DIVERSITY, ENDEMISM AND CONSERVATION OF CALIFORNIA MONKEYFLOWERS (PHRYMACEAE): A CASE STUDY IN *ERYTHRANTHE* SECTION *PARADANTHA*

A final project submitted to the Faculty of Claremont Graduate University in partial fulfillment of the requirements for the degree of Doctor in Philosophy in Botany

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APPROVAL OF THE REVIEW COMMITTEE

This dissertation has been duly read, reviewed, and critiqued by the Committee listed below, which hereby approves the manuscript of Naomi Fraga as fulfilling the scope and quality requirements for meriting the degree of Ph.D. in Botany.

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ABSTRACT

Diversity, endemism and conservation of California monkeyflowers (Phrymaceae): a case study in *Erythranthe* section *Paradantha*

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Plants placed in the genus *Mimulus* L. (Phrymaceae), as traditionally defined, are commonly known as monkeyflowers. These charismatic plants are exceedingly diverse in western North America with over 150 of the nearly 200 species worldwide occurring here. Nearly 60% (ca. 100) of the species native to western North American occur in California. However, Mimulus has recently undergone significant changes in taxonomy leaving the name Mimulus virtually absent from the California flora. Two genera that have been resurrected; *Erythranthe* Spach and *Diplacus* Nutt., account for nearly all of the species diversity in western North American Phrymaceae. *Erythranthe* is the most diverse of the genera segregated from Mimulus s.l., with 120 species currently recognized. *Erythranthe* section *Paradantha* (Phrymaceae) has recently been a source of floristic novelty, with five new species described from California and Nevada. *Erythranthe* section *Paradantha* is a relatively species rich lineage within which species identification has been challenging resulting in disagreement among taxonomic authorities. In this study, I examine species boundaries and relationships in *Erythranthe* section *Paradantha* in a phylogenetic context using a dense sampling scheme that benefits from extensive fieldwork. Results of this study will inform a taxonomic revision that also incorporates evidence from morphology and ecology.

DEDICATION

To my parents, Maria E. Fraga and Robert Fraga Sr., who have provided me with unconditional love and support throughout my life.

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CHAPTER ONE: REVISION OF *ERYTHRANTHE MONTIOIDES* AND *ERYTHRANTHE PALMERI* (PHRYMACEAE), WITH DESCRIPTIONS OF FIVE NEW SPECIES FROM CALIFORNIA AND NEVADA, U.S.A

Flowering plants form the structural basis and are a species-rich component of almost all terrestrial habitats, thus their study underpins ongoing efforts to conserve global biodiversity (Malcom et al. 2006; Joppa et al. 2011). Our knowledge of plant species, however, remains remarkably incomplete (Mabberley 2009) and basic biodiversity research, including species discovery, is needed. This is especially true for areas with high levels of diversity and endemism, such as western North America (Joppa et al. 2011). Notably, it has been estimated that 5% of the flowering plant species in western North America are yet to be described (Ertter 2000), and The Jepson Interchange (2012) reports 139 taxa, or 2% of the native California flora are newly described since *The Jepson Manual: Higher Plants of California* was published in 1993. The discipline of systematics offers essential information to conservation biology, especially with regard to the identification of taxa and distinct lineages that are in need of conservation. Undescribed species that remain uncollected or are unrecognized in herbaria or outdated taxonomic treatments result in inaccurate tallies of species diversity and may lead to incorrect identification of species (Soltis and Gitzendanner 1999; Bebber et al 2010), undoubtedly hampering conservation efforts. Resolving taxonomic issues and identifying the basic units of diversity, namely species, is vital for scientifically-based conservation measures to be established (Skinner et al. 1995; Joppa et al 2011).

The genus *Erythranthe* Spach. (Phrymaceae) formerly treated as part of *Mimulus* L. (see Barker et al. 2012 for modified taxonomic concepts), has a high incidence of rarity and endemism. Twelve sections and 110 taxa are currently recognized in *Erythranthe* (Barker 2012);

however, species delimitation and taxonomic relationships have been unclear, with as few as 50 taxa recognized in previous treatment (Grant 1924; Pennell 1951; Thompson 2012). The genus is particularly diverse in western North America, with more than 80% of species represented in this region (Barker et al 2012). At least 25 species of *Erythranthe* are currently listed by U.S. government agencies and native plant societies as sensitive, rare, or endangered, making *Erythranthe* a group of conservation concern (Colorado Rare Plant Field Guide 2012; California Native Plant Society Inventory of Rare and Endangered Plants 2012; Nevada Rare Plant Atlas 2012; Oregon Natural Heritage Information Center 2012; The Nature Conservancy 2012; The New England Wildflower Society 2012; Utah Rare Plants 2012; Washington Natural Heritage Program 2012; Wyoming Rare Plant Field Guide 2012). In several regional treatments of the group, some previously recognized rare species have been synonymized with more common species (Thompson 2002, 2012).

Erythranthe section *Paradantha* includes 16 species and is noted for having many endemic species, considerable variation in breeding systems, and problematic species delimitations (Beardsley et al. 2004; Grant 1924; Table 1.1). Taxonomic confusion has persisted in two species of section *Paradantha*: *E. montioides* and *E. palmeri* (Table 1.1). The most recent treatment took a conservative approach, placing three species into synonymy with *E. montioides* and one species into synonymy with *E. palmeri* (Thompson 2012). My work has yielded evidence for recognition of ten species where two species (i.e., *E. montioides* and *E. palmeri*) were previously recognized (Fig. 1.1; Table 1.1), including reinstatement of three species that were treated as synonyms and five that have been newly identified. Here I provide the necessary lectotype designations for *E. montioides*, describe five new species, provide revised descriptions for the five species previously treated as either *E. montoides* or *E. palmeri*, and clarify the

circumscriptions of these last two species. Taxonomy of the group has been previously reviewed by Gray (1886), Grant (1924), Greene (1885), Munz (1968), Pennell (1951), and Thompson (1993, 2012). A historical overview of taxonomic concepts for *E. montioides* and *E. palmeri* is presented below.

TABLE 1.1. Comparison of present treatment to selected historical (Grant 1924) and more recent (Thompson 2012) treatments of taxa included in *Erythranthe montioides* and *Erythranthe palmeri* by the last author.

Species treated in the current study	Other Synonyms	Grant (1924)	Thompson (2012)
Erythranthe barbata	*Mimulus deflexus*	*M. deflexus*	*M. montioides*
Erythranthe calcicola		*M. montioides*	*M. montioides*
Erytheranthe carsonensis	*M. rubellus* var. *latiflorus*	*M. montioides*	*M. montioides*
Erythranthe diffusa	*M. grantianus*	*M. diffusus*	*M. palmeri*
Erythranthe discolor		*M. discolor*	*M. montioides*
Erythranthe hardhamae		*M. palmeri*	*M. palmeri*
Erythranthe montioides		*M. montioides*	*M. montioides*
Erythranthe palmeri		*M. palmeri*	*M. palmeri*
Erythranthe rhodopetra		*M. palmeri*	*M. palmeri*
Erythranthe sierrae		*M. palmeri*	*M. palmeri*

Taxonomic overview of Erythranthe montioides

Erythranthe montioides was originally described by Asa Gray (1868) based on five specimens examined by him and cited in the protologue. These five syntypes were later found to represent three different species. Gray (1868) later determined two of the syntypes as *E. suksdorfii* (A.Gray) N.S. Fraga; this species continues to be recognized. The current study

reveals that the remaining three syntypes represent two distinct species such that a lectotype for *E. montioides* must be designated and a new species must be described. The original protologue described a range of morphological characteristics that are representative of the three species included among the five syntypes. The lectotype designated here for *E. montioides* maintains the most common usage of the name for a species that occurs in the high central Sierra Nevada in California.

Additionally, previous treatments, variously placed three species into synonymy with *E. montioides*: *Erythranthe barbata*, *Mimulus deflexus*, and *E. discolor*. *Erythranthe barbata* was described by Greene in 1884; however, he soon placed it into synonymy with *E. montioides* in his 1885 treatment of the group. Gray (1886) followed Greene and treated *E. barbata* as a synonym of *E. montioides*. *Erythranthe barbata* was later recognized by Grant (1924), Pennell (1951), and Munz (1968) before it was synonymized again with *E. montioides* by Thompson (1993, 2012). Note that although Grant recognized *E. barbata* as a synonym of *M. deflexus*, *M. deflexus* is a later name and is treated here as a synonym of *E. barbata*.

Erythranthe discolor was described by Grant (1924) in her monograph of *Mimulus*. This species was aptly named for its polymorphic flower color, and both morphs appear on the type specimen. This species was later recognized by Pennell (1951) and Munz (1968), however it was not accepted by others who treated it under *E. montioides* (Munz 1974; Thompson 1993, 2012). Grant's concept of the species was, in fact, confused with *E. montioide*s, as evidenced by her annotations; Grant frequently annotated specimens of *E. montioides* as *E. discolor*. *Erythranthe discolor* is endemic to the southern Sierra Nevada where it is known to hybridize with *E. barbata*; it is the subject of further studies of species boundaries and relationships in section *Paradantha* (Fraga unpubl.).

The current study has identified two additional species that were previously confused with *E. montioides* and are newly described here. *Erythranthe carsonensis* was included among the original syntypes of *E. montioides*; it is described as a new species here because the lectotype chosen for *E. montioides* represents a species that is endemic to the Sierra Nevada in California. *Erythranthe calcicola* has been consistently identified as *E. montioides* despite the fact that it can be easily distinguished morphologically from all other taxa that have been previously treated as *E. montioides*.

Taxonomic overview of Erythranthe palmeri

Erythranthe palmeri was described in 1876 by Gray. In his treatment of *Mimulus* for the Synoptical Flora of North America, he included *E. androsacea* (Curran ex Greene) N.S. Fraga as a variety of *E. palmeri*, but this species is easily segregated from *E. palmeri* based on floral and vegetative characteristics. Most authors including Green (1885), Grant (1924), Pennell (1951), Munz (1968), and Thompson (1993 2012) have recognized *E. androsacea* as a distinct species.

In her monograph, Grant (1924) segregated two species from *E. palmeri*: *E. diffusa* and *E. purpurea*. *Erythranthe purpurea* has consistently been recognized in subsequent treatments because it is easily distinguished from *E. palmeri* by floral and vegetative characters. *Erythranthe diffusa,* however, is distinguished morphologically from *E. palmeri* by more cryptic features including differences in ciliation on the margin of the calyx and gynoecium vestiture. Although it was previously recognized by Pennell (1951) and Munz (1968, 1974), *E. diffusa* has been synonymized with *E. palmeri* in more recent treatments (Thompson 1993, 2012). Here I recognize *E. diffusa* as a distinct species based on morphological and molecular characters. In addition, three species (*E. hardhamiae*, *E. rhodopetra*, *E. sierrae*) were discovered while

reviewing *E. palmeri* herbarium specimens and conducting field work, and are described here for the first time.

TABLE 1.2. Comparison of morphological features for species previously treated as *Erythranthe montioides*.

A.	*E. barbata*	*E. calcicola*	*E. carsonensis*	*E. discolor*	*E. montioides*
Leaf shape	linear to oblanceolate	lanceolate to ovate	linear to spatulate	linear to oblanceolate	linear to oblanceolate
Leaf width (mm)	0.5-2	2-8	1-5	1-4	0.5-2
Total corolla length (mm)	13-20	6-13	11-18	15-20	10-17
Tube-throat length (mm)	(5) 8-12	5-10	(5) 8-11	8-15	6-11
Limb width (mm)	6-13	3-7 (9)	7-15	7-15	7-15
Calyx margins	glabrous	ciliate	glabrous	glabrous	Ciliate
Flower color	Bicolored (maroon+yellow) or yellow	White or yellow	yellow	Yellow or pink	Yellow

TABLE 1.3. Comparison of morphological features for species previously treated as *Erythranthe palmeri.*

B.	*E. diffusa*	*E. hardhamae*	*E. palmeri*	*E. rhodopetra*	*E. sierrae*
Leaf shape	linear-oblanceolate to ovate	linear to oblanceolate	linear to lanceolate	Linear-oblanceolate to elliptic	linear to oblanceolate
Leaf width (mm)	1-10	1-3	1-4	1-10	1-11
Total corolla length (mm)	11-20	9-17	15-25	12-26	12-22
Tube-throat length (mm)	8-14	5-10	10-29	9-17	8-17
Limb width (mm)	6-14	7-11	8-15	16-25 mm	5-17
Calyx margins	glabrous	glabrous	ciliate	glabrous	Ciliate
Flower color	pink to purple	deep pink to purple	pink to purple	light pink	light pink to pink

MATERIALS AND METHODS

Data from field, herbarium, and molecular studies based on analysis of nuclear ribosomal

ITS and three non-coding chloroplast regions (*petA-psbJ*, *psbD-trnT, rpl32-trnL*; Fraga unpubl.) support the species concepts proposed here. Field studies were initiated in 2007 and have been conducted at more than 75 populations. Herbarium specimen records, databases (CCH; SEINet; and CNDDB), and literature reports were used to identify target populations for field surveys, including type localities. Populations were selected in order to sample each species throughout its known range. Several populations were visited more than once to permit collection of mature fruits and seeds, as well as flowering specimens. At each field site, data recorded included exact location (via Global Positioning System), habitat characteristics (i.e., elevation, slope, aspect, microhabitat, vegetation association, associated species), distinguishing morphological characteristics, life history attributes (i.e., abundance of plants, presence of pollinators), and conservation status (i.e., existing or potential threats or disturbances). Photographs were taken of living plants with common objects (pencils and coins) for scale. Seeds and herbarium specimens were collected for later study. Conservation assessments are based on criteria outlined by the California Native Plant Society (CNPS) Inventory of Rare and Endangered Plants (2012), and Natureserve (2012). Line drawings presented in the treatment are based on photographs, herbarium material, and descriptions provided to the illustrator.

Vegetative and floral measurements provided in the descriptions are all inclusive ranges from study of fresh material in the field, dried and pressed material collected in the field, and herbarium specimens. Qualitative characters were described from photographs, observations made in the field, and herbarium specimens. Terms used to describe morphological characters follow Grant (1924) and Thompson (2005). The ”calyx teeth” are extensions of the costa beyond the margin of the usually plicate calyx. The transition between the corolla tube and throat is gradual, thus the term “tube-throat” is used for the whole of the tube.

More than 500 herbarium specimens were examined from eleven herbaria: CAS/DS, DEVA, GH, MO, POM, RENO, RSA, SBBG, SD, UC/JEPS, and UNLV. Morphological measurements were taken from dried and pressed specimens. Herbarium specimens were databased and georeferenced to create accurate distribution maps; maps were prepared in ArcGIS 10.1 (ESRI 2012). Elevation ranges provided in the taxonomic treatment are compiled from herbarium specimen label data, and field sites for all species. Associated species lists include dominant species that are diagnostic of the vegetation association, annual plant species sharing similar habitats, and non-native species that are indicators of disturbance.

Figure 1.1. Diversity in corolla limb color, morphology and size in species previously included in *Erythranthe montioides*.—1. *Erythranthe barbata* (bicolored and yellow morph).—2. *Erythranthe calcicola* (white and yellow morph).—3. *Erythranthe carsonensis*..—4. *Erythranthe discolor* (yellow and pink morph).—5. *Erythranthe montioides*.

KEY TO SPECIES

1. Corolla yellow or white

    2. Leaves linear to spatulate, corolla with one large central red spot on the lower limb…..*Erythranthe carsonensis*

    2. Leaves linear-oblanceolate to ovate, corolla without one large central red spot on the lower limb

3. Corolla yellow, tube-throat funnelform, and tinged red on adaxial surface of tube throat…..*Erythranthe discolor* (in part)

3. Corolla yellow, white, or bicolored with the upper lip maroon, and the lower lip yellow, tube-throat funnelform to cylindric, and not tinged red on adaxial surface of tube-throat

4. Corolla yellow or white, 6-13 mm long, herbage glandular pubescent, calyx costa prominent…..*Erythranthe calcicola*

4. Corolla yellow, 10-20 mm long, herbage glabrous to minutely puberulent, with eglandular trichomes, calyx costa weak

5. Corolla yellow, lobes entire, tube throat funnelform to cylindric, palate glabrous to sparsely bearded with trichomes…..*Erythranthe montioides*

5. Corolla yellow or bicolored, lobes bifid, tube-throat cylindric, palate bearded with trichomes…..*Erythranthe barbata* (in part)

1. Corolla pink, purple, or bicolored with the upper lip maroon, and the lower lip yellow.

6. Calyx lobe margins ciliate

7. Leaf margins entire, never toothed; Limb deep pink to purple; stamens yellow Tranvserve Ranges…..*Erythranthe palmeri*

7. Leaf margins entire, or sometimes toothed; limb pale pink to pink; stamens white; Sierra Nevada…*Erythranthe sierrae*

6. Calyx lobe margins glabrous

8. Pedicels erect to ascending, not spreading horizontally with age

9. Corolla deep pink to purple with two yellow ridges on the lower limb and palate, corolla width (pressed) 7-15 mm…..*Erythranthe discolor* (in part)

9. Corolla pale pink to rose colored with a broad yellow palate, corolla width (pressed) 16-25 mm…..*Erythranthe rhodopetra*

8. Pedicels ascending to spreading, often spreading horizontally with age

10. Flowers yellow or bicolored with the upper lip maroon, and the lower lip yellow…..*Erythranthe barbata* (in part)

10. Flowers pink with two yellow ridges on the lower limb

11. Style distally pubescent, stigma included…..*Erythranthe diffusa*

11. Style glabrous, stigma equal with the tube-throat to exserted…..*Erythranthe hardhamiae*

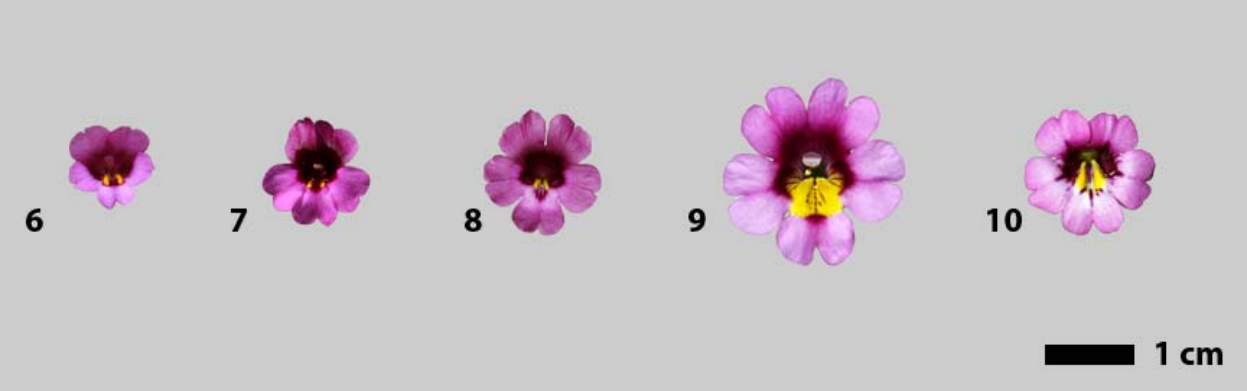

Figure 1.2. Diversity in corolla limb color, morphology and size in species previously included in *Erythranthe palmeri*.—6. *Erythranthe hardhamae*.—7. *Erythranthe diffusa*.—8. *Erythranthe palmeri*.—9. *Erythranthe rhodopetra*.—10. *Erythranthe sierrae*.

TAXONOMIC TREATMENT

ERYTHRANTHE BARBATA (Greene) N.S. Fraga "bearded monkeyflower" Phytoneuron 2012, ined.

Mimulus barbatus Greene, Bull. Calif. Acad. Sci. 1: 9. 1884.—TYPE: Location not provided on specimen label. (holotype, CAS digital image!; isotype: UC!)

Mimulus deflexus S. Watson. Proc. Amer. Acad. Arts 24: 84. 1889.—TYPE: U.S.A. California: Tulare Co., Long Meadow, June 1888, *Palmer 176* (holotype GH!; isotypes: MO!, NY digital image!, US digital image!).

Annual herb. Plants 2-15 cm tall × 0.5-7 cm wide; sparsely glandular pubescent. Stems erect, simple to branched, internodes 0.5-2 cm. Cotyledons persistent, oblanceolate to ovate, 1-6 mm long, with clasping bases. Leaves opposite, epetiolate; blades 5-19 mm long × 0.5-2 mm wide, linear to oblanceolate, palmately veined with three prominent veins from the base in wider leaves, margins entire. Flowers solitary in each axil, fruiting pedicels (5) 9-25 mm, exceeding calyx, erect to ascending, or spreading horizontally. Calyx 1-3 mm long × (2) 3-6 mm wide, campanulate, enlarging in fruit; the costa weak, darker than intercostal regions; calyx teeth equal, 0.5-1 mm long, acute and spreading, margins glabrous. Corolla12-20 mm long × 6-13 mm wide, bicolored, adaxial lip maroon-purple and abaxial lip yellow, or entirely yellow, lobes bifid, limb strongly zygomorphic; tube-throat (5) 8-12 mm long, cylindric, expanding abruptly to the limb, palate bearded, spotted with red markings. Stamens didynamous, 9-11 mm long; yellow, glabrous, included. Gynoecium 12-13 mm long, yellow; style glabrous; stigma lobes apically fringed, subequal, equal to corolla or slightly exserted from the orifice. Capsules 2-5 mm long, included to equal to calyx, cylindric, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.3-0.5 mm long × 0.2 mm wide, elliptic to ovoid, brown.

Representative specimens examined.—USA, California, Kern Co.: Trail to Little Cannell Meadow above Pine Flat, 7350 ft, 24 July 1964, *Twisselmann 9861a* (JEPS); Pine Flat, 7400 ft, 28 July 1965, *Twisselmann 11334* (JEPS, CAS); Bartolas Creek, near its summit, 6950 ft, 25 June 1966, *Twisselmann 12462* (CAS); Fay Creek at Little Cannell Meadow, 6400 ft, 26 June 1967, *Twisselmann 13396* (CAS, SD); Tulare Co.: SE end of Rode Flat, 7400 ft, 27 June 1967,

Twisselmann 13518 (CAS, JEPS, RSA, SBBG); Siberian Pass Creek, 11,000 ft, 25 July 1949, *Munz 14199* (RSA); W of South Fork Kern River, west of Kennedy Meadows, 6000 ft, 19 May 1986, *Ertter 6152* (RSA, UC); Big Meadow, 7800 ft, 26 June 1970, *Twisselmann 16879* (CAS, RSA); Chimney Creek, east of Chimney Creek Campground, 5800 ft, 30 May 1969, *Wheeler s.n.* (RSA); Kern Plateau, Dome Land, 8000 ft, 11 June 1972, *DeDecker 2924* (RSA); South Fork of Kern River at Tunnel Meadow, 9100 ft 25 July 1970, *Twisselmann et al. 16934* (JEPS, RSA); Long Meadow, 2200 m, 14 June 1904, *Hall & Babcock 5107* (CAS, POM, UC); Salmon Creek, Horse Meadow public campground, 7500 ft, 12 June 1960, *Wheeler 7704* (RSA); Head of Monache Meadow, South Fork of Kern River, 8050 ft, 14 July, 1950, *Munz 15021* (RSA); Cannell Meadow, 7000 ft, 15 June 1904, *Hall & Babcock* (UC); South Fork Kern River at Monache Meadow, 8000 ft, 12 August 1968, Twisselmann et al. 14779 (CAS, JEPS); Templeton Mountain near Kern Peak, 8700 ft, 5 July 1912, Jepson 4968 (JEPS); True Meadow, 6825 ft, 26 June 1967, *Twisselmann 13402* (JEPS); Poison Meadow, Kern Plateau, 7600 ft, 20 July 1962, *Twisselmann 7548* (CAS); 6 miles north of South Fork Kern River bridge on road to Troy Meadow, 7500 ft, 5 July 1967, *Howell & True 43146* (CAS) Cannell Meadows Southern Sierra Nevada Mountains, 7000 ft, 15 June 1904 *Hall & Babcock 5113a* (UC); Summit Meadow, Olancha Mountain, 9500 ft, 25 June 1904 *Hall& Babbcock 5278* (UC); Troy Meadows on upper Fish Creek, just off Sherman Pass Road, 20 June 1982, Sanders 2750 (UC); Lake on the ridge between Rattlesnake Meadow & Long Meadow, 7600 ft, 28 July, 1965, *Twisselmann 11316* (CAS); Horse Meadow, Kern Plateau, 7400 ft, July 1966, *Howell & True 41724* (CAS); Embree Mine jeep road, near the turn to the new road (S slope of Sherman Peak), 7300 ft, 2 August 1969, *Twisselmann 15903* (CAS, SD); Long Meadow, 7800 ft, 26 June 1970, *Twisselmann 16829* (CAS), Bakeoven Meadows, 8100 ft, 13 July 1950, 13 July 1950, *Howell 26801* (CAS); Ground

Hog Meadow, 8700 ft, 21 July 1942, *Ferris & Lorraine 10717*(DS); Fish Creek Campground, 9 miles NW of Kennedy Meadows, 7200 ft, 28 May 1973, *Keefe 13176* (CAS); Big Meadow to Manter Meadow, 7000ft, 3-6 July 1964, *Hardham 12096e* (CAS); Trout Creek, 7500 ft, 3-6 July 1964, *Hardham 12134a* (CAS); N end of Casa Vieja Meadows, 8300 ft, 30 June 1973, *Keefe 13-512* (CAS); Siberian Pass Creek, 11,000 ft, 25 July 1949, *Howell 25729* (CAS); Taylor Creek, S of Church Dome, 7200 ft, 1 October 1969, *Howell & True 46460* (CAS); 1.2 miles S of Troy Meadows, 7800 ft, 4 July 1967, *Howell & True 42982* (CAS); Lloyd's Meadow Basin: Lower Freeman Creek, 5500 ft, 14 May, 1971, *Shevock 240* (CAS); Fish Creek at the N end of Troy Meadow, 7600 ft, 30 July 1967, *Meng 457* (CAS, SBBG); 3 miles NE of Beach Meadow, 8200 ft, 7 August 1967, *Howell et al. 53789* (CAS); Cannell Meadow, 7200 ft, 28 August 1967, *Twisselmann 13619* (CAS); Paloma Meadows, 8500 ft, 16 July 1980, *Howell et al., 53864* (CAS); Inyo Co.: Horseshow Meadow, 10,000 ft, 14 August 1995, *DeDecker 6504* (RSA), Cottonwood Creek, 11,000 ft, 18 July 1949, *Munz 14046* (RSA); Cottonwood Lakes, 11,000 ft, 18 July 1949, *Munz 14057* (RSA); Manter Meadow, 7100 ft, 28 June, 1969, *DeDecker 2136* (RSA); Rock Creek near Mount Whitney, 9600 ft, 20 July 1912, *Jepson 5058* (JEPS).

Phenology and pollination biology.—Flowering occurs between May and August and fruiting between June and September. *Erythranthe barbata* has relatively large flowers, a narrow corolla tube that expands abruptly to the limb, and exhibits approach herkogamy. Presumably the beard of trichomes serve as an advertisement to pollinators. Based on evidence from corolla morphology, this species is presumed to be primarily outcrossing; but pollinators were not observed on this species over the course of this study.

Distribution and habitat.—*Erythranthe barbata* is endemic to the eastern Sierra Nevada in Kern, Tulare, and Inyo counties, California (Fig. 1.3). Plants primarily occur on decomposed granite at

the edges of meadows and streams but also occasionally in open sandy barrens and in the understory of lodgepole pine forest. *Erythranthe barbata* is associated with the following vegetation communities: pinyon-juniper woodland, montane coniferous forest, subalpine forest, riparian scrub, montane meadows, and alpine barrens. Elevation ranges from 1800-3400 m (5900-11,200 ft). Associated species include: *Abies concolor* (Gordon & Glend.) Hildebr., *Aquilegia formosa* Fisch. ex DC., *Achillea millefolium* L., *Artemisia douglasiana* Besser, *A. tridentata* Nutt., *Calocedrus decurrens* (Torr.) Florin, *Collinsia parviflora* Lindl., *Deschampsia danthonioides* (Trin.) Munro, *Erythranthe breweri* (Greene) G.L. Nesom & N.S. Fraga, *E. floribunda* (Douglas ex Lindl.) G.L.Nesom, *E. guttata* (Fisch, ex DC.) G.L.Nesom, *E. moschata* (Douglas ex Lindl.) G.L.Nesom, *E. primuloides* (Benth.) G.L.Nesom & N.S. Fraga, *Juncus* spp. L., *Perideridia parishii* (J.M. Coult. & Rose) A. Nelson & J.F. Macbr., *Phacelia exilis* (A. Gray) G.J. Lee, *Pinus balfouriana* Grev. & Balf., *P. contorta* Loudon subsp. *murrayana* (Grev. & Balf.) Critchf., *P. jeffreyi* Grev. & Balf., *P. monophylla* Torr. & Frém., *Polygonum polygaloides* Meisn. subsp. *kelloggii* (Greene) J.C. Hickman, *Quercus chrysolepis* Liebm., and *Q. wislizeni* A.DC.

Phylogenetic relationships and similar species.—*Erythranthe barbata* is inferred to share a close relationship with *E. discolor* (Fraga unpubl.). These species can be distinguished by corolla morphology and color throughout the majority of their range, but they are known to hybridize in the southern Sierra Nevada where they co-occur. *Erythranthe barbata* typically has bicolored flowers with a maroon-purple adaxial lip and a yellow abaxial lip, but occasionally plans have flowers that are entirely yellow. The frequency of yellow to bicolored plants can change from year to year. The corolla has a distinct cylindrical tube that is relatively narrow and expands abruptly to a bearded palate. In contrast, *E. discolor* has monochromatic flowers that are usually

yellow, less frequently pink, and the corolla tube-throat is funnelform and expanding gradually to a sparsely bearded to glabrous palate.

Etymology.—*Erythranthe barbata* is named for the beard of trichomes on the lower limb of the corolla.

Conservation concern.—*Erythranthe barbata* is not currently ranked by the California Native Plant Society (CNPS) as rare, threatened, or endangered. *Erythranthe barbata* is endemic to the southern Sierra Nevada in California and occurs in several high-use areas throughout its range. This species has been observed in areas that are subject to impacts from grazing, off-highway vehicle use, hiking trails, campgrounds, and road maintenance. It was considered by CNPS for ranking in 2006, but was rejected because it was too common (CNPS 2012). However, the conservation status of this species should be reevaluated in light of the current taxonomic revision. At the time of its evaluation by CNPS, populations that are currently identified as *E. discolor* and *E. montioides* may have been included within the distribution of *E. barbata*.

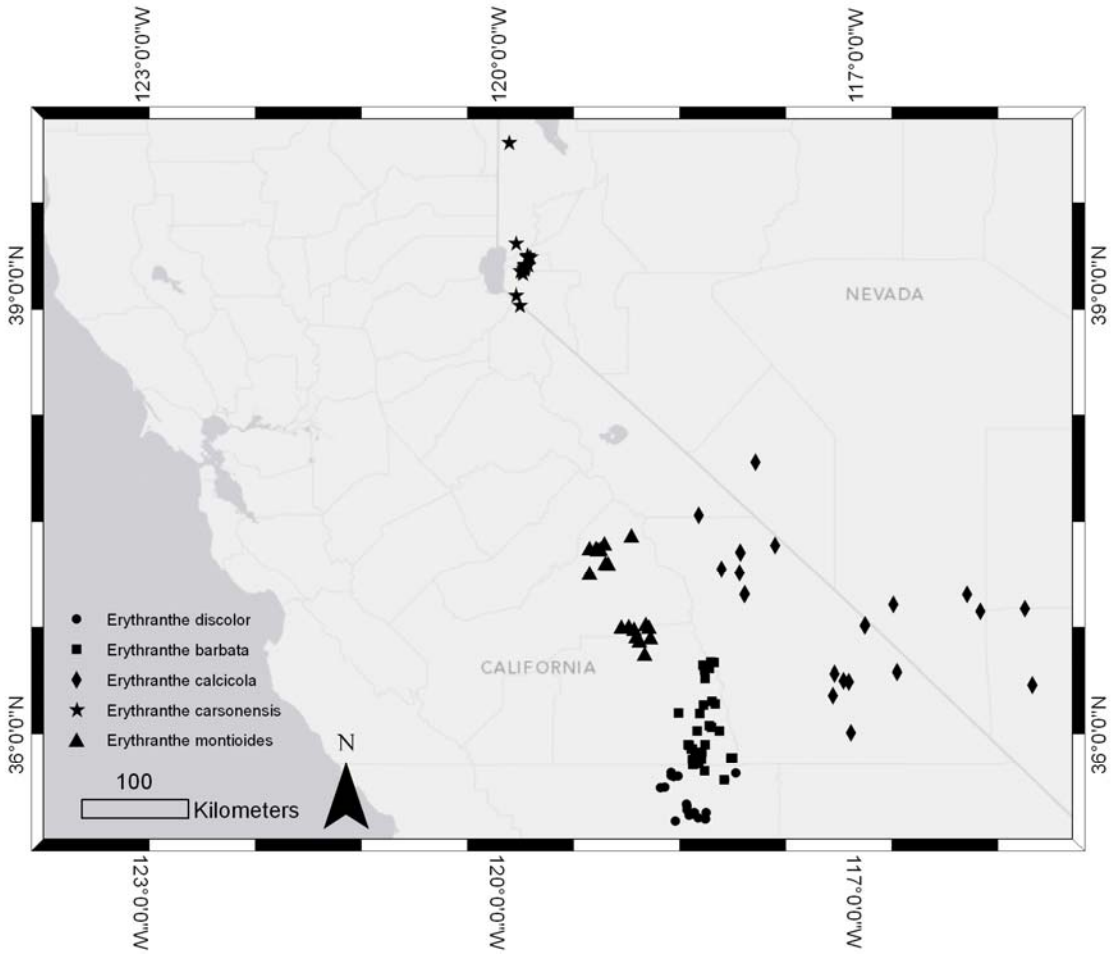

Figure 1.3. Distribution of species previously treated as *Erythranthe montioides*.

Erythranthe calcicola N.S. Fraga & D.A. York. "limestone monkeyflower".—TYPE: U.S.A, California, Inyo Co.: Death Valley National Park, Panamint Mountains, along a saddle 420 m NE of Aguereberry Point, 36°21'34"N, 117°02'35"W (NAD 83), 1780 m/5850 ft, 9 April 2004, *York & Schoenig 2849* (holotype:RSA!; isotypes: CAS!, US!).

Annual herb. Plants 2-15 cm tall × 1-8 cm wide; sparsely glandular pubescent. Stems erect, simple to branched, turning reddish with age; internodes 0.5-1.5 cm. Cotyledons persistent, ovate to round, 1-6 mm long, with clasping bases. Leaves opposite, epetiolate or with petioles short (0.5-1 mm long), connate at the base; blades 3-25 mm long × 2-8 (10) mm wide, lanceolate to ovate, palmatlely veined with three prominent veins from the base in wider leaves, margins

entire or sometimes toothed. Flowers solitary in each axil, fruiting pedicels 3-20 mm, exceeding calyx, erect to ascending. Calyx 4-8 mm long × 2-4 (5) mm wide, widely campanulate to cylindric, enlarging in fruit; costa prominent, darker than intercostal regions; calyx teeth equal, 0.5-1 mm long, acute to obtuse, margins ciliate. Corolla 6-13 mm long × 3-7 (9) mm wide, yellow or white with a yellow throat, early deciduous, lobes emarginate, limb weakly zygomorphic; tube-throat 5-10 mm long, cylindric, expanding gradually to the limb, palate sparsely bearded, spotted with red markings. Stamens didynamous, 3-9 mm long; yellow, glabrous, included. Gynoecium 5-10 mm long, light yellow to white; style glabrous; stigma lobes slightly apically fringed, subequal, included. Capsules 4-8 mm long, included to equal to calyx, cylindric, thin walled and fragile, dehiscing to base along both sutures. Seeds 0.5-0.9 mm long × 0.2-0.3 mm wide, elliptic to ovoid, brown.

Additional specimens examined.—USA. California, Inyo Co.: Death Valley National Park, Panamint Mountains, Panamint Mountains, ridge just E & below Aguereberry Point, 1780 m/5830 ft, 18 April 2001, *York et al. 2536* (DEVA); Death Valley National Monument, Panamint Mountains, Emigrant Canyon 2 miles E of Burro Spring on the Gold King mining claim, 1463 m 11 April 1978, *Holland & Schramm 1801* (UCR, UNLV); Death Valley National Monument, Panamint Mountains, Arrastra Spring, 5200 ft, 17 May 1978 (UNLV);Death Valley National Monument, Panamint Mountains, Wildrose Canyon, 4290 ft, 29 April 1973, *Fisher 1643* (UNLV); Death Valley National Monument, Funeral Mountains, Keane Canyon, 3800 ft, 30 April 1937, *Gilman 2317* (DEVA, RSA); Death Valley National Monument, Funeral Mountains, Keane Spring Canyon, 3000 ft, 30 April 1937, *Gilman 2318* (RSA);Death Valley National Monument, Funeral Mountains, near Kean Spring, 3700 ft 24 April 1978, *DeDecker 4600* (RSA);Death Valley National Monument, Funeral Mountains, Canyon NE of Red

Amphitheatre, 3750 ft, 7 May 1983, *Annable et al. 716* (UNLV); Saline Valley, 4700 ft 8 April 1967, *DeDecker 1671* (RSA); Saline Valley, 4900 ft 8 April, 1967, *Munz 18017* (RSA); Inyo Mountains, Marble Canyon, 5500 ft, 5 May 1962, *Raven 17550* (RSA); Inyo Mountains, "Teufel Canon", 5000 ft, 30 May 1939, *Jaeger s.n.* (RSA); Waucoba Road, 22.4 mi E of junction with Westgard Road, toward Eureka Valley, 5650 ft, 22 May 1976, *Davidson 3999* (RSA);Last Chance Range, west of Last Chance Spring, 6200 ft, 24 May 1978, *DeDecker 4688-a* (RSA); Death Valley National Park, N end of Saline Valley Road, ca. 14 miles south of Death Valley Road, 5600 ft, 8 April 2008, *Fraga et al.1995* (RSA); Death Valley National Park. Gold King Mining claim, off Wildrose Road, ca. 6 mi south of Hwy 190, 4900 ft, 17 April 2010, *Fraga et al. 3306* (RSA); Death Valley National Park. Ridge NE of Aguereberry Point, 5600 ft, 17 April 2010, *Fraga et al. 3308* (RSA); Death Valley National Park. SE slope above Wildrose Canyon. 4,400 ft, 24 April 2010, *Fraga & Prince 3310* (RSA); Death Valley National Park, gentle slope N of road to Aguereberry Point, ca. 2.6 mi E of Wildrose Road, 5200 ft, 24 April 2010, *Fraga & Prince 3315* (RSA). Death Valley Road, ca. 22 mi E of Hwy 168. N side of the road on slope. 5800 ft, 9 May 2011, *Fraga 3347* (RSA); Death Valley National Park: Marble Canyon off of Saline Valley Waucoba Road, 5900 ft, 9 May 2010, *Fraga 3348* (RSA); Mono Co: White Mountains, 1 mile up Coldwater Canyon in side drainage, 5450 ft, 15 April 1986, *Morefield & McCarty 3419* (RSA); —Nevada, Clark Co.:, Spring Mountains, ridge NE of Grassy Spring, 5,200 ft 14 May 1983, *Peterson & Lathrop 960* (UNLV); Spring Mountains, slopes west of Grassy Spring, 5500 ft 15 May 1983, *Peterson & Lathrop 965* (UNLV); Pintwater Range, E of Tim Spring 5800-6100 ft 5 May 1979, *Ackerman 30434* (UNLV, RENO); Nye Co.: Bajada west of Ranger Mountains on old Indian Spring Road. 24 April 1978, *Cochrane & Holland 991* (UNLV); Bare Mountains, south slope of Meiklejohn Peak, above Secret Pass, 5200 ft9 June

1995, *Niles et al. 4493* (UNLV); Nevada Test Site, along Mercury Highway, 20 miles N of Mercury on old road to Indian Springs, 3200 ft 24 April 1978, *Holland & Cochrane 1910* (UNLV); N and west end of Spotted Range, 4000 ft, 24 April 1969, Beatley 8033 (RSA, RENO); Esmeralda Co.: Silver Peak Range, 1.3 road miles west of Cave Springs on the Coyote Road from Silver Peak to Fish Lake Valley, 7200 ft, 25 June 1987, *Tiehm 11335* (RSA)

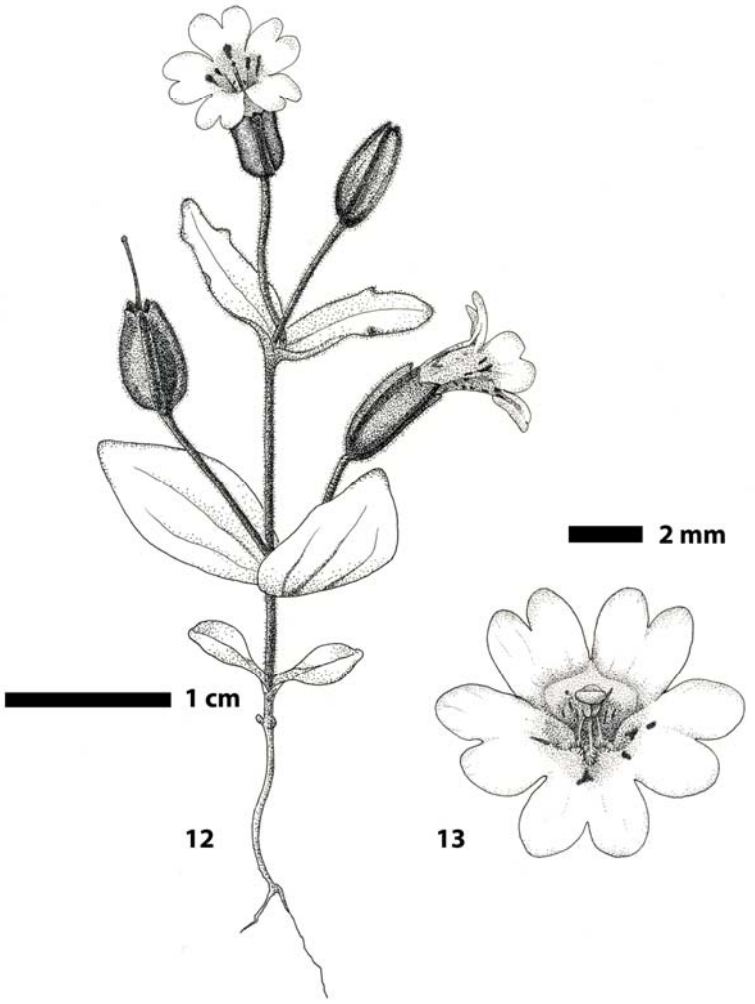

Figure 1.4. *Erythranthe calciola* N.S. Fraga & D.A. York.—12. Habit—13. Face view of corolla. Illustration by Michelle Thompson.

Phenology and pollination biology.—Flowering occurs between April and June; fruiting plants most commonly seen in May and June. *Erythranthe calcicola* has relatively small flowers that are early deciduous. Corollas were observed falling by mid-day and are presumed to be one-day flowers. Flowers of this species exhibit approach herkogamy but the distance between the stigma and anthers is sometimes less than 1mm, suggesting that this species has a mixed mating system with a mechanism to facilitate self-pollination with some frequency. No floral visitors were observed over the course of this study.

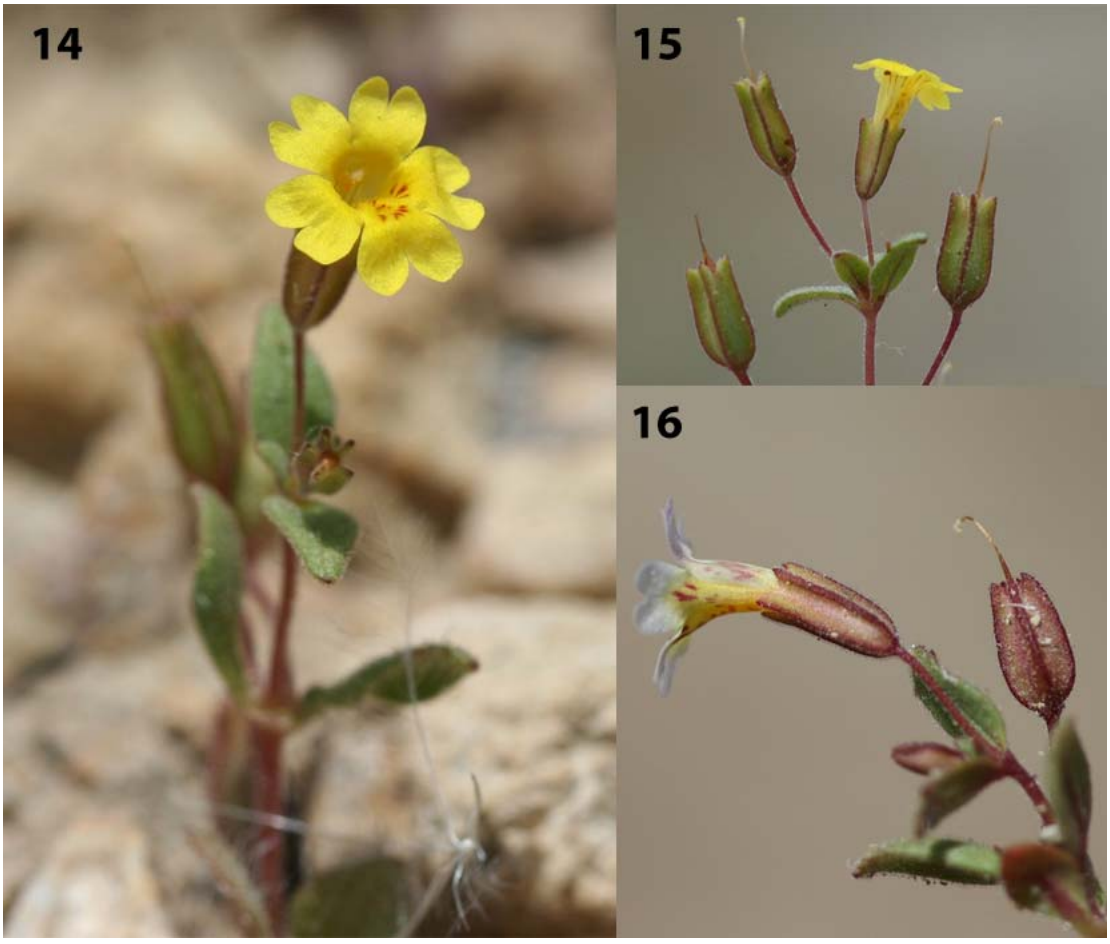

Figure 1.5. *Erythranthe calcicola*.—14. Habit.—15. Corolla and calyx with maturing fruit.—16. Lateral view of corolla and reddish calyx with maturing fruit.

