

1954

Genetic and Taxonomic Studies in *Gilia*: VI. Interspecific Relationships in the Leafy-stemmed *Gilias*

Verne Grant

Follow this and additional works at: <https://scholarship.claremont.edu/aliso>



Part of the [Botany Commons](#)

Recommended Citation

Grant, Verne (1954) "Genetic and Taxonomic Studies in *Gilia*: VI. Interspecific Relationships in the Leafy-stemmed *Gilias*," *Aliso: A Journal of Systematic and Floristic Botany*. Vol. 3: Iss. 1, Article 4.
Available at: <https://scholarship.claremont.edu/aliso/vol3/iss1/4>

GENETIC AND TAXONOMIC STUDIES IN GILIA

VI. INTERSPECIFIC RELATIONSHIPS IN THE
LEAFY-STEMMED GILIAS

VERNE GRANT*

INTRODUCTION

The Leafy-stemmed Gilias comprise a natural subdivision of the genus *Gilia*, family Polemoniaceae, technically known as the section *Eugilia*. The plants composing this section are herbaceous annuals with blue-violet flowers and stems which are more or less leafy throughout their length. They inhabit loose sandy soils in the more open communities of the Pacific slope of North America and of temperate South America. The attempts of various students to classify the group by traditional taxonomic methods have not proven entirely successful. A taxo-genetic study of the Leafy-stemmed Gilias was therefore undertaken in order to obtain experimental data bearing on the species problem in this group. The North American species have been delimited and described in previous papers of this series (parts I to V); the South American species are currently under investigation and will be reported on in a future communication. The present paper is concerned with the relationships between these species.

On morphological and ecological grounds, the Leafy-stemmed Gilias can be grouped into three assemblages of species. (i) The *Gilia tricolor* group consists of two species, *G. tricolor* Benth. (with two subspecies) and *G. angeleensis* V. Grant, both of which are diploid with 9 pairs of chromosomes (see part III). The members of the *Gilia tricolor* group are small plants which often form very extensive populations on the rolling foothills and plains of California behind the coast line. They are largely cross-pollinated by bees, but partly self-pollinated by these insects. (ii) Allied to the former is the *Gilia laciniata* group, which is represented in North America by the diploid species *G. millefoliata* Fisch. et Mey. (see part V), the tetraploid *G. clivorum* V. Grant (part V), and an island endemic *G. nevinii* Gray, and in South America by two or three species of diploids and tetraploids, which for the time being may all be referred to as *Gilia laciniata* Ruiz et Pavon sens. lat. The members of the *Gilia laciniata* group are mostly maritime plants, often with a prostrate habit of growth and very glandular herbage, which usually grow near the Pacific Ocean. Several of the species are autogamous in their breeding behavior. (iii) The *Gilia capitata* group consists of two diploid species, *G. capitata* Sims (with eight subspecies; see parts I and II) and *G. achilleaefolia* Benth. (part IV). These are plants of larger size which usually occur in disjunct local colonies in the hills and mountains on the Pacific slope of North America. Some races of *G. capitata* are self-incompatible and entirely cross-fertilizing, others are mainly but not entirely outcrossing; some races of *G. achilleaefolia* are mainly outcrossed but partly selfed, others are autogamous. A key to the species of *Eugilia* is presented in the taxonomic section of this paper.

The work on the Leafy-stemmed Gilias was begun in 1946 at the University of

*Rancho Santa Ana Botanic Garden.

Manuscript received for publication October 5, 1952.

California, Berkeley, continued from 1949 to 1950 at the Carnegie Institution of Washington, Stanford, and since 1950 has been carried on at the Rancho Santa Ana Botanic Garden. A part of the work was supported by a National Research Council Fellowship. Various aspects of the problem have been discussed at length with G. Ledyard Stebbins, Herbert L. Mason, and Harlan Lewis of the University of California; with Jens Clausen, David D. Keck, Wm. M. Hiesey, and Paul Grun of the Carnegie Institution of Washington; with Philip A. Munz of the Rancho Santa Ana Botanic Garden; and with Walter S. Flory of the Blandy Experimental Farm, Boyce, Virginia. The manuscript was reviewed in its early stages by Drs. Clausen and Grun, and in its later stages by Drs. Stebbins and Lewis, all of whom made valuable suggestions. The more than 2794 cross-pollinations were made by Mrs. Alva Grant, who also contributed many helpful suggestions. Marie Reiche and O. Velarde of Lima, Peru, kindly collected and sent seeds of *Gilia laciniata*. The author wishes to acknowledge his sincere gratitude to these colleagues for their interest, help and advice, and to the supporting institutions for material aid.

CROSSABILITY

Crosses have been attempted between all the North American species of Leafy-stemmed *Gilia* except *G. nevinii*; a tetraploid strain of *G. laciniata* from Peru has also been included in the crossing program. The crosses have been carried out under controlled conditions in a greenhouse, the female parents being isolated in breeding cages and emasculated from day to day. In most cases several strains were employed for each species; all strains were grown from seeds collected in the wild. The results obtained during the six hybridization seasons from 1947 to 1952 are summarized in table 1. This table shows that crosses performed within one species are usually successful, while interspecific crosses are usually unsuccessful.

Within a large or complex species like *G. capitata* or *G. achilleaefolia* there are definite barriers to crossing. Most of the strains of such species, however, intercross freely, and those which do not cross directly with one another can usually be hybridized via some intermediary strain. We see from the table that out of 46 hybrid combinations attempted, 32 yielded F_1 hybrids, mostly in large numbers. The F_1 hybrids were in all cases vigorous and fertile, and their F_2 progeny, though including some weak and malformed types, were on the whole quite viable.

Crosses between species of Leafy-stemmed *Gilia* give very different results. Some of the hybridizations yielded only masses of abortive seeds, others resulted in a mixture of abortive and apparently sound seeds but no F_1 hybrids, while 8 of the 68 combinations attempted produced small numbers of F_1 individuals, and only two combinations produced large numbers of hybrids. The most compatible combinations were *G. millefoliata* from Point Reyes Peninsula crossed by *G. achilleaefolia* from San Luis Obispo, and *G. millefoliata* ♀ × *laciniata* from Lima, Peru.

