined to the margins of a graded dirt road and to the active part of the disturbed watercourse that passes through a small part of the area occupied by the sympatric population. Apparent backcross individuals and other sorts of recombinant plants are rare and essentially confined to the highly disturbed margins of the road.

Site 3. In the town of Guerrero Negro, about 150 m east of the junction of the main road with the dirt road to the old wharf a few plants of *E. ventorum* (136) and a large *E. palmeri* population (116) occur. These species grow primarily around the borders of an approximately 700 m<sup>2</sup> area that has been severely disturbed by human activity (as evidenced by vehicle tracks, an old building foundation, and construction wastes). Only within this area of extreme disturbance hybrids (105 and 138) and their derivatives greatly outnumber individuals of the parent species. The range of variation in leaf shape (fig. 2) was essentially continuous from that of *E. ventorum* to that of *E. palmeri*.

Site 4. Just south of Millers Landing *Encelia ventorum* (114) occurs abundantly on the main mass of dunes and in lesser numbers on the smaller dunes nearer the shore. *Encelia palmeri* grows in patches between the smaller dunes and *Encelia laciniata* occurs along the northern margin of these dunes.

Less than 200 m inland from this site, in the lee of the dunes, we found other plants that in many ways resembled *E. laciniata* (fig. 4D) but had a more intensely green foliage (a result of less dense pubescence; fig. 3F). Also, their stigmas were bright yellow rather than brownish-purple as in other populations of *E. laciniata* and in *E. ventorum* and *E. palmeri*. The source of these differences was readily apparent, for here *E. ventorum* was in contact with a third species, *E. asperifolia* (132), which has deep green foliage and yellow stigmas. Clearly these laciniata-like plants (121 and 135) represented the hybrid product of *E. ventorum* and *E. asperifolia*.

Site 5. Just north of the Guerrero Negro airport *Encelia ventorum* (101) grows abundantly on the well-developed dunes. The nearest *Encelia palmeri* plants that we were able to find after a careful search were more than 1.5 km away. This suggests that pollinators can effectively transfer pollen between these species at least this distance, because we found two immature *E. laciniata* plants at the margin of an inland spur of these coastal dunes. They were in such poor condition that it seems unlikely that they would have reached reproductive age.

*Experimental hybrids.* To test the hybrid origin of *E. laciniata*, we crossed the supposed parents, *E. ventorum* and *E. palmeri*. The resulting hybrids had all the characteristics diagnostic of *E. laciniata* (figs. 3D and 4B).

Likewise, we crossed *E. ventorum* and *E. asperifolia* and got hybrids



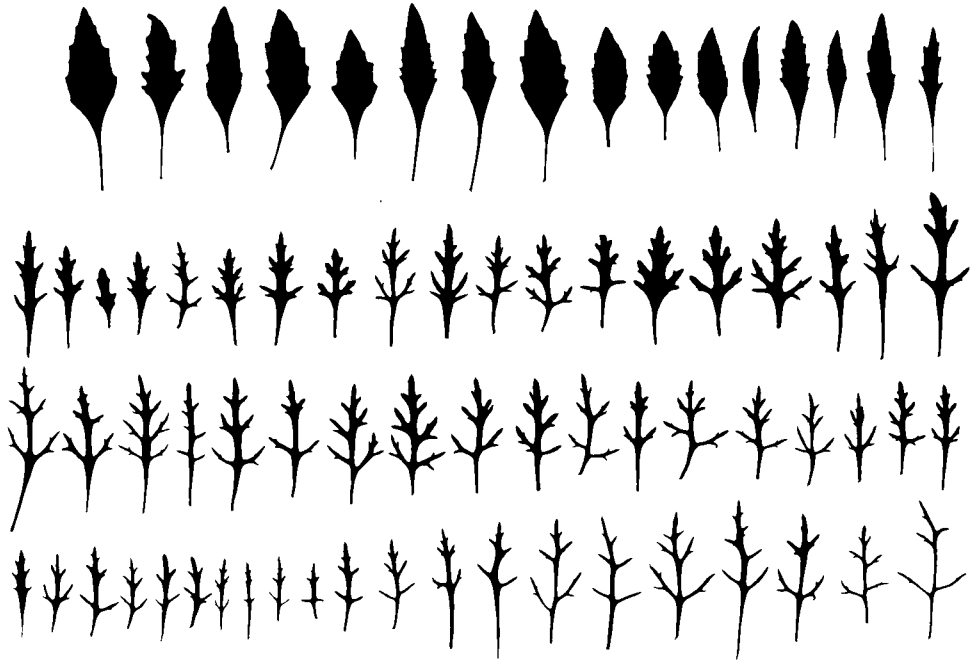


FIG. 5. Outcome of progeny test of *Encelia laciniata* fruits from site 1. Each leaf represents a different plant; leaves were taken from juvenile plants, which accounts for their small size.

indistinguishable from the *laciniata*-like plants found inland at site 4 (fig. 4E). Also, we intercrossed various individuals of *E. laciniata* grown from seedlings or cuttings collected from natural populations. The resulting progeny were highly variable, with some approaching the morphology of *E. ventorum* and others *E. palmeri* (fig. 4A). Intraspecific crosses in *E. ventorum* and *E. palmeri* produced only uniform progeny characteristic of their respective species.

