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Genetic and Taxonomic Studies in Gilia: III. The Gilia Tricolor Complex

Verne Grant

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GENETIC AND TAXONOMIC STUDIES IN GILIA

III. THE GILIA TRICOLOR COMPLEX

VERNE GRANT*

INTRODUCTION

Gilia tricolor, one of the handsomest species of *Gilia,* is a common element in the spring flora of northern California, where it often forms extensive stands. It is well known alike to the northern Californian settlers, who call it "Bird's-eye," and to European and North American gardeners. The purpose of the present paper is to investigate the relationships of this species.

A search among the annual members of the genus led to the finding of two species, both of them undescribed, which by their morphological characters may be regarded as fairly close relatives of *Gilia tricolor.* The first of these relatives is a plant of the northwestern border of the Mojave Desert which appears to link *Gilia tricolor* with the *Gilia tenuiflora* complex. A discussion of the desert allies of *Gilia tricolor* must await the completion of current studies in collaboration with Mrs. Alva Grant. The second relative of *Gilia tricolor* is a common but inconspicuous plant of southern California, which has been going under the name of *Gilia multicaulis*** in the manuals, but which is herein described as *Gilia angelensis.* Both *Gilia tricolor* and *G. angelensis* will be considered in the present paper.

A part of the work reported in this paper was accomplished during the tenure of a National Research Fellowship. The author takes this opportunity to thank Dr. Jens Clausen and his colleagues at the Carnegie Institution of Washington for much helpful counsel during the year of the fellowship. The author is grateful also to Mrs. Grant, who made the cross-pollinations and criticized the manuscript, making many helpful suggestions.

GENERAL DESCRIPTION

There is a close similarity between *Gilia tricolor* and *G. angelensis,* which has been overlooked in the past because of striking differences in the coloration and size of the flowers. *Gilia tricolor* has large corollas, usually brilliantly colored, with purple spots in the throat, whereas the flowers of *G. angelensis* are small, pale, and spotless. In habit and floral form, however, the two entities are very similar.

They are both rather small annual herbs with leafy stems. They both tend to form large populations on open foothills and plains. Where the plants are crowded by grasses or dwarfed by barren soils, the stems are simple and erect, but in more open and favorable situations the plants branch profusely at the

*Rancho Santa Ana Botanic Garden.

**The true *Gilia multicaulis* is a plant of the South Coast Range, which is specifically distinct from *Gilia angelensis.*

base and the branch stems spread horizontally before arching upward. There is no central leader in such cases (see fig. 1).

The flowers are borne in small glomerules or loose cymes at the tips of the branches. The calyx is predominantly green and herbaceous with narrow

Fig. 1. Growth habit, inflorescence and flowers of *Gilia tricolor* and *Gilia angelensis*. The strains were collected as seeds in the Inner Coast Range (near Byron) and cismontane southern California (near Perris), respectively, and grown at Stanford.

membraneous portions in the sinuses (fig. 2). The corolla is campanulate in form, with a short tube, a broad throat, and a rotately spreading limb. The tube is yellow or orange and the limb is some shade of blue-violet. As previously remarked, the inner surface of the throat is decorated with five pairs of purple spots in *Gilia tricolor,* but not in *G. angelensis* (fig. 3).

The flowers are protandrous, the anthers dehiscing several days before the stigma is mature. The stigma is exserted 1–2 mm. beyond the anthers at maturity. The flowers are canted so that the corolla limb faces outward from the periphery of the plant. The two lowermost stamens have relatively long upcurved filaments; the two lateral stamens are of medium length; and the uppermost stamen is short, being about half as long as the lower ones. The flowers are visited and pollinated by bees, which land and support themselves on the elongated lower pair of stamens while they introduce their heads into the expanded throat and suck nectar from the tube.

Three strains of *G. tricolor* (Hood Mt., Byron, and Parkfield) and one of *G. angelensis* (Perris) proved to be self-compatible in greenhouse tests.

GEOGRAPHICAL DISTRIBUTION

Gilia tricolor occurs in the Central Valley of California and in the lower slopes of the bordering mountain ranges. The plants in northern California tend on the whole to be more robust with large flowers grouped into glome-

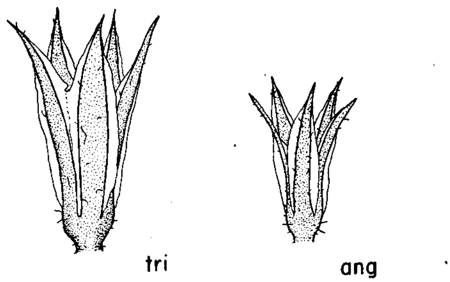

Fig. 2. Calyx of *Gilia tricolor* (from South Coast Range near Parkfield) and *Gilia angelensis* (from Perris). × 5.

rules, while the plants in the southern part of the range generally have smaller flowers borne solitary or in loose glomerules. These differences persist in garden progeny of wild strains and probably represent ecotypic responses to moister and drier habitats respectively. Mason and A. Grant (1948, 1951) have segregated the contrasting ecotypes as two subspecies, an arrangement which

