

A GUIDE TO UNDERSTANDING RECENT CLASSIFICATIONS OF THE FAMILY POLEMONIACEAE

Verne Grant

Section of Integrative Biology and Plant Resources Center, The University of Texas, Austin, Texas 78712

Abstract: Two very different systems of classification of the family Polemoniaceae—one a taxonomic system and the other a molecular cladistic system—have appeared recently. They are compared and reviewed. It is emphasized that taxonomy and cladistics use different basic systematic units (taxa or clades) and have different concepts of monophyly. Furthermore, taxonomy and molecular cladistics differ in the characters used in classification. Conflicts between molecular and reliable morphological characters occur in several parts of the family. The differences in methodology account for most of the incongruences between the two classifications of the family. In general, the methodological differences can be expected to yield incongruences between taxonomic and cladistic systems in any heterogeneous group of medium or large size. New suggestions are made about the early phylogenetic divergences in the Polemoniaceae. The tribes are reviewed from a taxonomic standpoint and a few changes are made.

Keywords: Polemoniaceae, cladistics, molecular systematics, phylogeny, taxonomy.

Two new systems of classification of the Polemoniaceae have appeared in the last two years (Grant, 1998, 1999; Grant and Day, 1999; Porter and Johnson, 2000). The Grant/Day system differs substantially and the Porter/Johnson one differs radically from all previous systems. Grant (1999) introduces one newly described genus and revives one old genus which is unfamiliar today. Porter and Johnson (2000) revive three old unfamiliar genera and describe five new genera. The two systems differ greatly from one another in the alignments at the tribal level and groupings at the generic level. The first purpose of this paper is to compare the two recent systems and show how they differ from previous standard systems and from one another.

When two groups of competent systematists study the same family in the same time period and come up with very different results, we seek an explanation. The explanation lies largely in the different approaches and methods used: those of molecular cladistics by Porter and Johnson, those of traditional taxonomy by Grant and Day. In this paper I will use the term taxonomy or the acronym TTES to include the

two subschools of traditional taxonomy and evolutionary systematics. Inevitably we are drawn into a comparison of taxonomy and cladistics.

A third effort is to reevaluate the Grant/Day system in the light of Porter and Johnson's evidence, to evaluate their system in the light of our evidence, and to see where the evidence points.

It is not within the scope of this paper to discuss each and every case of incongruence between the two systems. Research on problems in the Polemoniaceae is currently underway in several laboratories. The Porter and Johnson (2000) treatment will undoubtedly stimulate such research, and I hope this paper will too. As new results continue to appear in the literature, it becomes necessary to establish a cutoff point for the present paper, and that point is the appearance of Prather et al.'s paper in fall 2000.

COMPARISON OF THE SYSTEMS AND APPROACHES

Outlines of the two recent classifications showing their incongruences are pre-

TABLE 1. Classification system of Grant (1998, 1999) and Grant and Day (1999), with basic chromosome numbers and taxonomic notes added.

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- I. Subfam. Cobaeoideae.
1. Tribe Cantueae.
Cantua. $x = 9$.
Huthia.
 2. Tribe Cobaeaeae.
Cobaea. $2n = 52$, x prob. = 9. Genus revised recently by Prather (1999).
 3. Tribe Bonplandieae.
Bonplandia. $2n = 30$, x uncertain.
 4. Tribe Acanthogilieae.
Acanthogilia. $x = 9$.
 5. Tribe Loeseliaeae.
Loeselia. $x = 9$.
- II. Subfam. Polemonioideae.
6. Tribe Polemonieae.
Polemonium. $x = 9$.
Collomia. $x = 8$.
Allophyllum. $x = 9$ and 8. Recently expanded to include the sect. *Kelloggia* of *Gilia*.
Gymnosteris. $x = 6$.
Navarretia. $x = 9$. Formerly in *Gilia* tribe (Grant, 1959), but transferred to *Polemonium* tribe (in Grant, 1998).
Phlox. $x = 7$.
Microsteris. $x = 7$.
 7. Tribe Gilieae.
Gilia. $x = 9$ in five sections, = 9 and 8 in sect. *Giliandra*. Six sections: *Giliastrum*, *Giliandra*, *Gilmania*, *Gilia*, *Arachnion*, *Saltugilia*. Sect. *Kelloggia* containing the *G. leptalea* (A. Gray) E. Greene group transferred out as noted under *Allophyllum*.
Ipomopsis. $x = 7$.
Eriastrum. $x = 7$.
Langloisia. $x = 7$. Includes *Loeseliastrum*.
Tintinabulum. $x = 9$. Old genus recently resurrected for the former *Gilia* species: *G. campanulata* A. Gray, *G. filiformis* Parry ex Gray, and *G. inyoensis* I. M. Johnst.
 8. Tribe Leptodactyloneae. New tribe for genera formerly (Grant, 1959) in the *Gilia* tribe.
Leptodactylon. $x = 9$.
Linanthus. $x = 9$. Six sections were recognized in Grant (1959): sects. *Siphonella*, *Pacificus*, *Leptosiphon*, *Dactylophyllum*, *Linanthus*, *Dianthoides*. These were not restudied or reviewed in Grant (1998).
Maculigilia. $x = 9$. Recently described genus for the former *Gilia maculata* Parish or *Linanthus maculatus* (Parish) Milliken (Grant, 1999).

sented in Tables 1 and 2. As noted in the introduction, the Grant/Day system was arrived at by the methods of taxonomy (TTES). Its present form (in Table 1) is the latest stage in a process of gradual development, step by step, at the hands of many taxonomists over many decades. The Porter and Johnson system (Table 2) is a product of molecular cladistics. It represents a radical departure from any previous system.

