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Verne Grant

Alva Grant

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GENETIC AND TAXONOMIC STUDIES IN GILIA

XI. FERTILITY RELATIONSHIPS OF THE DIPLOID COBWEBBY GILIAS[1]

VERNE GRANT AND ALVA GRANT

CONTENTS

TAXONOMIC BACKGROUND

The Cobwebby Gilias *(Gilia* sect. *Arachnion)* are small to moderately robust annual herbs which germinate in winter and bloom in the spring. The plants form colonial populations of small or large size, numbering in the hundreds or millions of individuals. They grow on open sandy ground in a variety of habitats in the southwestern deserts and mountains.

With respect to chromosome number the Cobwebby Gilias fall into three series: diploids (with n=9), tetraploids, and octoploids. The one octoploid and the 12 known tetraploid species do not concern us further here. The purpose of the present paper is to describe the results of hybridization experiments involving the 15 diploid species.

The classification of the group has been set forth in an earlier paper to which the reader is referred for the taxonomic details (Grant and Grant, 1956). The system of classification adopted in 1956 has served as a framework on which to hang the taxogenetic data gathered in the experimental phase of the investigation and summarized in the present paper.

Prior to 1956 the taxonomy of the large-flowered Cobwebby Gilias was in a chaotic state. The basic taxonomic units, the subspecies, had not been blocked out and their distribution areas had not been delimited. A few widely accepted Latin names like "*Gilia tenuiflora*" and "*G. davyi*" were being applied indiscriminately to many different taxa. Some taxa were known by two or more names and other common entities remained undescribed. The task of linking up the subspecies into polytypic species had not been carried out. These and

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[1] The work described in this paper has been carried out since 1950 at the Rancho Santa Ana Botanic Garden. It was greatly facilitated from 1954 to 1957 by a research grant from the National Science Foundation. Valuable technical assistance was given by Mr. Richard Beeks and Dr. Howard Latimer. The charts were drawn by Mr. Richard Beasley.

other purposes were accomplished in the revision of 1956, which paved the way for a biosystematic analysis of the group.

The experimental studies have indicated further modifications in the system of classification, as was to be expected. For reasons which will appear later in this paper, the taxon we described as *Gilia leptantha vivida* should be transferred to *G. ochroleuca* and becomes *G. o. vivida.* A larger number of species is now recognized. For example, the southern race of *G. ochroleuca,* namely *G. o. exilis,* should be separated from the northern races as a distinct species, *G. exilis. Gilia austrooccidentalis, G. clokeyi* and *G. interior,* previously treated in the rank of subspecies, are now regarded as species, and *Gilia jacens* is newly described.

Certain species relationships have become evident. Thus *Gilia diegensis,* previously placed close to *G. latiflora,* is now transferred to the *Gilia brecciarum* group. *Gilia latiflora* is transferred to the *Gilia tenuiflora* group. Fairly close relationships have been discovered between *Gilia tenuiflora* and some of the reduced entities such as *G. interior* and *G. jacens.*

These and other results of the biosystematic investigation of the diploid Cobwebby Gilias are embodied in the revised classification system set forth in Table 1.

TABLE 1. SYSTEM OF CLASSIFICATION OF THE DIPLOID COBWEBBY GILIAS

I. GILIA OCHROLEUCA GROUP
    1. *Gilia ochroleuca* Jones. 3 subspecies: *bizonata, vivida, ochroleuca.*
    2. *Gilia exilis* (Gray) Abrams.
    3. *Gilia cana* (Jones) Heller. 5 subspecies: *cana, speciosa, bernardina, speciformis, triceps.*
    4. *Gilia mexicana* A. & V. Grant.
    5. *Gilia clokeyi* Mason.
    6. *Gilia aliquanta* A. & V. Grant. 2 subspecies: *aliquanta, breviloba.*

II. GILIA TENUIFLORA GROUP
    7. *Gilia tenuiflora* Bentham. 4 subspecies: *tenuiflora, arenaria, amplifaucalis, hoffmani.*
    8. *Gilia leptantha* Parish. 5 subspecies: *leptantha, purpusii, transversa, pinetorum, salticola.*
    9. *Gilia latiflora* Gray. 6 subspecies: *cuyamensis, latiflora, davyi, excellens, elongata, cosana.*
    10. *Gilia interior* (Mason & A. Grant) A. Grant.
    11. *Gilia austrooccidentalis* A. & V. Grant.
    12. *Gilia minor* A. & V. Grant.
    13. *Gilia jacens* A. & V. Grant.

III. GILIA BRECCIARUM GROUP
    14. *Gilia brecciarum* Jones. 3 subspecies: *brecciarum, neglecta, argusana.*
    15. *Gilia diegensis* (Munz) A. & V. Grant.

TAXONOMIC AND NOMENCLATURAL CHANGES

It is necessary to make several formal changes in the taxonomy of the diploid Cobwebby Gilias in order to make the classification of these plants consistent with the experimental findings.

A new diploid species was discovered in the southwestern desert area after the appearance of the revision of 1956. Though infrequent in herbarium collections, it was found to have a wide and natural distribution area from the Inyo Mts. of California to New Mexico. The name *Gilia clokeyi* described by Mason for an etiolated plant from the Charleston Mts. is applicable to this entity. In our revision (Aliso 3: 260) we had taken up this name for a subspecies of the tetraploid species *G. ophthalmoides* and had included in it several taxa which later field and herbarium studies have shown do not belong together. A revised description of *Gilia clokeyi* is given below.

GILIA CLOKEYI Mason
Madroño 6: 202, 1942.

Gilia ophthalmoides ssp. *clokeyi* A. & V. Grant, Aliso 3: 260, 1956, as to name but not as to concept or specimens cited.

Description.—Erect and often much branched annual. Basal leaves with narrow rachis, lateral lobes diverging at right angles from rachis. Pedicels of inflorescence arching out at a wide angle. Calyx not glandular, sometimes cobwebby, the lobes acute, sinus full and slightly keeled near base, tips of lobes red; calyx in fruit usually a little shorter than capsule, splitting to below middle. Corolla 3.5 to 5 mm. long with full throat, tube and lower throat yellow, upper throat white, lobes white to pale blue, tube included in calyx. Stamens well exserted, pollen white or very pale blue. Capsule ovate, full and round in lower half, narrowing strongly above, splitting the full length in dehiscing, the valves detaching easily. n=9.

Type.—*I. W. Clokey 8599,* north base of limestone ledge, 1200 m, Charleston Mts., Clark Co., Nevada, March 31, 1940. Univ. of California Herbarium 937,325.

Range.—Lower slopes of desert mountains below the pinyon zone and in the washes. Eastern California (Inyo and San Bernardino cos.), through southern Nevada (Clark Co.), in the southern half of Utah (Washington, Grand and San Juan cos.), northern Arizona (Mohave and Navajo cos.), to northwestern New Mexico (San Juan Co.). 1700 to 6200 ft. elevation. Flowering in April and May.

Note.—*Gilia clokeyi* is easily confused with *G. ophthalmoides,* but the two species may be distinguished by several characters, of which the following are most reliable. Corolla 3.5 to 5 mm. long, and corolla tube included in the calyx in *G. clokeyi;* corolla usually longer than 5 mm., and tube exserted from calyx in *G. ophthalmoides.* Corolla throat pale yellow below, white above in *G. clokeyi;* throat bright yellow in upper part in *G. ophthalmoides. Gilia clokeyi* is diploid and *G. ophthalmoides tetraploid.* The former occurs below the pinyon zone and the latter in the pinyon zone.

Representative Specimens.—CALIFORNIA: east side of Westgard Pass, Inyo Co., *V. & A. Grant 9836.* Kingston Mts., San Bernardino Co., *C. L. Hitchcock 6153.* NEVADA: Kyle Canyon, Charleston Mts., Clark Co., *I. W. Clokey 7639, E. K. Balls & R. Straw 19251, 19253-A, 19270, 19309, V. & A. Grant 9950.* UTAH: Mexican Hat, San Juan Co., *V. & A. Grant 10154.* La Sal Mts., San Juan Co., *V. & A. Grant 10152.* South of Hurricane, Washington Co., *F. W. Gould 1687.* ARIZONA: Mesquite to Littlefield, Mohave Co., *T. H. Kearney & R. H. Peebles 13202.* West of Beaver Dam, Mohave Co., *V. & A. Grant 9965.* NEW MEXICO: Shiprock to Farmington, San Juan Co., *V. & A. Grant 10140.* North of Farmington, San Juan Co., *V. & A. Grant 10141.*

A second new diploid species known from the inner South Coast Ranges of California is described here as *Gilia jacens.* The plants now referred to this species were included with misgivings in *Gilia brecciarum brecciarum* in the revision of 1956 (Aliso 3: 282-283).

Gilia jacens A. & V. Grant, sp. nov.

Description.—Low annual with spreading decumbent stems. Cobwebby pubescence rather dense on leaves and stems. Leaves deeply dissected, tending to be bipinnate, cauline leaves relatively well developed. Inflorescence glomerate. Calyx very pubescent, glandular or cobwebby, lobes and sinuses often purplish. Corolla slender, funnelform, 5-7 mm. long, deep violet with purple tube. n=9.

Herba annua brevis, ramis decumbentibus, pube foliorum ramarum et calycium dense araneoso-lanata, inflorescentia glomerata, corolla tenue 5-7 mm. longa obscuro-violacea.

Type.—*V. Grant 9980.* Valley between Stauffer Junction and Mt. Pinos, near Kern-Ventura county line, California, April 28, 1957. Rancho Santa Ana Botanic Garden Herbarium 111,283.

Range.—Sandy places in sagebrush, pinyon, scrub oak, and blue oak zones in inner South Coast Ranges, Kern Co. to northern Santa Barbara and Ventura cos., California. 3500 to 7000 ft. elevation. Flowering in April and May.

Note.—*Gilia jacens* resembles *G. brecciarum brecciarum* in habit of branching and flower size, *G. tenuiflora* in flower shape and color, and *G. leptantha* in leaf dissection. It may be distinguished from *G. brecciarum* and *G. leptantha* by the slender form and deep violet to purple color of the corollas and from *G. tenuiflora* by the smaller size of the corollas and the spreading habit of branching.

Representative Specimens.—CALIFORNIA: Ballinger Canyon, Cuyama Valley, Santa Barbara Co., *V. Grant 9365-4, 2682.* Ybarra Canyon, Temblor Mts., Kern Co., *E. C. Twisselmann 1973.*

Two other diploid taxa previously treated as subspecies of *Gilia inconspicua* are now regarded as separate species. These are *Gilia interior* and *G. austrooccidentalis.* For descriptions and ranges see Aliso 3: 253 and 254. The nomenclatural change elevating *interior* to species rank has been made (by A. Grant, *in* V. Grant, Natural History of the Phlox Family, 80, 1959). The new combination for *austrooccidentalis* is proposed here.

Gilia austrooccidentalis A. & V. Grant, comb. nov.

Gilia inconspicua ssp. *austrooccidentalis* A. & V. Grant, Aliso 3: 254, 1956.

The taxon *vivida,* described by us as a subspecies of *G. leptantha,* should be transferred to *G. ochroleuca.*

Gilia ochroleuca ssp. **vivida** A. & V. Grant, comb. nov.

Gilia leptantha ssp. *vivida* A. & V. Grant, Aliso 3: 238, 1956.

NEW CHROMOSOME COUNTS

No chromosome counts have been published for *Gilia mexicana* or *G. clokeyi* heretofore. It is desirable to place these on record here along with additional counts from new localities for three other small-flowered diploid species.

Gilia mexicana. n=9.
  Madera Canyon, Santa Rita Mts., Santa Cruz Co., Arizona; *V. Grant 9915, 9916.*
  Nogales to Patagonia, Santa Cruz Co., Arizona; *V. Grant 9920.*
Gilia clokeyi. n=9.
  Deep Springs, Inyo Co., California; *V. & A. Grant 9836.*
  Kyle Fan, Charleston Mts., Clark Co., Nevada; *V. & A. Grant 9950.*
  Mexican Hat, San Juan Co., Utah; *V. & A. Grant 10,154.*
Gilia minor. n=9.
  Aquila, Maricopa Co., Arizona; *V. & A. Grant 10,061-A, 10,061-B.*
Gilia austrooccidentalis. n=9.
  Simmler, San Luis Obispo Co., California; *Clare Hardham 3154.*
Gilia aliquanta. n=9.
  Plateau east of Leadfield, Nye Co., Nevada; *V. Grant 10,100.*

It should be noted that *Gilia jacens* from Ballinger Canyon, Santa Barbara Co., California *(V. Grant 2682)* is also diploid with n=9. This count was previously reported under the name *G. brecciarum brecciarum* in which this population was formerly included (Grant, Beeks and Latimer 1956).

BREEDING SYSTEMS

The diploid Cobwebby Gilias may be divided into two broad groups on the basis of their breeding system: the outcrossers and the inbreeders. The first group consists of the taxa with large showy flowers in which the stamens ripen ahead of the styles and on a different level. Most of the large-flowered Cobwebby Gilias are self-compatible, and although cross-pollination is promoted by the floral mechanism, self-pollination may occur too, especially toward the end of the blooming period. The plants are thus facultative rather than exclusive outcrossers. Self-incompatibility is of rare occurrence, being known only in some strains of *G. latiflora latiflora* and *G. latiflora excellens,* which are consequently obligate outcrossers. The cross-fertilizing Cobwebby Gilias are *G. ochroleuca* (except *G. o. ochroleuca*), *G. exilis, G. cana, G. tenuiflora, G. leptantha, G. latiflora, G. brecciarum* (except *G. b. brecciarum*), and *G. diegensis* (in part).

The second type of breeding system is found in the Cobwebby Gilias with small and inconspicuous flowers in which the stamens and styles ripen simultaneously and on the same level. Self-pollination occurs automatically in the early stage of flowering and accounts for most or even all of the seed output. The autogamous diploid Cobwebby Gilias are *Gilia ochroleuca ochroleuca, G. mexicana, G. clokeyi, G. aliquanta, G. interior, G. austrooccidentalis, G. minor, G. jacens, G. brecciarum brecciarum,* and some strains of *G. diegensis.*

It is not possible to draw a hard and fast line between the outcrossing and the inbreeding groups. *Gilia tenuiflora tenuiflora* and *G. diegensis* are somewhat intermediate between the two groups insofar as they have an intermediate and variable amount of cross-pollination. Among the autogamous species *Gilia aliquanta* has a higher rate of natural crossing than *G. clokeyi* or *G. mexicana.* In certain polymorphic populations of *G. leptantha leptantha* and *G. cana triceps* autogamous biotypes occur alongside outcrossing biotypes. *Gilia ochroleuca* and *G. brecciarum* consist of outcrossing races and inbreeding races. Most of the complicated facts can, however, be summarized both accurately and conveniently by the statement that eight species of diploid Cobwebby Gilia are predominantly cross-fertilizing and seven others are autogamous.

MATERIALS AND METHODS

Forty-six strains belonging to 15 species of diploid Cobwebby Gilias were intercrossed in 133 combinations, 67 of which led to the production of F_1 hybrids. In all, 2694 flowers were pollinated in crosses within and between the diploid species. The relationships of the diploid Cobwebby Gilias with the Leafy-stemmed Gilias and Woodland Gilias were investigated by cross-pollinating 528 flowers in 41 combinations, of which one was successful. Three species of Cobwebby Gilias, six of Leafy-stemmed Gilias, and three species of Woodland Gilias were used in the intersectional crosses. In all, 58 strains belonging to 24 species were intercrossed, 3222 flowers were artificially pollinated, 174 hybrid combinations attempted, and 68 types of F_1 hybrids produced and analyzed.

The plants were derived from seeds collected in the wild. A list of the taxa and strains employed in the hybridizations is given in Table 2. The map locations of the parental populations of these strains in California and Nevada are shown in Figure 1. Not shown on this map are two accessions from Arizona, one from the west central part of that state (*G. minor,* Wickenburg), and the other from the southeastern corner (*G. mexicana).*

The artificial cross-pollinations were made in an insect-free screenhouse. The normal precautions were taken to guard against contamination of cultures through mixing of pollen or seeds. The F_1 hybrids were scored for vigor, morphological characters, pollen fertility, and seed fertility. The extent of chromosome pairing and the subsequent course of meiosis were determined from examination of squashes of pollen mother cells. The vigor and in some cases the character segregation and fertility of the F_2 generations were recorded.

In summarizing the results in the various tables we have identified the strain of a given taxon by the first letter of its geographical source. Thus *Gilia clokeyi* from Deep Springs is designated as "*clokeyi* D" and *G. clokeyi* from Kyle Canyon as "*clokeyi* K." In cases where only one strain of a taxon was used no designation other than the taxonomic name is necessary.

CROSSABILITY

The ease of crossing of the taxa can be estimated in a general way from the number of hybrid individuals or hybrid seeds derived from a given number of flowers emasculated and cross-pollinated. The relevant figures are present in Table 3. Unfortunately an exact quantitative index cannot be derived from these data because of certain gaps in our information. The ratio of hybrid individuals to flowers pollinated is not entirely reliable because the germination of the seeds, hybrid or parental alike, is low. The germination percentage ranges from 1 to 25% for different desert strains and from 6 to 38% for different cismontane strains. The germination is also erratic from year to year. For example we obtained good seed germination with *G. ochroleuca ochroleuca* and *G. minor* in the winter of 1957-1958 and poor germination from the same seed lots in the slightly different winter of

1958-1959. Under these conditions of low and variable germination, which are apparently inherent in the Cobwebby Gilia populations themselves, the number of hybrid seedlings obtained from a given number of artificially pollinated flowers is not a precise measure of the crossability.

The number of apparently sound seeds produced per flower is a safer, but still not wholly reliable criterion. Seeds containing a viable embryo can usually be distinguished by their external appearance from inviable seeds, the former being plump and the latter shriveled. However, we have had cases of apparently good seeds resulting from hybrid crosses which have not germinated at all although the controls gave good germination; being small, they could not be recovered from the seed-bed for dissection and examination of the embryo. Other crosses yield seeds which range in a continuous series from obviously sound to obviously abortive, so that the dividing line between viability and inviability cannot be determined by inspection.

FIG. 1. Map localities of strains used in hybridizing. For identification of letters see Table 2.

The result of these and other conditions is that minor differences in the degree of crossability are obscured by experimental errors in the present study. Our data do, however, reveal marked differences in crossing behavior when comparisons are made on a broader scale. We cannot safely distinguish fine differences in the compatibility relationships of different combinations of subspecies. But we can know that a subspecies crosses much more easily with another subspecies in the same species than it does with a member of a different species group.

The ease of crossing of different biotypes in the same population was tested in four cases. Two forms of *G. latiflora davyi* from Mojave were crossed in 1950; 23 flowers when cross-

TABLE 2. LIST OF TAXA AND STRAINS USED IN HYBRIDIZATIONS.

All localities are in California unless otherwise specified. Collection numbers are those of the authors unless specified otherwise and refer to specimens in the Rancho Santa Ana Botanic Garden herbarium. The letters in parentheses refer to map localities in Figure 1.

