RHODORA, Vol. 107, No. 932, pp. 359–385, 2005

A MULTIVARIATE ANALYSIS OF *CYMOPTERUS GLOMERATUS*, FORMERLY KNOWN AS *C. ACAULIS* (APIACEAE)

FENG-JIE SUN[1]

Department of Plant Biology,
505 South Goodwin Avenue,
University of Illinois, Urbana, IL 61801
Current Address: Department of Crop Sciences,
352 NSRC, 1101 West Peabody Drive,
Urbana, IL 61801
e-mail: fsun@uiuc.edu
[1]Author for correspondence

GEOFFREY A. LEVIN

Center for Biodiversity,
Illinois Natural History Survey,
607 East Peabody Drive, Champaign, IL 61820
e-mail: glevin@inhs.uiuc.edu

STEPHEN R. DOWNIE

Department of Plant Biology,
505 South Goodwin Avenue,
University of Illinois, Urbana, IL 61801
e-mail: sdownie@life.uiuc.edu

ABSTRACT. Five infraspecific taxa have been recognized in *Cymopterus glomeratus* (= *C. acaulis*): vars. *glomeratus* (= *acaulis*), *fendleri*, *greeleyorum*, *higginsii*, and *parvus*. The results of previous phylogenetic analyses of DNA sequence and morphological data have supported the close association of these five varieties, although the relationships among them could not be discerned. The recognition of infraspecific taxa within *C. glomeratus* is controversial. Multivariate analysis of variance and principal component analysis of 288 specimens representing the morphological variability and geographic distribution of this species complex were conducted to test the validity of these infraspecific taxa. Results show that most of the characters previously used to recognize these varieties are highly variable within the taxa. Although analysis of variance demonstrated some statistical differences among the varieties, patterns were not consistent. No clearly separated clusters are revealed in the principal component analysis and all five varieties were intermixed on the plots of the principal components. On the basis of the results of both phylogenetic and multivariate analyses, we propose that plants in this species complex be recognized as one species, *C. glomeratus*, with no varieties. The nomenclature and typification of this species are presented.

Key Words: North American Apioideae, *Cymopterus acaulis*, *Cymopterus glomeratus*, multivariate analysis, principal component analysis

For more than a century considerable confusion has surrounded the proper delimitation of, and relationships among, the perennial endemic genera of western North American Apiaceae (Umbelliferae) subfamily Apioideae (Coulter and Rose 1888, 1900, 1909; Jones 1908), which includes the large genera *Cymopterus* Raf. and *Lomatium* Raf. This confusion ranges from intergeneric and infrageneric levels (Downie et al. 2002; Sun 2003; Sun and Downie 2004; Sun et al. 2004) to the infraspecific level (Cronquist 1997). It is difficult to circumscribe these taxa because of the overlapping variation in nearly all morphological characters, leading to disagreement among authors as to the taxonomic status of many plants (Cronquist 1997; Goodrich 1986; Hartman 1985; Hartman and Kirkpatrick 1986; Kartesz 1994; Mathias 1930).

Cymopterus glomeratus (Nutt.) DC. (= *C. acaulis* Raf.; plains spring-parsley) is one of two *Cymopterus* species recognized by Kartesz (1994) that have infraspecific taxa. Five varieties have been recognized under the invalid but widely used name *C. acaulis*: vars. *acaulis*, *fendleri* (A. Gray) Goodrich, *greeleyorum* J.W. Grimes & P.L. Packard, *higginsii* (S.L. Welsh) Goodrich, and *parvus* Goodrich. (We recognize that these combinations have never been made within *C. glomeratus* and we do not intend to do so, but for convenience we will refer to them by their varietal epithets under *C. acaulis* throughout this paper.) Plants of the *C. glomeratus* species complex are found in open places in sandy or clay soil in foothills and valleys, at elevations up to 2000 m. They are found from Canada to northern Mexico: specifically, from southern Alberta, Saskatchewan, and Manitoba to Oklahoma, Texas, and northern Chihuahua, Mexico. In the United States, they extend from southeastern Oregon, Idaho, Utah, and Arizona to western Minnesota, South Dakota, Nebraska, and Kansas (Figure 1; Cronquist 1997; Goodrich 1986; Mathias 1930; Mathias and Constance 1944–1945). Varieties *acaulis* and *fendleri* are widely distributed; the other three are restricted to several counties (Figure 1). Plants of this species can be distinguished from other taxa in the genus by a combination of morphological characters, although it is very unlikely that the genus *Cymopterus* is monophyletic (Downie et al. 2002; Sun 2003; Sun and Downie 2004; Sun et al. 2004). They are perennials with one or two pseudoscapes arising from the subterranean crown of a tapering taproot. Their leaves are two to three times pinnately dissected with few to several round to narrow lobes, and form a rosette at ground level. The plants produce several peduncles. Inflorescences are compact and the central umbellets are sessile or nearly so. The involucres are lacking or poorly developed. Bractlets of the involucel are more or less connate toward the base and often have two to three teeth. Flowers

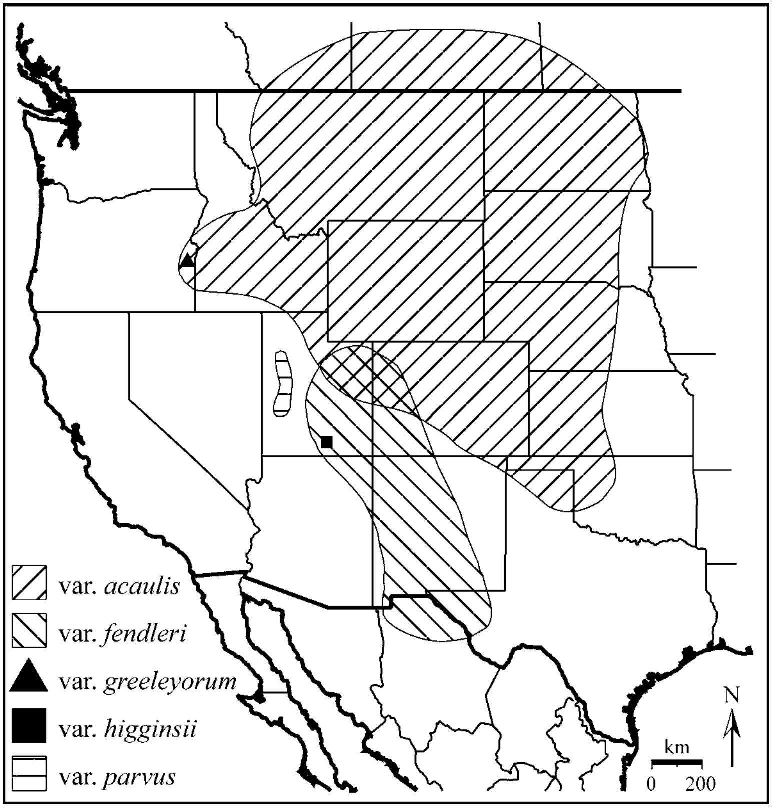

Figure 1. Map of western North America showing the distribution of the five varieties of *Cymopterus glomeratus*.

are yellow, purplish, or white. Fruits lack a carpophore and bear prominent wings that are merely wavy to strongly corrugate.

The monophyly of *Cymopterus glomeratus* has been confirmed by phylogenetic analyses of molecular (nuclear rDNA internal transcribed spacer and cpDNA *rps*16 intron and *trn*F-*trn*L-*trn*T DNA sequences) and morphological characters (Sun 2003; Sun and Downie 2004). However, resolution of relationships among the five varieties is unclear due to a lack of informative characters and conflicting tree topologies.

Recognition of infraspecific taxa within *Cymopterus glomeratus* has been controversial. Three of the five varieties (vars. *acaulis*, *fendleri*, and *higginsii*) historically were recognized at the species level (Goodrich 1986; Mathias 1930; Mathias and Constance 1944–1945;

Welsh 1976). Cronquist (1997) recognized only a single species with three varieties, synonymizing var. *higginsii* under var. *fendleri*, and var. *parvus* under var. *greeleyorum*. Following Cronquist's (1997) treatment, var. *acaulis* is sympatric with var. *fendleri* in the Uinta Basin of northeastern Utah and adjacent western Colorado, and with var. *greeleyorum* in Malheur County, Oregon, although var. *greeleyorum* is reputed to be ecologically separated from var. *acaulis* by being restricted to clay soil (Grimes and Packard 1981).

Flower color traditionally has been important in separating taxa within the *Cymopterus glomeratus* complex. Variety *acaulis* has white flowers, whereas var. *fendleri* is yellow-flowered. This difference was used to separate these taxa at the species level (Mathias 1930; Mathias and Constance 1944–1945). However, in practice, it is difficult to assign individual plants to variety, because the yellow petals fade to white when dried (Cronquist 1997; Goodrich 1986). Furthermore, such separation has been questioned by the presence of morphologically intermediate plants in their region of sympatry (Goodrich 1986; Figure 1). That vars. *greeleyorum* and *parvus* morphologically resemble var. *acaulis* but have yellow flowers like var. *fendleri* (Cronquist 1997; Goodrich 1986) further undermines the validity of using flower color to separate the varieties. Variety *higginsii* also resembles var. *fendleri* but has purple flowers. However, plants with purple flowers are also found outside the range of var. *higginsii* (pers. obs.). In addition, the morphological characters used to separate these varieties, such as the relative length of peduncle and leaf (Cronquist 1997; Goodrich 1986; Mathias 1930; Mathias and Constance 1944–1945) and the development of wavy fruit wings (Goodrich 1986), appear to be highly variable within the putative varieties and overlapping among them. Supposed morphological distinctions among the five varieties and their geographic distributions are summarized in Table 1.

To test the validity of infraspecific taxa within *Cymopterus glomeratus*, we conducted multivariate analysis of variance (MANOVA) and principal component analysis (PCA) of morphological characters scored from herbarium specimens. Heretofore, such studies of perennial endemic North American Apioideae have been few and have focused almost exclusively on *Lomatium* (Gilmartin and Simmons 1987; Mastrogiuseppe et al. 1985; Simmon and Gilmartin 1982). The objectives of this study were: 1) to examine quantitatively the patterns of morphological variation; 2) to determine the important morphological characters that contribute to the discrimination of any infraspecific taxa; and 3) to evaluate the taxonomic status of the infraspecific taxa in *C. glomeratus*.

Table 1. Characters traditionally used to separate the five varieties of *Cymopterus glomeratus* (*sensu* Kartesz 1994, as *C. acaulis*). Data from Cronquist (1997), Goodrich (1986), and Mathias and Constance (1944–1945).

Taxon	Petal Color	Peduncle Length	Bractlets	Fruit Wings	Geographic Distribution
Var. *acaulis*	White when fresh	Mostly equal to or shorter than leaves	Anthocyanic, or green and scarious, or green and herbaceous	Straight or slightly wavy; entire or obscurely erose	Central Saskatchewan and western Minn. to Okla., west to Mont., Wyo., central Idaho, southern Ore., and northeastern Utah
Var. *fendleri*	Yellow when fresh, fading to white/ cream when dried	Mostly equal to or longer than leaves	Mostly green and herbaceous	Straight or slightly wavy; mostly entire or obscurely erose	Northeastern Utah to northern Mexico, central N.M. to northeastern Ariz.
Var. *greeleyorum*	Yellow when fresh, fading to white/ cream when dried	Mostly shorter than leaves	Anthocyanic, or green and scarious, or green and herbaceous	Straight or slightly wavy; entire or obscurely erose	Malheur Co., Ore.
Var. *higginsii*	Purple when fresh	Mostly longer than leaves	Green and herbaceous	Straight or slightly wavy; entire or obscurely erose	Kane Co., Utah
Var. *parvus*	Yellow when fresh, fading to white/ cream when dried	Mostly shorter than leaves	Anthocyanic, or green and scarious, or green and herbaceous	Mostly strongly wavy and often erose	Millard and Tooele Cos., Utah

MATERIALS AND METHODS

We examined 686 herbarium specimens from the *Cymopterus glomeratus* species complex, borrowed from BM, BRY, CIC, GH, IDS, MO, NY, OSC, POM, RM, UC, US, and UTC (abbreviations as in Holmgren et al. 1990). Of these specimens, 288 had good locality data, were in good condition, and bore mature flowers or fruits. These specimens, which are listed in the Appendix, included the types of all five varieties and reflected the morphological variability exhibited by this species as well as representing populations from throughout the species' geographic range (Figure 1). The 288 specimens were used as operational taxonomic units (OTUs) to conduct the multivariate analyses.

