

NATURAL HYBRIDIZATION BETWEEN  
*MALACOTHRIX INCANA* AND *M. SAXATILIS* VAR.  
*IMPLICATA* (ASTERACEAE: LACTUCEAE) ON  
SAN MIGUEL ISLAND, CALIFORNIA

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ABSTRACT

Evidence from 1) plants grown in cultivation, 2) herbarium specimens, and 3) natural populations suggests that hybridization between the perennials *Malacothrix incana* and *M. saxatilis* var. *implicata* occurs on San Miguel Island, California. *Malacothrix incana* has yellow corollas, a chromosome number of  $2n = 14$ , and is self-compatible. *M. s.* var. *implicata* has white corollas, a chromosome number of  $2n = 18$ , and is self-incompatible. Three hybrids were grown in cultivation from achenes collected from *M. s.* var. *implicata* on San Miguel Island, and all had  $2n = 16$ . Hybrids in cultivation and in the field had pale yellow corollas. All hybrids had less than 4% stainable pollen and were intermediate between the parents in leaf and involucre morphology. Cross-pollinations between the parents in cultivation produced no hybrids, and hybrids apparently are relatively rare in natural populations. All of the evidence suggests that the parents are separated by generally effective isolating mechanisms and that hybridization in nature has not proceeded beyond the  $F_1$  level. Hybrids were found on San Miguel Island in all areas where the parents were seen together, and no single zone of hybridization was found. The presence of hybrids of different ages suggests that there have been several hybridization events. The parents have different habitat preferences, but changes in edaphic factors on San Miguel Island during historic time probably have allowed *M. incana* to invade areas occupied by *M. s.* var. *implicata* so that cross-pollination can occur often enough to produce hybrids.

Three of the ca. 24 species now included in *Malacothrix* (Asteraceae) are perennials. One, *M. xantii* A. Gray, behaves predominantly as an annual and is not considered here. The other two perennials are *M. incana* (Nutt.) Torr. & A. Gray, and the *M. saxatilis* (Nutt.) A. Gray complex. These two taxa are sufficiently morphologically distinct from the annuals and each other that they were considered separate genera by Nuttall (1841). The *M. saxatilis* complex originally included six species, but later taxonomic treatments (Williams 1957, Abrams and Ferris 1960) have reduced them to varietal rank. The corollas of *M. incana* are yellow and the chromosome number is  $2n = 14$ . Evidence from recent studies (Davis 1980) suggests that *M. incana* is closely related to diploid, annual

taxa that are endemic to the California islands. Members of the *M. saxatilis* complex have white corollas and a chromosome number of  $2n = 18$ . The complex is internally coherent but has no clear morphological or cytological relationship to any of the known annual species and is under current investigation by the senior author.

We observed that *M. saxatilis* var. *implicata* (Eastw.) Hall, endemic to the California islands, and *M. incana* were sympatric on San Miguel Island, California and evidence from a preliminary study (Philbrick 1980) suggested that hybridization was occurring. In the present paper, we report evidence that documents hybridization between these two taxa, and we discuss the evolutionary and systematic implications of this hybridization.

#### MATERIALS AND METHODS

Plants representing natural populations of *Malacothrix incana* and *M. s.* var. *implicata* were grown in UC soil mix B at the University of Louisville in a Sherer-Gillet walk-in chamber ( $2.0 \times 2.5 \times 2.5$  m). Photoperiod and temperature were reset every 15 days to match photoperiod and mean day and night temperatures for Los Angeles, California, over a 12 month cycle; these conditions were chosen for general studies of species of *Malacothrix* in cultivation and have been used for the past 12 years.

Beginning in 1974, plants were propagated from achenes taken from herbarium specimens at SBBG. Forty-nine plants of *M. incana* have been grown in the growth chamber: three from achenes of specimens collected at the mouth of the Santa Maria River, Santa Barbara Co.; one from an achene of a specimen from Santa Rosa Island; four from achenes of a single specimen collected at Montaña de Oro State Park, San Luis Obispo Co.; and 41 plants grown from achenes collected during trips to San Nicolas and San Miguel islands in 1984. Thirty-nine plants of *M. s.* var. *implicata* have been grown in the growth chamber: 15 from achenes collected on Anacapa Island in 1982; three from achenes collected on San Nicolas Island in 1984; 12 from achenes collected on San Miguel Island in 1984; and nine from achenes collected on Santa Cruz Island in 1985. Voucher specimens for all plants grown in cultivation are deposited at DHL.

