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GENETIC AND TAXONOMIC STUDIES IN *GILIA*IV. *GILIA* *ACHILLEAEFOLIA*

VERNE GRANT*

INTRODUCTION

On his expedition in the South Coast Range of California in the early 1830's, the botanical explorer David Douglas collected two quite dissimilar specimens, which Bentham subsequently described as *Gilia achilleaeifolia* and *G. multicaulis*. These entities happened to be so variable that later taxonomists, confronted with a greater representation of specimens and forced to interpret them on the basis of morphological characters alone, were led to confuse one of the entities, *Gilia achilleaeifolia*, with several races of *Gilia capitata*, and the other, *G. multicaulis*, with the species later distinguished as *Gilia engelensis* and *G. clivorum*. The original cleavage between *G. achilleaeifolia* and *G. multicaulis* which was established by Bentham in 1833, however, has been maintained in every manual, flora and monograph published since that date.

The results of intensive field studies and crossing experiments bring us to a very different disposition of these entities. The combined taxonomic and genetic studies show that *Gilia achilleaeifolia* and *G. multicaulis* together comprise a single species which is separated from the other species of its section by well-developed isolating mechanisms. The purpose of the following paper is to present the evidence bearing upon this conclusion and to propose an hypothesis to account for the extraordinary variability of the species.

The work on *Gilia achilleaeifolia*, which was commenced in 1946, was carried on during the year 1949-1950 at the Carnegie Institution of Washington, Stanford, California, with the support of a National Research Fellowship. Drs. Jens Clausen, William M. Hiesey, and David D. Keck made numerous helpful suggestions during the year of residence in Stanford. Mrs. Alva Grant made all the cross-pollinations, helped in the field work, and read the manuscript. The author wishes to express his appreciation to these individuals and to the supporting institutions.

VARIATION

Gilia achilleaeifolia (including *G. multicaulis*) occurs in canyons and on hillsides in the oak woodland and grassland savannah of the South Coast Range. The species consists of a series of discontinuous and disjunct local populations. These local colonies may number hundreds of individuals, or tens of thousands, but are in all cases limited in size and extent and separated by disjunctions from the nearest neighboring colonies. The most impressive feature about *Gilia achilleaeifolia* as one observes it in the field is the great variation from colony to colony. This variability is apparent even within a small neighborhood of populations, as in a single group of hills or mountain pass, and is repeated throughout the whole distribution area of the species.

Between populations.—The first step in the analysis of the variation pattern of *Gilia achilleaeifolia* was the measurement of 22 characters in 16 population samples

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collected throughout the range of the species. The eight characters which proved to be at once most uniform within the populations but most variable between populations were next measured in herbarium specimens from over 40 localities. This exercise confirmed the impression gained in the field that no two populations of *Gilia achilleaeifolia* are alike. The measurements were grouped according to the different natural areas occupied by the species in an effort to reveal, if possible, the existence of any geographical regularities in the variations. This effort was largely unsuccessful. Almost as wide a range of types can be found within any one area, such as the San Francisco Bay area, or San Benito County, or San Luis Obispo County, as can be found in the range of the species as a whole.

To simplify the presentation of the results, two of the characters, namely length of corolla and number of flowers in the cyme, have been plotted as idiographs on a distribution map (fig. 1). This map shows first that corolla length varies from 6 mm. to 21 mm. and size of inflorescence from 2 to 32 flowers, and secondly that these characters are to a certain extent independent of one another and of geographical position. There is, however, a correlation which is not brought out by the map in that the large-flowered types with capitate heads grow in sunny places, while the small-flowered forms with loose cymes tend to occur in shady habitats.

It was necessary to find out to what extent these and other differences between the populations were hereditary. In order to obtain information along this line, an experiment was set up at Stanford in 1950. Progenies of nine wild populations scattered through the range of the species (see fig. 2) were grown under relatively uniform environmental conditions. Part of the progeny of each natural population was grown in an experimental field exposed to full sunlight, while another part was grown in a shaded greenhouse. The plan was to let each strain be represented by 20 individuals in the sun plot and 20 individuals in the shade plot. Owing to adverse growing conditions the experiment could not be carried out according to the original plan, since some of the strains were finally represented by only a few individuals.

The data obtained from the experiment, while insufficient for statistical treatment, do nevertheless warrant some statements of a qualitative sort. Let us consider first the character of corolla length. The average length of corolla in the series of nine wild populations mapped on figure 2 is: Mt. Tamalpais, 6 mm.; Bear Creek, 10; Moraga Canyon, 11; Kings Mt., 7; Mt. Oso, 7; Pinnacles, 11; School Canyon, 19; San Luis Obispo, 21; Casmalia, 14. The average length of the corolla in the progenies of these populations grown in a uniform environment remained about the same as that of the plants in nature. There is consequently as great intercolonial variation in this character in the garden as there is in the wild.

The number of flowers in a typical cyme is more subject to environmental modifications. In a series of wild populations occurring in sunny habitats the average number of flowers per cyme is as follows: Bear Creek, 24; Moraga Canyon, 8; Mt. Oso, 5; Pinnacles, 8; School Canyon, 17; San Luis Obispo, 15; Casmalia, 20. The progeny of these populations when grown in a sun plot under relatively uniform environmental conditions produced about the same number of flowers per cyme as their parents in the natural habitats. The Bear Creek strain constituted an exception to this rule, in that the number of flowers in each inflorescence was appreciably less in the garden than in the wild (15 as compared with 24 flowers in an average cyme). Parallel samples of the same populations grown in the shady greenhouse had only one-half to one-third as many flowers per cyme as the plants grown in the sun (fig. 3).

