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ONE TAXON OR TWO: ARE *FRASERA UMPQUAENSIS* AND *F. FASTIGIATA* (GENTIANACEAE) DISTINCT SPECIES?

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ABSTRACT

Frasera fastigiata and *F. umpquaensis* are large, long-lived, perennial herbs with hollow stems, whorled leaves, large nectaries hidden by fringed hoods, and synchronized flowering. They differ in flower color and their ranges are disjunct. Some authors have treated them as conspecific due to their overall morphological similarity. The taxa can be distinguished by isozyme band patterns and by morphological traits including corolla color, relative lengths of corolla and calyx, and calyx lobe shape. Both isozyme differences and morphological differences are not completely fixed, but plants with one atypical feature can be identified by their combination of traits. The taxa should be recognized as distinct species.

Key Words: Conservation, *Frasera umpquaensis*, isozymes, rare plants.

Frasera umpquaensis M. Peck & Applegate (Peck and Applegate 1941) is a rare plant with a discontinuous range entirely west of the Cascade-Sierra axis from Lane Co., Oregon, to Trinity Co., California (Fig. 1). Young plants produce a rosette of slightly fleshy leaves, surprisingly lush in their upland habitat. After four to ten or more years, the long, thick rhizome puts up a flowering stalk that may exceed 1.7 m in height, bearing dozens of 1.2 cm-long, white to clear light green flowers that may have a purple tinge. Each of the four petal lobes bears a single large nectary surrounded and partly concealed by a fringed hood. Additional hairs arise below the nectaries, between the filaments. Flowering tends to be synchronized, with almost no plants over a large area flowering in some years and many flowering in other years. After fruiting, the plant returns to the rosette stage for four or more years. An individual plant may live for decades (Kaye 2001).

Frasera umpquaensis belongs to a group of four species characterized by this unusual life history, including synchronized flowering, and by tall, hollow stems and whorled leaves (Post 1958). The other three species are *F. caroliniensis* Walter of eastern North America, and the western species *F. speciosa* Douglas ex Griseb. and *F. fastigiata* (Pursh) A. Heller. *Frasera caroliniensis* and *F. speciosa* have more open inflorescences with larger, rotate, white or greenish corollas speckled with purple or brown. *Frasera speciosa* is unique in this group in having two nectaries on each petal and large, fringed scales (the corona) that originate below the nectaries and partially cover them (Beattie et al. 1973). *Frasera umpquaensis* and *F. fastigiata* have denser inflorescences with smaller, usually solid-colored flowers that do not open flat, and their corona is represented by a row of long hairs below the nectary, originating between the bases of the filaments (Table 1). *Frasera fastigiata* grows in Idaho and southeast Washington, while *F. umpquaensis* lives in southwest Oregon and northwest California (Fig. 1).

Frasera umpquaensis was said to differ from *F. fastigiata* in the corona hairs, the length and shape of the calyx lobes, and the corolla lobe width and apex shape (Card 1931; Peck and Applegate 1941; St. John 1941). Pringle (1990) stated that *F. fastigiata* can have corona hairs and implied that earlier illustrations omitting them (Card 1931) were in error, attributed the supposed calyx lobe differences to diverse interpretations of the words "lanceolate" and "linear" by different botanists, and dismissed supposed differences in corolla apex shape as variable within *Frasera* species. He summarized, "comparison of specimens from California identified as ... *F. umpquaensis* with specimens from the Blue Mountains of Oregon and from Idaho identified as ... *F. fastigiata* disclosed no differences by which the two taxa could be distinguished" (Pringle 1990, p. 186).

Pringle's (1990) rejection of *F. umpquaensis* species status had an air of finality, but botanists working with the plants were not satisfied. The color difference, the difference in average inflorescence size, and the 500-km disjunction between their ranges suggested that they were genetically

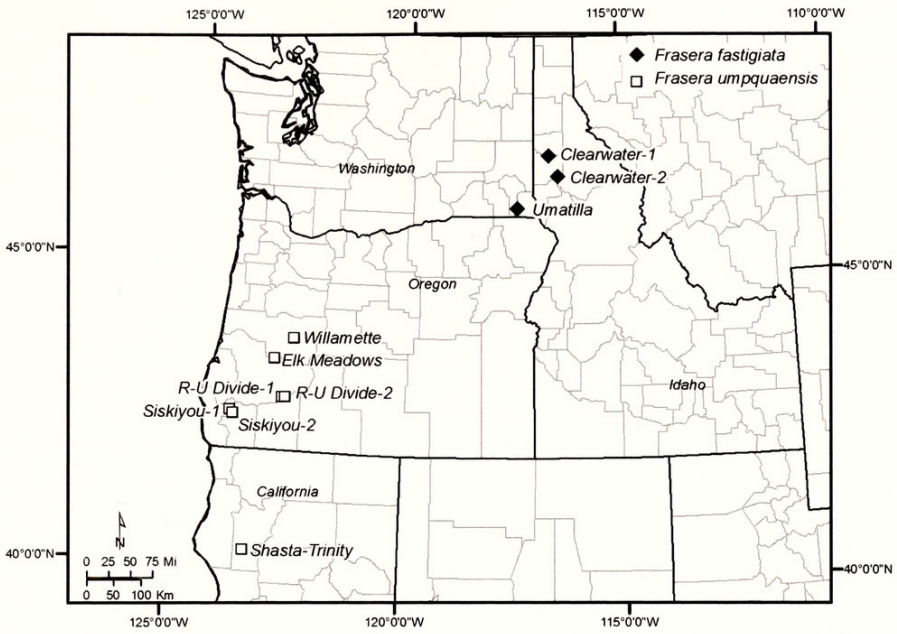

FIG. 1. Locations of populations of *Frasera fastigiata* and *F. umpquaensis* sampled for the isozyme study.

distinct and therefore should be treated as two species.

We report results of isozyme analysis and morphological studies of *F. umpquaensis* and *F. fastigiata* with the goal of clarifying their taxonomic status. We consistently use the name *F. umpquaensis* for the white to green-flowered plants of southwest Oregon and northern California, and *F. fastigiata* for the blue-flowered plants of Idaho and southeast Washington.

MATERIALS AND METHODS

Chromosomes

In October 2008, the somatic chromosome number of *Frasera umpquaensis* was determined by observation of mitosis in root tips of plants that had been grown at the Oregon State University greenhouse from seed collected in 2007 near the Elk Camp shelter, near Sourgrass Mountain in the Willamette National Forest, Lane Co., Oregon, at 4500 ft elevation. Excised root tips were pretreated in a saturated aqueous solution of p-dichlorobenzene at 4°C for 5 hr prior to fixation in Carnoy's fluid (95% ethyl alcohol and glacial acetic acid, 3:1 v:v). The root tips were hydrolyzed in a mixture of concentrated HCl and 95% ethanol (1:1 v:v) for 5–15 min, macerated in acetocarmine, and mounted with a small amount of Hoyer's solution (Beeks 1955). A Zeiss Photoscope III microscope equipped with phase-contrast optics was used to determine chromosome numbers in cells undergoing mitosis.

Isozymes

In the summer of 1996, two to five leaves per plant were collected from 75 individuals in three populations of *Frasera fastigiata* and 178 individuals in seven populations of *F. umpquaensis* (Table 2; Fig. 1). Leaf samples were shipped on ice to the National Forest Genetic Electrophoresis Laboratory (NFGEL). For each individual, three 7 mm diam. leaf discs were placed in a Tris buffer pH 7.5 (Gottlieb 1981) and stored at −70°C. On the morning of the run, samples were thawed, macerated, and absorbed onto 3 mm wide wicks prepared from Whatman 3MM chromatography paper.

