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GENETIC AND TAXONOMIC STUDIES IN GILIA

I. GILIA CAPITATA

Verne Grant*

1. Introduction

The capitate gilias of the family *Polemoniaceae,* a diverse group of herbaceous annuals ranging on the Pacific slope of North America from Baja California to British Columbia, present a pattern of variation and intergradation which has long confounded the taxonomist. In Jepson's Manual (Mason *ex* Jepson, 1925) the entire group was placed in *Gilia capitata* Dougl., whereas in Jepson's Flora (1943) four species were recognized, namely *G. capitata* Dougl., *G. staminea* Greene, *G. Chamissonis* Greene, and *G. achilleaefolia* Benth. Neither arrangement has proved very satisfactory. The group possesses far more geographical variation than was recognized in Jepson's Manual, but not the morphological discontinuity between allopatric types that might be implied by the treatment in Jepson's Flora. In the most recent taxonomic treatment of the genus *Gilia* (Mason and A. Grant *ex* Abrams' Flora, unpubl., cf. also Mason and A. Grant, 1948) *G. capitata* Dougl. is maintained as a species, but *G. staminea* and *G. Chamissonis* are treated as subspecies of *G. achilleaefolia* Benth.

The present study has grown out of the taxonomic researches of Prof. H. L. Mason and Mrs. Alva Grant in the genus *Gilia.* As stated by these authors, many of the taxonomic problems in *Gilia* are not capable of solution by traditional methods (Mason and A. Grant, 1948). The utilization of the techniques of experimental taxonomy, or of species genetics as this relatively new field may also be called, therefore becomes necessary. The study of the *Gilia capitata* complex has accordingly been approached in the following ways:

After a preliminary inspection of herbarium specimens, field studies were made, leading to a knowledge of the geographical and ecological relationships

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of the various natural entities. Population studies were carried out combined with statistical estimates. Plants from different habitats were raised in a uniform garden to obtain information about the nature of phenotypic variability. Progeny tests of natural populations were made to explore the pattern of genotypic variability. Artificial hybridizations were made to discover the ease of crossing, the fertility of the F_1 hybrids, and the segregation of taxonomic characters in later generation hybrids. Finally, the chromosomes of the natural entities and of their F_1 hybrids were studied. The evidence obtained from these investigations will be presented in the following chapters.

This evidence indicates that *Gilia capitata capitata, G. c. staminea* and *G. c. Chamissonis,* together with four other entities, compromise a typical polytypic species with well marked subspecies. It will be shown, moreover, that *G. c. capitata* and *G. c. staminea* contain all of the characters necessary to produce the whole polymorphic complex. Hybridization between these two subspecies, and between *G. c. capitata* and *G. c. Chamissonis,* is regarded as having given rise to the *Gilia capitata* complex as it is developed today from central California to Washington. The relationship of *Gilia achilleaefolia* Benth. to this group will be dealt with in a future paper. It may be remarked here also that studies of other members of the genus *Gilia* suggest that *G. capitata* is not a unit in itself, but may have affinities with both *G. abrotanifolia* Greene and *G. congesta* Hook. These too are problems for the future.

Most of the work reported in this paper was done while the author was a graduate student at the University of California. An earlier version of the present paper was submitted as a doctoral thesis in the Department of Botany of that institution. The author wishes to express his gratitude to the Chairmen of the Department of Botany and the Division of Genetics of the University of California for the many facilities which made the research possible. The factorial analysis was completed at a later date while the author enjoyed the support of a National Research Fellowship.

During the course of the research the author had much helpful guidance from Dr. G. L. Stebbins, Jr., on genetic matters. The counsel and teachings of Dr. Stebbins have been of great inspiration to the author in his work on *Gilia.* Drs. H. L. Mason and L. Constance were generous with their assistance in taxonomic questions. To all of these men the author is deeply indebted in many ways. In addition the author has enjoyed the constant benefit of Mrs. Alva Grant's intimate knowledge of the genus *Gilia,* and he takes this opportunity to acknowledge the very considerable technical assistance that she has rendered. It is a pleasure to acknowledge, finally, the invaluable assistance of Dr. Wm. M. Hiesey in the factorial analysis of the hybrids.

2. THE TAXONOMIC CHARACTERS

From an inspection of herbarium specimens, but even more from the observation of representative strains growing in the experimental garden, it has been found that the various subspecies of *Gilia capitata* differ from one another at nearly every phase of their growth. The morphological characters from the seedling to the seed have been tabulated in the case of several selected populations, representing both the extreme and the intermediate conditions, in Tables 1 and 2*.

As the extreme types we have *G. c. capitata* as represented by material from Fairfax and the Mayacama Mountains, *G. c. Chamissonis* from Point Reyes Peninsula, and *G. c. staminea* from Antioch. The characteristics of these plants may be briefly recapitulated as follows: *G. c. capitata* is a tall and slender plant of rocky hillsides; its leaves are twice dissected with usually narrow pinnae; the heads are glabrous or nearly so, and the stems may also be glabrous; the heads are narrow; the flowers are pallid to light blue-violet; the calyx lobes are acute; the corolla lobes are linear; the anthers are small, and the styles and stigmas are short; the capsule is indehiscent and few-seeded. (Figs. 1, 3, 4.)

Gilia capitata Chamissonis and *G. c. staminea* are plants of sandy soils; they

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*All measurements reported in this paper are taken from dried specimens, unless otherwise specified. Measurements of floral organs in the living state are roughly one-quarter to one-half greater than measurements of the same tissues when dried.

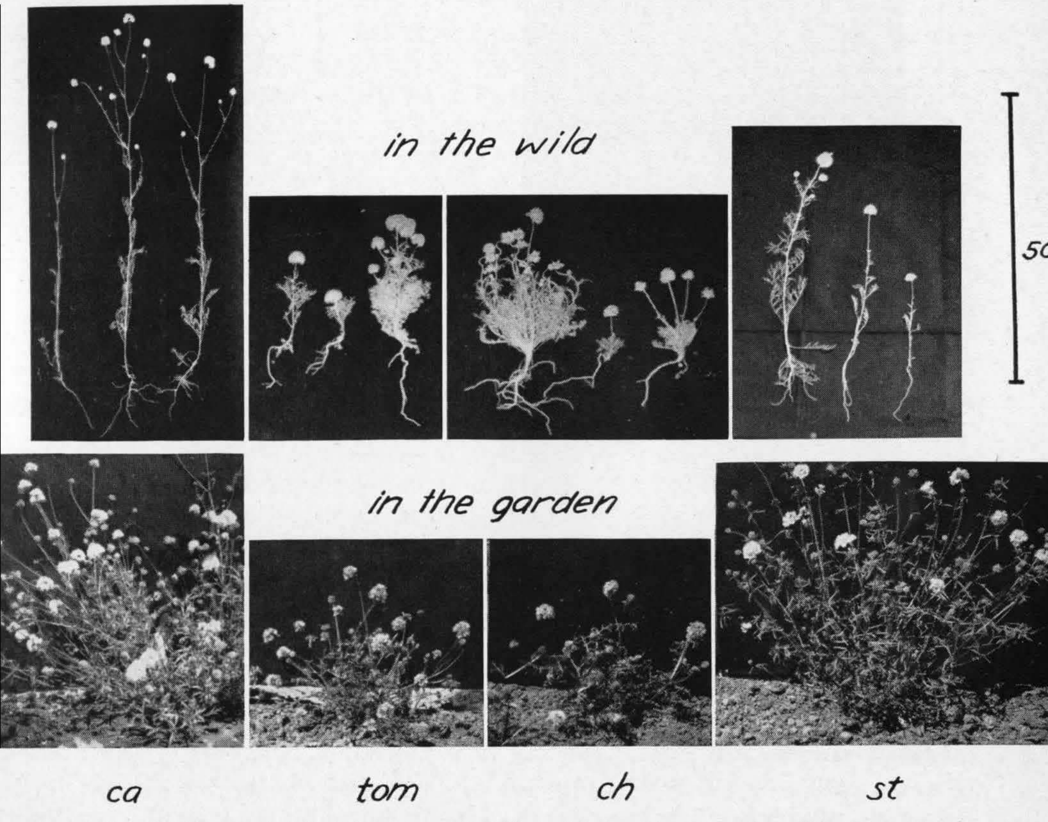


Fig. 1. Growth habit of four races of *Gilia capitata*. Above: in the wild. Below: in the garden. From left to right: *G. c. capitata,* Mayacama Mts. (ca); *G. c. tomentosa,* Tomales Bay (tom); *G. c. Chamissonis,* Pt. Reyes (ch); *G. c. staminea,* Antioch (st).

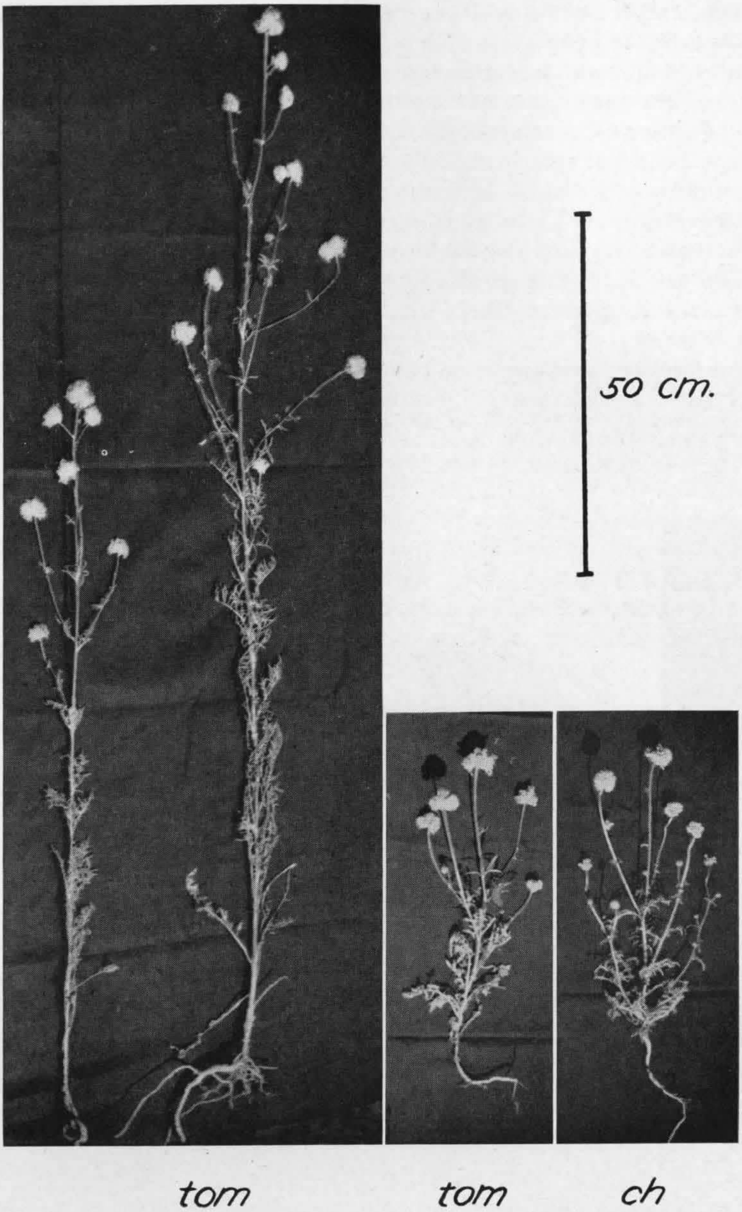
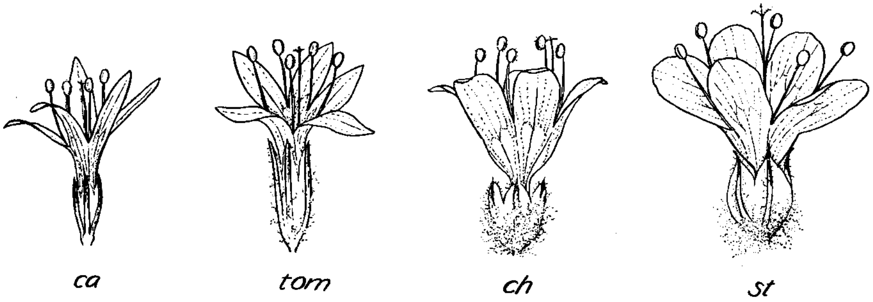


Fig. 2. Growth habit of three wild strains of *G. c. tomentosa* (tom) and *G. c. Chamissonis* (ch) from Tomales Bay.

develop deep taproots; the stems are glandular and the heads are densely floccose at the base; the calyx lobes are acuminate with a recurved tip; the corolla lobes are oval; the anthers are large, and the styles and stigmas are long; the capsule is many-seeded and dehiscent. In habit, *G. c. Chamissonis* is characterized by a basal rosette of leaves in the seedling and by a short, stocky form at maturity; the leaves are twice dissected and somewhat succulent; the floral heads are large; the corollas are of an intense shade of blue-violet. In all of the latter respects *G. c. staminea* is different: it is tall, slender, and relatively non-leafy at the base; its leaves are once dissected; the heads are narrow; and the flowers are a light blue-violet. (Figs. 1, 3, 4, 17).



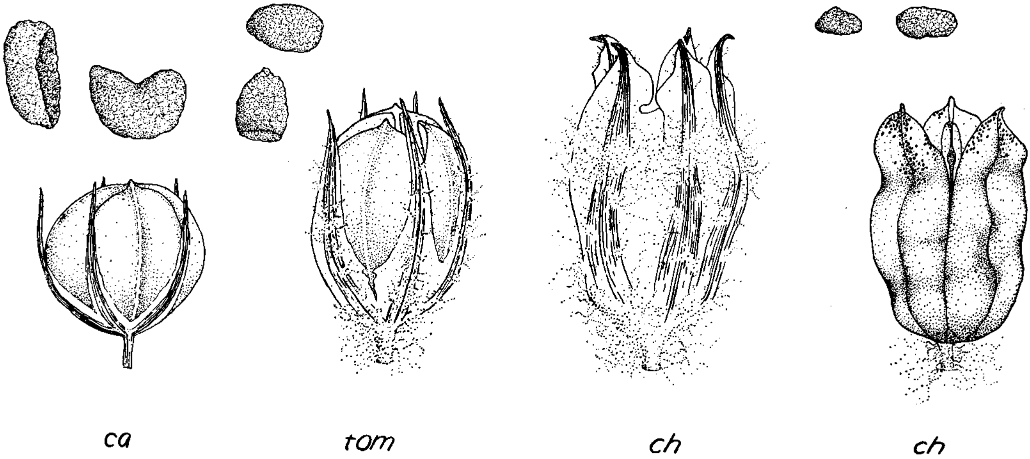


Fig. 3. Flowers of four races of *Gilia capitata*. Abbreviations as in Fig. 1. (× 2.)

Fig. 4. Capsules and seeds of three races of *Gilia capitata*. Abbreviations as in Fig. 1. The capsule of *G. c. Chamissonis* is shown both with and without the accrescent calyx. (× 6.)

The characters of fruit and seed deserve special mention. *Gilia capitata Chamissonis* and *G. c. staminea* possess a three-celled, dehiscent, many-seeded capsule. Under conditions of favorable pollination, eight or even ten seeds ripen in each cell. The individual seeds are small and angular, due to mutual compression during growth. At maturity the capsule splits open along its three valves, which then become recurved (as shown in Fig. 4), and the seeds

TABLE 1. Morphological characters of five populations of *Gilia capitata capitata*, *G. c. Chamissonis* and their intermediates. (Measurements refer to the plants in nature. All localities are in California.)

Subspecies	*capitata*	*tomentosa*	*pacifica*	*Chamissonis*	*Chamissonis*
Locality	Fairfax, Marin Co.	Tomales Bay, Marin Co.	Shelter Cove, Mendocino Co.	Tomales Bay, Marin Co.	Pt. Reyes, Marin Co.
Habitat	hillside	rocky bluff	hillside	sand dune	sand dune
Habit of seedling	no rosette	no rosette	no rosette	no rosette	rosette
Habit of mature plant:					
Stem	tall & slender	short & stocky	tall & slender	tall & stocky	short & stocky
Branching	branched in upper third of plant	branched from base	branched above	branched from base	branched from base
Root	shallow root	shallow root		deep taproot	deep taproot
Basal leaf:					
Length 2ry pinna, mm.	4–7	4–7	1–3	2–7	1–3
Width rachis, mm.	0.2–0.5	0.3–1.0	0.2–0.6	0.9–1.1	0.9–1.1
Pubescence of stem	glabrous to slightly floccose	floccose	stipitate glandular	stipitate glandular	stipitate glandular
Pubescence of head	glabrous	very floccose	glabrous	very floccose	very floccose
Floral head, diam., mm.	10–20	20–35	10–20	20–35	20–35
Color of corolla (Ridgway's standards)	light blue-violet	light blue-violet	light blue-violet	deep blue-violet	deep blue-violet
Calyx	not accrescent	slightly accrescent	accrescent	accrescent	accrescent
Calyx lobes, shape	acute	acute	acute	acuminate	acuminate
Calyx lobes, tip	straight	slightly recurved	slightly recurved	recurved	recurved
Calyx lobes, width, mm.	0.7–1.0	1.0–1.2	1.0–1.2	1.5–2.0	2.0–2.2
Color of sinuses	colorless	colorless	blue-violet	blue-violet	blue-violet
Corolla lobes, shape	linear	linear	linear	oval	oval
Corolla lobes, width, mm.	0.9–1.1	1.0–1.1	1.5–2.0	2.2–3.0	3.0–3.2
Style, length, mm.	6.5	8.0	7.0	6.5–8.5	9.0–9.5
Stigma, length, mm.	0.4	0.5–0.6	1.0–1.2	0.9–1.0	1.0–1.2
Capsule, dehiscence	indehiscent	tardily dehiscent	tardily dehiscent	dehiscent	dehiscent
Capsule, disarticulation	disarticulate	disarticulate	disarticulate	not disarticulate	not disarticulate
No. seeds per capsule	1–6	3–10	10–25	10–25	10–25

TABLE 2. Morphological characters of five populations of *Gilia capitata capitata, G. c. staminea* and their intermediates. (Measurements refer to plants in nature. All localities are in California.)

Subspecies	*capitata*	*mediomontana*	*mediomontana*	*pedemontana*	*staminea*
Locality	Mayacama Mts., Napa Co.	Yosemite Valley, Mariposa Co.	Mather, Tuolumne Co.	Mariposa, Mariposa Co.	Antioch, Contra Costa Co.
Habitat	wooded hillside	wooded hillside	wooded hillside	open hillside	open sand hill
Habit of mature plant	leafy at base		leafy at base	not leafy at base	not leafy at base
Diameter of stem at base, mm. (large individual)	2–3		2–3	3–4	3–7
Dissection of leaves	bipinnate	bipinnate	bipinnate	unipinnate	unipinnate
Width pinnae, mm.	1–2		2–6	1–2	1–2
Pubescence of head	glabrous	very floccose	very floccose	very floccose	very floccose
Earliness (av. no. days between germination & flowering in Berkeley	135		140		90
Color of corolla (Ridgway's standards)	pallid blue-violet		white	light blue-biolet	light blue-violet
Calyx	not accrescent	slightly accrescent	slightly accrescent	accrescent	accrescent
Calyx lobes, shape	acute	intermediate	intermediate	acuminate	acuminate
Calyx lobes, width mm.	0.7–0.9	1.0–1.3	0.8–1.0	1.2–1.9	1.7–2.0
Corolla lobes, shape	linear	linear	intermediate	intermediate	oval
Corolla lobes, width, mm.	0.6–0.9	1.0–1.2	1.6–2.1	1.8–2.1	2.8–3.2
Anther, length mm.	0.7	0.7	0.8	0.9	1.2
Filament, length mm.	1.5–2.5	2.5–3.0	2.5–3.5	2.8–3.2	3.0–5.0
Style, length mm.	3–6	6–7	6–7	6–7	10–12
Stigma, length mm.	0.4	0.6–0.8	0.6–0.8	0.6–0.8	1.0
Capsule, dehiscence	indehiscent	tardily dehiscent	tardily dehiscent	tardily dehiscent	dehiscent
Capsule, disarticulation	disarticulate	disarticulate	not disarticulate	somewhat disarticulate	not disarticulate
No. seeds per capsule	1–6		6–15	6–15 (?)	10–25

are shaken out individually with the swaying of the peduncle in the wind. If lateral force is applied to the dried capsules with a dissecting needle the pedicel breaks off below the calyx. The accrescent nature of the calyx is seen in Fig. 4.

Gilia capitata capitata in the Coast Ranges of north-central California has developed a very different constellation of fruit and seed characters. As shown for the Fairfax and Mayacama populations in Tables 1 and 2, the capsule is three-celled, indehiscent, few-seeded, and disarticulate. While young ovaries of these plants have as many as fourteen ovules, or about five per cell, it is the common condition for only one seed to mature in each cell, even with an abundance of pollinating bees. There may be as many as two seeds per cell, or as few as one seed in the entire capsule. The seeds are larger than those of *G. c. Chamissonis* or *G. c. staminea,* and are often perfectly ovoid without angles. The capsule, which is nearly globose, remains indehiscent throughout the summer, only splitting partly open along the sides with the first rains in the fall. If touched lightly with a dissecting needle, the capsule readily breaks off at the stipe and falls out of the non-accrescent calyx.

Gilia capitata capitata, as developed in its northern area in Oregon and Washington, lacks this specialization. It is also lacking in the maritime race of *G. capitata,* known as *G. c. tomentosa,* and in the Sierran race, *G. c. mediomontana.* The capsules of these plants have been described in Tables 1 and 2 and elsewhere in this paper as "tardily dehiscent," which is to say that the valves normally open only somewhat incompletely and without a full recurving of the lobes (cf. Fig. 4). Particular attention was paid to the relative forces necessary to cause the capsules of *G. c. tomentosa* from Tomales Bay to disarticulate. It was concluded that disarticulation here is more difficult than in *G. c. capitata* from the Mayacama Mountains, but easier than in *G. c. Chamissonis.* The accrescence of the calyx is also intermediate in the Tomales Bay plant with respect to *G. c. capitata* and *G. c. Chamissonis* (cf. Fig. 4).

3. GEOGRAPHICAL DISTRIBUTION

One of the most important facts brought out by Tables 1 and 2 is that intergradation between *G. c. capitata* and *G. c. Chamissonis* or *G. c. staminea* is very nearly complete. This is evident if the series of populations is compared with respect to a given quantitative character, such as the width of corolla or calyx lobes, the length of the filaments, styles or stigmas, or the number of seeds in the capsules. The question next arises: what are the geographical relationships of the extreme and the intermediate types?

Method

Measurements were obtained from a large sample of herbarium specimens, representing some 225 localities in all. Those characters which could be measured accurately—or at all—in a fairly large proportion of the specimens were then selected for scoring by Anderson's (1936) method for computing a hybrid index. The number of usable characters remaining when these conditions had been fulfilled was only six in the comparison of *G. c. capitata* with *G. c. Chamissonis,* and four in the comparison of *G. c. capitata* with *G. c. staminea* (cf.

Tables 3 and 4). The low number of characters employed, while unsatisfactory from the statistical point of view, nevertheless had the compensating advantage that it permitted the computation of the hybrid index for the largest possible number of stations.

As shown in Tables 3 and 4, the extreme types of *G. c. Chamissonis* or *G. c. staminea* receive an index value of two points for each character, the extreme type of *G. c. capitata* receives a zero for the same character, and intermediates are awarded one point for each character falling in the range between the two contrasted extremes. On this basis a specimen of "typical" *G. c. Chamissonis* will have a total score of twelve, "typical" *G. c. capitata* a total score of zero, and their artificial F_1 hybrid will receive a score of six. Similarly, in the comparison of *G. c. staminea* with *G. c. capitata*, the total possible score for *G. c. staminea* is eight, for *G. c. capitata* zero, and for their F_1 hybrid, four. The result of scoring the width of both calyx lobes and corolla lobes has probably been to attach greater weight to those characters, since they are very likely determined by the same genetic coefficient (Anderson and Ownbey, 1939); however, the author does not regard this weighting of perianth characters as disadvantageous.

TABLE 3. Score table used for computing the hybrid index of *Gilia capitata capitata, G. c. Chamissonis* and their intermediates.

Character	*Score Value*		
	0	*1*	*2*
Habit	tall and slender	intermediate	short & stocky
Floccosity of calyx	glabrous	sparsely floccose	very floccose
Calyx lobes, width mm.	0.6-1.1	1.2-1.9	2.0-2.4
Corolla lobes, width mm.	0.8-1.1	1.2-1.9	2.0-3.2
Stigma, length mm.	0.2-0.4	0.5-0.7	0.8-1.2
Capsule, dehiscence	indehiscent	tardily dehiscent	dehiscent
Total score	0 (=*G. c. capitata*)	6	12 (=*G. c. Chamissonis*)

TABLE 4. Score table used for computing the hybrid index of *Gila capitata capitata, G. c. staminea* and their intermediates.

Character	*Score value*		
	0	*1*	*2*
Floccosity of calyx	glabrous	sparsely floccose	very floccose
Calyx lobes, width mm.	0.6-1.1	1.2-1.4	1.5-2.4
Corolla lobes, width mm.	0.8-1.1	1.2-2.7	2.8-3.2
Stigma, length mm.	0.2-0.4	0.5-0.9	1.0-1.5
Total score	0 (=*G. c. capitata*)	4	8 (=*G. c. staminea*)

The scores obtained for the specimens were plotted as "pie diagrams" on a distribution map (Figs. 5, 6, 7). Populations of pure *G. c. capitata* are represented as white circles, pure *G. c. Chamissonis* or *G. c. staminea* as solid black circles, and intermediates as "pies" in which the amount of black varies with the magnitude of the score value. In general, it is assumed that the degree of resemblance of a specimen to *G. c. capitata* is proportionate to the amount of white, and conversely that its closeness to *G. c. Chamissonis* or *G. c. staminea* is indicated by the amount of black in the circle.

The Geographical Relationship of G. c. CHAMISSONIS *and* G. c. CAPITATA

The geographical relationship of *G. c. Chamissonis*, *G. c. capitata*, and their intermediates, known as *G. c. tomentosa* and *G. c. pacifica*, is shown on the first map (Fig. 5). *Gilia capitata capitata* appears to be uncontaminated by characters peculiar to *G. c. Chamissonis* in a strip of Coast Ranges away from the coast and south of the Oregon state line. *Gilia capitata Chamissonis*, in its extreme form, occurs in only two localities, the isolated sandy peninsulas of San Francisco and Point Reyes.

In the area enclosed by the rectangular frame, and shown in greater detail in Fig. 6, the sand dunes inhabited by *G. c. Chamissonis* and the rocky hillsides required by *G. c. tomentosa* approach within short distances of one another. In one case at Tomales Bay, populations of *G. c. Chamissonis* and *G. c. tomentosa*, flowering simultaneously, face one another across a distance of 475 feet. But the plants here are not as different from one another in their morphological characteristics as are the extreme types of *G. c. Chamissonis* and *G. c. capitata*. With respect to general habit they resemble each other more than they resemble their respective parental types; Fig. 2 shows a plant of *G. c. Chamissonis* from Tomales Bay, and a plant of *G. c. tomentosa* from the neighboring population. These pictures may be compared with Fig. 1 for *G. c. Chamissonis* of Point Reyes and *G. c. capitata* of the interior Coast Ranges. The dimensions of the flower parts and the nature of the capsule in the two adjoining populations, as summarized in Table 1, impart an impression of convergence also in respect to those characters.

The occurrence in adjacent habitats of convergent morphological types, isolated only partially by ecological factors, is a situation typical of that special aspect of hybridization followed by backcrossing known as introgression; and the conclusion may be tentatively advanced that the Tomales Bay plants are introgressive hybrids. The area outlined by the rectangle in Fig. 5, therefore, since it is characterized by the parallel development of evident backcross types of *G. c. Chamissonis* on the sandy areas, and of backcross types of *G. c. capitata* on the rocky bluffs (= *G. c. tomentosa*), may be regarded as an area of introgression.

