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TAXONOMY OF *ERYTHRANTHE SECT. ERYTHRANTHE* (PHRYMACEAE)

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ABSTRACT

Erythranthe sect. *Erythranthe* includes nine species: *E. cardinalis*, *E. cinnabarina*, *E. flammea*, *E. eastwoodiae*, *E. erubescens*, *E. lewisii*, *E. parishii*, *E. rupestris*, and *E. verbenacea*. **Erythranthe cinnabarina** Nesom, **sp. nov.**, includes the populations previously identified as *E. cardinalis* from three counties in southeastern Arizona — and is the phyletic sister of *E. cardinalis*. **Erythranthe erubescens** Nesom, **sp. nov.**, includes populations of the pink-flowered, Sierran race previously included within *E. lewisii* — and is the phyletic sister of *E. lewisii*. *Erythranthe lewisii* is narrowed in concept to the northern, magenta-rose-flowered race. **Erythranthe flammea** Nesom, **sp. nov.**, includes plants previously identified as *Mimulus nelsonii*, except for the type of *M. nelsonii*, which was a collection of the earlier-named *Mimulus verbenaceus*. Very rarely has such a complete array of evidence (geographic, ecological, morphological, genetic, phylogenetic) been available for the description of new species. A key to the species and a typification summary, morphological description, ecological summary, and county-level (in the USA) distribution map for each species are provided. A lectotype is selected for *E. rosea*, which is a synonym of *E. lewisii*.

The establishment of *Erythranthe* as a genus (Spach 1840) included only the type species, *E. cardinalis*. Greene (1885) reduced *Erythranthe* to a section of *Mimulus* and included *M. cardinalis*, *M. lewisii*, and *M. parishii*, but Grant's sect. *Erythranthe* (1924) included only the red-flowered species *E. cardinalis*, *E. verbenacea*, *E. rupestris*, and *E. nelsonii* — placing *E. lewisii* and *E. parishii* together in her broadly conceived sect. *Paradanthus*. Pennell (1951) included *E. cardinalis* and *E. lewisii* in sect. *Erythranthe*, placing *E. parishii* among the species of sect. *Paradanthus*. Pollen morphology of sect. *Erythranthe* is closely similar to that of the rest of the genus (Argue 1980), except for sect. *Simiola*. Molecular studies by Beardsley et al. (2003, 2004), however, securely establish the identity of sect. *Erythranthe* as a distinct group, including *E. parishii*, and its phyletic position within the genus and provide a well-documented hypothesis of relationships among the species (Fig. 1).

Attempted crosses between *Erythranthe cardinalis* and *E. lewisii* and various species of other *Erythranthe* sections (sects. *Mimulasia*, *Mimulosma*, *Monantha*, *Simiola*) as well as *Mimulus ringens* (*Mimulus* sensu stricto) were unsuccessful in producing progeny (Vickery 1966; Heisey et al. 1971).

Cytogenetic studies of sect. *Erythranthe* emphasizing crossing experiments were done by Carnegie researchers (Nobs & Heisey 1964, 1965; Heisey et al. 1971); these were largely repeated by Vickery (Vickery & Anderson 1967; Vickery 1978). Two main species groups were apparent through the crossing relationships — *M. lewisii* and *M. cardinalis* and the more eastern-distributed group of *M. eastwoodiae*, *M. verbenaceus*, *M. nelsonii*, and *M. rupestris* (the latter not included in the crossing experiments) — molecular analyses found that these groups constitute phylogenetic sisters.

The taxa of sect. *Erythranthe* are fewer and more unambiguously defined than those of sect. *Simiola*, yet taxonomic problems have remained. Especially significant have been the interpretation of the two morpho-geographic races of *E. lewisii* and of the long-disjunct populations in southeastern Arizona identified as *E. cardinalis*. Generalized distribution maps of the entities have been presented (e.g., Heisey et al. 1971; Vickery & Wullstein 1987; Beardsley et al. 2003) but the only formal taxonomic treatment of the whole group has remained that of Grant (1924).

The outline of taxonomy presented here is largely in agreement with that of Heisey et al. (1971) and Beardsley et al. (2003), except for the addition of two species in a reconsideration of the taxonomic status of the 'northern' (widespread, typical) and 'Sierra Nevada' (mostly California endemic) races of *E. lewisii* and the relationship between typical *E. cardinalis* and the populations from southeastern Arizona heretofore identified as *E. cardinalis.* The present study also clarifies issues of typification, provides morphological descriptions, clarifies the geographical distributions of *E. eastwoodiae* and *E. verbenacea,* confirms the distinction of *E. verbenacea,* and provides a name for the Mexican plants previously identified as *Mimulus nelsonii*.

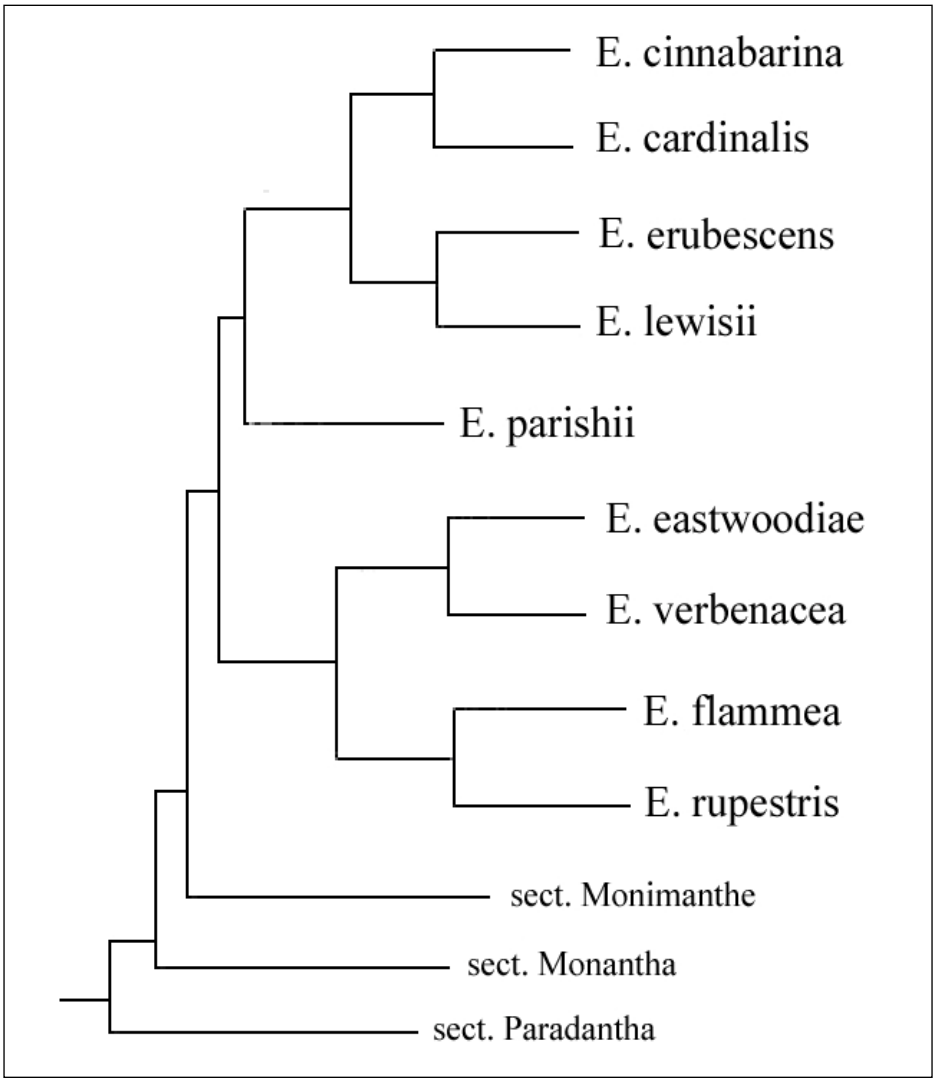
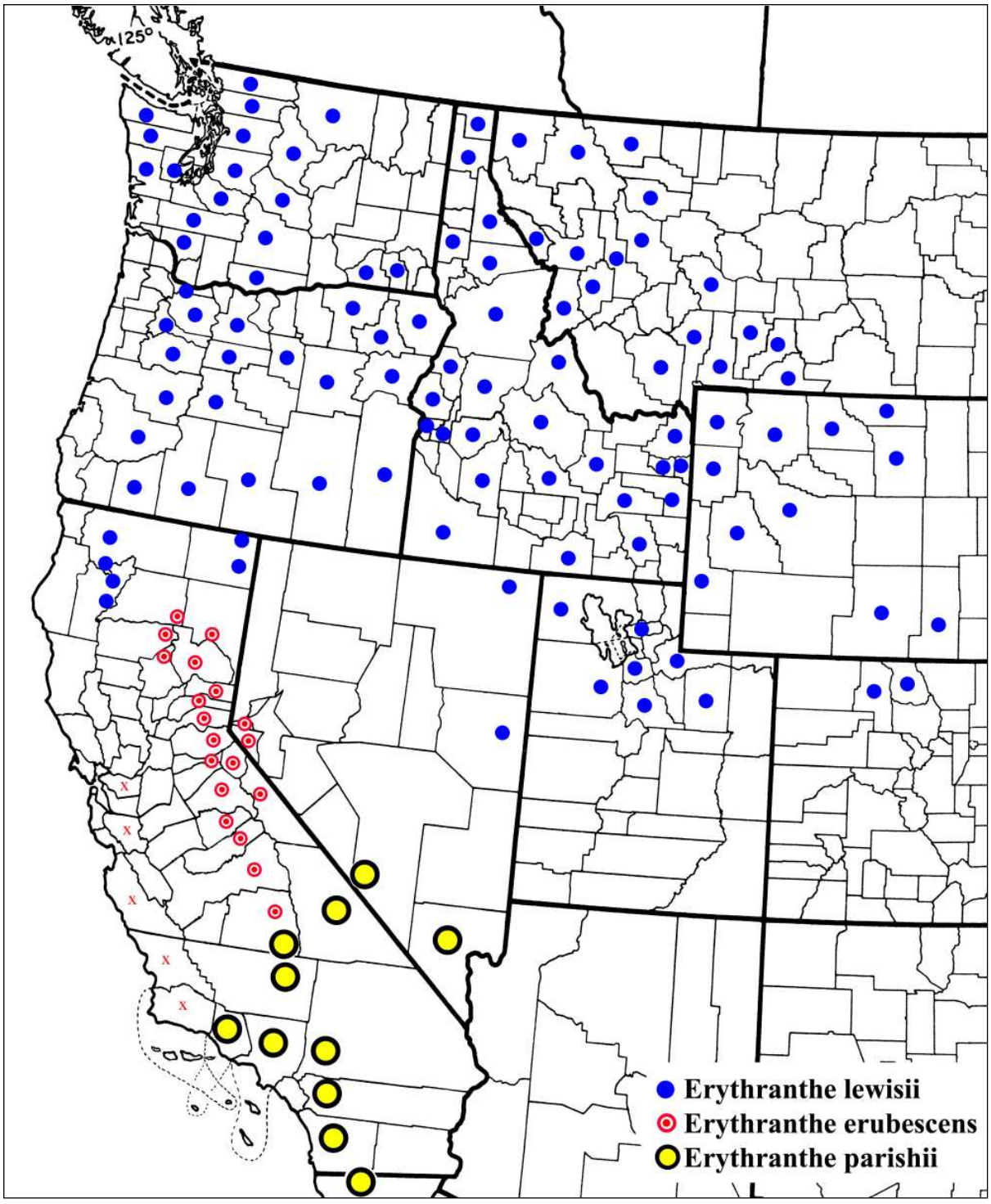
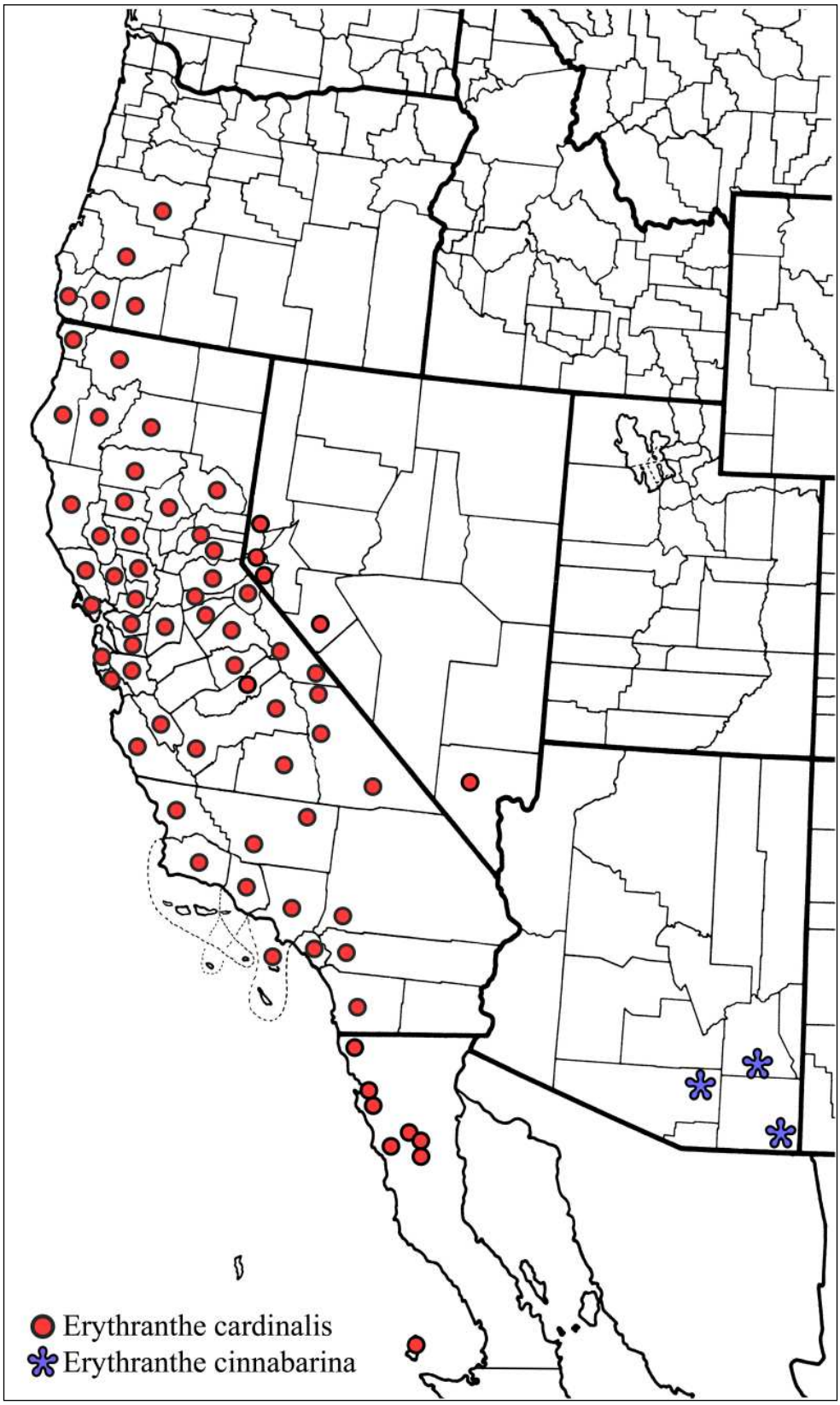