Methods of electrophoresis follow the general methodology of Conkle et al. (1982) except that most enzyme stains are somewhat modified as outlined in USDA Forest Service (1995). A lithium borate electrode buffer (pH 8.3) was used with a Tris citrate gel buffer, pH 8.3 (Conkle et al. 1982), to resolve alcohol dehydrogynase (ADH), leucine aminopeptidase (LAP), phosphoglucomutase (PGM), and phosphoglucose isomerase (PGI). A sodium borate electrode buffer (pH 8.0) was used with a Tris citrate gel buffer, pH 8.8 (Conkle et al. 1982), to resolve catalase (CAT), glutamate-oxaloacetate transaminase (GOT), triosephosphate isomerase (TPI), and uridine diphosphoglucose pyrophosphorylase (UGPP).A morpholine citrate electrode and gel buffer, pH 8.0 (USDA Forest Service 1995), was used to resolve diaphorase (DIA), florescent esterate (FEST), isocitrate dehydrogenase (IDH), and malate dehydrogenase (MDH). A Tris citrate electrode and gel buffer, pH 7.2 (USDA Forest Service 1995), was used to resolve phosphogluconate dehydrogenase (6PGD). All enzymes were resolved on 11% starch gels. Enzyme stain recipes follow USDA Forest Service (1995) except that GOT was stained using the recipe from Wendel and Weeden (1989). Two people independently scored each gel. When they disagreed, a third

TABLE 1. SELECTED MORPHOLOGICAL TRAITS OF THE FOUR SPECIES OF *FRASERA* WITH HOLLOW STEMS AND WHORLED LEAVES.

Trait	*F. umpquaensis*	*F. fastigiata*	*F. speciosa*	*F. caroliniensis*
Calyx lobes, at and after anthesis	longer than corolla lobes	shorter than corolla lobes	longer than corolla lobes	longer than corolla lobs
Calyx lobes, shape	usually linear or widest above the base, occasionally subulate	usually subulate (at least some calyx lobes on all plants subulate)	usually linear, or broadly subulate	lanceolate (sometimes to subulate)
Corolla color	white or light green, sometimes purple-tinged	deep blue to light purple, rarely white, occasionally spotted	white or light green with purple spots	white or light green with purple or brown spots
Corolla lobes, at anthesis	angled; corolla nearly campanulate	angled; corolla nearly campanulate	flat; corolla rotate	flat; corolla rotate
Corona	several long hairs	several, few, or no long hairs	scale(s) with several long hairs	short hairs
Nectaries	1 per corolla lobe	1 per corolla lobe	2 per corolla lobe	1 per corolla lobe
Filament length	3–4 mm	2.3–3.3 mm	6.5–8.5 mm	7–8 mm

person resolved the conflict. For quality control, 10% of the individuals were run and scored twice.

Two zones, designated 1 (faster) and 2 (slower), were resolved for each of the enzymes DIA, GOT, MDH, PGI, and TPI for a total of 18 enzyme systems.

Because the limited information available (Post 1958) suggested that these species might be hexaploid and there are no crossing studies to determine the inheritance of isozymes in *Frasera*, we were unable to provide a genetic interpretation for the complicated band patterns observed on the isozyme gels. Gels were therefore scored for (1) banding pattern, and (2) band presence/absence. This type of data results in a phenotypic (band pattern and presence) instead of genotypic (alleles and loci) analysis. The band pattern data were used to calculate the average phenotypic identities between pairs of populations using Hedrick's measure of phenotypic identity (Hedrick 1971).

Diversity measures within populations were calculated by several methods (after Chung et. al. 1991): (1) the number of bands found in each population, (2) percentage of the enzymes that yield more than one band pattern among individuals in a population, (3) the average number of band patterns per stain in a population, (4) the polymorphic index (PI), based on the frequency of occurrence of each band, and (5) the Shannon-Weaver Diversity Index (Shannon 1948) based on band pattern frequency.

Ordination was performed in the R statistical environment (R Development Core Team 2008). A simple pair-wise distance matrix was constructed from isozyme phenotypes using the function dist.gene from the R package 'ape' (Paradis et al. 2004). Kruskal's non-metric multidimensional scaling (NMS) was performed on the matrix of pair-wise distances using the R function isoMDS. In order to facilitate NMDS, zeros in the pair-wise distance matrix were replaced with the arbitrarily small value of 0.0001.

Morphology

We examined 27 sheets of *F. umpquaensis* representing 16 distinct collections and 137 sheets of *F. fastigiata* representing 105 distinct collections, from HSC, ID, ORE, OSC, UC, WILLU, and WTU (Appendix 1). Selected flowers were soaked in water and opened to observe the corona. Other traits we examined included flower color (when it could be determined from the label or dried material), number of leaves in each whorl, inflorescence width, relative length of calyx and corolla, lengths of filaments and petals, and length, width, and shape of calyx lobes. To examine the relationship between the two taxa with morphometric information, we used NMS as implemented in PC-ORD (McCune and

TABLE 2. *FRASERA UMPQUAENSIS* AND *F. FASTIGIATA* POPULATIONS USED IN THE ISOZYME STUDY. The *F. umpquaensis* populations are listed from north to south. NF = National Forest; BLM = Bureau of Land Management; RNA = Research Natural Area. TRS (township, range, and section) for Oregon and Washington are based on the Willamette Meridian; for Idaho, the Boise Meridian; and for California, the Humboldt Meridian. n = sample size.

Population	State	Location	T	R	S	n
F. fastigiata						
Clearwater-1	ID	Clearwater NF; Giant White Pine Campground	42N	3W	2	25
Clearwater-2	ID	Clearwater NF; Little Boulder Creek	39N	1W	33	25
Umatilla	WA	Umatilla NF; Asotin Creek	08N	43E	28	25
F. umpquaensis						
Willamette	OR	Willamette NF; Nevergo Creek	19S	3E	31	25
Elk Meadows	OR	Eugene District, BLM; Upper Elk Meadows RNA	23S	2W	35	25
R-U Divide-1	OR	Umpqua NF; Rogue-Umpqua divide	31S	1E	10	25
R-U Divide-2	OR	Rogue River NF; Rogue-Umpqua divide	31S	2E	8	27
Siskiyou-1	OR	Siskiyou NF; Bear Camp, Galice Ranger District	34S	10W	12	26
Siskiyou-2	OR	Medford BLM; Hobsen Horn Gravel Pit	34S	9W	34	25
Shasta-Trinity	CA	Shasta-Trinity NF; Fern Campground	1S	7E	36	25

Mefford 2006). Non-metric multidimensional scaling searches iteratively for an ordination with low stress, a measure of the relationship between ranked distances in multidimensional space to the ranked distances in the reduced ordination (Peterson and McCune 2001). The following quantitative traits were used: inflorescence width, filament length, length and width of the longer calyx lobe, difference in length between two adjacent sepals, petal length, and difference in length between petal and longer sepal. In addition, the qualitative trait of flower color was scored 1 = blue, 0 = non-blue (white or green). We used a random seed with 250 runs of real data to ensure the ordination had low stress. Monte Carlo simulations with 250 iterations were used to assess the probability that final stress could have been obtained by chance. A stability criterion of 0.0001 was used. Student's t-tests were performed in Microsoft Excel (Microsoft Corportation 2003) to test for significance of differences between the two taxa in sepal length and width, petal length, inflorescence width, and the difference between petal length and sepal length.