Crosses were also attempted between various kinds of Leafy-stemmed *Gilia* and members of other sections, namely the Woolly-leaved *Gilias* (*G. tenuiflora*, *G. sinuata*, etc.), the Woodland *Gilias* (*G. splendens*, *G. leptalea*, etc.), the *Gilia gilioides* group, and *Gilia congesta*. The morphological evidence indicates that the Woolly-leaved and the Woodland *Gilias* are phylogenetically closely related to the Leafy-stemmed *Gilias*, whereas *Gilia gilioides* and *G. congesta* are only distantly related and belong in separate subgenera. The table shows that all crosses between the Leafy-stemmed *Gilias* on the one hand, and the Woodland *Gilias*, the *Gilia gilioides* group, or *G. congesta* on the other, have failed, and that crosses between the Leafy-stemmed and the Woolly-leaved *Gilias* have failed in all but one instance. The one exceptional successful combination was a *tenuiflora* mother from Monterey County

TABLE 1. CROSSABILITY OF THE LEAFY-STEMMED GILIAS

Hybrid combination	No. of strains crossed	Total no. combinations	No. of successful combinations	No. of flowers pollinated	No. of capsules set	No. of abortive seeds	No. of sound seeds	No. F ₁ hybrids obtained
I. Intraspecific crosses.								
<i>capitata</i> × <i>capitata</i>	9	28	22	>1182	>470	some	many	many
<i>achilleaefolia</i> × <i>achilleaefolia</i>	9	15	7	168	130	many	1357	many
<i>tricolor</i> × <i>tricolor</i>	2	1	1	2	2	0	some	some
<i>angelensis</i> × <i>angelensis</i>	2	1	1	2	2	19	1	1
<i>clivorum</i> × <i>clivorum</i>	2	1	1	10	10	0	some	30
Total	24	46	32	>1364	>614	many	many	many
II. Interspecific, intrasectional crosses.								
<i>achilleaefolia</i> × <i>capitata</i>	10	11	0	231	many	many	14	0
<i>achilleaefolia</i> × <i>angelensis</i>	8	6	1	90	48	many	105	9
<i>achilleaefolia</i> × <i>tricolor</i>	8	7	0	72	54	many	2	0
<i>achilleaefolia</i> × <i>millefoliata</i>	5	5	1	69	63	many	250	56
<i>achilleaefolia</i> × <i>clivorum</i>	5	6	1	45	18	many	2	1
<i>capitata</i> × <i>angelensis</i>	3	2	0	23	17	many	10	0
<i>capitata</i> × <i>tricolor</i>	5	4	0	42	38	many	0	0
<i>capitata</i> × <i>millefoliata</i>	3	2	1	39	several		some	1
<i>capitata</i> × <i>clivorum</i>	6	5	3	85	64		some	6
<i>angelensis</i> × <i>tricolor</i>	5	4	0	33	24	many	some	0
<i>angelensis</i> × <i>millefoliata</i>	2	1	1	11	11	0	75	2
<i>tricolor</i> × <i>millefoliata</i>	5	6	0	24	24	many	3	0
<i>tricolor</i> × <i>clivorum</i>	2	1	0	30	28		0	0
<i>millefoliata</i> × <i>clivorum</i>	3	4	0	51	51		145	0
<i>laciniata</i> × <i>millefoliata</i>	2	2	2	30	22		500	many
<i>laciniata</i> × <i>clivorum</i>	2	2	0	36	35	many	0	0
Total	23	68	10	911	>497	many	>1106	many
III. Intersectional crosses.								
× Woolly-leaved Gilias	23	30	1	376	196	many	66	2
× Woodland Gilias	4	3	0	20	0	0	0	0
× <i>G. giloides</i> et aff.	11	14	0	>82	15		3	0
× <i>G. congesta</i>	2	2	0	41			0	0
Total	31	49	1	>519	211	many	69	2

crossed by an *achilleae-folia* father from San Luis Obispo. This cross yielded two F_1 individuals the first year it was made, but subsequent attempts to repeat the cross have failed.

Artificial hybridization between the species is apparently blocked at various stages between pollination and growth of the hybrid embryo. The foreign pollen may fail to stimulate the capsule to develop, or a capsule may be formed which contains only shrivelled seeds, or the capsule may contain sound seeds which fail to germinate under conditions which ensure full germination of seeds of the parental species. If the normal appearing seeds could be dissected and the hybrid embryo removed from the maternal tissues, it might be possible to obtain adult hybrids from some of the crosses which have so far proven wholly incompatible. Embryo culture is at present only a theoretical possibility in *Gilia*, however, owing to the technical difficulties posed by the minute size and hard coat of the seeds.

The evolutionary significance of the high degree of incompatibility between species of Leafy-stemmed *Gilia* becomes apparent when we realize that the ranges of the species overlap over broad areas in California. Sympatric occurrences are consequently very common. During the field work on the group, almost every possible pair of species has been found growing together and blooming simultaneously in the same or closely adjacent habitats (see fig. 1). The habitats of the Leafy-stemmed *Gilias* are also generally occupied by members of other sections of the genus and by other genera of Polemoniaceae. The strong incompatibility barriers permit these species to coexist in the same territory without excessive hybridization, which might expose them to the loss of their respective adaptations.

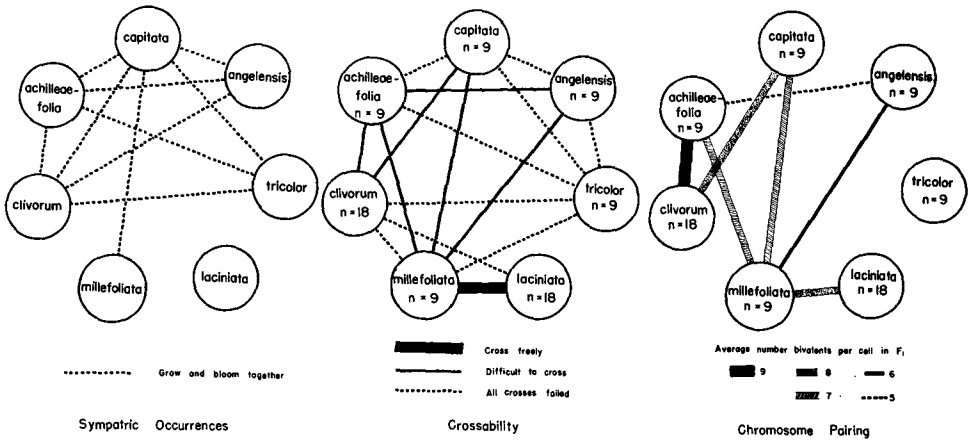


Fig. 1. Polygonal diagrams showing the sympatric occurrences and ease of crossing of seven species of Leafy-stemmed *Gilia* and the degree of chromosome pairing in their F_1 hybrids.

