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A multivariate analysis of *Pteryxia terebinthina* (Apiaceae)[1]

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SUN, F.-J. (Department of Plant Biology, 505 South Goodwin Avenue, University of Illinois, Urbana, IL 61801), G. A. LEVIN (Division of Biodiversity and Ecological Entomology, 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 *Pteryxia terebinthina* (Apiaceae). J. Torrey Bot. Soc. 135: 81–93, 2008.—Recognition of infraspecific taxa in *Pteryxia terebinthina* (vars. *albiflora*, *californica*, *foeniculacea*, and *terebinthina*) is controversial. Multivariate analysis of variance, principal component analysis, and discriminant analysis of 265 specimens representing the morphological variability and geographic distribution of the species complex were conducted to test the validity of these infraspecific taxa. Results show that var. *terebinthina* can be recognized by its unique fruit wing structure. There are statistically significant differences among the remaining varieties for most of the characters previously used to recognize these varieties, but all of these characters are overlapping among the taxa. No clearly separated clusters are revealed in the principal component analysis and discriminant analysis does not allow reliable recognition of the varieties. We therefore propose that this species complex be recognized as containing two varieties, *foeniculacea* and *terebinthina*.

Key words: discriminant analysis, multivariate analysis, North American Apioideae, principal component analysis, *Pteryxia terebinthina*.

Classification of the western North American species complex *Pteryxia terebinthina* (Hook.) J.M. Coult. & Rose (turpentine wavewing) has been controversial for more than one and a half centuries (Torrey and Gray 1840, Coulter and Rose 1900, Jones 1908, Rydberg 1917, Mathias 1930, Mathias and Constance 1944–1945, Kartesz 1994, Cronquist 1997). Its members can be distinguished from other taxa, both in *Pteryxia* (Nutt. ex Torr. & A. Gray) J. M. Coult. & Rose and in the closely-related genus *Cymopterus* Raf., by a combination of morphological characters, although it is very unlikely that either genus as currently circumscribed is monophyletic (Downie et al. 2002, Sun 2003, Sun and Downie 2004, Sun et al. 2004). These plants are distributed from Montana west to Washington, and south to Colorado, Utah, Nevada, and California, and they are often found in dry, open, often rocky or sandy places at elevations up to 2700 m (Mathias 1930, Mathias and Constance 1944–1945, Goodrich 1986, Constance 1993, Cronquist 1997). They are aromatic perennials possessing a stout to slender taproot and branching caudex. Their leaves are pinnately or ternate-pinnately dissected with numerous small and crowded ultimate segments. The inflorescences are spreading at anthesis with unequal rays and the flowers are uniformly yellow. The fruit wings are prominent and are strongly undulate (wavy or crisped) to nearly flat.

The currently recognized varieties (Kartesz 1994, Cronquist 1997) of *Pteryxia terebinthina*

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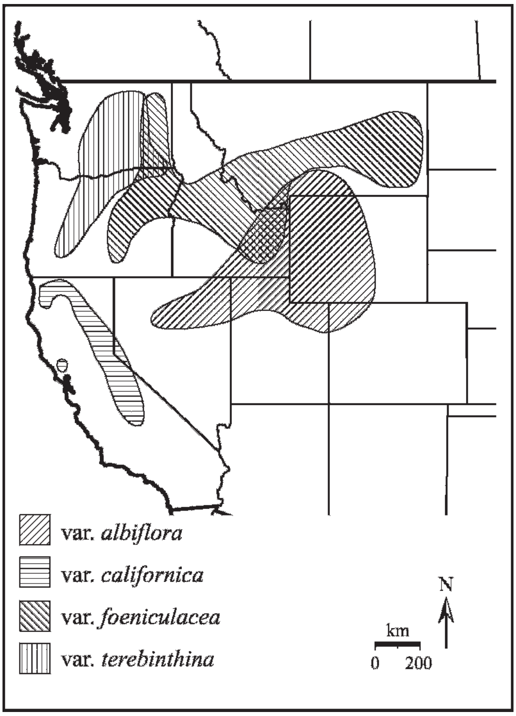

FIG. 1. Map of western North America showing the distribution of the four varieties of *Pteryxia terebinthina* as recognized by Kartesz (1994).

are fairly distinct geographically (Fig. 1): (1) var. *terebinthina* has a distribution centered on the Columbia Plateau of Washington and Oregon, mostly at low elevations and often in sand dunes; (2) var. *foeniculacea* is found from foothills to middle elevations in the mountains of the southern half of Montana and central Idaho, south to the border of the Snake River plain, and west into the mountains and foothills of northeastern and central Oregon (and eastern Washington) as far as the Maury and Ochoco Mountains; (3) var. *californica* grows in the southern Cascade Mountains and Sierra Nevada of California and adjacent mountains of extreme western Nevada, and extends west into the Klamath region of northwestern California; and (4) var. *albiflora* is found overlapping with var. *foeniculacea* on the eastern Snake River plain in Idaho, and extends eastward into Wyoming, and south to the mountains of northern Nevada, northern Utah, and northwestern Colorado.

Not only is the generic placement of the *Pteryxia terebinthina* complex uncertain, its classification is troublesome (Torrey and Gray 1840, Coulter and Rose 1900, Jones 1908, Mathias 1930, Mathias and Constance 1944–1945, Goodrich 1986, Kartesz 1994, Cronquist 1997). Major treatments of the group vary from recognizing up to six species to one species with four to five varieties in *Pteryxia* or three varieties in *Cymopterus* (Table 1). The fundamental problem is that the taxa are morphologically very similar. Torrey and Gray (1840) noted that *C. foeniculaceus* is "scarcely distinct" from *C. terebinthinus* and that *C. thapsoides* "is perhaps too near" that species. Similarly, Coulter and Rose (1900) stated that the species "are very difficult of discrimination" and Mathias (1930) commented that the varieties she recognized contained a "large number of intermediate forms" although they had distinct geographic ranges. Cronquist (1997) indicated that he "cannot sort the specimens [of *C. terebinthinus* var. *albiflorus* and var. *californicus*] appropriately without reference to the [geographic] data." The trend over time has been to recognize fewer taxa and in the currently prevailing treatments the complex is treated as a single species with four (Kartesz 1994) or three (Cronquist 1997) varieties in *Pteryxia* or *Cymopterus*, respectively.

In addition to the taxa presented in Table 1, *Pteryxia petraea* (M.E. Jones) J.M. Coult. & Rose has sometimes been treated as a variety of the *Pteryxia terebinthina* complex (Goodrich 1986, Constance 1993). *Pteryxia petraea* is widely distributed from southeastern Oregon and southwestern Idaho to Nevada and eastern California, and east from southern and eastern Utah and northwestern Colorado to northern Arizona and northwestern New Mexico. Morphologically, this species is quite distinct from all varieties of *P. terebinthina*: the upper lateral primary leaflets are equal or shorter than their internodes and often much smaller than the lower primary leaflets, while the lengths of the lower primary leaflets are longer than their widths, making the leaf blades skeleton-like. We agree with the many authors who maintain *P. petraea* as a distinct species (e.g., Mathias 1930, Mathias and Constance 1944–1945, Kartesz 1994, Cronquist 1997).

Phylogenetic analyses of nuclear ribosomal DNA internal transcribed spacer and chloroplast DNA *rps*16 intron and *trn*F-*trn*L-*trn*T sequences (Sun 2003, Sun and Downie 2004, Sun et al. 2004) have not been helpful in

Table 1. Major taxonomic treatments of the *Pteryxia terebinthina* complex. Authors of plant names are standardized according to Brummitt and Powell (1992).

