

# A multivariate analysis of *Pseudocymopterus* (Apiaceae)<sup>1</sup>

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SUN, F.-J. (Department of Plant Biology, 505 South Goodwin Avenue, University of Illinois, Urbana, IL 61801), G. A. LEVIN (Center for Biodiversity, Illinois Natural History Survey, 1816 South Oak Street, Champaign, IL 61820), AND S. R. DOWNIE (Department of Plant Biology, 505 South Goodwin Avenue, University of Illinois, Urbana, IL 61801). A multivariate analysis of *Pseudocymopterus* (Apiaceae). *J. Torrey Bot. Soc.* 133: 499–512. 2006.—Currently, *Pseudocymopterus* comprises two species, *P. montanus* and *P. longiradiatus*. *Pseudocymopterus montanus* is highly variable morphologically and in the past was subdivided into several poorly defined taxa. Multivariate analyses of 235 specimens reflecting the morphological variability exhibited by these plants and representing populations from throughout the ranges of both species were conducted to examine morphological discontinuities in *Pseudocymopterus*. Multivariate analysis of variance and principal component analysis confirmed that most of the characters previously used to recognize taxa within the complex are highly variable and overlapping among putative taxa. While no clearly distinguished clusters were revealed on the plots of the first three principal components, groups corresponding to *P. montanus* and *P. longiradiatus* were weakly separated from each other. Discriminant analysis using the same set of specimens showed that *P. montanus* and *P. longiradiatus* can generally be distinguished using a set of characters. These results are consistent with recent molecular analyses that revealed DNA sequence differences between these taxa. We therefore propose that *Pseudocymopterus* continues to be treated as having two species, *P. longiradiatus* and *P. montanus*, with no infraspecific taxa.

Key words: discriminant analysis, multivariate analysis, North American Apioideae, principal component analysis, *Pseudocymopterus longiradiatus*, *Pseudocymopterus montanus*.

Because of its great morphological variability and uncertain relationship to other Rocky Mountain umbellifers, much taxonomic confusion surrounds the genus *Pseudocymopterus* (mountain parsley, false spring-parsley, or

ligusticoid spring-parsley). Coulter and Rose (1888) erected *Pseudocymopterus* to include three species and two varieties. Two of those species were transferred from *Cymopterus*, and the third, *P. montanus* (A. Gray) J. M. Coult. & Rose, had been previously referred to doubtfully as either *Thaspium* or *Ligusticum*. Twelve years later, Coulter and Rose (1900) recognized one additional species. Rydberg (1906, 1917) elevated the two varieties of *P. montanus* to specific rank and, in so doing, recognized seven species of *Pseudocymopterus* from the Rocky Mountains and adjacent regions. In a monograph of *Cymopterus* and related genera, Mathias (1930) placed six of the species treated by Rydberg in synonymy under *P. montanus* and recognized six additional species of *Pseudocymopterus*, three of which were described originally in *Cymopterus*. She considered the species *P. montanus* as “one of the most polymorphic of the group” and described the characters used by Rydberg to delimit species in *Pseudocymopterus* as “extremely variable” or showing “all intergradations from one extreme to the other.” Mathias (1930) concluded that the

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characters upon which Rydberg's species had been based, such as flower color, plant height, and several features of the leaves, were "natural variations in a polymorphic species." She did admit, however, that the genus was difficult to circumscribe, for several of the species she recognized showed similarities to *Pteryxia*, *Cymopterus*, or *Aletes*. In a drastic change of treatment, 15 years later and without explanation, Mathias and Constance (1945) considered *Pseudocymopterus* as consisting of only *P. montanus* and transferred or returned all the other of Mathias' previously recognized species to either *Pteryxia* or *Cymopterus*. Subsequently, Cronquist (1961) expanded the limits of *Cymopterus* to include both *Pteryxia* and *Pseudocymopterus*, and in 1997, placed *Pseudocymopterus montanus* (and, possibly, *Pseudocymopterus davidsonii* (J. M. Coult. & Rose) Mathias) in synonymy under *C. lemmonii* (J. M. Coult. & Rose) Dorn (Cronquist 1997). Several of the species transferred by Cronquist were treated previously in the genus *Aletes* (Theobald et al. 1963, Weber 1984); Mathias and Constance (1945) had already included *Pseudocymopterus davidsonii* in *Pteryxia* (as *Pteryxia davidsonii* (J. M. Coult. & Rose) Mathias & Constance). In 1969, Mathias et al. described *Pseudocymopterus longiradiatus* Mathias, Constance & W. L. Theob. from the mountains of western Texas and adjacent southern New Mexico, and distinguished it from *P. montanus* by its longer rays, larger fruits with larger vittae, and ternate-pinnately decompose leaves (Mathias et al. 1969). Cronquist (1997) noted that the only technical character separating *Pseudocymopterus* from most *Cymopterus* species is the short, stiff pubescence at the top of the peduncle in the former, but that this did not "provide sufficient basis for a genus in [a] family of ill-defined genera." Currently, however, the prevailing treatment is to maintain recognition of the name *Pseudocymopterus* as distinct, with the genus comprising two species—*P. montanus* and *P. longiradiatus* (Mathias et al. 1969, Kartesz 1994). Some recent treatments recognize these species as *Cymopterus lemmonii* and *C. longiradiatus* (Mathias, Constance & W. L. Theob.) B. L. Turner (e.g., Cronquist 1997, Turner et al. 2003).

Plants of *Pseudocymopterus* in the commonly used sense, that is, comprising *P. montanus* and *P. longiradiatus*, are herbaceous, tap-

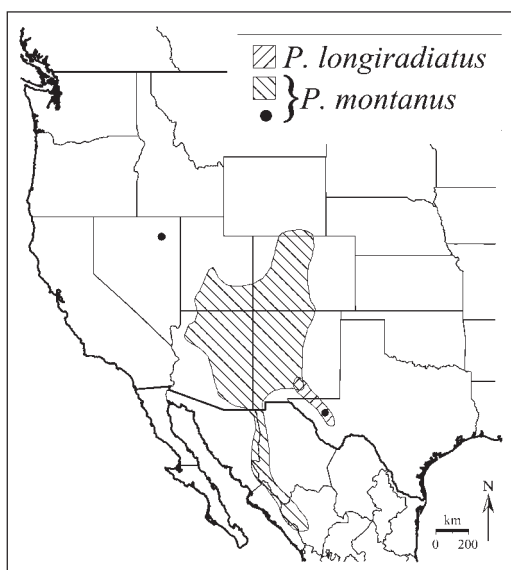


FIG. 1. Map of western North America showing the distributions of *Pseudocymopterus longiradiatus* and *P. montanus*.

rooted perennials of relatively xeric, open, montane, and subalpine meadows. Their umbels are borne on scapose stalks and the peduncles immediately beneath them are scabrous-hirtellous. The leaves are highly variable in size and degree of dissection, and are often carrot-like in aspect (Cronquist 1997). The flowers are yellow, orange, burnt red-orange, or purple, often fading white on herbarium sheets (Cronquist 1997). The wings on the fruits are all equally well-developed, or the dorsal wings may be reduced to low ridges or be completely absent (Hartman and Constance 1985). The genus is distributed from southern Wyoming to central Utah, disjunct in northeastern Nevada, and south to Arizona, New Mexico, western Texas, and Chihuahua, Sonora, and Durango, Mexico (Fig. 1). Its two species show partial geographic separation, with *P. longiradiatus* occurring at the southeastern extreme of the distribution of *P. montanus*. Although both species occur in the mountains of southern New Mexico, in western Texas *P. montanus* is reported only from Mt. Livermore (at elevations from 1800 to 3100 m), whereas *P. longiradiatus* occurs in the Davis and Guadalupe Mountains at generally lower elevations (Mathias et al. 1969, Turner et al. 2003).