The philosophical and methodological differences between TTES and cladistics, including molecular cladistics, are great; for characterizations of these and other schools of systematics see Stuessy (1990) and Mayr and Ashlock (1991). The differences that concern us here will be discussed under three headings: (1) the nature of the basic systematic units, the taxa or clades, and the criteria used for delimiting them; (2) policy

TABLE 2. Outline of the system of Porter and Johnson (2000) with notes. Numbers added to subfamilies and tribes for ease of reference.

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- I. Subfam. Acanthogilioideae.
 1. Tribe Acanthogilieae.
Acanthogilia. Regarded as basal in the family.
- II. Subfam. Cobaeoideae.
 2. Tribe Cantueae.
Cantua. Includes *Huthia*.
 3. Tribe Cobaeaeae.
Cobaea.
 4. Tribe Bonplandiaeae.
Bonplandia.
- III. Subfam. Polemonioideae.
 5. Tribe Polemonieae.
Polemonium.
 6. Tribe Loeseliaeae.
Loeselia.
Giliastrum. Formerly *Gilia* sect. *Giliastrum*.
Dayia. Contains the former *Gilia scabra* Brandegee group, related to *Giliastrum* and *Loeselia*.
Bryantiella. Set up for *Gilia glutinosa* Phil. and *G. palmeri* S. Wats. of the former sect.
Giliastrum.
Aliciella. Corresponds to *Gilia* sects. *Giliandra* and *Gilmania* of Grant (1998).
Ipomopsis. Two species transferred to other genera as noted below.
Microgilia. A segregate genus for the former *Ipomopsis minutiflora* (Benth.) V. E. Grant.
Eriastrum.
Langloisia. Narrow circumscription for the single species *L. setosissima* (Torr. & A. Gray) Greene.
Loeseliastrum. Circumscribed to include two species formerly in *Langloisia* plus *Ipomopsis depressa* (M. E. Jones) V. E. Grant.
7. Tribe Gilieae.
Collomia.
Allophyllum.
Navarretia. Expanded to include the former *Gilia* sect. *Kelloggia*, containing the *G. leptalea* (A. Gray) E. Greene group.
Gilia. Circumscribed to include sects. *Gilia* and *Arachnion* plus the *G. scopulorum* M. E. Jones group. Other sections of *Gilia* segregated as separate genera as noted elsewhere.
Saltugilia. A segregate of *Gilia sens. lat.* for the former *G. splendens* Dougl. ex Lindley group.
Lathrocasis. A new genus for the former *Gilia tenerrima* A. Gray.
8. Tribe Phlocidaeae.
Phlox.
Microsteris.
Gymnosteris.
Linanthus. Circumscribed to include *Leptodactylon*, *Linanthus* sects. *Linanthus* and *Dianthoides*, the former *Gilia campanulata* A. Gray group, and the former *Gilia maculata* Parish.
Leptosiphon. A segregate of *Linanthus sens. lat.* for the sections *Leptosiphon*, *Siphonella*, *Pacificus*, and *Dactylophyllum*.

with respect to paraphyletic groups; and (3) differences in the characters used or emphasized. Together, these differences account for many or most of the incongru-

ences between the two systems. Other factors that contribute to differences between the two systems are: (4) tendency toward splitting or lumping; (5) ways of interpret-

ing the molecular cladograms; and (6) the factor of taxonomic judgement.

This section will discuss topics 1 and 2. Taxa (since Darwin) are putatively monophyletic groups delimited on the criteria of similarity and difference, and arranged in hierarchies on the same criteria. In the pre-Darwin era the equivalent unit was a "natural" similarity group, one reflecting the Plan of Creation. The change in the theory of origins did not have much effect on the actual circumscription of the units since the criteria for circumscription remained the same. Clades are putative ancestor-descendant lineages. Cladistics groups organismic variation into hierarchical arrangements of clades. Thus taxa and clades represent different ways of grouping organismic variation.

The groupings and systems obtained by the taxonomic approach are not necessarily the same as those obtained by cladistics. In fact some incongruence between cladistic and taxonomic systems is inevitable. Consider a mid-size or large group containing an extant ancestral genus (A) and several different derived genera (D_1 , D_2 . . .). Cladistics will group these all in the same major clade, whereas a taxonomist will consider the character differences between the A and D genera and put them in different major groups.

An example is the disposition of the genus *Loeselia* in the alternative systems. Porter and Johnson (2000) consider *Loeselia* to be close to the ancestor of *Giliastrum*, *Eriastrum*, and several other genera, and group these together in the same tribe. However, *Loeselia* differs from *Giliastrum*, etc. in certain important characters (chromosome size, seed form, ecology), but resembles other primitive genera in these same characters. On this basis Grant (1959, 1998) places *Loeselia* in one tribe and the other taxa (*Gilia* sect. *Giliastrum*, *Eriastrum*, etc.) in a separate tribe.

