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## A PHYLOGENETIC CLASSIFICATION OF POLEMONIACEAE

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### ABSTRACT

Three hundred seventy nine species of Polemoniaceae are arranged in a phylogenetic classification composed of three subfamilies, eight tribes, and 26 genera. Nomenclature of one tribe is clarified and the circumscription of several tribes differs greatly from previous classifications. Five new genera, *Bryantiella*, *Dayia*, *Lathrocasis*, *Microgilia*, and *Saltugilia*, are proposed. In addition, four new species are described from the genera *Allophyllum*, *Dayia*, *Giliastrum*, and *Ipomopsis*. This treatment represents a major reclassification with 59 new combinations, and the application of several additional combinations not used in recent years.

Key words: *Allophyllum*, *Bryantiella*, classification, *Dayia*, *Giliastrum*, Gilieae, *Ipomopsis*, *Lathrocasis*, *Leptosiphon*, *Microgilia*, nomenclature, phylogeny, Polemoniaceae, *Saltugilia*, systematics.

### INTRODUCTION

Suprageneric classification in Polemoniaceae during the 20th century has undergone considerable flux, despite the appearance of relative stasis. In his monograph of Polemoniaceae for Engler's *Das Pflanzenreich*, Brand (1907) recognized 13 genera in two subfamilies and four tribes (Table 1). Investigations by a number of students of the family during the next 30 years led to Wherry's (1940) revision, which recognized 19 genera in three tribes and three subtribes. Almost 20 years later, Grant (1959) reevaluated the work of earlier students and synthesized these works with his own biosystematic and experimental studies to erect a classification of 18 genera in five tribes. This classification has served as the framework for sampling in comparative and evolutionary studies for forty years (Table 1). A number of broad comparative surveys, conducted in Polemoniaceae during this interval (e.g., Stuchlik 1967*a, b*; Taylor and Levin 1975; Harborne and Smith 1978; Smith et al. 1982; Wilken et al. 1982; Plitmann and Levin 1983, 1990; Carlquist et al. 1984; Steele and Vilgalys 1994; Johnson et al. 1996; Porter 1996), were interpreted in the framework of Grant's classification. As a result, some workers

suggested a revised taxonomy may better reflect the accumulating evidence of character distributions supporting alternative views of phylogenetic relationship (e.g., Smith et al. 1977; Day and Moran 1986; Johnson et al. 1996; Porter 1996). Of these studies, comparative DNA sequence analyses most forcefully stimulated the reexamination of Polemoniaceae classification. These data were clearly the impetus leading to Grant's (1998*a, b*) revised taxonomy of 20 genera in two subfamilies and eight tribes (Table 1). Similarly, these data have stimulated us to examine carefully many classes of characters and their distribution in Polemoniaceae. Grant's (1998*a, b*) newest classification, while in some instances remedying character conflict imposed by his earlier system (Grant 1959), inadequately reflects strongly supported and corroborated evidence for the underlying phylogeny of Polemoniaceae (Johnson et al. 1996; Porter 1996; Porter and Johnson 1998). Examination of both morphological and molecular data reveals well-corroborated patterns, providing evidence of the phylogeny of this family. Here we propose a new classification of Polemoniaceae, developed to reflect the phylogeny of this complex family.

Table 1. A comparison of major classifications of Polemoniaceae from the 1830s to the present. The classification of Reichenbach is a portion of his treatment of Convolvulaceae, within which he included Polemoniaceae.

Reichenbach 1837	Meisner 1839	Baillon 1890	Peter 1891
Gruppe Polemonieae	Tribus Polemonieae	Tribus Polemonieae	Tribus Polemonieae
<i>Cobaea</i>	<i>Bonplandia</i>	<i>Cantua</i>	<i>Bonplandia</i>
<i>Polemonium</i>	<i>Cantua</i>	<i>Collomia</i>	<i>Collomia</i>
	<i>Collomia</i>	<i>Loeselia</i>	<i>Gilia</i>
Gruppe Phloginae	<i>Gilia</i>	<i>Navarretia</i>	<i>Loeselia</i>
<i>Phlox</i>	<i>Hoitzia (Loeselia)</i>	<i>Phlox</i>	<i>Phlox</i>
	<i>Phlox</i>	<i>Polemonium</i>	<i>Polemonium</i>
	<i>Polemonium</i>		
Gruppe Gilieae		Tribus Cobaeae	Tribus Cobaeae
<i>Aegochloa (Navarretia)</i>		<i>Cobaea</i>	<i>Cobaea</i>
<i>Cantua</i>	Tribus Cobaeae		
<i>Collomia</i>	<i>Cobaea</i>		
<i>Courtoisia</i>		Tribus Bonplandieae	Tribus Cantueae
<i>Fentzelia</i>	Tribus Cyanantheae	<i>Bonplandia</i>	<i>Cantua</i>
<i>Gilia</i>	<i>Cyananthus</i>		
<i>Hoitzia (Loeselia)</i>			
<i>Leptosiphon</i>			
<i>Linanthus</i>			
<i>Welwitschia (Eriastrum)</i>			

#### MATERIALS AND METHODS

##### *Philosophy of Classification*

Classifications frequently function, for better or for worse, as proxies for phylogeny in comparative studies (e.g., Taylor and Levin 1975; Ricklefs and Renner 1994). The inferential accuracy achieved in such studies depends upon how well the classification accurately reflects phylogeny. Though it is not possible to literally observe the diversification events of the past, philosophical and methodological advances over the last 40 years have provided a valuable framework for reconstructing phylogeny. These tools, including cladistic analyses, have grounded systematics as a science based in hypothesis testing (classifications representing testable hypotheses of relationship), using repeatable methods, and providing a means for assessing the taxonomic value of a character or intrinsic levels of data support for a particular group. We do not suppose that systematics has reached a methodological pinnacle, that current algorithmic data analyses can resolve all of the complex diversification events produced by nature, nor that interpretation has no role in modern systematics. We do suggest, however, that appropriate tools for implementing strong inference (Platt 1964) in systematic studies exist. The application of these tools, while recent in origin relative to less explicit approaches, can provide important insights into phylogeny of use to all taxonomists involved in classifying organisms (see Mayr, 1995, for a similar conclusion albeit from a different perspective).

The classification presented here is an attempt to model what we have discovered regarding phylogeny in the *Phlox* family through our field and laboratory studies, observations, and primary literature (Fig. 1);

the classification reflects the phylogeny, rather than the phylogeny being *determined a posteriori* from the classification (Grant 1998a). Recognition of monophyletic groups has been central to our efforts. We use "monophyly" throughout this paper sensu Hennig (1966). That is, an ancestor and all of the descendants of that ancestor represent a monophyletic group. This corresponds to the term "holophyletic" of Ashlock (1971). As a classification criterion, monophyly has received its share of criticism (e.g., Cronquist 1987; Sosef 1997). Monophyly, however, provides a strong theoretical foundation for comparative biology (e.g., Donoghue and Cantino 1988; Snow 1996) and reflects our view that classifications should mirror evolutionary patterns of diversification.

The processes of diversification are the processes of evolution; that is, descent with modification. These processes have produced a genealogical connection, or phylogeny, between all organisms. Characters, whether morphological traits, palynology, flavonoid chemistry, reproductive biology, or DNA sequences, are the products of this genealogical descent as modified by mutation, drift, and selection. Each character may provide some degree of corroboration of the phylogeny, as well as some misleading information attributable to homoplasy or inaccuracies in homology assessment. It is through the synthesis of all lines of evidence that the most reliable estimation of the phylogeny of a group will be found and genealogical connections discovered.

The classification presented here reflects such a synthesis. Published DNA sequence analyses (Steele and Vilgalys 1994; Johnson and Soltis, 1995; Johnson et al. 1996, 1999; Porter 1996; Spencer and Porter, 1997; Porter and Johnson 1998; Prather and Jansen 1998;

Table 1. Continued.

Brand 1907	Wherry 1940	Grant 1959	Grant 1998
Subfam. Polemonioideae	" <i>Polemonium</i> Tribe"	Tribe Polemonieae	Subfam. Polemonioideae
Tribe Polemonieae	<i>Cobaea</i>	<i>Allophyllum</i>	Tribe Polemonieae
<i>Aliciella</i>	<i>Polemoniella</i>	<i>Collomia</i>	<i>Allophyllum</i>
<i>Collomia</i>	<i>Polemonium</i>	<i>Gymnosteris</i>	<i>Collomia</i>
<i>Gilia</i>		<i>Microsteris</i>	<i>Gymnosteris</i>
<i>Gymnosteris</i>	" <i>Collomia</i> Tribe"	<i>Phlox</i>	<i>Microsteris</i>
<i>Langloisia</i>	<i>Bonplandia</i>	<i>Polemonium</i>	<i>Navarretia</i>
<i>Navarretia</i>	<i>Cantua</i>		<i>Phlox</i>
<i>Phlox</i>	<i>Collomia</i>	Tribe Gilieae	<i>Polemonium</i>
<i>Polemonium</i>	<i>Gymnosteris</i>	<i>Eriastrum</i>	
	<i>Huthia</i>	<i>Gilia</i>	Tribe Gilieae
Tribe Bonplandieae	<i>Navarretia</i>	<i>Ipomopsis</i>	<i>Eriastrum</i>
<i>Bonplandia</i>		<i>Langloisia</i>	<i>Gilia</i>
<i>Loeselia</i>	" <i>Gilia</i> Tribe"	<i>Leptodactylon</i>	<i>Ipomopsis</i>
	" <i>Gilia</i> subtribe"	<i>Linanthus</i>	<i>Langloisia</i>
Subfam. Cobaeoideae	<i>Gilia</i>	<i>Navarretia</i>	
Tribe Cobaeae	<i>Hugelia</i> ( <i>Eriastrum</i> )		Tribe Leptodactylonae
<i>Cobaea</i>	<i>Ipomopsis</i>	Tribe Cobaeae	<i>Leptodactylon</i>
	<i>Langloisia</i>	<i>Cobaea</i>	<i>Linanthus</i>
Tribe Cantueae			
<i>Cantua</i>	" <i>Linanthus</i> subtribe"	Tribe Cantueae	Subfam. Cobaeoideae
<i>Huthia</i>	<i>Linanthastrum</i>	<i>Cantua</i>	Tribe Cobaeae
	<i>Linanthus</i>	<i>Huthia</i>	<i>Cobaea</i>
	<i>Leptodactylon</i>		
	" <i>Phlox</i> Tribe"	Tribe Bonplandieae	Tribe Bonplandieae
	<i>Loeselia</i>	<i>Bonplandia</i>	<i>Bonplandia</i>
	<i>Microsteris</i>	<i>Loeselia</i>	
	<i>Phlox</i>		Tribe Cantueae
			<i>Cantua</i>
			<i>Huthia</i>
			Tribe Loselieae
			<i>Loeselia</i>
			Tribe Acanthogilieae
			<i>Acanthogilia</i>

Bell et al. 1999; Fergussen et al. 1999; Bell and Patterson 2000), as well as an equal volume of unpublished DNA data, have contributed heavily toward phylogeny estimation in Polemoniaceae and hence this classification. DNA sequences remain the only broadly surveyed and published class of data at the family level in Polemoniaceae that have measurable levels of support. Even so, sequences and cladistic analyses are by no means the only source of evidence considered by us. We have attempted to evaluate and incorporate all published comparative and biosystematic data. In addition, when feasible, we have reexamined many morphological, palynological, and anatomical features ourselves to verify published interpretations and to characterize states for many species not previously reported. Preliminary cladistic analyses of comparative morphological data (Porter, unpubl.) provide very few inferred groups with even moderate support due to extensive homoplasy in these data; nonetheless, examining patterns of character distribution has been enlightening. In some instances, morphology was considered "more compelling" evidence of common an-

cestry than gene sequence data; in other instances, the reverse was true.

#### Scope and Format

Suprageneric classification primarily is of interest to systematists and comparative biologists, whereas interest in taxonomic changes involving generic circumscriptions and species relationships extends to government agencies, field biologists, and amateurs. Both types of change are understandably met with reserve and sometimes resistance. We have taken neither change lightly. We deliberated extensively between ourselves, and with others, on the bases and merit for all taxonomic change. We considered keeping some historical groups of doubtful monophyly for the sake of convenience and tradition while continuing to gather an "insurmountable body of evidence" before approaching the systematic community. At the same time, we surveyed and reviewed many classes of data with sufficient depth and breadth to express confidence in the composition of several lineages of Polemoni-



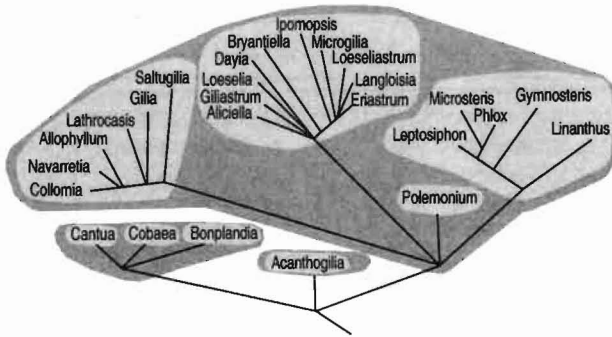


Fig. 1. Phylogenetic tree depicting hypothesized relationships between genera of Polemoniaceae. The structure of the tree is based upon comparative morphological and molecular (DNA sequences of nrITS, *cpmatK*, *cpmL-F*, and *mtnd1* intron) data. The circled groups represent major lineages, emphasized in the phylogenetic classification.

aceae not recognized by any currently accepted taxonomy. Ultimately, we abandoned tradition when corroborating data provided reasonable, substantive alternative hypotheses of phylogeny coupled with sufficient indication that the traditional groups in question were dubiously supported.

This classification is hierarchically arranged. Ranks of taxa are generally in correspondence with the traditional taxon inclusion of ranks in Polemoniaceae. However, taxa of equal rank are not intended to represent sister groups per se, or groups of equal age; taxa are simply monophyletic groups. Consistent with this form of presentation, taxa at lower ranks are presented alphabetically within the taxa of higher ranks to which they belong. Additionally, this classification is exclusive of subgeneric ranks other than species; infrageneric ranks are considered valuable, but their circumscription extends beyond the scope of this paper. Their omission here reflects neither endorsement nor rejection of the subgeneric and sectional classifications of others. Recent and forthcoming contributions (e.g., Porter 1998a; Prather 1999) address subgeneric and/or sectional classification of several genera in Polemoniaceae.

For each rank, the correct name of the taxon with full citation is provided. The nomenclature has been checked with the source literature, with the exception of Arnott's (1832) treatment in *Encyclopedia Britannica*, which was unavailable to us. For the sake of brevity, synonymy generally is not provided; however, some synonymy is included to clearly indicate circumscription of taxa. Following the family, subfamily, tribe, and genus names, brief descriptions are provided. A phylogenetic delineation, or "clade address," for supergeneric ranks follows. The phylogenetic delineation provides an explicit identification of the monophyletic group to which we associate a name, and specifies the meaning of a taxon name in terms of

ancestry and descent (de Queiroz 1997). This delineation (or definition) may take one of three forms: node-based, stem-based, or apomorphy-based (see de Queiroz and Gauthier 1990, 1992, 1994). Node-based definitions have the following form: the monophyletic group arising from the most recent common ancestor of taxon A and taxon B. In some cases we specify that the group is the "least incorporative," or the smallest monophyletic group that simultaneously includes two or more taxa. Less frequently, we employ a stem-based definition in the form: the most inclusive (or largest) monophyletic group that includes taxon C and taxon D, but does not include taxon A, or taxon B. Apomorphy-based definitions are of the form: the monophyletic group arising from the first common ancestor of taxon A to evolve a particular character. Because we are classifying under International Code of Botanical Nomenclature (ICBN) rules (Greuter et al. 1994), we have used type species to serve as taxon specifiers (taxon A or taxon B, above). The logic being that, for example, if the type of *Gilia* is within a clade, then the generic name must be associated with at least some portion of that clade. Following the phylogenetic delineation, the membership of each taxon is indicated. At the generic rank, a listing of species indicates membership. We have attempted to provide a complete and accurate listing of species; however, we do not consider ourselves experts in all genera, and some errors due to omission or inaccuracies may exist. Frequently, there are notes following the descriptions of the taxa that provide additional information regarding recognition. Following the classification, we present a generic key to Polemoniaceae.

## RESULTS AND DISCUSSION

An evaluation of molecular, morphological, palynological, karyological, phytochemical, and ecological data in Polemoniaceae provides an immediate realization of the immense complexity that has arisen during the diversification of this family. Homoplastic evolution is common. No fewer than eight genera possess some species occurring in very xeric habitats and other species that inhabit relatively mesic sites. Similarly, nine genera have species that display floral syndromes associated with hummingbird pollination (V. Grant and K. Grant 1965; Porter 1993), and ten genera display floral syndromes associated with hawkmoth pollination. At least six genera have both hawkmoth and hummingbird, as well as bee, fly, or beetle pollination. Given that multiple lineages appear to have undergone independent morphological change associated with shifts in habitat preference, and, at the same time, diversified greatly in pollination mechanisms, a high degree of homoplasy should not be surprising. Extensive homoplasy is reflected in the difficulty all workers in

Polemoniaceae have faced in elucidating higher-order relationships in this family: all but a few genera are defined by suites of characters and exclusive diagnostic features for supergeneric groups are elusive.

Hybridization may also have contributed to complex patterns of variation in the Phlox family. Hybridization has been suggested to play a role in species origins, both at the diploid (Grant 1959) and the polyploid (Day 1965; Tommerup and Porter 1996) levels, and has been hypothesized to have also played a role in the origin of more diverse lineages (Grant 1959). The patterns of distribution of morphological traits resulting from hybridization are varied and not easily predicted (McDade 1992). However, in the absence of substantive evidence for higher-order reticulation in the Phlox family, corroborative data supporting a model of simple divergence deserve consideration. Analytical methods under development that accommodate reticulate processes are promising (e.g., Hein 1993; Alroy 1995; Dickerman 1998), and such methods may provide new insights in Polemoniaceae in conjunction with additional data.

In Polemoniaceae, explicit analyses of congruence between nuclear and chloroplast genes reveal similar historic patterns of gene descent among genera for the regions surveyed (Johnson et al. 1995; Johnson 1996). Minor discrepancies exist between some species within genera, and in some weakly supported supergeneric relationships. Similarly, explicit comparisons of morphological data with DNA-based hypotheses show either no, or only weak conflict (Porter, unpubl.). Thus, while processes exist that can lead to discordance between gene-trees and species trees (e.g., Wendel and Doyle 1998), hard evidence for such discordance in the Phlox family does not currently exist. Furthermore, what is true for the gene, is true for the genotype and phenotype. Both morphology and gene sequences have the potential for providing misleading information, if approached with naiveté. However, they both have great promise if considered in concert and through corroboration. We contend that, in concert, morphological and molecular data provide an indication of the underlying phylogeny of Polemoniaceae.

This phylogenetic classification of Polemoniaceae (Table 2, and below) includes three subfamilies, eight tribes, and 26 genera for the 379 species of Polemoniaceae. Nomenclature for one tribe is clarified and the circumscription of several tribes greatly differs from previous classifications of this family (Table 1). We propose five new genera and describe four new species. This treatment represents a major reclassification, resulting in 59 new combinations. We restate our belief that an accurate and unambiguous reflection of phylogenetic relationships in classification supersedes the inconvenience of nomenclatural change. As with Grant (1998a: 744), we consider classifications to represent

Table 2. The proposed phylogenetic classification of Polemoniaceae.

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Subfam. Acanthogilioideae
Tribe Acanthogilieae
<i>Acanthogilia</i>
Subfam. Cobaeoideae
Tribe Bonplandiae
<i>Bonplandia</i>
Tribe Cantueae
<i>Cantua</i>
Tribe Cobaeae
<i>Cobaea</i>
Subfam. Polemonioideae
Tribe Gilieae
<i>Allophyllum</i>
<i>Collomia</i>
<i>Gilia</i>
<i>Lathrocasis</i>
<i>Navarretia</i>
<i>Saltugilia</i>
Tribe Loeseliaeae
<i>Aliciella</i>
<i>Bryantiella</i>
<i>Dayia</i>
<i>Eriastrum</i>
<i>Giliastrum</i>
<i>Ipomopsis</i>
<i>Langloisia</i>
<i>Loeselia</i>
<i>Loeseliastrum</i>
<i>Microgilia</i>
Tribe Phlocideae
<i>Gymnosteris</i>
<i>Leptosiphon</i>
<i>Linanthus</i>
<i>Microsteris</i>
<i>Phlox</i>
Tribe Polemonieae
<i>Polemonium</i>

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hypotheses that “can be tested, supported, falsified, or modified by subsequent evidence.” This classification is our attempt to incorporate concrete hypotheses of monophyly, based on our current understanding of phylogeny. We view this contribution as the commencement, rather than the consummation, of phylogenetic classification in the Phlox family, and welcome continued exploration of relationships. We anticipate additional, carefully considered data, both morphological and molecular, that may either corroborate or refute the hypotheses of relationships herein presented.

POLEMONIACEAE Juss.

*Gen. pl.*, p. 136, 1789.

Vines (*Cobaea*), small trees (*Cantua*), shrubs, perennial, biennial, or annual herbs. Flowers typically of five sepals, five fused petals, and five epipetalous or basally adnate stamens (but perianth and androecium consistently 4- or 6-merous in some *Linanthus*). Superior ovary of three fused and loculicidally dehiscent

carpels (bicarpellate in some *Navaretia*; septacidal in *Cobaea*, sometimes both loculicidal and septicidal in *Acanthogilia*). Petals convolute in aestivation (imbricate in some *Cantua*). Annular nectary disk present; ovules unitegmic and tenuinucellate; endosperm development nuclear. (including Cobaeaceae D. Don, *Edinburgh Philos. J.* 10: 109, 1824.) Type: *Polemonium* L.

*Phylogenetic delineation.*—The least incorporative monophyletic group of species that contains *Acanthogilia gloriosa*, *Bonplandia geminiflora*, *Cantua buxifolia*, *Cobaea scandens*, *Gilia laciniata*, *Loeselia cilata*, *Phlox glaberrima*, and *Polemonium caeruleum*.

*Membership.*—*Acanthogilia*, *Aliciella*, *Allophyllum*, *Bonplandia*, *Bryantiella*, *Cantua*, *Cobaea*, *Collomia*, *Dayia*, *Eriastrum*, *Gilia*, *Giliastrum*, *Gymnosteris*, *Ipomopsis*, *Langloisia*, *Lathrocasis*, *Leptosiphon*, *Linnanthus*, *Loeselia*, *Loeseliastrum*, *Microgilia*, *Microsteris*, *Navarretia*, *Phlox*, *Polemonium*, and *Saltugilia* (3 subfamilies, 26 genera, ~379 species).

Polemoniaceae, including *Cobaea*, are supported strongly by cladistic analyses as a monophyletic group that originated as part of an ericalean-ebenalean diversification. The sister family of Polemoniaceae is as yet uncertain (Johnson et al. 1996; Porter 1996; Nandi et al. 1998; Porter and Johnson 1998; Johnson et al. 1999). The origin of Polemoniaceae among ericalean and ebenalean families impacts the interpretation of traits heretofore considered characteristic of (i.e., putative synapomorphies for) the family. For example, tricarpelly is not uncommon in the ericalean-ebenalean families (e.g., Clethraceae, Diapensiaceae, and Fouquieriaceae), and therefore is doubtfully a synapomorphy for Polemoniaceae.

**Acanthogilioideae** J. M. Porter & L. A. Johnson,  
subfam. nov.

Frutex glandulosus. Foliis dimorphis, primariis spinosis persistentibus, alternis, et pinnatis, secundis lineari in fasciculis. Flores regulares et symmetrici. Corollae hypocrateriformis. Pollinis granum aureum, zonocolporatum, exino supraverrucato. Semina alatis. Typus: *Acanthogilia* A. G. Day et Moran.

Shrubs with persistent, alternate, spiny, pinnately lobed primary leaves and deciduous, linear secondary leaves that are axillary and fascicled on short shoots. Calyx and corolla radially symmetric, corolla salverform. Fruits dehiscing only about half the length, either loculicidal or both loculicidal and septicidal. Seeds winged. Type: *Acanthogilia* A. G. Day & Moran.

*Phylogenetic delineation.*—The monophyletic group descended from the first ancestor of *Acanthogilia gloriosa* to evolve persistent, spinescent primary leaves, formed by the lignification of the vascular bundles of

the leaf, and simultaneously zonocolporate pollen bearing verruca.

*Membership.*—*Acanthogilia*.