Torrey & Gray (1840)	Coulter & Rose (1900)	Mathias (1930)	Kartesz (1994)	Cronquist (1997)
Cymopterus albiflorus Torr. & A. Gray	*Pteryxia albiflora* (Torr. & A. Gray) Nutt. ex J.M. Coult. & Rose	*P. terebinthina* var. *albiflora* (Torr. & A. Gray) Mathias	*P. terebinthina* var. *albiflora*	*C. terebinthinus* var. *albiflorus* (Torr. & A. Gray) M.E. Jones
	P. calcarea (M.E. Jones) J.M. Coult. & Rose	*P. terebinthina* var. *calcarea* (M.E. Jones) Mathias	Synonym of *P. terebinthina* var. *albiflora*	Synonym of *C. terebinthinus* var. *albiflorus*
	P. californica J.M. Coult. & Rose	*P. terebinthina* var. *californica* (J.M. Coult. & Rose) Mathias	*P. terebinthina* var. *californica*	Synonym of *C. terebinthinus* var. *albiflorus*
C. foeniculaceus Torr. & A. Gray	*P. foeniculacea* (Torr. & A. Gray) Nutt. ex J.M. Coult. & Rose	*P. terebinthina* var. *foeniculacea* (Torr. & A. Gray) Mathias	*P. terebinthina* var. *foeniculacea*	*C. terebinthinus* var. *foeniculaceus* (Torr. & A. Gray) Cronquist
C. terebinthinus (Hook.) Torr. & A. Gray	*P. terebinthina* (Hook.) J.M. Coult. & Rose	*P. terebinthina* var. *terebinthina*	*P. terebinthina* var. *terebinthina*	*C. terebinthinus* var. *terebinthinus*
C. thapsoides Torr. & A. Gray	*P. thapsoides* (Torr. & A. Gray) Nutt. ex J.M. Coult. & Rose	Synonym of *P. terebinthina* var. *foeniculacea*	Synonym of *P. terebinthina* var. *foeniculacea*	Synonym of *C. terebinthinus* var. *foeniculaceus*

resolving the taxonomy of the *Pteryxia terebinthina* group. Results suggest that the complex most likely is not monophyletic, but relationships between its members and various species in the genera *Aletes* J.M. Coult. & Rose, *Cymopterus*, *Harbouria* J.M. Coult. & Rose, *Lomatium* Raf., *Oreoxis* Raf., *Musineon* Raf., *Pseudocymopterus* J.M. Coult. & Rose, and *Pteryxia* are poorly resolved. This is due to a lack of informative characters and significant incongruence between the nuclear and chloroplast DNA-derived trees. In contrast, phylogenetic studies of morphological characters support a close relationship among the varieties of *Pteryxia terebinthina* and between them and *P. petraea*, although again the monophyly of the group is poorly supported and no unique morphological synapomorphies have been identified for *P. terebinthina* (Sun 2003).

In the absence of clear phylogenetic results, we have chosen to explore morphological variation within the *Pteryxia terebinthina* complex using multivariate analysis of variance (MANOVA), principal component analysis (PCA), and discriminant analysis (DA) of morphological characters scored from herbarium specimens. The objectives of this study were to: 1) examine quantitatively the patterns of morphological variation; 2) determine the important morphological characters that contribute to the discrimination of any infraspecific taxa; and 3) evaluate the taxonomic status of the infraspecific taxa in *P. terebinthina* in light of both morphological and molecular data.

Materials and Methods. We examined 615 herbarium specimens from the *Pteryxia terebinthina* species complex, borrowed from BRY, ILL, K, MO, OSC, RM, UC, US, and UTC (abbreviations as in Holmgren et al. 1990). Of these specimens, 265 had complete locality data, were in good condition, and bore mature flowers or fruits. These specimens, which are listed in the Appendix, included the types of three varieties (*calcarea*, *californica*, and *terebinthina*) and reflected the morphological variability exhibited by the species and populations from throughout its geographic range (Fig. 1). The types of vars. *albiflora* and *foeniculacea* were incomplete and therefore could not be included in the quantitative analyses. The 265 specimens were used as operational taxonomic units (OTUs) in 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 the presence of an undulate fruit wing, were not included because they violate the assumptions of both MANOVA and PCA (Pimentel 1979). Nineteen quantitative characters were selected (Table 2). Data were collected using an Olympus dissecting microscope and a plastic ruler (accurate to 1 mm). The means of three to five 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. Six data sets were constructed and analyzed. The first three data sets were constructed from all 265 specimens: one matrix included flowering specimens only (48 OTUs and 16 characters); the second matrix included those specimens in fruiting condition (217 OTUs and 19 characters); the third matrix combined the OTUs of the previous two analyses (265) but with only the 16 non-fruit characters. As discussed below, *Pteryxia terebinthina* var. *terebinthina* differs in the qualitative character of having an undulate fruit wing (the fruit wing is straight in the other varieties). To explore variation among only the remaining varieties, another three data sets were constructed by excluding the OTUs of var. *terebinthina* from each of the first three data sets. The MANOVA was performed with SPSS ver. 14.0.1 for Windows (SPSS, Chicago, Illinois), 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. The *F*-tests to determine which, if any, characters differed significantly among the putative varieties were performed with and without Bonferroni correction, because although the characters may be independent, they were sampled from the same specimens. The PCA was conducted using NTSYSpc ver. 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, 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). The DA was conducted with SPSS vers. 14.0.1 for Windows, using all the characters simultaneously, the within-groups covariance matrix, and prior probabilities computed from the group sizes. The relatively small sample sizes for some of the varieties 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. Statistics for the 19 morphological characters are presented in Table 2. The MANOVA showed that all characters, except ultimate leaf segment length (character 9) and secondary ray length (character 16), differed significantly ($P < 0.05$, with or without Bonferroni correction) among the four varieties currently recognized in *Pteryxia terebinthina* (Kartesz 1994). Tukey tests, however, showed that for many characters the varieties belonged to overlapping homogeneous subsets (Table 2). Furthermore, ranges for all the varieties were overlapping for all characters. Thus, we found no quantitative characters that can be used individually to assign specimens to variety.

The PCA using all 265 specimens and 16 non-fruit morphological characters yielded

Table 2. Morphological characters and their statistics (mean ± standard deviation and range) for the four varieties currently recognized in *Pteryxia terebinthina* (Kartesz 1994). Sample sizes are indicated below the varietal epithet (flowering specimens/fruiting specimens). Characters that differ significantly ($P < 0.05$) among the varieties as shown by MANOVA F-tests are marked with asterisks. 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.

	Characters	*albiflora* (N = 9/111)	*californica* (N = 17/46)	*foeniculacea* (N = 18/35)	*terebinthina* (N = 4/25)
1.	Plant height (cm)*	24.2 ± 7.9^{A}	34.7 ± 14.0^{B}	30.8 ± 11.5^{B}	33.3 ± 8.2^{B}
		10.0–48.0	11.0–67.0	10.0–55.0	13.0–48.0
2.	Peduncle length (cm)*	19.4 ± 6.4^{A}	27.2 ± 12.1^{B}	23.7 ± 8.4^{AB}	25.8 ± 6.4^{B}
		8.0–38.0	8.0–55.0	8.5–42.0	10.6–41.0
3.	Leaf blade length (cm)*	7.9 ± 2.8^{A}	10.4 ± 3.8^{BC}	10 ± 4.0^{B}	12 ± 3.2^{C}
		3.8–17.0	4.5–22.0	3.5–18.0	5.5–17.0
4.	Leaf blade width (cm)*	6.5 ± 2.7^{A}	7.8 ± 4.1^{AB}	9.5 ± 5.3^{B}	9.5 ± 3.2^{B}
		1.8–16.5	2.5–20.0	3.8–36.0	3.8–15.0
5.	Leaf petiole length (cm)*	6.2 ± 2.9^{A}	7.4 ± 3.0^{AB}	8.4 ± 3.7^{B}	8.7 ± 2.9^{B}
		1.8–17.0	3.4–17.0	1.5–19.0	3.8–14.8
6.	Lowest leaflet length (cm)*	5.0 ± 2.2^{A}	5.9 ± 3.6^{AB}	6.5 ± 2.6^{BC}	7.3 ± 2.4^{C}
		1.5–11.0	1.5–15.3	2.2–13.5	2.8–11.0
7.	Lowest leaflet width (cm)*	2.5 ± 1.2^{A}	3.1 ± 2.5^{AB}	3.8 ± 2.0^{B}	3.8 ± 1.5^{B}
		0.8–6.5	0.8–13.0	1.2–10.0	1.5–6.5
8.	Number of pairs of lateral primary leaflets (pinnae)*	8.9 ± 1.2^{A}	9.5 ± 1.4^{B}	9.2 ± 1.3^{AB}	9.7 ± 1.0^{B}
		7–12	7–15	7–12	8–11
9.	Ultimate leaf segment length (mm)	2.1 ± 1.0	2.0 ± 0.8	2.1 ± 1.0	1.9 ± 1.0
		0.5–5.0	0.5–4.0	0.5–4.0	0.5–4.0
10.	Ultimate leaf segment width (mm)*	0.9 ± 0.3^{B}	0.9 ± 0.3^{B}	0.6 ± 0.2^{A}	0.7 ± 0.3^{B}
		0.5–1.5	0.5–1.5	0.2–1.0	0.5–1.5
11.	Length on the rachis between the first two pairs of leaflets (mm)*	30.8 ± 11.1^{A}	40.1 ± 15.6^{B}	38.5 ± 15.8^{B}	41.9 ± 12^{B}
		16.0–73.0	18.0–85.0	13.0–74.0	22.0–73.0
12.	Inflorescence (umbel) width (cm)*	5.0 ± 1.6^{A}	6.9 ± 3.1^{B}	5.0 ± 1.7^{A}	8.4 ± 2.9^{C}
		2.2–10.0	2.1–15.0	2.4–8.5	4.5–16.0
13.	Umbellet width (cm)*	1.4 ± 0.4^{AB}	1.5 ± 0.6^{B}	1.2 ± 0.4^{A}	1.9 ± 0.5^{C}
		0.3–2.4	0.5–3.0	0.6–2.2	1.2–2.9
14.	Primary ray number*	7.3 ± 1.4^{A}	9.0 ± 3.4^{B}	8.4 ± 2.0^{AB}	10.5 ± 3.5^{C}
		5–12	4–18	5–12	4–20
15.	Primary ray length (cm)*	2.2 ± 1.0^{A}	3.2 ± 1.8^{B}	2.0 ± 0.8^{A}	3.5 ± 1.2^{B}
		0.5–5.5	0.3–10.0	0.5–4.0	1.6–7.0
16.	Secondary ray length (mm)	4.1 ± 2.1	4.0 ± 2.1	3.6 ± 2.3	3.6 ± 2.1
		1.0–12.0	1.0–8.0	1.0–12.0	1.0–8.0
17.	Fruit length (mm)*	6.7 ± 1.2^{AB}	7.8 ± 1.7^{C}	6.2 ± 1.3^{A}	7.4 ± 1.8^{BC}
		4.0–10.0	5.0–12.0	4.0–9.0	5.0–11.0
18.	Fruit width (mm)*	4.4 ± 1.0^{A}	5.7 ± 1.7^{B}	3.9 ± 1.4^{A}	6.0 ± 1.8^{B}
		2.5–8.0	3.0–10.0	2.0–8.0	3.5–9.0
19.	Fruit wing width (mm)*	1.2 ± 0.4^{A}	1.7 ± 0.7^{B}	1.0 ± 0.5^{A}	1.8 ± 0.8^{B}
		0.5–3.0	0.5–3.0	0.5–2.5	1.0–4.0