The results of recent molecular systematic studies have done little to resolve the phylo-

genetic placement of *Pseudocymopterus* among other perennial Apiaceae subfamily Apioideae endemic to western North America, nor are they useful in supporting monophyly of the genus. Phylogenetic analyses of nuclear ribosomal DNA internal transcribed spacer (ITS) or chloroplast DNA *rps16* intron sequences placed *P. montanus* in a large polytomy with many other North American umbellifers, and maximum parsimony analysis of combined nuclear and chloroplast DNA data resulted in *P. montanus* comprising a poorly supported clade with *Cymopterus montanus* Nutt. ex Torr. & A. Gray and *C. multinervatus* (J. M. Coult. & Rose) Tidestr. (Downie et al. 2002). Subsequent studies of the same loci but with greater sampling of North American umbellifers including both species of *Pseudocymopterus* also yielded equivocal results with regard to the phylogenetic position of *Pseudocymopterus*, likely attributable to the rapid radiation of the group in western North America during the late Tertiary and Quaternary (Sun and Downie 2004, Sun et al. 2004). The results of phylogenetic analyses of combined ITS and *rps16* intron data showed the two examined accessions of *P. montanus* (from Arizona and Colorado) uniting with *Aletes macdougallii* J. M. Coult. & Rose, *Cymopterus beckii* S. L. Welsh and S. Goodrich, and *Pteryxia davidsonii* in a clade (Sun and Downie 2004). In a maximum likelihood analysis of these same combined data, the aforementioned clade is a weakly supported sister group to a clade comprising *Pseudocymopterus longiradiatus* and several accessions of *Aletes*, *Harbouria*, and *Oreoxis* (Sun and Downie 2004). While these molecular data do not support the monophyly of *Pseudocymopterus* and, instead, place them in two closely related clades, this relationship is not very well supported. Constraining *Pseudocymopterus* to monophyly results in minimal length trees just three steps longer than those without the constraint invoked, and both optimal and suboptimal sets of trees are not statistically different. Morphologically, *Pseudocymopterus montanus* and *P. longiradiatus* are extremely similar, and phylogenetic analyses of morphological characters support their sister group relationship, although no unique morphological synapomorphies have been identified for the genus (Sun 2003).

Because of the high degree of morphological variation exhibited by *Pseudocymopterus mon-*

*tanus* and its similarity to *P. longiradiatus*, further study of morphological differences within and between these taxa is appropriate. To examine morphological discontinuities within *Pseudocymopterus*, principal component analysis (PCA), multivariate analysis of variance (MANOVA), and discriminant analysis (DA) were conducted. The results were then evaluated in light of the aforementioned molecular results to ascertain the taxonomic status of these taxa.

**Materials and Methods.** We examined 566 herbarium specimens of *Pseudocymopterus*, borrowed from ARIZ, BRY, GH, ILL, JEPS, MICH, MO, NY, OSC, RM, SRSC, UC, UNM, US, UTC, and UTEP (acronyms as in Holmgren et al. 1990). Of these, 235 specimens (listed in the Appendix) had good locality data, were in good condition, and bore mature flowers or fruits. These specimens included the types of all species and varieties now submergered within *P. montanus*. They also reflected the morphological variability observed in *P. montanus* and *P. longiradiatus* and represented populations from throughout their ranges. These specimens were used as operational taxonomic units (OTUs) in the multivariate analyses.

We selected 21 characters based on previous taxonomic treatments and our own examination of herbarium specimens (Table 1). We did not include qualitative characters, such as flower color, because their use will violate the assumptions of the analytic methods we chose (Pimentel 1979). Data were collected using an Olympus dissecting microscope and a plastic ruler (accurate to 1 mm) from all herbarium specimens examined. The means of three to six measurements were calculated for each character on each herbarium sheet, depending upon the number of plants present. 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 235 specimens. The first matrix included only flowering specimens (152 OTUs and 18 characters). The second matrix contained those specimens in fruiting condition (83 OTUs and 21 characters). The third matrix combined the OTUs of the previous two matrices (235) but with only the 18 non-fruit characters.

Table 1. Morphological characters and their statistics (mean  $\pm$  standard deviation and range) for the two species currently recognized in *Pseudocymopterus*. Sample sizes are indicated following the species name (flowering specimens/fruitlet specimens). Characters that differ significantly ( $P < 0.05$ ) between the species as shown by MANOVA  $t$ -tests are marked with asterisks (same results with and without Bonferroni correction).

Character	<i>P. longiradiatus</i> (N = 18/7)	<i>P. montanus</i> (N = 134/76)
1. Plant height (cm)*	49.9 $\pm$ 21.3 21.0–99.0	36.4 $\pm$ 16.2 8.0–95.0
2. Peduncle length (cm)*	39.6 $\pm$ 19.0 14.0–90.0	27.6 $\pm$ 11.3 7.0–59.0
3. Leaf blade length (cm)*	9.8 $\pm$ 2.8 5.8–18.0	7.3 $\pm$ 2.7 3.3–20.0
4. Leaf blade width (cm)*	10.9 $\pm$ 3.6 6.4–20.0	5.9 $\pm$ 2.6 1.8–15.0
5. Leaf petiole length (cm)	9.7 $\pm$ 3.4 4.5–20.0	8.1 $\pm$ 3.9 2.2–25.0
6. Lowest leaflet length (cm)*	7.0 $\pm$ 2.1 4.2–12.0	4.0 $\pm$ 1.9 1.3–15.0
7. Lowest leaflet width (cm)*	4.9 $\pm$ 1.8 2.0–10.0	2.3 $\pm$ 1.3 0.2–7.2
8. No. of pairs of lateral primary leaflets (pinnae)	5.8 $\pm$ 0.7 4–7	5.7 $\pm$ 1.2 3–9
9. Ultimate leaf segment length (mm)	9.1 $\pm$ 3.4 3.5–18.0	12.2 $\pm$ 10.6 1.5–90.0
10. Ultimate leaf segment width (mm)*	2.7 $\pm$ 1.0 1.5–6.0	1.8 $\pm$ 0.8 1.0–6.0
11. Dist. between the first two pairs of leaflets (mm)*	37.6 $\pm$ 12.9 24.0–80.0	24.6 $\pm$ 8.1 9.0–57.0
12. Inflorescence (umbel) width (cm)*	7.9 $\pm$ 3.3 3.5–15.0	3.4 $\pm$ 1.7 1.5–23.0
13. Umbellet width (cm)*	1.4 $\pm$ 0.5 0.8–2.8	0.9 $\pm$ 0.3 0.4–2.2
14. Primary ray number*	9.9 $\pm$ 3.0 2–17	7.9 $\pm$ 2.3 3–15
15. Primary ray length (cm)*	3.4 $\pm$ 1.5 1.8–7.5	1.3 $\pm$ 0.6 0.4–3.5
16. Secondary ray length (mm)*	2.4 $\pm$ 1.0 1.0–5.0	1.2 $\pm$ 0.5 1.0–5.0
17. Bractlet length (mm)	3.9 $\pm$ 1.0 3.0–7.0	3.9 $\pm$ 1.1 2.5–8.0
18. Bractlet width (mm)*	0.6 $\pm$ 0.2 0.5–1.0	0.4 $\pm$ 0.2 0.2–1.0
19. Fruit length (mm)*	7.1 $\pm$ 1.0 6.0–9.0	5.0 $\pm$ 0.8 3.5–7.0
20. Fruit width (mm)	3.1 $\pm$ 0.6 2.0–4.0	3.5 $\pm$ 0.6 2.5–5.0
21. Wing width (mm)	1.1 $\pm$ 0.5 0.5–2.0	1.0 $\pm$ 0.2 0.5–1.5

Principal component analysis was conducted on each of the three data sets using NTSYSpc vers. 2.1 (Rohlf 2000). Identical parameters and procedures were used for all analyses. Each data matrix, OTUs (rows)  $\times$  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, which was used to generate the eigenvector and eigenvalue matrices. The SQRT (lambda) transformation was conducted 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 contributions of the characters to the overall variation among the OTUs were evaluated by examining the loadings (weights) of the characters on the principal components.

For those groups suggested by the PCA (only *Pseudocymopterus longiradiatus* and *P. montanus*; see Results), MANOVA was performed with SPSS vers. 13.0.1 for Windows (SPSS, Chicago, Illinois), using Type III sum of squares, and was followed by *t*-tests to determine which characters showed significant differences between the taxa. The *t*-tests were performed with and without Bonferroni correction, because although the characters may be independent, they were sampled from the same specimens. Discriminant analysis was conducted for the same groups with SPSS vers. 13.0.1 for Windows, using all the characters simultaneously, the within-groups covariance matrix, and prior probabilities computed from the group sizes. The small sample size for *P. longiradiatus* precluded using a random sample of the OTUs for calculating the discriminant function and then validating the model using the remaining OTUs, so cross-validation was conducted by classifying each OTU by the function derived from all the remaining OTUs ("leave-out-one" classification). The importance of the characters for distinguishing the groups was evaluated by examining both the standardized canonical discriminant function coefficients and the structure matrix (the pooled within-groups correlations between the characters and the standardized canonical discriminant function).

**Results.** The PCA of 18 non-fruit characters and 235 OTUs produced five components with eigenvalues greater than one. These account for about 76% of the total variation in the data set, with well over half of that represented by the first and second components (40.7% and 13.6%, respectively). Plots of the first three principal components (PC1, PC2, and PC3) are shown in Fig. 2. No clearly distinguished clusters were revealed. Specimens of *Pseudocymopterus longiradiatus* and *P. montanus* were weakly separated from each other on the first and second components, however, with about half the specimens of *P. longiradiatus* placed outside the cluster formed by nearly all the *P. montanus* specimens. The third principal component provided no segregation between these species. The types of all the segregates of *P. montanus* (indicated by filled circles in Fig. 2) fell within the range of *P. montanus* on all three components.

