

TAXONOMY OF THE POLEMONIACEAE: THE SUBFAMILIES AND TRIBES

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ABSTRACT

This paper presents a revised formal classification of the subfamilies and tribes of the Polemoniaceae based on a synthesis of new and old characters and on a traditional taxonomic approach. The genera are grouped into nine tribes and three subfamilies (Cobaeoideae, Polemonioideae, Acanthogilioideae). The five tropical and subtropical genera, which are basal in the family, fall into two primary groups: subfam. Cobaeoideae, containing *Cantua*, *Cobaea*, *Bonplandia*, and *Loeselia*; and subfam. Acanthogilioideae, containing *Acanthogilia*. The temperate herbaceous genera, which are derived, also fall into two primary groups. The subfam. Polemonioideae, related to and evidently derived from the Cobaeoideae, contains *Polemonium*, *Collomia*, *Navarretia*, *Phlox*, *Linanthus*, etc. The second main group of temperate herbaceous genera is the tribe Gilieae, which is related to the tribe Acanthogilieae and included in the same subfamily Acanthogilioideae with it. The Gilieae contains the genera *Gilia*, *Eriastrum*, *Ipomopsis*, etc. This system differs in numerous respects from the recent system of Porter and Johnson (Aliso, vol. 19(1), 2000), based on a molecular cladistic approach. Different goals and methods produce different results. It is suggested that other plant groups, which have been revised in recent times according to molecular cladistic evidence and criteria, should also be revised by taxonomic methods. Updated taxonomic classifications are needed for the useful features that they alone provide.

RESUMEN

En este trabajo se presenta una clasificación formal revisada de las subfamilias y tribus de las Polemoniaceae basada en una síntesis de caracteres nuevos y viejos mediante un método taxonómico clásico. Los géneros se agrupan en nueve tribus y tres subfamilias (Cobaeoideae, Polemonioideae, Acanthogilioideae). Los cinco géneros tropicales y subtropicales, que son basales en la familia, quedan en dos grupos primarios: subfam. Cobaeoideae, con *Cantua*, *Cobaea*, *Bonplandia*, y *Loeselia*; y subfam. Acanthogilioideae, con *Acanthogilia*. Los géneros herbáceos templados, que son derivados, también están en dos grupos primarios. La subfam. Polemonioideae, relacionada y evidentemente derivada de Cobaeoideae, contiene a *Polemonium*, *Collomia*, *Navarretia*, *Phlox*, *Linanthus*, etc. El segundo grupo principal de géneros herbáceos templados es la tribu Gilieae, que se relaciona con la tribu Acanthogilieae y está incluida también en la misma subfamilia Acanthogilioideae. Gilieae contiene los géneros *Gilia*, *Eriastrum*, *Ipomopsis*, etc. Este sistema difiere en numerosos aspectos del sistema reciente de Porter y Johnson (Aliso, vol. 19(1), 2000), basado en un método cladístico molecular. Diferentes objetivos y métodos producen resultados diferentes. Se sugiere que otros grupos de plantas, que han sido revisados recientemente con criterios y métodos cladistas moleculares deberían revisarse también por métodos taxonómicos. Las clasificaciones taxonómicas actualizadas se necesitan por las características que sólo ellas pueden ofrecer.

INTRODUCTION

Research on systematics of the Polemoniaceae is going on in several laboratories at present and is producing new evidence concerning relationships. This paper presents a revised classification of the primary subdivisions of the family—the subfamilies and tribes—in the light of the currently available information.

An earlier system (Grant 1959) was constructed before there was much pollen-morphological evidence or any DNA evidence. Both of these lines of evidence are very important for classification (see Materials and Methods for references). The two types of evidence were used in a recent system (Grant 1998; see Table 1).

I did not appreciate the full potential of the pollen evidence in 1998. It was used there to distinguish groups at low and middle taxonomic levels. In the revised system presented here it is used as a key character separating subfamilies.

An important molecular survey of the family was carried out by Johnson et al. (1996), using the chloroplast gene *matK* and a cladistic approach. This study recognized informal groupings based on the DNA cladograms, many of which differed from those in the Grant (1959) system. I took up some of these new groupings but rejected others in a revised taxonomic classification (Grant 1998, 1999; Grant & Day 1999). The taxonomic system of 1998–1999 differs significantly from the molecular cladistic groupings of Johnson et al. (1996).

Cladistic treatments of other organellar genes were made by various workers in this same period. The studies most relevant to this paper are listed in Materials and Methods. A complete list of molecular studies in the family up to 2000 is given by Porter and Johnson (2000).

