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## PHYLOGENY OF POLEMONIACEAE BASED ON NUCLEAR RIBOSOMAL INTERNAL TRANSCRIBED SPACER DNA SEQUENCES

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### ABSTRACT

Nuclear ribosomal internal transcribed spacer (ITS) DNA sequences are used to estimate the phylogeny of 53 members of Polemoniaceae, representing all but two genera of the family. Fitch parsimony analysis of equal-weighted nucleotide sites result in 1080 minimal-length trees. However, when alignment-ambiguous positions are removed and an 11:10 transition to transversion weighting is imposed only eight trees are found. These data are used to address two issues: 1) patterns of diversification in Polemoniaceae, and 2) the circumscription and monophyly of the genus *Gilia*. Although the monophyly of Polemoniaceae is well supported, relationships inferred among the earliest diverging lineages are altered by character weighting, treatment of indels, and taxon inclusion. In spite of the lack of reliable resolution at the basal nodes, ITS data provide evidence that *Gilia*, as currently interpreted, is polyphyletic and comprises at least five independent lineages.

Key words: DNA sequences, *Gilia*, Polemoniaceae, phylogeny.

### INTRODUCTION

The Polemoniaceae are a small, mostly New World, group of between 300 and 340 species (Grant 1959; Willis 1966; Cronquist 1981; Thorne 1992; Patterson 1993). Evolutionary relationships and classification within this family have long been controversial (Bentham 1845; Gray 1870; Kuntze 1891; Brand 1907; Rydberg 1913; Dawson 1936; Wherry 1940; Mason 1945; Mason and Grant 1948; Grant 1959; Cronquist 1984; Day and Moran 1986). Although generally considered a "natural" group by most authors, generic and species relationships within the family have remained obscure: the circumscription of species, genera and higher taxonomic groups differing radically from author to author. The most recent family-wide classification of Polemoniaceae is that of Grant (1959), who recognizes 18 genera, placed into five tribes (Table 1). Over the past 30 years, a broad spectrum of data has accumulated bearing on relationships within the family. These include family- and generic-level surveys of palynological (Stuchlik 1967; Loeblich 1964; Taylor and Levin 1975; Chuang et al. 1978; Timbrook 1986; Lord and Eckard 1986; Day and Moran 1986), histological (Carlquist et al. 1984), chemosystematic (Smith et al. 1977; Dean et al. 1978; Harborne and Smith 1978; Harborne 1980; Smith et al. 1982; Wilken et al. 1982; Kiredjiad and Smith 1985), and reproductive data (Grant and Grant 1965; Plitmann and Levin 1983; 1990). Although neither phenetic nor phylogenetic analyses have been conducted on the family using this wide array of morphological and chemical data (but

see Wilken and Hartman 1991), recent phylogenetic analyses of nucleotide sequences of the chloroplast gene *matK* (Steele 1991, 1992; Steele and Vilgalys 1994; Johnson and Soltis 1995; Johnson et al. 1996) suggest these tribes are not monophyletic. In light of these data, realignment of Grant's (1959) tribes appears inevitable. This study provides additional insight into classification and evolutionary history of Polemoniaceae from an independent source of evidence. Presented is a molecular phylogenetic study using sequences from the nuclear genes coding for ribosomal RNA, the internal transcribed spacers (ITS1 and ITS2).

### *Taxonomic Background*

The contrast between various classifications of Polemoniaceae has been reviewed by Grant (1959: 4). There is little consensus among historical classifications. The few general similarities (particularly for classifications since 1900) include: 1) the tendency to place the tropical genera *Cantua*, *Cobaea* and *Bonplandia* in separate tribes apart from the remainder of the so-called "temperate genera" (Brand 1907; 1908; Grant 1959); and 2) the inclusion of *Linanthus* and *Leptodactylon* in the same tribe with *Gilia* (Brand 1907; 1908; Wherry 1940; 1945; Grant 1959) while placing *Phlox* in a different tribe (Wherry 1940; 1945; Grant 1959). A particularly striking disparity among historical classifications in the family is the circumscription of the genus *Gilia*. These differences range from broad circumscriptions that include nearly all of



the "temperate genera" except *Polemonium*, *Phlox*, and *Collomia* (e.g., Bentham and Hooker 1876) to the present treatment by Grant (1959) that segregates *Allophyllum*, *Ipomopsis*, *Eriastrum*, *Langloisia*, *Loesiastrum*, and *Navarretia* from *Gilia*.

Grant's currently accepted tribal classification has not found support from recent molecular studies. Steele and Vilgalys (1994) provided evidence from cpDNA *matK* sequences that some genera included in tribe Polemoniaceae share more recent common ancestry with genera placed in tribe Gilieae. For example *Collomia* and *Allophyllum* (tribe Polemoniaceae) are more closely related to *Gilia* and *Navarretia* (tribe Gilieae) than to either *Phlox* or *Polemonium* (tribe Polemoniaceae). Indeed, Steele and Vilgalys suggest that there is no support for two temperate tribes, rather Polemoniaceae possess a single temperate lineage. These results were not only corroborated by Johnson and Soltis (1995) and Johnson et al. (1996) but due to the increased taxon sampling, evidence was presented that the genus *Gilia*, as currently circumscribed, is a polyphyletic assemblage. Some members of *Gilia* (e.g., *G. filiformis*) are more closely related to genera never associated with tribe Gilieae (e.g., *Phlox*) than to other members of *Gilia*.

This controversy over relationships within Polemoniaceae is problematic because Polemoniaceae have been used as a model system for the study of many aspects of character evolution and reproductive biology. The family as well as individual species have been used as primary examples for the pattern and modes of evolution of pollination mechanisms (Grant and Grant 1965; Galen and Kevan 1983; Paige and Whitham 1985, 1987a; Galen and Stanton 1989), evolution of plant sexual systems (Grant 1959; Schoen 1982a, b, c, 1983; Plitmann and Levin 1983, 1990), hybridization and its evolutionary consequences (Grant 1950, 1954a, b, 1957, 1979; Grant and Grant 1960; Day 1965; Levin 1979; Coyne 1974; Grant and Wilken 1987), natural selection on floral traits (Ellstrand 1983; Paige and Whitham 1985; Wolf et al. 1986; Ellstrand and Mitchell 1988; Campbell 1989; 1991), and evolution life history (Paige and Whitham 1987a, b). An accurate phylogenetic backdrop is necessary to interpret evolutionary changes in these traits (Donoghue 1989). The chloroplast phylogenies provide an important inroad into understanding the phylogeny of Polemoniaceae. However, a single gene phylogeny may not correspond with an organismal phylogeny (Dwyer et al. 1991; Doyle 1992; Neigel and Avise 1986; Sanderson and Doyle 1992). A phylogeny based on an independent source of data is both desirable and necessary to either corroborate or refute phylogenetic inferences from the chloroplast genome.

In this paper I provide a preliminary assessment of phylogenetic relationships of Polemoniaceae using

DNA sequences of the internal transcribed spacers (ITS1 and ITS2) of the nuclear ribosomal cistron. Because these spacer sequences are encoded in the nuclear genome, they represent an independent source of phylogenetic information from chloroplast sequences.

## METHODS

### Sampled Taxa

An attempt was made to include representatives of all of the 19 currently recognized genera of Polemoniaceae (Table 1). Because of the controversy over the limits of the genus *Gilia* and its relation to *Ipomopsis*, 13 species of *Gilia* (members of sections *Arachnion*, *Gilia*, *Giliandra*, *Giliastrum*, *Gilmania*, and *Saltugilia*) and five species of *Ipomopsis* (members of sections *Ipomopsis*, *Microgilia*, *Phloganthea* [including the *Giliopsis* group]). In addition, a largely unknown woody member of Polemoniaceae, *Gilia scabra* (treated by Grant 1959 as a synonym of *Linanthus nuttallii*), is also included. Only two genera are not represented. *Gymnosteris*, with two species, is not included because the DNAs did not sequence well enough for reasonable interpretation (nearly all of the nucleotide sites appeared polymorphic). In addition, the DNA sequence from *Huthia coerulea* is not included because it is unalignable with other Polemoniaceae sequences.

Selection of an outgroup for Polemoniaceae is problematical. In spite of most present classifications (Cronquist 1981; Takhtajan 1980; Thorne 1968, 1992), molecular data from the chloroplast gene *rbcL* (Olmstead et al. 1992; Chase et al. 1993) provide evidence that Polemoniaceae are more closely related to Ericalean groups, usually placed in the Dilleniidae, than to the Asteridae families with which they are traditionally placed: i.e., Convolvulaceae, Hydrophyllaceae, and Solanaceae (but see Anderberg 1992; Martin and Dowd 1991). In particular, chloroplast sequence data from *rbcL* (Olmstead et al. 1992) and *matK* (Johnson et al. 1996) place Fouquieriaceae as the sister group to Polemoniaceae. By contrast, the Chase et al. study of *rbcL* supports a close relationship between Polemoniaceae and Diapensiaceae. Close relationships between Polemoniaceae and both Diapensiaceae (Linnaeus 1753; Don 1822) and Fouquieriaceae (Humbolt et al. 1823; Nash 1903; Engler and Gilg 1924; Abrams 1951; Thorne 1977) have been suggested based on morphological evidence. Based on this evidence, I have selected Diapensiaceae and Fouquieriaceae as outgroups. Attempts were made to also include sequences from Solanales, e.g., *Nicotiana rustica* L. (Venkateswarlu and Nazar 1991); however, these sequences are unalignable.



### Collection and DNA Extraction

Material collected in the field was placed on ice for transport to storage at  $-80^{\circ}\text{C}$ . Total genomic DNA extracts from leaf material, powdered under liquid nitrogen, used a 2X CTAB protocol, modified from Doyle and Doyle (1987). In some cases a 4X CTAB (with 0.1% PVP-40) extraction buffer was used for species with high polysaccharide content. The DNAs were further purified using cesium chloride/ethidium bromide gradients (Maniatis et al. 1982). The DNAs of *Acanthogilia gloriosa* and *Gilia scabra* were extracted from leaf material desiccated using silica gel (Liston and Rieseberg 1990; Chase and Hillis 1991). The DNAs of six taxa were obtained from leaf fragments taken from herbarium collections (Table 1). Subsequently, all DNA samples obtained from herbarium specimens have been verified using freshly collected material, and in no case did the DNA sequences of ITS differ at more than a single, uninformative nucleotide site (Porter unpubl.).

### PCR Amplification and Sequencing

Sequencing was performed on 39 samples using the method of Sanger et al. (1977). Single-stranded DNAs for both strands of the two internal transcribed spacers of the nuclear ribosomal cistron, ITS1 and ITS2, were amplified directly by asymmetric polymerase chain reaction (PCR), using a 1:20 ratio of the primers "ITS5" (5'-GGA AGT AAA AGT CGT AAC AAG G-3') and "ITS2" (5'-GCT GCG TTC TTC ATC GAT GC-3') for the ITS1 spacer, and the primers "ITS3" (5'-GCA TCG ATG AAG AAC GCA GC-3') and "ITS4" (5'-TCC TCC GCT TAT TGA TAT GC-3') for the ITS2 spacer (White et al. 1990). PCR amplifications, PCR product purification and direct single-stranded DNA sequencing followed the procedures described by Baldwin (1992), except for the following modifications. The amplification of DNA from herbarium material employed a modified 10 $\times$  *Taq* polymerase reaction buffer consisting of 67mM Tris-HCl (pH 8.8), 2 mM  $\text{MgCl}_2$ , and 2 mg/ml bovine serum albumin (Pääbo et al. 1989; Pääbo 1990). The PCR products were electrophoresed using a 1.5% agarose gel (pre-stained with ethidium bromide) in a 1 $\times$  TBE (pH 8.3) buffer, to confirm the single-stranded product and purified using differential filtration in Millipore Ultra-Free-MC microfuge tubes (Millipore UFC-3 THK00). The purified DNAs were sequenced using the dideoxy chain termination reaction, following the procedures outlined in the TAQuence<sup>®</sup> kit (U. S. Biochemical Co.). Sequencing products were labeled using  $\alpha$ - $^{35}\text{S}$ dATP. To reduce base compressions, 7-deazadGTP was substituted for dGTP in all of the sequencing reactions. The gels were fixed in 5% acetic acid/5% methanol for 45 min and vacuum dried at

$80^{\circ}\text{C}$  for 1 hr. The autoradiographs were exposed for a minimum of 24 hr. All sequences were checked by sequencing the opposite strand.

Sequence data for 14 species were obtained using an Applied Biosystems Model 373A Automated DNA Sequencing System (Perkin Elmer). Template DNAs were prepared by symmetric PCR of the entire ITS region using a 1:1 ratio of primers ITS5 and ITS4. Direct cycle-sequencing of the ITS region followed manufacturers specifications, using the PRISM<sup>™</sup> DyeDeoxy<sup>™</sup> Terminator Kit (Perkin Elmer) and employed primers ITS2, ITS3, "ITS5I" (5'-AGG TG ACC TGC GGA AGG ATC ATT-3') and "ITS4I" (5'-GGT AGT CCC GCC TGA CCT GG-3'). Primers ITSP5I and ITSP4I are internal to and flanking ITS5 and ITS4, respectively. The four primers provide sequences for overlapping fragments that collectively cover both strands of the entire ITS region (ITS1, 5.8S and ITS2).

### Sequence Alignment

The 56 sequences were truncated to include only ITS1 and ITS2. Identification of the terminal ends of ITS1 and ITS2 was based on comparisons with published sequences for *Daucus carota* L., *Nicotiana rustica*, *Vicia faba* L., species of *Astragalus*, and representatives of *Madiinae* (Baldwin 1992, 1993; Venkateswarlu and Nazar 1991; Wojciechowski et al. 1993; Yokota et al. 1989). The two spacer regions were aligned separately, using PILEUP (Feng and Doolittle 1987; Higgins and Sharp 1987; see also Needleman and Wunch 1987), a multiple sequence alignment program of the University of Wisconsin Genetics Computer Group (UWGCG) software package. The alignment parameters were varied from GapWeight= 1.0 and GapLengthWeight= 0.1 to GapWeight= 5.0 and GapLengthWeight= 3.0. With higher gap and length penalty values, fairly large blocks of aligned sequences are produced, but single taxa are sometimes grossly misaligned. Low gap and length penalties result in alignments lacking grossly misaligned taxa, but with a greater frequency of gaps. Evenso, alternative alignments were evident. The resulting alignments were both analyzed directly and manually realigned and reanalyzed. The PILEUP aligned sequences were manually realigned to maximize the number of invariant nucleotide positions. The results presented refer to sequences which were realigned manually; however, the conclusions apply to both alignments.

### Phylogenetic Analysis

Estimations of phylogenetic relationships, based on combined ITS1 and ITS2 sequences, were obtained using Fitch parsimony as implemented in PAUP (version 3.0; Swofford 1991). A variety of heuristic approaches



Table 1. Classification of Polemoniceae, sensu Grant (1959) and collections utilized in the phylogenetic analysis of nrDNA internal transcribed spacer sequences. The cross (†) indicates those taxa for which herbarium collections were used for DNA extractions. The asterisk (\*) indicates those species for which cycle sequencing and automated sequencing procedures were used. Vouchers are cited and housed as indicated. The taxa included to serve as the outgroup are designated as such parenthetically.

