

CLASSIFICATION OF THE GENUS *GILIA* (POLEMONIACEAE)

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ABSTRACT

The body of knowledge concerning taxonomic characters in *Gilia* has increased greatly since the last previous infrageneric classification in 1959. The older and the newer information is combined to construct a new infrageneric classification, in which the species are grouped into three subgenera and seven sections. Five formerly poorly known species which have traditionally been in *Gilia* are excluded from the genus. Three of these are transferred to *Tintinabulum*, one to *Allophyllum*, and one to a new genus, *Maculigilia*. The very different approaches to classification of molecular cladistics and evolutionary systematics are currently being applied to *Gilia* and related genera; the two approaches are compared and discussed.

KEY WORDS: *Gilia*, *Allophyllum*, *Maculigilia*, Polemoniaceae, polyphyly

It was a common practice in the nineteenth century to group the temperate species of Polemoniaceae into four genera: *Polemonium*, *Phlox*, *Collomia*, and *Gilia* (Meisner 1836-1843; Bentham & Hooker 1876; Gray 1878; Peter 1897). *Polemonium* and *Phlox* have distinctive vegetative and floral characters which define them as genera, and consequently they have had a relatively stable taxonomic history. To a lesser extent this is also true of *Collomia*. *Gilia*, on the other hand, lacks distinctive vegetative and floral features, making generic definition difficult. It became a convenient catchall in the nineteenth century for species that did not fit into the other genera. Gray (1878), for example, adopted a very broad concept of *Gilia* which embraced twelve sections differing greatly from one another; and the treatment of *Gilia* by Bentham & hooker (1876) was very similar.

The trend toward all-inclusiveness in *Gilia* was reversed in the twentieth century as the plants became better known and more characters were found. The reverse trend was to segregate subgroups out of the old *Gilia* as separate genera. This process was started by Milliken (1904), a student of Jepson, and has continued to the present time. The net result is that the genus *Gilia* has been undergoing many and substantial changes in its constitution throughout its 200-year taxonomic history, unlike *Polemonium*, *Phlox*, and *Collomia*.

The genus problem in *Gilia* has two complementary aspects: delimitation of the genus as a whole, and recognition of natural sections and subgenera. The objectives are to identify the natural sections or subgenera; to group together those that belong to the same major monophyletic branch; to exclude subgroups that belong to other phylogenetic branches; and to use these inclusions and exclusions to determine the range of variation of the genus.

Three general classification systems of *Gilia* were proposed in the 1940s and 1950s: those of Mason & A. Grant (1948), Grant & Grant (1956), and Grant (1959). They all attempted to reflect the natural relationships of the subgroups as understood at the time. The 1959 system, which is still widely used, recognized five sections: *Giliastrum*, *Giliandra*, *Gilia*, *Saltugilia*, and *Arachnion*. It is in need of revision. The 1948 system contains some elements which were passed over in 1959, but will be taken up in the present revision.

Much research has been done on *Gilia* by many workers since 1959. The work has been carried out on several fronts. Our knowledge of morphological characters and chromosome numbers has increased. Non-traditional characters such as pollen morphology, flavonoids, chloroplast DNA, and ribosomal DNA have been introduced (Stuchlik 1967a, 1967b; Taylor & Levin 1975; Smith *et al.* 1977; Johnson *et al.* 1996; Porter 1977; Day, unpubl.). A sixth section of *Gilia*, section *Kelloggia*, has been set up (Day 1993a, 1993b). Two sections of the 1959 system, *Giliandra* and *Giliastrum* have been segregated as the genera *Aliciella* and *Giliastrum*, respectively (Porter 1998a, 1998b).

It is time to restudy and revise the system of classification of *Gilia* in the light of the new as well as the old evidence. This task is attempted here.

INTRODUCTION TO THE CLASSIFICATION

A survey of taxonomic characters was carried out in search for relatively conservative characters that identify groups of related species and distinguish such groups from one another. The diagnostically useful gross morphological characters and basic chromosome numbers are emphasized in the following descriptions of groups. The newer types of characters in pollen, flavonoids, and DNA are presented following the conventional characters.

A useful pollen character is the distribution of apertures. Two modes occur in *Gilia* and its close relatives: pantoporate (apertures scattered over grain) and zonocolporate (apertures in equatorial zone) (Stuchlik 1967a, 1967b; Taylor & Levin 1975; Chuang *et al.* 1978; Day, unpubl.).

Three main groups of flavonoids are found in *Gilia*, and these are designated as types A, B, and C (Smith *et al.* 1977). Type A consists of common flavonols (kaempferol, quercetin, myricetin); type B is 6-methoxyflavonols (patuletin, eupalitin, eupatolitin); type C is C-glycosylflavones (apigenin-based and luteolin-based) (Smith *et al.* 1977).

Variation in DNA sequences in a region of a chloroplast gene *matK* in *Gilia* and related genera is plotted in a cladogram (Johnson *et al.* 1996). Sequence variation in nuclear ribosomal DNA ITS is plotted on another cladogram (Porter 1997).

Variation in different types of characters is sometimes congruent and sometimes not. In the latter case, taxonomic judgment and weighting come into play. The observed distribution of characters, and my interpretation of them in cases of incongruence, are expressed in the following classification system. This system groups the species into three subgenera and seven sections. Five species are excluded from *Gilia* and transferred to other genera.

Only the essential nomenclature is given here. Additional synonyms for infrageneric taxa can be found in Grant (1959).

