

TAXONOMY OF THE POLEMONIACEAE: *GILIA* AND *LATHROCASIS*

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ABSTRACT

The infrageneric classification of *Gilia* is reviewed and revised on the basis of numerous phenetic and some molecular characters and by using a taxonomic approach. The result is a broadly defined multisection genus *Gilia* composed of two subgenera and seven sections (sects. *Gilia*, *Arachnion*, *Saltugilia*, *Giliastrum*, *Giliandra*, *Gilmania*, *Campanulastrum*), and a monotypic segregate genus (*Lathrocasis*). This system is compared with that of Porter and Johnson (2000) based primarily on molecular evidence and a cladistic approach. The two systems agree in some dispositions; in fact, the present system follows Porter and Johnson in recognizing *Lathrocasis*; but in other respects the two systems differ greatly. For example, the core genus *Gilia* is divided into six smaller genera in addition to *Lathrocasis* by Porter and Johnson. Basic differences between taxonomic and molecular cladistic approaches lead to the incongruences between alternative systems found here and elsewhere in the Polemoniaceae and in other plant families. These differences are discussed. A weakness of molecular cladistics is the attempt to classify groups by using DNA evidence primarily or exclusively. Better results can be obtained by combining the molecular characters with phenetic characters. There is a continuing need for new taxonomic revisions in the Polemoniaceae and other families that do this.

KEY WORDS: Cladistics, *Gilia*, *Lathrocasis*, molecular systematics, Polemoniaceae, taxonomy

RESUMEN

Se revisa la clasificación infragenérica de *Gilia* en base a numerosos caracteres fenéticos y algunos moleculares, usando una aproximación taxonómica. El resultado es el género multisección ampliamente definido *Gilia* compuesto de dos subgéneros y siete secciones (sects. *Gilia*, *Arachnion*, *Saltugilia*, *Giliastrum*, *Giliandra*, *Gilmania*, *Campanulastrum*), y un género monotípico segregado (*Lathrocasis*). Este sistema se compara con el de Porter y Johnson (2000) basado primariamente en pruebas moleculares y una aproximación cladística. Los dos sistemas concuerdan en algunas disposiciones; de hecho, el presente sistema sigue a Porter y Johnson en el reconocimiento de *Lathrocasis*; pero en otros aspectos los dos sistemas difieren enormemente. Por ejemplo, el núcleo del género *Gilia* se divide en seis géneros más pequeños en adición a *Lathrocasis* según Porter y Johnson. Las diferencias básicas entre la aproximación taxonómica y la cladística molecular dan lugar a incongruencias entre sistemas alternativos como se encuentra aquí y en otros estudios sobre Polemoniaceae así como en otras familias. Se discuten estas diferencias. Un punto débil de la cladística molecular es el intento de clasificar grupos usando primaria o exclusivamente DNA. Se pueden obtener mejores resultados combinando caracteres moleculares con caracteres fenéticos. Hay una necesidad creciente de nuevas revisiones taxonómicas en las Polemoniaceae y otras familias de igual comportamiento.

INTRODUCTION

In the nineteenth century, *Gilia* was treated as a catchall genus for the temperate herbaceous Polemoniaceae that did not fit into the well-defined genera *Polem-*

onium, *Phlox*, and *Collomia*. *Gilia* in that era was consequently very heterogeneous and was subdivided into numerous sections (Bentham & Hooker 1873–1876; Gray 1886; Peter 1897).

In the early twentieth century as the plants became better known morphologically and in the field, it became apparent that many of these sections were only remotely related to one another. Milliken (1904) started the process of reclassification by segregating *Navarretia* and *Linanthus* from *Gilia*. Her *Gilia* remained heterogeneous with six subgenera. Subsequent authors continued the process of pruning by spinning off *Eriastrum*, *Leptodactylon*, *Allophyllum*, *Ipomopsis*, etc. as separate genera, while retaining a polymorphous core genus *Gilia*.

Grant's (1959) treatment recognized a core genus *Gilia* composed of five interrelated sections (sects. *Giliastrum*, *Giliandra*, *Gilia*, *Arachnion*, *Saltugilia*). Section *Giliastrum* has been subdivided subsequently into two or three smaller sections (Grant 1999) (Table 1).

In 1959 I thought that the disparate elements had all been removed from *Gilia*, and Alva Day thought so too, but this was not the case. In later studies using pollen-morphological characters, Day (1993a, b) found a small group of species in *Gilia* sect. *Saltugilia* (the *G. leptalea* group) that did not belong in *Gilia*. It was not clear in 1993 where these species did belong. Day placed them in a section *Kelloggia* of *Gilia* for holding purposes, and later she and I transferred them to *Allophyllum* (Grant & Day 1999).

All these groupings and regroupings were made by taxonomists working within the conceptual framework of traditional or evolutionary taxonomy, using numerous phenetic characters, and changing the system gradually and progressively. In the year 2000, Porter and Johnson published a radically different classification of the *Gilia* complex and of the family as a whole. Their system was arrived at by the approach of molecular cladistics; they used DNA sequence variation in selected organellar genes as evidence, and interpreted this evidence according to cladistic concepts.

