A NEW LINEAGE-BASED TRIBAL CLASSIFICATION OF THE FAMILY CARYOPHYLLACEAE

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Understanding the relationships within the Caryophyllaceae has been difficult, in part because of arbitrarily and poorly defined genera and difficulty in determining phylogenetically useful morphological characters. This study represents the most complete phylogenetic analysis of the family to date, with particular focus on the genera and relationships within the large subfamily Alsinoideae, using molecular characters to examine the monophyly of taxa and the validity of the current taxonomy as well as to resolve the obscure origins of divergent taxa such as the endemic Hawaiian Schiedea. Maximum parsimony and maximum likelihood analyses of three chloroplast gene regions (matK, trnL-F, and rps16) from 81 newly sampled and 65 GenBank specimens reveal that several tribes and genera, especially within the Alsinoideae, are not monophyletic. Large genera such as Arenaria and Minuartia are polyphyletic, as are several smaller genera. The phylogenies reveal that the closest relatives to Schiedea are a pair of widespread, largely Arctic taxa, Honkenyra peploides and Wilhelmsia physodes. More importantly, the three traditional subfamilies (Alsinoideae, Caryophylloideae, and Paronychioideae) are not reflective of natural groups; we propose abandoning this classification in favor of a new system that recognizes major lineages of the molecular phylogeny at the tribal level. A new tribe, Eremogoneae Rabeler & W.L. Wagner, is described here.

Keywords: Alsinoideae, Caryophylloideae, Eremogoneae, molecular phylogeny, Schiedea.

Online enhancement: appendix table.

Introduction

The family Caryophyllaceae Juss., the pink or carnation family, is cosmopolitan and includes a number of common ornamental plants, such as carnations (Dianthus L.) and baby’s breath (Gypsophila L.). The family is primarily Holarctic in distribution, with diversity centered in the Mediterranean and Irano-Turanian regions (Bittrich 1993), and includes ~3000 species distributed among 88 genera (Rabeler and Hartman 2005). The number of genera declines to 82 if one accepts a broad concept of Silene (see Greuter 1995; Morton 2005a) or could increase to more than 120 if one accepts all the segregates of several of the large genera that have been proposed (see Oxelman et al. 2001; Tzvelev 2001). The most common classification (Pax and Hoffmann 1934; Bittrich 1993) of Caryophyllaceae includes three subfamilies based on characters of the stipules, petals, sepals, and fruits: Alsinoideae Burnett [Minuartioideae DC.], Caryophylloideae Arn., and Paronychioideae A. St. Hil. ex Fenzl [Illecebroideae Arn.].

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‡ Review of the recently released work by Takhtajan (2009) revealed that, unfortunately, three of the subfamily names used throughout this paper are not the oldest available names. The correct names, following Reveal (2007), are as follows: Alsinoideae Burnett (1835) is predated by Minuartioideae DC. in Beilschm. (1833), Paronychioideae A. St. Hil. ex Fenzl (1839) is predated by Illecebroideae Arn. (1835), and Polycarpoideae Burnett (1835) is predated by Polycarpioideae Beilschm. (1833).
numbers, number of floral parts, and the presence and nature of nectaries.

Possible morphological homoplasies and difficulty in determining morphological synapomorphies make the use of molecular phylogenetic data critical in understanding the relationships within the Caryophyllaceae (Smissen et al. 2002; Fior et al. 2006). Until recently, most of the molecular studies that have included members of the Caryophyllaceae have focused on the relationships of the families within the order Caryophyllales rather than on relationships within the family (Rettig et al. 1992; Downie and Palmer 1994; Downie et al. 1997; Cuénoud et al. 2002); these studies have revealed that the family is monophyletic (Rettig et al. 1992; Downie and Palmer 1994; Downie et al. 1997; Fior et al. 2006), supporting the continued inclusion of members of the Paronychioideae. Many of the more focused studies have been on the tribe Sileneae DC., especially the genus Silene L. (Desfexus and Lejune 1996; Oxelman and Lidén 1995; Oxelman et al. 1997, 2001; Eggens et al. 2007; Erixon and Oxelman 2008). In addition, a number of studies on genera within the Caryophyllaceae have been completed (Schiedea Cham. & Schltdl.: Solits et al. 1996; Scleranthus: Smissen et al. 2003; Schiedea: Wagner et al. 2005; Arenaria L. and Moehringia L.: Fior and Karis 2007; Polycarpon L.: Kool et al. 2007; Silene: Popp and Oxelman 2001) and are beginning to provide an understanding of the complexities of the family. Finally, a recent study by Brockington et al. (2009) has advanced our understanding of the order Caryophyllales and the placement of the Caryophyllaceae.

Relationships within the Caryophyllaceae and monophyly of the subfamilies were first investigated with molecular data by Smissen et al. (2002), who produced a phylogeny of 15 genera based on the chloroplast ndhF gene. A more comprehensive study of 38 genera in the Caryophyllaceae was performed by Fior et al. (2006), using a combination of chloroplast (matK) and nuclear ribosomal DNA (nrDNA; ITS) data. Both of these studies revealed that none of the three traditional subfamilies (Alsinoideae, Caryophyllioideae, and Paronychioideae) is monophyletic. Despite limited sampling, Smissen et al. (2002) concluded that all three subfamilies are polyphyletic. While the molecular phylogenies in Fior et al. (2006) are not well resolved, they do suggest that Alsinoideae (minus tribe Pycnophyileae Mattf.) and Caryophyllioideae together form a monophyletic group, with Paronychioideae forming a basal grade. Both studies demonstrate that the Alsinoideae tribe Scleranthae Link ex DC. is clearly separated from tribe Alsinae Lam. & DC., which itself is polyphyletic (Smissen et al. 2002; Fior et al. 2006).