*Progeny tests of natural populations.* To gain some understanding of the dynamics of populations in which *E. laciniata* occurs, we did progeny tests using fruits from *E. laciniata*, *E. ventorum*, and *E. palmeri* at site 1. This site was particularly interesting, because of the 100–200 m gap between the *E. ventorum* and *E. palmeri* populations. The 90 progeny from *E. laciniata* (125) were quite variable. Apparent backcrosses to *E. ventorum* predominated, but 12 individuals appeared to be backcrosses to *E. palmeri* (fig. 5). Some of these plants may well have been  $F_2$  recombinants. These results are certainly to be expected, because the progeny-tested *E. laciniata* plants occur at the margin of the *E. ventorum* population.

From fruits of *E. ventorum* (124) we obtained 220 plants, all but eight unquestionably *E. ventorum*. These eight agreed in all respects with *E. laciniata* and doubtless are the product of pollen from the *E. palmeri*

population 100–200 m away. The pollen flow against the prevailing winds strongly suggests insect pollinator activity, as do the size and sculpturing of *Encelia* pollen.

Three hundred fruits from *E. palmeri* (128) produced only *E. palmeri* progeny. We know from controlled crosses that *E. ventorum* pollen will function normally on *E. palmeri* stigmas to produce vigorous hybrids. Therefore, the lack of hybrids in this test must be attributed to other factors.

*Genetic system.* During these studies, we have repeatedly observed that hybrids among these species and their recombinant derivatives all have 18 pairs of chromosomes and regular meiosis and are as vigorous and fertile as their parents. Moreover, all parents, hybrids, and recombinants are strongly self-incompatible, with no instances of selfing seen in hundreds of test crosses.

#### DISCUSSION

A combination of field observations, progeny tests, and experimental crosses has shown conclusively that *Encelia* × *laciniata* Vasey & Rose (pro sp.) is of hybrid origin. The results reveal, moreover, that the description of *E.* × *laciniata*, as interpreted by several generations of collectors, includes two sorts of hybrids with one parental species in common. Most individuals identified as *E.* × *laciniata* are the hybrid product of *E. ventorum* and *E. palmeri* where they are sympatric along the Pacific coast of central Baja California. However, at a single locality south of Millers Landing, plants generally resembling *E.* × *laciniata* were found to be hybrids of *E. ventorum* and *E. asperifolia*. Other similar populations may very well exist along the coast to the north of this locality.

As is typical of hybrids, *E.* × *laciniata* plants are rigidly confined to areas of disturbance or to habitats that appear to be intermediate between those of their parent species. Without exception, we also observed that the greater the degree of habitat disturbance, the more frequent were hybrids and their derivatives, a phenomenon admirably elucidated in other plant groups by Anderson (1948, 1949) and Anderson and Anderson (1954). These sorts of field observations and our experimental analyses all point to the powerful role that selection plays in eliminating certain classes of progeny and thereby determining the variation patterns and distribution of taxa in these natural *Encelia* populations. Discerning and measuring selective factors is very difficult, especially in natural populations where so many components may interact to produce a final result. Consequently, we do not yet know precisely how selection is operating in these populations, but we have little doubt that it occurs and that it is extremely intense, if not absolute.

In this connection it is relevant that our experimental crossing program revealed these *Encelia* species and hybrids to be self-incompatible and fully interfertile, with no internal reproductive barriers. Hence, se-

lective forces would have to be great to overcome the interspecific pollen flow in these *Encelia* populations. For example, progeny tests of adjacent *E. palmeri* and *E. ventorum* populations at site 1 showed that even with a 100–200 m gap between the species, interspecific pollen flow still resulted in the production of hybrid embryos at a frequency of nearly 4%. Moreover, the natural hybrids at this site were completely confined to a narrow zone at the leeward edge of the sand dunes. This extremely precise and restricted distribution of hybrids must result from their complete selective elimination from other closely adjacent sites where fruits containing hybrid embryos no doubt are also dispersed. In addition, every hybrid plant appeared to be first generation; apparent backcrosses and other recombinants are totally lacking, despite the evidence from our progeny tests that they are generated in substantial numbers. This can only be accounted for by absolute post-dispersal selective forces preventing their survival. Furthermore, neither *E. ventorum* nor *E. palmeri* at this locality displayed any unusual amounts of variation indicative of effective gene flow between these species. Similarly, at site 2, where hundreds of plants of *E. ventorum* and *E. palmeri* are in intimate association, there was very little evidence of interspecific gene flow.