Figure 1. Phylogenetic relationships within and immediately outside of sect. *Erythranthe,* as indicated by Figures 2, 3, and 4 of Beardsley et al. (2003) and Figure 2 of Beardsley et al. (2004). Also see the summary in Figure 1 of Barker et al. (2012). Species added to sect. *Erythranthe* in the current study are *E. erubescens* and *E. cinnabarina. Erythranthe flammea* is the name of plants previously identified as *Mimulus nelsonii,* which is a synonym of *E. verbenacea.*

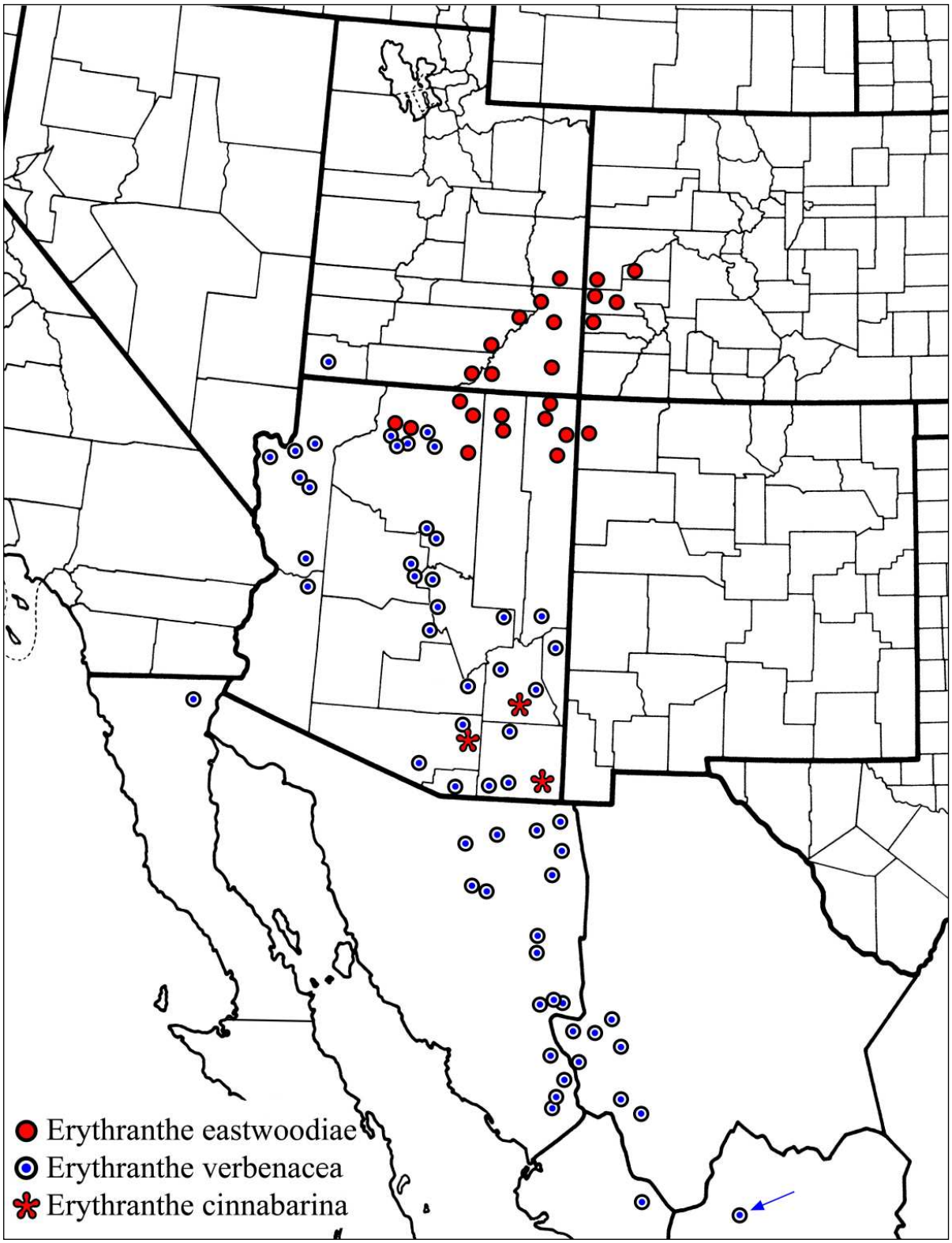
Formal nomenclature for *Erythranthe* and rationale for its separation (as a genus of more than 100 species) from *Mimulus* L. sensu stricto were presented by Barker et al. (2012). Previous detailed taxonomic studies of species groups at sectional rank within the genus have dealt with sect. *Achlyopitheca,* sect. *Mimulosma,* and sect. *Simiola* (Nesom 2012a, 2012b, 2012c).



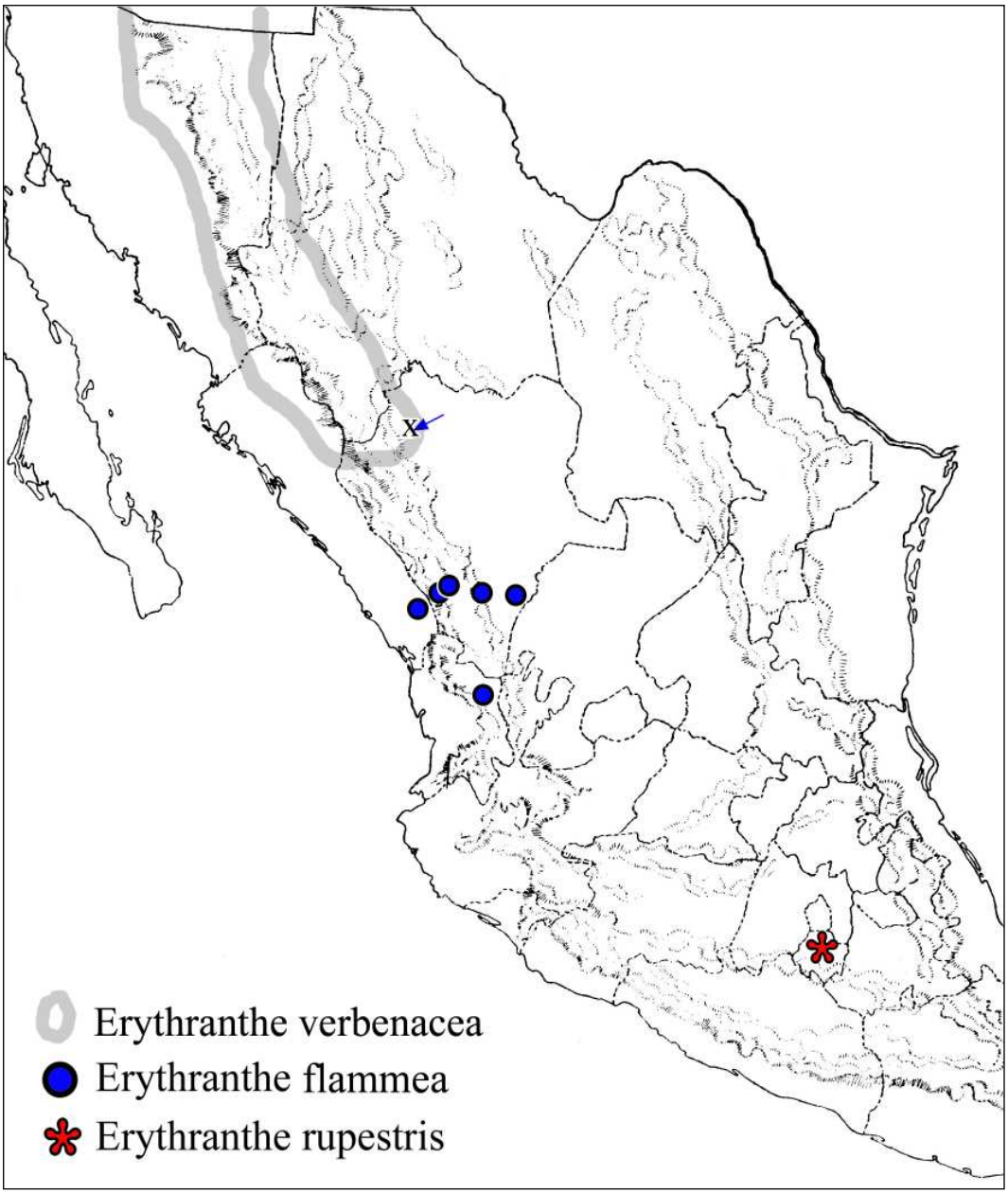
Map 1. Distribution of *Erythranthe lewisii*, *E. erubescens*, and *E. parishii*. The distribution of *E. lewisii* continues through southwestern Alberta and British Columbia into southern Alaska (see E-Flora BC 2013). The range of *E. parishii* extends slightly further southward into the Sierra San Pedro Martir of Baja California. Symbols in California and Nevada are placed within counties corresponding to the location of the populations, thus the portrayal of disjunction in northern California between *E. erubescens* and *E. lewisii* is accurate. "X"s show counties considered by Rogers (2010) as California coast range localities where David Douglas might have collected *Mimulus roseus* (within the area explored by Douglas in 1831-32) — Rogers concluded that the *M. roseus* type probably was from Santa Barbara County.



Map 2. Distribution of *Erythranthe cardinalis* and *E. cinnabarina*. Placement of symbols in larger counties indicates actual position of population systems.



Map 3. Distribution of *Erythranthe eastwoodiae*, *E. verbenacea*, and *E. cinnabarina*. Some localities for *E. eastwoodiae* are from DAVP-Utah (2014), COLO-Database (2014), and SEINET (2014). Collections documenting the disjunct population system of *E. verbenacea* in Baja California are cited in the text. The arrow points to the type locality of *Mimulus nelsonii*.



Map 4. Distribution of *Erythranthe flammea* and *E. rupestris*. Arrow points to type locality of *Mimulus nelsonii*, at the southern extremity of the range of *E. verbenacea* (shown in outline).

Species concepts and evolutionary overview

The population system from south-central Durango previously identified as *Mimulus nelsonii* (here as *Erythranthe flammea*) has been accepted in previous studies as a distinctive species. The present study more accurately represents its geography and morphology and provides an epithet, since the type of *M. nelsonii* is a plant of the earlier-named *M. verbenaceus*.

The formal description here of *Erythranthe erubescens* and *E. cinnabarina* provides a fuller and more accurate understanding of the evolutionary history of sect. *Erythranthe*. Both taxa previously have been recognized and discussed as unnamed variants within *E. lewisii* and *E. cardinalis*, respectively, but both deserve specific rank with justification equalling the other species of the section.

Species as recognized in sect. *Erythranthe*, as in 99% of other accepted species of vascular plants, are first "morphological (or morpho-geographic) species." The taxa of sect. *Erythranthe*, though, are remarkable in having been the subject of detailed experimental studies of their genetics and reproductive isolation (only *E. rupestris* has not been included in experiments), and thus, for the most part, can also be recognized as "biological species" in the sense of Mayr.

Geography enforces reproductive isolation between the sisters *Erythranthe erubescens* & *E. lewisii* and postzygotic isolation mechanisms (as documented) also are in effect. Differences in corolla color and shape between E. *erubescens* and *E. lewisii* may reflect the influence during speciation of selective pressure from pollinator preference. Primary pollinators of *E. erubescens* are the bumblebees *Bombus balteatus*, *B. centralis*, and *B. flavifrons*, and *B. vosnesenskii* (e.g., Heisey et al. 1971; Schemske & Bradshaw 1999) — *B. flavifrons* and *B. vosnesenskii* occur in the California Sierra Nevada and also in western Oregon where *E. lewisii* is sympatric with *E. cardinalis*; *Bombus balteatus* and *B. centralis* occur in the California Sierra Nevada but not in western Oregon (Koch et al. 2012), at least suggesting possibilities of pollinator-mediated selection.

Distinctions between the sisters *Erythranthe cardinalis* & *E. cinnabarina* probably evolved in allopatry, in view of their present wide disjunction. Experimental studies show that they are postzygotically isolated, but apart from their allopatry, possible prezygotic mechanisms have not been investigated. Primary pollinators of *E. cardinalis*, the hummingbirds *Calypte anna* and *Selasphorus rufus* (e.g., Heisey et al. 1971; Schemske & Bradshaw 1999), also occur in the range of *E. cinnabarina* (Cornell Lab of Ornithology 2014). Although the populations of *E. cinnabarina* occur in three geographically discrete and isolated systems, ecological and morphological variability within the species appears to be relatively narrow.