The Mt. Tamalpais and Kings Mt. populations, which were found growing in

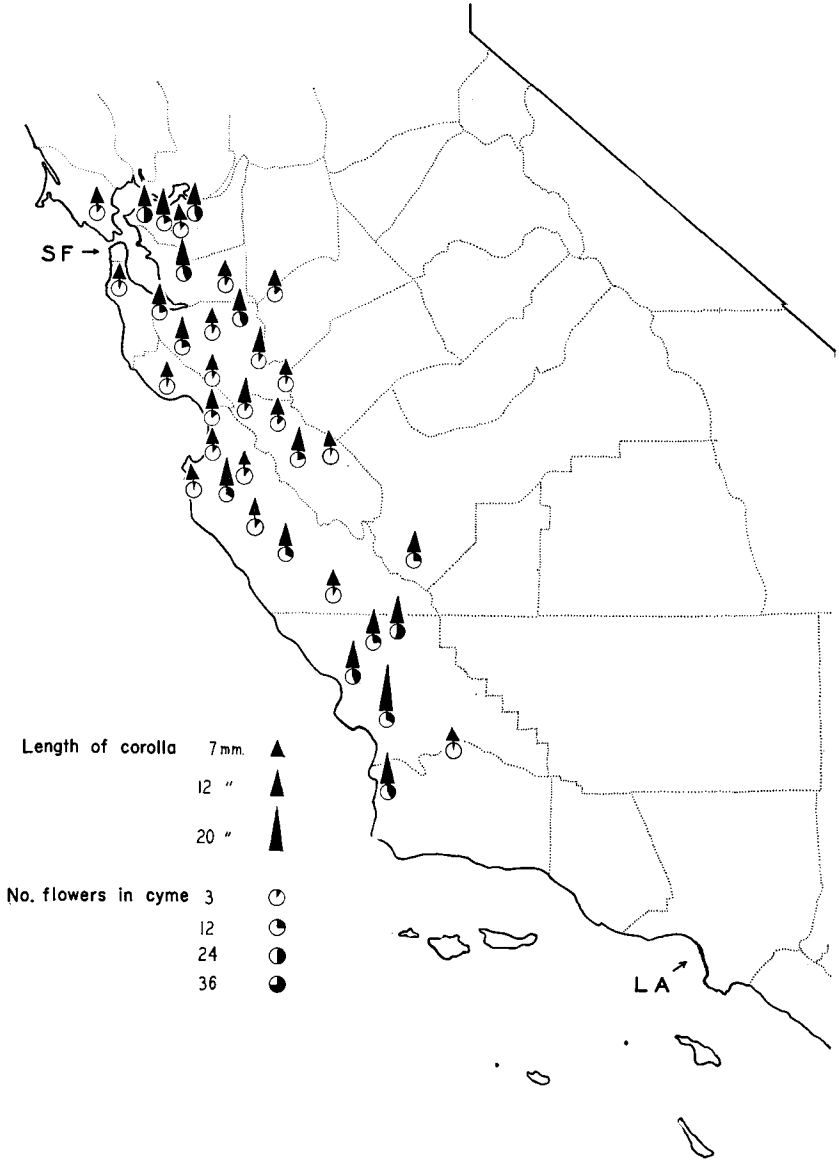


Fig. 1. Map showing the geographical distribution of two variable characters, corolla length and density of inflorescence, in *Gilia achilleaeifolia*. Each idiograph represents one population.

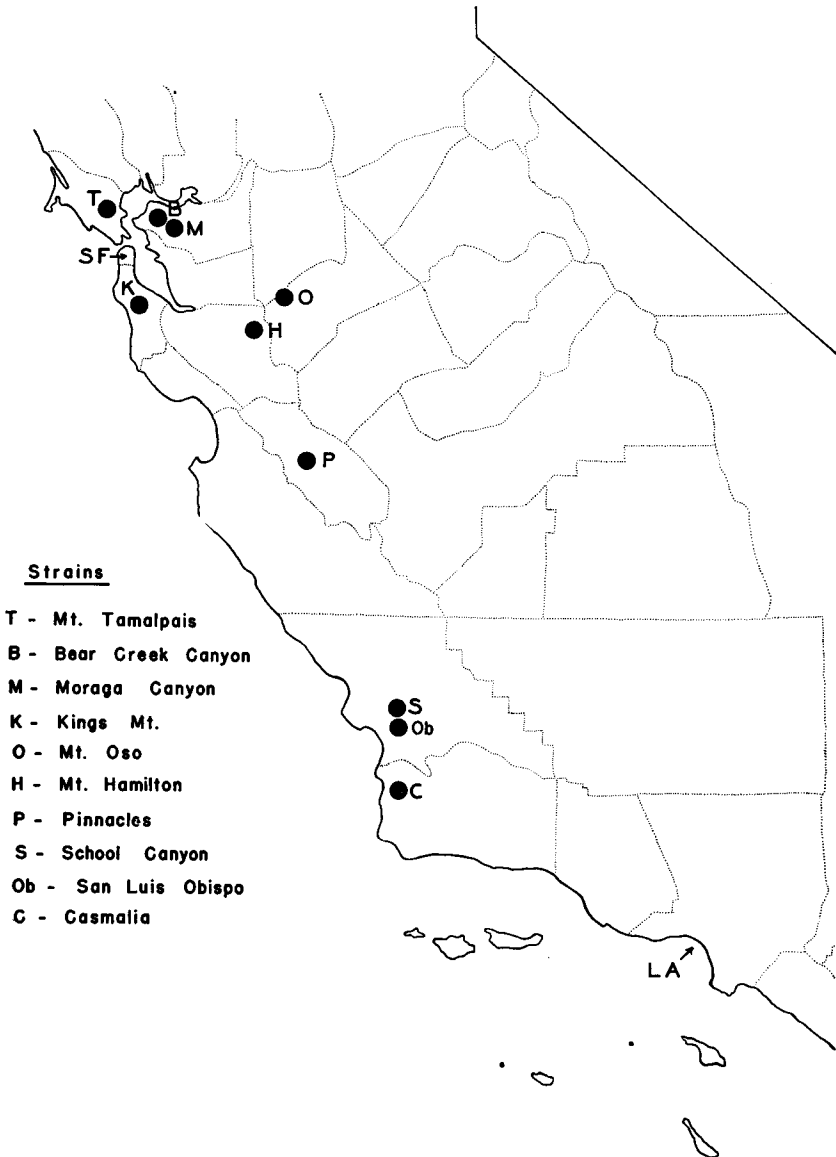


Fig. 2. The geographical location of some colonies of *Gilia achilleaeifolia* from which progeny were grown in the experimental garden.

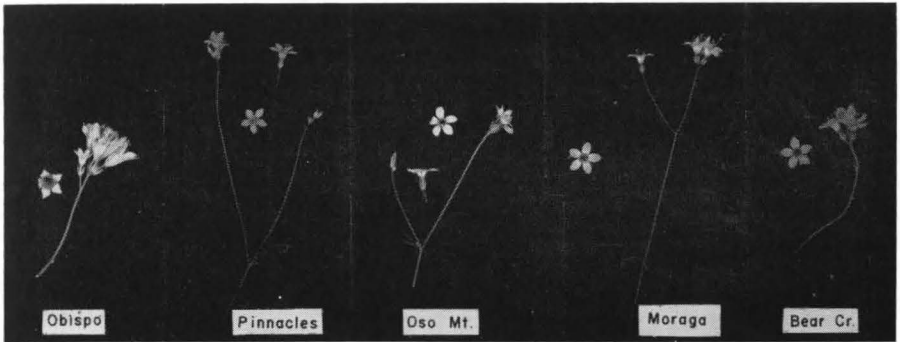


Fig. 3. Inflorescence and flowers in five strains of *Gilia achilleaeifolia* grown in the greenhouse at Stanford.

shady woods, had only about 3 flowers in a typical cyme. Progeny of these populations grown in the shady greenhouse produced the same number of flowers per inflorescence as their wild ancestors (fig. 3). Progeny grown in a sun plot, however, bore slightly denser inflorescences consisting of about 5 flowers each. The behavior of the populations from sunny and shady habitats when grown in experimental sun and shade plots may be construed as evidence that the size of the inflorescence is to a large extent hereditary. Furthermore, the norm of reaction in each population is apparently centered around the kinds of environmental conditions to which the population is naturally exposed, from which we might infer that the hereditary differences in size of inflorescence are adaptive.