Tribe Cantuaee (2: ca. 9)		
<i>Acanthogilia</i> (1 species)	<i>n</i> = 9	<i>A. gloriosa</i> (Brandeg.) Day & Moran. 2.4 km west of Punta Prieta, Baja California, Mexico. [J. M. Porter & K. D. Heil 7987; SJNM]
<i>Cantua</i> (ca. 12 species)	<i>n</i> = 27	<i>C. quercifolia</i> Cav. Cult. San Francisco State University, San Francisco, California. [R. Patterson sn; RSA]
<i>Huthia</i> (2 species)	<i>n</i> = ?	†* <i>H. coerulea</i> Brand. Arequipa, Peru. [O. Tovar 3543; MO]
Tribe Bonplandieae (2: ca. 17)		
<i>Bonplandia</i> (2 species)	<i>n</i> = 15	<i>B. geminiflora</i> Cav. Cult. San Francisco State University, San Francisco, California. [R. Patterson sn; RSA]
<i>Loeselia</i> (ca. 15 species)	<i>n</i> = 9	<i>L. glandulosa</i> (Cav.) Don. Patagonia Mountains, Santa Cruz County, Arizona. [J. M. Porter & C. Campbell 9231; AZ, SJNM]
Tribe Cobaeae (1: 19)		
<i>Cobaea</i> (19 species)	<i>n</i> = 27	<i>C. scandens</i> Cav. Cult. San Francisco State University, San Francisco, California. [R. Patterson sn; RSA]
	<i>n</i> = ?	† <i>C. baiurita</i> Standl. Puerto Vienda, Chiapas, Mexico. 20 Aug. 1967. [O. Clarke 293; AZ]
Tribe Polemonieae (5: ca. 102)		
<i>Allophyllum</i> (5 species)	<i>n</i> = 9	* <i>A. divaricatum</i> (Nutt.) A. Grant & V. Grant. Mt. Konociti, Lake County, CA. [J. M. Porter & L. Machen 10819; RSA]
	<i>n</i> = 9	<i>A. gilioides</i> (Benth.) Grant & Grant. 5 miles south of Oracle, Santa Catalina Mtns., Pinal County, Arizona. [J. M. Porter & L. Machen 8751; AZ, SJNM]
<i>Collomia</i> (15 species)	<i>n</i> = 8	* <i>C. grandiflora</i> Lindl. Libre Mtns., Los Angeles County, California. [T. Ross & S. Boyd 8142; RSA]
	<i>n</i> = 8	<i>C. linearis</i> Nutt. 10 miles northeast of Pogosa Springs, Archuleta County, Colorado. [J. M. Porter 8565; AZ]
<i>Gymnosteris</i> (2 species)	<i>n</i> = 6	—
<i>Phlox</i> (ca. 60 species)	<i>n</i> = 7	<i>P. stanburyi</i> (Torr.) Heller. 4 miles south of the junction of Nevada Highway 160 and US Highway 95, Nye County Nevada. [J. M. Porter 8841; SJNM]
	<i>n</i> = 7	* <i>P. (Microsteris) gracilis</i> E. Greene. Mt. Emma, Los Angeles County, California [J. M. Porter 10566; RSA]
<i>Polemonium</i> (ca. 20 species)	<i>n</i> = 9	<i>P. foliosissimum</i> Gray. Lizard Head Pass, along Colorado Highway 145, Dolores County, Colorado. [J. M. Porter 7526; SJNM]
Tribe Gilieae (8: ca. 200)		
<i>Eriastrum</i> (14 species)	<i>n</i> = 7	<i>E. diffusum</i> (Gray) Mason. Tucson Mountains, 4 miles west of Tucson, Pima County, Arizona. [J. M. Porter 8754; AZ]
<i>Gilia</i> (ca. 70 species)	<i>n</i> = 8	<i>G. caespitosa</i> Gray. Capitol Reef National Park, Wayne County, Utah [J. M. Porter & K. Heil 7352; SJNM]
	<i>n</i> = 9	†* <i>G. campanulata</i> Gray. 5 mi W Independence, Inyo County, CA [Kerr 638; RSA]
	<i>n</i> = 9	† <i>G. capitata</i> Sims. E of Washougal, Skamania County, Washington. 14 July 1984. [R. S. Halse 2900; AZ]
	<i>n</i> = 72	†* <i>G. crassifolia</i> Benth. Rio Molles, Endesa, Coquimbo, Chile. 5 Nov. 1970. [J. Simon 161; RSA]
	<i>n</i> = 9	* <i>G. filiformis</i> Gray. 12 mi E. Independence, Inyo County, CA [J. M. Porter & L. Machen 10849; RSA]
	<i>n</i> = 18	<i>G. flavocincta</i> A. Nels subsp. <i>australis</i> A. & V. Grant. Ca. 6 miles east of Roosevelt Reservoir, roadside, Pinal County, Arizona. [J. M. Porter 7060; SJNM]
	<i>n</i> = 9	† <i>G. foetida</i> Gil. ex Benth. Las Heras camino a Yalguaraz, Provincia de Mendoza, Argentina. 27 Dec. 1947. [R. Leal, 11,113; AZ]
	<i>n</i> = 9	<i>G. hutchinsifolia</i> Rydb. 5 mi S of Lathrop Wells, Nye County, Nevada. [J. M. Porter 8209; AZ, SJNM]
	<i>n</i> = ?	* <i>G. inyoensis</i> I. M. Johnston. Anchorite Pass, Mineral County, NV. [J. M. Porter & L. Machen 10842; RSA]
	<i>n</i> = 18	<i>G. latifolia</i> Wats. Cataract Canyon, Canyonlands National Park, San Juan County, Utah. [J. M. Porter & M. Heil 8804; AZ, SJNM]
	<i>n</i> = 9	* <i>G. maculata</i> Parish. Whitewater Canyon, Riverside County, CA. [J. M. Porter & L. Machen 10560; RSA]
	<i>n</i> = 8	<i>G. mcvickerae</i> M. E. Jones. Ca. 4 mi S of Panguitch on UT89, Garfield County, Utah. [J. M. Porter and L. Machen 7184; SJNM]

Table 1. Continued.

	<i>n</i> = 8	<i>G. nyensis</i> J. Reveal. Red001 burned area, Red Rock Canyon, Nevada Nuclear Test Site, Nye County, Nevada. [ <i>J. M. Porter</i> 8202; AZ]
	<i>n</i> = 9	<i>G. ochroleuca</i> M. E. Jones. Ca. 4 mi. S of Big Pine, Inyo County, California. [ <i>J. M. Porter</i> 8860; AZ, SJNM]
	<i>n</i> = 8	<i>G. pentstemonoides</i> M. E. Jones. N side of the Gunnison River, Cimarron, Montrose County, Colorado. [ <i>J. M. Porter</i> 7192; AZ, SJNM]
	<i>n</i> = 9	<i>G. rigidula</i> Benth. 7 miles southeast of Sonoita, Santa Cruz County, Arizona. [ <i>J. M. Porter</i> 8723; RSA, SJNM]
	<i>n</i> = 9	<i>G. scabra</i> Brandegee. Cerro Prietto, near San Hipalito, Viscaïno Desert, Baja California Sur, Mexico. [ <i>J. M. Porter and K. Heil</i> 7991; SJNM]
	<i>n</i> = 9	<i>G. scopulorum</i> M. E. Jones. Hualapai Indian Reservation, Mohave County, Arizona. 21 Apr. 1973. [ <i>P. S. Martin, sn</i> ; AZ]
	<i>n</i> = 9	* <i>G. splendens</i> Dougl. ex Lindl. Pacific Crest Trail, San Bernardino County, CA. [ <i>J. M. Porter</i> 10142; RSA]
	<i>n</i> = 9	<i>G. stellata</i> Heller. Roadside along AZ85, 9 mi N of Why, Pima County, AZ. [ <i>J. M. Porter</i> 9492; SJNM]
	<i>n</i> = 8	<i>G. subnuda</i> Gray. W of Steamboat Canyon, Apache County, AZ. [ <i>J. M. Porter &amp; K. Heil</i> 7355; SJNM]
	<i>n</i> = 18	† <i>G. tenerrima</i> A. Gray. 70 mi NW of Elko, Elko County, Nevada. 26 June 1937. [ <i>N. Nichols &amp; L. Lund</i> 206; AZ]
	<i>n</i> = 9	<i>G. tricolor</i> Benth. Cult. University of Arizona, seed from retail seed source. [ <i>J. M. Porter sn</i> ; AZ]
<i>Ipomopsis</i> (30 species)	<i>n</i> = 7	<i>I. gunnisonii</i> (Torr. and Gray) V. Grant. Navajo Mine, 12 miles south of Waterflow, San Juan County, New Mexico. [ <i>J. M. Porter</i> 9295; AZ, SJNM]
	<i>n</i> = 7	<i>I. multiflora</i> (Nutt.) V. Grant. Molino Basin, Santa Catalina Mountains, Pima County, Arizona. [ <i>J. M. Porter</i> 8052; AZ, SJNM]
	<i>n</i> = 7	<i>I. longiflora</i> (Torr.) V. Grant. 8 mi south of Safford, Greenlee County, Arizona. [ <i>J. M. Porter</i> 7142; SJNM]
	<i>n</i> = ?	†* <i>I. sonorae</i> (Rose) A. Grant. Sonora, Mexico. [ <i>T. R. VanDevender</i> 93-20; AZ, RSA]
	<i>n</i> = 7	† <i>I. tenuifolia</i> (Gray) V. Grant. 11 May 1980. Sierra San Pedro Martir, Mexico. [ <i>S. P. McLaughlin</i> 2465; AZ]
<i>Langloisia</i> (1 species)	<i>n</i> = 7	<i>L. setosissima</i> (Torr. & Gray) Greene subsp. <i>setosissima</i> . 4 miles south of the junction of Nevada Highway 160 and US Highway 95, Nye County Nevada. [ <i>J. M. Porter</i> 8561; SJNM]
	<i>n</i> = 7	<i>L. setosissima</i> (Torr. & Gray) Greene subsp. <i>punctata</i> (Cov.) Timbr. 4 miles south of the junction of Nevada Highway 160 and US Highway 95, Nye County Nevada. [ <i>J. M. Porter</i> 8840; SJNM]
<i>Leptodactylon</i> (7 species)	<i>n</i> = 9	* <i>L. pungens</i> (Torr.) Rydb. 3 mi S Natural Bridges Nat. Mon., Kane County, Utah. [ <i>J. M. Porter</i> 8561; SJNM]
	<i>n</i> = 9	<i>L. watsonii</i> (Gray) Rydb. Waterpocket Fold, Capitol Reef National Park, Wayne County, Utah. [ <i>J. M. Porter</i> 8571; SJNM]
<i>Linanthus</i> (41 species)	<i>n</i> = 9	<i>L. aureus</i> (Nutt.) Greene. 2 miles north of Searchlight, along US Highway 95, Clark County, Nevada. [ <i>J. M. Porter</i> 8822; AZ, SJNM]
	<i>n</i> = 9	* <i>L. bicolor</i> (Nutt.) Greene. Hayfork, Trinity County, CA. [ <i>J. M. Porter &amp; L. Machen</i> 10821; RSA]
	<i>n</i> = 9	<i>L. nuttallii</i> (Gray) Greene ex Mkn. 8 miles north of Granville, near Grey Peak, White Mountains, Greenlee County, Arizona. [ <i>J. M. Porter &amp; L. Machen</i> 9004; RSA, SJNM]
	<i>n</i> = 9	* <i>L. parryae</i> (Gray) Greene. Valyermo, Los Angeles County, CA. [ <i>J. M. Porter</i> 10553 RSA]
<i>Loeseliastrum</i> (2 species)	<i>n</i> = 7	<i>L. matthewsii</i> (Gray) Timbr. San Bernardino County, California. [ <i>J. M. Porter</i> 8869; SJNM]
	<i>n</i> = 7	<i>L. schottii</i> (Torr.) Timbr. 14 mi S of Parker, along AZ95, Yuma County, Arizona. [ <i>J. M. Porter</i> 8856; RSA]
<i>Navarretia</i> (32 species)	<i>n</i> = 9	<i>N. breweri</i> (Gray) Greene. Columbine Pass, Uncompahgre Plateau, Montrose County, Colorado. [ <i>J. M. Porter</i> 8599; RSA]
Diapensiaceae (Outgroup)	<i>n</i> = 6	*† <i>D. laponica</i> L. Mt. McKinley, Alaska. [ <i>M. Fay</i> 325; ARIZ]
Fouquieriaceae (Outgroup)	<i>n</i> = ?	<i>F. columnaris</i> (Kell.) Hendrickson. Cult., The University Mall, University of Arizona Campus, Tucson, Arizona. [ <i>J. M. Porter sn</i> ; SJNM]
	<i>n</i> = 6	<i>F. splendens</i> Engelm. Cult., Old Main, University of Arizona Campus, Tucson, Arizona. [ <i>J. M. Porter sn</i> ; SJNM]



was employed to help assure that all of the most parsimonious solutions were obtained. Initially, CLOSEST addition and TBR (tree bisection-reconnection) swapping was performed. This was followed by 100 replicates of RANDOM addition and TBR branch swapping. Finally, 500 replicates of RANDOM addition were carried out with no swapping, followed by TBR swapping on the resulting set of trees (Maddison 1991). This should insure that all minimal length tree are found, even if multiple "islands" of equally parsimonious trees exist. The data matrix was analyzed with equal weights at all nucleotide positions and using an 1.1 to 1 transition/transversion bias (based on estimates from Polemoniaceae sequences). Insertions and/or deletions (indels) were coded initially as missing data. Subsequent analyses treated indels as a "fifth nucleotide" (GAPMODE=FIFTHSTATE option in PAUP) and as additional binary characters.

### Robustness and Sampling

An assessment of the relative support for clades was performed using the decay index (Bremer 1988; Donoghue et al. 1992) and the bootstrap (Felsenstein 1985). Decay values were calculated for one, two and three steps longer than the shortest trees. My purpose is to identify only the weakly supported nodes. Bootstrap values were calculated from 100 replicate Fitch parsimony analyses, as implemented by PAUP 3.0, using heuristic searches based on CLOSEST addition and TBR branch swapping.

The distribution of tree-lengths, based on 10,000 randomly generated trees was evaluated for skewness (g1). A strongly left-skewed tree length distribution has been suggested to indicate that a data set is highly structured and likely contains strong phylogenetic signal (Goodman et al. 1979; Fitch 1984; Werman 1986; Hillis and de Sa 1988; Hillis and Dixon 1989; Hillis and Huelsenbeck 1992; Hillis 1991; Huelsenbeck 1991). However, this test actually assesses whether the g1 of a given data set deviates from the expected g1 of random data (see also Kallersjo et al. 1992).

To investigate the sensitivity of these data to taxon sampling, an analysis based on resampling terminal taxa was conducted. Lanyon's jackknife is a heuristic tool to explore the effect of taxon sampling on internal branch support and tree structure (Lanyon 1985a, b; Felsenstein 1988; Siddall 1995). Lanyon (1985a) points out that trees generated during this jackknife procedure simulate possible outcomes had the investigator failed to sample a taxon or if extinction had occurred. Clearly, taxon sampling (inclusion) can have profound consequences on assessment of monophyly (Doyle and Donoghue 1987; Gauthier et al. 1988; Donoghue et al. 1989; Novacek 1991). The manually realigned data matrix was analyzed by sequentially re-

moving each member of the ingroup, one at a time, and performing a parsimony analysis (CLOSEST addition, HOLD= 2, TBR branch swapping) on the resulting data sets (pseudoreplicates). In all cases, only the strict-consensus tree from analyses of each pseudoreplicate was retained. The trees were compared and pseudoreplicate-consensus trees were generated. This was done by first returning the excluded taxon from each pseudoreplicate run back into the pseudoreplicate strict-consensus tree. The excluded taxon was placed in the same position it is found in the strict-consensus tree from the analysis of the entire data set. This is based on the assumption that the analysis of the full data set provides evidence for the taxon's placement. After the excluded taxon is returned to the tree, a consensus of the entire set of trees was obtained, using strict and majority rule consensus procedures.

## RESULTS

### ITS Sequence Variation

The ITS1 regions of all representatives of Polemoniaceae, as well as the outgroups, were consistently larger than the ITS2 regions. Within Polemoniaceae the ITS1 region is generally 249–253 bases. Extremes beyond this range include the sequences of *Gilia rigidula* at 242 base pairs (bp) and *Gilia scabra* at 262 bp. The outgroups possessed the largest ITS1 sequence of this analysis, 267 bp. In Polemoniaceae, percent G+C content of ITS1 ranged from 42.2% in *Cobaea bairurita* to 65.0% in *Acanthogilia gloriosa*. ITS2 sequences were mostly between 188 and 193 bases, but ranged from 187 bp in *Phlox standsburyi* and *Linanthus nuttallii* to 195 in *Gilia foetida*. The ITS2 region of the outgroups was slightly larger, 196 bp. Percent G+C content of ITS2 in Polemoniaceae varied from 48.3% in *Cobaea bairurita* to 61.8% in *Acanthogilia gloriosa*.

### Alignment

Both ITS1 and ITS2 possess several highly conserved regions, flanked by more variable regions (Baldwin et al. 1995). The conserved regions are easily and nearly unambiguously aligned; however, the variable regions become increasingly difficult to align as pairwise distance increases. As a result, alignment of some taxa (i.e., outgroup taxa) should be viewed with skepticism. The variable regions of ITS in Polemoniaceae are frequently associated with short indels of one to a few nucleotides. Sequences of ITS1 and ITS2, aligned using variable weights in PILEUP produce similar alignments; however, the more variable regions seemed better aligned (i.e., there is a higher frequency of invariant sites) using GapWeight= 1.0 and GapLengthWeight= 0.1 (the aligned sequences us-



ing PILEUP are not shown). The manually realigned sequences are used in all of the following comparisons. Even so, the manually aligned sequence data set is not without alternative alignments and alignment in some regions remains ambiguous (Appendix I).

