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GENETIC AND TAXONOMIC STUDIES IN GILIA

XII. FERTILITY RELATIONSHIPS OF THE POLYPLOID COBWEBBY GILIAS

VERNE GRANT

INTRODUCTION

The Cobwebby Gilias are a taxonomically complex group of annual plants indigenous to the deserts and mountains of western North America and southern South America. My collaborator, Miss Alva Day (formerly Alva Grant), and I have been studying this plant group in the wild, the herbarium, the experimental garden, and the cytological laboratory for some 16 years.

These studies have been carried on with two interrelated objectives in mind. One of these objectives is purely taxonomic: to achieve a natural, or at least a relatively natural, system of classification of the Cobwebby Gilias. The other, theoretically more important objective is to gain an understanding of the evolutionary processes at work within this complex plant group and of the evolutionary patterns resulting from those processes. The two objectives are interrelated insofar as a sound taxonomy is the necessary foundation for a valid theoretical superstructure.

Several previous publications represent steps in the approach to the aforementioned goals. The first of these was a general taxonomic revision of the Cobwebby Gilias, or section *Arachnion,* based on the information available in 1956 (Grant and Grant, 1956). The taxonomic treatment of 1956, while now known to be inadequate in many details, was indispensable for all subsequent research on the group. The extensive occurrence of polyploidy in the group, and the identification of the numerous diploid species, the numerous tetraploid species, and the single octoploid, with $N = 9$, 18, and 36 respectively, were reported by Grant, Beeks, and Latimer (1956) and Grant (1959, pp. 175 ff.). The strength and distribution of sterility barriers within and between the diploid species are described by Grant and Grant (1960). The purpose of the present paper is to present the parallel findings, as regards fertility relationships and sterility barriers, among the polyploid species of Cobwebby Gilias and between them and the diploids.

SYSTEM OF CLASSIFICATION OF THE POLYPLOID COBWEBBY GILIAS

The polyploid Cobwebby Gilias, like their diploid relatives, are winter-germinating, spring-blooming, scapose annuals, which form colonial populations in sandy places in deserts and mountains. They differ from the diploids in several traits, two of which, namely stature and flower size, warrant special mention here. Whereas the plants attain a relatively large size under good natural growing conditions in many of the diploid taxa of Cobwebby Gilias, and are inherently small-sized in other diploid taxa, the polyploid Cobwebby Gilias range from medium to small in stature, with a high proportion of small-sized forms. The numerous taxa of diploid Cobwebby Gilias are about equally divided between showy, large-flowered, insect-pollinated types and small-flowered autogamous types, but the polyploid Cobwebby Gilias with only one exception possess small inconspicuous flowers and reproduce autogamously.

It should be noted, further, that the autogamous polyploid Cobwebby Gilias, like autogamous plants generally, reproduce predominantly by self-fertilization, but also undergo occasional outcrossing, which leads to a limited amount of gene exchange within and between the colonies.

As a consequence of their generally reduced plant size and flower size, the various polyploid taxa of Cobwebby Gilias look much alike, and also resemble the reduced diploid taxa. There are morphological differences between the taxa, to be sure, which can be found with sufficient study, but these character differences are relatively minor and difficult to use in ordinary taxonomic practice. All the autogamous Cobwebby Gilias, diploid and polyploid alike, have in fact traditionally been placed in one or two taxonomic species.

The discovery of strong sterility barriers between the taxa indicates that the traditional arrangement falls far short of portraying the true biological complexity of the group. The reduced diploid Cobwebby Gilias are now known to fall into at least nine well isolated species (Grant and Grant, 1960). It will be shown in this paper that the polyploid Cobwebby Gilias likewise comprise some 12 biological species, as known at the present time.

These polyploid species can be grouped fairly naturally into three main species groups, as follows:

I. GILIA INCONSPICUA GROUP. Cobwebby hairs (on herbage) fine; leaves with narrow rachis, and sometimes with long lobes, not clasping at base; tetraploid. Western North America.

II. GILIA SINUATA GROUP. Cobwebby hairs fine as in group I; leaves with very broad to medium-broad rachis, and with short to medium-sized lobes, leaf base often clasping; tetraploid. Western North America.

III. GILIA CRASSIFOLIA GROUP. Cobwebby hairs more coarse; leaves with fairly broad to fairly narrow rachis, not clasping at base; tetraploid and octoploid. Argentina and Chile.

As noted in the introduction, the system of classification of the Cobwebby Gilias proposed in 1956, which was based mainly on field and herbarium studies, served a useful purpose as a framework for the subsequent hybridization experiments. The accumulation of much additional evidence since 1956, especially from the taxogenetic studies themselves, but also from continuing field and herbarium work, makes it necessary to revise the systematic framework in a number of ways. The species of polyploid Cobwebby Gilia that are known and recognized at present are listed below. They are introduced here as a preliminary to the presentation of the taxogenetic data.

I. GILIA INCONSPICUA GROUP

1. *Gilia tweedyi* Rydberg. Eastern Oregon to Wyoming (Fig. 2). More field work is needed to clarify the distributional and morphological limits of this species.

2. *Gilia inconspicua* (Smith) Sweet. (Fig. 1A.) Sagebrush plains in the northern Great Basin (Fig. 2). Populations in central and northern Nevada and Utah present some unsolved taxonomic problems involving this species and the next one, *G. transmontana,* and

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Fig. 1. Form of the plant body in six species of polyploid Cobwebby Gilia.—(A) *Gilia inconspicua,* Blue Mt. Pass.—(B) *Gilia malior,* Mohave.—(C) *Gilia ophthalmoides* I, northern Arizona.—(D) *Gilia sinuata,* Morongo.—(E) *Gilia modocensis,* near Doyle.—(F) *Gilia crassifolia* 8X, Tecka. (× ¼)

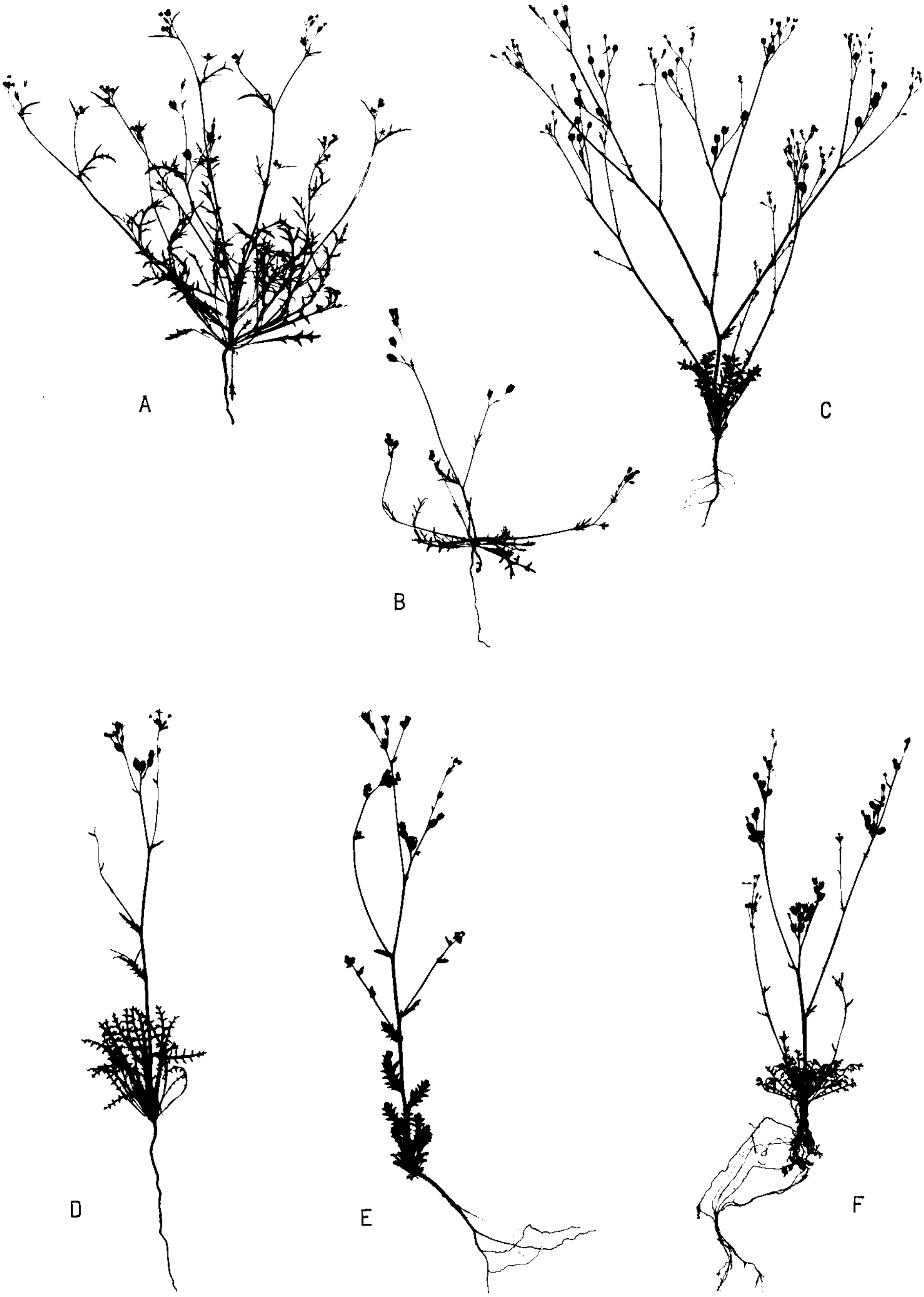

FIGURE 1

perhaps also *G. malior*. These problems cannot be solved in the herbarium, or even in the field alone, but will require further experimental work utilizing strains collected in the critical areas.

3. *Gilia transmontana* (Mason & A. Grant) A. Grant & V. Grant. Desert mountain slopes from the Mojave Desert to southwestern Utah (Fig. 2). Strains from different localities fall into two morphologically indistinguishable but intersterile series. The two fertility groups are not races in the usual sense, and will not be treated as subspecies, but on the other hand do not seem to be full-fledged sibling species either. The two known fertility groups are as follows:

(a) *G. transmontana* I. Mojave Desert, California.

(b) *G. transmontana* II. Beaverdam Mts., southwestern Utah, and probably also in southern Nevada.

4. *Gilia malior* A. Day & V. Grant. (Fig. 1B.) Desert foothills in the Mojave and Great Basin deserts, California and Nevada (Fig. 2). This species, formerly confused with *G. transmontana,* is relatively well understood now, as a result of intensive studies by Alva Day (Ph.D. thesis, in preparation).

5. *Gilia flavocincta* Nelson. Desert plains and valleys in the Sonoran Desert, Arizona and New Mexico (Fig. 2). In the revision of 1956 this entity was treated as a subspecies of *Gilia ophthalmoides,* which it resembles and largely replaces geographically. Subsequent field studies have revealed that the two entities are sympatric in central Arizona and remain distinct in their sympatric contacts. This observation together with the taxogenetic evidence to be presented later supports the separation of *G. flavocincta* from *G. ophthalmoides* as a distinct species. There are two morphologically different but interfertile and intergrading geographical races in *G. flavocincta.*

(a) *G. flavocincta* subsp. *flavocincta.* Large showy flowers. Central Arizona.

(b) *G. flavocincta* subsp. *australis.* Small inconspicuous flowers. Southern Arizona to New Mexico.