four components with eigenvalues greater than one (Pimentel 1979), which account for 75.2% of the total variation in the data set (46.6%, 12.5%, 9.8%, and 6.3%, respectively). Plots of the first three principal components (PC1, PC2, and PC3) are shown in Fig. 2. No clearly separated clusters are revealed and all varieties are intermixed on these plots. Furthermore, there are no clusters that correspond to specimens with undulate fruit wings. The fourth principal component also did not separate the OTUs into distinct clusters, nor did the any of the other PCAs, including or excluding var. *terebinthina* and using flowering or fruiting specimens separately or together (results not shown).

Table 3 lists the loadings on the first three components for the 16 non-fruit morphological characters from the combined analysis including all specimens (265 OTUs). The first (PC1) has relatively high positive loadings for plant height, peduncle length, leaf blade length and width, petiole length, lowest leaflet length and width, the length between the first two pairs of leaflets on the rachis, inflorescence width, and primary ray length. Thus, despite linear transformation, PC1 still largely reflects sorting by size, a common phenomenon in

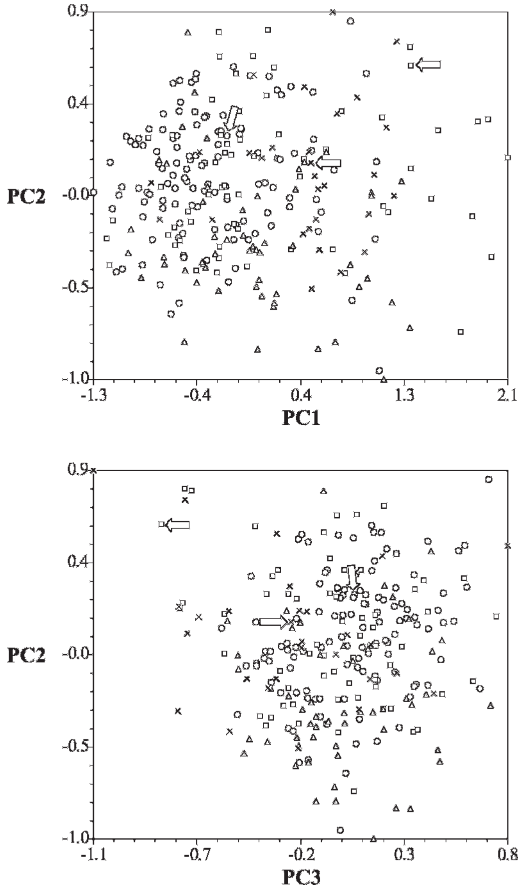

FIG. 2. Plots of principal components (PC) 1, 2, and 3 for the *Pteryxia terebinthina* complex (265 OTUs) using 16 non-fruit morphological characters. Varieties are indicated as follows: *albiflora* (circles), *californica* (squares), *foeniculacea* (triangles), and *terebinthina* (crosses). Arrows indicate type specimens of vars. *calcarea*, *californica*, or *terebinthina*.

PCA (Pimentel 1979). The second component (PC2) has a relatively high positive loading for umbellet width. The third (PC3) has relatively high positive loadings for the length and width of the ultimate leaf segment. The loadings for the analysis using fruiting specimens only from all varieties were very similar for the 16 non-fruit characters and gave high loadings to the three fruit characters, although as noted above no distinct clusters were apparent in component plots (results not shown). Nearly identical results (not shown) were found when var. *terebinthina* was excluded, illustrating the similarity of this variety to the others in the quantitative characters.

The DA also showed that the varieties are difficult to distinguish using quantitative characters alone. Although all the discriminant functions were statistically significant (Wilkes-Lambda values with $P < 0.05$), overall success at classification (cross-validated) was low, with only 62–72% of the specimens correctly classified, depending on the data set. Among the varieties, success was greater than 60% only for var. *albiflora*, which was correctly classified 81–85% of the time. Because specimens of this variety were much more numerous than the others (Table 2) and prior probabilities were calculated from group size, there is a bias toward correctly classifying this variety and misclassifying the others. If equal prior probabilities were assigned, correct classification for var. *albiflora* dropped to about 70%, correct classification of the other varieties increased slightly, and overall correct classification dropped to 61–68%.

Discussion. The varieties of *Pteryxia terebinthina* historically have been distinguished by a combination of quantitative and qualitative characters (Coulter and Rose 1900, Mathias 1930, Mathias and Constance 1944–1945, Cronquist 1997). However, some prior authors (Torrey and Gray 1840, Coulter and Rose 1900, Mathias 1930, Cronquist 1997) have recognized that many of the quantitative characters are highly variable within and overlapping among the putative varieties. Our results bear this out. Although MANOVA demonstrated that most of these characters differ statistically among the varieties (Table 2), the ranges of all the characters overlap so they cannot be used individually to distinguish among the varieties. Both PCA (Fig. 2) and DA showed that the varieties cannot be distinguished reliably using the quantitative characters in combination either.

The two qualitative characters that have been used to distinguish varieties in *Pteryxia terebinthina* are the presence of white (vs. yellow) flowers in var. *albiflora* and the presence of a strongly undulate (vs. straight) fruit wing in var. *terebinthina* (Coulter and Rose 1900, Rydberg 1917, Mathias 1930, Mathias and Constance 1944–1945). Plant specimens with white flowers have never been collected in the field, however, nor has their presence been otherwise confirmed (Cronquist 1997). For example, a specimen annotated as *Cymopterus terebinthinus* var. *albiflorus* [*Holmgren 14591* (NY 678535)] actually contains yellow flowers. In some Apiaceae, yellow

Table 3. Principal component loadings for the 16 non-fruit morphological characters on the first three components for the 265 OTUs of *Pteryxia terebinthina*. For each component, values with particularly large magnitudes are shown in bold.

Characters	PC1	PC2	PC3
1. Plant height (cm)	**0.8766**	0.0210	0.0937
2. Peduncle length (cm)	**0.8676**	0.0053	0.1109
3. Leaf blade length (cm)	**0.9086**	−0.2240	0.0516
4. Leaf blade width (cm)	**0.7468**	−0.3153	0.0575
5. Leaf petiole length (cm)	**0.7410**	−0.1940	0.1150
6. Lowest leaflet length (cm)	**0.8928**	−0.2525	0.0804
7. Lowest leaflet width (cm)	**0.8010**	−0.2631	0.1508
8. Number of pairs of lateral primary leaflets (pinnae)	0.5027	−0.2517	−0.3800
9. Ultimate leaf segment length (mm)	0.1658	0.3390	**0.7341**
10. Ultimate leaf segment width (mm)	0.1347	0.4421	**0.6646**
11. Length on the rachis between the first two pairs of leaflets (mm)	**0.8383**	−0.2248	0.1571
12. Inflorescence (umbel) width (cm)	**0.6996**	0.4840	−0.3279
13. Umbellet width (cm)	0.4733	**0.6396**	−0.3087
14. Primary ray number	0.5742	0.0013	−0.3197
15. Primary ray length (cm)	**0.6134**	0.5606	−0.1955
16. Secondary ray length (mm)	0.3793	0.5514	−0.0497

flowers fade to whitish when dried (Cronquist 1997, Sun et al. 2005), and it is reasonable to speculate that this was the case with the specimens used for the original description of *Cymopterus albiflorus* (Torrey and Gray 1840). Furthermore, plants identified as *Pteryxia terebinthina* var. *calcarea* because of their yellow flowers, but otherwise indistinguishable from var. *albiflora*, occur within the geographic range of var. *albiflora* (Cronquist 1997). Thus, it would appear that the epithet "*albiflora*" is a misnomer because all plants of *P. terebinthina* have yellow flowers in the field.