A characteristic feature of this area of introgression is that the *G. c. Chamissonis* types form extensive stands, whereas *G. c. tomentosa* exists in a few, discontinuous, small populations. This is no doubt largely a consequence of the wide distribution along the coast of sand dunes suitable for colonization by *G. c. Chamissonis*, in contrast to the limited number of rocky situations available for *G. c. tomentosa*, but there are some other implications. *Gilia* *capitata Chamissonis,* together with *Lupinus arboreus* Sims, *Phacelia distans* Benth., *Monardella undulata* Benth., *Oenothera micrantha* Hornem., *inter alia,* forms a characteristic sand dune flora, which appears to have been relatively little disturbed by man and grazing animals, although unfortunately that situation is today beginning to change in many places. The hillsides to the interior, however, have been very profoundly changed by man and his cattle, so that we cannot assume that *G. c. tomentosa* has always been as restricted in these hills as it is today.

The discovery of *G. c. tomentosa* among patches of *Stipa* bunchgrasses is very interesting in this connection, for it provides strong evidence of the relictual status of *G. c. tomentosa* on the maritime slopes of western Marin and Sonoma counties. Of great significance is the occurrence of a similar plant on Mount Diablo, in the interior county of Contra Costa, under circumstances such as to suggest that it has persisted there as a relict of the Pleistocene sea (cf. Jepson, 1925, pp. 10 and 220). The former wider distribution of *G. c. tomentosa* in the interior is also attested to by a specimen collected near Vallejo, Solano County, in 1886 (cf. Fig. 5).

Connecting links exist between *G. c. tomentosa* and *G. c. capitata.* On a serpentine outcrop less than two miles from Tomales Bay a colony was found which, in every feature except growth habit, resembled the maritime type of *G. c. tomentosa.* The difference in growth form, however, is the difference between stocky plants of 25 centimeters or so, and erect plants two meters tall (cf. Fig. 2). The same trend from short, stocky plants on the exposed maritime bluffs to robust types a short distance to the interior is repeated in a transect farther north, from Bodega Bay to the town of Bodega. Still farther inland, beyond the wind-swept hills and redwood-forested valleys, typical *G. c. capitata* is found in open woodland. Its stems and calyces are frequently lightly floccose, instead of glabrous, however, and in this respect it is reminiscent of the maritime race.

North of Bodega Bay *G. c. tomentosa* has been found in one or two stations. Farther north, in Mendocino County, this short, stocky, floccose plant is replaced on rocky hillsides by a gilia of bushy habit, with glandular stems and lightly floccose heads, corolla lobes of deep blue-violet and linear shape, short styles and long stigmas, and several other completely novel recombinations of the characters of *G. c. Chamissonis* and *G. c. capitata.* This marks the beginning of what may be termed an area of amalgamation, since here the germ plasms of the two original subspecies have been mixed, and backcross types of *G. c. Chamissonis* are nowhere encountered.

The area of amalgamation, as shown on the map (Fig. 5), extends from Mendocino County, California, to Coos County, Oregon. It is populated by several types, all of which, however, agree in possessing glandular stems and purple calyx sinuses, and in lacking densely floccose heads. One of the types is represented by the colony at the mouth of the Navarro River in Mendocino County, the characters of which have been mentioned in the preceding paragraph. The plant at Shelter Cove (summarized in Table 1) is distinguished from the Navarro type by corolla lobes of intermediate width, glabrous calyces,

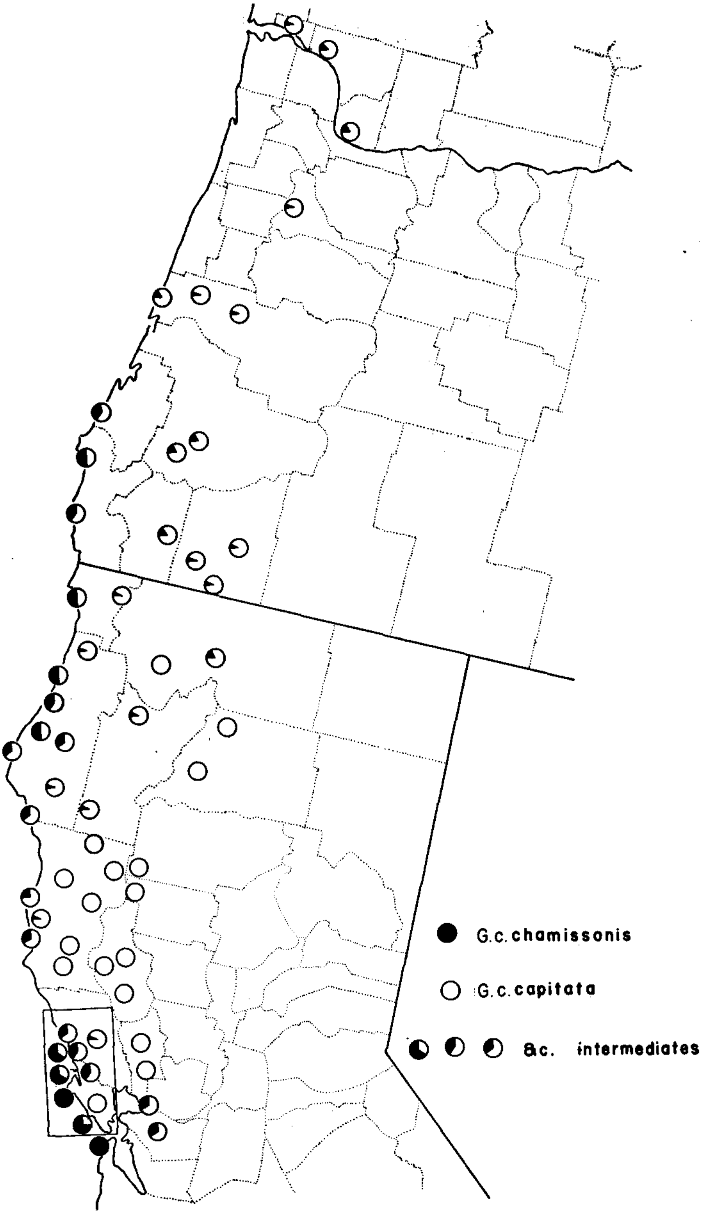


Fig. 5. The distribution of *G. c. capitata, G. c. Chamissonis,* and intermediate types along the Pacific Coast of California and Oregon. The amount of black in a circle is proportionate to the hybrid index of the specimen as computed from Table 3. Populations in eastern Oregon have not been plotted. The area within the rectangular frame has been enlargd in Fig. 6.

long stigmas, and somewhat pedicellate flowers. A plant on Cape Mendocino has loose, pedicellate heads with very accrescent calyces, two characters which strongly suggest introgression from *Gilia millefoliata* Fischer and Meyer in that region, but there the problem must rest for the present. All of the foregoing types are found close to the ocean, and may therefore be called *Gilia capitata pacifica* V. Grant.

The amalgamation of *G. c. Chamissonis* and *G. c. capitata* has evidently been something less than complete. This is perhaps a result of the critical isolating distances between suitable habitats on the immediate coast, which have permitted each one of several segregating or introgressive lines to become established here as a sort of *imperium in imperio.* Toward the interior the extreme types merge with *G. c. capitata* through a series of intermediate forms. Plants are found on the coastal plain which, by their tall, slender habit and disarticulating capsules, resemble typical *G. c. capitata,* but remain distinct from it by the purple calyx sinuses and the deeper color and greater width of the corolla lobes. Far to the interior and well up in the mountains of northern California and Oregon, specimens of *G. c. capitata* are marked with purple sinuses and tardily dehiscent capsules.

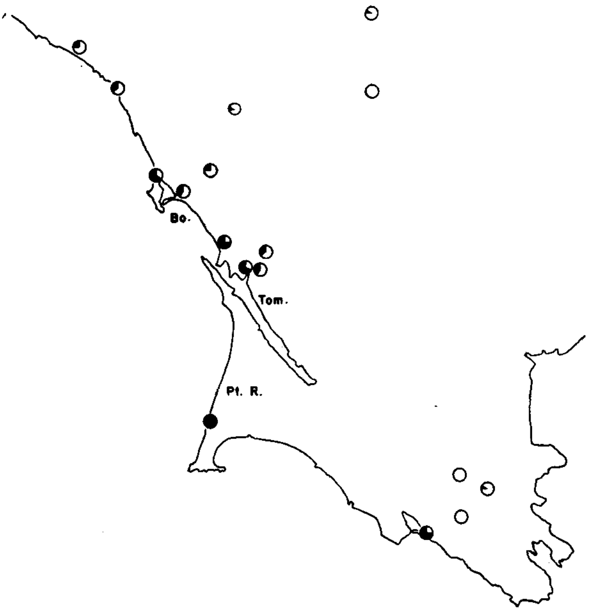


Fig. 6. The distribution of *G. c. capitata, G. c. Chamissonis,* and intermediate types in the area north of San Francisco Bay. Enlarged from Fig. 5, with the same symbols. Pt. R.=Point Reyes Peninsula; Tom=Tomales Bay; Bo.=Bodega Bay.

It is probable that the direct influence of *G. c. Chamissonis* never extended much farther north than Coos Bay, for relatively typical *G. c. capitata* has been collected on the Oregon coast at Florence. The calyx sinuses of this plant are, to be sure, purple, the capsules are tardily dehiscent, and the calyces are

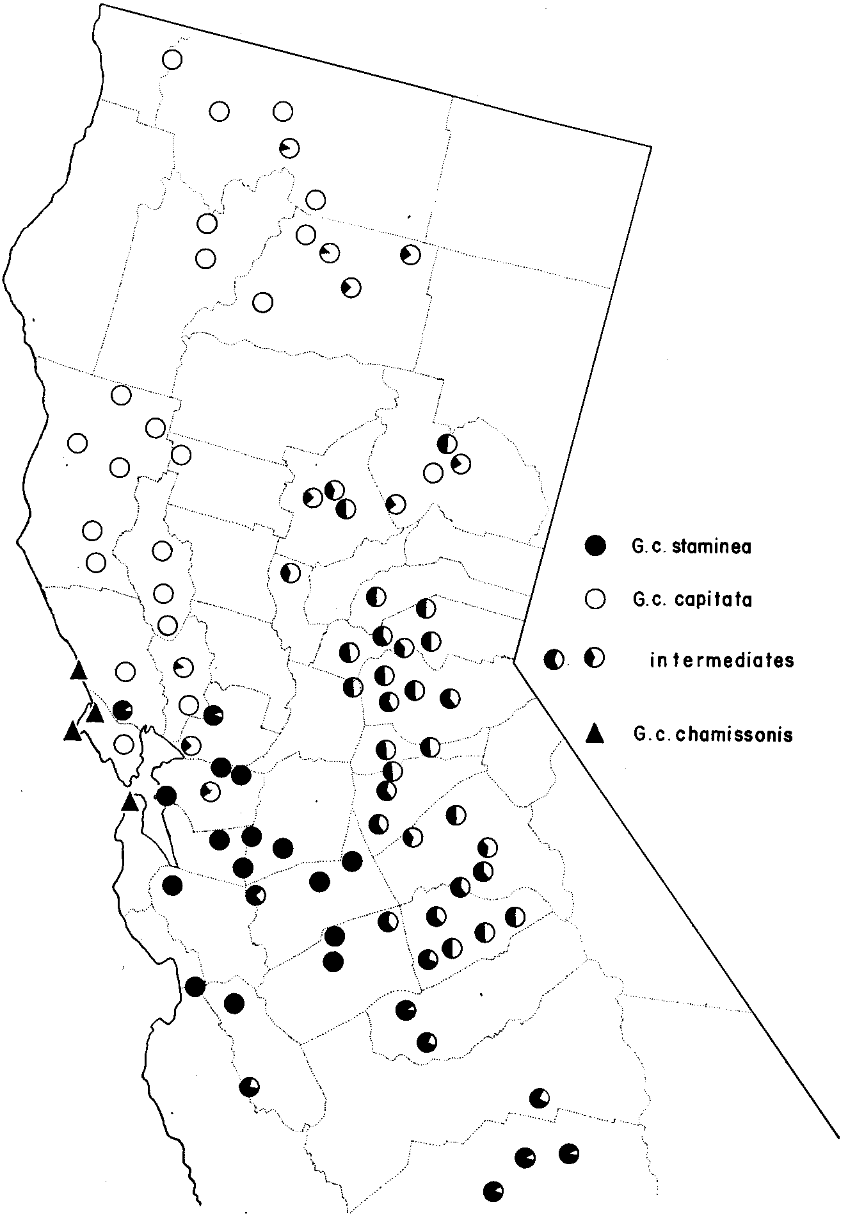


Fig. 7. The distribution of *G. c. capitata, G. c. staminea,* and intermediate types in California. The amount of black in a circle is proportionate to the hybrid index of the specimen as computed from Table 4.

floccose, but these are characters which, together with stigmas of intermediate length and capsules of intermediate seed number, are also found in a large proportion of the populations throughout Oregon and Washington. Various collections of *G. c. capitata* from the mouth of the Columbia River, which incidentally is the type locality of this entity, receive hybrid indices of 1, 2 and 3. It seems clear that the influence of *G. c. Chamissonis* has not been confined to areas where it is or was physically present, but has been felt far beyond the limits of its own range of distribution. Almost the entire northern branch of *G. c. capitata,* from northern California to British Columbia, falls within an area of contamination, where the combination of characters developed in the central Coast Ranges of California appears to have broken down under the pressure of introgression.

The Geographical Relationship of G. c. STAMINEA *and* G. c. CHAMISSONIS

Gilia capitata staminea is primarily a plant of the San Joaquin Valley of California, where it grows in open sandy fields. The known stations of this entity in the Coast Ranges are shown on the map (Fig. 7). They are from north to south: Petaluma, Sonoma County; Vaca Mountains, Solano County; Berkeley to Alameda, Alameda County; Cupertino, Santa Clara County; and Pajaro, Monterey County. The first-mentioned locality is based on a single specimen collected in the cemetery of Petaluma in 1934; when the author revisited this place in 1948 he found it so overgrown with grasses and other weeds as to virtually exclude the possibility that *G. c. staminea* is there today. *Gilia capitata staminea* has not been collected in Berkeley or Oakland since 1926; however, its former presence there is reliably documented by several independent collections, three of which were made in the late 19th century.

The chief paleogeographical significance of the localities just mentioned consists in the fact that every one of them lies along an estuary of an inland sea which inundated the San Joaquin Valley until Pliocene or Pleistocene time. Between Upper Miocene and Pliocene time (Reed, 1933, pp. 218 and 252) the sea withdrew from the tital channel between Bodega and Tomales bays and the interior; it withdrew from the Carquinez Straits, from the present Vaca Mountains, from the present southern arm of San Francisco Bay, and from the lower San Joaquin Valley. During the Pleistocene period the sea further retreated from the tidal gap between Monterey Bay and the southern San Joaquin Valley (op. cit., p. 273). If we can imagine that *G. c. staminea* or its progenitor grew on sand dikes at the edge of the Pliocene sea, much as it grows today in the Carquinez Straits by Antioch, then the subsequent uplift of the San Joaquin Valley would have resulted in a concentration of the entity in that newly exposed habitat. The uplift of the California coast would have stranded the outlying populations in the ancient tidal channels where they have persisted as relicts until modern times.

Gilia capitata Chamissonis occurs farther westward today, at the mouths of the old embayments. It is isolated from *G. c. staminea* by the slight geographical distance of the breadth of San Francisco Bay. The close morphological similarity of the two subspecies in characteristics other than habit and foliage almost demands that they have formerly been panmictic. It is a fact that *G. c.*

staminea on the eastern shores of San Francisco Bay and *G. c. Chamissonis* on the San Francisco peninsula are more similar in general habit than are *G. c. staminea* of the San Joaquin Valley and *G. c. Chamissonis* of Point Reyes.

The absence of *G. c. Chamissonis* in the sand dune areas bordering Monterey Bay is very interesting. *Gilia capitata staminea* occurs in the Pajaro Valley a short distance from the coast, which creates the opportunity for the selection of a maritime race of *Gilia capitata* in this area. The environmental conditions are apparently suitable for *G. c. Chamissonis.* Most of its associates on the San Francisco and Point Reyes peninsulas are present on the sand dunes of Monterey Bay. *Gilia capitata Chamissonis,* however, does not occur in this area at the present time.

The Geographical Relationship of G. C. STAMINEA *and* G. C. CAPITATA

In the Coast Ranges *G. c. staminea* has the geographical opportunity to meet *G. c. capitata* in only a limited number of places as shown on the map (Fig. 7). Here, for the most part, the two races are probably isolated both seasonally and ecologically. This is certainly the case in the Vaca Mountains, where *G. c. staminea* occurs on the sandy bottoms of canyons and flowers early, and *G. c. capitata* grows on rocky hillsides and flowers later. There is little or no evidence of gene exchange between the two subspecies anywhere in the Coast Ranges.

In the Sierra Nevada, however, the isolation of *G. c. staminea* and *G. c. capitata* has broken down on a large scale, permitting the population of those mountain slopes with a diversity of types. The characters of several Sierran populations are compared with the putative parental types in Table 2. Two general types can be distinguished in the Sierra Nevada. The first and more abundant of these occupies the Digger pine-Blue oak belt of the Sierra Nevada foothills; it has accordingly been named *Gilia capitata pedemontana* V. Grant. It resembles *G. c. staminea* rather closely, differing morphologically in its narrower corolla lobes, smaller anthers, tardily dehiscent capsules, etc. In addition, it is ecologically very different from *G. c. staminea* in that it grows on rocky hillsides and talus slopes. These are habitats with which *G. c. capitata* is usually associated.

Above the limits of *G. c. pedemontana,* in the Yellow pine-Black oak belt, a second type is found, which has been called *Gilia capitata mediomontana* V. Grant because it occurs in the middle altitudes. It resembles *G. c. capitata* but differs from it in its densely floccose heads, wider corolla lobes, longer stigmas, etc.; and it differs from *G. c. tomentosa* by its slender, tall habit and glandular stems.

Both *G. c. pedemontana* and *G. c. mediomontana,* in so far as they possess no characters peculiar to themselves alone and not developed to a more extreme degree in either *G. c. staminea* or *G. c. capitata,* would be judged by any experimental taxonomist to be introgressive hybrids of the latter two entities. It would probably be agreed, moreover, that *G. c. pedemontana* represents the product of repeated backcrossing onto a *G. c. staminea* stock and that *G. c. mediomontana* conversely is an introgressive type in the direction of *G. c. capitata.* This is the hypothesis which has prompted some experiments to be reported on in later chapters.

It remains to describe the geographical connection between *G. c. pedemontana* and *G. c. staminea* on the one hand, and between *G. c. mediomontana* and *G. c. capitata* on the other. In the central Sierra Nevada there is a distinct gap in the distribution of *G. c. pedemontana* and *G. c. staminea.* The latter entity drops out toward the east at the first rise above the valley floor. Above is the zone of rolling foothills which forms a suitable habitat for *Gilia tricolor* subsp. *diffusa* (Congdon) Mason and A. Grant, but not for *G. c. pedemontana.* That element begins where the topography becomes distinctly mountainous and wooded. In the northern Sierra Nevada *G. c. pedemontana* descends to low elevations around Chico, but this brings it to the margin of the Sacramento Valley where *G. c. staminea* is absent. In the southern Sierra Nevada, particularly in Fresno and Tulare counties, habitats for *G. c. pedemontana* occur at low elevations, leading to gene exchange with *G. c. staminea.*

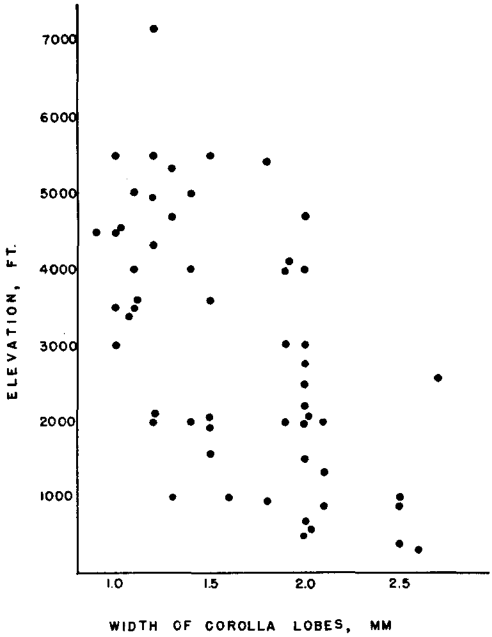


Fig. 8. Correlation between elevation in the Sierra Nevada and width of corolla lobe of *Gilia capitata.*

More field work will be necessary to clarify the relationship between *G. c. mediomontana* in the northern Sierran county of Plumas and *G. c. capitata* in the mountains of Shasta County. It appears that the two subspecies, one with floccose calyces and the other with glabrous calyces, are bridged by a third type with glandular calyces. Beyond the Sierra Nevada, in the Cascade Mountains through Oregon and Washington, *G. c. capitata* possesses characters

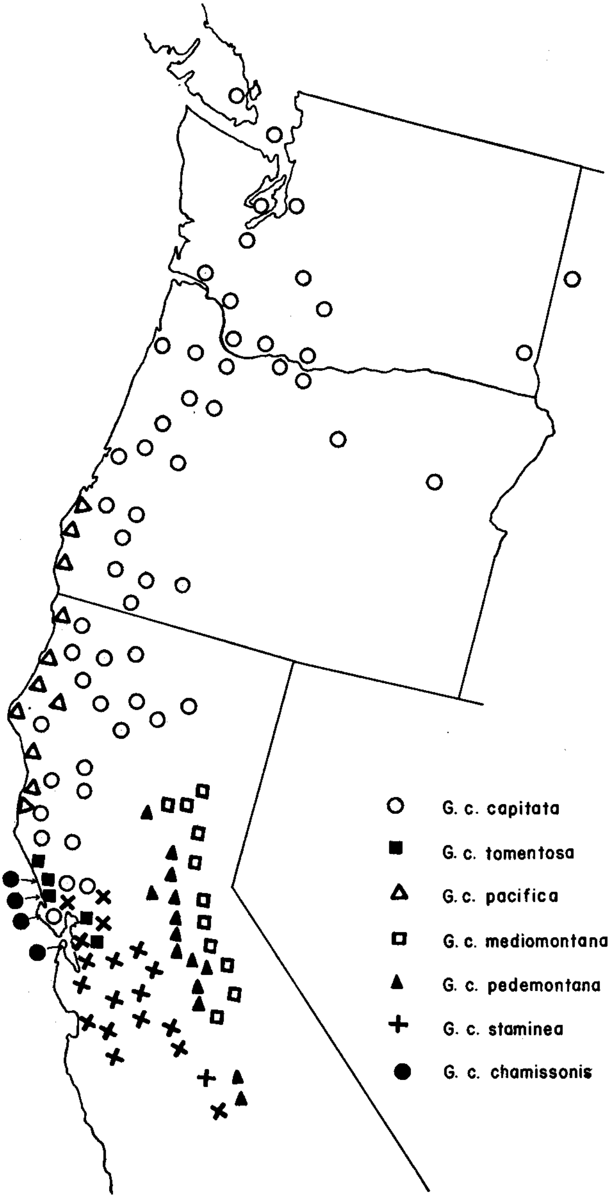


Fig. 9. The geographical distribution of the seven subspecies of *Gilia capitata*.

which signify a vast extension of the influence of *G. c. staminea* and *G. c. Chamissonis.*

Gilia capitata pedemontana and *G. c. mediomontana* are interrelated in the Sierra Nevada through a series of intergrading forms. The intermediate populations are not as frequent as might be expected by chance, however, and in practice it is usually easy to classify a specimen as one or the other. This point was tested by plotting the important diagnostic character of corolla lobe width against the elevation of the locality where the specimen was taken for some 56 localities along the length of the Sierra Nevada. The result took the form of the scatter diagram shown in Fig. 8. There is clearly a break between 2000 and 3000 feet. Below 2000 feet the corolla lobes are predominantly 1.5 mm. wide or more; above 3000 feet they are largely 1.5 mm. wide or less. The correlation of corolla lobe width with elevation is statistically significant, with $r = -.421$ at 55 degrees of freedom. The regression coefficient corresponds to an average decrease in corolla lobe width of 0.3 mm. for every 1000 feet rise in elevation.

Summary

This chapter may be summarized by a map showing the distribution of the seven named entities of *Gilia capitata* (Fig. 9). The entities, as will be seen from the map, replace one another geographically. Following various authors, both botanical and zoological (i.e., Clausen, Keck, and Hiesey, 1940; and Mayr, 1942), the present writer has adopted the view that geographical races should be treated taxonomically as subspecies. *Gilia capitata* has been treated, therefore, as a polytypic species composed of allopatric subspecies (cf. chap. 9 for the appropriate nomenclatorial changes and formal descriptions).

4. VARIABILITY

The causes of variation are frequently stated to be two-fold: environmental and genotypic. Data were obtained during the course of this study on both sources of variability in *Gilia capitata.* The range of environmental variation was measured by means of the cultivation of diverse ecotypes in a uniform garden; genotypic variation by means of progeny tests. The results of these experiments will be reported in the present chapter.

Ecological Analysis of the Taxonomic Characters

Reference has been made to the fact that the maritime capitate gilias are short and stocky, often with a basal rosette of leaves; that they always bear flowers more deeply colored than their inland relatives; and that they often have larger floral heads. The matter may be conveniently stated in the form of a table (Table 5). The question naturally arises as to what extent the differences in growth habit and flower color, by which the maritime races are together distinguished from the interior races, are due to environmental modifications.

An experiment was performed in the spring of 1947, in which plants of *G. c. Chamissonis* from Point Reyes, *G. c. tomentosa* from Tomales Bay, and *G. c. capitata* from the Mayacama Mountains in Napa County, were grown intermixed in a uniform garden in Berkeley. The positions of the parental populations with respect to the Berkeley garden are shown in Fig. 10.

Seventy-five individuals of each strain were represented in the garden plot. The three strains were completely randomized in the following fashion: each hill was assigned a number, starting with 1 in the northwest corner of the bed and ending with 224 in the southeast corner. Paper tickets similarly numbered from 1 to 224 were then shaken up in a basket and drawn at random in series of three. The first number drawn in each series determined the position of a plant of *G. c. capitata* in the garden, the second number a position for *G. c. Chamissonis,* and the third number a hill for *G. c. tomentosa.* The procedure was continued until all seventy-five plants of each strain had been assigned their places in the garden.

TABLE 5. Comparison of two climatic and two edaphic ecotypes of *Gilia capitata* with respect to growth habit and flower color.

	Maritime	*Interior*
Sand	*G. c. Chamissonis*	*G. c. staminea*
Corolla lobes oval	short and stocky	tall and slender
Capsule dehiscent	deep blue-violet fl.	light blue-violet fl.
Self-compatible	broad floral heads	narrow floral heads
Rocky hillside	*G. c. tomentosa*	*G. c. capitata*
Corolla lobes linear	short and stocky	tall and slender
Capsule indehiscent	light blue-violet fl.	pallid blue-violet fl.
Self-incompatible	broad floral heads	narrow floral heads

The plants were raised from bulk seed collected during the previous summer. The seeds were planted in flats of sand in December. The flats were watered down with distilled water and immediately placed in a cold-temperature room at 5° C. After two weeks stratification they were brought into the greenhouse. The seedlings upon germination were watered part of the time with O.25 N. Hoagland solution, or else with distilled water. The flats were removed outside in February, and the seedlings were set out in March. It was found that having the seedlings in plant bands two inches square, as supplied by nursery dealers, minimized the shock of transplanting, since the band and its contents were moved as a unit. If more than one seedling was present in a plant band, the supernumerary seedlings were eliminated in a random way by preserving for propagation only the seedling closest to the center of the two inch square.