As a taxon, the name Acanthogilioideae is redundant with Acanthogilieae, and *Acanthogilia*; recognition of this subfamilial rank is maintained for uniformity in treatment in this classification. However, as a monophyletic group, Acanthogilioideae are identified in a broader context that does not preclude the possibility that unknown species may also belong within this subfamily (i.e., more incorporative than only *Acanthogilia gloriosa*). Our exclusion of *Acanthogilia* from Cobaeoideae of Grant (1998a), and from our Polemonioidae, emphasizes the morphological intermediacy between this taxon, Cobaeoideae, and Polemonioidae. This monotypic taxon occupies a pivotal position with respect to the root of Polemoniaceae, and similarities in the morphological features of *Acanthogilia* exist with both subfamilies (Day and Moran 1986). For example, the verrucate pollen of *Acanthogilia* is reminiscent of the insulae (verrucae) on the pollen of *Cantua* (Day and Moran 1986). Even so, the pollen of *Acanthogilia* is zonocolporate, as is found in many members of Polemonioidae, rather than pantoporate, as is observed in Cobaeoideae (Stuchlik 1967a; Day and Moran 1986), and verrucate pollen also occurs in the *Giliastrum foetidum* (Gillies ex Benth.) J.M. Porter of the Polemonioidae. Like most members of Polemonioidae, *Acanthogilia* has a low, presumably diploid chromosome number of  $N = 9$ , in contrast to the high, presumably polyploid chromosome numbers of Cobaeoideae ( $N = 15, 26, 27$ ). Seedlings of *Cantua* and *Cobaea* are described as possessing “large cordate or ovate cotyledons” (Grant 1959: 9). The cotyledons of seedlings of *Acanthogilia* are linear and acute (Porter unpubl.), whereas the cotyledons of members of Polemonioidae vary from ovate to linear. Collectively, there seems to be no overwhelming morphological evidence supporting any specific sister relationship for *Acanthogilia*. In addition, molecular cladistic studies are unclear concerning the sister group relationship of *Acanthogilia*. This taxon may be sister to the so-called “tropical” genera (Cobaeoideae), the “temperate” genera (Polemonioidae), or to all other members of Polemoniaceae.

ACANTHOGILIEAE V. E. Grant  
*Amer. J. Bot.* 85: 744, 1998.

Shrubs with persistent, alternate, spiny, pinnately lobed primary leaves and deciduous, linear secondary leaves that are axillary and fascicled on short shoots. Calyx and corolla radially symmetric, corolla salverform. Seeds winged. Type: *Acanthogilia* A. G. Day & Moran.

*Phylogenetic delineation.*—See Acanthogilioideae, with which this taxon is redundant; recognition of this tribal rank is maintained for uniformity in treatment in this classification.

*Membership.*—Acanthogilia.

ACANTHOGILIA A. G. Day & Moran, *Proc. Calif. Acad. Sci.* **44**: 111–115, 1986.

Shrubs with persistent, alternate, spiny, pinnately lobed primary leaves and deciduous, linear secondary leaves that are axillary and fascicled on short shoots; glandular throughout. Calyx tube with a hyaline interval alternating with the herbaceous costae, the lobes with narrow hyaline margins, apex mucronate. Corolla funnelliform to salverform and mostly radially symmetric. Pollen zonocolporate, with semitectate exine (perforate or perreticulate), insulae (verrucae) present. Fruits dehiscent only about half the length, either loculicidal or both loculicidal and septicidal. Seeds winged.  $N = 9$ . One species.

ACANTHOGILIA GLORIOSA (Brandegee) A. G. Day & Moran, *Proc. Calif. Acad. Sci.* **44**: 115, 1986.

#### COBAEOIDEAE (D. Don) Arn.

*Encycl. Britannica ed. 7 v.5*, p.121, 1832.

(Cobaeaceae D. Don, *Edinburgh Philos. J.* **10**: 109, 1824.)

Vines, small trees, shrubs, or rarely herbs. Leaves alternate, simple and entire to pinnately lobed or compound. Calyx lobes nearly free (e.g., *Cobaea*) or fused, wholly herbaceous or hyaline between vasculature (e.g., *Cantua*). Corolla campanulate to tubular or salverform, medium to large, with epipetalous stamens inserted at corolla base or on tube. Seeds narrowly to broadly winged, rarely wingless (*Bonplandia*). Type: *Cobaea* Cav.

*Phylogenetic delineation.*—The least incorporative monophyletic group of species that includes *Bonplandia geminiflora*, *Cantua buxifolia*, and *Cobaea scandens*

*Membership.*—*Bonplandia*, *Cantua*, and *Cobaea* (three tribes, three genera, ~33 species).

This circumscription of subfamily Cobaeoideae differs from Grant (1998a) in excluding *Acanthogilia* and *Loeselia*. The former taxon is here accorded in its own subfamily; the latter is placed in Polemoniaceae. Encompassing considerable morphological diversity, Cobaeoideae separated early in the diversification of extant Polemoniaceae. The group as a whole is characterized by high, but not equivalent, chromosome numbers that may either stem from a single polyploid origin followed by several aneuploid changes, or multiple episodes of polyploidy and aneuploidy (Grant

1959; Johnson et al. 1996). Further investigations may allow a determination of which hypothesis explaining change in chromosome numbers in this group is most consistent with observed genome structure.

#### BONPLANDIEAE Baill.

*Hist. pl.* v.10, p.342, 1890.

Herbaceous to woody perennials, flowering the first year. Leaves alternate, broad, serrate or pinnately lobed, to linear and entire. Flowers axillary and paired. Calyx and corolla bilaterally symmetric. Seeds narrowly winged to wingless. Type: *Bonplandia* Cav.

*Phylogenetic delineation.*—The most incorporative monophyletic group of species that includes *Bonplandia geminiflora* and *B. linearis*, and shares a more recent common ancestor with *B. geminiflora* than with *Acanthogilia gloriosa*, *Cantua buxifolia*, *Cobaea scandens*, *Gilia laciniata*, *Loeselia ciliata*, *Phlox glaberrima*, or *Polemonium caeruleum*.

*Membership.*—*Bonplandia*.

As a taxon, Bonplandieae is redundant with *Bonplandia*; recognition of this tribal rank is maintained for uniformity in treatment in this classification.

BONPLANDIA Cav., *Anales Hist. Nat.* **2**: 131, 1800.

Herbaceous to woody perennials, flowering the first year. Leaves alternate, simple, broad to narrow and linear, entire, serrate or pinnately lobed. Inflorescence essentially cymose, but flowers appearing axillary and paired. Calyx campanulate to tubular, bilaterally symmetric, herbaceous, lacking any hyaline regions. Corolla bilaterally symmetric, tubular to salverform, geniculate, apex of corolla lobes retuse to truncate-erose. Stamens exserted, adnate to and inserted on the tube at about the midpoint, filaments pubescent at the base; pollen pantoporate, with striate-reticulate exine, spinule-like processes present. Seeds 1 per locule, narrowly winged to wingless.  $N = 15$ . Two species. Type: *Bonplandia geminiflora* Cav.

BONPLANDIA GEMINIFLORA Cav., *Anales. Hist. Nat.* **2**: 132, t. 20, 1800.

BONPLANDIA LINEARIS B. L. Rob., *Proc. Amer. Acad. Arts.* **43**: 24, 1907.

The two species of *Bonplandia* are distinguished on the basis of leaf and floral morphology: *Bonplandia geminiflora* has narrow to broad, serrate, lyrate or pinnately lobed (but highly variable) leaves, and corolla (20–)22–29 mm long with spreading lobes; whereas, *B. linearis* has narrow, linear, entire leaves, and corolla 15–18(–20) mm long with reflexed lobes. Rzedowski et al. (1995) suggest reducing *B. linearis* to synonymy under *B. geminiflora*, citing the highly variable leaf morphology. However, floral morphology provides ev-



idence contrary to such a treatment. Robinson (1907) described the corolla size of *B. linearis* as 20 mm, which falls between the ranges of the two species here cited. This raises the question as to whether the holotype of *B. linearis* (not seen) represents the large-flowered or the small-flowered species. If the former is true, then Rzedowski et al. (1995) are indeed correct, and there remains an undescribed, small flowered species of *Bonplandia*. Directed studies are needed in this genus.

#### CANTUEAE Peter

*Pflanzenfam.* IV 3a, p.45, 1891.

Branching shrubs to rarely small trees. Leaves alternate or fasciculate, coriaceous to fleshy, entire to deeply pinnately divided. Flowers tubular to salverform, imbricate or convolute in aestivation, calyx wholly herbaceous, or hyaline between vasculature. Seeds broadly winged. Type: *Cantua* Juss. ex Lam.

*Phylogenetic delineation.*—The most incorporative monophyletic group of species that includes *Cantua buxifolia* and *Cantua coerulea*, and that shares a more recent common ancestor with *Cantua quercifolia* than with *Acanthogilia gloriosa*, *Bonplandia geminiflora*, *Cobaea scandens*, *Gilia laciniata*, *Loeselia ciliata*, *Phlox glaberrima*, or *Polemonium caeruleum*.

*Membership.*—*Cantua*.

CANTUA Juss. ex Lam., *Encycl.* v.1, p.603, 1785.

Erect shrubs or small trees, mostly glandular or hairy. Leaves alternate or fascicled, coriaceous to soft, entire to sinuate or crenate-dentate, margins often revolute. Inflorescence corymbose to rarely of solitary flowers. Calyx thick and coriaceous, herbaceous, or hyaline except around the vasculature, tubular to campanulate, somewhat bilaterally symmetric. Corolla tubular, to funnelform or salverform, apex of corolla lobes deeply bilobed, retuse, retuse-apiculate, truncate-erose, to apiculate. Stamens included to exerted, adnate to and inserted on the tube at or below mid-tube, filaments glabrous or pubescent at the base, rarely papillose-hirsute the entire length; pollen pantoporate, reticulate exine, with insulae (verrucae). Many seeds per locule, the seeds small, broadly or narrowly winged. *N* = 27. Twelve species. Type: *Cantua buxifolia* Juss. ex Lam. Synonymy includes *Huthia* Brand, *Bot. Jahrb. Syst.* 42: 174, 175, 1908.

CANTUA BICOLOR Lem., *Fl. Serres Jard. Eur.* 3: 242, 1847.

CANTUA BUXIFOLIA Juss. ex Lam., *Encycl.* v.1, p.603, 1785.

CANTUA CANDELLA Brand, *Pflanzenr.* IV 250, p.22, 1907.

CANTUA COERULEA (Brand) J. M. Porter & L. A. Johnson, comb. nov.

Basionym: *Huthia coerulea* Brand, *Bot. Jahrb. Syst.* 42: 175, 1908.

CANTUA CUZCOENSIS Infantes, *Lilloa* 31: 102, 1962.

CANTUA FLEXUOSA (Ruiz & Pav.) Pers., *Syn. pl.* v.1, p.187, 1805.

CANTUA LONGIFLORA (Brand) J. M. Porter & L. A. Johnson, comb. nov.

Basionym: *Huthia longiflora* Brand, *Bot. Jahrb. Syst.* 50, *Beibl.* 111: 51, 1913.

CANTUA LONGIFOLIA Brand, *Feddes Repert. Spec. Nov. Regni Veg.* 20: 46, 1924.

CANTUA OVATA Cav., *Icon.* v.4, p.43, t. 363, 1797.

CANTUA PYRIFOLIA Juss. ex Lam., *Encycl.* v.1, p.603, 1785.

CANTUA QUERCIFOLIA Juss., *Ann. Mus. Natl. Hist. Nat.* 3: 118, 1804.

CANTUA TOMENTOSA Cav., *Icon.* v.4, p.43, t. 364, 1797.

*Cantua* is most certainly a monophyletic group, with a distribution restricted to the central and northern Andean highlands. The two species formerly treated as the genus *Huthia* share a similar distribution and have much in common morphologically with other *Cantua*. These species share a very similar pollen morphology with most *Cantua* (Stuchlik 1967a); they are similar to *C. quercifolia* in leaf morphology (i.e., margins are deeply sinuate to crenate dentate and glandular hairy); and they share a calyx morphology unique in the family (i.e., the calyx is hyaline except following the vasculature, where it is chlorophyllous, as found in *C. quercifolia*). Morphological evidence supports the hypothesis that *Huthia* is derived from within *Cantua* as presently circumscribed (see also Gibson 1967). Species limits are poorly known in this group. However, some regional floras provide rather thorough treatments for local areas (e.g., Gibson 1967; see also Infantes Vera 1962).

#### COBAEAE (D. Don) Meisn.

*Pl. vasc. gen.*, Tab. Diagn. 273, 180, 1840.

Vines. Leaves alternate, pinnate-compound with terminal leaflet modified into a tendril. Calyx lobes nearly free, herbaceous. Capsules with septical dehiscence. Seeds broadly winged. Type: *Cobaea* Cav.

*Phylogenetic delineation.*—The most incorporative monophyletic group of species that includes *Cobaea minor* and *Cobaea scandens*, and that shares a more recent common ancestor with *Cobaea penduliflora* than with *Acanthogilia gloriosa*, *Bonplandia geminiflora*, *Cantua buxifolia*, *Gilia laciniata*, *Loeselia ciliata*, *Phlox glaberrima*, or *Polemonium caeruleum*.

*Membership.*—*Cobaea*.

As a taxon, the name Cobaeae is redundant with *Cobaea*; recognition of this tribal rank is maintained for uniformity in treatment in this classification.

COBAEA Cav., *Icon.* v.1, p.11, 1791.

Tropical vines, somewhat woody at the base. Leaves alternate, pinnate-compound with terminal leaflet modified into a tendril. Inflorescences reduced to axillary, long pedunculate, solitary flowers. Calyx radially sym-

metric, lobes nearly free to the base, herbaceous, no hyaline portion. Corolla campanulate, to nearly rotate, large, radially to bilaterally symmetric, the lobes broad to narrow and caudate. Stamens included to exserted, adnate and affixed at the base of the corolla tube, base of filaments glabrous to densely hairy; pollen pantoporate, with reticulate exine. Capsules with septicial dehiscence. Seeds large, broadly winged.  $N = 26$ . Eighteen species. Type: *Cobaea scandens* Cav.

COBAEA AEQUATORIENSIS Aspl., *Svensk Bot. Tidskr.* **48**: 550, 1954.

COBAEA ASCHERSONIANA Brand, *Helios* **21**: 87, fig. 2, 1904.

COBAEA BIAURITA Standl., *Contr. U. S. Natl. Herb.* **17**: 457, pl. 30, 1914.

COBAEA CAMPANULATA Hemsl., *Garden (London)* **17**: 352, 1880.

COBAEA FLAVA A. Prather, *Brittonia* **48**: 114, 116, fig. 1, 1996.

COBAEA GRACILIS (Oerst.) Hemsl., *Garden (London)* **17**: 352, 1880.

COBAEA LUTEA D. Don, *Edinburgh Philos. J.* **10**: 112, 1824.

COBAEA MINOR M. Martens & Galeotti, *Bull. Acad. Sci. Brux.* **12**: 276, 1845.

COBAEA PACHYSEPALA Standl., *Contr. U. S. Natl. Herb.* **17**: 456, 457, pl. 29, 1914.

COBAEA PANEROI A. Prather, *Brittonia* **48**: 116, 117, fig. 2, 1996.

COBAEA PENDULIFLORA (H. Karst.) Hook. f., *Bot. Mag.* **95**, pl. 5757, 1869.

COBAEA PRINGLEI (House) Standl., *Contr. U. S. Natl. Herb.* **17**: 457, 1914.

COBAEA ROTUNDFLORA A. Prather, *Brittonia* **48**: 117, 119, fig. 3, 1996.

COBAEA SCANDENS Cav., *Icon.* v.1, p.11, pl. 16 & 17, 1791.

COBAEA SKUTCHII I. M. Johnston, *J. Arnold. Arbor.* **19**: 128, 1938.

COBAEA STIPULARIS Benth., *Pl. hartw.*, p.45, 1840.

COBAEA TRIANAE Hemsl., *Garden (London)* **17**: 353, 1880.

COBAEA TRIFLORA Donn. Sm., *Bot. Gaz. (Crawfordsville)* **13**: 75, 1888.

The great morphological divergence that distinguishes *Cobaea* from other Polemoniaceae (Standley 1914; Prather 1999) appears likely the result of anagenic change from a common ancestor within, but after, the initial diversification of this family, rather than indicative of a sister relationship between *Cobaea* and the rest of the family (Johnson et al. 1996; Porter and Johnson 1998; Johnson et al. 1999). Relationships within this genus are evaluated and discussed by Prather (1996, 1999).

#### POLEMONIOIDEAE (Juss.) Arn.

*Encycl. Britannica* ed. 7, v.5, p.121, 1832.

Annual, biennial, or perennial herbs, or shrubs. Leaves opposite or alternate, linear and entire to variously pinnately or palmately lobed, or pinnately or palmately compound. Flowers rotate, campanulate, tubular, funnelliform or salverform, radially or occasionally bilaterally symmetric. Seeds generally without wings, but occasionally with narrow wings (e.g., some species of *Aliciella*, *Loeselia*, and *Polemonium*). Type: *Polemonium* L.

*Phylogenetic delineation.*—The least incorporative monophyletic group of species that includes *Gilia laciniata*, *Loeselia ciliata*, *Phlox glaberrima*, and *Polemonium caeruleum*.

*Membership.*—*Aliciella*, *Allophyllum*, *Bryantiella*, *Collomia*, *Dayia*, *Eriastrum*, *Gilia*, *Giliastrum*, *Gymnosteris*, *Ipomopsis*, *Langloisia*, *Lathrocasis*, *Leptosiphon*, *Linanthus*, *Loeselia*, *Loeseliastrum*, *Microgilia*, *Microsteris*, *Navarretia*, *Phlox*, *Polemonium*, and *Saltugilia* (four tribes; 22 genera; ~330 species).

Polemonioideae, though not paralleling Cobaeoideae in extreme morphological features (e.g., arborescent or vining habit, very large flowers, high chromosome numbers, etc.), exceed Cobaeoideae in degree of morphological diversity. Species of Polemonioideae range from near leafless annuals to woody subshrubs. *Loeselia*, retained by Grant (1998a) in Cobaeoideae, is placed in Polemonioideae and certainly shares recent common ancestry with members of this subfamily as here circumscribed, to the exclusion of members of Cobaeoideae and Acanthogilioideae (Johnson et al. 1996; Porter 1996; Porter and Johnson 1998). This subfamily frequently is referred to as the “temperate group.” However, it should be noted that many members of Polemonioideae occur in the tropics and subtropics of North and South America, in addition to temperate regions. Tribal composition within our Polemonioideae differs substantially from that presented by Grant (1959, 1998a, b).

#### Gilieae J. M. Porter & L. A. Johnson, trib. nov.

Herbae annuae (vel perennes rariores ut in *Collomia*) erectae glandulosae vel glabrae. Folia alterna integra vel pinnatisecta (vel rara palmata). Folium caulinum foliis rosularibus simile vel deminutus, vel folium congestus infra inflorescenciam. Calyx fructifer accrescens vel rumpens. Flores regulares et symmetrici. Corollae infundibuliformis vel hypocrateriformis. Pollinis albi vel caerulei. Seminis pallidi vel atrobrunnei. Typus: *Gilia* Ruiz et Pavon

Annual herbs, rarely perennial (in *Collomia*); glandular throughout or primarily in the inflorescence. Leaves alternate, infrequently opposite below, entire to pinnately (rarely palmately) lobed; distributed variously throughout, in basal rosettes, or principally congested near the inflorescence. Calyx accrescent or rupturing with age, corollas radially symmetric, rarely somewhat bilaterally symmetric, funnelliform to salverform. Pollen blue or white, rarely yellow. Seeds light or dark. Type: *Gilia* Ruiz & Pav.

*Phylogenetic delineation.*—The least incorporative monophyletic group of species that includes *Collomia linearis*, *Gilia laciniata*, *Lathrocasis tenerrima*, *Navarretia involucrata*, and *Saltugilia grinnellii*.

*Membership.*—*Allophyllum*, *Collomia*, *Gilia*, *Lathrocasis*, *Navarretia*, and *Saltugilia* (6 genera, 95 species).

We formally describe Tribe Gilieae, following many years of misapplication of this tribal name. The use of Gilieae at the tribal rank (e.g., Grant 1959, 1997, 1998a) rests on Reichenbach's (1837) classification, subdividing Convolvaceae into three "Groups" (Gruppen): Polemoniariae, Hydroleae, and Convolvuleae. Polemoniariae are also divided into three groups (Phloginae, Gilieae, and Polemonieae) but no rank is specified. The Code does not provide a status for these rankless categories. It might be inferred that Reichenbach intended the designations to be equivalent to the tribal rank, given the ending of the names (e.g., Gilieae). But, because name endings were not standardized in 1837, and Reichenbach did not indicate a rank, such a supposition is groundless. Regardless, these names are subdivisions of Convolvaceae, not Polemoniaceae. Grant (1997) has suggested that in taking up Reichenbach's Gruppe Gilieae and treating it at the tribal level, in his 1959 Natural History of the Phlox Family, the name is legitimized, according to the code. While he did provide a description (p. 51) and indirectly cited the type (p. 120), Grant failed to identify that he was changing the rank of the taxon from unranked to tribe (i.e., *stat. nov.* or *trib. nov.*) or providing a new combination (transferring Gilieae from Convolvaceae to Polemoniaceae, i.e., *comb. nov.*), as required by the 1959 Code. Unlike an orthographic error, the rank of a taxon cannot be changed as a correction; the taxon clearly must be transferred in rank, or redescribed at the tribal rank. Rather than continue the confusion involving the application of Reichenbach's Gruppe Gilieae, we describe this tribe anew.

Tribe Gilieae, as here circumscribed, differs considerably in generic inclusion from that of Grant (1959, 1998a).

ALLOPHYLLUM A. D. Grant & V. E. Grant, *El Aliso* 3: 98, 99, 1955.

Annual herbs, erect to spreading, simple or divaricately branched, glandular. Leaves often forming a basal rosette, alternate, entire to once or twice pinnatifid, upper cauline leaves nearly palmate, lobes linear to narrowly oblanceolate, the tip not acute or mucronate. Flowers sessile to long pedicellate, somewhat congested or open inflorescences. Calyx tube with narrow hyaline intervals alternating with herbaceous costae, the lobes equal in length, not acute or mucronate. Corolla funnelliform, radially to bilaterally symmetric. Stamens equally or unequally inserted in the distal corolla tube, the filaments unequal or nearly equal in length; pollen pantoporate, with peritectate-perforate exine and spinule-like processes. Seeds one to three per locule, producing copious mucilage (i.e., spiracles)

when wetted.  $N = 8, 9$ . Six species. Type: *Allophyllum divaricatum* (Nutt.) A. D. Grant & V. E. Grant.

ALLOPHYLLUM DIVARICATUM (Nutt.) A. D. Grant & V. E. Grant, *El Aliso* 3: 101, 1955.

ALLOPHYLLUM GILIOIDES (Benth.) A. D. Grant & V. E. Grant, *El Aliso* 3: 105, 1955.

ALLOPHYLLUM VIOLACEUM (A. Heller) A. D. Grant & V. E. Grant, *El Aliso* 3: 106, 1955.

ALLOPHYLLUM GLUTINOSUM (Benth.) A. D. Grant & V. E. Grant, *El Aliso* 3: 104, 1955.

ALLOPHYLLUM INTEGRIFOLIUM (Brand) A. D. Grant & V. E. Grant, *El Aliso* 3: 102, 1955.

Cronquist (1984: 132) was "not convinced . . . that *Allophyllum* is actually more closely related to *Colomia* than to *Gilia*," and did "not see how it can reasonably be extracted from the remainder of the genus *Gilia*." Comparative DNA sequence data (Johnson et al. 1996, Porter 1996), however, strongly support the morphological evidence, cited by Grant and Grant (1955), providing additional support for the segregation of *Allophyllum*. As circumscribed here, *Allophyllum* does not include *Lathrocasis tenerrima* (for specific reasons, see below) as suggested by Grant (1998b); however, we include a previously undescribed species from southern Baja California, Mexico:

***Allophyllum nemophilophyllum*** J. M. Porter & L. A. Johnson, sp. nov.

Plantae annuae, glandulosae. Effusa ramosissima, humilis. Foliis lyrato-pinnatifidis alternis. Floribus laxe paniculatis, 2–5.5 mm longis, campanulatis; pedicellis tenuibus divaricatis, 11–33 mm longis; capsula subglobosa; ovarii loculi 1–2 ovulati. Semina palidae brunnea ovoidea, sub aqua dense mucilaginosae. *Typus*: R. Moran 8056.

Type.—Mexico. Baja California: Occasional in the shade of rocks, near San Juan Mine, Sierra San Borja, near 28°43'N, 113°38'W, elevation ca. 1200 m, 26 March 1960, R. Moran 8056 (holotype: RSA; isotypes: CAS, SD)

Delicate, erect to decumbent, annual herb, generally with a single stem, 2.5–20.0 cm tall, sparsely glandular villous; leaves (1)2.0–3.5 cm long, not forming a rosette, cauline, (simple) pinnately to usually bipinnately lobed with 3–7 segments, the lobes generally deeply toothed or lobed, ultimate segments 1–3 mm wide; inflorescence open sympodial, 1–2 flowers above the subtending bract, pedicels long dimorphic, (6)11–33 mm long in fruit; calyx 1.8–5.0 mm long in flower, 3.0–5.5 mm long in fruit, the lobes 1–4 mm long the hyaline portion equal in width with costae in flower and broader than costae in fruit; corolla white to pale blue, 2.0–5.5 mm long, the lobes 1.0–3.0 mm long, radially symmetric; stamens equally or subequally inserted on the upper tube, ca 0.5–1.0 mm long, anthers included to slightly exerted; capsule 3.0–4.0 mm, three-lobed, nearly globose, 1–2 seeds per locule,



seeds 1.3–2.0 mm long, rounded on one side, pale brown.