Porter and Johnson (2000) then used the available molecular evidence as the main basis for a formal system of the family. The primary clades or deepest branchings in the DNA cladograms become subfamilies in their system, the secondary clades become tribes, and the third-order clades become genera or small sets of genera. Formal taxonomic names are assigned to the groups. Good descriptions of phenetic characters are given for the groups. However, it is difficult to tell what role these phenetic characters play in defining the groups; sets of diagnostic characters are lacking. The groups are basically clades. Porter and Johnson (2000, p. 55) describe their system as “a phylogenetic classification of the Polemoniaceae.” It is what Mayr and Bock (2002) call a cladification.

Again, major differences exist between the cladistic system (Porter & Johnson 2000) and the taxonomic system (Grant 1998, 1999; Grant & Day 1999). A detailed analysis and discussion of these differences is given in Grant (2001). The incongruences persist in a comparison of the molecular cladistic system with the revised taxonomic system presented in this paper. Some of the differences are shown in Table 1.

TABLE 1. Comparison of recent classification systems of the family.

Grant 1959	Grant 1998, 1999; Grant and Day 1999
<i>Tropical and subtropical taxa</i> Tribe 1. Cantueae. <i>Cantua, Huthia</i> Tribe 2. Cobaeaeae. <i>Cobaea.</i> Tribe 3. Bonplandieae. <i>Bonplandia, Loeselia.</i> <i>Temperate taxa.</i> Tribe 4. Polemonieae. <i>Polemonium, Collomia, Allophyllum, Gymnosteris, Phlox, Microsteris.</i> Tribe 5. Gilieae. <i>Gilia, Ipomopsis, Eriastrum, Langloisia, Navarretia, Leptodactylon, Linanthus.</i>	Subfam. 1. Cobaeoideae. Tribe 1. Cantueae. <i>Cantua, Huthia.</i> Tribe 2. Cobaeaeae. <i>Cobaea.</i> Tribe 3. Bonplandieae. <i>Bonplandia.</i> Tribe 4. Loeselieae. <i>Loeselia.</i> Tribe 5. Acanthogilieae. <i>Acanthogilia.</i> Subfam. 2. Polemonioideae. Tribe 6. Polemonieae. <i>Polemonium, Collomia, Allophyllum, Navarretia, Phlox, Microsteris, Gymnosteris.</i> Tribe 7. Gilieae. <i>Gilia, Ipomopsis, Eriastrum, Langloisia, Tintinabulum.</i> Tribe 8. Leptodactyloneae. <i>Leptodactylon, Linanthus, Maculigilia.</i>
Porter and Johnson 2000	System proposed here (2003)
Subfam. 1. Acanthogilioideae. Tribe 1. Acanthogilieae. <i>Acanthogilia.</i> Subfam. 2. Cobaeoideae. Tribe 2. Cantueae. <i>Cantua (incl. Huthia).</i> Tribe 3. Cobaeaeae. <i>Cobaea.</i> Tribe 4. Bonplandieae. <i>Bonplandia.</i> Subfam. 3. Polemonioideae. Tribe 5. Polemonieae. <i>Polemonium.</i> Tribe 6. Loeselieae. <i>Loeselia, Giliastrium, Dayia, Bryantiella, Aliciella, Ipomopsis, Microgilia, Eriastrum, Langloisia, Loeseliastrium.</i> Tribe 7. Gilieae. <i>Collomia, Allophyllum, Navarretia, Gilia, Saltugilia, Lathrocasis.</i> Tribe 8. Phlocideae. <i>Phlox, Microsteris, Gymnosteris, Linanthus, Leptosiphon.</i>	Subfam. 1. Cobaeoideae. Tribe 1. Cantueae. <i>Cantua, (incl. Huthia).</i> Tribe 2. Cobaeaeae. <i>Cobaea.</i> Tribe 3. Bonplandieae. <i>Bonplandia.</i> Tribe 4. Loeselieae. <i>Loeselia.</i> Subfam. 2. Polemonioideae. Tribe 5. Polemonieae. <i>Polemonium, Collomia, Allophyllum, Navarretia.</i> Tribe 6. Phlocideae. <i>Phlox, Microsteris, Gymnosteris.</i> Tribe 7. Leptodactyloneae. <i>Leptodactylon, Linanthus, Maculigilia.</i> Subfam. 3. Acanthogilioideae. Tribe 8. Acanthogilieae. <i>Acanthogilia.</i> Tribe 9. Gilieae. <i>Gilia, Ipomopsis, Eriastrum, Langloisia, Tintinabulum.</i>

Cladists, on finding differences between cladistic and taxonomic systems of the same group, commonly attribute the differences to inadequacies in the taxonomy. Johnson et al. (1996) expressed this view of the Grant (1959) system very clearly. Indeed, the 1959 system was old and in need of repair in 1996. However, there are also other explanations to consider.