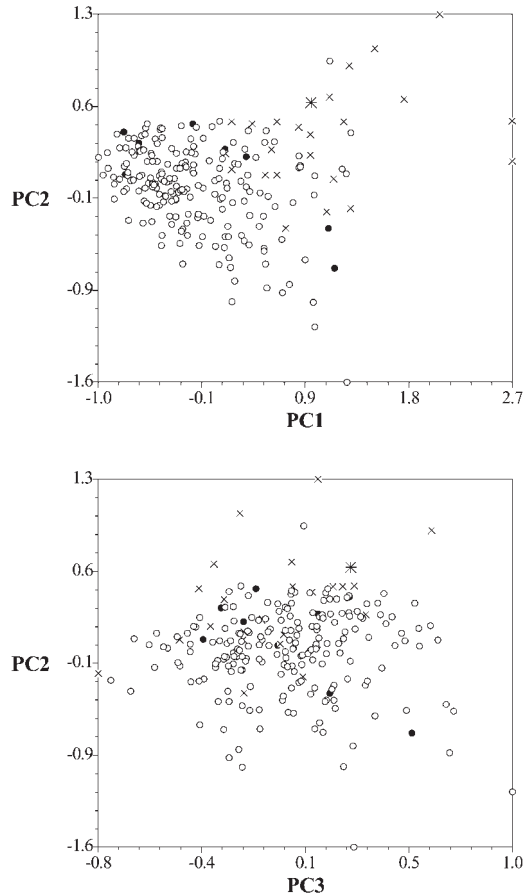


FIG. 2. Plots of principal components (PC) 1, 2, and 3 for *Pseudocymopterus* (152 flowering and 83 fruiting specimens) using 18 non-fruit morphological characters. OTUs identified as *P. longiradiatus* and *P. montanus* are indicated by x's and open circles, respectively. Type specimens of taxa generally synonymized with *P. montanus* are indicated as filled circles; the type specimen of *P. longiradiatus* is indicated as a star.

Table 2 lists the loadings for the 18 non-fruit characters on the first three components. PC1, which provided partial separation between *Pseudocymopterus longiradiatus* and *P. montanus*, had relatively high positive loadings for plant height, peduncle length, leaf blade length and width, lowest leaflet length and width, the distance between the first two pairs of leaflets, and the primary ray length, and somewhat lower positive loadings for umbel width and secondary ray length. PC2, which also provided partial separation between the species, had a relatively high negative loading for ultimate leaf segment length, and high positive loadings for umbellet width and



Table 2. Principal component loadings for the 18 non-fruit morphological characters on the first three components for the 235 OTUs of *Pseudocymopterus*. For each component, values with particularly large magnitudes are shown in bold.

Character	PC1	PC2	PC3
1. Plant height (cm)	<b>0.7870</b>	0.0108	0.2215
2. Peduncle length (cm)	<b>0.7916</b>	0.1085	0.1723
3. Leaf blade length (cm)	<b>0.8270</b>	-0.3205	-0.1643
4. Leaf blade width (cm)	<b>0.8756</b>	-0.1955	-0.1570
5. Leaf petiole length (cm)	0.5758	-0.4143	0.1016
6. Lowest leaflet length (cm)	<b>0.8604</b>	-0.2746	-0.1110
7. Lowest leaflet width (cm)	<b>0.7894</b>	-0.0843	-0.1216
8. Number of pairs of lateral primary leaflets (pinnae)	0.0524	0.4053	<b>-0.6158</b>
9. Ultimate leaf segment length (mm)	0.3501	<b>-0.6560</b>	0.4268
10. Ultimate leaf segment width (mm)	0.4818	-0.3224	0.1197
11. Distance between the first two pairs of leaflets (mm)	<b>0.8530</b>	-0.1292	-0.1434
12. Inflorescence (umbel) width (cm)	<b>0.6585</b>	0.4568	-0.0198
13. Umbellet width (cm)	0.5592	<b>0.5761</b>	0.2848
14. Primary ray number	0.3592	0.0145	<b>-0.6044</b>
15. Primary ray length (cm)	<b>0.7365</b>	0.4982	0.0591
16. Secondary ray length (mm)	<b>0.6296</b>	<b>0.5037</b>	0.1975
17. Bractlet length (mm)	0.1172	-0.2729	<b>-0.5361</b>
18. Bractlet width (mm)	0.1669	0.4614	0.0543

secondary ray length. In contrast, PC3 had relatively high negative loadings for the number of pairs of lateral primary leaflets, primary ray number, and bractlet length.

The PCA of fruiting specimens (83 OTUs and 21 characters; Fig. 3) gave similar results, with partial separation between *Pseudocymopterus longiradiatus* and *P. montanus* on the first two principal components, but no further separation within *P. montanus*. Characters with heavy loadings on the first two principal components from this data set were similar to those on the corresponding principal components from the previous data set, but leaf petiole length, umbellet width, and primary ray number were also heavily loaded on the first component (Table 3). Results from PCA of the data set of flowering specimens only (152 OTUs and 18 characters; plots of principal components are not shown) were very similar to those obtained from the other two data sets.

Comparison between specimens classified as *Pseudocymopterus longiradiatus* and *P. montanus* using MANOVA showed that the two taxa were significantly different (Wilks' Lambda  $P < 0.001$  for all three data sets). Most of the 21 characters, except for leaf petiole length, number of pairs of lateral primary leaflets, ultimate leaf segment length, bractlet length, fruit width, and wing width, differed significantly between these two taxa ( $t$ -tests,  $P < 0.05$ ; same results with and without Bonferroni correction), with means for *P.*

*longiradiatus* greater than those for *P. montanus* for all characters where the differences were significant (Table 1). Despite these statistical differences, however, there were no characters for which the ranges of the two taxa did not overlap extensively (Table 1).

The two taxa were generally distinguishable using DA. Cross-validation showed that using the 18 non-fruit characters for 235 OTUs resulted in correct classification for 21 of the 25 *Pseudocymopterus longiradiatus* specimens and 208 of the 210 *P. montanus* specimens, for an overall accuracy of 97.4%. Similarly, using all 21 characters for the 83 fruiting specimens allowed correct classification for 6 of the 7 *P. longiradiatus* specimens and 75 of the 76 *P. montanus* specimens (an overall accuracy of 97.6%). Standardized canonical discriminant function coefficients and the structure matrices from the two data sets are shown in Table 4. The relative importance of several characters differs considerably between the discriminant function coefficients and the structure matrix, suggesting collinearity among these characters. When that is the case, values in the structure matrix are better indicators of which characters allow better classification of the specimens (Norusis 2004). Characters that had relatively high values in both structure matrices were distance between the first two pairs of leaflets, umbel width, umbellet width, and primary ray length. In the non-fruit character analysis, leaf blade width, lowest leaflet length, and secondary ray length were also relatively

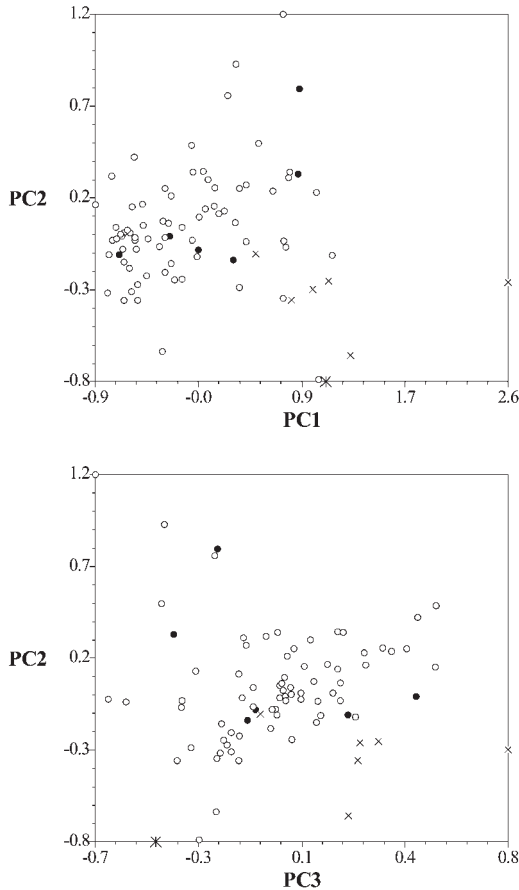


FIG. 3. Plots of principal components (PC) 1, 2, and 3 for 83 fruiting specimens of *Pseudocymopterus* using 21 morphological characters. OTUs identified as *P. longiradiatus* and *P. montanus* are indicated by x's and open circles, respectively. Type specimens of taxa generally synonymized with *P. montanus* are indicated as filled circles; the type specimen of *P. longiradiatus* is indicated as a star.

important, whereas in the analysis of fruiting specimens fruit length was relatively important.