Distribution and habitat.—*Erythranthe calcicola* (Fig. 4–5) is known from several mountain ranges in the northern Mojave Desert of eastern California and southwestern Nevada (Fig. 1.3): as follows. California: Funeral Mountains, Inyo Mountains, Last Chance Range, Panamint Mountains, White Mountains; Nevada: Bare Mountain, Pintwater Range, Sheep Range, Silver Peak Range, Spotted Range, Spring Mountains. Plants of this species primarily occur on talus slopes on substrates derived from carbonate rock and are associated with the following vegetation communities: creosote bush scrub, Joshua tree woodland, and juniper woodland. Elevation ranges from 915-2165 m (3000-7100 ft). Associated species include: *Antirrhinum kingii* S. Watson, *Ambrosia dumosa* (A. Gray) W.W. Payne, *Artemisia tridentata*, *Atriplex confertifolia* (Torr. & Frém.) S. Watson, *Chylismiella pterosperma* (S. Watson) W.L. Wagner & Hoch, *Coleogyne ramosissima* Torr., *Diplacus bigelovii* (A.Gray) G.L.Nesom & N.S. Fraga, *Ephedra nevadensis* S. Watson, *Ephedra viridis* Coville, *Eriogonum fasciculatum* Benth., *Ericameria linearifolia* (DC.) Urbatsch & Wussow, *Grayia spinosa* (Hook.) Moq., *Juniperus osteosperma* (Torr.) Little, *Krascheninnikovia lanata* (Pursh) A. Meeuse & A. Smit, *Larrea tridentata* (Sessé & Moc. ex DC.) Coville, *Linanthus filiformis* (A. Gray) J.M. Porter & L.A. Johnson, *Nama demissum* A. Gray, *Phacelia fremontii* Torr., *Pinus monophylla* Torr. & Frém., *Sphaeralcea ambigua* A. Gray, *Stipa speciosa* Trin. & Rupr., *Xylorhiza tortifolia* (Torr. & A. Gray) Greene, and *Yucca brevifolia* Engelm.

Phylogenetic relationships and similar species.—*Erythranthe calcicola* is morphologically similar to *E. rubella* (A.Gray) N.S. Fraga and is inferred to share a close relationship with this species (Fraga unpubl.). These species are easily distinguished by leaf shape and calyx morphology. The leaves of *E. calcicola* are lanceolate to ovate and the calyx is widely

campanulate to cylindric with margins ciliate. In comparison the leaves of *E. rubella* are linear to elliptic and the calyx is narrowly cylindric with glabrous margins.

Etymology.—The specific epithet and common name were chosen because *E. calcicola* appears to occur nearly exclusively on substrates of carbonate (limestone) origin.

Conservation concern.—All known occurrences for *E. calcicola* are on public lands administered by public agencies: Bureau of Land Management, Department of Defense, National Park Service, or the US Fish and Wildlife Service. *Erythranthe calcicola* is known from fewer than 20 occurrences and is therefore of limited distribution and should be considered for conservation status by the federal, state, and other agencies that manage this species. Historic mining operations and the presence of exotic plants species were the only visible disturbances observed over the course of field surveys conducted by this study.

Erythranthe carsonensis N.S. Fraga, "Carson Valley monkeyflower".—TYPE: U.S.A, Nevada, Carson City: Carson Valley, Eastern terminus of Clear Creek Road at the base of Prison Hill, 39° 7' 43.54"N, 119° 44' 19.23" W (NAD 83), 1460 m/4800 ft, 17 May 2010, *Fraga, Morefield, & Howle 3377* (holotype:RSA!; isotypes: US!, UC!).

Mimulus rubellus var. *latiflorus* S. Watson, United States Geological Exploration of the Fortieth Parallel. Vol. 5, Botany 226. 1871.—TYPE: U.S.A., Nevada, Carson City Co., Carson City, April 1868, *Watson 798* (GH!)

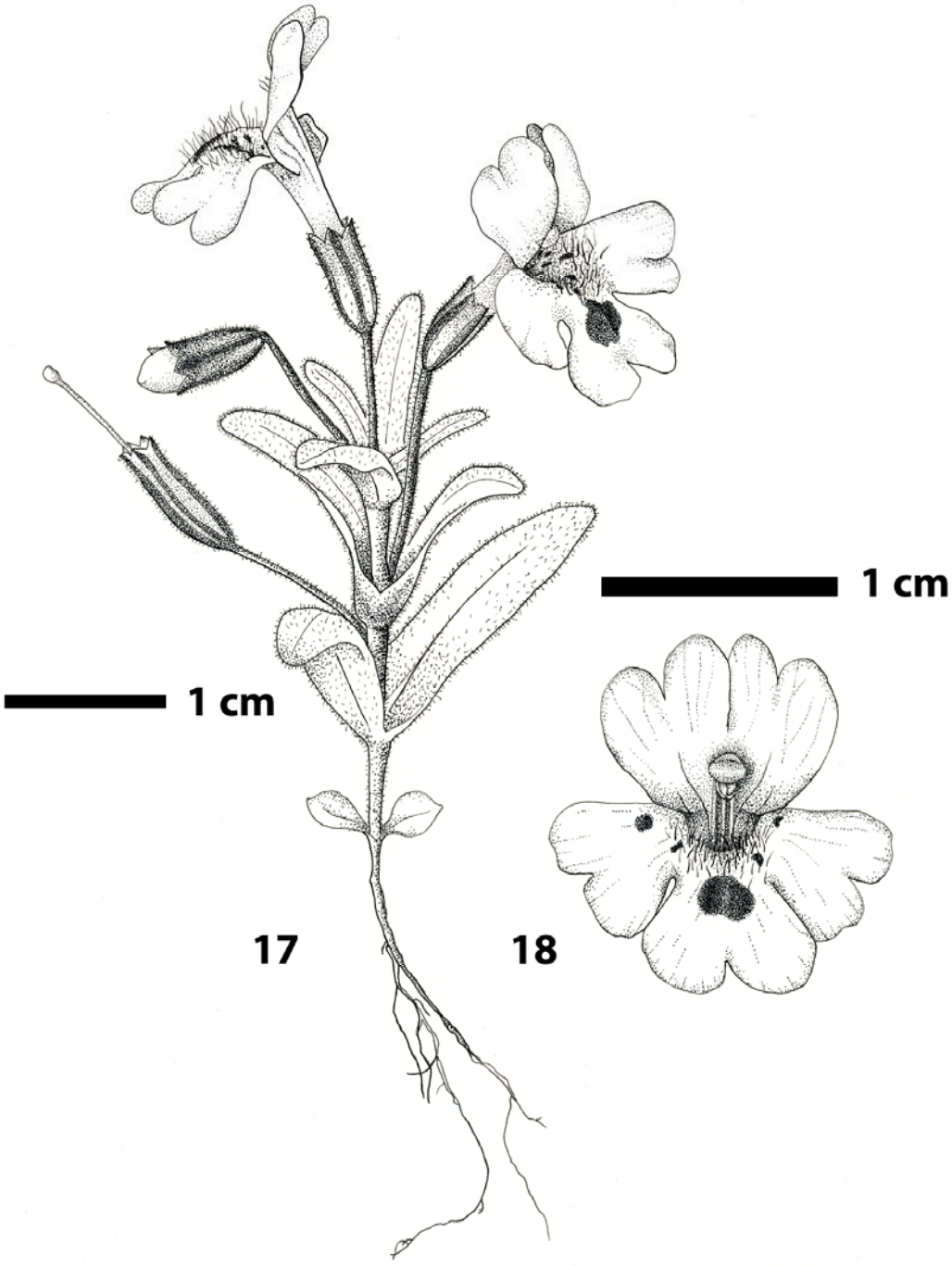

Figure 1.6. *Erythranthe carsonensis* N.S. Fraga.—17. Habit.—18. Face view of corolla. Illustration by Michelle Thompson.

Annual herb. Plants 1-7 cm tall × 1-4.5 cm wide; sparsely glandular. Stems erect, simple to branched, internodes (0.2-1), usually obscuring the stem. Cotyledons persistent, 0.2-1.2 mm long, round to reniform, with clasping bases. Leaves opposite, epetiolate, connate at the base; blades 3-17 mm long ×1-5 mm wide, linear to spatulate, palmately veined with three prominent veins from the base in wider leaves, margins entire. Flowers solitary in each leaf axil, fruiting pedicels 3-14 mm, exceeding calyx, ascending to erect. Calyx (3)5-7 mm long × 2-3(4) mm wide, campanulate to widely urn shaped, enlarging in fruit, costa prominent with sparse pubescence, and darker than the glabrous intercostal regions; calyx teeth equal, 0.5-1 mm long, acute and slightly recurved, margins glabrous. Corolla 11-18 mm long × 7-15 mm wide, yellow with red striations on the adaxial surface of the upper lobes, lobe bifid, strongly zygomorphic; tube-throat (5) 8-11 mm long, cylindric, expanding abruptly to the limb, palate bearded, and maculate with red markings and one large central spot. Stamens didynamous, 5-13 cm long; white to light yellow, glabrous, included. Gynoecium 6-15 cm long, yellow; style glabrous; stigma lobes apically fringed and subequal, equal with the throat to exserted from the orifice. Capsules 3-6 mm long, included in the calyx, campanulate, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.5-0.8 mm long × 0.1-0.2 mm wide, elliptic, brown.

Additional specimens examined.—USA. Nevada: Carson City: Eagle Valley: 0.5 mile south of Carson Hot Springs, 0.5 mile ENE of Lone Mountain summit, 4690 ft, 12 May 1991, *Morefield 5452* (RSA); Empire City, *Jones s.n.* (POM); Eagle Valley, 4743 ft, 7 June 1902, *Baker 1023* (POM); Eagle Valley, 4743 ft, 7 June 1902, *Baker 1029* (RSA); Topsy Lane south of Clear Creek. T14N R20E S.6, 4800 ft, 15 May 1979, *Genz 9097* (RENO); Corner of Topsy Lane and Hwy 395, on the north side of the road, 4800 ft, 15 May 2009, *Fraga & Morefield 2743* (RSA); Corner of Lynnette Ave and Arthur Dr., NE corner across from Nevada DOT building, 4800 ft,

16 May 2010, *Fraga 3370* (RSA); Corner of Old Hot Springs Road and Goni Road, 4700 ft, 16 May 2010, *Fraga 3371* (RSA); Douglas County: Near Trailhead parking for Faye-Luther Trail, 4850 ft, 15 May 2009, *Fraga 2744* (RSA); 5 miles south of Genoa, 27 April 1950, *Woodbury 23* (RENO); 3 miles south of Carson City, 4600 ft, 11 April 1941, *Solari 19* (RENO); On Gardenville Hwy, SW of Carson Indian Agency, 4700 ft, 24 April 1937, *Archer 5047* (RENO); Indian Hill, 3 miles south of Carson City near the Jacks Valley Road, April 13, 1976, 4850 ft, 13 April 1976, *Wise 4850* (RENO); Jacks Valley Management Area near Plymouth Drive turn off from Hwy 395, 4800 ft, 16 May 2010, *Fraga 3366* (RSA); Jacks Valley Management Area near Plymouth Drive turn off from Hwy 395, 4800 ft, 16 May 2010, *Fraga 3367* (RSA); James Lee Memorial Park near baseball field, USFS property, 4800 ft, 16 May 2010, *Fraga 3369* (RSA); Jacks Valley Management Area: W of elementary school and south of Jacks Valley Road, 5000 ft, 17 May 2010, *Fraga et al. 3372* (RSA); North side of Jacks Valley Road near Jacks Valley Management Area, 5100 ft, 17 May 2010; Fraga 3374; Washoe County: Franktown, 11May 1925, *P.A.L. s.n.* (RENO); Red Rock Canyon, T21N E 18E, 4800 ft, 30 April 1960, *Urrutia s.n.* (RENO); — California, Alpine County: near Fredericksburg, 23 May 2011, *Fraga & Matson 3803* (RSA).

Phenology and pollination biology.—Flowering occurs between late April and June and fruiting is most common in May and June. *Erythranthe carsonensis* has relatively large flowers, a long and distinct corolla tube that expands abruptly to the limb, which is bearded with trichomes. This species also exhibits approach herkogamy and has prominent nectar guide patterns on the palate. Based on evidence from corolla morphology, this species is presumed to be primarily outcrossing. Several insects were observed visiting this species, including skipper butterflies (Hesperiidae), and halictid bees (Halictidae).

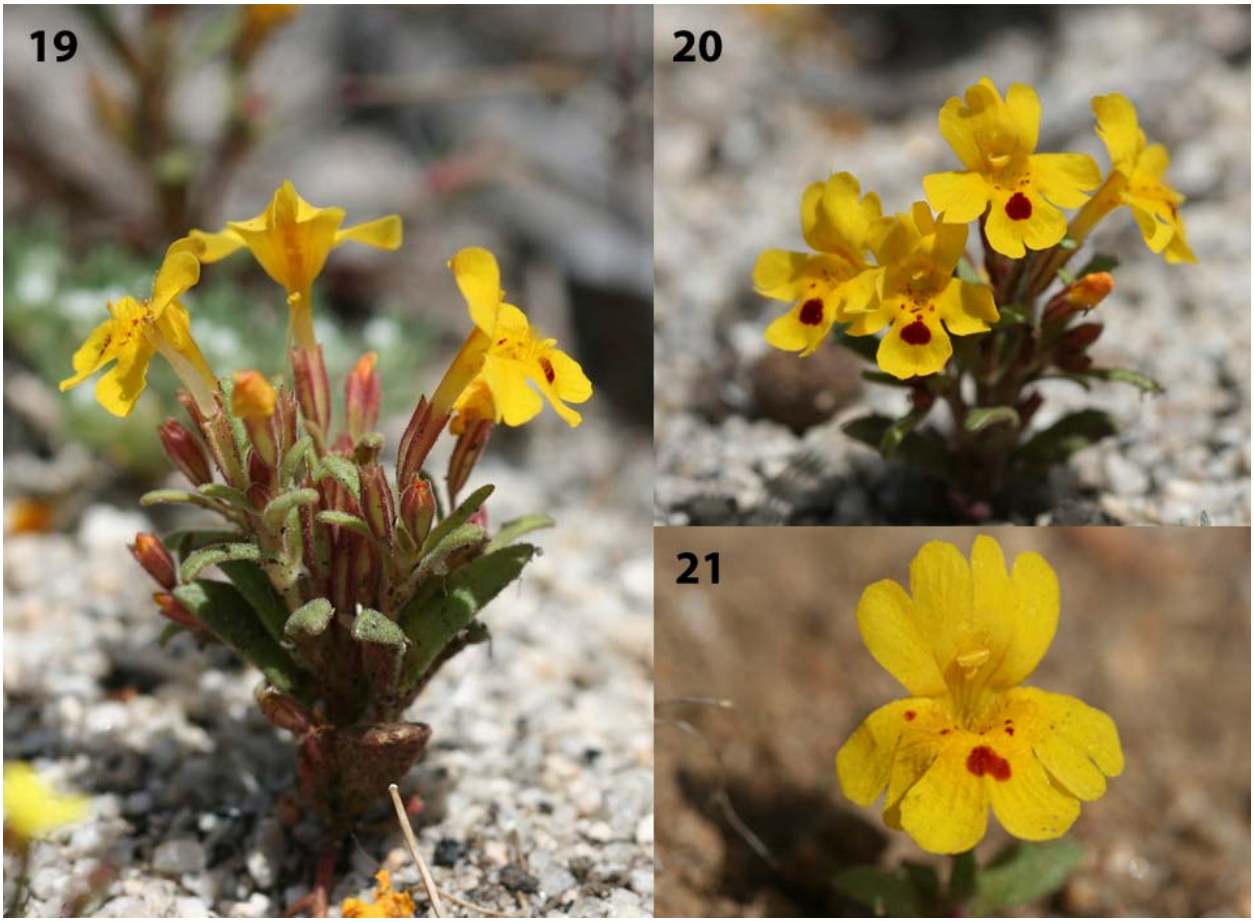

Figure 1.7. *Erythranthe carsonsensis*.—19. Plant habit with corolla lateral and abaxial view. —20. Plant habit with corolla face view.—21. Close up of corolla.

Distribution and habitat.—*Erythranthe carsonensis* (Fig. 1.7–1.8) is endemic to northwestern Nevada in Carson City, Douglas, and Washoe counties, and adjacent Alpine County in California (Fig. 1.3). There are ten known extant occurrences across its range; surveys of potential habitat may reveal additional occurrences. The majority of the known occurrences are located in Carson Valley region, with one disjunct occurrence documented in Red Rock Canyon approximately 36 miles to the north. This species occurs in open areas of Great Basin sagebrush/bitterbrush scrub in course granite soils on gentle to moderate slopes (0-15 percent), usually on north aspects but also occasionally on south-southwest aspects. Elevation ranges from 1400-1580 m (4600-5200 ft). Associated species include the following (* denotes non-native species): *Artemisia tridentata*

Nutt., **Bromus tectorum* L., *Calyptridium roseum* S. Wwatson, *Camissonia parvula* (Nutt. ex Torr. & A.Gray) P.H.Raven, *Cryptantha circumscissa* I.M.Johnst., *Chrysothamnus viscidiflorus* Nutt., *Descurainia pinnata* (Walter) Britton, *Diplacus nanus* (Hook. & Arn.) G.L.Nesom & N.S. Fraga, *Draba verna* L., *Ephedra viridis*, **Erodium cicutarium* (L.) L'Hér., *Erythranthe suksdorfii*, *Grayia spinosa*, *Gymnosteris nudicaulis* (Hook. & Arn.) Greene, *Layia glandulosa* Hook. & Arn., *Plectritis* (Lindl.) DC. sp., *Phacelia curvipes* Torr. ex S. Watson, *Phacelia linearis* (Pursh) Holz., *Plagiobothrys* sp. Fisch. & C.A. Mey., *Prunus andersonii* A. Gray, *Purshia tridentata* (Pursh) DC., **Sisymbrium altissimum* L., *Uropappus lindleyi* (DC.) Nutt., *Vulpia octoflora* (Walter) Rydb., *V. microstachys* (Nutt.) Munro, and *Zigadenus paniculatus* (Nutt.) S. Watson.

Phylogenetic relationships and similar species.—*Erythranthe carsonensis* is inferred to have a sister relationship with *E. suksdorfii* (Fraga unpubl.). These species are easily distinguished by corolla morphology and leaf shape. *Erythranthe carsonensis* has a longer corolla tube throat (8-11 mm) than *E. suksdorfii* (4-6 mm) and the corolla lobes are bifid. In contrast the lobes of *E. suksdorfii* are weakly notched to entire. The leaves of *E. carsonensis* are linear to spatulate and are clasping at the base, while the leaves of *E. suksdorfii* are linear to lanceolate or ovate and are not clasping at the base.

Etymology.—The specific epithet and common name allude to the Carson Valley region of Nevada, where this species primarily occurs.

Conservation concern.—Threats to *Erythranthe carsonensis* include loss of habitat due to development and agriculture, the presence and abundance of non-native species, and recreation. Evidence from herbarium specimen label data, literature, and personal observations indicate that development in the region has severely fragmented and reduced populations. Sereno Watson noted (1871) that this species formed “bright patches of color among the sage-brush in the lower

valleys." In 2010 a population that was observed to be marginal with less than 100 individuals was noted as "common" in 1979 (RENO 057126). Attempts to relocate historic occurrences from herbarium specimen records found several populations are now extirpated. Road maintenance, the presence and abundance of exotic plant species, the presence of off-highway vehicle trails, and a baseball park have been noted as sources of disturbance at extant occurrences. Because *E. caronensis* has a limited distribution, is known from few occurrences, and has several threats documented throughout its range, it is recommended that the species conservation status of this species be evaluated with Federal, State, and local agencies, and conservation organizations.

ERYTHRANTHE DIFFUSA (A.L. Grant) N.S. Fraga "Palomar monkeyflower" Phytoneuron 2012,

ined. *Mimulus diffusus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 257--258 1924 [1925].—TYPE: U.S.A., California, San Diego Co. Palomar, 29 May 1901, *Jepson & Hall 1959* (holotype: MO!; isotypes: DS!, JEPS, NY digital image!, UC!, US digital image!)

Mimulus grantianus Eastw., Proc. Calif. Acad. Sci. (ser. 4), 20: 153. 1931.—TYPE: U.S.A., California, San Diego Co., Campo, 23 April 1920, *Eastwood 9442* (holotype: CAS digital image!)

Annual herb. Plants 3.5-25 cm tall × 1-19 cm wide; minutely puberulent. Stems erect, simple to branched, internodes 1-4 cm. Cotyledons persistent, obovate to round, 0.2-1 mm long, with clasping bases. Leaves opposite, epetiolate or with petioles short (0.5-1); blades 2-18 mm long × 1-10 mm wide, linear-oblanceolate to ovate, palmately veined with three prominent veins from the base in wider leaves, margins entire or sometimes toothed. Flowers solitary in each axil, fruiting pedicels (2) 12-60 (-68) mm, exceeding calyx, erect to ascending, or spreading

horizontally. Calyx 4-7 mm long × (2) 3-6 mm wide, campanulate, enlarging in fruit; sometimes spotted red, costa weak, darker than intercostal regions; calyx teeth equal, 0.5-1 mm long, acute and spreading, with margins glabrous. Corolla 11-20 mm long × 6-14 mm wide, pink to purple, lobes emarginate, weakly zygomorphic; tube-throat 8-14 mm long, funnelform, expanding gradually to the limb, palate sparsely bearded with two yellow ridges. Stamens didynamous, 5-11 mm long; white, glabrous, included. Gynoecium 8-12 mm long, white to pink; style pubescent in the distal half; stigma lobes apically fringed, equal, included in the corolla. Capsules 3-6mm long, included in the calyx, campanulate, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.3-0.6 mm long × 0.1-0.2 mm wide, elliptic to ovoid, brown.

Representative specimens examined.—USA. California, Riverside Co: N slope of Agua Tibia Mtn., E of the Dripping Springs Alcove Area, 1640 ft, 3 May 1995, *Banks & Boyd 0200* (RSA); Shipley multi species reserve, SW of Tucalota Creek, 1601 ft, 28 Apr 1995, *Bramlet 2397* (RSA); San Mateo County Wilderness area, San Mateo Canyon 1200 ft, 12 May 1993, *Ross 7349* (RSA); Santa Ana Mountains, SE and E side of Elsinore Peak, 3300 ft, 7 May 1991, *Boyd 6158* (RSA); lower flank of range along the Bedford Truck trail on ridge between Bedford and McBribe Canyons, 2800 ft, 10 May 1991, *Boyd 6207* (RSA); along Thomas Mtn. Rd. West of Hwy 74 and south of Lake Hemet, 10 June 1980, *Busenberg 1988* (RSA); San Jacinto Mountains above Pine Cove, 6800 ft, 6 June 1949, *Cooper 2002b* (RSA); Upper San Juan Canyon, along San Juan Loop Trail, 1706 ft, 26 April 2003, *Roberts 5661* (RSA); San Jacinto Valley, Santa Rosa Hills, Simpson Park, 2460 ft, 13 April 2008, Wall 445 (RSA); San Diego Co: west face of Poser Mountain ca. 1/4 miles north of the intersection of Conejos Truck Trail and Viejas Grande Road, 2 April 1995, *Hirshberg 260* (RSA); Tecate Mountain, 3608 ft, 26 April 1969, *Moran 15835* (RSA, UC); north of Hauser Mountain: southwest of Morena Lake and northwest of

Cameron Corners, 1837 ft, *Rebman et al. 8930* (RSA); east side of El Prado Meadow at Laguna Camp, 5500 ft, 23 May 2010, *Fraga & Brock 3389* (RSA); MEX, Baja California: 5 km W of La Rumorosa, Sierra Juarez, 14 April 1979, *Moran s.n*. (RSA); East of main summit Sierra Blanca, 1175 m, 16 May 1976, *Moran 23241* (RSA); 9 miles SE of Tecate,12 May 1925, *Munz 9497* (RSA, UC); Sierra de Juarez, Laguna Hanson, Constitucion National Park, 1625 m, 28 May 1983, *Thorne et al. 55769* (UC).

Phenology and pollination biology.—Flowering occurs from late April to June and fruiting is most common in June and July. *Erythranthe diffusa* has relatively large flowers with distinctive yellow nectar guides and approach herkogamy. Based on evidence from corolla morphology, this species is presumed to be primarily outcrossing, but no insect visitors were observed over the course of this study.

Distribution and habitat.—*Erythranthe diffusa* is endemic to the Peninsular Ranges in southern California, USA, and Baja California, Mexico (Fig. 1.8). This species occurs in moist areas in openings of chaparral, dry meadows in pine and oak woodlands, grassland savanna, and riparian scrub. Elevation ranges from 300-2100 m (980-6800 ft). Associated species include: *Artemisia californica* Less., *Adenostoma fasciculatum* Hook. & Arn., *Ceanothus crassifolius* Torr., *Chaenactis glabriuscula* DC., *Collinsia concolor*Greene, *C. parviflora*, *Eriodictyon crassifolium* Benth., *Lasthenia californica* DC. ex Lindl., *Melica imperfecta* Trin., *Plantago erecta* E. Morris, *Platanus racemosa* Nutt., *Plagiobothrys tenellus* (Nutt.) A. Gray, *Populus fremontii* S. Watson, *Quercus agrifolia* Née, *Q. engelmannii* Greene, *Salvia apiana* Jeps., S. *mellifera* Greene, and *Zigadenus fremontii* (Torr.) Torr. ex S. Watson.

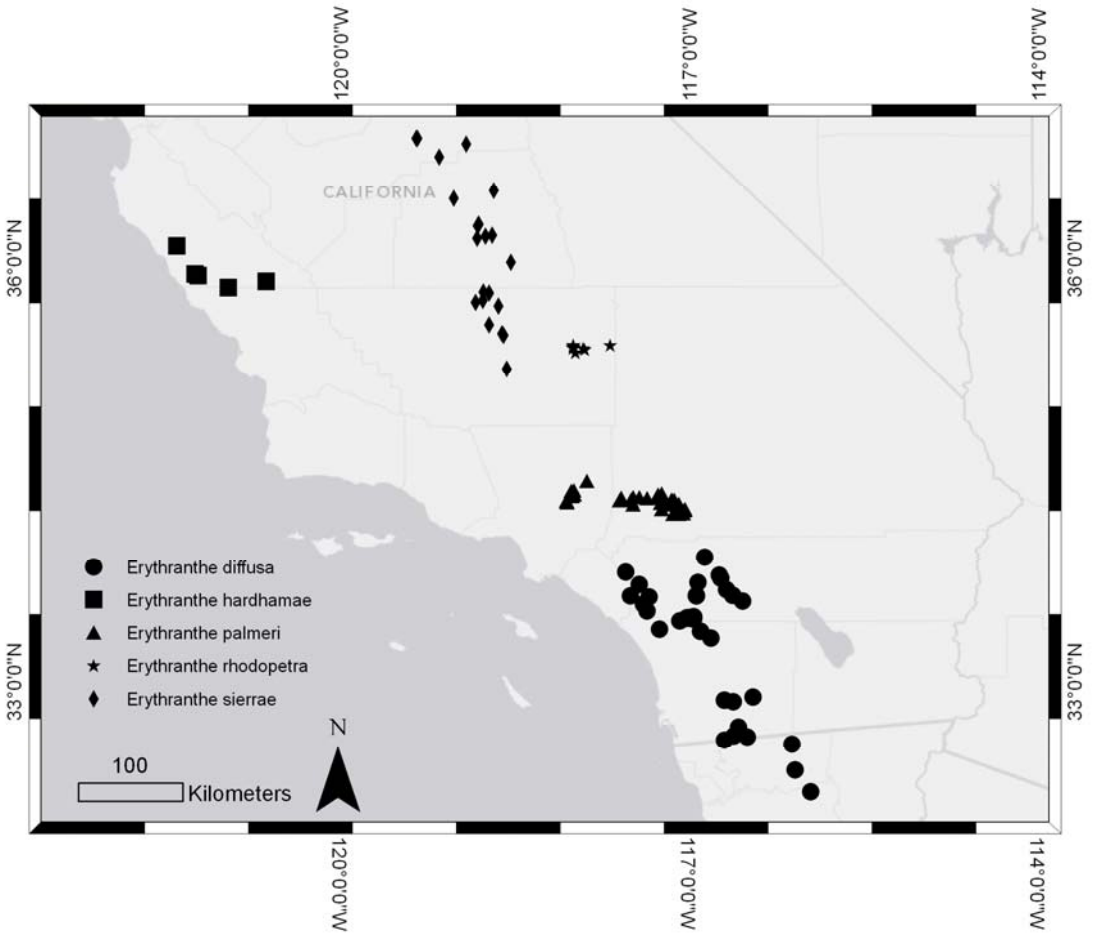

Figure 1.8. Distribution of species previously treated as *Erythranthe palmeri*

Phylogenetic relationships and similar species.—*Erythranthe diffusa* is inferred to have a close relationship with *E. purpurea* (Fraga unpubl), but *Erythranthe diffusa* is easily distinguished from *E. purpurea*. *Erythranthe diffusa* is generally taller (3.5-25 mm) than *E. purpurea*, has pink flowers, and pedicels that spread horizontally. In contrast *E. purpuea* is 3-10 mm tall, has pink to purple flowers with the upper lip darker than the lower lip, and pedicels erect to ascending and not spread horizontally.

Etymology.—*Erythranthe diffusa* is named for the diffuse branching habit which is characteristic of this species.

Conservation concern.—*Erythranthe diffusa* currently has a CNPS Rare Plant Rank of 4.3, which means it is uncommon in California but not very endangered, and a State Rank of S3.3 which means it is vulnerable but no current threats are known. Natureserve provides a Global Rank of G4Q, which means it is apparently secure considering the populations outside of the US, and is marked with a Q to denote the taxonomic uncertainty associated with this species (CNPS 2012). *Erythranthe diffusa* has a relatively widespread distribution and is known from western Riverside Co in California, USA to northern Baja California, Mexico. Anthropogenic change including development, grazing, off-highway vehicle use, road and trail maintenance, and power line development have all been documented as possible threats to known occurrences. Therefore the threat ranks for this species should be reassessed by the appropriate agencies.

ERYTHRANTHE DISCOLOR (A.L. Grant) N.S. Fraga "parti-colored moneyflower" Phytoneuron 2012, ined. *Mimulus discolor* A.L. Grant, Ann. Missouri Bot. Gard. 11: 257–258 1924 [1925].—TYPE: U.S.A., California, Kern Co., "gravelly slopes, Pah Ute Peak", *Purpus 5311* (holotype: MO!; isotypes: UC!, US digital image!)

Annual herb. Plants 5-12 (-15) cm tall × 05-4 cm wide; sparsely glandular pubescent. Stems erect, simple to branched, internodes1-3 cm. Cotyledons persistent, obovate to ovate, 0.3-1.1 mm long, with clasping bases. Leaves opposite, epetiolate or with petioles short (1-2 mm); blades 6-25 mm long ×1-4 mm wide, linear to oblanceolate, palmately veined with three prominent veins from the base in wider leaves, margins entire. Flowers solitary in each axil, fruiting pedicels 6-32 mm, exceeding calyx, erect to ascending. Calyx 4-8 mm long × 2-4 mm wide, campanulate, enlarging in fruit; costa weak and slightly darker than intercostal regions, sometimes red dotted; calyx teeth equal, 0.5-1 mm long, acute, erect to slightly spreading in fruit, margins glabrous.

Corolla 15-20 mm long × 7-15 mm wide, yellow and tinged red on adaxial surface of tube-throat, or deep pink to purple, lobes emarginate, strongly zygomorphic, tube-throat 8-15 mm long, funnelform, expanding abruptly to the limb, palate glabrous to sparsely bearded, mottled red on yellow plants and 2 yellow ridges on pink plants. Stamens didynamous, 11-13 mm long; yellow, glabrous, included. Gynoecium 13-14 mm long, white in yellow flowered plants, and pink to white in pink flowered plants; style glabrous; stigma lobes apically fringed, subequal, included in the corolla. Capsules 4-7 mm long, included in the calyx, campanulate, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.5-0.8 mm long × 0.2-0.3 mm wide, elliptic to ovoid, brown.

Representative specimens examined.—USA. California, Kern Co: Greenhorn Mountains, Little Poso Creek Falls, 4500 ft, 23 May 1937, *Benson 8344* (RSA); Greenhorn Mountains, Rancheria Road from Shirley Meadows Campground to Sawmill Road, 21 May 1989, *Harper s.n.* (RSA); Greenhorn Mountains, Rancheria Road near just south of Evans Flat Campground, 6100 ft, 13 Jun 2010, *Fraga & Brock 3474* (RSA); Kernville, 13 May 1891, *T.S. Brandegee s.n.* (UC); Fork of Cannell Creek on Pine Flat, 7100 ft, 10 July 1963, *Twisselmann 8674* (RSA); Piute Mountains, Piute Mountain Road, ca. 1.5-2 miles north of French Meadow, 7200 ft, 31 May 2008, *Fraga 2147* (RSA); Mouth of north fork of Esperanza Canyon, south of Marino Canyon at the east base of the Piute Mountains, 4300 ft, 18 April 2008, *Fraga et al. 2005* (RSA); 4 mi west on Piute Mountain Road from Kelso Valley Road, 5500 ft, 30 May 2010, *Fraga & De Groot 3413* (RSA); Piute Mountain/Saddle Springs Road, just east of Valley View Mine, 6725 ft, 12 June 2011, *Fraga & Jolles 3850* (RSA); Piute Mountains Brown Meadow, 7400 ft, 12 Jun 2011, *Fraga & Jolles 3855* (RSA); Piute Mountains; Piute Mountains Brown Meadow, 7400 ft, 12 Jun 2011,

Fraga & Jolles 3856 (RSA); Piute Mountains; Tulare Co: Cannell Meadows, 7000 ft, 15 June, 1904, *Hall & Babcock 5113* (UC).

Phenology and pollination biology.—Flowering occurs from April to June and fruiting is most common in June and July. *Erythranthe discolor* has two distinctive floral morphs—one is yellow with red spots on the palate, and the other is pink with two yellow ridges on the palate. Populations can be monomorphic (usually yellow) or mixed, with the yellow morph most often in higher frequency. *Erythranthe discolor* exhibits approach herkogamy and has relatively large flowers with trichomes and nectar guide patterns on the lower limb. Based on evidence from corolla morphology this species is presumed to be primarily outcrossing. Halictid bees (Halictidae) have been frequently observed visiting flowers of this species and are presumed to serve as the primary pollinators.

Distribution and habitat.—*Erythranthe discolor* is endemic to the southern Sierra Nevada in Kern and Tulare counties, California (Fig. 1.3). This species primarily occurs in decomposed granite in vernally wet depressions, swales, at the edges of streams, dry meadows, and in openings of pine forest, oak woodland, pinyon-juniper woodland, desert chaparral, and sagebrush scrub. Elevation ranges from 1310-2468 m (2800-8100 ft). Associated species include the following: *Abies concolor*, *Artemisia tridentata*, *Cercocarpus betuloides* Nutt., *Claytonia perfoliata* Willd., *Collinsia callosa* Parish, *C. parviflora*, *Erythranthe androsacea, E. barbata, E. floribunda*, *E. guttata*, *E. suksdorfii*, *Fremontodendron californicum* (Torr.) Coville, *Mimetanthe pilosa* (Benth.) Greene, *Muhlenbergia rigens*, *Phacelia exilis*, *Pinus jeffreyi*, *P. monophylla*, *Quercus chrysolepis*, *Q. kelloggii* Newb., *Q. wislizeni*, and *Salix lasiolepis* Benth.

Phylogenetic relationships and similar species.—*Erythranthe discolor* is inferred to share a close relationship with *E. barbata* (Fraga unpubl.). A putative hybrid swarm was observed in the

Scodie Mountains in the southern Sierra Nevada, where these two species overlap in distribution. See the expanded discussion under *E. barbata*.

Etymology.—The epithet for this species means "of different colors" and refers to the two color morphs that are present.

Conservation concern.—There are twenty known occurrences of *E. discolor*. There is currently little known regarding occurrence status and population trends, but recent surveys have found this *E. discolor* to be abundant where it occurs. Off-highway vehicle use, road maintenance, and campgrounds have been observed as possible sources of disturbance at known occurrences. Development has likely affected populations at lower elevations and several occurrences may have been extirpated in the vicinity of Kernville. *Erythranthe discolor* is of limited distribution and should be considered for conservation status by the federal, state, and other agencies that manage this species.

Erythranthe hardhamiae N.S. Fraga, "Santa Lucia monkeyflower" —TYPE: U.S.A, California, Monterey Co, Santa Lucia Mountains, mouth Los Burros Creek, 1 May 1960, *Hardham 5558* (holotype:RSA!; isotypes: CAS!, JEPS!).

Annual herb. Plants 2-13 cm tall × 1-13 cm wide; glabrous to minutely puberulent. Stems erect, simple to branched, internodes 1-3.5 cm. Cotyledons persistent, obovate-ovate, 0.1-1 mm long, with clasping bases. Leaves opposite, epetiolate; blades 2-12 mm long ×1-3mm wide, linear to oblanceolate, palmately veined with three prominent veins from the base in wider leaves, margins entire or sometimes toothed. Flowers solitary in each axil, fruiting pedicels 10-60 mm, exceeding calyx, erect to ascending, or spreading horizontally. Calyx 4-8 mm long × 2-4 mm wide, campanulate, enlarging slightly in fruit; costa weak, darker than intercostal regions,

sometimes spotted red; calyx teeth equal, 0.1-0.5 mm long, acute, with margins glabrous. Corolla 9-17 mm long × 7-11 mm long, deep pink to purple, lobes bifid, strongly zygomorphic; tube-throat 5-10 mm long, funnelform to cylindric, expanding abruptly to the limb, palate and orifice densely bearded with two yellow ridges. Stamens didynamous, 5-11 mm long; white, and included to occasionally exserted from the orifice. Gynoecium 7-12 mm long, pink, style glabrous, stigma lobes apically fringed, subequal, equal to the tube to exserted from the orifice. Capsules 2-5mm long, included in the calyx, cylindric, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.3-0.5 mm long × 0.1-0.2 mm wide, elliptic to ovoid, brown.

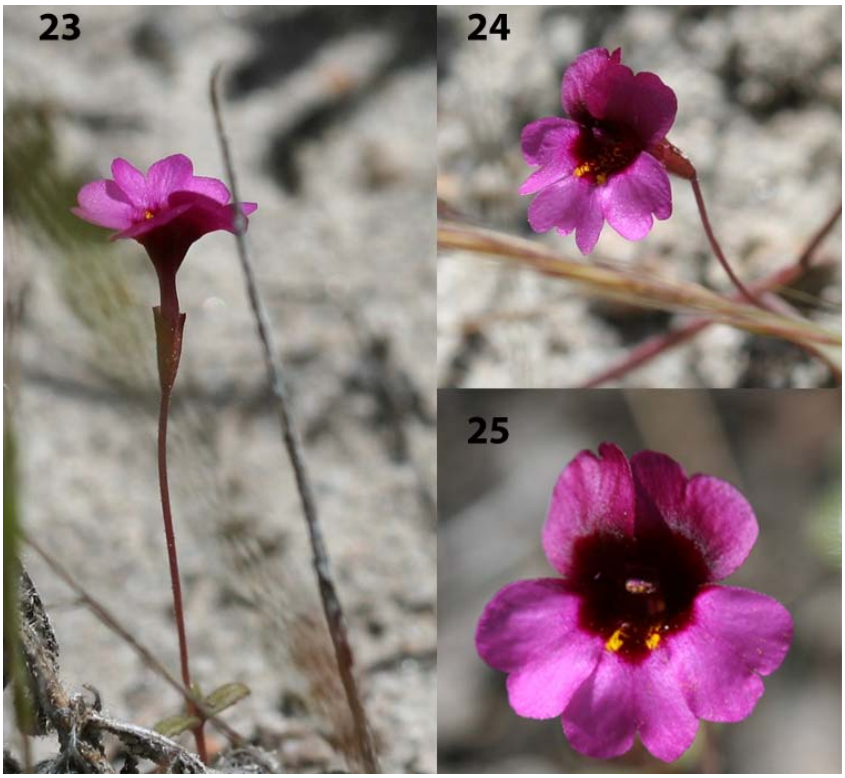

Figure 1.9. *Erythranthe hardhamae*.—.23. Plant habit.—24. Corolla lateral view.—25. Corolla face view.

Additional specimens examined.—USA, California, Monterey Co: Vineyard Canyon Road to Parkfield (E side of summit), 9 April 1961, *Hardham 6762* (JEPS); Vineyard Canyon Road, N

side of Road just E of summit 2300 ft, 2 May 2010, *Fraga 3344* (RSA), Santa Lucia Mountains: S of Los Burros Creek, 9 April 1961, *Hardham 5568* (SBBG); Santa Lucia Mountains Los Bueyes Creek Road, 2 April 1960, *Hardham 5480* (CAS, RSA, JEPS); Santa Lucia Mountains, road from San Antonio Mission to The Indians (Del Venturi Caves), 7 April 1960, *Hardham 5392* (JEPS); Santa Lucia Mountains, road from San Antonio Mission to The Indians (Del Venturi Caves), 7 April 1960, *Hardham 5392* (JEPS); San Luis Obispo Co: Santa Lucia Mountains,1 mi NW of Bee Rock, 1000 ft, 28 March 1960, *Hardham 5252* (JEPS, RSA, SBBG).

Phenology and pollination biology.—Flowering occurs from late March to May and fruiting is most common in May. *Erythranthe hardhamiae* has relatively large flowers with distinctive yellow nectar guides, an exserted stigma, and approach herkogamy. Based on evidence from corolla morphology, this species is presumed to be primarily outcrossing, but no pollinators were observed over the course of this study.

Distribution and habitat.—*Erythranthe hardhamiae* (Fig. 1.9) is endemic to the Coast and Inner Coast ranges in Monterey and San Luis Obispo counties, California (Fig. 1.8). This species occurs in sandy soils in openings of chaparral, and in sand filled crevices of sandstone outcrops. Elevation ranges from 300-500 m (1000-1650 ft). Associated species include the following (* denotes not native species): *Adenostoma fasciculatum*, *Camissonia* Link sp., *Chorizanthe* sp. R. Br. ex Benth., *Crassula connata* (Ruiz & Pav.) A. Berger, **Erodium botrys* (Cav.) Bertol., **E. cicutarium* (L.) Aiton, *Eriogonum fasciculatum* Benth., *Festuca microstachys* Nutt., **F. myuros* L., *Minuartia californica* (A. Gray) Mattf., *M. pusilla* (S. Watson) Mattf., *Nemacladus* sp. Nutt., and *Quercus chrysolepis*.

Phylogenetic relationships and similar species.—*Erythranthe hardhamiae* appears to be closely related to *E. androsacea* (Fraga unpublished). These species are easily distinguished from each

other by fruiting pedicel characters and corolla size. *Erythranthe hardhamiae* has pedicels that are 10-60 mm long and spread horizontally in fruit, and a limb that is 7-11 mm when pressed. In contrast *E. androsacea* has pedicles that are 5-30 mm long, are ascending to spreading in fruit, and do not spread horizontally, and a limb that is expended 3-7 mm when pressed.

Etymology.—*Erythranthe hardhamiae* is named in honor of Clare Butterworth Hardham (1918-2010). Hardham was a botanist who lived in Paso Robles, California; she studied the flora of the Santa Lucia Mountains. Her contributions have been many as evidenced by the many plants that bear her name in the region. Hardham collected specimens of *E. hardhamiae* at nearly all of the currently known locations.

Conservation concern.—There are eight known locations for *E. hardhamiae*; five are on lands managed by the Department of Defense (Fort Hunter Liggett), two are on private property, and one is on Los Padres National Forest. Grazing, road maintenance, the presence and abundance of exotic plant species, and development have all been noted as sources of disturbance. *Erythranthe hardhamiae* is of limited distribution and should be considered for conservation status by the federal, state, and other agencies that manage this species.

Erythranthe montioides (A. Gray) N.S. Fraga "montia-like monkeyflower", Phytoneuron 2012, ined. *Mimulus montioides* A. Gray, Proc. Amer. Acad. Arts 7: 380. 1868.—TYPE: U.S.A. California: Tulare Co., Mountains east of Visalia, 17-18 June 1864, *Brewer 2785* (lectotype, here designated: GH!).

