

## GEOGRAPHY OF *ERYTHRANTHE PARDALIS* (PHRYMACEAE), A SERPENTINE TOLERATOR

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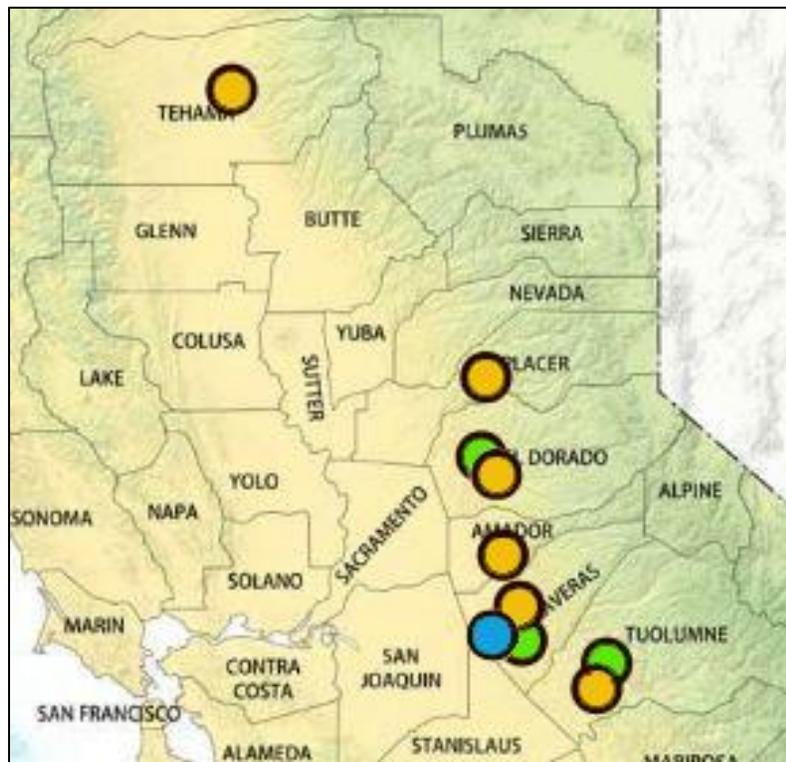
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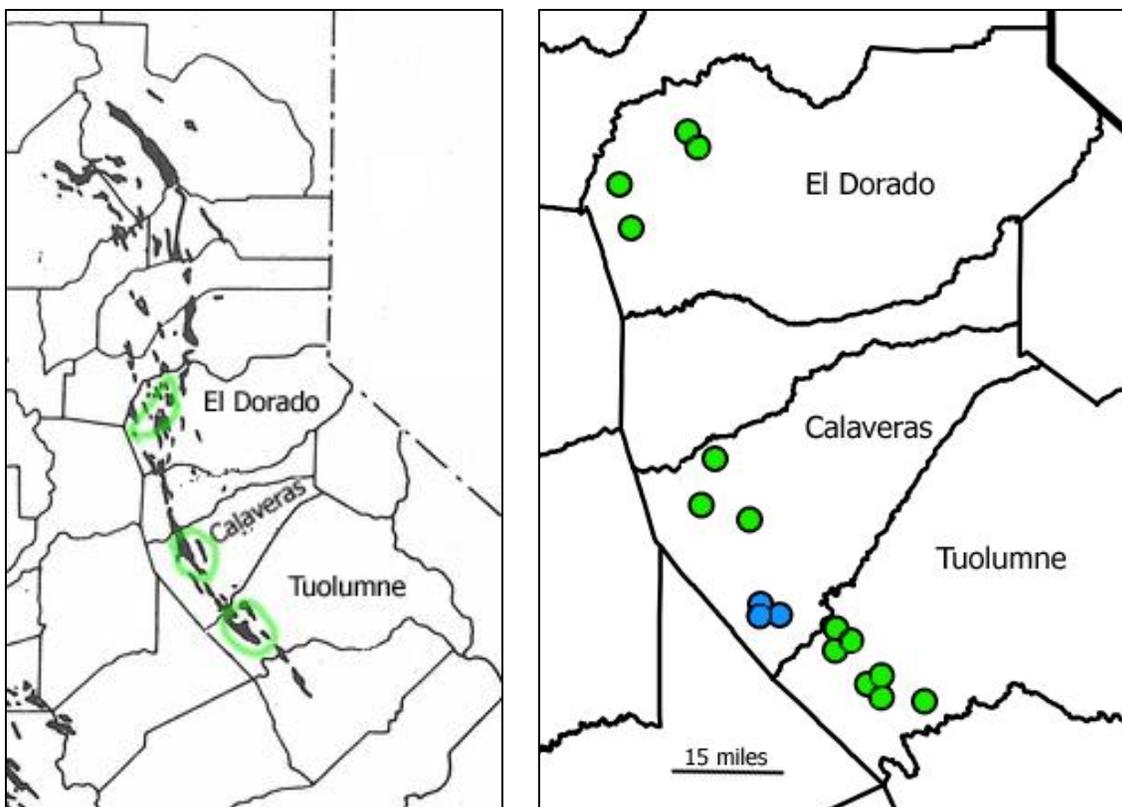
### ABSTRACT

Populations of *Erythranthe pardalis* occur in two separate regions of California — (a) Placer, El Dorado, Amador, Calaveras, and Tuolumne counties and (b) Tehama County. The Tehama County plants are disjunct from the more southern system by about 100 miles and all of the observations and collections there have been from igneous substrate. The type collection (from Tuolumne County) and others from the southern system occur on serpentine, but many occur on igneous and sedimentary substrate or on copper-contaminated sites. Detailed distribution maps are constructed from herbarium collections and observations posted on iNaturalist and Flickr; geological data are from label notes and from the Interactive Geologic Map of California.

*Erythranthe pardalis* is a member of sect. *Simiolus* (Nesom 2012) and characterized by an annual duration, small corollas (self-pollinating, fide Macnair et al. 1989), and especially by stipitate-glandular vestiture of the stems, leaves, and calyces — it is the only species of sect. *Simiolus* (with its putative sister, *E. serpentinicola*) with that vestiture. Morphological and geographic consistency provide the rationale for recognizing these plants as a single species. Natural hybrids are not known with any other species, except for the possibility of interaction with *E. nasuta* at one site (Nesom in prep.).



Map 1. County distribution of *Erythranthe pardalis*. Green symbols = serpentine. Gold symbols = non-serpentine. Blue = copper. A detailed map for each county is provided below (Maps 5-10).