In the Porter and Johnson (2000) system, the genus *Gilia* of Grant (1959, 1999) is broken up into seven genera, as shown in Table 1. With regard to one species group, the former *Gilia leptalea* group, both parties agree that it should come out of *Gilia*, but do not agree on where to put it (Table 1). The new monotypic genus *Lathrocasis* was set up for *Gilia tenerrima* (Porter & Johnson 2000); I did not at first accept *Lathrocasis* but do so now in this paper (Table 1). The genus *Gilia* of Porter and Johnson (2000) consists of *Gilia* sects. *Gilia* and *Arachnion* plus part of *Gilia* sect. *Saltugilia*. And their genus *Gilia* is separated at the tribal level from the other sections of *Gilia* (from *Gilia* subg. *Greeneophila*).

How do we explain the large differences between the two contemporaneous and up-to-date classifications of *Gilia* s. l.? Porter and Johnson (Johnson et al. 1996; Porter 1998; Porter & Johnson 2000) claim that *Gilia* s. l. is polyphyletic; their subdivided system is intended to correct the situation. I have argued

TABLE 1. Comparison of two current classifications of *Gilia* and certain gilioid taxa.

| Grant system (1999, 2001, this paper) | Porter and Johnson system (2000) | Tribe in PJ system |
|---|---|---------------------|
| <i>Gilia</i> subgen. <i>Gilia</i> | | |
| Sect. <i>Gilia</i> | Genus <i>Gilia</i> | <i>Gilieae</i> |
| Sect. <i>Arachnion</i> | Genus <i>Gilia</i> | <i>Gilieae</i> |
| Sect. <i>Saltugilia</i> | Genus <i>Saltugilia</i> | <i>Gilieae</i> |
| <i>Gilia</i> subgen. <i>Greeneophila</i> | | |
| Sect. <i>Giliastrum</i> | Genera <i>Giliastrum</i> , <i>Dayia</i> , <i>Bryantiella</i> | <i>Loeseliaceae</i> |
| Sect. <i>Giliandra</i> | <i>Aliciella</i> | <i>Loeseliaceae</i> |
| Sect. <i>Gilmania</i> | <i>Aliciella</i> | <i>Loeseliaceae</i> |
| Sect. <i>Campanulastrum</i> | <i>Linanthus campanulatus</i> group | <i>Phlocideae</i> |
| <i>Lathrocasis</i> (formerly in <i>Gilia</i>) | <i>Lathrocasis</i> | <i>Gilieae</i> |
| <i>Allophyllum leptaleum</i> group (formerly in <i>Gilia</i>) | <i>Navarretia leptalea</i> group (Formerly in <i>Gilia</i>) | <i>Gilieae</i> |

elsewhere (Grant 2001, 2003a, b) that the claim of polyphyly is not supported by the evidence, except in the *Gilia leptalea* group. The polyphyly issue will be discussed again later in this paper.

The difference between the alternative treatments of the *Gilia* complex can be adequately explained as a result of using the very different approaches of taxonomy and cladistics. The differences in working concepts and methods can be summarized briefly here (see Grant 2003a for review). First, the systematic units of taxonomy are similarity groups or taxa, those of cladistics are inferred phyletic lineages or clades. Second, taxonomy uses a traditional definition of monophyly: any group descended from a close common ancestor; whereas cladistics defines monophyly as a group consisting of **all** the descendants of the common ancestor. A given group can be monophyletic by the taxonomic definition but non-monophyletic by the cladistic definition.

Third, taxonomy employs any and all characters that are useful in distinguishing taxa. Phenetic cladistics sets some restrictions on the characters used. Molecular cladistics uses one or a few preselected DNA segments; the data are valuable but the database is very narrow. Fourth, taxonomy and molecular cladistics sample different parts of the overall genomes. The phenetic characters used in taxonomy are expressions of the chromosomal genome. The organellar DNA used in molecular cladistics is cytoplasmic in origin in the case of chloroplast and mitochondrial genes and is encoded in a special kind of chromosome site in the case of ribosomes.

Finally, there is always a subjective element when a cladogram is transformed into a system of taxa. Is a given clade going to be treated as a genus or a section?

These factors inevitably bring about some differences between taxonomic and molecular cladistic systems of the same plant group. They account for the differences in the tribal classification of the Polemoniaceae of Porter and

Johnson (2000) and Grant (2003b). And they will explain most of the differences in the treatment of the *Gilia* complex.

This brings us to the next question. In cases of incongruence between taxonomic and molecular cladistic systems of classification, which system comes closest to the goal of expressing natural or phylogenetic relationships? The short answer is: sometimes one system or approach, sometimes the other.

I have found the following modes in comparisons of taxonomic with molecular cladistic systems in the Polemoniaceae and other plant groups. (1) Each system is acceptable by its own standards. (2) A cladistic author applies the cladistic definition of monophyly to a taxonomic system which is natural by the taxonomic definition of monophyly, and the cladistic author then falsely accuses the taxonomic treatment of being non-monophyletic. (3) The molecular cladograms reveal a relationship which taxonomists had not noticed and which leads to a desirable revision in the taxonomy. (4) The DNA evidence is in conflict with a pattern of variation in reliable phenetic characters. This is likely to occur when the DNA evidence is derived from cytoplasmic organelles, especially chloroplasts, which are semi-independent of the chromosomal genome which determines most taxonomic characters. A chloroplast DNA cladogram may give a very distorted picture of the organismic relationships in a plant group.