Annual herb. Plants 3-9 cm tall × 1-13 cm wide; glabrous to minutely puberulent. Stems erect, simple to branched, internodes 0.5-1.5 cm. The cotyledons deciduous. Leaves opposite, epetiolate or with petioles short (0.5-1); blades 4-15 mm long × 0.5-2 mm wide, linear to

oblanceolate, palmately veined with three prominent veins from the base in wider leaves, margins entire. Flowers solitary in each axil, fruiting pedicels 3-15 mm, exceeding calyx, erect to ascending. Calyx is 3-6 mm long × 1-3 mm wide, campanulate, enlarging in fruit; costa weak, slightly darker than intercostal regions, sometimes spotted red; calyx teeth equal, 0.5-1 mm long, acute, margins ciliate. Corolla 10-17 mm long × 7-15 mm wide, yellow, lobes entire, strongly zygomorphic; tube-throat 6-11 mm long, funnelform, expanding gradually to the limb, palate glabrous to sparsely bearded spotted with red markings. Stamens didynamous, 7-8 mm long; yellow, glabrous, included. Gynoecium 10 mm long, white; style glabrous; stigma lobes apically fringed, equal, included. Capsules 3-5 mm long, included to calyx, campanulate, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.5-0.7 mm long × 0.2-0.3 mm wide, elliptic to ovoid, brown.

Additional specimens examined.—USA, California, Fresno Co: Markwood Meadows, 5800 ft, June 1900, *Hall & Chandler 339* (CAS, UC); Hume Lake Christian Camp, 5400 ft, 14 June 1998, *Schoenig 98-36* (UC); 7.2 km S-SE of Hume Lake, vicinity of Weston Meadow, T14Sm R28E, S11, NW1/4 of NE1/4, 1960 m, 28 June 1996, *York & Shevock 982* (CAS), On first road from Dinkey Creek Road, just west of Bald Summit, 13 July 2005, *Gowen 476* (JEPS); West end of Rabbit Meadow, west of Big Meadows, 7800 ft, 19 July 1979, *Heckard et al. 5142* (JEPS); -side of Kaiser Pass, near summit, 19 June 1997, *Wisura 5064* (RSA); Pittman Creek, above Huntington Lake, 27 July 1918, *Grant 1480* (RSA); trail to Nellie Lake, 8000 ft, 11 July 1917, *Grant 1080* (RSA); 9 miles south of general Grant National Park on road to Sequoia National Park, 26 July 1942, *Ferris & Lorraine 10827* (RSA, UC); Trail to Dinkey Lakes, Dinkey Lakes Wilderness, 8800 ft, 12 July 2008, *Fraga & Brock, 2366* (RSA); Tulare Co: Alta Trail, Giant Forest, 7500 ft, 8 August 1905, *Brandegee s.n.* (UC); SW of Stoney Creek Campground,

between Sequoia and Kings Canyon National Parks, 6400 ft, 18 June 1956, *Tillett & Sternback 486* (UC); along road between Moro Rock and Crescent Meadow, 18 June 2011, *Fraga et al. 3869* (RSA).

Phenology and pollination biology.—Flowering occurs from June to August and fruiting is most common in July and August. *Erythranthe montioides* exhibits approach herkogamy and has relatively large flowers. Based on evidence from corolla morphology this species is presumed to be primarily outcrossing. Solitary bees have been observed visiting flowers of this species and are presumed to serve as the primary pollinators.

Distribution and habitat.—*Erythranthe montioides* is endemic to the Sierra Nevada in Frenso and Tulare counties, California and is documented from 19 occurrences on Forest Service and National Park Service lands (Fig. 1.3). This species primarily occurs on the dry edges of meadows and in seasonally moist depressions in the open understory of mixed coniferous and lodgepole pine forest. Elevation ranges from 1645-2900 m (5400-9500 ft). Associated species include: *Abies magnifica, Arctostaphylos* Adans. sp., *Calocedrus deccurens*, *Ceanothus* L. sp., *Diplacus leptaleus* (A.Gray) G.L. Nesom, *Erythranthe laciniata* (A.Gray) G.L. Nesom, *Leptosiphon* Benth. sp., *Lewisia triphylla* (S.Watson) B.L. Rob., *Pinus contorta* subsp. *murrayana, P. jeffreyi, P. lambertiana*, and *P. monticola* D.Don.

Phylogenetic relationships and similar species.—*Erythranthe montioides* is inferred to share a close relationship with *E. palmeri* (Fraga unpublished). *Erythranthe montioides* is easily distinguished morphologically from *E. palmeri*. *Erythranthe montioides* has yellow flowers with entire lobes that are smaller (10-17 mm) than those of *E. palmeri* (15-25 mm). In contrast *E. palmeri* has pink flowers that are notched on each lobe.

Etymology.—*Erythranthe montioides* is named for its resemblance to the genus *Montia* L. (Montiaceae) and has been given the common name montia-like monkeyflower

Conservation concern.—*Erythranthe montioides* has been confused with other closely related species including *E. barbata*, *E. calcicola*, *E. carsonensis*, and *E. discolor*. It was previously thought to be a widely distributed species because of this taxonomic confusion. The majority of occurrences have not been surveyed in recent years; thus little information exists regarding population status and trends. Several hundred to several thousand individuals, however, were observed at Big Meadow and between Moro Rock and Crescent Meadow in 2010 and 2011. *Erythranthe montioides* should be evaluated for conservation status by the federal, state, and other agencies that manage this species.

Erythranthe palmeri (A. Gray) N.S. Fraga "Palmer's monkeyflower", Phytoneuron 2012, ined.

> *Mimulus palmeri* A. Gray Proc. Amer. Acad. Arts 12: 82. 1876.—TYPE: U.S.A. California: San Bernardino Co., Mohave River, 1 June 1876, *Palmer 321 ½* (holotype: GH!, isotypes: MO!, PH, UC!, US digital image!).

Annual herb. Plants 4-17 cm tall × 1-15 cm wide; minutely puberulent. Stems are erect, simple to branched, internodes 1-4 cm. Cotyledons persistent, obovate-ovate to round, 0.2-1 mm long, with clasping bases. Leaves opposite, epetiolate or with petioles short (0.1-1mm); blades are 3-17 mm long ×1-4 mm wide, linear to lanceolate, palmately veined with three prominent veins from the base in wider leaves, margins entire. Flowers solitary in each axil, fruiting pedicels 4-32 mm, exceeding calyx, erect to ascending, or spreading horizontally. Calyx 4-8 mm long × 2-4 mm wide, campanulate, enlarging in fruit; costa weak, darker than intercostal regions, sometimes red spotted; calyx teeth equal, 0.5-1 mm long, acute and spreading, margins ciliate. Corolla 15-25

mm long × 8-15 mm wide, pink to purple, yellow at the base of the tube, lobes emarginate, strongly zygomorphic; tube-throat 10-19 mm long, funnelform, expanding gradually to the limb, palate glabrous to sparsely bearded with two yellow ridges. Stamens didynamous, 8-12 mm long; yellow, glabrous, included. Gynoecium 12-16 mm long, pink; style glabrous; stigma lobes apically fringed, subequal, included. Capsules 3-5 mm long, included in the calyx, campanulate, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.5-0.9 mm long × 0.1-0.3 mm wide, elliptic to ovoid, brown.

Representative specimens examined.—USA, California, Los Angeles Co, San Gabriel Mountains: Upper Big Tujunga Canyon: margin of Big Tujunga Creek T2N R11W , NE/4 SE/4 SE/4 sec 5, 3980-4040 ft, 8 June 1990, *Ross et al. 2987* (RSA); Chilao Creek headwaters, T3N, R11W, NW/NE, sec 24, 5900 ft, 1 Jun 1968, *Wheeler s.n.* (RSA); Upper Big Tujunga at Vetter Gulch, 25 May 1963, *Wheeler 8258* (RSA); Pine Flats, 9 July, *Peirson 1124* (RSA); ca. 0.3 mi below Alder Saddle, along a dry branch of the S Fork of Little Rock Creek, 5300 ft, 30 June 1971, *Thorne & Tilforth 40764* (RSA); San Bernardino Co, San Bernardino Mountains: Near Mojave River, about 0.5 mi W of junction between roads to Hesperia and Lake Arrowhead, 3200 ft, 10 May 1979, *Thorne & Prigge 52892* (RSA); E of Running Springs, W of Deer Lick Station, 6000 ft, 29 May 1992, *Hirshberg 33* (RSA); Summit Valley on Hwy 173, 5.4 mi NE of Hwy 138 junction and 1 mi S of the Grass Valley Creek crossing, 3280 ft, 24 April 1993, *Sanders & Spilman 13774* (RSA); Fredalba, 5000 ft, 8 June 1919, *Munz & Johnston 2855* (RSA); Hunsakedr Flats, 5200 ft, 8 June 1919, *Munz & Johnston 2856* (RSA); Fish Camp, 6900 ft, 17 June 1921, *Johnston 2837* (RSA); Northeast of Rock camp station, North of Lake Arrowhead, 4785 ft, 21 May 2008, *Gross & Vanderplank 3420* (RSA); Intersection of FS Roads 3N34 (Pilot Rock Road) and 3N33, 4800 ft, 21 May 2008, *Fraga et al. 2092* (RSA); Keller Peak Road, 7200

ft, 11 June 2008, *Fraga & Kempton 2190* (RSA); Along OHV trail 1W17, north of Crab Flats, 5400 ft, 17 June 2008, *Fraga & Bell 2246* (RSA); 2.2 mi below junction for Smiley Park (along City Creek Road), 17 June 1953, *Bacigalupi et al. 4224* (JEPS); 9.7 mi above bridge crossing Deep Creek, Kinley Creek drainage, Deep Creek Grade, 4900 ft, 17 June 1953, *Bacigalupi et al. 4220* (JEPS); Horsthief Canyon, 15 May 1935, *Clokey & Anderson 6909* (JEPS); Strawberry Peak, 25 July 1901, *Abrams 1978* (DS).

Phenology and pollination biology.—Flowering occurs from April to July and fruiting is most common in June and July. *Erythranthe palmeri* exhibits approach herkogamy and has relatively large flowers. Based on evidence from corolla morphology this species is presumed to be primarily outcrossing. Solitary bees have been observed visiting flowers of this species and are presumed to serve as the primary pollinators.

Distribution and habitat.—*Erythranthe palmeri* is restricted to the San Gabriel and San Bernardino Mountains of the Transverse Ranges in Los Angeles and San Bernardino counties (Fig. 1.8). This species primarily occurs in decomposed granite in vernally wet depressions, swales, at the edges streams and creeks, dry meadows, and in openings of pine forest, oak woodland, and desert chaparral. Elevation ranges from 976-2200 m (3200-7200 ft). Associated species include the following (* denotes non-native species): **Bromus tectorum*, *Calochortus palmeri* S. Watson, *Castilleja lasiorhyncha* (A. Gray) T.I. Chuang & Heckard, *Ceanothus leucodermis* Greene, *Erythranthe breweri*, *E. guttata, E. suksdorfii*, *Eschscholzia californica* Cham., *Fremontodendron californicum*, *Gilia capitata* Sims, *Iris hartwegii* Baker var. *australis* Parish, *Phacelia mohavensis* A. Gray, *Pinus coulteri* Lamb. ex D. Don, *P. jeffreyi*, *Juncus mexicanus* Willd. ex Schult. & Schult. f., *Leptosiphon ciliatus* (Benth.) Jeps., *Madia minima* (A.

Gray) D.D. Keck, *Platystemon californicus* Benth, *Quercus kelloggii*, *Thysanocarpus laciniatus* Nutt., and *Trichostema austromontanum* F.H. Lewis.

Phylogenetic relationships and similar species.—*Erythranthe palmeri* is inferred to share a close relationship with *E. montioides* (Fraga unpublished). *Erythranthe palmeri* is easily distinguished morphologically from *E. montioides*. See discussion under *E. montioides* for distinguishing morphological features.

Etymology.—*Erythranthe palmeri* is named in honor of Edward Palmer (1829-1922), a botanist and explorer of the American West. Palmer collected the type specimen of *E. palmeri*.

Conservation concern.—*Erythranthe palmeri* has been confused with other closely related species including *E. diffusa*, *E. discolor* (pink form), *E. rhodopetra*, and *E. sierrae*. It was previously thought to be a widely distributed species because of this taxonomic confusion. *Erythranthe palmeri* is endemic to the Transverse Range in the San Gabriel and San Bernardino Mountains and is therefore of limited distribution. Off-highway vehicle use, road maintenance, hiking trails and campgrounds have all been observed as possible sources of disturbance to known occurrences. *Erythranthe palmeri* should be evaluated for conservation status by the federal, state, and other agencies that manage this species in light of clarification in taxonomy.

Erythranthe rhodopetra N.S. Fraga, "Red Rock Canyon monkeyflower".—TYPE: U.S.A, California, Kern Co, El Paso Mountains, Last Chance Canyon, Old Cuddhay Camp, 35°, 24', 40.2" N; 117°, 55', 40.1" W, 828m/2717 ft, 23 April 2011, *Fraga & Gardner 3787* (holotype: RSA!; isotypes: CAS!, UC!, US!).

Annual herb. Plants 5-15 (-21) cm tall × 1-15 cm wide; sparsely glandular pubescent. Stems erect, simple to branched, internodes 2-8 cm. Cotyledons persistent, obovate to ovate, 3-1.2 mm

long, with attenuate bases. Leaves opposite, petioles short (0.5-1 mm) to epetiolate; blades 5-22 mm long ×1-10 mm wide, linear-oblanceolate to elliptic, palmately veined with three prominent veins from the base in wider leaves, margins entire. Flowers solitary in each axil, fruiting pedicels 10-40 mm, exceeding calyx, erect to ascending. The calyx 5-10 mm long × 3-4 mm wide, campanulate to cylindric, enlarging in fruit; costa prominent and darker than intercostal regions; calyx teeth subequal and 0.5-1 mm long, acute and spreading, margins glabrous. Corolla 12-26 mm long × 16-25 mm wide, pink to rose colored, lobes bifid, weakly zygomorphic; tube-throat 9-17 mm long, funnelform, expanding abruptly to the limb, palate glabrous with a large yellow patch with dark pink longitudinal lines. Stamens didynamous, 10-13 mm long, yellow, glabrous, included. Gynoecium 12-14 mm long, pale pink to white; style glabrous; stigma lobes slightly apically fringed, subequal, included in the corolla. Capsules 4-8 mm long, included in the calyx, cylindric to campanulate, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.7-0.9 mm long × 0.2-0.3 mm wide, elliptic to ovoid, brown.

Additional specimens examined.—USA, California, Kern Co: Red Rock Canyon, 2300 ft, 14 March 1959, *DeDecker 1000* (RSA); Fremont Valley drainage; Red Rock Canyon north of Visitor's Center, 3 April 1993, *DeDecker 6378* (RSA); Near Ricardo, Red Rock Canyon, 29 March 1922, *Fultz 17074* (RSA); Red Rock Canyon, 1 April 1935, *Woglum 659* (RSA); Red Rock Canyon, 19 April 1958, *Munz & Gregory 23311* (RSA, UC); Red Rock Canyon, 1 May 1927, *Abrams 11856* (POM); Red Rock Canyon State Park, Hagen Canyon, 2200 ft, 12 April 2008, *Fraga et al. 1996* (RSA); North of Randsburg, 10 April 1922, *Pierce s.n.* (POM); Saltdale, Petrified Forest, 14 April 1933, *Johnston & Raiselis 17230* (RSA); El Paso Mountains, Petrified Forest, 20 April 1952, *Wheeler 6856* (RSA).

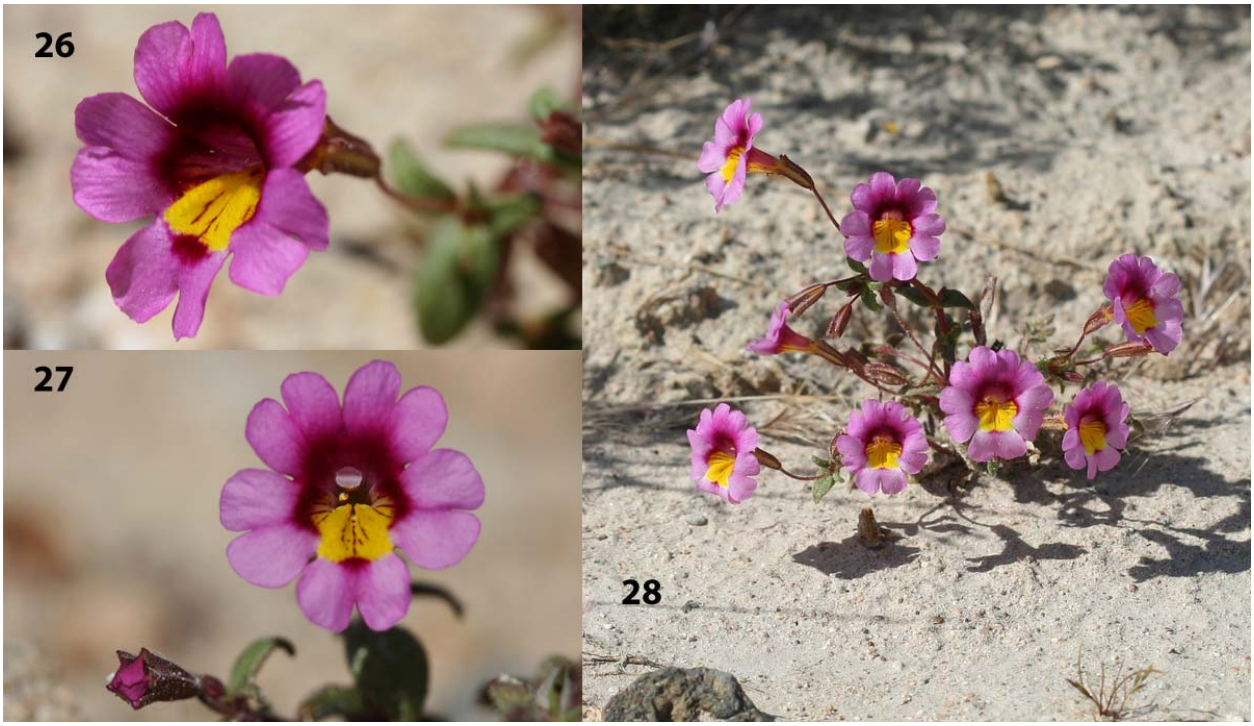

Figure 1.10. *Erythranthe rhodopetra*.—26. Corolla lateral view.—27. Corolla face view and floral bud.—28. Plant habit.

Phenology and pollination biology.—Flowering occurs from March to April and fruiting is most common in April and May. *Erythranthe rhodopetra* exhibits approach herkogamy and has very large flowers compared with the vegetative growth. Based on evidence from corolla morphology this species is presumed to be primarily outcrossing. Insect visitors were not observed visiting flowers of this species over the course of this study.

Distribution and habitat.—*Erythranthe rhodopetra* (Fig. 1.10) is endemic to the El Paso Mountains in Kern County, California (Fig. 1.8). This species occurs in highly compacted sandy soils in washes derived from sedimentary rock of the Ricardo Formation (Cox and Diggles 1986). The Ricardo Formation is of Miocene origin and is colorful with alternating bands of red, white, and brown and is composed of sandstones and consolidated conglomerates (Cox and Diggles 1986). Elevation ranges from 610-915 m (2000-3000 ft). Associated species include the

following (* denotes non-native species): **Bromus madritensis* L. subsp. *rubens* (L.) Husn., **B. tectorum*, *Calyptridium monandrum* Nutt., *Eremothera boothii* (Douglas) W.L. Wagner & Hoch, *Erythranthe guttata*, *Lepidium flavum* Torr., *Juncus bufonius* L., *Plagiobothrys arizonicus* (A. Gray) A. Gray, and *Platystemon californicus*.

Phylogenetic relationships and similar species.—*Erythranthe rhodopetra* appears to be closely related to *E. palmeri* (Fraga unpubl.). These species are easily distinguished from one another based on corolla size, corolla color, and nectar guide patterns. *Erythranthe rhodopetra* has a wider limb (16-25 mm) than *E. palmeri* (8-15 mm) and has pale pink flowers with a broad yellow palate and orifice. In contrast *E. palmeri* has deep pink flowers with two yellow ridges on the palate.

Etymology.—*Erythranthe rhodopetra* is named for the red sedimentary rocks of Red Rock Canyon State Park in Kern County, California. The species is endemic to the region and is associated with sandy canyon washes at the base of the red sedimentary cliffs.

Conservation concern.—*Erythranthe rhodopetra* occurs in less than ten populations within a120 sq km region and is therefore of limited distribution. All known occurrences are on public lands administered by the Bureau of Land Management or California State Parks. This species should be considered for conservation status by the federal, state, and other agencies that manage for this species. Historic mining operations, off-highway vehicle use, and the presence of exotic plants species were visible disturbances observed over the course of field surveys conducted by this study.

Erythranthe sierrae N.S. Fraga, “Sierra Nevada monkeyflower”.—TYPE: U.S.A, California, Kern Co, Sierra Nevada, Breckenridge Mountain, along Breckenridge Mountain Road, ca.

2 mi northwest of Breckenridge Campground, 35.4724°N, 118.6029°W, 5900 ft, *Fraga*, *Fraga*, & *Fraga 3445* (holotype: RSA!; isotypes: CAS!, UC!, US!).

Annual herb. Plants 4-20 cm tall × 2-19 cm wide; sparsely glandular pubescent. Stems erect, simple to branched, internodes 1-4 cm. Cotyledons persistent, obovate-ovate, 3-5 mm long, short petiolate with clasping bases. Leaves opposite, petioles short (0.5-1 mm) to epetiolate; blades (3-) 5-27 mm long ×1-11 mm wide, linear to oblanceolate, palmately veined with three prominent veins from the base in wider leaves, margins entire or sometimes toothed. Flowers solitary in each axil, fruiting pedicels (4-) 9-43 mm, exceeding calyx, erect to ascending. Calyx 4-8 mm long × 3-4 mm wide, campanulate, enlarging in fruit; costa weak and darker than intercostal regions; calyx teeth equal, 0.5-1 mm long, acute and spreading, margins ciliate. Corolla 12-22 mm long × 5-17 mm wide, pale pink to pink, lobes notched, weakly zygomorphic; tube-throat 8-17 mm long, funnelform, expanding gradually to the limb, palate with two yellow ridges. Stamens didynamous, 7-10 mm long; white, glabrous, included. Gynoecium 10-13 mm long, pink; style glabrous; stigma lobes apically fringed, subequal, included. Capsules, 3-6 mm long, included to equal to calyx, cylindric, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.5-0.8 mm long × 0.2-0.3 mm wide, elliptic to ovoid, brown.

Additional specimens examined.— USA, California, Kern Co: Greenhorn Mountain Range, Little Poso Creek Falls, 4500 ft, 23 May 1937, *Benson 8344* (POM); Greenhorn Range, 6000 ft., *Hall & Babcock 5050* (POM); Breckenridge Mountain, 6000 ft., 26 May 1928, *Bauer 213* (RSA); Howling Gulch near Woody, 1900 ft, *Smith 339* (RSA); Howling Gulch east of Woody Granite Road, 35.68991N,118.82803W, 30 May 2010, *Fraga et al. 3410* (RSA); Greenhorn Mountains, Summit between Glenville and Wood, 3000 ft, *Hughes 178* (POM); Keane, 1700 ft,

Jones s.n. (POM); N slope Breckenridge Mountain (at head of creek), 27 June 1965, *Twisselmann 11229* (JEPS); Breckenridge Mountain, 5700 ft, 6 June 2010, *Fraga et al. 3441* (RSA); Breckenridge Mountain Campground, 6600 ft, 4 July 2010, *Fraga & Brock 3514* (RSA); Rancheria Rd. (dirt road) south of Poso Flat Rd. and northwest below fire lookout. Near National Forest boundary and Oak Flat, 9 June 2005, *Gowen 432* (JEPS), Greenhorn Range, NW slope Basket Peak, 5250 ft, 27 June 1963, *Twisselmann 8546* (RSA); Fresno Co.: 100 meters W of Hume Lake Road, where USFS campground road forks off at Hume Lake, 36°, 47', 30" N; 118°, 54',00"W, 5300 ft, *Schoenig 37* (RSA); Just above Crawford Ranch, Pine Flat, Kings River about six miles below Trimmer; 650 ft, *Carter 48* (RSA, UC); Sand Creek, 6 May 1918, *Kelley s.n.* (JEPS); Tulare Co: North Fork of Tule River, 1 2/10 mi. above Milo, 2500 ft, 14 May 1933, *Wolf 4674* (RSA); Middle Fork of Tule River, 1750 ft, *Peirson 5619* (RSA); California Hot Springs to Durrwood, 11 May 1940, *Woglum 2713* (RSA); Tule River, 3000 ft, *Munz 3000* (RSA); 0.25 mile E of Milo junction and 7.5 miles N of Springville, *Robbins & Heckard 3535* (RSA); 1/4 mi NE Milo junction (7.5 mi N of Springville), 30 May 1953, *Heckard 456A* (RSA); Hills N of Springville, 800 ft, April1897, *Purpus 5048* (UC), Kaweah River Basin, 15 April 1901, *Hopping 111* (UC).

Phenology and pollination biology.—Flowering occurs from March to July and fruiting is most common in June and July. *Erythranthe sierrae* exhibits approach herkogamy and has relatively large flowers. Based on evidence from corolla morphology this species is presumed to be primarily outcrossing. Halictid bees (Halictidae) have been frequently observed visiting flowers of this species and are presumed to serve as the primary pollinators.

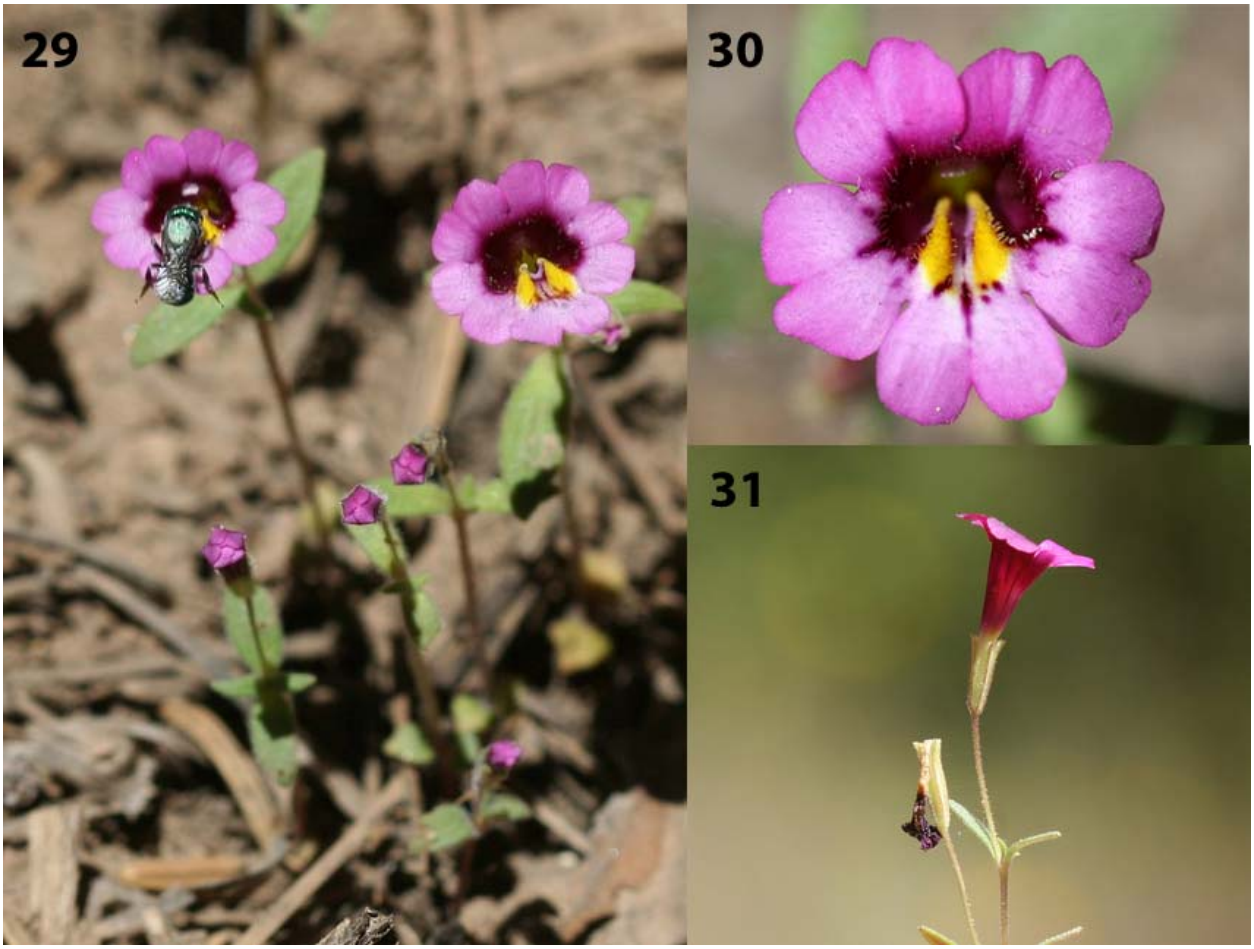

Figure 1.11. *Erythrathe sierrae*.—29. Habit, halictid (Halictidae) bee visiting flower, and floral buds.—30. Corolla face view.—31. Corolla lateral view and developing fruit.

Distribution and habitat.—*Erythranthe sierrae* is endemic to the Sierra Nevada in Kern, Fresno, and Tulare counties, California (Fig. 1.8). This species primarily occurs in decomposed granite in vernally wet depressions, swales, at the edges streams, dry meadows, and in openings of pine forest, and oak woodland. Elevation ranges from 200-2100 m (650-6800 ft). Associated species include the follwing: *Abies concolor*, *Claytonia perfoliata*, *Diplacus bolanderi* (A. Gray) G.L. Nesom & N.S. Fraga, *D. constrictus* (A.L. Grant) G.L. Nesom & N.S. Fraga, *Erythranthe breweri*, *E. floribunda*, *Nemophila maculata* Lindl. *Pinus jeffreyi*, *P. sabiniana* D. Don, *Phacelia*

curvipes, *Plagiobothrys* sp., *Quercus chrysolepis*, *Q. douglasii* Hook. & Arn., *Q. kelloggii*, *Ribes quercetorum* Greene.

Phylogenetic relationships and similar species.—*Erythranthe sierrae* is inferred to have a sister relationship with *E. gracilipes* (B.L. Rob.) N.S. Fraga (Fraga unpublished). These species are easily distinguished by corolla morphology. *Erythranthe sierrae* has corolla lobes that are more or less equal in size and a tube throat that is funnelform and expands gradually to the limb. In contrast, *E. gracilipes* has two reduced adaxial lobes that are smaller than the three abaxial lobes and a tube-throat that is cylindric and expands abruptly to the limb.

Etymology.—*Erythranthe sierrae* is endemic to the Sierra Nevada in California and is named for the range.

Conservation concern.—*Erythranthe sierrae* has a relatively widespread distribution and is known from Kern, Fresno, and Tulare counties in the foothills of the Sierra Nevada. Anthropogenic change including development, grazing, off highway vehicle use, road and trail maintenance, campgrounds, and the presence and abundance of exotic species have all been documented as possible threats to known occurrences. Several populations at lower elevations may be highly impacted from these disturbances with several populations possibly extirpated. This species should be reassessed for threats at known occurrences.

CHAPTER TWO: A Taxonomic Revision of *Erythranthe* Section *Paradantha* (Phrymaceae)

Mimulus L. s.l. commonly known as the monkeyflowers is a relatively well-known genus of flowering plants that forms a significant component of the diverse and rich flora of the western United States, especially in California. There have been numerous ecological and evolutionary studies centered on the group; in fact, the genus has been touted as an emerging model system for integration of ecological and genomic research, akin to the model organism *Arabidopsis* (DC.) Heynh. (Wu et al. 2007). Thus, *Mimulus* has prominence and name recognition among plant scientists worldwide. The genus formerly included at least 120 taxa that together have a worldwide distribution with centers of diversity in North America, Australia, and Asia (Beardsley and Olmstead 2002) but it has recently undergone an extensive taxonomic revision (Barker et al. 2012). Beardsley et al. (2004) provided a useful framework toward understanding relationships within the group and further supported an earlier study that provided evidence that *Mimulus* s.l. as traditionally circumscribed was not monophyletic (Beardsley and Olmstead 2002). The phylogenetic placement of the type species; *M. ringens* L., in an early-diverging lineage well separated from the majority of species included in *Mimulus* s.l. has resulted in a revised classification (Barker et al. 2012; Fig. 2.1). As a result, *Mimulus* s.s. (sensu stricto) has been reduced to seven species. Two genera, *Diplacus* Nutt. and *Erythranthe* Spach, contain the vast majority of western North American species formerly treated within *Mimulus*. Here I review the basis for recognition of these four genera (Table 2.1) and provide a taxonomic revision for a lineage of closely related species that comprise *Erythranthe* sect. *Paradantha* (A.L. Grant) G.L. Nesom & N.S. Fraga.

Table 2.1. Comparison of traits between *Mimulus* and segregate genera.

	Diplacus	*Erythranthe*	*Mimetanthe*	*Mimulus*
# of taxa	50	116	1	7
Distribution	NA	AS, NA, SA	NA	AU, AS, AF, NA
Corolla	marcescent	deciduous	marcescent to deciduous	deciduous
Calyx	tubular, plicate	tubular, plicate	partially seperated sepals, rounded	tubular, plicate
Pedicel length	shorter than length of calyx to sessile	longer than length of calyx	equal to longer than length of calyx	longer than length of calyx
Placentation	parietal	axile	parietal	axile
Fruit dehiscence	distal half of inner inner suture, sometimes distal 1/2 of outer suture	to base along both sutures	along 1/3-1/2 of both sutures	to base along both sutures
base chromosome #	8	14, 15, 16	UNK	8, 11, 12

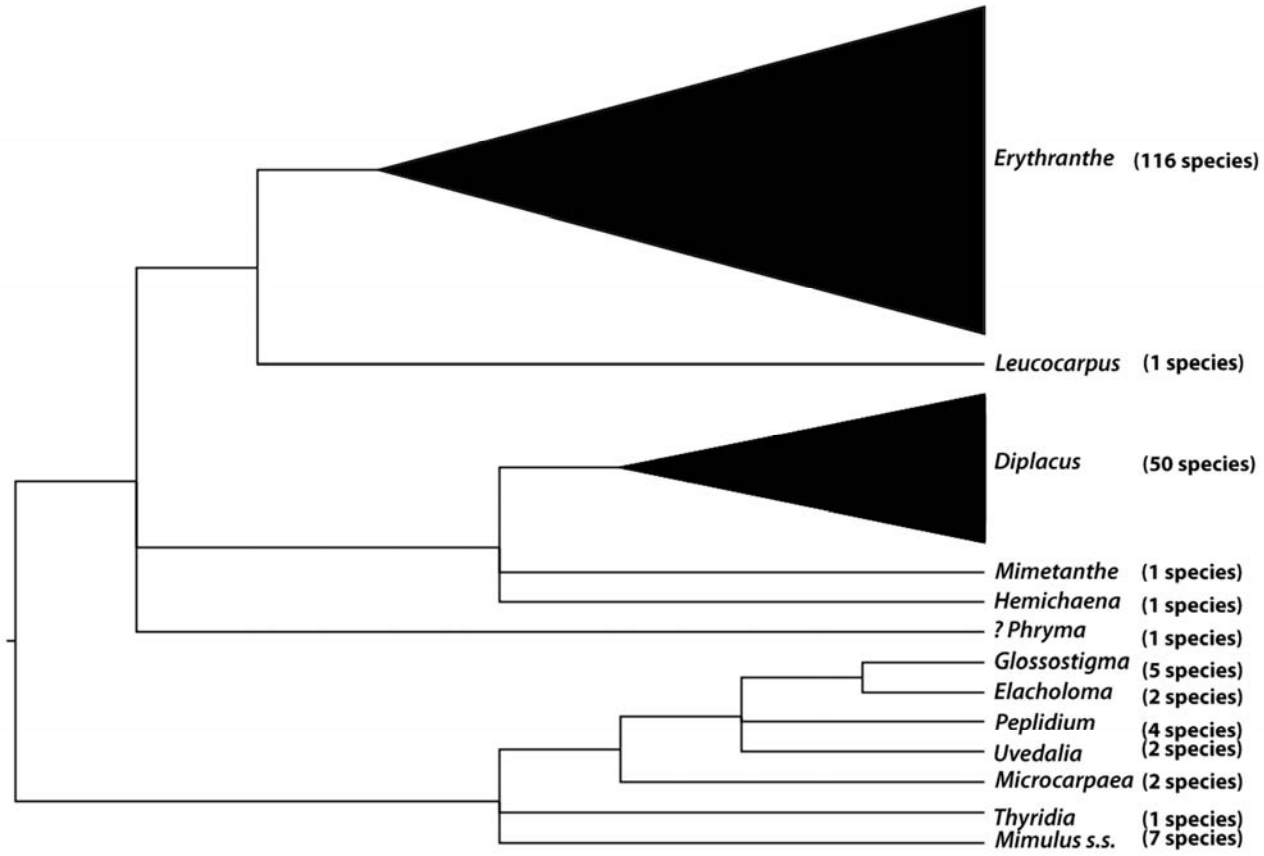

Figure 2.1. A summary of phylogenetic relationships among genera in Phrymaceae summarized from Beardsley et al. (2004) and Beardsley & Barker (2005). The position of Phryma is uncertain, but is placed based on an maximum likelihood analysis of combined chloroplast and nrDNA (ITS and ETS; Beardsley & Olmstead 2002).

TAXONOMIC HISTORY

Until recently the traditional broad circumscription of *Mimulus* included a large number of taxa that are now treated in *Erythranthe* and *Diplacus* (Beardsley et al. 2004; Barker et al. 2012). *Mimulus* as currently described is reduced to seven species and is distributed in North America, Africa, Asia, and Australia (Barker et al 2012). In *Species Plantarum*, Linnaeus (1753) published *Mimulus* with the description of a single species, *M. ringens*. Another species, *M. luteus* L., was added in the second edition of *Species Plantarum* (1763). By the turn of the eighteenth century, four species were recognized with the addition of *M. aurantiacus* Curtis and *M. alatus* Aiton, the former treated as a synonym of *M. glutinosus* (Wildenow 1800). The first comprehensive treatment of *Mimulus* was that of Bentham in his *Scrophulariaceae Indicae* (1835) which listed a total of 25 species. Almost 100 years years later, Grant (1924) treated 114 species of *Mimulus* in 12 sections. Other significant early works include Bentham (1846) who treated 31 species in *Prodromus*; Gray (1876) treated 29 species in his account of the botany of California for the Geological Survey of California; in *Studies in the Botany of California and Parts Adjacent*, Greene (1885) treated 33 species of *Mimulus* while recognizing the segregates *Diplacus* (six species) and *Eunanus* Benth. (19 species); and Pennell's (1951) *Illustrated Flora of the Pacific States* recognized 107 species. More recently, Thompson (1993, 2005, 2013), placed a number of earlier-accepted taxa in synonymy, thus considerably reducing the number of species treated within *Mimulus* s.l. for total of about 90 species.

The present treatment of *Mimulus* and its reduction to seven species reflects our current understanding of evolutionary relationships in Phrymaceae. The type species, *M. ringens*, is placed in an early-diverging lineage that is more closely related to six genera that occur in Australia and Asia than to the majority of the western North American species traditionally treated as *Mimulus* (Fig. 2.1). Three genera (*Diplacus*, *Mimetanthe*, and *Erythranthe*) have been

resurrected; these each well marked by morphology (Table 2.1) and together include most species that that have been traditionally treated as *Mimulus*. The current treatment required many name changes (at least 136 new combinations), but is based on the rules of priority and typification, and avoids the need to invoke conservation of the name *Mimulus* under a different type under the International Code of Botanical Nomenclature for Algae, Fungi, and Plants (McNiell et al. 2014).

As currently treated, *Diplacus* is endemic to North America and comprises six sections and 47 species (Barker et al. 2012). Historically, the concept of the genus emphasized shrubby habit and was restricted to what is now treated as *Diplacus* sect. *Diplacus* (Thompson 2005; Tulig and Nesom 2012). Under the current treatment, the genus has been expanded to include taxa that are of annual or perennial duration and have pedicels that are shorter than the calyx or absent, parietal placentation, and fruits that dehisce only along the distal half of the abaxial (inner) suture or not at all and only partially on the distal half of the adaxial (outter) suture (Thompson 2005). Phylogenetic patterns indicate that the woody perennial species are derived from ancestors of annual duration (Beardsley et al. 2004), and are well nested within the '*Diplacus*' clade (Fig. 2.1) recovered by Beardsley et al. (2004).). A number of taxonomic studies have focused on *Diplacus*, especially the shrubby perennial taxa (sect. *Diplacus*; McMinn 1951; Beeks 1962; Ezell 1970; Waayers 1996; Tulig 2000; Tulig and Clark 2000; Thompson 2005; Tulig and Nesom 2012). Also within *Diplacus*, *Eunanus*, once segregated as a genus, is currently treated at sectional rank (Barker et al. 2013).

Mimetanthe is a monotypic genus first described by Greene (1886). *Mimetanthe* was the only segregate genus that Grant recognized in her monograph of *Mimulus* (1924 Based on fruit characters, this species could be placed within *Diplacus*; however, there are several

morphological characters that distinguish it, including pedicel length, calyx with apically rounded segments, placentae fused in at least the proximal half of the fruit, capsule dehiscence along distal third of both sutures, and distinctive pollen referred to as type IV by Argue (1980).

Erythranthe was first described by Spach (1840) based on a single species with red flowers, *E. cardinalis*. It was soon placed into synonymy and reduced to sectional rank within *Mimulus*; it was not recognized again until its recent resurrection to reflect our current understanding of relationships within Phrymaceae (Barker et al. 2012). *Erythranthe* currently includes 12 sections and over 120 taxa (Barker et al. 2012). Notable, taxa that have been the subject of extensive ecological, evolutionary, and genetic studies (e.g. *E. cardinalis*, *E. guttata*, *E. lewisii, E. nasuta*) are placed in sections *Simiola* and *Erythranthe* (Wu et al. 2007). Species delimitation and phylogenetic relationships have been controversial in the group, with as few as 50 taxa recognized in previous treatments (Grant 1924; Pennell 1951; Thompson 2012). The genus is particularly diverse in western North America, with more than 80% of the species; the remaining species occur in South America and Asia (Barker et al. 2012).

Within *Erythranthe,* sect. *Paradantha* is noted for having many narrowly endemic species, considerable floral variation, and problematic species delimitations (Grant 1924; Beardsley et al. 2004; Table 2.2). Taxonomy of the group has been reviewed by Greene (1885), Gray (1886), Grant (1924), Munz (1968), Pennell (1951), and Thompson (1993, 2012). Taxonomic confusion has centered around two species of sect. *Paradantha*: *E. montioides* and *E. palmeri* (Table 2.2). The most recent treatment provided evidence for recognition of ten species where only two species (*E. montioides* and *E. palmeri*) were previously recognized (Fraga 2012). The present study recognizes 16 species.

Table 2.2. Species currently included in *Erythranthe* section *Paradantha*.

Species treated in the current study	Other Synonyms	Treatment in Grant 1924	Treatment in Thompson 2012
Erythranthe androsacea		*M. androsaceus*	*M. androsaceus*
Erythranthe barbata	*Mimulus deflexus*	*M. deflexus*	*M. montioides*
Erythranthe calcicola		*M. montioides*	*M. montioides*
Erythranthe carsonensis	*M. rubellus* var. *latiflorus*	*M. montioides*	*M. montioides*
Erythranthe diffusa	*M. grantianus*	*M. diffusus*	*M. palmeri*
Erythranthe discolor		*M. discolor*	*M. montioides*
Erythranthe gracilipes		*M. gracilipes*	*M. gracilipes*
Erythranthe hardhamiae		*M. palmeri*	*M. palmeri*
Erythranthe montioides		*M. montioides*	*M. montioides*
Erythranthe palmeri		*M. palmeri*	*M. palmeri*
Erythranthe purpurea	*M. purpureus* var. *pauxillus*	*M. purpureus* var. *purpurea*, *M. purpureus var. pauxillus*	*M. purpureus*
Erythranthe rhodopetra		*M. palmeri*	*M. palmeri*
Erythranthe rubella		*M. rubellus*	*M. rubellus*
Erythranthe shevockii		not treated	*M.shevockii*
Erythranthe sierrae		*M. palmeri*	*M. palmeri*
Erythranthe suksdorfiii		*M. suksdorfii*	*M. suksdorfii*

Erythranthe sect. *Paradantha* was erected by Grant (1924) as a highly variable group that was acknowledged to be artificial. Grant (1924) noted that species were placed in this section arbitrarily because they did not belong to any of the other well-established groups. Unsurprisingly, as then delimited, the section was found to be polyphyletic by Beardsley et al. (2004 Although Grant did not designate a type for the section, she noted that "*M. rubellus* is at the center of an assemblage of closely related species." In realigning the sectional classification of Phrymaceae (Barker et al. 2012), *E. rubella* was selected as the type for sect. *Paradantha* and thus the closely related species that Grant (1924) referred to as the "*Mimulus palmeri* group" are included in the section. *Paradantha* currently includes 16 species that resolve as a clade with

strong support in two independent studies (Beardsley et al. 2004, Fraga unpublished data, 2.2). Plants in the group are relatively diminutive annuals with highly variable floral morphology and corolla color (Fig. 2.2).

