

TAXONOMIC RELATIONSHIPS OF *GILIA MACULATA* (POLEMONIACEAE)

ROBERT PATTERSON

Department of Biology, San Francisco State University,
San Francisco, CA 94132

ABSTRACT

Gilia maculata is reassigned from its previous placement in *Linanthus*. It was described originally by Parish in 1892 as *Gilia maculata*, and placed in *Linanthus* by Milliken (1904). This species is poorly known because of its rarity and because of its very small size, causing it to be easily overlooked in the field. Rediscovery of a population of *G. maculata* provided the opportunity to study this taxon critically. Leaf arrangement and shape, indumentum, corolla and calyx morphology, and pollen exine morphology, argue against its unequivocal assignment to *Linanthus*, and favor its inclusion in *Gilia*.

Gilia maculata Parish (Fig. 1) is a systematic enigma. It is a minuscule, little-known desert annual that occurs near the western margins of the Little San Bernardino Mountains of southern California (Fig. 2). It has been regarded by most floristic treatments as *Linanthus maculatus* (Parish) Milliken, although it has few diagnostic features of *Linanthus*. Although botanists and governmental agencies have sought it because of its potentially rare status, it has seldom been seen or collected, and few specimens are present in herbaria, making study extremely difficult. Furthermore, its relationships with other species of *Linanthus* or *Gilia*, as well as with other Polemoniaceae, have never been examined critically. In April 1986, a substantial population of this species was located near the northwest entrance to Joshua Tree National Monument, providing enough material to conduct a more thorough study of the morphological relationships of this species.

TAXONOMIC HISTORY OF *GILIA MACULATA*

Parish's (1892) original description of *G. maculata* was as follows: "Inch high, diffusely branched from the base, sparsely pubescent; leaves entire, two lines long, broadly linear, thick and strongly carinate, obtuse, acerose; earlier flowers nearly sessile in the lower forks, later ones crowded above; calyx lobes nearly equal, much like the leaves but with a narrow hyaline membrane, ciliate; the narrowly campanulate tube of the corolla not exceeding the calyx, the limb rotate, two lines wide; filaments inserted on the base of the tube; anthers exserted; seeds few". Parish noted that the species was "... near *G. demissa* Gray, from which it differs in its entire leaves, obtuse