The progeny tests reveal the existence of conspicuous hereditary differences from strain to strain in habit of growth and other vegetative characters (see fig. 4). The strain from Casmalia, which grows on sand hills facing the ocean, retains its semi-maritime characteristics in the inland garden. It remains a relatively stocky plant with densely glandular stems, broad heads, and relatively intense pigmentation. The strains from San Luis Obispo and School Canyon, which grow on grassy hillsides only a few miles apart, differ in several constant vegetative characters. The School Canyon strain has a more slender habit with less leaves than the San Luis Obispo strain, and there are differences in pubescence as well. The Pinnacles strain, from the dry hot Inner Coast Range, remains a plant of slender stems and few leaves in the Stanford environment. The Bear Creek strain grows large in the garden

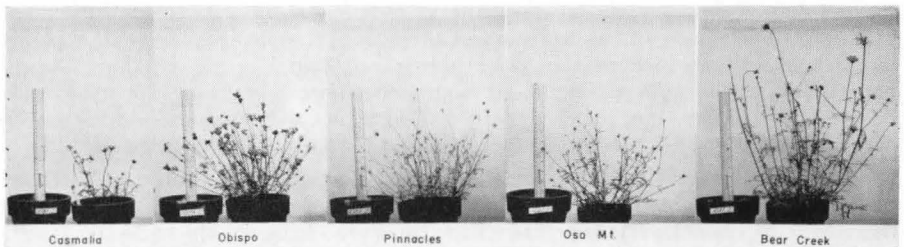


Fig. 4. Growth habit of five strains of *Gilia achilleaeifolia* as grown in the greenhouse at Stanford.

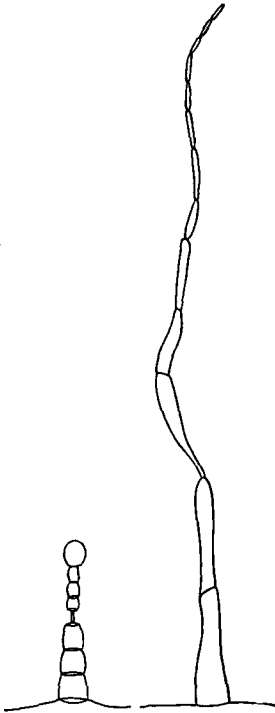


Fig. 5. Two types of calyx hairs found in *Gilia achilleaeifolia*. (x ca. 45.)

and preserves its distinctive glandulosity, deep pigmentation, leafiness, and fleshy calyx.

Within populations.—Several types of hairs may be distinguished on the calyx of *Gilia achilleaeifolia*. For our purpose it is necessary only to recognize short gland-tipped hairs and long woolly hairs (fig. 5). The types of calyx hairs do not only vary from population to population, but also show variations within the populations. Thus the School Canyon and San Luis Obispo colonies, which occupy hillsides only a few miles apart, differ in that the former colony possesses mainly long calyx hairs, while the latter is characterized largely by short glandular hairs. But among 31 progeny of the San Luis Obispo strain grown at Stanford, one individual possessed long woolly hairs on the calyx. Conversely, among 21 progeny of the School Canyon strain, two had short glandular hairs. Among nine F_1 hybrids between an individual from San Luis Obispo and an individual from School Canyon there were four plants like School Canyon in respect to calyx pubescence, two like the San Luis Obispo parent, two plants with a mixture of both pubescence types, and one plant with floccose hairs unlike those of their parent. This shows that some individuals in the natural populations are heterozygous for the genes controlling this character.

The population on Kings Mt. consisted of about equal numbers of hairy-stemmed and glabrous individuals. An individual in each class was selfed and was found to breed true to type. In this case, therefore, the individuals chosen for testing were homozygous for the genes controlling stem hairs. As will be shown later, the Kings Mt. strain is self-pollinating, while the School Canyon and San Luis Obispo strains are more or less outcrossing.

Two neighboring populations in the Mount Hamilton Range differed in the frequency of different types of hairs on the calyx. A population sample collected at Isabel Creek consisted of 14 individuals with long hairs and one with short hairs on the calyx, while a sample from Smith Creek contained only one plant with long hairs but nine with a mixture of long and short trichomes.

Some of the most striking intra-colonial variations proved to be non-hereditary. The colony on the grassy bank of Isabel Creek in the Mount Hamilton Range was composed of two types of individuals: tall plants with glomerate inflorescences containing about 15 flowers on short (1-2 mm. long) pedicels, and smaller individuals, one-half as tall as the former, with solitary flowers on long slender (15-20 mm. long) pedicels. Individuals representative of both types were transplanted in April to the shady greenhouse at Stanford. Inflorescences produced on the glomerate individuals after several weeks in the new environment consisted of solitary flowers on slender pedicels 20-25 mm. long. Progeny of the two types grown in a sun plot the next year were uniformly glomerate. We can conclude that the differences between the two types in the natural population were environmental modifications. The smaller individuals were shaded by the grass in the natural habitat, whereas the tall glomerate individuals received more light.

A similar situation was discovered in the population on Kings Mt. Here again long-pedicelled (10-60 mm.) and short-pedicelled (5-15 mm.) forms were encountered growing together in a single colony. Now, a plant similar to the long-pedicelled form has been described as a distinct species, *Gilia peduncularis*, complete with varieties and subvarieties. The status of this "species" can be judged from the fact that the differences between the long- and short-pedicelled types on Kings Mt. disappeared several weeks after transplantation to a greenhouse. In this shady environment both types of individuals became long-pedicelled. Progeny of the two types grown in a sun plot were uniformly short-pedicelled.

Ecological races.—Almost every local population in *Gilia achilleaeifolia* constitutes a separate race with distinctive characters. These races do not group themselves into broad geographical assemblages, as in most species including the related *Gilia capitata*, but the broader subdivision in the species is rather along ecological lines. The large-flowered races with dense heads occupy sunny hillsides in grassland and oak savannah; the small-flowered races with loose cymes occur in the shade of oak woodland or redwood forest; and there are numerous transitional forms in the semi-shade of open oak woods. The transplant studies mentioned in earlier paragraphs suggest that the dense-headed races grow with a minimum of phenotypic modification in sunny situations and similarly that the loose-flowered races are adjusted to the conditions prevailing in shady woods.

It has been found that the sun races, though self-compatible, are largely cross-pollinated by bees, whereas the shade races are largely self-pollinating. Let us consider the floral mechanism first in a typical large-flowered form, such as the School Canyon or Moraga Canyon strains (see figs. 3 and 6). The flowers, when open, are tipped to one side. A pair of long stamens and the style lie on the lower side of the flower. There is a short stamen above the entrance to the flower and a pair of medium length on either side. The stamens, which ripen before the stigma, are curved toward the entrance to the flower in their mature condition. At this time the style is pressed along the lower edge of the corolla. As the stigmas ripen they cover the center of the flower in a plane a millimeter or two beyond the anthers. In nature the flowers are visited and pollinated by bees, which settle on the lower side of the corolla, thrust their bodies into the expanded corolla throat to feed, and touch the

stigmas and lower anthers with the ventral portions of their bodies.