Only three species of sect. *Erythranthe* do not occur in sympatry with any other species — *E. eastwoodiae* (allopatric or perhaps parapatric with its sister *E. verbenacea*) and the sister pair E. *flammea* and *E. rupestris* — thus there is no natural test of their reproductive isolation. The geographic range of *E. cinnabarina* is mostly within that of *E. verbenacea* — the two are ecologically isolated and apparently rarely come into contact, but they are not sister species thus their sympatry does not provide an assessment of the development of reproductive isolation during speciation. *Erythranthe parishii* is parapatric with *E. cardinalis* in a small area of Tulare County where their ranges are contiguous (Fishman et al. 2013) — hybrids are formed where they come into contact (Paul Beardsley, pers. comm. 2014).

The geographic range of *Erythranthe cardinalis* completely encompasses that of *E. erubescens*. At the northern extension of its range (northwestern California and southwestern Oregon), *E. cardinalis* is sympatric with *E. lewisii*. Pollinator preference presumably plays a major role in isolating *E. cardinalis* and *E. lewisii* where they are sympatric, as it does with *E. cardinalis* and *E. erubescens*, but potential ecological distinctions (elevation, phenology) between *E. cardinalis* and *E. lewisii* have not been investigated.

In the molecular analysis of Beardsley et al. 2003), *Erythranthe cardinalis* and *E. lewisii* were interpreted to be sister species and that interpretation has been followed in subsequent studies (e.g., Ramsey et al. 2003; Angert & Schemske 2005; Angert et al. 2008; Fishman et al. 2013). In context of the species added in the present review, the phylogeny indicates that differentiation of hummingbird-pollination morphology preceded the speciation events that produced the two pairs of sister species — *E. lewisii* & *E. erubescens* and *E. cardinalis* & *E. cinnabarina*.

ERYTHRANTHE sect. **ERYTHRANTHE**

Erythranthe Spach, Hist. Nat. Veg. Phan. 9: 312. 1840. *Mimulus* sect. *Erythranthe* (Spach) Greene, Bull. Calif. Acad. Sci. 1: 108. 1885. **TYPE**: *Erythranthe cardinalis* (Dougl. ex Benth.) Spach, the only species in the protologue.

Perennial or (*E. parishii*) annual herbs, stems and leaves glabrous to puberulent or hirsute, usually glandular; leaf blades oblong or elliptic to oblanceolate, or narrowly lanceolate, shallowly toothed, palmately veined (3–5-nerved from the base); fruiting pedicels longer than calyces; calyces with sharp, definite angles and flat sides, lobes usually equal to subequal, usually apically caudate; corollas deciduous, relatively large (tube-throat 8–42 mm long), strongly red to purplish, magenta-rose, pink, or white, rarely yellow, limbs bilabiate, throat open, lobes shallowly notched to slightly retuse or entire, spreading to sharply reflexed; anther thecae white-villous (glabrous in E. parishii. x = 8.

Mexico

1. Stems prostrate with leafy stolons, cliff faces; Morelos ..... 9. **Erythranthe rupestris**
1. Stems erect, without stolons; Durango to the north and northwest.

2. Corolla tube-throats infundibular, exserted 2–11 mm beyond calyx margin; anther thecae spreading (non-reflexed); Baja California ..... 4. **Erythranthe cardinalis**
2. Corolla tube-throats tubular, exserted 13–25 mm beyond calyx margin; anther thecae reflexed.

3. Leaf blades elliptic to obovate, rhombic-ovate, or broadly spatulate, 50–75 mm x 15–26(–30) mm; corolla tube-throats 25–35 mm; calyx lobes ovate with a linear-triangular apex ..... 6. **Erythranthe verbenacea**
3. Leaf blades narrowly lanceolate, 60–95 mm x 7–15(–20) mm; corolla tube-throats 40–45 mm; calyx lobes narrowly triangular with a linear apex .....8. **Erythranthe flammea**

USA

1. Taprooted or fibrous-rooted, annual; fruiting pedicels 9–24 mm; corolla tube-throats 8–10 mm ..... 1. **Erythranthe parishii**
1. Rhizomatous and/or stoloniferous, perennial; fruiting pedicels (25–)30–95 mm (10–30(–40) mm in *E. eastwoodiae*); corolla tube-throats (15–)20–36 mm.

2. Corollas mostly light pink or magenta-rose to rose-purple or pink-purple; dorsal petals mostly free; anthers and stigma included; leaf margins denticulate to subentire or entire.

3. Corollas mostly magenta-rose, rose-purple, or pink-purple; calyx tube 12–15(–17) x 9–12 mm (pressed); widespread in northwestern USA ..... 2. **Erythranthe lewisii**
3. Corollas usually light pink; calyx tube 14–19 x 6–8 mm (pressed); Sierra Nevada of California ..... 3. **Erythranthe erubescens**

2. Corollas orange–red to scarlet or crimson; dorsal petals fused for most of length, erect; anthers and stigma exserted; leaf margins dentate to serrate.

4. Stems prostrate with leafy stolons; fruiting pedicels 10–30(–40) mm ..... 7. **Erythranthe eastwoodiae**
4. Stems erect to decumbent, rhizomatous but without stolons; fruiting pedicels (25–)50–120 (very rarely to 150) mm.

5. Corolla tube-throats tubular, exserted 13–25 mm beyond calyx margin; anther thecae reflexed ..... 6. **Erythranthe verbenacea**
5. Corolla tube-throats infundibular, exserted 2–11 mm beyond calyx margin; anther thecae spreading (non-reflexed).

6. Leaves adaxially glandular-villous on veins and lamina; calyx 17–28(–30) mm, lobes 4–7 mm, ovate to ovate-deltate, lobes apically attenuate-acute, not caudate; corolla tube-throat (15–)20–30 mm; California, Oregon, Baja California, 50–2300(–2800) m ..... 4. **Erythranthe cardinalis**
6. Leaves adaxially glabrous to minutely sessile- or stipitate-glandular; calyx (27–)29–34 mm, lobes 7–10 mm, ovate, abruptly attenuate to a linear-caudate apex; corolla tube-throat 29–36 mm; Arizona, 2100–3300 m ..... 5. **Erythranthe cinnabarina**

1. ERYTHRANTHE PARISHII (Greene) Nesom & Fraga, Phytoneuron 2012-39: 37. 2012. *Mimulus parishii* Greene, Bull. Calif. Acad. Sci. 1: 108. 1885. **TYPE**: **USA**. **California**. [San Bernadino Co.]: Cox Ranch, Mohave River, Aug 1882, *S.B. Parish & W.F. Parish 1465* (duplicates: F?, GH digital image!, M digital image!, PH 2 sheets digital images!, UC, US?, DS digital image!). On the handwritten label of the DS sheet, "Cox' Ranch" is crossed through and replaced by "Rock Spring." The GH sheet has "Bear Valley, San B. Mts., Aug 1882" but like the others, it is numbered *Parish & Parish 1465*.

In the protologue Greene cited: "On the Mohave slope of the San Bernadino Mountains, at Cox's Ranch, N side of San Bernadino Mts., Aug 1882; Parish Bros. No. 1465. Collected again in the summer of 1884, by the Rev. J.C. Nevin, and Mr. J.C. Oliver, in Los Angeles County, and by Mr. C.R. Orcutt, on the peninsula of Lower California in September of the same year." Grant (1924) cited the Parish collection as the "type" but did not distinguish among the duplicates (she cited "U.S., F, Calif., and Stanford, *type collection*"). Presumably the US specimen was the one that Greene had at hand in his description and would be the best choice for lectotype, but the species is not currently listed in the US type database (nor in the F type database).

Annual herbs, taprooted or fibrous-rooted. **Stems** erect, (3–)10–85 cm, mostly simple. **Herbage** villous-glandular to stipitate-glandular. **Leaves** cauline; blades oblanceolate to narrowly ovate or oblong, (8–)15–75 mm x 3–17 mm, palmately 3-veined, thin, apex acute to obtuse, base slightly narrowed, subclasping to clasping, margins distally denticulate to irregularly dentate; petioles absent. **Flowers** ca. 4–12, from medial to distal nodes. **Fruiting pedicels** 9–24 mm, ascending-erect. **Calyx** fruiting cylindric-campanulate, 8–13 mm, not inflated, slightly ridge-angled, villous-glandular to short stipitate-glandular, lobes subequal, 1–2 mm, deltate-apiculate, erect, glandular-ciliate. **Corollas** white to light lavender, pinkish, or rosy, palate ridges yellow, with or without small reddish spots on the palate and lower lip, tube-throats cylindric, 8–10 mm, exserted 1–3 mm beyond calyx, weakly bilabiate, lobe apices truncate to rounded, slightly erose, throats open. **Styles** glabrous. **Anthers** included, thecae spreading, glabrous. **Herkogamous** (weakly, stigma sometimes at essentially same level as upper pair of stamens). **Capsule** included, ellipsoid, slightly beaked, 6–10 mm. $2n = 16$ (as inferred from Fishman et al. 2013).

Flowering May–Aug. Wet, sandy streamsides, rocky riverbeds, canyon drainages; 400–2300 m; Calif., Nev.; Mexico (Baja California). Map 1.

In the molecular studies by Beardsley et al. (2003, 2004), *Erythranthe parishii* is sister to *E. cardinalis*/*E. cinnabarina*-*E. lewisii*/*E. erubescens*. Its annual duration, which is unique in the section, is derived from perennial ancestry. According to Fishman et al. (2013), *E. parishii* often co-occurs with *E. cardinalis* where their ranges are contiguous, presumably in Tulare County. Documentation of the presence of *E. parishii* in Nevada is in Lloyd and Mitchell (1973).

2. ERYTHRANTHE LEWISII (Pursh) Nesom & Fraga, Phytoneuron 2012-39: 36. 2012. *Mimulus lewisii* Pursh, Fl. Amer. Sept. 2: 427, plate 20. 1814 [1813]. **LECTOTYPE** (Reveal et al. 1999, p. 33): **USA**. [**Montana**.] Plate 20 (reproduced here as Fig. 2), Fl. Amer. Sept. 2: 427. 1814 [1813]. Protologue: "On the head springs of the Missouri, at the foot of Portage hill," 1805, *M. Lewis s.n.*

The Lewis collection was noted by Pursh to have been seen in the Lewis herbarium ("v.s. in Herb. Lewis nec non Lambert"), but no type material is now known to be extant (see Reveal et al. 1999), thus the protologue illustration becomes the lectotype. The type probably was collected either in the Great Falls area in Cascade Co., Montana, sometime from 21 Jun-14 Jul 1805 (as implied by the reference to "Portage Hill") or more likely along Trail Creek toward Lemhi Pass in Beaverhead Co., Montana, on 12 Aug 1805 (as implied by the reference to the "headsprings of the Missouri") (Reveal et al. 1999; UMDANSP 2008).

Mimulus roseus Dougl. ex Lindl., Edwards's Bot. Reg. 19 [n. ser., 6]: 1591, pl. 1591. 1 June 1833. **LECTOTYPE** (designated here): **USA**. **Oregon** or **Washington**. Plate 1591 (reproduced here as Fig. 6), Bot. Reg. 19: 1591. 1833. The illustrated plant was cultivated in London by the Horticultural Society from seeds sent by *David Douglas* (*s.n.*).

Lindley noted this in the 1833 Botanical Register protologue: "This beautiful Monkey-flower was sent by Mr. Douglas from Northern California in 1831. In his letter to the Horticultural Society he spoke of it as extremely rare, and the most striking object he had met with in that country. A very few grains of seed were all that reached England; and from those a small number of plants were obtained, one of which is now represented. ... Only a very small quantity of seed was saved last year, by means of which it has been preserved. ... It flowers in July and August."

Mimulus roseus previously has been treated as a synonym of a broadly construed *M. lewisii* (e.g., Hooker 1840; followed by Bentham 1846, Gray 1888, and Grant 1924) or else the name has not been considered even as a synonym (e.g., Greene 1885; Pennell 1951). With recognition here that the pink-flowered Sierra Nevadan plants of California constitute a species (*Erythranthe erubescens*, see below) distinct from typical, magenta-rose-flowered *E. lewisii*, the name *M. roseus* might be considered as the name for the Sierran plants, especially as Rogers (2010) accepted the protologue statement regarding California provenance and concluded that Douglas probably made the collection in Santa Barbara County, although it is outside of the currently known range of the species. Douglas collected in California in 1831 and 1832 but never reached the area where the Sierran race occurs (Map 1).

In addition to the protologue illustration (Fig. 6), three more of *Mimulus roseus* also were quickly published (Hooker 1834; Loddiges 1835; Don 1835; reproduced here as Figs. 7, 8, and 9, respectively) of plants probably from seeds immediately derived from the originally germinated plants. All four of the illustrations unequivocally show the magenta-rose corollas of typical *E. lewisii* — not the light pink of the California Sierran race. In contrast to Rogers's interpretation, it is thus reasoned here that Douglas collected the seeds of *M. roseus* in the Cascade Mountains close to the Columbia River or in the Blue Mountains east of Walla Walla, Washington, where he traveled through the range of *M. roseus* in July of 1830. On 11 October 1830, he shipped 3 chests of seeds (perhaps including *M. roseus*), but without dried plants, to London from the mouth of the Columbia river (fide Hooker 1836). The *Mimulus roseus* protologue was published 1 June 1833, thus it would have taken a little more than two years (ca. 31 months) for the seeds to travel to Europe, be received, reach the hands of horticulturalists and be grown to maturity, and then the illustration prepared. I have not seen the letter mentioned by Lindley (from Douglas to the Horticultural Society) or any reference to it.

This assumes that Lindley's comment that the seeds were received from Douglas in California in 1831 was mistaken (perhaps a clerical error in handling or labeling the seeds) or else that Douglas sent Oregon-collected seeds from California. If the latter proved to be correct, it would imply that Douglas took the seeds with him from the Columbia River to California and

shipped them from there to London in 1831. In a letter to W.J. Hooker (23 Nov 1831, from Monterey), Douglas wrote that "This, with many others, I trust you may yet have the pleasure of describing from living specimens, as I have sent to London upwards of one hundred and fifty nondescript plants, which I hope will bloom next season." Presumably these were California plants with bulbs or rhizomes or represented by cuttings, and according to the letter mentioned by Lindley in the protologue, Douglas did not consider *Mimulus roseus* to be "nondescript." Douglas later (23 October 1832, from the Columbia River, Oregon) wrote Hooker that he shipped "the whole of his California collection" — apparently referring to his dried specimens — from Hawaii on 8 September 1832.