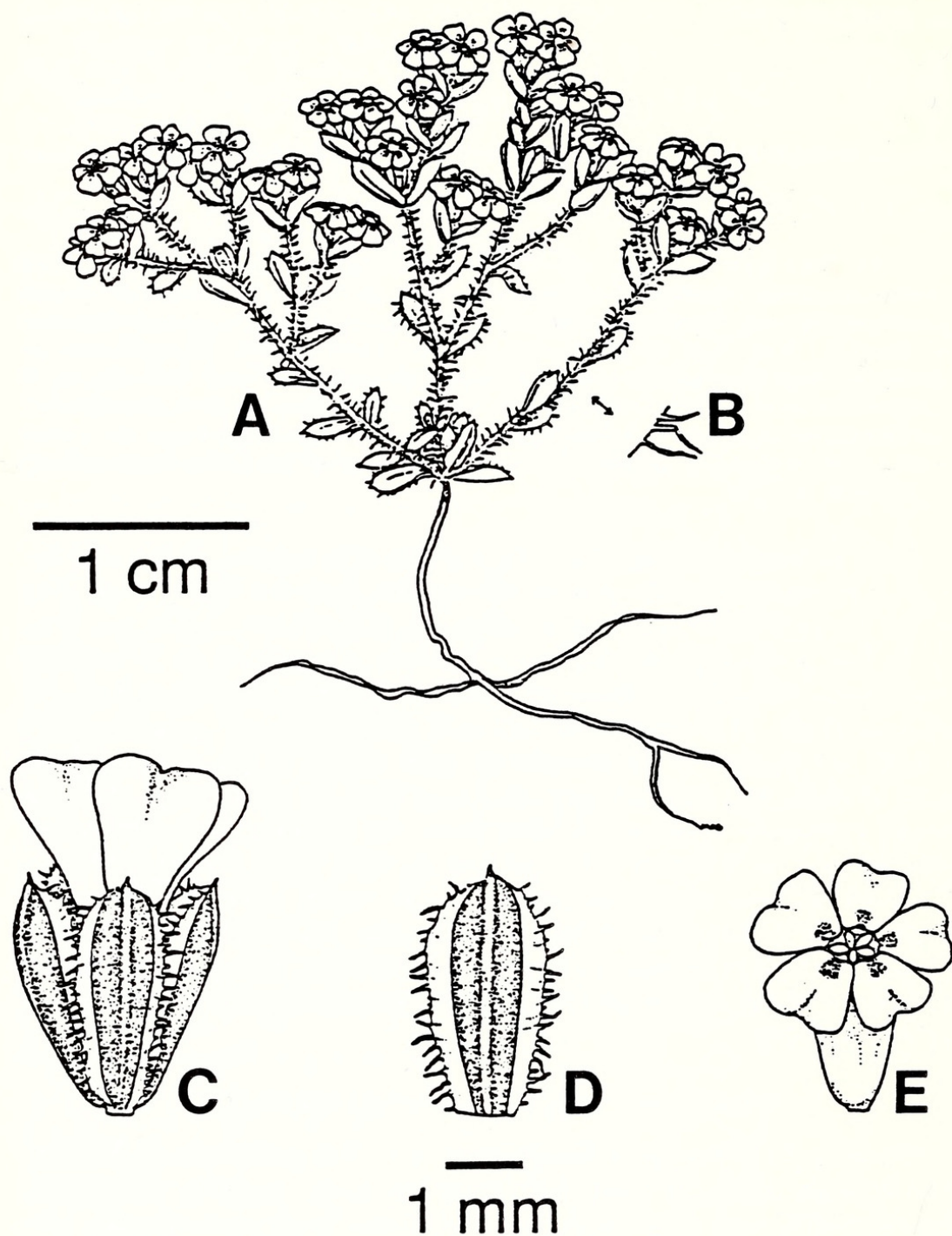


FIG. 1. *Gilia maculata*. A. Habit. B. Enlargement of trichomes. C. Flower at early anthesis. D. Calyx lobe showing hyaline margins. E. Face view of flower showing position of spots at base of corolla lobes.

and ciliate calyx-lobes, narrower corolla, and exserted anthers". The implication is that Parish considered the two species related based on an overall resemblance. It is not surprising that Parish did not recognize the new species as a member of *Linanthus*, because at that time most species recognized currently as *Linanthus* were included

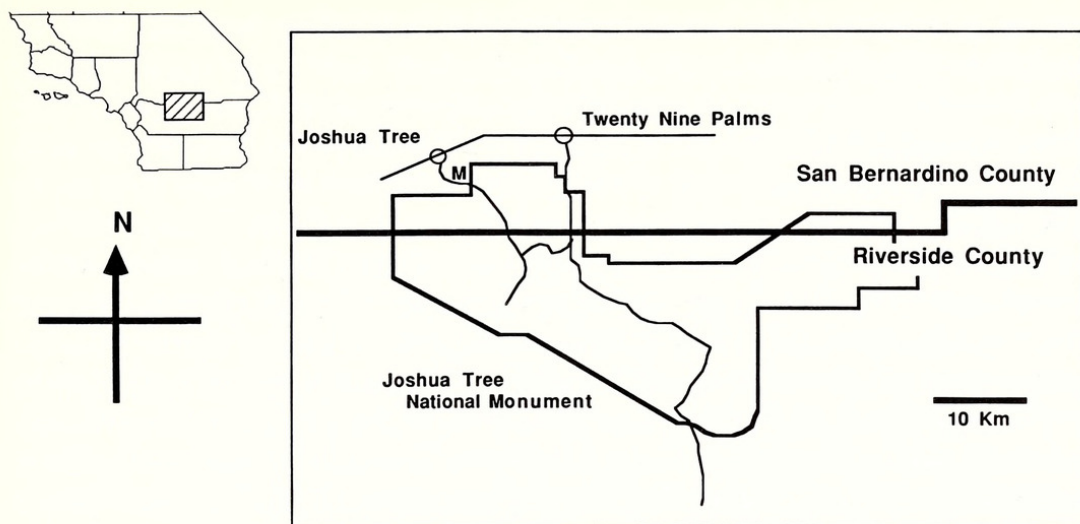


FIG. 2. Location of 1986 collection (M) of *Gilia maculata* (Bourell et al. 3000).

in *Gilia*. Although the genus name *Linanthus* dates from 1833, its common use did not begin until Greene's (1892) treatment.