Mortality of the seedlings in Berkeley was 20% of 75 individuals of *G. c. capitata,* 12% for *G. c. tomentosa,* and 7% for *G. c. Chamissonis. Gilia capitata tomentosa,* more than either of the other two strains, was infested by mildew. The hills in the garden bed were spaced one foot apart. This resulted in an unsatisfactory amount of crowding, as it turned out; the optimum distance between rows and hills for *Gilia capitata* is three feet.

Gilia capitata staminea was represented in a second garden bed in Berkeley by about thirty individuals transplanted as seedlings from nature. The position of the parental population at Antioch is not shown on Fig. 10; it would lie a short distance east of the edge of the map, in prolongation of the Sacramento-San Joaquin River. The fact that *G. c. staminea* was subjected to a different experimental treatment than the other three strains greatly restricts the statistical validity of a comparison between it and the other strains.

The appearance of plants of the four entities under natural conditions and in the garden may be visually compared in Fig. 1. The short and stocky maritime races retain their characteristic stature in Berkeley; the tall and slender interior types, on the other hand, remain tall in Berkeley, but become very bushy. The slender habit is developed among the culms of grasses in nature, and would appear to represent an environmental influence. The greater height of the interior plants in comparison with the maritime races is, however, genetically determined. This conclusion is borne out by the statistical data for plant height given in Table 6, where the results of the uniform garden experiment are summarized. Fig. 1 shows that *G. c. staminea* is not leafy at the base in cultivation, taking this characteristic also out of the realm of phenotypic modifications.

Differences in flower color, where they exist, are very marked in the capitate gilias. Nevertheless, it was desirable to have a standardized procedure by which the comparisons could be made with a minimum of personal error. The color of a flower was identified by placing a corolla lobe over a hole in a white pasteboard card and then moving the card over the color plates of Ridgway (1912) until the corolla lobe exactly matched a standard color. This procedure was always carried out with fresh materials in daylight, and was repeated on numerous occasions. Table 6 shows that the three subspecies, *G. c. Chamissonis, G. c. tomentosa,* and *G. c. capitata,* differ strongly from one another in nature with respect to flower color, with *G. c. tomentosa* occupying an intermediate position between the extremes. In Berkeley the differences, though still present, are less striking. It may be added that the flowers of *G. c. staminea* are light blue-violet in nature and light soft blue-violet in cultivation at Berkeley. The more intense coloration of the coastal races as compared with their inland representatives may therefore be concluded to be partly genotypic and partly phenotypic.

The breadth of the floral head is reduced in all subspecies in Berkeley over the natural condition. The amount of reduction is about the same for all three subspecies, however, and the similarity between *G. c. Chamissonis* and *G. c. tomentosa,* and their common divergence from *G. c. capitata,* in this character is preserved. Separate data from *G. c. staminea* show that it agrees with *G. c. capitata,* in Berkeley as in nature, in the possession of narrow heads.

A number of separate leaf measurements in Table 6 convey a general impression of partial, but only partial, convergence in Berkeley. For the opposite impression, of the unmistakable dissimilarity of the leaves in Berkeley plants, cf. Fig. 17. The rather great plasticity of leaves and other vegetative parts stands in marked contrast to the constancy of the dimensions of the flower parts under different environmental conditions (Table 6). This fact affords a measure of confidence in the selection of taxonomic characters from the latter organs in the capitate gilias.

It has been established that the differences between the maritime and inte-

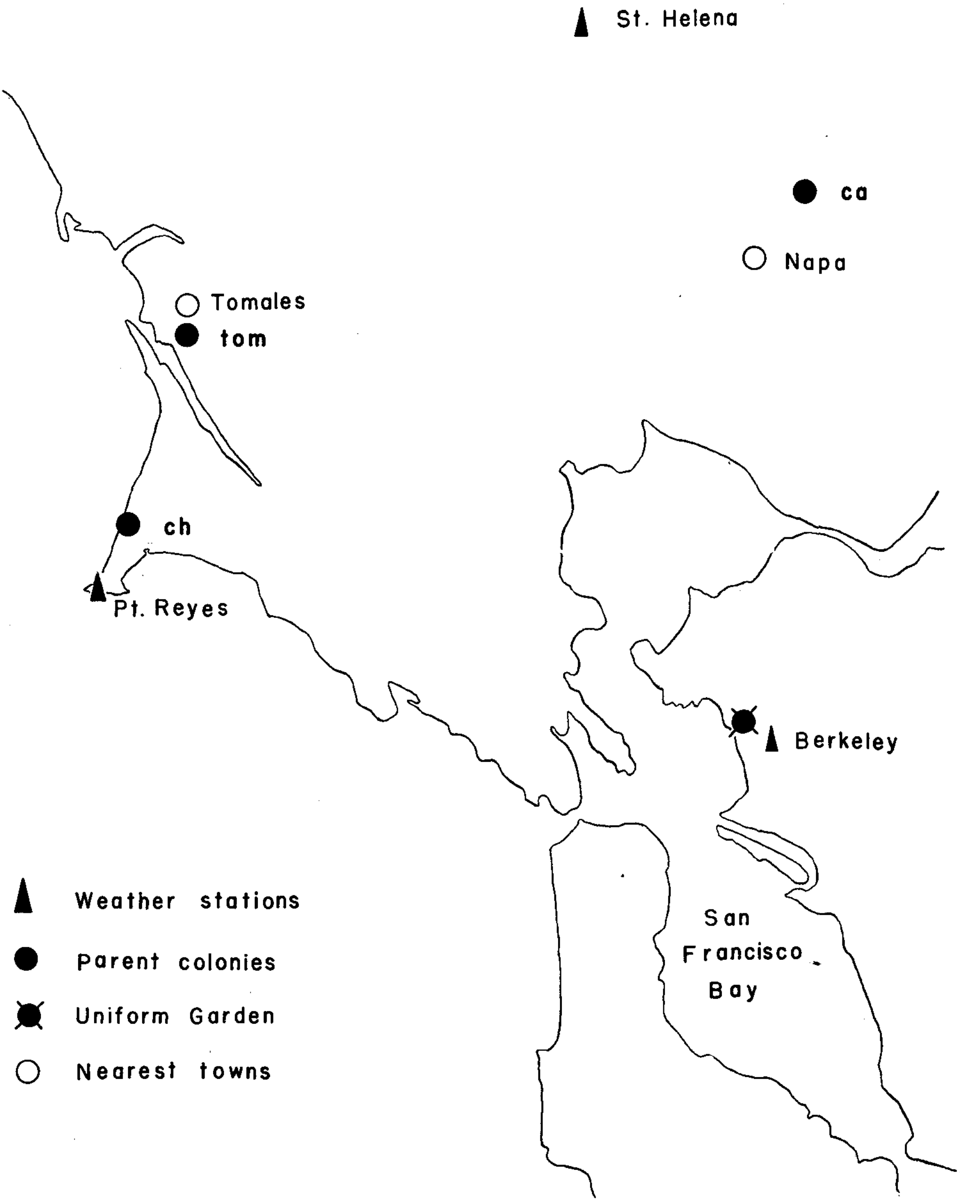


Fig. 10. The sites of the parental colonies of *Gilia capitata* in relation to the position of the uniform garden in Berkeley.

rior ecotypes of *Gilia capitata* consist to some extent of environmental modifications. When grown in a uniform garden in Berkeley the plants approach one another. The point of convergence, moreover, is a midpoint approximately equidistant between the extreme maritime and the extreme interior phenotypes. This is what one might expect, inasmuch as Berkeley is geographically and climatically intermediate between Point Reyes and the Coast Ranges of Napa County (Figs. 10-13). We may predict on the basis of these considerations that the transplanting of G. *c. capitata* to Point Reyes, or of *G. c. Chamissonis* to the Mayacama Mountains, would lead to pronounced environmental modifications in the direction of the phenotypes already existing at those stations, thus bearing out Turesson's (1922) principle of the parallelism of environmental modifications and genotypic responses.

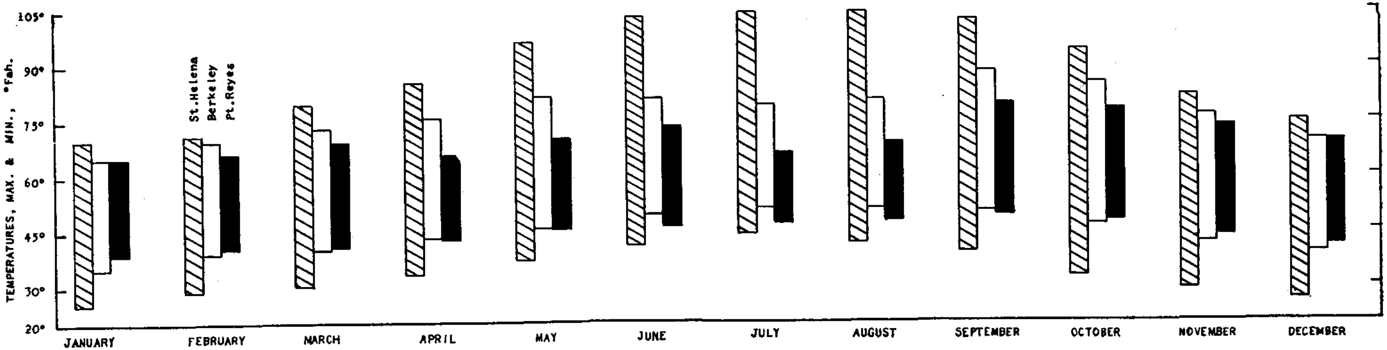
TABLE 6. Comparison of certain morphological characters of three ecotypes of *Gilia capitata* in the natural environment and in the uniform garden (in Berkeley).

		G. c. capitata	*G. c. tomentosa*	*G. c. Chamissonis*
Height of plant, cm.	nature	37±3	17±7	17±7
	garden	22±10	16±6	19±6
Basal leaf:				
width of rachis, mm.	nature	0.4	0.8	0.9
	garden	0.7	0.8	1.2
length of 1ry pinna, mm.	nature	15.6	9.9	8.1
	garden	16.8	14.6	14.7
width of 1ry pinna, mm.	nature	0.5	0.6	0.6
	garden	1.4	1.3	1.4
Floral head, diam., mm.	nature	19±3	25±7	25±4
	garden	13±3	16±4	16±4
Color of corolla, Ridgway	nature	*pallid* blue-violet	*light* blue-violet	*deep* blue-violet
	garden	*pale soft* blue-violet	*light soft* blue-violet	*deep soft* blue-violet
Width of corolla lobes, mm.	nature	0.6-0.9	1.0-1.1	3.0-3.2
	garden	0.6-0.9	1.0-1.1	3.0-3.2
Length of stigma, mm.	nature	0.4	0.5-0.6	1.0-1.2
	garden	0.4	0.5-0.6	1.0-1.2

Genotypic Variability within the Populations

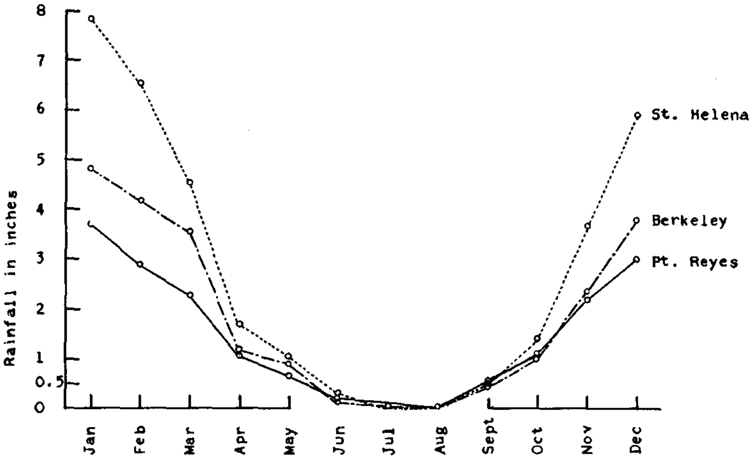
An important evolutionary factor in an entity is its inherent genotypic variability. This was explored by means of a progeny test for six populations of *Gilia capitata,* representing four subspecies. The populations tested were: *G. c. Chamissonis* from Point Reyes; *G. c. Chamissonis* from San Francisco; *G. c. tomentosa* from Tomales Bay; *G. c. capitata* from Mayacama Mountains, Napa County; *G. c. capitata* from Hatchet Mountain, Shasta County; and *G. c. mediomontana* from Mather, Tuolumne County.

The experimental design, which was suggested to the author by Prof. Stebbins, was as follows: twenty progenies were grown from one seed parent in the



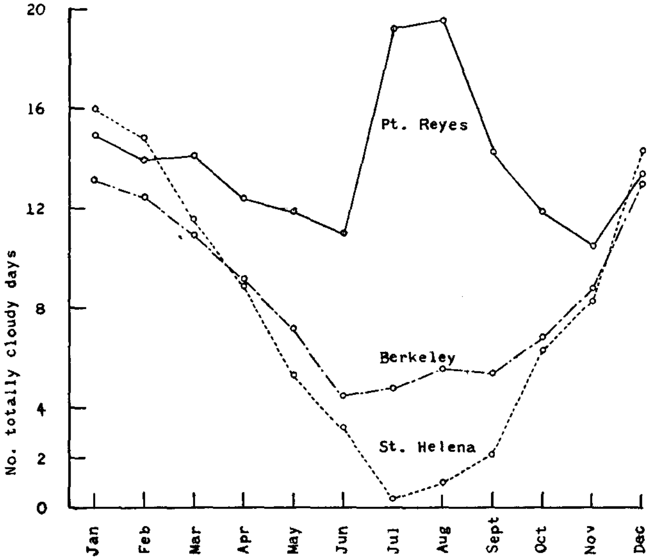
MAXIMUM AND MINIMUM TEMPERATURES THROUGHOUT THE YEAR AT 3 STATIONS NORTH OF SAN FRANCISCO BAY (10 YEAR AVERAGES).

Figs. 11-13. A comparison of the climates of St. Helena, which is near the population of *G. c. capitata;* Pt. Reyes, which is near the populations of *G. c. Chamissonis* and *G. c. tomentosa;* and Berkeley, the site of the uniform garden. All data from U. S. Weather Bureau.



Monthly distribution of rainfall at 3 stations north of San Francisco Bay (35 year averages).

Fig. 12



Distribution of cloudiness throughout year at 3 stations north of San Francisco Bay (10 year averages).

Fig. 13

natural population. These twenty plants from one parent will be referred to hereafter as "sisters," although, of course, they are probably only "half-sisters" in randomly cross-breeding organisms. A single progeny was also grown from each of twenty other seed parents in the same wild population. Each parental population was consequently represented in the experimental tract in Berkeley by twenty "cousins" as well as twenty "sisters."

In the original collection of the seeds by families, an effort was made to obtain a random sample of the parental population by harvesting only from plants occurring at regular intervals along a transect. The seeds were grown in flats, as already described in the previous section. An extra number of seeds of both sisters and cousins was planted to allow for the normal proportion of casualties at germination and establishment. To the extent that those casualties were replaced by healthy seedlings, some selection did unavoidably occur against the non-vigorous types in Berkeley. The progenies were grown in randomized plots, each plot consisting of two rows of sisters alternating with two rows of cousins. One of the assumptions of the experiment is that the amount of environmental variability is the same within every ten-foot-square plot of ground in the field.

The following morphological characters were selected for measurement: height of plant; length of terminal internode; diameter of head; width of corolla lobe; and number of seeds per capsule. The measurements, except for the last-mentioned character, were performed on living plants in the field. The dimensions of the corollas are therefore greater than reported elsewhere in this paper, where dried specimens were used. In the case of three populations, *G. c. Chamissonis* from Point Reyes, *G. c. tomentosa* from Tomales Bay, and *G. c. capitata* from the Mayacama Mountains, every plant was measured for all of the five characters; but due to lack of time only two critical measurements, those pertaining to the corolla and capsule, were taken for the samples of *G. c. mediomontana* from Mather and *G. c. capitata* from Hatchet Mountain. The progeny of *G. c. Chamissonis* from San Francisco appeared on scrutiny in the experimental field to be not significantly more or less variable than the progeny of *G. c. Chamissonis* from Point Reyes, and they were accordingly not measured at all.

In Table 7 the range, mean ($\bar{x}$), standard deviation (s), and coefficient of variability (C) are given for each character and each population. Under each population there are two sets of statistics, one for sisters and one for cousins, and in the case of seed number a third set of statistics is presented to describe the variability occurring within a single individual selected at random. This purely phenotypic variability must, of course, enter into the interpretation of comparative sister and cousin variabilities for the character in question. The coefficient of variability will be found to be the most satisfactory statistic for comparing the several populations with respect to characters by which they differ, one from another, in absolute size or number.

We may commence the analysis of the progeny test by regarding Fig. 14, where the variation pattern in three populations, *G. c. Chamissonis* from Point Reyes (CH), *G. c. tomentosa* from Tomales Bay (TOM), and *G. c. capitata* from Mayacama Mountains (CA), is compared with respect to four characters. In each population the uppermost line represents the variability between sisters, the lowermost line the variability between cousins, except in one case, where the variation within one individual has been shown in top position. The length of the line represents the range, the vertical bar the mean, and the horizontal bar the standard deviation.

The differences in range and mean between the three populations are chiefly of interest in connection with the taxonomic status of the characters thus compared. Since this point has been discussed in the preceding section it will be unnecessary to pursue it further here. The reader may nevertheless be interested in the graphic confirmation of the conclusion, previously stated, that *G. c. tomentosa* agrees with *G. c. capitata* in the width of its corolla lobes, with *G. c. Chamissonis* in the diameter of its floral heads, and is intermediate between them, but approaching *G. c. capitata,* in the number of seeds per capsule.

Comparing the variability of cousins with that of sisters of the same population, by means of the relative lengths of the horizontal bands, it is seen that the cousins are consistently more variable than the sisters, as would be expected in normally cross-breeding plants. The diameter of the heads constitutes an exception to this rule, the significance of which is not known.

The pattern of variation in a population is closely related to the breeding behavior of its individuals. It would be unnecessary to mention this point if *G. c. Chamissonis, G. c. tomentosa,* and *G. c. capitata* were alike in their breeding behavior. As will be shown in the next chapter, however, they are very different in this respect, *G. c. capitata* being fully self-incompatible, *G. c. Chamissonis* being self-compatible, and *G. c. tomentosa* being of reduced self-compatibility. On *a priori* grounds we should expect the variability of sisters to be less in *G. c. Chamissonis,* which may be more or less inbred, than in *G. c. capitata,* which is regularly outbred. In four out of five characters recorded in Table 7 this is the case. We should expect on the same *a priori* grounds that the pattern of sister variation would correspond with the pattern of the population as a whole, as represented by the cousins, most closely in *G. c. capitata* and least closely in *G. c. Chamissonis.* A striking difference in the means for sisters and cousins of the same population did, in fact, turn up in *G. c. Chamissonis,* where the number of seeds per capsule diverges significantly in the sisters as compared with the cousins (Fig. 14); however, a similar situation appears in *G. c. capitata* with respect to plant height (Table 7).

If we make the assumption that the self-compatible types may be partially inbred over a series of generations, then we might expect that the *excess* of cousin variability over sister variability would be greatest in self-compatible *G. c. Chamissonis* and least in *G. c. capitata.* This relationship can be expressed mathematically as the coefficient of variability of sisters ÷ coefficient of variability of cousins, in which the magnitude of the pure number is directly proportional to the excess of cousin variability over sister variability. The new coefficient, Csis. ÷ Ccous. as shown in Table 7, does, indeed, correspond to a relatively more uniform population of sisters than of cousins in *G. c.*

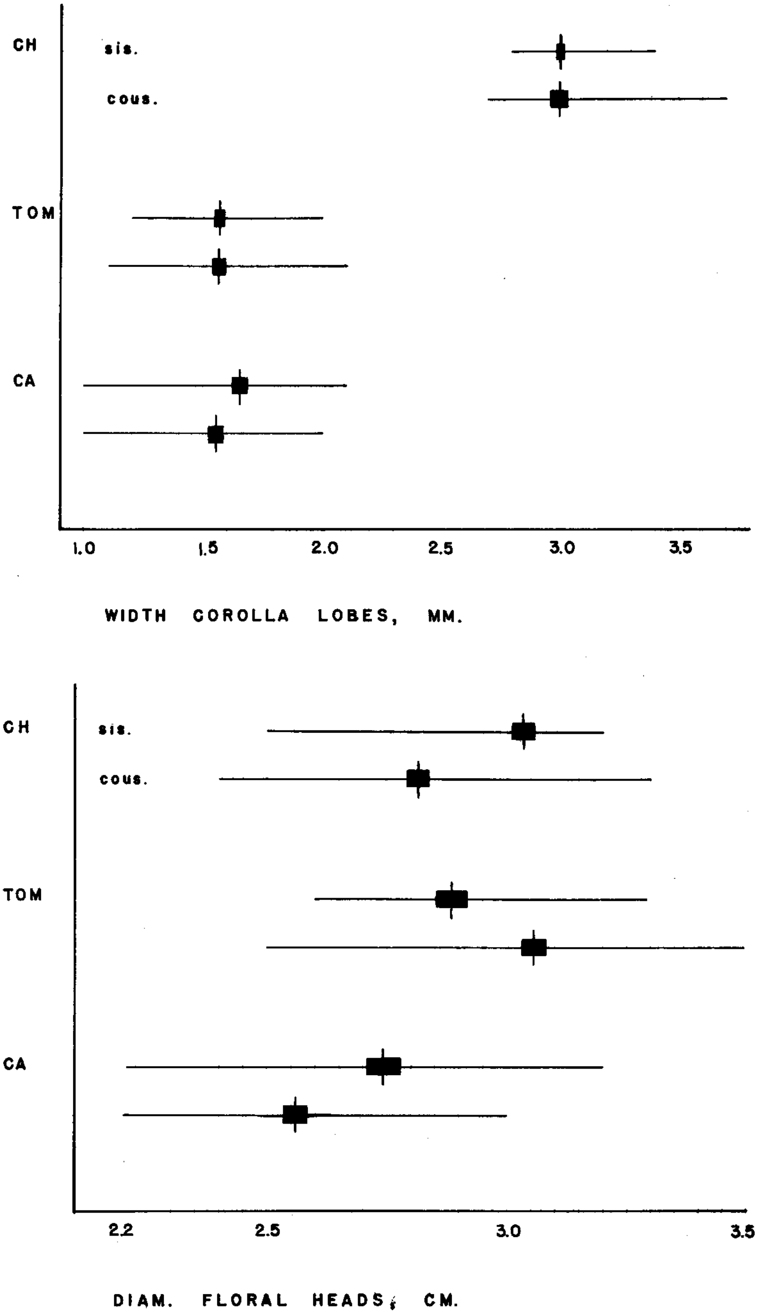
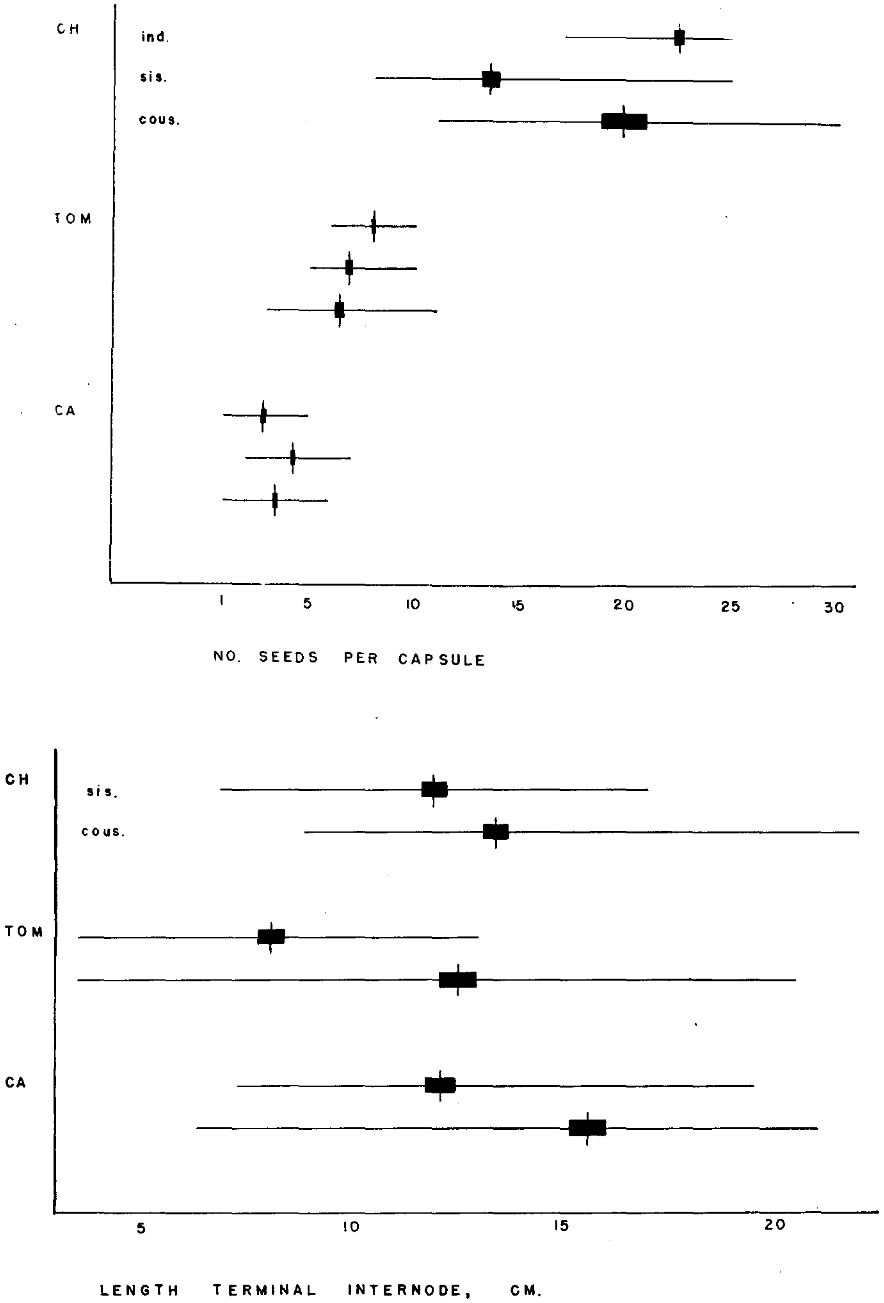


Fig. 14. Graphical representation of the measurements of four quantitative characters in a progeny test. The parental populations are *G. c. Chamissonis* from Pt. Reyes (ch); *G. c. tomentosa* from Tomales Bay (tom); and *G. c. capitata* from Mayacama Mts. (ca). The hori-



zontal line represents the range, the vertical bar the mean, and the horizontal band the standard deviation. The lower line for each population represents the statistics for cousins (cous.), the upper line the statistics for sisters (sis.), or in one case the statistics for one individual (ind.). All measurements were made on living plants.

TABLE 7. Comparative statistics for a progeny test of three populations of *Gilia capitata*. $\overline{X}$ = mean; s = standard deviation; C = coefficient of variability; Csis/Ccous = a ratio, the meaning of which is explained in the text. (All measurements from living plants.)

