Nesom, G.L. and N.A. Uelman. 2024. With rhizomes, *Erythranthe neoglaucescens*, sp. nov. (sect. *Simiolus*; Phrymaceae), via sympatric speciation. Phytoneuron 2024-51: 1–48. Published 15 July 2024. ISSN 2153 733X

# WITH RHIZOMES, *ERYTHRANTHE NEOGLAUCESCENS*, SP. NOV. (SECT. *SIMIOLUS*; PHRYMACEAE), VIA SYMPATRIC SPECIATION

**GUY L. NESOM**
Research Associate
Academy of Natural Sciences of Drexel University
Philadelphia, Pennsylvania
guynesom@sbcglobal.net

**NEIL A. UELMAN**
Los Angeles, California
neil.uelman15@gmail.com

## ABSTRACT

A population system from Butte and Tehama counties, California, essentially identical in morphology to *Erythranthe glaucescens* but rhizomatous rather than strictly annual, is recognized here as **Erythranthe neoglaucescens** Nesom & Uelman, **sp. nov.** The rhizomatous plants occur in a small area within the geographic range of typical *E. glaucescens*, in a constantly wet habitat (vs the summer-dry habitat mostly characteristic of typical *E. glaucescens*). The evolutionary transition to the rhizomatous form is interpreted here as an instance of sympatric speciation, the rhizomatous habit acquired (speculatively) through hybridization with *E. guttata*.

*Erythranthe glaucescens* (sect. *Simiolus*) is endemic to Butte, Shasta, and Tehama counties, California (Map 1). Plants are annual from a slender taproot or shallow fibrous roots and are characterized especially by their glabrous, glaucous, connate-perfoliate mid to distal cauline leaves (Figs. 5, 12-18). Flowers are relatively large, consistent with a predominantly outcrossing mating system (e.g., Ivey et al. 2023). Plants become senescent and die as the habitat dries (Figs. 19, 20).

Amos Heller in 1914 (March and July) made collections from along Big Chico Creek in Butte County that he identified as *Mimulus glaucescens*, but the plants are rhizomatous/stoloniferous (as noted in Nesom 2012; and see Nesom 2019 for more detailed comments). Dean Taylor collected the same entity in Tehama County in 1997 (Figs. 8), and he and Crystal Durbecq in 2006 independently collected it from along the West Branch Feather River (Figs. 6-7 and 9; details Figs. 21-36; Maps 2 and 3). Following a conversation with the first author in 2013, Taylor made a sample of live plants from the Feather River site for cultivation. He identified his 1997 and 2006 vouchers simply as *Erythranthe glaucescens* but later noted that a different species probably is represented (Taylor 2013, in tacit agreement with GLN). Two collections (*Hanson 18*, *Ivey 400;* Figs. 10, 11) were observed in the field to be rhizomatous and noted as such in the label data.

Here, we confirm the existence of a population system of rhizomatous "Erythranthe glaucescens" and distinguish it from the typical form, with its formal recognition as a distinct species.

**ERYTHRANTHE NEOGLAUCESCENS** Nesom & Uelman, **sp. nov.** **TYPE**: **California**. Butte Co.: West Branch Feather River, among rocks along the river margin just below the diversion dam upstream from the Retson Road Bridge, 39.93796, -121.53075, 3260 ft [1000 m], moist shaded volcanic cobble deposit under *Alnus rhombifolia* and mixed with *Athyrium filix-femina*, also abundant on crevices of the diversion dam wall and nearby cliffs, 22 Jun 2006, *N.A. Uelman 240* (holotype: RSA, Figs. 1 and 2; isotype: UC).

Similar to *Erythranthe glaucescens* (sect. *Simiolus*) in its glabrous, glaucous, connate-perfoliate mid to distal cauline leaves and relatively large, chasmogamous flowers; different in its rhizomatous habit and perennial duration and its constantly wet habitat.

Perennials, rhizomatous and/or stoloniferous, with leafy runners from basal nodes. **Stems** erect, simple or branched, terete, 30–80 cm, glabrous, glaucous. **Leaves** basal and cauline; petiole of basal and proximal cauline as long as or longer than blade, mostly glabrous; blade palmately 3–5-veined, (proximal) ovate to ovate-elliptic or orbicular-ovate, sometimes subcordate, 10–50 mm long, midcauline to distal orbicular, 5–45 mm wide, distinctly connate-perfoliate, base rounded to subcordate, margins of proximals denticulate to dentate or coarsely, irregularly toothed, sometimes lobed at base, of distals mostly entire, surfaces glabrous, glaucous. **Flowers** herkogamous, 3–50 (per stem) from distal nodes, chasmogamous. **Fruiting pedicels** 10–50 mm long, glabrous, glaucous. **Fruiting calyces** broadly campanulate, inflated, sagittally compressed, 7–16 mm long, glabrous, glaucous, throat closing. **Corollas** yellow, sometimes with a median splotch, abaxial limb densely dark yellow, others much lighter, throat floor and tube red-dotted, bilabiate, tube-throat funnelform, 12–20 mm, exserted 4–8 mm beyond calyx margin, limb expanded 14–36 mm. **Anthers** included, glabrous. **Styles** minutely hirtellous-puberulent. **Capsules** included, 6–11 mm. **Chromosome number** unknown.

Flowering (March-) May-July. Seepy cliff faces and among wet rocks at stream margins, perennially moist gravel, roadside seeps; 120-1000 meters elevation.

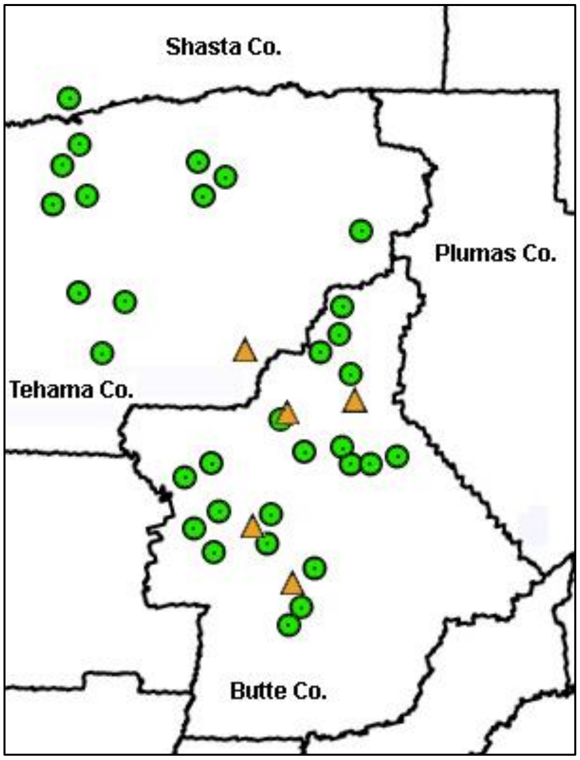
**Additional collections**. **California**. Butte Co.: Cañon of Big Chico Creek, 26 Mar 1914, *Heller s.n.* (MO); Cañon of Big Chico Creek, 2 Jul 1914, *Heller s.n.* (MO); Stirling City Quadrangle, along West Branch Feather River near the diversion dam and along the canal, 39.93908, -121.53183, on rocky cliffs and outcrops with water seeping out, mixed conifer forest, associated *Mimulus guttatus*, *Sedum spathifolium*, *Montia parviflora*, *Adiantum aleuticum*, 3270 ft [997 m], 18 May 2006, *Durbecq 8142* (SPIF); Upper Bidwell Park, ca. 2.5 air km E of Horseshoe Lake, directly W of Upper trail where it crosses a small perennially damp drainage N of Bear Hole, 39° 46' 56" N, 121° 45' 12" W, moist gravel in the understory of *Quercus douglasii* with abundant non-native grasses, 186 m, plants scattered, exhibit a perennial growth form with trailing stems rooting at the nodes, annual form of the species nearby on more open and rocky slopes, 3 Apr 2014, *Hanson 18* (SHSC); Centerville Rd [paralleling Butte Creek] ca. 0.8 km N of intersection with Honey Run Rd, 39.736° N, 121.701° W, wet seep on W side of road, 120 m, large plants spreading by rhizomes, 4 May 2021, *Ivey 400* (SHSC); vicinity of Stirling, West Branch Feather River, on the diversion dam and nearby cliffs just upstream from the Reston [= Retson] Road Bridge, 39.93796, -121.53075, 3260 ft [1000 m], moist shaded volcanic cobble deposit under *Alnus rhombifolia-Athyrium filix-femina* canopy, 28 Jun 2006, *Taylor 19554* (JEPS, SPIF). Tehama Co.: Pine Creek, Campbell Mound Quadrangle, 39° 58' 33" N, 121° 45' 14" W, dripping, shaded, vertical cliffs of volcanic mud flows, with *Adiantum pedatum*, *Mimulus* [Erythranthe] *cardinalis*, overshaded by *Torreya*, *Acer macrophyllum*, 1860 ft [567 m], 6 Jun 1997, *Taylor 16029* (UC).