Plants in cultivation were used in all cross-pollinations. Percentages of filled achenes were recorded for all crosses.

We examined 46 herbarium specimens of *M. incana*, *M. s.* var. *implicata*, and hybrids from Cuyler Harbor, San Miguel Island, and 98 specimens from other areas of the island. Forty-seven specimens of *M. incana* and *M. s.* var. *implicata* from other California islands, and 46 specimens of *M. incana* from mainland California also were studied. A list of specimens is available from the senior author.

We studied parents and hybrids in the field on flats near the Ranch

airstrip, slopes above Cuyler Harbor, north-facing slopes of San Miguel Hill, and slopes near the ocean at Tyler Bight during a visit to San Miguel Island, 24–27 May 1984.

Meiotic behavior in cultivated plants was studied using standard acetocarmine squash techniques, and 20 PMC's were analyzed for each plant studied. Pollen stainability was determined for plants from natural populations, plants in cultivation, and all herbarium specimens using 1% cotton blue-lactophenol; 100 pollen grains were analyzed for each specimen. For studies of mitosis, five-day-old seedlings from achenes from mainland and island locations were placed in 0.002 M 8-hydroxyquinoline for three hours, then fixed and root tips stained using the Feulgen technique.

Achenes for scanning electron microscopy (SEM) were mounted on stubs, coated with 9 nm gold, and viewed with either a Cambridge or an SPI Model 40 SEM.

## RESULTS

*Morphology of parents.* Morphological characters, as observed in the growth chamber, on herbarium specimens, and in natural populations, clearly distinguish *Malacothrix incana* from *M. s.* var. *implicata* (Table 1). The cauline leaves of *M. incana* have entire margins or possess broad, short lobes with blunt apices. Less often, the lobes are long and narrow (Fig. 1A). The leaves and stems are glabrous on some plants and densely tomentose on others. The outer phyllaries are ovate or broadly linear (Fig. 1A) and the surface of the receptacle is umbonate and without chaff. The corollas are yellow. The achenes have an inner pappus composed of a ring of bristles connate at their bases, but lack an outer pappus (Fig. 2A). The spines on the achene wall are less than 50  $\mu\text{m}$  long.

The cauline leaves of *M. s.* var. *implicata* are irregularly bipinnatifid with numerous, linear divisions; apices are generally attenuate-acute (Fig. 1C). The young leaves and stems are hairy, but glabrate at maturity. The outer phyllaries are lanceolate with acuminate apices (Fig. 1C). Chaff up to 40  $\mu\text{m}$  in length occurs on the surface of the receptacle. The corollas are white, with an abaxial lavender stripe on each ligule. The achenes have an inner pappus composed of bristles connate at their bases, and an outer pappus composed of white scarios teeth that extend above the apex of the achene wall (Fig. 2C). The achene surface is covered with spines, 110–170  $\mu\text{m}$  long.

*Cytology of parents.* Meiotic behavior appeared to be normal in 11 cultivated plants of *M. incana* and all had  $2n = 7_{11}$  (Fig. 3A); root tip mitosis was examined in eight plants and all had  $2n = 14$ . Meiotic behavior appeared normal in 10 cultivated plants of *M. s.* var. *implicata* and all had  $2n = 9_{11}$  (Fig. 3C); root tip mitosis was

TABLE 1. A COMPARISON OF FEATURES IN *Malacothrix incana*, *Malacothrix saxatilis* var. *implicata*, AND INTERSPECIFIC HYBRIDS. Mean  $\pm$  s.d. is given for stainable pollen; N = number of plants analyzed.