Characters used in the multivariate analyses were based on previous taxonomic treatments and our own examination of herbarium specimens. Qualitative characters, such as flower color, were not included because they violate the assumptions of both MANOVA and PCA (Pimentel 1979). It appeared that the maturity of the fruit and how the specimen was pressed influenced how wavy the fruit wing is, so we did not attempt to record this potential character. A total of 22 quantitative characters was selected (Table 2). The data were collected using an Olympus dissecting microscope and a plastic ruler (accurate to 1 mm). The means of three to six measurements were calculated for each character on each specimen, depending upon the number of plants per herbarium sheet. Characters were scored at the same developmental stage on each plant (i.e., flowering or fruiting). Measurements were taken from the best developed leaf and inflorescence available on a given specimen. Three data sets were constructed from these 288 specimens. One matrix included flowering specimens only (154 OTUs and 19 characters). The second matrix included those specimens in fruiting condition (134 OTUs and 22 characters). The third matrix combined the OTUs of the previous two analyses (288) but with only 19 non-fruit characters. Analyses were conducted on each of these three matrices. The MANOVA was performed with SPSS version 12.0.1 for Windows (SPSS, Chicago, IL), using Type III sum of squares, and was followed by Tukey tests using the harmonic mean sample size to determine the pattern of significant differences among the varieties. Principal component analysis was conducted using NTSYSpc version 2.1 (Rohlf 2000). Identical parameters and procedures were used for all analyses. We constructed data matrices with all characters and with those characters for which the varieties did not differ significantly, as shown by the MANOVA, eliminated. Each data matrix, OTUs (rows) ×

characters (columns), was standardized by column using a linear transformation in order to minimize the impact of size on the analysis (Pimentel 1979). The correlation coefficient was then used to calculate the interval matrix, and this matrix was used to generate the eigenvector and eigenvalue matrices. The SQRT (lambda) transformation was used for vector scaling. The standardized data matrix and the eigenvector and eigenvalue matrices were then used to generate a projection matrix. Finally, the standardized data were projected onto eigenvector values of the correlation matrix and the two dimensional views of the individual OTUs were plotted for the first three principal components. The relative importance of the characters for distinguishing the groups was evaluated by examining the loadings (weights) of the characters along the various constructed axes (principal components). In addition, a plot of peduncle length versus leaf blade length was generated because these two characters were previously considered important in distinguishing among the infraspecific taxa of *Cymopterus glomeratus* (Cronquist 1997; Goodrich 1986; Mathias 1930; Mathias and Constance 1944–1945).

RESULTS

For both the combined (288 specimens and 19 characters; Nos. 1–19; Table 2) and fruit (134 specimens and 22 characters; Nos. 1–22) data sets, MANOVA found that there were statistical differences among the varieties in the *Cymopterus glomeratus* species complex (Pillai's and Hotelling's traces and Wilks' Lambda all with $p < 0.001$). Statistics for the 22 morphological characters and the results of the Tukey tests are shown in Table 2. Three of the characters (Nos. 5, 8, and 14; Table 2) did not show significant differences among the varieties. In addition, for six characters (Nos. 9–11, 13, 16, and 19) the varieties showed significant differences, but due to small sample sizes for vars. *greeleyorum*, *higginsii*, and *parvus*, Tukey tests assigned all five varieties to a single homogeneous subset. Only four of the remaining characters separate the taxa into non-overlapping subsets. Characters 3 (pseudoscape length) and 7 (lowest leaflet length) distinguish var. *greeleyorum* from the other varieties, and characters 15 (primary ray number) and 22 (fruit wing width) separate vars. *greeleyorum* and *higginsii* from the other three varieties. There is a strong tendency—appropriately, given its name—for var. *parvus* to have the smallest (or fewest) means, and for vars. *greeleyorum* and *higginsii* to have the largest (or most) means, but except as noted previously these differences are insufficient to distinguish these varieties from one or more other

Table 2. Morphological characters and their statistics (mean ± standard deviation, with range in parentheses) for the five varieties traditionally recognized in *Cymopterus glomeratus*. Sample sizes for each variety are indicated below the varietal epithet (flowering specimens/fruiting specimens). Those characters that differ significantly ($p < 0.05$) among the varieties as shown by MANOVA are marked with an asterisk. Superscript letters show the results of Tukey tests using the harmonic mean sample size, with taxa in the same homogeneous subset ($p > 0.05$) sharing the same letter. Note that for six characters (Nos. 9–11, 13, 16, and 19) that showed significant differences, the taxa all belonged to the same homogeneous subset, probably as the result of the small sample sizes for vars. *greeleyorum*, *higginsii*, and *parvus*.

	Taxon				
Characters	*acaulis* (N = 83/69)	*fendleri* (N = 51/52)	*greeleyorum* (N = 3/3)	*higginsii* (N = 7/3)	*parvus* (N = 10/7)
1. Plant height (cm)*	8.7 ± 2.6^{AB} (4.5–17.0)	10.6 ± 3.7^{BC} (4.5–28.0)	10.8 ± 3.9^{BC} (7.0–18.0)	12.6 ± 4.2^{C} (7.0–20.0)	6.4 ± 1.1^{A} (5.0–8.5)
2. Peduncle length (cm)*	5.1 ± 2.7^{AB} (1.0–15.0)	7.9 ± 3.7^{BC} (2.0–25.0)	4.2 ± 2.8^{A} (1.5–8.0)	9.2 ± 4.1^{C} (4.5–17.0)	3.5 ± 1.0^{A} (2.5–5.5)
3. Pseudoscape length (cm)*	3.2 ± 1.3^{A} (1.0–7.5)	3.1 ± 1.2^{A} (1.0–7.5)	6.1 ± 2.3^{B} (3.5–10.0)	3.8 ± 1.3^{A} (2.0–6.5)	3.9 ± 1.0^{A} (2.2–5.0)
4. Leaf blade length (cm)*	3.9 ± 1.1^{AB} (2.0–8.0)	3.8 ± 1.1^{AB} (1.8–7.0)	3.6 ± 0.5^{A} (3.0–4.5)	4.7 ± 1.1^{B} (3.3–6.5)	3.3 ± 0.7^{A} (2.5–5.5)
5. Leaf blade width (cm)	3.4 ± 1.1^{A} (1.6–8.5)	3.1 ± 1.0^{A} (1.5–6.5)	3.6 ± 0.5^{A} (2.8–4.0)	3.3 ± 0.7^{A} (2.2–4.5)	2.9 ± 0.5^{A} (2.0–4.0)
6. Leaf petiole length (cm)*	5.0 ± 1.3^{AB} (2.7–9.0)	5.1 ± 1.5^{AB} (2.0–10.0)	5.5 ± 1.8^{B} (3.3–8.5)	4.7 ± 1.3^{AB} (2.8–7.0)	4.0 ± 0.8^{A} (2.8–6.0)
7. Lowest leaflet length (cm)*	2.1 ± 0.7^{A} (0.9–4.5)	1.7 ± 0.6^{A} (0.8–3.5)	2.9 ± 2.5^{B} (1.5–8.0)	2.0 ± 0.5^{A} (1.1–2.5)	1.7 ± 0.4^{A} (1.2–2.8)
8. Lowest leaflet width (cm)	1.5 ± 1.0^{A} (0.4–12.0)	1.3 ± 0.5^{A} (0.5–2.5)	1.5 ± 0.4^{A} (1.0–2.0)	1.5 ± 0.4^{A} (0.8–2.0)	1.1 ± 0.3^{A} (0.8–1.5)
9. Number of pairs of lateral primary leaflets (pinnae)*	4.7 ± 0.7^{A} (3–6)	5.1 ± 0.8^{A} (3–7)	5.3 ± 0.5^{A} (5–6)	5.0 ± 0.8^{A} (4–6)	4.9 ± 0.6^{A} (4–6)
10. Ultimate leaf segment length (mm)*	4.8 ± 2.1^{A} (2.0–14.0)	3.9 ± 1.6^{A} (1.0–10.0)	3.4 ± 1.7^{A} (2.0–6.5)	4.5 ± 1.1^{A} (2.5–6.5)	3.1 ± 0.9^{A} (1.8–4.5)

Table 2. Continued.

Characters	Taxon				
	acaulis (N = 83/69)	*fendleri* (N = 51/52)	*greeleyorum* (N = 3/3)	*higginsii* (N = 7/3)	*parvus* (N = 10/7)
11. Ultimate leaf segment width (mm)*	1.8 ± 0.6^{A} (1.0–5.0)	1.9 ± 0.6^{A} (1.0–4.0)	1.8 ± 0.5^{A} (1.5–2.5)	2.4 ± 0.7^{A} (1.5–3.5)	2.2 ± 0.5^{A} (1.5–3.0)
12. Length on the rachis between the first two pairs of leaflets (mm)*	14.4 ± 4.8^{AB} (6.0–32.0)	12.9 ± 4.3^{A} (3.0–25.0)	11.3 ± 2.5^{A} (9.0–16.0)	17.5 ± 4.0^{B} (12.0–25.0)	11.4 ± 2.6^{A} (8.0–15.0)
13. Inflorescence (umbel) width (cm)*	2.7 ± 0.7^{A} (1.0–4.5)	3.3 ± 1.7^{A} (1.6–18.0)	3.0 ± 0.8^{A} (2.0–4.0)	2.9 ± 0.9^{A} (1.8–4.5)	2.2 ± 0.4^{A} (1.5–2.5)
14. Umbellet width (cm)	1.2 ± 0.5^{A} (0.2–2.5)	1.3 ± 0.6^{A} (0.5–6.0)	1.4 ± 0.6^{A} (0.7–2.0)	1.2 ± 0.7^{A} (0.5–2.5)	1.1 ± 0.4^{A} (0.6–1.8)
15. Primary ray number*	4.4 ± 0.8^{A} (3–8)	4.5 ± 1.0^{A} (3–8)	6.0 ± 1.3^{B} (5–8)	5.6 ± 1.1^{B} (4–8)	4.4 ± 0.7^{A} (3–5)
16. Primary ray length (cm)*	0.4 ± 0.2^{A} (0.2–1.2)	0.5 ± 0.3^{A} (0.2–2.2)	0.5 ± 0.1^{A} (0.3–0.6)	0.3 ± 0.1^{A} (0.2–0.5)	0.3 ± 0.2^{A} (0.2–0.8)
17. Secondary ray length (mm)*	1.0 ± 0.0^{A} (1.0–1.0)	1.0 ± 0.1^{AB} (1.0–2.0)	1.2 ± 0.4^{AB} (1.0–2.0)	1.1 ± 0.3^{AB} (1.0–2.0)	1.2 ± 0.5^{B} (1.0–3.0)
18. Bractlet length (mm)*	4.7 ± 1.2^{AB} (2.5–9.0)	5.4 ± 1.5^{B} (3.0–10.0)	3.7 ± 1.0^{A} (3.0–5.0)	5.1 ± 1.3^{B} (3.0–7.0)	4.5 ± 1.1^{AB} (3.0–7.0)
19. Bractlet width (mm)*	1.6 ± 1.0^{A} (0.5–12.0)	2.1 ± 0.6^{A} (1.0–4.0)	2.2 ± 0.4^{A} (2.0–3.0)	2.1 ± 0.6^{A} (1.0–3.0)	2.0 ± 0.4^{A} (1.5–2.5)
20. Fruit length (mm)*	8.1 ± 1.8^{A} (5.0–13.0)	8.9 ± 1.6^{AB} (6.5–13.0)	9.0 ± 1.0^{AB} (8.0–10.0)	11.3 ± 3.5^{B} (8.0–15.0)	7.9 ± 1.0^{A} (7.0–10.0)
21. Fruit width (mm)*	6.2 ± 1.4^{AB} (3.0–10.0)	6.4 ± 1.3^{ABC} (4.0–10.0)	7.7 ± 0.6^{BC} (7.0–8.0)	8.3 ± 1.5^{C} (7.0–10.0)	4.6 ± 0.4^{A} (4.0–5.0)
22. Fruit wing width (mm)*	1.5 ± 0.5^{A} (1.0–3.0)	1.5 ± 0.5^{A} (1.0–3.0)	2.7 ± 0.3^{B} (2.5–3.0)	2.7 ± 0.6^{B} (2.0–3.0)	1.3 ± 0.3^{A} (1.0–1.8)

varieties. In no case do the characters separate the varieties by flower color, and for each character vars. *acaulis* and *fendleri* share at least one subset in common.