Parish's original description is not completely in accord with the holotype or with material collected in the field during this study. Contrary to his description, the leaves of the holotype are, in fact, obovate and certainly not acrose (it is possible that Parish was referring to a mucronate tip, which may be present in some specimens). Parish also omitted certain other features that distinguish *G. maculata* from other genera in the family. He neglected to state in his description that the leaves of this taxon were alternate. He did, however, describe the calyx lobes as ciliate, identifying an important character that sets *G. maculata* off taxonomically.

Milliken (1904) placed this species in *Linanthus*, although without any explicit justification. Moreover, her description of *L. maculatus* is not in complete accord with her inclusive description of the genus *Linanthus*. She described the leaves of *L. maculatus* as "... entire, the upper sometimes alternate, oblong ...", whereas her description of the leaves for the genus reads "... opposite and palmately parted, or rarely entire and linear". Thus, although Milliken's treatment dictated the taxonomic status under which this species has been recognized in all modern floras, it failed to distinguish this species clearly as a member of *Linanthus*. If, in fact, Milliken's key to genera of Polemoniaceae were used, *G. maculata* would be identified clearly as a member of *Gilia*.

Brand's (1907) concept of *Gilia* included most of the tribe Gilieae, including *Linanthus*. He recognized *G. maculata* as a member of sect. *Campanulastrum*, along with *G. parryae* and *G. bella* (= *Linanthus p.* and *b.*), *Gilia dactylophyllum* (= *L. demissus*), and three currently recognized species of *Gilia*, *G. campanulata*, *G. filiformis*, and *G. micromeria*. This treatment is particularly noteworthy be-

cause it is the earliest occasion where *G. maculata* is allied with *G. campanulata*. Phenetically *G. maculata* is probably most closely related to *G. campanulata*, although there are still substantial differences that distinguish them. Grant (1959) later combined sect. *Campanulastrum* with sect. *Giliastrum* under the latter name, although without providing justification.

Subsequent treatments continued to recognize this taxon as *Linanthus* without apparent concern for accuracy of the taxonomic placement. Jepson (1925, 1943) recognized *L. maculatus* but did not refer directly to its alternate leaves. Only in the genus description did he allude to *Linanthus* as having leaves "rarely with some uppermost alternate". Interestingly, in his Manual (1925) he placed *L. maculatus* with *L. demissus* and *L. parryae* in subgenus *Parrya*. Later, in his Flora of California (1943) Jepson included *L. bellus*, *L. concinnus*, and *L. dianthiflorus* in this subgenus, circumscribing what Grant (1959) later referred to as sect. *Dianthoides*. It is noteworthy that Jepson (1943) made a special comment in the generic description that *L. maculatus* (among other species) has entire leaves. He also commented on the narrow endemism shown by the range of *L. maculatus*. It is curious that, with the extra attention given to this species in his Flora, Jepson did not discuss the significance of alternate leaves in this species.

Mason omitted *L. maculatus* from the entire treatment of the Polemoniaceae in Abram's illustrated Flora of the Pacific States (1951). It is unclear whether this was an oversight, or whether it was due to a belief on Mason's part that this species did not belong in *Linanthus*. Munz (1959, 1974) included *L. maculatus* in his treatments, describing it accurately as having alternate leaves, but making no other special mention of this character.