Many plant groups have been studied with respect to both DNA markers and morphological or other phenetic characters. Sometimes the two kinds of characters are in agreement, sometimes they are not, and the latter situation is common. Rieseberg et al. (1996) list 34 seed plant genera in which discordance is found between DNA markers and phenetic characters. The type of DNA that is most common in the list of unreliable markers is chloroplast DNA. Unreliable chloroplast markers are found for example in: *Helianthus* (Rieseberg 1991; Rieseberg et al. 1991), *Quercus* (Whittemore & Schaal 1991), *Eucalyptus* (McKinnon et al. 1999), and *Gossypium* (Cronn et al. 2002).

In *Helianthus* (Rieseberg 1991; Rieseberg et al. 1991), *Quercus* (Whittemore & Schaal 1991), *Gossypium* (Cronn et al. 2002), and *Phlox* (Ferguson & Jansen 2002) it is possible to compare the reliability of chloroplast DNA with that of ribosomal DNA. In each case ribosomal DNA is more concordant with phenetic character variation than chloroplast DNA is.

The various sources of incongruence between taxonomic and molecular cladistic systems, listed above, all occur in the *Gilia* complex and other Polemoniaceae. Examples will be given in this paper.

Old taxonomic treatments are currently being revised by cladistic, mainly molecular cladistic, methods, but cladistic systems are not always right. There is a continuing need for up-to-date taxonomic treatments. Such treatments provide a choice for those who use classifications. With this goal in mind, I have recently revised and updated the tribal classification of the Polemoniaceae (Grant 2003b), and am doing the same here for the genus *Gilia*.

MATERIALS AND METHODS

I assembled as many characters as I could that distinguish major subgroups in *Gilia* s. l. These are mostly gross morphological features but also micromorphological or biochemical.

Among the microscopic characters that are useful in *Gilia* is corolla venation. The lower part of the corolla in *Gilia* has five sets of veins, one set for each corolla lobe, and each set has three parallel veins. The veins of a set branch above or distally. In some sections of the genus, the veins remain separate distally, while in other sections they anastomose distally (Day & Moran 1986; Day, pers. comm.).

The flavonoids in the genus fall into three groups, designated as types A, B, and C, and these types vary among the sections (Smith et al. 1977). Type A flavonoids are kaempferal, quercetin, and myricetin; type B is 6-methoxyflavonal; and type C is C-glycosylflavone (Smith et al. 1977).

A number of studies of DNA sequence variation have been made in the Polemoniaceae (listed in Porter & Johnson 2000; and Grant 2003b). For the purpose of this study I used mainly the papers of Johnson et al. (1996), Porter (1997, 1998), and Johnson and Weese (2000) which have the best coverage of the *Gilia* complex. Johnson et al. present cladograms of cpDNA *matK*, Porter of rDNA ITS, and Johnson and Weese of rDNA ITS, cpDNA *trnL*, and *matK*.

Recently Johnson et al. (2004) have published a survey of the fine structure of the seed coat in *Gilia* and related genera (see their SEM photographs).

The descriptions in the formal classification consist mainly of diagnostic characters. These serve to show the evidence supporting the classification. Good complete descriptions are given by Porter and Johnson (2000).

ANALYTICAL KEY TO THE MAIN GROUPS OF *GILIA* AND *LATHROCASIS*

1. Glandular hairs with tiny black tips; pollen white; seeds one per locule in capsule _____ Genus **Lathrocasis**
1. Glandular hairs where present with amber or colorless terminal glands; pollen blue, yellow or cream; seeds generally several or many per locule in capsule _____ Genus **Gilia**
2. Pollen blue; stamens inserted in sinuses of corolla lobes; annuals _____ **Gilia** subgen. **Gilia**
3. Pubescence of long fine intertwined white cobwebby hairs; stipitate glandular hairs often present also _____ **Gilia** sect. **Arachnion**
3. Cobwebby pubescence not present, pubescence consisting of multicellular trichomes and stipitate glandular hairs.
4. Plants scapose _____ **Gilia** sect. **Saltugilia**
4. Plants not scapose, cauline leaves ranging from large on lower stems to small on upper stems _____ **Gilia** sect. **Gilia**
2. Pollen generally yellow or cream, but blue in one species; stamens inserted in corolla tube, throat, or sinuses; perennials and annuals _____ **Gilia** subgen. **Greeneophila**
5. Plants usually branching from base with stems spreading, but sometimes single-stemmed; corolla generally campanulate or rotate; seeds mucilaginous when wet.
6. Small annuals with wiry stems and small flowers _____ **Gilia** sect. **Campanulastrum**
6. Perennials and some annuals; flowers showy or small _____ **Gilia** sect. **Giliastrum**

5. Plants scapose with a basal rosette and a central leader stem; corolla funnel-form or sometimes trumpet-shaped; seeds not mucilaginous when wet or only slightly so.

7. Lower leaves pinnate with a broad strap-shaped rachis and short lobes

Gilia sect. **Giliandra**

7. Lower leaves with a broad blade and lobed margin, the lobes sharp-tipped

Gilia sect. **Gilmania**

CLASSIFICATION

Genus 1. *Gilia* Ruiz & Pavon, Prod. Fl. Peruv. 25, t. 4. 1794. TYPE: *Gilia laciniata* Ruiz & Pavon.

Herbaceous perennials, biennials, or annuals, sometimes with a woody or soft woody base. Basal leaves well developed and upper cauline leaves much reduced in size, or moderately reduced in sect. *Gilia*. Generally spring blooming. Flowers usually in loose or glomerate cymes, or sometimes solitary or in capitate heads. Calyx lobes equal in length. Corolla frequently moderate-sized and showy, or small in many species. Pollen pores zonocolporate. Seeds small, angular, and sandy-colored, usually numerous in the capsule. Ancestral basic chromosome number $x = 9$ present in all sections; polyploidy common. Other characters vary between the subgenera and sections.

