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The phylogenetics and systematics of *Physaria kingii* (Brassicaceae)

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University of Northern Iowa

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THE PHYLOGENETICS AND SYSTEMATICS OF *PHYSARIA KINGII*
(BRASSICACEAE)

An Abstract of a Thesis

Submitted

in Partial Fulfillment

of the Requirements of the Degree

Master of Science

Jamie Minnaert-Grote

University of Northern Iowa

December 2014

ABSTRACT

The subspecies of *Physaria kingii* (S. Watson) O’Kane and Al-Shehbaz (Brassicaceae) have historically been a difficult group to delimit taxonomically based on morphology, geography, and ecology. The taxa have been moved between genera as well among varieties, subspecies, and full species many times over. This study addressed the systematics relationships of the subspecies of *P. kingii* using a combination of molecular (both nuclear and chloroplast DNA sequences), morphological, geographical, and ecological data. Three non-coding DNA regions were chosen: the internal transcribed spacer (ITS) region of nuclear ribosomal DNA and the chloroplast *rps* intron and the chloroplast *ndhC-trnV* intergenic spacer. Eighty-seven aligned sequences in total were selected and networks were constructed using SplitsTree for exploratory data analyses to identify any genealogical discordance for each of the regions in addition to a combined chloroplast region. With the prior knowledge of possible hybridization among *P. k.* subsp. *kaibabensis*, *P. k.* subsp. *wardii* (formerly included within *P. k.* subsp. *latifolia*), along with other taxa in the genus found on the Kaibab Plateau, *P. arizonica*, and *P. purpurea*, three networks for the ITS region were included to attempt to identify if hybridization is involved and, if so, to determine the maternal taxa. Additionally, Bayesian analyses were completed using each of the regions in addition to combining the chloroplast sequences. The nuclear and chloroplast regions produced statistically different results, so were not combined. The subspecies were not monophyletic and will remain as subspecies of *P. kingii*. There was a single taxonomic change, separating *P. wardii* from *P. kingii* subsp. *latifolia* and moving *P. wardii* to a subsp. of *P. kingii*.

Additionally, this dataset identified a possible relationship between *P. kingii* and *P. occidentalis* that suggested the *P. occidentalis* subspecies should be included under *P. kingii*. A more inclusive study will need to be done before determining this.

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This Study by: Jamie Minnaert-Grote

Entitled: The Phylogenetics and Systematics of *Physaria kingii* (Brassicaceae)

has been approved as meeting the thesis requirement for the

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DEDICATION

This is dedicated to my children Riana, Sydney, and Ainsley, the three most important people in my life and who constantly remind me that easier is not always better.

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CHAPTER 1

INTRODUCTION

This project addresses the relationships among the subspecies of *Physaria kingii* (S. Watson) O’Kane and Al-Shehbaz (Brassicaceae). There are currently seven recognized subspecies:

- *P. kingii* subsp. *kingii*
- *P. kingii* subsp. *bernardina* (Munz) O’Kane and Al-Shehbaz
- *P. kingii* subsp. *cobrensis* (Rollins and E.A. Shaw) O’Kane and Al-Shehbaz
- *P. kingii* subsp. *diversifolia* (Greene) O’Kane and Al-Shehbaz
- *P. kingii* subsp. *kaibabensis* (Rollins) O’Kane
- *P. kingii* subsp. *latifolia* (A. Nelson) O’Kane and Al-Shehbaz
- *P. kingii* subsp. *utahensis* (Rydberg) O’Kane.

Payson (1922) regarded this assemblage, which he characterized as the *utahensis* group, as “taxonomically the most perplexing group of them all” within the genus. Further, he noted that they seem to represent a “plexus of evolution”, implying that they are in a condition of change and not yet fully differentiated from one another. Similarly, Rollins and Shaw (1973) called this group the “most complex and taxonomically difficult species in the genus” and discuss the variability within the taxa and populations. Finally, O’Kane (2010) described these subspecies as making up a highly variable species that needs further molecular analysis.

Taxonomy and Systematic History

The attempt to delimit these taxa using morphological characters has been a turbulent journey with some of the taxa moving between genera as well as many moving among varieties, subspecies, and full species many times over. Beginning in 1885, S. Watson discovered and described the species *Vesicaria kingii* S. Watson, found in the West Humboldt Mountains in Nevada. A few years after discovering *V. kingii*, Watson (1888) distinguished *Lesquerella*, named for the paleontologist and bryologist Leo Lesquereux, from *Vesicaria* due to distinct character differences between the Old World and New World taxa. The American species have a distinct nerve that runs from the apex of the fruit to at least mid-septum. In addition, flowers are usually yellow, there are never solitary ovules, the trichomes are either stellate or lepidote, and the filaments are never toothed or appendaged. At the time, 52 *Lesquerella* species were recognized. Rollins and Shaw (1973) found that the original *V. kingii* specimens cited by Watson included representatives from two other species, *L. occidentalis* S. Watson and *L. wardii* S. Watson, but indicate that Watson later refined his concept of *L. kingii* to include only those that were first collected in Pershing Co., Nevada. This initial glimpse illustrates the tangled history that this group followed in the next 125 years.

Over the next 95 years, many new species were described and added to *Lesquerella*. Among these were *L. diversifolia* Green, which was discovered in the Wallow Mountains in Oregon and described by Green (1901) as “an exceedingly well marked species”. Maguire and Holmgren (1951) moved the species to *L. occidentalis* subsp. *diversifolia*

(Green) Maguire and Holmgren. Noting the resemblance, Rollins and Shaw (1973) combined *L. kingii* var. *sherwoodii* (M. Peck) C.L. Hitchcock, and *L. occidentalis* var. *diversifolia* (Green) C.L. Hitchcock into *L. kingii* subsp. *diversifolia* (Green) Rollins and E.A. Shaw, pointing out that this taxon is often confused with *L. occidentalis*. Peck (1934) first described *L. k.* var. *sherwoodii* as *L. sherwoodii* Peck. Later, Hitchcock and Cronquist (1964) reclassified this as a variety of *L. occidentalis*. He differentiated three *L. occidentalis* varieties, though he acknowledged that they appear to be “little more than growth forms”. Rollins and Shaw (1973) mention that *L. k.* subsp. *diversifolia* is closely related to *L. kingii* but have smaller fruits, shorter styles, more variability in leaf forms, and the two are geographically isolated.

Just two years after *L. k.* subsp. *diversifolia* was named, Rydberg (1903) described *L. utahensis* Rydberg remarking that there was some relation to *L. wardii*, sharing the same pubescence and habit. In their updated description of this taxon, Rollins and Shaw (1973) indicated that *L. utahensis* is closely related to *L. multiceps* Maguire, *L. wardii*, and *L. garetti* Payson. Welsh et al. (2003) also noted the similarities of this taxon to *L. wardii*, though they observed that the ranges are not overlapping, a common occurrence within this entire group as many are endemic to small regions.

L. latifolia Nelson, was first described in 1906 by Nelson. The holotype, collected in Meadow Valley Wash in southern Nevada, was considered *L. montana* (A. Gray) S. Watson by the collector, however Nelson disagreed, saying that geographically and morphologically it was unrelated, making it a new species. Rollins and Shaw (1973)

combined three taxa into *L. kingii* subsp. *latifolia* Rollins and E.A. Shaw: *L. latifolia*, *L. barnebyi* Maguire, and *L. occidentalis* subsp. *cusickii* (M.E. Jones) Maguire and Holmgren var. *parvifolia* Maguire and Holmgren. *L. barnebyi* was discovered by Ripley and Barneby in 1944 and described by Maguire (1950). He noted that this (*L. barnebyi*) was closely related to *L. utahensis* and *L. kingii* and that all three had variable pod shapes throughout their populations. Rollins and Shaw (1973) argued that while populations do differ from one another to some degree and they had been geographically isolated from one another for a substantial period of time, these were just populations within one species. The plants all had subglobose to elliptic fruits, glabrous inner valves, and 4–8 ovules per locule. To illustrate the plasticity of this group, Rollins and Shaw (1973) noted that the number of ovules per locule vary on a single plant and the fruit shape could vary within populations. It was also noted that certain populations resembled *L. wardii*. Welsh and Reveal (1977) moved *L. occidentalis* var. *parvifolia* Maguire and Holmgren to *L. kingii* var. *parvifolia* (Maguire and Holmgren) S.L. Welsh and Reveal, indicating that these were sometimes indistinguishable from *L. wardii*, but noting that the fruits differ apically: *L. wardii* was compressed and var. *parvifolia* was rounded. Watson (1888) first described *L. wardii* as a new species from the Aquarius Plateau of Utah. Rollins and Shaw (1973) noted that while the populations of *L. wardii* were homogenous within, compared to one another they showed significant divergence. They indicated that this was likely due to the populations being geographically isolated from one another. They also recognized that *L. kingii* and *L. utahensis* were likely closely related to *L. wardii*.

Welsh et al. (2003) mentioned that *P. kingii* var. *parvifolia* was most similar to *P. wardii* except in fruit shape.

In 1932, Munz 1932 described *L. bernardina* Munz, found in the San Bernardino Mountains near Bear Lake. Munz characterized this species as nearest to *L. kingii* and indicated that these taxa had been misidentified as *L. kingii* several times. Munz (1958) later changed this taxon to a subspecies of *L. kingii*.

It was forty additional years after *L. k.* subsp. *latifolia* was discovered before Rollins and Shaw (1973) described *L. kingii* var. *cobrensis* Rollins and E.A. Shaw from Elko County. They observed that the fruits were similar to *L. kingii* but differ in the geographic location, the recurved pedicels rather than sigmoid, and elliptic basal leaves rather than suborbicular.

The last of the taxa in this group, *L. kaibabensis* Rollins, was described by Rollins in 1982. He noted the similarities between *L. wardii* and *L. kaibabensis* suggesting they were closely related; however, he also found marked differences in the trichomes, fruits, and styles.

A closely linked species, *L. occidentalis* was first described as *Vesicaria occidentalis* Watson in (Watson) 1885 and was later moved to *Lesquerella* (Watson 1888). Rollins and Shaw (1973) believed that when Watson was reviewing these taxa he had little material to compare, thus he was uncertain about the taxonomic limits between *L. occidentalis*, *L. kingii*, and *L. douglassii* S. Watson. They also noticed that *L. occidentalis* had often been misidentified as *L. kingii* and *L. diversifolia*. In 1973, Rollins and Shaw

named two subspecies of this taxon, subsp. *occidentalis* and subsp. *cinerascens* (Maguire and A.H. Holmgren) Rollins and E.A. Shaw. They also indicated that while many populations differed from one another, differences were due to either edaphic conditions (California, Oregon) or geographic isolation (Idaho). *L. o.* subsp. *cinerascens* was sometimes confused with *L. utahensis* and *L. montana*, however, this taxon is compressed along the repleum where the others are not (Rollins and Shaw 1973).

In 2002, Al-Shehbaz and O’Kane merged *Lesquerella* with *Physaria* (Nuttall ex Torrey and A. Gray) A. Gray. Previous authors had voiced the belief that there were many morphological similarities between the two genera, including but not limited to leaf morphology, trichome type, and inflorescence (Al-Shehbaz and O’Kane 2002). O’Kane and Al-Shehbaz argued that morphological, molecular, ecological, and geographical data support the merger. Thus, they unified the two genera to make a single monophyletic genus. In addition, multiple taxa were moved to subspecific level including *P. k.* subsp. *bernardina*, *P. k.* subsp. *cobrensis*, *P. k.* subsp. *diversifolia*, and *P. k.* subsp. *latifolia*.

Holmgren (2004) raised *P. cobrensis* to species level and renamed *L. kaibabensis* as *P. kaibabensis*. B.L Turner (2004) subsequently moved *P. cobrensis* to a variety level of *P. kingii*, doing the same with *diversifolia* and *bernardina*. Finally, in 2007, O’Kane moved *kaibabensis* and *utahensis* to a subspecies of *P. kingii*. In addition, he combined *L. kingii* var. *parvifolia* and *P. wardii* into one taxon called *L. kingii* subsp. *latifolia*.

Morphology

Physaria consists of herbaceous annuals, biennials, and perennials. Most species are rosulate with silvery foliage, are generally pubescent with sessile stellate trichomes, and have flower petals that are commonly yellow, sometimes orange, and rarely white or purple. The fruits are silicles with valves that are typically pubescent outside, rarely pubescent inside, and have typically been important in the circumscription of *Physaria* (Rollins 1993; O’Kane 2010).

The *Physaria kingii* assemblage is comprised of small densely pubescent rosulate perennials. The trichomes have 3–7 rays that are bifurcate, doubly bifurcate, or 3-partite and can be either sessile or shortly stalked. The basal leaves are sub-orbicular, elliptic, or rhombic and can be entire, widened at the base, slightly lobed and sometimes sinuate. Cauline leaves are generally elliptic to nearly linear. These taxa have typical Brassicaceae flowers: actinomorphic bisexual flowers that are cruciform in shape, with clawed petals and tetradynamous stamens. The petals are yellow, cream-white, white or rarely purple and have fruits that are ellipsoid, obovoid or subglobose and apically rounded-acute or truncate. The valves are densely pubescent on the exterior and either pubescent or glabrous on the interior (Rollins and Shaw 1973; Holmgren 2005; O’Kane 2010).

As in most of *Physaria*, the fruits have historically been an important morphological feature used in identification. Though widely used in delineation, fruit and seed characteristics can be difficult to use as relationship indicators within the Brassicaceae family (O’Kane et al. 1996; Crespo et al. 2000; Koch and Al-Shehbaz 2000; Warwick

and Sauder 2005). Trichome morphology, however, correlates very well with phylogenetic data (Khalik 2005; Beilstein et al. 2006). Al-Shehbaz and O’Kane (2002) described *Physaria* trichomes as strictly stellate to stellate-peltate and nearly always tuberculate. They found that the presence or absence of trichomes on the inner valves, a feature found in some of the *P. kingii* subspecies, was mostly likely not an important distinguishing feature as they can vary within a population. However, they noted that within this genus it has been found to be a stable quality so may be a useful key character. As the fruits within this group are variable, it is yet unclear if they are valid relationship indicators.

Geographical Distribution and Ecology

While the Brassicaceae family has a worldwide distribution, the genus *Physaria* is largely found in North America with a few exceptions: one species extending into boreal Greenland and Russia and six South American species (O’Kane and Al-Shehbaz 2004; Al-Shehbaz et al. 2005; Al-Shehbaz and Prina 2009). Payson (1922) suggested that the origin of *Physaria* (*Lesquerella*) was likely in central Texas where the species then radiated outward in all directions. He explained that this was credible because Texas had the greatest concentration of *Physaria* species and greatest number of taxa with the largest amount of “primitive” characteristics. Payson also indicated that the ancestral species were likely calciphytes like so many in the modern genus.

The subspecies of *P. kingii* are found in the western United States in mostly arid montane habitats in calcareous, rocky soils that are often limestone- or dolomite-derived. (Rollins and Shaw 1973; O’Kane 2010; USDA FS 2014). O’Kane (2010) acknowledges

that the subspecies are geographically coherent with some overlapping ranges. The species range from California and Oregon to Utah and Arizona. With the current delineation of subspecies, four of the seven subspecies are endemic to geographically limited regions. *P. kingii* subsp. *diversifolia* (Figure 1) is found only in a small mountain range, the Wallowa Mountains, in northeastern Oregon. This taxon is geographically isolated from any other *P. kingii* subspecies but has overlapping ranges with *P. occidentalis* (Rollins and Shaw 1973; O’Kane 2010).

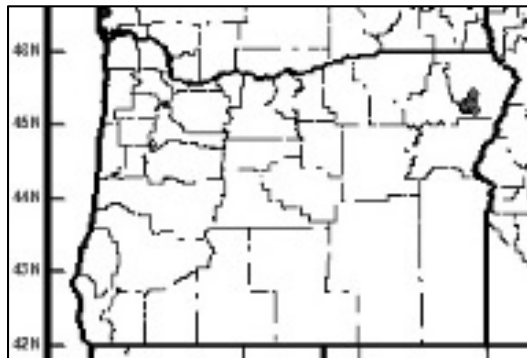


Figure 1. Map of *Physaria kingii* subsp. *diversifolia* individuals.

Similarly, *P. k.* subsp. *utahensis* (Figure 2) is an endemic found in Northern Utah in the Wasatch and Uintah Mountain ranges (Rollins and Shaw 1973; O’Kane 2010). The range picks up in northern Utah where *P. k.* subsp. *latifolia* ends (Holmgren 2005); however, *P. k.* subsp. *utahensis* does not have a range that overlaps with any other *P. kingii* subspecies.

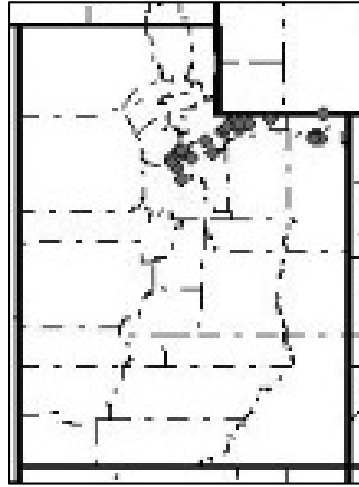


Figure 2. Map of *Physaria kingii* subsp. *utahensis* individuals.

Physaria kingii subsp. *bernardina* (Figure 3) is also geographically isolated from the others and being limited to San Bernardino Mountains near Bear Lake in southern California (Rollins and Shaw 1973; O’Kane 2010). In 1994 (USDA Forest Service 2014), *P. k.* subsp. *bernardina* was listed as endangered and added to the endangered species list. A draft recovery plan was made in 1997 (USFWS) for this and four other species endemic to the carbonate outcrops found in the region, but the plan has not moved past the draft stage. The draft recovery plan cited limestone mining, road construction, and deposit of mine overburden as the chief threats.

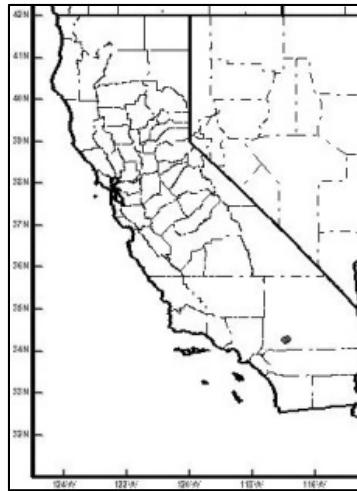


Figure 3. Map of *Physaria kingii* subsp. *bernardina* individuals.

The Kaibab Plateau in northern Arizona is the location of the final endemic subspecies, *P. k.* subspecies *kaibabensis* (Figure 4). O’Kane (2010, personal communication) suggests possible hybridization events with *P. k.* subsp. *latifolia*, and possibly *P. arizonica* or *P. purpurea*, two nearby *Physaria* species. This taxon is under review for protection under the Endangered Species Act. A petition was filed to list this along with 454 southwestern species as endangered or threatened with critical habitat in 2009. The Department of the Interior found that 67 of those species, including *P. k.* subsp. *kaibabensis*, warranted further study. The study is currently ongoing (USFWS 2014).

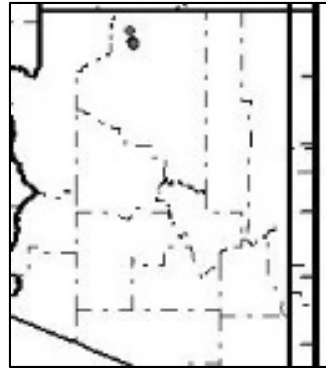


Figure 4. Map of *Physaria kingii* subsp. *kaibabensis* individuals.

The last three *P. kingii* subspecies have wider geographic ranges. *Physaria kingii* subsp. *kingii* (Figure 5) is found in California, Idaho, Nevada, and Oregon. *Physaria kingii* subsp. *latifolia* (Figure 7) is found in Arizona, California, Nevada, and Utah. Finally, *P. k.* subsp. *cobrensis* (Figure 6) is found throughout Nevada and in southern Idaho and possibly southeastern Oregon. These three taxa do have overlapping ranges, though *P. k.* subsp. *cobrensis* is found at lower elevations than the other two subspecies (Rollins and Shaw 1973; O’Kane 2010). Before being combined into *P. k.* subsp. *latifolia*, *P. wardii* (Figure 8) was considered geographically distinct by elevation, found only in high elevations in Utah (Rollins and Shaw 1973).

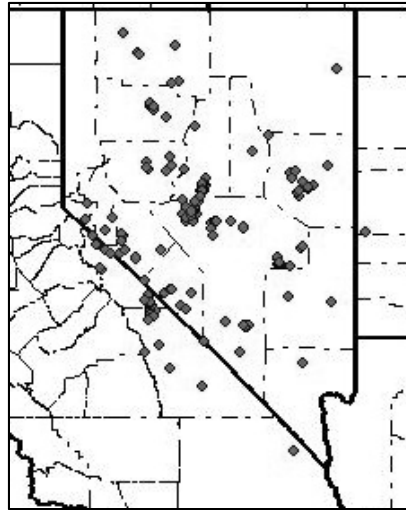


Figure 5. Map of *Physaria kingii* subsp. *kingii* individuals.

The related species, *P. occidentalis* subsp. *occidentalis*, has a wide range, growing in much of the western United States (Washington, Oregon, Idaho, California, and Nevada), whereas *P. o.* subsp. *cinerascens* is found only in Nevada and Utah. These overlap many of the *P. kingii* subspecies geographic ranges. Additionally, they grow in similar substrate, rocky calcareous soils (O’Kane 2010).

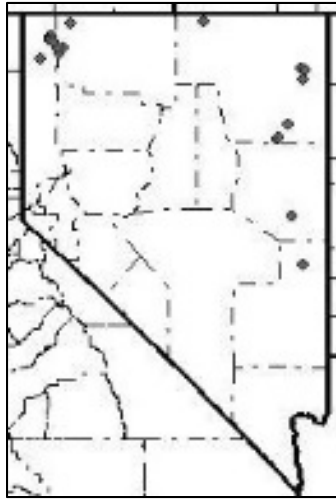


Figure 6. Map of *Physaria kingii* subsp. *cobrensis* individuals.

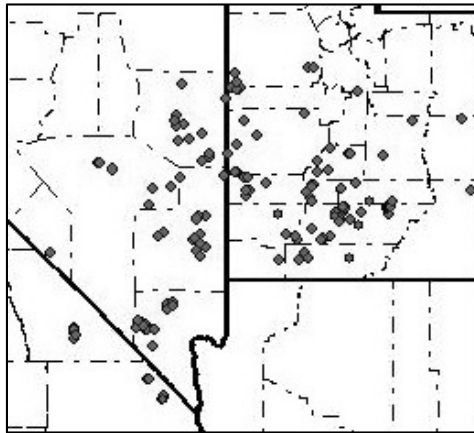


Figure 7. Map of *Physaria kindii* subsp. *latifolia* individuals.

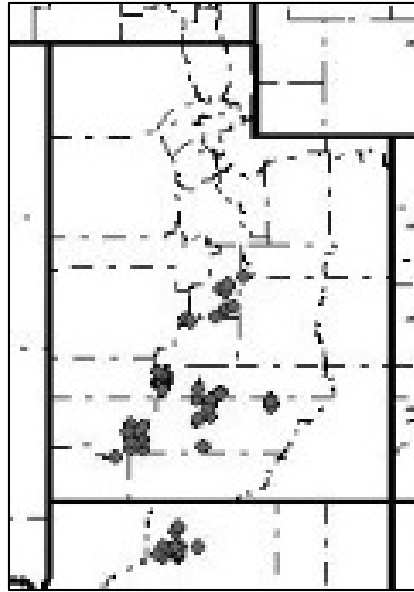


Figure 8. Map of *Physaria wardii* individuals.

Molecular Analysis

This study assumed a priori knowledge that these are closely related taxa that may exhibit hybridization, introgression, or incomplete lineage sorting events in their history (O’Kane, personal communication). With this knowledge, it was decided that a network analysis for the purpose of exploratory data analysis (EDA) would be conducted prior to constructing phylogenetic trees. EDA can provide information when data are net-like and give support for phylogenies (Huson 2008; Morrison 2010, 2012). Morrison (2010) describes the technique of EDA as a fishing expedition with prior knowledge of what will likely be caught but with intentions to catch anything available such as hybridization, introgression, recombination events, horizontal or lateral gene transfer, genome fusion,

ancestral polymorphisms, deep coalescence, as well as incomplete lineage sorting. Each of these can result in trees where individual genes differ from those of the population and may cause genealogical discordance making the analysis of the phylogeny more difficult (Baum and Smith 2013). For example, Gene 1 might suggest that species A is more closely related to species B than to species C, but Gene 2 indicates that species A is more closely related to species C than to species B.

While trees may force data into bifurcating forms, networks allow for and illustrate reticulation, quantifying the conflict that may be present in the evolutionary relationship between the taxa (Huson and Moulton 1996; Alain et al. 2000; Posada and Crandall 2001; Han 2003; Morrison 2012) where a tree would only indicate low support. If the data are tree-like, the network graph will result in a tree and will likely indicate the possible phylogenetic relationships (Dress et al. 1996; Huson 1998; Alain et al. 2000; Huson 2008; Morrison 2010).

Once an EDA was conducted, phylogenetic trees were produced using Bayesian inference. If the trees result in monophyletic groups, the taxa will be raised to species levels, if the groups are not monophyletic, they will remain as subspecies. An outgroup will be used to root the tree to compare the group of interest to a closely related species that is not in the group and will give directionality to the tree (Harrison and Langdale 2006; Michu 2007).

Many regions used for phylogenetic studies are slow-evolving and useful for higher-level systematics, making species and lower levels difficult or impossible to resolve. Faster evolving regions are available. However, even with these regions, there may be

fewer characters for analysis within a species, diminishing statistical power and making full resolution less likely (Barraclough and Nee 2001; Posada and Crandall 2001). To increase the phylogenetic signal, gaps will be coded and used as informative data. Simmons and Ochoterena (2000) contend that gaps are as much a part of the aligned sequence as nucleotides are so that excluding them would be discarding data (Wong et al. 2008). Further, inclusion of indels can improve branch support and even change the topology of the tree (Simmons et al. 2001; Egan and Crandall 2008). Ingvarsson et al. (2003) and Egan and Crandal (2008) suggest that gap inclusion may be more beneficial for the chloroplast regions because indel evolution may happen more frequently than base pair substitutions.

Using DNA from both nuclear and chloroplast regions may help phylogeny resolution (Baldwin et al. 1995; Sanderson and Driskell 2003). For this reason, we will be using a single nuclear region, ITS, and two chloroplast regions, *ndhC-trnV* and *rps*. ITS, internal transcribed spacer region, is made up of three pieces, ITS1, 5.8S rDNA ribosomal subunit, and ITS2 (Wojciechowski et al. 1999; Lavin et al. 2001; McMahon and Hufford 2004). The 5.8S subunit is highly conserved as one would expect in a region incorporated into ribosomes. The spacer units, ITS1 and ITS2, are not incorporated into the ribosome but are transcribed and it is hypothesized that they may be under evolutionary constraint due to this (Baldwin et al. 1995). For this reason, ITS has broad use among the angiosperms being the most widely used nuclear region below family level (Baldwin et al. 1995; Fuertes-Aguilar and Nieto-Feliner 2003; Nieto-Feliner and Rossello 2007).

In addition to the ability to be used across angiosperm families, ITS has proven a powerful resource for providing resolution in species level relationships and conflicting data sets (Baldwin et al. 1995; Nieto-Feliner and Rossello 2007). In particular, ITS has been useful when looking at reticulation patterns in relation to morphology confliction, patterns of variation that are inconsistent between taxonomic arrangement and geography, and to identify hybrids and progenitors (Sang et al. 1995; Fuertes Aguilar and Nieto-Feliner 2003).

Excluding ITS, noncoding chloroplast regions are the backbone of intergenic and interspecific phylogenetic studies (Baldwin 1992; Gielly and Taberlet 1994; Baldwin et al. 1995; Alvarez and Wendel 2003; Shaw et al. 2005). It is hypothesized that these regions evolve quickly and accrue insertions and deletions (indels) because there is less constraint, providing more variation thus higher phylogenetic signal (Gielly and Taberlet 1994; Shaw et al. 2005). The two chloroplast regions, the *rps* intron and *ndhC-trnV* intergenic spacer were chosen because they have worked well in the previous studies (Shaw et al. 2005, Lees 2010).

Aims of Study

The primary aim for this study was to resolve the relationships among the *Physaria kingii* taxa and to determine if they should remain as subspecies or if they needed to be raised to specific level. In addition, Welsh (2003), Holmgren (2005) and O’Kane (2007) agreed that morphologically, *P. wardii* was indistinguishable from *P. kingii* var. *parvifolia*. For this reason and based on morphology and preliminary genetic data from one nuclear gene region, O’Kane and Al-Shehbaz united the two into *P. kingii* subsp.

latifolia. One of the aims of this study is to determine if these should remain united or should be considered as two separate taxa.

Another target for this study was to look at the relationships between the Arizona taxa. *P. kingii* subsp. *latifolia* can have cream–yellow, cream–white, or white petals only on the Kaibab Plateau. There is a question of hybridization between this taxon, *P. kingii* subsp. *kaibabensis*, *P. arizonica*, and *P. purpurea*, all of which grow in the same region (O’Kane 2010). By looking at the nuclear DNA, it may be possible to determine if hybridization events have occurred.

Additionally, during the morphological study, it was discovered that *P. kingii* subsp. *kingii* found in the White Mountains in California sometimes has white flowers. DNA from some of these individuals will be included to determine if these are distinct or a phenotypic polymorphism within the same taxon.

Finally, there appears to be some conflict as to whether fruits are a good character for taxonomic description as most taxa in this group have variable pod shapes throughout their populations. Rollins and Shaw (1973) believed that ovule number may have been an important feature used to interpret relationships within this group. In addition, they discounted the presence or absence of trichomes on the inner valve as important in the delineation of species suggesting they may vary within a population. Further, Maguire and Holmgren drew treatment lines by altitude while Rollins and Shaw (1973) by geographic location. This study attempted to answer this question for this assemblage by reviewing and comparing a large number of specimens and their geographic locality.

CHAPTER 2

MATERIALS AND METHODS

Tissue Sources

The tissue for this study was obtained from three sources: leaf tissue dried on silica gel and DNA sequences provided by O’Kane; leaf tissue (ca. 20 mg unless otherwise specified) removed from borrowed voucher specimens; voucher collections and silica gel-dried leaf tissue collected by O’Kane and me in June 2013 from Arizona, California, Idaho, Nevada, Oregon, and Utah. Leaf tissue dried with silica gel was stored at –20°C. DNA was extracted from only one individual per population. If a voucher specimen had more than one individual, only one was sampled. Voucher information can be found in Table 1 and in Appendix A.

Physaria kingii specimens were requested from several herbaria: ASC, BRY, CAS, F, GH, MO, NY, RM, RSA, US, UTC, and WS (Holmgren et al. 1990). As specimens were received, individuals were examined to confirm identification. Many of the herbaria (BRY, CAS, F, NY, RM, RSA, US, UTC, and WS) included specimens of *Physaria occidentalis* among the collections suggesting that these should be included in the study. Taking into consideration that *P. kingii* subsp. *diversifolia* once belonged to the *occidentalis* complex and the morphology of both groups, it seemed rational to include samples of both *P. occidentalis* subspecies in the study.

Barraclough and Nee (2001) discussed the necessity for multiple representatives per taxon in phylogenetic research. Three representatives were chosen from each of the following: *P. kingii* subsp. *bernardina*, subsp. *utahensis*, subsp. *diversifolia*, and *kaibabensis*. Each of these taxa are endemics with limited geographic ranges. *Physaria kingii* subsp. *cobrensis* has a wider geographic range throughout Nevada thus eight specimens were sampled within this taxon to include multiple populations.

The remaining two taxa, *P. kingii* subsp. *latifolia* and subsp. *kingii*, are widespread, spanning four states each, so more samples were warranted. It was noted by Rollins and Shaw (1973) that *P. kingii* subsp. *latifolia* has several geographically isolated locations throughout the range that differ morphologically to some degree. In my observations, the same can be said about *P. kingii* subsp. *kingii*. For the above reasons, it is necessary to extensively sample within the wide geographic range of these subspecies. Thirty-seven specimens were chosen from *P. kingii* subsp. *latifolia* including representatives that were once recognized as *P. wardii*. Twenty-one specimens from *P. kingii* subsp. *kingii* were sampled.

Table 1. Voucher information and localities for specimens used for DNA studies. Voucher information is shown as collector(s) and collection number.

Taxon	Voucher Information	Locality
<i>P. k. subsp. bernardina</i>	Gross and Bell 4016 (RSA)	San Bernardino Co., CA
<i>P. k. subsp. bernardina</i>	Boyd and Marsh 1172 (RSA)	San Bernardino Co., CA
<i>P. k. subsp. bernardina</i>	Thorne, Tilforth, and Little 53154 (RSA)	San Bernardino Co., CA
<i>P. k. subsp. cobrensis</i>	Atwood, Jenkins, and Neiwert 13648 (BRY)	Cassia Co., ID
<i>P. k. subsp. cobrensis</i>	Holmgren and Holmgren 13614 (ISTC)	Elko Co., NV
<i>P. k. subsp. cobrensis</i>	Tiehm 11304 (GH)	Esmeralda Co., NV
<i>P. k. subsp. cobrensis</i>	Applegate 8326a (F)	Humboldt Co., NV
<i>P. k. subsp. cobrensis</i>	Tiehm 14454 (UTC)	Humboldt Co., NV
<i>P. k. subsp. cobrensis</i>	Minnaert–Grote and O’Kane 92 (ISTC)	Humboldt Co., NV
<i>P. k. subsp. cobrensis</i>	Williams and Tiehm 81–56–3 (UTC)	Lincoln Co., NV
<i>P. k. subsp. cobrensis</i>	Sanders 32871 (MO)	White Pine Co., NV
<i>P. k. subsp. diversifolia</i>	Maguire and Holmgren 27054 (US)	Wallowa Co., OR
<i>P. k. subsp. diversifolia</i>	Markow 12247 (RM)	Wallowa Co., OR
<i>P. k. subsp. diversifolia</i>	Minnaert–Grote and O’Kane 93 (ISTC)	Wallowa Co., OR
<i>P. k. subsp. diversifolia</i>	Minnaert–Grote and O’Kane 94 (ISTC)	Wallowa Co., OR
<i>P. k. subsp. diversifolia</i>	1887 (ISTC)	Wallowa Co., OR
<i>P. k. subsp. kaibabensis</i>	Holmgren, Holmgren and Joseph 13565 (ISTC)	Coconino Co., AZ
<i>P. k. subsp. kaibabensis</i>	Rollins and Rollins 79191 (ISTC)	Coconino Co., AZ
<i>P. k. subsp. kaibabensis</i>	Holmgren, Holmgren and Joseph 13564 (ISTC)	Coconino Co., AZ
<i>P. k. subsp. kaibabensis</i>	O’Kane 4213 (ISTC)	Coconino Co., AZ
<i>P. k. subsp. kingii</i>	Lloyd 2941 (UTC)	Inyo Co., CA
<i>P. k. subsp. kingii</i>	O’Kane and Minnaert–Grote 9842	Mono Co., CA
<i>P. k. subsp. kingii</i>	Grady 269 (ISTC)	Inyo Co., CA
<i>P. k. subsp. kingii</i>	Alexander and Kellog 3042 (UTC)	Inyo Co., CA
<i>P. k. subsp. kingii</i>	Maguire and Holmgren 26056 (UTC)	Mono Co., CA
<i>P. k. subsp. kingii</i>	Lavin 3323 (GH)	Mono Co., CA
<i>P. k. subsp. kingii</i>	Morefield and Ross 4705 (BRY)	Mono Co., CA
<i>P. k. subsp. kingii</i>	Smith 5206 (WS)	Franklin Co., ID
<i>P. k. subsp. kingii</i>	Tiehm 10418 (BRY)	Churchill Co., NV
<i>P. k. subsp. kingii</i>	Tiehm and Nachlinger 16157 (UTC)	Humboldt Co., NV
<i>P. k. subsp. kingii</i>	Tiehm 11000 (RM)	Lincoln Co., NV
		Table continues

Taxon	Voucher Information	Locality
<i>P. k. subsp. kingii</i>	Williams and Atwood 82–7–10 (GH)	Nye Co., NV
<i>P. k. subsp. kingii</i>	Leary, Niles, and Holland 3444 (BRY)	Nye Co., NV
<i>P. k. subsp. kingii</i>	Beatley s.n. (GH)	Nye Co., NV
<i>P. k. subsp. kingii</i>	Minnaert–Grote and O’Kane 91 (ISTC)	Nye Co., NV
<i>P. k. subsp. kingii</i>	Tiehm and Williams 6190 (GH)	Nye Co., NV
<i>P. k. subsp. kingii</i>	Williams and Tiehm 81–11–1 (UTC)	White Pine Co., NV
<i>P. k. subsp. kingii</i>	Holmgren and Holmgren 13633 (ISTC)	White Pine Co., NV
<i>P. k. subsp. kingii</i>	Costley 34 (RM)	Emery Co., UT
<i>P. k. subsp. kingii</i>	Holmgren and Holmgren 14050 (ISTC)	Piute Co., UT
<i>P. k. subsp. kingii</i>	Taye and Frost 2585 (UTC)	Piute Co., UT
<i>P. k. subsp. kingii</i>	Geer 15 (UTC)	San Pete Co., UT
<i>P. k. subsp. latifolia</i>	O’Kane 4211 (ISTC)	Coconino Co., AZ
<i>P. k. subsp. latifolia</i>	O’Kane 4212 (ISTC)	Coconino Co., AZ
<i>P. k. subsp. latifolia</i>	Minnaert–Grote and O’Kane 84 (ISTC)	Coconino Co., AZ
<i>P. k. subsp. latifolia</i>	Moseley and Mancuso 1734 (GH)	Franklin Co., ID
<i>P. k. subsp. latifolia</i>	Ackerman 76–224 (UTC)	Clark Co., NV
<i>P. k. subsp. latifolia</i>	Porter 4949 (BRY)	Clark Co., NV
<i>P. k. subsp. latifolia</i>	Windham 98–246 (ISTC)	Clark Co., NV
<i>P. k. subsp. latifolia</i>	Tiehm and Nachlinger 14776 (UTC)	Lincoln Co., NV
<i>P. k. subsp. latifolia</i>	Tiehm 13646 (BRY)	Nye Co., NV
<i>P. k. subsp. latifolia</i>	Beatley s.n. (GH)	Nye Co., NV
<i>P. k. subsp. latifolia</i>	Moore and Franklin 187 (MO)	White Pine Co., NV
<i>P. k. subsp. latifolia</i>	Tiehm and Williams 8727 (UTC)	White Pine Co., NV
<i>P. k. subsp. latifolia</i>	Higgins 1453 (MO)	White Pine Co., NV
<i>P. k. subsp. latifolia</i>	Reveal and Broome 8909 (ISTC)	Beaver Co., UT
<i>P. k. subsp. latifolia</i>	Holmgren and Holmgren 13795 (ISTC)	Garfield Co., UT
<i>P. k. subsp. latifolia</i>	Holmgren, Holmgren and Joseph 13588 (ISTC)	Garfield Co., UT
<i>P. k. subsp. latifolia</i>	Holmgren and Holmgren 13805 (ISTC)	Garfield Co., UT
<i>P. k. subsp. latifolia</i>	Minnaert–Grote and O’Kane 80 (ISTC)	Garfield Co., UT
<i>P. k. subsp. latifolia</i>	Atwood and Welsh 23949 (BRY)	Garfield Co., UT
<i>P. k. subsp. latifolia</i>	Holmgren and Holmgren 11784 (ISTC)	Garfield Co., UT
<i>P. k. subsp. latifolia</i>	Barnes, Harper, and Jolley 2863 (UVSC)	Iron Co., UT
<i>P. k. subsp. latifolia</i>	Minnaert–Grote and O’Kane 86 (ISTC)	Iron Co., UT
		Table continues

Taxon	Voucher Information	Locality
<i>P. k. subsp. latifolia</i>	Foster 5840 (BRY)	Juab Co., UT
<i>P. k. subsp. latifolia</i>	Shultz and Shultz 5228 (UTC)	Millard Co., UT
<i>P. k. subsp. latifolia</i>	Matthews 26 (UVC)	Millard Co., UT
<i>P. k. subsp. latifolia</i>	Welsh and Henriod 18038 (BRY)	Piute Co., UT
<i>P. k. subsp. latifolia</i>	Barnes 2163 (UVSC)	Tooele Co., UT
<i>P. k. subsp. utahensis</i>	Holmgren and Holmgren 13540 (ISTC)	Daggett Co., UT
<i>P. k. subsp. utahensis</i>	Salywon 3184 (ISTC)	Uintah Co., UT
<i>P. k. subsp. utahensis</i>	Holmgren and Holmgren 13651 (ISTC)	Salt Lake Co., UT
<i>P. wardii</i>	Maguire 19806 (UTC)	Beaver Co., UT
<i>P. wardii</i>	Holmgren, Holmgren, and Joseph 13600 (ISTC)	Garfield Co., UT
<i>P. wardii</i>	Holmgren, Holmgren, and Joseph 13598 (ISTC)	Garfield Co., UT
<i>P. wardii</i>	Holmgren and Holmgren 13795 (ISTC)	Garfield Co., UT
<i>P. wardii</i>	Welsh 21301 (BRY)	Iron Co., UT
<i>P. wardii</i>	O’Kane 4721 (ISTC)	Iron Co., UT
<i>P. wardii</i>	Windham 2396 (ISTC)	Kane Co., UT
<i>P. wardii</i>	Holmgren and Holmgren 14050 (ISTC)	Piute Co., UT
<i>P. o. subsp. cinerescens</i>	Rollins and Rollins 81305 (RM)	Power Co., ID
<i>P. o. subsp. cinerescens</i>	Tuhy 3683 (RM)	Juab Co., UT
<i>P. o. subsp. occidentalis</i>	Minnaert–Grote and O’Kane 95 (ISTC)	Butte Co., ID
<i>P. o. subsp. occidentalis</i>	O’Kane and Prather–O’Kane 4502 (ISTC)	Custer Co., ID
<i>P. o. subsp. occidentalis</i>	O’Kane 4497 (ISTC)	Wheeler Co., OR
<i>P. o. subsp. occidentalis</i>	Salywon 3194 (ISTC)	Box Elder Co., UT

DNA Extraction Procedures

Two procedures were used for DNA extraction. Initially a protocol developed by Carter and Milton (1993) and Huang et al. (2000) and modified by O’Kane was used. After an experiment quantifying the amount and the quality of extracted DNA, it was

determined that going forward Qiagen DNeasy Plant Mini Kits would be used. The experimental results indicated that both techniques resulted in approximately the same amount and quality of DNA, however, the Qiagen kit allowed for faster procurement, taking a few hours rather than one to two days.

