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By

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Professor Bruce Baldwin, Chair
Professor Brent Mishler
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Abstract

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This study investigated how habitat specialization affects the evolution and ecology of flowering plants. Specifically, a phylogenetic framework was used to investigate how trait evolution, lineage diversification, and biogeography of the western American flora are affected by two forms of substrate endemism: (1) edaphic specialization onto serpentine soils, and (2) host specialization of non-photosynthetic, holoparasitic Orobanchaceae.

Previous studies have noted a correlation between presence on serpentine soils and a suite of morphological and physiological traits, one of which is the tendency of several serpentine-tolerant ecotypes to flower earlier than nearby closely related populations not growing on serpentine. A phylogenetically uncorrected ANOVA supports this hypothesis, developed predominantly through previously published comparisons of conspecific or closely related ecotypes. However, comparisons among three models of trait evolution, as well as phylogenetic independent contrasts across 24 independent clades of plants that include serpentine tolerant species in California and with reasonably resolved phylogenies, revealed no significant affect of flowering time in each of these genera. Taken together, these results suggest eco-evolutionary scale dependence of flowering time, and that flowering time may be an exaptation that facilitates colonization of serpentine habitats.

To better understand the role that different substrates may play in diversification of the western American flora, additional studies were performed on a clade of parasitic plants in the Orobanchaceae endemic to the New World, long recognized as *Orobanche* sections *Gymnocaulis* and *Nothaphyllon.* First, a densely sampled phylogeny from specimens across the native geographic and host ranges of this clade was inferred using ribosomal nuclear DNA, a portion of the low-copy nuclear gene *waxy*, and three plastid regions. Several taxonomic species were found to be either non-monophyletic, or monophyletic but including several strongly supported sub-clades. In each case, these least-inclusive clades showed unique host associations, suggesting that host-switching may be an important driver of diversification. At a deeper phylogenetic scale, the monophyly of New World

broomrapes, coupled with phylogenetic evidence that the Eurasian genus *Diphelypaea* is nested within *Orobanche sensu lato* supports the resurrection of the genus *Aphyllon* to include all New World taxa traditionally recognized as *Orobanche* and diagnosable by a five-toothed calyx.

Finally, comparisons between the ranges of *Aphyllon* species and those of their hosts suggest that host specificity can also constrain biogeographic patterns in parasitic plants. Most strikingly, the closely related species *A. ludovicianum* and *A. chilense* both parasitize species of *Grindelia* in North and South America, respectively. Chronograms for both the tribe Orobancheae (*Aphyllon* and its holoparasitic relatives) and *Grindelia* were constructed using fossil and secondary calibration points, one of which was an inferred horizontal gene transfer event from an ancient leguminous host into the common ancestor of *Orobanche* and *Phelipanche*. These chronograms were used to reconstruct the historic biogeography using a dispersal-extinction-cladogenesis model. The dispersal of host and parasite lineages were both found to be from North America to South America, recapitulating a biogeographical pattern seen in many other lineages of land plants, with the dispersal of the *Aphyllon* lineage parasitic on *Grindelia* taking place somewhat after *Grindelia* began to diversify in South America. From a methodological standpoint, this study also demonstrates the general utility of using horizontal gene transfer events from well-dated clades to calibrate phylogenies in the absence of a fossil record.

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And to Nature, my teacher and muse.

CHAPTER 1:

Flowering time evolution of the California flora is independent of serpentine endemism

ABSTRACT

Comparative phylogenetic tests have been only recently applied to the many hypotheses about the role ultramafic (serpentine) soils play in the evolution and ecology of regional floras. An association between serpentine tolerance and early flowering has been observed at microevolutionary scales but not yet tested broadly across angiosperms. I used both hypothesis testing (phylogenetically independent contrasts) and model-selection approaches to compare published data of serpentine tolerance with flowering time using phylogenetic trees representing 24 clades of plants representing 27 genera and 17 families.

A total of 126 independent contrasts revealed no significant difference in flowering times across all clades or within any one clade except for the Thelypodieae (in which flowering time of serpentine-tolerant lineages was later). Similarly, an Ornstein-Uhlenbeck model with one optimal flowering time was preferred over a model with separate optima depending on serpentine tolerance in nearly all genera.

A phylogenetically uncorrected ANOVA found that serpentine tolerant species have an earlier distribution of flowering times compared to both endemic and non-tolerant species, and median flowering times of non-tolerant species show a bimodal distribution. Therefore, I conclude that long-term evolutionary responses of flowering time in a lineage that becomes tolerant of serpentine are variable across genera, with no significant overall bias towards earlier or later flowering. However, given that close relatives of serpentine-tolerant lineages tend to also flower relatively early, early flowering time may serve as an exaptation that allows species to better colonize serpentine habitats. In combination with previously published ecotype studies, these results illustrate the eco-evolutionary scale dependence of flowering time.

INTRODUCTION

Varied and contrasting edaphic regimes have long been understood as having a major influence on biodiversity and trait evolution at both large and small scales, particularly in plants. Continental-scale phylogenetic turnover and community structuring can be partly explained by soil gradients (Fine and Kembel 2011). At the population level, differences in soil type have been shown to be an ecological filter and a strong isolating mechanism of plant lineages even at short distances (MacNair and Christie 1983, Gardner and MacNair 2000, Moyle et al. 2012). Consequently, edaphic specialization has long been cited as a major factor governing plant distribution, reproductive isolation, and lineage splitting within genera (Humboldt and Bonpland 1805, Wallace 1895, Rajakaruna 2003, Baldwin 2005, Yost et al. 2012).

One of the starkest edaphic regimes is derived from ultramafic rock formations. These soils, broadly referred to as serpentine soils, are characterized by low calcium to magnesium ratios, generally low concentrations of plant essential macronutrients (N, P, K), and high concentrations of heavy metals (e.g. Mg, Fe, Ni). In addition to the harsh chemistry, serpentine soils show elevated soil temperatures and erosion compared to nearby nonserpentine areas (Walker 1954, Kruckeberg 2002). Serpentine soils are also thought to be more xeric (Walker 1954, Kruckeberg 2002, Harrison 2013), though this has been disputed by Raven and Axelrod (1978) and others (Eskelinen and Harrison 2015). In any case, the challenging serpentine-associated conditions for plants have led to distinctive floras on six continents (Kruckeberg 1985, Rajakaruna et al. 2009). In the tropical floras of Cuba and New Caledonia, 27% and 50% of endemic taxa are also endemic to serpentine soils. Among temperate regions, California has the most species-rich serpentine flora. Approximately 10% of California's endemic plant taxa are endemic to serpentine soils although those habitats represent less than 1.5% of the state's surface area (Kruckeberg 1985, Safford et al. 2005). These factors, in combination with a robust history of botanical study, have contributed to the region’s prominence as a model system for studying the evolutionary ecology of serpentine floras (Anacker 2011).

Given the intense selective regime imposed by serpentine soils, botanists and ecologists have long sought to identify morphological, physiological, and phenological adaptations that permit colonization of serpentine soils (e.g. Wulff 1943, Kruckeberg 1954, 1985, Wright et al. 2006, O’Dell and Rajakaruna 2011), as well as their genetic basis (e.g. Gailing et al. 2004). Studies in California and elsewhere have found that serpentine plants have increased tolerance to drought and heavy metal accumulation, reduced leaf size, shorter stature, elevated root to shoot ratios, greater tolerance and lower absorption of Mg, lower Ca levels but higher absorption, and earlier flowering phenology (Kruckeberg 1954, Schmitt 1980, Lee et al. 1997; Tyndall and Hull 1999; reviewed by Brady et al. 2005). However, very few of these hypotheses have been tested in a comparative phylogenetic framework. Independently comparing species on and off of serpentine soils does not account for their shared evolutionary history (Felsenstein 1985). Recent efforts have begun to address these deficiencies, especially in regards to macroevolution and diversification in California (e.g. Anacker et al. 2011, Anacker and Harrison 2012). However, more research is required to better understand trait evolution in these systems.

The focus of the present study was to test the hypothesis that the flowering time of plant lineages that invade serpentine soils is consistently earlier compared to non-serpentine plants. This has been a long-standing claim based mostly on observations of ecotypes that flower earlier on serpentine soils than do their non-serpentine conspecifics (Schmitt 1980, Brady et al. 2005). Serpentine soils are generally rocky and low in clay and organic matter, and therefore may desiccate more rapidly than non-serpentine soils. Accordingly, plants on California serpentines may preempt the earlier onset of summer drought conditions by flowering earlier, with a stronger shift expected among serpentine endemic taxa, which persist only on serpentine, than serpentine tolerant taxa, which are found in both serpentine and non-serpentine habitats. Here, I tested this flowering-time hypothesis using phylogenetically independent contrasts (PICs) and comparisons between three models of flowering-time evolution: (1) a Brownian motion (BM) model representing only genetic drift; (2), an Ornstein-Uhlenbeck model, which generalizes the BM model to include the effects of stabilizing selection on a given lineage, and; (3), and a multiple-optimum Ornstein-Uhlenbeck model, sometimes called a Hansen model, in which different trait optima (i.e. selective regimes) are permitted on different branches of the phylogeny. In the context of this study, the third model allowed for different flowering time optima between lineages growing on and off of serpentine soils. Finally, I use non-phylogenetic comparisons among flowering times of California native taxa to see if the ecotype-scale observations of earlier flowering time can be generalized to broad patterns across a regional flora, irrespective of evolutionary history.

MATERIALS AND METHODS

***Clade selection*—**Clade selection was based on three criteria: (1) at least one taxon of each clade must be endemic to serpentine soils in California, (2), a published molecular phylogeny including both plastid and nuclear sequence data and extensive taxonomic sampling must already exist, and (3) clades must represent independent origins of serpentine tolerance, such that no two sampled clades are sister to, or nested within, each other. Twenty-four clades were found to meet these criteria, including four of the top-five most important and four of the top-five most diverse serpentine genera in California (Safford et al. 2005). The fifth clade, *Hesperolinon*, has unclear taxonomic boundaries and phylogenetic relationships as a result of a recent, rapid radiation, making reliable ancestral-state reconstructions impractical (Schneider et al. 2016). Twenty-two of these clades were used by Anacker et al. (2011) as part of a large analysis of diversification onto serpentine soils. Phylogenies for the remaining clades were published subsequently: the Eriogonoideae (Kempton 2012) and Streptanthoid complex (= Thelypodieae) (Cacho et al. 2014). Tree topologies and branch lengths used from the studies of Anacker et al. (2011) and Kempton (2012) reflect a majority-rule consensus tree, whereas the Thelypodieae phylogeny of Cacho *et al.* (2014) is the maximum clade credibility tree from a BEAST analysis (see the original studies for full details).

I made several modifications to these phylogenies: Conspecific (or convarietal) terminals resolved as a clade were pruned to a single exemplar per taxonomic species, subspecies, or variety to match the resolution of trait data. Phylogenetic trees were made ultrametric using Sanderson's (2002) semi-parametric penalized likelihood algorithm implemented in the 'ape' package version 3.0-7 (Paradis et al. 2004) of the statistical program R version 2.15.1 (R Core Team 2012). The smoothing parameter, λ, was selected for each clade using a cross-validation algorithm. Outgroup taxa and ingroup tips for which no flowering time data were available (or in the case of a few Eriogonoideae, flower year-round) were pruned following the rate smoothing but prior to comparative analyses.

Trait data**—**Serpentine tolerance and serpentine endemism were treated as binary characters. Serpentine endemism was defined as taxa being naturally restricted to ultramafic soils, whereas serpentine tolerance was defined as any persistence on ultramafic soils regardless of where else the plants may be found and therefore also includes all serpentine endemic taxa. Character determinations followed a simplification of the ternary classification of Anacker *et al.* (2011) and Cacho et al. (2014), who relied on a database of serpentine affinity based on peer-reviewed and gray literature, expert assessment and observations, and herbaria records (Safford et al. 2005). Taxa not included in previous phylogenetic analyses were assessed for serpentine tolerance following Safford et al. (2005) and taxon descriptions in the revised *Jepson Manual* (TJM2; Baldwin et al. 2012).

Flowering time was treated as a continuous character by determining the midpoint of the flowering range as described by experts in published floras, similar to Bolmgren et al. (2003). Flowering time onset or conclusion are two other common ways to measure flowering phenology. However flowering time midpoint is probably a more stable measure of phenology than either onset or end of flowering time, which can be affected by population size (CaraDonna et al. 2014), and better reflective of the central tendency in the absence of detailed surveys of field populations or museum specimens, Flowering times of species native or naturalized to California, representing over 91% of study taxa, were taken from TJM2. Most of the remaining flowering time data came from the Flora of North America North of Mexico (FNA; Flora of North America Editorial Committee 1993+), with <1% from other sources such as the Flora of Baja California (Wiggins 1980), Flora of China (Zhengyi et al. 1994+, Brach and Song 2006), SEINnet (www.swbiodiversity.org), or the Lady Bird Johnson Wildflower Center (www.wildflower.org). Taxon nomenclature was standardized throughout. The resolution of flowering time ranges was usually month-to-month, resulting in semi-monthly (occasionally weekly) resolution of flowering time midpoint. All taxa included in this study were reported to have a unimodal distribution of flowering time.

Acknowledging the limitations inherent in this approach, including the coarseness of time record, and inability to control for latitude or elevation at the population level, flowering ranges from regional floras were used instead of mining herbarium record data for four reasons. First, substantial spatial, temporal, and taxonomic collection biases may exist in collections data, particularly across the geographic scales in this study. Using published floras allows for standardization across taxa, and expert understanding, which may offset some of these biases. Second, in some lineages floral morphology is not taxonomically diagnostic. For example, many Apiaceae are distinguished by fruit characters, so this phenophase may be overrepresented in herbaria collections. Unless the data were filtered, this would bias these records towards (in this example) later flowering. Third, published floras generally report longer flowering-time durations than direct analysis of herbarium data supports, perhaps due to the coarseness of the data, or temporal sampling bias in herbaria collections (Bolmgren et al. 2003, Bolmgren and Lönnberg 2005).

Finally, the taxonomic and geographic scope of this study (1205 taxa across North America) is much greater than other studies that have effectively used herbarium records to estimate phenological trends, generally from one or several well-curated herbaria (e.g. Primack et al. 2004, Lavoie and Lechance 2006, Calinger et al. 2013). Though most herbarium records in California have been digitized, records from neighboring states range from very low to moderate (Taylor 2014). However, rapid progress is being made in digitizing collection data, which hopefully will overcome this limitation in the future to the extent that it is not driven by collection bias.

Two species of *Ericameria* included in the analysis are spring-flowering while all other sampled taxa in the genus are fall-flowering; only the fall-flowering species were included. Whether those two species were scored as earlier or later did not qualitatively affect the results of independent contrasts; however, these taxa were pruned from the phylogenies and omitted from the model-testing analyses. Several species in the Eriogonoideae that flower year-round were also removed from analysis.

Trait data is presented in Appendix A and is also available as a .csv file with the published open-access version of this chapter at http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1767/full.

***Phylogenetic tests*—**The effect of serpentine tolerance on flowering time was tested using both PICs and likelihood comparisons between models that account for shifts in flowering time and those that do not. Blomberg's K statistic was also calculated for each genus to assess phylogenetic signal in flowering time at the within-clade level using the R package phytools (v. 0.5-64; Revell 2012). Significance testing was performed using a nonparametric tip randomization (1000 replicates).

Independent contrasts were performed using the 'aot' module in the program Phylocom 4.2 (Webb et al. 2008). This program allows for comparisons between a discrete independent, predictor variable (serpentine tolerance) and a continuous dependent variable (flowering time). Significance testing was done using a Wilcoxon signed-rank test on contrasts from each clade individually, as well as all contrasts together because of low sample sizes in the within-clade analysis, and because when pooled the data are not normally distributed ($p< 0.001$, Shapiro-Wilk normality test). To test whether lineages with a stronger relationship to serpentine were more likely to have different flowering time, analyses were repeated with taxa scored in two different ways: (1) serpentine endemics versus non-endemics, and (2) serpentine tolerant taxa (which includes all endemics) versus non-serpentine taxa. In both cases, trait values for serpentine tolerance were coded such that a positive contrast represents later flowering of the serpentine tolerant lineage, and a negative contrast represents earlier flowering. Although PICs assume trait evolution follows a BM model, this method has been found to be quite robust to violations of the BM assumption and branch length (Diaz-Uriatre and Garland 1996, Ackerly 2000) and my results from these analyses are consistent with the model-based approach also presented below.

Evolutionary model testing was conducted in R using the OUCH package version 2.8-2 (Butler and King 2004). Log-likelihoods were calculated for three different models of flowering time evolution: a one-parameter BM model, in which trait evolution follows a random walk, a two-parameter OU model with a single evolutionary optimum for flowering time, and a three-parameter OU model that estimates separate optimal flowering times for lineages on and off of serpentine. Because I was only interested in the shift of mean flowering time and not changes in other parameters caused by edaphic shifts (i.e. for attraction, α, and drift, σ^2), I did not use the more general model of Beaulieu et al. (2012). Ancestral character states of serpentine tolerance were reconstructed using a maximum likelihood analysis implemented in the R package 'picante' (Kembel et al. 2010) using either a symmetric or asymmetric rate matrix depending on the results of a likelihood ratio test. A preliminary study found that the ancestral-state reconstructions were relatively robust to the smoothing parameter (data not shown). The genus *Orthocarpus* was omitted from this analysis because it included only one serpentine tolerant taxon.

***Non-phylogenetic comparisons*—**In order to test the generalizability of the observation that serpentine floras flower earlier than non-serpentine floras, regardless of evolutionary history, nonphylogenetically corrected comparisons of serpentine endemic, tolerant, and non-tolerant species were made using a one-way analysis of variance (ANOVA). Bonferroni-corrected Wilcoxan signed-rank tests were used to determine significant differences in average flowering time among soil regimes. All 24 clades used in the phylogenetic analyses were used, but with complete sampling of all species, subspecies, and varieties native to California (i.e. minimally ranked taxa). Taxa not native to California were excluded so that a single source (TJM2) could be used for all flowering time data and to geographically constrain the area of comparison. Two additional genera that show extensive diversity on serpentine but lack suitable phylogenetic data were also included (*Lomatium* (Apiaceae) and *Packera* (Asteraceae)), resulting in a total of 1088 minimally ranked taxa, or 20% of California's native angiosperm flora.

RESULTS

***Independent contrasts*—**A total of 126 independent contrasts of flowering time from 24 clades of angiosperms containing 896 operational taxonomic units were identified. Lineages with serpentine tolerance were found to have flowering times slightly later than their non-serpentine sister lineages (+0.15 ± 0.10 months later, mean ± SE; Wilcoxon signed-rank test $P = 0.04$; Fig. 1.1a). However, this difference was driven mostly by a strong shift to later flowering time in serpentine-tolerant lineages within the Thelypodieae (+0.9 ± 0.2 months; $P = 0.002$), as flowering time shifts in serpentine-tolerant lineages from all remaining clades were not significantly different (+0.1 ± 0.1 months; $P=0.16$). At 42 nodes the serpentine tolerant lineages flowered earlier than their non-serpentine sister, at 67 nodes the serpentine tolerant lineages flowered later, and at 17 nodes there was no difference. Considered individually, no clade besides Thelypodieae showed a significant difference in flowering time (Table 1.1), although sample sizes (transitions between serpentine and non-serpentine states) were generally low. Two genera (*Layia* and *Orthocarpus)* had only one contrast apiece and therefore significance testing was not possible.

Considering only serpentine endemics, I found a similar stasis in flowering time (Fig. 1.1b). Only 48 contrasts were recovered: 13 in which the serpentine endemic lineage flowers earlier, 27 in which it flowers later, and eight with no difference. Taken together, serpentine endemics have a non-significantly later flowering time (0.27 ± 0.13 months later; P = 0.067). For most clades, within-group analyses were not possible due to a dearth of transitions to serpentine endemism (<2). One exception was in the Thelypodieae, in which serpentine-endemic lineages flower nearly a month later than their non-endemic sister lineages (+0.86 ± 0.25 months; P= 0.04).

Model comparisons—Of the three models of flowering time evolution tested, the preferred model for 18 of 23 clades was the single-optimum OU model, based on Akaike Information Criterion (AIC) scores (Fig. 1.2, Table 1.2). Using the Schwartz Information Criterion (SIC), which gives a higher penalty for over-parameterization, the single optimum OU model was preferred over the Hansen model in all but three clades. Among those for which the two-optimum Hansen model was preferred over the single-optimum OU model, the direction in flowering-time shift was variable. Only in *Cirsium* and Thelypodieae were the **Δ**AIC scores greater than 3, but the trait shifts were in opposite directions: Serpentine-tolerant lineages showing an earlier trait optimum in *Cirsium* but later in Thelypodieae (Fig. 1.2). Likewise, when only the two-optimum model is considered, the estimated parameters support an earlier flowering-time optimum among serpentine lineages in nine of 23 genera and a shift to later flowering time among serpentine lineages in the remaining 14. The BM model was preferred for *Trichostema, Layia,* and *Arctostaphylos*, though this may be an artifact of limited phylogenetic resolution or small phylogenetic trees. Estimated parameters for each clade are shown in Tables 1.2 and 1.3.

Phylogenetic signal in flowering time— Phylogenetic signal in flowering time among genera, as measured by Blomberg's K statistic was variable, but consistently less than 1, and significantly so for 8 of the 25 genera (Table 1.1). Blomberg's K was not correlated with the number of tips ($R^2 = 0.46$; F=2.179, P = 0.15).

Non-phylogenetic comparisons— Specialization to serpentine soils was found to affect flowering time (one way ANOVA, F=3.28, d.f.= 2, p=0.04). Taxa that are serpentine tolerant but not endemic flower earlier than both endemic taxa (Bonferroni-corrected Wilcoxan signed rank test p<0.02) and non-tolerant taxa (P< 0.01; Fig. 1.3), whereas serpentine endemics flower at the same time as their congeners found off of serpentine. For clade-specific results see Fig. 1.4.

DISCUSSION

Patterns of flowering time evolution—Natural selection can lead to directional evolution (Franks et al. 2007) or stasis (Evans et al. 1989) in flowering time. My results are consistent with selection acting upon flowering time, as evolutionary models that accounted for selection (OU models) were generally supported over non-adaptive Brownian motion models of evolution (Table 1.2). However, I found little to no evidence of selection causing a shift in flowering time of lineages on serpentine soils at the species level and above (Table 1.1, Table 1.2, Fig. 1.1, Fig. 1.2). Depending on the clade, serpentine habitats can select for either earlier *or* later flowering in serpentine tolerant lineages, but most commonly neither (Table 1.2, Fig. 1.2). Although lineages that are "serpentine tolerant" (i.e. with populations on and off of serpentine soils) flower significantly earlier than both serpentine endemics and species excluded from serpentine, (Fig. 1.3), these differences disappear when comparisons are controlled for shared evolutionary history.

While these data do not support the hypothesis that movement of a lineage onto or off of serpentine results in a unidirectional shift towards earlier or later flowering time in angiosperms, they should not be interpreted as evidence against the effect of edaphic factors on flowering time, just that patterns across scales and across clades are complex, with many processes acting independently, as evidenced by several genera in which a two optimum model is strongly favored (Fig. 1.2) but with opposing shifts. Flowering time is a relatively labile trait, with low phylogenetic signal. Blomberg's K statistic is lower than 1 in all 24 clades except for a single case (*Trichostema,* Table 1.1), indicating elevated trait evolution relative to what would be expected under a BM model. This is consistent with other regional-level studies of flowering plants (Du et al. 2015). Consequently, a real shift at very fine-scale phytogeographic levels, such as those observed in numerous ecotype studies of serpentine tolerant species such as *Gilia capitata, Leptosiphon androsaceus, L. bicolor*, the *Mimulus guttatus* complex, and *Collinsia sparsiflora* (Schmitt 1980, 1983, Brady et al. 2005; Wright et al. 2006) would not be observed, or evolutionarily relevant, at the deeper phylogenetic levels studied here. If this is the case, then these results are an example of discordance between microevolutionary process and macroevolutionary patterns (Jablonski 2007).

Four alternative explanations consistent with these data are discussed below. While it may be relatively straightforward to test them in particular cases, the large diversity across angiosperms makes it unlikely that a single explanation will apply universally. It remains a difficult task to determine the most important factors involved in the evolution of flowering time on serpentine, and to tease apart their relative effects so extrapolating the trends seen in fine-scale studies should be done with extreme caution.

***Countergradient variation*—**Countergradient variation is a pattern in which genetic influences on phenotype negatively co-vary with environmental effects on phenotype, resulting in minimal change in a given trait value over the gradient (Conover and Schultz 1995). In other words, phenotype shows minimal change because the differences in environmental and genetic contributions to phenotype between two ecotypes counteract each other. This process has been documented in over 60 species including serpentine and non-serpentine ecotypes (Conover et al. 2009). A full factorial study of riparian and serpentine ecotypes of the annual *Helianthus exilis* grown in potting soil and serpentine soil found that although serpentine genotypes took less time to flower compared to riparian genotypes grown in the same soil, both genotypes flowered earlier when grown on riparian soil compared to serpentine soil (Sambatti and Rice 2007). In this case, within a genotype, the environmental factors promoted later flowering when grown on serpentine, but within a phenotype, genetic differences caused earlier flowering of serpentine-adapted races. Curiously, a reverse example of countergradient variation was found in a reciprocal field-transplant study of *Collinsia sparsiflora*: serpentine genotypes flowered significantly later than non-serpentine genotypes when grown together but, regardless of genotype, transplants in serpentine soils flowered earlier (Wright et al. 2006). This finding is consistent with other reports of earlier-flowering serpentine ecotypes or populations (e.g.

Dyer et al. 2010). One key difference between the *H. exilis* and *C. sparsiflora* studies is that plants in the former study were kept well-watered with distilled water throughout the duration of the experiment. The delay in flowering observed by Sambatti and Rice may have resulted from delayed ontogeny due to edaphic factors such as low soil fertility (Walker 1954, Kruckeberg 1985, Cooke 1994). It is unclear the role that countergradient evolution plays at deeper taxonomic levels, but this phenomenon may contribute to the large number of serpentine/non serpentine sister lineages that show no difference in flowering time (Fig. 1.1).

Environmental heterogeneity within serpentine outcrops — This present study is limited to clades of plants important to the California flora and it is important to point out that serpentine soils (and consequently serpentine tolerant species) are not evenly distributed across the landscape. Serpentine soils are most abundant in northern and central montane California, including the Sierra Nevada, Klamath Ranges, and Coast Ranges (Kruckeburg 1985), and at elevations between 300 and 2300 meters (Burge and Salk 2014). However, aside from their parent material serpentine soils and outcrops show great variability, even edaphically— worldwide, 11 of the 12 major soil orders include some ultramafic soil types; (Rajakaruna and Bohm 1999, Jurjavcic et al. 2002, Alexander et al. 2007). Even within California, variation in aspect, topography, and hydrology can provide a number of different environments in a single patch of serpentine (Rajakaruna and Bohm 1999). This variation may be partially responsible for the conflicting information in the literature regarding water availability on serpentine compared to nearby non-serpentine soils, and likely responsible for variability in flowering time response (Raven and Axelrod 1978, Brady et al. 2005, Alexander et al. 2007). While serpentine soils generally have similar water holding capacity compared to non-serpentine soils (Burt et al. 2001), in western North America such soils are usually much rockier compared to other areas. Consequently, they may be better drained, with less soil to hold water per unit volume, factors that may contribute to the bareness of habitats associated with serpentine soils (Alexander et al. 2007, Cacho and Strauss 2014). However, Raven and Axelrod (1978) noted that some intermittent streams persist longer in the dry season in serpentine areas compared to elsewhere, and recent studies have demonstrated greater variance in both soil water capacity and plant cover on serpentine compared to non-serpentine soils (Harrison *et al.* 2004, Eskelinen and Harrison 2015). This is generally because such streams often have a fracture-driven hydrology rather than the more common pore-driven hydrology (Alexander et al. 2007). In this diversity of habitats it is possible for a clade to invade serpentine but not necessarily encounter a drier habitat. For example, the serpentine tolerant *Helianthus exilis* and serpentine endemic *Cirsium fontinale* are restricted to moist seeps that may remain wetter longer than sites in adjacent habitats. Therefore, even accepting the hypothesis that water availability plays a large role in flowering time differences, heterogeneity in hydrological regimes would be expected to result in heterogeneous responses in flower phenology such as those observed in this study.

***Biotic factors*—** Water availability is broadly recognized as a crucial abiotic factor in shaping serpentine soil communities and plant evolution (Kruckeberg 1985, Brady et al. 2005, Anacker and Harrison 2012). However, flowering phenology may respond more strongly to other biotic or abiotic factors in a given system. Increasing attention has been given to the role of pollinators, herbivores, and other biotic agents in affecting flowering phenology (Elzinga et al. 2007). Biotic interactions may put constraints on flowering time evolution or counteract selection of abiotic conditions (Evans et al. 1989, Pilson 2000, Levin 2006). Other times, biotic and abiotic factors can independently lead to convergence in plant traits. For example, sclerophylly, glaucousness, level of pubescence, decrease in specific leaf area, shrubbiness, and increase in root to shoot biomass ratios are associated with both herbivore resistance and xeric or low-nutrient environments, like serpentine soils (Brady et al. 2005, Alexander et al. 2007). The ways in which interactions between abiotic and biotic factors affect plant phenology in serpentine systems remain poorly studied and it may be that the evolutionary factors that drive plant phenology at deeper phylogenetic timescales studied here differ from those at fine (e.g. ecotypic) scales.

Earlier flowering time: an exaptation?— The difference in the distribution of flowering times between tolerant and both endemic and non-tolerant lineages noted in Fig. 1.3 is not independent of phylogeny. That is, species with earlier flowering are marginally more likely to persist on serpentine, although this is variable by clade. Therefore, instead of serpentine acting as a key selective agent following colonization, an earlier-flowering species may simply be more successful at initially colonizing serpentine. The key drivers of both species and trait composition in an area vary over spatial, temporal, and phylogenetic scales (Swenson et al. 2006, Cavender-Bares et al. 2009), and it is possible that earlier flowering time may have an ecological role and a short-term evolutionary role by isolating divergent populations, but little long-term evolutionary role at deeper time scales. This may explain why the distribution of serpentine endemic flowering times is similar to that of non-tolerant plants. Except in the case of founder-event speciation, a serpentine endemic can be thought of as a serpentine tolerant lineage that has been extirpated from non-serpentine soils (Anacker et al. 2011).

Among the clades studied, flowering times of non-tolerators formed a bimodal distribution (Fig. 1.3), consistent with reported patterns in the eastern United States, the Rocky Mountains, and Japan, (Kochmer and Handel 1986, Aldridge et al. 2011, CaraDonna et al. 2014). It is possible that non-tolerant lineages that show earlier peak flowering are more likely to give rise to serpentine tolerant lineages than those that flower later in the season. This hypothesis is supported by the phylogenetically corrected results, which suggest no difference between serpentine tolerant lineages and their closest relatives (Table 1.1, Fig. 1.1).

CONCLUSIONS

Phylogenetically independent contrasts and comparisons among three models of flowering time evolution both suggest that serpentine tolerance is not correlated with a unidirectional shift in flowering time. Comparing the results of phylogenetic methods with non-phylogenetic methods can provide stronger insight into the evolutionary ecology of unique edaphic conditions more than either can alone. Although serpentine tolerant plants show a slightly earlier distribution of flowering times than non-tolerant plants, this pattern is likely a result of ecological filtering, and not post-colonization adaptation. The contrast between these results and finer-scale ecotype studies suggest scale dependence of the major evolutionary factors (biotic or abiotic) governing flowering time phenology and evolution in this and other systems.

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Table 1.1. Colonization of serpentine has a variable effect on flowering time in 24 clades of angiosperms, based on phylogenetically independent contrasts. For each of 24 clades, the following is shown: Blomberg's K statistic for flowering time and P-value (ns = p ≥0.1), the number of phylogenetically independent contrasts, direction of average difference in flowering time of serpentine tolerant lineages compared to non-serpentine sister lineages, and associated P-values from the Wilcoxon signed-rank test. PICs were calculated using the 'aot' module of Phylocom 4.2. Significance testing was not performed on the serpentine endemic dataset due to a dearth of transitions.

		Blomberg's K (Flowering Time)		**Serpentine tolerant vs. non-serpentine**			**Serpentine endemic vs. not**	
Clade	No. OTUs	K	P	No. contrasts	Flowering time difference	P	No. contrasts	Flowering time difference
Allium	52	0.394	0.001	9	*later*	ns	5	*later*
Aquilegia	19	0.953	ns	2	*later*	ns	1	*later*
Arctostaphylos	46	0.988	ns	4	*later*	ns	3	*none*
Balsamorhiza	18	0.537	ns	2	*later*	ns	1	*later*
Calochortus	42	0.195	ns	8	*later*	ns	5	*later*
Calycadenia	16	0.721	0.004	3	*earlier*	ns	2	*later*
Ceanothus	52	0.643	0.001	9	*later*	ns	3	*earlier*
Cirsium	46	0.336	0.086	6	*later*	ns	2	*later*
Collinsia	17	0.522	0.074	6	*later*	ns	1	*later*
Ericameria[1]	22	0.536	ns	4	*earlier*	ns	1	*earlier*
	22	0.724	ns	4	*later*	ns	1	*earlier*
Eriogonoideae	129	0.203	0.001	9	*earlier*	ns	3	*later*
Erythronium	20	0.471	0.076	3	*earlier*	ns	1	*none*
Iris	19	0.666	0.009	4	*later*	ns	2	*earlier*
Layia	10	0.463	ns	1	*later*	ns	1	*later*
Lessingia	24	0.563	0.057	2	*later*	ns	2	*later*
Mimulus s.l.	71	0.163	ns	13	*later*	ns	1	*none*
Navarretia	35	0.327	ns	4	*earlier*	ns	3	*earlier*
Orthocarpus	5	0.729	ns	1	*earlier*	ns	1	*earlier*
Perideridea	16	0.274	ns	4	*later*	ns	2	*later*
Sanicula	14	0.253	ns	4	*earlier*	ns	1	*later*
Sidalcea	40	0.510	0.053	6	*earlier*	ns	1	*earlier*
Thelypodieae	51	0.722	0.019	8	*later*	0.002	4	*later*
Trichostema	11	1.221	0.028	3	*later*	ns	1	*later*
Trifolium	51	0.425	0.001	12	*later*	ns	1	*later*

[1] Two taxa in *Ericameria* have spring flowering times while the rest flower in the fall. Analyses were repeated by coding this as a shift to earlier flowering time (top values) or to a later flowering time (bottom values).

Table 1.2. Estimated free parameters, log likelihoods, and information criteria of three possible models of flowering time evolution on serpentine for each of 23 clades of angiosperms: An Ornstein-Uhlenbeck (OU) model with a single flowering time optimum, an OU model with separate optima for lineages that can grow on serpentine versus lineages excluded from serpentine (Hansen), and a Brownian motion (BM) model. Two spring-flowering species of *Ericameria* were omitted from the analysis because all other sampled taxa in the genus are fall flowering. The best-supported OU model for each support criterion for each genus is printed in bold. Underlined values indicate that the Brownian motion model was preferred over both OU models. Analyses were performed using the OUCH package (v. 2.8-2) of the statistical program R (v. 2.15.1).

	One Optimum OU				**Two optima OU (Hansen)**					**Brownian motion**		
Clade	θ	ln(L)	AIC	SIC	$\theta_{\text{non-serp.}}$	$\theta_{\text{serp.}}$	ln(L)	AIC	SIC	ln(L)	AIC	SIC
Allium	6.09	-70.76	**147.51**	**153.37**	6.34	5.87	-70.51	149.01	156.82	-73.18	150.36	154.26
Aquilegia	7.25	-20.88	**47.77**	**50.60**	7.26	7.24	-20.88	49.77	53.54	-21.10	46.19	48.08
Arctostaphylos	3.08	-60.52	127.05	**132.53**	2.91	3.44	-59.09	**126.18**	133.49	-59.90	123.80	127.46
Balsamorhiza	6.01	-13.42	**32.85**	**35.52**	6.10	5.80	-12.79	33.59	37.15	-16.55	37.11	38.89
Calochortus	6.23	-51.93	**109.85**	**115.06**	6.33	6.18	-51.79	111.58	118.53	-63.69	131.38	134.85
Calycadenia	7.63	-8.97	**23.95**	**26.26**	7.68	7.54	-8.93	25.85	28.94	-10.68	25.35	26.90
Ceanothus	4.67	-67.90	**141.79**	**147.65**	4.66	4.69	-67.90	143.79	151.60	-69.10	142.20	146.11
Cirsium	7.61	-42.75	91.50	95.89	7.86	6.83	-39.77	**87.54**	**93.40**	-47.48	98.95	101.89
Collinsia	5.78	-20.09	**46.17**	**48.67**	5.72	5.86	-20.05	48.09	51.43	-22.57	49.14	50.80
Ericameria	9.53	-24.39	**54.78**	**57.77**	9.53	9.61	-24.39	56.78	60.76	-26.97	57.94	59.93
Eriogonoideae	5.22	-214.94	**435.88**	**444.46**	7.26	7.35	-214.94	437.87	449.31	-231.22	466.43	472.15
Erythronium	5.33	-28.28	**62.55**	**65.54**	5.42	5.22	-28.23	64.46	68.44	-30.49	64.98	66.97
Iris	5.62	-16.38	**38.75**	**41.59**	5.60	5.64	-16.37	40.74	44.52	-18.70	41.40	43.29
Layia	5.66	-20.98	**47.97**	**51.10**	5.65	7.60	-20.94	49.88	54.06	-19.41	42.82	44.91
Lessingia	8.78	-29.87	**65.73**	**69.27**	8.61	9.37	-29.25	66.51	71.22	-31.82	67.64	70.00
Mimulus s.l.	6.00	-106.04	**218.07**	**224.86**	6.00	6.02	106.03	220.07	229.12	-128.97	261.94	266.46
Navarretia	6.31	-39.57	**85.15**	**89.81**	6.24	6.55	-39.07	86.15	92.37	-49.07	102.15	105.26
Perideridea	7.35	-20.27	46.53	**48.85**	6.46	7.61	-19.21	**46.42**	49.51	-23.09	50.17	51.72
Sanicula	4.81	-14.78	**35.57**	**37.48**	5.10	4.67	-14.16	36.33	38.88	-20.95	45.89	47.17
Sidalcea	6.39	-56.93	**119.86**	**124.93**	6.36	6.49	-56.89	121.78	128.54	-60.80	125.60	128.98
Thelypodieae	5.52	-78.42	162.84	168.64	5.34	6.73	-75.46	**158.92**	**166.65**	-81.51	167.01	170.88
Trichostema	8.12	-11.83	**29.66**	**30.85**	8.03	9.69	-11.65	31.29	32.88	-10.88	25.77	26.56
Trifolium	6.03	-72.98	151.95	157.75	6.32	5.06	-70.49	**148.99**	**156.71**	-76.49	156.98	160.84

θ, flowering time optimum, reported in months of the calendar year (1.0=Jan 1); ln(L), log-likelihood; AIC, Akaike Information Criterion; SIC, Schwartz Information Criterion.

Table 1.3. Estimated free parameters for three models of flowering time evolution on serpentine for 23 clades of angiosperms. The three models compared are an Ornstein-Uhlenbeck (OU) model with a single flowering time optimum, an OU model with separate optima for lineages growing on and off of serpentine (Hansen), and Brownian motion. Free parameters were estimated separately for each clade using the OUCH package (v. 2.8-2) of the statistical program R (v. 2.15.1).

	One optimum OU		Two optima OU (Hansen)		Brownian motion
Clade	**α**	**σ^2**	**α**	**σ^2**	**σ^2**
Allium	2.41	7.47	2.69	7.84	4.67
Aquilegia	2.83	2.99	2.84	2.99	0.59
Arctostaphylos	2.45	4.00	2.21	3.40	0.84
Balsamorhiza	138.74	72.22	73.00	35.42	0.79
Calochortus	26.14	36.98	28.60	39.97	4.83
Calycadenia	2.96	1.69	2.95	1.68	0.91
Ceanothus	1.39	3.39	1.39	3.38	2.05
Cirsium	6.06	11.10	8.92	12.97	3.78
Collinsia	6.42	8.50	7.45	9.70	1.97
Ericameria	3.29	4.77	3.26	4.73	1.98
Eriogonoideae	5.22	24.00	5.35	24.00	12.33
Erythronium	3.68	8.27	3.76	8.39	3.08
Iris	3.92	2.98	3.95	3.00	1.25
Layia	0.27	1.16	0.27	1.15	0.98
Lessingia	2.98	5.04	3.48	5.34	2.55
Mimulus s.l.	74.81	173.68	73.59	170.86	9.47
Navarretia	10.69	12.05	10.70	11.72	2.01
Perideridea	6.84	13.33	7.50	12.44	5.96
Sanicula	16.83	16.30	258.70	229.13	2.40
Sidalcea	3.48	7.66	3.52	7.72	2.91
Thelypodieae	2.70	7.66	3.53	8.43	3.56
Trichostema	0.55	1.45	0.59	1.44	1.05
Trifolium	2.62	7.81	3.36	8.38	4.03

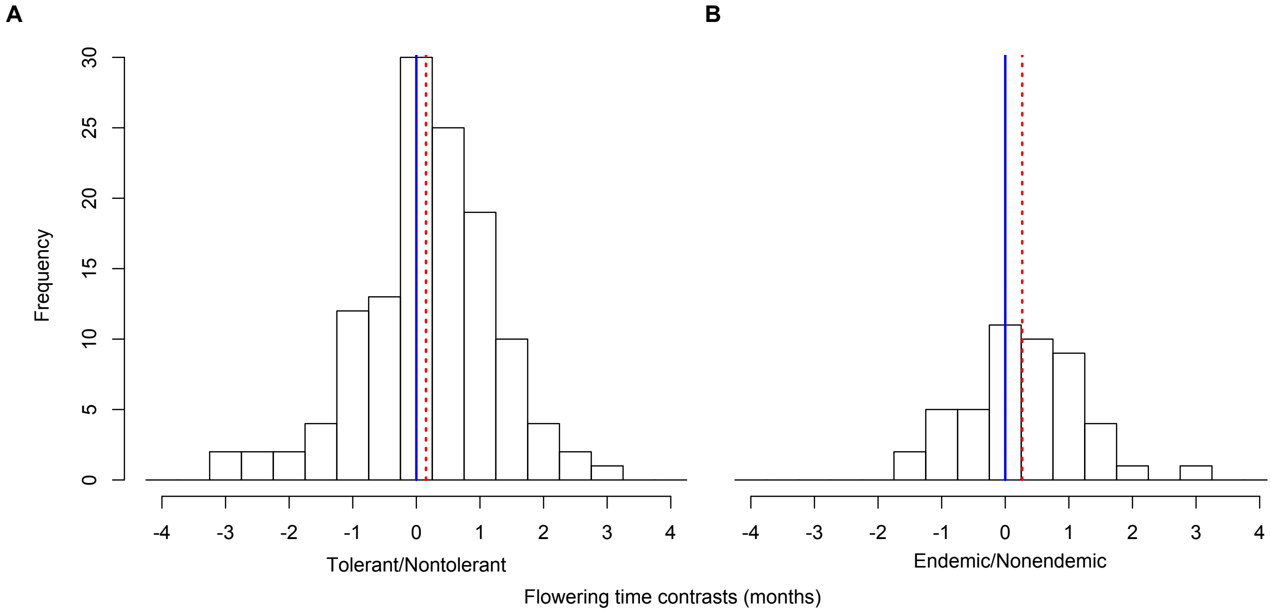

Fig. 1.1. Distribution of phylogenetically independent contrasts (PICs) of average flowering time for 24 clades of angiosperms in which there was a transition between **(A)** serpentine tolerance and exclusively non-serpentine occurrence (N=126), and **(B)** serpentine endemism and non-endemism (N=48). Positive contrasts represent the number of months later that the tolerant or endemic lineage flowers compared to its non-serpentine or non-endemic sister lineage. Blue solid lines indicate a value of zero; red dashed lines indicate the mean of all contrasts. PICs were calculated using the aot module of Phylocom 4.2.