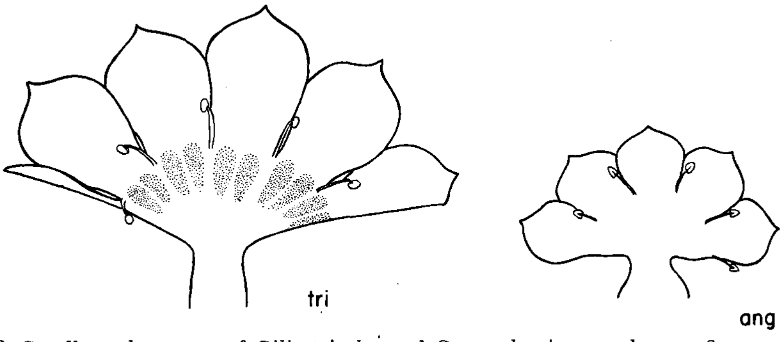

Fig. 3. Corolla and stamens of *Gilia tricolor* and *G. angelensis*, spread open. Same strains as in fig. 2. × 2½.

is adopted here. The intergradation between the two races is very gradual. Their respective areas — but not, unfortunately, their broad zone of intergradation — are shown in the distribution map (fig. 4).

The main area of *Gilia angelensis* lies in cismontane southern California. This species and *G. tricolor* are apparently wholly allopatric. They approach one another on opposite sides of Tejon Pass but do not meet, and there is no sign of intergradation or introgression between them.

Gilia angelensis and *G. capitata abrotanifolia* are sympatric over a wide area in the lower foothills and have numerous opportunities to hybridize.

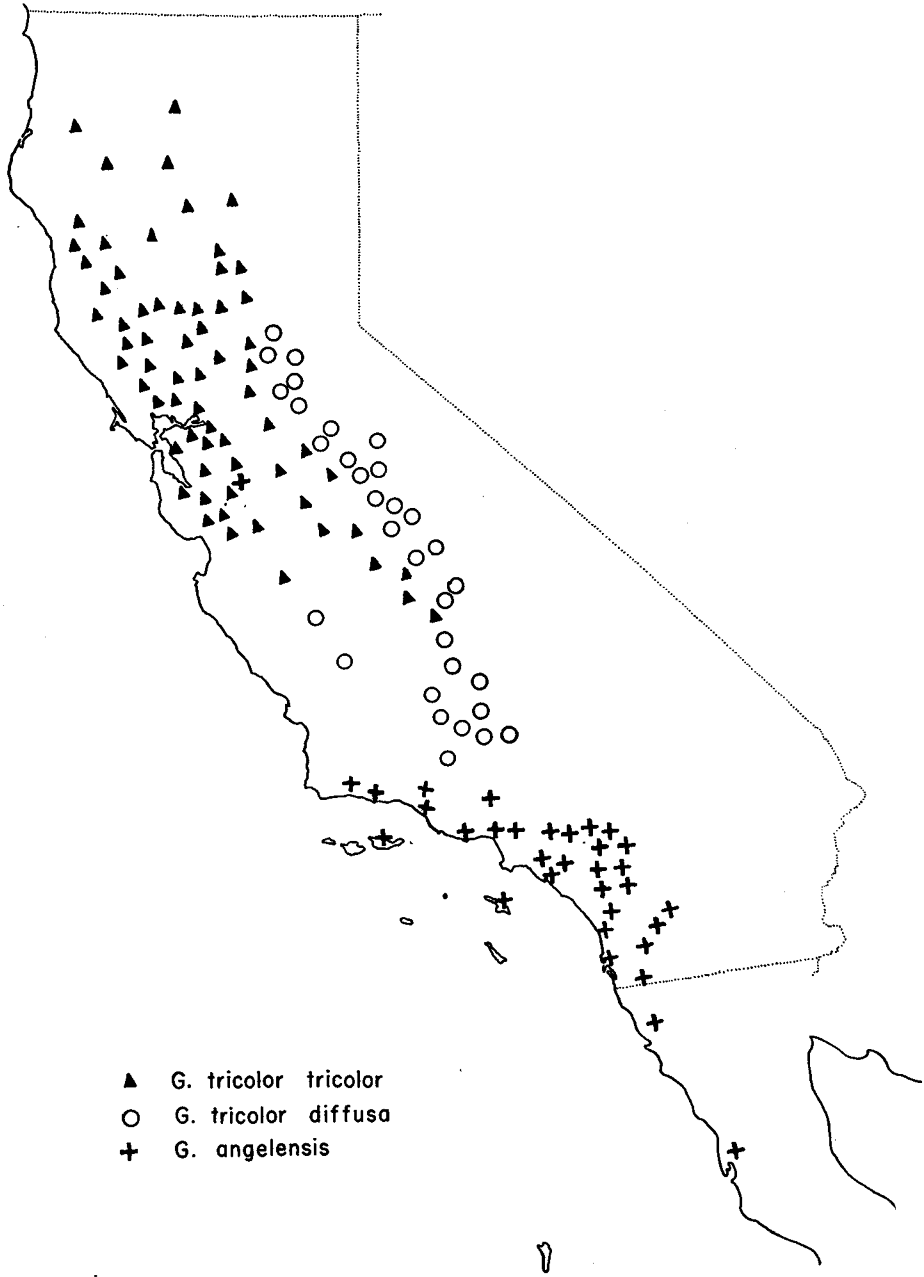

Fig. 4. Distribution map of *Gilia tricolor* and *G. angelensis*.