In both procedures, approximately 15–20 mg dried leaf tissue was ground with ca. 200 mg sterile silica sand using a mortar and pestle until it reached the consistency of fine powder. In the first procedure, the tissue was combined with 1 ml Extraction Buffer (100 mM Tris–HCl, pH 6.5; 1 M NaCl; 25 mM EDTA, pH 8.0; 175 mM sodium bisulfate; 1.5% w/v CTAB) and 0.5% v/v mercaptoethanol in a 2 ml microcentrifuge tube. After mixing vigorously, the tubes were incubated for one hour in a 65°C water bath and mixed occasionally. Approximately 1 ml Sevag (chloroform: isoamyl alcohol 24:1) was added to fill the tube, which was then emulsified and centrifuged at maximum speed (14,000 rpm) for five minutes. The aqueous layer was transferred to a new 2 ml microcentrifuge tube and combined with 1.1 ml Adsorption Buffer (6 M guanidine thiocyanate; 100 mM Tris; 5 mM Tris; 5 mM EDTA, pH 8.0; 1.8% w/v de-fined diatomaceous earth). The contents were mixed and incubated for five minutes at room temperature with frequent and gentle mixing. The tubes were centrifuged using a Spectrafuge 16M microcentrifuge for one minute at 8000 rpm. The supernatant was poured off and the pellet resuspended with 1–1.5 ml chilled Wash Buffer (80 mM potassium acetate; 8.4 mM Tris–HCl, pH 7.4; 40 mM EDTA, pH 8.0; 55% EtOH). This was centrifuged at maximum speed for one minute. The supernatant was removed and the pellet was resuspended with 1–1.5 ml 85% EtOH. The mixture was centrifuged for one additional minute at maximum speed. The

liquid was poured off and the tubes were inverted to dry overnight. The pellet was resuspended with 175 μ l TE (10 mM Tris-HCl, pH 8.4; 0.1 mM EDTA, pH 8.0), incubated for 10–15 minutes at 65°C and centrifuged for one minute at maximum speed. The liquid was transferred to a new 1.5 ml microcentrifuge tube. This was repeated with 75 μ l TE and the DNA solutions were combined. The microcentrifuge tubes were labeled and placed in a –20°C freezer for long-term storage.

The Qiagen DNeasy Mini Kit provided buffers, columns, and tubes for extraction purposes. Initially the Qiagen protocol provided in the kit was followed. The ground plant material was added to a 2 ml microcentrifuge tube with 400 μ l of Buffer AP1 and 4 μ l RNase A. The tubes were incubated in a 65°C water bath for 10 minutes with occasional mixing. One hundred thirty μ l Buffer AP2 were added, incubated on ice for five minutes, and then centrifuged for five minutes at maximum speed. The liquid was added to the provided QIA shredder column and centrifuged for two minutes at maximum speed. The flow-through was transferred to a new 2 ml microcentrifuge tube. Buffer AP3/E was added at a value of 1.5 times the volume of the flow through and mixed by pipetting. 650 μ l of the solution was added to the DNeasy Mini Spin Column and centrifuged for one minute at 9000 rpm. The flow-through liquid was discarded and the remaining mixture was added to the column and centrifuged. The column was added to a new 2 ml microcentrifuge tube, 500 μ l Buffer AW was added, this was centrifuged for one minute at 10,000 rpm, and the flow-through was discarded. The previous step was repeated and centrifuging for two minutes at max speed. The column was transferred to a new 2 ml microcentrifuge tube and 100 μ l of 65°C Buffer AE was added and

incubated at room temperature for five minutes. The column was centrifuged for one minute at 8000 rpm. One hundred μ l Buffer AE was again added, incubated for five minutes, and centrifuged for one minute at 8000 rpm. DNA solutions were labeled and placed in the -20°C freezer for long-term storage.

Drabkova et al. (2002) suggested modifications to the Qiagen procedure. These modifications were put into place in February 2013. The modifications were as follows: The initial incubation period was changed from 10 minutes to 30 minutes. Seventy-five μ l of preheated Buffer AE were added to the column instead of 100 μ l producing a more concentrated DNA solution. The incubation time for the Buffer AE in the column was changed to 10 minutes in place of five minutes. Kits purchased after January 2013 had modified buffer names. Buffer AP2 became Buffer P3, Buffer AP3/E became Buffer AW1 and Buffer AW became Buffer AW2.

Success of DNA extraction was visualized using UV illumination of a 1.1% agarose mini gel. The gels were run in SB Buffer (10 mM sodium hydroxide, pH 8.5 and boric acid) containing 15 μ l of 10 mg/ μ l ethidium bromide. The wells were filled with 2.5 μ l SB loading dye (13.5% Ficoll-400, 0.5% Orange-G, 6x SB buffer, 20mM EDTA) and 7.5 μ l DNA and run at 120 volts until the dye moved approximately 3 cm. Gels were placed on a UV illuminator and digital images were taken with a Kodak EDAS 290 Electrophoresis Documentation and Analysis System and Kodak 1D computer software.

Amplification of ITS Region

Polymerase chain reaction (PCR) was done using two thermocyclers, Biometra® TProfessional Basic Thermocycler Gradient and Biometra® TGradient, using 0.25 ml PCR microcentrifuge 8-tube strips. The total reaction volume was 25 μ l and consisted of 1 μ l DNA, 0.15 μ l taq polymerase, 2.5 μ l 10X Reaction Buffer (100 mM Tris-HCl, pH 8.8; 500 mM KCl, 17.5 mM MgCl₂; 5% v/v DMSO; 0.5% v/v Triton-X), 2.5 μ l rITS-F primer (Table 2), 2.5 μ l rITS-R primer (Table 2), 2.5 μ l 8 mM dNTP mix (10 μ l 100 mM dATP; 10 μ l 100 mM dCTP; 10 μ l 100 mM dGTP; 10 μ l 100 mM dTTP; 5 μ l 1 M Tris-Cl, pH 7.9; 455 μ l dH₂O); and 13.85 μ l ddH₂O. If an amplification was unsuccessful, 3 μ l of DNA was added to the reaction while decreasing the water volume to keep the total volume at 25 μ l. The thermocycler lid temperature was set to 104°C. The DNA was initially denatured for two minutes at 94°C. There were 30 cycles of the following: denaturation for 45 seconds at 94°C, primer annealing for one minute at 60°C, and extension for one minute at 72°C with an increase of 1 Δ t (s). There was a final extension period of 5 minutes at 72°C followed by a 16°C soak. An error in the programming on one thermocycler had an increase of 1 Δ t (s) during the annealing stage however this did not appear to adversely affect the reactions.

Table 2. Primer sequences. Primers rITS–F and rITS–R (Designed by O’Kane) Primers *rps*–F and *rps*–R (Oxelmann et al. 1997). Primers *ndhC*–F and *trnV*–R (Designed by O’Kane)

Primer	Primer Sequence	Genome
rITS–F	GTCGTAACAAGGTTTCCGTAGTGAACC	Nuclear
rITS–R	TCCGCTTATTGATATGCTTAAACTCAGC	Nuclear
<i>rps</i> F	GTGGTAGAAAGCAACGTGCGACTT	Chloroplast
<i>rps</i> R2	TCGGGATCGAACATCAATTGCAAC	Chloroplast
<i>ndhC</i> –F	TGCCAAAACAGGAATAGCAC	Chloroplast
<i>trnv</i> –R	TTTACCGAGCAGGTCTACGG	Chloroplast

Amplification of *rps* intron Region

PCR was done with 0.2 ml PCR microcentrifuge tubes or Fisher Scientific 0.25 ml 8-tube strips. Reactions had a total of 25 μ l and included 1 μ l DNA, 11.25 μ l ddH₂O, 5 μ l 5X Phusion HF Buffer provided with the Phusion enzyme, 2.5 μ l dNTPs, 2.5 μ l *rps*F primer (Table 2), 2.5 μ l *rps*R2 primer (Table 2), and 0.25 μ l Phusion II enzyme (Thermo Scientific). The lid temperature was set to 104°C. The first denaturation was for one minute at 98°C. There were thirty cycles of the following: denaturation at 98°C for 10 seconds, annealing at 66.8°C for 25 seconds, and extension for 30 seconds at 72°C. The final extension phase was for seven minutes at 72°C followed by a 16°C soak.

Amplification of *ndhC*–*trnV* Intergenic Spacer Region

PCR was done using 0.2 ml PCR microcentrifuge tubes or 0.25 ml Fisher Scientific strip 8-tube strips. The total volume for the reaction was 25 μ l and included 1 μ l DNA, 11.25 μ l ddH₂O, 5 μ l 5X Phusion HF Buffer, 2.5 μ l dNTP, 2.5 μ l *ndhC*–F primer (Table

2), 2.5 µl *trnV*-R primer (Table 2), and 0.25 µl Phusion II enzyme. The lid temperature was set to 104°C. The initial denaturation was 98°C for one minute. Thirty cycles of denaturation, annealing, and extension were set to 98°C for 10 seconds, 63°C for 25 seconds, and 66°C for 1 minute 30 seconds finishing with a 16°C soak.

Success of all PCR amplifications were determined by running a 1% agarose mini gel in SB buffer containing 15 µl of 10 mg/µl ethidium bromide. Wells were loaded with 2.5 µl SB loading dye, 2.0 µl PCR product, and 7.5 µl ddH₂O and run until the dye reached approximately 2.5 cm. The gels were digitized by using the Kodak EDAS 290 system.

DNA Sequencing

The PCR reactions were treated to remove excess dNTPs and primers before sequencing. The PCR products were plated in 96 well PCR plates and 1/5 volume (2.3 ul) Exonuclease I and Shrimp Alkaline Phosphatase (78 µl ddH₂O; 2 µl Exonuclease I, 10 U/ul; 20 µl Shrimp Alkaline Phosphatase, and 1 U/ul) were added and loaded into the thermocycler. The reaction was run for 15 minutes at 37°C followed by 80°C for 15 additional minutes.

PCR reactions were sent to Iowa State University's DNA Facility in Ames, Iowa. Samples were sequenced using the Sanger sequencing technique and run on an Applied Biosystems© 3730xl DNA Analyzer. Seven µl (15 ng/µl) of amplification primer (*rITS*-F and *rITS*-R; *rpsF* and *rpsR*; *ndhC*-F and *trnV*-R) was provided for each reaction, forward and reverse. The resulting sequences were provided as a chromatogram. Sequences were prepared using Chromas Lite version 2.1 (Chromas Lite, Technelysium,

Queensland, Australia). Forward and reverse strands were compared based on an alignment by Clustal X (Larkin et al. 2007) using default parameters. Polymorphic sites in the ITS region were coded using standard ambiguity codes (Fuertes-Aguilar and Nieto-Feliner 2003).

Phylogenetic Analysis

MAFFT version 7.110 (National Institute of Advanced Industrial Science and Technology 2013) was used for multiple sequence alignment using the G–INS–I strategy. IPAM/ $\kappa=2$ was chosen for the scoring matrix of nucleotide sequences as suggested in the parameters section of MAFFT when aligning closely related sequences (Kato and Standley 2013). Clustal was then used to save the alignments in FASTA format.

MEGA 5.0 (Tamura et al. 2011) was used to compute pairwise distances to eliminate duplicate sequences. A zero distance score indicated that sequences were identical and needed to be combined. MEGA 5.0 was also used to do a model test using automatic neighbor-joining tree with partial deletion and 95% site coverage cutoff.

Minimal changes to alignments were done using Bioedit (Hall 1999). Simple gap coding was completed with FastGap and coded with the presence or absence of gaps using as As and Cs (Borchsenius 2009); C was used for when a gap was present, A for when a gap was absent. Network analyses were done in SplitsTree 4 (Huson and Bryant 2006) for the *rps* intron, ITS, the *ndhC–trnV* intergenic spacer, and combined chloroplast regions.

Partition Finder (Lanfear et al. 2012) was first used to find the best partitioning scheme and then to compare user defined partitioning schemes to determine if nuclear and chloroplast regions could be combined. The program used linked branch lengths between partitions. The model selection was set to only models found within MrBayes using BIC as a metric. The BIC scores were then used to perform a likelihood ratio test using jModelTest (Posada 2008) to conclude if they were statistically different.

Bayesian analyses were done using Mr. Bayes version 3.2.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) with the CIPRES Science Gateway V.3.3 (Miller et al. 2010). Analyses were run for ITS, *rps* inton, *ndhC-trnV* intergenic spacer, and combined chloroplast regions. The data were partitioned with DNA in one partition and gaps in another. All data were set to run 50,000,000 iterations with a sample frequency every 1000 trees. Two separate runs were completed, each with four MCMC chains starting from a randomly chosen tree. The burn in value was set at 0.33 with the trees sampled during this portion discarded. The partitions were unlinked with a variable prior rate and an empirical prior state frequency. The stop value was set at 0.002 for convergence.

Scanning Electron Microscopy

Leaves were mounted on stubs and sputter coated with 0.5 μm gold. Trichome photographs were taken with a Vega 5136MM Scanning Electron Microscope in order to analyze size, shape, texture, ray number, and branching pattern.

Table 3. Voucher information for trichome SEM photographs.

Taxon	Voucher Information
<i>P. kingii</i> subsp. <i>bernardina</i>	Thorne, Tilforth, and Little 53154 (GH)
<i>P. kingii</i> subsp. <i>diversifolia</i>	Markow 12247 (RM)
<i>P. kingii</i> subsp. <i>cobrensis</i>	Tiehm 14454 (UTC)
<i>P. kingii</i> subsp. <i>kaibabensis</i>	Holmgren, Holmgren, and Joseph 13564 (ISTC)
<i>P. kingii</i> subsp. <i>kingii</i>	Maguire and Holmgren 25429 (F)
<i>P. kingii</i> subsp. <i>kingii</i>	Reveal s.n. (UTC)
<i>P. kingii</i> subsp. <i>kingii</i>	Tiehm and Williams 6190 (GH)
<i>P. wardii</i>	Holmgren, Holmgren, Joseph 13600 (UTC)
<i>P. wardii</i>	Maguire 19006 (RM)
<i>P. kingii</i> subsp. <i>latifolia</i>	Pinzl 2805 (GH)
<i>P. kingii</i> subsp. <i>utahensis</i>	Holmgren and Holmgren 13651 (ISTC)
<i>P. kingii</i> subsp. <i>utahensis</i>	Rollins and Rollins 81350 (MO)
<i>P. occidentalis</i> subsp. <i>occidentalis</i>	Cronquist 7097 (RM)
<i>P. occidentalis</i> subsp. <i>occidentalis</i>	Halse 1318 (RSA)

CHAPTER 3

RESULTS

Sequence Analysis

ITS Sequence Analysis

ITS (Appendix B) had fewer indels and fewer identical sequences among specimens when compared to the chloroplast regions. The sequences ranged from 652 to 655 bases in length; aligned they were 663 bases long; including coded gaps they were 683 base pairs long. In nine instances, two individuals had identical sequences, additionally there was one occurrence of three individuals with identical sequences, two instances of four individuals with a shared sequence, one instance of five individuals sharing a single sequence, and finally, there was one occurrence of six individuals with identical sequences (Table 4). In addition, there were fourteen single indels and three double indels.

Table 4. Specimens with identical ITS sequences

Number of taxa	Taxa	State
2	<i>P. k.</i> subsp. <i>bernardina</i> 53154 and 1172	CA
2	<i>P. k.</i> subsp. <i>diversifolia</i> 12247 and 94	OR
2	<i>P. k.</i> subsp. <i>kaibabensis</i> 79191 and 4213	AZ
2	<i>P. k.</i> subsp. <i>kaibabensis</i> 13564 and <i>P. wardii</i> 13600	AZ, UT
2	<i>P. k.</i> subsp. <i>kingii</i> 3444 and 3323	NV, CA
2	<i>P. wardii</i> 84 and 4211	AZ
2	<i>P. o.</i> subsp. <i>cinerascens</i> 81305 and 3194	ID, UT
2	<i>P. o.</i> subsp. <i>cinerascens</i> 1734 and subsp. <i>occidentalis</i> 5206	ID, UT
2	<i>P. o.</i> subsp. <i>occidentalis</i> 7097 and 4497	OR
3	<i>P. k.</i> subsp. <i>cobrensis</i> 14454, 8326a, and 92	NV
4	<i>P. k.</i> subsp. <i>kingii</i> 13633 , 9824 and subsp. <i>latifolia</i> 98246, 14776	NV
4	<i>P. k.</i> subsp. <i>latifolia</i> 13805 and <i>P. wardii</i> 21031, 80, and 13795	UT
5	<i>P. k.</i> subsp. <i>latifolia</i> 8909, 26 and <i>P. wardii</i> 2585, 4721, and 19806	UT
6	<i>P. k.</i> subsp. <i>latifolia</i> 11784, 13588 and <i>P. wardii</i> 86, 14050, and 2863	UT

As ITS is a nuclear region, it was possibly heterozygous. A site was considered polymorphic when the weakest peak reached at least 25% of the strength of the strongest peak in the chromatograph. There were 21 unique polymorphic sites found. One shared sequence, *P. k.* subsp. *kingii* 9824, 13633, *P. k.* subsp. *latifolia* 14776, 98246, had two polymorphic sites, one of which was shared with *P. k.* subsp. *kingii* 11000, 82710, 81111,

2941, 4705, and subsp. *diversifolia* 93. *Physaria kingii* subsp. *kaibabensis* 4213 and 79191 had nine unique polymorphic sites, by far the largest number found in this data set. The best model chosen for ITS was determined by MEGA to be K2+G+I. The average p distance, quantifying the similarity of sequences, was 0.02.

rps Intron Sequence Analysis

The *rps* intron (Appendix C) was the largest region sequenced with a range of 840 to 910 bases. Aligned these were 1023 bases long and when coded for gaps, the length was 1053 bases. There were six occurrences where two individuals had identical sequences, five instances where three individuals shared a sequence, three instances where four individuals had duplicate sequences, and one instance each of five, six, and eight individuals with identical sequences (Table 5).

Table 5. Specimens with identical *rps* intron sequences

Number of taxa	Taxa	State
2	<i>P. cordiformis</i> 283 and <i>P. k.</i> subsp. <i>kingii</i> 4705	CA
2	<i>P. k.</i> subsp. <i>diversifolia</i> 1887 and 12247	OR
2	<i>P. k.</i> subsp. <i>kingii</i> 82710 and 91	NV
2	<i>P. k.</i> subsp. <i>latifolia</i> 13596 and 13646	UT, NV
2	<i>P. k.</i> subsp. <i>latifolia</i> 14776 and 89	NV, UT
2	<i>P. k.</i> subsp. <i>latifolia</i> 13805 and <i>P. wardii</i> 80	UT
3	<i>P. k.</i> subsp. <i>bernardina</i> 53154, 4016, and 1172	CA
3	<i>P. k.</i> subsp. <i>kingii</i> 269, 26056, and 2941	CA
3	<i>P. k.</i> subsp. <i>utahensis</i> 13540, 3184, and 13651	UT
3	<i>P. wardii</i> 84, 4212, and 4211	AZ
3	<i>P. wardii</i> 21301, 86, and 2863	UT
4	<i>P. k.</i> subsp. <i>cobrensis</i> 14454, 92, subsp. <i>kingii</i> 11304, and <i>P. wardii</i> 34	NV, UT (<i>P. wardii</i>)
4	<i>P. k.</i> subsp. <i>kaibabensis</i> 13565, 13564, 4213, and <i>P. wardii</i> 13600	AZ, UT (<i>P. wardii</i>)
4	<i>P. k.</i> subsp. <i>kingii</i> s.n., 10418, 3444 and 3323	NV, CA (3323)
5	<i>P. k.</i> subsp. <i>kingii</i> 6190, 81111, 9824, 13633, and subsp. <i>latifolia</i> 98246	NV
6	<i>P. k.</i> subsp. <i>latifolia</i> 11784, 26, and <i>P. wardii</i> 14050, 19806, 13598, and 2585	UT
8	<i>P. k.</i> subsp. <i>cobrensis</i> 81563, subsp. <i>diversifolia</i> 93, subsp. <i>kingii</i> 11000 subsp. <i>latifolia</i> 5228, 8727, 2164, 49229 and <i>P. o.</i> subsp. <i>occidentalis</i> 7097	NV, CA (49229), OR (93, 7097), UT (5228, 2164)

This region had numerous indels, some quite long and of interest. There were ten unique single-gap sites, shared in some cases among multiple individuals. One region with a long region of repeated A's had indels ranging from one to five bases in length. Additionally, *P. k. subsp. latifolia* 4949 had an insertion of 37 bases found in no other individual. Another region had multiple repeats inserted, with gaps spanning from twenty-two to ninety-two bases in length. These repeats ranged from four to 24 bases with some duplications found two to three times in a row. The average p distance score was 0.0066 for the *rps* intron. The model chosen for all chloroplast regions including *rps* intron, *ndhC-trnV* intergenic spacer, and the combined chloroplast dataset was T92.

ndhC-trnV Intergenic Spacer Sequence Analysis

The *ndhC-trnV* intergenic spacer sequences (Appendix D) ranged from 396–622 bases in length. With gaps, there were 663 bases and when coded for gaps, there were 680 bases. Similar to the *rps* intron, there were multiple identical sequences shared with the smallest number shared being two and the largest twenty. There were two instances of two individuals with identical sequences, one occurrence with three individuals with an identical sequence, a single sequence shared by four individuals, one occurrence of six individuals with an identical sequence, one instance of seven individuals sharing one sequence, one occurrence of twelve individuals with a common sequence, and finally one sequence shared by twenty individuals (Table 6).

Table 6. Specimens with identical *ndhC-trnV* intergenic spacer sequences

Number of taxa	Taxa	State
2	<i>P. k.</i> subsp. <i>latifolia</i> 8727 and 49229	CA, NV
2	<i>P. o.</i> subsp. <i>occidentalis</i> 4497 and 7097	OR
3	<i>P. k.</i> subsp. <i>diversifolia</i> 12447, 93, 94	OR
4	<i>P. k.</i> subsp. <i>kingii</i> 26056, 16157, 2941, and 269	CA, NV (269)
6	<i>P. k.</i> subsp. <i>kaibabensis</i> 79191, 13564, 4213, and <i>P. wardii</i> 84, 4212, and 4211	AZ
8	<i>P. k.</i> subsp. <i>bernardina</i> 53153, 4016, 1172, subsp. <i>cobrensis</i> 81563, subsp. <i>kingii</i> 1100, 82710, 91, subsp. <i>latifolia</i> 5228	NV, UT (5228) CA (53153, 4016, 1172)
12	<i>P. k.</i> subsp. <i>cobrensis</i> 32871, 13648, 92, 14454, 8326a, subsp. <i>kingii</i> 11304, subsp. <i>latifolia</i> 13588, subsp. <i>utahensis</i> 13540, 3184, 13651, and <i>P. wardii</i> 1379, and 2396	NV, ID (13648), UT (13795, 2396, 13588, 13540, 3180, 13651)
20	<i>P. cordiformis</i> 283, <i>P. k.</i> subsp. <i>kingii</i> 10418, 3444, 13633, 6190, 3042, s.n., 81111, 3323, 10418, 4705, subsp. <i>latifolia</i> 76224, 11784, 98246, 8909, <i>P. o.</i> subsp. <i>cinerascens</i> 95, and <i>P. wardii</i> 86, 14050, and 34.	NV, CA (3042, 3323, 4705, 283), ID (95), UT (11784, 8909, 86, 14050, 34, 26)

Like the *rps* intron, there were numerous indels, however; there were few single-site gaps, only three spanning multiple individuals. The largest deletion, with 241 bases, was found in all *P. k.* subsp. *diversifolia* individuals. Also similar to the *rps* intron was a long stretch of A's with gaps in some specimens ranging from two to three bases in length. Additionally, there were two sites with duplications, each found in one representative, one was five bases in length and one was seven bases. Finally, the p distance between sequences was 0.0158.

Combined Chloroplast Sequence Analysis

The combined chloroplast dataset had a range of base lengths of 1297–1580 bases. When aligned, the total length was 1686 bases and with gaps coded was 1737 bases. Combining the chloroplast regions reduced the number of shared sequences substantially. There were four cases of two individuals each with identical sequences (Table 7).

Table 7. Specimens with identical combined chloroplast sequences

Number of taxa	Taxa	State
2	<i>P. k.</i> subsp. <i>bernardina</i> 53151 and 1172	CA
2	<i>P. k.</i> subsp. <i>kingii</i> 3444, 3323	NV, CA
2	<i>P. k.</i> subsp. <i>kingii</i> 13633 and subsp. <i>latifolia</i> 98246	NV
2	<i>P. k.</i> subsp. <i>latifolia</i> 11784 and <i>P. wardii</i> 14050	UT

Network Analyses

ITS Network Analysis

MEGA determined the model for ITS to be K2+G+I. The closest comparable model found in SplitsTree was the KP2+G+I model. The ITS network (Figure 9) had a large reticulated center with short internal edges and a shape between tree-like and net-like, leaning closer to a net-like form. Three taxa, *P. k.* subsp. *latifolia*, subsp. *kingii*, and *P. wardii*, were found distributed throughout the network with *P. k.* subsp. *kingii* from Nevada only found on approximately one-half. There were two major clusters protruding from the reticulated center. Looking at the major groupings, the conglomerate of Arizona *P. wardii*, *P. k.* subsp. *kaibabensis*, and *P. arizonica*, as well as one *P. wardii* from Utah, cluster tightly together showing a lot of reticulation at the end of a long set of parallel edges with short edges emerging from the network. With the Arizona *P. wardii* removed,

P. arizonica and *P. k. subsp. kaibabensis* cluster together. This can be seen in Figure 10. Similarly, when *P. k. subsp. kaibabensis* was removed, *P. arizonica* and the *P. wardii* found in Arizona were still clustered (Figure 11). Slightly set apart but still part of the same cluster were *P. k. subsp. kingii* s.n. and three *diversifolia*: 1887, 12247, and 94. While these were grouped together basally, they lie at the end of long edges. The other collection was largely *P. k. subsp. kingii* and *subsp. latifolia* and one single specimen of *subsp. diversifolia*. This cluster was primarily made up of individuals from Nevada however there were four *P. k. subsp. kingii* and one *P. k. subsp. latifolia* from California, three *P. k. subsp. latifolia* from Utah, and *P. k. subsp. diversifolia* was from Oregon.

Moving on to the smaller clusters, *P. k. subsp. cobrensis* grouped together with one exception, *P. k. subsp. cobrensis* 81563, found on the other side of the network with *P. k. subsp. latifolia* 5228. This is the only *P. k. subsp. cobrensis* sample found in Lincoln County, NV while the *P. k. subsp. latifolia* was in the neighboring Millard County UT. Looking closely at the *P. k. subsp. cobrensis* cluster, the northern Nevada specimens 8326a, 92, and 14454 clustered together with the one species found in southern Idaho, 13648. Also in that cluster but with more parallel edges separating them was 11304 from Esmeralda County, the southern-most *P. k. subsp. cobrensis* sampled. The one species from White Pine County, 32871, was grouped more closely with *P. purpurea*, a species outside of the *P. kingii* group. The reticulation connecting them had short edges however; *P. purpurea* was located at the end of a long edge.

Physaria kingii subsp. *utahensis* clustered basally with most of the Utah *P. k.* subsp. *latifolia* and *P. wardii* with short edged reticulation between; however, the *P. k.* subsp. *utahensis* lie at the end of a set of long parallel edges. Similarly, the *P. k.* subsp. *latifolia* and *P. wardii* were bundled at the end of multiple long parallel edges. Another group of interest was the three California *P. k.* subsp. *kingii* that grouped with *P. cordiformis*, a species found outside of this group. The reticulation among these taxa had long edges while the *P. k.* subsp. *kingii* specimens emerged on short edges and in one case an internal node found internally on *P. cordiformis*. The *P. cordiformis* species had a long edge that separated it from the *P. k.* subsp. *kingii*.

The *P. occidentalis* group, while mostly clustering together, does not stand out fully from the rest of the network, in one instance sharing a sequence with *P. wardii* 34. In addition, this group clustered slightly with *P. k.* subsp. *cobrensis*, *P. k.* subsp. *latifolia*, and further away with the *P. k.* subsp. *kingii* and *P. cordiformis* region. The one group that does stand alone is *P. k.* subsp. *bernardina* connected to the others only on the central reticulation.

SplitsTree provided fit indices for each network. The complete ITS network (Figure 9) had a fit of 94.164. The network excluding *P. wardii* from Arizona (Figure 10) had a fit of 94.328. Finally, the network with *P. k.* subsp. *kaibabensis* eliminated (Figure 11) had a fit of 94.546.

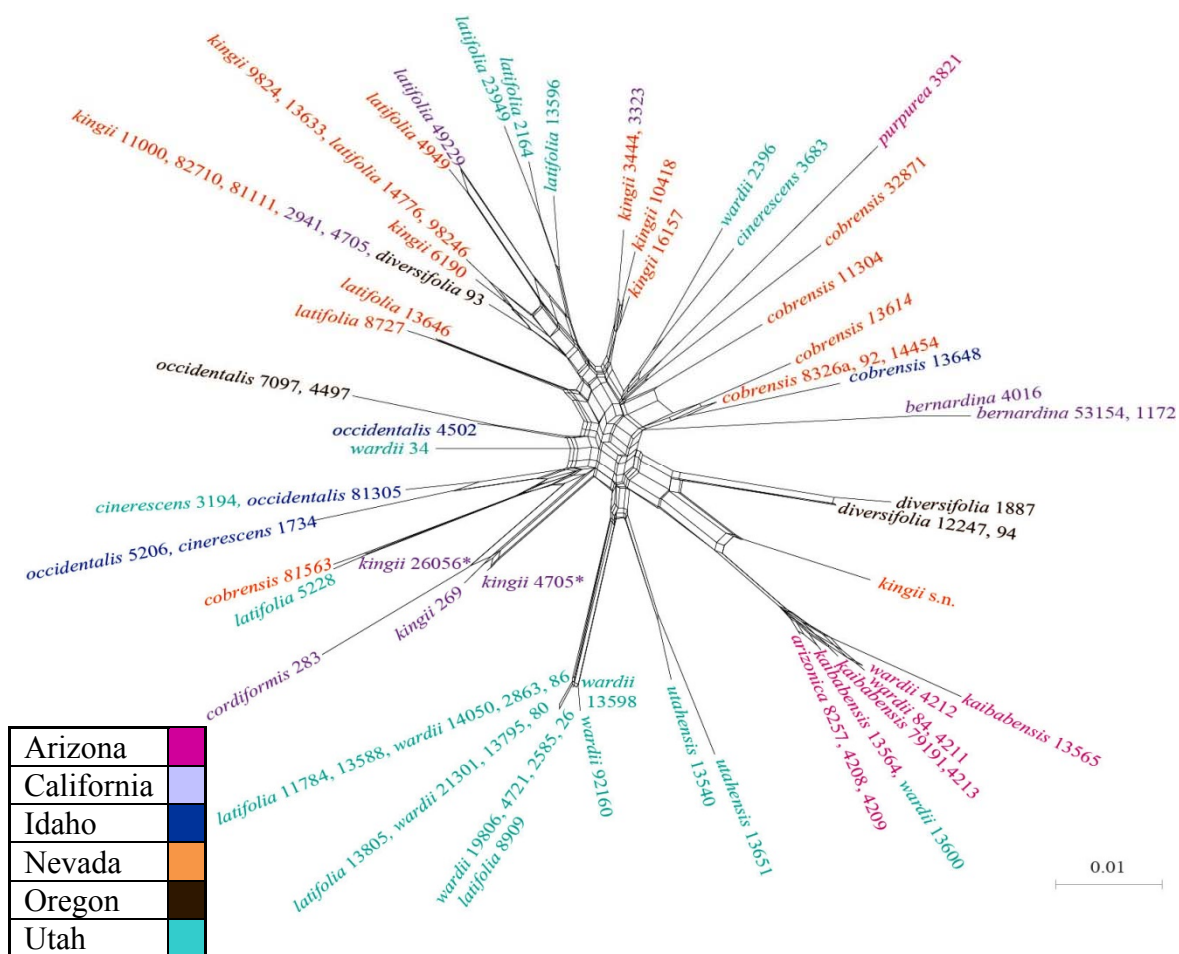


Figure 9. ITS network 1. Includes *P. arizonica* and *P. purpurea*, outgroup excluded. Color coded by state.

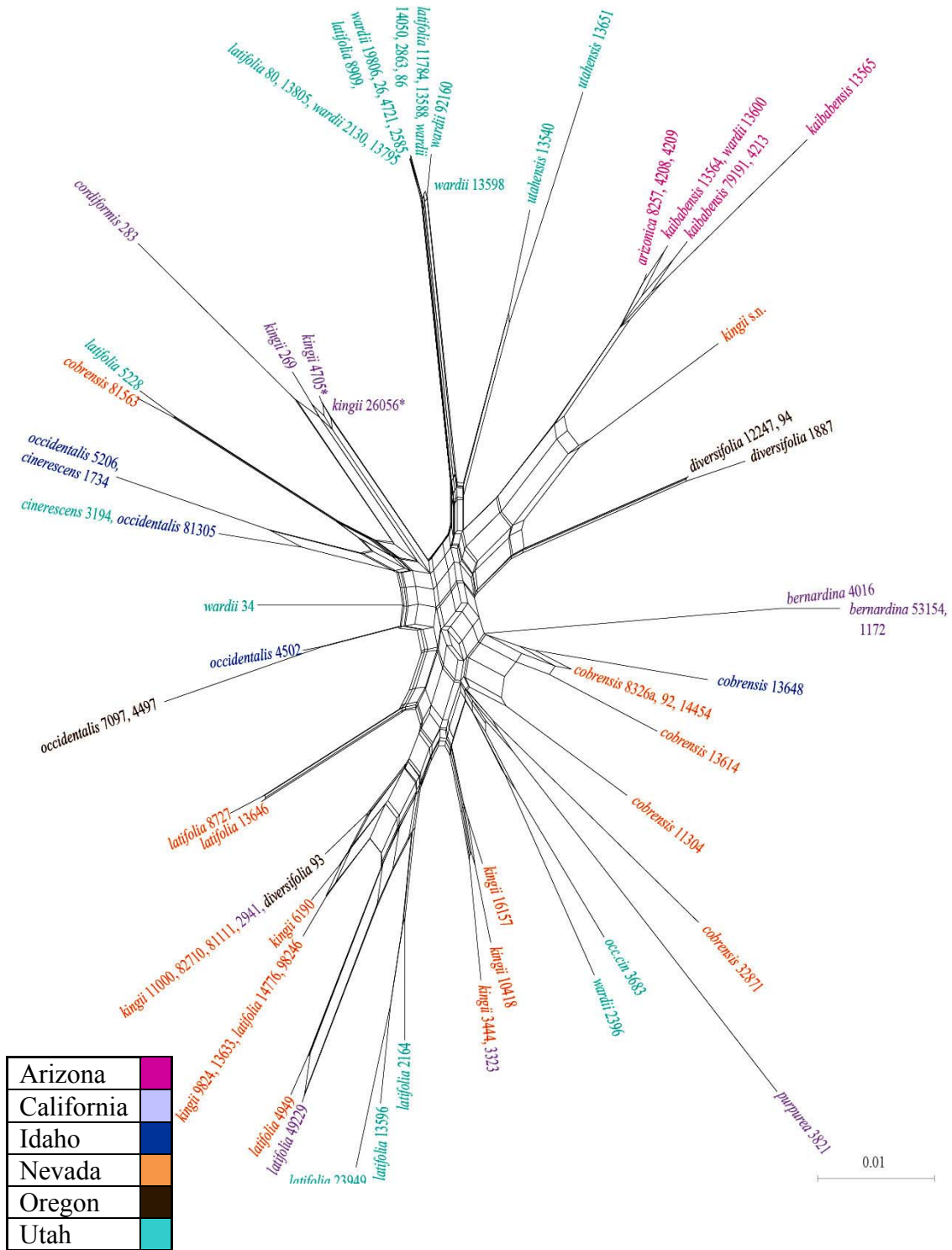


Figure 10. ITS network 2. Arizona *P. wardii* and outgroup removed. Color coded by state.