Because this species is not well known, and because the original diagnosis is scanty and not in complete agreement with the holotype material, an updated description is provided here based on material from the population collected in 1986:

Gilia maculata Parish, Bull. Torrey Bot. Club 19:93. 1892. (figs. 1, 3). — *Linanthus maculatus* (Parish) Milliken, Univ. Calif. Publ. Bot. 2:55. 1904. — TYPE: USA, California, Riverside Co., borders of the Colorado Desert, at Agua Caliente [Palm Springs], *W. G. Wright s.n.* (holotype: CAS!).

Diminutive ephemeral annual 1–3 cm high. Stems branching above the first 1 or 2 leaves, densely hairy with 1- to 4-celled trichomes throughout. Leaves alternate, fleshy, narrowly oblanceolate or oblong, sessile, mucronate, marginally ciliate with 1- to 2-celled, white hairs from the base to at least $\frac{1}{2}$ the length (often farther), the blade concave adaxially. Flowers borne in simple or compound cymes, sessile or subsessile, peduncle < 1 mm long; calyx lobes narrowly

oblanceolate or spatulate with mucronate tip, ca. 2 mm long, green, distinct nearly to base (only the adjacent membranes connected at base), glabrous, with membranous ciliate margins extending to the tip, the trichomes 2(–3) cells long, the terminal cell long-acuminate (Fig. 1B); corolla campanulate, tube ca. 1.5–2 mm long, yellow or yellow-green, slightly hairy on inner surface, throat <1 mm long, white, lobes broadly ovate-cordate, tips slightly concave, 1–1.5 mm long, white with cerise spot at base, spreading at right angle to the tube or (more commonly) reflexed, venation simple, open; stamen filaments attached to near base of corolla tube, narrowly lanceolate, 1.5–2 mm long; anthers oval, slightly exserted beyond corolla throat; pollen yellow, round, exine reticulate with 10–12 slit-like apertures distributed evenly on the surface of the grains; ovary triangular-ovate, ca. 0.5 mm long, style 1 mm long, stigma lobes <0.5 mm long. Seeds minuscule, dark reddish-brown, non-mucilaginous, 10–12 per capsule, \pm distributed evenly among locules; $n=9$.

Additional specimens. USA, CA, San Bernardino Co., rd from Joshua Tree to Joshua Tree Natl. Mon., ca. 3.5 km S of junction with CAL Hwy 62, 6 Apr 1986, *Bourell, Patterson, and Timbrook* 3000 (CAS); Coyote Holes, Joshua Tree National Monument, near line of Riverside and San Bernardino counties, 20 Apr 1924, *Munz* 7941; Chipmunk Trail, 28 Mar 1968, *Stebbins* 6650 (CAS!); 17 mi W of 29 Palms on rd to Morongo Valley, 950 m, 6 Apr 1937, *Daniels s.n.* (CAS!); ca. 5 mi N of Windmill Tank, 3600 ft, 2 Apr 1942, *Ripley and Barneby* 4273 (CAS!); 8 mi W of 29 Palms, 12 Apr 1935, *Keck* 3843 (CAS!).

Distribution and ecology. *Gilia maculata* occurs in moderately coarse sand in open areas of *Larrea-Yucca brevifolia* scrub as a member of the annual spring flora. It is extremely inconspicuous in its gray-green herbage and white corollas, and blends well with the substrate, even when in flower (Fig. 3). It is likely that this may be one reason why the species is so little known in the field and poorly represented in herbaria.

The population that was rediscovered in April 1986 occurs at 1000 m elevation. No other populations were found during this study. It remains uncertain as to whether this population is representative of other populations of this species; however, considerable area of similar habitat occurs throughout the region. The Joshua Tree population consisted of approximately 100 individuals in April 1986; the following year the population was reduced markedly in number, but individuals were found in the same area.