**Discussion.** Coulter and Rose (1888, 1900) recognized *Pseudocymopterus montanus* as comprising two varieties, vars. *tenuifolius* (A. Gray) J. M. Coult. & Rose and *purpureus* J. M. Coult. & Rose, differentiated primarily on the basis of flower color, size of plant, and degree of branching. Rydberg (1906) raised these varieties to specific rank and, later, recognized seven species of *Pseudocymopterus* native to the Rocky Mountains and adjacent regions (Rydberg 1917). These species were distinguished using flower color, plant height,

bractlet shape and its length relative to the flowers, and several features of the cauline and basal leaves. Mathias (1930), however, after examining "a large series of specimens," concluded that these characters vary considerably within each of Rydberg's species and overlap among them, and therefore were of no use for segregating these species. She placed six of Rydberg's species of *Pseudocymopterus* in synonymy under a polymorphic *P. montanus*, without recognizing infraspecific taxa. Mathias and Constance (1945) maintained this circumscription of *P. montanus*.

The results of this study support the treatment of *Pseudocymopterus montanus* by Mathias (1930) and Mathias and Constance (1945). Principal component analyses using many of the aforementioned characters resulted in no discernable clusters within *P. montanus* (Figs. 2 and 3). The types of the taxa synonymized with *P. montanus* by Mathias (1930; indicated by filled circles in the PCA plots) were distributed throughout a single large cluster, demonstrating that they represent different aspects of a highly variable species, but not distinct taxa. Many of the characters used to distinguish taxa in this group are vegetative and it is likely that variation reflects habitat differences (Mathias 1930), either from plasticity or micro-adaptation. Other characters vary even on the same plant; flower color, for example, can range from yellow through orange-purple to purple on a single individual. In any case, the characters do not support segregating these taxa at the specific or any infraspecific levels.

In contrast, the results provide some support for distinguishing *Pseudocymopterus longiradiatus* from *P. montanus*, the two species currently recognized in the genus. The two taxa were partially separated in PCA and can be distinguished fairly reliably using DA. Yet, we found no single character for which the two taxa did not overlap. In comparison with *P. montanus*, *P. longiradiatus* has longer rays, larger fruits, and ternate-pinnately decomposed leaves, in accordance with those differences outlined by Mathias et al. (1969). The results of PCA show that both primary and secondary ray lengths are heavily loaded on PC1 (Table 2) and fruit length is heavily loaded on PC2 (Table 3). Similarly, primary and secondary ray lengths and fruit length are among the best characters for distinguishing these taxa as shown by DA. (Umbel and

Table 3. Principal component loadings for the 21 morphological characters on the first three components for the 83 fruiting OTUs of *Pseudocymopterus*. For each component, values with particularly large magnitudes are shown in bold.

Character	PC1	PC2	PC3
1. Plant height (cm)	<b>0.8014</b>	0.2056	0.1268
2. Peduncle length (cm)	<b>0.7974</b>	0.1191	0.2109
3. Leaf blade length (cm)	<b>0.7540</b>	0.3208	-0.1232
4. Leaf blade width (cm)	<b>0.8868</b>	0.2132	-0.1087
5. Leaf petiole length (cm)	<b>0.7047</b>	0.4360	0.0131
6. Lowest leaflet length (cm)	<b>0.8263</b>	0.2439	-0.1349
7. Lowest leaflet width (cm)	<b>0.7599</b>	-0.0586	-0.0766
8. Number of pairs of lateral primary leaflets (pinnae)	-0.0658	-0.3383	0.4080
9. Ultimate leaf segment length (mm)	0.3924	<b>0.6485</b>	-0.4512
10. Ultimate leaf segment width (mm)	0.5973	0.1173	0.1585
11. Distance between the first two pairs of leaflets (mm)	<b>0.8707</b>	0.0346	0.0080
12. Inflorescence (umbel) width (cm)	<b>0.8243</b>	-0.3176	0.1913
13. Umbellet width (cm)	<b>0.6494</b>	- <b>0.5102</b>	-0.0096
14. Primary ray number	<b>0.6262</b>	-0.1739	0.2822
15. Primary ray length (cm)	<b>0.8106</b>	-0.1724	0.2391
16. Secondary ray length (mm)	<b>0.6610</b>	-0.2743	0.0038
17. Bractlet length (mm)	0.0670	-0.2980	-0.1558
18. Bractlet width (mm)	0.1312	-0.3541	0.2475
19. Fruit length (mm)	0.4678	- <b>0.5981</b>	-0.2829
20. Fruit width (mm)	0.0720	-0.4006	- <b>0.7326</b>
21. Wing width (mm)	0.3737	-0.3580	-0.4798

Table 4. Standardized canonical discriminant function coefficients and structure matrices (the pooled within-groups correlations between discriminating variables and standardized canonical discriminant functions) from the discriminant analyses comparing *Pseudocymopterus longiradiatus* and *P. montanus*. The analysis of 18 non-fruit characters included 25 specimens of *P. longiradiatus* and 210 specimens of *P. montanus*, and the analysis of all 21 characters included 7 specimens of *P. longiradiatus* and 76 specimens of *P. montanus*.

Character	18 Non-fruit characters		All 21 characters	
	Coefficient	Structure matrix	Coefficient	Structure matrix
1. Plant height (cm)	0.017	0.176	-0.243	0.182
2. Peduncle length (cm)	-0.635	0.211	0.034	0.210
3. Leaf blade length (cm)	-0.597	0.201	-0.278	0.103
4. Leaf blade width (cm)	0.542	0.395	0.613	0.238
5. Leaf petiole length (cm)	0.061	0.089	0.423	0.121
6. Lowest leaflet length (cm)	0.844	0.343	0.311	0.182
7. Lowest leaflet width (cm)	0.002	0.427	-0.168	0.235
8. Number of pairs of lateral primary leaflets (pinnae)	-0.480	0.012	-0.388	-0.048
9. Ultimate leaf segment length (mm)	-0.799	-0.067	-0.770	-0.045
10. Ultimate leaf segment width (mm)	0.266	0.235	-0.080	0.233
11. Distance between the first two pairs of leaflets (mm)	-0.011	0.328	-0.067	0.275
12. Inflorescence (umbel) width (cm)	0.217	0.501	0.552	0.501
13. Umbellet width (cm)	-0.047	0.330	0.377	0.433
14. Primary ray number	0.057	0.189	-0.315	0.192
15. Primary ray length (cm)	0.672	0.609	0.040	0.412
16. Secondary ray length (mm)	0.186	0.446	-0.319	0.204
17. Bractlet length (mm)	-0.087	0.017	0.260	0.040
18. Bractlet width (mm)	0.146	0.274	0.457	0.240
19. Fruit length (mm)	—	—	0.635	0.376
20. Fruit width (mm)	—	—	-1.054	-0.088
21. Wing width (mm)	—	—	0.471	0.112



umbellet width were also important in both PCA and DA, reflecting their association with ray lengths if ray divergence angles are similar in both taxa.) We observed, however, that large plants of *P. montanus* also have ternate-pinnately decompound leaves. We did not study vittae size due to limited fruiting material for dissection.

In addition to studies of combined molecular and morphological data, phylogenetic analyses of ITS and *rps16* intron sequences, separately or combined, support the recognition of *Pseudocymopterus montanus* as monophyletic (Sun 2003, Sun and Downie 2004). The two accessions of *P. montanus* included in these molecular studies, collected from Arizona and Colorado, differed by only 1 and 2 bp in their ITS and *rps16* intron regions, respectively. ITS sequence data for 10 additional accessions of *P. montanus* from throughout its range differed by 0 to 5 bp, representing up to 1.1% nucleotide divergence in pairwise comparisons (F.-J. Sun and S. R. Downie, unpubl. data). Both loci are quite conserved evolutionarily. By comparison, there were 7 and 11 bp differences between *P. montanus* and *P. longiradiatus* in their ITS and *rps16* intron regions, respectively, although there is some doubt whether the genus is monophyletic. These differences are similar to, or higher than, those obtained from interspecific comparisons of other Rocky Mountain umbellifers (Sun and Downie 2004). Phylogenetic analyses of molecular data place *P. montanus* and *P. longiradiatus* in two separate but closely related clades; in some trees, these clades are sister groups (Sun and Downie 2004). These relationships, however, are not very well supported, and representatives of additional genera (such as, *Aletes*, *Cymopterus*, *Harbouria*, *Oreoxis*, and *Pteryxia*) ally more closely to *P. montanus* or *P. longiradiatus* than these species do to each other. Similarly, cladistic analyses of morphological data show that the relationship between *P. montanus* and *P. longiradiatus* varies depending upon the analytical methods used (Sun 2003). Determination of the monophyly of *Pseudocymopterus* must come from further molecular studies of these plants, as well as consideration of the other perennial, endemic western North American genera putatively allied to *Pseudocymopterus*.