G. aliquanta:
    G. a. aliquanta, Red Rock Canyon, Kern Co. (9117) (A)
G. austrooccidentalis: Ballinger Canyon, Cuyama Valley, Santa Barbara Co. (9364-B, 9365-2, 9365-3) (B)
G. brecciarum:
    G. b. argusana, Randsburg, El Paso Mts., Kern Co. (9358) (C)
        Homewood Canyon, Argus Mts., Inyo Co. (9347) (D)
    G. b. brecciarum, Mt. Pinos, Ventura Co. (9409) (E)
    G. b. neglecta, Short Canyon, Mojave Desert, Kern Co. (9335) (F)
        Olancha Canyon, Sierra Nevada, Inyo Co. (9355) (G)
G. cana:
    G. c. cana, Rock Creek, Sierra Nevada, Mono Co. (9249) (H)
    G. c. speciosa, Short Canyon, Mojave Desert, Kern Co. (8860) (F)
    G. c. triceps, Homewood Canyon, Argus Mts., Inyo Co. (9344) (D)
        Wildrose Station, Argus Mts., Inyo Co. (I)
        China Lake, Mojave Desert, San Bernardino Co. (9341) (J)
        Panamint Mts., Inyo Co. (K)
G. clokeyi: Deep Springs east of Westgard Pass, Inyo Co. (9836) (L)
        Bradbury Wells, Death Valley, Inyo Co. (10,105) (M)
        Kyle Canyon, Charleston Mts., Clark Co., Nevada (9950) (N)
G. diegensis: Cuyamaca Mts., San Diego Co. (9225, 9227) (O)
        Anza junction, Riverside Co. (9234, 9235, 9236) (P)
        Temecula, Riverside Co. (9316) (Q)
        Santa Rosa Mt., Riverside Co. (R)
G. exilis: Dripping Springs, Riverside Co. (9317) (S)
        Fulmor Lake, San Jacinto Mts., Riverside Co. (16107) (T)
        Whitewater Canyon, Colorado Desert, Riverside Co. (9031) (U)
G. interior: Kern Valley, Sierra Nevada, Kern Co. (9110, 9112) (V)
        Democrat Springs, Kern Canyon, Kern Co. (8465) (W)
G. jacens: Ballinger Canyon, Cuyama Valley, Santa Barbara Co. (9365-4) (B)
G. latiflora:
    G. l. cuyamensis, Lockwood Valley, Ventura Co. (9420) (X)
    G. l. davyi, Mojave, Mojave Desert, Los Angeles Co. (Y)
        Gorman, Los Angeles Co. (9578) (Z)
    G. l. elongata, Red Rock Canyon, Kern Co. (A)
    G. l. excellens, Johannesburg, El Paso Mts., Kern Co. (9221) (C)
    G. l. latiflora, Apple Valley, Mojave Desert, San Bernardino Co. (RSABG 20683) (A′)
        Adelanto, Mojave Desert, San Bernardino Co. (8663) (B′)
G. leptantha:
    G. l. leptantha, Santa Ana River, San Bernardino Mts., San Bernardino Co. (9155) (C′)
    G. l. pinetorum, Mt. Pinos, Ventura Co. (16047, 16052) (E)
    G. l. purpusii, Kern River near Johnsondale, Sierra Nevada, Tulare Co. (9264) (D′)
        Isabella, Sierra Nevada, Tulare Co. (9220) (V)
    G. l. transversa, Cajon Pass, San Bernardino Co. (9385) (E′)
G. mexicana: Santa Rita Mts., Pima Co., Arizona (9915)
G. minor: Kramer junction, Mojave Desert, San Bernardino Co. (8851) (F′)
        Ballinger Canyon, Cuyama Valley, Santa Barbara Co. (9364-2, 9364-3, 9369-1, 9369-4) (B)
        Wickenburg, Maricopa Co., Arizona (9298)
G. ochroleuca:
    G. o. bizonata, Stauffer junction, Mt. Pinos, Ventura Co. (16040) (E)
    G. o. ochroleuca, Inyokern, Mojave Desert, Kern Co. (8858) (F)
    G. o. vivida, Big Pines, San Gabriel Mts., Los Angeles Co. (16055) (G′)
G. tenuiflora:
    G. t. tenuiflora, Arroyo Seco, Monterey Co. (Stebbins 3945) (H′)

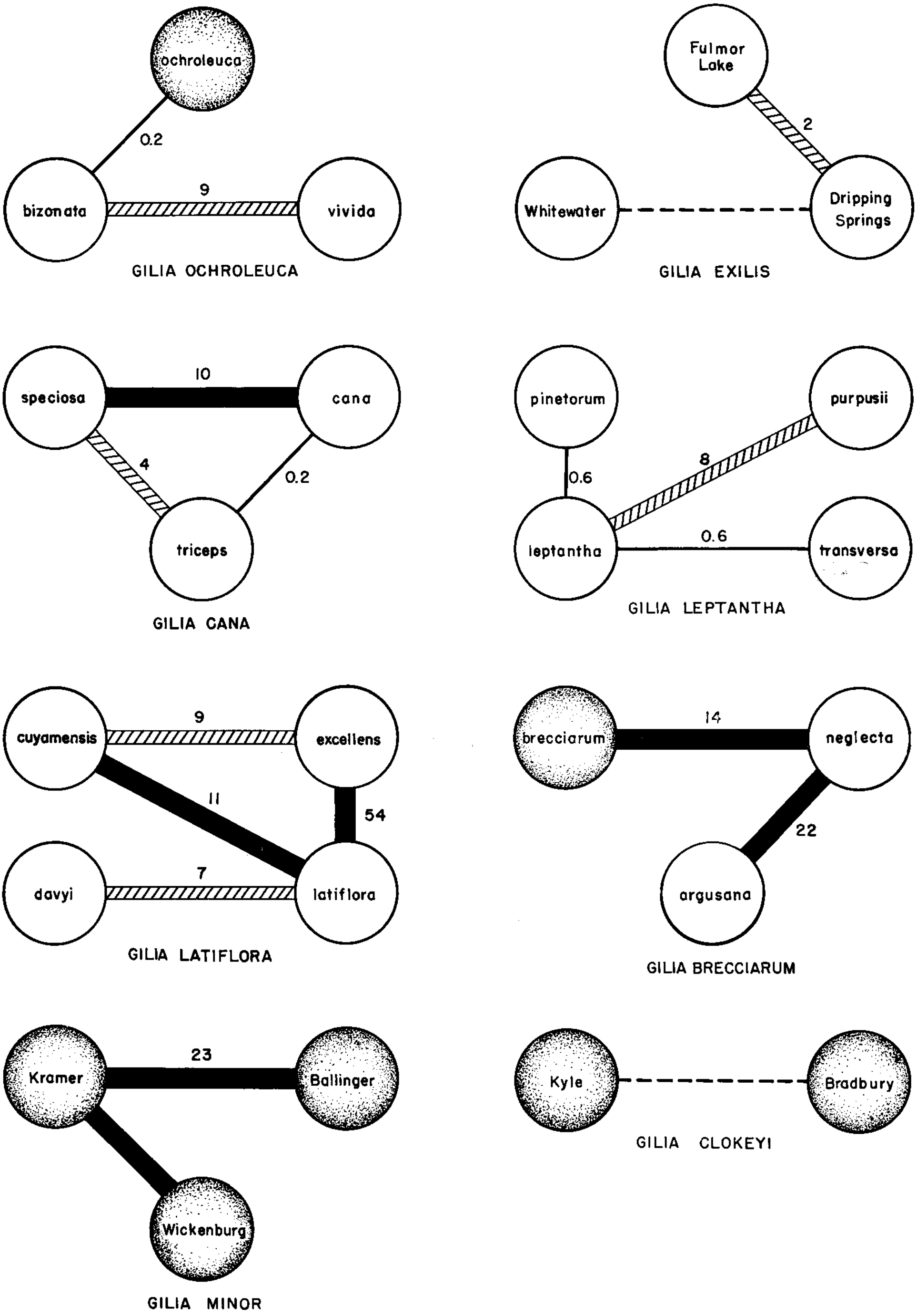

Fig. 2. Crossability of races. For explanation of symbols see Figure 3.

TABLE 3. CROSSABILITY.

Cross (♀ *parent listed first*)	*No. flowers pollinated*	*No. capsules set*	*No. abortive seeds*	*No. plump seeds*	*No.* F_1 *individuals*
I. CROSSES BETWEEN BIOTYPES OF THE SAME POPULATION					
G. exilis Dripping	7	7		89	43
G. latiflora davyi Mojave	23	23		610	∞
G. minor Ballinger	39	39	0	698	43*
G. austrooccidentalis Ballinger	47	40	few	674	40*
II. CROSSES BETWEEN RACES					
1. Gilia ochroleuca					
bizonata × vivida	6	2		21	15
vivida × bizonata	21	21		216	0
ochroleuca × bizonata	19	8	∞	2	1
bizonata × ochroleuca	10	1		4	0
2. Gilia exilis					
Whitewater × Dripping II	9	5	few	0	0
Fulmor × Dripping II	5	5		13	5
Dripping I & II × Fulmor	15	?		31	6
3. Gilia clokeyi					
Kyle × Bradbury	14	12	few	0	0
4. Gilia cana					
speciosa × cana	15	12		152	2
cana × triceps H	40	3		9	0
triceps H × speciosa	5	5	few	22	3
5. Gilia leptantha					
pinetorum × leptantha	16	12	39	9	1
leptantha × purpusii K	40	40		333	11
transversa × leptantha	12	9	few	24	2
leptantha × transversa	25	0		0	0
6. Gilia latiflora					
cuyamensis × excellens	35	29		330	0
cuyamensis × latiflora Ap	30	28		340	15
latiflora Ap × davyi M	2	1		23	9
davyi M × latiflora Ap	6	6	128	32	9
excellens × latiflora Ad	10	10		600	33*
latiflora Ad × excellens	57	57		2985	19*
7. Gilia minor					
Kramer × Ballinger	45	45	0	1055	48*
Kramer × Wickenburg	22	21	0	262	13
8. Gilia brecciarum					
brecciarum × neglecta S	21	20	0	288	39
argusana A × neglecta S	47	44	0	1011	19*
neglecta O × argusana R	35	32	0	784	61*
III. CROSSES BETWEEN SPECIES					
1. Gilia ochroleuca, exilis, and cana					
ochroleuca bizonata × exilis D I	24	23	∞	0	0
ochroleuca bizonata × exilis D II	22	21	∞	47	13
ochroleuca ochroleuca × exilis W	19	14	∞	?	19
ochroleuca bizonata × cana speciosa	29	10	5	54	14

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*from 350 seeds sown.

Cross (♀ *parent listed first*)	*No. flowers pollinated*	*No capsules set*	*No. abortive seeds*	*No. plump seeds*	*No. F_1 individuals*
ochroleuca ochroleuca × cana speciosa	25	18	few	1	0
ochroleuca vivida × cana triceps H	21	9	4	27	0
ochroleuca vivida × cana triceps C	34	12	few	23	0
cana triceps W × ochroleuca vivida	19	16	∞	23	1
exilis D II × cana triceps H	7	7		58	0
exilis D II × cana triceps C	16	10		54	0
2. Gilia tenuiflora, latiflora, and leptantha					
leptantha pinetorum × latiflora cuyamensis	39	32		496	several*
latiflora davyi M × tenuiflora	7	7		93	12
tenuiflora × latiflora davyi M	11	10		148	3
tenuiflora × latiflora davyi G	34	31		349	25
leptantha leptantha × latiflora latiflora Ap	24	24	few	160	10
latiflora latiflora Ap × leptantha leptantha	22	c.13	∞	98	19
latiflora latiflora Ap × leptantha pinetorum	12	8		90	9
leptantha pinetorum × latiflora latiflora Ap	22	c.16		136	1
latiflora latiflora Ap × leptantha purpusii K	17	0		0	0
tenuiflora × leptantha leptantha	29	?	∞	130	2
leptantha leptantha × tenuiflora	12	4		10	1
leptantha pinetorum × tenuiflora	12	0		0	0
tenuiflora × leptantha pinetorum	19	17		264	15
tenuiflora × leptantha purpusii K	20	19	∞	102	5
3. Gilia ochroleuca × G. tenuiflora, latiflora, and leptantha					
ochroleuca ochroleuca × latiflora elongata	8	2	4	1	0
latiflora latiflora Ap × ochroleuca bizonata	6	0	0	0	0
ochroleuca bizonata × latiflora latiflora Ap					
1951	16	0		0	0
1952	20	4	5	29	3
1956	20	14	∞	14	14
ochroleuca ochroleuca × latiflora latiflora Ap					
1951	4	4		7	0
1956	47	37	∞	0	0
ochroleuca bizonata × leptantha purpusii K	23	10		27	24
ochroleuca ochroleuca × leptantha purpusii K	22	10	few	5	0
ochroleuca bizonata × tenuiflora, 1951	23	0		0	0
1952	25	11	6	9	6
tenuiflora × ochroleuca bizonata	21	14	∞	18	1
ochroleuca ochroleuca × tenuiflora	3	1		1	0
leptantha pinetorum × ochroleuca vivida	39	15	∞	4	1
ochroleuca vivida × leptantha pinetorum	29	15	45	25	0
ochroleuca vivida × latiflora latiflora Ap, 1951	15	0		0	0
1952	24	9	27	36	0
4. Gilia cana, and exilis × G. tenuiflora, latiflora, and leptantha					
cana cana × leptantha purpusii K	40	25		105	4
latiflora davyi M × cana speciosa	10	?	∞	196	0
latiflora latiflora Ap × cana speciosa	4	4		69	1
cana speciosa × leptantha purpusii I	3	1		2	0
cana speciosa × leptantha purpusii K	5	2		3	1
tenuiflora × cana speciosa, 1950	5	4		69	0
1953	26	26	14	472	10
latiflora davyi M × cana triceps P	13	13	∞	30	0
latiflora elongata × cana speciosa	24	22	∞	0	0
exilis W × latiflora latiflora Ap	2	2		4	0
5. Gilia mexicana, clokeyi, and aliquanta					
clokeyi D × aliquanta	16	7	0	17	1
clokeyi D × mexicana	2	2	0	19	3
mexicana × aliquanta	22	7	0	51	0

Cross (♀ *parent listed first*)	*No. flowers pollinated*	*No. capsules set*	*No. abortive seeds*	*No. plump seeds*	*No.* F_1 *individuals*
6. Gilia ochroleuca, exilis, and cana × G. mexicana, clokeyi, and aliquanta					
aliquanta × ochroleuca bizonata	19	17	∞	0	0
ochroleuca bizonata × aliquanta	9	0	0	0	0
ochroleuca ochroleuca × aliquanta	23	15	0	19	0
exilis W × aliquanta	21	1		4	0
clokeyi K × ochroleuca ochroleuca	22	17	some	121	16
mexicana × ochroleuca ochroleuca	15	10	few	174	1
mexicana × exilis D	21	15	few	0	0
7. Gilia interior, austrooccidentalis, jacens, and minor					
minor K × interior D	2	1	0	0	0
minor K × interior K	19	12	∞	0	0
minor W × interior K	28	28	∞	3	0
minor B × jacens	6	0		0	0
minor K × jacens	40	40	∞	3	0
minor B × austrooccidentalis	54	54	∞	74	0
minor K × austrooccidentalis	50	50	0	452	20*
austrooccidentalis × jacens	46	42	0	518	140*
8. Gilia tenuiflora, latiflora, and leptantha × G. interior, austrooccidentalis, jacens, minor, and aliquanta					
austrooccidentalis × tenuiflora	28	?		233	82
jacens × tenuiflora	29	28		227	48
interior D × tenuiflora	8	8	21	25	21
interior K × tenuiflora	13	11	∞	17	7
minor K × tenuiflora	8	10	∞	2	0
minor B × tenuiflora	24	21	∞	4	0
interior K × latiflora latiflora Ap	18	16	∞	0	0
minor K × latiflora latiflora Ap	6	5	∞	0	0
aliquanta × latiflora latiflora Ap, 1953	14	15	few	0	0
1954	35	28	∞	26	0
aliquanta × leptantha purpusii K	22	14	few	0	0
9. Gilia ochroleuca, exilis, and cana × G. interior, austrooccidentalis, jacens, and minor					
minor K × ochroleuca ochroleuca	6	5	0	44	1
ochroleuca ochroleuca × minor K	4	2		18	0
ochroleuca ochroleuca × minor W	19	15	93	1	0
interior K × cana speciosa	24	21	∞	0	0
10. Gilia mexicana, clokeyi, and aliquanta × G. interior, austrooccidentalis, jacens, and minor					
interior K × aliquanta	18	9	∞	8	0
clokeyi D × minor K	6	5	0	44	2
minor K × clokeyi D	7	7	0	70	2
minor K × mexicana	3	3	0	7	2
clokeyi K × interior K	17	17	few	0	0
11. Gilia diegensis × G. brecciarum					
diegensis T × brecciarum brecciarum	48	40		772	6*
12. Gilia diegensis, and brecciarum × G. ochroleuca, exilis, and cana					
ochroleuca ochroleuca × brecciarum neglecta S	4	4		6	0
diegensis C × exilis D II	23	22	∞	62	2
brecciarum neglecta S × cana speciosa, 1951	24	22	∞	28	0
1954	38	36	∞	7	1
13. Gilia diegensis, and brecciarum × G. tenuiflora, latiflora, and leptantha					
diegensis A × leptantha pinetorum	9	11	∞	0	0
diegensis S × leptantha pinetorum	5	4	few	0	0

Cross (♀ parent listed first)	*No. flowers pollinated*	*No. capsules set*	*No. abortive seeds*	*No. plump seeds*	*No. F_1 individuals*
leptantha pinetorum × digensis S	16	0		0	0
tenuiflora × diegensis C	30	30	∞	2	0
brecciarum neglecta S × latiflora latiflora Ap	18	18	∞	14	0
leptantha pinetorum × brecciarum neglecta S	16	0	0	0	0
14. Gilia brecciarum × G. interior, austrooccidentalis, and aliquanta					
austrooccidentalis × brecciarum brecciarum	54	54		833	3*
interior K × brecciarum neglecta S	13	11	∞	6	0
aliquanta × brecciarum neglecta S	21	21	∞	0	0

pollinated yielded 610 seeds which in turn produced hundreds of F_1 seedlings. Two biotypes of *G. exilis* from Dripping Springs yielded 89 seeds and 43 F_1 individuals from seven flowers. Different color variants of *G. minor* and of *G. austrooccidentalis* from Ballinger Canyon also crossed freely. The average number of plump seeds per flower pollinated ranged from 13 to 26 in the different biotype crosses. These results indicate a seed fertility similar to that found under conditions of open pollination.

Weak and easily surmounted barriers to crossing are found between different geographical races of the same species (Fig. 2). Thus within *Gilia leptantha,* the Mt. Pinos race *(G. l. pinetorum),* Sierra Nevada race *(G. l. purpusii),* San Bernardino Mt. race *(G. l. leptantha),* and desert race *(G. l. transversa)* can be intercrossed to yield hybrids. The cross of the San Bernardino Mt. race by the Sierra Nevada race yielded 333 seeds from 40 flowers. That an incompatibility barrier exists is indicated by the finding of some abortive seeds in certain inter-subspecific combinations within *G. leptantha* (i.e., *pinetorum* × *leptantha*).

Similarly within *Gilia latiflora* the subspecies *latiflora, davyi, excellens,* and *cuyamensis* can be intercrossed in various combinations. A good seet set but no germination was obtained from the cross of *cuyamensis* × *excellens.* The races of *Gilia brecciarum* cross freely, as do the geographically widely separated races of *G. minor.*

Complete failure of crossing was found between two races of *G. exilis* and between two

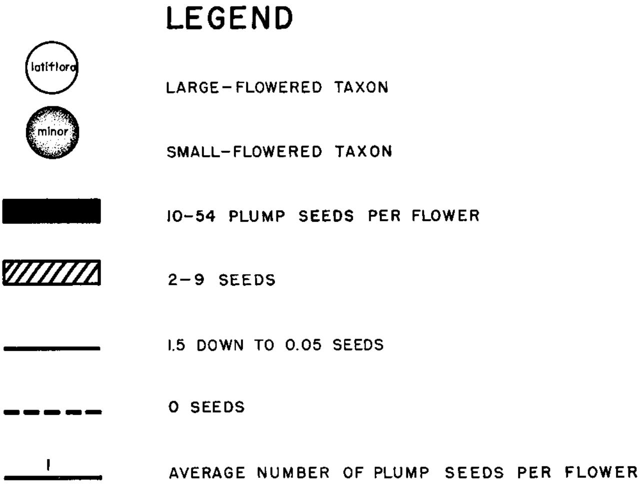

FIG. 3. Explanation of symbols used in Figures 2, 4, 5 and 6.

races of *G. clokeyi.* Within *Gilia ochroleuca,* the large-flowered races, *bizonata* and *vivida,* cross easily, but the small-flowered race, *ochroleuca,* is more difficult to cross with large-flowered forms.