This species is endemic to moist pockets of rocky, granitic slopes, mostly in the shade of larger rocks, 1000–2000 m., in the Sierra San Borja and Sierra la Asamblea, flowering March through April.

*Representative specimens*.—MEXICO. Baja California. Eastern end of Sierra San Luis, 26–30 mi N Punta Prieta 3000–3600 ft. 1 April 1950, H. Gentry & F. Cech 8909; Sierra San Borja, near San Juan Mine, 1200 m, 26 March 1960, R Moran 8056.

Restricted to desert mountains of the Vizciano phase of the Sonoran Desert, *Allophyllum nemophilophyllum* is ecologically unique in the genus: it is the only true subtropical, desert species. Morphologically it differs from all other species of *Allophyllum* in the exceptionally long pedicels (11–33 mm long). The small, white, radially symmetric flowers also serve to distinguish this species from *A. glutinosum* (with bilaterally symmetric, blue-violet flowers) and *A. gilioides* (with radially symmetric, dark blue-violet flowers), the only other representatives of this genus in Baja California, Mexico. As the specific epithet suggests, the lower cauline leaves are similar in morphology to some desert species of *Nemophila* (Hydrophyllaceae).

COLLOMIA Nutt., *Gen. Amer.* v. 1 126, 1818.

Annual or perennial herbs, erect to spreading, simple or divaricately branched, hairy or glandular. Leaves generally not forming a basal rosette, alternate, simple, entire or serrate to once pinnatifid, upper cauline leaves sessile. Flowers in terminal head-like inflorescences, rarely 1–3 in axils of leaves. Calyx tube with narrow, obscure hyaline intervals alternating with herbaceous portion, the lobes equal or unequal in length, sinuses pleated, calyx enlarging in fruit. Corolla funnelform to salverform, radially symmetric. Stamens equally or unequally inserted in the distal corolla tube, the filaments unequal or nearly equal in length; pollen zonocolporate or pantoporate, with striate, striate-reticulate, or reticulate exine. Seeds mostly one per locule (to three in two species), producing copious mucilage (i.e., spiricles) when wetted.  $N = 8$ . Fifteen species. Type: *Collomia linearis* Nutt.

COLLOMIA BIFLORA (Ruiz & Pav.) Brand, *Bot. Jahrb. Syst.* 36: 72, 1905.

COLLOMIA CAVANILLESII Hook. & Arn., *Bot. Beechey Voy.*, p.34, 1839.

COLLOMIA DEBILIS (S. Watson) Greene, *Pittonia* 1: 127, 1887.

COLLOMIA DIVERSIFOLIA Greene, *Pittonia* 1: 128, 1887.

COLLOMIA GRANDIFLORA Douglas ex Lindl., *Bot. Reg.* 14: sub. t. 1174, 1828.

COLLOMIA HETEROPHYLLA Douglas ex Hook., *Bot. Mag.* 56: t. 2895, 1829.

COLLOMIA LARSENII (A. Gray) Payson, *Univ. Wyo. Publ. Bot.* 1: 85, 1924.

COLLOMIA LINEARIS Nutt, *Gen. Amer.* v.1, p.126, 1818.

COLLOMIA MACROCALYX Leiberg ex Brand, *Feddes Repert. Spec. Nov. Regni Veg.* 17: 317 1921.

COLLOMIA MAZAMA Coville, *Proc. Biol. Soc. Wash.* 11: 35, 36, pl. 1, 1897.

COLLOMIA RAWSONIANA Greene, *Pittonia* 1: 221, 1888.

COLLOMIA RENACTA Joyal, *Brittonia* 38: 243, fig. 1, 1986.

COLLOMIA TENELLA A. Gray, *Proc. Amer. Acad. Arts* 8: 259, 1870.

COLLOMIA TINCTORA Kellogg, *Proc. Calif. Acad. Sci.* 3: 17, fig. 2, 1868.

COLLOMIA TRACYI H. Mason, *Madroño* 9: 254, 1948.

*Collomia* is often characterized in the literature as possessing an entirely herbaceous calyx. However, the accrescent calyces in *Collomia*, which are easily distinguished from all other genera in this family, are composed of wide, rhombic, herbaceous lobes connected  $\pm$  mid-length by a narrow yet identifiable membrane that folds outward at the sinus to form a pitcherlike projection. This arrangement gives the calyx a distinctive replicate or distended appearance. Most, if not all, species in this genus also possess explosively dehiscent capsules: in species with one seed per locule, each valve folds backwards lengthwise along the septae whereas in species with three seeds, each valve folds more or less horizontally between the seeds. The inclusion of *Collomia heterophylla* is supported equivocally by molecular cladistic analyses (Johnson and Porter unpubl.), but it is inferred to be part of a monophyletic *Collomia*, based on morphological and palynological evidence (Chuang et al. 1978).

GILIA Ruiz & Pav., *Fl. peruv. prodr.*, p.25, t. 4, 1794.

Annual herbs, glandular, variously hairy, or almost glabrous, generally with a basal rosette of leaves. Leaves highly dissected, 1–3 pinnatifid, to dentate or rarely entire, the ultimate segments sometimes toothed; cauline leaves alternate, becoming reduced above, often greatly so. Inflorescence cymose, the flowers in dense heads, glomerate, loose, or solitary. Calyx tube with hyaline intervals alternating with the herbaceous costae, the lobes with hyaline margins, acute to mucronate. Corolla funnelform to salverform, large and showy to very small and inconspicuous, the tube narrow often with a characteristic flared region (“throat”), lobes long or short, spreading. Stamens mostly equally inserted near the sinuses of the corolla lobes, the filaments equal or unequal in length; pollen zonocolporate, apertures rarely anomotreme, with striate or rugulate exine. Seeds many per locule, producing copious mucilage (i.e., spiricles) when wetted; each outer cell wall of the seed coat smooth when shed.  $N = 9, 18, 36$ . Thirty-nine species. Type: *Gilia laciniata* Ruiz & Pav.

GILIA ACHILLEIFOLIA Benth., *Edward's Bot. Reg.* 19: sub. t. 1622, 1833.

GILIA ACHILLEIFOLIA Benth. subsp. MULTICAULIS (Benth.) V. E. Grant & A. D. Grant, *El Aliso* 3: 298, 1956.

- GILIA ALIQUANTA A. D. Grant & V. E. Grant, *El Aliso* 3: 241, 242, fig. 10, 1956.
- GILIA ALIQUANTA A. D. Grant & V. E. Grant subsp. BREVILOBA A. D. Grant & V. E. Grant, *El Aliso* 3: 243, 1956.
- GILIA ALPINA (Wedd.) Brand, *Pflanzenr.* IV 250, p.107, 1907.
- GILIA ANGELENSIS V. E. Grant, *El Aliso* 2: 387, 388, figs. 1-4, 1952.
- GILIA AUSTRALIS (A. D. Grant & V. E. Grant) A. D. Grant & V. E. Grant, *Aliso* 4: 438, 1960.
- GILIA BRECCIARUM M. E. Jones, *Contr. W. Bot.* 12: 54, 1908.
- GILIA BRECCIARUM M. E. Jones subsp. NEGLECTA A. D. Grant & V. E. Grant, *El Aliso* 3: 283, fig. 21c, 1956.
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- GILIA FLAVOCINCTA A. Nelson, *Amer. J. Bot.* 21: 577, 1934.
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- GILIA LATIFLORA (A. Gray) A. Gray subsp. DAVYI (Milliken) A. D. Grant & V. E. Grant, *El Aliso* 3: 273, 1956.
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- GILIA OCHROLEUCA M. E. Jones subsp. VIVIDA (A. D. Grant & V. E. Grant) A. D. Grant & V. E. Grant, *Aliso* 4: 438, 1960.
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- GILIA TENUIFLORA Benth., *Edward's Bot. Reg.* 19: sub. t. 1622, 1833.
- GILIA TENUIFLORA Benth. subsp. AMPLIFUCALIS A. D. Grant & V. E. Grant, *El Aliso* 3: 246, 247, fig. 11b, 1956.
- GILIA TENUIFLORA Benth. subsp. ARENARIA (Benth.) A. D. Grant & V. E. Grant, *El Aliso* 3: 246, 1956.
- GILIA TENUIFLORA Benth. subsp. HOFFMANNII (Eastw.) A. D. Grant & V. E. Grant, *El Aliso* 3: 247, 1956.
- GILIA TRANSMONTANA (H. Mason & A. D. Grant) A. D. Grant & V. E. Grant, *El Aliso* 3: 266, 1956.
- GILIA TRICOLOR Benth., *Edward's Bot. Reg.* 19: t. 1622, 1833.
- GILIA TRICOLOR Benth. subsp. DIFFUSA (Congdon) H. Mason & A. D. Grant, *Madroño* 9: 209, 1948.
- GILIA TWEEDYI Rydb., *Bull. Torrey Bot. Club* 31: 634, 1904.
- GILIA VALDIVIENSIS Griseb., *Syst. Bemerk.* v.6, p.131, 1854.
- GILIA YORKII Shevock & A. G. Day, *Madroño* 45: 137, 139, Fig 1 A-G, 1999.

Our generic circumscription of *Gilia* differs substantially from that of Grant (1959; 1998a, b) and Day (1993b). Portions of *Gilia* sensu Grant are here placed in Tribe Loeseliaceae (i.e., *Aliciella* and *Giliastrum*), while others remain in Tribe Gilieae, but not within the genus *Gilia* (i.e., *Saltugilia*, *Lathrocasis*, and several *Navarretia*). With the removal of these disparate elements, *Gilia* is more cohesive morphologically and is strongly inferred to be monophyletic based on molecular data (Johnson et al. 1995; Johnson et al. 1996; Porter 1996; Johnson and Porter unpubl.). *Gilia*, as here circumscribed, includes predominantly rosette-forming annuals with cauline leaves that become reduced in size, but are lobed or toothed. Two morphological groups within *Gilia*, the cobwebby gilies and the leafy-stemmed gilies (Grant 1950, 1952a, b, 1954a, b, c; A. Grant and V. Grant 1956) are supported as monophyletic by molecular data. Two additional species with historically less certain placement (compare Grant and Grant 1954; V. Grant and A. Grant 1956; Grant 1959), *G. scopulorum* and *G. stellata*, are related closely to these larger groups and are retained in *Gilia*. *Gilia yorkii*, recently described as a member

of section *Saltugilia* (Shevock and Day 1999), is also retained in *Gilia*. In our estimation, this species belongs with the leafy-stemmed gilies with close affinities to *Gilia capitata*, but simply lacking a capitate inflorescence. The seeds of all gilies produce copious mucilage (i.e., spiricles) when wetted, and the outer wall of the testa is shed as an areolate, but not verrucate, sheet (with areoles defined by cell boundaries). Fine, tangled, white arachnoid-tomentum is also shared by most species, at least in the leaf axils, but often on leaves and in the inflorescence.

### **Lathrocasis** L. A. Johnson, gen. nov.

Plantae annuae, humiles, glandulis stipitatis ubique. Folia alterni, anguste lanceolati ad ensiformes, integra vel inferiora interdum lobati. Ramificatio sympodialis, effuse ramosissimus; ramis ramulisque filiformibus; pedicellis tenuibus divaricatis; inflorescentia laxo. Flores minuti; corolla infundibuliformis, calyx campanulatus. Pollinis granum anamocolporatum ad pantocolporatum vel raro bi-zonocolporatum, exino striato-reticulato. Capsula subglobosa, valvis effusis dehiscentiis; loculis 1-semenalis. Semina castanea, ovoidea, testa verrucata, sub aqua dense mucilaginoso. Ab *Gilia* Ruiz et Pavón in testa verrucosa, trichomatibus stipitati-glandularibus uniformiter, pedicellis retrorsis, et loculis uniovulatis differt. Typus: *Lathrocasis tenerrima* (A. Gray) L. A. Johnson

Annual herbs, densely stipitate glandular on stems and pedicels, sparsely glandular on leaves and calyces. Leaves alternate, narrowly lanceolate, entire, or infrequently with one or two linear to falcate lobes; basal rosette loose, sparse, or lacking. Upper leaves reduced, linear to ensiform. Branching sympodial, effuse, stems terminating in solitary flowers; pedicels filiform, divergent or retrorse. Flowers minute, usually <3.5 mm long; calyx campanulate, the herbaceous lobes equal, membrane margined, and fused to two-thirds their length; corolla funnellform from a short tube, barely to twice exceeding the calyx. Pollen anomotreme to pantotreme, rarely bizonotreme, apertures colporate, exine striate-reticulate. Seeds chestnut brown, ovoid, one per locule, producing copious mucilage (i.e., spiricles) when wetted; seed coat verrucate.  $N = 18$ . One species. Type: *Lathrocasis tenerrima* (A. Gray) L. A. Johnson

***Lathrocasis tenerrima*** (A. Gray) L. A. Johnson, comb. nov.

Basionym: *Gilia tenerrima* A. Gray, *Proc. Amer. Acad. Arts* 8: 277. 1870.

Inconspicuous and largely ignored, this species has recently been subjected to several generic realignments. Affinities with *Allophyllum* were suggested based largely on inaccurate interpretation of pollen morphology (Grant 1998b). Affinities with *Tintinabulum* (Grant and Day 1998) are similarly based on inaccurate characterization of trichome and floral characteristics (Johnson and Weese 2000). *Lathrocasis* possesses a distinct suite of morphological features that, considered as a whole, distinguish this taxon at

the generic level. This suite of characters includes the mostly entire, nonmucronate leaves, effuse branching with diverging to retrorse and threadlike pedicels, uniformity of short stipitate glands throughout, uniovulate locules, spiriferous seeds with verrucate seedcoats, minute funnellform flowers with simple vasculature, and stamens equally inserted approximately mid-tube. DNA sequence data (chloroplast *matK*, *trnL-F*, and nuclear ITS genes) of multiple populations of *L. tenerrima* corroborate this distinctive morphological characterization and show *Lathrocasis* well separated at the nucleotide sequence level from its nearest relatives in Gilieae (Johnson and Weese 2000).

*Lathrocasis* derives its name from the combination of the Greek “lathro-” (hidden, secret) and “kasis” (sister). True to its name, it is not clear presently whether *Lathrocasis* is sister to *Gilia*, a group composed of *Allophyllum*, *Collomia*, and *Navarretia*, or both of these groups combined (Johnson and Weese 2000).

NAVARRERIA Ruiz & Pav., *Fl. peruv. prodr.*, p.20, 1794.

Annual herbs, erect or prostrate, simple or divaricately branched, variously hairy, glandular or glabrous. Leaves generally not forming a basal rosette, alternate or lower most opposite, entire to once or twice pinnatifid; upper cauline leaves usually bracteate, sometimes palmately lobed to divided, acerose or spine-tipped. Flowers usually sessile and congested in a head-like inflorescences, but pedicellate and in pairs in *Navarretia capillaris*, *N. leptalea*, and *N. sinistra*. Calyx tube with hyaline intervals alternating with herbaceous costae,  $\pm$  unequal or rarely equal in length, mucronate to acerose. Corolla funnellform to salverform, lobes 4–5, spreading. Stamens mostly equally inserted near the sinuses of the corolla lobes, the filaments mostly equal in length; pollen pantocolporate or pantoporate, with striate, striate-reticulate, reticulate or pertectate-perforate exine, sometimes with spinule-like processes. Seeds one to many per locule, producing copious mucilage (i.e., spiricles) when wetted.  $N = 9$ . Thirty-one species. Type: *Navarretia involucrata* Ruiz & Pav.

NAVARRERIA ATRACTYLOIDES (Benth.) Hook. & Arn., *Bot. Beechey Voy.*, p.368, 1839.

NAVARRERIA BREWERI (A. Gray) Greene, *Pittonia* 1: 137, 1887.

NAVARRERIA CAPILLARIS (Kellogg) Kuntze, *Revis. gen. pl.* v.2, p.433, 1891.

NAVARRERIA COTULIFOLIA (Benth.) Hook. & Arn., *Bot. Beechey Voy.*, p.368, 1839.

NAVARRERIA DIVARICATA (A. Gray) Greene, *Pittonia* 1: 136, 1887.

NAVARRERIA DIVARICATA (A. Gray) Greene subsp. VIVIDOR (Jeps. & V. L. Bailey) H. Mason, *Abrams, Ill. fl. Pacific States* v.3, p.449, 1951.

NAVARRERIA ERIOCEPHALA H. Mason, *Madroño* 8: 196, 1946.

NAVARRERIA FILICAULIS (A. Gray) Greene, *Pittonia* 1: 134, 1887.

- NAVARRETIA FOSSALIS Moran, *Madroño* 24: 155, 1977.
- NAVARRETIA HAMATA Greene, *Pittonia* 1: 139, 1887.
- NAVARRETIA HAMATA Greene subsp. LEPTANTHA (Greene) H. Mason, *Abrams, Ill. fl. Pacific States* v.3, p.450, 1951.
- NAVARRETIA HAMATA Greene subsp. PARVILOBA A. G. Day, *Novon* 3: 336, 1993.
- NAVARRETIA HETERANDRA H. Mason, *Madroño* 8: 197, 1946.
- NAVARRETIA HETERODOXA (Greene) Greene, *Pittonia* 1: 134, 1887.
- NAVARRETIA INTERTEXTA (Benth.) Hook., *Fl. bor.-amer.* v.2, p.75, 1838.
- NAVARRETIA INTERTEXTA (Benth.) Hook. subsp. PROPINQUA (Suksd.) A. G. Day, *Novon* 3: 336, 1993.
- NAVARRETIA INVOLUCRATA Ruiz & Pav., *Syst. veg. fl. peruv. chil.*, p.43, 1798.
- NAVARRETIA JAREDII Eastw., *Zöe*, 5: 89, 1900.
- NAVARRETIA JEPSONII V. L. Bailey ex Jeps., *Fl. Calif.* v.3, p.154, 1943.
- Navarretia leptalea** (A. Gray) L. A. Johnson, comb. nov.  
Basionym: *Collomia leptalea* A. Gray, *Proc. Amer. Acad. Arts* 8: 261, 1870.
- Navarretia leptalea** subsp. **bicolor** (H. Mason & A. D. Grant) L. A. Johnson, comb. nov.  
Basionym: *Gilia leptalea* subsp. *bicolor* H. Mason & A. D. Grant, *Madroño* 9: 220, 1948.
- NAVARRETIA LEUCOCEPHALA Benth., *Pl. hartw.*, p.324, 1840.
- NAVARRETIA LEUCOCEPHALA Benth. subsp. BAKERI (H. Mason) A. G. Day, *Novon* 3: 337, 1993.
- NAVARRETIA LEUCOCEPHALA Benth. subsp. MINIMA (Nutt.) A. G. Day, *Novon* 3: 337, 1993.
- NAVARRETIA LEUCOCEPHALA Benth. subsp. PAUCIFLORA (H. Mason) A. G. Day, *Novon* 3: 337, 1993.
- NAVARRETIA LEUCOCEPHALA Benth. subsp. PLIEANTHA (H. Mason) A. G. Day, *Novon* 3: 337, 1993.
- NAVARRETIA MELLITA Greene, *Pittonia* 1: 134, 1887.
- NAVARRETIA MYERSII P. S. Allen & A. G. Day, *Novon* 3: 337, 1993.
- NAVARRETIA MYERSII P. S. Allen & A. G. Day subsp. DEMINUTA A. G. Day, *Madroño* 42: 34, 1995.
- NAVARRETIA NIGELLIFORMIS Greene, *Pittonia* 1: 132, 1887.
- NAVARRETIA NIGELLIFORMIS Greene subsp. RADIANS (J. T. Howell) A. G. Day, *Novon* 3: 339, 1993.
- NAVARRETIA PENINSULARIS Greene, *Pittonia* 1: 136, 1887.
- NAVARRETIA PROLIFERA Greene, *Pittonia* 1: 135, 1887.
- NAVARRETIA PROLIFERA Greene subsp. LUTEA (Brand) H. Mason, *Abrams, Ill. fl. Pacific States* v.3, p.448, 1951.
- NAVARRETIA PROSTRATA (A. Gray) Greene, *Pittonia* 1: 130, 1887.
- NAVARRETIA PUBESCENS (Benth.) Hook. & Arn., *Bot. Beechey Voy.*, p.368, 1839.
- NAVARRETIA ROSULATA Brand, *Pflanzenr.* IV 250, p.154, 1907.
- NAVARRETIA SETILOBA Coville, *Contr. U. S. Nat. Herb.* 4: 153, 1893.
- Navarretia sinistra** (M. E. Jones) L. A. Johnson, comb. nov.  
Basionym: *Gilia sinistra* M. E. Jones [as *sinister*], *Contr. W. Bot.* 10: 57, 1902.
- Navarretia sinistra** (M. E. Jones) L. A. Johnson subsp. **pinnatisecta** (H. Mason & A. D. Grant) L. A. Johnson, comb. nov.  
Basionym: *Gilia leptalea* subsp. *pinnatisecta* H. Mason & A. D. Grant, *Madroño* 9: 220, 1948.
- NAVARRETIA SQUARROSA (Eschsch.) Hook. & Arn., *Bot. Beechey Voy.*, p.368, 1839.
- NAVARRETIA SUBULIGERA Greene, *Pittonia* 1: 137, 1887.
- NAVARRETIA TAGETINA Greene, *Pittonia* 1: 137, 1887.
- NAVARRETIA VISCIDULA Benth., *Pl. hartw.*, p.324, 1840.

*Navarretia* historically has been recognized based on its spinescent-bracted capitate inflorescences and calyx with lobes of unequal length. Though named

concomitantly with *Gilia* (Ruiz and Pavon 1794), various authors have considered *Navarretia* and *Gilia* either congeneric (Gray 1870, 1886; Bentham and Hooker 1876; Baillon 1891), or at least closely related (Don 1838; Grant 1959; Cronquist 1984). Brand (1907) treated *Navarretia* separate from *Gilia*, but included species now recognized as members of *Eriastrum* within *Navarretia*. Brand's classification was later contested (e.g., Craig 1934; Mason 1945). Relationships between *Navarretia* and other genera never were explored fully by any of these authors.

Phylogenetic analyses of chloroplast *matK* (Johnson and Soltis 1995; Johnson et al. 1996) and nuclear ITS (Porter 1996; Spencer and Porter 1997) sequences provide strong evidence that *Navarretia* is closely allied with *Collomia*, *Allophyllum*, and three species formerly recognized in *Gilia* section *Kelloggia* (Day 1993a). *Navarretia* is here circumscribed to include these latter species (i.e., *N. capillaris*, *N. leptalea*, and *N. sinistra*). The recent placement of these three species in *Allophyllum* (Grant and Day 1998) is understandable given the close affinities of *Allophyllum* to *Navarretia* and *Collomia*. These three genera possess distinct gross morphologies, as do the "kelloggoid *Navarretias*". Even so, examination of the morphological traits, considered to be important indicators of relationship (Grant and Day 1998), provide support for placement of "kelloggoid *Navarretias*" in *Navarretia* rather than *Allophyllum* (Porter and Johnson unpubl.).

*Navarretia capillaris*, *N. leptalea*, and *N. sinistra* are distinguished from other *Navarretia* on the basis of architecture and traditional "key characters" (i.e., they lack a dense, spinescent inflorescence and possess calyx lobes of equal length). Their inclusion adds heterogeneity at the gross-morphological level to an otherwise cohesive group. Nevertheless, morphological and molecular data indicate these species are phylogenetically removed from *Gilia* and near *Navarretia*. In determining how best to treat *N. capillaris*, *N. leptalea*, and *N. sinistra* taxonomically, we at first considered erecting a new genus. Isozyme and distribution-wide population sampling of both chloroplast and nuclear genes, however, indicate these three species do not form an exclusive monophyletic group (Johnson, unpubl.). Ancient hybridization may be involved in the origin of at least some taxa. If so, their exact parentage has been obscured by time; nonetheless, ancestors of *Navarretia*, but not *Collomia* or *Allophyllum*, appear implicated most strongly (Johnson, unpubl.). By including *N. capillaris*, *N. leptalea*, and *N. sinistra* in *Navarretia*, we provide a treatment that emphasizes monophyly in the classification of these species. Any attempt to classify *N. capillaris*, *N. leptalea*, and *N. sinistra* in any single genus exclusive of *Navarretia* would make the alternative genus polyphyletic, and *Navarretia* paraphyletic.