This interpretation is supported by the observation that the species possessing the strongest barriers to crossing are those which, like *G. tricolor*, *angelensis*, *achilleae-folia*, *capitata* and *clivorum*, have the most numerous and varied contacts. The geographically most isolated species on the mainland of North America, *G. millefoliata*, crosses fairly easily with several other species. The most compatible combination so far discovered in the whole section involves the completely allopatric *Gilia laciniata* from South America. Although tetraploid, this species crosses as easily

with the diploid *G. millefoliata* as any two individuals of one population. The correlation between strength of the incompatibility barrier and frequency of sympatric contacts may be visualized in a general way by comparison of the two relevant polygonal graphs in fig. 1.

MORPHOLOGY OF THE HYBRIDS

The following interspecific hybrids were produced: (i) *millefoliata* ♀ from Point Reyes Peninsula × *capitata chamissonis* from the same locality; (ii) *millefoliata* ♀ from Point Reyes × *achilleaefolia* from San Luis Obispo; (iii) *angelensis* ♀ from Perris, Riverside County × *millefoliata* from Point Reyes; (iv) *angelensis* ♀ from Perris × *achilleaefolia* from Moraga Canyon, Contra Costa County; (v) *clivorum* ♀ from Grizzly Peak near Berkeley × *capitata staminea* from Antioch, Contra Costa County; (vi) the same strain of *clivorum* × *capitata abrotanifolia* from Kaweah River, Tulare County; (vii) *clivorum* ♀ from Strawberry Canyon near Berkeley × *capitata chamissonis* from Point Reyes; (viii) *achilleaefolia* ♀ from Kings Mt., San Mateo County × *clivorum* from Grizzly Peak; (ix) *millefoliata* ♀ from Point Reyes × *laciniata* from Lima, Peru, and the reciprocal; and (x) *tenuiflora* ♀ from Arroyo Seco, Monterey County × *achilleaefolia* from San Luis Obispo. Most of these strains have been described in earlier papers and documented by herbarium specimens in several California herbaria; specimens of the hybrids are preserved in the herbarium of the Rancho Santa Ana Botanic Garden.

The F_1 hybrids between species of Leafy-stemmed *Gilia* were vegetatively vigorous and flowered freely over a period of many weeks. The intersectional hybrid between *G. achilleaefolia* and *G. tenuiflora* was weak, and though it flowered it never produced mature stamens or carpels.

The hybrids were in general intermediate in morphology between the parental species. This is well shown, for example, by the character of the growth habit in the cross between *G. millefoliata* and *G. achilleaefolia* (fig. 2). *Gilia millefoliata* has long horizontal branches and a short central leader; the main branches of *G. achilleaefolia*, on the other hand, are erect, and one of them tends to assume the position of a central leader; and the F_1 hybrid has spreading branches and a moderately developed central leader. Table 2 shows the intermediate condition of various organs in the hybrids.

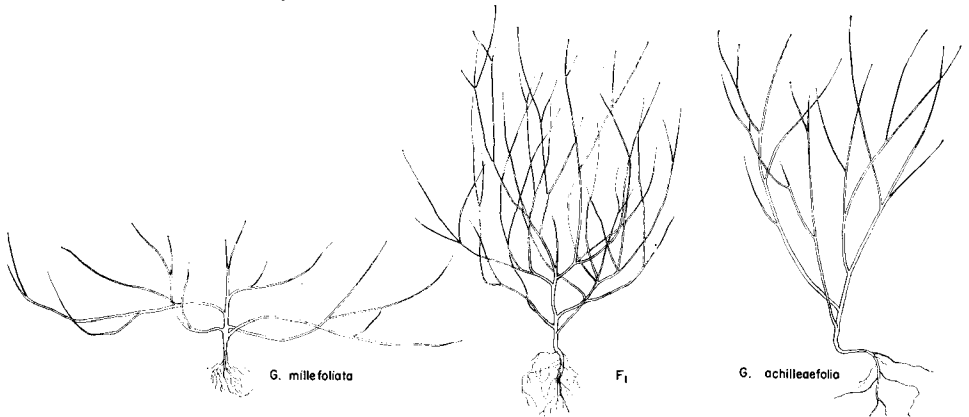


Fig. 2. Mode of branching of two species of *Gilia* and their F_1 hybrid, grown under uniform conditions. Inflorescences omitted from the drawings. x 0.13