RESULTS

Chromosomes

In 2008, counts of 78 chromosomes in each of 4 root tip cells undergoing mitosis confirmed that *F. umpquaensis* was polyploid and, because the base chromosome number in *Frasera* is 13 (Rork 1949), presumably hexaploid.

Isozymes

Frasera isozymes produced the variable, often complicated band patterns expected of polyploids. Tentative genetic interpretations could be developed only for the simpler band patterns, biasing genetic analysis against the more variable enzymes (MDH-2, PGI-1, TPI-1, and UGPP; Appendix 2) that most clearly distinguished the two taxa. Therefore, analyzing the isozyme patterns phenotypically, as patterns and bands, was more appropriate than genetic analysis for these *Frasera* species (Chung et al. 1991).

Most populations of *Frasera fastigiata* and *F. umpquaensis* were moderately to highly variable with 40–60% polymorphic loci (Table 3). The Willamette and Shasta-Trinity populations, isolated at the northern and southern ends of the *F. umpquaensis* range, respectively, were the least variable. In the Shasta-Trinity population all but two stains were monomorphic.

Although no fixed isozyme differences distinguished *F. fastigiata* from *F. umpquaensis*, overlap was slight in certain enzymes (e.g., MDH and PGI-1) and restricted to the Shasta-Trinity population in one enzyme (TPI-1). In general, Hedrick's measure of phenotypic similarity had high values for within-taxon comparisons and low values for between-taxon comparisons (Table 4). The NMS ordination based on the band patterns in individual plants resulted in two clusters corresponding to the two species (Fig. 2).

The geographically isolated Shasta-Trinity population of *F. umpquaensis* was relatively dissimilar to other *F. umpquaensis* populations (Table 4). When *F. umpquaensis* and *F. fastigiata* differed at an enzyme for which the Shasta-Trinity population was monomorphic, the Shasta-Trinity population shared its band pattern with other *F. umpquaensis* populations (e.g., for MDH, PGI-1, and PGM; Appendix 2). However, at one of its two variable enzymes (TPI-1), the Shasta-Trinity population had band patterns

TABLE 3. MEASURES OF PHENOTYPIC VARIATION IN ISOZYMES FOR TEN POPULATIONS OF TWO SPECIES OF *FRASERA*. The *F. umpquaensis* populations are listed from north to south.

Population	Sample size per stain	Bands	% polymorphic stains	Band patterns/stain (mean)	Polymorphic index	Shannon-Weaver diversity index
F. fastigiata	73.8					
F. fastigiata mean (SE)	24.6 (0.04)	44 (0.70)	53.7 (0.49)	2.13 (0.13)	3.87 (0.136)	0.4403 (0.008)
Clearwater-1	24.4	44	44.4	2.06 (0.38)	4.8932	0.4386
Clearwater-2	24.4	38	55.6	1.94 (0.25)	2.5920	0.3709
Umatilla	25.0	50	61.1	2.39 (0.39)	4.1248	0.5115
F. umpquaensis	177.6					
F. umpquaensis mean (SE)	25.4 (0.06)	41.3 (0.412)	39.7 (0.62)	1.83 (0.12	2.9207 (0.11)	0.3448 (0.012)
Willamette	25.0	39	27.8	1.39 (0.16)	1.9488	0.2184
Elk Meadows	24.9	47	55.6	2.33 (0.48)	4.6252	0.4978
R-U Divide-1	24.9	45	50.0	2.06 (0.33)	3.8592	0.4438
R-U Divide-2	27.0	47	55.6	2.28 (0.42)	4.7107	0.5415
Siskiyou-1	25.9	38	44.4	1.67 (0.20)	1.5136	0.2414
Siskiyou-2	24.9	41	33.3	1.89 (0.34)	2.7252	0.3513
Shasta-Trinity	25.0	32	11.1	1.22 (0.15)	1.0624	0.1195

otherwise observed only in the *F. fastigiata* populations. At the other (CAT), 60% of the individuals had a unique band pattern that seemed attributable to a unique allele. Therefore, Hedrick's distances indicate that the Shasta-Trinity population was as different from the northern *F. umpquaensis* population as from *F. fastigiata* populations (Table 4).

Morphology

Some traits reported to distinguish *F. umpquaensis* from *F. fastigiata* failed to separate the taxa consistently, but others were effective (Tables 5 and 6). Corona hairs were sometimes difficult to assess on herbarium specimens because chipping into the dried flowers often broke them, while soaking the flowers rendered them nearly transparent. The hairs often stuck to the fringed membrane that surrounds the nectary, and freeing them intact was difficult. Corona hairs were numerous and easy to see in all 19 *F. umpquaensis* flowers examined for them (Table 5). These hairs were also numerous in 18 of the 20 *F. fastigiata* specimens examined for them, but were often hard to see even when they were numerous. They were absent or sparse in flowers of two *F. fastigiata* specimens, varying among flowers in one inflorescence in one specimen (*Sondenaa 327*).

In *F. umpquaensis*, calyx lobes were longer than the mature corolla lobes (Table 5); in *F. fastigiata* they were shorter, and the difference was statistically significant (Table 6). However, in one of the 93 *F. fastigiata* specimens examined for this trait, *Bjork 7727*, the calyx lobes were clearly longer than the corolla on many of the mature flowers. Relative calyx length was often difficult to assess because the calyx lobes were longer than the corolla in bud, in both species. After anthesis the corolla lobes withered and folded, making comparisons of length misleading unless the flower was soaked and the corolla lobes unfolded.

In general, the two species were differentiated by calyx lobe shape (Table 5) and length (Tables 6). In *F. umpquaensis*, calyx lobes were usually linear (uniform in width) at least in the proximal half or lanceolate (widest above the base), though some were subulate (widest at the base and tapering uniformly to the tip). In *F. fastigiata*, all calyx lobes in most inflorescences and some calyx lobes in all inflorescences were clearly subulate. In both species, the two pairs of calyx lobes were sometimes found to differ in shape and/or length. Calyx lobes were significantly longer in *F. umpquaensis* than in *F. fastigiata* and corolla lobes were signficantly longer in *F. fastigiata*, although the the range of variation in these traits overlapped between the two species (Table 6).

TABLE 4. HEDRICK'S MEASURE OF SIMILARITY AMONG ISOZYME BAND PATTERN FREQUENCIES IN TEN POPULATIONS OF *FRASERA*. A value of 1.0 indicates identical variation in a population pair.