Examination of fine-scale morphological features yields support for this taxonomy despite gross morphological appearances. *Navarretia capillaris*, *N. leptalea*, and *N. sinistra* possess linear cotyledons as do most other *Navarretia* (but not *Allophyllum* or *Collomia*). They are also most similar to other *Navarretia* in seed morphology and seed germination requirements (involving long periods of moist chilling; Johnson pers. observ.). Additionally, *N. capillaris*, *N. leptalea*, and *N. sinistra* possess pantoporate pollen grains, a type ubiquitous in *Navarretia*, *Allophyllum*, and present in some *Collomia*, but unknown in *Gilia*. Exine sculpting, however, differs greatly among these species (Spencer and Porter 1997; Johnson unpubl.). *Navarretia capillaris* and *N. leptalea* have a striate-reticulate exine also found in *N. hamata* and *N. prolifera* (striate-reticulate type II of Spencer and Porter 1997); however, *N. leptalea* subsp. *bicolor* has variable pollen, some with the striate-reticulate exine similar to that of *N. breweri* (striate-reticulate type I of Spencer and Porter 1997). This contrasts with the rugulose, superficially pertectate pollen of *N. sinistra*, which in some ways is similar to the pollen of *N. leucocephala*, *N. plieantha*, *N. prostrata*, *N. myersii*, and *N. fossalis*, as well as *Allophyllum*. This exine diversity further supports the hypothesis that *N. capillaris* and *N. leptalea* form a lineage apart from *N. sinistra* (Johnson et al., 1994; Johnson 1996; unpubl.). Additional comparative surveys of micromorphological characters and two additional nuclear genes are underway to provide further insights into the history of these species (Johnson unpubl.).

**Saltugilia** (V. E. Grant) L. A. Johnson, gen. et stat. nov.

*Gilia* sect. *Saltugilia* V. E. Grant, *El Aliso* 3: 84, 1954, in part.

Plantae annuae. Folia basi caulis rosulata, pleraque bipinnatifida; folia caulini foliis rosularibus similibus vel deminutis, subulatis. Trichomata foliorum basium et caulis inferni uniseriata longe angustatus ferens glandula unicellularis. Trichomata inflorescentiae brevistipitata ferens glandis multicellularis. Inflorescentia cymosa, laxa. Corolla infundibuliformis, corolla fauce 5-maculatus flava. Stamina filamentis inaequalibus ad subequalibus. Pollinis granum caerulei, zonocolporatum, exino striato-reticulato. Seminibus pallidi brunnei, angulosi; testa verrucata, sub aqua dense mucilaginoso. Ab *Gilia* Ruiz et Pavón in testa verrucosa, et trichomatibus in pedicellis glandularibus stipitati-brevissimis multicellularis uniformiter et trichomatibus in foliis uniseriatis longibus glandibus minutis unicellularis differt. Typus: *Saltugilia grinnellii* (Brand) L. A. Johnson

Erect annual herbs; stems typically 1, much branched above, glabrous, glaucous, or glandular, mostly 15–100 cm in height. Leaves principally in a basal rosette, (1-)2(-3) pinnatifid, reduced upwards and ultimately subulate bracteate. Trichomes on lower leaves and stem translucent, tapering, terminating in a single, minute, globose, glandular cell (gland obscure;

appearing chain-like villous when dry). Trichomes on upper (and lower in some) stems, pedicels, and calyces short stalked and terminating in a flat-topped multicellular gland. Inflorescence cymose, loose, flowers borne singly or paired on unequal to subequal pedicels. Flowers mostly showy. Calyx lobes equal, the herbaceous costae narrower than and united above mid-length by a hyaline membrane. Corolla radially symmetric, funnellform, yellow spotted on throat. Stamens unequal to subequal, the shortest one often borne at right angles to the corolla wall. Pollen blue, zonocolporate, with striate exine. Seeds light tan, angular, many per locule, producing copious mucilage (i.e., spiracles) when wetted; seed coat verrucate. *N* = 9. Three species. Type: *Saltugilia grinnellii* (Brand) L. A. Johnson

***Saltugilia grinnellii*** (Brand) L. A. Johnson, comb. nov.

Basionym: *Gilia grinnellii* Brand, *Pflanzenr.* IV 250, p. 101, 1907. Synonym: *Gilia splendens* Dougl. of authors, *nomen nudum*.

***Saltugilia grinnellii*** (Brand) L. A. Johnson subsp. ***grantii*** (Brand) L. A. Johnson, comb. nov.

Basionym: *Gilia collina* Eastw. var. *grantii* Brand, *Pflanzenr.* IV 250, p.101, 1907.

***Saltugilia caruifolia*** (Abrams) L. A. Johnson, comb. nov.

Basionym: *Gilia caruifolia* Abrams, *Bull. Torrey Bot. Club* 32: 540, 1905.

***Saltugilia australis*** (H. Mason & A. D. Grant) L. A. Johnson, comb. nov.

Basionym: *Gilia splendens* subsp. *australis* H. L. Mason & A. D. Grant, *Madroño* 9: 213, 1948.

*Saltugilia* (= woodland *gilia*s) was first accorded nomenclatural status as a section of *Gilia* when Grant (1954c) placed *G. splendens*, *G. caruifolia*, and *G. australis* with *G. leptalea* and *G. capillaris*. A more recent circumscription of this section (Shevock and Day 1998) reflects the inclusion of *G. scopulorum* and *G. stellata* by Grant (1959), the removal of *G. leptalea* and *G. capillaris* by Day (1993a), and the inclusion of *G. yorkii* by Shevok and Day (1998). *Saltugilia grinnellii*, *S. caruifolia*, and *S. australis* are distinguished morphologically from these other taxa, and other *Gilia*, by the combination of leaf, trichome, and seed coat characteristics, despite sharing a similar habit with *Gilia*. This habit, consisting of a typically well-developed basal rosette of leaves subtending an erect, much branched but usually solitary stem bearing reduced leaves, is found elsewhere in Polemoniaceae, notably in *Aliciella* and *Ipomopsis sonora* (tribe Loeseliaceae) and, in a reduced form, in *Linanthus* (e.g., *L. campanulata* of tribe Phlocideae). Hybridization studies indicate *Saltugilia* is isolated reproductively from *Gilia* (Grant and Grant 1954; Johnson pers. observ.). Chloroplast and nuclear DNA sequences sampled widely from populations across the geographic range of these species also strongly support the removal of *Saltugilia* from *Gilia* (Johnson, 1996; Johnson et al., 1996;

Weese and Johnson unpubl.). *Saltugilia* is sister to a monophyletic group encompassing the remainder of Gilieae. The relationship between morphological and molecular variation at the population level among species of *Saltugilia* is being explored (Weese and Johnson unpubl.).

LOESELIEAE J. M. Porter & L. A. Johnson  
*Aliso* 17: 84, 1998.

Annual, biennial, and perennial herbs, or shrubs. Leaves alternate, rarely opposite (*Loeselia*), leafy throughout, or with leaves much reduced in the inflorescence of some annual species. Corollas bilaterally or radially symmetric, rotate, campanulate, funnel-form, or salverform. Ovary frequently glandular distally. Type: *Loeselia* L. Synonymy includes Loeseliae V. E. Grant, *Amer. J. Bot.* 85: 744. 1998.

*Phylogenetic delineation.*—The least incorporative monophyletic group of species that includes *Aliciella triodon*, *Dayia scabra*, *Eriastrum densifolium*, *Giliastrum rigidulum*, *Ipomopsis rubra*, and *Loeselia ciliata*.

*Membership.*—*Aliciella*, *Bryantiella*, *Dayia*, *Eriastrum*, *Giliastrum*, *Ipomopsis*, *Langloisia*, *Loeselia*, *Loeseliastrum*, and *Microgilia* (10 genera, 95 species).

Tribe Loeseliae, although diverse morphologically, has consistent support for monophyly from comparative DNA studies (Johnson et al. 1996; Porter 1996; Porter and Johnson unpubl.). Several notable evolutionary trends appear to be repeated in Loeseliae, including perennial habit, woody species, bilateral corollas, and aneuploid reduction (in *Aliciella*, *Giliastrum*, and the *Eriastrum*, *Ipomopsis*, *Langloisia*, *Loeseliastrum*, *Microgilia* group).

ALICIELLA Brand, *Helios* 22: 78, 1905.

Taprooted perennials, biennials, or annuals, mostly glandular pubescent. Leaves alternate, entire, or once- or twice-pinnatifid, leaf tips cuspidate, mucronate or aristate, often forming a basal rosette, cauline leaves reduced either  $\pm$  gradually or abruptly in size, but ultimately diminished. Inflorescence cymose, open. Calyx composed of herbaceous costae and hyaline intercostal regions, glandular. Corolla salverform to funnel-form, concolored, bicolored or tricolored, glandular or glabrous externally, glabrous internally, corolla veins often anastomosing at the base of the lobes and rarely also in the lobe,  $\pm$  radially symmetric. Stamens equally or unequally inserted in the distal corolla tube or in the sinuses of the corolla lobes, the filaments unequal or equal in length. Pollen zonocolporate and either striate-reticulate or reticulate, or zonoporate and pertectate, blue, yellow, or cream. Ovary glabrous, seeds not (or only slightly) becoming mucilaginous

when wetted.  $N = 8, 9, 16, 17, 18, 25$ . Twenty-one species. Type: *Aliciella triodon* Brand.

- ALICIELLA CESPITOSA (A. Gray) J. M. Porter, *Aliso* 17: 34, 1998.  
ALICIELLA FORMOSA (Greene ex Brand) J. M. Porter, *Aliso* 17: 33, 1998.  
ALICIELLA HAYDENII (A. Gray) J. M. Porter, *Aliso* 17: 31, 1998.  
ALICIELLA HAYDENII subsp. CRANDALLII (Rydb.) J. M. Porter, *Aliso* 17: 32, 1998.  
ALICIELLA HETEROSTYLA (S. Cochrane & A. G. Day) J. M. Porter, *Aliso* 17: 37, 1998.  
ALICIELLA HUMILLIMA (Brand) J. M. Porter, *Aliso* 17: 41, 1998.  
ALICIELLA HUTCHINSIFOLIA (Rydb.) J. M. Porter, *Aliso* 17: 35, 1998.  
ALICIELLA LATIFOLIA (S. Watson) J. M. Porter, *Aliso* 17: 43, 1998.  
ALICIELLA LATIFOLIA (S. Watson) J. M. Porter subsp. IMPERIALIS (S. L. Welsh) J. M. Porter, *Aliso* 17: 44, 1998.  
ALICIELLA LEPTOMERIA (A. Gray) J. M. Porter, *Aliso* 17: 38, 1998.  
ALICIELLA LOTTIAE (A. G. Day) J. M. Porter, *Aliso* 17: 40, 1998.  
ALICIELLA MCVICKERAE (M. E. Jones) J. M. Porter, *Aliso* 17: 28, 1998.  
ALICIELLA MICROMERIA (A. Gray) J. M. Porter, *Aliso* 17: 40, 1998.  
ALICIELLA NYENSIS (Reveal) J. M. Porter, *Aliso* 17: 36, 1998.  
ALICIELLA PENTSTEMONOIDES (M. E. Jones) J. M. Porter, *Aliso* 17: 30, 1998.  
ALICIELLA PINNATIFIDA (A. Gray) J. M. Porter, *Aliso* 17: 27, 1998.  
ALICIELLA RIPLEYI (Barneby) J. M. Porter, *Aliso* 17: 45, 1998.  
ALICIELLA SEDIFOLIA (Brandege) J. M. Porter, *Aliso* 17: 29, 1998.  
ALICIELLA STENOTHYRSA (A. Gray) J. M. Porter, *Aliso* 17: 30, 1998.  
ALICIELLA **subacaulis**(Rydb.) J. M. Porter & L. A. Johnson, comb. nov.  
Basionym: *Gilia subacaulis* Rydb., *Bull. Torrey Bot. Club* 30: 261, 1903.  
ALICIELLA SUBNUDA (A. Gray) J. M. Porter, *Aliso* 17: 33, 1998.  
ALICIELLA TENUIS (F. J. Sm. & Neese) J. M. Porter, *Aliso* 17: 35, 1998.  
ALICIELLA TRIODON (Eastw.) Brand, *Helios* 22: 78, 1905.

Formerly included in *Gilia* (Grant 1959, 1998b), *Aliciella* is more closely related to *Loeselia* and *Ipomopsis* than to *Gilia* (Johnson et al. 1996; Porter 1996), based on DNA sequence data. Morphologically, too, *Aliciella* differs from *Gilia* in chromosome number (most, but not all, species of *Aliciella* are  $N = 8$ ) and seed morphology (seeds do not produce copious mucilage; large seeded species tend to have an irregular wing). However, in spite of its small size, *Aliciella* is diverse morphologically and complicated by hybridization and polyploidy. Some species (e.g., *A. leptomeria* and *A. lottiae*) represent complexes with multiple polyploid origins (Tommerup and Porter 1996). The genus is also varied in pollination mechanisms and breeding systems (including the only verified instance of heterostyly in Polemoniaceae; Cochrane and Day 1994). For the subgeneric and sectional classification of *Aliciella*, see Porter (1998a).

**Bryantiella** J. M. Porter gen. nov.

Planta annua vel perennis, glanduloso-puberula. Caulis erectus, valde ramosus. Folia altera, linearia, integra vel pinnatisecta, segmentis linearibus. Flores solitarii vel ad 2 aggregati, breviter pedicellati. Corolla alba vel violacea, tubo brevi, incluso. Ovarium ovoideum vel subglobosum. Semina sub aqua dense mucilaginoso. Pol-

linis granum zonocolporatum, exino striato. Ab *Giliastrum* (Brand) Rydb. pollinibus albidus ad eburneus et exiniis striatis differt. Typus: *Bryantiella palmeri* (S. Wats.) J. M. Porter.

Plants stout annuals or perennials, 5–60 cm tall, glabrescent, glandular pubescent, or viscid throughout. Leaves narrowly linear, entire or pinnatifid, the lobes narrowly linear, axils sometimes with white hairs; cauline leaves reduced in size, ultimately bract-like. Flowers cymose, solitary or in pairs, pedicels 0.5–3.0 cm long. Calyx campanulate, 5-lobed or 5-cleft; the tube with a scarious region alternating with a green costa (lobe), glandular puberulent. Corolla rotate to campanulate, white, blue, violet, or deep pink, tube shorter than the calyx, lobes obovate to ovate, apiculate or denticulate. Stamens equally inserted low in the tube and included, glabrous; pollen zonocolporate with a striate exine. Ovary glabrous or glandular apically, fruit ovate capsule, longer than calyx; seeds tan to brown, becoming mucilaginous when wetted. Two species. Type: *Bryantiella palmeri* (S. Wats.) J. M. Porter.

***Bryantiella palmeri*** (S. Wats.) J. M. Porter, comb. nov.

Basionym: *Gilia palmeri* S. Wats. *Proc. Amer. Acad. Arts* 24: 61, 1889.

***Bryantiella glutinosa*** (Phil.) J. M. Porter, comb. nov.

Basionym: *Gilia glutinosa* Phil. *Linnaea* 30: 196, 1859.

Although traditionally included within *Gilia*, *Bryantiella* differs from the former in the lack of a persistent basal rosette of leaves and the perennial life history (sometimes persisting only a single year, appearing annual; Gibson 1967; Wiggins 1980). Ecologically, *Bryantiella* also differs from *Gilia*, being adapted to the driest deserts of both North America (San Felipe Desert) and South America (Atacama Desert). Phylogenetic inferences from the gene phylogenies of nr ITS and cp *trnL-F* noncoding regions (Porter et al. unpubl.) unambiguously place the relationships of *Bryantiella* (*B. palmeri*) within Tribe Loeseliaceae, near *Ipomopsis*, and away from *Gilia* s.s.

The two species were included in *Gilia* section *Giliastrum* by Grant (1959, but not 1998b). Unlike *Giliastrum* with yellow pollen, *Bryantiella* has white to cream-colored pollen. Pollen exine morphology of *Bryantiella* also differs from *Giliastrum* (see above) in that both species have striate exines with narrow lirae.

The generic name honors Susanna Bixby Bryant, founder of Rancho Santa Ana Botanic Garden (RSABG) and strong advocate for systematic research of California plants. Through RSABG, Susanna Bixby Bryant has provided both infrastructure and financial support that has contributed immensely to our knowledge of Polemoniaceae.

***Dayia*** J. M. Porter, gen. nov.

Perennes basibus lignosis vel saepiuscule suffrutescentes, erectae, glandulares. Folia alterna interdum subopposita, pinnatifida usque

subpalmata. Inflorescentia dense glandularis-puberulenta, thyrsoida e cymis redactis (1-) 2-floris composita. Corolla glabra, infundibuliformis vel hypocrateriformis, 14.0–22.0 mm longa, caerulea pallida atrolazulina varians. Stamina brevia, in tubo corollae inaequaliter vel aequaliter affixa, inclusa, vel in tubo superiori aequaliter affixa, exserta et declinata. Pollinis granum 5–7 zonocolporatum, exino striato-reticulato. Fructus capsularis leoninus usque aureo-brunneus. Semina 12–46 per loculo, minuta, ca. 1.2 mm longa, testis exterioris ubi madefactis fibrillae copiosae efferentis. Embryo achlorophyllus. Ab *Giliastrum* (Brand) Rydb. pollinibus caeruleis, exiniis striatis-reticulatis, corolla tubo longioribus, et seminibus minutis differt. Typus: *Dayia scabra* (Brandege) J. M. Porter

Erect, glandular, largely herbaceous perennials with woody base, or more frequently sub-shrubs. Leaves alternate to less often sub-opposite, pinnatifid to nearly palmate. Inflorescence densely glandular puberulent, composed of reduced (1-) 2-flowered cymes, forming a thyrsoid inflorescence. Corolla glabrous, funnellform to salverform, 14.0–22.0 mm long, pale to deep blue, with a distinct yellow or pale white center. Stamens subequally inserted on the corolla tube and included or equally inserted near the sinuses of the corolla lobes, declinate and exserted; pollen 5–7 zonocolporate with striatoreticulate exine. Fruit a tan to golden brown capsule; seeds 12–46 per cell, minute, ca. 1.2 mm long, the outer testa producing copious fibrils when wetted; embryo achlorophyllous. *N* = 9. Two species. Type: *Dayia scabra* (Brandege) J. M. Porter.

***Dayia scabra*** (Brandege) J. M. Porter, comb. nov.

Basionym: *Gilia scabra* Brandege, *Zoe* 5: 166. 1903.

*Dayia scabra* apparently is very local and restricted to several washes just north of Santa Rosalia, on the eastern coast of Baja California Sur, Mexico. Most of these areas are now under mine tailings and the continued existence of this species in the wild is in question. This species has been overlooked as a result of taxonomic confusion. Although the historical collections of *D. scabra* are representative and quite distinct, they have been misidentified inadvertently as *Linanthus nuttallii* (Grant 1959) or *Giliastrum rigidulum* (as *Gilia rigidula*, Wiggins 1980), or omitted (Day 1964) from treatments. Because this species is known so poorly, we provide a full description of *D. scabra*.

Erect herbaceous perennials with woody base or more frequently sub-shrubs, 15–65 cm high and 13–44 cm wide, much branched, the young parts glandular-pubescent with 3–5(–7) celled trichomes mostly less than 1 mm long, each tipped with a unicellular or multicellular yellowish gland. Woody base to 11–22 mm thick, the bark light to dark tan or gray, splitting into a network of narrow vertical strips. Branches ascending, branching pattern axillary along the primary axis, ultimately sympodial in the inflorescence, the branches flowering terminally, 9–40 cm long and 1.0–2.0 mm thick the first year, tan to somewhat anthocyanic, green terminally, subterete; internodes 1.0–



22.0 mm long, generally shorter than the leaves. Primary leaves alternate or rarely sub-opposite, pinnatifid to nearly palmate, 10.0–39.0 mm long, gradually reduced in size in the inflorescence, rachis 0.6–1.0 mm wide, 3–6 pairs of opposite to sub-opposite lobes, 9.0–35.0 mm long, 0.4–0.9 mm wide, often two pairs of lobes are located at the base of the mucronate tipped leaf, sparsely glandular. Inflorescence densely glandular puberulent, composed of reduced (1-) 2-flowered cymes, forming a thyrsoid inflorescence. Pedicels erect to spreading, pedicel of terminal flower 2–7 mm long, 0.2–0.4 mm thick, pedicel of lateral flower 5–14 mm long, 0.2–0.4 mm thick. Calyx 5.5–7.5 mm long, 3.0–4.0 mm in diameter at the sinuses, cylindric to campanulate, tapering to a rounded base, glandular externally, less so internally, calyx tube 3.0–4.3 mm long, segments (lobes) equal, erect, 1.2–3.2 mm long, attenuate-acute, with a weak mucro, green costae with three primary veins within, scarious margined except near the apex; sinuses v-shaped, the scarious intervals wider to about equal the chlorophyllous costae, generally not rupturing in fruit. Corolla funnelliform to salverform, 13.0–20.0 mm long, glabrous externally, pale blue, with a pale or white center, the orifice often with purple streaks, tube subequal or slightly longer than lobes, straight, 6.4–10.0 mm long, ca. 2.5–3.5 mm in diameter at 1/2 length, slightly flaring at the orifice, 3.0–5.0 mm wide; lobes 6.0–9.5 mm long, 4.0–6.0 mm wide at 1/2 length, oval to oblong or nearly orbicular, entire to emarginate, muriculopapillose within, the lobes convolute in bud, in anthesis spreading, with (15-)17–22(-24) close-spaced parallel veins per lobe, the veins not connected in the lobes. Filaments glabrous above, glandular papillose at the base, unequal in length, the shortest 3.0–4.0 mm long, the longest 6.0–7.0 mm long, sub-equally attached in the lower tube, the filaments superficially to distinctly adnate to the corolla tube, flowers protandrous; anthers 1.5–2.0 mm long, 0.2–0.6 mm wide, linear to linear-ovate, erect to versatile, mostly simultaneously dehiscent as the corolla lobes open, along the theca from the terminal point and downward, two to three anthers slightly exerted from the tube, the remaining anthers included. Pollen grains suboblate to spheroidal; apertures zonate, 5–7 colpi; exine striate, the lirae radiating from the apertures like lines of force in a magnetic field. Nectary disk green, ca. 2 mm wide shallowly cupped, the margin regularly undulate to form erect lobules opposite the calyx segments and spreading ones opposite the corolla lobes. Ovary three celled, 2.0–3.0 mm long, ca. 1.0 mm wide at the base, glandular at the apex; style 6.0–8.0 mm long, subequal to longer than the longest anthers; stigma lobes linear, acute, 0.8–2.5 mm long, spreading when receptive; ovules anatropous, unitegmic, axial placentation, 24–48 per cell. Fruit a capsule, obovoid, tan to golden

brown, often suffused with purple, 3.0–5.5 mm long, 1.5–3.5 mm in diameter, apex acute, loculicidally dehiscent, valves slightly recurving to erect, fruit shorter than the calyx. Seeds 12–46 per cell, minute, 0.8–1.5 mm long, 0.4–0.8 mm wide, ovoid, nearly round in cross-section, golden to pale tan, the outer testa with hygroscopic mucilage cells, producing copious fibrils when wetted. Embryo achlorophyllous, surrounded by a more or less thin layer of endosperm, the cotyledons ovate, equal to or slightly longer than the radical. Chromosomes:  $N = 9$ .

*Representative specimens examined.*—MEXICO, BAJA CALIFORNIA SUR: Santa Rosalia, 14 March 1900, *C. R. Orcutt s.n.* (UC; holotype); Wash just north of flying field, vicinity of Santa Rosalia, 15 March 1934, *R. S. Ferris 8700* (UC). Sandy flats, 4 mi N Santa Rosalia, 27°20'N, 112°19'W, 24 March 1974, *G. Webster 19625* (SDNHM). Cañada El Boleo, 4.5 km NNW Santa Rosalia, 7 November 1997, *A. Burquez s.n.* (RSA); 27°22'43"N, 112°19'29"W, Boleo Canyon, N of Santa Rosalia, 21 December 1997, *J. M. Porter & L. E. Machen 11524* (RSA).

In addition to *Dayia scabra*, a new species of this genus is described from the western coast of Baja California Sur, Mexico:

***Dayia grantii* J. M. Porter, sp. nov.**

Perennes basibus lignosis vel saepiuscule suffrutescens, erectae, glandulares. Folia alterna interdum subopposita, pinnatifida usque subpalmata. Inflorescentia dense glandularis-puberulenta, thyrsoida e cymis redactis (1-)2-floris composita. Corolla glabra, infundibuliformis vel hypocrateriformis, 14.0–22.0 mm longa, caerulea pallida atrolazulina varians, centro flavo distincto. Stamina in tubo superiori aequaliter affixa, exserta et declinata. Pollinis granum 5–7 zonocolporatum, exino striato-reticulato. Fructus capsularis leoninus usque aureo-brunneus. Semina 12–46 per loculo, minuta, ca. 1.2 mm longa, testis exterioris ubi madefactis fibrillae copiosae efferentis. Embryo achlorophyllus.  $N = 9$ . Typus: *K. Heil & J. M. Porter 6478*.

*Type.*—Mexico, Baja California Sur, Vizcaino Desert, 1.5 mi. N of San Hipolito turn-off, valley bottom at W foot of Cerro Prieto, 26 March 1991, *K. Heil & J. M. Porter 6478* (holotype: RSA!; isotypes: BRY!, SJNM!).