For the PCA using all 288 specimens and 19 non-fruit morphological characters, there are six components with eigenvalues greater than 1.0 (Pimentel 1979), which account for about 68% of the total variation in the data set (26.1%, 14.0%, 9.0%, 6.8%, 6.4%, and 5.7%, respectively). Plots of the first three principal components (PC1, PC2, and PC3) are shown in Figure 2. No clearly separated clusters are revealed and all varieties are intermixed on these plots. Furthermore, there are no clusters that correspond to differences in flower color. The remaining three principal components also did not separate the OTUs into distinct clusters, nor did the PCAs using flowering (154 OTUs × 19 characters) or fruiting (134 OTUs × 22 characters) specimens separately (results not shown). Similarly, PCAs of the combined data set of 288 OTUs using only 16 non-fruit characters (excluding characters 5, 8, and 14 which did not differ significantly among the varieties) provided no separation among the OTUs (results not shown).

Table 3 lists the character loadings from the combined analysis on the first three components. The first (PC1) has relatively high positive loadings for plant height, peduncle length, leaf blade length and width, petiole length, lowest leaflet length, and the length between the first two pairs of leaflets on the rachis. Thus, despite linear transformation, PC1 still largely reflects sorting by size, a common phenomenon in PCA (Pimentel 1979). The second component (PC2) has relatively high positive loadings for peduncle length, inflorescence width, umbellet width, and primary ray length, and thus sorts plants largely on inflorescence size. The third (PC3) has a relatively high positive loading for the number of pairs of lateral primary leaflets and relatively high negative loadings for the length and width of the ultimate leaf segment, thereby separating plants with numerous leaflets bearing small ultimate segments from those with few leaflets bearing large segments.

The plot of peduncle length versus leaf blade length for 255 OTUs of var. *acaulis* or var. *fendleri* is given in Figure 3. Most of the OTUs of var. *fendleri* have peduncles that are longer than the leaves, whereas OTUs of var. *acaulis* do not show a distinct pattern. In addition, both vars. *greeleyorum* and *parvus* have their OTUs about evenly divided between having peduncles that are shorter than the leaves and longer than the leaves, and all OTUs of var. *higginsii* have peduncles longer than the leaves (data not shown). Thus, these characters provide no clear separation among the varieties.

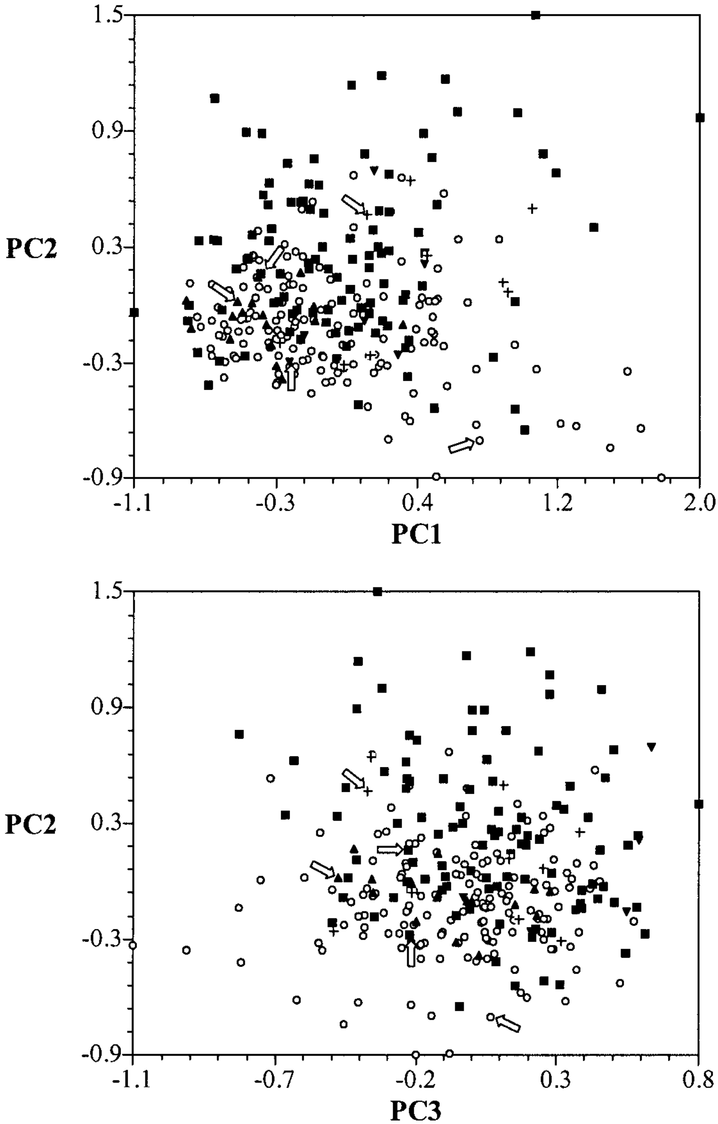

Figure 2. Plots of principal components (PC) 1, 2, and 3 for the *Cymopterus glomeratus* complex using 19 non-fruit morphological characters (Nos. 1–19; Table 2). Varieties are indicated as follows: *acaulis* (circles), *fendleri* (squares), *greeleyorum* (down triangles), *higginsii* (crosses), and *parvus* (up triangles). White-flowered OTUs are shown with open symbols, yellow-flowered with filled symbols, and purple-flowered with crosses. Arrows indicate type specimens.

Table 3. Principal component loadings for the 19 non-fruit morphological characters on the first three components for the *Cymopterus glomeratus* complex. For each component, values with particularly large magnitudes are shown in bold.

Characters	PC1	PC2	PC3
1. Plant height (cm)	**0.7324**	0.4523	0.1149
2. Peduncle length (cm)	**0.6079**	**0.5672**	0.0834
3. Pseudoscape length (cm)	0.1822	−0.0120	0.2559
4. Leaf blade length (cm)	**0.8758**	−0.2702	0.1161
5. Leaf blade width (cm)	**0.7547**	−0.4583	0.0498
6. Leaf petiole length (cm)	**0.7581**	0.0499	0.0858
7. Lowest leaflet length (cm)	**0.6732**	−0.4769	0.0213
8. Lowest leaflet width (cm)	0.5007	−0.3603	0.0518
9. Number of pairs of lateral primary leaflets (pinnae)	0.0917	−0.0424	**0.7889**
10. Ultimate leaf segment length (mm)	0.4882	−0.1698	−**0.6582**
11. Ultimate leaf segment width (mm)	0.3350	0.0887	−**0.6560**
12. Length on the rachis between the first two pairs of leaflets (mm)	**0.7982**	−0.3095	0.0442
13. Inflorescence (umbel) width (cm)	0.3178	**0.5674**	0.0455
14. Umbellet width (cm)	0.1365	**0.5033**	−0.0235
15. Primary ray number	0.2353	0.2860	0.2104
16. Primary ray length (cm)	0.2517	**0.6262**	0.0249
17. Secondary ray length (mm)	−0.0226	0.1008	−0.1647
18. Bractlet length (mm)	0.3920	0.4205	−0.1221
19. Bractlet width (mm)	0.1158	0.3437	−0.1331

DISCUSSION

Varieties in *Cymopterus glomeratus* traditionally have been distinguished based on a few quantitative morphological characters (peduncle length and leaf length), flower color, and to a lesser extent, geographic distribution. Multivariate analysis of quantitative characters shows that although there are statistical differences among the varieties for some characters, the differences are small and obscured by the considerable variation within the taxa. This is clearly demonstrated by the broadly overlapping homogeneous subsets of taxa defined by Tukey tests for most characters (Table 2). The most distinctive taxa are vars. *greeleyorum* and *higginsii*, which individually or together form separate subsets for a few characters, but even for these characters the ranges overlap among the varieties. The complete absence of distinct clusters

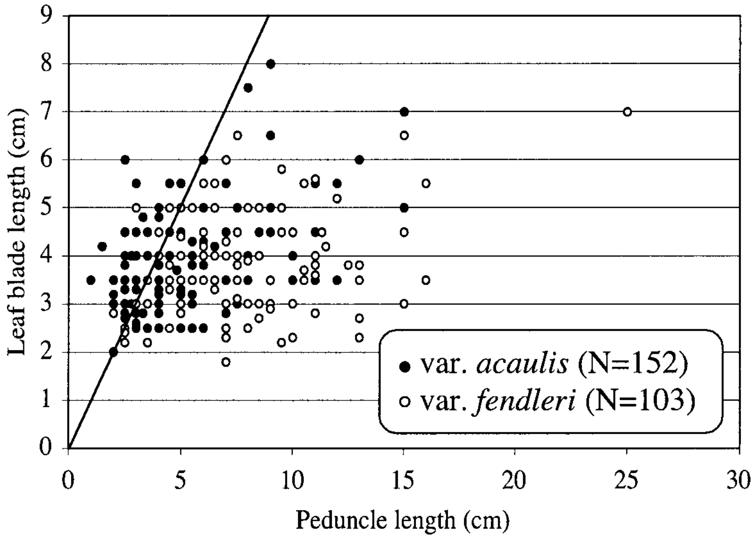

Figure 3. Scatter plot of peduncle length versus leaf blade length for 255 OTUs identified as two varieties of *Cymopterus glomeratus*. The diagonal line shows peduncle length equal to leaf blade length.

resulting from the PCA (Figure 2) further demonstrates the overlap among the varieties, and shows that infraspecific taxa cannot be distinguished by individual characters or combinations of characters.

A potential weakness of this study results from the small sample sizes for three of the varieties. These varieties are very narrowly distributed, thus specimens are rarely collected. This is the most likely cause of the seemingly contradictory finding for the six characters that differed significantly among the varieties, but Tukey tests assigned them all to a single homogeneous subset. However, even vars. *acaulis* and *fendleri*, for which we sampled more than 100 individuals each, overlapped considerably. The quantitative character combination most frequently used to distinguish them, peduncle length relative to leaf length, provides no separation between these taxa (Figure 3). For the other characters, differences between these varieties were small enough that they always shared membership in at least one homogeneous subset (Table 2).

A concern with all studies based solely on herbarium material is that variation reflects environmental plasticity rather than heritable genetic differences. We argue this is not a serious concern here because we found no consistent differences in the characters. Common garden experiments could be used to test for environmental effects, but we would not predict that the outcome would change the taxonomic conclusions. On the one hand, plasticity could be obscuring genetic differences among the plants, but even if that were true, the practical problem of distinguishing varieties would remain. On the other hand, some of the minor differences we observed, for example, the tendency of plants assigned to var. *parvus* to be at the small or fewest extremes for many characters, could be the result of environmental effects, further strengthening the case for not recognizing any varieties.