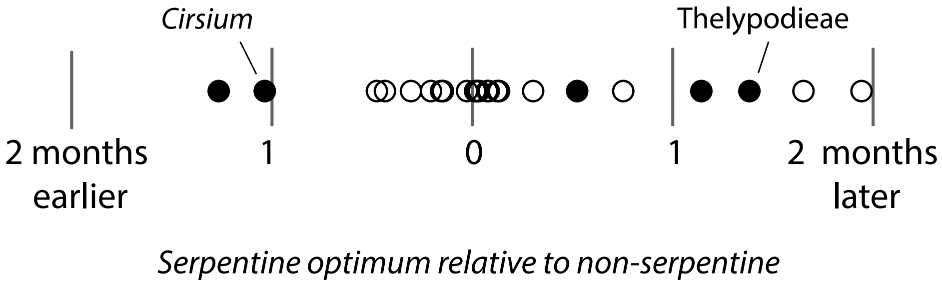

Fig. 1.2. Difference in estimated optimal flowering times of serpentine-tolerant lineages compared to non-tolerant lineages for 23 clades of angiosperms. Filled circles indicate clades for which a two-optimum model was preferred over a single-optimum OU model using the AIC, and circles are labeled if ΔAIC > 3.

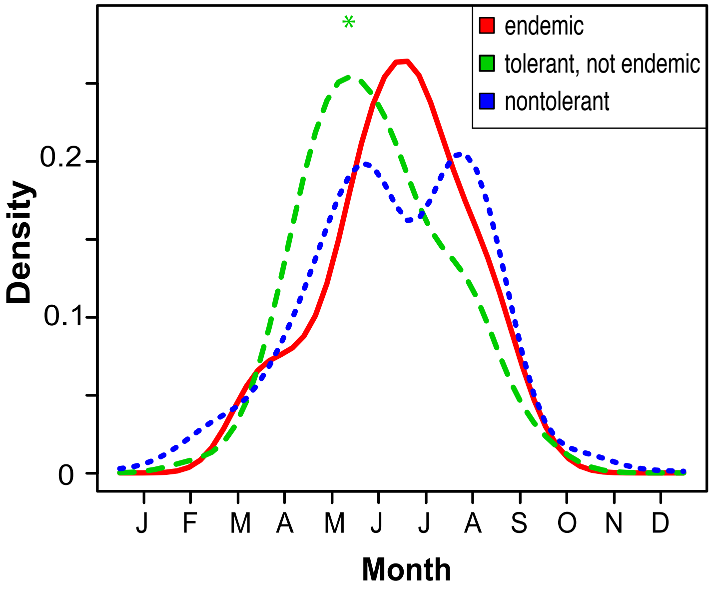

Fig. 1.3. Density plot of median flowering times for 1088 minimal-ranked taxa from 26 distinct clades found in California. Separate curves indicate serpentine endemics (red solid line, n=94), non-endemic serpentine tolerant taxa (green dashed line, n=221), and non-tolerant taxa (blue dotted line, n=773). Asterisk indicates significantly different mean flowering time from other distributions (Bonferroni-corrected Wilcoxan signed rank test, p < 0.02).

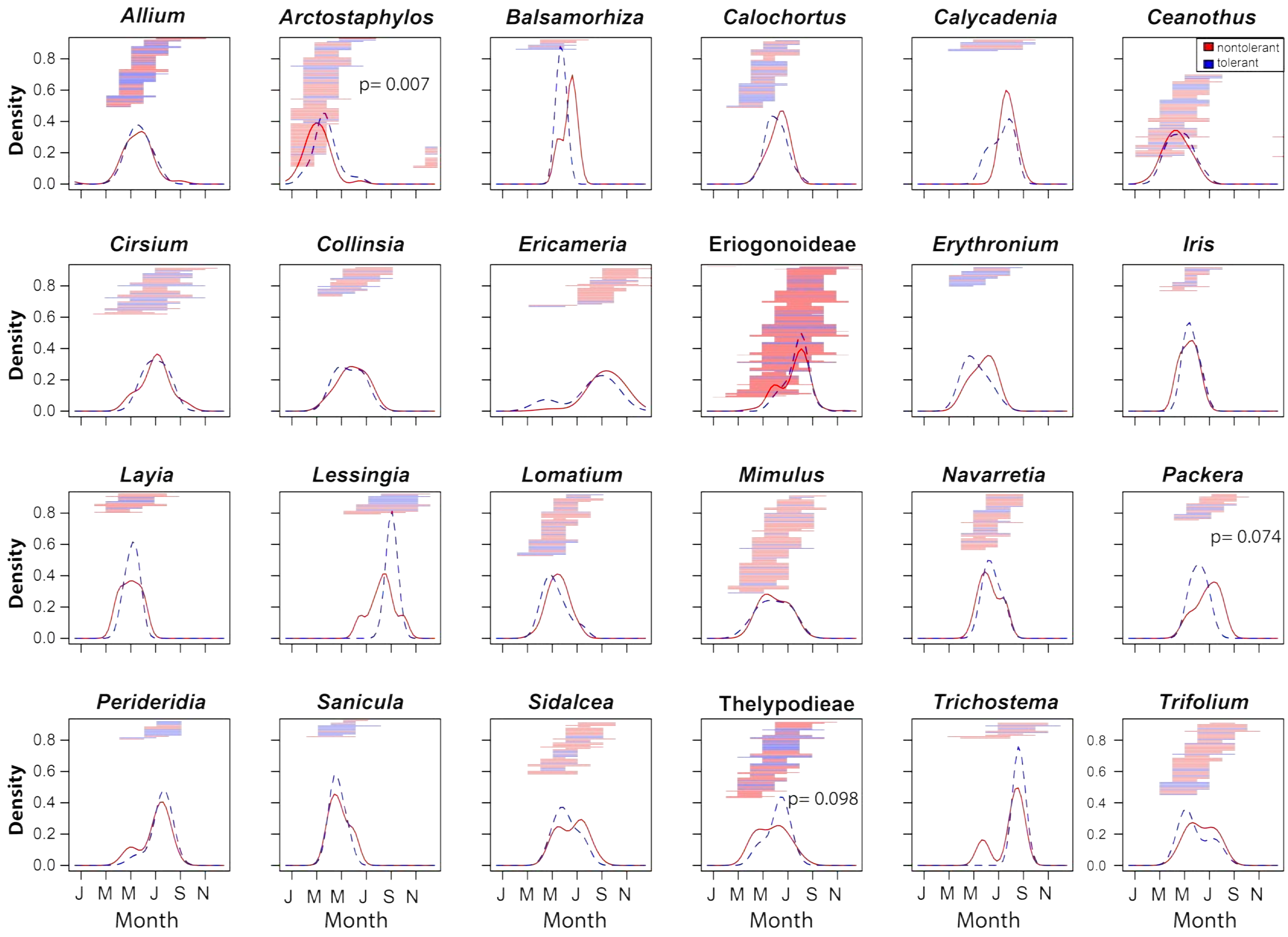

Fig. 1.4. Median flowering time density plots for serpentine tolerant (including endemics; blue dashed line) and non-tolerant plants (red solid line) of all California species in each of 24 clades of angiosperms (p-value from a two sample t-test shown if < 0.1). Colored bars represent flowering time ranges of each individual species. The genera *Orthocarpus* and *Aquilegia* were not included due to low sample sizes. Instead, *Lomatium* (Apiaceae) and *Packera* (Asteraceae), which have extensive diversity on California serpentine but lack well-resolved phylogenies, are shown.

CHAPTER 2:

Host-endemism and cryptic host-specific diversity among New World broomrapes

ABSTRACT

The broomrapes, *Orobanche s.l.* (Orobanchaceae), are common root-parasites found across Eurasia, Africa, and the Americas. All species native to the western-hemisphere, recognized as *Orobanche* sections *Gymnocaulis* and *Nothaphyllon*, form a clade that has a center of diversity in western North America, but also includes four disjunct species in central and southern South America. The wide ecological distribution coupled with moderate taxonomic diversity make this clade a valuable model system for studying the role, if any, of host switching in driving the diversification of plant parasites.

To infer a detailed phylogeny, two spacer regions of ribosomal nuclear DNA (ITS+ETS), three plastid regions, and one low-copy nuclear gene were sampled from 163 exemplars of *Orobanche* from across the native geographic and host ranges of currently accepted species. Together with comprehensive data on the parasites' native host ranges, associations between phylogenetic lineages and host specificity are tested.

Within the two currently recognized two species of *O.* sect. *Gymnocaulis,* seven strongly supported clades were found. Although regionally sympatric, members of these clades each had unique host associations. Strong support for cryptic host-specific diversity was also found in sect. *Nothaphyllon,* while other taxonomic species were well supported. This phylogenetic evidence supports a strong link between host specificity and host switching and diversification of parasitic plants.

INTRODUCTION

Parasitism is a highly successful life strategy that has evolved independently over sixty times among animals, at least twelve times among angiosperms, and repeatedly in protozoans and prokaryotes (Poulin and Morand 2000, Westwood et al. 2010). While the evolutionary significance of host-parasite associations has long been recognized (Kellogg 1913), the main evolutionary mechanisms involved in the generation and maintenance of such ecological and phylogenetic diversity are still poorly understood, especially among parasitic flowering plants (de Vienne et al. 2013, Joel et al. 2013).

The parasitic broomrapes, *Orobanche* sensu lato (s.l., alternatively circumscribed as the genera *Aphyllon* and *Myzorrhiza* in the New World and *Boulardia*, *Orobanche* sensu stricto (s.s.). and *Phelipanche* in the Old World: Schneeweiss 2013), have attracted significant attention as an important system for understanding the evolutionary consequences of parasitism. This attention is in part a result of their extensive worldwide diversity (at least 170 species; Ulrich et al. 1995), a detailed and well-supported understanding of their placement within the family Orobanchaceae as well as the relationships among major clades (Schneeweiss et al. 2004a, Park et al. 2008, McNeal et al. 2013, Schneeweiss 2013), and the significant economic damage caused by several Eurasian species to major agricultural systems worldwide (Joel et al. 2013).

Despite general interest in this group, relatively little is known about the role of host specificity in broomrape diversification. Understanding host-specificity of parasites is predicated on a comprehensive understanding of lineage boundaries in the host (e.g. Labrousse et al. 2001, Timko et al. 2012) and, more importantly for *Orobanche,* the parasite. That is, failure to recognize evolutionary diversity in the parasite results in an overestimation of host breadth and may limit the ability to understand the evolutionary processes responsible for speciation in plant parasites. Therefore, it is important to distinguish true host generalists from taxa that comprise several cryptic lineages artificially united on the basis of superficial similarity but distinguished genetically and ecologically. Host specificity to the family or genus level has been cited as a key factor in the differentiation and genetic isolation of three subspecies of the European *O. minor* (Thorogood et al. 2008, 2009), but this has not been broadly tested across other *Orobanche* lineages. Several recently described species of *Orobanche* in North America also have unique host preferences in the Asteraceae: *Orobanche riparia* parasitizes Helianthieae subtribe Ambrosiinae and *O. arizonica* parasitizes *Gutierrezia* spp. However, neither these species concepts nor those of the other American *Orobanche* species have ever been tested phylogenetically.

Inclusion of western hemisphere *Orobanche* (sections *Gymnocaulis* and *Nothaphyllon*) in phylogenetic studies has been limited to several exemplars included in larger genus- or family- level analyses. These studies, supported by karyological and morphological evidence, have shown that these two sections are sister groups and together are sister to an Old World clade corresponding to *Orobanche* sect. *Trionychon* (Schneeweiss et al. 2004a, Park et al. 2008), sometimes treated as the genus *Phelipanche* (Schneeweiss 2013). This larger clade is supported by a shared base chromosome base number of $x = 12$ (Heckard and Chuang 1973, Schneeweiss et al. 2004b).

Ecologically, *Orobanche* sections *Gymnocaulis* and *Nothaphyllon* parasitize a wide range of eudicot hosts, but most commonly perennial Asteraceae. Taxonomic diversity is concentrated in the California Floristic Province; however, species can be found across the Americas, as far north as the Alaska Peninsula and the Yukon Territory, east to Newfoundland, and south to central Mexico. Four poorly known species are found in South America. Affinities between South American *Orobanche chilensis* and North American *O. ludoviciana* have long been recognized (Beck 1890), but explicit biogeographic hypotheses for this or other such relationships within the clade have yet to be proposed.

The wide ecological and host diversity among western hemisphere *Orobanche*, as well as its tractable taxonomic diversity make it a valuable model system for understanding the main ecological and evolutionary processes affecting parasite diversification and speciation. Such investigations, however, are requisite for a robust understanding of evolutionary lineages, their host breadths, and their relationships. Specifically our goals were to (1) reconstruct a well-resolved phylogeny of western hemisphere *Orobanche* that could be used to develop a revised, natural taxonomy for the group, (2) evaluate the evolutionary significance of host switching in *Orobanche* sect. *Gymnocaulis* by comprehensively sampling across the geographic and host ranges of each taxon, (3) test the monophyly of longstanding taxa as well as recently described segregates, and (4) infer biogeographical relationships between North American and South American *Orobanche* spp.

MATERIALS AND METHODS

Taxon and population sampling— A total of 163 *Orobanche* populations were sampled either from fresh collected tissue or from herbarium collections: 57 from sect. *Gymnocaulis* and 106 from sect. *Nothaphyllon*. This data set includes at least one exemplar of all taxa of *Orobanche* recognized within the last 75 years except for *O. weberbaueri*, a poorly known taxon from southern coastal Peru, perhaps known only from the type. Denser population sampling across sect. *Gymnocaulis* enabled more comprehensive geographic and host-range sampling in the two currently recognized species of this section, *O. fasciculata* and *O. uniflora* (Fig. 2.1). Identifying the host-breadth for each taxon was challenging, as many collectors note the nearest living plant as the host species without confirming a haustorial connection, resulting in a proliferation of dubious records. Our criteria for accepting a host was that a host taxon must have been independently reported at several populations by more than one collector, or a haustorial connection to an identifiable fragment of host must be present on the herbarium voucher. For molecular phylogenetic analyses, one individual each of *O. gracilis* and *O. hederae* were used as outgroup (Park et al*.* 2008, McNeal et al. 2013). Sequence data for the *waxy* locus were not available for these outgroups, so instead two more distantly related outgroup taxa were used, *Castilleja ambigua* and *Triphysaria versicolor*. Specimen vouchers and host information are provided in Appendix B.

DNA extraction, amplification, and sequencing— DNA was extracted from dried floral tissue using a DNeasy Plant Mini Kit (Qiagen, Valencia, California), or using a CTAB protocol (Doyle and Doyle 1987). A total of six regions from the nuclear and plastid genomes were used to estimate the phylogeny: internal and external transcribed spacers of nuclear ribosomal DNA (ITS and ETS, respectively), introns 9–11 of the nuclear low-copy gene *waxy*, as well as the plastid trnL-trnF region (comprising the *trnL*$_{\text{UAA}}$ intron and the *trnL*$_{\text{UAA}}$-*trnF*$_{\text{GAA}}$ intergenic spacer) and the *matK* and *rps*2 genes. ITS, *matK*, and *rps*2 were selected based on their prior use in genus and family-level phylogenetic studies of *Orobanche* (Schneeweiss et al. 2004a, McNeal et al. 2013), and *waxy* for its use in the related hemiparasitic genus *Castilleja* (Tank and Olmstead 2008). The remaining two regions, ETS and trnL-trnF, were selected to provide additional rapidly evolving characters from the nuclear and plastid compartments, respectively. Due to difficulty assessing homology within some species of sect. *Nothaphyllon*, the *waxy* locus was mainly used to assess monophyly of sect. *Nothaphyllon* and to infer relationships within sect. *Gymnocaulis.*

Polymerase chain reaction (PCR) amplifications were performed using AccuPower PCR PreMix kits (Bioneer, Alameda, California) or by generating a master mix of 10 μL 5× Promega buffer, 4 μL of 25 mM $MgCl_2$, 1.25 μL of 10 mM dNTPs, 1 μL of 20 μM of each primer, and 0.25 μL of Go-Taq DNA Polymerase (Promega, Madison, Wisconsin) diluted to 50 μL. Complete information about primers, cycling parameters, and amplicon sizes are provided in Table 2.1. PCR products were purified using ExoSAP (USB Products, Cleveland, Ohio), and both DNA strands were sequenced using an ABI 3730 DNA analyzer (Applied Biosystems, Foster City, California). GenBank accession numbers for each sample are provided in Appendix A.

Sequence alignment and phylogenetic reconstruction— Sequences were checked for base-calling errors and assembled into contigs using Geneious v. 6.1.7 (Biomatters, Auckland, New Zealand). Sequence alignments were generated using the MUSCLE plug-in with default settings. Maximum likelihood (ML) and Bayesian inference (BI) analyses were conducted separately on the concatenated chloroplast DNA matrix (cpDNA), the concatenated ribosomal spacers (nrDNA), and the *waxy* locus using the CIPRES Science Gateway (Miller et al. 2010). The ML analyses were performed with RAxML-HPC2 v.8.2.6 (Stamatakis 2014) using the GTRCAT model with 25 rate categories and 1,000 rapid bootstrap (BS) replicates. The BI analyses were performed using MrBayes v. 3.2.6 (Ronquist et al. 2012). An AIC comparison implemented in jmodeltest2 (Darriba et al. 2002) was used to select a GTR + Γ substitution model (approximated using 4 rate categories). The estimated substitution rates for the nrDNA, cpDNA and *waxy* alignments were then used as priors in the MrBayes analysis. Default settings were used for other priors. Three independent runs of four chains each (one cold, three heated) were sampled every 1,000 generations for 2,500,000 generations. The first 20% of samples were discarded as burn-in. Convergence was assessed in several ways: the average standard deviation of split frequencies was <0.01, the potential scale reduction factor was close to 1.00 for all parameters, and the effective sample sizes (ESS) were >800.

RESULTS

Nuclear ribosomal DNA— Strongly supported clades in the Bayesian ITS/ETS analysis (Figure 2.1) were consistent with those identified by ML (data not shown). *Orobanche* sect.

Gymnocaulis and sect. *Nothaphyllon* were both resolved as monophyletic (Posterior probability (PP) =1.0, bootstrap support (BS)=100) and sister to each other. Within section *Gymnocaulis*, seven major clades were resolved (PP=1.0, BS ≥80). Under the current classification, three of these together correspond to a paraphyletic *O. fasciculata.* Plants from each of these clades showed unique host preferences: plants in two of these groups parasitize hosts of single genera, *Artemisia* (Asteraceae) and *Galium* (Rubiaceae). The third group of plants form a clade of generalists that parasitize numerous species within *Eriogonum* (Polygonaceae), *Eriophyllum* (Asteraceae), and *Eriodictyon* and *Phacelia* (Hydrophyllaceae)*.* The remaining four clades constituted a monophyletic *O. uniflora* (PP=1.0, BS=100). Three of these clades include parasites specific to hosts in the genera *Antennaria* and *Senecio* (Asteraceae)*,* on members of Saxifragaceae and Crassulaceae (Saxifragales s.s.), and on Apioideae (Apiaceae), respectively. These clades together are currently recognized as *O. uniflora* subsp. *occidentalis* and were resolved sister to the fourth clade corresponding to subsp. *uniflora*. Members of this clade parasitize *Rudbeckia* and several genera of Astereae in the Asteroideae.

Populations of the remaining American *Orobanche* species, representing sect. *Nothaphyllon,* were generally resolved in one of eight major clades (PP > 0.95, BS > 90): (1) A clade of populations from the western United States parasitic on *Artemisia* previously determined as one of three taxa: *O. parishii* subsp. *parishii*, *O. ludoviciana*, or *O. corymbosa*; (2) a taxonomically and ecologically diverse clade, the *O. californica* complex, which included *O. californica* and *O. vallicola*, as well as the remainder of *O. parishii* and *O. corymbosa* populations; (3) *O. pinorum*; (4) *O. tarapacana*; (5) the *Orobanche ludoviciana* complex, including *O. multiflora, O riparia*, *O. chilensis*, *O. tacnaensis, O arizonica*, the remainder of *O. ludoviciana,* and a collection from Hidalgo, Mexico (Yatskievych 85-215) that does match the morphology of any described species; (6) *O. valida*; (7) *O. cooperi* and *O. dugesii*; (8) *O. bulbosa*. Clades 6–8, found predominantly in southwestern North America, constituted a monophyletic group (PP=0.95, BS=77) that was sister to the rest of the section (clades 1–5). Resolution at the subspecific level of the paraphyletic *O. californica* was variable. For example, populations of subsp. *californica* along the central California coast parasitizing *Grindelia stricta* and those in far northern California and Washington parasitizing *Grindelia integrifolia* were resolved in separate strongly supported sub-clades within the *O. californica* complex (clade 2, above). Other subspecies, such as subsp. *grandis* and subsp. *condensa*, formed a polytomy. The polyploid *O. parishii* subsp. *brachyloba* was nested within one of three separate clades of *O. parishii* subsp. *parishii*.

***Plastid DNA*—** Strongly supported clades from the Bayesian analysis of three plastid regions (Fig. 2.2) were consistent with those identified by ML (data not shown). *Orobanche* sect. *Gymnocaulis* was resolved as monophyletic (PP=1.0, BS=100). Within sect. *Gymnocaulis*, six host-specific clades were resolved, congruent with the nrDNA results. Three of these were sub-clades of the monophyletic *O. uniflora* (PP=0.99, BS=97): a clade of plants parasitizing *Antennaria* and *Senecio* (PP=1.0, BS=93) and a less supported clade of plants parasitizing Apioideae (Apiaceae), Saxifragaceae and Crassulaceae (PP=0.71, BS=88), together corresponding to subsp. *occidentalis* (PP=1.0, BS=100) and sister to a clade of plants that parasitize several genera of Asteroideae corresponding to subsp. *uniflora* (PP=1, BS=100). *Orobanche fasciculata* was found to be paraphyletic: A strongly supported clade parasitizing *Artemisia* (PP=1.0, BS=100) was resolved sister to *O. uniflora*.

The remaining two clades of *O. fasciculata* were resolved as sister groups, one strongly supported and parasitizing *Galium* spp. in California and Oregon (PP=1.0, BS=100), and the other weakly supported and parasitizing a variety of distantly related core eudicot genera (PP= 0.65, BS <50).

Deep relationships within *Orobanche* sect. *Nothaphyllon* were generally well-resolved, albeit with variable support at the species and subspecies level. Populations of *O. bulbosa* formed a clade (PP=1.0, BS= 96) that was sister to the remainder of the section, which in turn was comprised of two well-supported subclades (PP=1.0, BS >95). The first included strongly supported clades corresponding to single taxa that diverged from the remainder of the subclade in succession: *O. valida* (PP=1.0, BS=100), *O. parishii* (PP=1.0, BS=100), and finally *O. tarapacana* (PP= 0.94, BS=72), which was sister to a clade of *O. cooperi, O. dugesii*, and one accession of *O. corymbosa* (PP=0.98, BS=68). The second well-supported subclade included the only sampled population of *O. pinorum* sister to the *O. californica* and *O. ludoviciana* complexes. Relationships within this subclade were poorly resolved, except for strong support of *O. riparia* + *O. arizonica*, *O. vallicola*, a clade of *O. californica* subsp. *californica* parasitic on *Eriophyllum staechadifolium*, and *O. chilensis* + several populations from central North America (PP=1.0, BS > 97).

waxy *locus*— *Orobanche* sect. *Gymnocaulis* and sect. *Nothaphyllon* were each resolved as monophyletic (PP=0.99, BS >75). Within sect. *Gymnocaulis,* five host-specific clades were resolved with strong support (PP > 0.92, BS > 73), congruent with both nrDNA and cpDNA results. These included a clade of plants parasitizing several genera in the Asteroideae corresponding to *O. uniflora* subsp. *uniflora*, as well as two clades together corresponding *O. uniflora* subsp. *occidentalis*— the first, which was comprised of plants parasitizing Saxifragaceae and Crassulaceae (Saxifragales s.s), and another that included a subclade of parasites on *Antennaria* and *Senecio* (Asteraceae) united in a moderately supported polytomy with several populations that parasitize Apioideae (PP= 0.89, BS= 0.74). The remaining two strongly supported clades include plants currently recognized as *O. fasciculata*: one was sister to *O. uniflora* and parasitizes *Artemisia*; the other parasitizes *Galium* and was sister to the remaining populations of *O. fasciculata*, which formed a third, weakly supported clade (PP=0.74, BS=67) including parasites on a variety of core eudicot hosts. In contrast to *Orobanche* sect. *Gymnocaulis*, infraspecific sampling density and phylogenetic resolution within *O.* sect. *Nothaphyllon* was limited, although conspecific populations of *O. valida, O. californica* subsp. *californica,* and *O. cooperi* as well as *O. chilensis* + *O. multiflora* were each resolved as monophyletic (PP > 0.94, BS > 90).

Tree files were uploaded to Open Tree of Life (http://www.opentreeoflife.org), study ID ot_732.

DISCUSSION

Host specificity and speciation— Among extant western hemisphere *Orobanche*, there exist many previously unrecognized, strongly supported host-specific lineages in both sect. *Gymnocaulis* and sect. *Nothaphyllon* that are strongly supported by both plastid and nuclear

DNA sequences (Figs. 2.1–2.3). This cryptic diversity has two complementary implications—one evolutionary, the other ecological. First, biodiversity within western hemisphere *Orobanche* is substantially richer than recognized by current taxonomy, perhaps because extensive reduction of structural characters in these parasites has limited the potential for morphological diagnosis of recently diverged evolutionary lineages. Second, the host breadth of each evolutionary lineage is narrower than previously assumed, although some lineages with wide host ranges are still present (e.g., *O. fasciculata* p.p.). Host-specificity in plant parasites has been correlated to various life history and other host traits such as weediness or perenniality (Schneweeis 2007). Host-switching has been cited as a driver of speciation of numerous parasites across the tree of life (Ricklefs et al. 2004, deVienne et al. 2013), including other lineages of parasitic plants (Norton and Carpenter 1998, Norton and Lange 1999, Bolin et al. 2011), as well as within the genus *Orobanche* (Thorogood et al. 2009). The evidence strongly supports this hypothesis. The abundance of host-specific clades found here suggests that host-switching may be an even more important driver of evolutionary divergence in parasitic plants than previously recognized.

Although some *Orobanche* taxa are specific to a single host species, most parasitize several closely related species that are unique and sometimes phylogenetically distant from the hosts of their nearest relatives. In many ways, *Orobanche* spp. occupy an ecological middle-ground between species like *Epifagus virginiana* (Orobanchaceae), which can only grow on *Fagus grandifolia*, and true generalists such as dodders (*Cuscuta* spp., Convolvulaceae) in which a single individual may parasitize numerous distantly related hosts (Press and Graves 1995). Therefore, it is unlikely that host-parasite co-speciation plays an appreciable role in driving diversification in western hemisphere *Orobanche* in contrast to some plant-animal, animal-animal, or prokaryote-animal host-parasite systems (de Vienne et al. 2013). Instead, that the more common mode—host switching followed by physiological specialization and divergence—appears to be dominant in this system.

Specialization and evolutionary divergence (cladogenesis) following host-switching is an expected outcome given the complex challenges of host detection, host invasion, and evasion or neutralization of host defenses, which may occur pre- or post-attachment. Pre-attachment host defenses may include reduced germination stimulants (i.e. strigolactones, Cameron et al. 2006, Xie et al. 2010), increased germination inhibitory compounds (Fernández-Aparicio et al. 2011), chemical inhibition of haustorial development (Pérez-de-Luque et al. 2005a, b), or structural fortifications to serve as a mechanical barrier to invasion. Potential hosts can repel parasitic plants following attachment using a variety of mechanisms that disrupt the flow of nutrients or block vessel elements (Goldwasser et al. 1999, 2000, Pérez-de-Luque et al. 2005a), initiate programmed cell death (Gurney et al. 2006), increase lignification and suberization of cell walls (Labrousse et al. 2001, Pérez-de-Luque et al. 2008), or elicit chemical defense through increased peroxidases or the transfer of toxins from the host to the parasite (Gurney et al. 2003). These multiple layers of incompatibility must be overcome for a successful invasion of the host, and provide the physiological basis for host specificity in parasitic Orobanchaceae (Yoder 1997, Yoshida and Shirasu 2009, Thorogood and Hiscock 2010). Consequently, distantly related hosts with more divergent physiologies likely require different invasion strategies. Various suites of host-specific traits may therefore represent different adaptive peaks for an *Orobanche* lineage.

Drès and Mallet (2002) cite a number of insect-plant systems to show how the formation of host-specific races may eventually lead to sympatric speciation of parasites through outbreeding depression, even in the presence of gene flow. The generalist clade of *O. fasciculata* shows poorly supported phylogenetic substructure and may provide the opportunity to explore this hypothesis in a plant-parasite system. Among the other host-specific clades of *O.* sect. *Gymnocaulis*, sympatric speciation following this model may already have occurred. The strong support for these clades by all three loci (nrDNA, cpDNA, and *waxy*) suggest minimal, if any, continued gene flow among these lineages, even between geographically neighboring populations. Isolation by host may also be reinforced by autogamy or apomixis, which is common in New World *Orobanche* species in contrast to more variable mating systems among species of Eurasian *Orobanche* and predominance of outcrossing among other lineages of parasitic angiosperms (Musselman et al. 1982, Jones 1989, Bellot and Renner 2013). Autogamy has been identified as the predominant mating system in *O. pinorum* with occasional outcrossing by bees (Ellis et al. 1999), is common among *O. fasciculata* parasitizing *Artemisia* (Reuter 1986), and has been anecdotally reported in *O. uniflora* subsp. *occidentalis and O. bulbosa* (K. L. Chambers 2952, OSC198410; Butterwick 5434 & Parfitt, ASU, JEPS; Schneider 1032, JEPS (Parfitt and Butterwick 1981)). Some populations of *Orobanche uniflora* subsp. *uniflora* are obligatorily parthenogenic, while other populations show a "wholly different…reproductive process" (Jenson 1951). As discussed previously, gene flow between different host-races is expected to be detrimental if parent taxa are adapted to separate hosts, since a hybrid may be adapted to neither of them.

Geographic differentiation may play a subordinate role in lineage diversification, and may be restricted to cases where sister clades parasitize closely related hosts, such as between the subspecies of *O. valida*, which both parasitize *Garrya*. Much more commonly, ranges are at least partially overlapping and closely related parasite lineages differing in their hosts can co-occur on a regional or even local scale. This is particularly well pronounced in sect. *Gymnocaulis*, discussed in detail below.

***Cryptic diversity in section* Gymnocaulis—**Cryptic lineages are found in both sections of New World *Orobanche* (e.g., a polyphyletic *O. parishii* subsp. *parishii* [Fig. 2.1]), but most extensively in *O.* sect. *Gymnocaulis*, in which over twice as many host-specific clades exist than commonly recognized taxa. Moreover, these cryptically distinct clades are often subtended by long stem branches relative to clades that represent different recognized species in sect. *Nothaphyllon.* This disparity, which is robust to the gene region(s) used (Figs. 2.1–2.3) may be due to more extensive reduction of morphological and thus diagnostic features in sect. *Gymnocaulis*, as well as more limited systematic and taxonomic study of this section (Achey 1933, Watson 1975) relative to sect. *Nothaphyllon* (Munz 1930, Collins 1973, Heckard 1973, Heckard and Chuang 1975, Collins and Yatskievich 2015). Similar levels of cryptic diversity may be found in other holoparasitic lineages, particular endoparasites like *Cytinus* (Cytinaceae) that show even more extensive morphological reduction than *Orobanche* and a more intimate host-parasite relationship (De Vega et al. 2008).

Each clade of *Orobanche* sect. *Gymnocaulis* shows at least partial range overlap with its sister group, with generally increasing overlap with decreasing phylogenetic distance (Fig. 2.4). The clade of *O. fasciculata* parasitic on *Galium* is entirely included within the range of its sister group, which is a generalist clade parasitic on various eudicot hosts. The clade of *O. fasciculata* parasitic on *Artemisia* grows coarsely sympatrically (i.e. sympatric at regional scales) with both subspecies of its sister group, *O. uniflora.* These subspecies, *O.* subsp. *uniflora* and *O.* subsp. *occidentalis*, once thought to be allopatric, are now known to co-occur based on a recent floristic discovery in southern British Columbia and subsequent reinterpretation of historic herbarium records. Most strikingly, the three closely related clades resolved within *O. uniflora* subsp. *occidentalis*, which parasitize species in the Asteraceae, Apiaceae, and Saxifragaceae plus Crassulaceae, respectively, share nearly entirely overlapping ranges at both coarse continental and local scales. For example, populations of all three clades can be found in Yosemite National Park and the adjacent Sierra National Forest.

Relationships in section **Nothaphyllon—** Host-specific species in sect. *Nothaphyllon* are also well-supported, including the recently described *O. arizonica*, *O. riparia,* and a clade currently recognized as *O. californica* subsp. *californica* that parasitzes *Eriophyllum stachaedifolium* on the central California coast, which is currently being described by the second author and George Yatskievych. Most other clades have distinct host associations, generally with perennial Asteraceae, but usually not specific to the species level (Fig. 2.1).

Most of the taxonomic diversity in *O.* sect. *Nothaphyllon* is concentrated in a large clade supported by nrDNA and cpDNA, which is composed of two subclades supported by nrDNA (Fig. 2.1) and morphological analysis (Heckard 1973, Collins 1973). The first subclade corresponds to the *O. californica* complex, which includes *O. californica* and its subspecies*, O. parishii, O. corymbosa,* and *O. vallicola.* The second clade represents the *O. ludoviciana* complex, which includes *O. ludoviciana* (except for populations parasitizing *Artemisia*), *O. multiflora,* the recently described *O. arizonica*, *O. riparia,* the disjunct South American species *O. chilensis* and *O. tacnaensis,* and a collection from Hidalgo, Mexico that does not fit the description of any described taxon (Yatskievych 85-215, ARIZ).

Several earlier-diverging lineages native to western North America are also strongly supported as monophyletic by both nrDNA and cpDNA, including *O. valida*, *O. bulbosa* and the recently revised *O. cooperi + O. dugesii* complex (Figs. 2.1, 2.2; Collins and Yatskievych 2015). However, relationships among these lineages are unclear: *O. bulbosa* is either resolved as sister to the rest of the section (nrDNA, Fig. 2.1) or as a grade with *O. bulbosa* diverging earliest (cpDNA, Fig. 2.2). The conflict among gene partitions is in most cases likely explained by incomplete lineage sorting, but in other cases may be a result of reticulate evolution. For example, based on its phylogenetic placement in two separate clades (Fig. 2.1), and morphological and host affinities (*Artemisia,* especially *A. tridentata*), *O. corymbosa* may represent a hybrid between *O. californica* and *O. ludoviciana*, both of which in part also parasitize *Artemisia.* In certain other cases, polyploidy may be a driver of speciation. Heckard and Chuang (1975) published detailed chromosome counts for most species. The octoploid *O. parishii* subsp. *brachyloba* forms a clade nested within *O. parishii* subsp. *parishii* (Fig. 2.1), its likely tetraploid progenitor (ploidy assignment based on chromosome base number of $x = 12$; for a more detailed discussion see Schneeweiss et al. 2004b), or if an allopolyploid, one of two parental lineages. Octoploid lineages have also been reported in *O. cooperi* and *O. corymbosa* subsp. *corymbosa* (but not *O. ludoviciana*). A full discussion of the systematics and taxonomy of these and other individual species is needed, but is beyond the scope of this study.

***Repeated dispersal to South America*—**The nrDNA phylogeny is evidence supporting the longstanding hypothesis that *O. chilensis* is closely related to *O. ludoviciana* and *O. multiflora* (Beck 1890), thereby contributing to the broadly recognized pattern amphitropical disjunction between the Great Plains of North America and northern Chile/southern Peru (Wen and Ickert-Bond 2009). Of the two other sampled *Orobanche* species from South America, *O. tacnaensis* was resolved with *O. chilensis*, but the two samples of *O. tarapacana* Phil. formed a separate, earlier-diverging lineage resulting from north-to-south dispersal. Phylogenetic placement of *O. tarapacana* is uncertain due to conflict between the nrDNA and cpDNA trees; *O. tarapacana* is sister to either the *O. ludoviciana* complex*,* the *O. cooperi* complex, or perhaps a hybrid between the two (Figs. 2.1, 2.2). The historical biogeography of these species and their hosts is investigated more thoroughly in Chapter 4.

CONCLUSIONS

Parasitic Orobanchaceae provides an exciting opportunity, and is becoming a model system for understanding plant parasitism at various levels of biological organization and scale (Joel et al. 2013, McNeal et al. 2013, Wicke et al. 2013, Yang et al. 2015). These results emphasize the importance of substrate endemism in the form of host specificity and host-switching as a driver of evolutionary divergence in obligate plant parasites. At least twice as many host-specific lineages exist in *O.* sect. *Gymnocaulis* compared to recognized taxa, and denser sampling in other clades such as *O.* sect. *Nothaphyllon* is likely to uncover more. This robust understanding of fine-scale evolutionary relationships provides the necessary phylogenetic framework to develop a more natural classification for this group, and understand genetic, ecological, functional, and life-history consequences of host-parasite associations more broadly.

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Table 2.1. Molecular regions used in the phylogenetic analyses of *Orobanche* sections *Gymnocaulis* and *Nothaphyllon*, approximate lengths of complete ingroup sequences, PCR primers (5'–3'), and thermocycling parameters. Two different forward primers for *rps*2 were used.

Gene region	**Approx. amplicon length**	**Primer sequences (5' – 3')**	**Reference**	**Thermocycling parameters**
ITS	590 bp	AB_101: TGG TCC CGT GAA GTG TTC G AB_102: CCG GTT CGC TG CCG TAA C	Schneeweiss et al. 2004a Schneeweiss et al. 2004a	94°C, 4min; 35x (95°C, 1 min; 48°C, 1 min; 72°C, 1 min); 72°C, 10min.
ETS	430 bp	ETS_B: ATA GAG CGC GTG AGT GGT G ETS_seq: (C) TGG CAG GAT CAA CCA GGT A	Beardsley and Olmstead, 2002 *(this dissertation)*	96°C, 2 min; 35x (94°C, 30s; 56°C, 30s; 72°C, 45s); 72°C, 3 min.
waxy (introns 9-11)	585-630 bp	waxy_9F-ORO: GAT GCT AAG CCW TTG TTG A waxy_11R: CCA TRT GGA ASC CAG TRT A	*(this dissertation)* Tank and Olmstead, 2009	92°C, 5min; 40x (94°C, 45s; 53.5°C, 45s; 72°C, 1min); 72°C, 5min.
matK 3' intron	680-760 bp	matK 8: CTT CGA CTT TCT TGT GCT matK_psbA5'R: AAC CAT CCA ATG TAA AGA CGG TTT	Steele and Vilgalys, 1994 Shaw et al. 2005	94°C, 5min; 40x (92°C, 1min; 51°C, 40s; 72°C, 1min); 72°C, 10min.
rps2	675 bp	rps2_2F: AAA TGG AAT CCT AAA ATG GC rps2_18F: GGR KAR AAA TGA CAA GAA GAT ATT GG rps2_661R: ACC CTC ACA AAT GCG AAT ACC AA	*(this dissertation)* dePamphilis et al. 1997 dePamphilis et al. 1997	94°C, 2min 30s; 35x (94°C, 1min; 50°C, 1min; 72°C, 1min); 72°C, 7min.
trnL–trnF spacer	710-810 bp	trnL 'c': CGA AAT CGG TAG ACG CTA CG trnF 'f': ATT TGA ACT GGT GAC ACG AG	Taberlet et al. 1991 Taberlet et al. 1991	94°C, 5min; 40x (92°C, 1min; 51.5°C, 1min; 72°C, 1min); 72°C, 5 min.