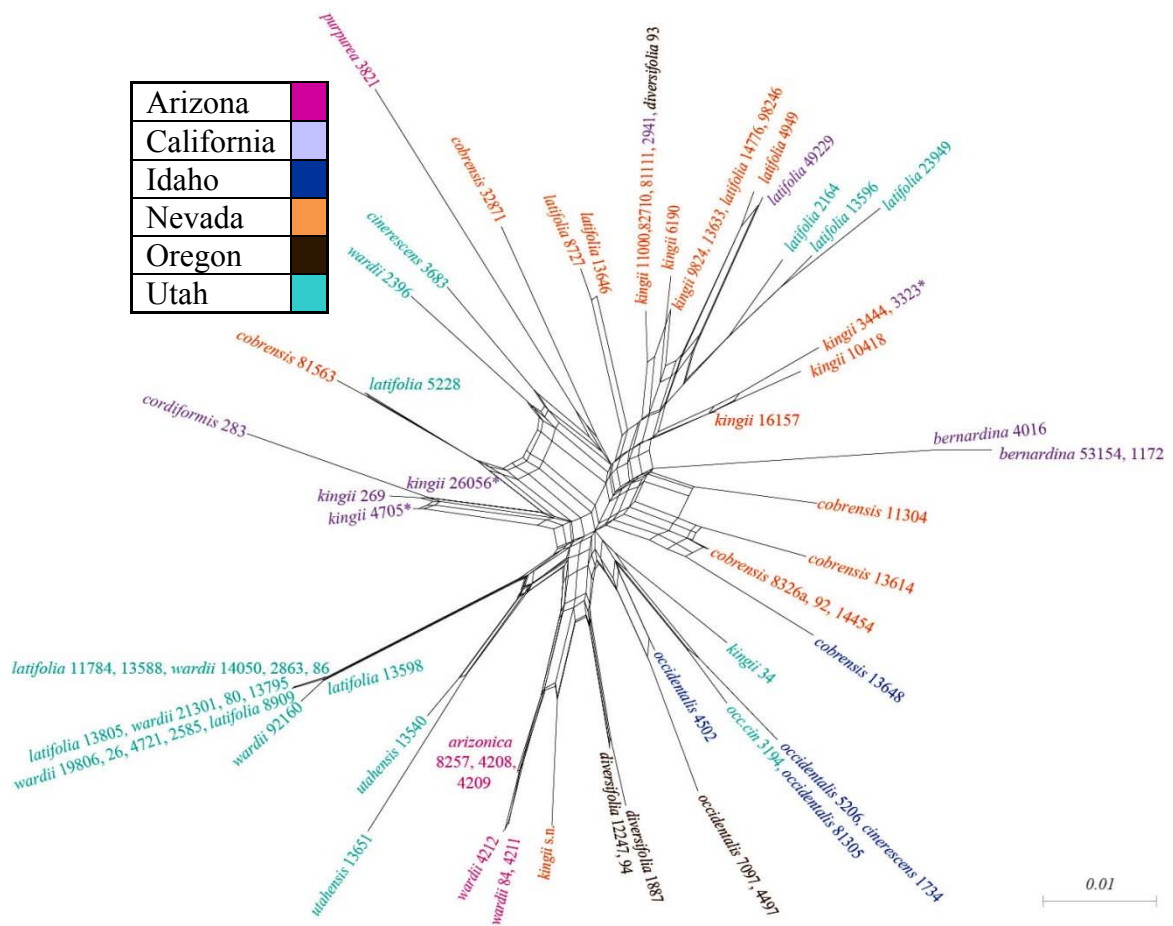


Figure 11. ITS network 3. *Physaria kingii* subsp. *kaibabensis* and outgroup excluded. Color coded by state.

rps intron Network Analysis

MEGA chose the best model for the *rps* intron, *ndhC-trnV* intergenic spacer and the combined chloroplast regions as T92. The closest model offered within SplitsTree for the same three regions was Jukes Cantor. The *rps* intron network had less overall reticulation than the ITS networks with longer internal edges, and three major clusters extending

outward (Figure 12). The bottom left portion of the network was more tree-like in form with the remaining network more net-like. Several subspecies were scattered throughout the network; these include *P. wardii*, *P. k.* subsp. *cobrensis*, subsp. *latifolia*, subsp. *kingii*, and *P. o.* subsp. *occidentalis*. The first cluster was made up of many long parallel edges with short edges protruding. This group included *P. k.* subsp. *kingii* from California and Nevada; all of the *P. k.* subsp. *diversifolia*; *P. k.* subsp. *cobrensis* 13614 and 81563, found in Nevada; *P. k.* subsp. *latifolia* from Nevada, California, and Utah; all of the *P. k.* subsp. *bernardina*; one *P. o.* subsp. *occidentalis* from Oregon, and *P. cordiformis*, both the *P. k.* subsp. *bernardina* and the *P. o.* subsp. *occidentalis* were separated from the others by single long edges.

Connecting the first cluster and the second was an internal node signifying a group of *P. k.* subsp. *latifolia* and *P. wardii*. The second large bundle included multiple *P. wardii* on the right side connected by long edged reticulation to *P. arizonica* as well as multiple *P. k.* subsp. *cobrensis*, a single *P. k.* subsp. *kingii*, and one *P. wardii*. *P. arizonica* was found on an internal node of the long edge of *P. k.* subsp. *cobrensis* 8326a.

Similar to the first two groups, the final was connected by long-edged reticulations. *P. o.* subsp. *cinerascens* 95 protruded from the network with a long edge with *P. k.* subsp. *kingii* 269, 26056, and 2941 found on an internal node. Further down another internal node included *P. k.* subsp. *latifolia* 13805 and *P. wardii* 80. Clustering together on the left side of this group were the Arizona taxa: *P. k.* subsp. *kaibabensis* and *P. wardii*. Two *P. wardii* from Utah were grouped with the Arizona cluster.

The more tree-like area had a small amount of reticulation in comparison to the rest of the network. This region included *P. k.* subsp. *latifolia* from Nevada and Utah, *P. k.* subsp. *cobrensis*, subsp. *utahensis*, *P. wardii*, *P. o.* subsp. *occidentalis*, and *P. o. cinerascens*. *Physaria kingii* subsp. *cobrensis* 32871 extends out on a long edge with a set of parallel edges internally from which *P. k.* subsp. *cobrensis* 13648 lays on a minimal edge. *Physaria kingii* subsp. *latifolia* 23949 was found on an interior node connecting *P. k.* subsp. *cobrensis* with *P. wardii*. The *P. k.* subsp. *utahensis* taxa emerge from many short parallel edges connected to *P. k.* subsp. *latifolia* 13596 and 13646. Finally, the fit index for the *rps* intron network was 94.156.

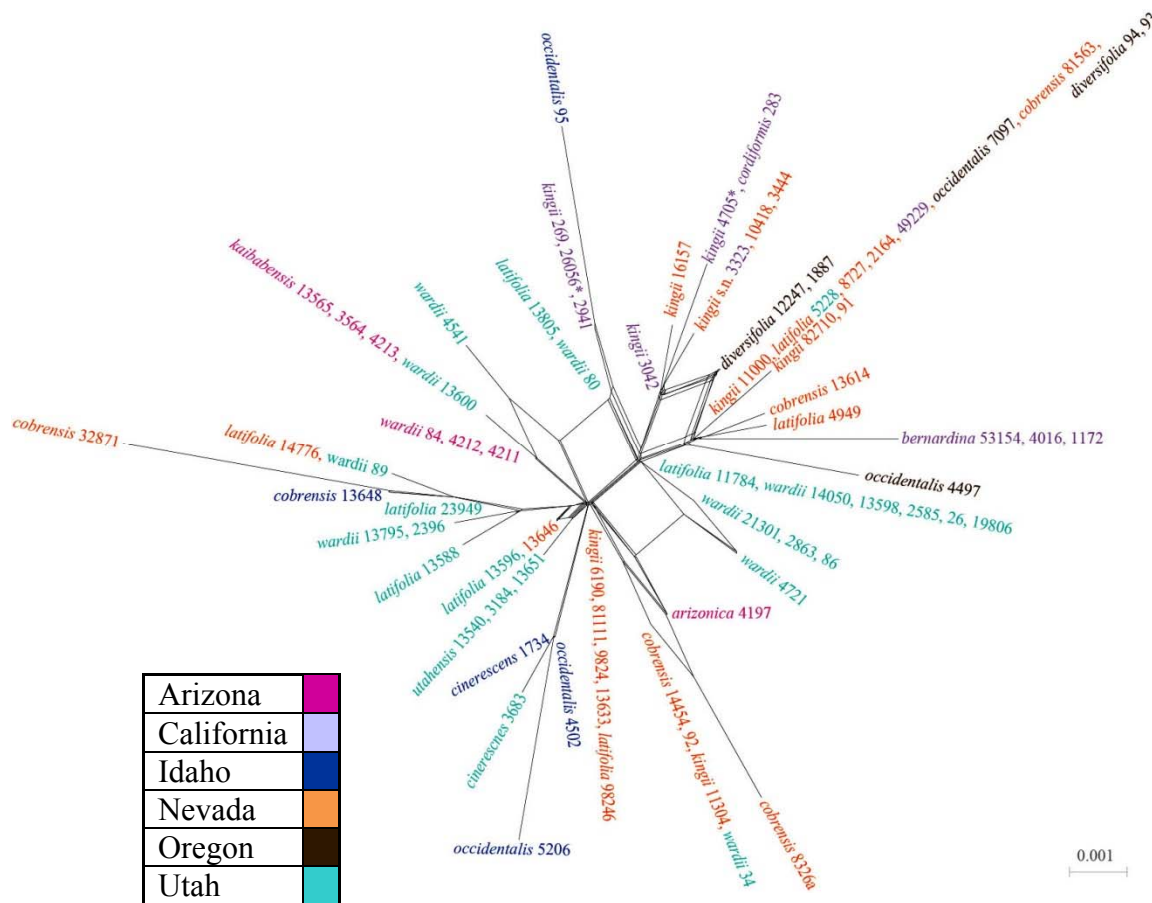


Figure 12. *rps* intron network. Outgroup excluded. Color coded by state.

ndhC-trnV Intergenic Spacer Network Analysis

The *ndhC-trnV* intergenic spacer network (Figure 13) had long-edged reticulations in the center similar to the *rps* intron though was more tree-like in form. It differs from the other networks in that it did not have large clusters of specimens. *Physaria kingii*

subsp. *latifolia* was found distributed throughout the network. On a lesser scale, *P. k.* subsp. *cobrensis* and subsp. *kingii* were also seen dispersed around the structure. The edges emerging from the network were mid length to long, with very few short edges. In addition, there were only two nodal individuals.

Starting from the top of the network, from a single node came four edges and in one case parallel edges. Three California *P. k.* subsp. *kingii* along with one from Nevada make up one edge, *P. k.* subsp. *latifolia* from Nevada another, most of the Arizona representatives in the third and the fourth had parallel edges, which was made up of *P. o.* subsp. *occidentalis* and subsp. *cinerascens*. The node itself was made up of a large variety of taxa with the same sequence including many *P. k.* subsp. *kingii*, a handful of subsp. *latifolia*, a large number of *P. wardii*, a single subsp. *kaibabensis*, one *P. o.* subsp. *occidentalis* and one *P. cordiformis*.

Coming from the same node, arose a single long edged reticulation with three mid-length edges protruding on one end and a single edge on the other. Of the three edges, two each held a single *P. k.* subsp. *latifolia*, both from Utah. The third held variable taxa that all had the same sequence including most of the *P. k.* subsp. *cobrensis*, all from Nevada save one 13648, from Idaho, all of the subsp. *utahensis*, a couple *P. wardii*, and a single subsp. *latifolia* from Utah. On the far side of the reticulation was a single *P. wardii* from Nevada. At the base, three edges stemmed from a single node. These were all Utah individuals including one *P. k.* subsp. *latifolia* and three *P. wardii*. *Physaria kingii* subsp.

latifolia 13805 was a node on the edge of *P. wardii* 80. *P. o.* subsp. *occidentalis* 11305 was the only specimen emerging from the center of the network.

On the other side of the structure, *P. k.* subsp. *cobrensis* 13614 came out by itself on a single edge. Separated from this by multiple reticulations, were three *P. k.* subsp. *latifolia* on two edges. A single Utah *P. k.* subsp. *latifolia*, 4949 on one and the other with *P. k.* subsp. *latifolia* from California and Nevada. Close by emerging on a single long edge was *P. k.* subsp. *latifolia* 2164 with connection to three *P. k.* subsp. *diversifolia* individuals at the other end of a set of parallel edges, also on a single long edge. The final grouping had two somewhat short edges with two *P. o.* subsp. *occidentalis* representatives from Oregon, 4497 and 7097, on one while the other had a variety of taxa including *P. k.* subsp. *kingii* from Nevada, a single Utah *P. k.* subsp. *latifolia*, a single *P. k.* subsp. *cobrensis* and all three *P. k.* subsp. *bernardina*. The fit index for the *ndhC-trnV* intergenic spacer network was 97.189.

Combined Chloroplast Network Analysis

The final network was the combined chloroplast (Figure 14). Combining the two sequences allowed for some resolution ending with a network that was more tree-like with less central reticulation, and two central nodes that gave rise to five clusters. Both *P. k.* subsp. *latifolia* and *P. k.* subsp. *kingii* were found in all five groups while *P. wardii* appeared in four of the five. One end was separated from the other clusters by long parallel edges. This contained *P. k.* subsp. *latifolia* from California, Nevada, and Utah, all subsp. *diversifolia*, two subsp. *cobrensis*, all of the subsp. *bernardina*, and a few subsp. *kingii* from Nevada. *P. o.* subsp. *occidentalis* 4497 was at the end of a long edge with a

short amount of internal reticulation from which *P. o.* subsp. *occidentalis* 7097 emerged. *Physaria kingii* subsp. *cobrensis* 13614 was separated somewhat by the others of this cluster by coming out further down the edge than the others which grouped around the tip.

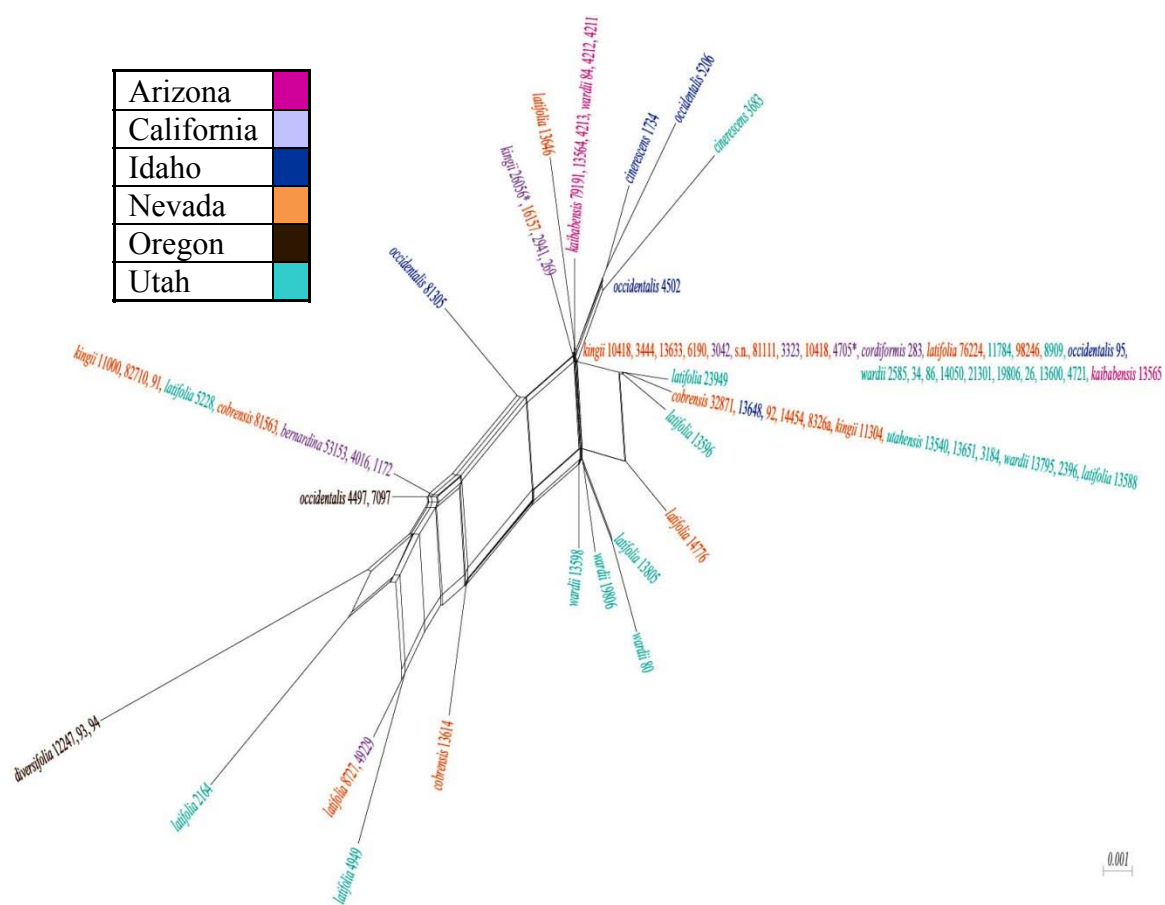


Figure 13. *ndhC-trnV* intergenic spacer network. Outgroup excluded. Color coded by state.

From the top-most central node emerged two groups on either side. The bottom was a small cluster that included only taxa from Utah including *P. k.* subsp. *latifolia* 86, and three *P. wardii* specimens. On the other side, a large cluster with a variety of taxa emerged with reticulation among the edges of this group. This collection included *P. k.* subsp. *latifolia* from Utah many *P. k.* subsp. *kingii* from Nevada and California, a few *P. wardii*, a single *P. o.* subsp. *occidentalis*, and *P. cordiformis*.

The final two groups broke off from short edged reticulation at the far end of the network. The top cluster included *P. o.* subsp. *occidentalis* and subsp. *cinerascens* on a long parallel edge with three single edges emerging from the tip. *P. o.* subsp. *occidentalis* 4502 was found at the node from which the three edges originated. Found at the basal node, *P. k.* subsp. *kingii* and subsp. *latifolia*, both from Nevada. On a set of parallel edges, the Arizona species bunch together and included one *P. wardii* specimen from Utah, 13600.

The final cluster had long edged reticulation from which both short and long edges arose. This group included a large variety of taxa including *P. k.* subsp. *kingii* from Utah and Nevada, many subsp. *cobrensis*, subsp. *utahensis*, subsp. *latifolia*, and *P. wardii*. Two of the *P. k.* subsp. *cobrensis* specimens, 32871 and 8326a, each had long edges with more groups of subsp. *cobrensis* emerging internally. Finally, the fit index for the combined chloroplast network was 97.467.

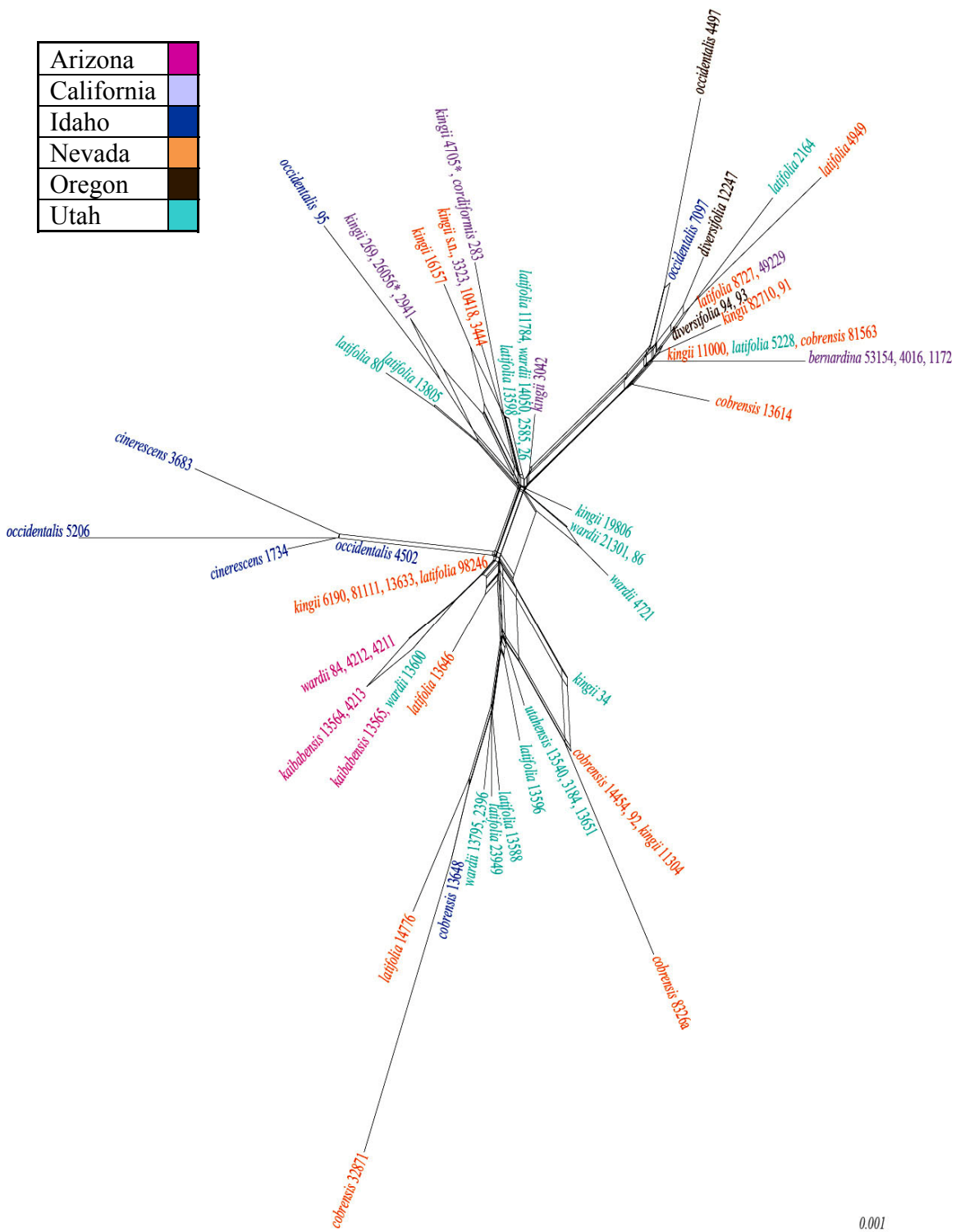


Figure 14. Combined chloroplast network. Outgroup excluded. Color coded by state.

Phylogenetic Analyses

ITS Bayesian Analysis

Overall the ITS phylogenetic tree (Figure 15) had high nodal support, with low support only found on a few internal nodes. *P. purpurea* was outside the *P. k.* subsp. *kingii* group. Within, most of the taxa were not shown to be monophyletic, with only *P. k.* subsp. *utahensis* and subsp. *bernardina* clustering together, however these were found within the whole of the *P. kingii* group. *Physaria kingii* subsp. *latifolia*, subsp. *kingii*, subsp. *cobrensis*, and *P. wardii* were found scattered throughout the tree. Both *P. o.* subsp. *occidentalis* and subsp. *cinerascens* were found clustered together on the tree but with no resolution between the two. Additionally, it was found within the *P. kingii* group. Lastly, the Arizona specimens group together with *P. arizonica*.

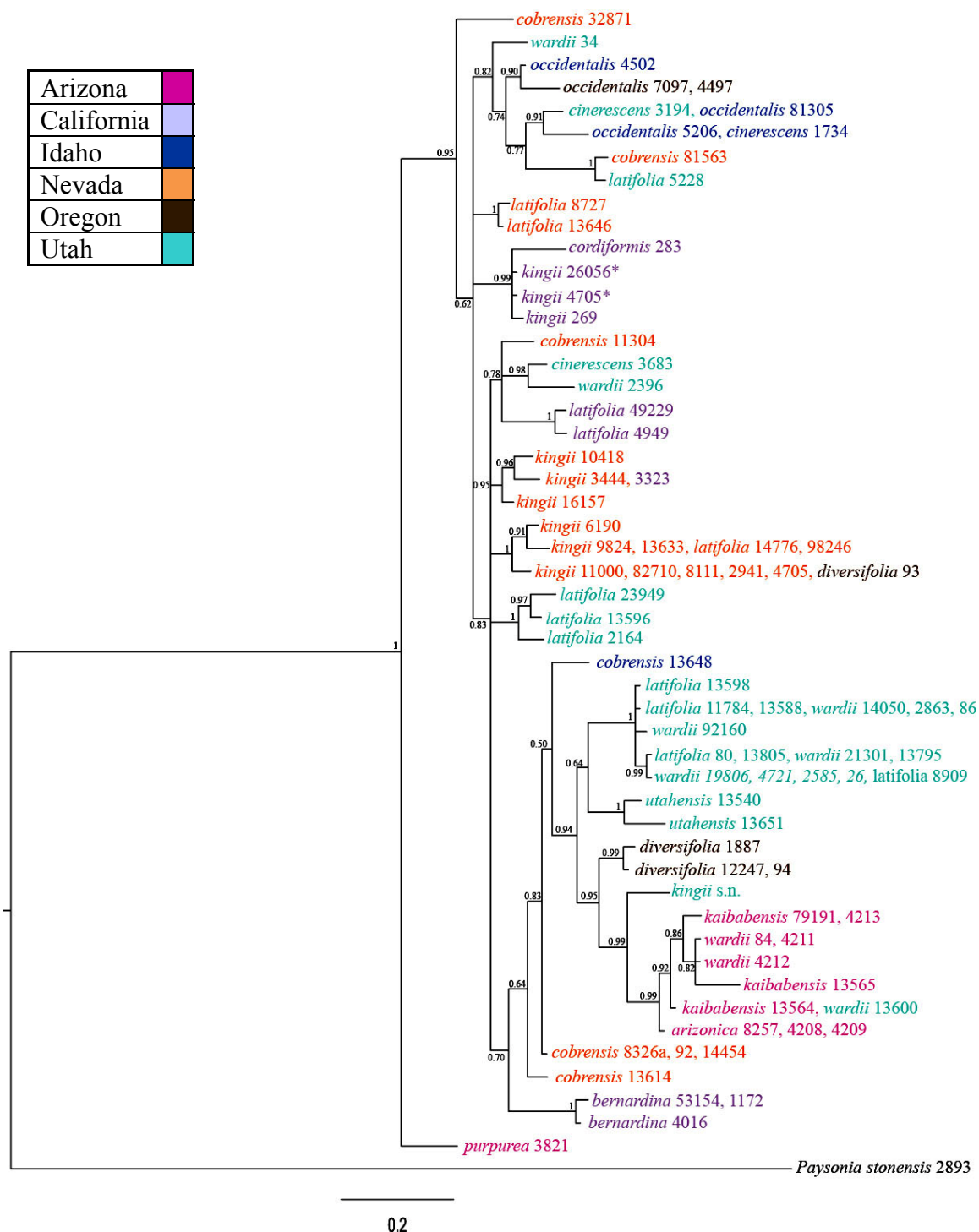


Figure 15. ITS Phylogeny. Includes posterior probabilities for nodal support. Color coded by state.

rps intron Bayesian Analysis

The *rps* intron phylogenetic tree (Figure 16) had little resolution. Nearly every taxon was found scattered throughout the tree. The branches that were bifurcating had posterior probabilities that ranged from 0.57–1. *P. arizonica* was found within the group and was sister to *P. k.* subsp. *cobrensis* 14454 and 92, subsp. *kingii* 11304, and *P. wardii* 34. The Arizona individuals, *P. k. subsp. kaibabensis* and *P. wardii*, were found to be sister to the Utah *P. wardii* 4541.

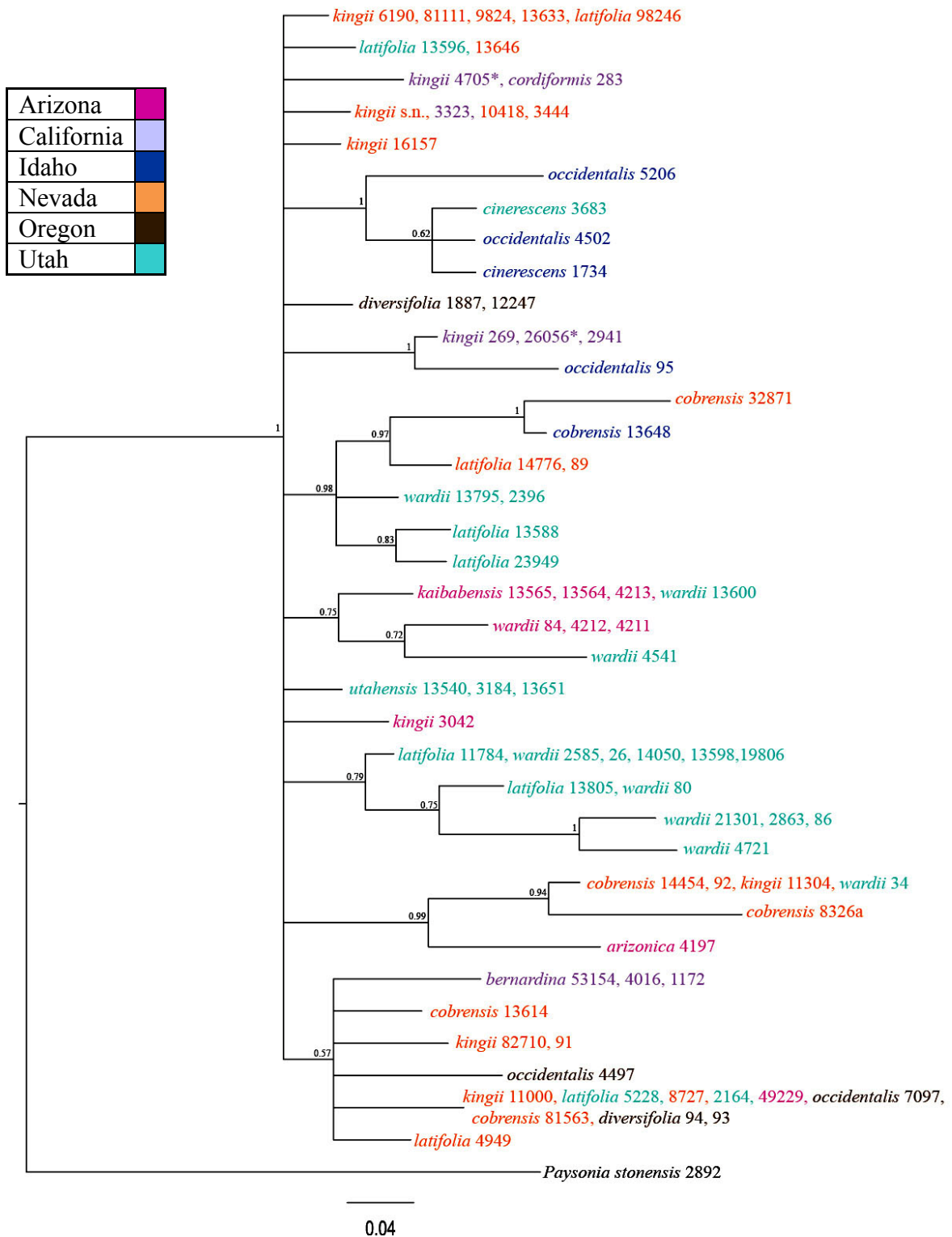


Figure 16. *rps* intron phylogeny. Includes posterior probabilities to show nodal support. Color coded by state.

ndhC-trnV Intergenic Spacer Bayesian Analysis

Similar to the *rps* intron tree, the *ndhC-trnV* intergenic spacer tree (Figure 17) had little resolution. There were no monophyletic taxa, in fact all taxa were spread throughout the phylogeny. *P. arizonica* was found within a large polytomy of *P. k.* subsp. *latifolia*, subsp. *cobrensis*, subsp. *utahensis* and *P. wardii*.

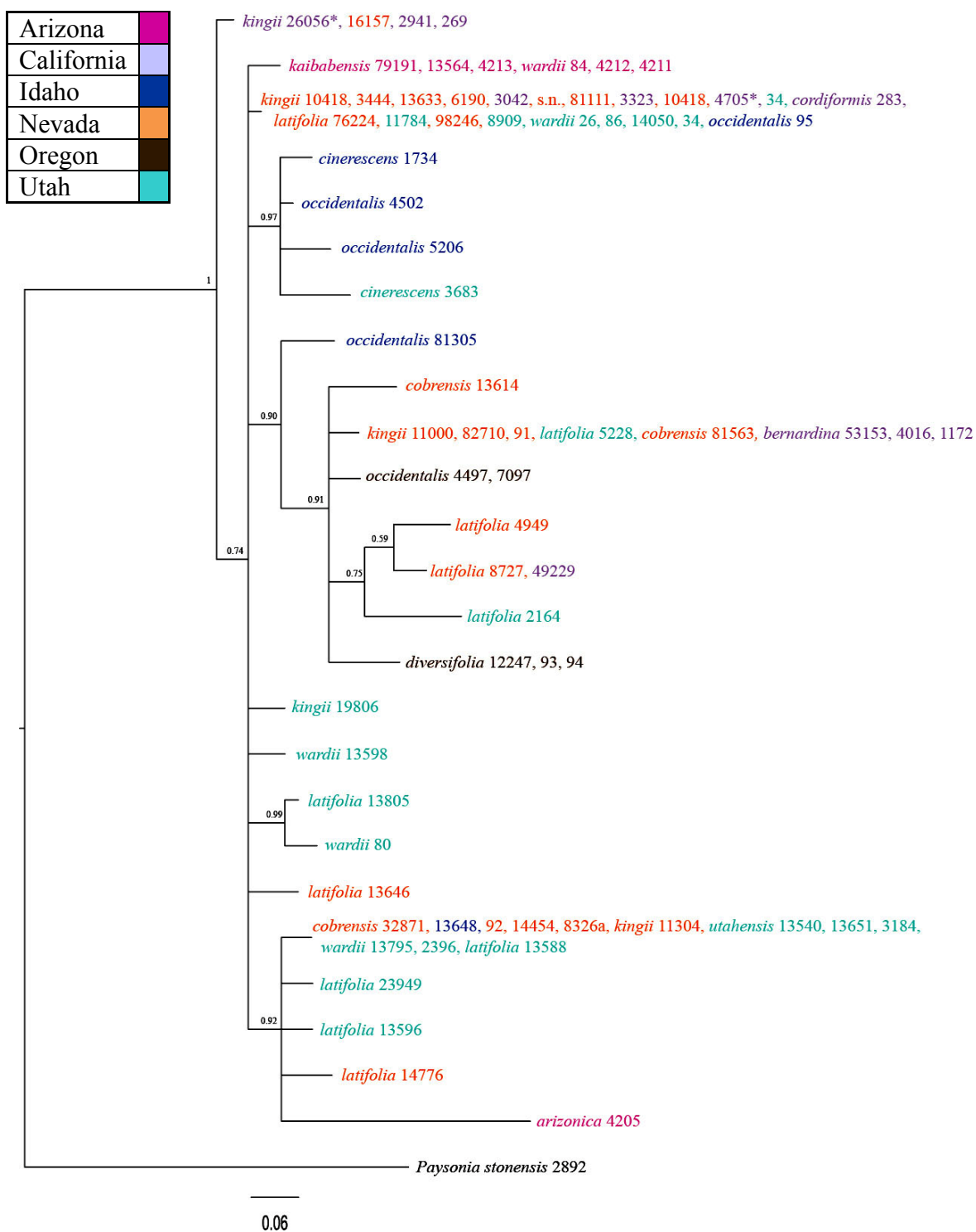


Figure 17. *ndhC-trnV* intergenic spacer phylogeny. Includes posterior probabilities for nodal support and color coded by state.

Combined Chloroplast Bayesian Analysis

Combining the chloroplast sequences increased the resolution in the tree a little, though there was still a large polytomy (Figure 18). The taxa were not monophyletic and like both the *rps* intron and the *ndhC-trnV* intergenic spacer, all of the taxonomic groups were spread throughout the tree. The Arizona taxa, *P. k.* subsp. *kaibabensis* and *P. wardii* were clustered together with the *P. k.* subsp. *latifolia* and sister to *P. wardii* 4541. *P. arizonica* was sister to a variety of *P. k.* subsp. *cobrensis*, subsp. *kingii*, and *P. wardii*.

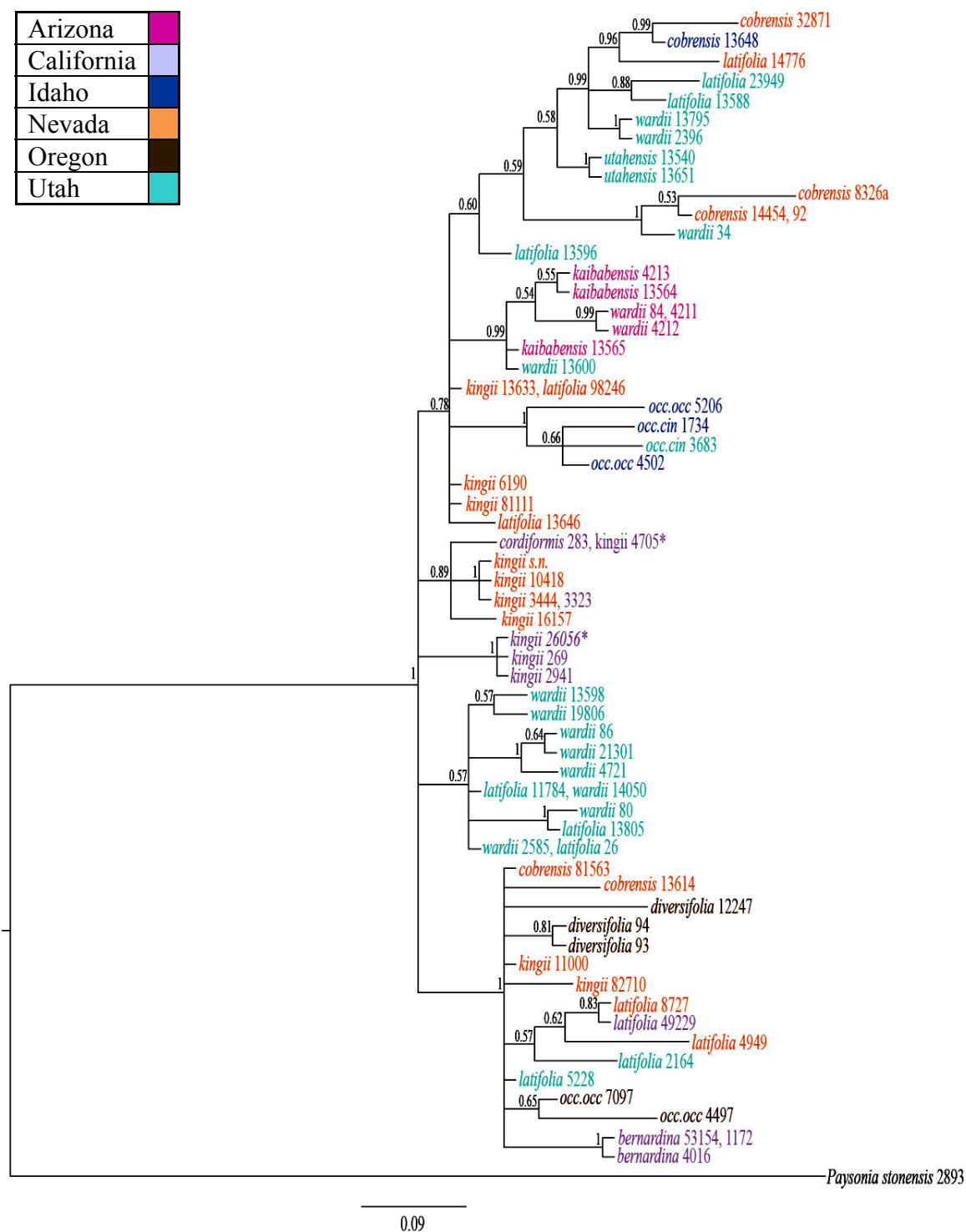


Figure 18. Combined chloroplast phylogeny. Includes posterior probability for nodal support. Color coded by state.

CHAPTER 4

DISCUSSION

Sequence Analyses

In this dataset, individuals from each of the subspecies frequently had identical sequences with others in the same taxon, with other subspecies within the *P. kingii* group, and at times with other species outside of the *P. kingii* group such as *P. occidentalis* and *P. cordiformis*, taxa outside of this species. In ITS, this was often seen with *P. k.* subsp. *latifolia*. Those found in Utah often had sequences identical to *P. wardii*, also found in Utah, while those found in Nevada often had sequences identical to *P. k.* subsp. *kingii* from Nevada. Hall (2011) indicated that average p-distance should be below 0.33 for a good phylogenetic analysis. P-distance scores as low as ITS (0.02), *rps* intron (0.0066), and *ndhC-trnV* intergenic spacer (0.0158) indicated highly similar sequences. Thus, the identical sequences were not remarkable. Additionally, these taxa could be related enough that gene flow is still happening in areas where taxa overlap such as in Utah and Nevada.