The foregoing description applies to plants growing in the spring months. In the latter part of the flowering season the stigmas stand closer to the anther and frequently come into contact with them. Since *Gilia achilleaeifolia* is self-compatible, as shown by self-pollination tests conducted on nine strains, the contact between the essential organs of a flower leads to seed formation. It might be concluded, therefore, that the large-flowered forms of *Gilia achilleaeifolia* are dependent upon bees for pollination during the height of the flowering season in spring, but are capable of automatic self-pollination toward the end of the season.

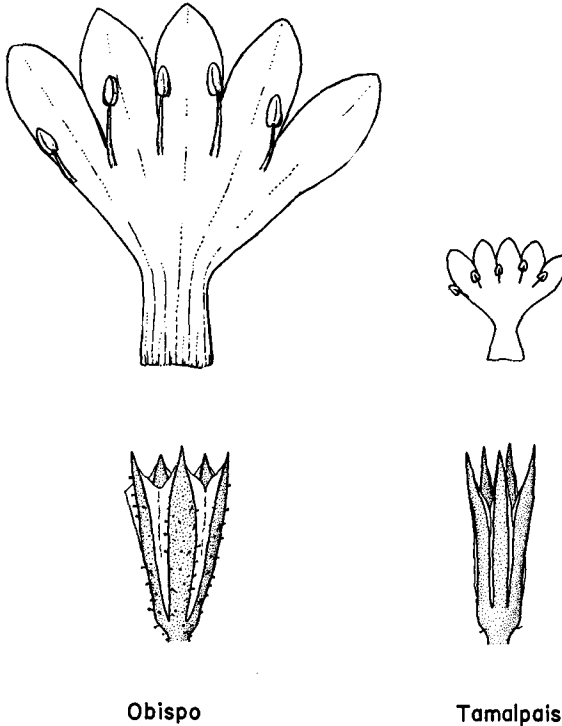


Fig. 6. Calyx and corolla of a large-flowered and a small-flowered strain of *Gilia achilleaeifolia*. There is complete intergradation between these extremes. (Calyx $\times 5$, corolla $\times 2.5$.)

This conclusion can be tested by isolating representative individuals in breeding cages. A healthy plant of the School Canyon strain which was thus isolated in early spring had set by the middle of May only one capsule on 67 flowers. A sister plant caged in July produced numerous capsules and only a few empty calyces under similar conditions of isolation. Spring and summer plants of the San Luis Obispo strain differed in a comparable fashion as to breeding behavior.

The first inbred generation derived from selfing flowers on an individual of the San Luis Obispo strain consisted largely of weak or inviable plants. Some of these died in the seedling stage, others developed into aberrant and male sterile indi-

viduals, and still others were weaklings which never attained a full and vigorous development. A small proportion of the inbred plants had normal vigor. Progeny grown from seeds harvested on the plants of the same strain in nature also included a few runts, but consisted predominantly of normally vigorous individuals. These facts suggest that the population contains some deleterious recessive genes which are brought to expression by selfing of the heterozygotes. Under conditions of open pollination outcrossing may predominate over self pollination so that only a small proportion of homozygotes is produced.

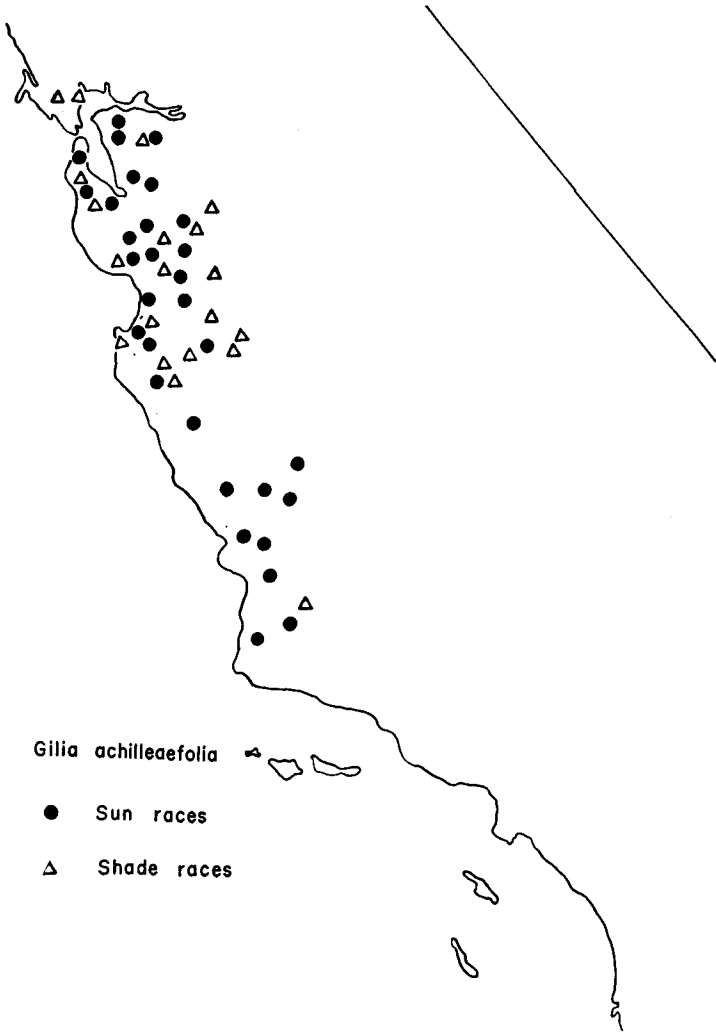


Fig. 7. Geographical distribution of the large-flowered, capitate sun races and the small-flowered, loosely cymose shade races of *Gilia achilleaeifolia*.

In the small-flowered types of *Gilia achilleaeifolia*, as typified by the Kings Mt. and Mt. Tamalpais strains (fig. 5), the stigmas and anthers occupy the same level from the very beginning of flowering. These types are consequently self-pollinating throughout the flowering season. An I_1 generation of the Kings Mt. strain was fully as vigorous as an open pollinated progeny of the same strain. This population probably consists therefore largely of homogygous individuals which have shed their deleterious recessive genes during generations of selfing and selective elimination. The breeding system of the self-pollinators probably has adaptive value in shady woods, where pollinating bees are scarce, just as the system of the large-flowered forms is suited to life on sunny hillslopes where bees are abundant.

The sun and shade races of *Gilia achilleaeifolia* thus differ, not only in tolerance of shade, size of corolla, and density of inflorescence, but also in floral mechanism and breeding behavior. The combination of characters in the sun and shade races probably help to adapt them to the ecological conditions which prevail in the niches which they respectively occupy. As sunny and shady habitats occur in close proximity throughout the South Coast Range, so too do the sun and shade races of *Gilia achilleaeifolia*. The map in figure 7 shows the absence of any geographical segregation between these two ecological races.