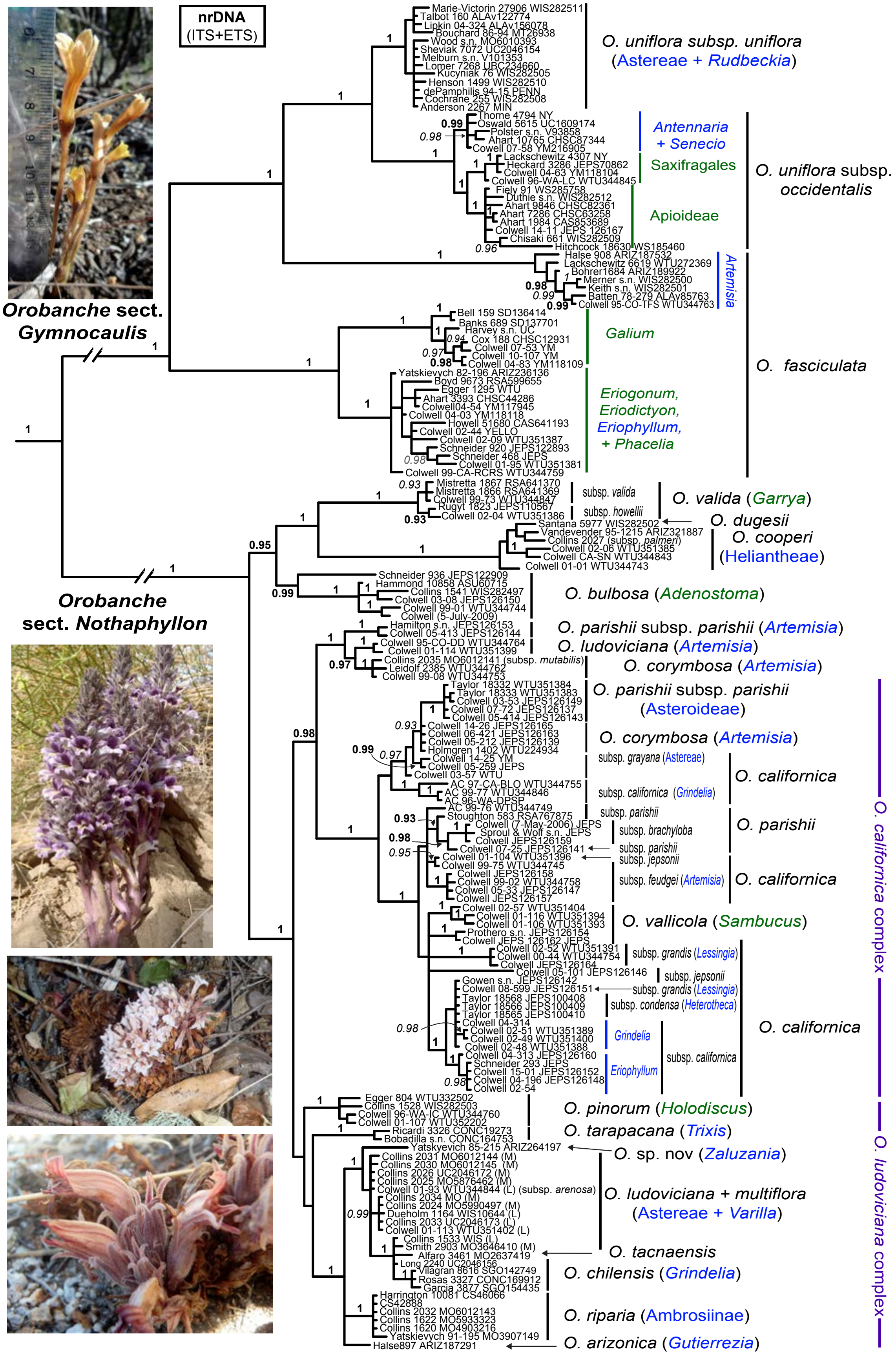
nrDNA
(ITS+ETS)
Orobanche sect. Gymnocaulis
Orobanche sect. Nothaphyllon
Marie-Victorin 27906 WIS282511
Talbot 160 ALAv122774
Lipkin 04-324 ALAv156078
Bouchard 86-94 MT26938
Wood s.n. MO6010393
Sheviak 7072 UC2046154
Melburn s.n. V101353
Lomer 7268 UBC234660
Kucyniak 76 WIS282505
Henson 1499 WIS282510
dePamphilis 94-15 PENN
Cochrane 255 WIS282508
Anderson 2267 MIN
O. uniflora subsp. uniflora
(Astereae + Rudbeckia)
Thorne 4794 NY
Oswald 5615 UC1609174
Polster s.n. V93858
Ahart 10765 CHSC87344
Cowell 07-58 YM216905
Antennaria + Senecio
Lackschewitz 4307 NY
Heckard 3286 JEPS70862
Colwell 04-63 YM118104
Colwell 96-WA-LC WTU344845
Saxifragales
Fiely 91 WS285758
Duthie s.n. WIS282512
Ahart 9846 CHSC82361
Ahart 7286 CHSC63258
Ahart 1984 CAS853689
Colwell 14-11 JEPS 126167
Chisaki 661 WIS282509
Hitchcock 18630 WS185460
Apioideae
O. uniflora subsp. occidentalis
Halse 908 ARIZ187532
Lackschewitz 6619 WTU272369
Bohrer1684 ARIZ189922
Merner s.n. WIS282500
Keith s.n. WIS282501
Batten 78-279 ALAv85763
Colwell 95-CO-TFS WTU344763
Artemisia
Bell 159 SD136414
Banks 689 SD137701
Harvey s.n. UC
Cox 188 CHSC12931
Colwell 07-53 YM
Colwell 10-107 YM
Colwell 04-83 YM118109
Galium
Yatskievych 82-196 ARIZ236136
Boyd 9673 RSA599655
Egger 1295 WTU
Ahart 3393 CHSC44286
Colwell04-54 YM117945
Colwell 04-03 YM118118
Howell 51680 CAS641193
Colwell 02-44 YELLO
Colwell 02-09 WTU351387
Schneider 920 JEPS122893
Schneider 468 JEPS
Colwell 01-95 WTU351381
Colwell 99-CA-RCRS WTU344759
Eriogonum, Eriodictyon, Eriophyllum, + Phacelia
O. fasciculata
Mistretta 1867 RSA641370
Mistretta 1866 RSA641369
Colwell 99-73 WTU344847
subsp. valida
Rugyt 1823 JEPS110567
Colwell 02-04 WTU351386
subsp. howellii
O. valida (Garrya)
Santana 5977 WIS282502
O. dugesii
Vandevender 95-1215 ARIZ321887
Collins 2027 (subsp. palmeri)
Colwell 02-06 WTU351385
Colwell CA-SN WTU344843
Colwell 01-01 WTU344743
O. cooperi (Heliantheae)
Schneider 936 JEPS122909
Hammond 10858 ASU60715
Collins 1541 WIS282497
Colwell 03-08 JEPS126150
Colwell 99-01 WTU344744
Colwell (5-July-2009)
O. bulbosa (Adenostoma)
Hamilton s.n. JEPS126153
Colwell 05-413 JEPS126144
O. parishii subsp. parishii (Artemisia)
Colwell 95-CO-DD WTU344764
Colwell 01-114 WTU351399
O. ludoviciana (Artemisia)
Collins 2035 MO6012141 (subsp. mutabilis)
Leidolf 2385 WTU344762
Colwell 99-08 WTU344753
O. corymbosa (Artemisia)
Taylor 18332 WTU351384
Taylor 18333 WTU351383
Colwell 03-53 JEPS126149
Colwell 07-72 JEPS126137
Colwell 05-414 JEPS126143
O. parishii subsp. parishii (Asteroideae)
Colwell 14-26 JEPS126165
Colwell 06-421 JEPS126163
Colwell 05-212 JEPS126139
Holmgren 1402 WTU224934
O. corymbosa (Artemisia)
Colwell 14-25 YM
Colwell 05-259 JEPS
Colwell 03-57 WTU
subsp. grayana (Astereae)
AC 97-CA-BLO WTU344755
AC 99-77 WTU344846
AC 96-WA-DPSP
subsp. californica (Grindelia)
O. californica
AC 99-76 WTU344749
Stoughton 583 RSA767875
subsp. parishii
Colwell (7-May-2006) JEPS
Sproul & Wolf s.n. JEPS
Colwell JEPS126159
subsp. brachyloba
Colwell 07-25 JEPS126141
subsp. parishii
O. parishii
Colwell 01-104 WTU351396
subsp. jepsonii
Colwell 99-75 WTU344745
Colwell JEPS126158
Colwell 99-02 WTU344758
Colwell 05-33 JEPS126147
Colwell JEPS126157
subsp. feudgei (Artemisia)
O. californica
Colwell 02-57 WTU351404
Colwell 01-116 WTU351394
Colwell 01-106 WTU351393
Prothero s.n. JEPS126154
Colwell JEPS 126162 JEPS
O. vallicola (Sambucus)
Colwell 02-52 WTU351391
Colwell 00-44 WTU344754
Colwell JEPS126164
subsp. grandis (Lessingia)
Colwell 05-101 JEPS126146
subsp. jepsonii
Gowen s.n. JEPS126142
Colwell 08-599 JEPS126151
subsp. grandis (Lessingia)
Taylor 18568 JEPS100408
Taylor 18566 JEPS100409
Taylor 18565 JEPS100410
subsp. condensa (Heterotheca)
Colwell 04-314
Colwell 02-51 WTU351389
Colwell 02-49 WTU351400
Colwell 02-48 WTU351388
Grindelia
Colwell 04-313 JEPS126160
Schneider 293 JEPS
Colwell 15-01 JEPS126152
Colwell 04-196 JEPS126148
Colwell 02-54
Eriophyllum
subsp. californica
O. californica
O. californica complex
Egger 804 WTU332502
Collins 1528 WIS282503
Colwell 96-WA-IC WTU344760
Colwell 01-107 WTU352202
O. pinorum (Holodiscus)
Ricardi 3326 CONC19273
Bobadilla s.n. CONC164753
O. tarapacana (Trixis)
Yatskyevich 85-215 ARIZ264197
O. sp. nov (Zaluzania)
Collins 2031 MO6012144 (M)
Collins 2030 MO6012145 (M)
Collins 2026 UC2046172 (M)
Collins 2025 MO5876462 (M)
Colwell 01-93 WTU344844 (L) (subsp. arenosa)
Collins 2034 MO (M)
Collins 2024 MO5990497 (M)
Dueholm 1164 WIS10644 (L)
Collins 2033 UC2046173 (L)
Colwell 01-113 WTU351402 (L)
O. ludoviciana + multiflora
(Astereae + Varilla)
Collins 1533 WIS (L)
Smith 2903 MO3646410 (M)
Alfaro 3461 MO2637419
O. tacnaensis
Long 2240 UC2046156
Vilagran 8616 SGO142749
Rosas 3327 CONC169912
Garcia 3877 SGO154435
O. chilensis (Grindelia)
Harrington 10081 CS46066
CS42888
Collins 2032 MO6012143
Collins 1622 MO5933323
Collins 1620 MO4903216
Yatskievych 91-195 MO3907149
O. riparia (Ambrosiinae)
Halse897 ARIZ187291
O. arizonica (Gutierrezia)
O. ludoviciana complex

Figure 2.1. Bayesian inference majority-rule consensus tree of 162 *Orobanche* populations inferred from nrDNA (ITS+ETS). Tip labels include the collection number followed by the herbarium accession number, if available. Posterior probabilities > 0.9 are shown in bold for nodes with > 70% maximum likelihood bootstrap support and in italics if BS < 70%. The internal branches leading to section *Gymnocaulis* and section *Gymnocaulis* have been shortened by a factor of ½. Host associations to the genus or higher taxonomic level are indicated in blue (Asteraceae) or green (other). Informally named clades in purple. Outgroup taxa are not shown. Photographs, from top to bottom: *O. fasciculata* parasitizing *Eriodicyton* sp. (Schneider 606); *O. cooperi* parasitizing *Hymenoclea salsola* (Schneider 415); *O. vallicola* parasitizing *Sambucus mexicana* (Schneider 316); O*. corymbosa* parasitizing *Artemisia tridentata* (Colwell 14-26).

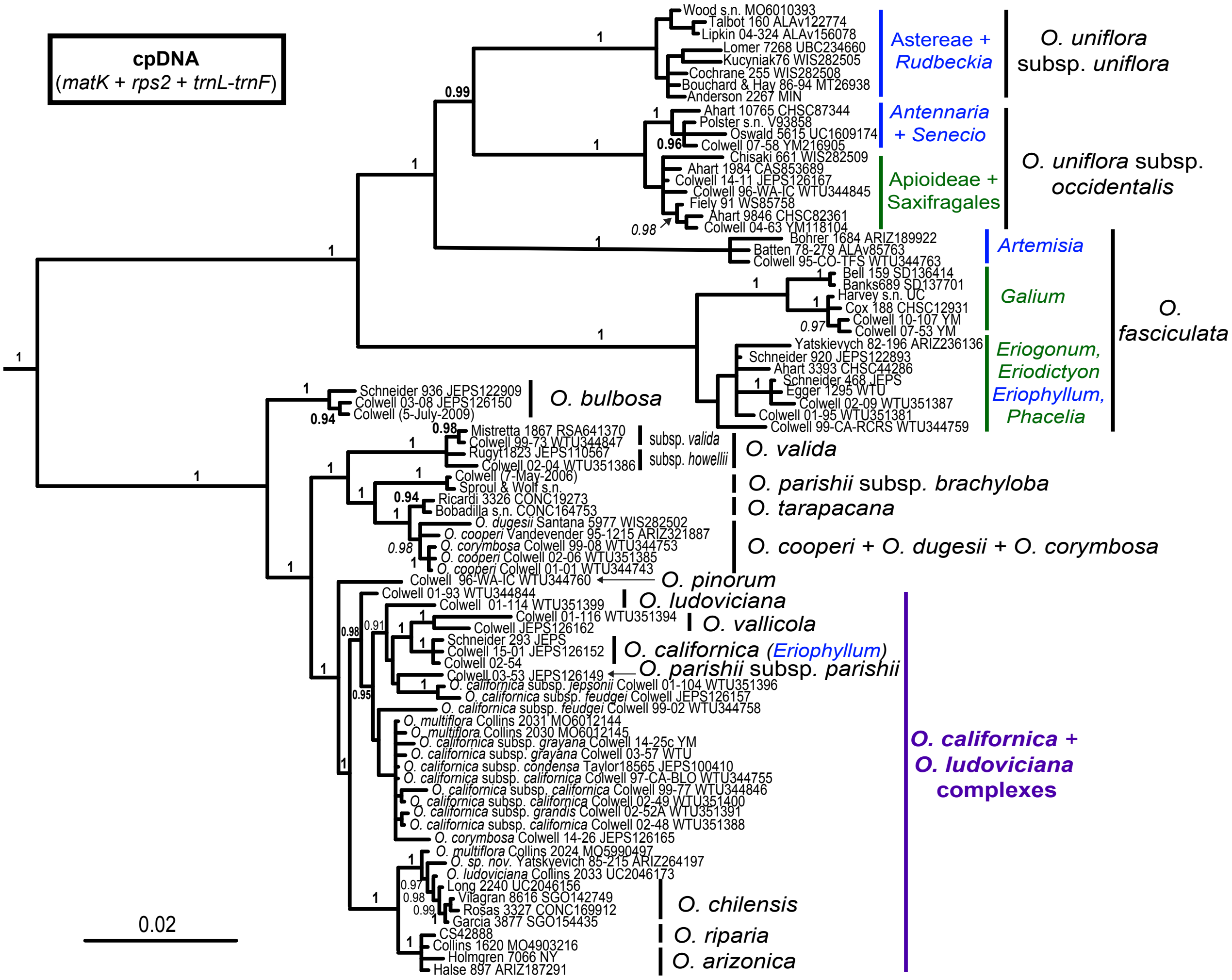

Figure 2.2. Bayesian inference majority-rule consensus tree of 86 *Orobanche* populations inferred from three concatenated cpDNA regions (*matK*, *rps2*, and trnL-trnF region). Tip labels consist of the taxon name (if not included in a sidebar), the collection number, and the herbarium accession numbers if available. Posterior probabilities > 0.9 are shown in bold for nodes with > 70% maximum likelihood bootstrap support and in italics if BS < 70%. Some host associations at the genus or higher taxonomic level are indicated in blue (Asteraceae) or green (other). For all others see Figure 2.1 or Appendix B. Informally named clades in purple. Outgroups not shown.

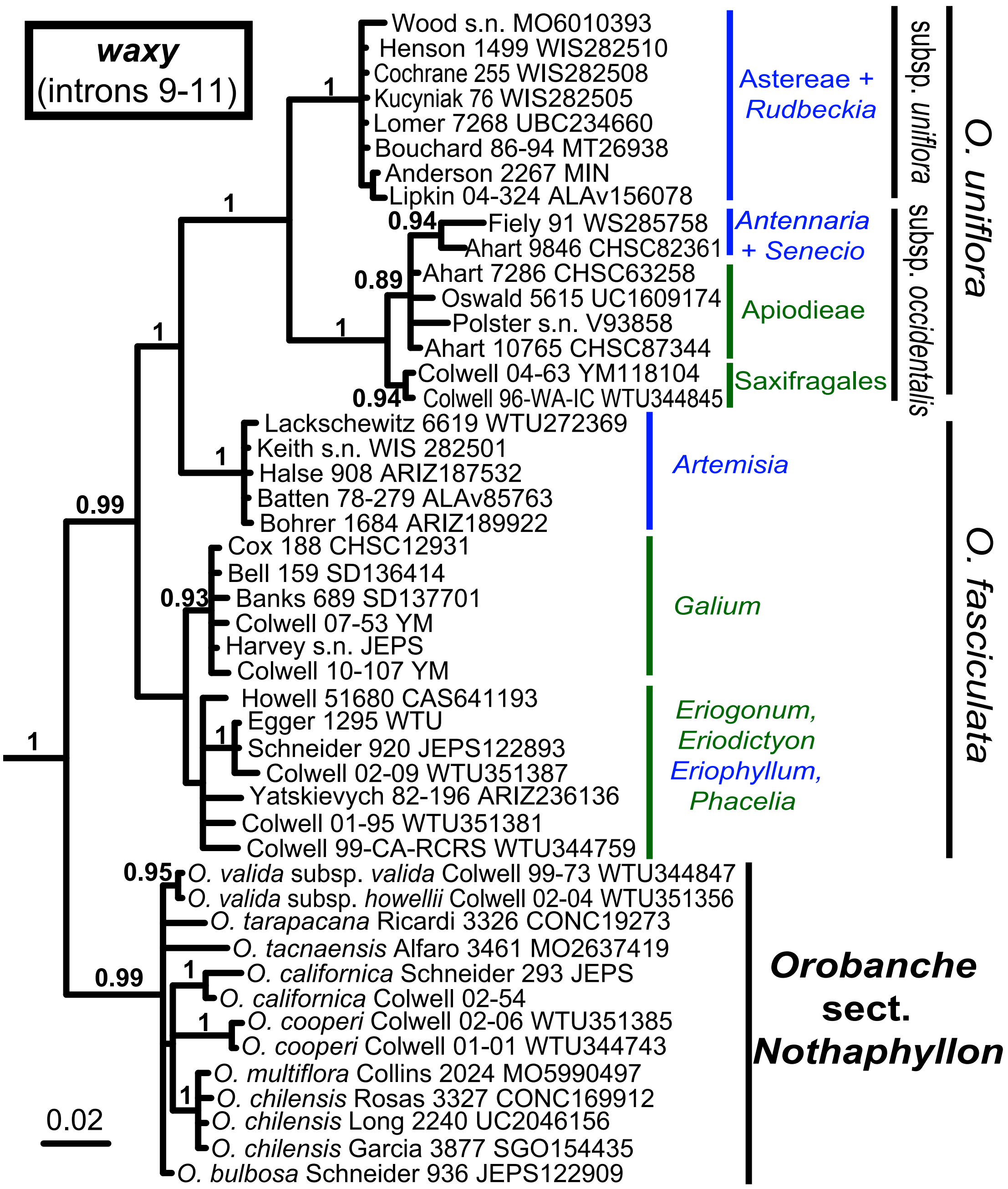

Figure 2.3. Bayesian inference majority-rule consensus tree of 47 *Orobanche* populations inferred from the *waxy* locus (introns 9–11). Tip labels consist of the taxon name (if not included in a sidebar), the collection number, and the herbarium accession numbers if available. Posterior probabilities > 0.8 are shown. All labeled nodes have ML bootstrap scores ≥ 74%. Host associations to the genus or higher taxonomic level for clades sect. *Gymnocaulis* are indicated in blue (Asteraceae) or green (other). For host associations of sect. *Nothaphyllon* see Figure 2.1 or Appendix A. Outgroups not shown.

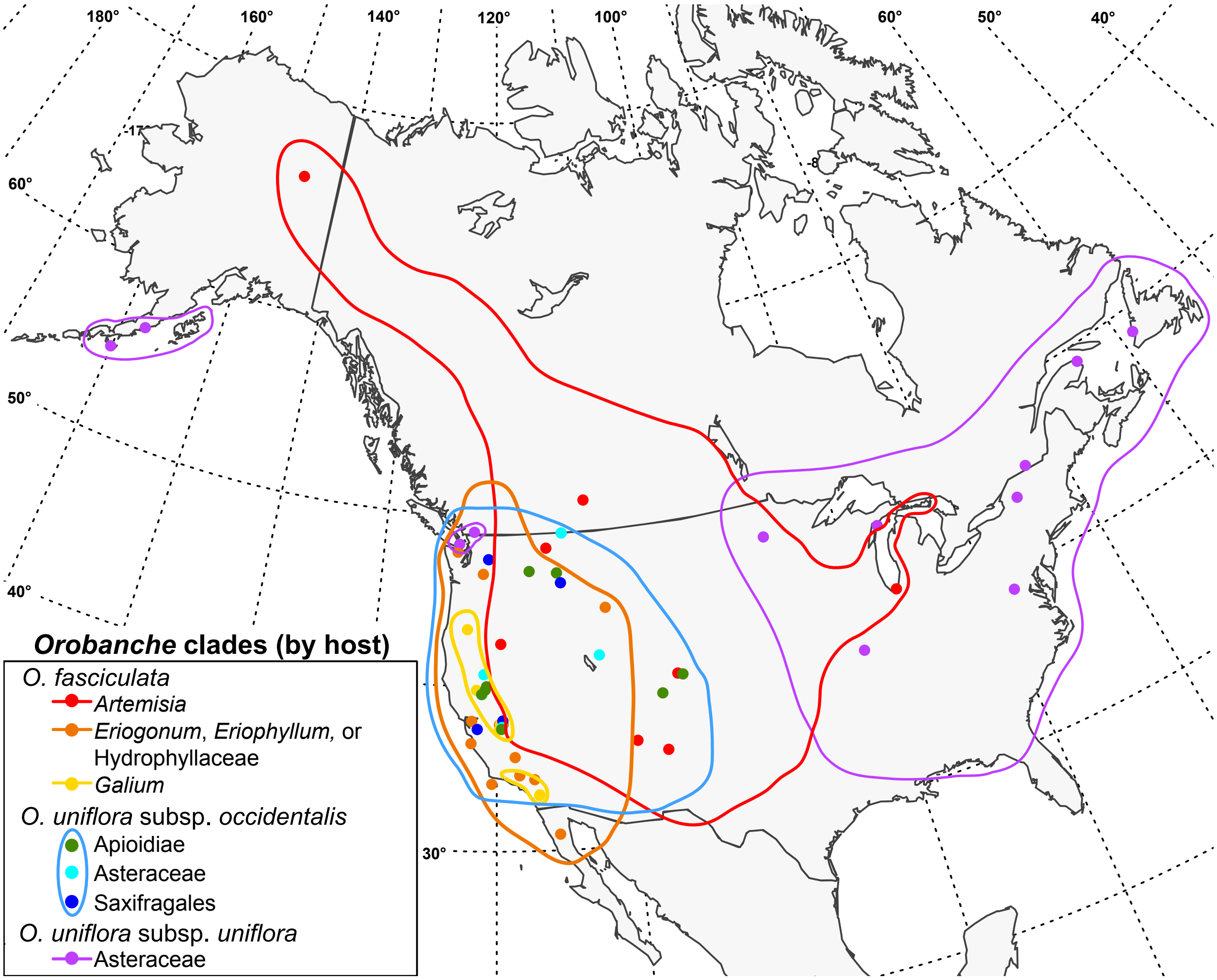

Figure 2.4. Range map of host-specific clades of *Orobanche* sect. *Gymnocaulis*. Colored circles represent individuals sampled in the phylogeny (Figs. 2.1–2.3). Colored lines show approximate range of each clade. Further study is needed to determine the range of each of the three host-specific lineages of *O. uniflora* subsp. *occidentalis,* which in this figure are treated as one unit. Range maps should be considered tentative, particularly in northern Canada and west-central United States, pending a thorough taxonomic and phytogeographical study.

CHAPTER 3:

Resurrection of the genus *Aphyllon*

ABSTRACT

Phylogenetic studies support a monophyletic clade of New World broomrapes (*Orobanche* sects. *Gymnocaulis* and *Nothaphyllon)* sister to the Old World genus *Phelipanche.* Therefore, I place the New World taxa in the genus *Aphyllon*, propose 21 new combinations, and provide a list of currently accepted taxa.

INTRODUCTION

Phylogenetic analysis of broomrapes and related holoparasites using nuclear DNA have found that the small eastern Mediterranean genus *Diphelypaea* Nicolson. is nested within *Orobanche* sensu lato (s.l.) as circumscribed by Beck (1890) (Schneeweiss et al. 2004a). Morphological and cytological differences between groups of taxa within *Orobanche* s.l. have led some botanists to adopt a narrow generic circumscription. In this taxonomic concept, *Orobanche* sensu stricto is limited to Old World species that lack bracteoles and have a base chromosome number of x = 19, a calyx divided to the base, and generally unbranched stems (Holub 1977, 1990). Other Old World broomrapes are treated as *Phelipanche* Pomel or the monotypic genus *Boulardia* F.W. Schultz (syn: *O.* sect. *Trionychon* Wallr. and *O. latisquama* (F.W. Schultz) Batt., respectively; Joel 2009, Schneweiss 2013).

Broomrape species native to the New World constitute two well-supported clades that together form a clade sister to *Phelipanche* (see Chapter 2). Taxonomically, these clades have been recognized as two separate genera *Aphyllon* (= *Orobanche* sect. *Gymnocaulis* Nutt.) and *Myzorrhiza* Phil. (= *O.* sect. *Nothaphyllon* (A. Gray) Heckard) by Holub (1977, 1990) and others (Schneweiss 2013), or more rarely, together as *Aphyllon* s.l (Gray 1876). However, neither of these generic taxonomies has been widely adopted among American botanists, in part because of the lack of available names for many taxa. Providing evidence to support the treatment of all New World broomrapes as *Aphyllon* and a providing list of recognized species (with homotypic synonyms) is the purpose of this chapter. New combinations are made where appropriate.

MATERIALS AND METHODS

In order to compare molecular branch lengths of major clades of *Orobanche* s.l, a maximum likelihood (ML) phylogram of *Aphyllon* and related holoparasites was inferred from 3 nuclear DNA loci (ITS, phytochrome A, and phytochrome B). All sequences were downloaded from Genbank, aligned, and concatenated into a supermatrix using SUMAC (Freyman 2015). The ML phylogeny was estimated using RAxML (Stamatakis 2014) with a GTR+ Γ nucleotide substitution model and 1000 rapid bootstrapping replicates.

Information about type specimens, basionyms, and synonomy of these new combinations was gathered by examining protologues and images of type specimens using major databases, including Tropicos (http://www.tropicos.org), JSTOR Global Plants (http://plants.jstor.org), and the International Plant Names Index (http://www.ipni.org). Types for all North American taxa and *O. weberbaueri* Mattf. have been designated by previous authors and are presented here. For three of the four South American taxa, typification would require more careful efforts beyond the scope of this study. No repository is given in the protologue for two syntypes of *Orobanche tacnaensis* Mattf. (Woitschach 71 and Meyen s.n.). The current existence of these specimens could not be verified, although a photograph of the Woitscach 71 (possibly from a specimen at B) is available at F. No specimens are cited by Rodolfo Phillipi in the protologues of the two taxa that he described.

RESULTS AND DISCUSSION

Molecular phylogenetic analyses have consistently supported a sister-group relationship between two strongly supported two American clades, representing *O.* sect. *Gymnocaulis* and *O.* sect. *Nothaphyllon* (McNeal et al. 2013, Fig. 2.1–2.3, Fig. 3.1). This relationship is supported by biogeography and synapomorphies such as a calyx with five fully developed lobes and a base chromosome number of $x = 12$, with polyploidy in most taxa (Heckard and Chuang 1975, Schneeweiss et al. 2004b). Holub (1977, 1991) has proposed treating the American broomrapes as two genera rather than one, though this was likely due to his erroneous belief based on vegetative morphology that *Orobanche* sect. *Nothaphyllon* is most closely related to *Phelipanche* and that *O.* sect. *Gymnocaulis* is allied to *O.* sect. *Orobanche* (Holub 1977).

The genus *Aphyllon* was described by Mitchell (1769), although it was not until nearly 80 years later that Asa Gray made a combination for *A. uniflorum* A. Gray. This species was the only broomrape included in his *Manual of the Botany of the Northern United States* (1848), though in the second edition (1856), Gray added two more species. Gray limited his generic concept for *Aphyllon* to taxa assignable to *O.* sect. *Gymnocaulis*, instead recognizing *O. ludoviciana* Nutt. in *Phelipaea* Tourn. ex. Desf. However, after a study of the Californian flora, Gray amended his generic concept for *Aphyllon* to include two sections, *Aphyllon* and *Nothaphyllon,* together containing all taxa native to the New World (Gray, 1876). Though expanded from Gray's initial circumscription, it was appropriate given Michell's original diagnosis of *Aphyllon* as having a five-toothed calyx ("semiquinquefidum"), a synapomorphy of New World broomrapes. A generation later, Rydberg (1906) proposed elevating Gray's *Aphyllon* sect. *Nothaphyllon* to genus rank on the basis of differences in habit and placentation using the available name *Myzorrhiza* Phil. However, the broader generic concept of *Orobanche* used by Beck (1890) has prevailed, particularly among American botanists.

Due to the biogeographical, morphological, cytological, and phylogenetic affinities of the New World broomrapes, I recommend treating them in a single genus, *Aphyllon,* composed of sections *Aphyllon* (=*O.* sect. *Gymnocaulis*) and *Nothaphyllon* (= *O.* sect. *Nothaphyllon*). Below, I present a key to sections and a list of recognized taxa in *Aphyllon*, proposing new combinations as necessary. Combinations are made at the most recently treated rank for the taxon in *Orobanche,* with the exception of *Orobanche uniflora* subsp. *occidentale* Greene, which is recognized at species rank under the available name *Aphyllon purpureum* (A. Heller) Holub due to its unique hosts, long molecular branch lengths, and recent discovery of sympatric populations of *A. purpureum* and *A. uniflorum* in southwestern British Columbia (Figs. 2.1–2.4). The treatment of *Aphyllon* sect. *Aphyllon* should be considered tentative; further taxonomic study is underway which will result in the recognition of several additional taxa.

KEY TO SECTIONS OF APHYLLON

1. Bracteoles subtending the calyx absent; pedicels much longer than flower (2-8x length); stems subterranean or rising to about ground level……..*Aphyllon* sect. *Aphyllon* (syn.: *O.* sect. *Gymnocaulis*)

1' Bracteoles subtending the calyx 2; pedicels equal to or shorter than flower, occasionally 2x length; stems usually rising above ground level……..*Aphyllon* sect. *Nothaphyllon* (syn.: *O.* sect. *Nothaphyllon*)

TAXONOMIC TREATMENT

***Aphyllon* Mitch.**, Diss. Brevis. Princ. Bot. 43. 1769.
Loxanthes Raf. Neogenyton 3. 1825. [TYPE— *Loxanthes fasciculatus* (Nutt.) Raf.]
Anoplanthus Endl., *nom. superfl.,* Gen. Pl. [Endlicher] pt. 10: 727. 1839.
Thalesia Raf. ex Britton, *nom. superfl.,* Mem. Torrey Bot. Club 5: 298. 1894.
TYPE— *Aphyllon uniflorum* (L.) Torr. & A. Gray, Manual 290. 1848.

Description

Herb, annual or rarely perennial, achlorophyllous, holoparasitic. Stems fleshy. Leaves reduced to scale-like bracts. Inflorescences terminal racemes, spikes, corymbs, or panicles. Calyx 5-toothcd. Corolla sympetalous, bilabiate to regular, tubular and often curved. Style long, stigma crateriform and peltate, or bilamellar. Fruit loculicidal capsules.
About 22 species: 18 in North America, 4 in South America.

Aphyllon sect. *Aphyllon*

Orobanche sect. *Gymnocaulis* Nutt., Gen. N. Amer. Pl. [Nuttall]. 2: 59. 1818.

Description

Stems subterranean or rising to about ground level. Pedicels long and slender, much longer than flower. Bracteoles subtending the calyx absent.

Species

***Aphyllon fasciculatum* (Nutt.) Torr & A. Gray**, Manual (ed. 2) 281. 1848.
Orobanche fasciculata Nutt., Gen. N. Amer. Pl. 2: 59. 1818.
Phelipaea fasciculata (Nutt.) Spreng., Syst. Veg. [Sprengel] 2: 818. 1825.
Loxanthes fasciculatus (Nutt.) Raf., Neogenyt. 3. 1825.
Anoplon fasciculatum (Nutt.) G. Don., Gen. Hist. 4: 633. 1838.
Anoplanthus fasciculatus (Nutt.) Walp., Repert. Bot. Syst. 3: 480. 1844.
Thalesia fasciculata (Nutt.) Britton, *Mem. Torrey Bot. Club* 5: 298. 1894.

TYPE— USA: “Missouri”, ca. 1811, *Nuttal s.n.,* (holotype, PH)

***Aphyllon purpureum* (A. Heller) Holub**, *Preslia* 70: 100. 1998.
Thalesia purpurea A. Heller, Bull. Torrey Bot. Club 24: 313. 1896.
Orobanche porphyrantha Beck, Pflanzenr. 96[IV,261]: 49. 1930.
Orobanche uniflora var. purpurea (A. Heller) Achey, Bull. Torrey Bot. Club 60: 445. 1933.
TYPE— USA: Idaho: Nez Perce Co.: near mouth of the Potlatch, 20 May 1896, *Heller 3099.* (no holotype designated; isotypes, CAS, DAO, K, MIN, MO, MSC, NDG, PH, US)

***Aphyllon uniflorum* (L.) Torr & A. Gray**, Manual (Gray) 290. 1848
Orobanche uniflora L., Sp. Pl. 2: 633. 1753.
Anoplanthus uniflorus (L.) Endl., Gen. Pl. [Endlicher] 727. 1839.
Thalesia uniflora (L.) Britton, *Mem. Torrey Bot. Club* 5: 298. 1894.
TYPE LOCALITY— USA: Virginia. (lectotype, *Clayton 387,* BM)

***Aphyllon* sect. *Nothaphyllon* A. Gray**, Bot. California [W.H. Brewer] 1: 584. 1876
Myzorrhiza Phil., Linnea 29: 36. 1858. [TYPE— *Myzorrhiza chilensis* Phil.]
Orobanche sect. *Myzorrhiza* Beck, Bibliotheca Botanica 4(19): 78. 1890.
Orobanche sect. *Nothaphyllon* (A. Gray) Heckard, Madroño 22: 41. 1973
TYPE— *Aphyllon californicum* (Cham. & Schltdl.) A. Gray, lectotype designated by Heckard, Madroño 22: 41. 1973.

Description

Stems clearly rising above ground. Pedicels equal to or shorter than flower. Bracteoles subtending the calyx 1 or 2.

Species

***Aphyllon arizonicum* (L.T. Collins) A.C. Schneid. comb. nov.**
Orobanche arizonica L.T. Collins, *Phytoneuron* 2015–48: 16, f. 1, 2, 4, 5, 6A, 7. 2015.
TYPE— USA: Arizona, Coconino Co.: near Tuba City, 1539 m, 27 September 1935, *Kearney & Peebles 12867* (holotype, ARIZ; isotype, US)

***Aphyllon californicum* (Cham. & Schltdl.)** A. Gray, *Bot. California* 1: 584. 1876.
Orobanche californica Cham. & Schltdl., *Linnea* 3: 134–136. 1828.
Phelypaea californica (Cam. & Schltdl.) G. Don, *Gen. Hist.* 4: 632. 1838.
Myzorrhiza californica (Cam. & Schltdl.) Rydb., *Bull. Torrey Bot. Club* 36: 696. 1909.

***Aphyllon californicum* subsp. *condensum* (Heckard) A.C. Schneid. comb. nov.**
Orobanche californica subsp. *condensa* Heckard, *Madroño* 22: 59–60, f. 1I-L, 5. 1973.
TYPE— USA: California: San Luis Obispo Co.: Yaro Creek, 25 May 1955, *Bacigalupi, Ferris & Robbins 5242* (holotype, JEPS; isotypes, NY, RSA, US, WTU)

***Aphyllon californicum* subsp. *feudgei* (Munz) A.C. Schneid. comb. nov.**

Orobanche grayana var. *feudgei* Munz, *Bull. Torrey Bot. Club* 57: 616–617, pl. 38, f. 8. 1930.
Orobanche californica subsp. feudgei (Munz) Heckard, *Madroño* 22: 62. 1973.
TYPE— USA: California: San Bernardino Co.: Baldwin Lake, 2 June 1924, *Munz 8177* (holotype, POM)

***Aphyllon californicum* subsp. *grande* (Heckard) A.C. Schneid. comb. nov.**
Orobanche californica subsp. *grandis* Heckard, *Madroño* 22: 60–62, f. 1P-R, 3A, 4E, 5. 1973.
TYPE— USA: California: Santa Barbara Co.: dunes at Surf, 22 July 1954, *H. M. Pollard* (holotype, UC; isotype, CAS)

***Aphyllon californicum* subsp. *grayanum* (Beck) A.C. Schneid. comb. nov.**
Orobanche grayana Beck, *Biblioth. Bot.* 4: 79. 1890.
Myzorrhiza grayana (Beck) Rydb., *Bull. Torrey Bot. Club* 36: 695. 1909.
Orobanche californica subsp. grayana (Munz) Heckard, *Madroño* 22: 54. 1973.
TYPE— USA: Oregon: banks of the Columbia River, 1825, *Douglas s.n.* (lectotype, K)

***Aphyllon californicum* subsp. *jepsonii* (Munz) A.C. Schneid. comb. nov.**
Orobanche grayana var. *jepsonii* Munz, *Bull. Torrey Bot. Club* 57: 617, pl. 38, f. 10. 1930.
Orobanche californica subsp. *jepsonii* (Munz) Heckard, *Madroño* 22: 57. 1973.
TYPE— USA: California: Colusa Co.: Princeton, October 1905, *H. P. Chandler s.n.* (holotype: POM, isotype: UC)

***Aphyllon chilense* (Phil.) A.C. Schneid. comb. nov.**
Myzorrhiza chilensis Phil., *Linnea* 29: 36–37. 1857.
Orobanche chilensis (Phil.) Beck, *Biblioth. Bot.* 4: 82–83. 1890.
TYPE— unknown.

***Aphyllon cooperi* A. Gray,** Proc. Amer. Acad. Arts 20: 307. 1885.
Orobanche ludoviciana var. cooperi (A. Gray) Beck, Biblioth. Bot. 4(Heft 19): 81. 1890
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TYPE LOCALITY— USA: Arizona: Fort Mojave (lectotype designated by Munz, Bull. Torrey Bot. Club 57: 620-21, *Cooper* s.n. in 1860-61, GH)

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Orobanche ludoviciana var. *latiloba* Munz, *Bull. Torrey Bot. Club* 57: 621–622, pl. 39, f. 18. 1930.
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***Aphyllon cooperi* subsp. *palmeri* (Munz) A.C. Schneid. comb. nov.**
Orobanche multicaulis var. *palmeri* Munz, *Bull. Torrey Bot. Club* 57: 613, pl. 38, f. 2. 1930.
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TYPE— Mexico, Durango, April-November 1896, *Palmer 7* (holotype: GH, isotypes, MO, UC)

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Myzorrhiza corymbosa Rydb., *Bull Torrey Bot. Club* 36: 696. 1909.
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TYPE— USA: Reynold's Creek, 2 July 1892, *Isabel Mulford s.n.* (holotype, NY; isotype, MO)

Aphyllon corymbosum **subsp.** ***mutabile*** **(Heckard) A.C. Schneid. comb. nov.**
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TYPE— USA: Rio Grande, 1845, *Gambel s.n.* (neotype designated by White & Holmes, Sida 19: 623, USA: Texas: Jim Wells Co., 19 April 1944, *Lundell & Lundell* 12809, LL; isoneotype, LL)

Aphyllon parishii **(Jeps.) A.C. Schneid. comb. nov.**
Orobanche californica var. *parishii* Jeps. *Man. Fl. Pl. Calif.* 952. 1925.
Orobanche parishii (Jeps.) Heckard. *Madroño* 22: 66. 1973.
TYPE— USA: California: San Bernardino Co.: Bear Valley, 1894, *S. B. Parish s.n.* (holotype, JEPS)

Aphyllon parishii **subsp.** ***brachylobum*** **(Heckard) A.C. Schneid. comb. nov.**
Orobanche parishii subsp. *brachyloba* Heckard, *Madroño* 22: 68–70, 2J, 3N, 5. 1973.
TYPE— USA: California: Ventura Co.: Dutch Harbor, San Nicolas Island, 23 April 1966, *Raven & Thompson 20794* (holotype, JEPS; isotypes, MO, RSA, SBBG)

Aphyllon pinorum **(Geyer ex Hook.) A. Gray**, Bot. California 1: 585. 1876.
Orobanche pinorum Geyer ex Hook., *Hooker's J. Bot. Kew Gard.* 3:297–298. 1851.
TYPE— USA: Idaho/Washington border, *Geyer 445* (holotype, K)

Aphyllon riparium **(L.T. Collins) A.C. Schneid. comb. nov.**

Orobanche riparia L.T. Collins, *J. Bot. Res. Inst. Texas* 3: 7–10, f. 1A-B, 2. 2009.
TYPE— USA: Indiana, Gibson Co.: Griffin, 16 August 1931, *Deam 50941* (holotype, IND; isotypes, A, F, GH, IND, MINN, WIS)

***Aphyllon robbinsii* (Heckard ex Colwell & Yatsk.) A.C. Schneid. comb. nov.**
Orobanche robbinsii Heckard ex Colwell & Yatsk., *Phytoneuron* 2016-58: 2. 2016.
TYPE— USA: California: San Francisco Co.: Lands End, 13 August 1956], *Deam 50941* (holotype, IND; isotypes, A, F, GH, IND, MINN, WIS)

***Aphyllon tacnaense* (Mattf.) A.C. Schneid. comb. nov.**
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SYNTYPES—: Peru: Tacna, 1890, *Woitschach 71* (photograph of type: F); Peru: Tacna, 1833, F. J. F. Meyen s.n.