At a very basic level, members of subfamily Alsinoideae are distinguished from the Caryophyllioideae by their free sepal and from the Paronychioideae by their exstipulate leaves (McNeill 1962). Members of subfamily Alsinoideae are thought to be most closely related to subfamily Caryophyllioideae, on the basis of “caryophyllad type” embryogeny, the development of diverticles of the embryo sac, and the shared character of sheathing leaf bases (Bittrich 1993). However, the monophyly of the Alsinoideae has been questioned because it may be either monophyletic, based on nectary gland characteristics, or paraphyletic, based on chromosome numbers. Fernandes and Leitão (1971) assumed that the Silenoideae (Caryophyllioideae) are nested within the Alsinoideae and that they represent an increase in chromosome number from the base number of n = 9 for the family. Characters that have been used to circumscribe subfamily Alsinoideae include exstipulate leaves; perigynous or hypogynous flowers; often conspicuous petals; free sepals; mostly open or semiclosed petal venation; epipetalous stamens, often with a nectar gland at the base and mainly capsulate; and dehiscent fruit. As Bittrich (1993) suggested, the circumscription of the Alsinoideae could be less clear if genera (e.g. Polycarpon and Spergula L.) with capsular fruits, which are most often regarded as members of the subfamily Paronychioideae, are included in the Alsinoideae; Leonhardt (1951) did so in his seven-subfamily classification of the family. This lack of clarity could also occur when authors recognize a narrow sense of the Paronychioideae as the family Illecebraceae (Hutchinson 1973). These genera differ from the “core” Alsinoideae in characters of embryology, leaf venation, and presence of stipules, suggesting that capsular fruits may have arisen more than once in the Caryophyllaceae. Furthermore, the genus Geocarpon Mack. (Alsinoideae) has tiny petals that could be interpreted as staminodes, a diagnostic feature of some of the Paronychioideae (Bittrich 1993).

Relationships within subfamily Alsinoideae, the largest of the Caryophyllaceae subfamilies, are poorly known. Bittrich (1993) placed the 28 genera of the Alsinoideae into five tribes, the Alsinae (23 genera), the Geocarpeae E.J. Palmer & Steyermark (consisting of a single species, Geocarpon minimum Mack.), the Habrosieae Endl. (consisting of a single species, Habrosia spinuliflora Fenzl.), the Sclerantheae (two genera), and the Pycnophyileae Mattf. (consisting of the single genus Pycnophyllum E.J. Remy; see also table 1). Characters of floral variation (loculicidal vs. both loculicidal and septicidal dehiscence, carpel number, presence or absence of petals, and sepal characteristics) have been used extensively in generic delimitation in the Alsinoideae. However, such characters are known to be highly evolutionarily labile or plastic and may not represent homologous characters for use in defining phylogenetic groups (Endress 1996; Hufford 1996). Because of possible homoplasies, the subfamilial classification, in particular relationships within the Alsinoideae, has remained problematic and should be examined by use of molecular characters. For example, McNeill (1973) described an example from Turkey that illustrates the difficulty, due to the convergence of morphological characters, of segregating two genera in different subfamilies, Stellaria L. (Alsinoideae) and Gypsophila L. (Caryophyllioideae).

One of the major questions within subfamily Alsinoideae involves the delimitation of the widespread genus Arenaria (Fernald 1919; Pax and Hoffmann 1934; Maguire 1951; McNeill 1980) and whether it should be broadly or more narrowly circumscribed. Another problem is that certain genera, such as the North American Geocarpon and the Hawaiian Schiedea Cham. & Schltdl., have obscure relationships with the remainder of the family. The single species of Geocarpon (G. minimum) was originally placed outside of the Caryophyllaceae in the Aizoaceae but also possesses some characters of the subfamilies Alsinoideae and Paronychioideae, and it was placed in its own tribe by Palmer and Steyermark (1950). Schiedea, which represents the fifth-largest radiation of angiosperms in the Hawaiian flora (Wagner et al. 1995, 2005; Solíes et al. 1996), is one of the most striking examples of adaptive radiation in the islands. Previous studies based on morphological
and molecular data suggest that *Schiedea* is monophyletic and the result of a single ancestral colonization to the archipelago (Wagner et al. 1995, 2005; Weller et al. 1995; Soltis et al. 1996); however, their ancestor and source area remain unresolved. The use of traditional classifications of the Alsinoideae and Caryophyllaceae to identify the closest relatives of the Hawaiian lineage is problematic, and a molecular phylogenetic analysis should contribute immensely to both subfamilial classification and placement of the Hawaiian Alsinoideae within the family.

Morphologically, the Hawaiian Alsinoideae appear to be most closely aligned to the large “Arenaria complex,” a group that traditionally includes the large genera *Arenaria* and *Minuartia* and up to nine smaller genera (McNeill 1962; Wagner et al. 1999). The specialized morphology of the nectaries of the Hawaiian genera suggest a possible relationship with *Minuartia* sect. *Greniera* Mattf., which consists of two serpentine endemic species in the western United States, one of which (*Minuartia douglasii* Mattf.) has a similar unusual nectary extension (Harris and Wagner 1995). Current studies of the ontogeny of nectary characteristics in Hawaiian Alsinoideae and *Minuartia* sect. *Greniera* (Harris and Wagner 1995; Wagner and Harris 2000) suggest that development of nectary tissue follows the same pathway in both lineages. Molecular phylogenetic analysis based on nrDNA sequences suggests, however, that *Minuartia* sect. *Greniera* is not as closely related to the Hawaiian genera as previously believed (Wagner et al. 2005); this is consistent with our results as well. Carlquist (personal communication to S. Weller) has suggested a New World origin for the group, while Ballard and Sytsma (2000) pointed to the Arctic region as the possible origin of *Schiedea*, after the surprising discovery, based on molecular data, of a subarctic origin for *Viola* L. These results necessitate identification of the sister group to the Hawaiian lineage and, as a consequence, reevaluation of relationships within the Alsinoideae on a worldwide basis by means of independently derived, molecularly based phylogenies. Thus, a more comprehensive phylogenetic perspective will allow us to address the possibility of convergent evolution in a complex, well-characterized morphological trait until recently considered a synapomorphy for the Hawaiian Alsinoideae and *Minuartia*.

We examine the phylogenetic utility of morphological characters used in traditional classifications of Caryophyllaceae, focusing on subfamily Alsinoideae and the origin of the Hawaiian endemic *Schiedea* and using the historical context provided by a phylogeny derived from molecular characters, including three chloroplast gene regions (*matK, trnL-F, and rps16*). The primary goals of this study are (1) to examine the monophyly and relationships of the three traditional subfamilies of Caryophyllaceae, (2) to examine the relationships within subfamily Alsinoideae (Caryophyllaceae) on a worldwide basis, and finally, (3) to clarify the position of the Hawaiian Alsinoideae (*Schiedea*) and their ancestral source area.