The basic consideration is that one system is a product of taxonomy and the other a product of cladistics. The two approaches have different criteria, goals, and methods. Taxonomy groups organisms according to similarity and difference, cladistics groups them into ancestor-descendant lineages. Taxa are not the same as clades. Taxonomy uses the traditional definition of monophyly whereas cladistics uses a special definition of its own. In taxonomy a monophyletic group is any group of organisms descended from a recent common ancestor; in cladistics a group to qualify as monophyletic must contain all the descendants of the common ancestor (see reviews of Mayr & Bock 2002, and Grant 2003).

The differences in the definition of a systematic unit and of monophyly automatically lead to incongruence between taxonomic and cladistic systems of the same group. A group circumscribed in a given way can be monophyletic in taxonomy but non-monophyletic in cladistics. And cladists frequently and incorrectly declare a taxonomic group to be non-monophyletic when it is monophyletic by the taxonomic definition. Many of the disagreements between the taxonomic and cladistic systems of the Polemoniaceae (and other plant groups) can be attributed to the differences in working concepts and definitions (see Grant 2001, 2003).

Where incongruences between rival systems are due to the use of different working concepts, one system cannot be said to be right and the other wrong; both systems may be right by their own respective standards. The view held by many cladists, including Johnson et al. (1996) in the Polemoniaceae, that a new cladistic treatment should replace a preexisting taxonomic treatment, is not justified insofar as it is based on the working concepts. In fact, one could argue just the opposite. We should have both cladistic systems and up-to-date taxonomic classifications, so that consumers of systematic biology can have a choice.

Other incongruences between taxonomic and cladistic systems of the Polemoniaceae are due to the evidence used. Here we are comparing taxonomy with molecular cladistics, phenetic characters with DNA sequence variation, and broad databases with narrow ones. This aspect will be considered in the Discussion section.

An up-to-date formal taxonomic classification of the Polemoniaceae is needed to complement the valuable cladistic treatment of Porter and Johnson (2000). The present paper deals with the subfamilies and tribes. An updated taxonomic treatment of the genera and sections of the temperate herbaceous Polemoniaceae is also needed. Work has begun on selected temperate genera.

MATERIALS AND METHODS

I compiled a list of conventional taxonomic characters from the older literature. I then sorted out the characters that distinguish groups at higher levels in the family, and set aside those that are diagnostically useful for genera and species. Character expressions were checked in the University of Texas Herbarium where desirable.

Family-wide surveys of particular microscopic and chemical characters are very helpful. Such surveys are available for: chromosomes (Grant 1959, ch. 6); pollen (Stuchlik 1967a, 1967b; Taylor & Levin 1975); wood anatomy (Carlquist et al. 1984); corolla venation (Day & Moran 1986); flavonoids (Smith et al. 1977, 1982); and organellar DNA (several authors listed below). The older studies of chromosomes size (in Grant 1959) need to be repeated by modern methods of determining DNA quantity.

Some of the characters vary at the upper taxonomic levels, and are used in this paper, while others vary at the generic and infrageneric levels. This is illustrated by the flavonoids.

The flavonoids occurring in the family fall into three main groups: (A) the common types, kaempferol, quercetin, and myricetin; (B) 6-methoxyflavonols; and (C) C-glycosylflavones (Smith et al. 1977). Variation in these is more useful taxonomically at the genus level than at the tribal level, and only a part of the flavonoid evidence is included in this paper. Smith et al.'s (1977) findings are recorded below for the four tropical genera. One aspect, the presence or absence of types B and C is recorded below for the temperate tribes.

Numerous features of the pollen show variation within the family. Day and Moran (1986) found that the spatial distribution of the pores is especially useful diagnostically. Most members of the family fall into one or the other of two contrasting character states: pantoporate (pores scattered over the grain) or zonocolporate (pores equatorial).

The corolla tube has five sets of three parallel and separate veins, one set for each corolla lobe. In most members of the family the veins anastomose to form a network in the corolla throat or lobes. In the tribe Leptodactyloneae, however, the veins are non-anastomosing. The character may not be well exhibited in small-flowered species of other tribes (Day & Moran 1986).

Family-wide studies of DNA sequences have been carried out with chloroplasts (*matK*, *ndhF*), mitochondria (*nad1B*), and ribosomes (*ITS*) (Steele & Vilgalys 1994; Johnson et al. 1996; Porter 1997; Porter & Johnson 1998; Prather et al. 2000). The DNA relationships are clearly portrayed in the cladograms, and I have used these in constructing the taxonomic classification. However, I have not found a way to express the molecular evidence in verbal terms for inclusion in the descriptions. The Porter and Johnson (2000) system is a good representation of the molecular clades (see Table 1).