		Width of corolla lobe, mm.					No. seeds per capsule					Diameter heads, cm.				
		Range	$\overline{X}$	s	C		Range	$\overline{X}$	s	C	Csis/Ccous	Range	$\overline{X}$	s	C	Csis/Ccous
G. c. Chamissonis	individual						17-25	22.5	2.41	10.7						
Pt. Reyes	sisters	2.8-3.4	3.04	.176	5.8		8-25	13.5	4.33	32.0		2.5-3.2	3.03	.25	8.2	
	cousins	2.7-3.7	3.00	.316	10.5	1.81	11-30	19.8	5.40	27.2	0.85	2.4-3.3	2.82	.25	8.9	1.08
G. c. tomentosa	individual						6-10	8.00	1.33	16.6						
Tomales Bay	sisters	1.2-2.0	1.58	.200	12.6		5-10	6.90	1.70	24.6		2.6-3.3	2.88	.33	11.4	
	cousins	1.1-2.1	1.58	.277	17.5	1.39	3-11	6.45	2.16	33.5	1.36	2.5-3.5	3.06	.27	8.8	0.77
G. c. capitata	individual						1-5	2.90	1.37	47.2						
Mayacama Mts.	sisters	1.0-2.1	1.66	.309	18.6		2-7	4.22	1.39	32.9		2.2-3.2	2.74	.35	12.8	
	cousins	1.0-2.0	1.56	.316	20.2	1.08	1-6	3.44	1.34	38.9	1-18	2.2-3.0	2.56	.24	9.3	0.73

		Length terminal internode, cm.					Height of plant, cm.				
		Range	$\overline{X}$	c	C	Csis/Ccous	Range	$\overline{X}$	s	C	Csis/Ccous
G. c. Chamissonis	individual										
Pt. Reyes	sisters	6.8-17.0	11.9	2.98	25.0		12-30	20.3	4.61	22.7	
	cousins	8.9-22.0	13.4	3.21	23.9	0.95	9.33	22.7	5.93	26.1	1.15
G. c. tomentosa	individual										
Tomales Bay	sisters	3.5-13.0	8.1	3.24	40.0		19-29	24.0	2.98	12.4	
	cousins	3.5-20.5	12.5	4.49	35.8	0.90	20-33	27.8	5.08	18.2	1.46
G. c. capitata	individual										
Mayacama Mts.	sisters	7.3-19.5	12.1	3.78	31.2		17-43	28.1	5.30	18.9	
	cousins	6.3-21.0	15.6	4.20	26.9	0.86	29-61	43.8	7.62	17.4	0.92

Chamissonis, as compared with *G. c. capitata,* for every character except one, and in that one the sisters and cousins of *G. c. Chamissonis* are very different in their means.

Another factor affecting the variation pattern is the size and structure of the population. In general, larger populations will possess a greater store of variability than smaller populations. The Mayacama population of *G. c. capitata* is large, ramified over a wide area on a brushy hillside, and is relatively immune to drastic reductions in the numbers of individuals, even during years of drought or grass fire. The Tomales Bay population of *G. c. tomentosa* is, by contrast, small, restricted in areal extent, and exposed to periodic fluctuations in size. In dry years on the coast the number of breeding individuals may be less than two hundred. The population of *G. c. Chamissonis* on Point Reyes is again extensive, but perhaps not so numerous or stable as the population of *G. c. capitata.* From the standpoint of population size, therefore, it would be expected that *G. c. tomentosa* would show less variation than *G. c. capitata.* A comparison of the C values for cousins in Table 7 shows that for three of the five characters, namely width of corolla lobes, number of seeds per capsule, and size of heads, this is indeed the case, and in a fourth character, height of plant, *G. c. tomentosa* is more uniform than *G. c. Chamissonis.* The population of *G. c. tomentosa* on its exposed maritime bluff is probably subjected to relatively strong selective pressures, by analogy with the case of *Achillea borealis* on the Bodega coast (Clausen, Keck and Hiesey, 1948, pp. 16-18), and this environmental selection would constitute another force operating to restrict variability in *G. c. tomentosa.*

TABLE 8. Comparative statistics for a progeny test of three populations of *Gilia capitata.* Explanation of symbols in Table 7. All Measurements from living plants.

		Width of corolla lobes, mm.				No seeds per capsule			
		Range	$\bar{X}$	s	C	Range	$\bar{X}$	s	C
G. c. capitata	individual					1-5	2.90	1.37	47.2
Mayacama Mts.	sisters	1.0-2.1	1.66	.309	18.6	2-7	4.22	1.39	32.9
	cousins	1.0-2.0	1.56	.316	20.2	1-6	3.44	1.34	38.9
G. c. capitata	individual					3-5	4.30	.68	15.8
Hatchet Mt.	sisters	1.1-1.9	1.51	.219	14.5	2-8	4.60	1.76	38.2
	cousins	1.0-1.9	1.56	.268	17.2	4-8	5.57	1.45	26.0
G. c. mediomontana	individual					7-12	9.4	1.65	17.5
Mather	sisters	1.8-2.7	2.27	.268	11.8	6-17	11.4	3.69	32.4
	cousins	2.1-2.9	2.32	.209	9.0	4-14	9.95	2.60	26.2

Population size can probably be removed as a variable factor in the comparison of the variability of *G. c. mediomontana* from the Sierra Nevada (Mather), *G. c. capitata* from the southern Cascade Mountains (Hatchet Mountain), and *G. c. capitata* from the Coast Ranges (Mayacama Mountains), since all these populations are large and continuous. As shown in Table 8 the cousin variability of the two former populations is less than that of *G. c. capi-*

tata from the Coast Ranges. It may be that environmental selection is more rigorous again in the Sierra Nevada and Cascade Mountains than in the central Coast Ranges, where relatively mild climatic conditions prevail. As regards the variability of sisters, *G. c. mediomontana,* which is probably self-compatible and partially inbred, is more uniform than *G. c. capitata,* which is obligately outbred.

The results of the progeny test lead us to the general conclusion that the inherent variability of natural populations, as typified by *Gilia capitata,* is restricted by two forces, inbreeding and natural selection.

Variation between Populations of the Same Entity

The variation pattern of the capitate gilias possesses two characteristic features. A given population is usually relatively uniform, as has been brought out in the preceding section, but neighboring populations of the same entity are frequently somewhat different in their morphological characters. Some examples of this latter phenomenon will be mentioned in the present section.

A very striking case of inter-colonial variation exists in *G. c. tomentosa,* where short, stocky forms, and tall, robust forms occupy adjacent habitats near both Tomales Bay and Bodega Bay (Fig. 2). Less spectacular, but not less real, are the habit differences of *G. c. Chamissonis* on opposite sides of San Francisco Bay. The Point Reyes plant forms a good basal rosette of leaves, it is short and stocky at maturity, and the flowering heads are large. The San Francisco plant does not possess such a well developed basal rosette and is somewhat looser in habit at maturity. The terminal peduncles are looser and more spreading, and the heads are less full than on Point Reyes. Inter-colonial variability appears to be especially well developed in *G. c. pacifica,* as has already been mentioned in the chapter on geographical distribution. Population studies are much needed in Mendocino and Humboldt counties, to supplement the excellent collections made by Mr. J. P. Tracy.

The existence of minor variants within subspecies is true also of the capitate gilias of the Sierra Nevada. *Gilia capitata mediomontana* is often possessed of light blue-violet flowers and stout, relatively simple stems. Populations of *G. c. mediomontana* around Mather in Tuolumne County have perfectly white flowers (in the living condition), and branch profusely at the base to produce numerous, brittle stems. A unique type of *G. c. mediomontana* occurs in Placer County, around Kyburz, which is distinguished from the rest of its subspecies by the possession of a conspicuous basal tuft of leaves, usually with wide pinnae. In Shasta County another variant, in this case distinguished by glandular hairs on the pedicels and calyces, has become established over a large area, and thus approaches the status of a subspecies.

Two adjacent populations of *G. c. capitata* in the Mayacama Mountains, one about 100 yards distant from the other, proved to differ by such physiological characters as seed germination and time of flowering, although in this case it is not certain that the differences are not due to environmental influences. One of the populations grew in an area which was burned over by a grass fire during the year when the seeds were collected. The other population occurred in the shade of an oak grove and was not affected by the fire. Seeds from the burned population germinated very much better than seeds from the shady grove, in the proportion of 61% to 32%; the germination test was replicated several times, always with a similar result (Grant, 1949b). During two successive seasons, progeny from the burned area flowered about two or three weeks earlier than progeny from the shady grove, in a randomized garden plot in Berkeley. Since the population in the oak grove has not come back during the two seasons since the seeds were first collected, it has not been possible to compare the two populations except on the basis of their behavior in 1946, the year of the fire. The F_1 generations of each of the two 1946 populations could, of course, be obtained by effecting *inter se* crosses within progenies grown from the original seed collection, and in this manner the existence of genetically determined earliness and seed germination could readily be determined.

There is variability between populations of *G. c. capitata*, and also within them, in respect to the presence of floccose or glandular hairs on the stem. Population studies of *G. c. capitata* near the coast as at Fairfax, Marin County, and Santa Rosa, Sonoma County, show that all of the individuals of those populations are floccose. In both the Mayacama Mountains and Hatchet Mountain, however, some individuals of a population are floccose and others are glandular. The progeny test described in the preceding section shows that the proportion of floccose individuals is greater in the Mayacama population (32%) than in the Hatchet Mountain population (12%). When more populations of *G. c. capitata* are known, it may turn out that the character of glandulosity varies in the manner of a cline, with the frequency of the gene for floccose hairs increasing from the interior toward the coast.

5. Compatibility and Fertility

Floral Biology

The flowers of the capitate gilias are protandrous. The anthers mature in the bud, force their way out of the expanding corolla, and dehisce a day or two after the flower has opened. Dehiscence of the anthers seems to be determined largely by the dessication of that organ in the sun. A longitudinal slit appears in each anther lobe, which, on recurving, brings about the extrusion of a mass of light blue pollen. Although the flowers of *Gilia capitata* are visited by a wide range of insects, most of the smaller types enter the corolla tube without touching the well exserted pollen masses, and effective pollination is carried out perhaps exclusively by bees and long-tongued flies. Especially important as pollinators of the capitate gilias in California are various members of the Anthophoridae and Dufoureidae.

At the time when the anthers first ripen, the style is an elevated club-shaped structure, with its future stigmatic lobes closely pressed against one another. The finding of *Gilia capitata* in this condition once led a botanist to describe a new species! Had Mr. Heller waited a few more days, he would have observed the three stigmas to open out and recurve. At this stage the stigmas are raised above the level of the anthers which still possess some good pollen. Self-pollination does not occur without the intervention of insect vectors, as will be brought out later.

It sometimes happens that an individual will reverse the normal sequence described above and produce its styles precociously. The floral head, in such cases, has the aspect of a pin cushion, with a dozen or more long, receptive styles protruding out of the unexpanded calyces. The corolla may or may not develop, and the anthers are abortive. This phenomenon has appeared invariably in plants of poor vigor, yet normal seeds will develop if the stigmas are pollinated. It is interesting to speculate that abnormal protogyny in *Gilia capitata* may be adaptive, in that it may enable a plant in unfavorable circumstances to complete its life cycle with the greatest brevity by the production of some seeds before it perishes.

The first flowers to open in *Gilia capitata* are the terminal flowers on the head. Several additional flowers peripheral to these then mature on each succeeding day until the whole head is in one or another stage of flowering. The head, at first globose, may eventually lose its regular shape by the proliferation of the apical group of flowers, and thus become conoidal. The first head to flower and fruit is followed in cymose order by other heads lower on the plant. With an abundance of water and suitable conditions of cultivation the capitate gilias can be maintained in flowering as long as three months in spring and summer. The last few flowers to develop in late summer are frequently diminutive in every proportion.

Method of Hybridization

Individuals of *G. c. Chamissonis* from Point Reyes, *G. c. tomentosa* from Tomales Bay, *G. c. capitata* from the Mayacama Mountains, and *G. c. staminea* from Antioch were intercrossed. All possible crosses were made, including the reciprocals. An entity was usually represented by four female parents and four male parents; however, in some of the crosses, only two pairs of parents were used. *Inter se* crosses were also made between a pair of individuals of the same entity. In addition, one individual of each entity was artificially selfed, while another individual of each entity was caged but not selfed artificially, in order to establish the presence or absence of autogamy or automatic selfing. A group of four F_1 plants of the same hybrid combination were caged and intercrossed to produce F_2 seeds. The F_1 hybrid of *G. c. capitata* and *G. c. Chamissonis* was backcrossed to both parental types under controlled conditions.

The female parents were enclosed in cheese-cloth breeding cages. The flowers were emasculated by jerking the five unripe anthers out of the bud with the aid of one prong of a pair of forceps. Every flower in a head was emasculated; unwanted heads were pinched off in the bud. The mature stigmas were pollinated by touching them individually with ripe anthers plucked from the desired male parent and held in a pair of forceps. The forceps were repeatedly sterilized in a vial of alcohol. Records were kept for each plant and for each head. The records for a head included the number of emasculations, the number of days of pollination, the number of capsules set, and the number of seeds per capsule.

Self-compatibility

Gilia capitata staminea and *G. c. Chamissonis* proved to be quite self-compatible and formed abundant seed with their own pollen. *Gilia capitata capitata,* as represented by two individuals, was fully self-incompatible and ripened no capsules at all with its own pollen. The cause of this self-incompatibility, whether due to inhibition of pollen-tube growth, or of embryonic development, or of still other stages in embryogeny, has not as yet been investigated. *Gilia capitata tomentosa* is of reduced self-compatibility, for it formed only a few capsules with one or two seeds in each capsule as a result of numerous self-pollinations. In this respect *G. c. tomentosa* is intermediate between *G. c. Chamissonis* and *G. c. capitata.*

Gilia capitata staminea and *G. c. Chamissonis,* although they are self-compatible, are not autogamous, and require the visits of insects if they are to be selfed. Individuals of these entities enclosed in cages and left to their own devices formed only minute capsules without seed.

Inter-compatibility

Foreign pollen took easily on all seed parents except *G. c. tomentosa.* Pollen of *G. c. staminea* or *G. c. Chamissonis* on several individuals of *G. c. tomentosa* apparently caused those plants to react vigorously: the foliage became spotty and yellowish, the anthers turned yellow and abortive, and capsule after capsule failed to develop. The proportion of capsules set to flowers emasculated, expressed as a percentage, is given for all of the crosses in Table 9 (in the column entitled "reproductive vigor of P"). There it is seen that scarcely one or two per cent of the flowers of *G. c. tomentosa* that were emasculated and pollinated by *G. c. staminea* or *G. c. Chamissonis* succeeded in forming ripe capsules. The F_1 hybrids resulting from those crosses, moreover, tended to be weaklings, as shown in the adjoining column. It may also be noted from Table 9 that *G. c. tomentosa* is less receptive to pollen of *G. c. capitata* than *G. c. capitata* is to pollen of *G. c. tomentosa.* The figures in this column are based on between three and seventeen heads, and fifty to 250 emasculations, for each cross.

The inter-compatibility relationships of the four entities were compared also with respect to the reduction in seed set. The number of seeds per capsule in seed parents used for hybrid crosses was compared with the seed set from the corresponding *inter se* crosses under the same greenhouse conditions. The seed set in the inter-subspecific crosses was expressed as a percentage of the average number of seeds per capsule in an *inter se* cross of the same subspecies. These percentages, which are based on between fifteen and 100 capsules for each cross (or only four in *G. c. tomentosa* ♀ × *G. c. Chamissonis),* are given in the first column of Table 9.

The most interesting thing about these figures is perhaps the suggestion of reciprocal differences in compatibility in the crosses between *G. c. staminea* and *G. c. Chamissonis, G. c. staminea* and *G. c. tomentosa, G. c. Chamissonis* and *G. c. tomentosa,* and *G. c. capitata* and *G. c. tomentosa.* In general, it appears that *G. c. staminea* is more compatible with *G. c. Chamissonis* or *G. c.*

tomentosa when *G. c. staminea* is the mother than when it is the pollen parent, and that *G. c. Chamissonis* and *G. c. capitata* are more compatible with *G. c. tomentosa* when they are the mothers rather than the pollen parents.

The existence of reciprocal differences in compatibility is confirmed for three of the four crosses by the data for reproductive vigor already mentioned (cf. crosses ii, v, and vi, Table 9). The respective sets of data may not be sufficiently independent, however, to make the confirmation very convincing, and in any case they are drawn from the same individual plants. It is therefore interesting to record the proportions of F_1 hybrids between *G. c. tomentosa* and *G. c. Chamissonis,* and *G. c. tomentosa* and *G. c. capitata,* occurring in progeny grown from plants in the uniform garden described in the preceding chapter.

TABLE 9. Summary of the breeding behavior of four subspecies of *Gilia capitata: G. c. Chamissonis* (ch), *G. c. staminea* (st), *G. c. capitata* (ca) and *G. c. tomentosa* (tom).

Hybrid Combination		Reaction of male gametophyte or embryo		Reaction of adult plant	
	♀ ♂	inter-compatibility of P's (*)	pollen fertility of F_1	reproductive vigor of P (**)	vegetative vigor of F_1
i)	st x ch	100%	51%	65%	vigorous
	ch x st	47	82	77	"
ii)	st x tom	91	17	55	"
	tom x st	29	53	2	weakling
iii)	st x ca	54	78	34	vigorous
	ca x st	67	83	42	"
iv)	ch x ca	41	73	70	"
	ca x ch	67	86	23	"
v)	ch x tom	76	85	71	"
	tom x ch	23	75	1	weakling
vi)	ca x tom	100	95	69	vigorous
	tom x ca	56	95	39	"

* = mean number seeds per capsule in seed parent used for hybrid cross ÷ mean number seeds per capsule in parents of same entity used for inter se cross x 100.

** = summation of (number of capsules matured per head ÷ number flowers emasculated in that head x 100).

The plants in that garden were randomized, as has already been stated, and were open pollinated by bees. Although the individual bees did not work over the plants at random, but confined their visits rather consistently to one subspecies at a time (Grant, 1949a), there is no reason to suppose that the inter-subspecific visits of the bees, when they did occur, would have resulted in the pollination of, say, *G. c. Chamissonis* by *G. c. tomentosa,* more frequently than of *G. c. tomentosa* by *G. c. Chamissonis.* Yet when 145 seedlings were raised from plants of *G. c. Chamissonis* in the uniform garden, 28 of them, or 20%, were F_1 hybrids with *G. c. tomentosa,* whereas out of 100 progeny of *G. c. tomentosa* no F_1 individual of *G. c. tomentosa* ♀ × *G. c. Chamissonis* was found. A similar but less extreme proportion was found in the progeny of *G. c. capitata* in the uniform garden, 58% of which were F_1s with *G. c. tomentosa,* as against only 32% of F_1s of *G. c. tomentosa* ♀ × *G. c. capitata* in the progeny of *G. c. tomentosa.*

These differences are statistically significant. They are not accounted for by the behavior of the bees, which was very closely observed. On the other hand, they are in agreement with the results of controlled hybridizations. It seems reasonably safe to conclude, therefore, that some members of the *Gilia capitata* complex, when they are combined in certain crosses, exhibit reciprocal differences in compatibility. These reciprocal differences are not correlated with the differences in length of style between the respective subspecies.

Pollen Sterility in F_1

Fresh pollen from ripe anthers of the F_1 hybrids was mounted in lactophenol and stained with aniline blue. The grains that filled out and took up a deep blue stain were counted as good, while the smaller, irregular, transparent, unstained grains were considered to be abortive. The slide was counted from one edge of the cover slip to the other (Garber, 1948). At least 400 pollen grains were counted on each slide. Every individual plant was at first replicated by counting pollen from a different head at a different time, but the replications proved to agree well with the original count (except in one case to be noted later), and that practice was finally discontinued.

TABLE 10. Frequency distribution of pollen fertility of sister F_1 hybrids from the same cross. Abbreviations as in Table 9.

		Per Cent Good Pollen									$\bar{X}$	Significance of difference in means
		10-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100		
i)	st x ch		1	1	2		2				51%	P<.01
	ch x st							3	3		82	
ii)	st x tom	3									18	
	tom x st					1					53	
iii)	st x ca						3	1		2	78	P=.50-.40
	ca x st						1	2	5	1	83	
iv)	ch x ca				1		2	3	2		73	P=.02
	ca x ch							2	5	2	86	
v)	ch x tom							1	3		85	
	tom x ch		1					2			75	
vi)	ca x tom						1			4	95	
	tom x ca									3	95	

The results, as summarized in Table 10, show that the hybrids exhibited a wide range of pollen fertility, from 16% good pollen to 98%. Even the lowest level of pollen fertility encountered, in the F_1 hybrid *G. c. staminea* ♀ × *G. c. tomentosa,* was still sufficiently high to enable the plants to produce a fairly good crop of sound seeds. In general, therefore, the F_1 hybrids were not so sterile as to be prevented from reproducing; on the contrary, most of them were as vigorous reproductively as the parental subspecies.

In crosses of other subspecies onto *G. c. tomentosa,* the F_1 generation included a large proportion of weakling individuals, as previously mentioned. In the progeny of *G. c. tomentosa* ♀ × *G. c. staminea,* for example, one individual was observed to become increasingly moribund, week by week. Its pollen was examined at two-week intervals with the following results: early May: 63% good pollen; late May: 46%; early June: anthers sterile with no pollen. The weakling hybrids of *G. c. tomentosa* usually failed to survive through the growing season; their elimination left the field occupied by the relatively few hybrids of *G. c. tomentosa* × *G. c. Chamissonis* that possessed good vigor and high fertility.

The crosses of *G. c. staminea* with *G. c. Chamissonis* and *G. c. tomentosa* led to reciprocal differences in the male sterility of the hybrids, such that the more sterile hybrids were those derived from a *G. c. staminea* mother. The reciprocal differences are not extremely great; they are, nevertheless, statistically significant (cf. Table 10, cross i), and in all probability are real. Since the reciprocally different hybrids were derived from different sets of parents, the question arises whether the respective *G. c. staminea* parents were themselves different in fertility.

The pollen of *G. c. Chamissonis, G. c. tomentosa,* and *G. c. capitata* appears to be both high and uniform in its fertility, or at least relatively so. Individuals of *G. c. staminea,* on the other hand, are characterized by a wide range of variation from 32% to 92% good pollen; the mean and standard deviation for fifteen individuals was 74% ± 22. The original *G. c. staminea* parents in the cross with *G. c. Chamissonis* yielded some dry pollen from herbarium specimens which showed little individual difference in fertility, as follows: i) *G. c. staminea* ♀ (46%) × *G. c. Chamissonis* gave a relatively sterile F_1, while *G. c. Chamissonis* ♀ × *G. c. staminea* (58%) gave a relatively fertile F_1. Similarly: ii) *G. c. staminea* ♀ (89%) × *G. c. tomentosa* gave a sterile F_1, and *G. c. tomentosa* ♀ × *G. c. staminea* (58%) yielded a relatively fertile hybrid.

These data do not of themselves suggest that the reciprocal differences in the F_1s are correlated with individual differences between the parents. However, the considerable heterozygosity of *G. c. staminea* with respect to some morphological characters, as well as the known variability of that entity in pollen fertility, require that these hybridization experiments be repeated, starting with inbred lines of *G. c. staminea,* and using the same individual parents to effect the reciprocal crosses. Perhaps then it can be established whether the reciprocal differences in hybrid sterility are due to individual differences within the population or to differences between the populations themselves.

The evidence for the existence of reciprocal differences in compatibility between populations as well as between individuals of the *Gilia capitata* complex has already been reported. That evidence would perhaps tend to strengthen the supposition that the observed reciprocal differences in hybrid sterility likewise constitute a population phenomenon. If that is so, a most remarkable situation exists in *Gilia capitata.* The compatibility relationships of the parents and the pollen fertility of the F_1s have been recorded in parallel columns in Table 9, where it may be seen that, with respect to the crosses involving *G. c. staminea* with *G. c. Chamissonis* or *G. c. tomentosa,* the reciprocal differences in compatibility are the very reverse of the reciprocal differences in pollen fertility. If a cross is easy to make *(G. c. staminea* ♀ × *G. c. Chamissonis),* the hybrid is relatively sterile, but if the crossability is low *(G. c. Chamissonis* ♀ × *G. c. staminea),* the hybrid is relatively fertile. Even more extreme contrasts in the reciprocal differences as to compatibility and hybrid fertility are manifested by *G. c. tomentosa* in combination with *G. c. staminea.*

Cases of reciprocal differences in hybrid sterility are not commonly encountered in the literature of plant breeding. The classical example occurs in the genus *Epilobium,* which has been the subject of thorough study in Germany. The reciprocal differences in pollen fertility of hybrids between the species pairs *E. parviflorum* and *E. roseum* (Lehmann, 1932), and *E. hirsutum* and *E. luteum* (Michaelis, 1933), have been attributed by those workers to differences in the cytoplasm of the respective parental species. The cytoplasm of the first-mentioned species of each pair is supposed to inhibit the action of the genes of the latter species, especially at the reproductive stage. The F_1 hybrid of *E. parviflorum* ♀ × *E. roseum,* or *E. hirsutum* ♀ × *E. luteum,* is sterile because of the deleterious combination of genes of *E. roseum* or *E. luteum* with the cytoplasm contributed by the maternal parent. In the reciprocal crosses, *E. roseum* ♀ × *E. parviflorum,* and *E. luteum* ♀ × *E. hirsutum,* the *E. roseum* or *E. luteum* genes are present with their own cytoplasm and the hybrids are fertile.

Reciprocal differences in hybrid sterility have also been reported for crosses between *Aquilegia vulgaris* and *A. chrysantha* (Skalinska, 1928). The manifestation of reciprocal differences in breeding behavior in *Gilia capitata* presents, however, some features not shared by the foregoing or any other examples known to the author. The situation in *Gilia capitata* constitutes a problem for future research.

Viability in F_2

The F_2 seedlings were on the whole normal and healthy in appearance. A distinct, though slight, barrier to interbreeding was nevertheless evident in the F_2 generation of certain of the crosses in the form of a small proportion of abnormal and inviable individuals. From 10 to 15 percent of the total number of seedlings grown in F_2 *G. c. staminea* × *G. c. tomentosa,* F_2 *G. c. Chamissonis* × *G. c. tomentosa,* F_2 *G. c. Chamissonis* × *G. c. capitata* were inviable and frequently underdeveloped. It may be noted that in the first two of the crosses mentioned a large proportion of individuals were also inviable in the F_1 generation (Table 11). In the remaining F_2 crosses only an occasional inviable seedling was found.

Summary

Four subspecies of *Gilia capitata,* namely *G. c. staminea from* Antioch, *G. c. Chamissonis* from Point Reyes, *G. c. tomentosa* from Tomales Bay, and *G. c. capitata* from the Mayacama Mountains, were crossed reciprocally with one another and were selfed. Each cross and its reciprocal was carried out with eight individual plants, or in some cases with four. Two individuals, or in some cases only one, were employed in making the selfs.

None of the entities are autogamous. *Gila capitata staminea* and *G. c. Chamissonis* are self-compatible, and *G. c. tomentosa* is of reduced self-compatibility. Two individuals of *G. c. capitata* proved to be totally self-incompatible.

The subspecies are compatible with one another in varying degrees. None of them are so incompatible that they cannot be crossed in the greenhouse, but some of the crosses, for example *G. c. tomentosa* ♀ × *G. c. Chamissonis* or *G. c. tomentosa* ♀ × *G. c. staminea*, are so difficult to make that F_1 hybrids would probably result only rarely under natural conditions, where the foreign pollen or hybrid embryo must compete with the products of the domestic pollen. One hundred progeny of plants of *G. c. tomentosa* in a mixed garden with *G. c. Chamissonis* thus yielded no F_1 hybrid of *G. c. tomentosa* by *G. c. Chamissonis.*

TABLE 11. Comparison of fertility in F_1 and viability in F_2 in inter-subspecific crosses of *Gilia capitata*. Abbreviations as in Table 9.