SYSTEM OF CLASSIFICATION

GILIA Ruíz & Pavón, *Prodr. Fl. Peruv.*, 25 and t. 4. 1794. TYPE SPECIES: *Gilia laciniata* Ruíz & Pavón.

Plants herbaceous; perennial, biennial or annual, sometimes with a woody or soft-woody base. Herbage with several types of pubescence, but not with dense coarse woolly hairs. Leaves alternate, with irregular pinnate teeth, lobes, or divisions, or entire-margined and linear in reduced forms. Usually spring blooming. Corolla mostly funnellform, sometimes campanulate, rotate, or salverform. Seeds angular, mostly sandy-colored, mostly mucilaginous when wet, but not mucilaginous in two sections. Chromosomes large, basic number $x=9$ in most sections, $x=8$ in sect. *Giliandra*.

Pollen zonocolporate, except in subg. *Kelloggia* where pantoporate. Flavonoids of type A and C widespread in genus; type B flavonoids found only in sections *Giliastrum* and *Gilmania* so far as known. (See preceding section for explanation of these terms.).

Widespread in western North America, also in temperate South America.

73 species as presently understood. These are grouped here in three subgenera and seven sections.

For the relationships of *Gilia* to the *Eriastrum-Ipomopsis-Langloisia* group and *Leptodactylon-Linanthus* group see Grant (1998). The relationships between *Gilia*, and *Tintinabulum* and *Macugilia* are considered later in the present paper.

Key to the Main Subgroups of *Gilia*

- A. Perennials or biennials, with woody base or herbaceous throughout.
 - B. Corolla campanulate or rotate. Pollen blue. Seeds mucilaginous when wet. ... sect. *Giliastrum*, in part
 - BB. Corolla funnelform, or occasionally salverform. Pollen yellow or white (except blue in 1 species of sect. *Giliandra*). Seeds not mucilaginous when wet.
 - C. Plants scapose. Basal leaves pinnately lobed or divided, with strap-shaped rachis. $x=8$sect. *Giliandra*, in part
 - CC. Plants not scapose. Leaves with broad blade. $x=9$. Rare..... sect. *Gilmania*, in part
- AA. Annual herbs.
 - D. Corolla campanulate..... *G. incisa* group in sect. *Giliastrum*
 - DD. Corolla funnelform, or occasionally salverform.
 - E. Seeds not mucilaginous when wet. Pollen yellow or white.
 - F. Plants scapose. Basal leaves pinnately lobed or divided, with strap-shaped rachis. $x=9$ or 8..... *G. leptomeria* group in sect. *Giliandra*
 - FF. Plants not scapose. Leaves with broad blade. $x=9$. Uncommon..... *G. latifolia* in sect. *Gilmania*
 - EE. Seeds mucilaginous when wet. Pollen blue.
 - G. Leaves with 1 or 2 linear finger-like lobes, or reduced and unlobed. Pollen pantoporate. Middle and high elevations in mountains. subg. *Kelloggia*
 - GG. Leaves dissected but not with lobes as in G. Pollen zonocolporate. Mainly at lower elevations, uncommon in middle elevations, and rarely at high elevations. subg. *Gilia*
 - H. Pubescence of interwoven fine cobwebby hairs. Basal leaf rosette present.sect. *Arachnion*
 - HH. Pubescence of straight multicellular hairs and stipitate glands. Basal leaf rosette present or absent.
 - I. Upper leaves well developed. No basal leaf rosette. Inflorescence usually a head or cluster..... sect. *Gilia*
 - II. Upper leaves much reduced. Basal leaf rosette present. Inflorescence an open cyme..... sect. *Saltugilia*

I. *GILIA* subg. *GREENEOPHILA* Brand, Pflanzenreich 250:144. 1907. TYPE SPECIES: *Gilia rigidula* Benth.

Perennials, sometimes with woody or soft-woody base, biennials, and annuals. Leaves with once pinnate teeth, lobes, or divisions. Corolla often concolored, sometimes bicolored. Pollen yellow, white, or blue. Seeds mucilaginous when wet or not so. Basic chromosome number $x=9$ and $x=8$.

Pollen zonocolporate. Flavonoids of types A, B, and C occur in sects. *Giliastrum* and *Gilmania*; no information on flavonoids in sect. *Giliandra*. Species representing the sections of this subgenus fall close together in the cladograms for *cpDNA* and *rnDNA*. They are remote from species of subg. *Gilia* on the same cladograms.

Center of distribution of the perennial and biennial members in northern México, Rocky Mountains, and intermountain region. Annuals widespread in western deserts. One section occurs also in temperate South America.

Three sections, sects. 1-3 as follows.

1. *GILIA* section *GILIASTRUM* Brand, Pflanzenreich 250:147. 1907. TYPE SPECIES: *Gilia rigidula* Benth.

Giliastrum Rydberg, *Fl. Rocky Mts.*, ed. 1, 699 and 1066. 1917.

Perennials with soft-woody base, and annuals. Lower leaves with a broad blade and once pinnate lobes, the lobes often sharp-tipped, or leaves linear. Corolla campanulate or rotate. Corolla concolored, violet or whitish, or bicolored, violet with a yellow center. Pollen blue in some species, no data for other species. Seeds sandy colored, mucilaginous when wet. $x=9$, $n=6$ found in one species.

Type B flavonoid is present.

Center of distribution in northern México and Texas. Secondary centers in Baja California and temperate South America.

Gilia incisa Benth., *G. insignis* (Brand) Cory & H.B. Parks, *G. foetida* Gill. ex Benth. (S. Amer.), *G. gypsophila* B.L. Turner, *G. ludens* Shinnery, *G. purpusii* K. Brandegee, *G. rigidula*, and *G. stewartii* I.M. Johnst. This species list is based on Turner (1994).