Although quantitative characters cannot reliably separate the varieties, flower color remains a potential basis for recognizing separate taxa. White-flowered var. *acaulis* has long been separated from yellow-flowered var. *fendleri*, but the presence of morphologically intermediate plants in the Uinta Basin weakens the case for such separation. There, "plants [of var. *acaulis*] with white flowers grow among those with yellow flowers, making it difficult if not impossible to recognize two taxa" (Goodrich 1986). The presence of other yellow-flowered varieties (i.e., *greeleyorum* and *parvus*) also makes the separation between vars. *acaulis* and *fendleri* questionable. Although Goodrich (1986) stated that the petals of var. *higginsii* are bright purple and remain so long after collection, we have found that the flower color varies even among flowers on a single plant. Purple flowers are also found on plants well outside the narrow geographic range of var. *greeleyorum* and that would be assigned to other varieties. Thus, flower color provides little or no justification for the recognition of infraspecific taxa in *Cymopterus glomeratus*.

Lastly, the distinctions among the five varieties of *Cymopterus glomeratus* based on their geographic distributions are not satisfactory. Variety *acaulis* is sympatric with var. *fendleri* in the Uinta Basin of northeastern Utah and adjacent western Colorado and with var. *greeleyorum* in Malheur County, Oregon, respectively. Variety *greeleyorum* is weakly ecologically separated from var. *acaulis* by being restricted to clay soil (Grimes and Packard 1981), whereas var. *acaulis* is found in both clay and sandy soil. The narrowly distributed var. *higginsii* is found in Kane County, Utah, where the widely distributed var. *fendleri* is also located. Based on available collections, var. *parvus* is separated from the other four varieties of *C. glomeratus*, although its distribution is close to var. *fendleri*. Because the habitats for these varieties are very similar to each other, and because no plants of this species complex are found immediately to the west of the areas where var. *parvus* is located, it is likely that localities containing var. *parvus* may represent the outer distribution boundary of this species complex. Apparently, the five varieties of *C.*

glomeratus are not geographically distinguishable based on their overlapping or adjacent distributions.

On the basis of the results presented herein, and the results of prior investigations that have confirmed the monophyly of the species (Sun 2003; Sun and Downie 2004), we propose that plants in this species complex be recognized as one morphologically variable species, *Cymopterus glomeratus*, with no varieties.

TAXONOMIC TREATMENT

Cymopterus glomeratus (Nutt.) DC., Prodr. 4: 204. 1830.

Selinum acaule Pursh, Fl. Amer. Sept. 2: 732. 1813 ["1814"]. *nom. illegit*., non *S. acaule* Cav. 1799. *Thapsia glomerata* Nutt., Gen. N. Amer. Pl. 1: 184. 1818. *Cymopterus acaulis* Raf., Herb. Raf. 2: 40. 1833. *nom. superfl. & illegit*. TYPE: UNITED STATES. "Upper Louisiana," 1811, *J. Bradbury s.n.* (LECTOTYPE designated by Mathias 1930: K!, photo at MO!; ISOLECTOTYPE: BM!). See discussion of typification and type locality below.

Ferula ? *palmella* Hook., Fl. Bor.-Amer. (Hooker) 1: 268. 1832. *nom. superfl. & illegit*. SYNTYPES: UNITED STATES. "the Missouri," 1811, *J. Bradbury s.n.* (SYNTYPE: photo at K!). CANADA. Saskatchewan: Carlton House, 1825–1827, *T. Drummond s.n.* (SYNTYPE: photo at K!).

Cymopterus fendleri A. Gray, Mem. Amer. Acad. Arts, n.s. 4: 56. 1849. *C. acaulis* var. *fendleri* (A. Gray) Goodrich, Great Basin Naturalist 46: 79. 1986. TYPE: UNITED STATES. New Mexico: Santa Fe Co., Santa Fe, gravelly hills, 1847, *A. Fendler 274* (HOLOTYPE: GH!; ISOTYPES: MO!, NY!, US!).

Coloptera parryi J.M. Coult. & Rose, Rev. N. Amer. Umbell. 50. 1888. *Cymopterus parryi* (J.M. Coult. & Rose) M.E. Jones, Zoe 4: 48. 1893. *Cymopterus glomeratus* var. *parryi* (J.M. Coult. & Rose) M.E. Jones, Proc. Calif. Acad. Sci., ser. 2, 5: 688. 1895. TYPE: UNITED STATES. Wyoming: Little Sandy, northwest Wyoming, 1873, *C.C. Parry s.n.* [HOLOTYPE: GH!; although the protologue did not indicate where the holotype was deposited, Coulter and Rose (1900) later stated that the holotype was at the Gray Herbarium].

Cymopterus decipiens M.E. Jones, Zoe 2: 246. 1891. TYPE: UNITED STATES. Utah: Cisco, 2 May 1890, *M.E. Jones s.n.* (HOLOTYPE: POM!; ISOTYPE: MO!).

Cymopterus leibergii J.M. Coult. & Rose, Contr. U. S. Natl. Herb. 7: 182. 1900. *C. glomeratus* var. *leibergii* (J.M. Coult. & Rose) M.E. Jones, Contr. W. Bot. 12: 25. 1908. TYPE: UNITED STATES. Oregon: Malheur Valley, near Harper Ranch, 12 Jun 1896, *J.B. Leiberg 2253* (HOLOTYPE: US!).

Cymopterus lucidus Osterh., Muhlenbergia 6: 59. 1910. TYPE: UNITED STATES. Colorado: Bent Co., west of Las Animas, 16 Jun 1909, *G.E. Osterhout 3905* (HOLOTYPE: RM!).

Cymopterus higginsii S.L. Welsh, Great Basin Naturalist 35: 377. 1976 ["1975"]. *C. acaulis* var. *higginsii* (S.L. Welsh) Goodrich, Great Basin Naturalist 46: 79. 1986. TYPE: UNITED STATES. Utah: Kane Co., E of None

Butte, 17 mi E of Glen Canyon City, 31 May 1975, *S.L. Welsh 12740* (HOLOTYPE: BRY!; ISOTYPE: MO!).

Cymopterus acaulis var. *greeleyorum* J.W. Grimes & P.L. Packard, Brittonia 33: 430. 1981. TYPE: UNITED STATES. Oregon: Malheur Co., clay soil, Sucker Creek Formation, Rockville area, just S of Leslie Gulch Rd jct. with Succor Creek Rd, T26S R46E S16, 2 May 1976, *P.L. Packard 76-3* (HOLOTYPE: NY!; ISOTYPES: OSC!, UTC!, NY!).

Cymopterus acaulis var. *parvus* Goodrich, Great Basin Naturalist 46: 79. 1986. TYPE: UNITED STATES. Utah: Tooele Co., Skull Valley, Stansbury Mtns., near 1/4 corner with sec 33, 32.7 km and 326 degree NW of Vernon, 7 Jun 1984, *S. Goodrich 20458* (HOLOTYPE: BRY!; ISOTYPES: NY!, RM!).

Mathias (1930) was aware that Pursh's *Selinum acaule* was a later homonym of *S. acaule* Cav. Unfortunately, she and most later authors continued to use this illegitimate name as the basionym for this species' name. Correcting this error requires use of the name *Cymopterus glomeratus* to replace the widely used, but incorrect, *C. acaulis*.

The type of *Selinum acaule* and hence of *Thaspia glomerata* has been the subject of some confusion. Mathias (1930) stated without any discussion that the type was at K, thereby inadvertently designating this as the lectotype. However Bradbury's material, studied by Pursh for the *Flora Americae Septentrionalis* (Pursh 1813), was in Lambert's herbarium, where Nuttall (1818) also reported seeing the specimen. Most of Lambert's herbarium eventually was obtained by PH (Rickett 1950). Unfortunately, Rickett (1950) was unable to locate any Bradbury material of this species at PH and therefore formally designated the Bradbury specimen at K as the lectotype. Ewan (1979) stated that the type was indeed at PH, but cited Rickett's publication as the basis for that claim. In addition, Cronquist (1997) reported that there was "original material" of this species at BM. We have seen a Bradbury specimen at BM and studied a high quality scanned image of his specimen at K (and a photograph of it at MO); but were unable to locate his collections of this species at PH or LIV, another herbarium that houses significant Bradbury material (Rickett 1950). Bradbury (1819) reported collecting this species only once, so the BM and K specimens would both appear to be original material, but neither bears Pursh's handwriting or any indication it came from Lambert's herbarium. Because we have been unable to locate the holotype, we therefore follow Mathias (1930) and Rickett (1950) and recognize the K specimen as the lectotype. The BM specimen should be treated as an isolectotype. The specimen at K (the then isotype of *S. acaule* Pursh) is also one of the syntypes of *Ferula* ? *palmella* Hook., making this name illegitimate.

The type locality is also problematic. Pursh (1813) gave only ''upper Louisiana,'' the locality used on most of Bradbury's collections in the Lambert herbarium (Rickett 1950). Later literature usually cites the type locality as ''on the alluvium of the Missouri, from the river Naduet to the Mahas.'' In modern terms, this is along the Missouri River between the Nodaway River and the Omaha Indian Reservation, and includes parts of Iowa, Kansas, Missouri, Nebraska, and South Dakota, although Bradbury collected mostly west of the river (Bradbury 1819; Rickett 1950). *Cymopterus glomeratus* does not occur in this region (Figure 1), however, reaching its eastern limit about 200 km to the west. This locality information comes from Bradbury's specimen list, which appeared in the second edition of his *Travels in the Interior of America* (Bradbury 1819). This edition was published eight years after his expedition, and his memory may have been faulty. The lectotype itself is labeled in unknown handwriting ''100 up the Missouri,'' which, assuming this to be river miles from the Missouri's mouth at the Mississippi River near St. Louis, the starting point of the expedition, lies in central Missouri, also outside the species' range. (The isolectotype has no specific locality information.) Rickett (1950) saw no other Bradbury specimens labeled like this, but did see two [*Erysimum asperum* (Nutt.) DC. and *Lesquerella ludoviciana* (Nutt.) S. Watson] labeled ''1100 miles up the Missouri.'' This would be in present-day north-central South Dakota, within the range of *C. glomeratus*. Bradbury (1819) also cited *E. asperum* as being important medicinally for the Arikara, who then lived in northern South Dakota (Parks 2001), corroborating the label locality. An additional consideration is that the type collection includes mature fruits, and Bradbury was in the Nodaway-Omahas region in the second half of April to very early May, too early for *C. glomeratus* to be fruiting in that part of its range, whereas he was in the Arikara area in early to middle June, when *C. glomeratus* would have been in late flower and fruit. Finally, Nuttall (1818), who was on the expedition with Bradbury, reported collecting this species on the ''open plains of the Missouri, commencing 40 miles below the confluence of the White River.'' This is in current-day south-central South Dakota, just within the range of *C. glomeratus*. Thus, despite Bradbury's (1819) statement, it is likely that the type of *Selinum acaule* and *Thaspia glomerata* came from South Dakota, perhaps about 1100 river miles up the Missouri from St. Louis.