Species	Population	Clearwater-1	Clearwater-2	Umatilla	Willamette	Elk Meadow	R-U Divide-1	R-U Divide-2	Siskiyou-1	Siskiyou-2
F. fastigata	Clearwater-1									
F. fastigata	Clearwater-2	0.894								
F. fastigata	Umatilla	0.723	0.747							
F. umpquaensis	Willamette	0.492	0.455	0.480						
F. umpquaensis	Elk Meadow	0.450	0.402	0.431	0.672					
F. umpquaensis	R-U Divide-1	0.573	0.533	0.497	0.767	0.781				
F. umpquaensis	R-U Divide-2	0.399	0.367	0.374	0.629	0.688	0.771			
F. umpquaensis	Siskiyou-1	0.621	0.673	0.576	0.766	0.702	0.774	0.680		
F. umpquaensis	Siskiyou-2	0.575	0.522	0.521	0.657	0.722	0.872	0.724	0.773	
F. umpquaensis	Shasta-Trinity	0.644	0.606	0.584	0.685	0.574	0.712	0.553	0.700	0.870

Flower color was difficult to assess on herbarium specimens because corollas in many older specimens of both species faded to tan. Flower color was not reported on the labels of the 16 *F. umpquaensis* specimens examined. Field workers report that the flowers are white to greenish, often lightly tinged with purple (Thomas Kaye personal observation; Jennifer Lippert, Willamette Natl. Forest, personal communication). Flower color was pale and greenish on the more recently collected herbarium specimens. Labels of the 21 *F. fastigiata* specimens that mentioned flower color reported it to be blue (including pale blue and "fairly deep blue"), purple, or lavender. Corollas of the more recent dried herbarium specimens varied from deep gentian blue to light purplish blue, with few exceptions (Table 5). One sheet (*Richards 116*) consisted of a shoot with blue corollas speckled with darker blue, and two shoots with pale flowers that may have been white in life. Flowers on several *F. fastigiata* specimens had inconspicuous darker speckles on blue corollas, and on a few sheets the speckles were relatively conspicuous (e.g., *Constance 1771*, *Williams & Goff 16*, and *Wilson 241*).

Nonmetric multidimensional scaling based on multiple morphometric traits produced a final stress of 6.188 and usually separated *Frasera fastigiata* from *F. umpquaensis* (Fig. 3). The two *F. fastigiata* that overlapped the cluster of *F. umpquaensis* were *Bjork 7727* which had sepals up to 2.3 mm longer than the petals, and the pale-flowered individual in *Richards 116*. Despite these anomalies, *Bjork 7727* could easily be assigned to *F. fastigiata* because of its blue flowers, subulate calyx lobes, and two cauline leaves per whorl. The pale-flowered plants in *Richards 116* had blue speckles and mostly subulate calyx lobes that were shorter than or barely longer than the corollas. Those traits, plus its occurrence in a population with blue flowered-plants, would lead to its correct identification.

DISCUSSION

Frasera umpquaensis and *F. fastigiata* are more similar to each other morphologically than they are to any other species, but they are not the same. Isozymes consistently distinguished the two taxa, although differences were not completely fixed (Fig. 2). The two taxa could be distinguished morphologically as well (Fig. 3), but as was true for isozymes, the differences were not completely fixed. Despite these occasional inconsistencies, all specimens could be easily identified to taxon when all traits were taken together. For example, a specimen that had an unexpected calyx length was typical of its taxon for other traits.

The past confusion over the differences between these taxa results in part from using

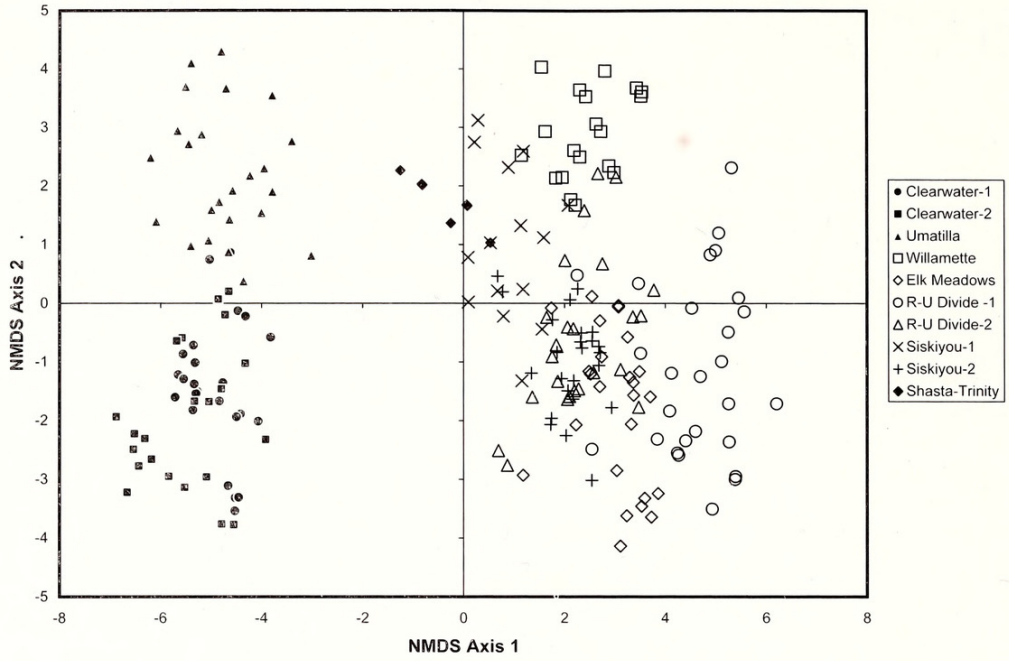

FIG. 2. Non-metric multidimentional scaling of isozyme band patterns in individual samples of *Frasera fastigiata* (dark symbols) and *F. umpquaensis* (open and shaded symbols).

unreliable traits (Peck and Applegate 1941; St. John 1941; Pringle 1990). Corona hairs do help differentiate the *umpquaensis-fastigiata* species pair from *F. speciosa*, which has fringed, membranous corona scales, and from *F. caroliniensis*, which has very short hairs (Table 1), but corona hairs are variable within *F. fastigiata* and hard to assess in both that species and *F. umpquaensis*. Corolla tip shape, too, is variable and hard to assess. Although calyx lobe shape tends to differentiate *F. fastigiata* from *F. umpquaensis*, it may vary even within an inflorescence.

When the appropriate traits are evaluated, *F. umpquaensis* and *F. fastigiata* are readily distinguished (Tables 5 and 6). *Frasera umpquaensis* has white to green flowers, calyx lobes that surpass the corolla, and usually longer, linear to lanceolate calyx lobes. In general, *F. fastigiata* has blue flowers, calyx lobes that are exceeded by the corolla (at anthesis), and shorter, subulate calyx lobes. Some *F. fastigiata* plants resemble *F. umpquaensis* in one of these traits, but not in all of them. In both species, calyx lobe shape may vary within the inflorescence.

Both isozyme variation and morphology indicate that these two taxa are genetically distinct. Their geographic separation suggests that the differences between the two will only become greater due to reproductive isolation. Because of this evidence, *Frasera umpquaensis* and *F. fastigiata* should be recognized as separate species.

TABLE 5. COMPARISON OF QUALITATIVE TRAITS OBSERVED IN *FRASERA UMPQUAENSIS* AND *F. FASTIGIATA*.

Trait	*F. fastigiata*	*F. umpquaensis*
Corolla color		
Sample size	n = 62	n = 15
Blue	62	0
Pale	1	15
Corolla lobes		
Sample size	n = 96	n = 16
>sepals	95	0
=sepals	5	0
<sepals	1	16
Calyx lobes widest		
Sample size	n = 44	n = 9
Base	44	2
Above	0	9
Mixed	4	2
Calyx lobe shape		
Sample Size	n = 21	n = 15
Lanceolate & linear	7	15
Subulate	19	1
Corona Hairs		
Sample size	n = 19	n = 9
0 to few	18	9
Many	1	0

Key to the Four Species of *Frasera* with Whorled Leaves and Wide, Hollow Stems

1. Corolla rotate, opening flat; filaments 6.5–8.5 mm long; petals white or green with purple-brown spots
   2. Nectary pit 1 on each corolla lobe; corona consisting of short hairs between the filament bases; range in eastern North America . . . . . *F. caroliniensis*
   2′ Nectary pits 2 on each corolla lobe; corona consisting of 1+ scale(s) with several long

TABLE 6. COMPARISON OF QUANITATIVE TRAITS OBSERVED IN *FRASERA UMPQUAENSIS* AND *F. FASTIGIATA*. For each species, trait values for the mean, standard deviation, standard error and range are provided. Values from the t-test of differences between means and the P-value are provided in the final two columns.