There is a ban on paraphyletic groups in cladistics. It is a corollary of the cladistic redefinition of monophyly. A monophyletic

group in the cladistic sense must contain *all* the descendants of a common ancestor. Taxonomy uses the old general definition of monophyly which does not have the restrictive phrase, "all descendants," and consequently paraphyly is not an issue, indeed is not considered at all, in circumscribing groups. Many groups that are paraphyletic by cladistic standards are good taxa by the criteria of taxonomy.

An example of the role of the paraphyly concept in classification building is provided by the section *Kelloggia* (the former *Gilia leptalea* group). Much evidence indicates that this group does not belong in *Gilia* (Grant and Day, 1999; Grant, 1999; Porter and Johnson, 2000). In molecular cladograms, the section *Kelloggia* appears as a basal branch in a *Navarretia* clade (Johnson et al., 1996; Spencer and Porter, 1997). However, *Kelloggia* differs markedly from *Navarretia* in morphological characters, as Porter and Johnson (2000) recognize. This problem could be resolved by setting *Kelloggia* up as a small genus. Porter and Johnson (2000, p. 68) consider but reject this solution; instead they sink *Kelloggia* in *Navarretia* to avoid paraphyly. Grant and Day (1999), on the other hand, transferred *Kelloggia* to *Allophyllum*, where it fits on morphological characters and is still close to but generically separate from *Navarretia*.

Taxonomic systems and cladistic systems can thus be expected to differ, given the conceptual and methodological differences between them, and often do differ (Mayr, 1995, 1997; Brummitt, 1997). Mayr (1997; Mayr and Bock, in prep.) distinguishes the two kinds of systems terminologically for the sake of clarity in discussion. Since taxonomy has a long history of building systems on the basis of similarity and difference, and of calling them classifications, Mayr reserves the term classification for systems of similarity groups, and proposes the term cladification for systems of clades. Brummitt (1997) has come to the same conclusion.

MOLECULAR AND NON-MOLECULAR CHARACTERS

The characters on which the two systems are based differ in the emphasis placed on DNA evidence, in the emphasis on morphology and other non-molecular features, and in the parts of the genome that are sampled by the methods used.

Grant and Day (Day, 1993a; Grant, 1998, 1999; Grant and Day, 1999), like other taxonomists, scan the entire range of characters (including molecular ones) in a search for those that differentiate groups, on the old premise that good taxonomic characters are where you find them. A further step is to find correlated associations of different characters, as these broaden the database for taxonomic alignments. It is particularly helpful to discover key diagnostic characters that are associated with other characters and serve as indicators of particular groups. An example is the cobwebby hairs that define the section *Arachnion* of *Gilia* and distinguish it from other sections of the genus (Mason and Grant, 1948). (The diagnostic characters used in the Grant/Day system are given in the references cited above; they cannot be given again here because of space limitations.)

Johnson et al. (1996) and Porter (1997), like other molecular cladists, pick a particular DNA segment at the outset, assay it systematically throughout the family, and run the data through a computer to produce cladograms. They use the molecular cladograms as the primary basis for cladification, as the following analysis shows.

The first family-wide molecular study of the Polemoniaceae by Steele and Vilgalys (1994) used a region of the chloroplast gene *matK*. Johnson et al. (1996) then carried out a much more extensive survey of the family using a different part of the same gene. An outline of the major clades found in their study is given in Table 3. Porter (1997) followed with a family-wide survey of nrDNA ITS. Porter and Johnson (1998) surveyed variation in a smaller number of

species in the mitochondrial gene *nad1b*. Prather et al. (2000) have carried out a family-wide study of another chloroplast gene, *ndhF*. The main clades found by them are outlined in Table 4.

To understand the basis for the particular groupings in the Porter and Johnson (2000) system it is necessary to compare it with the Johnson et al. (1996) cpDNA cladograms. A comparison of the three highest ranks of taxa with the three highest levels of clades is shown in Table 3. The groupings in the system follow closely the clades and subclades in the 1996 cladograms.

The three subfamilies in the system are coextensive with the three primary clades in the cladograms. Six of the seven tribes, including all of the temperate tribes, correspond exactly in circumscription with the secondary clades (Table 3). In the cladograms for the temperate clades, there are series of third-order subclades; these are mostly equivalent to genera in the system, but are sometimes equivalent to small sets of genera (Table 3).

The chloroplast 5' region of *matK*, is a good indicator of phylogenetic relationships and has contributed to some recent improvement in polemon classification. Furthermore, there is generally good congruence between the cladograms for it and those for other DNA segments assayed by Porter (1997) and Prather et al. (2000). This broadens the molecular support for Porter and Johnson's (2000) conclusions. Molecular cladograms are very good indicators, but we should not lose sight of the fact that the groupings they indicate are molecular clades, not taxa.

It is difficult to say what exactly the role of morphological and other non-molecular characters is in the Porter/Johnson system. The authors (2000, p. 56) favor synthesizing "all lines of evidence," and state that their classification "reflects such a synthesis." On the other hand, they (2000, p. 55) reject parts of the recent Grant classification that deviate from their molecular phylogeny.

