

**TAXONOMIC REVIEW OF THE  
*ERYTHRANTHE MOSCHATA* COMPLEX (PHRYMACEAE)**

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**ABSTRACT**

In a taxonomic reevaluation of the *Erythranthe moschata* complex, *E. moniliformis* (Greene) Nesom is treated as a synonym of the widespread *E. moschata*. The related species previously identified as *Erythranthe inodora* is maintained as distinct but the correct name for it is ***Erythranthe ptilota* Nesom, nom. et stat. nov.** (based on *Mimulus moschatus* var. *sessilifolius* A. Gray). ***Erythranthe willisii* Nesom, sp. nov.**, occurs abundantly on serpentine along the North Fork of the Feather River and in scattered nearby serpentine areas of east-central Butte Co and northeast Yuba Co. The new species is consistently morphologically differentiated from typical *E. moschata*, which is abundant in the immediate Plumas County region on non-serpentine substrate and closely sympatric with *E. willisii*. The morphological and geological discontinuity of the Feather River serpentine plants and their apparent genetic isolation from *E. moschata* support their taxonomic recognition. Distribution maps and photos of representative herbarium collections are provided for *E. moschata*, *E. ptilota*, and *E. willisii* as well as color photos of the new species *in vivo* and in natural habitat. Lectotypes are designated for *Mimulus moschatus* Dougl. ex Lindl., *Mimulus moschatus* var. *longiflorus* A. Gray, and *Mimulus moschatus* var. *sessilifolius* A. Gray.

The current manuscript (1) reevaluates the taxonomic status of *Erythranthe moniliformis* (sect. *Mimulosma*), concluding that it is not distinct as a species from *E. moschata*, (2) reviews aspects of the taxonomy and distinction of *E. inodora*, which is closely related to *E. moschata*, concluding that the correct name for the species previously identified as *E. inodora* is instead *Mimulus moschatus* var. *sessilifolius* (treated here at specific rank, using a substitute name), and (3) recognizes a *E. moschata*-like population system from serpentine exposures in the area of the North Fork of the Feather River as a previously undescribed species.

**1. Status of *Erythranthe moniliformis***

Earlier (Nesom 2012), I treated *Erythranthe moniliformis* as distinct from *E. moschata*, emphasizing a primarily erect habit and tendency toward sessile to subsessile and more densely arranged cauline leaves in *E. moniliformis* vs. a decumbent to procumbent habit and consistently petiolate leaves on longer internodes in *E. moschata*. In a review of this taxonomy, I am unable to confirm the existence of a discontinuity in morphology, geography, or ecology. Habit, leaf arrangement, size, and petiole length, and pedicel orientation may be correlated with habitat moisture. Rhizomes with small, tuber-like swellings can be observed over the whole *moschata/moniliformis* range, and there apparently are no consistent distinctions in vestiture and corolla size (although the names of Pennell's *M. macranthus* and Gray's *M. moschatus* var. *longiflorus* suggest corolla size was significant in recognition of those taxa). Figures 7–9 show aspects of the variation.

Support for the recognition of two species was provided by Argue's study of pollen morphology (1980, 1986) — pollen identified in his study as *Mimulus moschatus* produces supratectal processes (ornamented muri), while pollen of *M. moniliformis* lacks them (unornamented muri). The revised taxonomy here suggests that a larger sample of pollen might show different results. Argue found the same difference in 1980 between *M. moschatus* and *M. inodorus* but was not able to confirm that difference in 1986. The phylogenetic analysis by Whittall et al. (2006) included only a single sample identified as *M. moschatus* (Benton Co., Oregon, Whittall 46; voucher listed as OSC but not found there. *Erythranthe moschata* and *E. ptilota* both occur in Benton Co.).

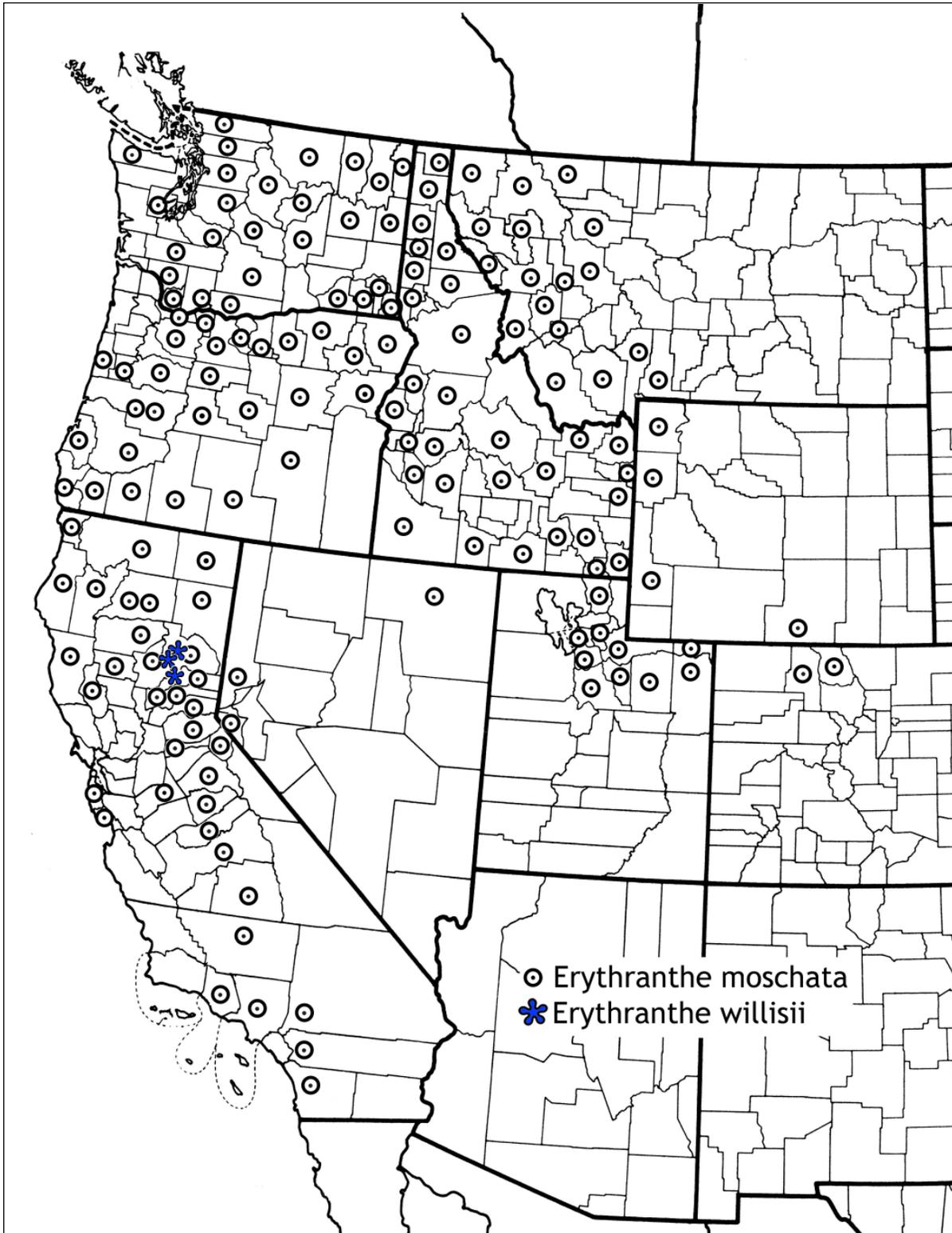


Figure 1. Distribution of *Erythranthe moschata* in the western USA. The distribution continues into southwestern Canada and is disjunct to the northeastern USA and adjacent Canada and Chile in South America. *Erythranthe willisii* is known only from Plumas Co. and immediately adjacent Butte and Yuba cos., California. Map records are from study at many herbaria, with additions from records/images from the Consortium of Pacific Northwest Herbaria.