	Frasera fastigiata					*Frasera umpquaensis*						
	n	mean	SD	SE	range	n	mean	SD	SE	range	t	P
Leaves/whorl												
Top whorl	45	2.89	0.53	0.08	2–4	15	3.4	0.51	0.13	3–4	−3.34	0.00264
2nd whorl	40	2.85	0.48	0.08	2–4	10	3.3	0.48	0.15	3–4	−2.63	0.01960
Inflorescence width (cm)	46	5.27	1.12	0.16	3.5–9	15	3.6	1.04	0.27	2.1–5.5	5.11	0.00000
Filament length (mm)	22	2.91	0.53	0.11	1.8–4	15	2.86	0.57	0.15	1.7–3.9	0.28	0.77906
Calyx length (mm)	42	8.44	1.84	0.28	4.4–12.8	30	10.08	1.57	0.29	7.3–14.2	−3.97	0.00017
Calyx width (mm)	42	1.35	0.40	0.06	0.7–2.2	30	1.53	0.40	0.07	0.9–2.3	−1.92	0.05860
Corolla length (mm)	21	9.94	1.46	0.32	6.7–13.4	15	8.29	1.37	0.35	5.3–10.8	3.43	0.00160
Calyx L–Corolla L (mm)	21	−1.50	1.30	0.28	−4.8–0.95	15	1.79	1.10	0.28	0.55–4.9	−7.97	0.00000

hairs between the filament bases; range in western North America . . . . . *F. speciosa*

1′ Corolla +/− campanulate, not opening flat; filaments 1.7–4 mm long; petals blue, white, or green, usually unspotted or inconspicuously spotted
3. Corollas usually pale to dark blue or purple; calyx lobes usually subulate, usually shorter than the corolla lobes (when corolla lobes fully expanded); inflorescence width 3.5–9 cm wide; range in Idaho and SE Washington . . . . . *F. fastigiata*

3′ Corollas white to green, sometimes purple-tinged; calyx lobes usually linear to lanceolate, longer than the corolla lobes; inflorescence 2.1–5.5 cm wide; range SW Oregon to NW California . . . . *F. umpquaensis*

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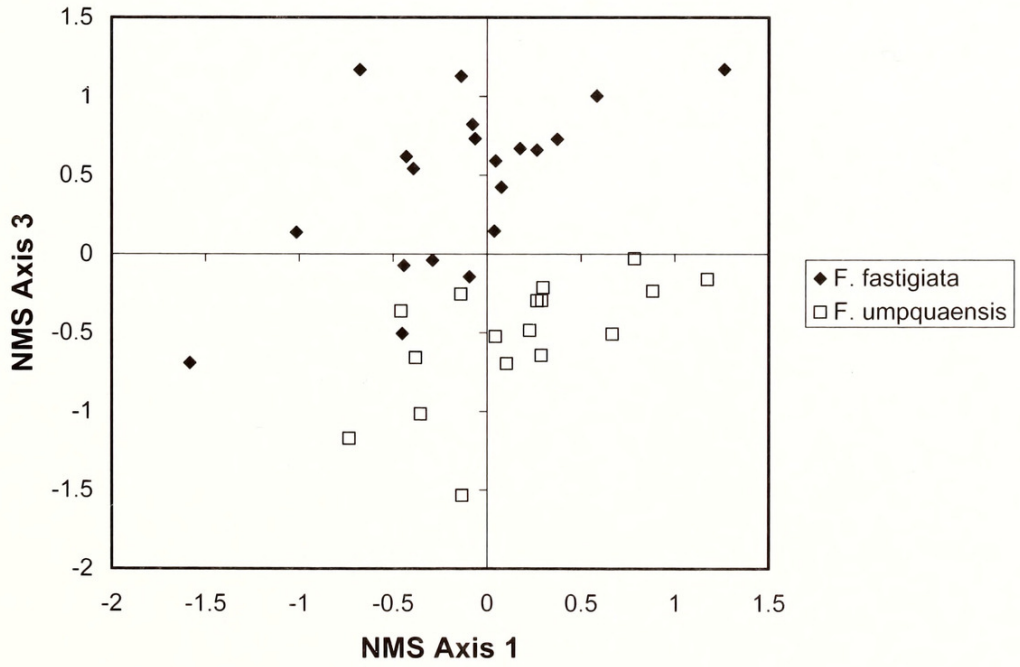

FIG. 3. Non-metric Multidimensional Scaling (NMS) of selected morphological traits in 17 specimens of *Frasera umpquaensis* and 20 specimens of *F. fastigiata*. Axes 1 and 3 explained the most variation in morphological traits.

Literature Cited

Beattie, A. J., D. E. Breedlove, and P. R. Ehrlich. 1973. The ecology of the pollinators and predators of *Frasera speciosa*. Ecology 54:81–91.

Beeks, R. M. 1955. Improvements in the squash technique for plant chromosomes. El Aliso 13:131–134.

Card, H. H. 1931. A revision of the genus *Frasera*. Annals of the Missouri Botanical Garden 18: 245–283.

Chung, M. G., J. L. Hamrick, S. B. Jones, and G. S. Derda. 1991. Isozyme variation within and among populations of *Hosta* (Liliaceae) in Korea. Systematic Botany 16:667–684.

Conkle, M. T., P. D. Hodgskiss, L. B. Nunnally, and S. C. Hunter. 1982. Starch gel electrophoresis of conifer seeds: a laboratory manual. USDA Forest Service General Technical Report PSW-64. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA.

Gottlieb, L. D. 1981. Gene number in species of Asteraceae that have different chromosome numbers. Proceedings of the National Academy of Sciences USA 78:3726–3729.

Hedrick, P. W. 1971. A new approach to measuring genetic similarity. Evolution 25:176–280.

Kaye, T. 2001. *Frasera umpquaensis* population monitoring plan, Medford District BLM: progress report. Unpublished report available at the Institute for Applied Ecology, 4550 SW Jefferson, Corvallis, OR.

McCune, B. and M. J. Mefford. 2006. PC-ORD. Multivariate Analysis of Ecological Data. Version 5. MjM Software, Gleneden Beach, OR.

Microsoft Corportation. 2003, Microsoft Office Excel 2003 (11.6355–6360) SP1.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Peck, M. E. and E. I. Applegate. 1941. A new *Frasera* from Oregon. Madroño 6:12.

Peterson, E. B. and B. McCune. 2001. Diversity and succession of epiphytic macrolichen communities in low elevation managed conifer forests in western Oregon. Journal of Vegetation Science 12:511–524.

Post, D. M. 1958. Studies in Gentianaceae. I. Nodal anatomy of *Frasera* and *Swertia perennis*. Botanical Gazette 120:1–14.

Pringle, J. S. 1990. Taxonomic notes on western American Gentianaceae. Sida 14:179–187.