The molecular evidence is often but not always in agreement with the phenetic evidence. In cases of a conflict I reexamine the phenetic evidence with the thought that it is best to have some phenetic characters to support the molecular characters. In the recent past (Grant 1998, 1999) and again for the present study I have found some such correlated phenetic and molecular characters, and have made the appropriate taxonomic changes. If, however, molecular evidence alone points in one direction, while two or more reliable phenetic characters point to a different taxonomic conclusion, I follow the phenetics. In other words, I do not assume that the molecular evidence is always the right guide to follow.

The descriptions in the formal system consist mainly of the character states of diagnostic characters. These can be regarded as the evidence supporting the taxonomic groupings. Good complete descriptions are given by Porter and Johnson (2000).

The nomenclatural paragraphs of the subfamilies and tribes contain the essential original names and recent names. Additional synonyms may be found in Grant (1959).

SYSTEM OF CLASSIFICATION

Fam. Polemoniaceae Juss. Polemoniaceae (as Polemonia) Juss.; Gen. Pl. 136. 1789. TYPE: *Polemonium caeruleum* L.

Various life forms from small trees to annual herbs. Leaves mostly alternate, but opposite in *Phlox*, *Leptodactylon*, and *Linanthus*. Floral plan 5-5-5-3. Corolla sympetalous with epipetalous stamens, usually radial, sometimes bilateral. Corolla veins mostly anastomosing in the corolla throat or lobes, but non-anastomosing in *Leptodactylon* and *Linanthus*. Ovary superior and 3-carpellary. Fruit generally a 3-celled capsule, but 1- or 2-celled in some species of *Navarretia*. Original basic number $x = 9$; polyploids and aneuploids common.

Mainly American hemisphere; several species in Eurasia. About 347 species. These are grouped here into three subfamilies and nine tribes. The species are listed for the tropical and subtropical tribes and genera. This is not feasible for the species-rich temperate groups; for these see the species lists in Grant (1959) and Porter and Johnson (2000).

ANALYTICAL KEY TO TRIBES

1. Seeds mostly winged (sometimes wingless); chromosomes small; tropical and subtropical.
2. Spiny desert shrub; deciduous green leaves in axils of spines; pollen zonocolporate; endemic in Baja California _____ **Acanthogilieae**
2. Not spiny desert shrubs with leaves as above; pollen pantoporate; widespread in American tropics and subtropics.
3. Calyx wholly herbaceous; individual flowers not subtended by bracts; life form varies.

- 4. Climbing vines; calyx sepals divided to base; leaves with terminal tendrils _____ **Cobaeaeae**
- 4. Not vines; calyx synsepalous; leaves without tendrils.
 - 5. Small trees and shrubs; Andes _____ **Cantueae**
 - 5. Perennial herbs; Mexico and Guatemala _____ **Bonplandiaeae**
- 3. Calyx membranous with no or only small herbaceous regions; individual flowers subtended by bracts; shrubs and herbs _____ **Loeseliaeae**
- 1. Seeds without wings; chromosomes mostly medium-sized to large, but small in 1 tribe; temperate and boreal.
 - 6. Pollen zonocolporate; seeds sandy or pale-colored; mostly in xeric habitats, common in deserts _____ **Gilieae**
 - 6. Pollen pantoporate; seed color varies; in various habitats.
 - 7. Seeds sandy or pale-colored; leaves opposite; leaves if cleft or divided are palmately so; chromosomes small _____ **Leptodactyloneae**
 - 7. Seeds dark brown or black; leaves alternate or opposite; leaves if divided are pinnately so; chromosomes large or medium-sized.
 - 8. Leaves alternate; leaves pinnately compound or lobed _____ **Polemonieae**
 - 8. Leaves opposite, or absent in 1 small genus; leaves simple and entire _____ **Phlocideae**

Subfam. 1. Cobaeoideae (D. Don) Arn., *Cobaeaceae* D. Don, *Edinburgh Philos. J.* 10:109–111. 1824. Subfam. *Cobaeoidea* Arn., *Encycl. Britannica*, ed. 7, 5:121. 1832. Subfam. *Cobaeoideae* Brand, *Pflzr.* 4(250):19. 1907. TYPE: *Cobaea scandens* Cav.

Various life forms from small trees to herbs, in tropical and subtropical zones. Seeds mostly winged, sometimes wingless. Pollen pantoporate. Chromosomes small.