Summarizing his California collections in the 23 Nov 1831 letter to Hooker, Douglas noted that "... to *Mimulus* I have also added several, among them the magnificent *M. cardinalis*, an annual, three or four feet high, handsomer than *M. luteus*." He had not earlier mentioned *M. luteus*, so it seems he assumed that *M. luteus* already would have reached England and been known — prior to the shipment of his California collections.

An undated specimen identified as *Mimulus lewisii*, with label data of "Oregon Douglas," is at GH (digital image!); the label is "Herb. A. Gray" on characteristic blue paper and the data are in Asa Gray's handwriting. Presumably Gray obtained this in 1838-39 on his first European trip. The preface of A Flora of North America (Torrey & Gray 1838, p. viii) noted that "We are under deep obligations to Mr. Bentham ... especially for a very full set of the plants collected by the late Mr. Douglas in Oregon and California, which were confided to him, as Secretary of the London Horticultural Society, for distribution." Bentham's reference (Scrophularineae Indicae, 1835) in the description of *M. roseus* to "Ad Columbia flumen, *Douglas*" surely alluded to this collection. None of Douglas's accounts mentions an encounter with *M. lewisii* on his first trip to the Pacific Northwest, thus this collection probably was made on the second trip. It was not, however, in the original material seen by Lindley.

The undated specimen at M (Fig. 2) was distributed with a printed label by the Horticultural Society of London and, although "D. Douglas" might be taken as the collector (as implied by the label), the plant probably was grown in London from seed, either from the original seed collection by Douglas or from descendants of the original cultivars.

Mimulus roseus var. *glabrior* Hook., Fl. Bor. Amer. 2: 100. 1840. **TYPE**: **CANADA**. **Alberta**. Protologue: "Mountains N of the Smoking River (*Drummond*); apparently very rare, or too early for the blossoming, for there are only two specimens in the collection, and only one in flower; and these are more glabrous than Mr. Douglas's specimens, which, as far as I know, were all gathered in California.—I think the *M. lewisii*, Ph. is probably a dwarf state of this species." (holotype: K? or E?). Thomas Drummond was in British Columbia on the Smoky River of west-central Alberta in August and September, 1826 (Geiser 1937).

Mimulus lewisii var. *exsertus* Coult. & Fisher, Bot. Gaz. 18: 302. 1893. **TYPE**: **USA**. **Colorado**. High mountains of northern Colorado, 1892, *G.E. Osterhout s.n.* (holotype: F digital image!).

Mimulus lewisii var. *tetonensis* A. Nels., Bot. Gaz. 34: 31. 1902. *Mimulus lewisii* forma *tetonensis* (A. Nels.) Macbr. & Pays., Contr. Gray Herb. 49: 67. 1917. **TYPE**: **USA**. **Wyoming**. Summit of Tetons above Lee's Lake, 11,000 ft, 26 Jul 1901, *E.D. Merrill & E.N. Wilcox 1072* (holotype: RM; isotype: NY digital image!).

Mimulus lewisii var. *alba* J.K. Henry, Fl. S. Brit. Columbia, 268. 1915. *Mimulus lewisii* forma *alba* (J.K. Henry) B. Boivin, Naturaliste Canad. 93: 1061. 1966 [published 1967]. **TYPE**: **CANADA**. **British Columbia**. As cited in the protologue: "With the species, Mt. Cheam; Crown Mt., North Vancouver." Specimens not located.

Perennial herbs, rhizomatous, sometimes described as having a musky odor. **Stems** erect, (15–)25–60(–75) cm, mostly simple. **Herbage** stipitate-glandular to glandular–villous, viscid. **Leaves** cauline; blades elliptic to ovate, ovate-lanceolate, or broadly lanceolate, (10–)25–75(–90) mm x 5–35 mm, 3–5-palmately veined from the base, margins denticulate with 2–5 pairs of teeth to subentire or entire, apex acute, base rounded or cuneate, subclasping; petioles absent. **Flowers** 2–6(–

10), axillary at leafy medial to distal nodes. **Fruiting** pedicels (25–)35–70 mm. **Calyx** broadly cylindric-campanulate, 15–22 mm, not inflated, stipitate-glandular to glandular–villous, lobes subequal, 3–5(–7) mm, deltate-triangular with caudate apices, erect, not ciliate. **Corollas** mostly rose-pink or magenta-rose to pink-purple or reddish purple, rarely crimson or pale violet, tube-throats infundibular, 22–28 mm, exserted 6–12 mm from the calyx, strongly bilabiate, lobe apices usually truncate to shallow convex and shallowly retuse, throats open. **Styles** 25–28 mm, glabrous. **Anthers** included, thecae spreading, white-villous. **Herkogamous**. **Capsule** included, cylindroid, 6–11 mm. 2*n* = 16 (Vickery et al. 1958, 1963, 1986; Nobs & Heisey 1965; Heisey et al. 1971).

Corolla color has been described as violet-red, rose-purple, rose, magenta, magenta-red, crimson, deep rose with orange spots on lip, reddish pink, pink-purple. Exceptions: "pinkish-white" in Yakima/ Skamania Co., Washington (Mt. Paddo, *Suksdorf 5779*, MO); "white or tinged with yellow," in Teton Co., Wyoming (as described in the protologue of *Mimulus lewisii* var. *tetonensis*). The type was described by Pursh as having a "beautiful pale purple" corolla with dark lines. White-flowered mutants occur sporadically (e.g., Wu et al. 2013, and see *M. lewisii* var. *alba*).

Flowering Jun–Sep. Stream banks, gravel bars, around springs, wet meadows, boggy areas, ditches, subalpine slopes, alpine meadows, wet talus, crevices; (1800–)2200–9500(–10,600) ft; Alta., B.C.; s Alaska, Idaho, Mont., Nev., Oreg., Utah, Wash., Wyo. Map 1.

Rationale for segregation of the Sierra Nevadan 'race' of *Erythranthe lewisii* as a distinct species is provided under *E. erubescens*.

3. ERYTHRANTHE ERUBESCENS Nesom, **sp. nov.** **TYPE**: **USA**. **California**. Nevada Co.: Ridge above Donner Pass, 7500 ft, 10 Aug 1903, *A.A. Heller 7141* (holotype: MO!; isotype: MO!).

Similar to typical *Erythanthe lewisii* but distinct in its light pink corollas (vs. mostly magenta-rose to purplish), more broadly cylindric calyx tubes (14–19 x 6–8 mm vs. 12–15(–17) x 9–12 mm), and its geographic range in the Sierra Nevada of California (vs. widespread from southern Alaska south to northern California, northern Utah, and northern Colorado. Genetically isolated and phylogenetically distinct from typical *E. lewisii*.

Perennial herbs, rhizomatous. **Stems** erect, 25–90 cm, mostly simple. **Herbage** stipitate-glandular to glandular–villous. **Leaves** cauline; blades elliptic to ovate, ovate-lanceolate, or lanceolate, (20–)30–90 mm x 5–25(–35) mm, palmately veined, margins denticulate with 1–4 pairs of teeth to subentire or entire, apex acute, base rounded or cuneate, subclasping; petioles absent. **Flowers** 2–8, axillary at leafy medial to distal nodes. **Fruiting** pedicels 45–90 mm. **Calyx** cylindric-campanulate, 15–22 mm, not inflated, stipitate-glandular to glandular–villous, lobes subequal to distinctly unequal, 5–7 mm, ovate with a linear-caudate apex, erect, not ciliate. **Corollas** light pink with darker pink stripes down the middle of each lobe, lower 3 lobes with a white basal patch, tube-throats infundibular, 20–30 mm, exserted 7–10 mm beyond calyx, strongly bilabiate, palate ridges yellow, lobe apices usually truncate and shallowly retuse, throats open. **Styles** 25–29 mm, glabrous. **Anthers** included, thecae spreading, white-villous. **Herkogamous**. **Capsule** included, narrowly cylindroid, 7–13 mm. 2*n* = 16 (Vickery et al. 1958, 1963, 1986; Heisey et al. 1971).

Corolla color has been described as rose, rose-pink, pink, pink and white with yellow throat, pink with a darker stripe down center of each lobe, striped on the throat.

Flowering Jul–Aug. Springs and seeps, meadows, cliffs, steep rocky slopes, ridges; (1400–)1800–3000(–3500) m; Calif. Map 1.

Students of sect. *Erythranthe* have recognized that two morpho-geographic races exist within what has been treated as the single species *Erythranthe lewisii* (e.g., Nobs & Heisey 1965; Heisey et al. 1971; Vickery & Wullstein 1987; Beardsley et al. 2003). The Sierra Nevada race (here segregated

as *E. erubescens*), essentially restricted to Sierran California, has mostly light pink corollas. The northern race (treated here as *E. lewisii* sensu stricto), widespread from southern Alaska south to northern California, northern Utah, and northern Colorado, has mostly magenta-rose corollas (compare Figs. 3-5 with 11-13). Corolla hue in *E. lewisii* is more variable than in *E. erubescens*.

Heisey et al. (1971) noted that the Sierra Nevada race also has narrower, more lanceolate and less dentate leaves with shorter-stalked glandular trichomes. "Conceivably, the Sierran plants could merit taxonomic recognition as a subspecies, but in the present report we prefer to regard them as two regionally and cytologically differentiated races" (p. 7).

Beardsley et al. (2003, p. 1407) made parallel observations: "Differences exist in corolla color, size, shape of leaves, and in stem and branching characteristics between [*Mimulus*] *lewisii* populations in the Sierra Nevada (Sierra Nevada race) and those in the Cascade and Rocky Mountains (Northern race). ... The results of our analysis of 474 AFLP fragments indicate two very well-supported clusters (100%) that correspond to the two races. All of the *M. lewisii* from the Sierra Nevada fall into one cluster and all the *M. lewisii* from the Cascades and the Rockies fall into another, with two exceptions. *Mimulus lewisii* [Northern race NCA 08] from the Siskiyou Mountains in northern California and *M. lewisii* [Northern race WA 02] from Poe Mountain in the Cascades in Washington appear to be intermediate between the two races. **The presence of intermediates between the races and the lack of substantive evidence for reproductive isolation in nature lead us to retain *M. lewisii* as one species at the present time**" (emphasis added).

It is not clear in what sense Beardsley et al. saw a lack of evidence for reproductive isolation in nature, because the two entities are allopatric where their ranges approach each other in northern California (Map 1); prezygotic reproductive isolation presumably is complete, even though plants might rarely occur sympatrically through long-distance dispersal. Both of the samples putatively showing intermediacy (Beardsley et al. p. 1403) are within the geographic range of *Erythranthe lewisii* sensu stricto; one of them (in Washington, Chelan Co.) is deeply imbedded among typical populations of the species; existence of the other (in northern California, Siskyou Co.), whether indicating rare introgression or perhaps variation remnant from an allopatric speciation event, surely does not deflect the view that two species can be recognized. Many species across many genera are recognized even though they may form natural hybrids with others.

Postzygotic isolation also separates the northern race from the Sierran race. "When any of four northern races (Warner Mountains, [Modoc Co.] California; Stevens Pass, Washington; Mount Rainier, Washington; and Logan Pass, Montana) are crossed among themselves in any combination, all the F1 hybrids show regular pairing at meiosis and high pollen fertility. The same is true when six races of *M. lewisii* from the central Sierra Nevada are intercrossed. Pollen infertility in each of these two groups of F1 hybrids ranges from 6 to 18 percent. In contrast, F1 hybrids between any of the northern and any of the Sierran group consistently show irregularities in chromosome pairing, with two sets of quadrivalents either in chains or rings at first metaphase, and a pollen infertility of 44–67 percent" (Nobs & Heisey 1965, p. 428). Hiesey et al. (1971) interpreted this incompatibility as arising from two pairs of reciprocal translocations. Observations by Vickery and Wullstein (1987) also indicate postzygotic isolation: artificial crosses between *E. erubescens* and *E. lewisii* produced relatively high seed set but viability of seeds produced by F1s was very low (noted to constitute a "moderate crossing barrier"), perhaps reflecting the same genetic system as observed earlier by the Carnegie group.

Difference between the two subgroups of *Erythranthe lewisii* also is reflected in their genetic compatibility with *E. cardinalis*. Sierran *E. lewisii* (= *E. erubescens*) and typical *E. cardinalis* are genetically interfertile (with normal meiosis) and hybrids potentially produce advanced segregants

that may closely resemble either parent (Nobs & Heisey 1964, 1965). "In contrast, members of the northern group of [*E.*] *lewisii* when crossed with the same races of [*E.*] *cardinalis* consistently show meiotic irregularities. Two sets of quadrivalents are evident at first metaphase in the majority of the pollen mother cells, and pollen infertility is high, 60–78 per cent" (Nobs & Heisey 1965, p. 428–429).

I am not able to confirm diagnostically consistent morphological differences between *Erythranthe lewisii* and *E. erubescens* noted by Heisey et al. (1971) and Beardsley et al. (2003). But in addition to the corolla color difference, a consistent distinction is observed here in calyx morphology — in *E. lewisii* the calyx tube is measurably shorter and broader, more barrel-shaped than tubular. Correspondingly, Vickery (1990) observed that corolla throat is larger and more open in *E. lewisii* than *E. erubescens* (ca 12–15 mm wide and high vs ca. 10 mm wide by 7 mm high) — this appears to be consistent with many photos available on the internet.