EXPERIMENTAL HYBRIDIZATION

Interstrain crosses.—The relationships between the various races of *Gilia achilleaeifolia* were investigated by means of artificial hybridizations. Nine strains were intercrossed in 15 combinations. The strain with the shorter style was used as the mother in all cases. The results are summarized in table 1 and portrayed graphically in figure 8. Reference to the table and figure shows that not all strains of *Gilia achilleaeifolia* can be crossed, some combinations yielding only masses of abortive seeds. If the geographical position of the parental strains is considered, by referring back to figure 2, it will be seen that the results form a fairly consistent picture.

The northern group of colonies cross freely among themselves. The only exception, Mt. Tamalpais \times Moraga Canyon, can perhaps be discounted for the time being, because of the inadequate sample of flowers pollinated. The southern group

TABLE 1. CROSSABILITY OF DIFFERENT STRAINS OF *GILIA ACHILLEAEIFOLIA*

♀ Parent	♂ Parent	No. flowers pollinated	No. capsules set	No. sound seeds	No. abortive seeds	No. F_1 hybrids
Mt. Tamalpais	Moraga Canyon	3	2	0	some	0
Mt. Tamalpais	Kings Mt.	7	5	71	0	25
Kings Mt.	Moraga Canyon	14	13	125	some	many
Kings Mt.	Pinnacles	6	5	0	many	0
Bear Creek	Moraga Canyon	13	15	610	0	many
Oso Mt.	Moraga Canyon	20	16	165	0	many
Moraga Canyon	Pinnacles	12	12	0	many	0
Pinnacles	Moraga Canyon	10	0	0	many	0
Bear Creek	San Luis Obispo	16	16	72	many	many
Moraga Canyon	School Canyon	9	9	3	many	0
School Canyon	San Luis Obispo	15	14	270	0	many
San Luis Obispo	Moraga Canyon	6	0	0	many	0
Casmalia	San Luis Obispo	11	11	41	some	many
Casmalia	Pinnacles	12	0	0	0	0
Pinnacles	San Luis Obispo	14	12	0	many	0

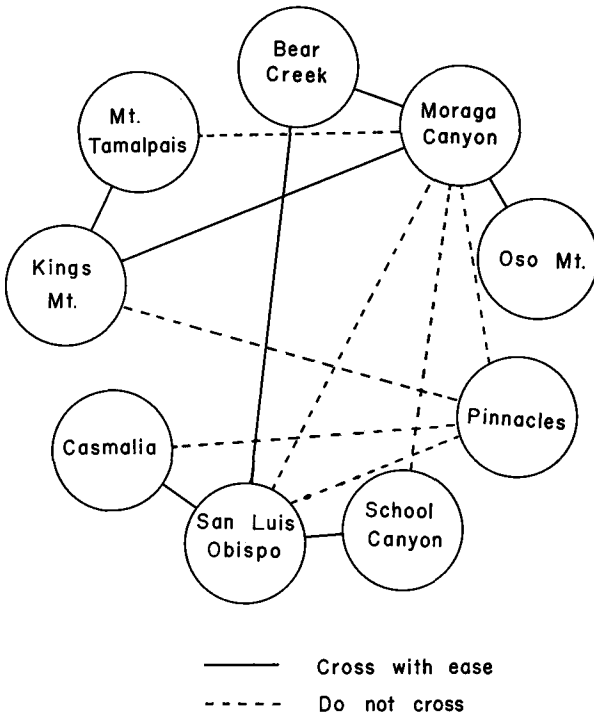


Fig. 8. Crossing diagram showing the compatibility relationships between different strains of *Gilia achilleaeifolia*.

of colonies likewise cross easily among themselves. But, with the exception of Bear Creek \times San Luis Obispo, the northern and the southern groups do not cross. The strain from Pinnacles, which occupies a central position on the map, does not combine with either the northern or the southern populations.

Gilia achilleaeifolia contains, therefore, at least three compatibility groups, a northern, a southern and a central group. No doubt further genetic exploration in this species would reveal the existence of still other compatibility groups and would give better definition to those which can be recognized from the preliminary crosses.

The first generation hybrids were all vigorous and fertile. F_2 progenies of over 200 individuals were grown from the crosses Kings Mt. \times Moraga Canyon and Bear Creek \times San Luis Obispo. These F_2 progenies were healthy and vigorous and included no weaklings or sublethal types.

The genetic barrier between some northern and some southern populations is thus confined to the parental generations. Once this barrier is breached, by means of some compatible combination such as Bear Creek \times San Luis Obispo, the northern and southern populations can exchange genes freely without the production of disharmonious recombinations. It appears probable, therefore, that the incompatibility barrier is the result of some fairly simple genic reaction and that the determining gene is represented in the different populations by different alleles.

Interspecific crosses.—Attempts were made to intercross nine strains of *Gilia achilleaefolia* with 16 strains representing 7 other species. Five of these species, namely *Gilia capitata*, *tricolor*, *angelensis*, *millefoliata* and *clivorum*, belong in the same section of the genus; the other two species, *Gilia tenuiflora* and *G. splendens*, belong to two related sections. Five hundred and forty-two flowers were cross-pollinated in 39 hybrid combinations; viable seeds were obtained in only four of the combinations.

The San Luis Obispo strain, representing the southern compatibility group, crossed easily with *Gilia millefoliata* to form numerous sound seeds and vigorous F_1 hybrids (Grant, 1952a). Three strains from the northern compatibility group, which is close to *Gilia millefoliata* geographically, did not cross with that species at all.

The strain from Moraga Canyon in the northern compatibility group, on the other hand, crossed with *Gilia angelensis* from southern California to yield nine hybrid individuals. The cross between the San Luis Obispo strain of *achilleaefolia* and *Gilia angelensis* has not been attempted.

For the rest, two F_1 hybrids were obtained between the San Luis Obispo strain and *Gilia tenuiflora*, and one hybrid between the Kings Mt. strain and *Gilia clivorum*. The F_1 hybrids were all completely sterile with either irregular meiosis or no sex cell formation at all (Grant, 1954).

Gilia achilleaefolia is thus well isolated from the species most closely related to it by strong incompatibility barriers which are reinforced by hybrid sterility. The sterility barriers are due, in part at least, to a repatterning of the chromosomes in the different species which prevents the formation of well-balanced gametes by their hybrids (Grant, 1954). This process has no known parallel within the species. The incompatibility barriers which isolate *G. achilleaefolia* from neighboring species, on the other hand, may be built up from some of the same genic elements as those which inhibit crossing within the species.

CYTOLOGY

Chromosome counts have been made from pollen mother cells of the following strains of *Gilia achilleaefolia* (see fig. 9):

San Luis Obispo, San Luis Obispo County.	VG 8557	n=9
Tres Pinos, San Benito County.	VG 8433	n=9
Moraga Canyon, Contra Costa County.	VG 8872	n=9
Kings Mt., San Maeo County.	VG 8903	n=9
Corte Madera Ridge, Mt. Tamalpais, Marin County. . .	VG 8878	n=9

The species had previously been counted as $2n=18$ by Flory (1937) and as $n=9$ by Sugiura (1940). Flory, who studied somatic chromosomes, was able to distinguish size differences ranging from a long pair 9 microns long to a short pair 4.5 microns long, and form differences between four pairs with subterminal centromeres and 5 with median or submedian centromeres. Through exchange of correspondence and specimens with Dr. Flory it has been possible to make certain that the horticultural material used in these cytological studies was in fact true *Gilia achilleaefolia* and not one of the entities formerly confused with it.