Hybridization is for the most part prevented by a strong incompatibility barrier. That it does sporadically occur, however, is indicated by several specimens which plainly show the influence of one species upon the other. A specimen from near Mentone in San Bernardino County (*V. Grant 8698*), for example, has characters suggesting introgression from *G.c.abrotanifolia* into *G. angelensis*, while a specimen from Santa Ana Canyon in Orange County (*P. A. Munz 2628*) bears indications of introgression in the opposite direction from *G. angelensis* into *G.c.abrotanifolia*. The perceptible effects of this hybridization between *G. angelensis* and *G. capitata abrotanifolia* are confined to a few restricted localities.

Gilia angelensis extends north along the coast to Santa Barbara County. Its existence in the South Coast Range beyond this point was not suspected until 1950 when a lone individual was found on the east slope of the Mount Hamilton Range, separated by more than two hundred miles from the nearest known station in Santa Barbara County. The best explanation for this disjunct distribution, so far as the author can see, is that *Gilia angelensis* was formerly established more or less continuously throughout the South Coast Range, but has subsequently vanished almost completely from this area. A large number of cismontane southern Californian species are known to range north through the South Coast Range to Mount Hamilton, as for example *Calochortus invenustus, Delphinium Parryi, Salvia mellifera, Malacothrix Clevelandii,* etc. (Sharsmith, 1945).

CHROMOSOME NUMBER

Both *Gilia tricolor* and *G. angelensis* have 9 pairs of chromosomes. The counts were obtained from propiono-carmine smears and paraffin sections of young anthers. Horticultural material of *G. tricolor* was previously determined as n = 9 by Langlet (1936) and Flory (1937). The author's counts are summarized below and illustrated in fig. 5.

G. tricolor tricolor; Inner Coast Range near Byron, Contra Costa Co.; *V. Grant 8640;* n = 9.

G. tricolor tricolor; South Coast Range near Parkfield, Fresno Co.; *D. D. Keck 6307;* n = 9.

G. tricolor diffusa; San Joaquin Valley near Tipton, Tulare Co.; *V. Grant 8654;* n = 9.

G. tricolor diffusa; Kern Canyon, Sierra Nevada, Kern Co.; *V. Grant 8466;* n = 9.

G. angelensis; Lytle Canyon, San Gabriel Mts., San Bernardino Co.; *V. Grant 8661;* n = 9.

G. angelensis; South Coast Range near Wheeler Hot Springs, Ventura Co.; *V. Grant 8706;* n = 9.

EXPERIMENTAL HYBRIDIZATIONS

Information concerning the genetic relationships of *Gilia tricolor* was sought by means of hybridization experiments. During the hybridization seasons of 1949, 1950 and 1951, four strains of *Gilia tricolor* were crossed with 21 strains, representing nine other species or species complexes. The number of flowers pollinated in each combination averaged about ten and ranged from

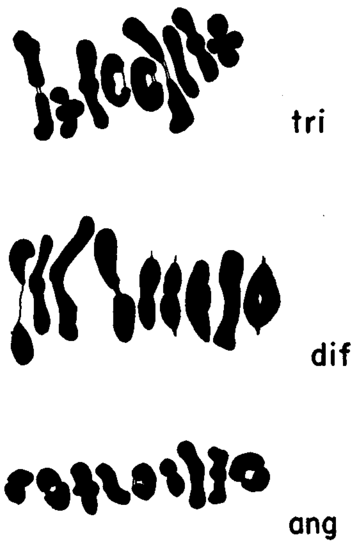

Fig. 5. Paired chromosomes of *Gilia tricolor* and *G. angelensis*. The strains are *G. tricolor tricolor* from Byron, *G. tricolor diffusa* from Tipton, and *G. angelensis* from Lytle Canyon. From camera lucida drawings of dividing pollen mother cells; chromosomes spread apart slightly in drawing. × 1600.

two or three up to 42. Reciprocal crosses were made wherever feasible, and where not the species with the shorter style was used as the female parent. The mothers were emasculated and isolated in breeding cages. A total of 43 hybrid combinations was attempted.

The following strains, grouped by species, were employed. They are all diploid, like *G. tricolor,* with n = 9, except *G. multicaulis* var. *clivorum, G. tenuiflora interior* from Cuyama Valley, and *G. sinuata,* which are tetraploid with n = 18.