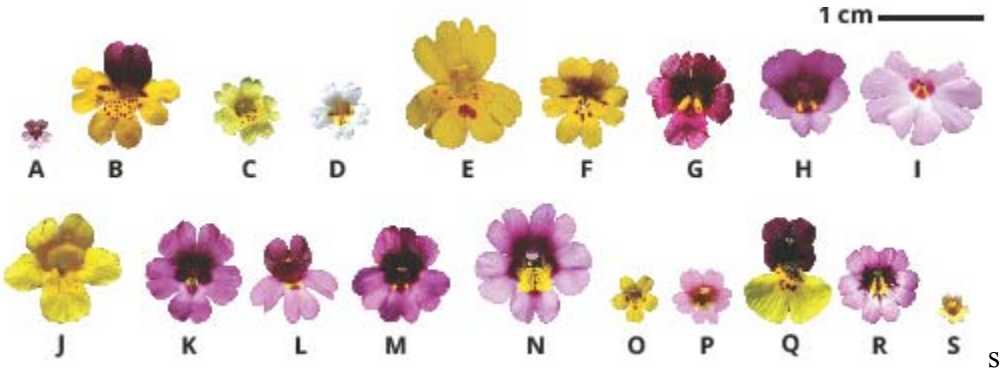

Fig. 2.2. Diversity in corolla limb color, morphology and size *Erythranthe* section *Paradantha*—A. *Erythranthe androsacea*.—B. *Erythranthe barbata* (bicolor form).—C. *Erythranthe calcicola* (yellow form).—D. *Erythranthe calcicola* (white form).—E. *Erythranthe carsonensis*.—F. *Erythranthe discolor* (yellow form).—G. *Erythranthe discolor* (pink form). —H. *Erythranthe diffusa*.—I. *Erythranthe gracilipes*. —J. *Erythranthe montioides*.—K. *Erythranthe palmeri*.—L. *Erythranthe purpurea*. —M. *Erythranthe hardhamiae*.—N. *Erythranthe rhodopetra*.—O. *Erythranthe rubella* (yellow form). —P. *Erythranthe rubella* (pink form).—Q. *Erythranthe shevockii*. —Q. *Erythranthe sierrae*.—Q. *Erythranthe suksdorfii*.

MATERIALS AND METHODS

***Field Studies*—**Between 2007 and 2012, 140 populations of all species included in *Erythranthe* sect. *Paradantha* and close relatives (outgroup taxa) were observed in the field. Herbarium specimen records, databases (CCH, SEINet, and CNDDB), and literature reports were used to identify target populations for field surveys, including type localities. Populations were selected in order to sample each species throughout its known range. Seeds and herbarium specimens were collected for later study. Several populations were visited more than once to permit collection of mature fruits and seeds, as well as flowering specimens. At each field site, data recorded included exact location (via Global Positioning System), habitat characteristics (i.e.,

elevation, slope, aspect, microhabitat, soil type, vegetation association, associated species), distinguishing morphological characteristics, life history attributes (i.e., abundance of plants, presence of pollinators), and conservation status (i.e., existing or potential threats or disturbances). Vouchers are deposited at RSA, and a duplicate set is at CAS. Seed collections are deposited at the Rancho Santa Ana Botanic Garden seed bank. Photographs were taken of living plants with common objects (pencils and coins) for scale (Fig. 2.3). In most cases photographs were taken with a Canon EOS Digital Rebel XTi 10.1 MP Digital SLR using a Canon Macro lens (100 mm). Flowers were photographed in lateral and face view.

Fig. 2.3. Variation in size and habit for species in *Erythranthe* section *Paradantha*—A. *Erythranthe androsacea* with a penny for scale.—B. *Erythranthe purpurea* with a pencil for

scale.—C. *Erythranthe diffusa* with a quarter for scale.—D. *Erythranthe montioides* with a hand for scale.

Measurements for Descriptions— Vegetative and floral measurements provided in the descriptions are all inclusive ranges from study of fresh material in the field, pressed and dried material collected in the field for this study, and mounted herbarium specimens. Plant height was measured from the ground to the tallest point on the plant (usually the inflorescence); plant width was measured from the two widest points on an individual plant (usually the width of the inflorescence); corolla width was measured on pressed specimens using the widest point on the limb; corolla tube length was measured from the base of the corolla to the opening of the lobes. Qualitative characters (e.g. corolla color) were described from photographs, field observations, and herbarium specimens. Associated species lists include dominant species that are diagnostic of the vegetation association, annual plant species sharing similar habitats, and non-native species that are indicators of disturbance.

Herbarium Studies—More than 500 herbarium specimens were examined from ten herbaria: CAS/DS, DEVA, GH, MO, RENO, RSA (including POM), SBBG, SD, UC/JEPS, and UNLV.

Line Drawings—Line drawings presented in the treatment are based on photographs, herbarium material, and descriptions provided to the illustrator.

Geographic Distributions and Elevation—Location information was entered into a database for all specimens examined. Herbarium specimens with label data that lacked precise geographic coordinates were georeferenced to provide latitude and longitude for mapping. Georeferenced locations were included only if there was a high degree of confidence (i.e., within 1 square mile) in establishing the location. County-level distribution maps were prepared in ArcGIS 10.1 (ESRI 2013). Elevation ranges for each taxon were compiled from field studies and label information on herbarium specimens examined (exceptional or dubious elevations are cited parenthetically).

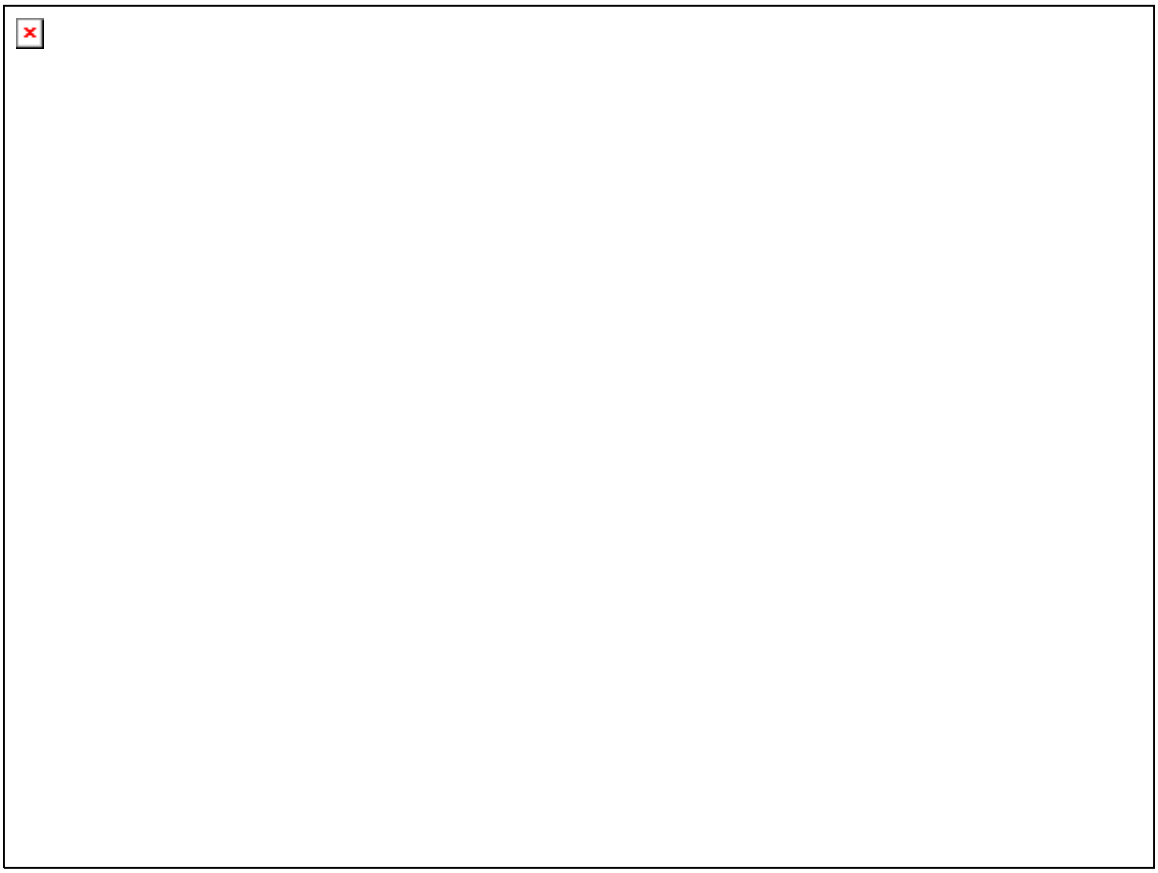

Fig. 2.4. Global distribution of *Erythranthe* section *Paradantha*

***Conservation Status*—**Assessment of conservations status was informed by range size as determined by fieldwork and herbarium specimens including observations of habitat quality including evidence of disturbance, current use of the area, and current status of populations. These data were assessed against criteria outlined by the California Native Plant Society (CNPS) Inventory of Rare and Endangered Plants (2013) and Natureserve (2013). In order to provide adequate conservation assessments I evaluated species based on criteria including rarity, unique evolutionary histories, endangerment, degree of threat, and risk of extinction (Meyers et al. 2000, Mace et al. 2003).

Duration and Habit— All species are diminutive annuals (Fig. 2.3). Plants range in size from less than 1 cm to no more than 40 cm tall with much of the variation apparently attributable to interannual variation in winter precipitation. Plants can be unbranched or highly branched.

Indumentum—Plants of species of *Erythranthe* sect. *Paradantha* can be nearly glabrous to sparsely puberulent or pubescent (following Thompson [2005], puberulence refers to presence of trichomes ≤ 0.5 mm long, whereas pubescence indicates presence of longer trichomes [mostly ≥1 mm]). Plants of all taxa have capitate glandular trichomes, with fewer having eglandular trichomes as well. Glandular trichomes are less than 0.5 mm long, but eglandular trichomes often exceed 1 mm.

Leaves— Leaves are simple, sessile to subsessile, usually with entire margins, but sometimes with toothed or revolute margins. Leaf margins can vary on a single plant. Leaf shape varies from linear to lanceolate, oblanceolate, ovate elliptic or spathulate. Paired leaves at a node are sometimes connate and slightly clasping at the base. Venation is palmate with three prominent main veins from the base of the leaf. The leaves are often reduced distally along a shoot.. Cotyledons are usually ovate to obovate, and persistent.

Inflorescence—Flowers are solitary from the leaf axils along the stem. The pedicels are long (2–70 mm), often presenting the flowers well above the height of the stem.

Calyx— Species have a persistent, tubular, plicate calyx (typical of Phrymaceae). The calyx lobes or "teeth" are extensions of the costa (veins) beyond the calyx margin. The calyx lobes are generally equal, and the presence or absence of cilia at the margin of the calyx appears to be an informative character for distinguishing morphologically similar species (e.g., *E. palmeri* vs. *E. diffusa*, *E. suksdorfii* vs. *E. rubella*). The calyx may be green, red, or straw colored, and often has

red spots at anthesis; the color is often darker on the costa and paler in the intercostal regions. The calyx enlarges as the fruit matures, and remains intact when the fruit dehisces.

Corolla—The corolla is generally bilabiate to funnelform and bilaterally symmetrical (*E. androsacea* and *E. suksdorfii* can have subradially symmetrical corollas). The five corolla lobes are typically equal; however, *E. gracilipes* and *E. shevockii* have highly modified corolla lobes that are unequal. The transition between the corolla tube and throat is gradual, thus the term "tubethroat" is used for the whole of the tube. The corollas are deciduous.

Corolla color ranges widely from white, yellow, pink, purple, to maroon. Corollas often have contrasting colors such as white, yellow, and red on the lower limb that may serve as pollinator guides. Two species (*E. barbata, E. shevockii*) have bicolored corollas with maroon upper lobes and a yellow lower limb. Four species exhibit corolla color polymorphisms: populations of *E. barbata*, *E. calcicola*, *E. discolor*, and *E. rubella* may be monomorphic or include plants with two color morphs (described below). The frequency of morphs within a population appears to change between years based on information provided on herbarium specimen labels and my field observations.

Androecium and Pollen—The stamens of plants in *Erythranthe* sect. *Paradantha* are didynamous and included in the corolla. Most flowers exhibit approach herkogamy where the anthers are positioned below the stigma. The distance between the anthers and stigma is reduced in some species (*E. androsacea*, *E. rubella,* and *E. suksdorfii*), likely indicative of a high degree of self-pollination. A survey undertaken by Argue (1981) found species of this group to have pollen with three apertures (tricolporate), a microreticulate exine pattern, lumina that were considered too small to measure, and polar and equatorial diameters of 25–40 μm and 21–43 μm, respectively.

***Gynoecium*—**The ovary has two carpels with many ovules; placentation is axile and the placentae are fused to form a central column (Grant 1924). The stigma has two flattened lobes that are sometimes fringed apically. The stigma can be included (equal to the corolla orifice) or exserted. The stigma lobes are touch-sensitive which brings the receptive surfaces together preventing further receipt of pollen unless the stigma reopens. Stigma closure is not limited to *Erythranthe* sect. *Paradantha*, but has been documented in many other members of the family Phrymaceae and other members of the order Lamiales including some Bignoniaceae, Lentibulariaceae, and Martyniaceae (Fetscher 1999; Thompson 2005).

***Fruits and Seeds*—** The fruit is a bilocular capsule with loculicidal dehiscence along both sutures to the base. There are many seeds per capsule (20–400). The seeds are small (0.3–0.9 mm long, 0.1–0.3 mm wide), brown, ovoid, and have reticulate patterns on the seed coat. Seeds have been shown to have minimal value in delimiting species within Phrymaceae because they are remarkably uniform in morphology (Grant 1924; Thompson 2005).

POLLINATION BIOLOGY

Several pollination strategies have been documented in *Erythranthe*, most notably insect, hummingbird, and self-pollination (Arathi and Kelly 2004; Schemske and Bradshaw 1999; Vickery 1990). In *Erythranthe* sect. *Paradantha*, halictid bees (sweat bees) and *Lepidoptera* have been observed visiting flowers; these presumably serve as pollinators although their effectiveness was not measured. Pollinators are attracted to flowers through visual guides that are displayed on the corolla such as spots, lines, contrasting colors, and the presence of trichomes on the lower lip; these presumably signal pollen or nectar rewards (Medel et al. 2003). In years of ample precipitation, populations will form large floral displays in dense patches, which may

increase pollinator services (Moeller et al. 2012). Self-pollination has been documented in this study; dissection of buds of *E. androsacea* in the field revealed stigmas covered with pollen. Floral traits that appear to correlate with self pollination include absence of herkogamy, reduced corolla size (corollas < 1 cm long), relatively early flowering time compared to closely related, sympatric species, and short flower duration (1–2 days). In addition, even in years when mass germination results in large floral displays in closely related species, dense floral displays are rarely observed in primarily self-pollinating species. Based on these traits *E. androsacea*, *E. rubella*, and *E. suksdorfii* are presumed to have high incidences of self-pollination.

ECOLOGY

All species in *Erythranthe* section *Paradantha* are winter annuals that germinate in response to precipitation in the late fall and winter months and have their active growing season in the spring. The majority of species occur in habitats that experience a Mediterranean-type climate where the majority of the precipitation falls in the winter (November-May), with an extended period of summer drought (June-October; Cowling et al. 2005). Species that occur in the Mojave and Great Basin deserts also experience a climate of predominately winter precipitation. One species, *E. rubella*, occurs in the Sonoran and Chihuanan deserts, both of which have substantial contributions to total annual precipitation from summer rains. This species does not, however, appear to germinate in response to summer rainfall. An examination of phenology from herbarium records finds that species in section *Paradantha* can be found blooming between the months of March and September. Flowering specimens collected from June to September are typically from higher elevations (above 1928 m [6000 ft]) where the blooming period is delayed due to snow pack and cool temperatures.

Species require ample precipitation for germination and, in years of drought, most seeds remain dormant to form an extensive seed bank. Interannual variation in preciptation yields corresponding variation in population sizes and density; sites where large, dense conspicuous patches are found in wet years can be sparsely populated or plants may be absent altogether in years of drought. Timing of precipitation may also be important. Plants appear to germinate most readily in response to early winter rains (November-January) and may have little to no germination response to precipitation in late winter and early spring (February-April).

DISTRIBUTION AND HABITATS

Distribution—All 16 species are endemic to western North America (Fig. 2.4); 11 (69%) are endemic to California and the majority of species occur in southern California. Only three species are known to occur above the 38th parallel (*E. carsonensis*, *E. rubella*, *E. suksdorfii*), and four taxa occur below the 33rd parallel. The latter four extend into Baja California, Mexico (*E. androsacea*, *E. diffusa*, *E. purpurea*, *E. rubella*), and *E. ruella* extends to mainland Mexico (Sonora). There is high species diversity and high rates of s69ympatry in the eastern Transverse Ranges (primarily the San Gabriel and San Bernardino mountains), and the southern Sierra Nevada in Kern and Tulare counties. Over 80% of species in this lineage are narrowly distributed and have global ranges of less than 10,000 sq km (3800 sq mi or ca. 2% of the land surface in California).

Elevation— Plants of *Erythranthe* section *Paradantha* have been found from 106 to 4,023 m. (350–13,200 ft) in elevation. *Erythranthe androsacea* and *E. sierrae* are the only species known to occur below 300 meters (1000 ft.). The lowest elevation occurrence known for *E. androsacea* is 106 m (350 ft) at the Ben Lomond sand hills of Santa Cruz County, California. These sand hills are notable for holding several endemic species, as well as several species of plants that

typically occur at higher elevations (e.g., *Pinus ponderosa* Lawson & C. Lawson, *Calyptridium monospermum* Greene). Beyond the Ben Lamond sand hills occurrence, the next known lowest elevation for *E. androsacea* is at 304 m (1000 ft). *Erythranthe sierrae* historically occurred at the base of the Sierra Nevada foothills and in the most upland regions of the Great Central Valley but many of these locations are presumed extirpated due to development for housing and agriculture. Most species occur between 300 and 2200 m. (1000–7000 ft) elev. in openings of shrublands, woodlands, or forests. One species, *E. barbata*, occurs above tree line in the alpine zone of the high Sierra Nevada. This is notable because annual plants are a globally rare life form above tree line and in alpine areas (Jackson 1985).

Habitats— Species typically occur in vernally wet habitats, often along ephemeral creeks and streams, swales, meadow edges, and moist depressions (Fig. 2.5d–e). Species adapted to more xeric conditions often occur on exposed rocky or sandy soils (Fig. 2.5a–c), typically in openings in full sun where there is little competition with larger plants. They often co-occur with other diminutive native annuals (Fig. 2.5). The majority of species in *Erythranthe* section *Paradantha* experience a Mediterranean climate with precipitation in winter and early spring, and prolonged drought in the summer months.

Edaphic Factors— Several species are restricted or nearly restricted to specific substrates. Plants of most species in the group occur in sandy or loamy soils of granitic origin. Species that occur on exceptional soil types include *E. calcicola*, *E. rubella*, *E. hardhamiae*, and *E. rhodopetra*. *Erythranthe calcicola* has a high affinity for limestone substrates on rocky talus slopes. *Erythranthe rubella* also occurs on limestone rock and also on granite. *Erythranthe hardhamiae* occurs on soils derived from sandstone and on serpentine. *Erythranthe rhodopetra* also occurs in soils derived from sandstone.

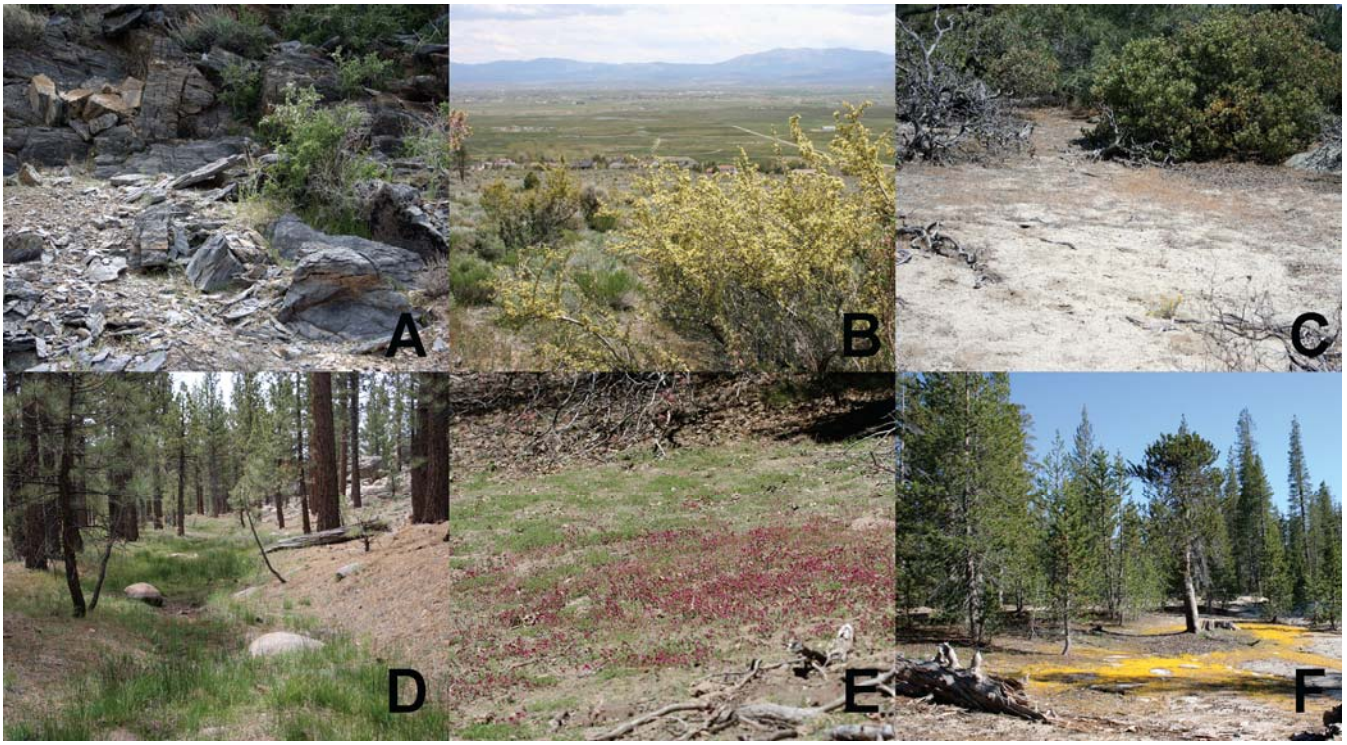

Figure. 2.5. Diversity of habitats for species in *Erythranthe* section *Paradantha*. A. Limestone south facing slope; habitat of *Erythranthe calcicola*.—B. Flats in sage brush scrub; habitat for *Erythranthe carsonensis*.—C. Sandy openings in chaparral and Jeffrey pine forest tranisition; habitat for *Erythranthe gracilipes*.—D. Seasonally wet creek in understory of Jeffrey pine forest; habitat for *Erythranthe palmeri*.—E. Sandy openings in Jeffrey pine forest; habitat for *Erythranthe sierrae*. —E. Sandy openings in lodgepole pine forest; habitat for *Erythranthe montioides*.

Site specificity and response to disturbance— Species of *Erythranthe* sect. *Paradantha* do not tolerate anthropogenic disturbance and are readily extirpated from highly disturbed sites. These plants can be taken as indicators of environmental quality for habitats in which they occur. Presumably, soil disturbance and damage to cyptogamic soil crusts formed by cyanobacteria, lichens, or bryophytes can create conditions that are less suitable for germination and/or establishment (DeFalco et al 2001). Competition with aggressive non-native species, especially weedy grasses (Poaceae), may also impact species persistence in the landscape (Rao et al. 2011).

Response to Fire— Two species have been documented to be more abundant post-fire, *E.*

gracilipes and *E. diffusa* (Keeley et al. 2005). Both occur at mid elevations (300–2100 m, 980–6800 ft) in chaparral to forest transitional habitats that are prone to wildfire. It is unknown how other species in the group respond to fire, but it is likely that *E. androsacea*, *E. hardhamiae*, and *E. sierrae* also have a positive germination response to fire based on the habitats in which they occur.

SPECIES DELIMITATION

Species delimitation in *Erythranthe* sect. *Paradantha* has been historically difficult with anywhere between seven and sixteen species recognized (Greene 1885; Gray 1886; Grant 1924; Munz 1968; Pennell 1951; Thompson 1993, 2012; this study). The treatment presented here employs a unified species concept: species are separately evolving lineages that can be identified from concordance of two or more attributes that indicate lineage separation and divergence (De Queiroz 2007). Attributes that may indicate distinct lineages and are used to distinguish species in the current treatment include reciprocal monophyly, geographic distance (taken as indicative of prezygotic reproductive isolation), ecological divergence, and morphological diagnosability. Assessment of reciprocal monophyly was determined from phylogenetic analysis based on data from nuclear ribosomal ITS and three non-coding chloroplast regions (*petA–psbJ*, *psbD–trnT*, *rpl32–*trnL; (chapter 3). Ecological divergence was determined based on fieldwork which yielded data on phenology and habitats. Morphological diagnosability was determined based on studies of plants in the field and herbarium.

KEY TO SPECIES

1. Corolla bicolored, upper lip marroon, lower lip yellow

   2. Upper lip with two maroon lobes, lower lip with three yellow lobes, leaves linear to oblanceolate, margins not revolute, leaf bases attenuate…..2. *Erythranthe barbata* (in part)

2. Upper lip with four maroon lobes, lower lip of one yellow bifid lobe, leaves lanceolate to ovate, margins revolute, leaf bases clasping…..14. *Erythranthe shevockii*

1. Corolla yellow, white, pink, or purple, not bicolored, upper and lower lip more or less the same color.

3. Calyx lobe margins glabrous

4. Corolla yellow.

5. Internodes much foreshortened and sometimes not evident, length 1–25 mm long, plants usually densely compact.

6. Corolla tubes 7–10 mm, distinct, from abruptly expanding throat, palate bearded and maculate…..4. *Erythranthe carsonensis*

6. Corolla tubes 4–6 mm, indistinct from the throat, palate glabrous, sometimes with red markings…..16. *Erythranthe suksdorfii*

5. Internodes elongate and distinct 5–40 mm, plants not densely compact

7. Floral tube distinct, cylindric, and expanding abruptly to the limb, palate bearded…..2. *Erythranthe barbata*

7. Tube-throat funnelform expanding gradullay to the limb, palate sparsely bearded to glabrous…..6.*Erythranthe discolor*

4. Corolla pink, or purple

8. Leaves with clasping bases

9. Corolla 3–8 mm long and 1–6 mm wide, weakly zygomorphic…..1. *Erythranthe androsacea*

9. Corolla 7–17 mm long and 7–11 mm wide, strongly zygomorphic

10. Adaxial lip of the corolla darker than abaxial lip, two adaxial lobes nearly entire…..11. *Erythranthe purpurea*

10., Adaxial and abaxial lip of the corolla the same color, all corolla lobes bifid…..8. *Erythranthe hardhamiae*

8. Leaves with attenutate bases

11. Corolla pale pink to rose-colored with a broad yellow palate, corolla width (pressed) 16–25 mm…..12. *Erythranthe rhodopetra*

11. Corolla deep pink to purple with two yellow ridges on the lower limb and palate, corolla width (pressed) 6–15 mm

12. Pedicels ascending to spreading, often spreading horizontally with age…..5. *Erythranthe diffusa*

12. Pedicels erect to ascending, not spreading horizontally with age…..6. *Erythranthe discolor*

3. Calyx lobe margins ciliate

13. Upper two lobes of the corolla much reduced, smaller than the lower three lobes, flowers rose to pink….7. *Erythranthe gracilipes*

13. Upper and lower lobes of the corolla more or less equal, flowers deep pink to purple, white or yellow.

14. Fruiting calyces becoming red, minutely glandular, costa prominent

15. Leaves lanceolate to ovate, 2–10 mm wide…..3. *Erythranthe calcicola*

15. Leeaves linear to elliptic, 1–5 mm wide….13. *Erythranthe rubella*

14. Fruiting calyces becoming straw colored, sometimes red spotted, minutely puberulent or glabrous, costa weak

16. Corolla yellow….9. *Erythranthe montioides*

16. Corolla pink

17. Leaf margins entire, never toothed; limb deep pink to purple; stamens yellow; eastern Transverse Ranges (San Gabriel and San Bernardino mountains)…..10. *Erythranthe palmeri*

17. Leaf margins entire or sometimes toothed; limb pale pink to pink; stamens white; Sierra Nevada and Tehachapi mountains…..15. *Erythranthe sierrae*

TAXONOMIC TREATMENT

1. ERYTHRANTHE ANDROSACEA (Curran ex Greene) N.S. Fraga "rock-jasmine monkeyflower" Phytoneuron 39: 1–60 (2012). .

Mimulus androsaceus Curran ex Greene, Bull. Calif. Acad. Sci. 1: 121. 1885.—TYPE: U.S.A. California: Tehachapi, Jun 1884, *Curran s.n*. (lectotype, here designated: CAS! isolectotypes: GH, PH, SD!, UC!)

Mimulus palmeri var. *androsaceus* (Curran ex Greene) A. Gray, Syn. Fl. N. America, 2 (1): 451. 1886.

Annual herb. Plants 0.5–10 cm tall, 0.5–7 cm wide, glabrous or minutely puberulent. Stems erect, simple to branched, internodes 0.1–1.5 cm. Cotyledons persistent, orbicular to ovate, 1–5 mm long, with clasping bases. Leaves opposite, epetiolate; blades 2–10 mm long, 1–5 mm wide, linear to lanceolate or ovate, palmately veined with three prominent veins from the base in wider leaves, margins revolute and entire or sometimes toothed. Flowers solitary in each axil, fruiting pedicels (5) 7–25 mm, exceeding calyx length, erect to ascending to spreading horizontally. Calyx 3–7 mm long, (2)3–6 mm wide, campanulate, enlarging in fruit; costa weak, darker than intercostal regions; teeth equal, 0.5–1 mm long, acute and spreading, margins glabrous. Corolla 3–8 mm long, 1–6 mm wide, pink to purple, lobes entire or notched, limb weakly zygomorphic to subradial; tube-throat 3–6 mm long, cylindric, expanding gradually to the limb, palate glabrous or sometimes sparsely bearded, sometimes with variable yellow or pink markings.

Stamens subequal to didynamous, 3–6 mm long; filaments and anthers straw-colored or brown, glabrous, included. Gynoecium 3–7 mm long, ovary brown to straw-colored, style and stigma pink, glabrous; stigma lobes apically fringed, subequal, equal to or slightly exserted from the orifice. Capsules 3–5 mm long, included to equal with the calyx, cylindric, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.3–0.5 mm long, 0.2 mm wide, elliptic to ovoid, light brown.

Representative Specimens Examined— U.S.A. California: Kern Co., near Kernville, Wofford Heights, 25 Mar 1960, *Howell 35179* (JEPS); between Kelso Creek and Kelso Valley road, 11 mi S of Hwy 178 W of Weldon, 1 mi NW of Bird Spring Pass road junction, 3 May 1985, *Heckard 6228* (JEPS); in sandy soil on stream terrace along road to Cortez Canyon W of Kelso Creek in Joshua Tree Woodland, 3560 ft, 16 Apr 1983, *Norris 368* (RSA); Cyrus Canyon E of Lake Isabella, 3000 ft, 9 Apr 2010, *Fraga 3193* (RSA); near mouth of South Fork Kern River Canyon below forest boundary near Bartolas Creek, N of Calif. Highway 178 and NW of the Bloomfield Ranch, 2900 ft, 20 Apr 1991, *Shevock 12019* (RSA); Lake Co., 1 mi SE Borax Lake (near road to Burns Valley), 16 Apr 1947, *Baker 11672* (JEPS); Los Angeles Co., San Andreas Rift Zone: just S of Bob's Gap, 30 Mar 1995, *Mistretta 1586* (RSA); Liebre Mountains region: Portal Ridge, N of the San Andreas Rift Zone, in the Cow Spring drainage along the Pacific Crest Trail, 3680 ft, 24 Mar 1998, *Boyd 10122* (RSA); San Gabriel Mountains, Southern California transmission line tower, vicinity of Aliso Canyon, W of the Angeles Forest Hwy, 1195 m, 16 Apr 2008, Mistretta 2457 (RSA); Modoc Co., N of Upper Rush Creek Public Camp, 2.5 mi E of Hwy 299, 18 May 1950, *Balls 14755* (RSA). Monterey Co., San Antonio *Lobb s.n.* (CAS); The Indians: ridge between Indians and Rooster Cr., 25 Apr 1960, *Hardham 5443* (RSA, CAS). Riverside Co., Santa Rosa Mountains, 30 May 1937, *Ramsey 2116* (POM); Kenworthy,

Thomas Valley, 4800 ft, 20 May 1922, *Johnston 5476* (POM); head of San Carlos Pass, Anza, 4500 ft, 21 May 1927, *Munz 10855* (POM). San Benito Co., 1 mile SW Buck Peak, ca. 1.5 miles W of Griswold Canyon, 18 Apr 1991, *Taylor 11613* (UC); Pinnacles National Monument, near intersection roads to Old Pinnacles Trail and Bear Gulch Day use area, 1300 ft, 4 Apr 2010, *Fraga 3190* (RSA); San Bernardino Co., N foot of the San Bernardino Mountains, Hwy 173, 5.4 miles NE of the junction with Hwy 138 and ca. 1 mile S of the Grass Valley creek crossing, 3281 ft, 11 Apr 1993, *Sanders 13731* (RSA, SD); San Bernardino Mountains, Baldwin Lake, Pavement Plain flat, S side of road, 26 May 1982, *Wallace 2009* (RSA).; Holcomb Valley Region: creek near intersection of 3N16 and 3N02, adjacent to mining claim, 7300 ft, 14 May 2008, *Fraga 2047* (RSA); ridgeline north of meadow near Broom Flat, 7800 ft, 26 Apr 2010, *Fraga 3320* (RSA); W Big Bear City (at E end on S side of lake), San Bernardino Mountains, Big Bear Lake, 14 June 1979, *Thorne 53080* (RSA, UC); San Bernardino National Forest: slope N of Baldwin Lake and Hwy 38, 6855 ft, 4 May 1978, *Thorne 53080* (RSA); San Bernardino National Forest, pebble plains S of Sugarloaf development, southern terminus of Maple St., 20 Jun 1998, *Schoenig 98–48* (UC); San Diego Co., Cuyamaca Mountains, vicinity of Cuyamaca Lake, at edge of meadow, N side of Hwy S-1, ca. 1 mile E of intersection with Hwy 79, 13 Apr 1994, *Hirshberg 268* (RSA), 50 yd N of road along Hwy 78, 2 miles E of Banner, 22 Feb 1986, *Reiser s.n.* (SD); San Luis Obispo Co., E side La Panza Range, Navajo Creek District, 11 May 1952, *Hoover 8186* (JEPS, SD); Santa Barbara Co., Hurricane Deck, 20 May 1957, *Hardham 1980* (JEPS); below Pine Corral Potrero (Sierra Madre Mountains, E fork of Lion Canyon), *Blakley 3414* (SBBG); Santa Clara Co., Lion Canyon, 19 May 1960, *Blakley 3414* (JEPS, RSA); 1 mi S Red Mountain (near summit of Del Puerto Road from Patterson to Mount Hamilton), 11 May 1963, *Breedlove 4936* (JEPS); headwaters Arroyo Bayo; Mount Hamilton Range, 30 Mar

1935, *Sharsmith 1703* (UC); 2.4 mi E of junction in San Antonio Valley (upper Arroyo del Puerto), 23 Apr 1963, *Raven 18233* (JEPS); between Arroyo del Puerto and Santa Clara Valley (W side of mountains), Mount Hamilton Range, Red Mountains, 24 Apr 1936, *Sharsmith 3617* (UC); Santa Cruz Co., 2 mi E Ben Lomond (on summit of divide between San Lorenzo River and Zayante Creek), 11 May 1947, *Stebbins 3742* (UC); Ben Lomond, 25 April 1890, *Brandegee s.n*. (UC); Ben Lomond sand hills, 9 May 1952, *Hesse 928* (JEPS); Tulare Co., Camp Mosquito Sequoia, 25 Apr 1909, *Sampson 414* (CAS); Ventura Co., 3.0 mi S Lockwood Valley road (on road to Thorn Meadows), San Emigdio Range, 12 May 1962, *Breedlove 2743* (JEPS); NW of Mt. Pinos, Noroeste Road W of Quatal Canyon Rd., 11 May 2005, *Gowen 319* (JEPS); about gravel in formerly moist fan in Pinyon-Juniper woodland, chaparral of Sandstone Campground on State Hwy 33 (399) in upper Sespe Creek watershed, 2 Jun 1967, *Smith 9636* (RSA); Rose Lake, 3600 ft, 8 Apr 1960, *Hardham 5388* (RSA, CAS); dry slope near Sandstone Public Camp, Route 33, in upper Sespe watershed, 4750 ft, 21 Jun 1967, *Chandler 3590* (RSA); junction of Thorne Meadows Road and Pine Springs Road, S of Frazier Mt. Park, U.S. 399 hwy, 5600 ft, 26 Apr 1962, *Olmsted 3362* (RSA); southwest end of the San Emigdio Mountains, far E end of Cowhead Potrero, near border with Kern Co., N and S side of Highway 95 (Cerro Noroeste Road), 5149 ft, 6 May 2008, *Gross 3328* (RSA).

MÉXICO: Baja California, 1/2 km S of El Condor, 4300 ft, 15 Apr 1979, *Moran 27027* (SD); 6 km SE of Japa, 4300 ft, 15 Apr 1979, *Moran 27042* (SD).

***Phenology and Pollination Biology*—**Flowering occurs between March and May; fruiting plants most commonly seen in May and June. *Erythranthe androsacea* has relatively small flowers (ca. 5 mm wide) and lacks herkogamy, suggesting frequent self-pollination. Self-pollination was

observed at two populations by dissecting floral buds to reveal stigmas covered with pollen. No visitors were observed on flowers of this species over the course of this study.

Distribution and Habitat— *Erythranthe androsacea* is a relatively widespread species occurring in several mountain ranges in California, US, and in Baja California, Mexico, including the Sierra Nevada, Coast Ranges, Transverse Ranges, and Peninsular Ranges. Plants primarily occur in decomposed granite in vernally moist areas including creek and stream edges, swales, and shallow depressions. *Erythranthe androsacea* is associated with the following plant communities: desert scrub, chaparral, oak woodland, riparian scrub, yellow pine forest. Elevation 106–2400 m (350–8000 ft). Associated species: *Artemisia tridentata* Nutt., *Cercocarpus betuloides* Nutt., *Collinsia parvifolia* Lindl., *Crassula connata* (Ruiz & Pav.) A. Berger, *Erythranthe suksdorffii*, *Eriogonum fasciculatum* Benth., *Fremontodendron californicum* (Torr.) Coville, *Juniperus californica* Carrière, *J. grandis* R.P. Adam, *Lomatium nevadense* (S. Watson) J.M. Coult. & Rose, *Microsteris gracilis* (Hook.) Greene, *Pinus jeffreyi* Grev. & Balf., *P. monophylla* Torr. & Fre´m, *P. ponderosa* Lawson & C. Lawson, *Poa secunda* J. Presl, *Purshia tridentata* (Pursh) DC., *Quercus chrysolepis* Liebm., and *Salix lasiolepis* Benth.

Phylogenetic Relationships and Similar Species—*Erythranthe androsacea* appears to be closely related to *E. hardhamiae, E. shevockii* and *E. purpurea* (Fraga chapter 3). Plants are easily distinguished from these other species by fruiting pedicel characters and corolla size. *Erythranthe hardhamiae* has pedicels 10–60 mm long that spread horizontally in fruit, and a limb that is 7–11 mm (pressed). In contrast, *E. androsacea* has pedicels 5–30 mm long that are ascending to spreading in fruit (not spreading horizontally), and a limb that is 3–7 mm (pressed).

Etymology—*Erythranthe androsacea* is named for resemblance of plants to those of the genus *Androsace* L. (Primulaceae), commonly known as rock-jasmine which is also the source of this monkeyflower's common name: 'rock-jasmine monkeyflower.'

Conservation Status—*Erythranthe androsacea* has a wide distribution but is relatively uncommon and is known from Kern, Lake, Los Angeles, Modoc, Monterey, San Benito, San Diego, San Luis Obispo, Santa Cruz, Santa Clara, Tulare, and Ventura counties in California and Baja California, Mexico. Anthropogenic change including development, grazing, off-highway vehicle use, road and trail maintenance, campgrounds, and the presence and abundance of exotic species have all been documented as threats to known occurrences. The species is widespread in California and does not have conservation status there; however it is known from only two occurrences in Baja California, Mexico, at the southern edge of its range. In Baja Californina it is being considered for a rarity lising of 2A which indicates that *E. androsacea* is rare in the California Floristic Province of Baja California, but is more common in the state of California (O'Brien et al. 2010, O'Brien personal communication).

2. ERYTHRANTHE BARBATA (Greene) N.S.Fraga "bearded monkeyflower" Phytoneuron 39: 1–60. 2012.

Mimulus barbatus Greene, Bull. Calif. Acad. Sci. 1: 9. 1884.—TYPE: Location not provided on specimen label (holotype: CAS digital image!; isotype: UC!)

Mimulus deflexus S.Watson. Proc. Amer. Acad. Arts 24: 84.1889.—TYPE: U.S.A. California: Tulare Co., Long Meadow, Jun 1888, *Palmer 176* (holotype GH!; isotypes MO!, NY digital image!, US digital image!).

Annual herb. Plants 2–15 cm tall, 0.5–7 cm wide, sparsely glandular pubescent. Stems erect, simple to branched, internodes 0.5–2 cm. Cotyledons persistent, oblanceolate to ovate, 1–6 mm long, with clasping bases. Leaves opposite, epetiolate; blades 5–19 mm long, 0.5–2 mm wide, linear to oblanceolate, palmately veined with three prominent veins from the base in wider leaves, margins entire. Flowers solitary in each axil, fruiting pedicels (5) 9–25 mm, exceeding calyx, erect to ascending, or spreading horizontally. Calyx 1–3 mm long (2) 3–6 mm wide, campanulate, enlarging in fruit; costa weak, darker than intercostal regions; calyx teeth equal, 0.5–1 mm long, acute and spreading, margins glabrous. Corolla 12– 20 mm long, 6–13 mm wide, bicolored, adaxial lip maroon– purple and abaxial lip yellow, or entirely yellow, lobes bifid, limb strongly zygomorphic; tube-throat (5) 8–12 mm long, cylindric, expanding abruptly to the limb, palate bearded, spotted with red markings. Stamens didynamous, 9–11 mm long; filiments and anthers yellow, glabrous, included. Gynoecium 12–13 mm long, ovary brown to straw colored, style and stigma yellow, glabrous; stigma lobes apically fringed, subequal, equal to corolla or slightly exserted from the orifice. Capsules 2–5 mm long, included to equal to calyx, cylindric, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.3–0.5 mm long, 0.2 mm wide, elliptic to ovoid, brown.

Representative Specimens Examined—U.S.A. California: Kern Co., trail to Little Cannell Meadow above Pine Flat, 7350 ft, 24 Jul 1964, *Twisselmann 9861a* (JEPS); Pine Flat, 7400 ft, 28 Jul 1965, *Twisselmann 11334* (JEPS, CAS); Bartolas Creek, near its summit, 6950 ft, 25 Jun 1966, *Twisselmann 12462* (CAS); Fay Creek at Little Cannell Meadow, 6400 ft, 26 Jun 1967, *Twisselmann 13396* (CAS, SD); Tulare Co., SE end of Rode Flat, 7400 ft, 27 Jun 1967, *Twisselmann 13518* (CAS, JEPS, RSA, SBBG); Siberian Pass Creek, 11,000 ft, 25 Jul 1949, Munz 14199 (RSA); W of South Fork Kern River, W of Kennedy Meadows, 6000 ft, 19 May

1986, Ertter 6152 (RSA, UC); Big Meadow, 7800 ft, 26 Jun 1970, *Twisselmann 16879* (CAS, RSA); Chimney Creek, E of Chimney Creek campground, 5800 ft, 30 May 1969, *Wheeler s.n.* (RSA); Kern Plateau, Dome Land, 8000 ft, 11 Jun 1972, *DeDecker 2924* (RSA); South Fork of Kern River at Tunnel Meadow, 9100 ft, 25 Jul 1970, *Twisselmann et al. 16934* (JEPS, RSA); Long Meadow, 2200 m, 14 Jun 1904, *Hall & Babcock 5107* (CAS, POM, UC); Salmon Creek, Horse Meadow public campground, 7500 ft, 12 Jun 1960, *Wheeler 7704* (RSA); head of Monache Meadow, South Fork of Kern River, 8050 ft, 14 Jul 1950, *Munz 15021* (RSA); Cannell Meadow, 7000 ft, 15 Jun 1904, *Hall & Babcock 5113a* (UC); South Fork of Kern River at Monache Meadow, 8000 ft, 12 Aug 1968, *Twisselmann et al. 14779* (CAS, JEPS); Templeton Mountain near Kern Peak, 8700 ft, 5 Jul 1912, *Jepson 4968* (JEPS); True Meadow, 6825 ft, 26 Jun 1967, *Twisselmann 13402* (JEPS); Poison Meadow, Kern Plateau, 7600 ft, 20 Jul 1962, *Twisselmann 7548* (CAS); 6 mi N of South Fork Kern River bridge on road to Troy Meadow, 7500 ft, 5 Jul 1967, *Howell & True 43146* (CAS); Summit Meadow, Olancha Mountain, 9500 ft, 25 Jun 1904, *Hall & Babcock 5278* (UC); Troy Meadows on upper Fish Creek, just off Sherman Pass Road, 20 Jun 1982, *Sanders 2750* (UC); lake on the ridge between Rattlesnake Meadow and Long Meadow, 7600 ft, 28 Jul 1965, *Twisselmann 11316* (CAS); Horse Meadow, Kern Plateau, 7400 ft, Jul 1966, *Howell & True 41724* (CAS); Embree Mine jeep road, near the turn to the new road (S slope of Sherman Peak), 7300 ft, 2 Aug 1969, *Twisselmann 15903* (CAS, SD); Long Meadow, 7800 ft, 26 Jun 1970, *Twisselmann 16829* (CAS); Bakeoven Meadows, 8100 ft, 13 Jul 1950, *Howell 26801* (CAS); Ground Hog Meadow, 8700 ft, 21 Jul 1942, *Ferris & Lorraine 10717* (DS); Fish Creek Campground, 9 mi NW of Kennedy Meadows, 7200 ft, 28 May 1973, *Keefe 13176* (CAS); Trout Creek, 7500 ft, 3–6 Jul 1964, *Hardham 12134a* (CAS); Siberian Pass Creek, 11,000 ft, 25 Jul 1949, *Howell 25729* (CAS); Taylor Creek, S of Church Dome, 7200 ft, 1

Oct 1969, *Howell & True 46460* (CAS); 1 2/10 mi S of Troy Meadows, 7800 ft, 4 Jul 1967, *Howell & True 42982* (CAS); Lloyd's Meadow Basin: Lower Freeman Creek, 5500 ft, 14 May 1971, *Shevock 240* (CAS); three mi NE of Beach Meadow, 8200 ft, 7 Aug 1967, *Howell et al. 53789* (CAS); Cannell Meadow, 7200 ft, 28 Aug 1967, *Twisselmann 13619* (CAS); Paloma Meadows, 8500 ft, 16 Jul 1980, *Howell et al. 53864* (CAS); Inyo Co., Horseshoe Meadow, 10,000 ft, 14 Aug 1995, *DeDecker 6504* (RSA); Cottonwood Creek, 11,000 ft, 18 Jul 1949, *Munz 14046* (RSA); Cottonwood Lakes, 11,000 ft, 18 Jul 1949, *Munz 14057* (RSA); Manter Meadow, 7100 ft, 28 Jun 1969, *DeDecker 2136* (RSA); Rock Creek near Mount Whitney, 9600 ft, 20 Jul 1912, *Jepson 5058* (JEPS).