Porter (1998b) is segregating section *Giliastrum* as a genus separate from *Gilia* to eliminate polyphyly. Grouping *Giliastrum* together with subgenus *Gilia* results in a polyphyletic genus according to Porter's phylogenetic hypothesis based on *nrDNA*. According to my phylogenetic hypothesis based on all available characters, section *Giliastrum* and subgenus *Gilia* have diverged widely, but nevertheless from a monophyletic taxon. See the last two sections of this paper. Separation of *Giliastrum* from subgenus *Gilia* is thus deemed unnecessary from a phylogenetic standpoint, and in addition, is undesirable taxonomically since it obscures the relationship between the two phyletic branches.

2. *GILIA* section *GILIANDRA* A. Gray, Proc. Amer. Acad. Arts 8:276. 1870. TYPE SPECIES: *Gilia stenothyrsa* A. Gray. *Aliciella* sect. *Giliandra* (A. Gray) J.M. Porter, Aliso 17:27. 1998.

Aliciella Brand, Pflanzenreich 250:150. 1907. TYPE SPECIES: *Gilia triodon* Eastwood.

Aliciella sect. *Aliciella* subsect. *Subnudae* J.M. Porter, Aliso 17:31. 1998. TYPE SPECIES: *Gilia subnuda* Torrey ex A. Gray.

Perennial herbs, sometimes woody-based, biennial herbs, and annuals. Plants with a basal leaf rosette and scapose upper parts. Lower leaves leathery, with a strap-

shaped rachis and once pinnate lobes or divisions. Corollas mostly funnelform, sometimes salverform, tubes slender or broad. Corollas showy, concolored, blue, red, or pink; or small and inconspicuous in most annual species. Pollen yellow or white, except blue in one species (*Gilia tenuis*). Seeds sandy colored, not mucilaginous when wet. $x=8$ throughout the section, $x=9$ occurs also in some annual species.

The species of this section fall into two subgroups. The perennial and biennial species with showy flowers and $x=8$ are basal. They occur in Utah, Colorado, and adjacent areas. The second subgroup consists of annuals, mostly with small flowers, they have both $x=8$ and 9 and polyploidy. They are derived and occur in the western deserts.

The center of distribution of the showy-flowered subgroup is in the Rocky Mountains and Colorado Plateau. The annuals range widely in the western deserts as noted above.

Showy-flowered perennial species: *Gilia caespitosa* A. Gray, *G. formosa* E. Greene ex Brand, *G. haydeni* A. Gray, *G. mcvickerae* M.E. Jones, *G. pentstemonoides* M.E. Jones, *G. pinnatifida* Moc. & Sessé, *G. sedifolia* Brandegees, *G. stenothyrsa* A. Gray, *G. subnuda*, and *G. tenuis* F.J. Sm. & Neese. Annual, mostly small-flowered species: *G. heterostyla* S.A. Cochrane & A.G. Day, *G. humillima*, *G. hutchinsifolia* Rydb., *G. leptomeria* A. Gray, *G. lottiae* A.G. Day, *G. micromeria* A. Gray, *G. nyensis* Reveal, *G. subacaulis* Rydb., and *G. triodon* Eastw. The list of perennial species is based on Porter (1998a), that of the annual species on Day (unpubl.).

Porter (1998a) has recently segregated *Giliandra* and *Gilmania* as a separate genus, *Aliciella*, in order to achieve monophyly. A genus containing *Giliandra*, *Gilmania*, and subgenus *Gilia* is polyphyletic according to Porter's phylogenetic hypothesis based on *mtDNA*. However, this combination is diverse, but monophyletic according to my phylogenetic hypothesis based on all available characters. See discussion in the last two sections of this paper. Separation of *Aliciella* from *Gilia* is deemed unnecessary phylogenetically and undesirable taxonomically for the same reasons as those given above with regard to *Giliastrum*.

3. *GILIA* section *GILMANIA* (Mason & A. Grant) V. & A. Grant, *Aliso* 3:299. 1956. TYPE SPECIES: *Gilia latifolia* S. Watson. *Gilia* subg. *Gilmania* Mason & A. Grant, *Madroño* 9:205. 1948. *Aliciella* subg. *Gilmania* (Mason & A. Grant) J.M. Porter, *Aliso* 17:43. 1998.

One species a woody-based perennial, another species an annual. Lower leaves with a broad blade and lobed margins, the lobes sharp-tipped. Corolla funnelform, pink. Pollen yellow. Seeds reddish-brown, not mucilaginous when wet. $x=9$.

Type B flavonoids present.

Deserts from southern California to Utah.

Gilia latifolia and *G. ripleyi* Barneby.

Mason & A. Grant (1948) set up a subgenus, *Gilmania*, for this distinctive small group; and Grant & Grant (1956) retained it in the rank of section. I later sank *Gilmania* into section *Giliastrum* (Grant 1959); this was a step in the wrong direction. Porter (1998a) has recently grouped sect. *Gilmania* with sect. *Giliandra* in the segregate genus *Aliciella*. I regard this as a step in another wrong direction. *Gilmania* does not fit well in either section, on conventional taxonomic characters, and is best treated as a third section coordinate with the other two.

II. *GILIA* subg. *GILIA*

Annual herbs. Leaves divided once pinnately to tripinnately, or entire margined and linear in reduced forms. Corolla mostly funnelform, sometimes salverform. Corolla concolored, or bicolored or tricolored with spots or rings. Pollen blue. Seeds mucilaginous when wet. $x=9$.