The aligned, combined sequences of ITS1 and ITS2 required, on average, gaps at 14.39% of the sites of any given sequence. The inclusion of the outgroup was responsible for gaps at 4.53% of these nucleotide positions. The combined data matrix, possesses 529 characters, of which 120 are invariant and 346 (65.28%) are potentially informative. The pair-wise levels of divergence range from 0.18% (between *Langloisia setosissima* subsp. *setosissima* and *Langloisia setosissima* subsp. *punctata*) to 42.4% (between *Diapensia lapponica* and *Cantua quercifolia*).

### Phylogenetic Analysis

All of the parsimony analyses of the full, equal-weighted data set, with indels treated as missing, resulted in recovery of the same 1080 minimum-length trees. For the data set including only potentially informative sites, the most parsimonious trees were of 1552 steps (tree length including all sites is 1646), with a consistency index (C.I.) of 0.423, retention index (R.I.) of 0.622, and rescaled consistency index (R.C.) of 0.263. The strict consensus tree (Fig. 1) shows that the primary areas of disagreement in the set of minimal length trees involves 1) relationships involving *Ipomopsis sonora* and *Loeseliastrum matthewsii* in the Loeseliae Clade, 2) relationship of *Gilia campanulata* within the Linanthieae Clade, and 3) relationships between three clades of *Gilia* species as well as *Gilia splendens*, within the Gilieae Clade. Aside from the basal nodes, the phylogenetic estimate is not highly sensitive to coding of the indel regions or transition-transversion weighting. Figure 2 shows the strict consensus trees from analyses that 1) treat each indel position as a fifth character state while all other sites are equally weighted, and 2) remove all indels and alignment-ambiguous positions while imposing a 1.0:1.1 transition to transversion weighting. In both analyses many fewer trees are recovered, 12 and 8 respectively. The topologies differ primarily in the inferred relationships of *Cobaea*, *Cantua*, *Bonplandia* and *Acanthogilia* to the remainder of Polemoniaceae. Both of these trees are very similar in structure to the full, equal-weighted analysis.

### Tree Support

**Bootstrap.**—The bootstrap 50% majority rule tree (not shown) is structurally identical to the strict consensus insofar as the majority rule tree is resolved. Many of the clades are supported with high bootstrap percentage values (see Fig. 1). Ten clades are supported by

values of 95% or greater. Hillis and Bull (1993), suggest that 70% bootstrap percentage values or greater might be a better estimate of a “95% confidence interval” for estimating the correct phylogeny. If this can be generalized to all data (but see Felsenstein and Kashino 1993), another 14 clades fall within the confidence limit.

Some portions of the trees, show little bootstrap support. In general the highest values are associated with the more terminal portions of the phylogeny. The values tend to decrease toward the more basal nodes. The only notable exception is the ancestral node of Polemoniaceae, that possesses a significant value of 99%.

**Decay index.**—The decay index is here employed to identify those clades that are weakly supported or may be prone to errors in phylogenetic estimation. Decay values shown in Fig. 1 range from one to three. In general, the most weakly supported nodes are the more basal nodes within Polemoniaceae. Again, the only exception to this trend is the ancestral node of Polemoniaceae.

**Lanyon's jackknife.**—The jackknife procedure required 53 analyses, the consensus of these analyses is shown in Fig. 3. The regions of the phylogeny that are affected by the inclusion of particular taxa are represented as unresolved polytomies. The lack of resolution indicates that a major portion of the phylogenetic estimate can change based solely on which terminal taxa are included in the analysis. However, it is the removal of *Acanthogilia* and the placement of *Cantua* that are responsible for much of the lack of resolution (i.e., the Loeseliae Clade). Resolved portions of the consensus tree represent relationships not effected by the current sampling. This includes the Gilieae Clade, the *Giliandra* clade, the *Gilia foetida*-*G. rigidula* clade, the Linanthieae Clade, the *Ipomopsis longiflora*-*I. multiflora*-*I. gunnisonii* clade, and the *Cobaea scanned*-*C. baurita* clade.

**Skewness of the distribution of random trees.**—One of the primary limitations to evaluation of the skewness of the distribution of sets of random trees for a data set of this size is that no 95% confidence limit for skewness values ( $g_1$ ) has been determined for data sets in excess of 25 terminal taxa (Hillis 1991; Hillis and Huelsenbeck 1992; Huelsenbeck 1991). However, as a conservative test, I have used the 95% confidence limit of the 25-taxon tree for those trees with 25 or more taxa (Hillis and Huelsenbeck 1992).

The distribution of tree length for a set of 10,000 trees based on all 56 sequences is significantly skewed, with a  $g_1$  statistic of  $-0.6622$ . Following Hillis (1991), I removed well-supported clades (as measured by bootstrap values of 95% or greater), except for one



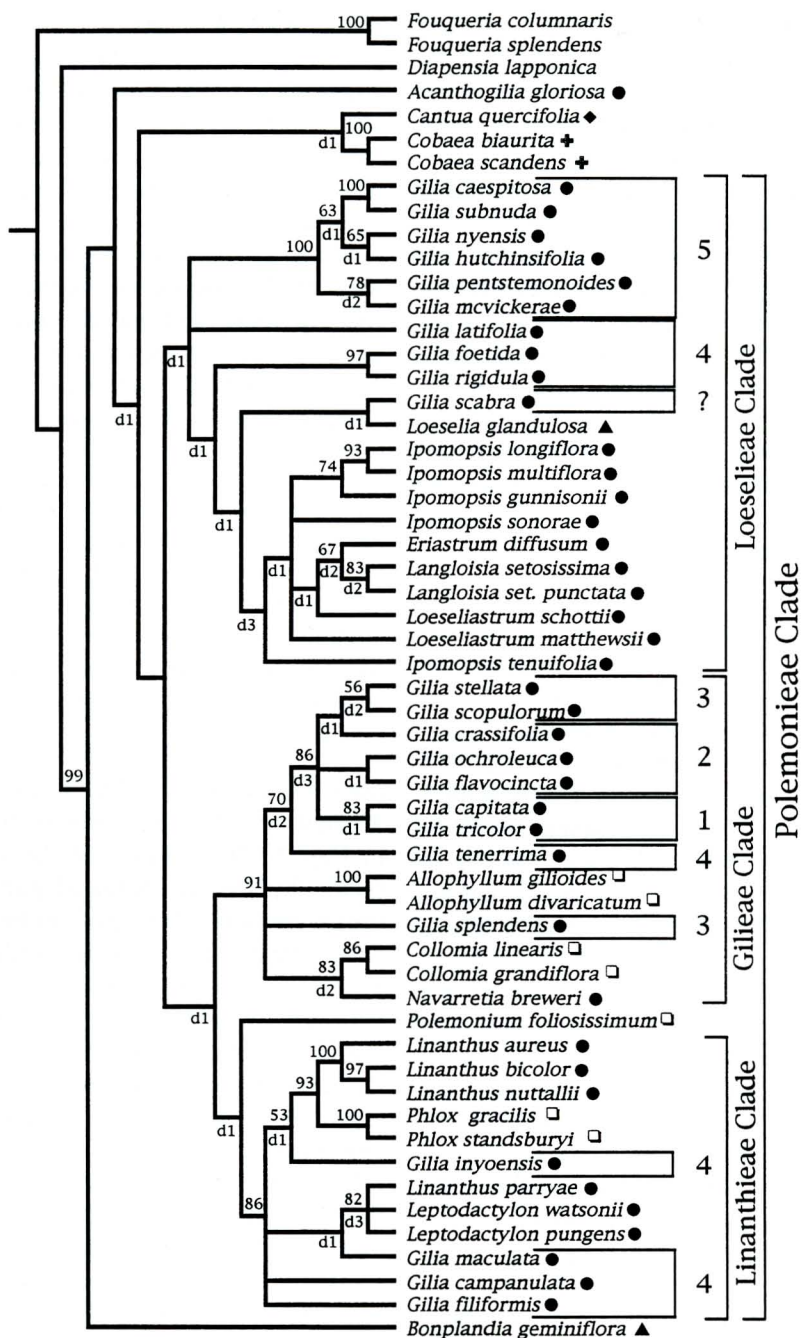
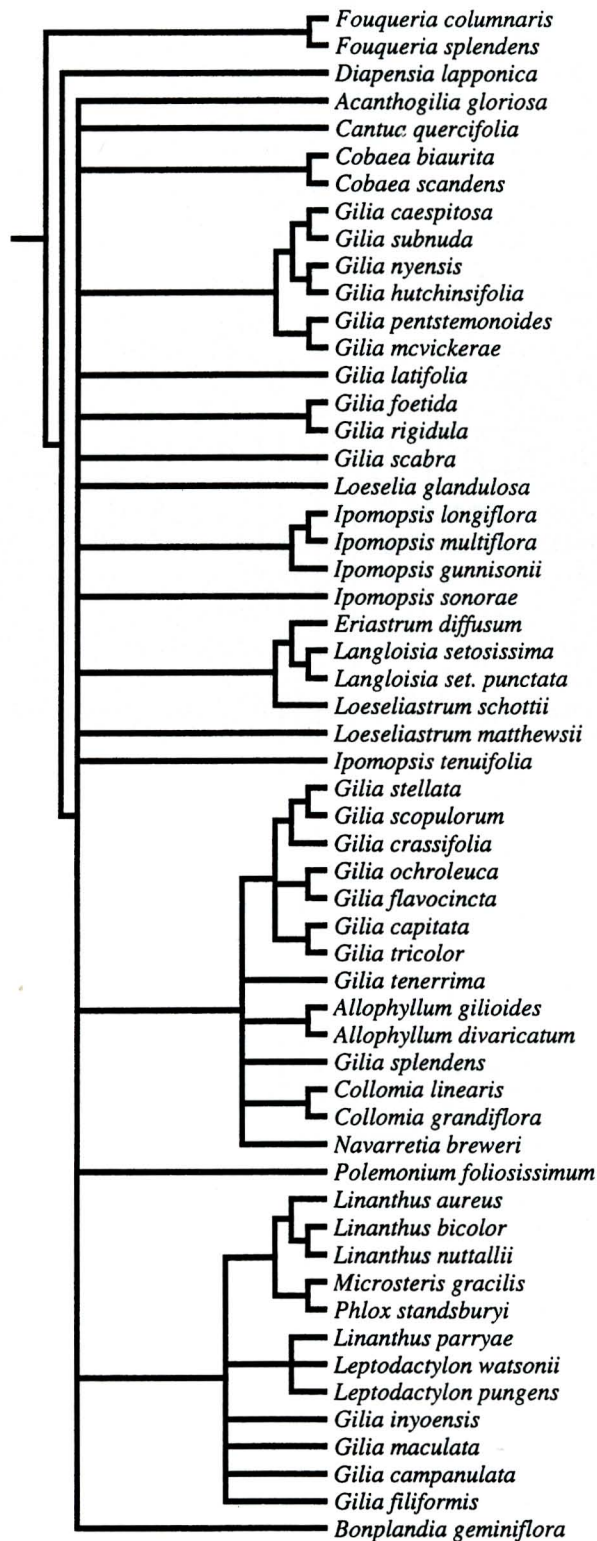


Fig. 1. The strict-consensus of 1080 trees of 1646 steps (CI = 0.423, RC = 0.263), resulting from the PAUP analysis of the manually realigned PILEUP alignment of 53 members of Polemoniaceae and three outgroup members. The number below each internode is the decay index for that branch, ranging from d1 to d3. The frequency at which clades occur in 100 bootstrap replications is shown as a percentage, above each internode. Tribal classification of Grant (1959) is indicated by the symbol following each ingroup taxon name (+ = Cobaeae; ♦ = Cantuaee; ▲ = Bonplandiae; □ = Polemonieae; ● = Gilieae). Intrageneric classification of *Gilia* is indicated by the numbered brackets (1 = sect. *Gilia*; 2 = sect. *Arachnion*; 3 = sect. *Saltugilia*; 4 = sect. *Giliastrum*; 5 = sect. *Giliandra*). *Gilia scabra* is labeled "?" because Grant erroneously considered it synonymous with *Linanthus nuttallii*.

randomly selected representative, leaving 46 taxa. Another set of 10,000 random trees was generated. Again, the distribution is significantly skewed:  $g1 = -0.4441$ . This was followed by removal of clades with bootstrap values of 90% or greater, save one representative, leaving 31 taxa, and skewness was determined. Similarly, the distribution remains significantly skewed ( $g1 =$

$-0.4881$ ). This process continued, using 21, 15, 12, 11, 10, nine, and eight taxa, each time removing members of the most well supported clades. In all cases, the  $g1$  value significantly differs from the expected value of random data. Similar results (Porter unpublished) are obtained from permutation tail probability tests (Faith and Cranston 1991).



## DISCUSSION

Sequence data from the two intergenic ITS spacers provide a compelling insight into some aspects of phylogeny. However, the phylogenetic inferences from ITS sequences contains both well-supported conclusions and highly questionable ones. In general, the weakly supported portions of the phylogeny are nodes associated with the earliest diverging lineages within the family. The lack of well-supported relationships at the base of the tree could be due to biological reasons or artifact. Biological reasons could include rapid diversification, low nucleotide substitution rate, or spurious long-branch attraction. Artifacts also could result from the difficulty in aligning the more divergent lineages and the treatment of the large blocks of question marks in the data matrix that result from indels. Fortunately, even with the ambiguity of relationships associated with the earliest diverging lineages, the robust portions of the phylogeny provides an understanding of relationships in Polemoniaceae that directly conflicts with current classification. This insight includes the pattern of diversification of the phlox family as well as issues of monophyly of the genera *Gilia*, *Ipomopsis* and *Linanthus*.

*Monophyly of Polemoniaceae*

The only well-supported node (based on bootstrap, decay and Lanyon's jackknife) in the basal region of the ITS phylogeny is the Polemoniaceae clade. Regardless of differential weighting of indels and/or transitions versus transversions, ITS sequences support the monophyly of Polemoniaceae. There is no support for the treatment of *Cobaea* as a separate family, Cobaeaceae (Don 1824). However, this study provides at best a weak test of the monophyly of Polemoniaceae. If the phylogeny is treated as unrooted, it can be recognized that a monophyletic Polemoniaceae is the result of the two longest branches (*Diapensia* and the *Fouqueria* clade) being united. These two lineages are characterized by nucleotide changes at nearly 30% of all potentially informative sites and between 37% and 50% of potentially informative sites not involving indels, raising the potential for long-branch attraction. This caution is tempered by the concordant support for a monophyletic Polemoniaceae from both chloroplast genes *matK* (Steele and Vilgalys 1994; Johnson et al. 1996) and *ndhF* (A. Prather, pers. comm.) and nuclear 18S sequences (as cited in Johnson et al. 1996).

*Diversification of Polemoniaceae*

The evolution and diversification of Polemoniaceae have been characterized by recent authors (e.g., Grant 1959) as a lineage of tropical origin that has radiated into the temperate regions. Grant postulates the inde-

Fig. 2. Lanyon's jackknife strict-consensus tree, identifying those regions of the phylogeny affected by taxon inclusion. Resolved portions of the tree indicate those nodes not influenced single taxon removal. Unresolved portions (compare with Fig 1) change based on the removal of a single terminal taxon.