The compatibility relationships between the species of the *Gilia ochroleuca* group can be visualized from the crossing diagram in Figure 4. The large-flowered species in this group can be intercrossed with varying degree of success. The small-flowered species are sometimes quite intercompatible and sometimes only moderately or slightly so, depending on the combination. Hybrids between the small- and large-flowered taxa within the *G. ochroleuca* group are difficult to produce.

An interesting difference was noted in 1954 in the crossability of *G. ochroleuca bizonata* from Mt. Pinos with different biotypes in the Dripping Springs population of *G. exilis.* The biotype designated "I" has a leaf dissection like that of *G. o. bizonata,* while biotype II has the simpler leaf dissection characteristic for *G. exilis.* The cross of *bizonata* ×

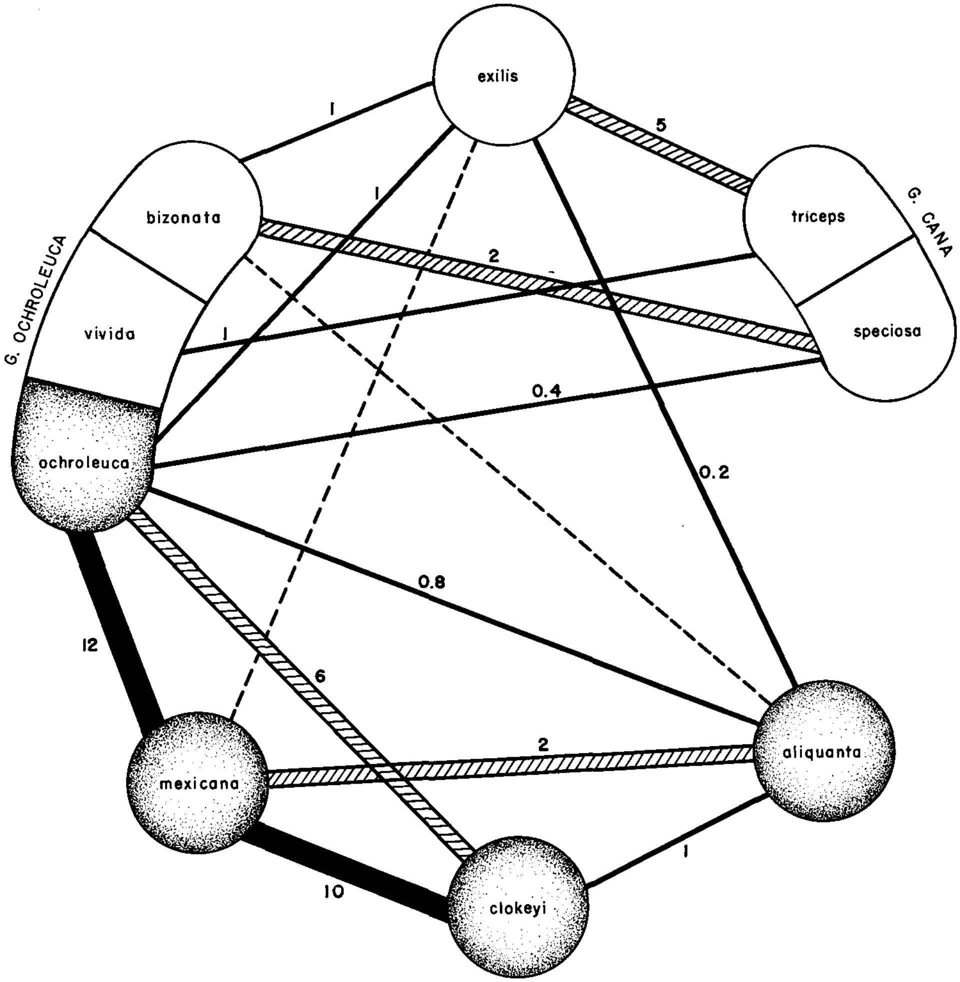

Fig. 4. Interspecific crosses within the *Gilia ochroleuca* group.

exilis I yielded no sound seeds, whereas the cross *bizonata* × *exilis* II resulted in the formation of numerous sound seeds and 13 hybrid individuals. The two biotypes cross freely between themselves to produce a fully fertile F_1. They evidently differ by genetic factors affecting their compatibility with foreign populations. Such genetic factors could be the basis for the strain to strain differences in crossability found in the Gilias and in numerous other plant groups which have been studied taxogenetically.

The pattern of crossing relationships is similar within the *Gilia tenuiflora* group (Fig. 5). Here the large-flowered species, *G. tenuiflora, leptantha,* and *latiflora,* are separated by compatibility barriers of medium strength. Some combinations of *G. latiflora* and *G. leptantha* produce hybrids readily, other combinations yield a reduced number of well formed seeds, and still other crosses yield numerous abortive seeds, or no seeds at all. Hybridization between most of the small-flowered species and between them and *G. tenuiflora* is moderately successful in the production of sound seeds. *Gilia minor* is more strongly isolated from other members of the species group.

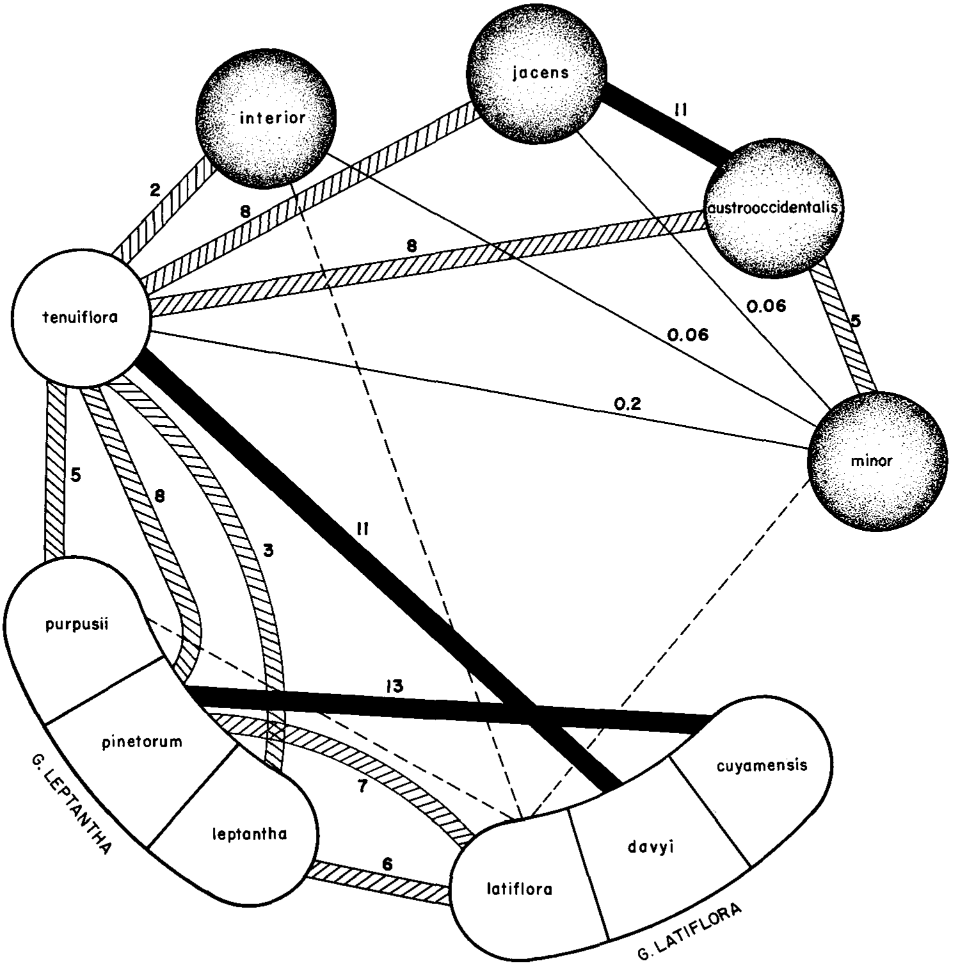

FIG. 5. Interspecific crosses within the *Gilia tenuiflora* group.

Crosses between the two species groups, the *Gilia ochroleuca* group × the *G. tenuiflora* group, are highly compatible in some combinations and highly incompatible in others. Figure 6 shows the varying degrees of crossability between different members of the two

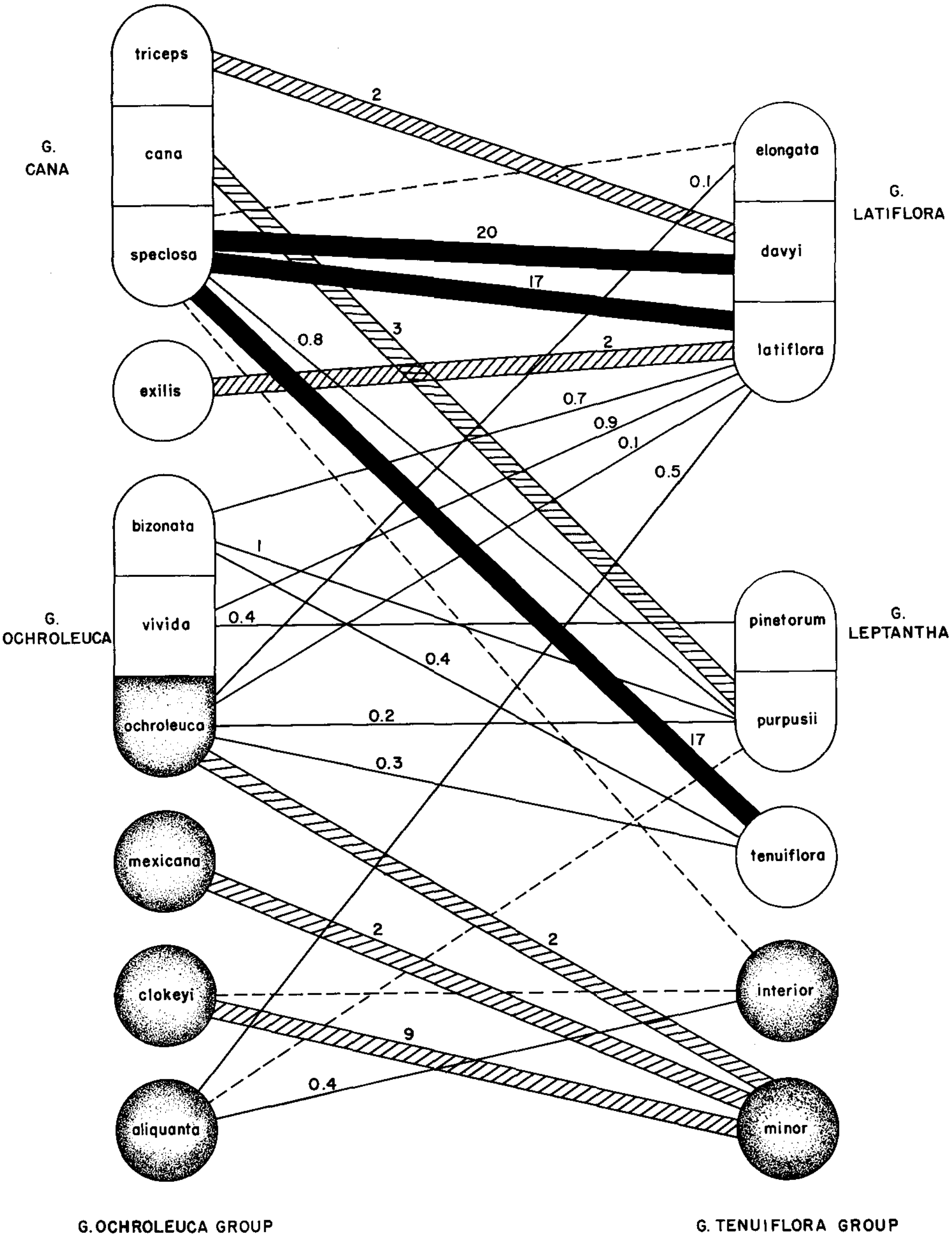

FIG. 6. Crosses between the *Gilia ochroleuca* group and the *Gilia tenuiflora* group.

species groups. In general, *G. ochroleuca* is strongly isolated from the *G. tenuiflora* group. Abortive seeds and no or reduced quantities of plump seeds are usually produced following crosses of *G. ochroleuca* × *G. tenuiflora* and its relatives. Some crosses which failed in one year were successful when repeated in another season, as *G. ochroleuca bizonata* × *G. latiflora latiflora*. *Gilia cana* on the other hand crosses fairly freely with *G. tenuiflora, leptantha,* and *latiflora*. In fact the average number of plump seeds per flower is the same for the crosses *G. cana* × *G. tenuiflora, leptantha,* and *latiflora* (7.3) as for crosses among the latter three species themselves (7.4). Crossability barriers of medium strength exist between the small-flowered taxa belonging to the respective species groups.

Gilia diegensis and *G. brecciarum* cross freely with one another, as shown in Figure 7.

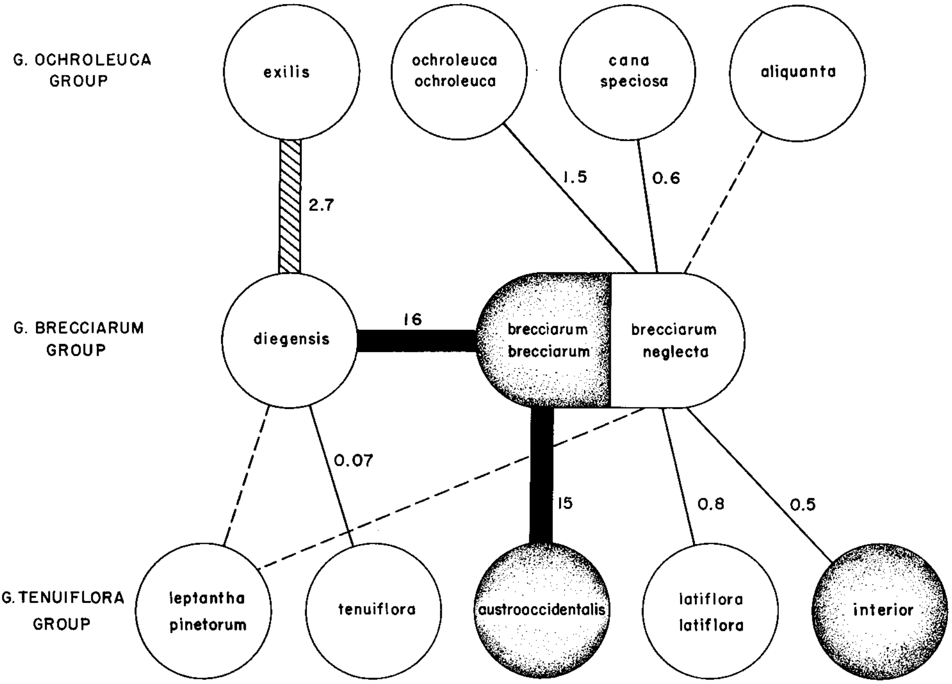

FIG. 7. Crosses involving the *Gilia brecciarum* group.

The *G. brecciarum* group is well isolated from most other species of Cobwebby Gilia by strong incompatibility barriers. Exceptions exist however; thus, *G. brecciarum brecciarum* crosses readily with *G. austrooccidentalis,* and hybrids between *G. diegensis* and *G. exilis* can be produced without too much difficulty. Despite repeated attempts, no hybrids have yet been produced between *G. diegensis* and the *G. tenuiflora* group, although we originally classified *G. diegensis* in the *G. tenuiflora* group on the basis of morphology and distribution.

The data of Table 3 were grouped according to the level of divergence of the taxa hybridized. Three different measures of crossability were calculated for the grouped data within each class. The three measures were the percent of the hybrid combinations attempted that yielded any F_1 progeny, the average number of plump seeds produced by each flower cross-pollinated, and the number of hybrid individuals derived from the pollination of ten flowers. The results are given in Table 4. This table shows that with respect to each of the three measures the crossability steadily decreases as the systematic relationships between the taxa become more remote.

The incompatibility barrier is manifested at different stages of flowering and fruiting. A Cobwebby Gilia flower pollinated with foreign pollen may fail to set a capsule; it may ripen a capsule which contains only or mainly shriveled seeds; a reduced number of sound seeds may form; or numerous plump seeds may develop but fail to germinate. There is evidently not one barrier but several. Latimer (1958) made a detailed study of the incompatibility barrier between *Gilia splendens* and *G. australis,* belonging to the related section *Saltugilia.* He resolved the block between these two species into several components: failure of the pollen tubes to reach the ovules, failure of fertilization, embryo failure, and disintegration of the endosperm.

TABLE 4. CROSSABILITY AT DIFFERENT TAXONOMIC LEVELS OF DIVERGENCE

Type of cross	*No. combinations attempted*	*% successful combinations*	*No. flowers pollinated*	*No. plump seeds per flower*	*No. hybrids per 10 flowers*
Between biotypes	4	100%	116	17.8	22
Between races	26	73%	562	15.2	12
Between species	103	43%	2016	3.7	3

Large-flowered taxa are generally difficult to cross with small-flowered taxa in the Cobwebby Gilias. It is often easier to cross two distantly related species with flowers of a similar size than to cross closely related forms differing in flower size. Thus the small-flowered *G. ochroleuca ochroleuca* crosses with difficulty with the closely related, large-flowered *G. o. bizonata,* but crosses fairly easily with the distantly related, small-flowered species *G. mexicana, G. clokeyi,* and *G. minor.* A large inequality in the respective length of style and pollen tubes may hinder crossing between *G. o. ochroleuca* and *G. o. bizonata;* conversely, the closer correspondence of style length and normal pollen tube growth between *G. o. ochroleuca* and other small-flowered species may favor cross-fertilization.

Reciprocal crosses between large- and small-flowered taxa are often more successful when the small-flowered and short-styled form is used as the female parent. For example, the cross *G. ochroleuca bizonata* ♀ × *G. aliquanta* did not yield any capsules, but the reciprocal cross *G. aliquanta* ♀ × *G. ochroleuca bizonata* produced a good set of capsules containing abortive seeds. The first and more incompatible combination involves a long-styled ♀ × short-styled ♂; the second combination in which at least capsules are formed involves a short-styled ♀ × a long-styled ♂. Similar reciprocal differences are found in crosses between the short-styled *G. diegensis* and the longer-styled *G. leptantha pinetorum,* capsules with abortive seeds being formed on *diegensis* mothers, but no capsules on *pinetorum* mothers.

The embryological causes of failure of crossing between the long-styled *Gilia splendens* and the short-styled *G. australis* in the section *Saltugilia* have been determined by Latimer (1958). Latimer has shown that the cross *G. splendens* ♀ × *G. australis* fails due to inability of the *australis* pollen tubes to reach the *splendens* ovules. The reciprocal combination, *G. australis* ♀ × *G. splendens,* fails for other reasons, primarily because of endosperm degeneration. In the first case pre-fertilization barriers were operative; in the second case where these were less significant other, post-fertilization barriers came into play.

Attention should be drawn to an interesting relationship, the causes of which are not yet understood. In several interspecific crosses the sympatric races of the two species have proven to be more compatible with one another than geographically separated races. The most compatible combination found between *G. leptantha* and *G. latiflora,* for example, was that involving *G. leptantha pinetorum* and *G. latiflora cuyamensis,* both of which occur naturally in the Mt. Pinos area. *Gilia jacens* and *G. austrooccidentalis,* both from Ballinger Canyon, are more compatible with one another than they are with the geographically distant strains of *G. minor* and *G. tenuiflora,* to which they are about equally closely related in other respects.