TABLE 2. MORPHOLOGY OF F₁ HYBRIDS IN THE LEAFY-STEMMED GILIAS

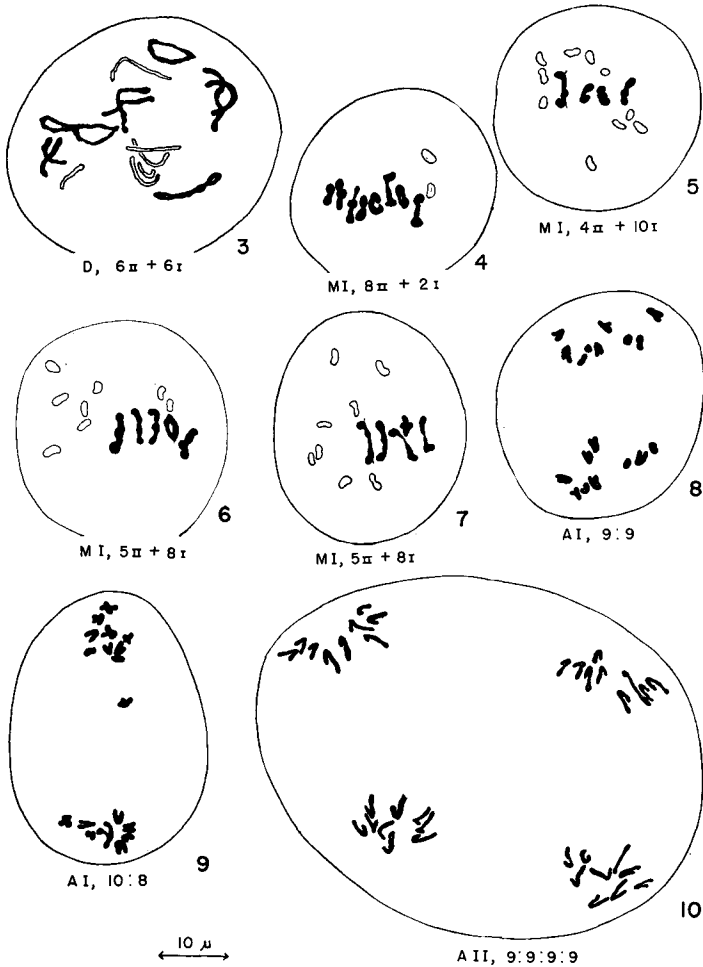
Character	Cross	P	F ₁	P
Branching	<i>mil*</i> × <i>ca</i>	branches long and horizontal	branches medium long & somewhat ascending	branches short and erect
	<i>ang</i> × <i>mil</i>	branches spreading and erect	branches partially erect	branches horizontal
	<i>mil</i> × <i>ach</i>	branches long and horizontal; leader short	branches spreading; leader moderately developed	branches erect; leader long
	<i>cli</i> × <i>ca</i>	stems short and much branched	intermediate	stems tall and sparsely branched
Pubescence	<i>ang</i> × <i>mil</i>	stem nearly glabrous	stems sparsely glandular	stems densely glandular
	<i>mil</i> × <i>ach</i>	stems densely glandular	stems moderately glandular	stems sparsely glandular
Inflorescence	<i>mil</i> × <i>ca</i>	glomerule of 5-6 flowers; pedicels 2-5 mm. long	head of 10-20 flowers; pedicels 1-2 mm. long	head of 50 flowers; pedicels 0.5-1.0 mm. long
	<i>cli</i> × <i>ca</i>	glomerule of 2-4 flowers; pedicels 2-10 mm. long	glomerule of 4-8 flowers; pedicels 1-3 mm. long	head of 50 flowers; pedicels 0.5-1.0 mm. long
Calyx	<i>mil</i> × <i>ca</i>	lobes acute, with flat green band 1 mm. wide flanked by narrow hyaline membranes 0.1-0.2 mm. wide	lobes subacuminate, with central green portion 0.6 mm. wide and hyaline border 0.6 mm. wide	lobes acuminate, with raised mid-rib 0.4 mm. wide bordered by broad hyaline wings 0.8 mm. wide
	<i>ang</i> × <i>mil</i>	tip of lobe pointed	tip of lobe subacute	tip of lobe rounded and obtuse
	<i>mil</i> × <i>lac</i>	lobes erect in one plane	intermediate	lobes flaring out
Corolla	<i>mil</i> × <i>lac</i>	corolla pale violet; throat prominent; purple spots in throat; lobes rounded at tip	corolla pale pinkish-violet; slight expansion in region of throat; faint reddish-violet spots; lobes very slightly pointed	corolla pale pink; no throat; no spots in corolla; lobes pointed
	<i>ang</i> × <i>ach</i>	lobes pointed	lobes very slightly pointed	lobes rounded
Stamens	<i>mil</i> × <i>ca</i>	filaments 0.4-0.6 mm. long	filaments 1.5 mm. long	filaments 4.0 mm. long
	<i>mil</i> × <i>ach</i>	filaments 0.4-0.6 mm. long	filaments 1.0 mm. long	filaments 1.5-2.0 mm. long
Style	<i>mil</i> × <i>ca</i>	4-6 mm. long	6 mm. long	9.0-9.5 mm. long
	<i>mil</i> × <i>ach</i>	4-6 mm. long	5-7 mm. long	12-13 mm. long

**mil*=*millefoliata*; *ca*=*capitata*; *ang*=*angelensis*; *ach*=*achilleaefolia*; *cli*=*clivorum*; *lac*=*laciniata*.

There is an interesting series of distinctions in the prominence of the purple spots in the corolla throat. These spots are very bright in *G. tricolor*, less bright but still quite prominent in *G. millefoliata*, and in *G. clivorum* they are usually plainly visible but dull. *Gilia capitata*, *achilleaefolia* and *laciniata* lack the purple spots altogether. Hybrids have never been obtained between *G. tricolor* and any other species. Hybrids between *G. millefoliata* and the spotless species always possess plain but dull corolla spots of a shade similar to that of *G. clivorum*, which is a

known hybrid derivative of *G. millefoliata* and *G. achilleaeifolia*. In hybrids of *G. clivorum* with the spotless species *G. capitata* or *G. achilleaeifolia*, the spots are present but faint. Four degrees of brightness can thus be distinguished in the corolla spots: very bright (as in *G. tricolor*); prominent (as in *G. millefoliata*); dull (as in the hybrids or hybrid derivatives of *G. millefoliata* with spotless species); and faint (as in hybrids of *G. clivorum* with spotless species).

The intermediacy of the F_1 hybrids with respect to a number of quantitative characters, like growth habit, size of inflorescence, form of the calyx, form and color of the corolla, and length of stamens and style, suggests that the differences between the species are determined by multiple factors for each character. This conclusion is



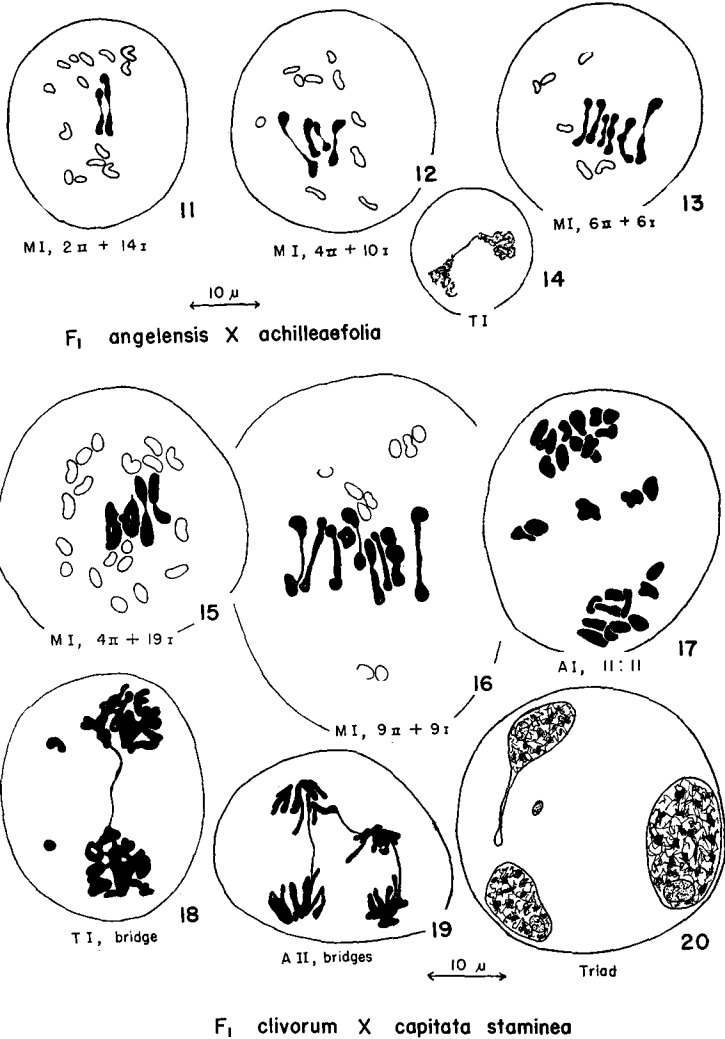
F_1 angelensis X millefoliata

Figs. 3-10. Meiosis in F_1 of *angelensis* ($n=9$) X *millefoliata* ($n=9$).