### Material and Methods

#### Taxonomic Sampling

This study represents the most comprehensive sampling of Caryophyllaceae taxa in a molecular phylogenetic study to date and includes a total of 126 species from 46 genera in the Caryophyllaceae worldwide (including 81 newly sequenced specimens), with particular emphasis on subfamily Alsinoideae and tribe Alsineae, from which 18 of the 28 genera were sampled (table 1). Sampling was initially designed to cover all putative outgroups to the Hawaiian *Schiedea* species in order to determine the source area for colonization. This included a focus on the “Arenaria complex” (McNeill 1962); we also sampled a number of the smaller genera in the Alsinoideae (e.g., *Honckenya* Ehrh. and *Wilhelmsia* Rchb., but not all were available, including *Brachystemma* D. Don) as well as six of the 10 subgenera of *Arenaria* and each of the four subgenera of *Minuartia*. Nine outgroup sequences from three families in the Caryophyllales (Achatocarpaceae, Amaranthaceae,

### Table 1

<table>
<thead>
<tr>
<th>Subfamily, tribe</th>
<th>Total genera sampled in Smissen et al. 2002</th>
<th>Genera (species) sampled in Fior et al. 2006</th>
<th>Genera (species) sampled in this study</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alsinoideae:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alsineae Lam. &amp; DC.</td>
<td>28</td>
<td>-</td>
<td>4 (4)</td>
</tr>
<tr>
<td>Geocarpeae E.J.Palmer &amp; Steyerm.</td>
<td>1</td>
<td>-</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Habrosieae Endl.</td>
<td>1</td>
<td>-</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Pycnophyllum Mattf.</td>
<td>1</td>
<td>-</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Scleranthae Link ex DC.</td>
<td>2</td>
<td>-</td>
<td>1 (1)</td>
</tr>
<tr>
<td>Caryophyloideae:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caryophyllae Lam. &amp; DC.</td>
<td>17</td>
<td>1 (1)</td>
<td>7 (11)</td>
</tr>
<tr>
<td>Drypideae Fenzl</td>
<td>1</td>
<td>-</td>
<td>0 (0)</td>
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<tr>
<td>Sileneae DC.</td>
<td>6</td>
<td>1 (1)</td>
<td>4 (9)</td>
</tr>
<tr>
<td>Paronochyloideae:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corrigioloideae Dumort.</td>
<td>2</td>
<td>0 (0)</td>
<td>2 (2)</td>
</tr>
<tr>
<td>Paronychiaceae Dumort.</td>
<td>15</td>
<td>4 (4)</td>
<td>7 (13)</td>
</tr>
<tr>
<td>Polycarpaeae DC.</td>
<td>16</td>
<td>4 (4)</td>
<td>6 (7)</td>
</tr>
<tr>
<td>Total</td>
<td>90</td>
<td>15 (15)</td>
<td>38 (79)</td>
</tr>
</tbody>
</table>
and Molluginaceae) were used to root the phylogenies. See table A1 in the online edition of the International Journal of Plant Sciences for a list of all specimens used in this study, including voucher and source information as well as GenBank accession numbers.

DNA Extraction, Amplification, and Sequencing

For the specimens newly sampled in this study, DNA was isolated from fresh, silica-dried, or herbarium leaf material with the Qiagen DNeasy DNA Plant Mini Kit (Qiagen, Valencia, California). For most specimens, the matK, trnL-F, and rps16 chloroplast gene regions were amplified; three independent regions were chosen to test for incongruence that may have resulted from chloroplast recombination, which was detected in the Sileneae by Erixon and Oxelman (2008), or from hybridization or lineage sorting, as hypothesized by Rautenberg et al. (2008). To amplify matK, the entire matK coding exon was amplified, together with a portion of the 5′ and 3′ exons for trnK (and associated intronic regions), with the primers trnK1F and trnK2R (see table 2 for primer source information) under the following polymerase chain reaction (PCR) parameters: 94°C for 4 min, followed by 30 cycles of 94°C for 1 min, 50°C for 1 min, and 72°C for 2.5 min. The cycling ended with 72°C for 7 min; the preparation then was held at 4°C. In some cases, because of the large fragment size generated from the above primers, two smaller overlapping fragments were amplified with 710F and Als11R for the 5′ end and with 980F and trnK2R for the 3′ end. Alisoideae-specific (Als11F, Als11R) and Caryophyllaceae-wide (Car11F, Car11R) primers were designed for sequencing the 3′ end of the coding region. In the middle of the coding region, the primers 980F and 980R were designed for sequencing Caryophyllaceae-wide samples. In addition, the primers 710F and trnK2R were used to sequence some samples. Amplification and sequencing of rps16 and trnL-F were more straightforward; rps16 was amplified with primers rpsF and rpsR, while trnL-F was amplified with trnL-F primers C and F and sequenced with primers C and F as well as E and D (Taberlet et al. 1991). Standard protocols were used for the amplifications and sequencing.

The total number of specimens analyzed for each of the three chloroplast regions is included in table 3. For the matK analysis, of the 135 total sequences, 70 were generated in this study and 65 were taken from previous studies and accessed through GenBank; most of these were analyzed in Fior et al. (2006). The combined data set included only those specimens that were newly sequenced in this study (81) and not those taken from GenBank, in order to have a more complete matrix; most of the newly sequenced specimens had all three genes sequenced, while seven were missing an rps16 sequence and 13 were missing a trnL-F sequence (table 3).

Sequence Alignments and Phylogenetic Analyses

Sequences were aligned manually by eye in PAUP* 4.0b10 (Swofford 2002). Regions for which homology assessments were ambiguous between a few taxa were replaced by question marks, whereas ambiguous regions across the majority of taxa were removed from the matrices before analyses. Insertions and deletions (indels) of more than 2 bp were scored as characters with the simple gap-coding method of Simmons and Ochoterena (2000) and were included in the maximum parsimony (MP) analyses (see table 3 for the numbers of indels scored). All MP analyses were performed in PAUP* 4.0b10 (Swofford 2002). In all MP analyses, characters were treated as unordered and equally weighted. For separate matK, rps16, and trnL-F data sets, a heuristic search with 10,000 random-addition replicates, tree bisection reconnection (TBR) branch swapping, Multrees on, and no more than 100 trees held at each step was performed, with all characters unordered and unweighted; these parameters were identical to those used in Fior et al. (2006). A combined analysis of all three chloroplast regions (not including GenBank matK sequences) was also performed with a heuristic search using 10,000 random-addition replicates, TBR branch swapping, and Multrees on. The total aligned lengths of the four matrices, including the number of indels, are listed in table 3. MP bootstrap analyses were run on all three separate and one