Relationships. The decision to place *G. maculata* into one of the currently recognized genera of Polemoniaceae or to erect a new genus must be weighed carefully. Any decision is completely dependent



FIG. 3. *Gilia maculata* in the field. Note size compared with coin.

on how well the existing genera are known taxonomically. The Polemoniaceae have been studied carefully by many authors, but systematic and ecological relationships among most members of the family are not well understood. Although *G. maculata* is most commonly included as a member of *Linanthus*, even superficial consideration of morphological characters does not support this alignment. The most commonly used defining feature for the genus *Linanthus* within the Polemoniaceae has been the presence of opposite leaves that are either a) palmately-divided with linear or narrowly lanceolate divisions or b) entire and linear. Presumably the entire leaves in certain species (e.g., *L. dichotomus* and relatives, *L. dianthiflorus*) represent a reduction of leaf lobes to one. *Linanthus* sensu stricto never has completely alternate leaves, although occasionally in some species the upper leaves near the inflorescence are subopposite. Inclusion of *G. maculata* as a member of *Linanthus* is out of accord with the morphological unity of the latter; it would be difficult to distinguish *Linanthus* as a discrete genus were *G. maculata* included. Bentham (1833), Greene (1892), and Milliken (1904), as well as nearly all subsequent authors, recognized the taxonomic importance of leaf morphology in this lineage, and I find no reason to diminish its value.

In addition to having alternate arrangement, the oblong-obovate

leaves of *Gilia maculata* represent a shape not found in any other species of *Linanthus*. This character appears to have been neglected as a distinguishing feature, although it is mentioned in several descriptions of the species (Jepson 1925, 1943; Munz 1959, 1974). Most species of *Linanthus* have linear or linear-lanceolate leaf lobes or leaves. The only species of *Linanthus* that have oblanceolate leaf lobes are in sect. *Leptosiphon* (e.g., *L. oblanceolatus*, *L. bicolor*); however, other morphological differences (corolla shape, leaf arrangement and divisions, inflorescence structure) between this section and *G. maculata* are so strong that similarity in leaf or leaf lobe shape can be regarded as an example of convergence.

Not only is the placement of *G. maculata* in *Linanthus* difficult based on the circumscription of the latter genus, there is no apparent morphological alliance between the former species and any existing species of *Linanthus*. Previously suggested relationships with other species of *Linanthus* are problematic. Parish (1892) and Jepson (1925, 1943) proposed an alliance with *L. demissus* (sect. *Dianthoides*) presumably founded on a superficial resemblance in habit and corolla morphology. Although both taxa are small desert annuals with white campanulate corollas with reddish basal spots on the lobes, other features do not support a close relationship. Pollen exine patterns of these two species are strikingly different (Fig. 4), and provide convincing evidence against a taxonomic alliance. *Linanthus demissus* has striate regions amid a reticulate exine, a pattern characteristic of certain species of *Linanthus* sect. *Dianthoides*. *Gilia maculata* lacks any striations and is uniformly reticulate, a pattern that occurs in certain species of *Gilia* and in most other *Linanthus* species. Inasmuch as pollen exine patterns have been extremely useful in helping to understand relationships in the Polemoniaceae (Stuchlik 1967a, b; Taylor and Levin 1975; Chuang et al. 1978; Day and Moran 1986; Timbrook 1986; Patterson, Golden, and Vagenas, unpubl.), this divergence suggests a strong taxonomic difference. Irrespective of relationships between *G. maculata* and other *Gilia* species as indicated by pollen morphology, taxonomic placement of *G. maculata* near *L. demissus* is not defensible. Additionally, *L. demissus* has palmately divided, opposite leaves (although upper leaves may occasionally be subopposite, the majority of the leaves remain opposite).

Other species within sect. *Dianthoides*, in which *G. maculata* was placed by Grant (1959), share few if any diagnostic characters with the latter species. Only *L. dianthiflorus* has simple leaves, but these are linear and opposite. Deeply cleft calyx tubes are present in *L. parryae*, *L. bellus*, and *L. demissus*, but they are not as deeply cleft as in *G. maculata*—there is always a fused portion, i.e., a calyx tube. Leaves of *L. bellus* and *L. parryae* are always opposite and palmately cleft.

One feature shared by *G. maculata* and most members of sect.