Tribe 1. Cantueae Peter, *Nat. Pflazfam.* 4(3a):45. 1891. TYPE: *Cantua buxifolia* Juss.

Small trees and shrubs. Leaves simple with broad blade or pinnately divided and narrow. Calyx wholly herbaceous and synsepalous. Corolla radial to bilateral. Seeds flat with broad wings. All three groups of flavonoids (A, B, and C) present (see Materials and Methods for explanation of these groups). $2n = 54$.

Distribution and taxa.—Andes. One genus, *Cantua*, with twelve species: *C. bicolor*, *C. buxifolia*, *C. candelilla*, *C. coerulea*, *C. cuzcoensis*, *C. flexuosa*, *C. longiflora*, *C. longifolia*, *C. ovata*, *C. pyrifolia*, *C. quercifolia*, *C. tomentosa*. The former small genus *Huthia* has been submerged in *Cantua* by Porter and Johnson (2000) and Alan Prather (pers. comm.) who is currently studying the group. I am following these authors.

Tribe 2. Cobaeaeae (D. Don) Meisn., *Cobaeaceae* D. Don, *Edinburgh Philos. J.* 10:109–111. 1824. Tribe *Cobaeaeae* Meisn., *Pl. Vasc. Gen.* 180, 273. 1839–1840. TYPE: *Cobaea scandens* Cav.

Climbing vines. Leaves pinnately compound with a terminal tendril. Flowers large and solitary. Calyx wholly herbaceous, sepals divided to base. Corolla radial. Seeds flat with broad wings. Has flavonoids of type A only. $2n = 52$.

Distribution and taxa.—Tropical forests from Mexico to Peru. One genus, *Cobaea*, with four sections and eighteen species: *C. aequatoriensis*, *C. ascher-*

soniana, *C. biaurita*, *C. campanulata*, *C. flava*, *C. gracilis*, *C. lutea*, *C. minor*, *C. pachysepala*, *C. paneroi*, *C. penduliflora*, *C. pringlei*, *C. rotundiflora*, *C. scandens*, *C. skutchii*, *C. stipularis*, *C. trianae*, *C. triflora*. See the recent monograph of Prather (1999).

Tribe 3. Bonplandieae Baill., Hist. Pl. 10:342. 1890. TYPE: *Bonplandia geminiflora* Cav.

Subshrubs with woody base and herbaceous shoot. Leaves simple with a broad blade and serrate margin or lobed. Calyx wholly herbaceous and synsepalous. Corolla bilateral. Seeds plump with narrow wings or wingless. Has flavonoids of type B only. $2n = 30$.

Distribution and taxa.—Mexico and Guatemala. One genus, *Bonplandia*, with two species, *B. geminiflora* and *B. linearis*.

Tribe 4. Loeseliaeae J.M. Porter & L.A. Johnson, Aliso 17:84. 8 Jun 1998. Tribe Loeseliaeae V.E. Grant; Amer. J. Bot. 85:744. 17 Jun 1998. TYPE: *Loeselia ciliata* L.

Subshrubs, perennial herbs, and annuals. Leaves simple with broad blade and entire or serrate margin. Inflorescence bracts with prominent veins subtend individual flowers; these are usually large and leaflike, but may be small. Calyx synsepalous and membranous with no or only small herbaceous regions. Corolla radial or bilateral. Seeds with narrow wings or wingless. Flavonoid groups A and C present, but type B absent. $2n = 18$.

Distribution and taxa.—Mexico to southern Texas and Arizona and to northern South America. Often in the temperate zone of tropical mountains. One genus, *Loeselia*, with fifteen species: *L. amplexans*, *L. caerulea*, *L. ciliata*, *L. cordifolia*, *L. glandulosa*, *L. grandiflora*, *L. greggii*, *L. hintoniorum*, *L. involucrata*, *L. mexicana*, *L. nepetifolia*, *L. pumila*, *L. purpusii*, *L. rupestris*, *L. rzedowski*. See Turner (1994) for a recent generic treatment.

Subfam. 2. Polemonioideae Brand., Pflzr. 4(250):30. 1907. TYPE: *Polemonium caeruleum* L.

Subshrubs, perennial herbs, and annuals, of temperate and boreal zones. Seeds not winged. Pollen pantoporate. Chromosomes mostly large or medium-sized, but small in one tribe.

Tribe 5. Polemonieae Arn., Encycl. Britannica, ed. 7, 5:121. 1832. Tribe Polemonieae Meisn., Pl. Vasc. Gen. 273. 1839. TYPE: *Polemonium caeruleum* L.