Distribution and taxa.—Widespread in western United States and Canada and northern Mexico; also in temperate South America. In arid or semiarid habitats, frequent in deserts. About 78 species.

Subgenus 1. *Gilia*

Leaves pinnately dissected, often bipinnate or tripinnate, but once pinnate or linear in reduced forms. Pubescence varies among the sections. Stipitate glandular hairs often present; they are medium-sized with a large terminal gland that is yellow or amber. Corolla usually funnellform, sometimes long-tubed and sub-salverform. Corolla veins anastomosing in distal part of corolla (see Materials and Methods for explanation of this character.) Stamens inserted in corolla lobe sinuses. Pollen blue. Seeds generally numerous in capsules, mucilaginous when wet. Flavonoids of type A and/or C present, but not type B. (See Materials and Methods for explanation of these types.) Basic chromosome number $x = 9$ throughout.

Section 1. *Gilia*

Plants with leafy stems, the leaves being the largest on lower stems and smaller but well developed on upper stems. Pubescence of multicellular trichomes and medium-sized stipitate glandular hairs. Inflorescence an open cyme, or a capitate head in some species. Corolla concolored or bi- or tricolored with purple spots on the throat and yellow tube. Corolla veins anastomosing. Flavonoids of type A found (see Materials and Methods for explanation).

Distribution and taxa.—Cismontane California to British Columbia and Baja California, and in Peru and Chile. Ten species: *G. achilleaefolia*, *G. angelensis*, *G. capitata*, *G. clivorum*, *G. laciniata* (S. Amer.), *G. lomensis* (S. Amer.), *G. millefoliata*, *G. nevinii*, *G. tricolor*, *G. valdiviensis* (S. Amer.).

Section 2. Arachnion A.D. & V.E. Grant, *Aliso* 3:214, 1956. TYPE: *Gilia latiflora* A. Gray. Plants scapose with a basal leaf rosette and central leader stem. Pubescence of long fine intertwined white cobwebby hairs; medium-sized stipitate glandular hairs often present also. Inflorescence an open cyme. Corolla often bi- or tricolored with contrastingly colored lobes, throat, and tube. Corolla veins anastomosing. Flavonoids of type C present.

Distribution and taxa.—Mountains and deserts of western North America, especially numerous in the Mojave desert; also in temperate South America. Twenty-five species: *G. aliquanta*, *G. austrooccidentalis*, *G. brecciarum*, *G. cana*, *G. clokeyi*, *G. crassifolia* (S. Amer.), *G. diegensis*, *G. flavocincta*, *G. inconspicua*, *G. interior*, *G. jacens*, *G. latiflora*, *G. leptantha*, *G. malior*, *G. mexicana*, *G. minor*, *G. modocensis*, *G. ochroleuca*, *G. ophthalmoides*, *G. salticola*, *G. sinuata*, *G. tenuiflora*, *G. tetrabreccia*, *G. transmontana*, *G. tweedyi*. The basic taxonomic treatment is that of Grant and Grant (1956).

Section 3. Saltugilia V.E. & A.D. Grant, *Aliso* 3:84, 1954. TYPE: *Gilia splendens* Douglas ex H.L. Mason & A.D. Grant, *Madroño* 9:212. 1948. Genus *Saltugilia* L.A. Johnson in Porter & Johnson, *Aliso* 19:69. 2000. Type designated by Johnson: *Saltugilia grinnellii* (Brand) L.A. Johnson. See Grant & Wendt (2003) for discussion of type.

Plants scapose with a basal leaf rosette and central leader stem. Pubescence of straight multicellular trichomes and stipitate glandular hairs, or with geniculate multicellular trichomes in *G. stellata*. Inflorescence an open cyme. Corolla usually concolored. Corolla veins anastomosing. Flavonoids of types A and C.

Distribution and taxa.—Central cismontane California to northern Baja California, and to western parts of desert. Woodland and desert habitats. Seven species: *G. australis*, *G. caruifolia*, *G. latimerii*, *G. scopulorum*, *G. splendens*, *G. stellata*, *G. yorkii*.

Gilia latimerii (T.L. Weese & L.A. Johnson) V.E. Grant, comb. nov. *Saltugilia latimeri* T.L. Weese & L.A. Johnson, *Madroño* 48:198. 2001. Related to *G. australis*.

Comment.—The species in sect. *Saltugilia* fall into two groups. The *G. splendens* group (*G. splendens*, *G. caruifolia*, *G. australis*, *G. latimerii*) is a natural interrelated group of woodland and desert species with mostly large flowers. The second group (*G. scopulorum*, *G. stellata*, *G. yorkii*) consists of small-flowered, mostly desert species which are similar to the *G. splendens* group in gross morphological characters. This was the basis for grouping them together in the same section in earlier studies (Grant & Grant 1954; Grant 1999).

However, the molecular evidence throws some doubt on this assumption. The *G. splendens* group and the second group form separate clades in the cladograms for chloroplast genes *matK* and *trnL* and ribosomal ITS (Johnson et al. 1996; Johnson & Weese 2000). A new character, sculpturing of the seed coat, also differs between the two groups (Johnson et al. 2004).

