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TAXONOMY OF *ERYTHRANTHE* SECT. *SIMIOLA* (PHRYMACEAE) IN THE USA AND MEXICO

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ABSTRACT

Erythranthe sect. *Simiola* includes 31 species from North America north of Mexico (some of them also occur in Mexico): *E. arenicola*, *E. arvensis*, *E. brachystylis*, *E. caespitosa*, *E. calciphila*, **Erythranthe charlestonensis** Nesom, sp. nov., **Erythranthe chinatiensis** Nesom, sp. nov., *E. corallina*, *E. cordata*, *E. decora*, *E. geyeri*, *E. glaucescens*, *E. grandis*, *E. guttata*, *E. hallii*, *E. inamoena*, *E. laciniata*, *E. marmorata* (including *Mimulus whipplei*), *E. michiganensis*, *E. microphylla*, *E. minor*, *E. nasuta*, *E. nudata*, *E. pardalis* (including *Mimulus cupriphilus*), *E. parvula*, **Erythranthe regni** Nesom, sp. nov., *E. scouleri*, *E. thermalis*, *E. tilingii*, *E. unimaculata*, and *E. utahensis*. Seven additional species, **Erythranthe brevinasuta** Nesom, sp. nov., *E. dentiloba*, **Erythranthe lagunensis** Nesom, sp. nov., *E. madrensis*, *E. pallens*, *E. pennellii*, and **Erythranthe visibilis** Nesom, sp. nov., are endemic to Mexico, while *E. glabrata* sensu stricto occurs only in Mexico, Central America, and South America. *Erythranthe geyeri*, *E. inamoena*, and *E. utahensis* have previously been treated within *M. glabratus*. The species are divided into 6 informal groups, several including subgroups. Provided here are a key to species, a description and distribution map for each species, and details of typification for all names, including synonyms. Lectotypes are designated for *Mimulus bakeri* Gandoger and ten taxa named by E.L. Greene: *M. arvensis*, *M. implexus*, *M. lucens*, *M. scouleri* var. *caespitosus*, *M. puberulus*, *Mimulus guttatus* var. *grandis*, *M. guttatus* var. *insignis*, *M. marmoratus*, *M. longulus*, and *M. subreniformis*.

KEY WORDS: *Mimulus* sect. *Simiolus*, *Mimulus guttatus*, *Erythranthe* sect. *Simiola*, *Erythranthe guttata*, *Erythranthe glabrata*

The species of *Erythranthe* sect. *Simiola* constitute a distinctive group in vegetative and floral morphology (Grant 1924) and in pollen morphology (Argue 1980). Molecular data indicate that the group is monophyletic (Beardsley et al. 2004) though relatively few species have been sampled. The species have previously been treated as *Mimulus* sect. *Simiolus* (see rationale for altered taxonomic concepts and nomenclature in Barker et al. 2012). The present study provides a taxonomic account of this group that differs substantially from most previous ones. The one closest in concept is that of Pennell (1951).

A number of the species of sect. *Simiola* currently serve as experimental organisms for various laboratories studying evolutionary processes (Dudash et al. 2005; Wu et al. 2008; and see further comments below), and sect. *Simiola* was the object of intensive investigation from about 1950 until the 1990s by R.K. Vickery and his students, who made hundreds of chromosome counts and interspecific and infraspecific crosses and from these data drew corresponding inferences about isolating mechanisms. Vickery, however, never provided a synthesis that correlated taxonomic concepts with data from biological studies and his only incursion into formal taxonomy involved the naming of several Mexican species. In what might be considered a summary of his studies (1978), he noted that *Mimulus guttatus* is "highly polytypic which has led many authors to propose one or another of its forms as distinct species or varieties. The segregant taxa include such distinct species as *M. glaucescens*, *M. laciniatus, M. nasutus*, *M. platycalyx,* and at least 20 other less clear-cut forms (Grant 1924; Pennell 1951)."

Because of ambiguous identifications and an emphasis on species concepts defined primarily by crossing relationships, many of Vickery's studies are difficult to interpret. Further, many of his evolutionary scenarios were predicated on a priori concepts of relationship that are not supported here.

Various botanists have studied the systematics of sect. *Simiola*, including Grant (1924), Campbell (1950), and Pennell (1935, 1947) and parts of the group have been considered in floristic treatments. Taxonomic assessments, however, have been variable in the ways they apportioned the variation and today there is little agreement on anything except for the status of a few seemingly clearly defined and mostly narrowly endemic species: *E. glaucescens*, *E. laciniata*, *E. michiganensis*, and *E. nudata*. *Erythranthe glabrata*, *E. guttata*, and *E. tilingii* are generally recognized, but varieties and subspecies have been recognized within each and there has been no agreement on patterns of variation or infraspecific nomenclature. Many superfluous names have been proposed for variants within sect. *Simiola* and significant disagreement exists in the placement of many names even as synonyms. Beardsley et al. (2004) remarked that "the species making up this section display a high degree of environmental plasticity," which is generally true, but such observations are likely also based in part on morphological variation across more than one species.

Grant (1924) recognized 10 species of *Mimulus* sect. *Simiolus* in North America (including extra-California regions) and 8 varieties (3 in *M. tilingii*, 5 in *M. guttatus*). Campbell (1950) recognized 4 species (excluding *M. glabratus*) and divided *M. guttatus* into 4 varieties. In the only broad treatment to recognize more narrowly defined variants, Pennell (1951) treated 20 species in sect. *Simiolus*, including *M. guttatus* with 4 varieties. For California, Munz (1959) recognized 7 species (including *M. guttatus* with 4 subspecies) and Thompson (1993) in the Jepson Manual — in the most recent overview of *Mimulus* sect. *Simiolus* — recognized only 5 species. *Mimulus guttatus* was described by Thompson (1993, p. 1043) as "Exceedingly complex; local populations may be unique but their forms intergrade over geog or elevation; variants not distinguished here." Thompson even reached across traditional boundaries to include *M. glabratus* var. *utahensis* as a synonym within his broadly interpreted *M. guttatus*.

***Mimulus* as a model study organism**

Evolutionary studies in *Mimulus* have emphasized isolating mechanisms and differentiation that can be documented at populational levels and small geographic scales. Evidence for the species status of *Mimulus michiganensis* (Posto & Prather 2003) and *M. cupriphilus* (Macnair 1989; Macnair & Cumbes 1989) has been provided along this avenue, and other segregates, especially from within *M. guttatus* in the broad sense, have been similarly recognized, though usually more tentatively. Evidence from biological studies suggests that isolating mechanisms among these plants are readily developed in local populations, thus it seems reasonable, at least as a working assumption, that some of such formally named variants might indeed be justifiably recognized at specific rank.

Darwin's investigation (1876) of inbreeding depression and development of self-fertility in *Mimulus luteus* L. was the forerunner of monkeyflower biology. More recent studies of evolutionary processes have centered primarily on populations identified simply as *Mimulus guttatus* (usually without varietal designation or formal qualification) and as *Mimulus nasutus* (e.g., Kiang & Hamrick 1978; Sweigart & Willis 2003; Hall et al. 2006; Martin & Willis 2007, 2010; Swiegart et al. 2008; Wu et al. 2010). The California endemics *M. glaucescens*, *M. laciniatus*, and *M. nudatus*, which are generally recognized in floristic accounts, also have sometimes been included as well as a few other taxa that are often treated as synonyms in these kinds of detailed studies, e.g., *M. caespitosus*, *M. cupriphilus*, *M. micranthus*, *M. platycalyx*, and *M. guttatus* var. *depauperutus* (e.g., Macnair 1989; Macnair & Cumbes 1989; Ritland 1989; Ritland & Ritland 1989; Fenster & Ritland 1992; Carr & Dudash 1996; Awadalla & Ritland 1997; Lin & Ritland 1997; Fenster & Carr 1997; Ritland & LeBlanc 2004).

The basis on which taxa in these evolutionary studies have been identified has rarely if ever been specified. Fenster and Carr (1997) referred to Munz and Keck (1968) for the identification of *Mimulus micranthus*. Ritland & Ritland (1989) provided line drawings of taxa as guides to the identity of the experimental plants (these drawings do show some diagnostic features, but that of *Mimulus nasutus* shows large, chasmogamous, long-styled flowers, which evidently are of some other species). Sweigart and Willis (2003) noted that "taxonomic classifications were verified using morphological characteristics as described by Abrams (1951)" (i.e., the treatment contributed by Pennell). Studies of "coastal perennial *M. guttatus*" by Lowry et al. (2008) apparently refer at least in large part (as established in pers. communication with Lowry) to *Erythranthe grandis* as treated in the present overview; the contrasting "inland annual *M. guttatus*" apparently is *Erythranthe microphylla*. Further, although most of these kinds of studies have indicated at least the general localities from which the plants were obtained, not a single one surveyed in the current taxonomic study has cited vouchers in documentation.

A clearer understanding of evolutionary patterns of variation in sect. *Simiola*, particularly including a knowledge of what discrete entities actually exist, surely would be valuable as these plants are being used in evolutionary studies in various labs in the USA and elsewhere (Phytozome 2011; mimulusevolution.org 2011; Mimulus Community 2011). Even with the barest taxonomic background, a group of these researchers recently received a five million dollar grant (NSF 2003) to study how new species arise by elucidating the molecular genetic basis of speciation mechanisms, concentrating on *Mimulus guttatus* and *M. nasutus* (sect. *Simiolus*) and *M. lewisii* and *M. cardinalis* (sect. *Erythranthe*).

Mimulus is used as a study organism because it provides "an excellent system for determining the genetic and genomic basis of adaptation and speciation," and [in *Mimulus*] "the integration of ecology and genetics with bioinformatics and genome technology offers great promise for exploring the mechanistic basis of adaptive evolution and the genetics of speciation" (Wu et al. 2008). As noted by Phytozome (2011), "*Mimulus* is uniquely suited for ecological and evolutionary studies because of its tremendous range of floral morphology (and associated pollinators), mating systems (selfing to outcrossing), growth forms (annual herbs to perennial woody shrubs), and habitat preference (desert to riparian to aquatic)."

As overstated by Phytozome, however, at least as regards sect. *Simiola*, "Unlike most plant genetic model systems, the ecology of *Mimulus* is known in great detail." Contrasting observations have been made. Meinke (1995, p. 7) referred to all populations of sect. *Simiola* in the Columbia River Basin of Oregon and Washington simply as the "*Mimulus guttatus*/*Mimulus nasutus* ecotype complex," noting that "Various ecotypes of *M. guttatus* occur throughout the entire CRB at most elevations and in virtually all mesic to aquatic habitats below high montane." Lowry and Willis (2010, p. 11) noted that "The *M. guttatus* species complex occurs across western North America as a mosaic of patchily distributed annual and perennial populations." If evolutionary patterns and species boundaries are not known, then the "ecology" surely cannot be known in a meaningful way. While it is clear, for example, that *Mimulus pardalis* and *M. nudatus* are adapted to serpentine substrates and are mostly restricted to them, hardly any generalization about the ecology of *M. guttatus* (in the broad sense of the authors noted above) can be made except that its relationship with the environment may differ greatly from one population to the next.

Phylogenetic hypotheses for the species of sect. *Simiola*

Little is known about phylogenetic relationships among entities of *Erythranthe* sect. *Simiola*. The molecular analysis by Beardsley et al. (2004) included only a few North American species: *Mimulus dentilobus* (probably *E. parvula* as identified here), *Mimulus glabratus* (probably the same as identified here), *Mimulus glaucescens*, *Mimulus guttatus* (sensu lato, otherwise unspecified), *Mimulus micranthus* (an ambiguous identification), *Mimulus nudatus*, *Mimulus tilingii* (sensu lato), *Mimulus wiensii* (presumably *E. madrensis* as identified here), and *Mimulus yecorensis* (*E. pallens* as identified here) and concluded essentially that "the relatively low genetic distances amongst taxa indicate that this clade is relatively young and that its constituent species are very closely related."

A study by Sweigart and Willis (2003) was aimed in part toward an understanding of relationships among a small group of species. The authors sampled various numbers of individuals from "39 *Mimulus guttatus* and 21 *M. nasutus* populations" as well as a few others (as identified in the study) of *M. laciniatus*, *M. nudatus*, *M. platycalyx*, and *M. tilingii*. DNA sequence variation at two nuclear loci was examined, the analysis shown in a neighbor-joining tree for each of the genes (Fig. 2, *m*CYCA; Fig. 3, *m*AP3). Nearly identical trees were shown by Sweigart et al. (2008), with the addition of tetraploid populations. A fuller phylogenetic value of these studies, however, perhaps awaits a reanalysis of the data based on accurate identification of the populations sampled. A subjective interpretation is offered here, based on the geographic locations of the sample populations, cross-references between populations included in the study, and cross-references by acronym to some of the same populations included in other studies from the Willis lab.

* Five populations of *Erythranthe grandis* show as a phylogenetically coherent group in Fig. 3.

* The middle, unresolved cluster of populations in Fig. 2 probably represents *E. microphylla*.

* The upper, weakly monophyletic cluster/clade ("66") in Fig. 2 probably is mostly *E. guttata* apparently intermixed with a few populations of *E. microphylla*, suggesting that introgression may be occurring (or that misidentifications are involved).

* Populations identified as *Erythranthe nasuta* (Figs. 2 and 3) show as strongly monophyletic. *Erythranthe laciniata* clusters with *E. nasuta* in Fig. 2 but not in Fig. 3. Populations identified as *E. nasuta* with "divergent sequences" are perhaps misidentifications of *E. microphylla*, hybrids/ introgressants between *E. nasuta* and *E. microphylla*, or some of each.

* The population of "*Mimulus platycalyx*" (Douglas Co., Oregon) does not cluster in Fig. 2 with any of *Erythranthe grandis*, *E. microphylla*, *E. guttata*, or *E. nasuta*. It perhaps is *E. arvensis* as identified in the current account, as Sweigart and Willis refer to *M. platycalyx* (= *Erythranthe microphylla*) as "highly selfing" (which it is not, but *Erythranthe arvensis* is).

Assumptions or hypotheses in a number of the evolutionary studies regarding progenitor-derivative relationships (particularly that one or another species is directly derived from *Mimulus guttatus*), sister relationships, or any other kind of relationship among taxa of sect. *Simiola* have been largely or completely speculative or else based on unwarranted assumptions. It has commonly been assumed (explicitly and implicitly) that *M. guttatus* is a primitive element of the section. This perhaps has been based on its relatively wide geographic range, wide variability, and perhaps its apparent perennial duration, but none of these justifies the assumption. Fishman and Willis (2008, p. 803) noted that "*M. guttatus* [is] the putative progenitor of other taxa in the complex," referring to Fenster and Ritland (1994). The cpDNA analysis of Fenster and Ritland compared populations identified as *M. laciniatus*, M. *micranthus*, *M. nasutus*, (obviously misidentified, from their illustration and description of it as herkogamous and outcrossing), and five populations of *M. guttatus* (surely misidentified at least in part, as they noted that "most populations of *M. guttatus* are annual.").

In their unrooted Wagner tree, *M. guttatus* appears as terminal taxon on four separate branches and on one of the branches it is indistinguishable from *M. nasutus*. The study concluded that *M. micranthus* and *M. laciniatus* evolved from diffent ancestors, which probably is true, but no vouchers were cited and the small number of taxa and the misidentifications render their study hardly meaningful.

Evolutionary processes and relationships

Many generalizations have been made about evolution within what has been presumed to be a single species. Hall and Willis (2006) documented "divergent natural selection for flowering time and local adaptation between two distinct populations of *Mimulus guttatus*." These two populations ("DUN" and "IM") are identified here with some certainty as *Erythranthe grandis* and *E. microphylla*. It is fair to say that these two species are "locally adapted" in the sense that their flowering time tracks conditions of moisture availability under which each grows, and flowering time may have been a significant factor in the evolutionary divergence of the clades of which two entities are members, but *E. grandis* and *E. microphylla* are not each other's closest relative in the hypothesis of relationships proposed below — they almost certainly arose from separate ancestors. Hall and Willis noted (p. 2474–2475) that "The extent to which local adaptation via flowering time divergence contributes to incipient ecological isolation or even speciation among *M. guttatus* populations is yet unknown, but our results suggest that it may be substantial. Under this scenario, much of the tremendous phenotypic diversity within this taxonomic species ["*Mimulus guttatus*"] is either directly caused or indirectly maintained by divergent, habitat dependent natural selection." At least in this instance, the distinction between *E. grandis* and *E. microphylla* appears to be indirectly maintained.

In a study using the same two populations (DUN and IM), Hall et al. (2006) posed this question: "Does life history divergence between these two populations have a genetic basis or is it completely environmentally dependent?" In the same perspective as in the Hall and Willis (2006) study, the question seems to be immediately answered by recognition that each population belongs to a different species and clade.

In the hypothesis here, the closest relatives of *Erythranthe grandis*, including *E. guttata* sensu stricto, share an essentially similar flowering regime and may occur in similar habitats. The same is true for *E. microphylla* and its closest relatives. This may help explain results that Hall et al. (2010) found surprising, i.e., that local adaptation in the same two populations of these species (DUN-*E. grandis* and IM-*E. microphylla*) is largely controlled by non-overlapping loci and that native genotypes were not uniformly locally adaptive. The perspective of still other studies using the DUN and IM populations (e.g., Arathi et al. 2002; Baker & Diggle 2011) may also be altered with the recognition that non-sister species are involved.

Other generalizations have been made about evolution within a broadly construed *Mimulus guttatus*. For example, Lowry et al. (2008) concluded that "the coast and inland populations collectively comprise distinct ecological races [of *Mimulus guttatus*]" and that "adaptations to widespread habitats can lead to the formation of reproductively isolated species." Again, what they considered ecological races are here regarded as distinct, non-sister species (*Erythranthe grandis* and *E. microphylla*).

Lowry and Willis (2010) observed that a chromosomal inversion polymorphism contributes to "adaptive divergence and reproductive isolation between annual and perennial ecotypes" of *Mimulus guttatus*. Most of the study populations were the perennial *Erythranthe grandis* and the annual *E. microphylla* (including the DUN and IM populations noted above). As interpreted in the present study, northernmost coastal perennial populations (BOB, TSG, BOB) and inland perennial populations (ANR, BOG, FAL, QNT) in the Lowry and Willis study probably were *E. guttata* (in the narrowed sense). One population of *E. nasuta* (SF), an inland annual, was included. They found that all annual populations had one inversion arrangement while all perennials had another, suggesting to them that the distribution of the two arrangements is "a function of the availability of soil moisture during summer months."

In a simpler perspective, in the Lowry and Willis study the distribution of the inversion arrangements is explained by common ancestry. Their study does not contradict a morphologically-based hypothesis that their "ecotypes" are instead better represented as four species and that among the four, the annuals *Mimulus microphyllus* and *M. nasutus* are related as a pair and the perennials *M. grandis* and *M. guttatus* are related as a pair. The data are better first interpreted outside of the assumption that all populations involved were of a single species.

Especially with the increased number of species in sect. *Simiola* recognized in the present study and different criteria for their identification, hypotheses of relationship should be reassessed based on objective criteria, and conclusions and generalizations in evolutionary studies should be reconsidered.

Duration and environmental modification

Species of *Erythranthe* sect. *Simiola* are commonly described as "perennial" or "annual" but what is meant by those descriptors is rarely explicit. The nature of the plant base at least sometimes appears to underlie the interpretation — perennials produce rhizomes or stolons and annuals are consistently fibrous-rooted or slenderly taprooted. Or, a shift in "annual/perennial life-history" in some cases appears to nearly equated with timing of flowering (van Kleunen 2007; Lowry & Willis 2010). Morphological features and timing of flowering associated with duration are closely tied to the adoption of narrower species concepts in the present study.

Mimulus guttatus has been described as variable in duration.

> "Plants annual and fibrous-rooted, or perennial by stout stolons, only rarely perennial from well-developed rhizomes, very variable in stature and vigor, sometimes dwarf and small-leaved, sometimes robust and nearly a meter high, and with the leaf blades up to nearly 1 dm long" Cronquist (1959, p. 344–345).
>
> Vickery (1973) distinguished "obligate annual forms" and "obligate perennial forms" of *M. guttatus*. He also (1974) characterized the species as comprising "facultative perennial or obligate annual plants."
>
> "While many inland populations of *M. guttatus* are annual, numerous inland perennial populations are found in areas of year-round soil moisture, such as on the edge of lakes or in rivers, hot springs, and alpine habitats (Lowry & Willis 2010, p. 4).

Others have viewed *M. guttatus* as perennial in duration.

> *"Mimulus guttatus* is a riparian species which maintains its populations largely by long life span and by growing profuse stolons as propagules in nature" (Kiang 1973).

Variation in duration within *Mimulus guttatus* has been described as occurring among "ecotypes" (e.g., Meinke 1995; Lowry & Willis 2010), "ecomorphs" (Wu et al. 2007), or "ecological races" (e.g., Lowry et al. 2008; Lowry & Willis 2010), and it commonly has been attributed to phenotypic response to environmental variation, for example as described below.

> "This species is the most common and the most polymorphic in the genus. It varies greatly with environmental conditions, especially in relation to the size of the stem, leaves, and

> flowers. ... The variety *grandis* of Greene is therefore considered to be a direct response to environment, the size of the parts being dependent on the amount of water available or on the vitality of the plant" (Grant 1924, p. 169).
>
> Dole (1992) characterized sites themselves as "perennial" (persistently wet) or "annual" (summer drying). "Plants [of *M. guttatus*] in annual sites die each summer due to lack of moisture (although they are occasionally facultative perennials, Vickery 1959), while those in perennial sites usually persist through the summer into the fall rainy season, hence continuing growth and reproduction (J. Dole, unpublished data)." (Dole 1992, p. 651).
>
> "In its native range where moisture is seasonally ephemeral, *M. guttatus* acts as a common annual. However, in areas where water is continuously available particularly in coastal areas, perennial individuals can be found (Dudash et al. 2005, p. 38).
>
> Using the number of stolons per plant as a possible response to varying conditions of water availability, Murren et al. (2006) observed "significant plasticity to water availability, with generally taller plants, larger stem diameters, lower leaf perimeter to area ratios, and greater stolon and sexual production in our wet treatment" (pp. 2599-2600) They noted that stolons were produced later in the season, "consistent with wet sites in the field where plants have a longer flowering season" (p. 2600).
>
> Van Kleunen (2007) regarded his study as documentation of adaptive evolution in life history traits, which he viewed as "plastic," connected with duration within the single species *M. guttatus*. He compared "plants of *Mimulus guttatus* originating from temporarily wet populations where the species has an enforced annual life-cycle" with "plants from permanently wet populations where the species has a perennial life-cycle" and found that the annuals invested significantly more in sexual reproduction and significantly less in vegetative reproduction, concluding that "natural watering conditions ... determine the life span of the species."
>
> "Members of the section *Simiolus* are hydrophilic plants growing by springs, bogs, lakes and small streams. *Mimulus guttatus* will grow in such habitats either as an annual, particularly is water is seasonal, or as a perennial where conditions are suitable. In some more arid places it also grows as a small unbranched annual when there is a lack of competition from better adapted species. This form flowers more quickly than conspecifics in a damper environment, and dies after producing only a few flowers" (Macnair 1989, p. 3).

Macnair, in the same publication (1989), noted that the duration of some species is genetically constrained.

> *Mimulus guttatus*, *M. nasutus*, *M. cupriphilus*, *M. nudatus*, and *M. laciniatus* "are probably functional annuals in many Californian populations. However, all *M. guttatus* populations studied have been only facultatively annual since in the glasshouse they will normally survive flowering. This is also true of *M. nasutus*. Although Vickery (1964) and Kiang (1973) describe this species as an annual, I have been able to maintain it as a perennial. The other three species appear to be obligate annuals. Since the annual/perennial distinction represents a fundamental difference in plant reproductive biology, this difference between *M. cupriphilus* [annual] and *M. guttatus* [perennial] is of considerable importance" (Macnair 1989, p. 11). [Author's note: *M. cupriphilus*, *M. laciniatus*, *M. nudatus*, and *M. nasutus* always are fibrous-rooted, never producing rhizomes or stolons or rooting at basal nodes.]

Hall et al. (2006) made a similar observation about "inland annual *Mimulus guttatus*" (presumably identified as *Erythranthe microphylla* in the current study).

> "Plants from these populations are facultative annuals due to seasonally dry environmental conditions, and they can be maintained indefinitely in standard greenhouse conditions" (p. 1831).

Presumably the fibrous-rooted plants maintained as "perennial" by Macnair and by Hall et al. did not develop rhizomes or stolons, thus the biological nature of this extended duration would not be homologous with that of *E. guttata*. It would be interesting to know if the potential of *E. microphylla* to be maintained "indefinitely" in the greenhouse also is found in other non-rhizomatous species of annual duration in nature.

It may be that some plants of *Erythranthe guttata* sensu stricto flower before developing rhizomes, thus appearing to be annual, but even the smallest flowering plants of this species (as regarded here) almost always have rhizomes or stolons. Further, I have not encountered a single published study that unequivocally documents the existence of variation in duration (rhizomatous vs. non-rhizomatous) among plants of any one *Mimulus* species, even though such an assumption has been made implicitly and explicitly in many studies.

In interpretation of the present study, there is a consistent distinction between species of fibrous-rooted or slenderly taprooted plants and species of rhizomatous plants. Various population systems of consistently fibrous-rooted or taprooted plants can be identified by syndromes of other morphological features and geography and are considered here as distinct evolutionary lineages, these for the most part identified as species. Potential for production of rhizomes, as in *Erythranthe guttata*, *E. grandis*, and *E. tilingii*, for example, also appears to be genetically controlled. It is not demonstrated, however, that rhizomes are consistently correlated with an ability in these herbs to persist in nature for more than a single season. The single explicit reference to this I have encountered in literature is this: "in perennial [persistently wet] sites, clones often appear several years old (as judged upon the size of genets with many stolons)" (Dole 1992, p. 651). By inference, *E. michiganensis* apparently perennates through rhizomes as all but one of its known populations are seed-sterile.

Ritland (1989) published observations of reproduction in *Erythranthe caespitosa*, where plants characteristically produce a mass of filiform rhizomes: "In the winter of 1983-1984, plants left outside in Vancouver were subject to subfreezing tempatures for a week. Most of the plants died except for a small (1–2 mm) nucleus of the vegetative meristem at the tip of each of the several branches of the plant. These small turions fragmented from the branch very easily and in spring grew into new plants."

Some consistently fibrous-rooted non-rhizomatous species (referred to in the present study as "annual") produce decumbent stems that characteristically root at the basal nodes (e.g., *Erythranthe arvensis*, *E. cordata*, *E. inamoena*). Whether this behavior makes them potentially similar in duration to rhizomatous species is not known. In *E. glaucescens* (as discussed below), which always is fibrous-rooted, plants from at least one locality have produced leafy runners from basal cauline nodes — the latter should be investigated toward the possibility that they are genetically different from the more characteristic expression without runners. In some plants of *E. guttata*, particularly in Colorado, and in *E. decora*, plants often produce numerous long, leafy runners from basalmost nodes, apparently in addition to rhizomes — whether these runners are strictly homologous (developmentally) to rhizomes produced elsewhere in the species also is an open question.

Murren et al. (2006) used eight populations of "*Mimulus guttatus*" from Lake and Napa counties, California, to study effects of Ca/Mg ratio and water on trait expression. Through field observations, they confirmed that all of the study populations "senesced at the end of the season and ultimately acted as annuals." Plants in some of the study populations were described as stoloniferous, apparently indicating that stolon production is not consistently correlated with perennial duration.

Production of rhizomes as a primitive feature in Phrymaceae may be a reasonable hypothesis, as some basal phyletic elements (Beardsley et al. 2004; Barker et al. 2012) are rhizomatous or otherwise perennial (e.g., *Mimulus ringens* and *Mimulus gracilis* are rhizomatous; *Leucocarpus perfoliatus* and species of *Hemichaena* are perennial but ligneous-taprooted). On the other hand, duration appears to be evolutionarily labile among (but not within) species of the family. It appears that the woodiness and perenniality of plants in *Diplacus* sect. *Diplacus* are derived from annual ancestors and such also may be the case in *Leucocarpus* and *Hemichaena*. Rhizome production in *Erythranthe* occurs in scattered species and species groups and may be derived in each of the instances. In sect. *Simiola*, rhizomes are produced in about half of the species and those species may all have arisen from annual, non-rhizomatous ancestors. In fact, it seems likely that the rhizomes of *E. tilingii* and those of *E. guttata* are not homologous.

Variation in flower size and morphology

Corolla size in some annual species of *Erythranthe* varies greatly. Especially notable in sect. *Simiola* are *E. arvensis*, *E. cordata*, *E. laciniata*, and *E. nasuta*. In these species flowers in the smaller range are cleistogamous but even the larger flowers, producing short but apparently chasmogamous corollas, are consistently autogamous in their arrangements of stamens and stigma.

Plants of *Erythranthe nasuta* vary greatly in stature and flowers of smaller plants are accordingly reduced in scale. Some plants produce only cleistogamous flowers, and even on a single plant short basal branches may bear numerous flowers consistently much smaller than those of the main branches. Kiang (1973, p. 229) observed that "flowers [of *E. nasuta*] are progressively reduced in size on a plant, and after ten nodes or so on the main stem, flowers often become so small [cleistogamous] as to be inconspicuous." Benedict (1993) noted that environmental stress resulted in production of cleistogamous flowers in *E. nasuta*.

Species in sect. *Simiola* that apparently produce only cleistogamous flowers are *Erythranthe brachystylis*, *E. brevinasuta*, *E. calciphila*, *E. hallii*, and *E. visibilis*. Species of the section with consistently autogamous pollination but apparently without cleistogamous corolla forms are *E. pardalis*, *E. geyeri*, and *E. inamoena*. Species with autogamous breeding and both corolla forms are *E. nasuta*, *E. laciniata*, *E. arvensis*, and *E. cordata*.

Corollas of some perennial species of *Erythranthe* sect. *Simiola* are highly variable in size. Some of the variation in *E. guttata* appears to be between populations, but plants sampled by collections often are relatively large and infrapopulational variation rarely is documented by herbarium collections. Grant (1924, p. 169) observed variation in single plants of *E. guttata*: "In several experiments, plants were marked early in the season which had corollas 3.5–4.5 cm. long; late in the summer, flowers produced on these same plants were less than half that length." Dole (1992, p. 655) observed that *E. guttata* populations "seemed to harbor relatively more genetic variation in stigma-anther distance [a common correlate of corolla length], as well as vegetative reproduction, stigma curl, corolla drop, and flowering date" than *E. microphylla* and *E. nasuta*. He speculated that high levels of self pollination resulting from anther-stigma contact in one population of *E. guttata* might reflect introgression of selfing features from *E. microphylla* at the same site. [The species identified by Dole as *E. microphylla* may have been the autogamous *E. arvensis*.]

Erythranthe guttata shows wide variation among populations in corolla size and anther/ stigma separation, but all appear to be essentially allogamous in nature. By growing experimental populations of *E. guttata* over five generations without pollinators, Bodbyl Roels and Kelly (2011) were able to induce pronounced changes in reduction of anther/stigma separation and in increased autogamous seed set. Similarly, in a population of *E. microphylla*, Fishman and Willis (2008) observed decreases in corolla width/length ratio and stigma–anther separation as a result of extreme pollen limitation. And at least in some populations of *E. guttata*, seed set in the absence of pollinators also may occur through delayed self pollination via corolla abscission. "Self pollination can occur as stamens, which are adnate to the corolla, drag anthers past the stigma as the corolla drops" (Dole 1992, p. 651).

In the annual *Erythranthe microphylla*, flowers as well as plants are highly variable in size. Dole's study (1992) suggests that variation in floral morphology in this species includes correlated variation in biology, the smaller flowers autogamous through stigma-anther contact prior to corolla abscission; larger flowers have separated stigmas and anthers and presumably are allogamous. In contrast, no unambiguous evidence of obligate autogamy in *E. microphylla* (in the sense of the present study) has been observed in the present study, even in the smaller corollas. In the smaller and narrower corollas, however, crowding of anthers and stigma, even when herkogamous, may lead to a higher incidence of self-pollination.

Lowry et al. (2012) studied "the genetic basis of variation in five anthocyanin phenotypes including calyx, corolla, and leaf coloration patterns that vary within and among populations of *Mimulus guttatus*," concluding that variation in calyx spotting is primarily controlled from a tandem array of three *R2R3-MYB* genes at a single major locus. They examined plants from over the whole geographic range of the species (identified without qualification in their study as *M. guttatus*; the genetic analysis included plants of *Erythranthe grandis* and *E. microphylla*) and found that the spotting was nonrandomly distributed — it is "most common in the Mediterranean regions of California [as mapped in their Fig. 3]. In the field, we have most commonly observed calyx spotting in populations that dry out quickly due to the onset of summer drought in California" (p. 90). Monthly precipitation was the climate variable most strongly correlated with the variation in spotting. An alternative explanation, however, for the non-random geographic distribution may simply be that the sampling of plants from California was biased toward *E. microphylla*, which, with its closest relatives, has a stronger tendency to produce anthocyanin pigments than *E. guttata* in the strict sense (pers. observ.). A realistic interpretation awaits accurate identifications.

Chromosome numbers

Chromosome numbers have been reported for North American populations of sect. *Simiola* in many studies and communications (see separate listing under Literature Cited) and Vickery has made generalizations regarding evolutionary and geographic trends. The most common chromosome number in the genus *Erythranthe*, $2n = 32$, is indicated by the molecular-phylogenetic study by Beardsley et al. (2004) to be the primitive one. Among sections of the genus, the greatest variation in chromosome number occurs in sect. *Simiola*, and $2n = 32$ characterizes some of those species as well. Many counts reported by Vickery et al. need to be verified because of problems in the initial identifications and inconsistent reporting of putative B-chromosomes.

No consistent attempt is made here to align each of the various chromosome counts with the publication in which it appeared. I have, however, studied vouchers for sect. *Simiola* deposited at UT by Vickery and students, and a number of these are cited where pertinent in the discussions.

A significant taxonomic insight from studies related to chromosome variation is the observation that crosses between different polyploid levels nearly always fail. Crosses between different dysploid levels produce hybrids that sometimes are sterile (Alam & Vickery 1973; Sweigart et al. 2008) but sometimes fertile. In a review of crossing relationships (Vickery 1974), one of two dysploid populations ($n = 13$ from New Mexico) of *Erythranthe nasuta* was almost completely genetically isolated from *M. guttatus*, but the other *n* = 13 population (from California) was more similar to *n* = 14 *E. nasuta* in its crossability. Identification of the seemingly aberrant population needs to be reassessed.

South American species

Six species of *Mimulus* sect. *Simiolus* were recognized by von Bohlen (1995) as native to Chile: (1) *M. cupreus* Dombrain, (2) *M. depressus* Phil., (3) *M. glabratus* Kunth sensu lato (including *M. andicola*, *M. externus*, *M. kingii*, *M. parviflorus*, *M. pilosiusculus*, *M. sylvaticus*, *M. tener*, and others), (4) *M. luteus* L. (including *M. nummularis*, *M. smithii*, *M. variegatus*, and others), (5) *M. acaulis* Phil. (= *M. minimus* von Bohlen = *M. nanus* Phil.), and (6) *M. naiandinus* Watson & von Bohlen. The species occur northward from Chile along the Andes to Columbia and others are recognized (Barker et al. 2012), apparently including some represented by synomyms as treated by von Bohlen: *M. andicola* Kunth, *M. laceratus* Pennell, *M. parviflorus* Lindl., and *M. pilosiusculus* Kunth. In view of the taxonomy proposed here for the North American species and the apparent ease with which isolating mechanisms are developed, it seems likely that further South American segregates will be recognized at specific rank.

Vickery divided the South American species between two subgroups (see further details below). Those of the *Mimulus glabratus* complex have a chromosome number of 2*n* = 92, presumably derived from a hexaploid ancestor on the base of x = 15. Those of the *Mimulus luteus* complex known cytologically have a chromosome number of 2*n* = 60, 62, and 64, the variation outside of x = 15 perhaps reflecting the presence of B chromosomes.

Species concepts

The approach and process of the present taxonomic study have been similar to those made by the author in many other genera of various families. Coherent morpho-geographical patterns have been sought and, once found, it is hypothesized that population systems showing such coherence reflect real evolutionary entities. Many of the perceived taxonomic problems in sect. *Simiola* apparently have largely been because of wide variability within species rather than variation within broadly intergrading complexes and most of the species in the present account are recognized with a strong degree of confidence. Interspecific hybrids apparently do occur but do not blur taxonomic boundaries to the extent where species cannot be recognized. For example, as noted by Sweigart and Willis (2003, p. 2491), "when populations of *M. guttatus* and *M. nasutus* live in sympatry, hybrids are frequently observed (Vickery 1964, 1974; Kiang and Hamrick 1978; Ritland 1991; Fenster and Ritland 1992). Nevertheless, the two species seem to maintain their phenotypic differences even in these sympatric sites, suggesting that the effects of hybridization may be limited."

Vickery (1978, p. 425-426), noted that "The *Mimulus guttatus* complex appears to be a large assemblage of more or less well-marked semispecies ... that has characteristics of both a superspecies, i.e., a series of allopatric semispecies toward the periphery of its range, and of a syngameon, i.e., of a cluster of sympatric semispecies toward the center of its range." An emphasis on crossing relationships in defining species such that much of this group becomes essentially a single species, the "*Mimulus guttatus* complex," or a superspecies or syngameon, does not fairly represent some of the apparently discrete patterns of variation that exist among these plants.

In a study of coastal perennial and inland annual "races of *Mimulus guttatus"* (as identified in the study), Lowry et al. (2008) concluded that the two population systems comprise distinct "ecological races." They perhaps were not considered species because F2 hybrids were successfully produced in all intercrosses among F1 progeny between the two races. On the other hand, they concluded (p. 2209) that they studied "two distinct morphologically and molecular genetically diverged groups [and that] "Nearly complete prezygotic isolation through a combination of geography, selection against immigrants, and flowering time isolation likely maintains the genetic differentiation of these coast and inland groups." "Striking morphological differences were found between coast and inland populations in the common garden greenhouse experiment" (p. 2202). "Geographically distant coastal populations (>1000 km apart from each other) are more closely related to each other than they are to adjacent inland populations" (p. 2209) and that "the coastal populations may be the result of a single evolutionary origin" (p. 2211).

In the perspective of the current account, the Lowry et al. (2008) study supports treatment of the coastal and inland population systems as distinct species. The difference in interpretation may simply reflect a difference in concept about the nature of species, but it seems more than semantic, as the authors noted (p. 2211) that "Although the coastal and inland races of *M. guttatus* appear to show approximately complete reproductive isolation, the process by which ecological races become good species remains unclear" (p. 2211) but that "adaptations to widespread habitats can lead to the formation of reproductively isolated species" (p. 2196). From the comments and photos in the publication, the two entities are identified here with strong probability as *Erythranthe grandis* (coastal perennial) and *E. microphylla* (inland annual). It is unlikely that they are in the process of evolutionary species divergence since they apparently are not each other's closest relative.

Lowry and Willis (2010) observed that a chromosomal inversion polymorphism contributes to "adaptive divergence and reproductive isolation between annual and perennial ecotypes" of *Mimulus guttatus*. Most of the study populations were the perennial *Erythranthe grandis* and the annual *E. microphylla* (including the DUN and IM populations noted above). As interpreted in the present study, northernmost coastal perennial populations (BOB, TSG, ALA) and inland perennial populations (ANR, BOG, FAL, QNT) in the Lowry and Willis study probably were *E. guttata* (in the strict sense). One population of *E. nasuta* (SF), an inland annual, was included. They found that all annual populations had one inversion arrangement while all perennials had another, suggesting to them that the distribution of the two arrangements is "a function of the availability of soil moisture during summer months."

In a simpler perspective, the distribution of the inversion arrangements is explained by common ancestry. The Lowry and Willis study does not contradict a morphologically-based hypothesis that their "ecotypes" are instead better represented as four species and that among the four, the annuals *M. microphyllus* and *M. nasutus* are related as a pair and the perennials *M. grandis* and *M. guttatus* are related as a pair. The data are better interpreted outside of the initial assumption that all populations involved were of a single species.

Scope of this study

The present study has been undertaken to provide a basis for the briefer account of sect. *Simiola* to be included in the taxonomic treatment of *Erythranthe* for the Flora of North America North of Mexico (Nesom & Fraga in prep.). Because geographic ranges of some of the mainly USA species include portions of Mexico and relatively few of the species appear to be endemic to Mexico, Mexican taxa and collections are reviewed here as well.

An attempt is made here to provide a complete account, with details of typification, of all the names proposed in sect. *Simiola* of North America. Online databases and digital images of type specimens (as cited here) have been helpful in this.

This account is based primarily on study of collections from ARIZ, BRIT-SMU-VDB, DAV-AHUC, MO, NMC, PH, SD, SRSC, TEX-LL, UC-JEPS, and UT. Further detailed study of additional collections, especially from Pacific Coast herbaria, surely will be able to improve interpretations and hypotheses presented here and likely even recognize additional taxa. All aspects of the present account warrant further study in both herbarium and field. Specimens are cited only for new species, some of the previously described ones that have not been generally recognized, and to clarify aspects of variation. Collections at herbaria above can be consulted in further documentation of the concepts.

ERYTHRANTHE sect. **SIMIOLA** (Greene) Nesom & Fraga, Phytoneuron 2012-40: 00. 2012. *Mimulus* sect. *Simiolus* Greene, Bull. Calif. Acad. Sci. 1: 109. 1885. **LECTOTYPE** (Nesom & Fraga 2011): *Mimulus guttatus* Fischer ex DC.

Annuals (fibrous-rooted or taprooted) or short-lived herbaceous **perennials** (rhizomatous or producing stolons or runners), glabrous to hirtellous, hirsute, or puberulent-glandular to villous-glandular with gland-tipped hairs. **Leaf blades** generally petiolate (especially proximally) and becoming sessile distally, ovate or elliptic to rotund (perfoliate in *M. glaucescens*, lyrate-dissected to pinnatifid in *M. laciniatus*), palmately veined. **Fruiting pedicels** usually longer than subtending leaves or bracts (shorter in *E. brachystylis*). **Fruiting calyces** commonly accrescent, lobes subequal to unequal, upper usually about 1.2–2 times longer than the others, in most species the lower lobes turning upward ca. 90º and folding over the lateral teeth, closing the throat. **Corollas** yellow (cream to pink or red in some South American species), commonly red-dotted along the throat and palate, strongly to weakly bilabiate or nearly symmetric, throat and palate usually with prominent ventral ridges. **Anthers** glabrous; anther pairs didynamous or equal in length, stigma above anthers (herkogamous) or at the same level (plesiogamous). **Placentation** axile, placentae fused in the basal half or for the whole length, remaining fused in fruit dehiscence; capsule dehiscent to base along outer suture or both sutures. $x = 8$, presumably ($2n = 26$, 28, 30, 32, 56, 62, and other dysploid numbers). **Capsules** included, generally short-stipitate, surfaces often transversly rugulose-ridged.

Fruiting calyx length is measured from the calyx base to the tip of the longest lobe. Corolla tube length is measured from the corolla base to the opening (sinus bases) of the lobes. Mature capsule lengths include the stipe.

The positions of stamen pairs and stigma often can be observed from within a pressed flower if it was pressed in an appropriate plane. If not, it is relatively simple to lift the upper corolla surface (as pressed) and make the observation. Flowers with didynamous stamens and the stigma above the upper stamens (herkogamous) are assumed in the present study to be allogamous. Those with both of the stamen pairs and the stigma at essentially the same level (plesiogamous; see Nesom 2012b) are assumed to be autogamous or at least partly so.

An informal infrasectional classification

Vickery (1974) observed that *Mimulus* sect. *Simiolus* "consists of at least five subgroups: (1) the ***M. guttatus* complex** (*M. guttatus*, *M. nasutus*, *M. laciniatus*, *M. platycalyx*, *M. glaucescens*); (2) the ***M. dentilobus* complex** (*M. dentilobus*, *M. madrensis*, *M. pennellii*, and several others later described by Vickery as new species); (3) the ***M. tilingii* complex** (*M. tilingii* var. *tilingii*, *M. tilingii* var. *corallinus*, *M. implexus*, *M. caespitosus*); (4) the ***M. glabratus* complex** (*M. glabratus* var. *glabratus*, *M. glabratus* var. *fremontii*, *M. glabratus* var. *utahensis*, and South American taxa *M. glabratus* var. *externus*, *M. pilosiusculus*, *M. andicola*); and (5) the ***M. luteus* complex** (South American: *M. luteus* "and its five varieties," *M. cupreus*, *M. acaulis*, *M. laceratus*).

A contrasting infrasectional classification is provided here as a guide to the North American species of *Erythranthe* sect. *Simiola* recognized in the current study, dividing them into six informal groups. The dentilobus, tilingii, and glabratus complexes of Vickery have analogs in the classification presented here. Placement of South American taxa is uncertain (see comments above) and they are not included.

The present arrangement is admittedly subjective, based on morphological similarity (main characters emphasized in defining the groups are listed) and personal experience with variability in each of the species. Plants are allogamous and perennial unless otherwise noted: * = autogamous; ^{A} = annual duration.

The classification here may be helpful in further investigating relationships. It also is offered partly as a potential balance to the exuberant postulation of ancestor-derivative relationships, sister relationships, and adaptive evolution within a single species often encountered in evolutionary studies of sect. *Simiola*. Based on the arrangement hypothesized here, the following correlates appear to be reasonable.

> * The suite of characters associated with autogamous fertility is heritable (subgroups B and C of the Microphylla group) as well as evolutionarily derivative (Guttata group, Madrensis group).
>
> * The closest relatives of *Erythranthe nasuta* apparently are *E. brevinasuta*, *E. laciniata*, and *E. pardalis*; species next most closely related to *E. nasuta* are those of the Microphylla group.
>
> * Annual duration is heritable (Microphylla group, subgroups A, B, and C) as well as evolutionarily derivative (Guttata group, Madrensis group).
>
> * Prolific rhizome production is heritable (Tilingii group and possibly the Decorus group, if the two are distinct).
>
> * Non-closing calyces are heritable (Glabrata group), variable within a species (Madrensis group, subgroup C of the Microphylla group), and evolutionarily derivative (Tilingii group).

1. **Glabrata group** (*E. glabrata*, *E. michiganensis*, *E. geyeri**, *E. regni**^{A}, *E. inamoena**). Perennial and annual, rhizomatous or rooting at proximal nodes, fibrous-rooted in *E. regni*; calyces not closing; flowers small and autogamous or (*E. michiganensis*) larger, chasmogamous and allogamous; central USA, Mexico, and South America. x = 15.

2. **Tilingii group** (*E. tilingii*, *E. minor*, *E. caespitosa*, *E. corallina*, *E. utahensis*). Perennial; flowers large, chasmogamous and allogamous; filiform rhizomes profusely produced; mostly high elevation (except for *E. utahensis*); western USA. x = 12?, 14, 15.

3. **Decora group** (*E. decora*, *E. scouleri*). Perennial; flowers large; rhizomes numerous; leaf margins closely toothed; styles densely hairy; Washington and Oregon. x = ?

4. **Guttata group** (*E. guttata*, *E. grandis*, *E. lagunensis*^{A}, *E. unimaculata*^{A}, *E. thermalis**^{A}, *E. arenicola*^{A}). Perennial and annual; leaves oblong or elliptic to obovate, margins remotely toothed; flowers relatively large and chasmogamous and allogamous; western USA and northwestern Mexico. x = 14.

5. **Microphylla group**.
Subgroup A. (*E. microphylla*^{A}, *E. glaucescens*^{A}, *E. marmorata*^{A}, *E. nudata*^{A}). Annual; flowers large or variable in size, chasmogamous and allogamous; basal and proximal cauline leaves often purplish on one or both surfaces; central California northward. x = 14.

Subgroup B. (*E. nasuta**^{A}, *E. brevinasuta**^{A}, *E. laciniata**^{A}, *E. pardalis**^{A}). Annual; flowers small (cleistogamous or slightly open, autogamous; basal and proximal cauline leaves often purplish (*E. nasuta*, *E. laciniata*); flowers often produced at all nodes, proximal to distal; Sierra Nevada of USA

(*E. laciniata*, *E. pardalis*) and broader (*E. nasuta*). x = 14. Perhaps arbitrarily separated from subgroup C.

Subgroup C. (*E. arvensis****A**, *E. brachystylis****A**, *E. charlestonensis****A**, *E. cordata****A**). Annual, often rooting at lower nodes; flowers often cleistogamous, all autogamous, produced from distal nodes; western USA. x = 14, 15.

Subgroup D. (*E. hallii****A**). Annual; flowers small, cleistogamous, produced from distal nodes; North-central Colorado. x = 16.

6. **Madrensis group.**
Subgroup A. (*E. madrensis*, *E. pallens*, *E. calciphila****A**, *E. pennellii*, *E. visibilis****A**). Perennial or annual; calyces 5-lobed or mostly 3-lobed; flowers small (allogamous or autogamous); western Mexico into southwestern USA. x = 16.

Subgroup B. (*E. chinatiensis* *, *E. dentiloba*, *E. parvula* *). Perennial, mat-forming; calyces 5-lobed or with tendency toward 3-lobed; flowers relatively small, allogamous or autogamous; corolla lobes laciniate to fimbriate; southwestern USA and northwestern Mexico. x = 16.

KEY TO SPECIES OF SECT. *SIMIOLA* IN THE USA AND CANADA

1. Fruiting calyces open at the throat, lateral calyx lobes mostly shallowly deltate to merely apiculate or absent, sometimes obscure or obsolete, not turned upward to close the throat.

  2. Perennial, arising from profusely produced, branching, filiform rhizomes; stems erect or basally decumbent-ascending and becoming erect distally; fruiting calyces (10–)11–17(–20) mm .... 10. **Erythranthe utahensis**
  2. Annual, fibrous-rooted, usually rooting freely at least at the proximal cauline nodes; stems erect, basally decumbent-ascending and becoming erect distally, or stems all prostrate; fruiting calyces 7–14 mm.

    3. Stems more or less quadrangular; distal and bracteal leaves densely villous on abaxial surfaces with vitreous, flattened, multicellular, eglandular hairs; flowers autogamous; western USA .... 27. **Erythranthe arvensis**
    3. Stems subterete; distal and bracteal leaves glabrous or villous-glandular; flowers allogamous or autogamous; eastern and central USA.

      4. Flowers herkogamous, corolla limb expanded 10–15 mm (pressed); Michigan .... 5. **Erythranthe michiganensis**
      4. Flowers plesiogamous, corolla limbs expanded 5–8 mm or 1–1.5 mm (pressed); southwestern USA.

        5. Fruiting calyces minutely hirtellous; stems often prostrate to decumbent but becoming fully erect at least in the inflorescence, commonly distinctly fistulose .... 4. **Erythranthe inamoena**
        5. Fruiting calyces glabrous to sparsely villous-glandular; stems prostrate to erect, not fistulose.

6. Stems prostrate and forming floating mats to decumbent-ascending to ascending or erect-ascending distally; calyces and pedicels glabrous or sparsely villous-glandular; calyces without purple-dots; tube-throats 6–8 mm, exserted 1–3 mm beyond calyx margins, limb expanded 5–8 mm (pressed) .... 2. **Erythranthe geyeri**
6. Stems erect to ascending-erect; calyces and pedicels glabrous; calyces purple-dotted; corolla tube-throats 9–12 mm, exserted 3–5 mm beyond calyx margins, limb expanded 1–1.5 mm (pressed) .... 3. **Erythranthe regni**

1. Fruiting calyces closed at the throat, lower lobes turned upward against the upper lobe.

7. Producing rhizomes or stolons.

8. Corolla lobes laciniate to fimbriate; plants procumbent and mat-forming.

9. Leaves densely villous-hirsute on both surfaces with thickened and flattened, stiff, whitish, gland-tipped hairs, calyces villous-hirsute, pedicels and distal stems stipitate-glandular; lower lip of corolla spreading .... 33. **Erythranthe parvula**
9. Leaves glabrous to moderately villosulous adaxially, glabrous abaxially, calyces glabrous to sparsely villosulous, pedicels and stems glabrous; lower lip of corolla strongly reflexing .. .. 34. **Erythranthe chinatiensis**

8. Corolla lobes entire or apically notched; plants procumbent to decumbent or erect to suberect.

10. Rhizomes filiform, usually branching, prolifically produced and forming a mass.

11. Leaves distinctly hirsutulous to softly hirsute on both surfaces with sharp-pointed, thick-walled, eglandular, and dull gray hairs .... 9. **Erythranthe corallina**
11. Leaves glabrous to sparsely villous-glandular or stipitate-glandular on both surfaces with blunt-tipped, thin-walled, minutely gland-tipped, and vitreous hairs.

12. Flowers 6–16, from proximal to distal nodes; corolla tube-throats 10–13 mm; fruiting pedicels (25–)40–75 mm; stems erect, 20–50 cm 10. **Erythranthe utahensis**
12. Flowers 1–3(–5) from distal nodes; corolla tube-throats 9–11 or 15–25 mm; fruiting pedicels 10–35(–40) mm; stems erect to erect-ascending or procumbent to decumbent or decumbent-ascending, 2–35 cm.

13. Stems procumbent or decumbent to decumbent-ascending, 3–10 cm, forming matted colonies; leaf blades 3–12 mm long, margins entire to mucronulate or barely denticulate; corolla tube-throats 15–18 mm ..... 7. **Erythranthe caespitosa**
13. Stems erect to erect-ascending, (2–)5–35 cm, plants solitary to weakly colonial; leaf blades mostly 5–35(–55) mm long, margins distinctly serrate to serrate-dentate or denticulate; corolla tube-throats 9–11 or 15–25 mm.

14. Corolla tube-throats 15–25 mm, exserted 5–10 mm beyond the calyx margin .... 6. **Erythranthe tilingii**
14. Corolla tube-throats 9–11 mm, exserted 1(–2) mm beyond the calyx margin .... 8. **Erythranthe minor**

10. Rhizomes broader than filiform, usually 1-few, not highly branched and forming a mass.

15. Lower cauline leaves narrowly oblong-obovate or oblong-elliptic to oblong-lanceolate, usually 3–4 times longer than wide, bases attenuate, margins shallowly and evenly callous-dentate; plants completely glabrous throughout; Columbia River region of Oregon .... 18. **Erythranthe scouleri**

15. Lower cauline leaves ovate to ovate-elliptic or broadly elliptic, usually 1–2 times longer than wide, bases rounded to truncate, margins shallowly and evenly callous-dentate (*E. decora*) or prominently and often irregularly dentate; plants glabrate to hirtellous or glandular-villous.

16. Leaf blades uniformly ovate-triangular to ovate-lanceolate with truncate bases, palmately (3–)5–7-veined; corolla tube-throats 18–26 mm; stems, pedicels, calyces, and leaf surfaces minutely hirtellous .... 17. **Erythranthe decora**

16. Leaf blades ovate-elliptic to ovate or suborbicular, with cuneate to rounded bases, subpinnately veined; corolla tube-throats (10–)12–20 mm or (14–)16–24 mm; vestiture of stems, pedicels, calyces, and leaf surfaces variable.

17. Stems (6–)15–65(–80) cm; pedicels, calyces, and distal stems variable in vestiture but not puberulent-glandular; corolla tube-throats (10–)12–20 mm, exserted 3–5 mm beyond the calyx margin; fruiting calyces 11–17(–20) mm .... 11. **Erythranthe guttata**

17. Stems (25–)50–120(–160) cm; pedicels, calyces, and distal stems densely puberulent with a mix of crinkly hairs and minutely stipitate-glandular hairs; corolla tube-throats (14–)16–24 mm, exserted (8–)10–15 mm beyond the calyx margin; fruiting calyces 15–22(–25) mm .... 12. **Erythranthe grandis**

7. Fibrous-rooted or taprooted, without rhizomes or stolons.

18. Corollas relatively large, chamogamous, tube-throats (6–)8–23 mm, exserted (2–)3–8 mm (sometimes 1 mm in smallest corollas of *E. microphylla*) beyond the fruiting calyx margin; fertilization allogamous (anther pairs at different level, stigma above upper anther pair) or (in *E. thermalis*) autogamous.