|                           | <i>M. incana</i>                                      | Hybrids  | <i>M. saxatilis</i> var. <i>implicata</i>      |
|---------------------------|---|--|--|
| Vestiture                 | stem and leaves densely hairy or essentially glabrous | stem and leaves densely hairy or essentially glabrous      | young stems and leaf axils with scattered hair |
| Receptacle                | umbonate, smooth, without chaff                       | umbonate, but with scattered chaff                         | foveolate, with chaff to 40 $\mu$ m long       |
| Corolla color             | dark yellow, with no adaxial stripes on ligules       | pale yellow, often with abaxial reddish stripes on ligules | white with abaxial lavender stripes on ligules |
| Achene wall               | spines on rims of lacunae 30–50 $\mu$ m long          | spines on rims of lacunae 70–80 $\mu$ m long               | spines on rims of lacunae 110–170 $\mu$ m long |
| Outer pappus              | none  | irregular scarious teeth                                   | dense ring of irregular scarious teeth         |
| Chromosomes at diakinesis | 2n = 7 <sub>II</sub>                                  | 2n = 16 <sub>I</sub>                                       | 2n = 9 <sub>II</sub>                           |
| Percent stainable pollen  | 94.8 $\pm$ 4.3 (N = 59)                               | 1.1 $\pm$ 2.6 (N = 45)                                     | 96.2 $\pm$ 3.3 (N = 32)                        |

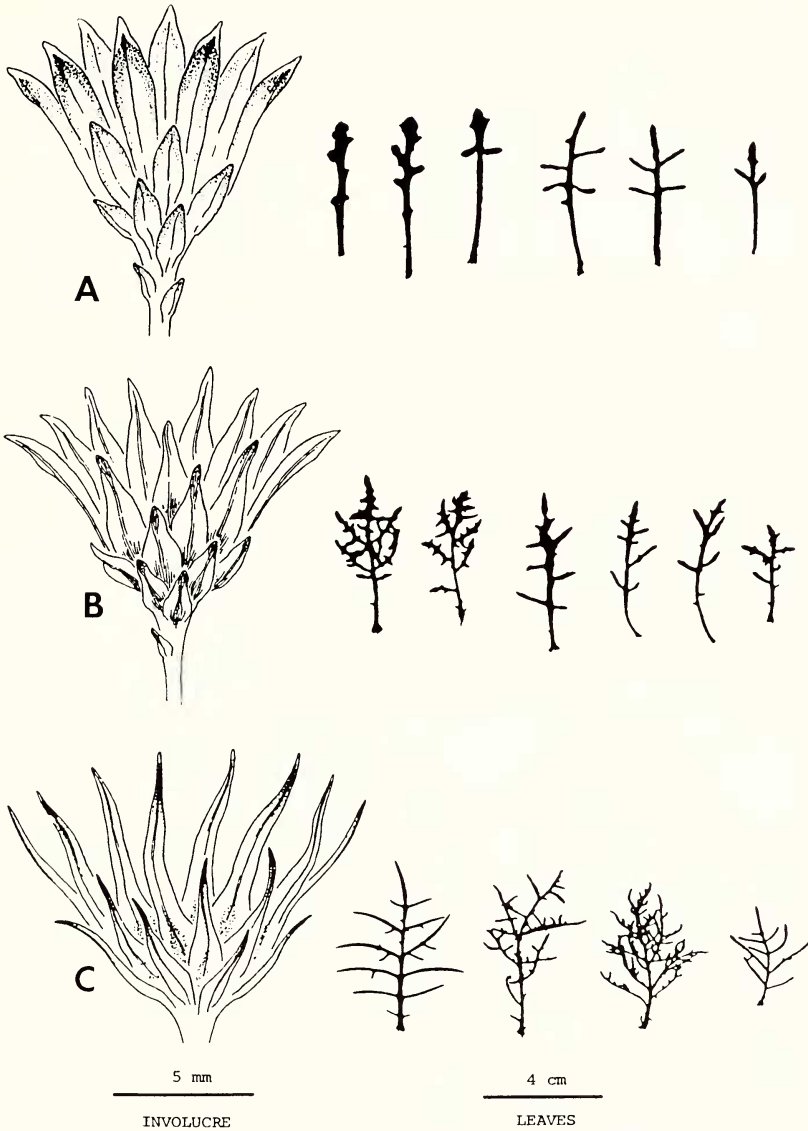


FIG. 1. Representative involucre and cauline leaves from plants grown in cultivation. A. *Malacothrix incana*. B. Hybrids between *M. incana* and *M. saxatilis* var. *implicata*. C. *M. saxatilis* var. *implicata*.