There may be reluctance to accept *Erythranthe neoglaucescens* at specific rank, given that rhizomatous *E. guttata* and annual *E. microphylla* often are regarded as conspecific ecotypes. Considered here, however, are two sympatric entities discontinuously distinct in a prominent and biologically significant feature.

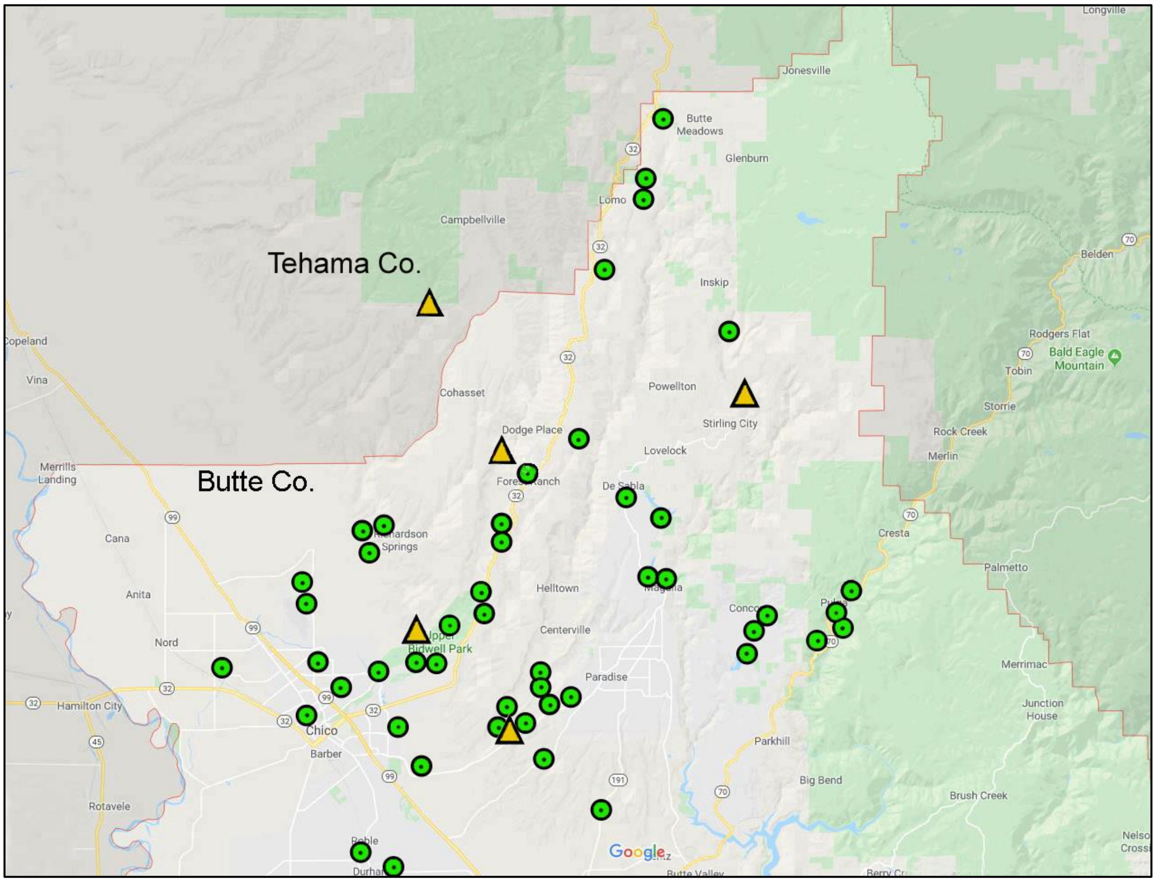
## Locality and habitat

The Heller collections of *Erythranthe neoglaucescens* are labeled with minimal locality information, but they are mapped here from along Big Chico Creek 1-2 miles southwest of Dodge Place (perhaps within Big Chico Creek Ecological Reserve) where local roads cross the creek — elevations along the creek there are about 500 meters.

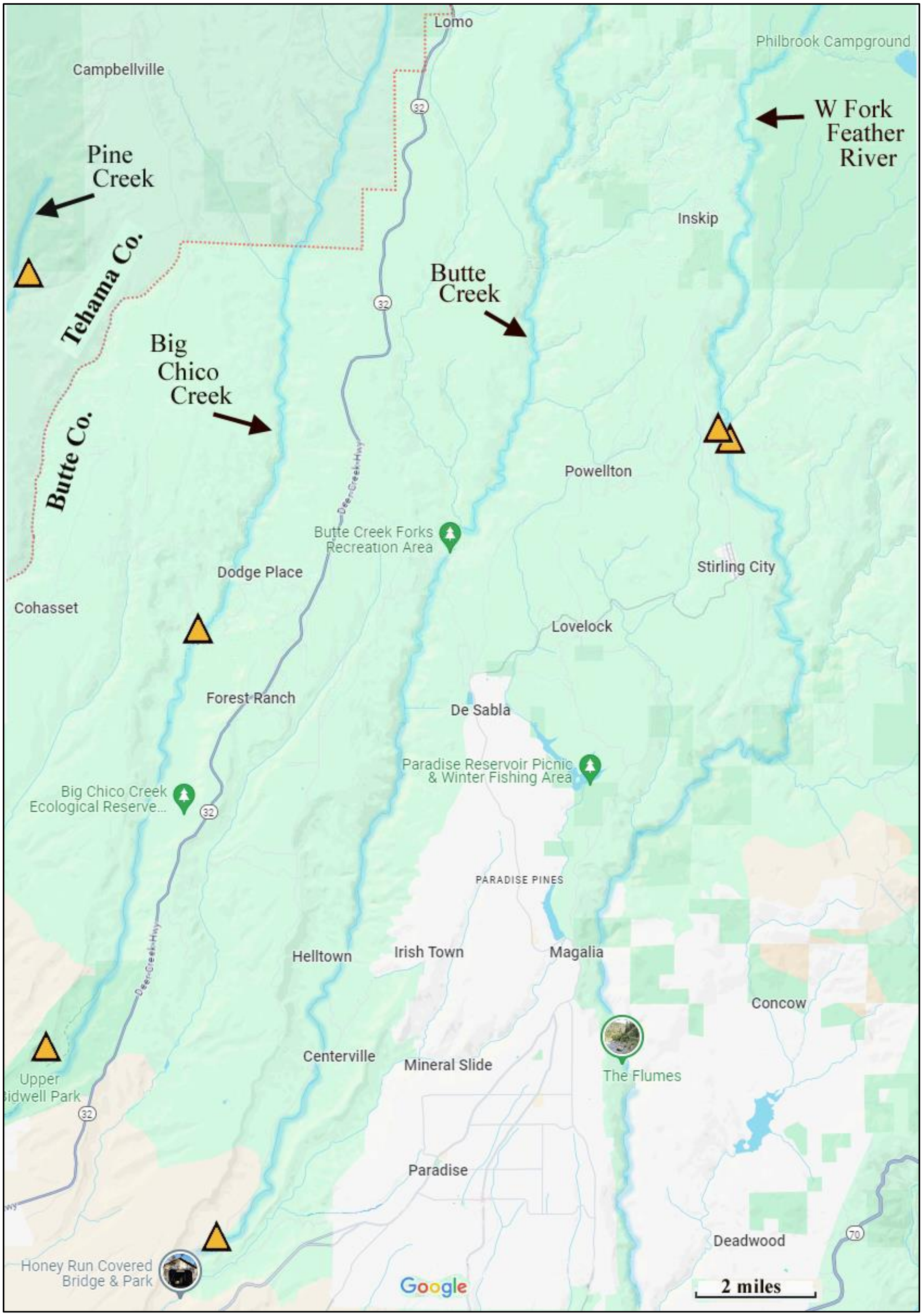
A search for *Erythranthe neoglaucescens* was made by Uelman on 22-23 June along Big Chico Creek and West Branch Feather River, but it was found only at the diversion dam site. Additional collections, however, indicate that it occurs more widely, even if rarely encountered.