19. Stems moderately to densely villous-glandular, at least proximally

20. Taprooted; stems, leaves, calyces, and pedicels moderately villous-glandular, without eglandular hairs; fruiting pedicels 15–45 mm; corolla tube-throats narrowly cylindric-funnelform .... 20. **Erythranthe marmorata**

20. Fibrous-rooted; stems, leaves, calyces, and pedicels moderately villous-glandular with gland-tipped hairs or mixed hirtellous and stipitate-glandular; fruiting pedicels 7–17 mm; corolla tube-throats infundibular.

21. Corollas tube-throats 11–20 mm, exserted 4–8 mm beyond the calyx margin; allogamous; coastal and near-coastal localities in Monterey, San Luis Obispo, and Santa Cruz cos., California ....13. **Erythranthe arenicola**

21. Corollas tube-throats 8–12 mm, exserted 1–2 mm beyond the calyx margin; autogamous; Yellowstone Natl. Park, Wyoming .... 14. **Erythranthe thermalis**

19. Stems delicately and minutely stipitate-glandular or glabrous to glabrate.

22. Corollas pale yellow to nearly white, palate dense-dark yellow, drying blue-green, tube-throats 9–14 mm; southern Arizona, New Mexico, Mexico .... 16. **Erythranthe unimaculata**

22. Corollas, including the palate, usually nearly evenly yellow, tube-throats (6–)8–23 mm; California, Nevada, Oregon, Washington, British Columbia.

23. Basal and proximal cauline leaves with blades lanceolate or oblong-lanceolate to ovate, distal narrower, narrowly spatulate to oblanceolate, 5–15(–30) mm x 1–5 mm; plants glabrous or stems, leaves, and pedicels minutely stipitate-glandular with hairs 0.05–0.1 mm, at least just above the nodes; Colusa, Glenn, Lake, Mendocino, Napa, and Sonoma cos., California .... 22. **Erythranthe nudata**

23. Basal and proximal cauline leaves with blades ovate or ovate-lanceolate to elliptic-ovate, orbicular-ovate, suborbicular, or depresssed-ovate, (3–)10–45 mm x 3–35 mm; plants glabrous and glaucous to hirtellous-glandular; distribution various.

24. Distal cauline leaves distinct, petioled or subclasping to narrowly perfoliate; stems and leaf surfaces not at all glaucous, stems and pedicels hirtellous or mixed hirtellous and stipitate-glandular, sometimes only short villous-glandular with gland-tipped hairs, sometimes completely glabrous below the inflorescence; corolla tube-throats (6–)8–16(–20) mm; California, Nevada, Oregon, Washington, British Columbia 19. **Erythranthe microphylla**

24. Distal cauline leaves distinctly connate-perfoliate and forming a flat disc; stems and leaf surfaces glabrous and glaucous; corolla tube-throats 12–23 mm; Butte and Tehama cos., California .... 21. **Erythranthe glaucescens**

18. Corollas relatively small, sometimes cleistogamous, tube-throats 4–14 mm, exserted 1–3 mm beyond the fruiting calyx margin; fertilization autogamous (anther pairs and stigma at about the same level).

25. Corolla tube-throats 7–14 mm, limb expanded 6–16 mm, apparently chasmogamous.

31. Distal leaves strongly auriculate-clasping and closely paired; flowers produced at distal nodes; stems glabrous.

32. Stems glabrous or sometimes minutely hirtellous in the inflorescence with deflexed hairs, eglandular; flowers 3–8(–16), from remote distal nodes; fruiting calyces (7–)9–14 mm; California, Nevada, Oregon, Washington, Idaho .... 27. **Erythranthe arvensis**

32. Stems sparsely and minutely stipitate-glandular; flowers (5–)12–16 in bracteate racemes; fruiting calyces (8–)15–18(–20) mm; Arizona, New Mexico, Texas, Colorado, Utah, Nevada; Mexico .... 29. **Erythranthe cordata**

31. Distal leaves not distinctly auriculate-clasping; flowers commonly from distal to proximal nodes; stems glabrous to sparsely hirtellous and/or finely villosulous-glandular.

33. Stems sparsely but distinctly finely villosulous-glandular proximally to distally; leaves finely villosulous-glandular .... 25. **Erythranthe pardalis**

33. Stems glabrous to sparsely hirtellous, finely villosulous-glandular above the nodes but not elsewhere; leaves eglandular.

34. Leaves as long as wide or wider than long (blades elliptic-ovate to broadly ovate, suborbicular, or depressed ovate), margins irregularly dentate to dentate-serrate or nearly lacerate-dentate, commonly doubly toothed; plants commonly producing tiny cleistogamous flowers on branches separate from those with larger flowers, corolla tube-throats (5–)8–12 mm .... 23. **Erythranthe nasuta**

34. Leaves longer than wide (blades elliptic to elliptic-obovate, oblanceolate, or oblong), margins commonly narrowly pinnately lobed or dissected, sometimes merely shallowly toothed; plants producing flowers of only one size, corolla tube-throats 4–6 mm .... 24. **Erythranthe laciniata**

25. Corolla tube-throats 4–10 mm, limb barely expanded or only 3–4 mm, clearly cleistogamous.

26. Fruiting calyces 6–10 mm, lobes usually 3 or 3–5 on the same plant, if 5 then with the 2 middle lobes much smaller than the lower pair .... 38. **Erythranthe calciphila**

26. Fruiting calyces mostly (7–)10–15 mm, lobes 5, all about equal size or the upper slightly longer.

27. Flowers and fruits subsessile to sessile, pedicels shorter than subtending leaves or essentially absent; Nye Co., Nevada .... 28. **Erythranthe brachystylis**

27. Flowers and fruits distinctly pedicellate, pedicels longer than subtending leaves; more widely distributed.

28. Distal leaves short-petiolate, hirsute to hirsutulous at least on adaxial surface; stems villous-glandular area at each axil, sometimes hirtellous distally; fruiting calyces with upper lobe usually distinctly longer than the lower and slightly falcate .... 23. **Erythranthe nasuta**

28. Distal leaves sessile or short-petiolate, glabrous or villous on one or both surfaces; stems usually glabrous; fruiting calyces with upper lobe not distinctly longer or falcate.

29. Fruiting calyces glabrous; (5–)7–10 mm 31. **Erythranthe hallii**

29. Fruiting calyces minutely hirtellous, (7–)9–14 mm.

30. abaxial surfaces of distal and bracteal leaves densely villous with long, vitreous, flattened, eglandular, multicellular hairs; middle and upper cauline leaves depressed-ovate to nearly reniform, distal sessile; stems, leaves, and calyces usually green; fruiting calyces commonly remaining open; stems erect to ascending, often rooting at lower nodes .... 27. **Erythranthe arvensis**

30. leaves glabrous or proximal leaves sometimes sparsely villous; middle and upper cauline leaves ovate to ovate-lanceolate, distal short-petiolate; stems, leaves, and calyces commonly dark purplish; fruing calyces closing; stems erect or ascending-erect, not rooting at lower nodes .... 30. **Erythranthe charlestonensis**

KEY TO SPECIES OF SECT. *SIMIOLA* IN MEXICO

1. Fruiting calyces open at the throat, lateral calyx lobes mostly shallowly deltate to lacking or merely apiculate, sometimes obscure or obsolete, lower lobes not curving upward in fruit.

  2. Fruiting calyces 10–13 mm, corolla tube-throats (7–)12–16 mm ...... 1. **Erythranthe glabratus**
  2. Fruiting calyces 4–12 mm, corolla tube-throats 5–11 mm.

    3. Fruiting calyces 4–6 mm, corolla tube-throats 5–6 mm; leaf surfaces puberulent-glandular .... 39. **Erythranthe visibilis**
    3. Fruiting calyces 7–14 mm, corolla tube-throats 6–12 mm; leaf surfaces glabrous.

      4. Stems more or less quadrangular .... 27. **Erythranthe arvensis**
      4. Stems subterete.

        5. Stems usually prostrate in flower, forming floating mats, occasionally becoming distally ascending-erect to erect, not distinctly fistulose; flowers 2–8(–12), usually from distal nodes but sometimes from most of them, very loosely racemose; corolla tube-throats 6–8 mm; fruiting pedicels 18–30 mm; fruiting calyces obtriangular to broadly obtriangular or deeply cupulate, glabrous to sparsely villous-glandular 2. **Erythranthe geyeri**
        5. Stems often prostrate to decumbent but becoming fully erect at least in the inflorescence, commonly distinctly fistulose; flowers (6–)8–18(–24), loosely to densely racemose, usually from distal nodes but sometimes from all nodes; corolla tube-throats 7–11 mm; fruiting pedicels 9–20 mm; fruiting calyces broadly cylindric-campanulate, minutely hirtellous .... 4. **Erythranthe inamoena**

1. Fruiting calyces closed at the throat, lateral lobes present or absent, lower lobes curving upward in fruit against the upper lobe.

  6. Stems mostly erect or ascending-erect from the base.

    7. Stems 4–30 cm; calyces 3-lobed; corolla tube-throats 5–7 mm .. 38. **Erythranthe calciphila**
    7. Stems 2–65(–100) cm; calyces 5-lobed; corolla tube-throats (in *E. nasuta* 5–)8–20(–26) mm.

      8. Rhizomatous or consistently rooting from proximal nodes.

        9. Rhizomatous; corolla tube-throats (10–)12–20(–26) mm, exserted 3–5 beyond calyx margin, limb expanded 12–24(–25) mm (pressed); styles 15–20 mm, exserted 6–9 mm beyond fruiting calyx margin; stigma above level of anthers, allogamous 11. **Erythranthe guttata**
        9. Rooting from proximal nodes; corolla tube-throats 8–14 mm, exserted 1–3 mm beyond calyx margin, limb expanded 9–14 mm (pressed); styles 7–10 mm, exserted 1–3 beyond fruiting calyx margin; stigma at same level as anthers, autogamous 29. **Erythranthe cordata**

      8. Fibrous-rooted.

        10. Corolla limb distinctly bilabiate, 7–17 mm wide (pressed); flowers herkogamous-allogamous; blade margins relatively evenly shallowly serrate-dentate to serrate, 1-toothed; pedicels villous glandular along whole length.

11. Corolla tube-throats exserted 3–4 mm beyond the calyx margin, palate and lower throat densely and dark yellow, drying blue-green, limbs expanded 8–17 mm wide (pressed); Arizona, New Mexico, Chihuahua Sonora . 16. **Erythranthe unimaculata**
11. Corolla tube-throats exserted 4–6(–7) mm beyond calyx margin, palate and lower throat not of a different color or hue, limbs expanded 7–10 mm wide (pressed); Baja California Sur .... 15. **Erythranthe lagunensis**

10. Corolla limb weakly bilabiate, 4–12 mm wide (pressed); flowers plesiogamous-autogamous; blade margins irregularly dentate to dentate-serrate or nearly lacerate-dentate, commonly doubly toothed; pedicels sparsely glandular-villous just above the nodes, otherwise glabrous.

12. Stems quadrangular; upper calyx lobe characteristically elongate, beaklike, margins entire; corolla lobe margins entire .... 23. **Erythranthe nasuta**
12. Stems terete; upper calyx lobe relatively short, often with 1-2 pairs of tiny teeth on the distal margins; corolla lobe margins sparsely denticulate .... 26. **Erythranthe brevinasuta**

6. Stems mostly procumbent, often rooting at the nodes, becoming erect in the inflorescence.

13. Corolla lobes fimbriate.

14. Leaves glabrous or rarely sparsely villosulous adaxially; stamen pairs at different levels, stigma above upper anther pair, allogamous .... 32. **Erythranthe dentiloba**
14. Leaves densely villous-hirsute to glabrous; both stamen pairs and the stigma at essentially the same level, autogamous.

15. Leaves densely villous-hirsute on both surfaces with thickened and flattened, stiff, whitish, gland-tipped hairs, calyces villous-hirsute, pedicels and distal stems stipitate-glandular; lower lip of corolla spreading .... 33. **Erythranthe parvula**
15. Leaves glabrous to moderately villosulous adaxially, glabrous abaxially, calyces glabrous to sparsely villosulous, pedicels and stems glabrous; lower lip of corolla strongly reflexing .... 34. **Erythranthe chinatiensis**

13. Corolla lobes entire or emarginate.

16. Stems, pedicels, calyces, and leaf surfaces moderately to densely villous-glandular to villosulous-glandular with hairs mostly 1–3 mm long; calyces 5-lobed .... 37. **Erythranthe pennellii**
16. Stems, pedicels, calyces, and leaf surfaces glabrous, or if glandular (*E. visibilis*) hairs mostly 0.2-0.8 mm long; calyces 3-lobed or essentially 3-lobed.

17. Fruiting calyces 4–6 mm; corolla tube-throats 5–6 mm; leaf surfaces puberulent-glandular .... 39. **Erythranthe visibilis**
17. Fruiting calyces 5–10 mm; corolla tube-throats 5–12 mm; leaf surfaces glabrous.

18. Fruiting pedicels 5–30 mm; fruiting calyces 5–8 mm; corolla tube-throats 5–9 mm, limbs 6–10 mm broad (pressed); autogamous .... 35. **Erythranthe madrensis**
18. Fruiting pedicels 25–60 mm; fruiting calyces 6–10 mm; corolla tube-throats 8–12 mm, limbs 8–12 broad (pressed); allogamous .... 36. **Erythranthe pallens**

1. ERYTHRANTHE GLABRATA (Kunth) Nesom, Phytoneuron 2012-40: 44. 2012. *Mimulus glabratus* Kunth, Nov. Gen. Sp. (quarto ed.) 2: 370. 1817. **TYPE**: **MEXICO**. [**Hidalgo**]. "Crescit prope Moran Mexicanorum, alt. 1330 hex. Floret Majo," *Humboldt and Bonpland s.n.* (holotype: B? or P?). "Type collection apparently not represented at the Museum d'Histoire Naturelle at Paris, France, and actual type at the Berlin Botanical Garden in Germany not verified."

Perennials, rhizomatous, all parts glabrous. **Stems** erect to decumbent-ascending, commonly emergent, (10–)25–50(–60) cm, commonly slightly fistulose, rooting at the nodes. **Leaves** cauline, basal usually absent at flowering, lower cauline or proximal to midcauline petiolate, petioles 5–20 mm, distal sessile, not connate, blades palmately 5–7 veined or proximal sometimes subpinnate, proximal broadly ovate, 25–50 mm, medial and distal orbicular to depressed-ovate, 10–40 mm, apices rounded, bases cuneate to rounded or subtruncate, margins shallowly dentate or dentate-serrate to merely mucronulate, with 8–12 teeth per side, rarely subentire. **Flowers** (4–)6–12, mostly from distal nodes. **Fruiting pedicels** 10–30(–40) mm. **Fruiting calyces** broadly campanulate-cylindric, 10–16 mm, not closing, sometimes purple-spotted or purple-tinged, lobes 5, the upper longest, apices rounded or rounded-mucronate. **Corollas** yellow, red-dotted, tube-throats narrowly funnelform, 9–13 mm, exserted 1–3 beyond the calyx margin, limb bilabiate, expanded. **Plesiogamous**; anther pairs at about the same level, stigma at or slightly below the anthers. **Capsules** 8–10 mm. 2n = 62.

Flowering (Jan-)Apr–Jul (–Aug, –Nov). Inundated places, lake and river sides, marshy areas, shallow ditches, moist gravel, steep arroyo banks, disturbed forest, roadsides; (500–, 1300–)1700–2800(–3200) m; Mexico, Guatemala, Nicaragua, South America (Colombia). Apparently completely absent between Guatemala and Colombia except for a single known locality in north-central Nicaragua (Sutton & Hampshire 2001). Map 1.

A detailed allozyme study of the *Mimulus glabratus* complex (Vickery 1990) indicates that four distinct groups can be recognized within what is identified here as *Erythranthe glabrata*, all with 2*n* = 62. As termed by Vickery, the (1) "Sierra Madre Occidental group" and the (2) "Chiapas-Guatemala group" have a sister relationship and together are sister to the (3) "Colombia group." Although the (4) "Sierra Madre del Sur group" is seemingly geographically interposed between 1 and 2, it is sister to the "Rio Grande group," which has a chromosome number of 2*n* = 60 and is the primarily Texan taxon recognized here as *Erythranthe inamoena*. The type of *M. glabratus* Kunth was collected in Hidalgo in south-central Mexico, thus that name in its strictest sense refers to the Sierra Madre del Sur group. These subgroups have not been distinguished in the present study.

The correct name for the most of the South American plants (south of Columbia) sometimes identified as *Mimulus glabratus* is *M. andicola* Kunth (= *Erythranthe andicola*). *Mimulus andicola* Kunth (1817) and *M. tener* Phil. (1891) were treated as synonyms of *M. glabratus* var. *glabratus* by Grant (1924). *Mimulus glabratus* var. *parviflorus* (Lindl.) A.L. Grant, *M. glabratus* var. *micranthus* (Phil.) B. Boivin, and *M. glabratus* var. *externus* Skottsb. are typified by South American plants.

2. ERYTHRANTHE GEYERI (Torrey) Nesom, Phytoneuron 2012-40: 43. 2012. *Mimulus geyeri* Torrey in Nicollet, Rep. Hydrogr. Upper Mississippi, 157. 1843. **TYPE**: **USA**. **North Dakota**. [Ramsey Co.:] Fresh water springs about Devil's Lake, 1 Aug 1839, *C.A. Geyer 119* (holotype: NY digital image! photo-PH!; isotypes: MO digital image!, PH!, US digital image!).

Mimulus jamesii Torrey & Gray ex Benth., Prodr. (DC.) 10: 371. 1846. *Mimulus glabratus* var. *jamesii* (Torrey & Gray) Gray, Synopt. Fl. N. Amer. ed. 2, 2(1): Suppl. 447. 1886. **LECTOTYPE** (Pennell 1935): **USA**. **Iowa**. [Pottawatamie Co.:] "Ad fontes planitiorum Missouriensium," along the Missouri River, 27 May 1820, *James s.n.* (NY digital image! photo-PH!; isolectotype: MO digital image!). Three collections were cited in the protologue:

"Ad fontes planitiorum Missouriensium (James!, Engelmann!), ad Devils Lake (iter Nicollet)." Pennell (1935, p. 120) noted that "Type, a specimen collected by Edwin James (according to his journal) in the present Pottawatomie County, Iowa, seen in Herb. New York Botanical Garden." At varietal rank within *M. glabratus*, the autonym var. *jamesii* has priority over var. *fremontii*.

Mimulus reniformis Engelm. ex Benth., Prodr. (DC.) 10: 371. 1846 [name only, included by Bentham in synonymy of *Mimulus jamesii*: "M. reniformis Engelm. mss."].

Mimulus jamesii var. *fremontii* Benth., Prodr. (DC.) 10: 371. 1846. *Mimulus glabratus* var. *fremontii* (Benth.) A.L. Grant, Ann. Missouri Bot. Gard. 11: 190. 1924. **TYPE**: **USA**. **Wyoming**. [Laramie Co.:] "In montium Windriver praeruptis," Rocky Mountains, 14 Jul 1842, *J.C. Fremont s.n.* (holotype: NY digital image! photo-PH!). Pennell (1935, p. 120) noted "Type, dated July 14, 1842, seen in Herb. New York Botanical Garden; from a manuscript also at that institution it appears that on that day Fremont was not in the Wind River Mountains, but actually on the high plains of what is now Laramie County, Wyoming."

Mimulus glabratus var. *oklahomensis* Fassett, Rhodora 41: 525. 1939. **TYPE**: **USA**. **Oklahoma**. Caddo Co.: Hinton, in Caddo Canyon, 26 Apr 1936, *D. Demaree 12338* (holotype: GH; isotype: MO!).

Perennials, rhizomatous, vestiture (in the northern part of the range, USA) of calyces, pedicels, and adaxial surfaces of distal leaves sparsely short-villous-glandular or (in New Mexico and Mexico) completely glabrous. **Stems** usually prostrate and forming floating mats, sometimes decumbent-ascending to ascending or erect-ascending distally, (3–)10–40 cm, rooting at the nodes. **Leaves** cauline, basal absent at flowering, blades palmately 3–5-veined, suborbicular to depressed-ovate or broadly elliptic-ovate to reniform, 6–25 mm x 5–30 mm, relatively even-sized or largest often at midstem, bracteal reduced, margins shallowly dentate to crenate-dentate with 3–7(–10) teeth per side, apex rounded, base cuneate to truncate or subcordate, all leaves short-petiolate or the distal sessile, petioles 3–10(–20) mm. **Flowers** 2–8(–12), usually from distal nodes but sometimes from most of them, very loosely racemose. **Fruiting pedicels** 18–30 mm. **Fruiting calyces** obtriangular to broadly obtriangular or deeply cupulate, (7–)8–12 mm, lateral lobes shallowly convex-mucronulate, not closing the throat, upper lobe ovate with rounded apex. **Corollas** yellow, sparsely red dotted or without red dots, tube-throats cylindric-funneform, 6–8 mm, exserted 1–3 mm beyond calyx margins, limb barely bilabiate, expanded 5–8 mm (pressed). **Styles** glabrous. **Plesiogamous**; anther pairs at about the same level, stigma at or slightly below the anthers. **Capsules** (4.5–5 mm in New Mexico) 5–8 mm, stipitate, included. $2n = 30$.

Flowering May–Aug(–Oct). Edges of flowing streams, marsh edges, drainage ditches, seepage areas, springs, muddy or moist banks; 200–2500 m (1500–2500 m in Arizona and New Mexico); USA, Mexico. Maps 2, 3.

Collections examined from the southwestern corner of the USA range. **Arizona**. Apache Co.: 2.5 mi NW of Fort Defiance, edges of water in small creek, 8 Oct 1965, *Crutchfield 921* (LL); road crossing of Chinle Creek between Dinnehotso and Mexican Water, 4900 ft, moist sand along stream, 17 Jul 1948, *Gould & Phillips 4797* (ARIZ); Canyon de Chelly Natl. Monument, sandy soil alongside stream in upper Canyon de Chelly, 6500 ft, 25 Jul 1971, *Halse 526* (ARIZ); 1 mi W of Tsaile Peak, 7500 ft, wet sites, 23 Aug 1934, *Howell 33* (ARIZ). Pinal Co.: Sacaton, "Little Gila," 2 Jun 1927, *Harrison 4201* (ARIZ).

Collections examined from **Texas**: Grayson Co.: at Carpenters Bluff, in spring, 23 Apr 1951, *Gentry 51-1382* (TEX). Hemphill Co.: Gene Howe Wildlife Management Area, 7 mi NE of Canadian, locally frequent in standing water of Persimmon Creek, 4 Jun 1957, *Rowell 5305* (TEX).

Erythranthe geyeri has commonly been regarded as conspecific with *E. glabrata* (as *Mimulus glabratus* var. *jamesii*), but typical *E. glabrata* has a different chromosome number and is sharply distinct in morphology, and the two are broadly sympatric in Mexico without intermediates. The allozyme study of the *Mimulus glabratus* complex (Vickery 1990) indicates that the USA Great Plains populations of *E. geyeri* are distinct from those in New Mexico and Mexico. Such a distinction is not made here but a study is needed to see if morphological evidence parallels the allozyme data.

Fassett distinguished *Mimulus glabratus* var. *oklahomensis* on the basis of its "flowers sometimes as large as those of var. *michiganensis*, with leaves like those of var. *Fremontii* (Benth.) Grant, and with pedicels more than twice as long as the subtending leaves." Besides the type collection in Caddo County, several other distinctly large-flowered collections of *Erythranthe geyeri* have been encountered among Oklahoma collections: Adair Co.: 1 mi SW of Watts on US 59, seepage area in a shaded bluff on Ballard Creek, 6 May 1958, *Wallis 6605* (SMU, TEX); Major Co.: near Cleo, edge of spring, 8 Jun 1913, *Stevens 782* (MO). Woodward Co.: Woodward, small, effluent stream from Boiling Springs, 2600 ft, 9 Aug 1964, *Vickery 2659*, cult. 7132, voucher for $2n = 30$ (UT).

These Oklahoma variants have flowers only at distalmost nodes and corolla tubes 10–11 mm long with limbs expanded 6–8 mm (pressed). The plants from Major County were collected past flower but the fruiting calyces are 12–13 mm long. The stems are erect from the base and produce rhizome-like runners from basal nodes. Large flowers suggest that these plants could be polyploid and their seemingly clustered geographic occurrence, apparently sympatric with typical *Erythranthe geyeri*, further suggests that they may represent an evolutionarily distinct entity. On the other hand, a chromosome count from a Woodward County collection is diploid and the relatively larger flowers apparently are autogamous, with anthers and stigma at the same level. Two other collections from the Boiling Springs area have smaller corollas of typical *E. geyeri* but have stigmas slightly above (ca. 1.5 mm) the level of upper anthers: Woodward Co.: Boiling Springs State Park: common in spring fed stream, 2 May 1953, *Goodman 5639* (SMU, UC); in stream below the spring-house, 1 May 1953, *Waterfall 11410* (SMU, TEX, UC).

In 1976, Vickery identified var. *oklahomensis* as the Great Plains variant of *Mimulus glabratus* (Hsu & Vickery 1976), and he later (Vickery 1984) cited collections that he identified as var. *oklahomensis* from Reno and Scott counties, Kansas, and from Custer and Thomas counties, Nebraska. He did not provide the criteria he used in identification of var. *oklahomensis.*

3. ERYTHRANTHE REGNI Nesom, **sp. nov. TYPE**: **USA**. **Arizona**. Yuma Co.: Kofa Mountains, ca. 50 mi N of Yuma, SE of Stone Cabin on Kofa Game Range at Horse Tank, wet soil surrounding pool, 16 Mar 1975, *W.E. Booth A-142* (holotype: ARIZ!).

Similar to *Erythranthe geyeri* in its open mature calyces, cleistogamous flowers, (in part in its) glabrous vestiture but different in its erect habit, apparently annual duration, larger leaves, purple-dotted calyces, and corollas with longer tube-throats and barely bilabiate limb.

Similar to *Erythranthe glabrata* in its open mature calyces, cleistogamous flowers, erect habit, prominently punctate leaves, and glabrous vestiture but different in its smaller calyces and corollas, flowers from all nodes, broader leaves (ratio) with fewer teeth, and annual duration.

Similar to *Erythranthe arvensis* in its erect habit, annual duration, open mature calyces, cleistogamous flowers but different in its glabrous vestiture and punctate leaves.

Similar to *Erythranthe cordata* in its erect habit and cleistogamous flowers but different in it glabrous vestiture, open mature calyces, and punctate leaves.

Annuals, fibrous-rooted, sometimes rooting at proximal nodes, completely glabrous. **Stems** erect to ascending-erect, 15–45 cm, sometimes becomes slightly fistulose. **Leaves** basal and cauline, basal petiolate, petioles 5–25(–30) mm, midcauline and distal sessile, not connate, blades palmately 5–7-veined or proximal sometimes subpinnate, largest basal or at midstem with distal slightly reduced, proximal ovate to depressed-orbicular, 15–20(–50) mm x 15–25(–50) mm, in size, medial and distal broadly depressed-ovate to obtriangular or flabellate, 15–35 x 15–40 mm, margins shallowly serrate-dentate, sometimes irregularly, to mucronulate or apiculate with (3–)5–7 teeth per side, rarely subentire, apices rounded, bases attenuate-cuneate. **Flowers** 6–16, from all nodes or from medial to distal. **Fruiting pedicels** 15–30 mm. **Fruiting calyces** broadly campanulate-cylindric, 7–9 mm, sparsely purple-dotted, lobe apices acute to obtuse-mucronulate, not closing the throat, upper lobe longest. **Corollas** yellow, apparently without red dots, tube-throats cylindric-funneform, 9–12 mm, exserted 3–5 mm beyond calyx margins, limb barely bilabiate or not at all, expanded 1–1.5 mm (pressed). **Styles** glabrous. **Plesiogamous**; anther pairs and stigma at about the same level. **Capsules** 4–5 mm, sessile, included.

Flowering Mar–May. Moist to wet, sandy loam soil; ca. 2800–3200 ft; Ariz.

Additional collections examined. **Arizona**. Yuma Co.: Kofa Mts., Kofa Game Range, in extremely moist, sandy loam soil, 2800 ft, 15 Apr 1953, *Crandall 150* (ARIZ); Kofa Mts., Kofa Game Refuge, High Tank 8, Upper Burro Canyon, 3200 ft, 31 Mar 1970, *Furlow 24* (ARIZ).

Erythranthe regni is endemic to the Kofa Mountains of Yuma County — all collections have been made from the Kofa Game Refuge. The epithet (genitive of *regnum*, kingdom) alludes to the Kofa Mountains, which are arid, volcanic remnants of Tertiary age. "Kofa" is a near acronym for the old King of Arizona gold mine, which stamped its property "K of A." The monkeyflower localities apparently are at higher elevations in the mountains — the three highest peaks in the area at about 1500 meters, 1350 meters, and 1100 meters.

4. ERYTHRANTHE INAMOENA (Greene) Nesom, Phytoneuron 2012-40: 44. 2012. *Mimulus inamoenus* Greene, Pittonia 5: 137. 1903. **TYPE**: **USA. Texas**. [Jeff Davis Co.:] Limpia Canyon, 25 Apr 1902, *S.M. Tracy* & *F.S. Earle 220* (holotype: ND-Greene!, photo-PH!; isotypes: MO!, PH!, TEX!, US digital image!).

Mimulus jamesii var. *texensis* A. Gray, Syn. Fl. N. Amer. 2(2): 277. 1878. **LECTOTYPE (**Pennell 1935, p. 118**)**: **USA. Texas**. [Travis Co.:] Austin, Apr 1843, *C. Wright s.n.* (GH; isolectotype: NY digital image!). The protologue noted only "Texas, Wright, Lindheimer, &c." — Pennell noted "Type, collected by Charles Wright at Austin, Texas in April, 1843, seen in Gray Herbarium of Harvard University."

Annuals, fibrous-rooted, rooting at proximal nodes and sometimes forming matlike colonies; stems, leaves, pedicels and calyx glabrous or the calyx hirtellous. **Stems** decumbent to decumbent-ascending at the base, becoming fully erect at least in the inflorescence, 10–30 cm, commonly distinctly fistulose (fleshy and hollow), mostly simple or few-branched from proximal nodes. **Leaves** basal and cauline or sometimes the basal deciduous by flowering, basal and lower to mid cauline petiolate, subsessile to sessile distally, blades ovate to broadly ovate or elliptic-ovate, (5–)15–35(–60) x (4–)10–35(–50) mm, becoming subreniform distally, margins dentate-serrate to shallowly dentate, 5–11 teeth per side, apex obtuse to rounded, base truncate to subcordate, petioles 10–70 mm. **Flowers** (6–)8–18(–24), loosely to densely racemose, sometimes produced from all nodes. **Fruiting pedicels** 9–20 mm, straight. **Fruiting calyces** broadly cylindric-campanulate, 7–11 mm, 5–9 mm wide (pressed), greenish or commonly purple-spotted, minutely hirtellous and scabrous, broadly cylindric, lobes deltate to shallowly deltate, lower slightly upturned (10º–45º) but not closing the throat, spreading ca. 45º, or sometimes deflexed 40º. **Corollas** yellow, red-spotted, tube-throats cylindric, 7–11 mm, exserted (1–)2–3(–4) mm beyond calyx margins, limb bilabiate, slightly expanded. **Styles** glabrous. **Plesiogamous**; anther pairs at about the same level, stigma at or slightly below the anthers. **Capsules** 4.5–6 mm, stipitate, included. 2n = 60.

Flowering Jan–Apr(–May). Edge of seeps and creeks, mud or gravel, shallow running water, wet crevices, canyon drainages; 800–2200 m in the trans-Pecos region and adjacent Mexico, 100–400 m in the Edwards Plateau. Texas; Mexico (Chihuahua, Coahuila). Map 3.

Chromosome vouchers. **USA**. **Texas**. Llano Co.: base of Enchanted Rock, sandy and rocky soil along spring fed stream, 1500 ft, 8 Jul 1960, *Vickery 2626*, cult 6278, voucher for *n* = 30 (UT); Enchanted Rock State Park, sand along stream, 1300 ft, 9 Apr 1966, *Vickery 2709*, cult. "7326 = 6278," voucher for *n* = 30 (UT).

Collections examined. **USA**. **Texas**. Numerous collections from almost every county indicated on Map 3. **MEXICO**. **Chihuahua**. Sierra de Hechiceros, Canon Encampanado, below (E) of Rancho Encampanado and above (W) of jct with Canon de Indio Felipe, canyon bottom woods with perennial stream, dry igneous mountains, along stream, 1300-1400 m, 27 Jul 1974, *Wendt & Adamcewicz 418* (TEX); Arroyo La Cristina, 0.3 mi up (E) from Mina Cerro Verde along road to Falomir, N of W part of Sierra Chorreras, 1200 m, arroyo with perennial water, general area of desert scrub, 22 Mar 1975, *Wendt & Lott 752* (TEX). **Coahuila**. Mpio. Zaragoza, Serranias del Burro, upper reaches of Cañon El Bonito, ca. 2.5 km above dam, 1700 m, in accumulations of soil in bed of drainage flowing over metamorphosed limestone in oak-pine woodland, 11 Apr 1976, *Riskind & Patterson 1946* (TEX); Sierra Maderas del Carmen, Cañon El Dos, ca. 1 mi below (SE) of Campo Dos, small moist meadow along stream in general area of coniferous forest, rhyolitic area, 2200 m, 3 Apr 1974, *Wendt et al. 129* (TEX); 1.6 mi S of El Club-Piedra Blanca-Huerfanita road that leaves the latter 6.2 mi W of Huerfanito, heading up limestone valley E of Sierra Maderas del Carmen, along small but apparently perennial stream in general area of desert scrub/grassland, 1325 m, 4 Apr 1974, *Wendt et al. 134* (TEX).

Erythranthe inamoena is distinctive in its lack of vestiture (usually completely glabrous), short corollas, flowers in racemes with reduced bracts and mostly at distal nodes, short and open-thoated fruiting calyces, erect and fistulose stems, and its apparent annual duration (fibrous-rooted but usually rooting at lower cauline nodes).

Pennell (1935) placed *Erythranthe inamoena* (as *Mimulus jamesii* var. *texensis*) as a synonym of typical *E. glabrata*, but the calyces (9–10 mm) and the corollas of the Texas plants are small, more like typical *E. geyeri* (as noted by Greene in the protologue of *Mimulus inamoenus*). Greene also correctly observed the difference in habit between *E. geyeri* (prostrate) and *E. inamoena* (at least flowering axes erect). *Erythranthe inamoena* is tetraploid, in contrast to the diploid *E. geyeri*.

Presumably because of its small corollas with autogamous fertility, *Erythranthe inamoena* has often been confused in identification with *E. cordata*, especially in the trans-Pecos region of Texas where the two are sympatric. The two usually can be distinguished by the following contrasts.

1. Calyces closed at maturity; flowering at distal nodes; pedicels and calyces minutely stipitate–glandular; fruiting calyces (8–)14–18(–20) mm; corolla tube-throats 8–14 mm .... **Erythranthe cordata**
1. Calyces open at maturity; flowering often at all nodes; pedicels and calyces glabrous; fruiting calyces (7–)8–11 mm; corolla tube-throats 7–11 mm .... **Erythranthe inamoena**

In Brewster, Presidio, and ValVerde counties, however, there are populations identified here as *E. inamoena* (based on proximal-to-distal distribution of flowers and the short mature calyces with open throats) that have sparsely stipitate-glandular pedicels and calyces. These might reflect introgression from *E. cordata* — typical populations of both species occur in Brewster and Presidio counties, but *E. cordata* has not been recorded from Val Verde County. Collections examined. **Texas**. Brewster Co.: along Calamity Creek, ca. 24 mi S of Alpine, in damp soil beneath bridge, 4500 ft, 2 Apr 1949, *Turner 459* (SRSC); Warnock & Johnston 17698 (SRSC). Presidio Co.: *Hinckley 3547* (SRSC); *Henrickson 11280* (TEX); *Warnock 18200* (SRSC-2 sheets); *Warnock 435* (SRSC); *Warnock & Powell 17767* (SRSC). Val Verde Co.: Indian Springs, formerly inundated SW-facing slope of large limestone blocks and boulders with large spring, 28 Jun 2002, *Poole 4606* (SRSC); 20-30 mi up Devil's River, along river at falls below Tawcett Lodge, frequent in mud, 2450 ft, 3 Apr 1953, *Warnock 11268* (SRSC).

5. ERYTHRANTHE MICHIGANENSIS (Pennell) Nesom, Phytoneuron 2012-40: 44. 2012. *Mimulus michiganensis* (Pennell) Posto & Prather, Syst. Bot. 28: 177. 2003. *Mimulus glabratus* subsp. *michiganensis* Pennell, Acad. Nat. Sci. Philadelphia Monogr. 1: 119. 1935. *Mimulus glabratus* var. *michiganensis* (Pennell) Fassett, Rhodora 41: 524. 1939. **TYPE**: **USA. Michigan**. Cheboygan Co.: banks of Niger Creek near Topinabee, 13 Jul 1925, *J.H. Ehlers 3240* (holotype: MICH digital image!; isotype: PH!).

Perennial, rhizomatous, commonly producing numerous leafy stolons from basal nodes, rooting at distal nodes, sometimes forming mats. **Stems** ascending-erect or basally decumbent, becoming erect in the inflorescence, 12–50(–70) cm, glabrous or minutely hirtellous and stipitate-glandular. **Leaves** cauline, basal absent at flowering, blades palmately 3–5-veined, broadly ovate to broadly ovate-elliptic or suborbicular, 8–30 mm x 7–30 mm, relatively even-sized or diminishing in size distally, bracteal reduced and slightly falcate (as pressed), margins evenly or unevenly dentate-serrate to dentate with 3–8 pairs of teeth per side, apices mostly rounded, bases truncate to cuneate, petioles 1–5(–15) mm, sessile at midstem and distally. **Flowers** 2–14, mostly from distal nodes or from medial to distal nodes. **Fruiting pedicels** 10–25 mm, spreading, villous-glandular to minutely villosulous-glandular. **Fruiting calyces** cylindric-campanulate, 7–10 mm, not closing, upper lobe ca. 2x longer than others and slightly upcurving, puberulous to softly hirtellous, mixed with longer stipitate-glandular hairs. **Corollas** yellow, sometimes faintly red-spotted, tube-throats cylindric-campanulate, 10–14 mm, exserted 5–8 mm beyond the calyx margin, limb bilabiate, expanded 10–15 mm (pressed). **Styles** glabrous. **Herkogamous**; anther pairs distinctly separated in level, stigma 0.5–2 mm above the upper anther pair. **Mature capsules** not observed. $2n = 30$ or rarely $2n = 28$ (Bliss 1986).

Flowering Jun–Aug(–Oct). Cold calcareous springs, seeps, depressions, streams, alkaline shorelines at the mouth of small drainages, steep moraine slopes, bluff bases, commonly within northern white cedar swamps; 500–900 m; Michigan (Benzie, Cheboygan, Emmet, Leelanau, Mackinac cos.). Map 3.

Erythranthe michiganensis is endemic to a small area in the Mackinac Straits and Grand Traverse regions of Michigan — known as extant from 15 sites and from 3 sites where now apparently extinct. Plants of all but one of the populations are essentially pollen-sterile and reproduce through rhizomes; those from the single partially fertile population have only 27–52% pollen stainability and regularly set selfed-fruits in the greenhouse. In interpopulational crosses between pollen-sterile individuals and pollen donor individuals from the partially fertile population, all the flowers survived to fruiting and all set fruit (Posto 2001).

Based on data from allozyme and RAPD studies, morphology, and crossing studies, Posto and Prather (2003) provided evidence in justification of treating *Erythranthe* [*Mimulus*] *michiganensis* at specific rank. It is "distinguished from the only other member of the *Mimulus glabratus* complex in the Upper Midwest, *M. glabratus* var. *jamesii* [= *E. geyeri*], by its relatively short pedicels (less than twice as long as the bracts), relatively large (17–27 mm) and irregularly spotted corolla, long style (6–14 mm), and large pistil (13–21 mm)." Differences between *E. geyeri* and *E. michiganensis* in the couplet below are as summarized by Posto and Prather.

1. Pedicels usually more than twice as long as the bracts; corollas 8–18 mm, sparsely spotted on tube; styles 2–6 mm; pistils 5–10 mm .... **Erythranthe geyeri**
1. Pedicels less than twice as long as the bracts; corollas 17–27 mm, irregularly spotted on lip and tube; styles 6–14 mm; pistils 13–21 mm .... **Erythranthe michiganensis**

The didynamous stamens of *E. michiganensis* and stigma positioned above the upper anther pair, along with the relatively large corollas with broadly expanded limb, are reflective of its allogamous breeding system and provide another contrast to *E. geyeri*, which is autogamous.

In the RAPD study, Posto and Prather found unique genetic markers in *Erythranthe michiganensis* and that all *E. michiganensis* individuals grouped in a distinct cluster in the UPGMA phenogram, nested among the individuals of *E. geyeri*. This result was consistent with an allozyme analysis by Vickery (1990). The less specialized breeding system of *E. michiganensis* suggests that it was not derived directly from *E. geyeri* and no RAPD evidence appeared to indicate that *E. guttata* was involved in the origin of *E. michiganensis*. The narrow geographic distribution of *E. michiganensis* lies within the wider range of *E. geyeri* and the two are known to co-occur at two sites, apparently without hybridization or morphologically intermediate individuals. A phylogenetic assessment of the Michigan endemic needs to be broadened, although similarities in vegetative morphology and calyx morphology suggest that *E. geyeri* surely must be among the closest relatives.

6. ERYTHRANTHE TILINGII (Regel) Nesom, Phytoneuron 2012-40: 44. 2012. *Mimulus tilingii* Regel, Gartenflora 18: 321, plate 631. 1869. *Mimulus langsdorffii* var. *tilingii* (Regel) Greene, J. Bot. (Brit. & Foreign) 33: 8. 1895. **TYPE**: **USA**. **California**. [Nevada Co.:] "In der Nahe von Nevada-City im Felsengebirge Californiens sammelte," *H.S.T. Tiling s.n.* (holotype: LE presumably). Regel grew it from seed sent by Dr. Tiling from the vicinity of Nevada City, California. The illustration seems diagnostic although the foliar vestiture would need to be examined to verify that it is not *Erythranthe corallina.*

Mimulus implexus Greene, J. Bot. (Brit. & Foreign) 33: 8. 1895. *Mimulus caespitosus* var. *implexus* (Greene) Peck, Man. Pl. Oregon, 655. 1941. **LECTOTYPE** (designated here): **USA**. **California**. [Nevada Co.:] Towards Castle Peak, 27 Jul 1895, *E.L. Greene s.n.* (ND-Greene 46291!, photo-PH!, photo-UT!; isolectotypes: ND-Greene!, UC!). The protologue provided only this: "It usually grows in dense masses among rocks along streamlets, but only in the higher Sierra Nevada of California." Greene noted that he had earlier (Bull. Calif. Acad. 1: 110. 1885) and mistakenly identified these plants as *M. tilingii*. He regarded *M. implexus* distinct particularly in the leaves, which are "not only of unusual thickness and fleshiness of texture; they are entirely covered by translucent dewy-looking particles, so that upon being handled, especially with moist hands, these particles burst, and cover the leaf surface at once with a thick albuminous slime."

Mimulus veronicifolius Greene, Leafl. Bot. Observ. Crit. 2: 7. 1909. **TYPE**: **USA**. **Washington**. [Clallam Co.:] Olympic Mountains, along rivulets, 5000 ft, Aug 1895, *C.V. Piper 2177* (holotype: ND-Greene!, photo-PH!, photo-UT!). The protologue noted "near implexus, excessively large corollas, 2 inches long and nearly 1.5 inches wide at the orifice." Plants of the type collection are relatively tall and suberect but have the very large corollas and intricately branched system of thin rhizomes characteristic of the species. Calyces and pedicels are minutely hirtellous.

Mimulus lucens Greene, Leafl. Bot. Observ. Crit. 2: 7. 1909. **LECTOTYPE** (designated here): **USA**. **Oregon**. [Baker Co.:] Along rivulets in deep woods, Powder River Mts., Aug 1896, *C.V. Piper 2518* (ND-Greene 43316!, photo-PH!, photo-UT!; isolectotype: ND-Greene!). "Akin to *M. implexus,* differing by much more slender stems which are weak and decumbent; leaves exactly ovate, truncate or subcordate at base, of such delicately succulent texture as to be clearly transparent when dried under pressure; calyx sparsely and finely villous." In the protologue, Greene cited *Piper 2518 and* 2519; the ND-Greene sheets (*Piper 2518*) have "Type" and "M. lucens Greene" in Greene's handwriting.

Mimulus implicatus Greene, Leafl. Bot. Observ. Crit. 1: 189. 1909. **TYPE**: **USA**. **California**. San Bernadino Co.: Mill Creek Falls, in the mountains back of San Bernadino, 5500 ft, 20 Jun 1901, *S.B. Parish 5063* (holotype: US digital image! Photo-JEPS!, photo-PH!; isotypes: NY digital image!, PH!). The PH label says "5,000 ft" but otherwise has the same collection data.

Perennial, rhizomatous from a mass of yellowish, branching rhizomes. **Stems** 2–35 cm, ascending-erect, usually freely branched, glabrous to sparsely stipitate-glandular or short glandular-villous. **Leaves:** blades 5–35 mm (30–55 mm in large-leaved forms), ovate to lanceolate-triangular or narrowly lanceolate (broadly ovate in large-leaved forms), glabrate to sparsely or moderately villous with thick-vitreous eglandular hairs, apex acute to obtuse or rounded, margins irregularly denticulate, palmately 3-5-veined, 1.5–3 cm, upper sessile, not perfoliate; petioles 0–25 mm. **Flowers** 1–3(–5), in distal axils. **Fruiting pedicels** 15–35(–40) mm, sparsely stipitate-glandular to short glandular-villous. **Fruiting calyces** broadly campanulate, 11–15 mm, closing, glabrous to sparsely stipitate-glandular or short glandular-villous, villous at the sinuses, generally purple-tinged and purple-dotted, lobes broadly ovate, blunt, unequal, the lower ones usually longer than the lateral, the upper at least twice as long as the others. **Corollas** yellow, red-dotted, tube-throats 15–28 mm, exserted 5–10 mm past calyx margin, limb bilabiate, expanded 14-30 mm across (pressed). **Styles** hirtellous. **Herkogamous**; anther pairs at different levels, stigma above upper anther pair. **Capsules** 5–7 mm, stipitate, included. $2n = 28, 56$.

Vouchers at UT for chromosome counts by Vickery: **$2n = 28$** (**California**, El Dorado Co., Mono Co.; **Utah**, Salt Lake Co.); **$2n = 56$** (**Utah**, Utah Co., *Vickery 2714*, cult. 7493).

Flowering Jul–Sep. Seeps, springs, streambanks, shallow rivulets, cliff bases, ledges and crevices, steep gravelly slopes, wet meadows; 6200-11,400 ft [1400–3400 m]. **Alberta** (Sheep Mountain, Waterton Lake, 28-31 Jul 1895, *Macoun 11,889*, ND-Greene); Ariz., Calif., Idaho, Mont., Nev., Wyo. Map 4.

The assertion that introgression has occurred between *Erythranthe tilingii* and *E. guttata* (Lindsay & Vickery 1967) is based on observations from northern Utah. Plants of the putative introgressants, from "the subalpine population from the Big Cottonwood Canyon," were noted by Lindsay and Vickery (1967, p. 453) as "typical of *M. guttatus* for the presence of underground stems which appears to be a residual *M. tilingii* trait from an ancient hybridization." In the UT herbarium, I identified a voucher as a plant of *E. utahensis*, for which $2n = 30$ and prolific rhizome production is characteristic. **Utah**. Utah Co.: Mount Timpanogos, 7800 ft, 6 Aug 1956, *Wiens s.n.*, $n = 15$ (UT), see Mukherjee and Vickery (1962). Also reported McArthur et al. (1972) as n = 15 for *E. tilingii* in Utah Co. are these (vouchers not seen): Mt. Timpanogos Trail, 2650 m, 1968, Vickery cult. 7714; Mt. Timpanogos Trail, 2745 m, 1968, Vickery cult. 7717; Emerald Lake, 3050 m, Vickery cult. 7716.

Erythranthe tilingii has generally been regarded as a widespread species of relatively high elevations, the plants arising from a system of thin rhizomes and producing mostly 1–3 large flowers per stem. It is sometimes considered to include one or several infraspecific entities. The present study divides this "complex" into four distinct entities, without unambiguous intergrades, each of which is treated at specific rank. One other species, *E. utahensis*, also is included — it has not previously been associated with this group of species.

(1) *Erythranthe tilingii* sensu stricto is relatively widespread over the western USA and is sympatric with *E. corallina* and *E. caespitosa*. Leaves are variable in size in *E. tilingii*, and particularly in Idaho

they may approach the small size of those of *E. caespitosa* but the leaf margins of *E. tilingii* are distinctly toothed and the stems are taller and more erect. Across the range of the species, plants sometimes produce very large leaves but these often can be seen to occur on plants with characteristically smaller leaves. This wide variability in size apparently does not occur in *M. caespitosus*.

(2) *Erythranthe minor* is characterized by very short corollas with relatively narrowly expanded limbs. Corollas of *E. tilingii* rarely may be equally as short but are produced on plants that are depauperate in other ways as well (e.g., **Oregon**. Klamath Co., *Epling 5555*, MO; **Washington**, Thurston Co., *Meyer 1590*, MO) — these scattered, small-flowered individuals are perhaps the reason Pennell regarded the range of *E. minor* to be wider than recognized here. The nodding calyces of *E. minor* also distinguish the species. Overall, the distinction of *E. minor* appears to be subtle but real, especially in view of its geographic coherence.

(3) *Erythranthe caespitosa* is endemic to northwestern and central Washington and the Selkirk Range of British Columbia — the plants have consistently small leaves with subentire margins and the stems are consistently procumbent to decumbent-ascending, usually forming matted colonies. *Erythranthe caespitosa* and *E. tilingii* apparently are sympatric in counties of northwestern Washington.

(4) *Erythranthe corallina* has hirsutulous to softly hirsute leaf surfaces and occurs only in the Sierra Nevada of California and adjacent Nevada (Washoe Co. and Carson City). Its chromosome number is reported as 2*n* = 48 and 56, compared to 2*n* = 28 and 56 in *E. tilingii*. Compared to *E. tilingii* sensu stricto, the leaf blades of *E. corallina* are relatively broader, the shape broadly ovate to orbicular-ovate, the plants are generally taller, and long-pedicellate flowers occasionally are produced from midstem or even proximal nodes. The hirsutulous to hirsute vestiture of eglandular hairs on both leaf surfaces is a reliably diagnostic feature and usually easily observed with a lens.

7. ERYTHRANTHE CAESPITOSA (Greene) Nesom, Phytoneuron 2012-40: 43. 2012. *Mimulus caespitosus* (Greene) Greene, J. Bot. (Brit. & Foreign) 33: 8. 1895. *Mimulus tilingii* var. *caespitosus* (Greene) A.L. Grant, Ann. Missouri Bot. Gard. 11: 154. 1924. *Mimulus scouleri* var. *caespitosus* Greene, Pittonia 2: 22. 1889. **LECTOTYPE** (designated here): **USA**. **Washington**. [Pierce Co.:] Lake Shore, on Mt. Rainier, 20 Aug 1889, *E.L. Greene s.n.* (ND-Greene 046468 photo-PH!, photo-UT!; isolectotypes: DS digital image!, ND-Greene-2 sheets!, NY digital image, PH!, UC! [with "TYPE" handwritten], US digital image!, WTU). Treated as a distinct species by Pennell (1951). When Greene raised this entity to specific rank in *Mimulus*, he intended only to reflect its disconnection from *M. scouleri* — he did not mention a relationship or similarity with *M. tilingii*.

Perennials, with slender rhizomes. **Stems** delicate, 3–10 cm, glabrous, minutely hirtellous, or stipitate-glandular, usually in masses, terete or flattish, decumbent at base, rooting at the lower nodes sometimes producing creeping, small-leaved runners. **Leaves**: blades orbicular to narrowly elliptic or ovate, 5–12 mm long, becoming larger distally, palmately 3-veined, often purple beneath, sparsely to moderately puberulent with minute stipitate-glandular hairs, margins denticulate to entire, apex obtuse, base cuneate to a short petiole, proximal leaves usually sublyrate, distal sessile to subsessile. **Flowers** 1–3, commonly solitary. **Fruiting pedicels** 10–30(–40) mm, sparsely to moderately villous with short, gland-tipped hairs, sometimes with an admixture of hirtellous hairs. **Fruiting calyces** broadly campanulate, 7–15 mm, closing, the short lobes obtuse to acute or mucronulate, lower pair upcurved, uppermost 3–5 mm and prominently protruding. **Corollas** yellow, dark red-spotted, tube-throats broadly funnelform to cylindric-funnelform, 15–18 mm, palate partially closed, lower lip deflexed-spreading lobes, upper lip with ascending lobes. **Styles** minutely hirtellous.

Herkogamous; anther pairs at different levels, stigma above upper anther pair. **Capsules** 4–5 mm, stipitate, included.

Flowering Jul–Sep. Alpine meadows and slopes, stream banks, wet rocks in streams, wet crevices, talus; 1100–2000(–2300) m. British Columbia (Selkirk Mts., Chilliwack Valley); Washington (Cascade and Olympic Mts.). Map 5.

8. ERYTHRANTHE MINOR (A. Nelson) Nesom, Phytoneuron 2012-40: 44. 2012. *Mimulus minor* A. Nelson, Proc. Biol. Soc. Wash. 17: 178. 1904. *Mimulus langsdorffii* var. *minor* (A. Nelson) Cockerell in Daniel, Fl. Boulder, Colorado, 213. 1911. **TYPE**: **USA**. **Colorado**. [Boulder Co.:] Arapahoe Pass (near Boulder), timberline, 1904, *D.M. Andrews 8* (holotype: RM fide Grant 1924, photo-PH!). Treated by Pennell (1951) as a distinct species occurring in the Hudsonian Zone from Oregon and Idaho south to Utah and New Mexico.

Mimulus luteus var. *alpinus* A. Gray, Proc. Acad. Philadelphia 15: 71. 1863 (non Lindley 1827). *Mimulus alpinus* (A. Gray) Piper, Contrib. U.S. Natl. Herb. 11: 510. 1906. *Mimulus langsdorffii* var. *alpinus* (A. Gray) Piper, Mazama 2: 99. 1901. *Mimulus langsdorffii* var. *alpinus* (A. Gray) Blankinship, Montana Agric. College Sci. Bull. 1: 98. 1905. **TYPE**: **USA**. **Colorado Territory**. Alpine and subalpine, 39-41°N, 1862, *C.C. Parry 135a* (holotype: GH photo-PH!). The protologue entry: "caulibus 3-pollicaribus e basi decumbente vel repente 1-3-floris; foliis plerisque sessilibus subintegerrimis. Alpine region, 135a coll. Parry, 1862. Very glabrous." The PH photo has a label of *Parry 235a*, 1862.