A similar pattern was found sporadically among the Woodland Gilias and the Leafy-stemmed Gilias. The sympatric strains of *Gilia splendens* and *G. australis* can be hybridized more readily than the allopatric populations of these two species (Grant and Grant, 1954; Latimer, 1958). Certain sympatric populations of *Gilia capitata* also cross more easily than allopatric populations (Grant, 1952). As regards *Gilia splendens* and *G. australis,* Latimer showed that the correlation of high crossability with sympatric occurrence holds good when the crossings are extended to a fairly large series of races of each species. He found also that the endosperm failed regularly in the unsuccessful allopatric crosses but was more normal in sympatric crosses. The question of why, in an evolutionary sense, the sympatric populations of two species sometimes come to have weaker barriers to crossing than populations which are not in contact with one another still remains to be answered.

MORPHOLOGY OF THE HYBRIDS

The F_1 hybrids produced during this investigation were fully vigorous in the vast majority of cases. The cross *G. cana triceps* Homewood × *G. cana speciosa* yielded two vigorous hybrids and one runt. From the cross of *G. tenuiflora* × *G. cana speciosa* we obtained 6 vigorous hybrids and 4 runts. Some runts appeared also in first generation progeny of the cross between *G. ochroleuca bizonta* × *G. latiflora latiflora.* The hybrids of *G. ochroleuca bizonata* ♀ × *G. tenuiflora* showed inhibitions in the development of various vegetative and floral parts, whereas the reciprocal hybrids *(tenuiflora* ♀ × *bizonata)* were fully vigorous. The F_1 of *G. leptantha pinetorum* × *G. latiflora latiflora* was male sterile.

Most of the F_1 hybrids were compared morphologically with their parents. Only a small proportion of the extensive data is presented in Table 5.

In most characters the hybrids are intermediate between the parental strains. This was the case in 88 out of 118 characters measured in 18 hybrid combinations. The intermediacy of the F_1s is manifested in every part of the plant body. Reference to Table 5 shows, for example, that the main branches are ascending in *Gilia tenuiflora,* decumbent in *G. ochroleuca bizonata,* and ascending but widely spreading in the F_1.

The flowers are borne in pairs on pedicels of nearly equal length in *G. ochroleuca bizonata.* The ultimate pair of pedicels is very unequal in length in *G. tenuiflora,* the ratio of shorter to longer being somewhere between 1 : 3 and 1 : 8. In the F_1 hybrid the ultimate pair of pedicels is unequal in length but less so than in *G. tenuiflora,* the ratio of shorter to longer being about 1 : 2. One flower of a pair blooms about one day ahead of the other in *G. o. bizonata;* the short-pedicelled flower blooms several days ahead of the long-pedicelled one in *G. tenuiflora;* and the short-pedicelled flower blooms about two days ahead of its mate in the F_1.

The stamens are almost equal in length in *G. o. bizonata,* quite unequal in *G. tenuiflora* which has one very short filament, and these organs possess an intermediate degree of unequalness in the hybrid. The stigma stands just at the orifice in *G. cana speciosa,* well above the orifice in *G. latiflora latiflora,* and occupies an intermediate position in the F_1.

In a fair number of characters (22 out of 118 scored) the F_1 is like one parent. Thus the capsule of *G. latiflora latiflora* is 5 mm. long, that of *G. leptantha pinetorum* 4 mm. long, and that of the F_1 4 mm. long. The stigma is exserted 3 mm. above the orifice in *G. tenuiflora,* 7-8 mm. in *G. leptantha pinetorum,* and 3 mm. in their hybrid. The pink color in the corolla limb of *G. leptantha leptantha* is dominant over the pale blue-violet color of *G. latiflora latiflora.*

TABLE 5. MORPHOLOGY OF HYBRIDS

Cross, P ♀ × P ♂	P ♀	F_1	P ♂
tenuiflora × ochroleuca bizonata	main branches ascending	ascending but widely spreading	decumbent
ochroleuca ochroleuca × ochroleuca bizonata	lateral branches 8-13 cm. long	25-30 cm. long	42-53 cm. long
tenuiflora × ochroleuca bizonata	herbage clear green	intermediate	grayish-green
tenuiflora × ochroleuca bizonata	upper half of stems glandular	upper one-third of stems sparsely glandular	upper stems glabrous & glaucous
ochroleuca bizonata × latiflora latiflora	leaf rachis narrow	intermediate	broad
tenuiflora × latiflora davyi	leaf rachis 1 mm. wide	2 mm. wide	4 mm. wide
tenuiflora × latiflora davyi	leaf lobes longer than width of rachis	equal to slightly longer than rachis width	shorter
minor × ochroleuca ochroleuca	leaf lobes short & broad, 1/4 or less than total length of leaf	lobes intermediate, 1/3 to 1/2 as long as entire leaf	lobes long & narrow, 1/2 or more as long as total length of leaf
tenuiflora × ochroleuca bizonata	ultimate pair of pedicels very unequal in length	ultimate pair slightly unequal	ultimate pair nearly equal
tenuiflora × leptantha pinetorum	longest pedicel in a flowering branch 30-35 mm. long	12-19 mm.	13-15 mm.
leptantha leptantha × tenuiflora	longest pedicel 15-19 mm. long	13-17 mm.	30-35 mm.
leptantha pinetorum × leptantha leptantha	uppermost flowering bract trifid	almost entire with very small side teeth	entire
minor × ochroleuca ochroleuca	calyx densely glandular	lightly glandular	glabrous
tenuiflora × ochroleuca bizonata	tips of calyx lobes recurved	slightly recurved	erect
latiflora latiflora × cana speciosa	corolla tube 6-8 mm. long	9-10 mm.	17-20 mm.
latiflora latiflora × cana speciosa	corolla throat 6 mm. long	3.5 mm.	3 mm.
ochroleuca ochroleuca × ochroleuca bizonata	corolla limb 3-4 mm. broad	7 mm.	12-13 mm.
ochroleuca bizonata × latiflora latiflora	orifice of corolla pale violet	white tinged with pale violet	white
ochroleuca bizonata × ochroleuca vivida	upper corolla throat pale grayish-violet	intermediate	dark purple
tenuiflora × ochroleuca bizonata	stamens very unequal in length	intermediate	almost equal in length
latiflora latiflora × leptantha leptantha	stamens exserted 3 mm.	5 mm.	8 mm.
latiflora latiflora × cana speciosa	stigma stands well above orifice	intermediate degree of exsertion	stigma at orifice
interior × tenuiflora	capsule ovoidal, approaching spheroidal	intermediate	short cylindrical

The F_1 hybrid was occasionally smaller in some feature than its smallest parent. For instance, the corolla limb is 14-15 mm. wide in *G. o. bizonata,* 18-20 mm. wide in *G. l. latiflora,* but only 10-13 mm. wide in their hybrid. The length of corolla tube and throat in these same plants is respectively 9, 12, and 7-8 mm. The corolla of the F_1 is thus smaller than that of either parent. Presumably in this and similar cases the genotypes of the two parental species interact to bring about an inhibition of development.

Anomalous character expressions appeared in the F_1 generation in a few instances. *Gilia ochroleuca bizonata* and *G. cana speciosa* both have a narrow leaf rachis, but their hybrid had a broad rachis. The upper part of the corolla throat is purple in *G. tenuiflora,* light grayish-violet in *G. o. bizonata,* but bright yellow in the F_1. In this case both parents carry genes for the production of yellow pigment in the corolla throat. This color is normally suppressed by other pigments in the species but can come to expression as a result of inhibition of the masking pigments in the hybrid.

The hybrids between *G. tenuiflora* and *G. ochroleuca bizonata* showed a number of reciprocal differences (Grant, 1956). The F_1s derived from a *tenuiflora* mother were fully vigorous with large flowers and well developed stamens; the hybrids from a *bizonata* mother were small plants with small leaves, small flowers and frequently abortive stamens. In the color of herbage, stem pubescence and shape of calyx lobes, the reciprocal hybrids differed from one another but resembled their female parents. The hybrids of *G. tenuiflora* and *G. leptantha leptantha* also differed reciprocally, the F_1s from a *leptantha* mother having longer pedicels, longer stamens, larger corolla lobes and duller corolla colors than those from a *tenuiflora* mother.

The F_2 generations were scored for morphological characters in only a few instances. A typical example is provided by corolla tube length in the cross *G. latiflora latiflora* × *G. cana speciosa.* The tube is 6-8 mm. long in *latiflora,* 17-20 in *speciosa,* 9-10 mm. in the F_1, and ranged from 6 to 14 mm. long in the F_2. The modal length of corolla tube in the F_2 population was 10 mm. The distribution of tube lengths among 41 F_2 individuals was as follows: 6 mm. *(3 individuals),* 7 mm. *(6)*, 8 mm. *(6)*, 9 mm. *(4)*, 10 mm. *(9)*, 11 mm. *(4)*, 12 mm. *(7)*, 14 mm. *(2)*. The width of the yellow region in the corolla throat varied in a similar intergrading manner between the respective parental conditions in this same F_2 generation. This and other F_2 populations presented the familiar aspect of continuous variation so commonly found in the progeny of plant hybrids.

HYBRID FERTILITY

The individuals composing wild populations of the Cobwebby Gilias are normally fertile as to pollen and seeds. Various degrees of infertility are exhibited by their interracial and interspecific hybrids. The data on hybrid fertility are summarized in Table 6. The pollen fertility was estimated from the percentage of well formed and well stained grains observed in a lactophenol-aniline blue mount. The percent of stainable pollen was scored for four sister hybrids wherever this many F_1 individuals were available for study. The separate averages for four or fewer sister hybrids were expressed as the range and their group average as the mean in Table 6.

Seed fertility of a hybrid was scored qualitatively into four classes. Hybrids producing nearly or quite as large quantities of seeds as the parental plants were classified as fertile; hybrids with a fair but obviously reduced seed output were considered semifertile; those producing only a few seeds under favorable conditions of pollination are regarded as highly sterile; and hybrids yielding no seeds at all are called completely sterile. The distinction between highly sterile and completely sterile may depend upon whether a given hybrid yields one or no seed in a season and is therefore an artificial division.

It is evident from Table 6 that the hybrids between different biotypes in the same population are fully fertile. The interracial hybrids are highly fertile as to seeds and vary from semifertile to highly fertile in their pollen (Fig. 8).

Hybrids between *G. ochroleuca* and *G. exilis,* representing related species in the *G. ochroleuca* group, are sterile. Only two seeds were harvested on the F_1 of *G. ochroleuca bizonata* × *G. exilis,* whereas 4000 seeds were harvested on the interracial hybrid *G. o. bizonata* × *G. o. ochroleuca.*

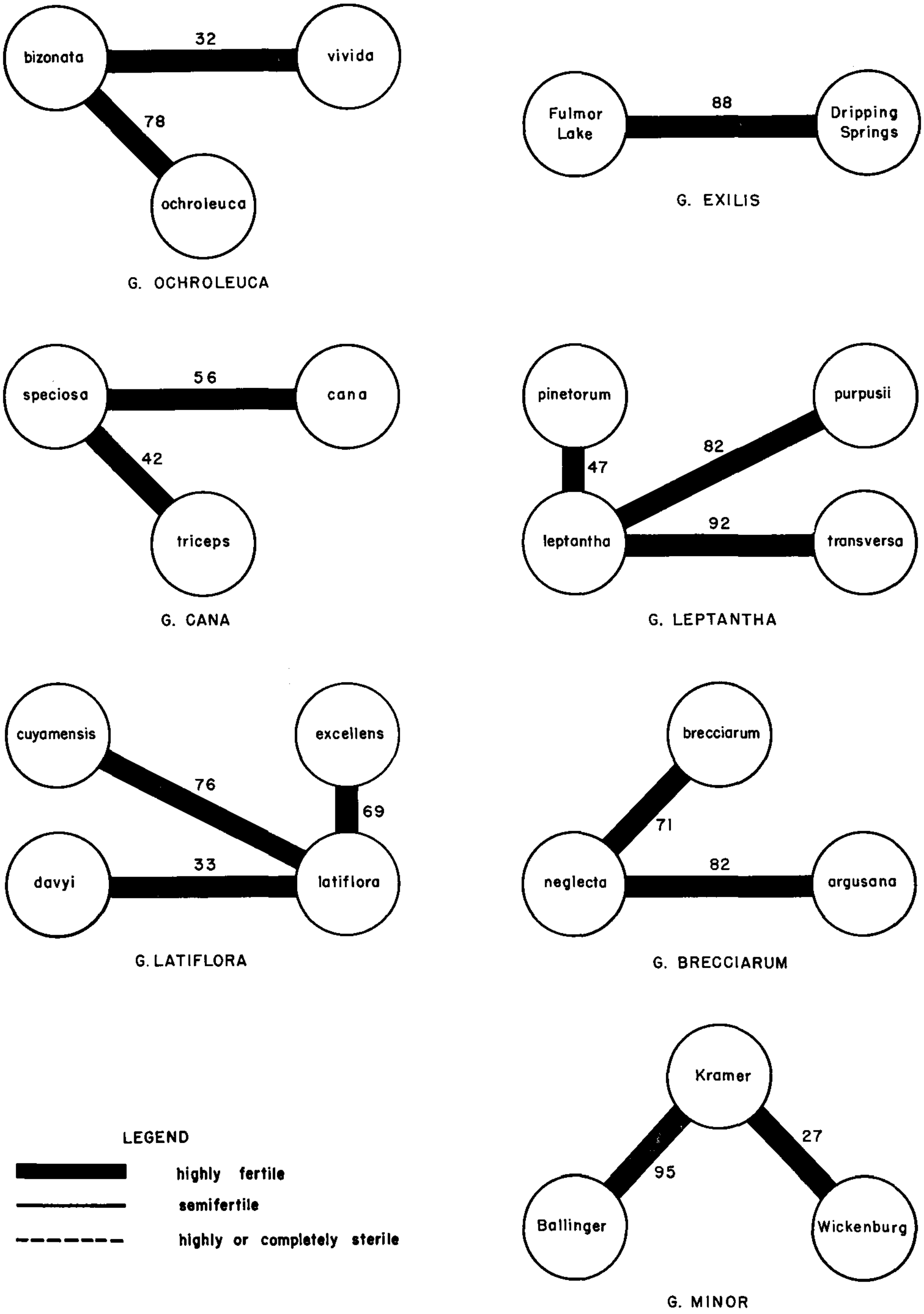

FIG. 8. Fertility of interracial hybrids. The figures are the average pollen fertility.

TABLE 6. FERTILITY OF F_1S AND VIGOR OF F_2S

	F_1 generation			F_2 generation	
Hybrid	*Pollen fertility, %* *range*	*mean*	*Seed fertility*	*% seed germination*	*% of vigorous seedlings*
I. HYBRIDS BETWEEN BIOTYPES					
G. exilis Dripping	95-98	96	fertile		
G. latiflora davyi Mojave			fertile		
G. minor Ballinger	95-98	97	fertile		
G. austrooccidentalis Ballinger	98-99	98	fertile		
II. INTERRACIAL HYBRIDS					
1. Gilia ochroleuca					
bizonata × vivida	22-46	32	fertile	9	93
ochroleuca × bizonata	78	78	fertile	2	70
2. Gilia exilis					
Fulmor × Dripping II	58-99	84	fertile	21	100
Dripping × Fulmor	70-99	92			
3. Gilia cana					
speciosa × cana	49-62	56	fertile	21	100
triceps H × speciosa	32-51	42	fertile	4	57
4. Gilia leptantha					
pinetorum × leptantha	47	47	fertile	11	38
leptantha × purpusii K	75-90	82	fertile	5	100
transversa × leptantha	90-95	92	fertile	8	100
5. Gilia latiflora					
cuyamensis × latiflora Ap	65-84	76	fertile	18	86
latiflora Ap × davyi M	14-63	33	fertile		
davyi M × latiflora Ap			fertile		
excellens × latiflora Ad	47-79	64	fertile	15	100
latiflora Ad × excellens	70-77	74	fertile		
6. Gilia minor					
Kramer × Ballinger	93-97	95	fertile		
Kramer × Wickenburg	20-37	27	fertile	3	

	F₁ generation			F₂ generation	
Hybrid	*Pollen fertility, %* *range*	*mean*	*Seed fertility*	*% seed germination*	*% of vigorous seedlings*
7. **Gilia brecciarum**					
brecciarum × neglecta S	47-84	71	fertile	18	36
argusana A × neglecta S	96-98	97	fertile	18	100
neglecta O × argusana R	18-97	66	fertile	15	70
III. INTERSPECIFIC HYBRIDS					
1. **Gilia ochroleuca group**					
ochroleuca bizonata × exilis D II	3-7	4	highly sterile		
ochroleuca ochroleuca × exilis W	1-3	2	semifertile	6	36
ochroleuca bizonata × cana speciosa	4-9	6	completely sterile		
cana triceps W × ochroleuca vivida	17	17	semifertile	40	100
clokeyi D × aliquanta	2	2	highly sterile	100	100
clokeyi D × mexicana	0-1	0.3	highly sterile	100	100
clokeyi K × ochroleuca ochroleuca	0-1	0.5	highly sterile		
mexicana × ochroleuca ochroleuca	4	4	highly sterile		
2. **Gilia tenuiflora group**					
leptantha pinetorum × latiflora cuyamensis	63-83	74	fertile	18	58
latiflora davyi M × tenuiflora	male sterile like ♀ P		fertile		61
tenuiflora × latiflora davyi M	19-20	20	fertile		52
tenuiflora × latiflora davyi G	20-35	28	fertile		100
leptantha leptantha × latiflora latiflora Ap	70-81	76	semifertile	17	29
latiflora latiflora Ap × leptantha leptantha	65-90	84	semifertile	17	71
latiflora latiflora Ap × leptantha pinetorum	34-46	42	fertile		
leptantha pinetorum × latiflora latiflora Ap	male sterile				
tenuiflora × leptantha leptantha	24-47	36			
leptantha leptantha × tenuiflora	43	43			
tenuiflora × leptantha pinetorum	15-81	46			
tenuiflora × leptantha purpusii K	20-40	32	fertile	13	100
minor K × austrooccidentalis	24-31	28	fertile	10	100
austrooccidentalis × jacens	10-20	16	fertile	18	100
austrooccidentalis × tenuiflora	16-35	26	semifertile to fertile	18	65
jacens × tenuiflora	16-27	22	semifertile	6	100
interior D × tenuiflora	0-2	1	fertile	17	86
interior K × tenuiflora	4-9	6	fertile	9	80

Hybrid	F₁ generation			F₂ generation	
	Pollen fertility, % *range*	*mean*	*Seed fertility*	*% seed germination*	*% of vigorous seedlings*
3. Gilia ochroleuca group × G. tenuiflora group					
ochroleuca bizonata × latiflora latiflora Ap	0.5-8	2	highly sterile	67	0
ochroleuca bizonata × leptantha purpusii K	4-15	8	semifertile	18	93
ochroleuca bizonata × tenuiflora	1	1	highly sterile		
tenuiflora × ochroleuca bizonata	1	1	highly sterile		
leptantha pinetorum × ochroleuca vivida	4	4	highly sterile		
cana cana × leptantha purpusii K	86-95	90	fertile	12	91
latiflora latiflora Ap × cana speciosa	34	34	fertile		98
cana speciosa × leptantha purpusii K	83	83	fertile	10	94
tenuiflora × cana speciosa	3-17	7	fertile	7	100
minor K × ochroleuca ochroleuca	0.5	0.5	completely sterile		
clokeyi D × minor K	0.5-1	1	highly sterile		
minor K × clokeyi D	1-3	2	highly sterile		
minor K × mexicana	0	0	highly sterile		
4. Gilia brecciarum group					
diegensis T × brecciarum brecciarum	25-30	28	fertile	9	100
5. Gilia brecciarum group × G. ochroleuca and G. tenuiflora groups					
diegensis C × exilis D II	1-3	2	completely sterile		
brecciarum neglecta S × cana speciosa	2	2	completely sterile		
austrooccidentalis × brecciarum brecciarum	11-14	12	fertile	20	100

The small-flowered species in the *G. ochroleuca* group, namely *G. ochroleuca ochroleuca, G. mexicana, G. clokeyi* and *G. aliquanta,* are also intersterile.