We are able to confirm that plants of *Pteryxia terebinthina* var. *terebinthina* have fruit wings that are much more undulate, or crisped, than plants that have been assigned to other varieties. In the absence of this character, clearly visible only on fairly mature fruits, specimens of var. *terebinthina* are indistinguishable from the other members of this species, as demonstrated by the results of both PCA and DA using quantitative characters. Although this is a single character and can be subject to uncertainty on many specimens, because the variety has a fairly distinct geographical range and in the region of geographic overlap with var. *foeniculacea* occurs at lower elevations, we support its continued recognition.

The results lead us to conclude that morphology allows recognition of only two varieties in *Pteryxia terebinthina*. Therefore, all names other than var. *terebinthina* must be synonymized under var. *foeniculacea*.

Taxonomic Treatment. Pteryxia terebinthina (Hook.) J.M. Coult. & Rose, Contr. U.S. Natl. Herb. 7: 171. 1900.

var. terebinthina.

Selinum terebinthinum Hook., Fl. Bor.-Amer. 1: 266. 1832. *Cymopterus terebinthinus* (Hook.) Torr. & A. Gray, Fl. N. Amer., 1: 624. 1840. *Pteryxia terebinthina* (Hook.) J.M. Coult. & Rose, Contr. U.S. Natl. Herb. 7: 171. 1900. Type: United States. [Washington: Walla Walla Co., or Oregon: Umatilla Co.], "barren sandy plains of the River Wallawallah," 1826, *D. Douglas s.n.* (holotype: K!).

var. foeniculacea (Torr. & A. Gray) Mathias, Ann. Missouri Bot. Gard. 17: 339. 1930.

Cymopterus foeniculaceus Torr. & A. Gray, Fl. N. Amer. 1: 624. 1840. *Pteryxia foeniculacea* (Torr. & A. Gray) Nutt. ex J.M. Coult. & Rose, Contr. U.S. Natl. Herb. 7:171. 1900. *Pteryxia terebinthina* var. *foeniculacea* (Torr. & A. Gray) Mathias, Ann. Missouri Bot. Gard. 17: 332. 1930. *Cymopterus terebinthinus* var. *foeniculaceus* (Torr. & A. Gray) Cronquist, Univ. Wash. Publ. Biol. 17: 529. 1961. Type: United States. [Oregon: county unknown], "Blue Mountains, E[t]. of W. Walla, " *T. Nuttall s.n.* (holotype: PH!; isotypes: NY!, GH!).

Cymopterus albiflorus Torr. & A. Gray, Fl. N. Amer. 1: 625. 1840. *Pteryxia albiflora* (Torr. & A. Gray) Nutt. ex J.M. Coult. & Rose, Contr. U.S. Natl. Herb. 7: 173. 1900.

Cymopterus terebinthinus var. *albiflorus* (Torr. & A. Gray) M.E. Jones, Contr. W. Bot. 10: 56. 1902. *Pteryxia terebinthina* var. *albiflora* (Torr. & A. Gray) Mathias, Ann. Missouri Bot. Gard. 17: 339. 1930. Type: United States. [Idaho, Utah, or Wyoming, county unknown], "Bear River, Rocky Mountains," *T. Nuttall s.n.* (holotype: PH!; isotypes: GH!, NY!).

Cymopterus thapsoides Torr. & A. Gray, Fl. N. Amer. 1: 625. 1840. *Pteryxia thapsoides* (Torr. & A. Gray) Nutt. ex J.M. Coult. & Rose, Contr. U.S. Natl. Herb. 7: 172. Type: United States. Oregon: [county unknown], rocky places in the Blue Mountains, *T. Nuttall s.n.* (holotype: PH).

Cymopterus calcareus M.E. Jones, Contr. W. Bot. 8: 32. 1898. *Pteryxia calcarea* (M.E. Jones) J.M. Coult. & Rose, Contr. U.S. Natl. Herb. 7: 173. 1900. *Pteryxia terebinthina* var. *calcarea* (M.E. Jones) Mathias, Ann. Missouri Bot. Gard. 17: 334. 1930. *Cymopterus terebinthinus* var. *calcareus* (M.E. Jones) Cronquist, Univ. Wash. Publ. Biol. 17: 529. 1961. Lectotype [designated by Coulter and Rose (1900)]: United States. Wyoming: Sweetwater Co., Green River, elev 6000 ft, 23 Jun 1896, *M.E. Jones s.n.* (lectotype: POM!; isolectotypes: MO!, US!).

Pteryxia californica J.M. Coult. & Rose, Contr. U.S. Natl. Herb. 7: 172. 1900. *Cymopterus californicus* (J.M. Coult. & Rose) M.E. Jones, Contr. W. Bot. 12: 27. 1908. *Cymopterus terebinthinus* var. *californicus* (J.M. Coult. & Rose) Jepson, Man. Fl. Pl. Calif. 730. 1925. *Pteryxia terebinthina* var. *californica* (J.M. Coult. & Rose) Mathias, Ann. Missouri Bot. Gard. 17: 337. 1930. Type: United States. California: Siskiyou Co., Sisson, 1897, *H.E. Brown s.n.* (holotype: US!).

Cymopterus elrodi M.E. Jones, Bull. Montana State Univ., Biol. Ser. 15: 41. 1910. *Pteryxia elrodi* (M.E. Jones) Rydb., Fl. Rocky Mts. 621. 1917. Type: United States. Montana: Ravalli Co., Alta, elev 4500 ft, 22 Jul 1909, *M.E. Jones s.n.* (holotype: POM; isotype: NY!).

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Appendix

Accessions of *Pteryxia terebinthina* used as OTUs in the multivariate analyses. These specimens are identified as varieties *albiflora*, *californica*, *foeniculacea*, or *terebinthina*, as treated by Kartesz (1994). In 23 instances, duplicate herbarium specimens from the same locality were examined. Herbarium acronyms are as in Holmgren et al. (1990).