Perennial, rhizomatous. **Stems, pedicels, and calyces** densely minutely hirtellous and eglandular or with a mixture of hirtellous and gland-tipped hairs. **Stems** erect to erect-ascending, 5–20 cm. **Leaves**: blades broadly ovate to elliptic-ovate or lanceolate, 8–25 x 5–15 mm, palmately 3-veined, both surfaces glabrous, margins shallowly dentate to denticulate, apex acute to obtuse, base cuneate to truncate, sessile to subsessile or proximal with petioles 1–3 mm. **Flowers** 1–3, from distal nodes. **Fruiting pedicels** 10–20 mm. **Fruiting calyces** 10–13 mm, closing, nodding 80º–100º, without purple dots. **Corollas** yellow, apparently without red dots, tube-throats tubular-funnelform, 9–11 mm, exserted from the calyx 0–1(–2) mm. **Styles** sparsely hirtellous. **Herkogamous**; anther pairs at different levels, stigma above upper anther pair. **Capsules** 5–8 mm, stipitate, included.

Flowering Jul–Aug(–Sep). Stream edges, lake edges, intermittent water courses, subalpine rill, roadside ditches, subalpine to alpine; 3000–3700 m; Colorado, New Mexico, Utah. Map 6.

The corollas of *Erythranthe minor* are distinctly shorter than those of typical *E. tilingii* and the geographic range of the species is set apart from *E. tilingii*. The morphological difference between the two is especially apparent by comparison of a set of specimens of one with the other. The range of *E. minor* is primarily in Colorado apparently extends into Utah (La Sal Mountains of Grand and San Juan counties) and into New Mexico (the Wheeler Peak area of Taos County).

The only collection seen from **New Mexico** is this: Taos Co.: Carson Natl. Forest, 8 mi from Red River town, bank of Goose Lake, 11,650 ft, 23 Aug 1968, *Correll & Correll 36261* (NMC).

9. ERYTHRANTHE CORALLINA (Greene) Nesom, Phytoneuron 2012-40: 43. 2012. *Mimulus corallinus* Greene, Erythea 4: 21. 1896. *Mimulus tilingii* var. *corallinus* (Greene) A.L. Grant, Ann. Missouri Bot. Gard. 11: 155. 1924. **TYPE**: **USA**. **California**. [Nevada Co.:] Washoe Mts., [protologue: "Plentiful along the western base of the Washoe Mountains beyond Truckee,"] 25 Jul 1895, *E.L. Greene s.n.* (holotype: ND-Greene, photo-UT!; isotype, as labeled: NY digital image!). The protologue (p. 21) noted "Plentiful along the western base of the Washoe Mountains beyond Truckee, but also near Summit Station, from the latter district it has been distributed by me under the name of M. Tilingii." Pennell (by annotation) identified this as *Mimulus tilingii*.

Mimulus minusculus Greene, Leafl. Bot. Observ. Crit. 2: 5. 1909. **TYPE**: **USA**. **California**. [Tulare Co.:] South Fork of Kern River, 8200 ft, 1875, *J.T. Rothrock 312* (holotype: US fide Greene in the protologue, but not included in US type database). Greene noted that "the whole plant is sparsely and minutely hispid-hirtellous."

Perennials, prolifically rhizomatous, rhizomes thin. **Stems** mostly erect to ascending-erect, 6–25(–38) cm, moderately hirsute to hirsutulous with deflexed hairs. **Leaves** basal and cauline, becoming larger distally or even-sized, blades ovate to broadly ovate, 15–45 mm, palmately 5-veined, hirsutulous on both surfaces with ascending hairs, eglandular, margins sharply dentate-serrate, apex obtuse, base mostly truncate to shallowly cordate, sessile or subsessile or proximal with petioles 1–15 mm. **Flowers** 1–3(–6), commonly solitary or mostly from distal nodes. **Fruiting pedicels** (10–)25–75 mm, glabrous or puberulent proximally with stipitate-glandular hairs. **Fruiting calyces** broadly cylindric-campanulate, 11–15 mm, not closing, sometimes purple-spotted, lobes shallowly deltate, lower pair slightly upcurved. **Corollas** yellow, red-spotted, tube-throats narrowly funnelform to broadly cylindric, 13–20 mm, limb expanded 12–22 mm (pressed). **Styles** sparsely hirtellous. **Herkogamous**; anther pairs at different levels, stigma above upper anther pair. **Capsules** 7–10 mm, stipitate, included. 2*n* = 48, 56?.

Flowering (May–)Jun–Aug. Creek banks, moraine water courses, bogs, marshes, wet meadows, roadside ditches; 4800–)5700–9000(–10,000) ft; California, Nevada. Map 7.

Before learning that *Erythranthe corallina* is the correct name for this species, I annotated various collections of it as *Erythranthe minuscula.*

For *Erythranthe corallina*, Vickery made chromosome counts of 2*n* = 48 from Tuolumne Co. (Porcupine Flats, 8000 ft, 17 Sep 1958, *Heisey 576* (UC, UT) and 2*n* = 56 from El Dorado Co. (8 mi from Calif. checking station along US Hwy 89, 7200 ft, summer 1963, *Wilson s.n.* (UT), identifying the vouchers as *Mimulus tilingii* var. *corallinus*. How the 2*n* = 48 population might have arisen in *E. corallina* is obscure, since its putative relatives apparently are 2n = 28 and 2n = 30. The species appears to be relatively uniform and it seems likely that it had but a single evolutionary origin. The voucher for the count of 2*n* = 56 needs to be reexamined on the possibility that it may be *E. utahensis*, and the count of 2n = 48 needs to be verified.

Two collections from the southern part of the range are of very low plants with decumbent-ascending stems (4–10 cm) and tiny ovate-triangular leaves (blades 5–10 mm x 3–6 mm) but the dense system of filiform rhizomes, flowers 1–3, and hirtellous foliar vestiture identify them as *Erythranthe corallina.* San Bernadino Co.: San Bernadino Mts., Bluff Lake, 7400 ft, 21-27 Jun 1895, *Parish 3606* (JEPS); eastern San Gabriel Hills, Lost Creek, W-facing canyon, on W-facing wet cliff face, 6800 ft, 22 Jul 1994, *Swinney 3088* (DAV). Other collections of *E. corallina* from Bluff Lake are typical in habit (e.g., *Clokey 5301* and *5305*, UC; *Grinnell 80*, UC) and similar compaction of the basal parts occurs sporadically elsewhere in the range of the species as well as in *E. tilingii.*

10. ERYTHRANTHE UTAHENSIS (Pennell) Nesom, Phytoneuron 2012-40: 44. 2012. *Mimulus glabratus* subsp. *utahensis* Pennell, Acad. Nat. Sci. Philadelphia Monogr. 1: 123, map 23. 1935. **TYPE**: **USA**. **Utah**. Millard Co.: along brook, Preuss Lake, near Clay's Ranch, 29 Aug 1919, *I. Tidestrom 11180* (holotype: PH!).

Perennial, prolifically rhizomatous, thin rhizomes. **Stems** erect or proximally decumbent-ascending and rooting at the nodes, 20–50 cm, glabrous or sparsely stipitate-glandular in the inflorescence. **Leaves** basal and cauline, even-sized or largest near midstem, sessile to subsessile except for proximal-most, blades orbicular or suborbicular to broadly elliptic, broadly ovate, or depressed ovate, 20–40(–75) mm x 12–35(–40) mm, both surfaces glabrous to glabrate or commonly sparsely stipitate-glandular and sparsely pilose with thin-walled hairs, often glaucous abaxially, margins entire or subentire to mucronulate or shallowly dentate or denticulate, apex rounded, base usually truncate to broadly cuneate; petioles absent or 2–10 mm. **Flowers** 6–16 in a loose raceme, distal bracts becoming much reduced. **Fruiting pedicels** (25–)40–75 mm, straight, stipitate-glandular to short villous with gland-tipped hairs. **Fruiting calyces** (10–)11–17(–20) mm, not closing, lobes convex-mucronulate, upper lobe slightly longer and triangular-blunt, stipitate-glandular or minutely hirtellous or a mixture, sometimes also with longer, thin-walled eglandular or glandular hairs. **Corollas** yellow, lower lip prominently darker yellow and sparsely purple-spotted, tube-throats narrowly funnelform to broadly cylindric, 10–15 mm, exserted 5–8 mm beyond calyx margin, limb weakly bilabiate, expanded 12–20 mm (pressed). **Styles** hirtellous. **Herkogamous**; anther pairs at different levels, stigma above upper anther pair. **Capsules** 5–8 mm, stipitate, included. $2n = 28, 30$.

Vouchers at UT for chromosome counts by Vickery: **$2n$ = 28** (**California**, Mono Co.; **Nevada**, Mineral Co.; **Utah**, Juab Co.); **$2n$ = 30** (**Nevada**, Elko Co. and White Pine Co.; **Utah**, Tooele Co. and Wayne Co.).

Flowering (Feb–)May–Aug(–Oct). Drainage ditches, springs, seeps, wet meadows, margins of ponds and small streams, marshy areas; 1400–2500 m; California (Fresno, Mono, Tuolumne), Colorado, Nevada, Utah. Map 7.

Colorado records as mapped from Delta, Montrose, and Saguache counties are from the database of collections from CU Museum-COLO (2009); collections from Montrose Co. were cited for subsp. *utahensis* by Pennell. California records for Fresno, Mono, and Tuolumne counties are vouchered by these: Fresno Co.: 6500 ft, 8 Jul 1949, *Bean 516*, Vickery cult. 5047 (UT). Mono Co.: Mono Lake, Rush Creek, 4 Sep 1948, *Mason 13646* (UC); by Mono Lake, 6440 ft, Jul 1948, *Stebbins 714* (UC). Tuolumne Co.: near the middle Fork of the Tuolumne River, 6000 ft, *Stebbins s.n.*, Vickery cult. 5047 (UT).

Erythranthe utahensis was treated as a distinct entity (as *Mimulus glabratus* subsp. *utahensis*) by Welsh et al. (2003). Holmgren (1983, p. 354) noted that "Subspecies *utahensis* Pennell is easily distinguished from the other subspecies of *M. glabratus*, but it can be too easily accomodated within the broad range of variability of *M. guttatus* DC." — he cited collections from Pennell's original documentation in recognizing at least the potential existence of subsp. *utahensis*. *Mimulus glabratus* subsp. *utahensis* was placed without comment as synonym of *M. guttatus* by Thompson (1993).

Erythranthe utahensis is characterized by its erect stems, prolifically produced filiform rhizomes, basal leaves short-petiolate to subsessile and cauline sessile, blades suborbicular to broadly ovate or depressed ovate with thin-walled villous-glandular hairs on both surfaces, margins subentire, proximal pedicels elongating to 75 mm, and calyces open at maturity. The species most closely similar to *E. utahensis* is *E. corallina* — both species have a dense system of thin rhizomes, thin and suborbicular leaf blades, long pedicels, open calyces, and large corollas. The two are sympatric where *E. utahensis* apparently touches into the Sierra Nevada of California. Plants of one collection have the taller habit of *E. utahensis* but with fewer flowers as in *E. corallina* and an apparently intermediate vestiture: Tuolumne Co.: Ackerson Creek, 4710 ft, 26 Aug 1949, *Vickery 191* (UT). The two species are distinguished by the following contrasts.

1. Flowers 1–6, from distal nodes only; corolla tubes 14–20 mm; fruiting pedicels 15–75 mm long; stems 6–25(–38) cm; leaf blades prominently dentate with sharp teeth, hairs of surfaces short, sharp-pointed, eglandular, thick-walled, and dull gray .... **Erythranthe corallina**

1. Flowers 6–16, from proximal to distal nodes; corolla tubes 10–13 mm; fruiting pedicels (25–)40–75 mm; stems 20–50 cm, leaf blades subentire to shallowly dentate, hairs of surfaces longer, apically blunt, gland-tipped, thin-walled and vitreous .... **Erythranthe utahensis**

Erythranthe utahensis previously has been regarded as a member of the '*Mimulus glabratus* complex' because of its similar chromosome number and presumably because of its calyx, which usually remains open at maturity. The distinctive rhizome system, however, as well as its foliar vestiture and its western USA geography, indicate that it belongs with the *E. tilingii* group. The allozyme analysis by Vickery (1990) places *Erythranthe utahensis* as more similar to Andean groups with $n = 46$ than to any other North American groups previously identified as *E. glabrata*, but the analysis did not include any other species of the *E. tilingii* group.

11. ERYTHRANTHE GUTTATA (Fischer ex DC.) Nesom, Phytoneuron 2012-40: 43. 2012. *Mimulus guttatus* Fischer ex DC., Cat. Pl. Horti Monsp., 127. 1813. *Mimulus langsdorffii* var. *guttatus* (Fischer ex DC.) Jepson, Fl. W. Mid. Calif., 406. 1901. **TYPE MATERIAL**: **USA. Alaska**. No other data, ca. 1803-1805, *G.H. Langsdorff s.n.* (CGE?; LE fide Tokarska-Guzik and Dajdok 2010; NY fide Pennell 1935). Figure 1.

The 1813 protologue is reproduced here:

"(141) MIMULUS GUTTATUS. M. foliis ovatis multinerviis denticulatis, inferioribus petiolatis, caulibus basi repentibus adscendentibus pilosiusculis projectura foliorum subtetragonis, pedicellis folio florali brevioribus. DC. *hort monsp. ined. t. 60.*

Hab. ..... Species affinis M. luteo cujus icon adest in *Feuill. peruv.*, sed differt: 1.º caule petiolique pilosis nec laevibus; 2.º foliis inferioribus longe petiolatis nec subsessilibus; 3.º dentibus foliorum inaequalibus nec regularibus; 4.º pedicellis folio brevioribus nec duplo longioribus; 5.º flore fere duplo minore; 6. º fauce piloso nec ut in icone Fewilleana glabro."

As a synonym of *Mimulus luteus* L., Bentham (1846, p. 370) listed "M. guttatus DC.! cat. hort. monsp. p. 127" and also cited the discussion and illustration of Langsforff's Mimulus (see notes below for *M. langsdorffii* J. Donn ex Greene 1895). Gray (Synopt. Fl., p. 448) also regarded the South American and western North American plants as conspecific, as *M. luteus*.

Grant (1924) did not specify a type for *M. guttatus*. Pennell (1935) noted that "Quite certainly the seeds of these garden plants were obtained from the same source as those of the plant figured in the Botanical Magazine 36: t. 1501. 1812 as *M. luteus*, being from Langsdorff who collected the plant, between 1806 and 1810, on Unalaska, one of the Fox Islands, Alaska. A probable duplicate of Langsdorff's specimen, or else its progeny in a Russian garden, as in Herb. New York Botanical Garden, labeled Mimulus guttatus F. Unalaschka. Fishcher." Pennell (1947) and Campbell (1950) essentially repeated Pennell's earlier account of the provenance.

The nature of Pennell's "certainty" about the source of the seeds is at least ambiguous, but he perhaps assumed that it was no coincidence that the Montpellier garden catalog and the Botanical Magazine article were published at essentially the same time and that Russian botanist F.E.L. Fischer also had access to the gatherings of Langsdorff. The plant illustrated in the Botanical Magazine of 1812 was said to be grown from seeds collected in Alaska by Langsdorff and initially sent to John Hunneman in England in about 1811. Tokarska-Guzik and Dajdok (2010) observed that Langsdorff collected the seeds during his voyage in 1805 to Marquis Island (1804-1808).

Mimulus rivularis Nutt., J. Philadelphia Acad. Nat. Sci. 7: 47. 1834. **TYPE**: **USA**. **Idaho** or **Oregon**. Head of Colum[bia River], [probably 1832], *N.J. Wyeth s.n.* (holotype: PH!; probable isotype: MO! see comments below). Protologue: "Stoloniferous; very smooth. Root leaves round oval, sharply crenate, petiolate, stem leaves similar, sessile. Flowers large, bright yellow. *Hab*. In the valleys of the Rocky Mountains."

The PH sheet hold four branches, all of which were identified by Pennell (by annotation) first as *Mimulus guttatus* and then as *M. puberulus*. Grant (1924) also apparently regarded all as equally pertinent to the type concept. Two separate collections and two separate labels, however, are mounted and the collections are not of the same entity.

The one longer and thicker stem has pedicels and calyces sparsely villous with gland-tipped hairs — it matches Nuttall's protologue and is the actual type. Immediately below this branch is mounted a small handwritten label (by Nuttall): "Mimulus luteus rivularis, Head of Colum. (Nutt f?? Wyeth)."

The three shorter and relatively thin stems have pedicels densely hirsutulous mixed with a few gland-tipped hairs. The accompanying label has a printed header: "US Geological and Geographical Survey of the Territories, SECOND DIVISION. J.W. Powell, in charge" with collection data as "Utah. [Sevier Co.:] Glenwood, 23 May 1875, *L.F. Ward 90*."

The collection at MO is labeled L.F. Ward 90, but it closely matches the morphology of the PH Nuttall collection — not those from Utah on the PH sheet — and it seems probable that the MO label was distributed with the wrong collection of plants. The MO sheet probably is part of the Wyeth-Nuttall collection and, if so, is thus an isotype.

Mimulus lyratus Benth., Scroph. Indicae, 28. 1835. *Mimulus guttatus* var. *lyratus* (Benth.) Pennell ex Peck, Man. Pl. Oregon, 654. 1941. **TYPE**: **USA**. **California**. The protologue notes only "California, *Douglas*" (holotype: K photo-MO!).

Mimulus glabratus var. *adscendens* A. Gray, Synopt. Fl. N. Am. ed. 2, 2, Suppl. 448. 1886. **TYPE**: **USA**. **Arizona**. [Coconino Co.:] Grand Canyon of the Colorado, 4 May 1885, *A. Gray s.n.* (holotype: GH photo-PH!). Protologue: "A large and robust form (as sometimes in Mexico), rising a foot or two high from the creeping base; branches freely racemosely flowered at summit; the upper and sometimes connate rounded leaves being much reduced and bracteiform. — *M. glabratus* (chiefly), Gray, Bot. Mex. Bound. 116. *M. hallii*, Greene, Bull. Calif. Acad. 113, but species not truly annual, nor calyx-teeth acute. The specimen of Hall described from [sic] was a cultivated one — Colorado and west to the Grand Cañon in N.W. Arizona, south to Mexico." *Hirtellous vestiture, eglandular.

Mimulus langsdorffii var. *argutus* Greene, J. Bot. (Brit. & For.) 33: 7. 1895. **TYPE**: **USA**. **Alaska**. The protologue cited "Sitka, *Barclay*; also Oregon, *Tolmie*, *Nuttall*, and others."

Mimulus langsdorffii var. *platyphyllus* Greene, J. Bot. 33: 7. 1895. **TYPE**: **CANADA**. **British Columbia**. Near Vancouver. "Collected long ago, on the shores of Nutka Sound, by Barclay."

Mimulus langsdorffii J. Donn ex Greene, J. Bot. (Brit. & Foreign) 33: 6. 1895. **TYPE**: **USA**. **Alaska**. ca. 1803-1805 or 1804-1808, *G.H. Langsdorff s.n.* (holotype: CGE?). Homotypic with *Mimulus guttatus*. Greene (1895) noted that "*M. langsdorffii* is an older name than *M. guttatus* for the North American type of this group," but Donn (J. Donn ex Sims, Bot. Mag. 36: sub pl. 1501. 1812) referred to the plant as "Langsdorff's Mimulus" — identifying it as *M. luteus* of Linnaeus, thus not validating a new epithet. Greene in 1895 attributed the earlier publication to "Donn in Sims."

As written by Sims in the protologue: "This beautiful species of MIMULUS was found by Dr. LANGSDORFF, who was attached, as naturalist, to the Russian embassy to China. He brought it, as we are informed, from Unashka, one of the Fox Islands, and seeds were transmitted to Mr. HUNNEMANN last spring, and through him to Mr. DONN, curator of the Botanical Garden at Cambridge, who kindly communicated to us in July last the specimen from which our drawing was made, under the name of MIMULUS *Langsdorfii*, which we should have adopted, had it proved, as was supposed, a new discovery. But the same species was found in Chili, by Father FEUILLEE, and has been long ago described and figured in his work, as above quoted. From him LINNAEUS inserted it in his Species Plantarum, with the specific name of *luteus*. It was found also in California and at Nootka, by Mr. ARCHIBALD MENZIES."

Mimulus grandiflorus J.T. Howell, Fl. N.W. Amer. 5: 520. 1901. **TYPE**: **USA**. **Oregon.** [Clackamas Co.:] Wet places along the Tualatin River near its mouth, Jul 1900, *T. Howell s.n.* (holotype: ORE digital image! photo-PH!). No type was cited, the protologue giving only this: "Growing in wet places along streams, western Oregon and Washington: beginning to flower early in May." Described as "stolons; stems 1-4 feet high; lower leaves sublyrate; calyx red-dotted, closed; infl. sparsely hairy; corolla 2 inches [5 cm]." The ORE[OSC] sheet has "Type specimen" handwritten on the label.

Mimulus hirsutus J.T. Howell, Fl. N.W. Amer. 5: 520. 1901 [non Blume 1826]. **TYPE: USA. Oregon.** [Clackamas Co.:] In the Tualitin River near its mouth, Jul 1900, *T. Howell s.n.* (holotype: ORE digital image!). No type was cited, the protologue giving only this: On wet rocks in the Tualatin and Willamette rivers Oregon: beginning to flower about the first of July." Described as 'stems stoutish, 1-2 feet high, stolons; calyx red-dotted, closed; lower leaves often laciniately lobed or lyrate; infl. hirsute; corolla 1 inch." The ORE[OSC] sheet has "Type specimen" handwritten on the original label and has been annotated later as "holotype."

Mimulus prionophyllus Greene, Leafl. Bot. Observ. Crit. 1: 190. 1905. **TYPE**: **USA**. **Arizona**. [Coconino Co.:] Willow Spring, 10 Jun 1890, *E. Palmer 527* (holotype: US digital image! photo-PH! photo-UC!).

Mimulus paniculatus Greene, Leaflets Bot. Observ. Crit. 1: 190. 1906. **TYPE**: **USA**. **California**. San Diego Co.: Witch Creek, May 1894, *R.D. Alderson s.n.* (holotype: ND-Greene!, photo-PH!, photo-UT!). The plant has fistulose stems like *M. petiolaris*.

Mimulus puberulus Greene ex Rydberg, Fl. Colorado, 311. 1906 [Greene, Leafl. Bot. Observ. Crit. 2: 4. 1909]. *Mimulus guttatus* var. *puberulus* (Greene ex Rydberg) A.L. Grant, Ann. Missouri Bot. Gard. 11: 170. 1924. **LECTOTYPE** (designated here): **USA**. **Colorado**. [Archuleta Co.:] Pagosa Springs, 27 Jul 1899, *C.F. Baker 587* (ND-Greene 046404!, photo-UT!; isolectotypes: F digital image!, MO! digital image!, ND-Greene!, NY digital image! photo-PH!; POM, RM, UC!, US digital image!). Greene (1909) cited *Baker 587*, "in my own herbarium," as the type. Grant (1924) referred to the name as published by Rydberg as a "nom. nud." and Rydberg apparently did not intend to publish the name as an innovation, perhaps assuming that Greene had already published it, but his key to species provides a morphological diagnosis. Rydberg's use of the name in 1906 can be taken as a valid publication.

Mimulus equinus Greene, Leafl. Bot. Observ. Crit. 1: 189. 1906. **TYPE**: **USA**. **California.** Lake Co.: In the "Horse Pasture," near the summit of Mt. Sanhedrin, 20 Jul 1902, *A.A. Heller 5924* (holotype: US digital image!; isotypes: CAS digital image!, NY digital image!, PH!).

Grant (1924) treated *Mimulus equinus* as a variety of *M. guttatus* (as *M. guttatus* var. *puberulus*), noting that it was distributed "in wet places in southern Colorado and northern New Mexico," and characterized by "stems densely pubescent above, often freely branched from the base; leaves puberulent or pubescent, usually grayish-green; pedicels shorter than the flowers, sometimes recurved in fruit; and corolla 2-3 cm. long." Pennell (1947, p. 166) noted that it "does not seem to me actually distinguishable from the common plant so widespread through the Rocky Mountain and Intermontane states, a plant distinguishable from true *M. guttatus* by its habitually smaller flowers. Were one to consider the two as separate species there are a number of names available for the common plant of the western United States, but as a subspecies the earliest trinomial is *puberulus*, which Dr. Grant intended to apply only to its pubescent extreme." *Hirtellous vestiture, eglandular.

Mimulus clementinus Greene, Leafl. Bot. Observ. Crit. 2: 5. 1909. **TYPE**: **USA**. **California**. [Los Angeles Co.:] San Clemente Island, off the coast of southern California, Jun 1903, *B. Trask s.n.* (holotype: US digital image! photo-PH!; isotype: NY digital image!).

Mimulus petiolaris Greene, Leafl. Bot. Observ. Crit. 2: 7. 1909. **TYPE**: **USA**. **California**. [Inyo Co.:] Argus Mountains, Shepherd Cañon, 800-2000 m, 28 Apr 1891, *F.V. Coville 740* with F. Funston (holotype: US digital image! photo-PH!; isotypes: MO!, NY digital image!, PH!).

Mimulus langsdorffii var. *minimus* J.K. Henry, Fl. S. Brit. Columbia, 268. 1915. **TYPE**: **CANADA**. **British Columbia**. Paisley Island, near Vancouver. The protologue: "Glabrous, stems 6-10 cm. high, corolla [20-40 mm] with one very large, light brown-purple spot on the lower lip. Paisley Island."

Mimulus guttatus subsp. *haidensis* Calder & Taylor, Canad. J. Bot. 43: 1398. 1965. **TYPE: CANADA**. **British Columbia**. Queen Charlotte Islands, Moresby Island, about 3 mi W of head of Cumshewa Inlet below north face of the Mt. Moresby, common along rocky-gravelly margins of steep facing runnel between 700 and 1300 ft, 31 July 1964, *J.A. Calder & R.L. Taylor 36391* (holotype: DAO; isotype: NY digital image!).

A collection identified and distributed as *Mimulus guttatus* subsp. *haidensis* is this: Queen Charlotte Islands, [Moresby Island,] ca. 20 mi S of Moresby Logging Camp, 29 Jul-2 Aug 1957, *Calder, Savile, and Taylor 23063* (UC!). Stems, pedicels, and calyces minutely hirtellous, eglandular.

Perennial, rhizomatous; stems, pedicels, and calyces villous-glandular or moderately to densely hirtellous with eglandular hairs or with a combination of glandular and eglandular hairs. **Stems** erect to ascending-erect, (6–)15–65(–80) cm, sometimes fistulose (up to 10 mm wide, pressed), sometimes rooting at proximal nodes. **Leaves** basal and cauline or basal absent at flowering, palmately or usually subpinnately 5–7-veined, proximal long-petiolate, blades 4–125 mm, ovate-elliptic to ovate or suborbicular, gradually or abruptly reduced in size distally, margins crenate to coarsely dentate, proximally shallowly toothed to irregularly small-lobed or lyrate-dissected, apices rounded to obtuse, bases rounded to cuneate to truncate, petioles absent or 1–95 mm. **Flowers** (1–)3–20(–28), mostly from distal nodes, sometimes in relatively compact racemes with reduced bracts. **Fruiting pedicels** 15–40(–60) mm. **Fruiting calyces** ovate-campanulate, 11–17(–20) mm, closing, nodding, usually without red markings. **Corollas** yellow, red-dotted, tube-throats infundibular, (10–)12–20 mm, exserted 3–5 mm beyond the calyx margin, limb bilabiate, expanded 12–24(–24) mm (pressed). **Styles** minutely hirsutulous to villosulous. **Herkogamous**; anther pairs at different levels, stigma above upper anther pair. **Capsules** 7–11(–12) mm, stipitate (stipes 1–1.5 mm), included. 2*n* = 28, 56.

Flowering Apr–Sep. Springs and seeps, marshes, beaver dams, along rivers, streams, and irrigation canals, loamy soil in conifer forest, wet and damp meadows, wet roadsides; 20–3200(–3700) m; British Columbia, Saskatchewan (Cypress Hills), Alberta (Cypress Hills); Alaska, Arizona, California, Colorado, Idaho, Montana, Nebraska, Nevada, Oregon, New Mexico, South Dakota, Texas, Washington, Wyoming; Mexico (Baja California, Chihuahua, Coahuila, Sonora); introduced in ne USA (Connecticut) and e Canada. Introduced in Europe (the introduction and spread of *Erythranthe guttata* in Europe is documented in detail by Tokarska-Guzik and Dajdok 2010). Map 9.

An eastern outlyer of *Erythranthe guttata*: **Nebraska**. <u>Keith Co.</u>: 2 mi W of Lemoyne, N side of Lake McConaughy, swampy springy flat along prairie creek, sandy soil, 11 Jun 1967, *Stephens 11540* (SMU). The leaf shape is suggestive of *E. geyeri* but the plants are erect and the corollas are relatively large (tubes 13–15 mm) with the stigma 2 mm above the longest anther pair.

A single collection is known from **Texas**: <u>Presidio Co.</u>: Chinati Mountains State Natural Area, Pelillos Canyon, at fork of Tinaja Prieta Canyon, riparian vegetation, in igneous gravel and bedrock, 4047 ft, 18 Sep 2004, *Lott et al. 5343* (TEX).

Even as more narrowly defined in the present study, *Erythranthe guttata* is markedly variable in morphology — particularly in stature, leaf shape, vestiture, flower size, and the distance of separation between anthers and stigma, and it ranges from subalpine and near-alpine habitats into desert situations where water is available. It seems probable that further study will distinguish distinct variants.

Sweigart and Willis (2003) found that nuclear DNA variation within populations of *Erythranthe guttata* (including *E. microphylla* in their concept) is exceptionally high compared to *E. nasuta*, where sequence similarity is high among (vs. within) populations.

Morphological variants.

Plants of *Erythranthe guttata* with extremely large corollas have been abundantly collected on the Aleutian Islands and Kokiak Island as well as in other Alaskan localities (e.g., Juneau, Amakuk, Yakutat Bay, Admiralty Island). Corolla tubes are 19–26 mm long and the limbs are expanded to 18–25 mm (pressed). The type collection by Langsdorff is one of these plants, as is the plant of *Mimulus langsdorffii* illustrated in the 1812 Botanical Magazine (Fig. 1). The plants are glabrous and relatively low in stature and perhaps represent an extreme in a continuum of variability, but patterns of variation in the species need to be investigated in detail (see further comments below under "Reported variation in ploidy level." The name *Erythranthe guttata* may prove to apply most appropriately only to Alaskan populations. Vickery et al. (1968) also observed that the tetraploid appeared to match the type of the species, based on their study of a "photograph of the De Candolle herbarium specimen of *M. guttatus*." A diploid also has been reported from the Aleutian Islands (see notes below), thus it appears that diploids and tetraploids may be sympatric in this area.

In scattered localities in California, both arid and more mesic, plants of *Erythranthe guttata* may become extremely tall (over 1 meter) with greatly expanded, fistulose stems and correspondingly large leaves (the type of *Mimulus petiolaris*, from Inyo Co., is like this) and similar plants have been collected in other states). Despite their striking appearance and a suspicion that such plants might be polyploid, their scattered and relatively common occurrence suggests that they are phenotypic variants within the morphological range of the diploid species.

In the area of El Dorado and Placer counties, California, plants of *Erythranthe guttata* are consistently relatively small and are commonly collected without rhizomes. When rhizomes do show, they are filiform. Corollas of these plants are relatively short and appear to be whitish or pale yellow with a darker palate. Further study in field and lab presumably would show whether such plants represent a distinct race.

Mimulus guttatus subsp. *haidensis* was described as "an endemic subalpine race" that occurs in and along the flanks of the Queen Charlotte Ranges on Graham Island and Moresby Island. It was distinguished on the basis of its hirtellous vestiture, but plants of similar hirtellous vestiture occur over the whole range of the species. A tetraploid chromosome number (2*n* = 56) was reported for subsp. *haidensis* from a total of five localities on Graham Island and Moresby Island (Calder & Mulligan 1968) and diploids (2*n* = 28) were documented from one locality on each of the two islands. At least one of the diploids has densely hirtellous stems, pedicels, and calyces — matching the morphology of subsp. *haidensis*: **British Columbia**. Queen Charlotte Islands, Graham Island, outskirts of Queen Charlotte City, 13 Jul 1957, *Calder et al. 22481* (MO, TEX). A duplicate of *Calder et al. 22481* (UC) has a mix of hirtellous and glandular hairs. *Calder et al. 36535* (UC) from Moresby Island has hirtellous pedicels but is otherwise completely glabrous. Without more documentation, the hypothesis that tetraploids represent a distinct morphological race in this area can be received only with low confidence.

Variation in vestiture does suggest, however, that regional differentiation has occurred within *Erythranthe guttata*. In all of Colorado, the Four Corners area, and north-central New Mexico, particularly, the vestiture of stems and calyces is consistently densely hirsute-hirtellous, without glandular hairs. Plants with similar vestiture also occur in Oregon, Washington, and British Columbia and in scattered localities elsewhere. In southern Oregon, California, and into Nevada and northwestern Arizona, vestiture is consistent in its villous-glandular nature, without eglandular hairs. Elsewhere in the geographic range the vestiture is a mix of hirsute-hirtellous (eglandular) and villous-glandular hairs. In this quick study, I have not been able to consistently correlate the pattern of vestiture with variation in other features.

The type of *Mimulus puberulus* Greene (Hinsdale Co., southern Colorado) has densely hirtellous-hirsutulous, eglandular vestiture on the stems, leaves, pedicels, and calyces and basal runners similar to the species in the rest of Colorado and northern New Mexico, but the plants produce relatively short corollas (but apparently herkogamous and allogamous) and the calyces have a relatively long upper lobe suggestive of *E. nasuta*. Plants of this region may come to be recognized as evolutionarily distinct, particularly if they should prove to be consistently tetraploid (see further comments below).

A collection similar to "*Mimulus puberulus*" also has been made from southeastern Arizona. These are small plants like those from northern New Mexico, with densely hirtellous-subvillous vestiture, but the corollas are very short and appear to be autogamous (plesiogamous) though they have an expanded limb. **Arizona**. Greenlee Co.: Hannagan Meadow area, 8900-9300 ft, 21 Jun 1962, *Schmidt 170* (ARIZ).

Lindsay and Vickery (1967) and Vickery et al. (1968) reported a chromosome count of 2*n* = 30 for a population of *Mimulus guttatus* from Cache Co., Utah ("Logan drainage," [Cache Valley,] Providence, 4500 ft, Vickery cult. 6177, UT), noting (1968, p. 213) that "the population is relatively uniform morphologically although its leaves are rounder and its calyces are blunter than is usual in *M. guttatus*. These traits suggest to us that this population may be showing the residual effects of previous introgression from *M. glabratus* var. *utahensis* Pennell." They also noted that because of pairing irregularities, the number might actually be 2*n* = 28 with a pair of B chromsomes. The voucher for the 2*n* = 30 count, however, seems better identified simply as *Erythranthe utahensis*. Claims by Vickery that hybridization and introgression also have occurred between *E. utahensis* and *E. guttata* in the Big Cottonwood and Provo drainages of Utah County are minimally and obliquely documented and need to be critically examined.

Reported variation in ploidy level.

Map 8 shows the USA localities of diploid and tetraploid chromosome numbers reported for plants identified as *Mimulus guttatus*. An account of most of the tetraploid counts is provided here.

* **Arizona** (Cochise Co.: [Huachuca Mts.,] Ramsey Canyon, 1646 m, Vickery cult. 7558, voucher not seen. Yavapai Co.: Verde Valley, 3 mi S of Camp Verde, by larger of 2 springs along the cliffs on the E edge of the river at Ward Ranch, 3010 ft, no date, *Vickery 2593*, cult. 6250, UT-2 sheets, cult. 6290, UT; Mia et al. 1964 and Vickery et al. 1968). Figure 2 in Vickery et al. shows 14 loosely paired quadrivalents.

* **New Mexico** (Grant Co.: Gila River, 4400 ft, Vickery cult. 6615, voucher not seen). The voucher for a tetraploid count of 2*n* = 56 from Catron Co. (Reserve, 5770 ft, *Vickery & Tai 7*, Vickery cult. 6613) is identified here as *Erythranthe cordata*, which otherwise is known as 2*n* = 30 from 6 separate counts. This count needs to be reassessed and is not mapped.

* **Arizona**. Mohave Co. As reported by McArthur et al. (1972): "*n* = 14, 28: Ariz., Mohave, Moccasin, 1525 m, 7555." No voucher was located at UT for this collection; see comments below for Kane Co., Utah.

* **Colorado** (La Plata Co.: Bayfield, Los Pinos River, 6750 ft, *Tai & Vickery 21*, Vickery cult. 6627, UT) and **New Mexico** (Rio Arriba Co.: Rio Chama, near bridge along Hwy 84, between river gravel bars and river-worn rocks on bars by the river, 7500 ft, *Tai & Vickery 16*, Vickery cult. 6622, UT); *Tai & Vickery 17* (cult. 6623, UT) was collected at the same locality; *Tai & Vickery 18* (cult. 6624, UT) was collected from the same vicinity, "near bridge on gravel bars, 6900 ft." The chromosome counts are from adjacent counties and this is the immedate region of plants noted above as possibly

representing an entity evolutionarily distinct from *E. guttata* (see comments above regarding *E. puberula*).

* **Colorado**. Grand Co.: Along the Rollins Pass road just above the Moffitt Tunnel, 10,000 ft, 1967, *Foreman s.n.*, McArthur cult. 7693-221 (UT). Another collection from Grand Co. is reported as diploid (2*n* = 28): Little Yellowstone Canyon, Shadow Mt. area, 14.5 mi N of Grand Lake, gravel at streamside, 9560 ft, 10 Aug 1966, *Douglas 61-488*, Vickery cult. 7139 (UT). Plants of both collections both have densely hirtellous vestiture and are very similar in other respects as well. It is not unreasonable to suppose that this is an instance of autotetraploidy, if the chromosome counts are correct.

* **Utah**. Kane Co. Two specimens at UT are vouchers for populations from which mixed diploid-tetraploid counts were obtained: Kane Co.: "Hundreds of plants growing in Sand Spring stream, [36º 51 N, 112º 46 W], 5100 ft; many very large one (up to 5 ft); cytology indicates mixed diploid-tetraploid population," 23 Jun 1969, *McArthur 25*, culture number "9554 = 7555," *n* = 14, 28. Kane Co.: "Thousands of plants growing in a ditch between lower two lakes at Three Lakes near Kanab. On a previous year I found no plants at this location, 5400 ft; cytology indicates mixed diploid-tetraploid population," 24 Jun 1969, *McArthur 26*, cult. 9555, n = 14, 28. Both voucher plants have thick-fistulose stems about 8 dm tall. These may represent instances of autotetraploidy. Sand Spring and Three Lakes are within ca. 12 kilometers of each other in Kane County. Moccasin, Arizona, in Mohave County, where diploids and tetraploids also were reported from a single population (see comments above), is near the Utah state line and only about 20 kilometers from these two Utah localities. The occurrence of these three, closely adjacent populations with variation in ploidy seems more than coincidental, or perhaps the phenomenon is more common than reported because of lack of sampling.

*** British Columbia**. Plants from the Queen Charlotte Islands apparently exist at diploid and tetraploid levels. It has been claimed that the tetraploids are morphologically distinct in having hirtellous, eglandular vestiture but they apparently are not different from some diploids in the Queen Charlotte Islands or from diploids in some other parts of the geographic range of the species. See comments above regarding *E. guttata* subsp. *haidensis*.

*** Alaska**. Vickery et al. (1968) reported a tetraploid chromosome count for a plant of *Erythranthe guttata*. from Admiralty Island (Gambier Bay, sea level to 1000 ft, Aug 1958, *Miller s.n.*, Vickery cult. 6152 (as published) or cult. 6250 (in UT). They observed bivalents frequently "paired in loose quadrivalent associations." Seed-grown plants of this individual produced hybrids in crosses with diploid plants from Contra Costa Co., California, but the F1s were sterile. Crosses of the Alaskan tetraploid with what Vickery et al. presumed was autotetraploid *E. guttata* from Arizona (Yavapai Co., *Vickery 2593*, see citation above) would not produce hybrids. Another chromosome count from Alaska has been reported as diploid, 2*n* = 28: Aleutian Islands, sea cliff on Amchitka Island, *Vickery 11452* (Vickery et al. 1981). Also diploid is "Vicinity of Juneau," *Vickery 5395*, as listed in Vickery (1978). See further comments above under "Morphological variants."

Figure 1. *Erythranthe guttata*. Illustration of *Mimulus langsdorffii* from Botanical Magazine (J. Donn ex Sims, Bot. Mag. 36: plate 1501. 1812). A large-flowered plant from Alaska, perhaps representing a tetraploid individual (see text).

12. ERYTHRANTHE GRANDIS (Greene) Nesom, Phytoneuron 2012-40: 43. 2012. *Mimulus grandis* (Greene) Heller, Muhlenbergia 1: 110. 1904. *Mimulus langsdorffii* var. *grandis* (Greene) Greene, J. Bot. (Brit. & Foreign) 33: 7: 1895. *Mimulus guttatus* var. *grandis* Greene, Man. Bot. San Francisco Bay, 277. 1894. **LECTOTYPE** (designated here): **USA**. **California**. [Solano Co.:] Rocky hills 5 mi E from Vallejo, 10 Apr 1874, *E.L. Greene s.n.* (ND-Greene! photo-PH!). No type was cited in 1894 protologue, which noted only "a conspicuous perennial of stream banks and some boggy places among the hills near the Bay."

Another collection of type material at ND-Greene is this: [Alameda Co.:] Berkeley, 20 Aug 1887, *E.L. Greene s.n.*; the label has handwritten "Mimulus grandis Greene." The label for the Solano County collection has "Mimulus ~~luteus~~ grandis" in Greene's handwriting.

Mimulus procerus Greene, Leafl. Bot. Observ. Crit. 2: 6. 1909. **TYPE**: **USA**. **California**. Monterey Co.: Santa Lucia Mountains, Jun 1898, *R.A. Plaskett 156* (holotype: ND-Greene! photo-PH!; isotypes: NY digital image!, US digital image!). Greene noted that the plant is "in every part hirtellous-puberulent."

Mimulus guttatus subsp. *litoralis* Pennell, Proc. Acad. Nat. Sci. Philadelphia 99: 165. 1947. **TYPE**: **USA**. **Oregon**. Lincoln Co.: Sea beach vic. Otter Rock, wet place, bluffs, 19 Jul 1939, *B. Maguire 17304* (holotype: PH!). Pennell noted that this is a "characteristic and magnificent plant that grows in masses along the rocky coast of Oregon and northern Cal[ifornia], where it replaces subspecies typicus."

Perennial, rhizomatous, sometimes rooting at lower nodes. **Stems, pedicels, calyces, and distal leaves** densely hirsutulous to softly hirtellous-puberulent to pilose-hirsutulous (hairs usually crinkly) and eglandular or with a mixture of hirtellous-puberulent and stipitate-glandular hairs, less commonly sparsely to densely stipitate-glandular or glandular-villous without hirtellous-puberulent vestiture. **Stems** erect, sometimes decumbent at the very base, (25–)50–120(–160) cm, usually fistulose (succulent-thickened and hollow). **Leaves**: basal and lower cauline petiolate, blades ovate to broadly elliptic, 25–60 x 20–40(–60) mm, margins crenulate to dentate, proximally sometimes sublyrate, apex rounded to obtuse, base truncate or truncate-cuneate to subcordate, petioles 10–80 mm, gradually reduced in size distally and becoming subsessile to sessile, bracteate in the inflorescence. **Flowers** 8–26, usually in bracteate racemes. **Fruiting pedicels** 10–35 mm. **Fruiting calyces** 15–22(–25) mm, 10–14 mm wide (pressed), closing, straight or nodding ca. 45º–100º. **Corollas** yellow, red-dotted within, tube-throats (14–)16–24 mm, long-exserted from calyx, limb broadly expanded. **Styles** hirtellous. **Herkogamous**; anther pairs at different levels, stigma above upper anther pair. **Capsules** 8–12 mm, stipitate, included. 2*n* = 28.

Chromosome vouchers. **California**. Monterey Co.: Pacific Grove, *Vickery 5001*, voucher for *n* = 14 (UT). San Mateo Co.: Piscadero, 30 ft, *Clausen 2083*, voucher for *n* = 14 (UT).

Flowering (Apr–)May–Jul(–Sep). Beaches, dunes, coastal bluffs, wet cliff faces, mud flats and seeps, marshes, drainage ditches, creeks, rarely in coastal sage scrub; 0–200(–800) m. California, Oregon. Map 10.

The densely puberulent vestiture of pedicels, calyces, and distal stems usually is diagnostic, especially in combination with the extra-sized flowers (corollas and mature calyces) and tall stature. Scattered collections are much shorter than normal but have large corollas and characteristic vestiture (e.g., San Mateo Co., Crystal Springs Lake, Apr 1903, *Elmer 4857* (MO); Santa Clara Co., along Cheboya Road W of Joseph Grant County Park, 6 May 1995, *Doo s.n.* (DAV). *Erythranthe grandis* characteristically occurs in coastal localities but it also is found in inland localities and habitats near the coast but well away from salt spray.

Large-flowered plants in coastal regions of Washington, British Columbia, and Alaska have a different vestiture and the corollas do not reach the size of *Erythranthe grandis* — these plants are an expression of *E. guttata*, as considered here.

Pennell (1951) placed *Mimulus grandis* in synonymy under typical *M. guttatus*.

13. ERYTHRANTHE ARENICOLA (Pennell) Nesom, Phytoneuron 2012-40: 43. 2012. *Mimulus guttatus* subsp. *arenicola* Pennell, Proc. Acad. Nat. Sci. Philadelphia 99: 166. 1947. **TYPE**: **USA**. **California**. Monterey Co.: Pacific Grove, sandy clay flat, 0–10 ft, 28 Jun 1940, *F.W. Pennell 26020* (holotype: PH!; isotypes: CAS digital image!, F digital image!, MICH digital image!, MO!, NY-2 sheets digital images!, UC!, US digital image!). Plants of the type collection are nearly glabrous except for minutely hirtellous calyces.

Annual, fibrous-rooted or slender taprooted. **Stems** 3–17 cm, erect, rarely prostrate to prostrate-ascending and rooting at the nodes (*Parish 11528*). **Stems**, leaves, calyces, and pedicels moderately glandular-villous with gland-tipped hairs or mixed hirtellous and stipitate-glandular. **Leaves** basal and cauline, basal short-petiole, cauline sessile, blades suborbicular to broadly ovate or depressed-ovate, 5–17 mm x 6–15 mm, palmately 3–5-nerved,. **Flowers** 1–6, at distal nodes. **Fruiting pedicels** 9–17 mm. **Fruiting calyces** ovoid-campanulate, 9–16 mm, closing, nodding. **Corollas** yellow, red-dotted, tube-throats infundibular, 11–20 mm, exserted 4–8 mm beyond the calyx rim, limb expanded 10–18 mm (pressed). **Styles** hirtellous. **Herkogamous**; anther pairs at different levels, stigma above the upper anther pair. **Capsules** ca. 5–12 mm, stipitate, included

Flowering Apr–Aug. Sandy beaches, especially in moist hollows among dunes, sea cliff bases, chaparral near beaches, mudstone outcrops; 0–100 m. California (Monterey, San Luis Obispo, Santa Cruz cos.). Map 11.

Pennell (1947, 1951) considered *Erythranthe arenicola* an endemic of Monterey County, but plants from adjacent San Luis Obispo and Santa Cruz counties also belong here. In addition to the Monterey Co. specimen (cited below), Vickery made collections of *E. guttata* and *E. grandis* at essentially the same locality. Most of the localities are at sea side but some are more than a mile inland.

California. Monterey Co.: along the coast, Monterey Peninsula, 30 Jul 1929, *Mathias 743* (MO); Monterey Peninsula, moist seeps in the dunes, Asilomar, Aug 1917, *Parish 11528* (MO); Monterey Peninsula, wet sand among dunes, 29 Aug 1957, *Thorne 18949* (UC); Pacific Grove, seep at high tide mark at the base of cliffs, in a moist pocket of rich soil, ca. 1/2 mi W of Lover's Point, 5 ft elevation, 13 Apr 1956, *Vickery 1*, cult. 5001 (UC, UT). San Luis Obispo Co.: Upper Prefumo Canyon Road, grassy area with scattered patches of chaparral, locally abundant on rock outcrop, flowers yellow with red dots, 29 Apr 1979, *Keil K13058* (TEX). Santa Cruz Co.: Plants of H-H Ranch, ca. 17 mi NW of Santa Cruz, on seasonal waterfall face in S fork of "Gulch #1," in sparse N coastal scrub, slope near vertical, 280 ft, on Santa Cruz mudstone outcrop with small pockets of soil, 800-1000 plants on waterfall face, all plants in population annual, 5 Jun 1983, *Buck 325* (JEPS); between Calif. 1 (Cabrillo Hwy) and Swanton Road, SE of Greyhound Rock and W and NW of old Seaside School (Swanton), no date or collector (JEPS).

Erythranthe arenicola is hypothesized here to be a derivative of *E. guttata* or *E. grandis*, retaining the allogamous breeding system of its putative ancestor but becoming reduced in size and duration.

14. ERYTHRANTHE THERMALIS (A. Nelson) Nesom, Phytoneuron 2012-40: 44. 2012. *Mimulus thermalis* A. Nelson, Bull. Torrey Bot. Club 27: 269. 1900. **TYPE**: **USA**. **Wyoming**. [Park Co.:] Upper Geyser Basin, on geyser formations, 3 Aug 1899, *A. Nelson* and *E. Nelson 6285* (holotype: RM photo-PH!; isotypes: MO!, NY-2 sheets digital images!).

Annual, without rhizomes or stolons, very occasionally with a basal, runner-like stem. **Stems** 1.5–10(–15) cm, erect, simple or branched from basal nodes. **Stems, pedicels, and calyces** moderately to densely stipitate-glandular to (less commonly) hirtellous and eglandular. **Leaves** basal and cauline, cauline 2–5 pairs, blades suborbicular to ovate, depressed-ovate, ovate-deltate or reniform, 4–15(–20) mm x 4–20 mm, palmately 3–5-nerved, basal and lower cauline short-petiolate, cauline subsessile to sessile, mostly 5–10 mm, margins evenly crenate-dentate to subentire, apices acute to obtuse or rounded, base cuneate to truncate or subcordate, petioles (basal and lower cauline) 3–20 mm. **Flowers** 1–5(–9), mostly at distal nodes. **Fruiting pedicels** 7–12 mm. **Fruiting calyces** ovate-campanulate 8–11 mm, closing, lobes unequal, deltate-triangular, upper longer than the others, ciliate or glabrous. **Corollas** yellow, red-dotted or apparently sometimes without red markings, tube-throats funnelform, 8–12 mm, exserted 1–2 mm beyond the calyx margin, strongly bilabiate, expanded 12–15 mm (pressed), throats open, palate villous. **Styles** hirtellous. **Plesiogamous**; anther pairs at about the same level, stigma at the level of the anthers. **Capsules** 5–6 mm, stipitate, included. $2n = 28$.

Flowering Mar–Aug. Hot, shallow, quick-drying soils around thermal pools and vents; 2200–2600 m; Wyoming (Park Co.). Not mapped.

Additional collections examined. **Wyoming**. Park Co.: Yellowstone National Park, on the "Formations" and frequent in YNP, 16 Jul 1912, *Churchill 723* (MO-2 sheets, mixed collection of *E. thermalis* and *E. guttata*); Yellowstone National Park, on volcanic soil, Jul 1930, *Demdas s.n.* (DAV); Yellowstone National Park, Firehole Lake (thermal spring), almost in water, 31 May 1958, *Hamlnechen s.n.*, voucher for $n = 14$ (UT); Yellowstone Park, Upper Geyser Basin, 24 Jul 1906, *Jepson 2531* (JEPS); Yellowstone Park, Upper Geyser Basin, on formations, 9 Sep 1887, *Kearney s.n.* (ND-Greene); Yellowstone Park, Gibbon Geyser basin, wet banks of hot streams, 10 Jun 1934, *Nelson & Nelson 1073* (MO, UC); Lower Geyser Basin, moist bank, 30 Jul 1951, *Sargent s.n.* (SMU); Firehole River, 3 mi SW of Old Faithful, West Thumb Road, growing next to hot spring, geyserite, 7800 ft, 26 Jun 1960, *Venrick 193* (MO) and *Venrick 194* (MO).

Erythranthe thermalis is recognized by its annual duration (without rhizomes), reduced stature and leaf size, and short but broad-limbed corollas with autogamous fertilization. It is endemic to Yellowstone National Park where it grows in hot, shallow, quick-drying soils around thermal pools and vents (not in thermally-influenced waters or creek edges; fide Margaret Kendrick, pers. comm.). Typical *E. guttata* (rhizomatous, allogamous) also grows in the immediately surrounding areas but apparently not in the hot soils.

After I had seen and annotated a number of these plants as *Mimulus thermalis*, the Fishman Lab website (2011) came to my attention — an informal discussion there of these thermal-soil plants appears to provide evidence supporting their treatment at specific rank. In addition to the reduced size, annual duration, and autogamy, adaptive differentiation among Yellowstone plants has produced a difference in phenology that apparently reinforces the autogamy in reducing gene flow. In the interpretation here, autogamy in these plants (as in many other examples in other genera and families) produces effective reproductive isolation, at least in the direction of outcrossing to selfing plants. A fuller assessment will be possible with eventual publication of studies conducted by the Fishman lab.

So interpreted, the Yellowstone situation is the only known example of sympatric speciation in *Erythranthe*. Evolutionary derivation of *E. thermalis* from *E. guttata* seems to be a secure hypothesis, given their morphological similarity and because the latter is the only species of sect. *Simiola* in northwestern Wyoming besides *E. tilingii* and *E. geyeri*, both of which are unlikely progenitors. Among the species of sect. *Simiola* in Wyoming, only *E. geyeri*, *E. guttata*, and *E. tilingii* have been recognized (Nelson & Hartman 1997; Dorn 2001). *Erythranthe thermalis* (as a species of *Mimulus*) has not been included even as a synonym.

A collection of *Erythranthe* aff. *guttata* from a hot springs area in Idaho is rhizomatous but the flowers are very small, outside the range of size for *E. guttata* but still allogamous, and it would be interesting to make further observations of these plants. Corolla tubes ca. 7 mm, styles 9–10 mm, the stigma exserted from the tube and beyond the anthers. **Idaho**. Blaine Co.: Ketchum and Guyer Hot Springs, margins of hot sulphur spring bogs, 5887 ft, 22 Jul 1911, *Nelson and Macbride 1278* (MO, UC).

15. ERYTHRANTHE LAGUNENSIS Nesom, **sp. nov. TYPE**: **MEXICO**. **Baja California Sur**. Arroyo San Bernardo ca. 3 km above Boca de la Sierra, near 23º 23, 109º 49, 500 m, in wet sand by stream, 19 Jan 1959, *R.V. Moran 7080* (holotype: SD; isotype: TEX).

Similar to *Erythranthe guttata* in overall habit, inflorescence, and vestiture but different in its annual duration (lacking rhizomes), stems apparently more commonly approaching decumbent, leaves broadly ovate to orbicular-ovate, and calyx lobes with denticulate margins.