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Orobanche valida Jeps., *Madroño* 1: 255-256. 1929.
Orobanche ludoviciana var. *valida* (Jeps.) Munz, *Bull. Torrey Bot. Club* 57: 621. 1930.
TYPE— USA: California: Rock Creek, San Gabriel Mountains, 2 June 1923, *F. W. Peirson 7937* (holotype: JEPS, isotype: RSA)

***Aphyllon validum* subsp. *howellii* (Heckard & L.T Collins) A.C. Schneid. comb. nov.**
Orobanche valida subsp. *howellii* Heckard & L.T Collins, *Madroño* 29: 98-100, f. 1A-E. 1982.
TYPE— USA: California: Mendocino Co.: Impassable Rock, 14 July 1951, *Donald V. Hemphill s.n.* (holotype: UC)

***Aphyllon vallicolum* (Jeps.) A.C. Schneid. comb. nov.**
Orobanche comosa var. *vallicola* Jeps., *Man. Fl. Pl. Calif.* 952. 1925.
Orobanche vallicola (Jeps.) Heckard, *Madroño* 22: 64. 1973.
TYPE— USA: California: Santa Clara Co.: Coyote, 14 October 1914, *W. L. Jepson 6196* (holotype: JEPS, isotypes: GH, MO)

***Aphyllon weberbaueri* (Mattf.) A.C. Schneid. comb. nov.**
Orobanche weberbaueri Mattf., *Notizbl. Bot Gart. Berlin-Dahlem* 8: 185. 1922.
TYPE— Peru: Camaná: Areuipa, Hafen Chala, 26 November 1915, *A. Weberbauer 7185.* (isotypes: GH, US)

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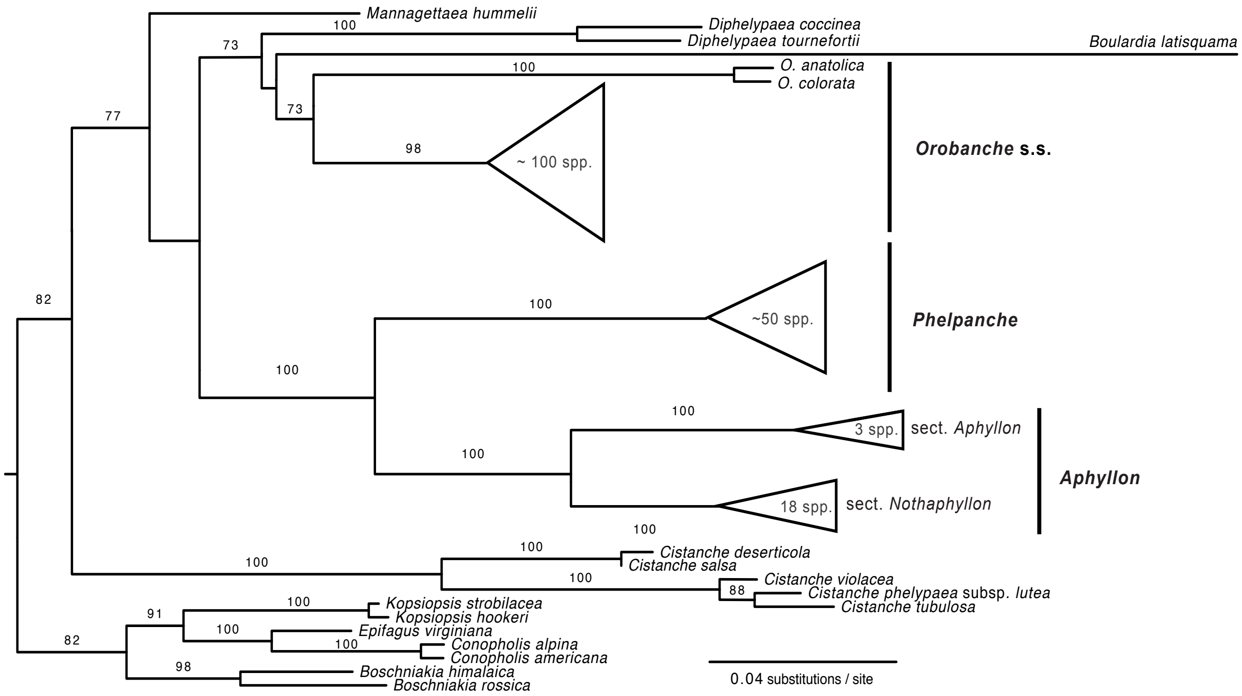

Figure 3.1. Maximum likelihood (ML) phylogram of *Aphyllon* and related holoparasite species inferred from 3 nuclear DNA loci (ITS, phytochrome A, and phytochrome B). Bootstrap scores of at least 70 % shown. Due to space constraints, several clades have been collapsed into triangles indicating the total recognized taxonomic diversity in that clade. For a more detailed and thorough study of phylogenetic relationships within *Aphyllon*, see Figures 2.1–2.3).

CHAPTER 4:

Parallel Pleistocene amphitropical disjunctions of a parasitic plant and its host

ABSTRACT

As shown in Chapter 2, closely related *Aphyllon* species in both North and South America are parasitic on *Grindelia.* However, the timing of these patterns and the processes to explain them are unknown. Therefore chronograms for the Orobanchaceae and *Grindelia* and their relatives were constructed using fossil and secondary calibration points, one of which was based on the inferred timing of horizontal gene transfer from a papilionoid legume into the common ancestor of *Orobanche* + *Phelipanche.* Elevated molecular evolution in the Orobanchaceae has hindered efforts to determine reliable divergence time estimates in the absence of a fossil record, however using a horizontal gene transfer event as a secondary calibration overcomes this limitation. These chronograms were used to reconstruct the biogeography of *Aphyllon*, *Grindelia,* and relatives using a DEC+J model implemented in RevBayes.

I infer two amphitropical dispersals of *Aphyllon* from North America to South America, with only a single dispersal in *Grindelia*. The dispersal of the *Aphyllon* lineage that is parasitic on *Grindelia* (0.41 Ma) took place somewhat after *Grindelia* began to diversify in South America (0.93 Ma). Although *Grindelia* and *Aphyllon* both dispersed to South America recently, *Grindelia* appears to have diversified more extensively post-colonization More broadly, recent Pleistocene glaciations probably have also contributed to patterns of diversity and biogeography of temperate northern hemisphere Orobancheae. In summary, parallel host-parasite amphitropical disjunctions in *Grindelia* and *Aphyllon* illustrate one means by which ecological specialization may result in non-independent patterns of diversity in distantly related lineages. This study also demonstrates the utility of using horizontal gene transfer events from well-dated clades to calibrate parasite phylogenies in the absence of a fossil record.

INTRODUCTION

Interactions between biogeography and ecology, that is, the interrelationship between species distributions and interspecific interactions, may strongly influence patterns of biodiversity (Sexton et al. 2009, Wiens 2011). Holoparasites, like other organisms that engage in obligate antagonistic or symbiotic interactions, require the presence of other species to complete their lifecycles. In such cases, strong links between biogeography, ecology, and perhaps also diversification are expected (Vanhove et al. 2016).

In chapter 2 I showed that all South American *Aphyllon* are phylogenetically nested within the temperate North American *A. ludovicianum* complex, but do not form a single monophyletic group. In one of these instances, a South American clade composed of *A. chilense* and *A. tacnaense* was found to be most closely related to two species native to the central United States, *A. ludovicianum* and *A. multiflorum*. Together, these four species are nested within the "*A. ludovicianum* complex", a clade that also includes two other North American taxa and the third sampled South American species, *A. tarapacanum* (Fig 2.1). This entire clade of parasites, like most species in *Aphyllon* sect. *Nothaphyllon,* parasitize perennial Asteraceae.

Within the *Aphyllon ludovicianum* complex, strong phylogenetic affinities exist between the hosts of North American and South American parasites. For example, species in the New World genus *Baccharis* have been reported as hosts for *A. ludovicianum* (e.g. *B. salicina* Torr. & A. Gray*, Collins 1323* WIS), and for several collections of South American *Aphyllon* (*B. polyantha* Kunth; *Vargas 3161*, MO; *Vargas 12880*, US), as well as occasional hosts of several other *Aphyllon* species. Similarly, *A. tarapacanum* has been reported on South American *Franseria* Cav. (e.g. Hutchison & Wright 7189; UC, US). Nuclear ribosomal and plastid DNA support different phylogenetic placements of *A. tarapacanum* (Fig. 2.1–2.3)*,* but in either case, close North American relatives parasitize other genera in the Ambrosiinae (Asteraceae). Specifically, *A. riparium* (supported by nrDNA evidence as a close relative) primarily parasitizes *Ambrosia artemisiifolia* L. and *Xanthium strumarium* L. (Collins et al. 2009), and *A. cooperi* (cpDNA) commonly parasitizes *Ambrosia dumosa*.

Most striking, however, is the *Aphyllon-Grindelia* Willd. host-parasite relationship: The primary hosts of *A. chilensis* are *G. chiloensis* (Cornel.) Cabrera and *G. ventanensis* Adr. Bartoli & Tortosa (Burkart, 1942), and its presumed closest North American relative, *A. ludovicianum,* commonly parasitizes *G. squarrosa* (Pursh) Dunal*. Grindelia* is also a host of the more distantly related *A. californicum* subsp. *californicum*.

The genus *Grindelia* (Asteraceae, Astereae), like *Aphyllon*, is restricted to the New World and has an amphitropical disjunction. Fine-scale taxonomic limits are somewhat controversial, with 25 to 50 recognized species native to North America and 26 recognized species native to South America (Bartoli and Tortosa 1999, Moore et al. 2012). This distribution appears to be the result of a single amphitropical disjunction event in *Grindelia*, with subsequent diversification in both North America and South America (Moore et al. 2012), although neither the timing of the dispersal and subsequent diversification nor the direction of dispersal were resolved in that study.

This current study was motivated by a desire to test this apparent case of parallel host-parasite American amphitropical disjunction and infer the relative timing of colonization. Specifically, the goals of this study are to (1) infer divergence times of major clades within *Grindelia* as well as *Aphyllon* and its holoparasitic close relatives in the Orobanchaceae, (2) test the hypothesis of two independent colonizations of South America by North American *Aphyllon,* and (3) compare the timing of these colonizations with the historical biogeography of *Grindelia.*

MATERIALS AND METHODS

***Orobanchaceae phylogeny* —** SUMAC version 1 (Freyman 2015) was used to download all Orobanchaceae and Paulowniaceae sequences from GenBank release 204 and to assemble a four-gene supermatrix (external transcribed spacer (ETS) and internal transcribed spacer region (ITS) of the nuclear ribosomal DNA, and low-copy nuclear genes phytochrome A and phytochrome B). Sampling within major clades outside the tribe Orobancheae (sensu McNeal et al. 2013, i.e., the clade of holoparasites that contains *Aphyllon*) was arbitrarily reduced to decrease computational time. Additional ETS and ITS sequences for both subspecies of *Aphyllon epigalium*, *A. purpureum*, and the undescribed clade of *A. fasciculatum* that parasitizes hosts other than species in the genus *Artemisia* L. were added manually for a total alignment of 160 minimum-ranked terminals. Final sequence alignments were generated using MAFFT v7.123b (Katoh and Standley 2013) and trimmed to form an aligned matrix of 5569 basepairs. GenBank accession numbers for sequences used in constructing the Orobanchaceae supermatrix are presented in Appendix C.

A chronogram of Orobanchaceae (including Rehmanniaceae) + Paulowniaceae was estimated using an uncorrelated lognormal relaxed clock model and a GTR+Γ substitution model for each gene partition, implemented in RevBayes v. 1.0.4 (Höhna et al. 2014). Rate variation across sites was modeled under a gamma distribution approximated by four discrete rate categories. The constant rate birth-death-sampling tree prior (Stadler 2009) was used with the probability of sampling species at the present (**ρ**) set to 0.08. **ρ** was calculated by dividing the number of extant species sampled in the supermatrix (160) by the estimated total number of species in Orobanchaceae (~2000), though sampling density was substantially higher within the Orobancheae than in other lineages. Branch rates were drawn from a lognormal prior with the mean and standard deviation given exponentially distributed hyperpriors with rate parameters of 0.25. Tree topology was fixed to the result of a maximum likelihood analysis performed on the same partitioned 4-gene dataset using RAxML v. 8.2.9 (Stamatakis 2014), which was generally consistent with topologies inferred using more thorough studies (McNeal et al. 2013; Fig. 2.1-2.3).

The Paulowniaceae + Orobanchaceae root age was calibrated based on the stem age of Paulowniaceae reported by Magallón et al. (2015) as part of a 5-gene, 792-taxon study of angiosperms with 137 node calibrations. To model the uncertainty in root age, the root node was given a uniform calibration density with a range of 57.02–28.08 Ma, representing the 95% HPD reported by Magallón et al. (2015), who used an uncorrelated lognormal Bayesian analysis run in BEAST.

Divergence times within Orobanchaceae were estimated using two independent stochastic nodes (Fig. 4.1). The calibration used to date the crown node of *Orobanche* s.l. (including the genera *Aphyllon, Diphelypaea* D.H. Nicolson*,* and *Phelipanche* Pomel) was based on a dated tree of the *albumin1* gene, which originated in parasitic Orobanchaceae through horizontal gene transfer from a papilionoid legume host approximately 16–11 Ma, before the divergence of *Orobanche* and *Phelipanche* (95% HPD: 16–6 Ma; Zhang et al. 2013). This node was modeled using a normal prior with a mean of 11 Ma and a standard deviation of 2.55. The other calibration was based on *Cistanche* Hoffmanns. ex Link pollen from a Neogene formation in Sebkha el Mellah, Algeria (Beucher 1971). Mueller (1981) reported the fossil as Pliocene, so the fossil age was conservatively fixed at 2.5 Ma, which represents the end of that epoch. Because the Miocene-Pliocene boundary is not well defined in this formation (see Beucher 1971, pp. 295, 398-399), the fossil could also be substantially earlier. The crown age of *Cistanche was treated* as a stochastic node with the waiting time to fossilization modeled by a lognormal prior with a mean of 10 and a standard deviation of 0.5. The waiting time to fossilization represents the time between the node being calibrated and the fossilization of a particular specimen in that lineage, as the probability of sampling the actual common ancestor are vanishingly small. In summary, the sampled prior ages had a mean of 12.5 Ma, and 95% were between 6.2 Ma and 29 Ma, reflecting the large uncertainty associated with this fossil date.

Four independent replicates of a Markov chain Monte Carlo (MCMC) were run for 5000 iterations as a pre-burnin to tune the proposals, then sampled every two iterations for 10,000 iterations. Each iteration consisted of 467 moves randomly scheduled from 369 different moves. The first 1000 samples of each run were discarded as burnin. Convergence was assessed using Tracer v. 1.6.0.

Grindelia *phylogeny* — The ITS and ETS alignment from Moore et al. (2012) was used for the analysis, with Genbank sequences from four additional outgroup taxa added and aligned by eye to allow for secondary time calibration: *Eurybia divaricata* (L.) G. L. Nesom (ITS: AY772423.1, ETS: AY772437), *E. radulina* (A. Gray) G. L. Nesom (ITS: EU200208.1, ETS: EU196489.1), *Symphyotrichum adnatum* (Nutt.) G. L. Nesom (ITS: JQ360444.1, ETS: JQ360214.1), and *S. drummondii* (Lindl.) G. L. Nesom var. *texanum* (E. S. Burgess) G. L. Nesom (ITS: U97603.1, ETS: AF516069.1). A backbone constraint tree was constructed in RAxML v 7.3.0 with the GTRGAMMA model of sequence evolution and made ultrametric using the chronos command in the 'ape' package (Paradis et al. 2004) in R (R Core Team 2016).

We gave the root age of the tree (the divergence between *Eurybia* (Cass.) Cass. and the remaining species) a uniform probability from 9.0–3.0 Ma (Fig. 4.2). This is the estimated divergence time between *Eurybia* and *Symphyotrichum* Nees plus *Grindelia* in the fossil-calibrated phylogeny of the Asteraceae reconstructed by Huang et al. (2016). No fossil or geological calibration points exist for internal nodes of the *Grindelia* phylogeny.

RevBayes v. 1.0.3 was used to produce a time-calibrated phylogeny, as described above for the Orobanchaceae. It was run for 10,000 iterations and sampled every 2 iterations, with a pre-burn-in of 5000 iterations and $\boldsymbol{\rho}$ set to 0.20. Each iteration consisted of 285 moves randomly scheduled from 297 different moves.

***Inferring historical biogeography*—** Ancestral geographic ranges were inferred using a DEC+J model implemented in RevBayes, which allows for sympatric speciation, allopatric speciation, and jump dispersal events. These reconstructions were performed across the time-calibrated maximum clade credibility (MCC) trees inferred above. The Orobanchaceae tree was pruned to include only members of the clade Orobancheae (*Aphyllon* and holoparasitic relatives) to prevent bias due to undersampling.

For the Orobancheae analysis, six non-overlapping biogeographic regions were used: (A) The California Floristic Province (CFP), (B) Western North America (except the CFP) to the Mississippi River basin and Hudson Bay, including Mexico and Central America, (C) Eastern North America, (D) Eurasia and Northern Africa, (E) Australia, and (F) South America (Fig. 4.3). Four independent MCMC replicates were run for 500 iterations as a pre-burnin to tune the proposals, then sampled every 10 iterations for 2,500 iterations, with the first 20% of samples discarded as burn-in. Each iteration consisted of three moves randomly scheduled from 11 different moves.

The *Grindelia* analysis used the same five regions delimited by Moore et al. (2012): (A) North America west of the Cascade-Sierra Nevada axis, (B) North America between the Cascade-Sierra Nevada axis and the crest of the Rocky Mountains, (C) North America east of the crest of the Rocky Mountains, (D) South America west of the crest of the Andes, and (E) South America east of the crest of the Andes (Fig. 4.4). Four independent MCMC replicates were run for 500 iterations as a pre-burnin to tune the proposals, then sampled every 10 iterations for 2,000 iterations. Each iteration consisted of five moves randomly scheduled from 12 different moves. The first 500 samples of each run were discarded as burnin.

RESULTS

Biogeography and divergence times in Orobanchaceae—Diversification of extant Orobanchaceae was relatively recent, with the family originating approximately 30 Ma, the origin of parasitism evolving shortly thereafter in the late Oligocene, and all but the earliest diverging lineages arising in the Neogene (Table 4.1, Fig. 4.1). Of the three clades of holoparasites in Orobanchaceae, the most species-rich, the tribe Orobancheae (sensu McNeal, 2013), is also the oldest, with a mean stem age of 26.2 Ma (95% HPD interval of 22.7–31.0 Ma) and a mean crown age of 16.8 Ma (14.2 –19.8 Ma), and arose from a widespread ancestor in the Northern Hemisphere (Eurasia/Northern Africa + Western North America + Eastern North America, PP = 0.37, Table 4.1).

Most early diversification of Orobancheae took place in Eurasia/Northern Africa (Fig. 4.3) with origination (stem ages) of the genera *Boulardia* F. W. Schultz*, Diphelypaea*, *Orobanche* s.s., *Phelipanche, Cistanche*, and *Mannagettaea* Harry Sm. all between 9 and 15 Ma, although crown ages for *Phelipanche* and the clade of *Orobanche* that excludes *O. anatolica* and *O. colorata* are much more recent (*Phelipanche:* 3.1 Ma, 95% HPD of 2.2–4.0 Ma; *Orobanche* 3.5 Ma, 2.6–4.4 Ma). The genus *Aphyllon* represents a single colonization from Eurasia/Northern Africa 7.1 Ma (5.6–8.7 Ma) into either the CFP (PP = 0.30) or elsewhere in western North America (PP = 0.30), with only recent, repeated colonizations of eastern North America. Other species of Orobancheae in eastern North America, in the genera *Conopholis* Wallr. and *Epifagus* Nutt., also arrived there from range expansion of a common western North American ancestor, albeit much earlier, in the Pliocene or late Miocene (Fig. 4.3).

Other *Aphyllon* lineages moved into the CFP from western North America and diversified in situ, such as the clade that includes *A. vallicolum, A. robbinsii, A. parishii* subsp. *parishii*, and all subspecies of *A. californicum* except subsp. *grayanum* (PP= 1.0; mean crown age 0.78 Ma [95% HPD 0.54–1.04 Ma]). Another example is the most recent common ancestor of *A. tuberosum* and *A. validum* (PP=0.83; mean crown age 2.6 Ma [1.9-3.3 Ma]), which diversified in the CFP as well as dispersing back out to form the lineage that became *A. cooperi* and *A. dugesii* in the deserts of western North America (PP = 0.73, Fig. 4.3).

We infer three amphitropical disjunctions caused by recent long distance dispersal events: two temperate American disjunctions in *Aphyllon*, and a third, of the rare Australian native *Orobanche cernua* var. *australiana* from a Northern Hemisphere Eurasian (or northern African) ancestor no earlier than 0.48 Ma (mean age 0.2 Ma; 95% HPD: 0.004–0.48 Ma, biogeography PP= 0.76). The two American amphitropical disjunctions resulted in two separate South American lineages from western North American ancestors. The first dispersal occurred ca. 1.4 Ma (0.97–1.8 Ma, PP = 0.71) and resulted in modern-day *A. tarapacanum*. The second occurred ca. 0.41 Ma (0.19-0.64, PP = 0.67) and resulted in the lineage that subsequently diversified into *A. tacnaense* and *A. chilense.*

***Biogeography and divergence times of* Grindelia—** *Grindelia* appears to have arisen very recently, with a crown age, which is also the basal split between North American and South American *Grindelia*, of approximately 1.40 Ma (95% HPD: 0.71–2.43 Ma; Table 4.1, Fig. 4.2). *Grindelia* was reconstructed, with high probability (PP = 0.92; Fig. 4.4), as having arisen in North America, east of the Continental Divide. The genus reached eastern South America sometime before the first branching event in the South American clade at ca. 0.93 Ma (95% HPD: 0.41–1.36 Ma; biogeography PP = 1.0). The diversification in North America began at approximately the same time, ca. 1.18 Ma (95% HPD: 0.57–2.04 Ma) in eastern North America, with a subsequent dispersal to western North America at ca. 0.63 Ma (95% HPD: 0.26–1.17 Ma) and from there to the Pacific states at ca. 0.18 Ma (95% HPD: 0.06–0.31 Ma) and subsequently to California at ca. 0.16 Ma (95% HPD: 0.04–0.25 Ma).

DISCUSSION

Parallel American amphitropical disjunctions— The difficulty of a successful long distance dispersal event is particularly acute for holoparasites or other extreme specialists, whose propagules must traverse a long distance and then also make contact with a host plant. The probability of successful colonization is therefore the product of the probabilities of both dispersal and establishment of the parasite, and the probabilities of prior dispersal and establishment of suitable hosts. Nonetheless, there is strong support for two independent dispersals of *Aphyllon* from western temperate North America to temperate South America within the last 1.8 million years (Table 4.1, Fig. 4.3). The more recent case was slightly preceded by the North to South American dispersal and subsequent diversification of *Grindelia* less than 2.5 Ma, a common host of South American *A. chilense* and closely related North American *Aphyllon* (Table 4.1, Fig. 4.4).

The timing and direction of dispersal in both clades is consistent with the timing and direction of many other reported temperate amphitropical American disjuncts (Wen and Ickert-Bond, 2009). In this case, assuming the parasite was unable to exploit any other hosts, the lag time between host and parasite colonization may reflect the time necessary for the *Grindelia* to establish in South America so that it would have a sufficient range, or perhaps more importantly density (Tsai and Manos 2010), to support the establishment of *Aphyllon*.

Recent biogeographic studies of parasitic plants have generally not considered the biogeography of potential hosts (e.g. Wolfe et al. 2005; Bendikshy et al. 2010). One reason may be that the phylogenetic breadth of their host associations due to frequent host switching at deeper phylogenetic levels, or host generalism in the case of many hemiparasites, does not provide a biogeographic constraint. However, the geographically and temporally parallel amphitropical disjunctions in *Aphyllon* and *Grindelia* illustrate a link between the ecology and biogeography of parasites and their host.

Historical biogeography of Orobancheae— Although holoparasitism likely emerged in the Miocene (Fig. 4.1), the origination of most extant diversity in the Orobancheae appears to have taken place in the last several million years, with the stem age of several large clades, most notably *Orobanche* s.s. (excluding *O. anatolica* and *O. colorata)* and *Phelipanche,* 2–3 times older than the crown age (Fig. 4.3). One process that may result in this "stemminess" is a high extinction rate, with internal nodes clustered near the present representing lineages that have not yet had time to go extinct. However, differentiating a constant high background extinction rate from variable or shifting diversification rates in the absence of a fossil record can be difficult (Nee 1994, Rabosky 2010).

Nonetheless, a high background extinction rate in the Orobancheae is an attractive hypothesis given the extreme specialization of holoparasitic Orobancheae to their hosts. Ecological specialization has been noted as an important contributor to extinction risk in many systems, although susceptibility to extinction and evolutionary trajectories more broadly may also depend on type of specialization (host-parasite, plant-pollinator, fundamental niche of plants etc., Munday 2004, Jiguet et al. 2007, Colles et al. 2009, Eskildsen et al. 2015).

In addition to intrinsic risk of extinction due to specialization, the dynamic climate of the Quaternary may also have played a role in the relative paucity of long-branch terminal taxa in *Orobanche, Phelipanche,* and to a lesser extent *Aphyllon*. Since the beginning of the Pleistocene, a series of five major ice sheet advances and retreats have swept across North America (Balco and Rovey 2010), resulting in alternating episodes of range contraction into refugia, followed by expansion or migration during interglacial periods (Shafer et al. 2010). These changes could have contributed to increased extinction rates by reducing population size or disrupting host-parasite associations. Contemporaneous glaciations in South America may have limited available habitat for colonization of hosts or parasites. On the other hand, the glacial/interglacial cycles may have also promoted speciation, as new opportunities for host-switching arose due to changes in plant assemblages, followed by reproductive isolation. Such host-switching may have led to the divergence of the genus *Kopsiopsis* (Beck) Beck, which became isolated in California and the Pacific Northwest following a host-shift to Ericaceae (Fig. 4.3). The remainder of this New World lineage, that is, the genera *Epifagus, Conopholis,* and *Boschniakia* C.A. Mey. ex Bong. have been present in eastern North America since the late Miocene or Pliocene, likely retreating into southeastern North America during the Pleistocene glaciations (Tsai and Manos 2010, Rodrigues and Stefanovic 2016).

Such environmental changes undoubtedly shaped the ranges of extant species, perhaps most obviously *Aphyllon uniflorum.* This species is primarily found in eastern North America, but also on the Alaska Peninsula and in far southwestern British Columbia, a vicariant pattern perhaps explained by recent glaciation. Historical species ranges, such as those inferred from population genetic analyses or fossil pollen records, are not taken into account in the ancestral state reconstructions performed here.

Other eastern North American *Aphyllon* species such as *A. fasciculatum and A. riparium* are also nested in the phylogeny, with western North America as the inferred origin of *Aphyllon*, which is also where extant taxonomic diversity is highest. Within western North America, I infer relatively frequent dispersal into and out of the CFP, in addition to recent *in situ* diversification in both the CFP and the rest of western North America (Fig. 4.3). This frequency of dispersal likely contributes to our difficulty in inferring the historical biogeography at these earlier nodes, or in being able to distinguish among alternative biogeographic hypothesis of California origins, western North American origins outside of California, or widespread ranges in both regions, in spite of the Sierra Nevada crest being a relatively strong biogeographical barrier today. One other important limitation in these analyses is uncertainty in tree topology. Incongruence between trees inferred using plastid and nuclear data at some deeper nodes (Fig. 2.1, Fig. 2.2) likely point to a more complicated biogeographical history of *Aphyllon* in western North America than presented here.

Though the biogeographical patterns of species in Eurasia and Africa are not the main focus of this study, these regions contain the majority of extant taxonomic and phylogenetic diversity within Orobancheae, particularly in the genera *Orobanche*, *Phelipanche*, and to a lesser extent *Cistanche*. As in North America, cooling and drying during the Pliocene followed by glacial/interglacial cycles likely greatly affected the diversification and extant ranges of the Orobancheae. Two centers of extant *Orobanche* and *Phelipanche* diversity, the Mediterranean and Caucasus, have been hypothesized as refugia for both plant and animal lineages during Pleistocene ice ages (Taberlet et al. 1998, Huwitt et al. 1999), although other processes may also have contributed to the high diversity in those regions (Feliner 2011). A more precise study of historical biogeography of Old World Orobancheae, with additional sampling of Eurasian taxa, would shed additional light on the range of the common holoparasitic ancestor and, by extension, how this lineage dispersed across the Northern Hemisphere.

***Historical Biogeography of* Grindelia—**Our analyses indicate that *Grindelia* diversified extremely recently in both North America and South America, more so than many of the other plants with which it co-occurs. For example, the estimated diversification time of the Californian species (that is, the species that are sister to *G. integrifolia* DC.) is 0.16 Ma, which is much more recent than almost all of the other groups that have significant ecological diversity in the CFP (Baldwin 2014). Similarly, compared to many other North American - South American disjuncts that show extensive diversification on the continent to which they dispersed, *Grindelia* arrived in South America through a long distance dispersal event much more recently, around 1.4 Ma (Figure 4, Wen and Ickert-Bond 2009). In contrast, other recent disjuncts, such as *Aphyllon*, have only one or two described species on the continent to which they dispersed.

Our finding of recent diversification for North American *Grindelia* is consistent with several lines of evidence from previous studies. First, North American species that have been tested are capable of hybridization with one another (although some species are separated by chromosomal rearrangements and only produce sterile hybrids; Dunford 1964, 1986). Second, many taxonomic species sampled in phylogenetic analyses are resolved as paraphyletic, which a combination of incomplete lineage sorting and recent hybridization (Moore et al. 2012), or taxonomic over-splitting. Third, there are some taxonomic difficulties, especially in the North American species, likely due to ecological diversification, and potential reproductive isolation in the field occurring more rapidly than strong morphological differentiation (Strother and Wetter 2006, Moore et al. 2014).

Despite these independent lines of evidence for recent diversification, it is possible that better calibrations in future analyses could change our age estimates. The only available calibration for this *Grindelia* phylogeny was a secondary calibration of the root node, based on a larger fossil-calibrated phylogeny of the Asteraceae as a whole (Huang et al. 2016). These authors used several fossil calibration points, but these calibration points were also all from relatively deep in the tree. Thus, it is possible that our 95% HPD intervals do not reflect the full uncertainty in the dating of these nodes, in which case the *Grindelia* may have been in South America for a longer period before establishment of *Aphyllon.*

Inferring divergence times by horizontal gene transfer— From a methodological standpoint, this study illustrates the utility of using horizontal gene transfer events as secondary calibration points to infer chronograms. The lack of fossils in the Orobanchaceae has required previous studies to rely on molecular-clock methods to infer divergence times (Wolfe et al. 2005). However, parasitic plants, which include nearly all members of the Orobanchceae, have accelerated rates of molecular evolution in the nuclear, plastid, and mitochondrial genomes (Bromham et al. 2013). Therefore, a molecular clock calibrated using a nonparasitic lineage should be systematically biased toward earlier parasite divergence times. It is difficult to meaningfully compare our findings with those of Wolfe et al. (2015) in that regard since the understanding of phylogenetic relationships at the generic level has changed and I used the more current Orobanchaceae + Paulownianceae root age estimate of Magallón et al. (2014). Further work to develop evolutionary models that explicitly incorporate horizontal transfer events could be used to more rigorously test these ideas in Orobanchaceae and other lineages of gene parasitic plants, nine of which have documented host-to-parasite horizontal gene transfers (Davis and Xi 2015).

CONCLUSIONS

Together, the patterns and timing of diversification in *Aphyllon* and *Grindelia* illustrate the role that host-parasite ecology can play in shaping biogeographical patterns. Out of three amphitropical disjunctions in the Orobancheae (one in Old World Orobanche, and two temperate American disjunctions in Aphyllon), the phylogenetic and host relationships are most Although *Aphyllon* and *Grindelia* appear to have taken different evolutionary trajectories following dispersal to South America (with only four described South American taxa in *Aphyllon* following two dispersal events, and *Grindelia* diversifying into 26 taxa following a single dispersal), the timing of their dispersals to South America are relatively congruent, with the dispersal of *Grindelia* occurring only slightly before the dispersal of *Aphyllon.* In the Northern Hemisphere, recent Pleistocene glaciations probably have also contributed to diversity and biogeography of temperate Orobancheae. Given the preponderance of host switches that have occurred in *Aphyllon*, it is uncertain if the existence of *Grindelia* directly enabled this lineage of *Aphyllon* to successfully colonize South America, but host availability should not be ignored in the context of parasite biogeography.

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Table 4.1. Divergence times with credible intervals (95% highest probability density [HPD]) and inferred historical biogeography of selected well–supported clades within Orobanchaceae and *Grindelia*. For a map of biogeographical regions, see Fig. 4.3 (Orobancheae) or Fig. 4.4 (*Grindelia*).

Clade	**Crown Age (Ma)**		**Biogeography**	
	Mean	**95% HPD**	**Region**	**Posterior Probability**
Orobanchaceae (incl. Rehmanniaceae)	29.8	25.9–35.2	–	–
Parasitic Orobanchaceae	27.3	23.5–32.0	–	–
Holoparasitic Orobancheae	16.8	14.2–19.8	Eurasia/ N. Africa + Western North America + Eastern North America	0.37
			Eurasia/North Africa + Eastern North America	0.26
Orobanche s.l. (incl. *Diphelypaea*)	13.9	11.7–16.4	Eurasia/ N. Africa	0.54
Aphyllon + *Phelipanche*	10.5	8.5–12.5	Eurasia/ N. Africa	0.41
Aphyllon	7.1	5.6–8.7	California Floristic Province	0.30
			Western North America	0.30
			California Floristic Province + Western North America	0.10
Aphyllon sect. *Aphyllon*	4.41	3.35–5.54	Western North America	0.33
			California Floristic Province + Western North America	0.33
Aphyllon sect. *Nothaphyllon*	2.79	2.05–3.61	California Floristic Province + Western North America	0.58
			California Floristic Province	0.29
A. ludovicianum complex[1]	1.39	0.97–1.82	Western North America	0.71
A. chilense + *A. tacnaense* + *A. ludovicianum* + *A. multiflorum*	0.41	0.19–0.64	Western North America	0.67

A. chilense + A. tacnaense	0.13	0.03–0.27	South America	1
Grindelia	1.40	0.71–2.43	Eastern North America	0.92
North American *Grindelia*	1.18	0.57–2.04	Eastern North America	0.98
Western N. American *Grindelia*	0.63	0.26–1.17	Western North America	1
Pacific Coast *Grindelia*	0.18	0.06–0.31	Pacific Coast	1
California *Grindelia*[2]	0.16	0.04–0.25	Pacific Coast	1
S. American *Grindelia*	0.93	0.41–1.36	Eastern South America	1

[1] The *A. ludovicianum* complex comprises *A. chilense, A. tacnaense, A. ludovicianum, A. multiflorum, A.* sp. nov., *A. arizonicum, A. riparium*, and *A. tarapacanum* (see Fig. 2.1).

[2] California *Grindelia* is the sister group to *G. integrifolia*.

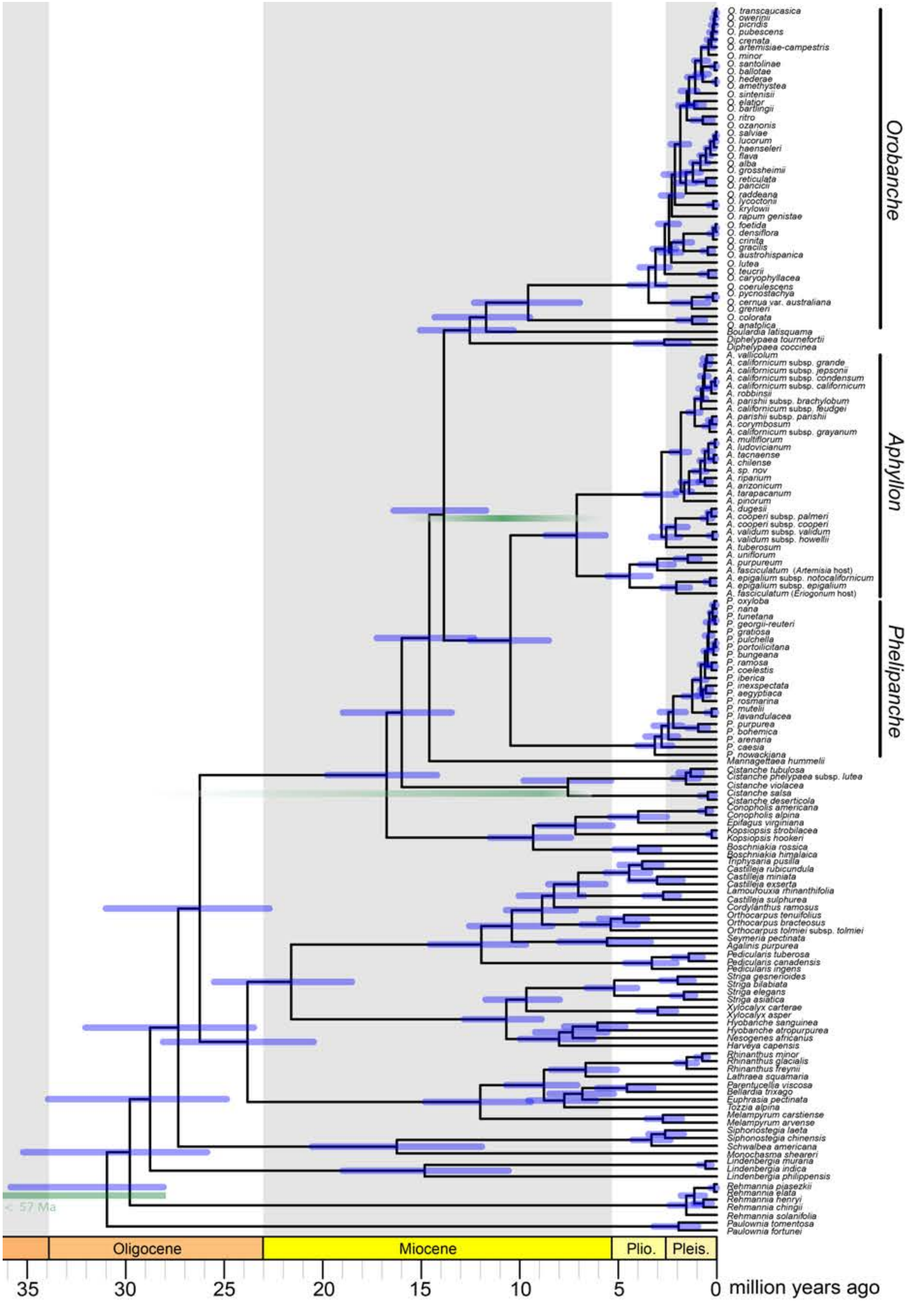
O. transcaucasica
O. owerinii
O. picridis
O. pubescens
O. crenata
O. artemisiae-campestris
O. minor
O. santolinae
O. ballotae
O. hederae
O. amethystea
O. sintenisii
O. elatior
O. bartlingii
O. ritro
O. ozanonis
O. salviae
O. lucorum
O. haenseleri
O. flava
O. alba
O. grossheimii
O. reticulata
O. pancicii
O. raddeana
O. lycoctonii
O. krylowii
O. rapum genistae
O. foetida
O. densiflora
O. crinita
O. gracilis
O. austrohispanica
O. lutea
O. teucrii
O. caryophyllacea
O. coerulescens
O. pycnostachya
O. cernua var. australiana
O. grenieri
O. colorata
O. anatolica
Boulardia latisquama
Diphelypaea tournefortii
Diphelypaea coccinea
A. vallicolum
A. californicum subsp. grande
A. californicum subsp. jepsonii
A. californicum subsp. condensum
A. californicum subsp. californicum
A. robbinsii
A. parishii subsp. brachylobum
A. californicum subsp. feudgei
A. parishii subsp. parishii
A. corymbosum
A. californicum subsp. grayanum
A. multiflorum
A. ludovicianum
A. tacnaense
A. chilense
A. sp. nov
A. riparium
A. arizonicum
A. tarapacanum
A. pinorum
A. dugesii
A. cooperi subsp. palmeri
A. cooperi subsp. cooperi
A. validum subsp. validum
A. validum subsp. howellii
A. tuberosum
A. uniflorum
A. purpureum
A. fasciculatum (Artemisia host)
A. epigalium subsp. notocalifornicum
A. epigalium subsp. epigalium
A. fasciculatum (Eriogonum host)
P. oxyloba
P. nana
P. tunetana
P. georgii-reuteri
P. gratiosa
P. pulchella
P. portoilicitana
P. bungeana
P. ramosa
P. coelestis
P. iberica
P. inexspectata
P. aegyptiaca
P. rosmarina
P. mutelii
P. lavandulacea
P. purpurea
P. bohemica
P. arenaria
P. caesia
P. nowackiana
Mannagettaea hummelii
Cistanche tubulosa
Cistanche phelypaea subsp. lutea
Cistanche violacea
Cistanche salsa
Cistanche deserticola
Conopholis americana
Conopholis alpina
Epifagus virginiana
Kopsiopsis strobilacea
Kopsiopsis hookeri
Boschniakia rossica
Boschniakia himalaica
Triphysaria pusilla
Castilleja rubicundula
Castilleja miniata
Castilleja exserta
Lamourouxia rhinanthifolia
Castilleja sulphurea
Cordylanthus ramosus
Orthocarpus tenuifolius
Orthocarpus bracteosus
Orthocarpus tolmiei subsp. tolmiei
Seymeria pectinata
Agalinis purpurea
Pedicularis tuberosa
Pedicularis canadensis
Pedicularis ingens
Striga gesnerioides
Striga bilabiata
Striga elegans
Striga asiatica
Xylocalyx carterae
Xylocalyx asper
Hyobanche sanguinea
Hyobanche atropurpurea
Nesogenes africanus
Harveya capensis
Rhinanthus minor
Rhinanthus glacialis
Rhinanthus freynii
Lathraea squamaria
Parentucellia viscosa
Bellardia trixago
Euphrasia pectinata
Tozzia alpina
Melampyrum carstiense
Melampyrum arvense
Siphonostegia laeta
Siphonostegia chinensis
Schwalbea americana
Monochasma sheareri
Lindenbergia muraria
Lindenbergia indica
Lindenbergia philippensis
Rehmannia piasezkii
Rehmannia elata
Rehmannia henryi
Rehmannia chingii
Rehmannia solanifolia
Paulownia tomentosa
Paulownia fortunei
Orobanche
Aphyllon
Phelipanche
< 57 Ma
Oligocene
Miocene
Plio.
Pleis.
35
30
25
20
15
10
5
0
million years ago

Figure 4.1. Bayesian Inference chronogram (maximum likelihood topology) of Orobanchaceae. Blue bars represent 95% HPD confidence intervals of node ages. Green bars represent priors on the root age (uniform), crown *Cistanche* (lognormal), and the most recent common ancestor of *Orobanche* and *Phelipanche* (normal).