Map 2a-b. County distribution of serpentine in the California Sierra (a) and serpentine-adapted (green) and of copper-adapted (blue) *Erythranthe pardalis* (b — collection and observation localities).

The geographic range of *Erythranthe pardalis* is restricted to a few counties in Sierran foothills of central California (Map 1). Populations appear to be scattered, but perhaps regionally clustered (Maps 2, 5-10) — collections and observations by California botanists and naturalists presumably approach a reasonably accurate picture of the distribution. The most obvious geographic discontinuity is between Tehama County populations and those in the larger area to the south, but distributional vacancies of smaller distances apparently occur elsewhere. Thus, as with many species, *E. pardalis* comprises populations and population systems among which reproductive isolation may be complete or nearly so. Potential for interbreeding among them has not been investigated.

### Serpentine and copper habitats

*Erythranthe pardalis* has been the subject of numerous publications, mostly related to genetic mechanisms of adaptation to copper-contaminated soil (e.g., Macnair & Watkins 1983; Macnair & Cumbes 1989; Macnair et al. 1989; Wright et al. 2103). The initial study was of copper-adapted plants of *E. microphylla* from the Keystone Union mine complex in Copperopolis, Calaveras County (Allen & Sheppard 1971), where plants grow on tailings and along a copper-contaminated creek. At two recently abandoned mines south of Copperopolis, Macnair (1989) concluded that some copper-adapted plants could be regarded as a distinct species of recent origin (= *Mimulus cupriphilus*) but he apparently was unaware that nearby plants of nearly identical morphology already had been named. Taxonomic confusion and ambiguity also have made interpretation difficult in other studies of these plants — it often is not clear whether "Mimulus guttatus" refers to *E. microphylla* or to *E. pardalis*.

The type locality of *Erythranthe pardalis* is serpentine habitat and the species has been characterized as a serpentine endemic or suggested to be one (e.g., Nesom & Fraga 2019), but it has been more commonly observed on igneous and sedimentary substrates (e.g., granite, andesite, basalt, pyroclastic flow, limestone, quartzite) as well as the copper-contaminated sites in Calaveras County. It

is a serpentine "tolerator" species rather than serpentine endemic (sensu Sianta & Kay 2019, 2021; Anaker et al. 2011). There are no obvious morphological differences between serpentine and non-serpentine plants, and plants from all substrates flower March through April, sometimes into May.

Serpentine adaptation is uncommon in species of sect. *Simiolus*. The only obligate serpentine species are *Erythranthe serpentinicola* from San Luis Obispo County and the sister pair *E. nudata* from Colusa, Glenn, Lake, Mendocino, Napa, and Sonoma counties and *E. percaulis* from Plumas County. *Erythranthe pardalis*, *E. microphylla*, and *E. glaucescens* occur on serpentine as well as non-serpentine habitats.

A strongly documented phylogenetic hypothesis for species of sect. *Simiolus* is not available but one in broad strokes, using available evidence (Nesom 2019), suggests that *Erythranthe pardalis* is most closely related to other annuals, e.g., *E. microphylla*, *E. nasuta*. There is no evidence that *E. pardalis* evolved from *E. guttata* in the strict sense (rhizomatous, constantly wet habitat) or from *E. microphylla* (annual, seasonally dry habitat, different growth form). Morphology similarity suggests that the recently described *E. serpentinicola* is the evolutionary sister of *E. pardalis* (Keil 2020) — if they are indeed sisters, then serpentine-adapted plants might be assumed to be ancestral (Fig. 1), with a broad tolerance that enables them to occur in a broader range of habitats, perhaps with local genetic adaptive adjustments. Macnair & Watkins (1983) found that copper-tolerant *E. microphylla* from Copperopolis did not show evidence of being at a severe disadvantage in an uncontaminated environment. Serpentine-adapted plants of *E. microphylla* (from Lake Co.) will grow on non-serpentine habitats (e.g., Palm et al. 2012), although not becoming as large as the non-serpentine plants.

In contrast, it is plausible that serpentine non-tolerance is the ancestral state in *Erythranthe pardalis*. It seems to be in *E. microphylla*, for which Selby & Willis (2018) noted that populations have "repeatedly and independently evolved serpentine tolerance" — its occurrence on serpentine is recorded in Lake, Marin, San Mateo, Sonoma, Tehama, and Trinity counties (Coastal Ranges, Map 4). Even with the wide range of *E. microphylla* (Map 3) and abundant occurrence of serpentine in northern and sierran California (Map 4a) and Oregon, these are the only localities where a serpentine habitat for the species has been recorded. Independent origin of these populations is plausible but, despite the claim otherwise, no evidence is at hand that would refute a hypothesis of common ancestry among any of them.