*Erythranthe moschata* occurs over a broad area (Fig. 1). The disjunct population systems of South America (Chile) and the northeastern USA probably are genetically distinct, and it would not be surprising if geographically restricted variants in the western USA are identified and perhaps named. For example, photographs (CalPhotos) from Tulare Co., California, show corollas with white patches on the sides of the lower lip — a feature similar to that in *E. norrisii*, an annual that also occurs in Tulare Co. (see Nesom 2012): Schoenig, 1 Jun 1991; Christie, 30 Aug 2003; Thorsted, 23 Jun 2016. Should this reflect introgression from *E. norrisii*, it would be the only instance I am aware of where genetic influence from another species shows in *E. moschata*. The "white-patch" pattern also is shown in plants of *E. moschata* from Siskiyou/Trinity County, California (see CalPhotos, Sheli Wingo).

Southern California plants (Los Angeles, San Bernardino, San Diego, and Riverside cos.) were previously identified as *E. inodora*, disjunct southward from the main range of the species (Nesom 2012). These plants tend to have large, often epetiolate or short-petiolate leaves and long pedicels, but the calyx lobes are variable in length and usually do not show the characteristic attenuate-apiculate apices. These are more reasonably identified within *E. moschata*.

An updated nomenclatural synopsis is provided here, with *Erythranthe moniliformis* included in synonymy of *E. moschata*.

**ERYTHRANTHE MOSCHATA** (Douglas ex Lindl.) Nesom, Phytoneuron 2012-39: 38. 2012. *Mimulus moschatus* Douglas ex Lindl., Bot. Reg. 13: plate 1118. 1827 [published 1828]. *Mimulus guttatus* var. *moschatus* (Douglas ex Lindl.) Prov., Fl. Canada 1: 439. 1862. **LECTOTYPE** (designated here): **USA. [Washington. Clark Co.]**: margins of ["grapy"] springs near Fort Vancouver, 1825, *D. Douglas s.n.* (GH! digital image!; isolectotype: BM digital image!). Lindley's discussion noted that Douglas found it "growing sparingly on the margins of springs in the country about the river Columbia, in North-West America." The illustration was made from a plant in the Garden of the Horticultural Society in August 1827. For the GH specimen, the locality is noted as "Margins of ["grapy"] springs near Fort Vancouver 1825;" for the BM specimen it is "Near ["grapy"] springs at Fort Vancouver 1825."

*Mimulus dentatus* var. *gracilis* A. Gray, Bot. Gaz. 7: 112. 1882. **TYPE: USA. California.** [Shasta Co. (label says "Plumas County":)] Lassen's Peak, 1882, *Mrs. R.M. Austin s.n.* (holotype: GH digital image!).

*Mimulus moniliformis* Greene, Bull. Calif. Acad. Sci. 1: 10. 1884. *Mimulus moschatus* var. *moniliformis* (Greene) Munz, Aliso 4: 99. 1958. *Erythranthe moniliformis* (Greene) Nesom, Phytoneuron 2012-39: 38. 2012. **TYPE: USA. California.** [Kern Co.]: Mt. Dyer, Jul 1980, *Mrs. R.M. Austin s.n.* (holotype: NDG digital image!). Protologue: "Common in dry rocky places of the Sierra, from 4,000 to 8,000 ft. In the collections of Bolander, Kellogg and others, this species occurs abundantly, and is named 'M. moschatus,' being confounded with the last species."

*Mimulus moschatus* var. *longiflorus* A. Gray, Synopt. Fl. N. Amer. (ed. 2) 2(1): 278. 1886. *Mimulus inodorus* Greene, Bull. Calif. Acad. Sci. 1: 119. 1885 [nom. et stat. nov., see comments below]. *Erythranthe inodora* (Greene) Nesom, Phytoneuron 2012-39: 38. 2012. **LECTOTYPE** (designated here): **California.** [Mariposa Co.]: Yosemite Valley and Mountain, 1865, *J. Torrey 381* (GH digital image!). Annotated by Gray as "var. *longiflorus*" for 'SYN. FL. N. AMER.'" Three other GH specimens were similarly marked by Gray as var. *longiflorus* and can be considered as original material:

[**Washington. Clark Co.**]: margins of ["grapy"] springs near Fort Vancouver, 1825, *D.*

*Douglas s.n.* — this also is the lectotype of *Mimulus moschatus* Douglas ex Lindl.

**California.** [Mariposa Co.]: Yosemite ["Yos"] Valley, 1866, *H.N. Bolander 6306*

**California.** [Mariposa Co.]: Cisco, 1870, *A. Kellogg & S. Brannan s.n.*

Gray's protologue on p. 278 noted only "The usual form in California, also in Oregon." In a further citation (p. 447), he noted "A form growing in drier soil, less viscid-villous, and with elongated corolla. — *M. moniliformis*, in part (the villous- and more or less viscous-pubescent plant), Greene, Bull. Calif. Acad. i. 119. Common especially in the Sierra Nevada." Greene's notes (p. 119) included *Mimulus dentatus* var. *gracilis* Gray in synonymy of his entry for *M. moniliformis*.

Greene did not cite a type for *Mimulus inodorus*; nor is there an NDG specimen marked as such; his protologue referred to "*M. moschatus*, Gray, Bot. Cal. I. 569, not of Dougl. *M. moschatus*, var. *longiflorus*, Gray, Syn. Fl. 278" and noted "Common in both the Coast Range and the Sierra Nevada, throughout California, and also in Oregon." In the Botany of California, Gray's entry for *M. moschatus* described the plants as petiolate; in the Synoptical Flora, he noted that var. *longiflorus* was "The usual form in California, also in Oregon."

My adoption of *Erythranthe inodora* as the name for the 'var. sessilifolius' plants (Nesom 2012) was in error. Pennell (1951) also used *Mimulus inodorus* at specific rank, clearly intending it for the 'var. sessilifolius' plants. Grant (1924) was perhaps the first to unambiguously ally the two names, citing *Mimulus inodorus* as a synonym of *Mimulus moschatus* var. *sessilifolius* A. Gray and noting that the entity occurs from British Columbia to southern California. She cited numerous specimens but not a type for either name.

*Mimulus crinitus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 186. 1924 [nom. nov]. *Mimulus acutidens* Reiche, Fl. Chile 6: 63. 1911 (not *M. acutidens* Greene 1885). **TYPE: CHILE.** Prov. Valdivia, en pantanos, *O. Buchtien 159* (holotype: SGO digital image!).