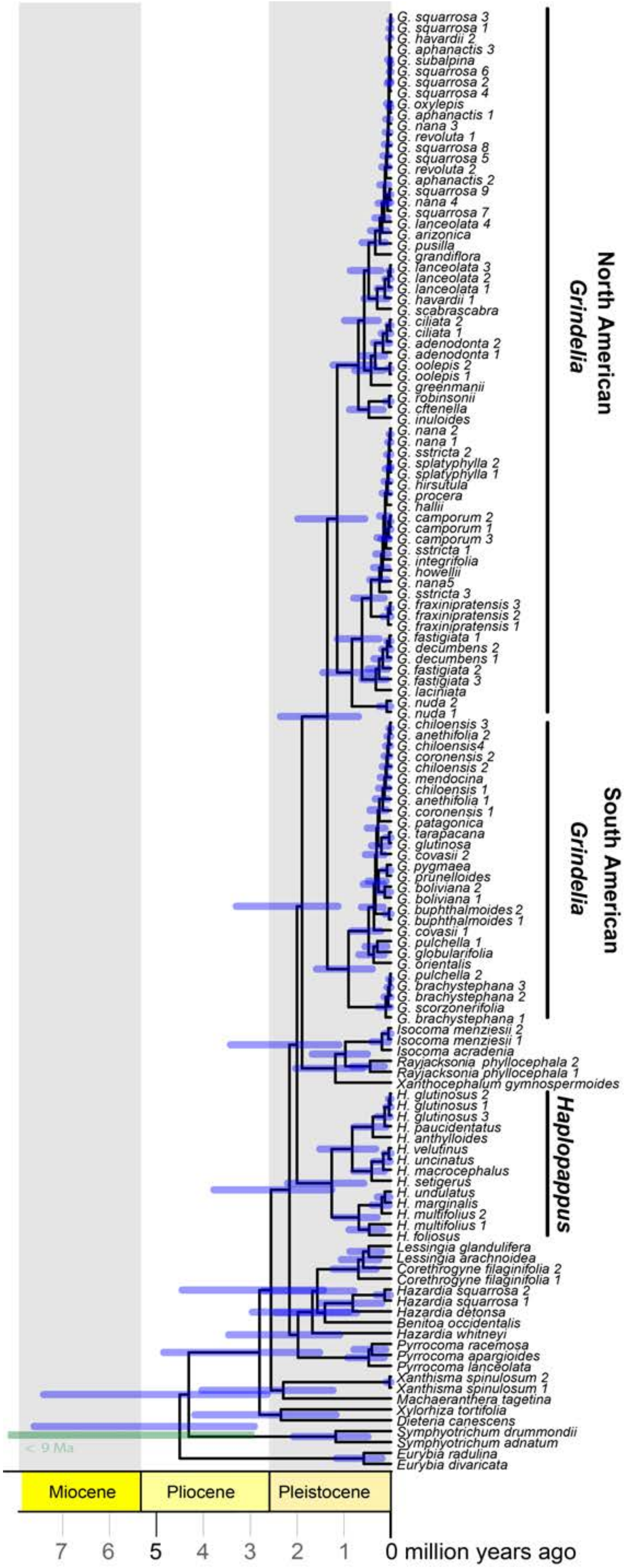
G. squarrosa 3
G. squarrosa 1
G. havardii 2
G. aphanactis 3
G. subalpina
G. squarrosa 6
G. squarrosa 2
G. squarrosa 4
G. oxylepis
G. aphanactis 1
G. nana 3
G. revoluta 1
G. squarrosa 8
G. squarrosa 5
G. revoluta 2
G. aphanactis 2
G. squarrosa 9
G. nana 4
G. squarrosa 7
G. lanceolata 4
G. arizonica
G. pusilla
G. grandiflora
G. lanceolata 3
G. lanceolata 2
G. lanceolata 1
G. havardii 1
G. scabrascabra
G. ciliata 2
G. ciliata 1
G. adenodonta 2
G. adenodonta 1
G. oolepis 2
G. oolepis 1
G. greenmanii
G. robinsonii
G. cftenella
G. inuloides
G. nana 2
G. nana 1
G. sstricta 2
G. splatyphylla 2
G. splatyphylla 1
G. hirsutula
G. procera
G. hallii
G. camporum 2
G. camporum 1
G. camporum 3
G. sstricta 1
G. integrifolia
G. howellii
G. nana5
G. sstricta 3
G. fraxinipratensis 3
G. fraxinipratensis 2
G. fraxinipratensis 1
G. fastigiata 1
G. decumbens 2
G. decumbens 1
G. fastigiata 2
G. fastigiata 3
G. laciniata
G. nuda 2
G. nuda 1
G. chiloensis 3
G. anethifolia 2
G. chiloensis4
G. coronensis 2
G. chiloensis 2
G. mendocina
G. chiloensis 1
G. anethifolia 1
G. coronensis 1
G. patagonica
G. tarapacana
G. glutinosa
G. covasii 2
G. pygmaea
G. prunelloides
G. boliviana 2
G. boliviana 1
G. buphthalmoides 2
G. buphthalmoides 1
G. covasii 1
G. pulchella 1
G. globularifolia
G. orientalis
G. pulchella 2
G. brachystephana 3
G. brachystephana 2
G. scorzonerifolia
G. brachystephana 1
Isocoma menziesii 2
Isocoma menziesii 1
Isocoma acradenia
Rayjacksonia phyllocephala 2
Rayjacksonia phyllocephala 1
Xanthocephalum gymnospermoides
H. glutinosus 2
H. glutinosus 1
H. glutinosus 3
H. paucidentatus
H. anthylloides
H. velutinus
H. uncinatus
H. macrocephalus
H. setigerus
H. undulatus
H. marginalis
H. multifolius 2
H. multifolius 1
H. foliosus
Lessingia glandulifera
Lessingia arachnoidea
Corethrogyne filaginifolia 2
Corethrogyne filaginifolia 1
Hazardia squarrosa 2
Hazardia squarrosa 1
Hazardia detonsa
Benitoa occidentalis
Hazardia whitneyi
Pyrrocoma racemosa
Pyrrocoma apargioides
Pyrrocoma lanceolata
Xanthisma spinulosum 2
Xanthisma spinulosum 1
Machaeranthera tagetina
Xylorhiza tortifolia
Dieteria canescens
Symphyotrichum drummondii
Symphyotrichum adnatum
Eurybia radulina
Eurybia divaricata
North American
Grindelia
South American
Grindelia
Haplopappus
< 9 Ma
Miocene
Pliocene
Pleistocene
7
6
5
4
3
2
1
0 million years ago

Figure 4.2. Bayesian Inference chronogram (maximum likelihood topology) of *Grindelia* and relatives (Asteraceae), reconstructed using RevBayes. Blue bars represent 95% HPD confidence intervals of node ages. The green bars represent the uniform prior on the root age.

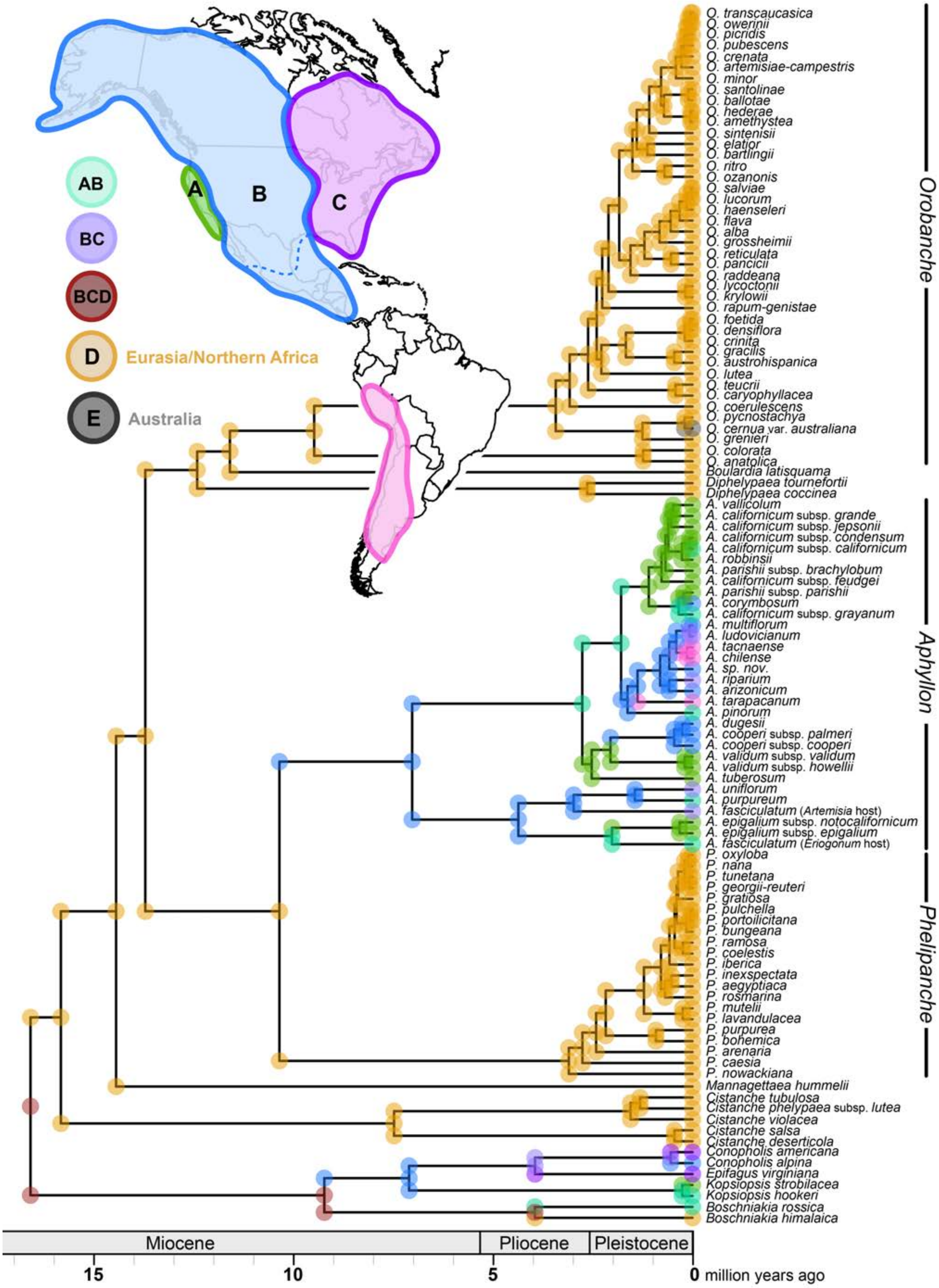
A
B
C
AB
BC
BCD
D Eurasia/Northern Africa
E Australia
O. transcaucasica
O. owerinii
O. picridis
O. pubescens
O. crenata
O. artemisiae-campestris
O. minor
O. santolinae
O. ballotae
O. hederae
O. amethystea
O. sintenisii
O. elatior
O. bartlingii
O. ritro
O. ozanonis
O. salviae
O. lucorum
O. haenseleri
O. flava
O. alba
O. grossheimii
O. reticulata
O. pancicii
O. raddeana
O. lycoctonii
O. krylowii
O. rapum-genistae
O. foetida
O. densiflora
O. crinita
O. gracilis
O. austrohispanica
O. lutea
O. teucrii
O. caryophyllacea
O. coerulescens
O. pycnostachya
O. cernua var. australiana
O. grenieri
O. colorata
O. anatolica
Boulardia latisquama
Diphelypaea tournefortii
Diphelypaea coccinea
A. vallicolum
A. californicum subsp. grande
A. californicum subsp. jepsonii
A. californicum subsp. condensum
A. californicum subsp. californicum
A. robbinsii
A. parishii subsp. brachylobum
A. californicum subsp. feudgei
A. parishii subsp. parishii
A. corymbosum
A. californicum subsp. grayanum
A. multiflorum
A. ludovicianum
A. tacnaense
A. chilense
A. sp. nov.
A. riparium
A. arizonicum
A. tarapacanum
A. pinorum
A. dugesii
A. cooperi subsp. palmeri
A. cooperi subsp. cooperi
A. validum subsp. validum
A. validum subsp. howellii
A. tuberosum
A. uniflorum
A. purpureum
A. fasciculatum (Artemisia host)
A. epigalium subsp. notocalifornicum
A. epigalium subsp. epigalium
A. fasciculatum (Eriogonum host)
P. oxyloba
P. nana
P. tunetana
P. georgii-reuteri
P. gratiosa
P. pulchella
P. portoilicitana
P. bungeana
P. ramosa
P. coelestis
P. iberica
P. inexspectata
P. aegyptiaca
P. rosmarina
P. mutelii
P. lavandulacea
P. purpurea
P. bohemica
P. arenaria
P. caesia
P. nowackiana
Mannagettaea hummelii
Cistanche tubulosa
Cistanche phelypaea subsp. lutea
Cistanche violacea
Cistanche salsa
Cistanche deserticola
Conopholis americana
Conopholis alpina
Epifagus virginiana
Kopsiopsis strobilacea
Kopsiopsis hookeri
Boschniakia rossica
Boschniakia himalaica
Orobanche
Aphyllon
Phelipanche
Miocene
Pliocene
Pleistocene
15
10
5
0 million years ago

Figure 4.3. Bayesian Inference chronogram (maximum likelihood topology) of Orobancheae biogeography, reconstructed using a DEC+J model implemented in RevBayes. Colored circles at tips represent the biogeographical range of each taxon. Circles on each node represent the reconstructed ancestral area of the most recent common ancestor of the two daughter lineages, while circles on either side of the node show the reconstructed areas immediately following cladogenesis. Each color represents a different biogeographical region or combination of regions as indicated by the map and legend in the upper left. The blue dashed line represents the southernmost extent of *Aphyllon* in North America.

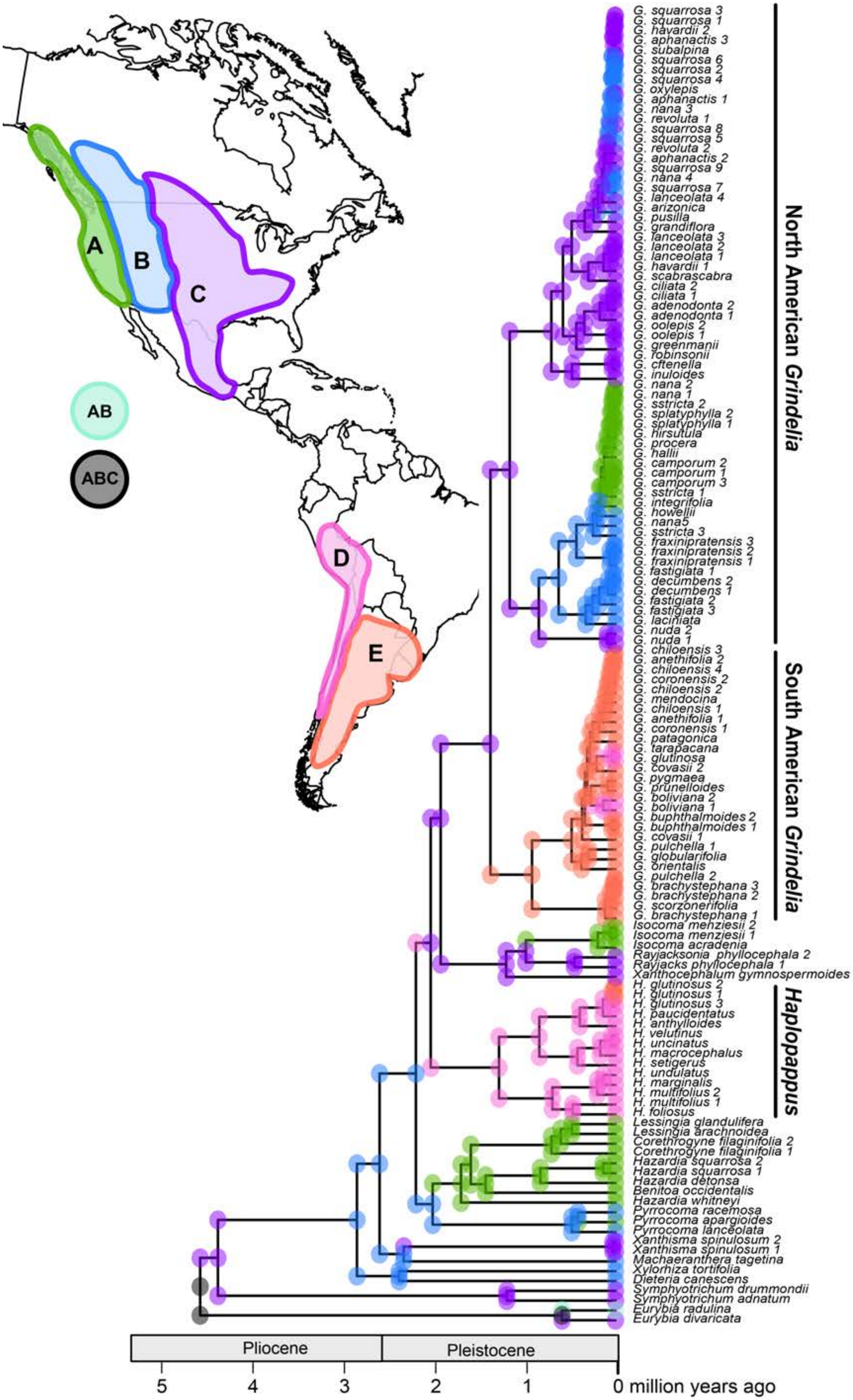
A
B
C
D
E
AB
ABC
G. squarrosa 3
G. squarrosa 1
G. havardii 2
G. aphanactis 3
G. subalpina
G. squarrosa 6
G. squarrosa 2
G. squarrosa 4
G. oxylepis
G. aphanactis 1
G. nana 3
G. revoluta 1
G. squarrosa 8
G. squarrosa 5
G. revoluta 2
G. aphanactis 2
G. squarrosa 9
G. nana 4
G. squarrosa 7
G. lanceolata 4
G. arizonica
G. pusilla
G. grandiflora
G. lanceolata 3
G. lanceolata 2
G. lanceolata 1
G. havardii 1
G. scabrascabra
G. ciliata 2
G. ciliata 1
G. adenodonta 2
G. adenodonta 1
G. oolepis 2
G. oolepis 1
G. greenmanii
G. robinsonii
G. cftenella
G. inuloides
G. nana 2
G. nana 1
G. sstricta 2
G. splatyphylla 2
G. splatyphylla 1
G. hirsutula
G. procera
G. hallii
G. camporum 2
G. camporum 1
G. camporum 3
G. sstricta 1
G. integrifolia
G. howellii
G. nana5
G. sstricta 3
G. fraxinipratensis 3
G. fraxinipratensis 2
G. fraxinipratensis 1
G. fastigiata 1
G. decumbens 2
G. decumbens 1
G. fastigiata 2
G. fastigiata 3
G. laciniata
G. nuda 2
G. nuda 1
G. chiloensis 3
G. anethifolia 2
G. chiloensis 4
G. coronensis 2
G. chiloensis 2
G. mendocina
G. chiloensis 1
G. anethifolia 1
G. coronensis 1
G. patagonica
G. tarapacana
G. glutinosa
G. covasii 2
G. pygmaea
G. prunelloides
G. boliviana 2
G. boliviana 1
G. buphthalmoides 2
G. buphthalmoides 1
G. covasii 1
G. pulchella 1
G. globularifolia
G. orientalis
G. pulchella 2
G. brachystephana 3
G. brachystephana 2
G. scorzonerifolia
G. brachystephana 1
Isocoma menziesii 2
Isocoma menziesii 1
Isocoma acradenia
Rayjacksonia phyllocephala 2
Rayjacks phyllocephala 1
Xanthocephalum gymnospermoides
H. glutinosus 2
H. glutinosus 1
H. glutinosus 3
H. paucidentatus
H. anthylloides
H. velutinus
H. uncinatus
H. macrocephalus
H. setigerus
H. undulatus
H. marginalis
H. multifolius 2
H. multifolius 1
H. foliosus
Lessingia glandulifera
Lessingia arachnoidea
Corethrogyne filaginifolia 2
Corethrogyne filaginifolia 1
Hazardia squarrosa 2
Hazardia squarrosa 1
Hazardia detonsa
Benitoa occidentalis
Hazardia whitneyi
Pyrrocoma racemosa
Pyrrocoma apargioides
Pyrrocoma lanceolata
Xanthisma spinulosum 2
Xanthisma spinulosum 1
Machaeranthera tagetina
Xylorhiza tortifolia
Dieteria canescens
Symphyotrichum drummondii
Symphyotrichum adnatum
Eurybia radulina
Eurybia divaricata
North American Grindelia
South American Grindelia
Haplopappus
Pliocene
Pleistocene
5
4
3
2
1
0 million years ago

Figure 4.4. Bayesian Inference chronogram (maximum likelihood topology) of *Grindelia* and relatives showing biogeography, reconstructed using a DEC+J model implemented in RevBayes. Colored circles on each node represent the reconstructed ancestral area of the most recent common ancestor of the two daughter lineages, while circles on either side of the node show the reconstructed areas immediately following cladogenesis. The map indicates which colors indicate which regions, with multiple-region states indicated by colored circles under the map.

Appendix A

Flowering time and serpentine tolerance trait data for 1205 minimum-ranked taxa in the study presented in Chapter 1

Column	Description
Clade --------------------------	The study clade including the sample
Genus -------------------------	Genus
species_infraspecies -------	Species epithet followed by infraspecific epithet (subspecies or variety) if applicable.
Serp. tolerance --------------	Categorizes the taxon into one of three groups based on the serpentine affinity score of Safford et al. (2005) or the flora treatment in the Jepson Manual ed. 2. **E** = serpentine endemic (Safford score > 4.5), **T =** tolerant but not endemic (Safford score between 0 and 4.5), and **N =** non-tolerant
Safford Index-----------------	Serpentine affinity on a scale of 1.0 to 6.25 representing increasing endemism, as determined by Safford et al. (2005). Taxa with no entry here were not included in Safford's database and are assumed to be not serpentine tolerant, unless otherwise specified in the Jepson Manual ed. 2. (Baldwin *et al.* 2012)
Onset---------------------------	flowering onset, as reported by the regional flora
Ending------------------------	flowering ending, as reported by the regional flora
Midpoint---------------------	flowering time midpoint, by Julian Day (Jan 1 = 1, Feb. 1 = 32, etc.) or by month (Jan 1 = 1.0, Feb. 1 = 2.0, etc.)
CA native---------------------	Is this taxon native to California? Based on the Jepson Manual ed. 2 (Baldwin *et al.* 2012).
Phylogeny--------------------	Did the available phylogenies include this taxon?

LITERATURE CITED

Baldwin, B. G., D. H. Goldman, D. J. Keil, R. Patterson, T. J. Rosatti, and D. H. Wilken, editors. 2012. *The Jepson manual: Vascular plants of California.* Second edition. University of California Press, Berkeley, California.

Safford, H. D., J. H. Viers, and S. P. Harrison. 2005. Serpentine endemism in the California flora: a database of serpentine affinity. *Madroño* 52: 222–257.

					Flowering time					
							Midpoint			
Clade	Genus	species_infraspecies	Serp. toler-ance	Safford Index	Onset	Ending	(day)	(mo)	CA native	Phylo-geny
Allium	Allium	abramsii	N		May	July	167	6.5	yes	yes
Allium	Allium	acuminatum	T	1.5	April	July	151.5	6	yes	no
Allium	Allium	amplectens	T	2.3	April	July	151.5	6	yes	yes
Allium	Allium	anceps	N		April	May	121	5	yes	yes
Allium	Allium	atrorubens_atrorubens	N		May	June	152	6	yes	yes
Allium	Allium	atrorubens_cristatum	N		May	June	152	6	yes	yes
Allium	Allium	bisceptrum	N		May	July	167	6.5	yes	no
Allium	Allium	bolanderi_bolanderi	T	1.1	May	August	182	7	yes	no
Allium	Allium	bolanderi_mirabile	T	2.3	May	July	167	6.5	yes	no
Allium	Allium	bolanderi_peninsulare	T		May	August	182	7	no	yes
Allium	Allium	brevistylum	N		June	August	197	7.5	no	yes
Allium	Allium	burlewii	N		April	July	151.5	6	yes	yes
Allium	Allium	campanulatum	T		May	August	182	7	no	yes
Allium	Allium	canadense_canadense	N		April	July	151.5	6	no	yes
Allium	Allium	cernuum	N		July	October	243	9	yes	no
Allium	Allium	cratericola	T	2.6	March	June	121	5	yes	yes
Allium	Allium	crispum	T	1.3	March	June	121	5	yes	yes
Allium	Allium	denticulatum	N		April	July	151.5	6	yes	yes
Allium	Allium	diabolense	E	6	April	June	136	5.5	yes	yes
Allium	Allium	diclamydeum	T		May	July	167	6.5	yes	yes
Allium	Allium	drummondii	N		March	June	121	5	no	yes
Allium	Allium	falcifolium	T	4.2	April	June	136	5.5	yes	yes
Allium	Allium	fimbriatum_fimbriatum	T		April	June	136	5.5	yes	yes
Allium	Allium	fimbriatum_mohavense	N		April	May	121	5	yes	no
Allium	Allium	fimbriatum_purdyi	E	5.4	April	June	136	5.5	yes	yes
Allium	Allium	geyeri	N		May	September	197	7.5	no	yes

Allium	Allium	goodingii	N		June	September	212.5	8	no	yes
Allium	Allium	haematochiton	N		March	May	106	4.5	yes	yes
Allium	Allium	hickmanii	N		March	May	106	4.5	yes	yes
Allium	Allium	hoffmanii	E	6.1	June	July	182	7	yes	yes
Allium	Allium	howelii_sanbenitense	N		April	May	121	5	yes	no
Allium	Allium	howellii_clokeyi	N		May	June	152	6	yes	no
Allium	Allium	howellii_howellii	T		March	April	91	4	yes	yes
Allium	Allium	hyalinum	T		March	May	106	4.5	yes	yes
Allium	Allium	jepsonii	E	5.4	May	July	167	6.5	yes	yes
Allium	Allium	lacunosum_davidsiae	N		April	May	121	5	yes	no
Allium	Allium	lacunosum_kernense	N		April	May	121	5	yes	no
Allium	Allium	lacunosum_lacunosum	T	3.8	April	May	121	5	yes	no
Allium	Allium	lacunosum_micranthum	T	4.3	April	May	121	5	yes	no
Allium	Allium	lemmonii	N		May	June	152	6	yes	yes
Allium	Allium	marvinii	N		March	April	91	4	yes	no
Allium	Allium	membranaceum	T	1.3	May	June	152	6	yes	yes
Allium	Allium	monticola	N		May	July	167	6.5	yes	no
Allium	Allium	munzii	N		April	May	121	5	yes	no
Allium	Allium	nevadense	N		April	June	136	5.5	yes	no
Allium	Allium	obtusum_conspicuum	T	1	May	June	152	6	yes	no
Allium	Allium	obtusum_obtusum	N		May	June	152	6	yes	yes
Allium	Allium	paniculatum_paniculatum	N		June	July	-30	0	yes	no
Allium	Allium	parishii	N		April	May	121	5	yes	no
Allium	Allium	parryi	N		May	July	167	6.5	yes	no
Allium	Allium	parvum	T		April	June	136	5.5	yes	yes
Allium	Allium	peninsulare_franciscanum	T	1.8	May	June	152	6	yes	no
Allium	Allium	peninsulare_peninsulare	N		April	May	121	5	yes	yes
Allium	Allium	platycaule	N		May	June	152	6	yes	yes
Allium	Allium	praecox	N		March	May	106	4.5	yes	yes
Allium	Allium	punctum	N		May	June	152	6	yes	yes
Allium	Allium	sanbornii_congdonii	E	5.6	June	July	182	7	yes	no

Allium	Allium	sanbornii_sanbornii	T	3.4	June	August	197	7.5	yes	yes
Allium	Allium	serra	T	2.6	April	May	121	5	yes	yes
Allium	Allium	sharsmithiae	E	5.1	April	May	121	5	yes	yes
Allium	Allium	shevockii	N		June	July	182	7	yes	yes
Allium	Allium	siskiyouense	T	2.8	April	June	136	5.5	yes	yes
Allium	Allium	stellatum	N		July	October	244	9	no	yes
Allium	Allium	tolmei_tolmei	N		April	July	151.5	6	yes	no
Allium	Allium	tribracteatum	N		March	May	106	4.5	yes	yes
Allium	Allium	triquetrum	N		March	April	91	4	yes	yes
Allium	Allium	tuolumnense	E	6.2	March	May	106	4.5	yes	yes
Allium	Allium	unifolium	T	1	May	June	152	6	yes	yes
Allium	Allium	validum	N		June	August	197	7.5	yes	yes
Allium	Allium	yosemitense	N		May	June	152	6	yes	yes
Aquilegia	Aquilegia	brevistyla	N		June	August	197.5	7.5	no	yes
Aquilegia	Aquilegia	canadensis	N		March	June	120.5	5	no	yes
Aquilegia	Aquilegia	coerulea_alpina	N		June	August	197.5	7.5	no	yes
Aquilegia	Aquilegia	coerulea_coerulea	N		mid-June	early September	212.5	8	no	yes
Aquilegia	Aquilegia	coerulea_ochroleuca	N		late June	August	207.5	7.75	no	yes
Aquilegia	Aquilegia	elegantula	N		May	July	166.5	6.5	no	yes
Aquilegia	Aquilegia	eximia	E	4.2	May	October	212.5	8	yes	yes
Aquilegia	Aquilegia	flavescens	N		June	August	197.5	7.5	yes	yes
Aquilegia	Aquilegia	formosa	T		April	September	182	7	no	yes
Aquilegia	Aquilegia	jonesii	N		June	July	182	7	no	yes
Aquilegia	Aquilegia	laramiensis	N		June	July	182	7	no	yes
Aquilegia	Aquilegia	pubescens	N		July	August	212.5	8	yes	yes
Aquilegia	Aquilegia	saximontana	N		July	August	212.5	8	no	yes
Aquilegia	Aquilegia	shockleyi	N		May	August	182	7	yes	yes
Aquilegia	Aquilegia	vulgaris	N		May	July	166.5	6.5	no	yes
Arctostaphylos	Arctostaphylos	andersonii	N		January	March	45.5	2.5	yes	yes
Arctostaphylos	Arctostaphylos	auriculata	N		February	March	61	3	yes	yes

Arctostaphylos	Arctostaphylos	bakeri	T	5.5	February	April	76	3.5	yes	yes
Arctostaphylos	Arctostaphylos	bakeri_sublaevis	E	6.3	February	April	76	3.5	yes	no
Arctostaphylos	Arctostaphylos	canescens_canescens	N		January	May	76	3.5	yes	no
Arctostaphylos	Arctostaphylos	canescens_sonomensis	T	2.5	March	May	105.5	4.5	yes	yes
Arctostaphylos	Arctostaphylos	catalinae	N		October	February	16	1.5	yes	yes
Arctostaphylos	Arctostaphylos	columbiana	T		March	May	105.5	4.5	yes	yes
Arctostaphylos	Arctostaphylos	confertiflora	N		February	March	61	3	yes	no
Arctostaphylos	Arctostaphylos	crustacea_crinita	N		February	April	76	3.5	yes	no
Arctostaphylos	Arctostaphylos	crustacea_crustacea	N		February	April	76	3.5	yes	no
Arctostaphylos	Arctostaphylos	crustacea_eastwoodiana	N		February	April	76	3.5	yes	no
Arctostaphylos	Arctostaphylos	crustacea_insulicola	N		February	April	76	3.5	yes	no
Arctostaphylos	Arctostaphylos	crustacea_rosei	N		February	April	76	3.5	yes	no
Arctostaphylos	Arctostaphylos	crustacea_subcordata	N		February	April	76	3.5	yes	no
Arctostaphylos	Arctostaphylos	cruzensis	N		January	March	45.5	2.5	yes	yes
Arctostaphylos	Arctostaphylos	densiflora	N		March	April	90	4	yes	yes
Arctostaphylos	Arctostaphylos	edmundsii	N		November	December	-30	0	yes	no
Arctostaphylos	Arctostaphylos	franciscana	E	6.2	January	April	60.5	3	yes	yes
Arctostaphylos	Arctostaphylos	gabilanensis	N		February	April	76	3.5	yes	no
Arctostaphylos	Arctostaphylos	glandulosa_adamsii	N		January	April	60.5	3	yes	no
Arctostaphylos	Arctostaphylos	glandulosa_crassifolia	N		October	February	60.5	3	yes	no
Arctostaphylos	Arctostaphylos	glandulosa_cushingiana	N		January	April	60.5	3	yes	no
Arctostaphylos	Arctostaphylos	glandulosa_gabrielensis	N		January	April	60.5	3	yes	no
Arctostaphylos	Arctostaphylos	glandulosa_glandulosa	N		January	April	60.5	3	yes	no
Arctostaphylos	Arctostaphylos	glandulosa_howellii	N		January	April	60.5	3	yes	no
Arctostaphylos	Arctostaphylos	glandulosa_leucophylla	N		January	April	60.5	3	yes	no
Arctostaphylos	Arctostaphylos	glandulosa_mollis	N		January	April	60.5	3	yes	yes
Arctostaphylos	Arctostaphylos	glauca	T		October	March	32	2	yes	yes
Arctostaphylos	Arctostaphylos	glutinosa	N		January	March	45.5	2.5	yes	no
Arctostaphylos	Arctostaphylos	hispidula	E	4.5	March	April	90	4	yes	yes
Arctostaphylos	Arctostaphylos	hookeri_hearstiorum	N		February	April	76	3.5	yes	yes
Arctostaphylos	Arctostaphylos	hookeri_hookeri	N		February	April	76	3.5	yes	yes

Arctostaphylos	Arctostaphylos	hookeri_ravenii	E	6.2	February	April	76	3.5	yes	yes
Arctostaphylos	Arctostaphylos	hooveri	N		February	April	76	3.5	yes	yes
Arctostaphylos	Arctostaphylos	imbricata	N		January	March	45.5	2.5	yes	yes
Arctostaphylos	Arctostaphylos	insularis	N		January	March	45.5	2.5	yes	no
Arctostaphylos	Arctostaphylos	klamathensis	T	3.9	May	July	166.5	6.5	yes	no
Arctostaphylos	Arctostaphylos	luciana	N		January	March	45.5	2.5	yes	no
Arctostaphylos	Arctostaphylos	malloryi	N		February	April	76	3.5	yes	no
Arctostaphylos	Arctostaphylos	manzanita_elegans	N		February	May	91.5	4	yes	no
Arctostaphylos	Arctostaphylos	manzanita_glaucesens	N		February	May	91.5	4	yes	no
Arctostaphylos	Arctostaphylos	manzanita_laevigata	N		February	May	91.5	4	yes	no
Arctostaphylos	Arctostaphylos	manzanita_manzanita	T		February	May	91.5	4	yes	yes
Arctostaphylos	Arctostaphylos	manzanita_roofii	N		February	May	91.5	4	yes	yes
Arctostaphylos	Arctostaphylos	manzanita_wieslanderi	N		February	May	91.5	4	yes	no
Arctostaphylos	Arctostaphylos	mewukka_mewkka	N		March	April	90	4	yes	yes
Arctostaphylos	Arctostaphylos	mewukka_truei	N		March	April	90	4	yes	no
Arctostaphylos	Arctostaphylos	montana_montana	T	4.9	February	April	76	3.5	yes	no
Arctostaphylos	Arctostaphylos	montanta_ravenii	E	6.2	February	April	76	3.5	yes	no
Arctostaphylos	Arctostaphylos	montaraensis	N		January	March	45.5	2.5	yes	no
Arctostaphylos	Arctostaphylos	montereyensis	N		January	March	45.5	2.5	yes	yes
Arctostaphylos	Arctostaphylos	morroensis	N		January	March	45.5	2.5	yes	yes
Arctostaphylos	Arctostaphylos	myrtifolia	N		January	February	32	2	yes	yes
Arctostaphylos	Arctostaphylos	nevadensis_knightii	N		May	July	166.5	6.5	yes	no
Arctostaphylos	Arctostaphylos	nevadensis_nevadensis	N		May	July	166.5	6.5	yes	no
Arctostaphylos	Arctostaphylos	nissenana	N		February	March	61	3	yes	yes
Arctostaphylos	Arctostaphylos	nortensis	T	2.8	March	May	105.5	4.5	yes	no
Arctostaphylos	Arctostaphylos	nummularia_mendocinoensis	N		March	May	105.5	4.5	yes	yes
Arctostaphylos	Arctostaphylos	nummularia_nummularia	N		March	May	105.5	4.5	yes	yes
Arctostaphylos	Arctostaphylos	obispoensis	E	5.7	February	March	61	3	yes	yes
Arctostaphylos	Arctostaphylos	ohloneana	N		February	March	61	3	yes	no
Arctostaphylos	Arctostaphylos	osoensis	N		October	February	16	1.5	yes	no
Arctostaphylos	Arctostaphylos	otayensis	N		January	March	45.5	2.5	yes	no

Arctostaphylos	Arctostaphylos	pacifica	N		January	March	45.5	2.5	yes	no
Arctostaphylos	Arctostaphylos	pajaroensis	N		October	February	16	1.5	yes	yes
Arctostaphylos	Arctostaphylos	pallida	N		January	March	45.5	2.5	yes	yes
Arctostaphylos	Arctostaphylos	parryana_desertica	N		January	March	45.5	2.5	yes	no
Arctostaphylos	Arctostaphylos	parryana_parryana	N		March	May	105.5	4.5	yes	yes
Arctostaphylos	Arctostaphylos	parryana_tumescens	N		March	April	90	4	yes	no
Arctostaphylos	Arctostaphylos	patula	T		April	June	136	5.5	yes	yes
Arctostaphylos	Arctostaphylos	pechoensis	N		January	March	45.5	2.5	yes	yes
Arctostaphylos	Arctostaphylos	pilosula	N		October	March	32	2	yes	yes
Arctostaphylos	Arctostaphylos	pringlei_drupacea	N		February	April	76	3.5	yes	yes
Arctostaphylos	Arctostaphylos	pumila	N		February	April	76	3.5	yes	no
Arctostaphylos	Arctostaphylos	pungens	T		February	March	61	3	yes	yes
Arctostaphylos	Arctostaphylos	purissima	N		January	March	45.5	2.5	yes	yes
Arctostaphylos	Arctostaphylos	rainbowensis	N		January	February	32	2	yes	no
Arctostaphylos	Arctostaphylos	refugioensis	N		October	February	16	1.5	yes	yes
Arctostaphylos	Arctostaphylos	regismonana	N		January	March	45.5	2.5	yes	no
Arctostaphylos	Arctostaphylos	rudis	N		October	February	1	1	yes	no
Arctostaphylos	Arctostaphylos	sensitiva	N		January	April	60.5	3	yes	no
Arctostaphylos	Arctostaphylos	silvicola	N		February	March	61	3	yes	yes
Arctostaphylos	Arctostaphylos	stanfordiana_decumbens	N		February	April	76	3.5	yes	no
Arctostaphylos	Arctostaphylos	stanfordiana_raichei	T	2.6	February	April	76	3.5	yes	no
Arctostaphylos	Arctostaphylos	stanfordiana_stanfordiana	N		February	April	76	3.5	yes	yes
Arctostaphylos	Arctostaphylos	tomentosa_bracteosa	N		October	March	32	2	yes	no
Arctostaphylos	Arctostaphylos	tomentosa_daciticola	N		October	March	32	2	yes	no
Arctostaphylos	Arctostaphylos	tomentosa_hebeclada	N		October	March	32	2	yes	no
Arctostaphylos	Arctostaphylos	tomentosa_tomentosa	T		October	March	32	2	yes	yes
Arctostaphylos	Arctostaphylos	uva_ursi	T		January	June	91	4	yes	yes
Arctostaphylos	Arctostaphylos	virgata	N		October	February	16	1.5	yes	no
Arctostaphylos	Arctostaphylos	viridissima	N		January	March	45.5	2.5	yes	yes
Arctostaphylos	Arctostaphylos	viscida_mariposa	N		February	April	76	3.5	yes	no
Arctostaphylos	Arctostaphylos	viscida_pulchella	E	5	February	April	76	3.5	yes	no