Map 1. Total distribution of *Erythranthe glaucescens* (circles) and *E. neoglaucescens* (triangles).



Map 2. Distribution of *Erythranthe glaucescens* (Butte Co.) and *Erythranthe neoglaucescens*.



Map 3. Distribution of *Erythranthe neoglaucescens* Big Chico Creek, Butte Creek, West Fork Feather River, and Pine Creek.

The monkeyflower habitats at the diversion dam site are primarily seepy and shaded cliff faces, cracks in the dam, canal margins, and the rocky creek margins (Figs. 25-31). Prominent associated species are *Alnus rhombifolia*, *Athyrium filix-femina*, *Epilobium ciliatum* subsp. *ciliatum*, *Adiantum aleuticum*, *Polystichum munitum*, and rhizomatous *Erythranthe guttata*. The plants seen by Taylor in 2006 growing from cracks in the diversion dam wall (Fig. 27) are still there.

Typical *Erythranthe glaucescens* has been collected in the vicinity of Lomo (Butte County) at elevations at the upper end of its range (1100-1400 meters, e.g., *Schlising 3803*-CHSC, *Schoenig 98-76*-UC).as well as along Big Chico Creek at lower elevations (350-500 meters, *Ivey 370*, *393*, *394*-CHSC and *Morgan 34*-CHSC). Collections of typical *E. guttata* also have been made from along Big Chico Creek, Butte Creek, and West Branch Feather River.

**ERYTHRANTHE GLAUCESCENS** (Greene) Nesom, Phytoneuron 2012-40: 43. 2012. *Mimulus glaucescens* Greene Bull. Calif. Acad. Sci. 1: 113. 1885. *Mimulus guttatus* var. *glaucescens* (Greene) Jepson, Man. Fl. Pl. Calif., 928. 1925. **TYPE**: **California**. Butte Co.: No other locality data, 1883, *Mrs. R.M. Austin s.n.* (holotype: NDG; isotype: CAS).

Annuals, slender-taprooted or fibrous-rooted. **Chromosome number**, 2n = 28. A full morphological description is given in Nesom and Fraga (2019). Besides great variability in height and number of flowers, which is characteristic of many annuals, conspicuous differences among plants of *Erythranthe glaucescens* are in toothing and lobing of proximal leaves and petiole length.

Flowering (March-) April through mid June. Seepage areas, wet rocks, moist cliffs, pool edges, rocky and gravelly stream banks, roadside ditches, serpentine outcrops, roadsides and roadcuts, low pastures, riparian woodlands, blue oak woodlands, chaparral, grasslands; 65–1050(–1170, see Fig. 16) meters.

## Biology of Erythranthe neoglaucescens

Runners of *Erythranthe neoglaucescens* anchor themselves in crevices and are often among moss mats. They root at the nodes and one plant often has multiple runners from basal nodes (Figs. 33-35). Rhizomes below the soil surface (Fig. 36) spread in all directions from the parent plant. Plants of *E. glaucescens* sometimes produce stems from basal nodes (e.g.. Figs. 17, 18) but such stems, regardless of ontogenetic stage, have not been observed to produce adventitious roots.

At the type locality, typical (rhizomatous) *Erythranthe guttata* grows in close proximity and in habitats similar to those of *E. neoglaucescens* — intermediates were not seen.

## Erythranthe neoglaucescens and Erythranthe guttata — Ivey et al. (2023), Vickery (1964)

Recent studies of *Erythranthe glaucescens* (Toll 2022; Ivey et al. 2023) apparently have involved only the annual form. With whole genome sequencing, Ivey et al. found evidence for extensive gene flow between *E. glaucescens* and *E. guttata* (the "Northern clade," as identified by Twyford and Friedman 2015, which includes both rhizomatous *E. guttata* and annual *E. microphylla*), especially where they occur in sympatry. The gene flow is asymmetric, "with higher migration rates from *M. glaucescens* into both lineages of *M. guttatus* than the reverse."

In view of the introgression, Ivey et al. noted that *Erythranthe glaucescens* maintains its morphological and ecological coherence, even though reproductive barriers appear to be weak or absent, except for ecogeographic isolation. "Seed germination [*glaucescens* and *guttatus* F1s from within and between conspecific populations and between species] was equally successful regardless of experimental cross type" and results suggest ”little opportunity for reproductive isolation via intrinsic post-zygotic reproductive isolation between *M. guttatus* and *M. glaucescens*" (Ivey et al., p. 1252). "The factors maintaining vegetative differences between [*E. glaucescens* and *E. guttata*] remain unclear" (p. 1256). In rhizomatous *E. guttata*, the DIV1 inversion on linkage group 8 (= LG8; Lowry and Willis 2010) presumably acts as a reproductive barrier, even if not a constraint on gene exchange, but the inversion was not among the 15 potential barriers evaluated by Ivey et al. nor was it mentioned in their report.

Ivey et al. referred to the "broad western North American distribution" of *Mimulus* [Erythranthe] *guttatus* and among their larger sampling were both annual plants (*Erythranthe microphylla*) and rhizomatous plants (*Erythranthe guttata* sensu stricto, from both the Southern clade and the Northern clade, sensu Twyford and Friedman) — as indicated by their discussion and a maximum likelihood phylogeny, principal components plot, and K-means clustering analysis (their Fig. 3A, B, and D). For evaluation of "Post-germination performance," Ivey et al. grew plants to maturity from progeny of within-population, between-population conspecific, and heterospecific crosses between (as *Mimulus*) *E. glaucescens* and *E. guttata*, noting there that "all populations studied for these experiments [presumably those within the 'Post-germination' evaluation] were functionally annual," but for the other categories in evaluation of pre-pollination and post-pollination barriers, no distinction was made among the forms of *E. guttata*. They identified their samples by locality but without vouchers, thus interpretation of almost all of their discussion is problematic, as it is not possible to determine whether reference to "*Mimulus guttatus*" refers to annual-nonDIV1 plants or to rhizomatous-DIV1 plants, evolutionary entities differing in morphology, biology, and geography.

Ivey et al. noted that Vickery (1964 — Vickery referencing his 1959 study) had reported strong postzygotic isolation between "*Mimulus glaucescens* and *Mimulus guttatus*." Of Vickery's 15 cultures of *M.* [Erythranthe] *guttatus*, only one (*Heisey 560*, Yosemite Junction) was characterized as annual, all the rest specifically as perennial. He cited vouchers for all samples, including collections by himself and others, but only *Vickery 190* (at UT, perennial) is in online collection databases, thus is the only one located for which the identity can be verified.