*Mimulus moschatus* var. *pallidiflorus* Suksdorf, Deutsche Bot. Monatsschr. 18: 154. 1900. **TYPE: USA. Washington.** Skamania Co.: Springs near Chenoweth, 7 Jul 1894, *W.N. Suksdorf 2320* (holotype: WS?; isotypes: F, ISC, NDG, NY, ORE, OSC, PH, UC, US, VT, WTU-2 sheets). Digital images! of all isotypes cited. Suksdorf did not specify where the holotype was located but his personal herbarium is at WS; all duplicates cited here were distributed with identical printed labels.

I earlier included var. *pallidiflorus* as a synonym of *Erythranthe inodora* (= *E. sessilifolia*) but the leaves are consistently petiolate in the large sample of plants distributed among the isotypes. The calyx lobes are narrowly triangular but lack the indurate tip and falcate curve characteristic of *E. inodora*. These plants are very similar to the type of *Mimulus acutidens* Reiche from Chile, treated here also as a synonym of *E. moschata*.

*Mimulus leibergii* A.L. Grant, Ann. Missouri Bot. Gard. 11: 231, plate 6, fig. 1. 1924. **TYPE: USA. California.** [Plumas Co.]: Mt. Pleasant, Spanish Peak Range, wet soil along creek, 6500 ft, 16 Jul 1900, *J.B. Leiberg 5171* (holotype: US digital image! photo-MO! photo-UC!).

*Mimulus macranthus* Pennell, Proc. Acad. Philad. 99: 160. 1947 **TYPE: USA. California.** Shasta Co.: Hatchet Mountain, 6 to 8 mi W of Burney, along stream in coniferous (*Pseudotsuga*) forest, 3900 ft, 7 Jun 1940, *F.W. Pennell 25710* (holotype: PH! digital image!; isotype: GH digital image!).

## 2. Status of *Erythranthe inodora*

Among plants often identified as *Erythranthe moschata* in the broad sense, those that I have previously recognized as *E. inodora* are morphologically and ecologically distinct and justifiably separated as a distinct species. In the nomenclatural review, however, the name *E. inodora* proves to be a synonym of typical *E. moschata* (comments above) and a new name is provided here for this species.

**ERYTHRANTHE PTILOTA** Nesom, **nom. et stat. nov.** *Mimulus moschatus* var. *sessilifolius* A. Gray, Synopt. Fl. N. Amer. (ed. 2) 2(1): 447. 1886 [not *Mimulus sessilifolius* Maxim. 1874 = *Erythranthe sessilifolia* (Maxim.) Nesom 2012]. **LECTOTYPE** (designated here): **USA. California:** [Butte Co.]: Chico, "last days of April" 1885, *A. Gray s.n.* (GH digital image!). Annotated by Gray as "*Mimulus moschatus* var. *sessilifolius* ... SYN FL. N. AMER. ed. 2."

In the original description of *Mimulus moschatus* var. *sessilifolius*, Gray did not cite a collection. The protologue noted "M. inodorus Greene, l.c., but the plant as strongly musk-scented as the ordinary species, at least in some cases." It also noted "Not rare in wet places, from San Bernardino Co., California, northward, and passing into the ordinary form in Oregon."

A syntype collection is mounted on the same sheet as the lectotype: **California**. San Bernadino ["San Bdino"] Co.: Temescal, tule swamps, Jun 1885, *W.S. Lyon 6* (GH digital image!) — but it lacks Gray's annotation (unless the anotation at the upper right-hand corner of the sheet, above the Chico plants, was meant to apply to both collections). The leaves are more or less sessile but the calyx lobes are not characteristic of 'sessilifolius' — this is a plant like those noted above from southern California that I earlier included within *Erythranthe inodora* (= *E. sessilifolia*) but which instead are interpreted here as intergrading variants of typical *E. moschata*.

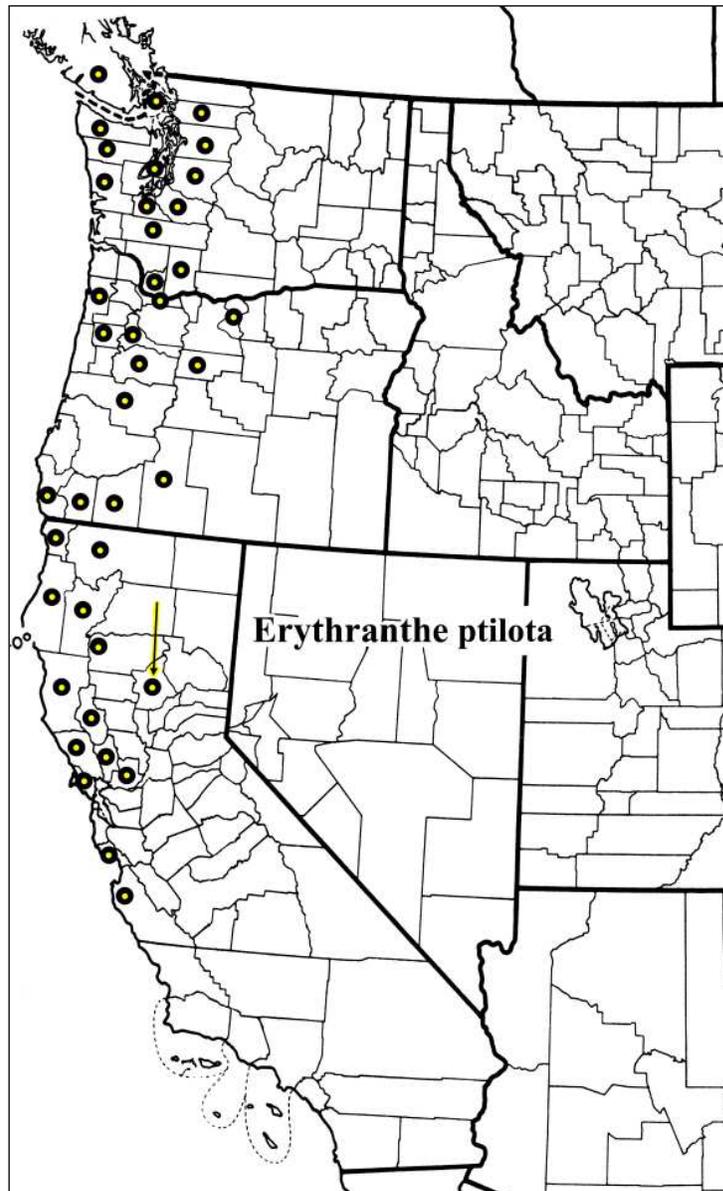


Figure 2. Distribution of *Erythranthe ptilota*. Arrow points to Butte Co., where the type collection was made. Additional collections from Butte Co. are cited in the text.

*Erythranthe ptilota* (Fig. 6) is recognized by its prostrate to decumbent or decumbent-ascending habit, large, consistently sessile leaves, densely villous vestiture, long pedicels, large calyces and corollas, hispid-hirtellous anthers, and particularly by its long, strongly unequal, linear-triangular, calyx lobes usually distally falcate. Leaves bases typically are truncate to rounded or subcordate. Rarely the leaves are short-petiolate, but in such cases, the distinctive leaf bases, vestiture, calyx morphology, and pubescent anthers are diagnostic. *Erythranthe ptilota* is widely sympatric with *E. moschata* but usually occurs at lower elevations and characteristically in wetter habitats. The epithet (Gr. *ptilotos*, winged, alludes to a fancied wing-like aspect of the pairs of sessile leaves).