Arctostaphylos	Arctostaphylos	viscida_viscida	T	2.2	February	April	76	3.5	yes	yes
Balsamorhiza	Balsamorhiza	careyana	N		(March-) May	June (-July)	143	5.75	no	yes
Balsamorhiza	Balsamorhiza	deltoidea	T		April	July	151.5	6	yes	yes
Balsamorhiza	Balsamorhiza	hookeri_hirsuta	N		May	July	166.5	6.5	yes	yes
Balsamorhiza	Balsamorhiza	hookeri_hispidula	N		May	July	166.5	6.5	yes	yes
Balsamorhiza	Balsamorhiza	hookeri_lagocephala	N		May	July	166.5	6.5	no	yes
Balsamorhiza	Balsamorhiza	hookeri_lanata	T		April	June	136	5.5	yes	yes
Balsamorhiza	Balsamorhiza	hookeri_neglecta	N		May	July	166.5	6.5	no	yes
Balsamorhiza	Balsamorhiza	incana	N		May	June (-July)	159	6.25	no	yes
Balsamorhiza	Balsamorhiza	macrolepis_macrolepis	T	2.5	March	July	136	5.5	yes	yes
Balsamorhiza	Balsamorhiza	macrolepis_platylepis	N		March	July	136	5.5	no	yes
Balsamorhiza	Balsamorhiza	rosea	N		April	May	121	5	no	yes
Balsamorhiza	Balsamorhiza	sagittata	N		May	August	182	7	yes	yes
Balsamorhiza	Balsamorhiza	sericea	E	6.2	May	June	151	6	yes	yes
Balsamorhiza	Balsamorhiza	serrata	N		April	June	136	5.5	yes	yes
Calochortus	Calochortus	albus_albus	T		April	June	136	5.5	yes	yes
Calochortus	Calochortus	albus_rubellus	T		April	June	136	5.5	yes	yes
Calochortus	Calochortus	amabilis	T		April	June	136	5.5	yes	yes
Calochortus	Calochortus	amoenus	T		April	June	136	5.5	yes	yes
Calochortus	Calochortus	argillosus	T		April	June	136	5.5	yes	yes
Calochortus	Calochortus	bruneaunis	N		May	August	182	7	yes	yes
Calochortus	Calochortus	catalinae	N		March	May	105.5	4.5	yes	yes
Calochortus	Calochortus	clavatus_avius	N		May	July	166.5	6.5	yes	no
Calochortus	Calochortus	clavatus_clavatus	T	4.5	April	June	136	5.5	yes	no
Calochortus	Calochortus	clavatus_gracilis	N		May	June	151	6	yes	no
Calochortus	Calochortus	clavatus_pallidus	T		April	July	151.5	6	yes	no
Calochortus	Calochortus	clavatus_recurvifolius	E		May	July	166.5	6.5	yes	yes
Calochortus	Calochortus	coeruleus	N		May	June	151	6	yes	yes
Calochortus	Calochortus	concolor	N		May	July	166.5	6.5	yes	no
Calochortus	Calochortus	davidsonianus	T		May	July	166.5	6.5	no	yes

Calochortus	Calochortus	dunnii	N		June	June	166.5	6.5	yes	yes
Calochortus	Calochortus	elegans	T	2	May	July	166.5	6.5	yes	yes
Calochortus	Calochortus	excavatus	N		April	May	121	5	yes	yes
Calochortus	Calochortus	fimbriatus	T	1.5	July	August	212.5	8	yes	no
Calochortus	Calochortus	flexuosus	N		April	May	121	5	yes	yes
Calochortus	Calochortus	greenei	E	6	June	July	182	7	yes	yes
Calochortus	Calochortus	invenustus	N		May	August	182	7	yes	no
Calochortus	Calochortus	kennedyi_kennedyi	N		April	June	136	5.5	yes	yes
Calochortus	Calochortus	kennedyi_munzii	N		April	June	136	5.5	yes	no
Calochortus	Calochortus	leichtlinii	T		June	August	197.5	7.5	yes	yes
Calochortus	Calochortus	longebarbatus_longebarbatus	N		June	August	197.5	7.5	yes	yes
Calochortus	Calochortus	luteus	T		April	June	136	5.5	yes	yes
Calochortus	Calochortus	macrocarpus	N		June	August	197.5	7.5	yes	yes
Calochortus	Calochortus	minimus	N		May	August	182	7	yes	yes
Calochortus	Calochortus	monanthus	N		June	June	166.5	6.5	yes	no
Calochortus	Calochortus	monophyllus	T		April	May	121	5	yes	yes
Calochortus	Calochortus	nudus	T	2.1	May	July	166.5	6.5	yes	yes
Calochortus	Calochortus	obispoensis	E	5.4	May	June	151	6	yes	yes
Calochortus	Calochortus	palmeri_munzii	N		June	June	166.5	6.5	yes	no
Calochortus	Calochortus	palmeri_palmeri	N		May	July	166.5	6.5	yes	yes
Calochortus	Calochortus	persistens	T		June	July	182	7	yes	yes
Calochortus	Calochortus	plummerae	N		May	July	166.5	6.5	yes	yes
Calochortus	Calochortus	pulchellus	E		April	June	136	5.5	yes	yes
Calochortus	Calochortus	raichei	E	6.2	May	August	182	7	yes	yes
Calochortus	Calochortus	simulans	N		May	July	166.5	6.5	yes	no
Calochortus	Calochortus	splendens	T		May	July	166.5	6.5	yes	yes
Calochortus	Calochortus	striatus	N		April	June	136	5.5	yes	no
Calochortus	Calochortus	superbus	T		May	July	166.5	6.5	yes	yes
Calochortus	Calochortus	syntrophus	N		May	June	151	6	yes	no
Calochortus	Calochortus	tiburonensis	E	6.1	May	June	151	6	yes	yes

Calochortus	Calochortus	tolmiei	T		April	July	151.5	6	yes	yes
Calochortus	Calochortus	umbellatus	T	2.9	March	May	105.5	4.5	yes	yes
Calochortus	Calochortus	uniflorus	T	1.7	April	June	136	5.5	yes	yes
Calochortus	Calochortus	venustus	T		May	July	166.5	6.5	yes	yes
Calochortus	Calochortus	vestae	T		May	July	166.5	6.5	yes	yes
Calochortus	Calochortus	weedii_intermedius	N		June	July	182	7	yes	yes
Calochortus	Calochortus	weedii_vestus	T	1	July	August	212.5	8	no	yes
Calochortus	Calochortus	weedii_weedii	N		May	August	182	7	yes	yes
Calochortus	Calochortus	westonii	N		May	June	151	6	yes	yes
Calycadenia	Calycadenia	fremontii	N		April	October	197.5	7.5	no	yes
Calycadenia	Calycadenia	hooveri	N		June	September	212.5	8	yes	yes
Calycadenia	Calycadenia	micrantha	N		June	October	228	8.5	yes	no
Calycadenia	Calycadenia	mollis	N		May	September	197	7.5	yes	yes
Calycadenia	Calycadenia	multiglandulosa	T	3.1	May	October	212.5	8	yes	yes
Calycadenia	Calycadenia	oppositifolia	T	2.6	April	July	151.5	6	yes	yes
Calycadenia	Calycadenia	pauciflora	E	5.3	April	September	182	7	yes	yes
Calycadenia	Calycadenia	spicata	N		May	September	197	7.5	yes	yes
Calycadenia	Calycadenia	truncata	T	2.1	May	October	212.5	8	yes	yes
Calycadenia	Calycadenia	villosa	N		May	September	197	7.5	yes	yes
Ceanothus	Ceanothus	arboreus	N		February	May	91.5	4	yes	yes
Ceanothus	Ceanothus	arcuatus	N		April	June	136	5.5	yes	no
Ceanothus	Ceanothus	confusus	T	1.3	February	April	76	3.5	yes	yes
Ceanothus	Ceanothus	cordulatus	T		May	July	166.5	6.5	yes	yes
Ceanothus	Ceanothus	crassifolius_crassifolius	T		January	April	60.5	3	yes	yes
Ceanothus	Ceanothus	crassifolius_planus	N		January	April	60.5	3	yes	no
Ceanothus	Ceanothus	cuneatus_cuneatus	T	1.5	February	May	91.5	4	yes	yes
Ceanothus	Ceanothus	cuneatus_fascicularis	N		February	May	91.5	4	yes	no
Ceanothus	Ceanothus	cuneatus_ramulosus	N		February	May	91.5	4	yes	no
Ceanothus	Ceanothus	cyaneus	N		April	June	136	5.5	yes	yes
Ceanothus	Ceanothus	dentatus	N		March	June	120.5	5	yes	yes
Ceanothus	Ceanothus	divergens	T	2	February	April	76	3.5	yes	yes

Ceanothus	Ceanothus	diversifolius	N		April	June	136	5.5	yes	yes
Ceanothus	Ceanothus	ferrisae	E	6.1	January	May	76	3.5	yes	yes
Ceanothus	Ceanothus	foliosus_foliosus	N		March	June	120.5	5	yes	no
Ceanothus	Ceanothus	foliosus_medius	T	4	March	June	120.5	5	yes	yes
Ceanothus	Ceanothus	foliosus_vineatus	T		March	June	120.5	5	yes	yes
Ceanothus	Ceanothus	fresnensis	N		May	June	151	6	yes	yes
Ceanothus	Ceanothus	gloriosus_exaltatus	N		March	May	105.5	4.5	yes	yes
Ceanothus	Ceanothus	gloriosus_gloriosus	N		March	May	105.5	4.5	yes	yes
Ceanothus	Ceanothus	gloriosus_porrectus	N		March	May	105.5	4.5	yes	yes
Ceanothus	Ceanothus	hearstiorum	N		March	April	90	4	yes	yes
Ceanothus	Ceanothus	herbaceous	N		March	August	151.5	6	no	yes
Ceanothus	Ceanothus	impressus_impressus	N		February	April	76	3.5	yes	yes
Ceanothus	Ceanothus	impressus_nipomensis	N		February	April	76	3.5	yes	no
Ceanothus	Ceanothus	incanus	N		April	June	136	5.5	yes	yes
Ceanothus	Ceanothus	integerrimus	T		May	July	166.5	6.5	yes	yes
Ceanothus	Ceanothus	jepsonii	E	6	March	April	90	4	yes	yes
Ceanothus	Ceanothus	lemmonii	T		April	May	121	5	yes	yes
Ceanothus	Ceanothus	leucodermis	T		April	June	136	5.5	yes	yes
Ceanothus	Ceanothus	maritimus	N		February	May	91.5	4	yes	yes
Ceanothus	Ceanothus	masonii	T	3.3	March	May	105.5	4.5	yes	yes
Ceanothus	Ceanothus	megacarpus_insularis	N		February	March	61	3	yes	yes
Ceanothus	Ceanothus	megacarpus_megacarpus	N		October	March	32	2	yes	yes
Ceanothus	Ceanothus	oliganthus_oliganthus	N		October	June	76	3.5	yes	no
Ceanothus	Ceanothus	oliganthus_orcuttii	N		February	June	106.5	4.5	yes	no
Ceanothus	Ceanothus	oliganthus_sorediatus	N		January	May	76	3.5	yes	yes
Ceanothus	Ceanothus	ophiochilus	N		March	April	90	4	yes	yes
Ceanothus	Ceanothus	otayensis	N		January	April	60.5	3	yes	no
Ceanothus	Ceanothus	palmeri	N		February	June	106.5	4.5	yes	yes
Ceanothus	Ceanothus	papillosus	T	1.5	March	May	105.5	4.5	yes	yes
Ceanothus	Ceanothus	parryi	N		April	May	121	5	yes	yes
Ceanothus	Ceanothus	parvifolius	N		May	July	166.5	6.5	yes	yes

Ceanothus	Ceanothus	perplexans	N		March	May	105.5	4.5	yes	no
Ceanothus	Ceanothus	pinetorum	N		May	June	151	6	yes	yes
Ceanothus	Ceanothus	prostratus_occidentalis	N		April	May	121	5	yes	no
Ceanothus	Ceanothus	prostratus_prostratus	T		April	June	136	5.5	yes	yes
Ceanothus	Ceanothus	pumilus	E	5.7	April	June	136	5.5	yes	yes
Ceanothus	Ceanothus	purpureus	N		February	April	76	3.5	yes	yes
Ceanothus	Ceanothus	rigidus	N		March	May	105.5	4.5	yes	yes
Ceanothus	Ceanothus	roderickii	T	1.7	April	June	136	5.5	yes	yes
Ceanothus	Ceanothus	sanguineus	N		April	June	136	5.5	yes	yes
Ceanothus	Ceanothus	sonomensis	T	1.3	March	April	90	4	yes	yes
Ceanothus	Ceanothus	spinosus	N		January	May	76	3.5	yes	yes
Ceanothus	Ceanothus	thyrsiflorus_griseus	N		February	June	106.5	4.5	yes	yes
Ceanothus	Ceanothus	thyrsiflorus_thyrsiflorus	T		March	June	120.5	5	yes	yes
Ceanothus	Ceanothus	tomentosus	T		February	May	91.5	4	yes	yes
Ceanothus	Ceanothus	velutinus	N		April	July	151.5	6	yes	yes
Ceanothus	Ceanothus	verrocosus	N		January	April	60.5	3	yes	yes
Ceanothus	Ceanothus	vestitus	N		March	May	105.5	4.5	yes	yes
Cirsium	Cirsium	andersonii	T		July	September	227.5	8.5	yes	yes
Cirsium	Cirsium	andrewsii	T	1.7	May	September	197	7.5	yes	yes
Cirsium	Cirsium	arizonicum_arizonicum	N		July	August	212.5	8	yes	no
Cirsium	Cirsium	arizonicum_tenuisectum	N		July	November	258	9.5	yes	no
Cirsium	Cirsium	arvense	N		June	September	212.5	8	no	yes
Cirsium	Cirsium	brevistylum	N		March	August	151.5	6	yes	yes
Cirsium	Cirsium	cymosum_canovirens	N		June	July	182	7	yes	yes
Cirsium	Cirsium	cymosum_cymosum	T	3	April	July	151.5	6	yes	yes
Cirsium	Cirsium	discolor	N		June	October	228	8.5	no	yes
Cirsium	Cirsium	douglasii_breweri	T	3	June	September	212.5	8	yes	yes
Cirsium	Cirsium	douglasii_douglasii	N		June	August	197.5	7.5	yes	no
Cirsium	Cirsium	eatonii	N		July	September	227.5	8.5	no	yes
Cirsium	Cirsium	edule	N		June	October	227.5	8.5	no	yes
Cirsium	Cirsium	fontinale_campylon	E	5.9	March	October	182	7	yes	no

Cirsium	Cirsium	fontinale_fontinale	E	6.1	May	August	182	7	yes	yes
Cirsium	Cirsium	fontinale_obispoense	E	6.1	April	October	197.5	7.5	yes	yes
Cirsium	Cirsium	hydrophilum_hydrophilum	N		June	September	212.5	8	yes	yes
Cirsium	Cirsium	hydrophilum_vaseyi	E	6.1	June	September	212.5	8	yes	no
Cirsium	Cirsium	mohavense	N		July	October	243	9	yes	yes
Cirsium	Cirsium	muticum	N		July	September	227.5	8.5	no	yes
Cirsium	Cirsium	neomexicanum	N		April	May	121	5	yes	yes
Cirsium	Cirsium	occidentale_californicum	N		April	July	151.5	6	yes	no
Cirsium	Cirsium	occidentale_candidissimum	N		April	September	182	7	yes	no
Cirsium	Cirsium	occidentale_compactum	N		February	July	122	5	yes	no
Cirsium	Cirsium	occidentale_coulteri	N		March	June	120.5	5	yes	no
Cirsium	Cirsium	occidentale_lucianum	T		April	July	151.5	6	yes	no
Cirsium	Cirsium	occidentale_occidentale	T		March	July	136	5.5	yes	yes
Cirsium	Cirsium	occidentale_venustum	T		May	July	166.5	6.5	yes	yes
Cirsium	Cirsium	palustre	N		July	August	212.5	8	no	yes
Cirsium	Cirsium	pitcheri	N		May	September	197	7.5	no	yes
Cirsium	Cirsium	praeteriens	N		June	July	182	7	yes	no
Cirsium	Cirsium	quercetorum	T		April	August	167	6.5	yes	yes
Cirsium	Cirsium	remotifolium_odontolepis	T	1	June	September	212.5	8	yes	yes
Cirsium	Cirsium	remotifolium_remotifolium	N		May	August	182	7	yes	no
Cirsium	Cirsium	remotifolium_rivulare	N		May	August	182	7	yes	no
Cirsium	Cirsium	rhothophilum	N		April	August	167	6.5	yes	yes
Cirsium	Cirsium	rydbergii	N		May	September	197	7.5	no	yes
Cirsium	Cirsium	scariosum_americanum	N		June	August	197.5	7.5	yes	no
Cirsium	Cirsium	scariosum_citrinum	N		May	September	197	7.5	yes	no
Cirsium	Cirsium	scariosum_congdonii	N		June	August	197.5	7.5	yes	yes
Cirsium	Cirsium	scariosum_loncholepis	N		April	September	182	7	yes	no
Cirsium	Cirsium	scariosum_robustum	N		June	July	182	7	yes	no
Cirsium	Cirsium	scariosum_scarioum	T		May	July	166.5	6.5	yes	yes
Cirsium	Cirsium	vulgare	N		May	October	212.5	8	no	yes
Cirsium	Cirsium	wheeleri	N		July	October	243	9	no	yes

Collinsia	Collinsia	antonina	N		March	April	90	4	yes	no
Collinsia	Collinsia	bartsiifolia	N		March	June	120.5	5	yes	yes
Collinsia	Collinsia	callosa	N		April	June	136	5.5	yes	yes
Collinsia	Collinsia	childii	N		(April-) May	July	143	5.75	yes	yes
Collinsia	Collinsia	concolor	N		April	June	136	5.5	yes	yes
Collinsia	Collinsia	corymbosa	N		April	June	136	5.5	yes	yes
Collinsia	Collinsia	grandiflora	N		April	July	151.5	6	yes	yes
Collinsia	Collinsia	greenei	E	5.2	April	August	167	6.5	yes	yes
Collinsia	Collinsia	heterophylla_austromontana	N		May	August	182	7	yes	no
Collinsia	Collinsia	heterophylla_heterophylla	T		March	June	120.5	5	yes	yes
Collinsia	Collinsia	linearis	T		May	July	166.5	6.5	yes	yes
Collinsia	Collinsia	multicolor	T	1.1	March	May	105.5	4.5	yes	yes
Collinsia	Collinsia	parryi	N		April	May (-June)	128	5.25	yes	yes
Collinsia	Collinsia	parviflora	T		March	July	136	5.5	yes	yes
Collinsia	Collinsia	rattanii	N		May	August	182	7	yes	yes
Collinsia	Collinsia	sparsiflora_collina	N		March	April	90	4	yes	no
Collinsia	Collinsia	sparsiflora_sparsiflora	T	1.7	March	May	105.5	4.5	yes	no
Collinsia	Collinsia	tinctoria	T		May	August	182	7	yes	yes
Collinsia	Collinsia	torreyi_brevicarinata	N		May	July	166.5	6.5	yes	no
Collinsia	Collinsia	torreyi_latifolia	N		June	August	197.5	7.5	yes	no
Collinsia	Collinsia	torreyi_torreyi	N		May	August	182	7	yes	no
Collinsia	Collinsia	torreyi_wrightii	N		May	August	182	7	yes	yes
Collinsia	Collinsia	violacea	N				105.5	4.5	no	yes
Ericameria	Ericameria	albida	N		August	November	273.5	10	yes	yes
Ericameria	Ericameria	arborescens	T	1.3	August	November	273.5	10	yes	yes
Ericameria	Ericameria	bloomeri	N		July	October	243	9	yes	yes
Ericameria	Ericameria	brachylepis	N		September	December	304.5	11	yes	yes
Ericameria	Ericameria	cooperi	N		March	June	120.5	5	yes	yes
Ericameria	Ericameria	cuneata_cuneata	N		September	November	289	10.5	yes	yes
Ericameria	Ericameria	cuneata_macrocephala	N		September	November	289	10.5	yes	no

Ericameria	Ericameria	cuneata_spathulata	N		September	November	289	10.5	yes	no
Ericameria	Ericameria	discoidea_discoidea	N		July	September	227.5	8.5	yes	yes
Ericameria	Ericameria	discoidea_linearis	N		July	September	227.5	8.5	no	yes
Ericameria	Ericameria	ericoides	N		September	November	289	10.5	yes	yes
Ericameria	Ericameria	fasciculata	N		July	October	243	9	yes	yes
Ericameria	Ericameria	gilmanii	N		August	September	243	9	yes	yes
Ericameria	Ericameria	greenei	T	2	July	September	227.5	8.5	yes	no
Ericameria	Ericameria	laricifolia	N		September	October	274	10	yes	yes
Ericameria	Ericameria	linearifolia	T		March	May	105.5	4.5	yes	yes
Ericameria	Ericameria	nana	N		July	November	258	9.5	yes	yes
Ericameria	Ericameria	nauseosa	T		August	October	258.5	9.5	yes	yes
Ericameria	Ericameria	ophitidis	E	5.5	July	August	212.5	8	yes	yes
Ericameria	Ericameria	palmeri_pachylepis	N		August	December	289	10.5	yes	no
Ericameria	Ericameria	palmeri_palmeri	N		September	November	289	10.5	yes	yes
Ericameria	Ericameria	paniculata	N		June	December	258.5	9.5	yes	yes
Ericameria	Ericameria	parishii	N		July	October	243	9	yes	yes
Ericameria	Ericameria	parryi_aspera	N		July	September	227.5	8.5	yes	yes
Ericameria	Ericameria	parryi_imula	N		July	September	227.5	8.5	yes	yes
Ericameria	Ericameria	parryi_latior	N		July	September	227.5	8.5	yes	yes
Ericameria	Ericameria	parryi_monocephala	N		July	September	227.5	8.5	yes	yes
Ericameria	Ericameria	parryi_nevadensis	N		July	September	227.5	8.5	yes	yes
Ericameria	Ericameria	parryi_vulcanica	N		July	September	227.5	8.5	yes	yes
Ericameria	Ericameria	suffruticosa	N		July	September	227.5	8.5	yes	yes
Ericameria	Ericameria	teretifolia	N		September	November	289	10.5	yes	yes
Eriogonoideae	Acanthoscypus	parishii_abamsii	N		June	August	197.5	7.5	yes	no
Eriogonoideae	Acanthoscypus	parishii_cienegensis	N		June	September	212.5	8	yes	no
Eriogonoideae	Acanthoscypus	parishii_goodmaniana	N		May	September	197	7.5	yes	no
Eriogonoideae	Acanthoscypus	parishii_parishii	N		June	October	228	8.5	yes	yes
Eriogonoideae	Aristocapsa	insignis	N		May	June	151	6	yes	yes
Eriogonoideae	Centrostegia	thurberi	N		March	July	136	5.5	yes	yes
Eriogonoideae	Chorizanthe	angustifolia	N		April	July	151.5	6	yes	yes

Eriogonoideae	Chorizanthe	biloba_biloba	N		May	August	182	7	yes	yes
Eriogonoideae	Chorizanthe	biloba_immemora	N		May	September	197	7.5	yes	no
Eriogonoideae	Chorizanthe	brevicornu_brevicornu	N		February	July	122	5	yes	yes
Eriogonoideae	Chorizanthe	brevicornu_spathulata	N		April	July	151.5	6	yes	no
Eriogonoideae	Chorizanthe	breweri	E	5.4	March	July	136	5.5	yes	no
Eriogonoideae	Chorizanthe	clevelandii	N		May	September	197	7.5	yes	no
Eriogonoideae	Chorizanthe	corrugata	N		February	May	91.5	4	yes	no
Eriogonoideae	Chorizanthe	cuspidata_cuspidata	N		April	July	151.5	6	yes	no
Eriogonoideae	Chorizanthe	cuspidata_villosa	N		May	August	182	7	yes	no
Eriogonoideae	Chorizanthe	diffusa	N		April	July	151.5	6	yes	yes
Eriogonoideae	Chorizanthe	douglasii	N		April	July	151.5	6	yes	no
Eriogonoideae	Chorizanthe	fimbriata_fimbriata	N		March	July	136	5.5	yes	no
Eriogonoideae	Chorizanthe	fimbriata_laciniata	N		March	July	136	5.5	yes	yes
Eriogonoideae	Chorizanthe	flava	N		February	April	76	3.5	no	yes
Eriogonoideae	Chorizanthe	inequalis	N		April	May	120.5	5	no	yes
Eriogonoideae	Chorizanthe	leptotheca	N		May	August	182	7	yes	no
Eriogonoideae	Chorizanthe	membranacea	N		April	July	151.5	6	yes	yes
Eriogonoideae	Chorizanthe	obovata	N		May	July	166.5	6.5	yes	yes
Eriogonoideae	Chorizanthe	orcuttiana	N		March	May	105.5	4.5	yes	no
Eriogonoideae	Chorizanthe	palmeri	E	4.9	May	August	182	7	yes	yes
Eriogonoideae	Chorizanthe	parryi_fernandina	N		April	June	136	5.5	yes	yes
Eriogonoideae	Chorizanthe	parryi_parryi	N		May	June	151	6	yes	no
Eriogonoideae	Chorizanthe	polygonoides_longispina	N		April	June	136	5.5	yes	yes
Eriogonoideae	Chorizanthe	polygonoides_polygonoides	N		April	June	136	5.5	yes	no
Eriogonoideae	Chorizanthe	procumbens	N		April	June	136	5.5	yes	yes
Eriogonoideae	Chorizanthe	pungens_hartwegiana	N		April	July	151.5	6	yes	no
Eriogonoideae	Chorizanthe	pungens_pungens	N		April	July	151.5	6	yes	no
Eriogonoideae	Chorizanthe	rigida	N		February	June	106.5	4.5	yes	yes
Eriogonoideae	Chorizanthe	robusta_hartwegii	N		April	July	151.5	6	yes	no
Eriogonoideae	Chorizanthe	robusta_robusta	N		May	September	197	7.5	yes	no
Eriogonoideae	Chorizanthe	spinosa	N		April	July	151.5	6	yes	yes

Eriogonoideae	Chorizanthe	staticoides	N		April	July	151.5	6	yes	yes
Eriogonoideae	Chorizanthe	uniaristata	T	2.7	April	July	151.5	6	yes	yes
Eriogonoideae	Chorizanthe	valida	N		June	August	197.5	7.5	yes	no
Eriogonoideae	Chorizanthe	ventricosa	N		May	September	197	7.5	yes	no
Eriogonoideae	Chorizanthe	watsonii	N		April	August	167	6.5	yes	yes
Eriogonoideae	Chorizanthe	wheeleri	N		April	June	136	5.5	yes	no
Eriogonoideae	Chorizanthe	xanti_leucotheca	N		April	June	136	5.5	yes	no
Eriogonoideae	Chorizanthe	xanti_xanti	N		April	July	151.5	6	yes	yes
Eriogonoideae	Dedeckera	eurekensis	N		June	October	228	8.5	yes	yes
Eriogonoideae	Dodecahema	leptoceras	N		May	June	151	6	yes	yes
Eriogonoideae	Eriogonum	acaule	N		May	July	166.5	6.5	no	yes
Eriogonoideae	Eriogonum	alatum_alatum	N		June	October	228	8.5	no	yes
Eriogonoideae	Eriogonum	alpinum	E	6.1	July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	ammophilum	N		June	September	212.5	8	no	yes
Eriogonoideae	Eriogonum	ampullaceum	N		July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	annuum	N		April	November	212.5	8	no	yes
Eriogonoideae	Eriogonum	apiculatum	N		May	November	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	apricum_apricum	N		June	October	228	8.5	yes	no
Eriogonoideae	Eriogonum	apricum_prostratum	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	arborescens	N		April	October	197.5	7.5	yes	yes
Eriogonoideae	Eriogonum	arcuatum_arcuatum	N		June	October	228	8.5	no	yes
Eriogonoideae	Eriogonum	argillosum	T	3.1	March	October	182	7	yes	no
Eriogonoideae	Eriogonum	baileyi_baileyi	N		May	October	212.5	8	yes	yes
Eriogonoideae	Eriogonum	baileyi_praebens	N		June	October	228	8.5	yes	no
Eriogonoideae	Eriogonum	batemanii	N		June	September	212.5	8	no	yes
Eriogonoideae	Eriogonum	bicolor	N		April	July	151.5	6	no	yes
Eriogonoideae	Eriogonum	bifurcatum	N		May	June	151	6	yes	no
Eriogonoideae	Eriogonum	brachyanthum	N		April	November	212.5	8	yes	yes
Eriogonoideae	Eriogonum	breedlovei_breedlovei	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	breedlovei_shevockii	N		June	October	228	8.5	yes	no
Eriogonoideae	Eriogonum	brevicaule_brevicaule	N		June	September	212.5	8	no	yes

Eriogonoideae	Eriogonum	butterworthianum	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	caespitosum	N		April	July	151.5	6	yes	yes
Eriogonoideae	Eriogonum	callistum	N		May	August	182	7	yes	no
Eriogonoideae	Eriogonum	cedrorum	N		May	October	212.5	8	yes	no
Eriogonoideae	Eriogonum	cernuum	N		April	October	197.5	7.5	yes	yes
Eriogonoideae	Eriogonum	cithariforme_agninum	N		May	October	212.5	8	yes	no
Eriogonoideae	Eriogonum	cithariforme_cithariforme	N		May	October	212.5	8	yes	no
Eriogonoideae	Eriogonum	clavellatum	N		May	July	166.5	6.5	no	yes
Eriogonoideae	Eriogonum	compositum_compositum	T	1.7	April	July	151.5	6	yes	yes
Eriogonoideae	Eriogonum	congdonii_congdonii	E	5.1	July	September	227.5	8.5	yes	yes
Eriogonoideae	Eriogonum	contiguum	N		April	June	136	5.5	yes	no
Eriogonoideae	Eriogonum	contortum	N		May	August	182	7	no	yes
Eriogonoideae	Eriogonum	correllii	N		July	October	243	9	no	yes
Eriogonoideae	Eriogonum	corymbosum_corymbosum	N		July	October	243	9	no	yes
Eriogonoideae	Eriogonum	covilleanum	T	3	April	August	167	6.5	yes	no
Eriogonoideae	Eriogonum	crocatum	N		April	July	151.5	6	yes	yes
Eriogonoideae	Eriogonum	dasyanthemum	T	3	May	October	212.5	8	yes	no
Eriogonoideae	Eriogonum	davidsonii	N		May	September	197	7.5	yes	yes
Eriogonoideae	Eriogonum	deflexum_baratum	N		July	October	243	9	yes	yes
Eriogonoideae	Eriogonum	deflexum_nevadense	N		June	October	228	8.5	yes	no
Eriogonoideae	Eriogonum	diclinum	T	3.2	June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	douglasii_meridionale	N		April	June	136	5.5	yes	no
Eriogonoideae	Eriogonum	eastwoodianum	N		May	September	197	7.5	yes	yes
Eriogonoideae	Eriogonum	effusum	N		June	September	212.5	8	no	yes
Eriogonoideae	Eriogonum	elatum_elatum	N		May	October	212.5	8	yes	yes
Eriogonoideae	Eriogonum	elatum_villosum	T	3.3	June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	elegans	N		May	November	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	elongatum_elongatum	N		July	November	258	9.5	yes	yes
Eriogonoideae	Eriogonum	eremicola	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	eremicum	N		June	September	212.5	8	yes	yes
Eriogonoideae	Eriogonum	esmeraldense_esmeraldense	N		May	October	212.5	8	yes	yes

Eriogonoideae	Eriogonum	esmeraldense_toiyabense	N		June	September	212.5	8	no	yes
Eriogonoideae	Eriogonum	evanidum	N		July	October	243	9	yes	yes
Eriogonoideae	Eriogonum	exaltatum	N		May	October	212.5	8	yes	no
Eriogonoideae	Eriogonum	fastigiatum	N		March	April	90	4	no	yes
Eriogonoideae	Eriogonum	flavum_flavum	N		June	September	212.5	8	no	yes
Eriogonoideae	Eriogonum	giganteum_compactum	N		May	October	212.5	8	yes	no
Eriogonoideae	Eriogonum	giganteum_formosum	N		May	September	197	7.5	yes	no
Eriogonoideae	Eriogonum	gilmanii	N		May	September	197	7.5	yes	no
Eriogonoideae	Eriogonum	glandulosum	N		May	November	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	gordoni	N		May	October	212.5	8	no	yes
Eriogonoideae	Eriogonum	gracile_incultum	N		July	October	243	9	yes	no
Eriogonoideae	Eriogonum	gracilipes	N		July	September	227.5	8.5	yes	yes
Eriogonoideae	Eriogonum	grande_grande	N		March	October	182	7	yes	yes
Eriogonoideae	Eriogonum	grande_rubescens	N		April	September	182	7	yes	no
Eriogonoideae	Eriogonum	grande_timorum	N		April	October	197.5	7.5	yes	no
Eriogonoideae	Eriogonum	greggii	N		July	May	351	12.5	no	yes
Eriogonoideae	Eriogonum	havardii	N		May	September	197	7.5	no	yes
Eriogonoideae	Eriogonum	heermannii_argense	N		April	November	212.5	8	yes	no
Eriogonoideae	Eriogonum	heermannii_floccosum	N		May	October	212.5	8	yes	no
Eriogonoideae	Eriogonum	heermannii_hermannii	N		May	November	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	heermannii_humilius	N		June	October	228	8.5	yes	no
Eriogonoideae	Eriogonum	heermannii_occidentale	N		July	October	243	9	yes	no
Eriogonoideae	Eriogonum	heermannii_sulcatum	N		April	October	197.5	7.5	yes	no
Eriogonoideae	Eriogonum	heracleoides_heracleoides	N		May	September	197	7.5	yes	yes
Eriogonoideae	Eriogonum	hieracifolium	N		June	October	228	8.5	no	yes
Eriogonoideae	Eriogonum	hirtellum	E	6.2	July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	hirtiflorum	T	3.3	May	October	212.5	8	yes	no
Eriogonoideae	Eriogonum	hoffmannii_hoffmannii	N		July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	hoffmannii_robustius	N		August	November	273.5	10	yes	yes
Eriogonoideae	Eriogonum	hookeri	N		June	October	228	8.5	yes	no
Eriogonoideae	Eriogonum	incanum	N		June	September	212.5	8	yes	no

Eriogonoideae	Eriogonum	inerme_hispidulum	N		May	September	197	7.5	yes	no
Eriogonoideae	Eriogonum	inerme_inerme	N		May	August	182	7	yes	no
Eriogonoideae	Eriogonum	intrafractum	N		May	October	212.5	8	yes	yes
Eriogonoideae	Eriogonum	kelloggii	E		May	August	182	7	yes	no
Eriogonoideae	Eriogonum	kennedyi_alpigenum	N		July	August	212.5	8	yes	no
Eriogonoideae	Eriogonum	kennedyi_austromontanum	N		June	August	197.5	7.5	yes	yes
Eriogonoideae	Eriogonum	kennedyi_kennedyi	N		April	July	151.5	6	yes	no
Eriogonoideae	Eriogonum	kennedyi_pinicola	N		May	June	151	6	yes	no
Eriogonoideae	Eriogonum	kennedyi_purpusii	N		May	July	166.5	6.5	yes	no
Eriogonoideae	Eriogonum	lachnogynum	N		July	October	243	9	no	yes
Eriogonoideae	Eriogonum	latens	N		June	August	197.5	7.5	yes	no
Eriogonoideae	Eriogonum	leptocladon_leptocladon	N		June	October	228	8.5	no	yes
Eriogonoideae	Eriogonum	libertini	E	6.1	June	August	197	7.5	yes	no
Eriogonoideae	Eriogonum	lobbii	N		June	August	197.5	7.5	yes	no
Eriogonoideae	Eriogonum	longifolium	N		May	October	212.5	8	no	yes
Eriogonoideae	Eriogonum	luteolum_caninum	E	5.5	May	October	212.5	8	yes	no
Eriogonoideae	Eriogonum	luteolum_luteolum	T	3.8	July	November	258	9.5	yes	no
Eriogonoideae	Eriogonum	luteolum_pedunculatum	E		June	October	228	8.5	yes	yes
Eriogonoideae	Eriogonum	luteolum_saltuarium	N		July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	maculatum	N		April	November	212.5	8	yes	yes
Eriogonoideae	Eriogonum	maifolium_cupulatum	N		June	August	197.5	7.5	yes	no
Eriogonoideae	Eriogonum	marifolium_marifolium	N		June	August	197.5	7.5	yes	yes
Eriogonoideae	Eriogonum	mensicola	N		July	October	243	9	yes	no
Eriogonoideae	Eriogonum	micothecum_schoolcraftii	N		July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	microthecum_alpinum	N		July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	microthecum_ambiguum	N		July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	microthecum_corymbosoides	N		July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	microthecum_johnstonii	N		July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	microthecum_lacus-ursi	N		July	August	212.5	8	yes	no
Eriogonoideae	Eriogonum	microthecum_lapidicola	N		June	October	228	8.5	yes	no
Eriogonoideae	Eriogonum	microthecum_laxiflorum	N		June	October	228	8.5	yes	no

Eriogonoideae	Eriogonum	microthecum_panamintense	N		July	October	244	9	yes	no
Eriogonoideae	Eriogonum	microthecum_simpsonii	N		June	October	228	8.5	yes	yes
Eriogonoideae	Eriogonum	mohavense	N		May	September	197	7.5	yes	no
Eriogonoideae	Eriogonum	molestum	N		May	September	197	7.5	yes	yes
Eriogonoideae	Eriogonum	molle	N		March	July	137.5	5.5	no	yes
Eriogonoideae	Eriogonum	multiflorum_multiflorum	N		August	November	273.5	10	no	yes
Eriogonoideae	Eriogonum	multiflorum_riograndis	N		August	November	273.5	10	no	yes
Eriogonoideae	Eriogonum	nealleyi	N		June	September	212.5	8	no	yes
Eriogonoideae	Eriogonum	nervulosum	E	6.2	May	October	212.5	8	yes	no
Eriogonoideae	Eriogonum	nortonii	N		May	August	182	7	yes	no
Eriogonoideae	Eriogonum	nudum_auriculatum	N		May	October	212.5	8	yes	no
Eriogonoideae	Eriogonum	nudum_decurrens	N		July	October	243	9	yes	no
Eriogonoideae	Eriogonum	nudum_deductum	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	nudum_indictum	T	1.5	May	October	212.5	8	yes	no
Eriogonoideae	Eriogonum	nudum_murinum	N		May	October	212.5	8	yes	no
Eriogonoideae	Eriogonum	nudum_nudum	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	nudum_oblongifolium	T	2	May	October	212.5	8	yes	no
Eriogonoideae	Eriogonum	nudum_paralinum	N		June	October	228	8.5	yes	no
Eriogonoideae	Eriogonum	nudum_pauciflorum	N		June	October	228	8.5	yes	yes
Eriogonoideae	Eriogonum	nudum_psychicola	N		June	October	228	8.5	yes	no
Eriogonoideae	Eriogonum	nudum_pubiflorum	N		June	October	228	8.5	yes	no
Eriogonoideae	Eriogonum	nudum_regirivum	N		August	November	273.5	10	yes	no
Eriogonoideae	Eriogonum	nudum_scapigerum	N		July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	nudum_westonii	N		May	September	197	7.5	yes	no
Eriogonoideae	Eriogonum	nummulare	N		July	October	243	9	yes	yes
Eriogonoideae	Eriogonum	nutans_nutans	N		May	September	197	7.5	yes	yes
Eriogonoideae	Eriogonum	ochrocephalum_ochrocephalum	N		May	June	151	6	yes	yes
Eriogonoideae	Eriogonum	ordii	N		March	July	136	5.5	yes	yes
Eriogonoideae	Eriogonum	ovalifolium_caelestinum	N		July	August	212.5	8	yes	no
Eriogonoideae	Eriogonum	ovalifolium_depressum	N		June	August	197.5	7.5	yes	no

Eriogonoideae	Eriogonum	ovalifolium_eximium	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	ovalifolium_monarchense	N		June	August	197.5	7.5	yes	no
Eriogonoideae	Eriogonum	ovalifolium_nivale	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	ovalifolium_ovalifolium	N		April	August	167	6.5	yes	no
Eriogonoideae	Eriogonum	ovalifolium_purpureum	N		April	August	167	6.5	yes	yes
Eriogonoideae	Eriogonum	ovalifolium_vineum	N		May	June	151	6	yes	no
Eriogonoideae	Eriogonum	palmerianum	N		March	October	182	7	yes	yes
Eriogonoideae	Eriogonum	panamintense	N		May	October	212.5	8	yes	no
Eriogonoideae	Eriogonum	parishii	N		June	October	228	8.5	yes	yes
Eriogonoideae	Eriogonum	pauciflorum	N		May	September	197	7.5	no	yes
Eriogonoideae	Eriogonum	pelinophilum	N		May	July	166.5	6.5	no	yes
Eriogonoideae	Eriogonum	pendulum	E	6.2	July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	pharnaceoides_pharnaceoides	N		July	November	258	9.5	no	yes
Eriogonoideae	Eriogonum	plumatella	N		April	October	197.5	7.5	yes	no
Eriogonoideae	Eriogonum	polypodum	N		July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	prattenianum_avium	N		July	August	212.5	8	yes	no
Eriogonoideae	Eriogonum	prattenianum_prattenianum	N		May	July	166.5	6.5	yes	yes
Eriogonoideae	Eriogonum	prociduum	N		May	July	166.5	6.5	yes	no
Eriogonoideae	Eriogonum	pusillum	N		February	August	137.5	5.5	yes	yes
Eriogonoideae	Eriogonum	pyrolifolium_coryphaeum	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	pyrolifolium_pyrolifolium	T		July	September	227.5	8.5	yes	yes
Eriogonoideae	Eriogonum	racemosum	N		June	October	228	8.5	no	yes
Eriogonoideae	Eriogonum	reniforme	N		February	August	137.5	5.5	yes	no
Eriogonoideae	Eriogonum	rixfordii	N		June	December	258.5	9.5	yes	yes
Eriogonoideae	Eriogonum	rosense	N		July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	roseum	N		May	November	227.5	8.5	yes	yes
Eriogonoideae	Eriogonum	rupinum	N		July	September	227.5	8.5	yes	yes
Eriogonoideae	Eriogonum	saxatile	N		May	October	212.5	8	yes	yes
Eriogonoideae	Eriogonum	shockleyi_shockleyi	N		May	August	182	7	yes	yes
Eriogonoideae	Eriogonum	siskiyouense	E	5.4	July	September	227.5	8.5	yes	yes