Phenology and Pollination Biology—Flowering occurs between May and August and fruiting between June and September. *Erythranthe barbata* has relatively large flowers, a narrow corolla tube that expands abruptly to the limb, and exhibits approach herkogamy. Presumably the beard of trichomes on the lower limb serves as an advertisement to pollinators. Based on evidence from corolla morphology, this species is presumed to be primarily outcrossing; but pollinators were not observed on flowers of this species over the course of this study.

Distribution and Habitat—*Erythranthe barbata* is endemic to the eastern Sierra Nevada in Kern, Tulare, and Inyo counties, California. Plants primarily occur on decomposed granite at the edges of meadows and streams but also occasionally in open sandy barrens and in the understory of lodgepole pine forest. *Erythranthe barbata* is associated with the following vegetation communities: pinyon-juniper woodland, montane coniferous forest, subalpine forest, riparian scrub, montane meadows, and alpine barrens. Elevation 1800–3400 m (5900–11,200 ft). Associated species: *Abies concolor* (Gordon & Glend.) Hildebr., *Aquilegia formosa* Fisch. ex DC., *Achillea millefolium* L., *Artemisia douglasiana* Besser, *A. tridentata*, *Calocedrus decurrens*

(Torr.) Florin, *Collinsia parviflora*, *Deschampsia danthonioides* (Trin.) Munro, *Erythranthe breweri* (Greene) G.L.Nesom & N.S.Fraga, *E. floribunda* (Douglas ex Lindl.) G.L.Nesom, *E. guttata* (Fisch. ex DC.) G.L.Nesom, *E. moschata* (Douglas ex Lindl.) G.L.Nesom, *E. primuloides* (Benth.) G.L.Nesom & N.S.Fraga, *Juncus* L. spp., *Perideridia parishii* (J.M.Coult. & Rose) A.Nelson & J.F.Macbr., *Phacelia exilis* (A.Gray) G.J.Lee, *Pinus balfouriana* Grev. & Balf., *P. contorta* Loudon subsp. *murrayana* (Grev. & Balf.) Critchf., *P. jeffreyi*, *P. monophylla*., *Polygonum polygaloides* Meisn. subsp. *kelloggii* (Greene) J.C.Hickman, *Quercus chrysolepis*, and *Q. wislizeni* A.DC.

Phylogenetic Relationships and Similar Species—*Erythranthe barbata* is inferred to share a close relationship with *E. discolor* (Fraga unpubl.). These species can be distinguished by corolla morphology and color throughout the majority of their range, but they are known to hybridize in the southern Sierra Nevada where they co-occur. *Erythranthe barbata* typically has bicolored flowers with a maroon-purple adaxial lip and a yellow abaxial lip, but occasional plants have flowers that are entirely yellow. The frequency of yellow versus bicolored plants can change from year to year. The corolla has a distinct cylindrical tube that is relatively narrow and expands abruptly to a bearded palate. In contrast, *E. discolor* has monochromatic flowers that are usually yellow, less frequently pink, and the corolla tube-throat is funnelform and expands gradually to a sparsely bearded to glabrous palate.

Etymology—*Erythranthe barbata* is named for the beard of trichomes on the lower limb of the corolla.

Conservation Status—*Erythranthe barbata* is not currently ranked by the California Native Plant Society (CNPS) as rare, threatened, or endangered. *Erythranthe barbata* is endemic to the southern Sierra Nevada in California and occurs in several high-use areas throughout its range.

This species has been observed in areas that are subject to impacts from grazing, offhighway vehicle use, hiking trails, campgrounds, and road maintenance. It was considered by CNPS for ranking in 1994, but was rejected because it was too common (CNPS 2012, Skinner et al. 1994). However, the conservation status of this species should be reevaluated in light of the current taxonomic revision because at the time it was considered as a possible synonym of *E. montioides*. At the time of its evaluation by CNPS, it was considered as a possible synosnym of *E. monitoides* and populations that are currently identified as *E discolor* and *E. montioides* may have been included within the distribution of *E. barbata*.

3. ERYTHRANTHE CALCICOLA N.S.Fraga & D.A.York, "limestone monkeyflower". Aliso 30: 54–58, 58–59. 2012.—TYPE: U.S.A. California: Inyo Co., Death Valley National Park, Panamint Mountains, along a saddle 420 m NE of Aguereberry Point, 36.219340N, 117.029350W (NAD 83), 1780 m/5850 ft, 9 Apr 2004, *York & Schoenig* 2849 (holotype: RSA!; isotypes: CAS!, US!).

Annual herb. Plants 2–15 cm tall, 1–8 cm wide, glandular pubescent. Stems erect, simple to branched, internodes 0.5–1.5 cm. Cotyledons persistent, ovate to round, 1–6 mm long, with clasping bases. Leaves opposite, epetiolate or with petioles short (0.5–1 mm long), connate at the base; blades 3–25 mm long, 2–10 mm wide, lanceolate to ovate, palmately veined with three prominent veins from the base in wider leaves, margins entire or sometimes toothed. Flowers solitary in each axil, fruiting pedicels 3–20 mm, exceeding calyx, erect to ascending. Calyx 4–8 mm long, 2–4 (5) mm wide, widely campanulate to cylindric, enlarging in fruit; costa prominent, darker than intercostal regions; calyx teeth equal, 0.5–1 mm long, acute to obtuse, margins ciliate. Corolla 6–13 mm long, 3–7 (9) mm wide, yellow or white with a yellow throat, lobes emarginate,

limb weakly zygomorphic; tube-throat 5–10 mm long, cylindric, expanding gradually to the limb, palate sparsely bearded, spotted with red markings. Stamens didynamous, 3–9 mm long; filaments and anthers yellow, glabrous, included. Gynoecium 5–10 mm long, ovary brown to straw colored, style and stigma light yellow to white, glabrous; stigma lobes slightly apically fringed, subequal, included. Capsules 4–8 mm long, included to equal to calyx, cylindric, thin walled and fragile, dehiscing to base along both sutures. Seeds 0.5–0.9 mm long, 0.2–0.3 mm wide, elliptic to ovoid, brown.

Representative Specimens Examined—U.S.A. California: Inyo Co., Death Valley National Park, Panamint Mountains, Panamint Mountains, ridge just E & below Aguereberry Point, 1780 m/ 5830 ft, 18 Apr 2001, *York et al. 2536* (DEVA); Death Valley National Monument, Panamint Mountains, Emigrant Canyon 2 mi E of Burro Spring on the Gold King mining claim, 1463 m 11 Apr 1978, *Holland & Schramm 1801* (UCR, UNLV); Panamint Mountains, Arrastra Spring, 5200 ft, 17 May 1978, *Schramm & Holland 1996* (UNLV); Panamint Mountains, Wildrose Canyon, 4290 ft, 29 Apr 1973, *Fisher 1643* (UNLV); Funeral Mountains, Keane Canyon, 3800 ft, 30 Apr 1937, *Gilman 2317* (DEVA, RSA); Funeral Mountains, Keane Spring Canyon, 3000 ft, 30 Apr 1937, *Gilman 2318* (RSA); Funeral Mountains, near Kean Spring, 3700 ft, 24 Apr 1978, *DeDecker 4600* (RSA); Funeral Mountains, canyon NE of Red Amphitheatre, 3750 ft, 7 May 1983, *Annable et al. 716* (UNLV); Saline Valley, 4700 ft, 8 Apr 1967, *DeDecker 1671* (RSA); Saline Valley, 4900 ft, 8 Apr 1967, *Munz 18017* (RSA); Inyo Mountains, Marble Canyon, 5500 ft, 5 May 1962, *Raven 17550* (RSA); Inyo Mountains, Teufel Canon, 5000 ft, 30 May 1939, *Jaeger s.n*. (RSA); Waucoba Road, 22.4 mi E of junction with Westgard Road, toward Eureka Valley, 5650 ft, 22 May 1976, *Davidson 3999* (RSA); Last Chance Range, W of Last Chance Spring, 6200 ft, 24 May 1978, *DeDecker 4688a* (RSA); N end of Saline Valley Road, ca. 14 mi

S of Death Valley Road, 5600 ft, 8 Apr 2008, *Fraga et al. 1995* (RSA); Gold King Mining claim, off Wildrose Road, ca. 6 mi S of Hwy 190, 4900 ft, 17 Apr 2010, *Fraga et al. 3306* (RSA); ridge NE of Aguereberry Point, 5600 ft, 17 Apr 2010, *Fraga et al. 3308* (RSA); SE slope above Wildrose Canyon, 4400 ft, 24 Apr 2010, *Fraga & Prince 3310* (RSA); Death gentle slope N of road to Aguereberry Point, ca. 2.6 mi E of Wildrose Road, 5200 ft, 24 Apr 2010, *Fraga & Prince 3315* (RSA); Death Valley Road, ca. 22 mi E of Hwy 168, N side of the road on slope, 5800 ft, 9 May 2011, *Fraga 3347* (RSA); Marble Canyon off Saline Valley, Waucoba Road, 5900 ft, 9 May 2010, *Fraga 3348* (RSA); Mono Co., White Mountains, 1 mi up Coldwater Canyon in side drainage, 5450 ft, 15 Apr 1986, *Morefield & McCarty 3419* (RSA). Nevada: Clark Co., Spring Mountains, ridge NE of Grassy Spring, 5200 ft, 14 May 1983, *Peterson & Lathrop 960* (UNLV); Spring Mountains, slopes W of Grassy Spring, 5500 ft, 15 May 1983, *Peterson & Lathrop 965* (UNLV); Pintwater Range, E of Tim Spring, 5800–6100 ft, 5 May 1979, *Ackerman 30434* (UNLV, RENO); Nye Co., Bajada W of Ranger Mountains on old Indian Spring Road, 24 Apr 1978, *Cochrane & Holland 991* (UNLV); Bare Mountains, S slope of Meiklejohn Peak, above Secret Pass, 5200 ft, 9 Jun 1995, *Niles et al. 4493* (UNLV); Nevada Test Site, along Mercury Highway, 20 mi N of Mercury on old road to Indian Springs, 3200 ft, 24 Apr 1978, *Holland & Cochrane 1910* (UNLV); N and W end of Spotted Range, 4000 ft, 24 Apr 1969, *Beatley 8033* (RSA, RENO); Esmeralda Co., Silver Peak Range, 1.3 road mi W of Cave Springs on the Coyote Road from Silver Peak to Fish Lake Valley, 7200 ft, 25 Jun 1987, *Tiehm 11335*(RSA).

***Phenology and Pollination Biology*—**Flowering occurs between April and June; fruiting plants most commonly seen in May and June. *Erythranthe calcicola* has relatively small flowers that are early deciduous. Corollas were observed falling by mid-day and are presumed to be one-day flowers. Flowers of this species exhibit approach herkogamy but the distance between the stigma

and anthers is sometimes less than 1 mm, suggesting that this species has a mixed mating system with a mechanism to facilitate self-pollination with some frequency. No floral visitors were observed over the course of this study.

Distribution and Habitat.—*Erythranthe calcicola* is known from several mountain ranges in the northern Mojave Desert of eastern California and southwestern Nevada as follows; Funeral Mountains, Inyo Mountains, Last Chance Range, Panamint Mountains, White Mountains (California); Bare Mountain, Pintwater Range, Sheep Range, Silver Peak Range, Spotted Range, Spring Mountains (Nevada). Plants of this species primarily occur on talus slopes on substrates derived from carbonate rock and are associated with the following vegetation communities: creosote bush scrub, Joshua tree woodland, and juniper woodland. Elevation 915–2165 m (3000–7100 ft). Associated species: *Antirrhinum kingii* S.Watson, *Ambrosia dumosa* (A.Gray) W.W.Payne, *Artemisia tridentata*, *Atriplex confertifolia* (Torr. Fre´m.) S.Watson, *Chylismiella pterosperma* (S.Watson) W.L.Wagner & Hoch, *Coleogyne ramosissima* Torr., *Diplacus bigelovii* (A.Gray) G.L.Nesom & N.S.Fraga, *Ephedra nevadensis* S.Watson, *Ephedra viridis* Coville, *Eriogonum fasciculatum*, *Ericameria linearifolia* (DC.) Urbatsch & Wussow, *Grayia spinosa* (Hook.) Moq., *Juniperus osteosperma* (Torr.) Little, *Krascheninnikovia lanata* (Pursh) A.Meeuse & A.Smit, *Larrea tridentata* (Sesse´ & Moc¸. ex DC.) Coville, *Linanthus filiformis* (A.Gray) J.M.Porter & L.A.Johnson, *Nama demissum* A.Gray, *Phacelia fremontii* Torr., *Pinus monophylla*, *Sphaeralcea ambigua* A.Gray, *Stipa speciosa* Trin. & Rupr., *Xylorhiza tortifolia* (Torr. & A.Gray) Greene, and *Yucca brevifolia* Engelm.

Phylogenetic Relationships and Similar Species—*Erythranthe calcicola* is morphologically similar to *E. rubella* and is inferred to share a close relationship with this species (Fraga unpubl.). These species are easily distinguished by leaf shape and calyx morphology. The leaves of *E.*

calcicola are lanceolate to ovate and the calyx is widely campanulate to cylindric with margins ciliate. In comparison, the leaves of *E. rubella* are linear to elliptic and the calyx is narrowly cylindric with glabrous margins.

Etymology—The specific epithet and common name were chosen because *E. calcicola* appears to occur nearly exclusively on substrates of carbonate (limestone) origin.

Conservation Status—All known occurrences for *E. calcicola* are on public lands administered by public agencies: Bureau of Land Management, Department of Defense, National Park Service and US Fish and Wildlife Service. *Erythranthe calcicola* is known from fewer than 20 occurrences and is therefore of limited distribution and should be considered for conservation status by the federal, state, and other agencies that manage this species. Historic mining operations and the presence of exotic plant species were the only visible disturbances observed over the course of field surveys for this study.

4. ERYTHRANTHE CARSONENSIS N.S.Fraga, "Carson Valley monkeyflower". Aliso 30: 59, 61,62. 2012.—TYPE: U.S.A. Nevada, Carson City: Carson Valley, eastern terminus of Clear Creek Road at the base of Prison Hill, 39.7943.540N, 119.44919.230W (NAD 83), 1460 m/4800 ft, 17 May 2010, *Fraga, Morefield, & Howle* 3377 (holotype: RSA!; isotypes: US!, UC!).

Mimulus rubellus var. *latiflorus* S.Watson, United States Geological Exploration of the Fortieth Parallel. vol. 5, botany: 226. 1871.—TYPE: U.S.A. Nevada, Carson City Co., Carson City, Apr 1868, *Watson 798* (GH!).

Annual herb. Plants 1–7 cm tall, 1–4.5 cm wide, sparsely glandular. Stems erect, simple to branched, internodes 0.2–1 cm, usually obscuring the stem. Cotyledons persistent, round to

reniform , 0.2– 1.2 mm long, with clasping bases. Leaves opposite, epetiolate, connate at the base; blades 3–17 mm, long 1–5 mm wide, linear to spatulate, palmately veined with three prominent veins from the base in wider leaves, margins entire. Flowers solitary in each leaf axil, fruiting pedicels 3–14 mm, exceeding calyx, ascending to erect. Calyx (3) 5–7 mm long, 2–3 (4) mm wide, campanulate to widely urn shaped, enlarging in fruit, costa prominent, and darker than the glabrous intercostal regions; calyx teeth equal, 0.5–1 mm long, acute and slightly recurved, margins glabrous. Corolla 11–18 mm, long 7–15 mm wide, yellow with red striations on the adaxial surface of the upper lobes, lobes bifid, limb strongly zygomorphic; tube-throat (5) 8–11 mm long, cylindric, expanding abruptly to the limb, palate bearded, and maculate with red markings and one large central spot. Stamens didynamous, 5–13 mm long; filaments and anthers white to light yellow, glabrous, included. Gynoecium 6–15 mm long, ovary brown to straw colored, style and stigma yellow, glabrous; stigma lobes apically fringed and subequal, equal with the throat to exserted from the orifice. Capsules 3–6 mm long, included in the calyx, campanulate, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.5– 0.8 mm long, 0.1–0.2 mm wide, elliptic, brown.

Representative Specimens Examined—U.S.A. California: Alpine Co., near Fredericksburg, 23 May 2011, *Fraga & Matson 3803* (RSA). Nevada: Carson City, Eagle Valley, 0.5 mi S of Carson Hot Springs, 0.5 mi ENE of Lone Mountain summit, 4690 ft, 12 May 1991, *Morefield 5452* (RSA); Empire City, *Jones s.n*. (POM); Eagle Valley, 4743 ft, 7 Jun 1902, *Baker 1023* (POM); Eagle Valley, 4743 ft, 7 Jun 1902, *Baker 1029* (RSA); Topsy Lane S of Clear Creek, 4800 ft, 15 May 1979, *Genz 9097* (RENO); corner of Topsy Lane and Hwy 395, on the N side of the road, 4800 ft, 15 May 2009, *Fraga & Morefield 2743* (RSA); corner of Lynnette Avenue and Arthur Drive, NE corner across from Nevada DOT building, 4800 ft, 16 May 2010, *Fraga 3370*

(RSA); corner of Old Hot Springs Road and Goni Road, 4700 ft, 16 May 2010, *Fraga 3371* (RSA); Douglas Co., near trailhead parking for Faye-Luther Trail, 4850 ft, 15 May 2009, *Fraga 2744* (RSA); 5 mi S of Genoa, 27 Apr 1950, *Woodbury 23* (RENO); 3 mi S of Carson City, 4600 ft, 11 Apr 1941, *Solari 19* (RENO); on Gardenville Hwy, SW of Carson Indian Agency, 4700 ft, 24 Apr 1937, *Archer 5047* (RENO); Indian Hill, 3 mi S of Carson City near the Jacks Valley Road, 4850 ft, 13 Apr 1976, *Wise 4850* (RENO); Jacks Valley Management Area near Plymouth Drive turn-off from Hwy 395, 4800 ft, 16 May 2010, *Fraga 3366* (RSA); near Plymouth Drive turn-off from Hwy 395, 4800 ft, 16 May 2010, *Fraga 3367* (RSA); James Lee Memorial Park near baseball field, 4800 ft, 16 May 2010, *Fraga 3369* (RSA); W of elementary school and S of Jacks Valley Road, 5000 ft, 17 May 2010, *Fraga et al. 3372* (RSA); N side of Jacks Valley Road near Jacks Valley Management Area, 5100 ft, 17 May 2010, *Fraga 3374* (RSA); Washoe Co., Franktown, 11 May 1925, *P.A.L. s.n.* (RENO); Red Rock Canyon, 4800 ft, 30 Apr 1960, *Urrutia s.n.* (RENO)

***Phenology and Pollination Biology*—**Flowering occurs between late April and June and fruiting is most common in May and June. *Erythranthe carsonensis* has relatively large flowers (Fig. 2.3), a long and distinct corolla tube that expands abruptly to the bearded limb. This species also exhibits approach herkogamy and has prominent nectar guide patterns on the palate. Based on evidence from corolla morphology, this species is presumed to be primarily outcrossing. Several insects were observed visiting this species, including skipper butterflies (Hesperiidae), and halictid bees (Halictidae).

Distribution and Habitat*—*Erythranthe carsonensis is endemic to northwestern Nevada in Carson City, Douglas, and Washoe counties, and adjacent Alpine County in California. There are ten known extant occurrences across its range; surveys of potential habitat may reveal additional

occurrences. Most known occurrences are located in Carson Valley region, with one disjunct occurrence documented in Red Rock Canyon approximately 36 mi to the north. This species occurs in open areas of Great Basin sagebrush/bitterbrush scrub in coarse granite soils on gentle to moderate slopes (0–15 percent), usually on N aspects but also occasionally on S–SW aspects. Elevation 1400–1580 m (4600–5200 ft). Associated species (* denotes non-native species): *Artemisia tridentata*, **Bromus tectorum* L., *Calyptridium roseum* S.Watson, *Camissonia parvula* (Nutt. ex Torr. & A.Gray) P.H.Raven, *Cryptantha circumscissa* I.M.Johnst., *Chrysothamnus viscidiflorus* Nutt., *Descurainia pinnata* (Walter) Britton, *Diplacus nanus* (Hook. & Arn.) G.L.Nesom & N.S.Fraga, *Draba verna* L., *Ephedra viridis*, **Erodium cicutarium* (L.) L'He´r., *Erythranthe suksdorfii*, *Grayia spinosa*, *Gymnosteris nudicaulis* (Hook. & Arn.) Greene, *Layia glandulosa* Hook. & Arn., *Plectritis* (Lindl.) DC. sp., *Phacelia curvipes* Torr. Ex S.Watson, *Phacelia linearis* (Pursh) Holz., *Plagiobothrys* Fisch. & C.A.Mey. sp., *Prunus andersonii* A.Gray, *Purshia tridentata*, **Sisymbrium altissimum* L., *Uropappus lindleyi* (DC.) Nutt., *Vulpia octoflora* (Walter) Rydb., *V. microstachys* (Nutt.) Munro, and *Zigadenus paniculatus* (Nutt.) S.Watson.

Phylogenetic Relationships and Similar Species—*Erythranthe carsonensis* is inferred to have a sister relationship with *E. suksdorfii* (Fraga unpubl.). These species are easily distinguished by corolla morphology and leaf shape. *Erythranthe carsonensis* has a longer corolla tube-throat (8–11 mm) than *E. suksdorfii* (4–6 mm) and the corolla lobes are bifid. In contrast, the lobes of *E. suksdorfii* are weakly notched to entire. Leaves of *E. carsonensis* are linear to spatulate and are clasping at the base, whereas leaves of *E. suksdorfii* are linear to lanceolate or ovate and are not clasping at the base.

Etymology—The specific epithet and common name allude to the Carson Valley region of Nevada where this species primarily occurs.

Conservation Status—Threats to *Erythranthe carsonensis* include loss of habitat due to development and agriculture, the presence and abundance of non-native species, and recreation; off-highway vehicle trails, and a baseball park have been noted as sources of disturbance at extant occurrences. Evidence from herbarium specimen label data, literature, and personal observations indicate that development in the region has severely fragmented and reduced populations. Sereno Watson noted (1871) that this species formed "bright patches of color among the sage-brush in the lower valleys." A population that was observed to be marginal with frewer than 100 individuals in 2010 had been noted as (plants) "common" in 1979 (RENO 057126). Attempts to relocate historic occurrences from herbarium specimen records found several populations that are now extirpated. Because *E. carsonensis* has a limited distribution, is known from few occurrences, and has several threats documented throughout its range, it is recommended that the species' conservation status be evaluated with Federal, State, and local agencies, and conservation organizations.

5. ERYTHRANTHE DIFFUSA (A.L.Grant) N.S.Fraga "Palomar monkeyflower'' Phytoneuron 39: 1–60. 2012.

Mimulus diffusus A.L.Grant, Ann. Missouri Bot. Gard. 11: 257–258.1924 [1925].—TYPE: U.S.A. California: San Diego Co., Palomar, 29 May 1901, *Jepson 1959* (holotype: MO!; isotypes: DS!, JEPS, NY digital image!, UC!, US digital image!).

Mimulus grantianus Eastw., Proc. Calif. Acad. Sci. (ser. 4) 20: 153. 1931.—TYPE: U.S.A. California: San Diego Co., Campo, 23 Apr 1920, *Eastwood 9442* (holotype: CAS digital image!).

Annual herb. Plants 3.5–25 cm tall, 1–19 cm wide, minutely puberulent. Stems erect, simple to branched, internodes 1–4 cm. Cotyledons persistent, obovate to round, 0.2–1 mm long, with clasping bases. Leaves opposite, epetiolate or with petioles short (0.5–1); blades 2–18 mm long, 1–10 mm wide, linear-oblanceolate to ovate, palmately veined with three prominent veins from the base in wider leaves, margins entire or sometimes toothed. Flowers solitary in each axil, fruiting pedicels (2) 12–60 (–68) mm, exceeding calyx, erect to ascending, or spreading horizontally. Calyx 4–7 mm long, (2) 3–6 mm wide, campanulate, enlarging in fruit; sometimes spotted red, costa weak, darker than intercostal regions; calyx teeth equal, 0.5–1 mm long, acute and spreading, margins glabrous. Corolla 11–20 mm long, 6–14 mm wide, pink to purple, lobes emarginate, limb weakly zygomorphic; tube-throat 8–14 mm long, funnelform, expanding gradually to the limb, palate sparsely bearded with two yellow ridges. Stamens didynamous, 5–12 mm long; filaments and anthers white, glabrous, included. Gynoecium 8–12 mm long, ovary white to pink, style and stigma white to pink, style pubescent in the distal half; stigma lobes apically fringed, equal, included in the corolla. Capsules 3–6 mm long, included in the calyx, campanulate, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.3–0.6 mm long, 0.1–0.2 mm wide, elliptic to ovoid, brown.

Representative Specimens Examined—U.S.A. California: Riverside Co., N slope of Agua Tibia Mtn., E of the Dripping Springs Alcove Area, 1640 ft, 3 May 1995, *Banks 0200* (RSA); Shipley multi species reserve, SW of Tucalota Creek, 1601 ft, 28 Apr 1995, *Bramlet 2397* (RSA); San Mateo County Wilderness area, San Mateo Canyon, 1200 ft, 12 May 1993, *Ross 7349* (RSA);

Santa Ana Mountains, SE and E side of Elsinore Peak, 3300 ft, 7 May 1991, *Boyd 6158* (RSA); lower flank of range along the Bedford Truck trail on ridge between Bedford and McBribe Canyons, 2800 ft, 10 May 1991, *Boyd 6207* (RSA); along Thomas Mtn. Rd. W of Hwy 74 and S of Lake Hemet, 10 Jun 1980,*Busenberg 1988* (RSA); San Jacinto Mountains above Pine Cove, 6800 ft, 6 Jun 1949,*Cooper 2002b* (RSA); Upper San Juan Canyon, along San Juan Loop Trail, 1706 ft, 26 Apr 2003, *Roberts 5661* (RSA); San Jacinto Valley, Santa Rosa Hills, Simpson Park, 2460 ft, 13 Apr 2008,*Wall 445* (RSA); San Diego Co., W face of Poser Mountain ca. 1/4 mi N of the intersection of Conejos Truck Trail and Viejas Grande Road, 2 Apr 1995, *Hirshberg 260* (RSA); Tecate Mountain, 3608 ft, 26 Apr 1969, *Moran 15835* (RSA, UC); N of Hauser Mountain: SW of Morena Lake and NW of Cameron Corners, 1837 ft, *Rebman et al. 8930* (RSA); E side of El Prado Meadow at Laguna Camp, 5500 ft, 23 May 2010, Fraga & *Brock 3389* (RSA).

MÉXICO. Baja California: 5 km W of La Rumorosa, Sierra Juarez, 14 Apr 1979, *Moran s.n.* (RSA); E of main summit Sierra Blanca, 1175 m, 16 May 1976, *Moran 23241* (RSA); 9 mi SE of Tecate, 12 May 1925, *Munz 9497* (RSA, UC); Sierra de Juarez, Laguna Hanson, Constitución National Park, 1625 m, 28 May 1983, *Thorne et al. 55769* (UC).

Phenology and Pollination Biology—Flowering occurs from late April to June and fruiting is most common in June and July. *Erythranthe diffusa* has relatively large flowers with distinctive yellow nectar guides and approach herkogamy. Based on evidence from corolla morphology, this species is presumed to be primarily outcrossing, but no insect visitors were observed over the course of this study.

Distribution and Habitat—*Erythranthe diffusa* is endemic to the Peninsular Ranges in southern California, USA, and Baja California, MexicoThis species occurs in moist areas in openings of

chaparral, dry meadows in pine and oak woodlands, grassland savanna, and riparian scrub. Elevation 300–2100 m (980–6800 ft). Associated species include: *Artemisia californica* Less., *Adenostoma fasciculatum* Hook. & Arn., *Ceanothus crassifolius* Torr., *Chaenactis glabriuscula* DC., *Collinsia concolor* Greene, *C. parviflora*, *Eriodictyon crassifolium* Benth., *Lasthenia californica* DC. ex Lindl., *Melica imperfecta* Trin., *Plantago erecta* E.Morris, *Platanus racemosa* Nutt., *Plagiobothrys tenellus*(Nutt.) A.Gray, *Populus fremontii* S.Watson, *Quercus agrifolia* Ne´e, *Q. engelmannii* Greene, *Salvia apiana* Jeps., *S. mellifera* Greene, and *Zigadenus fremontii* (Torr.) Torr. ex S.Watson.

Phylogenetic Relationships and Similar Species—*Erythranthe diffusa* is inferred to have a close relationship with *E. purpurea* (Fraga unpubl.), but is easily distinguished from that species. *Erythranthe diffusa* is generally taller (3.5–25 cm) has pink flowers, and pedicels that spread horizontally. In contrast, *E. purpurea* is 3–10 cm tall, has pink to purple flowers with the upper lip darker than the lower lip, and pedicels erect to ascending.

Etymology—*Erythranthe diffusa* is named for the diffuse branching habit which is characteristic of this species.

Conservation Status—*Erythranthe diffusa* currently has a CNPS Rare Plant Rank of 4.3, which means it is uncommon in California but not very endangered, and a California State Rank of S3.3 which means it is vulnerable but no current threats are known. In northwestern Baja California this species is being considered for a rank of 2A which means that it is considered rare in the California floristic province of Baja California but is more common in the state of California (O'Brien et al. 2010, O'Brien personal communication). Natureserve provides a Global Rank of G4Q, which means it is apparently secure considering the populations outside of the US, and is marked with a Q to denote the taxonomic uncertainty associated with this species (CNPS 2013).

Erythranthe diffusa has a relatively widespread distribution. It is known from western Riverside Co. in California, USA, to northern Baja California, Mexico. Anthropogenic change including development, grazing, off-highway vehicle use, road and trail maintenance, and power line development have all been documented as possible threats to known occurrences. Therefore the threat ranks for this species should be reassessed by the appropriate agencies.

6. ERYTHRANTHE DISCOLOR (A.L.Grant) N.S.Fraga, "parti-colored monkeyflower" Phytoneuron 39: 1–60.2012.

Mimulus discolor A.L.Grant, Ann. Missouri Bot. Gard. 11: 257–258.1924 [1925].—TYPE: U.S.A. California: Kern Co., "gravelly slopes, Pah Ute Peak", *Purpus 5311* (holotype: MO!; isotypes: UC!, US digital image!).

Annual herb. Plants 5–12 (–15) cm tall, 0.5–4 cm wide, densely glandular puberulent. Stems erect, simple to branched, internodes 1–3 cm. Cotyledons persistent, obovate to ovate, 0.3–1.1 mm long, with clasping bases. Leaves opposite, epetiolate or with petioles short (1–2 mm); blades 6–25 mm long, 1–4 mm wide, linear to oblanceolate, palmately veined with three prominent veins from the base in wider leaves, margins entire. Flowers solitary in each axil, fruiting pedicels 6–32 mm, exceeding calyx, erect to ascending. Calyx 4–8 mm long, 2–4 mm wide, campanulate, enlarging in fruit; costa weak and slightly darker than intercostal regions, sometimes red dotted; calyx teeth equal, 0.5–1 mm long, acute, erect to slightly spreading in fruit, margins glabrous. Corolla 15–20 mm long, 7–15 mm wide, yellow and tinged red on adaxial surface of tube-throat, or deep pink to purple, lobes emarginate, limb strongly zygomorphic, tube-throat 8–15 mm long, funnelform, expanding abruptly to the limb, palate glabrous to sparsely bearded, mottled red on yellow flowered plants and 2 yellow ridges on pink flowered

plants. Stamens didynamous, 11–13 mm long; filaments and anthers yellow, glabrous, included. Gynoecium 13–14 mm long, ovary yellow, style yellow, and stigma white in yellow-flowered plants, and pink to white in pink-flowered plants, glabrous; stigma lobes apically fringed, subequal, included in the corolla. Capsules 4–7 mm long, included in the calyx, campanulate, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.5–0.8 mm long, 0.2–0.3 mm wide, elliptic to ovoid, brown.

Representative Specimens Examined—U.S.A. California: Kern Co.:,Greenhorn Mountains, Little Poso Creek Falls, 4500 ft, 23 May 1937, *Benson 8344* (RSA); Greenhorn Mountains, Rancheria Road from Shirley Meadows Campground to Sawmill Road, 21 May 1989, *Harper s.n.* (RSA); Greenhorn Mountains, Rancheria Road just S of Evans Flat Campground, 6100 ft, 13 Jun 2010, *Fraga & Brock 3474* (RSA); Kernville, 13 May 1891, *T.S. Brandegee s.n.* (UC); fork of Cannell Creek on Pine Flat, 7100 ft, 10 Jul 1963, *Twisselmann 8674* (RSA); Piute Mountains, Piute Mountain Road, ca. 1.5–2 mi N of French Meadow, 7200 ft, 31 May 2008, *Fraga 2147* (RSA); mouth of N fork of Esperanza Canyon, S of Marino Canyon at the E base of the Piute Mountains, 4300 ft, 18 Apr 2008, *Fraga et al. 2005* (RSA); 4 mi W on Piute Mountain Road from Kelso Valley Road, 5500 ft, 30 May 2010, *Fraga & De Groot 3413* (RSA); Piute Mountain/Saddle Springs Road, just E of Valley View Mine, 6725 ft, 12 Jun 2011, *Fraga & Jolles 3850* (RSA); Piute Mountains Brown Meadow, 7400 ft, 12 Jun 2011, *Fraga & Jolles 3855* (RSA); Piute Mountains, Piute Mountains Brown Meadow, 7400 ft, 12 Jun 2011, *Fraga & Jolles 3856* (RSA); Piute Mountains; Tulare Co., Cannell Meadows, 7000 ft, 15 Jun 1904, *Hall & Babcock 5113* (UC).

Phenology and Pollination Biology—Flowering occurs from April to June and fruiting is most common in June and July. *Erythranthe discolor* has two distinctive floral morphs—one is yellow

with red spots on the palate, and the other is pink with two yellow ridges on the palate. Populations can be monomorphic (usually yellow) or mixed, with the yellow morph most often in higher frequency. *Erythranthe discolor* exhibits approach herkogamy and has relatively large flowers with trichomes and nectar guide patterns on the lower limb. Based on evidence from corolla morphology this species is presumed to be primarily outcrossing. Halictid bees (Halictidae) have been frequently observed visiting flowers of this species and are presumed to serve as the primary pollinators.

Distribution and Habitat—*Erythranthe discolor* is endemic to the southern Sierra Nevada in Kern and Tulare counties, California. This species primarily occurs in decomposed granite in vernally wet depressions, swales, at the edges of streams, dry meadows, and in openings of pine forest, oak woodland, pinyon-juniper woodland, desert chaparral, and sagebrush scrub. Elevation 1310–2468 m (4300–8100 ft). Associated species: *Abies concolor*, *Artemisia tridentata*, *Cercocarpus betuloides*, *Claytonia perfoliata* Willd., *Collinsia callosa* Parish, *C. parviflora*, *Erythranthe androsacea*, *E. barbata*, *E. floribunda, E. guttata*, *E. suksdorfii*, *Fremontodendron californicum*, *Mimetanthe pilosa* (Benth.) Greene, *Muhlenbergia rigens*, *Phacelia exilis*, *Pinus jeffreyi*, *P. monophylla, Quercus chrysolepis*, *Q. kelloggii* Newb., *Q. wislizeni*, and *Salix lasiolepis*.

Phylogenetic Relationships and Similar Species—*Erythranthe discolor* is inferred to share a close relationship with *E. barbata* (Fraga unpubl.). A population of plants that are intermediate in morphology between *E. barbata* and *E. discolor* was observed in the Scodie Mountains in the southern Sierra Nevada, where these two species overlap in distribution (See the expanded discussion under *E. barbata*). *Erythranthe discolor* also shares a complicated relationship with a

group of populations that may represent an underscribed species, however more information is needed to resolve this relationship.

Etymology—The epithet for this species means "of different colors" and refers to the two color morphs that are present.

Conservation Status—There are twenty known occurrences of *E. discolor*. There is currently little known regarding occurrence status and population trends, but recent surveys have found *E. discolor* to be abundant where it occurs. Off-highway vehicle use, road maintenance, and campgrounds have been observed as possible sources of disturbance at known occurrences. Development has likely affected populations at lower elevations and several occurrences may have been extirpated in the vicinity of Kernville. *Erythranthe discolor* is of limited distribution and should be considered for conservation status by the California Native Plant Society and land managers where this species occurs.

7. ERYTHRANTHE GRACILIPES (B.L. Rob.) N.S. Fraga, "slender monkeyflower" Phytoneuron 39: 1–60 (2012).

Mimulus gracilipes B.L. Rob., Amer. Acad. Arts Sci. 26: 176. 1891.—TYPE: U.S.A. California: Mariposa Co., Mormon Bar, 20 Apr 1889, *Congdon s.n*. (holotype: GH!)

Annual herb. Plants 5–15 cm tall, 2–5 cm wide, glandular puberulent. Stems erect, simple to branched, internodes 0.5–2 cm. Cotyledons persistent, orbicular to ovate, 2–6 mm long, with clasping bases. Leaves opposite, epetiolate; blades (3) 7–13 mm long, 1–3 mm wide, ;elliptic to ovate, palmatley veined with three prominent veins from the base in wider leaves, margins entire or sometimes toothed. Flowers solitary in each axil, fruiting pedicels 8–25 mm, exceeding the calyx, erect to ascending. Calyx 4–7 mm long, 1–4 mm wide, campanulate, enlarging in fruit;

costa weak, darker than the intercostal regions; calyx teeth equal 0.5–2 mm long, acute to obtuse, and erect, margins ciliate. Corolla 10–17 mm long, 5–15 mm wide, pink to rose-lavender, abaxial lobes bifid, two adaxial lobes much reduced and smaller than the three abaxial lobes, limb strongly zygomorphic; tube-throat 6–10 mm long, cylindric, expanding abruptly to the limb, palate glabrous to sparsely bearded with two yellow ridges, the orifice dark pink.Stamens didynamous, 5–7 mm long, filaments and anthers white, glabrous, included. Gynoecium 6–7 mm long, ovary pink, style and stigma pink, glabrous, fringed, included. Capsules 4–5 mm long, included to equal to the calyx, cylindric, thin walled, fragile, dehiscing to the base along both sutures. Seeds 0.2–0.3 mm long, 0.1–0.2 mm wide, round to ovoid, brown.

***Representative Specimens Examined*—**U.S.A. California: Fresno Co., Above the North Fork Kings River on forest road 11S12, 3.4 miles from Balch Camp, 2600 ft, 17 Apr 1982, *Shevock 9180* (CAS); Ca. 43 km NE of Fresno, 5.3 km E of Tollhouse, 1015 m, 23 May 1988, *York 2124* (CAS, JEPS); 2.8 mi E USFS road 10S02 (along USFS Road 10S69); Haslett Basin, 2900 ft, 13 May 1975, *Haines 75142* (CAS, JEPS); just SW of United States Forest Service engineer's camp (Haslett Basin along Nutmeg Creek), Haslett Basin, Nutmeg Creek, 1850 ft 11 May 1975, *Haines 75245* (JEPS); 4 mi s of Highway 180 (2 mi n of Fresno-Tulare line, 1/2 mi w of Miramonte store, overlooking Mill Creek 100 yds downstream from Sand Creek Road), Miramonte, Junction of Mill Creek with Sand Creek Road, 3095 ft, 1 May 1960, *Linderman s.n.* (JEPS); 4.7 mi E Auberry (on Auberry Road), 3000 ft, 20 May 1963, *Weiler 63120* (JEPS); Auberry Road, 3700 ft, 25 Apr 1941, *Petersen 316* (JEPS); Both sides of Forest Road 9S07 2.3 mi N of Auberry Rd., Jose Basin, 3608 ft, 15 May 1998, *Schoenig s.n.* (UC); ca. 20 mi from Auberry (road 9S07 off railroad grade, ca. 1/4 mi E of road), 4200 ft, 24 Apr 1962, *Kirkhart 9* (JEPS); Sierra National Forest (USFS), Music quad, utility corridor, SCE hydroelectric towers &

access road, 3642 ft, 18 May 2003, *Walker s.n.* (SD); Madera Co., 0.3 mi W of Ahwahnee; Fresno Flats; in subdivision near the junction of Windy Gap Drive and Primrose Lane,2400 ft, 22 Apr 1996, *Taylor 15609* (JEPS); South Fork, 2700 ft, 10 May 1954, *Barneby 11449* (CAS); Mariposa Co., Bootjack Ranch, Apr 1892, *Congdon s.n.* (CAS); Pea Ridge Road, 5 Apr 1903, *Congdon s.n*. (UC), near Mormon Bar, 12 May 1893, *Congdon s.n.* (UC); Hales Ranch, May 1892, *Congdon s.n.* (UC).

Phenology and Pollination Biology—Flowering occurs from April to May and fruiting is most common in June. *Erythranthe gracilipes* has a distinctive corolla morphology where the two upper lobes are highly reduced compared to the lower three lobes. The limb expands abruptly from the tube-throat making the corolla appear nearly salverform. Pollinators were not observed as a part of this study, however given the unique symmetry of this species and the size of the flower relative to the vegetative body, this species is presumed to be primarily outcrossing.

Distribution and Habitat—*Erythranthe gracilipes* is endemic to the western foothills of the Sierra Nevada in Fresno, Madera and Mariposa counties, California. This species occurs in open areas in shallow decomposed granite soils often on the edges of large granite boulders primarily in openings in burned chaparral, yellow pine forest, and foothill woodland communities. Elevation 500–1300 m (1640–4300 ft). Associated species: *Arctostaphylos viscida* Parry subsp. *mariposa* (Dudley) P.V. Wells, *Ceanothus cuneatus* Nutt., *Collinsia tinctoria* Benth., *Eriodictyon californicum* (Hook. & Arn.) Torr., *Heteromeles arbutifolia* (Lindl.) M. Roem., *Leptosiphon filipes* (Benth.) J.M. Porter & L.A. Johnson, *Linanthus dichotomus* Benth., *Lupinus citrinus* Kellogg, *L. stiversii* Kellogg, *Madia exigua* (Sm.) A. Gray, *Malacothrix clevelandii* A. Gray, *Plagiobothrys tenellus* (Hook.) A. Gray, *Pinus jeffreyi, P. sabiniana* D.Don, *Quercus kelloggii*, *Q. wislizeni*, *Selaginella hansenii* Hieron., and *Trifolium willdenovii* Spreng.

Phylogenetic Relationships and Similar Species—*Erythranthe gracilipes* is inferred to have a sister relationship with *E. sierrae* (Fraga unpubl.). These species are easily distinguished by corolla morphology. *Erythranthe sierrae* has corolla lobes that are more or less equal in size and a tubethroat that is funnelform and expands gradually to the limb. In contrast, *E. gracilipes* has two reduced adaxial lobes that are smaller than the three abaxial lobes and a tube-throat that is cylindric and expands abruptly to the limb.

Etymology—The slender stalked monkeyflower, *Erythranthe gracilipes*, is a diminutive plant with slender stems and pedicels. The specific epithet is derived from gracilis which means slender.

Conservation Status—*Erythranthe gracilipes* has a CNPS rare plant rank of 1B.2 which means it is rare and fairly endangered in California. Only known from about 13 occurrences in the foothills of the Sierra Nevada, California (CNPS 2012), this species is a narrow endemic. Populations have been impacted by housing development and road maintenance and construction.

8. ERYTHRANTHE HARDHAMIAE N.S.Fraga, "Santa Lucia monkeyflower" Aliso 30: 64, 23–25. 2012.—TYPE: U.S.A. California: Monterey Co., Santa Lucia Mountains, mouth Los Burros Creek, 1 May 1960, *Hardham 5558* (holotype RSA!; isotypes CAS!, JEPS!).