Flowering (May–)Jun–Sep. Creek banks, gravel bars, flood plains, shallow ditches and natural drainage, swales, damp banks, wet sand, moist soil in coniferous woods, seeps, marshes, bogs; 0–3200(–6200) ft; British Columbia; Calif., Oreg., Wash. Figure 2.

- a. Cauline leaves sessile (proximal sometimes short-petiolate or subpetiolate), blades 30–70 mm; fruiting pedicels (15–)22–50 mm; calyx lobes linear-lanceolate to narrowly triangular with linear-acuminate apices, 5–9 mm; anthers strongly to weakly hirsute-hirtellous ..... **Erythranthe ptilota**  
 a. Cauline leaves petiolate to sessile or subsessile, blades (10–)15–40(–50) mm; fruiting pedicels (7–)10–40 mm; calyx lobes triangular to linear-lanceolate or narrowly triangular-acuminate, 2–4 mm; anthers glabrous or subglabrous ..... **Erythranthe moschata**

The lectotype of *Erythranthe ptilota* is a Butte County collection, which, although slightly disjunct to the west from the main system of the species, is characteristic in morphology and habitat of the species as it occurs elsewhere. Additional Butte County collections of *E. ptilota* are cited here.

Butte Co.: Upper Bidwell Park, ca. 10 mi NE of Chico, ca. 3/4 air mi W of Hwy 32, ca. 45 yds E of Ten Mile House Road, ca. 55 yds SE of the gate, wet soil along small flowing stream, meadow, 884 ft, 30 Jun 2009, *Ahart 15,978* (CHSC); along Bald Rock Road 1.7 mi S of N jct with Hwy 162, 7.6 mi NE of S jct with Hwy 162, ca. 1/4 mi E of the road, marsh in yellow pine forest, 3160 ft, 6 Jun 1980, *Banchero 201* (CHSC); ca. 1.2 mi N of Coutolenc and Coutolenc-Hupp roads, 0.7 mi S of jct Skyway and Coutolenc roads, seep in yellow pine forest, 3000 ft, 17 Jun 1980, *Banchero 247* (CHSC); along Concow Road 1.3 mi N of jct with Hwy 70, 0.3 mi N of town of Concow, streamside in yellow pine forest, 1700 ft, 19 Jun 1980, *Banchero 254* (CHSC); Butte Creek Canyon, ca. 300 ft, 21 Jul 1967, *Bowlin 48* (CHSC); damp sand at S edge of Butte Creek, ca. 2.1 mi S of Skyway [Road] and ca. 1/4 mi E of Hwy 99 bridge, 29 Aug 1987, *Castro 213* (CHSC, UCD); Bidwell Park near bottom of Ten Mile House Road, E side of Big Chico Creek near N end of park property, edge of perennial meadow drainage, ca. 720 ft, 12 Jun 2004, *Fischer 684* (CHSC); Chico, 28 Jul 1916, *Hazeltine s.n.* (UCD); Five-Mile Dam, 14 Aug 1923, *Heller 13816* (WTU); along Butte Creek just below the dam, 0.4 mi along the creek NE of Hwy 99 bridge, 3.6 mi SE of jct Hwy 32 in Chico, gravelly border of creek, 225 ft, scattered plants, 15 Jun 2013, *Nesom CA2013-1* (CAS); Upper Bidwell Park, Chico, near retaining wall along Chico Creek at E end of Centennial Ave., moist, sandy and rocky creek bed, 280 ft, 27 May 1983, *Oswald 565* (CHSC); Upper Bidwell Park, Chico, 100 ft N of Upper Park Road at Diversion Dam, seep in open area in foothill woodland, 420 ft, 2 Jun 1983, *Oswald 614* (CHSC).

### 3. A new species from California

During study of monkeyflowers in the CAS-DS and CHSC herbaria in June 2013, collections of two entities of *Erythranthe*, both from serpentine in the North Fork Feather River canyon in Plumas Co., California, came to my attention as potentially undescribed species and I went to the locality later on the same trip. I did not find the plants of sect. *Simiolus* described soon after as *E. percaulis* (Nesom 2013), but Steve Schoenig and David Popp recently found them there in abundance (Schoenig 2016). The Serpentine Canyon plants of the *E. moschata* complex (sect. *Mimulosma*), however, were abundant and conspicuous and I made observations and collections and took photographs (among Figs. 13–22). This population system is recognized here at specific rank.

**ERYTHRANTHE WILLISII** Nesom, *sp. nov.* **TYPE: California.** Plumas Co.: [North Fork] Feather River canyon, wet serpentine slope, ca. 2800 ft, 26 Jun 1951, *J.T. Howell 27540* (holotype: CAS! Fig. 10; isotype: RSA!).

Similar to *Erythranthe moschata* but distinct in its combination of dense vestiture (stems, leaves, calyces), thick and relatively compact rhizomes, tendency for thick stems, common axillary branching at the distal nodes, short pedicels, leaves epetiolate-sessile with rounded to subcordate bases, strong tendency for purple abaxial leaf coloration, stems long and multinodal, colonies often spreading over a large area, and habitat consistently over serpentine.

**Perennials**, rhizomatous, rarely rooting at proximal nodes, commonly forming large colonies; rhizomes white, usually highly branching. **Vestiture:** stems, leaves, and pedicels densely glandular-villous with gland-tipped hairs mostly 1–2 mm, calyces densely glandular-villous. **Stems** simple or usually branched, erect to ascending, decumbent, or prostrate, 7–45 cm, nodes (2–)4–15 or more. **Leaves** mostly cauline, basal not persistent; sessile to subsessile, petiole absent or sometimes 1–2 mm long at proximal nodes; blades ovate or elliptic-ovate, pinnately veined, often bicolor (purplish abaxially), midcauline 10–35 x 6–18 mm, base rounded to subcordate, margins coarsely serrate-dentate to denticulate or subentire, apex short-attenuate to acute, obtuse, or rounded. **Flowers** 2 per node, at all nodes or sometimes mostly from medial to distal nodes. **Fruiting pedicels** 4–20(–25) mm. **Fruiting calyces** campanulate to cylindrical-campanulate, 7–10 mm, weakly inflated, ridged-angled to winged-angled, lobes subequal, triangular to linear-lanceolate, erect to slightly spreading. **Corollas** weakly bilabiate to essentially radially symmetric, yellow with fine, red to brownish lines in tube and throat and onto proximal portion of lower 3 lobes; tube-throat narrowly funnellform, 12–15 mm, extending beyond calyx margin; lobes oblong-obovate, apex rounded to notched, limb 9–12 mm wide (pressed). **Styles** glabrous. **Anthers** included, glabrous or slightly hirtellous to scabrous. **Herkogamous.** **Capsules** 4–5 mm, included. **Chromosome number** unknown.

Flowering May–Sep. Seepage, drainage margins, moist soil, talus, cracks and crevices, talus, soil derived from serpentine; (1600–)2300–3000 ft; along North and East branches of the North Fork Feather River in Plumas Co. and closely adjacent areas of east-central Butte and northeastern Yuba cos., Calif..