Pollen zonocolporate. Flavonoids of type B absent so far as known. Species of the three sections in this subgenus fall close together on the cladograms for *cpDNA* and *mtDNA*. They are remote from the species of subg. *Greeneophila* on the same cladograms.

Center of distribution in California, occurring in regions with summer-dry climates and in deserts. Ranging through other parts of western North America, and recurring in temperate South America.

Three sections, nos. 4-6 as follows.

4. *GILIA* section *GILIA*

Annual herbs with well-developed upper leaves. Pubescence of straight multicellular hairs and stipitate glands. Inflorescence usually a head or cluster. Corollas funnelform, concolored or tricolored.

Center of distribution in cismontane California. Ranging north to British Columbia; recurring in temperate South America.

Gilia achilleaefolia Benth., *G. angelensis* V. Grant, *G. capitata* Sims, *G. clivorum* (Jepson) V. Grant, *G. laciniata* Ruiz & Pavón (S. Amer.), *G. lomensis* V. Grant (S. Amer.), *G. millefoliata* Fischer & C. Meyer, *G. nevinii* A. Gray, *G. tricolor* Benth., and *G. valdiviensis* Griseb. (S. Amer.).

5. *GILIA* section *SALTUGILIA* V. & A. Grant, *Aliso* 3:84. 1954. TYPE SPECIES: *Gilia splendens* Douglas.

Annual herbs with well-developed basal leaves and reduced upper leaves. Pubescence of straight multicellular hairs and stipitate glands. Inflorescence cymose. Corollas funnelform, concolored.

Center of distribution in southern California. Ranging to central California mountains and to southwestern deserts.

Gilia australis (H. Mason & A.D. Grant) V. Grant & A.D. Grant, *G. caruifolia* Abrams, *G. scopulorum* M.E. Jones, *G. splendens* H. Mason & A.D. Grant, *G. stellata* A.A. Heller, and *G. yorkii* ined. *Gilia yorkii* is a new species (Shevock & Day, in press).

6. *GILIA* section *ARACHNION* A. & V. Grant, *Aliso* 3:214. 1956. TYPE SPECIES: *Gilia latiflora* A. Gray.

Annual herbs with a basal leaf rosette and scapose upper body. Pubescence of fine cobwebby hairs especially in leaf axils. Inflorescence cymose. Corollas mostly funnellform, sometimes salverform. Corollas usually tricolored.

Center of distribution in southern California mountains and Mojave Desert. Ranging to other areas of western North America; recurring in temperate South America.

Gilia aliquanta A.D. Grant & V. Grant, *G. austro-occidentalis* (A.D. Grant & V. Grant) A.D. Grant & V. Grant, *G. brecciarum* M.E. Jones, *G. cana* (M.E. Jones) A.A. Heller, *G. clokeyi* H. Mason, *G. crassifolia* Benth. (S. Amer.), *G. diegensis* (Munz) A.D. Grant & V. Grant, *G. flavocincta* A. Nels., *G. inconspicua* (Smith) Sweet, *G. interior* (H. Mason & A.D. Grant) A.D. Grant, *G. jacens* A.D. Grant & V. Grant, *G. latiflora* (A. Gray) A. Gray, *G. leptantha* Parish, *G. malior* A.G. Day & V. Grant, *G. mexicana* A.D. Grant & V. Grant, *G. minor* A.D. Grant & V. Grant, *G. modocensis* Eastw., *G. ochroleuca* M.E. Jones, *G. ophthalmoides* Brand, *G. sinuata* Douglas ex Benth., *G. salticola* Eastw., *G. tenuiflora* Benth., *G. tetrabreccia* A.D. Grant & V. Grant, *G. transmontana* (H. Mason & A.D. Grant) A.D. Grant & V. Grant, and *G. tweedyi* Rydb.

III. *GILIA* subg. *KELLOGGIA* Mason & A. Grant, *Madroño* 9:219. 1948. TYPE SPECIES: *Gilia capillaris* Kellogg.

Medium-sized to small annual herbs. Herbage glandular-puberulent, or glabrous. Upper and lower leaves about the same size. Leaves with 1 or 2 linear finger-like lobes, or unlobed and entire. Corolla funnellform, concolored or bicolored. Pollen blue, pantoporate, the sexine striated or with spinules. Capsule containing 1-6 seeds per locule. Seeds mucilaginous when wet. $x=9$.

No information on flavonoids, and only one puzzling record of DNA sequences.

Center of distribution in mountains of central California, Nevada, and Oregon. Disjunct populations in Idaho and Colorado.

7. *GILIA* section *KELLOGGIA* Day, Novon 3:332. 1993.

Characters of the subgenus.

Gilia capillaris Kellogg, *G. leptalea* (A. Gray) E. Greene, and *G. sinistra* M.E. Jones.

The species of subgenus *Kelloggia* are similar in habit, and floral and seed characters to those of subgenus *Gilia*, and occur in the same geographical area. For these reasons the species assigned here to the subgenera *Kelloggia* and *Gilia* were formerly thought to be closely related.

However, the discovery of pantoporate pollen in the species of *Kelloggia* (Day, unpubl. data) indicates that it is isolated from the subgenera *Gilia* and *Greeneophila*, which have zonocolporate pollen (Stuchlik 1967a, 1967b; Day, unpubl. data).

What are the true relationships of *Kelloggia*? Pollen characters and leaf form point to a relationship with *Allophyllum*. But more evidence is needed to determine the best taxonomic disposition of *Kelloggia*.