Porter and Johnson (2000) treat the *G. splendens* group as a segregate genus, *Saltugilia*, and leave the second group (*G. scopulorum* etc.) in their genus

Gilia. I of course believe that these groups should be treated at the rank of section rather than genus. Otherwise I agree that there is a problem concerning the closeness of the relationships between the two groups and within the second group itself. More morphological, breeding, and molecular studies are desirable to clarify the relationships. In the meantime we have the practical problem of making a place for the second group in the classification system. In the present system, the species of the second group are retained in the sect. *Saltugilia* until we know better what to do with them.

Subgenus 2. *Greeneophila* Brand, *Pflanzenreich* 4(250):144. 1907. TYPE: *Gilia rigidula* Benth.

Leaves with broad blades, or pinnately divided, or linear in reduced forms. Small or tiny glandular hairs, short-stalked, the glands translucent and colorless, or herbage sometimes glaucous in sect. *Campanulastrum*. Corolla varying in form: campanulate, rotate, funnelform, or trumpet-shaped. Corolla veins anastomosing or non-anastomosing (see section descriptions). Stamens often inserted in corolla tube or throat, but sometimes in sinuses (see section descriptions). Pollen yellow or cream, but blue in one species (in sect. *Giliastrum*). Seeds generally numerous in capsules; mucilaginous or non-mucilaginous (see section descriptions). Flavonoids of type B (6-methoxyflavonols) present in sects. *Giliastrum* and *Gilmania*; no data for the other sections. Basic number $x = 9$ present in all sections; $x = 9$ and 8 in sect. *Giliandra*.

Section 4. *Giliastrum* Brand, *Pflanzenreich* 4(250):147. 1907. TYPE: *Gilia rigidula* Benth. *Giliastrum* Rydb., *Fl. Rocky Mts.*, ed. 2, 699, 1066. 1922. *Bryantiella* J.M. Porter, *Aliso* 19:70. 2000. TYPE: *Gilia palmeri* S. Wats., *Proc. Amer. Acad. Arts* 24:61. 1889. *Dayia* J.M. Porter, *Aliso* 19:71. 2000. TYPE: *Gilia scabra* T.S. Brandegee, *Zoe* 5:166, 1903.

Perennial herbs with a soft woody base and some annuals, stems branching from base. Leaf consisting of a broad blade with serrate margin, or blade cleft and with lobes, or reduced to a narrow linear rachis with narrow lobes. Corolla generally campanulate or rotate, rarely funnelform (in *G. scabra*); large or small. Corolla violet, blue, pink, or white, sometimes with a yellow tube. Corolla veins separate and non-anastomosing, except in *G. rigidula* where they do anastomose (see Materials and Methods). Stamens inserted in corolla base or throat. Pollen usually yellow, sometimes white, blue in one species (*G. scabra*). Seed coat mucilaginous when wet. Basic number $x = 9$; $n = 6$ and 12 occur in *G. insigne*.

Distribution and taxa.—Colorado and Kansas to Texas and northern Mexico and Baja California, also in temperate South America. Often in semiarid or arid plains and deserts. Twelve species: *G. castellanosii* (S. Amer.), *G. foetida* (S. Amer.), *G. glutinosa* (S. Amer.), *G. incisa*, *G. insigne*, *G. gypsophylla*, *G. ludens*, *G. palmeri*, *G. purpusii*, *G. rigidula*, *G. scabra* (includes *Dayia grantii* J.M. Porter pending further study), *G. stewartii*. See Turner (1994) for a treatment of the Texas and Mexican species. Porter and Johnson (2000) treat *Giliastrum* as a genus.

Gilia castellanosii (J.M. Porter) V.E. Grant, comb. nov. *Giliastrum castellanosii* J.M. Porter, *Aliso* 19:75. 2000.

Comment.—*Gilia scabra* of Baja California was poorly understood for many years. Brandegee (1903), who described it, stated that it was related to *Gilia floribunda* in section *Siphonella*. These are old names for *Linanthus nuttallii*. When compiling a list of species names in the 1950s, I followed Brandegee and listed *Gilia scabra* as a synonym of *Linanthus nuttallii* (Grant 1959, p. 140). I did not see herbarium material until much later. Recently Porter has studied this species in the field and laboratory, and gives a full description of its morphology (Porter and Johnson 2000). He also presents molecular evidence as noted below. Porter proposes a new genus, *Dayia*, for *D. scabra* and the closely related *D. grantii*. *G. (or D.) scabra* seems to fit into sect. *Giliastrum*, though it does differ from other species of *Giliastrum* in having funnelform corollas and blue pollen. Alva Day also views *G. scabra* as a member of sect. *Giliastrum* (pers. comm.).

The molecular evidence consists of sequence variation for the chloroplast gene *matK* and ribosomal ITS (Johnson et al. 1996; Porter 1997; Prather et al. 2000). Molecular evidence could help greatly to clarify the relationships of *Gilia scabra*, but in fact only raises more questions. In the DNA cladograms, *Gilia scabra* forms a clade consisting of itself and *Loeselia glandulosa*. This result is puzzling. *Gilia* sect. *Giliastrum* is only distantly related to *Loeselia* (Grant 2003b). *Gilia scabra* does not have the phenetic characters of *Loeselia*. In the cladograms *Gilia scabra* is adjacent to a *Giliastrum* clade, but *Loeselia glandulosa* seems very much out of place. The possibility of mislabelling plant material suggests itself. The assays of *Gilia scabra* and *Loeselia glandulosa* should be repeated. For the present it seems best to treat *G. scabra* as a member of sect. *Giliastrum*. In the future, with more study, it might be assigned to a new section, *Dayia*, related to sect. *Giliastrum*.