R Development Core Team. 2008, R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Website http://www.r-project.org [accessed 09 July 2010].

Rork, C. L. 1949. Cytological studies in the Gentianaceae. American Journal of Botany 36:687–701.

Shannon, C. E. 1948. A mathematical theory of communication. Bell System Technical Journal 27:379–423, 623–656.

St. John, H. 1941. Revision of the genus *Swertia* (Gentianaceae) of the Americas and the reduction of *Frasera*. American Midland Naturalist 26:1–29.

USDA Forest Service. 1995, National forest genetic rlectrophoresis laboratory standard operating procedures. NFGEL, USDA Forest Service, Placerville, CA.

Wendel, J. F. and N. F. Weeden. 1989. Visualization and interpretation of plant isozymes. Pp. 5–45 *in* D. E. Soltis and P. S. Soltis, (eds.), Isozymes in plant biology. Dioscorides Press, Portland, OR.

Appendix 1

Specimens Examined

Specimens are from the herbaria of Humboldt State University (HSC), Oregon State University (OSC), Shasta-Trinity National Forest (S-T NF), University of California (UC), University of Idaho (ID), University of Oregon (ORE, at OSC), University of Washington (WTU), Willamette University (WILLU, at OSC). * = measured for morphological study.

Frasera fastigiata: IDAHO. **Benewah Co.**: slopes of Plummer Butte southeast of Plummer, 17 May 1961, *Baker 16101* (ID); Lolo Creek Road, 47°13.345′ 116°50.734′, 10 June 2003, *Brunsfeld 2659* (ID); Mary Minerva McCroskey Memorial State Park, near park entrance, T43N R4W S30, 47°3′31.18″ 116°51′57.46″, 1 June 2004, *Brunsfeld 2974* (ID); Mary Minerva McCroskey Memorial State Park, ca. 1.5 mi W of park entrance, 47°3′37.06″ 117°59′36.960″, 1 June 2004, *Brunsfeld 3023* (ID); St. Joe National Forest, upper slopes of St. Joe Baldy in vicinity of saddle between St. Joe Baldy and Reed's Baldy, on ridge running to top of St. Joe Baldy from the saddle., 30 June 1996, *Fox 656* (ID); summit of Moose Mtns., 19 June 1927, *Jones 607* (WTU); near Chatcolet, 12 May 1928, *Warren 893* (WTU). **Clearwater Co.**: Elk Butte Summit and Lookout, 11 July 2002, *Brunsfeld 2191* (ID); Elk Butte south face, near summit, 27 July 1976, *Cavanaugh 20* (ID); Freemon Creek, Brown's Creek meadows, 28 July 1929, *Cook s.n.* (WTU); Weipe, 22 June 1937, *Davis 271-37* (WTU); 8 mi NE of Dent, along the north fork of the Clearwater River, 3 May 1941, *Weber 2115* (WTU). **Idaho Co.**: 9 mi W of Grangeville, 22 June 1937, *Christ 7715* (ID); 10.0 mi S of Grangerville on Nez Perce NF Road 4649, headwaters of N Fk White Bird Creek, W side of road at edge of forest near base of road embankment, T29N R3E S34, 29 July 1989, *Ertter 8822* (UC); Nezperce National Forest, Wild Horse Corral, 25 July 1952, *Evanko ABE-19* (ID); ca. 10 mi S of Sweet Water, along highway, 1 July 1949, *Hitchcock 19162* (UC, WTU); ½ mi SW of Whitebird Summit, T29N R2E S5, 19 June 1950, *Jones 79* (WTU); Nez Perce National Forest, 12 mi S of Grangeville along the Grangeville-Salmon Road #221, near Cayuse Meadows, T29N R3E S34 SE 1/4, 16 June 1995, *Sondenaa 135* (ID); Nez Perce Naitonal Forest, Pinnacle Ridge. 14.8 mi S of Grangeville on FS Rd 221, then 4.4 mi W of FS Rd 1870, T28N R3E S7 SW 1/4, 21 June 1996, *Sondenaa 327* (ID*). **Kootenai Co.**: Mica Peak area, Clearwater Bioregion, about 5.5 mi N of Setters, lower south slopes of Mica Peak, occasional along Bozard Creek Road, 47°33′ 117°2′, 4 June 2003, *Bjork 7727* (ID*); Coer d'Alene, 30 May 1928, *Christ 92* (ID*); (no location), July 1891, *Leiberg 213* (UC); (nono location), 1890, *Leiberg 217* (ORE); (no location), July 1891, *Leiberg s.n.* (ORE). **Latah Co.**: Paradise Hills, April 1900, *Abrams 611* (UC); 8 mi E of Moscow on Troy road, 2 June 1960, *Aller s.n.* (ID*); on slope Near Paradise Creek, Moscow Mtns., about 6 mi NE of Moscow, 16 June 1951, *Bacon s.n.* (WTU); NE of Moscow, 22 June 1939, *Baker 1235* (ID); Thatana Hills, Moscow Mountain, 24 June 1939, *Baker 1301* (ID);