Gilia cana and *G. ochroleuca* are separated by a sterility barrier which is strongly developed between the races *bizonata* and *speciosa* but present in a weaker form between the races *vivida* and *triceps.* No seeds at all were set on three hybrid individuals of *G. ochroleuca bizonata* × *G. cana speciosa,* whereas the F_1 of *G. cana triceps* × *G. ochroleuca vivida* produced a fair amount of good pollen and ten sound seeds.

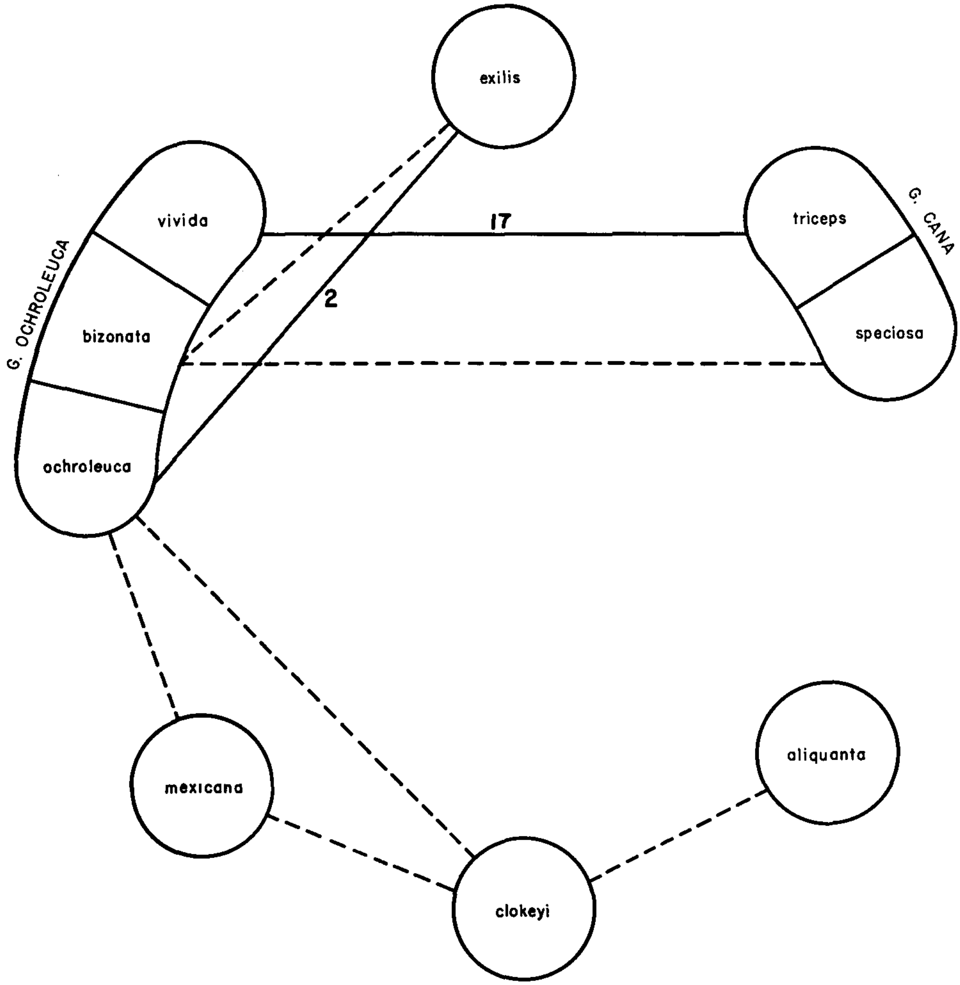

FIG. 9. Fertility of interspecific hybrids in the *Gilia ochroleuca* group. Legend as in Figure 8.

In the *Gilia tenuiflora* group the large-flowered species, *G. tenuiflora, G. leptantha* and *G. latiflora,* produced semifertile or fertile hybrids in every combination attempted (Fig. 10). *Gilia austrooccidentalis* in this same group also produced fertile or semifertile hybrids with *G. minor, G. jacens* and *G. tenuiflora* (Fig. 10). The hybrid between *G. tenuiflora* and *G. interior* was pollen sterile but seed fertile. The hybrid of *G. tenuiflora* × *G. jacens* was semifertile.

Most hybrids between the *G. ochroleuca* group and the *G. tenuiflora* group are highly or completely sterile (Fig. 11). The F_1 of *G. ochroleuca bizonata* × *G. latiflora latiflora* Apple Valley was first grown in 1953; three individuals which were open pollinated during several weeks produced a total of three seeds. The cross was repeated in 1956 and a new F_1 generation raised in 1957. Eight hybrid individuals bloomed ten weeks in the greenhouse without setting any seeds. The hybrids were used as females in artificial backcrosses with *G. o. bizonata* but were fruitless under these conditions also. Four additional hybrid individuals were set out with some individuals of *G. latiflora latiflora* in an isolation plot where they bloomed for ten weeks and were abundantly visited by bees. No seeds were set by the open pollinated plants either.

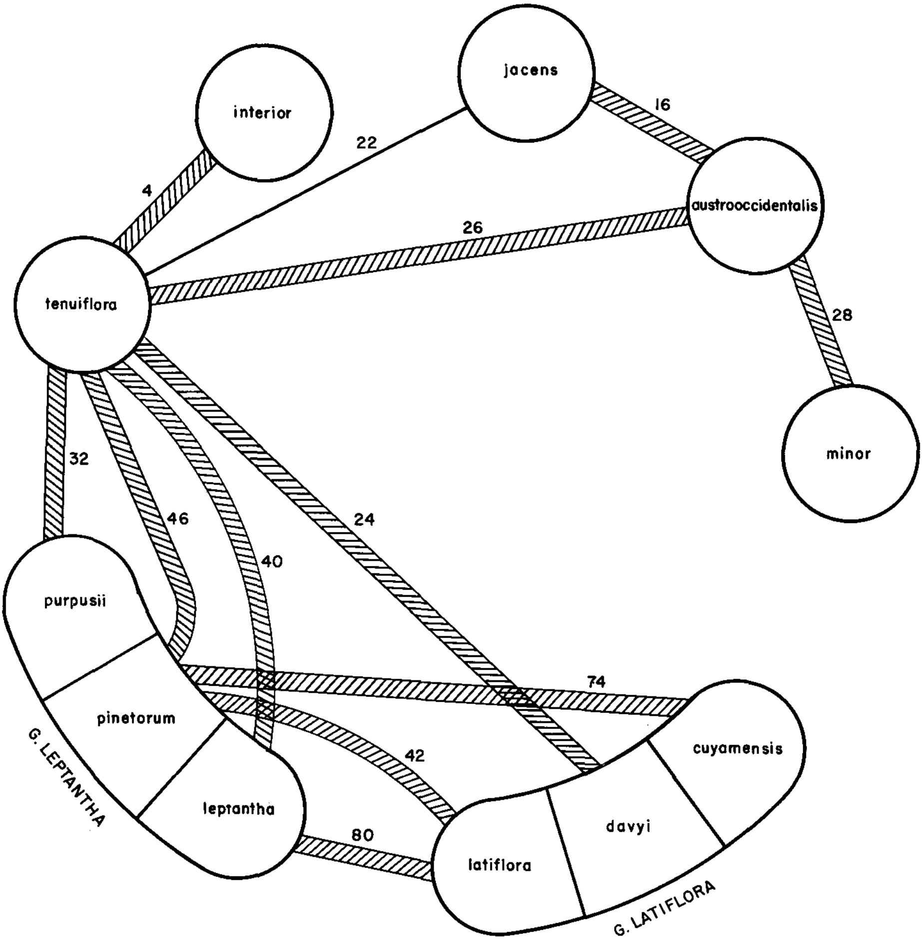

FIG. 10. Fertility of interspecific hybrids in the *Gilia tenuiflora* group. Legend as in Figure 8.

Strong sterility barriers also separate the small-flowered entities belonging to the two species groups, as shown in Figure 11.

Certain hybrid combinations between the two species groups were exceptional in being fertile or semifertile. *Gilia cana* produced fertile hybrids with the large-flowered members of the *G. tenuiflora* group. The F_1 of *G. cana speciosa* from Short Canyon × *G. leptantha purpusii* from the Kern River several thousand feet higher in the Sierra Nevada had 83% good pollen and produced 511 plump seeds on one hybrid individual. *Gilia leptantha purpusii* also ranges down the desert slopes of the Sierra Nevada into Short Canyon where it grows sympatrically with *G. cana speciosa.* Natural hybrids of *speciosa* × *purpusii* were found in Short Canyon in 1958 and were observed to be highly sterile as to both pollen and seeds. A distinct sterility barrier thus exists between the two species in the zone of their overlap. It would be interesting to determine the fertility of this same hybrid combination under experimental conditions.

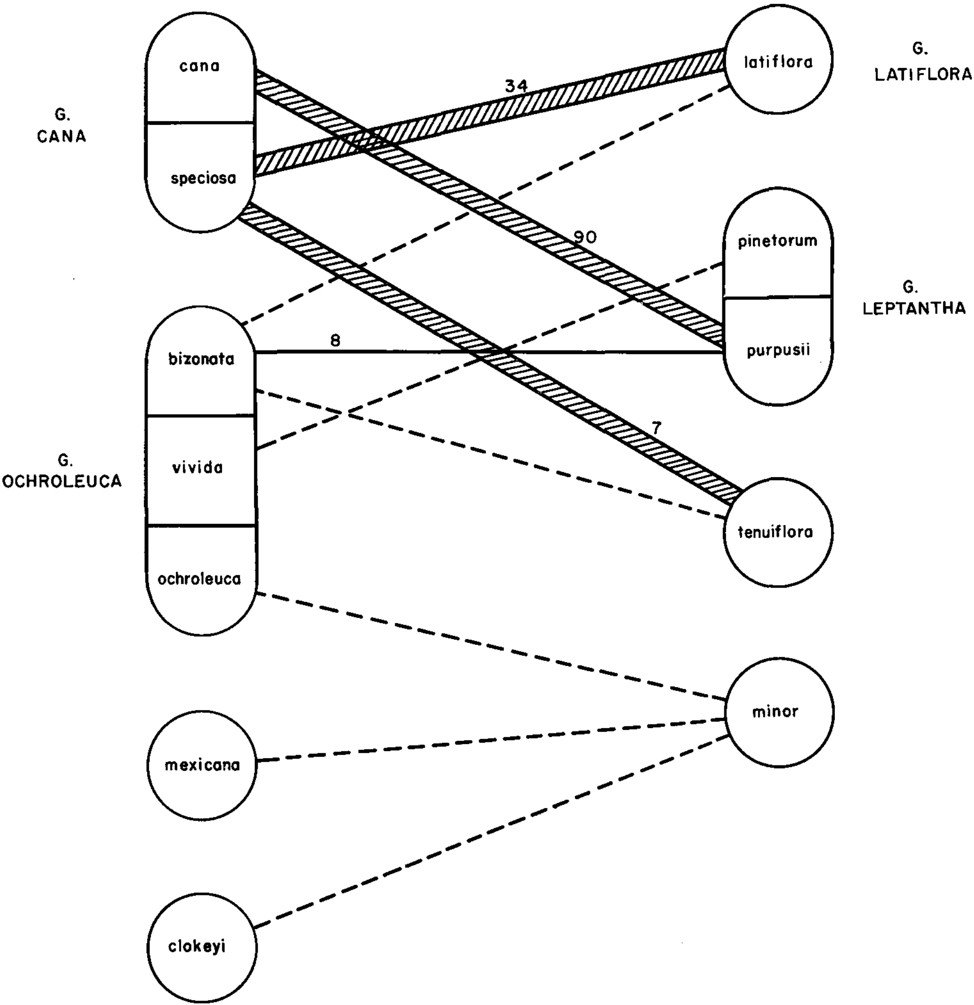

Fig. 11. Fertility of hybrids between the *Gilia ochroleuca* group and the *Gilia tenuiflora* group. Legend as in Figure 8.

Gilia diegensis not only crosses readily with *G. brecciarum brecciarum,* as noted in a previous section, but also forms a fertile hybrid with that species (Fig. 12). The hybrid between *G. brecciarum* and *G. austrooccidentalis* also produced numerous good pollen grains and sound seeds. Complete sterility characterized the hybrids obtained between the *G. brecciarum* group and the *G. ochroleuca* group (Fig. 12).

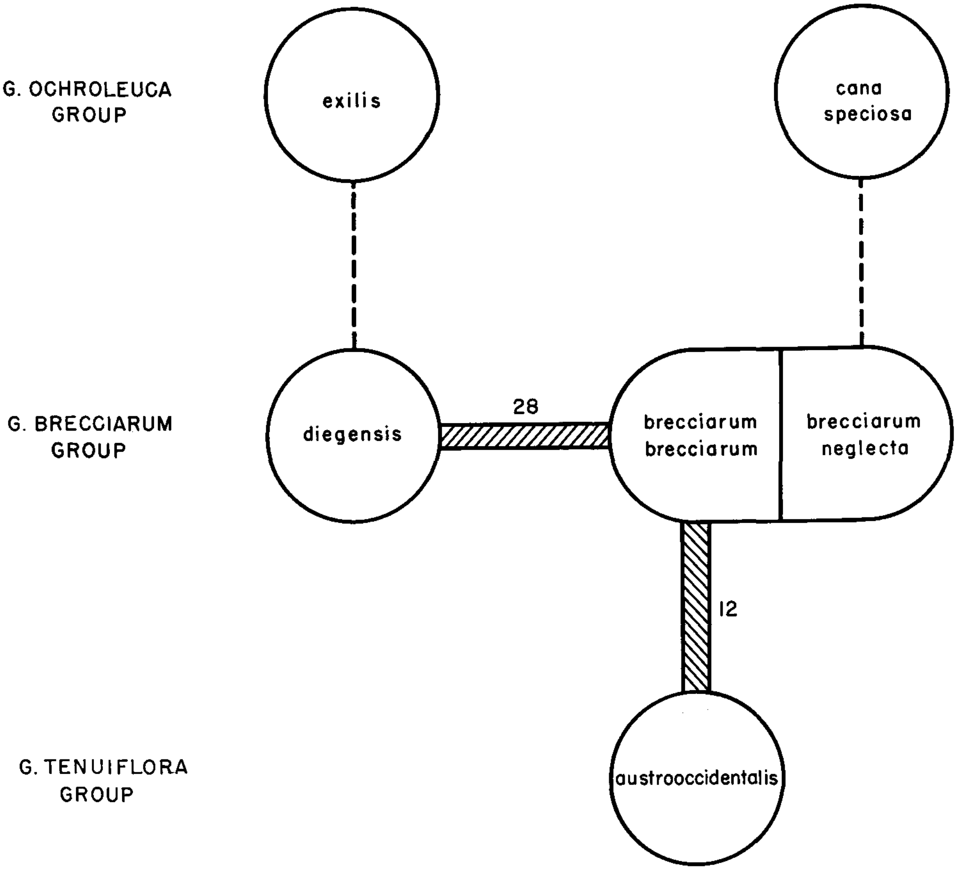

FIG. 12. Fertility of hybrids involving the *Gilia brecciarum* group. Legend as in Figure 8.

CYTOLOGY OF THE HYBRIDS

Meiosis is normal in the Cobwebby Gilias with rare exceptions. Fifty-two pollen mother cells of *G. cana speciosa* from Short Canyon were examined at metaphase I or diakinesis; 49 of these cells had nine bivalents; two had eight bivalents and two univalents; and one had a chain of four chromosomes. The average amount of pairing for this sample was 8.96 bivalents per cell. Of 67 cells at anaphase, 65 were normal with no lagging chromosomes or bridges; a laggard was seen in one cell at anaphase I and one in another cell at anaphase II. In 67 cells at metaphase I in *G. latiflora latiflora* from Apple Valley, 66 had nine bivalents and one had eight bivalents and two univalents; the chromosome pairing averaged 8.98 bivalents per cell. In a sample of 29 clear anaphases in this plant one cell showed an aberration, a bridge. Similar results pointing to normal meiosis were obtained with *G. tenuiflora* from Arroyo Seco.

This is not always the case however. The species of the *Gilia tenuiflora* group often form variable hybrid populations where they come into contact. The individuals in these populations exhibit varying degrees of sterility of pollen and seeds, which is frequently associated with irregularities of meiosis. For example one individual of *G. leptantha purpusii* from Old Isabella with about 1% good pollen had reduced metaphase pairing with a range of six to nine bivalents and a mode of seven bivalents per cell. Laggards were frequent at anaphase in this plant.

Fertile and meiotically regular plants were used as parents for hybridizations in the present study. The meiotic behavior of the F_1 hybrids is recorded in Table 7. The figures given in the table are derived from samples of 20 to 70 or more cells for each stage of meiosis.

Different races of the same species generally produce hybrids with essentially normal meiosis. *Gilia ochroleuca bizonata,* a large-flowered race of the pinyon-juniper belt, and *G. o. ochroleuca,* a small-flowered desert race, are so well differentiated morphologically and ecologically that a special relationship between them had not been suggested prior to the taxonomic revision of 1956; yet their hybrid has perfectly regular meiosis (Fig. 13). Meiosis was nearly as normal in the interracial hybrid *G. ochroleuca bizonata* × *G. o. vivida.* Other race hybrids have shown the same amount of regularity at meiosis with close to nine bivalents in each metaphase cell and no or only occasional laggards at anaphase (Fig. 13). Chains or bridges may or may not be frequent depending on the particular hybrid combination.

Hybrids between species within the *Gilia tenuiflora* group likewise exhibit a high degree of pairing (Fig. 14). The hybrid of *G. latiflora latiflora* from the Mojave Desert with *G. leptantha leptantha* from yellow pine forest in the San Bernardino Mts. had nine bivalents in 36 cells examined at first metaphase and eight bivalents in 12 other cells. The average pairing was 8.75 bivalents per cell. Fifty-six out of 65 cells in anaphase I were clear of laggards and nine other cells had one or two laggards; the amount of lagging seen at anaphase II and the sporad stage was comparable. The course of meiosis was similar in the hybrid of *G. latiflora latiflora* × *G. leptantha pinetorum* from Mt. Pinos.

The greatest reduction in pairing seen in any hybrid within the *Gilia tenuiflora* group was five bivalents in several cells of *G. tenuiflora* × *G. leptantha.* Lagging of chromosomes at anaphase was on the whole fairly common in the interspecific hybrids of the *G. tenuiflora* group, as reference to Table 7 will show. Chains and bridges were also present at metaphase or anaphase respectively in many of these hybrids.

Chromosome pairing in the F_1 of *G. tenuiflora* × *G. interior* ranged from six to nine bivalents per cell, with 47 of the 53 PMC's analyzed having seven or eight bivalents (Fig. 14). Lagging of the univalents was common. Chains of three and occasionally four chromosomes were seen in 19% of the metaphase I figures, and chromatid bridges were common at anaphase. This hybrid produced a reduced amount (4 to 9%) of good pollen. The plants did however set seeds abundantly in spite of the low pollen fertility. The course of meiosis was similar in the hybrids of *G. tenuiflora* with *G. austrooccidentalis* and *G. jacens.*

A marked reduction in chromosome pairing is found in the hybrid *G. ochroleuca ochroleuca* × *G. exilis.* Full bivalent pairing was not seen once in a sample of 63 cells, whereas two cells had only one bivalent, and cells with as few as six or five bivalents were common. The range of pairing in this hybrid is shown in Figure 15.

The hybrids of *G. ochroleuca ochroleuca* with *G. mexicana* and *G. clokeyi* have low pairing, averaging 6.3 and 3.7 bivalents per cell respectively (Fig. 15). The F_1 of *G. clokeyi* × *G. aliquanta* has medium variable pairing with a range from one to nine bivalents per cell and a mean of 4.5 (Fig. 16). As would be expected from the disturbed meiosis, these hybrids were all highly sterile.