---

Table 2

<table>
<thead>
<tr>
<th>Name</th>
<th>Sequence (5′ to 3′)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>trnK1F</td>
<td>CTC AAC GGT AGA GTA CTC</td>
<td>Manos and Steele 1997</td>
</tr>
<tr>
<td>trnK2R</td>
<td>AAC TAG TCG GAT GGA GTA G</td>
<td>Steele and Vilgalys 1994</td>
</tr>
<tr>
<td>Als11F</td>
<td>ATC TTT CGC ATT ATT ATA G</td>
<td>This study</td>
</tr>
<tr>
<td>Als11R</td>
<td>GCA CGT ATA GCA CTT TGG T</td>
<td>This study</td>
</tr>
<tr>
<td>Car11F</td>
<td>GTG CTA GAA CTT TGG CTC G</td>
<td>This study</td>
</tr>
<tr>
<td>Car11R</td>
<td>CGA GCC AAA GATT CTA GCA C</td>
<td>This study</td>
</tr>
<tr>
<td>980F</td>
<td>TGG TCT CAA CCA AGA AGA AT</td>
<td>This study</td>
</tr>
<tr>
<td>980R</td>
<td>ATT TCT TCT TGG TGG AGA CCA</td>
<td>This study</td>
</tr>
<tr>
<td>710F</td>
<td>GTA TCG CAC TAT GTW TCA TTT GA</td>
<td>Johnson and Solitis 1995</td>
</tr>
<tr>
<td>rpsF</td>
<td>GTG GTA GAA AGC AAC GTG CTA CTT</td>
<td>Popp and Oxelman 2001</td>
</tr>
<tr>
<td>rpsR</td>
<td>TCG GGA TCG AAC ATC AAT TGC AAC</td>
<td>Popp and Oxelman 2001</td>
</tr>
<tr>
<td>trnL-F, primer C</td>
<td>CGA AAT CGG TAG AGC GTA CG</td>
<td>Taberlet et al. 1991</td>
</tr>
<tr>
<td>trnL-F, primer D</td>
<td>GGG GAT AGA GGG ACT TGA AG</td>
<td>Taberlet et al. 1991</td>
</tr>
<tr>
<td>trnL-F, primer E</td>
<td>GGT TCA AGT CCC TCT ATC CC</td>
<td>Taberlet et al. 1991</td>
</tr>
<tr>
<td>trnL-F, primer F</td>
<td>ATT TGA ACT GGT GAC AGC AG</td>
<td>Taberlet et al. 1991</td>
</tr>
</tbody>
</table>
combined data set; for the separate data sets, the same parameters as those used in Fior et al. (2006) were used, which involved a heuristic search with 10,000 bootstrap replicates, with 10 random-addition replicates and TBR branch swapping, saving 10 trees at each replicate; for the combined data set, a heuristic search was conducted with 1000 bootstrap replicates, TBR branch swapping, Multrees on, and 10 random-addition replicates, holding 10 trees at each step. Maximum likelihood (ML) analyses also were performed for all three chloroplast regions separately and combined with the Web-based program RAxML (Stamatakis et al. 2005) using the GTR model with 1000 bootstrap replicates (Stamatakis et al. 2008); they were performed at least twice for each data set to ensure the stability of the topology.

Results

Phylogenetic Analyses

The statistics from the MP analyses, including the total number of sequences in the matrices and their aligned length, the number of indels, the number of parsimony-informative characters, tree length, and the consistency and retention indices for the separate chloroplast and combined data sets, are listed in table 3. The ML analyses resulted in trees with the following likelihood (–ln L) scores: \( matK = -24, 507.8522; rps16 = -8985.9028; trnL-F = -10, 683.8514; \) combined = \(-39, 025.4385 \). Results from the separate and combined ML analyses are consistent with, but somewhat better resolved and better supported than, the strict consensus trees from the MP analyses; results from the two ML analyses resulted in consistent topologies and indicate that the ML analyses did not get caught in local optima. The separate \( rps16 \) and \( trnL-F \) ML and MP analyses are not shown but are consistent with the \( matK \) and combined analyses in the main Alsinoideae groupings (figs. 1, 2, clades A–E); however, the deeper nodes are unresolved.

Finally, observations of the relative positions of the outgroup families (Achatacarpaceae, Amaranthaceae, and Molluginaceae) are incongruent between the \( matK \) and combined analyses (figs. 1, 2), possibly because of limited sampling. Both, however, place Molluginaceae in a proximal position to the Caryophyllaceae, which is not consistent with the results of Caénoud et al. (2002), who sampled widely within the order.

Taxonomic Groupings

The phylogenetic analyses presented here (figs. 1, 2) demonstrate that subfamilies Alsinoideae and Paronychioideae as usually delimited are not monophyletic; subfam. Paronychioideae is a basal paraphyletic grade, while tribe Pycnophylleae, usually included in subfam. Alsinoideae, is nested within it. In both the \( matK \) and combined analyses, members of tribe Corrigioleae Dumort. (Corrigiola L. and Telephium L.) are monophyletic and sister to the rest of the family. The tribe Paronychieae Dumort. is polyphyletic, with one main clade including Paronychia Miller, Gymnocarpus Forssk., and Hernia L., while the genus Diceranthus Webb is nested within a clade of the polyphyletic tribe Polycarpaeae DC. Tribe Polycarpaeae consists of a clade including Polycarpus L. and Loeflingia L. and a clade including Spergula and Spergularia L.; the latter clade is more closely related than the former to the Alsinoideae + Caryophyllideae clade. The South American Alsinoideae genus Pycnophyllum is nested within the first Polycarpaeae clade, sister to Drymaria.

In the \( matK \) analysis (fig. 1), Paronychia Mill. is itself paraphyletic, with Gymnocarpus and Hernia nested within it. Chaudhri (1968) recognized three subgenera in his revision of the Paronychia: the chiefly New World Paronychia, the southeastern United States endemic Siphonochlaena (Torrrey & A. Gray) Chaudhri, and the Old World Anoplychia (Fenzl) Chaudhri. The “divergent” species in our analysis, Paronychia kapatla (Hacq.) A. Kern, is a member of the Old World assemblage.

In both the \( matK \) and combined analyses (figs. 1, 2), the Alsinoideae are also demonstrated to be paraphyletic, because the monophyletic Caryophyllideae are nested within, but the two together are well supported as a monophyletic group. Rapid diversification of the family, inferred from extremely short branch lengths, obscures relationships among the major clades of the Alsinoideae (A–C) and Caryophyllideae (D and E); however, a number of important results are elucidated. The Caryophyllideae consist of two main lineages, which include (1) Dianthus, Saponaria L., Gypsophila, and their relatives (clade D) and (2) Silene L. and its relatives (clade E); these correspond to tribes Caryophylleae Lam. & DC. and Sileneae DC., respectively. In the \( matK \) analysis (fig. 1), Dianthus is paraphyletic, with Velezia L. nested within it, and Lychnis and Silene are both polyphylectic, with Lychnis nested within Silene; although there is reduced sampling in the combined analysis (fig. 2), results are consistent, suggesting that Lychnis is paraphyletic, with Silene within it. If Viscaria Bernh. is treated as a separate genus (Liden et al. 2001), i.e., Lychnis viscaria L. in the combined analysis (fig. 2), then Lychnis would be a sister group to Silene, with Viscaria as a sister to Lychnis + Silene.