Hybrid combination (including reciprocal)	Percent good pollen in F_1	Percent viable seedlings in F_2	No. seedlings in F_2
st × ch	66	96	223
st × tom	35	90	60
st × ca	80	98	46
ch × ca	80	90	240
ch × tom	80	85	65
ca × tom	95	100	24

Reciprocal differences in compatibility exist which cannot be explained on the basis of differences in style length. The following crosses are distinctly easier to make in the direction indicated than in the reciprocal direction: *G. c. staminea* ♀ × *G. c. Chamissonis; G. c. staminea* ♀ × *G. c. tomentosa; G. c. Chamissonis* ♀ × *G. c. tomentosa;* and *G. c. capitata* ♀ × *G. c. tomentosa.* This conclusion is based on the breeding data and substantiated in the case of the last two crosses by a test of the progeny of numerous individuals of each subspecies, grown intermixed in a garden and open-pollinated by bees. It was found that, while 100 progeny of *G. c. tomentosa* plants yielded no F_1s of *G. c. tomentosa* ♀ × *G. c. Chamissonis,* the reciprocal hybrids, *G. c. Chamissonis* ♀ × *G. c. tomentosa,* comprised 20% of the progeny of *G. c. Chamissonis* plants in the same garden.

The F_1 hybrids are vigorous in all crosses except *G. c. tomentosa* ♀ × *G. c. staminea* and *G. c. tomentosa* ♀ × *G. c. Chamissonis.* The pollen fertility is relatively high in most crosses; in no cross was the sterility of the F_1s so great as to preclude the production of abundant sound seeds. A distinct, though relatively slight, barrier to interbreeding is present in the F_2 generation of three of the crosses in the form of a small proportion of inviable individuals. The crosses in question are: *G. c. staminea* × *G. c. tomentosa; G. c. Chamissonis* × *G. c. tomentosa;* and *G. c. Chamissonis* × *G. c. capitata.*

Reciprocal differences in pollen fertility were found in two crosses involving *G. c. staminea.* The following crosses lead to more fertile hybrids than their reciprocals: *G. c. Chamissonis* ♀ × *G. c. staminea; G. c. tomentosa* ♀ × *G. c. staminea.* The reciprocal differences in pollen fertility of the F$_1$s are just the reverse of the reciprocal differences in compatibility of the parents. These hybridizations should be repeated with relatively pure lines.

Gilia capitata capitata, which is quite different morphologically from *G. c. staminea* or *G. c. Chamissonis*, is not isolated from either of those subspecies by any genetic barrier up to the F$_2$ generation. *Gilia capitata staminea* and *G. c. Chamissonis,* on the other hand, which are very close morphologically, are separated by partially developed barriers of incompatibility or pollen sterility.

Gila capitata tomentosa, used as a female parent, is difficult to cross with the other subspecies, and the mothers react to the foreign pollen by manifesting symptoms of lethality. The F$_1$ hybrids tend to be weak and inviable. In these respects *G. c. tomentosa* behaves unlike any of the other subspecies; however, in its breeding behavior with *G. c. staminea,* it shows an interesting resemblance to *G. c. Chamissonis* (cf. Table 9, crosses i and ii); and in its self-compatibility reactions it is intermediate between *G. c. Chamissonis* and *G. c. capitata.*

TABLE 12. The mean number of seeds per capsule in parents and F$_1$s in intersubspecific crosses in *Gilia capitata.* Mean is based on about 20 capsules from about 10 plants. All plants were abundantly open pollinated by bees.

Hybrid combination		Mean no. seeds per capsule		
P$_a$	P$_b$	P$_a$	F$_1$	P$_b$
G. c. capitata ×	*G. c. Chamissonis*	3	10	20
G. c. capitata ×	*G. c. staminea*	3	7	20
G. c. capitata ×	*G. c. tomentosa*	3	6	6
G. c. Chamissonis ×	*G. c. tomentosa*	20	10	6
G. c. staminea ×	*G. c. tomentosa*	20	12	6
G. c. Chamissonis ×	*G. c. staminea*	20	16	20

6. Cytology

The chromosomes of the capitate gilias are large, few in number (9 pairs), dissimilar, and easily stained. The author has encountered technical difficulties only in the examination of early stages of meiotic prophase. *Gilia capitata* should form suitable material for many cytogenetic studies. In the present study the importance of the chromosomes in determining relationships has been diminished by the fact that the entities all have the same number of them, and that their behavior at meiosis in the F$_1$ hybrids is quite regular.

Method

Most of the cytological work was done with pollen mother cells; the study of root and shoot tips occupied a subsidiary role. Floral buds were collected preferably at mid-day, when the temperatures were moderately high but

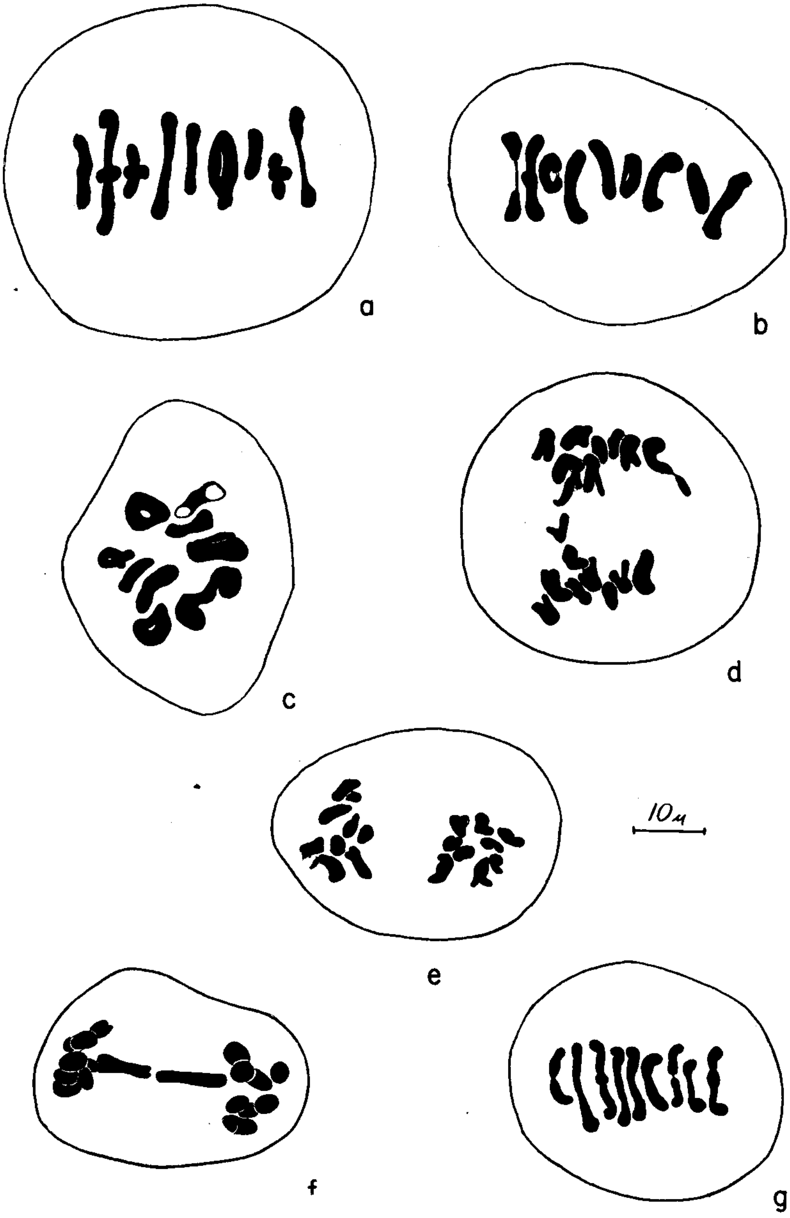


Fig. 15. Meiosis in the seven subspecies of *Gilia capitata*. PMC's. a—*G. c. capitata*, Mayacama Mts., chromosomes spread out in drawing; b—*G. c. Chamissonis*, Pt. Reyes, chromosomes spread out in drawing; c—*G. c. staminea*, Antioch; d—*G. c. mediomontana*, Yosemite Valley; e—*G. c. pedemontana*, Kaweah; f—*G. c. tomentosa*, Tomales Bay; g—*G. c. pacifica*, Cape Mendocino, chromosomes spread out in drawing. (× 900.)

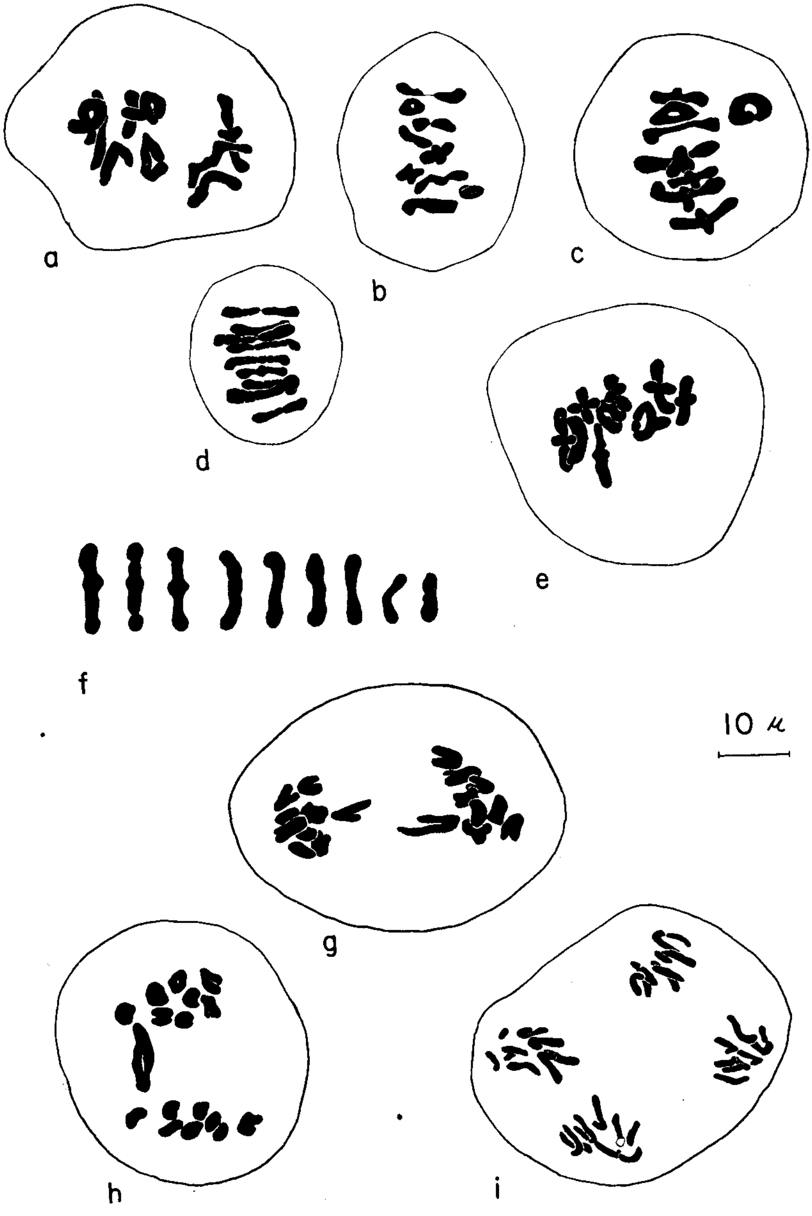


Fig. 16. Meiosis in F_1 hybrids between subspecies of *Gilia capitata*. PMC'c. a—*G. c. staminea* ♀ × *G. c. tomentosa*, diakinesis, this hybrid had 16% good pollen; b—*G. c. capitata* ♀ × *G. c. Chamissonis*, metaphase I; c—*G. c. tomentosa* ♀ × *G. c. Chamissonis*, metaphase I; d—*G. c. capitata* ♀ × *G. c. staminea*, metaphase I; e—*G. c. staminea* ♀ × *G. c. tomentosa*, metaphase I, this hybrid had 16% good pollen; f—*G. c. staminea* ♀ × *G. c. Chamissonis*, metaphase I, chromosomes rearranged in drawing, this hybrid had 35% good pollen; g—same hybrid, anaphase I; h—same hybrid, anaphase I, note slow separation of one pair of chromosomes; i—same hybrid, anaphase II. (× 900.)

before the plants had begun to wilt.. They were fixed for at least 48 hours in a solution of 4 parts chloroform: 3 parts absolute alcohol: 1 part glacial acetic acid. The acetic acid was added to the other components just prior to making the fixation. PMC's from young anthers were stained with aceto-carmine plus as much iron as could be worked into the solution from the tips of the dissecting needles. The slide was heated for about eight minutes on a rack suspended over a beaker of boiling water, then smeared. In order to prevent the cytoplasm from later turning dark, the PMC's were immediately destained by flushing the slide with 50% acetic acid to which a few drops of aceto-carmine had been added (Bradley, 1948). The slides were made permanent by diffusion of euparol under the cover slips in an alcohol vapor chamber (Bradley, op. cit.). Drawings of meiotic figures were made with a Bausch and Lomb camera lucida at a magnification of × 2300.

The Chromosomes of the Entities

Gilia capitata was found to have nine pairs of chromosomes, confirming the earlier report of Flory (1934) based on nursery plants of *G. c. capitata.* The author's counts may be summarized in tabular form (cf. also Fig. 15):

G. c. capitata	n=9	Mayacama Mts., Napa Co.	V. Grant	7702
			V. Grant	7985
		Hatchet Mt., Shasta Co.	V. Grant	8023
G. c. tomentosa	n=9	Tomales Bay, Marin Co.	V. Grant	7991
G. c. pacifica	n=9	Cape Mendocino, Humboldt Co.	J. P. Tracy	18225
G. c. Chamissonis	n=9	Point Reyes, Marin Co.	V. Grant	7662
G. c. staminea	n=9	Antioch, Contra Costa Co.	V. Grant	7925
			H. L. Mason	12566
G. c. pedemontana	n=9	Calaveras River, Calaveras Co.,	V. Grant	8498
		Kaweah River, Tulare Co.	V. Grant	8481a
G. c. mediomontana	n=9	Yosemite Valley, Mariposa Co.	V. Grant	8610

According to Flory (op. cit.), who studied somatic divisions in root tips, five pairs of chromosomes in *G. c. capitata* have median centromeres and four have subterminal centromeres. The chromosomes range in length from over 6μ to 3.5μ.

Meiosis in the F_1 Hybrids

Numerous clear figures were seen at metaphase I with regular pairing; numerous clear anaphases were seen with no bridges (Fig. 16). No micronuclei were found at telophase I or II. A pair of univalents was observed in several preparations. An F_1 hybrid of *G. c. staminea* ♀ × *G. c. Chamissonis* with 35% good pollen was selected for detailed study at metaphase and later stages. The first metaphase in this hybrid is shown in Fig. 16f. Twenty-eight cells were counted at anaphase I, all of them showing 9-9 segregations. Of 67 cells at telophase I, 66 had no laggards or micronuclei, and only one had a possible laggard. Thirty-four quartets at telophase II showed no micronuclei, while four additional quartets possessed one or two blebs which might be interpreted as micronuclei.

The Cause of Pollen Abortion

The stage of pollen abortion was determined in both the above relatively sterile hybrid individual of *G. c. staminea* ♀ × *G. c. Chamissonis,* and in an equally sterile F_1 of *G. c. staminea* ♀ × *G. c. tomentosa.* The microspores developed normally out of the tetrads while the anther enlarged from 0.9 mm. long (*G. c. staminea* ♀ × *G. c. Chamissonis)* to 1.9 mm. long. At the latter stage, with the anthers enveloped in the still colorless floral bud, a differentiation began to appear between full and shriveled pollen grains. The good grains were binucleate, whereas the abortive grains remained uninucleate. The first postmeiotic mitosis was not itself observed, but the circumstantial evidence suggests that pollen abortion begins at that first critical hurdle in the development of the male gametophyte.

From what has previously been stated with regard to the course of meiosis in the most sterile F_1s, it is obvious that no gross structural rearrangements of the chromosomes or irregularities of meiosis exist which could account for the observed proportion of abortive pollen. On the other hand, several possible invisible situations, subsumed by the term cryptic structural hybridity (Stebbins, 1945), can be imagined which would lead by independent assortment to the production of microspores deficient for small segments necessary for normal development. Such deficient spores would be particularly likely to fall out the moment they undertook to perform their first complicated function, namely nuclear division. It is, of course, possible that the male sterility of the hybrids of *Gilia capitata* is brought about by the action of genes as well as of segments of chromosomes. Only future research can reveal whether it is necessary to postulate also a complementary effect of the cytoplasm in order to explain the reciprocal differences in pollen sterility.

7. FACTORIAL ANALYSIS

Hybrid Vigor

All F_1s, except *G. c. tomentosa* ♀ × *G. c. staminea* and *G. c. Chamissonis,* exhibited the phenomenon of heterosis. This phenomenon was manifested in several ways: the F_1 hybrids produced more growth of the vegetative parts than the parents; and the duration of the flowering season was about six weeks longer in the F_1s than in the parents. It has been noted elsewhere (Grant, 1949b) that the germination percentage of the F_1 seeds was greater than the mean of their parents. Hybrid vigor was not evident in the F_2 generation. It was conspicuously apparent again, however, in the B_1 generations of *G. c. capitata* and *G. c. Chamissonis.* Two inbred lines of *G. c. staminea,* derived by selfing of two individuals (cf. ch. 5), have been carried to the third generation with some depression in vigor.

The Intermediacy of the F_1s

With respect to most of their characters, such as growth habit, leaf shape, earliness, flower color, dimensions of floral parts, etc., the F_1 hybrids are intermediate between the parental entities. Illustrations of leaf and corolla bring out the intermediacy of the F_1s in these characters (Figs. 17-18). The average

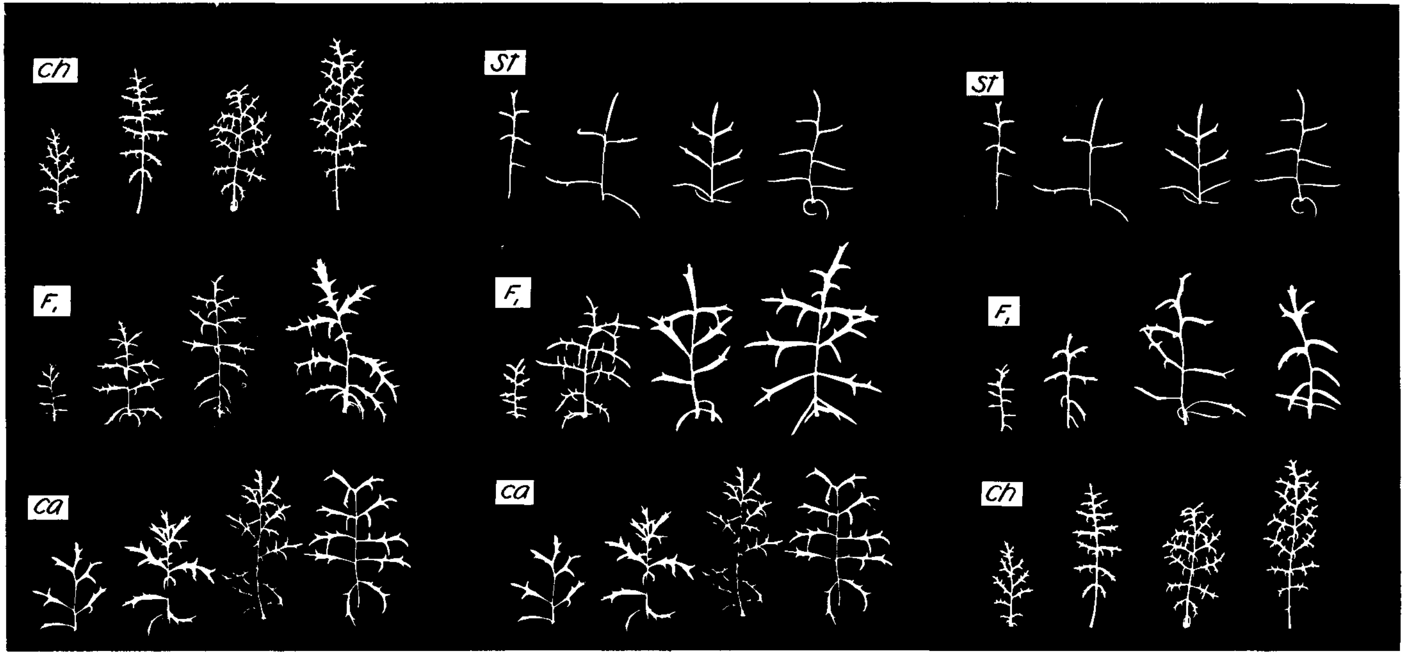


Fig. 17. Silhouettes of basal leaves of three subspecies of *Gilia capitata* and their F_1 hybrids. The subspecies are *G. c. capitata*, Mayacama Mts. (ca); *G. c. Chamissonis*, Pt. Reyes (ch); and *G. c. staminea*, Antioch (st). The four leaves represented in each strain are from four sister plants grown in Berkeley from the same seed parent.

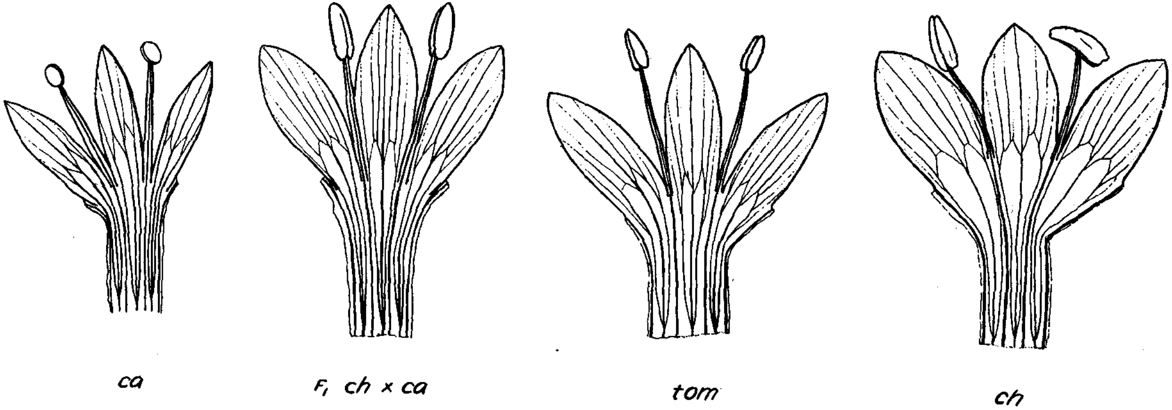


Fig. 18. A portion of the corolla and androecium in several members of *Gilia capitata*. Left: *G. c. capitata*, Mayacama Mts. (ca). Right: *G. c. Chamissonis*, Pt. Reyes (ch). Center: F_1 *G. c. Chamissonis* × *G. c. capitata;* and *G. c. tomentosa*, Tomales Bay (tom). (× 4.)

number of seeds per capsule for about twenty capsules on about ten individual plants is given in Table 12. This table reveals that the number of seeds per capsule is intermediate in most of the F_1 hybrids except *G. c. Chamissonis* × *G. c. staminea.* In the latter hybrid the possible influence of pollen or ovule sterility is evident in a seed number lower than expectation. Reciprocal differences in morphological characters, with the possible exception of this special case of seed set, were not found.

Segregation

Stem pubescence.—Floccose-stemmed individuals of *G. c. capitata* were crossed with glandular-stemmed individuals of *G. c. Chamissonis.* Their F_1 had glands on the stem. The F_2 segregated as follows: 172 individuals with glandular stems: 43 individuals with floccose stems. The author must confess that he is somewhat embarassed to have to report such an unusually close agreement with a 3:1 ratio! That the situation is not entirely simple, however, is indicated by two other F_2 populations. Floccose-stemmed *G. c. tomentosa* crossed with glandular-stemmed *G. c. Chamissonis* and *G. c. staminea* gave in the F_1 glandular-stemmed individuals, as in the cross *G. c. capitata* × *G. c. Chamissonis.* In F_2 *G. c. tomentosa* × *G. c. staminea,* however, there were: 33 glandular individuals: 17 floccose individuals: 4 individuals with both glands and floccose hairs on the stem. Similarly in F_2 *G. c. tomentosa* × *G. c. Chamissionis* there were 33 glandular individuals: 15 floccose individuals: 6 individuals both glandular and floccose.

A certain amount of lethality was present in the aforementioned two F_2s of *G. c. tomentos*a (cf. ch. 5). There is no reason to assume that the lethal factors are not distributed at random with respect to the genes for stem pubescence. The eleven inviable individuals in the F_2 of *G. c. tomentosa* × *G. c. Chamissonis,* if their genotype for stem pubescence were known, might tip the actual ratio in any one of several directions; one cannot help but note, however, that if a linkage existed between the genes for lethality and those for glandulosity, an approximately 3:1 ratio would have been obtained in the F_2s of *G. c. tomentosa* with *G. c. Chamissonis* and *G. c. staminea,* as was observed in the F_2 of *G. c. capitata* × *G. c. Chamissonis.*

The existence of different degrees of glandulosity and floccosity in both of the foregoing F_2 populations suggests that more genes than one are segregating for stem pubescence. The existence of a certain proportion of recombination types in the form of individuals with both types of stem pubescence probably points toward the same conclusion. To judge from the phenotypes of both the parents and the hybrids, the radius of action of the gene for floccose hairs tends to be in the lower part of the stem, while the effect of the gene for glandular hairs is more intensely expressed on the upper part of the stem. It seems possible that in a uniformly short-stemmed F_2 from short-stemmed parents, such as the F_2 *G. c. tomentosa* × *G. c. Chamissonis,* the radius of action of the respective genes may overlap. Such an overlap in gene action might have some bearing on the occurrence of recombination types.

It is probable, in conclusion, that the difference between glandular hairs and floccose hairs on the stem is essentially a difference in the action of two alleles of a single gene. Other genes, which govern the nature of pubescence in other parts of the plant, may well influence the expression of the genes for stem pubescence. What other genetic factors are involved in this character is not known.

Earliness.—*G. c. staminea* flowers within 83-97 days after germination in Berkeley, whereas *G. c. Chamissonis and G. c. tomentosa* flower within 128-142 days. The F_1 hybrids between the early and late races flower in 112-118 days. The relatively small range for the F_1 hybrids shows that they are more uniform than the parental strains in time of flowering. The flowering time in an F_2 population of 212 individuals of *G. c. staminea* × *G. c. Chamissonis* stretched out over a period of 44 days, which nearly bridged the extremes between the parental types. Five individuals flowered after a growth period of 89 to 92 days; another 20 individuals flowered after 129 to 132 days; a large proportion of the individuals, numbering 161 in all, flowered in an intermediate period of 105 to 116 days; and the remaining 26 individuals ranged in their flowering time between the extreme and intermediate classes. An essentially similar though less complete picture was presented by the 54 individuals grown in F_2 *G. c. staminea* × *G. c. tomentosa.*

One would expect, on the basis of a binomial distribution, to recover both parental types in 2/16 of the individuals of an F_2 population segregating for two genes of equal and additive effect; in 2/64 of the F_2 individuals segregating for three such genes; and in 2/256 of the F_2 individuals segregating for four polymeric genes. The recovery of the parental types in 2/17 of the F_2 individuals in the present instance suggests that the difference in flowering time between *G. c. Chamissonis* and *G. c. staminea* may be due to a difference in about two genes of approximately equal effect.

Leaf dissection.—The lower cauline leaves are unipinnate in *G. c. staminea,* bipinnate in *G. c. Chamissonis,* and slightly bipinnate or intermediate in the F_1 (Fig. 17). A classification of 208 individuals of the F_2 generation into parental and intermediate types gave the following results: 76 bipinnate: 85 intermediate: 47 unipinnate. In the F_1s of *G. c. staminea* × *G. c. capitata* and *G. c. tomentosa,* on the other hand, the bipinnate condition exhibits a small degree of dominance (Fig. 17). A relatively high proportion of bipinnate leaves are recovered in the F_2 generation. The ratio in F_2 *G. c. staminea* × *G. c. capitata* is: 31 bipinnate: 10 intermediate: 3 unipinnate; and in F_2 *G. c. staminea* × *G. c. tomentosa:* 33 bipinnate: 11 intermediate: 6 unipinnate.