TABLE 7. MEIOTIC BEHAVIOR OF HYBRIDS

Hybrid	*Metaphase pairing*		*Anaphase lagging*			*Structural aberrations*	
	No. bivalents per cell		*% cells with laggards or micronuclei at:*			*% cells with*	
	mean	range	AI	AII	Tetrad	chains	bridges
I. INTERRACIAL HYBRIDS							
ochroleuca bizonata × ochroleuca vivida	8.9	8-9	0	1			
ochroleuca ochroleuca × ochroleuca bizonata	9.0	9-9	0	0		0	0
cana triceps H × cana speciosa	8.6	6-9	0	0	3	0	6
leptantha pinetorum × leptantha leptantha	8.8	8-9	2			0	0
leptantha leptantha × leptantha purpusii K	8.8	8-9	+*	+		13	
latiflora latiflora Ap × latiflora excellens	8.9	8-9	+		2	16	
minor K × minor B	9.0	9-9	0	0	0	0	0
minor K × minor W	9.0	8-9	0	0			0
brecciarum brecciarum × brecciarum neglecta S	8.9	8-9	6		0	0	0
II. INTERSPECIFIC HYBRIDS							
1. Gilia ochroleuca group							
ochroleuca bizonata × exilis D	7.9	4-9	31	42	13	+	20
ochroleuca ochroleuca × exilis W	6.0	1-8	40	66	60	13	3
ochroleuca bizonata × cana speciosa	5.1	2-8	50	45	26	0	15
cana triceps W × ochroleuca vivida	8.1	6-9	47	54	57	0	4
clokeyi D × aliquanta	4.5	1-9	100	100		0	8
clokeyi D × mexicana	1.1	0-4	75	75	+	0	7
clokeyi K × ochroleuca ochroleuca	3.7	2-6	75	92		13	
mexicana × ochroleuca ochroleuca	6.3	2-9	7				
2. Gilia tenuiflora group							
tenuiflora × latiflora davyi M	8.9	8-9	25	28	10		0
latiflora latiflora Ap × leptantha leptantha	8.8	8-9	14	6	10	0	0
latiflora latiflora Ap × leptantha pinetorum	8.6	7-9	12	20	2	0	8

Hybrid	*Metaphase pairing*		*Anaphase lagging*			*Structural aberrations*	
	No. bivalents per cell		*% cells with laggards or micronuclei at:*			*% cells with*	
	mean	range	AI	AII	Tetrad	chains	bridges
tenuiflora × leptantha leptantha	7.3	5-9	47	64	41	5	14
tenuiflora × leptantha pinetorum	7.5	5-9	34	50	22	35	9
tenuiflora × leptantha purpusii K	7.8	6-9	33	28	28	8	11
minor K × austrooccidentalis	8.7	8-9	24	11	19	14	0
austrooccidentalis × jacens	7.9	6-9	+	+	+	20	10
austrooccidentalis × tenuiflora	7.9	6-9	+	+	+	25	
jacens × tenuiflora	8.5	7-9	45	50	18	0	10
interior D × tenuiflora	7.7	6-9	30	40	13	19	9
3. Gilia ochroleuca group × G. tenuiflora group							
ochroleuca bizonata × latiflora latiflora Ap	4.3	0-8	38	76	81	1	2
ochroleuca bizonata × leptantha purpusii K	3.0	0-7	39	75	42	5	11
leptantha pinetorum × ochroleuca vivida	6.9	4-9	+	+		+	+
latiflora latiflora Ap × cana speciosa	8.4	6-9	7	25	9	3	3
cana speciosa × leptantha purpusii K	8.7	7-9	13		7	3	0
tenuiflora × cana speciosa	7.9	4-9	29	14	9	26	
minor × ochroleuca ochroleuca	2.8	1-5					
clokeyi D × minor K	4.6	2-7	88			9	
minor K × mexicana	1.7	0-4					
4. Gilia brecciarum group							
diegensis T × brecciarum brecciarum	7.8	6-9			6	13	
5. Gilia brecciarum group × G. ochroleuca group							
diegensis C × exilis D	2.3	0-6	+	+	85	0	
brecciarum neglecta S × cana speciosa	5.6	3-8	71	56	66	7	16

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*The symbol + means present in undetermined frequency.

The hybrid *G. clokeyi* × *G. mexicana* is almost asynaptic. Out of 54 cells studied in metaphase I, 19 had no bivalents, and only three cells had as many as three or four bivalents (Fig. 16). Although lagging was found in most of the anaphase cells in this hybrid, the number of lagging chromosomes per cell was unaccountably small in relation to the number of unpaired chromosomes present at metaphase. The chromosome number at the two poles at anaphase I was frequently unequal.

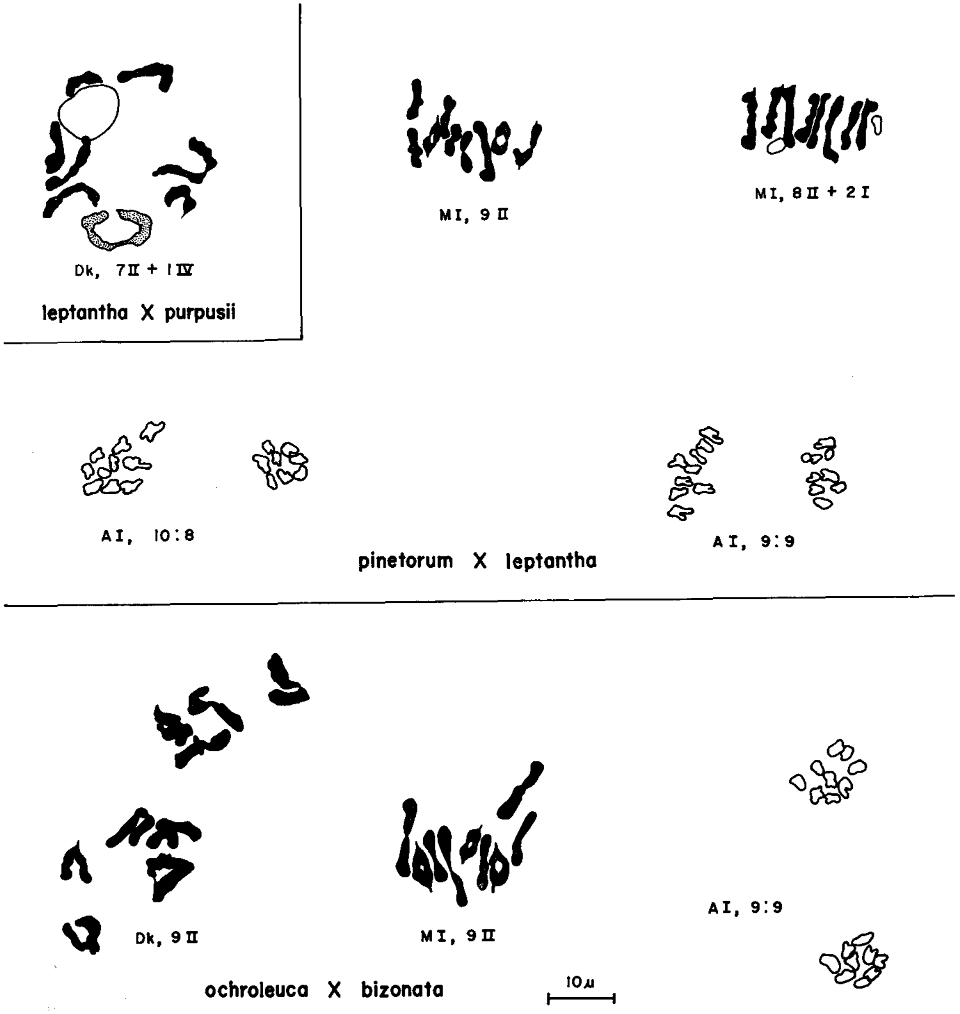

FIG. 13. Meiosis in interracial hybrids. *Gilia leptantha* above, and *Gilia ochroleuca* below. Bivalents shown black, univalents white, and chains stippled.

Two of the foregoing hybrids gave rise spontaneously to tetraploid F_2 progeny. The F_2 generations of *G. clokeyi* × *G. aliquanta* and *G. clokeyi* × *G. mexicana* each consisted of two individuals which were vigorous and fertile with 44 to 88% good pollen. These plants had 36 chromosomes. Pairing at metaphase was predominantly in 18 bivalents, or frequently as $17_{\text{II}} + 2_{\text{I}}$. Trivalents were occasionally seen. The meiosis of these tetraploids was however quite regular (Fig. 16).

A strong reduction in chromosome pairing is characteristic of the sterile interspecific hybrids between the *Gilia ochroleuca* group and the *G. tenuiflora* group. Seventy-three metaphase cells in the hybrid of *G. ochroleuca bizonata* × *G. latiflora latiflora* presented a range from zero to eight bivalents with the great bulk of the cells having three to six bivalents (Fig. 17). Only one cell among the 73 analyzed had as many as eight bivalents; this exceptional cell is depicted in Figure 17. Lagging of chromosomes was common at anaphase. Even lower pairing was found in the interspecific combination *G. ochroleuca bizonata* × *G. leptantha purpusii* with an average of three bivalents per cell.

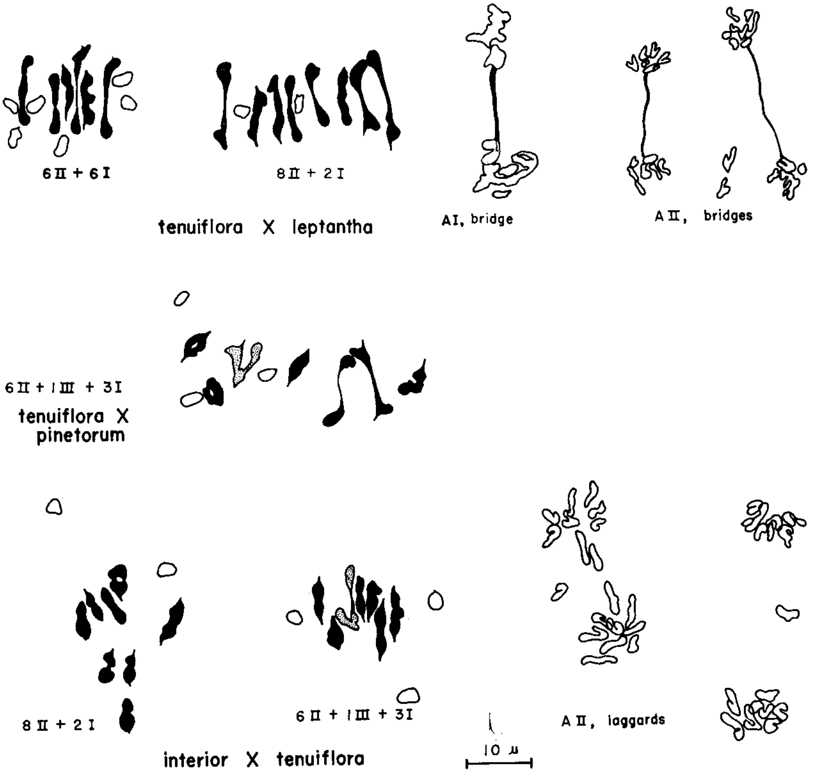

Fig. 14. Meiosis in interspecific hybrids in the *Gilia tenuiflora* group. Symbolism as in Figure 13.

Low pairing characterizes also the hybrids between the small-flowered members of the two species groups. Thus the hybrids of *G. minor* with *G. clokeyi, G. ochroleuca ochroleuca* and *G. mexicana* have average bivalent frequencies of 4.6, 2.8, and 1.7 respectively (Fig. 18). A translocation chain composed of a metacentric chromosome and two adjacent chromosomes with subterminal centromeres was seen repeatedly in the hybrid *G. clokeyi* × *G. minor* (Fig. 18).

Gilia cana speciosa and *G. ochroleuca vivida* within the *G. ochroleuca* group form hybrids with the large-flowered species of the *G. tenuiflora* group which have a higher degree of pairing than that just described (Fig. 17).

Gilia diegensis and *G. brecciarum brecciarum* which cross fairly freely and produce a semifertile hybrid also show much (though incomplete) chromosome homology at meiosis. The average bivalent frequency for 45 PMC's was 7.8; the maximum of nine bivalents was found in six of these cells; most cells had eight or seven bivalents. Chains of three chromosomes were not uncommon. Pairing in the hybrids of the *G. brecciarum* group with the *G. ochroleuca* group was strongly reduced.

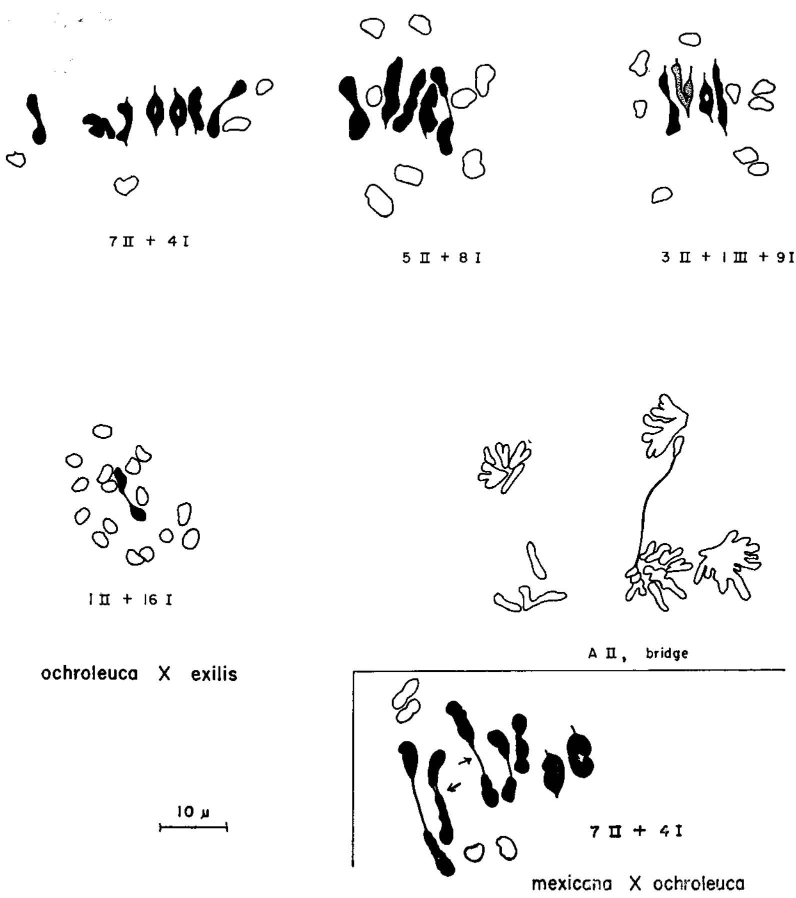

FIG. 15. Meiosis in interspecific hybrids in the *Gilia ochroleuca* group. *Gilia ochroleuca ochroleuca* × *G. exilis* above, *G. mexicana* × *G. ochroleuca ochroleuca* below. Note two heteromorphic bivalents indicated by arrows. Symbolism as in Figure 13.

The reduction in chromosome pairing which is so characteristic of the species hybrids in the Cobwebby Gilias is probably due in large measure to differences in the structural arrangement of the different species. Many of the associations of three and four chromosomes observed at metaphase in the hybrids appear to be translocation chains. Many though not all of the anaphase bridges are probably the result of crossing over in inversions.

Heteromorphic bivalents are found commonly in the hybrids. Many were seen in *G. diegensis* × *G. exilis, G. ochroleuca bizonata* × *G. cana speciosa, G. ochroleuca bizonata* ×

G. latiflora latiflora, G. mexicana × *G. ochroleuca ochroleuca, G. clokeyi* × *G. mexicana*, and *G. clokeyi* × *G. minor*. The cell of *bizonata* × *latiflora* with $8_{II} + 2_{I}$ shown in Figure 17 has a bivalent composed of one large and one small chromosome on the righthand side of the figure; it will be noted that the leftover univalents also differ in size. Heteromorphic bivalents are shown also in Figures 15, 16 and 18 for three other hybrids.

The recovery of bivalent pairing in the tetraploid progeny of two of the hybrids which

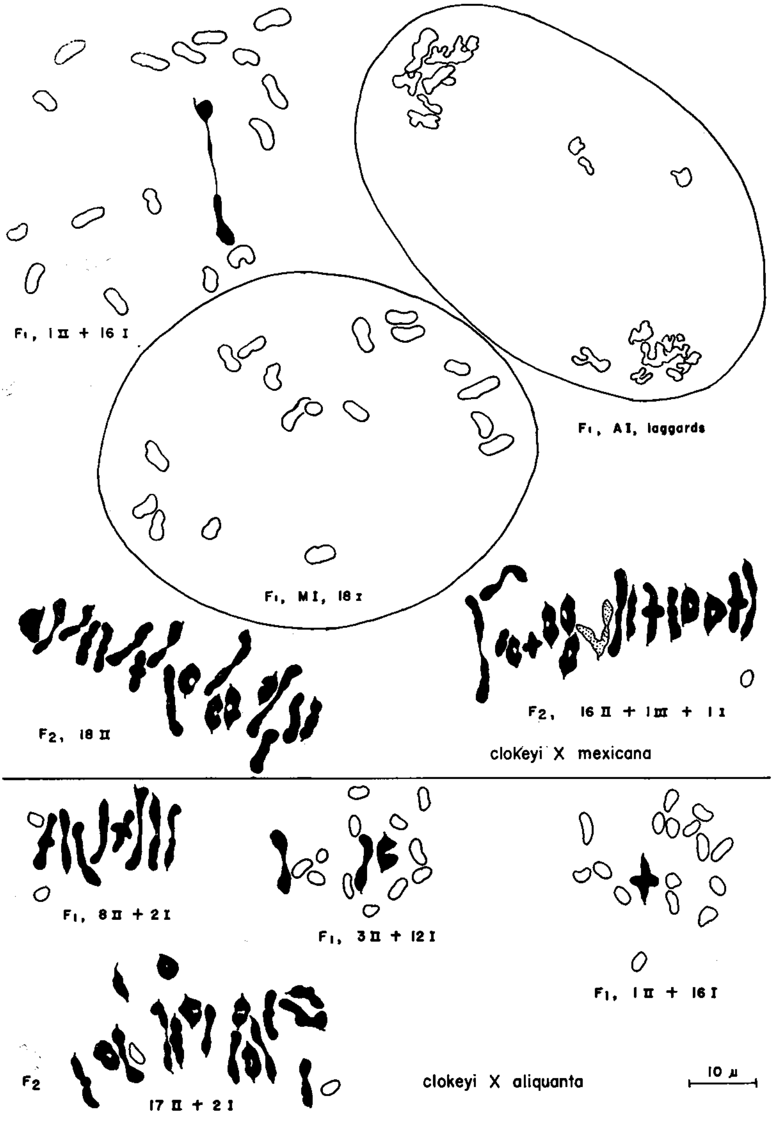

FIG. 16. Meiosis in two diploid hybrids of *Gilia clokeyi* and in their tetraploid F_2 progeny. *Gilia clokeyi* × *G. mexicana* above, *G. clokeyi* × *G. aliquanta* below.