ACKNOWLEDGMENTS. The authors thank Deborah S. Katz-Downie for assistance in the laboratory; the curators of the herbaria cited in the text for access to specimens; Vicki Noble, Sharon McDonald, and Walter Kittredge for scanning type specimens; Jason Koontz and two anonymous reviewers for comments on the manuscript; and Kanchi Gandhi for help with the nomenclature. This work was supported by National Science Foundation grants DEB 9407712 and DEB 0089452 to S.R.D., and by Francis M. and Harlie M. Clark research support grants, a Herbert Holdsworth Ross Memorial Fund award, a Program in Ecology and Evolutionary Biology Summer Research Fellowship, and travel grants from the Graduate College, the John R. Laughnan Fund, and the Program in Ecology and Evolutionary Biology to F.J.S. This paper represents a portion of a Ph.D. dissertation submitted by F.J.S. to the Graduate College of the University of Illinois at Urbana-Champaign.

LITERATURE CITED

BRADBURY, J. 1819. Travels in the Interior of America, in the Years 1809, 1810, and 1811, 2nd ed. Sherwood, Neely, and Jones, London, U.K.

COULTER, J. M. AND J. N. ROSE. 1888. Revision of North American Umbelliferae. Wabash College, Crawfordsville, IN.

——— AND ———. 1900. Monograph of the North American Umbelliferae. Contr. U. S. Natl. Herb. 7: 1–256.

——— AND ———. 1909. Supplement to the monograph of the North American Umbelliferae. Contr. U. S. Natl. Herb. 12: 441–451.

CRONQUIST, A. 1997. Apiaceae, pp. 340–427. *In*: A. Cronquist, N. H. Holmgren, and P. K. Holmgren, eds., Intermountain Flora: Vascular Plants of the Intermountain West, U. S. A., Vol. 3, Part A. The New York Botanical Garden, Bronx, NY.

DOWNIE, S. R., R. L. HARTMAN, F.-J. SUN, AND D. S. KATZ-DOWNIE. 2002. Polyphyly of the spring-parsleys (*Cymopterus*): Molecular and morphological evidence suggests complex relationships among the perennial endemic genera of western North American Apiaceae. Canad. J. Bot. 80: 1295–1324.

EWAN, J. 1979. Introduction, pp. 5–117. *In*: F. T. Pursh, Flora Americae Septentrionalis [facsimile reprint of 1814 edition]. J. Cramer, Vaduz, Liechtenstein.

GILMARTIN, A. J. AND K. S. SIMMONS. 1987. Relationships of *Lomatium* among other genera of Apiaceae. Pl. Syst. Evol. 157: 95–103.

GOODRICH, S. 1986. Utah flora: Apiaceae (Umbelliferae). Great Basin Naturalist 46: 66–106.

GRIMES, J. W. AND P. L. PACKARD. 1981. New taxa of Apiaceae, Hydrophyllaceae, and Saxifragaceae from Oregon and Idaho. Brittonia 33: 430–434.

HARTMAN, R. L. 1985. A new species of *Cymopterus* (Umbelliferae) from southern Idaho. Brittonia 37: 102–105.

——— AND R. S. KIRKPATRICK. 1986. A new species of *Cymopterus* (Umbelliferae) from Northwestern Wyoming. Brittonia 38: 420–426.

HOLMGREN, P. K., N. H. HOLMGREN, AND L. C. BARNETT. 1990. Index Herbariorum. The New York Botanical Garden, Bronx, NY.

JONES, M. E. 1908. New species and notes. Contr. W. Bot. 12: 1–81.

Kartesz, J. T. 1994. A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland, 2nd ed. Biota of the North American Program of the North Carolina Botanical Garden. Timber Press, Portland, OR.

Mastrogiuseppe, J. D., J. G. Steven, K. S. Simmons, and G. K. Brown. 1985. Morphological and cytotaxonomic evaluation of *Lomatium tuberosum* (Apiaceae). Brittonia 37: 252–260.

Mathias, M. E. 1930. Studies in the Umbelliferae. III. A monograph of *Cymopterus* including a critical study of related genera. Ann. Missouri Bot. Gard. 17: 213–476.

——— and L. Constance. 1944–1945. Umbelliferae, pp. 43–295. *In*: North American Flora, Vol. 28B. The New York Botanical Garden, Bronx, NY.

Nuttall, T. 1818. The Genera of North American Plants, Vol. 1. Printed for the author by D. Heartt, Philadelphia, PA.

Parks, D. R. 2001. Arikara, pp. 365–390. *In*: R. J. DeMallie, ed., Plains, Handbook of North American Indians, Vol. 13. Smithsonian Institution, Washington, DC.

Pimentel, R. A. 1979. Morphometrics: The Multivariate Analysis of Biological Data. Kendall/Hunt Publishing Co., Dubuque, IA.

Pursh, F. T. 1813 ["1814"]. Flora Americae Septentrionalis or, a Systematic Arrangement and Description of the Plants of North America. White, Cochrane, and Co., London, U.K.

Rickett, H. W. 1950. John Bradbury's explorations in Missouri Territory. Proc. Amer. Philos. Soc. 94: 59–89.

Rohlf, F. J. 2000. NTSYSpc: Numerical Taxonomy and Multivariate Analysis System, version 2.1. Exeter Publishing, Ltd., Setauket, NY.

Simmon, K. S. and A. J. Gilmartin. 1982. Toward infrageneric taxa of *Lomatium* (Umbelliferae): A natural alliance. Abstr. Bot. Soc. Amer., Misc. Ser. Publ. 162: 107.

Sun, F.-J. 2003. A phylogenetic study of *Cymopterus* and related genera (Apiaceae). Ph.D. dissertation, Univ. Illinois, at Urbana-Champaign, IL.

——— and S. R. Downie. 2004. A molecular systematic investigation of *Cymopterus* and its allies (Apiaceae) based on phylogenetic analyses of nuclear (ITS) and plastid (*rps*16 intron) DNA sequences. S. African J. Bot. 70: 407–416.

———, ———, and R. L. Hartman. 2004. An ITS-based phylogenetic analysis of the perennial, endemic Apiaceae subfamily Apioideae of western North America. Syst. Bot. 29: 419–431.

Welsh, S. L. 1976 ["1975"]. Utah plant novelties in *Cymopterus* and *Penstemon*. Great Basin Naturalist 35: 377–378.

APPENDIX

Specimens of *Cymopterus glomeratus* included in the multivariate analyses and their identifications, as treated by Kartesz (1994, as *C. acaulis*). Herbarium acronyms follow Holmgren et al. (1990).

Variety *glomeratus* (= *acaulis*)

CANADA. Manitoba: Carberry, Assiniboine River, sand hills above River, 0.5 mi W, elev 10858 ft, 29 May 1967, *Baldwin 6089* (MO); District De Souris, 1 mi SE of

Goodlands, arid ridge at the foot of the Head of Tortue, 3 Jun 1960, *Boivin 13421* (RM).