Erect herbaceous perennials with woody base or more frequently sub-shrubs, (18)30–60 cm high and 20–50 cm wide, much branched, the young parts glandular-pubescent with 2–8(10) celled trichomes mostly less than 0.10–0.33 mm long, each tipped with a unicellular or multicellular yellowish gland. Woody base to 8.5 mm thick, the bark light to dark tan or gray, splitting into a network of narrow vertical strips. Branches ascending, branching pattern axillary along the primary axis, ultimately sympodial in the inflorescence, the branches flowering terminally, 8–30 cm long 1–4 mm thick the first year, tan to strongly anthocyanic becoming gray, chlorophyllous terminally, subterete; internodes 0.5–55.3 mm long, mostly 5.0–12.0 mm, generally shorter than the leaves. Primary

leaves alternate or rarely sub-opposite, pinnatifid to nearly palmate, 8.0–32.6 mm long, gradually reduced in size in the inflorescence, rachis 0.6–1.3 mm wide, (1)2–4 pairs of opposite to sub-opposite lobes, 5.0–12.6 mm long, 0.6–1.1 mm wide, often two sets of lobes are located at the base of the mucronate tipped leaf, sparsely glandular. Inflorescence densely glandular puberulent, composed of reduced (1-) 2-flowered cymes, forming a thyrsoid inflorescence. Pedicels erect to spreading, pedicel of terminal flower 1.0–3.2 mm long, 0.35–0.60 mm thick, pedicel of lateral flower 5.0–10.5 mm long, 0.30–0.60 mm thick. Calyx 5.5–7.5 mm long, 1.7–3.0 mm in diameter at the sinuses, cylindric, tapering to a rounded base, densely glandular externally, less so internally, tubular for 3.3–4.8 mm (the lower  $\frac{2}{3}$  to  $\frac{3}{4}$ ), segments (lobes) equal, erect or somewhat out-curved, 1.2–3.0 mm long, triangular lanceolate, pungent-acuminate, aristate, with three primary veins within, scarious margined except near the apex; sinuses v-shaped, the scarious intervals about equal to the chlorophyllous costae, generally not rupturing in fruit. Corolla funnellform to salverform, 14.0–22.0 mm long, glabrous both externally and internally, pale to deep blue, with a distinct yellow center, tube shorter than lobes, straight, 6.0–9.0 mm long, ca. 3.0 mm in diameter at  $\frac{1}{2}$  length, slightly flaring at the orifice, 4.0–5.0 mm wide; lobes 8.5–12.0 mm long, 6.0–9.5 mm wide at  $\frac{1}{2}$  length, oval to oblong or nearly orbicular, entire to emarginate, muriculopapillose within, the lobes convolute in bud, in anthesis spreading, with (15-)17–22(-24) close-spaced parallel veins per lobe, the veins not connected in the lobes. Filaments glabrous, 13.5–17.6 mm long, sub-equally attached in the upper tube, the filaments superficially to distinctly adnate to the corolla tube, filaments declinate, flowers protandrous; anthers 3.5–4.5 mm long, 0.6–0.8 mm wide, linear to linear-ovate, erect to versatile, mostly simultaneously dehiscent as the corolla lobes open, along the theca from the terminal point and downward, well exerted from the corolla tube but slightly shorter than the lobes. Pollen grains suboblate to spheroidal; apertures zonate, 5–7 colpi; exine striate, the lirae radiating from the apertures like lines of force in a magnetic field. Nectary disk green, ca. 2 mm wide shallowly cupped, the margin regularly undulate to form erect lobules opposite the calyx segments and spreading ones opposite the corolla lobes. Ovary three celled, 3.0–4.0 mm long, ca. 1.0 mm wide at the base, glabrous; style 10.0–15.0 mm long, subequal to longer than the anthers; stigma lobes linear, acute, 1.5–2.0 mm long, spreading when receptive; ovules anatropous, unitegmic, axial placentation, 24–48 per cell. Fruit a capsule, obovate, tan to golden brown, often suffused with purple, 6.0–9.0 mm long, 2.5–3.5 mm in diameter, apex acute, loculicidally dehiscent, valves slightly recurving to erect, fruit shorter than the calyx.

Seeds 12–46 per cell, minute, ca. 1.2 mm long, 0.6 mm wide, ovoidal, nearly round in cross-section, golden to pale tan, possessing no vestiges of a wing, the outer testa with hygroscopic mucilage cells, producing copious fibrils when wetted. Embryo achlorophyllous, surrounded by a more or less thin layer of endosperm, the cotyledons ovate, equal to or slightly longer than the radical. Chromosomes:  $N = 9$ .

*Dayia grantii* apparently is endemic to a very small region of the Vizcaino desert, along the western coast of northern Baja California Sur. It is known only from the type locality, at the western foot of Cerro Mesa (a.k.a. Cerro Prieto) between San Hipolito and Punta Prieta, 24 km south of Ciudad Bahia Ascuncion. This species occurs along a wash and on adjacent alluvial slopes, associated with *Encelia palmeri*, *Fouquieria dugettii*, *Jatropha cinera*, *Euphorbia miser*, *Bursera hindsiana*, and *Krameria sp.*, at approximately 50 ft. elevation. Flowering occurs in (December) February through March (April) in response to winter rains, and again sporadically through the summer in response to the less frequent summer rains. A self-incompatible species, based on *ex situ* crossing studies, the flowers of *Dayia grantii* open during the morning and remain open for several days. Observations of insect visitation are limited; but, butterflies, anthophorid bees, and bombylid bees frequent the flowers.

*Representative specimens examined.*—MEXICO, BAJA CALIFORNIA SUR: Vizcaino Desert, between Cerro Prieto and Punta Prieta, near San Hipolito, 19 March 1950, *H. S. Gentry 8850* (ARIZ, RSA); 1.5 mi. N of San Hipolito turn-off, valley bottom at W foot of Cerro Prieto, 26 March 1991, *K. D. Heil & J. M. Porter 6478* (BRY, RSA, SJNM); 1.5 mi. N of San Hipolito turn-off, valley bottom at W foot of Cerro Prieto, 15 March 1994, *J. M. Porter 11324* (RSA).

*Dayia* is similar in general appearance to both *Ipomopsis* and *Giliastrum*; however, morphological data, as well chromosome number, provide evidence that it is isolated from these genera. The haploid chromosome counts (from dividing pollen mother cells) of *D. scabra* and *D. grantii* are  $x = 9$ . This contrasts with all known members of *Ipomopsis*, which possess a base chromosome number of  $N = 7$  (Grant 1959). Pollen of both *D. scabra* and *D. grantii* is blue, with a thick striate-reticulate exine; seeds are minute; and a well developed corolla tube (6–9 mm long; longer than the calyx) is present. This differs from all members of *Giliastrum*, that have yellow, pertectate pollen grains, larger seeds, and a very short corolla tube (less than 5 mm long; shorter than the calyx).

Given the relationship between *Dayia* and *Loeselia* inferred by ITS (Porter 1996) and *matK* (Johnson et al. 1996) sequence data, it is important to note the great morphological differences between *Dayia* and *Loeselia* that parallels the large number of nucleotide changes that distinguish these genera. A well-characterized genus of Polemoniaceae, members of *Loeselia*

possess simple, dentate leaves and large, wingless or winged seeds. In addition, most members of *Loeselia* have bilaterally symmetric flowers (except *L. mexicana*) and a shrubby to subshrubby habit. By contrast, *Dayia* possess pinnatifid leaves and minute, wingless seeds and radially symmetric corollas. Further, in molecular phylogenetic analyses of nrITS and cp *trnL-F*, including all species of tribe Loeseliaceae, *Dayia* does not share immediate and exclusive common ancestry with *Loeselia*, nor with *Giliastrum*, nor with *Ipomopsis* (Porter et al. unpubl.).

The DNA studies of Johnson et al. (1996) and Porter (1996) included "*Gilia scabra*" in their analyses. Following the nomenclatural changes provided here, the DNA sample used in these studies actually represents *Dayia grantii*.

The generic name honors Alva G. Day, who has contributed much to the understanding of morphological diversity in Polemoniaceae. The specific epithet of *Dayia grantii* honors Verne E. Grant, who has dedicated much of his research to developing an understanding of the diversification process in the genus *Gilia* and Polemoniaceae as a whole.

ERIASTRUM Wooton & Standl., *Contr. U. S. Natl. Herb.* **16**: 160, 1913.

Annual or perennial herbs, sometimes woody, erect, branching from the base, glabrous to woolly, rarely glandular. Leaves alternate, simple, entire, or once-pinnatifid, not forming a basal rosette, leaf tips cuspidate or mucronate, cauline leaves  $\pm$  gradually reduced in size. Inflorescence mostly terminal and head-like, less often in few-flowered cymes, usually woolly. Calyx composed of herbaceous costae and hyaline intercostal regions, lobes unequal in length, hairy or glandular. Corolla salverform to funnelform, radially or bilaterally symmetric. Stamens equally inserted in the distal corolla tube or in the sinuses of the corolla lobes, the filaments unequal or equal in length. Pollen zonocolporate, mostly anomotreme or pantocolporate with striate, striate-reticulate, or reticulate exine, occasionally pertectate with striations, blue, yellow, or cream. Ovary glandular apically or glabrous, seeds becoming mucilaginous when wetted.  $N = 7$ . Fourteen species. Type: *Eriastrum filifolium* (Nutt.) Wooton & Standl.

- ERIASTRUM ABRAMSII (Elmer) H. Mason, *Madroño* **8**: 90, 1945.  
 ERIASTRUM BRANDEGEEAE H. Mason, *Madroño* **8**: 88, 1945.  
 ERIASTRUM DENSIFOLIUM (Benth.) H. Mason, *Madroño* **8**: 73, 1945.  
 ERIASTRUM DENSIFOLIUM (Benth.) H. Mason subsp. AUSTROMONTANUM (T. T. Craig) H. Mason, *Madroño* **8**: 74, 1945.  
 ERIASTRUM DENSIFOLIUM (Benth.) H. Mason subsp. ELONGATUM (Benth.) H. Mason, *Madroño* **8**: 73, 1945.  
 ERIASTRUM DENSIFOLIUM (Benth.) H. Mason subsp. MOHAVENSIS (T. T. Craig) H. Mason, *Madroño* **8**: 74, 1945.  
 ERIASTRUM DENSIFOLIUM (Benth.) H. Mason subsp. SANCTORUM (Milliken) H. Mason, *Madroño* **8**: 75, 1945.  
 ERIASTRUM DIFFUSUM (A. Gray) H. Mason, *Madroño* **8**: 76, 1945.

- ERIASTRUM EREMICUM (Jeps.) H. Mason, *Madroño* **8**: 78, 1945.  
 ERIASTRUM EREMICUM (Jeps.) H. Mason subsp. YAGERI (M. E. Jones) H. Mason, *Madroño* **8**: 78, 1945.  
 ERIASTRUM FILIFOLIUM (Nutt.) Wooton & Standley, *Contr. U. S. Natl. Herb.* **16**: 160, 1913.  
 ERIASTRUM HOOVERI (Jeps.) H. Mason, *Madroño* **8**: 89, 1945.  
 ERIASTRUM LUTEUM (Benth.) H. Mason, *Madroño* **8**: 81, 1945.  
 ERIASTRUM PLEURIFLORUM (A. Heller) H. Mason, *Madroño* **8**: 75, 1945.  
 ERIASTRUM PLEURIFLORUM (A. Heller) H. Mason subsp. SHERMANHOYTAE (T. T. Craig) H. Mason, *Madroño* **8**: 75, 1945.  
 ERIASTRUM SAPPHIRINUM (Eastw.) H. Mason, *Madroño* **8**: 79, 1945.  
 ERIASTRUM SAPPHIRINUM (Eastw.) H. Mason subsp. DASYANTHUM (Brand) H. Mason, *Madroño* **8**: 80, 1945.  
 ERIASTRUM SPARSIFLORUM (Eastw.) H. Mason, *Madroño* **8**: 86, 1945.  
 ERIASTRUM SPARSIFLORUM (Eastw.) H. Mason subsp. HARWOODII (T. T. Craig) H. K. Harrison *Phytomorph.* **18**: 401, 1968.  
 ERIASTRUM VIRGATUM (Benth.) H. Mason, *Madroño* **8**: 84, 1945.  
 ERIASTRUM WILCOXII (A. Nelson) H. Mason, *Madroño* **8**: 85, 1945.  
 ERIASTRUM TRACYI H. Mason, *Madroño* **8**: 87, 1945.

The genus *Eriastrum*, although weakly characterized morphologically (Mason 1945), can be distinguished from other genera provided a set of traits is considered (e.g., sagittate anthers, calyx with unequal lobes, and arachnoid lanate pubescence). However, as noted by Mason (1945), some *Eriastrum* species lack one or the other of these traits.

Most authors (Craig 1934; Mason 1945; Harrison 1972) have disagreed with Brand's (1907) inclusion of *Eriastrum* within *Navarretia*. For example Grant (1959) suggests a close relationship between *Eriastrum*, *Ipomopsis*, and *Langloisia*. Both chloroplast and nuclear DNA sequence data (Johnson et al. 1996; Porter 1996) support Grant's hypothesis. Further, the morphological and molecular data provide support that *Eriastrum*, as circumscribed by Grant (1959) and Mason (1945), is a monophyletic group.

Even though there is little debate regarding generic delimitation of *Eriastrum*, species and subspecies boundaries are problematic (compare Mason 1945 and Patterson 1993). We follow the species recognized in the two most recent monographic/revisional studies (Mason 1945; Harrison 1972). Thorough comparative studies of this genus are needed.

GILIASTRUM (Brand) Rydb., *Fl. Rocky Mts.*, pp.699 & 1066, 1917.

Perennial (also annual?) herbs, flowering the first year, glandular puberulent, with sparse nonglandular trichomes, or glabrous. Leaves alternate, entire, toothed to pinnatifid, gradually reduced in size in the inflorescence. Flowers perfect, in dichasia. Calyx campanulate, 5-lobed or 5-cleft; the tube with a scarious region alternating with a green costa (lobe) and ruptured by the fruit. Corolla rotate-funnelform, the lobes much longer than the tube, external surface glabrous, internal tube pubescent or glabrous. Stamens equally

inserted in the lower portion of the corolla tube, filaments pubescent, papillate or glabrous basally. Apex of ovary glandular puberulent to glabrous. Pollen yellow, zonocolporate, peritectate to semitectate, or striate exine, often with spinule-like processes, rarely with insulae (verrucae). Fruit a loculicidal capsule, ellipsoidal or globose in shape. Seeds several per carpel, seed coat producing mucilage when wetted.  $N = 6, 9, 10, 12, 18$  (Porter 1998b). Nine species. Type: *Giliastrum rigidulum* (Benth.) Rydb.

- GILIASTRUM ACEROSUM (A. Gray) Rydb., *Fl. Rocky Mts.*, pp.699 & 1066, 1917.  
 GILIASTRUM FOETIDUM (Gillies ex Benth.) J. M. Porter, *Aliso* 17: 83, 84, 1998.  
 GILIASTRUM GYPSOPHILUM (B. L. Turner) J. M. Porter, *Aliso* 17: 84, 1998.  
 GILIASTRUM LUDENS (Shinners) J. M. Porter, *Aliso* 17: 84, 1998.  
 GILIASTRUM INSIGNE (Brand) J. M. Porter, *Aliso* 17: 84, 1998.  
 GILIASTRUM INCISUM (Benth.) J. M. Porter, *Aliso* 17: 84, 1998.  
 GILIASTRUM PURPUSII (K. Brandegeee) J. M. Porter, *Aliso* 17: 84, 1998.  
 GILIASTRUM PURPUSII (K. Brandegeee) J. M. Porter subsp. PLATYLOBUM (I. M. Johnst.) J. M. Porter, *Aliso* 17: 84, 1998.  
 GILIASTRUM PURPUSII (K. Brandegeee) J. M. Porter subsp. STEWARTII (I. M. Johnst.) J. M. Porter, *Aliso* 17: 84, 1998.  
 GILIASTRUM RIGIDULUM (Benth.) Rydb., *Fl. Rocky Mts.*, p.1066, 1917.

Retrospectively, it is remarkable that a genus, as cohesive and well marked as is *Giliastrum*, has remained entangled with an unrelated group of species (i.e., *Gilia*, see Grant 1959, 1998b; Turner 1994a). *Giliastrum* floral morphology is quite different from *Gilia*. Species of *Giliastrum* have short tubes, large, rotate lobes, and bright yellow pollen. *Giliastrum* displays a pattern of corolla vasculature that lacks anastomoses in the corolla lobes, a pattern not documented in *Gilia* (Day and Moran 1986), as here circumscribed.

*Giliastrum* exhibit an unusual floral "behavior." Members of this genus have flowers that open and close at specific times of the day. *Giliastrum acerosum*, *G. ludens*, and *G. rigidulum* possess flowers that open in the early afternoon and close at dusk. By contrast, *G. insigne* and *G. purpusii* have flowers that open with the early morning sun, but close around noon. This phenomenon is particularly striking at locations where representatives of the two types occur sympatrically. The flowers of *G. foetidum* open in the early morning and remain open until late afternoon, providing a third, contrasting pattern.

In addition to the eight species cited above, a new species is described from Argentina:

***Giliastrum castellanosii* J. M. Porter, sp. nov.**

Perennis, glanduloso-pilosa. Caules erecti, ramosi, 12–20 cm alti. Folia pinnatifida, segmentis linearibus. Flores terminales, solitarii vel ad 2–3 aggregati, breviter pedicellati. Corolla 11–15 mm longa, lobis oblongis. Ovarium ovoideum, superne ciliatum. Semina sub aqua

dense mucilaginoso. Pollinis granum 5–7 zonocolporatum, exino striato, verrucato. Typus: A. *Castellanos* 30,732.

Type.—ARGENTINA, Prov. Catamarca, Agua Negra. 9 February 1930. A. *Castellanos* 30.732. (holotype: BA!; isotypes: F!, LIL!).

Erect perennial herb, 10–20 cm. tall, woody and branching from the base, densely glandular-puberulent throughout. Leaves ovate in outline, 10–25 mm long, pinnatifid with 5–8 linear, entire lobes, cuspidate or mucronate at apex, leaves little reduced in size in the inflorescence. Flowers arranged in terminal or axillary cymes, solitary or 2–3 in number, on short peduncles 1–1.5 cm long; calyx shortly campanulate, 4.5–7.0 mm long (in fruit somewhat larger), lobes 2.5–5.0 mm in length, lanceolate, acute to acuminate, the scarious intercostal membranes continuing along the lobe margins; corolla 11–15 mm long, rotate to campanulate, pale blue, lobes obovate, acute, 7–12 mm long, 6–8 mm broad; stamens exerted from tube but not longer than corolla lobes, filaments equally inserted ca 1–2 mm above the base of corolla, free portion ca. 7 mm long, glabrous, anthers 1.5 mm long, yellow; ovary fusiform to elliptic-ovoid, ca. 2 mm long, glandular puberulent on the upper portion, style sparsely glandular at base, equal to the stamen, 6–7 mm long, stigma lobes ca. 1 mm long; mature capsule oblong, 5–7 mm. long, equal to or slightly exceeding calyx, valves 2–2.5 mm wide; each locule containing numerous small, brown seeds, 0.8–1.4 mm long, 0.4–0.7 mm wide, seed coat becoming mucilaginous when wetted.

Apparently *Giliastrum castellanosii* is very local and restricted. The only known collections are from the same region, toward the northern end of Valle de Chaschuil, near the Cordillera de San Buenaventura, in the Andes Mountains of western Catamarca, Argentina.

Representative specimens.—ARGENTINA. Prov. Catamarca. Dept. Tinogasta, Quebrada de los Amancayes, Sierra Buenaventura, 2400 m, 9 February 1930, *Schreiter* 6338 (BA, LIL); Agua Negra. 9 February 1930. A. *Castellanos* 30.732 (BA, F, LIL).

Closely related to *Giliastrum foetidum*, *G. castellanosii* differs from the former in both vegetative and floral traits. The leaves of *G. castellanosii* have linear lobes, dissected to the midrib, contrasting with the broadly lobed leaves that are often shallowly lobed in *G. foetidum*. The flowers of *G. castellanosii* are pale blue, 15 mm long or less, with obovate, acute lobes. *Giliastrum foetidum* has pink corollas, usually more than 15 mm long, with ovate, rounded lobes. In addition, pollen of *G. castellanosii* is zonocolporate, with a rugulose exine, covered with small, but sometimes densely arranged, verrucae. *Giliastrum foetidum* (Prov. Mendoza, Cruz del Paramillo, C. A. O'Donnell 1172, LIL) has zonocolporate pollen with a striate exine, bearing both highly scattered verrucae and spinule-like



processes. These are strikingly different exine sculpting patterns. Although these two *Giliastrum* species occur at similar elevations, *G. castellanosi* occurs farther north in Prov. Catamarca, whereas *G. foetidum* is found to the south, in Prov. Mendoza and Prov. San Juan.

The specific epithet honors A. Castellano, eminent botanist of Argentina, who has contributed much to the knowledge of Cactaceae of Argentina (and Polemoniaceae, through his collections).

IPOMOPSIS Michx., *Fl. bor.-amer.* v.1, p.141, 1803.

Annual or perennial herbs, sometimes woody, erect, branching from the base, variously hairy or glandular. Leaves alternate, entire, or once- or twice-pinnatifid, leaf tips cuspidate, or mucronate, sometimes forming a basal rosette, cauline leaves  $\pm$  gradually reduced in size. Inflorescence cymose, thyrsoïd, or terminal and head-like. Calyx composed of herbaceous costae and hyaline intercostal regions, hairy or glandular. Corolla salverform or campanulate, radially or bilaterally symmetric. Stamens equally or unequally inserted in the distal corolla tube or in the sinuses of the corolla lobes, the filaments unequal or equal in length. Pollen zonocolporate with striate, striate-reticulate or reticulate exine, blue, yellow, or cream. Ovary glandular apically or glabrous, seeds becoming mucilaginous when wetted.  $N = 7, 14$ . Twenty-nine species. Type: *Ipomopsis rubra* (L.) Wherry.

- IPOMOPSIS AGGREGATA (Pursh) V. E. Grant, *El Aliso* 3: 360, 1956.  
 IPOMOPSIS AGGREGATA (Pursh) V. E. Grant subsp. ATTENUATA (A. Gray) V. E. Grant & A. D. Grant, *El Aliso* 3: 360, 1956  
 IPOMOPSIS AGGREGATA (Pursh) V. E. Grant subsp. BRIDGESII (A. Gray) V. E. Grant & A. D. Grant, *El Aliso* 3: 361, 1956  
 IPOMOPSIS AGGREGATA (Pursh) V. E. Grant subsp. CANDIDA (Rydb.) V. E. Grant & A. D. Grant, *El Aliso* 3: 360, 1956  
 IPOMOPSIS AGGREGATA (Pursh) V. E. Grant subsp. CARMENENSIS Henr., *Aliso* 11: 591, 1987.  
 IPOMOPSIS AGGREGATA (Pursh) V. E. Grant subsp. COLLINA (Greene) Wilken & Allard, *Syst. Bot.* 11: 11, 1986).  
 IPOMOPSIS AGGREGATA (Pursh) V. E. Grant subsp. FORMOSISSIMA (Greene) Wherry, *Aliso* 5: 5, 1961.  
 IPOMOPSIS AGGREGATA (Pursh) V. E. Grant subsp. TEXANA (Greene) Wherry, *Aliso* 5: 7, 1961.  
 IPOMOPSIS AGGREGATA (Pursh) V. E. Grant subsp. WEBERI V. E. Grant & Wilken, *Bot. Gaz. (Crawfordsville)* 147: 367, 1986).  
 IPOMOPSIS ARIZONICA (Greene) Wherry, *Aliso* 5: 7, 1961.  
 IPOMOPSIS CONGESTA (Hook.) V. E. Grant, *El Aliso* 3: 361, 1956.  
 IPOMOPSIS CONGESTA (Hook.) V. E. Grant subsp. CREBRIFOLIA (Nutt.) A. G. Day, *Madroño* 27: 112, 1980.  
 IPOMOPSIS CONGESTA (Hook.) V. E. Grant subsp. FRUTESCENS (Rydb.) A. G. Day, *Madroño* 27: 112, 1980.  
 IPOMOPSIS CONGESTA (Hook.) V. E. Grant subsp. MONTANA (A. Nelson & P. B. Kenn.) V. E. Grant, *El Aliso* 3: 361, 1956  
 IPOMOPSIS CONGESTA (Hook.) V. E. Grant subsp. NEVADENSIS (Tidestr.) Kartesz & Gandhi, *Phytologia* 72: 88, 1992.  
 IPOMOPSIS CONGESTA (Hook.) V. E. Grant subsp. PALMIFRONS (Brand) A. G. Day, *Madroño* 27: 112, 1980.  
 IPOMOPSIS CONGESTA (Hook.) V. E. Grant subsp. PSEUDOTYPICA (Constance & Rollins) A. G. Day, *Madroño* 27: 112, 1980.