Ontogenetic studies of two geographically distinct populations of *Erythranthe lewisii* and two of *E. erubescens* have revealed differences in the development of pedicels, ovaries, stamens, calyx tubes, sepals, and corollas (Hazle 2001). The ovary of *E. erubescens* is separated from the nectary by a deep invagination that does not occur in *E. lewisii* (see Hazle & Canne Hilliker 2005, Figs. 8, 9, and 10). Differences in corolla bud shape carry forward into mature corollas (*E. erubescens* with more forward-projecting lobes, *E. lewisii* with more recurved lobes) — the lower lip, including the villous palate ridges, of *E. erubescens* forms a more extended landing platform, a subtle but consistent difference (compare Figs. 4 and 5 with Figs. 11, 12, and 13). Vickery (1990) observed that the corolla lobes of *E. erubescens* are "thrust forward" while in *E. lewisii* they are "gently recurved."

In sum, typical *Erythranthe lewisii* (the northern race) and the Sierra Nevada population system are discontinuously distinct in morphology and reproductively isolated by prezygotic and postzygotic barriers. This provides a complete rationale for regarding both as distinct species.

4. ERYTHRANTHE CARDINALIS (Dougl. ex Benth.) Spach, Hist. Nat. Veg. 9: 313. 1840. *Mimulus cardinalis* Dougl. ex Benth., Scroph. Ind., 28. [17 Nov] 1835. *Diplacus cardinalis* (Dougl. ex Benth.) Groenl., Rev. Hort., sér. 4, 6: 137. 1857. **TYPE**: **USA**. **California**. "California," 1831, *D. Douglas s.n.* (holotype: K presumably; isotypes: GH digital image!, NY digital image!). Bentham's publication slightly preceded that of John Lindley (Trans. Hort. Soc. London n. ser., 2: 70, pl. 3. 1835 ["read" 4 Nov 1835; probably published in Dec 1835 or early 1836]), which also described *Mimulus cardinalis* (and illustrated it — see Fig. 14).

Specimens at BR and M (digital images!) perhaps are type material, but if so the label data are misleading (if not incorrect): each label is printed, distributed from "Herb. Soc. Hort. Lond.," with "Nova California, Douglas, 1833." Douglas was in the Pacific Northwest in 1833, north of the range of *Erythranthe cardinalis*. The type was collected somewhere between Santa Barbara and San Francisco, as he explored in that area of California in 1831 (Hooker 1836; Rogers 2010); all of his California specimens presumably were shipped to England from Hawaii on 8 September 1832 (see comments under *Mimulus roseus*).

Mimulus cardinalis var. *exsul* Greene, Leaflets Bot. Observ. Crit. 2: 2. 1909. **TYPE**: **MEXICO**. **Baja California**. Cedros Island, 18-20 Mar 1889, *E. Palmer 681* (holotype: US digital image!; isotype: PH).

Mimulus cardinalis var. *griseus* Greene, Leaflets Bot. Observ. Crit. 2: 2. 1909. **TYPE**: **USA**. **California**. [Los Angeles Co.]: Santa Catalina Island, moist places, esp. stream banks, May 1896, *B. Trask s.n.* (holotype: US digital image!; isotypes: MO!, PH).

Mimulus cardinalis var. *rigens* Greene, Leaflets Bot. Observ. Crit. 2: 2. 1909. **TYPE**: **USA**. **California**. [San Bernadino Co.]: Vicinity of San Bernadino, 1000-1500 ft, 10 Jul 1896, *S.B. Parish 4189* (holotype: US digital image!; isotypes: MIN digital image!, MO 2 sheets!, NY digital image!, PH).

Perennial herbs, rhizomatous, not stoloniferous. **Stems** mostly erect to ascending, 25–75 cm, freely branched. **Herbage** sparsely to densely glandular-villous to glabrate. **Leaves**: blades elliptic-ovate to ovate or obovate, 20–90(–110) mm x 10–38(–60) mm, palmately veined, thickened, adaxially glandular-villous on veins and lamina, apex acute, base acuminate, subclasping, margins irregularly serrate to dentate; petiolar region short or absent. **Flowers** 2–12, axillary at leafy medial to distal nodes. **Fruiting pedicels** 30–90(–120) mm. **Calyx** cylindric to cylindric-campanulate, 17–28(–30) mm, not inflated, hispid-hirsute to hirsute, lobes subequal, 4–7 mm, ovate to ovate-deltate, apically attenuate-acute, not caudate, usually ciliate. **Corollas** scarlet to orange–red, rarely yellow, throat yellowish with red stripes, tube-throats infundibular, (15–)20–30 mm, exserted 2–11 mm beyond calyx margin, limbs strongly bilabiate, throats open, palate yellow–villous, red, without spots or stripes. **Styles** glabrous. **Anthers** exserted, thecae spreading, densely white-villous. **Herkogamous**. **Capsule** included, narrowly oblong, 10–16 mm. 2*n* = 16 (Vickery et al. 1958, 1963, 1986; Nobs & Heisey 1965; Heisey et al. 1971).

Flowering May–Sep. Moist to wet places along streams and lakes, creek beds, canyon, arroyo, and ravine bottoms, around springs and seepage areas, floodplains, moist clearings and woods edges; (5–)50–2300(–2800) m (see Angert & Schemske 2005); Calif., Nev., Oreg.; Mexico (Baja California). Map 2.

Vickery (1992) noted that yellow-flowered populations of *Erythranthe cardinalis* occur on Cedros Island, Baja California, and in the Siskyou Mountains of Oregon. They also have been collected on Santa Cruz Island, California.

Erythranthe cardinalis has sometimes been regarded as a member of the New Mexico flora, based on the supposition (or prediction) by Martin and Hutchins (1981) that the species occurs in that state. No documenting record, however, has been encountered in the present study for *E. cardinalis* or for *E. verbenacea* or *E. cinnabarina.*

Erythranthe cardinalis is completely sympatric in overall geographic range with *E. erubescens*, partially sympatric with *E. lewisii* (Maps 1, 2), but interbreeding is rare between *E. cardinalis* and either of the other two in natural populations— in one natural sympatric population of *E. cardinalis* and *E. erubescens*, Ramsey et al. (2003) found 2 of 2336 progeny to be hybrids. Heisey et al. (1971) observed that artificial F1 hybrids between the same two are abundantly obtained, vigorous, and fertile but, apparently in contrast, Vickery and Wullstein (1987) observed low seed set in artificial F1s between *E. erubescens* (Placer Co., California) and two samples of typical *E. cardinalis* (Los Angeles and San Mateo cos., Calilfornia). Ramsey et al. (2003) found that *E. cardinalis-erubescens* hybrids had lower seed set, lower pollen viability (ca. one-third that of the parental species), and significantly lower seed mass than the parents, but they found little or no reduction in seed germination, survival, growth, and flowering of F1 hybrids. F2 segregants (*cardinalis-erubescens*) display a wide variety of form and color (Bradshaw et al. 1995). Hybrids apparently are not known between *E. cardinalis* and *E. lewisii* sensu stricto.

Compared to postzygotic barriers to gene flow, prezygotic isolation between *Erythranthe cardinalis* and *E. erubescens* is stronger (Ramsey et al. 2003). Prezygotic barriers are reflected first in their elevational segregation and then in differential pollinator visitation. Habitats of *E. cardinalis* are at (5–)50–2300(–2800) meters, while *E. erubescens* occurs at (1300–)1800–2800(–3500) meters. The two co-occur only along larger watercourses at mid-elevation sites (in the Yosemite region, the shared distribution limit is 1200–1600 meters—Angert & Schemske 2005; Angert 2006 (or 1200–1500 meters—Angert et al. 2008). As noted by Heisey et al. (1971), "seeds of [*M. erubescens*] from high elevations are occasionally carried by streams to lower sites occupied by *M. cardinalis* and establish ephemeral populations" — they studied one such site on the floor of Yosemite Valley at 1300 meters. Where the two do co-occur, their specialization to different pollinators almost

completely restricts gene flow. *Erythranthe erubescens* is bumblebee-pollinated while *M. cardinalis* is hummingbird-pollinated, the animal preferences influenced primarily by corolla color, size, and shape and nectar reward. Floral traits of these two species and their genetic basis have been the subject of numerous studies (e.g., Bradshaw et al. 1995, 1998; Schemske & Bradshaw 1999).

5. ERYTHRANTHE CINNABARINA Nesom, **sp. nov. TYPE**: **USA**. **Arizona**. Cochise Co.: Chaperon Canyon, at road, cold living brook, 7300 ft, 1 Jul 1907, *Blumer 1551* (holotype: MO!; isotypes: ARIZ!, NMC!).

Similar to typical *Erythranthe cardinalis* in its spreading anther thecae, relatively short-exserted corolla tube, and its reflexing corolla lobes but distinct in its generally larger leaves with reduced vestiture, fewer flowers, larger calyx and corolla, apically caudate calyx lobes, and its separate geographical range. See details in couplet 6 of USA key above.

Perennial herbs, rhizomatous. **Stems** mostly erect to ascending, 25–60 cm, freely branched. **Leaves**: blades elliptic to oblong-elliptic, elliptic-lanceolate, or broadly lanceolate, 60–125 mm x 25–46 mm, palmately veined, thickened, adaxially glabrous to minutely (lens) stipitate- or sessile-glandular, abaxially minutely short glandular-villous along the veins, glabrous on lamina, apex acute, base narrowly auriculate, clasping to subclasping, margins shallowly dentate with sharp-pointed teeth; petiolar region absent. **Flowers** 2–4(–8), axillary at leafy distal nodes. **Fruiting pedicels** 50–95 mm. **Calyx** cylindric-campanulate, (27–)29–34 mm x 9–12 mm (pressed), not inflated, minutely stipitate- or sessile-glandular, lobes subequal, 7–10 mm, ovate, abruptly attenuate to a linear-caudate apex, usually ciliate. **Corollas** deep orange, dull orange, red-orange, deep scarlet, tube-throats tubular, 29–36 mm, exserted 7–12 mm beyond calyx margins, limbs strongly bilabiate, throats open, yellow-orange with dark red stripes leading onto the basal part of the lobes, without spots, palate ridges raised, red, densely short-villous with yellowish hairs. **Styles** glabrous. **Anthers** exserted, thecae spreading, densely white-villous. **Herkogamous**. **Capsule** included, narrowly oblong, 14–18 mm. $2n = 16$, as inferred from Nobs and Heisey (1965) and from Heisey et al. (1971).

Flowering Jun–Aug(–Sep). Canyons, ravines, stream beds and margins, riparian vegetation, mixed conifer forest; 2100–3300 m; Arizona. Maps 2, 3.

Erythranthe cinnabarina occurs in habitats at elevations of 2450–3100 meters in Cochise Co. (Chiricahua Mts.), Graham Co., (Pinaleno Mts.), and Pima Co. (Santa Catalina Mts.). *Erythranthe verbenacea*, with which it sometimes has been confused, occurs at lower elevations (350–2600 meters) and ranges over most of the state (Apache, Cochise, Coconino, Gila, Graham, La Paz, Maricopa, Mohave, Pima, Pinal, Santa Cruz, Yavapai cos.). *Erythranthe cinnabarina* apparently occurs alone (without *E. verbenacea*) in the Pinaleno Mts. and in the Chiricahua Mts., but both species have been abundantly documented in the Santa Catalina Mts., where they sometimes closely co-occur in areas of elevational overlap (e.g., at Marshall Gulch, at ca. 2500 meters; at Bear Wallow Campground, ca. 2600 meters).

Additional collections examined. **USA**. **Arizona**. Cochise Co., **CHIRICAHUA MTS.**: no other data, *Bloomer n-13* (ARIZ); Chiricahua Wilderness Area, Greenhouse Trail, 1/4 mi E of Cima Cabin, where trail crosses creek, 8780 ft, with *Pseudocymopteris*, *Veratrum*, *Viola*, *Fragaria*, 3 Jul 1975, *Leithliter 94* (ASU); East Turkey Creek, moist sandy soil in creek bottom, 6300 ft, 22 Jun 1960, *McCormick et al. 174* (ARIZ); Turkey Creek Canyon, 3 air mi SSW of Paradise, 7 air mi W of Portal, in the canyon W of the intersection of the road to Paradise and the Forest Service road to Onion Saddle, in soil collected between boulders present in the creek, with *Juniperus deppeana*, *Pinus chihuahuana*, *Pseudotsuga*, *Picea*, *Quercus gambelii*, *Juglans*, *Hedeoma hyssopifolium*, *Habenaria sparsiflora*, 6800–7000 ft, 9 Sep 1986, *Ward 86-034* (NMC). Graham Co: **PINALENO MTS.**: Upper Marijilda Canyon, below Shannon Camp, along creek, 9000 ft, 6 Aug 1972, *Bingham 2-18* (ASU); riparian zone at Grant Creek just below compgrounds in Mexico conifer forest, 8500 ft, 28 Jul 1988,

Bricker 331 (ASU); along AZ Hwy 366, ca. 1.5 mi NW of Hospital Flat, scattered in stream-bed under mixed conifers, 8700 ft, 7 Sep 1980, *Jenkins 3127* (ARIZ); Grant Creek, 6300 ft, 21 Jun 1983, *Johnson 1175* (ASU); Mount Graham, Jul 1927, *Kearney 4502* (ARIZ); junction of Grant Creek and Swift Trail, 10 mi E of Clark Peak Trailhead, along creek in moist mixed coniferous forest, 2665 m, 6 Aug 1990, *Lowry s.n.* (ARIZ); branch of Ash Creek, 1.1 mi NE of Columbine Work Center, along stream, 9200 ft, with *Heracleum*, *Actaea*, *Epilobium angustifolium*, 25 Jul 1989, *McLaughlin 5622* (ARIZ); Marijilda Canyon, in water and in moist soil, 8500 ft, 3 Sep 1944, *Pultz 1080* (ARIZ); Coronado Natl. Forest, adjacent to FS 803, 7.8 mi E of FS 287, S-facing slope, in gravelly alluvium, Subalpine Coniferous Forest, with *Populus tremuloides*, *Pinus flexilis*, *Pseudotsuga menziesii*, 10,000 ft, 16 Jul 1995, *Villalba 2289* (NMC). Pima County, **SANTA CATALINA MTS.**: 20 mi NE of Tucson, Ski Bowl winter sports area, along stream, 8 Jul 1964, *Baad 444* (VDB); Upper Sabino Creek, 1 mi W of Summerhaven, streamside, 8000 ft, 27 Jun 1960, *Barr 60-69* (ARIZ); Mount Lemmon, Jul 1965, *Hesselberg s.n.* (ARIZ); 32 mi NE of Tucson via Catalina Hwy. in Bear Wallow, mixed conifer forest, wet gulley, 8200 ft, 24 Jul 1965, *Matthews 471* (ASU, VDB); Marshall Gulch, 7600 ft, 28 Jun 1917, *Shreve s.n.* (ARIZ); Mount Lemmon, Bear Wallow Camp grounds, 8000 ft, 28 Aug 1938, *Smith 14169* (ARIZ); Upper Sabino Creek, Turkey Run Rd, 1 mi W of Summerhaven, wet stream bed, with *Mimulus gutattus* and *Platanthera limosa*, 8100 ft, 24 Jul 2008, *Tedford 814* (ARIZ); Marshall Gulch, 20 Jun 1907, *Thornber 4191* (ARIZ); Soldiers Camp, 7 Aug 1908, *Thornber s.n.* (ARIZ); Upper Sabino Canyon, in ravine, along small flowing stream, SE & NW 20 d slope, gneiss with quartzite, Stand #17, riparian mixed conifer forest, with *Abies concolor*, *Pseudotsuga menziesii*, 8500 ft, 10 Jul 1962, *Whittaker & Niering s.n.* (ARIZ).