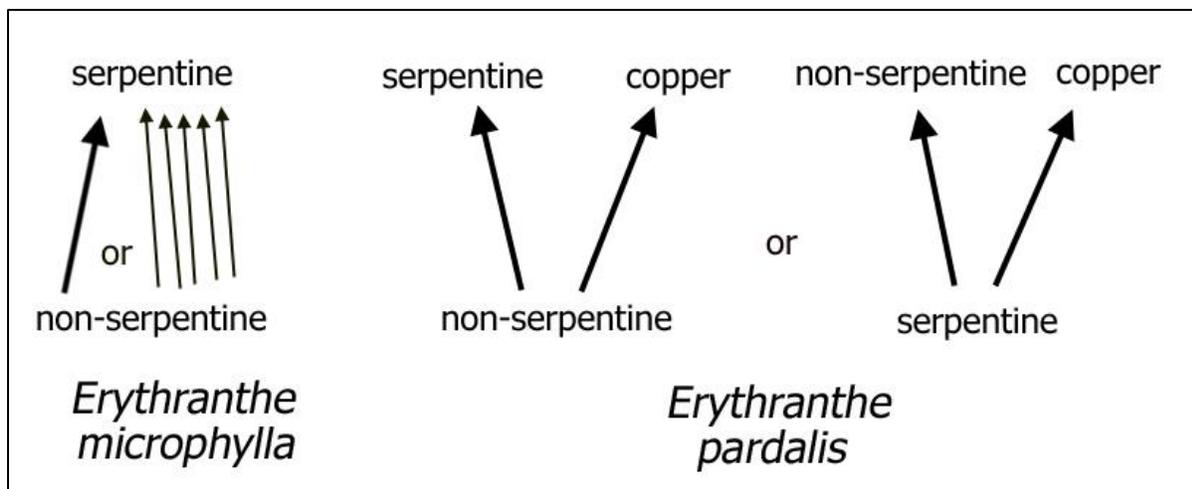
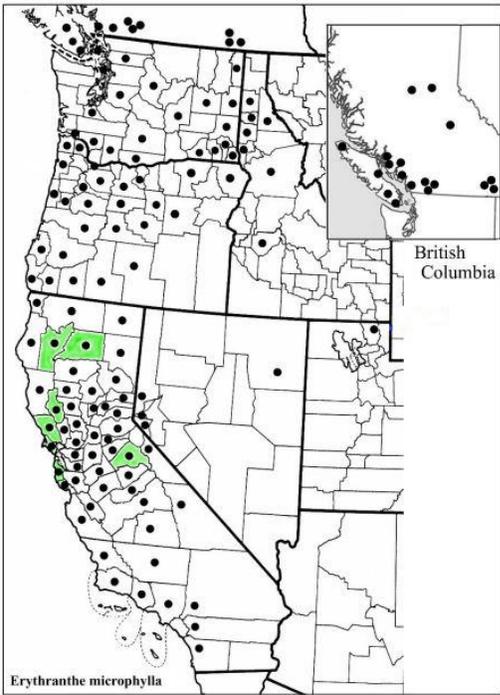
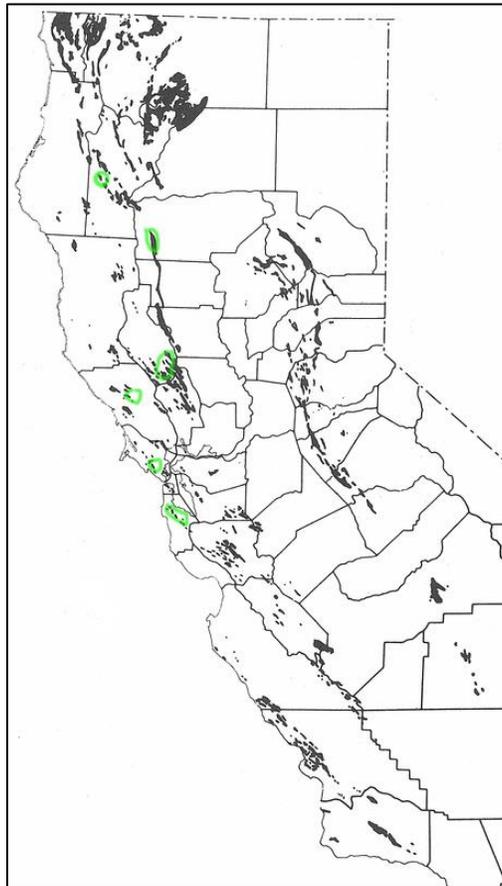
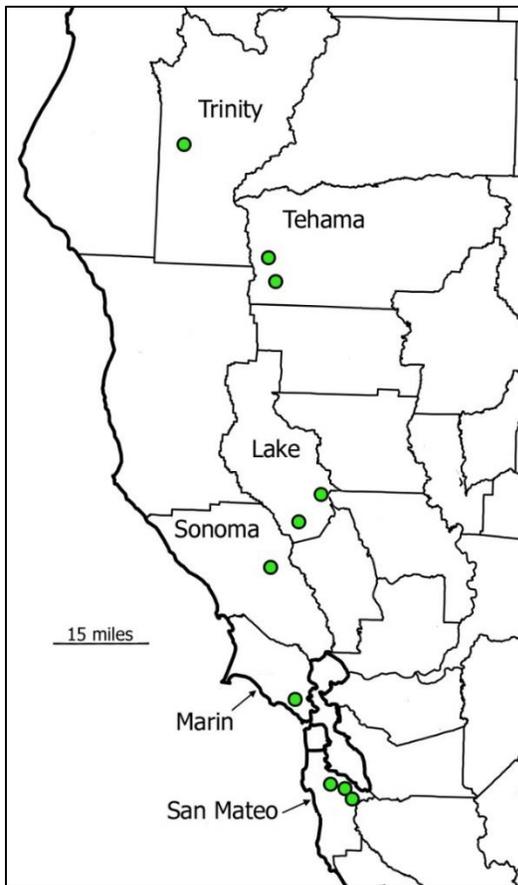


Figure 1. Pathways of adaptation. In *Erythranthe microphylla*, adaptation to serpentine via a single event or multiple, independent events. In *E. pardalis*, adaptation from an ancestral condition to non-serpentine or serpentine.



Map 3. Distribution of *Erythranthe microphylla* (from Nesom 2019). Serpentine-adapted populations are in green-shaded counties.



Map 4a-b. Distribution of serpentine-adapted *Erythranthe microphylla* in California Coastal Ranges and (b) serpentine in California (a).

### Genetic control of substrate tolerance

Selby and Willis (2018) located the area mediating serpentine tolerance in *Erythranthe microphylla*, identifying it as a major QTL with effects modified by causal alleles — they noted that the same QTL confers serpentine tolerance in distantly separated populations (Lake and Tuolumne counties). "The serpentine allele is largely dominant with heterozygotes having only slightly reduced survival rates relative to serpentine homozygotes." A common garden study indicated that each population is better adapted to its home soil than to the "foreign" soil.

Copper tolerance in *Erythranthe microphylla* (from the town of Copperopolis) is controlled by a single, dominant "supergene" (Macnair 1981, 1983; Macnair & Christie 1983; Smith & Macnair 1983; McNair et al. 1993; Smith & Macnair 1998), with effects sometimes modified by other minor genes (modifiers"). Wright et al. (2013) noted that control in *E. microphylla* is by a "dominant allele at a single Mendelian locus." The region mediating copper tolerance is on chromosome 9, that for serpentine tolerance on chromosome 13 (e.g., Selby & Willis 2018). The same gene for copper tolerance is used by both *E. microphylla* and *E. pardalis* (Macnair & Cumbes 1983). Nickel tolerance in *E. microphylla* is controlled by still other genes and is not correlated with serpentine tolerance (Tilstone & Macnair 1997; Hughes et al. 2001).

*Erythranthe pardalis* occurs intermixed with *E. microphylla* at the McNulty and Star Excelsior mine sites, and the two species also occur in close proximity over serpentine in the Red Hills area southwest of Chinese Camp. Naturally occurring intermediates have not been documented — reproductive isolation presumably results (at least in part) from differences in corolla morphology, i.e., small and selfing in *E. pardalis*, larger and outcrossing in *E. microphylla*. F<sub>1</sub> and F<sub>2</sub> hybrids and backcrosses, however, were produced between copper-tolerant *E. pardalis* from the McNulty mine and *E. microphylla* from the town of Copperopolis (Macnair & Cumbes 1983). F<sub>1</sub>s, F<sub>2</sub>s, and F<sub>3</sub>s were produced between *E. pardalis* (identified as such, not as *Mimulus cupriphilus*) and *E. marmorata* (large corollas, outcrossing; from Knights Ferry in Stanislaus Co. — voucher not cited or located; Hughes et al. 2001). Crosses apparently have not been attempted between serpentine-tolerant and -intolerant plants of *E. pardalis*.