- IPOMOPSIS CONGESTA (Hook.) V. E. Grant subsp. VIRIDIS (Cronquist) A. G. Day, *Madroño* 27: 112, 1980.  
 IPOMOPSIS EFFUSA (A. Gray) Moran, *Madroño* 24: 143, 1977.  
 IPOMOPSIS GOSSYPIFERA (Gillies ex Benth.) V. E. Grant, *El Aliso* 3: 361, 1956.  
 IPOMOPSIS GUNNISONII (Torr. & A. Gray) V. E. Grant, *El Aliso* 3: 361, 1956.  
 IPOMOPSIS GUTTATA (A. Gray) Moran, *Madroño* 24: 145, 1977.  
 IPOMOPSIS HAVARDI (A. Gray) V. E. Grant, *El Aliso* 3: 361, 1956.  
 IPOMOPSIS LAXIFLORA (J. M. Coul.) V. E. Grant, *El Aliso* 3: 361, 1956.  
 IPOMOPSIS LONGIFLORA (Torr.) V. E. Grant, *El Aliso* 3: 361, 1956.  
 IPOMOPSIS LONGIFLORA (Torr.) V. E. Grant subsp. AUSTRALIS R. A. Fletcher & W. L. Wagner, *Madroño* 31: 20, 1984.  
 IPOMOPSIS MACOMBII (Torr.) V. E. Grant, *El Aliso* 3: 361, 1956.  
 IPOMOPSIS MACROSIPHON (Kearney & Peebles) V. E. Grant & Wilken, *Syst. Bot.* 17: 687, 1992.  
 IPOMOPSIS MULTIFLORA (Nutt.) V. E. Grant, *El Aliso* 3: 357, 1956.  
 IPOMOPSIS PINNATA (Cav.) V. E. Grant, *El Aliso* 3: 357, 1956.  
 IPOMOPSIS POLYANTHA (Rydb.) V. E. Grant, *El Aliso* 3: 357, 1956.  
 IPOMOPSIS POLYCLADON (Torr.) V. E. Grant, *El Aliso* 3: 361, 1956.  
 IPOMOPSIS PRINGLEI (Gray) Henr., *Aliso* 11: 594, 1987.  
 IPOMOPSIS PUMILA (Nutt.) V. E. Grant, *El Aliso* 3: 361, 1956.  
 IPOMOPSIS ROSEATA (Rydb.) V. E. Grant, *El Aliso* 3: 361, 1956.  
 IPOMOPSIS RUBRA (L.) Wherry, *Bartonia* 18: 56, 1936.  
 IPOMOPSIS SANCTI-SPIRITUS Wilken & R. A. Fletcher, *Brittonia* 40: 48, 1988.  
 IPOMOPSIS SONORAE (Rose) A. Grant, *El Aliso* 3: 361, 1956.  
 IPOMOPSIS SPICATA (Nutt.) V. E. Grant, *El Aliso* 3: 361, 1956.  
 IPOMOPSIS SPICATA (Nutt.) V. E. Grant subsp. CAPITATA (A. Gray) V. E. Grant, *El Aliso* 3: 361, 1956.  
 IPOMOPSIS SPICATA (Nutt.) V. E. Grant subsp. ORCHIDACEA (Brand) Wilken & R. L. Hartm., *Syst. Bot.* 16: 156, 1991.  
 IPOMOPSIS SPICATA (Nutt.) V. E. Grant subsp. ORCHIDACEA (Brand) Wilken & R. L. Hartm. var. ORCHIDACEA (Brand) Dorn, *Vasc. pl. Wyo.*, p.299, 1988.  
 IPOMOPSIS SPICATA (Nutt.) V. E. Grant subsp. ORCHIDACEA (Brand) Wilken & R. L. Hartm. var. CEPHALOIDEA (Rydb.) Wilken & R. L. Hartm., *Syst. Bot.* 16: 157, 158, 1991.  
 IPOMOPSIS SPICATA (Nutt.) V. E. Grant subsp. ROBRUTHIAE Wilken & R. L. Hartm., *Syst. Bot.* 16: 158, fig. 6, 1991.  
 IPOMOPSIS SPICATA (Nutt.) V. E. Grant subsp. TRIDACTYLA (Rydb.) Wilken & R. L. Hartm., *Syst. Bot.* 16: 155, 1991.  
 IPOMOPSIS TENUIFOLIA (A. Gray) V. E. Grant, *El Aliso* 3: 357, 1956.  
 IPOMOPSIS TENUITUBA (Rydb.) V. E. Grant, *El Aliso* 3: 361, 1956.  
 IPOMOPSIS TENUITUBA (Rydb.) V. E. Grant subsp. LATILOBA V. E. Grant & Wilken, *Bot. Gaz. (Crawfordsville)* 149: 446, 1988.  
 IPOMOPSIS THURBERI (Torr.) V. E. Grant, *El Aliso* 3: 361, 1956.  
 IPOMOPSIS WENDTII Henr., *Aliso* 11: 589, 1987.  
 IPOMOPSIS WRIGHTII (A. Gray) Shinnery, *Sida* 1: 178, 1963.

The segregation of *Ipomopsis* from *Gilia* (Grant 1956), ignored or rejected by some authors (Cronquist 1984; Welsh et al. 1993), has been supported overwhelmingly by molecular data (Steele and Vilgalys 1994; Johnson et al. 1996; Porter 1996). Although chromosome numbers of *Ipomopsis* ( $N = 7$ ) are consistently different from that of *Gilia* ( $N = 9$ ), the morphological traits that distinguish these genera are surprisingly cryptic. Rather than any single feature, trends and combinations of traits distinguish *Ipomopsis*. *Ipomopsis* has many perennial species (*Gilia* species are annual; *Aliciella*, *Giliastrum*, *Eriastrum* and *Dayia* also have perennial species) and bilateral corollas are

common (*Gilia* species have mostly radial corollas). Some species of *Ipomopsis* have thyrsoid inflorescences, an architecture never found in *Gilia* nor most other genera (save a few species of *Aliciella*). These traits, while singly not separating every species of *Ipomopsis* from *Gilia*, are helpful if considered together.

In addition to the 28 species noted above, a new species from Sinaloa, Mexico is here described:

***Ipomopsis monticola* J. M. Porter & L. A. Johnson, sp. nov.**

Perennis. Caules erecti, ramosi, 40–70 cm alti. Folia pinnatifida, segmentis 3–7(–9) angustissimis, filiformia. Flores terminales, solitarii vel ad 2 aggregati, pedicellatis 3–9 mm longis. Corolla rubra vel rosea, 19–22 mm longa, lobis oblongis. Ovarium ovoideum, superne ciliatum. Pollinis granum 8–9(–12) zonocolporatum, exino reticulato vel striato-reticulato. Typus: *D. E. Breedlove & R. F. Thorne 18342*.

*Type*.—MEXICO, Estad. Sinaloa, Mpio. Badiraguato, Sierra Surutato, 3 mi N of Los Ornos, along road to Ocurahui. 2 October 1970. *D. E. Breedlove & R. F. Thorne 18342*. (holotype: RSA!; isotype: CAS).

Erect perennial herb, 40–70 cm tall, somewhat woody and branching from the base, sparsely hairy below with long nonglandular, white trichomes and shorter glandular hairs. Leaves ovate in outline, 20–50 mm long, pinnatifid with 3–7(–9) narrowly linear, the terminal lobe 15–33 mm long, ca 0.3(–0.4) mm broad, lateral lobes 10–27 mm long, 0.2–0.4 mm broad, entire lobes, tips mucronate-acuminate, leaves reduced in size in the inflorescence, mostly 3-lobed. Flowers in terminal or axillary cymes, solitary or in pairs, on short, densely glandular peduncles 3–9 mm long. Calyx shortly campanulate, 5.5–6.0 mm long (in fruit to 7.0 mm), tube 3.0–3.5 mm in length, lobes narrowly lanceolate to linear, acute to acuminate, the scarious intercostal membranes ca. 1.0 mm wide, much wider than the green costal portion (0.2–0.4 mm wide). Corolla 19–22 mm long, funnellform to salverform, red or pink, lobes ovate, margins denticulate and somewhat apiculate, 4.5–5.0 mm long, 3.5–4.0 mm broad. Stamens included to slightly exerted, filaments white, equally inserted in the upper tube, free portion 2.5–3.0 mm long, glabrous, anther ovoid, 1.0 mm long, yellow; pollen oblate spheroidal, 46.4–57.8  $\mu$  (equatorial), 41.5–51.0  $\mu$  (polar), 8–9(–12) zonocolporate apertures, exine striato-reticulate. Ovary fusiform to elliptic-ovoid, ca. 2 mm long, glandular puberulent on the upper portion, style sparsely glandular at base, slightly longer than the stamen, stigma lobes 1–1.5 mm long; mature capsule ovoid-oblong, 5–7 mm. long, equal to or slightly exceeding calyx. Seeds unknown.

Known only from the type collection in the Sierra Surutato, Sinaloa, Mexico, this species occurs on

steep, moist slopes at 6500 ft elevation, associated with *Alnus*, *Styrax*, *Mahonia*, *Clethrea*, *Pinus*, *Quercus*, and *Juglans*.

*Ipomopsis monticola* is apparently quite uncommon, and has been mistaken for *I. aggregata*. It differs in having ovate corolla lobes that lack the more attenuate apex observed in *I. aggregata*. It also differs in having a glandular ovary and filiform leaf lobes, whereas *I. aggregata* has a glabrous ovary and linear (but not filiform) leaf lobes. In some other respects it is similar to *I. wendtii*, of Coahuila, Mexico (Henrickson 1987). For example, both possess pink corollas, with ovate lobes, and are associated with pine-oak woodlands in the mountains of Mexico. However, *I. monticola* lacks the enlarged calyx characteristic of *I. wendtii*, possesses a longer corolla tube (14.0–17.0 mm in *I. monticola* vs. 8–11 mm in *I. wendtii*), and differs in pollen morphology. *Ipomopsis wendtii* has oblate spheroidal pollen, 38.3–48.0  $\mu$  (equatorial), 35.3–40.0  $\mu$  (polar), 6–7(–8) zonocolporate apertures, with a heterobrochate, reticulate exine, unlike pollen of *I. monticola* (see above). Phylogenetic analyses of chloroplast *trnL-F* DNA sequences strongly support relationships between *I. monticola*, *I. pinnata*, and *I. pringlei*; however, nuclear sequences (ITS) provides ambiguous resolution concerning *I. monticola* (Porter et al. unpubl.).

LANGLOISIA Greene, *Pittonia* 3: 30, 1896.

Annual herbs, branching from the base, hairy with branched trichomes but not glandular. Leaves alternate, simple, linear to oblanceolate, dentate to once-pinnatifid, lateral lobes with 2–3 bristles, not forming a basal rosette, cauline leaves little reduced in size. Inflorescence mostly terminal and head-like, subtending bracts with bristle-tipped lobes. Calyx composed of herbaceous costae and narrow hyaline intercostal regions, lobes equal in length, bristle tipped. Corolla funnellform, radially symmetric. Stamens equally inserted below the sinuses of the corolla lobes, the filaments equal in length. Pollen zonocolporate and striate to striate-reticulate, blue or white; Ovary glabrous apically, seeds becoming mucilaginous when wetted. *N* = 7. One species.

LANGLOISIA SETOSISSIMA (Tort. & A. Gray) Greene, *Pittonia* 3: 30, 1896.

LANGLOISIA SETOSISSIMA (Tort. & A. Gray) Greene subsp. PUNCTATA (Coville) Timbrook, *Madroño* 33: 169, 1986.

Generic delimitation of *Langloisia* is discussed by Timbrook (1986), wherein he cites compelling morphological and phytochemical evidence for the segregation of *Langloisia* and *Loeseliastrum*. *Langloisia* has branched trichomes (but lacks glands), has a radially symmetric corolla, equally inserted straight filaments, white to blue pollen, reticulate seed coat sculpturing, and possesses three different 6-methoxyflavonols,

while lacking the common flavonols, kaempferol and quercetin. In contrast, *Loeseliastrum* has unbranched trichomes (and also glands), has a bilaterally symmetric corolla, unequally inserted sigmoid filaments, yellow pollen, linear seed coat sculpturing, and possesses the common flavonols, kaempferol and quercetin while lacking the 6-methoxyflavonols. Indeed, morphological evidence for the segregation of *Langloisia* and *Loeseliastrum* is overwhelming.

LOESELIA L., *Gen. pl.* 276, 1754.

Perennial shrubs, herbs or annuals, glandular puberulent, with sparse nonglandular trichomes, or glabrous. Leaves alternate or opposite, simple, entire, dentate or aristate. Flowers perfect, in bracteate dichasia or congested in head-like inflorescences. Calyx campanulate to tubular, radially or slightly bilaterally symmetric; with herbaceous costae and scarious sinuses, or entirely scarious. Corolla funnellform to salverform, radially to strongly bilaterally symmetric, external surface glandular to glabrous, internal tube glandular pubescent or glabrous. Stamens equally inserted in the mid to lower portion of the corolla tube, filaments pubescent, papillate or glabrous. Apex of ovary glandular puberulent to glabrous. Pollen pantoporate, pertectate exine with fine striations and spinule-like processes. Fruit a loculicidal capsule, ellipsoidal or globose in shape. Seeds several per carpel, lacking a wing or rarely narrowly winged, seed coat producing mucilage when wetted.  $N = 9$ . Thirteen species. Type: *Loeselia ciliata* L.

LOESELIA AMPLECTANS (Hook. & Arn.) Benth, *Prodr.* v.9, p.320, 1845.

LOESELIA CAERULEA (Cav.) G. Don, *Gen. hist.* v.4, p.248, 1838.

LOESELIA CILIATA L., *Sp. pl.*, p.628, 1753.

LOESELIA CILIATA L. subsp. **echinophylla** (Brand) J. M. Porter & L. A. Johnson, comb. nov.

Basionym: *Loeselia ciliata* L. var. *echinophylla* Brand, *Pflanzenr.* IV 250, p.178, 1907.

LOESELIA CORDIFOLIA Hemsl. & Rose, *Hooker's Icon. Pl.* 26: t. 2551, 1899.

LOESELIA GLANDULOSA (Cav.) G. Don, *Gen. hist.* v.4, p.248, 1838.

LOESELIA GLANDULOSA (Cav.) G. Don subsp. CONGLOMERATA (Kunth) Brand, *Pflanzenr.* IV 250, p.177, 1907.

LOESELIA GLANDULOSA (Cav.) G. Don subsp. **nepetifolia** (Cham. & Schltld.) J. M. Porter & L. A. Johnson, comb. nov.

Basionym: *Hoitzia nepetaefolia* Cham. & Schltld., *Linnaea* 6: 385, 1834.

LOESELIA GRANDIFLORA Standl., *J. Wash. Acad. Sci.* 17: 527, 1927.

LOESELIA GREGGII S. Watson, *Proc. Amer. Acad. Arts* 18: 117, 1883.

LOESELIA INVOLUCRATA G. Don, *Gen. hist.* v.4, p.248, 1838.

LOESELIA MEXICANA (Lam.) Brand, *Pflanzenr.* IV 250, p.174, 1907.

LOESELIA PUMILA (M. Martens & Galeotti) Walp., *Repert. bot. syst.* v.6, p.527, 1846.

LOESELIA PURPUSII Brandege, *Univ. Calif. Publ. Bot.* 3: 389, 1909.

LOESELIA RUPESTRIS Benth, *Prodr.* v.9, p.319, 1845.

LOESELIA RZEDOWSKII McVaugh, *Acta. Bot. Mex.* 11: 11, 1990.

A morphologically heterogeneous group in many respects, *Loeselia* is monophyletic, as evidenced by leaf morphology, phylogenetic analyses of chloroplast and nuclear DNA sequences (Porter et al. in prep), and pollen morphology. All species of *Loeselia* possess a pollen type (see above) unique in Polemoniaceae (Porter and Allen unpubl.). Many species are morphologically cohesive and distinctive from other species, but others display considerable racial variation. We provide two recombinations of distinctive racial variants of two widespread species, based on comparative morphology and gene sequence data, resulting from a molecular phylogenetic analysis of *Loeselia* (Porter et al. in prep.).

Nearly all classifications of Polemoniaceae prior to that of Brand (1907) include *Loeselia* in the same tribe (or "Gruppe") as species here included in tribe Loeseliaceae (along with others; see Table 1). It was with Brand's (1907) treatment that *Loeselia* was isolated into another tribe, along with *Bonplandia*; however, both were still included in subfam. Polemonioideae. Grant (1959, 1998a) associates *Loeselia* with the "tropical genera" of subfam. Cobaeoideae. In spite of this taxonomic assignment, Grant (1959; 1998b) suggests that *Loeselia* is involved in the origin of *Ipomopsis* and *Giliastrum* (his "*Gilia* sect. *Giliastrum*"). Although Grant's (1998a, b) general thesis of relationships (subfamilial, tribal, and within "*Gilia*") is without support from molecular data (morphological data being equivocal), there is evidence for common ancestry between *Loeselia*, *Giliastrum*, and *Ipomopsis*, along with the other genera here included in Loeseliaceae. Nomenclature and species delimitation in *Loeselia* remains in an unsatisfactory state and revisional work is needed. At least four named taxa have had their types destroyed and neither lectotypes nor neotypes have been identified (Turner 1994b).

LOESELIASTRUM (Brand) Timbrook, *Madroño* 33: 170, 1986.

Annual herbs, branching from the base, bearing uniseriate eglandular trichomes and glandular trichomes. Leaves alternate, simple, linear to oblanceolate, entire, dentate to once-pinnatifid, lateral lobes with 1 acerose bristle or mucronate, not forming a basal rosette, cauline leaves little reduced in size. Inflorescence mostly terminal and head-like, or solitary in the leaf axils, subtending bracts with bristle-tipped lobes. Calyx composed of herbaceous costae and narrow hyaline intercostal regions, lobes equal in length, bristle tipped. Corolla funnellform, bilaterally symmetric. Stamens subequally inserted below the sinuses of the corolla lobes, the filaments unequal in length. Pollen zonocolporate and striate to reticulate, yellow or gold.



Ovary glandular apically. Seeds becoming mucilaginous when wetted.  $N = 7$ . Three species. Type: *Loeseliastrum matthewsii* (Brand) Timbrook.

LOESELIASTRUM **depressum** (M. E. Jones ex A. Gray) J. M. Porter & L. A. Johnson, comb. nov.

Basionym: *Gilia depressa* M. E. Jones ex A. Gray, *Proc. Amer. Acad. Arts* 16: 106, 1880.

LOESELIASTRUM MATTHEWSII (A. Gray) Timbrook, *Madroño* 33: 171, 1986.

LOESELIASTRUM SCHOTTII (Torr.) Timbrook, *Madroño* 33: 172, 1986.

The segregation of *Loeseliastrum* from *Langloisia* has been discussed by Timbrook (1986) and is supported by morphological evidence; *Loeseliastrum* is related to *Langloisia* and *Eriastrum* more closely than to *Gilia*, as suggested by Timbrook. We include *Loeseliastrum depressum*, formerly treated within *Ipomopsis* (Grant 1956; 1959), in this small genus. Although morphological data is somewhat equivocal, *L. depressum* shares bilaterally symmetric flowers, glandular trichomes (in addition to long nonglandular trichomes), subequally inserted filaments that are unequal in length, and corolla vasculature with veins connected only well above the base of the corolla lobe, with *Loeseliastrum*. The corolla vasculature trait has not been observed in *Ipomopsis* (Day and Moran 1986), and in *Loeseliastrum* occurs only in *L. matthewsii*. This is noteworthy because chloroplast *trnL-F* DNA sequences provide evidence supporting the hypothesis that *L. depressum* and *L. matthewsii* share immediate common ancestry (Porter et al. in prep.). It must be recognized, however, that nuclear ITS sequences support (albeit weakly) *L. depressum* as sister to *Loeseliastrum*, *Langloisia*, and *Eriastrum* (but not to *Ipomopsis*).

**Microgilia** J. M. Porter & L. A. Johnson, gen. et stat. nov.

Planta glaberrima vel minute glanduloso-puberula. Caulis erectus. Folia altera, linearia, integra vel pinnatisecta, segmentis 2–3 linearibus. Flores solitarii vel ad 2(-3) aggregati, breviter pedicellati. Corolla alba vel violacea pallida. Ovarium ovoideum, superne ciliatum. Semina sub aqua dense mucilaginoso. Pollinis granum bi-zonocolporatum, exino striato. Ab *Ipomopsis* Michx. calyceibus lobis inaequalis, pollinis granis bi-zonocolporatis, et loculis uniovulatis differt. Typus: *Microgilia minutiflora* (Benth.) J. M. Porter et L. A. Johnson

Erect, taprooted woody annuals with a strong  $\pm$  linear central leader giving rise to linear ascending branches; stipitate glandular, rarely appearing glabrate. Cotyledons long-linear; foliage leaves not forming a basal rosette, cauline, trifid with linear, filiform segments, or entire and linear to filiform. Flowers short pedicellate to nearly sessile, solitary, appearing mostly axillary but actually terminal on short axillary shoots. Calyx composed of herbaceous costae and hyaline intercostal regions fused beyond mid-tube, the lobes un-

equal to subequal in length, spinulose tipped, and narrower than the connecting membrane, the membrane truncate or nearly so when expanded. Corolla salverform, white or pale blue, with radial symmetry. Stamens subequally inserted in the distal corolla tube, the filaments unequal to equal in length; pollen bizonocolporate with a striate exine. Ovary glandular apically, style often persisting in fruit. Seeds one per locule, flattened but shallowly convex on one side with a narrow longitudinal ridge on the other, appearing narrowly winged by the presence of copious spiracles that expand when wetted.  $N = 7$ . One species. Type: *Microgilia minutiflora* (Benth.) J. M. Porter & L. A. Johnson.

**Microgilia minutiflora** (Benth.) J. M. Porter & L. A. Johnson, comb. nov.

Basionym: *Gilia minutiflora* Benth., *Prodr.* v.9, p.315, 1845.

Morphologically, *Microgilia* is separated from *Ipomopsis* (see Grant 1956), by its calyx, with unequal lobes (also found in *Eriastrum*), and bizonate pollen (found only rarely in some *Lathrocasis* individuals). Pollen morphology is intriguing because the bizonotreme condition is somewhat intermediate between zonotreme (found in *Ipomopsis*) and pantotreme (found in some *Eriastrum* species). Molecular cladistic analyses (Johnson, 1996; Johnson et al. 1996; Porter et al. unpubl.) provide weak support for sister group relationship between *Microgilia* and a clade composed of *Eriastrum*, *Langloisia*, and *Loeseliastrum*. Collectively, morphological and molecular evidence support the segregation of *Microgilia*.

PHLOCIDAE Dumort.

*Anal. fam. pl.*, p.25, 1829.

Subshrubs or annual herbs. Leaves opposite or the uppermost alternate, rarely only lowermost leaves opposite, or foliage leaves entirely lacking (*Gymnosteris*); entire to pinnately lobed or palmately compound. Corollas radially symmetric, campanulate, funnelform or salverform. Pollen yellow, white, or orange. Seeds light or dark. Type: *Phlox* L. Synonymy includes Phlogieae (Rchb.) J. M. Porter & L. A. Johnson, *Aliso* 17: 84. 1998; Leptodactyloneae V. E. Grant, *Amer. J. Bot.* 85: 746. 1998; and Gruppe Polemoniariae, Phloginae Rchb., *Handb. Nat. Pflzsystems ed. 1*, p.194. 1837.

**Phylogenetic delineation.**—The most incorporative monophyletic group of species that includes *Gymnosteris nudicaulis*, *Leptosiphon androsaceus*, *Linanthus dichotomus*, and *Phlox glaberrima*, and that shares a more recent common ancestor with *Linanthus filiformis* than with *Aliciella triodon*, *Polemonium caeruleum*, or *Saltugilia grinnellii*.

**Membership.**—*Gymnosteris*, *Leptosiphon*, *Linanthus*, *Microsteris*, and *Phlox*, (5 genera, 127 species).

Tribe Phlocideae incorporates Grant's (1998a) Tribe Leptodactyloneae, and three members of Grant's Tribe Polemonieae. All of these genera display a tendency toward possessing opposite leaves (Grant 1959); however, not all species in this tribe have opposite leaves (Mason 1941). Similarly, most species possess salverform corollas, but other forms are also found. Nuclear and chloroplast gene sequences also support the monophyly of Phlocideae (Johnson et al. 1996; Porter 1996).

**GYMNOSTERIS** Greene, *Pittonia* 3: 303, 1898.

Annual herbs, stems naked or nearly so, but bearing persistent cotyledons. Leaves reduced to a whorl of entire, basally connate involucre bracts, subtending a more or less capitate inflorescence. Inflorescences cymose, more or less congested or reduced to a single flower. Calyx almost entirely hyaline, save the herbaceous lobes. Corolla salverform, the tube narrow, lobes somewhat large (to 6.0 mm long) to very short, spreading, acute to rounded apically. Stamens equally inserted on the distal corolla tube; pollen pantoporate, with reticulate exine. Seeds 3 or more per locule, producing copious mucilage when wetted.  $N = 6$ . Two species. Type: *Gymnosteris nudicaulis* (Hook. & Arn.) Greene.

*GYMNOSTERIS NUDICAULIS* (Hook. & Arn.) Greene, *Pittonia* 3: 304, 1898.