G. tricolor tricolor; Hood Mt. Range, North Coast Range, Sonoma Co.; *VG 8873.*

G. tricolor tricolor; Inner Coast Range near Byron, Contra Costa Co.; *VG 8640.*

G. tricolor tricolor; South Coast Range near Parkfield, Fresno Co.; *D. D. Keck 6294.*

G. tricolor diffusa; San Joaquin Valley near Tipton, Tulare Co.; *VG 8654*

G. angelensis; Lytle Canyon, San Gabriel Mts., San Bernardino Co.; *VG 8661.*

G. angelensis; interior Southern California valley near Perris, Riverside Co.; *VG 8700.*

G. achilleaefolia; South Coast Range near San Luis Obispo, San Luis Obispo Co.; *VG 8557.*

G. achilleaefolia; Moraga Canyon, Inner Coast Range, Contra Costa Co.; *VG 8505.*

G. achilleaefolia; Bear Creek Canyon near Orinda, Coast Range, Contra Costa Co.; *VG 8424.*
G. multicaulis; Kings Mt., Coast Range, San Mateo Co.; *VG 8903.*
G. capitata capitata; Mayacama Mts., North Coast Range, Napa Co.; *VG 7702.*
G. capitata Chamissonis; Pt. Reyes Peninsula, Marin Co.; *VG 8645.*
G. capitata staminea; San Joaquin River near Antioch, Contra Costa Co.; *VG 7879.*
G. millefoliata; Pt. Reyes Peninsula, Marin Co.; *VG 7909, 8419.*
G. multicaulis clivorum; Grizzly Peak, Coast Range, Alameda Co.; *VG 8536.* (This is the only available taxonomic name for this species, which is quite distinct from *G. multicaulis.*)
G. tenuiflora interior; Cuyama Valley, Inner South Coast Range, Ventura Co.; *H. L. Mason 14014.* (This entity is specifically distinct from *G. tenuiflora.*)
Gilia 8859; east scarp of Sierra Nevada near Inyokern, Kern Co.; *VG 8859.*
G. tenuiflora; Arroyo Seco, South Coast Range, Monterey Co.; *G. L. Stebbins 3945.*
G. latiflora; Mojave Desert near Mojave, Kern Co.; *VG 8816.*
G. latiflora triceps; Panamint Mts. near Wildrose, Inyo Co.; *VG 8821.*
G. sinuata; Morongo Basin, desert slope of San Bernardino Mts., San Bernardino Co.; *VG 8842.*
G. sinuata; Mojave Desert near Kramer, San Bernardino Co.; *VG 8846.*
G. ochroleuca transmontana; Mojave Desert near Kramer, San Bernardino Co.; *VG 8847.*
G. gilioides gilioides; Pinnacles, Inner South Coast Range, San Benito Co.; *VG 8712.*
G. gilioides volcanica; Sierra Nevada near Groveland, Tuolumne Co.; *D. D. Keck 6456.*

Interstrain crosses within *Gilia tricolor* proved to be fully compatible. Interspecific crosses involving *G. tricolor,* however, were almost without exception incompatible.

No capsules at all were formed as a result of cross-pollinations between *G. tricolor* and *G. gilioides* or *G. sinuata.* Crosses between *G. tricolor* and *G. angelensis, achilleaefolia, capitata, millefoliata,* and *tenuiflora* usually resulted in a set of capsules and the formation of numerous shrivelled and inviable seeds. Reciprocal crosses between *G. tricolor* and *G. tenuiflora interior* and *G. 8859* yielded some sound seeds, which either developed into selfs or did not germinate at all.*

No natural hybrids of *Gilia tricolor* have ever been found. It thus appears that gene exchange between *G. tricolor* and other species of *Gilia* is blocked, both in nature and in the breeding plot, by a strong barrier of incompatibility.

*Since the above was written, crosses have been attempted between *G. tricolor* and two more species of *Gilia,* both of which are diploid. These are: *G. Abramsii;* Mt. Pinos, Ventura Co.; *VG 16040;* and true *G. tenuiflora interior;* Democrat Hot Springs and Kern Valley, Kern Co.; *VG 9107* and *17568.* The last-mentioned species is quite distinct from the Cuyama Valley plant currently going under the same name. In crosses between *G. tricolor* and *G. Abramsii* the capsules did not plump up, while crosses with *G. tenuiflora interior* led to small capsules containing shrivelled seeds.

The nature of the block — whether it operates during pollen tube growth, fertilization, or embryo development — has not been investigated.

Gilia angelensis was crossed with 13 strains belonging to 6 other species of *Gilia* in 17 different combinations. The following strains, grouped by species, were employed. They all have the same chromosome number as *G. angelensis,* with the exception of *G. tenuiflora interior* from Cuyama Valley, which is tetraploid.

G. *angelensis;* interior valley near Perris, Riverside Co.; *VG 8700.*

G. *angelensis;* Lytle Canyon, San Gabriel Mts., San Bernardino Co.; *VG 8661.*

G. *angelensis;* Isabel Creek, Mt. Hamilton Range, Santa Clara Co.; *VG 8891.*

G. *tricolor tricolor;* Hood Mt. Range, North Coast Range, Sonoma Co.; *VG 8873.*

G. *tricolor tricolor;* Inner Coast Range near Byron, Contra Costa Co.; *VG 8640.*

G. *tricolor diffusa;* San Joaquin Valley near Tipton, Tulare Co.; *VG 8654.*

G. *achilleaefolia;* Isabel Creek, Mt. Hamilton Range, Santa Clara Co.; *VG 8889.*

G. *achilleaefolia;* Moraga Canyon, Coast Range, Contra Costa Co.; *VG 8505.*

G. *achilleaefolia;* Pinnacles, Inner South Coast Range, San Benito Co.; *VG 8716.*

G. *multicaulis;* Kings Mt., Coast Range, San Mateo Co.; *VG 8903.*

G. *multicaulis;* below Corte Madera ridge, North Coast Range, Marin Co.; *VG 8878.*

G. *capitata staminea;* San Joaquin River near Antioch, Contra Costa Co.; *VG 7879.*

G. *capitata abrotanifolia;* foothills of San Bernardino Mts. near Mentone, San Bernardino Co.; *VG 8699.*

G. *millefoliata;* Pt. Reyes Peninsula, Marin Co.; *VG 8419.*

G. *tenuiflora interior;* Cuyama Valley, Inner South Coast Range, Ventura Co.; *H. L. Mason 14014.*

G. *splendens australis;* Morongo Basin, desert slope of San Bernardino Mts., San Bernardino Co.; *VG 15985.*

The geographically isolated strain of *Gilia angelensis* from the Mount Hamilton Range crossed readily with a southern Californian strain (Lytle Canyon) and produced vigorous and fertile F_1 and F_2 hybrids. Most, but not all, interspecific crosses of G. *angelensis* were unsuccessful.