6. *Gilia ophthalmoides* Brand. (Fig. 1C.) Pinyon woodland in mountains from eastern California to Colorado and New Mexico (Fig. 2). The strains from different localities fall into three fertility groups. One or more of these, and particularly *G. ophthalmoides* III, may have to be elevated to the rank of species when more is known about the situation.

(a) *G. ophthalmoides* I. Widespread.

(b) *G. ophthalmoides* II. Sweetwater Mts., eastern California.

(c) *G. ophthalmoides* III. Mogollon Mts., New Mexico, and probably elsewhere in New Mexico and Arizona.

II. GILIA SINUATA GROUP

7. *Gilia sinuata* Douglas, hereafter referred to as *Gilia sinuata* I. (Fig. 1D.) Widespread in desert plains and washes in the Mojave Desert, Great Basin, and Colorado Basin, from California north to Washington and east to Colorado (Fig. 3).

8. *Gilia sinuata* II. Superstition Mts., Arizona, and probably elsewhere in the Sonoran Desert. This plant is recognizably different from the true *Gilia sinuata* (or *G. sinuata* I) of the more northern desert plains, and is intersterile with it. There are various reasons for believing that *Gilia sinuata* II may be a distinct species, and it is provisionally treated as such here, although more evidence is needed to confirm this suggestion and to justify the formal

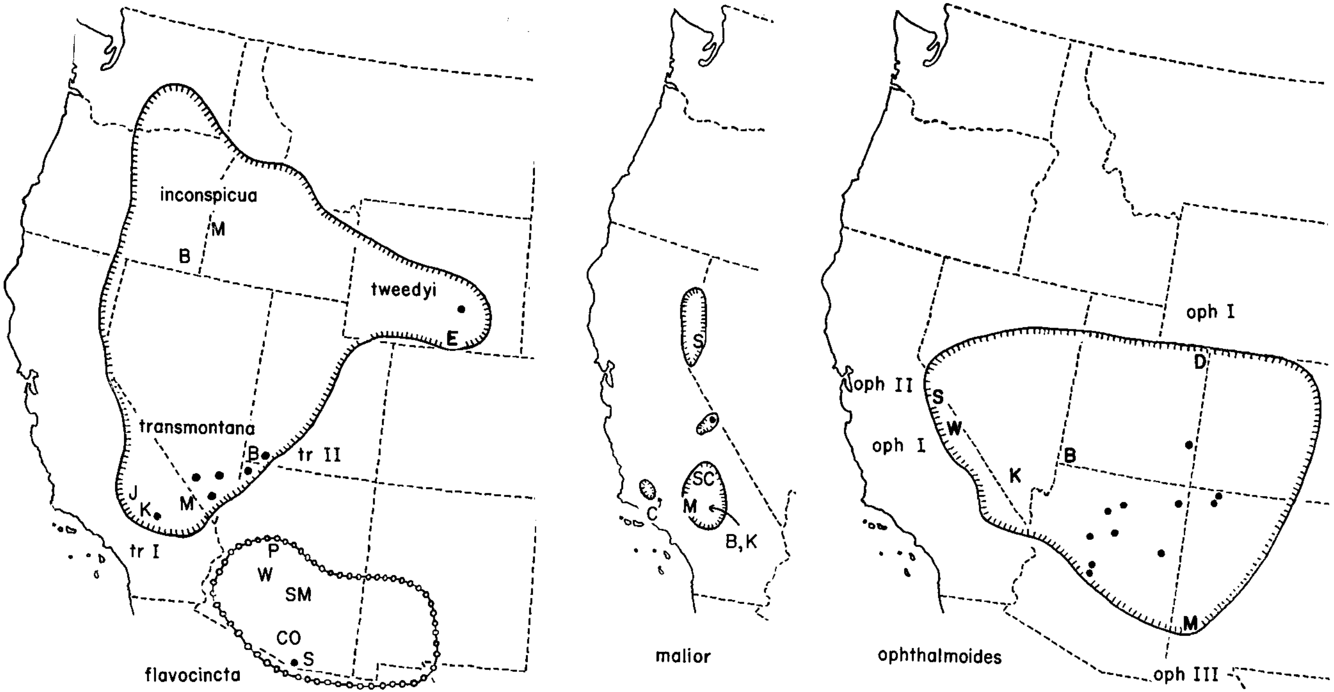

Fig. 2. Geographical distribution of the members of the *Gilia inconspicua* group. Local populations determined for chromosome number are shown as either dots or letters. Strains used in the crossing program are indicated by letters and are further identified in Table 1.

taxonomic description. *Gilia sinuata* II seems to have reached a higher level of evolutionary divergence from its congeners than have the intersterile populations in *Gilia transmontana.* It appears to be related to *Gilia sinuata* I in much the same way that *G. tetrabreccia* is related to *G. modocensis,* namely as a more or less localized allopatric species.

9. *Gilia modocensis* Eastwood. (Fig. 1E.) High desert plains from eastern Oregon through Nevada to southern California (Fig. 3).

10. *Gilia tetrabreccia* A. Grant & V. Grant. Mountain slopes on Mt. Pinos and neighboring mountains, south-central California (Fig. 3).

III. GILIA CRASSIFOLIA GROUP

11. *Gilia crassifolia* 4X. Plains and mountains, Argentina and Chile (Fig. 3). *Gilia crassifolia* Bentham, *sens. lat.,* encompasses a wide diversity of forms which need critical taxonomic study. Three strains have been grown and hybridized in Claremont from seeds kindly collected by Drs. A. Soriano and J. Hunziker in Argentina. Even this limited sample of strains proves to contain two specifically distinct forms, one tetraploid and the other octoploid, which will be referred to in this paper as *Gilia crassifolia* 4X and *G. crassifolia* 8X respectively.

12. *Gilia crassifolia* 8X. (Fig. 1F.) Patagonia (Fig. 3).

TAXONOMIC CHANGES

Two changes in the formal classification of the tetraploid Cobwebby Gilias will be made here. The first of these is the proposal of *Gilia flavocincta* subsp. *australis* as a new combination, and the second is the description of *Gilia malior* as a new species.

Gilia flavocincta subsp. **australis** A. Day & V. Grant, comb. nov.

Gilia ophthalmoides subsp. *australis* A. Grant & V. Grant, Aliso 3: 263. 1956.

Gilia malior A. Day & V. Grant, sp. nov.

Description.—Annual herb with erect central stem and leafy base; secondary branches somewhat decumbent, numerous in mature plants and arising from axils of basal leaves; middle internodes elongate, much exceeding the cauline leaves. Lower stems and leaves cobwebby-pubescent. Basal leaves pinnately lobed; rachis 1–2 mm wide; lobes linear, longer than the width of the rachis. Upper leaves much reduced, having a prominent central lobe and small lateral lobes. Inflorescence diffusely cymose, in 1–3–flowered units, each subtended by a bract. Flowers maturing in sequence on unequal pedicels which elongate strongly as capsules mature. Calyx lightly glandular-pubescent and often blotched or uniformly red-violet in color. Calyx sinus-membrane smooth or slightly puckered, U-shaped, high in the sinuses, or in one sinus deeper and V-shaped. Corolla 6–11 mm long, slightly exserted, or to twice as long as calyx; tube stout, gradually flaring into narrow throat; lobes oval, rounded at apex. Corolla tube and part of throat purple, generally blending into yellowish color above; uppermost throat yellow or white, or tube and throat entirely purple; lobes violet. Capsule ovoidal, included in, or sometimes slightly exserted from calyx at maturity, dehiscent along the valve sutures, and detachable from receptacle. Seeds medium to relatively large in size, weighing 30–60 mg each on the average. $N = 18$. (Fig. 1B.)

Herba annua, ramis ascenderibus; tubus corollae purpureus; capsula ovoidea; semina medio-grandis; planta tetraploidea.

Type.—V. Grant & A. Grant 10,053, buttes south of Mohave, Kern Co., California, March 14, 1958. Rancho Santa Ana Botanic Garden Herbarium 118,170.

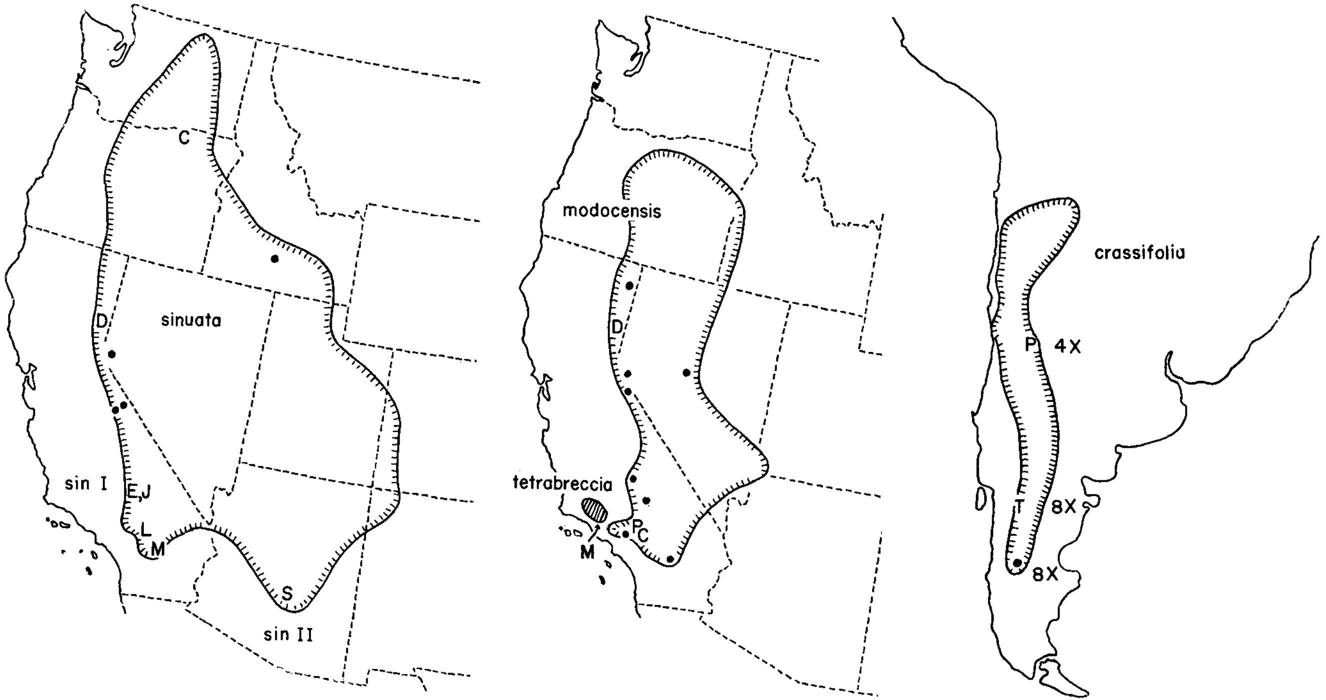

Fig. 3. Geographical distribution of the members of the *Gilia sinuata* group in western North America and of the *Gilia crassifolia* group in temperate South America. Local populations determined for chromosome number are shown as either dots or letters. Strains used in the crossing program are indicated by letters and are further identified in Table 1.

Range.—Arid foothills and plains, from 1800 to 5000 ft. elevation; western Mojave Desert north to the west-central Great Basin and west to the inner South Coast Ranges; southern California to northeastern California and northwestern Nevada. (See map in Fig. 2.)