Only in the highly disturbed site 3 at Guerrero Negro did the situation approach what might be termed a hybrid swarm. Within about a 700 m<sup>2</sup> area of greatest disturbance, F<sub>1</sub> hybrids, apparent backcross plants, and various other recombinants composed nearly the entire population. The extreme alteration of the habitat apparently produced an array of unusual microenvironments that were suitable for the survival of various recombinant *Encelia* individuals. Such an extensive array of recombinants has not been observed elsewhere in natural *Encelia* populations, but similar recombinant arrays of plants easily were produced experimentally among F<sub>2</sub> progenies.

Collectively, all of these natural examples (which might be termed natural experiments) together with our experimental findings consistently point to the overriding importance of post-dispersal selective forces in these *Encelia* populations.

One might assume that pollinator behavior would favor intraspecific pollination in these plants. Nevertheless, it is quite apparent from our progeny tests that pollinator activities generate numerous hybrids and their derivatives. Accordingly, it is difficult to think of pollinators serving an effective isolating function. Rather, they appear to be principally a means of providing sufficient intraspecific progeny to allow each species to continue occupying the sites to which it is best adapted.

In this connection, it is significant that in certain intermediate sites, or where habitats are disturbed to the extent that the parental species are apparently no longer at a selective advantage, we can find hybrids and recombinants not just surviving but composing nearly the entire population. This same phenomenon occurs in the well-studied interspecific interactions of *Salvia apiana* and *S. mellifera* (Anderson and Anderson

1954), despite their pronounced divergence of pollination mechanisms and temporal modes of reproduction, which for the most part appear to be absent in *Encelia*. In the case of the salvias, it is particularly difficult to accept the interpretation that the "permissiveness" (reduced competition) of an open or disturbed habitat is the essential reason for the appearance and success of hybrids and their derivatives. If these products of hybridization were not adaptively superior in locally altered habitats, it is hard to imagine how they could largely or entirely replace the parent species just within these altered sites, as described by Anderson and Anderson (1954). Moreover, when one considers how seldom these *Salvia* hybrids are produced by the exceptional event of interspecific pollination, coupled with the hybrids' substantially reduced reproductive capacity (Grant and Grant 1964), it becomes all the more difficult to accept the displacement of the parent species by hybrids and their derivatives on the basis of relaxed selection. With these salvias, as well as with *Encelia* species, only extremely intense to absolute post-dispersal selection capable of overcoming the influence of the pollinators adequately explains the characteristics of these populations.

The occurrence of hybrids and recombinants in natural *Encelia* populations is indisputable evidence of pollinator infidelity. What is more, our progeny tests have shown conclusively that various sorts of interspecific recombinant individuals are generated in substantial numbers in sympatric *Encelia* populations, whether they are manifested as mature survivors or not. Clearly, we cannot look to pollinators as the agents maintaining the discreteness of these plant species. Instead, we must conclude that without other essentially omnipotent post-dispersal selective forces eliminating or confining the products of interspecific gene flow, the resulting trickle of genes between these *Encelia* species, no matter how small, would in time bring about their merger and ultimate homogeneity.

ACKNOWLEDGMENTS. We thank Daniel I. Axelrod, Gregory J. Lee, Barbara K. Rugeley, and Krista J. Thompson for their assistance in the field, Gerald D. Carr for helpful comments on an early draft of this manuscript, and Reid Moran for his valuable suggestions for improving the manuscript.

#### LITERATURE CITED

- ANDERSON, E. 1948. Hybridization of the habitat. *Evolution* 2:1-9.  
———. 1949. *Introgressive hybridization*. New York: John Wiley.  
——— and B. R. ANDERSON. 1954. Introgression of *Salvia apiana* and *Salvia mellifera*. *Ann. Missouri Bot. Gard.* 41:329-338.  
BAKER, K. F., ed. 1957. The U. C. system for producing healthy container-grown plants. Univ. Calif. Agric. Exp. Sta. Manual 23.  
BLAKE, S. F. 1913. A revision of *Encelia* and related genera. *Proc. Amer. Acad. Arts* 49:346-396.  
GRANT, K. A. and V. GRANT. 1964. Mechanical isolation of *Salvia apiana* and *Salvia mellifera* (Labiatae). *Evolution* 18:196-212.

- JOHNSON, A. F. 1977. A survey of the strand and dune vegetation along the Pacific and southern gulf coasts of Baja California, Mexico. *J. Biogeography* 7:83-99.
- LEWIS, H. and C. EPLING. 1959. *Delphinium gypsophilum*, a diploid species of hybrid origin. *Evolution* 13:511-525.
- SHREVE, F. and I. L. WIGGINS. 1964. *Vegetation and flora of the Sonoran Desert*, vol. 2. Stanford: Stanford Univ. Press.
- VASEY, G. and J. N. ROSE. 1889. List of plants collected by Dr. Edward Palmer in Lower California in 1889. *Proc. U.S. Natl. Mus.* 11:535.
- WIGGINS, I. L. 1980. *Flora of Baja California*. Stanford: Stanford Univ. Press.