Reciprocal crosses between G. *angelensis* and G. *splendens australis* led to no set of capsules from a total of 18 flowers pollinated.

Crosses between G. *angelensis* and G. *tricolor* and *capitata* resulted in the formation of capsules with numerous shrivelled and inviable seeds. Such capsules rarely contained a few well plumped seeds which did not germinate. A cross of G. *tenuiflora interior* by G. *angelensis* followed a similar pattern, in that 21 flowers produced 20 capsules with numerous abortive seeds and a single sound seed, which did not germinate.

There was considerable variation in crossability between *G. angelensis* and the different strains of *G. achilleaefolia* and *multicaulis*. Some crosses resulted only in the formation of abortive seeds, while other combinations proved more compatible. A cross of *G. angelensis* by *G. multicaulis* from Kings Mt. led to 52 plump seeds plus numerous abortive seeds from 23 flowers, but none of the seeds germinated. *Gilia angelensis* crossed by *G. achilleaefolia* from Moraga Canyon gave 46 sound seeds plus numerous abortive ones from 14 flowers, and from these seeds 9 F_1 hybrids were grown.

Gilia angelensis appears to be fairly compatible with *G. millefoliata,* for 11 capsules were set on as many flowers, and yielded 75 sound seeds and no shrivelled ones. Two F_1 hybrids were grown to maturity.

The first generation hybrids between *G. angelensis* and *G. achilleaefolia* and *millefoliata* were vigorous but highly sterile, with 1% and less than 1% good pollen respectively. The plants of F_1 *angelensis* × *millefoliata* set no seeds from sister crossings in the greenhouse during the first few weeks of flowering. Early in June, then, the hybrids were interplanted with the *angelensis* parent in the experimental field, in an attempt to backcross them under conditions of open pollination. Although they bloomed freely for seven weeks in the open field, they set no seeds. The F_1 of *angelensis* × *achilleaefolia* Moraga Canyon was likewise completely seed sterile.

Chromosome pairing was much reduced in both hybrids. The average number of bivalents per cell at metaphase I was 6.2 in F_1 *angelensis* × *millefoliata,* and 4.6 in F_1 *angelensis* × *achilleaefolia,* as compared with 9 in the parental species. The numerous univalents that resulted from this failure of pairing lagged at anaphase and produced micronuclei in the sporads. It is evident that there is only a moderate degree of chromosome homology between *G. angelensis* and either *G. achilleaefolia* or *millefoliata*. A detailed analysis of meiosis in these interspecific hybrids will be presented in a forthcoming paper.

It appears, in summary, that *G. tricolor* and *G. angelensis* are separated from other species, and from one another, by strong incompatibility barriers. The incompatibility barrier of *G. angelensis* can be breached in the direction of *G. achilleaefolia* and *G. millefoliata*. The resulting F_1 hybrids of *G. angelensis* are then too sterile to reproduce themselves either as F_2s or backcrosses.

PHYLOGENETIC RELATIONSHIPS

A study of phylogenetic trends in the Polemoniaceae suggests that *Polemonium,* with its perennial life-form, leafy stems, alternate compound leaves, loose cymose inflorescence, herbaceous calyx, blue-violet campanulate corolla, predominantly mesic ecology, and 9 pairs of large chromosomes with median centromeres, is a primitive genus in the family. The characteristics possessed by many other genera of Polemoniaceae — such as annual habit, prickly or reduced leaves, leafless stems and basal rosettes, membraneous accrescent calyces, long-tubed salverform corollas or reduced self-pollinating flowers, adaptation to desert climates, reduced chromosome numbers of $n = 8$, 7 and 6, and small chromosomes with subterminal centromeres — seem to represent various specializations on the fundamental pattern of plant form laid down in *Polemonium*. On the basis of current views concerning phylogenetic trends in angiosperms it is theoretically possible to derive *Gilia* and various other genera from some prototype with the characters of *Polemonium,* whereas any attempt to read the series in the opposite direction meets with grave difficulties.

If *Gilia* descended from a *Polemonium*-like ancestor, then the most primitive species of *Gilia* will be that which most closely resembles *Polemonium. Gilia tricolor* possesses a number of characteristics which on this basis would be regarded as primitive for the annual *Gilias.* The stems are leafy; the inflorescence is a loose cyme; the calyx is predominantly herbaceous with only a very narrow hyaline portion in the sinuses; the corolla is campanulate; the 9 pairs of chromosomes are large; and the northern strains at least are adapted to a moist climate. The purple spots in the corolla-throat represent, of course, a specialization acquired during the evolutionary history of the species.