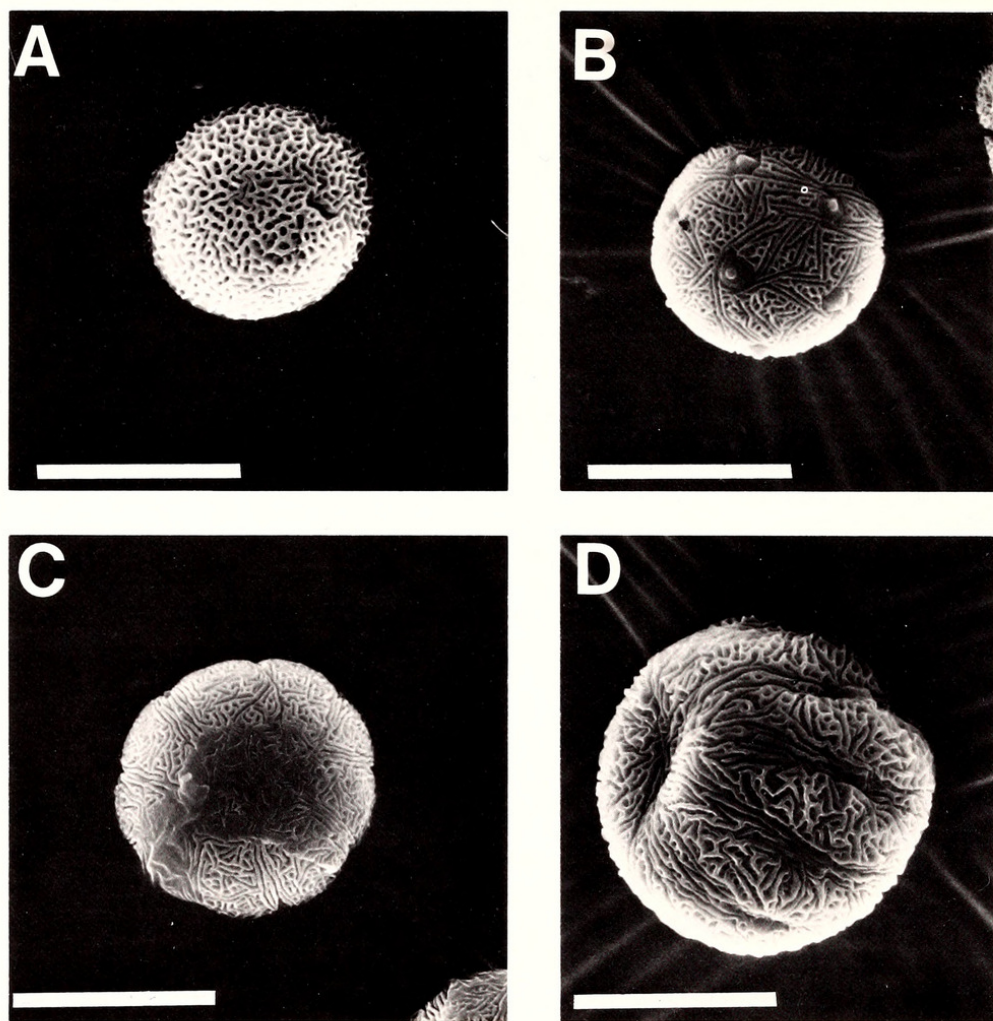


FIG. 4. Scanning electron micrographs of pollen grains. A. *Gilia maculata*. B. *Linanthus demissus*. C. *G. campanulata*. D. *G. inyoensis*. Bar represents 20 μ m.

Dianthoides is the presence of red marks at the base of the corolla lobes. In this respect the corolla of *L. demissus* is similar superficially to that of *G. maculata*; however, it is likely that this represents convergence in corolla color pattern. Presence of red spots on corolla lobes is common in many species of *Linanthus*, and is present as a character in sects. *Pacificus* and *Leptosiphon*, as well as in *Dianthoides*. An argument in support of corolla color pattern as indicative of close relationship in this case negates the importance of other features such as leaf arrangement and shape. The latter characters have had a major role in distinguishing genera within the family, but corolla color patterns have rarely been regarded as important generic diagnostics. As Grant (1965) points out, although evolution of floral morphology (including color patterns) has been a major factor in speciation in the Polemoniaceae, it is apparent that similar color patterns have evolved more than once across generic lines.