Variety *albiflora*

UNITED STATES. Colorado: Moffat Co., Flat Tops/White River Plateau, Thornburg Mtn, ca 18 air mi NE of Meeker, elev 7000 ft, 8 Jun 1991, *Vanderhorst 2436* (RM); near mouth of Pool Canyon, ca 1.2 mi SW of Chew Ranch, elev 5510 ft, 1 Jun 1987, *O'Kane 3015* (RM). Routt Co., Flat Tops/White River Plateau, above Williams Fork, ca 13 air mi SSW of Hayden, elev 6800–7200 ft, 22 Jun 1990, *Hartman 25622* (BRY, RM). Idaho: Bannock Co., Red Hill at Pocatello, Range 34 E-Township 6 S, 5 Jun 1941, *Davis 3169* (UC). Bingham Co., ca 15 mi S of Idaho Falls and W of Snake River, elev 4600 ft, 5 Jul 1965, *Call 2432* (UC). Blaine Co., lava beds NW of Little Park, elev 4940 ft, 11 Jun 1981, *Harrison 13437* (RM). Bonneville Co., Caribou Mtn, rock slides near summit, 19 Jul 1923, *Payson & Armstrong 3557* (ILL); Caribou Range, Southeastern end of Big Elk Mtn, 9 air mi S of Palisades Dam, elev 8800 ft, 24 Jul 1971, *Holmgren & Marttala 5616* (UC, UTC). Butte Co., 1.1 mi NW of Arco near Big Lost River crossing, elev 5200 ft, 8 Jul 1953, *Call 829* (UC); 20 mi S of Arco, on Blackfoot Rd, 8 Jun 1941, *Christ 12260* (UC). Cassia Co., 17 air mi SW of Oakley, 1 mi N of Idaho-Utah State line, Goose Creek drainage near Shoe Spring, 22 Jun 1982, *Atwood & Goodrich 8969* (BRY); Lower Beaver Dam Creek below Emery Ranch, elev 5100 ft, 10 Jun 1985, *Atwood & Rosentrader 11162* (BRY). Madison Co., Butte, W of Rexburg, elev 5000 ft, 18 Jun 1938, *Cronquist & Davis 2055* (MO); Rexburg and Butte, 18 Jun 1938, *Davis 309* (UC). Oneida Co., ca 15 mi ESE of Rockland, elev 5000 ft, 5 Jul 1978, *Welsh et al. 17252* (BRY). Montana: Carbon Co., S facing slopes above the N Fork Grove Creek, ca 6 mi SW of Red Lodge, elev 6600 ft, 24 Jun 1986, *Lesica 3893* (RM). Gallatin Co., Bridger Mts, Bozeman, 17 Jul 1905, *Blankinship 226* (MO). Nevada: Elko Co., 1.8 road mi N of the Nontello Fork on the road to Goose Creek from Thousand Springs Valley, W side of Rock Springs Creek, elev 5400 ft, 12 Jun 1985, *Tiehm 9653* (RM); ca 1 mi NW on Cobre, S facing slope, elev 5960 ft, 19 Jun 1979, *Foster 7936* (BRY); Cold Springs Mtn, 0.3 road mi W of road summit on road from Hwy 93 to the O'Neil Basin, elev 6800 ft, 11 Jun 1985, *Tiehm 9644* (UC); Delano Mtn, 2.3 road mi N of the Twelve Miles Ranch Rd to Montello on the road to Crittenden Reservoir, elev 5200 ft, 8 Jun 1987, *Tiehm 11194* (RM); Goshute Valley on road to Montello, 6.3 mi NE of Hwy I-80 on Nev Hwy 30, elev 5900 ft, 13 Jun 1985, *Williams & Tiehm 85-52-3* (UTC); Pilot Range, W of Wendover, elev 4800 ft, 27 May 1942, *Ripley & Barneby 4618* (RM); 25 mi E of Wells on old Hwy paralleling Southern Pacific railroad, elev 6000 ft, 13 May 1940, *Train 3664* (UTC). Utah: Box Elder Co., 0.1 mi E of jct US Hwy 89 and Temple Fork Rd, 17 mi NE of Logan, 8 Jul 1982, *Horner-Till 800* (UTC); Bear River Canyon, 20 Jun 1909, *Smith 1681* (UTC). Cache Co., 3 mi up Logan Canyon, 5 Jun 1937, *Passey s.n.* (UTC); all over Canyon and ridges, W ridge of Spring Hollow, 2 May 1936, *Maguire 13738* (UTC); Grouse Creek Mtns, Bovine Mtns, Devil's Playground, elev 5400 ft, 6 Jun 1996, *Dixon & Hardy 219* (BRY); Kelton Rd, 5.5 km E of Utah Hwy 30, 28 air km SSW of Rosette, elev 1570 m, 2 Jun 1979, *Holmgren & Holmgren 9224* (UTC); N facing slope of the Selev Lake Formation, Goose Creek drainage, 0.25 mi S of Utah-Idaho State line, elev 5020 ft, 24 Jun 1989, *Franklin 6714A* (BRY); near Blue Creek on Hwy 30S, 15 mi SE of Snowwille, 31 May 1955, *Clarke 8* (UC); W slopes of Little Mtn, 15 mi WNW of Brigham City, 4 Jun 1982, *Neese 11555* (BRY, RM); 0.25 mi above mouth of dry canyon, 4 Jun 1937, *Cronquist 540-37* (RM, UTC); in sage type under Maple, W ridge of Spring Hollow, elev 5300 ft, 2 Jun 1936, *Maguire 13741* (UC, UTC); Sardine Canyon, 14 May 1934, *Maguire 17752* (RM). Daggett Co., 12 mi S of Manila Ashley Forest, elev 8400 ft, 20 Jun 1934, *Harrison & Larsen 7894* (MO); 4 mi S of Manila, Sheep Creek Campground, elev 6500 ft, 20 Jun 1979, *Welsh et al. 32* (BRY); Ashley National Forest, 12 mi S of Manila, elev 8400 ft, 20 Jun 1934, *Harrison & Larson 7894* (BRY); Ashley National Forest, Flaming Gorge National Recreation area, E side of Flaming Gorge Reservoir, 1.5 mi N of Antelope Campground, elev 6600 ft, 26 May 1992, *Goodrich 24045* (BRY); Browns Hole, Red Canyon, E of Goslin Mtn, elev 6100 ft, 30 May 1988, *Clark & Charlesworth 5089* (BRY); ca 4.5 mi due SE of Manila, elev 7100 ft, 26 Jun 1979, *Welsh & Moore 18657* (BRY); Southwestern Wyoming and adjacent Utah, Flaming Gorge National Recreation area, elev 6080–7040 ft, 5 Jun 1995, *Refsdal & Goodrich 3591* (RM). Rich Co., Bear Lake, E side, hillside and beach front, elev 7500 ft, 12 Jul 1982, *Thorne 2117* (BRY, RM); Crawford Mtns, Braizer Canyon, elev 7600 ft, 28 Jun 1981, *Thorne & Thorne 1376* (BRY); S Eden Canyon, 2 mi E of lake shore, elev 5980 ft, 16 Jul 1984, *Shaw & Mueller 3541* (UTC); W facing red rock slides, 6 mi N of S end of Bear Lake near Scout Camp, elev 4500 ft, 28 Jun 1965, *Call 2422* (UC). Tooele Co., Dutch Mtn, 21 Jun 1891, *Jones s.n.* (RM); Detroit, S end of the Dugway Range, ca 85 air mi SW of Salt Lake City, 25 May 1891, *Jones s.n.* (RM); Dugway, 26 May 1891, *Jones s.n.