It seems altogether possible that the change to a more arid climate in western North America during late Tertiary times, as described by Axelrod (1948, 1950), may have stimulated the following evolutionary changes. A perennial mesic form of *Polemonium* withdrew from some center of origin in the Southwest to moister regions, leaving behind a mesic annual better able to cope with the new drier conditions. As the climate became even more arid, that daughter species, which was an ancient form of *G. tricolor,* was itself forced to retreat to a more northern area, but not before it had given rise to at least two new drought-enduring types.

One of these is the reduced, small-flowered *Gilia angelensis,* which is adapted to the warm dry climate now prevailing in cismontane southern California,

Character	*G. capitata, achilleaefolia, millefoliata.*	*G. tricolor, angelensis.*	*G. tenuiflora interior, tenuiflora, latiflora, etc.*
Range	Pacific slope		desert and desert border
Habit	plants usually without a basal rosette; upper cauline leaves usually well developed		plants with a basal rosette; upper cauline leaves much reduced
Pubescence	floccose or glandular hairs		fine woolly hairs
Calyx	anthocyanin, if present, located in sinus membranes		in herbaceous portion
Ecology	mostly moderate sunlight in wooded or foggy areas	intense sunshine of open plains and hills	
Size	plants grow very large in experimental garden (except *millefoliata)*	plants remain small in garden	
Inflorescence	dense head or tight glomerule	loose cyme	
Corolla	concolored (except *millefoliata);* limb erect and ascending (except *millifoliata);* remaining open in dark weather	bicolored or tricolored; limb rotately spreading; usually closing in dark weather	

and which has points of similarity in turn with *G. capitata abrotanifolia* and *G. achilleaefolia.* The other offspring of *G. tricolor* on this hypothesis is *G. tenuiflora interior* and *G. 8859,* adapted to the semi-desert climate prevailing in the upper San Joaquin Valley and adjacent mountain ranges, from which may have developed in turn the complex of forms in the desert proper, namely *G. latiflora, tenuiflora* and their allies. A thin thread of crossability remains between *G. angelensis* and *G. achilleaefolia.*

The tabulation on page 384 summarizes the likenesses and differences between the *Gilia tricolor* complex and the two most closely related complexes.

TAXONOMY

The *Gilia tricolor* complex is distinguished from all other species groups by the following combination of characters: leafy stems, predominantly herbaceous calyx, campanulate corolla with a limb 4 mm. or more wide when pressed flat, and exserted style. The members of the *Gilia tricolor* group may be separated by the following key.

Corolla 8–16 mm. long, with prominent purple spots in the throat and a bright yellow or orange tube; central and northern California.
  Flowers solitary on long peduncles, corolla 8–10 mm. long and 7–9 mm. broad across the limb...... *G. tricolor diffusa*
  Flowers in 2–5-flowered glomerules on short pedicels; corolla 11–16 mm. long and 9–14 mm. broad across the limb .... *G. tricolor tricolor*
Corolla 7–8 mm. long, without spots in the throat and with a pale yellow tube; cismontane southern California.. *G. angelensis*

GILIA TRICOLOR Benth.

Annual herbs; plants branching divaricately from base, 8–40 cm. high, stems floccose or glabrous below and glandular above; lower cauline leaves uni- or bipinnately dissected, 1–4 cm. long, the segments narrow to nearly filiform, the upper cauline leaves reduced and apparently palmate; calyx somewhat accrescent, the lobes acute, with a central green herbaceous band about 1 mm. wide flanked by very narrow hyaline wings joining below into a hyaline sinus 0.1–0.5 mm. wide; corolla campanulate, 8–16 mm. long, 2–3 times longer than calyx, deciduous, frequently lightly pubescent on outer surface, tricolored, the limb pale to deep blue-violet, the tube and lower portion of the throat yellow to orange, and the throat marked with 5 pairs of purple spots, the lobes rotately spreading; stamens inserted equally in the sinuses of the corolla, the filaments unequal in length, there being a lowermost long pair 2–3 mm. long, a lateral pair of medium length, and a short upper one about half the length of the long filaments; style exserted, stigmas 2–3 mm. long; capsule ovoid, dehiscent, 16–36-seeded; seeds ovoid, 1.0–1.5 mm. long, brown; $n = 9$.

Range.—Foothills and open plains of central and northern California from the upper San Joaquin Valley to the Trinity Mts., 20–4000 ft.

GILIA TRICOLOR subsp. TRICOLOR Benth.

Gilia tricolor Benth., Bot. Reg., under t. 1622, 1833 (type seen).

Gilia nivalis Hérincq, Rev. Hort. **22**: 86, 1850.

Flowers solitary or in 2–5-flowered glomerules, pedicels 2–30 mm. long; calyx 4–7 mm. long in flower, 6–8 mm. long in fruit, floccose, the sinuses purple; corolla 11–16 mm. long, the limb 9–14 mm. wide when pressed flat, the lobes 5–8 (or sometimes 4) mm. wide.

Type.—California, *Douglas,* 1833. Royal Botanic Gardens, Kew.

Range.—Open grassy plains and hill slopes of Central Valley from Tulare County to Tehama County, Central and North Coast Ranges from San Benito County to Humboldt and Trinity counties, northern Sierra Nevada in Plumas and Lassen counties, and southern Cascade Mts. in Shasta County. 20–2000 ft. Sympatric with *Gilia gilioides, G. multicaulis* var. *clivorum, G. capitata.* Flowers March-April, sometimes in February in south and in May in north.