Annual herbs, fibrous-rooted, without rhizomes but sometimes rooting at proximal nodes. **Stems** terete, erect to ascending-erect or decumbent-ascending, 12–40 cm. **Pedicels, calyces, distal leaves, and distal portions of stems** moderately to densely short-villous-glandular with gland-tipped hairs 0.2–1.0 mm, rarely mixed with short, sharp-pointed, eglandular hairs (hirtellous-hirsute). **Leaves** basal and cauline, basal usually largest, very gradually or very little reduced in size distally until an extended inflorescence, cauline blades mostly broadly ovate to orbicular-ovate, (7–)15–40 mm x (5–)10–35 mm, sessile or basal and proximal with petioles 2–15 mm, usually not punctate (see comments below), palmately (3–)5–7 veined, veins basal to suprabasal, margins shallowly serrate-dentate, 5–10 pairs of teeth per side, sometimes doubly toothed. **Flowers** 3–15(–26), from mid to distal nodes. **Fruiting pedicels** 7–20(–30) mm, nodding 30º–90º. **Fruiting calyces** 7–14 mm, ovoid, sometimes red-spotted, closing, lobes 5, triangular-acute, upper lobe slightly longer, upper lobe sometimes denticulate with 1–2 pairs of small teeth distally. **Corollas** yellow, red-spotted on palate and base of lower lip, tube-throats funnelform-tubular, 7–12(–14) mm, exserted 4–6(–7) mm beyond calyx margin, limbs bilabiate, 7–10 mm wide (pressed). **Styles** hirtellous with ascending hairs. **Herkogamous**; stamen pairs usually separated but stigma barely above the upper pair, sometimes apparently plesiogamous. **Capsules** 5–7 mm, stipitate, included.

Flowering Jan–Apr(–May). Along streams, arroyos, springs, oak and oak-pine woods, riparian woods, dry subtropical deciduous woods, dry washes; (200–)500–2000 m; Mexico (Baja California Sur). Map 12.

Additional collections examined. **MEXICO**. **Baja California Sur**. From San Jorge to San Francisquito and La Chuparosa, E side of Sierra de la Victoria, Arroyo Santa Rita, 23º 29-31' N, 109º 47-55' W, in granitic sand, with *Populus brandegeei*, *Quercus devia*, *Lysiloma microphylla*, and *Dodonea viscosa*, 840 m, 11 Apr 1955, *Carter & Ferris 3316* (SD); from San Jorge to San Francisquito and La Chuparosa, E side of Sierra de la Victoria, La Chuparosa, open rolling ridge tops with *Pinus edulis*, *Nolina beldingii*, *Quercus devia*, *Arbutus peninsularis*, and *Lepechinia hastata*, 1800 m, at spring, 23º 29-32' N, 109º 47-55' W, 12 Apr 1955, *Carter & Ferris 3353* (SD, TEX); Sierra de la Laguna, Camp. Palo Extrano, 23º 31' N, 109º 56' W, arroyo con agua, bosque de pino y encino, 1850 m, 15 Mar 1987, *Dominguez 440* (SD); Mpio. La Paz, Sierra de la Victoria, Paraje de Cano "El Chalete," 23º 36' N, 109º 55' W, bosque de encinos, 1670 m, 12 Feb 1997, *Dominguez L. 1758* (SD), *Dominguez L. 1759* (SD); Rancho Santo Domingo (Arroyo), 23.43532º N, 110.02034º W, 497 m, 16 Apr 2008, *Dominguez L. 4027* (SD); Sierra La Laguna, Agua El Saltito, Rancho La Burrera, 23.512268º N, 110.041275º W, selva baja caducifolia, 514 m, 30 May 2008, *Dominguez L. 4096* (SD); Sierra Laguna, La Laguna, granitic gravel of dry wash, oak-pine forest, 6000 ft, 24 Mar 1939, *Gentry 4405a* (ARIZ); Sierra La Laguna, Reserva de la Biosfera, El Saltito de La Burrera, 23.51109º N, 110.04442º W, arroyo, selva baja caducifolia, 535 m, 28 Mar 2008, *Leon de la Luz*

8073 (SD); Cape region, El Chorro, near 23º 26' N, 109º 48' W, near canyon mouth, wet sand by stream, 200 m, 30 Apr 1959, *Moran 7285* (SD); Cape region, La Laguna, 23º 33' N, 109º 58' W, 1700 m, 27 May 1965, *Sloan s.n.* (SD); Cape region, E slopes of the Sierra de la Victoria, El Reparito, W from Caduaño, along stream in moist sand, ca. 2300 ft, 8 May 1959, *Thomas 7810* (SD); southern outskirts of Miraflores, in wet sand at margin of arroyo, [23º 21' N, 109º 45' W], 8 Jan 1959, *Wiggins 14735* (ARIZ).

Most of these plants previously have been identified as *Erythranthe guttata* but the annual duration is distinctive and they are far disjunct from the nearest populations of typical *E. guttata* in Baja California (the northern state). The toothing of the calyx margins is seen elsewhere in the genus only in *E. brevinasuta*, suggesting that ancestry of these two endemics of Baja California Sur may be close.

Gentry 4403a from La Laguna is distinctive in its low, procumbent habit, hirtellous vestiture, tiny leaves, relatively small calyces and corollas, and punctate leaves, but it is regarded here as a depauperate individual of *Erythranthe lagunensis*. *Sloan s.n.*, also from La Laguna, has an ascending habit with longer stems and larger leaves and corollas, but it has hirtellous vestiture and punctate leaves. *Dominguez 4027* has minutely hirtellous calyces; *Thomas 7810* has pedicels mixed hirtellous and villous-glandular; *Moran 7080* (the type) has calyces mixed hirtellous and villous-glandular. This mirrors the variability in vestiture found in *E. guttata*.

16. ERYTHRANTHE UNIMACULATA (Pennell) Nesom, Phytoneuron 2012-40: 44. 2012. *Mimulus unimaculatus* Pennell, Notul. Nat. Acad. Nat. Sci. Philadelphia 43: 5. 1940. **TYPE**: **USA**. **Arizona**. [Gila Co.:] Sierra Ancha, rim of Pueblo Canyon, 13 May 1931, *G.J. Harrison 7892* (holotype: PH!; isotype: ARIZ!).

Annual, shallowly fibrous-rooted or slender taprooted. **Stems** erect or basally ascending-erect, sometimes rooting at proximal nodes, (2–, 8–)10–30(–50, –100) cm, terete, becoming fistulose in larger plants, stems and pedicels delicately short glandular-villous to stipitate-glandular, often glabrous below the inflorescence. **Leaves** mostly cauline or basal sometimes persistent, proximal short-petiolate, sessile above, connate-perfoliate distally, blades ovate-lanceolate to ovate or broadly ovate-elliptic, midcauline 12–40(–50) x 10–25(–45) mm, proximal sometimes subpinnately nerved, usually with (1–)2 pairs arising from the midvein above the blade base, becoming palmately nerved distally, vestiture a mix of 3 kinds of hairs: sharp-pointed hirtellous, vitreous-flattened, and gland-tipped, margins shallowly dentate-serrate to serrate with 7–12 teeth per side, apex rounded to obtuse, base rounded to truncate or cuneate, petioles 4–10(–15) mm, reduced and bractlike in the inflorescence. **Flowers** (1–)3–14, mostly from midstem and above. **Fruiting pedicels** 10–40 mm, straight. **Fruiting calyces** broadly campanulate, 9–13(–15) mm, closing, nodding 30º–90º, sparsely glandular-villous to stipitate-glandular, lobes triangular-ovate to broadly triangular, upper distinctly longest. **Corollas** pale yellow to nearly white, palate and lower throat densely and dark yellow, drying blue-green, red-spotted, tube-throats funnelform to subinfundibular, (7–)9–14 mm, exserted 3–4 mm beyond the calyx margin, limbs bilabiate, broadly expanded (8–17 mm pressed), palate densely bearded. **Styles** hirtellous. **Herkogamous**; anther pairs at different levels, stigma above upper anther pair. **Capsules** 5–8 mm, stipitate, included. 2n = 28.

Flowering Jan–Jun. Stream and canal sides, pool edges, canyon bottoms, sand, gravel, and mud, tropical deciduous, riparian, and pine-oak forests; 200–2000 m. Arizona (Cochise, Gila, Pima, Santa Cruz cos.), New Mexico (Dona Ana Co.); Mexico (Chihuahua, Sonora). Map 13.

Erythranthe unimaculata is recognized by its annual duration (fibrous-rooted, without stolons or rhizomes), delicate-glandular vestiture, mostly sessile to subsessile, often widely spaced leaves,

Figure 2. *Erythranthe unimaculata*, isotype ARIZ

closed fruiting calyces, and relatively large, pale yellow to nearly white corollas with a dark yellow palate that dries blue-green (Fig. 3). The breeding system is allogamous. The plants commonly are single-stemmed but sometimes produce decumbent-ascending stems branching from the very base of the plant, these sometimes rooting at proximal nodes (e.g., *Pringle 889*, *Palmer 16* and *17*, *Ward & Soreng 82-008*; Vickery's greenhouse cultures of *Gentry 8078* from Chihuahua). Plants of *Blumer 3433a* from the Rincon Mts. are unusually small (1.5-3 cm tall, with 1-2 flowers). Without the basal parts, plants of *E. unimaculata* sometimes may be difficult to distinguish from *E. guttata*.

Figure 3. Flowers of *Erythranthe unimaculata*, from the ARIZ isotype

Additional collections examined. **USA**. **Arizona**. Cochise Co.: **Chiricahua Mts.**: S. Fork of Cave Creek Canyon, 5300 ft, 31 Mar 1962, *Barr 62-185* (ARIZ); *Blumer 162* (ARIZ); Price Canyon, cold springs, 22 Jul 1907, *Goodding 2299* (MO); Cave Creek Recreation Park, in running water, 5000 ft, 18-19 Jun 1930, *Goodman & Hitchcock 1224* (MO); marginal aquatic in Cave Creek, South Fork Road, 0.5 mi from jct of Road 42 and S. Fork Road, 5200 ft, 20 Apr 1989, *Holloway & Cowley 41* (MO); Cave Creek area, 3500 ft, 1 Apr 1941, *Kimball s.n.* (ARIZ); 1 mi below Rustler Park cattle guard, near water, 7900 ft, 7 Jun 1960, *McCormick 116* (ARIZ); Cave Creek Canyon, stream bed, 31 May 1929, *Peebles & Loomis 5860* (ARIZ); Rucker Canyon, along stream near upper road crossing, ca. 6300 ft, 8 Jun 1980, *Toolin 793* (ARIZ). **Dragoon Mts.**: West Cochise Stronghold, drainage among high boulders, 22 Apr 1962, *Goodding 60-63* (ARIZ). **Huachuca Mts**.: roadside in Scotia Canyon, wet soil by stream, 5900 ft, 2 Jun 1991, *Bowers 3503* (ARIZ); Miller Canyon, along old trail in canyon bottom in pine-oak forest, 7300 ft, 30 May 1992, *Fishbein 372* (ARIZ); along stream, May 1912, *Goodding 1321* (ARIZ); Ft. Huachuca Military Reservation, head of Garden Canyon, along shallow soil water courses, 13 May 1958, *Goodding 116-58* (ARIZ); canyon above Sunnyside, near edge of charco, 13 May 1958, *Goodding 132-58* (ARIZ). Gila Co.: **Sierra Ancha Wilderness Area, Tonto Natl. Forest**: Hunt Spring, at top of Devils' Chasm, off trail 140 ca. 1.5 mi from trailhead, 6500 ft, 13 Jun 1992, *Imdorf 800* (ARIZ); along Trail 139 at Trailside Spring, moist soil, with *Juglans major*, *Vitis arizonica*, *Rhus radicans*, and mixed conifer forest upland, 6800 ft, 22 May 1993, *Imdorf 1243* (ARIZ). Pima Co.: **Baboquivari Mts.**: Brown Canyon, E slope of the Buenos Aires National Wildlife Refuge, *Platanus racemosa-Celtis reticulata* riparian forest in canyon bottom in oak woodland-desert grassland transition, ca. 1220 m, common annual in water in streambed, 6 May 1999, *Reina G. 99-101* et al. (UT). **Rincon Mts.**: Manning Camp, springy soils on rocks, 1 Oct 1909, *Blumer 3433a* (UC). **Santa Catalina Mts.**: Upper Sabino Creek, 1 mi W of Summerhorn, ca. 8000 ft, 27 Jun 1960, *Barr 60-70* (ARIZ); Molino Creek, along creek bank in shade, 10 Apr 1985, *Bennett 8744* (ARIZ); ca. 5 mi N of Mt. Lemmon lodge, dirt road above Peppersauce, seeping sandy bank, small spring, 7 Jul 1967, *Crutchfield 3323* (LL); Mt. Lemmon Road, 7000 ft, 6 May 1925, *Nichol s.n.* (ARIZ); Mt. Lemmon, 30 May 1927, *Peebles 4081* (ARIZ); Jun 1907, *Thornber & Lloyd 4334* (ARIZ); Sabino Canyon, 1 Apr 1894, *Toumey 103* (UC); Sabino Canyon, 3 Apr 1894, *Toumey 104* (UC). Santa Cruz Co.: Tumacacori Natl. Historic Park/Guevavi Unit, semi-desert grassland, dry benches E off Santa Cruz River, ca. 3400 ft, 20 Mar 2001, *Guertin 142* (ARIZ); Cottonwood Canyon SW of the Santa Rita Mts., moist soil below dam, 16 Mar 1975, *Kaiser 550* (ARIZ); White House Canyon, along streams, 5200 ft, 22 Apr 1917, *Shreve 5176* (ARIZ); Santa Rita Mts., Cave Creek Canyon, streambed, 6200-6800 ft, 3-4 May 1975, *Van Devender s.n.* (ARIZ). **New Mexico**. Dona Ana Co.: W base of Organ Mts., Dripping Springs Canyon, 11 mi E of northern Las Cruces, slow-moving water of a constantly moist, N-facing depression of an unbroken quartz monzonite outcrop, with *Preissia*, *Aquilegia chrysantha*, and mosses, 6000 ft, 25 Apr 1982, *Ward & Soreng 82-008*, voucher for $2n = 28$ (MO); Organ Mts., 16 Apr 1893, *Wooton s.n.* (MO). **MEXICO**. **Chihuahua**. Sierra Charuco, Arroyo Hondo, igneous rocky canyon slope in pine-oak forest, riparian, 4500-5500 ft, 16-30 Apr 1948, *Gentry 7995* (ARIZ) and *8078* (ARIZ); Sierra Charuco, *Gentry 8078* [Vickery greenhouse cults. 5322, 5323, 28 Jan 1950] (UT); Ricardo Flores Magón, side of isolated pool in sandy soil, 21 Jun 1964, *Miller M64-9* (UT); 14 mi S of Nueva Casa Grandes, wet sand and gravel by Rio Casas Grandes, 21 Jun 1964, *Miller M64-10* (UT); vicinity of Chihuahua, ca. 1300 m, 8-27 Apr 1908, *Palmer 16* (MO) and *Palmer 17* (MO); river gravel, Chihuahua, 14 Apr 1886, *Pringle 889* (MO); Mpio. Ocampo, Parque Nac. Cascada Basaseachic, in the box canyon at the base of the fall, ca. 1700 m, 26 Apr 1985, *Spellenberg et al. 8021* (NMC); Mpio. Ocampo, Parque Nac. Cascada Basaseachic, in the barranca at the base of the falls, wet clayey soil near base of falls, 1570 m, 25 Apr 1987, *Spellenberg et al. 9054* (NMC); Mpio. Ocampo, Parque Nac. Cascada Basaseachic, moist sandy soil along river between top of falls and campground area, 2000 m, 17 Jun 1993, *Spellenberg et al. 11862* (NMC); Mpio. Ocampo, S-facing igneous cliff with waterfall in pine and oak woods, in most grass on cliff, 2190 m, 17 Jun 1993, *Spellenberg et al. 11905* (NMC); near Colonia Garcia in the Sierra Madres, 7500 ft, 9 Jun 1899, *Townsend & Barber 28* (MO); Mpio. Ocampo, Cascada de Basaseachic, Rio Basaseachic, pine-oak forest, 1800 m, very common herb in water in stream, flrs yellow, 4 Jun 1999, *Van Devender 99-219* et al. (NMC, UT); 2 blocks N of the plaza in old Casas Grandes, 4800 ft, 29 Apr 1976, *Vickery greenhouse cult. 12,181* (UT); willow-shaded stream near Janos, KM 196 on Mexico Rte 2, between Janos and La Ascension, 4250 ft, 29 Apr 1976, *Vickery 2863* (UT); KM 92, Mexico 28 at Fcoindera bus stop, in drying sandy areas of stream in partial shade, 10 Jun 1976, *Vickery 2917* (UT); Colonia Pacheco, S part of town, "Townsite Pasture," at the Marion Wilson Ranch and adjoining pastures, gravelly, grussy, and sandy soil derived from extrusive igneous rock, creekS and a river, 2000 m, 1-2 Aug 1972, *Wilson et al. 8579* (ARIZ). **Sonora**. 37 mi NE of Cajeme, on road to Tesopaco, 4 Mar 1933, *Mallery 18* (ARIZ); Mpio. Yecora, Arroyo Los Garambullos, 0.5 km SE of Tonichi, 180 m, uncommon annual in mud at edge of river, flrs white, 30 May 1999, *Reina G. 99-114* et al. (UT); Arroyo El Pilladito, near Tepoca, stream canyon in tropical deciduous forest, 500 m, very common annual in moist soil along canal, "possibly small plants of larger *M. guttatus* types," 2 Apr 2000, *Reina G. 2000-198* et al. [Vickery greenhouse cult. no. 14356] (UT); 13 mi (by road) N of Arizpe, 31 Mar 1959, *Turner 59-51* (ARIZ); Cienega ca. 1 mi E of

Rancho Agua Fria on Rio Saracachi (E of Cucurpe), 9 Apr 1977, *Van Devender s.n.* (ARIZ); upper end of bend in Rio Cuchujaqui at Rancho El Conejo, 12.4 km (by air) S of Alamos, 240 m, uncommon annual under *Taxodium* in moist soil at edge of river, 7 May 1992, *Van Devender 92-581* (ARIZ); below village of Guajaray on Arroyo Guajaray, 6.5 km (by air) NNW of jct with Rio Mayo, tropical deciduous forest in rocky stream canyon, 270 m, scattered in cobbles near arroyo, 18 Mar 1993, *Van Devender 93-450* (ARIZ-2 sheets); Rio Cuchujaqui at El Paso, 150 m, uncommon annual on bank of river, 25 Feb 1995, *Van Devender 95-92* (ARIZ); Arroyo Los Huerigos (tributary of Arroyo San Nicolas) at Mexico 16, 9.3 km E of Tepoca, 3.5 km WNW (by air) of San Nicolas, *Populus brandegei* riparian gallery forest, 650 m, very common annual at edge of stream, 9 Mar 1996, *Van Devender 96-53* (ARIZ); 1.5 km SW of Santa Ana on road to Guadalupe Tayopa, rocky canyon with *Populus brandegei*, tropical deciduous forest on slopes, 775 m, common annual in moist gravel along stream, 21 Feb 1997, *Van Devender 97-210* (TEX); Arroyo Los Huerigos (= A. El Moro, A. San Nicolas), 9.3 km E of Tepoca on Mex 16, 3.5 km (by air) WNW of San Nicolas, *Populus monticola* riparian gallery forest, 650 m, locally common annual in mud at edge of stream, 13 Apr 1999, *Van Devender 99-73* (UT) and *Van Devender 99-78* (UT); Arroyo Tepoca, ca. 1.7 km (by air) NW of Curea, 420 m, locally very common annual in moist soil along stream, 31 May 1999, *Van Devender 99-139* et al. (UT); along Rio Yecora, ca. 1 km (by air) NW of Yecora, 1530 m, solitary herb in moist soil at edge of stream, 2 Jun 1999, *Van Devender 99-186* et al. (UT). Mpio. Onavas, Arroyo de la Uvalamita, Rancho La Mula, 25.5 km SE of Rio Yaqui on Mex. 16, palm-*Bursera* canyon in tropical deciduous forest, 685 m, locally common annual in water at canyon bottom, 1 Apr 2000, *Van Devender 2000-187* et al. (UT); Mpio. de Imuris, 5 km N of Mesa del Romero, 19 km N of Imuris on Mex. 15, Arroyo, Bambuto drainage, cottonwood-willow forest, 980 m, 25 May 2009, *Van Devender 2009-246* (NMC).

17. ERYTHRANTHE DECORA (A.L. Grant) Nesom, Phytoneuron 2012-40: 43. 2012. *Mimulus decorus* (A.L. Grant) Suksdorf, Werdenda 1: 37. 1927. *Mimulus guttatus* var. *decorus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 173. 1924. **TYPE**: **USA**. **Oregon**. [Clackamas Co.:] Vicinity of Oregon City, wet meadow, 11 Jun 1905, *M.W. Lyon, Jr. 59* (holotype: MO! digital image! photo-PH!; isotypes: CAS digital image!, NY digital image!, US digital image!).

Perennial, rhizomatous (perhaps prolifically so), sometimes producing numerous, long, remotely leafy runners from basal cauline nodes; distal stems, pedicels, calyces, and both leaf surfaces densely and minutely hirtellous (or leaf surfaces sometimes glabrate), pedicel vestiture often slightly deflexed. **Stems** erect, 20–100 cm, simple. **Leaves** cauline, basal mostly absent by flowering, all except distalmost petiolate, blades broadly ovate-triangular to ovate-lanceolate, 20–50(–60) x 10–30(–40) mm, palmately (3–)5–7-veined, apices acute, bases rounded to truncate to shallowly cuneate, petioles 8–25 mm (proximal) to 3–5 mm (distal). **Flowers** (1–)2–7(–14), from distal nodes. **Fruiting pedicels** 18–35(–40) mm. **Fruiting calyces** ovoid, 15–19 mm, green or sometimes red-spotted, closing, lobes deltate to shallowly ovate, apiculate, 1–3 mm, sinuses villous. **Corollas** yellow to chrome yellow, usually red-spotted on floor of throat and tube, tube-throats broadly funnelform-infundibular, 18–26 mm, exserted (8–)10–15 mm beyond calyx margin, limb bilabiate,expanded 22–30 mm (pressed). **Styles** minutely and prominently hirsutulous to villosulous with ascending to spreading hairs. **Herkogamous**; anther pairs at different levels, stigma above upper anther pair. **Capsules** 8–10 mm, stipitate, included.

Flowering May–Aug. River banks, stream sides, dripping banks, moist meadows; 1000–1600 m. Idaho, Oregon, Washington. Map 14.

Erythranthe decora is distinct in its uniformly ovate to ovate-lanceolate leaf blades with truncate bases and regularly toothed margins, relatively long internodes, rhizomatous habit, mostly unbranched stems, often with with leafy runners from basal nodes, large corollas, hairy styles, and minutely hirtellous stems, pedicels, calyces, and leaf surfaces. The thin, densely produced rhizomes suggest a relationship with the *E. tilingii* group.

Plants of a collection from Idaho appear to be widely disjunct but they are a good match for those of *Erythranthe decora* in Washington. **Idaho**. Clearwater Co.: Morris Creek drainage, near headwaters of Morris Creek and Old Growth Cedar Grove, along FR 1969d, 0.5 mi from jct of FR 1969, ca. 1.3 air mi N of Shattuck Butte, 12.2 mi NNE of Elk River by road, riparian area along Morris Creek dominated by *Carex* sp., *Phalaris arundinacea*, and *Alnus* sp., 4300 ft, plants occasional along wet stream banks, 21 Jul 1996, *Richardson 478* (UC).

Two collections are mapped (Map 14) from citations by Grant (1924): **Oregon**. Multnomah Co.: Portland, along a mountain stream, 3 Jul 1903, *Lunnell s.n.* (RM); [Linn Co.:] Calapooya Valley, swampy ground, 3500 ft, 17 Jul 1899, *Barber s.n.* (RM).

18. ERYTHRANTHE SCOULERI (W.J. Hooker) Nesom, Phytoneuron 2012-40: 44. 2012. *Mimulus scouleri* W.J. Hooker, Fl. Bor.-Amer. 2: 100. 1838. *Mimulus guttatus* subsp. *scouleri* (W.J. Hooker) Pennell, Proc. Acad. Nat. Sci. Philadelphia 99: 166. 1947. **TYPE**: **USA**. **Oregon**. Columbia River, no date, *Dr. Scouler s.n.* (holotype: K, apparently seen by Pennell, photo-PH!). The photo at PH is of a plant collected by Douglas in 1825. The protologue noted that "There are no flowers to these specimens ..." and provided only a brief description: "glaberrimus, caule erecto basi ramoso, foliis petiolatis lanceolatis dentatis 5-nerviis floralibus brevioribus subovatis, pedunculis folio brevioribus, calycibus demum inflatis."

Perennial (presumably rhizomatous, full base not seen), completely glabrous throughout. **Stems** erect, 15–80 cm, simple, producing long, sparsely leafy runners from basal nodes. **Leaves** cauline, basal mostly absent at flowering, blades (basal to medial) oblong-elliptic to oblong-lanceolate, 25–60 mm x 8–18 mm, palmately (3–)5–7 veined to subpinnate, margins evenly and very shallowly dentate or crenate to mucronate or mucronulate with 10–20 teeth per side, sometimes more deeply toothed at the very base, proximal and medial petiolate with bases attenuate to a petiolar region 10–25 mm, distal sessile. **Fruiting pedicels** 20–25 mm. **Fruiting calyces** 13–14 mm, closing, lobes deltate-acuminate, subequal. **Corollas** yellow, apparently without red markings, tube-throats infundibular, 20–24 mm, exserted ca. 10–15 mm beyond calyx margin, limb bilabiate,expanded 22–30 mm (pressed). **Styles** minutely and prominently hirsutulous to villosulous with ascending to spreading hairs. **Herkogamous**; anther pairs at different levels, stigma above upper anther pair. **Capsules** not seen.

Flowering May–Aug. Seeps, river and creek banks; ca. 1000 m. Oregon. (John Day River, a tributary of the Columbia River, in Clatsop, Grant, Wheeler, Sherman, and Gilliam cos.). Map 14.

Additional collections examined. **Oregon**. [Clatsop Co.:] S shore of Columbia River, above Astoria, 1883, *Meehan 15739* (MO); John Day, 20 Aug 1902, *Sheldon 10181* (UC); John Day, near Tongue Point, 20 Aug 1902, *Sheldon 11136* (MO).

Erythranthe scouleri is distinctive in its oblong-elliptic leaves with long-tapering bases and closely toothed margins, completely glabrous vestiture, long, leafy runners from basal cauline nodes, large corollas with broad limbs, and prominently hairy styles. Several features of the species are interpreted here as suggestive of a close relationship to *E. decora*, particularly its very large corollas, hairy styles, closely toothed leaf margins, tall, simple, and erect stems, numerous runners, and its geographic range.

Erythranthe scouleri was treated as a distinct species by Howell, (Fl. N.W. Amer. 5: 520. 1901) and by Pennell (1951), but it was subsequently recognized as a synonym or infraspecific entity within *Mimulus guttatus* — or sometimes not recognized even as a synonym. Pennell (1947, p. 166) noted this: "We need to know whether the narrow-leaved *Mimulus scouleri* Hook., from along the Columbia River, be actually a local subspecies of *M. guttatus*, or if it pertain to abnormally narrow-leaved individual plants. The Academy's herbarium shows specimens resembling Scouler's type from near Astoria in Clatsop County, Oregon, where they were gathered by Thomas Meehan in 1883, not far from Scouler's locality of a half century earlier; and from the John Day valley farther east in Oregon, gathered by E.P. Sheldon in 1902 (his number 10181)."

Erythranthe scouleri is not represented among Oregon's formally listed RTE species (Oregon Biodiversity Information Center 2010), but perhaps this is at least in part because of the current encompassing concept of *E. guttata*.

19. ERYTHRANTHE MICROPHYLLA (Benth.) Nesom, Phytoneuron 2012-40: 44. 2012. *Mimulus microphyllus* Benth., Prodr. (DC.) 10: 371. 1846. *Mimulus langsdorffii* var. *microphyllus* (Benth.) A. Nels. & Macbride, Bot. Gaz. 61: 44. 1916. *Mimulus guttatus* var. *microphyllus* (Benth.) Pennell ex Peck, Man. Pl. Oregon, 654. 1941. **TYPE**: **USA**. **Washington**. [Wahkiakum Co.:] "In rupibus ad flum. Oregon, (Douglas!)" (holotype: K). Pennell (1951, p. 710) noted that the locality visited by Douglas is "Tongue Point, in the present Wahkiakum County, Washington." Treated as a distinct species by Pennell (1951), who noted that its range is "Cascade Mountains and coastal forests from northern Washington to northern California, east to central Idaho."

Mimulus luteus var. *depauperatus* A. Gray, Geol. Surv. Calif., Botany 1: 567. 1876. *Mimulus guttatus* var. *depauperatus* (A. Gray) A.L. Grant, Ann. Missouri Bot. Gard. 11: 170. 1924. **TYPE**: **USA**. **California**. [Mendocino Co.:] banks of Navarro River, under moist rocks, [Apr] 1865, *H.N. Bolander 4516* (GH photo-PH!). In the protologue synonymy Gray cited *M. microphyllus* and "*M. tenellus*, Nutt. herb., not of Bunge" and some have interpreted *M. microphyllus* and var. *depauperatus* as homotypic (e.g., Holmgren 1984). In the Synoptical Flora, Gray noted (p. 448) that this is "an extreme depauperate form, either seedling or showing the creeping stolons; ... Grows with the larger forms on Columbia River; specimens exactly like those of Douglas from the same district (except that some show the stoloniferous base) were received from Mrs. Barrett." Gray may have included *M. longulus*, with extremely reduced corollas, in his concept of var. *depauperatus*, but the GH type appears to show the larger corollas of *M. microphyllus*.

Mimulus tenellus Nutt. ex A. Gray [in synonymy under *M. luteus* var. *depauperatus*], Geol. Surv. Calif., Botany 1: 567. 1876; Proc. Amer. Acad. Arts 11: 98. 1876 [not *M. tenellus* Bunge, Enum. Pl. Chin. Bor. 49. 1833].

Mimulus laxus Pennell ex Peck, Man. Pl. Oregon, 655. 1941. **TYPE**: **USA**. **Oregon**. Deschutes Co.: Elk Lake, gravelly shore, 27 Jul 1931, *F.W. Pennell 15547* (holotype: PH!; isotypes; CAS digital image!, F digital image!, MO!, NY digital image!, UC!, US digital image!).

Mimulus glareosus Greene, Pittonia 1: 282. 1889. **TYPE**: **USA**. **California**. Lake Co.: Gravelly margins of moutain streams, 30 Aug 1888, *E.L. Greene s.n.* (holotype: ND-Greene! photo-PH!; isotype: UC). The protologue noted "Most related to *M. laciniatus* of the Sierra Nevada; the calyx like that of *M. nasutus*."

Mimulus guttatus var. *insignis* Greene, Man. Bot. San Francisco Bay, 277. 1894. *Mimulus langsdorffii* var. *insignis* (Greene) Greene, J. Bot. (Brit. & Foreign) 33: 7. 1895. *Mimulus nasutus* var. *insignis* (Greene) A.L. Grant, Ann. Missouri Bot. Gard. 11: 181. 1924. **LECTOTYPE**(designated here): **USA**. **California**. [Napa Co.:] Napa River Basin, low meadows near La Lomita, 26 Apr 1893, *W.L. Jepson s.n.* (ND-Greene 46297!; isolectotype: ND-Greene!; probable isolectotypes: JEPS, UC-3 sheets). The ND-Greene label has handwritten by Greene "Mimulus guttatus D.C. var. insignis Greene."

The protologue noted only "of Napa and Sonoma counties, and the most beautiful *Mimulus* in our flora." Besides the collection designated here as lectotype, other collections from Sonoma County are at ND-Greene and identified as var. *insignis*. The JEPS collection has been referred to as the holotype, as the label (apparently written by Jepson) notes that it is "The very type": La Lomita, near Yountville, 26 Apr 1893, *W.L. Jepson 8m* (JEPS!; duplicates: UC-3 sheets!).

Mimulus nasutus var. *insignis* was inadvertently and incorrectly referred to as "var. *eximius* (Greene) Grant" by J.T. Howell (Marin Fl., 242. 1949).

Mimulus langsdorffii var. *californicus* Jepson, Fl. W. Mid. Calif., 407. 1901. **TYPE**: **USA**. **California**. [Solano Co.:] Vacaville, 20 Mar 1901, *W.L. Jepson 1198a* (holotype: JEPS digital image! photo-PH!). An annotation by Thomas Robbins in 1953 notes this: "The original description states only that this variety is 'Common in the Sacramento and Coast Range Valleys. Apr-May.' This collection is cited as the type ... by Jepson in Fl. Calif. ined. ms." As described by Pennell (1951): "[blade base] rounded or cordate to petiole (often obscured by extra lobules on petiole)."

Mimulus platycalyx Pennell, Proc. Acad. Nat. Sci. Philadelphia 99: 167. 1947. **TYPE**: **USA**. **California**. Mariposa Co.: Yosemite National Park, 1 mi. S of Wawona, mossy soil over granitic rock, 4500 ft, 28 May 1940, *F.W. Pennell 25580* (holotype: PH!; isotypes: CAS digital image!, NY digital image!, UC, US digital image!). On the holotype, some plants have a hirtellous vestiture of stiff, sharp-pointed hairs mixed with a few gland-tipped hairs; others have calyces and pedicels moderately villous with loose, gland-tipped hairs. Otherwise, they are similar in morphology and all would appear to be from the same population.

Annual, fibrous-rooted. **Distal stems and pedicels** hirtellous (hairs commonly deflexed) or mixed hirtellous and stipitate-glandular, sometimes only short villous-glandular with gland-tipped hairs, stems commonly completely glabrous below the inflorescence. **Stems** erect, (3–)5–30(–45) cm, usually simple, sometimes with numerous branches from basal cauline nodes, sometimes distinctly 4-angled. **Leaves** usually basal and cauline or basal sometimes absent at flowering, basal or proximal to medial petiolate, becoming sessile distally, blades ovate or ovate-lanceolate to elliptic-ovate, suborbicular, or depresssed-ovate, (3–)10–35 mm x 3–25 mm, palmately 3–5-veined, often purplish, glabrous to sparsely or moderately hirtellous, eglandular, margins shallowly crenate to sharply crenate-serrate, with 5–10 teeth per side, basal and proximal often irregularly incised near the petiole and sublyrate, apices acute to obtuse-rounded, bases rounded to truncate or subcordate, petioles 3–25(–35) mm. **Flowers** 1–8(–14), mostly from distal nodes. **Fruiting pedicels** 8–30(–50) mm. **Fruiting calyces** ovoid-campanulate to broadly cylindric-campanulate, (7–)9–16(–20) mm, strongly to weakly closing, nodding 30º–90º, sometimes red-tinged or red-dotted, minutely hirtellous, hairs sometimes reduced to the basal cells or altogether absent and the calyx glabrous. **Corollas** yellow to golden-yellow or orangish-yellow, commonly red-spotted, sometimes with a large red blotch on the lower lip (Napa and Sonoma counties), tube-throats broadly funnelform to infundibular, (6–)8–16(–20) mm, exserted (1–)2–6(–8) mm beyond the calyx margin, limb bilabiate, expanded 8–25 mm (pressed), palate villous. **Styles** sparsely hirtellous. **Herkogamous**; anther pairs at different levels, stigma above upper anther pair. **Capsules** 6–9(–11) mm, stipitate, included. $2n = 28, 56$.

Flowering Mar–Jul. Rock depressions, rocky ridges, cliff faces, road cuts, wet meadows, seeps, stream banks, drying ponds and ephemeral stream channels, vernal springs over serpentine, roadsides and roadside ditches, dry banks, lava soil, loam, clay, gravel, yellow pine, oak-pine, mixed oak, oak-chaparral; 20–1700(–2200, –2600) m; California, Idaho, Nevada, Oregon, Washington; British Columbia. Map 17.

A tetraploid population identified as *Erythranthe microphylla* was discovered in San Luis Obispo Co., California (Lowry et al. 2008). Upon finding that plants of the SLO population (identified in the study as the "inland annual race of *Mimulus guttatus*") had more than two alleles at multiple loci, an analysis with flow cytometry revealed the tetraploidy.

A report of 2*n* = 15 for this species (Vickery et al. 1968, as *Mimulus platycalyx*, from San Mateo Co., California) is regarded here as 2*n* = 14, as the authors originally surmised might be the case. Vickery (1974, p. 69) noted that "the 15th pair of chromosomes [may be] B chromosomes. Actually the present crossing results strengthen that hypothesis considerably" and in that publication (p. 43), he reported the number as "n = 14 + 1 B chromosome."

Erythranthe microphylla is characterized by its annual duration (fibrous-rooted), usually simple stems, relatively widely spaced leaves, glabrous to hirtellous vestiture, open corollas, and calyces closing at the throat. Even in the smallest corollas, the stigma is positioned above the upper anther pair, indicating that all are primarily allogamous. Some plants have basal and lower cauline leaves with exaggeratedly and irregularly toothed-incised margins, especially in Lake and Napa counties (whence the types of *Mimulus glareosus* and *M. guttatus* var. *insignis*, respectively), but a similar tendency can be seen over most of the geographic range.

Plants of *Erythranthe microphylla* vary greatly in height, leaf size, and flower size (the larger flowers approaching the size of those in *E. grandis* and *E. decora*) yet all seem to be within the expression of a single species. Some collections have been made to show this striking range of size within a population, multiple collections from a single county or general locality show the wide variability, and an observant collector made this label observation "Flowers varying in size and number with the vigor of the plant" (Coos Co., Oregon, *Cronquist 6853*, MO). Plants of the Sierra Nevada, mostly south of El Dorado County, commonly are in the smaller size range and are those identified by Pennell as *Mimulus platycalyx*. The type of *Mimulus microphyllus* also was described from smaller plants.

Problems in identification can be encountered when small plants of *Erythranthe microphylla* and *E. guttata* are collected without the base. Without a clear indication that rhizomes are part of the plant, small individuals of *E. guttata* can be very similar to *E. microphylla* but the latter contrasts in its 4-angled stems, different branching pattern (see Baker and Diggle 2011, who studied *E. microphylla* and *E. grandis*), pedicels glabrous or sometimes sparsely glandular, never hirtellous, and corollas often more golden yellow (with slightly added orange).

20. ERYTHRANTHE MARMORATA (Greene) Nesom, Phytoneuron 2012-40: 44. 2012. *Mimulus marmoratus* Greene, Erythea 3: 73. 1895. **LECTOTYPE** (designated here): **USA**. **California**. Stanislaus Co.: Knight's Ferry, [moist rocks,] 9 Apr 1895, *F.W. Bancroft s.n.* (ND-Greene 046328!, photo-PH!, photo UT!; isolectotype: ND-Greene 046329!). Fig. 4 (lectotype).

Mimulus whipplei A.L. Grant, Ann. Missouri Bot. Gard. 11: 184. 1924. **TYPE**: **USA**. **California**. [Calaveras Co.:] Hillsides and rocky places, Murphy's, 14 May 1854, *J.M. Bigelow s.n.* (holotype: GH digital image!, photo-PH!; isotype: US digital image!). Fig. 3 (holotype and isotype).

Annual, taprooted; stems, pedicels, leaves, and calyces commonly densely villous-glandular, sometimes less densely so. **Stems** erect, 7–28 cm, unbranched or branched from the base. **Leaves** mostly cauline or the basal persistent, blades ovate or broadly ovate to elliptic-ovate or depressed-ovate, (10–)15–30 mm x 6–15 mm, palmately (3–)5-veined, margins shallowly to coarsely dentate, apices acute, bases truncate to shallowly cuneate, proximal to medial petiolate, petioles 7–15 mm. **Flowers** axillary from middle to distal nodes. **Fruiting pedicels** 15–45 mm. **Fruiting calyces** broadly campanulate, 9–12 mm, sharply nodding, often densely purple-spotted, densely hirtellous or less commonly to sparsely stipitate-glandular, densely villous at the sinuses, closed, teeth broadly triangular-acute, unequal, the upper scarcely twice the length of the others. **Corollas** yellow, red-spotted in throat with a large red blotch at base of lower lip, tube-throats narrowly cylindric-funnelform, 10–12 mm, exserted 4–5 mm beyond calyx margin, limbs bilabiate, abruptly expanded 14–20 mm. **Styles** glabrous to sparsely hirtellous. **Herkogamous**; anther pairs at different levels, stigma above upper anther pair. **Capsules** 6–9 mm, stipitate, included.

Flowering Mar–May. Not known but apparently not over serpentine; ca. 100–900 m. California, Stanislaus and Calaveras cos. (Stanislaus River drainage) and Amador Co. (Mokelumne River drainage). Map 20. Figs. 3, 4, 5, and 6.

Additional collections examined. **California**. Amador Co.: Mokelumne River, 1892, *Hansen s.n.* (ND-Greene); Mokelumne River, 1892, *Hansen s.n.* (ND-Greene); Mokelumne River and immediate tributaries, Fischer's Cabin, 1200 ft, 13 May 1896, *Hansen 473* (ND-Greene).

The label for *Hansen 473* specifies "Amador and Calaveras Counties," but Hansen's 1892 and 1893 collections give only "Mokelumne River" as the locality. The Mokelumne River crosses or forms the border of five California counties: Alpine, Amador, Calaveras, San Joaquin, and Sacramento, and placement of the Amador County symbol on Map 20 assumes that all three Hansen collections were made at or near the same place.

Erythranthe marmorata is recognized by its erect, taprooted habit and annual duration, villous-glandular vestiture, ovate-petiolate leaves; flowers from middle to distal nodes, long, narrow corolla tubes abruptly flaring into a broad limb, lower middle corolla lobe with a large red blotch, and fruiting calyces dark-spotted and sharply nodding. On two of the five plants of the lectotype sheet, the lower nodes have produced adventitious roots, but this perhaps was in response to partial burial of the stem, because the other three plants, as well as the two on the isolectotype and those of the other collections (Figs. 5 and 6), have slender taproots.

The species most similar to *Erythranthe marmorata* are *E. microphylla*, *E. pardalis*, and *E. nasuta* — all three are annuals and placed here in the *E. microphylla* group (subgroups A and B). *Erythranthe pardalis* is partially sympatric with *E. marmorata* in Calaveras and Amador counties and the range of *E. marmorata* is completely within the ranges of both *E. microphylla* and *E. nasuta*. Contrasting features of *E. marmorata* with these three species are given here.

> *Erythranthe microphylla*: roots consistently fibrous; cauline vestiture usually glabrous below the inflorescence; leaves glabrous to sparsely or moderately hirtellous, eglandular; flowers commonly produced mostly from distal nodes; corolla tubes usually broadly funnelform to infundibular; lower corolla lobe without a prominent red blotch.
>
> *Erythranthe pardalis*: cauline vestiture sparsely and more delicately glandular; flowers usually produced at all nodes, including the basal; corolla tubes shorter and the flowers autogamous; lower corolla lobe without a prominent red blotch.
>
> *Erythranthe nasuta*: cauline vestiture usually glabrous except at the nodes; leaves characteristically hirtellous on one or both surfaces; flowers often chasmogamous and cleistogamous on a single plant; corollas short-tubed, barely chasmogamous to cleistogamous and the flowers autogamous; calyces with a longish, protruding upper lobe.

In the present study, a realistic concept of *Erythranthe marmorata* was not formed until after study of the type material at ND-Greene in January 2012. It seems likely that collections of *E. marmorata* may be present among the large number of specimens examined earlier at UC-JEPS, where they presumably would have been identified as *E. microphylla*. The likelihood that I identified them as either *E. nasuta* or *E. pardalis* is small.

Grant (1924) treated *Mimulus marmoratus* as a synonym of *M. guttatus* var. *arvensis*. Pennell (1951) treated it as a synonym of *M. nasutus*, apparently basing his assessment on examination of a photo at PH of the ND-Greene type. Beyond that, *M. marmoratus* has been treated variously in synonymy except, apparently, in two places.

> * The Mcnair website (The *Mimulus* Page 1996), notes that *Mimulus marmoratus* "appears to be restricted to a small area of Calaveras County, California. It is obligately annual and appears to be self-fertilising. We found it growing on the basalt and conglomerate at the top of Table Mountain, Calaveras Co, in a situation *M. guttatus* would be unable to grow." An accompanying photo shows a plant identified as *M. marmoratus* from Knight's Ferry (near Table Mountain) — an unequivocal identification is not possible from the photo but the seemingly procumbent habit, subpinnately multi-veined leaves, and the very small (see lens cap for comparative size) and relatively small-limbed corollas without prominent red markings on the lobes strongly suggest that it is *Erythranthe floribunda* (Douglas ex. Lindl.) Nesom of sect. *Mimulosma* (Nesom 2012a). This also would be consistent with Mcnair's description of the species as "self-fertilizing," which *E. marmorata* certainly is not.
>
> * The CalPhotos website (2010) provides photos by Dean Wm. Taylor of plants identified as *Mimulus marmoratus* from Mariposa County. The ovate-lanceolate, subpinnately multi-veined leaf blades and the relatively large and relatively broad-limbed corollas with prominently massed red dots at the base of the lower three lobes indicate that these plants are *Erythranthe geniculata* (Greene) Nesom of sect. *Mimulosma.*

The identity of *Mimulus whipplei* has long been problematic. According to CNPS (2011), "many recent searches have not rediscovered this plant" and it has remained known only from the type collection. Within *Erythranthe*, the lack of mature calyces on the type has prevented an unequivocal decision even regarding its position in the genus. Grant (1924) placed it among the species of *Mimulus* sect. *Simiolus*, while Pennell (1951) placed it in sect. *Paradanthus*, keying it among the smaller set of species now regarded as *Erythranthe* sect. *Mimulosma* (Nesom 2012a). Grant's protologue did not compare *M. whipplei* with any other species nor did she provide any comments in distinction — her key to species seemingly identifies it as closer to South American species than to those of sect. *Simiola* in the western USA, emphasizing the glandular-villous stems and open corolla throats of *M. whipplei*. Nor did Pennell comment on his placement of the species.

Remarkably, the type of *Mimulus whipplei* was collected from a locality only about 15 miles northeast of the type locality of *M. marmoratus*, and the two taxa are similar in general aspect and especially in their long-tubed corollas with broadly flaring limbs. Examination of the type of *M. marmoratus* in the Greene herbarium confirmed that both taxa are villous-glandular, taprooted annuals. Argue (1980, p. 83) noted that an examination of the pollen of *M. whipplei* "should quickly resolve the disagreement over its proper placement" since species of sect. *Simiolus* have irregularly synaperturate (usually ± spiraperturate) pollen, a type unique within all of *Mimulus* sensu lato. In sum, it is clear that the names *M. marmoratus* and *M. whipplei* apply to the same species.

Figure 4. *Mimulus whipplei*, holotype (GH) and isotype (US).

Figure 5. Lectotype (ND-Greene) of *Mimulus marmoratus*.

Figure 6. *Erythranthe marmorata* from Calaveras Co., California (see comments in text).

Figure 7. *Erythranthe marmorata* from "Mokelumne River," probably in Calaveras Co., California (see comments in text).

21. ERYTHRANTHE GLAUCESCENS (Greene) Nesom, Phytoneuron 2012-40: 43. 2012. *Mimulus glaucescens* Greene, Bull. Calif. Acad. Sci. 1: 113. 1885. *Mimulus guttatus* var. *glaucescens* (Greene) Jepson, Man. Fl. Pl. Calif., 928. 1925. **TYPE**: **USA**. **California**. Butte Co.: 1883, *Mrs. R.M. Austin s.n.* (holotype: ND-Greene! photo-PH!, photo-UT!; isotype: CAS digital image!).

Annual, slender taprooted or fibrous-rooted, mostly glabrous and more or less conspicuously glaucous. **Stems** erect, (5–)30–60(–80) cm, simple or branched, terete, occasionally quadrangular above, rarely with runners from basal nodes. **Leaves** basal and cauline, proximal ovate to ovate-elliptic or orbicular-ovate, sometimes subcordate, 10–50 mm, palmately 3–5-veined, margins denticulate to dentate or coarsely and irregularly toothed, occasionally lobed at the base, petioles slender, as long as or much longer than the blade, sometimes pubescent or villous, distal leaves few, sessile, orbicular, 5–45 mm wide, connate-perfoliate below the inflorescence and disc-like, margins nearly entire or with small scattered teeth. **Flowers** 1–16, commonly from distal nodes, sometimes from nearly all. **Fruiting pedicels** 10–50 mm. **Fruiting calyces** broadly campanulate, 7–16 mm long, closing, lobes short, broadly triangular, blunt to acute, the upper slightly longer. **Corollas** yellow, lower lip densely dark yellow, others much lighter, red-dotted on floor of throat and tube, sometimes with a median blotch, tube-throats 12–23 mm, exserted 4–8 mm beyond the calyx margin, bilabiate, limb expanded 14–36 mm (pressed). **Styles** minutely hirtellous-puberulent. **Herkogamous**; anther pairs at different levels, stigma above upper anther pair. **Capsules** ca. 5–11 mm, stipitate, included. 2*n* = 28.

Flowering Mar–May(–Jun). Seepage areas, wet rocks, moist cliffs, pool edges, gravelly stream banks, serpentine outcrops, roadsides and roadcuts, low pastures, riparian woodland, blue oak woodland, chaparral, grassland; 80–900(–1100) m; California (Butte and Tehama cos.). Map 18.

The basal leaves of *Erythranthe glaucescens* are very similar to those of *E. microphylla* — often nearly round in outline, with irregularly toothed margins, and often puplish. Corollas of *E. glaucescens* are widely variable in size, also similar to the situation in *E. microphylla*.

The Mcnair website (Macnair 1996) makes this observation regarding *Erythranthe glaucescens*: "Pennell [1951] suggests that it is annual, but it behaves as a perennial in the glasshouse, unlike the obligate annual segregants of *M. guttatus*." In the present study, all collections seen of *E. glaucescens* except two (both from a single locality) have been fibrous-rooted or slenderly taprooted and clearly annual. Plants from one locality produced filiform, small-leaved runners from basal cauline nodes: **California**. Butte Co.: Canon of Big Chico Creek, 26 Mar 1914, *Heller s.n.* (MO) and 2 Jul 1914, *Heller s.n.* (MO). Mcnair did not say what observations led him to interpret the duration of *E. glaucescens* as perennial.

22. ERYTHRANTHE NUDATA (Curran ex Greene) Nesom, Phytoneuron 2012-40: 44. 2012. *Mimulus nudatus* Curran ex Greene, Bull. Calif. Acad. Sci. 1: 114. 1885. **TYPE**: **USA**. **California**. Lake Co.: Kelsey Mountain, Jun 1894, *Mrs. Curran s.n.* (CAS?; not located at ND-Greene).

Annuals, glabrous or stems, leaves, and pedicels minutely stipitate-glandular with hairs 0.05–0.1 mm, at least just above the nodes. **Stems** erect or ascending, (5–)9–30 cm, terete, simple or branched from basal nodes, branches mostly reddish-purple. **Leaves** scattered, proximal blades lanceolate or oblong-lanceolate to ovate, distal narrower, narrowly spatulate to oblanceolate, 5–15(–30) mm x 1–5 mm, margins denticulate to proximally dentate-lobed, bases attenuate, long-petioled (petioles mostly 5–30 mm), the upper sessile and mostly linear, not perfoliate. **Flowers** 1–8, often in proximal or medial to distal axils. **Fruiting pedicels** 10–35 mm, erect in flower, spreading to divaricate or rarely recurved in fruit. **Fruiting calyces** ovate-campanulate, 6–13 mm, closing, lobes nearly equal, obtuse to acute, lower upcurved over the lateral ones and nearly closing the orifice.

Corollas yellow, red-spotted on floor of the throat and tube, tube-throats cylindric-funnelform, 8–12 mm, exserted 2–4 mm beyond calyx margin, bilabiate, limb expanded 8–12 mm (pressed). **Styles** glabrous. **Herkogamous**; anther pairs at different levels, stigma above upper anther pair. **Capsules** 6–7 mm, stipitate, included.

Flowering Apr–Jun. Open gravelly seeps on serpentine outcrops, serpentine crevices, springs, stream sides, gravelly creek beds, roadside drainages and swales; 250–700 m; California (Colusa, Glenn, Lake, Mendocino, Napa, and Sonoma cos.). Map 18.

Erythranthe nudata is distinct in its annual duration, few, inconspicuous, and narrow leaves, long and spreading-divaricate pedicels, and large corollas. The plants apparently are true to serpentine substrate. A presumption that *E. guttata* is its "progenitor" (Gardner & Macnair 2000) is without documentation or any other kind of justification.

23. ERYTHRANTHE NASUTA (Greene) Nesom, Phytoneuron 2012-40: 44. 2012. *Mimulus nasutus* Greene, Bull. Calif. Acad. Sci. 1: 112. 1885. *Mimulus langsdorffii* var. *nasutus* (Greene) Jepson, Fl. W. Calif., 407. 1901. *Mimulus guttatus* var. *nasutus* (Greene) Jepson, Man. Fl. Pl. Calif., 928. 1925. **LECTOTYPE** (Grant 1924, p. 179): **USA**. **California**. Sonoma Co.: Knights Valley, Apr 1877, *H.T. Edwards s.n.* (GH; isolectotype: NY digital image!). The lectotype selection was made from collections noted in the protologue: "Our earliest specimens were collected in 1877, in Sonoma County, Cal. at Knight's Valley and Skaggs' Springs, by Mr. Henry Edwards. Mrs. R.M. Austin sent it from Butte County in 1883; while Mrs. Curran obtained fine specimens last year in localities as far apart as Lake and Kern counties." No specimen matching any of these possible collections was located at ND-Greene.

Greene (1885) made these observations about the new species: "Its calyx is more uniformly spotted than in the true *M. guttatus*, from which it is most obviously distinct by its quadrangular winged stem, its inflorescence, racemose almost from the very base, and its small corolla, but especially by the peculiar calyx, the upper tooth of which not only almost equals the tube in length but is rendered singularly conspicuous by the enfolding about it, of the lower ones; which latter thus disappear entirely from the profile, if we may so speak, thus suggesting the specific name." Latin, *nasutus*, large-nosed.

Mimulus luteus var. *gracilis* A. Gray ex Torrey, Rep. U.S. Mex. Bound., Botany 2(1): 115. 1859. *Mimulus guttatus* var. *gracilis* (A. Gray ex Torrey) G.R. Campbell, Aliso 2: 328. 1950. **LECTOTYPE** (Campbell 1950, p. 336): **USA**. **California**. Napa Co.: on rocks, Mar 1852, *G. Thurber 498* (GH, photo! in Campbell 1950). Protologue: "Copper Mines, New Mexico, and near Cruces; *Bigelow*. Gila valley; *Schott*. Napa county, California; *Thurber*. San Luis Obispo; *Parry*."

Mimulus subreniformis Greene, Erythea 3: 67. 1895. **LECTOTYPE** (designated here): **USA**. **California**. Shasta Co.: Burney Falls, 30 May 1894, *M.S. Baker and F. Nutting s.n.* (ND-Greene 46422! photo-PH!, photo-UT!; isolectotypes: ND-Greene!, UC!).

Mimulus cuspidatus Greene, Leafl. Bot. Observ. Crit. 2: 6. 1909. **TYPE**: **USA**. **California**. [Stanislaus or Tuolumne Co.:] [protologue: "wet shades among rocks along the upper Stanislaus River, ... late June, 1889," *E.L. Greene s.n.* (holotype: NG-Greene! photo-PH!; isotype: DS digital image!). The ND-Greene sheet has no label but is marked in Greene's hand as "Type!"

Mimulus erosus Greene, Leafl. Bot. Observ. Crit. 2: 4. 1909. **TYPE**: **MEXICO**. **Baja California**. Santa Agueda, 4 Mar 1890, *E. Palmer 233* (holotype: US digital image! photo-PH!).