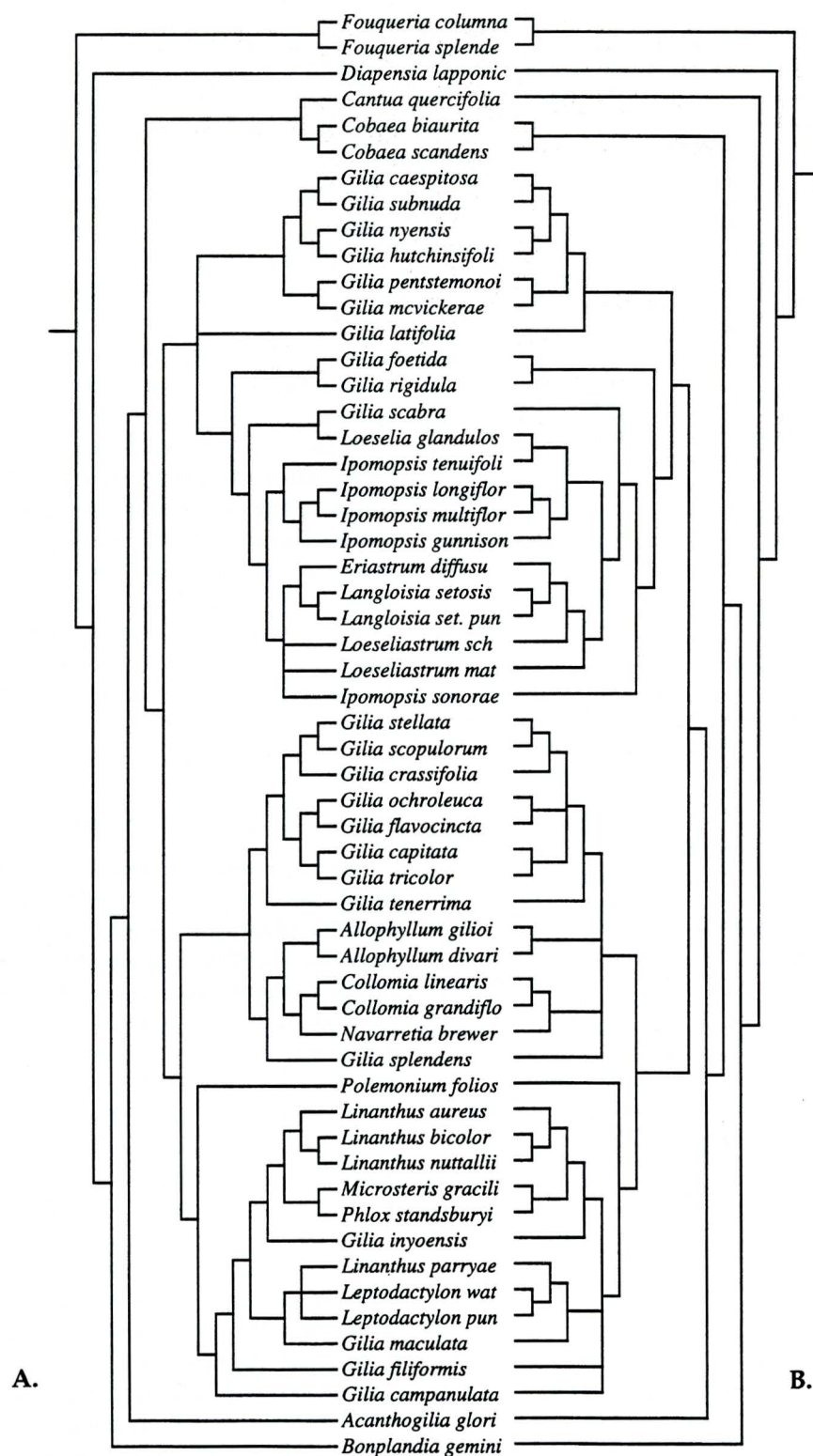


Fig. 3. Comparison of two parsimony analyses differing in the weighting of gaps and transitions vs. transversions. Tree A is the strict consensus of 12 trees, resulting from the analysis in which no transition/transversion bias is imposed but all gap positions were treated as a fifth nucleotide state (GAPMODE = FIFTHSTATE option in PAUP). The analysis for tree B utilized a 1.1 to 1.0 transition to transversion bias but all gap and alignment-ambiguous positions were removed. Tree B is the strict consensus of the resulting eight trees.

pendent origin of two temperate lineages, tribes Polemoniaceae and Gilieae, from different tropical groups (tribes Cobaeae and Bonplandiae, respectively). This tropical-temperate distinction has persisted. The phylogenetic inference based in *matK*, presented by Steele and Vilgalys (1994), is suggested to support a tropical origin although the strict consensus tree shows ambiguous relationships between the included genera of tropical distribution. Steele and Vilgalys also propose a single "temperate" lineage, rather than two. Johnson et al. (1996) present a more complete *matK* phylogeny in which *Cantua*, *Cobaea*, and *Bonplandia* form a "tropical clade." Aside from *Acanthogilia*, the remaining genera are included in a large "temperate clade." Given that *Acanthogilia* is not tropical in distribution, the ancestral condition, if reconstructed using parsimony, is dependent on the distribution of the outgroups. Because Diapensiaceae are temperate in distribution and Fouquieriaceae are subtropical to tropical the ancestral character state assignment is ambiguous.

The phylogeny based on nucleotide sequences from ITS 1 and 2 show *Acanthogilia*, *Cantua*, *Cobaea*, and *Bonplandia* as a paraphyletic group, positioned as the earliest diverging lineages of the family. This could be interpreted as support for a tropical origin of Polemoniaceae. However, the relationships between these four genera, as inferred by ITS, have been shown to change based on taxon inclusion, character weighting (indels and transition-transversion) and how alignment-ambiguous sites are treated. It is difficult to argue that the ITS phylogeny is error free in this region. Given the uncertainty of relationships at the basal nodes the ancestral character state assignment is also uncertain. The question of a tropical origin for the family remains unanswered. Such determination again requires a more rigorous assessment of sister and outgroup relationships for Polemoniaceae than is presented here or in previous studies (e.g., Chase et al. 1993; Steele and Vilgalys 1994; Johnson et al. 1996).

The ITS spacer sequences support the remaining genera of Polemoniaceae (i.e., *Gilia*, *Ipomopsis*, *Eriastrum*, *Langloisia*, *Loeseliastrum*, *Loeselia*, *Allophyllum*, *Collomia*, *Navarretia*, *Phlox*, *Linanthus*, *Lepidodactylon* and *Polemonium*) as a monophyletic group. This lineage has been referred to as the "Temperate Clade" (Steele and Vilgalys 1994; Johnson et al. 1996). While it is true that the majority of species in this clade occur in temperate regions, such a characterization may obscure the geographic patterns associated with diversification and dispersal within the lineage. This lineage includes several clades that are either wholly or partly tropical in distribution. For example, *Loeselia* ranges from southernmost Arizona, USA, through Mexico and Central America to Columbia, but all species occur in the tropics of Mexico.

Similarly, *Gilia* section *Giliastrum* (exclusive of *Gilia tenerrima*, *G. filiformis*, *G. campanulata*, *G. inyoensis*, and *G. maculata*) occurs not only in the temperate southwestern United States, but also the subtropical and tropical latitudes of both Mexico and South America (Peru, Bolivia, and Argentina). These examples serve to point out this clade includes tropical, subtropical, temperate, and even boreal lineages. It is not evident where the early diversification took place. Indeed, Grant's (1959) hypothesis of several independent lineages dispersing to and radiating within the temperate regions cannot be ruled out. For convenience I will refer to this clade as the Polemoniaceae Clade (Fig. 1).

The Polemoniaceae Clade is comprised of members from three of Grant's (1959) tribes (tribes Gilieae, Polemoniaceae, and Bonplandiae). None of these three tribes is supported as monophyletic (Fig. 1). Rather, three primary lineages, in addition to the genus *Polemonium*, make up this clade in all of the most parsimonious trees. The support for relationships between these clades is weak, but the membership of the three lineages is consistent regardless of weighting of transitions vs. transversions or indels and it is corroboration from other molecular phylogenetic studies (Steele and Vilgalys 1994; Prather 1995; Johnson et al. 1996). I refer to these clades as the Loeseliaeae, Gilieae, and Linanthieae Clades (Fig. 1). Note that the endings are used to distinguish the clades from generic names and are not intended to imply a particular hierarchic rank.

The Loeseliaeae Clade, which includes *Gilia* section *Giliandra*, *Gilia* section *Giliastrum* (exclusive of *Gilia campanulata*, *G. inyoensis*, *G. maculata* and *G. filiformis*), *Gilia scabra*, *Loeselia*, *Ipomopsis*, *Langloisia*, *Loeseliastrum*, and *Eriastrum*, is the sister group to the remaining members of the Polemoniaceae Clade. The members of this clade have traditionally been included within tribe Gilieae, with the exception of *Loeselia*, which has been placed in Bonplandiae (Grant 1959). The potential relationship between *Loeselia* and certain members of tribe Gilieae was recognized by Grant (1959), given his hypothesis that tribe Gilieae has its origin within or near *Loeselia*. Support, as measured by bootstrap, jackknife and decay, is low for many of the nodes within the Loeseliaeae Clade. Even so, the phylogenetic inference is highly consistent with that of *matK* (Johnson et al. 1996). Several noteworthy points can be made concerning the phylogenetic inferences based on ITS sequences. First, the two subspecies of *Langloisia setosissima* are supported as the sister group of *Eriastrum*. The sister group of this (the *Eriastrum*-*Langloisia* Clade) is *Loeseliastrum schottii*, supporting Timbrook's (1986) assertion that *Langloisia s.s.* and *Loeseliastrum* do not represent a monophyletic group. This represents a direct conflict between ITS and phylogenetic inferences from chloro-



plast *matK* (Johnson et al. 1996) and *trnL* intron (Porter, unpubl.) sequences, that support *Langloisia* and *Loeseliastrum* as sharing most recent common ancestry. Second, note that *Ipomopsis* is not monophyletic. The placement of *Ipomopsis tenuifolia* as sister to *Ipomopsis*, *Eriastrum*, *Langloisia*, and *Loeseliastrum* is not surprising, given that this member of the *Gilia* group was formerly included in *Loeselia* (Gray 1876; 1886). *Ipomopsis sonora* is also not unambiguously more closely related to other *Ipomopsis* species than to other genera. There may be three lineages, representing a grade, included in the current circumscription of *Ipomopsis*. The paraphyly of *Ipomopsis* is corroborated by chloroplast DNA sequence data (Johnson et al. 1996; Porter, unpubl.) and a more detailed ITS analysis of the *Loeselia* Clade (Porter, in prep.). Third, the members of *Gilia* within this clade are neither monophyletic (although, *Gilia* section *Gilia* is monophyletic) nor closely related to those *Gilia* associated with the type (i.e., *Gilia* section *Gilia*, type = *G. laciniata* R. & P.). In fact, *Gilia* section *Giliastrum*, as circumscribed by Grant (1959) is polyphyletic. In addition, *Gilia scabra*, considered by Grant (1959: 140) synonymous with *Linanthus nuttallii*, is suggested to share common ancestry with *Loeselia*.

The *Gilieae* Clade includes *Allophyllum*, *Collomia*, *Navarretia*, *Gilia* sections *Saltugilia*, *Arachnion*, *Gilia*, and one member of section *Giliastrum*. Historically, *Allophyllum* has been variously treated within *Collomia* (Bentham 1845; Gray 1870), close to *Collomia* in tribe *Polemonieae* (Grant and Grant 1955; Grant 1959), or included within *Gilia* (Nuttall 1848; Brand 1907; Mason and Grant 1948; Cronquist 1984), in tribe *Gilieae*. *Navarretia* has been of equally uncertain affiliation: included within *Gilia* by Gray (1870); allied with *Collomia*, *Cantua* and *Gymnosteris* in the *Collomia* tribe (Wherry 1945); or within Tribe *Gilieae*, near *Langloisia* and *Leptodactylon* (Grant 1959). It is perhaps not surprising that ITS sequences support a close relationship between *Navarretia*, *Collomia*, *Allophyllum* and a portion of what is now considered *Gilia*. Even so, this is a striking noncorrespondance with traditional taxonomy because it not only segregates only a portion of *Gilia* and allies it with *Navarretia* (both members of Grant's tribe *Gilieae*), but also strongly supports the relationships between this group and two members of tribe *Polemonieae*, *Allophyllum* and *Collomia*. The monophyly of the *Gilieae* Clade, supported here by ITS sequences, is both well supported in terms of bootstrap values and Lanyon's jack-knife analysis and also corroborated by sequence data from the chloroplast gene *matK* (Steele 1992; Steele and Vilgalys 1994; Johnson and Soltis 1995). The correspondence between ITS and *matK* gene phylogenies and the relative robustness of this portion of the ITS

phylogeny strongly supports the monophyly of this group.

Perhaps the most intriguing of the hypothesized relationships based on ITS sequence data involves the *Linanthieae* Clade. This clade is comprised of the genera *Linanthus*, *Leptodactylon* and *Phlox*, as well as four species of *Gilia* currently included in section *Giliastrum*. The *Linanthieae* Clade is well supported but very inconsistent with current classification. Although there is a long history associating *Linanthus* and *Leptodactylon* together (Gray 1870; Brand 1907; Wherry 1940; 1945; Grant, 1959) and they are currently both included in tribe *Gilieae*, *Phlox* (currently in tribe *Polemonieae*) has not been considered closely related. While floral morphology of *Leptodactylon* has been compared with that of *Phlox* (Gray 1870), no direct relationship was espoused. It is noteworthy that *Linanthus*, *Phlox* and *Leptodactylon* all possess pantoporate pollen grains (Marticorena 1961; Stuchlik 1967; Taylor and Levin 1975), very similar leaf flavonoid and phenolic chemistry (Smith et al. 1977; Dean et al. 1978; Smith et al. 1982), and possess opposite leaves, an unusual trait in *Polemoniaceae*.

The *Linanthieae* Clade is also intriguing because four species of *Gilia* (*G. campanulata*, *G. inyoensis*, *G. filiformis*, and *G. maculata*) are also members. These species have historically been closely aligned (see for example Brand 1907); however, most treatments prior to 1989 maintained *G. maculata* in *Linanthus*, while the remaining species were retained in *Gilia* sect. *Giliastrum*. Patterson (1989) has cautiously argued that, in spite of the unique traits possessed by *G. maculata*, there is sufficient morphological similarity between *Gilia campanulata*, *G. inyoensis*, *G. filiformis* and *G. maculata* to include them in the same genus, i.e., *Gilia*. ITS sequence data, presented here, supports in essence Patterson's proposition; however, this group of species is related not to members of *Gilia*, but to *Linanthus*, *Leptodactylon* and *Phlox*. It is also important to note that ITS sequences do not support the monophyly of these species.

#### *Gilia* is not monophyletic

The genus *Gilia* has remained, over the last 100 years, a recurring taxonomic problem, the circumscription of which has changed radically. Mason and Grant (1948) correctly point out that all of the herbaceous genera of the *Polemoniaceae*, with the exception of *Polemonium* and *Phlox*, have historically been placed in *Gilia*. One of the most broad interpretations of the genus was that of Asa Gray (1886). While recognizing that *Gilia* was "certainly a polymorphous . . . genus" (Gray 1870: 262), he included the currently recognized genera *Langloisia*, *Loeseliastrum*, *Gymnosteris*, *Leptodactylon*, *Linanthus*, *Navarretia*, *Ipomopsis* and *Er-*



*iastrum* within *Gilia*. The most recent classification of the family (Grant 1959) has maintained all these segregate genera. However, as noted above, Cronquist (Cronquist 1959; Cronquist 1984) has included *Ipomopsis* and *Allophyllum* within *Gilia*.

ITS sequence data provide insight into this conflict. The monophyly of representatives of *Gilia* sects. *Gilia* (here represented by *G. capitata* and *G. tricolor*), *Arachnion* (represented by *G. crassifolia*, *G. ochroleuca* and *G. flavocincta*), *Saltugilia* (represented by *G. stellata* and *G. scopulorum*), and *Giliastrum*, sensu Grant 1959 (represented by *G. tenerrima*) is supported (Fig. 2). Conspicuously absent from this clade are *Gilia scabra* and members of *Gilia* sects. *Giliastrum* (represented by *G. foetida*, *G. rigidula*, *G. latifolia*, *G. campanulata*, *G. inyoensis*, *G. filiformis*, and *G. maculata*), and *Giliandra* (represented by *G. caespitosa*, *G. subnuda*, *G. pentstemonoides*, *G. mcvickerae*, *G. hutchinsifolia* and *G. nyensis*). All of these samples, except *G. campanulata*, *G. inyoensis*, *G. filiformis*, and *G. maculata* (in the Linanthieae Clade), are within the Loeseliae Clade. The most parsimonious placement of any one of these species into the Gilieae Clade requires between 27 and 51 steps (ACCTRANS reconstruction). Moreover, if representatives of *Gilia* sensu Grant (1959) are constrained to be monophyletic, three minimal-length trees are found of tree length 1693, 47 steps longer than the unconstrained analysis. The inclusion of representatives of *Ipomopsis* into *Gilia* (as proposed by Cronquist) does not ameliorate this situation. If *Ipomopsis* is constrained to be included in *Gilia*, sensu Cronquist, the eight trees found are 59 steps longer than the unconstrained analyses. Including additional taxa to make the representatives of *Gilia* monophyletic—if one considers the minimal-length ITS trees—will result in a group as morphologically diverse as Gray's circumscription of *Gilia*. If this is considered an unacceptable treatment (i.e., considering the Polemoniaceae Clade as a single genus, *Polemonium*), then the genus *Gilia* must be recognized in the more strict sense (i.e., *G. tenerrima* and its sister group), it will be necessary to remove those clades that do not share common ancestry.