## Speciation and phylogeny

The evolutionary transition to *Erythranthe neoglaucescens* presumably was a local adaptation perhaps involving few loci, with plants of annual *E. glaucescens* in a maximally wet habit for the species (i.e., with protracted presence of water — e.g., Figs. 21-23 vs its characteristic, quickly summer-dry habitat — e.g., Figs. 19, 20) acquiring the ability to produce runners/stolons/rhizomes. Extensive gene flow documented by Ivey et al. suggests that the basis of rhizome production in *E. neoglaucescens* may have been acquired via gene transfer from rhizomatous *E. guttata* to annual *E. glaucescens*, even though the loci in *E. guttata* are within the recombination-suppressed inversion sequence. This provides a plausible mechanism for the seemingly abrupt origin of a life history/reproductive strategy similar to *E. guttata*. Typical *E. guttata* occurs in a constantly wet or saturated habitat and *E. glaucescens* sometimes occurs in the same habitat (biotic sympatry" sensu Grant 1981) along Big Chico Creek and West Branch Feather River.

It seems impossible to demonstrate that divergence of the two entities did not begin in allopatry, but the *Erythranthe neoglaucescens* populations are within the geographic range of *E. glaucescens* (Map 1) and the evolutionary transition in habit and life history appears to be an instance of sympatric speciation (e.g., Coyne and Orr 2004; Coyne 2007). The existence of intrinsic post-zygotic isolation between *E. glaucescens* and *E. neoglaucescens* might rule out sympatric speciation (Coyne and Orr 2004) but evidence for this is not at hand.

Morphological intermediates between *Erythranthe glaucescens* and *E. neoglaucescens* have not been encountered. What mechanism may be responsible for the apparent isolation is not evident unless a habitat difference is involved. At the extremes, their habitats differ in amount and timing of moisture but those of typical *E. glaucescens* are variable. Constant water may be more available at higher elevations and it is possible that the collections of *E. neoglaucescens* from 120 and 186 meters are from populations dispersed from higher and perhaps more characteristic localities. There appears to be little or no distinction in phenology (pers. observ.) or in elevation. Polyploidy is unusual in sect *Simiolus* but the chromosome number of *E. neoglaucescens* is unknown.

In species with the DIV1 inversion, rhizomes (and their mostly interconvertible equivalents, stolons and runners) are reasonably assumed to be derived from a common ancestor, their genetic basis within the inversion linkage (Coughlan and Willis 2018; summary discussion in Nesom 2019). Placement of *Erythranthe tilingii* and *E. caespitosa* in the rhizomatous clade (Phylogeny 1) is parsimonious but speculative without a resolved phylogeny — *E. tilingii* lacks the DIV1 inversion and there is suggestion that a relationship to the DIV1 taxa may not be so close (e.g., Oneal et al. 2014; Ivey et al. 2023). The loci influencing perenniality, however, predate the inversion and arose and were fixed in the perennial ancestor to the inversion taxa (Coughlan and Willis 2018).

Stems of *Erythranthe arvensis* and closely similar species (annual plants of sect. *Simiolus*, see Phylogeny 1) often are proximally decumbent in wet habitats and develop adventitious roots — but such stems apparently do not become rhizomatous and probably are not homologous with rhizomes elsewhere in the section. Perennial (rhizomatous or adventitiously rooting) and annual species occur in both the Glabrata and Madrensis groups of sect. *Simiolus*. Annual *E. thermalis* is derived from sympatric perennial *E. guttata*, retaining the inverted squence (Kolis et al. 2022; as surmized by Nesom 2019) but using loci from outside of the inversion.

An understanding of homologies in sect. *Simiolus* awaits genetic analysis and a robust phylogenetic hypothesis. With recognition, however, that *Erythranthe neoglaucescens* and *E. glaucescens* are evolutionary sisters, this pair offers a more effective approach toward understanding the genetic basis of rhizome production than beginning with the assumption that *E. guttata* (rhizomatous) and *E. microphylla* (annual) are conspecific ecotypes or a progenitor-derivative pair.

If hybridization is involved in the origin of *Erythranthe neoglaucescens*, a tangentially analogous example might be in the origin of the widespread European *E.* x *robertsii* (Vallejo-Marin and Lye 2013), a triploid, seed- and pollen-sterile hybrid between introduced diploid *E. guttata* and South American tetraploid *E. lutea*. Hybrids coexist with *E. guttata* in several spontaneous populations. *Erythranthe peregrina* in Scotland (Vallejo-Marin 2012) is a fertile hexaploid, apparently from genome doubling in *E.* x *robertsii*. All chromosome counts for *E. glaucescens* are diploid; all for *E. guttata* and *E. microphylla* in California have been diploid; the number is unknown for *E. neoglaucescens* — thus a comparison to the hybrid origin of *E.* x *robertsii* may not be pertinent.

## Primitive in sect. Simiolus — annual or perennial?

In the Guttata group, annual duration appears to be evolutionarily primitive (Nesom 2012, 2014a, 2014b, as summarized in 2019; Coughlan and Willis 2018). Non-rhizomatous annuals are the prevalent life form in most American species most closely related to sect. *Simiolus* (Beardsley et al. 2004), and the developmental origin of rhizomes may be relatively simple (correlated life history features add complexity). Coughlan and Willis (2018, p. 2) observed that inside the DIV1 inversion sequence, genetic diversity in sect. *Simiolus* perennials is much lower than in annuals, although measurements of diversity throughout the rest of the genome are relatively similar between annual and perennial *Mimulus guttata* (= *Erythranthe microphylla* and *E. guttata*), "in line with the hypothesis that the perennial orientation of the inversion is derived and experienced a relatively old selective sweep." In a more equivocal assessment, Coughlan et al. (2023, p.7), noted that rhizomes in *E. guttata*, *E. decora*, and *E. tilingii* may have evolved independently or existed as a shared polymorphism in the common ancestor, or else they may have originated via introgression from other species. In a diametric view, Kolis et al. (2022) observed that for stolons (or rhizomes), "their loss is diagnostic of drought-associated annualization in *Mimulus* … ."

*Erythranthe unimaculata* (Arizona, New Mexico, Chihuahua, Sonora) is a species of annual plants otherwise closely similar in morphology to perennial *Erythranthe guttata* and should be considered in evaluations of life history polarity. Perennial (rhizomatous or adventitiously rooting) and annual species both occur in the Glabrata and Madrensis groups of sect. *Simiolus*. Recently described and morphologically isolated *E. mitodes* (Colorado) of sect. *Simiolus* apparently is annual — its stems are creeping and often apparently pendent but do not develop adventitious roots.

In the closely related genus *Diplacus*, most abundantly represented in California, annuals are the primitive form, perennials found only in the derived *D. aurantiacus* group = sect. *Diplacus* (Beardsley et al. 2004). In the strongly Mediterranean climate of California, it is not surprising that annuals are the predominant life form in Phrymaceae — ancestral species and genera are in other regions of the world. All of species of the mostly American genera *Hemichaena*, *Leucocarpus*, *Mimulus* sensu stricto, and *Phryma* are perennial (Barker et al. 2012). Plants of all species of Asian *Erythranthe* sects. *Mimulasia* and *Sinopitheca* are perennnial. The Asian genus *Cyrtandromoaea*, recently recognized as a basal member of Phrymaceae (Liu et al. 2019), also includes only perennial species. While annual duration appears to be primitive in the Guttata group of sect. *Simiolus*, perenniality probably is primitive in the family.

## ACKNOWLEDGEMENTS

Comments on the manuscript from Bruce Baldwin are greatly appreciated.

## LITERATURE CITED

Barker, W.R., G.L. Nesom, P.M. Beardsley, and N.S. Fraga. 2012. A taxonomic conspectus of Phrymaceae: A narrowed circumscription for *Mimulus*, new and resurrected genera, and new names and combinations. Phytoneuron 2012-39: 1–60.

Beardsley, P.M., S.E. Schoenig, J.B. Whittall, and R.G. Olmstead. 2004. Patterns of evolution in western North American *Mimulus* (Phrymaceae). Amer. J. Bot. 91: 474–489.

Coughlan, J.M. and J.H. Willis. 2018. Dissecting the role of a large chromosomal inversion in life history divergence throughout the *Mimulus guttatus* species complex. Molec. Ecol. 28: 1343–1357.

Coughlan, J.N., M.W. Brown, and J.H. Willis. 2021. The genetic architecture and evolution of life-history divergence among perennials in the *Mimulus guttatus* species complex. Proc. Roy. Soc. B 288: 1–10.