Gilia is the only genus in which *G. maculata* can readily be incorporated based on comparative morphology. *Gilia* is a large, mor-

phologically diverse, polythetic genus. Its circumscription is difficult, and it is most easily recognized by lacking characters that are present in other genera. Leaves are always alternate in *Gilia*, but leaf, trichome, and floral morphology in *Gilia* is extremely diverse. The basic chromosome number in the genus is $x=9$, as it is for *Linanthus* (Grant 1959; Patterson 1979).

Gilia was partitioned into five sections (Table 1) by Grant (1959), each of which is morphologically and ecologically diverse. *Gilia maculata* has morphological features that ally it with members of sect. *Giliastrum* Brand. This section ranges from perennials such as *G. ripleyi* to diminutive annuals like *G. campanulata* and *G. inyoensis*. It is also poorly understood from a taxonomic viewpoint (Grant 1965). One character that distinguishes it from other sections of *Gilia* is the presence mostly of campanulate or rotate corollas. This feature is present not only in *G. maculata*, but also in three other small desert annuals: *G. campanulata*, *G. inyoensis*, and *G. tenerrima*.

Another character by which these four species are allied is calyx morphology. The calyx is divided into five lobes to near the base (the lobes actually appearing distinct), with membranous margins that extend most to all of the length of the calyx lobes (Fig. 1D). This feature is absent in other species of *Gilia*.

Pubescence features also appear to ally these species while illustrating the complex interrelationships among them. All four species are moderately to densely pubescent on their stems, leaves, and calyx lobes. The trichomes are generally 2- to 4-celled long, and uniseriate. They show a further similarity among these species in that cells appear to alternate in orientation with respect to one another, forming a "chain link" structure (Fig. 1B). Slightly different trends in cell number exist among different species and on different organs, but irrespective of these differences, trichome morphology provides an additional argument for including *G. maculata* within sect. *Giliastrum*.

Despite similarities among *Gilia maculata* and the other three species cited above, it is notably distinct in other characters. In particular, no other species of *Gilia* have ciliate leaf margins and calyx lobes. Furthermore, the pollen exine pattern of *G. maculata* is different from that of any other *Gilia* species, especially that of *G. campanulata* or *G. inyoensis* (Fig. 4). Pubescence type and pollen exine morphology are regarded generally as conservative characters and have been used in numerous instances as taxonomically valuable characters throughout the Polemoniaceae (Grant 1959; Patterson 1977; Timbrook 1986; Gordon-Reedy in press). Therefore, although affinities exist between *G. maculata* and certain other species of sect. *Giliastrum*, strong differences remain, rendering the problem of relationships with the remainder of the genus far from solved.

TABLE 1. FEATURES OF THE FIVE SECTIONS OF *GILIA* (SENSU GRANT 1959).

	<i>Giliastrum</i> (including <i>G. maculata</i>)	<i>Giliandra</i>	<i>Gilia</i>	<i>Arachnion</i>	<i>Salpigilia</i>
Duration	Annuals and perennials	Annuals and perennials	Annuals	Annuals	Annuals
Lower leaves	Mostly not deeply lobed	Once-pinnate	1-3 Pinnate	1-3 Pinnate	1-3 Pinnate or linear
Upper leaves	Similar to lower leaves	Reduced	Reduced	Very reduced	Reduced or well-developed and entire
Corolla shape	Campanulate or rotate	Funnelform	Funnelform	Funnelform	Funnelform
Pollen color	Yellow or blue	Mostly yellow, rarely blue	Blue	Blue	Blue

A case for and against a new genus. It is inevitable that, as more taxonomic information has become available in the Polemoniaceae, reassessments have appeared, often necessitating recognition of new taxa above the level of species. Day and Moran (1986) recently accumulated evidence in favor of reassigning the former *Ipomopsis gloriosa* to a new genus, *Acanthogilia*; the combination of characters in this taxon precluded unequivocal placement in any previously existing genus. Timbrook (1986) similarly reaffirmed the generic status of *Loeseliastrum*, formerly a section of *Langloisia*. A strong case might be made for a similar treatment of *G. maculata*, inasmuch as it does not ally very closely with any known member of *Gilia*, and certainly not with *Linanthus* or any other existing genus in the family. Morphologically it represents a mosaic of features from different genera, lacking all of the defining characters of even the more variable genera in the family. However, a large number of unsolved questions remain about relationships within *Gilia* as well as among *Gilia* and other genera. Other genera in the Gilieae are reasonably well-circumscribed and distinct, even though they may share a suite of characters with *Gilia*. Based on information presently available, *Gilia maculata* does not possess any character or combination of characters that clearly set it apart at the generic level. Further studies of character distribution in this species and in the remaining species of *Gilia* may provide an alternative insight on this problem.