Distinguishing Characters.—*Gilia malior* closely resembles and is easily confused with *G. transmontana, G. minor,* and *G. aliquanta.*

The plants now treated as *Gilia malior* were formerly placed in *G. transmontana.* In the previous taxonomic treatment of the latter species the authors stated: "The specimens interpreted as belonging to *G. transmontana* . . . may actually belong to more than one natural entity. The information is not yet at hand, however, for dealing with the variations in *G. transmontana* in a satisfactory way." (Grant and Grant, 1956, p. 266). Since 1956 Alva Day has made an intensive analysis of the problem, the main results of which will be reported elsewhere, enabling us to separate *G. malior* from *G. transmontana* proper as follows.

Gilia malior differs from the related tetraploid species, *G. transmontana,* in: (1) corolla lobe form (corolla lobes broad with rounded apex in *G. malior,* narrow with acute apex in *G. transmontana*); (2) corolla lobe color (corolla lobes violet in *G. malior,* pale-violet to white and the lower sides streaked with violet in *G. transmontana*); (3) corolla tube color (corolla tube deep purple in *G. malior,* weak purple striated with yellow in *G. transmontana*); (4) pollen color (bright blue in *G. malior,* pale blue in *G. transmontana*); (5) plant habit (secondary branches often strongly decumbent in *G. malior,* somewhat spreading but mainly erect in *G. transmontana*); and (6) seed size (seeds weigh 30–60 mg in *G. malior,* 20–30 mg in *G. transmontana*).

Gilia malior differs from *G. minor* in: (1) chromosome number ($2N = 36$ in *G. malior,* $2N = 18$ in *G. minor*); (2) capsule form and exsertion (capsule ovoidal and usually included in calyx in *G. malior,* subcylindrical and strongly exserted from calyx in *G. minor*); (3) capsule disarticulation (capsule valves detach from receptacle in *G. malior,* remain strongly attached to receptacle in *G. minor*); (4) calyx pubescence (calyx lightly glandular in *G. malior,* densely glandular in *G. minor*); (5) corolla lobe form (corolla lobes with rounded apex in *G. malior,* with pointed apex in *G. minor*); and (6) seed size (seeds weigh 30–60 mg. in *G. malior,* 10–20 mg. in *G. minor*).

Gilia malior differs from *G. aliquanta* in: (1) chromosome number ($2N = 36$ in *G. malior,* $2N = 18$ in *G. aliquanta*); (2) corolla length (6–11 mm. in *G. malior,* 6–22 mm. in *G. aliquanta*); (3) stigma and stamen exsertion (stigma and stamens barely above orifice in *G. malior,* strongly exserted in *G. aliquanta*); (4) calyx pubescence (lightly glandular in *G. malior,* glabrous in *G. aliquanta*).

Representative specimens.—CALIFORNIA. San Luis Obispo County: *E. C. Twisselmann 1840,* Temblor Mts.; *C. B. Hardham 3154,* Simmler; *V. & A. Grant 8696, 9097, 17,559,* Cuyama Valley. San Bernardino County: *V. & A. Grant 10,045, 10,046,* Kramer Hills. Lassen County: *V. & A. Grant 9798,* Litchfield. NEVADA. Washoe County: *H. L. Mason 13,984,* Steamboat Springs; *V. & A. Grant 9795,* Sparks; *P. Train 3604,* Red Rock.

MATERIALS AND METHODS

Field trips were taken to various parts of western North America over a period of many years to collect living strains of the autogamous Cobwebby Gilias for use in the artificial hybridization program. These strains have been grown from seed in Claremont and determined for chromosome number. The geographical localities of the known polyploid populations are indicated by the dots and letters on the distribution maps in Fig. 2 and 3.

The polyploid strains used in hybridizing are shown by letters on these maps and are further identified in the list given in Table 1.

TABLE 1. *List of species and strains used in hybridizations.*

The index letters of the strains are employed as abbreviations in the crossing diagrams and tables, and, in the case of the polyploid species, also in the distribution maps. The collection numbers of the strains are those of the author unless otherwise specified and refer to voucher specimens in the herbarium of the Rancho Santa Ana Botanic Garden.

POLYPLOIDS

I. GILIA INCONSPICUA GROUP
  1. *Gilia tweedyi.*
    (E) Encampment, Carbon Co., Wyoming. (9725)
  2. *Gilia inconspicua.*
    (M) Marsing, Owyhee Co., Idaho. (9816)
    (B) Blue Mountain Pass, Malheur Co., Oregon. (9819)
  3. *Gilia transmontana.*
    (a) *G. transmontana* I
      (K) Kramer Hills, San Bernardino Co., California. (9902, 10046-A)
      (J) Johannesburg, El Paso Mts., Kern Co., California. (8847)
      (M) Mountain Pass, east of Baker, San Bernardino Co., California. (9060)
    (b) *G. transmontana* II
      (B) Beaverdam Mts., Washington Co., Utah. (9972)
  4. *Gilia malior.*
    (C) Cuyama Valley, Santa Barbara Co., California. (8696)
    (K) Kramer junction, and south of Kramer Hills, San Bernardino Co., California. (10049, 10045)
    (B) Boron, San Bernardino Co., California. (9907)
    (M) Mohave, Kern Co., California. (A. Day 60–107)
    (SC) Short Canyon, Inyokern, Inyo Co., California (9337)
    (S) Sparks, Washoe Co., Nevada. (9795)
  5. *Gilia flavocincta.*
    (a) *G. f.* subsp. *flavocincta*
      (W) Wickenburg, Maricopa Co., Arizona. (9297)
      (SM) Superstition Mts., Pinal Co., Arizona (10067, 10068, 10069)
    (b) *G. f.* subsp. *australis*
      (P) Paulden, Yavapai Co., Arizona. (10129)
      (CO) Canyon del Oro, near Tucson, Pima Co., Arizona. (2728)
      (S) Sonoita, Pima Co., Arizona. (9923, 9924)
  6. *Gilia ophthalmoides.*
    (a) *G. ophthalmoides* I
      (W) Westgard Pass, White Mts., Inyo Co., California. (9431)
      (K) Kyle Canyon, Charleston Mts., Clark Co., Nevada. (E. K. Balls 19276)
      (B) Beaverdam Mts., Washington Co., Utah. (9969)
      (D) Dinosaur National Monument, Uintah Co., Utah. (9705)
    (b) *G. ophthalmoides* II
      (S) Sweetwater Mts., Mono Co., California. (P. A. Munz 21118)
    (c) *G. ophthalmoides* III
      (M) Mule Creek, Grant Co., New Mexico. (P. A. Munz 23327)

II. GILIA SINUATA GROUP
  7. *Gilia sinuata* I.
    (M) Morongo Valley, Riverside Co., California. (9895)
    (L) Lucerne Valley, San Bernardino Co., California. (9946)
    (E) El Paso Mts., Kern Co., California. (9557)
    (J) Johannesburg, Kern Co., California.
    (D) Doyle, Lassen Co., California. (2947–A)
    (C) Columbia River, Umatilla Co., Oregon. (9811)
  8. *Gilia sinuata* II.
    (S) Superstition Mts., Pinal Co., Arizona. (10070)

Table 1. *List of species and strains used in hybridizations. (Continued)*

POLYPLOIDS

- II. Gilia sinuata group
  - 9. *Gilia modocensis.*
    - (C) Cajon Pass, San Bernardino Co., California. (15993)
    - (P) Phelan, San Bernardino Co., California. (15995)
    - (D) Doyle, Lassen Co., California. (2947–B)
  - 10. *Gilia tetrabreccia*
    - (M) Mt. Pinos, Ventura Co., California. (16042)
- III. Gilia crassifolia group
  - 11. *Gilia crassifolia* 4X.
    - (P) Puente del Inca, Depto. Las Heras, Prov. Mendoza, Argentina. (J. Hunziker 6316)
  - 12. *Gilia crassifolia* 8X.
    - (T) Tecka, Terr. Chubut, Argentina. (2294, 2959, from seed collection by A. Soriano)

DIPLOIDS

- IV. Gilia ochroleuca group
  - 13. *Gilia ochroleuca.*
    - (a) *G. o.* subsp. *ochbroleuca*
      - (Y) Inyokern, Kern Co., California. (8858)
    - (b) *G. o.* subsp. *bizonata*
      - (M) Mt. Pinos, Ventura Co., California. (16040)
  - 14. *Gilia exilis.*
    - (D) Dripping Springs, Riverside Co., California. (9317)
    - (W) Whitewater Canyon, Colorado Desert, Riverside Co., California. (9031)
  - 15. *Gilia cana.*
    - (a) *G. c.* subsp. *triceps*
      - (W) Wildrose Canyon, Panamint Mts., Inyo Co., California. (8821)
      - (T) Trona, Inyo Co., California. (9342, 9343)
      - (C) China Lake, Mojave Desert, Kern Co., California. (9341)
    - (b) *G. c.* subsp. *speciosa*
      - (S) Short Canyon, Inyokern, Inyo Co., California. (8860)
  - 16. *Gilia clokeyi*
    - (D) Deep Springs, east of Westgard Pass, Inyo Co., California. (9836)
    - (K) Kyle Canyon, Charleston Mts., Clark Co., Nevada. (9950)
  - 17. *Gilia aliquanta.*
    - (R) Red Rock Canyon, Kern Co., California. (9117)
- V. Gilia tenuiflora group
  - 18. *Gilia tenuiflora.*
    - (a) *G. t.* subsp. *tenuiflora*
      - (A) Arroyo Seco, Monterey Co., California. (G. L. Stebbins 3945)
  - 19. *Gilia leptantha.*
    - (a) *G. l.* subsp. *pinetorum*
      - (M) Mt. Pinos, Ventura Co., California. (16047, 16052)
  - 20. *Gilia latiflora.*
    - (a) *G. l.* subsp. *latiflora*
      - (A) Apple Valley, Mojave Desert, San Bernardino Co., California. (RSABG 20683)
    - (b) *G. l.* subsp. *davyi*
      - (M) Mohave, Kern Co., California.
  - 21. *Gilia interior.*
    - (K) Kern Valley, Sierra Nevada, Kern Co., California. (9110, 9112)
    - (D) Democrat Springs, Kern Canyon, Kern Co., California. (8465)
    - (H) Hobo Springs, Kern Canyon, Kern Co., California. (9108)
  - 22. *Gilia minor.*
    - (K) Kramer junction, Mojave Desert, San Bernardino Co., California. (8851)
    - (SK) South of Kramer Hills, San Bernardino Co., California. (9222)
    - (W) Wickenburg, Maricopa Co., Arizona. (9298)

TABLE 1. *List of species and strains used in hybridizations. (Continued)*

DIPLOIDS

V. GILIA TENUIFLORA GROUP
  23. *Gilia jacens.*
      (B) Ballinger Canyon, Cuyama Valley, Santa Barbara Co., California. (9365–4)

VI. GILIA BRECCIARUM GROUP
  24. *Gilia brecciarum.*
      (a) *G. b.* subsp. *brecciarum*
        (H) Halleluja junction, Plumas Co., California. (9669)
      (b) *G. b.* subsp. *neglecta*
        (S) Short Canyon, Inyokern, Inyo Co., California. (9335)

The taxogenetic exploration of the polyploid Cobwebby Gilias is adequate for some species and in some geographical areas, in which a sufficient number of strains has been employed in the hybridization program, but is only in a preliminary stage in the case of other, more sparsely sampled species or areas. Owing to limitations of time and resources, it has not yet been possible to analyze the relationships of the members of the *Gilia inconspicua-transmontana* complex in central and northern Nevada, of the *Gilia sinuata* complex in Arizona, of *Gilia crassifolia* in South America, and so on.