In contrast to the lack of post-zygotic reproductive barriers in *Erythranthe pardalis*, a strong barrier between *E. microphylla* and the serpentine-obligate *E. nudata* is conferred by hybrid seed lethality. The two occur within meters of each other at some sites (Gardner & MacNair 2000; Toll & Willis 2018). Hybrids were detected in field-produced seed only when *M. nudatus* was the maternal parent (Gardner & Macnair 2000).

### METHODS

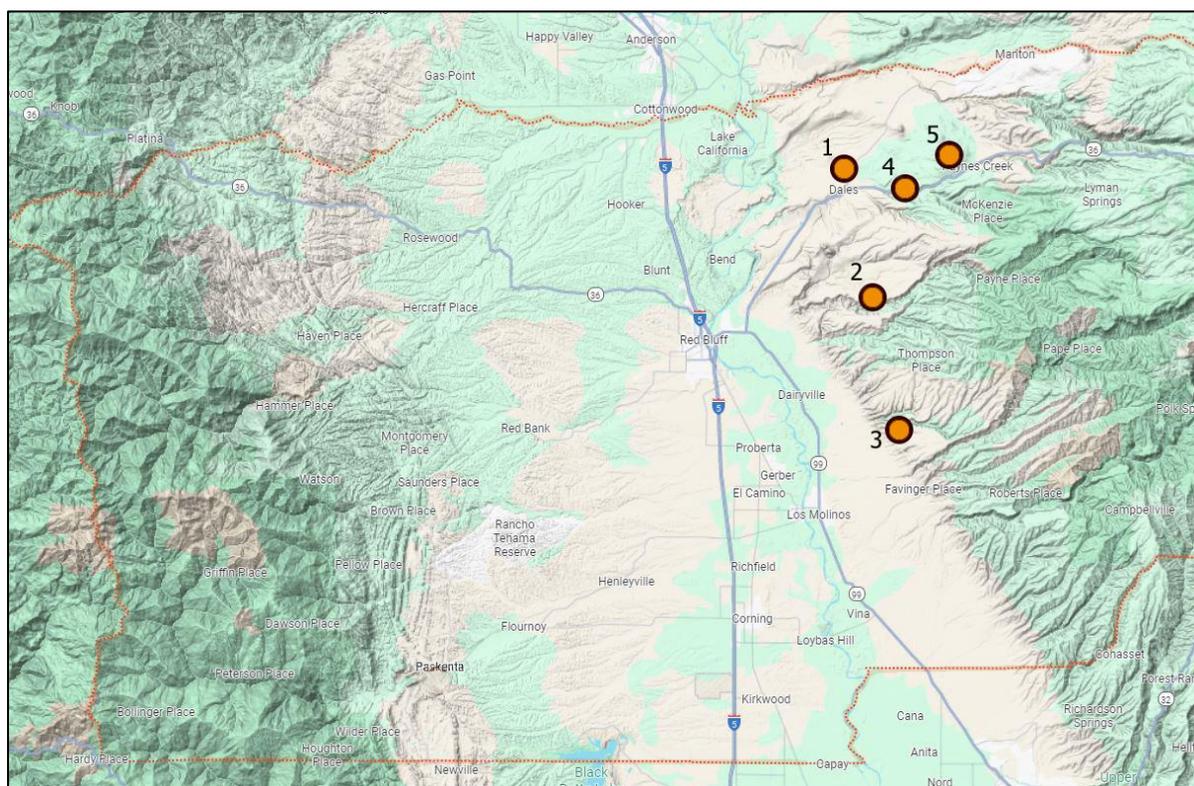
Maps were constructed using data from herbarium collections and from photographically documented observations on iNaturalist and Flickr. All of these are cited and numbered in the Appendix — they can be located by county and then by number on the maps. All cited collection records (at least specimen images) and photos have been examined and confirmed to be accurate. Records are mapped either as "serpentine" or "non-serpentine" — the latter includes substrates ranging from igneous to sedimentary, as indicated in each citation.

Geological information recorded on collection labels is assumed to be accurate — collections from serpentine substrate are usually specified as such. iNaturalist observations rarely provide habitat information except through inference from photos, but they provide geographic coordinates that allow precise mapping and determination of geology using the Geologic Map of California (Jennings 2020) and the Interactive Geologic Map of California (NGMDB -- USGS/AASG 2025).