Gilia palmeri of Baja California and *G. glutinosa* of Peru and Chile have been treated as a related amphitropical species pair in sect. *Giliastrum* (Grant 1959). Porter proposes to treat them as a new bitypic genus, *Bryantiella* (Porter & Johnson (2000)). The phenetic characters to support this change are not impressive. Porter has some molecular evidence from cpDNA and rDNA to support this proposal but this is unpublished (Porter & Johnson 2000, p. 71). I think these two species belong in sect. *Giliastrum*, and Alva Day (pers. comm.) is of the same opinion.

Section 5. *Giliandra* A. Gray, Proc. Amer. Acad. 8:276. 1870. TYPE: *Gilia stenothyrsa* A. Gray. *Aliciella* sect. *Giliandra* J.M. Porter, *Aliso* 17:27. 1998. *Aliciella* Brand, *Pflanzenreich* 4(250):150. 1907. TYPE: *Gilia triodon* A. Eastwood.

Woody-based perennials, short-lived perennials, biennials, and annuals. Plants scapose with a basal leaf rosette, central leader stem, and cymose inflorescence. Lower leaves leathery, pinnate, with a strap-shaped rachis and short lobes. Flow-

ers showy in the perennial and biennial species, mostly small and inconspicuous in the annual species. Corolla in the large-flowered species funnellform or sometimes trumpet-shaped; blue, red, or pink. Corolla veins anastomosing (see Materials and Methods). Stamens inserted in corolla tube or sinuses. Pollen mostly yellow or cream-colored, rarely blue. Seeds not mucilaginous or only slightly so when wet. Two basic numbers, $x = 9$ and 8 ; $n = 8$ is common in the perennial and biennial species; polyploids are common in the annual species.

Distribution and taxa.—Colorado Plateau, Rocky Mountains, and adjacent plains for the perennial and biennial species; Mojave desert and neighboring deserts for the annual species. Nineteen species. *G. caespitosa*, *G. formosa*, *G. haydenii*, *G. heterostyla*, *G. humillima*, *G. hutchinsifolia*, *G. leptomeria*, *G. lottiae*, *G. mcvickerae*, *G. micromeria*, *G. nyensis*, *G. pentstemonoides*, *G. pinnatifida*, *G. sedifolia*, *G. stenothyrsa*, *G. subacaulis*, *G. subnuda*, *G. tenuis*, *G. triodon*.

Gilia humillima (Brand) A.G. Day ex V.E. Grant, comb. nov. *Aliciella triodon* var. *humillima* Brand, Pflanzenreich 4(250):150. 1907. *Aliciella humillima* J.M. Porter, Aliso 17:41.1998.

Comment.—Porter (1998) has recently revised sect. *Giliandra*, and treats it as a genus, *Aliciella*. He includes the *Gilia latifolia* group in *Aliciella*, whereas I assign it to a neighboring section, *Gilmania*. Porter's (1998) treatment contains much information about the geographical distribution, habitats, chromosome numbers, and other features of the species.

Section 6. *Gilmania* (H.L. Mason & A.D. Grant) V.E. Grant & A.D. Grant, Aliso 3:299. 1956. TYPE: *Gilia latifolia* S. Wats. *Gilia* subgen. *Gilmania* H.L. Mason & A.D. Grant, Madroño 9:205. 1948. *Aliciella* subgen. *Gilmania* J.M. Porter, Aliso 17:43. 1998.

Woody-based perennials and annual herbs. Plants scapose with a basal rosette, central leader, and cymose inflorescence. Lower leaves with a broad blade, lobed margin, and sharp-tipped lobes. Corolla funnellform, pink. Corolla venation not recorded. Stamens inserted in corolla tube. Pollen yellow. Seeds not mucilaginous or only slightly so when wet. Basic number $x = 9$.

Distribution and taxa.—Deserts from southeastern California to Utah. Two species: *G. latifolia* (annual) and *G. ripleyi* (perennial).

Section 7. *Campanulastrum* Brand, Pflanzenreich 4(250):144. 1907. TYPE: *Gilia campanulata* A. Gray. *Gilia* subgen. *Campanulastrum* H.L. Mason & A.D. Grant, Madroño 9:219. 1948. *Tintinabulum* Rydb., Fl. Rocky Mts., ed. 2, 698, 1065. 1922. TYPE: *Gilia filiformis* Parry ex A. Gray. *Gilia* subgen. *Tintinabulum* H.L. Mason & A.D. Grant, Madroño 9:220. 1948.

Small annuals. Stems very slender and wiry, branching from base and spreading. Pubescence glandular-puberulent, or commonly glabrous in *G. filiformis*. Leaves small and linear. Flowers solitary. Corolla campanulate, small, yellow or cream. Veins non-anastomosing (A. Day, pers. comm.). Stamens inserted in corolla throat or tube. Pollen yellow. Seeds mucilaginous when wet. Basic number $x = 9$, diploids.

Distribution and taxa.—Desert mountains, California to Utah and Arizona. Three species: *G. campanulata*, *G. filiformis*, *G. inyoensis*.

Comment.—Some phenetic characters of sect. *Campanulastrum* relate it to sect. *Giliastrum*, other characters relate it to sects. *Giliandra* or *Gilmania*. The molecular cladograms for ribosomal ITS and chloroplast genes *trnL* and *matK* show a *Campanulastrum* clade adjacent to a *Giliandra* clade (Johnson and Weese 2000). These authors list the species under generic names, *Linanthus* and *Aliciella*.