Evidence for recognizing *Erythranthe cinnabarina* at specific rank, distinct from *E. cardinalis*, is unequivocal and compelling. In fact, very rarely has such a complete array of evidence been available for the description of a new species. The Arizona system is geographically long-disjunct from the typical *E. cardinalis* (Map 2), adapted to a different ecology, and documented to be genetically distinct, phylogenetically distinct, and distinct in morphology. Even without knowledge of their genetics, if plants of 'cinnabarina' morphology occurred in California, where they would have been subject to general comparative study, the discontinuity surely would have been recognized earlier.

Molecular studies show the two entities to have a evolutionary sister relationship. In the molecular analysis of sect. *Erythranthe* (Beardsley et al. 2003), the disjunct Arizona populations identified as *Erythranthe cardinalis* (cited as *PB 2001-01* WTU and *PB 2001-02* WTU, but vouchers not at WTU; both collected from the same population in Marijilda Canyon of the Pinaleno Mts., Arizona, fide Paul Beardsley, pers. comm.) cluster as sister to those from Oregon, California, and Mexico (*Vickery 11315*, UT) — based on AFLPs analyzed by neighbor-joining and parsimony.

Nobs and Heisey (1965) found that at least one reciprocal translocation in *Erythranthe cinnabarina* distinguishes it from populations of typical *E. cardinalis*. "A race of *Mimulus cardinalis* from the Santa Catalina Mountains [Marshall Gulch] of Arizona when crossed with any of several *M. cardinalis* races from the Pacific coast or the central Sierra Nevada in California produces F1 hybrids that have one tetravalent or trivalent plus a single chromosome in about 50 percent of the pollen mother cells. Others show regular pairing of all eight chromosomes, but often one or two pairs are loosely attached. ... Pollen infertility increases to 20–35 percent in F1 hybrids with the Arizona race, compared with 3–7 percent in various hybrids between five coastal and Sierran races. Pairing at meiosis is highly regular in the Sierran group, with no evidence of any structural differences among any of the pairs of chromosomes" (p. 427). Pollen fertility in the F1s was reduced 20–30% (Nobs & Heisey 1967). Heisey et al. (1971) noted that the Arizona 'cardinalis' "is genetically differentiated by a mild sterility barrier that appears to be the result of a reciprocal translocation between two pairs of chromosomes" but pointed to an illustration (their Fig. 9, lower right) of irregular meiotic pairing in

an F1 hybrid between *E. cardinalis* from Marshall Gulch and *E. lewisii* from Logan Pass, Montana. Vickery & Wullstein (1987) found that seed viability of F1 hybrids between typical *E. cardinalis* and *E. cinnabarina* [from Pima Co., Arizona] was very low, constituting a "strong crossing barrier."

The genetic distinction between *Erythranthe cinnabarina* and *E. cardinalis* also can be seen in their genetic relationship to *E. erubescens* and *E. lewisii*. *Erythranthe cinnabarina* is postzygotically isolated from both *E. erubescens* and *E. lewisii* — "The Arizona races of *M. cardinalis* show a high degree of genetic incompatibility with either the northern or Sierran races of *M. lewisii*. The F1 hybrids in both instances are about 87 percent sterile, and in some cultures they are sublethal" (Nobs & Heisey 1965, p. 429). In contrast, typical *E. cardinalis* is interfertile with *E. erubescens* (see comments above).

Vickery and Wullstein (1987, p. 340), following Heisey et al. (1971, 7), referred to *Erythranthe cinnabarina* as the "narrow-leafed race" of *E. cardinalis* and separated it in their key from typical *E. cardinalis* by a narrower leaf outline — but this is essentially the reverse of what is observed here, based on nearly all specimens available for examination. Nor do the measurements of calyx and corolla size by Vickery and Wullstein show the marked differences between the two species recorded in the present study.

Despite continuing confusion of *Erythranthe verbenacea* and the *E. cardinalis*-like plants (*E. cinnabarina*) in Arizona (see comments below), their distinction also is clear, with *E. cinnabarina* having different corolla morphology, different anther thecae orientation, larger, broader leaves with reduced vestiture, and different ecology. I have not seen any collection that might be indicative of hybridization, perhaps because of the demonstrated genetic incompatibility between the two. "The most highly developed genetic barrier in the *Erythranthe* section appears between the intercompatible [*E. verbenacea*, *E. eastwoodiae*, and *E. nelsonii*] ... and *M. cardinalis*. The Arizona and California forms of *M. cardinalis* are about equally incompatible with the *M. verbenaceous-eastwoodiae-nelsonii* complex" (Nobs & Heisey 1965, p. 428).

Contrasts between the two species are outlined in the couplet below.

1. Corolla tube-throat exserted 7–12 mm, exserted 3–10 mm beyond calyx margin; anther thecae reflexing; leaves 60–120 x 25–46 mm, adaxially glabrous to minutely (lens) stipitate- or sessile-glandular, abaxially minutely short glandular-villous along the veins, glabrous on lamina; habitats at 2450–3100 meters ..... **Erythranthe cinnabarina**
1. Corolla tube-throat exserted 13–25 mm beyond calyx margin; anther thecae straight, spreading; leaves 50–75 mm x 15–26(–30) mm, sparsely to densely glandular-villous on both surfaces; habitats at 350–2600 meters ..... **Erythranthe verbenacea**

6. ERYTHRANTHE VERBENACEA (Greene) Nesom & Fraga, Phytoneuron 2012-39: 37. 2012. *Mimulus verbenaceus* Greene, Leafl. Bot. Observ. Crit. 2: 2. 1909. *Mimulus cardinalis* Dougl. ex Benth. var. *verbenaceus* (Greene) Kearney & Peebles, J. Washington Acad. Sci. 29: 491. 1939. **TYPE**: **USA**. **Arizona**. [Yavapai Co.]: In crevices in the perpendicular walls of the cañon where the water drips out, Clear Creek, Camp Verde, 9 Aug 1891, *J.W. Toumey s.n.* (holotype: US digital image!). The US sheet has a handwritten annotation by Greene as "Mimulus verbenaceus, Type."

Mimulus lugens Greene, Leafl. Bot. Observ. Crit. 2: 3. 1909. **TYPE**: **USA**. **Arizona**. [Cochise Co.]: Fort Huachuca, 26 Apr-21 May 1890, *E. Palmer 441* (holotype: US digital image!). The US sheet has a handwritten annotation by Greene as "Mimulus lugens, Type."

Mimulus nelsonii A.L. Grant, Ann. Missouri Bot. Gard. 11: 144. 1925 ("1924"). *Erythranthe nelsonii* (A.L. Grant) Nesom & Fraga, Phytoneuron 2012-39: 37. 2012. **TYPE**: **MEXICO**. **Durango**. Sierra Madre, 30 mi N of Guanaceví, 8000-9000 ft, 18 Aug 1898, *E.W. Nelson 4775* (holotype: US digital image!; isotypes: K digital image!, PH digital image!).

Perennial, rhizomatous. **Stems** erect to decumbent, 20–60 cm, usually simple, weakly 4-angled. **Herbage** sparsely to densely glandular-villous. **Leaves** cauline; blades elliptic to obovate, rhombic-ovate, or broadly spatulate, 50–75 mm x 15–26(–30) mm, 3-5-palmately veined from the base, margins coarsely serrate distally or along the whole length, apex acute to obtuse, base subcordate, subclasping, petioles absent. **Flowers** 2–12, axillary at leafy medial to distal nodes. **Fruiting pedicels** 45–90(–110, rarely to 150) mm. **Calyx** campanulate 20–28 mm, weakly inflated, sparsely glandular-villosulous to stipitate-glandular, lobes subequal, 5–6 mm, ovate to ovate-triangular with a linear-triangular apex, erect. **Corollas** crimson, often tinged with yellow, tube-throats tubular, 25–35 mm, exserted 13–25 mm beyond calyx margin, strongly bilabiate, lower lip spreading, upper lip erect, lobe apices truncate, often emarginate, throats open, ventral ridges raised, dark red, densely short-villous. **Styles** glabrous. **Anthers** exserted, thecae reflexed, white-villous. **Herkogamous** (strongly to weakly). **Capsule** included, cylindric, 15–22 mm. 2*n* = 16 (Vickery et al. 1958, 1963, 1986; Nobs & Heisey 1965; Heisey et al. 1971).

Flowering Jun–Sep. Stream edges and beds, floodplains, around seeps and springs, canyon bottoms, moist cliff crevices and ledges; 350–2600 m; Ariz., Utah; Mexico (Baja California, Chihuahua, Sinaloa, Sonora, Durango). Map 3.

The populations of *Erythranthe verbenacea* in Baja California are long-disjunct from the main range, occurring there on the east side of the Sierra Juarez in the vicinity of Tajo Canyon (a.k.a. Cantillas Cañon or Tantillas Cañon). Specimens examined. **MEXICO**. **Baja California**. Tajo (Cantillas) Canyon, 10 Sep 1952, *Harbison 44828* (SD, UC); Tajo (Cantillas) Canyon, 21 Apr 1955, *Harbison 111* (CAS-2 sheets); Tajo Cañon, E side of Sierra Juarez, 32º 16' N, 115º 55' W, wet sandy soil in shade of large boulder, 900 m, 8 Sep 1957, *Moran 6081* (CAS, SD); Sierra Juarez, between El Topo and Laguna Hanson, Rancho Rodeo del Rey, extreme NE part of the Ranch in the upper part of Tajo Canyon, 33.2208º N, 115.897º W, schist substrates, riparian, 1600 m, 21 Jun 2007, *Rebman 13597* (SD); Cantillas Canyon, desert canyon, 1 Apr 1953, *Schwenkmeyer s.n.* (SDSU fide SEINET). Typical *E. cardinalis* in Baja California occurs further west and south and is allopatric with *E. verbenacea*. See other comments following *E. cardinalis*.

Vickery (1992) noted that yellow-flowered morphs of *Erythranthe verbenacea* occur "in a population" at Vasey's Paradise in the Grand Canyon (Coconino County), 32 miles downstream from Lees Ferry.

Populations of *Erythranthe verbenacea* in the vicinity of Oak Creek Canyon in southern Coconino Co., Arizona (documented by numerous collections), have leaves with a narrow, lateral, undulating, purple stripe across the mid lamina (Fig. 19). The coloration is retained even in dried specimens. A similar pattern of leaf coloration occurs in *E. flammea* (Fig. 20).

Grant (1924) recognized *Mimulus verbenaceus* as a species distinct from *M. cardinalis*, a distinction later confirmed by Carnegie researchers (e.g., Nobs & Heisey 1965; Heisey et al. 1971) and by Vickery and Wullstein (1987), who found a strong crossing barrier between the two (see comments under *Erythranthe cinnabarina*). Kearney and Peebles (1942, 1960) and Shreve and Wiggins (1964) treated *M. verbenaceus* as a variety of *M. cardinalis*, while Holmgren (1984) and Welsh et al. (2003) have regarded it as a synonym of *M. cardinalis*. It currently is treated as a synonym of *M. cardinalis* by USDA (2014) and Kartesz (2014).

In Grant's description of *Mimulus nelsonii*, she remarked only that it "is unique in the section [*Erythranthe*] on account of its unequal calyx-teeth and its short style" (1924, p. 144). She did not provide comparative measurements of style length and I cannot find that it differs from *E. verbenacea* in that feature. The calyx lobes are indeed unequal in length and in this feature apparently stand apart

from typical *E. verbenacea* — this population in the Guanaceví area, at the very southernmost extension of the *E. verbenacea* range (Map 3) — is otherwise identical to *E. verbenacea*. It might be regarded as a peripheral variant of the latter, but it unequivocally is not the same species as occurs along Hwy 40 between Cd. Durango and Mazatlan, here recognized as *E. flammea*.

Molecular data (Beardsley et al. 2003) indicate that *Erythranthe verbenacea* is sister to *E. eastwoodiae* and phyletically distinct from *E. cardinalis*/*E. cinnabarina*, which is sister to *E. lewisii*/ *E. erubescens*. In addition to distinction in shape and length of the corolla tube-throat (infundibular and shorter in *E. cardinalis*/*E. cinnabarina* vs. cylindric and longer in *E. verbenacea* — see key couplet 5; also see the couplet as part of discussion under *E. cinnabarina*), corolla lobes in *E. cardinalis* are reflexed while the adaxial corolla lobes of *E. verbenacea* are spreading. This is evident in living plants (see many photos via internet) but more difficult to see in pressed material. Another contrasting feature noted by Grant (1924), Heisey et al. (1971), and Beardsley et al. (2003) is anther thecae orientation — thecae are reflexed 45º in *E. verbenacea* and *E. eastwoodiae*, in contrast to the spreading (non-reflexed) lobes of *E. cardinalis*.