There were more individuals that had identical sequences in both of the chloroplast regions than in ITS, with more in the *ndhC-trnV* intergenic spacer than the *rps* intron. As the *rps* intron is a longer region, it is expected to have more mutations. These data also support Egan and Crandall's (2008) finding that chloroplast DNA has a larger proportion of indels, as well as Baldwin et al. (1995) that ITS has more point mutations than length mutations and fewer indels. Perhaps the most notable indel was the

deletion found in all of the *P. k.* subsp. *diversifolia* in the *ndhC–trnV* intergenic region, a deletion of 241 bases out of the total 664 bases, approximately 36% of the total length, though this deletion was not enough to separate subsp. *diversifolia* from the *P. kingii* group.

Phylogenetic Analyses

Results provided by a network are different from that of a phylogenetic tree. A network provides clusters of similar taxa that are more alike to one another than to those outside the cluster, separating individuals into groups (Dress et al. 1996, Morrison 2012). In addition, an internal node may represent extant taxa, indicating there is no unique pattern separating it from the others in the network, whereas phylogenetic trees have internal nodes that only represent ancestral speciation events (Barracough and Nee 2001, Morrison 2010, 2012).

When incompatibilities are found within the network data, whether from hybridization, homoplasy, recombination, or other evolutionary processes, loops or parallel edges are formed (Posada and Crandall 2001). Thus, networks with more reticulation reveal more conflicts among the data (Dress et al. 1996). The edge lengths in a network represent the number of differing characters between taxa and indicate the significance of the split (Dress et al. 1996; Morrison 2010, 2012). In addition, a network that is more tree-like in form indicates compatibility among the data whereas a net-like form shows weak compatibility and provides little information (Dress et al. 1996; Huson 2008).

As was seen in Figure 9, the ITS network was more net-like in form with a large reticulated center. As mentioned, reticulation indicates conflict, arising from underlying evolutionary processes that are present. This network had a large central area of reticulation likely revealing incomplete lineage sorting which suggests that genetic drift and selection have not had enough time to separate the lineages. Further, the net-like form of the ITS network indicated that there was much conflict and little compatibility within data so little could be extrapolated.

While as a whole the ITS network provided little information, there were some regions that provided some interesting clues as to what the phylogenetic tree might look like. For instance, *P. k.* subsp. *bernardina* looked as if it was separate from the rest of the *P. kingii* group as there was little reticulation other than that found centrally and it lays at the end of a long edge. Furthermore, while *P. k.* subsp. *utahensis*, only found in Utah, clustered with *P. k.* subsp. *latifolia* and *P. wardii* specimens from Utah, subsp. *utahensis* lays at the end of a long edge indicating they were different from the other taxa. Finally, the *P. occidentalis* group, while mostly clustering together, also aggregated with those within the *P. kingii* group, a good indication that they are closely related.

Networks can give insight as to whether hybridization events have happened. To discover if *P. kingii* subsp. *kaibabensis* was hybridizing or is possibly a hybrid, samples from two *Physaria* species outside this group, *P. arizonica* and *P. purpurea*, but found on the Kaibab Plateau were included in the dataset. The ITS networks and trees indicate that *P. purpurea* is outside of the *P. kingii* group due to the long edge and very little

reticulation. *P. arizonica*, however, clustered with the *P. kingii* specimen from Arizona, *P. wardii* from Arizona, and single *P. wardii* from Utah. To test the relationships, three ITS networks were constructed, one with *P. kingii* subsp. *kaibabensis*, *P. wardii* from Arizona, and *P. arizonica*; one with *P. kingii* subsp. *kaibabensis* removed; and one with the *P. wardii* from Arizona removed. In all three networks (Figures 9-11) *P. arizonica* clustered with the other Arizona taxa indicating there were likely hybridization events involving all three taxa and possibly pointing to introgression.

Looking at the ITS tree (Figure 15), *P. arizonica* is sister to *P. kingii* subsp. *kaibabensis* and *P. wardii* with high support, a posterior probability of 0.99. *P. arizonica* was also included in the chloroplast trees to see if we could discover the maternal species. In the *rps* intron tree (Figure 16), *P. arizonica* did not cluster with the other Arizona species but was sister to a group that included *P. kingii* subsp. *cobrensis*, subsp. *kingii*, and subsp. *wardii* with a posterior probability of 0.99. In the *ndhC-trnV* intergenic spacer tree (Figure 17), *P. arizonica* was in a polytomy with *P. kingii* subsp. *latifolia*, subsp. *utahensis*, subsp. *cobrensis*, subsp. *kingii* and *P. wardii*, with a posterior probability of 0.92. This suggested that *P. arizonica* was not the maternal species; the data does not give firm evidence as to the relationships among the Arizona taxa other than hybridization events have likely occurred.

Morphologically, the *P. wardii* in Arizona are unlike others in this taxon in that they have glabrous inner valves rather than pubescent inner valves, and more ovules per ovary (8–12 ovules per ovary compared to 4). At this point, we cannot conclusively determine

which is the hybrid species. However, it is my suspicion that these are not in fact *P. wardii* but are the product of hybridization between *P. k.* subsp. *kaibabensis* and *P. arizonica*. Without further work, it is impossible determine the hybrid from the parent species.

The *rps* intron network had less reticulation and longer internal edges than the ITS network. This indicated that there was less conflict within this dataset. With many of the subspecies found throughout the network, it is likely that subspecies will not be monophyletic. Additionally, there were more individuals at internal nodes in the *rps* intron than in ITS (ten compared to five) showing that there were many sequences that were not significantly different from the sequences surrounding them.

Unlike in ITS, *P. k.* subsp. *utahensis* in the *rps* intron network did not cluster with *P. wardii* but, rather, was found with two individuals of *P. k.* subsp. *latifolia* that had identical sequences, one from Nevada and one from Utah. Additionally, the *P. k.* subsp. *utahensis* were at the end of a short edge, unlike in ITS, indicating there was little difference between it and the other taxa in this cluster. The *P. occidentalis* group was found scattered throughout the network similar to ITS, which again indicated that these are likely very closely related to *P. kingii*.

The network for *ndhC-trnV* intergenic spacer (Figure 13) was more tree-like than those of the *rps* intron or ITS, indicating less conflict and more compatible data. Most of the taxa were found throughout the network similar to the other networks illustrating that there would be little resolution in the phylogenetic trees. While there were more shared

sequences, this region had taxa on only two internal nodes indicating that the sequences were more unique from one another. The *P. occidentalis* group was found throughout, similar to the other networks, again suggesting that these were very closely related to *P. kingii*. *P. kingii* subsp. *bernardina* had an identical sequence with individuals of subsp. *kingii*, subsp. *latifolia* and subsp. *cobrensis*. Additionally *P. kingii* subsp. *utahensis* had an identical sequence with individuals of subsp. *cobrensis*, subsp. *kingii*, subsp. *latifolia* and with *P. wardii*. This indicated that these taxa were not different and will remain subspecies of *P. kingii*, rather than full species.

The combined chloroplast network (Figure 14), provided better resolution than either separate chloroplast network; however, it also indicated that the taxa would not be monophyletic. Of note, *P. kingii* subsp. *bernardina* was found as separate at the end of a long edge however internally there was a lot of reticulation shared with other taxa suggesting that this will still be found as a subspecies of *P. kingii*.

Each network output using SplitsTree was graded by fitness to indicate how accurate the portrayal was. A higher fit measure suggests a more accurate representation (Dress et al. 1996). Each of the networks, all three ITS, *rps* intron, *ndhC-trnV* intergenic spacer, and the combined chloroplast, had high fit measures, 94.164, 94.328, 94.546, 94.156, 97.189, 97.467 respectively. This indicated that the data provided by the networks were an accurate portrayal.

Neither the nuclear nor the chloroplast trees provided support for the *Physaria kingii* group (Figures 15-17). None of the taxa were monophyletic indicating that these should

all remain as subspecies of *P. kingii*. Additionally, if *P. wardii* and *P. k.* subsp. *latifolia* were a single taxon, more clustering of the two would be expected. Looking strictly at shared sequences, *P. kingii* subsp. *latifolia* and *P. wardii* individuals had identical sequences three instances in ITS and *rps* intron but only once in *ndhC–trnV* intergenic spacer. Interestingly the identical sequences were found only from among the *P. kingii* subsp. *latifolia* from Utah and not those collected in Nevada or California. Comparably, *P. kingii* subsp. *latifolia* had identical sequences in *ndhC–trnV* with every other subspecies in *P. kingii*, except subsp. *diversifolia*, and to two taxa outside of the group, *P. cordiformis* and *P. occidentalis* subsp. *occidentalis*. *P. wardii* had identical sequences with *P. k.* subsp. *kingii*, subsp. *cobrensis*, and subsp. *kaibabensis* in addition to subsp. *latifolia*. In *ndhC–trnV*, *P. wardii* had identical sequences as *P. k.* subsp. *kingii*, subsp. *utahensis*, subsp. *cobrensis*, subsp. *kaibabensis*, subsp. *latifolia*, *P. occidentalis*, and *P. cordiformis*.

Looking at the trees and networks, in ITS (Figures 9, 10, 11, and 15) many *P. k.* subsp. *latifolia* from Utah cluster with both subsp. *utahensis* and *P. wardii* but can also be found in other areas of the tree. Further, *P. k.* subsp. *latifolia* from Nevada and California do not group together with *P. wardii* and can be found throughout the rest of the tree. The same can be said for the *rps* intron tree (Figure 16). There is some clustering of *P. k.* subsp. *latifolia* from Utah with *P. wardii* but both can be found throughout the tree not clustering together. The *ndhC–trnV* tree (Figure 17) has is no clustering of these two taxa. The combined chloroplast tree (Figure 18) does show some clustering but with low support and, in one case, *P. wardii* was found sister to *P. k.* subsp. *cobrensis*.

Morphologically *P. wardii* can look similar to *P. k.* subsp. *latifolia* with rounded acute apices and longer than wide fruits, though often obcompressed, as Nelson (1906) initially noted, or they can also look somewhat like *P. k.* subsp. *kingii* with truncate apices, somewhat swollen valves on either side of the replum, and sometimes even oblate. These morphological differences do not separate out neatly on the trees. The *P. wardii* individuals with truncate apices often clustered with *P. k.* subsp. *latifolia* whereas the individuals with rounded-acute apices did not cluster with *P. k.* subsp. *latifolia*. Based on the molecular and morphological data, the *P. k.* subsp. *latifolia* and *P. wardii* will be separated into two distinct taxa, both as subspecies of *P. kingii*. *P. wardii* will be renamed *P. k.* subsp. *wardii* (Watson) Minnaert-Grote and O’Kane.

This study did not initially intend to examine whether *P. occidentalis* was included within *P. kingii*. However, after suggestions from multiple herbaria and close morphological and taxonomic investigation, it was clear that they are closely related. While we did not include enough data to conclusively accept that the *P. occidentalis* species should be included within *P. kingii*, the results of this study suggest this. In every phylogenetic tree (Figures 15-18), *P. occidentalis* was found to be not monophyletic. Further studies with more population level sampling should be done before making *P. occidentalis* a member of the *P. kingii* subspecies.

A few specimens of *P. kingii* subsp. *kingii* found only in the White Mountains in Mono County, California had white, rather than yellow, petals. Two representatives (4705 and 26056, indicated with a star in the trees and networks) were included in the

molecular portion of the study to determine if these were a new taxon or a polymorphism of *P. kingii* subsp. *kingii*. In the ITS tree (Figure 15), both individuals were in a polytomy with *P. k.* subsp. *kingii* 269 from neighboring Inyo Co. and *P. cordiformis*, also found in California. The polytomy had a posterior probability of 0.99. In the *rps* intron tree 4705 had an identical sequence as *P. cordiformis* and 26056 and other California *P. k.* subsp. *kingii* individuals, 269 and 2941, had identical sequences. The former were sister to *P. o.* subsp. *occidentalis* 95 with a posterior probability of 1. The *ndhC-trnV* intergenic spacer sequences provided the least amount of data with 26056 and three other *P. k.* subsp. *kingii* having identical sequences. These individuals were outside of the rest of the *P. kingii* group with a posterior probability of 1. Individual 4705, as well as individuals from *P. k.* subsp. *kingii*, subsp. *latifolia*, *P. cordiformis*, *P. wardii* and *P. o.* subsp. *occidentalis* had identical sequences that were within a large polytomy with a posterior probability of 0.74. The combined chloroplast tree (Figure 18) provided no resolution of this issue. While the California individuals often clustered together, they were also found with individuals from Nevada. Further, the white flowers did not always cluster together. At this point, it appears that the white petaled individuals are phenotypic variants of *P. kingii* subsp. *kingii*. Of note, it seems likely that there is a close relationship between *P. cordiformis* and *P. kingii*, something that should be evaluated in future studies.

Further resolution for each of these questions may possibly have been answered by combining nuclear and chloroplast regions. Partition Finder provided BIC scores which were put into jModelTest. This program determined that the two were significantly

different, thus nuclear and chloroplast regions could not be combined. This suggested that either the two regions were evolving at different rates or have different histories.

Plastic Traits

The question of whether these taxa should stay as subspecies, be elevated to species, or neither remains. Morphologically, each of these taxa are different. Geographically, these taxa are allopatric except for *P. k.* subsp. *kingii*, subsp. *latifolia*, subsp. *cobrensis*, and subsp. *wardii*, which have overlapping ranges. However, on a molecular level there is very little, if any, support for the present taxonomy. This group could benefit from a better nuclear region for molecular work, one that is less constrained. However, thus far, that has been difficult for the genus *Physaria* (Mensen 2013). With little difference in noncoding regions, it is likely that protein-coding regions have even fewer differences. Thus, morphological variations seen among both species and within populations are likely due to phenotypic plasticity.

Phenotypic plasticity is the ability within a single genotype to alter development, physiology, chemistry, morphology, behavior, and life history based on environmental cues that can be internal or external, abiotic or biotic (West-Eberhard 1989; Sultan 2000; Agrawal 2001; Price et al. 2002; Schlichting and Smith 2002). Traditionally, the genotype was described as the blueprint that leads the way, which was then followed by the phenotype, the visual representation of the genotype (Sultan 2000; Ghalambor et al. 2007); however, this way of thinking has been reevaluated. Sultan (2000) defines a genotype as providing a “repertoire of environmentally contingent phenotypic

possibilities” while describing the phenotype as the result of complex systems influenced by interacting genes, gene products, and the environment.

Schlichting and Smith (2002) suggest that plasticity may involve selective up or down regulation patterns of expression. Additionally, environmental influences may alter the interaction of genes and their products within the transcriptome and the proteome. The environment can influence signaling, cross talk of separate signaling pathways, as well as constraints and may possibly modify gene expression within a single genotype. Further, not all genes are transcribed at all times and not all proteins or polypeptides are active at once so the environment may act on different genes at different times (Schlichting and Smith 2002).

While some authors still believe evolution by natural selection on phenotypically plastic traits do not produce adaptive evolutionary responses (de Jong 2005), many others believe that phenotypic plasticity is important not only in the development and function of organisms but also in the adaptive evolution of species (West–Eberhard 1989; Sultan 2000; Ghalambor et al. 2007). McArthur and Wilson (1967) suggested that phenotypic changes were the first to occur and selection on those changes caused genetic differentiation. Plasticity would allow establishment into new niches whether this is new habitat, environmental condition, or a change in fruit or leaf shape that offer some fitness advantage. The traits that allowed the individuals to survive in these niches or to become more fit, later become genetically assimilated so that the environmental stimulus that initially produced those traits would be no longer needed (Baldwin 1896, Ghalambor et

al. 2007). Increased divergence due to phenotypic fixation would likely include an increase in genetic modification before diversifying (West–Eberhard 1989). West–Eberhard (1989) postulates that only those phenotypes that are expressed may be acted upon by selection, and the environment is the determining factor of which phenotypes are exposed to modification.

In the *P. kingii* group, this could be illustrated by looking at *P. k.* subsp. *diversifolia* which can grow in moist habitats on creek banks. While there is genetically little difference between this and the others in the *P. kingii* group, something, likely a plastic trait, has allowed it to move into a new niche, different from the arid habitats that the others are found in. Another example is *P. k.* subsp. *latifolia* which has an overlapping range with that of *P. k.* subsp. *kingii*. *Physaria kingii* subsp. *latifolia* have fruits that are longer than wide with rounded apices as well as glabrous inner valves while subsp. *kingii* have wider than long fruits with truncate apices and they generally have pubescent inner valves. Environmental pressures, abiotic or biotic, have changed the fruit shapes in these taxa in different ways and while natural selection or drift may be acting on these traits, the genotype has not yet caught up so that molecularly they still have the same genotype.

In colonizing species, studies have shown that there is little genetic differentiation in wide ranging populations, which may facilitate the ability to move into new niches or environmental conditions without the extensive time needed to adapt and evolve through natural selection or drift (Sultan 2000; Schlichting and Smith 2002; Ghalambor et al. 2007). Plastic organisms may be more competitive or tolerant to stressful conditions and

allow persistence while giving directional selection time to act on other traits thus aiding in diversification (Schlichting and Smith 2002; Ghalambor et al. 2007). West–Eberhard (1989) describes functional plasticity as a clay figure, malleable enough to be remodeled without falling apart. Additionally, she suggested that once isolation has occurred, rapid speciation could occur. While *Physaria* is not a weedy genus to any degree, plasticity may help explain the rapid diversification of the genus *Physaria* and the unresolved phylogenetic trees.

While some authors believe that plasticity increases diversification, others believe plasticity stunts it. Some suggest that if a genotype is sufficiently plastic and there is increased fitness, it is unlikely that natural selection will occur to make genetically distinct populations (Sultan 2000; Price et al. 2002). Schlichting and Smith (2002) propose that the most fit individuals should have low plasticity. Fitness however, is difficult to quantify as it is a combination of traits, both positive and negative. Speciation caused by phenotypic fixation may also be constrained by the rest of the genome with the multiple forms competing for genomic support (West-Eberhard 1989). de Jong and Behera (2002) stress that there is little empirical evidence on either side of the argument.

Williams et al. (1995) used a population transplant experiment on fountain grass, *Pennisetum setaceum* (Forssk.) Chiov, in Hawaii in an attempt to discover how the environment plays a role in plastic response. These plants showed little genetic variation but strong morphological, physiological, and reproductive differences in varying environments on the island. There were differing hypotheses to explain these results

including that the plasticity provides such a good match to the environments that there was no evolution because there was no opportunity for directional selection to act. Another hypothesis suggested that there was not enough genetic variation for selection to occur (Ghalambor et al. 2007). A hypothesis not taken into account was the time frame. According to Ghalambor et al. (2007), these plants have only been on the island for 100 years, while evolution could take thousands.

Galloway and Fenster (2000) postulate that in numerically small populations, like many *P. kingii* populations, drift may overwhelm selection, which stunts the potential genetic variation. Thus, differentiation may take longer periods of time. When considering that *Physaria* is a recent genus, *P. kingii* could be considered to be in its infancy and one could assume that there has not been sufficient time for differentiation, but given another 10,000 years or so of selective pressure and drift, genetic assimilation and divergence may occur.

Key to the Subspecies of *Physaria kingii*

1. Fruits wider than long, truncate apically.
 2. Inner valves glabrous; fruiting pedicels recurved; Nevada.....
 *P. k.* subsp. *cobrensis* p 86
 2. Inner valves pubescent; fruiting pedicels erect, ascending, or sigmoid, sparingly recurved.
 3. Basal leaf blades margins sinuate or lobed, sometimes lyrate, rarely entire; Wallowa or Elkhorn Mountains, Oregon.....
 *P. k.* subsp. *diversifolia* p 88
 3. Basal leaf blades margins entire, lobed, or shallowly toothed; California, Idaho, Nevada, Utah.
 4. Basal leaf blades elliptic, suborbicular, rhombic, deltoid, or ovoid; 4–6 ovules per ovary; California, Idaho, Nevada.....
 *P. k.* subsp. *kingii* p 79
 4. Basal leaf blades suborbicular, rhombic, or subdeltate; 4-8-(16) ovules per ovary; Utah.....
 *P. k.* subsp. *wardii* (in part) p 104
1. Fruits longer than wide, rounded to acute apically.
 5. Inner valves pubescent..... *P. k.* subsp. *wardii* (in part) p 104
 5. Inner valves glabrous
 6. Petals white; styles 0.5–3 (5) mm; Kaibab Plateau, Arizona.....
 *P. k.* subsp. *kaibabensis* p 91
 6. Petals yellow (occasionally cream yellow or cream white on Kaibab Plateau); styles 1-11 mm; Arizona, California, Nevada, Utah.

7. Plants erect; styles 4–11 mm; ovules 4–6 per ovary; San Bernardino Mountains, California
 *P. k.* subsp. *bernardina* p 83

7. Plants ascending, erect, decumbent, or prostrate; styles 1–8 mm; 4–16 ovules per ovary; n. Arizona, e. California, Nevada, Utah.

8. 4–8 ovules per ovary; n. Utah, Wasatch and Uinta Mountains *P. k.* subsp. *utahensis* p 99

8. 8–16 ovules per ovary; Arizona, e. California, Nevada, Utah

9. Petals yellow; styles 1–8 mm; ovules 8–16 per ovary; e. California, Nevada, Utah
 *P. k.* subsp. *latifolia* p 95

9. Petals yellow, cream yellow, or cream white; styles 1–3 mm; ovules 8–12 per ovary; Kaibab Plateau, Arizona
 *P. k.* subsp. *kaibabensis* x *P. arizonica* p 108

Species Description

Physaria kingii (S. Watson) O'Kane and Al-Shehbaz subsp. *kingii*

TYPE: United States. Nevada, Pershing County: West Humboldt Mountains. June 1868, *Watson 82* (Lectotype chosen by Payson (1922), GH; Isolectotypes: NY, US).

Plants perennial (Figure 19); rosulate; simple, not thickened caudex; densely pubescent; trichomes (Figure 21) have large tubercles throughout; bifurcate, 3 partite, or doubly bifurcate; 4–5 rays. Stems prostrate, decumbent, or ascending; 1–35 cm long, with many stems. Basal leaves gradually narrows to petiole; 0.5–5.5 (8) cm long; 1–14 (21) mm wide; entire, lobed, toothed or rarely lyrate margins; suborbicular, elliptic, rhombic, deltoid, or ovoid. Cauline leaves 3–22 (34) mm long; 1–7 mm wide; margins entire, rarely toothed; spatulate or oblanceolate; often second opposite the pedicels. Sepals 3–5 (6) mm long; green or yellow-green; 1–2 mm wide; lanceolate. Petals yellow (or white in the White Mountains in Mono County, California); 5–9 mm long; blade oblanceolate; anthers 1–2 mm long; style 1–6 mm long. Fruiting pedicels 4–14 mm long; sigmoid or sometimes recurved (when recurved it is a few on a plant, not all of the pedicels as in *P. k. subsp. cobrensis*); often second; fruit (Figure 20) 2–6 mm long; 2–6 mm wide, generally wider than long; subglobose, obovoid, oblate, or obdeltate with truncate apices, sometimes retuse, but often rounded when immature. Inner fruit valves usually pubescent to varying degrees; some are densely covered while some have only a few scattered trichomes. A few populations are glabrous internally. Ovules 4 (6) per ovary; septum can be entire and often wrinkled, fenestrate with a small hole in the center, (or reduced to a

thin rim around the replum similar to *P. k.* subsp. *cobrensis*). Seed reddish brown; subglobose; 2 mm long. $2n=12$.



Figure 19. *Physaria kingii* subsp. *kingii* in flower. (9842) Photo by S.L. O'Kane

Physaria kingii subsp. *kingii* grows in a variety of soils including white clay, sandstone, dolomite, limestone, granite, (basalt), igneous, volcanic rock, slate talus or gravelly/sandy loam. This taxon is commonly found on rocky slopes, dry open hillsides, roadcuts, windswept ridge tops, bluffs, rock outcrops, and loose screes in elevations ranging from 1450 m to 3800 m, though most commonly between 2100 m to 3200 m.



Figure 20. *Physaria kingii* subsp. *kingii* fruiting raceme. Photo from the Quinn Canyon Range in southern Nevada (Minnaert–Grote and O’Kane 91). Photo by author.

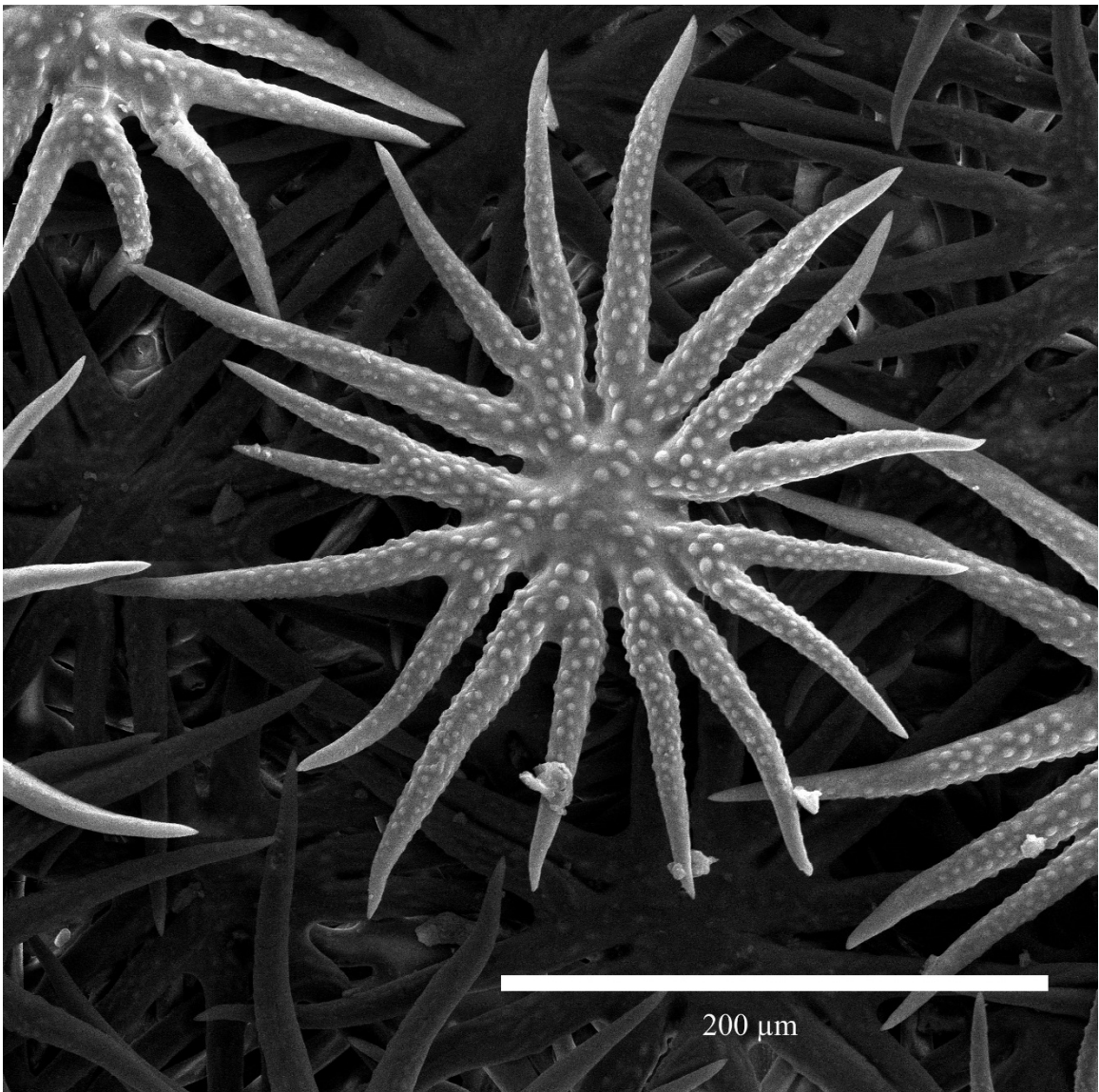


Figure 21. *Physaria kingii* subsp. *kingii*. Photo of trichome of adaxial surface of basal leaf [Maguire and Holmgren 25429 (F)].

The range of *P. k.* subsp. *kingii* overlaps with subsp. *latifolia*. These can be distinguished from one another by fruit shape, ovule number, trichome form, and generally by the presence of trichomes on the inner valves, although there are some populations of *P. k.* subsp. *kingii* that have glabrous inner valves. Additionally, *P. k.* subsp. *kingii* overlaps with subsp. *cobrensis*, though subsp. *kingii* is generally found at higher elevations. *Physaria kingii* subsp. *cobrensis* tends to be smaller overall, have glabrous inner valves, and have recurved pedicels throughout the entire plant. Further, they can be differentiated by ovule number in combination with the septum, which forms a thin rim around the replum, a form rarely found in *P. k.* subsp. *kingii*.

Physaria kingii subsp. *bernardina* (Munz) O’Kane and Al–Shehbaz

TYPE: UNITED STATES. California, San Bernardino County: north side of Bear Lake, at the east end of Bear Valley, San Bernardino Mts., 16 May 1924, *Pierson 4600* (Holotype: POM; Isotypes: GH, JEPS, RM, RSA).

Plants perennial (Figure 22); rosulate; simple, not thickened caudex; densely pubescent; trichomes tuberculate (Figure 23); 5 rays, doubly bifurcate or 3 partite; rays slightly webbed or fused at the base; bipartite to 3-partite. Stems 3.5–17.5 cm long; few to many; unbranched. Erect basal leaves; 1–4 cm long; 3–8 mm wide; margins entire, (weakly toothed); elliptical, obovate, or ovate; can be flat, often folded sometimes cupped. Cauline leaves 0.5–1.2 cm long; 0.1–2.5 mm wide; oblanceolate, spatulate, sometimes +/- linear; usually flat but sometimes cupped. Sepals 4–7 mm long; 1–4 mm wide; yellow-green; lanceolate. Petals yellow; 0.5–1 cm long; blade oblanceolate; anthers

1.5–2.2 mm long; styles 0.4–1.1 cm long. Pedicels 0.6–1.2 cm long; loosely sigmoid; ovate, obovate, or subglobose. Fruits 3–8 mm long; 2–5 mm wide; rounded acute apices; glabrous inner valves; 4–6 ovules per ovary; fenestrated septum with a small hole. Seeds 1.5–2 mm, reddish brown, ovoid to globose, slightly flattened.



Figure 22. *Physaria kingii* subsp. *bernardina* in flower. Photo by Gary A. Moore.

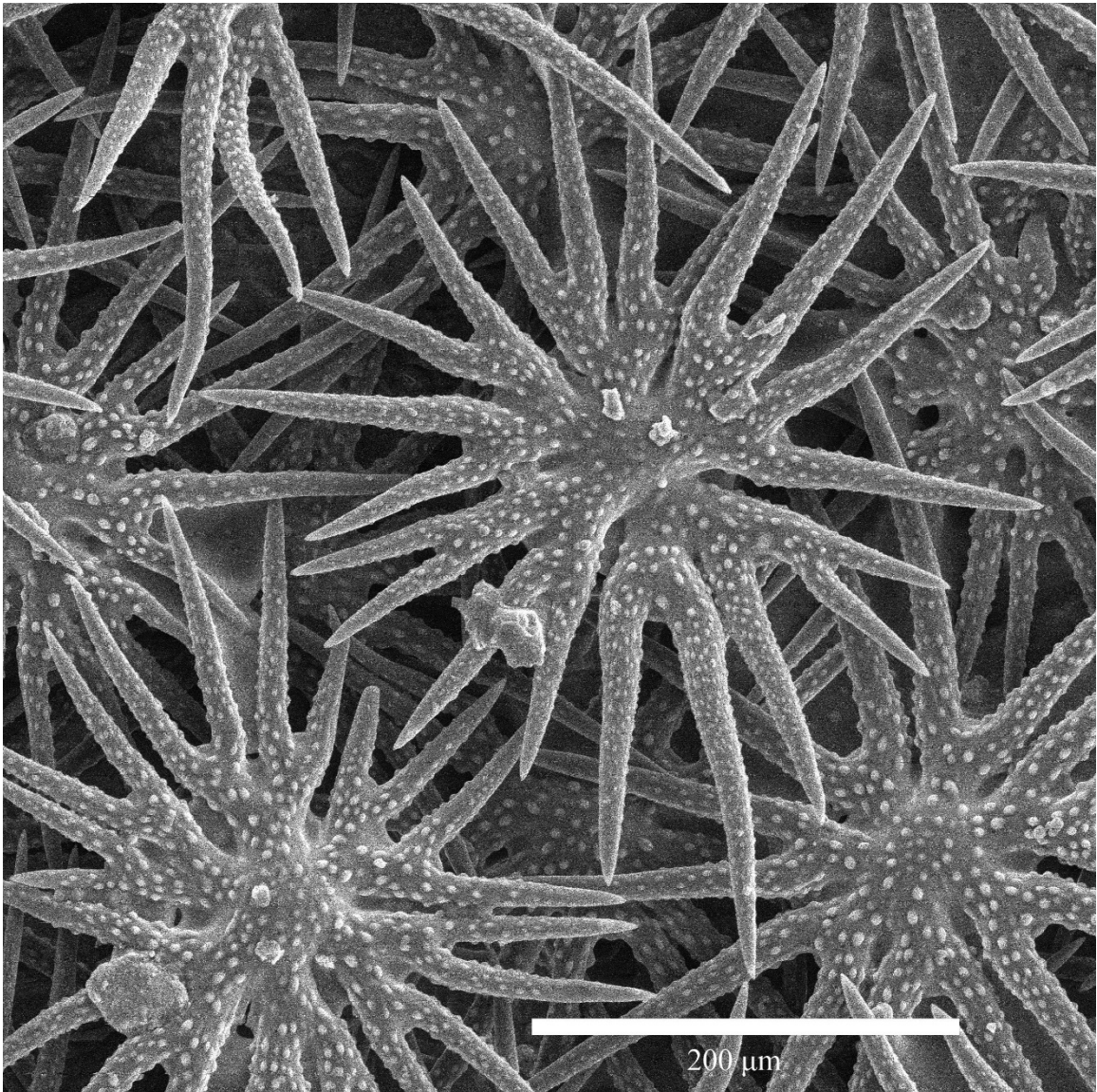


Figure 23. *Physaria kingii* subsp. *bernardina*. Photo of adaxial surface of basal leaf [Thorne, Tilforth, Little 53154 (GH)].

Physaria kingii subsp. *bernardina* grows on bedrock of carbonate materials, usually limestone. These can be found on outcrops in forest understory and open rocky slopes

under pines from 2000 m to 2800 m. These are endemic to the San Bernardino Mountains near Bear Lake in San Bernardino County, California. The range does not overlap with any other taxa in the *P. kingii* group.

Physaria kingii subsp. *cobrensis* (Rollins and E.A. Shaw) O’Kane and Al-Shehbaz

TYPE: UNITED STATES. Nevada, Elko County: 30 miles east of Wells on Cobre old highway paralleling Southern Pacific Railroad, *Train 3665*, (Holotype: GH; Isotypes: NY, UC).

Perennial rosulate plants; simple, rarely branched, not thickened caudex; densely pubescent; trichomes (Figure 24) with 5–6 rays, these bifurcate or doubly bifurcate; large tubercles throughout, low-umbonate centrally. Stems 1–19 cm long; many stems; unbranched; prostrate (ascending). Basal leaves erect; 0.6–4 cm long; 1–10 mm (13) wide; margins often toothed or lobed, sometime entire, rarely lyrate; often rhombic sometime obovoid, elliptic or ovoid; often cupped. Cauline leaves 5–20 mm long; 1–5 (6) mm wide; margins toothed or entire; oblanceolate, sometimes broadly so, subrhombic, or spatulate. Sepals yellow green or green; lanceolate; 4–6 mm long; 0.5–1.5 mm wide. Petals yellow; oblanceolate; 6–8 mm long; anthers 1–1.5 mm long; styles 1–6 mm long. Pedicels 2–15 mm long; recurved, sometimes slightly sigmoid; secund; cordate, obdeltate, subglobose, obovate, and rarely ovoid. Fruit 2–6 mm long; 2–7 mm wide; truncate apices; glabrous valves; 8 (12) ovules per ovary; septum is a thin rim around the outside with a large hole in the center. Seeds 1–2 mm; yellow/green-brown when immature but mature to an orange-brown; subglobose or ovoid.

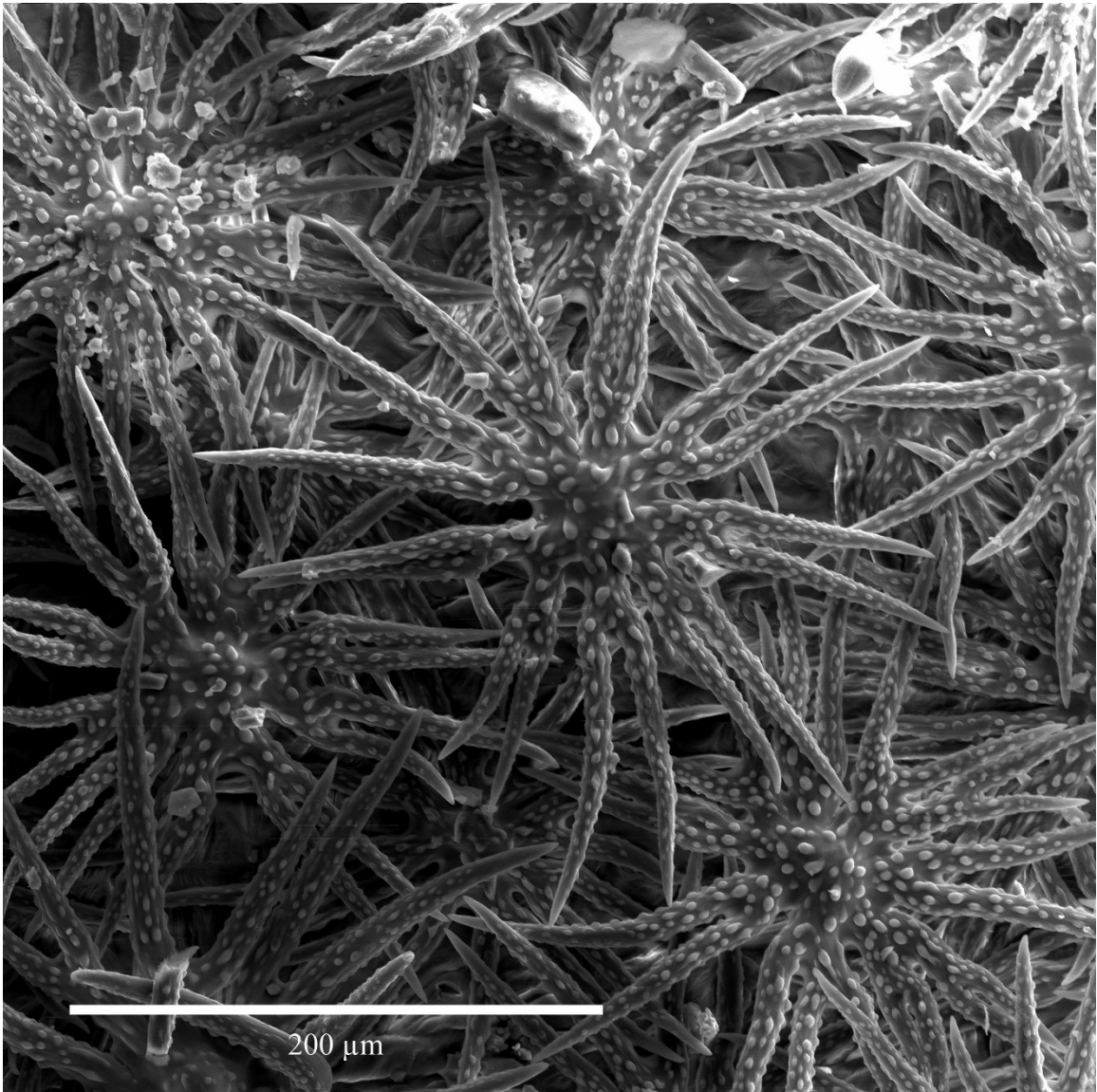


Figure 24. *Physaria kingii* subsp. *cobrensis*. Photo of adaxial surface of basal leaf [Tiehm 14454 (UTC)].