The current study together with results of previous phylogenetic analyses of molecular

data supports continuing the long practice of synonymizing all the segregates of *Pseudocymopterus montanus* within a single polymorphic species with no infraspecific taxa. The question remains how to treat *P. longiradiatus*. *Pseudocymopterus montanus* and *P. longiradiatus* can generally be distinguished using a set of characters, and molecular data demonstrate that although they are closely related within a larger complex containing other western North American umbellifers, they exhibit sequence differences. Until evidence to the contrary is available, and in order to maintain stability of classification, we continue to recognize two species in *Pseudocymopterus*.

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### Appendix

Accessions of *Pseudocymopterus* used as OTUs in multivariate analyses. These specimens are identified as *P. montanus* or *P. longiradiatus*, as treated by Kartesz (1994) and in accordance with the results of this study. In 11 instances, duplicate herbarium specimens from the same locality were examined. Herbarium acronyms are as in Holmgren et al. (1990).

#### *Pseudocymopterus montanus*

UNITED STATES. ARIZONA: Apache Co., Apache-Sitgreaves National Forest, Rt 56 at Terry Flat, 6–10 mi E of US Rt 666, elev 2800–3000 m, 27 Jun 1992, *Miller et al. 7641* (MO). Cochise Co., upper Miller Canyon, Huachuca Mtns, 18 Aug 1909, *Goodding 421* (MO, RM); Huachuca Mtns, Jun 1887, *Lemmon 392* (holotype of *Peucedanum lemmonii*; US); Montane Plateau, 26 Jun 1912, *Goodding 1089* (RM); Fly Peak Trail near Rustler Park, Chiricahua Mtns, elev 8600 ft, 7 Jul 1964, *Barr 64–347* (UC); Rustler Park, Chiricahua Mtns, elev 8600 ft, 4 Jul 1985, *Sanders 5858* (UC); Rustler Park, Chiricahua Mtns, 21 Jul 1961, *Barnum 1180* (BRY); Rustler Park, Chiricahua Mtns, 22 Sep 1931, *Jones s.n.* (MO). Coconino Co., San Francisco Mtns, elev 9000–11300 ft, 11 Aug 1923, *Hanson & Hanson 783* (MO); Mt Humphreys, Jul 1883, *Rusby 632* (syntype of *Pseudocymopterus montanus* var. *purpureus*; US); Kaibab Forest, elev 8000 ft, 19 Jul 1930, *Goodman & Hitchcock 1633* (RM); Flagstaff, 11 Aug 1907, *Thornber 2084* (MO); in the vicinity of Flagstaff, elev 7000 ft, 8 Jul 1898, *MacDougal 256* (UC); Coconino Forest, San Francisco Mtns, elev 10500 ft, 10 Jul 1918, *Pearson 581* (RM); near Flagstaff, elev 7000 ft, 23 Aug 1922, *Hanson A215* (MO); Coconino Forest, Wild Bill Pasture 3, elev 7700 ft, 18 Aug 1967, *Gierisch 3206* (RM); Kendrick Peak, along Trail #22, trailhead at parking lot at the end of US Forest Service Rd 171A, elev 10100 ft, 5 Aug 1983, *Ricketson 573* (MO); Kendrick Peak, along Trail #22, trailhead at parking lot at the end of US Forest Service Rd 171A, elev 8700 ft, 5 Aug 1983, *Ricketson 527* (MO); Kendrick Peak, between Trail #22, US Forest Service Rd 171A, SE of Kendrick Peak lookout tower, elev 8500 ft, 28 Apr 1983, *Ricketson 663* (MO). Gila Co., Forest Sierra Ancha, Workman Creek near Main Dam, elev 6500 ft, 23 May 1961, *Pase 1210* (RM); N Peak,

Matzatzal Mtns, elev 1800 m, *Collom 136* (MO); Sierra Ancha Area, Parker Canyon below Natural Drainages, elev 4000 ft, 13 May 1967, *Pase 1746* (RM); Tonta National Forest, elev 5600 ft, 26 Sep 1935, *Little 4103* (RM). Navajo Co., Mogollon Rim, along Hwy 277, 0.3 to 1.9 mi E of the Gila Co. line, ca 27 air mi NE of Payson, elev 7475 ft, 9 Oct 1982, *Sanders et al. 3210* (UTC); W slope of the Chusta Mtns, 6 mi E of Lukachukai, 9 Jun 1983, *Spellenberg & Soreng 7126* (UC). Pima Co., 32 mi NE of Tucson via Catalina Hwy in Bear Wallow, Santa Catalina Mtns, elev 8200 ft, 24 Jul 1965, *Matthews & Matthews 456* (UTC). COLORADO: Archuleta Co., Piedra, Chimney Rock Trail, 21 Jun 1924, *Schmall 1235* (RM); Pagosa Springs, 9 Jul to 19 Aug 1917, *Bethel 5722* (RM); San Juan National Forest, 1911, *Keplinger 134* (RM). Boulder Co., Roosevelt National Forest, near Yankee Doodle Lake, 26 Aug 1957, *Gierisch 1980* (RM). Clear Creek Co., mountains at the head waters of Clear Creek, Clear Creek Canyon near Georgetown, 8 to 27 Jul 1885, *Patterson 41* (UC); Brookvale, Indian Park, 17 Jun 1918, *Churchill s.n.* (MO); Empire, elev 8500 ft, 15 to 25 Jul 1903, *Tweedy 5601* (RM). Conejos Co., along Alamosa Creek, near Capulin, 5 Jul 1935, *Ramaley 15029* (OSC); 0.6 mi SE of Gun Sight Pass, 0.6 mi NE of Fish Lake, elev 3750 m, 2 Aug 1987, *Douglas 1751* (BRY); Massey Creek, 1.5 mi NW of Cold Springs, 1.1 mi SSE of River Springs Guard Station, elev 9200 ft, 18 Jun 1986, *Douglas 1025* (RM). Costilla Co., upper slope of saddle at head of N Fork Whiskey Creek, BAR NI Ranch, Culebra Range, elev 12600 ft, 16 Aug 1987, *Neely 4672b* (RM); head of Duling Creek, ca 1 mi N of Lost Lake, Culebra Range, elev 11850 ft, 19 Aug 1987, *Neely 4763* (RM, RM). Custer Co., San Isabel Forest, elev 10200 ft, 15 Jul 1938, *McCready AM-132* (RM). Eagle Co., Flat Tops/White River Plateau, Deer Park, ca 7 air mi W of Burns, elev 9200 ft, 21 Jul 1991, *Vanderhorst 3419* (RM); Flat