confirmed by the finding of continuous variation in the tetraploid F_2 , F_3 and F_4 progeny of one of the crosses, *G. millefoliata* \times *achilleaeifolia* (see part V).

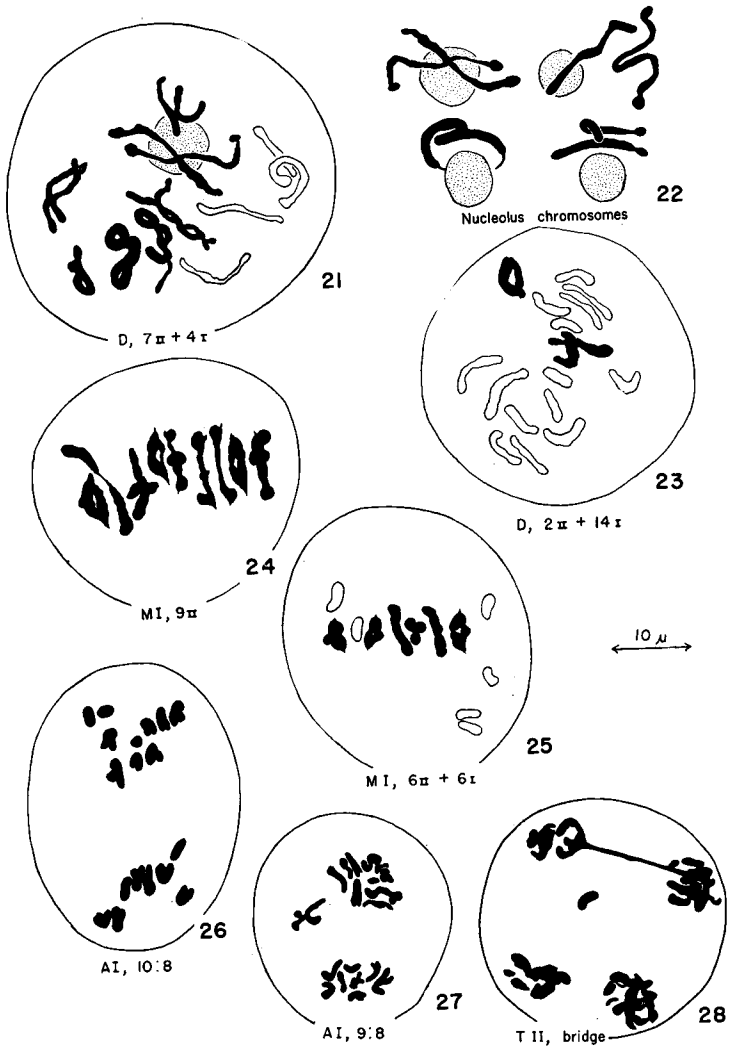
CYTOGENETICS OF THE HYBRIDS

Meiosis was studied in the F_1 hybrids and in the parental species by means of propiono-carminе squashes of pollen mother cells. The plants referred to in the following account were grown either in the experimental field or in 6 inch pots of



Figs. 11-14. Meiosis in F_1 of *angelensis* ($n=9$) \times *achilleaeifolia* ($n=9$). Figs. 15-20. Meiosis in F_1 of *clivorum* ($n=18$) \times *capitata staminea* ($n=9$). Fig. 17 shows an anaphase I cell with 11 chromosomes at each pole and 5 lagging chromosomes; figs. 14, 18 and 19 show chromatid bridges; fig. 20 shows a triad with a micronucleus.

good soil in the greenhouse. The cytological preparations were made permanent by infiltration of euparal in an alcohol vapor chamber (Bradley 1948). The chromosomes were drawn at bench level with a camera lucida; in metaphase and anaphase figures the chromosomes were sometimes spread apart slightly in drawing. The scale of the drawings is indicated in figs. 3 to 33 by the double arrow, which measures

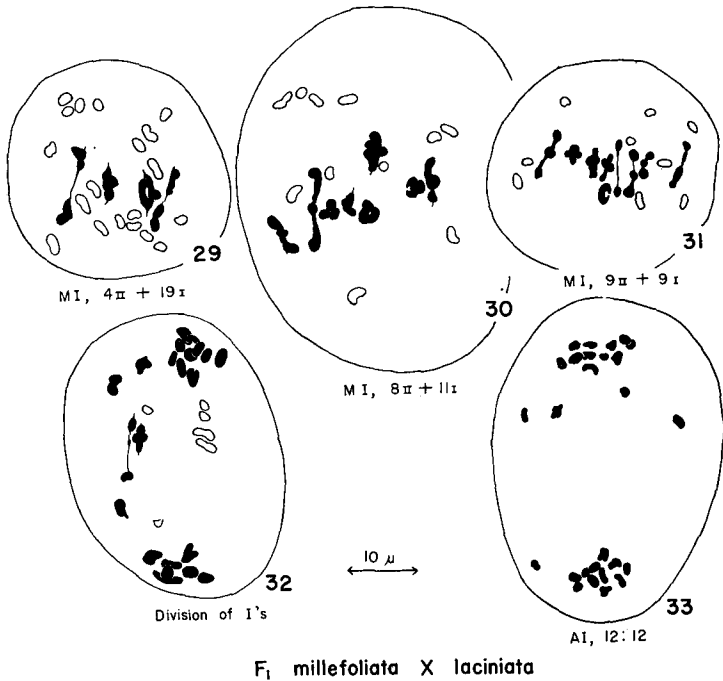


F₁ millefoliata X capitata chamissonis

Figs. 21-28. Meiosis in F₁ of *millefoliata* (n=9) X *capitata chamissonis* (n=9). Fig. 21 shows a cell in diakinesis with 7 bivalents containing 15 chiasmata; fig. 22 shows the same pair of nucleolus-organizing chromosomes as seen in different cells at diakinesis; fig. 27 shows a lagging chromosome in the process of division.