Mimulus bakeri Gandoger, Bull. Soc. Bot. Fr. 66: 219. 1919. **LECTOTYPE** (designated here): **USA**. **California**. Napa Co.: Mt. St. Helena, colonies common among streamlets, 20 Apr 1903, *C.F. Baker 2608* (CAS digital image!; isolectotypes: LY?, ND-Greene!, NY digital image!). Gandoger also cited "Amer. occid. Oregon (*Cusick n. 1627*!)." Regarding his set of four new species, *M. bakeri*, *M. puncticalyx*, *M. parishii*, and *M. puberulus*, Gandoger noted that "Sequentes e polymorpho *Mimulo nasuto* Greene desumptae sunt." Two sheets at UC are labeled "Eastern Oregon Plants, wet rocks, not rare, 15 Jun 1897, *W.C. Cusick 1627*" thus they apparently are not duplicates of the holotype nor do they match the protologue, even though Cusick's collection number is the same.

Mimulus parishii Gandoger, Bull. Soc. Bot. Fr. 66: 219. 1919 [non Greene 1885]. **TYPE**: **USA**. **California**. [San Bernadino Co.:] "California ad S. Bernadino," *S.B. Parish 4741* (holotype: LY?). A possible isotype is at MO: San Bernadino Co.: Vicinity of San Bernadino, 1000-2500 ft, Apr 1897, *S.B. Parish s.n.* (MO!).

Mimulus puberulus Gandoger, Bull. Soc. Bot. Fr. 66: 219. 1919 [non Greene ex Rydb. 1906]. **TYPE**: **USA**. **Washington**. Klickitat Co.: Bingen, riverbank, 17 Apr 1905, *W.N. Suksdorf 5016* (holotype: LY?; isotypes: US digital image!, WS photo-PH!). The WS sheet was photographed at the 'home of W.N. Suksdorf."

Mimulus puncticalyx Gandoger, Bull. Soc. Bot. Fr. 66: 219. 1919. **TYPE**: **USA**. **Washington**. [Klickitat Co.:] Ad Bingen, no date, *W.N. Suksdorf 2775* (holotype: LY?; isotypes: PH-2 sheets!, WS photo-PH!).

Annual, fibrous-rooted or slender taprooted. **Stems** erect to ascending-erect or decumbent, 2–35(–100) cm, usually 4-angled or sometimes shallowly 4-winged, usually thin-wiry but sometimes fistulose, simple or branched from proximal nodes, glabrous except for a consistently small, villous-glandular area just above the nodes, sometimes hirtellous distally. **Leaves** basal and cauline or basal absent at flowering, proximal to medial petiolate, sessile distally, petioles 3–35 mm, narrowly flanged at the base, blades elliptic-ovate to broadly ovate, suborbicular, or depressed ovate, (5–)10–49(–80) mm x (3–)10–25(–60) mm, palmately 3–5-nerved, proximal largest and persistent, apices acute to obtuse, bases cuneate to truncate or subcordate, margins irregularly dentate to dentate-serrate or nearly lacerate-dentate, commonly doubly toothed, 4–9 main teeth per side, sometimes sublacerate to sublyrate basally, more or less tinged with red on the lower surface or purple-spotted, glabrous or often hirtellous on one or both surfaces with dull, terete, sharp-pointed, eglandular hairs. **Flowers** (1–)2–12(–20), usually from distal nodes but sometimes from medial to distal. **Fruiting pedicels** (3–)7–20(–40) mm, glandular-villous on upper side at the axils, otherwise nearly glabrous. **Fruiting calyces** ovoid-campanulate, (5–)10–15(–19) mm, nodding 30º–180º, closing, upper lobe prominently elongate 1.5–3 x beyond the lower and nose-like, glabrous to minutely hirtellous or appressed-hirtellous, minutely short-ciliate at the sinuses, frequently purple-tinged or purple-spotted. **Corollas** yellow, usually with a red-spotted throat and a red blotch at the base of the lower lip, tube-throats broadly cylindric, (5–)8–12 mm, exserted (0–)1–2 mm beyond calyx margin, limb weakly bilabiate, expanded ca. 6–12 mm (pressed). **Styles** minutely scabrous to glabrous. **Plesiogamous**; anther pairs and stigma at the same level. **Capsules** (4–)5–9(–10) mm, stipitate, included. $2n = 28$ (various localities), $2n = 26$ (California, Tuolumne Co.; New Mexico, Dona Ana Co.: San Augustine Pass, 4500 ft, 30 Oct 1946, *Norwell s.n.*, Vickery cult. 5018, voucher for $2n = 26$, UT).

Flowering (Mar–)Apr–Jun(–Jul). Cliff faces, ledges, crevices, and bases, wet rocks in rivers, stream sides, sand bars, mossy seeps, wet clay banks, moist fields, sandy soil, depressions over granite, roadsides; (30–)600–2300(–3200) m; California, Nevada, Oregon, Washington, Idaho, Arizona, New Mexico; Canada (British Columbia); Mexico (Baja California, Sonora). Map 21.

Erythranthe nasuta is characterized by its annual duration (fibrous-rooted), 4-angled stems, broadly ovate leaves commonly with irregularly toothed margins, calyces with longish, protruding upper lobe, short corollas (autogamous — chasmogamous or cleistogamous), and glandular vestiture only in the axils. At least the distal and bracteal leaves consistently have hirtellous to hirsutulous adaxial surfaces, even in the smallest of plants. *Erythranthe nasuta* has been abundantly collected in Arizona, particularly in Pima County, where the variability in plant size nearly matches that found in California.

Collections examined from Mexico. **Baja California**. San Juanico (8 mi N), rocky arroyo margin, 8 Mar 1939, *Gentry 4305* (ARIZ). **Sonora**. Canyon of the Rio Magdalena, 12 mi above Imuris, 22 Mar 1934, *Shreve 6565* (ARIZ).

As observed in the introduction, plants of *Erythranthe nasuta* produce flowers that vary significantly in size, even on a single plant. Plants with only the tiny cleistogamous flowers (mature calyces 5–7 mm) are so distinctive that upon encountering what appeared to be a population system of them, with tiny leaves and decumbent to procumbent, filiform stems, I first thought they perhaps represented a distinct species. Here it is tentatively concluded that they are variants within the morphological range of the species. Collections examined. **California**. Kern Co.: Greenhorn Mts., ca. 2 mi from Alta Sierra, along old road from Alta Sierra to Wofford Heights, 18 May 1976, *Howell 51729* (MO); Greenhorn Range, 2.4 mi W of Wofford, mossy seep, 4300 ft, with Juncus kellogii, etc. 12 May 1969, *Howell and True 45586A* (MO). Kings/Kern Co.: Mt. Stanford, wet ground, Jul 1890, *Sonne 263* (MO). Mono Co.: White Mts., along N fork of Cottonwood Creek, 0.1 mi above its confluence with Tres Plumas Creek, 2.8 mi S 88 E of Eva Belle Mine, moist granite crevices facing 20 WSW above creek with *Rosa*, *Artemisia*, and *Holodiscus*, 11 Jul 1987, *Morefield 4603* (MO). Tulare Co.: White Chief, Mineral King, 9700 ft, 1 Jul 1966, *Rice 242* (DAV); Cherry Hill Road, 2.1 mi above Dry Creek, chaparral, 5000 ft, dense colony growing on a recently moist sheet of decomposed granite, 2 Aug 1969, *Twisselman 15914* (JEPS, MO).

Similarly, plants of *Erythranthe nasuta* sometimes encountered with thick-fistulose stems up to one meter tall and and with very large fruiting calyces (16–19 mm) appear remarkably distinct and might be considered 'gigas' forms reflecting the influence of polyploidy. Regarding his collection *8158* from Madera Co., cited below, Heller (1906, p. 249) made this observation: "growing about large flat granite rocks on the edge of a stream. The plants were large and robust, many of them fully three feet high and much branched. Ordinarily it is of rather low growth." These phenotypically gigas forms, however, appear to grade into the range of variation more characteristic of the species. Representative collections of the "gigas" form. **California**. Butte Co.: ca. 2 mi SE of Jarbo Gap, W side of the North Fork of the Feather River, sand bar, near the Poe Power House, 9 Jun 1987, *Ahart 5735* (MO). Calaveras Co.: Camp Nine Road, NE of Vallecito, 1100-2000 ft, 5 Apr 1978, *Howell 52778* (VDB). Madera Co.: hills about 5 mi above Pollasky, 12 Apr 1906, *Heller 8158* (MO). Napa Co.: Mt. St. Helena, colonies common along streamlets, 20 Apr 1903, *Baker 2608* (LL, MO). Sonoma Co.: on a wet bank in clay soil in Knight's Valley, upper Sonoran Life Zone, 20 Apr 1940, *Heller 15545* (MO). Ventura Co.: North Fork Ventura River, wet rocks, 750 m, 2 May 1935, *Clokey 6916* (MO).

Erythranthe nasuta and *E. guttata*.

A number of evolutionary studies have focused on differentiation and isolation between outcrossing *Erythranthe guttata* and self-fertilizing *E. nasuta*, but whether the plants involved were identified by the same criteria as in the present study is not known. Mating system and pollen–pistil interactions are said to cause most of the isolation between the two (Kiang & Hamrick, 1978; Diaz & Macnair, 1999; Martin & Willis 2007). Sweigart et al. (2006) found that one incompatibility allele (at hms2) appears to be widespread and perhaps fixed throughout the geographic range of *E. nasuta*. Another allele (hms1) is restricted to some Oregon populations (Linn Co.) of *E. guttata* (the identity ambiguous by reference to the present study).

Fishman et al. (2002) identified in *Erythranthe nasuta* more than 20 loci of small to moderate effects underlying species differences in floral morphology related to mating system divergence. Most of those loci appeared to influence variation in aspects of floral size and shape.

Several populations of small-flowered, autogamous tetraploids that resemble *Erythranthe nasuta* were discovered on Vancouver Island and the Gulf Islands of southwestern Canada as well as in southwestern Oregon (Benedict 1986). On Vancouver Island these plants were growing sympatrically with diploid *E. nasuta* and diploid "*Mimulus guttatus*" (as identified in the study) and Benedict hypothesized that these two species were the parents of the tetraploid. Sweigart et al. (2008) extended the study and found the tetraploid to be "widespread and common from northern California to British Columbia." Fixed heterozygosity at allozyme loci was further evidence for Benedict of an alloploid origin for the tetraploids, and patterns of molecular variation supported the hypothesis that they were two independent alloploid origins of the tetraploids (Sweigart et al. 2008).

Two distinct haplotypes occur at each of the nuclear genes *mCYCA* and *mAP3* in each of the tetraploids (Sweigart et al. 2008). One haplotype shares near-identity with sequences from *M. nasutus*; the second is similar to but does not exactly match any members of the *M. guttatus* complex sampled by Sweigart et al. Populations of the tetraploid commonly have individuals with "*M. nasutus*-like haplotypes" mixed with those of "*M. guttatus*-like haplotypes."

The tetraploids resemble *Mimulus nasutus* at least in being annual, small-flowered obligate selfers. As noted by Benedict (p. 122), they are "Very similar to *M. nasutus*. All characters overlap to a degree with *M. nasutus* but, under favorable growth conditions, the following structures tend to be more enlarged in *M. nasutus*: [height, stem width, calyx length, leaves, pedicel length, stipe length]." Benedict and Sweigart et al. found that the tetraploids are nearly completely reproductively isolated from their putative parents — *E. nasuta* and some expression of *E. guttata* in the broad sense. Benedict provided the following key couplet.

1. Pistil included within or equal to calyx; corolla tube-throat nearly cylindrical; plants 5–50 cm tall, large ones with quadrangular winged stem; diploid .... **Mimulus nasutus**
1. Pistil usually exserted from calyx (up to 3 mm), corolla tube-throat narrowly funnel-shaped (infundibular); plants 5–25 cm tall, stems tending to quadrangular but not winged; tetraploid .... **Mimulus sp.**

The species identified in these studies as *Mimulus guttatus* perhaps is *Erythranthe microphylla* as identified in the present account, as Benedict indicated that these plants are annual, which excludes *E. guttata* in the present sense. On the other hand, she referred to *Mimulus platycalyx* (here placed as a synonym of *E. microphylla*) and distinguished it from "annual *Mimulus guttatus*," even noting that she found "*Mimulus platycalyx*" growing close to populations of the tetraploid in Oregon. An understanding of the biology and taxonomy in this situation remains incomplete.

The tetraploid has not been distinguished in the current study (with one possible exception, below), but I have examined relatively little material from Oregon and Washington, and it is possible that I simply overlooked the variants before becoming aware of the differences noted by Benedict, which is the only place its morphology has been characterized.

I have examined one collection from northern Oregon that perhaps are similar in origin to the tetraploids above. Multnomah Co.: Base of Multnomah Falls in damp area, 280 ft, 22 Aug 1969, *McArthur 33,* Vickery cult. 9562, voucher for *n* = 28 (UT). These plants have erect stems apparently from a rhizomatous base, the stems, pedicels, calyces, and leaves are minutely hirtellous and eglandular, the fruiting calyces are 8–11 mm long and apparently not closing, and the corollas are light yellow with a dark yellow palate, sparsely spotted throat, and tubes 10–12 mm long, little at all exserted beyond the calyx margin . If the rhizomatous morphology and tetraploid chromosome number within this population are correct as observed and consistent, it would justifiably be treated as a distinct species (a previously undescribed one, and different from the plants discussed by Benedict).

The chromosome number was reported by McArthur et al. (1972), who identified it as *Mimulus guttatus*, but the the tiny, autogamous flowers immediately remove it from that species.

24. ERYTHRANTHE LACINIATA (A. Gray) Nesom, Phytoneuron 2012-40: 44. 2012. *Mimulus laciniatus* A. Gray, Proc. Amer. Acad. Arts 11: 98. 1876 [January]. **TYPE**: **USA**. **California**. [Mariposa Co.:] On the South Fork of the Merced at Clark's Ranch, 1872, *C. Sulivan and A. Gray s.n.* (holotype: GH).

Mimulus eisenii Kellogg, Proc. Calif. Acad. Sci., ser. 1, 7: 89. 1876 [August or later]. **TYPE**: **USA**. **California**. [Fresno Co.:] Near Fresno, no date, *Dr. G. Eisen s.n.* (holotype: CAS digital image! photo-PH!, fragment UC!).

Annual, slender taprooted or fibrous-rooted. **Stems** erect, 3–38 cm, simple or branched from the base, glabrous to sparsely hirtellous, finely villosulous glandular above the nodes but not elsewhere. **Leaves** cauline, basal deciduous by flowering, blades elliptic to elliptic-obovate, oblanceolate, or oblong, 3–55 mm, margins commonly narrowly pinnately lobed or dissected, sometimes merely shallowly toothed, all petiolate or distally subsessile, petioles absent or 1–35 mm. **Flowers** 2–8, from medial to distal nodes. **Fruiting pedicels** 5–25 mm, nodding 30º–140º at the calyx base. **Fruiting calyces** cylindric-campanulate, 8–10 mm, closing, red-spotted ± glabrous, upper lobe slightly longer than the others. **Corollas** yellow, red-spotted in the throat and the larger usually with a single large red blotch on the lower lip, tube-throats 4–6 mm, exserted 1–2 beyond the calyx margin, limb weakly to strongly bilabiate, expanded ca. 5–6 mm (pressed). **Styles** glabrous. **Plesiogamous**; anther pairs and stigma at the same level. **Capsules** 5–7 mm, stipitate, included. $2n = 28$.

Flowering Apr–Jul(–Aug). Cracks, depressions, and seeps in granite outcrops, ledges, talus and scree, rocky stream sides, rocky slopes, roadsides, intermittent drainages; 900–2300(–2900, –3300) m; California (Amador, Butte, Fresno, Madera, Mariposa, Tulare, Tuolumne cos.). Map 18.

As in *Erythranthe nasuta*, the upper calyx lobe in *E. laciniata* tends to be narrowly lanceolate to triangular (nose-like) and perceptibly falcate, curving slightly upward both in flower and in fruit. The upper lobe is not so prominently protrusive as it often is in *E. nasuta.*

Corollas size is variable in *Erythranthe laciniata* but size of those with open throats (vs. much reduced in size and apparently cleistogamous) is not strongly correlated with size of the individual plant. Those on some plants, however, are all or nearly all greatly reduced and apparently cleistogamous. Even the larger corollas apparently are autogamous — the anther pairs are slightly separated or equal in level and the stigma is in the middle of the anthers or at the level of the upper pair.

Plants from Butte County identified here as *Erythranthe laciniata* are disjunct from the main range and have much larger and more highly dissected leaves.

25. ERYTHRANTHE PARDALIS (Pennell) Nesom, Phytoneuron 2012-40: 44. 2012. *Mimulus pardalis* Pennell, Proc. Acad. Nat. Sci. Philadelphia 99: 164. 1947. **TYPE**: **USA**. **California**. Tuolumne Co.: Red Hills above Peoria Flat, crevices of serpentine rock, 1600 ft, 11-16 Apr 1919, *R.S. Ferris 1602* (holotype: DS digital image!; isotypes: JEPS, PH!, POM).

Mimulus cupriphilus M. Macnair, Bot. J. Linn. Soc. 100: 3. 1989. **TYPE**: **USA**. **California**. Calaveras Co.: McNulty mine, copper-contaminated soil, "April 13-20th 1987," *M. McNair s.n.* (holotype: BM as cited; isotype: JEPS as cited in the protologue but not located at JEPS). Mcnair perhaps intended the JEPS specimen cited below (identified by Mcnair as *M. cupriphilus*) as an isotype but it is not a duplicate of the cited holotype. In any case, the Mcnair collection at JEPS is unequivocally identified as *Erythranthe pardalis.*

Annual, fibrous-rooted or taprooted; stems, calyx, and pedicels short and delicately stipitate-glandular; distal stems and pedicels minutely puberulent-glandular with gland-tipped hairs 0.1–0.4 mm (to 1 mm on proximal portions of stems). **Stems** decumbent-ascending with distal portion erect, 5–30 cm, simple or sometimes branched from proximal to medial nodes. **Leaves** mostly cauline, basal usually absent at flowering, all petiolate or distal-most becoming subsessile, proximal and medial petioles 8–20 mm, distal 1–2 mm, blades mostly ovate or broadly ovate to depressed-ovate, palmately 3-veined, proximal and medial 7–22 mm x 6–18 mm, sometimes largest at midstem, sparsely villous to puberulent-glandular with vitreous, gland-tipped hairs, less commonly glabrous, apices obtuse to obtuse-acuminate, margins shallowly dentate-serrate with 2–3(–5) teeth per side mostly distally, bases rounded or cuneate to a gradually attenuate petioles 1–12 mm. **Flowers** 2–12, usually evenly distributed from proximal to distal nodes. **Fruiting pedicels** 10–35 mm. **Fruiting calyces** cylindric-campanulate, 8–11 mm, nodding 45º–180º, consistently dark purple-spotted, glabrous to sparsely puberulent-glandular, sometimes minutely hirtellous, lobes triangular-acute, uppermost longest, lower two closing upward against the upper. **Corollas** yellow, without prominent red spots or sometimes sparsely red-spotted on floor of throat, tube-throats narrowly funnelform to cylindric, 7–10(–12) mm, exserted 1–3 mm beyond calyx margin, limb bilabiate, expanded 8–12 mm (pressed), palate villous. **Styles** glabrous. **Plesiogamous**; anther pairs in larger corollas slightly separated and stigma at level of upper pair or both anther pairs and stigma at the same level; in smaller corollas (without expanded limb and barely exserted beyond calyx margin) both anther pairs and stigma at the same level. **Capsules** 4–6 mm, stipitate, included. $2n = 28$.

Flowering (Mar–)Apr–May. Crevices of serpentine rock, stony red soils, red clay, among boulders, along streams, ditches, tailings at copper mines; 100–700 m. California (Amador, Calaveras, El Dorado, Placer, Tehama, Tuolumne cos.). Map 19.

Erythranthe pardalis (Fig. 8) is recognized by its annual duration (fibrous-rooted or taprooted) and relatively delicate habit, ovate to depressed-ovate leaves toothed mostly on the distal margins, small, autogamous flowers produced from all nodes (proximal to distal), dark-spotted calyces, and glandular cauline and foliar vestiture. The plants occur primarily on serpentine rocks and soil but also grow on copper tailings at mine sites. The plants in Tehama County, disjunct from the main range, perhaps are not on serpentine.

Mimulus cupriphilus was viewed by Mcnair (1989; Mcnair et al. 1989; Mcnair & Cumbes 1989) as a narrow endemic restricted to copper-contaminated substrates — he knew it only from three populations at two closely situated copper mines near Copperopolis in Calaveras County and was unable to find it on nearby copper outcrops or mine sites. He hypothesized that *M. cupriphilus* is an immediate derivative of *M. guttatus* — "It is probable that this species [*M. cupriphilus*] evolved on one or both of these copper mines from copper tolerant *M. guttatus*" (Mcnair & Cumbes 1989, p. 219). Mcnair (1989, p. 13) suggested that *M. cupriphilus* probably evolved "within the last 150 years, and most probably within the last 50" — corresponding to the time period in which copper mines in central California were intensively worked.

The reasoning upon which this hypothesis was based is quoted here (Mcnair & Cumbes 1989, p. 212): "The origin of this form [*Mimulus cupriphilus*] is unknown, but it is not unlikely that it evolved in the recent past close to its present location. It is very improbable that a widespread species could have gone previously undescribed in California. It is possible that it is a rare undescribed species, which evolved a tolerant race only on these two mines: however, rare species are unlikely to evolve tolerance simply because they will not have the genetic resources to do so (Mcnair, 1987). Also, despite a diligent search of the surrounding area, no nontolerant populations of this form have been found. It is not an unreasonable hypothesis to suggest therefore that this form represents a recent evolutionary event."

It remains possible that populations of *Erythranthe pardalis* on copper substrate are physiologically specialized from the more widespread serpentine plants (though the same gene may not responsible for both tolerances (e.g., Mcnair & Smith 1987). The "copper" populations of *E. cupriphila*, however, appear to utilize the same gene (genetic locus) for copper tolerance as the local copper tolerant populations of *E. guttata*, an observation emphasized by Mcnair and Cumbes in their speculative scenario for the evolutionary derivation of *Mimulus cupriphilus*. In view of the broader perspective of species relationships hypothesized here, however, the hypothesis that *E. pardalis* evolved directly from *E. guttata* was in part a correlate of the absence of taxonomic perspective. And given the discovery that *Mimulus cupriphilus* is a synonym of *Mimulus pardalis,* there is no reason to believe that the evolutionary age of this species differs significantly from its relatives.

Figure 8. *Erythranthe pardalis*. Isotype DS.

Using progeny from experimentally produced reciprocal crosses and backcrosses between *Mimulus guttatus* and *M. cupriphilus*, Mcnair and Cumbes (1989) studied genetic systems governing flowering time, floral morphology, plant size, and duration. The observation by Mcnair of putative natural cupriphilus-guttatus hybrids at one site needs to be confirmed and, if confirmed, documented, as only anecdotal observation was provided.

Erythranthe pardalis and its putative close relative *E. nasuta* occur sympatrically and it is possible that some plants in Tuolumne and Calaveras counties might even be pardalis-nasuta hybrids, but they produce the tiny flowers on short stems from basal nodes that are characteristic of *E. nasuta* but not *E. pardalis*: e.g., Calaveras Co.: *Heckard 5507* (UC) and *Robbins 3524* (UC); Tuolumne Co.: *Ferris 1626* (UC) and *Hoover 1336* (UC).

Additional collections examined. **California**. Amador Co.: Jackson, 1892, *Hansen s.n.* (ND-Greene); Silver Lake, 20 Sep 1892, *Hansen s.n.* (ND-Greene); Middle Fork, 1500 ft, Apr 1893, *Hansen 135* (MO); Fisher's Cabin, 2000 ft, Apr 1892, *Hansen 473* (MO, ND-Greene, UC); New York Falls, 2000 ft, Apr 1892, *Hansen 1286* (MO, UC); Middle Fork, 1500 ft, Apr 1892, *Hansen 1288* (MO); Ione, 300 ft, 25 Mar 1896, *Hansen 1517* (MO, ND-Greene); Elsie's Creek, 2700 ft, May 1896, *Hansen 1626* (ND-Greene); N of Falls, 2000 ft, 18 Jul 1896, *Hansen 1795* (ND-Greene); N face of steep canyon and rocky places near stream, in foothill woodland, in red clay, 4 mi E of Plymouth, on road to Fiddletown, 30 Mar 1961, *Ramsey 29* (JEPS-2 sheets). Calaveras Co.: Table Top Mt., SE face, 700 ft, Copperopolis Quad, 16 Apr 1936, *Belshaw 1896* (UC); 5 mi NE of Valley Springs on road to Fosteria, in moist ditch on slope with *Pinus sabiniana*, 3 May 1963, *Breedlove 4788* (SMU); Pardee Reservoir, Pardee Lake, W of McAfee gulch at S end of the gulch, W of the Coast to Crest Trail just before it heads down into the gulch, burned ca. 5 years ago, 1032 ft, 17 May 2005, *CNPS SN Foothill Team SNFN0249b* (DAV); Table Mt., 7 mi S of Copperopolis on road to State Hwys 108 and 120, on top of old lava flow, 1100 ft, 27 Apr 1963, *Lloyd 2444* (JEPS); McNulty Mine, copper-contaminated stream, [greenhouse grown], “seeds collected from dead plants, May 1985; plants grown August 1986,” *Mcnair s.n.* (JEPS); ca. 7 air mi SW of Copperopolis, Star & Excelsior Mine, tailings pile from copper mine, 800 ft, 7 Apr 1998, *Taylor 16283* (JEPS), *16285* (JEPS-2 sheets), and *16286* (JEPS-2 sheets). El Dorado Co.: 2 mi NW of Clarksville, SE slope of Bass Lake, under and along edge of serpentine rocks, 5 May 1967, *Crampton 7859* (AHUC); near San Andreas, 24 Apr 1941, *Eastwood and Howell 8710* (UC); along Rose Creek at its mouth on the Stanislaus River, 12 Apr 1981, *Heckard 5505* (JEPS); along Stanislaus River (E side), ca. 3 air mi NNW of Columbia, ca. 880 ft, 12 Apr 1981, *Heckard 5507* (JEPS). Placer Co.: Iowa Creek Road ca. 2 mi from I-80 near entrance to Auburn State Recreation Area, at creek crossing, ca. 1700 ft, boulders at base of open S-facing slope, only at edge of boulder, herbage ± slimy, 8 Apr 1989, *Ertter 8173* (MO, TEX, UC). Tehama Co.: Dales Lake Ecological Reserve, W side of Manton Rd (A6) ca. 2 mi N of Dales Station on Hwy 36, ca. 14 mi NE of Red Bluff, localized population in crevices on a shaded outcrop on the S edge of the basalt ridge crossing the NE corner of the reservoir, blue oak woodland, 740 ft, 10 Apr 1995, *Oswald & Ahart 6642* (JEPS). Tuolumne Co.: 1.8 mi N of the Tuolumne-Mariposa county line, moist rocky serpentine soil along the large rock outcrops above Hwy 49, 19 Mar 1974, *McNeal 1383* (UT); Red Hills area, W of Chinese Camp, along Minnow Gulch, moist crevices of ultrabasic rock, 1000 ft, 8 Apr 1973, *Stebbins 9033* and *9039* (JEPS); Peoria Pass, Peoria Pass Road, 2.5 road mi N of Hwy 120, low relief serpentine hills E from the roadway, deep red, weathered serpentine clay in open *Ceanothus cuneatus* chaparral burned the previous summer, 26 Mar 1998, *Taylor 16268* (JEPS-2 sheets); Peoria Basin, slopes at SE edge of basin ca. 1 mi E of Peoria Pass Rd, stony red weathered serpentine soils dominated by *Ceanothus cuneatus* chaparral, 900 ft, 15 Apr 1998, *Taylor 16328* (UC); Stanislaus River 2 mi downstream from Tulloch Lake dam, shaded northerly slopes at base of Table Mt., in stony red soils dominated by *Quercus douglasii-Aesculus californica*, 490 ft, 15 Apr 1998, *Taylor 16313* (MO, UC).

26. ERYTHRANTHE BREVINASUTA Nesom, **sp. nov. TYPE**: **MEXICO**. **Baja California Sur**. Sierra Guadalupe, W of Mulege, S of Rancho San Sebastian, near Ranchos San Fernando, El Cochí, Gueribo, and San Andrés, 26º 59' 20" N, 112º 27' 33" W, volcanic slopes and canyon, *Lysiloma divaricata*, ca. 900 m, 27 Oct 1997, *J.P. Rebman 4592* (holotype: SD!).

Similar to *Erythranthe nasuta* in its flowers produced from basal to distal nodes, small corollas and autogamous flowers, relatively broad leaf blades with irregularly serrate margins, hirtellous vestiture of bracteal leaves, pedicels sparsely glandular-villous just above the nodes; different in its terete stems, short upper calyx lobe and tendency for tiny teeth on the calyx lobes, denticulate corolla lobes, stems decumbent-ascending to ascending from the base, lack of basal branches that produce tiny cleistogamous flowers, and southern distribution disjunct from the range of *E. nasuta*.

Annual herbs, fibrous-rooted. **Stems** decumbent-ascending to ascending from the base, sometimes rooting a lower nodes, 6–30 cm, thin to thickened, simple or branched from proximal nodes, glabrous except for a small glandular-villous area on the pedicels just above the nodes. **Leaves** cauline, basal absent by flowering, largest proximally, gradually reduced in size distally, proximal petiolate, petioles 5–20 mm, distal sessile, basal to medial blades ovate to elliptic-ovate or depressed ovate, 10–45 mm x 12–40 mm, palmately 3–5 veined, margins irregularly serrate-dentate, usually doubly toothed with 3–6 main teeth per side, uppermost bracts usually sparsely to densely hirtellous on both surfaces, other leaves glabrous. **Flowers** 3–15, from medial to distal nodes or sometimes from proximal to distal. **Fruiting pedicels** 7–30 mm, sparsely villous-glandular just above the nodes, otherwise glabrous. **Fruiting calyces** ovoid-campanulate, 7–9 mm, nodding 45–90, closing, upper lobe slightly longer, not nose-like, glabrous or less commonly minutely hirtellous, margins prominently villous at the sinuses, usually sparsely purple-dotted, upper lobe commonly with a pair of distal, shallowly dentate teeth. **Corollas** yellow, red-dotted in throat, usually with a larger red splotch on the lower lip, tube-throats narrowly funnelform, 8–10 mm, exserted 3–5 mm beyond the calyx margin, limb weakly bilabiate, expanded 4–7 mm (pressed), each lateral lobe margin with 1–3 shallow denticles or apiculae. **Styles** glabrous. **Plesiogamous**. **Capsules** 4–5 mm, stipitate.

Flowering (Oct–)Dec–Mar. Volcanic slopes and canyon bottoms, sandy stream and pond edges, seepy slopes; 30–900 m; Mexico (Baja California, Baja California Sur). Map 12.

Additional collections examined. **MEXICO**. **Baja California**. Arroyo San Pedro, near San Pedro, occasional in wet sand, ca. 350 m, 28º 30' N, 113º 30' W, 11 Mar 1966, *Moran 12525* (SD). **Baja California Sur**. Canyon below La Victoria, W of Notri, 25º 52.5' N, 111º 25' W, small hanging valley, 540 m, 21 Mar 1960, *Carter 3929* with Ferris (SD); [Mpio. Loreto], 15 mi SSW of San Javier, Arroyo Santo Domingo, along stream bed of Arroyo Santo Domingo, 29 Mar 1970, *Crutchfield & Turner 3639* (TEX); Sierra Giganta, Arroyo Hondo [N of Cerro Giganta], riparian in canyon bottom, 14 Dec 1938, *Gentry 4138* (ARIZ); 8 mi N of San Juanico, rocky arroyo margin, 8 Mar 1939, *Gentry 4305* (ARIZ); Arroyo San Juan, 26º 26' N, 112º 44' W, ca. 30 m, by seepage-fed pond (with ducks), 14 Feb 1973, *Moran 20115* (SD).

These plants might be treated as a geographic outlyer within *Erythranthe nasuta*, but their formal segregation here emphasizes the differences in stem and corolla morphology and stem orientation. Also, the tendency to produce calyx lobes with toothed margins suggests that *E. brevinasuta* may share genetic background with the even more southern *E. lagunensis*. Lack of a prominent "beaked" calyx also is a distinctive difference, but there is variability in this feature within the range of typical *E. nasuta*. The choice of epithet is intended to point to the short calyx beak while alluding to the possible close relationship of the two species, although it perhaps is likely that *E. brevinasuta* is closer to *E. lagunensis* and thence to *E. guttata*.

The terete stems of *Erythranthe brevinasuta* contrast sharply with those of *E. nasuta*. The latter has 4-angled stems (to narrowly 4-winged on thicker stems) — a distinctive and consistent diagnostic feature in combination with the cleistogamous flowers, annual duration, and characteristic leaf shape and vestiture. Even on the smallest plants of *E. nasuta*, the 4-angled morphology can be seen by looking just above the nodes.

The shallowly denticulate corolla margins of *Erythranthe brevinasuta* suggest that the species might share ancestry with *E. dentiloba* and its relatives, since this feature is not encountered elsewhere in the genus, but the overall morphology is much more similar to *E. nasuta*.

27. ERYTHRANTHE ARVENSIS (Greene) Nesom, Phytoneuron 2012-40: 43. 2012. *Mimulus arvensis* Greene, Pittonia 1: 37. 1887. *Mimulus langsdorffii* var. *arvensis* (Greene) Jepson, Fl. W. Mid. Calif., 407. 1901. *Mimulus guttatus* var. *arvensis* (Greene) Grant, Ann. Missouri Bot. Gard. 11: 174. 1924. *Mimulus guttatus* subsp. *arvensis* (Greene) Munz, Aliso 4: 99. 1958. **LECTOTYPE** (designated here): **USA**. **California**. [San Mateo Co.:] Belmont, May 1886, *E.L. Greene s.n.* (ND-Greene! photo-PH!; isolectotypes: PH 2 sheets!).

In the protologue, Greene noted that "This plant was first known to me in a specimen or two brought from Lake County in 1884 by Mrs. Curran. I have mentioned it on page 112 of the first volume of California Academy Bulletin, under *M. microphyllus*. In the spring of 1886 I was surprised to find it common in wheat fields among the growing grain, in both San Mateo and Marin counties, not far from San Francisco. It is strictly annual and very unlike the common *M. guttatus* to which, under the name of *M. luteus*, a large number of our species and subspecies were until recently referred. In the districts named the large perennial will be met with in the same field with the annual, if a streamlet or springy place exist; and this not rarely 5 feet high, bearing a truly magnificent panicle of racemes, sometimes the whole cluster nearly 2 feet long, and half as broad; and the annual here defined will be in seed and dying while its neighbor of the streamlets is not yet in full flower toward the end of April."

In addition to the collection from San Mateo Co, there is another relevant sheet at PH: California. [Marin Co.:] Pt. Reyes, 15 Apr 1886, *E.L. Greene s.n.* (PH!). Each of the three sheets has a label with handwritten identification by Greene as "*Mimulus arvensis* Greene." The PH sheets from Belmont were annotated by Pennell as isotypes of *M. arvensis.*

In the protologue Greene speculated that *Mimulus arvensis* might be the same as *M. lyratus*. Both taxa were treated as distinct species by Pennell (1951); Grant (1924) treated *M. arvensis* as *M. guttatus* var. *arvensis* but *M. lyratus* as a synonym of typical *M. guttatus*. *Mimulus lyratus* is regarded here as a synonym of *M. guttatus.*

Mimulus longulus Greene, Leafl. Bot. Observ. Crit. 2: 4. 1909. **LECTOTYPE** (designated here): **USA**. **Nevada**. [Elko Co.:] Deeth, in low meadows along the Humboldt River, [protologue: "margins of spring pools that in summer have gone dry,"] 26 Jul 1896, *E.L. Greene s.n.* (ND-Greene 46314!, photo-PH!; isolectotype: NG-Greene!). "The species can only be compared with my *M. Hallii* of Colorado; and that is low, with rather crowded leaves and flowers; has also a calyx with much more unequal teeth and these closely connivent." Treated as a distinct species by Pennell (1951), who noted that it occurs on the "Columbia Plateau of eastern Washington and Oregon eastward and southward to Montana, Utah, and Arizona." The bracts have little or no villous vestiture.

Mimulus micranthus Heller, Muhlenbergia 8: 132. 1912. *Mimulus nasutus* Greene var. *micranthus* (Heller) A.L. Grant, Ann. Missouri Bot. Gard. 11: 182. 1924. *Mimulus guttatus* var. *micranthus* (Heller) G.R. Campbell, Aliso 2: 332. 1950. *Mimulus guttatus* subsp. *micranthus* (Heller) Munz, Aliso 4: 99. 1958. **TYPE**: **USA**. **California**. Santa Clara Co.: Twenty-seven Mile Drive near Congress Springs, 13 May 1904, *A.A. Heller 7410* (holotype: BKL?; isotypes: CAS digital image!, MO!, MSC, NY digital image!, PH!, UC!, US digital image!).

Mimulus hallii var. *alvordensis* Pennell ex Peck, Man. Pl. Oregon, 655. 1941. **TYPE**: **USA**. **Oregon**. [Harney Co.:] Alvord Ranch, lower flanks of Steins Mts., 2 Jul 1927, *L.F. Henderson 7129* (holotype: PH!). Annotated by Pennell in 1945 as "TYPE" of var. *alvordensis* then in 1939 as "*Mimulus longulus* Greene." The protologue gives only this: "Wet, somewhat alkaline soil, Harney and Malheur cos."

Annual, taprooted or fibrous-rooted, sometimes rooting at proximal cauline nodes if decumbent. **Stems** erect to decumbent-ascending, 5–70 cm, simple or branched from proximal to medial nodes, usually 4-angled, fistulose to very narrow, glabrous or sometimes minutely hirtellous in the inflorescence with deflexed hairs, eglandular. **Leaves** basal and cauline or basal absent by flowering, often largest at midstem or above, reduced in size distally, blades ovate to orbicular, orbicular-ovate, oblong-ovate, or (midddle and upper cauline) depressed-ovate to nearly reniform, (5–)10–35(–45) mm x 6–26(–50) mm, palmately 3–5-veined, glabrous except for bracts densely villous abaxially or sometimes on both surfaces with vitreous eglandular hairs (completely glabrous in Baja California), margins denticulate or subentire to distinctly dentate, on larger plants the proximal characteristically lacerate-lobed to pinnatifid at the margin base, apex rounded, base rounded to truncate, subcordate, or shallowly cordate, distal broadly orbicular to depressed-ovate, sessile, petioles 3–20(–90) mm. **Flowers** 3–8(–16), from remote distal nodes. **Fruiting pedicels** 5–40(–90) mm, glabrous. **Fruiting calyces** ovate-campanulate, (7–)9–14, lobes turning up and closing the throat or not and the throat remaining open, with or without red dots, faces minutely hirtellous. **Corollas** yellow, usually red-spotted, tube-throats cylindric-funnelform, (7–)8–12 mm, exserted (0–)1–2(–)3 mm beyond calyx margin, limb weakly bilabiate to subcylindric and nearly regular, expanded 5–10 mm (pressed). **Styles** glabrous. **Plesiogamous**; anther pairs not separated in level, stigma at the same level. **Capsules** (5–)6–7 mm, stipitate, included. 2*n* = 28.

Flowering Apr–Jun(–Jul). Hills, ridges, clay banks, stream banks, moist woods; 30–1900(–2300 in Nevada) m; California, Nevada, Oregon; Mexico (Baja California). Map 15.

Additional collections examined. **MEXICO**. **Baja California**. 2 km SE of El Chocolate, 31º 30.5' N, 116º 23.5' W, local in wet soil, 275 m, 11 Mar 1979, *Moran 26692* (SD); Sierra La Asamblea, NE of El Crucero (jct of Hwy 1 and road to Bahia de Los Angeles), riparian zone in the vicinity of Rancho San Luis, 29º 16' 35" N, 114º 02' 41" W, Vizcaino desert, 1000 m, 20 Apr 2004, *Rebman 9872* (SD); Sierra La Libertad, vicinity of the abandoned Rancho El Paraiso, along the riparian area of Arroyo El Paraiso, 28.5424º N, 113.631º W, Sonoran desert, 745 m, 25 Apr 2009, *Rebman 17265* (SD); Canyon del Diablo, E slope of Sierra San Pedro Martir, reached via Santa Clara, 4200 ft, 31 Mar 1973, *Taylor 2306* (UC). **CANADA**. **British Columbia**. [Chilliwack-Fraser Canyon Co.:] Aspen Grove along edge of shallow lake in rich humus, 3500 ft, 26 Jun 1934, *Went 43* (UC). **USA**. **California.** Alameda Co.: Berkeley, Apr 1893, *Michener & Bioletti s.n.* (ND-Greene); "Boswell's" damp rocky places, 300 ft, 10 Feb 1900, *Tracy 513* (TEX). Humboldt Co.: Alder Point on Eel River, shady wet ground around spring, 500 ft, corolla yellow, not spotted, 22 May 1903, *Tracy 1883* (TEX); 2 mi N of Laytonville, moist clay bank in shade, 7 Jun 1937, *Heller 15892* (MO); Alton, 100-300 ft, 9 Jun 1912, *Tracy 3688* (MO). Lake Co.: Hough's Springs, 7 May 1928, *Abrams 12530* (MO). Marin Co.: Tiburon, Jun 1886, *Greene s.n.* (ND-Greene); Mendocino Co.: N of Cahto Peak ca 5 airmiles W of Laytonville, Stoten Opening at head of Elder Creek on W side of Signal Peak, moist ground along streamlet, ca. 3800 ft, flrs yellow, appearing cleistogamous, 14 May 1989, *Ertter 8467* (TEX); 6.3 mi E of Dos Rios, along Poonbiurry Road between Dos Rios and Covelo, along small stream in wet soil, 28 May 1949, *Wiggins 12145* (SMU, UT). Modoc Co.: Davis Creek, Jun 1895, *Austin s.n.* (ND-Greene); Napa Co.: hills E of St. Helena, 23 Apr 1915, *Jepson 6238* (UC). San Mateo Co.: San Mateo, 21 Apr 1894, *Burnham s.n.* (BH, as cited by Grant 1924). Santa Clara Co.: Stanford University, 25 Apr 1902, *Abrams 2370* (MO); foothills near Stanford University, 2 May 1902, *Baker 881* (ND-Greene); Alviso, 1892, *Bioletti s.n.* (ND-Greene); summit of the first ridge west of Los Gatos, 9 May 1904, *Heller 7393* (MO); Smith Creek, foot of Mt. Hamilton, 10 May 1907, *Heller*

8517 (MO); hills west of Los Gatos, ca. 7000 ft, 30 Apr 1980, *Heller 8936* (MO). Sonoma Co.: near Windsor, 18 Apr 1902, *Heller & Brown s.n.* (MO); Shellville, May 1892, *Michener & Bioletti s.n.* (ND-Greene). Siskyou Co.: Metcalf's ranch, NE base of Mt. Eddy, open places in the forest, ca. 3800 ft, 20 Jun 1919, *Heller 13256* (MO). **Idaho.** Bear Lake Co.: Georgetown Canyon, 8 air mi NE of Georgetown, in cold spring water, 13 Jul 1978, *Shultz 2753* (UT). Canyon Co.: Squaw Butte, gravelly wet places, 3500 ft, 29 May 1910, *Macbride 143* (MO). Cassia Co.: Raft River Geothermal Area, 17 mi S of Malta, along lower Cottonwood Creek, 5000 ft, 22 Jun 1976, *Allan 796* (UT); Basin, 7 Jul 1964, *Harper 1157* (UT). Owyhee Co.: Hot Hole, East Fork Bruneau, wet woods, 3 Jul 1912, *Nelson & Macbride 1908* (MO, SMU). **Nevada.** Elko Co.: Star Canyon, SE of Deeth, 5600 ft, 10 Jul 1912, *Heller 10569* (MO, UC); Jarbridge, by a spring, 7000 ft, 6 Jul 1912, *Nelson & Macbride 1959* (MO, SMU); Route 40, 2-3 miles SE of Deeth, slow-flowing brook in meadow, 5400-5500 ft, 22 Jul 1938, *Pennell and Schaeffer 23430* (PH 2 sheets!). Humboldt Co.: Paradise Valley, NE of Winnemuca, irrigated meadow, 4700 ft, 24 Jun 1967, *Gentry 1633* (UC). White Pine Co.: 2 mi NE of Hamilton, moist spring, 8000 ft, 8 Jul 1946, *McMillan et al. 80* (UT). **Oregon.** Grant Co.: 3 mi above Prairie, wet sunny places along W Fork of Dixie Creek, 18 Jun 1925, *Henderson 5493* (MO-2 sheets). Harney Co.: damp ground 5 mi N of Wagontire, 22 Jun 1941, *Peck 20858* (UC). Jackson Co.: Queen's Branch, 18 Jun 1892, *Hammond 311* (MO). Klamath Co.: along Hwy 66 ca. 10.5 mi E of Klamath River crossing at Boyles Reservoir, moist to wet meadow area, *Juncus* dominant, bordered by *Pinus ponderosa* forest, ca. 4400 ft, 25 Jun 1995, *Taylor 15134* (UC). Linn Co.: Big Meadows, springy places, 1370 m, 26 Jul 1894, *Leiberg 533* (UC). **Utah**. Box Elder Co.: Raft River Mts., Dunn Canyon, Middle Fork, moist loam soil in seeps under aspen, frequent, 7000 ft, 31 Jul 1943, *Maguire & Holmgren 22188* (UC). **Washington**. Stevens Co.: Loon Lake, wet meadows, common, 23 Jun 1903, *Beattie & Chapman 2101* (UC).

Erythranthe arvensis is characterized by its annual duration (fibrous-rooted or taprooted) but commonly rooting at proximal cauline nodes, glabrous, fistulose stems with nodes few and remotely spaced, depressed-ovate leaves with margins often sublyrate (lacerate-lobed to subpinnatifid) at the base, distal leaves and bracts densely villous with vitreous eglandular hairs, other leaves (proximally) glabrous, and corollas varying in size from relatively small but perhaps chasmogamous (the type of *Mimulus arvensis*) to even smaller (cleistogamous; the type of *Mimulus micranthus*). The breeding system is consistently autogamous — in larger to smaller corollas.

The plants in Baja California are considerably disjunct from the main range and they are completely glabrous, lacking the vitreous hairs on the bracts. The calyces are consistently open at maturity. More detailed study may show them to be distinct in other ways.

A diagnostic feature of *Mimulus arvensis* has been described as its relatively short and even-sized calyx lobes that do not turn upward to close the orifice, and this commonly is an evident feature. In fact, however, even among collections cited by Grant, some plants have a longer upper calyx lobe and lower lobes that turn upward in variable degrees.

Leaf morphology of *Erythranthe arvensis* often is very similar to that of *E. microphylla* and the two perhaps hybridize. An example of a possible hybrid is this: **California**. Lake Co.: 27 mi from Montcello, boggy ground along roadside, 25 Apr 1943, *Ensign 337* (DAV). This is a tall plant with racemes on side branches, large, closed fruiting calyces (13–18 mm), densely villous distal bracts, and relatively short corolla tubes (12–14 mm) with the stigma only very slightly above the upper anther pair.

Some plants from the Cosumnes River Preserve in Sacramento Co. (e.g., *PeBenito et al. 31*, *Popp 17na*, DAV) have overall morphology of *Erythranthe arvensis*, including villous bracts, but the corollas are slightly longer than typical and the anther pairs are separated with the stigma at or slightly above the upper pair. This might reflect genetic influence from typical *E. microphylla*, which occurs in the same area. In Cold Canyon, Solano County, plants (DAV) identified here as *E. arvensis* have hirtellous stems and leaves, perhaps indicating genetic influence of some other species.

A collection from the Stanislaus River shows plants with the vegetative morphology of *Erythranthe arvensis* and with non-closing calyces but the corollas are longer with expanded limbs and the stigma well above both pairs of stamens. A hybrid with *E. guttata* or *E. microphylla*?, but more than a single plant apparently is represented on the two sheets. **California**. Tuolumne/ Stanislaus/ San Joaquin Co.: Stanislaus River, [no other locality data,] 17 Jun 1889, *Greene s.n.* (ND-Greene-2 sheets).

A series of plants from southeastern Oregon, may well warrant recognition at specific rank if they further prove to be consistent in morphology. A total of 25 individuals on two sheets have the aspect of *Erythranthe arvensis* but the stems of all are consistently sparsely retrorse-hirtellous. The plants are 2–14 cm tall. Harney Co.: 12 mi W of Vale, seepage slope, 21 Jun 1948, *Peck 25313* (UC); 5 mi E of Harper, seepage slope, 21 Jun 1948, *Peck 25313* (UC). The two collections are labeled with the same collection number but apparently are from slightly different locations: the distance between Vale and Harper is about 21 miles.

Plants of *Leiberg 533* from Linn Co., Oregon, are large and have the typical vegetative aspect of *Erythranthe arvensis*, but the pedicels, bracts, and calyces have a mix of eglandular-hirtellous and glandular hairs, atypical of the species. Plants from Stevens Co., Washington, are typical; those from British Columbia have a typical aspect and vestiture except for a slight admixture of hirtellous hairs.

Identification of Utah and southern Idaho populations as *Erythranthe arvensis* is a tentative hypothesis, as there appears to be little difference between them and the Colorado system of *E. hallii*, which is tightly coherent morphologically and geographically, but these plants need to be studied in the context of the larger group of annuals with autogamous flowers, as discussed under *E. charlestonensis*.

28. ERYTHRANTHE BRACHYSTYLIS (Edwin) Nesom, Phytoneuron 2012-40: 43. 2012. *Mimulus brachystylis* Edwin, Leafl. W. Bot. 7: 137. 1954. **TYPE**: **USA**. **Nevada**. Nye Co.: Moist loam around a spring on a steep north slope in Sunnyside Canyon about 5 mi N of Ione, 7000 ft, 14 Jul 1930, *K.H. Beach and L.E. Mills 881* (holotype: US digital image!, Fig. 9; isotype: UC!). The holotype includes about 10 plants, the isotype 7 plants.

Annuals, fibrous-rooted, less commonly taprooted, apparently sometimes producing thin runners from basal nodes. **Stems** erect, 6–22 cm, 4-angled, filiform to slightly thickened but not distinctly fistulose, glabrous. **Leaves** basal and cauline, blades ovate to depressed-ovate or suborbicular, margins undulate to subentire or weakly and irregularly dentate, apices rounded, bases truncate to subcordate, proximal petiolate, distal subsessile to sessile, proximal and medial glabrous, distal villous with thin-walled, flattened, vitreous hairs, with an admixture of eglandular, sharp-pointed hairs. **Flowers** 4–10, from medial to distal nodes. **Fruiting pedicels** 5–10 mm in proximal axils, shorter than or equalling subtending leaves, 1–5 mm distally and the calyces appearing sessile or subsessile, glabrous. **Fruiting calyces** broadly elliptic-ovoid, 10–13 mm, apparently not closing at the throat or only slightly so, red-tinged to sparsely purple-dotted or without dots, minutely hirtellous, lobes subequal, upper slightly longer than the others. **Corollas** yellow, apparently without red markings, tube-throats narrowly cylindric, 7–9 mm, exserted 0–1 mm beyond the calyx margin, limb weakly bilabiate or hardly at all, expanded ca. 3 mm (pressed). **Styles** glabrous. **Plesiogamous**; anther pairs and stigma at the same level. **Capsules** 4–5 mm, stipitate, included.

Known only from the type collection in Nye Co., Nevada. Map 15.

Type.
Mimulus brachystylis Edwin
Leaflets of Western Botany
april 16, 1954 Vol VII; No 6.
G. EDWIN, U.S. NATIONAL ARBORETUM HERBARIUM

PLANTS OF NYE COUNTY NEVADA
Mimulus (a peculiar form of M. guttatus DC. ?)
RuaV!
Moist loam around a spring on a steep north slope
in Sunnyside Canyon about 5 miles north of Ione.
Elevation 7000 feet.
With Mimulus (#879).
Kay H.Beach # 881 July 14, 1940
Laura E.Mills

Figure 9. *Erythranthe brachystylis*. Holotype of *Mimulus brachystylis*, US.

Erythranthe brachystylis is very similar to *E. arvensis*. Both are annual in duration and produce depressed-ovate leaves, the distal with vitreous-villous surfaces, and tiny corollas barely exserted from the calyx and probably cleistogamous (the protologue of *Mimulus brachystylis* notes "style much shorter than the shorter pair of stamens, scarcely 3–3.5 mm long"). The vestiture of the distal leaves includes an admixture of eglandular sharp-pointed hairs, sometimes encountered in *E. arvensis*, though not typical, perhaps reflecting introgression from *E. nasuta*.

The distinction of *Erythranthe brachystylis* from *E. arvensis* is primarily in its foreshortened pedicels and more inflated fruiting calyces. The fruiting calyces appear to be subsessile or on pedicels shorter or only equalling the subtending leaves. The difference is qualitative but produces a distinctive aspect.

29. ERYTHRANTHE CORDATA (Greene) Nesom, Phytoneuron 2012-40: 43. 2012. *Mimulus cordatus* Greene, Leafl. Bot. Observ. Crit. 2: 5. 1909. **LECTOTYPE** (Pennell by annotation in 1941, formally designated here): **USA**. **New Mexico**. [Grant Co.:] Bear Mountain, near Silver City, about 5000 ft, 24 Apr 1903, *O.B. Metcalfe 28* (US digital image! photo-PH!; isolectotypes: DS digital image!, MO-2 sheets!, ND-Greene!, NY digital image!, PH!, UC!). Noted in the protologue: "part of [O.B. Metcalfe's] n. 28 as in U.S. Herb., the other specimens under that distribution number being of a very different species." The US sheet has a fruiting plant of *E. cordata* and four separate flowering branches of *E. geyeri*; Pennell in 1941 annotated the sheet to indicate that the single plant of *E. cordata* is the "TYPE." All plants on the DS, MO, ND-Greene, NY, PH, and UC sheets are *E. cordata*. Treated as a distinct species by Pennell (1951), who described the range as "southern California and northern Lower California, east to southern New Mexico."

Mimulus maguirei Pennell, Notul. Nat. Acad. Sci. Philadelphia 43: 6. 1940. **TYPE**: **USA. Arizona.** Coconino Co.: 2 mi W of Williams, Mt. Spring Ranch, among sedges under *Pinus ponderosa* in small swamp, 6500 ft, 26 Jun 1935, *B. Maguire et al. 12214* (holotype: PH!). Annotated by F.W. Pennell in 1945 as *Mimulus longulus* Greene (a synonym of *Erythranthe arvensis*).

Annual, fibrous–rooted, sometimes producing leafy runners from basal nodes, stems often rooting at proximal nodes and appearing rhizome-like. **Stems** mostly erect, 12–40 cm, very rarely apparently greater than 100 cm, mostly simple, commonly fistulose, distinctly stipitate-glandular with fine, minute, gland–tipped hairs. **Leaves** basal and cauline, basal persistent, basal and lower cauline petiolate, petioles 6–20(–40) mm, blades orbicular to broadly elliptic-ovate or oblong-elliptic, basal largest, basal and midcauline 15–30(–50) mm, gradually reduced in size distally to as small as 6 mm, cauline mostly sessile, not connate, becoming broadly ovate to narrowly reniform, palmately 3–5(–7)-veined, margins shallowly and evenly to unevenly dentate, apex obtuse to rounded, base cuneate to truncate or shallowly cordate. **Flowers** (5–)10–16 in bracteate racemes. **Fruiting pedicels** 10–30(–45) mm, minutely stipitate-glandular. **Fruiting calyces** (8–)14–18(–20) mm, nodding 45º–90º, closing, apparently without red dots, upper lobe longest, 1.5–2 mm, sparsely stipitate-glandular to hirsutulous (or mixed glandular-hirsutulous), or glabrous. **Corollas** yellow, red-spotted, lower lip deeper yellow, tube-throats 8–14 mm, exserted 1–3 mm beyond calyx margin, limb weakly to strongly bilabiate, expanded 9–14 mm across (pressed). **Styles** glabrous. **Plesiogamous**; anther pairs and stigma at the same level. **Capsules** 5–7 mm, stipitate, included. $2n = 60$.