studied in eight plants and all had  $2n = 18$ . Pollen stainability of *M. incana* and *M. s.* var. *implicata* was 80% or more in all growth chamber plants, herbarium specimens, and natural populations. All plants of *M. s.* var. *implicata* in growth chamber conditions were



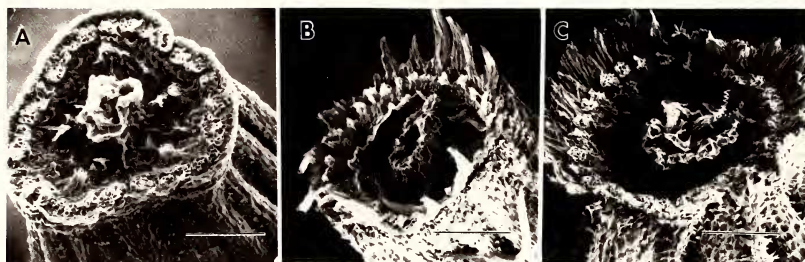


FIG. 2. Scanning electron micrographs of the apical portions of achenes of parents and hybrid. A. *Malacothrix incana*. B. Hybrid between *M. incana* and *M. saxatilis* var. *implicata*. C. *M. saxatilis* var. *implicata*. (Bars = 100  $\mu$ m.)

found to be self-incompatible. In contrast, all plants of *M. incana* were found to be self-compatible.

*Growth chamber experiments.* We were unable to obtain mature hybrid plants from achenes produced by cross-pollinations in cultivation. Fifty-four filled achenes were produced from 12 crosses involving *M. s.* var. *implicata* as the female parent and *M. incana* as the male parent. From these, only five plants were produced, and all were of non-hybrid origin. These individuals were possibly products of the mentor effect, in which the presence of foreign compatible pollen allows the self-incompatibility mechanism to be bypassed (Nettancourt 1977). Achenes taken from *M. incana* following cross-pollinations with *M. s.* *implicata* produced only non-hybrid plants.

Three hybrid plants were grown in the growth chamber from wild achenes. One plant was grown from an achene taken from a specimen of *M. s.* var. *implicata* collected at Cuyler Harbor in 1973. The other two hybrids were grown from achenes collected in 1984 from plants identified in the field as *M. s.* var. *implicata*: one at Tyler Bight and one at Cuyler Harbor. All three hybrids had less than 4% stainable pollen, and 16 univalents were observed in meiosis in all specimens (Fig. 3B).

Hybrids from all sources were intermediate between the parents in leaf and involucre morphology (Fig. 1B). The stems and leaves of the hybrids varied from glabrate to densely tomentose. Receptacles were umbonate with scattered chaff. Achenes had an inner pappus and an outer pappus composed of white, scarious teeth (Fig. 2B). The outer pappus of hybrids was consistently less well-developed than the outer pappus of *M. s.* var. *implicata*. The achene walls of hybrids had spines that were 70–80  $\mu$ m long.

In the growth chamber and in the field, corollas of hybrids were pale yellow and often had a reddish streak along the abaxial surface of each ligule. One of the cultivated hybrid plants grew at a faster rate and flowered sooner during its first year of growth than indi-

