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Verne Grant

Alva Grant

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GENETIC AND TAXONOMIC STUDIES IN GILIA

VII. THE WOODLAND GILIAS

VERNE GRANT* AND ALVA GRANT

HISTORY OF THE SECTION

Present studies indicate that the subgenus Gilia is composed of three natural sections. The first of these, the Leafy-stemmed Gilias or section Eugilia, has been treated in previous papers of this series. The second, the Woolly-leaved Gilias of the desert and bordering mountain ranges (sect. Eugilia of Mason and A. Grant, 1948), is currently under investigation by the present authors. The third group, and the one which forms the subject of this paper, is the Woodland Gilias or section Saltugilia, which has not heretofore been recognized as a taxonomic unit.

In 1831 and 1832 David Douglas travelled in the South Coast Range of California, where he saw and collected both Gilia splendens, a Woodland Gilia, and G. tenuiflora, a typical Woolly-leaved Gilia. Douglas apparently regarded his collections as belonging to distinct species, for he sent G. splendens home to England under the name it now enjoys and made no similar notation about G. tenuiflora which was named by Bentham. The members of the Royal Horticultural Society, who grew the plants from seed in England, evidently did not agree with Douglas, however, and published both species under the name Gilia tenuiflora. Thus began a confusion which lasted for over a century. Gilia splendens was until 1898 known simply as G. tenuiflora Benth. from then until 1948 it was known as G. tenuiflora var. altissima Parish.

One of the important accomplishments of the revisional study of Gilia by Mason and A. Grant (1948) was the restoration of G. splendens as a species distinct from G. tenuiflora. This separation was made possible by the discovery of a character, the type of hairs on the leaves and lower stems, which marks off two large series of forms. In the treatment of Mason and A. Grant, the Gilia splendens series and the G. tenuiflora series were both retained within one section. The present paper takes the next logical step of raising the G. splendens group to the level of an independent section.

Extensive field studies on Gilia during the past several years have enabled the authors to recognize a number of striking similarities between Gilia splendens and G. leptalea, which point to a hitherto unnoticed relationship between these two species and their respective allies. The systematic position of the G. leptalea group has been fluctuating and unsatisfactory in the earlier treatment of Gilia. Brand (1907) and Milliken (1904) simply placed it in a large undifferentiated section Eugilia together with various Woolly-leaved and Leafy-stemmed Gilias. Gray (1886) and Mason and A. Grant (1948) tried to indicate the relationships of the G. leptalea group more precisely, the former by including it in the same section (Courtoisia) with Collomia heterophylla and Gilia glutinosa (Benth.) Gray, the latter by designating a separate subgenus (Kelloggia) for this group together with G. minutiflora and G. tenerrima.

*Rancho Santa Ana Botanic Garden.
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Time has taken care of the section *Courtoisia* of Gray, which is now nothing more than a synonym for species groups belonging to two or even three genera of Polemoniaceae. The proposal of Mason and A. Grant deserves closer attention. The opinion of the present authors is that the subgenus *Kelloggia*, based primarily on the possession of undissected linear leaves, does not reflect any natural relationships, but rather brings together the end products of reduction series in three distinct evolutionary lines. *Gilia tenerrima* seems to belong in the subgenus *Campanulastrum* (Brand) Mason and A. Grant, which as construed by the present authors would include also *G. campanulata, filiformis, inyoensis* and *sonorae*, all of which are delicate annuals. A study of the characteristics of *Gilia minutiiflora* indicates that it belongs in the subgenus *Ipomopsis* (Michx.) Milliken, which the senior author prefers to regard as including the following series of species: (i) *G. rubra, aggregata et aff., tenuifolia, candida*; (ii) *G. multiflora, macombii, thurberi, longiflora, laxiflora*; (iii) *G. congesta, roseata, spicata, minutiiflora, gunnisonii, pumila, gossypifera, depressa, polycladon*. Reduced needle-like leaves are found in *G. tenuifolia* as well as in *G. minutiiflora* in this subgenus. The relationships of the *G. leptalea* group, finally, as noted above, seem to lie in the direction of *G. splendens*.

The *G. splendens* and *G. leptalea* groups have a number of common characteristics in their growth habit, flowers, and ecology. They are erect annual herbs with a strong central leader and abundant well-developed lateral branches. The pubescence of the herbage is the same, consisting of villous or glandular hairs. The inflorescence is cymose and the flowers are borne on long slender pedicels. The corolla is pink in both *G. splendens* and *G. leptalea*, though it becomes blue-violet or white in related species. Some populations belonging to both species groups have yellow corolla throats and pairs of purple dots present at the bases of the corolla lobes. The corolla throat tends to be long, slender and tapering in both *G. splendens* and *G. leptalea*. In both species groups there are members with one or more stamens inserted in the middle of the corolla throat. The pollen is bright blue so that the anthers frequently show through the thin wall of the corolla. Finally, the plants characteristically form colonies in the semi-shade of openings in coniferous forest of the Pacific Slope of North America. This ecological similarity has suggested both the common and the Latin names of the section, Woodland Gilia and *Saltugilia*.

The section *Saltugilia* is regarded as consisting of five species belonging to two species groups. The following classification is adopted:

(i) The *G. splendens* group.
1. *G. splendens* Dougl. (2 subspecies: *splendens* and *grantii*).
3. *G. australis* (Mason & A. Grant) V. & A. Grant.

(ii) The *G. leptalea* group.
4. *G. leptalea* (Gray) Greene (with 3 subspecies: *leptalea, pinnatisecta*, and *bicolor*).
5. *G. capillaris* Kell.

The classification within each species group is essentially the same as that proposed earlier by Mason and A. Grant (1948). The only innovations are the raising of *G. splendens* ssp. *australis* Mason & A. Grant to the level of a distinct species, and the substitution of the name *G. splendens* ssp. *grantii* (Brand) V. & A. Grant for *G.s.grinnellii* (Brand) Mason & A. Grant. The formal taxonomy is set forth in a later section of this paper.
The characteristics of growth habit, leaf, inflorescence and flower of the *G. splendens* group are illustrated in figures 1 to 4. The geographical distribution of the three species is shown in the maps of figures 5 to 7. Inspection of these illustrations shows that *G. splendens* is a scapose plant with a basal rosette of deeply dissected leaves and a diffuse cymose inflorescence with solitary flowers. The plants are capable of growing to a fairly large size under favorable conditions, attaining 12 dm. in height and branching profusely in the experimental garden. *Gilia carrifolia* is similar in growth habit, growing to an even larger size and bearing bigger leaves in the garden. *Gilia splendens* and *G. carrifolia* differ in a number of floral characteristics. The first named species has pink corollas with a long tube and slender tapering throat and short stamens inserted in the sinuses of the lobes; in *G. carrifolia*, by contrast, the corolla is pale blue-violet with a more campanulate form and has long exserted stamens attached to the middle of the short corolla throat. The map (fig. 5) shows that *G. splendens* and *G. carrifolia* are wholly allopatric, the former species occurring in the South Coast Range and the San Gabriel, San Bernardino and San Jacinto Ranges, and the latter ranging from the Cuyamaca, Laguna and Palomar Mountains to the San Pedro Martir Range. The habitats occupied by each species are similar insofar as they consist usually of openings in pine woods.

Fig. 1. Growth habit of *Gilia carrifolia* from Palomar Mt. and *G. splendens* grantii from the San Gabriel Mountains. Plants grown in Claremont.
Fig. 2. Growth habit of *Gilia australis* from Morongo Canyon, Riverside County. Plant grown in Claremont.

Fig. 3. Basal leaves of the *Gilia splendens* group. The strain of *G. splendens splendens* is from Morongo Canyon; the other entities are represented by the same strains as in figs. 1 and 2. From plants grown in Claremont.
The common and widespread form of *G. splendens* is a plant with a medium-short corolla tube. At higher elevations in the San Gabriel Mountains there is a distinctive long-tubed race with bright pink flowers known as *G. splendens* ssp. *grantii* (fig. 4). The altitudinal relationship of this long-tubed form to typical *splendens* can be visualized from the map of figure 6. There is more or less continuous intergradation from subspecies *splendens* to subspecies *grantii* with increase of elevation. *Gilia splendens* descends below the pine belt on the desert slopes of the San Bernardino and San Jacinto Ranges, where a third race has evolved with paler blue-violet flowers, a shorter corolla tube, and a more sparing development of the leaves composing the basal rosette. These characteristics are constant under cultivation in a coastal garden. It would be appropriate to give this race a formal Latin designation were it not for the fact that the features by which it would have to be distinguished are not ordinarily clearly discernable in dried herbarium specimens.