Annual herb. Plants 2–13 cm tall, 1–13 cm wide, glabrous to minutely puberulent. Stems erect, simple to branched, internodes 1–3.5 cm. Cotyledons persistent, obovate to ovate, 0.1–1 mm long, with clasping bases. Leaves opposite, epetiolate; blades 2–12 mm long, 1–3 mm wide, linear to oblanceolate, palmately veined with three prominent veins from the base in wider leaves, margins entire or sometimes toothed. Flowers solitary in each axil, fruiting pedicels 10– 60 mm, exceeding calyx, erect to ascending, or spreading horizontally. Calyx 4–8 mm long, 2–4 mm

wide, campanulate, enlarging slightly in fruit; costa weak, darker than intercostal regions, sometimes spotted red; calyx teeth equal, 0.1–0.5 mm long, acute, with margins glabrous. Corolla 9–17 mm long, 7–11 mm wide, deep pink to purple, lobes bifid, limb strongly zygomorphic; tube-throat 5–10 mm long, funnelform to cylindric, expanding abruptly to the limb, palate and orifice densely bearded with two yellow ridges. Stamens didynamous, 5–11 mm long; filaments and anthers white to pink, and included to occasionally exserted from the orifice, glabrous. Gynoecium 7–12 mm long, ovary pink, style and stigma pink, glabrous, stigma lobes apically fringed, subequal, equal to the tube to exserted from the orifice. Capsules 2–5 mm long, included in the calyx, cylindric, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.3–0.5 mm long, 0.1–0.2 mm wide, elliptic to ovoid, brown.

Representative Specimens.—U.S.A. California: Monterey Co., Vineyard Canyon Road to Parkfield (E side of summit), 9 Apr 1961, *Hardham 6762* (JEPS); Vineyard Canyon Road, N side of road just E of summit, 2300 ft, 2 May 2010, *Fraga 3344* (RSA); Santa Lucia Mountains, S of Los Burros Creek, 9 Apr 1961, *Hardham 5568* (SBBG); Santa Lucia Mountains, Los Bueyes Creek Road, 2 Apr 1960, *Hardham 5480* (CAS, RSA, JEPS); Santa Lucia Mountains, road from San Antonio Mission to The Indians (Del Venturi Caves), 7 Apr 1960, *Hardham 5392* (JEPS); San Luis Obispo Co.: Santa Lucia Mountains, 1 mi NW of Bee Rock, 1000 ft, 28 Mar 1960, *Hardham 5252* (JEPS, RSA, SBBG).

Phenology and Pollination Biology—Flowering occurs from late March to May and fruiting is most common in May. *Erythranthe hardhamiae* has relatively large flowers with distinctive yellow nectar guides, an exserted stigma, and approach herkogamy. Based on evidence from corolla morphology, this species is presumed to be primarily outcrossing, but no pollinators were observed over the course of this study.

Distribution and Habitat—*Erythranthe hardhamiae* is endemic to the Coast and Inner Coast ranges in Monterey and San Luis Obispo counties, California. This species occurs in sandy soils in openings of chaparral, and in sand-filled crevices of sandstone outcrops. Elevation 300–500 m (1000–1650 ft). Associated species (* denotes non-native species): *Adenostoma fasciculatum*, *Camissonia* Link sp., *Chorizanthe* R.Br. ex Benth. sp., *Crassula connata*, **Erodium botrys* (Cav.) Bertol., **E. cicutarium* (L.) Aiton, *Eriogonum fasciculatum*, *Festuca microstachys* Nutt., **F. myuros* L., *Minuartia californica* (A.Gray) Mattf., *M. pusilla* (S.Watson) Mattf., *Nemacladus* Nutt. sp., and *Quercus chrysolepis*.

Phylogenetic Relationships and Similar Species—*Erythranthe hardhamiae* appears to be closely related to *E. androsacea* (Fraga unpubl.). These species are easily distinguished from each other by fruiting pedicel characters and corolla size. *Erythranthe hardhamiae* has pedicels that are 10–60 mm long and spread horizontally in fruit, and a limb that is 7–11 mm when pressed. In contrast, *E. androsacea* has pedicels that are 5–30 mm long, are ascending to spreading in fruit, and do not spread horizontally, and a limb that is extended 3–7 mm when pressed.

Etymology—*Erythranthe hardhamiae* is named in honor of Clare Butterworth Hardham (1918–2010). Hardham was a botanist who lived in Paso Robles, California; she studied the flora of the Santa Lucia Mountains. Her contributions have been many as evidenced by the many plants that bear her name in the region. Hardham collected specimens of *E. hardhamiae* at nearly all of the currently known locations.

Conservation Status—There are eight known locations for *E. hardhamiae*; five are on lands managed by the Department of Defense (Fort Hunter Liggett), two are on private property, and one is in Los Padres National Forest. Grazing, road maintenance, the presence and abundance of

exotic plant species, and development have all been noted as sources of disturbance. *Erythranthe hardhamiae* is of limited distribution and should be considered for Conservation Status by the federal, state, and other agencies that manage this species.

9. ERYTHRANTHE MONTIOIDES (A.Gray) N.S.Fraga "montia-like monkeyflower" Phytoneuron 39: 1–60. 2012.

Mimulus montioides A.Gray, Proc. Amer. Acad. Arts 7: 380.1868.—TYPE: U.S.A. California: Tulare Co., mountains E of Visalia, 17–18 Jun 1864, *Brewer 2785* (lectotype designated by Fraga, 2012: GH!).

Annual herb. Plants 3–9 cm tall, 1–13 cm wide, glabrous to minutely puberulent. Stems erect, simple to branched, internodes 0.5–1.5 cm. Cotyledons deciduous. Leaves opposite, epetiolate or with petioles short (0.5–1 mm); blades 4–15 mm long, 0.5–2 mm wide, linear to oblanceolate, palmately veined with three prominent veins from the base in wider leaves, margins entire. Flowers solitary in each axil, fruiting pedicels 3–15 mm, exceeding calyx, erect to ascending. Calyx is 3–6 mm long, 1–3 mm wide, campanulate, enlarging in fruit; costa weak, slightly darker than intercostal regions, sometimes spotted red; calyx teeth equal, 0.5–1 mm long, acute, margins ciliate. Corolla 10–17 mm long, 7–15 mm wide, yellow, lobes entire, limb strongly zygomorphic; tube-throat 6–11 mm long, funnelform, expanding gradually to the limb, palate glabrous to sparsely bearded, spotted with red markings. Stamens didynamous, 7–11 mm long, filaments and anthers yellow, glabrous, included. Gynoecium 10–13 mm long, ovary yellow to white, style and stigma white; glabrous; stigma lobes apically fringed, equal, included. Capsules 3–5 mm long, included to calyx, campanulate, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.5–0.7 mm long, 0.2–0.3 mm wide, elliptic to ovoid, brown.

Representative Specimens Examined—U.S.A. California: Fresno Co., Markwood Meadows, 5800 ft, Jun 1900, *Hall & Chandler 339* (CAS, UC); Hume Lake Christian Camp, 5400 ft, 14 Jun 1998, *Schoenig 98–36* (UC); 7.2 km S–SE of Hume Lake, vicinity of Weston Meadow, 1960 m, 28 Jun 1996, *York & Shevock 982* (CAS), on first road from Dinkey Creek Road, just W of Bald Summit, 13 Jul 2005, *Gowen 476* (JEPS); W end of Rabbit Meadow, W of Big Meadows, 7800 ft, 19 Jul 1979, *Heckard et al. 5142* (JEPS); E side of Kaiser Pass, near summit, 19 Jun 1997, *Wisura 5064* (RSA); Pittman Creek, above Huntington Lake, 27 Jul 1918, *Grant 1480* (RSA); trail to Nellie Lake, 8000 ft, 11 Jul 1917, *Grant 1080* (RSA); 9 mi S of General Grant National Park on road to Sequoia National Park, 26 Jul 1942, *Ferris & Lorraine 10827* (RSA, UC); trail to Dinkey Lakes, Dinkey Lakes Wilderness, 8800 ft, 12 Jul 2008, *Fraga & Brock, 2366* (RSA); Tulare Co.: Alta Trail, Giant Forest, 7500 ft, 8 Aug 1905, *Brandegee s.n.*(UC); SW of Stoney Creek Campground, between Sequoia and Kings Canyon National Parks, 6400 ft, 18 Jun 1956, *Tillett & Sternback 486* (UC); along road between Moro Rock and Crescent Meadow, 18 Jun 2011, *Fraga et al. 3869* (RSA).

Phenology and Pollination Biology—Flowering occurs from June to August and fruiting is most common in July and August. *Erythranthe montioides* exhibits approach herkogamy and has relatively large flowers. Based on evidence from corolla morphology and population densities this species is presumed to be primarily outcrossing. *Erythranthe monitoides* was observed in dense populations forming large floral displays in a year of ample precipitation. Solitary bees which are presumed to serve as the primary pollinators were observed visiting flowers within these large floral displays.

Distribution and Habitat—*Erythranthe montioides* is endemic to the Sierra Nevada in Fresno and Tulare counties, California, and is documented from 19 occurrences on Forest Service and

National Park Service lands. This species primarily occurs on the dry edges of meadows and in seasonally moist depressions in the open understory of mixed coniferous and lodgepole pine forest. Elevation 1645–2900 m (5400–9500 ft). Associated species: *Abies magnifica*, *Arctostaphylos* Adans. sp., *Calocedrus decurrens*, *Ceanothus* L. sp., *Diplacus leptaleus* (A.Gray) G.L.Nesom, *Erythranthe laciniata* (A.Gray) G.L.Nesom, *Leptosiphon* Benth. sp., *Lewisia triphylla* (S.Watson) B.L.Rob., *Pinus contorta* subsp. *murrayana*, *P. jeffreyi*, *P. lambertiana*, and *P. monticola* D.Don.

Phylogenetic Relationships and Similar Species—*Erythranthe montioides* is inferred to share a close relationship with *E. palmeri* (Fraga unpubl.) but is easily distinguished morphologically from that species. *Erythranthe montioides* has yellow flowers with entire lobes that are smaller (10–17 mm) than those of *E. palmeri* (15–25 mm). In contrast, *E. palmeri* has pink flowers that are notched on each lobe.

Etymology—*Erythranthe montioides* is named for its resemblance to the genus *Montia* L. (Montiaceae) and has been given the common name montia-like monkeyflower.

Conservation Status—*Erythranthe montioides* has been confused with other closely related species including *E. barbata*, *E. calcicola*, *E. carsonensis*, and *E. discolor*. It was previously thought to be a widely distributed species because of this taxonomic confusion. The majority of occurrences have not been surveyed in recent years; thus little information exists regarding population status and trends. Several hundred to several thousand individuals, however, were observed at Big Meadow and between Moro Rock and Crescent Meadow in 2010 and 2011. *Erythranthe montioides* should be evaluated for Conservation Status by the federal, state, and other agencies that manage this species.

10. ERYTHRANTHE PALMERI (A.Gray) N.S.Fraga "Palmer's monkeyflower" Phytoneuron 39: 1–60 (2012).

Mimulus palmeri A.Gray, Proc. Amer. Acad. Arts 12: 82. 1876.—TYPE: USA. California, San Bernardino Co.: Mohave River, 1 Jun 1876, *Palmer 321* (holotype GH!, isotypes MO!, PH, UC!, US digital image!).

Annual herb. Plants 4–17 cm tall, 1–15 cm wide; minutely puberulent. Stems are erect, simple to branched, internodes 1–4 cm. Cotyledons persistent, obovate/ovate to round, 0.2–1 mm long, with clasping bases. Leaves opposite, epetiolate or with petioles short (0.1–1 mm); blades are 3–17 mm long, 1–4 mm wide, linear to lanceolate, palmately veined with three prominent veins from the base in wider leaves, margins entire. Flowers solitary in each axil, fruiting pedicels 4–32 mm, exceeding calyx, erect to ascending, or spreading horizontally. Calyx 4–8 mm long, 2–4 mm wide, campanulate, enlarging in fruit; costa weak, darker than intercostal regions, sometimes red spotted; calyx teeth equal, 0.5–1 mm long, acute and spreading, margins ciliate. Corolla 15–25 mm long, 8–15 mm wide, pink to purple, lobes emarginate, strongly zygomorphic; tube-throat 10–19 mm long, funnelform, expanding gradually to the limb, palate glabrous to sparsely bearded with two yellow ridges. Stamens didynamous, 8–12 mm long, flaments and anthers yellow, glabrous, included. Gynoecium 12–16 mm long, ovary yellow, style and stigma pink, glabrous; stigma lobes apically fringed, subequal, included. Capsules 3–5 mm long, included in the calyx, campanulate, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.5–0.9 mm long, 0.1–0.3 mm wide, elliptic to ovoid, brown.

Representative Specimens Examined—U.S.A. California: Los Angeles Co., San Gabriel Mountains, Upper Big Tujunga Canyon, margin of Big Tujunga Creek T2N R11W, NE/4 SE/4 SE/4 sec 5, 3980–4040 ft, 8 Jun 1990, *Ross et al. 2987* (RSA); Chilao Creek headwaters, T3N,

R11W, NW/NE, sec 24, 5900 ft, 1 Jun 1968, *Wheeler s.n.* (RSA); Upper Big Tujunga at Vetter Gulch, 25 May 1963, *Wheeler 8258* (RSA); Pine Flats, 9 Jul, *Peirson 1124* (RSA); ca. 0.3 mi below Alder Saddle, along a dry branch of the S Fork of Little Rock Creek, 5300 ft, 30 Jun 1971, *Thorne & Tilforth 40764* (RSA); San Bernardino Co., San Bernardino Mountains, near Mojave River, about 0.5 mi W of junction between roads to Hesperia and Lake Arrowhead, 3200 ft, 10 May 1979, *Thorne & Prigge 52892* (RSA); E of Running Springs, W of Deer Lick Station, 6000 ft, 29 May 1992, *Hirshberg 33* (RSA); Summit Valley on Hwy 173, 5.4 mi NE of Hwy 138 junction and 1 mi S of the Grass Valley Creek crossing, 3280 ft, 24 Apr 1993, *Sanders & Spilman 13774* (RSA); Fredalba, 5000 ft, 8 Jun 1919, *Munz & Johnston 2855* (RSA); Hunsaker Flats, 5200 ft, 8 Jun 1919, *Munz & Johnston 2856* (RSA); Fish Camp, 6900 ft, 17 Jun 1921, *Johnston 2837* (RSA); NE of Rock camp station, N of Lake Arrowhead, 4785 ft, 21 May 2008, *Gross & Vanderplank 3420* (RSA); intersection of Forest Service roads 3N34 (Pilot Rock Road) and 3N33, 4800 ft, 21 May 2008, *Fraga et al. 2092* (RSA); Keller Peak Road, 7200 ft, 11 Jun 2008, *Fraga & Kempton 2190* (RSA); along OHV trail 1W17, N of Crab Flats, 5400 ft, 17 Jun 2008, *Fraga & Bell 2246* (RSA); 2.2 mi below junction for Smiley Park (along City Creek Road), 17 Jun 1953, *Bacigalupi et al. 4224* (JEPS); 9.7 mi above bridge crossing Deep Creek, Kinley Creek drainage, Deep Creek Grade, 4900 ft, 17 Jun 1953, *Bacigalupi et al. 4220* (JEPS); Horsethief Canyon, 15 May 1935, *Clokey & Anderson 6909* (JEPS); Strawberry Peak, 25 Jul 1901, *Abrams 1978* (DS).

***Phenology and Pollination Biology*—**Flowering occurs from April to July and fruiting is most common in June and July. *Erythranthe palmeri* exhibits approach herkogamy and has relatively large flowers. Based on evidence from corolla morphology this species is presumed to be

primarily outcrossing. Solitary bees have been observed visiting flowers of this species and are presumed to serve as the primary pollinators.

Distribution and Habitat—*Erythranthe palmeri* is restricted to the San Gabriel and San Bernardino Mountains of the Transverse Ranges in Los Angeles and San Bernardino counties. This species primarily occurs in decomposed granite in vernally wet depressions, swales, at the edges of streams and creeks, dry meadows, and in openings of pine forest, oak woodland, and desert chaparral. Elevation 976–2200 m (3200–7200 ft). Associated species (* denotes non-native species): **Bromus tectorum*, *Calochortus palmeri* S.Watson, *Castilleja lasiorhyncha* (A.Gray) T.I.Chuang & Heckard, *Ceanothus leucodermis* Greene, *Erythranthe breweri*, *E. guttata*, *E. suksdorfii*, *Eschscholzia californica* Cham., *Fremontodendron californicum*, *Gilia capitata* Sims, *Iris hartwegii* Baker var. *australis* Parish, *Phacelia mohavensis* A.Gray, *Pinus coulteri* Lamb. ex D.Don, *P. jeffreyi*, *Juncus mexicanus* Willd. ex Schult. & Schult.f., *Leptosiphon ciliatus* (Benth.) Jeps., *Madia minima* (A.Gray) D.D.Keck, *Platystemon californicus* Benth., *Quercus kelloggii*, *Thysanocarpus laciniatus* Nutt., and *Trichostema austromontanum* F.H.Lewis.

Phylogenetic Relationships and Similar Species—*Erythranthe palmeri* is inferred to share a close relationship with *E. montioides* (Fraga unpubl.) but plants of these taxa are easily distinguished morphologically (see discussion under *E. montioides*). Etymology.—*Erythranthe palmeri* is named in honor of Edward Palmer (1829–1922), a botanist and explorer of the America West. Palmer collected the type specimen of *E. palmeri.*

Conservation Status—*Erythranthe palmeri* has been confused with other closely related species including *E. diffusa*, *E. discolor* (pink form), *E. rhodopetra*, and *E. sierrae*. It was previously thought to be a widely distributed species because of this taxonomic confusion. *Erythranthe*

palmeri is endemic to the Transverse Range in the San Gabriel and San Bernardino Mountains and is therefore of limited distribution. Off-highway vehicle use, road maintenance, hiking trails, and campgrounds have all been observed as possible sources of disturbance to known occurrences. *Erythranthe palmeri* should be evaluated for Conservation Status by the federal, state, and other agencies that manage this species in light of clarification in taxonomy.

11. ERYTHRANTHE PURPUREA (A. L. Grant) N.S. Fraga, "purple monkeyflower". Phyroneuron 39: 1–60 (2012).

Mimulus purpueus A.L. Grant, Annals of the Missouri Botanical Garden 11: 255–256. 1924 [1925]. —TYPE: U.S.A. California: San Bernardino Co., San Bernardino Mountains, Bear Valley, 6000 ft, Jun 1886, *Parish 1862* (holotype: DS; isotype: UC!)

Mimulus purpureus var. *pauxillus* A.L. Grant, Annals of the Missouri Botanical Garden 11: 256 1924 [1925]. —TYPE: Mexico. Baja California, San Pedro Martir, 15 May 1893, *Brandegee s.n.* (holotype: GH; isotype: US digital image!)

Annual herb. Plants 3–10 cm tall, 1–9 cm wide, minutely puberulent. Stems erect, simple to branched, internodes 0.2–1.6 cm. Cotyledons persistent, ovate to obovate, 1–5 mm long, with clasping bases. Leaves opposite, epetiolate; blades 4–15 mm long, 1–5 mm wide, elliptic to lanceolate, palmately veined with three prominent veins from the base in wider leaves, margins entire and revolute or sometimes toothed. Flowers solitary in each axil, fruiting pedicels 13–57(–70) mm, exceeding calyx, erect to ascending to spreading horizontally. Calyx 3–8 mm long, 2–4 mm wide, campanulate, enlarging in fruit; costa prominent, darker than intercostal regions; calyx teeth equal, 0.5–1 mm long, acute and spreading, margins glabrous. Corolla 7–15 mm long, 8–11 mm wide, pink to purple purple, the adaxial lip darker than abaxial lip, two adaxial lobes nearly

entire, the 3 abaxial lobes notched, limb strongly zygomorphic; tube-throat 7–13 mm long, cylindric to funnnelform, expanding gabruptly to the limb, palate bearded, sometimes with yellow markings. Stamens didynamous, 7–12 mm long; filaments and anthers purple, glabrous, included. Gynoecium 10–16 mm long, ovary pink to purple, style and stigma purple, glabrous; stigma lobes apically fringed, subequal, at or slightly exserted from the orifice. Capsules 3–8 mm long, included to equal to the calyx, cylindric, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.3–0.5 mm long, 0.2–0.3 mm wide, elliptic to ovoid, light brown.

Representative Specimens—USA. California, San Bernardino Co.: San Bernardino Mountains, Holcomb Valley, north side of the road near site of Belleville, upper Caribou Creek, 2245–2317 m, 26 May 1996, Sanders 18188 (UCR); Rebel Ridge at Big Bear Lake, 6800 ft, 14 Jun 1967, D. *Myrick 1691* (SBBG); Along road to Fish Hatchery, south of Baldwin Lake, 2104 m, 29 May 1932, *Peirson 9968* (RSA), Holcomb Valley, N of Big Bear Lake, 17 Jun 1962, *Campbell s.n.* (CAS, RSA); Holcomb Valley, just E of Holcomb Valley Campground, just NE of intersection of SBNF roads 3N16 and 3N05, 2236 m, 8 Jun 2010, *Wood 1976* (RSA); Shallow pond and grassy swales on placer working, just W. of Holcomb Valley Campground, 12–13 Jun 1979, *Thorne 53503*, (RSA); North from Holcomb Valley Road (FS 3N16) at junction with Van Dusen Canyon Road (FS 3N09), east of Holcomb Valley Campground past open area to Caribou Creek, 2256 m, 4 Jun 2008, *Gross 3426* (RSA); near E end Big Bear Lake (along California 18), 6800ft, 29 May 1966, *Holmgren 2602* (UC); Bear Valley, 2073 m, 10 Jun 1922, *Munz 5651* (CAS, POM. UC), Bear Valley; dry slope about 1/2 mile west of boat landing, 2043 m, 22 Jun 1926, *Munz 10450* (POM), Holcomb Valley, 2241 m, 6 Jul 1926, *Munz 10655* (POM), Big Bear Valley, 6500 ft, 4 Jul 1920, *Harwood 4349* (POM); Margin of Big Bear Lake at E end on south side west of Big Bear City, 6749 ft, 14 Jun 1979, *Thorne 53082* (RSA, SD, UC); Placer workings just W of

Holcomb Valley Campground, 2248 m,2–3 Jun 1980, *Thorne 54320* (RSA, UC); E. of Holcomb Valley; in drainage way at west edge of Arrastre Flat, 2284 m, 15 Jun 1905, *Thorne 53222* (RSA, UC); Big Bear Valley, Maple Lane near the town of Sugarloaf, 4 Jun 1905, *Krantz s.n.* (RSA); W edge of Arrastre Flat, ca. 0.5 mi N of intersection of FS Roads 3N16 (Holcomb Valley Road) and 3N32, 4 Jun 2008, *Fraga 2157* (RSA); ca. 0.15 mi Wt of Poligue Canyon Road (2N09) and 0.4 miles S of Old Baldy Council Camp. Adjacent to Bike trail, 10 Jun 2008, *Fraga 2179* (RSA). MÈXICO, Baja California: Sierra San Pedro Martir, 0.75 mi from entrance gate to National Park, 6 Jun 2009, *Fraga 2893* (RSA); upper east end of Vallecitos, 31 May 1976, *Moran 23311* (RSA); Hike several miles in thru Vallecitos to upper meadow and beyond, nearly to eastern crest, 2560 m, *Thorne 60921* (RSA); Fields south of La Grulla, 6500 ft, 29, May, 1958, *Powell 62* (UC), South of Vallecitos in wet, open meadow near Cerro la Botella Azul, 28 Jun 1998, *Rebman 5401* (SD).

Phenology and Pollination Biology—Flowering occurs from May to June and fruiting is most common in June and July. *Erythranthe purpurea* exhibits approach herkogamy, has relatively large flowers compared with the vegetative growth, and trichomes and contrasting colors on the lower limb (yellow and dark purple markings on a light lavender limb). Based on evidence from corolla morphology, this species is presumed to be primarily outcrossing. Insect visitors were not observed visiting flowers of this species over the course of this study.

Distribution and Habitat—*Erythranthe purpurea* has a disjunct distribution, most collections are San Bernardino County, California in the San Bernardino Mountains of the Transverse Ranges in the U.S., but the plant is also know from sites ca. 402 km (250 mi) south in the Sierra San Pedro Martir of Baja California, Mexico. This species primarily occurs in loamy to sandy soils of decomposed granite in vernally wet depressions, swales, at the edges of streams and

creeks, dry meadows, often in thick pine duff in openings of pine forest, and riparian woodlands. Elevation 1900–2800 m (6200–9200 ft). Associated species: *Abies concolor*, *Allium parryi* S. Watson, *Artemisia tridentata*, *Collinsia parvifolia*, *Erythranthe androsacea*, *E. exigua* (A. Gray) G.L. Nesom & N.S. Fraga, *E. suksdorfii*, *Juncus bryoides* F.J. Herm., *Juniperus grandis* R.P. Adams, *Leptosiphon breviculus* (A. Gray) J.M. Porter & L.A. Johnson, *Mimetanthe pilosa* (Benth.) Greene, *Phacelia curvipes* S. Watson, *Plagiobothrys tenellus* (Hook.) A. Gray, *Populus tremuloides* Michx., *Pinus jeffreyi*, and *Viola douglasii* Steud.

Phylogenetic Relationships and Similar Species—In her treatment of *Mimulus*, Grant (1924) recognized one infraspecific taxon of this species, *Mimulus purpureus* var. *pauxilis*. This taxon was distinguished for its small stature and presumably because it is geographically separated from the majority of the populations of the species. A review of additional specimens since its original description does not reveal any significant difference in size between plants found in the U.S. and Mexico. Plants in Mexico do not appear to be morphologically distinct, therefore I do not recognize the variety at this time. In an analysis of ITS sequence data, *Erythranthe purpurea* forms a clade with and is presumably closely related to *E. androsacea*, *E. shevockii*, these results are further supported by morphological evidence; these taxa have similar leaves that are somewhat succulent and are often enrolled at the margins (Fraga unpublished).

Etymology—*Erythranthe purpurea* is named for its purple corolla. The corolla is dark purple on the upper limb and light purple to lavender on the lower limb. This species is commonly referred to as little purple monkeyflower.

Conservation Status—*Erythranthe purpurea* is a narrow endemic restricted to twenty-two known sites in the Holcomb Valley, and Bear Valley regions in the San Bernardino Mountains, U.S., and is disjunct in the Sierra San Pedro Martir in Baja California, Mexico where it is known

from four locations. Threats to this species include modification to its habitat via housing and commercial development, off highway vehicle use, cattle grazing, hydrological alteration, and invasion by non-native species (Fraga 2008). *Erythranthe purpurea* has a CNPS rare plank rank of 1B.2 which means that it is rare and fairly threatened in California (CNPS 2013). In Mexico this species has been evaluated for Conservation Status and has been recommended for 1B ranking in Northwestern Baja California which means this species is considered rare and endangered in the California floristic province in Baja California and elsewhere (O'Brien et al. 2010, O'Brien personal communication).

12. ERYTHRANTHE RHODOPETRA N.S.Fraga, "Red Rock Canyon monkeyflower". Aliso 30: 66–67. 2012.—TYPE: U.S.A. California: Kern Co., El Paso Mountains, Last Chance Canyon, Old Cuddhay Camp, 35.249, 40.20N; 117.55940.10W, 828 m/2717 ft, 23 Apr 2011, *Fraga 3787* (holotype: RSA!; isotypes: CAS!, UC!, US!).

Annual herb. Plants 5–15 (–21) cm tall, 1–15 cm wide; sparsely glandular pubescent. Stems erect, simple to branched, internodes 2–8 cm. Cotyledons persistent, obovate to ovate, 1.2–3 mm long, with attenuate bases. Leaves opposite, short petiolate (0.5–1 mm) to epetiolate; blades 5–22 mm long, 1–10 mm wide, linear-oblanceolate to elliptic, palmately veined with three prominent veins from the base in wider leaves, margins entire. Flowers solitary in each axil, fruiting pedicels 10–40 mm, exceeding calyx, erect to ascending. Calyx 5–10 mm long, 3–4 mm wide, campanulate to cylindric, enlarging in fruit; costa prominent and darker than intercostal regions; calyx teeth subequal and 0.5–1 mm long, acute and spreading, margins glabrous. Corolla 12–26 mm long, 16–25 mm wide, pink to rose colored, lobes bifid, limb weakly zygomorphic; tube-throat 9–17 mm long, funnelform, expanding abruptly to the limb, palate glabrous with a large yellow patch

with dark pink longitudinal lines. Stamens didynamous, 10–13 mm long, filaments and anthers yellow, glabrous, included. Gynoecium 12–14 mm long, ovary pink to purple, style and stigma pale pink to white; style glabrous; stigma lobes slightly apically fringed, subequal, included in the corolla. Capsules 4–8 mm long, included in the calyx, cylindric to campanulate, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.7–0.9 mm long, 0.2–0.3 mm wide, elliptic to ovoid, brown.

Representative Specimens—U.S.A. California: Kern Co.,Red Rock Canyon, 2300 ft, 14 Mar 1959, *DeDecker 1000* (RSA); Fremont Valley drainage; Red Rock Canyon N of Visitor's Center, 3 Apr 1993, *DeDecker 6378* (RSA); near Ricardo, Red Rock Canyon, 29 Mar 1922, *Fultz 17074* (RSA); Red Rock Canyon, 1 Apr 1935, *Woglum 659* (RSA); Red Rock Canyon, 19 Apr 1958, *Munz & Gregory 23311* (RSA, UC); Red Rock Canyon, 1 May 1927, *Abrams 11856* (POM); Red Rock Canyon State Park, Hagen Canyon, 2200 ft, 12 Apr 2008, *Fraga et al. 1996* (RSA); N of Randsburg, 10 Apr 1922, *Pierce s.n.*(POM); Saltdale, Petrified Forest, 14 Apr 1933, *Johnston & Raiselis 17230* (RSA); El Paso Mountains, Petrified Forest, 20 Apr 1952, *Wheeler 6856* (RSA).

Phenology and Pollination Biology—Flowering occurs from March to April and fruiting is most common in April and May. *Erythranthe rhodopetra* exhibits approach herkogamy and has very large flowers compared with the vegetative growth. Based on evidence from corolla morphology this species is presumed to be primarily outcrossing. Insect visitors were not observed visiting flowers of this species over the course of this study.

Distribution and Habitat—*Erythranthe rhodopetra* is endemic to the El Paso Mountains in Kern County, California. This species occurs in highly compacted sandy soils in washes derived from sedimentary rock of the Ricardo Formation (Cox and Diggles 1986). The Ricardo Formation is

of Miocene origin and is colorful with alternating bands of red, white, and brown and is composed of sandstones and consolidated conglomerates (Cox and Diggles 1986). Elevation 610–915 m (2000–3000 ft). Associated species (* denotes non-native species): **Bromus madritensis* L. subsp. *rubens* (L.) Husn., **B. tectorum*, *Calyptridium monandrum* Nutt., *Eremothera boothii* (Douglas) W.L.Wagner & Hoch, *Erythranthe guttata*, *Lepidium flavum* Torr., *Juncus bufonius* L., *Plagiobothrys arizonicus* (A.Gray) A.Gray, and *Platystemon californicus*.

Phylogenetic Relationships and Similar Species—*Erythranthe rhodopetra* appears to be closely related to *E. palmeri* (Fraga unpubl.). These species are easily distinguished from one another based on corolla size, corolla color, and nectar guide patterns. *Erythranthe rhodopetra* has a wider limb (16–25 mm) than *E. palmeri* (8–15 mm) and has pale pink flowers with a broad yellow palate and orifice. In contrast, *E. palmeri* has deep pink flowers with two yellow ridges on the palate.

Etymology—*Erythranthe rhodopetra* is named for the red sedimentary rocks of Red Rock Canyon State Park in Kern County, California. The species is endemic to the region and is associated with sandy canyon washes at the base of the red sedimentary cliffs.

Conservation Status—*Erythranthe rhodopetra* is known from fewer than ten populations within a 120 km^2 region and is therefore of limited distribution. All known occurrences are on public lands administered by the Bureau of Land Management or California State Parks. This species should be considered for Conservation Status by federal, state, and other agencies that manage for this species. Historic mining operations, off highway vehicle, and presence of exotic plants species weredisturbances observed over the course of field surveys conducted by this study.

13. ERYTHRANTHE RUBELLA (A. Gray ex. Torr.) N.S. Fraga, "redstem or little redstem monkeyflower" Phytoneuron 39: 1–60. 2012.

Mimulus rubellus A. Gray ex. Torr, Rep. U.S. Mex. Bound. 2: 116. 1859.—TYPE: U.S.A. New Mexico: Dona Ana Co., Organ Mountains, Apr, *Bigelow 770*, (lectotype designated by Grant, 1924 [1925]: GH!; isolectotype: US digital image!).

Mimulus gratioloides Rydb., Bull. Torr. Bot. Club 28: 27 1901.—TYPE: U.S.A. Colorado: Butte, 5 miles southwest of La Veta, 22 May 1900, *Rydberg 5660* (holotype: NY digital image!)

Annual herb. Plants 3–32 cm tall, 1–11 cm wide; minutely puberulent to glandular pubescent. Stems erect, simple to branched, internodes 0.5–4 cm. Cotyledons persistent, obovate to reniform, 2–6 mm long, with attenuate bases. Leaves opposite, epetiolate; blades , 5–22(–30) mm long, 1–5 mm wide, linear to elliptic, palmately veined with three prominent veins from the base in wider leaves, margins entire or sometimes toothed. Flowers solitary in each axil, fruiting pedicels 2–18 mm, exceeding calyx, erect to ascending. Calyx 4–9 mm long, 2–4 mm wide, cylindric, enlarging in fruit; costa prominent and darker than intercostal regions; calyx teeth subequal and 0.5–1 mm long, acute, margins ciliate. Corolla 5–9 mm long, 3–5 mm wide, yellow or pink, lobes notched, limb weakly zygomorphic; tube-throat 4–10 mm long, cylindric, expanding abruptly to the limb, palate glabrous with a large yellow patch with dark pink longitudinal lines. Stamens didynamous, 10–13 mm long, filaments and anthers yellow, glabrous, included. Gynoecium 5–9 mm long, ovary yellow or pink, style and stigma yellow or pink; style glabrous; stigma lobes entire subequal, included in the corolla. Capsules 3–8 mm long, included in the calyx, cylindric, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.4–0.6 mm long, 0.2–0.3 mm wide, elliptic to ovoid, brown.

***Representative Specimens Examined*—**U.S.A. Arizona: Coconino Co., Shoshoni Point, Grand Canyon National Park, 7 May 1978, *Engard s.n.* (UNLV); Mohave Co., Grand Canyon-Parashant National Monument, volcanic cone west of road to Whitmore Canyon Overlook, 15 Apr 2003, *Atwood 29122* (UNLV); Pima Co., Tucson Mountains Park, south end of Camino de Oeste, Oeste Wash near head of David Yetman Trail, 29 Feb 1992, *Van Devender 92–298* (RSA). California, Inyo Co.: Death Valley National Park. Road to Gold King Mining claim, off Wildrose Road, ca. 6 mi south of Hwy 190, 17 Apr 2010, *Fraga 3305* (RSA); Death Valley National Park. Gentle slope north of road to Aguereberry Point. ca. 2.6 mi east of Wildrose Road, 24 Apr 2010. *Fraga 3316* (RSA); San Bernardino Co.: North Fork of Lytle Creek, on slopes along north side of the canyon, northeast of Paiute Campground, 20 May 2004, *Fraga 1201* (RSA); Nevada, Clark Co.: Lucky Strike Canyon, Spring Mountains, 14 May 1983, Peterson 930 (UNLV), 0.5 mile NW of La Madre Spring, northern Red Rock Canyon Recreation, 28 Apr 1990, *Leary 3940* (UNLV); SSW end of Indian Ridge near Cold Creek Road, 13 May 1978, *Thorne 51515* (UNLV); Utah, Washington Co: 11 May 1973, *Meyer 2639*.

***Phenology and Pollination Biology*—**Flowering occurs between April and August; fruiting plants most commonly seen in May through September. *Erythranthe rubella* has relatively small flowers and lacks herkogamy, suggesting that self-pollination may occur frequently. This species has two floral color morphs. Populations display either pink or yellow flowers but mixed populations have not been observed. No floral visitors were observed on this species over the course of this study

Distribution and Habitat*—Erythranthe rubella*is a widely distributed species occurring primarily in mountainous regions throughout Arizona California, Colorado, Nevada, New Mexico, Texas, Utah, and Wyoming in the US and Baja California Norte, and Sonora Mexico.

Plants primarily occur in substrates derived from carbonate, granitic, and volcanic rocks, sometimes in vernally moist areas but also on dry, rocky often south facing slopes. *Erythranthe rubella* is associated with the following vegetation communities: desert scrub, oak woodland, pine-oak woodland, pinyon-juniper woodland, riparian forest, and yellow pine forest. Elevation 300–3050 m (1000–10800 ft). Associated species: *Ambrosia salsola* (Torr. & A. Gray) Strother & B.G. Baldwin, *Artemisia tridentata*, *Castilleja chromosa* A. Nelson, *Coleogyne ramosissima*, *Encelia farinosa* A. Gray ex Torr., *Eriogonum fasciculatum*, *Juniperus grandis*, *J. deppeana* Steud., *J. osteosperma* (Torr.) Little, *Populus tremuloides*, Pinus jeffreyi, *P. monophylla*, *P. ponderosa*, *Prosopis velutina* Wooton, *Pseudotsuga menziesii* (Mirb.) Franco, *Purshia tridentata*, *Quercus chrysolepis*, and *Q. turbinella* Greene.

Phylogenetic Relationships and Similar Species—*Erythranthe rubella* is morphologically similar to *E. calcicola* and is inferred to share a close relationship with this species (Fraga unpubl.). These species are easily distinguished by leaf shape and calyx morphology. The leaves of *E. rubella* are linear to elliptic and the calyx is narrowly cylindric with glabrous margins. In comparison the leaves of *E. calcicola* are lanceolate to ovate and the calyx is widely campanulate to cylindric with margins ciliate.

Etymology—*Erythranthe rubella* is named for the red tinge the plants get as they age and mature fruits develop, and thus this plant also has the common name of red stem or little red stem monkeyflower.

Conservation Status—*Erythranthe rubella* is a widely distributed species compared to most species in *Erythranthe* section *Paradantha,* and may in fact have the largest range size in the section. This species has Conservation Status in one state where it is found infrequently; it is ranked as S1 or critically imperiled in Wymoning by Natureserve (2013). It has been evaluated

for Conservation Status in Baja California Mexico where it has been given a rank of 2B as a species that is rare in California Floristic Province of Baja California, Mexico, but more common elsewhere (O'Brien et al. 2010, O'Brien personal communication).

15. ERYTHRANTHE SHEVOCKII (Heckard & Bacig.) N.S. Fraga, "Kelso Creek monkeyflower" Phytoneuron 39: 1–60. 2012.

Mimulus shevockii Heckard & Bacig., Madroño 33: 271–276: 1986.—TYPE: U.S.A, California: Kern Co., West side of Kelso Creek along the dirt road to Cortez Canyon, 16 Apr 1983, *Shevock 10319* (holotype JEPS!, isotypes CAS, GH, MO!, NY digital image!, RSA!, SBBG!, US digital image!

Annual herb. Plants 2–12 cm tall, 0.5–4.5 cm wide, minutely puberulent or glabrous. Stems erect, simple to branched, internodes 0.5–2.1 cm. Cotyledons persistent, obovate to ovate, 3–10 mm long, short petiolate with clasping bases. Leaves opposite, epetiolate; blades 3–10 mm long, 1–5 mm wide, lanceolate to ovate, palmately veined with three prominent veins from the base in wider leaves, margins entire and revolute. Flowers solitary in each axil, fruiting pedicels 10–22 mm, exceeding calyx, erect to ascending. Calyx 4–7 mm long, 2–5 mm wide, campanulate, enlarging in fruit; costa weak and darker than intercostal regions; calyx teeth equal, 0.5–1 mm long, acute and spreading, margins glabrous. Corolla 9–15 mm long, 8–15 mm wide, with two maroon adaxial lobes, two maroon lateral lobes, and one yellow central bifid lobe, limb strongly zygomorphic; tube-throat 8–12 mm long, cylindric, expanding abruptly to the limb, palate bearded, with with red spots. Stamens didynamous, 7–10 mm long, filaments and anthers maroon, glabrous, equal with the orifice. Gynoecium 10–14 mm long, ovary maroon, style and stigma maroon, glabrous; stigma lobes apically fringed, subequal, exserted. Capsules 5–6 mm

long, included to equal to calyx, cylindric, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.5–0.7 mm long, 0.2–0.3 mm wide, elliptic to ovoid, brown.

***Representative Specimens*—**U.S.A. California: Kern Co., Kelso Creek. Between the creek and Kelso Valley Road, 11 miles south of state highway 178, 11 May 1983, *Bacigalupi 9346* (JEPS, SBBG, SD); Kernville, 3000 ft,17 Apr 1932, *Bangsberg s.n*. (JEPS); Southern Sierra Nevada Range Piute Mountains, lower Esperanza Canyon at eastern base of Sorrell Peak and western edge of Kelso Valley, 1372–1463 m, 1 May 2008, *Boyd 11977* (RSA); East base of Piute Mountains southeast of Isabella Lake, ca. 1.0 mile west of Kelso Creek road on Cortez Canyon Road, 3599 ft , 19 Apr 1986, *Ertter 5979* (SD, UC); Southern Sierra Nevada, Along Dirt Road west of Kelso Valley Road, extension of Snow Street", 1037 m, 2 Apr 2005, *Fraga 1533* (RSA); 11 mi s Highway 178 (between Kelso Creek and Kelso Valley Rd., W of Weldon (1 mi nw of Bird Spring Pass Rd. jct.), 3 May 1886, *Heckard 6225* (JEPS, SD); Kelso Canyon,3000 ft, 29 Apr 1973, *Luthey 341* (CAS), Cyrus Canyon, E of Sierra Way, Kern Plateau, Kern River Drainage, 3200 ft, 16 Apr 1983, *Norris 370* (CAS, JEPS); 100 meters S of South Kelso Valley Road. Across from address 3858, 3400 ft, 24 Mar 1998, *Schoenig 98-3* (UC); Along Kelso Creek on a dirt road to Cortez Canyon, 3500 ft, 25 Apr 1982, *Shevock 9321* (CAS, JEPS, RSA); Along the dirt road to Cortez Canyon, W side of Kelso Creek, 3500 ft, 2 Apr 1983, *Shevock 10266*, (CAS, JEPS, RSA); Cyrus Canyon, 2 miles E of Sierra Way Road, Kern Plateau, Kern River Drainage, 3200 ft, 8 Apr 1983, *Shevock 10267* (CAS, JEPS, SBBG); Cortez Canyon, tributary of Kelso Creek, 4100 ft, 16 Apr 1983, *Shevock 10320* (CAS, RSA); Kelso Creek Road, 1 mile N of Bird Springs Pass Road then 100 yards W toward Kelso Creek, South Fork Kern River, 3375 ft, 16 Apr 1983, *Shevock 10322* (CAS, JEPS, RSA); Cyrus Canyon, E of Sierra Way, Kern Plateau, Kern River Drainage, 3200 ft, 16 Apr 1983, *Shevock 10327* (CAS, JEPS, RSA); Along the E side

of Kelso Creek Approximately 1/2 mil S of Bird Springs Pass Road, along Kelso Creek Road, then 1/4 mile W towards Kelso Creek, 3600 ft, 7 May 1983, *Shevock 10368* (CAS, JEPS, RSA); Along the dirt road just S of Bob Rabbit Canyon toward Cortez Canyon, west of Kelso Creek, 3250 ft, 7 May 1983, *Shevock 10383* (CAS. JEPS, RSA); Kelso Creek Canyon between the Piute and Scodie Mountains, 3500 ft, 11 Apr 1992, *Shevock 12108* (CAS); Cyrus Canyon, 3900 ft, 26 Apr 1971, *Twisselmann 17640* (CAS); Cyrus Canyon, E of Kern Valley, 3200 ft, 24 Apr 1968, *Twisselmann, 14087* (CAS. JEPS, SBBG).

Phenology and Pollination Biology.—Flowering occurs between March and April and fruiting between April and May. *Erythranthe shevockii* has relatively large flowers with bright, contrasting colors on the corolla (the upper limb is maroon, the lower limb is yellow with red spots on the palate). In addition flowers exhibits approach herkogamy, have a beard of trichomes on the lower limb, and forms large floral displays in years of ample precipitation. Presumably the beard of trichomes and contrasting colors serve as an advertisement to pollinators. Based on evidence from corolla morphology and population densities, this species is presumed to be primarily outcrossing. Halictid bees (sweat bees) and small flower beetles were observed visiting flowers during field studies especially in populations that formed large floral displays.

Distribution and Habitat.—*Erythranthe shevockii* is restricted to the southern Sierra Nevada in Kern County. This species primarily occurs on flat openings on decomposed granite in course sandy soils in Joshua Tree woodland and Junuper woodland Elevation 900–1400 m (3000– 4600 ft). Associated species: *Anisocoma acaulis* Torr. & A.Gray, *Ambrosia salsola*, *Tetrapteron graciliflorum* (Hook. & Arn.) W.L. Wagner & Hoch, *Canbya candida* Parry ex. A.Gray, *Cylindropuntia echinocarpa* (Engelm. and J.M.Bigelow) F.M. Knuth, *Diplacus fremontii (*Benth.) G.L. Nesom, *Ephedra nevadensis* S.Watson, *Ericameria linearifolia* (DC.) Urbatsch

and Wussow, *E. nauseosa* (Pall.) G.L. Nesom & G.I. Baird, *Eriogonum fasciculatum*, *Eriophyllum pringlei* A.Gray, *Erythranthe androsacea*, *Leptosiphon aureus* (Nutt.) J.M. Porter & L.A. Johnson), *L. parryae* (A.Gray) Greene, *Lupinus concinnus* J.Agardh, *Pectocarya penicillata* (Hook. and Arn.) A.DC., *P. setosa* A.Gray, and *Salvia dorrii* (Kellogg) Abrams.