Perennial and annual herbs. Leaves alternate. Leaves pinnately compound (in *Polemonium*) or simple and pinnately lobed, or simple and entire in reduced forms (in the other genera). Capsule locules commonly containing 1 to few seeds each; sometimes many-seeded in *Navarretia*. Seeds dark brown or black, sometimes plump and rounded, sometimes small. Pollen generally pantoporate, but

zonocolporate in some species of *Collomia*. Flavonoids of type C absent; type B absent in *Polemonium* and *Allophyllum*, but present in *Collomia* and *Navarretia*. Chromosomes medium-sized or large, $x = 9$ and 8 .

Distribution and taxa.—North America, extending to Eurasia. Genera: *Polemonium*, *Collomia*, *Allophyllum*, *Navarretia*. About 78 species.

Polemonium is set apart from the other three genera by leaf form and some molecular characters (Johnson et al. 1996). It could well be separated in a tribe of its own, as in the Porter and Johnson (2000) system. On the other hand, it is allied to the other genera by seed and pollen characters and by other molecular evidence (Prather et al. 2000). A conservative disposition is made here.

Tribe 6. Phlocideae Dumort., Anal. Fam. Pl., 25. 1829. Gruppe Phloginae Rchb., Handb. Nat. Pflzsystems, ed. 1, 194. 1837. Tribe Phlogieae Rohb. ex J.M. Porter & L.A. Johnson, Aliso 17:84. 1998. TYPE: *Phlox glaberrima* L.

Subshrubs, perennial herbs, and some annuals. Leaves or at least the lower leaves opposite; true leaves absent in the small genus *Gymnosteris*. Leaves simple with narrow blade and entire margin. Capsule locules mostly 1-seeded. Seeds brown, sometimes plump and rounded, sometimes small. Flavonoids of type B lacking, but type C present. Chromosomes medium-sized or large, $x = 7$ and 6 .

Distribution and taxa.—North America, extending to Asia. Genera: *Phlox*, *Microsteris*, *Gymnosteris*. About 66 species.

Phlox ($x = 7$) could be derived from *Collomia* ($x = 8$) in the Polemonieae. *Microsteris* ($x = 7$) is a reduced annual derived from a perennial *Phlox*. *Gymnosteris* ($x = 6$) is a reduced leafless annual formerly thought to be close to *Collomia*; but phenetic and molecular evidence now indicate that its closest relative is *Phlox* or *Microsteris* (Porter & Johnson 2000). See Ferguson and Jansen (2002) on molecular relationships in *Phlox*.

Tribe 7. Leptodactyloneae V.E. Grant, Amer. J. Bot. 85:746. 1998. TYPE: *Leptodactylon californicum* Hook & Arn.

Subshrubs, perennial herbs, and annuals. Leaves mostly opposite. Leaves palmately divided, or simple and entire in reduced forms. Corolla veins non-anastomosing, in contrast to other tribes (see explanation in Materials and Methods). Capsule locules containing several to many seeds each, rarely 1-seeded. Seeds sandy or pale-colored, or sometimes brown in *Leptodactylon*. Flavonoids of types B and C present. Chromosomes small, $x = 9$.

Distribution and taxa.—Semiarid and arid habitats including deserts in western North America. Genera: *Leptodactylon*, *Linanthus*, *Maculigiia*. About 50 species.

In the system of Porter and Johnson (2000), *Linanthus* s.l. is subdivided into two genera, *Linanthus* s.s. and *Leptosiphon*, on cladistic grounds. These two taxa are indeed well differentiated, but they are also united by some common characters, and they could be treated as either subgenera of one genus or two

separate genera. A conservative treatment as *Linanthus* s.l. is preferred here because it shows the relationships of the two branches. *Maculigilia* is a recent segregate genus for the old distinctive desert species *Gilia maculata* (see Patterson 1989; Grant 1999). *Maculigilia maculata* is probably a derivative of some xerophytic member of *Linanthus*.

Leptodactylon and *Linanthus* form a closely related and isolated genus pair. This group was formerly placed in the tribe Gilieae on macroscopic characters (Grant 1959), but the more recent evidence of flavonoids and *cpDNA* and *nrDNA* point to a relationship with *Phlox* (Smith et al. 1977, 1982; Johnson et al. 1996; Porter 1997). *Leptodactylon/Linanthus* is placed in the tribe Phlocideae in the Porter and Johnson (2000) system.

However, in other characters, *Leptodactylon* and *Linanthus* are unlike the Phlocideae (or Polemonieae); namely, palmate leaves, non-anastomosing corolla veins, sandy or pale-colored seeds, small chromosomes, and an affinity for semi-arid and arid habitats. The present treatment attempts to resolve the similarities and important differences by placing these genera in a separate tribe Leptodactyloneae next to the Phlocideae. This makes for a better definition of both tribes.