Tops/White River Plateau, Derby Mesa, ca 18 air mi NNW of Eagle, elev 8200 ft, 11 Jun 1990, *Vanderhorst 392* (RM); Gore Range, Eagles Nest Wilderness Area, central 1 km W of Lower Piney Lake, elev 2800 m, 30 Jun 1986, *Hogan & Arapkiles 15* (RM); Gore Range, Eagles Nest Wilderness Area, central along Deluge Creek in forest of aspen and lodgepole, elev ca 3000 m, 19 Jun 1987, *Hogan & Arapkiles 239* (UTC). El Paso Co., Pikes Peak region, elev 8250 ft, 16 Jul 1920, *Johnston 2578* (UC). Garfield Co., Flat Tops Wilderness, Blair Mtn, ca 17 air mi NNW of Glenwood Springs, elev 10800 ft, 24 Aug 1991, *Vanderhorst 4471* (RM); Flat Tops Wilderness, Devils Causeway, ca 34 air mi NNE of Glenwood Springs, ca 4 air mi NE of Trappers Lake, elev 11600 ft, 13 Jul 1990, *Vanderhorst 1026* (RM); Flat Tops/White River Plateau, limestone ridge above Bison Lake, ca 13 air mi N of Glenwood Springs, elev 11000 ft, 6 Aug 1991, *Vanderhorst 3855* (RM). Gilpin Co., along State Rt 119, 7.6 mi S of Boulder and Gilpin Co. line, elev 9000 ft, 30 Jun 1985, *Nelson & Nelson 7916* (RM). Grand Co., Gore Pass on Hwy 84, Routt National Forest, elev 9000 ft, 1 Aug 1962, *Porter & Porter 9180* (RM); Park Range, ca 9 air mi WSW of Kremmling, elev 8600 ft, 6 Jun 1989, *Kastning et al. 1498* (RM); Park Range, ca 95 mi WSW of Kremmling, elev 8500 ft, 11 Aug 1989, *Kastning et al. 2594* (RM); Rocky Mountain National Park, 1 mi NE of Columbine Lake, elev 8700 ft, 30 Jul 1936, *Sawyer & Rutter 85* (UC); Sulphur Springs, 8 Aug 1907, *Osterhout 3586* (RM). Gunnison Co., Gunnison Watershed, Keblar Pass, elev 10000 ft, 14 Aug 1901, *Baker 789* (RM); Black Mesa, elev 9800 ft, 3 Jul 1964, *Gierisch 2885* (RM); Gunnison and Pitkin Co. border, Elk Mtns, alpine ridge S of Taylor Pass, elev 3850 m, Jul to Aug 1986, *Matthews 1883* (RM); steep slope on W side of E River across from Avery Peak Campground, along Co. Rd, 3 Jul 1984, elev 9700 ft, *Wilken 14049* (BRY). Huerfano Co., E Indian Creek, elev 2400–2700 m, 1 Jun 1900, *Rydberg & Vreeland 5794* (RM). Jackson Co., Park Range, ca 19 air mi W of Walden, on trail to Lake Katherine, elev 8920–9400 ft, 21 Jun 1989, *Kastning 1784* (RM); Park Range, ca 23 air mi NW of Walden, by Big Creek Falls, elev 9100–9400 ft, 20 Jun 1989, *Kastning et al. 1751* (RM); Park Range, near Buffalo Ridge-Seven Lakes Trailhead, ca 2 mi S of WY state line, ca 34 air mi NNE of Steamboat Springs, elev 9600 ft, 6 Aug 1989, *Snow 5457* (RM); Park Range, near jct of US Forest Service Rds 600 and 689, ca 0.5 mi N of Big Creek Lake, ca 22 air mi NW of Walden, elev 8900 ft, 6 Aug 1989, *Snow 5282* (RM). La Plata Co., hills above Mancos, elev 8000–9000 ft, 26 Jun 1898, *Baker 137* (MO); N bank of Animas River, ca 0.4 mi ENE of confluence with Cascade Creek, elev 2356 m, 1 Jul 1985, *Baker 85129* (UTC); San Juan National Forest, elev 10800 ft, 5 Jun 1934, *Loughridge 112* (RM). Larimer Co., above Beaver Creek, elev 9500–12000 ft, 7 Jul 1896, *Crandall 1388* (RM); 1 mi N of the confluence of Two and One Half Creek and the Laramie River along the river, elev 8640 ft, 14 Jul 1974, *Phillips 135* (RM); Aspen Grove, ca 40 mi NW of Fort Collins, 11 Jun 1971, *Crawford 283* (RM); Cameron Pass, 2 Aug 1913, *Osterhout 5017* (RM); Hwy 7, ca 4 mi S of Estes Park, 3 Jun 1971, *Hartman 3110* (RM); Long's Peak Inn, 11 Sep 1915, *Osterhout 5465* (RM); Roosevelt National Forest, pine slopes above Cache La Poudre River near Sleeping Elephant Campground, ca 40 mi W of Fort Collins, elev 8300 ft, 11 Aug 1965, *Feddema 3364* (RM); Stove Prairie, 17 Aug 1912, *Osterhout 4770* (RM). Las Animas Co., Wilkins Park, BAR NI Ranch, between Whiskey Creek and Wilkins Creek, Culebra Range, elev 9900 ft, 13 Aug 1987, *Neely 4539* (RM). Montezuma Co., Montezuma Forest, along Forest boundary, W of Bild Creek, elev 9700 ft, 3 Aug 1922, *Rose R-84* (RM); San Juan National Forest, Cascade Creek, ca 4 mi S of Purgatory Ski Resort, elev 8000 ft, 13 Aug 1986, *Kass 2561* (RM). Montrose Co., Uncompahgre Forest, elev 9500 ft, 21 Jun 1939, *Lanconter et al. 65* (RM); Uncompahgre Plateau, Love Mesa Rd 500, 1 mi from jct with Rd 402, elev 9450 ft, 24 Jul 1982, *Siplivinsky & Beck 4316* (RM). Ouray Co., Miners Creek, elev 11000 ft, 21 Jun 1940, *Tiedemann T-25* (RM). Park Co., ca 4 mi N of Grant, road from Georgetown, 3 Jun 1971, *Crawford 267* (RM); Front Range, Pike National Forest, slopes E of Jefferson Creek, ca 5 air mi NW of Jefferson, elev 10220 ft, 29 Jun 1994, *Ranne 51* (RM); Mosquito Range, ca 1 mi SE of Mt Bross, S of Dolly Varden Gulch, elev 12200 ft, 30 Jun 1985, *Neely 3061* (UTC). Rio Blanco Co., near Pagoda Peak, elev 9000 ft, Aug 1899, *Baker 508* (RM); Flat Tops Wilderness, Mirror Lake Trail, ca 30 air mi E of Meeker, ca 6 air mi NW of Trappers Lake, elev 9600–10000 ft, 15 Jul 1990, *Vanderhorst 1120* (RM); Flat Tops Wilderness, Park Creek, ca 22 air mi N of Glenwood Springs, elev 9200–10000 ft, 12 Aug 1990, *Vanderhorst 1667* (RM); Flat Tops/White River Plateau, Sleepy Cat Peak, ca 23 air mi ENE of Meeker, elev 10200–10500 ft, 12 Aug 1991, *Vanderhorst 4075* (RM); Flat Tops/White River Plateau, Burro Mtn, ca 6 air mi S of Buford, elev 9900–10100 ft, 28 Jun 1990, *Hartman 26398* (RM). Routt Co., Flat Tops/White River Plateau, Bear River, ca 8 air mi SW of Yampa, elev 9000 ft, 3 Jul 1991, *Vanderhorst 3048* (BRY); Flat Tops/White River Plateau, on the divide between Egeria and Sunnyside Creeks, ca 1 air mi SSW of Harper Reservoir, ca 11 air mi SSW of Yampa, ca 34 air mi SSW of Steamboat Springs, elev 10000 ft, 28 Jun 1990, *Nelson 19165* (RM); Park Range, at jct of US Forest Service Rd 129 and dirt road leading around NW side of Steamboat Lake, elev 8000 ft, 4 Aug 1989, *Snow 5096* (RM); Park Range, ca 13 air mi ESE of Yampa, ca 29 air mi SSE of Steamboat Springs, ca 2 air mi SSE of Lynx Pass on Morrison Creek Rd, elev 9000 ft, 31 Jul 1989, *Nelson & Nelson 17402* (RM); Park Range, ca 22 air mi NNE of Steamboat Springs, along the N Fork of the Elk River, elev 8250 ft, 27 Jun 1989, *Kastning et al. 1939* (RM); Park Range, Gold Creek Drainage, near Mtn Zirkel Wilderness boundary, ca 21 air mi NE of Steamboat Springs, elev 8500 ft, 10 Aug 1989, *Snow 5675* (RM). Teller Co., near divide, 22 Jun 1939, elev 9000 ft, *Ehlers 7603* (RM). NEW MEXICO: Bernalillo Co., Saudia Rim, Saudia Mtns, elev 10500 ft, 12 Jul 1930, *Nelson 529* (RM); Tierra Blanca Canyon, elev 7300 ft, 24 Aug 1915, *Chapline 379* (RM); vicinity of Albuquerque, Sandia Crest, Rt 14-S to summit of Crest, elev 5000–10500 ft, 17 Jun 1977,