The most consistent and recognizable features of *Erythranthe willisii* are the long stems, sometimes reaching at least 45 cm long and often with many, relatively crowded nodes, epetiolate-sessile leaves with rounded to subcordate bases, and short pedicels, characteristically no longer than the subtending leaves (except sometimes the distal ones where subtending leaves are distinctly reduced in size) (Figs. 10, 11, 12). Sessile to subsessile leaves occur in *E. moschata*, especially in the California Sierra, but petiole length and leaf base shape are variable within populations; lack of petioles and a rounded/subcordate base are fixed characters in *E. willisii* (as they are also in *E. ptilota*). The wide-spreading colonies of *E. willisii* are not produced in either *E. moschata* or *E. ptilota*. In the field, the dense vestiture is a prominent feature, but this is harder to distinguish in pressed specimens. Phenology and flower morphology of *E. willisii* and *E. moschata* appear to be similar.

**Additional collections examined (Serpentine Canyon area). California. Plumas Co.:** [Main population system]: W side of Chips Creek, just S of bridge on Hwy 70, ca. 1.25 mi SW of Belden, uncommon, damp rocky soil of gravel bar, 2346 ft, 8 Oct 2006, *Ahart 13,399* (CHSC); W side of Carbon Road, ca. 1/8 mi S of Mosquito Creek, ca. 5 air mi NE of Belden, W side of [N Branch] N Fork Feather River, damp, rocky, bare, disturbed serpentine soil, 2600 ft, 11 Sep 1997, *Ahart 7895* (CHSC, JEPS); 21 mi from Quincy on Hwy 24 [1950's Hwy 24 has become the current Hwy 70], N Fork Feather River, 2500 ft, loose tangled mats to 3 feet across, scattered on seeps in scree and on granite rock, 30 Aug 1950, *Balls 15,507* (RSA, WTU); East Branch North Fork Feather River, 762 m, 24 May 1946, *Follett 143* (JEPS, RSA); 2.5 mi E of Rich Bar (along State Hwy 24), moist places along the highway in serpentine, 22 May 1941, *Heller 16140* (UC); Feather River canyon, seepage in serpentine area E of Rich Bar, 19 May 1968,

*McClintock & Roderick s.n.* (CAS); NE side Chips Creek on Hwy 70 along N Fork Feather River, 1.3 mi SW (below) Belden Powerhouse, base of roadcut in soil, 2340 ft, uncommon, 15 Jun 2013, *Nesom CA2013-4* (UC); Caribou Road along North Branch North Fork Feather River, between Hwy 70 and Mosquito creek, between Queen Lily and North Fork Campgrounds, wet soil by road, base of serpentine slope, 2450 ft, common, 15 Jun 2013, *Nesom CA2013-5* (CAS); Caribou Road along North Branch North Fork Feather River, N side of North Fork Campground, 2.2 mi N of jct Hwy 70, dry slopes beside road, 2460 ft, common, 15 Jun 2013, *Nesom CA2013-6* (CAS, UC); Caribou Road along North Branch North Fork Feather River, 2.8 mi N of jct Hwy 70, at inflow of Mosquito Creek on W side of road, large colony on seepy rocks and soil, 2650 ft, 15 Jun 2013, *Nesom CA2013-7* (BRIT, CHSC, CAS, RSA, UC, UCSB); 4 mi W of Virgilia, East Branch, N Fork Feather River, ca. 2500 ft, 2 Jun 1963, *Rose 63081* (CAS, RSA); Serpentine Canyon, Rich Bar-Virgilia, perennial plant communities growing in wet places on rocky serpentine talus, 16 Aug 1997, *Sanchez-Mata & Rodrigues-Rojo s.n.* (UCD); Feather River Canyon, Caribou Road, 3000 ft, 26 Aug 2002, *Shapiro s.n.* (UCD).

**Additional collections examined (outlying localities).** Butte Co.: Ca. 3/4 mi NE of Pulga, N side of Hwy 70, ca. 1/8 mi W of Poe Dam, S edge of North Fork Feather River, damp sand, 1416 ft, 11 Sep 2006, *Ahart 13,294* (CHSC); S side of Hwy 70, ca. 1/4 mi W of Bear [Ranch] Creek jct with N Fork Feather River, ca. 0.5 mi W of Arch Rock Tunnel rest stop, [ca. 5.5 mi NE of Pulga, serpentine] 1600 ft, 6 Oct 1980 [fruiting], *Taylor 3361* (CHSC, Fig. 12). Plumas Co.: Flood plain of Spanish Creek at mouth of Wapaunsie Creek, [ca. 5 mi W of Quincy on Bucks Lake Road, E side of Snake Lake Road at jct with Bucks Lake Rd, serpentine], hydraulic mining gravels, 3600 ft, 16 Jul 1976, *Howell 51910* (CAS, Fig. 11); beside small stream on ridge between Onion Creek and Middle Fork Feather River, N of Strawberry Valley along Quincy-LaPorte Road, [E of Sly Creek Reservoir, serpentine], 15 Sep 1948, *Wiggins 12054* (DS). Yuba Co.: Gravel bar along Slate Creek [ca. 2 mi NE of Strawberry Valley], yellow pine forest, 1250 m, 12 Aug 1980, *Ahart 2547* (CAS).

This *Erythranthe* is named for Duke University molecular geneticist John Willis, who has encouraged and mentored many in the study of evolutionary problems approached through monkeyflowers — his lab a wellspring of monkeyflower momentum. Great person, too, with good humor. He and his students (in reluctance to accept taxonomic changes) may choose to refer to these plants as "the Willis population system formerly known as *Mimulus moschatus*" or "the *Mimulus* named for John," or perhaps they'll just murmur "ecotype," but in any case the plants will invite molecular attention. The epithet is in the genitive case, as I feel confident that the species will eventually become his.

### Locality and habitat

*Erythranthe willisii* is a more or less continuous population system along several miles in the canyon of the East Branch North Fork of the Feather River with exposed serpentine. Plants and colonies are dense in some areas, less so and more scattered in others, growing on cracks and crevices and cliff bases and on talus and bare soil along the Feather River Highway (Hwy 70). Road construction through this area, creating large exposures of bare serpentine and maintaining disturbed roadsides of serpentine-derived soil, probably has increased the density of the plants.

Caribou Road (toward the town of Caribou, along the North Branch North Fork Feather River) diverges from Hwy 70 about 1.5 miles east of Belden, and *Erythranthe willisii* is common along its roadbanks for about two miles, to the area where Mosquito Creek merges with the North Branch (Fig. 4).

Other smaller serpentine exposures occur in Plumas Co., on either side of the Serpentine Canyon area, as well as in east-central and southeastern Butte Co. and northeastern Yuba Co., and *Erythranthe willisii* also has been collected from several of these areas (Fig. 3). This area of serpentine is known as the "Feather River complex," a northwest-southeast trending ultramafic belt, mainly of serpentinite and peridotite, about 33 miles long and 2 to 4 miles wide. Most of it is in

Plumas County but parts reach into Sierra, Nevada, Placer, and El Dorado counties (Alexander et al. 2007). It is the northernmost ultramafic body in the Sierra Nevada (Kruckeberg 1984).

Typical *Erythranthe moschata* occurs in close sympatry with *E. willisii*, the two entities separated by substrate. The only apparent intermediate I have seen is *Taylor 3361* (from ca. 4 miles north of Pulga, Fig. 12; cited with the collections of *E. willisii*) — it has long stems with crowded nodes and short-pedicelled flowers in pairs at nearly all nodes, but the leaves are distinctly petiolate along the whole length of the stem.