Subfam. 3. Acanthogilioideae (V.E. Grant) J.M. Porter & L.A. Johnson, *Aliso* 19:60. 2000. Tribe Acanthogilieae V.E. Grant; *Amer. J. Bot.* 85:744. 1998. TYPE: *Gilia gloriosa* Brand., *Acanthogilia gloriosa* A.G. Day & R. Moran.

Shrubs, subshrubs, and herbs of arid habitats, commonly in deserts. Seeds winged or wingless. Pollen zonocolporate. Chromosomes mostly medium-sized or large, but small in one tribe.

Tribe 8. Acanthogilieae V.E. Grant, *Amer. J. Bot.* 85:744. 1998. TYPE: *Gilia gloriosa* Brand., *Acanthogilia gloriosa* A.G. Day & R. Moran.

Spiny desert shrub. Leaves dimorphic, with primary leaves modified as persistent spines, and small deciduous green leaves in the axils of the spines. Capsule locules containing 1–6 seeds each. Seeds flat with broad wings. Chromosomes small, $x = 9$.

Distribution and taxa.—Endemic in central Baja California. One genus and species *Acanthogilia gloriosa*. Detailed information about this interesting taxon is given by Day and Moran (1986).

Tribe 9. Gilieae (Rchb.) V.E. Grant, *Nat. Hist. Phlox Fam.* 120. 1959. Gruppe Gilieae Rchb.; *Handb. Nat. Pflzsystems*, ed. 1, 194, 1837. Tribe Gilieae J.M. Porter & L.A. Johnson; *Aliso* 19:63. 2000. TYPE: *Gilia laciniata* Ruiz & Pav.

Subshrubs, perennial herbs, and annuals; not spiny. Leaves not dimorphic; leaves pinnately divided or dissected with narrow segments, or small and linear in reduced forms. Capsule locules usually many-seeded. Seeds sandy or pale-colored, mostly angular, sometimes banana-shaped. Pollen generally

zonocolporate, but deviating toward pantoporate in some species of *Eriastrum*. Flavonoids of type B present; type C uncommon (occurs in *Gilia* and *Langloisia*) or absent (*Gilia*, *Ipomopsis*). Chromosomes mostly medium-sized, sometimes large; $x = 9, 8$, and 7 .

Distribution and taxa.—Widespread in arid habitats, common in deserts. The genera as treated here are *Gilia*, *Tintinabulum*, *Ipomopsis*, *Eriastrum*, *Langloisia*. About 105 species.

A broad concept of *Gilia* as a genus composed of six sections is adopted here and elsewhere (Grant 1999, 2001). *Gilia* s.l. with a basic chromosome number of $x = 9$ in all sections (and $x = 8$ in part of one section) is basal in the tribe. *Tintinabulum* ($x = 9$) is a small specialized genus close to *Gilia*. *Ipomopsis*, *Eriastrum*, and *Langloisia* with $x = 7$ appear to be derivatives of *Gilia* (Grant 2001).

Molecular cladists consider *Gilia* s.l. to be polyphyletic, and split it up into a series of small genera (Johnson et al. 1996; Porter & Johnson 2000). I contend that this viewpoint is based, first, on the cladistic definition of monophyly and, second, on an overreliance on the molecular cladograms, and that *Gilia* s.l. is monophyletic by the traditional definition of monophyly (Grant 1999, 2001).

PHYLOGENY

The Polemoniaceae is evidently derived from an ericalean stock (Brown 1938; Porter & Johnson 1998; Johnson et al. 1999). The basal living forms of the family are the tropical and subtropical genera. There are five of these (*Cantua*, *Cobaea*, *Bonplandia*, *Loeselia*, *Acanthogilia*), all very different from one another. In this group *Cantua* comes closest to the ericalean stock, while the other genera exhibit derived characters of one sort or another.

The subtropical desert shrub, *Acanthogilia*, differs markedly from *Cantua*, but also shares some inconspicuous but significant characters with it (Day & Moran 1986). These workers suggest (p. 125) that “*Acanthogilia* may be a specialized desert descendant of a diploid line also ancestral to *Cantua*.”