Taxonomic importance of Gilia maculata. Questions of evolutionary and taxonomic importance remain in which *G. maculata* may provide some insight. Its previous placement within and without *Linanthus* reemphasizes the point that there is a great deal that is not understood clearly about the relationship between *Linanthus* and *Gilia*. For example, just as *G. maculata* has been moved from *Linanthus* in this study, Moran (1977) removed *L. uncialis* from *Gilia*. In neither case are morphological features problematic or difficult to measure; rather, both of these species are poorly known, being uncommon and inconspicuous in the field, and poorly represented in herbaria. This underscores the need for considerable caution in assessing taxonomic relationships when some or all members of a group are not completely understood. It is also noteworthy that both of these species have been placed in *Linanthus* sect. *Dianthoides* and *Gilia* sect. *Giliastrum*. This situation suggests that an evolutionary connection between *Gilia* and *Linanthus* might be sought among these two sections. Such an hypothesis is attractive in exploring further the relationships between these genera. The position of *G. maculata* in the California flora also remains unknown. Its isolation in the Little San Bernardino Mountains, a region not particularly well-associated with isolated and endemic plant species, is not readily explained; neither is its geographic disjunction

by over 300 km from its postulated nearest relatives, *G. inyoensis* and *G. campanulata*. In addition, not only is there minimal information about population size in this species, but virtually nothing is known about its reproduction (e.g., pollination, seed production, dispersal). Prior to attempting to answer questions about evolution in this species, considerably more information must be gathered regarding the ecology, distribution, and reproductive biology of *G. maculata*.

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ANNOUNCEMENT

RELOCATION OF UC AND JEPS TO INTERIM QUARTERS

During March and April 1989, the UC and JEPS collections will be temporarily relocated to a site several miles from the UC-Berkeley campus; the staff will move in May or June. The herbaria will be housed at the off-campus site until renovation of new quarters in the Life Sciences Building is completed at the end of 1992. Interim quarters will be fully functional and accessible to researchers. We expect to retain our phone numbers, and mail addressed to "University Herbarium" or "Jepson Herbarium" (but *not* "Department of Botany") will be delivered to our new location.

The move is being coordinated in such a way as to minimize disruption of research needs. Loans will generally be unaffected, other than potential minor delays in processing. We do ask that shipments to UC of routine exchange, returned loans, and similar low-priority transactions be kept to a minimum until June 1989, so that our staff can concentrate on the move.

Visitors during March and April 1989 should contact us in advance to determine whether or not their groups have been moved, and what needs to be done to bring the researcher and specimens together. Except for the day or two that any group of specimens is in transit, they should be accessible at one place or the other, but special arrangements will need to be made to provide access to the new quarters until June 1989.

The location of the interim quarters is at 6701 San Pablo Avenue, two blocks south of Ashby Avenue at the junction of Berkeley, Oakland, and Emeryville. The herbaria will occupy a minor portion of a huge warehouse owned by the University, commonly referred to as the Merchant Building. The facility is easily accessed by automobile from Interstate Highway 80 at the Ashby Exit. For public transportation, take a bus from the Ashby BART Station west along Ashby Avenue to San Pablo Avenue.

Eastern Hemisphere collections of spermatophytes (except Asteraceae, Apiaceae, Myrtaceae, and Ranunculaceae) will continue to be housed at the annex established five years ago adjacent to campus. After renovation is complete, however, these collections will be reintegrated into the main herbarium. Until then, visitors who expect to see these specimens should make arrangements in advance.



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