*Dwyer 14019* (MO). Colfax Co., ca 1.5 mi N of Black Lake, elev 2720 m, 5 Aug 1998, *Sivinski 4530* (RM); Philmont Scout Ranch, near Cimarron, trail 2 mi SE of Black Mtn Camp, elev 8400 ft, 8 Jul 1968, *Hartman 2320* (RM). Grant Co., NW of Silver City, ca 10 air mi SW side of Bear Mtn, in a S-draining canyon that crosses road ca 2 mi W of pass, 4 Oct 1980, *Spellenberg & Ward 5897* (UC); Coppermine Creek, 1851, *Wright 1107* (holotype of *Thaspium* ? *montanum* var. ? *tenuifolium*; GH). Hidalgo Co., Peloncillo Mtns, Clanton Canyon, 11 Aug 1977, *Wagner & Sabo 3465* (MO). Lincoln Co., Capitan Mtn near summit, along Forest Service Rd 56, elev 2900 m, 1 Aug 1976, *Wagner & Sabo 2212* (MO); near Monjeau Lookout, Sacramento Mtns, ca 6 mi NE of Sierra Blanca Peak, 17 Jul 1968, *Moir 68-45* (RM). Mora Co., Rt 3, 3.9 mi E of Taos Co. line, elev 8600 ft, 12 Aug 1984, *Hill 15093* (UC). Otero Co., ca 0.5 mi N of Sierra Blanca Peak, Sacramento Mtns, elev 11200 ft, 10 Jul 1968, *Moir 68-59* (UTC); on Sierra Blanca Peak, elev 11800 ft, 22 Jul 1995, *Scott 9449* (RM); Sacramento Mtns, 8 Aug 1899, *Wootton s.n.* (RM); Sacramento Mtns, upper Russia Canyon, ca 0.2 mi E of Hwy 64, elev 8900 ft, 24 Jun 1984, *Worthington 12147* (RM). San Miguel Co., mountains near Pinos Altos, 26 Jun 1936, *Stewart s.n.* (MO); top of range between Sapello and Pecos Rivers, elev 11000 ft, 1 to 4 Aug 1900, *Cockerell s.n.* (lectotype of *Pseudocymopterus montanus* var. *multifidus*; NY); Pecos Wilderness, Forest Rds 645 and 156, between Terrero Mine and summit of Elk Mtn, Santa Fe Mtns, elev 11400–11661 ft, 19 Aug 1984, *Hill 15320* (UC); Santa Fe Forest, Jack's Creek Trail #259, elev 9900 ft, 5 Jul 1973, *Moir 138* (RM); Santa Fe Forest, Windsor Creek, Pecos River, elev 8500 ft, 7 Sep 1976, *Pase 2091* (RM). Santa Fe Co., sunny declivities at the foot of the mountains, along Santa Fe Creek, 1847, *Fendler 276* (holotype of *Thaspium* ? *montanum*; GH); Santa Fe Canyon, 9 mi E of Santa Fe, elev 8000 ft, 2 Jun 1897, *Heller & Heller 3651* (MO); Santa Fe Forest, Osha Creek, elev 8800 ft, 21 Jul 1923, *Renner 159* (UC). Socorro Co., Bear Mtns, May 1887, *Rusby 148 1/2* (MO). Taos Co., Hwy 64, hillside, La Sombra Forest Camp, Carson National Forest, 16 Jul 1955, *Mathias 3000* (UC, UC); Hwy 64, Palo Flechado Pass, 16 Jul 1955, *Mathias 3001* (UC); Sangre de Cristo Mtns, 0.5 mi N of summit of Mallette Canyon Rd, 5.4 mi NNW of Red River, elev 10500 ft, 17 Aug 1973, *Holmgren & Holmgren 7263* (UTC); Sangre de Cristo Mtns, Costilla Creek Canyon, hills N of the creek, 12 mi SE of Amalia, elev 9000 ft, 16 Aug 1973, *Holmgren 7222* (UC); Sangre de Cristo Mtns, W slope of Wheeler Peak, above Williams Lake, elev 11200 ft, 21 Aug 1973, *Holmgren & Holmgren 7323* (UC, UTC). UTAH: Beaver Co., 1 mi E of Buffer Lake Rd, vicinity of Big John Flats, 19 Jul 1940, *Maguire 19673* (UTC); 12.5 mi E of Beaver, Fishlake National Forest, Tushar Mtns, N Fork of Three Creek, elev 8700 ft, 13 Jul 1982, *Goodrich 17259* (RM); 15 mi E of Beaver, Fishlake National Forest, Tushar Mtns, Big Flat, elev 9600 ft, 13 Jul 1982, *Goodrich 17263* (RM); rocky breaks, N Delano Peak, elev 11600 ft, 20 Jul 1940, *Maguire 19696* (UC, UTC). Garfield Co., Garfield Range, elev 3700 m, 20 Jun 1903, *Clements s.n.* (RM); Aquarius Plateau, Dixie Na-

tional Forest, Posy Lake, 15 mi N of Escalante, elev 8800 ft, 12 Aug 1965, *Holmgren et al. 2436* (BRY, UTC); Aquarius Plateau, at the head of Poison Creek, 4 Aug 1905, *Rydberg & Carlton 7426* (holotype of *Pseudocymopterus versicolor*; NY); at the edge of the timber, overlooking the E Fork of Bull Creek, Henry Mtns, ca 25 mi S of Hanksville, elev 10000 ft, 5 Jul 1961, *Cronquist 9432* (OSC, UTC); Iron Spring Draw, Escalante Mtns, elev 3037 m, 20 Jul 1978, *Reese 934* (UTC); SC Paunsaugunt-Sevier, E slope of Table Mtn, elev 9925 ft, 4 Aug 1977, *Foster & Foster 4942* (BRY). Grand Co., 2 mi N of Warner Ranger Station, elev 9200 ft, 19 Jul 1933, *Maguire et al. 17738* (UTC); La Sal Mtns, elev 10500 ft, 31 Jul 1924, *Payson & Payson 4091* (MO); N base of Haystack Mtn, elev 9300 ft, 9 Jul 1933, *Maguire et al. 17740* (UTC); ridge S of Beaver Creek and SW of Don's Lake on the La Sal Mtns, elev 9800 ft, 29 Jul 1988, *Richardson 87B* (BRY). Iron Co., from N edge of Cedar Breaks, elev 10300 ft, 12 Aug 1938, *Hitchcock et al. 4596* (RM); Cedar Breaks National Monument, near Chessmen Overlook, elev 3530 ft, 21 Jun 1984, *Higgins 14477* (RM); Cedar Breaks Rim, elev 10400 ft, 13 Aug 1939, *Maguire 17571* (UTC); Dixie Forest, Midway Summit, elev 9800 ft, 19 Jul 1968, *Pfister 178* (RM); E side of Cedar Breaks National Monument, elev 10500 ft, 23 Jun 1940, *Maguire 18979* (UTC); jct Hwy 14 & 143, ca 19 road mi SE of Cedar City, elev 3000 m, 27 Jun 1985, *Neese 17113* (RM); on slopes above Alpine Lake, Cedar Breaks National Monument, elev 10000 ft, 13 Aug 1939, *Maguire 17590* (UTC). Piute Co., SW ridge of Mt Belknap, ca 10 mi WSW of Marysvale, elev 11200–11700 ft, 21 Jul 1984, *Tuhy & Johnson 1693* (UTC). San Juan Co., Abajo Peak, Abajo Mtns, elev 11360 ft, 19 Aug 1995, *Foster 283* (RM); Abajo Peak, elev above 11000 ft, 1 Jul 1932, *Maguire & Redd 2002* (UTC); La Sal Mtns, just S of La Sal Pass, 30 air km SE of Moab, elev 3080 m, 14 Aug 1984, *Holmgren et al. 10692* (BRY, UTC); N slope just N of the larger of the two Bears Ears, ca 21 air mi W of Blanding, elev 8400 ft, 29 Jun 1961, *Cronquist & Holmgren 9386* (UTC); S peak, NW exposure, 10 mi due W of Monticello, elev 10200 ft, 13 Jul 1993, *Huber 195* (BRY); SE slope La Sal Mtns, ca 1.7 mi ESE of Mtn Peale, elev 9760 ft, 26 Jul 1986, *Franklin 4037* (BRY); Yellow Pine woodland, Kigalia Ranger Station, Elk Ridge, elev 8200 ft, 23 Jun 1932, *Maguire & Redd 2006* (UTC). Sanpete Co., 18.5 mi W of Ferron, Manti-La Sal National Forest, Wasatch Plateau, Black Fork Creek, elev 9120 ft, 10 Aug 1982, *Goodrich & Lewis 17416* (BRY); CC Price-Ferron, 21 mi due S of Mt Pleasant, elev 10700 ft, 12 Aug 1977, *Welsh et al. 16125* (BRY); CC Price-Ferron, Skyline Drive E of Manti, elev 10700 ft, 28 Jul 1977, *Clark 2884* (BRY); Manti-La Sal National Forest, head of Manti Canyon, Skyline Drive, elev 10000 ft, 4 Jul 1942, *Plummer 205* (RM); Manti-La Sal National Forest, base of West Sanpete Peak, elev 10600 ft, 25 Aug 1976, *Lewis 4521* (UTC); Manti-La Sal National Forest, Skyline above the Cove, elev 10400 ft, 3 Aug 1978, *Lewis 5587* (BRY); Manti-La Sal National Forest, Middle Forks Park, Skyline Drive, Wasatch Plateau, elev 10500 ft, 8 Aug 1940, *Maguire 20027* (UTC); on flat plateau at top of S Fork, Manti