*Gilia australis* is a smaller plant with simpler leaves and small whitish flowers which does not attain a large size either in nature or the experimental garden (figs. 2-4). It ranges from San Bernardino County, California, to the southern half of Baja California (fig. 7). It occurs in hotter and drier habitats than either *G.*
Splendens or *G. carifolia*, namely in sandy washes of the foothills and plains below the pine belt. The reduction of stem and leaf size in *G. australis* may be among the features which have enabled this species to occupy successfully the desert and semi-desert environments. Despite the generally clear-cut ecological isolation of *G. australis* from either *G. splendens* or *carifolia*, there are several localities at least where the species come into immediate contact. These localities are indicated in figure 5. *Gilia australis* occurs sympatrically with the desert race of *G. splendens* on the desert slopes of the San Bernardino Range and the foothills of the San Jacinto Range. It occurs sympatrically with *G. carifolia* on Palomar Mt. and perhaps elsewhere as well.

Fig. 5. Geographical distribution of *Gilia splendens* and *G. carifolia*. The region within the rectangle is enlarged in fig. 6.
Fig. 6. Distribution of *Gilia splendens splendens* and *G.s.grantii* in the San Gabriel Mountains.

*Gilia leptalea* differs most conspicuously from *G. splendens* in having leafy stems and in lacking a basal rosette. The leaves, moreover, are usually simple and linear instead of pinnately compound. The manner of branching, the inflorescence, and the general form of the flowers are, however, similar in the two species. Both the differences and the resemblances are seen by comparing figure 8 with the previous figures. *Gilia leptalea* is polytypic and consists of three well-marked geographical races. These are: (i) a race of relatively tall plants with simple linear leaves and a long slender corolla throat (*G.l.leptalea*, fig. 8); (ii) a race similar to the foregoing except that the leaves are pinnate and bear 1 to 3 pairs of simple lateral lobes (*G.l.pinnatisecta*); and (iii) a race of smaller plants with a short corolla throat which is yellow instead of pink (*G.l.bicolor*, fig. 8).

The geographical distribution of these races is seen in figures 10 and 11. *Gilia leptalea pinnatisecta* occurs in the North Coast Range of California; *G.l.leptalea* occurs in the Cascade Mountains of Oregon and northern California south through the Sierra Nevada and is known from Steens Mountains in eastern Oregon; *G.l.bicolor* is restricted to the Sierra Nevada where it occupies an altitudinal zone above that of typical *leptalea*.

*Gilia capillaris* is similar in habit to *G. leptalea* (fig. 9). The chief difference between the two species lies in the floral characters. *Gilia capillaris* has short corollas, a glandular instead of a glabrous calyx, an included instead of an exserted style, and stamens inserted wholly in the sinuses of the corolla lobes rather than partly in the middle of the throat. In one common form of the species the plants are relatively tall and well branched, whereas in another form the habit is dwarfish. The two extreme forms, which are connected by a complete series of intergradations, are depicted in figure 9. The dwarf form seems to represent a high montane ecotype of the species.

The area of distribution of *G. capillaris*, as shown in figure 10, is the largest of any species of Woodland Gilia. It ranges through the Cascade Mountains from northern Washington to northern California, occurs in various mountain ranges of eastern Washington and eastern Oregon, continues south through the Sierra Nevada, and recurs on at least four mountain peaks in southern California. Although *G. capillaris* reaches higher elevations than *G. leptalea*, there is a fairly broad altitudinal zone where the ranges of the two species overlap. This leads to frequent
sympatric contacts. Several mixed colonies were found by the authors during the course of the field studies; another was reported by Jepson (1943: 176); and a number of others can be inferred from herbarium specimens. The known sympatric occurrences of *G. capillaris* and *G. leptalea* are indicated in figure 11. In the cases known to the authors there is some ecological segregation of the two species, with *G. leptalea* tending to occur in richer soil and *G. capillaris* in drier and sandier spots.

In the southern part of its range *G. capillaris* occurs in the territory of *G. splendens* and *G. caruifolia*. Here again the species are segregated into different ecological niches, with *G. capillaris* occurring mostly at higher elevations. Whether mixed colonies exist containing *G. capillaris* in combination with either *G. splendens* or *caruifolia* is not known.

Fig. 7. Geographical distribution of *Gilia australis*.

The chromosome counts thus far obtained for the Woodland Gilias indicate that all members of this group are diploid with $n=9$. The counts are tabulated below and the chromosomes are shown in figure 12. The herbarium specimens documenting these counts are filed in the herbarium of the Rancho Santa Ana Botanic Garden. *Gilia leptalea bicolor* remains to be counted.

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<td><em>G. australis</em></td>
<td>Morongo Canyon, Riverside Co.</td>
<td>15985</td>
<td>n = 9</td>
</tr>
<tr>
<td><em>G. leptalea leptalea</em></td>
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<td>8925</td>
<td>n = 9</td>
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<tr>
<td><em>G. capillaris</em></td>
<td>Sonora Pass, Tuolumne Co.</td>
<td>18001</td>
<td>n = 9</td>
</tr>
</tbody>
</table>
Fig. 8. Growth habit and flowers of *Gilia leptalea leptalea* from Kyburz, El Dorado County, and *G.i.bicolor* from Ebbett's Pass, Alpine County. From pressed specimens of plants collected in nature. Scale of the habit photographs shown in centimeters; flower photographs enlarged.
Tests performed on caged plants of various strains of Woodland Gilias have furnished evidence of the existence of several different breeding systems in this group. A typical system is that found in *G. leptalea leptalea* from Mather, Tuolumne County, and *G. splendens grantii* from Cow Canyon, Los Angeles County. The plants when isolated in breeding cages do not set capsules or seeds in the absence of insect visits. This result is readily understandable, since in typical flowers the style well exceeds the stamens. If the flowers are artificially self-pollinated, however, a full complement of sound seeds is produced. The plants are thus self-compatible but dependent upon external agents for pollination.
Gilia carujofolia from Palomar Mountain deviates from this condition in being self-incompatible. Fifteen flowers of this strain when selfed completely failed to ripen either capsules or seeds, whereas crosses between sister individuals of this strain were fully inter-compatible.

A deviation in the opposite direction of self-compatibility combined with automatic self-pollination is found in G. australis from Morongo Canyon, Riverside County, and in the desert race of G. splendens from the same locality. These strains proved to be fully autogamous in greenhouse tests. Inspection of the floral mechanism of G. capillaris growing in the wild suggests that it is also autogamous.

In consequence of their small inconspicuous flowers and their autogamous habit,
the wild populations of *G. australis* and *G. capillaris* probably consist of more or less homozygous lines. Insect visits resulting in cross-pollination are probably of occasional occurrence.

With the other species, which have large showy flowers and lack the capacity for automatic selfing, animal visitations might be expected to occur regularly. A search was made for the pollinating agents of these species. The records are most complete for *G. splendens*, which was studied from this point of view at seven localities in
three mountain ranges. Additional pollination records were obtained in one population each of *G. leptalea leptalea* and *G. caruifolia*.

The floral mechanism of *G. splendens* consists of the following elements (see fig. 4). The corolla is funnelform with a pink limb, a throat which is pale bluish-violet in the upper parts and yellow below, and a dark reddish tube. The flowers are held out laterally with the lowermost corolla lobes extended outward slightly and the uppermost ones retracted. The stamens are of unequal length, the lowermost ones being exserted 2 mm. beyond the orifice of the corolla throat, and the uppermost stamen being only half as long and curved over the orifice. The style lies on the lower side of the corolla and is exserted well beyond the anthers. The anthers ripen before the stigma becomes receptive.

![Meiolic chromosomes of the species of Woodland Gilia. From camera lucida drawings of dividing pollen mother cells. Chromosomes sometimes spread apart in drawing.](Fig. 12)

There is nectar at the base of the corolla tube. The entrance to this nectar is through the orifice of the corolla throat, which is usually 3 mm. in diameter and 5 or 6 mm. long and which tapers into the slender tube. The length of the corolla tube is subject to geographical variation. Some typical measurements of the length of the tube are: 3-4 mm. in the desert race of *G. splendens* in Morongo Canyon; 5 mm. in the San Jacinto Mountains; 6 mm. in the San Bernardino Mountains; 17 mm. in *G.s.grantii* on Mt. Wilson in the San Gabriel Range.

The most frequent visitor of the flowers of *G.s.splendens* was the bee fly *Bombbylius lancifer* Osten Sacken* (Bombyliidae), which was found in all populations.