The cited collection by Balls from 1950 is noted to have been from granite and apparently is outside the extent of the exposed serpentine, but these plants are typical *E. willisii*. Fide measurement through Google Earth, "21 [road] miles from Quincy" is in the vicinity of Belden, probably slightly west of it (Fig. 4). This is outside the mapped serpentine exposure but plants in soil along the roadcut base west of Belden at Chip's Creek (*Nesom CA2013-4*, Fig. 4) are typical *E. willisii*, as is the plant collected by Ahart (13,399) which he noted as "uncommon," in a gravel bar of Chips Creek along Hwy 70. Collections of typical *E. moschata* have been made in the close vicinity of typical *E. willisii* near Chips Creek and Belden (e.g., *Banchemo 147* and *158*, CHSC). *Head s.n.* (CAS) from a "granite crack" near Camp Rogers, slightly further south (Fig. 4), appears to be typical *E. moschata*, perhaps with slightly denser than normal vestiture.

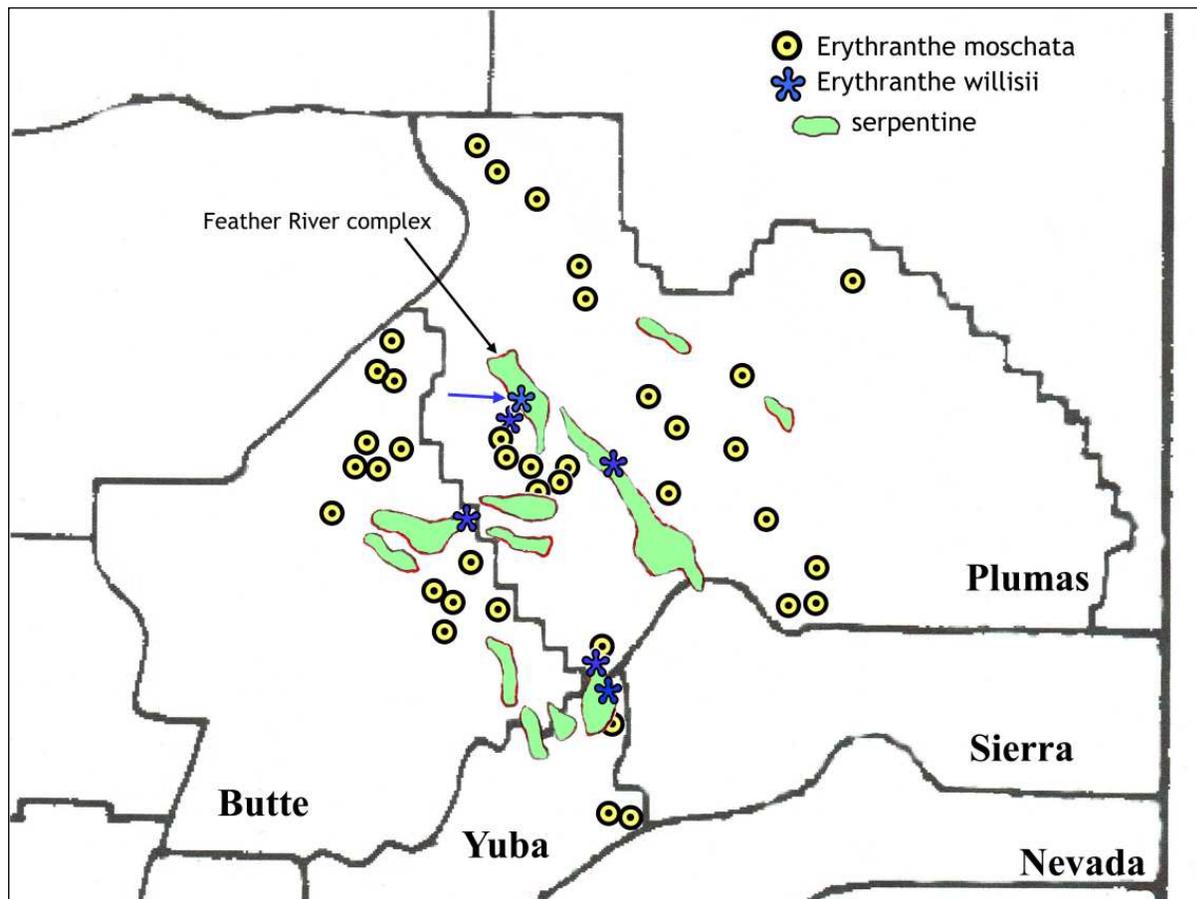


Figure 3. Distribution of *Erythranthe willisii* and typical *E. moschata* in Butte, Plumas, and Yuba counties, California, in relation to serpentine exposures. Blue arrow points to the main (most dense) population system of *E. willisii*. Serpentine exposures continue southward into Sierra and Nevada counties (and further, off map).

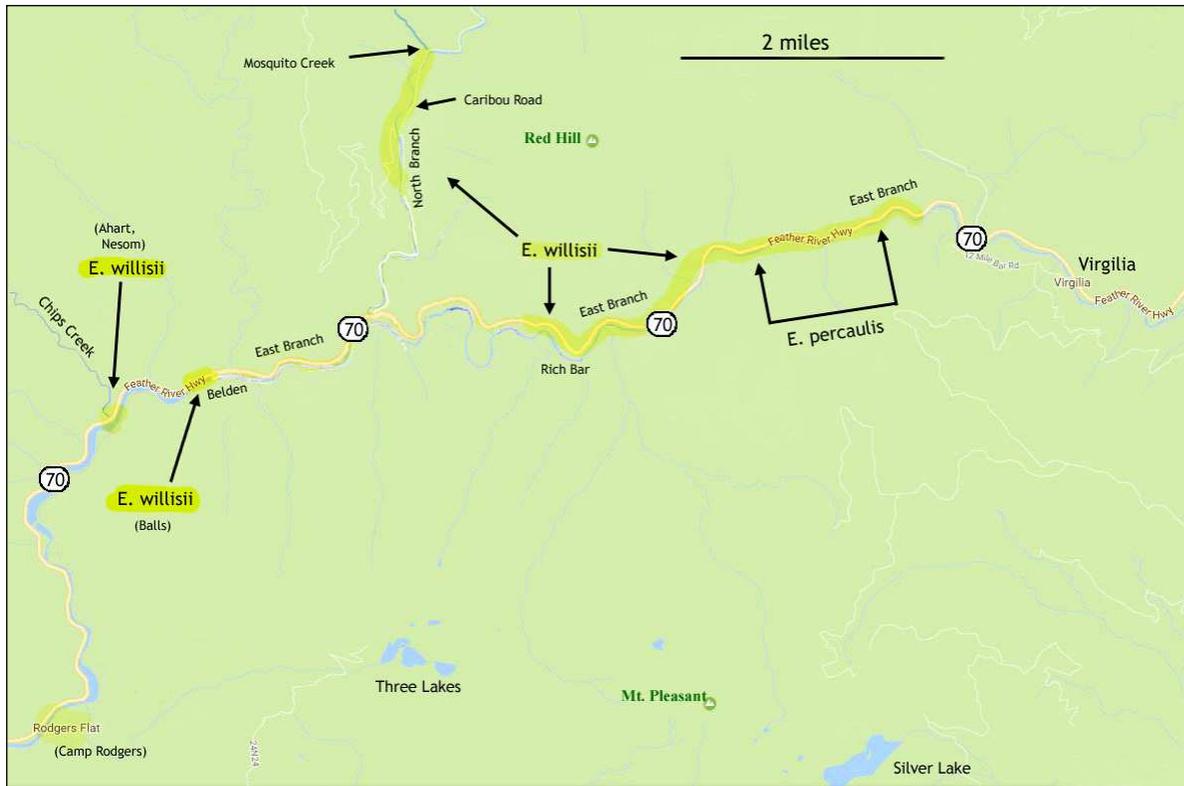


Figure 4. North Fork of the Feather River (North and East branches), showing known localities for *Erythranthe willisii*. *Erythranthe percaulis* also is endemic to the Feather River serpentine complex but is more restricted in extent.