UNITED STATES. Unknown State: "Upper Louisiana," 1811, *Bradbury s.n.* (BM). Colorado: Baca Co., ca 13 mi N of Pritchett, 17 May 1990, *Brooks 19735* (BM); Spring Field, 20 May 1914, *Osterhout 5061* (BM); Bent Co., hillsides along the Arkansas River near Hasty, elev 4000 ft, 3 May 1947, *Porter 4109* (BM); Boulder Co., N edge of turtle-back sandstone, S facing slope of Gunbarrel Hill, 10 mi NE of Boulder, 17 Apr 1947, *Weber 3265* (UTC); Douglas Co., Denver, dry soil, elev 5300 ft, 15 May 1918, *Clokey 3041* (UC); El Paso Co., "Cemetery" prairie, Colorado Springs, 14 Jun 1912, *Churchill 619* (MO); Garfield Co., Flat Tops/White River Plateau, Main Elk Creek, ca 4 air mi N of New Castle, elev 5800–6700 ft, 23 May 1990, *Hartman & Vanderhorst 24525* (RM); Flat Tops/White River Plateau, Grand Hogback, ca 5 air mi N of Rifle, elev 5800 ft, 25 May 1991, *Vanderhorst 2172* (RM); Huerfano Co., high plains, N of Walsenburg, elev 6500 ft, 27 May 1938, *Ehlers 6787* (RM); Larimer Co., elev 5000 ft, 1 May 1895, *Patterson 3934* (MO); Fort Collins, elev 5000 ft, 3–24 May 1896, *Crandall s.n.* (UC); Moffat Co., Cedar Springs, Draw-Wild Horse Ridge, SW of Maybell, elev 1950 m, 8 May 1990, *Goodrich 23093* (BRY); sandy hills near Maybell, 14 May 1948, *Beetle & Porter 5503* (RM); Montrose Co., Paradox Valley, on knoll, E of Paradox, elev 5240 ft, 25 Apr 1986, *Franklin 2834* (BRY, RM); Otero Co., S of La Junta, elev 4200 ft, 25 May 1962, *Gierisch 2490* (RM); Prowers Co., fine river bottom dirt, amongst heavy, low growth, near the Arkansas River, elev 3610 ft, 28 May 1984, *Kent & Brock 82* (MO); Pueblo Co., 3 mi N of Pueblo, elev 4700 ft, 3 May 1947, *Porter 4119* (RM); Rio Blanco Co., 0.2 mi E of Piceance Creek and 0.9 mi NNE of Square South Ranch, elev 1855 m, 27 May 1982, *O'Kane & Sigstedt 82-144* (RM); 0.3 mi N of Hatch Gulch and 2.4 mi SSW of Square South Ranch, elev 1945 m, 27 May 1982, *O'Kane & Sigstedt 82-150* (RM); 10 road mi W of Rangely on Hwy, 20 Apr 1995, *Goodrich 24763* (BRY); 8.6 mi S of Dinosaur, along Hwy 64, 3 May 1978, *Neese & England 4339* (BRY); overlooking White R, 10 mi W of Rangely, elev 6000 ft, 1 May 1982, *Neese 11273* (BRY); Routt Co., Flat Tops/White River Plateau, hills above Colorado River, ca 1 air mi NW of McCoy, elev 7000 ft, 12 May 1991, *Vanderhorst 2033* (RM); Weld Co., New Windsor, 4 Jun 1909, *Osterhout 4139* (RM); Yuma Co., Bonny Reservoir, ca 2 mi E, 8 May 1971, *Hermann 23527* (RM). Idaho: Ada Co., Snake River below Swan Falls, 19 Apr 1937, *Tucker 666* (IDS); Butte Co., 1 mi W of May's ranch, Howe, dry clay desert, 12 Apr 1939, *Mays s.n.* (IDS); 5 mi S of Howe, on W side of Co. Rd leading toward Arco, elev 5000 ft, 20 May 1958, *Passey & Hugie 104* (UTC); Canyon Co., without locality, May 1936, *Davis 29A-36* (IDS); ca 4 mi due E of Homedale, exposed fine sandy-silty lakebeds on hill, elev ca 2400 ft, 30 Mar 1986, *Ertter 5872* (UC); Greenleaf, 28 Apr 1935, no collector indicated, *s.n.* (IDS); Clark Co., S end of Beaverhead Mtns, 289 mi from Dubois, elev 5400 ft, 25 May 1981, *Goodrich 15424* (BRY); Custer Co., benchland across river from Challis, elev ca 5200 ft, 14 Jun 1944, *Hitchcock & Muhlick 8961* (IDS); Bureau of Land Management forest, lower Morgan Creek, elev 6000 ft, Jul 1967, *Morgan 47* (UTC); Gooding Co., 5 mi S of Bliss, 30 Apr 1983, *Branchfield 26* (IDS); dry clay hill below Bliss, 11 May 1946, *Davis 4459* (IDS); Lemhi Co., Salmon, 16 May 1936, *Davis 34-35* (IDS). Kansas: Gove Co., 14 mi W and 12 mi S of Gove, Chalky prairie flats below bluffs along Smoky Hill River, 21 May 1980, *McGregor 31705* (RM); Morton Co., 6 mi N and 4 mi W of Elkhart, 22 May 1984, *McGregor 35408* (RM). Montana: Carbon Co., Lloyd's cabin, elev 4200 ft, 10 May 1983, *Lichvar 5584* (RM); Carter Co., 200 m S of the Carter Rimrock Rd, Ekalaka Hills, Custer National Forest, elev 1158 m, 6 Apr 1986, *Mooers & Mooers 1081* (BRY); Custer Co., 7 mi SW of Miles City along Hwy 10, 6 May 1957, *Calder et al. 20569* (UC). Nebraska: Deuel Co., 2 mi N and 0.5 mi W of Big Springs, prairie pasture hillside, 17 May 1970, *Stephens 38082* (UC); Sioux Co., on the S side of the University pastures, 16 May 1963, *Rittenhouse 125* (UTC); Sheridan Co., Metcalf Public Hunting Grounds, 13 mi N of Hay Springs, 4 Apr 1964, *Nixon 14* (RM). North Dakota: Benson Co., Pleasant Lake, 11 Jun 1912, *Lunell s.n.* (MO); Billings Co., near Medora and Theodore Roosevelt National Memorial Park, in the badlands, elev 2500 ft, 7–10 Jun 1967, *Porter & Porter 10338* (RM); Emmons Co., on hills above Oahe Reservoir, 13 mi W and 4.5 mi S of Hazelton, 6 May 1972, *Williams 872* (MO); Griggs Co., sandy prairie, river valley, 9 May 1952, *Stevens 1323* (UC); Logan Co., lower slopes of Shell Butte at W end, 13.5 mi S and 3 mi W of Napoleon, 13 May 1972, *Williams 875* (MO). Oklahoma: Harper Co., 10 mi S of Buffalo, 19 Apr 1935, *Goodman 2393* (MO). Oregon: Malheur Co., 6.3 mi S of the jct of Hwy 201 and the road leading to Succor Creek State Park, elev 2640 ft, 25 May 1975, *Halse 1164* (OSC); beside the large brown and white ash deposit on the S side of the road, one mi below Succor Creek Canyon, elev 3800 ft, 15 Apr 1974, *Frohlich DF-74-1* (UC); gravelly hilltops, near Rockville, 24 May 1927, *Henderson 9251* (OSC); loose ground on hill near Symes' Ranch, Owyhee river, up Watson, 27 Apr 1927, *Henderson 9290* (OSC); N end of Succor Creek Rd, ca 9 air mi W of Homedale, Idaho, 7.6 mi from Rt 19 (second major ash area), elev 2700 ft, 28 Apr 1989, *Ertter 8384* (UC); on road to Succor Creek State Park, 9.35 mi from Hwy 95, 23 Apr 1988, *Hart 1209* (UC); SW of Harper, elev ca 2800 ft, low hills of yellowish, rocky welded tuff with pockets of heavy black soil, scattered on S slope, 4 Apr 1986, *Joyal 1034* (OSC). South Dakota: Butte Co., Newell, 1 May 1913, *Carr s.n.* (RM); Fall River Co., 9 mi SW of Hot Springs, open prairie hillside, woods above, dry rocky red soil, 1 May 1970, *Stephens 37677* (UC). Utah: Daggett Co., 23 km SE of Dutch John, between Rye Grass and Sears Canyons, elev 5500 ft, 3 May 1985, *Goodrich & Welsh 21516* (BRY); Flaming Gorge National Recreation Area, Ashley National Forest, E side of Flaming Gorge Reservoir, 9–10 mi E of Manila, elev 6050 ft, 26 May 1992, *Goodrich 24049* (BRY); Flaming Gorge National Recreation Area, Ashley National Forest, E side of Flaming Gorge Reservoir, Brinegar Ranch, elev 6040–6080 ft, 11 May 1993, *Goodrich 24036* (BRY); Duchesne Co., along roadside of US Hwy 40, ca 4 mi W of Duchesne, 28 Apr 1965, *Walker 514* (BRY); Grand Co., head of Sego Canyon, Wasatch formation, 10 May 1990, *Baird 3238* (RM); mesa top, Selev and Marble Canyons, Dolores Triangle, 2 mi W of Colorado boundary, elev 1750 m, 13 May 1997, *Atwood & Welsh 22088* (BRY); Uintah Co., 0.5 mi E of Big Wash, elev 5060 ft, 14 May 1979, *Foster 7556* (BRY); 0.6 mi NE of old Bonanza Hwy at Deadman Bench Divide, elev 5950 ft, 29 May 1993, *Stone 1593* (BRY); 10 mi of Vernal, Ashley National Forest, Uinta Mtns, N side of Red Mtn, elev 7300 ft, 22 May 1986, *Goodrich 22026* (BRY); *ibid., Goodrich 22025* (RM); 5 mi NW of Dinosaur National Monument, elev 5500 ft, 24 Apr 1933, *Graham 7517* (MO); among Greasewood, W side of Green River, 20 mi S of Vernal, elev 4700 ft, 4 May 1935, *Graham 8756* (MO); ca 30 mi S of Ouray, Buck Canyon Rd, elev 5800 ft, 18 May 1978, *Neese & Peterson* 4721 (BRY); E side of Green River, 5 May 1999, *Atwood & Evenden 24313* (BRY); N of Skull Pass Quarry, 20 mi S of Vernal, elev 5000 ft, 9 May 1933, *Graham 7642* (MO); S of the Rim Rock, 0.6 mi in rounded hills, 22 May 1988, *Thorne & Thorne 6181* (BRY); sand hills, N of Green River, 9 mi SSE of Vernal, elev 5000 ft, 27 Apr 1933, *Graham 7531* (MO); Tridell, 8 Apr 1972, *Goodrich s.n.* (UTC); Tridell, elev 5700 ft, 31 May 1975, *Goodrich 4065*

(UTC); on rocky slope of bench near Uteland Mine, along Green River, below Ouray, elev 4800 ft, 17 May 1935, *Graham 8898* (MO); W side of Green River, S of mouth of Sand Wash, elev 4500 ft, 27 May 1933, *Graham 7889* (MO). Wyoming: Albany Co., Sand Creek, 31 May 1900, *Nelson 6978* (RM); on the red hills N of the city, Laramie, 31 May 1899, *Nelson & Nelson 6829* (RM); Big Horn Co., without locality, *s.d., Worthley 147* (RM); along Elk Creek Rd, E of Manderson, 8 air mi W of Manderson, elev 4000 ft, 29 May 1980, *Current 759* (RM); Big Horn Mtns, Medicine Lodge Canyon, elev 5000 ft, 26 May 1980, *Hartman & Dueholm 11161* (RM); 2 mi S and 2 mi W of Lovell, 7 Jun 1964, *Despain 10* (RM); Campbell Co., 2 mi S of Walcott jct, on Hwy 130, 18 May 1971, *Hartman 3086* (RM); ca 1.5 mi N of Hwy 387, along Hwy 50, near Belle Fourche River, elev 5200 ft, 30 May 1978, *Hartman & Dueholm 5770* (RM); ca 18 air mi SSE of Reno jct, elev 4800 ft, 3 Jun 1978, *Hartman & Dueholm 5878* (RM); ca 4 mi NW of Rockypoint, elev 4200 ft, 24 May 1978, *Dueholm & Hartman 1353* (RM); Hwy 59, less than 1 mi N of Converse Co., elev 4700 ft, 21 May 1978, *Hartman & Dueholm 5240* (RM); Carbon Co., N Platte River Valley, Haystack Mtns, Cheyenne Ridge, ca 0.75 mi NW of Hwy 351, on W side of Seminoe Reservoir, elev 6600–6700 ft, 15 May 1993, *Fertig 13498* (RM); Converse Co., Southeastern Plains, above Lost Creek on Harris or Co. Rd 58, ca 2.5 air mi S of Lost Springs, ca 23 air mi E of Douglas, elev 4969–5020 ft, *Nelson 25221* (RM); Southern Powder River Basin, ca 1.5 mi S and ca 1.7 mi E of the Cheyenne River on Clareton or Co. Rd 39, ca 5.5 air mi NE of Dull Center, ca 62.5 air mi NNE of Douglas, elev 4360–4420 ft, 24 May 1993, *Nelson 25134* (RM); Crook Co., 0.5 mi SW of Hulett, elev 3800 ft, 30 May 1935, *Ownbey 606* (UTC); Black Hills, Sourdough Creek, W of Seely Rd, ca 6.4 air mi N of Hulett, elev 4000 ft, 23 May 1983, *Marriott 2150* (RM); ca 1 mi NW of Lightning Flats, elev 4200 ft, 24 May 1978, *Hartman & Dueholm 5415* (RM); ca 2 air mi SW of Oshoto, elev 4000 ft, 23 May 1978, *Hartman & Dueholm 5362* (RM); Fremont Co., 14.75 mi and 52 degrees from Lander, above flood plain of Little Wind Rd, elev 5300 ft, 26 Apr 1980, *Goodrich 13740* (RM); banks of the Popo Agie River, S of Lander, elev 5400 ft, 6–11 Jun 1965, *Scott 409* (RM); Bridger Mtns, E end of Copper Mtn and N of Point of Mtn road, ca 16 air mi N of US Hwy 20–26, elev 6200–6600 ft, 6 Jun 1996, *Fertig 16542* (RM); Crooks Gap Rd, 1 mi S of Jeffrey City, elev 6400 ft, 3 Jun 1985, *Hartman 20451* (RM); edge of Moneta Hills, ca 3.75 air mi NNE of Moneta, elev 5630–5730 ft, 20 May 1986, *Haines 5928* (RM); Sheep Mtn, ca 11 air mi SE of jct US Hwy 287 and Wyo Hwy 28, elev 6200–7200 ft, 31 May 1985, *Hartman & Haines 20162* (RM); Goshen Co., 5 mi N of Ft Laramie, elev 4300 ft, 21 May 1977, *Hammel 464* (RM); Southern Powder River Basin/Southeastern Plains, Goshen Hole, Little Red Bill Hill and vicinity, ca 5.5 air mi W of Yoder, ca 15.5 air mi SW of Torrington, elev 4310–4394 ft, 27 May 1993, *Nelson 25475* (RM); Hot Springs Co., SW of Thermopolis, elev 4800 ft, 14 May 1978, *Hardy 732* (BRY); Johnson Co., ca 22 air mi N of Linch, ca 28.5 air mi NE of Kaycee, above the Powder River on the Iragaray Ranch, elev 4400 ft, 28 May 1979, *Nelson 2737* (RM); Laramie Co., Cheyenne, May 1902, *Nelson 8846* (RM); Cheyenne, Jun 1897, *Clement 521* (RM); Lincoln Co., basins and mountains of SW benchland between Zieglers Wash and Dry Mouddy Creek, ca 9 air mi WNW of Granger, elev 6460–6500 ft, 3 Jul 1995, *Nelson & Refsdal 36122* (RM); Green River Basin, ca 5.3 air mi W of Fontenelle Dam, elev 6940 ft, 3 Jun 1995, *Cramer 5474* (RM); Green River Basin, Holden Hill above Fontenelle Reservoir, ca 8.5 air mi NW of Fontenelle Dam, elev 6900 ft, 5 Jun 1995, *Cramer 5601* (RM); overthrust Belt, Moxa, on E bank of Ham's Fork River, 0.1 mi E of US Hwy 30, ca 15.5 air mi SE of Opal, elev 6500 ft, 10 May 1995, *Fertig & Struttmann 15621* (RM); Natrona Co., ca 10 air mi SW of Casper, elev 6000 ft, 2 Jun 1988, *Hartman & Brown 23589* (RM); E rim of Bates Hold, 1.5–2 air mi N of Carbon Co. line, elev 6600 ft, 21 May 1993, *Fertig 13517* (RM); Platte River Valley, Alcova reservoir, Cottonwood Creek campground, ca 2 air mi SW of Alvoca, on slopes E of reservoir, elev 5600–5700 ft, 21 May 1993, *Fertig 13541* (RM); Southeastern Plains, at the Oregon Trail Historical Site on the Emigrant Trail, across the North Platte River from Guernsey, elev 4320–4400 ft, 19 May 1993, *Nelson 24828* (RM); Southern Powder River Basin, ca 3 air mi SSE of Powder River and ca 1 air mi NW of Middle Casper Creek crossing, elev 5890–5910 ft, 24 Jun 1993, *Hartman 38317* (RM); Southern Powder River Basin, N of Coal Draw off Co. Rd 116, ca 3 air mi N of Midwest, elev 4800–4920 ft, 17 May 1993, *Nelson 24784* (BRY); Wyo Hwy 220, ca 6 air mi W of Alcova, elev 6300 ft, 10 May 1981, *Hartman & Fonken 12546* (RM); Niobrara Co., Southern Powder River Basin, along Wyo Hwy 270 just W of intersection with Wyo Hwy 272, ca 2 air mi NE of Lance Creek, ca 22.5 air mi NNW of Lusk, elev 4500–4640 ft, 20 May 1993, *Nelson 25011* (RM); Southern Powder River Basin, between Alum Creek and Old Woman Creek Hills, ca 19.7 air mi ENE of Lance Creek, ca 25 air mi NNE of Lusk, elev 4250–4420 ft, 20 May 1993, *Nelson 24976* (RM); Park Co., Absaroka Mtns, Aldrich Creek Drainage and vicinity, elev 7600 ft, 10 Jun 1983, *Hartman et al. 14827* (RM); Absaroka Mtns, N Fork Shoshone River Drainage, ca 3 mi N of Hwy 14, along Elk Fork Creek Trail, elev 6300 ft, 19 May 1980, *Evert 1755* (RM); Absaroka Mtns, N–S trending ridge immediately W of Clearwater Creek, ca 0.125 mi N of Hwy 14, 16 and 20, elev 6200 ft, 4 Jun 1989, *Evert 16361* (RM); Sublette Co., Green River Basin, ca 1.5 air mi E of Marbleton, elev 6900–7000 ft, 21 Jun 1995, *Cramer & Kellett 6561* (RM); Green River Basin, ca 11.5 air mi N of Big Piney on the E side of US Hwy 189, elev 7100 ft, 28 May 1995, *Cramer 5222* (RM); Green River Basin, ca 12.5 air mi SW of Big Piney, elev 7700 ft, 12 Jun 1995, *Cramer 6016* (RM); Green River Basin, ca 6.8 air mi ENE of Farson on the N side of Wyo Hwy 28, elev 6700 ft, 26 May 1995, *Cramer 5102* (RM); Green River Basin, Elk Mtn, ca 22.5 air mi NE of Farson, elev 7400 ft, 30 May 1995, *Cramer 5251* (RM); Green River Basin, Little Colorado Desert, The Frog, ca 5.5 air mi NE of La Barge, elev 6975, 5 Jun 1995, *Cramer 5670* (RM); slopes S of Figure Four Canyon Rd, 16 Jun 1993, *Kass 3768* (BRY); Sweetwater Co., 21 mi W of Green River, 19 Jun 1923, *Payson & Armstrong 3207* (MO); basins and mountains of SW Flaming Gorge National Recreation Area, S peninsula at the confluence of Blacks Fork and Green River, ca 17 air mi S of Green River, elev 6120–6246 ft, 20 Jun 1995, *Nelson et al. 35447* (RM); ca 2 air mi NE of Superior, plains above and steep escarpment below Zerkel Mesa with sandstone outcrops, elev 7600 ft, 24 May 1981, *Hartman 12603* (UC); ca 32 mi NW of Green River, 3 May 1985, *Welsh 23343* (BRY); Great Divide Basin, flats on NE side of Bush Rim, ca 0.3 mi E of Chicken Springs, elev 7260 ft, 29 May 1994, *Fertig & Struttmann 14747* (RM); Green River Basin, ca 17 air mi NW of Farson, elev 6900 ft, 17 Jun 1995, *Cramer & Kellett 6233* (RM); river bank of Green River, 6 mi NW of Green River, 13 Jun 1971, *Hatch 1261* (UTC); Uinta Co., 7 mi E of Mountainview along Hwy 414, sand hills and adjacent clay knolls, S of Hwy, 12 May 1989, *Atwood 13580* (BRY); basins and mountains of SW along Leavitt Creek below the S end of Cottonwood Bench, ca 7 air mi ESE of Mountainview, ca 39.5 air mi E of Evanston, elev 6700–6860 ft, 18 Jun 1995, *Nelson & Refsdal 35183* (RM); Overthrust Belt, badlands on N side of Wyo Hwy 414, ca 6 air mi ESE of Mountainview, NE of Crooked Canyon, ca 1.5 mi SE of Graham Reservoir #3, elev 6600–6680 ft, 13 May 1995, *Fertig & Struttmann 15645* (RM);