Meiosis was examined in 25 pollen mother cells of the F_1 hybrid between the Kings Mt. and Moraga Canyon strains and was found to be perfectly regular.

ORIGIN OF THE VARIATION IN *GILIA ACHILLEAEFOLIA*

It is becoming increasingly clear in studies on the biology of angiospermous species that extraordinary variability is frequently the result of hybridization. In

many cases, where polyploidy or apomixis or structural heterozygosity is involved, it is possible to obtain cytogenetic proof of hybridization. In other cases we must rely on morphological evidence and on the nature of the variation pattern. The variability in *Gilia achilleaeifolia* far exceeds the norm for species of *Gilia*. There are reasons for believing that this abnormal variability is a consequence of hybridization.

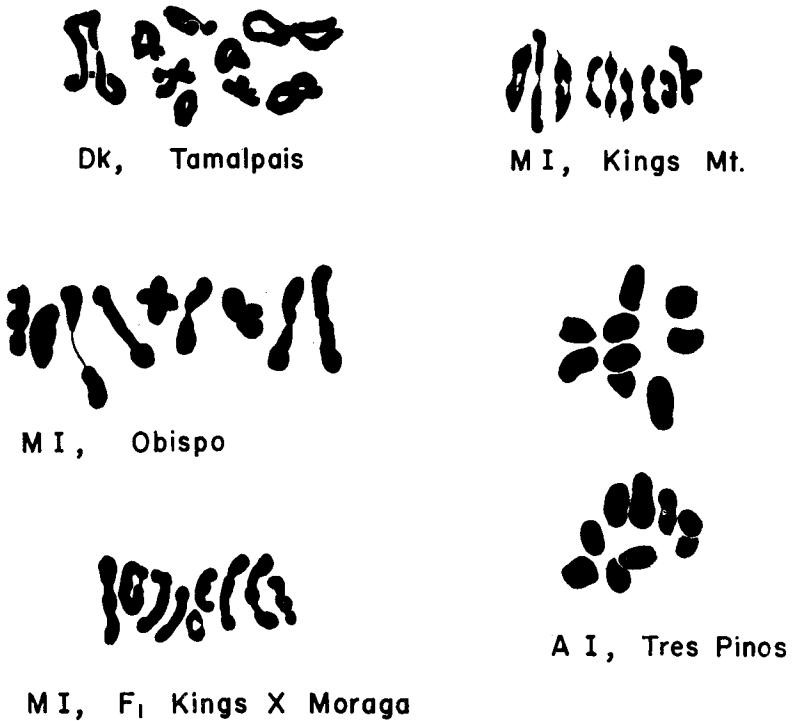


Fig. 9. Paired chromosomes in several strains and one inter-strain hybrid of *Gilia achilleaeifolia*. From camera lucida drawings of dividing pollen mother cells. The chromosomes in the MI figures were spread apart slightly in drawing. (x 2700.)

Gilia achilleaeifolia is intermediate between *Gilia capitata* and the *G. tricolor* complex in a large number of characters. The inflorescence in *G. capitata staminea* or *G.c.abrotanifolia* is a globose head composed of about 50 flowers on pedicels 1 mm. long or less; that of *G. tricolor* or *G. angelensis* is a loose cyme composed of 1 to 5 flowers on pedicels 2 to 40 mm. long; that of *G. achilleaeifolia* varies from a fan-shaped head of 15 to 25 flowers to a loose cyme of 2 to 7 flowers and the length of the pedicels varies from 1 mm. to 60 mm. The calyx lobes consist of a broad herbaceous portion about 1 mm. wide flanked by narrow hyaline margins in *G. tricolor*; of narrow green midribs less than half a millimeter wide flanked by broad hyaline sinuses in *G. capitata staminea* or *G.c.abrotanifolia*; and the calyx lobes of *G. achilleaeifolia* span the gap with a herbaceous portion varying from 0.2 to 1.0 mm. broad and averaging in most populations about 0.6 mm. in breadth.

The corolla lobes are ascending with rounded margins in *G. capitata*; they are rotately spreading with pointed tips in the *G. tricolor* complex; and vary in *G. achilleaeifolia* from ascending to spreading and from rounded to slightly pointed. The inner surface of the corolla tube is blue-violet in *G. capitata*; yellow to greenish in the *G. tricolor* complex; and varies in different populations of *G. achilleaeifolia* from blue-violet to green. The stamens are shorter than the corolla lobes in *G. achilleaeifolia* as they are also in the *G. tricolor* complex, while the stamens and corolla lobes are of about equal length in *G. capitata*. The ratio between the longest and shortest stamen in a series of *G. tricolor* populations is 10 to 5; the stamens of *G. capitata* are almost equal in length with a ratio between the longest and shortest members of 10 to 9; in a series of *achilleaeifolia* populations this ratio averages 10 to 7 and ranges in some cases down to 10:5.

Gilia tricolor itself possesses a character which disqualifies it as an ancestor of *G. achilleaeifolia*. That character is the purple spots in the corolla throat. Some of the products of hybridization between *G. tricolor* and *G. capitata* would be expected to retain at least the vestiges of these spots, yet there is no trace of purple markings in the corolla throat of any *achilleaeifolia* population. A spotless type of *Gilia tricolor* may have existed in former times, however, and the related species *G. angelensis* lacks corolla spots today. Hybridization between some spotless member, living or extinct, of the *Gilia tricolor* complex and *G. capitata staminea* or *G.c. abrotanifolia* might thus have produced *G. achilleaeifolia*.

All attempts to cross contemporary populations of the *Gilia tricolor* complex with *G. capitata* have failed, but this does not mean that former populations may not have been able to cross in nature. Indeed, natural hybridization seems to occur sporadically between *Gilia angelensis* and *G. capitata abrotanifolia* in southern California (Grant, 1952b). The introgressive products of this hybridization, as exemplified by plants from Santa Ana Canyon, could easily pass as *G. achilleaeifolia*. The resemblance in habit, inflorescence, calyx, size and color of corolla, fullness of corolla throat, and length of stamens is very striking.

The hypothesis of a hybrid origin of *G. achilleaeifolia* would explain the presence of incompatibility barriers between different strains of this species. The putative parental species, *G. capitata* and *G. tricolor*, are themselves separated by very strong incompatibility barriers, which result in the production of masses of shrivelled seeds following cross-pollinations. The genetic factors responsible for this incompatibility might conceivably be recombined in the progeny derived from hybridization between the original species, so that the hybrid derivatives are isolated both from the parental species and from one another. Intraspecific incompatibility barriers associated with a high degree of morphological variability are found also in *Elymus glaucus* in the Sierra Nevada (Snyder, 1950, 1951; Stebbins, unpublished) and in *Clarkia deflexa* in the South Coast Range (Lewis, unpublished). Both species appear to have arisen by hybridization. The authors therefore quite plausibly suggest that the intraspecific barriers are derived genetically from the barriers which isolated the original parental species. This explanation would apply equally well to the case of *Gilia achilleaeifolia*.