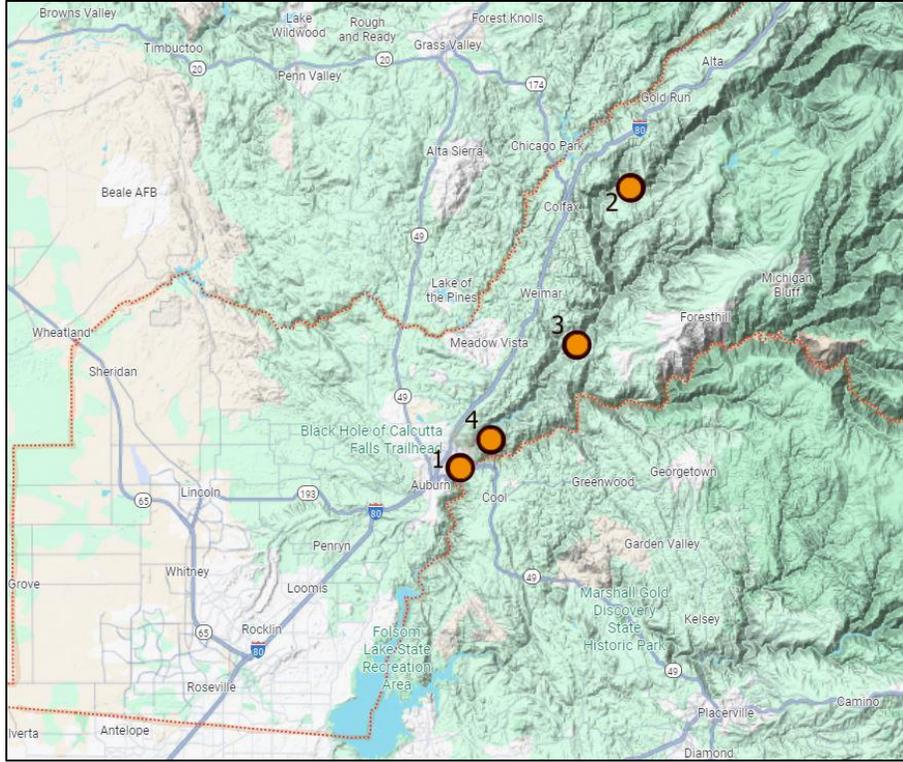
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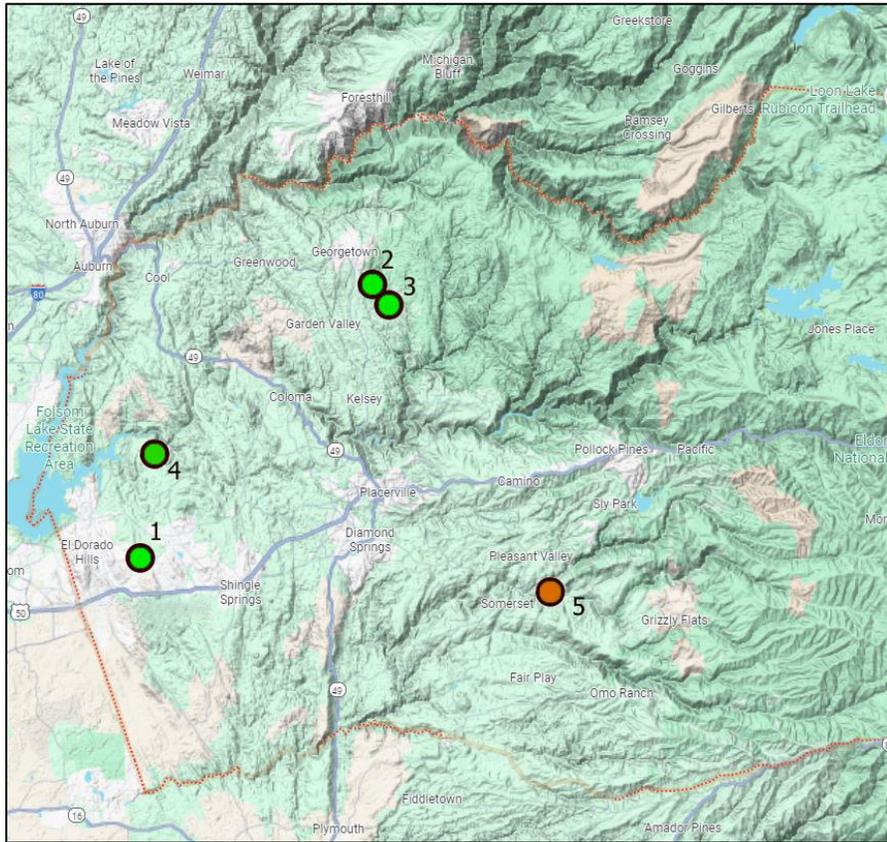
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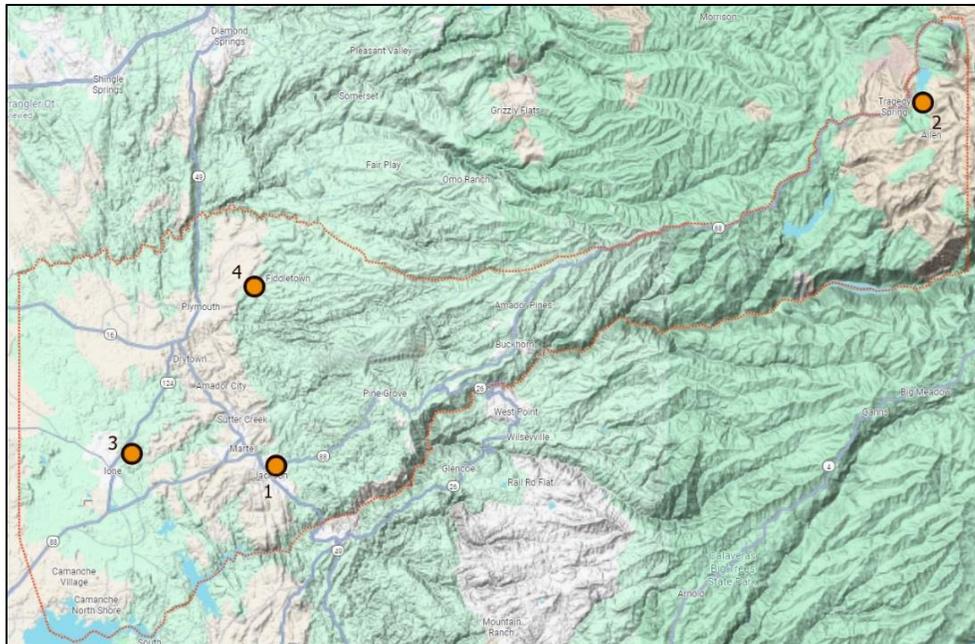
Map 5. Distribution of *Erythranthe pardalis* in Tehama County.