The Porter/Johnson (2000) treatment

TABLE 3. Three levels of major clades in the cpDNA cladograms of Johnson *et al.* (1996), and comparison with the taxonomic system of Porter and Johnson (2000). Johnson *et al.* (1996) assign informal names to many of the clades; the names are listed here, sometimes in a modified form. Numbers are assigned to the primary and secondary clades for ease of identification. The taxa of Porter and Johnson (2000) that are equivalent to the various clades are listed in parentheses.

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- I. *Acanthogilia* Clade. (=Subfam. Acanthogilioideae)
 - 1. Same clade. (=Tribe Acanthogilieae)
 - II. Tropical Clade. (=Subfam. Cobaeoideae)
 - 2. *Cantua* Clade. (=Tribe Cantueae)
 - 3. *Cobaea*—*Bonplandia* Clade. (=Tribes Cobaeae and Bonplandiae)
 - III. Temperate Clade. (=Subfam. Polemonioideae)
 - 4. *Polemonium* Clade. (=Tribe Polemonieae)
 - 5. *Ipomopsis*—*Gilia subnuda* Clade. (=Tribe Loeseliae)
 - Gilia* sect. *Giliandra* Clade. (=Aliciella)
 - Gilia* sect. *Giliastrum* Clade. (=Giliastrum)
 - Clade of *Loeselia glandulosa* and *Gilia scabra*. (=Loeselia and Dayia)
 - Ipomopsis* Clade. (=Ipomopsis, Eriastrum, Langloisia, and Loeseliastrum)
 - 6. *Allophyllum*—*Gilia splendens* Clade. (=Tribe Gilieae)
 - Saltugilia* Clade. (=Saltugilia)
 - Gilia tenerrima* Clade. (=Lathrocasis)
 - Clade of True Gilias. (=Gilia sens. str.)
 - Allophyllum* Clade. (=Allophyllum, Collomia, and Navarretia.)
 - 7. *Phlox*—*Gilia filiformis* Clade. (=Tribe Phlocideae)
 - Leptodactylon* Clade. (=recircumscribed genus *Linanthus*)
 - Gilia filiformis* Clade. (=an element in recircumscribed *Linanthus*)
 - Gymnosteris* Clade. (=Gymnosteris)
 - Phlox* Clade. (=Phlox and Microsteris)
 - Linanthus ciliatus* Clade. (=Leptosiphon)

includes extensive morphological descriptions, particularly of the genera, and is in fact an excellent source of morphological information. Macromorphological and micromorphological characters of diagnostic value are listed in the descriptions, but these are often not used in sorting out the taxa. I could find no alignments in the system that were incongruent with the molecular

cladograms. The grouping of genera in several tribes agrees with the molecular cladograms but is at variance with significant morphological character differences, as will be seen in later sections.

Readers may notice the absence of references to morphological cladistics. No family-wide morphological cladograms have been published as of this writing.

TABLE 4. Two levels of named clades in the cladogram for the chloroplast gene *ndhF* (Prather *et al.*, 2000). This table lists the genera or sections in the clades; for the particular species involved see Prather *et al.* Number designations are added.

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- I. Cobaeoideae Clade.
 - 1. *Acanthogilia* Subclade. *Acanthogilia*.
 - 2. Core Cobaeoideae. *Cobaea*, *Bonplandia*, *Cantua*, *Huthia*.
 - II. Polemonioideae Clade.
 - 3. *Polemonium* Subclade. *Polemonium*.
 - 4. Gilieae Subclade. *Allophyllum*, *Collomia*, *Gilia* sect. *Kelloggia*, *Navarretia*.
 - 5. Linanthieae Subclade. *Gymnosteris*, *Linanthus*, *Phlox*, *Microsteris*.
 - 6. Loeseliae Subclade. *Ipomopsis*, *Eriastrum*, *Langloisia*, *Aliciella*, *Giliastrum*, *Loeselia*.

TABLE 5. Sections of *Gilia* in treatments of Grant and Day, and segregate genera in treatment of Porter and Johnson.

Grant (1959). Sects. <i>Giliastrum</i> , <i>Giliandra</i> , <i>Gilia</i> , <i>Arachnion</i> , <i>Saltugilia</i> .
Day (1993a, 1993b). Sects. <i>Giliastrum</i> , <i>Giliandra</i> , <i>Gilia</i> , <i>Arachnion</i> , <i>Saltugilia</i> , <i>Kelloggia</i> . The latter (the <i>Gilia leptalea</i> [A. Gray] E. Greene group) was regarded as very different from other <i>gilia</i> s and was segregated from <i>Saltugilia</i> as a separate section.
Grant (1999), Grant and Day (1999). Subgen. <i>Greeneophila</i> : sects. <i>Giliastrum</i> , <i>Giliandra</i> , <i>Gilmania</i> . Subgen. <i>Gilia</i> : sects. <i>Gilia</i> , <i>Arachnion</i> , <i>Saltugilia</i> . Sect. <i>Kelloggia</i> , the <i>Gilia campanulata</i> A. Gray group, <i>G. tenerrima</i> A. Gray, and <i>G. maculata</i> Parish removed from <i>Gilia</i> . <i>Kelloggia</i> and <i>G. tenerrima</i> placed in <i>Allophyllum</i> .
Porter and Johnson (2000). <i>Gilia sens. str.</i> reduced to sects. <i>Gilia</i> and <i>Arachnion</i> plus the <i>G. scopulorum</i> M. E. Jones group. Other sections elevated to genera: <i>Giliastrum</i> , <i>Aliciella</i> (=sects. <i>Giliandra</i> and <i>Gilmania</i>), and <i>Saltugilia</i> . <i>Dayia</i> and <i>Bryantiella</i> split off <i>Giliastrum</i> . Segregate genus <i>Lathrocasis</i> set up for <i>G. tenerrima</i> . Sect. <i>Kelloggia</i> transferred to <i>Navarretia</i> .