Eriogonoideae	Eriogonum	spathulatum	N		July	October	243	9	no	yes
Eriogonoideae	Eriogonum	spectabile	N		July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	spergulinum_pratense	N		July	August	212.5	8	yes	no
Eriogonoideae	Eriogonum	spergulinum_reddingianum	N		June	September	212.5	8	yes	yes
Eriogonoideae	Eriogonum	spergulinum_spergulinum	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	sphaerocephalum_halimioides	N		May	July	166.5	6.5	yes	no
Eriogonoideae	Eriogonum	sphaerocephalum_sphaerocephalum	N		May	July	166.5	6.5	yes	yes
Eriogonoideae	Eriogonum	strictum_anserinum	N		May	August	182	7	yes	no
Eriogonoideae	Eriogonum	strictum_greenei	E	5.9	June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	strictum_proliferum	E	6	June	September	212.5	8	yes	yes
Eriogonoideae	Eriogonum	temblorense	N		May	September	197	7.5	yes	no
Eriogonoideae	Eriogonum	tenellum_ramossissimum	N		April	December	228	8.5	no	yes
Eriogonoideae	Eriogonum	ternatum	E	6.2	June	August	197.5	7.5	yes	no
Eriogonoideae	Eriogonum	thornei	N		May	July	166.5	6.5	yes	no
Eriogonoideae	Eriogonum	tomentosum	N		May	October	212.5	8	no	yes
Eriogonoideae	Eriogonum	tripodum	E	5.3	May	July	166.5	6.5	yes	no
Eriogonoideae	Eriogonum	truncatum	N		April	August	167	6.5	yes	no
Eriogonoideae	Eriogonum	twisselmannii	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	umbellatum_ahartii	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	umbellatum_argus	T	3	June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	umbellatum_bahiiforme	T	3.5	July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	umbellatum_canifolium	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	umbellatum_chlorothamnus	N		July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	umbellatum_covillei	N		July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	umbellatum_dichrocephalum	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	umbellatum_dumosum	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	umbellatum_furcosum	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	umbellatum_glaberrimum	N		July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	umbellatum_goodmannii	T	3.3	May	September	197	7.5	yes	no
Eriogonoideae	Eriogonum	umbellatum_humistratum	T	4.5	June	September	212.5	8	yes	no

Eriogonoideae	Eriogonum	umbellatum_juniporinum	N		June	October	228	8.5	yes	no
Eriogonoideae	Eriogonum	umbellatum_lautum	N		July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	umbellatum_minus	N		July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	umbellatum_modocense	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	umbellatum_munzii	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	umbellatum_nelsoniorum	T		July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	umbellatum_nevadense	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	umbellatum_polyanthum	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	umbellatum_smallianum	N		July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	umbellatum_speciosum	N	4.2	June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	umbellatum_subaridum	N		June	October	228	8.5	yes	yes
Eriogonoideae	Eriogonum	umbellatum_torreyanum	N		July	September	227.5	8.5	yes	no
Eriogonoideae	Eriogonum	umbellatum_versicolor	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	ursinum_erubescens	N		June	September	212.5	8	yes	no
Eriogonoideae	Eriogonum	ursinum_ursinum	T	1.1	May	September	197	7.5	yes	yes
Eriogonoideae	Eriogonum	vestitum	N		March	November	197	7.5	yes	no
Eriogonoideae	Eriogonum	villiflorum	N		April	July	151.5	6	no	yes
Eriogonoideae	Eriogonum	vimineum	T	1	May	September	197	7.5	yes	yes
Eriogonoideae	Eriogonum	viridescens	N		April	November	212.5	8	yes	no
Eriogonoideae	Eriogonum	watsonii	N		May	September	197	7.5	no	yes
Eriogonoideae	Eriogonum	wrightii_membranaceum	N		July	October	243	9	yes	yes
Eriogonoideae	Eriogonum	wrightii_nodosum	N		August	February	321	11.5	yes	no
Eriogonoideae	Eriogonum	wrightii_olanchense	N		July	August	212.5	8	yes	no
Eriogonoideae	Eriogonum	wrightii_subscaposum	N		June	September	212.5	8	yes	yes
Eriogonoideae	Eriogonum	wrightii_trachygonum	N		July	October	243	9	yes	no
Eriogonoideae	Eriogonum	wrightii_wrightii	N		July	October	243	9	yes	yes
Eriogonoideae	Eriogonum	zionis_coccineum	N		July	September	227.5	8.5	no	yes
Eriogonoideae	Goodmania	luteola	N		April	August	167	6.5	yes	yes
Eriogonoideae	Hollisteria	lanata	N		March	July	136	5.5	yes	yes
Eriogonoideae	Johanneshowellia	crateriorum	N		May	September	197	7.5	no	yes
Eriogonoideae	Johanneshowellia	puberula	N		May	September	197	7.5	yes	yes

Eriogonoideae	Lastariaea	coriacea	N		February	June	106.5	4.5	yes	yes
Eriogonoideae	Mucronea	californica	N		March	August	151.5	6	yes	yes
Eriogonoideae	Mucronea	denudata_gracilis	N		January	May	76	3.5	yes	no
Eriogonoideae	Mucronea	perfoliata	N		March	July	137.5	5.5	yes	yes
Eriogonoideae	Nemacaulis	denudata_denudata	N		March	August	152	6	yes	yes
Eriogonoideae	Oxytheca	dendroidea_dendroidea	N		June	October	228	8.5	yes	yes
Eriogonoideae	Oxytheca	perfoliata	N		April	August	167	6.5	yes	yes
Eriogonoideae	Oxytheca	watsonii	N		June	October	228	8.5	yes	yes
Eriogonoideae	Sidotheca	caryophylloides	N		June	September	212.5	8	yes	yes
Eriogonoideae	Sidotheca	emarginata	N		February	August	137.5	5.5	yes	no
Eriogonoideae	Sidotheca	trilobata	N		April	September	182	7	yes	yes
Eriogonoideae	Stenogonum	salsuginosum	N		April	September	182	7	no	yes
Eriogonoideae	Systenotheca	vortreidei	T	3.1	May	July	166.5	6.5	yes	yes
Erythronium	Erythronium	albidum	N		February	April	76	3.5	no	yes
Erythronium	Erythronium	americanum	N		April	April	105.5	4.5	no	yes
Erythronium	Erythronium	californicum	T	2.7	March	April	90	4	yes	yes
Erythronium	Erythronium	citrinum_citrinum	T	4.3	March	May	105.5	4.5	yes	no
Erythronium	Erythronium	citrinum_roderickii	T	4.7	March	June	120.5	5	yes	yes
Erythronium	Erythronium	elegans	N		May	June	151	6	no	yes
Erythronium	Erythronium	grandiflorum_candidum	N		April	June	136	5.5	no	yes
Erythronium	Erythronium	grandiflorum_grandiflorum	T		April	July	151.5	6	yes	yes
Erythronium	Erythronium	helenae	E	4.5	March	May	105.5	4.5	yes	yes
Erythronium	Erythronium	hendersonii	T	2.5	April	July	151.5	6	yes	yes
Erythronium	Erythronium	klamathense	T		April	July	151.5	6	yes	yes
Erythronium	Erythronium	mesochoreum	N		March	May	105.5	4.5	no	yes
Erythronium	Erythronium	montanum	N		June	August	197.5	7.5	no	yes
Erythronium	Erythronium	multiscapoideum	T	3	March	May	105.5	4.5	yes	yes
Erythronium	Erythronium	oregonum	N		March	May	105.5	4.5	yes	yes
Erythronium	Erythronium	pluriflorum	N		May	July	166.5	6.5	yes	yes
Erythronium	Erythronium	purpurascens	T	1	May	August	182	7	yes	yes
Erythronium	Erythronium	pusaterii	N		May	July	166.5	6.5	yes	no

Erythronium	Erythronium	quinaultense	N		May	May	136	5.5	no	yes
Erythronium	Erythronium	revolutum	N		March	July	136	5.5	yes	yes
Erythronium	Erythronium	taylorii	T		March	May	105.5	4.5	yes	yes
Erythronium	Erythronium	tuolumnense	T	2.5	March	June	120.5	5	yes	yes
Iris	Iris	bracteata	E	5.8	May	May	136	5.5	yes	yes
Iris	Iris	chrysophylla	N		May	June	151	6	yes	yes
Iris	Iris	douglasiana	T		May	July	166.5	6.5	yes	yes
Iris	Iris	fernaldii	N		April	April	105.5	4.5	yes	yes
Iris	Iris	forrestii	N		May	June	151	6	no	yes
Iris	Iris	hartwegii_australis	N		May	June	151	6	yes	yes
Iris	Iris	hartwegii_columbiana	N		May	May	136	5.5	yes	yes
Iris	Iris	hartwegii_hartwegii	N		May	June	151	6	yes	yes
Iris	Iris	hartwegii_pinetorum	N		May	May	136	5.5	yes	yes
Iris	Iris	innominata	E	5.8	May	June	151	6	yes	yes
Iris	Iris	longipetala	N		March	June	120.5	5	yes	no
Iris	Iris	macrosiphon	N	1.1	March	May	105.5	4.5	yes	yes
Iris	Iris	missouriensis	N		May	July	166.5	6.5	yes	no
Iris	Iris	munzii	N		April	April	105.5	4.5	yes	yes
Iris	Iris	purdyi	T		April	May	121	5	yes	yes
Iris	Iris	tenax_gormanii	N		May	May	136	5.5	no	yes
Iris	Iris	tenax_klamathensis	N		May	May	136	5.5	yes	yes
Iris	Iris	tenax_tenax	N		June	August	197.5	7.5	no	yes
Iris	Iris	tenuissima	T		May	May	136	5.5	yes	yes
Iris	Iris	tenuissima_purdyiformis	N	1.5	April	May	121	5	yes	yes
Iris	Iris	thompsonii	T		April	May	121	5	yes	yes
Layia	Layia	carnosa	N		April	July	151.5	6	yes	no
Layia	Layia	chrysanthemoides	N		March	June	120.5	5	yes	no
Layia	Layia	discoidea	E	6.1	April	June	136	5.5	yes	yes
Layia	Layia	fremontii	N		February	May	91.5	4	yes	no
Layia	Layia	gaillardioides	N		March	August	151.5	6	yes	no
Layia	Layia	glandulosa	N		February	July	122	5	yes	yes

Layia	Layia	heterotricha	N		April	June	136	5.5	yes	no
Layia	Layia	hieracioides	N		April	July	151.5	6	yes	no
Layia	Layia	jonesii	T	3.5	March	May	105.5	4.5	yes	no
Layia	Layia	leucopappa	N		March	April	90	4	yes	no
Layia	Layia	munzii	N		March	April	90	4	yes	no
Layia	Layia	pentachaeta_albida	N		March	May	105.5	4.5	yes	no
Layia	Layia	pentachaeta_pentachaeta	T		March	June	120.5	5	yes	no
Layia	Layia	platyglossa	N		February	July	122	5	yes	no
Layia	Layia	septentrionalis	T	3.2	April	June	136	5.5	yes	no
Lessingia	Benitoa	occidentalis	T	4.1	June	November	243	9	yes	no
Lessingia	Corethrogyne	filaginifolia	T	1.3	July	November	258	9.5	yes	yes
Lessingia	Lessingia	arachnoidea	E	6.2	July	October	243	9	yes	yes
Lessingia	Lessingia	germanorum	N		June	November	243	9	yes	yes
Lessingia	Lessingia	glandulifera_glandulifera	N		May	October	212.5	8	yes	yes
Lessingia	Lessingia	glandulifera_peirsonii	N		May	September	197	7.5	yes	yes
Lessingia	Lessingia	glandulifera_tomentosa	N		August	November	273.5	10	yes	yes
Lessingia	Lessingia	hololeuca	T	2.5	June	October	228	8.5	yes	yes
Lessingia	Lessingia	leptoclada	T		July	October	243	9	yes	yes
Lessingia	Lessingia	micradenia_glabrata	E	5.1	August	October	258.5	9.5	yes	yes
Lessingia	Lessingia	micradenia_micradenia	E	5.3	July	October	243	9	yes	yes
Lessingia	Lessingia	nana	N		June	October	228	8.5	yes	yes
Lessingia	Lessingia	nemaclada	T	2	July	October	243	9	yes	yes
Lessingia	Lessingia	ramulosa	E	5.4	July	October	243	9	yes	yes
Lessingia	Lessingia	tenuis	N		May	July	166.5	6.5	yes	yes
Lessingia	Lessingia	virgata	N		June	October	228	8.5	yes	yes
Lomatium	Lomatium	bicolor_leptocarpum	N		April	May	121	5	yes	no
Lomatium	Lomatium	californicum	N		April	June	136	5.5	yes	no
Lomatium	Lomatium	canbyi	N		April	May	121	5	yes	no
Lomatium	Lomatium	caruifolium_caruifolium	N		March	May	105.5	4.5	yes	no
Lomatium	Lomatium	caruifolium_denticulatum	N		April	May	121	5	yes	no
Lomatium	Lomatium	ciliolatum	E	6	June	July	182	7	yes	no

Lomatium	Lomatium	congdonii	E	6.2	March	June	120.5	5	yes	no
Lomatium	Lomatium	dasycarpum_dasycarpum	T	3.6	March	June	120.5	5	yes	no
Lomatium	Lomatium	dasycarpum_tomentosum	N		March	May	105.5	4.5	yes	no
Lomatium	Lomatium	dissectum_dissectum	N		May	July	166.5	6.5	yes	no
Lomatium	Lomatium	dissectum_multifidum	N		April	July	151.5	6	yes	no
Lomatium	Lomatium	engelmannii	E	5.8	June	August	197.5	7.5	yes	no
Lomatium	Lomatium	foeniculaceum_fimbriatum	N		April	June	136	5.5	yes	no
Lomatium	Lomatium	foeniculaceum_inyoense	N		June	July	182	7	yes	no
Lomatium	Lomatium	foeniculaceum_macdougalii	N		May	June	151	6	yes	no
Lomatium	Lomatium	grayi	N		May	June	151	6	yes	no
Lomatium	Lomatium	hallii	N		May	August	182	7	yes	no
Lomatium	Lomatium	hendersonii	N		March	June	120.5	5	yes	no
Lomatium	Lomatium	hooveri	E	5.9	April	May	121	5	yes	no
Lomatium	Lomatium	howellii	T	6.1	May	June	151	6	yes	no
Lomatium	Lomatium	insulare	N		February	April	76	3.5	yes	no
Lomatium	Lomatium	lucidum	N		April	May	121	5	yes	no
Lomatium	Lomatium	macrocarpum	T	2.7	April	June	136	5.5	yes	no
Lomatium	Lomatium	marginatum_marginatum	E	5	March	May	105.5	4.5	yes	no
Lomatium	Lomatium	marginatum_purpureium	E	5	March	May	105.5	4.5	yes	no
Lomatium	Lomatium	martindalei	N		May	June	151	6	yes	no
Lomatium	Lomatium	mohavense	N		April	May	121	5	yes	no
Lomatium	Lomatium	nevadense_nevadense	N		April	July	151.5	6	yes	no
Lomatium	Lomatium	nevadense_parishii	N		April	July	151.5	6	yes	no
Lomatium	Lomatium	nudicaule	N		April	June	136	5.5	yes	no
Lomatium	Lomatium	observatorium	T	1.4	March	May	105.5	4.5	yes	no
Lomatium	Lomatium	parryi	N		May	June	151	6	yes	no
Lomatium	Lomatium	parvifolium	T		February	May	91.5	4	yes	no
Lomatium	Lomatium	peckianum	N		May	May	136	5.5	yes	no
Lomatium	Lomatium	piperi	N		March	May	105.5	4.5	yes	no
Lomatium	Lomatium	plummerae	N		May	June	151	6	yes	no
Lomatium	Lomatium	ravenii	N		April	June	136	5.5	yes	no

Lomatium	Lomatium	repostum	T	3.2	April	May	121	5	yes	no
Lomatium	Lomatium	rigidum	N		April	May	121	5	yes	no
Lomatium	Lomatium	shevockii	N		April	May	121	5	yes	no
Lomatium	Lomatium	stebbinsii	N		March	May	105.5	4.5	yes	no
Lomatium	Lomatium	torreyi	N		May	August	182	7	yes	no
Lomatium	Lomatium	tracyi	E	6.1	May	June	151	6	yes	no
Lomatium	Lomatium	triternatum_macrocarpum	N		April	July	151.5	6	yes	no
Lomatium	Lomatium	triternatum_triternatum	T	2.8	April	July	151.5	6	yes	no
Lomatium	Lomatium	utriculatum	T	1.7	February	May	91.5	4	yes	no
Lomatium	Lomatium	vaginatum	T		April	May	121	5	yes	no
Mimulus	Mimulus	alsinoides	N		March	June	120.5	5	yes	yes
Mimulus	Mimulus	androsaceus	N		March	June	120.5	5	yes	yes
Mimulus	Mimulus	angustatus	N		March	June	120.5	5	yes	yes
Mimulus	Mimulus	aurantiacus_aridus	N		March	June	120.5	5	yes	yes
Mimulus	Mimulus	aurantiacus_aurantiacus	T		March	June	120.5	5	yes	yes
Mimulus	Mimulus	aurantiacus_grandiflorus	N		March	June	120.5	5	yes	yes
Mimulus	Mimulus	aurantiacus_parviflorus	N		March	June	120.5	5	yes	no
Mimulus	Mimulus	aurantiacus_puniceus	N		March	June	120.5	5	yes	yes
Mimulus	Mimulus	bicolor	T		April	June	136	5.5	yes	yes
Mimulus	Mimulus	bigelovii_bigelovii	N		February	June	106.5	4.5	yes	yes
Mimulus	Mimulus	bigelovii_cuspidatus	N		February	June	106.5	4.5	yes	no
Mimulus	Mimulus	bolanderi	N		April	July	151.5	6	yes	yes
Mimulus	Mimulus	breviflorus	N		May	June	151	6	yes	yes
Mimulus	Mimulus	brevipes	N		April	July	151.5	6	yes	yes
Mimulus	Mimulus	brewerii	N		June	August	197.5	7.5	yes	yes
Mimulus	Mimulus	cardinalis	N		May	September	197	7.5	yes	yes
Mimulus	Mimulus	clevelandii	N		April	June	136	5.5	yes	yes
Mimulus	Mimulus	congdonii	T		March	May	105.5	4.5	yes	yes
Mimulus	Mimulus	constrictus	N		May	August	182	7	yes	yes
Mimulus	Mimulus	cusickii	N		May	August	182	7	yes	yes
Mimulus	Mimulus	dentatus	N		May	August	182	7	yes	yes

Mimulus	Mimulus	douglasii	T	2.7	February	April	76	3.5	yes	yes
Mimulus	Mimulus	evanescens	N		July	July	197	7.5	yes	no
Mimulus	Mimulus	exiguus	N		June	July	182	7	yes	yes
Mimulus	Mimulus	filicaulis	N		May	July	166.5	6.5	yes	yes
Mimulus	Mimulus	floribundus	T		April	July	151.5	6	yes	yes
Mimulus	Mimulus	fremontii_fremontii	N		March	June	120.5	5	yes	yes
Mimulus	Mimulus	fremontii_vandenbergensis	N		May	June	151	6	yes	no
Mimulus	Mimulus	glabratus	T		June	August	197.5	7.5	yes	yes
Mimulus	Mimulus	glaucescens	T	3.8	March	May	105.5	4.5	yes	yes
Mimulus	Mimulus	gracilipes	N		April	May	121	5	yes	yes
Mimulus	Mimulus	guttatus	T		March	August	151.5	6	yes	yes
Mimulus	Mimulus	inconspicuus	N		April	June	136	5.5	yes	yes
Mimulus	Mimulus	johnstonii	N		May	August	182	7	yes	yes
Mimulus	Mimulus	kelloggii	T		March	June	120.5	5	yes	yes
Mimulus	Mimulus	laciniatus	N		May	August	182	7	yes	no
Mimulus	Mimulus	latidens	N		April	June	136	5.5	yes	yes
Mimulus	Mimulus	latifolius	N		March	April	90	4	yes	no
Mimulus	Mimulus	layneae	T	2.9	May	August	182	7	yes	yes
Mimulus	Mimulus	leptaleus	N		June	August	197.5	7.5	yes	yes
Mimulus	Mimulus	lewisii	N		June	August	197.5	7.5	yes	yes
Mimulus	Mimulus	mohavensis	N		April	May	121	5	yes	yes
Mimulus	Mimulus	montiodes	N		March	June	120.5	5	yes	yes
Mimulus	Mimulus	moschatus	N		June	August	197.5	7.5	yes	yes
Mimulus	Mimulus	nanus_jepsonii	N		May	August	182	7	yes	yes
Mimulus	Mimulus	nanus_mephiticus	N		May	August	182	7	yes	yes
Mimulus	Mimulus	nanus_nanus	T		May	August	182	7	yes	yes
Mimulus	Mimulus	norrisi	N		March	May	105.5	4.5	yes	yes
Mimulus	Mimulus	nudatus	E	5.6	May	June	151	6	yes	yes
Mimulus	Mimulus	palmeri	N		March	June	120.5	5	yes	yes
Mimulus	Mimulus	parishii	N		May	August	182	7	yes	yes
Mimulus	Mimulus	parryi	N		April	July	151.5	6	yes	yes

Mimulus	Mimulus	pictus	N		March	May	105.5	4.5	yes	yes
Mimulus	Mimulus	pilosus	N		April	August	167	6.5	yes	yes
Mimulus	Mimulus	primuloides_linearifolius	T	4	July	August	212.5	8	yes	yes
Mimulus	Mimulus	primuloides_primuloides	N		June	August	197.5	7.5	yes	no
Mimulus	Mimulus	pulchellus	N		April	July	151.5	6	yes	yes
Mimulus	Mimulus	pulsiferae	N		April	June	136	5.5	yes	yes
Mimulus	Mimulus	purpureus	N		June	July	182	7	yes	yes
Mimulus	Mimulus	pygmaeus	N		May	June	151	6	yes	yes
Mimulus	Mimulus	rattanii	N		April	July	151.5	6	yes	yes
Mimulus	Mimulus	ringens	N		April	June	136	5.5	yes	yes
Mimulus	Mimulus	rubellus	N		April	June	136	5.5	yes	yes
Mimulus	Mimulus	rupicola	N		February	June	106.5	4.5	yes	yes
Mimulus	Mimulus	shevockii	N		April	May	121	5	yes	yes
Mimulus	Mimulus	suksdorfii	N		May	August	182	7	yes	yes
Mimulus	Mimulus	tilingii	N		July	September	227.5	8.5	yes	yes
Mimulus	Mimulus	torreyi	T		May	August	182	7	yes	yes
Mimulus	Mimulus	traskiae	N		March	April	90	4	yes	no
Mimulus	Mimulus	tricolor	N		March	June	120.5	5	yes	yes
Mimulus	Mimulus	viscidus_compactus	N		April	July	151.5	6	yes	no
Mimulus	Mimulus	viscidus_viscidus	N		April	July	151.5	6	yes	yes
Mimulus	Mimulus	whitneyi	N		May	September	197	7.5	yes	yes
Navarretia	Navarretia	atractyloides	T		May	July	166.5	6.5	yes	yes
Navarretia	Navarretia	breweri	T		June	August	197.5	7.5	yes	yes
Navarretia	Navarretia	capillaris	N		June	August	197.5	7.5	yes	no
Navarretia	Navarretia	cotulifolia	N		May	June	151	6	yes	no
Navarretia	Navarretia	divaricata_divaricata	N		June	August	197.5	7.5	yes	no
Navarretia	Navarretia	divaricata_vividior	N		June	August	197.5	7.5	yes	yes
Navarretia	Navarretia	eriocephala	N		May	June	151	6	yes	yes
Navarretia	Navarretia	filicaulis	T		June	July	182	7	yes	yes
Navarretia	Navarretia	fossalis	N		April	June	136	5.5	yes	yes
Navarretia	Navarretia	gowenii	T		May	June	151	6	yes	no

Navarretia	Navarretia	hamata_hamata	N		April	June	136	5.5	yes	yes
Navarretia	Navarretia	hamata_leptantha	N		April	June	136	5.5	yes	yes
Navarretia	Navarretia	hamata_parviloba	N		April	June	136	5.5	yes	yes
Navarretia	Navarretia	heterandra	N		May	June	151	6	yes	yes
Navarretia	Navarretia	heterodoxa	T	2.8	May	June	151	6	yes	no
Navarretia	Navarretia	intertexta_intertexta	N		May	July	166.5	6.5	yes	yes
Navarretia	Navarretia	intertexta_propinqua	N		June	August	197.5	7.5	yes	yes
Navarretia	Navarretia	jepsonii	E	5.6	April	June	136	5.5	yes	yes
Navarretia	Navarretia	leucocephala_bakeri	N		April	July	151.5	6	yes	yes
Navarretia	Navarretia	leucocephala_leucocephala	N		April	May	121	5	yes	yes
Navarretia	Navarretia	leucocephala_minima	N		June	August	197.5	7.5	yes	yes
Navarretia	Navarretia	leucocephala_pauciflora	N		May	June	151	6	yes	yes
Navarretia	Navarretia	leucocephala_plieantha	N		May	June	151	6	yes	yes
Navarretia	Navarretia	mellita	N		May	July	166.5	6.5	yes	yes
Navarretia	Navarretia	mitracarpa	E	5.9	May	July	166.5	6.5	no	yes
Navarretia	Navarretia	myersii_deminuta	N		April	May	121	5	yes	yes
Navarretia	Navarretia	myersii_myersii	N		May	May	136	5.5	yes	no
Navarretia	Navarretia	nigelliformis_nigelliformis	N		April	June	136	5.5	yes	no
Navarretia	Navarretia	nigelliformis_radians	N		May	July	166.5	6.5	yes	yes
Navarretia	Navarretia	ojaiensis	N		May	July	166.5	6.5	yes	no
Navarretia	Navarretia	peninsularis	N		June	August	197.5	7.5	yes	yes
Navarretia	Navarretia	prolifera_lutea	N		May	July	166.5	6.5	yes	no
Navarretia	Navarretia	prolifera_prolifera	N		May	June	151	6	yes	yes
Navarretia	Navarretia	prostrata	N		April	July	151.5	6	yes	yes
Navarretia	Navarretia	pubescens	T	2	May	July	166.5	6.5	yes	yes
Navarretia	Navarretia	rosulata	E	6	May	July	166.5	6.5	yes	yes
Navarretia	Navarretia	setiloba	T		April	July	151.5	6	yes	yes
Navarretia	Navarretia	sinistra_pinnatisecta	T		June	August	197.5	7.5	yes	no
Navarretia	Navarretia	sinistra_sinistra	N		June	August	197.5	7.5	yes	no
Navarretia	Navarretia	squarrosa	N		June	August	197.5	7.5	yes	yes
Navarretia	Navarretia	subuligera	N		April	August	167	6.5	yes	yes

Navarretia	Navarretia	tagetina	N		April	June	136	5.5	yes	yes
Navarretia	Navarretia	viscidula	N		June	July	182	7	yes	yes
Orthocarpus	Orthocarpus	bracteosus	N		June	August	197.5	7.5	yes	yes
Orthocarpus	Orthocarpus	cuspidatus_copelandii	N		June	August	197.5	7.5	yes	no
Orthocarpus	Orthocarpus	cuspidatus_cryptanthus	N		June	August	197.5	7.5	yes	no
Orthocarpus	Orthocarpus	cuspidatus_cuspidatus	N		June	August	197.5	7.5	yes	yes
Orthocarpus	Orthocarpus	imbricatus	N		June	August	197.5	7.5	yes	yes
Orthocarpus	Orthocarpus	luteus	N		July	August	212.5	8	yes	yes
Orthocarpus	Orthocarpus	pachystachyus	E		May	June	151	6	yes	yes
Packera	Packera	bernardina	N		May	July	166.5	6.5	yes	no
Packera	Packera	bolanderi	N		May	July	166.5	6.5	yes	no
Packera	Packera	breweri	N		April	June	136	5.5	yes	no
Packera	Packera	cana	N		June	August	197.5	7.5	yes	no
Packera	Packera	clevelandii	E	5.8	May	August	182	7	yes	no
Packera	Packera	eurycephala_eurycephala	T	3.8	May	June	151	6	yes	no
Packera	Packera	eurycephala_lewisrosei	E	5.8	April	June	136	5.5	yes	no
Packera	Packera	ganderi	N		April	May	121	5	yes	no
Packera	Packera	greenei	E	5.3	May	July	166.5	6.5	yes	no
Packera	Packera	hesperia	N		April	June	136	5.5	yes	no
Packera	Packera	indecora	N		June	August	197.5	7.5	yes	no
Packera	Packera	ionophylla	N		June	August	197.5	7.5	yes	no
Packera	Packera	layneae	E	4.9	April	June	136	5.5	yes	no
Packera	Packera	macounii	E	5.1	May	July	166.5	6.5	yes	no
Packera	Packera	multilobata	N		May	July	166.5	6.5	yes	no
Packera	Packera	pauciflora	N		July	August	212.5	8	yes	no
Packera	Packera	pseudaurea	N		June	July	182	7	yes	no
Packera	Packera	streptanthifolia_streptanthifolia	N		May	August	182	7	yes	no
Packera	Packera	subnuda	N		June	September	212.5	8	yes	no
Packera	Packera	werneriifolia	N		July	August	212.5	8	yes	no
Perideridia	Perideridia	americana	N		April	July	151.5	6	no	yes

Perideridia	Perideridia	bacigalupii	E	4.6	June	August	197.5	7.5	yes	yes
Perideridia	Perideridia	bolanderi_bolanderi	T		June	August	197.5	7.5	yes	yes
Perideridia	Perideridia	bolanderi_involucrata	T		June	August	197.5	7.5	yes	yes
Perideridia	Perideridia	californica	N		April	May	121	5	yes	yes
Perideridia	Perideridia	erythrorhiza	T				228	8.5	no	yes
Perideridia	Perideridia	gairdneri_borealis	T		June	August	197.5	7.5	yes	yes
Perideridia	Perideridia	gairdneri_gairdneri	N		June	July	182	7	yes	no
Perideridia	Perideridia	howellii	N		July	August	212.5	8	yes	yes
Perideridia	Perideridia	kelloggii	T	2.1	July	August	212.5	8	yes	yes
Perideridia	Perideridia	lemmonii	T		July	August	212.5	8	yes	yes
Perideridia	Perideridia	leptocarpa	E	5.6	June	August	197.5	7.5	yes	yes
Perideridia	Perideridia	oregana	T	1.7	July	August	212.5	8	yes	yes
Perideridia	Perideridia	parishii_latifolia	N		June	August	197.5	7.5	yes	yes
Perideridia	Perideridia	parishii_parishii	N		June	August	197.5	7.5	yes	no
Perideridia	Perideridia	pringlei	T	3.7	April	June	136	5.5	yes	yes
Sanicula	Sanicula	arctopoides	N		February	May	91.5	4	yes	yes
Sanicula	Sanicula	arguta	T		March	April	90	4	yes	yes
Sanicula	Sanicula	bipinnata	T		April	May	121	5	yes	yes
Sanicula	Sanicula	bipinnatifida	T	1.8	March	May	105.5	4.5	yes	yes
Sanicula	Sanicula	canadensis	N		May	July	166.5	6.5	no	yes
Sanicula	Sanicula	crassicaulis	T		March	May	105.5	4.5	yes	yes
Sanicula	Sanicula	graveolens	N		March	May	105.5	4.5	yes	yes
Sanicula	Sanicula	hoffmannii	T	1.8	March	May	105.5	4.5	yes	yes
Sanicula	Sanicula	laciniata	T		March	May	105.5	4.5	yes	yes
Sanicula	Sanicula	maritima	N		April	May	121	5	yes	no
Sanicula	Sanicula	peckiana	E	5.3	May	May	136	5.5	yes	yes
Sanicula	Sanicula	saxatilis	N		May	June	151	6	yes	yes
Sanicula	Sanicula	tracyi	T	2.1	March	May	105.5	4.5	yes	yes
Sanicula	Sanicula	tuberosa	T		March	July	136	5.5	yes	yes
Sidalcea	Sidalcea	asprella_asprella	T		May	June	151	6	yes	no
Sidalcea	Sidalcea	asprella_nana	T		June	August	197.5	7.5	yes	yes

Sidalcea	Sidalcea	calycosa	N		March	July	136	5.5	yes	yes
Sidalcea	Sidalcea	celata	T		May	June	151	6	yes	no
Sidalcea	Sidalcea	covillei	N		May	June	151	6	yes	yes
Sidalcea	Sidalcea	diploscypha	T	2.6	April	May	121	5	yes	yes
Sidalcea	Sidalcea	elegans	T		June	July	182	7	yes	no
Sidalcea	Sidalcea	gigantea	N		July	September	227.5	8.5	yes	no
Sidalcea	Sidalcea	glaucescens	T		June	August	197.5	7.5	yes	yes
Sidalcea	Sidalcea	hartwegii	T	1.6	April	June	136	5.5	yes	yes
Sidalcea	Sidalcea	hickmanii_anomala	E	5.6	May	June	151	6	yes	yes
Sidalcea	Sidalcea	hickmanii_napensis	N		May	May	136	5.5	yes	no
Sidalcea	Sidalcea	hickmanii_parishii	N		June	August	197.5	7.5	yes	yes
Sidalcea	Sidalcea	hickmanii_pillsburiensis	N		July	July	197	7.5	yes	no
Sidalcea	Sidalcea	hickmanii_viridis	E	6.3	May	June	151	6	yes	no
Sidalcea	Sidalcea	hirsuta	N		April	June	136	5.5	yes	no
Sidalcea	Sidalcea	keckii	T	3	April	May	121	5	yes	yes
Sidalcea	Sidalcea	malachroides	N		April	August	167	6.5	yes	yes
Sidalcea	Sidalcea	malviflora_californica	N		March	June	120.5	5	yes	yes
Sidalcea	Sidalcea	malviflora_dolosa	N		June	July	182	7	yes	yes
Sidalcea	Sidalcea	malviflora_laciniata	N		March	June	120.5	5	yes	yes
Sidalcea	Sidalcea	malviflora_malviflora	N		March	July	136	5.5	yes	yes
Sidalcea	Sidalcea	malviflora_patula	N		May	August	182	7	yes	yes
Sidalcea	Sidalcea	malviflora_purpurea	N		May	June	151	6	yes	yes
Sidalcea	Sidalcea	malviflora_rostrata	N		April	May	121	5	yes	no
Sidalcea	Sidalcea	multifida	N		May	July	166.5	6.5	yes	yes
Sidalcea	Sidalcea	neomexicana	N		April	June	136	5.5	yes	yes
Sidalcea	Sidalcea	oregana_eximia	N		June	August	197.5	7.5	yes	no
Sidalcea	Sidalcea	oregana_hydrophila	N		July	September	227.5	8.5	yes	yes
Sidalcea	Sidalcea	oregana_oregana	N		May	September	197	7.5	yes	yes
Sidalcea	Sidalcea	oregana_spicata	N		June	August	197.5	7.5	yes	yes
Sidalcea	Sidalcea	oregana_valida	N		June	September	212.5	8	yes	yes
Sidalcea	Sidalcea	pedata	N		May	August	182	7	yes	yes

Sidalcea	Sidalcea	ranunculacea	N		June	August	197.5	7.5	yes	no
Sidalcea	Sidalcea	reptans	N		June	August	197.5	7.5	yes	no
Sidalcea	Sidalcea	robusta	N		April	June	136	5.5	yes	yes
Sidalcea	Sidalcea	setosa	N		June	July	182	7	yes	no
Sidalcea	Sidalcea	sparsifolia	N		March	June	120.5	5	yes	yes
Sidalcea	Sidalcea	stipularis	N		June	August	197.5	7.5	yes	yes
Thelypodieae	Caulanthus	amplexicaulis	T		April	August	167	6.5	yes	yes
Thelypodieae	Caulanthus	anceps	N		March	May	105.5	4.5	yes	yes
Thelypodieae	Caulanthus	californicus	N		February	April	76	3.5	yes	yes
Thelypodieae	Caulanthus	cooperi	N		March	April	90	4	yes	yes
Thelypodieae	Caulanthus	coulteri	N		March	July	136	5.5	yes	yes
Thelypodieae	Caulanthus	crassicaulis	N		April	July	151.5	6	yes	yes
Thelypodieae	Caulanthus	flavescens	T	2.3	March	May	105.5	4.5	yes	yes
Thelypodieae	Caulanthus	glaucus	N		April	June	136	5.5	yes	yes
Thelypodieae	Caulanthus	hallii	N		April	May	121	5	yes	yes
Thelypodieae	Caulanthus	heterophyllus	N		March	May	105.5	4.5	yes	yes
Thelypodieae	Caulanthus	inflatus	N		March	May	105.5	4.5	yes	yes
Thelypodieae	Caulanthus	lasiophylla	T		March	June	120.5	5	yes	yes
Thelypodieae	Caulanthus	major	N		May	July	166.5	6.5	yes	yes
Thelypodieae	Caulanthus	pilosus	N		March	July	136	5.5	yes	yes
Thelypodieae	Caulanthus	simulans	N		March	June	120.5	5	yes	yes
Thelypodieae	Sibaropsis	hammittii	N		March	April	90	4	yes	yes
Thelypodieae	Stanleya	elata	N		May	July	166.5	6.5	yes	yes
Thelypodieae	Stanleya	pinnata_pinnata	N		April	September	182	7	yes	yes
Thelypodieae	Stanleya	viridiflora	N		May	July	166.5	6.5	yes	no
Thelypodieae	Streptanthella	longirostris	N		March	June	120.5	5	yes	yes
Thelypodieae	Streptanthus	barbatus	E	5.6	June	August	197.5	7.5	yes	yes
Thelypodieae	Streptanthus	barbiger	E	6	May	August	182	7	yes	yes
Thelypodieae	Streptanthus	batrachopus	E	6.1	May	June	151	6	yes	yes
Thelypodieae	Streptanthus	bernardinus	N		June	August	197.5	7.5	yes	yes
Thelypodieae	Streptanthus	brachiatus	E	5.6	June	July	182	7	yes	yes

Thelypodieae	Streptanthus	bracteatus	N		April	June	136	5.5	no	yes
Thelypodieae	Streptanthus	breweri	E	5.7	May	July	166.5	6.5	yes	yes
Thelypodieae	Streptanthus	callistus	N		April	May	121	5	yes	no
Thelypodieae	Streptanthus	campestris	N		May	June	151	6	yes	yes
Thelypodieae	Streptanthus	carinatus	N		February	April	76	3.5	no	yes
Thelypodieae	Streptanthus	cordatus_cordatus	N		April	July	151.5	6	yes	yes
Thelypodieae	Streptanthus	cordatus_piutensis	N		June	July	182	7	yes	no
Thelypodieae	Streptanthus	cutleri	N		February	April	76	3.5	no	yes
Thelypodieae	Streptanthus	diversifolius	N		April	July	151.5	6	yes	yes
Thelypodieae	Streptanthus	drepanoides	E		May	July	166.5	6.5	yes	yes
Thelypodieae	Streptanthus	farnsworthianus	N		May	June	151	6	yes	yes
Thelypodieae	Streptanthus	fenestratus	N		May	June	151	6	yes	yes
Thelypodieae	Streptanthus	glandulosus_albidus	E	5.3	April	July	151.5	6	yes	no
Thelypodieae	Streptanthus	glandulosus_glandulosus	T	1.9	April	July	151.5	6	yes	yes
Thelypodieae	Streptanthus	glandulosus_hoffmanii	T	3	May	July	166.5	6.5	yes	no
Thelypodieae	Streptanthus	glandulosus_niger	E	6.1	May	July	166.5	6.5	yes	no
Thelypodieae	Streptanthus	glandulosus_pulchellus	E	4.9	May	June	151	6	yes	no
Thelypodieae	Streptanthus	glandulosus_secundus	T	3.5	April	June	136	5.5	yes	no
Thelypodieae	Streptanthus	glandulosus_sonomensis	E		May	July	166.5	6.5	yes	no
Thelypodieae	Streptanthus	gracilis	N		June	September	212.5	8	yes	no
Thelypodieae	Streptanthus	hesperidis	E	6.1	May	July	166.5	6.5	yes	yes
Thelypodieae	Streptanthus	hispidus	N		March	June	120.5	5	yes	no
Thelypodieae	Streptanthus	howellii	E	6.1	June	July	182	7	yes	yes
Thelypodieae	Streptanthus	hyacinthoides	N		May	June	151	6	no	yes
Thelypodieae	Streptanthus	insignis_insignis	T	4	March	May	105.5	4.5	yes	no
Thelypodieae	Streptanthus	insignis_lyonii	T	3.3	April	May	121	5	yes	no
Thelypodieae	Streptanthus	longisiliquus	N		May	July	166.5	6.5	yes	yes
Thelypodieae	Streptanthus	maculatus	N		April	May	121	5	no	yes
Thelypodieae	Streptanthus	morrisonii	E	6.1	May	September	197	7.5	yes	yes
Thelypodieae	Streptanthus	oblanceolatus	N		June	July	182	7	yes	no
Thelypodieae	Streptanthus	oliganthus	N		June	August	197.5	7.5	yes	no