Flowering (Jan–)Mar–Jun. Springs, seeps, stream edges, muddy banks, flood plains, marshes and swamps, wash bottoms, wet depressions, wet places among boulders; (600–)800–2400(– ca. 3000) m. Arizona, California, Colorado, Nevada, New Mexico, Texas, Utah. Map 16.

A collection identified as *Erythranthe cordata* by the present author, voucher for $n = 28$ (Catron Co., N.M., as cited below), needs to be rechecked for identity since six other chromosome counts for *E. cordata* have been $2n = 60$ (San Bernadino Co., Calif.; Grant Co., N.Mex.; Brewster, Culberson, Jeff Davis, and Presidio cos., Tex.). The chromosome number of *E. cordata* may indicate that it is not as closely related to *E. arvensis* ($2n = 28$) as hypothesized here.

Collections examined. **MEXICO**. **Chihuahua**. 5 mi SW of Rancho Los Nogales along Piedras Verdes River, riparian, 5350 ft, 9 Jul 1997, *Spencer et al. 393* (TEX). **Coahuila**. Mpio. Ocampo, Sierra del Carmen, Rcho. Morteros y Rcho. San Isidro, ca. 178 km de Musquiz por la brecha Muzquiz-Boquillas del Carmen (carr. 53), 1300 m, matorral rosetofilo, 27 Mar 1992, *Carranza et al. 1327* (ARIZ); Mpio. Ocampo, Sierra Maderas del Carmen, moist zone along creek below Campo 5 in Oso Canyon, 29 May 1975, *Riskind & Patterson 1836g* (LL). **Sonora**. Palm Canyon, Sierra Baviso, 17 mi SE of Magdalena on road to Cucurpe, seep on N-facing slope, 19 Mar 1978, *McCarten 2725* (ARIZ); Dead Bull Canyon, near Arizpe, riparian, 17 Mar 1982, *Thompson & Davis 82-31* (ARIZ); ca. 5 mi E of Esqueda along road to reservoir, in canyon, ca. 4000 ft, 6 Apr 11979, *Toolin 259* (ARIZ); Rio de los Alisos (Rio Magdalena), 28.6 m S of Nogales along Mex Rte 15, in wet sandy mud, with *Populus fremontii* and *Platanus wrightii*, 14 Mar 1980, *Toolin 543* (ARIZ); Palm Canyon, Sierra Baviso, 17 mi SE of Magdalena, streamside, 13 Feb 1977, *Van Devender s.n.* (ARIZ); Rio Moctezuma, Moctezuma, Barisómari, 27 Jun 1938, *White 341* (ARIZ); Rio Bavispe, Colonia Oaxaca, at water's edge, 7 Jul 1938, *White 456* (ARIZ); Aguaje de Bacatejaca, between Granados and Bacadéhuachi, grassland, 7 Jul 1940, *White 2917* (ARIZ).

Representative collections examined. **USA. Arizona**. Cochise Co.: Chiricahua Mts., E of Onion Saddle, 7200 ft, 31 Mar 1962, *Barr 62-190* (ARIZ); Chiricahua Mts., Barfoot Park, 8000-8250 ft, 19 Sep 1906, *Blumer 1399* (ARIZ); Mule Mts., Bisbee, wet places, Apr 1909, *Goodding 53* (UT), *Goodding 60* (ARIZ); Huachuca Game Preserve, Tinker Canyon, in edge of water, 14 Apr 1950, *Goodding 123-50* (ARIZ); Dragoon Mts., canyon below Van Horn Mine Cabin, 5 May 1953, *Goodding 58-53* (ARIZ); Ft. Huachuca Military Reservation, Kino Spring, 22 Apr 1961, *Goodding 17-61* (ARIZ-2 sheets). Coconino Co.: lower part of Oak Creek Canyon, wet area, ca. 5000 ft, 8 May 1934, *Ferguson & Ottley 5046* (UC). Gila Co.: 2 mi N of Greenback Creek at Bouquet Ranch, ca. 5 mi N of Theodore Roosevelt Lake, cattle tank/spring, bank's edge, 3 Apr 1991, *Baker 8161* (ARIZ); Fort Apache Indian Reservation, Rock Creek crossing of Canyon Inn-Medicine trail, on and adjacent to seeps-wet soils, ca. 4000 ft, 26 Apr 1967, *Granfelt 67-58* (ARIZ). Graham Co.: Turkey Creek, 6 mi W of Point of Pines, 70 mi E of San Carlos, flood plain of creek, ponderosa pine, 6200 ft, 24 Jul 1952, *Bohrer 436* (ARIZ); Graham Mts., Tripp Canyon, 15 mi S of Pima, along water course, 9 Apr 1935, *Moeller 10573* (ARIZ). Maricopa Co.: 4 mi S of Wickenburg, Palm Lake, marsh, 12 May 1966, *Crutchfield 1526* (LL); Sauceda Mts., 1500 ft, 27 Mar 1960, *Johnson s.n.* (ARIZ); Lake Pleasant Regional Park, area #6, Cottonwood Creek, in creek, 27 Mar 1965, *Lehto 4729* (ARIZ); Route 88, Apache Trail, Tortilla Flats, muddy bank of pool, 29 Mar 1940, *Pennell & Gibson 24968* (ARIZ); Sierra Estrella above Santa Cruz Village, small plants on N-facing slope of wet cliff base, 570 m, 2 Apr 1985, *Rea 608* (ARIZ). Mohave Co.: Black Mts., 3 mi E of Sitgreaves Pass, spring, 26 Mar 1967, *Barr 67-97* (ARIZ); Cerbat Mts., 2 mi E of Chloride, 4500 ft, in mats in seep on cliff, 20 Apr 1979, *Bowers 1659* (ARIZ); Outer Gorge, Toroweap, Saddle Horse Canyon, Devils's Bathtub, under juniper, 4500 ft, 10 May 1952, *Cottam 13251* (UT); along Trout Creek ca. 6 km downstream of Ash Creek [ca 34.88° N, 113.65° W], grus and granite substrate, with *Fraxinus velutina* and *Acacia greggii*, 3600 ft, 18 Apr 2006, *Rink 4727* (ARIZ). Pima Co.: Organ Pipe Cactus Natl. Monument area, Dripping Spring, 15 Apr 1952, *Cottam 12817* (ARIZ, UT); Puerto Blanco Mts., Dripping Springs, moist soil near spring, 2300 ft, 18 Mar 1945, *Darrow 2443* (ARIZ); Ajo Mts., Alamo Canyon, 2500 ft, 14 Mar 1939, *Nichol s.n.* (ARIZ); northern Santa Rita Mts., moist wash bottom in desert grassland, 4450 ft, 5 Apr 1986, *McLaughlin 3334* (ARIZ); along Arivaca Creek, 5.5 mi NW of Arivaca, walnut, ash, cottonwood, *Sambucus mexicana*, *Vitis arizonica*, 3450 ft, 3 Apr 1988, *McLaughlin 4498* (ARIZ); Buenos Aires Natl. Wildlife Refuge, unnamed canyon on S side of Las Guijas Mts., moist face of Mesquite Root Dam, 3600 ft, 23 Mar 1989, *McLaughlin 5476* (ARIZ); Saguaro Natl. Monument, canyon near Sweetwater Trail, wet depression in limestone bedrock, 3499 ft, 7 Mar 1989, *Rondeau 89-57* (ARIZ); Fort Lowell, Rillito River, 25 Apr 1903, *Thornber 5386* (ARIZ); Sabino Canyon, Santa Catalina Mts, 2 May 1903, *Thornber 5498* (TEX); Santa Catalina Mts., Sabino Canyon, common along water courses, 3000-5000 ft, 5 Apr 1913, *Thornber s.n.* (ARIZ); Tucson, 1 May 1894, *Toumey s.n.* (UC). Pinal Co.: Sacaton, Gila River bottom, 25 Mar 1932, *Harrison & Kearney 8383* (ARIZ). Santa Cruz Co.: Pajarito Mts., Sycamore Canyon, ca. 1/4 mi below Hank & Yank Spring, in water of stream in narrow canyon, oak woodland, ca. 4000 ft, 7 Apr 1974, *Longwell s.n.* (ARIZ); San Rafael State Park, Parker Canyon, wash in sandy soil with *Chilopsis linearis*, *Chrysothamnus nauseosus*, 28 Mar 2001, *McLaughlin 9096* (ARIZ); Santa Rita Mts., 6 Apr 1935, *Nelson 1398* (UC); mountains between Ruby and the Tucson-Nogales hwy, "Massacre Camp," rocky stream banks, 12 Apr 1935, *Nelson & Nelson 1478* (MO); Sonoita River, near Patagonia, 4000 ft, 22 Mar 1925, *Shreve s.n.* (ARIZ); mts. near Patagonia, Apr 1908, *Thornber 2905* (ARIZ-2 sheets). Yavapai Co.: Prescott Natl. Forest, Milk Creek, 7 mi N of Wagoner, riparian, 3900 ft, 28 Apr 1968, *Carpenter s.n.* (SMU); Bradshaw Mts., 22 Jun 1892, *Toumey s.n.* (UC). **California**. San Bernadino Co.: Deet[?] Canyon between Whipple Mts., and Black Meadows Wash, Power Line Rd, Parker Dam, marshy ground, bottom of canyon, 21 Apr 1940, *Alexander & Kellogg 1186* (UC 667449); Whipple Mts., sandy wash, in seep, 25 Apr 1940, *Alexander & Kellogg 1220* (UC); Whipple Mts., marshy meadow in a deep canyon, Vickery cult. 5063, seeds from UC 667449, "1 to 3 ft in nature but only 6 inches to 1 ft in greenhouse," voucher for *n* = 30 (UC, UT-3 sheets); Mohave Desert, W slope of Providence Mts., 6 airline mi E of Kelso in Cornfield Spring Canyon, *Larrea*-*Yucca schidigera*, wet gravel along stream banks, 3400 ft, 28 May 1941, *Wolf 10818* (UC). **Nevada**. Clark Co.: Pintwater Range, Tim Spring, 4800 ft, 22 Jul 1978, *Ackerman 31231* (UC); Opal Mts., Delaney Canyon, 2 mi S of Nelson, 4200 ft, 27 Apr 1938, *Train 1512* (UC). Nye Co.: W Frenchman, exclosure above Cane Springs pond, 4000 ft, 2 Jun 1967, *Beatley 3999* (JEPS); NW Yucca Flat, Whiterock Spring, seepage area, 5000 ft, 16 Jun 1967, *Beatley & Bostick 4109* (JEPS). **New Mexico.** Catron Co.: Blue River, Apache Natl. Forest, growing on gravel at edge of water, 25 Aug 1966, *Crutchfield 2084* (LL); 10 mi S of Reserve, S of jct of NM Hwy 12 with US 80, shallow rocky stream, open sunny area, 5800 ft, 28 Jun 1963, *Vickery & Tai 7*, cult. no. 6613, voucher for *n* = 28 (UT); Gila Cliff Dwellings Natl. Monument, 15 May 2001, *West 448* (ARIZ). Dona Ana Co.: Organ Mts., May 1891, *Wooton s.n.* (NMC); Organ Mts., Filmore Canyon, 15 May 1899, *Wooton s.n.* (NMC); Organ Mts., Filmore Cañon, 26 May 1905, *Wooton s.n.* (NMC); Organ Mts., 28 May 1905, *Wooton s.n.* (UC). Grant Co.: Foxtail Canyon on Gila River, wet granitic sand, 27 Apr 1966, *Crutchfield 1381* (LL); Burro Mts, W.C. Silby's Range, Gila Forest, 1880-2180 m, 22 Oct 1919, *Eggleston 16440* (PH); 4.5 mi N of 516 Ranch, Mogollon Creek, with *Quercus*, *Juniperus*, *Juglans*, *Rhus*, *Platanus*, 11 Jun 1935, *Maguire et al. 11936* (MO); 2.5 mi N of Pinos Altos, wet shaded hillside about spring in canyon, 24 Apr 1947, *McVaugh 8043* (TEX); mountains near Pinos Altos, 26 Jun 1936, *Stewart s.n.* (MO); Mangus Springs, 17 road mi NW of Silver City, growing in Mangus Spring at its intersection with the sandy arroyo of Mangus Creek, which passes under US-180, 4800 ft, 12 May 1981, *Ward & Salazar 82-013*, voucher for *n* = 30 (NMC). Hidalgo Co.: Guadalupe Canyon, 15 mi E of jct with road to Douglas, Arizona, *Juniper-Agave-Yucca* zone, sandy soil along edge of creek, 4200 ft, 20 Apr 1968, *Hess 1776* (NMC); Peloncillo Mts., Hwy 80 at Granite Gap, sandy wash, 4500 ft, 30 Apr 1983, *Worthington 10,133* (UT). Luna Co.: wet places in old creek bed, canyon E of road, foothills E of Cook's Peak, 12 mi NW of Florida Station, 29 Apr 1947, *McVaugh 8130* (TEX-2 sheets); Florida Mts., NW side of mts., SE of Capitol Dome, 5300 ft, 30 Apr 1983, *Worthington 10133* (UT). San Juan Co.: 10 mi W of Farmington, seep area, 27 Jun 1963, *Tai & Vickery 1* (UT). Sierra Co.: 1 mi W of Hillsboro, 5600 ft, 1 May 1905, *Metcalfe 1537* (MO-2 sheets, NMC, TEX-2 sheets). Socorro Co.: Water Canyon, Cibola Natl. Forest, in S Baldy area, small spring in canyon, pine-oak-juniper, 3 Jun 1965, *Crutchfield 112* (LL, NMC); mountains SE of Patterson, 5800 ft, 16 Aug 1900, *Wooton s.n.* (NMC). **Texas**. Brewster Co.: Alpine Creek below Kokernut Springs, 18 May 1946, *Cory 53186*, Vickery cult. 5373, voucher for *n* = 30 (UT); Big Bend Natl. Park, Tornillo Creek near Hot Springs, 20 Apr 1948, *Whitehouse 19715* (SRSC). Culberson Co.: W side of Beach Mt., ca. 7 mi NW of Van Horn, edge of seep, 7 Sep 1963, no collector cited, *Vickery cult. 6296*, voucher for *n* = 30 (UT). El Paso Co.:

ca. 20 mi E of El Paso, frequent in wet places among boulders at Hueco Tanks, 4000 ft, 5 Apr 1958, *Warnock & Johnston 16158* (MO, SRSC, TEX); Hueco Mts., Hueco Tanks, dried bottom and edges of pond, silty soil, 20 Aug 1946, *Waterfall 6606* (MO); Franklin Mts., Ash Canyon, 0.5 mi SE top N Franklin Mt., in mesic canyon among rhyolite boulders at springs and seeps, 29 Apr 1978, *Worthington 2711* (TEX). Jeff Davis Co.: near Ft. Davis, Limpia Creek, in shallow pools, 10 Oct 1926, *Palmer 32152* (TEX); Davis Mts., wet ground about spring, 8 Jun 1928, *Palmer 34402* (MO); Limpia Canyon, 5000 ft, 30 Jun 1962, *Tai & Vickery 12*, cult. 6618, voucher for *n* = 30 (UT); Davis Mts., frequent along Limpia Canyon, Wild Rose Pass, 4700 ft, 24 May 1949, *Warnock 8652* (SRSC). Presidio Co.: Tapia Canyon, 12.4 mi E of Redford, in wet sand and seepage, 16 Apr 1965, *Correll 30859* (LL); Pinto Canyon near Ruidosa, abundant in spring water, 13 Apr 1919, *Hanson 590* (MO); Fresno Creek, 5 mi upstream from road to Lajitas, 12 Jul 1982, *Johnston & Warnock 3682*, Vickery cult 6294, voucher for *n* = 30 (UT); W side of Chinati Mts., infrequent in moist areas below dam in lower Tinaja Prieta Canyon, 3900 ft, 10 Nov 1988, *Warnock 275* (SRSC). **Utah**. Kane Co.: Cottonwood Wash Canyon, 26.5 mi SE of the jct of the Cottonwood Wash road and Utah Hwy 54 at Cannonville, at Cottonwood Wash Spring, 5100 ft, 7 Jun 1967, *Reveal 819* (TEX). Washington Co.: Zion Natl. Park, Horse Pasture Plateau, where Potato Hollow ends at cliffs edge, wet marsh below small reservoir, 6750 ft, 22 Jun 1965, *Holmgren 1995* (TEX); Zion Natl. Park, Emerald Pool Trail, 4000 ft, 6 May 1935, *Weight 838z* (UT).

Erythranthe cordata is characterized by its fibrous-rooted habit (annual in duration, without rhizomes but commonly rooting at the lower nodes), short corollas and autogamous fertility (anthers and stigma at the same level), closed calyces, sparsely villous-glandular vestiture (lacking hirtellous, eglandular hairs), and stems commonly fistulose in larger plants. The abbreviated corollas with autogamous fertility of *E. cordata* are diagnostic and separate it from *E. guttata*. The difference in chromosome number also points to their evolutionary distinction.

The following contrasts, using style length even when corollas are absent, usually provide a distinction between the two species.

1. Corolla tubes 8–14 mm, exserted 1–3 mm beyond calyx margin, limb expanded 9–14 mm (pressed); styles 7–10 mm, exserted 1–3 beyond fruiting calyx margin; plesiogamous .... **Erythranthe cordata**
1. Corolla tubes (10–)12–20(–26) mm, exserted 3–5 beyond calyx margin, limb expanded 12–24(–25) mm (pressed); styles 15–20 mm, exserted 6–9 mm beyond fruiting calyx margin; herkogamous .... **Erythranthe guttata**

In the interpretation here, plants of *Erythranthe cordata* are highly variable in size — from tiny fibrous-rooted plants with nearly filiform stems to much larger individuals with fistulose stems rooting at proximal nodes. Label comments for a Kane Co., Utah, population of *E. cordata* (*Reveal 819*) are congruent with the observations of the present study over the whole range of the species: "This population is exceedingly variable as the plants range from less than 1 cm high to over 8 dm high; growing both in seeps where the plants are large to sandy flats along the stream where the plants are 1-4 dm high, to grassy flats where the same plants were as small as 1 cm."

Erythranthe cordata and *E. nasuta* are sympatric in Arizona and southeastern New Mexico and small plants of each species may be very similar in aspect, both with cleistogamous corollas and both with reduced vestiture. Those of *E. nasuta* can be recognized by the distal and bracteal leaves with hirtellous to hirsutulous adaxial surfaces — a lens usually is required to see this feature and it sometimes is most obvious around the leaf margins. A possible hybrid between the two, with the aspect of *E. cordata* but leaves, pedicels, and calyces with a mixture of stipitate-glandular and eglandular-hirtellous hairs, is this: **Arizona**. Yavapai Co.: Black Canyon, 2000 ft, 14 Apr 1960, *Demaree 42259* (ARIZ).

30. ERYTHRANTHE CHARLESTONENSIS Nesom, **sp. nov.** **TYPE**: **USA**. **Nevada**. Clark Co.: Charleston Mts., Griffith's Mine, moist sloping rock, 2400 m, 25 Jun 1938, *I.W. Clokey 8116* (holotype: UC!; isotypes: MO-2 sheets!, TEX-2 sheets!).

Annual, fibrous-rooted; stems, leaves, calyces commonly dark purplish. **Stems** erect, 4–16(–24) cm, simple, slender, weakly 4-angled, glabrous. **Leaves** basal and cauline or basal deciduous, largest at midstem or above, cauline relatively few on long internodes, blades regularly ovate to ovate-lanceolate, 5–16(–20) x 3–11 mm, palmately 3-veined, proximal glabrous to sparsely villous on both surfaces, distal and bracteal sparsely villous adaxially with vitreous, flattened, eglandular hairs, sparsely hirtellous to glabrous abaxially, margins shallowly and evenly crenulate to serrate-dentate or denticulate, apices acute to obtuse, bases truncate to subcordate, proximal to distal all short-petiolate (1–3 mm). **Flowers** (1–)4–7, often from all nodes but commonly beginning about midstem. **Fruiting pedicels** 6–19 mm, deflexed 45º–90º at the calyx glabrous or villous-glandular near the nodes. **Fruiting calyces** 10–13 mm, closing, sometimes purple-dotted, minutely hirtellous, sometimes also sparsely glandular, margin villous at the sinuses, upper lobe not prominently protruding or only slightly so. **Corollas** yellow, sparsely red-dotted, tube-throats narrowly cylindric, 4–6 mm, exserted 0.5–1 mm beyond calyx margin, limb barely expanded, nearly regular. **Styles** glabrous. **Plesiogamous**; anther pairs and stigma at the same level. **Capsules** 6–8 mm, stipitate, included.

Flowering Apr–Jul(–Aug). Grassy slopes, damp soil, moist rocks; (900–)1700–2400(–2800) m. Arizona, Nevada. Map 15.

Additional collections examined. **Arizona**. Mohave Co.: 20 mi from Kingman, Union Pass, [ca. 2600 ft], 30 May 1893, *Wilson 25* (UC). **Nevada**. Clark Co.: Charleston Mts., McFarland Springs, grassy slope, 2425 m, 4 Jul 1938, *Clokey 8115* (SMU, UC); Charleston Mts., Fletcher Canyon, damp soil with *Pinus scopulorum*, 2250 m, 20 Jul 1939, *Clokey 8493* (UC); Charleston Mts., Griffith's Mine, moist sloping rock, 2400 m, 12 Jul 1939, *Clokey 8494* (UC); Charleston Mts., Vic Wilson's Ranch, Right Hand Canyon, 3 May 1939, *Maguire 16603* (UC); Timber Mt., Highland Spring, 15 mi NW of Bell Ranch, 5000 ft, 25 Apr 1938, *Train 1487* (UC). Elko Co.: Ruby Mts., Terrace Guard Station, 8500 ft, 13-18 Aug 1941, *Mills & Beach 1460* (UC).

The epithet of the new species refers to the Charleston Mountains (a.k.a. Spring Mountains) of Clark County, where the plants have been most abundantly collected. This population system is recognized here at specific rank because it is relatively constant in morphology and it cannot be definitely associated with any of the other annuals with autogamous flowers that occur in the region –– *Erythranthe arvensis*, *E. brachystylis*, *E. cordata*, *E. nasuta*, and *E. hallii*. The species is characterized by its annual duration, autogamous flowers, small stature and commonly purplish color of stems and leaves, regularly ovate, short-petiolate leaves with shallowly crenate margins and (distal leaves) sparsely villous to glabrous adaxial surfaces, hirtellous calyces without a prominently longer upper lobe, and lack of glandular hairs.

Individuals of all of these six species may flower when as small as 2–5 centimeters high, and the distinctions among them at such small sizes commonly are subtle. There is no feature of *E. charlestonensis* without overlap in the other species, but the same is essentially true of all of the species. Each has its own distinctive and relatively consistent constellation of characters and distinctive geographical range. Overlap in morphology may reflect hybridization and introgression, or it might be reflective of the ancestral genome from which they all probably arose — or both.

Erythranthe hallii has a relatively more northern distribution (Map 15) and its leaves and calyces and very thin and greenish; plants often are completely glabrous or the distal leaves and bracts are slightly villous adaxially. The chromosome number has been reported as 2*n* = 32, distinct from the 2*n* = 28 of *E. nasuta* and 2*n* = 30 of *E. cordata*.

Erythranthe arvensis has a more western and northern distribution (Map 15) and rarely develops purple coloration. The plants, including the calyces, usually are glabrous except for the distal leaves and bracts, which are prominently and diagnostically silvery-villous adaxially. At least the middle and upper cauline leaves typically are depressed-ovate to nearly reniform in outline, and the calyces of *E. arvensis* tend to remain open at maturity. The narrow endemic *E. brachystylis* (Map 15) is most similar to *E. arvensis*.

Erythranthe nasuta (Map 21) occurs sympatrically with *E. charlestonensis*. Even in smallest sizes, it is characterized by a noticeably longer upper calyx lobe and by distal leaves and bracts that are moderately to densely hirsutulous-hirtellous on both surfaces at least around the proximal margins. Leaf margins are variable but often, as in the larger plants, unevenly and shallowly dentate with sharp teeth.

Erythranthe cordata (Map 16) in a characteristically larger growth expression occurs sympatrically with *E. charlestonensis*. Pedicels and calyces of *E. cordata* are sparsely to moderately villous-glandular. The presence of hirtellous vestiture distinguishes it from small individuals of *E. cordata*.

31. ERYTHRANTHE HALLII (Greene) Nesom, Phytoneuron 2012-40: 43. 2010. *Mimulus hallii* Greene, Bull. Calif. Acad. Sci. 1: 113. 1885. *Mimulus guttatus* var. *hallii* (Greene) A.L. Grant. Ann. Missouri Bot. Gard. 11: 172. 1924. **LECTOTYPE** (Grant 1924, p. 173): **USA**. **Colorado**. [Jefferson Co.:] about Golden City, in shady ravines, at lower altitudes only, 1871, *E. Hall and J.P. Harbour 398* (MO!). Protologue: "Collected by Hall & Harbour apparently, and also later by the writer, in 1871. ... It is remarkable for having, for the size of the plant, the smallest corollas of any of the species." Identified by Weber and Wittmann (1992) as "a very depauperate modification" of *Mimulus guttatus*.

Annual, fibrous-rooted. **Stems** erect, 2–8 cm, simple, slender, 4-angled, sometimes apparently rooting at lower nodes if proximally decumbent, glabrous. **Leaves** basal and cauline or basal deciduous, largest at midstem or above, cauline relatively few on long internodes, blades ovate to ovate-lanceolate, 5–11 x 3–9 mm, palmately 3-veined, glabrous or the distal and bracteal leaves sparsely villous with vitreous, flattened, eglandular, multicellular hairs, margins very shallowly dentate or denticulate, apices acute to obtuse, bases truncate to cuneate, basal and lower to mid cauline with petioles 1–4 mm, sessile distally. **Flowers** (1–)4–ca. 10, sometimes from all nodes but usually beginning about midstem. **Fruiting pedicels** 6–14 mm, usually deflexed ca. 90º at the calyx. **Fruiting calyces** (5–)7–10 mm, closing, sometimes red-dotted, glabrous, margin villous at the sinuses, upper lobe not prominently protruding or only slightly so **Corollas** yellow, often red-dotted, tube-throats narrowly cylindric, 4–6 mm, exserted 0.5–1 mm beyond calyx margin, limb barely expanded, nearly regular. **Styles** glabrous. **Plesiogamous**; anther pairs and stigma at the same level. **Capsules** 4–6 mm, stipitate, included 2*n* = 32 (voucher from Grand Co., *Douglas 61-480*, UT).

Flowering May–Aug. Ledges, seeps, along streams, wet meadows; 1900–3200 m; Colorado (Boulder, Clear Creek, Grand, Jefferson, Larimer counties). Map 15.

Additional collections examined. **Colorado.** Boulder Co.: Boulder, stream, 5700 ft, 20 Jun 1906, *Daniels 25* (MO); along trail from Buckingham campground to Fourth of July Mine, wet meadows, 9500 ft, 13 Aug 1979, *Teare and Taylor 1339* (DAV); seepage over granite slabs at base of

S-facing slope in *Pinus ponderosa* woodland along Boulder Creek, 5600 ft, 21 Jun 1979, *Taylor and Teare 7396A* (DAV); beside a spring near summit of Flagstaff Mt., just W of Boulder, 7000 ft, 18 May 1949, *Weber 4653* (TEX, UC); 8 mi W of Lyons, South St. Vrain Canyon, 6300 ft, 12 Jun 1922, *Wiegand & Upton 4257* (MO). Clear Creek Co.: Georgetown, damp places, 18 Jul 1892, *Patterson 294* (MO, UC). Grand Co.: Devil's Staircase, East Inlet, 3.5 mi E of Grand Lake, Shadow Mt. area, moss banks on cliff in temporary seep areas, ca. 9000 ft, 20 Jul 1961, *Douglas 61-315* (UT); North Inlet 1/4 mi below Cascade Fall, 3 mi NE of Grand Lake, shaded ledge, under overhanging, S-facing cliffs, 8800 ft, 7 Aug 1961, *Douglas 61-480*, voucher for *n* = 16 (UT); Little Yellowstone Canyon, 14.5 mi N of Grand Lake, Rocky Mt. Natl. Park, gravel at streamside, 9560 ft, 10 Aug 1961, *Douglas 61-488* (UT). Jefferson Co.: Morrison, moist soil, 1970 m, 3 Jun 1921, *Clokey 4287* (UC); Morrison, 27 Jul 1889, *Greene s.n. (*ND-Greene). Larimer Co.: Estes Park, moist ground, 29 Jun 1912, *Churchill s.n.* (MO); Loveland, 55 mi above dam in Big Thompson Canyon, in seep on rocky ledge, no date, *Vickery cult 7313* (UT).

Erythranthe hallii may be an eastern vicariant of *E. arvensis*. — both have a tendency to root at basal nodes and distal and both have bracteal leaves villous with vitreous, flattened, eglandular, multicellular hairs although this vestiture is barely developed and often absent in *E. hallii*. The only reported chromosome number from the Colorado plants, 2*n* = 32, also appears to be distinct among possible relatives of *E. hallii*, and if the count is correct, the species perhaps is not so closely related to others of the Microphylla group.

Erythranthe hallii is endemic to the same area of Colorado and has the same chromosome number as *E. gemmipara*. The latter, however, is different in calyx morphology and molecular data (Beardsley et al. 2004) indicate that it is distantly related to sect. *Simiolous*. *Erythranthe gemmipara* is treated by Barker et al. (2012) as a monotypic section of the genus.

32. ERYTHRANTHE DENTILOBA (B. Rob. & Fernald) Nesom, Phytoneuron 2012-40: 44. 2012. *Mimulus dentilobus* B. Rob. & Fernald, Proc. Amer. Acad. Arts 30: 120. 1894. **TYPE**: **MEXICO**. **Sonora**. Nacori, 3750 ft, 4 Dec 1890, *C.V. Hartman 288* (holotype: GH photo-PH!; isotypes: NY digital image!, US digital image!). Fig. 8.

Perennial, rhizomatous, mat-forming. **Stems** prostrate, 5–15 cm, rooting at the nodes, glabrous to very sparsely glandular. **Leaves** cauline, petiolate, blades ovate to braodly ovate or orbicular, depressed-ovate, 2–10(–17) x 2–10(–20) mm, palmately 3-veined, surfaces glabrous or rarely sparsely villosulous-glandular adaxially with vitreous flattened hairs, commonly punctate adaxially, margins dentate to dentate-serrate with 3–5 teeth per side, apices mostly obtuse, bases truncate to cuneate, petioles 1–4 mm. **Flowers** axillary, usually 1 per stem at distal nodes. **Fruiting pedicels** 5–25 mm, glabrous. **Fruiting calyces** cylindric-ovoid, 5–7 mm, lobes 5 or 3(+2), closing, nodding 45º–90º. **Corollas** yellow, red-dotted, tube-throats funnelform, 5–7 mm, exserted 2–3 mm beyond calyx margin, limb bilabiate, expanded 6–9 mm (pressed), lobes fimbriate. **Herkogamous**; anther pairs at different levels, stigma above upper anther pair. 2*n* = 32.

Flowering Mar–Sep(–Oct). Springs, seeps, canyon bottoms, cliff faces, rocks in water, moist banks; 500–2300 m; Mexico (Baja California, Chihuahua, Sinaloa, Sonora). Map 22.

Additional collections examined. **MEXICO. Baja California Sur.** N side of Cerro de la Giganta, western branch of Arroyo Hondo, near spring, ca. 700-800 m, 28 Nov 1947, *Carter et al. 2077* (ARIZ); Sierra Giganta, above Pto. Escondido, moist rocks in canyon bottom, 2000 ft, 22 Apr 1938, *Gentry 3772* (ARIZ, MO); Sierra de las Palmas, La Champagna, S of Santa Rosalia, in seeps, *Nolina* grassland over undulating broken terrain of volcanic mountain top, 27-29 Apr 1952, *Gentry & Fox 11792* (ARIZ); canyon above Puerto Escondido, 13 Mar 1937, *Rempel 161* (ARIZ). **Chihuahua.** S slope, Barranca del Cobre, in arroyo, short tree forest, 4200 ft, 11 Apr 1963, *Caddell 1062* (BRIT);

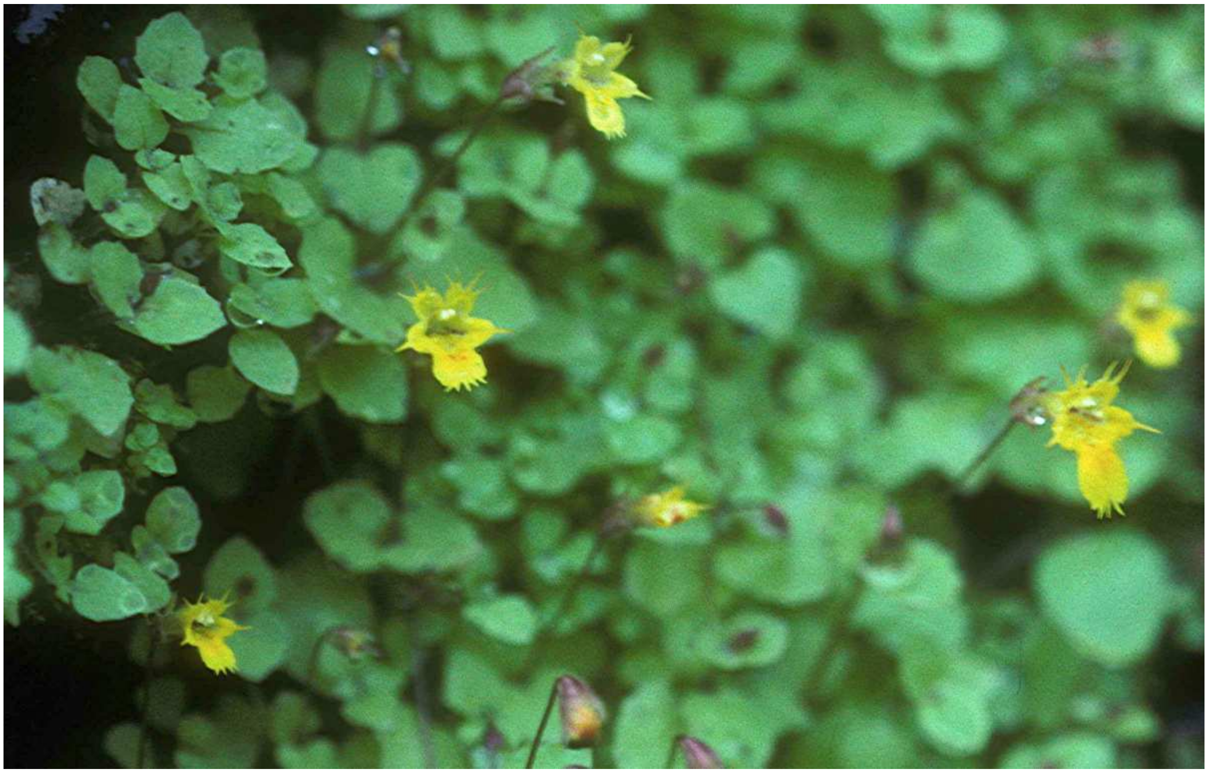

Figure 10. *Erythranthe dentiloba*, photo by Mark Egger, used by permission. Sonora, Mexico, along Mex. Hwy 16 between Trigo Colon and Maycoba, 17 Aug 1998.

Sierra Charuco, Arroyo Hondo, pine forest spring, on moist rocks, 11 Sep 1935, *Gentry 1765* (ARIZ); Guicorichi, Rio Mayo, meadow spring, on rocks at water edge, 8 Oct 1935, *Gentry 1990* (ARIZ, UC); Sierra Charuco, Rancho Byerly, rocky igneous slopes, pine-oak forest, 5000–5800 ft, 17-25 Apr 1948, *Gentry 8085* (ARIZ, UC); Sierra Charuco, Arroyo Hondo, igneous rocky canyon slope in pine-oak forest, aquatic, 4500-5500 ft, 16-30 Apr 1948, *Gentry 8073* (ARIZ, UC); Mpio. Temosachi, Nabogame, pine-oak-cypress forest, 1800 m, 12 Oct 1988, *Laferriere 1946* (ARIZ); Mpio. Temosachi, Nabogame, arroyo, 1800 m, 24 Apr 1987, *Laferriere 372* (ARIZ); Parque Nacional de Cascada Basaseachic, in the barranca at the base of the falls, wet, bare, slick rock at the base of the trail on steep N slope, shaded with *Abies*, *Ostrya*, *Acer*, 1600 m, forming dense mats on the rocks where moist, 11 Nov 1989, *Mahrt & Spellenberg 79* (NMC); Sierra Obscura, spring seep, 1600 m, 26 Mar 1985, *Martin s.n.* (ARIZ); Sierra Obscura between Rancho El Oso and Sawmill at El Serrichito, basaltic soils, 2000 m, 7-9 Nov 1986, *Martin et al. s.n.* (ARIZ); Canon de Lopez, 1350 m, 17 Mar 1988, *Martin s.n.* (ARIZ); Mpio. Ocampo, Parque Nacional de Cascada Basaseachic, barranca to W of falls, at base of dry cliffs in more or less open, dry *Pinus durangensis-Quercus hypoleucoides* woods, ca. 1800 m, 26 Apr 1985, *Spellenberg et al. 8030* (NMC); near Chuichupa in the Sierra Madres, 31 Aug 1899, *Townsend & Barber 388* (NMC); Cascada de Basaseachic, Rio Basaseachic, pine-oak forest, common herb in moist soil at edge of stream, 4 Jun 1999, *Van Devender 99-215* (NMC); Cascada de Basaseachic, Rio Basaseachic, pine-oak forest, abundant herb on wet rock surface under waterfall, 1800 m, 4 Jun 1999, *Van Devender 99-220* (NMC). **Sinaloa.** 5 mi N of El Palmito, slopes and ledges of barranca with *Pinus* and *Quercus*, 2300 m, 28 Oct 1973, *Breedlove 35728* (MO); Sierra Surotato, Los Pucheros, Penasco, pine-oak-madrono forest, in seep of cavern on calcareous cliff, 5500-6500 ft, 17-24 Mar 1945, *Gentry 7220* (ARIZ). **Sonora.** Rio Mayo region, KM 196 on Hwy 16, Tithonia stop W of Tepoca, 950 m, 14 Mar 1988, *Ferguson s.n.* (ARIZ); Agua Salado, 15 mi NE of Los Tanques by road, below seep in small side canyon along road from Los Tanques to Las Chinacas, tropical deciduous forest, 500 m, 15 Mar 1992, *Fishbein et al. 87* (ARIZ);

along Hwy 16, 3.6 mi E of Rio Maycoba crossing, N-facing cliff with seeps in oak woods, 1400 m, mat-forming herb, 7 Sep 1995, *Fishbein et al. 2516* (ARIZ); Rio Mayo, San Bernadino, arroyo, water in rocks, Toiwe, 25 Feb 1935, *Gentry 1353* (ARIZ, UC); Los Tepalcates on old road to Bermudez, 1450 m, 15 Mar 1988, *Martin s.n.* (ARIZ); Los Cien Pinos, 1700 m, 16 Mar1988, *Martin s.n.* (ARIZ); Sahuarivo to Coroqui, upper short tree forest, 900 m, 18 Mar 1992, *Martin et al. s.n.* (ARIZ); 18.3 mi E of the Rio Yaqui bridge near Tonichi, on the road to Carrizal and Santa Rosa, canyon with many palms, 3200 ft, locally common perennial herb along a stream, mat-forming, 27 Mar 1983, *Sanders 3717* (UC); Mpio. de Alamos, Arroyo El Cobre, ca. 9 km (by air) N of Guirocoba below (just W of) Choquincahui (El Cobre), among mosses and liverworts in the moistened soil of a seep along the arroyo bank, riparian tropical deciduous forest, 520 m, 17 Mar 1995, *Steinmann et al. 621* (ARIZ).

All plants of sect. *Simiola* with laciniate-lobed corollas (Mexico, Arizona, New Mexico, and Texas) have generally been identified as *Mimulus dentilobus*, but these occur as three, morphologically distinct, widely allopatric population systems, each of which is treated here as a separate species. There is no evidence of intermediacy. *Erythranthe dentiloba* is the only one of the three with an allogamous breeding system.

33. ERYTHRANTHE PARVULA (Woot. & Standl.) Nesom, Phytoneuron 2012-40: 44. 2012. *Mimulus parvulus* Woot. & Standl., Contr. U.S. Natl. Herb. 16: 171. 1913. **TYPE**: **USA**. **New Mexico**. Grant Co.: "vicinity of Silver City, Fort Bayard, Santa Rita, Fierro, the Mimbres Valley and East Canyon tributary to it, and on the G.O.S. Ranch, in canyons withing 10 miles of the ranch house," Rocky Canyon, 29 Aug 1911, *J.M. Holzinger s.n.* (holotype: US digital image!; isotype: MO!). The US sheet has the date "9 August" handwritten on the label, but the MO sheet has "Aug 29." Because the printed label gives the range of collection dates as "Aug. 27 to Sept. 12, 1911" presumably the handwritten date on the US label was in error and the correct date is August 29.

Perennial, rhizomatous, mat-forming. **Stems** prostrate, 5–15 cm, sometimes rooting at the nodes, stipitate-glandular distally. **Leaves** cauline, petiolate, blades ovate to orbicular-ovate or depressed-ovate, 3–11 mm x 3–9 mm, palmately 3-veined, villous-hirsute on both surfaces, densely so adaxially, margins shallowly denticulate to dentate with 3–5 teeth per side, apices acute to obtuse, bases truncate to cuneate, petioles 1–4 mm. **Flowers** axillary, few and scattered at distal nodes. **Fruiting pedicels** 7–15 mm, minutely stipitate-glandular. **Fruiting calyces** cylindric-ovoid, 4–5 mm, closing, nodding 45º–90º, 5-lobed, moderately to densely villous-glandular. **Corollas** yellow, red-dotted, tube-throats funnelform, 6–8 mm, exserted 4–5 mm beyond calyx margin, limb bilabiate, expanded 4–6 mm (pressed), lobes fimbriate. **Plesiogamous**; anther pairs barely separated in level and essentially contiguous, stigma even with upper anther pair. 2n = 32 (**Arizona**. Maricopa Co.: along Eagle Creek, *Vickery 13007*, UT). Fig. 9.

Flowering Apr–Sep. Wet vertical rock faces, ledges, and rocky slopes, seepy wash banks; 500–2400(–3400) m. Arizona, New Mexico; Mexico (Sonora). Map 23.

Additional collections examined (ASU fide SEINet). **MEXICO. Sonora.** 4 mi E of Rancho Diablo in Cajón Bonito, on the SW-facing bare rock, 1 May 1976, *Mason 3199* (ARIZ). **USA. Arizona.** Graham Co.: Upper Gila River drainage, on Bonita Creek, near mouth of Midnight Canyon, in mats on rocky W-facing canyon wall, a few inches to 1 ft above water, ca. 3800 ft, 21 Jun 1978, *McGill 2391* (ARIZ, ARIZ digital image!); Aravaipa Canyon, east end, near confluence with Turkey Creek, S-facing seepage cliffs above creek, vertical cliffs and ledges (rhyolite?), riparian vegetation, 3000 ft, 2 Apr 1977, *Reeves 5456* (ARIZ). Greenlee Co.: 5 or 6 mi SE of Morenci, Eagle Creek Hot Springs, canyon, 5000 ft, 29 Jan 1977, *Bissonette 7460* (ARIZ); Eagle Creek above confluence with Gila river, upstream from pump station, vertical conglomerate canyon walls, 6 Sep 1998, *McGill 7003* (ARIZ); Eagle Creek, narrow riparian canyon and hillside, 3700 ft, 29 Jun 1977, *Minckley s.n.*

(ARIZ). Maricopa Co.: Lower Camp Creek, seep spring in face of cliff, N slope, silt on rock cliff, 1600 ft, 14 Sep 1952, *Blakley B-1597* (ARIZ); Superstition Mountains, Le Barge Canyon, along stream 2340 ft, 7 Apr 1963, *Lehto 1719* (ARIZ) and *1719-b* (ARIZ): Camp Creek, 2.1 road mi W of confluence with Verde River, wash bank with seeps, 7 Jun 1977, *McGill 1415* (ARIZ, ASU). Pinal Co.: Peralta Canyon in Superstition Mountains foothills 1900 ft, 21 Mar 1965, *Lehto 4631* (ARIZ). Yavapai Co.: Tangle Creek; ca 2 km SE of Tangle Peak and ca. 5 km NW of the Verde River, SE-facing seep, prostrate annual in wet soil at base of small, shallow caves, 762 meters, 12 April 1992, *Baker 8815* (ARIZ). **New Mexico**. Catron Co.: Little Creek, 4 mi S of Gila Cliff Dwellings, Gila Natl. Forest, attached to rock cliff in dripping wet area, 6 Jun 1965, *Crutchfield 139* (LL); Mogollon Mountains at Whitewater Spring, 10,200 ft, 9 Sep 1980, *Fletcher 4879* (UNM, fide SEINet); upper end of Snow Lake in the Gila National Forest, gravel and silty loam of mud flats, 7300 ft, 12 Sep 1990, *Hutchins 12740* (UNM, fide SEINet). Grant Co.: Bear Canyon, 6 mi E of Gila, forming dense mats on moist vertical sides of overhanging cliffs, 5000 ft, 23 May 1935, *Maguire et al. 11662* (UC).

Figure 11. *Erythranthe parvula*, habit, flower, and leaf. Photos by Russ Kleinman, Bill Norris, and Kelly Kindscher, Western New Mexico Univ. Dept. of Natural Sciences and the Dale A. Zimmerman Herbarium. Vascular plants of the Gila Wilderness. **New Mexico**, Grant Co., Black Range, Rocky Canyon, 4 Jun 2009.

34. ERYTHRANTHE CHINATIENSIS Nesom, **sp. nov. TYPE**: **USA**. **Texas**. Presidio Co.: Chinati Mtns. State Natural Area, Pelillos Canyon, deep pool at foot of dam, Boulder Canyon, a large steep, bowl-shaped igneous area N side of Chinati draining off Chinati Peak, riparian area and seeps from crevices in igneous rock face of canyon wall, 3775 ft, associates include *Salix gooddingii*, *Cephalanthus*, *Juglans microcarpa*, *Tecoma stans*, *Brickellia*, *Perityle dissecta*, *Mimulus dentilobus*, and small frogs, mat-forming, flrs yellow, upper lobes paler than middle lower lobe, reddish maroon spots in throat, 17 Sep 2004, *Lott et al. 5316* (holotype: TEX). Fig. 10.

Different from *Erythranthe dentiloba* in its autogamous flowers and strongly reflexed lower corolla lip. Different from *Erythranthe parvula* in its nearly glabrous leaves and its strongly reflexed lower corolla lip. Similar to both species in its prostrate habit, 5-lobed calyces, and fimbriate corolla lobes.

Perennial, rhizomatous, mat-forming. **Stems** prostrate, 5–20 cm, sometimes rooting at the nodes, glabrous. **Leaves** cauline, petiolate, blades ovate to broadly ovate or orbicular-ovate, 4–15(–22) mm x 4–15(–18) mm, palmately 3–5(–7) veined, glabrous to moderately villosulous adaxially with vitreous, flattened, eglandular or minutely gland-tipped hairs, glabrous abaxially, margins shallowly denticulate or merely mucronate to mucronulate with 3–6 teeth per side, apices acute to obtuse, bases truncate to cuneate, petioles 2–10(–20) mm. **Flowers** axillary, few and scattered at distal nodes. **Fruiting pedicels** 10–20 mm, glabrous. **Fruiting calyces** ellipsoid, 5–6 mm, closing, nodding 45º–90º, 5-lobed, glabrous to sparsely villosulous-glandular. **Corollas** yellow, red-dotted, tube-throats funnelform 7–8 mm, exserted 4–5 mm beyond calyx margin, limb bilabiate, expanded 6–7 mm (pressed), lobes fimbriate. **Plesiogamous**; anther pairs barely separated in level and essentially contiguous, stigma even with upper anther pair.

Flowering Mar–Sep. Seeps in vertical cliff faces, wet bluffs; 900–2300 m; Texas (Presidio Co.). Map 23.

Additional collections examined. **USA**. **Texas**. Presidio Co.: S side of Chinati Peak, locally common perennial herb in moist shaded area near seep spring, igneous soils, ca. 6900 ft, 7 Jun 1977, *Butterwick & Lott 3784* (TEX); near falls in Mexican Canyon, 27 Nov 1942, *Hinckley 2645* (SRSC); S side of Bofecillos Mts., under overhanging rock where water drips continually in Tapada Creek, ca. 2700 ft, 4 Mar 1944, *Hinckley 2918* (SRSC); S Chinati Mts., right fork of Tinaja Prieta Canyon, in moist soil of perennially wet seep, with mosses and Aquilegia, 15 Apr 1978, *Lott 58* (SRSC); Chinati Mountains State Natural Area, Pelillos Canyon, deep pool at foot of dam, riparian area and seeps from crevices in igneous rock face of canyon wall, 3775 ft, mat-forming, 17 Sep 2004, *Lott 5316* (SRSC); Chinati Mountains State Natural Area, Pelillos Canyon, between the dam and Tinaja Prieta fork, canyon bottom woodland of *Salix*, *Juglans*, *Cephalanthus*, and *Quercus*, 3910 ft, 25 Mar 2005, *Lott et al. 5449* (TEX); near head of trail between Barnett Bros. ranch on Horse Creek and S side of Chinati Mts., hanging in mats vertically permanently wet cliffs, ca. 2000 m, flrs apparently 4-lobed, the upper lobe broad, 21 Jul 1945, *McVaugh 7472* (LL, SMU); Big Bend State Park, Tapado Canyon, 2963 ft, 6 Mar 2009, *Morey* color photo (SRSC); Mexicano Falls and 0.5 air mi SE in Arroyo Segundo, Big Bend Ranch, wet, mossy cliff face, locally common decumbent perennial, corolla yellow, 27 Aug 1984, *Poole 2568* (TEX); Chinati Peak and canyons N and E of the peak, overhanging and seeping bluffs, mat-forming subsucculent, flowers yellow with red spot on lower, larger petal, 7 Jun 1977, *Powell & Powell 3095* (LL, SRSC); Tapado Canyon below Redford, limestone soil, sparse on slopes, 5 Feb 1960, *Warnock 19100* (SRSC); midslopes of Chinati Peak, rare at limestone seep, 5700 ft, 27 Mar 1959, *Warnock & Powell 17779* (SRSC).

The leaves of the type collection are at the upper range of variation in size measured for the species.

HOLO TYPE OF: Erythranthe chinatiensis Nesom

! B. L. Turner 2005

257 TX

Flora of Texas
Plant Resources Center (TEX-LL), University of Texas at Austin

Scrophulariaceae: *Mimulus dentilobus* Robins. & Fern.

TEXAS: Presidio Co: Chinati Mtns. State Natural Area. Pelillos Canyon, deep pool at foot of dam. 29° 51' 39" N; 104° 28' 35" W. Elev. 3775'

Riparian area & seeps from crevices in igneous rock face of canyon wall. Assoc. Salix gooddingii, Cephalanthus, Juglans microcarpa, Tecoma stans, Brickellia, Perityle dissecta, Mimulus dentilobus, small frogs.

Mat-forming. Fls yellow, upper lobes paler than middle lower lobe; reddish-maroon spots in throat.

Emily J. Lott w/ S. P. Rankin, M. L. Butterwick & P. R. Manning
5316
September 17, 2004

Figure 12. *Erythranthe chinatiensis*, holotype TEX.

Herbarium of Southwest Texas State Univ.
Mimulus dentilobus Robins. & Fern.
det. David E. Lemke 1991

The University of Texas Herbarium (LL, TEX)
Mimulus dentilobus B. L. Robins. & Fern.
Det: B. L. Turner, 25 Sep 1997

University of Texas - Austin (LL, TEX)
00025022

THIS SPECIMEN
RECORDED BY THE
TEXAS NATURAL
HERITAGE PROGRAM
JMP 4 X 1984

THE LUNDELL HERBARIUM
University of Texas
PLANTS OF TEXAS

Mimulus dentilobus B.L. Robinson & Fern.

PRESIDIO CO.: Locally common perennial herb in moist shaded area near seep spring on south side of Chinati Peak. In igneous soils at ca. 6900 ft. elevation.

June 7 1977
M. Butterwick & E. Lott #3784

Figure 13. *Erythranthe chinatiensis*, *Butterwick & Lott 3784*, TEX.

Figure 14. *Erythranthe chinatiensis.* Big Bend Ranch State Park, Tapado Canyon, 2963 ft, 6 Mar 2009. Photograph by Roy Morey, mounted on herbarium sheet at TEX.

35. ERYTHRANTHE MADRENSIS (Seem.) Nesom, Phytoneuron 2012-40: 44. 2012. *Mimulus madrensis* Seem., Bot. Voy. Herald 9: 322, plate 58. 1856. **TYPE**: **MEXICO**. [**Durango**]. In swamps, on the road from Durango to Tepic," 1850, *B. Seemann 2110* (holotype: K, fide Pennell 1935; apparent isotype: BM fide Vickery 1973). The illustration in the protologue (Fig. 11 in the present account) shows the diagnostic features, including the 3-lobed calyx. The relatively long corollas and protruding style, suggestive of allogamy, are similar to *E. pallens*, but the narrowly expanded limb, short pedicels, and small leaves are those of *E. madrensis* as described here. Fig. 11.

Mimulus wiensii Vickery, Madroño 22: 161. 1973. **TYPE**: **MEXICO**. **Durango**. W of El Salto, on wet banks near KM 1155 on the Durango-Mazatlan road, 2615 m, 24 Aug 1959, *D. Wiens 2643*, voucher for *n* = 16 (holotype: UT digital image; isotype: UT digital image!).

Perennial, rhizomatous, mat-forming, all parts glabrous, stems and leaves (abaxially) commonly purplish. **Stems** prostrate to decumbent, rooting at the nodes, 5–12 cm, often ascending to ascending-erect or erect in the inflorescence. **Leaves** mostly cauline, broadly ovate to orbicular-ovate, blades 2–10 x 2–8 mm, palmately 3–5-veined, bases cuneate to truncate, apices mostly obtuse, margins shallowly dentate to mucronate, 2–6 teeth per side, adaxial surfaces minutely punctate, all petiolate, petioles 1–6 mm. **Flowers** 1–5(–7), mostly at distal nodes. **Fruiting pedicels** 5–30 mm. **Fruiting calyces** ovoid, 5–8 mm, closing, nodding, lobes usually 3, sometime the 2 middle lobes slightly developed or represented by a mucro at veins end, apices mostly rounded. **Corollas** yellow, red-dotted, tube-throats narrowly funnelform, 5–9 mm, exserted 2–4 mm beyond calyx margin, limb bilabiate, expanded 6–10 mm (pressed). **Plesiogamous**; anther pairs barely separated in level and contiguous, stigma at same level as upper anther pair. **Capsules** 2.5–3 mm. 2n = 16.