Moscow Mountain, 2 July 1939, *Baker 1372* (ID); along the Troy Road 4 mi E of Moscow, 14 May 1949, *Baker 5847* (ID); slope above Gnat Creek, about 4 mi NE of Moscow, 13 May 1952, *Baker 8875* (ID*, UC, WTU); east slope of Tomer's Butte, 5 mi SE of Moscow, 15 May 1952, *Baker 8885* (ID, WTU); along Skyline Drive, 2 mi W of Highway 95 junction, T43N R4W S13, 9 June 1960, *Baker 15881* (ID*); Moscow Mt., 5 mi NE of Moscow, 22 June 1960, *Baker 15954* (ID); Moscow Mts., 12 May 1906, *Botany Class s.n.* (ID); St. Joe National Forest, north side of Moscow Mountain between Rock Creek and Hatter Creek, T47N R4W S21, 30 May 2002, *Brunsfeld 2002* (ID); south slope of Moscow Mountain, 5 mi NE of Moscow, 19 June 1950, *Chichester 149* (ID); Crumarine Creek, 5 mi NE of Moscow, 23 June 1950, *Chichester 288* (ID); north slope of Moscow Mountain, 5 mi NE of Moscow, 26 June 1950, *Chichester 476* (ID); south slope and banks of Crumarine Creek, 13 May 1954, *Chichester 880* (ID*); Crumarin Ridge, S of East Twin, Palouse Range, 18 June 1954, *Chichester 984* (ID); Crumarine creek Drainage at base of Moscow Mountain (Palouse Range), 17 June 1954, *Chichester 1111* (ID); Shatuna [?] Ridge, 1 June 1937, *Daubenmire 37285* (WTU); north slope NW of The Twins, 12 June 1936, *Dillon 587* (UC, WTU); Cedar Mt., 20 May 1916, *F. L. P. 411* (WTU); Moscow, July 1915, *Gail s.n.* (ID*); Moscow Mt., Moscow, 1916, *Gail s.n.* (ID); Moscow, 1930, *Gail s.n.* (ID); ca. 1 mi S of Deary on Highway 3 (2290 State Hwy 3), farm on east side of highway, west side of patch of small woods ca. 1/4 mi from residence and buildings, 46°47.030′ 116°33.5′, 20 May 2003, *Hill 286* (ID); 3 mi S of Thorp, 27 May 1944, *Hitchcock 8395* (WTU); southern base of Moscow Mountain, 7 May 1954, *Johnson 34* (ID); intersection of Randall Flat Rd. and Beulah Rd. approx. 2 mi N of the junction of Randall Flat Rd. and Hwy. 8., *Jonassen 19* (WTU); on Gold Hill N of Potlatch; USGS Potlatch Quadrangle 15 min series, T42N R4W S21 SE 1/4 SE 1/4 SE 1/4, 10 May 1976, *McMahon 31* (WTU); along northeastern slopes of Tomer's Butte, 2.5 mi SE of Moscow, T38N R5W S23, 23 July 1955, *Nisbet 86* (ID); 1/4 mi E of Robinson Lake, T39N R4W S6, 5 May 1958, Moscow Mt., 3 May 1930, *Nyberg s.n.* (WTU); *Oppe 68* (ID); above Big Meadow and Big Meadow Creek, N of Troy (3.4 mi up road from picnic area, 1.7 mi up from holding pond), T40N R4W S14, 3 July 2002, *Parks 49* (ID*); (no location), 16 July 1893, *Piper 1618* (ORE, UC, WTU); (no location), 16 July 1893, *Piper s.n.* (ORE); Moscow, 26 April 1895, *Ransom s.n.* (ID); summit of Bald Mountain, 17 July 1955, *Richards 116* (ID*); Moscow Mt., 6 June 1925, *Ridout s.n.* (WTU); Moscow Mts., 28 April 1906, *Simpson s.n.* (ID); Cedar Mt., 5 June 1921, *St. John 6036* (UC, WTU); Lunch Bucket Ridge, T40N R1W S36 SW 1/4, 13 June 1972, *Wagner 48* (ORE); near Viola, Moscow Mts., 1 June 1924, *Warren 874* (WTU); along trail to ridgetop to Three Tree Butte, 9 June 1974, *Wellner 167* (ID). **Lewis Co.**: S of Grangerville, 18 June 1939, *Baker 1188* (ID*); 1 mi S of Forest, IDD, on Merek Rd., 6 June 2002, *Brunsfeld 2031* (ID); along Forest Road, 1.1 mi N of Forest, T33N R3W S36 NW corner, 16 August 2002, *Parks 135* (ID). **Nezperce Co.**: 2 mi S of Zaza, 9 October 1927, *Hardin 377* (WTU); about Lake Waha, 24 June 1896, *Heller 3285* (UC); Benton Meadows, Craig Mountain, ca. 6.5 mi S of Waha, T32N R4W S15 NE 1/4, 5 June 1993, *Mancuso 900* (ID); top of Winchester grade, 6 June 1951, *Torrell 78* (ID). **ShoshoneCo.**: north slope, Freezeout Saddle, 14 mi E of Clarkia, 20 July 1958, *Baker 15359* (ID); Freezout Saddle, St. Joe National Forest, 14 mi E of Clarkia, 5 July 1963, *Baker 16429* (ID*); 12 mi W of Clarkia, 1 July 1961, *Daubenmire 6114* (WTU); on Freezout Rd ca. 1 mi beyond Freezout Saddle at junction with first rd. to right, along ridgeline to N & E, along E-W portion of ridgeline, T42N R3E S1 NE 1/4, 8 July 1996, *Fox 702* (ID); Squaw Springs, 17 June 1969, *Swalley s.n.* (ID); vicinity of Windy Peak, 18 July 1941, *Wilson 241* (UC, WTU). **Undetermined Co.**: Elk River, 19 June 1927, *Gail s.n.* (ID); Ingham's Mt., 12 June 1892, *Lake s.n.* (WTU); Strohm Canyon, 26 May 1957, *Laughlin 168* (ID); Carder Ranch, River Hill, 23 May 1912, *Rust 42* (ID); Viola Grade, 18 May 1927, *Williams s.n.* (ID). WASHINGTON. **Asotin Co.**: S of Anatone, 2 June 1950, *Baker 6738* (ID, WTU); along summit of Blue Mountains, overlooking Indian Tom Creek, 30 mi SW of Asotin, T7N R43E S1, 25 June 1949, *Cronquist 5902* (ID, UC*, WTU); Blue Mountains, S of Smyth Rd., W of Washington 129, about 2 mi (air) SW of Anatone, 46°6′ 117°9′, 30 May 1998, *Fishbein 3392* (ID,WTU*); 2 mi W of Anatone, 15 May 1926, *Gissell s.n.* (WTU); Petty Ridge, 15 mi SW of Asotin, T8N R44E S20, 10 June 1959, *Hitchcock 21832* (WTU); near Anatone, 21 May 1922, *St. John 9757* (WTU). **Columbia Co.**: foothills of Blue Mountains between Godman Guard Station and Dayton, 2 August 1950, *Kruckeberg 2537* (WTU); Stockade Springs, 7/6 1927, *St. John 8288* (WTU). **Garfield Co.**: Powell Camp, near Clearwater Ranger Stateion, Blue Mountains, T9N R42E S, 14 June 1936, *Constance 1771* (WTU*); Umatilla National Forest, intersection of Forest Road 40 and Forest Road 4022, 27 June 1997, *Williams 16* (OSC, WTU*). **Spokane Co.**: (no location), 5 June 1889, *Suksdorf 938* (UC); Latah Creek, 28 July 1916, *Suksdorf 8965* (WTU). **Whitman Co.**: Kamiack Butte, June 1897, *Elmer 802* (UC, WTU); Kamiack Butte, 12 June 1952, *King 52-100* (WTU*); near top of Kamiak Butte in dense woods, 28 May 1922, *Parker 406* (OSC, WTU); along ridge, Kamiak Butte, 21 May 1921, *St. John 5887* (WTU). **Undetermined Co.**: Palouse, 15 July 1892, *Henderson s.n.* (WTU); Palouse country, July 1880, *Marsh s.n.* (WTU), UNDETERMINED STATE. Santianne Creek Bottom, 27 July 1895, *Leiberg 1064* (ORE, UC).

Frasera umpquaensis: CALIFORNIA. **Trinity Co.**: near Pickett Peak, close to the town of Mad River, 40°20′52.39″ 123°22′2.7″, 16 July 1979, *Clifton 7842* (HSC*); near Pickett Peak, 40°20′58″ 123°22′8″, 28 June 1980, *Copeland 293* (HSC*); near Pickett Peak, 40°20′58″ 123°22′8″, 28 June 1980, *Copeland 294* (HSC*); Hayfork Ranger District, Picket Peak Lookout Road, T1S R7E S7 (Humboldt Meridian), 19 July 2001, *Erwin 1099* (S-T NF*); north slopes of Pickett Peak, South Fork Mountain, T1S R7E S27 (Humboldt Meridian), 9 July 1971, *Sawyer 2416* (HSC*). OREGON: **Curry Co.**: Bear Camp summit, T34S R10W S12, 16 July 1979, *Hess, R. s.n.* (OSC*). **Douglas Co.**: Upper Elk Meadows, 32 km SSE of Cottage Grove, T23S R2W S35 SE 1/4, 25 July 1979, *Christy, J. 2529* (ORE*); Umpqua National Forest, Rogue-Umpqua Divide; below Bald Ridge, T31S R1E S2, 30 June 1979, *Fosback, J. s.n.* (OSC*); Huckleberry Gap Glades, 5 August 1924, *Ingram, D. 1507* (ORE*,OSC); Rogue-Umpqua Divide 22 mi W of Crater Lake, 31 July 1916, *Peck, M. 4497* (WILLU*); alpine slopes of Abbott Butte, Rogue River Nat. Forest, 2 July 1936, *Thompson, J. 13067* (WILLU*, WTU*). **Jackson Co.**: near

Anderson Camp, Rogue-Umpqua Divide, upper waters of Rogue River, northeastern Jackson County, 11 July 1929, *Applegate, E. 5930* (UC*, WILLU); mainly on the Umpqua drainage (W) side of the Rogue-Umpqua Divide, 1 mi NE of Butler Butte, Rogue River Nat'l Forest, 28 June 1950, *Kruckeberg 2010* (UC,WTU); Woodruff Meadows, 5 July 1925, *Pendleton, R. s.n.* (OSC*). **Undetermined Co.**: along drainage of the east fork of Abbot Creek, ca. 20 mi W of Crater Lake, near Abbott Butte; to the SE of Elephant Head at 5100 ft, 6 July 1972, *Mitchell 215* (OSC*); along drainages of the E fork of Abbott Creek, ca. 20 mi W of Crater Lake, near Abbott Butte, 42°56′ 122°31′, 27 July 1972, *Mitchell 299* (OSC*).