In both the \( matK \) and combined analyses, the Alsinoideae are polyphyletic, composed of major clades A–C (figs. 1, 2), as well as having the Caryophyllideae tribes Caryophyllaceae

<table>
<thead>
<tr>
<th>Spacer</th>
<th>Sequences</th>
<th>bp</th>
<th>Indels</th>
<th>PI characters</th>
<th>Trees</th>
<th>L (steps)</th>
<th>CI</th>
<th>RI</th>
</tr>
</thead>
<tbody>
<tr>
<td>( matK )</td>
<td>135</td>
<td>1764</td>
<td>7</td>
<td>861 (48.8%)</td>
<td>236,819</td>
<td>4067</td>
<td>.4699</td>
<td>.7573</td>
</tr>
<tr>
<td>( rps16 )</td>
<td>74</td>
<td>768</td>
<td>2</td>
<td>338 (43.9%)</td>
<td>88,989</td>
<td>1512</td>
<td>.5357</td>
<td>.7059</td>
</tr>
<tr>
<td>trnL-F</td>
<td>68</td>
<td>888</td>
<td>2</td>
<td>380 (42.7%)</td>
<td>13,155</td>
<td>1881</td>
<td>.5183</td>
<td>.6448</td>
</tr>
<tr>
<td>Combined</td>
<td>81</td>
<td>3420</td>
<td>11</td>
<td>1454 (42.5%)</td>
<td>576</td>
<td>6474</td>
<td>.5263</td>
<td>.7008</td>
</tr>
</tbody>
</table>

Note. Table shows the total aligned length (bp), the number of parsimony-informative (PI) characters, the total number of trees, the shortest tree length (L), the consistency index (CI), and the retention index (RI) for all separate and combined data sets.
Fig. 1 Maximum likelihood (ML) phylogeny from analysis of matK sequences from GenBank and those generated in this study (table A1). Numbers above the branches represent ML bootstrap (BS) values, while those below are for maximum parsimony (MP) BS values (a missing value represents an MP BS value of <50). Branches with dashed lines collapse in the MP strict consensus tree. Circled letters indicate major clades discussed in the text; squared letter refers to the other part of the figure (A or B). The taxonomy shown here along the right-hand side of the phylogeny indicates the three-subfamily system (Alsinoideae, Caryophylloideae, and Paronychioideae) of Pax and Hoffmann (1934) and the associated tribes from Bittrich (1993); alongside this is the tribal alignment proposed in this article. Subgenera of Arenaria and Minuartia follow McNeill (1962) and are denoted by three-letter codes. Arenaria: Are = Arenaria, Ere = Eremogone, Ers = Eremogoneastrum, Lei = Leiopteris, Odo = Odontostemma, Por = Porphyrantha. Minuartia: Hym = Hymenella, Min = Minuartia, Rho = Rhodalsine, Spr = Spergella. Superscripts next to taxon names indicate instances of differing topology in the MP strict consensus tree. 1: Loeflingia hispanica and Dicheranthus plocamoides are sister to each other (BS = 54) and are basal in the clade. 2: Silene campanula and Silene italicata are sister to each other (BS = 60) and sister to Silene acaulis + Silene rothmaleri.
Fig. 2  Maximum likelihood (ML) phylogeny from analysis of combined matK, trnL-F, and rps16 sequences. Numbers above the branches represent ML bootstrap (BS) values, while those below are for maximum parsimony (MP) BS values (a missing value represents an MP BS value of <50). Branches with dashed lines collapse in the MP strict consensus tree. Circled letters indicate major clades discussed in the text. The taxonomy
Rhodalsine to each other (BS = 1). Arenaria L., Eremogone F. Williams, and combined analyses (fig. 1), tribe Alsineae is clearly polyphyletic, with Alsineae tribes Geocarpeae and Scleranthieae, as well as Caryophylloideae tribe Drypideae (Drypis spinosa L.), nested within it, while one species, M. geniculata, that has sometimes been placed in the separate genus Rhodalsine J. Gay is nested within the Paronychioideae.

Within the Alsinoideae, there are a number of important taxonomic issues that were resolved in our phylogenetic analyses, especially related to the large genera Arenaria and Minuartia. In both the matK and combined analyses (figs. 1, 2), Arenaria is polyphyletic. Clade C consists of Arenaria subg. Eremogone (Fenzl) F. Williams and Eremogoneastrum F. Williams, along with Minuartia subg. Spergella (Fenzl) McNeill. Within clade C, Arenaria subg. Odontostemma (G. Don) F. Williams is included in a clade with Pseudostellaria Pax and Lepyrodictis, while members of Arenaria subg. Arenaria, Leiopsis McNeill, and Porphyrantha (Fenzl) McNeill, as well as members of the genus Moehringia, form a clade; Arenaria subg. Arenaria is itself polyphyletic, consisting of two lineages in the combined analysis (fig. 2) and three in the matK analysis (fig. 1). In the matK analysis (fig. 1), Moehringia is also demonstrated to be polyphyletic.


Another genus within the Alsinoideae that was shown to be paraphyletic is Stellaria. In the matK analysis (fig. 1), Stellaria has Myosoton aquaticum (L.) Moench (sometimes treated as Stellaria aquatica [L.] Scop.) and Plettkea cryptantha Mattf. nested within it.

The results from these phylogenetic analyses have shown that the genera most closely related to the endemic Hawaiian genus Schiedea are Honckenya and Wilhelmsia. In both the matK and combined analyses, the genus Schiedea is monophyletic, with bootstrap support of 100, and related to the unspecific genera Honckenya and Wilhelmsia. In the matK analysis (fig. 1), it is sister to Wilhelmsia, followed by Honckenya, in both the MP and ML analyses. In the combined analysis, the ML tree places Honckenya as more closely related to Schiedea, while in the MP tree, Honckenya and Wilhelmsia are sister to each other and to Schiedea. In all analyses, Schiedea, Honckenya, and Wilhelmsia are in clade A, with members of Alsinoideae tribes Geocarpeae, Scleranthieae, and Alsineae.