Wyo Hwy 414, 7 road mi SE of Mountainview, elev 7200 ft, 6 Jul 1983, *Hartman 15757* (RM); Washakie Co., W of Worland, on the lower part of the Fifteen Mile Drainage area, elev 4100–4300 ft, 16 May 1962, *Nichols 368* (RM); Weston Co., Black Hills, Lak Reservoir on Stockade Beaver Creek, ca 5 air mi ESE of Newcastle, elev 4400 ft, 21 Apr 1984, *Marriott et al. 6113* (RM); Southern Powder River Basin, Thunder Basin National Grasslands, above Little Thunder Creek on Lynch Rd, just S of Wyo Hwy 450, ca 12 air mi ENE of Clareton, ca 38.5 air mi SW of Newcastle, elev 4300–4400 ft, 24 May 1993, *Nelson 25164* (RM).

Variety *fendleri*

UNITED STATES. Arizona: Apache Co., desert region S of Petrified Forest, 27 May 1935, *Nelson & Nelson 2158* (RM); Coconino Co., 10 mi SW of Tuba City, elev 4000 ft, 22 Apr 1941, *Cutler 4649* (UC); ca 55 mi N of Flagstaff, E side of Hwy 89, elev 5000 ft, 8 May 1985, *Neese & House 16772* (BRY); Rim of Canyon Diablo, Two Guns, elev 5000 ft, 24 May 1961, *Demaree 44227* (UC); Navajo Co., 1 mi SE of Winslow, elev 4800 ft, 25 Apr 1961, *Chacon s.n.* (UC). Colorado: Archuleta Co., 1.5 mi S of Hwy 160 on road to Arboles, just E of Chimney Rock, elev 6500 ft, 16 Jun 1951, *Weber & Livingston 6215* (RM); Delta Co., 3.3 mi ESE of Hwy 92, Gunnison Rd crossing, 9 mi E of Delta, elev 5400 ft, 10 May 1983, *Neese 13225* (BRY); 8.6 mi SW of Delta, Co. Rd 348, then on gravel road towards Columbine Pass, 0.8 mi NE of Montrose Co. line, elev 5200 ft, 11 Apr 1982, *Hartman & Dueholm 13943* (RM); Garfield Co., 19 mi S of Douglas Pass, along Hwy 39, 3 May 1978, *Neese & England 4358* (BRY); ca 4 mi SSW of Parachute, Grand Valley, elev 5200 ft, 10 May 1985, *Welsh et al. 23362* (RM); Mesa Co., ca 4 mi S of Clifton, elev 4900 ft, 14 May 1984, *Welsh et al. 22748* (BRY); ca 4.5 mi E of Highline Lake and 6.9 mi N of US Hwy 50, elev 4840 ft, 14 Jun 1983, *Peterson & Kennedy 83-200* (RM); just W of West Selev Creek, ca 16 air km NW of Mack, elev 1450 m, 25 May 1976, *Cronquist 11431* (BRY); SE end of Sinbad Valley at head of Selev Creek Canyon, elev 5600 ft, 26 May 1983, *Atwood 9261* (BRY); Montezuma Co., Cortez, 10 May 1925, *Nelson 10403* (MO, RM). New Mexico: Bernalillo Co., Albuquerque, 21 Jul 1926, *Palmer 31160* (MO); on the mesa, ca 2 mi E of Albuquerque, elev 5000 ft, 1915, *Kammerer 47* (MO); Albuquerque, May 1900, *Harward s.n.* (MO); McKinley Co., 5 mi N of Crown Point, elev 6700 ft, 2 Jun 1977, *Peabody et al. 1358* (BRY); San Juan Co., Four Corners, elev 5500 ft, 20 Apr 1941, *Cutler 4618* (MO) Blanco, N and NE slopes of sandstone outcrop just on NW edge of town, elev 5400 ft, 2 May 1982, *Hartman & Fonken 13967* (RM); Chaco Canyon National Monument, NW Hwy 57, 6.6 road mi towards Blanco Trading Post from Visitors Center, elev 6000 ft, 31 May 1987, *Hartman & D'Alcamo 22674* (RM); foot of mesas, NE of San Juan Power Plant, ca 5 mi W slope, 16 May 1978, *Allan 855* (BRY); Navajo Mine, E of Mason Pit, in sandy soil, ca 17 air mi SW of Fruitland, 7 Jun 1983, *Spellenberg & Soreng 7095* (RM); near Old Well, 8 Jun 1979, *Kramp 146A* (UC); NM 44, 4.5 mi E of Nageezi, elev 6800 ft, 11 Apr 1982, *Hartman & Dueholm 13941* (RM); W of Hogback Ridge and 5 mi W of San Juan Power Plant, 31 May 1975, *Harper NM82* (BRY); S of Four Corners Power Plant, ca 2 mi on Bisto Rd, San Juan and Chico River Drainage area, SE slope, elev 5450 ft, 18 May 1978, *Allen 879* (BRY); S of Burnham Trading Post, N of Teec-ni-di-tso Wash, 7–14 Jun 1980, *Shultz 720* (UTC); Santa Fe Co., gravelly hills, Santa Fe, 1847, *Fendler 274* (MO); hills at Santa Fe, elev 7300 ft, 15 May 1897, *Heller & Heller 3539* (MO); Torrance Co., 3 mi W of Negra, 6 Jun 1977, *Wagner & Sabo 3036* (MO).