* (MO). Uintah Co., 3 mi NE of Roosevelt, on Duchesne River Formation, 10 Jun 1976, *Goodrich 5862* (BRY); between Maeser and Lapoint, ca 1 mi S of Hwy 121, elev 5400 ft, 8 Jun 1976, *Goodrich 5740* (BRY); Twelve Mile Wash between Maeser and Lapoint, ca 1 mi S of Hwy 121, 8 Jun 1976, *Goodrich 5737* (RM). Wyoming: Big Horn Co., Big Horn Mtns, ca 25.5 air mi E of Greybull, ca 12 air mi N of Hyattville on alkali road, elev 7000 ft, 10 Jul 1979, *Nelson 3416* (RM); Big Horn Mtns, Cold Spring Rd, ca 8 air mi NE of Hyattville, elev 7000 ft, 26 May 1980, *Hartman & Dueholm 11224* (RM); W slopes of the mountains, 10–15 mi E of Kane, elev 8500 ft, 22 Jun 1936, *Williams & Williams 3075* (MO); head of Powder River, mountain side, 19 Jul 1901, *Goodding 332* (MO). Carbon Co., ca 7 air mi NE of Savery, elev 6800 ft, 14 Jun 1979, *Hartman & Coffey 8961* (RM). Fremont Co., Red Canyon Rim, ca 14 air mi SSE of Lander, elev 6100–6500 ft, 20 Jun 1986, *Haines 6641* (RM). Hot Springs Co., Bighorn Basin, ridge along N side of Grass Creek Rd, ca 6 mi W of Wyo Hwy 120, elev 5800 ft, 27 Jun 1993, *Evert 25337* (RM). Lincoln Co., ca 1.8 mi due E of Idaho-Wyoming State line, elev 6400 ft, 1 Jul 1986, *Franklin 3666* (BRY); elev 6840 ft, 3 Jul 1982, *Dorn 3730* (RM); Green River Basin, ca 13.5 air mi NE of Kemmerer, elev 7100–7250 ft, 4 Jul 1995, *Cramer 7137* (RM); Southern Selev River Range and vicinity, badlands area ca 1 air mi N of Round Mtn, ca 11 air mi NE of Kemmerer, elev 7000–7480 ft, 28 May 1994, *Hartman & Cramer 45706* (RM); Southern Selev River Range and vicinity, Dempsey Ridge, ca 15.5 air mi WNW of Kemmerer, elev 7800–8000 ft, 30 Jul 1995, *Cramer & Kellett 9928* (RM); Southern Selev River Range and vicinity, Southern Sublette Range, ca 7 air mi N of Cokeville, elev 6140–7600 ft, 28 Jun 1994, *Cramer & Kellett 1229* (RM); Targhee National Forest, W slope of Snake River Range, ridge leading to Observation Peak, ca 8 air mi N of Alpine jct, elev 9600–10000 ft, 1 Aug 1991, *Markow 4615* (BRY); upper Green River Basin, Muddy Creek, ca 6 air mi W of US Hwy 189, elev 6800–6900 ft, 19 May 1993, *Hartman 37256* (BRY); W facing sparsely forested steep rocky slopes on both sides of Sheep Gulch, 1/8 mi from the confluence with Snake River, elev 5700 ft, 4 Jul 1965, *Call & Call 2430* (UC); Wyoming Range, Willow Creek, 9.6 km S of confluence with Hoback River, just above Adams Creek, 12 air km SE of Hoback jct, elev 1990 m, 2 Aug 1978, *Holmgren & Holmgren 9068* (BRY). Natrona Co., Powder River, 27 Jun 1910, *Nelson 9389* (RM). Park Co., Absaroka Mtns, N Fork Shoshone River Drainage, on ridge between Cougar and Pagoda Creeks, ca 4 mi S of US Hwy 14, 16, and 20, elev 8600 ft, 22 Jul 1981, *Evert 3277* (UC); Absaroka Mtns, divide between Moss and Clearwater Creeks, ca 1.5–2.5 mi N of Hwy 14, 16 and 20, elev 7600–8300 ft, 6 Jul 1989, *Evert 17591* (RM); Absaroka Range, N Fork of Shoshone River drainage, N ridge of Ptarmigan Mtn on divide between Cougar and Pagoda Creeks, ca 3.9 mi E of Elk Fork Creek, ca 5 mi S of US Hwy 14, 16, and 20, elev 10200 ft, 30 Jul 1996, *Fertig 16978* (RM); Northern Absarokas, Battleship Mtn, ca 2.5 air mi NW of Dead Indian Pass, ca 24.3 air mi NW of Cody, elev 6400–6600 ft, 18 Jul 1985, *Nelson 12547* (RM); Northern Absarokas, rim of natural corral and ridge above, elev 7200 ft, 17 Jul 1985, *Hartman 20919* (RM); Northern Absarokas, S end of Bald Ridge, ca 3–4 air mi NE of Dead Indian Pass, ca 23 air mi NW of Cody, elev 7500 ft, 17 Jul 1985, *Nelson 12508* (BRY, RM). Sublette Co., Green River Basin, ca 5.5 air mi E of Fontenelle Dam, elev 6550–6600 ft, 18 Jul 1995, *Cramer & Kellett 8350* (RM); Green River Basin, Flat Top, ca 10.5 air mi SE of Big Sandy, elev 7400–7530 ft, 13 Jul 1995, *Cramer & Kellett 7997* (RM); Green River Basin, formation just NW of Squaw Teat, ca 4 air mi S of Elkhorn jct, elev 7200–7537 ft, 20 Jun 1994, *Cramer 972* (RM); Horse Creek, W of Merna, 17 Jul 1922, *Payson & Payson 2737* (RM); plains between Eden and Big Piney, 6 Jul 1922, *Payson & Payson 2585* (MO); upper Green River Basin, Cretaceous Mtn/Hogsback Ridge area, ca 9.5 air mi NNW of La Barge, elev 7200–7480 ft, 20 May 1993, *Hartman 37374* (RM); upper Green River Basin, Cretaceous Mtn/Hogsback Ridge area, mesa with radio tower, ca 10.5 air mi SSW of Big Piney, elev 7300–7400 ft, 24 Jul 1993, *Hartman 41779* (RM); Wind River Range, Little Sheep Mtn, ca 27 air mi N of Pinedale, W of Gypsum Creek and US Forest Service Rd 102, elev ca 9600 ft, 10 Aug 1980, *Spellenberg & Soreng 5757* (UC). Sweetwater Co., Green River, elev 6000 ft, 23 Jun 1896, *Jones s.n.* (isolectotype of *Pteryxia terebinthina* var. *calcarea*; US); Green River Basin, Green River, ca 13 air mi N of Daniel jct, elev 7600 ft, 15 Jul 1995, *Cramer & Kellett 8274* (RM); Steamboat Mtn, elev 8400 ft, 8 Jul 1980, *Dueholm 10458* (RM); summit of Steamboat Mtn, elev 8400 ft, 8 Jul 1980, *Dueholm 10459* (RM); Freighter Gap, elev 7400 ft, 9 Jul 1980, *Dueholm 10532* (RM); 18 mi from Green River, Flaming Gorge National Recreation area, S Chimney Rock, elev 6400–6600 ft, 15 Jun 1988, *Goodrich & Atwood 22524* (BRY); 46 mi E of Rock Springs along Hwy 430, 17 Jun 1997, *Atwood 22695* (BRY); ca 2 air mi SW of Pine Butte, elev 7400 ft, 16 Jul 1980, *Dueholm 10580* (RM); Leucite Hills, Superior, W of Zirkel Mesa, elev 7500 ft, 7 Jul 1973, *Albee 1454* (UTC); Potter Mtn, elev 7400–8000 ft, 7 Jul 1980, *Dueholm 10394* (RM). Teton Co., Hoback Canyon, elev 7500 ft, 25 Jun 1933, *Williams 1180* (MO); W slope of Wind River Range, Fish Creek/Moccasin Basin area, along S Fork of Fish Creek between Buck and Devils Basin Creeks, ca 34 air mi ENE of Jackson, elev 8000 ft, 23 Aug 1990, *Nelson & Fertig 20134* (RM); W slope of Wind River Range, S Fork of Fish Creek between Purdy and Hackamore Creeks, elev 7750–7800 ft, 25 Aug 1990, *Hartman & Fertig 28424* (RM); W Slope of Wind River Range, adjacent to Forest Service Rd 30410 and Cottonwood Creek, ca 26 air mi E of Jackson, elev 7600 ft, 6 Jul 1990, *Fertig 3057* (RM); Teton Pass Mts, E of Victor, Idaho, elev 7500 ft, 22 Jul 1920, *Payson & Payson 2073* (MO). Uinta Co., 1–2 mi W of Piedmont, elev 7200 ft, 6 Jul 1983, *Hartman 15754* (RM); 2.75 mi N of Lonetree, elev 2300 m, 2 Jul 1999, *Goodrich 26060* (BRY); basins and mountains of Southwestern Wyoming, Bridger Butte, ca 5.5 air mi WSW of Fort Bridger, ca 25.5 air mi E of Evanston, elev 7300–7500 ft, 7 Jul 1995, *Nelson & Refsdal 36453* (RM); basins and mountains of Southwestern Wyoming, lower E flank of Hickey Mtn, ca 3 air mi NNW of Lonetree, elev 7600–7820 ft, 13 Jul 1995, *Refsdal 5305* (RM); basins and mountains of SW Wyoming, Wildcat Butte between Church Butte Rd and I-80 at Sweetwater Co., ca 14.8 air mi NE of Lyman, ca 49 air mi ENE of Evanston, elev 6820–6980 ft, 18 Jul 1995, *Nelson & Refsdal 35210* (RM); ca 5 mi N and 25 degrees W of Lonetree, E side of Hickey Mtn, elev 7800 ft, 30 Jun 1982, *Goodrich & Atwood 17172*