Another difference in the character basis of the two systems is this. The morphological characters that are used extensively in the Grant/Day system are characters of a type known in angiosperms to be determined by chromosomal genes that exhibit Mendelian behavior (cf. Grant, 1975). The genetic material assayed and used by Porter and Johnson (Johnson et al., 1996; Porter, 1997; Porter and Johnson, 2000), on the other hand, is derived mainly from chloroplasts and mitochondria, which are separate from the chromosomal genome. These organelles represent a very small part of the total genome.

The organeller DNA segments are regarded as good indicators of relationship since variation in them is usually correlated with variation in other more central characters and gene systems; but it is hazardous to regard them as infallible indicators. Different genes or gene systems can evolve at different rates. Evolutionary change can level off in genes affecting physiological processes, for instance, but go on in gene-controlled morphological characters.

An example of this is found in the hominoids. Humans and great apes are very similar in blood types and some other proteins, but are different in morphology and behavior. This suggests that evolutionary change in some biochemical and physiological features slowed down or even stopped in the common ancestor, but morphologi-

cal and behavioral change continued to occur in the subsequent human and ape lineages (cf. Grant, 1991, pp. 349–353). We have an apparently similar case in the Polemoniaceae. The tropical genera *Cantua*, *Cobaea*, and *Bonplandia* are quite close in the molecular cladograms but are very different in morphology.

GILIA

A major difference of opinion and policy exists between taxonomists and cladists in regard to the circumscription of the genus *Gilia*. Taxonomists have generally been comfortable with a broadly defined genus *Gilia* composed of five or six sections, whereas Porter and Johnson (2000) favor splitting *Gilia* into a series of segregate genera (Table 5).

Johnson et al. (1996) sounded the keynote for a policy of splitting in their paper presenting family-wide cladograms for the chloroplast gene *matK*. *Gilia* species do not form a single clade but are dispersed among other temperate genera (Table 3). Johnson et al. (2000) concluded that *Gilia* as it was circumscribed in 1996 was “extremely” polyphyletic. Porter’s (1997) family-wide study of ribosomal DNA ITS pointed to the same conclusion.

The next step was to sort out the monophyletic groups in the polyphyletic genus. Porter (1998a, 1998b) started the

process by setting up the segregate genera *Giliastrum* and *Aliciella*, and Porter and Johnson (2000) extended the process with the segregation of additional new genera (Table 5).

The charge of extreme polyphyly levelled at recent treatments of *Gilia* (Johnson et al. 1996) is jarring to long-term students of the genus. To us this epithet applies to the *Gilia* of the early 1900s. Many botanists have labored since then to prune out the disparate elements. The task was not finished by 1996, but it was well advanced then.

But is *Gilia* as circumscribed by Grant (1959) and Day (1993a) (Tables 1 and 5) really polyphyletic to any serious extent? The claim of Johnson et al. (1996) that it is needs to be analyzed with respect to both the semantics and the evidence.

Johnson et al. (1996) did not say which sense of the term polyphyly they were using, but undoubtedly they mean polyphyly *sensu* cladistics. A group can be monophyletic in evolutionary systematics, where the general definition of monophyly is used, but not be monophyletic in cladistics.

The genus *Gilia* in recent classifications has included a number of poorly known species which were assigned to the closest section for storage until they could be studied further and placed where they belong. These species show up in the DNA cladograms, and Johnson et al. (1996) highlight them as examples of polyphyly (Table 3). But this is not polyphyly in any meaningful sense of the term; it is an artifact of standard taxonomic procedure.

Kelloggia is an example of false polyphyly. The species involved (the *Gilia leptalea* group) were long thought to belong in *Gilia* (Grant, 1959), but were found to be out of place in *Gilia* by Day on pollen, seed, leaf and other characters (Day, 1993b, unpubl.). *Kelloggia* was retained in *Gilia* for several years with this knowledge in mind for lack of any alternative place to put it, until Grant and Day (1999) transferred it to another genus, *Allophyllum*. Several other

disparate species or species groups were also transferred out of *Gilia* recently, namely the *G. campanulata* group, *G. tenerrima*, and *G. maculata* (Grant, 1999; Grant and Day, 1999) (Tables 1 and 5).

With *Kelloggia* and other misfits out of the picture, we can return to the question of polyphyly. Polyphyly is not the only conclusion that can be drawn from the DNA cladograms of Johnson et al. (1996). An alternative interpretation of the cladograms, not considered by the cladist school, is consistent with the conclusion that a broadly defined genus *Gilia* is monophyletic in the traditional sense.