The polyploid Cobwebby Gilias listed in Table 1, comprising 37 strains in 12 species, have been intercrossed in numerous (54) combinations. The polyploid Cobwebby Gilias have also been hybridized with 12 diploid species of the section, as represented by a total of 24 strains. The species and strains of diploids are also listed in Table 1. Altogether, 2049 flowers were cross-pollinated in 106 hybrid combinations.

The cross-pollinations were made in an insect-free screenhouse in Claremont with normal safeguards against contamination of cultures. The F_1 hybrids were grown in the screenhouse and scored for vigor, morphological characters, pollen fertility, and seed fertility. The degree of chromosome pairing in the hybrids was determined from examination of propiono-carmine squashes of dividing pollen mother cells.

CROSSABILITY

The polyploid Cobwebby Gilias have been crossed *inter se* and with their diploid relatives in 106 hybrid combinations. The hybrid combinations attempted and the results obtained are listed in Table 2, where the data are classified according to the taxonomic level of divergence of the strains crossed. The average crossing behavior of these plants at the different levels of divergence is then presented in summary form in Table 3.

The ease of crossing of the polyploid Cobwebby Gilias can be measured in various ways: by the proportion of the flowers pollinated that set capsules, by the production of abortive seeds, by the average number of plump seeds per flower pollinated, and by the number of F_1 hybrids grown from these seeds. These measures are given for the various crosses individually in Table 2 and for the crosses pooled in groups according to taxonomic level in Table 3. The crossing behavior of different biotypes from the same population may be taken as the control. The tables show that, compared with this standard of reference, strong crossability barriers exist between the polyploid species in most combinations.

Variability within a population in respect to compatibility with another population is shown by the results of separate crosses between the same two strains of *G. ophthalmoides.* The cross between *G. ophthalmoides* II from Sweetwater Mts. × *G. ophthalmoides* I from Westgard Pass was carried out with two biotypes of the Westgard population, one possessing a yellow and the other a purple corolla tube. The Sweetwater plants, used as female parents, were pollinated by one or the other Westgard biotypes under uniform

Table 2. *Crossability of the polyploid Cobwebby Gilias.*

Cross (♀ parent listed first)	No. flowers pollinated	No. capsules set	No. abortive seeds	No. plump seeds	Ave. no. seeds per flower	No. F_1 individuals
I. CROSSES BETWEEN BIOTYPES OF THE SAME POPULATION						
inconspicua M, violet × yellow tube	28	24	0	313	11.2	75
malior B, small × larger flowers	18	17		149	8.3	0
flavocincta SM, short × long tube	11	11	2	109	9.9	26
II. CROSSES BETWEEN RACES						
1. Between interfertile races						
inconspicua, M × B	21	20	0	275	13.1	26
transmontana I, M × K	17	17	0	184	10.8	16
malior, C × SC	50	50		752	15.0	3
malior, C × S	28	24	0	251	9.0	29
malior, M × S	25	23		236	9.4	∞
flavocincta, S × CO	21	21		789	37.6	41[a]
flavocincta, P × CO	18	17	0	308	17.1	111
flavocincta, CO × W	22	?	+	132	6.0	8
ophthalmoides I, W narrow throat × B	23	16	+	59	2.6	0
ophthalmoides I, W broad throat × B	23	15	+	168	7.3	42
ophthalmoides I, K × D	34	32	0	250	7.4	14
sinuata I, C × D	26	19	0	673	25.9	48[b]
sinuata I, D × E	29	17	0	88	3.0	14
sinuata I, E × L	16	15	0	370	23.1	27
sinuata I, M × L	10	3	+	2	0.2	0
modocensis, P × D	20	17	∞	10	0.5	3
2. Between different fertility groups						
transmontana, I M × II B	18	17	+	139	7.7	64
ophthalmoides, II S × I W yellow tube	19	19		154	8.1	101
ophthalmoides, II S × I W purple tube	20	14	∞	0	0	0
III. CROSSES BETWEEN POLYPLOID SPECIES						
1. Within Gilia inconspicua group						
tweedyi E × *inconspicua* M	24	22	+	0	0	0
tweedyi E × *malior* S	28	21	∞	124	4.4	21
tweedyi E × *ophthalmoides* I W	23	20	∞	11	0.5	1
transmontanaa I K × *inconspicua* M	10	6	∞	0	0	0
inconspicua M × *transmontana* II B	9	5	0	42	4.7	15
transmontana II B × *inconspicua* M	11	8	+	36	3.3	17
malior S × *inconspicua* M	24	24	0	215	9.0	30
transmontana I M × *malior* S	29	25	3	191	6.6	10
malior C × *transmontana* I M	26	25		284	10.9	35
transmontana I K × *malior* K	4	1	0	3	0.8	0
transmontana I M × *flavocincta* CO	30	15		4	0.1	0
malior S × *flavocincta* CO	24	21	∞	1	0.04	0
inconspicua M × *ophthalmoides* I W	23	20		387	16.8	77
transmontana I M × *ophthalmoides* I W	22	22	+	186	8.4	28
malior S × *ophthalmoides* I W	25	21		270	10.8	56

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[a] from 400 seeds.

[b] from 300 seeds.

Table 2. *Crossability of the polyploid Cobwebby Gilias.*

Cross (♀ parent listed first)	No. flowers pollinated	No. capsules set	No. abortive seeds	No. plump seeds	Ave. no. seeds per flower	No. F_1 individuals
1. Within Gilia inconspicua group. ***(continued)***						
ophthalmoides I D × *flavocincta* CO	24	22	∞	0	0	0
ophthalmoides II S × *flavocincta* W	11	11	0	77	7.0	5
2. Within Gilia sinuata group						
sinuata I M × *sinuata* II S	22	22		322	14.6	12
modocensis P × *sinuata* I E	18	15		93	5.2	15
modocensis D × *sinuata* I D	45	33	∞	3	0.1	0
tetrabreccia M × *modocensis* P	23	21	4	269	11.7	2[c]
3. Between the Gilia inconspicua, sinuata, and crassifolia groups						
transmontana I J × *sinuata* I M	5	5	+	22	5.5	0
transmontana I J × *sinuata* I J	2	2		0	0	0
sinuata I J × *transmontana* I J	3	1		7	2.3	0
malior C × *modocensis* C	18	18	2	203	11.3	53
modocensis P × *flavocincta* CO	20	3	+	0	0	0
crassifolia 4X P × *ophthalmoides* I K	22	22		10	0,4	0
crassifolia 4X P × *ophthalmoides* I D	32	30	∞	9	0.3	0
crassifolia 4X P × *sinuata* I D	14	13	∞	0	0	0
crassifolia 8X T × *inconspicua* B	14	13	∞	3	0.2	3
modocensis P × *crassifolia* 8X T	36	30		251	7.0	35
crassifolia, 8X T × 4X P	25	12	+	12	0.5	0
IV. CROSSES BETWEEN POLYPLOID AND DIPLOID SPECIES						
1. Gilia inconspicua and transmontana × diploids						
jacens B × *inconspicua* M	15	13		0	0	0
transmontana I J × *tenuiflora* A	7	2	+	0	0	0
transmontana I J × *latiflora* M	8	4	∞	1	0.1	0
transmontana I J × *cana* W	8	4	∞	3	0.4	0
transmontana I M × *cana* T	45	31	∞	18	0.4	0
transmontana I M × *minor* SK	23	17	∞	1	0.04	0
transmontana I K × *clokeyi* K	23	20	+	∞	∞	0
2. Gilia malior × diploids						
malior B × *aliquanta* R	27	20	+	0	0	0
malior S × *aliquanta* R	22	15	∞	3	0.1	0
aliquanta R × *malior* B	10	8	0	0	0	0
clokeyi D × *malior* B	27	16	∞	17	0.6	0
malior C × *ochroleuca* M	20	11	∞	12	0.6	0
malior C × *ochroleuca* Y	25	18	∞	0	0	0
ochroleuca Y × *malior* C	5	1	0	3	0.6	0
malior C × *tenuiflora* A	6	6		14	2.3	0
malior C × *latiflora* M	12	8	0	42	3.5	6
malior C × *latiflora* A	27	23	+	211	7.8	4
malior C × *minor* K	36	12	∞	2	0.1	0
minor K × *malior* C	27	15	∞	1	0.04	0
minor W × *malior* S	22	20	∞	1	0.04	0
malior C × *interior* D	11	11	+	100	9.1	2
malior C × *interior* H	8	6	+	48	6.0	4

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[c] poor germination.

Table 2. *Crossability of the polyploid Cobwebby Gilias.*

Cross (♀ parent listed first)	No. flowers pollinated	No. capsules set	No. abortive seeds	No. plump seeds	Ave. no. seeds per flower	No. F_1 individuals
2. Gilia malior × diploids *(continued)*						
malior C × *interior* K	6	5	1	51	8.5	(d)
malior C × *brecciarum* S	24	24	∞	54[e]		0
3. Gilia flavocincta × diploids						
flavocincta CO × *ochroleuca* M	21	21	∞	243	11.6	65
exilis W × *flavocincta* CO	4	4		32	8.0	0
flavocincta CO × *exilis* D	23	22	∞	452	19.6	295
flavocincta CO × *cana* S	19	18	∞	255	13.4	5
cana C × *flavocincta* CO	18	5	1	51	2.8	0
flavocincta W × *cana* C	14	11	+	75	5.4	1
flavocincta CO × *tenuiflora* A	18	18	∞	133	7.4	3
tenuiflora A × *flavocincta* CO	6	2	∞	0	0	0
tenuiflora A × *flavocincta* W	19	19	∞	0	0	0
flavocincta CO × *latiflora* A	44	43	∞	0	0	0
latiflora A × *flavocincta* W	10	0		0	0	0
minor K × *flavocincta* CO	19	18	∞	31	1.6	13
minor W × *flavocincta* W	19	19	∞	25	1.3	0
interior K × *flavocincta* W	25	18	∞	0	0	0
4. Gilia sinuata I × diploids						
sinuata M × *cana* W	3	3		0	0	0
sinuata M × *tenuiflora* A	8	7	33	28	3.5	0
sinuata J × *tenuiflora* A	3	3	∞	0	0	0
sinuata M × *latiflora* A	7	7	7	89	12.7	14
sinuata M × *latiflora* M	4	4		6	1.5	0
5. Gilia modocensis and tetrabreccia × diploids						
ochroleuca Y × *modocensis* C	5	2		0	0	0
modocensis C × *tenuiflora* A	5	5	∞	3	0.6	3
modocensis C × *latiflora* A	22	22	17	374	17.0	24
modocensis P × *leptantha* M	25	21		198	7.9	3
minor K × *modocensis* C	11	8	+	0	0	0
modocensis P × *brecciarum* S	28	24	∞	2	0.1	0
modocensis C × *brecciarum* S	20	12	∞	0	0	0
modocensis P × *brecciarum* H	29	18	∞	0	0	0
tetrabreccia M × *brecciarum* S	33	23	∞	7	0.2	0

[d] seeds not sown.
[e] some were selfs.

environmental conditions. The cross Sweetwater ♀ × yellow-tubed Westgard yielded numerous sound seeds and numerous F_1 hybrids. By contrast, the cross of Sweetwater ♀ × purple-tubed Westgard produced a mass of abortive seeds and no sound seeds.