10 microns. The proportion of viable pollen produced by the hybrids and species was estimated from lactophenol mounts of the grains stained with aniline blue; the plump, well stained grains were counted as good, and the empty shrivelled grains as inviable.

Meiosis is normal in all the species. The chromosomes are regularly paired in bivalents at diakinesis and metaphase I; no univalents or multivalents have been seen in any species at this stage. At anaphase the chromosomes separate to the poles in an orderly manner; no lagging chromosomes or chromatid bridges have been found. The sporads contain four microspores and no micronuclei. A high proportion (95% or more as a rule) of normal pollen grains is formed. The species are uniformly fertile as to seeds. Meiosis is likewise essentially normal, and fertility is high, in the intraspecific hybrids, as reported in previous papers (parts I to V).



Figs. 29-33. Meiosis in F₁ of *millefoliata* (n=9) X *laciniata* (n=18). Fig. 32 shows an early anaphase with some chromosomes already at the poles, 2 bivalents still at the equatorial plate, and 3 univalents which have divided; fig. 33 shows a cell in anaphase I with 12 chromosomes at or near each pole and in addition 3 lagging chromosomes.

The interspecific hybrids, by contrast, have all exhibited marked irregularities at meiosis. The data on chromosome pairing and anaphase separation are summarized in tables 3 and 4 and illustrated in figures 3 to 33. Reference to table 3 shows that a varying number of bivalents and univalents was formed in all of the hybrids. The maximum possible number of bivalents was found most frequently in the two hybrids, *achilleaefolia* X *clivorum* and *clivorum* X *capitata*, whereas *angelensis* X *millefoliata*, with a modal number of 6-7 bivalents, and *angelensis* X *achilleae-*

TABLE 3. METAPHASE PAIRING IN F₁ HYBRIDS IN THE LEAFY-STEMMED GILIAS

Hybrid	Chromosome number	No. cells with a given no. bivalents										Total no. cells	Mean no. bivalents per cell
		9	8	7	6	5	4	3	2	1	0		
<i>angelensis</i> × <i>millefoliata</i>	18		6	23	22	13	3	1				68	6.2
<i>angelensis</i> × <i>achilleaeifolia</i>	18		1	4	11	20	15	8	3	1		63	4.6
<i>millefoliata</i> × <i>achilleaeifolia</i>	18	3	11	20	12	9						55	6.8
<i>achilleaeifolia</i> × <i>clivorum</i>	27	32	1									33	9.0
<i>clivorum</i> × <i>capitata</i>	27	18	32	22	11		1					114	8.0
<i>millefoliata</i> × <i>capitata</i>	18	22	40	37	19	11	3	2				134	7.2
<i>millefoliata</i> × <i>laciniata</i>	27	33	22	9	1	4	1		1			71	8.0

folia, with a modal number of 4-5 bivalents, had the least amount of bivalent formation.

Many of the bivalents were paired as closely in the hybrids as in the parental species. This observation is confirmed by data on chiasma frequencies in two of the hybrids and their respective parents. Thus in the F₁ of *millefoliata* × *capitata chamissonis* the mean number of chiasmata per bivalent was 1.83 at diakinesis and 1.18 at metaphase. This is less than the normal chiasma frequency of the *millefoliata* parent (2.30 and 1.85 at the two stages respectively), but close to that of the *chamissonis* parent (1.84 and 1.12 respectively). Similarly, the F₁ of *millefoliata* × *achilleaeifolia* had on the average 1.17 chiasmata per bivalent at metaphase, which is not significantly different from the average 1.16 chiasmata formed by the *achilleaeifolia* parent at this same stage.

A trivalent chain was seen at first metaphase in two cells in the hybrid of *angelensis* × *millefoliata*. A chain of four chromosomes was found in one prometaphase cell of *millefoliata* × *capitata chamissonis*. These configurations indicate that *G. millefoliata* is differentiated from *G. angelensis* and *G. capitata chamissonis* by a translocation.

TABLE 4. BEHAVIOR OF CHROMOSOMES AT ANAPHASE IN F₁ HYBRIDS IN THE LEAFY-STEMMED GILIAS

Hybrid	Per cent of cells with:			Chromatid bridges at: Anaphase I or II
	Lagging chomosomes or micronuclei at:			
	Anaphase I	Anaphase II	Sporad stage	
<i>angelensis</i> × <i>millefoliata</i>	28% (14 cells)	15% (13 cells)	47% (17 sporads)	0.0% (27 cells)
<i>angelensis</i> × <i>achilleaeifolia</i>	26 (27)	64 (11)	90 (39)	5.0 (38)
<i>millefoliata</i> × <i>achilleaeifolia</i>	27 (40)	96 (23)	87 (39)	3.2 (63)
<i>achilleaeifolia</i> × <i>clivorum</i>	57 (7)	100 (10)	100 (12)	0.0 (17)
<i>clivorum</i> × <i>capitata</i>	65 (161)	79 (119)	56 (115)	10.8 (120)
<i>millefoliata</i> × <i>capitata</i>	12 (87)	48 (40)	37 (123)	2.1 (140)
<i>millefoliata</i> × <i>laciniata</i>	39 (44)	100 (2)	55 (65)	0.0 (46)

The univalents were often associated in pairs at diakinesis, though not joined by chiasmata. Figure 23 shows a cell in prometaphase in the hybrid of *millefoliata* × *capitata chamissonis* with 7 unsynapsed "pairs" of chromosomes. In this same hybrid the nucleolus-organizing chromosomes were sometimes joined by a single chiasma, sometimes associated along their length but not connected, and sometimes unassociated (fig. 22).

The univalents frequently lagged as anaphase, so that with higher numbers of univalents and at later stages of meiosis the distributions of the chromosomes became increasingly irregular. Bridge configurations were found at both the first and second divisions in four of the hybrids, as many as three bridges being present in a single cell (fig. 19). In consequence of all these irregularities, most of the sporads contained either less than the normal four nuclei or else supernumerary micronuclei.