Variation.—Relatively uniform. Depauperate specimens from hot, dry areas in the Coast Range, such as Lake County, frequently resemble *G. tricolor diffusa.* The coloration of the corolla is intense in the northern and pale in the southern part of the range. There is complete intergradation with *G. tricolor diffusa.*

Specimens cited.—CALIFORNIA. San Benito Co.: Panoche Pass, *D. D. Keck 5234.* Santa Clara Co.: Pacheco Pass, *L. R. Abrams 10739;* Gilroy, *C. F. Baker 1942;* Evergreen, *J. B. Davy 63;* Mt. Hamilton, *C. F. Baker 634, H. L. Mason 7199.* Alameda Co.: east of Livermore, *R. S. Ferris 9431;* Sunol, *H. L. Mason 1310.* Contra Costa Co.: Byron, *V. Grant 8640;* Mt. Diablo, *H. M. Hall 1727, H. L. Mason 5118, M. L. Bowerman 569, 2864.* Napa Co.: Napa River, *W. L. Jepson (1893);* St. Helena, *C. Hunt (1921).* Lake Co.: Lakeport, *T. S. Brandegee (1884).* Sonoma Co.: Santa Rosa, *A. A. Heller 5211.* Mendocino Co.: Blue Rock, *A. Eastwood (1902).* Humboldt Co.: Phillipsville, *J. P. Tracy 5467;* Trinity River Valley, *J. P. Tracy 15733.* Fresno Co.: Fresno, *H. L. Mason 8172.* Merced Co.: Merced, *A. Eastwood (1917).* San Joaquin Co.: Linden, *F. W. Gunnison (1896).* Sacramento Co.: Fair Oaks, *M. S. Baker (1900).* Yolo Co.: Winters, *A. Eastwood 14219.* Colusa Co.: Colusa Junction, *T. S. Brandegee (1889);* Leesville, *Brandegee (1889).* Sutter Co.: Marysville Buttes, *A. A. Heller 11801.* Butte Co.: Oroville, *A. A. Heller 10724;* Clear Creek, *H. E. Brown (1897).*

GILIA TRICOLOR subsp. DIFFUSA (Congdon) Mason and A. Grant.

Gilia tricolor subsp. *diffusa* Mason and A. Grant, Madroño **9**: 209, 1948.

Gilia diffusa Congdon, Erythea **7**: 186, 1900 (type seen).

Gilia tricolor var. *longipedicellata* Greenm., Rhod. **6**: 154, 1904.

Gilia inconspicua subsp. *sinuata* var. *oreophila* subvar. *diffusa* Brand, Pflzr. **IV, 250**: 105, 1907.

Flower solitary on long peduncles 1–4 cm. long; calyx 3–4 mm. long in flower, 4–7 mm. long in fruit, floccose or glandular, the sinus purple or colorless; corolla 8–10 mm. long, the limb 7–9 mm. wide when pressed flat, the lobes 3–4 mm. wide.

Type.—New Coulterville Road, Mariposa County, California. *J. W. Congdon, May 3, 1898.* Univ. of California Herbarium.

Range.—Dry open plains and rolling foothills of upper San Joaquin Valley in Kern and Tulare counties, Sierra Nevada foothills as far north as Placer County, and Inner Coast Range north to Fresno County. 300–4000 ft. Sympatric with *Gilia gilioides, G. tenuiflora interior, G. capitata staminea, G. capitata pedemontana*. Flowers March-May.

Variation.—Relatively uniform, intergrading with *G. tricolor tricolor*.

Specimens cited.—CALIFORNIA. Kern Co.: Keene, *F. W. Pennell 25100;* Bakersfield, *V. Grant 8458;* Kern Canyon, *V. Grant 8466, H. L. Mason 11731, 8006;* Havilah, *H. L. Mason 8375;* Woody, *V. Grant 8478.* Tulare Co.: Exeter, *H. L. Mason 11711;* Grapevine, *P. S. Woolsey (1898);* Three Rivers, *L. R. Abrams 10803, V. Grant 8485.* Fresno Co.: Coalinga, *V. Grant 8453, 8456.* Madera Co.: Northfork, *R. Bacigalupi 2297;* Coarsegold, *V. Grant 8491.* Mariposa Co.: Blochmans Ranch, *A. Eastwood 4239;* Coulterville, *V. Grant 8521.* Tuolumne Co.: French Flat, *R. S. Ferris 1541.* Amador Co.: Drytown, *G. Hansen 1557;* Ione, *G. Hansen 1580.* El Dorado Co.: Placerville, *K. Brandegee (1907);* Shingle Springs, *H. L. Mason 4505.*

Gilia angelensis sp. nov.

Herba annua usque ab basi ramescens 7–70 cm. alta; caulibus glabris vel floccosis ad basim aliquando supra mediam partem glandulosis; capitulis pluribus; floris circa 5 (1–10), pedicellis 2–3 mm. longis; calycibus florentibus 3–4 mm. longis, fructiferis accrescentibus, floccosis rare glabris, lobis acutis cum parte media lata (0.3–0.7 mm.) et viridi et margine 0.1–0.3 mm. lata ad sinum; corollis campanulatis 7–8 mm. longis, calycibus duplicibus longioribus, limbo coeruleo-violaceo, tubo pallido flavo, lobis ovatis 2–3 mm. latis; stylo exserto, stigmate 1 mm. longa; capsula ovoidea, seminibus 20–30, 0.5–1.0 mm. longis; n = 9.