The question is how to express the relationships in the taxonomic system. Sect. *Campanulastrum* does not fit neatly into any one of the other sections in subgen. *Gilia*. Including the *Gilia campanulata* group in sect. *Giliastrum* as in Grant (1959) is not the answer. Segregating it as a genus *Tintinabulum* (Rydberg 1922; Grant 1999) obscures the relationship. Treating this group as a section in subgen. *Greeneophila* seems to be the best solution.

Genus 2. *Lathrocasis* L.A. Johnson, *Aliso* 19:67. 2000. TYPE: *Gilia tenerrima* A. Gray.

Small annuals with small flowers. Stems branching from base and ascending. Leaves linear, with one or two lateral lobes, or simple. Pubescence of tiny stipitate glandular hairs with a black dot-like head. Corolla broad-throated funnelform, white or bluish with yellow spots in throat. Corolla veins branching but not anastomosing (Johnson & Weese 2000; Day, unpubl.). Stamens inserted in corolla throat. Pollen white. Pollen exhibiting an unusual zonocolporate condition with the pores in a broad equatorial band (Grant & Day 1999). Seeds rounded, 1 per locule, mucilaginous when wet. Flavonoids not reported. $2n = 36$, $x = 9$. See Johnson and Weese (2000) for a more detailed morphological description.

Distribution and taxa.—One species, *L. tenerrima*. Western mountains from Sierra Nevada, California, to Montana, Wyoming, and Utah.

Comment.—*Gilia tenerrima* possesses a unique combination of characters making it difficult to place in the system. On the basis of some characters, Day and I formerly placed this species in or near the *Gilia campanulata* group (Day 1993a; Grant & Day 1999). However, the more recent molecular evidence does not support this assignment (Johnson & Weese 2000).

A cladogram for rDNA ITS shows *G. tenerrima* as a clade adjacent to the sections *Saltugilia*, *Arachnion*, and *Gilia*. Cladograms for chloroplast genes *trnL* and *matK* agree with the ribosome cladogram (Johnson and Weese 2000). *Gilia tenerrima* is widely separated from *G. campanulata* in all three cladograms. It also differs from the *G. campanulata* group in seed coat sculpturing (Johnson et al. 2004).

In fact, *G. tenerrima* falls outside the range of variation of the genus *Gilia* as described in this paper. It differs from *Gilia* as described here in the type of glandular pubescence, seed shape and number, pollen color, and distribution of pores on the pollen grains.

Gilia tenerrima resembles *Allophyllum* in a number of phenetic characters (Grant 1999; Grant & Day 1999). However, this indication of relationships is not supported by the molecular evidence. *Gilia tenerrima* and *Allophyllum* fall in separate major clades in the molecular cladograms of Johnson and Weese (2000).

Johnson and coworkers set up a new monotypic genus, *Lathrocasis*, for *G. tenerrima* (Porter & Johnson 2000; Johnson & Weese 2000). This is a good solution for the taxonomic problem and is followed here.

Future study of *L. tenerrima* should include cytotaxonomic work. The few populations that have been chromosome-counted are tetraploid. Diploids could well turn up with further exploration and they might shed some light on the ancestry of the known tetraploid form.

DISCUSSION

Phylogenetic Relationships in the *Gilia* Tribe

The tribe Gilieae as defined by Grant (2001, 2003b, this paper) contains the temperate herbaceous members of the family with zonocolporate pollen, as contrasted with other temperate herbaceous groups which have pantoporate pollen. The tribe consisted of the genera *Gilia*, *Ipomopsis*, *Eriastrum*, *Langloisia*, and *Tintinabulum* in the recent treatments (Grant 2001, 2003b). In the present treatment, *Tintinabulum* is reduced to a section of *Gilia* (sect. *Campanulastrum*), and *Lathrocasis* is taken up, resulting in a tribe composed of *Gilia*, *Lathrocasis*, *Ipomopsis*, *Eriastrum*, and *Langloisia*.

The genera fall into two grades with respect to the basic chromosome number, which is $x = 9$ in *Gilia* and *Lathrocasis*, and $x = 7$ in *Ipomopsis*, *Eriastrum*, and *Langloisia*. $X = 9$ is the ancestral condition in the Polemoniaceae and $x = 7$ is derived (Grant 1959).

Gilia is regarded as basal in the tribe and the seven-paired genera as advanced. The latter do exhibit some advanced phenetic characters, such as bracteate flowering heads in *Eriastrum*, bilateral corollas in *Langloisia*, and hummingbird and hawkmoth flowers in *Ipomopsis*. The summer-blooming habit of *Eriastrum* and lowland species of *Ipomopsis* may be an advanced trait.

The woody-based perennials in *Gilia* sect. *Giliastrum* appear to be basal within *Gilia*. The other sections represent branches in a series of radiations. The California-centered annual gilies (sects. *Gilia*, *Arachnion*, *Saltugilia*) are one such major branch. Section *Giliandra* with $x = 9$ and also the reduced number $x = 8$ is another.

The seven-paired genera *Eriastrum* and *Ipomopsis* can be viewed as offshoots of one or two sections of perennial gilies in subgen. *Greeneophila*. The small desert genus *Langloisia* seems to be an offshoot of *Eriastrum*. *Lathrocasis* ($x = 9$) appears to be related to the California-centered annual gilies.