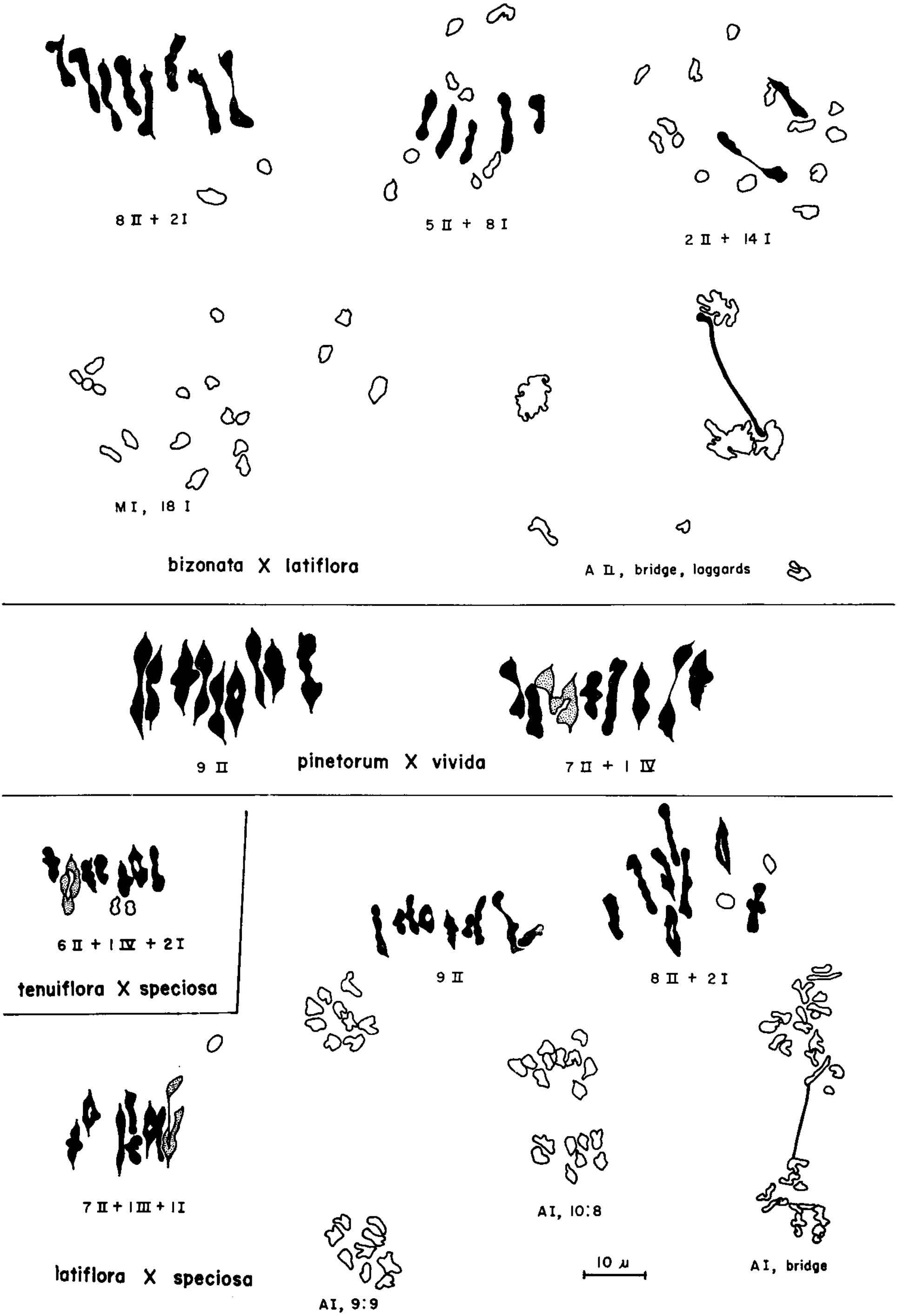
8 II + 2I
5 II + 8 I
2 II + 14 I
MI, 18 I
bizonata X latiflora
A II, bridge, laggards
9 II
pinetorum X vivida
7 II + 1 IV
6 II + 1 IV + 2I
tenuiflora X speciosa
9 II
8 II + 2 I
AI, 10:8
7 II + 1 III + 1 I
latiflora X speciosa
10 μ
AI, bridge
AI, 9:9

FIG. 17

had reduced pairing on the diploid level is further evidence for the structural differentiation of the chromosomes of the species involved.

The reduction in pairing seen at metaphase does not appear to represent a falling apart of bivalents formed earlier in meiosis. The lack of pairing at metaphase appears rather to be a continuation of a situation which exists already in prophase. We can trace the asynapsis back to diakinesis and diplotene in some of the hybrids, as for example *Gilia minor* × *G. mexicana* (Fig. 18).

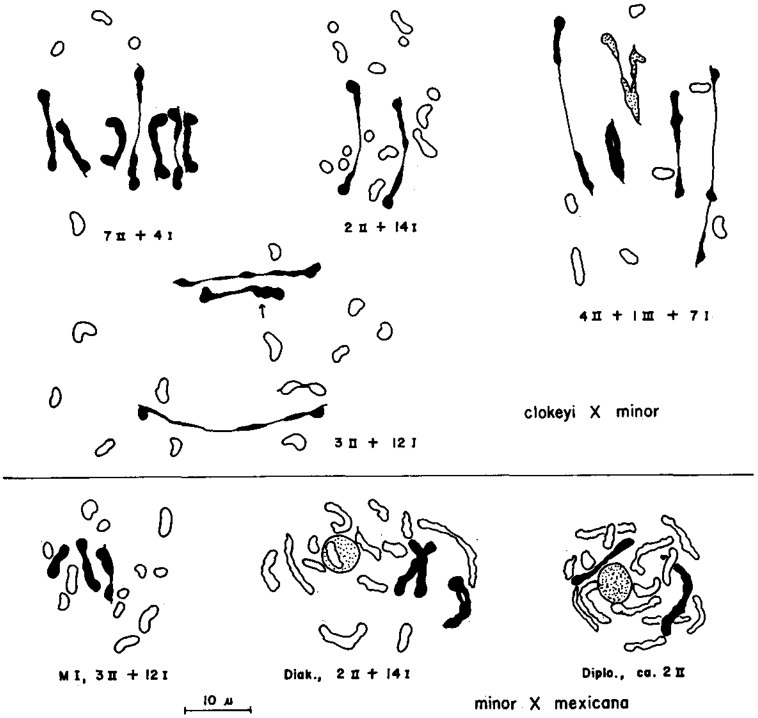

FIG. 18. Meiosis in hybrids between autogamous members of the *Gilia ochroleuca* group and the *G. tenuiflora* group. *Gilia clokeyi* × *G. minor* above. Note dividing univalent near the attenuated bivalent; note also the heteromorphic bivalent marked by the arrow. *Gilia minor* × *G. mexicana* below.

There is a good general correlation between degree of chromosome pairing and degree of fertility of a hybrid, and it is fair to conclude that much, though probably not all, of the hybrid sterility is due to aberrations of meiosis and the consequent formation of unbalanced chromosome complements in the meiotic products. The races and species of the *Gilia tenuiflora* group, for example, are genomically similar and form fertile or semifertile hybrids. The genomically distinct *Gilia tenuiflora* and *G. ochroleuca* groups, on the other hand, are highly intersterile. But this intersterility of the two groups is least where the chromosome

FIG. 17. Meiosis in hybrids between the large-flowered members of the *Gilia ochroleuca* group and the *G. tenuiflora* group. *Gilia ochroleuca bizonata* × *G. latiflora latiflora* above; *G. leptantha pinetorum* × *G. ochroleuca vivida* in the middle; *G. tenuiflora* × *G. cana speciosa* at middle left; and *G. latiflora latiflora* × *G. cana speciosa* below.

homology is greatest, as between *G. cana* and the large-flowered species of the *G. tenuiflora* group. In the case of two hybrids and their polyploid derivatives, sterility was correlated with poor chromosome pairing in the F_1 generation and fertility with regular bivalent pairing in the F_2.

The pairing data can be condensed in the following statements. (1) One genome occurs with modifications throughout the *Gilia tenuiflora* group. We may call this the T genome. (2) *Gilia ochroleuca, G. exilis, G. cana* and *G. mexicana* possess related but differentiated genomes. A genome which may be designated **O** is common to these species but takes a different form in each species, thus O_{och}, O_{ex}, O_{can}, O_{mex}. (3) A third genome, **C**, is found in *Gilia clokeyi.* (4) The chromosomes of *G. aliquanta* are structurally different from those of *G. clokeyi.* We have not yet had a hybrid between *G. aliquanta* and *G. ochroleuca* or its relatives available for cytological analysis. Direct evidence regarding the chromosome homology between these two species is thus lacking, and so we do not know whether the chromosomes of *G. aliquanta* comprise another subgenome of the **O** group or whether they form a separate genome. (5) *Gilia brecciarum* and *G. diegensis* have related but well differentiated chromosome sets, which may be designated collectively as the **B** genome, and individually as the subgenomes $\mathbf{B}_{br}$ and $\mathbf{B}_{di}$. The **B** genome is known to pair poorly with the **O** genome, but its pairing relations with the **T** genome remain to be determined. These categorical generalizations are shown graphically in Figure 19.

The designation of well differentiated genomes by different letters and subgenomes by the same letter with different subscripts is apt to imply a qualitative distinction which does not exist. Chromosomes of the **O** genome are able to pair to some extent with chromosomes of the T genome. Conversely, hybrids between closely related taxa produce occasional pollen mother cells with low pairing. The amount of homology between two chromosome sets is a relative matter. Furthermore, the degree of pairing at metaphase I is not a precise measure of homology anyway. Bivalent formation is the result of various factors which cannot usually be separated in practice; it is not only the result of structural homology but is affected also by meiotic genes, chiasma frequency, chromosome length, and various environmental conditions.

Nevertheless, a genomic classification may be a useful device for grouping and simplifying a body of data so that the overall pattern can be grasped. No harm can come from such an exercise so long as the complexities are duly recognized. In this respect a genomic classification is no different from other kinds of classification used in biology. All classifications of biological materials are oversimplifications of complex phenomena, but we could not operate without them.

VIGOR OF THE F_2s

Weak, dwarfed and semilethal types were found in the progenies of a majority of the hybrids grown (see Table 6). An F_2 generation often displayed a continuous variation from fully vigorous individuals through plants slightly smaller or weaker than normal to obviously inviable types. In such cases scoring the seedlings into just two categories, vigorous and inviable, for the purpose of calculating percentages was an uncertain operation, and the figures given in Table 6 consequently represent general trends rather than precise measures.

The F_2 progeny of *G. latiflora latiflora* ♀ × *G. leptantha leptantha* can be compared with the progeny from the reciprocal cross, *leptantha* ♀ × *latiflora,* from the standpoint of vigor. Seventy-one percent of the F_2s of *latiflora* × *leptantha* but only 29% of the F_2s of *leptantha* × *latiflora* were vigorous. There were many more runts in the latter F_2 population than in the former. The gametic fertility of the reciprocally different F_1 hybrids and the germination of the two lots of F_2 seeds were nearly equal.

Many inviable genotypes were apparently eliminated in the stage of seed germination.

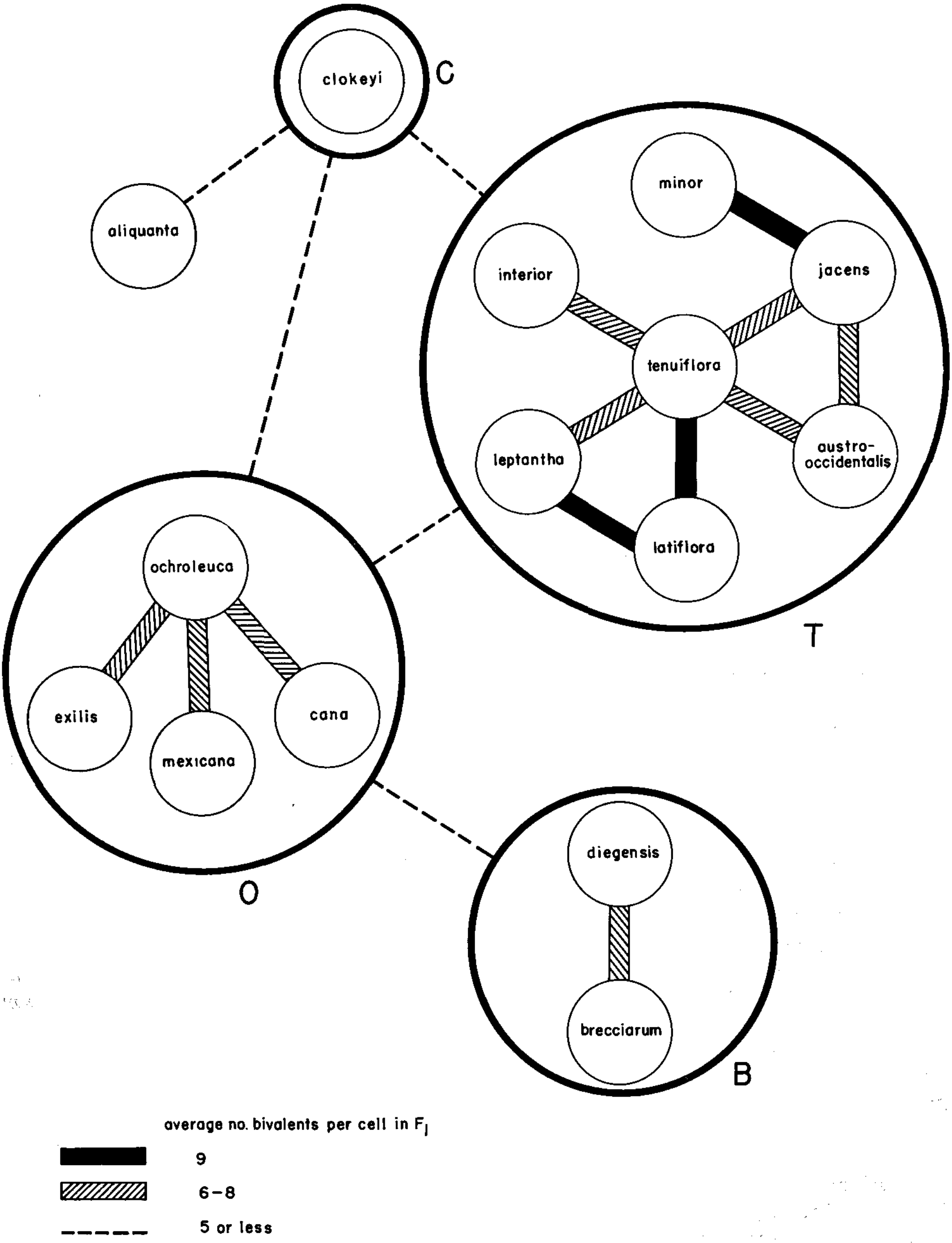

FIG. 19. Genome groups.

The low germination percentages of F_2 seeds recorded in Table 6 are partly a manifestation of hybrid breakdown and partly due to the normally reduced and erratic germination of the parental strains themselves. Thus 4000 F_2 seeds of *G. ochroleuca ochroleuca* × *G. o. bizonata* gave rise to only 98 seedlings. This represents a germination of 2% which could cover up a great deal of hybrid breakdown in an early embryonic stage. We cannot be sure that cryptic hybrid breakdown is occurring here, however, because we often get as little as 2% germination from seed lots of the *ochroleuca* parent.

On the other hand it is significant that some F_2 populations show high germination and a low frequency of vigorous seedlings *(G. ochroleuca bizonata* × *G. latiflora latiflora),* while other F_2s have low germination but a relatively high level of vigor in the seedling stage *(G. ochroleuca bizonata* × *G. leptantha purpusii)*. Such cases can readily be explained by the hypothesis that a certain proportion of inviable genotypes is weeded out of an F_2 population either at the stage of germination or during seedling growth. Some of the reduced seed germination in at least some of the F_2 populations is attributable to hybrid breakdown.

The sterile hybrids *G. clokeyi* × *G. mexicana* and *G. clokeyi* × *G. aliquanta* produced 26 and two seeds respectively which developed into two vigorous individuals in each cross. These F_2 progeny were tetraploid and fertile. The two F_2 individuals of *G. clokeyi* × *G. mexicana* had 44 and 88% good pollen, and the two individuals in the F_2 of *G. clokeyi* × *G. aliquanta* 62 and 80% good pollen.

RELATIONSHIPS OF ARACHNION TO OTHER SECTIONS OF GILIA

Numerous attempts have been made to cross Cobwebby Gilias with related sections of the genus, the Leafy-stemmed Gilias and the Woodland Gilias. The most commonly used strains of Cobwebby Gilia have been *G. tenuiflora* from Arroyo Seco and *G. latiflora latiflora* from Apple Valley; *G. ochroleuca bizonata* and *G. o. vivida* have also been employed in the crossings. These Cobwebby Gilias were intercrossed with *G. tricolor, angelensis, achilleaefolia, capitata staminea, clivorum,* and *laciniata* among the Leafy-stemmed Gilias, and with *G. splendens, australis,* and *stellata* among the Woodland Gilias.

In all, 442 flowers were pollinated in crosses between the sections *Arachnion* and *Gilia* (Leafy-stemmed Gilias), and 86 flowers in crosses of *Arachnion* with *Saltugilia* (Woodland Gilias). Almost the only result of these crossings was the production of abortive seeds. The average number of sound seeds obtained per flower pollinated in the intersectional crosses was 0.004. This figure can be compared with an average yield of 3.7 plump seeds per flower from all interspecific crosses within the section *Arachnion.*

Two sound seeds were harvested following the cross-pollination of 12 flowers of *G. tenuiflora* by *G. achilleaefolia* from San Luis Obispo (sect. *Gilia*). Two F_1 hybrids were grown in 1950. They were weak and never produced anthers or seeds. Attempts to repeat the cross in a subsequent year were unsuccessful.

We have never been able to produce an artificial hybrid between *Arachnion* and *Saltugilia.* However Mr. E. K. Balls collected sterile hybrids of *G. cana triceps* × *G. scopulorum* (sect. *Saltugilia*) growing with the parental species in the Panamint Mts. in 1958.

These findings show that Cobwebby Gilias can cross very rarely with Leafy-stemmed and Woodland Gilias. The other two sections of the genus, *Giliastrum* and *Giliandra,* are more distantly related.

NATURAL RELATIONSHIP

Relationship in the evolutionary sense may be defined as "the degree of genotypical similarity" (Müntzing 1930: 323). There are many indicators of genotypical similarity: morphological likeness, ecological and geographical distribution, ease of crossing, vigor and fertility of hybrids, extent of chromosome pairing. No one of these is an infallible criterion.

Morphological similarity may arise by parallel evolution as well as by descent from a common ancestor. Conversely, related taxa may appear dissimilar morphologically as a result of the predominating action of a relatively few genes. The sum total of the genotypic similarities is greater between the morphologically different but interfertile *Gilia diegensis* and *G. brecciarum brecciarum* than between the morphologically and ecologically similar but intersterile *G. diegensis* and *G. leptantha pinetorum.*

This is not to imply that interfertility necessarily takes priority over morphological resemblances in estimating the degree of relationship. The various elements in a fertility relationship, such as crossability, hybrid fertility, and chromosome pairing, may reflect general genotypic similarities, but they may also reflect the action of a few particular genes. The biotypes I and II of the Dripping Springs race of *Gilia exilis* are perfectly interfertile and differ in only a few genes. If we knew only the crossing behavior of Biotype II with *G. ochroleuca bizonata* we would judge that *Gilia exilis* and *Gilia ochroleuca* were moderately compatible with one another; if we were to base our judgments on hybridization experiments involving only Biotype I we would conclude that the two species were highly incompatible.

Low chromosome pairing in hybrids may reflect differences of a very fundamental sort between the genomes of the parental species. It may also reflect the action of one or a few genes, which are capable of obscuring close genomic relationships. This hazard of genome analysis has been discussed among others by Gaul (1954). Several of the hexaploid species of *Geum* sect. *Eugeum,* such as *Geum rivale, urbanum, molle, silvaticum* and *hispidum,* have homologous or partly homologous genomes. Hybrids of *Geum macrophyllum* and related species with the main branch of the section are asynaptic. But this does not mean that *Geum macrophyllum* and its relatives fall in a different genome group, for certain combinations like *Geum macrophyllum* × *G. aleppicum* do show full chromosome pairing. The low pairing in most hybrids of *G. macrophyllum* is probably genic rather than structural in origin (Gajewski, 1957, 1959).