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*The Diptera mentioned herein were identified by Dr. F. R. Cole of Redlands, California.*
studied. This insect lowers itself into the corolla throat while hovering. By inserting its head in the throat and probing into the tube with its long proboscis, which varies from 5 to 10 mm. long in the different individuals collected, it can easily reach the nectar in the typical and the desert races of *G. splendens*. In the process of sucking the nectar, the insect receives pollen on its under surface where it is in a position to be conveyed to the stigma of another flower. Syrphid-flies belonging to the *Syrphus americanus* group were also found visiting the flowers in the San Bernardino Mountains.

A second class of visitors of *G.s.splendens* consists of various kinds of solitary bees, of which *Halictus sisymbrii* Cockerell* and *Doufourea sp.* were collected. The bees settle on the extended lower stamens and climb into the corolla throat, getting the pollen on their venter in the process. In one locality where *G.s.splendens* was growing with *G. capitata abrotanifolia* and *Streptanthus* there were honeybees working on the shallower flowers of the latter species, but none on the former, as though they had become conditioned to the fact its flowers were too long and slender to be successfully visited by them.

*The bees mentioned in this paper were named by Mr. P. M. Timberlake of the Citrus Experiment Station, Riverside, California.*
Gilia splendens grantii with its extremely long corolla tube might be expected to be visited by some kind of insect with an equally long proboscis. As a matter of fact, however, the most prominent visitor of this plant is the same species of bee fly, Bombylus lancifer, as is found on the shorter-tubed G. splendens splendens. By inserting its whole head in the corolla throat, this insect can just reach to the upper part of the tube. Yet it was found systematically working over the flowers and thus was probably obtaining some satisfaction from them. Another bombylid collected on the flowers was Aphoeabantus sp. which has a short snout. In addition two species of bees were found, Halictus sisyphri Cockerell and H. tripartitus Cockerell. An insect visitor with a proboscis long enough to reach to the bottom of the elongated corolla tube of G. s. grantii has not as yet been found but might turn up with further observations.

Anthaxia aeneogaster Castelnau, a black buprestid beetle which sits on the corolla limb, eating the lobes and the pollen, is commonly found in the populations of both subspecies of G. splendens in the San Bernardino and San Gabriel Ranges. This
beetle flies with agility from flower to flower and might carry some pollen. It is probably not a very effective pollinator, however.

The floral mechanism of *G. leptalea*, as exemplified by a typical case, a strain from Kyburz, El Dorado County (fig. 8), is in general similar to that of *G. splendens*. The faintly sweet-scented corollas are again funnel-form with a rotately spreading limb and a long tapering throat and slender tube, which together measure 10 or 11 mm. long. The orifice of the throat is 2 mm. in diameter. The corolla lobes and throat are pink and the tube is yellow. The flower is canted to one side and in this position the two lowermost stamens are exserted about 1 mm. beyond the throat, the anthers of the two lateral stamens stand at the orifice of the throat, and the uppermost anther is inside the throat about 1 mm. from the orifice. The style is exserted. There is nectar at the base of the tube.

Bombylid flies (*Lepidanthrax inaurata* Coquillett and *Oligodranes setosus* Cresson) and a megachilid bee (*Dianthidium ulkei davidsoni* (Cockerell)) were found on these flowers. The insects settle on the flowers and burrow into the throat in order to suck the nectar at the base of the tube. This action of course results in their touching the essential organs. The small size of the bombylid flies which visit *G. leptalea*, with bodies 4 to 6 mm. long, is correlated with the relatively small dimensions of the *leptalea* flowers; the larger-flowered *G. splendens* is visited by larger-bodied beeflies which are 6 to 10 mm. long.

*Gilia caruifolia* presents some different features. The flowers are pale blue-violet instead of pink. Small purple spots are present in pairs at the base of the corolla lobes and there is some yellow in the throat. The corolla throat is broadly expanded, being as broad as it is long, and the tube is relatively short. The stamens are well exserted. Small solitary bees (*Halictus tripertitus*) were found visiting the flowers of the Palomar Mt. strain of this species. Alighting on the exserted stamens and style, the bees enter the broad corolla throat to suck the nectar. Their venter becomes blue with pollen, which rubs off onto the stigma.

A melyrid beetle (*Listrus sp.*) was also found in the flowers of *G. caruifolia*. The same or a related species of beetle has commonly been observed in flowers of *Calochortus* in the same region. Unpublished studies indicate that it is a regular and effective pollinator of the *Calochortus* flowers. It probably contributes to the pollination of *G. caruifolia* also.

Although the list of insect visitors of the Woodland Gilias would be greatly extended by further collecting, it is believed that the main outlines are now evident. Beeflies, assisted by solitary bees and syrphid-flies, are the principal pollinators of the slender pink flowers of *G. splendens* and *G. leptalea*. The more open, blue-violet flowers of *G. caruifolia* are pollinated largely by bees. Various kinds of beetles are occasional visitors. *Gilia australis* and *G. capillaris* are largely self-pollinated.

**FERTILITY RELATIONSHIPS**

**Crossability.**—The following strains of Woodland Gilia were grown in the experimental garden and intercrossed: *G. splendens splendens*, Morongo Canyon, Riverside County; *G. splendens grantii*, Cow Canyon, San Gabriel Mountains, Los Angeles County; *G. caruifolia*, Palomar Mt., San Diego County; *G. australis*, Morongo Canyon, Riverside County; *G. leptalea leptalea*, Mather, Tuolumne County.

Numerous attempts to grow a wide variety of strains of *G. leptalea* and *G. capillaris* were unsuccessful due to failure of germination of the seeds. Refrigeration of the seeds was attempted but may not have been as long or as extreme as that which obtains in the natural habitats. This factor restricted the analysis of compatibility
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<th>No. of sound seeds</th>
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<td>× Woolly-leaved Gilias</td>
<td>5</td>
<td>5</td>
<td>0</td>
<td>64</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>9</td>
<td>11</td>
<td>0</td>
<td>112</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>0</td>
</tr>
</tbody>
</table>

*Underdeveloped.
relationships almost entirely to the *G. splendens* group. A strain of *G. leptalea* was, however, transplanted to the garden one year and was crossed with the *G. splendens* group, which sheds some light on the ability of the two groups to hybridize.

The results of the crosses are summarized in table 1. This table shows that two extremely different races of *G. splendens*, one from the desert and the other from the high San Gabriel Mountains, cross freely and produce abundant F₁ hybrids. These two races of *G. splendens* also crossed very readily with *G. caruifolia*. The compatibility was greater in combinations involving the desert race of *splendens* than in those involving *G. grantii*.

*Gilia australis* was crossed to two strains of *G. splendens*, of which one was sympatric with it in nature and the other allopatric. It is of interest to note that only the former cross succeeded. Sixteen F₁ hybrids resulted from the crossing of 12 flowers of *australis* by *splendens* from Morongo Canyon; 22 flowers of *australis* crossed by *G. splendens grantii* from Cow Canyon yielded no F₁ individuals at all. Crosses of *G. australis* with *G. caruifolia* were likewise unsuccessful.

All attempts to obtain hybrids of the *G. splendens* group with either *G. leptalea* or the other two sections of the subgenus have been unsuccessful. *Gilia stellata* from Morongo Canyon crossed by *G. splendens* from the same locality—hence another cross between sympatric strains—set 4 underdeveloped capsules which contained two abortive seeds and one apparently sound seed which did not germinate.* In every other case the wide crosses did not lead even to the development of the capsules.

Hybrid sterility.—F₁ hybrids were obtained in the following combinations: (i) *G. splendens splendens* ♀ × *G. splendens grantii*; (ii) *G. splendens splendens* ♀ × *G. caruifolia*; (iii) *G. caruifolia* ♀ × *G. splendens grantii*; (iv) *G. australis* ♀ × *G. splendens splendens*.

The interracial hybrid of *G. splendens* was fertile. Six individuals determined for pollen fertility ranged from 6 to 25% good pollen and averaged about 12% good pollen. Seed fertility of these plants was high. The hybrids between *G. splendens* and *G. caruifolia* were likewise fertile. There was no significant difference in this respect between the two combinations, one involving *G.s.splendens* and the other *G.s.grantii*. Nine F₁ individuals ranged from 5 to 22% good pollen and averaged 14% good pollen. These plants set seeds freely. Most individuals of the hybrid of *G. australis* × *splendens* were fertile. Five individuals ranged in per cent of good pollen from 8 to 27%, a sixth plant had only 1% good pollen, and the average for all individuals was 12%. Most of the 16 plants were fully fertile as to seeds, but several individuals were semi-sterile. We can conclude that the species of the *G. splendens* group are interfertile.

Hybrid viability.—The F₁ generation of the interracial hybrid of *G. splendens* and of the interspecific hybrid of *G. splendens* × *caruifolia* was represented by fully vigorous individuals. Some of the individuals in F₁ of *G. australis* × *splendens* were vigorous, others were dwarfed as will be described later.