Phylogenetic Relationships and Similar Species—In an analysis of *ITS* sequence data, *E. shevockii* forms a strongly supported clade with *E. androsacea* and *E. purpurea*. These results are further supported by morphological evidence: these taxa share leaves that are somewhat succulent and are often enrolled at the margins and connate at the base (Fraga unpublished). However these taxa can be easily distinguished by their corolla morphology.

Etymology—*Erythranthe shevockii* is named for James R. Shevock (1950–), an American Botanist and who first understood the species to be new; he did extensive field work prior its publication (HUH 2013). The common name Kelso Creek monkeyflower refers to the region (Kelso Valley) where this species occurs in Kern County, California.

Conservation Status—*Erythranthe shevockii* has a CNPS rare plant rank of 1B.2 which means it is rare and fairly endangered in California; it is a narrow endemic, known only from about 11 occurrences in the southern Sierra Nevada (CNPS 2013). Populations have been impacted by housing development, cattle grazing, agriculture (orchards), lake inundation, and road maintenance and construction. This species has been considered for federal listing but rejected because the U.S. Fish and Wildlife Service concluded that current threats warranteing listing had not been identified also the range of *E. shevockii* could be greater than understood at the time of the proposed rule such that potential habitat required surveying (Fraga 2007).

15. ERYTHRANTHE SIERRAE N.S.Fraga, "Sierra Nevada monkeyflower". Aliso 30: 67–68, 22. 2012.—TYPE: U.S.A. California: Kern Co., Sierra Nevada, Breckenridge Mountain, along Breckenridge Mountain Road, ca. 2 mi NW of Breckenridge Campground, 35.4724N, 118.6029W, 5900 ft, *Fraga, Fraga, & Fraga 3445* (holotype: RSA!; isotypes: CAS!, UC!, US!).

Annual herb. Plants 4–20 cm tall, 2–19 cm wide, sparsely glandular pubescent. Stems erect, simple to branched, internodes 1–4 cm. Cotyledons persistent, obovate to ovate, 3–5 mm long, short petiolate with clasping bases. Leaves opposite, short petiolate (0.5–1 mm) to epetiolate; blades (3–) 5–27 mm long, 1– 11 mm wide, linear to oblanceolate, palmately veined with three prominent veins from the base in wider leaves, margins entire or sometimes toothed. Flowers solitary in each axil, fruiting pedicels (4–) 9–43 mm, exceeding calyx, erect to ascending. Calyx 4–8 mm long, 3–4 mm wide, campanulate, enlarging in fruit; costa weak and darker than intercostal regions; calyx teeth equal, 0.5–1 mm long, acute and spreading, margins ciliate. Corolla 12–22 mm long, 5–17 mm wide, pale pink to pink, lobes notched, limb weakly zygomorphic; tube-throat 8–17 mm long, funnelform, expanding gradually to the limb, palate with two yellow ridges. Stamens didynamous, 7–10 mm long, filaments and anthers white, glabrous, included. Gynoecium 10–13 mm long, ovary pink to brown, style and stigma pink, glabrous; stigma lobes apically fringed, subequal, included. Capsules 3–6 mm long, included to equal to calyx, cylindric, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.5–0.8 mm long, 0.2–0.3 mm wide, elliptic to ovoid, brown.

***Representative Specimens*—**U.S.A. California: Kern Co., Greenhorn Mountain Range, Little Poso Creek Falls, 4500 ft, 23 May 1937, *Benson 8344* (POM); Greenhorn Range, 6000 ft, *Hall & Babcock 5050* (POM); Breckenridge Mountain, 6000 ft, 26 May 1928, *Bauer 213* (RSA);

Howling Gulch near Woody,1900 ft, *Smith 339* (RSA); Howling Gulch E of Woody Granite Road, 35.68991N,118.82803W, 30 May 2010, *Fraga et al. 3410* (RSA); Greenhorn Mountains, summit between Glenville and Wood, 3000 ft, *Hughes 178* (POM); Keane, 1700 ft, *Jones s.n.* (POM); N slope Breckenridge Mountain (at head of creek), 27 Jun 1965, *Twisselmann 11229* (JEPS); Breckenridge Mountain, 5700 ft, 6 Jun 2010, Fraga et al. 3441 (RSA); Breckenridge Mountain Campground, 6600 ft, 4 Jul 2010, *Fraga & Brock 3514* (RSA); Rancheria Rd. (dirt road) S of Poso Flat Rd. and NW below fire lookout, near National Forest boundary and Oak Flat, 9 Jun 2005, *Gowen 432* (JEPS); Greenhorn Range, NW slope Basket Peak, 5250 ft, 27 Jun 1963, *Twisselmann 8546* (RSA); Fresno Co., 100 m W of Hume Lake Road, where USFS campground road forks off at Hume Lake, 36.479300N; 118.549000W, 5300 ft, *Schoenig 37* (RSA); just above Crawford Ranch, Pine Flat, Kings River about 6 mi below Trimmer, 650 ft, *Carter 48* (RSA, UC); Sand Creek, 6 May 1918, *Kelley s.n.* (JEPS); Tulare Co., N fork of Tule River, 1 2/10 mi above Milo, 2500 ft, 14 May 1933, *Wolf 4674* (RSA); middle fork of Tule River, 1750 ft, *Peirson 5619* (RSA); California Hot Springs to Durrwood, 11 May 1940, *Woglum 2713* (RSA); Tule River, 3000 ft, *Munz 3000* (RSA); 1/4 mi E of Milo junction and 7.5 mi N of Springville, *Robbins & Heckard 3535* (RSA); 0.25 mi NE of Milo junction (7.5 mi N of Springville), 30 May 1953, *Heckard 456A* (RSA); hills N of Springville, 800 ft, Apr 1897, *Purpus 5048* (UC); Kaweah River Basin, 15 Apr 1901, *Hopping 111* (UC).

***Phenology and Pollination Biology*—**Flowering occurs from March to July and fruiting is most common in June and July. *Erythranthe sierrae* exhibits approach herkogamy and has relatively large flowers. Based on evidence from corolla morphology and floral display due to patch size this species is presumed to be primarily outcrossing. Halictid bees (Halictidae) which are

presumed to serve as the primary pollinators have been frequently observed visiting flowers of this species especially in populations that form dense patches.

Distribution and Habitat—*Erythranthe sierrae* is endemic to the Sierra Nevada in Kern, Fresno, and Tulare counties, California. This species primarily occurs in decomposed granite in vernally wet depressions, swales, at the edges of streams, dry meadows, and in openings of pine forest and oak woodland. Elevation 200–2100 m (650–6800 ft). Associated species: *Abies concolor*, *Claytonia perfoliata*, *Diplacus bolanderi* (A.Gray) G.L.Nesom & N.S.Fraga, *D. constrictus* (A.L.Grant) G.L.Nesom & N.S.Fraga, *Erythranthe breweri*, *E. floribunda, Nemophila maculata* Lindl. *Pinus jeffreyi*, *P. sabiniana Phacelia curvipes*, *Plagiobothrys* sp., *Quercus chrysolepis*, *Q. douglasii* Hook. & Arn., *Q. kelloggii*, *Ribes quercetorum* Greene.

Phylogenetic Relationships and Similar Species—*Erythranthe sierrae* is inferred to have a sister relationship with *E. gracilipes* (B.L.Rob.) N.S.Fraga (Fraga unpubl.). These species are easily distinguished by corolla morphology: *E. sierrae* has corolla lobes that are more or less equal in size and a tubethroat that is funnelform and expands gradually to the limb. In contrast, *E. gracilipes* has two reduced adaxial lobes that are smaller than the three abaxial lobes and a tube-throat that is cylindric and expands abruptly to the limb.

Etymology—*Erythranthe sierrae* is endemic to the Sierra Nevada in California and is named for the range.

Conservation Status—*Erythranthe sierrae* has a relatively widespread distribution and is known from Kern, Fresno, and Tulare counties in the foothills of the Sierra Nevada. Anthropogenic change including development, grazing, off highway vehicle use, road and trail maintenance, campgrounds, and the presence and abundance of exotic species have all been documented as possible threats to known occurrences. Several populations at lower elevations may be highly

impacted from these disturbances with several populations possibly extirpated. This species should be reassessed for threats at known occurrences.

16. ERYTHRANTHE SUKSDORFII (A. Gray, Syn.) "Suksdorff's monkeyflower" Phytoneuron 39: 1–60. 2012.

Mimulus suksdorfii A. Gray, Fl. N. America 2 (1, Suppl.): 450. 1886.—TYPE: U.S.A. Washington: Yakima Co., on rocks Mount Paddo, 7000–8000 ft, 19 June 1886, *Suksdorf 487* (lectotype designated by Grant, 1924 [1925]: GH!; isolectotype: WU)

Annual herb. Plants 0.5–10(–13) cm tall, 0.5–6(–8) cm wide, minutely puberulent. Stems erect, simple to branched, internodes 0.1–2.5 cm. Cotyledons persistent, ovate to elliptic, 0.1–0.5 mm long, short petiolate with clasping bases. Leaves opposite, epetiolate; blades, 2–20(–25) mm long, 0.5–4 mm wide, linear to lanceolate or ovate, palmately veined with three prominent veins from the base in wider leaves, margins entire. Flowers solitary in each axil, fruiting pedicels 3–6 mm, exceeding calyx, erect. Calyx 3–6 mm long, 2–3 mm wide, campanulate, enlarging in fruit; costa weak and darker than intercostal regions; calyx teeth equal, 0.5–1 mm long, acute and spreading, margins glabrous. Corolla 6–8 mm long, 2–3 mm wide, yellow, lobes entire or weaklynotched, limb weakly zygomorphic; tube-throat 4–6 mm long, cylindric, expanding gradually to the limb, palate with red markings, glabrous. Stamens subequal to didynamous, 4.5–6 mm long, filaments and anthers yellow, glabrous, included. Gynoecium 4.5–8 mm long, ovary yellow, style and stigma yellow, glabrous; stigma lobes apically fringed, subequal, included. Capsules 3–6 mm long, included to equal to calyx, cylindric, thin walled and fragile, dehiscing to the base along both sutures. Seeds 0.2–0.3 mm long, 0.4–0.6 mm wide, elliptic to ovoid, brown.

***Representative Specimens*—**U.S.A. California: Alpine Co., Sagebrush Flat, 0.5 mile west of Monitor Pass, 8300 ft, 10 Jul 1963, *Howell 39739* (CAS); Scossa Canyon, along Airport Road (Indian Creek Reservoir road) 0.5 miles Southeast of Diamond Valley Road, Dutch Valley, 5400 ft, 5 May 1974, *Taylor 3331* (UC); El Dorado, near Eagle Falls, Emerald Bay, Lake Tahoe, 6500 ft, 10 Jun 1925, *Howell 1140* (CAS); Fresno Co., Ruby Lake Grade, vicinity of Huntington Lake, 1 Aug 1926, *Klyver s.n.* (DS); Sierra Nevada; Central Sierra Nevada region Bubbs Creek, 3049 m, 23 Jul 1948, *Munz 12473* (RSA); 100 yds below Mono Creek Diversion Dam Rd. (at a point 75 yds above Bear Creek Diversion Dam Rd. Jct., on a short road down to a dump), 7000 ft, 20 Jun 1953, Quibell 2335 (JEPS); Colby Meadows, 9800 ft, 17 Jul 1952, *Raven 4377*, (CAS); West side of Hell-for-Sure Pass,11000 ft,11 Aug 1952, *Raven 5038* (CAS); Bench Lake,10450 ft, 23 Jul 1956, *Raven 9785* (CAS, JEPS); Inyo Co. slope S Lone Pine Creek Canyon; E slope of Sierra Nevada, 6950 ft, 2 Jun 1942, *Alexander & Kellogg 2909* (UC); Sierra Nevada, Onion Valley, 9000 ft, 27 Jul 1942, *Alexander & Kellogg 3175* (UC); Mosquito Flat, Rock Creek, 10,000 ft, 1 Aug 1932, *Crafts 612* (CAS); Inyo Mountains: Eureka Valley drainage; summit on road to Papoose Flat from N.,2759 m, 20 Jun 1980, *DeDecker 5055* (RSA, UC), McAfee Meadow, White Mountains., 11700 ft, 23 Jul 1930, *Duran s.n.* (SD); Kearsarge Pass Trail,10500 ft, 31 Jul 1948, *Howell 25236* (CAS), Cottonwood Creek,10200 ft, 18 Jul 1949, *Howell 25444* (CAS); Sierra Nevada; Southern Sierra Nevada region west shore Long Lake, Rock Creek Lake Basin, 10660 ft, 1 Aug 1931, *Peirson 9490* (RSA);White Mountains; head of Wyman Canyon, 3201 m, 28 Jul 1952, *Roos 5854* (RSA), Above Little Lakes Valley on trail to Ruby Lake. Upper Rock Creek drainage, 10700 ft, 16 Aug 2011, *Fraga & Brock 3887* (RSA); Lassen Co.: 7.0 mi N of Madeline (about 1 mi N of Sage Hen siding on Southern Pacific Rail Road, just E of U.S. Highway 395), on Southern Pacific Rail Road, 5500 ft, 28 Jun 1957, *Bacigalupi 5990* (JEPS);

SW Harvey Valley ca. 200 m NE of Whitehorse Well, ca. 6 mi N if USFS Bogart Work center, 1700 m, 3 Jun 1991, *Corbin 620*, (RSA); Great Basin Province; Modoc Plateau, Champs, 1524 m, 19 Jun 1897, *Jones s.n.*, (POM); Champs Flat Rd (Lassen 105, Forest 32N28Y) junction with Lassen 21 (32N02) to Eagle Lake (on w edge of valley, between Poison Lake and Susanville), Pine Creek Valley, 5680 ft, 3 Jun 1993, *Oswald 5486*, (UC); Los Angeles Co., San Gabriel Mountains, SW of Pinon Hills, 0.3 mi. S of mouth of Mescal Canyon and reservoir, 12 Jun 1998, *Swinney 6957* (RSA); San Gabriel Mountains, Lily Springs area on N slope of Mt. Hawkins, drainage of S Fork Big rock Creek, 2439 m, 28 Jun 1974, *Thorne 44749* (RSA); Madera Co., Ridge N of San Joaquin Mountain., 31 Jul 1941, *Howell 16622* (CAS); NW Merced Peak (slopes about Ottoway Lake. headwters of Illilouette Creek); Yosemite National Park, Ottoway Creek drainage, 9750 ft, 14 Jul 1941, *Mason 12524* (JEPS); Sink along Hwy to Canby, Several miles N of Quarantin Station, 14 Jun 1936, *Baker 8313* (RSA, UC); N of Upper Rush Creek Public Camp, 2.5 miles E of Hwy 299., 5700 ft, 18 May 1950, *Balls 14754* (CAS, RSA); Near Perez, 15 Jun 1940, *Eastwood & Howell 8276* (CAS, POM); Bodie,8374 ft, 27, Jul 1945, *Alexander & Kellogg 4315* (DS, UC); Nevada Co., 400 ft SW of fish observation post at Sagehen Creek Station, west of State Highway 89, 1951 m, 26 Jun 1964, *Schmid 89*, (RSA); Meadow at intersection of Boca-Hobart Mills road and Dry Creek road, just north of Prosser Reservoir, 5865 ft, 2 Jun 1974, *True & Howell 7724* (CAS); Lookout on old Donner Summit Highway,7000 ft, 10 Jun 1973,*Williams s.n.* (CAS); Plumas Co., Gravel bars along a small stream, on the S side of County Road 111 (Beckwourth Genesee Road), 50 yards E of Forest Road 24N08, Red Clover Valley, about 2 miles (air) N of the N end of Lake Davis, 5406 ft, 16 Jun, *Ahart 14105* (JEPS) Sierra Valley near Beckwourth,4880 ft, 18 Jun 1962, *Howell 37802* (CAS); Sandy Flat, 5,8 miles E of Beckwourth , 4900 ft, 19 Jun 1962, *Howell 37870* (CAS);

Plumas, 5.8 mi E Beckwourth; Sierra Nevada,4900 ft, 19 Jun 1962, *Howell 37870* (JEPS); Riverside Co., San Jacinto Mountains region Mount San Jacinto State Park, Hidden Lake, 2652 m, 7 Sep 3006, *Fraga 1736* (RSA); Tahquitz Valley, San Jacinto Mountains, 7200 ft, 6 Jul 1922, *Munz 5995* (CAS); San Jacinto Mountains region Tahquitz Valley,2317 m, 6 Jul 1922, *Munz 5995* (POM); San Bernardino Co., high up on s flanks Clark Mountain, 6900 ft, 30 Apr 1952, *Bacigalupi 3695* (JEPS); San Bernardino Mountains region, W side of Broom Flat, near Forest Service road 2N04, 2332 m, 29 Apr 2010, *Bell 860* (RSA), San Bernardino Mountains, approximately 0.75 air mile N of Onyx peak along forest service road 1N01 (Pipes Road), 2678 m, 2 Jun 2010, *Bell 1247* (RSA); San Bernardino Mountains, Tributary to Greenlead Creek adjacent to Holcomb Valley Road (3N16), 2195–2226 m, 27 May 2009, *Fraga 2808* (RSA); San Bernardino Mountains region N from Holcomb Valley Road (3N16) at junction with Van Dusen Canyon Road (3N09), 2256 m, 4 Jun 2008, *Gross 3425* (RSA); San Gabriel Mountains: NE slope Mount San Antonio. Headwaters of west fork of north fork Lytle Creek, 2713 m, 15 Jul 1968, *Wheeler s.n.* (RSA); San Bernardino Mountains Lower portion of Wildhorse Meadow, 2561–2607 m, 27 May 2009, *White 13001* (RSA); Santa Barbara Co., at summit of road at Big Pine Mountain. San Rafael Mountains, 6250 ft, 25 Jun 1963, Smith 8342 (JEPS); Siskiyou Co., Caldwell Butte, E slope, Lava Beds National Monument, 1646 m, 16 May 1950, *Balls 14710* (RSA); Tulare Co., near Mineral King, Sierra Nevada, 8800 ft, 7 Aug 1891, *Coville 1524* (UC); Sierra Nevada: Bighorn Plateau (Tawny Point) Sequoia National Park, 11600 ft, 14 Jul 1963, *DeDecker 1557* (RSA); Franklin Pass Trail, 8000 ft, 18 Jul 1951, Howell 27875 (CAS), Sierra Nevada; Central Sierra Nevada region Franklin Pass Trail, Mineral King and vicinity, 2439 m, 18 Jul 1951, *Howell 27875* (RSA); Tunnel Meadow Sierra Nevada, Kern Plateau, South Fork of Kern River, 9100 ft, 25 Jul 1970, Twisselmann 16937, (JEPS); Round Meadow, 9000 ft, 14 Jul

1971, *Twisselmann, 18032* (CAS); Tuolumne Co., Near Parson's Lodge, Tuolumne Meadows, 9 Aug 1944, *Howell 20192*, (CAS); Eagle Meadow, 20 Jun 1936, *R. F. Hoover 1349* (JEPS); Mount Dana Sierra Nevada, 12900 ft, 7 Aug, *Sharsmith 5503* (UC); Ventura Co., Mount Pinos region Dirt road to Mt Pinos summit and condor observation site, beyond the public parking area, just below the fork in the road, 2591 m, 24 Jun 1978, *Davidson 7372* (POM), Rose Lake Sespe drainage, 3600 ft, 8 Apr 1960, *Hardham 5388* (JEPS).

Phenology and Pollination Biology—Flowering occurs between April and August; fruiting plants most commonly seen in May through September. *Erythranthe suksdorfii* has relatively small flowers and lacks herkogamy, suggesting that self-pollination may occur frequently. Self-pollination was observed at one population when floral buds were dissected revealing stigmas covered with pollen. No floral visitors were observed on this species over the course of this study.

Distribution and Habitat—*Erythranthe suskdorfii* is a widely distributed species occurring primarily in mountainous regions throughout Arizona California, Colorado, Idaho, Montana, Nevada, Oregon, Utah, Washtington, Wyoming in the US. Plants primarily occur in decomposed granite in vernally moist areas on theedges of creeks, streams and in swales and shallow depressions. *Erythranthe suksdorfii* is associated with the following vegetation communities: meadows, sagebrush scrub, pinyon-juniper woodland, mixed coniferous forest, white fir forest, yellow pine forest. Elevation 1000–4200 m (3290–13800 ft). Associated species: *Abies concolor*, *Artemisia tridentata*, *Cercocarpus ledifolius* Nutt., *Chrysothamnus viscidiflorus* (Hook.) Nutt., *Collinsia parvifolia*, *Diplacus nanus*, *Ephedra viridis*, *Ericameria nauseosa*, *Erythranthe androsacea*, *E. breweri*, *E. guttata*, *Juniperus grandis*, *Lewisia rediviva* Pursh, *Navarretia breweri* (A. Gray) Greene, *Pinus jeffreyi*, *P. lambertiana*, *P. monophylla*, *Purshia tridentata*.

Phylogenetic Relationships and Similar Species—*Erythranthe suksdorfii* is inferred to have a sister relationship with *E. carsonensisi* (Fraga unpubl.). These species are easily distinguished by corolla morphology and leaf shape, but share similar growth habitat in that plants are often highly compact with short internodes. See discussion under *Erythranthe carsonsensis* for further information.

Etymology—*Erythranthe suksdorfii* is named for Wilhelm Nikolaus Suksdorf (1850–1932) who was born in Holstein Germany and later immigrated to Bingen, Washington, U.S. where he lived for 57 years (Jones 1933). Suksdorf was an avid plant collector who sent his specimens to Asa Gray at Harvard University Herbarium. The type for *E. suksforfii* was one such specimen. Suksdorf noted in correspondence to Gray that his collection of *E. suksdorfii* (*487*) "is a species I have not found before. The corolla is light yellow, its lobes nearly equal and all emarginate".

Conservation Status—*Erythranthe suksdorfii* is a widely distributed species occurring throughout the western North America. This species has Conservation Status in states where it is found less frequently (Natureserve 2013). *Erythranthe suksdorfii* has a global rank of G4 or apparently secure, but has subnational ranks (S) of S1 or critically imperiled in British Columbia, Canada; S2 or imperiled in the state of Washington, S3 or vulnerable in Montane and Wyoming, and S4 or apparently secure in Nevada. This species is unranked regionally in the states of Arizona, California, Colorado, Idaho, New Mexico, Oregon, and Utah (Natureseve 2013).

CHAPTER THREE: Phylogeny of *Erythranthe* section *Paradantha* (Phrymaceae), a lineage of monkeyflowers native to western North America.

A central goal of plant systematics is to catalogue, organize and understand the evolutionary history of all plant diversity on earth. Despite over 260 years of effort, it is estimated that nearly 20% or 70,000 of the world's flowering plant species still remain to be described (Bebber et al. 2010). Monographs, taxonomic treatments and regional floristic studies continue to be of vital importance in our pursuit of species discovery and documentation (Bebber et al. 2010, 2013). Moreover, understanding of patterns of diversity greatly informs studies in the related fields of ecology and evolutionary biology and, further, the use, management and conservation of natural resources. To meet the goal of cataloging the world's plant diversity, there have been calls for more studies integrating fieldwork, collections, and molecular phylogenetic analysis to advance our understanding of diversity at low taxonomic levels (Bebber et al. 2010, 2013, Daly et al. 2001, Joppa et al. 2011). Combining these efforts towards an integrated approach to documenting diversity can be particularly useful in groups of organisms that have been historically challenging and problematic with regard to taxonomy.

Erythranthe Spach (Phrymaceae; previously included in *Mimulus* L.) is one such group. The genus has been the subject of pervasive taxonomic disagreement, and controversies continue to exist especially at low taxonomic levels (Barker et al. 2012, Beardsley et al. 2004, Whitall et. al. 2006, Nesom 2012a, b). *Erythranthe* sect. *Paradatha* is a relatively species-rich lineage within which species identification has been challenging owing to disagreement among taxonomic authorities (Grant 1924, Munz 1968, Pennell1951, Thompson 1993, 2012, Fraga 2012). In this study, I examine species boundaries and relationships in *Erythranthe* sect.

Paradatha in a phylogenetic context using a dense sampling scheme that benefits from extensive fieldwork. Results of this study inform a taxonomic revision that also incorporates evidence from morphology and ecology (Fraga chapter 2).

Mimulus s.l., as formerly constituted, was a species rich genus in Phrymaceae (Lamiales), a relatively small family with an estimated 200 taxa that occur worldwide (Barker et al. 2014, Beardsley and Olmstead 2002). *Mimulus* s.l. has recently undergone extensive taxonomic revision based on phylogenetic study and assessment of morphological synapomorphies (Barker et al. 2012, Beardsley et al. 2004). The results of this research provided the framework for revision of the generic and sectional classification of Phrymaceae (Barker et al. 2012). Some of the resultant segregate genera (e.g., *Diplacus* Nutt., *Erythranthe*) continue to be a source of newly described species (Fraga 2012; Nesom 2012a, 2013a, 2013 b). As important, species delimitation, especially in species-rich lineages, continues to challenge taxonomists (Fraga 2012, Nesom 2012a, 2012 b). Recently published taxonomic studies in Phrymaceae have advanced our understanding of relationships among major lineages in the family, but also call attention to the complexities and taxonomic controversies that exist with regard to species delimitations and relationships at the species level (Nesom 2012a, 2012b, Fraga 2012, Tulig and Nesom 2012). To better understand species boundaries and inform species-level comparative studies, dense sampling among and within species is needed in order for phylogenetic studies to have the power to assess monophyly of species and to improve understanding of relationships among species (Beardsley et al. 2004).

Despite the widespread claim that there has been nearly complete or dense taxon sampling in phylogenetic studies within Phrymaceae (77–95%; Beardsley et al. 2004, Grossenbacher 2011, Ogutcen et al. 2014, Silvertown et al. 2006), reevaluation of this claim in

the context of the revised taxonomy indicates that only 55% (ca. 110/200 taxa) of the family's total species diversity has been sampled for phylogenetic studies. When one considers all heterotypic synonyms, percent of taxa sampled only decreases further (Fig. 31); although inclusion in studies of these previously recognized taxa are warranted to test current hypotheses of species delimitation. Sampling in Phrymaceae for the study of Beardsley et al. (2004) was designed to investigate interspecific relationships among western North American taxa such that multiple accessions were only included for widespread and 'difficult' taxa. It is important to realize, however, that inclusion of multiple accessions has the potential to reveal complex patterns (e.g., putatively conspecific accessions not monophyletic) owing to processes operating near the species level (e.g., incomplete lineage sorting, hybridization). Moreover, increased sampling for molecular phylogenetic studies may reveal challenges owing to recent divergence and therefore limited sequence variation among closely related species, as is the case in *Erythranthe* sect. *Simiola*, an enigmatic lineage with considerable species richness yet little divergence among species in loci sampled for phylogenetic analysis to date (Beardsley et al. 2004).

Erythranthe is the most diverse of the genera segregated from *Mimulus* s.l., with 120 species currently recognized (Barker et al. 2013; Nesom and Fraga in prep); only 29% of taxa have been sampled in previously published phylogenetic studies (Fig 3.1; Beardsley et al. 2003, 2004, Whitall et al. 2006). Determining interspecific relationships and increasing our understanding of species boundaries in *Erythranthe* are especially important because it is considered a model system for understanding adaptation and speciation (Wu et al. 2008), and is a group of conservation concern (Beardsley et al. 2004, Fraga 2012, Whitall et al. 2006). *Erythranthe* includes notable species that have been the subject of extensive ecological,

evolutionary, and genetic studies (e.g., *Erythranthe cardinalis*, *E. guttata*, *E. lewisii* (Pursh) G.L. Nesom & N.S. Fraga, *E. nasuta* (Greene) G.L. Nesom) in sections *Simiola* and *Erythranthe* (Wu et al. 2008). In addition, several studies have examined putative sister species to investigate the evolution of species traits in a phylogenetic context (Grossenbacher and Whitall 2012; Grossenbacher et al. 2013, Ogutcen et al. 2014). Unfortunately, several of these putative sister species pairs are taxonomically uncertain and/or are not supported as sister taxa by rigorous phylogenetic work, including taxa placed in *Erythranthe* sect. *Paradantha* (e.g., *Erythranthe androsacea*/*E. shevockii*, *E. gracilipes*/*E. palmeri, E. montioides*/*E. suksdorfii*). Rigorous phylogenetic research is critical to inform taxon sampling for these and other kinds of comparative studies.

Section *Paradantha* of *Erythranthe* was erected by Grant (1924), who viewed it as a highly variable group that was likely to be artificial. Grant (1924) noted that species were placed in this section because they did not belong to any of the other well-established groups. Unsurprisingly, as then delimited, the section was found to be polyphyletic by Beardsley et al. (2004). As currently treated, the section resolves as a clade with strong support (Beardsley et al. 2004) and is one of the most diverse lineages in the genus with 16 species recognized at present. Plants in the group are relatively diminutive annuals that are known for their highly variable floral morphology and corolla color (Fig. 3.2). The section is restricted to western North America (Fig. 3.3). In this study I present a molecular phylogenetic analysis focusing on *Erythranthe* sect. *Paradatha*. Sampling is greatly expanded compared to previous studies, both in terms of accessions and of data. Sequence data from nuclear ribosomal ITS and three non-coding regions from the chloroplast genome (*petA-psbJ*, *psbD-trnT*, *rpl32-trnL*) were generated to examine species limits, monophyly and relationships.

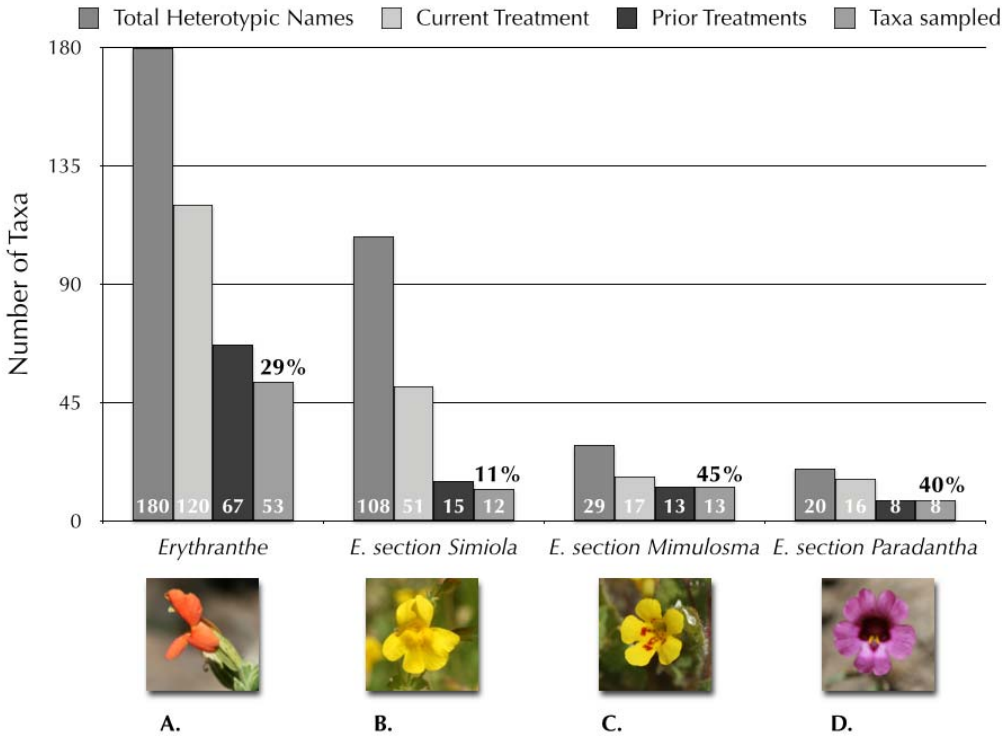

Figure 3.1. Comparison of the total number of named taxa, the number of taxa recognized currently (Nesom and Fraga in prep), the number of taxa recognized in prior treatments (Thompson 2012), and the percent sampled in previous phylogenetic studies (Beardsley et. al. 2003, 2004, Whitall 2004) for *Erythranthe* and the three most diverse sections in the genus (Sections *Simiola*, *Mimulosma*, and *Paradantha*). Photos are representative of taxa in each lineage. A. *Erythranthe cardinalis*, B. *Erythranthe guttata*, C. *Erythranthe geniculata*, D. *Erythranthe palmeri*.

MATERIALS AND METHODS

Sampling—The study includes 90 accessions for 16 species that represent all named taxa in *Erythranthe* sect. *Paradantha* (Appendix A). Multiple accessions (2–11) where included for all taxa except for *E. hardhamiae* (one sample). An effort was made to sample throughout the range of each taxon including type localities when possible (Fig. 3.3). Outgroup sampling was broad and included eight species from five of the twelve section in *Erythranthe* to enable a more

rigorous test of monophyly of *Erythranthe* sect. *Paradantha*. This is important because several accessions included in the study represent newly described species that have been placed in *Erythranthe* but have not been previously sampled in phylogenetic studies (Fraga 2012).

Figure 3.2. Selected species of *Erythranthe* section *Paradantha*. A. *Erythranthe rhodopetra* (scale bar = 5mm). B. Pink and yellow morph of *Erythranthe discolor* (scale bar = 15mm). C. *Erythranthe carsonensis* (scale bar = 10mm). D. *Erythranthe* "*susannae*" sp nov. (scale bar = 20mm). E. *Erythranthe shevockii* (scale bar = 12mm). F. *Erythranthe rubella* (scale bar = 20 mm).

DNA extraction, amplification and Sequencing—Genomic DNA was extracted from dried leaf material using a modified CTAB extraction protocol (Doyle and Doyle 1987). The source material included field collected silica-gel preserved whole-plant material and, in a few instances, samples from herbarium specimens. Extractions were suspended in 100 µL 1 × TE buffer and quantified using a spectrophotometer (BioSpec-1601 DNA/ Protein/Enzyme Analyzer, Shimadzu Corporation, Columbia, Maryland). Following quantification, DNA aliquots were diluted to a concentration of 5 ng/µL for use in PCR reactions.

The nuclear ribosomal ITS (nrITS) region was amplified using primers 18SF and 26SR (CGATTGAATGGTCCGGTGAAG and AGGACGCTTCTACAGACTACAA, respectively; Rydin et al. 2004) at an annealing temperature of 62C. Chloroplast regions were chosen from those described by Shaw et al. (2007) after an initial screening of five: *rps16-trnK*, *trnQ-5'rps16*, *petA-psbJ*, *psbD-trnT*, and *rpl32-trnL*. The last three were selected based on ease of amplification and high levels of variability. Primers, annealing temperatures and PCR conditions for these non-coding chloroplast regions followed protocols outlined Shaw et al. (2007). All PCR amplifications were performed using GoTaq polymerase (Promega, Madison, Wisconsin) in an ammonium sulfate buffer; products were amplified on a PTC-100 thermal cycler (MJ Research, Waltham, Massachusetts) in 25 μL reactions. Additives included 5% DMSO for nrITS and 2% bovine serum albumin (BSA) for non-coding chloroplast regions; these improved product yield and specificity. PCR products were cleaned by polyethylene glycol (PEG) precipitation (Johnson and Soltis 1995) prior to cycle sequencing.

Cycle sequencing reactions (20 μL) were carried out in both directions with ABI Prism Big Dye Terminator solution (Applied Biosystems, Foster City, California) using the same primers as in PCR. Products of sequencing reactions were purified by passing through Sephadex G-50 (GE Healthcare, Anaheim, California) in a 96-well filtration plate. Sequencing was performed on an ABI 3130xl genetic analyzer (Applied Biosystems, Foster City, California) at Rancho Santa Ana Botanic Garden.

Sequence Alignment and Phlogenetic Inference— Sequences were assembled and edited in Geneious version R8 , aligned using MUSCLE version 3.7 as implemented in Geneious followed by manual adjustments in Geneious (Kearse et al., 2012). Previously published nrITS sequences were downloaded from GenBank and added to the nrITS data matrix. Data from the

four target loci where assembled into five data sets, nrITS, *petA-psbJ*, *psbD-trnT*, *rpl32-trnL*, and concatenated chloroplast sequences. The best-fit model of evolution for each data set was evaluated using jModeltest2 v. 2.1.7 (Dariba et al. 2012), under both the Akaike information criterion (AIC) and Bayesian information criterion (BIC). Phylogenies were then inferred using Bayesian inference in Mr Bayes version 3.2.2 (Ronquist and Huelsenbeck, 2003) and Maximum Likelihood using RaxML version 8 (Stamatakis et al. 2008) on the CIPRES cluster (Miller et al. 2009). Bayesian analyses were run for 10,000,000 generations. Trees were saved every 200th generation and the burn-in value was set to ignore the first 25% of trees. Clade support was determined by Bayesian posterior probabilities (Li et al., 2000). Bootstrapping was carried out with 1,000 replicates for the RaxML analyses. Gaps were not coded but were treated as missing data. Data sets consisting of concatenated loci were treated as single partitions.

RESULTS

Characteristics of the datasets — After alignment, the total number of positions in each data set was: 927 base pairs (bp) for nrITS, 1045 bp for *petA-psbJ*, 1580 bp for *psbD-trnT*, 1029 bp for *rpl32-trnL*, and 3654 bp for the total concatenated chloroplast (cpDNA) data set (Table 3.1). Less than 5% of sequences lacked more than 20% of sequence length or were lacking entirely in each matrix (Appendix A). The characteristics of each data matrix are summarized in Table 3.1. The nrITS region was the least variable (13.38%) among sampled loci and provided the fewest parsimony informative characters (69). The most variable loci where *psbD-trnT* with 478 variable sites (30.25% of the total sites) and *rpl32-trnL* with the most parsimony informative characters (167). The models of evolution selected were: GTR + G for nrITS and GTR + I + G for *petA-psbJ*, *psbD-trnT*, *rpl32-trnL* and the concatenated cpDNA dataset, respectively.

Table 3.1. Summary statistics for each data set.

Data set	Total length (bp)	Parsimony-informative characters (*n*)	Polymorphic sites (*n*)	variability (%)	missing data (%)	Model	Accessions
nrITS	927	69	124	13.38%	8.50%	GTR + G	91
petA-psbJ	1045	95	214	20.48%	15.30%	GTR + I + G	86
psbD-trnT	1580	172	478	30.25%	12.60%	GTR + I + G	86
rpl32-trnL	1029	167	273	26.53%	18.80%	GTR + I + G	85
cpDNA concatenated	3654	434	965	26.41%	17.10%	GTR + I + G	89

Phylogenetic relationships inferred from the nrITS analysis—The nrITS analysis provides support for 12 of the 16 named species based on multiple conspecific samples resolving as monophyletic or as paraphyletic with respect to closely related species. In other cases, monophyly cannot be rejected because some samples are unresolved or placed without strong support (Fig. 3.4). Species supported in the nrITS analyses include: *E. barbata*, *E. calcicola*, *E. carsonensis*, *E. diffusa*, *E. gracilipes*, *E. montioides*, *E. palmeri*, *E. purpurea*, *E. rhodopetra*, *E. rubella*, *E. shevockii*, and *E. sierrae*. Samples for species that exhibit flower color polymorphisms (*E. barbata*, *E. calcicola*, *E. discolor*, and *E. rubella*) did not segregate by color (e.g., sample 37 for *E. rubella* has pink corollas but groups with yellow-flowered samples 84 and 97), providing support for my field observations that species are able to maintain multiple color morphs within a population or across a species range. Samples of *E. discolor* are largely unresolved in the nrITS analysis. Taxa that resolve as polyphyletic in the nrITS analysis include: *E. androsacea* and *E. suksdorfii*. The nrITS analysis does not provide sufficient resolution to infer many relationships among species (Fig. 3.4).

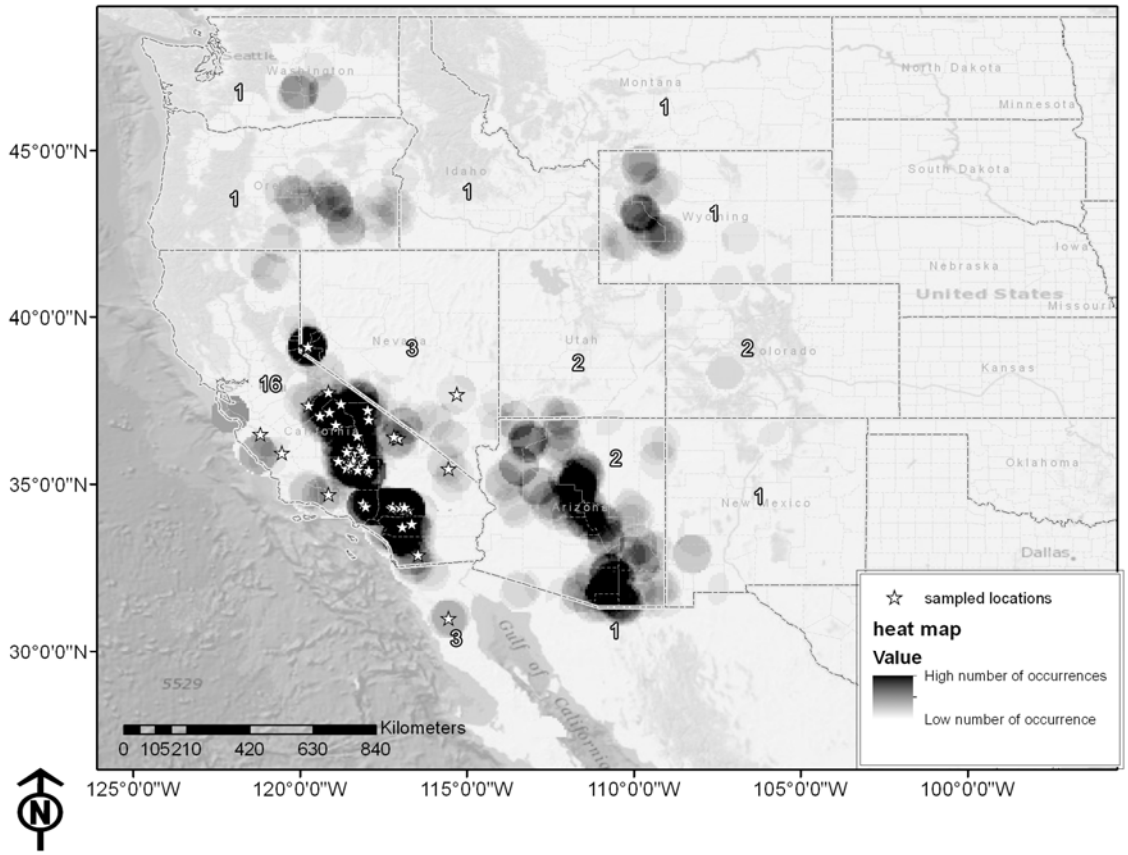

Figure 3.3. Map of sampling locations of *Erythranthe* section *Paradantha* for this study superimposed on a heat map of known occurrences of species in the group. The geographic range of *Erythranthe* section *Paradantha* extends throughout western North America in the USA to Baja California, Mexico, but the density of populations is highest in California and the sampled range for this study. The number of species that occurs in each state is indicated on the map.

Phylogenetic relationships inferred from the cpDNA analysis — The cpDNA results provide support for three species that resolve as monophyletic with strong support: *Erythranthe calcicola*, *E. montioides*, and *E. rhodopetra* (Fig. 3.5). Samples of *E. shevockii* are mostly unresolved, but are in a well-supported clade with two close relatives: *E. androsacea* and *E. purpurea*. The majority of samples for two species pairs endemic to the Sierra Nevada resolve as paraphyletic: *E. gracilipes*/*sierrae* and *E. barbata*/*discolor*. The cpDNA results provide improved resolution to infer relationships between major species groups (Fig. 3.5).Two major species groups are recovered with strong support in the cpDNA results (Clades 1 and 2; Fig.3.5). Clade 1 includes

two well-supported clades: a clade of primarily purple flowered species (marked by a square) and five taxa endemic to the Sierra Nevada (*E. barbata*, *E. discolor*, *E. gracilipes*, *E. sierrae*, *E.* "*susannae*;" marked by a circle). Clade 2 includes species that have yellow corollas, and a subset of samples for the species that are endemic to the Sierra Nevada that where also recovered in Clade 1 (*E. barbata*, *E. discolor*, and *E. "susannae"*). Two samples of *E. rubella* resolve as sister to the rest of Clade 2. Several samples of *E. androsacea* are placed in Clades 1 and 2. *Erythranthe* "*susannae*" is placed with *E. barbata* and *E. discolor* in Clades 1 and 2. Four species show significant discordance in the cpDNA results: *Erythranthe androsacea*, *E. rubella*, *E. suksdorfii* and *E. "susannae"*

Table 3.2: A list of species assemblages

Sierra Nevada group	Pink flowered group	Yellow flowered group	Self pollinating taxa
E. barbata	E. androsacea	E. calcicola	E. androsacea
E. discolor	E. diffusa	E. carsonensis	E. suksdorfii
E. gracilipes	E. hardhamiae	E. montioides	E. rubella
E. sierrae	E. palmeri	E. rubella	
E. "susannae"	E. purpurea	E. suksdorfii	
	E. rhodopetra		
	E. shevockii		

Comparison between nrITS and cpDNA analyses.— Results of the phylogenetic analyses for the nrITS (Fig. 3.4) and concatenated cpDNA (Fig. 3.5) datasets are largely incongruent. Species as currently delimited (Fraga 2012) are mostly supported in the nrITS results (12/16), but are generally not supported by the cpDNA phylogeny (4/16). Three species form reciprocally monophyletic groups in both the nrITS and cpDNA analyses: *E. calcicola*, *E. montioides*, and *E. rhodopetra*. Species that show discordance in both the nrITS and cpDNA results include: *E. androsacea*, *E. barbata*, *E. discolor E.* "*susannae*", and *E. suksdorfii*. The nrITS results lack

sufficient resolution to infer relationships between species, but the cpDNA results provide improved resolution for understanding relationships between major groups of species.