## Conclusions

Sequences of the two internal transcribed spacers, ITS1 and ITS2, have been demonstrated to provide reliable phylogenetic estimates for portions of Polemoniaceae. The bootstrap, decay index, Lanyon's jackknife, and distribution of the tree length of random trees provide support for much of the phylogenetic inference. These include the *Giliandra* clade, *Gilia foetida*-*G. rigidula* clade, the *Allophyllum*-*Gilia* clade, the *Linanthus*-*Phlox*-*Leptodactylon* clade, and the *Ipomopsis gunnisonii*-*I. longiflora*-*I. multiflora* clade. Un-

fortunately, resolution of relationships among most of the major lineages, representing the basal radiation of the family, is suspect. Even given this limitation, ITS data unambiguously fail to support the current classification of Polemoniaceae that recognizes two temperate tribes, Polemoniaceae and Gilieae (Table 1). Rather, all of the genera, exclusive of *Bonplandia*, *Cantua* (and presumably *Huthia*), *Cobaea*, and *Acanthogilia*, are within a single clade, with members of Grant's tribes, Polemoniaceae and Gilieae variously related. Further, it has been shown that ITS sequence data does not support *Gilia*, as currently circumscribed, as a monophyletic group. The taxa now treated as *Gilia* represent at least five independent lineages, and potentially more (Fig. 1).

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## Appendix 1

	10	20	30	40	50	60	70	80	90	100	110
<i>Fouquieria columnaris</i>	TCGATACCTGCCTAGCAGAACGACCTGTGAACTCGT	CTCCAAATGAGGTGAT	TCGC	GGGTGGGC	CTCC	GGTCCCCCGTGGGGAA	CCTTCTCGGGGAAGCG				
<i>Fouquieria splendens</i>	TCGATACCTGCCTAGCAGAACGACCTGTGAACTCGT	CTCCAAATGAGGTGAT	TCAY	GGGTGGGC	CTCT	GGTCCCTCCCGTGCAGAA	CCTTATCGGGGAACG				
<i>Diapensia lapponica</i>	TCGATATCTGCACAGCAGAACGACCCGCGAACTAGTATTCTCACTTTG	GGAGAT	GCATTGGGCGGTC	TAAT	CCCCCT	CCTTTGTGCT	CTCCAC	....GCC			
<i>Acanthogilia gloriosa</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTGTATTCAAACTTCGGGTGGC	ACG	GGCTGTGGC	CTC	GGTCCCT	CGCCCGTTCC	CCCT	...CGGGA			
<i>Cantua quercifolia</i>	TCGAAA	CTGTCCCGAAACACGACCCGTGAACTTGTATTCTCAYATCGGGT	GC	ATG	GTCGATCGG	CTTC	GGTCCCT	CGGCCATTGCTACCCCGTTGGTGGT	GT		
<i>Bonplandia geminiflora</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTCGT	TAAACATATCGGG	GC	AC	TCGGC	CTTC	GGA	CT	CCGGTCTCGG	GTGTTTT	GCCCTCGT
<i>Cobaea biaurita</i>	TCGAAACCTGCATRGACAGAAAGACCYGTGAACCTTAT	TTTTAAACTCAG	TGGC	ATG	ATTGGGGA	CTYC	GGTCCCT	CCTTTGTGTY	CCCTTT	RCTGTGTTG	
<i>Cobaea scandens</i>	TCGAAACCTGCATGGCAGAAAGACCTGTGAACTTAT	TTTTAAACTCAG	TGGC	ATG	ATTGGGGA	CTTC	GGTCCCT	CATTTGTGTC	CCCTTT	GCT	GTG
<i>Gilia caespitosa</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAAACTAAA	TCGGGTGGC	ACG	AGCATGGTC	CTTT	GGTCCA	AACTCGTTGC	CCCCA	GCTGGGT		
<i>Gilia subnuda</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAAACTAAA	TCGGGTGGC	ACG	AGCATGGTC	CTTT	GGTCCA	AACTCGTTGC	CCCCA	GCTGGGT		
<i>Gilia pentstemonoides</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAAACTAAA	TCGGGTGGC	ACG	GGCATGSSS	CTTT	GGTCCCT	AGCCCGTTGC	CCCCA	GCTGGGT		
<i>Gilia mcvickerae</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAAACTAAA	TCGGGTGGC	ACG	GRCATGGTC	CTTT	GGTCCCT	AGCTCGTTGC	CCCCA	GCTGGGT		
<i>Gilia nyensis</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAAACTAAA	TCGGGTGGC	ACG	AGCATGGT	CTTC	GGTCCCT	AGCTCGTTGC	CCCCA	GCTGGGT	T	
<i>Gilia hutchinsifolia</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAAACTAAA	TCGGGTGGC	ACG	AGCATGGTC	CTTT	GGTCCCT	ACCTCGTTGC	CCCCA	GCTGGGT		
<i>Gilia latifolia</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAAACTACA	TCGGGTGGC	ACG	GGCGTCGTA	CTCC	GGTCCCT	CGTTCGTTGC	CCCTT	GCTGGGTGT		
<i>Gilia foetida</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAAACTAAA	TCGGGA	GC	ACG	GTCGTGGAC	CTTT	GGTCCCT	TGCTCG	TGC	CCC	A
<i>Gilia rigidula</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAAACTAAA	TCGGGT	GC	ACG	GTCGTGGAC	CTTC	GGTCCA	CGATCGATGC	CCC	A	
<i>Gilia scabra</i>	TCGAAACCTGTCTAGCAGAACGACCCGCGAACTTGTAACTAACA	CCGGGT	GC	ACG	GACGTGGAC	CTCC	GGTCCCT	TGGCCGTTGC	ACCCA	GCCGGAT	
<i>Loeselia glandulosa</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAACTAACA	CTCGGTGGC	GCG	GGCGTGGG	CTTTT	GGTCCCT	CGCTCGTTGC	CCCCA	GCCGACA		
<i>Ipomopsis longiflora</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAACTAACA	TCGGGTGGC	ACG	GGTGTGGTC	CTAT	GGTCCCT	CCCCCGTTGC	CACCTA	GCTGACA		
<i>Ipomopsis gunnisonii</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAACTAACA	TCGGGTGGC	ACG	GGTGTGGTC	CTAT	GGTCCCT	CACCCATTGC	CCCTA	GCTGACG		
<i>Ipomopsis multiflora</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAACTAACA	TCGGGTGGC	ACG	GGTGTGGTC	CTAT	GGTCCCT	CCCCCGTTGC	CCCTA	GCTGCCA		
<i>Ipomopsis tenuifolia</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAACTAACA	TCGGGTGGC	AC	GGCGTGGTC	CTTTT	GGTCCCT	CGCCCGTTGC	CCCTA	GCTGACT		
<i>Ipomopsis sonora</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAACTAACA	TCAGGT	GCTCGG	GGTGGGTC	CTTC	GGTCCCT	CGCTCGTTGC	CCCTA	GCCGACA		
<i>Eriastrum diffusum</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAACTAACA	TTGGGCGGC	ACG	GGTGTGGC	CTCTAT	GGTCCCT	CGCTCGTTGC	CCCTA	GCCGACA		
<i>Loeseliastrum matthewsii</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAACTAACA	TCGGGTGGC	ACG	GGTGTGGTC	CTWT	GGTCCY	CGCTCGTTGC	CCCTA	GCTGACA		
<i>Loeseliastrum schottii</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAACTAACA	TTGGGTGGC	ACG	GGTGTGGTC	CTTT	GGTCCCT	CGCTCGTTGC	CCCTA	GCTGACA		
<i>Langloisia setosissima</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAACTAACA	TTGGGTGGC	ACG	GGCTTGGTC	CTCT	GGTCCCT	CGCTCGTTGC	CCCTA	GCCGGCA		
<i>Langloisia set. punctata</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAACTAACA	TTGGGTGGC	ACG	GGCTTGGTC	CTCC	GGTCCCT	CGCTCGTTGC	CCCTA	GCCGGCA		
<i>Gilia stellata</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAACTAACA	TCGGGTGGT	GCG	GGCTTGTATCTC	...	GGTACG	CGCTCGTTCC	CCCCAC	GCTAGGA		
<i>Gilia crassifolia</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTAACTAACA	TCAGGTGG	GCG	GGCTTGTATCTC	...	GGTACT	CGCTCGTTCC	CCCCAC	GCTAGGA		
<i>Gilia scopulorum</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTAGGGTGGT	GCG	GGCGTGTATCTC	...	GGTACT	CGCTCGTTCC	CCC	AC	GCTAGGA		
<i>Gilia ochroleuca</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTAGGGTGG	GCG	GGTGTGTATCTC	...	GGTACT	CGCTCGTTCC	CCCCAC	GCTAGGA			
<i>Gilia flavocincta</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTAGGGTGGC	GGTGTGTATCTT	...	GGTACT	ACGCTCGTTCC	...	CCCCAC	GCTAGGA			
<i>Gilia tenerrima</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTWGGGTGGT	GYG	GGCGTGTATCTC	...	GGTACT	TGCHCGTTCC	...	CCCCAC	GCTAGGA		
<i>Gilia capitata</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTAGGGTGGT	GCG	GGTGTGTATCTC	...	GGTACT	CGCCCGTTCC	...	CACCTC	GCTAGGA		
<i>Gilia tricolor</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTTGGGTGGT	RCG	GGTGTGTATCTC	...	GGTACT	CGCTCGTTCC	...	CCCCAC	GCTAGGA		
<i>Allophyllum gilioides</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTTCGGGTGGT	ACG	GGCGTGTATCTC	...	GGTACT	CGCTCGTTCC	...	CCCCAC	GCTAGGA		
<i>Allophyllum divaricatum</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTTCGGGTGGT	ACG	GGCGTGTATCTC	...	GGTACT	CGCTCGTTCC	...	CCCCAC	GCTAGGA		
<i>Gilia splendens</i>	TCGAGACCTGTCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTTCGGGTGGC	TCG	GGCGTGTATCTC	...	GGTACT	CGCCCGTTGC	...	CCCCAC	GCTAGGA		
<i>Collomia linearis</i>	TCGACAC	TGCATAGCAGAACGACCCGCGAACTTGTATTCAAAACTTCGGGTGGT	GCG	GGTGTGTATCTC	...	GGTACT	CGCTCGTTAC	...	CCCCAC	GCTAGGA	
<i>Collomia grandiflora</i>	TCGACACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTTCGGGTGGT	GCG	GGTGTGTATCTC	...	GGTACT	CGCTCGTTAC	...	CCCCAC	GCTAGGA		
<i>Navarretia breweri</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTTCGGGTGGT	GCG	GGCATGTATCATC	...	GGTACT	CGCTCGTTAC	...	CCCCAC	GCTAGGA		
<i>Polemonium foliosissima</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTTCGGGTGGC	ACG	ARCGTAGTA	CTTC	GGTACT	CGCCCGTYGC	...	CCCTC	GCTGTGA		
<i>Linanthus aureus</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTTGGGGGTGACG	AC	TTGTG	CTTC	GGTACT	...	CACGTTGC	...	CCCTT	GCTGGTG	
<i>Linanthus parryae</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTTCGGGTGGC	ACA	TG	TTGTG	CTTC	GGTACT	CGCATGTTGC	...	CCCTT	TGCTGGTG	
<i>Gilia maculata</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTTCGGGTGGT	GCG	GAC	ATGTG	CTTC	GGTACT	TGTCCGTTGC	...	CCCTT	GCTGGTG	
<i>Gilia campanulata</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTTCGGGTGGT	ATG	GCG	TTGTG	CTTC	GGTACT	CGCCCGTTGC	...	CCCTT	GCTGGTG	
<i>Gilia inyoensis</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTTCGGGTGGT	GCG	GCG	TTGTG	CTTC	GGTACT	CGCCCGTTGC	...	CCCTC	GCTGGTG	
<i>Gilia filiformis</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTTCGGGTGGC	GCG	GCG	TTGTG	CTTC	GGTACT	CGTCCGTTGC	...	CCCTC	GCTGGTG	
<i>Phlox gracilis</i>	TCGACACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTTCGGGTGGT	GCG	TGC	TTCT	CTTC	CGCCCGT	TGCTCG	TGCT	TGCT	TGCT	TGCT
<i>Phlox standsburyi</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTTCGGGTGGT	GCG	TGC	TTCT	CTTC	CGCCCGT	TGCTCG	TGCT	TGCT	TGCT	TGCT
<i>Leptodactylon watsonii</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTTCGGGTGGT	GCA	GCG	TTGTG	CTTC	GGTACT	CGCTCGTTGC	...	CCCTT	TGCTGGTG	
<i>Leptodactylon pungens</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTTCGGGTGGC	GCA	TGC	TTGTG	CTTC	GGTACT	CGCTCGTTGC	...	CCCTT	TGCTGGTG	
<i>Linanthus bicolor</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTTCGGGTGGT	GAT	GAC	TTGTG	CTTC	GGTACT	TGTATGTTGC	...	CCCTT	GCTGGTG	
<i>Linanthus nuttallii</i>	TCGAAACCTGCCTAGCAGAACGACCCGCGAACTTGTATTCAAAACTTCGGGTGGT	GAC	AC	TTGTG	CTTC	GGTACT	TGCACGTTGC	...	CCCTT	GCTGGTG	

Appendix 1. Aligned nrDNA ITS1 and ITS2 nucleotide sequences from 53 representatives of Polemoniaceae and three outgroup members. Nucleotide sites are numbered 5' to 3', beginning with the first base of ITS1. Position 278 is the final base of ITS1 and position 279 is the first base of ITS2 (the 5.8S region has been removed). Nucleotide coding follows standard IUB-IUPAC codes. Gaps at nucleotide positions are denoted by dots.