Annual herbs; plants erect, spreading, usually branching from base, 7–70 cm. high; stems glabrous or floccose below, sometimes glandular above; basal and lower cauline leaves unipinnately or bipinnately dissected, 2–5 cm. long, the ultimate segments somewhat falcate, 5–15 mm. long, 0.5–1.5 mm. wide, the upper cauline leaves smaller, pinnate, frequently appearing as if palmate, the axils of the leaves floccose; inflorescence cymose, the heads several, terminal on naked peduncles 1–5 cm. long, usually about 5-flowered, sometimes 1–10-flowered, the pedicels 2–3 mm. long; calyx in flower 3–4 mm. long, accrescent, floccose, or sometimes glabrous, the lobes acute, with a broad flat central green portion 0.3–0.7 mm. wide flanked on both sides by straight-margined hyaline wings 0.1–0.3 mm. wide at the sinus, these colorless or blue-violet; corolla campanulate, 7–8 mm. long, twice as long as the calyx, the limb pallid blue-violet to white, the tube pale yellow, the limb 4–6 mm. wide when pressed flat, the lobes rotately spreading, oval, with an acute tip, 2–3 mm. wide; stamens inserted in the sinuses of the corolla, the filaments about 1 mm. long; style exserted, stigmas 1 mm. long; capsule ovoid, dehiscent, 20–30-seeded; seeds 0.5–1.0 mm. long, brown; n = 9.

Type.—Sandy plains at mouth of Lytle Creek Canyon, east end of San Gabriel Mts., San Bernardino Co., California. *V. Grant 8661,* April 25, 1949. Rancho Santa Ana Botanic Garden Herbarium. Named for the Los Angeles area, which is in the center of its distribution.

Range.—Loose soil of outwash plains, sunny hillsides and canyons, from Baja California through cismontane southern California to Santa Barbara County, and on Santa Catalina and Santa Cruz islands; rare in Mount Hamilton Range; 800–6300 ft. Often sympatric with *Gilia capitata abrotanifolia,* rarely with *G. achilleaefolia, G. multicaulis* var. *clivorum*. Flowers March-May.

Variation.—Relatively uniform. Some specimens suggest that hybridization may occasionally occur with *G. capitata abrotanifolia.*

Specimens cited.—MEXICO. Baja California: Santo Domingo, *I. L. Wiggins 4483, 4501;* n. Ensenada, *H. F. Copeland (1947).* CALIFORNIA. San Diego Co.: San Diego, *K. Brandegee (1905, 1906);* Warner Hot Springs, *C. B. Wolf 8495;* Ramona, *I. L. Wiggins 2486.* Riverside Co.: Elsinore, *P. A. Munz 12024;* Santa Ana River, *P. A. Munz 2628;* Perris, *L. R. Abrams 13676, C. B. Wolf 6314;* Banning, *F. W. Gould 2148.* San Bernardino Co.: Upland, *I. Johnston 41, 47;* San Bernardino, *S. B. Parish 6903, V. Grant 8694.* Los Angeles Co.: Claremont, *H. P. Chandler (1897), P. A. Munz 3240,* Saugus, *G. B. Grant 5433.* Ventura Co.: Seacliff, *B. S. Angier 26;* Wheeler Hot Springs, *V. Grant 8706.* Santa Barbara Co.: Solvang, *B. O. Schreiber 1649.*

Herbaria consulted.—University of California, California Academy of Sciences, Stanford University, Pomona College, and Rancho Santa Ana Botanic Garden.

Summary

Gilia tricolor possesses a number of characteristics, such as leafy stems, campanulate corolla, herbaceous calyx, and mesic ecology, which suggest that it is derived from some *Polemonium*-like ancestor, and is the progenitor in turn of at least two series of annual *Gilias.* One of the descendants of *Gilia tricolor,* on this hypothesis, is *G. tenuiflora interior* and an undescribed relative from the mountains bordering the Mojave Desert, which gave rise successively to the complex of forms centering around *G. tenuiflora* and *G. latiflora* in the desert proper. The other line of evolution from *G. tricolor* leads to the reduced drought-enduring *G. angelensis* sp. nov. of southern California, which is related in turn to *G. achilleaefolia* and *G. capitata abrotanifolia.*

Gilia tricolor ($n = 9$) is isolated from the other 9-paired annual species by very strong incompatibility barriers. *Gilia angelensis* ($n = 9$) crosses fairly readily with certain strains of *G. achilleaefolia* and *G. millefoliata* in the breeding plot, and hybridizes to a limited extent with *G. capitata abrotanifolia* in nature, but is separated from the other diploid annual species by strong incompatibility barriers. The experimental hybrids of *G. angelensis* are highly sterile with reduced chromosome pairing, and the field hybrids with *G. capitata abrotanifolia* are apparently fertile only as backcrosses. The reproductive isolation separating *Gilia tricolor* and *G. angelensis* from other species of *Gilia,* and from one another, is therefore very nearly complete.

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