As Gajewski points out (1957: 349), "... In the group of species from the genus *Geum* covered by the present investigation no simple relation is apparent between hybrid fertility and the systematic position, the degree of morphological differentiations or the degree of polyploidy of the parental species. . . . The processes of morphological and cytological differentiation only partly coincide with the physiological and genic differences on which hybrid sterility depends."

One or a few gene differences can thus produce effects on the morphology, crossability, fertility or cytology of hybrids similar to the effects of extensive genotypic differentiation during phylogenetic divergence. Because of the ever present possibility that fundamental genotypic similarities may be hidden from view by a few gene-controlled processes, we are on safer ground in inferring close relationships where we find positive evidence for them than in postulating remote relationships on negative evidence. Evidences of close relationship between two taxa are conclusive. Evidences of distant relationships must be looked at critically and checked against the possibility that they are an expression of relationship-obscuring genes.

A further consequence of the potential effects of particular genes in hybridization studies is that we must take our evidences of relationship where we find them, to borrow an axiom from classical taxonomy. We cannot arrange comparative morphology, fertility data, and cytological evidence in any kind of hierarchy for the assaying of relationships. Our glimpse into the degree of similarity between any two genotypes may be afforded by one kind of evidence in one instance and by another kind of evidence in another instance. Whichever line of evidence does reveal closeness of relationship must be weighed heavily in the final synthesis.

It follows that we cannot simply throw the different types of data, those from morphological, fertility, and chromosomal studies, into a hopper and count on receiving in the discharge a more reliable estimate of relationships than we would arrive at by a use of critical judgment. The idea of an aggregate index of genotypical similarities, in which the separate lines of evidence are pooled, sounds attractive enough in theory. For the present at least the working biosystematist usually finds it necessary to proceed like the classical taxonomist before him; that is, he weights his data before he adds them. The biosystematist may consider a larger number of lines of evidence than the classical taxonomist could, but he has not given up the use of taxonomic judgment.

All degrees of genotypical similarity or dissimilarity exist. We find a wide range and many intermediate conditions of relationship among the diploid Cobwebby Gilias studied in this investigation. This fact increases the desirability of placing the study of natural relationships on a quantitative basis. The desirability and the feasibility of having a quantitative measure of genotypical similarity are, however, two entirely different matters. But even though we cannot quantify the different degrees of relationship found in the Cobwebby Gilias, we can still recognize certain modal conditions, which will be described in the next section.

PATTERNS OF RELATIONSHIPS IN THE COBWEBBY GILIAS

Gilia ochroleuca consists of three well differentiated geographical races: *G. o. bizonata* in the pinyon-juniper zone of the South Coast Ranges and southern Sierra Nevada; *G. o. vivida* on the crest of the San Gabriel Mts.; and *G. o. ochroleuca* in the Mojave Desert. These races cross freely (with the exception of combinations between the small-flowered and large-flowered forms), and the F_1 hybrids are highly fertile with normal meiosis.

The three large-flowered species of the *Gilia tenuiflora* group are largely allopatric but overlap on the margins of their ranges (Fig. 20). *Gilia tenuiflora* occurs in the interior valleys of the South Coast Ranges and on the coast at Monterey Bay and on Santa Rosa Island. *Gilia leptantha* is distributed in a series of disjunct areas in the pine belt of the southern California mountains and extends into the western margin of the Mojave Desert. *Gilia latiflora* occurs on sandy plains and valleys of the western Mojave Desert, ranging through Antelope Valley to the arid interior valleys of the South Coast Range. Each of these species is composed of well differentiated, intergrading races which have been given formal recognition as subspecies.

The races composing these species are interfertile. So in general are the species themselves. The compatibility and sterility barriers and the meiotic irregularities are not significantly greater between *G. tenuiflora, G. leptantha* and *G. latiflora* than they are between the subspecies within each of these species.

The three large-flowered species in the *Gilia tenuiflora* group have largely allopatric distributions, sometimes hybridize naturally along their zones of contact, and are known to be interfertile. If consideration were to be given only to these facts the taxa might be combined into one large polytypic species.

On the other hand, the morphological differences between the three main constituents of the *Gilia tenuiflora* group are as great as those which accompany good species barriers elsewhere in the genus *Gilia* and indeed in the section *Arachnion.* Furthermore, these entities coexist sympatrically in various combinations without extensive hybridization. As shown in Figure 20, both *G. tenuiflora* and *G. latiflora* occur in the inner Coast Range valleys of San Luis Obispo County from Cholame to Simmler. *Gilia latiflora* and *G. leptantha* occur close together on Mt. Pinos and on the desert slopes of the San Gabriel and San Bernardino Mts. Reducing the three species to one huge polytypic species would misrepresent their morphological and geographical relationships.

For purposes of formal taxonomy we suggested in 1956 and still believe that *Gilia tenuiflora, G. leptantha* and *G. latiflora* should be treated as separate species. As evolutionists we may add that they appear to form a closely related assemblage, the major members of which are at a stage of divergence just beyond that of geographical races but falling short of that characterizing mature species. This divergence involves genetic factors determining different morphologies, different ecological requirements, and partial internal barriers to gene exchange. It is perhaps appropriate to regard *Gilia tenuiflora, G. leptantha* and *G. latiflora* neither as species nor subspecies but as "semispecies" (Grant, 1957).

Similar considerations apply in the case of *Gilia ochroleuca* and *G. exilis*. These two entities are closely related and are largely but not entirely allopatric. *Gilia exilis* occurs mainly to the south of *G. ochroleuca* in the mountains of southern California, but isolated stations are found far to the north within the territory of *G. ochroleuca bizonata*. Some sympatric occurrences and a definite sterility barrier argue in favor of placing *G. ochroleuca* and *G. exilis* in separate species. Yet it must be admitted that this separation cannot be consistently maintained on grounds of morphology and the range of variation.

Whatever doubts may be entertained regarding the taxonomic treatment of some of the entities within either group, the specific status of the groups themselves is quite clear. *Gilia ochroleuca* is sympatric with different representatives of the *Gilia tenuiflora-leptantha-latiflora* group over an extensive area in southern California (Fig. 21). Populations of the two groups grow side by side in numerous localities without hybridization.

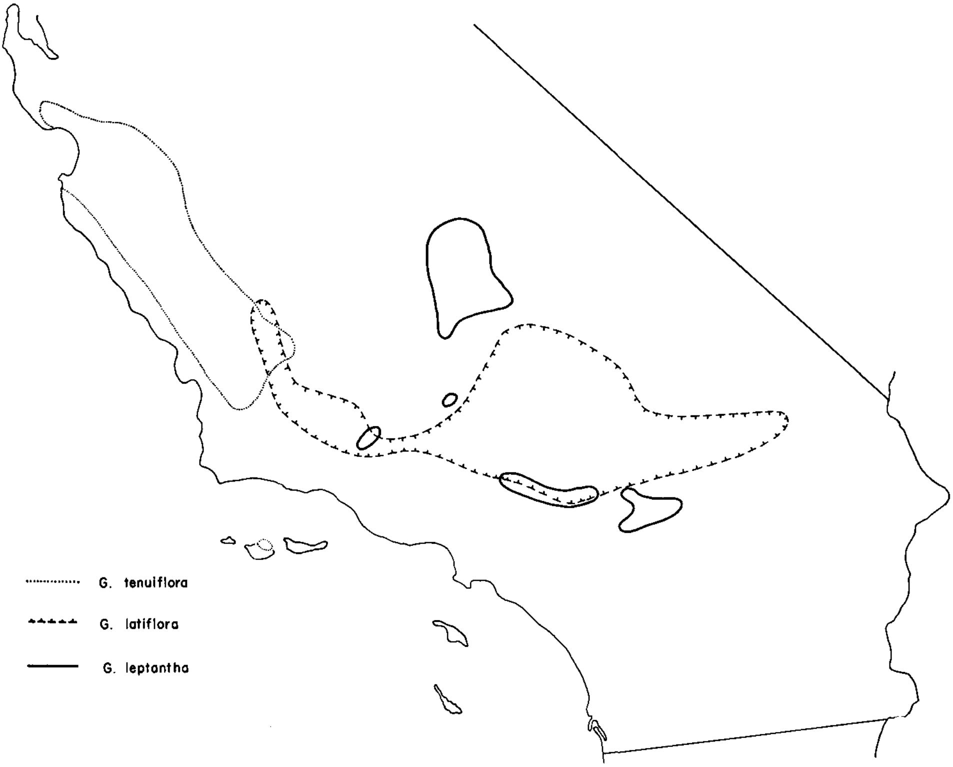

FIG. 20. Geographical relationships of *Gilia tenuiflora, G. leptantha,* and *G. latiflora.*

A whole complex of characters differentiates *Gilia ochroleuca bizonata, G. exilis* and *G. cana triceps* on the one hand from the *G. tenuiflora-leptantha-latiflora* assemblage on the other, which is why they have been placed in different species groups. The ultimate pairs of flowers in the inflorescence are borne on pedicels of nearly equal length in the *Gilia ochroleuca* group and on very unequal pedicels in the *G. tenuiflora* group. The corolla throat is full and abruptly expanded in the first group and gradually flaring in most members of the second group. The upper corolla throat and orifice are pale violet in the first group, whereas a rim of white is present in the orifice in the second. In the *G. ochroleuca* group the stamens are subequal and the capsule globular; in the *G. tenuiflora* group the stamens are quite unequal and the capsule oblong-ovoidal.

These morphological differences are among the most extreme found in the section *Arachnion.* They mark a basic and original divergence in the phylogeny of the section.

Ecologically, *Gilia ochroleuca bizonata* occurs in pinyon-juniper woodland, an old and stable plant community. Most of the races of *Gilia leptantha* occur in another relatively old community, the yellow pine forest. It is logical to assume that the species associated with ancient vegetation types are more likely to be ancient themselves than related species occurring in desert habitats of recent origin. The ecological associations of some members of the *Gilia ochroleuca* and *G. tenuiflora* groups thus support the hypothesis that these taxa are ancient in comparison with most of their congeners. If these species are ancient, then the event of speciation which marked their divergence must also have occurred relatively early in the phylogeny of the section.

The extreme morphological divergence and the extensive sympatry of *Gilia ochroleuca-exilis* and *Gilia tenuiflora-leptantha-latiflora* point to the conclusion that these two groups have reached the stage of full-fledged species. The taxogenetic evidence is in agreement with the other lines of evidence. There is a very strong sterility barrier between the two groups. Chromosome pairing is much reduced in their hybrids.

The two divergent lines of evolution have not, however, remained completely isolated during their history of sympatric contacts. They have hybridized sporadically. This hybridization has led to the formation of some of the existing taxa. The large-flowered Cobwebby Gilia on the crest of the San Gabriel Range, the taxon *vivida,* is a member of the *Gilia ochroleuca* fertility group and constitutes a geographical race of that species. Yet it possesses a complex of morphological characters which point to a relationship with the *Gilia tenuiflora* group and which account for its having been described originally as a subspecies of *G. leptantha.* It could have acquired these characters most readily by introgression from *Gilia leptantha* into a preexisting population of *Gilia ochroleuca* with features like those still preserved in *G. o. bizonata.*

The chromosome pairing relationships of *vivida* are very interesting. Whereas the hybrids of *G. ochroleuca bizonata* with *G. leptantha* have an average of three bivalents per cell at metaphase and a range of zero to seven, the hybrids of *G. ochroleuca vivida* with *G. leptantha* show much better pairing, with a mean of seven and a range of four to nine bivalents.

Gilia cana is classified in the *G. ochroleuca* group on the basis of its morphological characters. However, most races of *G. cana* approach the *G. tenuiflora* group morphologically and have probably derived many of their features from that group by introgression. In short, *Gilia cana* is somewhat intermediate between the two species groups but fits more naturally into the *G. ochroleuca* group than in the *G. tenuiflora* complex.

As Figure 6 shows, *Gilia cana* crosses more easily with the *G. tenuiflora* group than does any other member of the *G. ochroleuca* group. In fact the crossability between *Gilia cana* and *G. tenuiflora-leptantha-latiflora* is about the same as that between the latter three semispecies themselves. The average number of plump seeds harvested per flower was 7.3 for all crosses between *G. cana* and *G. tenuiflora, leptantha* and *latiflora;* the corresponding figure for the interspecific crosses between *G. tenuiflora, leptantha* and *latiflora* was 7.4

The artificial hybrids of *Gilia cana* with the large-flowered species of the *G. tenuiflora* group are fertile or semifertile. One hybrid observed in nature was highly sterile. The fertility of the artificial hybrids is associated with a relatively high degree of chromosome pairing, the average bivalent frequency being 7.9, 8.4 and 8.7 in different hybrid combinations between the two groups. For comparison, *Gilia ochroleuca bizonata* forms on the average only three or four bivalents in hybrids with the same members of the *G. tenuiflora* complex.

Gilia cana and *G. ochroleuca vivida,* which have independently acquired germplasm from the *G. tenuiflora* group, produce a semifertile hybrid with an average of eight bivalents per cell. The hybrid of *G. cana* with *G. ochroleuca bizonata* was by contrast completely sterile and had a mean of five bivalents in each nucleus.

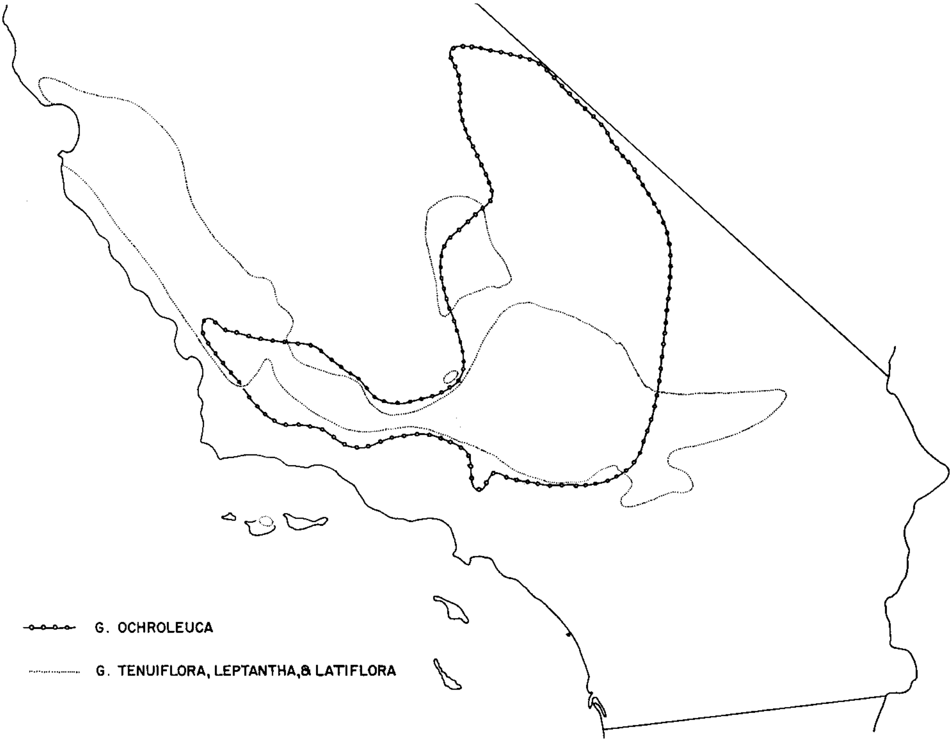

FIG. 21. Geographical relationships between *Gilia ochroleuca* and the *G. tenuiflora-leptantha-latiflora* assemblage.

It is interesting that both the morphological gap and the sterility barrier between the *Gilia ochroleuca* and the *G. tenuiflora* groups should be partially bridged in two taxa, *G. o. vivida* and *G. cana,* which are probably of hybrid origin between the species groups. The two ways in which the populations *vivida* and *cana* reveal their relationship to the *G. tenuiflora* group, their morphological resemblances and interfertility, could have a common cause. The chromosomes of *vivida* and *cana* are more similar in structural arrangement to the *G. tenuiflora* genome than are the chromosomes of other, more extreme members of the *G. ochroleuca* group. The introgression from one species group into the other was an influx of chromosome segments which would be expected to affect both the visible traits and the chromosome pairing relationships of the recipient population.

There are theoretical grounds for expecting that long-continued hybridization between intersterile species should lead, under conditions of cross-fertilization, to the elimination of the sterility barrier as a result of the smoothing out of the genomic differences (Grant, 1958). The cross-fertilizing taxa, *G. ochroleuca vivida* and *G. cana,* which in all probability originated from hybrids between intersterile members of the *G. ochroleuca* and *G. tenuiflora* groups, bridge the sterility barrier between the ancestral species groups, as demanded by the hypothesis. The genotypic similarities between two phylads may become greater or less during the course of their evolutionary history.

The existence of bridging genomes presents one more difficulty for genome analysis in addition to those arising from the influence of meiotic genes, of cytological conditions unrelated to structural homology, or of environmental factors. Suppose that two species, A and B, differ in enough structural arrangements so that bivalent formation cannot take place normally in their hybrid. A third entity of introgressive origin, A_b, however, has a greater number of structural arrangements in common with A than B does, and similarly A_b is more homologous with B than A is. The chromosomes of A_b can pair frequently with their partial homologues in either the A or the B genomes. The structural differences have been reduced by introgression up to a certain threshhold level where bivalent formation can take place regularly. If a taxogeneticist happens to work with the entity carrying the bridging genome, he may be misled into concluding that the chromosomes are more or less homologous throughout the entire group.

Genome analysis is usually carried out with a random collection of phylogenetically uncontrolled strains, representing what happens to be available to the investigator. The conclusions derived from genome analysis will be most reliable, however, when the investigator understands the group as a whole, and knows its taxonomic and geographical as well as its cytogenetic aspects. Then he will be in a better position to estimate whether the strains and taxa used as parental types represent introgressed or extreme members of the complex.

SUMMARY

The 15 diploid species of Cobwebby Gilia may be classified into three species groups on the basis of the combined morphological and genetic evidence. These groups, as shown in Table 1, are the *Gilia ochroleuca* group, the *G. tenuiflora* group, and the *G. brecciarum* group.

The races of several species are known to cross freely with one another to form fertile or semifertile hybrids with complete or nearly complete chromosome pairing.

The closely related species *G. tenuiflora, G. leptantha,* and *G. latiflora,* have largely allopatric but marginally overlapping distributions. These and some other species are more or less interfertile and possess different modifications of the same genome (T). Such incompatibility, sterility and inviability barriers as exist between the three species are not much stronger than those found between the races of one species.

Gilia ochroluca, G. exilis and *G. cana* form another group of interrelated species with largely but not entirely allopatric distributions. Sterility barriers of medium strength separate these species. These and other members of the *G. ochroleuca* group possess different but related subgenomes (O_{och}, O_{ex}, etc.).

Gilia ochroleuca and the *Gilia tenuiflora-leptantha-latiflora* complex occur sympatrically over an extensive area. The two phylads differ in a whole complex of morphological characters. Strong barriers to crossing exist between them. The hybrids that can be obtained are highly or completely sterile and have a low degree of chromosome pairing.

Natural hybridization between the divergent phylads has however given rise to certain taxa, namely *G. ochroleuca vivida* and *G. cana,* with relationships in both camps. These taxa are morphologically intermediate between the two species groups and bridge the sterility barrier which separates the extreme members of the opposing groups. The chromosomes of *G. ochroleuca vivida,* which belong to the O genome, are more similar in structural arrangement to the T genome than are the chromosomes of the morphologically extreme members of the *G. ochroleuca* group.

Gilia brecciarum and *G. diegensis* form a fertility group and genome group distinct from either the *G. ochroleuca* or the *G. tenuiflora* complex.

Hybridization between the Cobwebby Gilias and other sections of the genus is opposed by very strong incompatibility barriers. Only two intersectional hybrids are known, an artificially produced one between *G. tenuiflora* and *G. achilleaefolia* (a Leafy-stemmed Gilia), and a natural hybrid between *G. cana triceps* and *G. scopulorum* (of the Woodland Gilias). Both of these hybrids were completely sterile.

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