	120	130	140	150	160	170	180	190	200	210	220
<i>Fouquieria columnaris</i>	TGCTCCGAGCAATGCACGCAGCTGCACGGCGAA	GGGTGCGCTTCTCTGGAACAAACGAA	CCCCGGCGCG	AACGTGCGCAAGGAAAC	TTAACAAAGAGATC	.TCG					
<i>Fouquieria splendens</i>	TGCTCTGAGCAATGCACGCAGTTGCACGGCAGG	GGGTGCGCTTCTCCGAAAAACAAACGAA	CCCCGGCGCG	AGCCGCGCAAGGAAAC	TTAACAAAGAGATC	.TCG					
<i>Diapensia lapponica</i>	TGGAGTGTGC.TCGTATCCCTTTCCGGGGGCCAC	GGGTGCAC	.CTC	.GAGGACAAC	AA	CCCCGGCGCG	AATAGTGCCAAGGAATT	TAAACAT	TGAGTGCCCAT		
<i>Acanthogilia gloriosa</i>	GTGCA...TC.CGCGGCC	....CCGCGCGCG	GCTCGCATTTCCCGGCCAACAAACGAA	CCCCGGCGCGG	CATGCG	CAAGGAACT	GTAACACAGAGAGCC	.T	G		
<i>Cantua quercifolia</i>	GACCACTCGCCACGCGGTGAGCTTCTGGTGATGGTTCGCTTCCGACAAACCAACGAA	CCCCGGCGCG	.CATGTG	CAAGGAATT	GTAACGAAGA	....TTG					
<i>Bonplandia geminiflora</i>	CGGGATGCACGCACCGCGCGCGGAAASTCGCGAGGCGTGTATTTCTCGGCAACCGAACAAACCCCCGGCGCGG	CA	...CCAAGGAAC	TTG	AACAAAGAGAGC	.TTG					
<i>Cobaea baurita</i>	ATGCARTTGTTCATAGCGAGAGCTCTGTCAACTAC	TGTATTTTTCAGCACATTAACGAA	CTCCGGCGCGG	TATGTGCCAAGGAAAW	RWAATAAAGAGTGC	.TTG					
<i>Cobaea scandens</i>	ATGCAGTTGTTCATAGCGAGAGCTCTGTCAACTAC	TGTATTTTTCAGCACATTAACGAA	CTCCGGCGCGG	TATGTGCCAAGGAAAW	GAAATAAAGAGTGC	.TTG					
<i>Gilia caespitosa</i>	GTGCA...TT.CATGGCC	....TATGGCAA	TGGTTGCACCTTCTTGGCACAKTAACGAA	CCCCGACGCG	TGTGCGTCAAGGAATT	GTAACAAAGAGAGC	.TTG				
<i>Gilia subnuda</i>	GTGCA...TT.CATGGCC	....TATGGCAA	TGGTTGCACCTTCTTGGCACATTAACGAA	CCCCGACGCG	TGTGCGTCAAGGAATT	GTAACAAAGAGAGC	.TTG				
<i>Gilia pentstemonoides</i>	GTGCA...WT.CAAGGCC	....TATGGCAA	TGATTGCACCTTCCGGGCACATTAACGAA	CCCCGGCGCG	TATGCGTCAAGGAATT	GTAACAAAGAGAGC	.TTG				
<i>Gilia mcvickerae</i>	GTGCA...TT.CAAGGCC	....TATGGCAA	TGATTGCACCTTCCGGGCACATTAACGAA	CCCCGGCGCG	TATGCGTCAAGGAATT	GTAACAAAGAGAGC	.TTG				
<i>Gilia nyensis</i>	GTGCA...TT.CATGGCC	....TTTGGCAA	TGTTTGCACCTTCTCGGCACATTAACGAA	CCCCGACGCG	TTTGCCTCAAGGAAAT	GTAACAAAGAGAGC	.TTG				
<i>Gilia hutchinsifolia</i>	GTGCA...TC.CATGGCC	....TATGGCAA	TGGCTGCACCTTCCCGGCACATTAACGAA	CCCCGGCGCG	TGTGCGTCAAGGAATT	GTAACAAAGAGAGC	.TTG				
<i>Gilia latifolia</i>	GTGCA...TT.CACGGCC	....TACGGTTTGTGGATGCACCTTCCGGGCACATTAACGAA	CCCCGGCGCG	TATGCGTCAAGGAATT	GTAACAAAGAGAGC	.TTG					
<i>Gilia foetida</i>	GTGCA...AT.CACGACC	....TATGGCAA	GGTTGTGCTTCTTGGCACATTAACGAA	CCCCGGCGCG	TATGCG	CAAGGAATT	GTAACAAAGAGAGC	.TTG			
<i>Gilia rigidula</i>	GTGCA...AT.CACGGCC	....TACGGCAG	GGTTGTGCTTATAGCAAT	AACTAACCCCCGGCGCG	TACGCGTCAAGGAATT	ATAACAAATACAGC	.TT				
<i>Gilia scabra</i>	GTGCT...CT.CACGGCC	....TTCGGGTG	TGTTTGCACCT	.CGGCAAACTAACGAA	CCCCGGCGCG	TACGCGCAAGGAATT	GTAACAAAGAGAGC	.TTG			
<i>Loeselia glandulosa</i>	GTGCT...AT.CATGGCC	....TACGGCGA	TGGTTGCACCT	.CGGCGTTTTAACTAA	CCCCGGCGCG	TAAGCG	CAA	...TT	GTAACAAAGAGAGC	.TTG	
<i>Ipomopsis longiflora</i>	GTGCA...CT.CACGGCC	....TCTGGCAA	TGTTTGCACCT	.CGGCAAACTAACGAA	CCCCGGCGCG	TGTGCG	CAAGGAATT	GTAACAAAGAGAGC	.TTG		
<i>Ipomopsis gunnisonii</i>	GTGCA...CT.CATGGCC	....TATGGCAA	TGTTTGCACCT	.AACGCAAACTAACGAA	CCCCGGCGCG	TGTGCGCAAGGAATT	GTAACAAAGAGAGC	.TTG			
<i>Ipomopsis multiflora</i>	GTGCA...CT.CACGGCC	....TCTGGCAA	TGTTTGCACCT	.CGGCAAACTAACGAA	CCCC	GCGCAG	TGTGCG	CAAGGAATT	GTAACAAAGAGAGC	.TTG	
<i>Ipomopsis tenuifolia</i>	GTGCA...CT.CRTGGCC	....TATGGCAA	TGTTTGCACCT	.TTGGCACATTAACGAA	CCCC	GCGCAG	TGTGCGCAAGGAATT	GTAACAAAGAGAGC	.TTG		
<i>Ipomopsis sonora</i>	GTGCA...CT.CGCGCT	....TAGGCGA	GGTTCGCACTT	.CGGCACATTAACGAA	CCCCGGCGCG	TGTGCGCAAGGAATT	GTAACAAAGAGAGC	.TTG			
<i>Eriastrum diffusum</i>	GTGCA...CT.CA	.....GCAA	TGTTT	CACCT	.AGGCACCTTAACGAA	CCCCGGCGCG	TGTGCG	CAAGGAATT	GTAACAAAGAGAGC	.TTG	
<i>Loeseliastrum matthewsii</i>	GTGCA...CT.CACGGCC	....TATGGCWATTGTTTGCACCT	.CGGCACATTAACGAA	CCCCGGCGCG	TGTGCG	CAAGGAATT	GTAACAAAGAGAGC	.T			
<i>Loeseliastrum schottii</i>	GTGCA...CT.CACGGCC	....TATGGCTG	TGTTTGCACCT	.CGGCACATTAACGAA	CCCCGGCGCG	TGTGCG	CAAGGAATT	GTAACAAAGAGAGC	.TTG		
<i>Langloisia setosissima</i>	GTGCA...CT.CACGGCC	....TATGGCAA	TGTTTGCACCT	.CGGCACATTAACGAA	CCCCGGCGCG	TGTGCG	CAAGGAATT	GTAACAAAGAGAGC	.TTG		
<i>Langloisia set. punctata</i>	GTGCA...CT.CACGGCC	....TATGGCAA	TGTTTGCACCT	.CGGCACATTAACGAA	CCCCGGCGCG	TGTGCG	CAAGGAATT	GTAACAAAGAGAGC	.TTG		
<i>Gilia stellata</i>	GTGTA...AT.CACGGCC	....TCGGCAA	TGCTTGCACCTTCCCGGCACATCAACGAA	CCCCGGCGCG	TCTGCG	CAAGGAAT	ATAACAAAGAGAGCT	.TTG			
<i>Gilia crassifolia</i>	GTGGA...AG.CACGGCC	....TCGGCAA	TGCTTGCACCTTCCCGGCACATCAACGAA	CCCCGGCGCG	TCTGCG	CAAGGAAT	GTAACAAAGAGAGCT	.TTG			
<i>Gilia scopulorum</i>	GTGTA...AT.CATGGCC	....TCGGCAA	TGTTTGTACTTCCCGGTACATCAACGAA	CCCCGGCGCG	TCTGCG	CAAGGAAT	GTAACAAAGAGAGCT	.TTG			
<i>Gilia ochroleuca</i>	GTGTA...AG.CACGGCC	....TCGGCAA	TGCTTGCACCTTCCCGGCACATCAACGAA	CCCCGGCGCG	TCTGCG	CAAGGAAT	GTAACAAAGAGAGCT	.TTG			
<i>Gilia flavocincta</i>	GTGTA...AG.CACGGCC	....WCGCAA	TGCTTGCACCTTCCCGGCACATCAACGAA	CCCCGGCGCG	TCTGCG	CAAGGAAT	GTAACAAAGAGAGCT	.TTG			
<i>Gilia tenerima</i>	GTGTA...AT.CAYGGCY	....TCGGCAA	TGCTAGCACTTCCCGGCACATCAACGAA	CCCCGACGCG	TATGCG	CAAGGAAT	GTAACAAAGAGAGCT	.TTG			
<i>Gilia capitata</i>	ATGTA...AT.CACGGCC	....TCGGCAA	TGCTTGCACCTTCCCGGCACATCAACGAA	CCCCGGCGCG	TCTGCG	CAAGGAAT	GTAACAAAGAGAGCT	.TTG			
<i>Gilia tricolor</i>	GTGTA...AT.CACGGCC	....TCGGCAA	TGCTTGCACCTTCCCGGCACATCAACGAA	CCCCGGCGCG	TTTGCCTCAAGGAAT	GTAACAAAGAGAGCT	.TTG				
<i>Allophyllum gilioides</i>	GTGTA...AT.CATTGCC	....TCGGCAA	TACTTGCACCTTCCCTAG	CATTAACGAA	CCCCGGCGCG	TATGCG	CAAGGAAT	GTAACAAAGAGAGCT	.TTG		
<i>Allophyllum divaricatum</i>	GTGTG...AT.CATTGCC	....TCGGCAA	TACTTGCACCTTCCCTAG	CATTAACGAA	CCCCGGCGCG	TATGCG	CAAGGAAT	GTAACAAAGAGAGCT	.TTG		
<i>Gilia splendens</i>	GTGTA...AT.CACGGCC	....TCGGCAA	TGCTTGCACCTTCCCGGCACATCAACGAA	CCCCGGCGCG	TATGCG	CAAGGAAT	GTAACAAAGAGAGCT	.TTG			
<i>Collomia linearis</i>	GTGTA...AT.CAAGGCC	....TCGGCAA	TGCTTGCACCTTCCCGGCACATCAACGAA	CCCCGGCGCG	TATGCG	CAAGGAAT	GTAACAAAGAGAGCT	.TTG			
<i>Collomia grandiflora</i>	GTGTA...AT.CAAGGCC	....TTGGCAA	TGCTTGCACCTTCCCGGCACATCAACGAA	CCCCGGCGCG	TACGCG	CAAGGAAT	GTAACAAAGAGAGCT	.TTG			
<i>Navaretia breweri</i>	GTGTA...AT.CAAGGCC	....TTGGCAA	TGCTTGCACCTTCCCGGCACATCAACGAA	CCCCGGCGCG	TATGCG	CAAGGAAT	GTAACAAAGAGAGCT	.TTG			
<i>Polemonium foliosissimum</i>	GTGCA...CG.CACTGCC	....TCGGCAA	TGCTTKC	.CTTCCCGACACATTAACGAA	CCCCGGCGCG	TATGCG	CAAGGAAT	GTAACAAAGAGAGC	.TTG		
<i>Linanthus aureus</i>	GAGCA...TC.CATGGTC	....TCGGCTA	TGTTTGTCTTCCCGGCACCTTAACGAA	CCCCGGCGCG	AATGTG	CAAGGAAT	GTAACAAAGAGAGC	.TTG			
<i>Linanthus parryae</i>	GTACA...TT.CATAGCT	....TTGGCGA	TGCTTGTCTTCCCGGCACCTTAACGAA	CCCCGGCGCG	AATGTGCCAAGGAAT	GTAACATAGACAGC	.TTG				
<i>Gilia maculata</i>	GTGCA...TT.CAT	.GCC	....TCGGCGA	TGCTTG	GCTTCCCGGCACCTTAACGAA	CCCCGGCGCG	TATGCG	CAAGGAAT	GTAACATAGACAGC	.TTG	
<i>Gilia campanulata</i>	GCGCA...TT.CATGGCC	....TTGGCAA	TGTTTGTGCTTCCCGGCACCTTAACGAA	CCCCGGCGCG	AATGTGCCAAGGAAT	GTAACAAAGAGAGC	.TTG				
<i>Gilia inyoensis</i>	GTGCA...TT.CATTGCC	....TCGGCAA	TGCTTGTGCTTCCCGGCACCTTAACGAA	CCCCGGCGCG	TATGCG	CAAGGAAT	GTAACAAAGAGAGC	.GTG			
<i>Gilia filiformis</i>	GTGCA...TT.CATGGCC	....TCGGCAA	TGTTTGTGCTTCCCGGCACCTTAACGAA	CCCCGGCGCG	TATGCG	CAAGGAAT	GTAACAAAGAGAGC	.TTG			
<i>Phlox gracilis</i>	GTGCA...TC.CATTGCC	....CCGGCAA	TGCATGCGCTTCCCGG	.CTTAACGAA	CCCCGGCGCG	TATGTGCCAAGGAAT	GTAACAAAGAGAGC	.TTG			
<i>Phlox standsburyi</i>	GTGCA...TT.CATGGCC	....TCGGCAA	TGCTTGTGCTTCCCGGCACCTTAACGAA	CCCCGGCGCG	TATGTGCCAAGGAAT	GTAACAAAGAGAGC	.TTG				
<i>Leptodactylon watsonii</i>	GTGCA...TT.CATGGCC	....TCGGCAA	TGCTTGTGCTTCCCGGCACCTTAACGAA	CCCCGGCGCG	TATGCG	CAAGGAAT	GTAACATAGACAGC	.TTG			
<i>Leptodactylon pungens</i>	GTGCA...TC.CATGGCC	....TCGGCGA	TGCTTGTGCTTCCCGGCACCTTAACGAA	CCCCGGCGCG	TATGCG	CAAGGAAT	GTAACATAGACAGC	.TTG			
<i>Linanthus bicolor</i>	GAGCA...TC.CATT	.CC	....TTGTGTA	TGTTTGTCTTCCCGGCACCTTAACGAA	CCCCGGCGCG	AATGTGCCAAGGAAT	GTAACAAAGAGAGC	.TTG			
<i>Linanthus nuttallii</i>	GAGCA...TC.CATTGCC	....TAGTGTA	TGGTGTCTTCCCGGCACCTTAACGAA	CCCCGGCGCG	AATGTG	CAAGGAAT	GTAACAAAGAGAGC	.TTG			