P. k. subsp. *cobrensis* grow in gravelly, rocky, or coarse sand, basalt pebbles in loam, clay, or white clay soils. Commonly, they are found on rocky flats, bare knolls, arid

planes, or valley floors. While the range overlaps with *P. k.* subsp. *kingii* and subsp. *latifolia*, they are found at lower elevations, from 1500 m to 2000 m. Their most distinguishing feature is the recurved pedicels and their septa, which are a thin rim around the outside of the replum, a trait rarely found in *P. kingii* subsp. *kingii*.

Physaria kingii subsp. *diversifolia* (Greene) O’Kane and Al-Shehbaz

TYPE: UNITED STATES. Oregon, Wallowa County: dry mountainsides, Wallowa Mts., 7000 feet alt., 6 August 1899 *Cusick 2304* (Holotype: ND-G; Isotypes: F, GH, MO, UC, US, WS)

Plants perennial (Figure 25); rosulate; simple, rarely branched, not thickened caudex; densely pubescent. Trichomes (Figure 26) with 4–5 rays, these bifurcate, doubly bifurcate, or 3-partite; slightly webbed at the base of the rays; small tubercles found only on the rays, centrally smooth; umbonate. Stems 5–27 cm long; few to many; unbranched; prostrate or ascending. Basal leaves erect; ascending to spreading; 1–5.5 cm long; 0.2–1.5 cm wide; widened at base, toothed, lobed, or sinuate; elliptical, ovoid, obovoid, or lyrate; often folded. Cauline leaves 0.2–1.9 cm long; 1–4.5 mm wide; margins entire, oblanceolate or spatulate; involute or cupped. Sepals green or yellow-green; lanceolate; 3.5 mm long; 1–1.5 mm wide. Petals yellow; 5–7 mm long; oblanceolate; anthers 0.5–1 mm long; styles 1–3 mm long. Fruiting pedicels 0.4–1.9 cm long; sigmoid, rarely erect, or recurved but sparingly not throughout the whole plant; second. Fruits globose or oblate; 2–4 mm long; 2.5–5 mm wide; apices truncate;

pubescent inner valves; entire or fenestrate septum with a small hole; 4–6 ovules per ovary. Seeds 1–2 mm long; flattened; reddish brown; ovoid. $2n=10$.



Figure 25. *Physaria kingii* subsp. *diversifolia* in flower. Photo from the moist bank of Hurricane Creek in Wallowa Mountains of Oregon (Minnaert–Grote and O'Kane 93). Photo by S.L. O'Kane Jr.

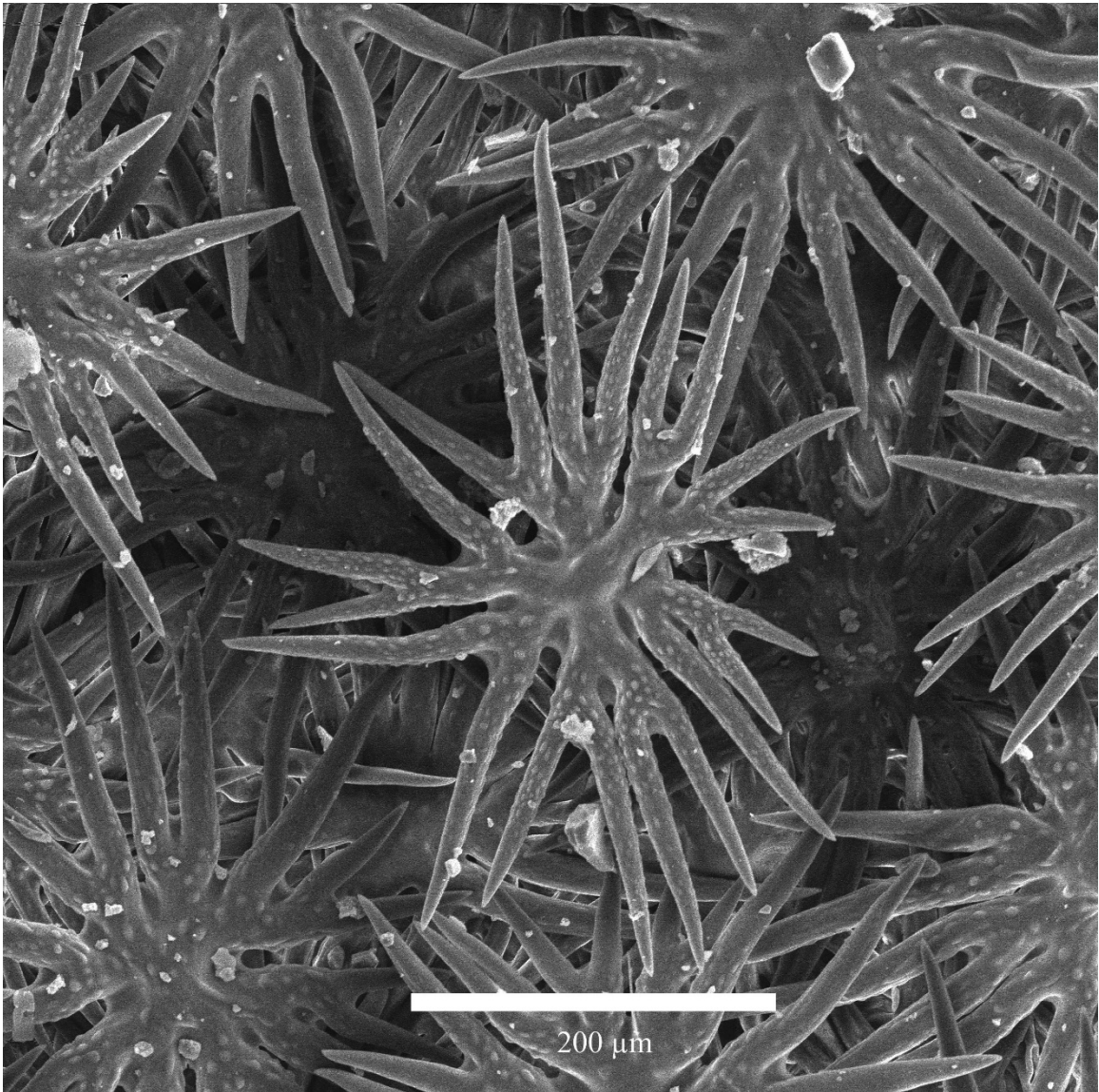


Figure 26. *Physaria kingii* subsp. *diversifolia*. Photo of adaxial surface of a basal leaf [Markow 12247 (RM)].

Physaria kingii subsp. *diversifolia* is found on gravelly flood banks, dry rocky creek beds, dry stony slopes above creeks, crystalline marble on dry bare cliffs, and moist

shady coniferous woods along creek, features that distinguish this taxa from the others which grow in arid ecosystems. These are often found in lodgepole pine and cottonwood communities at elevations from 1400 m to 2650 m. *Physaria kingii* subsp. *diversifolia* is endemic to the Wallowa and Elkhorn Mountains and has a region that does not overlap with others in the *P. kingii* group. Similar to *P. k.* subsp. *kingii*, they have fruits that are longer than wide, have pubescent inner valves, and have 4–6 ovules.

Physaria kingii subsp. *kaibabensis* (Rollins) O’Kane and Al-Shehbaz

TYPE: UNITED STATES: Arizona, Coconino County: limestone-clay knolls, open park-like meadow area, 18.6 mi s. of Jacob Lake on road to the n. entrance to Grand Canyon Natl. Park, 8 June 1979, *Rollins and Rollins 79191* (Holotype: GH, Isotypes: BRY, MO, NY, UC, US)

Plants rosulate perennials (Figure 27); simple, not thickened caudex; densely pubescent with large tubercles densely covering the entirety; trichomes with 5–6 rays, these bifurcate, doubly bifurcate, or 3-partite. Stems prostrate; 1.5–9.5 cm long; few to many; unbranched. Basal leaves 0.9 – 3.5 cm long; 0.2–0.8 cm wide; margins entire, deltoid, elliptic, ovate, or suborbicular; often cupped. Cauline leaves 2–10 mm long; 1–2 mm (3) wide; entire margins; oblanceolate or spatulate; often cupped or involute. Sepals green or yellow-green; 4–4.5 mm long; 1 mm wide; lanceolate. Petals white; (3)–5–6 mm long; oblanceolate; anthers 1–2 mm long; styles 0.5–2.5 mm long, short in comparison with others in this group. Pedicels 3–9–(13) mm long; erect or loosely sigmoid; not second; inflorescence congested at the tips of the raceme. Fruits longer than wide;

ellipsoid to ovoid; 3–5–(6) mm long; 2–3–(4) mm wide; rounded acute apices; glabrous inner valves; entire septums; 6–8 ovules per ovary. Seeds 1–1.5 mm long; yellow/green to orange/brown in color; ovate to subglobose.



Figure 27. *Physaria kingii* subsp. *kaibabensis* in flower. Note the white petals. Photo from the Kaibab Plateau in northern Arizona (O'Kane 4213). Photo by S.L. O'Kane Jr.



Figure 28. *Physaria kingii* subsp. *kaibabensis* in fruit. Photo from the Kaibab Plateau in northern Arizona (Minnaert–Grote and O'Kane 83). Photo by S.L. O'Kane Jr.

Physaria kingii subsp. *kaibabensis* (Figure 30) grow on gentle rocky slopes in rocky limestone soils in open meadow areas. It is endemic to the Kaibab Plateau in northern Arizona, with an elevation range of 2200 m to 2700 m.

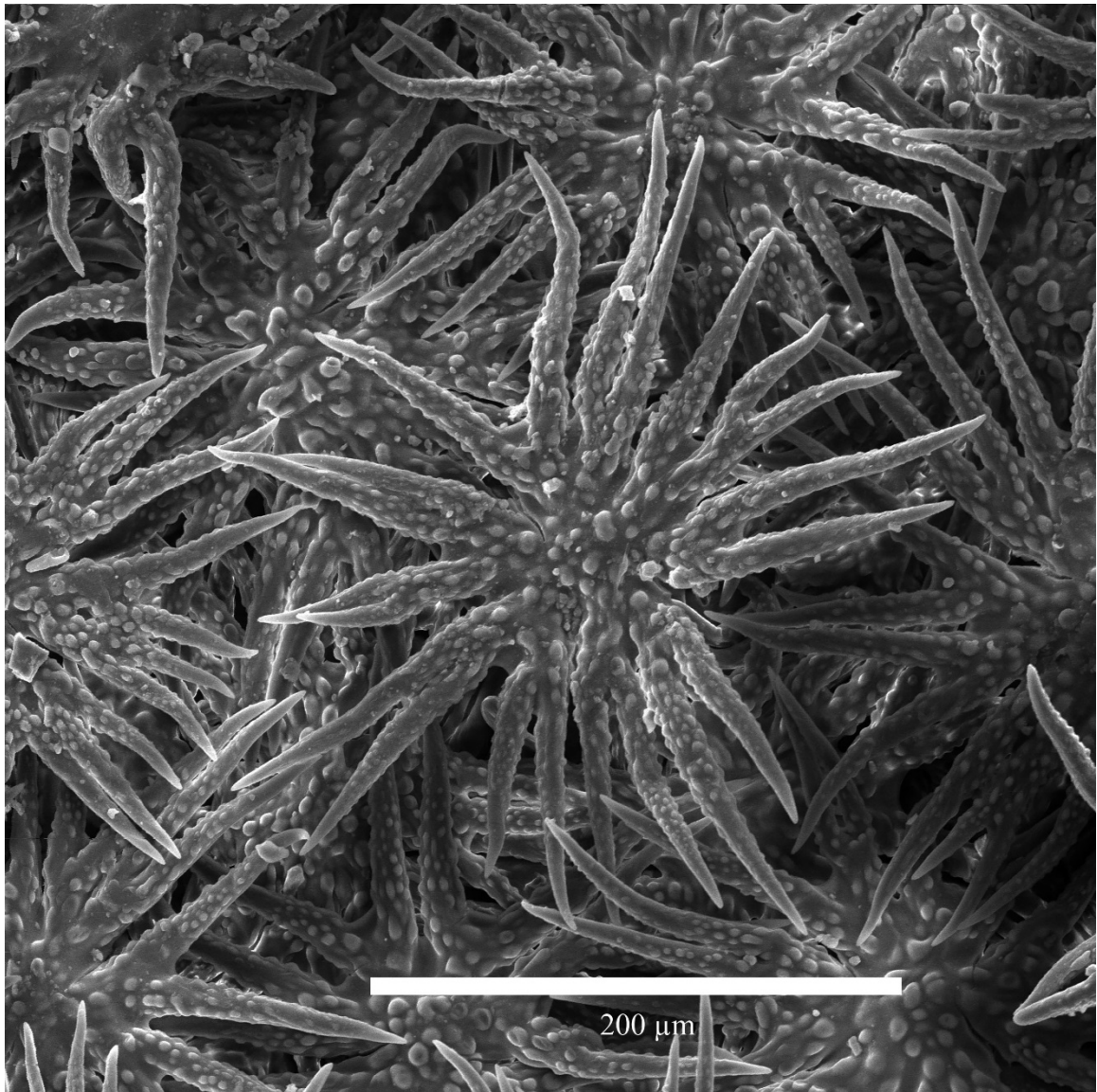


Figure 29. *Physaria kingii* subsp. *kaibabensis*. Photo of adaxial surface from a basal leaf [Holmgren, Holmgren, and Joseph 13564 (ISTC)].



Figure 30. *Physaria kingii* subsp. *kaibabensis* habitat. Photo highlights the meadow community from the Kaibab Plateau in northern Arizona (Minnaert–Grote and O’Kane 83). Photo by S.L. O’Kane Jr.

Physaria kingii subsp. *latifolia* (A. Nelson) O’Kane and Al–Shehbaz

TYPE: UNITED STATES. Nevada, Lincoln County: Karshaw, Meadow Valley Wash, 26 April 1902, *Goodding* 625 (Holotype: RM; Isotypes: GH, MO, US).

Plants perennial (Figure 31); rosulate; densely pubescent; caudex simple; rarely branched; not thickened. Trichomes (Figure 32) with 5-6 rays; tuberculate or smooth;

umbonate; bifurcate to 3-partite. Stems 2–32 cm long; rarely branched; prostrate to decumbent. Basal leaves 0.5–7.5 cm long; 2–17 (25) mm wide; usually entire but can be shallowly lobed or toothed; deltate; elliptic (sometimes widely), ovate, suborbicular; rhombic, spatulate, rarely lyrate; often slightly cupped. Cauline leaves 2–16 (22) mm long; 0.5–9 mm wide; entire, rarely toothed; oblanceolate, spatulate, near linear, or elliptic; often second opposite the pedicels. Sepals green or yellow-green; 4–7–(9) mm long; 0.5–2 mm wide; oblanceolate. Petals yellow; 6–9–(11) mm long; anthers 0.5–2 mm long; styles 1–8 mm long. Fruiting pedicels 3–15 mm long; erect when immature, weakly or strongly sigmoid; second. Fruit subglobose, ovoid, rarely obdeltate; 3–9 mm long; 2–6.5 mm wide; apices rounded or round–acute; glabrous inner valves; septum usually entire, less commonly fenestrate with small hole; 8–16 ovules per ovary. The ovule number appears to be population based although one plant had fruits with 8, 12, and 16 ovules. Seeds 1–2 mm, green/yellow in color when immature and often globose as they mature they turn a darker orange/brown and ovoid in shape. $2n=10$.

Similar to *P. k.* subsp. *kingii*, subsp. *latifolia* has a wide range of substrates where it will grow. It can be found on limestone-, igneous-, granite-, basalt-, and volcanic tuff-derived soils in dry sandy, rocky, chip, cobble, or gravel. These taxa grow on roadsides, meadows, rock outcrops, barren exposed ridges or ledges, slopes, and in shady canyon bottoms and flats in pine–juniper or sage communities from 1150 m to 3000 m, though it is most common between 1500 m to 2800 m.



Figure 31. *Physaria kingii* subsp. *latifolia* in fruit. Photo from the Highland Range in Lincoln County Nevada (Minnaert–Grote and O’Kane 89). Photo by S.L. O’Kane Jr.

Physaria kingii subsp. *latifolia* has overlapping ranges with *P. k.* subsp. *kingii*, subsp. *cobrensis*, and subsp. *wardii*. They can be differentiated from subsp. *kingii* and subsp. *cobrensis* by fruit shape and from subsp. *wardii* by the absence of trichomes on the inner valves. Fruit shape, ovule number, and elevation may also aid in distinguishing these taxa, however, there are some overlapping of ranges.

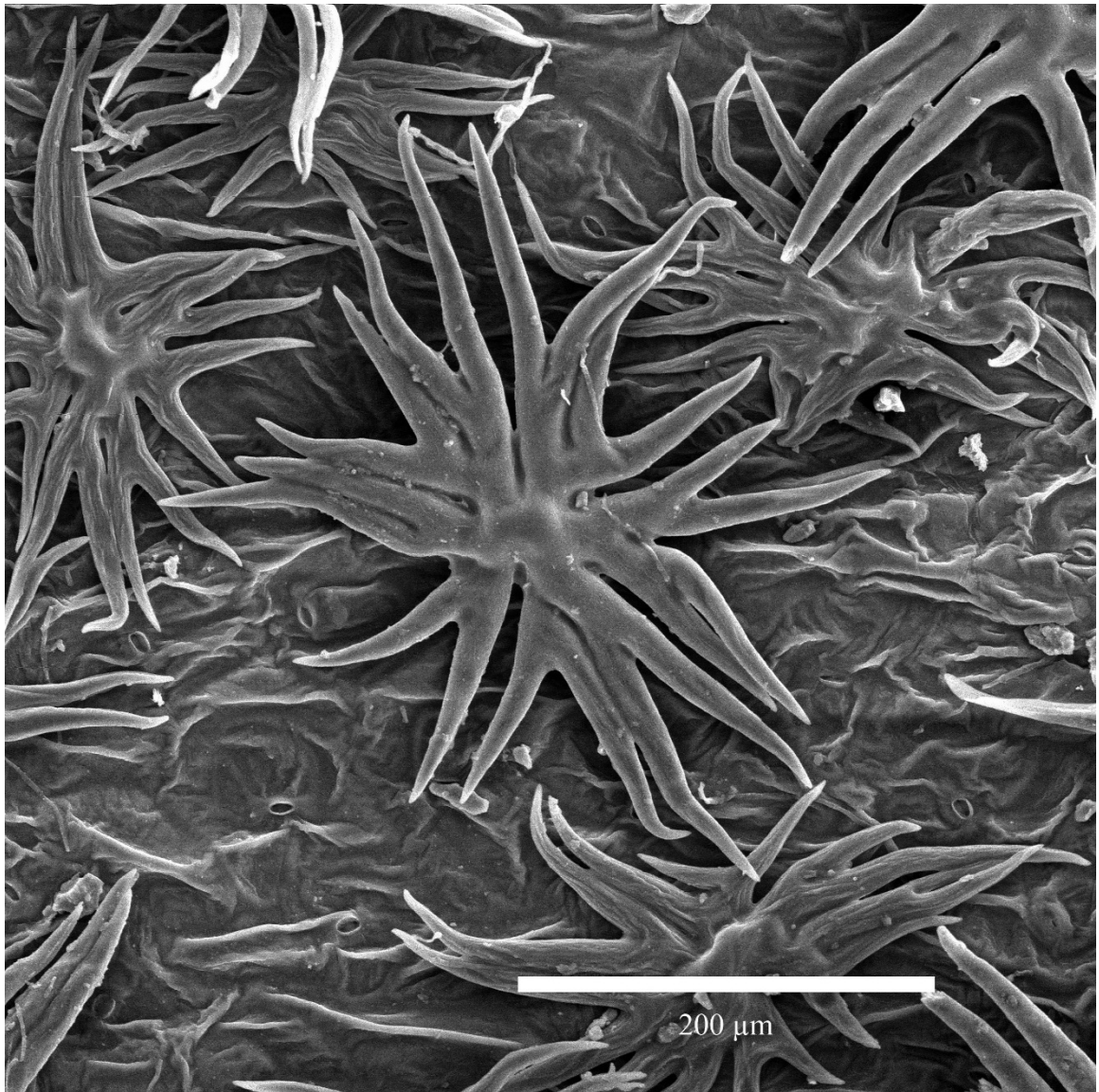


Figure 32. *Physaria kingii* subsp. *latifolia*. Photo from the abaxial side of a basal leaf [Pinzl 2805 (GH)].

Physaria kingii subsp. *utahensis* (S. Watson) O’Kane and Al-Shehbaz

TYPE: UNITED STATES: Utah, Utah County: American Fork Canyon, 9000 ft, 31 July 1880, *Jones 1354* (Holotype: NY; Isotypes: ARIZ, DS, MO, POM, US).

Plants perennial (Figure 33); rosulate; branched or simple, not thickened caudex; densely pubescent; trichomes (Figure 35) with 5–6 rays that are bifurcate, doubly bifurcate, or 3-partite; with shallow tubercles found only on the rays. Stems prostrate to decumbent; 2–15–(19) cm long; few to many; unbranched. Basal leaves 0.6–6 cm long; 2–16 (26) mm wide; margins generally entire but can be shallowly toothed or lobed; ovoid, obovoid, or elliptic and less commonly suborbicular, deltate, or subrhombic. Leaves are highly variable even on an individual plant. The leaves found in the Uinta Mountains appear to grow larger than in the Wasatch Mountains. Cauline leaves 3–26 (36) mm; 1–6 mm wide; margins entire; spatulate, oblanceolate, or obovate. Sepals green or yellow-green; lanceolate; 4–6 (7) mm long, 1–1.5 mm wide. Petals yellow; oblanceolate; 6–11 (19) mm long; anthers 0.5–2 mm long; styles 2–6 (7) mm long. Fruiting pedicels 2–10 mm long; erect to sigmoid; can be second or clustered at the tips of the raceme. Fruits (Figure 34) ovate, subglobose, longer than wide; 2–6 mm long; 1.5–4 (4.5) mm wide; apices rounded-acute, a few appear somewhat weakly truncate on subglobose fruits; glabrous inner valves; entire (fenustrate) septum; 4–8 ovules per ovary, sometimes variable on a single plant. Seeds 1–2 mm long; ovate to subglobose; yellow/brown when immature and as they mature they turn an orange/brown in color.



Figure 33. *Physaria kingii* subsp. *utahensis* in fruit. Photo by Tony Frates.

Physaria kingii subsp. *utahensis* is found on dry gravelly, stony, sandy, talus, or loamy soils that are granitic- or limestone-derived. It is most often found in windswept crests, stony ridges, leeward slopes, rock crevices, open spaces between rocks, alpine tundra, subalpine meadows, or rocky outcrops in spruce-pine communities. This taxon is endemic to the Wasatch and Uinta Mountain ranges in northern Utah at elevation ranging from 2350 m to 3500 m, though is more common at higher elevations from 2700 m to 3500 m. The range does not overlap with any other in the *P. kingii* group.



Figure 34. *Physaria kingii* subsp. *utahensis* fruiting raceme. Photo by Tony Frates.

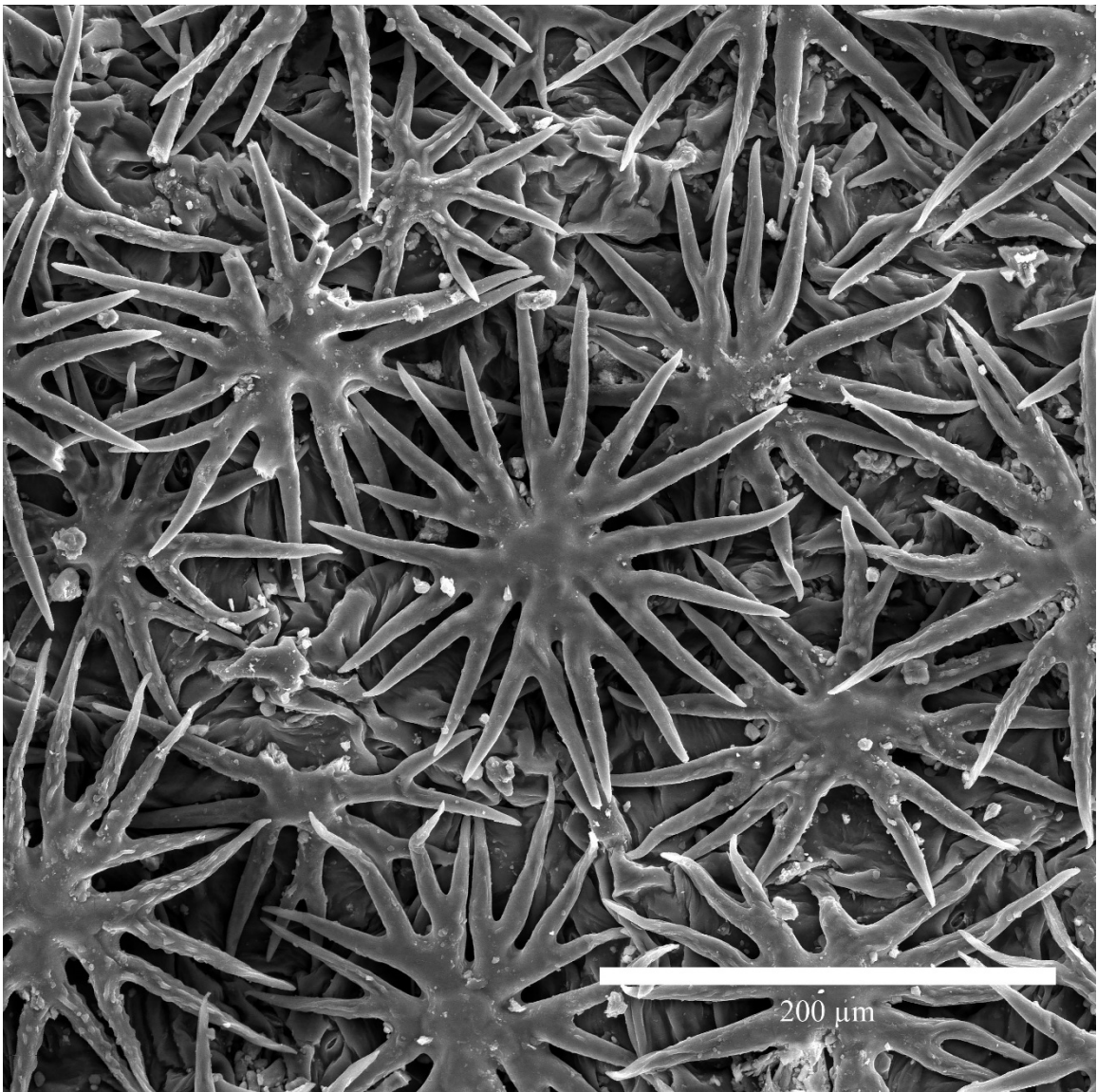


Figure 35. *Physaria kingii* subsp. *utahensis*. Photo of adaxial side of basal leaf [Holmgren and Holmgren 13651 (ISTC)].

Physaria kingii subsp. *wardii* (S. Watson) Minnaert–Grote and O’Kane [to be published]

TYPE: UNITED STATES. Utah, Garfield, County: Aquarius Plateau, 11000 ft, 15 August 1875, *L.F. Ward 589* (Holotype: GH; Isotypes: F, MO, US).

Plants perennial (Figure 36); rosulate; caudex simple or branched, not thickened; densely pubescent; trichomes (Figure 37) with 4–6 rays; tuberculate throughout; bifurcate, doubly bifurcate, or 3–partite. Stems 2–18 cm long though smaller plants are more common; unbranched; prostrate or decumbent to ascending. Basal leaves 0.5–8 cm long; 2–22 mm wide; entire, lobed, or toothed margins; elliptic, sometimes widely so, suborbicular, rhombic, subdeltate, or rarely lyrate; often cupped or slightly involute. Cauline leaves 2–17 mm long; < 1–7 mm wide; margins entire; oblanceolate, spatulate, or rarely widely elliptic; often second opposite the pedicels. Sepals green to yellow-green; 3–7 mm long; 1–2 mm wide; elliptic to ovate. Petals yellow; oblanceolate; 5–9 mm long; anthers 0.5–1.5 mm long; styles 2–5–(1,7) mm long. Pedicels 2–7–(12) mm long with larger rounded-acute fruits on longer pedicels; erect to loosely sigmoid; second or congested at the tips. Fruits elliptic, subglobose, ovoid, or obovoid; 1–7 mm long; 2–7 mm wide; apices varying degrees of rounded/acute to truncate; inner valves pubescent; ovules per ovary 4–8–(12), variable even on a single plant (12 seen only once); septum can range from entire to fenestrate with a small hole centrally, to rarely a thin rim around the outside of the replum. Seed size 1–2 mm, greenish brown when immature but mature to an orange brown, ovate or subglobose. $2n=12$.



Figure 36. *Physaria kingii* subsp. *wardii* in flower and fruit. Photo from near Escalante Canyon summit in southern Utah (Minnaert–Grote and O’Kane 80). Photo by S.L. O’Kane.

Physaria kingii subsp. *wardii* grows in stony, rocky, talus slopes, igneous sandy gravel, soils derived from ash flow tuff, sandy soil overlying mudstone, white shale formation, volcanic gravel, limestone, marbled chiprock, gravelly to sandy loam granite soils, hard clay soils, pink limestone, white or pink claron formation, silty

meadows and dry loam at base of lava flows. It can be found on exposed ridges, roadside or disturbed slopes, open meadows, alpine meadows, ridge tops, rock outcrops, exposed rocky slopes, rocky knolls, and alpine tundra in spruce-fir, sage, pinyon-juniper, or aspen communities with elevations from 2550 m to 3500 m.

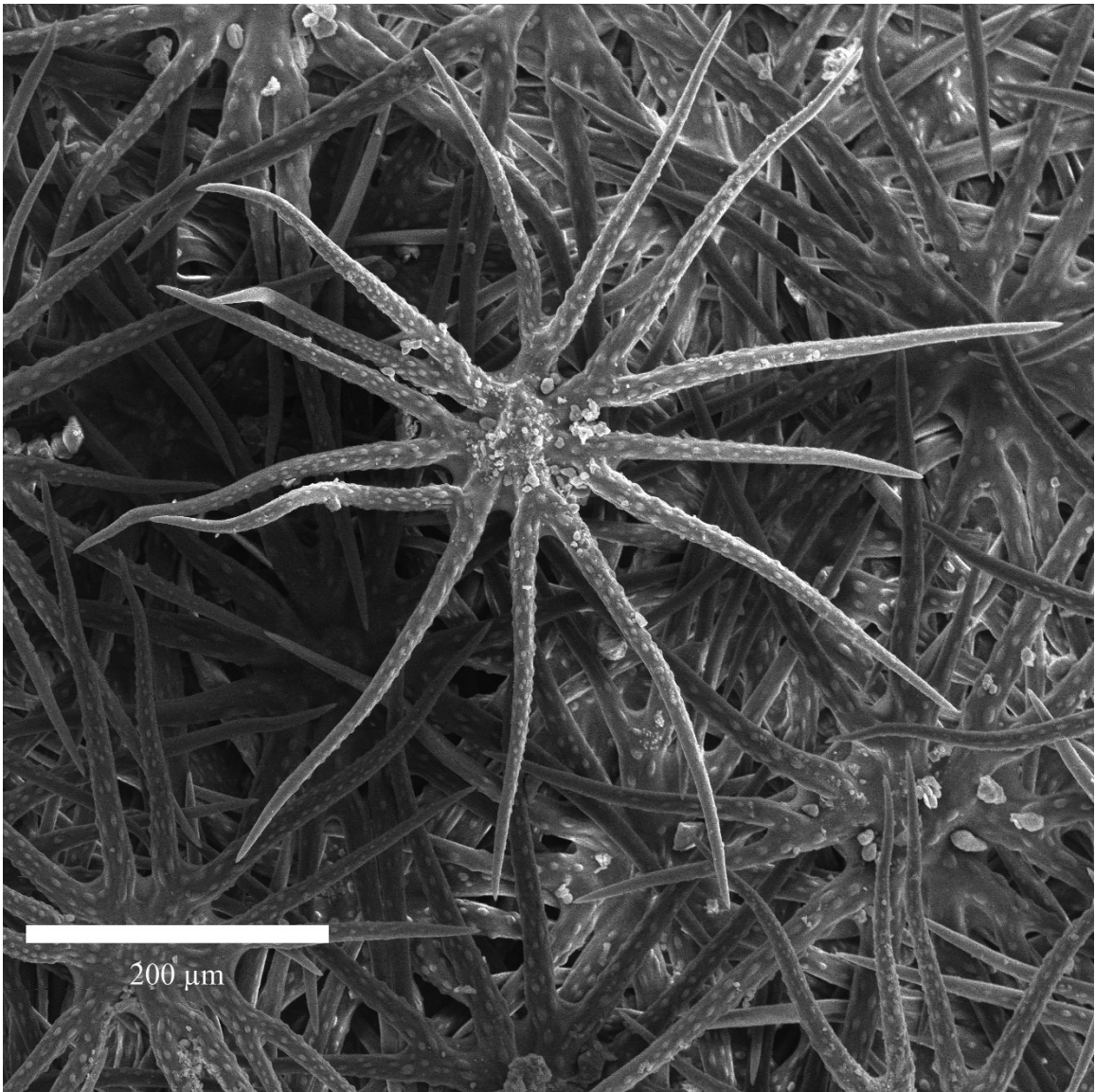


Figure 37. *Physaria kingii* subsp. *wardii*. Photo from the adaxial surface of a basal leaf [Holmgren, Holmgren and Joseph 13600 (UTC)].



Figure 38. *Physaria kingii* subsp. *wardii* habitat. Image highlights the ecological habitat near the summit of Escalante Canyon in southern Utah (Minnaert–Grote and O’Kane 80). Photo by S.L. O’Kane.

Physaria kingii subsp. *kaibabensis* x *Physaria arizonica*

Plants perennial (Figure 39); rosulate; caudex not thickened; densely pubescent. Basal leaves 1–4 cm long, 5–22 mm wide. Cauline leaves 4–20 mm long, 1–10 mm wide. Sepals 4–6 mm long; 1–1.5 wide. Petals 7–10 mm long; styles similar to *P. k.* subsp. *kaibabensis*, 1–3 (5)mm long; pedicels 3–11 mm, fruits 2–6 mm long; 2–3 mm wide; rounded acute apices; glabrous inner valves; 8–12 ovules per ovary; entire septum. It is found where the range of *P. kingii* subsp. *kaibabensis* nears the range of *P. arizonica* on the Kaibab Plateau in northern Arizona, with an elevation range of 2200 m to 2700 m (Figure 40).



Figure 39. *Physaria kingii* subsp. *kaibabensis* x *Physaria arizonica* in fruit. Photo from north rim of the Grand Canyon in northern Arizona (Minnaert–Grote and O’Kane 84). Photo by S.L. O’Kane Jr.



Figure 40. *Physaria kingii* subsp. *kaibabensis* x *Physaria arizonica* (Minnaert-Grote and O'Kane 84) habitat. Photo highlights the ecological habit on the northern rim of the Grand Canyon in northern Arizona. Photo by S.L. O'Kane Jr.

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APPENDIX A

SPECIMENS EXAMINED

Physaria kingii subsp. *kingii*

UNITED STATES: Arizona: Maricopa County: Adams Mesa, Tonto Forest. 2000' elevation; T3N, R8E, S8; 16 March 1929; *Bushnell 8* (RM). **California: Inyo County:** Canyon east of divide, Cerro Gordo Peak, on loose bank of road. 7500-7800' elevation; 28 June 1942; *Alexander and Kellogg 3042* (CAS, GH, NY, US, UTC). White Mountains, alpine slopes along White Mtn Rd near pullout by Patriarch Grove, NE of Redding Canyon. 3068m elevation; 37°22.98'N 118°10.89'W; 9 July 2007; *Grady 269* (ISTC). So. slope of Pine Alpha Bristlecone stand. 10600' elevation; 5 May 1961; *Mooney, St. Andre, and Wright 52* (CAS). Head of Silver Canyon. 10500' elevation; 7 June 1961; *Mooney, St. Andre, and Wright 123* (CAS). Bristlecone Pine Forest, crests South of Hillside Springs, Independence Quadrangle. 10200' elevation; 6 July 1957; *DeDecker 682* (RSA). Inyo Mountains, Trail to Seep Hole Spring. 12 May 1940; *Kerr s.n.* (CAS). White Mts, Reed Flat, on dry flat, edge of Bristle-cone Pine Forest, 10300' elevation; 18 June 1955; *Munz 21009* (CAS, NY, RSA). Mollie Gibson Canyon, common along wash. About 3 miles up canyon from Westgard Pass Road. 7950' elevation; 11 July 1964; *Lloyd 2941* (RM, UTC). Wyman Canyon, 0.5 miles south of mine shacks. On rocky slopes. 8000' elevation; 22 June 1963; *Lloyd 2817* (GH). On the ridge 0.3 miles due east of Mollie Gibson Mine, Deep Springs Valley drainage. Carbonate colluvium sloping 10°N. 8300' elevation; T7S

R35E S16; 8 June 1984; 2046 (NY). **Mono County:** South of Conway Summit, 0.7 mile south of Virginia Lakes Road on Jordan Basin Road. 384.786°N 11911.701°W; 8340 ft elevation; 7 June 2013 *O’Kane and Minnaert-Grote 9842* (ISTC). Sweetwater Mountains, on dry, rocky slope under white fir, branch of Sweetwater Canyon. 8300’ elevation; 17 July 1944; *Alexander and Kellogg 3902* (CAS). White Mts, betw. Naval Research Lab. Stations at high elevations on slopes of White Mt Pk. July 1951; *Vollmer and Beane 235* (CAS). White Mts, frequent, sandy soil near stream, vic of meadow at head of Crooked Creek. 2 August 1945; *Maguire and Holmgren 26056* (GH, NY, US, UTC). White Mts, frequent, broad sagebrush saddle above head of Wyman Creek, 1 mi. W. of Blank Mt. 1 August 1945; *Maguire and Holmgren 26052* (GH, NY, UTC). White Mts, frequent, stony sagebrush ridge between Cottonwood Creek and Crooked Creek. 12000’ elevation; 2 August 1945; *Maguire and Holmgren 26084* (NY, UTC). White Mts, frequent, stony sagebrush slopes, S.E. of Campito Meadow. 10800’ elevation; 6 August 1945; *Maguire and Holmgren 26120* (NY, UTC). Frequent, stony sagebrush slopes southeast of Campito Meadow. 10800’ elevation; 6 August 2012; *Maguire and Holmgren 26102* (UTC). Quaking Aspen Canyon on northeast side of Wheeler Peak above Sweetwater, Nevada. 9000’ elevation; 10 July 1977; *Breedlove 42996* (CAS). Quaking Aspen Canyon on northeast side of Wheeler Peak above Sweetwater, Nevada. 9000’ elevation; 29 May 1978; *Breedlove 43583* (CAS). Meadow with *Populus tremuloides* and *Ribes*. Slopes with *Pinus monophylla*, *Artemisia tridentata* and *Purshia* at town site of Masonic (upper). 8900’ elevation; 12 June 1979; *Breedlove 43763* (CAS). Steep walled

canyon. Quaking Aspen Canyon on Northeast side of Wheeler Peak above Sweetwater. 9000' elevation; 24 May 1979; *Breedlove 43713* (CAS). Limestone outcrops just N of mouth of Lundy Canyon into Mono Basin. 8000' elevation; T2N, R25E, S11; 13 July 1977; *Taylor 6511* (CAS). Sheep Mountain. 11900' elevation; 15 July 1971; *Larson s.n.* (CAS). North of WM Research Sta 1. Dolomite substrate, sandstone-dolomite. 10800' elevation; 1 August 1962; *Mooney, St. Andre, and Wright 892* (CAS). On road to Virginia Lakes, 3.3 miles west of Conway Summit. 9000' elevation; 15 June 1941; *Cantelow s.n.* (CAS). Fishlake Valley Drainage, top of ridge forming the N wall of the N Fork of Perry Aiken Creek, 0.8 miles N66° E of White Mtn Peak. 12420' elevation; T3S,R34E,S32,SE ¼; 25 July 1987; *Morefield and Ross 4705* (BRY, GH, MO, NY). Growing on rocky metamorphic limestone +/- 200 west of the lower mine tunnel at the copper mine in a canyon northeast of Copper Mountain. 7850' elevation; T2N, R25E, S11, NE ¼ ; 7 July 1963; *Reveal and Reveal s.n.* (CAS, NY, UTC). Vicinity of University of California White Mountain Research Station, White Mountains just North of Inyo-Mono County line. 10200' elevation; 11 August 1951; *Tucker 2227* (CAS). Masonic Mountain head of Masonic Gulch, northerly aspect. 8000' elevation; T6N, R26E, S17; 25 May 1979; *Genz 9160* (NY). Sweetwater Mountains, east side, East Walker River drainage, open area on ridge between Ferris Canyon and Greek Creek. 10200' elevation; 20 July 1984; *DeDecker 5672* (MO). Sweetwater Mtns, S end, S slope of Wheeler Peak. 11200' elevation; T7N, R24E, S36; 22 July 1981; *Lavin 3323* (GH). Masonic Mountains, Bodie Hills, E slope. 8900' elevation; T6N, R26E, S28; 11 June 1980; *Lavin SW32* (GH).