7. ERYTHRANTHE EASTWOODIAE (Rydb.) Nesom & Fraga, Phytoneuron 2012-39: 36. 2012. *Mimulus eastwoodiae* Rydb., Bull. Torrey Bot. Club 40: 483. 1913. **TYPE**: **USA**. **Utah**. [San Juan Co.:] San Juan River, near Bluffs, 1200-1500 m, 25-29 Aug 1911, *P.A. Rydberg* and *A.O. Garrett 9883* (holotype: NY digital image!; isotypes: NY digital image!, RENO digital image!, RM, US digital image!, UT!).

Perennial, stoloniferous, sometimes also rhizomatous. **Stems** scandent to pendent, 5–30(–40) cm, mostly simple. **Herbage** villous-glandular to minutely stipitate-glandular with gland-tipped hairs, often a mixture of longer and much shorter hairs. **Leaves** cauline; blades flabellate distally to obovate to oblanceolate or elliptic, (5–)13–40(–55) mm x 8–20(–25) mm, largest near midstem or distally, palmately 3-veined, thick, apex acute, base cuneate or rounded, subclasping, margins coarsely serrate on distal half; petioles absent. **Flowers** 2–8, axillary at leafy medial to distal nodes. **Fruiting pedicels** 10–30(–40) mm. **Calyx** cuneate-cylindric to cylindric, 15–23(–27) mm, not inflated or weakly so, glabrous or minutely stipitate-glandular to sparsely glandular-villosulous, lobes subequal, 4–7 mm, triangular-acuminate, ciliate. **Corollas** scarlet to orange-red or orange, caducous, tube-throats narrowly funnelform, 20–30 mm, exserted 5–15 beyond calyx, limb strongly bilabiate, throats open, palate puberulent, red, not spotted or striped. **Styles** glabrous. **Anthers** exserted, thecae reflexed, villous. **Herkogamous**. **Capsule** included, elliptic, 6–10 mm. $2n = 16$ (Vickery et al. 1963; Nobs & Heisey 1965; Heisey et al. 1971).

Flowering May–Sep(–Nov); seepage in sandstone overhangs, cave roofs, walls, crevices, and cliff bases, pinon-juniper woodland; 900–2000 m; Ariz., Colo., N.Mex., Utah. Map 3.

The range of *Erythranthe eastwoodiae* appears to be essentially contiguous with that of *E. verbenacea* in the Grand Canyon region, but among the specimens I have studied, there has been no evidence of hybridization.

8. ERYTHRANTHE FLAMMEA Nesom, **sp. nov. TYPE**: **MEXICO**. **Durango**. Sierra Madre Occidental, between Mazatlán and Durango, 2 mi E of El Espinazo, 20.5 mi E of El Palmito, ledges of cliff face, in spring water, 8600 ft, 8 Jun 1962, *P.C. Hutchinson 2506* (holotype: MO!; as noted on the label, duplicates distributed to E, F, G, HEID, K, M, MEXU, MICH, NY, P, S, UC, US, WIS).

Differing from *Erythranthe verbenacea* in its reduced vestiture, longer and narrower leaves, longer corolla tube-throats, and narrowly triangular calyx lobes with an elongate, linear apex.

Perennial, rhizomatous. **Stems** erect, often laxly, 15–50 cm, moderately to densely short glandular-villous. **Leaves** cauline; blades narrowly lanceolate, 30–95 mm x 7–15(–20) mm, palmately 3-veined from the base, Hwy 40 populations with a broad, lateral, often arching, maroon stripe at the distal 1/2–1/3, moderately to densely short glandular-villous, margins sharply serrate on distal 2/3–2/5 with 8–16(–25) pairs of teeth or denticles, apex acute, base narrowly subcordate, subclasping; petioles absent. **Flowers** 6–10(–12), axillary at leafy medial to distal nodes. **Fruiting pedicels** 50–90 mm. **Calyx** broadly cylindrical, 34–37 mm, tube 20–25 mm, sparsely short villous-glandular, lobes subequal, narrowly triangular with a linear apex, 7–11 mm, erect. **Corollas** crimson-red, tube-throat cylindrical, 40–45 mm, exserted 18–20 mm beyond calyx, strongly bilabiate, throat ampliate, lobes of upper lip erect, those of lower lip shorter and spreading. **Styles** glabrous. **Anthers** exserted, thecae reflexed, densely white-villous; style exserted, glabrous. **Herkogamous** (weakly, the stigma slightly or not at all beyond level of upper pair of anthers). **Capsule** included, cylindroid, 10–12 mm. $2n = 16$ (Vickery et al. 1963; Nobs & Heisey 1965; Heisey et al. 1971). Figures 20, 21.

Flowering Jan–Jul. Cliffs, steep banks and hillsides, canyon slopes, usually in seepage or near waterfalls, pine and pine-oak woods; 6500–9000 ft; Mexico (Durango, Nayarit, Sinaloa). Map 4.

Additional collections. **MEXICO**. **Durango**. Moist area along Mex Hwy 40 near crest of mts. between Durango and MazatIan, 9000 feet, 3 Jun 1963, *Bell 17703* (ASU, SMU); 10 to 12 mi W of La Ciudad (38 to 40 mi W of El Salto), along road to Mazatlan from Cd. Durango, steep, moist canyon slope in pine-oak forest, 8300 ft, 15 Jun 1951, *Gentry 10611* with Gilly (ARIZ); 99.1 mi W of Durango City via Hwy 40 (Mazatlan-Durango hwy), next to waterfall, uncommon, 7930 ft, 11 Jan 1977, *Goldberg 77-68* with Inouye (ARIZ); Mpio. de Súchil, Arroyo El Temascal, 4 km al SW de Piedra Herrada (La Michilia), a orilla de arroyo, muy abundante, 3 May 1981, *S. Gonzalez and M. Gonzalez 1638* (ASU digital image!, MO); along Mexican Hwy 40 from Durango to Mazatlan, along mountainous roadside, with pines and some open grasslands, 6200-8595 ft, 1 Jun 1966, *Pearce 2324* (ARIZ); Mpio. El Salto, Sierra Madre Occidental, along Hwy 40 at the eastern end of El Espinazo de Diablo, 11.3 mi SW of La Ciudad, 16 mi E of Revolcaderos, humid pine-oak forest on SE-facing cliffs and steep banks, on a roadside seep, 7800 ft, uncommon preennial, flowering & fruiting, 26 Mar 1984, *Sanders 4881* (ARIZ); Mpio. El Salto, above Los Bancos, near km post 162 on Hwy 40 (Durango-Mazatlan), dry and rather brushy S-facing slopes near the rim of the plateau, but also with localized seeps and springs, pine-oak forest with *Ceanothus*, *Cercocarpus*, *Alnus*, and *Arbutus*, area heavily grazed, 8036-8397 ft, 14 Apr 1999, *Sanders 22648* (UCR); ca. 11.5 mi W of La Ciudad along Mex 40, on and around a spring flowing of a rock cut, 30 Mar 1974, *Taylor & Taylor 15830-B* (BRIT); Mex Hwy 40, near KM 161, among large granite boulders, by mountain stream in pine-oak forest, 7850 ft, 12 May 1976, *Vickery cult. no. 12,217* (MO); 50 km S of Cd. Durango on road to La Flor, 6800 ft, 10 May 1981, *Walker 81-24* (ARIZ). **Nayarit**. Mpio. El. Nayar, 100 airline km NNE of Tepic, rocky ridge with *Pinus*, *Quercus*, and *Arbutus* dissected by a grassy, spring-filled valley along the Arroyo Santa Rosa W of Santa Teresa, 2095 m, 21-24 Oct 1979, *Breedlove 44516* (MO). **Sinaloa**. On the Durango-Villa Union hwy at Km. 1164, ca. 1 mi NW of El Palmito, a small stream drains the area, flowing into the drainage of the Rio Balahurte, massive cliffs present, pine-oak forest, 6500 ft, 27 Apr 1966, *Hubbell s.n.* (ARIZ).

These plants (including all those in published chromosome, genetic, and phylogenetic studies) have previously been identified as *Mimulus nelsonii*, but the type of *M. nelsonii* clearly belongs with the earlier-described *M. verbenaceus* and is now placed there as a synonym. When Grant (1924) described *M. nelsonii*, she knew it only from the type from north-central Durango — she did not see any collections from the area to the south where all collections of *Erythranthe flammea* have been made.

Plants from southeast of Cd. Durango and in northern Nayarit should be studied more closely in comparison to those between Cd. Durango and Mazatlan, as the collections cited here (*Gonzalez &*

Gonzalez 1638, *Walker 81-24; Breedlove 44516*) tend to have broader, more densely toothed leaves (10–16(–25) pairs of teeth or denticles along the distal 2/3 vs. 8–12 pairs along the distal 2/5) without a purple cross-stripe. The calyx lobes, however, have linear apices and the corolla tube-throat is elongate (ca. 40 mm), and the close geography of all these populations suggests that they are most closely related among themselves.

9. ERYTHRANTHE RUPESTRIS (Greene) Nesom & Fraga, Phytoneuron 2012-39: 37. 2012. *Mimulus rupestris* Greene, Leafl. Bot. Obs. Crit. 2: 3. 1909. **TYPE**: **MEXICO**. **Morelos**. Sierra de Tepoxtlan, wet cliffs, 7500 ft, 6 May 1900, *C.G. Pringle 8348* (holotype: US digital image!; isotypes: K digital image!, MO!, NDG digital image!, PH digital image!, POM, S digital image!).

Perennial, rhizomatous. **Stems** mostly prostrate to ascending, often laxly, 5–15 cm, frequently rooting at the nodes, densely and finely glandular-villous. **Leaves** cauline; blades oblanceolate to elliptic-oblanceolate, 20–45 mm x 6–20 mm, palmately 3-veined from the base, green on both sides, moderately to densely short glandular-villous, margins shallowly to coarsely serrate on distal 1/2 with 3–5 pairs of teeth, apex acute, base gradually attenuate, slightly subclasping or not at all; petioles absent. **Flowers** 2–6 at distal nodes. **Fruiting pedicels** 20–30 mm. **Calyx** cylindric, 17–20 mm, tube 14–16 mm, moderately short glandular-villous, not ciliate, lobes subequal, triangular to ovate-triangular with a slightly attenuate apex, 3–5 mm, erect. **Corollas** crimson-red, tube-throat cylindric, 25–30 mm, exserted 13–15 mm beyond calyx, strongly bilabiate, throat ampliate, lobes of upper lip longer, erect, those of lower lip shorter and spreading. **Styles** glabrous. **Anthers** exserted, thecae reflexed, densely white-villous; style exserted, glabrous. **Herkogamous** (weakly, the stigma barely above level of upper pair of anthers). **Capsule** included, ellipsoid, 6–8 mm. $2n = 16$ (as inferred from Vickery et al. 1986).

Flowering Apr–May. Wet cliffs; 5900–7500 ft; Mexico (known only from the type and collections from near the type locality in north-central Morelos). Map 4.

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Figure 2. *Erythranthe lewisii*. Plate 20 (the lectotype) from Pursh's *Flora Americae Septentrionalis*, 1814. The corolla was described as "beautiful pale purple" with dark lines.

Figure 3. *Erythranthe lewisii*. Pierce Co., Washington, Mt. Rainier National Park. Photo © Walter Siegmund, 25 August 2010. From Wikipedia.

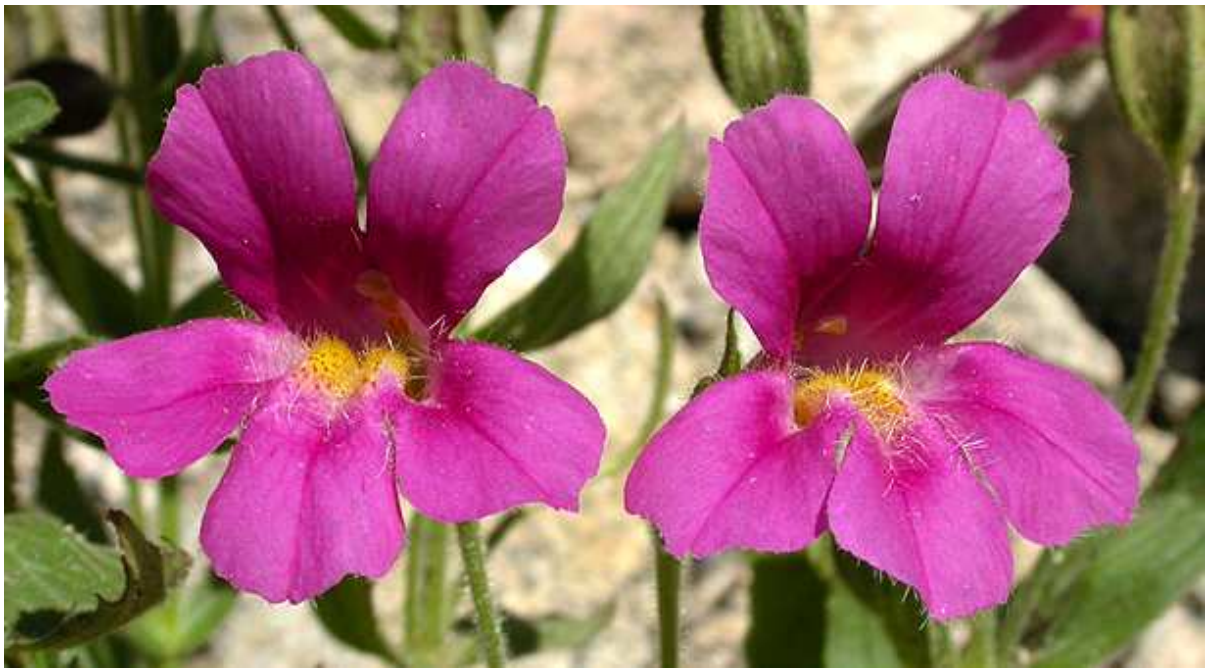

Figure 4. *Erythranthe lewisii*. Baker Co., Oregon, Elkhorn Mountains. Photo © Christopher L. Christie, 21 August 2004.