DNA evidence might shed light on the problem. The only DNA record of the section published so far is for *cpDNA* *matK* in *Gilia sinistra* (Johnson *et al.* 1966). It places *G. sinistra* in a group of five *Navarrettia* species in the cladogram. This result is out of line with the phenetic evidence concerning both *Kelloggia* and *Navarrettia*. Further molecular studies are needed.

EXCLUSION AND REASSIGNMENT OF FIVE SPECIES

Five species of annuals with reduced vegetative and floral characters, assigned to *Gilia*, have been poorly understood throughout this century. The species in question are *G. campanulata* A. Gray, *G. inyoensis* I.M. Johnst., *G. filiformis* Parry *ex* A. Gray, *G. maculata* Parish, and *G. tenerrima* A. Gray. The first four are desert annuals and the last one is montane. The relationships of these species to the main subgroups of *Gilia* have not been obvious from the usual taxonomic characters, leaving it up to successive workers to place them as best they can in the system. Much more has become known about these plants in the last ten years, however, and it is time for a reassessment.

The five species do not fit well into any of the seven sections recognized in the present treatment. If they were to remain in *Gilia*, additional sections would have to be set up for them. This is a plan that I considered and tried to implement but in the end discarded. The species are not only misfits in *Gilia*, but show signs of relationship to other genera. Therefore, it seems best to take them out of *Gilia* and place them in other genera. I am resurrecting the long dormant genus *Tintinabulum* of Rydberg (1917) for *G. campanulata*, *G. inyoensis*, and *G. filiformis*. A new genus *Maculigilia* is set up for *G. maculata*; and *G. tenerrima* is transferred to *Allophyllum*.

TINTINABULUM Rydberg, *Fl. Rocky Mts.*, ed. 1, 698 and 1065. 1917. TYPE SPECIES: *Gilia filiformis* Parry ex A. Gray. *Gilia* subg. *Tintinabulum* Mason & Grant, *Madroño* 9:220. 1948.

Gilia subg. *Greeneophila* sect. *Campanulastrum* Brand, *Pflanzenreich* 250:144. 1907. TYPE SPECIES: *Gilia campanulata* A. Gray. *Gilia* subg. *Campanulastrum* Mason & A. Grant, *Madroño* 9:219. 1948.

Small desert annuals with a spreading habit. Stems very slender. Leaves alternate, reduced, lanceolate to linear. Flowers solitary on slender pedicels. Corolla narrowly to broadly campanulate. Corolla yellow or bicolored yellow and white. Pollen yellow. Seeds mucilaginous when wet. $x=9$.

Center of distribution northern Mojave Desert, ranging through deserts to Utah and Arizona. Three species.

Tintinabulum filiforme (Parry ex A. Gray) Rydberg, *Fl. Rocky Mts.*, ed. 1, 698 and 1065. 1917. BASIONYM: *Gilia filiformis* Parry ex A. Gray, *Proc. Amer. Acad. Arts* 10:75. 1874.

Tintinabulum campanulatum (A. Gray) V. Grant, *comb. nov.* BASIONYM: *Gilia campanulata* A. Gray, *Proc. Amer. Acad. Arts* 9:279. 1870.

Tintinabulum inyoensis (I.M. Johnston) V. Grant, *comb. nov.* BASIONYM: *Gilia inyoensis* I.M. Johnston, *Contrib. Gray Herb.* 75:39. 1925.

These three species differ from the rest of *Gilia*, or from *Gilia* as delimited here, in spreading habit with very slender stems, and differ from most sections of *Gilia* in campanulate corollas. In my old treatment (Grant 1959) I included them in *Gilia* sect. *Giliastrum* on what now seem to be superficial resemblances. Mason & A. Grant (1948) had previously assigned them to two adjacent small subgenera of *Gilia*, subg. *Campanulastrum* and subg. *Tintinabulum*, which was on the right track. They could be retained in *Gilia* as a third subgenus.

However, in growth habit and floral characters, the plants resemble *Linanthus* sect. *Dactylophyllum* (the *L. aureus* [Nutt.] E. Greene group). Furthermore, they cluster with *Leptodactylon* and *Linanthus* in the cladograms for *nrDNA* (Porter 1997) and *cpDNA* (Johnston *et al.* 1996).

These indications of a relationship with *Linanthus*, particularly the DNA evidence, tilt the scales in favor of segregating the group at the genus level. Rydberg's (1917) small genus *Tintinabulum* is a good place for them. The genus *Tintinabulum* is assigned to the tribe Gilieae.

MACULIGILIA V. Grant, *genus novum*. TYPE SPECIES: *Gilia maculata* Parish.

Herbae annuae diminutivae, hirsutae. Folia integra, oblongata vel oblanceolata. flores in capitulis terminalibus. Corolla campanulata, maculata. Pollen flavus, pantoporatus. Semina rubicunda brunnea, sub aqua immutata. Chromosomae $x=9$.

Small annuals with spreading habit. Stems with dense cover of long hairs. Leaves fleshy, entire, oblong or oblanceolate. Inflorescence a dense cluster. Calyx lobes free with ciliated membranous margins. Corolla campanulate, corolla lobes notched at tip. Corolla tricolored with white lobes and throat, yellow tube, and red spots on lobes. Pollen yellow, pantoporate. Seeds dark reddish brown, not mucilaginous when wet. $x=9$.

Colorado Desert, California, rare. One species.