Discussion

Results from the phylogenetic analysis of three chloroplast gene sequences (matK, trnL-F, and rps16) reveal several important taxonomic and biogeographic discoveries, including that (1) the subfamilies within Caryophyllaceae as currently delimited are not natural groups and should be abandoned, (2) the species-rich alsinoid genera Arenaria and Minuartia and several other genera are not natural groups and require both reorganization and further study to better reflect phylogenetic relationships, (3) several smaller genera are nested within larger genera, such as Myosoton Moench and Plettkea Mattf. (in Stellaria) and Velezia (in Dianthus), and (4) the closest relatives to the endemic Hawaiian genus Schiedea are a pair of circumboreal taxa, Honckenya peploides (L.) Ehrh. and Wilhelmsia physes (Fisch. ex Ser.) McNeill.

The traditional three-subfamily subdivision of the Caryophyllaceae is not reflected in our results, suggesting that the morphological characters used to delimit them are unreliable because of extensive convergent evolution. This is consistent with results from prior phylogenetic studies, including Smis-
sen et al. (2002) and Fior et al. (2006). One possible scenario would be to treat the three tribes of the Paronychioideae as subfamilies and have the species-rich part of the family, ~2500 of the ~3000 species (R. K. Rabelet, unpublished data), constitute one large subfamily (Alsinoidae + Caryophylloideae); this arrangement seems rather unconventional at best. We believe that a better course of action would be to abandon subfamilies within the Caryophyllaceae and instead recognize at least 11 tribes based on the well-supported lineages from our phylogenetic analyses. Outside of those, we propose to accommodate the relationships we have found within the Alsinoidae. Most of these tribes are in current use in the sense we use here (Bittrich 1993) and have a recognized morphological basis as well. There is some uncertainty in this classification, which we summarize below.

Within subfamily Paronychioideae, results from this study agree with those of Fior et al. (2006), in which this subfamily is a basal grade of taxa, with tribe Corrigioleae monophyletic and sister to the remainder of the subfamily, a monophyletic tribe Paronychieae, and a polyphyletic tribe Polycarpeae. Smissen et al. (2002) found that subfamily Paronychieae did not form a basal grade but was polyphyletic, with Spergularia more closely related to alsinoid taxa than to members of the tribe Polycarpeae. Recognizing tribe Sperguleae Dumort., as Pax and Hoffmann (1934) and Eckhardt (1964) did, is appropriate because Spergula and Spergularia clustered outside of the Polycarpeae, closer to but not inside of the Alsinoidae-Caryophylloideae clade. This intermediate position seems consistent because these taxa share some alsinoid characters (Bittrich 1993; Smissen et al. 2002).

Paronychia’s being paraphyletic is consistent with the ITS results of Oxelman et al. (2002), where the “divergent” species in our analysis, Paronychia kapela (Hacq.) A. Kern, also clustered with Herniaria. While this suggests that the Old World subg. Anoplonychia (Fenzl) Chaudhri, a group of more than 40 species (Chaudhri 1968), may deserve generic recognition, we agree with Oxelman et al. (2002) that further study is warranted, since no study has yet been focused on sampling the diversity within either Paronychia or Herniaria, genera of ~110 and 45 species (Bittrich 1993), respectively.

In our new tribal classification, the subfamily Paronychioideae is abandoned and replaced by four tribes: Corrigioleae (the clade Corrigiola + Telephium), Paronychieae (the clade Gymnocarpos + Herniaria + Paronychia), Polycarpeae (the clade containing Dicrhanthus, Loeflingia, Ortega L., Polycarpon, and Drymaria, as well as Pycnocephylum, formerly in the Alsinoidae), and Sperguleae (the clade including Spergularia, Spergula, and Rhodalsine [Minuartia subg. Rhodalsine]; figs. 1, 2; table A1). The conate styles of Pycnocephylum, an anomaly in the Alsinoidae (Bittrich 1993), are also found in other members of the Polycarpeae. One other consequence of this classification is that the presence of stipules can no longer be used as a defining character for the Polycarpeae and the Sperguleae; only the Corrigioleae and the Paronychieae will be consistently stipulate.

This study provided a better-resolved phylogeny of the Caryophylloideae and Alsinoidae than the previous study by Fior et al. (2006), as a result of both increased taxonomic sampling and additional molecular characters. While the “backbones” of the separate and combined analyses were not resolved in this study, they likewise were neither well supported nor resolved in the phylogenies of Fior et al. (2006). This may be due to short branch lengths after rapid radiation. Most of the Alsinoidae and a nested Caryophylloideae form a monophyletic group; this is consistent with the view of Bittrich (1993), who hypothesized this on the basis of caryophyllal type embryogeny in these subfamilies, while Paronychieae have the solanad type.

Subfamily Caryophylloideae was shown to be monophyletic (except for tribe Drypideae) and nested within Alsimoidae in this study, consistent with the findings of Fior et al. (2006) but not those of Smissen et al. (2002); in the latter study, tribe Sileneae was resolved as sister to Scleranthus (subfamily Alsimoidae tribe Scleranthaeae). Treating the Caryophylloideae as tribes Caryophylleae and Sileneae (clades D and E, respectively; figs. 1, 2) is consistent with both traditional and molecular studies and current usage (Bittrich 1993). The increased sampling of Dianthus in our matK analysis showed that the genus Dianthus is paraphyletic, with Velezia rigidus nested within it (fig. 1); just like Paronychia, Dianthus is a very large genus (~300 species; Bittrich 1993) that has not been broadly sampled. Our matK analysis identified a paraphyletic Silene with Lycnis nested within it, which is consistent with results of other studies, including Oxelman and Lidén (1995; ITS and 5.8S), Oxelman et al. (1997; rps16), Erixon and Oxelman (2008), and Rautenberg et al. (2008; SIX1 and Y1). Our combined analysis showed that Silene and Lycnis were sister to each other, consistent with findings of Popp and Oxelman (2004; RNA polymerase gene family, ITS, and rps16), Oxelman et al. (2001; ITS and rps16), and Fior et al. (2006); this may be due to the more limited sampling in those analyses. However, independent data indicate that the incongruence between these molecular phylogenies may be due to a reticulate history (Delichère et al. 1999; Frajman et al. 2007). Oxelman (personal communication 2009) indicates that part of the problem may also rest with a misidentified sequence of Lycnis coronaria in GenBank, which may be the matK sequence used in our study. We could not test whether this sequence is identical to one from Silene gallica because none are currently available. Further work with new sequences and better sampling should help resolve the issue. The results of the combined analysis (fig. 2) do concur with those of Frajman et al. (2009; rps16 and ITS) in showing that the genus Viscaria, here shown as Lycnis viscaria, should be recognized because it is a sister taxon to Silene + Lycnis.