APPENDIX 2. ISOZYME BAND PATTERN FREQUENCIES IN POPULATIONS OF *FRASERA UMPQUAENSIS and F. FASTIGIATA*. See Methods for enzyme abbreviations.

		F. fastigiata			*F. umpquaensis*						
Enzyme	Pattern	Clearwater-1	Clearwater-2	Umatilla	Willamette	Elk Meadows	R-U Divide-1	R-U Divide-2	Siskiyou-1	Siskiyou-2	Shasta-Trinity
6PGD	A	1.000	0.960	0.960	1.000	0.240	1.000	1.000	1.000	0.960	1.000
6PGD	B		0.040								
6PGD	C					0.480					
6PGD	D			0.040		0.280					
6PGD	F									0.040	
ADH	A	1.000	1.000	0.840	1.000	0.875	0.840	1.000	1.000	1.000	1.000
ADH	C					0.125	0.160				
ADH	D			0.160							
CAT	A	0.360	0.240	0.120	1.000	1.000	0.760	0.778	0.846	1.000	0.080
CAT	B						0.120				0.320
CAT	C	0.240	0.120	0.240			0.120	0.222	0.115		
CAT	D			0.120					0.039		
CAT	E	0.320	0.480	0.480							
CAT	F	0.080	0.160	0.040							
CAT	J										0.600
DIA-1	A	1.000	1.000	1.000	0.400	1.000	1.000	0.111	1.000	1.000	1.000
DIA-1	B				0.080						
DIA-1	C							0.519			
DIA-1	D							0.370			
DIA-1	E				0.520						
DIA-2	A	0.889	1.000	0.680	1.000	0.261	1.000	0.593	0.391	1.000	1.000
DIA-2	B			0.120		0.739		0.407	0.609		
DIA-2	C	0.111		0.200							
FEST	A	1.000	0.920	0.720	0.400	1.000	1.000	0.667	0.731	1.000	1.000
FEST	B			0.200	0.600			0.333	0.269		
FEST	C		0.040	0.040							
FEST	D		0.040	0.040							
GOT-1		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GOT-2	A				1.000	0.360	0.480	0.482		0.042	
GOT-2	B	0.680	0.960	0.040			0.480	0.222	0.846	0.500	1.000
GOT-2	C	0.160		0.880			0.040	0.148	0.077	0.291	
GOT-2	D	0.160	0.040	0.080		0.280			0.077	0.083	
GOT-2	E					0.080				0.042	
GOT-2	F					0.280		0.148			
GOT-2	G									0.042	
IDH	A	1.000	1.000	0.760	1.000	1.000	1.000	1.000	1.000	1.000	1.000
IDH	B			0.240							
LAP	A					0.960	0.880	1.000		0.920	
LAP	B	1.000	0.880	0.960	0.280	0.040			0.923	0.040	1.000
LAP	C		0.120	0.040	0.720		0.120		0.077	0.040	
MDH-1		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

APPENDIX 2. CONTINUED.

Enzyme	Pattern	*F. fastigiata*			*F. umpquaensis*						
		Clearwater-1	Clearwater-2	Umatilla	Willamette	Elk Meadows	R-U Divide-1	R-U Divide-2	Siskiyou-1	Siskiyou-2	Shasta-Trinity
MDH-2	A				1.000	1.000	0.680	0.963	1.000	0.400	1.000
MDH-2	B	0.120	0.200	1.000							
MDH-2	C	0.680	0.760							0.040	
MDH-2	D	0.080									
MDH-2	E						0.240	0.037		0.440	
MDH-2	F						0.040			0.120	
MDH-2	G	0.120	0.040				0.040				
PGI-1	A				0.800	0.880	1.000	1.000	1.000	1.000	1.000
PGI-1	B	0.120	0.280	0.440							
PGI-1	C	0.800	0.240	0.200							
PGI-1	D	0.080	0.360	0.360							
PGI-1	E		0.120			0.120					
PGI-1	G				0.200						
PGI-2	A	1.000	1.000	1.000	1.000	1.000	0.800	0.037	0.885	0.600	1.000
PGI-2	B							0.704	0.038	0.040	
PGI-2	C						0.200	0.259	0.077	0.360	
PGM	A				1.000		0.417	0.222	0.923		1.000
PGM	B	1.000	0.920	0.040				0.074			
PGM	C		0.080								
PGM	D			0.520							
PGM	E			0.160							
PGM	F			0.120		0.040					
PGM	G			0.040		0.120	0.083	0.037		1.000	
PGM	H					0.360		0.037			
PGM	I			0.040							
PGM	J							0.037			
PGM	N			0.080							
PGM	O					0.440		0.074			
PGM	P						0.500				
PGM	S					0.040		0.482	0.077		
PGM	T							0.037			
TPI-1	A	0.120	0.600	1.000							0.200
TPI-1	B	0.160	0.360								
TPI-1	C	0.040									
TPI-1	D	0.040									
TPI-1	E	0.200									
TPI-1	F	0.200	0.040								0.480
TPI-1	G	0.240									
TPI-1	H				1.000	0.960	1.000	1.000	1.000	1.000	0.320
TPI-1	I					0.040					
TPI-2	A	0.720	0.280	1.000	1.000	0.640	0.440	0.222	1.000	0.600	1.000

APPENDIX 2. CONTINUED.

		F. fastigiata			*F. umpquaensis*						
Enzyme	Pattern	Clearwater-1	Clearwater-2	Umatilla	Willamette	Elk Meadows	R-U Divide-1	R-U Divide-2	Siskiyou-1	Siskiyou-2	Shasta-Trinity
TPI-2	B					0.320	0.440	0.630		0.120	
TPI-2	C					0.040	0.120	0.148		0.280	
TPI-2	D	0.280	0.720								
UGPP	A	0.760	1.000	0.640			0.160				
UGPP	B				0.400	0.040					
UGPP	C				0.560	0.320	0.320		0.039	0.120	
UGPP	D				0.040	0.120	0.080				
UGPP	E			0.200		0.040	0.040	0.296	0.807	0.440	1.000
UGPP	F					0.080	0.360	0.371	0.154	0.440	
UGPP	G							0.074			
UGPP	H					0.080		0.259			
UGPP	I						0.040				
UGPP	J	0.240									
UGPP	K					0.160					
UGPP	L			0.160		0.120					
UGPP	M					0.040					