Flowering Mar–Aug. Wet crevices, ledges, cliff faces, seepage in road cuts, rocks at waterfalls and in streams, stream banks, moist banks and ditches; (1000–)1500–2800(–3300) m. Mexico (Chihuahua, Durango, Jalisco, Michoacan, Sinaloa, Sonora). Map 24.

Additional collections examined. **MEXICO. Chihuahua.** Mpio. Batopilas-Mpio. Urique, between Basogochic and Quirare in pine-oak forest near small stand of *Abies durangensis*, small clumps in rock crevices along arroyo, 6870 ft, 3 Jun 1978, *Bye 8570* (TEX); Mpio Guachochi-Mpio Urique, S side of Barranca del Cobre between Napuchi and Rio Urique near KM 69.6 of Creel-Guachochi road in open pine-oak forest, along moist seepage area of road cut, forming mat on perpendicular moist soil surface, 31 May 1980, *Bye 9725* (TEX); shallow canyon (Arroyo El Revention?), below Saguaribo, just below cascada, on rocks under cascada, 1600 m, 17 Mar 1992, *Fishbein 158* (ARIZ); Sierra des Papas, Son-Chi, rock in flowing water, 20 Oct 1933, *Gentry 641M* (ARIZ); Sierra Charuco, Arroyo Hondo, igneous rocky canyon slope in pine-oak forest, seep, 4500-5500 ft, 16-30 Apr 1948, *Gentry 8159* (ARIZ, UC); Mpio. Temosachi, Nabogame, 12 km NW of Yepachic, in stream, 1800 m, 1 Nov 1986, *Laferriere 347* (ARIZ); Mpio. Temosachi, Nabogame, trailing, pine-oak-cypress forest, arroyo, 1800 m, 21 Mar 1988, *Laferriere 2262* (ARIZ, TEX); Cascada Basaseachic, top of falls, ashy volcanic rocks, 1900 m, 17 Mar 1986, *Martin et al. s.n.* (ARIZ); 80 km SW of El Vergel on road to Guadalupe y Calvo, 3.2 km S of bridge in Turuachi, deep canyon, area of pines and oaks, abundant on wet rocks around seepage, ca. 2600 m, 26 Aug 1983, *Nesom 4971* (TEX); Barranca del Cobre, ca. 54 mi S of Creel and 6 mi SW of the road intersection at Cafe La Casita on the road to La Bufa, vicinity of Basigochi, pine-oak woodland on mountain slope of volcanic ash, 7500 ft, locally common perennial, 22 Mar 1984, *Sanders 4772* (UC-2 sheets); Mpio. Ocampo, canyon to S of fall, thin soil over wet, slick rock along river, 26 Apr 1985, *Spellenberg et al. 8007* (NMC); Parque Nacional de Cascada Basaseachic, in the box canyon at the base of the falls, matted on river bank at base of falls, ca. 1700 m, 26 Apr 1986, *Spellenberg et al. 8448* (NMC); Parque Nacional de Cascada Basaseachic, in the barranca at the base of the falls, in wet clayey soil near base of cliffs, 1570 m, 25 Apr 1987, *Spellenberg et al. 9058* (NMC). **Durango.** Sierra Madre Occidental, between Mazatlan and Durango, 2 mi E of El Espinazo, 8600 ft, 8 Jun 1962, *Hutchinson 2507* (UC); 12.5 mi W of La Ciudad, rocky seepage bluff, 8050 ft, 22 Jul 1975, *LeDoux et al. 2032* (LL); 39 road mi SW of El Salto on Hwy 40, dripping wet granitic seepage cliff ca. 50 mi high, ca. 2400 m, 21 Jul 1969, *Marcks & Marcks 1204* (LL); 21.7 mi NE of El Paraiso, Sinaloa, on road between Villa Union and El Salto, wet ledge in seepage, 8400 ft, 29 Sep 1953, *Ownbey 1982* (UC); 3.4 mi E of El Palmito, 2 Apr 1970, *Powell & Turner 1866* (TEX); along Mex Hwy 40, 2 mi W of Las Bancos and 22 mi E of El Palmito, 13 mi W of La Ciudad, steep dripping cliffs and slopes along and above road, 27 Sep 1973, *Reveal 3548* (TEX); 111 road mi N of Santiago Papasquiaro on road to Topia, 5 mi W of Cienega Nuestra Senora, pine-oak-madrone-juniper woods, 2420 m, shaded creek

Figure 15. *Erythranthe madrensis*, line drawing from the 1856 protologue.

bank and gravelly creek bed, 18 Sep 1982, *Spellenberg 6711* (NMC); Mpio. Mezquital, 37 km SW de Mezquital, en lugares con mucha humedad, bosque de encino-pino con *Arbutus*, 2450 m, 6 Mar 1985, *Tenorio L.* 8078 (ARIZ); crest of the Sierra Madre, ca. KM 177 on Hwy 40, ca. 32 km W of La Ciudad, wet roadside ditch, ca. 2185 m, 12 May 1976, *Vickery 2903*, cult. 12,220 (SRSC, UC); roadcuts on steep mountainside, Hwy 40 just W of La Fraguita, 1.1 mi E of turnout to El Indio (13.2 mi E of the Sinaloa border, ca. 2400 m, 16 Mar 1983, *Whittemore 83-023* (TEX). **Jalisco**. Mpio. Mezquitic, 15 km despues de bajio del Tule hacia Bolanos, postrada, in colonias donde escurre el agua de un manantia, 12 Mar 1991, *Chazaro & Sorensen 6574* (TEX); NE slopes of Nevado de Colima, above Canoas de Leoncito, steep mountain sides in alder-zacaton zone, 3100–3300 m, 13 Sep 1952, *McVaugh 12896* (MICH, SMU!, US). **Michoacan.** Distr. Coalcoman, Barroloso, bank of stream, 2250 m, 20 Oct 1939, *Hinton 15349* (ARIZ, LL, MO, TEX); near El Barroloso, *McVaugh 22835* (MICH, US); Mpio. Tzitzio, 3 km al S de Mil Cumbres camino a Villa Longin, 2500 m, hierba postrada sobre rocas, en ladera humeda, 11 Oct 1983, *Martinez S. 4811* (MO); just E of Morelia along hwy (KM 212.3), dense patch on vertical, mossy, dripping bank, 23 Aug 1976, *Wonderly 347* (NMC). **Sinaloa.** Sierra Monterey, Quebrada de Platano, moist cliffs by waterfall, canyon in oak forest, 3000 ft, 12 Mar 1940, *Gentry 5909* (ARIZ); Sierra Surotato, Los Pucheros, rocky stream bank, openly forested slope of pine-oak-madrono, 5500-6500 ft, 17-24 Mar 1945, *Gentry 7213* (ARIZ, UC); Sierra Suotato, above La Jolla, riparian, pine-oak zone, 5000-6000 ft, 17-24 Mar 1945, *Gentry 7285* (ARIZ). **Sonora**. Canada La Ventana (Arroyo El Otro Lado), 2.5 km (by air) ESE of Yecora, rocky stream canyon in pine-oak forest, 1520 m, moist bank above stream, 1 Oct 1998, *Reina G. 98-1991* (ARIZ).

Erythranthe madrensis is distinct in its prostrate stems forming mats, small, petiolate leaves with minutely punctate adaxial surfaces and usually purplish abaxially, glabrous vestiture, 3-lobed calyces, and small, bilabiate but autogamous flowers.

36. ERYTHRANTHE PALLENS (Greene) Nesom, Phytoneuron 2012-40: 45. 2012. *Mimulus pallens* Greene, Leafl. Bot. Observ. Crit. 2: 4. 1909. **TYPE**: **MEXICO**. **Durango**. Santiago Papasquiaro, Apr-Aug 1896, *E. Palmer 55* (holotype: US digital image! photo-PH!, photo-UC!; isotypes: MO!, NY digital image!, UC!).

Mimulus yecorensis Vickery, Madroño 44: 391. 1997 [publ. 1998]. **TYPE**: **MEXICO**. **Sonora**. 17 km E of Yecora on Mexico Hwy 16, mossy banks of small stream in pine forest, 26 Apr 1982, *D.A. Polhemos s.n.* [Vickery culture no. 13257] (holotype: UT!; isotypes: CAS digital image!, GH, MICH digital image!, MO!, NY digital image!, SRSC!, UC!, US digital image!). Voucher for chromosome count of n = 32. Vickery (1973, 1997) studied the type of *Mimulus madrensis* (he stated that he borrowed material from K) and placed it as a synonym of *M. glabratus* var. *fremontii.*

Annual, fibrous-rooted, rhizomatous, sometimes mat-forming, all parts glabrous, stems and leaves (abaxially) sometimes purplish. **Stems** procumbent to decumbent, 3–18 cm commonly rooting at the nodes, ascending to ascending-erect in the inflorescence. **Leaves** basal and cauline, 1–3(–4) pairs, basal short-petiolate (petioles 1–2 mm), sessile distally, blades broadly elliptic to ovate-elliptic or suborbicular, 4–12 x 3–9 mm, adaxial surfaces minutely punctate, bases cuneate to truncate-rounded, apices rounded, margins shallowly crenate to dentate with 2–6 teeth per side. **Flowers** 1–6(–8), from all nodes to mostly distal nodes. **Fruiting pedicels** 25–50 mm. **Fruiting calyces** campanulate-ovoid, 6–10 mm, closing, nodding 30–90º, lobes 3, apices, rounded. **Corollas** yellow, red-spotted in the floor of throat and tube, tube-throats narrowly funnelform, 8–12 mm, exserted 3–5 mm beyond the calyx margin, limb bilabiate, expanded 8–12 mm (pressed). **Herkogamous**; anther pairs at different levels, stigma above the upper anther pair. **Capsules** 2.5–3.5 mm. 2*n* = 32.

Flowering Mar–Sep. Wet rocks at waterfalls and in streams, stream banks, springs, shady wet ravines; 1250–2700 m. Mexico (Chihuahua, Durango, Sinaloa, Sonora). Map 24.

Additional collections examined. **MEXICO. Chihuahua**. NE slope of Sierra Mohinora, in wet soil along stream (tributary of Rio del Soldado) in gorge of conifer forest, near La Rocha, 7500 ft, 14-15 Oct 1959, *Correll & Gentry 23097* (LL); Mpio. Temosachi, Nabogame, pine-oak-*Cupressus arizonica* forest, 1800 m, 3 Dec 1987, *Laferriere 1288* (NMC); Mpio. Ocampo, area of Cascada de Basaseachic, steep-sided canyon of Rio Durazno, S of parking area and campground, ca. 1950-2000 m, edge of pool along riverbank with cover of other herbs, 17-20 Oct 1986, *Nesom & Vorobik 5618* (TEX); Barranca del Cobre, ca. 54 mi S of Creel and 6 mi SW of the road intersection at Cafe La Casita on the road to La Bufa, vicinity of Basigochi, pine-oak woodland on mountain slope of volcanic ash, 7500 ft, locally common perennial, 22 Mar 1984, *Sanders 4772* (UC-2 sheets); 24 km from Creel and along roadside to and at the Cascadas de Cusarare, on wet rocks at the base of a waterfall, 7140 ft, 26 Aug 1990, *Swagel 253* (MO); near Colonia Garcia in the Sierra Madres, 7400 ft, 12 Sep 1899, *Townsend and Barber 324* (MO); Mpio. Ocampo, Cascada de Basaseachic, bosque de pino-encino, 1250 m, 14 Apr 1995, *Yen & Estrada 4119* (BRIT) and *4129* (BRIT). **Durango.** Distr. Santiago Papasquiaro, NE of Ataes, on rocks in brook, pine forest, 8000 ft, 20 Apr 1943, *Lundell 13019* (LL-2 sheets); San Ramón, Apr 21–May 18 1906, *Palmer 87* (MO, UC); 111 road mi N of Santiago Papasquiaro on road to Topia, 5 mi W of Cienega Nuestra Senora, pine-oak-madrone-juniper woods, 2420 m, shaded creek bank and gravelly creek bed, 18 Sep 1982, *Spellenberg 6712* (NMC). **Sinaloa.** Sierra Surotato, Los Pucheros, riparian in pine-oak-madrono forest, 5500-6500 ft, 17-24 Mar 1945, *Gentry 7232* (ARIZ, UC). **Sonora.** 11 mi E of Yecora, along road between Yecora and Maicova, on bank of small stream, with *Pinus latifolia* and *Pinus chihuahuana*, 5200 ft, 27 Mar 1975, *Karpiscak 75-16* (ARIZ); Hwy 16 to Yecora, *Platanus* spring, 1700 m, 13 Mar 1990, *Martin & Ferguson s.n.* (ARIZ); 5.2 km W of Yecora on Mex 16, pine-oak forest, 1720 m, in moist soil near stream, 11 Mar 1996, *Van Devender 96-93* (ARIZ).

Erythranthe pallens (tetraploid) is similar to *E. madrensis* (diploid) in its mat-forming habit, glabrous vestiture, and punctate adaxial leaf surfaces but differs in its longer pedicels, larger calyces, longer corollas with broader limbs, and its allogamous fertility. The two have nearly congruent geographic distributions except that *E. madrensis* is mapped here further south (but see comments below). A hypothesis of autoploid origin for *E. pallens* is plausible except for the presumably more specialized autogamous fertility of the putative ancestor (*E. madrensis*).

Apparently closely adjacent colonies of *Erythranthe pallens* and *E. madrensis* were recognized in the field as distinct by Spellenberg in north-central Durango. His *6712* (*E. pallens*) was described as "corollas yellow" and has fruiting pedicels 15–30 mm and corolla tubes 9–10 mm with limbs expanded 10–12 mm; the flowers are allogamous. His *6711* (*E. madrensis*) was described as "corollas yellow, red-spotted within" and has fruiting pedicels 12–25 mm and corolla tubes 6–7 mm with limbs expanded 6–8 mm; the flowers are autogamous.

The close similarity of these entities is emphasized by variability in *Erythranthe madrensis* that approaches *E. pallens*. A greenhouse-grown plant of *E. madrensis* from seeds collected along Hwy 40 west of La Ciudad, Durango (*Vickery 2903*, UC!), has nearly the same aspect as *E. pallens* (large leaves, long pedicels, and relatively larger) but still has autogamous corollas. *McVaugh 12896* from Nevado de Colima in Jalisco is identified here as *E. madrensis* but is larger than normal (fruiting calyces 8 mm, fruiting pedicels 15–30 mm, corolla tubes 9–10 mm, exserted 4–5 mm). *Wonderly 347* from Michoacan also is identified as *E. madrensis* but has larger corollas and slightly didynamous stamens, the mode of fertility ambiguous from the specimen. The distinction and relationship between the Jalisco and Michoacan collections need further study.

37. ERYTHRANTHE PENNELLII (Gentry) Nesom, Phytoneuron 2012-40: 45. 2012. *Mimulus pennellii* Gentry, Madroño 9: 24. 1947. **TYPE**: **MEXICO**. **Sinaloa**. Africa, Sierra Tacuichamona, on rocks in water, 2000–3000 ft, 19 Feb 1940, *H.S. Gentry 5691* (holotype: MICH digital image!; isotypes: ARIZ-2 sheets!, MO!, PH!). The physiography and vegetation in the region of the type locality of *Mimulus pennellii* (Sierra Tacuichamona) were described in detail by Gentry (1946).

Perennial, rhizomatous, often mat-forming; stems, pedicels, calyces, and leaf surfaces moderately to densely villous with vitreous, multicellular, flattened hairs mostly 1–3 mm long with minute, dark-colored gland at the tip of each. **Stems** ascending-erect to decubent-ascending, 10–30 cm, rooting at proximal nodes, finely villosulous-glandular to densely villous-glandular. **Leaves** mostly cauline, blades orbicular to suborbicular, broadly ovate, or depressed-ovate, mostly 5–15(–30) mm x 6–17(–35) mm, largest at the base or near midstem, gradually or slightly reduced in size up to uppermost nodes, moderately to densely villous on both surfaces, proximal sharply cuneate to a petiolar base 1–5(–10) mm, distal becoming sessile, primarily palmately 5-veined with secondary reticulum evident, margins shallowly and regularly dentate to dentate-serrate with 3–6(–10) thick, mucronate-tipped teeth per side, apices mostly rounded. **Flowers** 2–6, mostly at distal nodes. **Fruiting pedicels** 15–25 mm, spreading-ascending. **Fruiting calyces** ovoid, 6–8 mm, closing, nodding lobes 5, triangular-acute, the upper ca. 1–2 times longer. **Corollas** yellow, red-spotted, tube-throats funnelform, 6–8 mm, exserted 2–3 mm beyond calyx margin, limb bilabiate, expanded 6–8 mm (pressed). **Plesiogamous**; anther pairs and stigma at essentially the same level. **Capsules** ca. 3 mm.

Flowering Jan–May. Wet places in canyons, cliff faces, rocks in water, flood plains, riparian forest, oak forest; 300–1500 m. Mexico (Sinaloa, Sonora). Map 25.

Additional collections examined. **MEXICO. Sinaloa**. [Mpio. Badiraguato], Puerto a Tamiapa, moist bank in canyon bottom, oak forest, 4500 ft, 5 May 1940, *Gentry 5866a* (ARIZ). **Sonora**. Arroyo Guajaráy, Cajón del Ardilla, growing in wet place near mouth of canyon in riparian forest with *Eupatorium collinum*, *Heliocarpus*, *Celtis iguanea*, *Montanoa rosei*, 375 m, 15 Mar 1994, *Fishbein et al. 1569* (ARIZ); Los Conejos, Rio Mayo, Saluchi W, small arroyo, growing in rocks out of which water seeping, 25 Oct 1934, *Gentry 1111* (ARIZ); 10 mi W of Nuri by old road to Texopaco, on small cliff above perennial stream, 24 Mar 1975, *Goldberg s.n.* (ARIZ); 5 km SW of Santa Barbara by road, at the entrance to a cave in El Palmarito canyon, 1000 m, 16 Mar 1990, *Martin s.n.* (ARIZ); ca. 5 km S of Santa Barbara, cave next to Mesa Redonda, 900 m, 14 May 1990, *Martin s.n.* (ARIZ); 1 mi N of Nuri, flood plain of the Rio Nuri, in sand in recent flood channel, 25 Mar 1975, *Spaulding 75-3-41* (ARIZ); below the village of Guajaráy on Arroyo Guajaráy, 6.5 km (by air) WNW of jct with Rio Mayo, tropical deciduous forest in rocky stream canyon, 270 m, in cobbles near stream, 19 Mar 1993, *VanDevender 93-476* (ARIZ); ca. 1 km (by air) NW of Yecora, along Rio Yecora, 1530 m, in moist soil or recently dried rocky stream beds, 2 Jun 1999, *Van Devender 99-181* (ARIZ).

Among the species of sect. *Simiola*, *Erythranthe pennellii* is distinctive in its combination of decumbent stems rooting at the nodes and forming mats, stipitate-glandular to villosulous-glandular or villous-glandular vestiture of vitreous, flattened hairs, orbicular to broadly ovate leaves with regularly dentate margins and short petioles, consistently 5-lobed calyces with middle lobes often reduced in size, and small corollas and autogamous fertilization.

In its habit, leaf morphology, and geography *Erythranthe pennellii* is most similar to *E. pallens* and *E. calciphila*, moreso to *E. calciphila* in its glandular vestiture and small corollas (autogamous). It is distinct from *E. calciphila* in its mostly decumbent stems with adventitious roots, deciduous basal leaves, and consistently 5-lobed calyces.

38. ERYTHRANTHE CALCIPHILA (Gentry) Nesom, Phytoneuron 2012-40: 43. 2012. *Mimulus calciphilus* Gentry, Madroño 9: 2. 1947. **TYPE**: **MEXICO**. **Sinaloa**. Sierra Surotato, Los Pucheros, pine-oak-madrono, openly forested slope, 5500–6500 ft, calcareous peñasco, shady slope, 17-24 Mar 1945, *H.S. Gentry 7217* (holotype: MICH digital image!; isotypes: ARIZ!, F digital image!, PH!).

Mimulus minutiflorus Vickery, Madroño 44: 392. 1997. **TYPE**: **MEXICO**. **Durango**. Km 165.5 on Mexico Hwy 40, in ephemerally moist, sunny areas in the pine forest, 2220 m, 12 May 1976, *R.K. Vickery, Jr. 2901* [Vickery culture no. 12,218] (holotype: UT!; isotypes: CAS digital image!, GH, MICH digital image!, MO! digital image!, SRSC!, UC!, UT!). Voucher for *n* = 32. Types distributed by Vickery were from greenhouse-grown plants that were rooting at lower nodes -- atypical in nature but seen in a few other collections besides the type.

Annual, usually fibrous-rooted, without rhizomes or stolons; stems, pedicels, and calyces minutely stipitate-glandular. **Stems** usually erect, sometimes decumbent-ascending, 4–30 cm, rarely rooting at proximal nodes, delicately villosulous-glandular along the whole length. **Leaves** basal and cauline, all petiolate, palmately 3(–5)-veined, blades orbicular-ovate to oblong-ovate, 7–28 mm x 5–22 mm, margins shallowly dentate to denticulate with 3–6 teeth per side, apices rounded to obtuse, base truncate to shallowly cuneate; petioles 1–3 mm, cauline blades slightly or hardly reduced in size from the basal but becoming subsessile to sessile (1–3 pairs of cauline leaves), surfaces villous with thin-walled, vitreous, eglandular or minutely gland-tipped hairs, commonly also minutely stipitate-glandular. **Flowers** 1–6(–10), axillary at all nodes. **Fruiting pedicels** 15–30(–55) mm, sometimes minutely hirtellous and minutely stipitate-glandular, sometimes short glandular-villous. **Fruiting calyx** ovoid, 5–6 mm in flower, 6–10 mm in fruit, thin, usually 3(–5)-nerved, closing, nodding ca. 90° at maturity, lobes usually 3 or 3 and 5 on the same plant, if 5 then with the 2 interpolated lobes much smaller than the lower pair. **Corollas** light yellow, red-spotted, tube-throats narrowly funnelform, 5–7 mm, exserted 1–2 mm beyond calyx margin, limb barely bilabiate, expanded 2–4 mm. **Styles** glabrous. **Plesiogamous**; anther pairs and stigma at essentially the same level. **Capsules** 2–4 mm, stipitate, included. 2*n* = 30, 32. Figs. 12, 13.

Flowering Mar–Sep(–Nov). Rocky knobs, moist boulders, wet rock faces, road cuts, seepage, springs, usually in pine or pine-oak woods; 1800–2500 m; Arizona; Mexico (Chihuahua, Durango, Sinaloa, Sonora). Map 25.

Additional collections examined. **USA. Arizona.** <u>Cochise Co.</u>: Mule Mts., Bisbee, wet places, Apr 1909, *Goodding 52* (ARIZ); Huachuca Mts., Glance Canyon, moist spot under rock ledges, 29 Sep 1949, *Goodding 874-49* (ARIZ); Bisbee, in creeks, Apr 1909, *Harris 21* (ARIZ); Chiricahua Mts., Cave Creek Canyon, 22 Sep 1929, *Harrison et al. 6186* (ARIZ); Chiricahua Mts., Coronado Natl. Forest, 1/8 mi W of Rustler Park Ranger Station, along Bootlegger Trail (USFS Trail 257) to Long Park, on moist rock faces of granite boulders, continual water supply from seepage, nearly total shade of *Pinus ponderosa*, assoc. flora of Douglas fir, gambel oak, aspen, *Salvia*, *Artemisia*, *Senecio*, *Bromus*, 8400 ft, 11 Sep 1986, *Ward 86-062*, voucher for chromosome count of *n* = 15 (MO). **MEXICO. Chihuahua.** Cerro Quicorichi, Rio Mayo, riparian, on moist rocks above water, 6000 ft, 6 Oct 1935, *Gentry 1941* (ARIZ); canyon E of Hidalgo del Parral, seepage at foot of dam, 12 Nov 1957, *Knobloch 749* (LL); Mpio. Temosachi, Nabogame, pine-oak-*Cupressus arizonica* forest, 1800 m, 21 Mar 1988, *Laferriere 1394* (TEX); Mpio. Guadalupe y Calvo, meadow on S side of village of Turuachi, 0.4 mi NW of bridge crossing in Turuachi, SW of Rio Verde 46 mi SW of El Vergel, area of pine and scattered oaks, 22 Aug 1988, *McDonald & Nesom* 2526 (TEX); Sierra Obscura, 1 mi W of Rancho El Oso, 2000 m, 26 Mar 1985, *Martin s.n.* (ARIZ); 49.9 mi SW of El Vergel on Hwy 24, in Turuachi Canyon, 0.7 mi S of bridge at Turuachi, area of oak-pine, base of N-facing slope/seepage area, scattered on vertical, wet rock face of road cut below seepage area, 2200 m, 24 Aug 1984, *Nesom & Lewis 5141* (TEX); Santa Rosa, 30 May 1960, *Pennington 256* (TEX); Sierra Madre, springy places, 29 Sep 1887, *Pringle 1347* (ND-Greene); Mpio. Ocampo, 8 mi toward San

Juanito from jct of Tomochic-Yepachic road, 7 mi NW of Yoquiva, steep N slope, igneous, with *Quercus sideroxyla*, *Q. rugosa*, doug fir, ca. 8000 ft, 27 Apr 1985, *Spellenberg et al. 8061* (NMC); Mpio. Ocampo, ca. 1 km W of W boundary of Parque Nacional Cascada de Basaseachic, 21 km from the Cahuisori-Ocampo road on the road to Candameña, 10.5 km below Cruz Verde at the crossing of the Rio Candameña, ca. 1.6 air mi N of Candameña, among *Platanus*, *Acacia*, 965 m, two plants only on a sand bar, 25 May 1994, *Spellenberg & Miller 12062* (NMC); Mpio. Ocampo, ca. 1 km W of W boundary of Parque Nacional Cascada de Basaseachic, 11 km from the Cahuisori-Ocampo road on the road to Candameña, 0.3 km below Cruz Verde, steep SE-facing canyon at the top of Barranca Composante, oaks, 1900 m, in seep in cleft in rock, 23 Sep 1994, *Spellenberg et al. 12125* (NMC); 18 air km SSE of Cuahtemoc, above Cuisuiriachic at mine, on La Bufa, vertical rock face, among wet moss, 6800 ft, 14 Apr 1984, *Spellenberg & Soreng 7704* (NMC); Sierra La Brena, 13 mi SW of Altamirano, just W of Los Azules on high rocky knob in pine-oak woodland, 7200-7400 ft, 26 Sep 1998, *Spencer & Atwood 1244* (TEX); Mpio. Ocampo, road to Candameña, 5 km before Cruz Verde, open, rocky, NE-facing slope, 6000 ft, 23 Sep 1994, *Todsen s.n.* (NMC); 5 mi SE of Colonia Garcia, 12 Sep 1899, [*Townsend & Barber*] *324* (ND-Greene); 20 mi SW of Chuichupa, 31 Aug 1899, [*Townsend & Barber*] *388* (ND-Greene). **Durango**. 25 km E of El Palmito, along highway, steep moist cliff, ca. 2300 m, Mar 1965, *Breedlove 7231*, Vickery cult. 7169, voucher for *n* = "$32^{\pm}$, $48^{\pm}$, $64^{\pm}$" (SRSC, UC); Santiago Papasquiaro and vicinity, Apr and Aug 1896, *Palmer 55* (UC); 111 road mi N of Santiago Papasquiaro on road to Topia, 5 mi W of Cienega Nuestra Senora, steep, rocky W face, of mesic canyon bottom next to stream, pine-fir-oak-madrone-juniper woods, 2420 m, on mossy rock, 18 Sep 1892, *Spellenberg & Zimmerman 6741* (NMC); KM 165.5 on Mex Hwy 40, in ephemerally moist sunny areas in the pine forest, 2220 m, 12 May 1976, *Vickery 2901*, cult. 12,218, greenhouse grown, voucher for n = 32 (UC); 2 km W of Los Bancos, Hwy 40 at KM 165.5, in moss all over the wet cliffs, 7550 ft, 12 May 1976, *Vickery* [*2901*], field-collected (UC-2 sheets). **Sinaloa.** Along Hwy 40, 1.5-3 mi below El Palmito , ca. 45 mi NE of Concordia and ca. 3 mi S of the Durango state line, locally common beside a seep, 6400 ft, 30 Dec 1983, *Sanders et al. 4463* (ARIZ). **Sonora.** Sierra de los Ajos, W-facing slope, spring at head of Hoya del Packard, 2300 m, 10 Oct 1992, *Felger et al. 92-893* (ARIZ); Mesa El Campanero, along road between Puerto de la Cruz and microwave station, ca. 0.4 mi N of microwave tower, 2100 m, seep in side of cliff in pine-oak forest, 9 Sep 1995, *Fishbein et al. 2603* (ARIZ); Mesa El Campanero W of Yecora, headwaters of El Reparo (Yaqui River), fir-*Cupressus*-*Pinus* ravine, 2100 m, 2 Jul 1992, *Martin & Barber s.n.* (ARIZ).

Figure 16. *Erythranthe calciphila*, *Spencer & Atwood 1244*, from northwestern Chihuahua.

Erythranthe calciphila is recognized by its annual duration (fibrous-rooted), short, erect stems with few, even-sized leaves (the basal often persistent), delicate stipitate-glandular vestiture, 3-lobed calyces relatively large in fruit, and very small corollas with autogamous fertilization. Plants rarely root at proximal nodes — an example from Sierra Obscura, Chihuahua (*Martin s.n.*) has the basal portion of the stem rooting at nodes; these plants also have lateral calyx lobes more prominently developed than characteristic for the species.

Figure 18. *Erythranthe calciphila* in natural habitat. Photo by Mark Egger, used by permission. Sinaloa, Mexico, along Mex. Hwy 40, below (and W of) El Palmito, on barranca cliffs, 1 Sep 1997.

39. ERYTHRANTHE VISIBILIS Nesom, **sp. nov.** **TYPE**. **MEXICO**. **Michoacan**. Vicinity of Morelia, Cerros San Miguel, 2200 m, Dec 1910, *G. Arsene 5310* (holotype: MO). Figure 19.

Distinct among species of sect. *Simiola* in its combination of terrestrial habitat, prostrate stems rooting at the nodes, small, villosulous-glandular leaves, glandular pedicels, tendency for 3-lobed calyces, and tiny, autogamous flowers on short pedicels.

Annual (probably; basal parts not observed), mat-forming. **Stems** procumbent, 2–10 cm, rooting at the nodes, glabrous. **Leaves** drying very thin and translucent, cauline, petiolate to subpetiolate, petioles 1–3 mm, blades ovate or ovate-elliptic to depressed-ovate, 5–14 mm x 5–14 mm, palmately 3–5-veined, adaxial surfaces sparsely to moderately puberulous with vitreous, thin-walled, gland-tipped hairs ca. 0.2–0.8 mm, not punctate, margins subentire to barely mucronulate or shallowly but sharply dentate-serrate, 3–5 teeth per side, apices obtuse to rounded, bases cuneate to subcordate. **Flowers** 1–3, apparently mostly at distal nodes. **Fruiting pedicels** 4–11 mm, minutely stipitate-glandular with hairs ca. 0.1 mm. **Fruiting calyces** broadly obovate-campanulate, 4–6 mm, variably closing or not at all, nodding, lobes 3–5, the middle sometimes much reduced, upper lobe longest. **Corollas** yellow, apparently without red markings, tube-throats cylindric, ca. 5–6 mm, barely exserted if at all beyond the calyx margin. **Plesiogamous**; anther pairs and stigma at essentially the same level. **Capsules** 2–3 mm, included.

Known only from the type collection and one other from the same locality. Map 24.

Additional collection examined. **MEXICO**. **Michoacan**. Vicinity of Morelia, Cerros San Miguel, 2200 m, 10 Feb 1912, *Arsene 9936* (MO).

Figure 19. *Erythranthe visibilis*, type collection. Insets contrast mature calyx morphology, closed vs. open.

The epithet is an affirmation of the existence of these plants, despite their diminishingly small size and delicate aspect. *Erythranthe visibilis* has the smallest flowers of any species in sect. *Simiola*. The two collections cited here were annotated by A.L. Grant and by F.W. Pennell as "Mimulus glabrata var. jamesii" (that entity identified here as *Erythranthe geyeri*). Habitat information is lacking for the collections but the plants are prostrate and mat-forming and in a terrestrial habit, growing intermixed with two species of delicate moss. The calyces are variably 5-lobed to 3-lobed, sometimes with reduced middle lobes (thus tending toward 3-lobed) and the throat also is variable from closed to open, the two lower lobes turning sharply upward or not (Fig. 19).

Erythranthe visibilis is a member of the primarily Mexican *E. madrensis* group, particularly in view of the calyx morphology, relatively reduced size, and geography. The range of *E. madrensis* reaches Michoacan (Map 23) and depauperate plants of that species rarely may approach the approximate small size of *E. visibilis*, but nowhere in the range of *E. madrensis* does it produce glandular pedicels or leaves, which are characteristic of *E. visibilis*.

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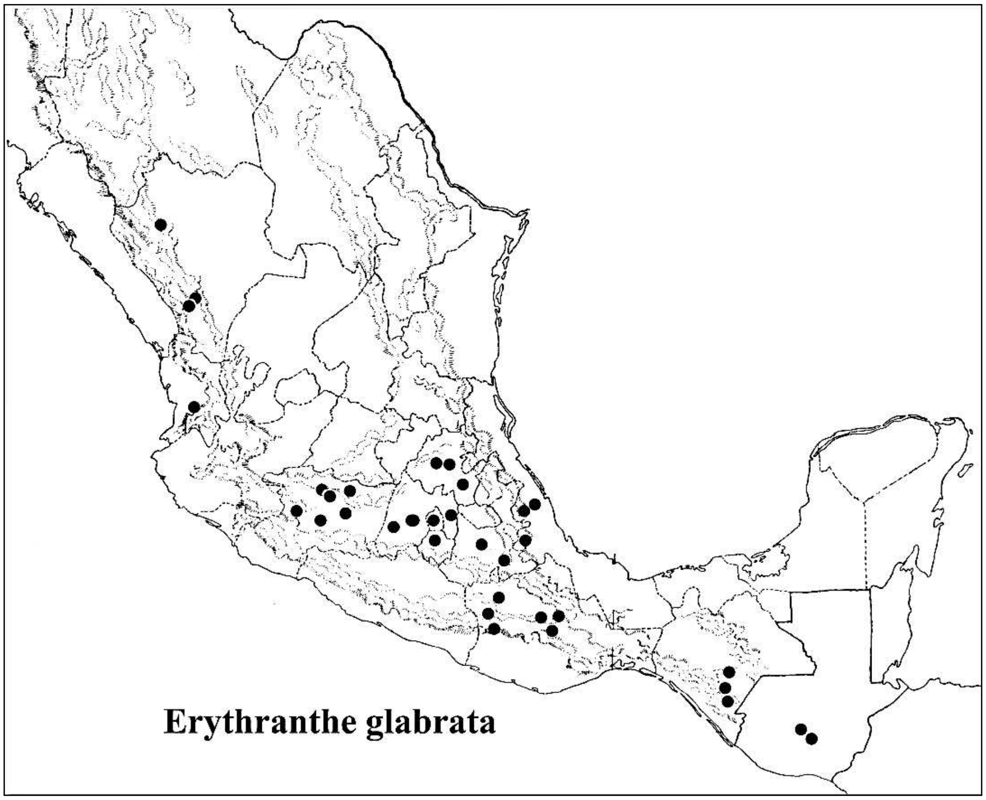
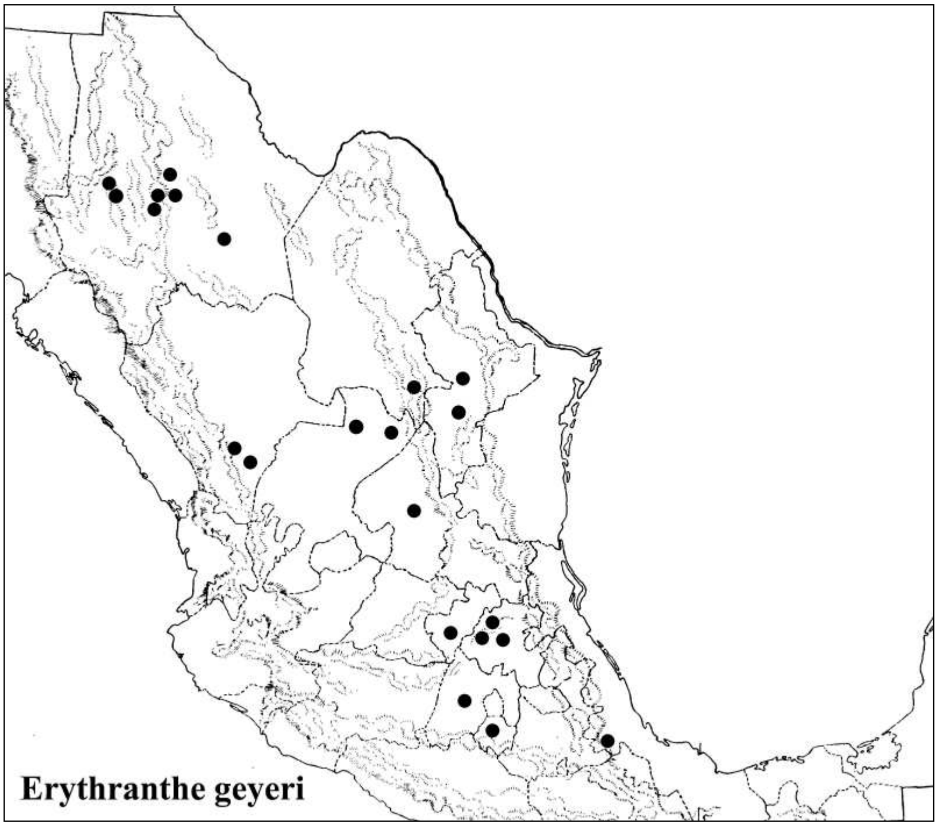
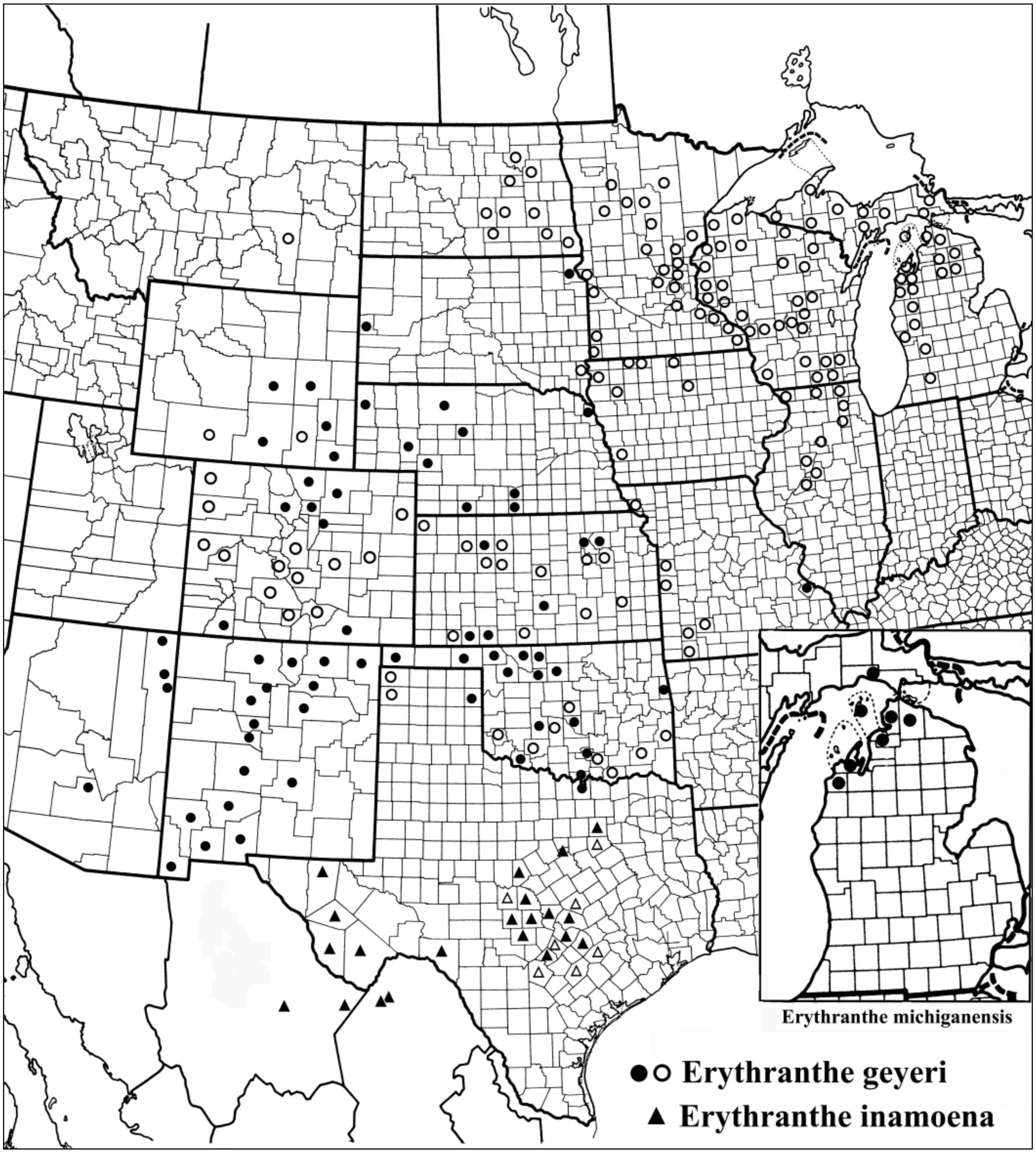


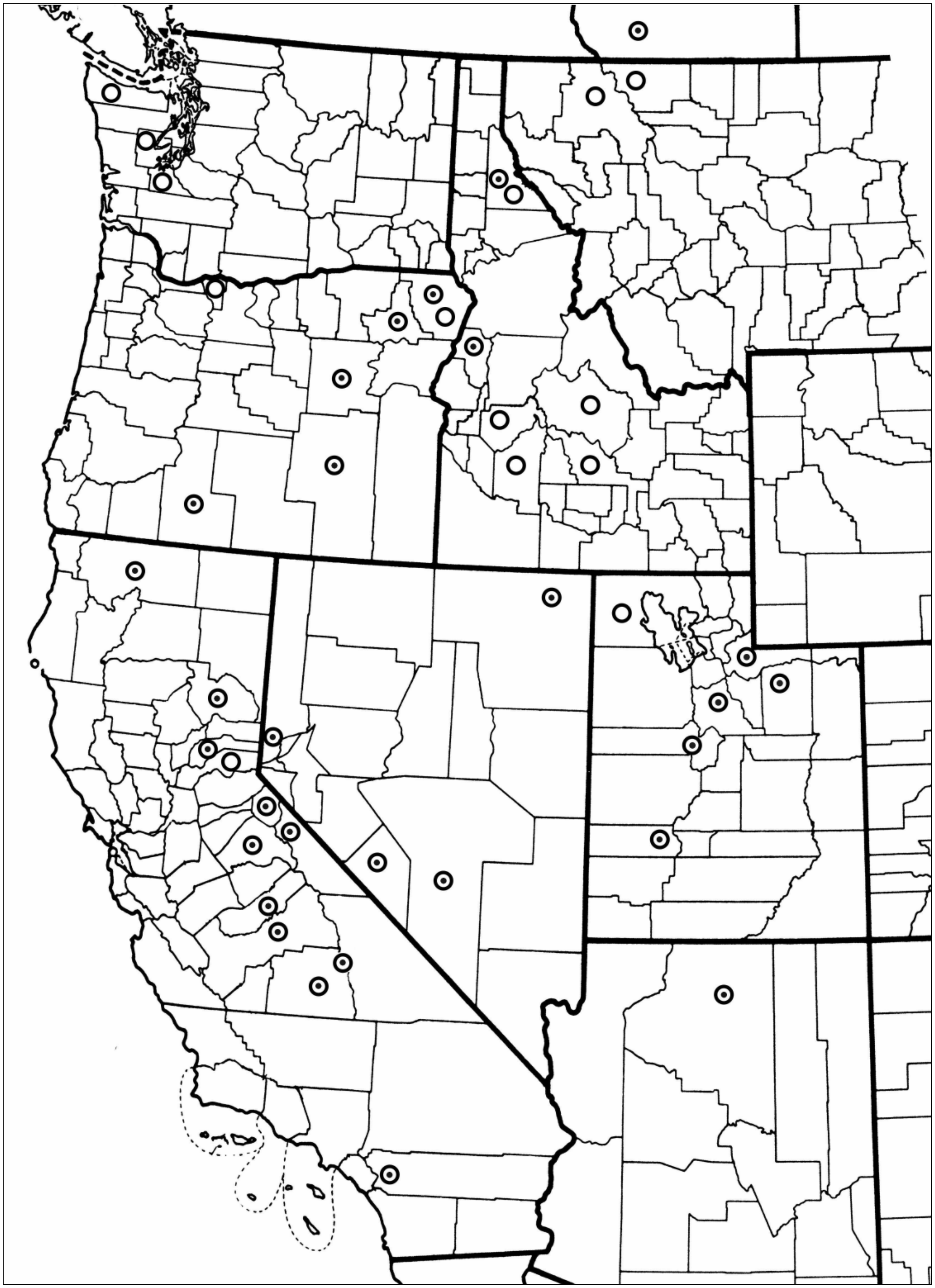
Map 1. Distribution of *Erythranthe glabrata*.



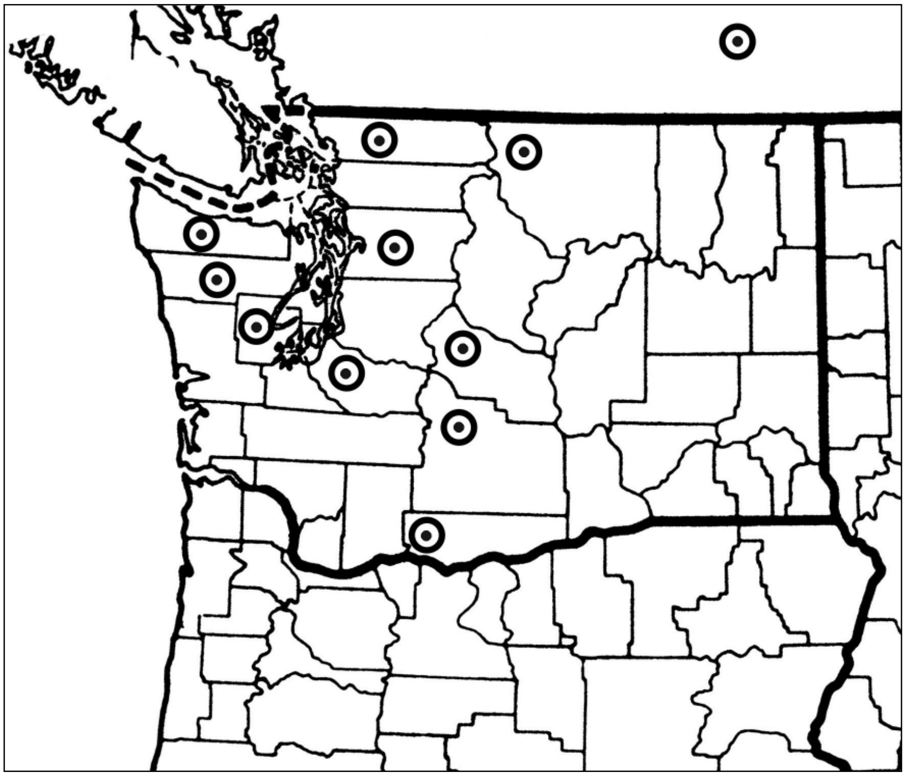
Map 2. Distribution of *Erythranthe geyeri* in Mexico.



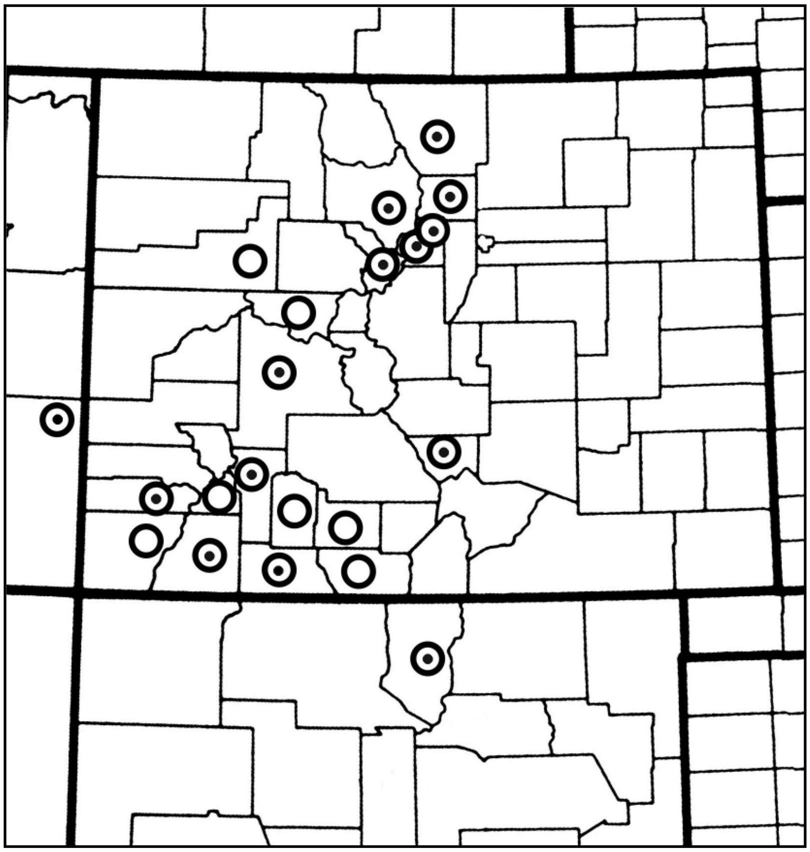
Map 3. Distribution of *Erythranthe inamoena*, *E. geyeri* in the USA, and *E. michiganensis*. Hollow symbols are records from literature. Missouri distribution records for *E. geyeri* added from Weber et al. (2000).



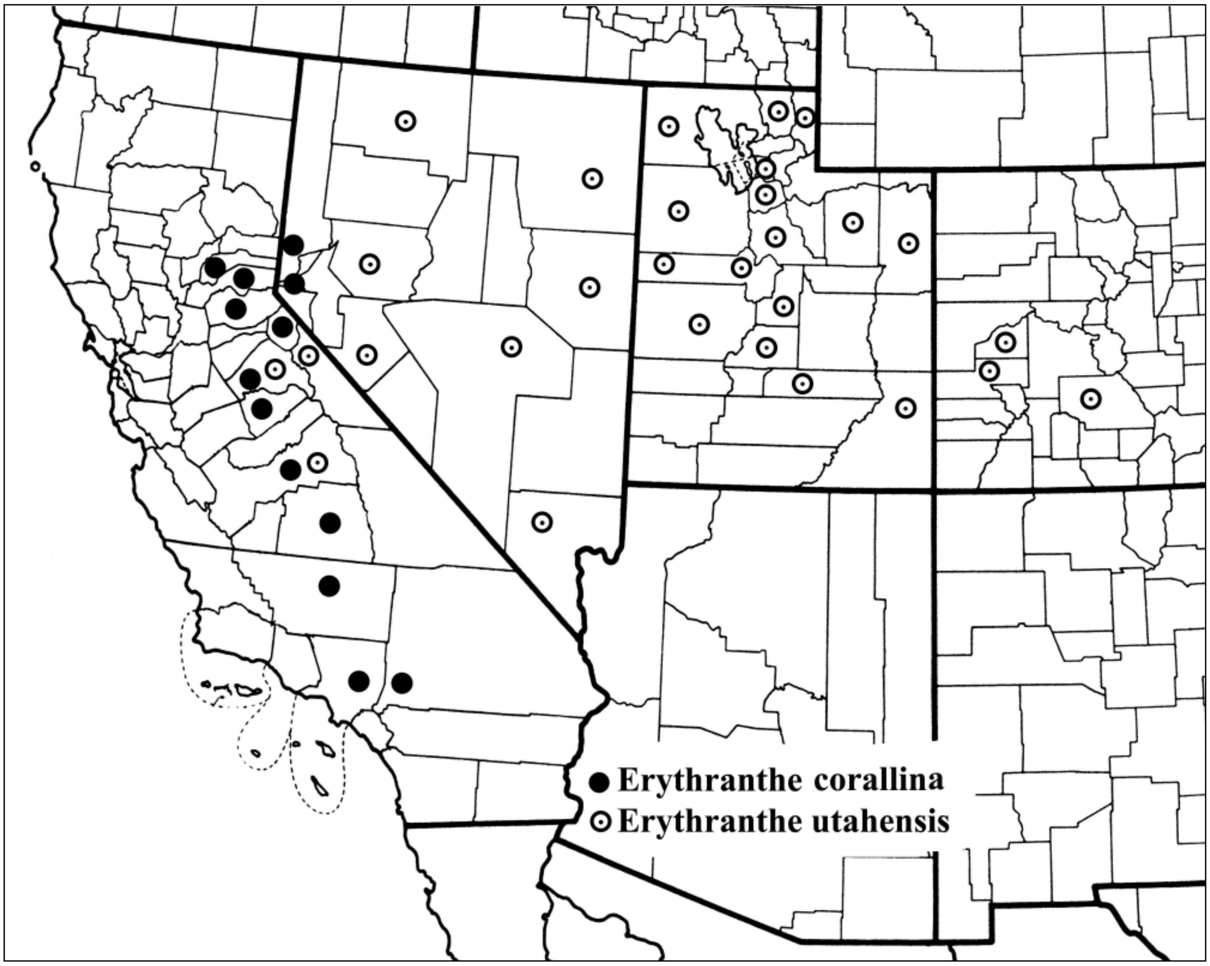
Map 4. Distribution of *Erythranthe tilingii*. Symbols without dots are records from literature.