Maculigilia maculata (Parish) V. Grant, *comb. nov.* BASIONYM: *Gilia maculata* Parish, Bull. Torrey Bot. Club 19:93. 1892. *Linanthus maculatus* (Parish) Milliken, Univ. California Publ. Bot. 2:55. 1904.

This rare species was described as a *Gilia* by Parish in 1892, but transferred to *Linanthus* by Milliken (1904) and retained there by later students (e.g., Jepson 1943; Grant 1959). Patterson (1989) rediscovered the species in the wild and made a thorough study of it. The above diagnosis is based on Patterson's more detailed description. Patterson concluded that the species does not belong in *Linanthus*, but can be accommodated in *Gilia* though it is unique there.

Species *maculata* differs from the present sections of *Gilia* in its calyx, pubescence, and leaf blades, and from all sections except *Kelloggia* in having pantoporate pollen.

The species does, however, share some distinctive characters in common with section *Gilmania*. Namely, seed characters, pollen color, and desert ecology. These characters suggest a relationship with section *Gilmania*.

But the molecular evidence points in a different direction. In the cladogram for nrDNA ITS (Porter 1997), *Maculigilia maculata* clusters with *Leptodactylon* and *Linanthus*. It is also close to the *Tintinabulum campanulatum* group which is close to *Leptodactylon* and *Linanthus* in the cladogram.

Nevertheless, *Maculigilia maculata* is well outside the range of variation of these genera. Therefore, it is segregated into a monotypic genus of its own which seems to lie somewhere between *Linanthus* and *Gilia*. *Maculigilia* is assigned tentatively to the tribe Leptodactyloneae.

Allophyllum tenerrimum (A. Gray) V. Grant, *comb. nov.* BASIONYM: *Gilia tenerrima* A. Gray, Proc. Amer. Acad. Arts 8:277. 1870. *Navarrettia tenerrima* Kuntze, *Revisio Gen. Pl.* 2:433. 1891.

Small annual herb with spreading habit. Leaves, flowers, and capsules much reduced. Pubescence stipitate-glandular with a slender stalk bearing a black gland. Leaves alternate, oblanceolate to linear with 1 or 2 lobes, or not lobed and entire. Flowers solitary, small. Corolla tube and throat white and lobes pale blue. Pollen grains approaching pantoporate, with fine spinules on the tectum. Capsule globular, containing usually 1 seed per locule, valves usually falling off at maturity. Seeds rounded, ovoid, brown; mucilaginous when wet. $x=9$; $2n=36$.

Mid and high elevations in mountains, eastern Oregon and Sierra Nevada of California to Wyoming and Utah.

This species has been included in *Gilia* in almost all treatments since Gray (1878). In some modern treatments it has been placed close to the *Gilia leptalea* group which is now *Gilia* sect. *Kelloggia* (Mason & A. Grant 1948, 1951; Grant 1959). It is, however, quite distinct within *Gilia*.

Stuchlik (1967a, 1967b) and Day (unpubl.) noted that species *tenerrimum* is similar to *Allophyllum* in pollen morphology. Day (unpubl.) noted other similarities to *Allophyllum* in pubescence and gross morphology. The trichomes, leaf form, capsules, and seeds of species *tenerrimum* are characteristic of *Allophyllum* but not of *Gilia*. This evidence supports the conclusion that the species belongs to *Allophyllum*, a conclusion with which Day agrees (pers. comm.). *Allophyllum tenerrimum* is amply different from the typical *Allophyllum* -- *A. gilioides* (Benth.) A.D. Grant & V. Grant, *A. glutinosum*, etc. -- but many of the differences can be attributed to the reduced nature of *A. tenerrimum*.

In the DNA cladograms (Johnson *et al.* 1996; Porter 1997), *Allophyllum tenerrimum* occurs close to both *Allophyllum* and *Gilia* subg. *Gilia*.

PHYLOGENY

The characters and character combinations used to delineate the subgenera and sections of *Gilia* can be used to infer a probable phylogeny. The two subgenera, *Greeneophila* and *Gilia*, represent two main branches in the inferred phylogenetic tree (Figure 1). Of these two, the subgenus *Greeneophila* contains the most primitive characters.

The *Gilia rigidula* group (in subg. *Greeneophila* sect. *Giliastrum*) exhibits the primitive life-form or woody-based perennials. It approaches the most primitive genus *Loeselia* in life-form and is similar to it in sequences of *cpDNA* and *rnDNA* (Johnson *et al.* 1996; Porter 1997). The *G. rigidula* group occurs with *Loeselia* in northern México and Texas, and is probably derived from a *Loeselia*-like ancestor in this area (Grant 1959, 1998).

The perennial members of the other sections of subgenus *Greeneophila* exhibit some derived features as compared with section *Giliastrum*, and appear to be side-branches derived from a *Gilia rigidula*-like ancestor. The perennial species of section *Giliandra* have colonized the Rocky Mountains and Colorado Plateau. The centers of distribution of the perennial members of subgenus *Greeneophila* thus lie in a region from northern México to the Rocky Mountains and Colorado Plateau.

All three sections of subgenus *Greeneophila* have given rise to reduced annuals which have colonized western deserts.

The subgenus *Gilia* with its three interrelated sections (*Gilia*, *Saltugilia*, and *Arachnion*) consists entirely of annuals. The showy-flowered species are the basal members of this subgenus. These have their center of distribution and probable center of origin in California. The derived small-flowered members are widespread in the western deserts and mountains where they intermingle with the reduced annuals of subgenus *Greeneophila*.