Coyne, J.A. 2007. Sympatric speciation. Current Biol. 17: R787–R788.

Coyne, J.A. and H.A. Orr. 2004. Speciation. Sinauer Associates, Sunderland, Mass.

Grant, V. 1981. Plant Speciation (ed. 2). Columbia Univ. Press, New York.

Ivey, C.T., N.M. Habecker, J.P. Bergmann, J. Ewald, M.E. Frayer, and J.M. Coughlan. 2023. Weak reproductive isolation and extensive gene flow between *Mimulus glaucescens* and *M. guttatus* in northern California. Evolution 77: 1245–1261.

Kolis, K.M., C.S. Berg, T.C. Nelson, L. Fishman. 2022. Population genomic consequences of novel life history and mating system adaptation to a geothermal soil mosaic in yellow monkeyflowers (*Mimulus guttatus*). Evolution 76: 765–781.

Liu, B., Y.-H. Tan, S. Liu, R.G. Olmstead, D.-Z. Min, Z.-D. Chen, N. Joshee, B.N. Vaidya, R.C.K. Chung, and B. Li. 2019. Phylogenetic relationships of *Cyrtandromoea* and *Wightia* revisited: A new tribe in Phrymaceae and a new family in Lamiales. J. Syst. Evol. 58: 1–17.

Lowry, D.B. and J.H. Willis. 2010. A widespread chromosomal inversion polymorphism contributes to a major life-history transition, local adaptation, and reproductive isolation. PLoS Biol. 8: e1000500.

Nesom, G.L. 2012. Taxonomy of *Erythranthe* sect. *Simiola* (Phrymaceae) in the USA and Mexico. Phytoneuron 2012-40: 1–123.

Nesom G.L. 2014a. Updated classification and hypothetical phylogeny of *Erythranthe* sect. *Simiola* (Phrymaceae). Phytoneuron 2014-81: 1–6

Nesom G.L. 2014b. Further observations on relationships in the *Erythranthe guttata* group (Phrymaceae). Phytoneuron 2014-93: 1–8

Nesom, G.L. 2019. Update 2019: Classification and hypothetical phylogeny of *Erythranthe* sect. *Simiolus* (Phrymaceae). Phytoneuron 2019-31: 1–6.

Nesom, G.L. and N. Fraga. 2019. *Erythranthe*. Pp. 372–425, in Flora of North America North of Mexico, Vol. 17. Oxford Univ. Press, New York and Oxford.

Oneal, E., D.B. Lowry, K.M. Wright, Z. Zhu, J.H. Willis. 2014. Divergent population structure and climate associations of a chromosomal inversion polymorphism across the *Mimulus guttatus* species complex. Molec. Ecol. 23: 2844-2860.

Taylor, D.W. 2013. Shield-bracted monkeyflower (*Erythranthe glaucescens*) is probably 2 species. California Blog Spot, August 3 and September 26. No longer accessible.

Toll, K. 2022. Perfoliate leaves reduce herbivory in the shield-bracted monkeyflower (*Mimulus glaucescens*). Ecology 104: e33876.

Twyford, A.D. and J. Friedman. 2015. Adaptive divergence in the monkey flower *Mimulus guttatus* is maintained by a chromosomal inversion. Evolution 69: 1476–1486.

Vallejo-Marin, M. 2012. *Mimulus peregrinus* (Phrymaceae): A new British allopolyploid species. PhytoKeys 14: 1–14.

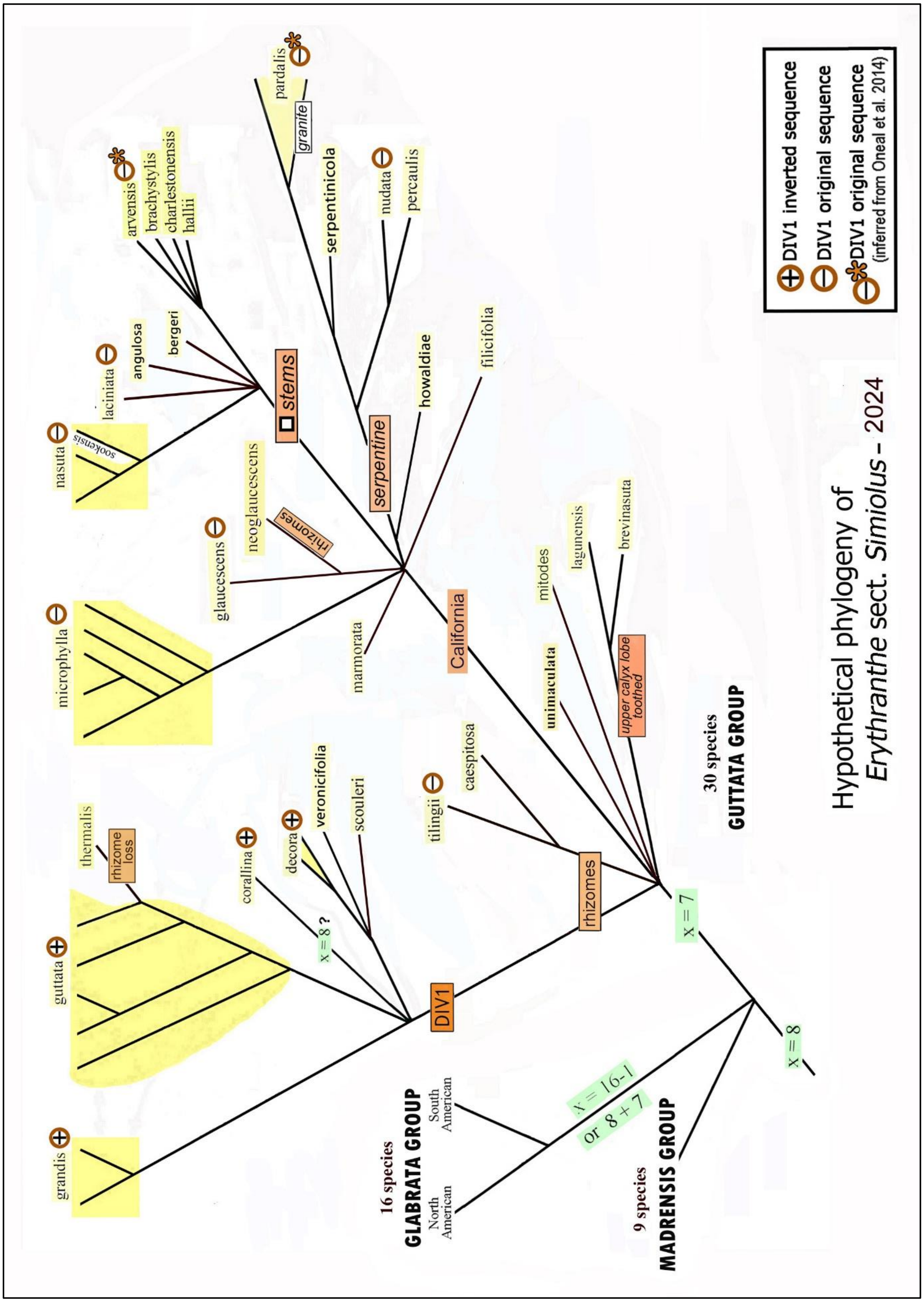
Vallejo-Marin, M. and G. Lye. 2013. Hybridisation and genetic diversity in introduced *Mimulus* (Phrymaceae). Heredity 110: 111–122.

Vickery, R.K., Jr. 1959. Barriers to gene exchange within *Mimulus guttatus* (Scrophulariaceae). Evolution 13: 300–310.

Vickery, R.K., Jr. 1964. Barriers to gene exchange between members of the *Mimulus guttatus* complex (Scrophulariaceae). Evolution 18: 52–69.

---

Phylogeny 1. Hypothetical phylogeny of *Erythranthe* sect. *Simiolus*, relationships largely unresolved, modified from a similar diagram (Nesom 2019), where a detailed discussion is given. Apomorphies are shown where information is available; otherwise species are grouped by morphological similarity and geography. In this interpretation, sect. *Simiolus* includes 55 species.