Thelypodieae	Streptanthus	platycarpus	N		March	April	90	4	no	yes
Thelypodieae	Streptanthus	polygaloides	E	5.7	May	July	166.5	6.5	yes	yes
Thelypodieae	Streptanthus	sparsiflorus (=platycarpus)	N		March	April	90	4	no	yes
Thelypodieae	Streptanthus	tortuosus	T	1.4	April	September	182	7	yes	yes
Thelypodieae	Streptanthus	vernalis	E		March	May	105.5	4.5	yes	yes
Thelypodieae	Streptanthus	vimineus	T		May	July	166.5	6.5	yes	no
Thelypodieae	Thelypodium	brachycarpum	T	3.3	April	August	167	6.5	yes	no
Thelypodieae	Thelypodium	crispum	N		June	August	197.5	7.5	yes	yes
Thelypodieae	Thelypodium	flexuosum	N		April	June	136	5.5	yes	yes
Thelypodieae	Thelypodium	howellii_howellii	N		May	July	166.5	6.5	yes	no
Thelypodieae	Thelypodium	integrifolium_affine	N		June	October	228	8.5	yes	no
Thelypodieae	Thelypodium	integrifolium_complanatum	N		June	August	197.5	7.5	yes	yes
Thelypodieae	Thelypodium	laciniatum	N		April	August	167	6.5	yes	yes
Thelypodieae	Thelypodium	milleflorum	N		April	August	167	6.5	yes	no
Thelypodieae	Thelypodium	stenopetalum	N		May	August	182	7	yes	no
Thelypodieae	Thysanocarpus	conchuliferus	N		March	April	90	4	yes	no
Thelypodieae	Thysanocarpus	curvipes	N		February	June	106.5	4.5	yes	yes
Thelypodieae	Thysanocarpus	laciniatus_hitchcockii	N		March	May	105.5	4.5	yes	no
Thelypodieae	Thysanocarpus	laciniatus_laciniatus	N		March	May	105.5	4.5	yes	no
Thelypodieae	Thysanocarpus	laciniatus_rigidus	N		February	May	91.5	4	yes	no
Thelypodieae	Thysanocarpus	radians	N		March	April	90	4	yes	no
Trichostema	Trichostema	arizonicum	N		July	October	243	9	no	yes
Trichostema	Trichostema	austromontanum_austromontanum	N		July	October	243	9	yes	yes
Trichostema	Trichostema	austromontanum_compactum	N		July	August	212.5	8	yes	no
Trichostema	Trichostema	lanatum	N		April	July	151.5	6	yes	yes
Trichostema	Trichostema	lanceolatum	T		June	November	243	9	yes	yes
Trichostema	Trichostema	laxum	T	4	June	October	228	8.5	yes	yes
Trichostema	Trichostema	micranthum	N		July	September	227.5	8.5	yes	yes
Trichostema	Trichostema	oblongum	N		June	September	212.5	8	yes	yes
Trichostema	Trichostema	ovatum	N		July	October	243	9	yes	yes

Trichostema	Trichostema	parishii	N		March	July	136	5.5	yes	yes
Trichostema	Trichostema	rubisepalum	E	5.4	July	September	227.5	8.5	yes	yes
Trichostema	Trichostema	ruygtii	N		June	October	228	8.5	yes	no
Trichostema	Trichostema	simulatum	N		July	September	227.5	8.5	yes	yes
Trifolium	Trifolium	albopurpureum	T		March	June	120.5	5	yes	yes
Trifolium	Trifolium	amoenum	N	1.3	April	June	136	5.5	yes	yes
Trifolium	Trifolium	andersonii_andersonii	N		May	August	182	7	yes	no
Trifolium	Trifolium	andersonii_beatleyae	N		May	August	182	7	yes	yes
Trifolium	Trifolium	angustifolium	N		April	May	121	5	no	yes
Trifolium	Trifolium	arvense	N		July	July	197	7.5	no	yes
Trifolium	Trifolium	barbigerum	N		April	June	136	5.5	yes	yes
Trifolium	Trifolium	beckwithii	N		May	August	182	7	yes	yes
Trifolium	Trifolium	bifidum_bifidum	T		April	June	136	5.5	yes	yes
Trifolium	Trifolium	bifidum_decipiens	N		April	June	136	5.5	yes	no
Trifolium	Trifolium	bolanderi	N		June	July	182	7	yes	yes
Trifolium	Trifolium	breweri	N		May	August	182	7	yes	yes
Trifolium	Trifolium	buckwestiorum	N		May	June	151	6	yes	yes
Trifolium	Trifolium	campestre	N		April	May	121	5	no	yes
Trifolium	Trifolium	ciliolatum	N		March	June	120.5	5	yes	yes
Trifolium	Trifolium	cyathiferum	N		May	August	182	7	yes	yes
Trifolium	Trifolium	depauperatum_amplectens	N		April	June	136	5.5	yes	no
Trifolium	Trifolium	depauperatum_depauperatum	T		March	May	105.5	4.5	yes	yes
Trifolium	Trifolium	depauperatum_truncatum	N		April	June	136	5.5	yes	no
Trifolium	Trifolium	dichotomum	T		April	June	136	5.5	yes	yes
Trifolium	Trifolium	dubium	T		April	July	151.5	6	no	yes
Trifolium	Trifolium	eriocephalum_eriocephalum	T		May	August	182	7	yes	yes
Trifolium	Trifolium	fragiferum	N		May	August	182	7	no	yes
Trifolium	Trifolium	fucatum	T	1.3	April	June	136	5.5	yes	yes
Trifolium	Trifolium	glomeratum	N		March	May	105.5	4.5	no	yes
Trifolium	Trifolium	gracilentum	T	1	March	June	120.5	5	yes	no

Trifolium	Trifolium	grayi	N		April	June	136	5.5	yes	no
Trifolium	Trifolium	gymnocarpon	N		May	June	151	6	yes	yes
Trifolium	Trifolium	hirtum	T		April	May	121	5	no	yes
Trifolium	Trifolium	howellii	N		July	August	212.5	8	yes	yes
Trifolium	Trifolium	hybridum	N		May	October	212.5	8	no	yes
Trifolium	Trifolium	hydrophilum	N		April	June	136	5.5	yes	no
Trifolium	Trifolium	incarnatum	N		May	August	182	7	no	yes
Trifolium	Trifolium	jokerstii	N		March	May	105.5	4.5	yes	yes
Trifolium	Trifolium	kingii_dedeckerae	N		May	July	166.5	6.5	yes	no
Trifolium	Trifolium	lemmonii	N		May	July	166.5	6.5	yes	yes
Trifolium	Trifolium	longipes_atrorubens	N		June	September	212.5	8	yes	no
Trifolium	Trifolium	longipes_elmeri	E	5.3	June	September	212.5	8	yes	yes
Trifolium	Trifolium	longipes_hansenii	N		June	September	212.5	8	yes	no
Trifolium	Trifolium	longipes_multipedunculatum	N		June	September	212.5	8	yes	no
Trifolium	Trifolium	longipes_oreganum	T	4	June	August	197.5	7.5	yes	no
Trifolium	Trifolium	longipes_shastense	N		June	September	212.5	8	yes	no
Trifolium	Trifolium	macraei	N		March	May	105.5	4.5	yes	yes
Trifolium	Trifolium	macrocephalum	N		April	May	121	5	yes	yes
Trifolium	Trifolium	microcephalum	T	1.4	April	August	167	6.5	yes	yes
Trifolium	Trifolium	microdon	T		March	June	120.5	5	yes	yes
Trifolium	Trifolium	monanthum_grantianum	N		June	August	197.5	7.5	yes	no
Trifolium	Trifolium	monanthum_monanthum	N		June	August	197.5	7.5	yes	yes
Trifolium	Trifolium	monanthum_parvum	N		June	August	197.5	7.5	yes	no
Trifolium	Trifolium	monanthum_tenerum	N		June	August	197.5	7.5	yes	no
Trifolium	Trifolium	obtusiflorum	N		April	July	151.5	6	yes	yes
Trifolium	Trifolium	oliganthum	T		March	June	120.5	5	yes	yes
Trifolium	Trifolium	olivaceum	N		April	May	121	5	yes	no
Trifolium	Trifolium	palmeri	N		March	May	105.5	4.5	yes	yes
Trifolium	Trifolium	polyodon	N		April	June	136	5.5	yes	yes
Trifolium	Trifolium	productum	T		June	August	197.5	7.5	yes	yes
Trifolium	Trifolium	productum	N		June	August	197.5	7.5	yes	no

Trifolium	Trifolium	reflexum	N		June	July	182	7	no	yes
Trifolium	Trifolium	siskiyouense	N		June	July	182	7	yes	no
Trifolium	Trifolium	subterraneum_brachycalyx	T		March	April	90	4	no	yes
Trifolium	Trifolium	subterraneum_subterrane	T		March	April	90	4	no	yes
Trifolium	Trifolium	subterraneum_yanninicum	T		March	April	90	4	no	yes
Trifolium	Trifolium	trichocalyx	N		April	June	136	5.5	yes	no
Trifolium	Trifolium	variegatum_geminiflorum	N		April	July	151.5	6	yes	no
Trifolium	Trifolium	variegatum_major	N		April	July	151.5	6	yes	no
Trifolium	Trifolium	variegatum_variegaum	N		April	June	136	5.5	yes	yes
Trifolium	Trifolium	willdenovii	T	1.3	March	June	120.5	5	yes	yes
Trifolium	Trifolium	wormskioldii	N		May	October	212.5	8	yes	yes

Appendix B

Vouchers, host associations, and Genbank Accession numbers for 163 *Orobanche* populations and outgroup taxa sampled for the phylogenetic analysis in Chapter 2.

Host associations in plain text were confirmed based on a haustorial connection or otherwise designated as the host by the collector. Host taxa printed in italics are inferred based on lists of co-occurring plants reported by the collector.

Collection #	Accession #	Taxon	Host	ITS	ETS	matK	rps2	trnL-trnF spacer	waxy
Halse 4905	WTU 333630	Castilleja ambigua							FJ939224
Halse 897	ARIZ 187291	O. arizonica		KX161146	KX160998	KX160824	KX160921	KX161298	
Homgren 7066	NY	O. arizonica				KX160825	KX160922		
Collins 1541	WIS 282497	O. bulbosa		KX161150	KX161002				
Colwell (5-July-2009)			Adenostoma fasciculatum	KX161147	KX160999	KX160826		KX161299	
Colwell 03-08	JEPS 126150	O. bulbosa	Adenostoma fasciculatum	KX161148	KX161000	KX160827	KX160923	KX161300	
Colwell 99-01	WTU 344744	O. bulbosa	Adenostoma fasciculatum	KX161149	KX161001				
Hammond 10858	ASU 60715	O. bulbosa		KX161151	KX161003				
Schneider 936	JEPS 122909	O. bulbosa	Adenostoma fasciculatum	KX161152	KX161004	KX160828	KX160924	KX161301	KX160874
Colwell 02-48	WTU 351388	O. californica subsp. californica	Grindelia stricta	KX161153	KX161005	KX160830	KX160926	KX161306	
Colwell 02-49	WTU 351400	O. californica subsp. californica	Grindelia stricta	KX161154	KX161006	KX160831	KX160927	KX161305	
Colwell 02-51	WTU 351389	O. californica subsp. californica	Grindelia stricta	KX161155	KX161007				
Colwell 02-54		O. californica subsp. californica	Eriophyllum staechadifolium	KX161258	KX161100	KX160872	KX160996	KX161377	KX160896
Colwell 04-	JEPS 126148	O. californica	Eriophyllum	KX161259	KX161101				

196		subsp. californica	staechadifolium						
Colwell 04-313	JEPS 126160	O. californica subsp. californica	Eriophyllum staechadifolium	KX161260	KX161102				
Colwell 04-314		O. californica subsp. californica	Grindelia stricta	KX161156	KX161008				
Colwell 15-01	JEPS 126152	O. californica subsp. californica	Eriophyllum staechadifolium	KX161261	KX161103	KX160871		KX161376	
Colwell 96-WA-DPSP	WTU	O. californica subsp. californica	Grindelia integrifolia	KX161157	KX161009				
Colwell 97-CA-BLO	WTU 344755	O. californica subsp. californica	Grindelia integrifolia	KX161158	KX161010	KX160829	KX160925	KX161303	
Colwell 99-77	WTU 344846	O. californica subsp. californica	Grindelia integrifolia	KX161159	KX161011	KX160832	KX160928	KX161304	
Schneider 293	JEPS	O. californica subsp. californica	Eriophyllum staechadifolium	KX161262	KX161104	KX160873	KX160997	KX161378	KX160920
Taylor 18565	JEPS 100410	O. californica subsp. condensa	Heterotheca villosa var. minor	KX161160	KX161012	KX160833	KX160929	KX161307	
Taylor 18566	JEPS 100409	O. californica subsp. condensa	Heterotheca villosa var. minor	KX161161	KX161013				
Taylor 18568	JEPS 100408	O. californica subsp. condensa	Heterotheca villosa var. minor	KX161162	KX161014				
Colwell (18-June-2006)	JEPS 126157	O. californica subsp. feudgei		KX161163	KX161017	KX160835	KX160931	KX161308	
Colwell (8-June-2006)	JEPS 126158	O. californica subsp. feudgei	Artemisia tridentata	KX161167	KX161018				
Colwell 05-33	JEPS 126147	O. californica subsp. feudgei	Artemisia tridentata	KX161164					
Colwell 99-02	WTU 344758	O. californica subsp. feudgei		KX161165	KX161015	KX160834	KX160930		
Colwell 99-75	WTU 344745	O. californica subsp. feudgei		KX161166	KX161016				
Colwell (18-Sept-2006)	JEPS 126164	O. californica subsp. grandis	Lessingia filaginifolia and Isocoma menziesii	KX161168	KX161022				
Colwell 00-44	WTU 344754	O. californica subsp. grandis	*Lessingia filaginifolia*	KX161169	KX161019				
Colwell 02-52	WTU 351391	O. californica subsp. grandis	Lessingia filaginifolia	KX161170	KX161020	KX160836	KX160932	KX161309	
Colwell 08-599	JEPS 126151	O. californica subsp. grandis	Lessingia filaginifolia	KX161171	KX161021				

Colwell 03-57	WTU	O. californica subsp. grayana	*Eucephalus breweri*	KX161172	KX161023	KX160837	KX160933	KX161310	
Colwell 05-259	JEPS 126145	O. californica subsp. grayana	Erigeron sp.	KX161173	KX161024				
Colwell 14-25	YM	O. californica subsp. grayana	Euthamia occidentalis	KX161174	KX161025	KX160838	KX160934	KX161302	
Allen s.n. (=Colwell 05-101)	JEPS 126146	O. californica subsp. jepsonii		KX161177	KX161028				
Colwell 01-104	WTU 351396	O. californica subsp. jepsonii	Artemisia tridentata	KX161176	KX161027			KX161311	
Gowen s.n.	JEPS 126142	O. californica subsp. jepsonii		KX161178	KX161029				
Garcia 3877	SGO 154435	O. chilensis		KX161179	KX161030	KX160840	KX160936	KX161313	KX160875
Long 2240	UC 2046156	O. chilensis	Grindelia ventanensis	KX161181	KX161031	KX160841	KX160937	KX161314	KX160876
Rosas 3327	CONC 169912	O. chilensis		KX161182	KX161032	KX160842	KX160938	KX161315	KX160877
Vilagran 8616	SGO 142749	O. chilensis		KX161183	KX161033	KX160843	KX160939	KX161316	
Colwell 01-01	WTU 344743	O. cooperi	*Hymenoclea salsola*	KX161185	KX161035	KX160844	KX160940	KX161319	KX160878
Colwell 02-06	WTU 351385	O. cooperi	*Encelia farinosa*	KX161186	KX161036	KX160845	KX160941	KX161317	KX160879
Colwell 97-CA-SN	WTU 344843	O. cooperi	*Ambrosia dumosa*	KX161184	KX161034				
Van Devender 95-1215	ARIZ 321887	O. cooperi		KX161188	KX161038	KX160846	KX160942	KX161318	
Collins 2027	UC2046163	O. cooperi subsp. palmeri	Viguiera stenoloba	KX161187	KX161037				
Colwell 05-212	JEPS 126139	O. corymbosa		KX161189	KX161039				
Colwell 06-421	JEPS 126163	O. corymbosa		KX161190	KX161040				
Colwell 14-26	JEPS 126165	O. corymbosa	Artemisia tridentata	KX161191	KX161041			KX161320	
Colwell 99-08	WTU 344753	O. corymbosa	Artemisia tridentata	KX161192	KX161042			KX161321	
Holmgren 1402	WTU 224934	O. corymbosa	Artemisia sp.	KX161175	KX161026				
Leidolf 2385	WTU 344762	O. corymbosa	Artemisia sp.	KX161193	KX161043				
Collins 2035	MO 6012141	O. corymbosa subsp. mutabilis		KX161194	KX161044				

Santana 5977	WIS 282502	O. dugesii		KX161195	KX161045	KX160847	KX160943	KX161322	
Ahart 3393	CHSC 44286	O. fasciculata	Eriophyllum lanatum	KX161206			KX160948		
Banks 689	SD 137701	O. fasciculata	Galium andersonii	KX161207	KX161052		KX160993	KX161373	KX160886
Batten 78-279	ALA v85763	O. fasciculata	Artemisia frigida	KX161208	KX161053		KX160950	KX161324	KX160884
Bell 159	SD 136414	O. fasciculata	Galium sp.	KX161209	(>200 bp)		KX160994	KX161374	KX160887
Bohrer 1684	ARIZ 189922	O. fasciculata	*Artemisia pacifica*	KX161210	KX161054			KX161325	KX160888
Boyd 9673	RSA 599655	O. fasciculata	Eriogonum fasciculatum		KX161055				
Colwell 01-95	WTU 351381	O. fasciculata	*Phacelia hastata*	KX161197		KX160849	KX160945	KX161327	KX160881
Colwell 02-09	WTU 351387	O. fasciculata	Eriogonum compositum	KX161198		KX160850	KX160946	KX161330	KX160882
Colwell 02-44	YELLO	O. fasciculata	Eriogonum flavum	KX161199					
Colwell 04-03	YM 118118	O. fasciculata	*Ericameria arborescens*	KX161200	KX161046				
Colwell 04-54	YM 117945	O. fasciculata	Eriogonum wrightii subsp. subscaposum	KX161201	KX161047				
Colwell 04-83	YM 118109	O. fasciculata	Galium aparine	KX161202	KX161048				
Colwell 07-53	YM	O. fasciculata	Galium sp.	KX161203	KX161049		KX160992	KX161371	KX160883
Colwell 10-107	YM	O. fasciculata	Galium bolanderi	KX161204	KX161050			KX161370	KX160917
Colwell 95-CO-TFS	WTU 344763	O. fasciculata		KX161205	KX161051			KX161323	
Colwell 99-CA-RCRS	WTU 344759	O. fasciculata		KX161196		KX160848	KX160944	KX161326	KX160880
Cox 188	CHSC 12931	O. fasciculata	Galium sp.	KX161211		KX160854	KX160995	KX161375	KX160919
Egger 1295	WTU	O. fasciculata		KX161212	KX161056	KX160852	KX160949	KX161331	KX160889
Halse 908	ARIZ 187532	O. fasciculata	Artemisia tridentata	KX161213	KX161057				KX160890
Harvey s.n.	UC	O. fasciculata	Galium oreganum	KX161214	KX161058		KX160991	KX161372	KX160918
Howell 51680	CAS 641193	O. fasciculata	Phacelia egena	KX161215	KX161059				KX160891
Keith s.n.	WIS 282501	O. fasciculata	*Artemisia sp.*	KX161216	KX161060		KX160951		KX160893
Lackschewitz 6619	WTU 272369	O. fasciculata	Artemisia dracunculus	KX161217	KX161061				
Merner s.n.	WIS 282500	O. fasciculata		KX161218	KX161062				
Schneider 468	JEPS	O. fasciculata	Eriodictyon sp.	KX161219	KX161063	KX160851	KX160947	KX161329	
Schneider 920	JEPS 122893	O. fasciculata	Eriogonum nudum	KX161220	KX161064	KX160853		KX161332	KX160885

Yatskievych 82-196	ARIZ 236136	O. fasciculata	Eriodictyon angustifolium & Eriastrum densifolium	KX161221	(>200 bp)			KX161328	KX160894
Schneeweiss 7	WU	O. gracilis	Chamaecytisus sp.			HG803179	HG803179		
	herb. Sanchez-Pedraja 12213	O. gracilis		EU655600					
Schneider 124	JEPS 121581	O. hederae	Hedera helix	KX161222			KX160952		
Collins 1533	WIS	O. ludoviciana	Grindelia squarrosa	KX161180	KX161069				
Collins 2033	UC 2046173	O. ludoviciana	Ambrosia	KX161227	KX161070	KX160839	KX160935	KX161312	
Colwell 01-113	WTU 351402	O. ludoviciana	Chrysopsis villosa	KX161223	KX161065				
Colwell 01-114	WTU 351399	O. ludoviciana		KX161224	KX161066	KX160855	KX160953	KX161333	
Colwell 95-CO-DD	WTU 344764	O. ludoviciana	Artemisia sp.	KX161225	KX161067				
Dueholm 1164	WIS 10644	O. ludoviciana	Chrysopsis villosa var. villosa	KX161228					
Colwell 01-93	WTU 344844	O. ludoviciana subsp. arenosa	Chrysopsis villosa	KX161226	KX161068		KX160954	KX161334	
Collins 2024	MO 5990497	O. multiflora	Hetertheca latifolia	KX161230	KX161072	KX160857	KX160956	KX161336	KX160895
Collins 2025	MO 5876462	O. multiflora	Varilla texana	KX161231	KX161073				
Collins 2026	UC 2046172	O. multiflora	Varilla texana	KX161232	KX161074				
Collins 2030	MO 6012145	O. multiflora	Gutierrezia sarothrae	KX161233	KX161075	KX160858	KX160957	KX161337	
Collins 2031	MO 6012144	O. multiflora	*Gutierrezia sp.*	KX161234	KX161076	KX160859	KX160958	KX161338	
Collins and Heil 2034	MO	O. multiflora	Hetertheca villosa	KX161235	KX161077				
Smith 2903	MO 3646410	O. multiflora		KX161236	KX161078				
Colwell (4-May-2006)	JEPS 126159	O. parishii subsp. brachyloba	Isocoma menziesii var serpiphylla	KX161241	KX161082				
Colwell (7-May-2006)		O. parishii subsp. brachyloba		KX161243	KX161084	KX160861	KX160960		
Sproul & Wolf s.n.		O. parishii subsp. brachyloba		KX161242	KX161083	KX160860	KX160959	KX161339	
Colwell 03-53	JEPS 126149	O. parishii subsp. parishii	Gutieriezia microcephala	KX161244	KX161085	KX160862	KX160961	KX161341	

Colwell 05-413	JEPS 126144	O. parishii subsp. parishii	Artemisia dracunculus	KX161245	KX161086				
Colwell 05-414	JEPS 126143	O. parishii subsp. parishii	*Iva axillaris*	KX161238					
Colwell 07-25	JEPS 126141	O. parishii subsp. parishii	Lessingia filaginifolia	KX161237	KX161079				
Colwell 07-72	JEPS 126137	O. parishii subsp. parishii	Iva axillaris	KX161239	KX161080				
Colwell 99-76	WTU 344749	O. parishii subsp. parishii		KX161240	KX161081				
Hamilton s.n.	JEPS 126153	O. parishii subsp. parishii	Artemisia dracunculus	KX161246	KX161087				
Stoughton 583	RSA 767875	O. parishii subsp. parishii			KX161088				
Taylor 18332	WTU 351384	O. parishii subsp. parishii	Chrysothamnus nauseosus subsp. consimilis	KX161248	KX161090				
Taylor 18333	WTU 351383	O. parishii subsp. parishii	Gutierrezia microcephala	KX161247	KX161089				
Collins 1528	WIS 282503	O. pinorum	Holodiscus discolor	(>200 bp)					
Colwell 01-107	WTU 352202	O. pinorum	*Holodiscus discolor*	KX161249	KX161091				
Egger 804	WTU 332502	O. pinorum		KX161251	KX161093				
Collins 1620	MO 4903216	O. riparia	Xanthium strumarium and Ambrosia artemisiifolia	KX161253	KX161095	KX160864	KX160963	KX161343	
Collins 1622	UC 2046176	O. riparia	Ambrosia trifida	KX161254	KX161096				
Collins 2032	MO 6012143	O. riparia	Dicoria brandegi	KX161255	KX161097				
Harrington 10081	CS 46066	O. riparia		KX161257	KX161099				
Yatskievych 91-195	MO 3907149	O. riparia	Ambrosia trifida and Xanthium pennsylvanicum	KX161252	KX161094				
	CS 42888	O. riparia	Xanthium sp.	KX161256	KX161098	KX160865	KX160964	KX161344	
Yatskyevich 85-215	ARIZ 264197	O. sp. nov.	Zaluzania triloba	KX161229	KX161071	KX160856	KX160955	KX161335	
Alfaro 3461	MO 2637419	O. tacnaensis		KX161263	KX161105			KX161345	KX160897

Bobadilla s.n.	CONC 164753	O. tarapacana		KX161264	KX161106	KX160866	KX160965		
Ricardi 3326	CONC 19273	O. tarapacana			KX161107		KX160966	KX161346	KX160898
Ahart 10765	CHSC 87344	O. uniflora subsp. occidentalis	Senecio aronicoides	KX161269	KX161113		KX160970	KX161354	KX160899
Ahart 1984	CAS 853689	O. uniflora subsp. occidentalis	Perideridea bolanderi subsp. involucrata	KX161270	KX161114		KX160976	KX161351	
Ahart 7286	CHSC 63258	O. uniflora subsp. occidentalis	Perideridea kelloggii	KX161271	KX161115		KX160973	KX161350	KX160903
Ahart 9846	CHSC 82361	O. uniflora subsp. occidentalis	Perideridea sp.	KX161272	KX161116		KX160975		KX160904
Chisaki 661	WIS 282509	O. uniflora subsp. occidentalis	*Asteraceae sp.*	KX161273	KX161117		KX160982		
Colwell 04-63	YM118104	O. uniflora subsp. occidentalis	Sedum obtusatum	KX161266	KX161110		KX160974	KX161348	KX160902
Colwell 07-58	YM216905	O. uniflora subsp. occidentalis	*Senecio aronicoides*	KX161267	KX161111		KX160969	KX161353	
Colwell 14-11	JEPS 126167	O. uniflora subsp. occidentalis	Osmorrhiza brachypoda	KX161268	KX161112		KX160972	KX161349	
Colwell 96-WA-IC	WTU 344845	O. uniflora subsp. occidentalis	Lithophragma bulbifera and Montia perfoliata	KX161265	KX161109		KX160971	KX161347	KX160901
Duthie s.n.	WIS 282512	O. uniflora subsp. occidentalis		KX161274	KX161118				
Fiely 91	WS 285758	O. uniflora subsp. occidentalis	Lomatium macrocarpum and Eriogonum heracleoides	KX161275	KX161119		KX160977	KX161352	KX160907
Heckard 3286	JEPS 70862	O. uniflora subsp. occidentalis	*Saxifraga californica*		KX161120				
Hitchcock 18630	WS 185460	O. uniflora subsp. occidentalis	Lomatium sp.		KX161108				
Lackschewitz 4307	NY	O. uniflora subsp. occidentalis	Saxifraga spp. and Suksdorfia	KX161276	KX161121				
Oswald 5615	UC 1609174	O. uniflora subsp. occidentalis	Antennaria rosea	KX161277	KX161122		KX160968	KX161356	KX160906
Polster s.n.	V93858	O. uniflora subsp. occidentalis		KX161278	KX161123		KX160967	KX161355	KX160905
Thorne 4794	NY	O. uniflora subsp. occidentalis	Antennaria rosea	KX161279	KX161124				

Anderson 2267	MIN	O. uniflora subsp. uniflora	Solidago canadensis	KX161280	KX161125		KX160981	KX161361	KX160900
Bouchard and Hay 86-94	MT 26938	O. uniflora subsp. uniflora		KX161281	KX161126		KX160979		KX160908
Cochrane 255	WIS 282508	O. uniflora subsp. uniflora		KX161282	KX161127		KX160985	KX161362	KX160913
dePamphilis 94-15	PENN	O. uniflora subsp. uniflora		AY209297					
Henson 1499	WIS 282510	O. uniflora subsp. uniflora		KX161283	KX161128				KX160914
Kucyniak 76	WIS 202505	O. uniflora subsp. uniflora	Solidago sp.	KX161284	KX161129		KX160984	KX161358	KX160912
Lipkin 04-324	ALA v156078	O. uniflora subsp. uniflora	Solidago lepida	KX161285	KX161130		KX160980	KX161360	KX160909
Lomer 7268	UBC 234660	O. uniflora subsp. uniflora	*Solidago lepida*	KX161286	KX161131		KX160983	KX161357	KX160910
Marie-Victorin 27906	WIS 282511	O. uniflora subsp. uniflora	*Senecio pseudoaureus*		KX161134				
Melburn s.n.	V 101353	O. uniflora subsp. uniflora		KX161287					
Sheviak 7072	UC 2046154	O. uniflora subsp. uniflora	*Solidago sp.*	KX161288	KX161132				
Talbot 169	ALA v122774	O. uniflora subsp. uniflora	Solidago multiradiata	KX161289	KX161133		KX160978	KX161359	
Wood s.n.	MO 6010393	O. uniflora subsp. uniflora	Solidago sp.	KX161290	KX161135			KX161363	KX160911
Colwell 02-04	WTU 351386	O. valida subsp. howellii		KX161291	KX161136	KX160867	KX160986	KX161364	KX160915
Ruygt 1823	JEPS 110567	O. valida subsp. howellii	*Garrya sp.*		KX161137		KX160987	KX161365	
Colwell 99-73	WTU 344847	O. valida subsp. valida		KX161292	KX161138	KX160868	KX160988	KX161367	KX160916
Mistretta 1866	RSA 641369	O. valida subsp. valida	Garrya flavescens and Cercocarpus betuloides		KX161139				
Mistretta 1867	RSA 641370	O. valida subsp. valida	*Garrya flavescens*		KX161140			KX161366	
Colwell (01-Aug-2006)	JEPS 126162	O. vallicola	Sambucus mexicana	KX161293	KX161141	KX160869	KX160989	KX161368	
Colwell 01-	WTU 351393	O. vallicola	Sambucus mexicana	KX161294	KX161142				

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Colwell 01-116	WTU 351394	O. vallicola	*Sambucus mexicana*	KX161295	KX161143	KX160870	KX160990	KX161369	
Colwell 02-57	WTU 351404	O. vallicola	Sambucus mexicana	KX161296	KX161144				
Prothero s.n.	JEPS 126154	O. vallicola		KX161297	KX161145				
Egger 1259	WTU	Triphysaria versicolor subsp. versicolor							FJ939226

Appendix C

GenBank accession numbers for DNA sequences used in the Orobanchaceae phylogenetic analysis

Regions with missing data are marked with a dash (–).

	Gene Region			
Taxon	ETS	ITS	PhyA	PhyB
Agalinis purpurea	–	EU827858.1	AM233922.1	KC542198.1
Aphyllon arizonicum	KX160998	KX161146	–	–
Aphyllon californicum subsp. californicum	KX161005	KX161153	AM233989.1	KC542244.1
Aphyllon californicum subsp. condensum	KX161012	KX161160	–	–
Aphyllon californicum subsp. feudgei	KX161015	KX161164	–	–
Aphyllon californicum subsp. grande	KX161019	KX161169	–	–
Aphyllon californicum subsp. grayanum	KX161024	KX161173	–	–
Aphyllon californicum subsp. jepsonii	KX161028	KX161177	–	–
Aphyllon chilense	KX161031	EU600371.1	–	–
Aphyllon cooperi subsp. cooperi	KX161036	KX161186	–	–
Aphyllon cooperi subsp. palmeri	KX161037	KX161187	–	–
Aphyllon corymbosum	KX161041	KX161191	AM233990.1	KC542245.1
Aphyllon dugesii	KX161045	KX161195	–	–
Aphyllon epigalium subsp. epigalium	KX161049	KX161211	–	–
Aphyllon epigalium subsp. notocalifornicum	KX161052	KX161207	–	–
Aphyllon fasciculatum (Artemesia host)	KX161053	KX161208	AM233992.1	KC542248.1
Aphyllon fasciculatum (Eriogonum host)	KX161064	KX161220	–	–
Aphyllon ludovicianum	KX161070	KX161227	KC542191.1	KC542246.1
Aphyllon multiflorum	KX161072	KX161230	–	–
Aphyllon parishii subsp. brachylobum	KX161083	KX161242	–	–
Aphyllon parishii subsp. parishii	KX161085	KX161244	–	–
Aphyllon pinorum	KX161091	AY209292.1	AM233994.1	KC542247.1
Aphyllon purpureum	KX161110	KX161266	–	–
Aphyllon riparium	KX161095	KX161253	–	–
Aphyllon robbinsii	KX161104	KX161262	–	–
Aphyllon sp nov.	KX161071.1	KX161229.1	–	–
Aphyllon tacnaensis	KX161105	KX161263	–	–
Aphyllon tarapacanum	KX161107	KX161264	–	–
Aphyllon tuberosum	KX161000	KX161148	–	–
Aphyllon uniflorum	KX161125	KX161280	–	–
Aphyllon validum subsp. howellii	KX161136	KX161291	–	–
Aphyllon validum subsp. validum	KX161138	KX161292	–	–
Aphyllon vallicolum	KX161143	KX161295	–	–

Bellardia trixago	–	JF900513.1	AM233930.1	KC542203.1
Boschniakia himalaica	–	AY911212.1	KC542187.1	KC542204.1
Boschniakia rossica	–	AY911214.1	AM233932.1	KC542206.1
Castilleja exserta	EF103614.1	EF103688.1	AM233939.1	KC542212.1
Castilleja miniata	EF103642.1	EF103712.1	AM233941.1	KC542214.1
Castilleja rubicundula	EF103610.1	EF103685.1	AM233942.1	KC542215.1
Castilleja sulphurea	AF478977.1	AF478944.1	AM233945.1	KC542290
Cistanche deserticola	–	AB217873.1	–	–
Cistanche phelypaea subsp. lutea	–	AY209300.1	–	–
Cistanche salsa	–	AB217872.1	–	–
Cistanche tubulosa	–	AB217871.1	–	–
Cistanche violacea	–	AY209304.1	–	–
Conopholis alpina	–	KC480324.1	AM233949.1	KC542216.1
Conopholis americana	–	AY209289.1	AM233950.1	KC542217.1
Cordylanthus ramosus	EF103662.1	EF103725.1	AM233951.1	–
Diphelypaea coccinea	–	AY209284.1	–	–
Diphelypaea tournefortii	–	AY209285.1	–	–
Epifagus virginiana	–	AY209290.1	AM233954.1	KC542221.1
Euphrasia pectinata	–	AY596811.1	–	–
Harveya capensis	–	AF120224.1	–	–
Hyobanche atropurpurea	–	AF120213.1	AM233964.1	KC542230.1
Hyobanche sanguinea	–	AF120220.1	AM233967.1	–
Kopsiopsis hookeri	–	AY209291.1	AM233931.1	KC542205.1
Kopsiopsis strobilacea	–	AY911215.1	AM233933.1	KC542207.1
Lamourouxia rhinanthifolia	–	–	AM233969.1	KC542293.1
Lathraea squamaria	–	AM503877.2	AM233973.1	KC542234.1
Lindenbergia indica	–	KC480288.1	AM233976.1	–
Lindenbergia muraria	–	KC480289.1	AM233977.1	KC542235.1
Lindenbergia philippensis	–	AY911231.1	AM233978.1	KC542236.1
Mannagettaea hummelii	–	KC480355.1	KC542190.1	–
Melampyrum arvense	–	AM503874.2	AM233919.1	KC542237.1
Melampyrum carstiense	–	EU259252.1	AM233979.1	KC542238.1
Monochasma sheareri	–	KC480363.1	AM233985.1	KC542241.1
Nesogenes africanus	–	–	AM233986.1	–
Orobanche alba	–	AY209245.1	–	–
Orobanche amethystea	–	AY209274.1	–	–
Orobanche anatolica	–	AY209283.1	–	–
Orobanche artemisiae-campestris	–	AY209264.1	–	–
Orobanche austrohispanica	–	AY209241.1	–	–
Orobanche ballotae	–	AY960729.1	–	–
Orobanche bartlingii	–	AY209260.1	–	–
Orobanche caryophyllacea	–	AY209237.1	–	–
Orobanche cernua var. australiana	–	AY209230.1	–	–

Orobanche coerulescens	–	AY209235.1	–	–
Orobanche colorata	–	AY209281.1	–	–
Orobanche crenata	–	AY209266.1	–	–
Orobanche crinita	–	AY209244.1	–	–
Orobanche densiflora	–	AY209243.1	AM233991.1	–
Orobanche elatior	–	AY209275.1	–	–
Orobanche flava	–	AY209254.1	–	–
Orobanche foetida	–	EU655603.1	–	–
Orobanche gracilis	–	AY209238.1	AM233993.1	–
Orobanche grenieri	–	AY960728.1	–	–
Orobanche grossheimii	–	AY209277.1	–	–
Orobanche haenseleri	–	AY209253.1	–	–
Orobanche hederae	–	AY209273.1	–	–
Orobanche krylowii	–	KF359500.1	–	–
Orobanche lucorum	–	AY209251.1	–	–
Orobanche lutea	–	AY209279.1	–	–
Orobanche lycoctoni	–	AY960724.1	–	–
Orobanche macrolepis	–	AY209288.1	–	–
Orobanche minor	–	AF437315.1	AY348568.1	KC542249.1
Orobanche owerinii	–	AY209265.1	–	–
Orobanche ozanonis	–	AY960723.1	–	–
Orobanche pancicii	–	JN796923.1	–	–
Orobanche picridis	–	AY209269.1	–	–
Orobanche pubescens	–	AY209268.1	–	–
Orobanche pycnostachya	–	AY881143.1	–	–
Orobanche raddeana	–	AY209257.1	AM233995.1	KC542250.1
Orobanche rapum-genistae	–	AY209280.1	–	–
Orobanche reticulata	–	AY209256.1	–	–
Orobanche ritro	–	EU655617.1	–	–
Orobanche salviae	–	AY209252.1	–	–
Orobanche santolinae	–	EU655604.1	–	–
Orobanche sintenisii	–	AY209276.1	–	–
Orobanche teucrii	–	AY209236.1	–	–
Orobanche transcaucasica	–	AY209261.1	–	–
Orthocarpus bracteosus	EF103666.1	AY911243.1	AM233997.1	KC542251.1
Orthocarpus tenuifolius	EF103671.1	EF103734.1	AM233998.1	KC542252.1
Orthocarpus tolmiei subsp. tolmiei	–	EF103726.1	–	–
Parentucellia viscosa	KM408188.1	KC480377.1	–	–
Paulownia fortunei	–	KJ563196.1	–	–
Paulownia tomentosa	AF478974.1	AF478941.1	AM234001.1	KC542195.1
Pedicularis canadensis	–	HG424091.1	–	–
Pedicularis ingens	–	HG424135.1	–	–
Pedicularis tuberosa	–	AY949661.1	AM234008.1	KC542261.1

Phelipanche aegyptiaca	–	KC811152.1	–	–
Phelipanche arenaria	–	AY960733.1	–	–
Phelipanche bohemica	–	AY960734.1	–	–
Phelipanche bungeana	–	AY209330.1	–	–
Phelipanche caesia	–	AY209351.1	–	–
Phelipanche coelestis	–	AY209329.1	–	–
Phelipanche georgii-reuteri	–	AY960746.1	–	–
Phelipanche gratiosa	–	EU581773.1	–	–
Phelipanche iberica	–	AY960742.1	–	–
Phelipanche inexspectata	–	AY960739.1	–	–
Phelipanche lavandulacea	–	EU581718.1	–	–
Phelipanche mutelii	–	AY960735.1	–	–
Phelipanche nana	–	KM925016.1	–	–
Phelipanche nowackiana	–	AY209352.1	–	–
Phelipanche oxyloba	–	AY209319.1	–	–
Phelipanche portoilicitana	–	AY960743.1	–	–
Phelipanche pulchella	–	AY960741.1	–	–
Phelipanche purpurea	–	EU581717.1	–	–
Phelipanche ramosa	–	EU581794.1	AM233996.1	–
Phelipanche rosmarina	–	EU581735.1	–	–
Phelipanche tunetana	–	AY209324.1	–	–
Rehmannia chingii	–	DQ069313.1	–	–
Rehmannia elata	–	DQ069315.1	–	–
Rehmannia henryi	–	DQ272447.1	–	–
Rehmannia piasezkii	–	DQ069316.1	–	–
Rehmannia solanifolia	–	DQ069314.1	–	–
Rhinanthus freynii	–	GU445319.1	AM234013.1	KC542266.1
Rhinanthus glacialis	–	FJ790041.1	AM234014.1	KC542267.1
Rhinanthus minor	–	FJ790040.1	AM234015.1	KC542268.1
Schwalbea americana	–	AY911252.1	AM234017.1	KC542270.1
Seymeria pectinata	–	AY911253.1	–	–
Siphonostegia chinensis	–	JN133286.1	AM234020.1	KC542271.1
Siphonostegia laeta	–	JN381014.1	–	KC542272.1
Striga asiatica	–	EU253604.1	AM234024.1	–
Striga bilabiata	–	AY911255.1	AM234025.1	–
Striga elegans	–	AY911256.1	KC542193.1	KC542276.1
Striga gesnerioides	–	AY911257.1	AM234026.1	KC542275.1
Tozzia alpina	–	–	AM234031.1	KC542278.1
Triphysaria pusilla	AF478976.1	AF478943.1	–	–
Xylocalyx asper	–	KC480411.1	AM234033.1	KC542279.1
Xylocalyx carterae	–	KC480412.1	AM234036.1	–