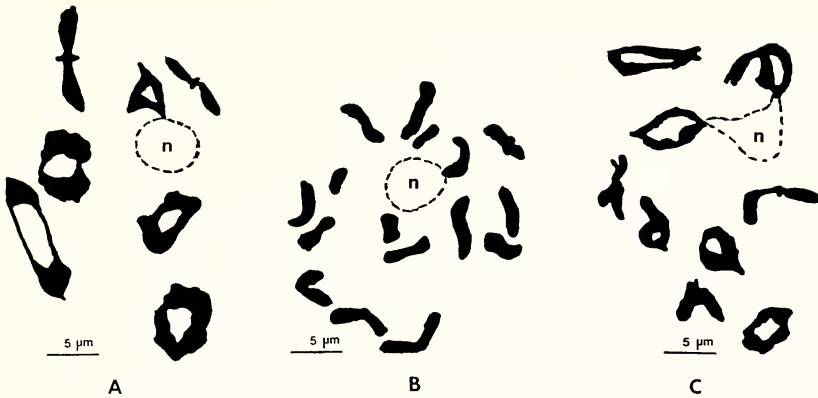


FIG. 3. Meiotic configurations at diakinesis in PMC's of parents and hybrid. A. *Malacothrix incana*, 7<sub>n</sub>. B. Hybrid between *M. incana* and *M. saxatilis* var. *implicata*, 16<sub>n</sub>. C. *M. s.* var. *implicata*, 9<sub>n</sub>.

viduals of either parent growing with it. The other two hybrid plants died after flowering in their first year of growth. Cross-pollinations between cultivated hybrids with either *M. s.* var. *implicata* or *M. incana* produced abortive ovaries.

*Field observations.* On San Miguel Island in 1984, *M. incana* was found on the flats and slopes across the surface of the island and on the slopes, bluffs, and unstabilized sand dunes near the ocean. Along the west slope of San Miguel Hill, *M. incana* was abundant and grew scattered on stabilized sand. In contrast, *M. s.* var. *implicata* was not observed on the upper flats and slopes of the island, but was common on the slopes and bluffs adjacent to the ocean.

We found 38 putative hybrids on San Miguel Island, 20 on the slopes above Cuyler Harbor, 14 above Tyler Bight, two above Cardwell Point, one in Willow Canyon, and one in upper Cañada del Mar. These hybrids were found in a variety of habitats on the island, but occurred only where the parents also were present. Parents and hybrids occasionally were intermixed, with one of the taxa growing among the stems of the others. Parents and hybrids were vigorous and well-developed on the north-facing slopes above Cuyler Harbor, but were noticeably less robust on the southwest-facing slopes above Tyler Bight. All the hybrids had light yellow corollas and leaves intermediate in morphology between those of the parents; stainable pollen ranged from 0–4%. In 113 mature heads (1–7 from each plant) collected in the field, 10 normal-appearing achenes were found among a total of 9615. None of these achenes germinated when planted; five had poorly developed embryos, but the others contained embryos that appeared to be normal.

Although *M. incana* was found on unstabilized sand dunes and

on stabilized sand, hybrids were found only on stabilized sand. The composition of the vegetation was conspicuously different, however, in different areas where hybrids were found. The following descriptions of three areas on the north-facing slopes above Cuyler Harbor illustrate some of these vegetation differences: 1) *M. incana* abundant, few plants of *M. s.* var. *implicata* present, patches of bare soil interspersed among the herbaceous cover; 2) *M. incana* uncommon, *M. s.* var. *implicata* common as part of a shrubby assemblage that included *Lupinus albifrons* Benth., *Baccharis pilularis* DC., and *Haplopappus venetus* (HBK) Blake; 3) parents relatively uncommon, no bare soil patches visible, no shrubby vegetation present. Hybrids were generally well-developed with thick basal stems 2–4 cm in diameter, and evidence of previous years' growth could be seen. Estimates of the ages of hybrid plants on San Miguel Island were made using evidence from a study of the rate of increase in stem diameter of a hybrid plant growing in cultivation for six years. From this comparison, most wild hybrid plants appeared to be four years of age or older, but one flowering hybrid was found with a stem diameter and branching pattern that suggests it was no more than two years old.

*Pollinators.* Thirty-one pollinating and herbivorous insects were collected from *Malacothrix* parents and hybrids (Miller and Davis 1985). Three species of insects were collected from both parents and the hybrids, and the parents shared an additional four species of visitors that were not observed on the hybrids. Both parents and hybrids were in flower with up to 250 open flower heads on individual plants. On parents and hybrids, the heads opened about 0700 h and among the first visitors to the two parents was the native bee *Agapostemon texanus* Cresson, which appears to be the major pollinator of *Malacothrix* species on San Miguel Island. The relatively large, metallic green females were numerous in the morning hours, and a majority of the pollen taken from 11 females of this species from San Miguel Island was from *Malacothrix*. On four occasions we saw individuals of *A. texanus* move from flowers of one parent to flowers of the other parent.