Hypothetical phylogeny of *Erythranthe* sect. *Simiolus* – 2024

Figure 1. *Erythranthe neoglaucescens*, holotype, representing larger plants in the population. *Uelman 240* (RSA).

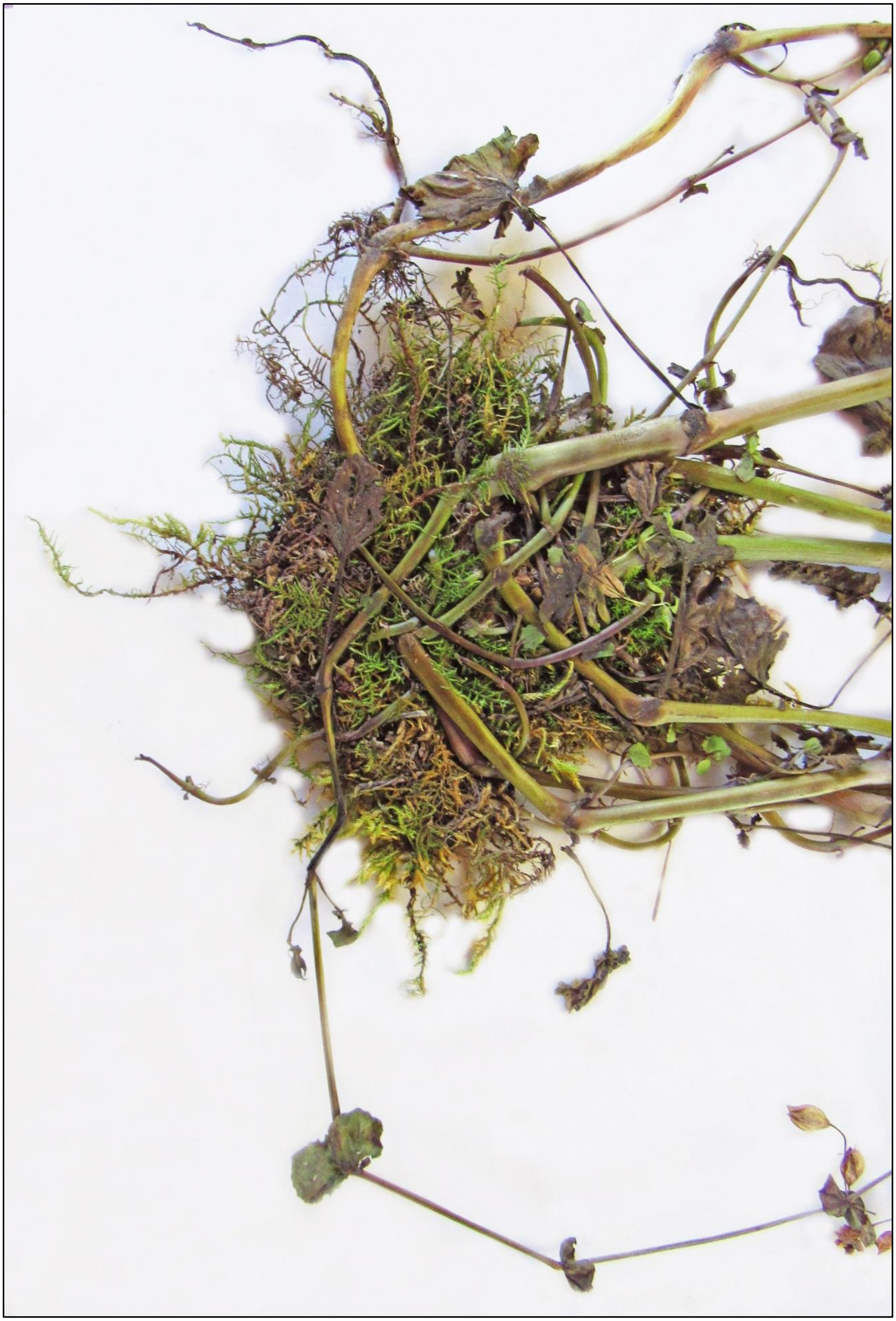


Figure 2. *Erythranthe neoglaucescens*, detail from holotype in Figure 1.

Figure 3. Base of plants of *Erythranthe neoglaucescens* (*Taylor 19554*, JEPS, SPIF). Rhizomes, leafy runners.

Figure 4. Base of plants of *Erythranthe neoglaucescens* (*Taylor 16029*, UC). Leafy runners, rhizomes.

Figure 5. Base of plants of typical *Erythranthe glaucescens* from Butte County, representative collections. Shallow fibrous roots and slender taproots.

Family: SCROPHULARIACEAE – 257 - CA

PLANTS OF CALIFORNIA
FLORA OF THE SIERRA NEVADA
(Jepson Manual nSNH region)

*Mimulus glaucescens* Greene

**BUTTE COUNTY: West Branch Feather River;** growing on the diversion dam and nearby cliffs just upstream from the Reston Road Bridge, vicinity of Striling, T24N R4E SW1/4 of NE1/4 Section 16, Stirling City 7½' USGS quadrangle; alt. 3260 ft.; moist shaded volcanic cobble deposit under *Alnus rhombifolia-Athyrium felix femina* canopy.

Latitude/Longitude (GPS, NAD27) 39.93796/-121.53075

**Dean Wm. Taylor** #19554 28 June 2006

SPI FORESTRY DIVISION - RARE PLANT PROGRAM

Floral and vegetative traits measured for study of the associations between morphological evolution and species diversification in monkey flowers (*Mimulus* spp.)

**Research Annotation** Chris Muir, Amy Angert 2017
**University of British Columbia Herbarium**

Figure 6. *Erythranthe neoglaucescens*. *Taylor 19554* (JEPS).

Sierra Pacific Industries - Forestry
SPIF00923

As of 2008 SPI Accession #08470

Family: SCROPHULARIACEAE – 257 - CA

PLANTS OF CALIFORNIA
FLORA OF THE SIERRA NEVADA
(Jepson Manual nSNH region)

***Mimulus glaucescens*** Greene

**BUTTE COUNTY: West Branch Feather River;** growing on the diversion dam and nearby cliffs just upstream from the Reston Road Bridge, vicinity of Stirling, T24N R4E SW1/4 of NE1/4 Section 16, Stirling City 7½' USGS quadrangle; alt. 3260 ft.; moist shaded volcanic cobble deposit under *Alnus rhombifolia-Athyrium filix-femina* canopy.

Latitude/Longitude (GPS, NAD27) 39.93796/-121.53075

**Dean Wm. Taylor** #19554 28 June 2006

SPI FORESTRY DIVISION - RARE PLANT PROGRAM

Figure 7. *Erythranthe neoglaucescens*. West Branch Feather River. *Taylor 19554* (JEPS).

Figure 8.  *Erythranthe neoglaucescens*.  Pine Creek, Tehama County.  *Taylor 16029* (UC).

Sierra Pacific Industries - Forestry
SPIF00921

SPI Forestry Division Rare Plant Program
*Mimulus glaucescens*
Scrophulariaceae Shield-Bracted Monkey Flower

Along West Branch Feather River near the diversion dam and along the canal. 24N04E SE 1/4 of NW 1/4 of Section 16. Growing on ocky cliffs and outcrops with water seeping out in a mixed conifer forest. Associated plants: Mimulus guttatus, Sedum spathulifolium, Montia parviflora, and Adiantum aleuticum.

County: Butte
Quadrangle: Stirling City, CA
Collector: Crystal Durbecq
Date Collected: 5/18/2006
Lat: 39.93908
Lon: -121.53183
Elevation: 3270
Accession# 08142

Figure 9. *Erythranthe neoglaucescens*. West Branch Feather River, *Durbecq 8142* (SPIF).