Subgenus *Gilia* is united with subgenus *Greeneophila* by some common characters, but is also amply different from *Greeneophila* in morphology and center of distribution. It is also far removed from the subgenus *Greeneophila* in the cladograms for *cpDNA* *matK* and *nrDNA* ITS (Johnson *et al.* 1996; Porter 1997).

It is suggested that the three sections of subgenus *Gilia* branched off from an ancestor in or near the *G. rigidula* group in California in response to climatic changes toward summer-dry conditions. Such climatic changes occurred in the Middle Pliocene, Late Pliocene, and Xerothermic phase of the Quaternary (Axelrod 1948, 1950; Raven & Axelrod 1978). The hypothesis presumes that the ancestor disappeared from the California area as the climate became unfavorable for it, creating the present systematic gap. Sections *Saltugilia* and *Arachnion* then went on to radiate in the deserts as desert areas expanded in the Late Pliocene and Xerothermic time.

An origin of subgenus *Gilia* from the perennial *G. rigidula* group presents no particular theoretical difficulties. The *G. rigidula* group has given rise to the annual *G. incisa* group in Texas. There is not much difference between *G. incisa* and reduced plain-flowered species of subgenus *Gilia*, such as *G. angelensis* and *G. australis*.

The third subgenus *Kelloggia* does pose a problem. On general morphological characters, it has been allied to the other far-western annual gilies. However, it has pantoporate pollen (Day, unpubl. data). This is a primitive condition in the family, and occurs in *Loeselia* among other genera, whereas the rest of *Gilia* including the *G. rigidula* group has the derived condition of zonocolporate pollen (Stuchlik 1967a, 1967b; Taylor & Levin 1975; Day, unpubl. data).

This suggests that subgenus *Kelloggia* is not as closely related to the western annual gilies as has been thought, is not derived from the *Gilia rigidula* group, and may have an independent origin with some unknown ancestor with pantoporate pollen (Figure 1). If this suggestion is confirmed, *Kelloggia* does not belong in *Gilia*.

A number of cases exist in *Gilia* and its relatives where a given group exhibits evidence of relationships in two different directions. Some characters of the group in question, group X, indicate a relationship with group A, other characters of group X relate it to group B, and A and B are too distantly related to be able to hybridize. Subgenus *Kelloggia* is one example of this. *Maculigilia* is another; one set of characters suggests a relationship with *Gilia* section *Gilmania*, while another set indicates a relationship with *Linanthus*. Other such cases are noted in the preceding sections.

What are the phylogenetic explanations of the apparently bipolar relationships? One explanation is convergence which is common and widespread. Convergent evolution has produced desert annuals with reduced vegetative characters and small flowers in four sections (*Giliastrum*, *Giliandra*, *Saltugilia*, *Arachnion*); the similar-

appearing species were grouped together in the same artificial section *Eugilia* of older authors. Another source of bipolar relationships may be the retention of disparate elements in the genotype from ancient hybridization events; this is a possibility that we know very little about. We should also consider horizontal gene transfer between remotely related groups, which may be more common in nature than we realize.

DISCUSSION

Until recently all systematic studies of *Gilia* and other Polemoniaceae were carried out within the framework of either traditional taxonomy or evolutionary systematics (cf. Grant 1998). Studies of DNA sequence variation in Polemoniaceae including *Gilia* began in the 1990s, and the DNA evidence has been analyzed and interpreted according to the procedures of cladistics (Steele & Vilgalys 1994; Johnson *et al.* 1996; Porter 1997, 1998a).

The philosophy and methods of traditional taxonomy and evolutionary systematics, on the one hand, and those of molecular cladistics on the other, are very different, and lead to different conclusions in some cases. I have discussed the differences as regards the family Polemoniaceae elsewhere (Grant 1998), and will discuss the differences with respect to *Gilia* here.

Johnson *et al.* (1996) and Porter (1997, 1998a) state emphatically that *Gilia* is polyphyletic; indeed, "extremely" polyphyletic (Johnson *et al.* 1996). Actually, the phrase "extreme polyphyly" applies better to the historical catchall genus *Gilia* of the nineteenth century than it does to the *Gilia* of recent times. Successive generations of botanists have labored throughout the twentieth century to make *Gilia* more natural or less polyphyletic, and much progress has been made.

What is the standard of reference for determining the polyphyly or monophyly of a taxonomic group? For Johnson *et al.* (1996) and Porter (1997, 1998a, 1998b) there is only one standard. It is the cladogram or gene tree of a particular DNA segment. Johnson *et al.* (1996) and Porter (1997) go directly from the clades in their DNA cladograms to informal taxonomic groups, as I have shown in my analysis of their work (Grant 1998). Porter (1998a, 1998b) takes it a step further by converting several of the informal taxa into formal ones. Porter's (1998a) subdivisions of *Aliciella* conform closely to the set of clades and subclades in his *nrDNA* cladogram (Porter 1997). *Gilia* species occur in different clades of the DNA cladograms, and it is on this basis that *Gilia* is said to be extremely polyphyletic (Johnson *et al.* 1996; Porter 1997, 1998a).

There is another standard of reference for monophyly/polyphyly, namely, the system of classification built up by the methods of traditional taxonomy and evolutionary systematics. These methods include consideration of all possible characters and weighting of characters in cases of conflict in the evidence. They are responsible for almost all of the progress that has been made toward a phylogenetically natural classification of *Gilia* and allied genera.