Two other biotypes in the Westgard population of *G. ophthalmoides* I are distinguished by the shape of the corolla throat and also by their crossing behavior with the Beaverdam Mt. race of the same species. The broad-throated biotype of the Westgard population produces numerous hybrids with the Beaverdam race, whereas the narrow-throated biotype does not (Table 2). Similar biotype differences in crossability with a foreign entity were found previously in the diploid Cobwebby Gilia, *G. exilis* from Dripping Springs (Grant and Grant, 1960, p. 447).

The variation in crossability may occur also at a higher level of divergence as between different strains. Thus *G. inconspicua* from Marsing is separated by a relatively weak incompatibility barrier from *G. transmontana* II Beaverdam but by a strong barrier from *G. transmontana* I Kramer. In the hybrid combination *G. modocensis* ♀ × *G. sinuata* I, the sympatric races from Doyle are very difficult to cross, whereas the allopatric races of the same species cross fairly easily.

TABLE 3. *Crossability of the polyploid Cobwebby Gilias 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	3	67%	57	10.0	17.7
Between races	19	84%	440	11.0	11.6
Between polyploid species belonging to the same species group	22	64%	480	5.3	6.8
Between polyploid species belonging to different species groups	10	33%	166	3.0	5.5
Between polyploid and diploid species	52	27%	906	2.9	4.9

Most crosses between a tetraploid and a diploid species were difficult to make, here as in other plant groups. However, the tetraploid species *G. flavocincta,* which occupies a geographically isolated position in Arizona, proved to be an exceptionally good crosser with different strains of the diploid species *G. cana, ochroleuca, exilis,* and *tenuiflora.* The crosses of *G. flavocincta* Canyon de Oro ♀ × *exilis, cana,* and *ochroleuca* yielded 20, 13, and 12 plump seeds for every flower pollinated, which is better than the average seed harvest from interracial or inter-biotype crosses in this group.

In summary, with rare exceptions different geographical races of the same species of polyploid Cobwebby Gilias cross freely or fairly freely under experimental conditions, as shown by Fig. 4. A very few interspecific crosses were also easy to make. But in the great majority of the interspecific combinations it was either difficult or impossible to produce F_1 hybrids, as shown by Table 3 and Fig. 5.

VIABILITY OF THE HYBRIDS

Most of the F_1 hybrids were normal in vigor. Inviable F_1s were produced in three crosses. The F_1 hybrid of *G. tweedyi* Encampment × *ophthalmoides* I Westgard Pass was inviable and never flowered. The plants in the F_1 generation of *G. flavocincta* Canyon de Oro × *tenuiflora* Arroyo Seco were all semilethal runts with few or no flowers, and so were their few F_2 progeny. The F_1 generation of *G. modocensis* Phelan × *sinuata* I El Paso Mts. consisted of 14 vigorous plants and one inviable runt. The two F_2 plants produced by this hybrid were both vigorous (but sterile).

The F_2 generations were scored for vigor in every case in which the F_1 hybrid was fertile enough to produce F_2 progeny. The F_2 families derived from interracial hybrids frequently consisted of scores or hundreds of plants, but in some crosses consisted of ten or fewer plants. The F_2 progenies descended from such interspecific hybrids as were not completely sterile were usually small, ranging in numbers from two to 19 plants in most cases, and attaining the maximum numbers of 59 and 64 plants in two crosses.

The F_2 progenies generally varied in vigor from normal plants at one extreme to inviable types at the other. The proportion of inviable or weak individuals differed from cross to

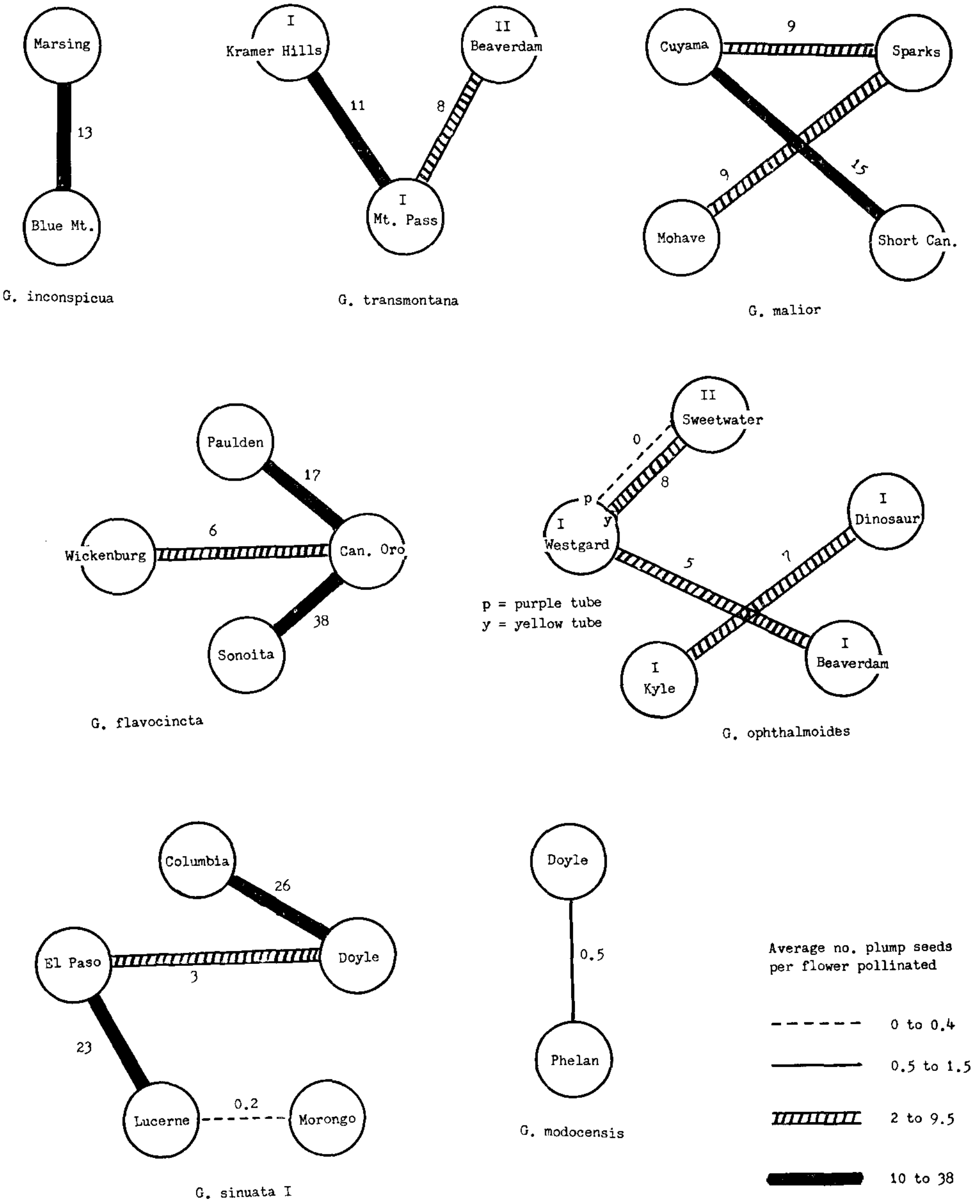
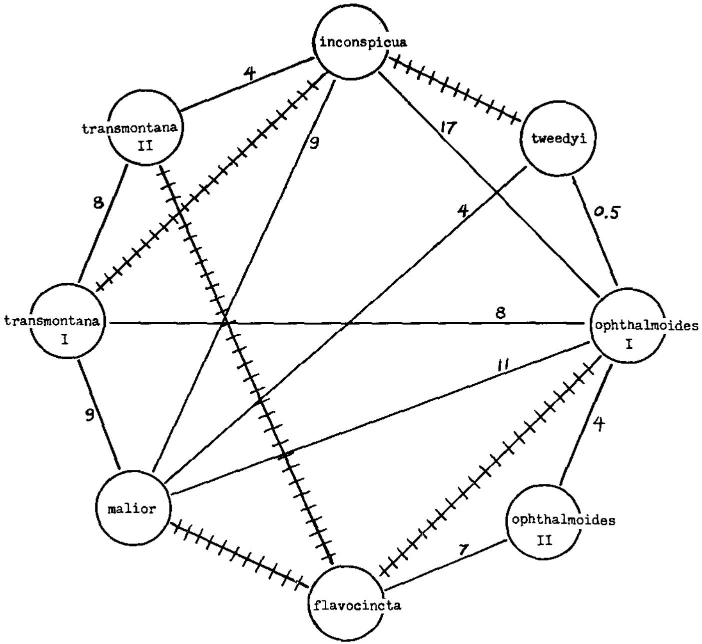
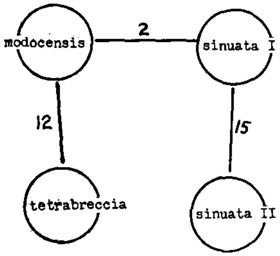


Fig. 4. Ease of crossing between different races or fertility groups of the same species in the tetraploid Cobwebby Gilias.



Gilia inconspicua group

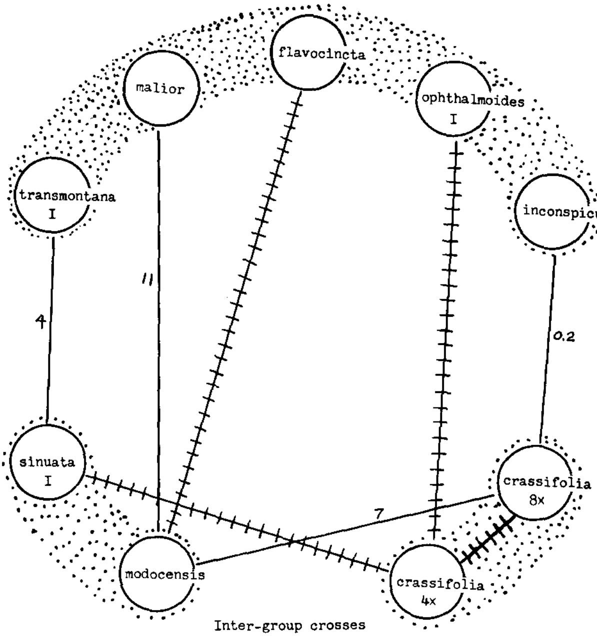


Gilia sinuata group

┼┼┼┼┼┼ cross failed completely

—— hybrid obtained

6 ave. no. plump seeds per flower



Inter-group crosses

Fig. 5. Crossability of different polyploid species of Cobwebby Gilias.

cross, as shown in Table 4. The F_2 generations derived from several interracial and one interspecific cross contained, in fact, no inviable or weak individuals; while in other F_2 generations from either interracial or interspecific crosses 12%, 33%, 57%, 92% or some similar proportion of the individuals were weak or inviable; and two interspecific hybrids gave rise to all inviable F_2s.

HYBRID FERTILITY

The pollen fertility of the F_1 hybrids and, in some crosses, of their F_2 progeny was estimated from the percentage of well-formed and well stained grains (in a lactophenol-aniline blue mount). The percentage of well-formed pollen was scored on four sister hybrids wherever this many F_1 individuals were available for study.