HERBARIUM OF CALIFORNIA STATE UNIVERSITY, CHICO

***Erythranthe glaucescens*** (DC.) S.F. Blake

Butte County, **CALIFORNIA** Elevation 186 m.
T22N, R2E, NE¼ of NE¼ of sec. 9. Richardson Springs 7.5' quad.
Lat: N 39° 46' 56" Long: W 121° 45' 12" NAD83

Southern Sierra Nevada Foothills. Upper Bidwell Park, approximately 2.5 air km east of Horseshoe Lake. Directly west of Upper Trail where it crosses a small perennially damp drainage north of Bear Hole. Growing in moist gravel in the understory of *Quercus douglasii* with abundant non-native annual grasses. Other associates include *Artemesia douglasiana, Sidalcea calycosa* ssp *calycosa, Toxicodendon diversilobum* and *Hypericum perforatum.* Plants exhibit a perennial growth form with trailing stems rooting at the nodes; plants scattered. Annual form of the species occurs nearby on more open and rocky slopes.

Tim Hanson 18 3/IV/2014

Figure 10. *Erythranthe neoglaucescens*. Upper Bidwell Park (near Big Chico Creek), *Hanson 18* (CHSC).

**FLORA OF CALIFORNIA**
Butte County

*Mimulus glaucescens* Greene

Centerville Rd. about 0.8 km N of intersection with Honey Run Rd. Wet seep on W side of road. Large plants spreading by rhizomes. 39.736°N; 121.701°W; 120 m elevation.

Christopher T. Ivey 400 4 May 2021

Figure 11. *Erythranthe neoglaucescens*. Centerville Road (paralleling Butte Creek), *Ivey 400* (SHSC).

*Erythranthe glaucescens* (Greene) G.L.Nesom
syn. acc. to Jepson Interchange 2020-07-09
UC Davis Center for Plant Diversity (DAV)

**HERBARIUM OF CALIFORNIA STATE UNIVERSITY, CHICO**
BUTTE COUNTY, CALIFORNIA

Mimulus glaucescens Greene

Corolla yellow, with red spots on lower lip. Large population, ca. 0.5 mi sw of Hwy 32 on Crown Pt Rd, 11 mi nw of Chico. Paradise West Quad. 7.5', T23N, R2E, se corner sec. 24. Steep, moist road cut in chaparral with sandy loam soil. Associates: Mimulus kelloggii, Pityrogramma triangularis, Garrya fremontii. Elevation 1800 ft.

**Coll.** F.J. Fuller **No.** 20 **Date:** 18/IV/82
**Det.** F.J. Fuller **Date:** 18/IV/82

Figure 12. *Erythranthe glaucescens*, small plants. Butte County, 550 m. *Fuller 20* (DAV).

Figure 13. *Erythranthe glaucescens*, intermediate (normal) sized plants. Butte County, ca. 70 m, *Hoover 11,137* (OBI).

Figure 14. *Erythranthe glaucescens*, large and small plants. Butte County, ca. 80 m, *Asa Gray s.n.* (GH).

Figure 15. *Erythranthe glaucescens*, large and intermediate plants. Butte County, 60 m, *Moyer 173* (GH).

SPI Forestry Division Rare Plant Program
*Erythranthe glaucescens*
PHRYMACEAE Shield-bracted monkeyflower

Millie THP. Growing at seep in forestry regeneration unit. Lat/Lon in NAD27.

County: Tehama
Quadrangle: Devils Parade Ground
Collector: Matthew C. Berger
Date Collected: 6/26/2018
District: Stirling
Lat: 40.07134
Lon: -121.63142
Elevation: 3845'
Accession# 10061

Figure 16. *Erythranthe glaucescens*, mature calyces with shape suggesting influence of *E. arvensis*. Tehama County, 3845 ft (1170 m) at the uppermost elevation for the species, *Berger 10061* (SPIF).

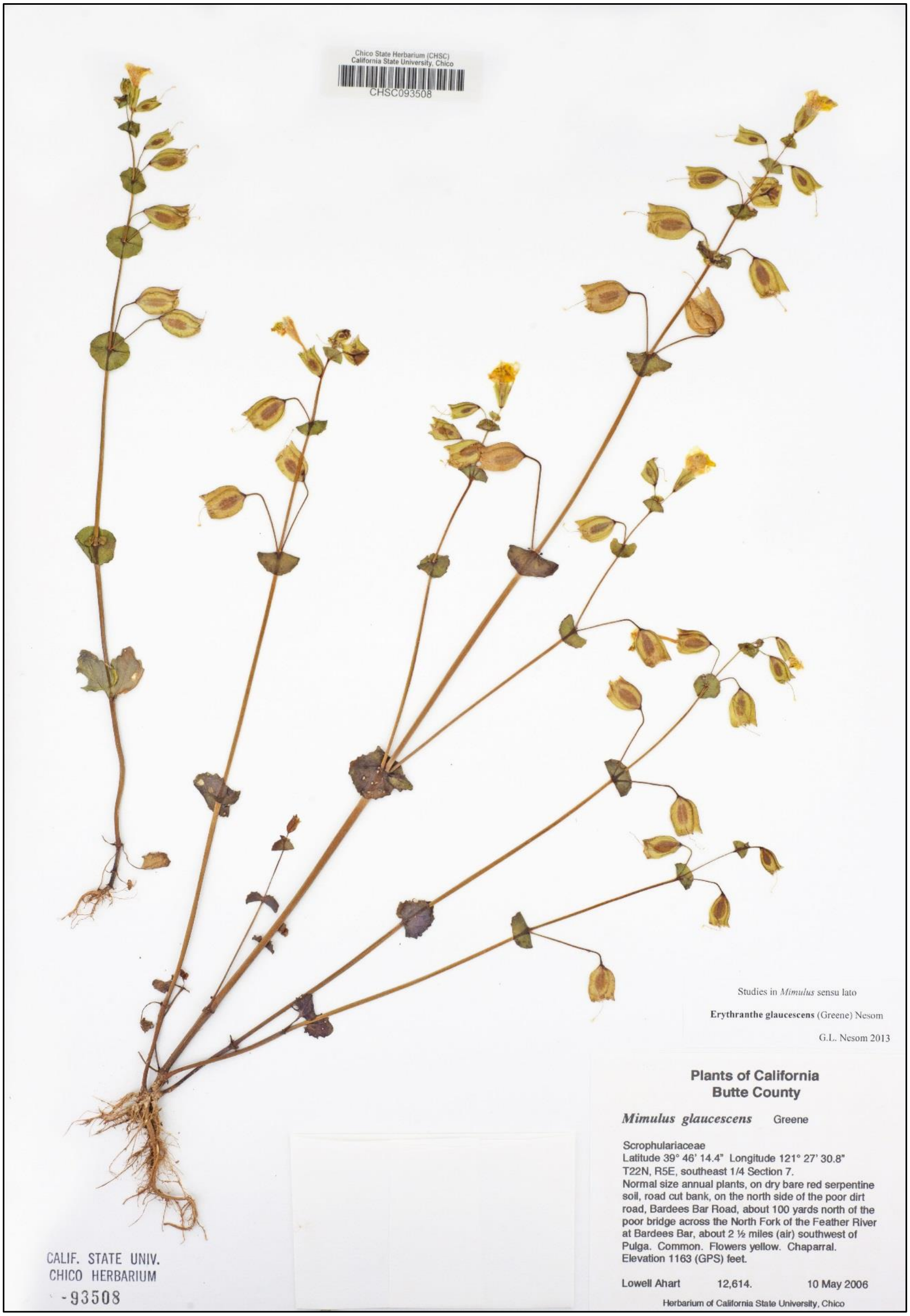


Figure 17. *Erythranthe glaucescens*, stems from basalmost nodes. Butte County, 354 m, *Ahart 12,614* (CHSC).