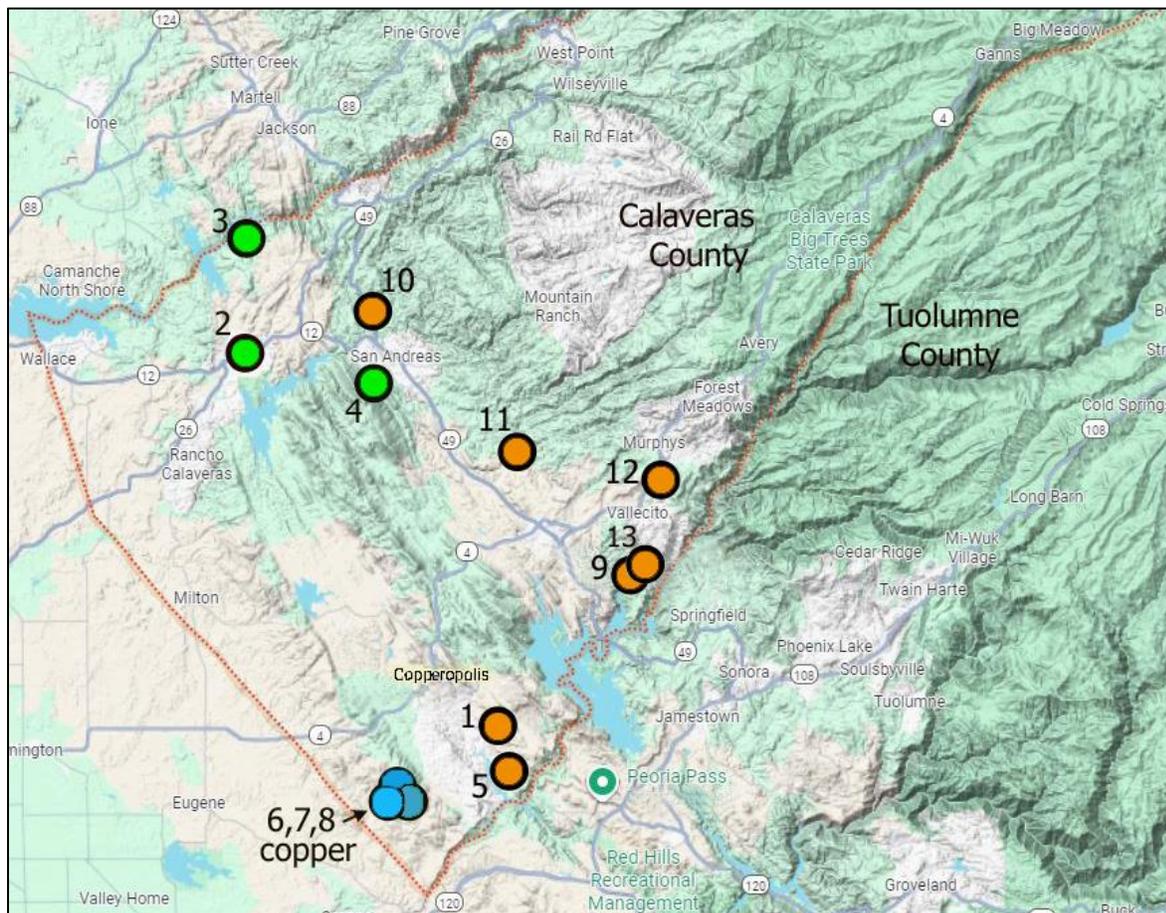
Map 6. Distribution of *Erythranthe pardalis* in Placer County.



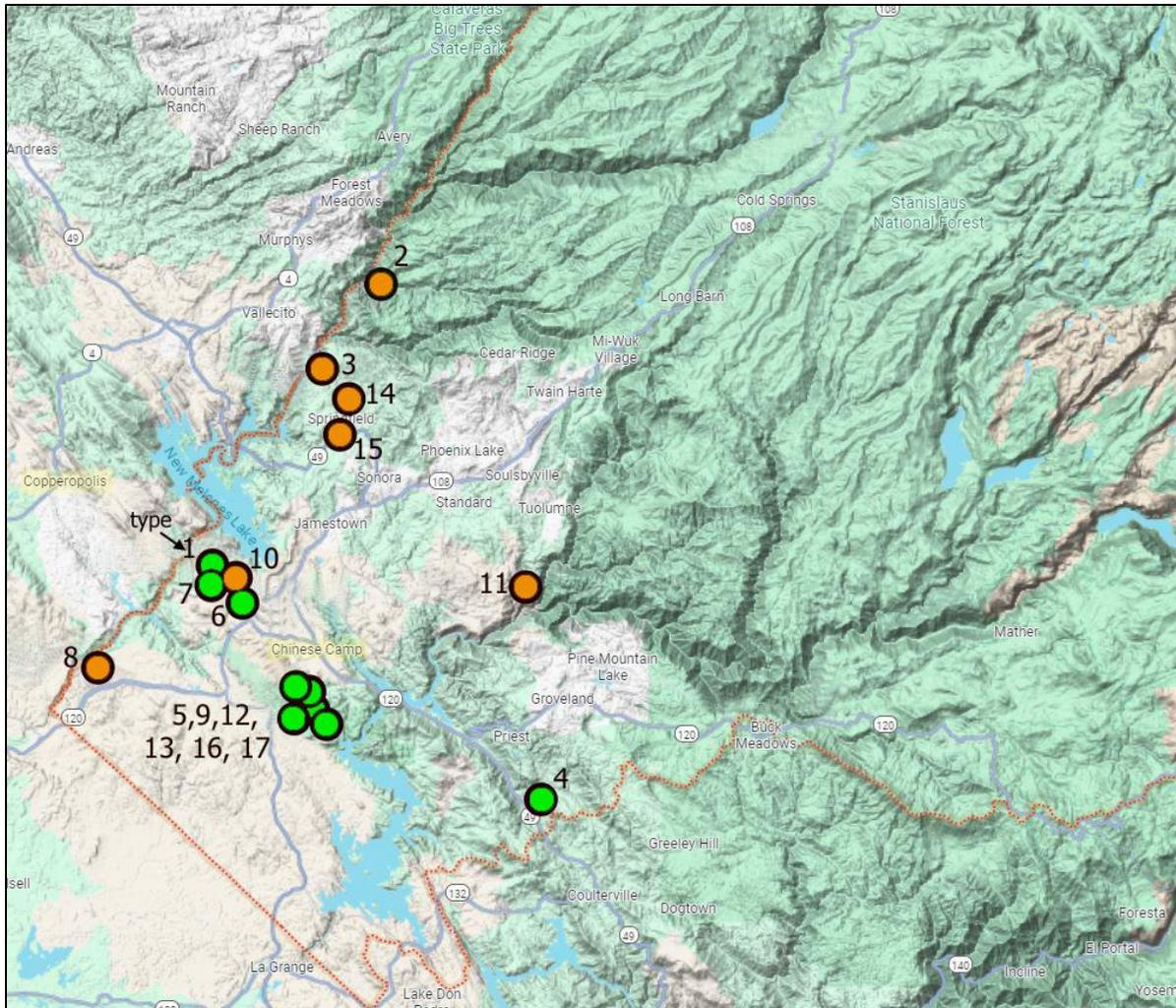
Map 7. Distribution of *Erythranthe pardalis* in El Dorado County.



Map 8. Distribution of *Erythranthe pardalis* in Amador County. Early collections by George Hansen (see Appendix) have no locality other than a name that could not be located in this study (see Hansen 1895; Jepson 1928). The Silver Lake locality seems out of place.



Map 9. Distribution of *Erythranthe pardalis* in Calaveras County.



Map 10. Distribution of *Erythranthe pardalis* in Tuolumne County.