F₂ progeny were derived from sib crossings of these hybrids. The number of

---

*The systematic position of *G. stellata* Heller, a diploid species of the Sonoran and Mojave Deserts, is not clear. Some populations of this species resemble *G. australis*, others resemble *G. scopulorum*, another desert species. The latter in turn approaches *G. latifolia* which belongs in a separate subgenus with *G. leptomeria*, *stenothyrsa* and other Rocky Mountain and Great Basin species. *Gilia stellata* together with *G. scopulorum* thus bridges the gap between two subgenera... Further study will probably clarify the tangled relationships in this part of the genus.*
individuals in each family in the seedling stage ranged from 40 in *splendens* × *splendens* to 148 in *splendens* × *caruifolia*. The seedling progeny were in general vigorous and healthy with only a small fraction of weak or dead individuals. A similar proportion of weak seedlings was found in cultures of the parental strains.

The seedlings of both the F₂s and the parents were planted out in the experimental field in order to obtain information on the viability of mature plants in the F₂ generation. Unfortunately the plot selected for this purpose was not well suited for Woodland Gilias, with the result that all cultures suffered large losses due to unfavorable environmental conditions. The chief difficulty seemed to be a rotting of the root crown causing eventual death of the plant; other deleterious factors were strong west winds, depredations of rats, and excessively strong insolation. Seventy-three per cent of the plants of *G. caruifolia* were dead or dying on June 9, and 38% and 25% respectively of the populations of *G.s.splendens* and *G.s.grantii* were lost. Under these circumstances the fact that about 50% losses occurred in the various F₂ populations is of little or no significance for the problem at hand.

Each F₂ family contained, in addition to the plants of essentially normal growth which had become weak, sick or dead as a result of an unfavorable response to the environment, also some stunted individuals with malformed leaves or buds and generally retarded development. These runts are a familiar phenomenon in the later generation progeny of interracial and interspecific hybrids in *Gilia*, and apparently represent segregates which lack some genes or gene combinations necessary for normal growth. Genetically inviable individuals of this sort constituted about 5% of the F₂ populations in the interracial hybrid of *G. splendens* and of the interspecific hybrids of *G. splendens* with *G. caruifolia*, and about 28% of the F₂ population of *G. splendens* with *G. australis*. No aberrant dwarfs were found in the population of the parental strains. There is consequently a definite loss of viability in the F₂ generation of crosses between all species and certain races of the *G. splendens* group.

The most striking manifestation of gene-controlled disturbances of normal development was found in progeny of *G. australis* crossed by the sympatric strain of *G. splendens*. Inbred and outcrossed progeny of the parental strains are normal in appearance and general growth. Out of 16 F₁ hybrids, 8 were normal and 8 were runts. The latter produced abnormal red-tipped leaves and never flowered. The F₂ generation derived from two of the normal F₁ plants started out with 64 seedlings, which at an early stage were 100% vigorous and normal in appearance. The 64 seedlings were set out in the experimental plot, where 10 of them died. The remaining 64 individuals segregated into two clear-cut classes: 36 normals and 18 red-leaved non-flowering runts.

The factorial basis of this phenomenon cannot be determined with the scanty data available. The simple division of the F₁ and F₂ progeny into two classes, normals and runts, can probably be explained by some equally simple Mendelian mechanism involving a semilethal gene. The fact that inviable individuals are not found in intraspecific progenies indicates that the semilethal gene carried by one of the parental species is expressed only in interaction with some portion of the genotype of the other species. This case of hybrid inviability, which has some points in common with "corky" in *Gossypium* (Stephens 1946, 1950) and the lethal factor in *Crepis* (Hollingshead 1930), deserves a thorough analysis.

**CYTOLOGY OF THE HYBRIDS**

The course of meiosis in two interspecific hybrids, as revealed by studies of smear preparations of dividing pollen mother cells, is summarized in tables 2 to 4 and
TABLE 2. METAPHASE PAIRING IN F₁ HYBRIDS IN THE WOODLAND GILIAS.
ALL HYBRIDS HAVE 18 CHROMOSOMES

<table>
<thead>
<tr>
<th>Hybrid</th>
<th>No. cells with a given no. bivalents</th>
<th>Total no. cells</th>
<th>Means no. bivalents per cell</th>
</tr>
</thead>
<tbody>
<tr>
<td>australis X s. splendens</td>
<td>9 19 8 6 1</td>
<td>43</td>
<td>7.7</td>
</tr>
<tr>
<td>caruifolia X s. splendens grantii</td>
<td>10 15 1 1</td>
<td>27</td>
<td>8.3</td>
</tr>
</tbody>
</table>

illustrated in figures 13 and 14. Inspection of a third hybrid, that of G. caruifolia with G. splendens splendens, indicated that its meiotic behavior was essentially similar to that of G. caruifolia X G. splendens grantii.

Table 2 reveals a high degree of pairing in the two interspecific hybrids, with an average of about 8 out of a possible number of 9 bivalents per cell. The few unpaired chromosomes which are frequently present at first metaphase often lag at first anaphase (table 3). A somewhat higher frequency of laggards occurs at second anaphase. These lagging chromosomes account for the 13 to 20% of tetrads with micronuclei and for the small amount of micropollen in the mature anthers.

Among the anaphase cells which contain no laggards, moreover, it is not uncommon to find irregular distributions of chromosomes to the two poles, such as 8:10 or 7:11. Of the 14 anaphase cells in which the chromosomes could be counted, less than half had 9:9 distributions. Both hybrids were similar in this respect.

TABLE 3. BEHAVIOR OF CHROMOSOMES AT ANAPHASE IN F₁ HYBRIDS IN THE WOODLAND GILIAS

<table>
<thead>
<tr>
<th>Hybrid</th>
<th>Percent of cells with lagging chromosomes or micronuclei at:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Anaphase I</td>
</tr>
<tr>
<td>australis X s. splendens splendens</td>
<td>7% (27 cells)</td>
</tr>
<tr>
<td>caruifolia X s. splendens grantii</td>
<td>10% (48)</td>
</tr>
</tbody>
</table>

Chains of 3 and 4 chromosomes were of rather frequent occurrence in G. caruifolia X s. splendens, and were found also in G. australis X s. splendens (table 4). The latter hybrid commonly formed chromatid bridges at anaphase. Such configurations were less common but did occur in the hybrid of G. caruifolia and G. splendens (fig. 14, lower right). The multivalents and the bridges indicate that the species of the G. splendens group differ in respect to some gross translocations and inversions.

All of these visible irregularities of chromosome segregation, as well as the imperceptible unbalances resulting from pairing and crossing over of only partially homologous chromosomes, contribute to the amount of shrivelled and inviable pollen reported in the previous section.

TABLE 4. CHROMOSOMAL ABERRATIONS IN F₁ HYBRIDS IN THE WOODLAND GILIAS

<table>
<thead>
<tr>
<th>Hybrid</th>
<th>Percent of cells with:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Multivalents (MI)</td>
</tr>
<tr>
<td>australis X s. splendens splendens</td>
<td>2.3% (44 cells)</td>
</tr>
<tr>
<td>caruifolia X s. splendens grantii</td>
<td>22.9% (35 cells)</td>
</tr>
</tbody>
</table>
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MORPHOLOGY OF THE HYBRIDS

The morphological characteristics of the F₁ hybrids are summarized in table 5. This table shows that with respect to morphology and flowering time the hybrids were in general intermediate between the parents. The F₂ generation derived from four of the F₁ hybrids segregated into a more or less continuous array of variations for each quantitative character. The complexity of some of these characters is illustrated by the silhouettes of basal leaves of the parents, F₁, and six F₂ individuals of one of the crosses (fig. 15).