	230	240	250	260	270	280	290	300	310	320	330
	.	.	.	ITS1	.	<-----[.----->	ITS2	.	.	.	.
<i>Fouquieria columnaris</i>	CCCCCGGCGCTCC	GTTCGCGGATGCACG	.GGGACGGTTGCATCTTTTC	ACGAAACATCGCGTCGCTCCCCACCCC	TCGCCCCGTTGC	GGGCGCGGGTGTTCGAGG					
<i>Fouquieria splendens</i>	CCCCCGACGCTCC	GTTCGCGGATGCACG	.GGGACGGTTGCATCTTTTC	ACGAAACATCGCGTCGCTCCCCACCCC	TCGCCCCCTTGT	GGGCGCGGGTGTTCGAGG					
<i>Diapensia lapponica</i>	TTCCCTCTTGC	CCCGGTTTACTCGGGTGTAGGGGGAAGTTGG	TGTCCTCTGAA	AAACATCGCGTCGCCCCAACCCCTCTCCCTTTTGTGGT	TAGTGAGGAGTTTGGGG						
<i>Acanthogilia gloriosa</i>	TC.CGGAGGCCCC	GTTCGCGGGTGA	CGAAGGGCGG	TGCCATCTGA	C.ACAATACATCTCGTCGCTCCCAACC	.TCTGCCCTCAC	GGGAGCGGGCAATG	GGA			
<i>Cantua quercifolia</i>	TCCGTCCCTCG	CCCGTTCACGGGTGT	CGAAGGGGCG	CGGCATCD	A.C.GCAATGATTGCGTCGCCCCAAACCC	.TGTCCCTCGG	GGAATCRG	.ATTG	GS		
<i>Bonplandia geminiflora</i>	CC.CGGAGGCCCG	CTTCG	.GGT.C	CGAAGGGCAA	TGCCATCTTA	C.TCAATACATCGCGTCGCCCCAACCC	TTACCCCTTCG	GGCGTGACGGGCTTG	GGA		
<i>Cobaea baurita</i>	TC.CTCCTTTCC	CATTATATGG	.GT	CAAAGGGCAA	TGTCRTCTTA	C.ACAATACATCTCGTCGCTCCCAACC	.TATTTCCACAA	GAAAKYRTGTTGTT	CGA		
<i>Cobaea scandens</i>	TC.CTCCTTTCC	CATTATATGGGTGT	CAGAGGGCAA	TGTCGTCTTA	CAACAATACATCTCGTCGCTCCCAACC	.TATTTTCYACAA	GAAATGTTGTTGTT	CGA			
<i>Gilia caespitosa</i>	TT.TGGAAGCCCC	GTTCGCGGGTGC	CGAAGTGCAA	TGCCATCTKA	C.AAAAAACATCGCGTCGCCCCAACCC	.TATTCCTTTG	GGATTTGAGGTATTG	GGA			
<i>Gilia subnuda</i>	TT.TGGAAGCCCC	GTTCGCGGGTGC	CGAAGG	CAA	TGCCATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.TCTTCCTTTG	GGATTTGATGTATTG	GGA		
<i>Gilia pentstemonoides</i>	TT.TGGAAGTCCC	GTTCGCGGGTGC	CGAAGGACAA	TGCCATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.TATTCCTTTG	GGATTTAAGGTATTG	GGA			
<i>Gilia mcvickerae</i>	TT.TGGAAGCCCC	GTTCGCGGGTGC	CGAA	GACAA	TGCCATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.TATTCCTTTG	GGATTTAAGGTATTG	GGA		
<i>Gilia nyensis</i>	TT.CGAAGGCCCC	GTTCGCGGGTGC	CGAAGAACAA	TGCCATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.TATTCCTTTG	GGATTTAAGGTATTG	GGA			
<i>Gilia hutchinsifolia</i>	TT.CGGAGGCCCC	GTTCGCGG	GTGC	TGAAGGGCAA	TGCCATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.TATTCCTTTG	GGAATTAMGGTCTTG	GGA		
<i>Gilia latifolia</i>	TC.TCAAAGCCCC	GTTCGC	GCTGC	CGAAGG	CAA	TG.CATCTTA	C.ACGAAACATCGCGTCGCCCCAACCC	.TATTCCTCTG	GGAGTTACGGTTTTT	GGA	
<i>Gilia foetida</i>	TC.CGGATGCCTC	GTTCGCGGKKG	GGAAGGGCAA	TGCCATCTTA	C.TCAAAACATCGCGTCGCCCCAACCC	.CTTCCCTATG	GGAATCGGTGCTTG	GGA			
<i>Gilia rigidula</i>	...AGAAGCCTC	GTTCGCGAGTGC	.AAGGGTAT	TGCCATCTTA	C.WMAAAACATCGCGTCGCCCCAATC	.TCTTCCCATTG	GGA	GATGGTTTG	GGA		
<i>Gilia scabra</i>	TC.CGGAAGCCCC	GTTCGCGGGCGT	GGAAGGGCAA	CGCCATCTTG	C.AACAAACATCGCGTCGCCCCAACCC	.CTTCCCTCTG	GGGATTGCGGCGTTG	GGA			
<i>Loeselia glandulosa</i>	CC.TGGAAGCCCC	GTTCGCGGGTGT	GGAAGGGCAGATGCGATCTTA	C.TCAAAACATCGCGTCGCCCCAACCC	.TATTTCCCTTG	GGATTCGTGTTGTTG	GGA				
<i>Ipomopsis longiflora</i>	TTGCGGAA	CCCC	GTTCAGGGTGC	GGAAGTGCAA	TGCAATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.TATTTCCCTTG	GAAATGTGGTGTGTT	GGA		
<i>Ipomopsis gunnisonii</i>	CT.CGAAAGCCCC	GTTCGCGGRWGC	AAGAAGGGCAA	TGCAATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.TATTTCCCTTAG	GGAATACGGTGTGTTG	GGA			
<i>Ipomopsis multiflora</i>	TT.CRGAAGCCCC	GTTCGCGGGTGC	GGAAGTGCAA	TGCAATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.TATTTCCCTTG	GGAATGAGGTATTG	GGA			
<i>Ipomopsis tenuifolia</i>	TC.CGGAAGCCCC	GTTCGCGGGTGC	GGAAG	GCAA	TGCCATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.TCTTCCCTTCG	GGAATGTGGTCTTG	GGA		
<i>Ipomopsis sonora</i>	TT.CGGAAGCCCC	GTTCGCGGGTGC	AGAAG	GACATTGCCATCTTA	C.AAAAA	CTAAGCGTCGCGTCGCCCCAATCTTCCCTCCG	GGAAGCACGGTCTTG	GGA			
<i>Eriastrum diffusum</i>	TC.CGGAAG	CCC	GTTCGC	GGTGCGGAAGGGCAG	TG.CATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.TCTT	CCTCT	.GGAATCGGTGCTTG	GGA	
<i>Loeseliastrum matthewsii</i>	TT.CGGAAGCCCC	GTTCGCGGGTGC	CGAAGKCAA	TG.CATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.TCTT	CCTCT	.GGAATTACGGTCTT	GGA		
<i>Loeseliastrum schottii</i>	TT.CGGAAG	CCC	GTTCGCGGGTGC	CGAAGG	CAA	TG.CATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.TCTTCCCTCTG	GGGATTACGGTCTTG	GGA	
<i>Langloisia setosissima</i>	TC.CGGAAGCCCC	GTTCGCGGGTGC	GGAAGGGCAA	TGCCATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.TCTT	CCTCT	.GGAATTACGGTCTTG	GGA		
<i>Langloisia set. punctata</i>	CT.TGGAAGCCCC	GTTCGCGGGTGC	TGAAGGGCAT	TGCCATCTTA	C.AAAAAATATCGCGTCGCCCCAACCC	.TCTTCCCTACG	GGAATCATGG	TTG	GGG		
<i>Gilia stellata</i>	TT.TCGATGCCCC	GTTCGCGGGTGC	TGAAGGGCAAG	GCCATCTTA	C.AAAAAATATCGCGTCGCCCCAACCC	.TCTTCCCTAAG	GGAATCATGG	TTG	GG		
<i>Gilia crassifolia</i>	CT.TGGAAGCCCC	GTTCGCGGGTGC	TGAAGGGCAAG	GCCATCTTA	C.AAAAAATATCGCGTCGCCCCAACCC	.TCTTCCCTATG	GGAATCATGG	GTG	GGG		
<i>Gilia scopulorum</i>	CT.TAGATGCCCC	GTTC	CGCGTGC	TGAAGGGCAAG	GCCATCTTA	C.AAAAAATATCGCGTCGCCCCAACCC	.TCTTCCCTACG	GGAATCATGG	TTG	GGG	
<i>Gilia ochroleuca</i>	CT.TGGATGCCCC	GTTCGCGGGTGC	TGAAGGGCAAG	GCCATCTTA	C.AAAAAATATCGCGTCGCCCCAACCC	.TCTTCCCTAAG	GGAATCATGGTTCG	GGA			
<i>Gilia flavocincta</i>	CC.TGGATGCCCC	GTTCGCGGGTGC	TGAAGGGT	TAGTGACATC	TA.CAAAAAACATCGCGTCGCTCCCAACC	.TCTTCCCTATG	GGAATCATGG	TTTG	GGA		
<i>Gilia tenerrima</i>	CT.TGGATGCCCC	GTTCGCGGGTGC	TGAAGGGCAAG	GCCATCTTA	C.AAAAAATATCGCGTCGCCCCAACCC	.TCTTCCCTACG	GGAATCATGG	TTTG	GGK		
<i>Gilia capitata</i>	CT.TGGATGCCCC	GTTCGCGGGTGC	TGAAGGTCAAC	GCCATCTTA	C.AAAAAATATCGCGTCGCCCCAACCC	.TCTTCCCTATG	GGAATCATGG	TTTG	GGG		
<i>Allophyllum gilioides</i>	TT.CGGAAGCCCC	GTTCGCGGGTGC	TGAAGGGCAA	TGCCATCTTA	C.AATATACATCGCGTCGCCCCAACCC	.TCTTCCCTATG	GGAATCATGK	TCTG	GGA		
<i>Allophyllum divaricatum</i>	TT.CGGAAGCCCC	GTTCGCGGGTGC	TGAAGGGCAA	TGCCATCTTA	C.AATATATTACGCGTCGCCCCAACCC	.TCTTCCCTATG	GGAATCATGG	TTTG	GGA		
<i>Gilia splendens</i>	CT.TGGATGCCCC	GTTCGCGGGTGC	TGAAGGGCAA	TGCCATCTTA	C.AAAAA	CATCGCGTCGCCCCAACCC	.TCTTCCCTATG	GGAATCATGG	TGTG	GGA	
<i>Collomia linearis</i>	CT.TGGATGCCCC	GTTCGCGGGTGC	TGAAGTGCAA	TGCCATCTTG	C.AAAAAACATCGCGTCGCCCCAACCC	.TCATCCCTATG	GGATCTTTG	TTTG	GGA		
<i>Collomia grandiflora</i>	CT.TGGATGCCCC	GTTCGCGGGTGC	TGAAGGGCAA	TGCCATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.TCATCCCTATG	GGAAGCATGG	TTTG	GGA		
<i>Navarretia breweri</i>	CT.TGGACGCCCC	GTTTCGCGGGTGC	TGAAGTGCAA	TGCCATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.TA	TCCTACG	GGAATCATGG	TTTG	GGA	
<i>Polemonium foliosissimum</i>	C..CAGAAGCCC	.GTTCGCGGGTGC	.GAAGTGAAC	.GCG	TCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.TCATTCCTTTG	GGAATCACGGTCTTG	GGA		
<i>Linanthus aureus</i>	TC.TGGAAGCCCC	GTTCGCGGGTGC	CAAAGGGCAT	TGCCATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.ATTCCCTTTG	GGAATCACGGTCTTG	TTG	GGA		
<i>Linanthus parryae</i>	TC.CGGAAGCCCC	GTTCGCGGGTGC	GGAAGGGCAT	TGCCATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.TTTCCTCTG	GGAATCATGGGCTTG	GGA			
<i>Gilia maculata</i>	TC.CAGAAGCCCC	GTTCGCGGGTGC	CGAAGGGCAT	TG.CATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.TTTCCTTTG	GGAATCACGGGATTG	GGA			
<i>Gilia campanulata</i>	TC.TGGAAGCCCC	GTTCGCGGGTGC	GGAAGGGCAT	TGCCATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.TTTCCTTTG	GGAATCACGGGATTG	GGA			
<i>Gilia inyoensis</i>	TC.TCGAAGCCCC	GTTCGCGGGTGC	TGAAGGGCAT	TGCCATCTTA	C.AAAAAACTTCGCGTCGCCCCAACCC	.CTTTCCTTTG	GGAATCACGGGCTTG	GGA			
<i>Gilia filiformis</i>	TC.CGGAAGCCCC	GTTCGCGGGTGC	CGAAGGGCAT	TGCCATCTTA	C.AAAAAACTTCGCGTCGCCCCAACCC	.TTTCCTTTG	GGAATCACGGGCTTG	GGA			
<i>Phlox gracilis</i>	TC.TGGAAGCCCC	GTTCGCGGGTGC	CGAAGGGCAC	TGCCATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.ATTCCCTTCG	GGAATCAATGGTTG	GGA			
<i>Phlox standsburyi</i>	TC.CGGAAGCCCC	GTTCGCGGGTGC	CGAAGGGCAT	TGCCATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.ATTTCCTTCG	GGATTCACGGTCTTG	GGA			
<i>Leptodactylon watsonii</i>	TC.CGGAAGCCTC	GTTCGCGGRWGC	GGAAGGGCAT	TGCCATCTTA	C.AAAAAACATCGCGTCGCCCCAACCC	.TTTCCTTTT	GGAATCACGGGCTTG	GGA			
<i>Leptodactylon pungens</i>	TC.CGGAAGCCCC	GTTCGCGGGTGC	GGAAGGGCAT	TGCCATCTTA	C.AAAAAACTACGCGTCGCCCCAACCC	.TTTCCTTTG	GGAATCACGGGCTTG	GGA			
<i>Linanthus bicolor</i>	TC.TTGAAGCCCC	GTTCGCGGGTGC	AAAAGGACAA	TGCCATCTTA	C.AAAAAACTACGCGTCGCCCCAACCA	.ATT	CCTTTT	GGAATCACGGTCTTG	GGA		
<i>Linanthus nuttallii</i>	CC.TGGAAGTCCC	GTTCGCGGGTGC	CAAAGGGCAT	TGCCATCTTA	C.AAAAAACATCGCGTCGCCCCAATCC	.ATT	CCTCTT	GGAATCATGGTCTTG	GGA		

Appendix 1. Continued.