The number of stainable pollen grains produced by the hybrids was in all cases very low, ranging from 1.5% down to 0.5% of the total output of pollen. All of the hybrids were completely sterile. Forty luxuriant individuals of *millefoliata* × *achilleaeefolia* which were grown under conditions of open pollination in the experimental field set no seeds whatever on the diploid level after flowering freely for three and a half months. The hybrids of *millefoliata* × *laciniata* were similarly open pollinated by bees during three months without producing any seeds. The hybrids of *angelensis* × *millefoliata* were interplanted with the *angelensis* parent in the experimental field, where they bloomed for seven weeks without setting seeds.

The data on meiotic behavior in the interspecific hybrids suggest that one of the main causes of hybrid sterility in the Leafy-stemmed Gilias consists of structural rearrangements of the chromosomes which interfere with normal chromosome pairing and hence with the formation of well balanced gametes. It has been possible to demonstrate the existence of chromosomal sterility between two of the species, *G. millefoliata* and *G. achilleaeefolia*, by obtaining their allotetraploid derivative, which is characterized in general by full fertility and regular bivalent pairing (Grant 1952c). The existence of chromosomal sterility does not, however, necessarily mean that other types of hybrid sterility are absent. Analysis of the raw allotetraploid just mentioned reveals, indeed, a segregation for independent but closely associated systems of genic factors which bring about sterility of pollen and seeds respectively (see part V). Genic sterility is thus superimposed on chromosomal sterility. In addition, the segregating allotetraploids produce numerous dwarfish individuals and inviable recombinations, which bear witness to the presence of general disharmonies between the genotypes of the two species (op. cit.).

The intersectional hybrid between *G. achilleaeefolia* and *G. tenuiflora* performed quite differently from the intrasectional crosses. The two hybrid individuals were somewhat weak and never reached the stage of meiosis. They evidently suffered from some genotypic derangement which prevented the normal development of the sex organs.

The species of Leafy-stemmed *Gilia* are thus separated by chromosomal sterility and, in some cases at least, also by gametic genic sterility, while a species of Leafy-stemmed *Gilia* is separated from a species of Woolly-leaved *Gilia* by diplontic genic sterility.

GENOME ANALYSIS

The pairing data are summarized graphically in figure 1. The degree of chromosome pairing in the *angelensis-millefoliata-achilleaeefolia* triangle indicates that the three parental species possess essentially different genomes. The *capitata-millefoliata-achilleaeefolia* triangle is completed in a more indirect manner. Figure 1 shows that

although the hybrid between *G. capitata* and *G. achilleaefolia* has not been produced, the pairing relationships have been determined between these two species and *G. clivorum*. It has been established that the tetraploid *G. clivorum* contains genomes of *G. achilleaefolia* and *G. millefoliata* (part V). The triploid hybrid between *G. clivorum* and *G. achilleaefolia* exhibited the "Drosera" type of chromosome pairing, with the regular formation of 9 bivalents and 9 univalents. If the chromosomes of *G. capitata* were completely homologous with those of *G. achilleaefolia*, the triploid hybrid of *clivorum* \times *capitata* should also have had regular pairing in 9 bivalents. This was not the case. The hybrid of *G. clivorum* and *G. capitata* usually paired in less than 9 chromosomes of the complements and often formed chromatid bridges. The chromosomes of *G. capitata* cannot, therefore, be fully homologous with those of *G. achilleaefolia*. We can conclude that the three species, *G. capitata*, *G. millefoliata* and *G. achilleaefolia* possess different genomes between which only partial homology exists. The pairing in the triploid hybrid of *laciniata* \times *millefoliata*, resulting in 2 to 9 bivalents and 23 to 8 univalents, indicates that *G. laciniata* is not an autopolyploid. This species possesses two genomes, neither one of which is completely homologous with the *millefoliata* genome.

Some chromosome pairing occurs in all the hybrids, but complete pairing does not occur in any hybrid with the sole exception of the hybrid between *G. clivorum* and one of its diploid ancestors. The mean number of bivalents per cell ranges from 4.6 to 8.0. The chromosomes of the various species of Leafy-stemmed Gilia are therefore homologous in respect to some segments and non-homologous in others. A high degree of homology may exist between particular chromosomal segments in certain species as indicated by the fact that the hybrids form as many chiasmata per bivalent as one of their parents. But the genomes of the species, taken as a whole, are different.

These genomes seem to be differentiated in respect to a series of structural rearrangements, most of which are probably fairly small since the configurations indicative of gross structural hybridity are of rare occurrence in the F_1 s. Morphological differences exist between the somatic chromosomes of *G. tricolor*, *millefoliata*, *achilleaefolia* and *capitata* (Flory 1934, 1937; Grant, unpublished). As might be expected, therefore, heteromorphic bivalents are sometimes found in the interspecific hybrids (Grant 1952c). Nearly all the hybrids form occasional chromatid bridges at anaphase of meiosis, which indicate that the parental species differ by one or more paracentric inversions. One of the hybrids with a relatively low degree of pairing, *millefoliata* \times *achilleaefolia*, produced a fertile allotetraploid with regular bivalent pairing (part V). These facts justify the conclusion that the differentiation of the species has been accompanied by a repatterning of their chromosomes.

TAXONOMY

The section *Eugilia* consists of herbaceous annuals with blue-violet flowers borne in loose cymes, small glomerules or capitate heads; the stems are more or less leafy throughout their length, in distinction to some related sections which consist of rosette plants; and the herbage is frequently covered with coarse white hairs or minute stipitate glands. There are seven species on the Pacific slope of North America, mostly in cismontane California, and two or three species in temperate South America.

Bentham in his treatment of 1833 used the name *Eugilia* in approximately the same sense in which it is used here, that is, he included *G. tricolor*, *achilleaefolia*, *capitata*, *laciniata*, etc., in this section, while placing *G. tenuiflora* and other species in other sections of the genus. In his treatment of 1845, however, Bentham included

the extraneous elements *G. congesta*, *G. rigidula*, *G. crassifolia* and others in *Eugilia*. With the treatments of Gray (1886) and Brand (1907) the section *Eugilia* became even more unnatural. The Leafy-stemmed Gilias were once more defined as a natural group by Milliken (1904) and Mason and A. Grant (1948). But both Milliken and Mason and A. Grant referred them to the subgenus *Capitata*, reserving the name *Eugilia* for the related group of desert annuals which we have designated as the Woolly-leaved Gilias, viz. *G. tenuiflora* and its relatives. Since the first species of *Gilia* described, *G. laciniata* from Peru, is a Leafy-stemmed *Gilia* and not a Woolly-leaved *Gilia*, the correct name for the section to which it belongs is *Eugilia*. The name *Capitata* must therefore be regarded as a later synonym of *Eugilia*, and a suitable Latin name will have to be found for the Woolly-leaved Gilias.