### TABLE 5. MORPHOLOGY OF F₁ HYBRIDS IN THE WOODLAND GILIAS

<table>
<thead>
<tr>
<th>Character</th>
<th>Cross</th>
<th>P</th>
<th>F₁</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habit</td>
<td>s. splen* × s. gran</td>
<td>sparse foliage</td>
<td>intermediate</td>
<td>dense cluster of basal leaves</td>
</tr>
<tr>
<td></td>
<td>s. splen × car</td>
<td>sparse foliage</td>
<td>intermediate</td>
<td>dense cluster of basal leaves</td>
</tr>
<tr>
<td>Stem</td>
<td>s. splen × s. gran</td>
<td>glabrous</td>
<td>sparsely glandular</td>
<td>glandular</td>
</tr>
<tr>
<td></td>
<td>car × s. gran</td>
<td>glabrous</td>
<td>sparsely glandular</td>
<td>densely glandular</td>
</tr>
<tr>
<td></td>
<td>s. splen × s. gran</td>
<td>glabrous</td>
<td>sparsely glandular</td>
<td>densely glandular</td>
</tr>
<tr>
<td></td>
<td>aus × s. splen</td>
<td>densely hirsute</td>
<td>hirsute</td>
<td>glabrous</td>
</tr>
<tr>
<td>Flowering time</td>
<td>s. splen × s. gran</td>
<td>early</td>
<td>intermediate</td>
<td>late</td>
</tr>
<tr>
<td></td>
<td>s. splen × car</td>
<td>early</td>
<td>intermediate</td>
<td>late 26.6 mm.</td>
</tr>
<tr>
<td></td>
<td>s. splen × s. gran</td>
<td>14.4 mm.</td>
<td>20.5 mm.</td>
<td>24.5 mm.</td>
</tr>
<tr>
<td></td>
<td>car × s. gran</td>
<td>13.5 mm.</td>
<td>15.2 mm.</td>
<td>14.4 mm.</td>
</tr>
<tr>
<td></td>
<td>aus × s. splen</td>
<td>7.1 mm.</td>
<td>9.7 mm.</td>
<td>intense pink</td>
</tr>
<tr>
<td></td>
<td>s. splen × s. gran</td>
<td>pale violet</td>
<td>pale pink</td>
<td>intense pink</td>
</tr>
<tr>
<td></td>
<td>car × s. gran</td>
<td>pale violet</td>
<td>pale pink</td>
<td>gradually tapering</td>
</tr>
<tr>
<td></td>
<td>s. splen × s. gran</td>
<td>abruptly dilated</td>
<td>slightly dilated</td>
<td>2.0 mm.</td>
</tr>
<tr>
<td></td>
<td>car × s. gran</td>
<td>3.5 mm. long</td>
<td>broad but tapering</td>
<td>tapering</td>
</tr>
<tr>
<td></td>
<td>s. splen × s. gran</td>
<td>broadly expanded</td>
<td>spots present</td>
<td>pair of purple spots</td>
</tr>
<tr>
<td></td>
<td>car × s. gran</td>
<td>no trace of purple spots</td>
<td>some flowers have faint pinkish spots, other flowers on the same individual have none</td>
<td>at base of each lobe</td>
</tr>
<tr>
<td></td>
<td>car × s. gran</td>
<td>pair of purple spots</td>
<td>none</td>
<td>no spots</td>
</tr>
<tr>
<td>Stamina, exsertion</td>
<td>s. splen × car</td>
<td>barely exserted above orifice of throat</td>
<td>well exserted, but not as long as corolla lobes</td>
<td>as long as corolla lobes</td>
</tr>
<tr>
<td></td>
<td>car × s. gran</td>
<td>as long as lobes</td>
<td>about half as long as lobes</td>
<td>half as long as lobes</td>
</tr>
<tr>
<td>Stamina, insertion</td>
<td>s. splen × car</td>
<td>in sinuses of corolla lobes</td>
<td>in sinuses</td>
<td>in sinuses</td>
</tr>
<tr>
<td></td>
<td>car × s. gran</td>
<td>in middle of throat</td>
<td>in sinuses</td>
<td>in middle of throat</td>
</tr>
<tr>
<td>Style</td>
<td>s. splen × car</td>
<td>shorter than corolla</td>
<td>almost as long as corolla</td>
<td>longer than corolla</td>
</tr>
<tr>
<td>Capsule</td>
<td>s. splen × s. gran</td>
<td>slightly exceeding the fructing calyx</td>
<td>1/3 longer than fructing calyx</td>
<td>twice as long as fructing calyx</td>
</tr>
</tbody>
</table>

*s. splen=splendens splendens; s. gran=splendens grantii; car=caruifolia; aus=australis.
Fig. 15. Basal leaves of *G. caruiifolia*, *G. splendens splendens*, their *F₁* hybrid, and six *F₂* progeny. x 0.4
As previously mentioned, both the F$_2$s and samples of the parental strains were planted out in an experimental plot in which they did not thrive. *Gilia caruifolia* was the most unsuccessful of the parental types in this environment; only one-quarter of the plants of this species survived in good condition, whereas about three-quarters of the individuals belonging to the other species remained alive and vigorous. It was interesting, therefore, to find in going down the rows of the F$_2$ of *G. caruifolia X splendens grantii* that the *grantii*-like segregates far outnumbered the *caruifolia*-like types. It is probable that the F$_2$ individuals resembling *G. caruifolia* were selected against in the Claremont environment by the same factors which so strongly reduced the population of *G. caruifolia*.

This selective discrimination against many of the genotypes in the experimental plot made it impossible to carry out a more detailed analysis of the inheritance of the taxonomic characters. The intermediacy of the F$_1$ hybrids and the appearance of continuous variation in their F$_2$ progeny suggest that these characters are determined by multiple factors.

**Evolution**

The phylogeny of the Woodland Gilias can be reconstructed with considerable plausibility on the basis of what is now known concerning the group. The two species groups, one centering around *G. splendens*, the other around *G. leptalea*, evidently represent two major branches of a phylogenetic tree. The closest approximations of the two branches, both morphologically and geographically, are reached in *G. splendens splendens* and in *G. leptalea pinnatisecta*. Both entities occur in the Coast Ranges, the former in the south and the latter in the north. Each entity possesses slender pink flowers, often with small purple spots, which are self-compatible but cross-pollinated by beetles and solitary bees. *Gilia leptalea pinnatisecta*, of all the forms of the *G. leptalea* group, alone has fairly well dissected leaves, which must have been the ancestral condition of the group. This plant approaches *G. splendens* in both distribution and several morphological characters.

Not all of the common resemblances of the *G. leptalea* and *G. splendens* groups, however, are found in the two Coast Range races just mentioned. *Gilia leptalea* resembles *G. caruifolia* more than *G. splendens* in having some of its stamens inserted in the corolla throat rather than in the sinuses of the lobes. On the other hand, *G. splendens* resembles *G. leptalea bicolor* more than *G. l. pinnatisecta* in the yellow color of the lower part of the corolla throat. The ancestors of the two species groups thus probably had more characters in common than do *G. splendens splendens* and *G. leptalea pinnatisecta* today. The latter entities have diverged widely from the ancestral types and have lost some of the characteristics which they previously possessed and which were preserved in other descendants of each line.

Each branch of the Woodland Gilias has given rise to an offshoot of reduced, self-pollinating plants fitted for more extreme environments than prevail in the ancestral coniferous forest. In the *G. leptalea* group the specialized offshoot is *G. capillaris*, which has colonized areas with long cold winters. Regions with this type of climate are found today in the high interior mountain ranges but were more widespread at lower elevations during the Pleistocene period. The reduced autogamous offshoot of the *G. splendens* group is *G. australis*, which has colonized the arid coastal plain of southern California and Baja California and has invaded the Mojave Desert. The arid environments in which it finds itself are, like the cold environments inhabited by *G. capillaris*, geologically recent (Axelrod 1950).

The direction of evolution in the Woodland Gilias, as inferred from general phylogenetic considerations, is clearly from an ancestral type adapted to a relatively
equable climate, as found today in the California Coast Ranges, toward derived types fitted respectively for frigid and for arid climates, as found in the present day high mountains and deserts. In their evolutionary development, therefore, the Woodland Gilias have kept pace with the major climatic changes in western North America since the latter part of Cenozoic time.

With respect to their broader relationships the Woodland Gilias seem to stand between the Leafy-stemmed and the Woolly-leaved Gilias. In the *G. leptalea* group the upper cauline leaves are well developed as in the Leafy-stemmed Gilias, whereas the *G. splendens* group consists of scapose plants like the Woolly-leaved Gilias. The types of hairs on the stems, leaves and calyces of the Woodland Gilias are the same as those found in the Leafy-stemmed Gilias. The inflorescence, consisting of solitary flowers borne in pairs on long pedicels, is like that of the Woolly-leaved Gilias. The area of distribution of the Woodland Gilias on the Pacific Slope of North America and into the Mojave Desert overlaps broadly with that of the Leafy-stemmed Gilias on the Pacific Slope and the Woolly-leaved Gilias in the deserts and bordering mountain ranges.

The evolutionary pattern developed in the Woodland Gilias is different in several ways from that of either the Leafy-stemmed or the Woolly-leaved Gilias. The elements composing the evolutionary pattern of the Leafy-stemmed Gilias have been described in previous publications (Grant 1953, 1954). That section consists of a number of sympatric species which come into contact in innumerable localities but which are isolated by exceedingly strong barriers of incompatibility and hybrid sterility. Despite these barriers to crossing, some hybridization does occur and accounts for the fact that the species are poorly defined and have been the subject of much disagreement among systematists. Two of the species of Leafy-stemmed Gilia are allotetraploids.