Within subfamily Alsinoidae, as frequently defined, there are a number of important taxonomic conclusions that arise from this study. The increased resolution of this study confirms the polyphylly of tribe Alsiniae (sensu Bittrich 1993), which was not well resolved in Fior et al. (2006); this conclusion is consistent with the findings of Smissen et al. (2002; ndhF). We also demonstrated that the tribes Geocarpeae and Scleranthaeae are nested with taxa in Bittrich’s Alsiniae, suggesting that the tribal alignment in the Alsinoidae must be reconsidered and most likely more finely subdivided; we have proposed such a revision (figs. 1, 2; table A1). Our results are consistent with those of Smissen et al. (2003; ITS) in showing tribe Pycnocephylleae more closely related to the formerly circumscribed tribe Polycarpeae, into which we now include Pycnocephylum (figs. 1, 2; table A1).
Before molecular investigations of the Alsinioideae, there were various attempts at grouping the genera within tribe Alsiniae. Pax and Hoffmann (1934) recognized two subtribes on the basis of whether the capsules opened by entire or split valves. This concept matches, with only one exception (the genus *Lepyrodiclis*), the members of clade A (entire valves) and clades B + C (split valves) that have traditionally been included in that tribe. McNeill (1962) recognized three “aggregations,” not necessarily representing natural relationships, within the Alsiniae, along with a divergent *Schiedea* (which he hypothesized was aligned with the Paronychioideae): (1) the *Stellaria-Cerasium* group (including *Myosoton, Holosteum* L., *Moenchia* Ehrh., and maybe *Pseudostellaria*), (2) the *Sagina* group (including *Colobanthus*), and (3) the *Arenaria* group (including *Minuartia, Moehringia, Wilhelmsia, Lepyrodiclis, Brachystemma*, and *Honckenya* as well as *Thylacospernum* Fenzl, *Thrya* Boiss. & Balansa, *Gooringia* Williams, *Reicheldea* Pax, and *Buffonia* L.).

Our study confirms that McNeill’s first group, with the addition of *Arenaria* subg. *Odonostemma* and *Lepyrodiclis* (in clade B; figs. 1, 2), would constitute tribe Alsiniae sensu stricto (type: *Stellaria media* [L.] Vill.). Most of these genera have petals deeply cleft (rarely jagged or nearly entire) or rarely absent and, except for *Lepyrodiclis*, capsules dehiscing by twice as many valves as styles. In both the matK and combined analyses, the Andean South American *Plettkea* is nested inside *Stellaria*, sister to the Arctic North American *Stellaria crassipes* Hultén (figs. 1, 2). The nesting of *Plettkea* and *Myosoton* (one species native to Eurasia) within *Stellaria* illustrates a third example of a genus of Caryophyllaceae of more than 100 species that should be the focus of broad sampling and is one of several examples of taxa with indehiscent fruits clustering with genera with capsular fruits. The appearance of *Arenaria chamissonis* Maguire in this clade in the combined analysis reinforces Morton’s (2005b) comments on the uncertain generic placement of this taxon; recent treatments have considered it to be a species of either *Arenaria* or *Stellaria*, but it was originally described as *Cheirleria dicranoides* Cham. & Schlldl., a genus described by Linnaeus to accommodate a single species now included in *Minuartia*.

McNeill’s (1962) second group, *Sagina* and *Colobanthus*, is a monophyletic group in this study; however, it is clustered with a portion of *Minuartia* subg. *Minuartia* in a clade that also includes *Buffonia* and *Drypis* (clade A, fig. 1), to form what we propose as tribe Saginiae. Each of these genera, except *Drypis*, have petals entire or rarely absent and capsules dehiscing by as many valves as styles. *Sagina, Colobanthus,* and *Buffonia* have mostly four or five styles, while the *Minuartia* species here have three. The inclusion of *Drypis*, a spiny perennial from the eastern Mediterranean with hooded sepal, bifid petals, and an indehiscent fruit, is an unexpected result. It is often placed in its own tribe (Drypideae Fenzl) within the Caryophyllidoideae because of a number of anomalous features (see Bittrich 1993). While it clearly clusters away from the rest of the Caryophyllidoideae, we suggest that further study is warranted to determine whether it should be retained in the Saginiae or tribe Drypideae should be recognized.

The *Arenaria* “group” does not form a cohesive group, let alone a monophyletic one, as *Arenaria* and *Minuartia* are both polyphyletic and genera such as *Wilhelmsia, Lepyrodiclis,* and *Honckenya* are not closely aligned (figs. 1, 2). *Schiedea* may indeed have a number of morphological features that are “divergent” from many Alsinioideae; based on his anatomical study of flowers and fruits, Rohweder (1970) proposed, but did not publish, the tribe “Alsinidendreae” to segregate it within the Alsinioideae. Our study does show that, contrary to McNeill’s (1962) suspicion, *Schiedea* is clearly not related to the Paronychioideae. The morphologically diverse taxa *Schiedea, Wilhelmsia, Honckenya, Scleranthus,* and *Geocarpus,* as well as members of *Minuartia* subg. *Hymenella* and several species of *Minuartia* subg. *Minuartia,* form a highly supported monophyletic clade that is here treated as the tribe Sclerantheae. The inclusion of *Geocarpus* and *Scleranthus,* genera that were formerly in separate tribes of the Alsinioideae, complicates the morphological diagnosis of this clade, in part because of the highly reduced morphology of these taxa. Other than the fact that all of the genera except *Scleranthus* have as many capsule valves as styles, it is difficult to locate morphological features that would unite the assemblage. Most are apetalous, with *Honckenya, Wilhelmsia,* and *Minuartia* having entire petals. In both the combined and separate analyses, results are consistent with those of Smissen et al. (2003; ITS) in demonstrating that in *Scleranthus,* Northern Hemisphere species (*Scleranthus perennis, Scleranthus annuus*) are sister to Southern Hemisphere ones (*Scleranthus biflorus*), while we did not find that *Sagina* and *Colobanthus* were as closely related to *Scleranthus* as they are to other taxa. Further study, especially involving *Minuartia* senso latu, is required in this clade; it may reveal morphological and/or molecular data that support further splitting of this tribe.

The delimitation of groups within *Arenaria* has often been disputed, with concepts ranging from a broad, all-inclusive *Arenaria* (Fernald 1919; Maguire 1951), recognizing *Minuartia, Arenaria, Moehringia,* and up to nine other genera (McNeill 1962), to splitting *Minuartia* into many segregates, e.g., six additional genera to cover the Arctic taxa (Löve and Løve 1976). We demonstrate here not only that these genera should not be united into an all-inclusive “*Arenaria* group” but also that *Arenaria* and *Minuartia* are both polyphyletic.