Sweetwater Mountains, east side, East Walker River drainage, open area on ridge between Ferris Canyon and Green Creek. 10200' elevation; 20 July 1984; *McDecker 5674* (GH). White Mountains, Ancient Bristlecone Pine Forest, Patriarch Grove, 0.5 miles south of the parking lot, 16 airline miles northeast of Bishop. 11400' elevation; T5S, R34E, S12; 18 July 1972; *Holmgren and Holmgren 6237* (GH, NY). 1.3 miles N35°E of Sheep Mountain above Cottonwood Basin, Fishlake Valley drainage. 11630' elevation; T5S, R34E, S1; 8 July 1984; 2308 (NY). White Mountains. 8000' elevation; 22 June 1963; *Menzies s.n.* (CAS). **San Bernardino County:** 11 air miles E of Cima, at Kingstone Mine in Keystone Canyon of New York Mts, in granite slopes with oak-pinyon vegetation. 5900' elevation; 16 May 1973; *Henrickson 9667* (CAS). Lemhi Forest, head of Bear Creek. 8000' elevation; 28 May 1932; *Jacobs 200* (RM). **Nevada: Churchill County:** Clan Alpine Range, War Canyon, about 2 road miles NW of Clan Alpine Ranch Road, unsurveyed. Pinyon-juniper zone. 6000' elevation; 14 June 1991; *Pinzl 9561* (GH). Clan Alpine Mts, War Canyon, 5.5 road miles west of main Edwards Creek Valley road. Plants growing with *Artemisia* on rocky hillsides. 6400' elevation; T29N, R36E, S25; 18 May 1986; *Tiehm 10418* (BRY, CAS, GH, NY, RM). Clan Alpine Mts, Byers Canyon on east side, 1.7 road miles west of the main Edwards Creek Valley road. 5700' elevation; T20N, R37E, S1; 24 May 1984; *Tiehm 8513* (BRY, CAS, GH, NY, RM, UTC). Clan Alpine Mts, Bernice Canyon on the NW side of the range, .6 miles east of the 1st creek crossing. Plants growing on steep, loose screes below rock outcrops. 4700' elevation; T22N, R37E, S14; 5 June 1984; *Tiehm 8578* (BRY, CAS, GH, NY, UTC). Cox Canyon, W

side of the Stillwater Range. 5000' elevation; T21N, R33E, S22; 23 May 1979; *Tiehm and Birdsey 4947* (GH, MO, NY, UTC). Pine Grove Hills, rocky outcrop east of Pine Grove Summit. 8400' elevation; T9N R26E; 16 June 1983; *Mooney 1070* (GH).

Stillwater Mts, Freeman Basin. 7000' elevation; 1 June 1975; *Lott s.n.* (NY).

Stillwater Range, Middle Fork of Pete Canyon. 6000' elevation; 2 June 1977; *Lott 113* (NY, UTC). Extreme SW corner of the T20N and R40E. Benchmark 6129 New Pass. 6129' elevation; 8 May 1974; *Baily 74-667-3* (CAS). **Douglas County:** Pine Nut Mountain, ridge E of Bald Mountain on the road to Rickey Canyon, S end of the range. 8450' elevation; T11N, R22E, S22; 30 June 1998; *Tiehm 12552* (BRY, CAS, NY, UTC). Pine Nut Mts, Bald Mt, ridge northeast of the peak. 9000' elevation; T11N, R22E, S16; 17 July 1982; *Tiehm and Lavin 7361* (GH). Pine Nut Mts, Sunrise Basin, plants common in open rocky areas. 8000' elevation; T14N, R22E, S23-24; 25 June 1977; *Tiehm and Williams 3568* (CAS, NY). Taylor Valley (RisueCanyon), NW end of Sweetwater Mtns. 7600' elevation; T8N, R123E; 24 June 1980; *Lavin and Wharff SW55* (NY). **Esmeralda County:** Silver Peak Range, McAfee Canyon near head of the canyon at the divide between White Wolf Canyon, about 10 air miles east of Dyer. 7600' elevation; T3S, R37E, S17; 4 May 1986; *Tiehm 10306* (BRY, GH, NY, RM, RSA). Silver Peak Range, high ridge between Mohawk Mine and High Peak in the middle of the range. 8800' elevation; T2S, R38E, S30; 28 May 1994; *Tiehm 12075* (BRY, CAS, MO, NY). Mt. Sabb, Palmetto, rocky slopes. 8000-9000' elevation; May-October 1898; *Purpus 5863* (US). White Mountains, W rim of Mustang Mtn, 0.3 miles N33° E of Kennedy Point. Owens Valley drainage. 10170'

elevation; T1S R33E S4; 5 July 1986; *Morefield and McCarty 4063* (BRY, NY). Palmetto Mountains, E of Pigeon Spring, Lida Quadrangle. 7000' elevation; 1 June 1957; *DeDecker 652* (RSA). Montezuma Range, 14.2 road miles west of Highway 93 on the main road into the range from the south side which leads to a relay tower. 7200' elevation; T3S, R41E, S10; 17 June 1987; *Tiehm 11304* (CAS, GH, NY). Between Red Mtn and High Peak, 6.3 mi from Silver Peak in the Silver Peak Range. T2S, R38E, ca S22; 18 May 1988; *Williams and Tiehm 88-14-3* (BRY, NY). Gravelly slope on west side of Lida Pass, in pinyon-juniper woodland. 1 June 1960; *Raven and Verity 15471* (RSA). Ridge South of Queen Mine. 10500' elevation; 4 September 1926; *Ferris 6747* (CAS). **Eureka County:** Frequent, sandy soil, assoc. sagebrush, 5 mi. S. Sadler's R., 55 mi S. Elko. 22 May 1941; *Holmgren 829* (UTC). Low gravelly clay bluff on W slope of Sulpher Creek Range 25 miles NNW of Eureka. 24 May 1982; *Barneby 17827* (NY). **Humboldt County:** Santa Rosa Range, ridge crest west of Abel Creek at south end of range. 8600' elevation; T41N, R38E, S3; 19 June 1985; *Tiehm 9733* (BRY, CAS, GH, NY, RM, UTC). Sonoma Range, ridge on N side Water Canyon, about 4 miles from Water Canyon Road. 8000' elevation; 40°54.10N 117°37.03'W, WGS-1984; T35N, R39E, S7; 8 June 2007; *Tiehm and Nachlinger 15453* (CAS, NY). Jackson Mts, hills north of the North Fork of Jackson Creek, 2.4 airmiles SE of Parrot Peak. 7400' elevation; 41°20.335'N 118°26.435'W, WGS-1984; T40N, R32E, S18; 17 June 2010; *Tiehm and Nachlinger 16157* (CAS, NY, UTC). Jackson Mts near the Iron King Mine. Plants common with tall sagebrush on rocky hills, also on roadcuts. T40N, R32E, S29; 3 June 1979; *Tiehm and Birdsey*

4989 (CAS, GH, MO, NY, UTC). West Humboldt Mountains, west slope of Star Peak, 7800' elevation; 31 July 1912; *Heller s.n.* (CAS). Sonoma Range, ridge top between Water Canyon and Thomas Creek Canyon. Exposed rocky ridge top. 8400' elevation; T35N, R38E, S19; 10 July 1964; *Holmgren and Reveal 1395* (GH, NY, UTC). Pine Forest Range, Leonard Creek drainage near Duffer Peak. 9000' elevation; 43N, R28E; 28 June 1964; *Holmgren and Reveal 1163* (UTC). Jackson Mountains, Jackson Creek drainage, Iron King Mine, 49 airline miles south of Denio. 8000' elevation; T40N, R32E, S29; 31 May 1970; *Holmgren and Holmgren 4082* (BRY, GH, NY). Jackson Mountains, area around Iron King Mines, 48.5 airline miles south of Denio. 7600' elevation; T40N, R32E, S29; 17 June 1970; *Holmgren, Fay, and Bethers 4254* (NY, RM). Jackson Mountain, among sagebrush on rocky steep slope, igneous rocks above Iron King Mine, ridge NE of Iron King Mine. 8600' elevation; T40N, R32E, S29; 15 June 1979; Rollins, Rollins, *Tiehm, and Williams 79253* (GH, NY). **Lander County:** Fish Creek Basin in the middle of the range. 5600' elevation; T27N, R42E, S7; 25 June 1980; *Tiehm 6051* (CAS, GH, MO, NY, RM, RSA).

Toiyabe Forest, Big Creek and Kingston Canyon. 1800-2400m elevation; *Hitchcock 807* (US). Toiyabe Forest, Bunker Hill, dry ground. 2250-3400m elevation; 29 July 1913; *Hitchcock 858* (US). Toiyabe Forest, Bunker Hill, dry hill. 2250-3400m elevation; 29 July 1913; *Hitchcock 848* (US). Divide between Kingston Canyon and Big Creek Canyon, N end of Toiyabe Mts. 8700' elevation; T17N R43E S34/35; 18 July 1980; *Ertter and Strachan 3745* (BRY, CAS, GH, NY, UTC). Toiyabe Range, Toiyabe Nat'l Forest, head of Sheep Canyon ESE of Arc Dome, loose slate talus on

warm S. slope. 10500' elevation; T11N, R41E; 20 June 1985; *Atwood, Ermouick, and Smith* 11283 (BRY). Toiyabe Mts, crest of Range between Kingston Creek and Santa Fe Creek. 10800' elevation; T16N, R43E, S2, SW ¼; 16 July 1981; *Neese, Goodrich, and Welsh* 10724 (BRY, NY). Along south slope of Kingston Canyon, 1-3 mi. below Ranger Station. 10 June 1937; *Goodner and Hennig* 195 (NY). Toiyabe Range, Toiyabe National Forest, lower slopes of Bunker Hill above Mahogany Canyon, 0.5 miles west of Kingston Canyon and Kingston Ranger Station. 8200' elevation; 20 May 1960; *Sharsmith* 4782 (GH, RM, UTC). Kingston Ranger Station. 7500' elevation; 15 June 1930; *Linsdale and Linsdale* 52 (CAS, UTC). Toiyabe Range, E Birch Creek and slopes to the W. 8000' elevation; T17N R43E; 20 June 1988; *Kolar and Knight* 1833 (NY). Toiyabe Range, Kingston Creek Canyon at the mouth of Spring Canyon, 16.3 km (10.1 mi) from State Route 376. 2345m (7700') elevation; 39°16'47"N 117°09'15"W; T16N R43E S4; 5 July 2001; *Holmgren and Holmgren* 14407 (NY). Toiyabe Range, Big Creek, rock hillsides. 7000' elevation; 7 June; *Train* 234 (US). Kingston Canyon. 29 July 1913; *Kennedy* 4192 (CAS). Toiyabe Range, Toiyabe NF, right Fork Birch Creek. 8200' elevation; 18 June 1977; *Goodrich s.n.* (GH). Toiyabe Range, Toiyabe NF, North Fork Big Cr, gravelly slopes near the head of the drainage. 8400' elevation; 2 July 1977; *Goodrich s.n.* (GH). Toiyabe Range, Toiyabe NF, Big Creek south wall of the canyon near Big Creek Campground, inside the 1964 burn. 7000' elevation; 28 May 1977; *Goodrich* 7716 (GH, UTC). Toiyabe Range, Toiyabe NF, along the crest of the range between Kingston Canyon and Frenchman Creek. 10600' elevation; 14 July 1978; *Goodrich* 11830 (NY). Bunker

Hill. 29 June 1931; *Linsdale and Linsdale 510* (CAS). Pahrnagat Range, Logan Pass on main road on south side of Mt Irish. 7100' elevation; T4S, R59E, S6; 10 May 1987; *Tiehm 11000* (BRY, CAS, NY, RSA). **Lincoln County:** Clover Mountains, 5.1 miles South of Caliente on the Ella Mountain road at junction with Sawmill Canyon Road. 5600' elevation, 14 May 1987, *Tiehm and Williams 11009* (BRY, CAS, NY, RM). **Lyon County:** Pine Grove Hills, crest of the range at the road junction from Rockland Canyon. 8300' elevation; T9N, R26E; 19 June 1991; *Tiehm and Nachlinger 12058* (CAS, NY). Slope along Rough Creek. 7500' elevation; 17 May 1980; *Breedlove 44707* (CAS, NY). **Mineral County:** Excelsior Mountains, 2.8 road miles N of junction to Cow Camp on main road north from Huntoon Valley to Rattlesnake Flat. 7200' elevation; T4N, R31E, S11; 20 June 1998; *Tiehm and Nachlinger 12502* (BRY, CAS, UTC). East slopes Wassuk Range, above Cory Canyon. 9000' elevation; 10 September 1938; *Archer 7011* (GH). Wassuk Range, Mt Grant, 0.5 km North, 0.3 km west of the summit of Mt. Grant. 3350m (11000') elevation; 12 July 1977; *Bell and Johnson 552* (WS). Bodie Hills; Mt. Hicks area near the peak. 9400' elevation; T5N, R28E, S24; 13 July 1983; *Tiehm and Lavin 8114* (BRY, CAS, GH, NY, UTC). Pilot Mountains, .8 road miles west of Pilot Peak on main road back to Telephone Canyon. 9000' elevation; T6N, R36E, S29; 23 May 1988; *Tiehm and Williams 11675* (CAS, GH, NY, RM). Wassuk Range, Powell Canyon near road summit. 8400' elevation; T6N, R29E, S25; 20 June 1983; *Tiehms and Williams 7931* (CAS, NY, UTC). Mount Grant, on slope below summit. 10700' elevation; 13 July 1945; *Alexander and Kellogg 4461* (CAS, UTC). Big Indian Mine, road to Cory Canyon.

9500' elevation; 12 July 1945; *Alexander and Kellogg 4445* (CAS). Wassuck Range, Mt Grant, excavated area near southern boundary of Hawthorne Army Ammo Depot.

9000' elevation; 9 July 1983; *Mooney 1087* (GH). **Nye County:** Near Plot 64, north side of Rainier Mesa. Yucca/Kawich drainage basin. 7500' elevation; 11 June 1964; *Beatley and Carl s.n.* (GH, MO). Grapevine Mtns, Sarcobatus/Death Valley drainage, Death Valley Nat Mon, summit, along old rd at head of Phinney Cyn, ca. 2 airline mi se. of Grapevine Peak. 7550' elevation; 5 May 1970; *Reveal 2231* (CAS, GH). No. Topopah Drainage Basin, local, below repeater site, so. face of Shoshone Mtn, at saddle on Topopah Rd. 6800' elevation; 25 May 1970; *Beatley s.n.* (RSA). North Pahute Mesa, occasional on disturbed site near UE19g. 6500' elevation; 9 July 1967; *Beatley s.n.* (GH). Toiyabe Range, Toiyabe National Forest, McLeod Creek, 29 miles 196° from Austin. 8600' elevation; 12 July 1979; *Goodrich s.n.* (GH). Crest of Toiyabe Mts. at head of Stewart Creek, ca. 90 km south of Austin. 3200m; T12N, R41E., S34; 5 July 1973; *Cronquist 11000* (BRY, GH, NY, US, WS). Quinn Canyon Range; 9.3 road miles east of Nyala Road (FAS 827); on road to Cherry Creek summit, 1.5 miles from summit. 7200' elevation; 16 June 1980; *Pinzl 3079* (GH).

White River Valley, Sunnyside area, .4 miles southwest of Hot Creek Campground. 5200' elevation; T6N, R61E, S17; 22 July 1980; *Tiehm and Williams 6190* (GH, NY). Indian Valley, 16 mi. S. of the Reese River Ranger Sta. 7000' elevation; 7 July 1945; *Maguire and Holmgren 25671* (CAS, NY, US, UTC, WS). Toiyabe Range, gravelly broad sagebrush ridge between Stewart Creek and Sawmill Creek. 9500' elevation; 23 July 1945; *Maguire and Holmgren 25915* (CAS, NY, UTC, WS).

Toiyabe Range, Mohawk Canyon, frequent, loose light sandy soil on West facing slope. 7500' elevation; 14 June 1945; *Maguire and Holmgren 25429* (F, GH, NY, UTC). Toiyabe Range, Mohawk Canyon, frequent, loose calcareous soil in sparse juniper. 9 July 1945; *Maguire and Holmgren 25685* (GH, NY, UTC). Toquima Range, rocky ridge on south side of Pine Creek Canyon. 10000' elevation; 17 July 1945; *Maguire and Holmgren 25824* (NY, US, UTC). Quinn Canyon Range, 3 mi west of Cherry Creek Summit. 20 June 1945; *Maguire and Holmgren 25548* (NY, UTC). Quinn Canyon Range, ridge north of Cherry Creek Pass. 20 June 1945; *Maguire and Holmgren 25533* (GH, NY, UTC). Indian Creek near jct with Reese River, 2 miles south of Warners, Toiyabe Nat'l Forest. 7000' elevation; 29 June 1976; *McPherson 76-1-4* (CAS). Toquima Mountain Range, Toiyabe Mountains, Stewart Creek Campground. 8600' elevation; 38°N 116°50-57'W; 6 June 1979; *Smith 1187* (UTC). White River Valley, .5 mi W of Hot Creek Campground. 5500' elevation; T6N, R61E, S3; 24 May 1979; *Thorne 539* (BRY, GH). Pahute Mesa, south end. Forty-Mile drainage basin. 7000' elevation; 22 June 1964; *Beatley s.n.* (GH). Northern Rainier Mesa, near Plot 64. Kawich/Yucca drainage basin. 7400' elevation; 4 June 1967; *Beatley s.n.* (CAS, GH). Echo Mountain area, southern Pahute Mesa. Forty-Mile drainage basin. 6500' elevation; 25 June 1964; *Beatley and Carl s.n.* (GH). Rainier Mesa, west slope. 6000' elevation; 3 June 1964; *Beatley and Carl s.n.* (GH). Quinn Canyon Range, 4.8 miles North of Cherry Creek Summit. 7310' elevation; 38°11.54'N 115°36.37'W; 6 June 2013; *Minnaert-Grote and O'Kane 91* (ISTC). Toiyabe Range, 1.3 miles due S of Ophir Summit along the Toiyabe Crest

Trail between North Twin River and Last Chance Creek; 0.8 miles WNW of South Toiyabe Peak. 10160' elevation; T12N, R41E, S12, NE ¼ NW ¼; 28 June 1991; *Morefield and Frolli 5493* (NY). Jct of Rainier Mesa Rd and turn-off to Holmes Rd, no. Rainier Mesa, so. Belted Range. Yucca/Forty Mile drainage basin. 7400' elevation; 10 June 1968; *Reveal 1212* (GH). Quinn Canyon Range, along a low ridge west of the Cherry Creek Summit Road, 4.5 miles north of Cherry Creek Summit and 0.3 miles south of the Humboldt National Forest line. 6200' elevation; 20 May 1976; *Reveal 4405* (BRY, GH, NY, UTC). Quinn Canyon Range, summit of Cherry Creek Canyon. 7650' elevation; 20 May 1976; *Reveal 4404* (NY). Wisconsin Creek. 8500' elevation; 25 May 1930; *Linsdale and Linsdale 3a* (CAS). Mohawk Ranger Station. 8000' elevation; 17 June 1931; *Linsdale and Linsdale 216* (CAS). Quinn Canyon Division, near mouth of Bruno Canyon. 6500' elevation; 4 June 1975; *Lewis 3335* (UTC). Hot Creek Range, west side of Morey Peak, N of saddle btw Six-Mile Canyon and N Six-Mile Spring. Ca T9N, R50E; 17 August 1983; *Mooney 1230* (GH). W side of the Quinn Canyon Range, 0.9 mi uphill from Forest Service Boundary. 6000' elevation; T4N, R57E, ca S5; 13 May 1982; *Williams and Atwood 82-7-10* (GH, NY). East side of Shoshone Range, South Fork of Barrett Creek. 8400' elevation; T14N, R39E unsurveyed; 4 July 1980; *Williams, Lott, and Tiehm 80-176-14* (BRY, CAS, GH, NY, UTC). Toquima Range, Toiyabe National Forest, Pine Creek Canyon. 8200' elevation; T11N, R45E; 13 July 1964; *Holmgren and Reveal 1442* (BRY, NY, UTC, WS). Shoshone Mountains, Toiyabe National Forest, 1.1 miles east of Union Canyon Summit, in East Union Canyon. 2300m elevation; T12N,

R39E, S24; 4 June 1996; *Leary, Niles, and Holland 3444* (BRY). Western slope of the Toiyabe Range, a few miles west of Ophir Summit. 13 June 1979; *Rollins and Rollins 79222* (GH). Toiyabe Mountains, rocky open ridge among dwarf sagebrush, ½ mile W of Ophir Summit. 13 July 1979; *Rollins and Rollins 79227* (BRY, F, MO, NY, RM, US). Cherry Creek summit, Quinn Canyon Range. 7450' elevation; 10 June 1966; *Barneby 14402* (CAS, NY). Toiyabe Mountains, South Twin River, 6 miles west of canyon mouth. 7500' elevation; 10 July 1938; *Rollins and Chambers 2535* (CAS, RM, UTC). Toiyabe Mountains, 15 miles west of Round Mountain, watershed of Jet Creek. 9500' elevation; 10 July 1938; *Rollins and Chambers 2505* (CAS, US, UTC). Toiyabe NF, Toiyabe Range, McLeod Creek, 29 miles 196° from Austin. 8600' elevation; N39°5'25" W117°13'8"; 12 July 1979; *Goodrich 13434* (BRY). Toiyabe Range, Toiyabe NF, Summit Cr. 37 miles 197° from Austin. 7800' elevation, N38°58'28" W117°16'7"; 25 June 1979; *Goodrich s.n.* (GH). Toiyabe Range, Toiyabe NF, along crest of the range between Aiken Cr, and Washington Canyon. 10500' elevation; T15N, R43E, S17, SW ¼; 5 August 1978; *Goodrich 12123* (RM, UTC). Toiyabe Range, Toiyabe NF, San Juan drainage. 8550' elevation; T14N, R42E, S8, SE ¼; 1 June 1978; *Goodrich 11213* (RM). Toiyabe Range, Toiyabe NF, crest of range at Ophir Pass. T13N, R41E, S36; 30 June 1978; *Goodrich s.n.* (GH). Toiyabe Range, Toiyabe NF, along the crest of the range between Aiken Cr, and Washington Canyon. 10500' elevation; T15N, R43E, S17, SW ¼; 5 August 1978; *Goodrich s.n.* (GH). Toiyabe Range, Toiyabe National Forest, San Juan drainage. 8550' elevation; T14N, R42E, S8; 1 June 1978; *Goodrich s.n.* (GH). Shoshone

Range, Toiyabe National Forest, N.F.K. Barrett Canyon. 8200' elevation; 4 May 1977; *Goodrich 6874* (GH). Toiyabe Range, Toiyabe NF, big ridge between Stewart Cr. and Twin Rivers; 19 miles and 303° from town of Round Mtn. 11200' elevation; N38°51'30" W117°21'5"; 17 July 1979; *Goodrich 13510* (BRY). Toquima Range, Shoshone Mt, Toiyabe NF, head of Bull Frame Canyon, ca 7 mi and 318° from Belmont. 10550' elevation; N38°40'23" W116°57'48"; 7 July 1979; *Goodrich and Smith 13273* (BRY). Toiyabe National Forest, 10-15 mi. SE of ranger stn. Clear Creek toward Ophir Creek Summit. 8500' elevation; 30 June 1976; *McPherson 76-2-6* (CAS). **Pershing County:** West Humboldt Mountains, Star Creek Canyon on east side of the range, South side of Star Creek. 7800' elevation; T31N, R34E, S27; 31 May 1985; *Tiehm 9543* (BRY, CAS, GH, NY, RM, UTC). West Humboldt Mts, head of Star Canyon on the east side of the range. Plants growing in protected outcrops near the ridgetop. 9300' elevation; T31N, R34E, S20; 4 July 1984; *Tiehm 8895* (NY). Humboldt Range, ridge on north side of Humboldt Canyon on northwest end of range, .4 miles West of Yana Point. 7800' elevation; T31N, R34E, S8 (unsurveyed); 13 June 1989; *Tiehm and Nachlinger 12004* (BRY, CAS, NY, RM, WS). West Humboldt Range, north of Star Peak, SW of Lakeview Mine. 8300' elevation; T31N, R34E, S8, SE ¼; 14 July 1978; *Tiehm and Williams 4546* (NY). W. Humboldt Mts, above Unionville. 6600' elevation; 6 June 1943; *Ripley and Barneby 5620* (CAS, NY). Upper limits of Juniper zone and above, dry ridge north of Star Creek, East of Star Peak. 16 June 1946; *Ownbey and Ownbey 2867* (CAS, NY). **White Pine County:** Egan Range, 0.5 road miles W of Highway 50 at Keystone Junction on

Highway 267 to Ruth, S side of the highway. 6780' elevation; T16N, R62E, S3; 15 June 2000; *Tiehm and Nachlinger 13244* (NY). SE end of Long Valley on east side of the road, 10.4 road miles north of highway 50. 6400' elevation; T19N, R59E, S8; 9 June 1983; *Tiehm and Williams 7875* (BRY, GH, NY, UTC). Egan Range, .5 road mile west of highway 50 on the road to Ruth. 6770' elevation; T16N, R62E, S3; 10 June 1983; *Tiehm and Williams 7880* (BRY, CAS, GH, NY, UTC). White River Valley, Jakes Wash. Pinyon-juniper-mound-forming comm, white sandy clay knolls. 6400' elevation; T15N, R60E, S24; 5 June 1980; *Thorne, Welsh, Welsh, and Chatterley 988* (BRY, RM). E end of Jake's Valley, ca 13 mi S of Hwy 50. 6400' elevation; T16N, R60E (unsurveyed); 22 May 1981; *Williams and Tiehm 81-11-1* (BRY, CAS, GH, NY, UTC). US Highway 50, 2.1 km (1.3 mi) northwest of Ruth turnoff. 2075m (6800') elevation; 39°17'51"N 114°58'32"W; T17N R62E S34; 28 June 1999; *Holmgren and Holmgren 13633* (ISTC, NY, UTC). Thirty miles west of Ely then 4.5 miles north of Ruby Lake Road. 22 June 1984; *Atwood 10230* (GH, NY). Butte Mountains, summit of Long Valley Canyon, about 45 km (28 mi) air distance northwest of downtown Ely. 2200m (7220') elevation; 39°32'50"N 115°14'02"W; T19N R60E S4, NW ¼; 7 June 2002; *Holmgren and Holmgren 14652* (NY, UTC). 1.8 km (1.1 mi) along the Ruth road from US Highway 50. 2075m (6800') elevation; 39°16'53"N, 114°58'26"W; T16N R62E S3; 28 June 1999; *Holmgren and Holmgren 13628* (NY). Stone clay flats among juniper, 16 miles n.-w. of Ely. 7400' elevation; 9 June 1966; *Barneby 14397* (CAS, NY, US). 1.1 miles northwest of the Ruth Road on Highway 50 to Eureka, north of the highway. 7000' elevation; T17N, R62E, S27; 21

May 1985; *Tiehm 9436* (BRY, CAS, GH, NY, RM, UTC, WS). Along US Hwy. 50, 7 miles west of Ely. 2074m elevation; T17N, R62E, S28; 25 May 1976; *Halse 1352* (CAS, NY). Spring Valley, Cooper Canyon on bajada, 0.5 mi from Spring Valley Rd. 6400' elevation; T20S, R66E, S5; 3 May 1980; *Thorne and Harrison 815* (BRY).

Physaria kingii ssp. *bernardina*

UNITED STATES: California: San Bernardino County: San Bernardino Mts, North side of Bear Lake. 6,700' elevation; 6 July 1924; *Johnston s.n.* (RM).

Dolomitic, rocky slope along Caribou Creek in Van Dusen Canyon. 1.8 mi. north of junction with Hwy 38 in Big Bear City. 7100-7300' elevation; 15 June 1979; *Thorne, Tilforth, and Little 53154* (GH, RSA). San Bernardino Mtns, North shore, east end Big Bear Lake. ½ mile E of Stanfield. Cutoff on rocky limestone slope between two churches. 6,850' elevation; 7 May 1980; *Bennett and Wilson s.n.* (CAS). San Bernardino Mountains region, Survey along the west ridgeline of Sugarloaf Mountain. From 34.21189N 116.86998W, off of Forest Service Road (2N21) to a knoll NW of Sugarloaf. Near 34.20440N 116.82124W. This collection site. Slightly sloping NE. 2488-2777m/8160-9110' elevation; near 34.20987°N, 116.84163°W; T2N R1E S35, SE1/4; Moonridge 7.5 quad; 1 June 2009; *Gross and Bell 4016* (RSA). San Bernardino Mountains, Bear Valley area. North shore of Baker Lake about 1 mi east of Stanfield Cut-off.

11 June 1985; *Boyd and Marsh 1172* (RSA).

Physaria kingii ssp. *cobrensis*

UNITED STATES: Idaho: Bonneville County: BLM land, Hells Half Acre Lava Flow, western edge ca 3 miles S of Hwy 20, ca 23 miles W of Idaho Falls. In barren small playa-like shallow depressions at W base of flow with small, nearly “desert pavement-like basalt pebbles at surface. 5150’ elevation; T2N R34E S8 SW ¼; 19 June 1983; *Henderson and Cholewa 6576* (RM). **Cassia County:** Sawtooth National Forest, Ca 2.4 airline mi S of Ibex Peak, Twin Falls R.D. 5700’ elevation; T16S, R20E, S2 SWNE; 21 June 1989; *Atwood, Jenkins, and Neiwert 13648*. **Nevada, Elko County:** Owyhee Desert, 1.5 road miles WNW of Butte Springs on Bob Johnson Road past Hat Peak. 5175’ elevation; T46N, R49E, S11; 10 June 1999; *Tiehm and Nachlinger 12888* (NY). Butte Valley, on the road to Te-Moak Indian Reservation, 5.8 air miles SSE of Odgers Range. 6200’ elevation; T27N, R62E, S29; 19 June 1984; *Tiehm and Williams 8730* (BRY, CAS, GH, NY, RM). 10 miles N of Currie. 6200’ elevation; 29 June 1945; *Ripley and Barneby 6445* (CAS, NY). Foothills of Pequor Range, near Oasis. 6150’ elevation; 27 May 1944; *Ripley and Barneby 4611* (NY). Pequop Mountains, foothills on the east side along the old US Highway 40 now paralleling Interstate 80, 4 km (2.5 mi) northwest of Oasis-Montello exit. 1880m (6170’) elevation; 41°03’16”N 114°31’32”W; T37N, R66E, S28; 27 June 1999; *Holmgren and Holmgren 13614* (ISTC, NY, UTC). Butte Valley, 2.9 km (1.8 mi) west of the valley road from a turnoff 39.7 km (24.7 mi) south of US Highway 93, 10.5 km (6.5 mi) air distance west-southwest of Currie. 1980m (6500’) elevation; 40°11’08”N 115°02’19”W; T27N, R61E, S25; 28 June 1999; *Holmgren and*

Holmgren 13624 (NY, UTC). Butte Valley, along the valley road 38.1 km (23.7 mi) south of US Highway 93, 9 km (5.6 mi) south of Odgers Range, 6 km (9.5 mi) air distance west-southwest of Currie. 6300' elevation; 40°11'54"N 115°00'24"W; T27N, R62E, S20; 27 June 1999; *Holmgren and Holmgren 13622* (NY). 30 mi. E of Wells on Cobre old Highway paralleling Southern Pacific R.R. 13 May 1940; *Train 3665* (NY). **Humboldt County:** Sheldon Antelope Range, Badger Creek Road to Summit Lake, approximately 1 mile SE of Mahogany Mt. 6050' elevation; T43N, R24E; 12 May 1981; *Pinzl 3931* (GH). High Rock Canyon Hills, 0.4 road miles SE of Black Buttes road on road to Chukar Gulch. 6180' elevation; 41°25.606'N 119°16.091'W; T41N, R24E, S32; 20 May 2004; *Tiehm 14454* (ASC, NY, RSA, UTC). West end of Wildcat Gorge at southeast end of Shoestring Valley, east of Stevens Camp. 5650' elevation; T42N, R24E, S32; 5 June 1985; *Tiehm and Schoolcraft 9600* (BRY, CAS, GH, NY RM, RSA, WS).

West head of Thousand Creek. 6 June 1933; *Applegate 8326a* (CAS, F). 43 miles from Cedarville, CA, on road 8A, SW side of road. 5857' elevation; 41°40.52'N 119°25.41'W; 9 June 2013; *Minnaert-Grote and O'Kane 92* (ISTC) Charles Sheldon Wildlife Refuge, rocky area, near hwy 8A. 43 miles northeast of Cedarville, California. 6 June 1981; *Rollins and Rollins 81229* (BRY, MO, NY, RM, US).

Lincoln County: Lake Valley, 4.2 rd mi E of Highway 93. 6000' elevation; T6N, R66E, Sec. 36; 12 June 1981; *Williams and Tiehm 81-56-3* (UTC). **Washoe County:** Antelope Flat, east of Hayes Canyon Range, Nellie Spring turnoff from road, which has been numbered "34". 5800' elevation; T40N, R21E, S27, NW ¼; 23 April 1990;

Pinzl 8942 (GH, NY). Sheldon National Wildlife Refuge, 1.2 road miles N of Badger Mt Road on highway 8A, W of highway. 6000' elevation; T44N, R23E, unsurveyed; 13 June 1995; *Tiehm 12126* (BRY, MO, NY, RSA, UTC). Southwest side of Badger Mt., .8 air miles E of Wall Canyon Ranch. 5850' elevation; T43N, R23E, S34; 20 June 1978; *Rogers and Tiehm 947* (CAS, NY, UTC). **White Pine County:** Steptoe Valley, near work camp in vicinity of Connors Pass Well, north side of road from Hwy 50/93 (Connors Pas 7.5'). 2080m (6822') elevation; 39°02'32"N 114°43'59"W, 13 June 2006; *Sanders 32871* (MO).

Physaria kingii subsp. *diversifolia*

UNITED STATES: Oregon: Wallowa County: Wallowa Mountains, Ice Lake Trail. 26 June 1937; *Eastwood and Howell 3412* (CAS, F, NY, US). Wallowa Mountains, Hurricane Forest Creek Camp, frequent, gravelly flood bands under open lodge-pole pine and cottonwood,. 4200' elevation; 19 July 1946, *Maguire and Holmgren 26686* (BRY, CAS, F, GH, MO, NY, RM, US, WS). Wallowa Mts, Dry stony slopes above Slickrock Creek in vic of Hurricane Creek. 16 August 1946; *Maguire and Holmgren 27054* (NY, US, UTC). Growing in "crystalline marble" on dry bare cliffs of the Matterhorn, with *Penstemon* and *cassipe*. 8500' elevation; R44E T4S S11; 8 August 1963; *Mason 6430* (GH). Thin sandy soil on steep limestone cliffs of Marble Point, with *Valeriana*, *Berberis*, and *Anemone*, near snow. 6900' elevation; R43E T3S S24; 5 July 1964; *Mason 6918* (GH). Bed of Deadman Creek. 5500' elevation; 17 August 1963; *Mason 6511* (GH). 5 miles southwest of Joseph, up Hurricane Creek Road. 4700' elevation; 2 June 1963; *Mulligan and Mosquin 2692*

(CAS, NY). Ice Lake, Wallowa Mts. 10 July 1935; *Jones 7019* (GH). Wallowa-Whitman National Forest, 4.8 miles from Highway 82 on Hurricane Creek Road, south of the town of Joseph. 4870' elevation; 45°19.31N 117°18.24W; 10 June 2013; *Minnaert-Grote and O'Kane 93* (ISTC). Wallowa-Whitman National Forest, 5.4 miles from Highway 82 on Hurricane Creek Road, south of the town of Joseph. 45°18.75N 117:18.39W; 10 June 2013; *Minnaert-Grote and O'Kane 94* (ISTC). Above Aneroid Lake, 7 mi. S of Wallowa Lake. 8000' elevation; 22 July 1936; *Rose 36589* (CAS, F). Strong Bank of upper Hurricane Creek. 20 July 1944; *Peck 22449* (GH). Dry talus slope, Ice Lake. 11 July 1934; *Peck 18434* (CAS, NY). Lower East slope of Lostine Canyon, 18 miles above Lostine. 22 July 1933; *Peck 17859* (NY). Wallowa-Whitman National Forest, east side of Hurricane Creek Trail, 100 yds N of Slickrock Creek ca 2.5 air mi S of Hurricane Creek Trail parking area, ca 8 air mi S of Joseph. 5800' elevation; T3S R44E S27; 17 July 2001, *Markow 12247* (RM). Near Enterprise. 23 May 1923; *Sherwood 427* (GH).

Ice Lake Trail. 7000' elevation; 9 July 1961; *Mason 1237* (GH). In shady, moist coniferous woods along Hurricane Creek. Ca. 5000' elevation; R44E T3S S3; 23 June 1962; *Mason 5032* (GH).

Physaria kingii subsp. *kaibabensis*

UNITED STATES: Arizona: Coconino County: Kaibab Plateau, 19 miles S of Jacob Lake on turnoff to Eastside Game Rd, exposed limestone knoll above sinkhole ½ mile E of Grand Canyon Hwy. 22 June 1979; *Ertter and Strachan 2900* (NY, UTC). Ca. 12 miles S of Jacob Lake, Collected from the tops of dry rocky hills that

exist in meadows. 23 May 1984; *Schaack 1221* (ASC, NY). Jacob Lake, Kaibab Forest, moderate W. slope, coarse limestone gravel soil with *Erigeron*, *Aster*. 7500' elevation; 7 June 1927; *Storm 207* (BRY, RM). Kaibab Forest, near V.T. Resort, rock outcrop on forest border in partial shade. 8775' elevation; 14 July 1927; *Peirson 7390* (CAS). Kaibab Plateau, V.T. Park, rocky soil. 4 July 1953; *Merkle 762* (CAS). 18 miles South of Jacob Lake on Highway 67. 8573' elevation; 4 June 2013; *Minnaert-Grote and O'Kane 83* (ISTC). 15.8 miles south of jctn 89A/67 in Jacob Lake on rte 67 toward Grand Canyon Natl Park (north side). 8380' elevation; 18 June 1993; *Rebman and Dierig 1901* (NY). Kaibab Plateau, north end of Pleasant Valley. 10 June 1949; *Goodding 165-49* (CAS). North Kaibab National Forest, ponderosa pine forest. 2384m elevation; UTM 12S 4063812N 397033E [NAD27]; 14 June 2009; *McMaster and Markgraf 232* (ASC). Kaibab Plateau, Arizona Route 67, 25.7 km (16 mi) south of Jacob Lake and 21 km (13 mi) air distance south-southeast. Rocky exposed slope east of the highway with *Potentilla hippiana*. 2625m (8610') elevation; 36°31'45"N 112°09'02"W; T36N R2E S11; 21 June 1999; *Holmgren, Holmgren, and Joseph 13564* (CAS, ISTC, NY). Kaibab Plateau, Pleasant Valley, Arizona Route 67, 30.4 km (18.9 mi) south-southeast of Jacob Lake and 25.5 km (16 mi) air distance. 2620m (8600') elevation; 36°29'44"N 112°07'57"W; T36N R2E S24; 21 June 1999; *Holmgren, Holmgren, and Joseph 13565* (ISTC, NY, RSA, UTC). Limestone ledge, 2 mile north of Kaibab Lodge, north of Grand Canyon National Park. 8800' elevation; 23 July 1941; *Munz 16976* (CAS). 18.6 miles South of Jacob Lake on road to the North entrance to Grand Canyon National Park. 8 June 1979; *Rollins and Rollins*

79191 (NY). Open rocky knolls and crevices of weathered limestone rocks, near State Hwy 67, 20.1 miles south of Jacob Lake. 11 July 1986; *Rollins and Rollins 86216* (NY, RM, UTC). Limestone knolls, 21 miles south of Jacobs Lake. 8200' elevation; 13 August 1967; *Rollins 57332* (NY). Limestone chip and rocky slope, 17 miles south of Jacob Lake. 8000' elevation; 13 August 1957; *Rollins 57333* (F, NY). Kaibab National Forest, 18.6 miles south of Jacob Lake on Highway 67. 2530m elevation; 36°29.97'N 112°8.15'W; 18 May 1998; *O'Kane 4213* (ISTC).