The same features are found in an even more marked degree in the Woolly-leaved Gilias (V. & A. Grant, unpublished). Here the taxonomic picture is very bewildering. This is evidently due to the existence of a large number of entities which are sympatric and which consequently enjoy many and varied opportunities for hybridization. There is definite evidence that such hybridization has occurred and has modified the variation pattern of the group. Three tetraploid species have so far been discovered in this section, of which two are known and the third suspected to be of hybrid origin. Nevertheless, natural hybridization is opposed by very strong internal barriers. The incompatibility barriers are so strong in the Woolly-leaved Gilias that attempts to obtain artificial interspecific hybrids almost invariably fail. Those rare hybrids which can be produced are then usually highly sterile.

In the Woodland Gilias, by contrast, the species lines are clearly drawn for all to read. A satisfactory treatment of these species was worked out on the basis of conventional taxonomic methods (Mason and A. Grant, 1948). The experimental work conducted on the group since that date has not changed the picture in any essential way. Polyploidy has not been found in the group. The innovation of combining the *G. leptalea* and *G. splendens* groups into one new section was based on morphological and ecological similarities first perceived during field studies, and was neither supported nor rejected by the genetic data.

The simple taxonomic structure of the Woodland Gilias is probably a result of a phylogenetic development which has been almost entirely dendritic and divergent. In short, hybridization has apparently played only a minor role in the production of new variations in this group. The unimportance of hybridization is due chiefly to the lack of opportunities. There are relatively few species and they are largely
allopatric. Clusters of related species growing together, such as are commonplace in other sections of the genus, are not met with in the Woodland Gilias. It is not at all unusual to find three species of Leafy-stemmed Gilia, or four, five or even six species of Woolly-leaved Gilia, growing together and blooming simultaneously in one locality. The great majority of habitats contain only one species of Woodland Gilia; the finding of two species in the same place is definitely a rarity, and probably represents the maximum aggregation which occurs.

Where two species of Woodland Gilia do come into contact, as occurs most frequently with *G. leptalea* and *G. capillaris* in the Sierra Nevada (fig. 11), there is morphological evidence of introgressive hybridization. *Gilia capillaris* has acquired longer corollas in one such locality near Frendonyer Pass, Lassen County, so that the population approaches *G. leptalea* slightly in appearance; it has acquired a yellow corolla throat in Sonora Pass, Tuolumne County, causing the population to simulate the neighboring populations of *G. leptalea bicolor*. In the relatively few places where *G. splendens* comes into contact with *G. australis*, as on the lower slopes of the San Bernardino and San Jacinto Ranges, introgression may similarly be inferred from the special characteristics assumed by the indigenous populations of *G. splendens*: the paler corollas with less pink and more blue-violet in the limb and throat, the shorter corolla tube, the more sparse development of basal leaves; and in at least one case the self-pollinating habit characteristic of *G. australis*. The Woodland Gilias do not lack the ability, but rather the opportunity, for hybridization on a wide scale.

The largely allopatric distributions of the few species of Woodland Gilias seem to be correlated with another unique feature of their evolutionary pattern. In this group, unlike other sections of the subgenus, the internal barriers to gene exchange between species are weak. The species of the *G. splendens* group cross more or less freely with one another. The hybrids are partially fertile and set seeds in abundance. It is possible to grow large F₂ populations from seeds harvested on these hybrids. Interspecific hybrids in other sections are usually completely sterile in the garden so that no F₂ progeny can be grown at all. Pairing and separation of the chromosomes at metaphase and anaphase is more nearly regular in hybrids in the *G. splendens* group than in hybrids of either the Leafy-stemmed or the Woolly-leaved Gilias. The relatively slight differentiation of the chromosomes may account in part for the weak sterility barriers.

The behavior of the sympatric strains of *G. australis* and *G. splendens* from Morongo Canyon in crosses with one another is interesting in this connection. The strains cross freely. However, some of the F₁ individuals were semi-sterile and half of the total number were inviable. One-quarter of the F₂ progeny were inviable. The peculiar appearance, uniform expression and regular ratios of the inviable types suggests that they are produced by semilethal factors carried by the sympatric populations. This phenomenon did not occur in the crosses of allopatric strains of the *G. splendens* group.

Dobzhansky (1950) has applied the concepts of "challenge" and "response" to the evolutionary activities of living populations. The coexistence of several closely related species in the same habitats is a kind of challenge, to which the species may respond by the development of internal barriers capable of preventing, reducing or at least regulating the flow of genes between them. Such barriers are seen to exist between *G. splendens* and *G. australis* in at least one locality where they occur together. But for the most part the Woodland Gilias have lacked that challenge and have not made that response.
Section **Saltugilia**, sect. nov. **WOODLAND GILIAS**.


Herba annua ramosa; caulibus et foliis villosis vel glandulosis; floribus solitariis axillaribus; corollis saepe puniceis, faucibus saepe flavis, lobis base aliquando purpureo-maculatis; faucibus corollarum saepe longis et tenuibus; staminibus in medio faucium vel in sinu aliquando insertis.

Erect annuals with a strong central leader and usually abundant, well-developed lateral branches; herbage villous, with multicellular chain-like trichomes, or glandular, with stipitate glands, the upper branches of inflorescence glandular; inflorescence cymose, the flowers borne on long slender pedicels; corolla often pink, sometimes blue-violet or white, often striated with dark violet or purple on the outer surface, the throat often yellow, small purple spots sometimes present in pairs at the base of the lobes; corolla throat often long, slender and tapering; stamens sometimes inserted in the middle of the corolla throat, or otherwise in the sinus, pollen bright blue, the anthers showing through the wall of the corolla.

Characteristically plants of openings in coniferous forest; but some of the races occur also in oak woodland and chaparral, and *G. australis* has invaded the desert.

**Type.** — *Gilia splendens* Doug.

**Relationships.**—With the Leafy-stemmed Gilias and the Woolly-leaved Gilias in the subgenus *Cilia*.

**Herbaria consulted.**—California Academy of Sciences; University of California, Berkeley; Dudley Herbarium, Stanford; Oregon State College; University of Oregon; Pomona College; Rancho Santa Ana Botanic Garden. The authors are grateful to the curators of these herbaria for many favors.

**KEY TO THE WOODLAND GILIAS**

Plants scapose; basal leaves bi- or tri-pinnate or sometimes once pinnate; capsule containing 12-70 seeds. South Coast Range and southern California.

Stamens inserted in sinus of corolla, shorter than corolla lobes; flowers pink to whitish or pale violet. Monterey Co. to Baja California and in the Mojave Desert.

Flowers large, 10-36 mm. long; corolla limb usually pink; style exserted.

Corolla tube short, 9 mm. long or less; limb bright pink. Widespread .............................................. 1a. *G. splendens splendens*

Corolla tube long, 10 mm. or more long; limb very intense pink. Higher elevations in San Gabriel Mts. .................................................. 1b. *G. splendens grantii*

Flowers small, 5-9 mm. long; corolla limb whitish or pale violet; style included ............ 3. *G. australis*

Stamens inserted in middle of corolla throat, exserted beyond corolla lobes; flowers blue-violet. San Diego Co. to Baja California .......... 2. *G. caruifolia*

Plants not scapose; basal and lower cauline leaves simple and entire or occasionally with small lateral lobes; capsules containing 6-12 seeds. Washington to northern California, infrequent in southern California.

Flowers large, 8-18 mm. long, about 3 times the length of calyx; some of the stamens inserted in middle of corolla throat; style exserted; calyx usually glabrous.

Leaves simple and entire. Cascade Mts. from Washington to northern California and Sierra Nevada.

Corolla throat pink or violet, long and slender, 5-7 mm. long .................. 4b. *G. leptalea leptalea*

Corolla throat yellow or white, short, 4-5 mm. long .................. 4c. *G. leptalea bicolor*

Leaves with 1-3 pairs of small lateral lobes. North Coast Ranges ......... 4a. *G. leptalea pinnatisecta*

Flowers small, 3-6 mm. long, about twice the length of calyx; stamens all inserted in sinuses of corolla; style included; calyx glandular .................. 5. *G. capillaris*

*Dr. Philip A. Munz has given helpful advice on the nomenclatural problems.*
1a. Gilia splendens subsp. splendens.

Gilia tenuiflora var. altissima Parish, Erythea 6: 90, 1898. (lectotype seen).
Gilia tenuiflora subsp. eu-tenuiflora var. genuina subvar. altissima Brand, Pflzr. 4 (250): 102, 1907.