Three of the subgenera of *Arenaria* that we sampled should be recognized as genera: *Arenaria, Odontostemma* Benth. (*Arenaria* subg. *Odontostemma*), and, especially via its placement in a separate clade, *Eremogone* Fenzl (*Arenaria* subg. *Eremogone* and *Eremogoneastrum*). *Eremogone* has been adopted for the recent *Flora of North America* treatment (Hartman and Rabeler 2004; Hartman et al. 2005). We propose that *Eremogone* (clade C, figs. 1, 2) and *Thylacospernum* (clade C, fig. 2) should constitute a new tribe *Eremogoneae* Rabeler & W.L. Wagner; *Thylacospernum* is tentatively included in this tribe because it is absent from the matK analysis and weakly supported in the combined analysis (fig. 2).

We place *Arenaria* sensu stricto and *Moehringia* in tribe *Arenarieae* Kitt. (figs. 1, 2; table A1), the plants having petals entire or rarely absent and capsules dehiscing by twice as many valves as styles. While members of the *Eremogoneae* have narrow, grasslike leaves, most species of *Arenaria* have broader, often ovate to lanceolate leaves. Although *Moehringia* is easily characterized by a unique appendaged seed, we also demonstrate that there is little support for recognizing it
as a genus separate from Arenaria; this is consistent with the results of Fior and Karis (2007; ITS and matK).

Similarly, our results show that three of the subgenera of Minuartia should also be removed from Minuartia. Minuartia platypylla and several other closely related species (not sampled here) from the Canary Islands and Mediterranean coasts, currently placed in Minuartia subg. Rhodalsine, would be better treated as members of the genus Rhodalsine. These taxa appear to be related to Spargularia, which, as McNeill (1962) noted, they closely resemble except for lacking stipules; we place both of these genera in the tribe Sparguleae. Because of the distinctive quadrangular stems and spreading sepals and capsule valves of the Mexican endemic Minuartia moehrin-gioides, its retention in Minuartia as the only member of Minuartia subg. Hymenella was questioned by McNeill (1962). It is clear from our results that it should now be removed and regarded as the only member of a unspecific genus, Triplateia Bartl. (Hymenella Moq. & Sessé ex Ser. in DC. [1824] non E.M. Fries [1822]). Although our results suggest that Minuartia subg. Spergella belongs within Eremogone, no previous study of this distinctive taxon gives support for this; re-establishment of Phlebanthia Rchb. to accommodate the two or three species currently recognized in the subgenus Spergella may be a wiser interim step.

While results also suggest that Minuartia subg. Minuartia should be split (figs. 1, 2) into a Eurasian-Holarctic and a North American clade, this result must be tempered by the limited sampling in this study. Sampled taxa belong to seven of the 12 sections recognized by McNeill (1962). Since one of the “missing” five sections is Minuartia, a group of ~50 mostly Mediterranean species, we cannot postulate into which clade Minuartia sensu stricto would be placed. Another missing section is sect. Uninerviae (Fenzl) Mattf., a section of six to eight species most diverse in southeastern North America. Given its occurrence near the native range of Geocarpus minimu and the North American Minuartia taxa clustering with Sagina, it would be most interesting to see where Minuartia sect. Uninerviae would be placed. Our results show that molecular data do support some of the segregates proposed by Löve and Löve (1976), which were primarily based on differences in morphological and taxonomic traits. Since the nine taxa sampled here would be placed in eight(!) different genera by Löve and Löve (1976), it is evident that Minuartia must be more completely sampled before any additional conclusions can be drawn.

Results from this study confirmed prior phylogenetic analyses that showed that the Hawaiian genus Schiedea is monophyletic and the result of a single colonization event to the islands (Solis et al. 1996; Wagner et al. 2005). An important and surprising result from this study was the identification of the closest living relatives of Hawaiian Schiedea: the unspecific genera Honckenya and Wilhelmstia, primarily from the Arctic and subarctic regions of both Eurasia and North America. Wilhelmstia is similar to Honckenya in habitat, but their resemblance was previously hypothesized to be due to convergence associated with their riparian or maritime habitats (McNeill 1962, 1980; Wagner 2005a, 2005b). Further study with the addition of samples of Minuartia sect. Uninerviae will help to resolve whether the Hawaiian Schiedea did originate from the Arctic via North America.

While we have proposed a classification with 11 tribes, we realize that there are several limitations that could expand it to include additional tribes. Several taxa, if/when sampled, could produce changes in the scheme. The placement of Drypis within the Saginae is tentative; it may be better segregated as tribe Drypideae. While we were unable to obtain Habrosia spinuliflora, an eastern Mediterranean herb and the only member of tribe Habrosieae, Smissen et al. (2003) included it in their ITS2 study. The sequence most closely related to Habrosia was Drypis; should tribe Habrosieae be maintained, or do these taxa together form a tribe? From a short ITS2 sequence, Smissen et al. (2003) was able to place Pentastemonodiscus monochlamydeus Rech.f., a highly reduced plant from Afghanistan, within the family but not within a subfamily; placement near Scleranthus, as suggested by Bittrich (1993), was not confirmed. The current composition of the Sclerantheae would be subject to change if a broadly based study of Minuartia were to be completed. As noted above, we did not sample a member of Minuartia sect. Minuartia; resolution of the placement of Minuartia sensu stricto might allow subdividing our Sclerantheae into more morphologically consistent groups.

Our results provide the most in-depth understanding of the relationships within the Caryophyllaceae, especially within the large, often recognized subfamily Alsinoidae, and clarify the position of some morphologically divergent lineages as well as confirming that the classification within the family is in need of significant revision. Several steps were taken in this article to revise the classification on the basis of molecular data, including abandoning the traditional three-subfamily system in favor of one based on tribes. We propose segregating the Caryophyllaceae into at least 11 tribes based on highly supported monophyletic groups; further study with increased sampling and morphological data may warrant recognizing additional tribes within the family.

**Description of Tribe Eremogoneae**

W.L. Wagner, tribus nov.


Plants perennial, rarely annual. Leaves filiform to subulate, often long-linear and grasslike, congested in the vegetative rosettes and at or near base of flowering stems, apex often acutate. Inflorescence of one or more terminal cymes, sometimes compressed to headlike, sometimes flowers solitary. Flowers weakly perigynous, rarely strongly so (Tylacospermum). Sepals with scarious margins, often broad.

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