Physaria kingii subsp. latifolia

California: Inyo County: Panamint Range, exposed ridge North of Mahogany Flat, head of Wild Rose Canyon. 8100' elevation; 31 May 1938; *Crum 2051* (CAS). Panamint Mts, Wild Rose Canyon, Flat under pinyons. 7500' elevation; 8 May 1932; *Munz 12531* (RSA). Panamint Mountains, Wild Rose Canyon, under *Pinus monophylla* on steep rocky slope. 7700' elevation; 12 July 1947; *Roos and Roos 2835* (CAS). Panamint Mountains, Wild Rose summit. 8500' elevation; 28 April 1931; *Coville and Gilman 238* (US). Panamint Mountains, sandy soil, upper part of Surprise Cañon. 7800' elevation; 15 June 1928; *Howell 3939* (CAS). Panamint Mountains, slope of Baldy. 16 September 1931; *Coville and Gilman 47* (US). Panamint Mountains, slope southward from Wild Rose summit. 8600' elevation; 16 September 1931; *Coville and Gilman 36* (US). Panamint Mtns, Hanaufrah Canyon, slope of the trail to Telescope Peak. 20 June 1935; *Gilman 1798* (US). **Modoc County:** Upper slopes of Warner Mtns near Patterson Lake. Dry gravelly slopes above the timber. 9000' elevation; 31 July 1983; *Schoolcraft 1124* (NY). **Mendocino County:**

California Forest, Red Rock D#4, gravel soil, barren ridge top. 6250' elevation; 24 June 1923; *Cronemiller 613* (CAS, RM). **San Bernardino County:** E Mojave Desert, New York Mts, Caruthers Canyon below Giant Ledge Mine on limestone rocks and mine tailings. 6100' elevation; 13 May 1977; *Thorne, Tilforth, DeBuhr, et al.49323* (CAS, GH). Caruthers Canyon, near Hard Cash Mine, 2.9 mi. N of New York Mts. road. 6200' elevation; 29 April 1973; *Thorne 43351* (GH, NY). New York Mts, Keystone Canyon. 5800' elevation; 28 May 1977; *Thorne, Wisurna, Davidson, and Prigge 49229* (GH). Eastern Mohave Desert, New York Mtns, loose soil near Keystone Spring. 5200' elevation; 4 May 1935; *Munz 13737* (CAS, UTC). 7 miles East of Jacob Lake. 6950' elevation; 9 June 1942; *Ripley and Barneby 4915* (NY). New York Mountains, Keystone Canyon, common on rocky slopes at this altitude. 5700' elevation, 15 May 1940, *Alexander and Kellogg 1476* (GH). NY Mountains, 4th of July Canyon, on dry, rocky slope above the Old Giant Ledge Mine. 5800' elevation; 11 May 1940; *Alexander and Kellogg 1408* (UTC). New York Mountains, 4th of July Canyon, quite common under pinyon pine and on rocky slopes, upper canyon. 5800' elevation; 13 May 1940; *Alexander and Kellogg 1439* (CAS). N side of Clark Mountain, 5.2 mi NNW of Mountain Pass. 7400' elevation; 20 May 1972; *Prigge and Henrickson 150* (NY). E. Mojave Desert, New York Mountains, Keystone Canyon. 5500' elevation; 10 May 1978; *Prigge and Thorne 2932* (GH). East side of New York Mountains, Keystone Spg toward head of Keystone Canyon. 6000-6200' elevation; 28 May 1977; *Davidson 5813* (NY, RSA). Mojave Desert, Clark Mtn, 1 mi So. of Coliseum Mine. 6000' elevation; 28 May 1935; *Wolf 7074* (CAS). New York

Mountains, Keystone Canyon, On loose talus detritus. 5600' elevation, 10 May 1978, *Thorne and Prigge 51338* (RSA). E. Mojave Desert, New York Mts, Caruthers Canyon, upper end near Hard Cash Mine, on rocky slopes in pinyon-juniper woodland. 6200' elevation; 31 May 1973; *Thorne and Tilforth 43696* (GH, NY).

Nevada: Clark County: Desert Game Range, 2 mi S of Mormon Well (ne of Corn Creek Headquarters). 6880' elevation; 31 May 1958; *Janish 1128a* (CAS). Charleston Mountains, ridge south side of Lee Cañon, in limestone. 8450' elevation; 26 July 1913; *Heller 11004* (CAS, GH, MO, NY, US). Charleston Mountains, Camp No. 1 and 2, Charleston Park Resort. 7700' elevation; 19 May 1939; *Alexander 547* (CAS). Sheep Range, NW of Pine Nut Camp. 7000' elevation; 29 May 1976; *Ackerman 76-224* (NY, UTC). Charleston Mountains, Deer Creek. 8250' elevation; 13 June 1939; *Alexander 772* (GH). Sheep Mountains, Hidden Forest, on limestone slope. 7700' elevation; 22 May 1940; *Alexander and Kellogg 1533* (GH). Sheep Mtns, Hidden Forest, floor of Canyon. 7700' elevation; 21 May 1940 ; *Alexander and Kellogg 1510* (CAS, GH). Charleston Mountains, Lee Canyon. Calcareous gravels under pines. 9000' elevation; 13 June 1943; *Ripley and Barneby 4986* (NY). Charleston Mountains, Kyle Cañon, Yellow pine-aspen belt. 25 May 1919; *Tidestrom 9627* (US). Kyle Canyon, gravelly gentle slopes and flats. 2225m elevation; 10 May 1936; *Clokey 7100* (NY). Kyle Canyon, gravelly gentle slopes and flats. 2200-2270m elevation 19- 21 June 1939; *Clokey 8358* (BRY, CAS, F, GH, MO, NY, RM, RSA, US, UTC, WS). Kyle Canyon, fill at bridge, yellow pine belt. 2300' elevation; 3 June 1936; *Clokey 7101* (GH, NY). McFarlane Springs, openings, yellow pine belt. 2425m

elevation; 1 June 1937; *Clokey 7534* (GH, NY). Canyon East of Mountain Springs. 1400' elevation; 22 April 1939; *Clokey 8350* (CAS). Kyle Canyon below CCC Camp. 2200m elevation; 10 May 1936; *Clokey 7100* (NY, UTC). Northwest Spring Mountains, Indian Springs/Pahrump; Wheeler Pass, Nevada Hwy 52. 7650' elevation; 1 July 1970; *Beatley and Reveal s.n.* (GH, NY). Spring Mountains, common, area of spring above old camp and Adams Ranch, upper Clark Cyn nw. of Charleston Peak, sw. face of no. -cent. 9000' elevation; 22 July 1971; *Beatley, Ackerman, and Bamberg s.n.* (GH). Sheep Range, NE Las Vegas Valley drainage basin. Common on ridge no. of Hidden Forest Camp, on gravelly limestone soil. 8000' elevation; 13 June 1968; *Reveal 1282* (GH). Toiyabe National Forest, Lee Canyon Ski Area. 20 May 1987; *Porter 4949* (BRY). Wheeler Pass, 2 mi W of Willow Sp. 1190m elevation; T18S, R55E, S10; 18 May 1987; *Thorne and Atwood 5236* (BRY, NY). Sheep Range, N of Las Vegas near Mormon Pass, ca 3.94 km SW of Wamp Spring. In gravelly, limestone soil on gentle N-facing slope with *Pinus*, *Juniperus*, *Artemisia*, and *Ephedra*. 6700' elevation; 36°37'27"N 115°06'33"W (WGS84 Datum); T15S, R61E, S14; 28 May 1998; *Windham 98-246* (BRY, ISTC, MO). Sheep Range, 2.5 km (1.6 mi) north of Mormon Wells picnic site, 53 km (33 mi) airline distance north of downtown Las Vegas. 1950m (6400') elevation; T15S, R61E; 27 May 1979; *Holmgren, Holmgren, and Barneby 9204* (BRY, GH, NY, RM, RSA). McFarlane Spring Wash, shady canyon bottom in pine needles. 7800' elevation; 20 June 1938; *Train 2020* (GH). Sheep Range, Mormon Pass area, Mormon Well Rd. 6600' elevation; 16 June 1973; *Ackerman 3360* (UTC). **Esmeralda County:** Magruder

Mountain, Magruder Ridge in limestone boulders. 2652m (8700') elevation; T6S, R40E, S16, SE ¼; 27 June 1995; Holland, Niles, *Landau, and Leary* 5272 (NY).

Lincoln County: West side of Delamar Mountains, West Oak Springs/Oak Springs. 5850' elevation; 12 May 1980; *Pinzl* 2805 (GH). North of Pioche. 5600' elevation; June 18, 1944; *Ripley and Barneby* 6350 (NY). NE end of the Pahranaagat Range, 6.6 road miles NW of highway 93 on the Coal Valley road, near the summit. 5600' elevation; T3S, R60S, sec. 7; 16 May 1982; *Tiehm* 6919 (GH). Pahranaagat Range, Mt. Irish at the north end of the range. 8400' elevation; T3S, R59E, S31; 15 June 1987; *Tiehm* 11274 (NY). Delamar Mts, 0.5 road miles E of Highway 93 from Caliente on road to West Oak Springs. 5850' elevation; T4S, R65E, S16; 2 May 2005; *Tiehm and Nachlinger* 14776 (ASC, CAS, F, MO, NY, UTC). Delamar Mountains, 1.7 road miles Northeast of Willow Creek on road to Indian Basin. 5450' elevation; 37°26.793"N 114°38.319"W, WGS-1984; T6S, R66E, S6; 8 June 2011; *Tiehm and Nachlinger* 16336 (NY). Delamar Mountains, 1.8 miles West of Oak Springs Summit on Highway 93, then 0.5 mi Northeast on dirt road. 5900' elevation; 23 June 1984; *Tiehm and Williams* 7984 (BRY, CAS, GH, NY, RM). Clover Mountains, 9 miles South of Caliente on Ella Mountain Road, near Cabin Pines Campground. 6000' elevation T5S, R67E; 23 June 1983; *Tiehm and Williams* 7979 (GH, NY, RM).

Highland Range, Manhattan Gap on the main road from Pan American mine north around the range. 7200' elevation; T1N, R66E, S9; 17 May 1987; *Tiehm and Williams* 11031 (CAS, NY, RM, RSA). Meadow Valley Wash, 5.1 road miles South

of Caliente on Elgin Road, Hardy Canyon just West of Etna. 4500' elevation; T4S, R66E; 16 May 1985; *Tiehm, Williams and Ertter 9420* (GH, NY). Highland Range, above Caliente. 6400' elevation; 26 May 1945; *Ripley and Barneby 6406* (NY). Highland Range, west of Caliente. 6400' elevation; 19 May; *Ripley and Barneby 3492* (NY). West side of Highland Range, west of the town of Pioche. 6436' elevation; 37°55.01'N 114°37.05'W; 5 June 2013; *Minnaert-Grote and O'Kane 89* (ISTC). Near Elgin in Meadow Valley between the Clover and Delamar Mountains. 11 May 1975; *Shultz, Shultz, and Lowrey 1657* (UTC). Egan Range, Shingle Pass Road, 4.4 miles East of Nevada Hwy 318, 23 air miles South of Lund. 6200' elevation; 26 May 1995; *Holmgren and Holmgren 12351* (NY). **Nye County:** Monitor Range, Toiyabe NF, Danville Canyon, ca 20 mi and 55° from Belmont with sagebrush. 9400' elevation; N38°45'20" W116°34'28"; 30 June 1979; *Goodrich 13067* (BRY). Hot Creek Range, ridge E of Sixmile Summit between North and South Sixmile Canyons. 9300' elevation; T9N, R50E, S12; 5 July 2001; *Tiehm 13646* (BRY, CAS, NY). South Twin River. 6500' elevation; 1 May 1930; *Linsdale and Linsdale s.n.* (UTC). Hot Creek Range, Sixmile Summit between north and south Sixmile Canyons. 8800' elevation; T9N, R50E, S11; 5 June 2001; *Tiehm and Nachlinger 13599* (BRY, CAS, NY, RSA, UTC). Table Mountain, head of Barley Creek, gravelly sagebrush slopes above Scuffe Pasture. 9800' elevation; 10 July 1945; *Maguire and Holmgren 25693* (GH, MO, NY, UTC). 1 mile NE of Hot Creek Campground. 5220' elevation; T6N, R61E, S8; 5 June 1979; *Thorne 555* (BRY). Quinn Canyon Range, Cherry Creek summit, along road in Pinyon-juniper

vegetation. 13 July 1983; *Mooney 1111* (GH). Timber Mtn, N side. 8800' elevation; 27 June 1979; *Williams; Birdsey, and Tiehm 79-109-1* (CAS, NY, UTC). **White Pine County:** 6 miles N of Ely. 6300' elevation; 14 June 1944; *Ripley and Barneby 6271a* (NY). Spring Valley, south end of Baking Powder Flat, 3.7 mi east of US 93 on South Highline Road. 5775' elevation; T11N, R66E S36; 17 June 1980; *Pinzl 3103* (GH). Due W of Ragsdale Springs, about 6 miles. 7000-8000' elevation; 24 May 1937; *Moore and Franklin 187* (MO). Snake Range, Mt Washington, north side near the end of the road from the Pole Canyon Mine. 10200' elevation; T12N, R68E, S11; 27 June 1985; *Tiehm 9785* (BRY, CAS, NY). Cherry Creek Range, Pinenut Canyon, 2.7 road miles northeast of Butte Valley road near the Last Chance Mine. 8600' elevation; T24N, R62E, S25; 19 June 1984; *Tiehm and Williams 8727* (CAS, NY, RM, UTC). Spring Valley, 20 mi due of Ely. 6000' elevation; T15N, R66E, S1; 20 May 1980; *Harrison and Thorne 13231* (BRY, NY). 12 miles NW Ragsdale Springs. 26 May 1937; *Moore and Franklin 249* (F). Nevada Forest, Benchland, east of Mud Spring. 6500' elevation; 27 May 1937; *Moore M-583*, (RM). Egan Range, 14 miles NW of Ely. 7000' elevation; 20 June 1948; *Ripley and Barneby 9280* (NY). Summit of Baker Pass, 15 miles east of Baker. 29 May 1968; *Higgins 1453* (F, MO, NY). Snake Range, west side of range between Pole Canyon and Lincoln Canyon. 7000' elevation; Approx. T12N., R68 E, S20 or 21; 14 June 1964; *Holmgren and Reveal 931* (NY). Along US Hwy 50, 10.6 miles east of junction with US Highway 93, within a few hundred feet of (lower edge of) hwy. 2 November 1964, *Brown s.n.* (CAS). **Utah: Beaver County:** Wah Wah Mtns, E slope, base of volcanic cliffs.

7000' elevation; T28S, R15W, S29; 26 May 1978; Ostler and *Anderson 1128* (BRY). Wah Wah Mtns, ca 2.5 mi W of Summit turn N. 6800' elevation; T26S, R16W, S19, SE; UTM Zone: 12 275897 4267818; 12 May 1997; *Aitken 377* (UTC). Tushar Mountains, along Utah Highway 153, on low gravelly hills north of road above Mercant Valley just southwest Dead End Road, 11.7 air miles east of Beaver. 8625' elevation; 38°18'12"N, 112°25'19"W; T29S, R5W, S9, NE ¼; 17 June 2008; *Reveal and Broome 8909* (ISTC, NY). Desert Game Range, 2 miles south of Mormon Well (northeast of Corn Creek Headquarters). 6880' elevation; 31 May 1958; *Janish 1128* (CAS). New York Mountains, Mohave Desert, Fourth of July Canyon. 18 March 1932; *Jaeger s.n.* (CAS). Wah Wah Mtns, east side of Lime Point. 6080' elevation; T26S, R16W, S25, SE; UTM Zone 12 274321 4265606; 12 May 1997; *Aitken 383* (UTC). WahWah Mtns, Pine Grove Canyon at mouth. 29 April 1980; *Baumann s.n.* (BRY). Hamlin Valley, ca 1.25 miles S of Millard Co. line, ca. 100 m E of Nev state line. 6240' elevation; T26S, R20W, S14, NW ¼ of NE ¼; 2 June 1980; *Welsh and Chatterley 19560* (BRY). **Cache County:** In Logan Cyn, at Tony Grove Lake. Subalpine confier comm., on limestone, in loamy shallow pockets. 8400' elevation; T13N, R3E, S6; 28 July 1984; *Thorne, Chandler, and Franklin 3351* (RM).

Duchesne County: Ashley National Forest, 15.5 miles due S of Duchesne, S end of Cottonwood Ridge above Sowers Canyon. 8820' elevation; T16S, R16W, S30; 18 May 1989; *Franklin 6459* (NY). **Emery County:** Sandy, gravelly soil in pinyon-juniper woodland on the San Rafael Swell south of Eagle Canyon, ca 25 km airline southeast of Moore. 2100m elevation; T22S, R9E, S33; 23 May 1976; *Cronquist*

11413 (BRY, NY). West Tavaputs Plateau, Book Cliffs, Horse Canyon-Lower Range Creek road, 13.5 km (8.7 mi) south of bottom of Horse Canyon. 2010m (6600') elevation; 39°23'06"N 110°18'26"W; T16S, R14E, S36; 31 May 1992, *Holmgren and Holmgren 11676* (NY). **Garfield County:** Henry Mts, just north of Mt Pennell, about 40 mi south of Hanksville with scattered sagebrush and pinon pine on rocky, granitic ridge top leading to The Horn from the south. 9000' elevation; 20 June 1961; *Cronquist and Holmgren 9312* (NY). Area of Big Lake. 9900' elevation; T31S, R2E, S28; 30 May 1979; *Lewis 5917* (BRY). Bryce Canyon. 20 June 1932; *Weight B32 204* (US). 3 mi. N of Barker Reservoir past the Gap, mountain meadow. 2925m elevation; 25 June 1982; *Nixon 11391* (BRY). 5 mi s of Boulder, frequent, sandy soil, associated with juniper and pinyon pine. 3 June 1948; *Holmgren and Nielson 7758* (CAS, RS, UTC, WS). Aquarius Plateau, Powell Nat'l Forest, frequent, open park, Aspen-Spruce. 10000' elevation; 29 June 1940; *Maguire 19207* (RM, UTC). Canyon NE of Tropic. 6112' elevation; N 37°39.628' W 111°57.879'; T36S, R2W, S24; 20 June 1998; *Atwood and Welsh 23949* (BRY). Steep Creek east face Boulder Mt, on dry slopes. 8000-9000' elevation; 25 June 1938; *Beck s.n.* (BRY). Between Barker Reservoir and Round Willow Bottom Reservoir. 2880m elevation; 25 June 1982; *Nixon 11362* (BRY). Sheep Cr. Drainage, about 4 airline miles sw of Cannonville, 6.7 miles up the Sheep Cr. Road from the Cottonwood Wash Road. 6600' elevation; T37S, R3W, S31; 4 June 1967; *Reveal, Gentry, and Davidse 774* (MO). 1.6 mi N of Hwy 12 on road to Losee Canyon. Slope below sandstone goblins of Paunsaugunt Plateau. Turn off to Losee Canyon on Hwy 12 about 1.9 mi E of junction with Hwy

89. 29 April 1997; *Hufford 1778* (WS). Bryce Cr. Drainage, 3 miles w of Tropic, in a small meadow along springfed streamlets. 3 June 1967; *Reveal, Gentry, and Davidse 744* (GH, MO). Aquarium Plateau, Big Lake. T31S, R2E, S28, SE ¼; 13 June 1989; *Franklin 6570* (BRY, RM). Box-Death Hollow Wilderness. Along ridgetop between Sand Creek and Right Fork Death Hollow. 7700' elevation; T33S, R3E, S27E NW; 31 May 1989; *Franklin 6523* (BRY). Canyon above Tropic. 6500' elevation; 28 May 1894; *Jones 5312d* (US). Markagunt Plateau, 13.4 km (8.3 mi) west of US 89 on Mammoth Creek road (US Forest Service road 067). 2345m (7700') elevation; T37S, R7W, S13; 14 June 1992; *Holmgren and Holmgren 11784* (ISTC). Aquarius Plateau, Coyote Hollow, 8.4 km (5.2 mi) west of Escalante-Bicknell Road, along Clayton Guard Station Road. 2880m (9450') elevation; 38°00'15"N 111°1'55"W; T32S, R1E, S21; June 2000; *Holmgren and Holmgren 13805* (ISTC, NY, UTC). Henry Mountains, 3.7 km (2.4 mi) southwest of Bull Creek Pass, 35.5 km (22 mi) air distance south-southwest of Hanksville. 2900m (9515') elevation; 38°03'59"N 110°49'02"W; T31S R10E S33; 25 June 1999; *Holmgren, Holmgren and Joseph 13596* (ISTC, NY, UTC). Henry Mountains, McMillan Spring Campground, 8.4 km (5.2 mi) southwest of Bull Creek Pass, 35.5 km (22 mi) air distance south-southwest of Hanksville. 2600m (8530') elevation; 38° 05'00"N 110° 51'00"W; T31S, R10E, S31; 25 June 1999; *Holmgren, Holmgren, and Joseph 13588* (ISTC, NY, UTC). Aquarius Plateau, about 42 km (26 mi) north of Escalante and 34 km (21 mi) air distance north (347°). 3050m (10000') elevation; T31S, R2E, S33; 9 June 1984; *Holmgren and Holmgren 10612* (NY). Henry Mountains, 0.3 km (0.2 mi) west of Bull Creek Pass at

the turnoff to Burnt Ridge, 33.5km (20.5 mi) air distance south-southwest of Hanksville. 3150 m (10335') elevation; T31S, R10E, S27; 25 June 1999, *Holmgren, Holmgren and Joseph 13597* (NY, UTC). Henry Mountains, junction of Bull Creek Pass and Granite Creek roads, 4.6km (2.6 mi) northeast of Bull Creek Pass, 13.5 km (19.5 mi) air distance south-southwest of Hanksville. 2825 m (9270') elevation; T31S, R10E, S23; 25 June 1999, *Holmgren, Holmgren, and Joseph 13601* (NY, UTC). 18 mi SW of Panguitch, limestone chip, ridge bordering Panguitch Lake on the south. 25 June 1983; *Rollins, Rollins, and Road 83150* (BRY, NY, RM, UTC).

Summit of Boulder Mt. 13.5 due SSW of Antimony. Volcanic gravel, in meadows. 10400' elevation; T33S, R1W, Sec 11; 30 June 1974; *Welsh and Moore 13799* (BRY, NY). Aquarius Plateau, ca 1 mi N of Big Lake and 21 air mi S of Loa. T31S, R2E, S21 SE4 of SW4; UTM Zone 12, 439379E, 4216495N, NAD27; 27 July 2005; *Fertig 22135*(UTC). **Iron County:** Markagunt Plateau, 10.5 air mi SSW of Parowan, summit of Second Left Hand Canyon. 3100m elevation; T36S, R8W, S5; 9 August 1986; *Neese 17614* (BRY). 100 yards north of the Junction of Highway 143 and FR to Brian Head. 10359' elevation; 5 June 2013; *Minnaert-Grote and O'Kane 86* (ISTC). 27 June 1936; *Gierisch 14* (UTC). **Juab County:** 3 mi SW of Six Mile Ranch. 5000' elevation; T10S, R17W, S19; 18 April 1978; *Foster 5840* (BRY).

6 miles SW of Callao, East slope. 6000' elevation; T11S, R19W, S12; 18 April 1978; *Foster 5828* (BRY). Foothills at base of Deep Creek Mtns. 6200' elevation; 24 May 1995; *Armstrong and Johnson 503* (BRY). Just e of CCC Camp. 4500' elevation; T11S, R17W, S16; 18 April 1978; *Foster 5864* (BRY). Deep Cr Mtns, Thomas

Creek. 6500' elevation; T11S, R18W; 12 May 1981; *Kass 223* (BRY). Deep Creek Mtns, ca 0.5 mi E of Nubold Ranch. 6500' elevation; T13S, R19W, S7; 6 June 1978; *Welsh, Foster, and Henriod 16796* (BRY). **Kane County:** Between Glendale and Orderville. 20 June 1933; *Eastwood and Howell 817* (CAS). Alton East, dry, rocky soil in mountain shrub. T40S, R5W, S14; 9 June 1975; *Holmgren 16055* (NY). At Drip Bench Mark on Four Mile Bench caprock of Wahweap formation. 6300' elevation; 29 April 1974; *Welsh and Atwood 12379* (BRY, NY). **Millard County:** House Range, Sawtooth Mt, Notch Peak. 9000' elevation; N 39°09.348' W113°24.468'; 11 June 1999; *Tilley and Atwood 497* (BRY). Pruess Lake. 5500' elevation; T22S, R19W, S20; 2 May 1964; *Matthews 26* (BRY). Warm Point Ridge, Desert Experimental Range. 6000' elevation; T25S, R18W, S25; 30 April 1964; *Wood 97* (BRY). Sand dune area southwest of White dunes. 4760' elevation; T15S, R6W, S24; 9 June 1981; *Shultz and Shultz 5228* (UTC). Along St Route 21, pass dividing Snake Valley from Pine Valley, 41.8 km (26 mi) southeast of the Nevada border. 1905m (6250') elevation; 38°37'02"N 113°50'02"N; T25S R18W S22; 29 May 2000; *Holmgren and Holmgren 13748* (NY). **Piute County:** Mountains north of Bullino Creek, near Marysvale. 23 July 1905; *Rydberg and Carlton 7160* (NY, RM). Marysvale in Bullion Canyon. 9000' elevation; 5 June 1894; *Jones 5397b* (NY, RM). Tushar Mts, Beaver District, along 2 mile Creek, ca 6 mi due SW of Marysvale. 10000' elevation; T28S, R4W, S4; 16 August 1978; *Welsh and Henriod 18038* (BRY). **San Juan County:** La Sal Forest, La Sal Ranger Station pasture. 7000' elevation; 14 May 1924; *Olsen 0-56* (RM). **Sevier County:** East foothills of Pavant

Range, ca. 4 miles due NW of Aurora. 6200' elevation; T21S, R2W, S13; 15 May 1978; *Welsh 16516* (BRY). E foothills of Pavant Range, ca. 4 miles NW of Aurora. 6200' elevation; T21S, R2W, S13; 27 April 1978; *Welsh 16497* (BRY). Pavant Mts, ca. 4 miles NNW of Aurora. 5500' elevation; T21S, R2W, S13; 12 June 1978; *Welsh, Welsh, and Henriod 16940* (BRY). Joseph City. 13 May 1899; *Jones s.n.* (NY, RSA). Salina Cañon. 8000' elevation; 15 June 1894; *Jones 5441* (NY, RM). Head of Salina Canyon. 8000' elevation; 15 June 1894; *Jones 5441* (RM). Fish Lake National Forest, 7.5 mi W of Richfield, grassy sagebrush-covered hillside, off road to Ranger Station. 24 June 1983; *Rollins and Rollins 83137* (CAS, MO, NY, RM). Salina Canyon, 20 mi above Salina, in humus under junipers, on limestone. 7100' elevation; 7 June 1966; *Barneby 14381a* (NY). Fishlake Forest, Fishlake Hightop. 9500' elevation; 23 July 1941; *Robinette R-54* (RM). **Tooele County:** Rush Valley, along the Faust Rd (Poney Express Trail Rd), ca 10.5 road miles W of the junction with Utah Highway 73, S of the rd. 1603m (5259') elevation; 40°10'51"N 112°23'30"W; T7S, R5W, S27, NE ¼; 26 April 2002; *Barnes 2164* (UVSC). Rush Valley, along the Faust Rd (Pony Express Trail Road) S of the railroad crossing, ca. 11.5 road miles W of junction with Utah Highway 73. 1603m (5259') elevation; 40°11'N 112°22'W; T7S, R5W, S27, NE ¼; 3 May 2002; *Barnes 2170* (UVSC). Rush Valley, along County Highway 20556 (dirt road), ca. 8.4 road miles SW of the junction with Utah Highway 73. 1591m (5217') elevation; 40°9'39"N 112°18'30"W, WGS84; 3 May 2005; Angus 177. Clifton Hills. 6240' elevation; T8S, R18W, S35; 19 May 1981; *Kass 245* (BRY). **Washington County:** ZNP, Horse Pasture Plateau, south end of West Rim Trail, east of Phantom

Valley. Temple Cap member, Carmel Fma, with oakbrush and manzanita. T40S, R10W, S32 NW; 10 July 1987; *Thorne and Franklin 5511* (BRY, NY, RM). Zion National Park, Horse Pasture Plateau along West Rim Trail of Zion Canyon. 7300' elevation; T40S, R10W, S29; 22 June 1965; *Holmgren, Reveal and La France 1979* (BRY, NY, UTC). **Wayne County:** N end of Henery Mtns, Saw Mill Basin Rd, ca 3.5 mi S of Fairview Ranch. Pinyon-juniper comm., on gravelly bench above Bull Cr. 6200' elevation; 7 May 1982; *Atwood and Welsh 8663* (BRY). Fish Lake National Forest, Elkhorn Campground, hillside NW of the campground entrance. T27S, R4E, S15, NW ¼; 16 June 1986; *Porter 3905* (BRY). Capitol Reef National Park, Moenkopi Formation, hilltop near Pleasant Creek. 1800m elevation; T30S, R7E, S20, SW ¼; 25 April 1988; *Fleming 552* (BRY). Elk Horn GS near Loa and Thousand Lake Mt. T27S, R4E, S15; 10 June 1991; *Anderson 66* (UVSC). Capitol Reef National Park, Pleasant Creek area, hilltop near the creek. T30S, R7E, S20, SW ¼; 8 May 1988; *Fleming 610* (BRY). Ca. 7 miles WSW of Loa. 8200' elevation; T28S, R1E, S24; 16 June 1977; *Welsh 14968* (BRY). **Washington: Kittitas County:** Wenatchee National Forest, Swauk Creek campground. Sculpture Rock trail at summit. 3800' elevation; T21N, R17E, S12, SW ¼, SW ¼; 6 May 1983; *Brown 48* (WS). Wenatchee National Forest, Wenatchee Mts, Sulpture Rock Trail south Swauk Creek Cpgd. 3800' elevation; T21N, R17E, S12, SW ¼ SW ¼; 8 May 1983; *Grable 9755* (WS).

Physaria kingii subsp. *utahensis*

UNITED STATES: Utah: Daggett County: Uinta Mountains, U.S. Highway 191, 8.8km (5.5 mi) south of the junction with Utah Route 44, 6 km (3.7 mi) north of Uintah County Line. 2500m (9200') elevation; 40°47'52"N, 109°27'45"W; T1N R22E S20; 19 June 1999; *Holmgren and Holmgren 13540* (ISTC, NY). Near Utah State Hwy 44, 28 miles north of Vernal. 19 June 1981; *Rollins and Rollins 81350* (F, MO, NY, RM). **Duchesne County:** Uinta Mountains, south fork of Rock Creek. 9975' elevation; T2N, R8W, S25, SE ¼ of SE ¼; 2 August 1995; *Huber 2691* (RM, UTC). Uinta Mtns, openings of Engelmann spruce, limestone substrate, head of Dry Canyon, 4.5 mi due W. of Moon Lake. 11050' elevation; T2N, R6W, S18, NE1/4; 18 July 1994; *Huber 1859* (NY, UTC). Uinta Mountains, Lake Fork Mountain. 10800' elevation; T2N, R5W, S15, NW ¼ of NW ¼; 2 July 1998; *Huber and Wedig 3764* (NY). Uinta Mtns, ca 4 km due south of Granddaddy Lake. 3465m elevation; 40°33'29"N 110°48'16"W; 7 August 2002, *Harris and Snyder 3202* (UVSC). Uinta Mtns, Ashley NF, 15.25 km 22 degrees N of Tabiona, Big Ridge, head of Cirque Basin with clumps of Krummholz spruce. 10650' elevation, T1N, R7W, S14, NE1/4; 21 July 1983, *Goodrich 19163* (NY). **Elko County:** Mountains southeast of Silver Lake, near the headwaters of the Big Cottonwood Creek. 1 August 1905; *Rydberg and Carlton 6563* (NY). Big Cottonwood Cañon, between Silver Lake and the summit of Mount Majestic. 28 June 1905; *Rydberg and Carlton 6423* (NY). Big Cottonwood Cañon between Silver Lake and summit of Mt Majestic. 28 June 1905; *Rydberg and Carlton 6411* (NY, RM). **Salt Lake County:** Big Cottonwood Canyon,

from type locality of *L. garrettii* Payson. 2 August 1936; *Garrett 7356* (F). 1.15 mi SSE of Brighton Store. 9600' elevation; T3S, R3E, S2, SW4, NE4; 9 August 1991; *Tuhy 3650* (NY). Upper Maybird Gulch, ca .4 mi NE of the Pfeifferhorn, top and E side of low rocky ridge on basin floor in coarse-soil microsites. 10100-10300' elevation; T3S, R2E, S22, E2SW4SE4; 9 September 1991; *Tuhy 3704* (RM). 1.5 mi above Alta on Albion Basin Road, talus, cliffs above timberline. 3200m elevation; T3S, R3E, S4; 7 July 1984; *Higgins 14492* (NY, RM). Central Wasatch Range, Albion Basin, at the head of Little Cottonwood Canyon, slope south of the campground. 2915m (9560') elevation; 40°34'27"N 11°36'37"W; T2S R3E S9; 15 August 1999; *Holmgren and Holmgren 13651* (ISTC, NY). Central Wasatch Range, Little Cottonwood Canyon, near the Sunset Peak trail on the west side of the ridge, west-northwest of the peak. 10400' elevation; 40°34'47"N 111°35'59"W; T2S, R3E, S3; 16 August 1999; *Holmgren and Holmgren 13653* (NY). Central Wasatch Range, head of Big Cottonwood Canyon, Catherine Lake, rocky open area near the south lake shore. 3040m (9980') elevation; 40°34'43"N 111°35'31"W; T2S R3E S3; 16 August 1999, *Holmgren and Holmgren 13656* (NY). Wasatch Mountains, near Lake Mary, above Brighton. 9400' elevation; 30 July 1957; *Rollins and Vickery 57268* (F, MO, NY, RM). Wasatch Mts, north-facing slope just east of Lake Mary, above Brighton. 9300' elevation; 30 July 1957; *Rollins and Vickery 57269* (MO, NY). Albion Basin, Little Cottonwood Canyon, ½ mi east of Albion Campground. 9500' elevation; T3S, R3E; 4 August 1984; *Shaw 3604* (UTC). **Summit County:** Fishlake Forest (Fillmore), Ridge south of Burnt Hollow, Juniper, ridgetop. 7800' elevation;

22 June 1922; *Miller 104* (RM). SW base of Mt Elizabeth, edge of lodgepole woods, open valley of Mill Creek, 6 mi SE. 8500' elevation; 13 August 1933; *Hermann 5887* (MO). Wasatch Forest, District 6, Bear River trail crossing Blacks Fork Ranger Station. 8500' elevation; 10 August 1922; *McDonald 82* (RM). North slope Uinta Mountains, Wasatch National Forest, ca. 27 air miles SSE of Evanston WY, 0.3 mi E of Deadman Pass. Steep east-west ridge with gravelly limestone cliffs. 10440-11170' elevation, T1N R11E S4, also S5; 19 August 1995, *Refsdal 7325* (RM). North Slope Uinta Mountains, Wasatch National Forest, ca 27.5 air mi SSE of Evanston, WY. 11000-11580' elevation; T1N, R11E, S4 also S9, S10, and S15; 19 August 1995; *Refsdal 7383* (RM). 6 mi due NE of Kamas, near summit of Hoyt Peak. 10200' elevation; T1S, R7E, S31, NE ¼; 14 September 1980; *Neese and Neese 9839* (NY). Uintah Mts, peaks east of east fork of Bear River. 11000' elevation; 17 July 1928; *Goodman 528* (RM). Uintah Mts, divide between E Fork of Bear River and Black's Fork. 10000' elevation; 9 July 1930; *Goodman and Hitchcock 1505* (CAS, F, MO, NY, RM). Divide between East Fork of Bear River and Black's Creek, in sandy soil on shrub-covered slope. 10000' elevation; 27 July 1957; *Beaman and Stone 1475* (MO, NY, RM). Stony ridge on top of peak near West Fork of Bear River. 11000' elevation; 7 July 1926; *Payson 4901* (CAS, NY, RS). Uintah Mts, ridge east of East Fork of Bear River, dry rocky soil. 11000' elevation; 17 July 1928; *Payson 628* (RM). China Meadows, ca 1000 meters N on ATV trail from N parking lot of China Meadows trailhead, where trail is just W of large oxbow of East Fork of Smiths Fork River, disturbed roadside and roadcut. 9163' (2793m) elevation; 40°56'4.62"N

110°13'23.22"W; WGS84; 2 July 2010, *Hansen and Hansen 53* (UVSC). Growing in gravel, off Utah Route 150, near Wasatch Ranger Station, 9.7 mi W of Utah/Wyoming border. 4 June 1979; *Rollins and Rollins 79158* (MO, Y, RM). Uinta Mtns, Wasatch NF, 26 air mi NE of Kamas, Mill City Cr. - Whitney Rd. 9100' elevation; T2N, R9E, S36, SE ¼ SE ¼; 28 June 1984; *Goodrich 20608* (NY). Wasatch-Cache National Forest, Table Top rim above W. Fork Blacks Fork, windswept crest and leeward slopes. 3270m elevation; 40°53'67"N 110°41'45.90"W; 16 July 2008, *Goodrich 27463* (BRY). **Uintah County:** Ashley National Forest, 1 mi. E of Hwy 191 on Diamond Mt. Plateau Rd, ca. 28 mi. N of Vernal. 2394m elevation; 18 July 1996; *Salywon 3184* (ISTC). Dyer Mtn, ca 27 mi NW of Vernal, off the Red Cloud Loop Road, opposite Kane Hollow. NW-facing open, rocky hillside. 10100' elevation; T1S, R21E, S16, NW1/4; 14 August 1982; *Albee 5343* (UTC). Ca. 20 mi due N of Vernal. 8400' elevation; T1S, R22E, S20; 28 June 1979; *Neese and Moore 7942* (NY). Uintah Mts, Dyer Mine, rocky ridges. 5 July 1902; *Goodding 1258* (MO, NY, RM). East end of the Uinta Mountains, in limestone areas, Kane Hollow, 28 km (17.5 mi) airline distance n of Vernal. 2620m (8600') elevation; T1S, R21E, S23; 30 June 1976; *Holmgren and Holmgren 8320* (NY). Uinta Mountains, Diamond Mountain Road, along Reader Creek, 2.1km (1.3) mi e of US Highway 191, 30.5 (19 mi) air distance north-northeast of downtown Vernal. 2470m (8100') elevation; 40° 43'03"N 109° 26'56"W; T1S R22E S21; 19 June 1998; *Holmgren and Holmgren 13190* (NY). Uinta Mountains, 0.8 mi on Diamond Mt Plateau road from Utah Highway 44, the junction of which is 23.8 miles north of Vernal. 8179' elevation;

T1S, R22E, S21; 7 June 1971; *Holmgren and Holmgren 5075* (NY, RM). East end of the Uinta Mountains, top of Dyer Mountain, about 32 km (20 mi) airline distance north of Vernal. 10200' elevation; T1S, R21E, S16; 1 July 1976; *Holmgren and Holmgren 8333* (CAS, NY, UTC). **Utah County:** Wasatch Mts, Mt Timpanagos. 8 August 1927; *Garrett 3770* (F). Wasatch Mtns, Lone Peak Wilderness Area, ridge either side of Pfeifferhorn. 10800-11300' elevation; T3S, R2E; 23 July 1983; *Franklin 305* (NY). Ridge N of Box Elder Peak, coarse-soil covered ledges of low granitic outcrop, along ridge crest. Ca. 9640' elevation; T4S, R2E, S2, NW4, NE4, NW4; 7 August 1991; *Tuhy 3639* (NY). NW part of Mineral Basin, ca 2 mi S of Alta, rocky E and SE facing slopes. 10500' elevation; T3S, R3E, S17, SW4NW4; 18 July 1991; *Tuhy 3617* (NY). Upper Dry Ck Canyon, ca 1 mi S of the Pfeifferhorn, granitic outcrops. Fill material forming E slope of platform for radar installation. 9400' elevation; T3S, R2E, S34, W2NW4NE4; 13 September 1991; *Tuhy 3708* (RSA). Manti Forest, north of Indianola in foothills. 6500' elevation; 21 May 1928; *Humphrey 107* (RM). Uinta Forest, head of Nobleetts Creek. 8000' elevation; 14 June 1932; *Larson 98* (RM). **Wasatch County:** In soil among granitic rocks, well vegetated herbaceous comm. W of saddle btwn. pts 10321 and 10315, ca 1.4 mi SSE of Brighton Store. 10404' elevation; T3S, R3E, S2, SE4, SW4; 9 August 1991; *Tuhy 3649* (UTC). 24.2 mi SE from hwy 189 and 40 jct on roadside in Strawberry Valley. 12 May 1971; *Loosli 35* (BRY).