These results indicate that the degree of dissection of the leaves in *Gilia capitata* is determined by a small number of genes. The alleles for the bipinnate condition are in general dominant over the alleles for unipinnate leaves. This dominance of the bipinnate condition is, moreover, much greater in *G. c. capitata* and *G. c. tomentosa* when crossed with *G. c. staminea* than it is in *G. c. Chamissonis* crossed with that entity.

Corolla lobe width.—The corolla lobe is about 1 mm. wide in *G. c. capitata,* about 3 mm. wide in *G. c. Chamissonis,* and intermediate in the F_1 hybrid (Fig. 18). In the F_2 generation, as shown in Table 13, the distribution of corolla

Table 13. Frequency distribution of corolla lobe widths in F_2 and B_1 of *G. c. capitata* (ca) x *G. c. Chamissonis* (ch).

	Width of corolla lobe, mm.																						N
	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	2.1	2.2	2.3	2.4	2.5	2.6	2.7	2.8	2.9	3.0	
P ca	+	+																					
P ch																					+	+	
F_1											+	+											
F_2		1		3	3	9	13	11	23	20	36	21	11	12	7	6	2	2	1	3			184
B_1 (ca x ch) x ca		2	2	1	2	1	4			1	3												16
B_1 (ca x ch) x ch												1		1		1			1		3	1	8

Table 14. Frequency distribution of stigma lengths in F_2 and B_1 of *G. c. capitata* (ca) x *G. c. Chamissonis* (ch).

	Length of stigma, mm.													N
	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	
P ca	+	+												
P ch												+	+	
F_1				+	+									
F_2			1	11	43	57	33	24	3	2	1		1	176
B_1 (ca x ch) x ca	1	3	9	1	1	1	1							17
B_1 (ca x ch) x ch					3	1	3			1	1			9

lobe widths approaches a normal frequency distribution. The two reciprocal backcrosses show little or no overlap in range. A pure parental type is recovered only once in 184 individuals in F_2, but in the frequency of 1 in 8 in B_1 (*G. c. capitata* × *G. c. Chamissonis)* × *G. c. capitata*. The results presented in Table 13 suggest that the difference in the width of the corolla lobes between *G. c. capitata* and *G. c. Chamissonis* is a difference determined by about four genes of approximately equal action.

Stigma length.—The F_2 between *G. c. capitata* with short stigmas and *G. c. Chamissonis* with long stigmas segregates for stigma length, as shown in Table 14. The recovery of one parental type in 176 individuals in F_2 indicates, as in the case of corolla lobe width, that the number of segregating genes cannot be less than three, or more than five, and is probably about four. The inheritance of stigma length differs in one important respect, however, from the inheritance of corolla lobe size. The F_1 between a race with short stigmas and one with long stigmas is not intermediate, but approaches the former parent. The distribution of stigma lengths in F_2 is similarly skewed in the direction of short stigmas (cf. Table 14). The distribution of types in B_1 *(G. c. capitata* × *G. c. Chamissonis)* × *G. c. Chamissonis,* furthermore, is skewed so as to extend into the range of the reciprocal backcross types. A possible explanation of these results is that of the approximately four genes controlling stigma length in *Gilia capitata,* one is a major gene exhibiting dominance, and the others are modifier genes of equal effect.

Calyx pubescence.—The calyx of *G. c. capitata* is glabrous, while that of *G. c. Chamissonis* and *G. c. tomentosa* is very floccose. The F_1 hybrids between the glabrous and floccose races are moderately floccose. Four phenotypic classes may be recognized in the F_2 generations, as follows: very floccose (like the *G. c. Chamissonis* parent), moderately floccose (like the F_1), sparsely floccose, and glabrous (like the *G. c. capitata* parent). The actual ratios observed in 215 individuals of F_2 *G. c. capitata* × *G. c. Chamissonis* were: 45 very floccose: 100 moderately floccose: 49 sparsely floccose: 21 glabrous. A much smaller F_2 population of *G. c. capitata* × *G. c. tomentosa* gave a similar distribution: 8 very floccose: 12 moderately floccose: 4 sparsely floccose: 0 glabrous. In B_1 *(G. c. capitata* × *G. c. Chamissonis)* × *G. c. capitata* the following distribution was observed: 0 very floccose: 8 moderately floccose: 8 sparsely floccose: 2 glabrous; in the reciprocal backcross onto *G. c. Chamissonis* the ratio was: 7 very floccose: 2 moderately floccose: 0 sparsely floccose: 0 glabrous.

The fact that the F_1 between *G. c. Chamissonis* or *G. c. tomentosa* and *G. c. capitata* is not intermediate but is closer to the former parent than to the latter, indicates that the genes determining the floccose condition of the calyx exercise a partial dominance over their opposite alleles. The skewness of the distribution in F_2 and B_1 toward the floccose condition is in agreement with this conclusion. The high proportion of pure parental types recovered in F_2, about 2/6, indicates that the number of genes cannot be much greater than two.

Capsule dehiscence.—In *G. c. capitata* the capsule is indehiscent; in *G. c. Chamissonis* and *G. c. staminea* it is fully dehiscent; and in the F_1s it is indehiscent. Segregation in F_2 gives the following distribution of types: in F_2 *G. c.*

TABLE 15. Correlations between characters in inter-subspecific F_2 hybrids in *Gilia capitata*. r = correlation coefficient; n = size of sample; p = probability that a given value of r is due to chance alone; L = linkage probably present; O = linkage probably absent; (1) = see footnote; P = positive correlation between parental characters; N = negative correlation between parental characters.

Hybrid combination	Character pair		r	n	p	presence of linkage	direction of correlation
F_2 ca x ch	Stem pubescence	Calyx pubescence	+.338	215	<.01	L	P
	"	Corolla color	+.240	201	<.01	L	P
	"	Corolla lobe width	+.110	184	>.05	O	P
	"	Stigma length	+.084	176	>.05	O	P
	"	Calyx lobe reflexion	+.016	186	>.05	O	P
	"	Capsule dehiscence	+.004	157	>.05	O	P
	"	Seed size	—.061	59	>.05	O	N
	Calyx pubescence	Corolla color	+.237	201	<.01	L	P
	"	Corolla lobe width	+.072	184	>.05	O	P
	"	Stigma length	+.216	176	<.01	L	P
	"	Calyx lobe reflexion	—.065	186	>.05	O	N
	"	Capsule dehiscence	—.066	157	>.05	O	N
	"	Seed size	—.196	59	>.05	O	P
	Corolla color	Corolla lobe width	+.095	185	>.05	O	P
	"	Stigma length	+.108	174	>.05	O (1)	P
	"	Calyx lobe reflexion	+.098	174	>.05	O	P
	"	Capsule dehiscence	+.166	147	<.05	L	P
	"	Seed size	—.040	54	>.05	O	P
	Corolla lobe width	Stigma length	+.116	172	>.05	O	P
	"	Calyx lobe reflexion	+.039	159	>.05	O	P
	"	Capsule dehiscence	+.079	135	>.05	O	P
	"	Seed size	—.116	49	>.05	O	P
	Stigma length	Calyx lobe reflexion	+.167	153	<.05	L	P
	"	Capsule dehiscence	+.348	128	<.01	L	P
	"	Seed size	—.074	46	>.05	O	P

Hybrid combination	Character pair		r	n	p	presence of linkage	direction of correlation
	Calyx lobe reflexion	Capsule dehiscence	+.190	157	=.01	L	P
	"	Seed size	—.208	59	>.05	O	P
	Capsule dehiscence	Seed size	—.086	57	>.05	O	N
F_2 st x tom	Stem pubescence	Earliness	+.239	50	>.05	O (2)	P
F_2 st x ch	Earliness	Leaf dissection	—.163	208	<.05	L	N
	"	Leaf lobe shape	+.040	206	>.05	O	P
	Leaf dissection	Leaf lobe shape	+.599	208	<.01	L (3)	P

(1) Statistically significant correlation could be established with a sample about 150 individuals larger than the one studied; the internal structure of the data suggests that linkage may be present.
(2) This value of r would be statistically significant with a sample of only 70 individuals, hence the possibility of linkage cannot be ruled out.
(3) This may be due to developmental correlation rather than to linkage.

capitata × *G. c. Chamissonis*: 127 indehiscent: 19 tardily dehiscent: 9 fully dehiscent; and in F_2 *G. c. capitata* × *G. c. staminea*: 31 indehiscent: 4 tardily dehiscent: 3 fully dehiscent. A dominance of the genes determining indehiscence of the capsule is clearly indicated by these results. The recovery of the homozygous recessive type in respectively 1/17 and 1/19 of the individuals in the F_2 generations of the two crosses may mean that the difference between dehiscence and indehiscence of the capsule is due to differences in about two genes.

Seed size.—This quantitative character was measured in terms of the weight in milligrams of ten seeds on each individual plant. The seeds of the *G. c. capitata* parent have an average weight of 0.8 mg. per seed; those of *G. c. Chamissonis* 0.2 mg., and the F_1 0.5 mg. The measurements on 59 individuals in F_2 reveal a segregation for seed size with a peak in the intermediate values and a recovery of 6 parental types in all. It seems probable from these results that the differences in seed size between *G. c. capitata* and *G. c. Chamissonis* can be resolved into differences in two or possibly three genes. Since the size of the seeds is inversely correlated with the number of seeds per capsule, it is probable that one set of genes is responsible for both characters. The fact that the ovules are about equally numerous and equally large in both parents, and that the differences appear largely in the fruiting stage, raises some interesting questions concerning the time of action of the genes controlling seed size.

Growth habit.—The F_2s between the short and stocky race, *G. c. Chamissonis*, and the tall and slender races, *G. c. capitata* and *G. c. staminea*, segregate for habit of growth. The segregation differs from the previously mentioned cases, however, in that it does not yield to analysis in terms of a small number of genes. A total of 430 individuals were grown in the F_2s of parental races having opposite growth form. The tall and slender habit of one parent appeared in several individuals in these F_2 populations. The short and stocky form of the *G. c. Chamissonis* parent, however, was not recovered in the F_2s. These facts suggest that growth habit is determined by more than four, and perhaps by many, genes. It is of interest to note that the F_2 between two short and stocky races, *G. c. Chamissonis* and *G. c. tomentosa,* did not segregate for growth form.

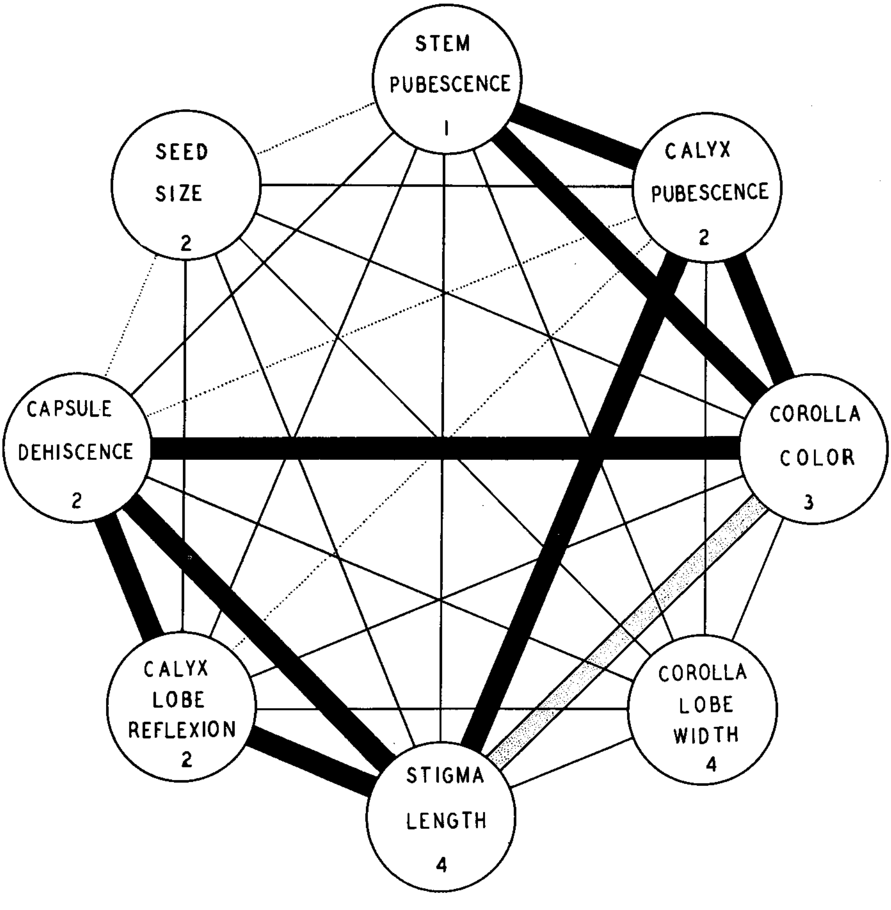


Fig. 19. Diagram of linkage between characters segregating in F_2 *G. c. capitata* × *G. c. Chamissonis*. The solid bands indicate statistically significant correlation; the stippled band indicates nearly significant correlation; the solid lines show positive but insignificant correlation between parental characters; the dotted lines show negative insignificant correlation between the parental characters. The estimated minimum number of genes segregating for each character is shown at the bottom of the circle.

Linkage

The F_2 between *G. c. capitata* and *G. c. Chamissonis* segregates for at least twenty morphological characters. It proved feasible in practise to measure and study the correlations between eight of these characters, paired in various combinations, in a sample totalling 215 individuals. Supplementary results were obtained for three characters in a sample of 215 individuals of F_2 *G. c. staminea* × *G. c. Chamissonis,* and for two characters in 54 individuals of F_2 *G. c. staminea* × *G. c. tomentosa.* Since the eight segregating characters in the F_2 *G. c. capitata* × *G. c. Chamissonis* are, in the aggregate, determined by differences in about twenty genes, and since these genes are borne on but nine chromosomes, one would expect to find linkage.

The results of the computations of correlations between the different pairs of characters are summarized in Table 15. The first thing to be noted in this table is that evidence of linkage between various pairs of characters does indeed exist. Only two among the eleven characters studied, namely corolla lobe width and seed size, failed to show some linkage.

TABLE 16. Linkage groups in *Gilia capitata.*

Chromosome:								
I	II	III	IV	V	VI	VII	VIII	IX
Stem pubescence								
Calyx pubescence *1	Calyx pubescence *2							
Corolla color *1	Corolla color *2	Corolla color *3						
	Stigma length *1	Stigma length *2	Stigma length *3					
		Capsule dehiscence *1	Capsule dehiscence *2					
			Calyx reflexion *1					
Earliness *1 (?)					Corolla lobe width		Seed size	

The strength of the linkages between the remaining nine characters, as inferred from the absolute magnitude of the correlation coefficients where 1 = perfect correlation and 0 = no correlation, is in no case very great. The highest correlation coefficient listed in Table 15 is that between the dissection and the reflexion of the leaf lobes (r = +.60). There is no basis for deciding at present to what extent this correlation between two leaf characters may be a purely developmental phenomenon due to an effect caused by a single gene, and to what extent it may be due to linkage of different genes. The remaining statistically significant values of r in Table 15 range in magnitude from .35 down to .16.

Characters which are linked together may be independently linked to other characters. The picture which emerges from the data of Table 15 is one of an interlocking system of weak linkages (Fig. 19). The principal elements in this system are twofold: first, the multiple factors responsible for one character difference are located on different chromosomes, and are consequently assorted independently of one another; and secondly, they are linked independently of one another with the multiple factors responsible for various other character differences. This system of linkage can be visualized in the concrete with the aid of Fig. 19 and Table 16, which are a systematization of the data of Table 15.

The direction of linkage is in all cases except one, earliness vs. leaf dissection, toward the parental combination of characters. This is what one would expect on the assumption that the alleles which are linked together in each parental type have been established in the racial germ plasm during a long period of evolution. One might also expect on the basis of chance that the statistically insignificant correlation coefficients, as determined by the null hypothesis at the 5% level, would bear algebraic signs at random with respect to the parental combination of characters. An examination of Table 15 will reveal that this expectation is by no means fulfilled. The sign of r points in the direction of linkage of the parental characters in eighteen of the twenty-two insignificant correlation coefficients listed in this table. That this result could come about by chance alone is so improbable as to require no serious consideration*. This points to the conclusion that with a larger sampling of the F_2 a greater proportion of character pairs would show significant correlations than are shown by the present data.

The Taxonomic Significance of the Artificial Hybrids

The hybrid indices, used in chapter 3 to provide a numerical expression for the similarities and dissimilarities between the primary races of *Gilia capitata* and the types intermediate between them, measure differences due to at least 21 genes in the comparison of *G. c. capitata* and *G. c. Chamissonis* (Table 3), and at least 14 genes in the comparison of *G. c. capitata* and *G. c. staminea* (Table 4). The pie diagrams which were constructed from the hybrid indices and plotted on maps (Figs. 5-7) reveal differences between populations ranging from 0 to at least 21 or 14 genes for the characters scored. The inference drawn from the geographical distribution of the morphologically intermediate types was that their similarities with both extreme types are due to their possession of a mixture of genes from the two primary races. The study of the artificial F_2 populations should be of interest in connection with the hypothesis of the hybrid derivation of the morphologically intermediate types.

In F_2 *G. c. capitata* × *G. c. Chamissonis* several individuals were obtained which match existing types of *G. c. pacifica*. The B_1 *(G. c. capitata* × *G. c. Chamissonis)* × *G. c. Chamissonis* included individuals which are similar to

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*$\chi^2 = 8.9$; 1 degree of freedom; $p < .01$.

the introgressive type of *G. c. Chamissonis* in the area from Tomales Bay to Bodega Bay (Fig. 6). The B_1 *(G. c. capitata* × *G. c. Chamissonis)* × *G. c. capitata* yielded some individuals similar to the introgressive type of *G. c. capitata* in the north coast line from Mendocino County, California, to southern Oregon, as well as other individuals indistinguishable from pure *G. c. capitata.* In the F_2 between *G. c. capitata* and *G. c. staminea* some individuals were found which match *G. c. pedemontana.*

Although the characters of *G. c. tomentosa* were synthesized individually in the F_2 *G. c. capitata* × *G. c. Chamissonis* (cf. Fig. 18), they were not recombined in any one plant. The multifactorial basis of growth form is probably one of the chief obstacles in the synthesis of *G. c. tomentosa* out of its putative parental materials. This difficulty might of course be overcome by the application of more refined methods of plant breeding than have been employed to date. Such methods would almost inevitably require a combination of repeated hybridization and artificial selection. The synthesis of an artificial *G. c. tomentosa,* like the origin of the naturally occurring race, would probably be possible only by a selection of gene recombinations. Whereas *G. c. pacifica* represents a series of more or less simple recombination types of *G. c. capitata* and *G. c. Chamissonis,* and is readily recovered in a fairly small F_2 population, *G. c. tomentosa* is apparently a more highly selected line and does not appear in the F_2 generation.

The parental ensemble of characters was as a rule never recovered in F_2. The only exception to this rule was the occurrence of several individuals resembling *G. c. staminea* in the F_2 of *G. c. Chamissonis* × *G. c. staminea.* This latter cross, however, segregated relatively little and only for the characters which differentiate the parental races. This evidence indicates that the morphological similarities between *G. c. Chamissonis* and *G. c. staminea* are the result, not of convergent evolution, but of close affinity due to former gene exchange.

8. EVOLUTION

The purpose of the present chapter is to consider the evolutionary processes and steps by which the members of *Gilia capitata* have come to possess their present characters and distributions.

Adaptation

The ultimate source of new organic characteristics presumably lies in the process of mutation (Dobzhansky, 1941). If the term mutation is conceived in the broadest possible sense, the assertion will perhaps be acceptable to most modern students of evolution, or at least to neo-Darwinists. But how long is the time lag between the event of a mutation and its expression in a group of organisms? In a diploid, sexually reproducing, extensively panmictic organism (such as *Gilia capitata*) the establishment of a new mutation may be more or less immediate or it may be postponed for many generations. The passage from "the chemical level of mutation to the biological level of adaptation" (Darlington, 1939) will be immediate when the new mutation is immediately and intrinsically favorable and can thus come under the direct influence of natural selection. It will be delayed if the new mutation is of itself adaptively neutral and favorable to its possessor only in combination with other mutations or under other environmental circumstances.

The recombination of different mutations which are adaptively neutral when taken singly but which improve the efficiency of the organism in their harmonious action as a collective whole, together with the storage of those mutations for future reference, constitutes the great biological role of sexual reproduction. Sex in combination with diploidy has permitted organic populations to maintain a storehouse of variability, where new mutations may be stored and grow old before they are put to use. The gene causing the stems of *Gilia capitata capitata* to be floccose is at least old enough to have become widely dispersed throughout large areas of the Coast Ranges and Cascade Mountains without, however, having attained "the biological level of adaptation." But that mutation, which is shifting and infrequent in the Mayacama and Hatchet Mountain populations of *G. c. capitata,* has become established in the pure and homozygous condition in populations closer to the coast. Evidently, under certain circumstances, the provision of old mutations is drawn upon. Sexual reproduction is the key to the storehouse of variability; it enables organisms to get at old mutations and in many cases spares them the bother of making new ones.

The foregoing statement is not controverted by the fact that certain genes may habitually mutate in a certain way, so that their individual possessors may arrive independently of one another at the same condition. For, if parallel mutation had been an efficacious source of variability in the history of living organisms, sex and diploidy might not have arisen. It follows that the possession on the part of distinct individuals of the same mutation, or of its phenotypic expression, is in the great majority of cases presumptive evidence of common descent. The occurrence of the gene for floccose hairs on the stem in populations of *G. c. capitata* as far apart as the interior and the maritime Coast Ranges might, of course, be the result of exceptional parallel mutation. But that is improbable. The improbability of the parallel development of the same phenotype in independent lines, moreover, increases with the number of mutations involved. This is the theoretical basis for the conclusion that morphological characters which are known to be governed by many genes cannot as a rule be shared by different individuals in any other way than through sexual reproduction.

In the species complex to which *Gilia capitata* belongs the failure of genetic isolating barriers has led to sexual reproduction not only between individuals of the same kind, but also between individuals belonging to different systematic categories. Hybridization, which represents a vast extension of the possibilities of sexual reproduction, by opening up the storehouse of old mutations to members of distinct subspecies or species, has played a major role in the diversification of the *Gilia capitata* complex. The reproductive structure of that complex, with its decentralization of the stores of variability into partially isolated geographic units, has permitted opposing subspecies to differ from one another by many characters, and yet to share some of the genes controlling the blocks of characters by which they differ. *Gilia capitata pedemontana,* for instance, has the oval corolla lobes of *G. c. staminea,* but they resemble those of *G. c. capitata* in being narrow, and numerous other examples could be mentioned.

Has *G. c. pedemontana,* in drawing upon the genic supplies of *G. c. staminea* and *G. c. capitata,* been guided by natural selection, so that old mutations in each parental stock have only reached the biological level of adaptation in the inter-subspecific hybrid? Or has the peculiar constellation of characters of *G. c. pedemontana* been arrived at by the introgression of genes without the guidance of natural selection? We cannot form an accurate opinion about the adaptive value of particular characters by merely scrutinizing them. We are left, therefore, with two alternatives: speculation, or the more laborious project of a selection experiment. Of the two methods of inquiry only the former affords any hope at the present moment. In the opinion of the author both processes, selection and fortuitous introgression, have been at work in molding the subspecies of *Gilia capitata.*

In our example of *G. c. pedemontana* it is difficult to see any other factor than introgression in the production of corolla lobes of intermediate width and stigmas of intermediate length, etc. On the other hand, the acquisition by *G. c. pedemontana* of physiological properties enabling it to grow on rocky hillsides, a characteristic habitat of *G. c. capitata,* probably represents a case of the recombination of the morphological characters of one entity with the ecological characters of the other under the directing influence of natural selection. Again, with *G. c. tomentosa,* the tardily dehiscent capsules bear more the aspect of the loss of an adaptation than of the gain of a new one, since they are intermediate in character; but the short and stocky growth form, shared with *G. c. Chamissonis,* suggests an adaptive response to a maritime habitat.

In summary, hybridization between subspecies is just an extension on the grand scale of combination and recombination within populations (cf. also Stebbins, 1950, ch. 7). It occurs originally without reference to natural selection. Yet it increases enormously the field of operation of natural selection.

Hybridization

The structure of the ecospecies *Gilia capitata* differs from that of many polytypic species in that the geographical races do not here blend into one another gradually, but the transition is accomplished in a series of discrete morphological and geographical stages. Where certain of the subspecies, for example *G. c. capitata* and *G. c. staminea,* or *G. c. capitata* and *G. c. Chamissonis,* meet they not only intergrade, but they hybridize. The great diversity of types produced by *G. c. capitata* and *G. c. Chamissonis* along the northern coast of California, and called for purposes of classification *G. c. pacifica,* is no mere intergradation. The development of backcross races of both *G. c. staminea* and *G. c. capitata* in the Sierra Nevada is not simple intergradation; it is introgressive hybridization, which would be superfluous in the absence of some form of reproductive isolation between the original parental types.

Let us consider the evidence bearing upon this conclusion. Of the subspecies of *Gilia capitata* supposed to be of introgressive origin, *G. c. tomentosa* is the best known genetically. A consideration of the arguments for and against the occurrence of introgression from *G. c. Chamissonis* into *G. c. tomentosa* may prove instructive.

The author was first led to the hypothesis that *G. c. tomentosa* is an introgressive hybrid of *G. c. capitata* with *G. c. Chamissonis* by the discovery of a plant of the general characters of *G. c. capitata* in the geographical range of *G. c. Chamissonis,* and by the observation of similarities in their phenotypes which almost demanded that they share some of the same genes. The morphological differences between *G. c. tomentosa* and *G. c. Chamissonis,* moreover, were largely the differences between *G. c. capitata* and *G. c. Chamissonis.* The close proximity of certain colonies of *G. c. Chamissonis* and *G. c. tomentosa* made the circumstantial evidence very compelling.

Certain valid objection might, however, be raised against the original hypothesis. The progeny test described in an earlier chapter, for example, failed to establish greater variability in *G. c. tomentosa* than in its putative parents. Furthermore, the marker gene "gland" from *G. c. Chamissonis* has not been found in natural populations of *G. c. tomentosa.* There is, finally, the incompatibility of *G. c. tomentosa* with *G. c. Chamissonis.*

But let us examine the difficulties created by rejection of the hypothesis of introgression. *Gilia capitata tomentosa* is intermediate between *G. c. capitata* and *G. c. Chamissonis* in at least fourteen characters, including such imponderables as self-compatibility and seedling mortality in Berkeley. In most of its morphological characters, *G. c. tomentosa* tends to approach *G. c. capitata* more than *G. c. Chamissonis.* In its breeding behavior with *G. c. staminea,* however, it reacts like *G. c. Chamissonis.* The fruit and seed characters of *G. c. tomentosa* can be explained with the greatest degree of probability by assuming that they are the product of genes of *G. c. capitata* in interaction with genes from *G. c. Chamissonis;* quite similar fruit and seed characters were, in fact, synthesized in the artificial F_2 of *G. c. capitata* and *G. c. Chamissonis.* Gene exchange would seem to be established by these facts.