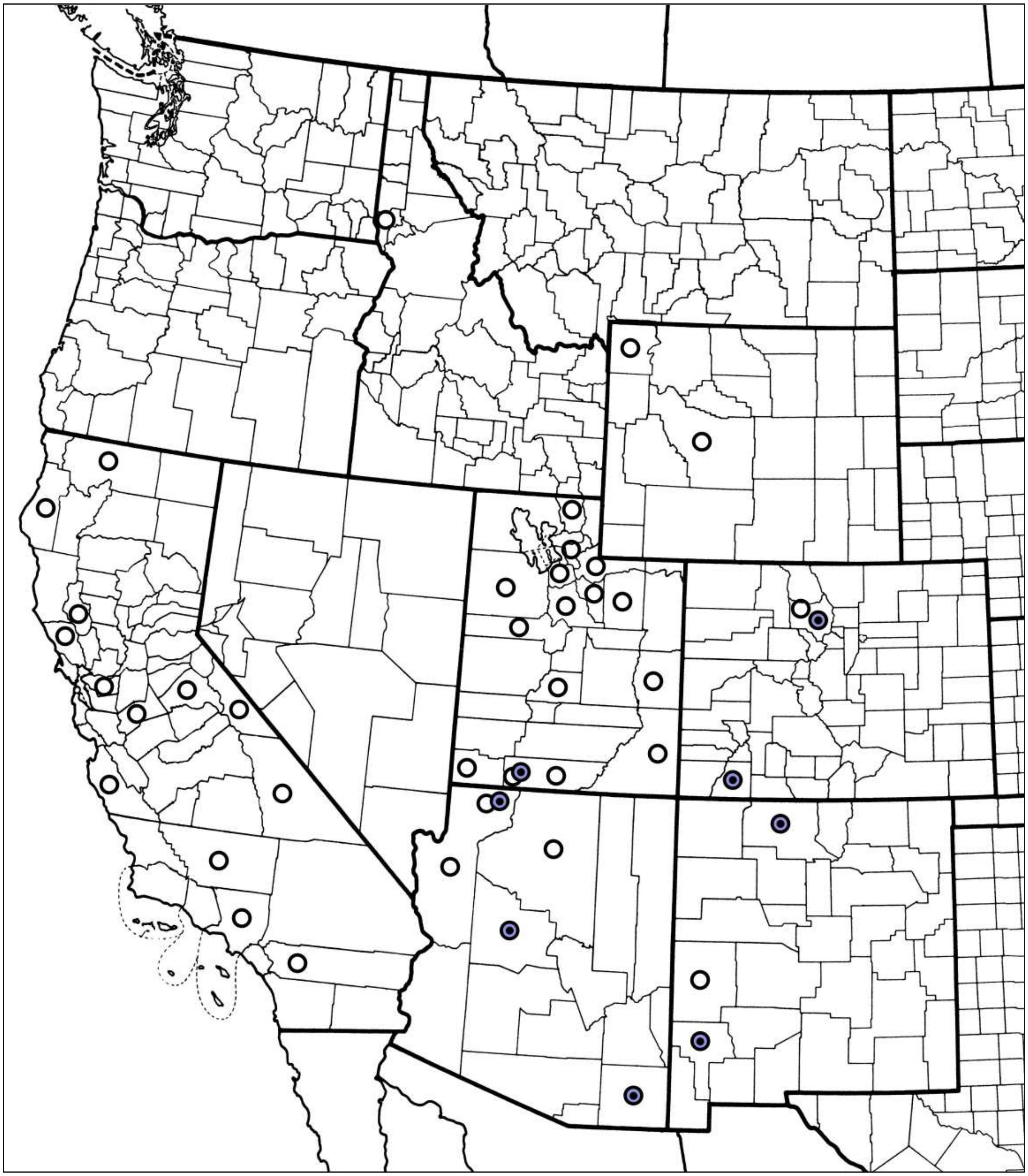
Map 5. Distribution of *Erythranthe caespitosa*.



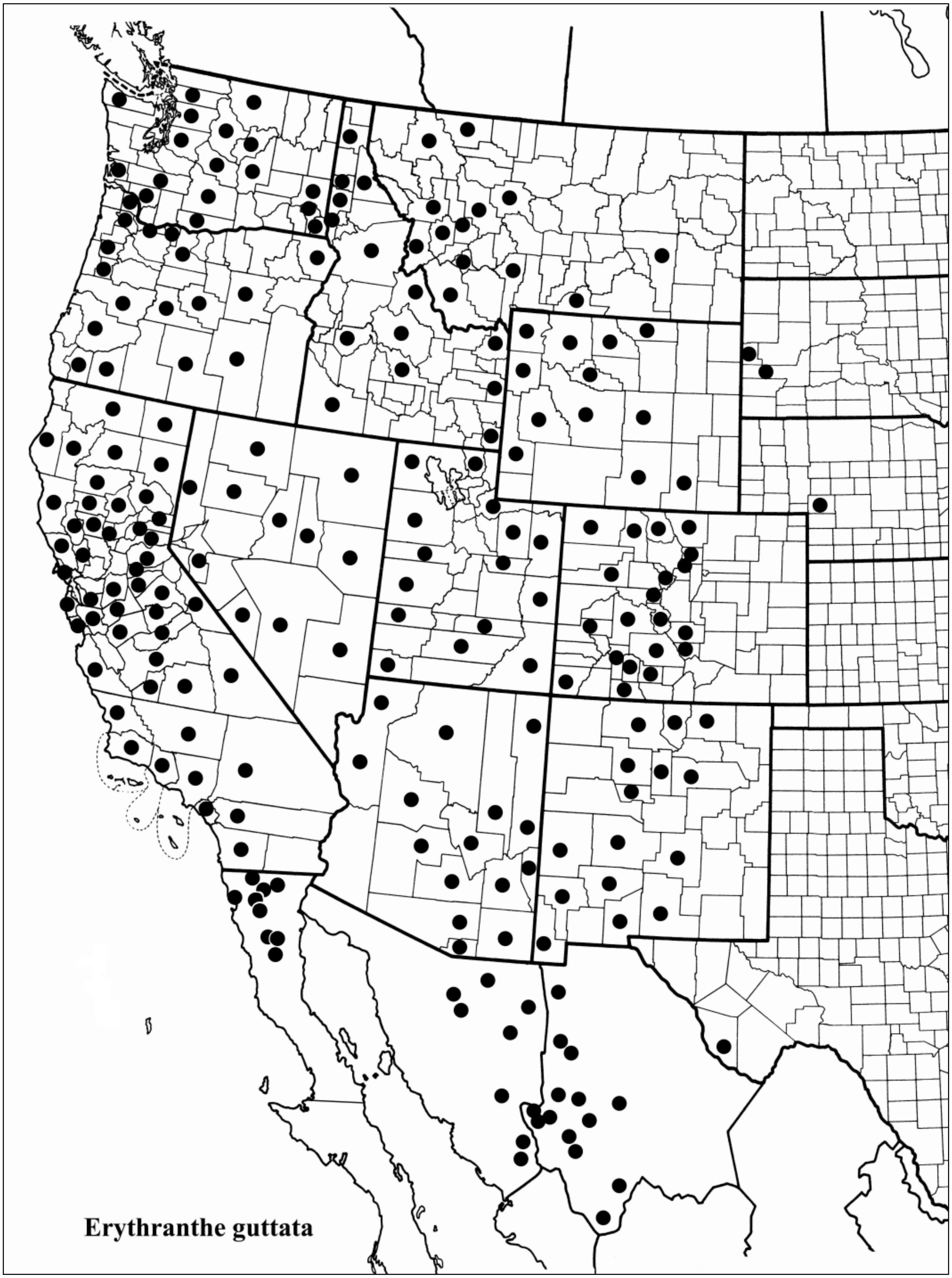
Map 6. Distribution of *Erythranthe minor*. Symbols without dots are records from literature.



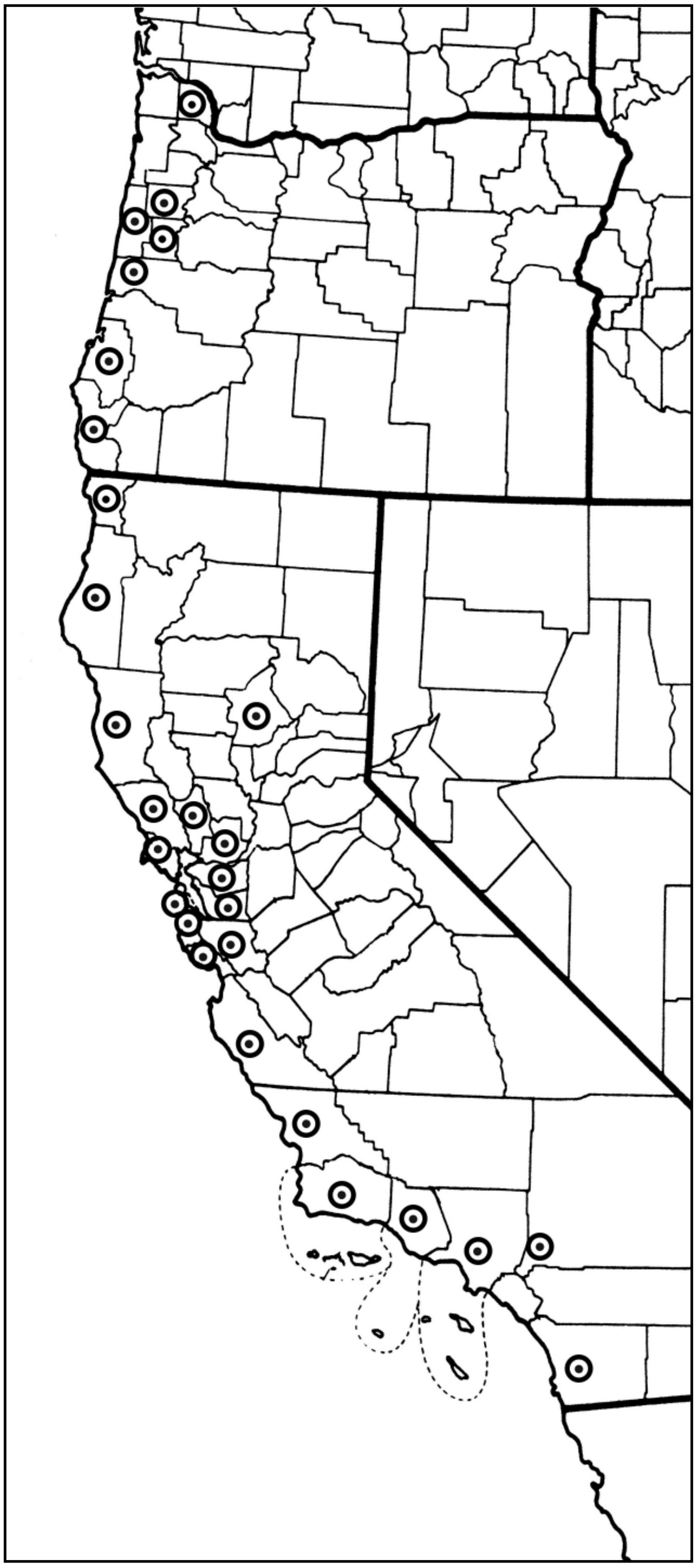
Map 7. Distribution of *Erythranthe utahensis* and *E. corallina*.



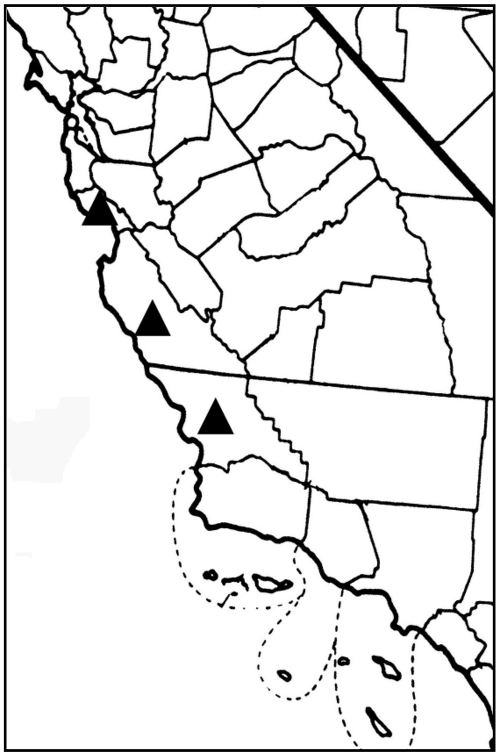
Map 8. Chromosome counts reported from the USA for plants identified as *Mimulus guttatus*. Open circles are diploid; dotted blue circles are tetraploid, Overlapping symbols in Mohave Co., Arizona, and Kane Co., Utah, denote single populations with both ploidy levels. Tetraploids also are reported from Canadian coastal localities (British Columbia) and Alaska. See text for further comments.



Map 9. Distribution of *Erythranthe guttata* (in the sense of the present study) in the USA and Mexico. The complete distribution in Mexico is shown.



Map 10. Distribution of *Erythranthe grandis*.



Map 11. Distribution of *Erythranthe arenicola*

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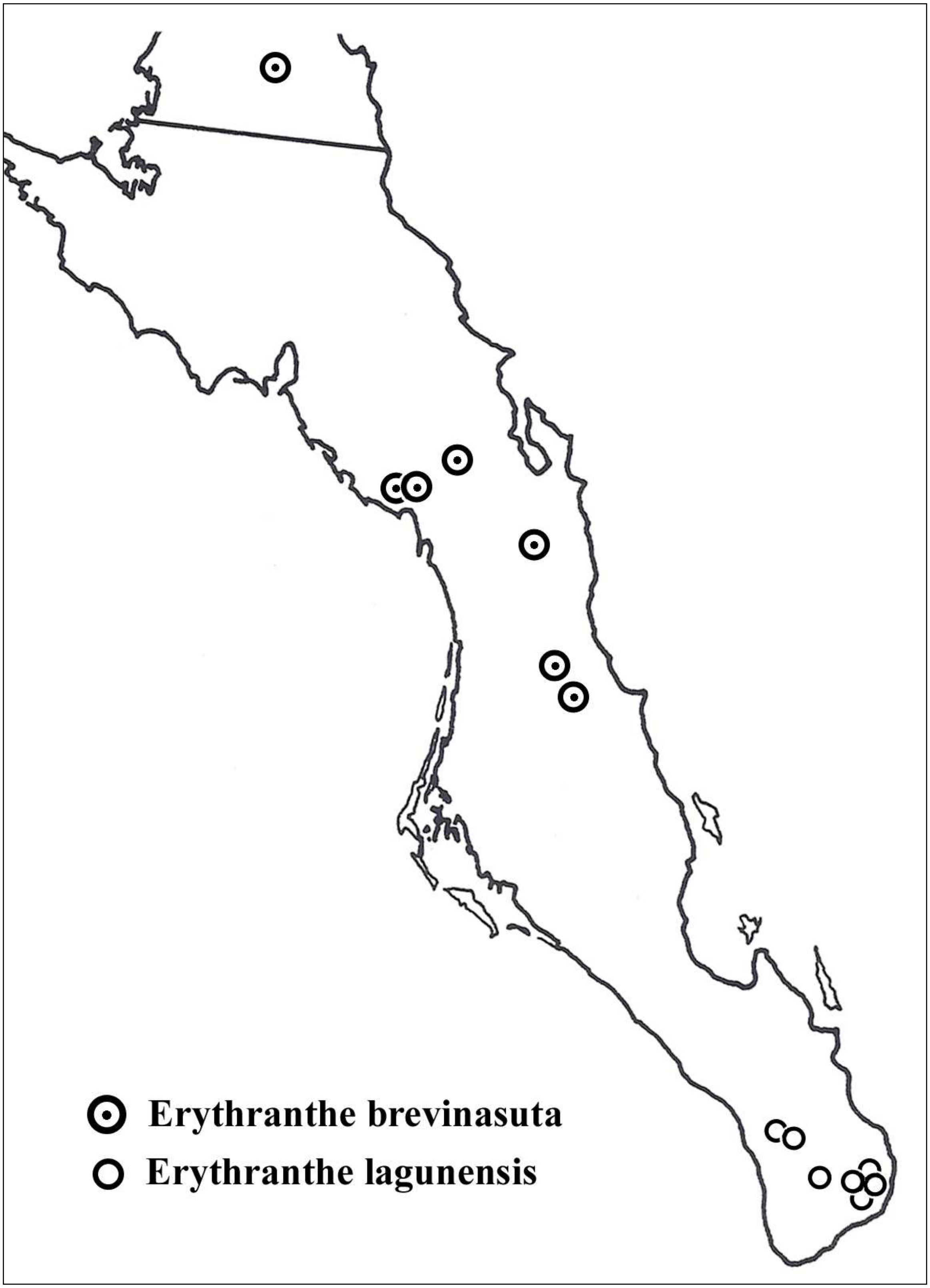
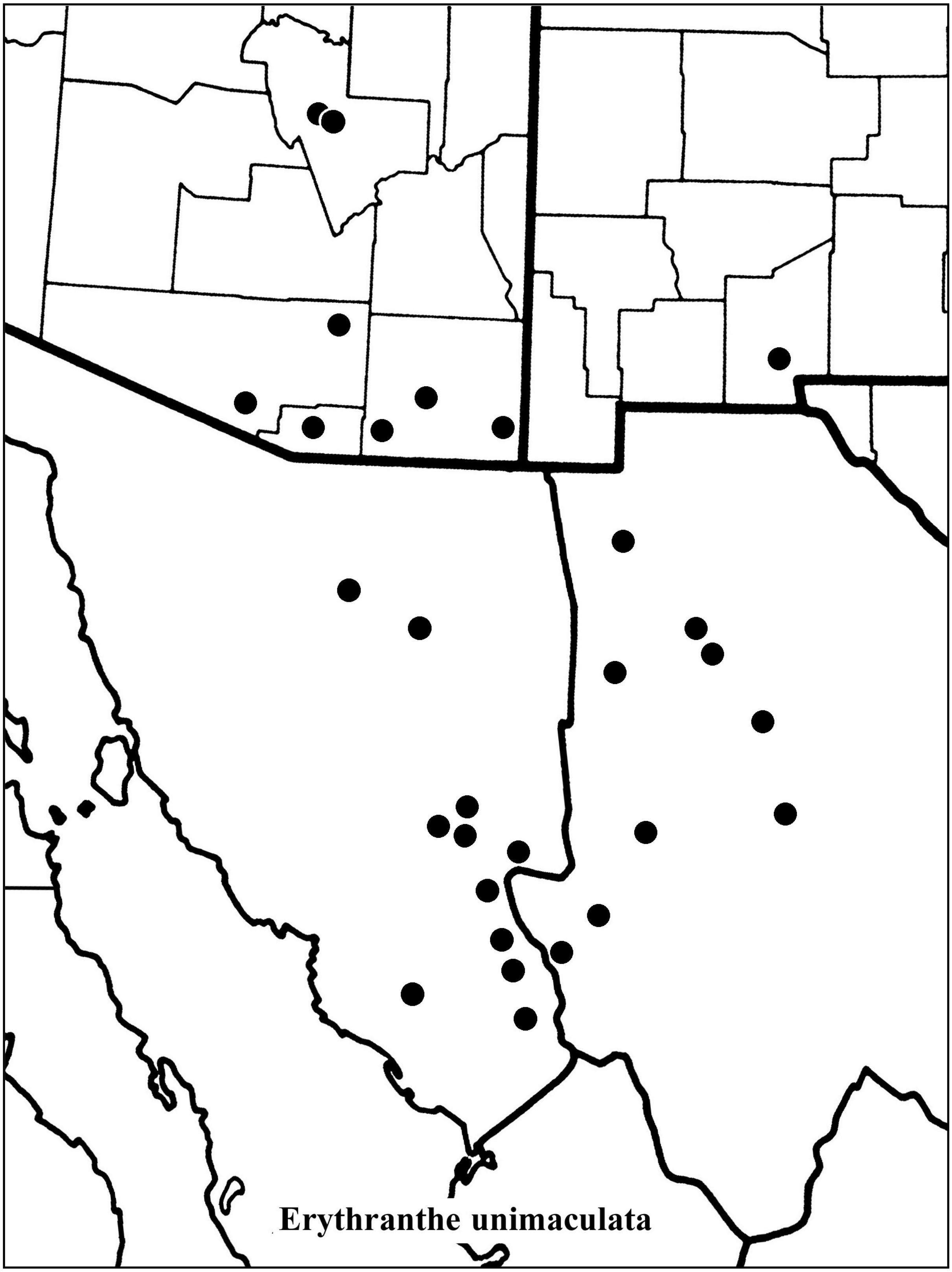
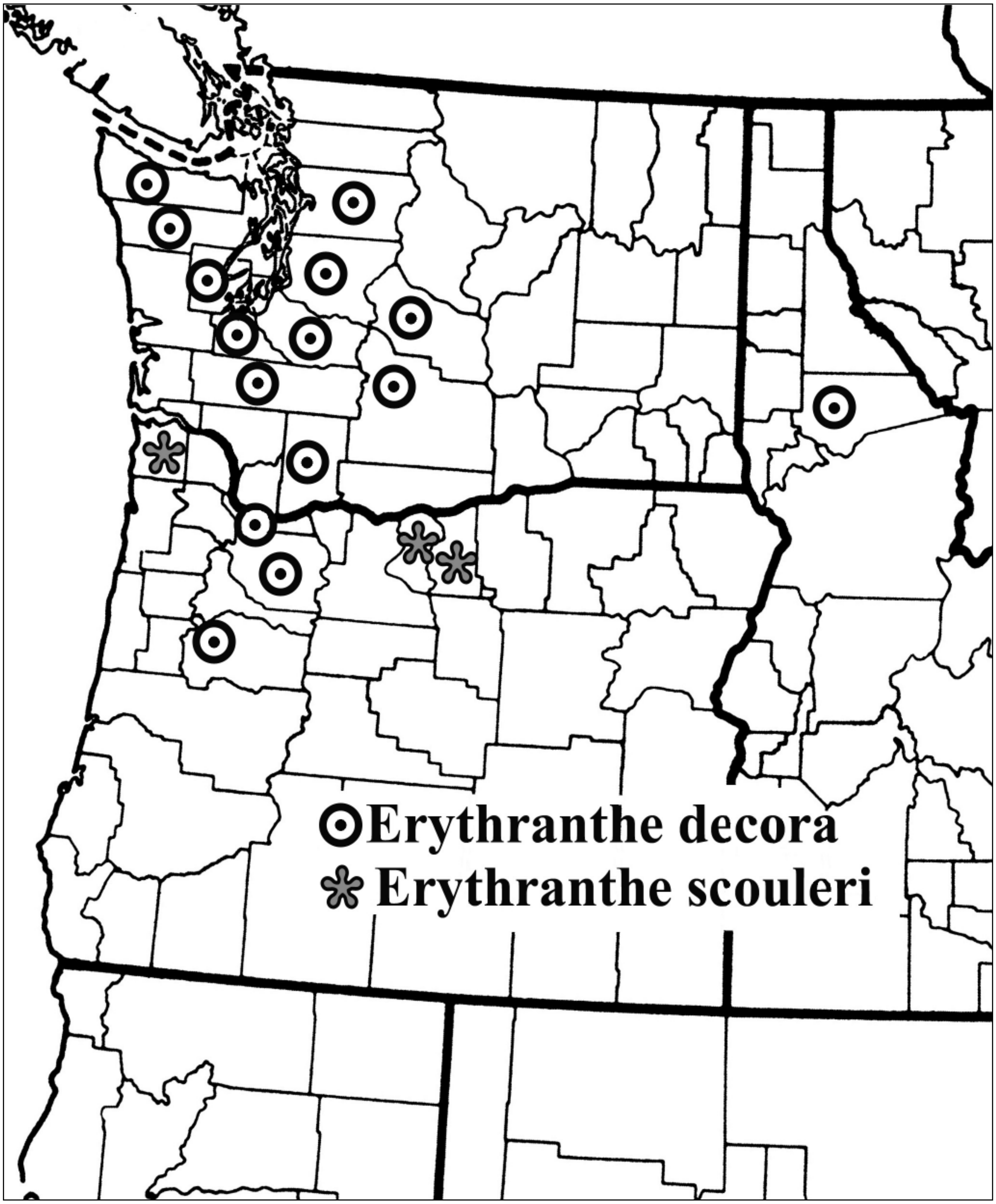


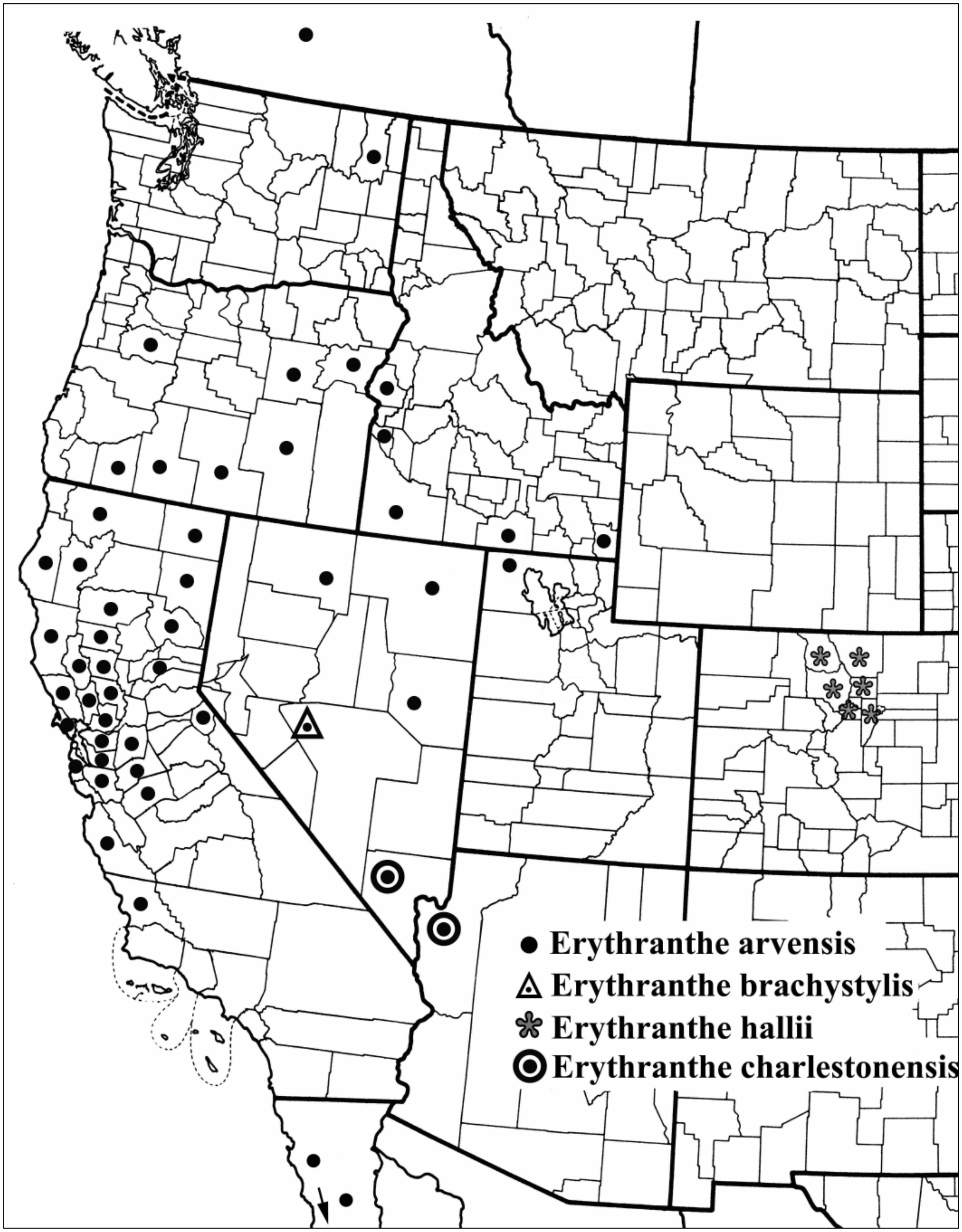
Map 12. Erythranthe brevinasuta and E. lagunensis.



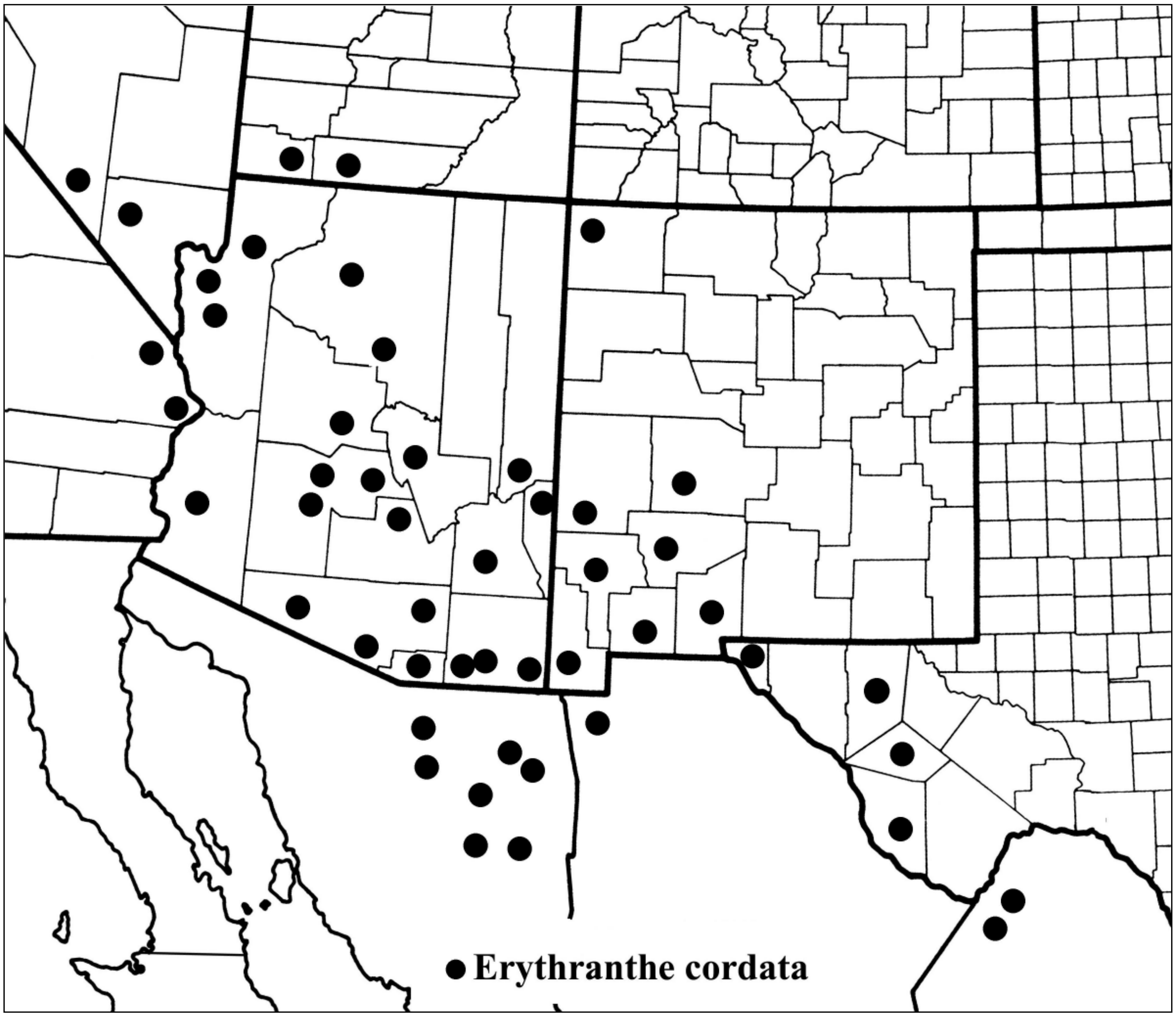
Map 13. Distribution of *Erythranthe unimaculata*.



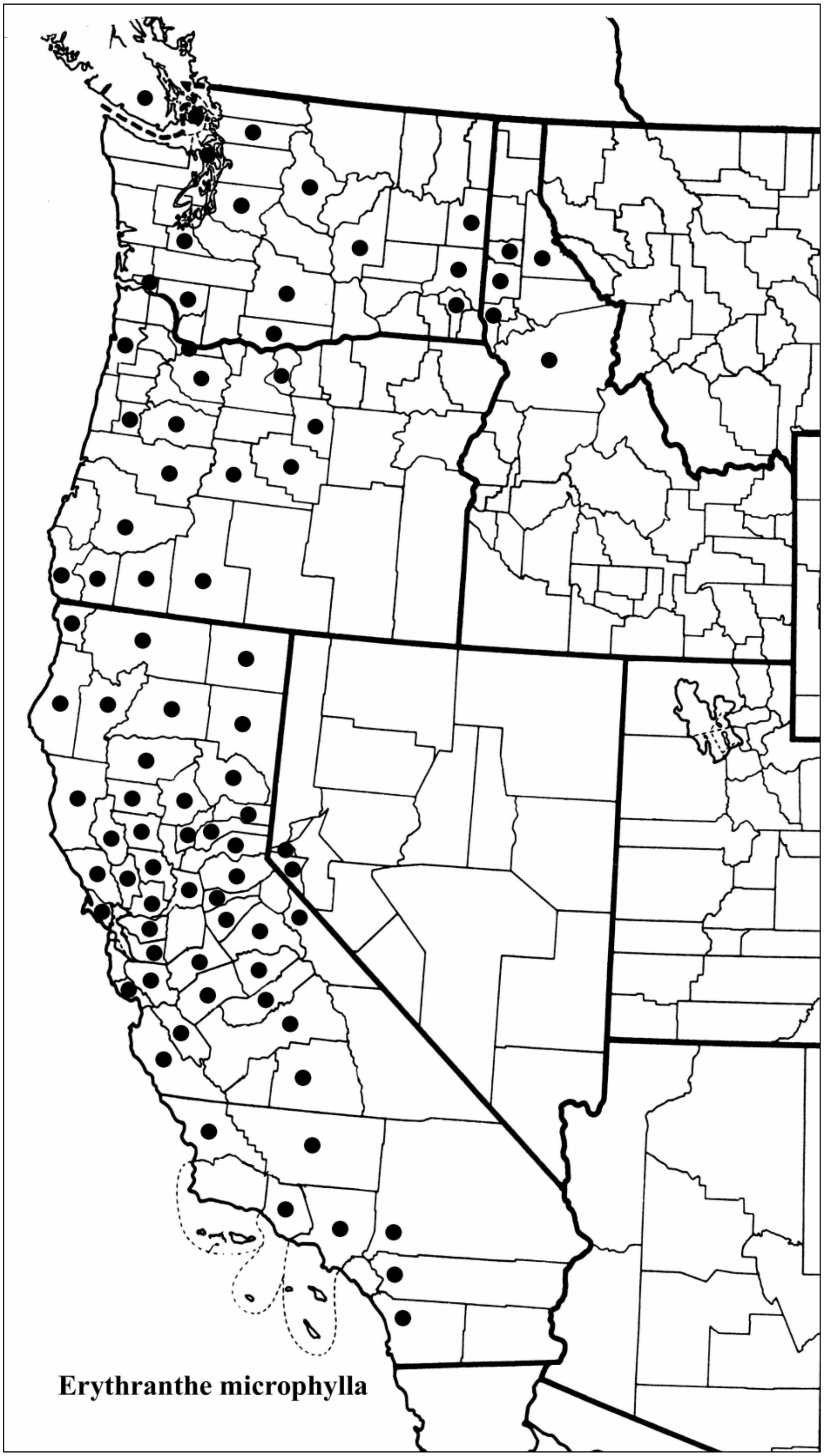
Map 14. Distribution of *Erythranthe decora* and *E. scouleri*.



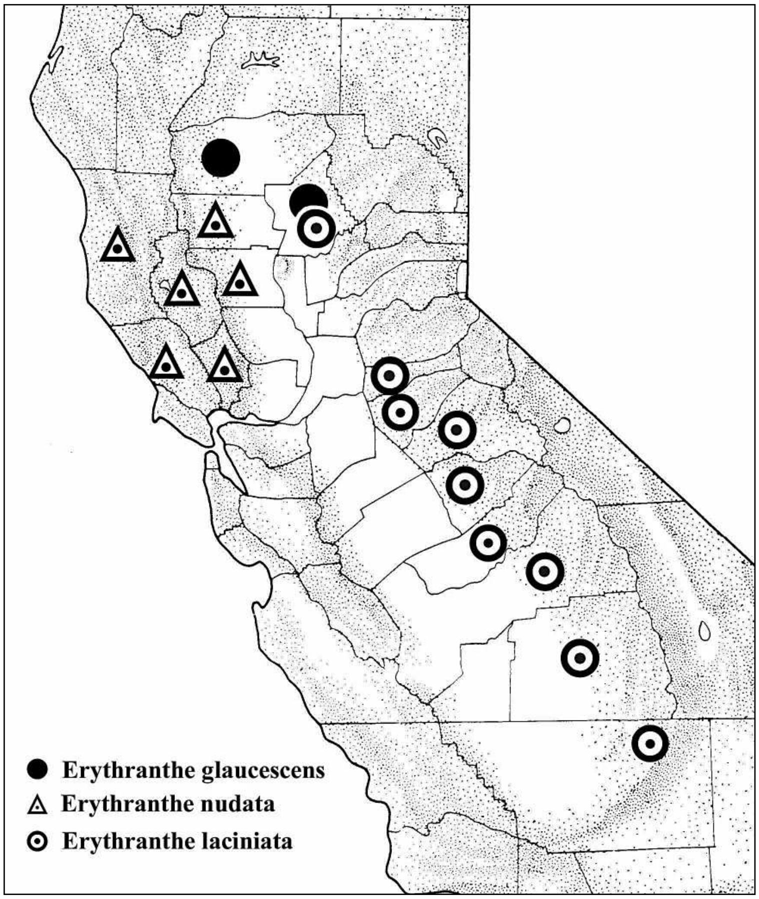
Map 15. Distribution of *Erythranthe arvensis*, *E. brachystylis*, and *E. hallii*. Study of herbaria in Oregon and Washington (under-represented in the current study) may show that *E. arvensis* is more common in that region.



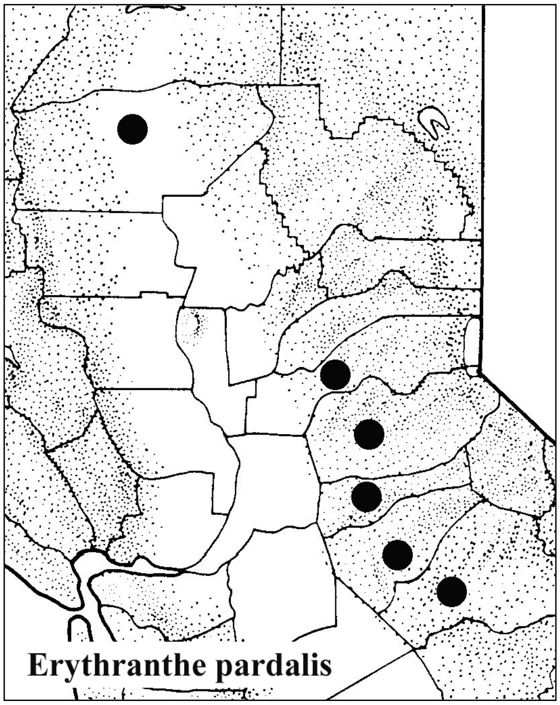
Map 16. Distribution of *Erythranthe cordata*.



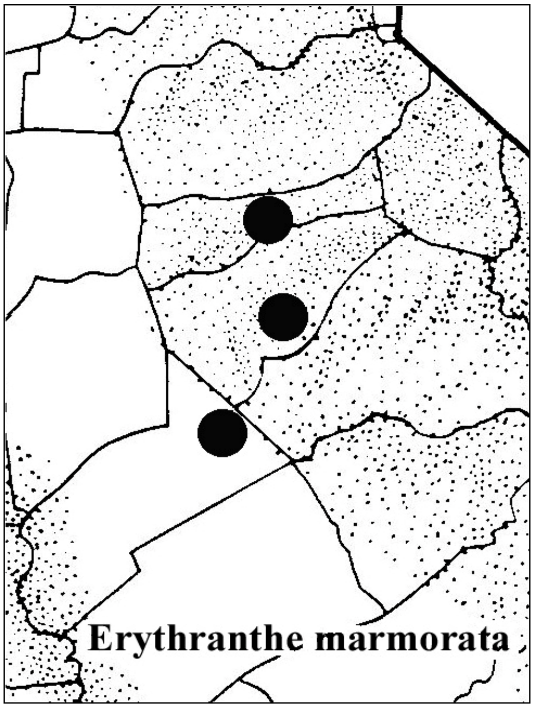
Map 17. Distribution of *Erythranthe microphylla*.



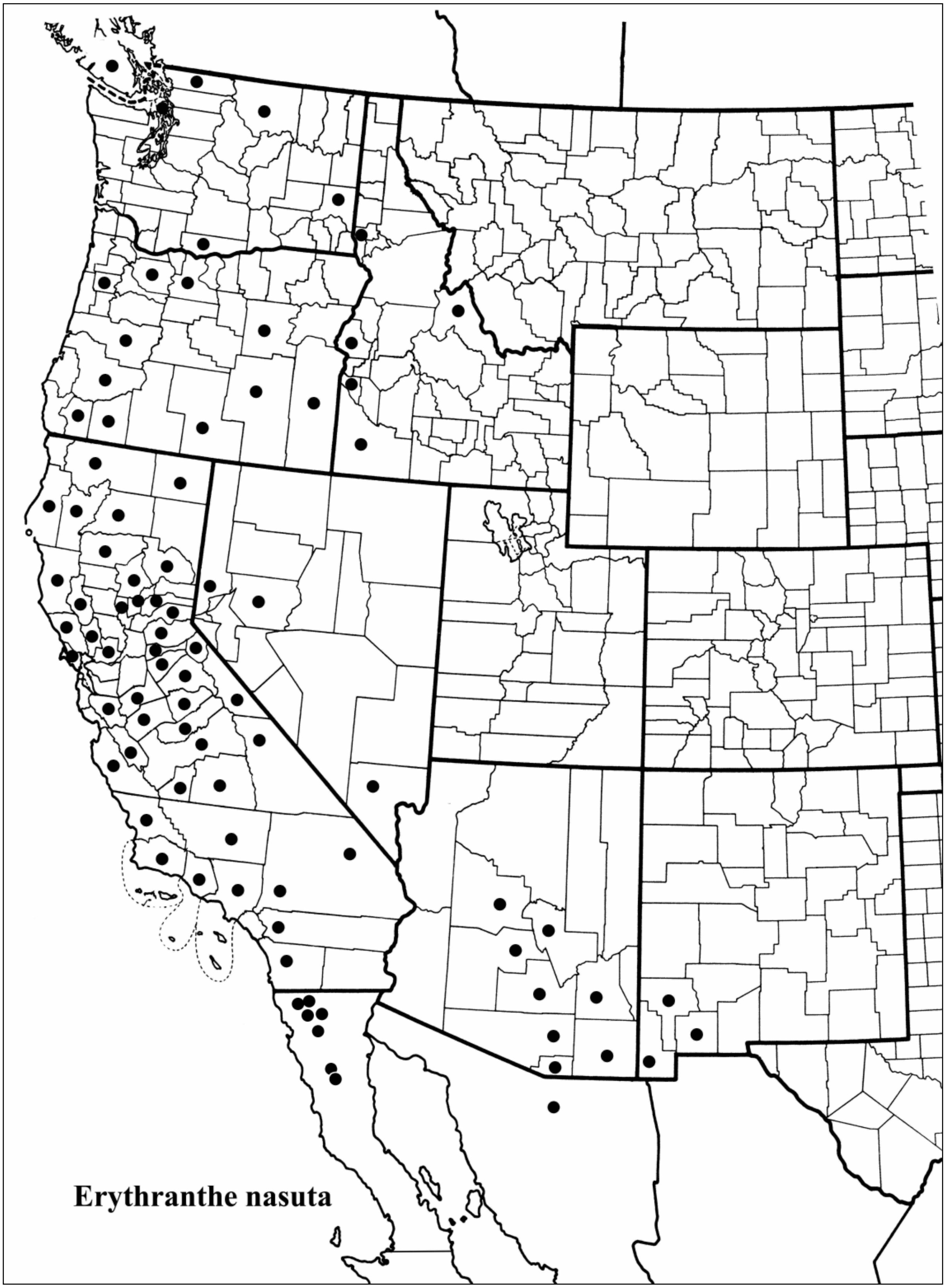
Map 18. Distribution of *Erythranthe laciniata*, *E. glaucescens*, and *E. nudata*.



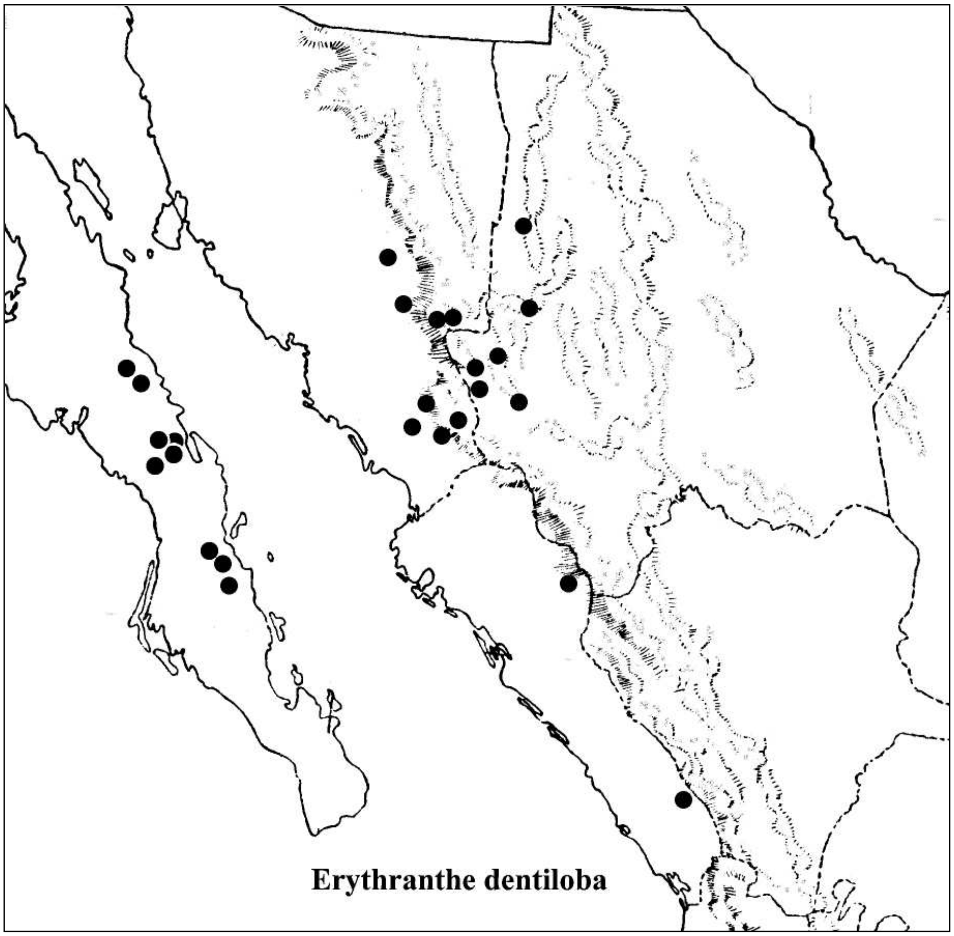
Map 19. Distribution of *Erythranthe pardalis*.



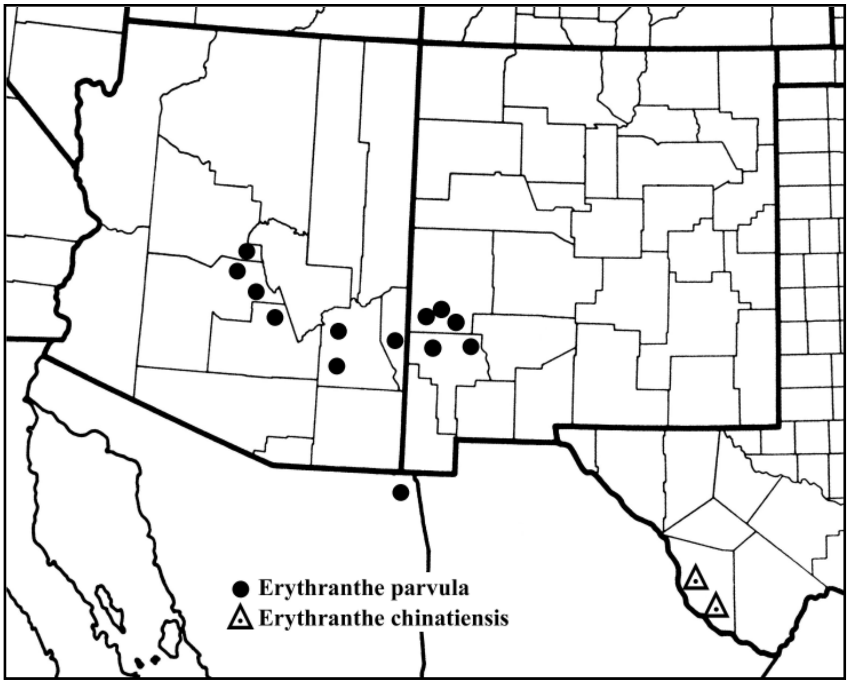
Map 20. Distribution of *Erythranthe marmorata*.



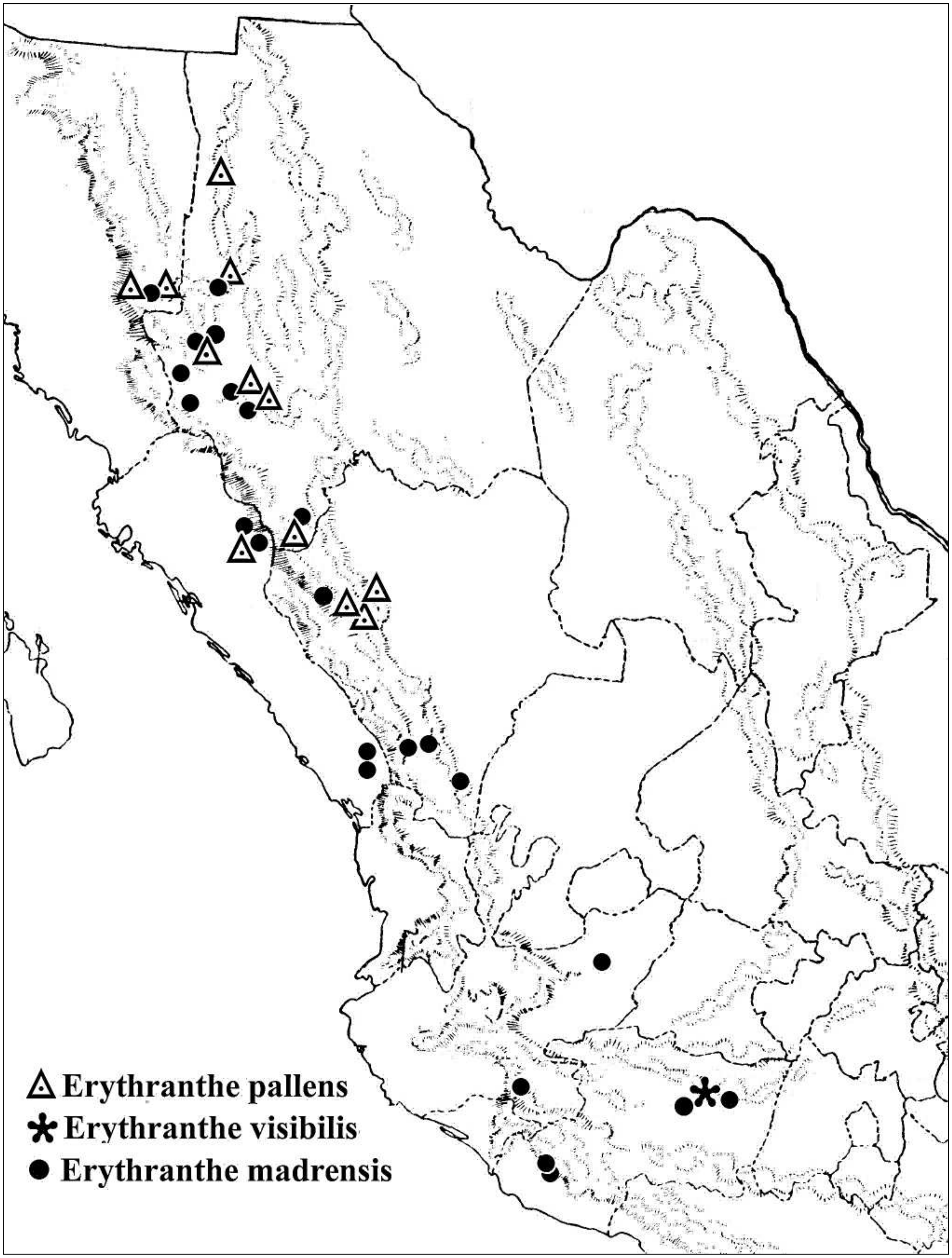
Map 21. Distribution of *Erythranthe nasuta*.



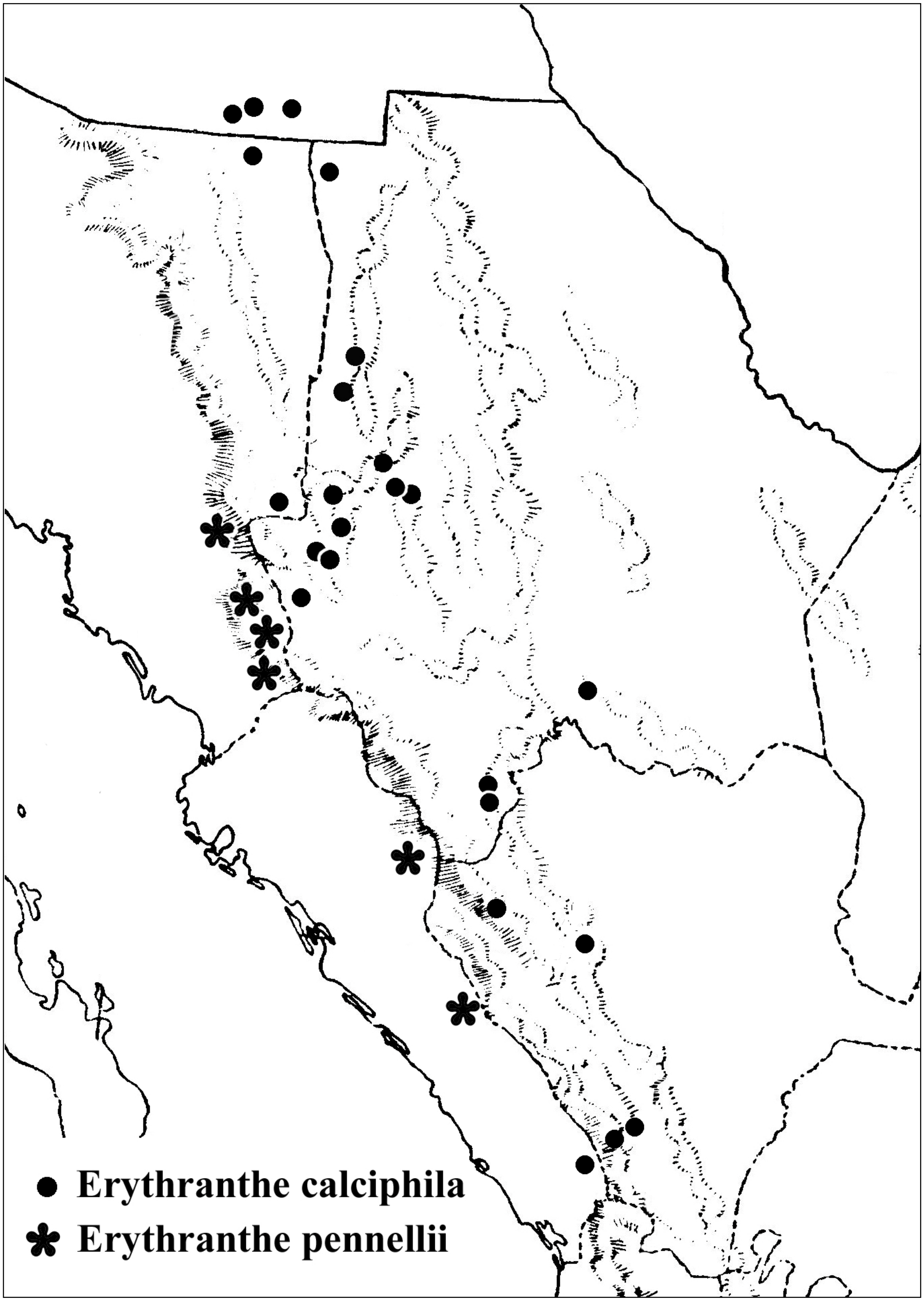
Map 22. Distribution of *Erythranthe dentiloba*.



Map 23. Distribution of *Erythranthe parvula* and *E. chinatiensis.*



Map 24. Distribution of *Erythranthe madrensis*, *E. pallens*, and *E. visibilis.*



Map 25. Distribution of *Erythranthe calciphila* and *E. pennellii*. In the USA, *E. calciphila* occurs in the Chiricahua, Dragoon, and Huachuca Mountains of Cochise Co., Arizona.