One of the significant characters is the spatial distribution of pores on the pollen grains, whether pantoporate or zonocolporate. Another is ecological preferences: mesic or xeric. The pollen pore character has proven to be a valuable marker for revising the classification of species groups and genera (Day & Moran 1986; Grant & Day 1999), and can be extended to higher taxa. *Cantua* and three related genera (*Cobaea*, *Bonplandia*, and *Loeselia*, comprising the subfamily Cobaeoideae) are pantoporate and mesophytic. *Acanthogilia* is zonocolporate and xerophytic. Day and Moran’s (1986) hypothesis can be rephrased as the suggestion of an early split between the ancestors of the pantoporate Cobaeoideae and the ancestor of the zonocolporate *Acanthogilia*. The molecular evidence of Prather et al. (2000) is in agreement with this hypothesis.

This split persists in the derived, temperate, mainly herbaceous tribes. Day

and Moran (1986) point to characters which *Gilia* and its close relatives share with *Acanthogilia*. The tribe Gilieae, as circumscribed here and in Grant (1998), is zonocolporate and xerophytic. It could well have an unknown ancestor in common with *Acanthogilia*.

The mid-Eocene plant *Gilisenium* from Utah is close to *Gilia* in a number of characters (Lott et al. 1998). It is desirable to determine its pollen pore character, if possible.

The tribes Polemoniaceae and Phlocideae are pantoporate and generally mesophytic. They may be derived from a *Bonplandia*-like ancestor in the Cobaeoideae. The Polemoniaceae and Phlocideae extend into cold northern areas and are the only representatives of the family in northeastern North America and Eurasia. The Leptodactyloneae is also pantoporate and is related to the Phlocideae but is xerophytic.

The two main temperate phylads often occur in the same area, especially in western North America, where some species or groups have crossed over from one type of habitat to another. In this situation the two phylads have given rise to species of annuals which converge in their general morphological characters. For example, some small-flowered species of *Allophyllum* (Polemoniaceae) closely resemble certain small-flowered species of *Gilia* (Gilieae), and were mistakenly treated as *Gilia* until recently (Grant 1999; Grant & Day 1999).

DISCUSSION

Several causal factors contribute to the numerous differences between the taxonomic and molecular cladistic systems of the Polemoniaceae. Two of these are theoretical: (1) the use of different systematic units, namely, taxa and clades; and (2) the application of different definitions of monophyly. These two factors were discussed in the introduction. The two approaches also use different evidence and this of course leads to different results. We will consider here: (3) differences in the types of characters used; and (4) differences in the range and breadth of the database.

(3) Molecular systematists working in the Polemoniaceae (and other plant groups) use DNA sites in chloroplasts and mitochondria, which are parts of the cytoplasmic genome. Phenetic characters used in taxonomy are determined mainly by the chromosomal genome (see Grant 1975, 2003, for review). Discordance between plastid and mitochondrial evidence, on the one hand, and phenetic characters on the other, can be expected and is often found. Ribosomes, also used in molecular systematics of Polemoniaceae and other families, are a part of the chromosomal genome. They can vary independently of plastids and mitochondria, and for that matter, independently of unlinked chromosomal genes. Here again, incongruence between the various sources of evidence can be expected (see Grant 2003, for further discussion).

(4) Molecular cladistic treatments of the Polemoniaceae (and those of other

plant groups) are based on one or a few genes. The treatment of Johnson et al. (1996) blocks out informal systematic groups on the basis of one chloroplast gene. Taxonomic systems, by contrast, are based on numerous phenetic characters determined by scores or hundreds of genes and gene systems (Grant 1975, for review). These contrasts between approaches represent the extremes. Modern taxonomists utilize the DNA evidence of molecular systematists. And many molecular cladists incorporate phenetic characters in reaching their conclusions.

Factors (1) and (2) bring about different results but do not affect the accuracy of the results, as noted in the introduction. The type and range of characters (factors 3 and 4) do have an effect on the robustness of the results. Molecular cladograms are essentially gene trees, or character phylogenies to use an older term. Single characters often work well in one part of a group but break down elsewhere in the same group. If the goal is a natural classification of whole organisms, one must assemble a broad range of characters, some of which may conflict with others, and one should then follow the weight of the evidence, as is standard procedure in taxonomy.

Taxonomic classifications thus have certain methodological advantages. Another advantage lies in the area of convenience and desirability. Named similarity groups, and hierarchies of such groups, are generally useful for identification, information retrieval, and cataloging. It would be difficult to write a flora, using clades instead of taxa, and such a flora would be difficult to use if it were written (see Diggs & Lipscomb 2002).

For several reasons, therefore, it is desirable to make an updated taxonomic classification of the Polemoniaceae available. But why stop with the Polemoniaceae. Numerous other plant groups have been revised recently by molecular cladistic methods, but are represented in the literature by old taxonomic treatments. These groups should also be re-revised by taxonomists, using the new molecular evidence, but handling all the evidence by taxonomic methods. Plant taxonomy has much work to do.

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