(RM, UTC); basins and mountains of Southwestern Wyoming, E end of Sage Creek Mtn, ca 5.3 air mi N of Lonetree, elev 8200–8420 ft, 23 Jul 1995, *Refsdal 5883* (RM); US 189, 8.7 road mi NE of I-80, elev 7000 ft, 6 Jul 1983, *Hartman 15735* (RM); Wyo Hwy 412, 7.7 road mi NW of Carter, elev 7000 ft, 6 Jul 1983, *Hartman 15745* (RM). Washakie Co., Big Horn Basin, along Wyo Hwy 434, ca 10 mi S of Tensleep, elev 5000 ft, 27 Jun 1981, *Evert 2900* (RM); Big Horn Basin, ca 20 mi NW of Thermopolis, along Wyo Hwy 120, elev 5000 ft, 3 Jul 1983, *Evert 5308* (RM); ca 1 mi N of Mud Creek Rd, elev 4700 ft, 10 Jun 1981, *Martin 1543* (RM).

Variety *californica*

UNITED STATES. California: Alpine Co., 0.5 mi S of Lake Alpine, Big Trees (Alpine), elev 7700 ft, 19 Jul 1935, *Howden 23* (UC); near Red Lake, elev 8000 ft, 27 Jun 1947, *Johnson 134* (UTC); on slopes and ridges around Frog Lake, ca 1 km S of Hwy 88 at Carson Pass, 16 Jul 1988, *McNeal 3328* (BRY). Amador Co., along the margins of a large meadow area above Hwy 88, 8.1 mi NE of Lumberyard, El Dorado National Forest, 28 Jun 1981, *McNeal 2564* (BRY). Butte Co., Butte Meadows quad, on S side of Old Humboldt Rd, on rocky slope beneath power lines, ca 0.9 mi W of Butte Meadows Forestry Station, elev 4400 ft, 6 Jul 1980, *Taylor 3073* (MO); Jonesville, elev 1700 m, 13 Jul 1929, *Copeland 390* (RM); little summit near Butte Meadows, 22 Jun 1914, *Heller s.n.* (MO); Summit of the Sierra Nevada above Jonesville, elev 7000 ft, on the summit of a ridge ca rocks, 26 Jun 1915, *Heller 12029* (ILL). Calaveras Co., rocky location near Auto Camp, Big Meadow, N Fork of Stanislaus River region, elev 6500 ft, 23 Jul 1935, *Peirson s.n.* (UC). El Dorado Co., Toiyabe National Forest, 1.5 mi W of Raymond Peak, elev 8500 ft, 21 Jul 1947, *Johnson JJ-191* (RM). Fresno Co., Collins Meadow, elev 7500 ft, Jul 1900, *Hall & Chandler 541* (UC); Granite Basin, 30 Jul 1910, *Clemens s.n.* (RM); Hutchinson Meadow area, Piute Canyon, S Fork of San Joaquin River, above old Forest Service Cabin on W side of French Creek, just above its jct with Piute Creek, 21 Aug 1955, *Quibell 5944* (UC); Sierra National Forest, San Joaquin Experimental Range, Huntington Lake, elev 7000 ft, 4 Jul 1937, *Biswell B-159* (RM). Humboldt Co., rocky river bar, Trinity River Valley, at Willow Creek, elev 500 ft, 3 Jun 1929, *Tracy 8600* (UC, UTC); Trinity River Valley, Willow Creek, elev 500 ft, 28 Apr 1929, *Tracy 8549* (UTC). Lassen Co., Lassen's Peak, elev 6000 ft, 8 Jul 1897, *Jones s.n.* (MO). Madera Co., granitic soil near Whiskey Creek, 1 mi NW of Ellis Meadow, Sierra Nevada, elev 5500 ft, 1 Jul 1938, *Constance 2390* (UTC). Mariposa Co., Yosemite National Park, near Tioga Rd, elev 7000 ft, 12 Aug 1930, *Standford 1920* (RM). Mono Co., 0.2 mi E of Sonora Pass, elev 9500 ft, 10 Aug 1938, *Constance 2456* (UTC); 1 mi W of lower end of Lower Twin Lake, elev 8700 ft, 10 Jul 1937, *Hendrix 323* (UC). Nevada Co., near Castle Peak, 31 Jul 1903, *Heller 7070* (MO, RM, UC); on bank above Hwy near ASUG Lodge, near Norden, 26 May 1944, *Jorgensen 445* (MO). Plumas Co., Sierra City NW quad, on ridge between Florentine Canyon and Spencer Lakes, ca 5 mi SW of Johnsville, elev 7000 ft, 11 Aug 1982, *Taylor & Swanson 4967* (MO). Shasta Co., Summit City, elev 8000 ft, 26 Jul 1900, *Jones 6339* (MO, OSC); Shasta National Forest, along Swift Creek Trail, elev 2500 ft, 25 Jun 1912, *Dayton 92* (RM); Shasta National Forest, Dunsmuir quad, Sims Lookout, ca 11 mi S of Castella, N facing slope, elev 3696 ft, 10 Jun 1980, *Taylor 2806A* (MO); hillsides in Sacramento River Gorge, 1 mi N of Coram on road to Kennett, 8 Jun 1938, *Mathias 1386* (RM, UTC); Little Shoeinhorse Mtn (Squaw Creek watershed), elev 5250 ft, E facing slope, 17 Jun 1992, *Taylor 12788* (UC); near Selev Creek, Sierra Nevada Mtns, elev 1400 ft, Jun 1903, *Hall & Babcock 4015* (UC); Shasta-Trinity National Forest, border of Castle Crags State Park, along roadside, closest city Castella, elev 680 m, 23 Jun 1993, *Merello et al. 706* (MO); Sierra Nevada Mtns, lava beds, elev 4000 ft, Jun 1903, *Hall & Babcock 4230* (UC); Squaw Creek canyon, on limestone cliffs, 0.5 mi E of Squaw Creek Fire Control Station, along Forest Rd 27, elev 1750 ft, 19 Apr 1992, *Taylor 12600* (UC); Waters Gulch Trail, 0.9 mi W of the trailhead located on Packers Bay Rd, ca 0.5 mi N of Packers Bay Marina, elev 1200 ft, 27 Apr 1994, *Oswald & Ahart 6153* (UC); near Middle Creek Station, 3 Jun 1905, *Heller 7953* (MO). Sierra Co., Tahoe National Forest, road to Weber Lake, 3.2 mi W of state Hwy 89, elev 1950 m, 12 Jun 1993, *Schmidt et al. 843* (MO). Siskiyou Co., forest on Spring Hill near Sisson, 9 Jun 1928, *Heller 14597* (RM); gravely creek bed, along Sacramento Creek, ca 2 mi SW of Mount Shasta, 10 Jul 1962, *Barclay et al. 1328* (UC); road to Walker Post Office, 4 mi W of Yreka, elev 4000 ft, 14 May 1942, *Constance & Rollins 2924* (UTC); Spring Hill near the town of Mt Shasta, 22 Jul 1921, *Heller 13585* (ILL); Whitney Creek foot of Mt Shasta, bank on roadside, 19 Jul 1923, *Perison 3951* (UC); Sisson, 1897, *Brown s.n.* (holotype of *Pteryxia terebinthina* var. *californica*; US). Sonoma Co., 0.2 mi W on Harrison Grade Rd from jct with Stoetz Lane, elev 480 ft, 18 Apr 1984, *Utech et al. 84-164* (RM); along and just above creekbed, headwaters of Big Austin Creek, vicinity of "The Cedars," near Layton Chromite Mine, elev 875 ft, 30 May 1956, *Bacigalupi 5663* (RM, UC); hillsides above a disturbed area, 3 mi N of Occidental on the road to Monte Rio, 3 Apr 1976, *McNeal 1880* (BRY); serpentine area on the Fred McMurray Ranch, 1 mi NW of Lafayette School, ca 5 mi E of Guerneville, 4 Jun 1950, *Nobs et al. 672* (UC). Tulare Co., above S end of Crescent Meadow, 3 mi from Giant Forest, Sequoia National Park, 27 Jun 1940, *Cronquist 2130* (MO); dry slopes below W side of Elizabeth Pass, elev 9500 ft, 26 Aug 1938, *Sharsmith 3855* (UC); Jordan Peak, 3 air mi due N of Camp Nelson, ca 25 air mi ENE of Porterville, SW facing slope SW of lookout, elev 9100 ft, 5 Aug 1988, *Ertter & Shevock 7884* (RM); Lloyd Meadow, between 0.75 to 0.5 mi N of Soda Spring on Freeman Creek, near trail to Trout Meadow, W slope among rocks of a low outcropping, elev ca 5600 ft, 24 Jul 1964, *Smith 1312* (RM, UC). Nevada: Carson City, elev 5000 ft, 29 May 1897, *Jones s.n.* (UTC). Douglas Co., Pine Nut Mtns, N ridge of Bullionville, N of Bald Mtn, elev 9000 ft, 17 Jul 1982, *Tiehm & Lavin 7370* (RM); Toiyabe National

Forest, N of Snowslide Canyon, elev 6500 ft, 9 Jul 1946, *Crane BC-12* (RM). Washoe Co., 4.5 mi S of Mount Rose, elev 8300 ft, 29 Jul 1939, *Hitchcock & Martin 5565* (UTC); E side of Mt Rose, elev 8450 ft, *Heller 10942* (RM); along headwaters of Incline Creek, elev 8300 ft, 29 Jul 1940, *Mason 12348* (UTC).