The following key will facilitate identification of the species of *Eugilia*.

- A. Flowers in capitate heads (rarely in few-flowered glomerules or solitary); calyx composed of relatively narrow herbaceous bands and broad hyaline sinuses; corolla lobes mostly erect and ascending in living plants; corolla concolored; (*Gilia capitata* group)
- Heads globose, 25-100-flowered; stamens exserted. Widespread from Baja California to British Columbia but rare in South Coast Ranges. *G. capitata*
- Heads fan-shaped or inflorescence loosely cymose, 2-25-flowered; stamens included. South Coast Ranges. *G. achilleaeifolia*
- AA. Flowers solitary or in loose cymes or small glomerules; calyx composed of broad herbaceous bands and narrow hyaline sinuses; corolla lobes mostly rotately spreading in living plants; corolla con-, bi- or tri-colored.
- B. Corolla campanulate, the limb 5-14 mm. wide when pressed flat; style exserted, the stigmas raised well above the anthers; corolla deciduous after anthesis; (*Gilia tricolor* group).
- Corolla throat bearing 5 pairs of prominent purple spots, the limb blue-violet and tube bright yellow or orange; corolla 8-16 mm. long. Northern California south to Tehachapi Mts. *G. tricolor*
- Corolla throat not spotted, the limb white or pale violet and tube pale yellow; corolla 7-8 mm. long. Southern California. *G. engelensis*
- BB. Corolla funnellform, the limb 3-5 mm. wide when pressed flat; style included, the stigmas at or only slightly above the level of the anthers; corolla often persistent for awhile upon the ripening capsule; (*Gilia laciniata* group.)
- Corolla tube much longer than the throat or limb; leaves dissected into very narrow linear segments. Insular. *G. nevini*
- Corolla tube equal to throat or limb; leaf segments more or less broad. Mainland.
- Corolla throat usually with purple spots; capsules 25-50-seeded; peduncle much elongated in fruit. California and Oregon.
- Stems densely glandular; fruiting calyx 8-11 mm. long; pollen white; spots in corolla throat very dark and conspicuous. Coastal sand-dunes north of San Francisco Bay. *G. millefoliata*
- Stems floccose below, never densely glandular; fruiting calyx 5-6 mm. long; pollen blue (rarely white); spots in corolla throat moderately dark and inconspicuous. South Coast Ranges and coast south of San Francisco Bay *G. clivorum*
- Corolla throat lacking purple spots; capsules 20-25-seeded; peduncle very little elongated in fruit. Peru to Chile and Argentina. *G. laciniata* sens. lat.

SUMMARY

The Leafy-stemmed Gilias comprise a natural subdivision of the genus *Gilia* (section *Eugilia*, family Polemoniaceae), which has its primary center of distribution in California and a secondary center in temperate South America. The nine or ten species are all annual herbs which grow on loose sandy or rocky soils in open habitats. The prevailing mode of reproduction in the group is by a combination of cross-fertilization and selfing; several races of *G. capitata* are self-incompatible and

therefore entirely cross-breeding; *G. millefoliata*, *G. clivorum*, *G. laciniata* in part, and several races of *G. achilleaeifolia* are autogamous. The species are sexual, possess a normal meiotic cycle, and are predominantly diploid with $n=9$; two species, *G. clivorum* and *G. laciniata* (in part), are tetraploid with $n=18$.

Crosses between different strains of the same species are usually, though not invariably, successful, and the hybrids are nearly always vigorous and fertile. *Gilia millefoliata* ($n=9$) from the California coast crosses freely with *G. laciniata* ($n=18$) from the Peruvian coast. Crosses between the different North American species are very difficult to make. The strong incompatibility barriers may have evolved as mechanisms to enable the species to grow sympatrically.

In their morphological characters, the F_1 hybrids are intermediate between the parental species. Allotetraploid derivatives of one of the F_1 hybrids segregated into a continuous array of variations. These facts are consistent with the view that the morphological differences between the species are determined by multiple factors.

The interspecific hybrids are nearly always characterized by a pronounced reduction of chromosome pairing at meiosis. They are consequently highly sterile. Analysis of two hybrid triangles and one additional triplod hybrid reveals the existence of at least six different diploid genomes in the section. The chromosomal differences between the species apparently consist of a few gross paracentric inversions and reciprocal translocations and many small structural rearrangements.

LITERATURE CITED

- Bentham, G. 1833. *Eugilia*. Bot. Reg. 19, under table 1622.
- . 1845. *Eugilia*. in de Candolle, Prodrum systematis naturalis regni vegetabilis. Paris. 9: 311-313.
- Bradley, Muriel. 1948. A method for making aceto-carminic squashes permanent without removal of the cover slip. Stain Tech. 23: 41-44.
- Brand, A. 1907. *Eugilia*. in Engler, Das Pflanzenreich. Leipzig. 4. 250: 94-112.
- Flory, W. S. 1934. A cytological study on the genus *Phlox*. Cytologia 6: 1-18.
- . 1937. Chromosome numbers in the Polemoniaceae. Cytologia, Fujii Jub. Vol., 171-180.
- Grant, V. 1950. Genetic and taxonomic studies in *Gilia*. I. *Gilia capitata*. El Aliso 2: 239-316.
- . 1952a. idem. II. *Gilia capitata abrotanifolia*. El Aliso 2: 361-373.
- . 1952b. idem. III. The *Gilia tricolor* complex. El Aliso 2: 375-388.
- . 1954a. idem. IV. *Gilia achilleaeifolia*. El Aliso 3: 1-18.
- . 1954b. idem. V. *Gilia clivorum*. El Aliso 3: 19-34.
- . 1952c. Cytogenetics of the hybrid *Gilia millefoliata* \times *achilleaeifolia*. I. Variations in meiosis and polyploidy rate as affected by nutritional and genetic conditions. Chromosoma 5: 372-390.
- Gray, A. 1886. *Eugilia*. in Synoptical Flora of North America. 2nd ed., New York. 2(1): 146-149.
- Mason, H. L. and Grant, Alva. 1948. Some problems in the genus *Gilia*. Madroño 9: 201-220.
- Milliken, Jessie. 1904. A review of Californian Polemoniaceae. Univ. Calif. Publ. Bot. 2: 1-71.