*GYMNOSTERIS PARVULA* (Rydb.) A. Heller, *Muhlenbergia* 1: 3, 1900.

Affinities of *Gymnosteris* lie with *Phlox* and *Microsteris* (Johnson et al. 1996) rather than *Collomia* (Wherry 1944; Grant 1959, 1998a). *Gymnosteris* pollen is nearly identical to that of *Phlox* (Stuchlik 1967a; Taylor and Levin 1975), and seeds produce copious mucilage when wetted that appears to be truly mucilaginous in origin (as does *Microsteris*), rather than the expansion of obvious spiracles as observed in *Collomia* (Schnopf and Deichgraber 1983). Also, the congested inflorescence of *Gymnosteris*, although similar to those found in *Collomia*, is equally similar to those found in *Phlox* and elsewhere in Phlocideae. Chloroplast and nuclear DNA sequences strongly support this view (Johnson 1996; Johnson and Soltis 1998).

*LEPTOSIPHON* Benth., *Edward's Bot. Reg.* 19: sub. t. 1622, 1833.

Low to erect and slender annuals, or perennials, sometimes woody at the base. Leaves opposite, palmately lobed, rarely entire (*L. floribundus* subsp. *hallii*), with 3–9 lobes, nearly glabrous to scabrous, tomentose or glandular. Inflorescence either open or head-like, flowers pedicellate, rarely sessile (*L. lemmonii*). Corolla salverform to funnellform, often with a ring of hairs within the tube. Stamens equal in length,

attached at the same level in the corolla, pollen yellow, pantoporate, rarely pantocolporate, with pilate, reticulate exine. Seeds becoming mucilaginous when wetted, or remaining unchanged.  $N = 9, 18$ . Thirty-one species of western North America and Chile. Type: *Leptosiphon androsaceus* Benth. Synonymy includes *Siphonella* A. Heller, *Muhlenbergia* 8: 57, 1912; and *Linanthis* Ewan, *Jour. Wash. Acad. Sci.* 32: 139, 1942.

*LEPTOSIPHON ACICULARIS* (Greene) Jeps., *School fl. Pacif. Coast.* p.77, 1902.

*LEPTOSIPHON ambiguus* (Rattan) J. M. Porter & L. A. Johnson comb. nov.

Basionym: *Gilia ambigua* Rattan, *Bot. Gaz. (Crawfordsville)* 11: 339, 1886.

*LEPTOSIPHON ANDROSACEUS* Benth., *Edward's Bot. Reg.* 19: sub. t. 1622, ii, 1833.

*LEPTOSIPHON aureus* (Nutt.) J. M. Porter & L. A. Johnson comb. nov.

Basionym: *Gilia aurea* Nutt., *Proc. Acad. Nat. Sci. Philadelphia* 4: 11, 1848.

*LEPTOSIPHON aureus* subsp. *decorus* (A. Gray) J. M. Porter & L. A. Johnson comb. nov.

Basionym: *Gilia aurea* var. *decora* A. Gray, *Proc. Amer. Acad. Arts* 8: 264, 1870.

*LEPTOSIPHON BICOLOR* Nutt., *Proc. Acad. Nat. Sci. Philadelphia* 4: 11, 1848.

*LEPTOSIPHON bolanderi* (A. Gray) J. M. Porter & L. A. Johnson comb. nov.

Basionym: *Gilia bolanderi* A. Gray, *Proc. Amer. Acad. Arts* 8: 263, 1870.

*LEPTOSIPHON breviculus* (A. Gray) J. M. Porter & L. A. Johnson comb. nov.

Basionym: *Gilia brevicula* A. Gray, *Proc. Amer. Acad. Arts* 12: 79, 1876.

*LEPTOSIPHON CILIATUS* (Benth.) Jeps., *School fl. Pacif. Coast.* p.77, 1902.

*LEPTOSIPHON croceus* (Eastw.) J. M. Porter & L. A. Johnson comb. nov.

Basionym: *Linanthis croceus* Eastw., *Pl. hartw.*, p.325, 1849.

*LEPTOSIPHON filipes* (Benth.) J. M. Porter & L. A. Johnson comb. nov.

Basionym: *Gilia filipes* Benth., *Pl. hartw.*, p.325, 1849.

*LEPTOSIPHON floribundus* (A. Gray) J. M. Porter & L. A. Johnson comb. nov.

Basionym: *Gilia floribunda* A. Gray, *Proc. Amer. Acad. Arts* 8: 267, 1870.

*LEPTOSIPHON floribundus* subsp. *glaber* (R. Patt.) J. M. Porter & L. A. Johnson comb. nov.

Basionym: *Linanthis floribundus* (A. Gray) Milliken subsp. *glabrus* R. Patt., *Madrño* 24: 45, figs. 1 & 2a, 1977.

*LEPTOSIPHON floribundus* subsp. *hallii* (Jeps.) J. M. Porter & L. A. Johnson comb. nov.

Basionym: *Siphonella floribunda* (A. Gray) Jeps. var. *hallii* Jeps., *Fl. Calif.* v.3 pt. 2, p.219, 1943.

*LEPTOSIPHON GRANDIFLORUS* Benth., *Edward's Bot. Reg.* 19: sub. t. 1622, ii, 1833.

*LEPTOSIPHON harknessii* (Curran) J. M. Porter & L. A. Johnson comb. nov.

Basionym: *Gilia harknessii* Curran, *Bull. Calif. Acad. Sci.* 1: 12, 1884.

*LEPTOSIPHON jamauensis* (Moran) J. M. Porter & L. A. Johnson comb. nov.

- Basionym: *Linanthus jamaensis* Moran, *Madroño* 24: 147, 148, 149, 150, fig. 1, 1977.
- LEPTOSIPHON **jepsonii** (D. W. Schemske & C. Goodwillie) J. M. Porter & L. A. Johnson comb. nov.  
Basionym: *Linanthus jepsonii* D. W. Schemske & C. Goodwillie, *Madroño* 43: 453, 455, 456, 457, fig. 1, 1996.
- LEPTOSIPHON **latisectus** (E. G. Buxton) J. M. Porter & L. A. Johnson comb. nov.  
Basionym: *Linanthus latisectus* E. G. Buxton, *Madroño* 41: 178, 1994.
- LEPTOSIPHON **laxus** (Vasey & Rose) J. M. Porter & L. A. Johnson comb. nov.  
Basionym: *Gilia laxa* Vasey & Rose, *Proc. U. S. Natl. Mus.* 11: 531, 1889.
- LEPTOSIPHON **lemmonii** (A. Gray) J. M. Porter & L. A. Johnson comb. nov.  
Basionym: *Gilia lemmonii* A. Gray, *Syn. fl. N. Amer.* v.2, p.394, 1878.
- LEPTOSIPHON **liniflorus** (Benth.) J. M. Porter & L. A. Johnson comb. nov.  
Basionym: *Gilia liniflora* Benth., *Edward's Bot. Reg.* 19: sub. t. 1622, iii, 1833.
- LEPTOSIPHON **melingii** (Wiggins) J. M. Porter & L. A. Johnson comb. nov.  
Basionym: *Leptodactylon melingii* Wiggins, *Contr. Dudley Herb.* 1: 173, 1933.
- LEPTOSIPHON **montanus** (Greene) J. M. Porter & L. A. Johnson comb. nov.  
Basionym: *Linanthus montanus* Greene, *Erythea* 3: 120, 1895.
- LEPTOSIPHON **nudatus** (Greene) J. M. Porter & L. A. Johnson comb. nov.  
Basionym: *Linanthus nudatus* Greene, *Erythea* 3: 120, 1895.
- LEPTOSIPHON **nuttallii** (A. Gray) J. M. Porter & L. A. Johnson comb. nov.  
Basionym: *Gilia nuttallii* A. Gray, *Proc. Amer. Acad. Arts* 8: 267, 1870.
- LEPTOSIPHON **nuttallii** subsp. **howellii** (T. W. Nelson & R. Patt.) J. M. Porter & L. A. Johnson comb. nov.  
Basionym: *Linanthus nuttallii* (A. Gray) Milliken subsp. *howellii* T. W. Nelson & R. Patt., *Madroño*, 32: 102, 1985.
- LEPTOSIPHON **nuttallii** subsp. **pubescens** (R. Patt.) J. M. Porter & L. A. Johnson comb. nov.  
Basionym: *Linanthus nuttallii* (A. Gray) Milliken subsp. *pubescens* R. Patt., *Madroño* 24: 43, figs. 1 & 2c, 1977.
- LEPTOSIPHON **oblanceolatus** (Brand) J. M. Porter & L. A. Johnson comb. nov.  
Basionym: *Gilia oblanceolata* Brand, *Pflanzenr.* IV 250, p.136, 1907.
- LEPTOSIPHON **pachyphyllum** (R. Patt.) J. M. Porter & L. A. Johnson comb. nov.  
Basionym: *Linanthus pachyphyllum* R. Patt., *Madroño* 24: 44, figs. 1 & 2f, 1977.
- LEPTOSIPHON **parviflorus** Benth., *Edward's Bot. Reg.* 19: sub. t. 1622, ii, 1833.
- LEPTOSIPHON **pusillus** (Benth.) J. M. Porter & L. A. Johnson comb. nov.  
Basionym: *Gilia pusilla* Benth., *Edward's Bot. Reg.* 19: sub. t. 1622, iii, 1833.
- LEPTOSIPHON **pygmaeus** (Brand.) J. M. Porter & L. A. Johnson comb. nov.  
Basionym: *Gilia pygmaeus* Brand, *Pflanzenr.* IV 250, p.134, 1907.
- LEPTOSIPHON **pygmaeus** subsp. **continentalis** (Raven) J. M. Porter & L. A. Johnson comb. nov.  
Basionym: *Linanthus pygmaeus* (Brand.) J. T. Howell subsp. *continentalis* P. H. Raven, *Aliso* 5: 334, 1965.
- LEPTOSIPHON **rattanii** (A. Gray) J. M. Porter & L. A. Johnson comb. nov.  
Basionym: *Gilia rattanii* A. Gray, *Syn. fl. N. Amer. ed. 2* v.2, p.407, 1886.
- LEPTOSIPHON **septentrionalis** (H. Mason) J. M. Porter & L. A. Johnson comb. nov.  
Basionym: *Linanthus septentrionalis* H. Mason, *Madroño* 4: 159, pl. 28, figs. a-e, 1938.
- LEPTOSIPHON **serrulatus** (Greene) J. M. Porter & L. A. Johnson comb. nov.  
Basionym: *Linanthus serrulatus* Greene, *Erythea* 3: 120, 1895.

Not treated at the generic level since Jepson's School Flora (Jepson 1902), *Leptosiphon* was first recognized in the same communication relegating *Linanthus* to generic status (Bentham 1833), and historically has been a recognized genus in classifications (Reichenbach 1837; see Table 1). Some morphological support for the distinction between *Leptosiphon* and *Linanthus* was indicated by Wherry (1961: 10), but he did not make nomenclatural changes:

The aim of this note has been to point out that, if calyx characters are given adequate consideration, the so-called genus *Linanthus* is polyphyletic. The small group of its members which includes the generitype, and so here is termed colloquially the eulinanthus section, seems to have arisen from the *Leptodactylon* complex. Most of them have on the other hand evolved from perennials which may be assigned to the genus *Linanthastrum*, and so could be classed as generically distinct from *Linanthus* Bentham (1833), *sens. strict.*

Although all of the details of Wherry's note have not found support, his hypotheses of relationship between *Linanthus* sect. *Linanthus* and *Leptodactylon*, and between *Linanthastrum* (= *Leptosiphon nuttallii* and relatives) and much of what previously has been referred to as "*Linanthus*" is endorsed strongly by molecular phylogenetic analyses (Johnson et al. 1996; Porter 1996; Bell et al. 1999; Bell and Patterson 2000). *Leptosiphon*, as here circumscribed, includes taxa formerly included in *Linanthus* sections *Siphonella*, *Leptosiphon*, *Pacificus*, and *Dactylophyllum*.

LINANTHUS Benth., *Edward's Bot. Reg.* 19: sub. t. 1622, 1833.

Low to erect and slender annuals, or perennials, sometimes woody at the base. Leaves opposite or alternate, entire, palmately, or sometimes pinnately lobed, with 1-9 lobes. Inflorescence either open or head-like, flowers sessile or shortly pedicellate. Corolla salverform, funnelform, or campanulate, sometimes vesperine. Stamens equal in length, attached at the same level in the corolla, pollen yellow, pantoporate, with minutely reticulate or striate-reticulate exine. Seeds not becoming mucilaginous when wetted in many species, but becoming mucilaginous in others. *N* = 9, 18. Twenty-four species of western North America. Type: *Linanthus dichotomus* Benth. Synonymy includes *Fenzlia* Benth., *Edward's Bot. Reg.* 19: sub. t.

1622, 1833; *Leptodactylon* Hook. & Arn., *Bot. Beechey Voy.*, p.369, 1839; *Maculigilia* V. E. Grant, *Phytologia* **84**: 78, 79, 1999; and *Tintinabulum* Rydb. Fl. Rocky Mts. p.698 [p.1065], 1917 [1918].

LINANTHUS ARENICOLA (M. E. Jones) Jeps. & V. Bailey ex Jeps., *Fl. Calif.* v.3, pt. 2, p.205, 206, 1943.

LINANTHUS BELLUS (A. Gray) Greene, *Pittonia* **2**: 256, 1892.

LINANTHUS BIGELOVII (A. Gray) Greene, *Pittonia* **2**: 253, 1892.

LINANTHUS **californicus** (Hook. & Arn.) J. M. Porter & L. A. Johnson comb. nov.

Basionym: *Leptodactylon californicum* Hook. & Arn., *Bot. Beechey Voy.*, p.369, 1839.

LINANTHUS **campanulatus** (A. Gray) J. M. Porter & L. A. Johnson, comb. nov.

Basionym: *Gilia campanulata* A. Gray, *Proc. Amer. Acad. Arts* **8**: 279, 1870.

LINANTHUS **caespitosus** (Nutt.) J. M. Porter & L. A. Johnson comb. nov.

Basionym: *Leptodactylon caespitosum* Nutt., *Proc. Acad. Nat. Sci. Philadelphia* **4**: 12, 1848.

LINANTHUS CONCINNUS Milliken, *Univ. Calif. Publ. Bot.* **2**: 53, 1904.

LINANTHUS DEMISSUS (A. Gray) Greene, *Pittonia* **2**: 257, 1892.

LINANTHUS DIANTHIFLORUS (Benth.) Greene, *Pittonia* **2**: 254, 1892.

LINANTHUS DICHOTOMOUS Benth., *Edward's Bot. Reg.* **19**: sub. t. 1622, 1833.

LINANTHUS **filiformis** (C. Parry ex A. Gray) J. M. Porter & L. A. Johnson, comb. nov.

Basionym: *Gilia filiformis* C. Parry ex A. Gray, *Proc. Amer. Acad. Arts* **10**: 75, 1874.

LINANTHUS **glabrum** (R. Patt. & M. Yoder-Williams) J. M. Porter & L. A. Johnson, comb. nov.

Basionym: *Leptodactylon glabrum* R. Patt. & M. Yoder-Williams, *Syst. Bot.* **9**: 161, 162, 1984.

LINANTHUS **inyoensis** (I. M. Johnst.) J. M. Porter & L. A. Johnson, comb. nov.

Basionym: *Gilia inyoensis* I. M. Johnst., *Contr. Gray Herb.* **75**: 39, 1925.

LINANTHUS **jaegeri** (P. A. Munz) J. M. Porter & L. A. Johnson comb. nov.

Basionym: *Gilia jaegeri* P. A. Munz, *Bull. S. Calif. Acad. Sci.* **31**: 68, 1932.

LINANTHUS JONESII (A. Gray) Greene, *Pittonia* **2**: 254, 1892.

LINANTHUS KILLIPII H. Mason, *Madroño* **9**: 251, 1948.

LINANTHUS MACULATUS (Parish) Milliken, *Univ. Calif. Publ. Bot.* **2**: 55, 1904.

LINANTHUS ORCUTTII (C. Parry & A. Gray) Jeps., *Man. fl. pl. Calif.*, p.804, 1925.

LINANTHUS PARRYAE (A. Gray) Greene, *Pittonia* **2**: 256, 1892.

LINANTHUS **pungens** (Torr.) J. M. Porter & L. A. Johnson comb. nov.

Basionym: *Cantua pungens* Torr., *Ann. Lyceum Nat. Hist. New York* **2**: 221, 1826.

LINANTHUS UNCIALIS (Brandegee) Moran, *Madroño* **24**: 151, 1977.

LINANTHUS **veachii** (C. Parry ex Greene) J. M. Porter & L. A. Johnson comb. nov.

Basionym: *Gilia veachii* C. Parry ex Greene, *Bull. Calif. Acad. Sci.* **2**: 198, 1885.

LINANTHUS WATSONII (A. Gray) Wherry, *Aliso* **5**: 10, 1961.

LINANTHUS VISCAINENSIS Moran, *Madroño* **24**: 152, 153, 154, figs. 3 & 4, 1977.

*Linanthus*, while morphologically diverse, is evidently monophyletic as here circumscribed (Johnson et al. 1996; Porter 1996; Bell et al. 1999; Bell and

Patterson in press). Species formerly treated as the genus *Leptodactylon* are, without question, within this monophyletic group. This is supported not only by molecular phylogenetic studies, but also morphology (Wherry 1961; see also Fig. 1 a & c, in Patterson 1977). For example, with the exception of *Linanthus californicus*, all of the species formerly of *Leptodactylon* possess vespertine flowers, as is found in *Linanthus* section *Linanthus* (*Linanthus arenicola*, *L. bigelovii*, *L. dichotomous*, *L. jonesii*, and *L. viscaïnensis*).

We also include section *Dianthoides*, which, along with *L. maculatus*, *L. campanulatus*, *L. inyoensis*, and *L. filiformis*, are a grade leading to the remainder of *Linanthus*. While it may seem desirable to remove some of these to another genus (e.g., *Tintinabulum* and *Maculigilia*, Grant 1998b), such an attempt, without additional generic circumscription ("splitting"), gives taxonomic status to a paraphyletic group. While *L. maculatus*, *L. campanulatus*, *L. inyoensis*, and *L. filiformis* all possess alternate leaves (at least above the lowest nodes), seemingly discordant with *Linanthus*, it is important to also observe that *L. arenicola*, *L. californicum*, *L. pungens*, and *L. viscaïnensis* also possess alternate leaves. Moreover, the floral morphology of *L. maculatus*, *L. campanulatus*, *L. inyoensis*, and *L. filiformis* is strikingly similar to members of sect *Dianthoides* in having a calyx with a short tube, and rotate to campanulate corolla with red marks near the orifice of the corolla tube.

It is noteworthy that only a decade has passed since *Linanthus maculatus* was returned to *Gilia* (Patterson 1989). This decision was based on a comparative morphological study that demonstrated great morphological similarity between *L. maculatus* and three species of "Gilia" (*L. campanulatus*, *L. inyoensis*, and *L. filiformis*). Recent comparative DNA studies of nrITS (Porter 1996; Bell et al. 1999), and cp *trnL-F* (Johnson and Porter, unpubl.) support Patterson's (1989) assertions regarding affinities among these species; however, all four species share most recent common ancestry with *Linanthus*, rather than *Gilia*.

Close examination of Porter (1996) reveals that *Linanthus inyoensis* was inferred (albeit weakly) to share common ancestry with *Phlox*, *Microsteris* and *Leptosiphon*, in some analyses of nr ITS sequences (and also cp *trnL-F*, Johnson and Porter unpubl.). While no additional molecular data has been surveyed that suggests these independent chloroplast and nuclear genes are revealing erroneous inferences of relationship for this species (due to introgression, lineage sorting, or systematic error), there is an overwhelming similarity between *L. inyoensis* and *L. campanulatus* (the two were considered conspecific by some authors: e.g., Jepson 1957). They differ primarily in flower size. Rather than recognize a new, monotypic genus based



upon flower size and weak molecular evidence, we include *L. inyoensis* within *Linanthus* and recommend further study of this species.

MICROSTERIS Greene, *Pittonia* 3: 300, 1898.

Annual herbs, stems erect and branched. Leaves opposite below, alternate above, simple and entire. Inflorescences cymose, reduced to a pair or single flowers. Calyx tube with hyaline intervals alternating with the herbaceous costae, the lobes with hyaline margins. Corolla salverform, the tube narrow, lobes short, spreading, somewhat notched apically. Stamens unequally inserted on the corolla tube. Pollen pantoporate, with reticulate exine. Seeds one per locule, producing copious mucilage when wetted. *N* = 7. One species.

MICROSTERIS GRACILIS (Dougl. ex Hook.) Greene, *Pittonia* 3: 300, 1898.

MICROSTERIS GRACILIS (Dougl. ex Hook.) Greene subsp. HUMILIOR (Greene) H. Mason, *Abrams. Ill. fl. Pacific States* v.3, p.413, 1951.

*Microsteris* is generally considered to include a single, polymorphic species with perhaps two widespread races. These races differ largely in architecture and flower size: subsp. *gracilis* is unbranched with larger flowers, subsp. *humilior* is branched with small flowers (see Cronquist 1984). In actuality, morphological variation across western North America is much more complicated and appears to involve phenotypically plastic traits. Moreover, *Microsteris* occurs in an incredibly diverse array of habitats, ranging from alpine slopes to Sonoran Desert washes. A nearly identical degree of variation is observed in South America, both in terms of morphology and habitat. *Microsteris* may be more diverse than previously indicated. Directed research is required to determine the limits of geographically partitioned genetic diversity (subspecies) and the role of phenotypic plasticity in the diversification of *Microsteris*.

PHLOX L., *Gen. pl. ed. 1*, p.52, 1737.

Annual or perennial herbs, stems erect to decumbent, sometimes cushion-like or mat-forming. Leaves opposite, the uppermost sometimes alternate, simple, entire, often connate at the base. Inflorescences cymose, sometimes reduced to a single flower. Calyx tube with hyaline intervals alternating with the herbaceous costae, the lobes with hyaline margins. Corolla salverform, the tube narrow, lobes large, spreading, acute to notched apically. Stamens unequally inserted on the corolla tube; pollen pantoporate, with reticulate exine. Seeds 1(–4) per locule, not producing copious mucilage when wetted. *N* = 7. About 69 species. Type: *Phlox glaberrima* L.

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- PHLOX ADSURGENS Torr. ex A. Gray, *Proc. Amer. Acad. Arts* 8: 256, 1870.
- PHLOX ALBOMARGINATA M. E. Jones, *Zöe* 4: 367 & 368, 1894.
- PHLOX ALBOMARGINATA M. E. Jones subsp. DIAPENSIODES (Rydb.) Wherry, *Notul. Nat. Acad. Nat. Sci. Philadelphia*, 87: 11, 1941.
- PHLOX ALYSSIFOLIA Greene, *Pittonia* 3: 27 & 28, 1896.
- PHLOX AMABILIS Brand, *Pflanzenr.* IV 250, p.74, 1907.
- PHLOX AMOENA Sims, *Bot. Mag.* 32: t. 1308, 1810.
- PHLOX AMOENA Sims subsp. LIGHTHIPEI (Small) Wherry, *Morris Arbor. Monogr.* 3. (*Gen. Phlox*), p.55, 1955.
- PHLOX AMPLIFOLIA Britton, *Man. fl. n. U. S.*, p.757, 1901.
- PHLOX ANDICOLA E. E. Nelson, *Revis. W. N. Amer. Phlox.*, p.11, 12 & 13, 1899.
- PHLOX ANDICOLA E. E. Nelson subsp. PARVULA Wherry, *Morris Arbor. Monogr.* 3. (*Gen. Phlox*), p.151, 1955.
- PHLOX AUSTROMONTANA Coville, *Contrib. U. S. Natl. Herb.* 4: 151, 1893.
- PHLOX AUSTROMONTANA Coville subsp. DENSE (Brand) Wherry, *J. Wash. Acad. Sci.* 29: 519, 1939.
- PHLOX AUSTROMONTANA Coville subsp. PROSTRATA (E. E. Nelson) Wherry, *J. Wash. Acad. Sci.* 29: 518, 1939.
- PHLOX BIFIDA Beck, *Amer. J. Sci.* 11: 170, 1826.
- PHLOX BIFIDA Beck subsp. STELLARIA (A. Gray) Wherry, *Castanea* 16: 99, 1951.
- PHLOX BOREALIS Wherry, *Morris Arbor. Monogr.* 3. (*Gen. Phlox*), p.126, fig. p.125, 1955.
- PHLOX BUCKLEYI Wherry, *J. Wash. Acad. Sci.* 20: 26, 1930.
- PHLOX CESPITOSA Nutt., *J. Acad. Philadelphia n. s.* 7: 41, 1834.
- PHLOX CAROLINA L., *Sp. pl. ed. 2*, v.1, p.216 & 217, 1762.
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- PHLOX CAROLINA L. subsp. ANGUSTA Wherry, *Morris Arbor. Monogr.* 3. (*Gen. Phlox*), p.108, 1955.
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- PHLOX DOLICHANTHA A. Gray, *Proc. Amer. Acad. Arts* 12: 310, 1887.
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- PHLOX FLORIDANA Benth., *Prodr.* v.9, p.304 & 305, 1845.