The molecular cladistic approach of Porter and Johnson (2000) and Johnson

et al. (2004) leads to a very different classification, as mentioned in the introduction (see also Grant 2001). First, *Gilia* s. l. is broken up into numerous smaller genera (Table 1). Second, the segregate genera are assigned to three different tribes (Table 1).

Third, these tribes contain mixtures of genera with different ancestral roots as indicated by phenetic characters. For example, Porter and Johnson (2000) group the equivalent of Grant's *Gilia* subgen. *Gilia* together with *Allophyllum* and *Collomia* in their tribe *Gilieae* (Table 1). This is a non-monophyletic grouping according to strong phenetic evidence (Grant 1998, 2001, 2003b). The tribe *Loeseliae* of Porter and Johnson (2000) is also non-monophyletic, containing a mixture of *Loeselia* and most of *Gilia* subgen. *Greeneophila* (Table 1). *Loeselia* and *Gilia* have different roots and are assigned to different subfamilies in the taxonomic system (Grant 2003b).

***Gilia* Is Not Polyphyletic**

Johnson et al (1996) state that *Gilia* s. l. is polyphyletic, repeating the statement several times for emphasis. The same conclusion is stated in other molecular systematic papers (Porter 1998; Porter & Johnson 2000; Weese & Johnson 2001). The authors do not present an explicit verbal justification for their claim. However, it is clear from the context that the basis for their conclusion is a broad incongruence between the existing taxonomic classification of *Gilia* s. l. and their molecular cladograms.

The comprehensive family-wide cladograms of Johnson et al. (1996) were the forerunner of a reclassification of the family as a whole including the *Gilia* complex. The molecular evidence consisted of the sequence variation in the chloroplast gene *matK*. Johnson et al. (1996) made the assumption that the cladograms for *matK* provide a reliable guide for the phylogeny of the species in the family. The clades were assigned informal taxonomic names.

Porter and Johnson (2000) set out to construct a phylogenetic classification system based on molecular evidence; and in practice they took up the cpDNA *matK* clades of Johnson et al. (1996) and transformed these into formal taxonomic groups with taxonomic names. The primary and secondary molecular clades became subfamilies and tribes respectively. Third-order clades became genera or small sets of genera. Evidence from studies of other DNA regions played a supporting role: rDNA ITS (Porter 1997, 1998) and rDNA ITS and cpDNA *trnL* (Johnson & Weese 2000).

Full descriptions of phenetic characters were attached to the taxonomic groups of Porter and Johnson (2000), but it is difficult to see what effect, if any, the phenetic characters had on the circumscription of the groups. In cases of conflict between molecular and phenetic evidence, the molecular evidence routinely prevails.

A comparison of the Porter and Johnson (2000) system with other systems

before 2000 is thus a comparison of a cladistic system based primarily on DNA data with a taxonomic classification based primarily on phenetic characters.

In the molecular cladograms of Johnson et al. (1996), clades containing the subgroups of *Gilia* s. l. are scattered in different positions on the graph, and other genera such as *Eriastrum* and *Ipomopsis* lie between them. This topology indicates non-monophyly in cladistics, which uses the cladistic definition of monophyly; and it is probably the basis for Johnson et al.'s (1996) conclusion that *Gilia* is "extremely" polyphyletic. However, the topology is quite consistent with the concept of monophyly used by taxonomic students of *Gilia*. This is an example of a "false accusation" of polyphyly, as mentioned in the introduction.

The pattern of the molecular cladograms is consistent with the phylogenetic hypothesis that *Gilia* s. l. is a basal multisection genus in the tribe *Gilieae*. The sections differ in molecular as well as phenetic characters. Some sections of *Gilia* have given rise to derived genera such as *Eriastrum* and *Ipomopsis*, and these lie between sections of *Gilia* in the cladograms. The same pattern is seen in molecular cladograms of other plant groups and is often misinterpreted as evidence for polyphyly (see Grant 2003a).

Actually, the molecular evidence is in reasonably good agreement with the taxonomic classifications of *Gilia* s. l. The big incongruence is between the taxonomic classification and the molecular-based system. This suggests that the incongruence, or much of it, has developed in the process of converting molecular clades into taxa.

The Genus Concept in *Gilia*

The goal in both evolutionary taxonomy and molecular cladistics is to circumscribe genera so that they are natural or monophyletic. Beyond this basic goal, it is possible, in either school, to adjust the boundaries in various ways ranging from lumping to splitting. The two schools also apply different criteria for circumscription: significant phenetic differences between genera in evolutionary taxonomy, distinctive molecular clades in molecular cladistics. The results are seen in current treatments of *Gilia* where one school's sections are another school's genera.

Alva Day and I and other earlier evolutionary taxonomists such as Herbert Mason (Mason & Grant 1948) have favored a broad multisection genus *Gilia* because the broad circumscription expresses the interrelationships of the subbranches. Splitting the sections off as a series of segregate genera (*Aliciella*, *Giliastrum*, etc.) obscures their interrelationships. Having one generic name (*Gilia*) for a related set of sections, rather than a different generic name for each subdivision, reinforces the sense of interrelationship, and in addition reduces the memory burden, and facilitates preliminary identification in the field or herbarium.

Gilia s. l. is more difficult to define diagnostically than its constituent sec-

tions, but it can be defined. *Gilia* as treated here is a genus of temperate herbaceous Polemoniaceae that has zonocolporate pollen, a basic chromosome number of $x = 9$, a spring-blooming habit, and generally angular seeds.

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