Gilia sensu lato has two subgenera (*Greeneophila* and *Gilia*), corresponding to two main phyletic branches, and three sections in each subgenus, corresponding to secondary branches (Table 5). The subgenera are well differentiated in morphological characters (*cf.* Grant, 1999). They also form separate clades in cladograms for chloroplast and ribosomal DNA (Johnson et al., 1996; Porter, 1997) (Table 3). Subgen. *Greeneophila* and particularly sect. *Giliastrum* possess a number of ancestral characters, while subgen. *Gilia*, consisting of annual herbs, is probably derived from a *Giliastrum*-like ancestor (Grant, 1998, 1999). The sections in both subgenera are well differentiated morphologically. Most of the sections sort out as separate clades in the DNA cladograms (Johnson et al., 1996; Porter, 1997) (Table 3).

At a higher taxonomic level, the subgenera and sections share a number of morphological and chromosomal characters in common, including the basic number $x = 9$ ($x = 9$ and 8 in sect. *Giliandra*) (Grant, 1959, 1999). This pattern suggests that *Gilia sensu lato* is a well developed and relatively old monophyletic group which has produced two primary branches and six secondary branches.

The genera *Ipomopsis*, *Eriastrum*, and *Langloisia* are related to *Gilia sensu lato* by various characters, and are most closely related to subgenus *Greeneophila* (Grant,

1959, 1998; Grant and Day, 1999). Other characters in these three genera are advanced in comparison with *Greeneophila*, for example a basic number of $x = 7$, suggesting that they are derived from a *Greeneophila*-like ancestor (Grant, 1998; Grant and Day, 1999; Table 1). In the DNA cladograms the three afore-mentioned genera form a subclade that branches off the clade of *Gilia* subgen. *Greeneophila* (Johnson et al., 1996; Porter, 1997). The pattern of branching in the DNA cladogram is consistent with the phylogenetic hypothesis of a basal *Gilia* with diverse branches, some of which gave rise to the derived genera *Ipomopsis*, *Eriastrum*, and *Langloisia*.

The question of how to delimit *Gilia*, whether broadly or narrowly, comes down to a matter of preference for splitting or lumping. *Gilia* could be split up in a number of ways: the two subgenera could be elevated in rank to genera; Porter and Johnson (2000) adopt another possible way. But unnecessary splitting at the genus level has definite disadvantages; it obscures the relationships between the component sections, and it multiplies generic names where one name would be sufficient.

PRIMARY DIVERGENCES

The primitive characters in the Polemoniaceae, those in which the family approaches its ericalean ancestors, are scattered among the six tropical and subtropical genera (*Cantua* to *Loeselia* in Table 1; for characters cf. Grant, 1998; Porter and Johnson, 2000). The temperate groups are generally agreed to be derived.

The position of pores in the pollen grains has been found to be a relatively conservative character that marks primary subdivisions in the family. Five of the six tropical/subtropical genera have pantoporate pollen. Only *Acanthogilia* in the tropical/subtropical group has the contrasting condition of zonocolporate pollen. The zonocolporate condition also characterizes the genera of the temperate tribe Gilieae sensu

Grant (Day and Moran, 1986; Grant, 1998, 1999; Grant and Day, 1999). The correlation of the contrasting character states with the primary taxonomic subdivisions holds up very well but breaks down in some species of *Collomia* (with zonocolporate pollen), *Eriastrum* (with pantoporate pollen), and *Allophylum tenerrimum* (with a variable intermediate condition) (Grant, 1999; Grant and Day, 1999; Porter and Johnson, 2000). These exceptions need further study.

The systematic distribution of the porate condition supports the conclusion that pantoporate pollen is an ancestral character in the family and zonocolporate pollen is derived (Day and Moran, 1986; Grant and Day, 1999). A plausible phylogenetic hypothesis is that an early split occurred in the tropical/subtropical polemons between the preponderant pantoporate members and an ancestor of the zonocolporate *Acanthogilia*.

Acanthogilia is a desert shrub with specialized vegetative characters; it is apparently a dead end. But it shares some characters with the pantoporate *Cantua*, on the one hand, and with the zonocolporate *Gilia* sect. *Giliastrum* on the other hand (Day and Moran, 1986). The phylogenetic hypothesis therefore postulates that the early split yielded a zonocolporate species, now extinct, which became the ancestor of *Acanthogilia* in one line and of *Gilia* sect. *Giliastrum* in another line. *Gilia* sect. *Giliastrum* has characters which can be regarded as ancestral for the other sections of *Gilia* and the other genera of the tribe Gilieae, as noted in the preceding section (Grant, 1959, 1998, 1999).

The zonocolporate condition is considered a good indicator of phylogenetic relationships because it is associated with other characters that distinguish the tribe Gilieae (*sensu* Grant) from other temperate genera and tribes of the family. Porter and Johnson (2000) list the pollen pore character in their genus descriptions but do not use it in making tribal groupings. This leads to differences between Porter/Johnson and Grant/

Day in hypothesized phylogenies and phylogenetic classifications.