Canyon, Wasatch Plateau, elev 10000 ft, 12 Jul 1962, *Holmgren 236* (UTC); S slope, Wagon Road Ridge, 12 Jul 1941, *Harrison & Harrison 10431* (UTC); Skyline Summit above the Great Basin Experiment Station between Orangeville and Ephraim, elev 10200 ft, 5 Aug 1973, *Holmgren & Holmgren 7811* (UC, UTC); on N facing slope, Manti-La Sal National Forest, Wasatch Plateau, elev near 10000 ft, 28 Jul 1961, *Holmgren 44* (UTC); Great Basin Experiment Station, Wasatch Plateau, 6 Jul 1924, *Harris C24537* (MO). Sevier Co., Elkhoe Ranger Station, elev 10500 ft, 20 Jul 1940, *Gutzman G-2* (RM); White Mtn, Sern Wasatch Range, ca 14 mi NW of Emery, elev 3440 m, 6 Aug 1983, *Tuhy 1058* (UTC); Wasatch Mtns, Mt Terrell, elev 3075 m, 27 Aug 1908, *Tidestrom 1811* (holotype of *Pseudocymopterus tidesstromii*; US). Wayne Co., Dixie Forest, Bluebell Knoll Enclosure, Boulder Top, elev 11000 ft, 18 Aug 1966, *Lewis 1206* (RM). WYOMING: Albany Co., in aspen woods, Pole Mtn region, elev 8300 ft, 15 Jul 1946, *Porter 4020* (RM); Laramie Range, Pole Mtn District, Medicine Bow National Forest, W of Eagle Rock, N facing slope, elev 8200–8400 ft, 23 Jul 1964, *Aslamy 157* (RM); Laramie Range, Pole Mtn region, elev 8000–8600 ft, 27 Jul 1965, *Porter & Porter 9987* (UC); Laramie Range, Pole Mt region, E of Laramie, elev 8300 ft, 1 Aug 1960, *Porter & Porter 8464* (RM); Middle Crow Creek, Medicine Bow National Forest, ca 12 mi E of Laramie, elev 7500 ft, 6 Aug 1965, *Feddema 3235* (RM); Pole Mtn region, elev 8200 ft, 10 Jun 1946, *Porter 3838* (UTC); near Sherman, 29 Jul 1893, *Greene s.n.* (UC); Sherman and Buford, 27 Jul 1913, *MacBride 2556* (RM); Tie City, 20 Jul 1900, *Nelson 7667* (holotype of *Pseudocymopterus sylvaticus*, RM; isotype of *Pseudocymopterus sylvaticus*, MO). Carbon Co., Saw Mill Creek, 25 May 1895, *Nelson 1238* (RM); Sierra Madre Mtns, Medicine Bow Forest, ca 13 air mi SW of Encampment, ca 29.5 air mi S of Saratoga at Hog Park, elev 8400 ft, 24 Jul 1978, *Nelson & Nelson 1901* (RM); Sierra Madre, ca 1.4 air mi N of state line, ca 16 air mi SE of Encampment, along Middle Fork Big Creek, elev 8500 ft, *Nelson 16169* (RM); Sierra Madre, Cunningham Park, ca 17 air mi SE of Encampment, elev 8100 ft, 17 Aug 1986, *Williams 413* (RM). Laramie Co., elev 7400 ft, 3 Jul 1984, *Dorn 4069* (RM); elev 7500 ft, 3 Jul 1984, *Dorn 4062* (RM).

MEXICO. CHIHUAHUA: Meadow Valley, Sierra Madre Mtns, elev 7000 ft, 17 Sep 1903, *Jones s.n.* (MO); on Hwy 16, ca 30 mi W of the La Junta jct, near mountain village, elev 6950 ft, 19 Jul 1975, *Ellis et al. 16* (MO); Majalca, 18 to 20 Aug 1935, *LeSueur Mex-13* (MO); vicinity of Madera, elev 2250 m, 27 May to 3 Jun 1908, *Palmer 276* (MO); District Guerrero, Municipio de Guachochic, Cusarare, S of Creel, Guachochic Rd, vado of Arroyo Cusarare, moist flat and flood plain above Arroyo Cusarare and below cultivated fields, elev 6900 ft, 11 Aug 1972, *Bye 2710* (UC); District of Guerrero, Basuchil, ca 10 mi NW of Minaca, elev 2200 m, 8 May 1929, *Mexia 2508* (UC, MO); District of Guerrero, Municipio de Bocoyna, N facing slope at bend of Rio Oteros W of Creel, elev 7600 ft, 30 Jul 1974, *Bye 6637* (UC); Municipio de Ignacio Zaragoza, 12 mi E of Ignacio Zaragoza, 15 mi SW

of Buenaventura, pass through Sierra la Catarina, elev 8000 ft, N slope ca 0.25 mi S of highway, 30 Oct 1989, *Spellenberg et al. 10057* (RM); Municipio Ocampo, Parque Nacional de Cascada Basaseachic, on N slope at overlook, ca 1 air km S of Cascada, elev 2100 m, 24 Apr 1987, *Spellenberg et al. 9049* (RM); summit of Mesa El Campanero between Yecora, Sonora, and Bermudez, elev 2120 m, 17 Aug 1985, *Turner & Martin #85–33* (UC); 6 mi W of Madera along main gravel road to the Rio Papigochic, E slope of ridge, 22 Sep 1984, *Lavin 4951* (UC); foothills of the Sierra Madre Mtns, 19 Sep 1887, *Pringle 1250* (UC); Municipio Madera, 12 Oct 1994, *Spellenberg et al. 12255* (UC); Nabogame, elev 1800 m, 5 Sep 1988, *Laferriere 1917* (UC). DURANGO: Otinapa, 25 Jul to 5 Aug 1906, *Palmer 439* (MO). SONORA: Municipio de Yecora, above Restaurant Puerto de la Cruz on road to Mesa del Campanero, elev 1800 m, 6 Aug 1996, *Traub s.n.* (RM).

*Pseudocymopterus longiradiatus*

UNITED STATES. NEW MEXICO: Eddy Co., Last Chance Canyon, elev 4700 ft, 25 Apr 1999, *Worthington 28171* (RM); 32 mi W of Carlsbad, S Texas Hill Canyon Research Natural Area, elev 4920 ft, 28 Apr 1988, *Dunmire 1058* (UNM); Guadalupe Mtns, Middle Rocky Arroyo, arroyo bottom, elev 5000 ft, 16 May 1979, *Fletcher 3814* (UNM); Guadalupe Mtns, in the S Fork of Big Canyon, 24 May 1982, *Knight 1980* (UNM). Otero Co., Sacramento Mtns, ca 3 mi SSW of Bent, canyon bottom, SW side of Domingo Peak, elev 7200 ft, 7 Aug 1990, *Sivinski 1546* (UNM); Sacramento Mtns, West Side Rd, ca 3 air mi S of High Rolls, elev 2300 m, 31 Jul 1998, *Sivinski 4515* (UNM); Lower Dog Canyon, Sacramento Mtns, 14 May 1978, *W.H.P. 658* (UNM); Alamo National Forest, Haynes Canyon, 10 Aug 1911, *Barlow s.n.* (MO); Guadalupe Mtns, ca 0.5 mi NW of Powers Well, elev 5960 ft, 5 May 2001, *Worthington 30492* (UTEP). TEXAS: Brewster Co., in lower and middle canyon, on E side of Mt Ord, elev 4600 ft, 7 Apr 1947, *Warnock et al. 3807* (SRSC); in lower portion of limestone canyon, NE side of Mt Ord, Gage Estate, 11 mi S of Alpine, 7 Apr 1947, *Warnock et al. 4738* (SRSC). Culberson Co., Guadalupe Mtns National Park, on trail from Bush Mtn to Pine Springs, 4 Jun 1973, *Northington 426* (ARIZ); Pine Springs Canyon on the trail to Guadalupe Peak, ca 0.5 mi due W of the campground, 3 Jun 1987, *Higgins 17183* (BRY); N facing canyon, ca 9 mi N of Van Horn, *Correll & Rollins 23805* (MO); upper McKittrick Canyon, Guadalupe Mtns, by dry stream bank, elev 6000 ft, 22 Jun 1947, *Meyer & Meyer 2186* (isotype of *Pseudocymopterus longiradiatus*; UTC); Guadalupe Mtns, lower South McKittrick Canyon, elev 6000 ft, 18 May 1958, *Warnock & Johnston 16528* (SRSC); Guadalupe Mtns, S McKittrick Canyon, elev 6200 ft, 30 Apr 1961, *Warnock 18239* (SRSC); Guadalupe Mtns, lower Smith Canyon, near Frijole, elev 6000 ft, 3 May 1947, *Warnock & McVaugh 5406* (SRSC); Guadalupe Mtns, in upper Pine Spring Canyon, elev 7000 ft, 3 May 1947, *Warnock & McVaugh 5436* (SRSC); Guadalupe Mtns, in shady spots, elev 8000 ft, 21 Jun 1958, *Johnston 3184* (SRSC);



Guadalupe Mtns, McKittrick Canyon, 20 May 1991, *Whitefield s.n.* (SRSC); Guadalupe Mtns, McKittrick Canyon, canyon bottom ca 0.5 to 1 mi trail E of Pratt Cabin (picnic area), elev 5200 ft, 13 Jun 1983, *Freeman & Worthington 10741* (UTEP); Guadalupe Mtns, vicinity of Frijole Post office, elev 8000 ft, 10 Aug 1930, *Grassl 134* (MICH). Jeff Davis Co., Little Aguja Canyon, elev 1550 m, 17 Jun 1931, *Moore & Steyermark 3131* (MO); rocky hills above Limpia Creek near Wild Rose Pass, ca 15 mi NE of Fort Davis, 10 Apr 1947, *McVaugh 7891* (MICH).