Estimates of the seed fertility of the hybrids were obtained by comparing their seed output with that of the parental species under the same generally favorable conditions for growth and self-pollination in the experimental screenhouse. On this basis four categories of seed fertility could be recognized: high fertility, semisterility, high sterility, and complete sterility. A hybrid with approximately the same seed output as the parental species was classified as highly fertile; hybrids producing a definitely reduced quantity of seeds were considered semisterile; and hybrids yielding few or no seeds were considered highly or completely sterile respectively. Seed fertility was usually but not invariably well correlated with pollen fertility.

The data on hybrid fertility are presented in Table 4 and are summarized graphically in Figs. 6 and 7.

The F_1 hybrids between morphologically distinguishable biotypes of the same population were produced and studied in two crosses: in the Marsing population of *G. inconspicua* and in the Superstition Mt. strain of *G. flavocincta.* The inter-biotype hybrids were highly fertile as to both pollen and seeds in both cases, as is evident from Table 4 and Fig. 6; they were, in fact, as fertile as the parental types.

A similar high degree of fertility is found in some, though not all, F_1 hybrids between geographical races of a species. Thus the races of *Gilia malior* from such widely separated areas as the Great Basin of Nevada (Sparks), the South Coast Ranges of California (Cuyama), and the Mojave Desert (Mohave and Short Canyon) are highly interfertile. Other fertile or semisterile hybrids between more or less widely separated races of a species are shown in Fig. 6.

Most of the species hybrids, on the other hand, were highly or completely sterile, while some other interspecific hybrids were semisterile (Fig. 7). Four sister individuals of the hybrid of *G. crassifolia* 8X Tecka × *inconspicua,* for example, flowered freely for ten weeks, producing between 7 and 29% of apparently good pollen grains which regularly fell onto the stigmas, yet formed only a few seeds in all this time. The hybrid of *G. modocensis* × *crassifolia* 8X, with a smaller proportion (1–3%) good pollen, was completely sterile as to seeds. The great majority of the triploid hybrids derived from crosses between tetraploid and diploid species were completely sterile (Table 4).

The hybrids between *G. transmontana* I and II, and between *G. ophthalmoides* I and II, produced only 4 or 5% of well-formed pollen and were highly sterile as to seeds. The sterility barrier between groups I and II is thus similar in strength to that separating good species in the autogamous Cobwebby Gilias generally. In their morphological and geographical relationships, on the other hand, these fertility groups behave as races. More complete information about the situation in *Gila transmontana* and *G. ophthalmoides* is needed.

The fertility of the F_2s was measured in several cases. Among interracial crosses, the

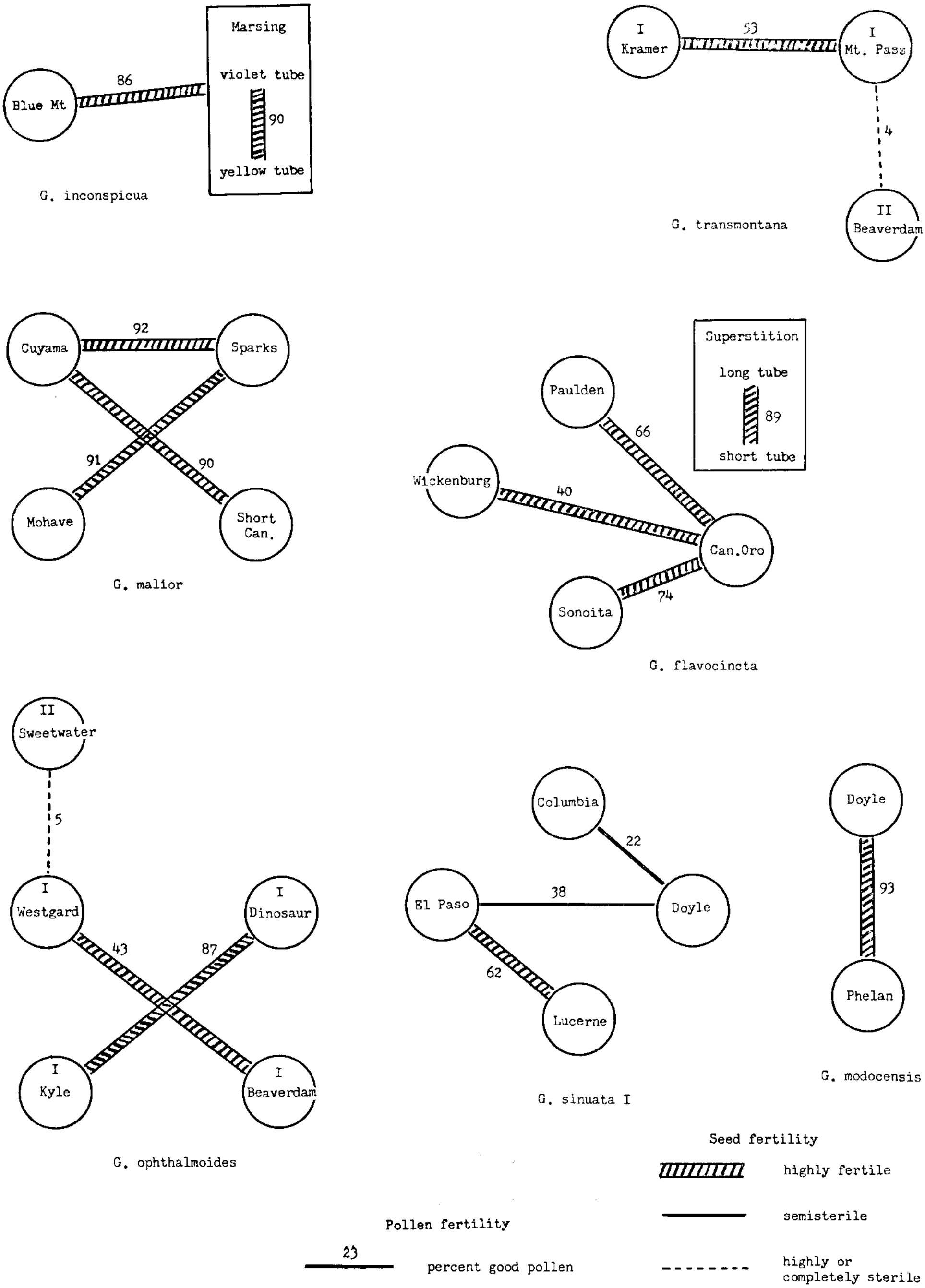


Fig. 6. Fertility of F_1 hybrids between races or fertility groups of the same species.

TABLE 4. *Fertility of F_1s and vigor of F_2s.*

	POLLEN FERTILITY, %			
HYBRID	RANGE	MEAN	SEED FERTILITY	F_2 GENERATION
I. HYBRIDS BETWEEN BIOTYPES				
inconspicua M, violet × yellow tube	72–99	90	highly fertile	51% vigorous
flavocincta SM, short × long tube	76–96	89	highly fertile	
II. FERTILE RACE HYBRIDS				
1. Within Gilia inconspicua group				
inconspicua, M × B	71–96	86	fertile	43% vigorous
transmontana I, M × K	45–65	53	fertile	100% vigorous, fertile
malior, C × SC	89–92	90	fertile	
malior, C × S	83–96	92	fertile	71% vigorous
malior, M × S	89–93	91	fertile	
flavocincta, S × CO	58–83	74	fertile	poor germination
flavocincta, P × CO	59–74	66		
flavocincta, CO × W	19–60	40	fertile	100% vigorous
ophthalmoides I, K × D	80–92	87	fertile	poor germination
ophthalmoides I, W × B	26–50	43	fertile	poor germination
2. Within Gilia sinuata group				
sinuata I, D × E	27–60	38	semisterile	poor germination, semifertile
sinuata I, E × L	51–81	62	fertile	poor germination, 67% vigorous
sinuata I, C × D	12–31	22	semisterile	poor germination, 50% vigorous
modocensis, P × D	87–98	93	fertile	poor germination
III. HYBRIDS BETWEEN FERTILITY GROUPS ASSIGNED TO THE SAME SPECIES				
transmontana, I M × II B	3– 8	4	highly sterile	
ophthalmoides, II S × I W	2– 9	5	highly sterile	several vigorous F_2s, one with 28% good pollen

TABLE 4. *Fertility of F_1s and vigor of F_2s.*

HYBRID	POLLEN FERTILITY, %		SEED FERTILITY	F_2 GENERATION
	RANGE	MEAN		
IV. INTERSPECIFIC HYBRIDS				
1. Within Gilia inconspicua group				
tweedyi E × *malior* S	1– 3	2	highly sterile	
inconspicua M × *transmontana* II B	8–19	12	semisterile	poor germination
transmontana II B × *inconspicua* M	4–15	10	semisterile	67% vigorous
malior S × *inconspicua* M	0.6– 3	2	highly sterile	88% vigorous
inconspicua M × *ophthalmoides* I W	3– 6	5	highly sterile	8% vigorous
transmontana I M × *malior* S	2– 5	3	semisterile	84% vigorous
malior C × *transmontana* I M	1– 4	3	highly sterile	highly sterile
transmontana I M × *ophthalmoides* I W	13–18	16	semisterile	100% vigorous
malior S × *ophthalmoides* I W	4– 8	6	highly sterile	several weak F_2s
ophthalmoides II S × *flavocincta* W	3– 7	5	highly sterile	
2. Within Gilia sinuata group				
sinuata, I M × II S	1– 7	5	semisterile	none vigorous
modocensis P × *sinuata* I E	4– 5	4	highly sterile	2 F_2s highly sterile
tetrabreccia M × *modocensis* P	1– 2	1	completely sterile	
3. Between polyploid species groups				
malior C × *modocensis* C	0.5– 3	1	highly sterile	vigorous but highly sterile
crassifolia 8X T × *inconspicua* B	7–29	21	highly sterile	
modocensis P × *crassifolia* 8X T	1– 3	2	completely sterile	
4. Gilia inconspicua group × diploids				
malior C × *latiflora* A	1– 1	1	completely sterile	
malior C × *latiflora* M	1– 1	1	completely sterile	
flavocincta CO × *ochroleuca* M	1– 3	2	no data	
flavocincta CO × *exilis* D	1– 9	2	completely sterile	
flavocincta CO × *cana* S	1–15	5	highly sterile	
flavocincta W × *cana* C	1– 1	1	completely sterile	
flavocincta CO × *tenuiflora* A	7	7	highly sterile	sublethal runts
minor K × *flavocincta* CO	0.5–2.0	1	completely sterile	
5. Gilia sinuata group × diploids				
sinuata I M × *tenuiflora* A	0.5	0.5	completely sterile	
sinuata I M × *latiflora* A	0– 2	1	completely sterile	
modocensis C × *tenuiflora* A	0.5	0.5	completely sterile	
modocensis C × *latiflora* A	1– 1	1	completely sterile	
modocensus P × *leptantha* M	1– 2	1	completely sterile	

F_2 plants of *G. transmontana* I Mt. Pass × *transmontana* I Kramer were highly fertile, and those of *G. sinuata* I Doyle × *sinuata* I El Paso Mts. were semifertile. The plants composing the F_2 generation of the interspecific cross, *G. malior* × *transmontana* were highly sterile, like the F_1 hybrids. The F_1 hybrids of *G. modocensis* × *sinuata* produced a total of four F_2 seeds which in turn gave rise to two F_2 individuals. These had 4% and 10% good pollen and were completely sterile as to seeds after ten weeks of self-pollination in the screenhouse.