## APPENDIX. Voucher information for geographic/geological records

### AMADOR COUNTY

1. Jackson, [ca. 38° 20' 53" N, 120° 46' 24" W], [volcanic and ultramafic in the vicinity], 1892, *Hansen s.n.* (NDG)
2. Silver Lake, [ca. 38° 40' N, 120° 07' W], [Tv<sup>p</sup>/gr<sup>Mz</sup>; Mesozoic granite], 20 Sep 1892, *Hansen s.n.* (NDG)
0. Not mapped. Sequoia gigantea region, Middle Fork [Mokelumne River] [?, perhaps in Calaveras Co.], 1500 ft, Apr 1893, *Hansen 135* (DS, MO, RSA);
0. Not mapped. Sequoia gigantea region, Fisher's Point (or Fisher's Cabins) [on the Mokelumne River, fide Jepson 1928] [not located], 2000 ft, Apr 1892 or 1893, *Hansen 473* (MO, NDG, UC).
0. Not mapped. Sequoia region, New York Falls [?not located], 2000 ft, Apr 1892, *Hansen 1286* (GH, MO, UC);
0. Not mapped. 0. Middle Fork [Mokelumne River] [?, perhaps in Calaveras Co.], 1500 ft, Apr 1892, *Hansen 1288* (DS, MO)

0. Not mapped. Norte Bar, 1000 ft, Apr 1895, *Hansen 1050* (DS).
3. Ione [ca. 38° 21' N, 120° 57' W], 300 ft, [sedimentary, volcanic, and ultramafic in the vicinity], 25 Mar 1896, *Hansen 1517* (MO, NDG)
0. Not mapped. Elsie's Creek [Giant Sequoia area fide Jepson 1928] [perhaps in Calaveras Co., Big Trees area, 38°17' N 120°19' W, where Hansen made other collections], [area of volcanics], 2700 ft, May 1896, *Hansen 1626* (DS, NDG)
0. Not mapped. N of Falls [?not located], 2000 ft, 18 Jul 1896, *Hansen 1795* (NDG)
4. 4 mi E of Plymouth, on road to Fiddletown, [ca. 38.504 N, 120.7823 W], N face of steep canyon and rocky places near stream, in foothill woodland, in red clay, [Pzcc; metasedimentary/limestone], 30 Mar 1961, *Ramsey 29* (JEPS-2 sheets)

### CALAVERAS COUNTY

1. Copperopolis Quad, Table Top Mtn, SE face, 37.898903 N, 120.57212 W, wet places along cleavage planes on 100% slope of latite butte, [Tm; andesite, basalt?], 700 ft, 16 Apr 1936, *Belshaw 1895* (UC)
2. Road to Fosteria [Paloma] 5 mi NE of Valley Springs, [ca. 38.20 N, 120.80 W], in moist ditch on slope, [um; serpentine], with *Pinus sabiniana*, 3 May 1963, *Breedlove 4788* (SMU)
3. Pardee Reservoir, Pardee Lake, W of McAfee Gulch at S end of the gulch, W of the Coast to Crest Trail just before it heads down into the gulch, [um; serpentine], burned ca. 5 years ago, 1032 ft, 17 May 2005, *CNPS SN Foothill Team SNFN0249b* (DAV)
4. near San Andreas, [probably serpentine, W of town], 24 Apr 1941, *Eastwood & Howell 8710* (CAS, UC)
5. Table Mtn, 7 mi S of Copperopolis on road to State Hwys 108/120, top of old lava flow, 1100 ft, 27 Apr 1963, *Lloyd 2444* (JEPS)
6. McNulty Mine, [37 54' 45" N, 120 43' 26" W], copper-contaminated stream [in area of volcanic and metavolcanic], [greenhouse grown], "seeds collected from dead plants, May 1985; plants grown August 1986," *McNair s.n.* (JEPS)
7. McNulty mine, copper-contaminated soil, "April 13-20th 1987," *McNair s.n.* (BM, JEPS – type collection of *Mimulus cupriphilus*)
8. ca. 7 air mi SW of Copperopolis, Star & Excelsior Mine, [37.915 N, 120.72778 W], tailings pile from copper mine [in area of volcanic and metavolcanic], 800 ft, 7 Apr 1998, *Taylor 16283* (JEPS), *16285* (JEPS-2 sheets), and *16286* (JEPS-2 sheets)
9. W of Parrott's Ferry Road near Coyote Creek Cave; 38.05919 N, 120.47979 W; [ls; Mesozoic granite, quartz monzonite, granodiorite, and quartz diorite], (no substrate photo); *denizs*, 29 Mar 2024 **iNaturalist**
10. Hwy 49 NW of San Andreas; 38.22045 N, 120.70005 W; [Pzv; Paleozoic metasedimentary], (substrate photo not illustrative); *Damon Tighe*, 26 Mar 2017 **iNaturalist**
11. Above San Domingo Creek, NW of Altaville; 38.12228 N, 120.59630 W; [Pzv; Paleozoic metasedimentary], (no substrate photo); *Matt Berger*, Mar 2023 **iNaturalist**
12. Ca 1.5 mi S of Murphys on Hwy 4; 38.11460 N, 120.45327 W; [Pz or ls; Paleozoic metasedimentary rocks, dolomite? or quartzite?], (substrate photo); *Matt Berger*, Mar 2023 **iNaturalist**
13. Natural Bridge on Coyote Creek, [ls; limestone], 1500 ft, 1976, *Menzies 142* (CAS).

### EL DORADO COUNTY

1. 2 mi NE of Clarksville, SE slope of Bass Lake, 38.676111 N, 121.078056 W, under and along edge of large serpentine rocks, 5 May 1967, *Crampton 7859* (AHUC, CHSC, DAV)

2. Traverse Creek Special Interest Area; 38.87655 N, 120.81697 W; [um; serpentine], (substrate photo); *Matt Berger*, 19 Mar 2019 **iNaturalist**
3. Traverse Creek Special Interest Area; 38.87391 N, 120.81846 W; [um; serpentine], (substrate photo not illustrative); *Thomas Taylor*, 12 Apr 2023 **iNaturalist**
4. S side of South Fork American River, 3/4 mi NW of mouth of Weber Creek, 38.7617878 N, 121.0162034 W, dry sandy soil along river, 600 ft, moist, shady boulders, [pyroxene outcrop within area of gabbro], 23 April 23 1978, *Stebbins 7839* (CAS).
5. Happy Valley Road, 1.1 mi NE (69°) of Somerset, just W of the bridge over the Cosumnes River (38.654 N, 120.666 W), pine forest and riverside chaparral, 1785 ft, plants under 15 mm tall were abundant, growing with *Sedum spathulifolium* on a wet, mossy, rock bank, the tall plants were uncommon and grew from rock cracks along with the small specimens, [Mzg; granite], 14 May 2010, *Helmkamp 16041* (BRIT, ex UCR)