Corolla limb usually pink, sometimes pale pinkish-violet, tube 3-6 mm. long, total length of corolla when pressed flat 10-23 mm.; longest filaments 1-2 mm. long; stigma exerted 1-5 mm. beyond anthers.

Type.—Plants grown by the Royal Horticultural Society in England in 1834-1836, and illustrated in Edwards' Botanical Register, from seeds sent from California by David Douglas under the name of Gilia splendens. Douglas collected in the South Coast Range of California between Monterey and Santa Barbara counties in the years 1831 and 1832, and it is here that he probably found the species.

The type of G. tenuiflora var. altissima Parish must be designated for nomenclature.
tural purposes. The type locality is given as foothills of the San Bernardino Mountains. An inspection of Parish collections in California herbaria reveals that the earliest collection from this locality, and the first one to be recognized as distinctive by the collector, is S. B. and W. F. Parish 1592, May 1881, Dudley Herbarium 119565. The specimen is labelled *Gilia tenuiflora* Benth. and bears the notation "A peculiar, large-flowered form." This specimen should be regarded as the type of *G. tenuiflora* var. *altissima*.

The type of *G. grinnellii* Brand was *F. Grinnell*, July 4, 1904, Switzer's Trail, Mt. Wilson, Los Angeles Co., California, in the Berlin Herbarium. The type specimen was destroyed during World War II, according to information received from Prof. G. Helmcke of Berlin. An effort to reconstruct Brand's concept of *grinnellii* meets with difficulties since the various lines of evidence are not wholly consistent with one another. Brand's cotypes at the California Academy of Sciences, for example, refer to as many different entities as there are specimens cited, none of which exist at the type locality. This line of evidence can only be ignored for purposes of typification. Brand's description of *G. grinnellii* narrows the range of possibilities to either the typical form of *G. splendens* or the long-tubed race of higher elevations in the San Gabriel Range. Mason and A. Grant (1948) considered that *grinnellii* was the long-tubed race. The statement of Brand that the corolla tube is 5 times longer than the calyx in *grinnellii*, and only 2 to 3 times longer in typical *splendens* (*tenuiflora altissima* in Brand's treatment), stands in favor of this interpretation. But Brand also gives the length of the corolla in *grinnellii* as 22 mm., and in typical *splendens* as 25 mm. This comparison would lead to the interpretation that *grinnellii* is synonymous with typical *splendens*. Brand's own statements therefore afford no certain criterion for identifying the entity which he named. The final recourse exists of designating a new type. There is a topotype collected by F. Grinnell, June 22, 1910, on Switzer's Trail at 3500 ft. elevation in the San Gabriel Mts., Dudley Herbarium 72993. This specimen is designated as the neotype of *G. grinnellii*. It would be classified by the present authors as typical *splendens* approaching the long-tubed race.

Range.—Openings in pine or oak woods or chaparral in the South Coast Range from Monterey County to Ventura County and in the San Gabriel, San Bernardino and San Jacinto Mountains of southern California, and on the desert slopes of the latter two ranges. From 1000-7700 feet elevation. In bloom from April to July. Sympatric with *G. australis, achilleaefolia, capitata abrotanifolia, exilis, sinuata, stellata*.


1b. Gilia splendens subsp. grantii, comb. nov.


Corolla limb intense pink, tube 10-18 mm. long, total length of corolla when pressed flat 20-36 mm.; longest filaments 2-3 mm. long; stigma exserted 2-5 mm. beyond anthers.

Range.—Open sandy or gravelly slopes, in the coniferous forest belt, San Gabriel Mountains, Los Angeles County. From 2700-7000 ft. elevation and above the zone inhabited by subspecies splendens. Blooms from May to July. Sympatric with G. exilis.

Variation.—Intergrades with subspecies splendens.

Specimens cited: CALIFORNIA. Los Angeles Co.: Mt. Wilson, V. & A. Grant 16029, 16030, 16031, 16032, H. L. Mason 3744; Rock Creek, F. W. Peirson 7933; San Antonio Canyon, F. W. Peirson 457, 7343, H. L. Mason 3773; Cow Canyon, V. & A. Grant 16006.

2. GILIA CARUIFOLIA Abrams

Gilia arenaria subsp. exilis var. caruifolia Brand, Pflzr. 4 (250): 104, 1907.

Scapose annuals 3-6 or even 12 dm. tall, with an erect central leader and numerous branches spreading from the base; base of plant with numerous large, bi- or tri-pinnate leaves, with narrow rachis and deeply-cut segments, 3-7 or even 30 cm. long, upper stems clothed only with reduced linear bracts, entire margined or with a pair or two of short lateral lobes; herbage glabrous, the stems glaucous, the upper branches of inflorescence glandular; inflorescence cymose, the flowers borne in pairs on pedicels of unequal length subtended by a bract, pedicels 1-10 mm. long; calyx 3-4 mm. long, the lobes 1 mm. long; corolla funnelform with a broad limb and short tube, the tube 3-5 mm. long, throat 3 mm. long and 3 mm. in diameter at orifice, the limb 15-20 mm. in diameter, the lobes oval, 5-8 mm. long and 3-5 mm. wide, spreading or often somewhat ascending, total length of corolla when pressed flat 7-14 mm., corolla limb pale blue-violet, often with a pair of purple spots at the base of each lobe, upper part of throat whitish with yellow spots, lower throat and tube pale blue-violet; stamens inserted in middle of throat about 1 mm. below sinuses, unequal in length, the uppermost stamen being about 1 mm. shorter than the others, the longer filaments measuring 6-7 mm. long, pollen blue; style lying on lower side of corolla, exserted, the stigmas 2-3 mm. beyond anthers at maturity; capsule 4 mm. long, 2-3 mm. wide, slightly to twice exceeding the accrescent calyx, containing 12-20 seeds; seeds brown, 1 mm. long; n = 9.

Type.—Dry hills between Cuyamaca Lake and Oriflamme Canyon, Cuyamaca Mountains, San Diego County, California, June 28, 1903. L. Abrams 3940. New York Botanical Garden Herbarium.

Range.—Sandy soils in openings in pine woods or chaparral, mountains from San Diego County, California, to the San Pedro Martir Range in Baja California. 4500-7500 feet elevation. In bloom from May to August. Sympatric with G. australis, sinuata, diegensis.

Variation.—Fairly uniform. Individual variation exists within colonies with respect to such characters as shape of leaf lobes and presence of purple and yellow markings in the corolla throat.

Specimens cited: CALIFORNIA. San Diego Co.: Hot Springs Mt., Annette Carter 1832; Palomar Mt., P. A. Munz 8229, V. & A. Grant 16018; Oak Grove, F. W. Peirson 2295; Cuyamaca Mts., L. Abrams 3940, M. E. Jones (1926); Jacumba, M. E. Jones (1926).

3. GILIA AUSTRALIS comb. nov.

G. splendens subsp. australis Mason & A. Grant, Madroño 9: 213. 1948 (type seen).

Small scapose branched annuals, to 30 cm. tall, with a basal rosette; lower leaves villous, stems glabrous, glandular in the inflorescence, sometimes sparsely pubescent throughout; leaves mainly basal, these once, twice or thrice pinnate, 2-7 cm. long, the rachis narrow, 1 mm. wide, the lateral lobes 3-6 on each side, well spaced, nar-
row, 5-15 mm. long and usually dissected into secondary divisions, upper cauline leaves reduced to entire linear bracts a few mm. long; inflorescence cymose, the flowers borne in pairs on pedicels of unequal length subtended by a bract, the pedicels 4-26 mm. long, calyx 2-4 mm. long, the lobes acute and erect; corolla small, funnelform, twice or thrice the length of the calyx, measuring 5-10 mm. long when lobes are pressed out flat, the tube itself 2-3 mm. long, limb 4-9 mm. in diameter, pale violet or whitish with yellow spots in throat and outer surface of lobes commonly streaked with purple; stamens inserted in sinuses, equal in length, short, 0.5-1.5 mm. long, pollen blue; style included, stigmas 1 mm. long, touching the anthers; capsule ellipsoidal, equaling to twice exceeding the accrescent calyx, 4-6 mm. long, about twice as long as wide, containing 20-30 ovoidal, light-brown seeds 0.5-1.0 mm. long; n=9.

Type.—Temecula Valley, Riverside County, California, H. L. Mason 3195. May 2, 1926. University of California Herbarium 748763.*

Range.—Sandy places in the foothills and adjacent plains of the coastal mountains of southern California and Baja California from San Bernardino County (34° lat.) to Santa Domingo (25° lat.), and into the Mojave Desert from the San Bernardino and San Jacinto Mts. to the Old Dad Mts. and Joshua Tree National Monument; 400-4100 ft. Blooms from March to May, in some localities as early as February. Sympatric with G. splendidens, caruifolia, sinuata, stellata, abramsii.