	340	350	360	370	380	390	400	410	420	430	440
<i>Fouquieria columnaris</i>	GCGGAAG.ATGG..	CCCCCGTGC	CGCTCAGT	GCTCGCGT	CGGCCTAAAA	AGAGTCCC..	CGGCGACTG	ACG.TCACGA..	CAAGTGGTGGT	TGAC.AAA..	CCGTT.GCG
<i>Fouquieria splendens</i>	GCGGAAG.ATGG..	CCCCCGTGC	ACATCAGT	GCGCGT	CGGCCTAAAA	AGCGAGTCCCT..	CGACGACTG	ACG.TCACGA..	CAAGTGGTGGT	TGAC.AGA..	CCGTT.GCA
<i>Diapensia lapponica</i>	GCGGAAG.TTGG..	CCCCCGTGC	ACAGTCTCT	CTGCGGTC	CGGCCAAAATA..	CAGTCCATC	GAGAAAWTAT	GTACACGA..	CATCTGGTGGT	TGAC.AAA..	CTTAC.GAG
<i>Acanthogilia gloriosa</i>	GCGGAAA.TTGG..	TCTCCCGTGC	CACAC.GCTG.	CGCGGTTGG	CCTAAAAA..	AGAGTCGA..	CGTGGACGAGCG.	TCACAG..	CATGTGGTGGT	TGTC.AGA..	CCGTT.GCG
<i>Cantua quercifolia</i>	GCRGAGA.TTGG..	CCTCCCGTGC	ACATCGTTG.	AGCGGTTGG	CCCTAAATA..	AGTGGA..	CGTTGATGGGCG.	TCACGA..	CATGTGGTGGT	TGTGCCAACCGTT..	GCG
<i>Bonplandia geminiflora</i>	GCGGAAA.TTGG..	TCTCCCGTGC	CGCTAGCCG.	TGCGGTTGG	CCTAAAAA..	CGAGTGA..	CGTGGACGAGCG.	TCACAA..	CATGTGGTGGT	TGAACAAA..	CCGTT.GCG
<i>Cobaea biaurita</i>	GCGGAAAGTTGGCCTCTCCTGTGCACATTGTTG.	TGTGGTTGG	CCTAAAAAT..	TGAGTSCA..	CGTGGATGAG	AGTTGCGAA..	CAAGTGGTGGT	TGTC.AAG..	CCGTT.GCG		
<i>Cobaea scandens</i>	GCGGAAG.TTGG..	TCTCCTGTGC	ACATGTTG.	TGTGGTTGG	CCTAAAAAT..	TGAGTGA..	CGTGATGAGAGT	TCGCAA..	CAAGTGGTGGT	TGTC.AAG..	CCGTT.GCA
<i>Gilia caespitosa</i>	GCGGAAA.TTGG..	TCTCCCGTGC	TTTT.TCTG.	TGCGGTTGG	CCTAAAAA..	CGAGTCGA..	CGTGGGCGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.SAG
<i>Gilia subnuda</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ATTT.TCTG.	TGCGGTTGG	CCTAAAAA..	CAAGTCGA..	CGTGGGCGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCR
<i>Gilia pentstemonoides</i>	GCRGAAA.TTGG..	TCTCCCGTGC	TCTT.WTTG.	TGCGGTTGG	CCTAAAAA..	AGAGTAGA..	CGTGACGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Gilia mcvickerae</i>	GCGGAAA.TTGG..	TCTCCCGTGC	TCTT.TCTG.	TTCGGTTGG	CCTAAAAA..	AGAGTMGA..	CGTGGACGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Gilia nyensis</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ATTTCTCTG.	TGCGGTTGG	CCTAAAAA..	AGAGTCGA..	CGTGGACGAA	CGC.TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Gilia hutchinsifolia</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ATTTCTG.	TGCGGTTGG	CCTAAAAA..	AGAGTCGA..	CGTGGACGAA	CGC.TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Gilia latifolia</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ATTTGTTG.	TGCGGTTGG	CCTAAAAA..	TGAGTCGA..	CGTGGACGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Gilia foetida</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACTCTGTTG.	TGCGGTTGG	CCTAAATA..	AGAG.CGG.	CGTGGGCGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Gilia rigidula</i>	GCGGAGA.TTGG..	TCTCCCGTGC	ACTATGTTG.	TGCGGTTGG	CCTAAAAA..	AGAGTCGG.	CGTGGATGAGCG.	TCACAA..	CWAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Gilia scabra</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACTCTGTTG.	AGCGGTTGG	CCTAAATA..	CGAGTCGA..	CGTGAACGAGCG.	TCACAA..	CATGTGGTGGT	TGAC.TGA..	CCGTT.GCG
<i>Loeselia glandulosa</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACTCAGATG.	CGCGGTTGG	CCTAAATA..	AGAGTCGG.	CGTTGACGAA	CGC.TCACAA..	CATGTGGTGGT	TGAC.AAA..	TCGTT.GCG
<i>Ipomopsis longiflora</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACTCTG.TG.	TGCGGTTGG	CCTAAATA..	AGAGTCGA..	CGTGGACGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Ipomopsis gunnisonii</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACTCTGTTG.	TGCGGTTGG	CCTAAATA..	AGAGTCGA..	CGTGGATGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCA
<i>Ipomopsis multiflora</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACTTTGTC.	CTKCGGTTGG	CCTAAATA..	AGAGTCGA..	CGTGGACGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Ipomopsis tenuifolia</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACTCTGCG.	G.TGCGGTTGG	CCTAAATA..	AGAGTCGA..	CGTGGACGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Ipomopsis sonora</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACTCTGTTG.	TGCGGTTGG	CCTAAACA..	AGAGTCGA..	CGTGGACGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Eriastrum diffusum</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACTCTGATG.	TGCGGTTGG	CCTAAATA..	AGAGTCGA..	CGTGGGKAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTTGGCG
<i>Loeseliastrum matthewsii</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACTCTGTTGCTCGCGGTTGG	CCTAAATA..	AGAGTCGA..	CGTGGGCGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG	
<i>Loeseliastrum schottii</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACTCTGTTG.	CGCGGTTGG	CCTAAATA..	AGAGTCGA..	CGTGGGCGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Langloisia setosissima</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACTCTGCTG.	TGCGGTTGG	CCTAAATA..	AGAGTCGA..	CGTGGGCGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Langloisia set. punctata</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACTCTGCTG.	TGCGGTTGG	CCTAAATA..	AGAGTCGA..	CGTGGGCGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Gilia stellata</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACACCGATG.	CGCGGTTGG	CCTAAATA..	TGAGTCGA..	CGTGACGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Gilia crassifolia</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACATCGATG.	CGCGGTTGG	CCTAAATA..	TGAGTCGA..	CGTGGACGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Gilia scopulorum</i>	GCGGAAA.TTGG..	CCTCCCGTGC	ACACYGATG.	CGCGGTTGG	CCTAAATA..	AGAGTYGA..	CGTGGACGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Gilia ochroleuca</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACACCGATG.	CGCGGTTGG	CCTAAATA..	AGAGTTGA..	CGTGGACGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Gilia flavocincta</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACATCGATG.	CGCGGTTGG	CCTAAATA..	AGAGTTGA..	CGTGGACGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT..CG
<i>Gilia tenerrima</i>	GCGGAAA.TTGG..	TCTCCCGTGC	TGACCGTTG.	YGCGGTTGG	CCTAAATA..	AGAGTCGA..	CGTGGACGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Gilia capitata</i>	...GAGA.TTGG..	TCTCCCGTGC	ACTCCGATG.	CGCGGTTGG	CCTAAATA..	AGAGTTGA..	CGTGGACGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Gilia tricolor</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACTCCGATG.	CGCGGTTGG	CCTAAATA..	AGAGTTGA..	CGTGGACGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Allophyllum gilioides</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACTTCGTTG.	TGCGGTTGG	CCTAAATA..	AGAGTTGA..	CGTGAACGAGCG.	TCATAA..	CATGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Allophyllum divaricatum</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACTACGTTG.	TGCGGTTGG	CCTAAATA..	AGAGTTGA..	CGTGAACGAGCG.	TCATAA..	CATGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Gilia splendens</i>	GCGGAAG.TTGG..	TCTCCCGTGC	ACAATGCTG.	CGCGGTTGG	CCTAAACA..	AGAGTTGA..	CGTGGACGAGCG.	TTACAA..	C?AGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Collomia linearis</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACATCGTTG.	CGTGGTTGG	CCTAAATA..	AGAGTGA..	CGTGAACGAGCG.	GTACAA	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Collomia grandiflora</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACATCGTTG.	CGTGGTTGG	CCTAAATA..	AGAGTGA..	CGTGAACGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Navarretia breweri</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACATGTTG.	CGTGGTTGG	CCTAAATA..	AGAGTGA..	CGTGGACGAGCG.	TCACAA..	CAAGTGGTGGT	TGTC.AAA..	CCGTT.GCG
<i>Polemonium foliosissima</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACGCTGTTG.	TGCGGTTGG	CCTAAATA..	AGAGTCGA..	CGTGKACGAGCG.	TCACAA..	CAAGTGGTGGT	TGTT.AAA..	CCGTT.GCG
<i>Linanthus aureus</i>	.CGGAGA.TTGG..	TCTCCCGTGC	ACT.GTTG.	TGTGGTTGG	CCTAAATA..	AGAGTTGG.	CGTGTACGAGT.	CSACAA..	CRATTGGTGGT	TGTTAAWRGCTTTGGCC	
<i>Linanthus parryae</i>	GCGGAGA.TTGG..	TCTCCCGTGC	ACTTTGTTG.	TGCGGTTGG	CCTAAATA..	AGAGTCGA..	CGTGTGCTGCG.	TCACAA..	CAATTGGTGGT	TGTTATAAACTTTT..	GCC
<i>Gilia maculata</i>	GCGGAGA.TTGG..	TCTCCCGTGC	ACTTTGCTG.	TGCGGTTGG	CCTAAATA..	AGAGTCGA..	CGTGGACGTCG.	TCACAA..	CAATTGGTGGT	TGTTT.AAAACCGAT.	GCC
<i>Gilia campanulata</i>	GCGGAGA.TTGG..	TCTCCCGTGC	ACAACGCTG.	CGCGGTTGG	CCTAAATA..	AGAGTCGA..	CGTGGACGTCG.	TCACAA..	CAATTGGTGGT	TGTTT.AAAACCGAT.	GCC
<i>Gilia inyoensis</i>	GCGGAGA.TTGG..	TCTCCCGTGC	ACTTCGCTG.	CGCGGTTGG	CCTAAATA..	AGAGTCGA..	CGTGGAGGAGCG.	TCACAA..	CAATTGGTGGT	TGTTT.AAGACCTTTTGGCC	
<i>Gilia filiformis</i>	GCGGAGA.TTGG..	TCTCCCGTGC	ACTTTGTTG.	TGCGGTTGG	CCTAAATA..	AGAGTCGA..	CGTGGACGAGCG.	TCACAA..	CAATTGGTGGT	TGTTT.AAAACCGTTT.	GCC
<i>Phlox gracilis</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACTTCGGTG.	TGCGGTTGG	CCCAATTT..	AGAGT.GA.	CGCGGACTAGCG.	ACACAA..	CAATTGGTGGT	TGTTT.AAAACCTTCA.	GCC
<i>Phlox standsburyi</i>	GCGGAAA.TTGG..	TCTCCCGTGC	ACTTCGGTG.	TGCGGTTGG	CCCTAAATA..	AGAGT.GA.	CGTGGACTAGCG.	ACACAA..	CAATTGGTGGT	TGTTT.AAAACCTTTA.	TCC
<i>Leptodactylon watsonii</i>	GCGGAGA.TTGG..	TCTCCCGTGC	ACTTTGTTG.	TGCGGTTGG	CCTAAATA..	AGAGTCGA..	CGTGTACGTCG.	TCACAA..	CAATTGGTGGT	TGTTTATAAAACCTTTT.	GCC
<i>Leptodactylon pungens</i>	GCGGAGA.TTGG..	TCTCCCGTGC	ACTTTGTTG.	TGCGGTTGG	CCTAAATA..	AGAGTCGA..	CGTGTACGTCG.	TCACAA..	CAATTGGTGGT	TGTTTATAAAACCTTTT.	CCC
<i>Linanthus bicolor</i>	GCGGAGA.TTGG..	TCTCCCATAC	ATCAT.GTTG.	TGTGGTTGG	CCTAAATA..	AGAGTCGG.	CATGAGTGAGT.	TCACAA..	CAATTGGTGGT	TGTTT.AAAACCTTTT.	GCC
<i>Linanthus nuttallii</i>	GCGGAGA.TTGG..	TCTCCCGTGC	ACTCTGTTG.	TGTGGTTGG	CCTAAATA..	AGAGTCGG.	CGTGAATGAGT.	CCACAG.	CAATTGGTGGT	TGTTTATAAAACCTTTT.	GCC



	450	460	470	480	490	500	510	520
<i>Fouquieria columnaris</i>	TTTCCTGTCG	TGCGTCGCA	TCGTCGCAACGGGCTGG	...CTCAC	...GTGACCC	TGAAG	TG	..CGGTAACAG
<i>Fouquieria splendens</i>	TTTCCTGTCG	TGCGTCGCA	TCGTCGCTACGGGCCGG	...CTCAT	...GTGACCC	TGAAG	CG	..CGGTAACAGCTGTCGCTCGACC
<i>Diapensia lapponica</i>	CCT	..TGTCG	TGA	TC	...TTCTCGCCGATGT?GCA	..CTTTA	...TGACCC	TGATG
<i>Acanthogilia gloriosa</i>	CTGT	TGTTG	TGCGT	GCT	TCGTCCTCC	TCGT	AA	..CTCCA
<i>Cantua quercifolia</i>	TTGCC	GTTG	TGCGT	..CG	TCGTCCTCCGG	...AA	..GCKCCA	..TAGACCC
<i>Bonplandia geminiflora</i>	TT	CCTGTTGTTG	GT	..CG	TTCTCCCCGG	..TT	AG	CGCTCCG
<i>Cobaea biaurita</i>	TTAT	TGTTG	TCTGA	..CC	TCGTCTCTC	...TACAA	..CWCCA	..TTGACCT
<i>Cobaea scandens</i>	TTAT	TGTTG	TCTGA	..CC	TCGTCTCTG	...AAAA	..CTCCA	..TTGACCT
<i>Gilia caespitosa</i>	TTGC	TGTTG	TGCGT	..TT	TCATCTCT	TCGTCGA	..CCCCA	..TTGACCC
<i>Gilia subnuda</i>	TTGC	TGATG	TGCGT	..TT	TCATCTCT	TCGTCGA	..CCCCA	..TTGACCC
<i>Gilia pentstemonoides</i>	TTGC	TGTTG	TGCGT	..TT	TCATCTCT	TCGTCGA	..CTACA	..TTGACCC
<i>Gilia mcvickerae</i>	TTGC	TGTTG	TGCGT	..TT	TCATCTCT	TCGTCGA	..CTCCA	..TTGACCC
<i>Gilia nyensis</i>	TTGC	TGTTG	TACGT	..TT	TCATCTCT	TCGTCGA	..CTCCA	..TTGACCC
<i>Gilia hutchinsifolia</i>	TTGC	TGTTG	TACGT	..TT	TCATCTCT	TCGTCGA	..CTTCA	..TTGACCC
<i>Gilia latifolia</i>	TTGC	TGTTG	TGCGT	..TA	CCGTCTCT	TCGCCAA	..CTCCA	..TTGACCC
<i>Gilia foetida</i>	TTGT	TGTTG	TGCGT	TA	AGTCGTGCTY	CGTCCAGCCTTACATAGTTGACCC	TGTTG	CA
<i>Gilia rigidula</i>	TTGT	TGTTG	TGCGC	TA	A	TCCT	CT	TCGTCAA
<i>Gilia scabra</i>	TGGT	TGTTG	TGCGT	CA	TCGTACTCA	CCGTTGG	..TTCCG	..TGGACCC
<i>Loeselia glandulosa</i>	TTGT	TGTTG	TAGCGT	CA	CAGCCGTCTGT	ACGCSAA	..CTCAA	..TTGACCC
<i>Ipomopsis longiflora</i>	TTGC	TGTTG	TGCGT	CA	CCGTCTCT	ACGTCAA	..CTCCA	..ATGACCC
<i>Ipomopsis gunnisonii</i>	ATTG	TGTTG	WGCCT	AA	KCATCTCT	ATGTMGA	..CTCCA	..ATGACCC
<i>Ipomopsis multiflora</i>	TTGC	TGTTG	TGCGT	CA	TGTCTCT	CCGTCAA	..CTCCA	..ATGACCC
<i>Ipomopsis tenuifolia</i>	TTGC	TGTTG	TGCGT	CA	CCGTCTCT	CCGTCAA	..CTCAA	..TTGACCC
<i>Ipomopsis sonora</i>	TTGT	TGTTG	TGCGT	CG	TCGTCCGCT	CAGTCGA	..CTCCA	..ACGACCC
<i>Eriastrum diffusum</i>	TTGCGT	TGTTG	TGCGT	GCGGTCGTCTCT	CCGTGMA	..CTCCA	..TTGACCC	TGTTG
<i>Loeseliastrum matthewsii</i>	TTGC	TGTTG	AGCGT	CA	CGGTCTCT	CCGTCAA	..CTCCA	..ATGACCC
<i>Loeseliastrum schottii</i>	TTGM	TGTTG	TGCGT	CA	TCGTCTCT	CCGTCAA	..CTCCA	..TTGACCC
<i>Langloisia setosissima</i>	TTGC	TGTTG	TGCGT	CA	TCGTCTCT	CCGTCAA	..CTCCA	..TTGACCC
<i>Langloisia set. punctata</i>	TTGC	TGTTG	TGCGT	CA	TCGTCTCT	CCGTCAA	..CTCCA	..TTGACCC
<i>Gilia stellata</i>	TTGT	TGTTG	TGCGT	TA	TCGTCTCT	CCGTCAA	..CTCCA	..TTGACCC
<i>Gilia crassifolia</i>	TTGT	TGTTG	TGCGT	TA	TCGTCTCT	CCGTCAA	..CTCCA	..TTGACCC
<i>Gilia scopulorum</i>	TTGT	TGTTG	TGCGT	TA	TCGTCTCT	CCGTCAA	..CTCCA	..TTGACCC
<i>Gilia ochroleuca</i>	TTGT	TGTTG	TGCGT	TA	TCGTCTCT	CCGTCAA	..CTCCA	..TTGACCC
<i>Gilia flavocincta</i>	TTGT	TGTTG	TGCGT	TA	TCGTCTCT	CCGTCAA	..CTCCA	..TTGACCC
<i>Gilia tenerima</i>	TTGT	TGTTG	TGCGT	TT	TCGTCTCT	WCCTCWA	..CTCCA	..TTGACCC
<i>Gilia capitata</i>	TTGT	TGTTG	TGCGT	TA	TCGTCTCT	CGTACAG	..CTCCA	..TTGACCC
<i>Gilia tricolor</i>	TTGT	TGTTG	TGCGT	TA	TCGTCTCT	CGTACAT	..CTCCA	..TTGACCC
<i>Allophyllum gilioides</i>	TTAT	TGTTG	TAGCGT	TAGTTGTTCTCT	TCGTTAA	..CTCCA	..TTGACCC	TGTTG
<i>Allophyllum divaricatum</i>	TTAT	TGTTG	GCGT	TA	TGTTCTCT	TCGTTAA	..CTCCA	..TTGACCC
<i>Gilia splendens</i>	TTGC	TGTTG	TGCGT	CT	TCGCCCTCT	TCGTCAA	..CTCCA	..TTGACCC
<i>Collomia linearis</i>	TTGT	TGTTG	TGCGT	TA	TGTTCTCT	CCGTCAA	..CTCCA	..TTGACCC
<i>Collomia grandiflora</i>	TTGT	TGTTG	TGCGT	TG	TGTTCTCT	CCGTCAA	..CTCCA	..TTGACCC
<i>Navarretia breweri</i>	TTGT	TGTTG	WGCCT	TA	TGTTCTCT	TCGTCAA	..CTCCA	..TTGACCC
<i>Polemonium foliosissima</i>	TTGC	TGTTG	WGCCT	TA	SCGTCTCT	TCGTMGG	..CTCCA	..TTGACCC
<i>Linanthus aureus</i>	TTACATGTTG	TG	...TGCTTGT	TTCCG	...MTGT	..CTCCA	..AKGACCC	TTGTTG
<i>Linanthus parryae</i>	TTGC	TGTTG	TGCGT	TG	TCGTCTCT	TC	..CGA	..CTCCA
<i>Gilia maculata</i>	TTAC	TGTTG	TGCGT	TA	ACGTCTCT	TCGTCGA	..CTCCA	..TTGACCC
<i>Gilia campanulata</i>	TTAC	TGTTG	TGCGT	TG	TCGTCTCT	TCGTCGT	..CTCCA	..TTGATCC
<i>Gilia inyoensis</i>	TTAC	TGTTG	TGCGT	CG	TGTTCTCT	TCGTCGG	..CTCCA	..TTGACCC
<i>Gilia filiformis</i>	TTAC	TGTTG	TGCGT	TG	TCGTCTCT	TCGTCGA	..CTCCA	..TTGACCC
<i>Phlox gracilis</i>	TTAC	TGTTG	TTCGT	CTTTGCTCTCT	...TCTA	..CTCCA	..TTGACCC	TGTTG
<i>Phlox standsburyi</i>	TTAC	TGTTG	TGCGT	CTTTGCTCTCT	...TCTA	..CTCCA	..TTGACCC	TGTTG
<i>Leptodactylon watsonii</i>	TTGC	TGTTG	TGCGT	TG	TCGTCTCT	...TCCGA	..CTCCA	..TTGACCC
<i>Leptodactylon pungens</i>	TTGC	TGTTG	TGCGT	TG	TCGTCTCT	...TCCGA	..CTCCA	..TTGACCC
<i>Linanthus bicolor</i>	T	..CTGTTG	TGCG	..CTGTTG	...GCTGT	..TTCCA	..ATGACCC	TGTTG
<i>Linanthus nuttallii</i>	TTACATGTTG	TGCG	..CT	TGCTCAT	...GTTAT	..CTCCA	..ATGACCC	TGTTG