MEIOSIS IN THE HYBRIDS

Chromosome pairing and separation at meiosis are normal in the polyploid species of Cobwebby Gilias. These processes are altered in varying degrees in the artificial hybrids. The amount of pairing in bivalents and in higher associations for the various hybrids is summarized in Table 5. The data presented in the table are based on the analysis of between 20 and 50 pollen mother cells for each hybrid in the majority of cases; in several hybrids it was not possible to obtain more than about 10 analyzable cells.

In the fertile and semifertile race hybrids the chromosomes pair normally and completely in bivalents or are subject to slight reductions of pairing. This is shown by the data in Table 5 and illustrated in Fig. 8 for two hybrids between widely separated geographical races of *Gilia sinuata* I. All 22 cells analyzed in the hybrid Columbia River × Doyle had 18 bivalents plus 1 univalent. The presence of the univalent cannot be accounted for at present, since the parental strains that were examined or reexamined for chromosome number had exactly 18 pairs of chromosomes, but it is quite possible that some individuals belonging to either the Columbia River or Doyle population carry an extra pair and contributed the extra chromosomes to the hybrid. The formation of 18 bivalents was the typical condition in the other race hybrid of *Gilia sinuata* I, namely Doyle × El Paso Mts., though occasional cells had 17 II + 2 I or 16 II + 4 I (Fig. 8).

The sterile tetraploid interspecific hybrids, by contrast, all exhibit much reduction in pairing along with the formation of large numbers of univalents which lag in anaphase. Chains of three or four chromosomes are occasional in some hybrids and fairly frequent in others. The hybrids between *G. transmontana* I and II and between *G. ophthalmoides* I and II behave like interspecific hybrids in their cytology as well as in sterility. A series of typical metaphase configurations for the various hybrids in the *Gilia inconspicua* group is shown in Fig. 9. Greatly reduced pairing is found in the 54-chromosomes hybrids between the South American octoploid, *G. crassifolia*, and the North American tetraploid species *G. modocensis* and *G. inconspicua* (see Fig. 10). Fig. 11 summarizes graphically the pairing relationships between the polyploid species of Cobwebby Gilia.

The triploid hybrids derived from crosses between certain tetraploid and diploid species have about 9 II + 9 I on the average, while in other triploid hybrids the chromosome pairing is considerably less than 9 II. These observations as well as those on the chromosome behavior in the tetraploid hybrids have an obvious bearing on the problem of the origin of the tetraploid species. This large problem goes beyond the scope of the present paper. It may be mentioned, however, that at this writing Miss Alva Day has nearly completed a detailed study of the origin of two of the tetraploid species, *G. transmontana* and *G. malior,* from their diploid ancestors.

The F_2 progeny of meiotically irregular interspecific hybrids were examined cytologically in two cases, in *G. modocensis* × *sinuata* I and in *G. malior* × *modocensis.* In both cases the F_2 individuals exhibited much reduction of pairing, with numerous univalents, and were moderately to completely sterile. The later generation progeny of the hybrid *G. malior* × *modocensis* have been studied cytogenetically to the F_9 generation. The results of this study,

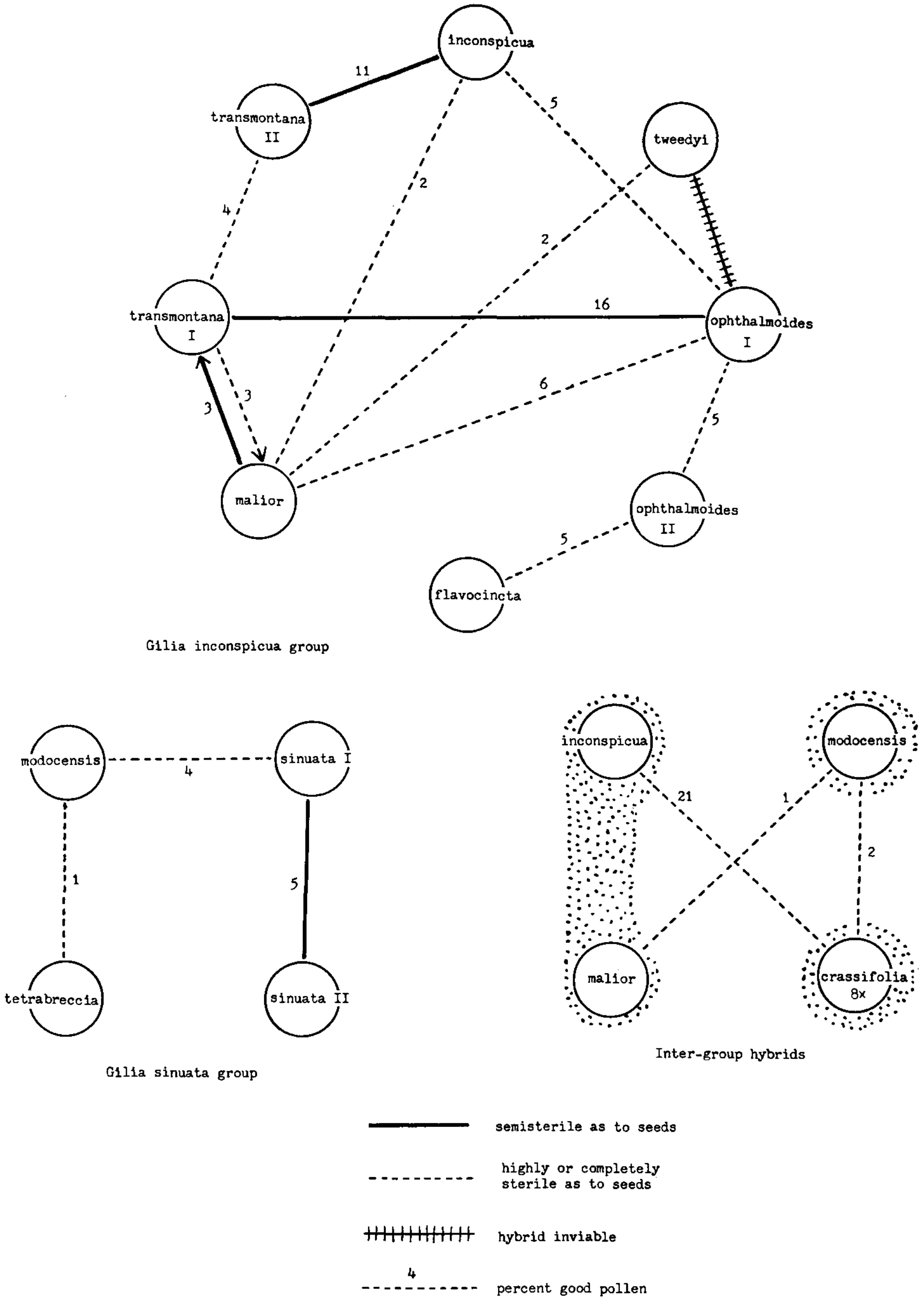


Fig. 7. Fertility of interspecific F_1 hybrids in the polyploid Cobwebby Gilias.

which will be presented elsewhere, provide good evidence that the observed sterility is predominantly chromosomal but partly genic in nature.

Table 5. *Metaphase pairing in F_1 hybrids.*

HYBRID	NO. BIVALENTS PER CELL[a]		% CELLS WITH
	MEAN	RANGE	III OR IV
I. FERTILE RACE HYBRIDS			
1. Within Gilia inconspicua group			
inconspicua, M × B	17.8	16–18	0
malior, C × S	18.0	18–18	0
malior, M × S	18.0	18–18	
flavocincta, CO × W	18.0	17–18	0
ophthalmoides I, K × D	17.8	17–18	0
ophthalmoides I, W × B	17.9	16–18	0
2. Within Gilia sinuata group			
sinuata I, D × E	17.7	16–18	4
sinuata I, C × D	18.0	18–18	0
modocensis, P × D	18.0	18–18	
II. HYBRIDS BETWEEN FERTILITY GROUPS ASSIGNED TO THE SAME SPECIES			
transmontana, I M × II B	10.8	9–13	11
ophthalmoides, II S × I W	11.2	9–13	23
III. INTERSPECIFIC HYBRIDS			
1. Within Gilia inconspicua group			
tweedyi E × *malior* S	9.6	6–14	8
transmontana II B × *inconspicua* M	14.0	11–16	4
malior S × *inconspicua* M	9.7	8–13	
inconspicua M × *ophthalmoides* I W	9.8	6–15	50
transmontana I M × *malior* S	9.2	7–11	
malior C × *transmontana* I M	9.1	7–15	
transmontana I M × *ophthalmoides* I W	13.9	12–16	7
malior S × *ophthalmoides* I W	3.4	1– 6	8
ophthalmoides II S × *flavocincta* W	6.7	3–12	high
2. Within Gilia sinuata group			
sinuata, I M × II S	13.5	12–16	+
modocensis P × *sinuata* I E	10.5	8–15	37
tetrabreccia M × *modocensis* P	8.5	4–12	
3. Between polyploid species groups			
malior C × *modocensis* C	6.0	1–10	3
crassifolia 8X T × *inconspicua* B	11.9	10–14	33
modocensis P × *crassifolia* 8X T		7–11	high
4. Tetraploids × diploids			
malior C × *latiflora* M	5.7	2– 9	5
flavocincta CO × *exilis* D		2– 6	
flavocincta W × *cana* C	6.2	4– 8	13
minor K × *flavocincta* CO	4.5	2– 7	5
sinuata I M × *latiflora* A	9.9	8–12	38
modocensis C × *latiflora* A	9.1	7–11	65

[a] Where occasional III were present in a cell, these were scored as bivalents for statistical purposes.

DISCUSSION

The small-flowered and predominantly self-pollinating Cobwebby Gilias occur widely throughout the arid regions of western North America and southern South America. These reduced annual plants look much alike in their general features throughout their extensive distribution area. In various fine details of morphology they also exhibit considerable variation, both individual variation within a colony and geographical variation between areas (see Fig. 1). The two aspects of the variation pattern, the general similarities and the relatively inconspicuous differences, are reflected in opposing tendencies in the taxonomic treatment of this group of plants. One traditional treatment has been to place all the North American forms in one taxonomic species, *Gilia inconspicua,* and all the South American forms in another, *Gilia crassifolia.* The other tendency has been to recognize a series of named taxa treated either as species (i.e., *Gilia inconspicua, G. sinuata, G. tweedyi,* etc.) or as varieties (*Gilia inconspicua* var. *sinuata, G. sinuata* var. *tweedyi,* etc.).

Representative forms of the small-flowered Cobwebby Gilias have been grown in Claremont from seeds collected in many natural populations scattered over the distribution area of the group (Fig. 2 and 3). The garden-grown plants have been compared with respect to their morphological characters, determined for chromosome number, and intercrossed in most of the possible hybrid combinations. The evidence obtained from the garden studies has been correlated with observations of the morphology and ecology of the plants in nature.