An older phylogenetic hypothesis proposed that *Loeselia* is close to the ancestor of *Gilia* sect. *Giliastrum* (Grant, 1959, 1998, 1999; Porter and Johnson, 2000). This is supported by molecular evidence and some morphological characters. The difficulty with this hypothesis is that *Loeselia* has pantoporate pollen (Stuchlik, 1967). The available evidence is thus conflicting. Exploration of more characters in more species of *Loeselia* may help to clear up the problem.

The position of the Eocene genus *Gilisenium* in the early phylogeny of the family remains to be determined (Lott et al., 1998). It looks like a giliod polemon. Its pollen characters are unknown at present.

LINANTHUS

The Grant (1959) taxonomic system grouped the linanthoid polemons into one minor shrubby genus (*Leptodactylon*) and a large diverse herbaceous genus (*Linanthus*) subdivided into six sections. The molecular cladistic approach reveals two major clades. One clade contains *Leptodactylon* and two sections of the old *Linanthus* including the section *Linanthus*; the other contains four sections of the old *Linanthus* including the section *Leptosiphon* (Johnson et al., 1996; Bell et al., 1999). These clades are treated as separate genera, *Linanthus* and *Leptosiphon* (Porter and Johnson, 2000). The realignment is believed to be in the interest of monophyly (Bell et al., 1999; Porter and Johnson, 2000).

However, the realignment is not in the interest of similarity-based classification. The old comprehensive genus *Linanthus* was diverse but was held together by common leaf, habit, and chromosome characters. The diversity was expressed in the set of sections. The old *Linanthus* could be seen as a moderately large monophyletic genus which had radiated in various directions. The taxonomic advantage of the old classification is lost when two molecular clades

are sorted out and converted into genera which are poorly defined on non-molecular characters.

Let us return to the issue of monophyly. In the course of revising the linanthoid polemons, Porter and Johnson (2000) transferred the former *Gilia campanulata-filiformis* group (or *Tintinabulum*, Table 1) to the new segregate genus *Linanthus* (Table 2). *Linanthus* and *Leptodactylon* have pantoporate pollen, whereas the *Gilia campanulata-filiformis* group is zonocolporate (Stuchlik, 1967). The transfer thus makes the new *Linanthus* polyphyletic on the basis of the very good pollen pore character.

The molecular cladograms reveal a third clade, *Phlox*, nested within the linanthoid polemons (Johnson et al., 1996; Bell et al., 1999; Prather et al., 2000). This suggests that *Phlox* may have originated as an offshoot of some branch of the old genus *Linanthus*, and indeed Porter and Johnson show it as such in their phylogenetic tree (2000, p. 58).

Cladistic doctrine requires that *Linanthus* and *Phlox* be grouped together in some suprageneric category to avoid paraphyly, and Porter and Johnson place them both in their tribe Phlocideae (Table 2). However, *Linanthus* and *Phlox* are very different in leaf form, seeds, and chromosomes. Since paraphyly is a non-problem in taxonomy we are free to segregate *Linanthus* and *Phlox* into separate tribes and still claim monophyly for *Linanthus*.

TRIBES

The tribes of Porter and Johnson (2000) are major molecular clades (Table 3), while those of Grant (1998) are suprageneric multi-character taxa. The two sets of tribes coincide in some cases and differ in others (Tables 1 and 2), as expected in a comparison of taxonomic and cladistic classifications. Here we review and evaluate the various tribes from the standpoint of TTES. Some changes in the 1998 system of tribes are made in the light of the more recent

proposals of Porter and Johnson (2000); in other cases no changes are deemed necessary.

Four of the five tropical/subtropical tribes are the same in the two systems (tribes 1–4 in Tables 1 and 2). The fifth tribe in this geographical group, the *Loeselia* tribe, differs between the two systems.

The tribe Loeseliae of Porter and Johnson (2000) contains *Loeselia* and a series of temperate genera (*Giliastrum*, *Eriastrum*, etc.) (Table 2). *Loeselia* shares a suite of characters with the pantoporate tropical genera, as mentioned in a previous section (and cf. Grant, 1998), and it differs in these same characters from the zonocolporate temperate genera in the Porter/Johnson circumscription of the tribe. This tribe is not a monophyletic group when the morphological evidence is considered, nor is it a good taxon on the criterion of similarity and difference. It is better to retain the *Loeselia* tribe as it is in Grant (2000) and Table 1.

The tribe Gilieae of Porter and Johnson (2000) contains a mixture of four pantoporate genera (*Collomia*, *Allophyllum*, *Navarretia*, *Lathrocasis*) and two zonocolporate genera (*Gilia sens. str.*, *Saltugilia*; Table 2). This tribe is polyphyletic on the premise that the pollen pore character is a good indicator of phylogeny. There is no reason at present to make any changes in the composition of the tribe Gilieae *sensu* Grant (Table 1).

The tribe Polemonieae (*sensu* Grant, 1998) contains *Polemonium*, *Collomia*, *Allophyllum*, *Navarretia*, *Gymnosteris*, *Phlox*, and *Microsteris* (Table 1). Some changes are needed here. The tribe Polemonieae (*sensu* Porter and Johnson, 2000) contains only the genus *Polemonium* (Table 2), and this seems to be a good way to treat it. *Polemonium* forms a separate major clade in all the molecular cladograms (Johnson et al., 1996; Porter, 1997; Porter and Johnson, 1998; Prather et al., 2000). It is also distinct morphologically. I follow Porter and Johnson on this.