Species assemblages— Three species assemblages (i.e., collections of species that are inferred to share close relationships) are revealed by examination of the nrITS and the cpDNA analyses: the Sierra Nevada group, the purple-flowered group, and the yellow-flowered group (Figs 3.4–3.5; Table 3.2).

The Sierra Nevada group includes taxa endemic to the Sierra Nevada in California (i.e., *E. barbata*, *E. discolor*, *E. gracilipes*, *E. sierrae*, and *E. "susannae"*) that are inferred to share a close relationship. The Sierra Nevada group consists of three clades in the nrITS analysis, two of which lack strong support; relationships among these clades are not resolved but monophyly of the three together cannot be rejected. In the cpDNA results, the Sierra Nevada group resolves as two well-supported clades with most accessions placed in Clade 1 and a smaller subset in Clade 2. These two clades are not, however, sister taxa; instead they are separated by numerous strongly supported branches (Fig. 3.5).

The purple-flowered group includes mostly pink and purple-flowered species that are native to desert and montane/desert transitional habitats in the Mojave Desert and Peninsular and Transverse Ranges (Table 3.2). Most samples that represent species included in the group resolve as a clade in both the nrITS and cpDNA results (i.e., *E. androsacea*, *E. diffusa*, *E. hardhamiae*, *E. purpurea*, *E. shevockii*); *E. palmeri* and *E. rhodopetra* are included in this clade in the cpDNA results but are unresolved in the nrITS results (Fig. 3.4). Several samples of *E. androsacea* that are included in the purple-flowered group in the nrITS results are placed elsewhere by the cpDNA data.

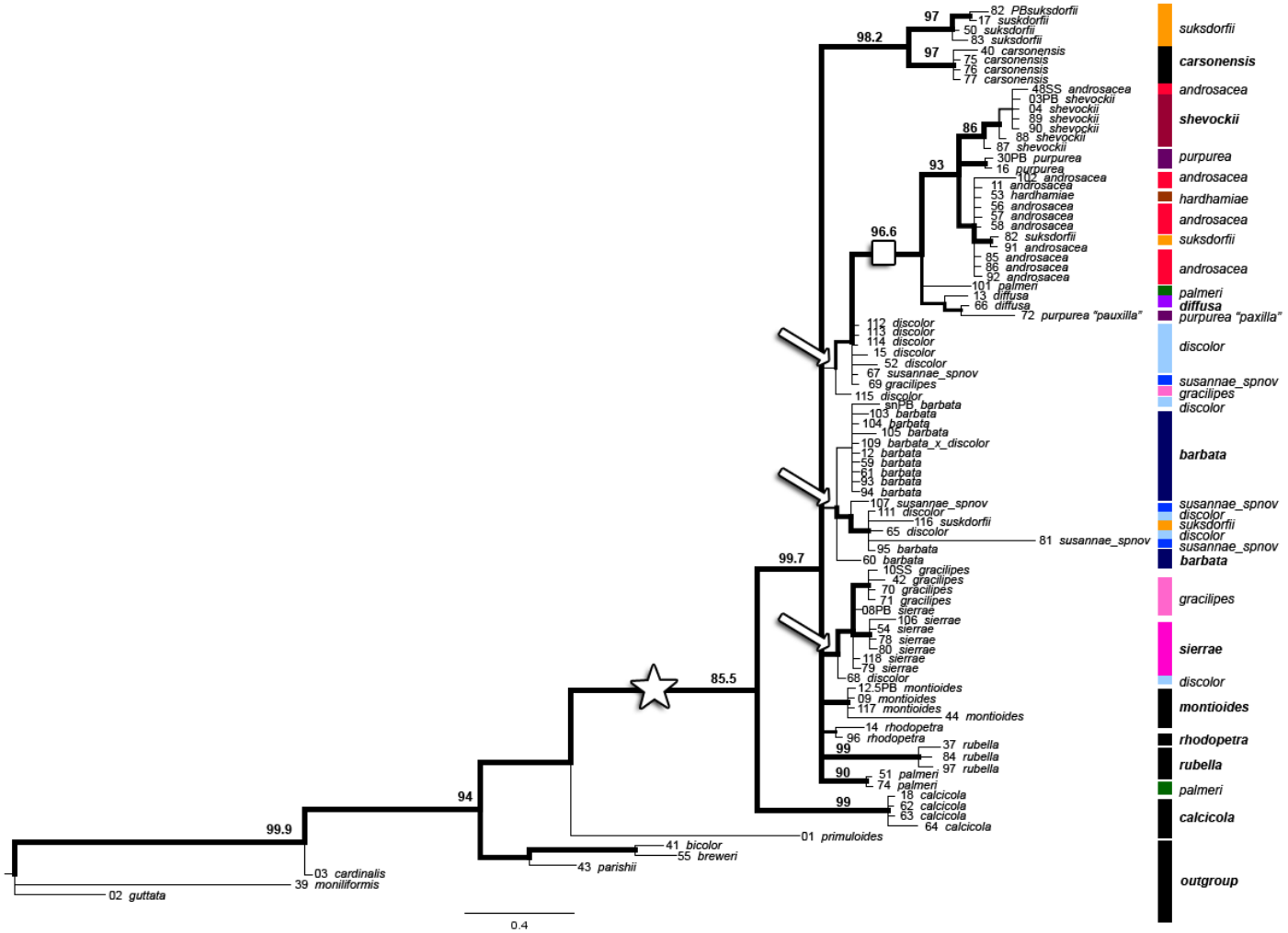

Figure 3.4. Phylogeny based on nrITS inferred by ML and Bayesian analyses; mean branch lengths are inferred by Bayesian analysis. Bold branches have a posterior probability of > 95%. Branches are labeled above with ML bootstrap values. Star indicates *Erythranthe* section *Paradantha*. The purple flowered clade is marked by a square. Taxa in the Sierra Nevada group are marked by arrows. Black bars to the right mark monophyletic species, color-coded bars mark accessions that are con-specific but not monophylyetic (e.g., most accessions of *E. suksdorfii* form a clade but two accessions are placed with other taxa).

Results weakly support the existence of a third group of taxa with yellow flowers: *Erythranthe calcicola, E. carsonensis*, *E. montioides, E. rubella, E. suksdorfii.* Results from analysis of the cpDNA data support this group as a clade except that one clade of the Sierra Nevada group is nested within it (i.e., the clade marked with a circle and an ML BS value of 97 in Fig. 3.5), as are many accessions of *E. androsacea* and an additional accession of *E. barbata* (94). In addition, accession 97 of *E. rubella* is placed distantly (basal to the pink flowered group in Clade 1). *Erythranthe carsonensis* and *E. suksdorfii* are strongly supported as sister taxa in the nrITS analysis, but two accessions of *E. suksdrofii* (82, 116) are placed elsewhere in the cpDNA results. Accessions of *E. montioides* and *E. rubella* are monophyletic in the nrITS results but with relationships otherwise unresolved; monophyly of these together with the *E. carsonensis* + *E.* s*uksdorfii* clade could not be rejected. Lastly, accessions of *E. calcicola* form a clade that is sister to all other species of *E.* sect. *Paradantha* in the nrITS results.

Self-pollinating taxa—Of the three species that are presumed to be primarily self-pollinating due to aspects of floral morphology (Fraga in prep), *E. androsacea*, *E. suskdorfii*, and *E. rubella*, only the latter is monophyletic, and only inferred so by nrITS sequences. All samples of *E. androsacea* are part of the purple-flowered group in the nrITS results but are not monophyletic; accessions of this species are placed in both Clades 1 and 2 in the cpDNA results. *Erythranthe rubella*, although monophyletic based on nrITS, is polyphyletic in the cpDNA results. The majority of samples of *E. suskdrofii* resolve together in the nrITS results; in the cpDNA results they are polyphyletic but all are placed in Clade 2.

Recently described species—Five species have been recently described in *Erythranthe* sect. *Paradantha* based on field observations, morphology, geography, habitat differences, and preliminary phylogenetic results (Fraga 2012); these include: *Erythranthe calcicola*, *E.*

carsonensis, *E. hardhamiae*, *E. sierrae*, and *E. rhodopetra*. Evidence from one or both analyses supports recognition of these newly described species except for *E. hardhamiae* for which only one sample was included. Three of the five newly described species are well supported as monophyletic in the nrITS results (*E. calcicola*, *E. carsonensis*, *E. rhodopetra*); two of these are also well supported in the cpDNA results (*E. calcicola*, and *E. rhodopetra*). *Erythranthe carsonensis* and *E. sierrae* are paraphyletic with respect to close relatives in the cpDNA and the nrITS results respectively.

DISCUSSION

Species delimitation and identification have been historically difficult within *Erythranthe* sect. *Paradantha*. This can be attributed in part to a reduction in vegetative morphology owing to small stature, and variation in corolla color and nectar guide patterning within species (Fraga unpubl.). As currently treated, species in sect. *Paradantha* are recovered as a monophyletic group with robust support in independent analyses of nuclear and cpDNA sequence data. Taxon sampling is greatly improved in this study with 100% of the named species sampled compared to 50% in a previous study (Beardsley et al. 2004). Phylogenetic results provide some level of support for the recognition of most species (12/16); however, samples from six taxa show significant discordance in one or more analysis (*E. androsacea*, *E. barbata*, *E. discolor*, *E. rubella*, *E. suksdrofii* and *E.* "*susannae*"). Species that are inferred to self-pollinate frequently (*E. androsacea*, *E. rubella*, *E. suksdrofii*) show the most significant discordance between the nrITS and cpNDA analyses. Phylogenetic results presented here provide new insight with regard to species limits, relationships, and evidence of hybridization.

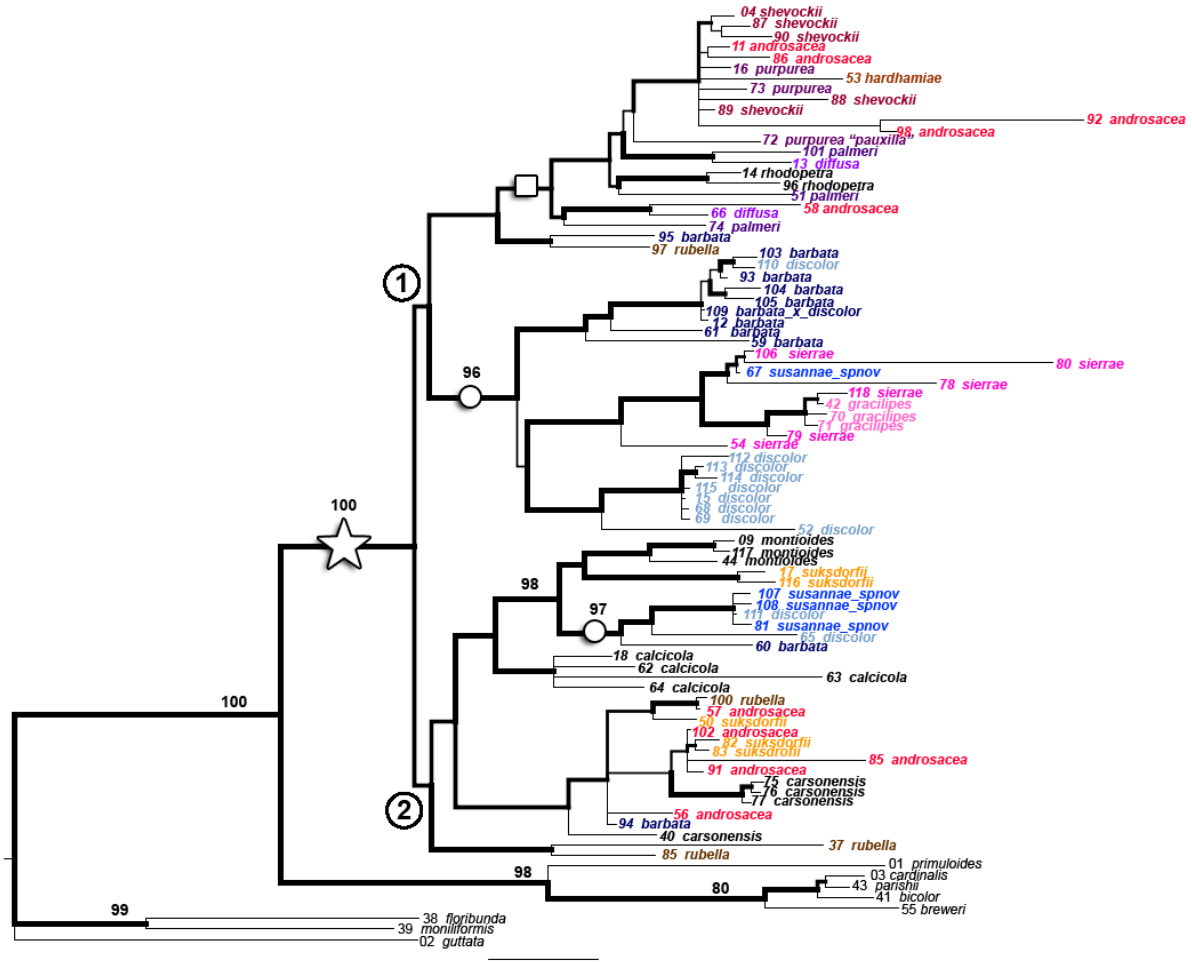

Figure 3.5. Phylogeny based on the concatenated chloroplast alignment inferred by ML and Bayesian analyses; mean branch lengths inferred by Bayesian analysis. Bold branches have a posterior probability of > 95%. Branches are labeled below with ML bootstrap values. Star indicates *Erythranthe* section *Paradantha*. Taxa in the Sierra Nevada group are marked by circles. The purple flowered clade is marked by a square. Monophyletic or paraphyletic species (e.g. *E. carsonensis*) names are black and bold, accessions that are con-specific but not monophylyetic are color coded.

Evidence of hybridization—*Erythranthe androsacea*, *E. barbata*, *E. discolor*, *E. rubella*, *E. suksdorfii* and *E. "susannae"* are polyphyletic in one or more analysis (nrITS or cpDNA). Such patterns can arise through hybridization between species, convergent evolution, or by the retention of ancestral variation (i.e., incomplete lineage sorting; Maddison and Knowles 2006). This study provides evidence for recent (e.g. *E. androsacea* x *E. suksdorfii*) and ancient gene flow (e.g. Sierra Nevada group in Clade 2; Fig. 3.5) in *Erythranthe* sect. *Paradatha*. Species in sect. *Paradantha* have a high degree of niche conservatism with the majority of species occurring in vernally wet habitats in montane to desert transition zones (Fraga unpubl.). Because species share similar habitats and have overlapping geographic distributions, high rates of sympatry are expected. Approximately 25% (23/90) of the accessions sampled for this study where sympatric with other species in sect. *Paradantha*, with up to four species occurring at a single site (Appendix A). This study provides evidence of hybridization for at least three species pairs in sect. *Paradantha*: *Erythranthe androsacea* x *E. shevockii*, *E. barbata* x *E. discolor*, and *E. androsacea* x *E. suksdorfii*.

Evidence of hybridization based on intermediate morphology has rarely been documented in sect. *Paradantha*; however field observations have revealed at least two instances of hybridization inferred from morphology: *E. androsace* x *shevockii* and *E. barbata* x *discolor* (accession 109; Fig. 3.7). Hybridization in sect. *Paradantha* is further supported by evidence of gene flow in the phylogenetic results. For example, accession 98-4SS of *E. androsacea* is included in a well-supported clade with multiple samples of *E. shevockii* in the nrITS analysis (Fig. 3.4) and is the only accession of *E. androsacea* that does not group with the remaining conspecific samples. Importantly accession 98-4SS (*E. androsacea*) was collected at a location where it was sympatric with *E. shevockii*. Additional accessions of *E. androsacea* (11 and 86)

where also collected at sites where it was sympatric with *E. shevockii*, but these accessions do not show evidence of hybridization (Fig. 3.4–3.5).

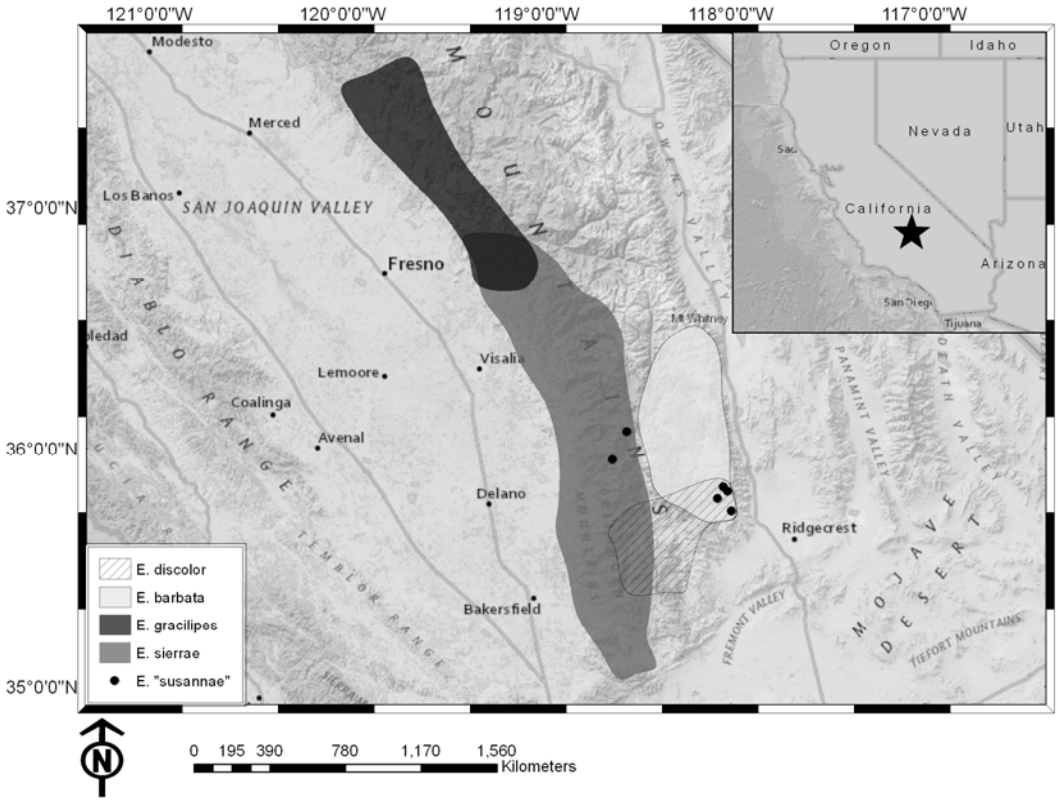

Figure 3.6. A map of the distribution of the Sierra Nevada group. The star on the inset map indicates the region depicted in California, USA.

Erythranthe barbata and *E. discolor* are inferred to share a close relationship and have range overlap in the southern and northeastern portion of their ranges respectively (Fig. 3.6). Three accessions where sampled from a location in the region of overlap where plants where observed to be intermediate in morphology between *E. barbata* and *E. discolor* (Fig. 3.7a). Accessions were tentatively identified to species as follows: *E. barbata* (103; bicolored corolla) and two samples of *E. discolor* (109; yellow corolla and 110, pink corolla; Fig. 3.7a). Sample 110 for *E. discolor* was difficult to amplify for the nrITS region and therefore was not included in the analysis (Appendix A). However all three samples were included in the cpDNA results;

these sequences and the two accessions that amplified for nrITS (103, 109) are placed with the majority of *E. barbata* accessions in both analyses. All accessions collected at this site were more similar to *E. discolor* in vegetative and corolla morphology than to *E. barbata* but the phylogenetic results indicate that these plants are more genetically similar to *E. barbata*. Additional population level sampling in this geographic region could provide insight into the extent of hybridization and species boundaries between *E. barbata* and *E. discolor*.

Erythranthe androsacea and *E. suksdorfii* both have relatively small flowers (< 10 mm) compared with other species in *E.* sect. *Paradantha* and are presumed to be primarily self-pollinating (Fraga unpubl.). There is, however, evidence of gene flow between these two species based on discordance between the nrITS and cpDNA results for specific samples. Sample 82 of *E. suksdorfii* is placed in a well-supported clade with many accessions of *E. androsacea* in the nrITS results; it was collected at a location where it was sympatric with sample 11 (*E. androsacea*) and is also geographically proximal to that of accession 91 (*E. androsacea*; ca. 5 air km apart). Accession 82 (*E. suksdorfii*) is placed with other *E. suksdorfii* accessions that resolve as sister to *E. carsonensis* (inferred closest relative of *E. suksdofii*) in the cpDNA analysis. Conversely samples of *E. androsacea* (accessions 91 and 57) are placed with conspecfic samples in the nrITS results, but have conflicting results in the cpDNA phylogeny where these accessions group with sympatric accessions of *E. suksdorfii* (50 and 82). These results point to recent geneflow between *E. androsacea* and *E. suksdorfii* where they co-occur in different parts of their range (Transverse Ranges and southern Sierra Nevada) and suggest that *E. androsacea* is frequently the pollen donor, while *E. suksdorfii* is the ovule parent. Sampling throughout the range of *E. androsacea* and *E. suksdorfii* at sympatric sites could provide additional insight into the frequency of hybridization and whether the direction of hybridization is consistently skewed.

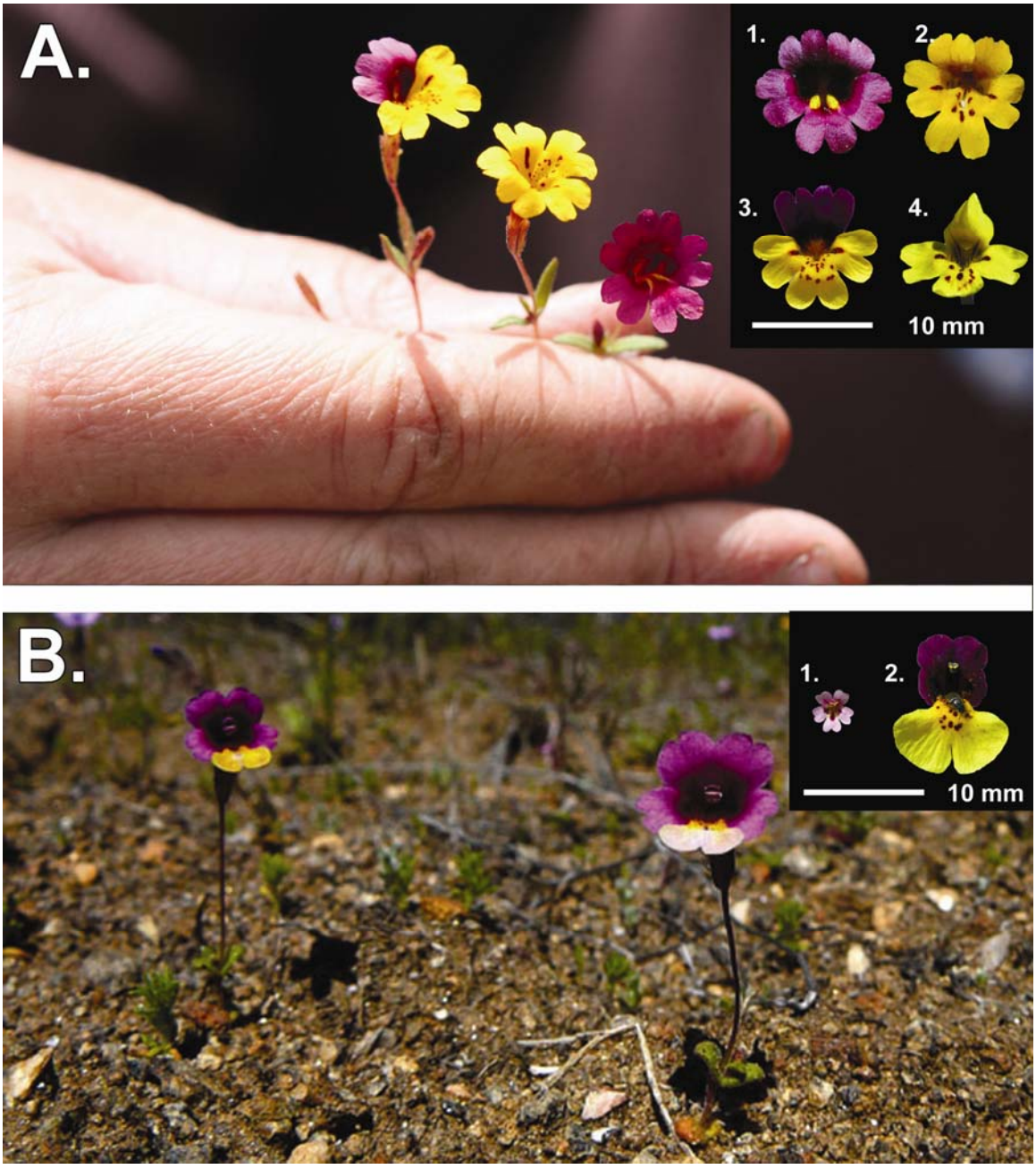

Figure 3.7**.** Individuals of putative hybrid origin. A. Three floral morphs of *Erythranthe barbata* x *E. discolor*. A1–4 putative parents: A1. *E. discolor* (pink morph), A2. *E. discolor* (yellow morph), A3. *E. barbata* (bicolored morph), A4. *E. barbata* (yellow morph). B. *Erythranthe androsacea* x *E. shevockii* (photo by Tim Thomas). A1–2 putative parents. B1. *E. androsacea*, B2. *E. shevockii*.

Evidence of incomplete lineage sorting—*Erythranthe sierrae* and *E. gracilipes* are paraphyletic with respect to each other in both analyses (nrITS and cpDNA). These taxa are inferred to be sister species; their paraphyletic relationship is putatively due to incomplete lineage sorting.

Flower color polymorphism—Corolla color ranges widely in *Erythranthe* sect. *Paradantha* from white, yellow, pink, purple, to bicolored flowers with maroon upper lobes and a yellow lower limb (Appendix A). Four species are known to display corolla color polymorphisms within or between populations: *Erythranthe barbata*, *E. calcicola*, *E. discolor*, and *E. rubella*. As a part of this study, all color morphs within a species where sampled (with at least two samples per color morph) to evaluate flower color variation within species in a phylogenetic context (Appendix A). Understanding corolla color variation within a species is important in the context of proper species identification. Corolla color has been used frequently as a key character in *Erythranthe* to segregate closely related and morphologically similar species (Thompson 2012), and misidentification due to flower color polymorphism is frequent on herbarium specimens. For example, the yellow color morph of *E. barbata* has been commonly misidentified as *E. montioides*, the pink color morph of *E. discolor* is commonly misidentified as *E. palmeri*, and the pink color morph of *E. rubella* is commonly misidentified as *E. breweri* (*E. breweri* is a closely related species but is not placed in sect. *Paradantha*). Based on phylogenetic results there is no evidence that conspecific samples of different color morphs segregate by color. The maintenance of floral color polymorphisms (specifically pink and yellow) is frequent in the family Phrymaceae with at least 10 examples in *Diplacus* and *Erythranthe*. Further study is needed to understand the genetic and ecological basis for maintenance of flower color polymorphisms across this diverse lineage.

Sierra Nevada group—The Sierra Nevada group (*E. barbata*, *E. discolor*, *E. gracilipes*, *E. sierrae*, and *E.* "*susannae*") is inferred to be closely related based on shared habitat preferences (vernally wet open areas in woodland and forest understory), biogeography (all endemic to the southern Sierra Nevada) and the phylogenetic results presented here. The Sierra Nevada group occurs in a region that is topographically diverse and heterogeneous with respect to precipitation gradients and habitat type, but these taxa currently appear to be isolated primarily based on geographic distribution and topography (Fig. 3.7). *Erythanthe barbata* is consistently placed in Clades 1 and 2 by the cpDNA results, as sister to the remaining members of the Sierra Nevada group (Fig. 3.5). *Erythranthe barbata* and *E. discolor* share a close relationship and there is evidence of hybridization where these two species overlap in distribution (Fig. 3.6). *Erythranthe "susannae*" was identified as a morphological variant of *E. discolor* during field observations. The distribution of *E. "susannae"* is primarily within the range of overlap between *E. barbata* and *E. discolor.* This taxon is hypothesized to be a result of hybridization between *E. barbata* and *E. discolor*, based on consistent placement with *E. barbata* and *E. discolor* within the nrITS ands cpDNA analysis and its geographic distribution. However, more study is needed to test the hypothesis of a hybrid origin for *E. "susannae"* and to determine its degree of reproductive isolation.

Erythranthe graclipes and *E. sierrae* are inferred to share a sister relationship. *Erythranthe sierrae* is a newly described species, collections of which were previously misidentified as *E. palmeri* (Fraga 2012). The accession of *E. palmeri* that was included in the study of Beardsley et al. (2004) is here identified as *E. sierrae*. The results from this study corroborate results recovered in the analysis of Beardsley et al. (2004) that supported a sister relationship between *E. gracilipes* and *E. sierra* (as *E. palmeri* in his earlier study).

Samples from the Sierra Nevada group placed in Clade 2 may provide evidence of a distant introgression event and subsequent chloroplast capture for a subset of the species (*E. barbata*, *E. discolor* and *E. "susannae"*; Fig. 3.5). The accessions recovered in the Sierra Nevada group in Clade 2 of the cpDNA phylogeny are also recovered as a clade in the nrITS results (accessions 107, 11, 65, 81 and 60) indicating that they share a close relationship. Relationships between accessions of species in Sierra Nevada group in Clade 1 is mirrored in Clade 2, suggesting a recurrent pattern among these species.

Purple-flowered group—The purple-flowered group is inferred to be closely related based on biogeography (Mojave Desert, Peninsular Ranges, and Transverse Ranges) habitat preference (desert to montane/desert transition habitats), and results of the phylogenetic analyses. *Erythranthe androsacea*, *E. hardhamiae*, *E. shevockii*, and *E. purpurea* share a close relationship and also a number of morphological traits (clasping cotyledons and nearly succulent leaves). Increased sampling is needed for *E. hardhamiae* (only one sample was included in the current study) to determine its phylogenetic placement within the purple-flowered group, and to assess monophyly. The single accession of *E. hardhamiae* included in the study is nested within accessions of *E. androsacea* in the nrITS results and is unresolved in the cpDNA results. *Erythranthe purpurea* occurs in the San Bernardino Mountains and is disjunct 400 km south in the Sierra San Pedro Martir in Baja California, MX. More sampling is needed in Baja California to better understand the relationship between the northern US populations with the Mexican populations to the south and to further explore biogeographic patterns in this lineage.

Additional samples are also needed of *E. diffusa*, a relatively widespread species in that it occurs in southern California Peninsular Ranges, USA, south to Baja California, MX. This species has relatively wide habitat preferences and occurs in openings of chaparral vegetation, in

the understory of oak and pine forest, and in dry meadows; plants also occur across a wide elevational range (300–2100 meters).

Erythranthe rhodopetra is a narrow endemic native to the Mojave Desert in Kern County. Its relationship with other taxa in *E*. sect. *Paradantha* is unresolved. Sampling additional genetic markers is warranted to improve structure within the phylogeny and increase understanding of species relationships in this group.

Erythranthe palmeri is endemic to the Transverse Ranges in Los Angeles and San Bernardino counties. Only one sample was included from the western portion of its range in the San Gabriel Mountains; the relationship of this accession (101) to the other two *E. palmeri* accessions (74 and 51) is unresolved. More sampling is needed throughout the range of the species to determine relationships between the western and eastern populations.

Yellow-flowered group—*Erythranthe carsonensis* and *E. suksdorfii* likely share a close relationship based on both the nrITS and cpDNA results. Interestingly, these species have strongly asymmetric geographic distributions; *E. carsonensis* is a globally rare species endemic to the Carson Valley region of Nevada and adjacent California whereas *E. suksdorfii* is one of the most widespread species in the lineage and occurs throughout western North America. A previous study suggests that differences in climate niche breadth explained the most variation in geographic range size among North American monkeyflowers (*Diplacus* and *Erythranthe*) than other environmental factors (Sheth et al. 2014). In addition Grossenbacher et al. (2013) found that most recently formed sister species of *Diplacus* and *Erythranthe* differ most in their geographic range size.

Self-pollinating species—Three taxa (*E. androsacea*, *E. rubella*, *E. suksdrofii*) are presumed to have high incidences of self-pollination based on floral traits that appear to correlate with self

pollination including: absence of herkogamy, reduced corolla size (< 1 cm long), relatively early flowering time compared to other closely related sympatric species, short flower duration (1–2 days), and relatively small population sizes leading to sparse floral displays (Fraga unpubl.). Results presented here for the self-pollinating species suggests either problems with the current taxonomy, perhaps indicative of frequent convergence on small flower size and cryptic lineages associated with the evolution of self-fertilization, or surprisingly frequent hybridization with closely related species. More sampling across the broad geographic distribution of *E. androsacea*, *E. suksdorfii* and *E. rubella*, including documentation of ploidy level, could help increase understanding of reproductive biology, species boundaries, and aid in identifying evolutionary processes that may be involved in discordance between cp and nuclear results for this group. These data will ultimately inform taxonomic classification of the group.

Current species delimitation—Recent taxonomic work has improved taxonomic classification within *Erythranthe* sect. *Paradantha* and has yielded evidence for recognition of ten species where two species (i.e., *E. montioides* and *E. palmeri*) were previously recognized, including reinstatement of three species (*E. barbata*, *E.* discolor, and *E. diffusa*) and the description of five new species that are supported by the phylogenetic results (including strong support for *E. calcicola*, *E. carsonensis*, *E. rhodopetra*, *E. sierrae*): More sampling is needed with regard to *E. hardhamiae* (only one accession currently included). *Erythranthe* "*susannae*" is an undescribed putatively new species of hybrid origin (*E. barbata* x *E. discolor*); further study is needed to determine if this taxon warrants taxonomic status. t

Conclusions—Diversity in *Erythranthe* sect. *Paradantha* is greater than had been previously documented. Most species belong to narrowly endemic lineages that are vulnerable to habitat loss and warrant conservation consideration. There is evidence for hybridization between closely

(*E. barbata* x *E. discolor*) and more distantly (*E. androsacea* x *E. suksdorfii*) related species. Both recent and considerably older / deeper in the tree. Hybridization may an important evolutionary process in this lineage. There is also evidence of incomplete lineage sorting between *E. sierrae* and *E. gracilipes*.

APPENDIX A

Sample		Species	Author	Collector		Number	Flower color	GenBank accession number			
								ITS	petA-psbJ	psbD-trnT	rpl32-trnL
11	*	E. androsacea	(Curran ex Greene) N.S. Fraga	Fraga	RSA	2002	pink	X	X	X	X
56	*	E. androsacea	(Curran ex Greene) N.S. Fraga	Fraga	RSA	3450	pink	X	X	X	X
57	*	E. androsacea	(Curran ex Greene) N.S. Fraga	Fraga	RSA	2047	pink	X	X	X	X
58		E. androsacea	(Curran ex Greene) N.S. Fraga	Fraga	RSA	3190	pink	X	X	X	X
85		E. androsacea	(Curran ex Greene) N.S. Fraga	Fraga	RSA	3355	pink	X	X	X	X
86	*	E. androsacea	(Curran ex Greene) N.S. Fraga	Fraga	RSA	3193	pink	X	X	X	X
91	*	E. androsacea	(Curran ex Greene) N.S. Fraga	Fraga	RSA	3414	pink	X	X	X	X
92		E. androsacea	(Curran ex Greene) N.S. Fraga	Porter	RSA	14995	pink	X	X	X	X
98		E. androsacea	(A. Gray) N.S. Fraga	Mistretta	RSA	2457	pink		X		
102	*	E. androsacea	(Curran ex Greene) N.S. Fraga	Fraga	RSA	3811	pink	X	X	X	X
48SS		E. androsacea	(Curran ex Greene) N.S. Fraga	Schoenig	UC	98-48	pink	AY575400			
12	*	E. barbata	(Greene) N.S. Fraga	Fraga	RSA	2152	bicolor	X	X	X	X
59		E. barbata	(Greene) N.S. Fraga	Fraga	RSA	3760	yellow	X	X	X	X
60		E. barbata	(Greene) N.S. Fraga	Fraga	RSA	3597	yellow	X	X	X	X
61		E. barbata	(Greene) N.S. Fraga	Fraga	RSA	2270	bicolor	X	X	X	X
93		E. barbata	(Greene) N.S. Fraga	Fraga	RSA	2270	bicolor	X	X	X	X
94		E. barbata	(Greene) N.S. Fraga	Fraga	RSA	2265	bicolor	X		X	
95		E. barbata	(Greene) N.S. Fraga	Fraga	RSA	3596	bicolor	X	X	X	X
103	*	E. barbata	(Greene) N.S. Fraga	Fraga	RSA	3810	bicolor	X	s	X	X
104		E. barbata	(Greene) N.S. Fraga	Fraga	RSA	3826	bicolor	X	X	X	X
105		E. barbata	(Greene) N.S. Fraga	Fraga	RSA	3827	yellow	X	X	X	X
109	*	E. barbata x discolor	(A.L. Grant) N.S. Fraga	Fraga	RSA	3808	yellow	X	X	X	X
snPB		E. barbata	(Greene) N.S. Fraga	Schoenig			unknown	AY575405			
18		E. calcicola	N.S. Fraga & D.A. York	Fraga	RSA	1995	yellow	X	X	X	X
62		E. calcicola	N.S. Fraga & D.A. York	Fraga	RSA	3315	white	X	X	X	X
63		E. calcicola	N.S. Fraga & D.A. York	Fraga	RSA	3347	yellow	X	X	X	X
64		E. calcicola	N.S. Fraga & D.A. York	Fraga	RSA	3308	white	X	X	X	X
40		E. carsonensis	N.S. Fraga	Fraga	RSA	2743	yellow	X	X	X	X
75		E. carsonensis	N.S. Fraga	Fraga	RSA	3367	yellow	X	X	X	X
76		E. carsonensis	N.S. Fraga	Fraga	RSA	3370	yellow	X	X	X	X
77	*	E. carsonensis	N.S. Fraga	Fraga	RSA	3377	yellow	X	X	X	X

13		E. diffusa	(A.L. Grant) N.S. Fraga	Wall	RSA	445	pink	X	X	X	X
66		E. diffusa	(A.L. Grant) N.S. Fraga	Fraga	RSA	3389	pink	X	X	X	X
15	*	E. discolor	(A.L. Grant) N.S. Fraga	Fraga	RSA	2005	pink	X	X	X	X
52		E. discolor	(A.L. Grant) N.S. Fraga	Fraga	RSA	2147	yellow	X	X	X	X
65	*	E. discolor	(A.L. Grant) N.S. Fraga	Fraga	RSA	3474	yellow	X	X	X	X
68	*	E. discolor	(A.L. Grant) N.S. Fraga	Fraga	RSA	2151	pink	X	X	X	X
110	*	E. discolor	(A.L. Grant) N.S. Fraga	Fraga	RSA	3809	pink		X		X
111		E. discolor	(A.L. Grant) N.S. Fraga	Fraga	RSA	3846	yellow	X	X	X	X
112	*	E. discolor	(A.L. Grant) N.S. Fraga	Fraga	RSA	3850	yellow	X	X	X	X
113	*	E. discolor	(A.L. Grant) N.S. Fraga	Fraga	RSA	3851	pink	X	X	X	X
114		E. discolor	(A.L. Grant) N.S. Fraga	Fraga	RSA	3855	pink	X	X	X	X
115		E. discolor	(A.L. Grant) N.S. Fraga	Fraga	RSA	3856	pink	X	X	X	X
42		E. gracilipes	(B.L. Rob.) N.S. Fraga	Fraga	RSA	2654	pink	X	X	X	X
69		E. gracilipes	(B.L. Rob.) N.S. Fraga	Fraga	RSA	2687	pink	X	X	X	X
70		E. gracilipes	(B.L. Rob.) N.S. Fraga	Fraga	RSA	2688	pink	X	X	X	X
71		E. gracilipes	(B.L. Rob.) N.S. Fraga	Fraga	RSA	2694	pink	X	X	X	X
10SS		E. gracilipes	(B.L. Rob.) N.S. Fraga	Schoenig	UC	98-10	pink	AY575407			
53		E. hardhamiae	N.S. Fraga	Fraga	RSA	3344	pink	X	X	X	X
9		E. montioides	(A. Gray) N.S. Fraga	Fraga	RSA	2366	yellow	X	X	X	X
44		E. montioides	(A. Gray) N.S. Fraga	Fraga	RSA	3040	yellow	X	X	X	X
117		E. montioides	(A. Gray) N.S. Fraga	Fraga	RSA	3869	yellow	X	X	X	X
12.5PB		E. montioides	(A. Gray) N.S. Fraga	Beardsley	WTU	98-012.5	yellow	AY575404			
51		E. palmeri	(A. Gray) N.S. Fraga	Fraga	RSA	2092	pink	X	X	X	X
74		E. palmeri	(A. Gray) N.S. Fraga	Fraga	RSA	3540	pink	X	X	X	X
101		E. palmeri	(A. Gray) N.S. Fraga	Fraga	RSA	2169	pink	X	X	X	X
16		E. purpuea	(A.L. Grant) N.S. Fraga	Fraga	RSA	2157	purple	X	X	X	X
72		E. purpuea	(A.L. Grant) N.S. Fraga	Fraga	RSA	2893	purple	X	X	X	X
73		E. purpuea	(A.L. Grant) N.S. Fraga	Fraga	RSA	2161	purple	X	X	X	X
30PB		E. purpuea	(A.L. Grant) N.S. Fraga	Beardsley	WTU	98-030	purple	AY575402			
14		E. rhodopetra	N.S. Fraga	Fraga	RSA	1996	pink	X	X	X	X
96		E. rhodopetra	N.S. Fraga	Fraga	RSA	3786	pink	X	X	X	X
37		E. rubella	(A. Gray) N.S. Fraga	Fraga	RSA	2880	pink	X	X	X	X
84		E. rubella	(A. Gray) N.S. Fraga	Fraga	RSA	3305	yellow	X	X	X	X
97		E. rubella	(A. Gray) N.S. Fraga	Bell	RSA	2448	yellow	X	X	X	X
100		E. rubella	(A. Gray) N.S. Fraga	Tiehm	RSA	14875	yellow			X	X
4		E. shevockii	(Heckard & Bacig.) N.S. Fraga	Fraga	RSA	1533	bicolor	X	X	X	X

87	*	E. shevockii	(Heckard & Bacig.) N.S. Fraga	Fraga	RSA	1990	bicolor	X	X	X	X
88	*	E. shevockii	(Heckard & Bacig.) N.S. Fraga	Fraga	RSA	3192	bicolor	X	X	X	X
89		E. shevockii	(Heckard & Bacig.) N.S. Fraga	Fraga	RSA	1994	bicolor	X	X		
90		E. shevockii	(Heckard & Bacig.) N.S. Fraga	Fraga	RSA	2001	bicolor	X	X	X	X
03PB		E. shevockii	(Heckard & Bacig.) N.S. Fraga	Schoenig	UC	98-03	bicolor	AY575403			
54		E. sierrae	N.S. Fraga	Fraga	RSA	3443	pink	X	X	X	X
78		E. sierrae	N.S. Fraga	Fraga	RSA	3514	pink	X	X	X	X
79		E. sierrae	N.S. Fraga	Fraga	RSA	3410	pink	X	X	X	X
80		E. sierrae	N.S. Fraga	Fraga	RSA	3445	pink	X	X	X	X
106	*	E. sierrae	N.S. Fraga	Fraga	RSA	3847	pink	X	X	X	X
118		E. sierrae	N.S. Fraga	Fraga	RSA	3867	pink	X	X	X	X
08PB		E. sierrae	N.S. Fraga	Beardsley	WTU	98-008	pink	AY575406			
17		E. suksdorfii	(A. Gray) N.S. Fraga	Fraga	RSA	2421	yellow	X	X	X	X
50	*	E. suksdorfii	(A. Gray) N.S. Fraga	Fraga	RSA	2046	yellow	X	X	X	X
82	*	E. suksdorfii	(A. Gray) N.S. Fraga	Fraga	RSA	2004	yellow	X	X	X	X
83	*	E. suksdorfii	(A. Gray) N.S. Fraga	Fraga	RSA	3376	yellow	X	X	X	X
116		E. suksdorfii	(A. Gray) N.S. Fraga	Fraga	RSA	3887	yellow	X	X	X	X
082PB		E. suksdorfii	(A. Gray) N.S. Fraga	Beardsley	WTU	98-082	yellow	AY575401			
67	*	E. susannae sp. nov	ined.	Fraga	RSA	3448	pink	X	X	X	X
81		E. susannae sp. nov	ined.	Fraga	RSA	3592	pink	X	X	X	X
107		E. susannae sp. nov	ined.	Fraga	RSA	3841	pink	X	X	X	X
108		E. susannae sp. nov	ined.	Fraga	RSA	3838	pink		X	X	X
41		E. bicolor	(Hartw. ex Benth.) G.L. Nesom & N.S. Fraga	Fraga	RSA	2689	bicolor	X	X	X	X
55		E. breweri	Greene) G.L. Nesom & N.S. Fraga	Fraga	RSA	3541	pink	X	X	X	X
3		E. cardinalis	(Douglas ex Benth.) Spach	Fraga	RSA	1932	red	X	X	X	X
38		E. floribunda	(Douglas ex Lindl.) G.L. Nesom	Fraga	RSA	2941	yellow		X	X	X
2		E. guttata	(Fisch. ex DC.) G.L. Nesom	Fraga	RSA	1933	yellow	X	X	X	X
39		E. moniliformis	(Greene) G.L. Nesom	Fraga	RSA	2945	yellow	X	X	X	X
43		E. parishii	(Greene) G.L. Nesom & N.S. Fraga	Fraga	RSA	2285	pink	X	X	X	X
1		E. primuloides	(Benth.) G.L. Nesom & N.S. Fraga	Fraga	RSA	1935	yellow	X	X	X	X

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