Variety *foeniculacea*

UNITED STATES. Idaho: Blaine Co., on ridge between N fork of Wood River and Murdock Creek, 11 mi N of Ketchum, 6800 ft, 17 Jun 1941, *Cronquist 2490* (UTC); Sawtooth National Forest, Boulder Mtns, 12.5 mi N of Ketchum, head of W Fork of Trail Creek, elev 10000 ft, 16 Aug 1981, *Atwood & Goodrich 8464* (BRY). Bonneville Co., open slopes near base of peak, 19 Jul 1923, *Payson & Armstrong 3563* (ILL). Butte Co., base level reefs along Hwy, 2 mi N of Midway, 13 Jun 1941, *Cronquist 2348* (UTC); ca 2 mi W of Big Lost River Bridge along Hwy 20/26, then NW along old paved road 0.7 mi, elev 5100 ft, 6 Jun 1967, *Atwood 881* (BRY); near jct of T-20 and T-17, elev 4900 ft, 14 May 1984, *Moseley 244* (RM); Southeastern base of the Lemhi Range, ca 1.7 mi N of Hwy 22, 1.0 mi NE of jct Hwy 33, elev 5300 ft, *Cholewa & Henderson 587* (RM). Caribou Co., Aspen Range, Middle Sulphur Canyon at W boundary of Caribou National Forest, 5 air mi E of Soda Springs, 15 Jun 1978, *Shultz & Shultz 2573* (UTC). Custer Co., across river from Challis, elev ca 5200 ft, 13 Jun 1944, *Hitchcock & Muhlick 8957* (UTC); Challis Creek, elev 6000 ft, 19 Jul 1916, *Macbride & Payson 3315* (MO, RM, UC); Morgan Creek, 10 mi N of Challis, talus slopes on N side of canyon, 26 Jun 1984, *Atwood 10320* (RM). Fremont Co., Fall River drainage, near Fall River and US 191, elev 5050 ft, 16 May 1972, *Lindsay 995* (BRY). Lemhi Co., in ditch along Hwy 93 beside Salmon River, ca 32 mi N of Challis, 21 Jun 1980, *Hart & Hunter 442* (RM); ca 20 mi N of Challis, to E of Salmon River, 16 Jun 1944, *Hitchcock & Muhlick 9033* (UTC); Salmon Forest, Big Creek, elev 5600 ft, 18 Jun–Jul 1928, *Green 101* (RM); Salmon National Forest, Rams Fork, 1 mi above Allison Ranch, elev 5500 ft, 17 Jun 1928, *White 11* (RM); Salmon National Forest, Salmon River Mtns, 37 mi from Salmon, elev 5500 ft, 27 May 1981, *Goodrich et al. 15485* (BRY); Salmon River, 1/8 mi N of Twelve Miles Creek on rock slides and in rocks on both sides of river, elev 4300 ft, 8 Jul 1953, *Call 826* (UC). Valley Co., alpine slopes of high ridge W of Cascade, Payette National Forest, 7500 ft, *Thompson 13848* (UTC, MO). Washington Co., Weiser, elev 2200 ft, 6 Jul 1899, *Jones 6348* (MO); Cuddy Mts, elev 6000 ft, 11 Jul 1899, *Jones 6350* (MO). Montana: Lewis and Clark Co., at the base of an E facing slope above Hunters Gulch just above the road crossing, elev 4200 ft, 30 Jun 1985, *Lesica 3467* (UC). Ravalli Co., both sides of the W Fork Bitterroot Hwy, 0.5 mi E of the Trapper Peak Job Corps Camp, elev 4130 ft, 9 Jul 1976, *Lackschewitz 6625* (RM). Oregon: Baker Co., Hell's Canyon Dam, 30 mi NE of Halfway, open, rocky cliffs and gravel, elev 1650 ft, 28 Apr 1991, *Brooks s.n.* (OSC); Cornucopia, 27 Jul 1931, *Jones 29053* (MO); Elkhorn Range, Hunt Mtn, montane to subalpine S slope, Pine Creek drainage, elev 5500–7700 ft, 23 Jul 1985, *Joyal 996* (OSC); rocky slopes of Wallowa Mtns, near Cornucopia, 18 Jul 1936, *Thompson 13328* (UC); Wallowa Mtns, NE side of Red Mtn, 8 air km N of Cornucopia, elev 2440 m, 13 Jul 1980, *Holmgren et al. 9608* (UTC). Crook Co., rocks of Camp Creek, Maurey's Mtns, 1 Jul 1901, *Cusick 2627* (MO, UC, RM); Ochoco National Forest, elev 2800 ft, 31 May 1919, *Ingram B-797* (RM); Ochoco Pass, Ochoco National Forest, elev 5000 ft, 10 Jul 1955, *Clarke 25* (UC). Deschutes Co., Deschutes Canyon, vicinity of Radmond, among rocks, 1 May 1921, *Whited 257* (RM). Grant Co., Blue Mountains Experimental Forest, elev 4700 ft, 17 May 1936, *Kauffman 25* (RM); all over N slope of summit, Baldy Mtn, Malheur National Forest, elev ca 7000 ft, 21 Jul 1962, *Kruckeberg 5496* (RM); in W rim of High Lake Basin, elev 8200 ft, 4 Aug 1946, *Maguire & Holmgren 26833* (UC, UTC). Umatilla Co., Umatilla, 28 Jun 1930, *Jones 25259* (MO). Wallowa Co., Wallowa Mtns, near the lake, elev 5000–6000 ft, 23 Aug 1898, *Cusick 2085* (MO, UC); Pacific NW Wallowa, elev 7800 ft, *Reid 756* (RM). Wheeler Co., dry sterile slope, 3 mi N of Mitchell, 5 Jul 1942, *Peck 21576* (OSC). Washington: Asotin Co., mouth of Grand Ronde, 9 May 1925, *John 3518* (MO). Columbia Co., Blue Mtns, below Table Rock, elev 6150 ft, 20 Jul 1935, *Constance et al. 1262* (MO); Tallow Flat, 25 Jun 1913, *Darlington 245* (RM). Spokane Co., 10 mi N of Spokane, Clark Springs, 8 Jul 1902, *Kreagen 119* (UC, UTC). Whitman Co., Wawawai, May 1897, *Elmer 770* (MO, US).

Variety *terebinthina*

UNITED STATES. Oregon: Gilliam Co., 6 mi E of Arlington, N slope, elev 235 ft, 11 May 1940, *Detling 4168* (OSC, UC). Morrow Co., in sand, 0.5 mi E of Boardman, 30 Apr 1950, *Cronquist 6240* (OSC); near Boardman, 14 Jun 1928, *Thompson 4778* (MO). Sherman Co., 3 mi E of Rufus, Columbia River Gorge, elev 300 ft, 29 May 1940, *Constance & Beetle 2688* (RM). Umatilla Co., 1 mi NE of Hermiston, desert, 23 May 1930, *Hills 11* (OSC); 7 mi E of Umatilla, 15 Jun 1937, *Meyer 934* (UC); Umatilla, elev 500 ft, 1 Jun 1905, *Jones s.n.* (MO); Hermiston, in S edge of town, 28 Jun 1919, *Lawrence 2353* (OSC). Washington: Adams Co., on partly stabilized sand dunes, ca 10 mi W of Washtucna, 31 May 1950, *Cronquist 6486* (OSC); sand hills at Sand Dunes State Park, ca 5 mi W of Washtucna, 29 May 1966, *Hitchcock 24479* (UC). Benton Co., on Hwy 14, 0.5 mi N of Plymouth, ca 1 mi N of the Umatilla Bridge, elev 500 ft, 1 Jun 1974, *Denton 3445* (OSC); Paterson, 11 May 1951, *Dana s.n.* (OSC); Horn Rd, observatory turn-off, elev 480 ft, 28 Apr 1984, *Baird 539* (RM); on banks of Columbia River (Umtanum Ridge), elev 400 ft, 18 Jun 1983, *Baird 199* (BRY); Pit 30, between the 200 area, elev 730 ft, 17 May 1993, *McKinnon & Sackschewsky 327* (BRY). Chelan Co., May 1972, *Tiedemann 280* (RM); sagebrush slopes near Wenatchee, 11 Jun 1933, *Thompson 8997* (RM, UC). Ferry Co., sandy hills along Columbia River ca 1 mi N of Hellgate, elev above 1290 ft, 12 Jun 1940, *Rogers 660* (UTC). Franklin Co., 3 mi S of Hanford, 23 May 1944, *Hitchcock & Muhlich 8187* (RM); NE end, near corner of Rd 68 and Dent Rd, elev 530 ft, 9 May 1984, *Baird 690* (BRY); upper Sonoran, 8 mi N of Kahlotus, 7 Jul 1935, *Constance & McMurray 1143* (MO). Grant Co., 0.2 mi S of jct to Royal City on both sides of road, just N of railroad bridge and dam to Wanapum Lake at Beverly, 28 May 1973, *LeDoux & Dunn 957* (UC); 1 mi W of O'Sullivan Dam, on open sandy hills, 12 Jun 1959, *Hitchcock & Muhlick 21870* (UC). Walla Walla Co., Wallula, 5 Apr 1923, *Wareen 3072* (MO); sandy grounds of the Wallawallah River, 1826, *Douglas s.n.* (holotype of *Pteryxia terebinthina* var. *terebinthina*; K). Yakima Co., Falcon Valley, 3 Jun–Jul 1883, *Suksdorf s.n.* (MO); 15 mi N of Centerville, in Rattle-snake Hills, 23 May 1944, *Hitchcock & Muhlick 8201a* (UTC).