4. GILIA LEPTALEA (Gray) Greene

Erect annuals, 5-35 cm. tall; stems well branched, or sometimes simple, glandular more or less throughout their length; leaves linear, arcuate, 1-5 cm. long, simple, or sometimes with 1-3 pairs of linear lateral lobes, glandular; inflorescence cymose, the flowers borne in pairs on pedicels 3-40 mm. long; calyx slender, 3-4 mm. long, the lobes acuminate, about 1 mm. long, usually glabrous, sometimes glandular; corolla funnelform, 8-18 mm. long, about 3 times the length of the calyx, the throat mostly long and slender, 4-7 mm. long, 3 mm. wide, the lobes oval, 3-5 mm. long and 2.0-2.5 mm. wide, limb bright pink, a pair of dark violet or purple spots sometimes present at base of each lobe, throat pink, violet, yellow or white, tube bright to pale yellow, throat and tube often striated with purple or dark violet; stamens unequally inserted, some in the sinuses, others in the middle of the throat 1-2 mm. below the sinuses, the filaments unequal in length, 1-3 mm. long, some anthers well included, others slightly exserted; style exserted, stigma 2-3 mm. beyond anthers; capsule 3-4 mm. long, equalling but not exceeding the accrescent calyx, containing 6-12 seeds; seeds brown, 1 mm. long, angular; n=9.

Range.—Openings in coniferous forest, Pacific Slope from the Columbia River, Oregon, to Lake County, California, through the mountains of Siskiyou and Shasta counties, California, to the Sierra Nevada, and thence south to Tulare County. 2000 to 8500 feet elevation. Blooms from June to September.

4a. GILIA LEPTALEA subsp. PINNATISECTA Mason & A. Grant


Leaves pinnate with 1-3 pairs of simple lateral lobes, the blade narrow to broadly linear, 1-6 mm. broad; corolla throat as in subspecies leptalea.

*Gilia australis: Heller is a manuscript name which was cited by Brand (Pflz. 4 (250): 115, 1907) as a synonym of Gilia aggregata arizonica. The mere citation of a name as a synonym does not constitute valid publication, according to Article 46 of the rules of nomenclature. Since a name which has not been validly published has no claim to priority (Art. 22), the name australis of Mason and A. Grant, which was properly published, can be used in the rank of species.

Range.—North Coast Range from Humboldt County to Lake County, California. 1000 to 7000 feet. June to August.


4b. Gilia leptalea subsp. leptalea


Gilia leptalea Greene, Erythea 4: 58, 1896.

Gilia leptalea subsp. eu-leptalea Brand, Pflzr. 4 (250): 97, 1907.

Leaves linear and entire; corolla throat long, slender, gradually tapering to the tube, 5-7 mm. long, pink or violet.

Type.—The lectotype is H. N. Bolander 4918, Yosemite Valley, California, 1866. Gray Herbarium, Harvard University.* This is one of several specimens cited by Gray in the original description. The herbarium label bears the legend "leptalea n. sp. A. Gray" in Gray’s handwriting.

Range.—Cascade Mountains from Oregon to Shasta and Lassen counties, California, Steens Mts. in eastern Oregon, and through the Sierra Nevada to Tulare County. 4500-8000 feet elevation, usually at lower elevations than subspecies bicolor. Blooms from June to August. Sympatric with Gilia capitata.


4c. Gilia leptalea subsp. bicolor Mason & A. Grant

Gilia leptalea subsp. bicolor Mason & A. Grant, Madroños 9: 220, 1948. (type seen).

Leaves simple and entire; corolla throat short, more or less abruptly tapering to the tube, 4-5 mm. long, yellow or white.


Range.—Sierra Nevada from Plumas County to Fresno County. 6000-9700 feet elevation, usually above subspecies leptalea in areas where both occur. Blooms from July to September.


5. Gilia capillaris Kell.


Gilia linearifolia Howell, Fl. N. W. Amer. 461, 1903.


Gilia subalpina Greene ex Brand, loc. cit. (cotypes seen).

Gilia columbiana Piper ex Brand, loc. cit., as a synonym.

*Dr. R. C. Foster of the Gray Herbarium kindly loaned type material of this entity.
Erect annuals, 2-35 cm. tall; stems well branched, or sometimes simple, stipitate glandular throughout their length; leaves simple, or rarely with a pair of lateral lobes at base, linear, sometimes slightly arcuate, 0.5-5.0 mm. wide, glandular, lower and middle cauline leaves 1-4 cm. long, the upper cauline leaves becoming progressively smaller; inflorescence cymose, the first flowers to mature being terminal on short pedicels and subsequent flowers being borne on longer pedicels which arise in the axils of the first; calyx slender, 3-4 mm. long, the lobes acuminate and about equal in length to the tube, glandular, green, often with purple streaks on the lobes or in the sinus; corolla funnelform, 3-6 mm. long, about twice the length of the calyx, pale violet, pink or white, often striated with purple, the tube sometimes yellow, the throat sometimes possessing purple spots; stamens inserted in the sinuses, the filaments equal in length and point of insertion, 0.5 mm. long, the anthers bright blue, visible through the wall of corolla in dried specimens; stigmas 0.5-1.0 mm. long, included, touching the anthers; capsule ovoid, 3-4 mm. long, equalling the calyx, containing 6-12 brown seeds 1.0-1.5 mm. long.


Range.—On sandy soils of mountain slopes and flats, often in openings in coniferous forest, frequently springing up following the melting of snow patches. 2500-7500 ft. elevation in northern part of range, or washing down rivers to lower elevations (at 200 ft. near mouth of Jager Creek in Humboldt Co.), 5000-10500 in Sierra Nevada, and 5000-8500 ft. in southern California. Blooms from July to August and even into September in north, from June to August in Sierra Nevada, and in June and July in southern California.

Cascade Mountains of Washington and Oregon, occasional in mountains of eastern Washington and Oregon, in the North Coast Range of California as far south as Mendocino County, throughout the Sierra Nevada, on Mt. Pinos in Ventura County, and through the San Bernardino and San Jacinto Mountains to Palomar Mt. in San Diego County.

Sympatric with G. leptalea, G. tenuiflora purpusii.

Variation.—The common form of the species throughout most parts of its range is a tall robust plant. In the Sierra Nevada south of Lake Tahoe the plants tend to be dwarf annuals only a few centimeters tall. In the central Sierras the corolla tube is sometimes yellow (i.e., V. & A. Grant 8991, Slate Creek, Mono Co.) which corresponds to the coloration of G. leptalea in this same area and may point to the occurrence of introgression.


SUMMARY

The Woodland Gilias comprise a new section (Saltugilia) of the subgenus Gilia. The section contains two species groups: the G. splendens group, in southern California and Baja California, includes G. splendens, caruifolia, and australis; the
G. leptalea group in northern California, Oregon and Washington consists of G. leptalea and G. capillaris. So far as known all species are diploid with n=9. The distinctive characteristics of the section, the species and the subspecies are summarized on page 84.

The two branches of the section converge in G. splendens of the South Coast Range and G. leptalea pinnatisecta of the North Coast Range of California. These are plants of openings in coniferous forest, which occur in a region characterized by relatively mild and moist winters. The plants are self-compatible but require insect visits for pollination. The slender funnelform pink flowers are pollinated chiefly by bombylid flies and also by solitary bees. The most divergent members of the two branches of the section are reduced self-pollinating plants which live in extreme environments of recent geological age: G. australis of arid coastal plains and deserts, and G. capillaris of the frigid zones of high mountains.

The species of the G. splendens group were intercrossed. In most cases they were found to cross freely and to yield fertile hybrids from which large F₂ generations could be derived. At meiosis in the hybrids most of the chromosomes were paired in bivalents, but there was some lack of pairing, and some of the pairing which did occur resulted in the formation of chains or bridges. Sympatric strains of G. splendens and G. australis when crossed produced a definite proportion of inviable individuals in F₁ and F₂.

Attempts to cross the G. splendens group with G. leptalea, with several members of the Leafy-stemmed and Woolly-leaves Gilias, and with G. stellata of the leptomeria group, were unsuccessful.

The species of Woodland Gilia are largely allopatric and only rarely come into contact with one another. Hybridization is consequently a minor factor in the production of new variations in this group. This fact is reflected in a simple taxonomy which is the expression of a dendritic rather than a reticulate phylogeny. The weak development of compatibility and sterility barriers in the G. splendens group is correlated with the paucity of sympatric contacts between the species.

**LITERATURE CITED**


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