Figure 5. *Erythranthe lewisii*. Beartooth Mountains in Park County, Montana. Photos by Steve Torna, August 2013; used by permission from his Knowledge and Light website.

Figure 6. *Mimulus roseus*. From protologue in Edwards's Botanical Register by John Lindley (1833). Corolla color described as "rosea." Illustration by Sarah Ann Drake.

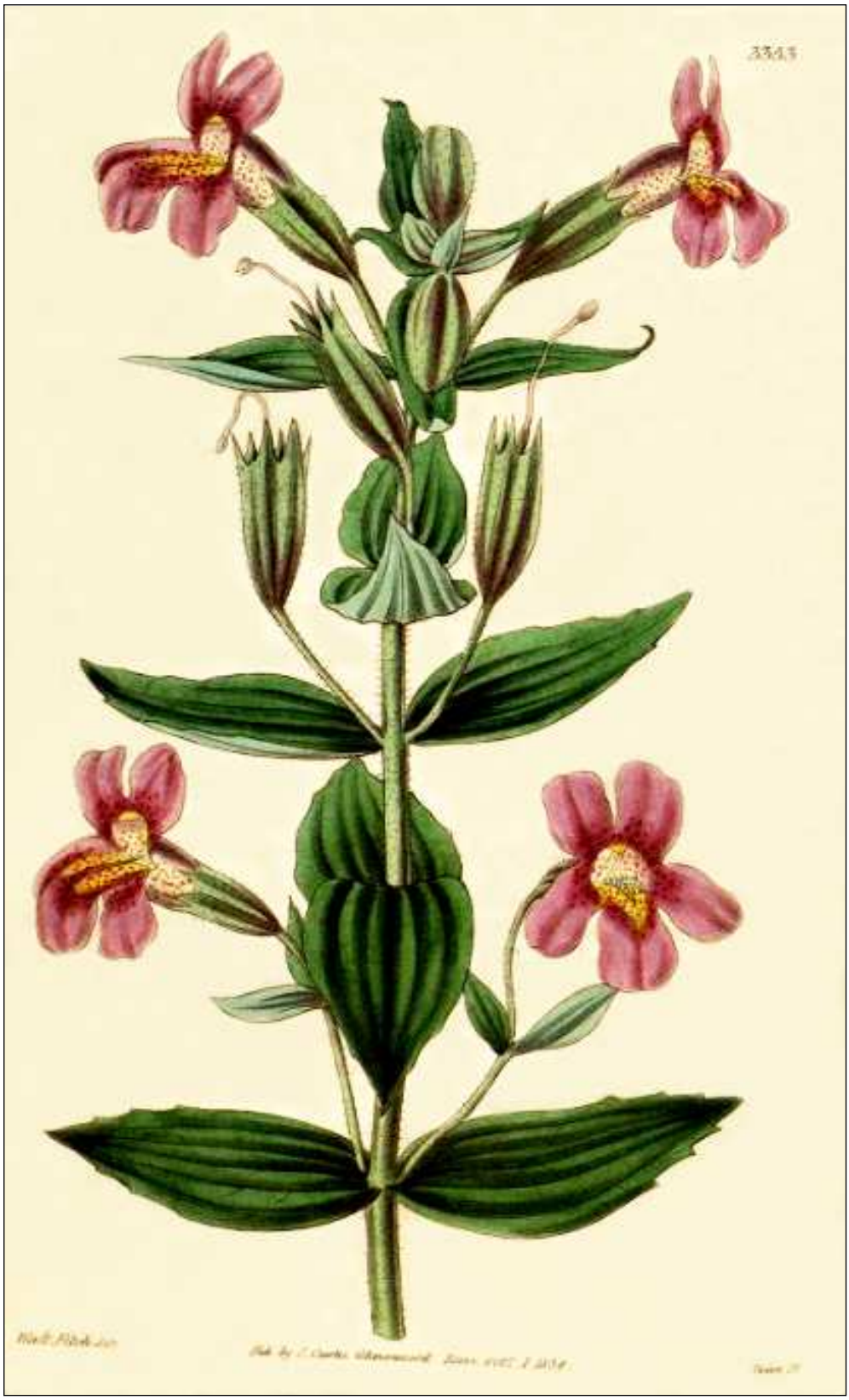

Figure 7. *Mimulus roseus*. From entry in Curtis's Botanical Magazine by William Jackson Hooker (1834). Corolla described as of a "beautiful rose-colour." Illustration by Walter Fitch.

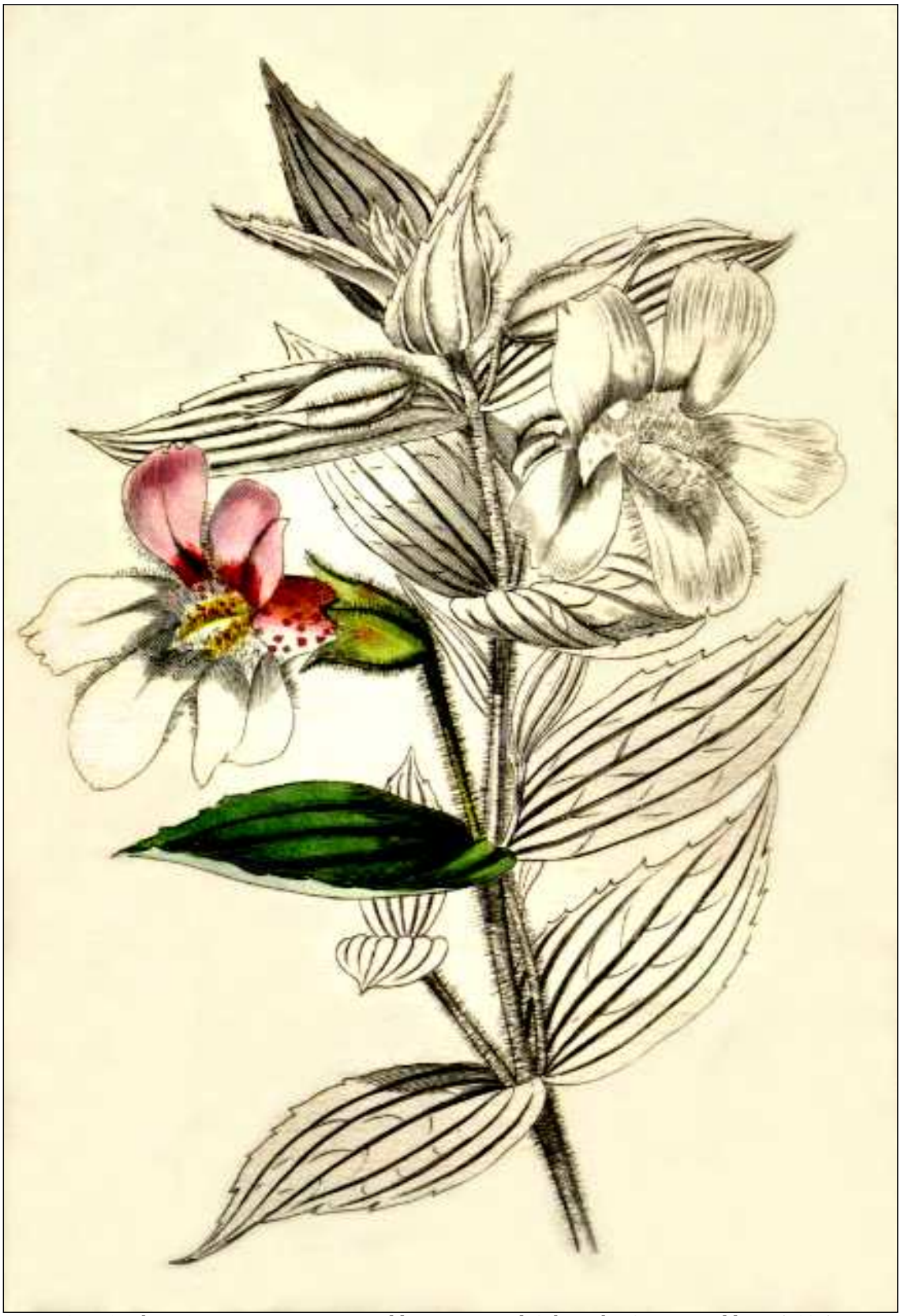

Figure 8. *Mimulus roseus*. From entry in Loddiges Botanical Cabinet by George Loddiges (1835). No description was provided apart from the illustration by George Cooke.

Figure 9. *Mimulus roseus*. From entry in The British Flower Garden by David Don (1835). Corolla described as of a "deep rose-colour." "We are indebted to Mr. Knight, of the Exotic Nursery, King's Road, Chelsea, for the specimen whence our drawing was taken." Illustration by J.T. Hart.

Figure 10. *Mimulus roseus*. Herbarium M, distributed by the "Herb. Hort. Soc. London" but probably not type material. Rather the plant probably was grown in London from seed, either from the original California seed collection of 1831 by D. Douglas or from descendants of the original cultivars.

Figure 11. *Erythranthe erubescens.* Top left, Fresno Co., California; photo by Brother Alfred Brousseau, 1 Aug 1986. © 1995 Saint Mary's College of California. Top right, Madera Co., California; photo © Jeffrey Pippen, 10 Jul 2007. Bottom, Mariposa Co., California, photo © John Game, 1 Jul 2000.

Figure 12. *Erythranthe erubescens.* Alpine County, California, Ebbett's Pass. Photo by J.T. Vale, 1 Aug 1974. CalAcademy slide #T 107,885.

Figure 13. *Erythranthe erubescens.* "California." Photo by Brother Alfred Brousseau.

Figure 14. *Mimulus cardinalis*. From entry in the Transactions of the Horticultural Society of London by John Lindley (1835). Illustration by Sarah Anne Drake.

Figure 15. *Erythranthe cardinalis.* In the flood channel of Seiad Creek, near Seiad Valley, Siskyou Co., California. © 2011 Aaron Schusteff, photo 3 July 2007.

Figure 16. *Erythranthe cinnabarina*, Pinaleno Mts., Graham Co., Arizona, 24 June 2012. Photo by Bob Beatson, Flickr, used by permission. Note the large leaves, large flowers, and few-flowered inflorescences.

Figure 17. *Erythranthe cinnabarina*, Pinaleno Mts., Graham Co., Arizona, 24 June 2012. Photo by Bob Beatson, Flickr, used by permission. Note apparent "infolding" of margins of upper petal pair, which seems to be the reverse of the direction of folding in *E. cardinalis*. The apparent yellow-hairy palate ridges also are not characteristic of *E. cardinalis.*

Figure 18. *Mimulus verbenaceus*. Painting by Mary Vaux Walcott (1925). As noted by Rogers (2010), this plant was from along the Bright Angel Trail in the Grand Canyon, Coconino Co. Arizona. It was identified by Walcott as *M. cardinalis* but instead clearly is *M. verbenaceus.*

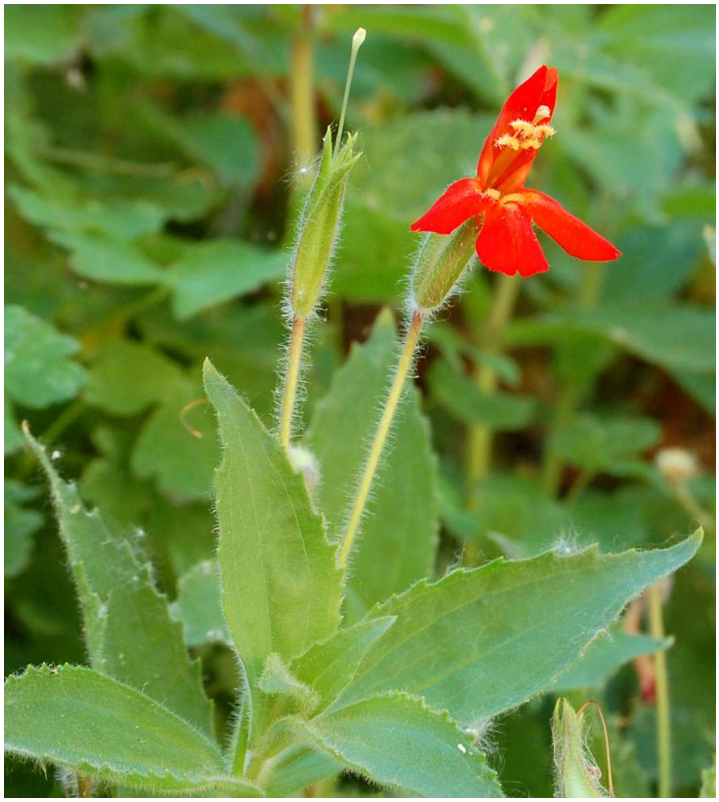

Figure 19. *Erythranthe verbenacea*. Mazatzal Mts., Pima Co., Arizona. Photo by M. J. Plagens, 17 May 2008. From Wikipedia.

Figure 20. *Erythranthe verbenacea*. Oak Creek Canyon, Coconino Co., Arizona, 23 May 2009. The purple stripe across the leaf lamina apparently is consistenstly characteristic of plants of the Oak Creek Canyon area. Photo by Thomas H. Kent at FloraFinder.com.

Figure 21. *Erythranthe flammea*. Along Hwy 40, W of La Rumarosa, Durango, Mexico. Photo by Mark Egger, 14 Apr 1999. The purple stripe across the leaf lamina is characteristic of the species in the Cordilleran populations but not elsewhere.

Figure 21. *Erythranthe flammea*. Durango, Mexico, same population as above. Photo by Mark Egger, 14 Apr 1999.