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- PHLOX HIRSUTA E. E. Nelson, *Revis. W. N. Amer. Phlox.*, p.28 & 29, 1899.
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- PHLOX MESOLEUCA Greene, *Leaflets Bot. Obs.* **1**: 152, 1905.
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- PHLOX PANICULATA L., *Sp. pl. ed. 1*, p.151 & 152, 1753.
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PHLOX VIRIDIS E. E. Nelson subsp. LONGIPES (M. E. Jones) Wherry, *Morris Arbor. Monogr.* 3. (*Gen. Phlox*), p.88, 1955.

PHLOX VISCIDA E. E. Nelson, *Revis. W. N. Amer. Phlox.*, p.24 & 25, 1899.

*Phlox* is characterized by simple, entire leaves, salverform corolla, stamens unequally inserted on the corolla tube, and pantoporate pollen with reticulate exine. However, all of these traits are also found in one or another of the closely related genera, *Leptosiphon*, *Linanthus*, and *Microsteris*. Thus, in spite of the morphological cohesiveness, there are apparently few unambiguous synapomorphies for *Phlox*. Although some species are distinctive, intergradation is common in many species groups (Wherry 1955) and hybridization has been proposed to play a major role in the origin of species in some groups (e.g., Levin and Smith 1965; Levin 1966). The hybrid origin of some *Phlox* species is consistent with recent ITS sequence analyses (Ferguson et al. 2000).

There has been little controversy regarding generic limits, save the debate concerning the inclusion of *Microsteris* within *Phlox* (Mason 1941). Recent molecular cladistic analyses with improved sampling in *Phlox* (Ferguson et al. 2000), taken together with previous studies (Johnson et al. 1996; Porter 1996), provide evidence that *Microsteris* is the sister group to *Phlox*, rather than sharing close relationship to other annual *Phlox* species (Mason 1941). Thus, segregation of *Microsteris* from *Phlox* rests on the relative importance placed on distinguishing characters, such as seed coat mucilage and flower size, in generic delimitation (see also Grant 1998a).

#### POLEMONIEAE Dumort.

*Anal. fam. pl.*, p.25, 1829.

Perennial or annual (*Polemonium micranthum*) herbs. Leaves pinnately compound. Calyx accrescent, regular; corolla regular, rotate, campanulate or funnel-form. Stamens usually inserted equally. Seeds dark, angular, and shiny. Type: *Polemonium* L.

*Phylogenetic delineation.*—the most incorporative monophyletic group of species that includes *Polemonium caeruleum* and *P. micranthum*, and shares a more recent common ancestor with *Polemonium viscosum* than with *Aliciella triodon*, *Gilia laciniata*, *Gymnos-teris nudicaulis*, *Loeselia ciliata*, *Phlox glaberrima*, or *Saltugilia grinnellii*.

*Membership.*—*Polemonium*.

As a taxon, the name Polemonieae is redundant with *Polemonium*; recognition of this tribal rank is maintained for uniformity in treatment in this classification.

POLEMONIUM L., *Sp. pl. ed. 1*, v.1, p.162, 1753.

Perennial (one annual) herbs, stems generally erect, often glandular. Leaves alternate, pinnately compound, or very deeply pinnatifid, the terminal leaflet confluent with the rachis. Inflorescences variously cymose. Calyx tube mostly herbaceous, rarely with a very narrow or shallow hyaline interval alternating with the broad herbaceous costae, the lobes lacking hyaline margins. Corolla campanulate to funnellform, rarely nearly rotate. Stamens equally inserted on the mid to lower corolla tube, pollen pantoporate, with striate or reticulate exine. Seeds 1–10 per locule, producing copious mucilage when wetted. *N* = 9. About 28 species. Type: *Polemonium caeruleum* L.

POLEMONIUM ACUTIFLORUM (Willd. ex Roem. & Schult.) *Syst. Veg.* v.4, p.792. 1819.

POLEMONIUM BOREALE Adams, *Mem. Soc. Imp. Naturalistes Moscou* 5: 92, 1817.

POLEMONIUM BRANDEGEEI (A. Gray) Greene, *Pittonia* 1: 126, 1887.

POLEMONIUM CAERULEUM L., *Sp. pl.* v.1, p.162, 1753.

POLEMONIUM CAERULEUM L. subsp. VILLOSUM (Rud. ex Georgi)

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POLEMONIUM OCCIDENTALE Greene, *Pittonia* 2: 75, 1890.

POLEMONIUM OCCIDENTALE Greene subsp. LACUSTRE Wherry, *Amer. Midl. Naturalist* 34: 376, fig. 2, 1945.

POLEMONIUM PAUCIFLORUM S. Watson, *Proc. Amer. Acad. Arts.* 23: 280, 1888.

POLEMONIUM PAUCIFLORUM S. Watson subsp. HINCKLEYI (Standl.) Wherry, *Amer. Midl. Naturalist* 27: 747, 1942.

POLEMONIUM PAUCIFLORUM S. Watson subsp. *melindae* (J. Rzedowski, G. Calderon de Rzedowski & J. Villarreal) J. M. Porter & L. A. Johnson comb. nov.

Basionym: *Polemonium melindae* J. Rzedowski, G. Calderon de Rzedowski & J. Villarreal, *Acta Bot. Mex.* 31: 58, 60, 61, Fig. 1, 1995.

POLEMONIUM PAUCIFLORUM S. Watson subsp. STENOCALYX (Standl.) Wherry, *Amer. Midl. Naturalist* 27: 754, 1942.

POLEMONIUM PECTINATUM Greene, *Cal. Acad. Sci. Bull.* 1: 10, 1884.

POLEMONIUM PULCHELLUM Bunge, *Ledeb. Fl. altaic.* v.1, p.283, 1829.

POLEMONIUM PULCHERRIMUM Hook., *Bot. Mag.* 57: t. 2979, 1830.

- POLEMONIUM PULCHERRIMUM Hook. subsp. DELICATUM (Rydb.) Brand, *Pflanzenr.* IV 250, p. 35, 1907.
- POLEMONIUM PULCHERRIMUM Hook., subsp. LINDLEYI (Whearty) V. E. Grant, *Bot. Gaz. (Crawfordsville)* **150**: 163, 1989.
- POLEMONIUM REPTANS L. *Syst. nat. ed. 10*, v.2, p.925, 1759.
- POLEMONIUM SUMUSHANENSE Lu & Ma, *Acta. Sci. Nat. Univ. In-tramongol.* **20**: 392, 1989.
- POLEMONIUM VANBRUNTTIAE Britton *Bull. Torrey Bot. Club* **19**: 224, tab. 131, 1892.
- POLEMONIUM VISCOSUM Nutt., *Proc. Acad. Nat. Sci. Philadelphia* **4**: 10, 1848.

*Polemonium* is well characterized and cohesive morphologically, with perhaps the exception of *Polemonium micranthum*—the only annual species in this genus. However, species boundaries in some cases are complex and blurred by hybridization, convergent evolution, or both. Whereas monophyly of this genus is certain, it's sister group relationship is less clear. Species level systematic research for the genus as a whole is greatly needed, although the tufted alpine species have been investigated (Grant 1989). It is difficult convincingly to support close relationships between *Polemonium* and other members of Polemoniaceae using morphological data, a difficulty that may historically lie in seeking relationships with specific genera (i.e., members of tribe Polemonieae, sensu Grant) rather than with a broader group of genera. Mitochondria (Porter and Johnson 1998) and chloroplast (Johnson et al. 1996; Prather pers. comm.) DNA sequences provide evidence supporting the sister relationship between *Polemonium* and the remainder of Polemoniaceae, whereas nuclear ITS sequences show, but only weakly support, a sister relationship only with Phloceae.

*Key to the Genera of Polemoniaceae*

Identification of taxa within Polemoniaceae can be challenging for novice students of this family. This is due, in part, to the inherent complexity of morphological evolution and high degree of homoplasy that exists in characters useful in writing keys. Additionally, although distinguishing characters or character sets exist for all genera, some of these features are not readily observed in the field with typical magnifications of 10×–20× (e.g., pollen morphology, chromosome number, corolla venation, and fine-scale gland features). Furthermore, exceptional taxa abound for almost any single “key” characteristic. Difficulty in Polemoniaceae identification is also aggravated by available taxonomic keys that overlook exceptional taxa or present highly generalized or even inaccurate character descriptions. Nearly all keys to genera, of which we are aware, will fail for at least some species of a number of genera. We attempt here to present an artificial taxonomic key that will accurately place species within their respective genera using traits that can be observed in the field. We minimized or eliminated, when

possible, the use of traits that are obscure or difficult to observe (e.g., chromosome number), and contrasts of degree (e.g., slightly vs. densely); however, we do occasionally employ traits that require careful observation (e.g., seed coat mucilage/fibrils). By attempting to avoid generalizations and encompassing global, rather than only regional diversity, this key is somewhat complex. We hope the additional complexity is offset by the accuracy achieved in Polemoniaceae determination.

This key requires representative material possessing both flowers and mature fruit. Seed coat traits such as mucilage are readily observed in mature seed; however, maturing ovules generally will not display this feature. Further, pollen color and corolla pigmentation patterns are best noted from fresh material (both features are critical for species level determination). When the term “tube” is used below in reference to the corolla, this refers to the fused portion of the corolla, including both the parallel and the flared portions. Finally, it is essential to note that phenotypic plasticity is common in Polemoniaceae. It is particularly evident, for example, in the drought-stressed, diminutive forms of *Gilia* or etiolated forms collected in dense stands of grasses or shrubs. These abnormal forms may be challenging to key to genus, and even more challenging to correctly determine to species with any key.

The superscript preceding a generic name denotes the number of times the genus occurs in the key. If no superscript is present, the genus is determined in only one place.

- 1. Leaves pinnate-compound, at least the lowest leaflets with a short petiolule . . . . . **2**
- 1. Leaves simple, entire to deeply lobed or pinnatifid, or palmate-compound; if pinnatifid, then all lobes continuous with the rachis . . . . . **4**
- 2. [1.] Leaves terminating in a dichotomous tendril; lianas; seeds flat, winged, more than 10 mm; fruit dehiscence septical . . . . . *Cobaea*
- 2. Leaves terminating in a leaflet confluent with the rachis; herbaceous perennials (one annual), not a vine; seeds less than 8 mm, often angular; fruit dehiscence loculicidal . . . . . **3**
- 3. [2.] Calyx appearing completely herbaceous (a narrow hyaline margin sometimes present along base of lobes, shortly intruding in the intercostal region), apex not mucronate . . . . . <sup>2</sup>*Polemonium*
- 3. Calyx with herbaceous costa and membranous intercostal region, lobe margins often scarious margined, apex of lobes mucronate . . . . . <sup>4</sup>*Giliastrum* (*G. purpusii* subsp. *purpusii*)
- 4. [1.] Vegetative leaves above the cotyledons reduced and fused at the base to form involucrel bracts; filaments apparently lacking (< 0.5 mm) . . . . . *Gymnosteris*
- 4. Vegetative leaves present and well developed; involucrel bracts, if present, not fused at the base; filaments present (> 0.5 mm) . . . . . **5**
- 5. [4.] Innermost bracts subtending calyx membranous on proximal margin or bearing window-like regions;



- leaves simple, dentate; corolla bilaterally symmetric, sometimes only slightly so . . . . . *Loeselia*
- 5. Bracts subtending calyx (if present) herbaceous; leaves and corolla various . . . . . 6
- 6. [5.] Subshrubs, shrubs or small trees; at least the lower portion of plants woody . . . . . 7
- 6. Annuals or rosette forming short-lived perennials, generally herbaceous, lacking a persistent, woody, above-ground stem, woody caudex may be present . . . . . 21
- 7. [6.] Leaves dimorphic, primary leaves pinnate, becoming persistent pinnate spines, axillary leaves linear on short shoots . . . . . *Acanthogilia*
- 7. Leaves various but not dimorphic, primary leaves not becoming persistent pinnate spines . . . . . 8
- 8. [7.] Calyx bilaterally symmetric or at least the calyx lobes unequal in length . . . . . 9
- 8. Calyx radially symmetric . . . . . 12
- 9. [8.] Leaves palmate and sessile, or pinnate-trifid and then leaves opposite . . . . . <sup>9</sup>*Linanthus*
- 9. Leaves entire, dentate, lyrate-pinnatifid, or pinnatifid with (2–)5–16 lobes and then leaves alternate . . . . . 10
- 10. [9.] Stamen filaments affixed in the sinus of the corolla lobes, inflorescence capitate; inflorescence, bracts and calyx floccose to woolly pubescent . . . <sup>3</sup>*Eriastrum*
- 10. Stamen filaments affixed in the lower (proximal) corolla tube; inflorescence variable: cymose, corymbose, to flowers in pairs or solitary, but not capitate; inflorescence, bracts and calyx glandular to glabrous, but not floccose or woolly . . . . . 11
- 11. [10.] Corolla tube geniculate, bearing a sharp bend at mid-tube; seeds oblong, wingless or with a very narrow, incomplete wing . . . . . *Bonplandia*
- 11. Corolla tube straight or curved, but not geniculate, seeds ovate, flat with a more or less broad wing . . . . . *Cantua*
- 12. [8.] Leaves opposite, at least the lower cauline leaves . . . . . 13
- 12. Leaves alternate throughout . . . . . 15
- 13. [12.] Stamen filaments unequally affixed in the corolla tube . . . . . <sup>2</sup>*Phlox*
- 13. Stamen filaments equally affixed in the corolla tube or sinus of the corolla lobes . . . . . 14
- 14. [13.] Corolla glandular externally, opening diurnally; leaves palmate, with 3–9 acute but soft and pliable lobes . . . . . <sup>3</sup>*Leptosiphon*
- 14. Corolla glabrous externally, opening at night; leaves palmate to pinnate, with 3–9 rigid and pungent lobes . . . . . <sup>9</sup>*Linanthus*
- 15. [12.] Corolla lobe longer than corolla tube . . . . . 16
- 15. Corolla lobe shorter than corolla tube . . . . . 18
- 16. [15.] Anthers and pollen yellow to nearly orange . . . . . <sup>4</sup>*Giliastrum*
- 16. Anthers and pollen cream colored to bright blue . . . . . 17
- 17. [16.] Anthers and pollen cream colored . . . . . <sup>4</sup>*Bryantiella*
- 17. Anthers and pollen blue . . . . . *Dayia*
- 18. [15.] Inflorescence capitate and head-like . . . . . <sup>3</sup>*Ipomopsis*
- 18. Inflorescence thyrsoid, or variously cymose, but not capitate . . . . . 19
- 19. [18.] Leaves mostly palmate and sessile, the lobes rigid and pungent tipped; flowers opening nocturnally . . . . . <sup>9</sup>*Linanthus*
- 19. Leaves linear and simple, or variously pinnatifid, lobes never rigid and pungent tipped; flowers opening diurnally . . . . . 20
- 20. [19.] Plants open and diffusely branching, densely glandular (nearly viscid), lacking eglandular hairs; flowers solitary or in pairs, radially symmetric; filaments attached at the mid-tube . . . . . <sup>4</sup>*Bryantiella*
- 20. Plants more or less strict and thyrsoid, branching from the base, sometimes somewhat open, bearing eglandular, white trichomes and sometimes glandular trichomes (not viscid); corolla bilaterally symmetric (rarely radial); filaments attached above the mid-tube . . . . . <sup>3</sup>*Ipomopsis*
- 21. [6.] Calyx wholly green (herbaceous) in flower, or carinate with a narrow intercostal membrane that terminates in a spout-like projection at the apex of the sinus . . . . . 22
- 21. Calyx with a well-defined hyaline intercostal membrane (sometimes narrow); calyx sinuses not pleated or expanded (though the entire calyx may be accrescent), and not terminating in a spout-like projection . . . . . 23
- 22. [21.] Calyx wholly green, accrescent, sinus not pleated in fruit; corolla rotate campanulate; . . . . . <sup>2</sup>*Polemonium* (*P. micranthum*)
- 22. Calyx with a narrow intercostal membrane that terminates in a spout-like projection at the apex of the sinus; sinus of calyx pleated to expanded in fruit; corolla funnelform to salverform, . . . . . *Collomia*
- 23. [21.] Leaves primarily opposite on lower stem, generally cauline, leaves often alternate in inflorescence or on distal portions of branches . . . . . 24
- 23. Leaves alternate, cauline and/or with a rosette (lower-most nodes sometimes subopposite to opposite) . . . . . 30
- 24. [23.] Stamen filaments unequally affixed in the corolla tube . . . . . 25
- 24. Stamen filaments equally affixed in the corolla tube . . . . . 26
- 25. [24.] Seeds not producing mucilage when wetted; perennial or annual; calyx accrescent and usually not splitting; most or all leaves opposite . . . . . <sup>2</sup>*Phlox*
- 25. Seeds producing mucilage when wetted; annual; calyx accrescent and usually splitting in the intercostal region, the lobes spreading; lower leaves opposite, upper alternate . . . . . *Microsteris*
- 26. [24.] Leaves pinnate-lobed, lobes pungent or spine-tipped; plants perennial; flower parts 4–6 . . . <sup>9</sup>*Linanthus*
- 26. Leaves palmate-lobed or entire, or if pinnate-lobed, then plants annual; leaf lobes sometimes acute or sharp, but not spine-tipped; flower parts in 5's . . . . . 27
- 27. [26.] Inflorescence a dense head, or geminate in small clusters . . . . . 28
- 27. Inflorescence not a dense head, variously cymose . . . . . 29
- 28. [27.] Corolla campanulate to short-funnelform . . . <sup>9</sup>*Linanthus*
- 28. Corolla salverform or funnelform, tube long exerted from the calyx, filamentous, < 1 mm wide, or if 1–2 mm wide, then the flared proximal (“throat”) region much shorter than the rest of the tube . . . . . <sup>3</sup>*Leptosiphon*
- 29. [27.] Flowers nocturnal (except in one race of *L. dichotomous*), mostly or all sessile to subsessile . . . <sup>9</sup>*Linanthus*
- 29. Flowers diurnal, on thread-like pedicels, or scattered in the axils of leaves and branches . . . . . <sup>3</sup>*Leptosiphon*
- 30. [23.] Calyx lobes unequal in length . . . . . 31
- 30. Calyx lobes equal in length . . . . . 34
- 31. [30.] Inflorescence of one or more congested, usually capitate units . . . . . 32
- 31. Inflorescence open, consisting of 1–3-flowered units, neither capitate nor subcapitate . . . . . 33

32. [31.] Inflorescence arachnoid hairy, with tangled white hairs ..... <sup>3</sup>*Eriastrum*
32. Inflorescence glandular, villous, or glabrous, but not arachnoid hairy ..... <sup>2</sup>*Navarretia*
33. [31.] Plant glandular puberulent to subglabrous; calyx glabrous to glandular; corolla salverform, 4–7 mm long, white or pale bluish ..... <sup>2</sup>*Microgilia*
33. Plant rarely viscid glandular and usually slightly floccose; calyx glabrous to floccose; corolla salverform, 8–12(-14) mm long, sapphire-blue with tube distally yellow ..... <sup>3</sup>*Eriastrum*
34. [30.] Lower cauline leaves palmate-lobed, more than three lobes ..... 35
34. Lower cauline leaves simple to pinnatifid, sometimes trifid, but not palmate-lobed (upper cauline leaves of inflorescence sometimes somewhat palmate) ..... 36
35. [34.] Leaves sessile, lobes divided to base, or nearly so ..... <sup>9</sup>*Linanthus*
35. Leaves with a distinct petiole usually longer than the lobes ..... <sup>5</sup>*Ipomopsis*
36. [34.] Leaf and calyx lobes bristle-tipped ..... 37
36. Leaf and calyx lobes obtuse, acute, mucronate, or rarely aristate but both not bristle-tipped ..... 38
37. [36.] Corolla bilaterally symmetric, leaf bristles solitary ..... <sup>2</sup>*Loeseliastrum*
37. Corolla radially symmetric, leaf bristles in 2's or 3's ..... *Langloisia*
38. [36.] Corolla rotate, campanulate or shortly funnelform, the lobes longer than the corolla tube ..... 39
38. Corolla funnelform to salverform, the lobes shorter than the corolla tube ..... 44
39. [38.] Calyx divided nearly to base, margin of lobe scarious, rarely ciliate ..... 40
39. Calyx fused to form a tube  $\frac{1}{2}$  or more the length of the lobes, margin of lobe scarious, but never ciliate ..... 41
40. [39.] Stems 1–12(-15) cm tall; corolla 3–7(-9) mm long, the lobes mostly less than 5 mm long, with yellow, purple or red markings below the lobes ... <sup>9</sup>*Linanthus*
40. Stems 10–70 cm tall; corolla (5-)8–17 mm long, the lobes mostly more than 5 mm long; corolla tube with a distinct yellow or whitish eye .... <sup>4</sup>*Giliastrum*
41. [39.] Corolla less than 4 mm long ..... 42
41. Corolla greater than 5 mm long ..... 43
42. [41.] Basal leaves narrowly lanceolate to oblanceolate, entire or with 1 or 2 lobes ..... <sup>2</sup>*Lathrocasis*
42. Basal leaves once-pinnatifid, the lobes nearly at right angles to the rachis ..... <sup>2</sup>*Aliciella*
43. [41.] Pollen cream colored to white ..... <sup>4</sup>*Bryantiella*
43. Pollen yellow to orange-yellow ..... <sup>4</sup>*Giliastrum*
44. [38.] Calyx divided nearly to base, margin of lobe scarious, rarely ciliate ..... <sup>9</sup>*Linanthus*
44. Calyx fused to form a tube  $\frac{1}{2}$  or more the length of the lobes, margin of lobe scarious, but never ciliate ..... 45
45. [44.] Ovules and seeds 1 per locule and upper leaves narrow, linear-entire or pinnate-trifid ..... 46
45. Ovules and seeds > 1 per locule, or if only 1, then upper leaves  $\pm$  palmate-compound and plants mephic ..... 47
46. [45.] Plants with one type of trichome (stipitate glandular) throughout; pedicels longer in length than the calyx; branching pattern divergently spreading ..... <sup>2</sup>*Lathrocasis*
46. Plants with glandular and eglandular trichomes; pedicels mostly shorter in length than the calyx; branching pattern ascending ..... <sup>2</sup>*Microgilia*
47. [45.] Seeds not mucilaginous or producing spiricles when wetted ..... <sup>2</sup>*Aliciella*
47. Seeds mucilaginous or producing spiricles when wetted ..... 48
48. [47.] Flowers arranged in one or more dense, thyrsoid, spiciform, or cymose-capitate inflorescences .... 49
48. Flowers in more open inflorescence, pedicellate, or if subsessile, then flowers scattered along stem (sympodial) ..... 51
49. [48.] Leaves once to twice pinnatifid, the segments usually toothed; corolla usually funnelform with a well-developed flared "throat" ..... <sup>2</sup>*Gilia*
49. Leaves entire to once pinnatifid, the segments not toothed; corolla narrowly funnelform to salverform, lacking a well-developed flared "throat" ..... 50
50. [49.] Leaves lance-elliptic, entire or dentate; corolla slightly bilaterally symmetric ..... <sup>2</sup>*Loeseliastrum*
50. Leaves pinnatifid or entire and then linear; corolla various ..... <sup>5</sup>*Ipomopsis*
51. [48.] Seeds dark brown to black; leaves more or less uniformly distributed throughout, reducing only gradually upwards, the upper cauline leaves  $\pm$  palmately lobed, or entire (and then similar to the lower leaves) or (rarely) twice pinnatifid, if palmate-lobed, then central lobe more broad than the lateral ones ..... 52
51. Seeds, greenish, tan, light brown or light gray; leaves frequently clustered in a basal rosette, upper cauline leaves simple and entire (and then different from the basal leaves), or pinnatifid, sometimes reduced and bract-like, the central lobe equal or narrower than the lateral lobes ..... 53
52. [51.] Trichomes, at least some, > 0.5 mm long and often longer, glandular or eglandular, mostly > 1 type or length throughout; cotyledons spatulate .. *Allophyllum*
52. Trichomes < 0.3 mm long, glandular,  $\pm$  uniform in ype throughout; cotyledons linear ..... <sup>2</sup>*Navarretia*
53. [52.] Corolla salverform or funnelform and then bilaterally symmetric ..... <sup>5</sup>*Ipomopsis*
53. Corolla campanulate to funnelform,  $\pm$  radially symmetric ..... 54
54. [53.] Apex of ovary glandular ..... <sup>4</sup>*Bryantiella*
54. Apex of ovary eglandular ..... 55
55. [54.] Trichomes on basal leaves translucent, minutely gland tipped; inflorescence glands subsessile, diameter of gland > length of stalk, more abundant on pedicel than calyx; pedicels and calyx without long stalked hairs. .... *Salugilia*
55. Trichomes on basal leaves eglandular white arachnoid (present at least in axils), or white geniculate, or translucent; if translucent, inflorescence glands long stalked, diameter of gland < length of stalk and generally equally abundant on pedicel and calyx, or inflorescence trichomes including long hairs ..... <sup>2</sup>*Gilia*

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