Serpentine exposures in the very northern tip of Yuba County and immediately adjacent Plumas County (Fig. 3) also bring *Erythranthe willisii* and *E. moschata* in close proximity. The latter has been collected at Strawberry Valley (*Rose 39233*, CAS) and 3.6 miles northeast of Strawberry Valley (*Howell 54089*, CAS) — both localities close cited collections of *E. willisii* from Plumas Co. (*Wiggins 12054*) and Yuba Co. (*Ahart 2547*).

After studying many hundreds of collections of *Erythranthe moschata* sensu lato from over its entire range, I have not seen a single one, except for those of *E. willisii*, with locality data specifying a serpentine/ultramafic substrate. Such collections may have been made (typical *E. moschata* occurs in areas of exposed serpentine in California, Oregon, and Washington), with the collector unaware of the geology, but even if so, I have not seen any cluster of collections except for *E. willisii* that unambiguously suggests the existence of a variant population system.

### Distinction and taxonomic rationale

Features among the set that defines *Erythranthe willisii* can be seen within the limits of populational variation over the range of typical *E. moschata*, but they occur coherently and with consistency in *E. willisii*. The distinctive morphology of *E. willisii* has been previously appreciated — plants clearly of the species were cultivated at the University of California Botanical Garden and photographed in 1968; Figure 20a & b). The degree of difference among recognized species of *Erythranthe* often is small, but *E. willisii* can confidently be recognized, especially in view of its ecological specialization and close sympatry with *E. moschata*.

*Erythranthe willisii* may be a direct derivative of *E. moschata*, but this cannot be known with assurance without an understanding of the relationship among *E. willisii*, *E. moschata*, and *E. pilota*.

Rhizomes are derived within sect. *Mimulosma* (as inferred from the phylogenetic hypothesis of Whittall et al. 2006), and these three are the only rhizomatous species of the section. They presumably are most closely related among themselves. The above-ground stolons or runners of *E. jungermannioides* are independently derived — its closest relatives are species of the "Columbia River/Snake River clade," which otherwise are taprooted or fibrous-rooted annuals without stolons.

The regionally patchy occurrence of serpentine exposures underlies the habitat isolation of *Erythranthe willisii* in the Feather River area. It exists in close sympatry with typical *E. moschata* in the area of the Feather River complex (Fig. 3) and there is no evidence of intergradation between them, although occasional hybrids may be formed. Gene flow between *E. willisii* and *E. moschata* presumably is inhibited by a reduced ability of the serpentine plants to compete on substrates where *E. moschata* is common (Anacker et al. 2010; Anacker 2014) and by the probable inviability of non-serpentine immigrants (of *E. moschata*) onto the serpentine.

The serpentine plants might be considered primarily a physiologically differentiated population system (a locally adapted population/ an ecological race/ an ecotype) within *Erythranthe moschata* but the morphological discontinuity and the ecogeographic isolation of *E. willisii* position it securely along the speciation continuum (e.g., Lowry & Gould 2016).

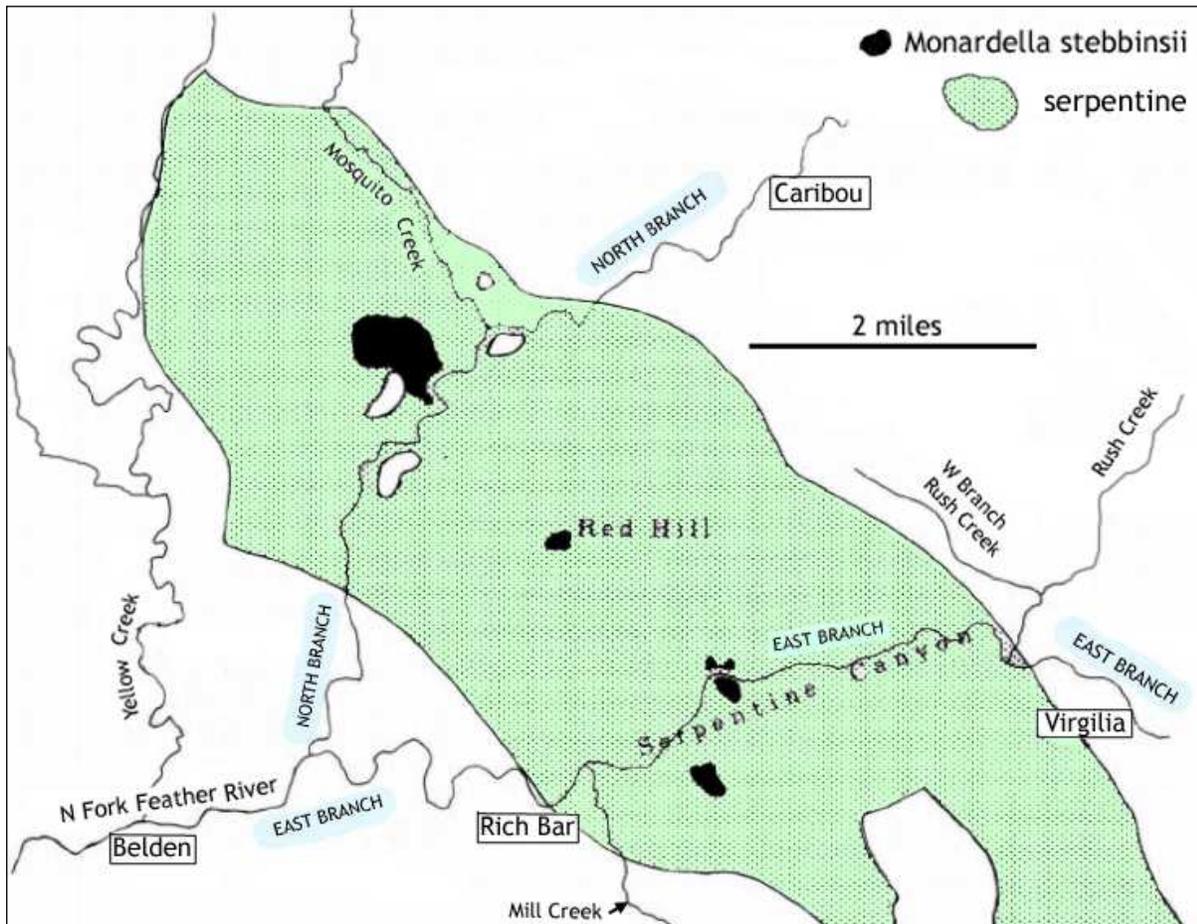


Figure 5. North end of the Feather River complex (exposed ultramafic belt) in Plumas Co., California. The distribution of *Monardella stebbinsii* is similar to that of *Erythranthe willisii*, except that *E. willisii* is more common and more broadly spread through the Feather River complex. Map adapted/modified from Hardham and Bartel (1990); scale is similar to Figure 4.