The difficulties of the hypothesis of introgression will perhaps be removed by setting the date of introgression in the geological past. The hypothesis is thereby liberated from the corollary assumption that the introgressive populations should exhibit greater variability than the parental types. *Gilia capitata tomentosa* is a stabilized intermediate. It is stabilized both because it is old (cf. ch. 3), and because the selective pressures are relatively strong in its maritime habitat (cf. ch. 4). The absence of glandular stems in *G. c. tomentosa* may be due to the effects of natural selection in the later history of this subspecies. The cline exhibited by populations of *G. c. capitata,* in which the gene frequency of "gland" decreases from the interior toward the coast (cf. ch. 4) does suggest a selective discrimination against glandular stems or some other character linked with them in the maritime Coast Ranges. The slight incompatibility of *G. c. tomentosa* with *G. c. Chamissonis,* finally, constitutes no barrier to introgression at all, since the natural hybrid would have to be formed only a few times.

Factors in the Evolutionary History of GILIA CAPITATA

One of the major factors in the evolution of the *Gilia capitata* complex has probably been the ecological opportunity of hybrid types to develop (Epling, 1947; Anderson, 1948). This is particularly so in those cases, apparently not rare in the cenospecies to which *Gilia capitata* belongs, where the reproductive isolation of different systematic groups has been due to ecogeographic factors rather than to hybrid sterility or incompatibility. Orogenic and climatic changes accomplish the breakdown of the ecogeographic barriers in certain regions, permitting the flow of genes from one species or subspecies into another. Sexual reproduction on the grand scale leads to the production of diverse new types, some of which prove successful in the colonization of the diverse new habitats.

Let us suppose that *G. c. capitata* existed in late Tertiary time in the northern Coast Ranges, then an archipelago, and in the Cascade Mountains. Let us suppose, further, that in the same epoch *G. c. Chamissonis* was present on the Pacific strand and that *G. c. staminea* occurred on the strand of the Pliocene sea.

The uplift of the San Joaquin Valley in Pliocene and Pleistocene time exposed a sandy plain suitable for the maximum development of *G. c. staminea,* and there its center of distribution lies today. But *G. c. staminea* has never been found in the adjacent Sacramento Valley. In attempting to explain this fact, it may be pertinent to recall that the northern branch of the Great Valley of California has had a very different geological history from the San Joaquin Valley. The last marine transgression in the Sacramento Valley was during the Cretaceous period (Reed, 1933). The exposure of the Sacramento Valley to colonization by land plants thus probably occurred in a geological period long before *G. c. staminea* was in a position to exploit it. This historical situation is reflected in the generally more mature soil and vegetation of the Sacramento Valley, in comparison with the loose sands and pioneering annuals of the San Joaquin Valley.

The ecogeographic isolation of *G. c. staminea* and *G. c. capitata* in the California Coast Ranges has been maintained to the present day. In the Sierra Nevada, however, the isolation of those two entities has broken down on a large scale. It may be that the great Pleistocene uplift of the Sierra Nevada brought about the intermingling of *G. c. capitata,* as a microthermal immigrant from the Cascade Mountains on the higher slopes, with *G. c. staminea,* persisting since the Pliocene on the lower plains. The shorter growing season in the Sierra Nevada caused the flowering times of the two entities to overlap, by stimulating phenotypic or genotypic changes or both, and so abolished the seasonal isolation which still prevails in the Coast Ranges. Sexual reproduction on the level of subspecies or species thereupon led to the production of new recombination types, some of which were well fitted to survive on the flanks of a rapidly changing range of mountains.

The breakdown of ecogeographic isolation between *G. c. Chamissonis* and *G. c. capitata* along the California coast may have been a consequence of the uplift of the coastal plain or of other orogenic changes in that region during the Pleistocene epoch. The resulting hybridization between the two entities has led to an incomplete mixture of their respective germ plasms, however, and *G. c. pacifica* comprises more than one morphological type (due in part, it must be added, to apparent introgression from *G. millefoliata*). Introgression of *G. c. Chamissonis* into *G. c. capitata,* to give rise to *G. c. tomentosa* in the area north of San Francisco Bay, may also have occurred during the Pleistocene epoch. Subsequent to this introgression, at any rate, *G. c. tomentosa* was able to extend its range over an area from Marin and Sonoma counties to Mount Diablo.

An hypothesis of the evolutionary history of a group of organisms is usually unverifiable. This circumstance constitutes a serious limitation in most discussions of phylogeny. The probable accuracy of a phylogenetic hypothesis may be greatly increased, however, by the application of certain methods of species genetics. One such method, the analysis of genomes, has hitherto been used with some success in tracing phylogenies in groups, the constituent entities of which differ by numerical or structural changes of the chomosomes. Another method, which apparently has not been exploited as yet, may be the genetic investigation, not only of a given species, but also of its associates.

For example, one or another representative of the *Phacelia distans* complex frequently grows in association with *G. c. staminea* in the San Joaquin Valley, with *G. c. Chamissonis* from San Francisco to Bodega Bay, with *G. achilleaefolia* in Santa Barbara and San Luis Obispo counties, and sometimes with *G. c. capitata* in the Coast Ranges. Other species of *Phacelia* are frequently found with *Gilia* in other parts of their respective ranges. This close association of the two genera in nature today suggests that they may have paralleled one another in their migrations and evolution. To the extent that this is true, conclusions about relationships in one genus may be checked against evidence concerning the other genus. The species genetics of the members of a flora, as well as of the members of a genus, may prove capable of strengthening many phylogenetic hypotheses.

9. TAXONOMY

The morphological relationships of *Gilia capitata* to the other capitate gilias are shown by means of the following key. In the taxonomic treatment which follows only *Gilia capitata* will be considered.

Key to the Capitate Gilias

Perennial or biennial herbs; Rocky Mts. and adjacent plains, west through Great Basin to the Pacific states .... *G. congesta* Hook and *G. spicata* Nutt.

Annual herbs; Pacific states
  Heads 8–25-flowered, fan-shaped; South Central Coast Ranges of California .... *G. achilleaefolia* Benth.

Heads 25–100-flowered, globose; rare in South Central Coast Ranges
  Heads 25–50-flowered; calyces sparsely floccose; pedicels 1–2 mm. long; Southern California north to southern Sierra Nevada. . . . . *G. abrotanifolia* Greene
  Heads 50–100-flowered (rarely fewer); calyces densely floccose with a nest of white hairs at base of head, or else glabrous, rarely sparsely floccose or glandular; pedicels 1 mm. long or less; central California from Sierra Nevada, San Joaquin Valley and North Central Coast Ranges north to British Columbia. . . . . *G. capitata* Sims

GILIA CAPITATA SIMS

Annual herbs, tall and slender or short and stocky; stems stipitate glandular, floccose or glabrous, simple or cymosely branched, 10–100 cm. high; basal and lower cauline leaves uni- or bipinnately dissected, 4–10 cm. long, the rachis winged, 0.2–1.1 mm. wide, the primary pinnae 5–20 mm. long, the ultimate segments somewhat falcate, 0.2–5.0 mm. wide, the upper cauline leaves smaller, 0.5–6.0 cm. long, on a short rachis, pinnate, but the 3–7 slender lobes appearing as though palmate, the axils of the leaves usually floccose; inflorescence capitate, the heads 1-several, terminal on naked peduncles 1–20 cm. long, globose, tending to proliferate, 14–40 mm. broad, 50–100-flowered, the flowers, subsessile on pedicels 1 mm. or less long, maturing in cymose order; calyx glabrous, floccose, or rarely glandular, the lobes acute or acuminate, 0.6–2.5 mm. wide at the base, 2.0–2.5 mm. long, the midrib green, the margins and sinus membrane-hyaline, blue-violet or colorless; corolla funnelform, 6–13 mm. long, the lobes oval or linear, 0.7–3.3 mm. wide, erect and approximate, pallid to deep blue-violet or white; stamens inserted in the sinuses of the corolla, exserted, the filaments 1.8–5.0 mm. long, the anthers 0.7–1.2 mm. long, dehiscing by 2 longitudinal slits, extruding masses of light-blue pollen; style exserted, 4–12 mm. long, the 3 stigmatic lobes recurving at maturity, 0.2–1.5 mm. long; capsule globose to ovoid, dehiscent to indehiscent, sometimes disarticulating on the stipe above the calyx, 1–30 seeded; seeds ovoid or ovoid-angled, 1.0–2.3 mm. long, brown, the coat verrucose, becoming gelatinous when wetted.

Range.—Central California to British Columbia and east to western Idaho; open fields or sunny hillsides, 10–7,000 ft.

Key to the Subspecies of GILIA CAPITATA

Corolla lobes linear, 0.7–2.0 mm. wide; calyx lobes acute, the tip straight or only very slightly recurved; capsule disarticulating on the stipe above the calyx; heads glabrous to densely floccose.
  Heads densely floccose at the base.
    Stems floccose; stigmas 0.5–0.6 mm. long. . . . . *2. tomentosa*
    Stems glandular; stigmas 0.6–1.0 mm. long. . . . . *4. mediomontana*

Heads glabrous or sparsely floccose, but not densely floccose at the base.
  Calyx sinuses blue-violet; stigmas 0.4–0.9 mm. long; corolla lobes 1.0–2.0 mm. wide; capsule 10–25-seeded . . . . *3. pacifica*
  Calyx sinuses colorless; stigmas 0.2–0.4 mm. long; corolla lobes 0.7–1.1 mm. wide; capsule 1–6– (10–) seeded . . . . *1. capitata*

Corolla lobes oval, 1.5–3.3 mm. wide; calyx lobes accuminate with a recurved tip; capsule not disarticulating; heads densely floccose.
  Capsules tardily dehiscent, 6–15-seeded; stigmas 0.6–1.0 mm. long; anthers 0.8–1.0 mm. long; corolla lobes 1.5–2.5 mm. wide; plants shallowly rooted . . . . *5. pedemontana*
  Capsules freely dehiscent, 10–25-seeded; stigmas 0.9–1.2 mm. long; anthers 1.0–1.2 mm. long; corolla lobes 2.2–3.3 mm. wide; plants with taproots.
    Corolla deep blue-violet; leaves bipinnately dissected; plants short and stocky, leafy at the base; herbage with a mephitic color . . . . *7. Chamissonis*
    Corolla light blue-violet; leaves unipinnately dissected; plants taller, not leafy at the base; herbage without a distinct odor . . . . *6. staminea*

1. **Gilia capitata** subsp. **capitata** stat. nov.

Gilia capitata Sims, Bot. Mag. **53**: t. 2698, 1826. (type seen)
G. capitata alba Orcutt, W. Amer. Sci. **7**:132, 1891.
G. pallida Heller, Muhl. **1**:43, 1904. (type seen)
G. glandulifera Heller, Muhl. **2**:114, 1906. (type seen)
G. tenuisecta Heller, Muhl. **2**:115, 1906.
G. capitata var. *trisperma* Brandegee *ex* Brand, Pflzr. 4^{250}:112, 1907.
G. capitata var. *glandulifera* Brand, Ann. Conserv. et Jardin Bot. Genève **15** & **16**:331, 1913.

Plants tall and slender, relatively shallow rooted; stem glabrous, glandular, or very slightly floccose, relatively slender, 1–3 mm. in diameter at base, simple, becoming cymosely branched in the upper third of the plant, erect, 20–80 cm. high; basal and lower cauline leaves bipinnately dissected, the rachis narrow, 0.2–1.0 mm. wide, the ultimate pinnae 1–7 mm. long, 0.2–1.0 mm. wide; heads 14–40 mm. broad; calyx glabrous, rarely glandular, or sparsely floccose, not at all accrescent, the lobes acute, 0.6–1.0 mm. wide at the base, about 2 mm. long, straight-tipped, the margins and sinus membrane colorless, or rarely tinged with blue-violet; corolla 6–8 mm. long, the lobes linear, 0.7–1.1 mm. wide, 2–4 mm. long, pallid to light blue-violet; filaments 1.8–3.8 mm. long, anthers about 0.7 mm. long; style 4.0–7.5 mm. long, stigmas 0.2–0.4 mm. long; capsule globose or subglobose, indehiscent or tardily dehiscent, disarticulating on the stipe above the calyx, 1–6- (or 10-) seeded; seeds ovoid or ovoid-angled, 1.6–2.1 mm. long.

Type.—Vicinity of Fort Vancouver, Washington, *Douglas.*

Range.—Coast Ranges from Marin County, California, to British Columbia and east to western Idaho; in open vegetation on rocky soils of well drained, sunny slopes, 500–6,000 ft. May-July.

Variation.—*Gilia capitata capitata* occurs in its extreme form in the California Coast Ranges from Napa County and interior Marin County to interior Mendocino County. In this area the subspecies is represented by plants with indehiscent capsules containing normally only one to three seeds. This would be presumably the form described by Brandegee as *Gilia capitata* var. *trisperma* from Trinity County, California, of which the type is no longer in existence. From Shasta County, California, north through Oregon and Washington, including the type locality at the mouth of the Columbia River, the capsules tend to be tardily dehiscent and to bear two or three seeds in each locule. The simplest hypothesis to account for the loss of capsule specialization in the northern branch of *G. c. capitata* is that introgression of genes has occurred from *G. c. Chamissonis* and/or *G. c. staminea,* with their primitive, dehiscent, many-seeded capsules.

The flowering heads of *G. c. capitata* are typically glabrous. A minor variant exists in Shasta County, however, in which the calyces and pedicels are glandular *(Grant 8023)*; this is the *Gilia glandulifera* of Heller. Some specimens from the neighboring county of Butte, which by their corolla characters should probably be classified as *G. c. pedemontana,* likewise exhibit a glandular calyx [*Gulick* (1929), *Austin 833,* Morrison (1932)].

The pubescence of the stem shows some geographical variation which, like that of the calyx, has been found not to be of systematic importance. *Gilia capitata capitata* is floccose in the maritime Coast Ranges in Marin and Sonoma counties, California, and is more or less glandular in the interior counties and towards the north. Two thoroughly investigated populations near the coast, one at Fairfax, Marin County, the other at Santa Rosa, Sonoma County, proved to be 100% floccose; a population in the Mayacama Mountains of Napa County was composed of both glandular and floccose individuals, with the glandular individuals constituting 68% of the total; and a fourth population, on Hatchet Mt., Shasta County, was composed of 88% of glandular individuals. All of the populations of *G. c. Chamissonis* and most of the populations of *G. c. staminea* are 100% glandular. Mass collections of *G. c. capitata* from Oregon and Washington are much to be desired. The indication that the expression of glands on the stem is due to the action of a single dominant gene suggests the following generalization. The gene for floccose hairs on the stem is floating in different populations at varying frequencies; but its frequency increases in a clinal fashion toward the maritime Coast Ranges in Marin and Sonoma counties, where it has become established in populations in the homozygous condition.

A second trend between the interior and the coast is noted in the color of the corollas, which are pallid blue-violet in the interior Coast Ranges and light blue-violet in Marin and Sonoma counties.

Specimens cited.—CALIFORNIA. Marin Co.: Bolinas Road, *Brandegee* (1907); Mt. Tamalpais, *Jepson* (1891); Ross Valley, *Eastwood* (1896); Fairfax, *Grant 8575;* Carson country, *Howell 15540, 19630, 21814;* San Rafael hills, *Howell 23126.* Sonoma Co.: Santa Rosa, *M. S. Baker 593, Grant 7960.* Napa Co.: Calistoga, *Tracy 1838;* Mt. St. Helena, *Chandler 7592, Grant 7965;* Mayacama Mts., *Grant 7985.* Lake Co.: Oat Hill Mine, *Wiggins 6718;* Williams to Bartlett Springs, *J. Clausen 1022;* Middletown, *Grant 7966.* Glenn Co.: Adler Springs, *Baker 10054.* Tehama Co.: Government Flat, *Eastwood 9819.* Mendocino Co.: Ukiah, *Bolander 3914;* Round Valley, *Goddard 618;* Hopland to Mountain House, *Heller 15336;* Laytonville, *Davy 5307;* Comptche, *Walker 393;* Mendocino Pass, *Grant 8247.* Humboldt Co.: Hupa, *Manning;* Klamath River, *Chandler 1521;* French Camp Ridge, *Tracy 13995.* Trinity Co.: Trinity Summit, *Tracy 14345, 15652;* Weaverville, *Yates 345;* Ruth, *Tracy 10238.* Siskiyou Co.: Gazelle, *Heller 8081.* Shasta Co.: Redding, *Heller 16153;* McCloud River, *Heller 13017;* Hatchet Mt., *Grant 8023.* OREGON. Klamath Co.: Swan Lake Valley, *Applegate 3637.* Jackson Co.: Siskiyou Mts., *Applegate 5503;* Ragsdale Butte, *Hitchcock 5026;* Table Mt., *Ch. Mason 1214.* Josephine Co.: Grant's Pass, *Prescott 5438.* Coos Co.: Brewster Canyon, *Peck 4820.* Douglas Co.: Riddle, *Peck 4846,* Roseburg, *Peck 4842.* Lane Co.: Willamette River, *Henderson 14527;* Linslaw, *Detling 3024;* Florence, *Peck 13521.* Marion Co.: Detroit, *Peck 1581;* Salem, *Peck 677.* Clackamas Co.: Canby, *Morrill 140.* Wheeler Co.: Shelton Park, *Peck 21553.* Baker Co.: Sumpter, *Peck 10400.* Tillamook Co.: Trask River, *Morrill 189.* Wasco Co.: Dalles, *Peck 14869.* Hood River Co.: Hood River, *Peck 2271.* Washington Co.: Cornelius Pass, *Constance 2764;* Columbia River Highway, *Mason 3520.* WASHINGTON. Wahkiakum Co.: Grays River, *St. John 8774.* Cowlitz Co.: Longview, *Meyer 616.* Clark Co.: East Mill, *English 1143;* Knapp, *St. John 9218;* Vancouver, *Thompson 908.* Skamania Co.: Stevenson, *Meyer 937;* Prindle, *Suksdorf 9114.* Klickitat Co.: Rockland, *Suksdorf 11216;* Bingen, *Thompson 11540.* Yakima Co.: Yakima, *Brandegee* (1882). Lewis Co.: Mt. Rainier National Park, *Piper 3314.* Thurston Co.: Olympia, *Heller 4040.* King Co.: Seattle, *Shumway 7141.* Whidby Island: *Gardner 205.* San Juan Island: Friday Harbor, *Peck 12821.* BRITISH COLUMBIA. Vancouver Island: Shawnigan, *Anderson 689.* IDAHO. Kootenai Co.: *Sandberg 7141.*

2. **Gilia capitata** subsp. **tomentosa** comb. nov.
Gilia achilleaefolia subsp. *Chamissonis* var. *tomentosa*
Eastwood *ex* Brand, Pflzr. 4^{250}: 111, 1907. (Type seen, see below.)

Plants short and stocky, or sometimes tall and robust, usually from a well developed taproot; stems floccose, slender or stout, 1-10 mm. in diameter at base, branching from near base, or in robust forms from the middle, 10–25 cm. high, or to 2 m. high; basal leaves bipinnately dissected, the rachis 0.3–1.0 mm. wide, the ultimate pinnae 4–7 mm. long, about 1.0 mm. wide, axils of the leaves floccose; heads 15–30 mm. broad; calyx densely floccose, slightly accrescent, the lobes acute, 1.0–1.2 mm. wide at the base, about 2.5 mm. long, the tip very slightly recurved, margins and sinus membrane colorless; corolla 7–10 mm. long, lobes linear, 1.0–1.1 mm. wide, 4 mm. long, light blue-violet; filaments 3–4 mm. long, anthers 1.0 mm. long; style 6–8 mm. long, stigmas 0.5–0.6 mm. long; capsule ovoid, tardily dehiscent, disarticulating on the stipe above the calyx, 3–10-seeded; seeds ovoid or ovoid-angled, 1.9–2.2 mm. long.

Type.—Bodega Point, Sonoma County, California, *Eastwood 4826,* June 29, 1915. Calif. Acad. Sci. The original type *(Eastwood 2)* having been destroyed in the San Francisco earthquake and fire of 1906, the above cited topotype, which Miss Eastwood has identified as the same plant (oral comm., Oct. 19, 1948), may now be designated as the type specimen.

Range.—Near the coast, Marin and Sonoma counties, California; rocky maritime bluffs and outcrops, 50–500 ft.; also on Mt. Diablo, Contra Costa County, at 3000 ft. Frequently with *Phacelia californica* Cham. May-July.

Variation.—Two distinct types of growth form are comprised under the epithet *Gilia capitata tomentosa.* The first and more abundant of these is a stocky form; but two populations have been found, in each case not more than several miles distant from the nearest stocky types, in which the plants are erect and very tall *(Grant 8593, 8596).* A possible intergrade between *G. c. tomentosa* and *G. c. capitata* has been found on a serpentine ridge near Occidental, Sonoma County *(Carter 1842; Morley 592).* In general, however, *G. c. tomentosa* is today well isolated ecologically from *G. c. capitata.*

Specimens cited.—CALIFORNIA. Marin Co.: Tomales Bay, *Schreiber 580;* Tomales, *Grant 7653, 8593.* Sonoma Co.: Bodega Bay, *Eastwood 4826, Heller 15631, Chandler 696;* Bodega, *Grant 8596;* Fort Ross, *Grant 8599.* Contra Costa Co.: Mt. Diablo, *Bowerman 2253.* Solano Co.: Vallejo, *Towle* (1886).

3. **Gilia capitata** subsp. **pacifica** subsp. nov.

Planta ampla vel tenuis; radix comparate brevis; caulis glandulosus, amplus vel tenuis, ad basim 1–5 mm. diam., infra plerumque ramosus, 25–50 cm. altus; folia inferiores bipinnatisecta, rachis 0.2–1.0 mm. lato, pinnae ultimae 3–10 mm. longae, 0.2–1.0 mm. latae; capitulum 12–40 mm. latum; calyx floccosum (non dense), vel glabrum, accrescens, lobae acutae, ad basim 1.0–1.5 mm. latae, 2.0–2.5 mm. longae, costa viridis, margo et sinus coerulei-violaçei; corolla 6–8 mm. longa, lobae lineares, 1.0–2.0 mm. latae, 3–4 mm. longae, coeruleae-violaceae vel clarae coeruleae-violaceae; filamentum 2.5–4.0 mm. longum, anthera 0.6–1.0 mm. longa; stylus 5.5–9.0 mm. longus, stigmae 0.4–0.9 mm. longae; capsula ovoidea, dehiscens facile vel lente, disarticulans in stipite supra calyce, vel non disarticulans, seminibus 10–25; semen ovoideum vel ovoideum-angulum, 1.3–2.0 mm. longum.

Plants stocky or slender, relatively shallow rooted; stems glandular, slender or stout, 1–5 mm. in diameter at base, usually branched from near base, 25–50 cm. high; basal leaves bipinnately dissected, the rachis 0.2–1.0 mm. wide, the ultimate pinnae 3–10 mm. long, 0.2–1.0 mm. wide; heads 12–40 mm. broad; calyx floccose (but not densely so), or glabrous, accrescent, the lobes acute, 1.0–1.5 mm. wide at the base, 2.0–2.5 mm. long, the midrib green, the margins and sinuses blue-violet; corolla 6–8 mm. long, the lobes linear, 1.0–2.0 mm. wide, 3–4 mm. long, blue-violet or light blue-violet; filament 2.5–4.0 mm. long, anthers 0.6–1.0 mm. long; style 5.5–9.0 mm. long, stigmas 0.4–0.9 mm. long; capsule ovoid, freely or tardily dehiscent, disarticulating on the stipe above the calyx, or not disarticulating, 10–25–seeded; seeds ovoid or ovoid-angled, 1.3–2.0 mm. long.

Type.—Ocean bluffs just south of the mouth of Navarro River, Mendocino County, California, *V. Grant 8601,* July 8, 1948. U.C. Herbarium.

Range.—Near the coast, Mendocino County, California, to Coos County, Oregon; in sandy or rocky soils on exposed hillsides, 30–1000 ft., or ascending to 4000 ft. Frequently with *Gilia millefoliata* Fisch. & Mey. May-August.

Variation.—*Gilia capitata pacifica* is a variable entity with respect to most of the characters by which its parental subspecies, *G. c. capitata* and *G. c. Chamissonis,* are distinguished. Single populations appear to be uniform in the sense that little or no segregation can be observed for the same characters of habit, flower, capsule and seeds, which differ markedly from one population to the next. The nature of variation in *G. c. pacifica,* and, in particular, the fact that it is mainly between populations and not within them, might indicate that former mass hybridization between *G. c. Chamissonis* and *G. c. capitata* has been followed by the isolation in distinct localities of different segregating lines, between which there has been relatively little subsequent gene exchange. *Gilia capitata pacifica* intergrades with *G. c. capitata* in northwestern California and southwestern Oregon, where the blue-violet markings of the calyx sinuses of the former entity penetrate to the interior and to high altitudes in the mountains.

Specimens cited.—CALIFORNIA. Mendocino Co.: Mouth of Navarro River, *Grant 8601;* s.e. of Shelter Cove, *Tracy 6319;* Fort Bragg, *Peirson 3811.* Humboldt Co.: Cape Mendocino, *Tracy 15962;* Alton, *Tracy 3672, 3756;* Bridgeville, *Parks 793;* Bear River Ridge, *Tracy 14879;* Buckspot, *Tracy 2188;* Kneeland Prairie, *Tracy 3068;* Trinidad, *Tracy 2583.* Del Norte Co.: Crescent City, *Abrams 8333.* OREGON. Curry Co.: Humbug Mt., *Radcliff* (1943); Gold Beach, *Leach* (1928). Coos Co.: Bandon, *Thompson 12794.*

4. **Gilia capitata** subsp. **mediomontana** subsp. nov.

Planta tenuis; radix comparate brevis; caulis glandulosus, rare non glandulosus, tenuis, ad basim 1–2 mm. diam., simplex, supra cymose ramosus, 15–40 cm. altus; folia inferiores uni- vel bi-pinnatisecta, rachis 0.7–1.0 mm. lata, pinnae ultimae 1–4 mm. latae; capitulum 12–25 mm. latum; calyx dense floccosum, aliquando accrescens, lobae acutae, ad basim 0.8–1.2 mm. latae, circa 2 mm. longae, mucronibus leviter recurvatis, marginibus et sinubus non pigmentibus; corolla 5–8 mm. longa, lobae lineares, 1.0–1.4 (1.8) mm. latae, 2–4 mm. longae, pallidae coeruleae-violaceae vel albae et deinde cumutantes clarae coeruleae-violaceae siccandae; filamentum 2.5–4.0 mm. longum, anthera 0.7–1.0 mm. longa; stylus 6–7 mm. longus, stigmae 0.6–1.0 mm. longae; capsula subglobosa vel ovoidea, lente dehiscens, disarticulans in stipite supra calyce, seminibus 3-10; semen ovoideum vel ovoideum-angulum, 1.6–2.3 mm. longum.

Plants slender with relatively shallow roots; stems glandular, rarely nonglandular, relatively slender, 1–2 mm. in diameter, simple, becoming cymosely branched above, 15–40 cm. high; basal and lower cauline leaves uni- or bi-pinnately dissected, the rachis 0.7–1.0 mm. wide, the ultimate pinnae 1–4 mm. wide; heads 12–25 mm. broad; calyx densely floccose, sometimes accrescent, the lobes acute, 0.8–1.2 mm. wide at the base, about 2 mm. long, tip very slightly recurved, the margins and sinuses colorless; corolla 5–8 mm. long, the lobes linear, 1.0–1.4 (1.8) mm. wide, 2–4 mm. long, pale blue-violet or white and then turning pale blue-violet on drying; filaments 2.5–4.0 mm. long, anthers 0.7–1.0 mm. long; style 6–7 mm. long, stigmas 0.6–1.0 mm. long; capsule subglobose to ovoid, tardily dehiscent, disarticulating on the stipe above the calyx, 3–10–seeded; seeds ovoid or ovoid-angled, 1.6–2.3 mm. long.

Type.—Yosemite Valley, Mariposa County, California, *L. R. Abrams 4435,* June 20, 1911. U. C. Herbarium.