The great genetic variability of *G. achilleaeifolia*, which extends to morphological and ecological characteristics and to isolation barriers, and the intermediacy of this species in a large number of characters, may thus be a result of hybridization between some member of the *G. tricolor* group and *G. capitata staminea* or *G.c. abrotanifolia*.

TAXONOMY

It would be desirable from a taxonomic standpoint to be able to segregate the confusing array of variations in *Gilia achilleaeifolia* into a convenient number of usable categories. Unfortunately, there are no constant morphological characters by which to distinguish all or even most of the members of the different known compatibility groups. A natural classification according to the principal Mendelian populations would therefore be unworkable in practice. There are conspicuous morphological differences between the sun races and the shade races which could be used for purposes of classification. But this subdivision of the species cuts across the Mendelian populations; it follows ecological, but not geographical, lines. A workable classification according to the major morphological and ecological types would thus not be phylogenetic. One could, of course, set out to name every small group of populations, such as the Casmalia type, the San Luis Obispo type, the Pinnacles type and so on, but the resulting system of classification would then be difficult to use. The best arrangement, perhaps, is to simply recognize that innumerable genetic races exist, without benefit of Latin names, in *Gilia achilleaeifolia*.

GILIA ACHILLEAEFOLIA Benth.

- Gilia achilleaeifolia* Benth., Bot. Reg. 19, under t. 1622, 1833. (type seen.)
G. multicaulis Benth., Bot. Reg. 19, under t. 1622, 1833. (type seen.)
G. multicaulis var. *tenera* Gray, Proc. Am. Acad. 8: 278, 1870. (type seen.)
G. oreophila Greene, Baker's West Am. Pl. 1: 9, 1902. (nomen nudum, type seen.)
G. peduncularis Eastwood ex Milliken, Univ. Calif. Publ. Bot. 2: 34, May 1904. (type seen.)
G. multicaulis var. *alba* Milliken, op. cit. 35, 1904.
G. multicaulis var. *eximia* Milliken, op. cit. 35, 1904. (type seen.)
G. pedunculata Eastw., Bot. Gaz. 37: 446, June 1904. (type seen.)
G. pedunculata var. *calycina* Eastw., op. cit. 447, 1904. (type seen.)
G. pedunculata var. *minima* Eastw., op. cit. 447, 1904. (type seen.)
G. peduncularis var. *typica* Brand, Pflzr. 4(250): 107, 1907. (in part as to specimens cited.)
G. peduncularis var. *typica* subvar. *calycina* Brand, op. cit. 108, 1907.
G. multicaulis subsp. *eu-multicaulis* Brand, op. cit., 109, 1907.
G. multicaulis subsp. *eximia* Brand, Pflzr. 4(250): 110, 1907.
G. inconspicua subsp. *sinuata* var. *oreophila* (Greene) Brand, op. cit., 105, 1907.
G. multicaulis var. *peduncularis* Jeps., Fl. Calif. 3(2): 187, 1943.
G. multicaulis subsp. *peduncularis* Mason and A. Grant, Madroño 9: 209, 1948.

Annual herbs; plants erect, tall and spreading, or sometimes trailing, 6-70 cm. high, branching from base; stems glabrous, or sparingly floccose below, often lightly glandular above, rarely glandular throughout; basal and lower cauline leaves unipinnate or bipinnate, 4-10 cm. long, the primary lobes 5-15 mm. long, the ultimate segments somewhat falcate, 1-25 mm. long and 0.5-2.0 mm. wide, the upper cauline leaves smaller, 0.5-4.0 cm. long, pinnate, frequently appearing as if palmate, the axils of the leaves floccose; inflorescence densely or loosely cymose, the cymes several, terminal on naked peduncles 1-15 cm. long, either consisting of fan-shaped heads of 8-25 or usually about 15 flowers subsessile on pedicels 1-2 mm. long, or of open cymes consisting of 2-7 flowers on pedicels 1-60 mm. long; calyx in flower 3-7 mm. long, accrescent, floccose, or with glands on the tips of the lobes, or sometimes glandular throughout, the lobes acute, with a flat herbaceous portion 0.2-0.8 mm. wide flanked on both sides by straight-margined hyaline wings 0.1-0.3 mm. wide at the sinus, these blue-violet or colorless; corolla funnellform, 5-21 mm. long, less than twice as long to 3 times longer than the calyx, blue-violet, the throat often expanded and approximately as long as the tube, the limb 4-8 mm. wide when

pressed flat, the lobes erect and ascending or rotately spreading, oval, 1-4 mm. wide, sometimes with an acute tip; stamens inserted in the sinuses of the corolla, included, the filaments 0.5-3.0 mm. long; style exerted, 1-2 mm. longer than corolla at maturity, or only slightly exerted, stigma 1-2 mm. long; capsule ovoid, dehiscent, 10-18-seeded; seeds ovoid, angular, 1-2 mm. long, brown; $n=9$.

Type.—"California," Douglas, 1833. Royal Botanic Gardens, Kew. Judging by the morphological characters of the type specimen, as well as by the illustration in Bot. Reg. 20, t. 1682, 1834, the type locality of *Gilia achilleaefolia* would lie in the central part of the South Coast Ranges in the general area of Monterey County. The characters of the Douglas type of *Gilia multicaulis* are such as to suggest that it also was collected in this same region. Neither the type specimen nor the illustration in Bot. Reg. support the opinion of Jepson and Hoover (Fl. Calif. 3(2): 186, 1943) that the Douglas collection is the plant of the South Coast Ranges and southern California later described as *Gilia abrotanifolia* Greene.

Range.—Loose soil of open, sunny hillsides, bluffs, and canyons, or shaded slopes in oak woodland, 200-4000 ft.: South Coast Ranges from Marin and Contra Costa counties to northern Santa Barbara County, California. Sympatric with *Gilia capitata*, *G. clivorum*, *G. splendens*, *G. tenuiflora*, *G. gilioides*. Flowers May-June.

Variation.—There is complete intergradation between the robust large-flowered capitate forms of sunny places (exemplified by the Douglas collection of *Gilia achilleaefolia*), through spreading small-flowered types growing in sunlight (exemplified by the Douglas specimen of *Gilia multicaulis*), to weak plants with a few small flowers on elongated pedicels in shady woods (the equivalents of *Gilia peduncularis* Eastw.). These various types have no well-marked geographical segregation.