Studies in *Mimulus* sensu lato

**Erythranthe glaucescens** (Greene) Nesom

G.L. Nesom 2013

HERBARIUM OF CALIFORNIA STATE UNIVERSITY, CHICO

Plants of California

Mimulus glaucescens Greene

Corolla golden-yellow with orange-brown dots. Substantial population, ca. .8 km sw of Pulga 120 m n of North Fork of Feather River, along Pulga Rd., ca. 100 m from juncture with Hwy 70. Moist area at edge of rocky talus. Associates: Potentilla glandulosa, Lomatium sp. and Erythronium multiscapoideum.
T 22 N, R 5 E, Sec 6.
Elevation 495 m.
Coll. Marc P. Hayes No. 6 Date: 22/IV/77
Det. M.P. Hayes Date: 22/IV/77

Figure 18. *Erythranthe glaucescens*, stems from basalmost nodes. Butte County, 495 m, *Hayes 6* (CHSC).

Figure 19. *Erythranthe glaucescens*, population with many plants flowering, some apparently senescent (left side), Gray Davis Dye Creek Preserve, Tehama County. iNaturalist photo by Kaden Ashdown, 28 May 2023. The congested appearance of these plants might suggest a clonal group, but the numerous, strictly erect stems are more characteristic of closely spaced annuals.

Figure 20. *Erythranthe glaucescens*, totally senescent, Butte County. iNaturalist photo by Chloe Novak, 2 Aug 2022.

Figure 21. *Erythranthe glaucescens*, edge-of-water habitat, Big Chico Creek Ecological Reserve, Butte County. iNaturalist photo by Jon Aull, 4 May 2021.

Figure 22. *Erythranthe glaucescens*, edge-of-water habitat near Forest Ranch, Butte County. iNaturalist photo by Ashley Obar, 20 April 2024.

Figure 23. *Erythranthe glaucescens*, edge-of-water habitat. Paynes Creek, Tehama County. iNaturalist photo by "toadprince," 2 July 2023.

Figure 24. West Branch Feather River at the diversion dam site and type locality of *Erythranthe neoglaucescens*. Photo by Uelman, 23 June 2024.

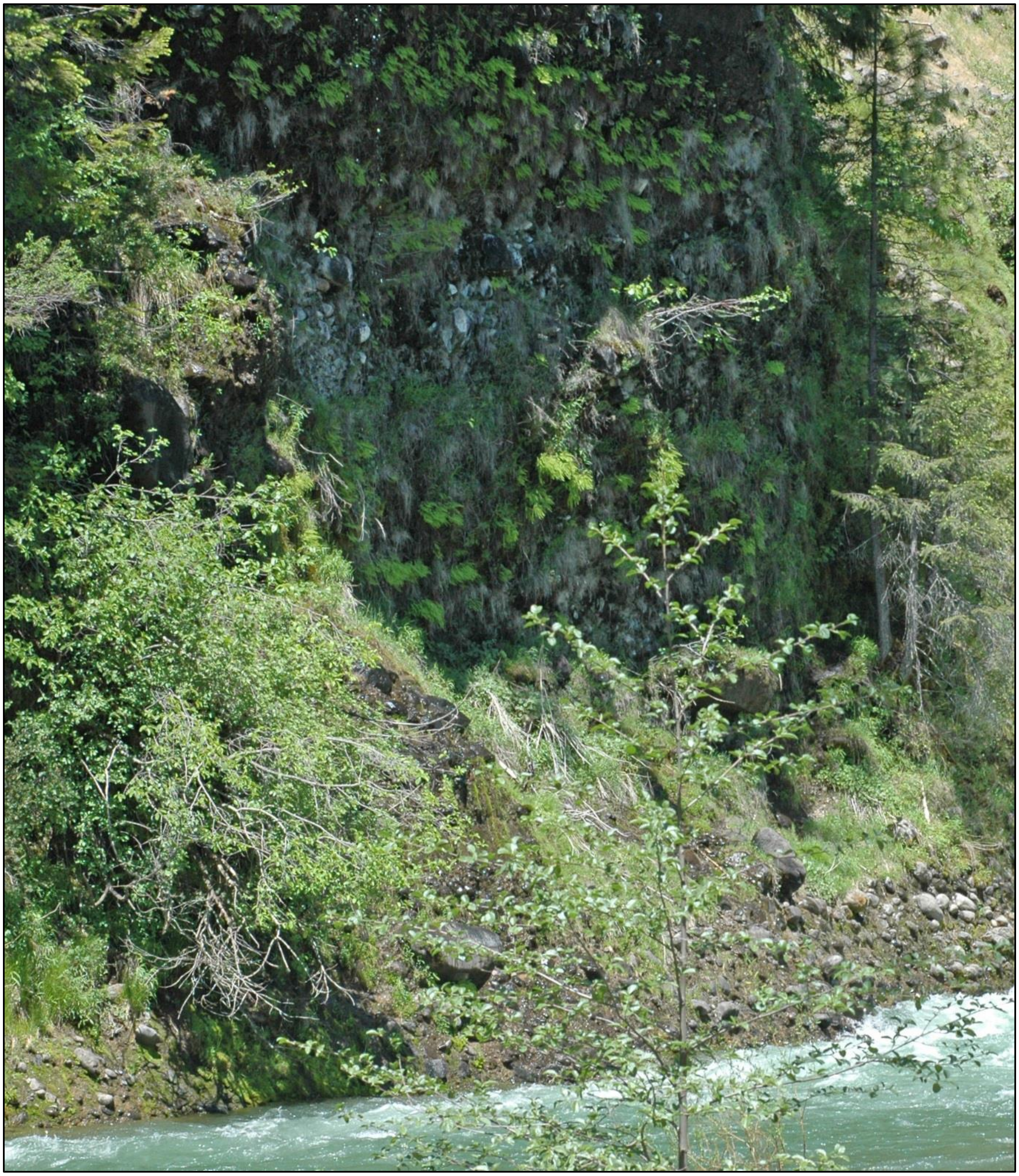


Figure 25. *Erythranthe neoglaucescens*. Cliffside habitat, near diversion dam of West Branch Feather River, near type locality and site of *Taylor 19554*. Photo by Dean W. Taylor, 28 June 2006. The collection by Crystal Durbecq (Fig. 6) apparently was made from here or else a similar habitat close by.

Figure 26. Diversion dam on the West Branch Feather River, type locality of *Erythranthe neoglaucescens*. Photo by Uelman, 23 June 2024.

Figure 27. *Erythranthe neoglaucescens* on wall of diversion dam of West Branch Feather River, at the type locality and site of *Taylor 19554*. Photo by Dean W. Taylor, 28 June 2006.

Figure 28. Canal at diversion dam on West Branch Feather River, at the type locality of *Eyrthranthe neoglacescens*. Photo by Uelman, 23 June 2024.

Figure 29. *Erythranthe neoglaucescens*, edge of pool of West Branch Feather River below diversion dam. Type locality. Photo by Uelman, 23 June 2024.

Figure 30. *Erythranthe neoglaucescens*, edge of pool of West Branch Feather River below diversion dam. Type locality. Photo by Uelman, 23 June 2024.

Figure 31. *Erythranthe neoglaucescens*, edge of pool of West Branch Feather River below diversion dam. Type locality. Photo by Uelman, 23 June 2024.

Figure 32. *Erythranthe neoglaucescens*, connate-perfoliate midcauline leaves. Type locality. Photo by Uelman, 23 June 2024.

Figure 33. *Erythranthe neoglaucescens*, leafy runners from basal nodes. Type locality. Photo by Uelman, 23 June 2024.

Figure 34. *Erythranthe neoglaucescens*, leafy runners from basal nodes. Type locality. Photo by Uelman, 23 June 2024.

Figure 35. *Erythranthe neoglaucescens*, leafy runner. Cultivated by Dean Taylor from the diversion dam site, West Branch Feather River. Photo by Dean W. Taylor (from Taylor 2013).

Figure 36. *Erythranthe neoglaucescens*, root mass with filiform fibrous roots and thicker white rhizomes. Type locality. Photo by Uelman, 23 June 2024.

Figure 37. *Erythranthe neoglaucescens*. Type locality. Photo by Uelman, 23 June 2024.

Figure 38. *Erythranthe neoglaucescens*, rotated 90° from natural position. Type locality. Photo by Uelman, 23 June 2024.

Figure 39. *Erythranthe neoglaucescens,* mature calyces. Type locality. Photo by Uelman, 23 June 2024.