Utah: Carbon Co., Bluff, S of Gordon Creek, 3 mi W of Price, elev 5800 ft, 12 May 1981, *Welsh 20420a* (BRY); US 50-6, 3 mi NW of Price, elev 5800 ft, 29 May 1982, *Hartman 13987* (RM); Duchesne Co., 21.6 mi S of Hwy 40, Castle Peak-Sand Wash Rd, 9 mi S of Pariette Bench, elev 5400 ft, 26 Apr 1978, *Neese et al. 4258* (BRY); Emery Co., ca 2 mi ESW of Green River, elev 4200 ft, 4 Jun 1978, *Welsh & Welsh 16742* (BRY); 10.4 mi E of Green River Bridge along I-70, elev 1354 m, 26 May 1991, *Atwood 14908* (BRY); roadside along Hwy 24, 4 mi S of I-70, 24 May 1980, *Neese 8719* (BRY); San Rafael Desert, along Hwy 24, 1 mi S of I-70, elev 4350 ft, 19 May 1979, *Harris & Harris 146* (BRY); San Rafael Swell, Big Hole Wash, elev 5150 ft, 22 May 1979, *Harris 217* (BRY); sandy slopes near Goblin Valley, 50 mi SW of Green River, elev 5000 ft, 25 May 1961, *Cronquist 9090* (UC); Green River, 23 May 1914, *Jones s.n.* (UC); Garfield Co., along Orange Cliffs road, E of Hwy 95, elev 4500 ft, 11 May 1983, *Welsh et al. 21962* (RM); Eggnog Spring, Bullfrog Creek, W of Henry Mtns, 6 May 1965, *Welsh 3991* (BRY); Glen Canyon National Recreation Area, ca 11 mi due N of Hite, elev ca 3900 ft, 28 Apr 1983, *Welsh 21782* (RM); Henry Mtns, along roadside between Eggnog and Saleratus Creeks, elev 4500 ft, 24 Apr 1976, *Neese 1628* (BRY); Ticaboo Canyon, 15 mi below Hite along the Colorado River, 2 May 1954, *Holmgren & Goddard 9954* (UTC); Grand Co., Porcupine Canyon, Red Hills, elev 4160 ft, 8 May 1985, *Franklin 1433* (BRY); 1.5 mi N of Crescent jct, Thompson Pass Rd, 25 May 1988, *Nelson & Tibbetts 5205F* (BRY); 1.5 mi N of National Forest boundary, elev 6650 ft, 22 May 1984, *Goodrich et al. 20421* (BRY); 10 air mi E of Moab, just S of Maloy Park, elev 7300 ft, 27 May 1983, *Atwood 9269* (BRY); 14 mi NW of Moab, Upper Courthouse Wash, vicinity of Mill Canyon Rd, elev 4560 ft, 14 May 1988, *Franklin 6025* (BRY); 2 mi SE of Cisco, elev 4500 ft, 24 May 1983, *Neese 13349* (BRY, RM); 5.5 mi S of Crescent jct, 25 mi NW of Moab, elev 4650 ft, 16 May 1983, *Goodrich & Atwood 18143* (BRY); at Colorado-Utah border, 1 mi S of Coates Creek, 20 air mi S of I-70, elev 6200 ft, 25 May 1983, *Neese 13400* (BRY); Bartlett Wash, 17 mi NW of Moab, elev 4700 ft, 16 May 1983, *Goodrich & Atwood 18152* (BRY); Desert Valley, NW of Moab, 15 Jun 1944, *Holmgren & Hansen 3311* (UTC); E of Moab, elev 6320 ft, 10 May 1986, *Chandler et al. 2863* (RM); Ida Gulch, 2.5 mi SE Hwy 128 along Colorado River, E of Castle Valley Rd, elev 1400 m, 11 May 1986, *Thorne et al. 4627* (BRY); Seven-Mile Mesa, 9.6 mi SE of Dewey Bridge, elev 5800 ft, 8 Jun 1976, *Lowrey et al. 390* (UTC); Kane Co., ca 1.6 mi E of Little Valley on Grand Bench Rd, 26 Mar 1972, *Atwood 3530* (BRY); Coyote Canyon and adjacent mesa tops, elev 3900–4000 ft, 11 Apr 1982, *Welsh & Neese 21002A* (BRY); Middle Rock Creek Drainage, ca 25 mi NE of Page, AZ, elev ca 3900 ft, 13 Apr 1987, *Tuhy & Holland 2883* (UTC); near Cottonwood Spring, 17 May 1992, *Higgins 18791* (BRY); W of Hole in the Rock, near Soda, 17 May 1992, *Higgins 18766* (BRY); San Juan Co., flats, ca 0.5 mi NE of Castle Butte, ca 10 mi SSW of Hite, 3 May 1987, *Tuhy & Holland 3088* (BRY); 2.5 mi E of Hwy 47-262 jct, 14 mi S of Blanding, elev 5200 ft, 17 May 1983 ,*Atwood & Goodrich 9213* (RM); 4 mi E of Clay Hills, 28 Apr 1966, *Rooney 234* (BRY); ca 75 mi W of Blanding and 10 mi E of Hite, elev 4200 ft, 16 May 1961, *Cronquist 9037* (UC); along White Rim Rd, N of Turks Head, Canyonlands National Park, 18 May 1968, *Welsh 7088* (BRY); along wash leading out of Arch Canyon, where it joins Comb Wash, 18 mi SW of Blanding, elev 5000 ft, 14 May 1961, *Cronquist 9012* (UC); E bank of Green River, ca 8 mi down stream from Mineral Bottom at Foot Bottom, elev 4000 ft, 2 May 1983, *Welsh 21803* (BRY); Major N–S flowing wash, tributary of Castle Creek, elev 5350 ft, 27 May 1985, *Neely & Carpenter 2575* (UTC); Muley Point, Glen Canyon National

Recreation Area, elev 6200 ft, 8 Jun 1983, *Welsh 22242* (RM); on Comb Ridge just above the drop off to Butler Wash, N of Hwy 163 approximately 0.5 mi, accessed by the old abandoned Hwy, elev 4500 ft, 11 Apr 2000, *Davis 546* (UTC); W of Bluff, elev 4000 ft, 7 Apr 1933, *Anderson & Larsen 5987* (UTC); Uintah Co., Uinta Basin, Snake John Reef, NE of Hwy, 12 May 1982, *Neely & Thorne 727* (UTC); 1 mi W of Rainbow, elev 6000 ft, 4 Jun 1965, *Holmgren et al. 1809* (UTC); 6 mi out of Mountainview towards Lonetree, 23 Jun 1953, *Holmgren & Tillett 9464* (UTC); 6.2 mi from Dinosaur Quarry, elev 5300 ft, 26 May 1979, *Goodrich 12309* (BRY); 7–8 km S of Cliff Ridge and ca 40 air km SE of Vernal, 21 May 1976, *Cronquist 11408* (UTC); along Hwy 40 ca 8 mi W of Vernal, elev 5500 ft, 19 May 1978, *Neese & England 4769* (BRY); Asphelev Ridge, 5–6 mi SW of Vernal, 29 Apr 1976, *Shultz 1843-b* (UTC); ca 2.5 mi from Dinosaur Quarry, elev 4900 ft, 25 May 1979, *Goodrich 12284* (BRY); ca 25 mi due SE of Roosevelt, mouth of Pariette Draw, elev 4700 ft, 8 May 1978, *Neese 4453* (BRY); ca 5.5 mi SE of Jensen on Cliff Ridge, elev 5300 ft, 19 May 1982, *Neese & Snyder 11402* (BRY); ca 6 mi NE of Ouray, Ledta Bench, elev 4900 ft, 13 Jun 1979, *Neese & Neese 7577* (BRY); drainage to the W of Willow Creek, Ouray Rd, elev 5140 ft, 15 May 1979, *England 1735* (BRY); elev 5740 ft, 6 May 1982, *Kass 744* (BRY); S end of White River bridge, S of Ouray, 1 May 1965, *Blaylock 56* (BRY); Snake John Ridge, elev 5500 ft, 13 May 1982, *Thorne et al. 1706* (RM); Southern Canyon Quadrangle, 4.5–5 mi S of Bonanza, along Evacuation Creek, elev 5100–5300 ft, 11 Jun 1975, *Howard & Shultz 1975* (UTC); steep hills, ca 7 mi SW of Vernal, S of Hwy 40, 3 mi along road to abandoned oil well, elev 5300 ft, 25 Apr 1978, *Neese 4251* (BRY); Steinaker Reservoir Management area, elev 5700 ft, 13 May 1980, *Neese & White 8626* (BRY); Tridell, desert in Duchesne River Formation, 15 Apr 1978, *Goodrich 10821* (BRY); Wayne Co., 1.5 mi NW Fairview Ranch, N slopes of Henry Mtns, elev 4900 ft, 9 May 1947, *Harrison 11177* (BRY); ca 5 mi N of Cainville, W side of N Cainville Mesa, 18 May 1976, *Welsh et al. 13113* (BRY); Main Fork Happy Canyon, elev ca 5700 ft, 28 Apr 1987, *Tuhy & Holland 2964* (UTC); Millard Canyon, elev 4640 ft, 10 May 1983, *Welsh & Holland 21932* (RM); Millard Canyon Benches, elev ca 4400 ft, 10 May 1983, *Welsh & Chatterley 21882* (RM); Millard Canyon, elev 5150 ft, 10 May 1983, *Welsh & Chatterley 21859* (UTC).

Variety *greeleyorum*

UNITED STATES. Oregon: Malheur Co., without locality, 26 Mar 1937, *Tucker 650* (RM); near Rockville School on Succor Creek, white ash hillside, E facing, elev 3900 ft, 24 May 1975, *Ertter 117/5* (CIC); large ash deposit ca 1 mi below Succor Creek Canyon, 14 May 1974, *Packard 74-23* (CIC); large brown and white ash deposit on the NW side of the road, ca 1 mi below Succor Creek Canyon, elev 3800 ft, 14 May 1974, *Packard 74-36* (CIC); McBride Creek Rd, exposure of Sucker Creek Formation ash, elev 3900 ft, 24 May 1989, *Smithman et al. LS-2045* (CIC); Rockville area, just S of Leslie Gulch Rd jct with Succor Creek Rd, 2 May 1976, *Packard 76-3* (NY).

Variety *higginsii*

UNITED STATES. Utah: Kane Co., near stock pond, elev 1450 m, 27 Mar 1995, *Armstrong & Chapman 501* (BRY); 3.2 mi N of Hwy 89 via Cottonwood Wash/Coyote Creek Rd, elev 1400 m, 3 May 1992, *Atwood & Holland 17473* (BRY); Coyote Bench, E of Coyote Creek ca 2 mi, 24 Apr 1996, *Atwood & Furniss 20820*

(BRY); elev 4640 ft, 17 Mar 1995, *Chapman s.n.* (BRY); elev 4550 ft, 17 Mar 1995, *Chapman s.n.* (BRY); E of None Butte, ca 17 mi E of Glen Canyon City, 31 May 1975, *Welsh 12740* (BRY); ca 30 mi E of Glen Canyon City, 23 Apr 1973, *Atwood 4549* (MO); Coyote Creek, ca 10 air mi ENE of Big Water, elev 4640 ft, 1 May 1991, *Franklin 7339* (MO); badland, rim rocks, tropic shale formation, elev 1300 m, 9 May 1992, *Thorne & Zupan 10111* (OSC); 31 mi S of Escalante, on road to Hole-in-the-rock, 25 Jun 1965, *Collotzi et al. 582* (UTC).

Variety *parvus*

UNITED STATES. Utah: Millard Co., 6 mi from Oak City, elev 5200 ft, 30 Apr 1981, *Goodrich 15311* (BRY); 4 mi from Oak City, elev 5040 ft, 30 Apr 1981, *Goodrich 15312* (BRY); 1 mi from Oak City, elev 5120 ft, 30 Apr 1981, *Goodrich 15313* (BRY); Canyon Mtns-Sevier Desert, 6 mi from Oak City, elev 5200 ft, 19 May 1981, *Goodrich 15404* (BRY); 39 mi E of Garrison, Tule Valley, elev 4840 ft, 3 May 1982, *Goodrich 16528* (BRY); 37 mi E of Garrison, Tule Valley, just NE of the dry lake bed, elev 4800 ft, 3 May 1982, *Goodrich 16529* (BRY, RM); 24.5 mi SW of Delta, Sevier Desert, elev 4800 ft, 1 Jun 1983, *Goodrich 18312* (BRY, RM); 28 mi NW of Milford, head of Wah Wah Valley, elev 1450 m, 1 Jun 1983, *Goodrich 18325* (BRY); Tooele Co., 1 mi E of Dugway (E area), elev 1475 m, 7 Jun 1984, *Goodrich 20460* (BRY); Indian Rice Grass, Dunefield, NW of English village, W of Cedar Mtns, Dugway proving Ground, elev 1375 m, 7 Jun 1993, *Johnson 351* (BRY); elev 1550 m, 24 May 1991, *Clark 5357* (BRY); Skull Valley, elev 5000 ft, 3 May 1980, *Taye 777* (BRY); 32.7 km and 326 degree NW of Vernon, Skull Valley-Stansbury Mtns, near 1/4 corner with Sec 33, elev 5200 ft, 7 Jun 1984, *Goodrich 20458* (RM, NY); Stansbury Mtns-Skull Valley, 32.7 km NW of Vernon, elev 5200 ft, 7 May 1984, *Goodrich 20251* (RM).