The largest flowered forms are found in the hills of San Luis Obispo County between the towns of San Luis Obispo and Arroyo Grande. The plants of this area are remarkable for their robust habit of growth and their exceedingly large corollas, which here attain the extreme length of 21 mm. and thrice exceed the calyx. In all other parts of the range the corollas are similar in size and but twice the length of the calyx. The large-flowered forms of northern Santa Barbara County, south of San Luis Obispo, have corollas 12-14 mm. long, while north of San Luis Obispo, the corollas measure 9-12 mm. long.

The large-flowered forms are known to approach the ocean only in northern Santa Barbara County, and here a maritime ecotype has evolved on hills facing the sea. This plant, with its smaller, more deeply colored flowers crowded into denser heads and its more glandular stems, apparently occupies a position in relation to the main body of its species analogous to that of the race *chamissonis* in *Gilia capitata*. These two parallel developments, occurring some two hundred miles apart on the California coast line, have sometimes been grouped together in taxonomic treatments on account of their superficial resemblances.

Some specimens of *Gilia achilleaefolia* in the southern part of its range possess characters—a subglobose head with sessile or sub-sessile flowers, broad hyaline calyx wings, and partially exerted stamens—which suggest introgression from *G. capitata*. This hybridization appears to involve *G. capitata staminea* in the case of populations in the Inner South Coast Range southwest of Coalinga (F. W. Peirson 5638, P. A. Munz 9160). Farther south in Santa Barbara and Ventura counties it is difficult to separate *G. achilleaefolia* from *G. capitata abrotanifolia*.

Specimens cited: CALIFORNIA. Santa Barbara Co.: Casmalia, *V. & A. Grant 8550*; Santa Maria, *A. Eastwood 414*, *H. L. Mason 8318a*; Cuyama River, *A. Eastwood (1896)*, *V. & A. Grant 8709*. San Luis Obispo Co.: San Luis Obispo, *R. S. Ferris 7534*, *B. Miossi 207*, *V. & A. Grant 8555*, *8557*, *8562*; Atascadero, *V. & A. Grant 8568*. Monterey Co.: Jolon, *H. L. Mason 11760*; Arroyo Seco, *G. L. Stebbins 3946*; Carmel Valley, *A. A. Heller 6525*, *C. M. Belshaw 430*, *V. & A. Grant 17596*; Tassajara Springs, *V. & A. Grant 17599*, *17602*; Monterey, *A. Eastwood (1900)*, *J. Clemens (1905)*; Pt. Lobos, *H. L. Mason 9214*. San Benito Co.: Pinnacles, *V. & A. Grant 8445*; Panoche Pass, *V. & A. Grant 8436*, *8444*; Tres Pinos, *V. & A. Grant 8432*; Idria, *I. L. Wiggins 9386*. Santa Clara Co.: Gilroy, *A. Eastwood 4308*; Los Gatos, *A. A. Heller 7396*; New Almaden, *H. L. Mason 6933*; Alum Rock Park, *R. L. Pendleton 684*; Mt. Hamilton, *H. K. Sharsmith 745*, *1117*, *V. & A. Grant 8508*; Pacheco Pass, *H. L. Mason 12560*; Searsville Dam, *H. L. Mason 1019*. Santa Cruz Co.: Felton, *H. L. Mason 3369*. San Mateo Co.: Blenheim, *A. Eastwood (1901)*; Kings Mt., *D. D. Keck 2931*. Alameda Co.: Sunol, *L. Constance 2234*; Stony Brook Canyon, *V. & A. Grant 7694*, *7930*; Cedar Mt., *V. & A. Grant 7624*; Berkeley, *C. M. Belshaw 583*. Contra Costa Co.: Moraga Canyon, *V. & A. Grant 8504*, *8505*; Orinda, *V. & A. Grant 8424*; Mt. Diablo, *M. L. Bowerman 2869a*, *2059*, *V. & A. Grant 17592*. Marin Co.: Mt. Tamalpais, *H. L. Mason 1337*, *J. T. Howell 19391*, *21976*; San Rafael Hills, *J. T. Howell 17977*; Mill Valley, *J. T. Howell 14605*.

Herbaria consulted: Specimens were studied in the herbaria of the University of California, Berkeley, the California Academy of Science, Stanford University, Pomona College, and the Rancho Santa Ana Botanic Garden. Special material was borrowed from the Gray Herbarium and from Kew. The writer wishes to acknowledge his gratitude to the curators of these herbaria for many kindnesses.

List of excluded names: The following names, applying to *Gilia achilleaeifolia* or to some related species, are doubtful and should be excluded from synonymy.

Gilia stricta Scheele, *Linnaea* 21: 755, 1848. (nomen dubium) This name is based on a plant cultivated in Germany. The origin of the cultivated strain is not stated, no specimen appears to have been preserved, and the description is inadequate for identification of the name.

Gilia multicaulis var. *stricta* Brand, *Pflzr.* 4(250): 110, 1907. (nomen dubium)

Gilia multicaulis var. *detonsa* Gray ex Milliken, *Univ. Calif. Publ. Bot.* 2: 35, 1904. (nomen dubium) This name is attributed to Gray by Milliken in her review of California Polemoniaceae. There is, however, no record of prior publication by Gray himself, and there is no material labelled *detonsa* in the Gray Herbarium. Milliken, who must therefore be regarded as the author of the name, gave as the type locality the Berkeley hills and cited in addition a specimen from San Luis Obispo County. Unfortunately she did not provide us with the means, either by her taxonomic description, or the annotation of specimens, or a sufficiently precise citation of specimens, of distinguishing her variety *detonsa* from some other kinds of *gilia*s growing in the two areas mentioned. No specimen can be found in the University of California Herbarium or Jepson Herbarium or, as previously remarked, in the Gray Herbarium to which the name *detonsa* can definitely be applied.

SUMMARY

Gilia achilleaeifolia (n=9) is a highly variable species of the South Coast Range of California. There is genetic variation within, and to a greater extent between, the populations in respect to morphological characters and ecological tolerances. Populations in sunny habitats usually possess large flowers grouped in heads and are more or less outcrossed by bees, while populations of shaded woods have small flowers in loose cymes and are self-pollinating. The latter types correspond to *G. multicaulis* and *G. peduncularis* of the manuals.

Strains representing the major morphological and ecological types were intercrossed. There are no barriers to gene exchange between strains from the same geo-

graphical area, but gene exchange between a northern, a southern and a central group of populations is blocked by an incompatibility barrier. One strain belonging to the northern incompatibility group did cross successfully with a strain in the southern group of populations to yield a fertile F_1 hybrid and fully vigorous F_2 progeny. The barrier between the northern and southern populations is thus restricted to the incompatibility reaction of the parental types.

Gilia achilleaefolia is isolated from the other species of *Gilia* by strong incompatibility barriers reinforced by hybrid sterility.

In many of its features *Gilia achilleaefolia* lies between the *G. tricolor* complex and *G. capitata staminea* or *G.c.abrotanifolia*. Morphological intermediacy associated with great genetic variability is a known result of hybridization. The hypothesis is proposed that the intermediate and variable species *G. achilleaefolia* is a product of hybridization in some past age between a member of the *G. tricolor* complex and *G. capitata staminea* or *G.c. abrotanifolia*.

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