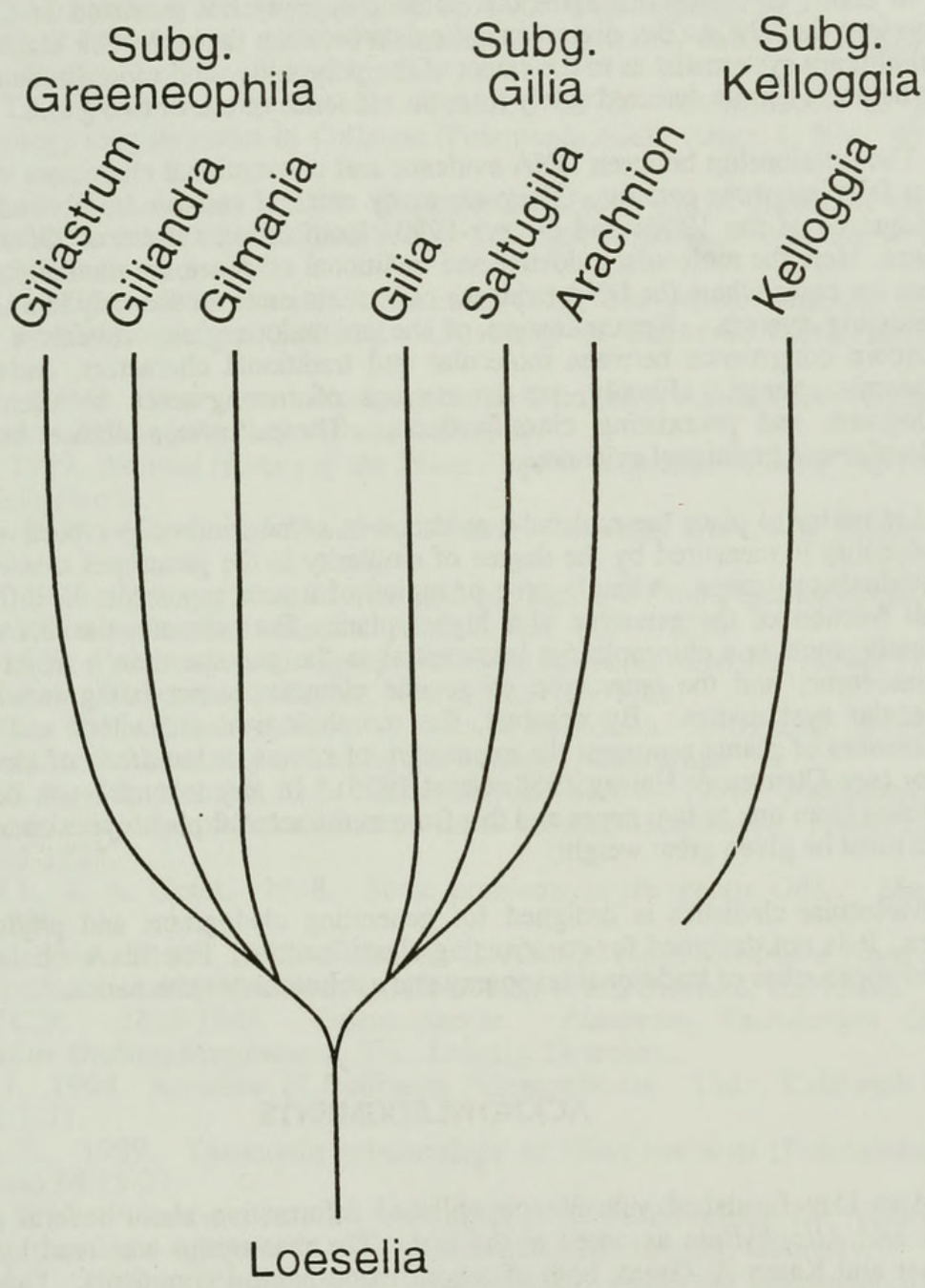


Figure 1. Proposed phylogeny of the main subgroups of the genus Gilia.

In short, all parties can agree that some polyphyly has persisted in *Gilia* and its allies into the 1990s. But disagreement exists between the molecular cladists and this evolutionary systematist as to the extent of the polyphyly, and more fundamentally, as to whether it can be detected solely from the evidence of one or two genes.

The relationship between DNA evidence and conventional characters in *Gilia* and allies falls into three patterns. There are many areas of congruence between the DNA cladograms of the 1990s and the pre-1990 classification system of *Gilia* and allied genera. Here the molecular evidence and traditional evidence are mutually supportive. There are cases where the DNA evidence calls attention to an anomaly in a sector of the preexisting system. Reexamination of the anomalous group reveals a previously unknown congruence between molecular and traditional characters, and leads to a taxonomic change. Finally, we have cases of incongruence between the DNA cladograms and preexisting classifications. These force a choice between the molecular and traditional evidence.

Let us try to place the molecular evidence in some kind of perspective. Natural relationship is measured by the degree of similarity in the genotypes of two or more individuals or groups. A single gene or region of a gene represents an infinitesimally small fraction of the genotype of a higher plant. Furthermore, the DNA of a cell organelle such as a chloroplast is less central to the genome than a major gene in a chromosome, and the latter type of genetic element is not being tested in plant molecular systematics. By contrast, the morphological characters and ecological preferences of plants represent the expression of scores or hundreds of chromosomal genes (see Clausen & Heisey 1958; Grant 1975). In any incongruence between the evidence from one or two genes and that from multifactorial phenotypic characters, the latter must be given great weight.

Molecular cladistics is designed for generating cladograms and phylogenies of genes. It is not designed for constructing classifications. For this we have the time-tested approaches of traditional taxonomy and evolutionary systematics.

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