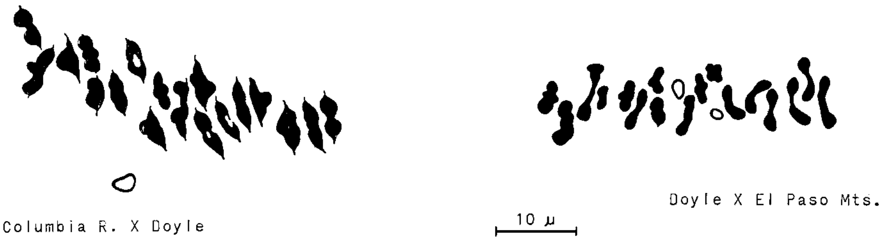


Fig. 8. Chromosome pairing at metaphase I in two semifertile interracial hybrids of *Gilia sinuata* I. Bivalents are shown black and univalents white.

The cytotaxonomic studies indicate that the small-flowered Cobwebby Gilias fall into two series: diploids (N = 9), and polyploids, mainly tetraploids (N = 18) but also one octoploid (Grant, Beeks, and Latimer, 1956).

The hybridization studies carried out with the diploid strains show that strong internal barriers to gene exchange are present between many of these forms, as reported in the previous paper in this series (Grant and Grant, 1960). The known incompatibility and sterility barriers, when related to the evidence of morphology, ecology, and geographical distribution, reveal the existence of some ten intersterile species of small-flowered Cobwebby Gilias on the diploid level.

Many of the forms of polyploid Cobwebby Gilias, as shown in the present paper, are likewise separated by strong internal barriers of incompatibility, hybrid inviability, hybrid sterility, and hybrid breakdown. In the early years of the hybridization program, in fact, we encountered strong barriers to crossing between every pair of morphologically different forms of polyploid Cobwebby Gilia which we attempted to cross, and such F_1 hybrids as we did succeed in producing were invariably highly sterile with low chromosome pairing. In later years, with a larger sample of strains available from different geographical localities, it was possible to demonstrate the absence or weak development of internal breeding barriers between geographically separated populations in many instances, as well as the

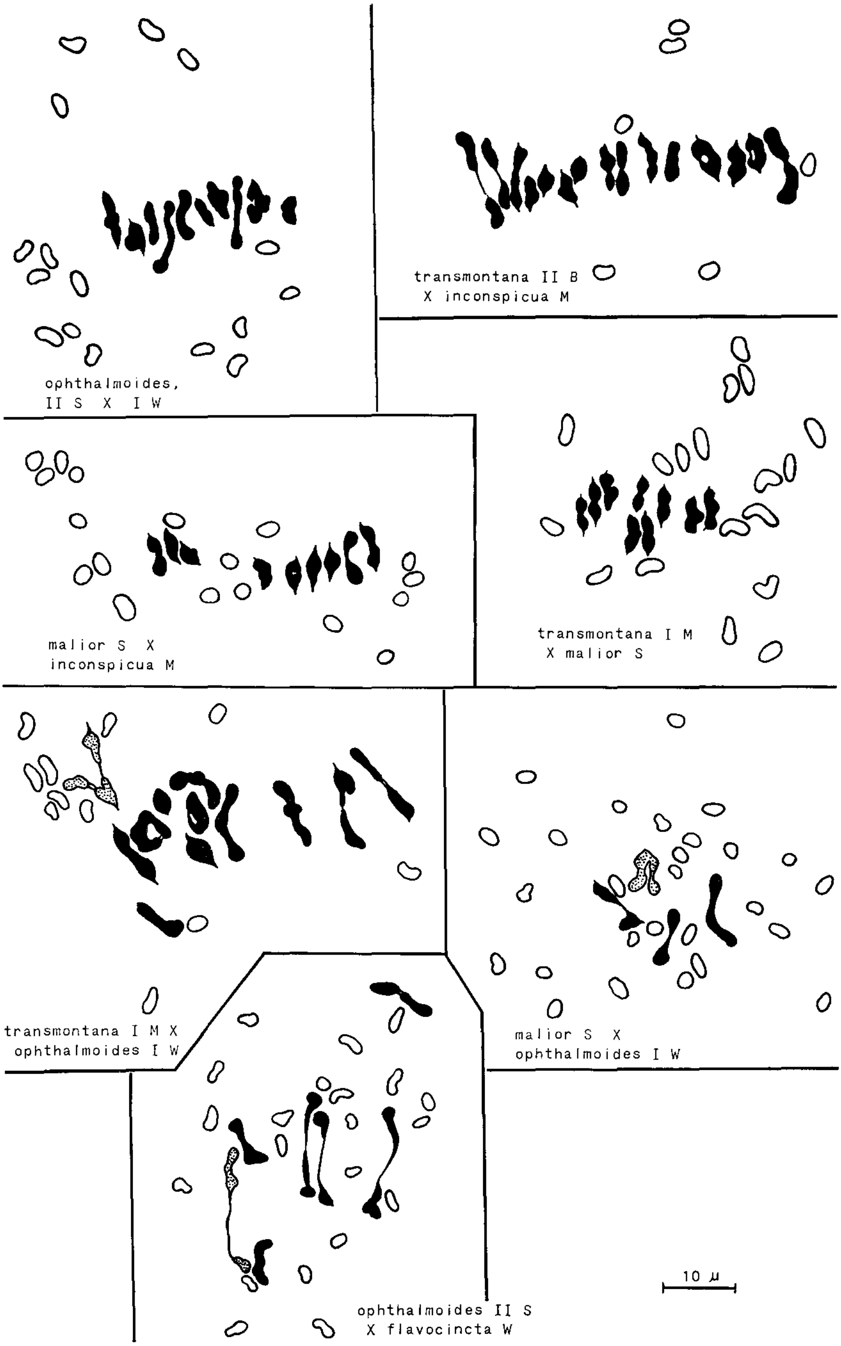

ophthalmoides, II S X I W
transmontana II B X inconspicua M
malior S X inconspicua M
transmontana I M X malior S
transmontana I M X ophthalmoides I W
malior S X ophthalmoides I W
ophthalmoides II S X flavocincta W
10 μ

Figure 9

strong development of such barriers between allopatric or sympatric populations in other combinations.

For example, populations of *Gilia sinuata* living hundreds of miles apart—one on the Columbia River, a second in northeastern California, and a third in the Mojave Desert—cross more or less freely *inter se* in the experimental garden to produce fertile or semifertile hybrids, thus behaving as geographical races. A similar array of interfertile races is found within the related and morphologically slightly different *Gilia modocensis* in the same general territory. But *Gilia sinuata* and *G. modocensis,* which coexist in the same territory, where they generally grow in different habitats, the former in low desert washes and the latter in high desert plains, but also frequently side by side in the same habitat, are prevented from interbreeding by strong incompatibility and sterility barriers. These two entities must, consequently, be regarded as separate species.

The distribution of the sterility barriers in the polyploid Cobwebby Gilias, as correlated with the evidence of morphology, ecology, and geographical distribution, enables us to block out twelve intersterile species. A brief review of these species is given on pages 480 to 484, and their geographical areas, insofar as known, are shown in the distribution maps in Fig. 2 and 3.

Fig. 10. Chromosome pairing in the sterile F_1 hybrid of *Gilia modocensis* (Mojave Desert) × *G. crassifolia* 8X (Patagonia). This hybrid between a tetraploid and an octoploid species was hexaploid with 54 chromosomes. Bivalents shown black, univalents white, chains stippled.

The polyploid species are isolated from the diploid species by strong crossability and sterility barriers, as would be expected.

Most of the relationships between populations of polyploid Cobwebby Gilias encountered in this study can be assigned unequivocally to either the racial or the specific level of systematic divergence. However, some interesting situations of an intermediate type

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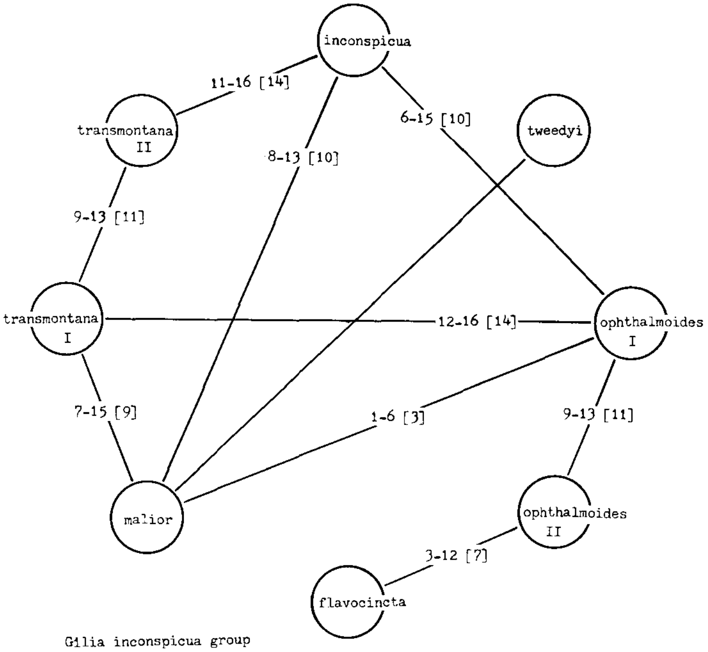
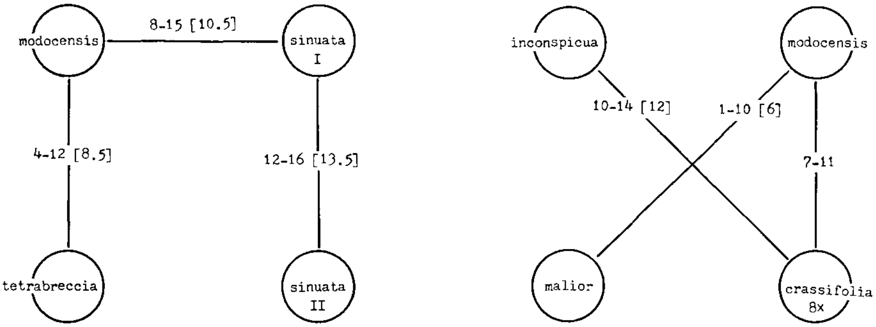
Fig. 9. Chromosome pairing in seven sterile F_1 hybrids in the *Gilia inconspicua* group. The hybrids are all tetraploid ($2N = 36$). Drawings made by camera lucida; chromosomes moved apart slightly in drawing in several instances. Bivalents are shown black, univalents white, and chains stippled.



Gilia inconspicua group



Gilia sinuata group

Inter-group hybrids

Fig. 11. Degree of chromosome pairing in interspecific F_1 hybrids in the polyploid Cobwebby Gilias. The parental species are tetraploid ($N = 18$) in all cases except *Gilia crassifolia* 8X which is octoploid, and complete pairing in the hybrids would therefore be 18 II. The observed numbers of II or III per pollen mother cell, both range and mean for a sample of about 20 to 50 cells, are recorded for each hybrid.

have also been found. *Gilia transmontana,* for example, forms a series of interfertile populations in the Mojave Desert from the Kramer Hills in the west to Mountain Pass in eastern California; but a population still farther east, in the Beaverdam Mts. of southwestern Utah, which is indistinguishable morphologically from the Mojave Desert strains, forms highly sterile and meiotically irregular hybrids with the latter. Similar cases of intraspecific sterility, or of what appears to be best identified as such, are found in *Gilia ophthalmoides.*

SUMMARY

The small-flowered Cobwebby Gilias, diploid and polyploid forms taken together, comprise a flock of intersterile sibling species, some 23 of which have been identified, mapped, and assayed as to fertility relationships.

ACKNOWLEDGMENTS

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