### PLACER COUNTY

1. Iowa Creek Road ca. 2 mi from I-80 near entrance to Auburn State Rec Area, at creek crossing, [ca. 38.91 N, 121.044 W], [Mzv; Mesozoic volcanic and metavolcanic rocks], boulders at base of open S-facing slope, ca. 1700 ft, only at edge of boulder, herbage ± slimy, 8 Apr 1989, *Ertter 8173* (MO, TEX, UC)
2. Along North Fork American River just east of confluence with Secret Ravine; 39.11710 N, 120.89727 W; [Mzv; Mesozoic volcanic and metavolcanic], (substrate photo does not match Mzv, but not serpentine); *Kate Morozova*, 29 Mar 2025 **iNaturalist**
3. Auburn State Rec Area, along North Fork American River at bridge crossing of Ponderosa Way; 38.99961 N, 120.93965 W; [J; Jurassic sedimentary], (no substrate photo); *lheislein*, 1 May 2024 **iNaturalist**
4. Auburn State Rec Area, along Lake Clementine Road; 38.93204 N, 121.02839 W; [m; pre-Cenozoic metasedimentary and metavolcanic], (substrate photo); *hrodgers07*, 13 Mar 2024 **iNaturalist**

### TEHAMA COUNTY

1. Dales Lake Ecological Reserve, W side of Manton Road (A6) ca. 2 mi N of Dales Station on Hwy 36, ca. 14 mi NE of Red Bluff, blue oak woodland, localized population in crevices on a shaded outcrop on the S edge of the basalt ridge crossing the NE corner of the reservoir, [Qrb; Quaternary pyroclastic and volcanic mudflow deposits], 740 ft, 10 Apr 1995, *Oswald & Ahart 6642* (CHSC, JEPS)
2. E of Red Bluff, near Hogsback Road, "a single plant in a basalt rock crevice on a steep slope," *Mark Egger*, 8 Apr 2025 **FLICKR**
3. Gray Davis Dye Creek Preserve, 40.110613 N, 122.011939 W; [Tv<sup>p</sup>; Tertiary pyroclastic and volcanic mudflow deposits], *Scott Hardage*, 15 Mar 2025 **iNaturalist**
4. Between Dales and Paynes Creek, [ca. 40.32 N, 122.03 W, coordinates from the symbol location]; [Tv<sup>p</sup>; Tertiary pyroclastic and volcanic mudflow deposits], *cmccarron*, Apr 2025 **iNaturalist**
5. Top of knob NE of Paynes Creek, 40.34180 N, 121.94315 W; [Qrv; Holocene volcanic flow rocks], *Rob Irwin*, 16 Apr 2021 **iNaturalist**

### TUOLUMNE COUNTY

1. Red Hills above Peoria Flat, crevices of serpentine rock, 1600 ft, 11-16 Apr 1919, *Ferris 1602* (DS, JEPS, PH, POM — type collection of *Mimulus pardalis*)
2. Along Rose Creek at its mouth on the Stanislaus River, [ca. 38.107 N, 120.397 W], [probably Paleozoic metasedimentary], 12 Apr 1981, *Heckard 5505* (JEPS)

3. Along Stanislaus River (E side), ca. 3 air mi NNW of Columbia, [ca. 38.05 N, 120.44 W], [area of volcanics intermixed with limestone], ca. 880 ft, 12 Apr 1981, *Heckard 5507* (JEPS)
4. Above Hwy 49, 1.8 mi N of the Tuolumne-Mariposa county line, 37.7762989 N, 120.268516 W, moist rocky serpentine soil along the large rock outcrops above Hwy 49, 19 Mar 1974, *McNeal 1383* (OSC, UT)
5. Red Hills area, W of Chinese Camp, along Minnow Gulch, moist crevices of ultrabasic rock, 1000 ft, 8 Apr 1973, *Stebbins 9033* and *9039* (JEPS)
6. Peoria Pass, Peoria Pass Road, 2.5 road mi N of Hwy 120, low relief serpentine hills E from the roadway, deep red, weathered serpentine clay in open *Ceanothus cuneatus* chaparral burned the previous summer, 26 Mar 1998, *Taylor 16268* (JEPS-2 sheets)
7. Peoria Basin, slopes at SE edge of basin ca. 1 mi E of Peoria Pass Rd, stony red weathered serpentine soils dominated by *Ceanothus cuneatus* chaparral, 900 ft, 15 Apr 1998, *Taylor 16328* (JEPS)
8. Stanislaus River 2 mi downstream from Tulloch Lake dam, [37.855 N, 120.634 W], shaded northerly slopes at base of Table Mt., in stony red soils [Tertiary volcanic flow, hornblende near rhyolite] dominated by *Quercus douglasii*-*Aesculus californica*, 490 ft, 15 Apr 1998, *Taylor 16313* (MO, UC)
9. Red Hills Road S of Chinese Camp; 37.85371 N, 120.45514 W; [um; serpentine]; *Annie Zell*, 1 April 2024 **iNaturalist**
10. Peoria Basin; 37.92368 N, 120.51108 W; [Mzv/um border] (substrate photo shows andesite, not serpentine); *chloe and trevor*, 29 Apr 2023 **iNaturalist**
11. Slightly N of Tuolumne River slightly W of confluence with N Fork; 37.90250 N, 120.2685 W; [Pz/ls; limestone, schist?, quartzite], (substrate photos); *chloe and trevor*, 30 Apr 2023 **iNaturalist**
12. Red Hills Road SW of Chinese Camp; 37.85247 N, 120.45877 W; [um; serpentine, (substrate photos); *Matt Berger*, 19 Mar 2024 **iNaturalist**
13. Red Hills Road SW of Chinese Camp; 37.85304 N, 120.45613 W; [um; serpentine], (substrate photo not illustrative); *Matt Berger*, 19 Mar 2024 **iNaturalist**
14. NW of Columbia; 38.04330 N, 120.41600 W; [gr<sup>Mz</sup> but evidently slightly misplaced; Mesozoic diorite, (substrate photo); *Matt Berger*, Mar 2023 **iNaturalist**
15. Town of Springfield; 38.02054, 120.41377; [gr<sup>Mz</sup> but evidently slightly misplaced; Mesozoic diorite, (substrate photo); *Matt Berger*, Mar 2023 **iNaturalist**
16. Red Hills Road, SW of Chinese Camp; 37.85409 N, 120.45352 W; [um; serpentine], (substrate photo); *Morgan Stickrod*, 9 Mar 2025 **iNaturalist**
17. Red Hills Road, SW of Chinese Camp; 37.8541 N, 120.45372 W; [um; serpentine, (substrate photos); *Naomi Fraga*, 19 Mar 2024 **iNaturalist**