Potentially related to the evolutionary position of *Erythranthe willisii* is the discovery of hybrid incompatibility in California monkeyflowers of sect. *Simiolus* as an incidental by-product of natural selection for copper tolerance (Wright et al. 2013) — the copper tolerance and hybrid lethality are controlled by distinct but tightly linked loci. In the Wright et al. study, the heavy metal tolerance is expressed in a species (*Erythranthe pardalis* (Pennell) Nesom) otherwise restricted to serpentine.

Recognition of species, however, carries no requirement for intrinsic postzygotic isolation — many clear and broadly recognized species have been found capable of hybridizing and backcrossing with others when brought into contact experimentally. Some theorists have narrowed the definition of species ("good" species, "full" species, biological species) to populations in advanced stages of evolutionary divergence, where intrinsic postzygotic isolation is strong (see Lowry 2012; Lowry & Gould 2016), but taxonomists and others interested in diversity usually operate in good confidence on the basis of morphology, geography, and ecology (see Nesom 2014 for an unusual instance where new monkeyflower species have been recognized with a full range of information, including genetic, in support of the decision).

Five other endemic plant taxa are known from the Feather River complex: *Erythranthe percaulis* Nesom, *Monardella follettii* (Jeps.) Jokerst, *Monardella stebbinsii* Hardham & Bartel (see Fig. 5), *Packera eurycephala* var. *lewisrosei* (Howell) Bain, and *Sedum albomarginatum* Clausen. All are restricted to the Serpentine Canyon area and nearby serpentine exposures in Plumas and Butte counties; records for the two monardellas disjunct in counties further south are based on misidentifications (fide Mark Elvin, pers. comm., 2017). The relationship between the two putative varieties of *Packera* appears to be analogous to that between *E. moschata* and *E. willisii* — populations of typical *P. eurycephala* occur both on and off serpentine but none are in Plumas and Butte counties; only plants on serpentine in Plumas and Butte counties have the 'lewisrosei' morphology).

*Erythranthe percaulis* grows in close association with *E. willisii* in one area of the Feather River canyon (Schoenig 2016) — the locality is indicated on Figure 4. The first known collection of *E. percaulis* is this: Plumas Co.: 2.5 mi E of Rich Bar, moist places along the hwy in serpentine, 22 Mar 1941, *Heller 16139* (WTU). Two other monkeyflower species have been collected or observed on the Feather River serpentine: *Erythranthe microphylla* (pers. observ. 2013) and *Diplacus mephiticus* (*Bacigalupi et al. 8867*, JEPS; *Galen Smith s.n.*, JEPS).

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I am grateful to John Strother for comments on typification of *Mimulus inodorus* and *M. moschatus* var. *sessilifolius*, to Naomi Fraga for observations on *Erythranthe moschata* in southern California, to Steve Schoenig for photos of *E. willisii*, to Kim Kersch and Amy Kasameyer (UC-JEPS) for photos of the *Diplacus mephiticus* specimens from the Feather River locality, and to Joe Lippert (BRIT) for providing specimen images. Loans from CAS-DS and CHSC to BRIT were essential for this review and are much appreciated, as is hospitality during personal study at CHSC, RSA-DS, UC-JEPS, UCD, and WTU.

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Figure 6. *Erythranthe pilota*, representative specimen from Marin Co., California.



Figure 7. *Erythranthe moschata*, representative specimen from El Dorado Co., California. Leaves are short-petiolate to sessile with obtuse bases.



Figure 8. *Erythranthe moschata*, representative specimen from El Dorado Co., California.



Figure 9. *Erythranthe moschata*, representative specimen from Modoc Co., California



Figure 10. Holotype of *Erythranthe willisii*.



Figure 11. *Erythranthe willisii*, representative specimen from Plumas Co., California.



Figure 12. *Erythranthe willisii*, possibly with genetic influence of *E. moschata*. The long, multinodal stems and short pedicels are characteristic of *E. willisii* but the distinct petioles are not.



Figure 13. Habitat of *Erythranthe willisii* and *E. percaulis*. Serpentine Canyon along Hwy 70, ca. 2 miles west of Virginia. Photo by Steve Schoenig, 24 May 2016



Figure 14. *Erythranthe willisii* in Serpentine Canyon ca. 5 miles east of Belden, at base of cliff and roadcut. Photo by G. Nesom, 15 Jun 2013. Extensive colonies are characteristic of the species.



Figure 15. *Erythranthe willisii* in Serpentine Canyon ca. 5 miles east of Belden, in seep near base of roadcut. Photo by G. Nesom, 15 Jun 2013.



Figure 16. *Erythranthe willisii* in Serpentine Canyon ca. 5 miles east of Belden, seepage on face of serpentine cliff/roadcut . Photo by G. Nesom, 15 Jun 2013.



Figure 17a & b. *Erythranthe willisii* in Serpentine Canyon ca. 2 miles west of Virgilia, ledges of serpentine roadcut and cliffs. Photos by Steve Schoenig, 24 May 2016.



Figures 18a & b. *Erythranthe willisii* on north side of Caribou Road along North Branch North Fork Feather River, north of Queen Lily Campground. Photos by G. Nesom, 15 Jun 2013.



Figure 19a & b. *Erythranthe willisii*. A (top). Serpentine Canyon, ca. 2 miles west of Virgilia. Photo by Steve Schoenig, 24 May 2016. B (bottom). Caribou Road at crossing of Mosquito Creek. Photo by G. Nesom, 15 Jun 2013. Note essentially sessile leaves with truncate to rounded or subcordate base, flowers at numerous nodes, and short pedicels.



Figure 20a & b. *Erythranthe willisii* in Serpentine Canyon, ca. 2 miles west of Virgilia. Photos by Steve Schoenig, 24 May 2016. Flowers are herkogamous even though the stigma is well within the tube.



Figure 21a & b. *Erythranthe willisii*. Grown in the University of California Berkeley Botanical Garden, originally from "Rich Bar, Plumas County." Photos by Robert Potts©California Academy of Sciences. A. (top). 25 Aug 1968 (CalAcademy slide #T 41300; fide CalPhotos). B (bottom). 7 Sep 1968 (CalAcademy slide # T 41299). The top photo apparently was taken with a filter – it shows a perfect bulls-eye pattern characteristic of a radially symmetric corolla, although the red markings and the palate ridges are those of bilabiate morphology, where a runway pattern (at least of UV reflectance) might be expected (see Peterson et al. 2015 for examples of different UV patterns in sect. *Simiolus* corollas). This suggests a possible isolating mechanism in the *E. moschata* complex, assuming that the reflectance pattern varies within or among the species.



Figure 22. *Erythranthe willisii*, showing relatively thick, congested rhizomes. Hwy 70 along North Fork Feather River, vicinity of Chips Creek, ca. 1 mile west of Belden. Photo by G. Nesom, 15 Jun 2013.