In their tribe Phlocideae, Porter and Johnson (2000) group *Linanthus* and its relatives with *Phlox* and its relatives (Table 2). This is supported by molecular cladograms but is a disparate grouping on cytological and morphological characters. Taxonomic classification is better served in my opinion by retaining a separate tribe Leptodactyloneae for the linanthoid group (Grant, 1998, 1999; Table 1).

The remaining genera are *Collomia*, *Allophyllum*, *Navarretia*, *Gymnosteris*, *Phlox*, and *Microsteris*. They can be and have been grouped together on seed, leaf, and chromosome characters (Table 1). If these characters are emphasized they could define a comprehensive tribe Phlocideae. However, the molecular cladograms indicate that the six genera fall into two separate groups: (1) *Collomia*, *Allophyllum*, *Navarretia*; and (2) *Gymnosteris*, *Phlox*, *Microsteris* (Johnson et al., 1996; Prather et al., 2000). If the molecular evidence is followed, the genera should be classified into two tribes: (1) tribe Phlocideae (*Gymnosteris*, *Phlox*, *Microsteris*); and (2) *Collomia* tribe (*Collomia*, *Allophyllum*, *Navarretia*).

To summarize, the tropical/subtropical genera can be grouped into five tribes as in Table 1. For the temperate genera, the tribes Gilieae and Leptodactyloneae can be retained as in Table 1, and the tribe Polemonieae as in Table 2. The other temperate genera (*Collomia*, *Allophyllum*, *Navarretia*, *Gymnosteris*, *Phlox*, *Microsteris*) could be grouped either in one broadly defined tribe Phlocideae, or split up in a narrow tribe Phlocideae and a *Collomia* tribe along the lines indicated in the preceding paragraph. Further study is desirable to clarify this question.

DISCUSSION

The incongruences between alternative systems of the Polemoniaceae should be viewed in the context of the larger paradigm differences between taxonomy and cladistics.

A standard research protocol of molecular plant cladistics is to take an existing taxonomic treatment of a plant group, subject the group to a molecular cladistic analysis, detect incongruences, conclude that the molecular indicators are right, and go on to recommend or make revisions in the classification in accordance with the cladograms. Papers exemplifying this approach are numerous and include Johnson et al. (1996) for the Polemoniaceae.

There are other conclusions that can be drawn from the same set of incongruences, as shown in this paper. The molecular indicators are likely to be right in some cases but not necessarily in every incongruence. Non-molecular characters may be the best indicators in some instances. More generally, we can't conclude that one system is more correct, that is, more true to phylogeny, than the other for two reasons. First we don't know the real phylogeny; we are comparing an inferred cladistic phylogeny with an inferred taxonomic one. Furthermore, since taxonomic and cladistic methods measure different variables—lateral vs. vertical relationships—a cladistic analysis is not a valid test of a taxonomic classification.

Various authors give high praise to the cladistic philosophy and methodology and relegate taxonomy to the sidelines or to the past (e.g., de Quieroz, 1997; Judd et al., 1999; Cantino and de Queiroz, 2000). Some cladists contemplate a future world in which cladistics has replaced taxonomy and taxonomic nomenclature (e.g., de Quieroz, 1997; Cantino and de Queiroz, 2000). This would be a world of clades.

Taxonomy is the only field of biology that blocks out sets of similarity groups of whole organisms. Named taxa when delimited by thorough study are very useful entities. A taxon often possesses one or more pivotal characters which enable us to form a concept of it; the concept of the group combined with its name is then useful in recognition, identification, and communication. The taxonomic name is sometimes

a code for the key character (e.g., Monocotyledoneae, Umbelliferae).

Major clades indicate phylogenetic trends but are often too heterogeneous to permit the formation of recognition concepts. The cladistic order Ericales of the Angiosperm Phylogeny Group (1998) and Judd et al. (1999) consists of several earlier taxonomic orders and ranges through a series of stages from primitive to advanced. The tribe Loeseliae of Porter and Johnson (2000) has the same problem on a smaller scale, as noted previously. Woese (1998, 2000) segregates the Eubacteria and Archaeobacteria into separate clades in order to connect the Archaeobacteria up with the eukaryotes, but in so doing he dissolves a good taxon.

Many groups in society—bird-watchers, wildlife managers, horticulturists, etc.—have a need for similarity-difference classifications of the organisms they deal with, and taxonomy provides this. The genealogy of the organisms in question is of only secondary interest to them.

A statement of William Whewell in his *History of the Inductive Sciences* (1859, book 16) gives us something to think about. "Systematic botany" (meaning traditional taxonomy in our terms) is founded on "the ideas of Likeness and Difference," just as astronomy is founded on "the ideas of Space and Time." The two fields can trace their histories to "the earliest times."

ACKNOWLEDGMENTS

I discussed the problem with Ernst Mayr, Alva Day, and Tom Wendt. Billie L. Turner, Beryl Simpson, Alan Prather, Jerry Brand, Karen Grant, and an anonymous reviewer read the manuscript. I thank these individuals for their helpful suggestions.

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