#### DISCUSSION

Evidence from the present study suggests that hybridization between *Malacothrix incana* and *M. saxatilis* var. *implicata* occurs on San Miguel Island when the two are found in sympatry. Hybrids are less abundant than the parents. For example, only 20 hybrids were found along the slopes above Cuyler Harbor where thousands of plants of each parent occur. The presence of a young hybrid plant on the island and the wide range of apparent ages of the other hybrids suggest that hybridization is a continuing phenomenon.



We have found no evidence that natural hybridization has proceeded beyond the  $F_1$  level and the production of  $F_2$  segregates is improbable. All of the hybrids were sterile, less than 0.1% of the achenes from heads of hybrids were filled, and no chromosome associations were observed in hybrids grown in the growth chamber. Parents and hybrids were identified easily in nature, as herbarium specimens, or in the growth chamber; no combinations of character states were found that suggested segregation beyond the  $F_1$  level.

The achenes of the parents are dispersed easily because of their small size (length ca. 1 mm), light weight (ca. 0.05 mg), and the presence of a ring of inner pappus bristles that may remain attached to the fruit and can function as a parachute. Achenes from mature heads of cultivated parents often were seen floating in the air from one end of the growth chamber to the other. During each growing season, seedlings of *M. incana* regularly appeared in pots containing mature plants of other species of *Malacothrix*. Because of the almost constant wind and its relatively high velocity on San Miguel Island, it is likely that achenes of both species have had a chance to be distributed throughout the island. The general pattern of distribution of *M. incana* and *M. s.* var. *implicata* on San Miguel Island, however, suggests that each species has different habitat preferences. This view is supported by observations from San Nicolas Island where both *M. incana* and *M. s.* var. *implicata* are found and by the distribution of *M. incana* on mainland California. At mainland sites, *M. incana* is restricted to coastal strand communities where stable sand dunes are found. Williams and Potter (1972) found that *M. incana* was restricted to the stable dune area at Morro Bay State Park (San Luis Obispo Co.) where it formed conspicuous scattered colonies. On San Nicolas Island, we recently found *M. incana* to be distributed widely on portions of the island where the substrate is stabilized sand and also near the ocean on stabilized or unstabilized sand dunes. We found *M. s.* var. *implicata* growing only on more compacted sandy-clay soils, either on bluffs away from the main beach areas or along the ocean on the leeward side of the island. We found no habitats on San Nicolas Island where *M. incana* and *M. s.* var. *implicata* were sympatric.

Johnson (1980) suggested that recurrent episodes of vegetation stripping and soil erosion have occurred during late Pleistocene to recent historic time on San Miguel Island. Historic stripping episodes have followed droughts, overgrazing, and farming activities. Landscape modification has included dune encroachments and wind erosion. An aerial photograph taken on 1 April 1960 (Johnson 1980) showed strips of sands that ran from one side of the island to the other. The distribution of *M. incana* across the slopes of Green Mountain and San Miguel Hill is generally correlated with these stabilized sandy areas. Such changes in edaphic factors apparently

have played the primary role in allowing *M. incana* and *M. s.* var. *implicata* to grow sympatrically.

Natural hybridization between *Malacothrix incana* and *M. saxatilis* var. *implicata* suggests a relationship between the *M. saxatilis* complex and the main body of *Malacothrix*. With respect to most morphological features, however, the *M. saxatilis* complex is less similar to *M. incana* and related annual species than it is to some of the mainland annual species. For example, an outer pappus similar in construction to the one in the *M. saxatilis* complex is found in *M. glabrata* A. Gray, and the receptacles of most annual mainland species are foveolate and bear chaff. White corollas similar to those in the *M. saxatilis* complex are found in *M. floccifera* (DC.) Blake, but the latter has no outer pappus. Natural hybridization between *M. incana* and *M. s.* var. *implicata* and the fact that a number of morphological features of the *M. saxatilis* complex occur in other species in the genus support the idea that *Malacothrix* is natural as currently defined. There is no extant mainland species with a suite of morphological features that match it with members of the *M. saxatilis* complex, however, and the precise placement of the complex in *Malacothrix* remains to be determined.

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