Range.—Sierra Nevada of California, from Mariposa County to Plumas County; in rocky soil of sunny hillsides or open woods, 3000–7000 ft. Frequently with *Pinus ponderosa* Dougl., *Libocedrus decurrens* Torr., *Quercus Kelloggii* Newb. May-July.

Variation.—This entity represents *G. c. capitata* under the influence of *G. c. staminea* at higher elevations in the Sierra Nevada. Intergradation with *G. c. pedemontana* at lower elevations is complete. More field work will be necessary, however, to establish the connection between *G. c. mediomontana* and *G. c. capitata* in Plumas and Shasta counties.

Specimens cited.—CALIFORNIA. Mariposa Co.: Yosemite Valley, *Abrams 4435, Saunders* (1906); Wawona, *Mason 4862.* Tuolumne Co.: South Fork Tuolumne River, *Eastwood 147;* Strawberry Lake, *Wiggins 6830;* Pikes Peak, *Quick 1835;* Mather, *Mason 650, 2116, Keck 1115.* Amador Co.: Panther Creek, *Hansen 1135.* Eldorado Co.: Kyburz, *Grant 7995.* Placer Co.: American River, *Geldern* (1912); Mammoth Springs, *French 383;* Blue Canyon, *Walker 1323.* Sierra Co.: Cedar Glen, *Jones* (1920), Downieville, *Kennedy* (1909). Butte Co.: Yankee Hill, *Heller* (1937); Jarboe Pass, *Heller 15112.* Plumas Co.: Taylorsville, *Clemens* (1920); Greenville, *Clemens* (1920), *Heller 8822;* Cascade, *Grant 8579;* Camel Peak, *Grant* 8587; Lexington Hill, *Lewis 475.*

5. **Gilia capitata** subsp. **pedemontana** subsp. nov.

Planta alta; radix comparate brevis; caulis glandulosus, rare non glandulosus, comparate amplus, ad basim 2–10 mm. diam., simplex, vel supra cymose ramosus, 30–90 cm. altus; folia inferiores uni- vel bi-pinnatisecta, pinnae ultimae 1–5 mm. latae; capitulum 15–30 mm. latum; calyx dense floccosum (rare sparse floccosum vel glandulosum), accrescens, lobae acuminatae, ad basim 1.0–1.9 mm. latae, 2.5–3.0 mm. longae, mucronibus recurvatis, marginibus non pigmentibus; corolla 7–11 mm. longa, lobae ovatae, 1.5–2.5 mm. latae, 3–5 mm. longae, clare coeruleae-violaceae; filamentum 2.2–3.2 mm. longum, anthera 0.8–1.0 mm. longa; stylus 6–7 mm. longus, stigmae 0.6–1.0 mm. longae; capsula ovoidea, lente dehiscens, non disarticulans, seminibus 6–15; semen ovoidum-angulum, circa 1.5 mm. longum.

Plants tall with relatively shallow roots; stems glandular, rarely non-glandular, relatively stout, 2–10 mm. in diameter, simple, or cymosely branched above, 30–90 cm. high; basal and lower cauline leaves uni- or bi-pinnately dissected, the ultimate pinnae 1–5 mm. wide; heads 15–30 mm. broad; calyx densely floccose (rarely sparsely floccose or glandular), accrescent, the lobes acuminate, 1.0–1.9 mm. wide at the base, 2.5–3.0 mm. long, tip recurved, the margins colorless; corolla 7–11 mm. long, the lobes oval, 1.5–2.5 mm. wide, 3–5 mm. long, light blue-violet; filaments 2.2–3.2 mm. long, anthers 0.8–1.0 mm. long; style 6–7 mm. long, stigmas 0.6–1.0 mm. long; capsule ovoid, tardily dehiscent, not disarticulating, 6–15-seeded; seeds ovoid-angled, about 1.5 mm. long.

Type.—West-facing slope 1.4 miles south of North Fork of Calaveras River, on Highway 49, Calaveras County, California, *V. Grant 8498,* May 11, 1948. U. C. Herbarium.

Range.—Sierra Nevada of California, from Tulare County to Butte County; in rocky soil of sunny hillsides or open woods, 200–5000 ft. With *Pinus Sabiniana* Dougl. and *Quercus Douglasii* H. & A., or in the lower borders of the

Pinus ponderosa forest, frequently with *Gilia abrotanifolia* Greene or *G. tricolor* subsp. *diffusa* Mason & A. Grant. April-June.

Variation.—*Gilia capitata* subsp. *pedemontana* may be regarded as a branch of *G. c. staminea* in the Sierran foothills which has received characters of *G. c. capitata.* It intergrades today with *G. c. mediomontana* at higher elevations, while in the southern Sierra Nevada the occurrence of habitats suitable for it at low elevations leads to intergradation with *G. c. staminea* of the valley floor *(Parks 563, Hoover 4000, 522).* In the central Sierra Nevada *G. c. pedemontana* is relatively uniform, although there is some variation in the dimensions of the floral parts. The most evident variants of *G. c. pedemontana* occur in the northern Sierra Nevada, particularly in Butte County, where forms with sparse floccosity of heads *(Heller 13384a, Constance 2827)* or with glandular calyces [*Gulick* (1929), *Austin 833, Morrison* (1932)] exist.

Specimens cited.—CALIFORNIA. Tulare Co.: Three Rivers, *Grant 8432.* Fresno Co.: Dunlap, *Parks 563.* Mariposa Co.: Cathay, *Eastwood 4376;* Mariposa, *Grant 8529;* Mariposa to Bear Valley, *Grant 8528;* south of Coulterville, *Grant 8524;* El Portal, *Carter 587, Michael* (1922); Bear Creek Lodge, *Schreiber 823.* Tuolumne Co.: Twain Harte, *Alexander 3671.* Calaveras Co.: Copperopolis, *Davy 1356, 1397;* North Fork Calaveras River, *Grant 8498;* Mokelumne Hill, *Grant 8499.* Amador Co.: Irishtown, *Hansen 1160.* El Dorado Co.: Placerville, *Robbins 1089;* Diamond Springs, *Belshaw 819.* Sacramento Co.: Folsom, *Copeland 610.* Placer Co.: Newcastle, *Ingrim* (1933); Colfax, *Sonne* (1891); American Valley, *Lemmon* (1883); Weimar, *Grant 7970.* Nevada Co.: Grass Valley, *Mason 3281;* Nevada City, *Eastwood 610.* Butte Co.: Cresta, *Pattee* (1923).

6. **Gilia capitata** subsp. **staminea** comb. nov.

Gilia staminea Greene, Erythea **3**:105, 1895 (type examined for the author by Dr. Delisle of the Greene Herbarium.)
G. capitata var. *staminea* Brand, Pflzr. 4^{250}:111, 1907.
G. dissecta Heller *ex* Brand, l.c., as a synonym.
G. capitata var. *achilleaefolia* Mason *ex* Jepson, Man. Fl. Pl. Calif., 795, 1925.
G. achilleaefolia subsp. *staminea* Mason & A. Grant, Madroño **9**:208, 1948.

Plants tall with taproots; stem glandular or rarely non-glandular, relatively stout, 2–10 mm. in diameter at base, simple, or cymosely branched above, 10–60 cm. high; basal and lower cauline leaves unipinnately dissected, the rachis 0.3–1.5 mm. wide, the pinnae 8–35 mm. long, 0.3–2.0 mm. wide; heads 15–30 mm. broad; calyx densely floccose, accrescent, the lobes acuminate, 1.5–2.5 mm. wide at the base, about 2.5 mm. long, tip recurved, margins colorless or blue-violet; corolla 7–13 mm. long, the lobes oval, 2.2–3.3 mm. wide, 3–5 mm. long, light blue-violet; filaments 3–5 mm. long, anthers 1.0–1.2 mm. long; style 10–12 mm. long, stigmas 1.0–1.5 mm. long or rarely less; capsule ovoid, dehiscent, not disarticulating, 10–25-seeded; seeds ovoid-angled, 1.0–1.5 mm. long.

Type.—"Very common throughout the interior of California." Information kindly provided by Dr. A. L. Delisle, Curator of Greene and Nieuwland Herbaria, University of Notre Dame, in correspondence with the author, indicates that Greene collected *G. staminea at* Alameda, California,, in 1891 and determined as *G. staminea* specimens from Antioch, California. The type specimen of *G. capitata staminea* is hereby designated as *Greene 40709,* Alameda, California, May 1891. Greene Herbarium, Univ. of Notre Dame.

Range.—San Joaquin Valley, California, from Kern County to Contra Costa County, and sporadically in the Coast Ranges from San Benito County to Solano and Sonoma counties; sandy flats or sand hills, 20–200 ft., or ascending to 1000 ft. Frequently with *Phacelia distans* Benth., *Gilia tricolor* Benth. or *Gilia tricolor* subsp. *diffusa* (Congdon) Mason & A. Grant. March-May (or June).

Variation.—Gilia capitata staminea is relatively uniform in the northern part of the San Joaquin Valley, where it is developed in its extreme form. Its relationship with *G. c. capitata* in the Sierra Nevada has resulted in the production of *G. c. pedemontana* and *G. c. mediomontana.* In the north-central Coast Ranges, however, where *G. c. staminea* occurs in the territory of *G. c. capitata,* the two races have evidently had little contact with one another. This is the case, for instance, in the Vaca Mts., in Solano and Yolo counties, where populations of "typical" *G. c. staminea* (Gates Canyon, Weldon (Mix) Canyon) lie within seven or eight miles of "typical" *G. c. capitata* (Putah Canyon). The isolation here is due to seasonal and ecological factors, with *G. c. staminea* flowering earlier than *G. c. capitata* and growing on the sandy flats rather than the rocky hillsides. The relationship of *G. c. staminea* with *G. abrotanifolia* in the southern San Joaquin Valley remains to be investigated.

Specimens cited.—CALIFORNIA. Madera Co.: Madera, *Hoover 4000;* Chowchilla, *Hoover 522.* Merced Co.: Atwater, *Grant 8496;* Merced River at Highway 99, *Wolf 8737;* Hilmer, *Mason 12566;* Livingston, *Davy 1687;* Merced to Gustine, *Grant 8530, 8532.* Stanislaus Co.: Modesto, *Evans* (1901); Oakdale, *Grant 8497;* El Puerto Canyon, *Hoover 858.* San Joaquin Co.: Manteca, *Grant 8510;* French Camp, *Sanford 98;* Lathrop, *Brandegee* (1907); Midway, *Schreiber 148.* Contra Costa Co.: Antioch, *Baker 2805, Rose 33090, Davy 892, Mason 5159, Grant 7925;* north of Kirker Pass, *Brewer 1118.* Solano Co.: Gates Canyon, *Heller 5389.* Sonoma Co.: Petaluma, *Ott 9.* Alameda Co.: Berkeley, *Mason 3209, Davy 828;* Oakland, *Chestnut 1888;* Brushy Peak near Livermore, *Belshaw 650;* Corral Hollow, *Hoover 3027.* Santa Clara Co.: Cupertino, *Pendleton 790.* Monterey Co.: Pajaro, *Chandler 365.* San Benito Co.: Pinnacles, *Howell 11142.*

7. **Gilia capitata** subsp. **Chamissonis** comb. nov.

Gilia Chamissonis Greene, Erythea 3:105, 1895.
G. achilleaefolia subsp. *Chamissonis* Brand, Pflzr. 4^{250}:111, 1907, in part.
G. achilleaefolia var. *Chamissonis* Nels. & Mcbr., Bot. Gaz. **61**:34, 1916.
G. capitata var. *regina* Jepson, Man. Fl. Pl. Calif., 795, 1925.
G. Chamissonis var. *regina* Jepson, Fl. Calif. 3:185, 1943.

Plants short and stocky with deep taproot; seedling often forming a rosette; herbage somewhat succulent with a mephitic odor; stems very glandular, relatively stout, 2–5 mm. in diameter at base, branching from near base, 15–70 cm. high; basal leaves bipinnately dissected, the rachis 0.9–1.1 mm. wide, the ultimate pinnae 1–4 mm. long, 0.5–2.0 mm. wide; heads 25–35 mm. broad; calyx densely floccose, accrescent, the lobes acuminate, 1.5–2.2 mm. wide at the base, about 2.5 mm. long, tip recurved, margins and sinuses blue-violet; corolla 9–10 mm. long, the lobes oval, 2.2–3.2 mm. wide, 3.0–3.5 mm. long, deep blue-violet; filaments 2.5–5.0 mm. long, anthers 1.0 mm. long; style 6.5–9.5 mm. long, stigmas 0.9–1.2 mm. long; capsule ovoid, dehiscent, not disarticulating, 10–25-seeded; seeds ovoid-angled, 1.0–1.7 mm. long.

Type.—Sand hills of San Francisco, *E. L. Greene.*

Range.—Near the coast, San Francisco to Bodega Bay, Sonoma County, California; sand dunes, 20–200 ft. Frequently with *Phacelia distans* Benth., *Monardella undulata* Benth., *Oenothera micrantha* Hornem., *Lupinus arboreus* Sims, *Gilia millefoliata* Fisch. & Mey. May-July. (A specimen collected at Gray's Harbor, Washington, in 1892 *(Henderson 2401)* is probably best accounted for as an introduction in ship's ballast.

Variation.—Notwithstanding its restricted area of distribution, *G. c. Chamissonis* presents three well-marked morphological types. The extreme form of *G. c. Chamissonis,* with the seedling rosette, occurs on Pt. Reyes Peninsula. Its distinctness was recognized by Jepson, who called it *G. Chamissonis* var. *regina.* The plant from the sand hills of San Francisco is similar; however, the rosette is less well defined, the heads lack the fullness of the Point Reyes form, and the general habit is somewhat looser. The possibility that these differences are merely environmental has been eliminated by growing members of both races together in a uniform garden in Berkeley. The third variant of *G. c. Chamissonis* occurs on sandy areas around Tomales Bay and Bodega Bay in Marin and Sonoma counties where, exposed to introgression from *G. c. tomentosa,* the rosette character has been lost, the growth form has become looser, and the corolla lobes have become distinctly narrower.

A gilia growing near the ocean in Santa Barbara and San Luis Obispo counties has long been referred to *G. c. Chamissonis.* On herbarium sheets the resemblance is very close indeed. The aspect of the plant in nature, however, leaves no doubt that its relationships are with the *G. achilleaefolia* group. The angle of the corolla lobes, for example, which are rotately spreading rather than erect and ascending, constitutes an important feature that would not be preserved in herbarium specimens. This and other characters, including its occurrence on rocky hillsides rather than dune sands, indicate that the Santa Barbara plant need *not* be regarded as another variant of *G. c. Chamissonis.*

Specimens cited.—CALIFORNIA. San Francisco Co.: San Francisco, *Baker 2846, Davy 184, Brandegee* (1905), *Kennedy 4668, Grant 7997.* Marin Co.: Pt. Reyes Peninsula, *Mason 11840, Grant 7992;* Bolinas Bay, *Brandegee* (1905); Tomales Bay, *Grant 8589, 8590;* Dillon Beach, *Grant 8591.* Sonoma Co.: Bodega Bay, *Grant 8598.*

Specimens from the following western herbaria have been inspected:

University of California at Berkeley
Stanford University
California Academy of Sciences
Oregon State College
Willamette University
University of Washington
Yosemite National Park
College of the Pacific

Sacramento Junior College
Chico State College
Santa Rosa Junior College
State College of Washington

10. CONCLUSIONS AND SUMMARY

Conclusions

Gilia capitata (Polemoniaceae) is a polytypic species composed of the following subspecies from central California to British Columbia: *G. c. capitata,* Coast Ranges from San Francisco Bay to British Columbia and east in the Cascade Mountains; *G. c. tomentosa,* maritime bluffs of Marin and Sonoma counties, and Mount Diablo; *G. c. pacifica,* coastal plain of northern California and southern Oregon; *G. c. mediomontana,* Sierra Nevada of California above 3000 ft.; *G. c. pedemontana,* Sierra Nevada below 3000 ft. (with local exceptions); *G. c. staminea,* San Joaquin Valley and scattered localities in the Coast Ranges; *G. c. Chamissonis,* coastal sand dunes from San Francisco Bay to Bodega Bay. For a brief recapitulation of the characters of these subspecies the reader may refer to the diagnostic key in chapter 9.

On the basis of their morphological characters and geographical ranges two basic types may be recognized within the complex. They are: *G. c. capitata,* a plant of rocky hillsides, with (usually) glabrous heads, acute calyx lobes, linear corolla lobes, short stigmas, and indehiscent, few-seeded capsules; and *G. c. Chamissonis* and *G. c. staminea,* plants of sand dunes or sandy plains, with densely floccose heads, acuminate calyx lobes, oval corolla lobes, long stigmas, and dehiscent, many-seeded capsules. The morphological characters and geographical distribution of the remaining subspecies suggest that they have been derived from introgressive hybridization between the primary subspecies. *Gilia capitata tomentosa* and *G. c. pacifica* appear to be the products of introgression from *G. c. Chamissonis* into *G. c. capitata; G. c. mediomontana* appears to be the product of introgression from *G. c. staminea* into *G. c. capitata;* and *G. c. pedemontana* appears to be the product of introgression in the reverse direction from *G. c. capitata* into *G. c. staminea.*

Gilia capitata tomentosa and *G. c. capitata,* with linear corolla lobes and indehiscent or tardily dehiscent capsules, and *G. c. Chamissonis* and *G. c. staminea,* with oval corolla lobes and fully dehiscent capsules, form two vicarious pairs of ecotypes. The first-mentioned ecotype of each pair is maritime, possesses a short, stocky habit of growth, broad heads, and deep blue-violet flowers. The last-mentioned ecotype of each pair is interior, and is distinguished from the maritime ecotype by a slender, tall growth form, narrow heads, and pale blue-violet flowers. The cultivation of samples of the four ecotypes in a uniform garden in Berkeley, which is climatically intermediate between the maritime and interior stations, led to convergence of the strains with respect to their differences in growth habit and flower color. The convergence was incomplete, however, and the strains were amply distinct in their growth habit in Berkeley. It is concluded that the vegetative characters and flower color of the ecotypes, as phenotypically expressed in their natural habitats, are the result of both genotypic responses and environmental modifications, paralleling one another and additive in their effect.

The genotypic variability of four subspecies of *Gilia capitata* was measured by means of progeny tests of natural populations. The variability of cousins, or progenies from randomly selected seed parents in the natural population, was compared with the variability of sister progenies from one seed parent in that same population. Furthermore, the variability of one population was compared with that of another. The variability of cousins was consistently greater than the variability of sisters in the same population for four of the five characters measured. The sister variability was less in the self-compatible types *(G. c. Chamissonis, G. c. mediomontana)* than in the self-incompatible types *(G. c. capitata, G. c. tomentosa)*. The cousin variability was less in populations presumably exposed to relatively strong selective pressures (maritime Coast Ranges, Sierra Nevada, Cascade Mountains) than in populations existing under milder climatic conditions (Mayacama Mountains). The cousin variability of small populations *(G. c. tomentosa)* was less than that of large and extensively ramified populations *(G. c. capitata* in Mayacama Mountains). Among the forces operating to restrict the inherent variability of natural populations of *Gilia capitata*, therefore, are selfing, small size of population, and environmental selection.

Representatives of *G. c. capitata, G. c. tomentosa, G. c. Chamissonis* and *G. c. staminea* were intercrossed and selfed. None of the members of *Gilia capitata* are autogamous; *G. c. Chamissonis* and *G. c. staminea* are self-compatible; *G. c. capitata* is self-incompatible; and *G. c. tomentosa* is of reduced self-compatibility. All of the subspecies of *Gilia capitata* are compatible *inter se* except *G. c. tomentosa*. This plant is difficult to cross onto as a female parent. Reciprocal differences in compatibility, not correlated with differences in style length, thus exist between *G. c. tomentosa* and the other types, and also in the cross between *G. c. Chamissonis* and *G. c. staminea*. The F_1 hybrids are vigorous in all crosses except *G. c. tomentosa* ♀ × *G. c. staminea* and *G. c. Chamissonis*. The pollen fertility of the F_1s was relatively high in most crosses, and in no case was so low as to preclude the production of abundant sound seeds. A suggestion of reciprocal differences in pollen fertility, correlated inversely with the reciprocal differences in compatibility, was found in the crosses of *G. c. staminea* with *G. c. Chamissonis* and *G. c. tomentosa*. A small proportion of inviable individuals was found in the F_2 generations between *G. c. tomentosa*, and *G. c. Chamissonis* and *G. c. staminea*. A slight though distinct barrier to gene exchange thus exists in each generation up to F_2 between *G. c. tomentosa* on the one hand and *G. c. Chamissonis* and *G. c. staminea* on the other.

The subspecies of *Gilia capitata* all have nine pairs of chromosomes. Meiosis in F_1 hybrids of all crosses, even the most sterile, was essentially normal. The microspores commence to abort at the time of the first post-meiotic mitosis.

The subspecific differences in stem pubescence are determined by the action of a single gene; the differences in calyx pubescence, calyx lobe reflexion, capsule dehiscence, seed size, and earliness are controlled by two genes; the differences in corolla color are due to about three genes; the racial differences in corolla lobe width and stigma length are caused by differences in about four genes; growth form is controlled by more than four and probably by many genes. The gene for glandular hairs on the stem is dominant over the allele for floccose hairs. The genes for bipinnate dissection are dominant over the alleles for unipinnate dissection of the basal leaves; the genes for floccose calyces are dominant over those for glabrous calyces; the alleles for indehiscent capsules are dominant over those for dehiscent capsules; the genes determining short stigmas are dominant over the alleles determining long stigmas; and dominance is exhibited by the genes for the tall and slender habit over the alleles for the short and stocky habit. The factors determining the foregoing and some other characters are distributed on nine chromosomes in an interlocking system of weak linkages (cf. Fig. 19).

The synthesis of *G. c. pacifica* in F_2 *G. c. capitata* × *G. c. Chamissonis,* and of *G. c. pedemontana* in F_2 *G. c. capitata* × *G. c. staminea,* indicates that the two intermediate entities are more or less simple recombination types of their respective parents. The synthesis of a type of *G. c. Chamissonis* in B_1 *(G. c. capitata* × *G. c. Chamissonis)* × *G. c. Chamissonis* suggests that the naturally occurring populations are a backcross or introgressive type The failure to synthesize *G. c. tomentosa* in its entirety in F_2 *G. c. capitata* × *G. c. Chamissonis,* and the indication that this entity could only be bred with the supplementary aid of artificial selection, suggests that, unlike *G. c. pacifica,* it is a fairly highly selected line. The dominance of the gene for glands on the stem over the allele for floccose hairs, together with the universal occurrence of floccose stems in *G. c. tomentosa,* even in populations separated by only a few hundred feet from glandular-stemmed *G. c. Chamissonis,* proves that introgression from *G. c. Chamissonis* into *G. c. tomentosa* is not occurring today. The general lack of segregation in F_2 *G. c. Chamissonis* × *G. c. staminea,* except for the few characters by which they differ, indicates that these two subspecies have diverged from a common panmictic population.

Natural hybridization within *Gilia capitata* is viewed as a special aspect of sexual reproduction, by which new biological types are created out of the raw materials of the parental entities and are delivered over to natural selection. In many cases this hybridization is beneficial to the species, for it increases the possibilities of adaptation in a changing environment. The most important barriers to gene flow in the species complex to which *Gilia capitata* belongs thus appear to consist of ecogeographic factors rather than hybrid sterility or incompatibility. Where old and previously remote habitats have been brought into closer proximity by orogenic and climatic changes, the existing species or subspecies have met and produced new types, some of which have successfully colonized the new environments.

The great uplift of the Sierra Nevadan axis in the Pleistocene epoch may have for the first time permitted the intermingling of *G. c. capitata,* as an immigrant from the Cascade Mountains on the higher slopes, with *G. c. staminea,* persisting since the Pliocene on the lower plains. Introgression, being to the mutual advantage of both entities under the conditions of rapid environmental change, thereupon led to the conversion of *G. c. capitata* into *G. c. mediomontana,* and of *G. c. staminea* into *G. c. pedemontana.* The uplift of the coastal plain in northern California, meanwhile, may have brought *G. c. capitata* into contact with *G. c. Chamissonis,* leading to the production of *G. c. pacifica.* Introgression of *G. c. Chamissonis* into *G. c. capitata* to produce *G. c. tomentosa* in the area north of San Francisco Bay may also have occurred during the Pleistocene epoch, for a disjunct population of *G. c. tomentosa* with the characters it acquired by introgression exists as a Pleistocene relict on Mount Diablo.

Summary

1. *Gilia capitata* (Polemoniaceae) is a polytypic species composed of seven named subspecies from central California to British Columbia. There are two basic morphological types within the complex, typified by *G. c. capitata* and the pair of subspecies *G. c. Chamissonis* and *G. c. staminea.* The characters and distribution of the remaining subspecies suggest their origin through introgressive hybridization between the primary subspecies.

2. *Gilia capitata tomentosa* and *G. c. capitata,* as well as *G. c. Chamissonis* and *G. c. staminea,* are two vicarious pairs of ecotypes, each with a maritime and an interior member. Cultivation in a uniform garden in Berkeley led to partial convergence of these ecotypes with respect to their differences in growth habit and flower color. Their vegetative characters, as phenotypically expressed in nature, are thus the cumulative result of both genotypic responses and environmental modifications.

3. Genotypic variability of several of the subspecies was measured by means of progeny tests of natural populations. Greater uniformity was found in partially inbred entities than in self-incompatible entities, in populations of small size than in large and ramified populations, and in populations exposed to strong selective pressures than in populations existing under relatively mild climatic conditions. Subspecies supposed to be of introgressive origin were not more variable than the putative parental subspecies.

4. *Gilia capitata capitata, G. c. tomentosa, G. c. Chamissonis,* and *G. c. staminea,* when intercrossed, produce mostly vigorous and fertile hybrids. Weak but distinct barriers to gene exchange exist between *G. c. tomentosa* on the one hand, and *G. c. Chamissonis* and *G. c. staminea* on the other, in all generations from P to F_2. Reciprocal differences in compatibility and pollen fertility, inversely correlated with one another, exist between *G. c. tomentosa* and *G. c. Chamissonis* and *G. c. staminea.*

5. The subspecies of *Gilia capitata* all have nine pairs of chromosomes. Meiosis in the F_1 hybrids of all crosses, even the most sterile, was essentially normal.

6. A single gene determines the difference between glandular and floccose hairs on the stem. Two genes control the inter-subspecific differences in calyx pubescence, calyx lobe reflexion, capsule dehiscence, seed size, earliness; three genes the differences in corolla color; about four genes are responsible for the

interracial differences in corolla lobe width and stigma length; growth habit is controlled by many genes.

7. Several linkage groups are recorded. The linkages are weak and interlocking.

8. *Gilia capitata pacifica* was synthesized in F_2 *G. c. capitata* × *G. c. Chamissonis; G. c. pedemontana* was synthesized in F_2 *G. c. capitata* × *G. c. staminea;* the introgressive type of *G. c. Chamissonis* was synthesized in B_1 *(G. c. capitata* × *G. c. Chamissonis)* × *G. c. Chamissonis.* The characters of *G. c. tomentosa* were synthesized but were not recombined in any one individual in F_2 *G. c. capitata* × *G. c. Chamissonis;* that intermediate entity is a product of selection as well as of hybridization and recombination. The general lack of segregation in F_2 *G. c. Chamissonis* × *G. c. staminea* indicates that these entities have diverged from a common panmictic population.

9. The universal presence of floccose stems in *G. c. tomentosa,* which is the homozygous recessive condition, proves that introgression from glandular-stemmed *G. c. Chamissonis* into that entity is not occurring today. The evidence of geographical distribution and the nature of variability in populations suggest that introgression in *Gilia capitata* occurred largely during the Pleistocene epoch.

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