Physaria kingii subsp. *wardii*

Arizona: Coconino County: Growing on a flat, open slope in fine-textured soil. 6525' elevation; UTM zone 12, 421785E 3938179N; 31 August 2005; *Christie 1061* (ASC). Kaibab Plateau, Kaibab National Forest, Forest Rd 425 on way to Thunder River Trail. 2149m elevation; 17 May 1998; *O'Kane 4211* (ISTC). 16 miles South of Jacob Lake on Grand Canyon Hwy across Kaibab Plateau, dry soil between road and meadow near *Eleocharis* -- rimmed pond on W side of road. T36N, R2E; 22 June 1979; *Ertter and Strachan 2891* (CAS, NY, UTC). Kaibab Plateau, Trail Canyon, near US Highway 89A 89A, 9.5 km (5.9 mi) east of Jacob Lake. 2125m (6970') elevation; 36°43'56"N 112°07'49"W; T39N, R2E, S36; 22 June 1999; *Holmgren, Holmgren, and Joseph 13568* (ISTC). Kaibab Plateau, Jolly Sink. 10 June 1949; *Goodding 200-49* (CAS). Kaibab Plateau, South Canyon, Piñon-Juniper belt. 29 April 1949; *Goodding 78-49* (CAS). Saddle Canyon, Kaibab NF, Pinyon, Kaibab Limestone formation. 1300m elevation; T34N, R4E, S22, NE ¼; 25 April 1996; *Atwood and Furniss 20827* (NY). Kaibab Plateau, Le Fevre Ridge off FS Road ca. 0.8 miles W of US Alt 89, ca. 4 air miles NW of Jacob Lake and ca. 4.5 air miles SSW of Le Fevre Scenic Outlook. 7450' elevation; T39N, R1E, S22, SW4 of NE4; 18 June 2005; *Fertig 21981* (NY). Rim of Grand Canyon, near Locust Point, North Rim of Grand Canyon on FR 294,. 7620' elevation; 4 June 2013; *Minnaert-Grote and O'Kane 84* (ISTC). Kaibab National Forest, trail head to Thunder River at end of Forest Road 292A. 2134m elevation; 36° 26'3"N 112° 25'43"W; 18 May 1998; *O'Kane 4212* (ISTC). 4 1/2 mi e of Jacob Lake junction. Gentle slope near road

beneath ponderosa pine in pine duff. 2141m elevation; 36°43'53"N 112° 9'10"W; 13 May 1998; *O'Kane and Windham 4200* (ISTC). Ca 2.75 mi NW of Babbit Lake.

Utah: Beaver County: Tushar Mtns, Fishlake National Forest, along Forest Service road #123 leading NNE out of Big John Flat to Shelly Baldy Peak, on very steep, rocky, S-facing hillside. 10711' elevation; T28S, R5W, S23; UTM – 378323 m.E by 4246964 m.N (Zone 12, NAD 27); 8 July 2008; *Kelsey, Kelsey, and White 08-95* (MO). Tushar Mts: Poison Creek, NW facing slope, gravelly soil. 11400' elevation; T28S, R5W, S14; 19 July 1993; *Taye 5213* (BRY, NY, RM). Tushar Range, 1 mi N Puffer Lake Rd., via Big John Flats Rd. 9000' elevation; 25 July 1940; *Maguire 19853* (NY, UTC). Tushar Mtns, 16.2 mi E of Beaver along Hwy 153, N along road from Big John Flat to Mud Lake, 0.3 mi N of crossing of Poison Creek. 10890' elevation; T28S, R5W, S14, NW ¼, SW ¼; 21 July 1991; *Arnou 6804* (BRY, NY). Tushar Mts, Fish Lake Forest, Merchant Creek, ca 11.5 mi due ENE of Beaver. 8600' elevation; T29S, R5W, S9; 29 June 1978; *Welsh, Welsh, and Welsh 17179* (BRY, NY, RM, UTC). Tushar Mountain Range, Fish Lake NF, ca ¼ mi ENE of Dbno Peak, Beaver Rd. 11200' elevation; T28S, R5W, S13; 30 May 2002; *Madsen 1424* (RM). Tushar Mtns, Merchant Creek. 8800' elevation; T29S, R5W, S3; 11 June 1984; *Taye 2209* (BRY). Tushar Mtns, Beaver Canyon. 8500' elevation; T29S, R5W, S17; 1 July 1984; *Taye 2523* (BRY, UTC). Tushar Mtns, N facing slope, City Creek Pk. 11000' elevation; T29S, R4W, S5, SW ¼, SW ¼; 29 July 1991; *Taye 5119* (BRY, NY). Tushar Mtns, Delano Pk, on W slope. 11000' elevation; T28S, R5W, S 23; 3 July 1984; *Taye 2549* (BRY, NY, RSA). Tushar Range, 1 mi N Big John Flats, basin

Beaver River, W fork. 10000' elevation; 24 July 1940; *Maguire 19806* (UTC).

Tushar Mtns, vicinity of Puffer Lake and Lake Peak. 10000-11200' elevation; 24 July 1964; *Bosworth 35* (BRY, NY). Tushar Mountains, dugway above Big John Flat. 3050-3150m elevation; T28S, R5W, S22 and S27; 27 July 1991; *Atwood 16175* (BRY, NY, RM). 15 mi east of Beaver along Highway 153. Meadow 1/2 mile above Merchant Creek Dam. 2550m elevation; T29S, R5W, S9; 26 July 1991; *Atwood 16123* (BRY, RM). Tushar Mtns, Fishlake Natl Forest, ridge top between South Fork Bullion Canyon and The Pocket. T28S, R5W; 3 August 1981; *Atwood 8213* (BRY).

Fishlake National Forest, Puffer Lake, common on rocky slopes. 10000' (3050 m.) elevation; 26 June 1930; *Keck 639* (RSA). Tushar Mountains, along the dirt road toward Mt. Belknap-Delano Peak saddle along the West Fork of Merchant Creek; 1.8 miles north of Utah Highway 153, this junction 15 miles east of Beaver, in a mountain meadow associated with grasses and adjacent *Artemisia* on volcanic soils and rocky slopes near the meadow. 9000' elevation; 8 July 1977; *Reveal and Reveal 4693* (BRY, NY, RSA, UTC). Tushar Mtn, Fishlake NF, N Puffer. 9650' elevation; T29S, R5W, S1 SW ¼; 17 August 1983; *Bascom and Mendenhall 78* (BRY). Tushar Mtns, ENE of Beaver on slope below Mud Lake, ca 2.04 km ENE of the summit (11321) of Shelly Baldy Peak. 10725' elevation; 38°11'28"N 112°24'11"W (WGS84 Datum); T28S, R5W, S15; 29 June 2001; *Windham and Windham 2517* (NY). Tushar Mountains, Fishlake National Forest, Merchant Creek, ½ mile northeast of Utah 153, (Beaver junction road). 8500' elevation; T29S, R5W, S8; 23 July 1965; *Holmgren, Reveal, and La France 2249* (BRY, NY, UTC). Northern approach to Mt. Delano, 5.4

miles northeast of State Highway 153. 9 July 1986; *Rollins and Rollins 86207* (NY, RM). Near summit of high ridge on road to Mt Baldy and Mt Belknap from the south. 11000' elevation; 9 July 1986; *Rollins, Rollins, and Florence 86210* (NY, RM, UTC). Tushar Mtns, Fishlake NF, 12.5 mi 81 dg E of Beaver, N Fk Three Cr, disturbed rocky slope at the edge of a spruce, aspen comm. 8700' elevation; T29S, R5W, S10, SW ¼; 13 July 1982; *Goodrich 17257* (BRY, RM). Tushar Mts, Beaver District, vicinity of Mud Lake, 10.5 mi due SW of Marysvale, alpine meadows and slopes above timberline, igneous sandy gravel. 10800' elevation; T28S, R5W, S15; 3 August 1978; *Welsh 17949* (BRY, NY, RM). **Emery County:** East Mountain, Manti Forest. 9700' elevation; 1 September 1936; *Costley 34* (RM). **Garfield County:** Henry Mts, open, rocky, granitic slope overlooking the east fork of Bull Creek, about 25 miles south of Hanksville. 10000' elevation; T31S, R10E, S22; 5 July 1961; *Cronquist and Holmgren 9434* (NY, UTC). Powell Forest, west edge Boulder top. 11000' elevation; T31S, R3E, S11; 12 August 1942; *Ellison 842-50* (RM). Aquarius Plateau, Mountain Meadow, moist soil. 10000' elevation; 24 June 1936; *Beck and Tanner s.n.* (BRY). Henry Mts, 4.6 miles sw of Lonesome Beaver C.G. at Burned Ridge. 9700' elevation; 30 July 1967; *Gentry and Davidse 1752* (F, NY, RM, UTC). Henry Mtns, Mt. Ellen. 9000' elevation; 24 July 1894; *Jones 5664c* (US). Aquarius Plateau, 30 mi North of Escalante, knoll of exposed rubble. 9800' elevation; 10 August 1957; *Rollins 57318* (F, NY, RM). Henry Mtns, Bromide Pass. 11000' elevation; 27 May 1894; *Jones 5695a* (NY). Henry Mts, S. rim Bull Creek Basin, frequent, slopes, Hudsonian. 9000-10000' elevation; 2 July 1940; *Maguire 19365* (UTC). 2 mi S.W. of Panguitch Lake,

frequent with Sage, dry loam base of recent lava flow. 23 June 1940; *Maguire 19017* (UTC). Henry Mountains, high east facing slopes between Sawmill Basin and the summit of Mt. Ellen. 2400-3445m elevation; 19 June 1953; *McVaugh 14664* (NY). Aquarius Plateau, Clayton Guard Station Road; 8 km (5 mi) north of Escalante Canyon Summit. 3150m (10335') elevation; 37°52'30"N 111°52'21"W; T34S, R1W, S2; 3 June 2000; *Holmgren and Holmgren 13791* (NY). SC Aquarius Plateau, 18 mi SSW of Bricknell. 10000' elevation; T31S, R2E, S27; 1 June 1977; *Neese and White 2991* (BRY, RM). Top Aquarius Plateau, near Posy Lake. 8500' elevation; 1 July 1938; *Beck s.n.* (BRY). Aquarius Plateau, Posy Lake. 8500' elevation; 1 July 1938; *Beck s.n.* (BRY). SC Aquarius, 14 mi due SSW of Bicknell. 9400' elevation; T31S, R2E, S10; 22 June 1977; *Neese and White 3286* (BRY). Henry Mts, on Bromide Peak, dry rock slope. 8800' elevation; 19 April 1934; *Harrison, Empey and Larsen 7464* (BRY). 4.8 miles North of Escalante Canyon Summit along FR FH17 head. 10440' elevation; 37°52.72'N 111°52.20'W; 3 June 2013; *Minnaert-Grote and O'Kane 80* (ISTC). North Mountain of Henry Mountains, granite saddle in rocky soil. Approx. 10400' elevation; 21 June 1963; *Nelson s.n.* (UTC). Dixie NF, Escalante RD, found on white/pink talus slopes on, S of Canaan Peak. 2750-2833m elevation; 7 July 2000; *Madsen 966* (BRY). Henry Mtns, Mt Ellen. 11000' elevation; 1894; *Jones s.n.* (NY). Aquarius Plateau, Clayton Guard Station Road, 10.6 km (6.6 mi) north of Escalante Canyon Summit. 3180m (10435') elevation; T33S, R1W, S35; 3 June 2000; *Holmgren and Holmgren 13795* (ISTC, NY, UTC). Henry Mountains, 0.5 km (0.3mi) west of Bull Creek Pass, 33 km (20.5mi) air distance south-southwest of

Hanksville. Steep slope above the road. 3200m (10500') elevation; 38° 04'57"N 110° 47'56"W; T31S R10E S27; 25 June 1999; *Holmgren, Holmgren, and Joseph 13600* (ISTC, NY, UTC). Henry Mountains, 0.3 km (0.2 mi) west of Bull Creek Pass, 33.5 km (20.5 mi) air distance south-southwest of Hanksville. 3150m (10335') elevation; 38°05'01"N 110° 48'22"W; T31S, R10E, S27; 25 June 1999; *Holmgren, Holmgren, and Joseph 13598* (ISTC, NY, UTC). Aquarius Plateau, 17 airline miles northwest-north of Escalante, 1 mi west of Escalante-Bicknell road on Clayton G.S. turnout. 9000' elevation; T32S, R2E, S20; 11 August 1970; *Holmgren and Holmgren 4724* (BRY, NY, RM). Aquarius Plateau at the head of Poison Creek. 4 August 1905; *Rydberg and Carlton 7403* (NY). 8 mi SW of Panguitch Lake, ca 26 mi SW of Panguitch, granitic rocks and gravel, exposed ridge. 25 June 1983; *Rollins, Rollins, and Roads 83154* (BRY, NY, RM). 2 miles SW of Panguitch Lake, ca. 20 mi sw of Panguitch, lava rock flat. 25 June 1983; *Rollins, Rollins, and Roads 83152* (BRY, NY, RM, RSA, UTC). **Iron County:** Common, stony soil, 1/2 mi s of summit of Brian Head Peak. 10800' elevation; 23 June 1940; *Maguire 19006* (RM, UTC). SC Markagunt, 4 mi N of Horse Lake. 9500' elevation; T34S, R7W, S29; 17 June 1977; *Foster and Foster 4231* (BRY). Brian Head summit, 11 air miles due S of Parowan. 3400m elevation; T36S, R9W, S12, SW ¼; 27 June 1985; *Neese and Neese 17117* (BRY, NY). Cedar Breaks, two miles northeast of Lodge. 26 June 1942; *Degener and Peiler 16448* (RM). Dixie NF, 1.5 mi s of Brian Head and 0.75 mi n of Cedar Breaks National Monument, along hwy 143. T36S, R9W, S14; 25 July 1979; *Atwood 7408* (BRY). Brian Head, view area the summit of the mountain, W side of Brian Head

Peak Rd (FR 047). 3461m (11353') elevation; 37°40'54"N 112°49'50"W, WGS84; 19 June 2002; *Barnes, Harper, and Jolley 2863* (UVSC). Cedar Breaks, rocky ground near base of Brian Head. 10750' elevation; 20 July 1927; *Peirson 7516* (RSA). Brian Head. 3250-3446m elevation; T36S R9W S12; 29 July 1999; *Higgins 20700* (BRY, NY). Brian Head, sandy to rocky slopes. 11307' elevation; T36S, R8W, S12; 20 July 1984; *Higgins 14615* (BRY). Markagunt Plateau, Dixie NF, E slope of Brian Head, ca 0.7 km ENE of the summit of the mountain. In rocky volcanic soil on gentle, SE-facing slope. 11150' elevation; Brian Head Quad (7 ½ min); T36S, R9W, S12; UTM 4172025 m.N by 339250 m.E (Zone 12); 30 June 1992; *Windham 92-160* (ISTC). Hurricane, Pine Springs, S slope, sage comm., hard clay soil. 8680' elevation; T38S, R11W, S12; 8 July 1977; *Foster and Foster 4570* (BRY). Markagunt Plateau, on a ridge ca 1.1 ca air mi E of the summit of Brian Head. 3377m (11075') elevation; 37°40'43"N 112°48'40"W; 24 June 2003, *Jolley and Van Buren 2003-29* (UVSC). Markagunt Plateau, Brian Head by Cedar Breaks National Monument. 11300' elevation; 25 July 1980; *Kass and Hreha 116* (NY). Marbleized chip-rock and rocky areas, near summit between Beaver and Junction, State Hwy 153. 10400' elevation; 10 July 1986; *Rollins and Rollins 86212* (BRY, NY, RM, UTC). SC Markagunt, Brian Head Peak. 11000' elevation; T36S, R9W, S12; 21 July 1977; *Welsh and Clark 15598* (BRY). Markagunt Plateau, Cedar Breaks National Monument, North Viewpoint along highway 148. Grassy brow of ridgeline in white, chalky limestone soil of Claron Formation surrounded by spruce-fir forest. 3175m elevation; 37° 39'26"N 112° 50'2"W; 31 May 2000; *O'Kane 4721* (BRY, ISTC, NY). Silty Brian

Head Form, ca 1/2 mi s of Brian Head Peak. Meadow along drainage. 10800' elevation; T36S, R9W, S12; 17 July 1982; *Welsh 21301* (BRY, NY). Cedar Breaks vicinity, Engelmann spruce woods and margin of breaks, Pink limestone memb. Caron fma. 10400' elevation, T35S, R9W, S17; 17 July 1982; *Welsh 21293a* (BRY).

Kane County: NE of Kanab along the crest of Deer Spring Point near end of access road, ca. 3.31 km NNE of Sand Spring. In sandy soil overlying mudstone on gentle N-facing slope with *Pinus*, *Juniperus* and *Artemisia*. 7130' elevation; 37°18'33"N 112°10'53"W (WGS84 Datum); T40S, R3W, S30; 9 May 2001; *Windham 2396* (ISTC, MO, NY). **Millard County:** Along Hwy 50-26, 10 mi W of Salina. 6000' elevation; T21S, R2W, S4; 24 May 1980; *Neese 8692* (BRY, GH, NY). Desert Experimental Range, Warm Point Ridge. 6000' elevation; T25S, R18W, S25; 30 April 1964; *Matthews 7* (BRY). **Piute County:** Tushar Mountains, Fish Lake Natl.Forest, head of Bullion Canyon, and W of Marysvale and SE of Mt Baldy. 10000' elevation; T27S, R5W; 18 July 1981; *Atwood 8048* (BRY). Tushar Mtns, ridge crest at head of S Fork Bullion Canyon. 11840' elevation; T28S, R5W, S13; 3 July 1984; *Taye and Frost 2585* (BRY, UTC). Tushar Mtns, Fishlake NF, 1.2 miles n of Mud Lake (summit). 11300' elevation; T28S, R5W, S10, NE1/4; 30 August 1983; *Bascom and Mendenhall 180* (BRY). Fishlake Nat. Forest, at the alluvial areas of Wades Canyon. 6000' elevation; T30S, R4W, S21, NE ¼; 7 July 1979; *Greenwood s.n.* (BRY). Tushar Mountains, north-facing slope at the head of Pine Creek (Bullion) Canyon, 16 km (10 mi) air distance west-southwest of downtown Marysvale. 3480m (11415') elevation; 38°23'35"N 112°24'00"W; T28S R5W S10; 14 July 1 2000;

Holmgren and Holmgren 14050 (ISTC, NY, UTC). Tushar Mountains, Mt. Brigham, Krumholtz comm. Delano Peak Tuff Intrusive. 11250' elevation; T28S, R4W, S8, SW4; 18 July 1991; *Kass and Taye 3289* (BRY). Rocky knoll in an open meadow, 10.5 miles W of Junction. 9 July 1986; *Rollins and Rollins 86205* (BRY, NY, RM, UTC). Bullion Canyon, mountain above Two-mile Creek, 10 road miles W of Marysvale. 7 July 1986; *Rollins and Rollins 86199* (BRY, NY, RM, UTC). Tushar Range, high ridge between Mount Edna and Mount Brigham. 7 July 1986; *Rollins and Rollins 86200* (BRY, NY, RM, UTC). Tushar Mts, Beaver Dist, head of Bullion Creek, ca 9 mi due WSW of Marysvale. 10000' elevation; T28S, R5W, S2; 17 August 1978; *Welsh and Henriod 18146* (BRY, NY, RM). Tushar Mts, Beaver District, Mt Brigham, ca 7 mi SW of Marysvale. 11200' elevation; 16 August 1978; *Welsh and Henriod 18080* (BRY). Tushar Mts, head of Bullino Canyon, 9 mi. WSW of Marysvale. 10000' elevation; T28S, R5W, S1; 28 July 1976; *Welsh, Taylor, and Atwood 14101* (BRY, NY). Parker Mt, 6 mi due east of Angle. 9200' elevation; T29S, R1W, S36; 29 July 1976; *Welsh, Taylor, and Moore 14182* (BRY). Tushar Mts, Fish Lake Forest, Grindstone Flat, ca 6.5 mi NW of Circleville. 9600' elevation; T29S, R4W, S31; 29 June 1978; *Welsh, Welsh, and Welsh 17190* (BRY). Tushar Mts, Mountain east of Mt. Belknap, 12 miles west of Marysvale. 11000' elevation; 21 July 1951; *Rollins 51221* (F, NY). Brigham Peak, Marysvale. 11700' elevation; 29 August 1894; *Jones 5958a* (NY, RSA). **San Pete County:** Manti Forest, rocky clay loam soil. 9400' elevation; 6 September 1912; *Willey 341* (RM). Santi National Forest, Great Basin Experiment Station. *Sampson 30380* (RM). Manti National

Forest, Great Basin Expt. Sta. near Alpine Physical Factor Station. 10000' elevation; 1 August 1925; *Forsling and Nelson 260* (RM). Manti Forest, Head of Ephaim Canyon. 9800' elevation; 2 August 1916; *Geisler 47* (RM). Ferron Mountain. 940m elevation; T19S, R34E, S35; September 1990; *Geer 15* (UTC). Manti Forest, Great Basin Expt. Sta., Philadelphia flat. 10000' elevation; 20 June 1919; *Hall 890* (RM). Manti Forest. 10500' elevation; 6 September 1912; *Willey 341* (RM). **Sevier County:** SE slope of the Valley Mountains, ca 3.57 km NW of junction of State Routes 63 and 256. On gentle, E-facing slope in rocky soil derived from white shale formation. 5675' elevation; T21S, R1W, S18; UTM – 4314450 m.N by 416750 m.E (Zone 12); B.L.M. Aurora Quad (7 ½ min.); 2 May 192 ; *Windham and Windham 92-15* (MO, NY). **Wayne County:** SC Boulder, 13 miles due South of Bicknell. 11000' elevation; T30S, R4E, S30; 21 June 1977; *Neese and White 3267* (BRY).

Physaria occidentalis subsp. *cinerascens*

Idaho, Butte County: Cahllis National Forest, 4.1 miles on road to Howe Mountain, FR557 then 0.4 miles on FR 560. 7916' elevation; 15 June 2013; *Minnaert-Grote and O'Kane 95* (ISTC). **Idaho: Custer County:** White Knob Mountains, Challis National Forest, S side of Copper Basin, E side of The Swamps, ca 10 mi SW of Mackay. 8350' elevation; T5N, R23E, S6, NW ¼; 22 June 1984; *Moseley 309* (RM). **Idaho: Franklin County:** Bear River Range, Cache NF, upper Logan River area, around summit of Wilderness Peak (Peak 9460), ca. 1 mi W of Gibson Lakes, ca. 5 mi SE of Mapleton. 9100-9460' elevation; T16S, R41E, S10, SE4; 16 July 1990; *Moseley and Mancuso 1734* (GH). **Power County:** 6.3 mi E of western boundry of Sawtooth

National Forest. 13 June 1981; *Rollins and Rollins 81305* (RM). **Nevada: Esmeralda County:** South end of the Silver Peak Range, Magruder Mt, frequent, stony north facing slopes. 5 July 1945; *Maguire and Holmgren 25649* (NY, UTC, WS). Summit of Gold Mtn. 8000' elevation; 23 June 1930; *Keck 573* (CAS). **Eureka County:** Roberts Creek Mts, ridge east of Roberts Creek Peak. 9800' elevation; T23N, R50E; 4 August 1984; *Tiehm and Nachlinger 9135* (NY). Fish Creek Range, just southwest of Eureka, ridge north of Prospect Peak. 8700' elevation; T19N, R53E, S34; 19 July 1983; *Tiehm and Williams 8201* (NY). Roberts Mtn, near BM 8830. 8800' elevation; T23N, R50E, S33; 9 June 1988; *Kolar and Knight 1801* (NY). **Nye County:** North end of Railroad Valley, 8 air miles due east of Duckwater. 5750' elevation; T12N, R57E, S3; 15 May 1981; *Tiehm 6433* (NY). **Pershing County:** E. Humboldt Mts. 10000' elevation; August 1860; *Watson 82* (NY). W. Humboldt Mtns. 8500' elevation; June 1860; *Watson 82* (NY). **White Pine County:** Ruby Mts, just northeast of a mine area on the north side of Bourne Canyon, on south side of Little Bald Mt. 8000' elevation; T24N, R57E, S34; 22 May 1985; *Tiehm and Lindsey 9452* (NY). Mokomoke Mts, 1 road mile south of Hamilton on the road to Shermantown. 8400' elevation; T16N, R58E, S16; 17 June 1984; *Tiehm and Williams 8693* (NY). Butte Mountains, north of highway 50 near the turn to Illipah Creek Reservoir. 6900' elevation; T17N, R58E, S12; 9 June 1983; *Tiehm and Williams 7877* (NY). Moorman Ridge, just east of the Hamilton Road on highway 50 to Ely, south of the highway. 6800' elevation; T17N, R58E, S13; 14 May 1985; *Tiehm, Williams, and Ertter 9389* (NY). U.S hwy 50, 0.5 km (0.3 mi) east of the Hamilton-Illipah turnoff, 45 km (28

mi) air distance west-northwest of downtown Ely. 2150m (6900') elevation; T17N R58E S13; 28 June 1999; *Holmgren and Holmgren 13634* (NY). Northern Snake Range, Mt. Moriah, w face of mountain. 11200' elevation; T16N, R69E; 6 July 1966; *Holmgren and Reveal 2814* (NY, RSA). **Utah, Beaver County:** Wah Wah Mtn, on alluvium of east side, 11 airline miles south of Wah Wah Pass (Utah 21). 6700' elevation; T28S, R15W, S29; 13 July 1969; *Holmgren and Kern 3714* (NY). On the WNW side of Grampian Hill above Frisco townsite. 7000' elevation; T27S, R13W, S23; 8 June 1998; *Atwood, Evenden, and Armstrong 23806a* (NY, RM). **Box Elder County:** Raft River Mts, Sawtooth National Forest, 6.6 ESE of Yost. 2753m elevation; 20 July 1996; *Salywon 3194* (ISTC). Ridgecrest SW of Wolf pass, ca ¾ mi NE of Mt Nebos, N Summit. 10900' elevation; T11S, R2E, S30, NW4, SW4; 13 August 1991; *Tuhy 3658* (NY). Raft River Mountains, just south of saddle between One Mile Creek and George Creek canyons, 6.5 km (4 mi) air distance southeast, 122° of Yost. 2260m (7400') elevation; T14N, R14W, S17; 10 June 1984; *Holmgren, Holmgren, and Keller 10483a* (ISTC, NY). Raft R. Mountains, Sawtooth NF, 4 mi se of Yost. 7600' elevation; 21 June 1982; *Goodrich and Atwood 17065* (NY). **Juab County:** S summit of Mt Nebo. 11870' elevation; T11S, R1E, S36, NE4SE4SE4; 22 August 1991; *Tuhy 3683* (RM). Rocky summit North Peak, Mt. Nebo. 10200' elevation; 7 July 1959; *Cottam, Anderson, Rowland, and Ream 15576* (MO). Crevices of weathered rock outcrops, main ridge crest, ca .4 mi NNE of Mt. Nebo's North Summit. 11420' elevation; T11S, R1 ½ E, S30, NE4 of S2; 16 August 1991; *Tuhy 3670* (RM). Uinta NF, N of Mt Nebo at head of Pole Canyon, ca 1.33 km N of

the summit of Wolf Pass. 10625' elevation; 39°50'35"N 111°45'03"W; T11S, R2E, S19; UTM – 4410400 m.N by 435775 m.E (Zone 12); 28 June 1996; *Windham 96-211* (ISTC). **Millard County:** 7000' elevation; T19S, R14W, S25; 27 June 1981; *Kass and White 493* (BRY). **Toole County:** Stansbury Mtns, summit of Deseret Peak, W facing slope. 11020' elevation; T4S, R7W; 7 July 1978; *Taye 164* (NY). Stansbury Mountains, North Willow Canyon, on quartzite outcrop of ridge crest. 8150' elevation; T3S, R7W; 4 June 1979; *Taye 453* (NY).

Physaria occidentalis ssp. *occidentalis*

California: Placer County: On Truckee River. 18 July 1886; *Sonne s.n.* (F). **Mono County:** Warren Mt, Modoc Forest. 8600' elevation; 2 July 1917; *Smith 67* (RM). **Siskiyou County:** Trinity Mountains, Shasta NF, summit of Mt Eddy, 8.4 air mi SW of Weed. 2752m elevation; 41°19.178'N 122°28.733'W; 17 July 2007; *Grady 310* (ISTC). **Idaho: Bingham County:** Blackfoot Mountains, Wolverine Creek-Sellars Creek summit, hilltop west of pass. 220m (7220') elevation; 43°17'08"N, 111°52'35"W; T1S, R39E, S34; 18 June 2003; *Holmgren and Holmgren 14797* (ISTC). **Blaine County:** Smoky mountains. 9500' elevation; 13 August 1916; *Macbride and Payson 3770* (RM). NE of Sun Valley above Trail Creek along Forest Rd 408. Steep, SW-facing slope of limestone fragments. 2195m elevation; 43°47'23"N 114°15'38"W; 29 June 1998; *O'Kane and Prather-O'Kane 4501* (ISTC). **Cassia County:** Sawtooth National Forest. 1910; *Woods 56a* (RM). **Custer County:** Boulder Mts, Sawtooth Nat. For, talus slides on west base of Ryan Peak. 11000' elevation; 1 August 1944; *Hitchcock and Muhlick 10576* (RM). Lemhi Forest,

above Grouse Creek slide. 7300' elevation; T12N, R21E, S1; 20 May 1929; *Cusick 81* (RM). Antelope Pass on east side of Copper Basin. 2723m elevation; 43°46'16"N 113°45'51"W; 29 June 1998; *O'Kane and Prather-O'Kane 4502* (ISTC). **Franklin County:** Franklin Basin Road, forest and high elevation meadows. 7850' elevation, 42°05.42'N 111°37.11'; 25 June 2004; *Smith 5206* (NY, WS). **Lemhi County:** Salmon Forest, ½ mile above Yellowjacket Ranger Station. 7000' elevation; 5 July 1930; *Gutzman 9* (RM). Lemhi Forest, bar west of Grouse Creek. 5500' elevation; 6 May 1928; *Schulze 53* (RM). **Nevada: White Pine County:** Snake Range, Mt. Washington, just south of the peak near the ancient bristlecone forest. 11200' elevation; T12N, R68E; 22 August 1988; *Tiehm 11907* (NY). **Oregon: Grant County:** Serpentine talus slopes overlooking Field's Creek, 17 mi se of Dayville. 3400' elevation; T13S, R28E., S35; 6 June 1953; *Cronquist 7097* (RM, RSA). 10 mi s of John Day on Hwy 395. 1189m elevation; 44°17'5"N 118°57'52"W; 25 June 1998; *O'Kane and Prather-O'Kane 4498* (ISTC). **Harney County:** Steins Mtns, near Wild Horse Creek. 15 July 2012; *Cusick 2036* (US). **Umatilla County:** East Birch Creek Rd, 7 mi se Pilot Rock. Rocky outcropping on s-facing slope. 1800' elevation; T2S, R32E, S12, NW ¼ SE ¼; 25 April 1976; *Grable 6289* (WS). **Wallowa County:** On talus of lava cap, high ridge east of meadow, 1 ½ mi. below Aneroid Lake. 12 July 1950; *Kruckeberg 2264* (RSA). On talus of lava cap, high ridge east of meadow, 1 ½ mi. below Aneroid Lake. 12 July 1950; *Kruckeberg 2264* (RSA). Along John Day River 8.6 mi west of Spray on Highway 19. Gravelly loam from basalt at base of old lava flow. 533m elevation; 44°48'24"N 119°56'32"W; 25 June 1998; *O'Kane*

4497 (ISTC). **Wheeler County:** Dry rocky sagebrush slopes along John Day Valley near Spray. 17 April 1935; *Thompson 11339* (RSA). W. end of Mitchell at Jct. U.S. Hwy 26 and State Hwy 207. 2800' elevation; T11S, R21E, S36; 11 May 1976; *Halse 1318* (CAS, RSA, UTC). Dry rocky sagebrush slopes along John Day Valley near Spray. 17 April 1935; *Thompson 11339* (RSA). **Utah: Iron County:** SC Markagunt, E slope, Wasatch Formation. 10350' elevation; T36S, R9W, S24; 19 July 1977; *Foster and Foster 4643* (BRY, NY). **Juab County:** N ridge of North Peak ca 1/4 mi N of summit. On boundary of Juab and Utah counties. 10800' elevation; T11S, R2E, S19, SW4SE4SW4; 16 August 1991; *Tuhy 3668* (RM). **Tooele County:** Stansbury Mtns, Deseret Peak, rocky quartzite, south-facing slope. 9500' elevation; T4S, R7W, S22; 4 July 1980; *Taye 979* (NY). **Utah County:** Spur ridge along N side of North Basin, ca .4 mi SE of Mt. Nebo's N summit. Crevices and ledges of N and E facing rock outcrops. 10650' elevation; T11S, R1 ½ E, S31, SE4 of N2; 15 August 1991; *Tuhy 3665* (RM).


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Bermudiana 4016 ..... 140 140 ..... 170 170 ..... 180 180 .....
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kingii 16157 ..... 140 140 ..... 170 170 ..... 180 180 .....
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cordifolia 283 ..... 140 140 ..... 170 170 ..... 180 180 .....
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laticfolia 2164 ..... 140 140 ..... 170 170 ..... 180 180 .....
laticfolia 13595 ..... 140 140 ..... 170 170 ..... 180 180 .....
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Physalis_sicomenis 2093 ..... 140 140 ..... 170 170 ..... 180 180 .....

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bernardina 53154 4016 1
 cehrensii 13614
 kingii 6190 8111 9824
 latifolia 13596 13646
 kingii 4705 cordii formis
 kingii s n 3323 10418
 kingii 16157 ab1
 occ occ 5206
 kingii 1887 diversifoli
 kingii 82710 91
 kingii 269 26056 2941
 occ 95
 occ occ 4497 ab1
 cob 32871 ab1
 cehrensii 13648
 wardii 13795 2396
 kaib 13565 13564 4213 1
 utah 13540 3184 13651
 latifolia 14776 89
 latifolia 13588
 kingii 3042 ab1
 kingii 1986 2585 latif
 latifolia 84212 4211
 latifolia 2949
 latifolia 13805 wardii
 latifolia 86 wardii 213
 wardii 4721 ab1
 kingii 11000 lat 5228 8
 wardii 4541 ab1
 cob 14454 92 kingii 113
 AR124197
 cehrensii 8326a
 occ cin 3683 ab1
 occ occ 4502 ab1
 latifolia 1734 ab1
 latifolia 4949
 Paysonia_ston_2892

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 TTGTTTCTAT-TTTTATCTA-180
 TTGTTTCTAT-TTTTATCTA-190


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bernardina 53154 4016 1
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kingii 8190 8111 9824
latifolia 13596 13646
kingii 4705 cordiiFormis
kingii s 3323 10418
kingii 16157 ab1
occ occ 5206
kingii 1887 diversifoli
kingii 82710 91
kingii 269 26056 2941
occ 95
occ occ 4497 ab1
cob 32871 ab1
cobrensis 13648
wardii 13795 2396
kaib 13565 13564 4213 1
usab 13540 3184 13651
latifolia 14776 89
latifolia 13588
kingii 3042 ab1
kingii 19806 2585 latif
latifolia 23949
latifolia 13805 wardii
latifolia 86 wardii 213
wardii 4721 ab1
kingii 11000 lat 5228 8
wardii 4541 ab1
cob 14454 92 kingii 113
AR124197
cobrensis 8326a
occ cin 3683 ab1
occ occ 4502 ab1
latifolia 4734 ab1
latifolia 4949
Paysonia_ston_2892
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kingii 269 26056 2941 CAGAAATGAGAAAT-CAAATTTGATTCGAAAAAAGAGACAAACAAAAAAGGGTTAGAGACTACTCAAT-AAAAAAGTACTTAAGGATTCCTCCTGAGATATTTGAGAGATATTTAACTTGAGT
occ 95 CAGAAATGAGAAAT-CAAATTTGATTCGAAAAAAGAGACAAACAAAAAAGGGTTAGAGACTACTCAAT-AAAAAAGTACTTAAGGATTCCTCCTGAGATATTTGAGAGATATTTAACTTGAGT
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latifolia 1734 ab1 CAGAAATGAGAAAT-CAAATTTGATTCGAAAAAAGAGACAAACAAAAAAGGGTTAGAGACTACTCAAT-AAAAAAGTACTTAAGGATTCCTCCTGAGATATTTGAGAGATATTTAACTTGAGT
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APPENDIX D

ndhC-trnV INTERGENIC SPACER SEQUENCE ALIGNMENT

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cob 33871 13688 92 14454 8266a kibzii 11304 13540 13651 3114 wardii 13795 2396 latifolia 13588
kalbebeemii 7191 3354 4213 latifolia 84 4212 4211
kibzii 10418 3448 13633 6190 3042 b B1111 3383 10418 4705 2585 cordiformis 283 latifolia 76224 11784 98246 8909 13600 26 86 ccc 95 wardii 14050 34
latifolia 1734 ab1
ccc ccc 4502 16157 2941 269
kibzii 26036 16157 2941 269
latifolia 23545
latifolia 23545
latifolia 23536
ccc ccc 3206
ccc ccc 3465 ab1
kibzii 13598
kibzii 13598
latifolia 13805
wardii 80
latifolia 14776 ab1
ccc ccc 3683 ab1
latifolia 13646
cobbeemii 13664
kibzii 11000 82710 82710 91 lat 5328 cob 81963 hemmardina 53153 4016 1172
ccc ccc 4497 7097
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Peysonia spum 2892
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