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UPDATED CLASSIFICATION AND HYPOTHETICAL PHYLOGENY OF *ERYTHRANTHE* SECT. *SIMIOLA* (PHRYMACEAE)

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ABSTRACT

Revised versions of the informal classification and phylogenetic diagram of the 50 species of *Erythranthe* sect. *Simiola* are presented, with comments on rationale for the arrangements. Three main lineages are recognized: the Madrensis group (x = 8), the Glabrata group (x = 15), and the Guttata group (x = 7). Within the Guttata group, species of the Nudata and Tilingii subgroups apparently do not intergrade with others. *Erythranthe glaucescens*, *E. corallina*, *E. unimaculata*, and perhaps *E. cupriphilus* also appear to be morphologically isolated, as are *E. brevinasuta* and *E. lagunensis*, which occur in Baja California and Baja California Sur apart from others of sect. *Simiola*.

An infrasectional classification of the 50 species of *Erythranthe* sect. *Simiola* is outlined here. The current version is modified from the original presented in a taxonomic revision of sect. *Simiola* (Nesom 2012). An associated phylogenetic diagram (Fig. 1) is modified from an earlier one shown as part of a commentary (Nesom 2013) noting that assumptions regarding patterns of relationships within sect. *Simiola* should be considered in context of the whole group of species.

The arrangement of species in the classification is based primarily on morphological similarities, geography, and chromosome number. The phylogenetic diagram provides a visualization of the classification and incorporates a few elements regarding evolutionary polarity. The phylogenetic hypothesis is largely subjective and highly unresolved but at least provides a starting point, extending the analysis of Beardsley et al. (2004), for more detailed study.

The phylogenetic study by Beardsley et al. (2004) included 11 species of *Erythranthe* sect. *Simiola* (identities not confirmed, see comments in Nesom 2012). The closest relatives of sect. *Simiola* are indicated to be sect. *Exigua* (comprising the single species *E. exigua*) and the sister pair sect. *Mimulosma* (20 species; base chromosome number x = 8) and sect. *Mimulasia* (11 species; base chromosome number x = 8). x = 8 also is the base for other *Erythranthe* sections for which a chromosome number is known (i.e., sects. *Erythranthe*, *Monimanthe*, *Paradantha*, and *Simigemma*), except for x = 9 in sect. *Monantha* (comprising *E. primuloides* and *E. linearifolia*). Thus x = 8 is assumed to be the primitive number for sect. *Simiola*. It also is the base number for all the Phrymaceae, according to analysis by Beardsley et al. The position of the x = 7 lineage of sect. *Simiola* as derivative compared to the Madrensis and Glabrata groups is reflected in the Beardsley et al. analysis.

Broad features of the classification/phylogeny and related observations

1. The Madrensis group (x = 8) and Glabrata group (x = 15) are positioned as coordinate to the rest of sect. *Simiola* because of their distinction in chromosome number and geography. A base chromosome number of x = 15 in the Glabrata group presumably is either a doubled chromosome number minus one pair (x = 2 x 8 – 1) or else a combination of x = 8 and x = 7 genomes, perhaps originating through hybridization between an x = 8 plant and one from the Guttata group (thus x = 8 + 7). Compared to the Guttata group, the Madrensis and Glabrata groups have more eastern and southern distributions (central and southwestern USA through Mexico and into Andean South America).

1. **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. Base chromosome number = 16 (or 8).

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. Base chromosome number = 16 (or 8).

2. **Glabrata group**

Subgroup A - North American (_E. michiganensis_, _E. geyeri_*, _E. inamoena_*, _E. cordata_*^{A}, _E. regni_*^{A}, _E. utahensis_). Perennial and annual, rhizomatous or rooting at proximal nodes, annual and without rhizomes in _E. regni_; calyces not closing; flowers small and autogamous or (_E. michiganensis_) larger, chasmogamous and allogamous; central USA, Mexico. Base chromosome number = 15

Subgroup B - South American (_E. acaulis_, _E. andicola_, _E. cuprea_, _E. depressa_, _E. glabrata_, _E. lacerata_, _E. lutea_, _E. naiandina_, _E. parviflora_, _E. pilosiuscula_, and perhaps others). Perennial and annual, rhizomatous or rooting at proximal nodes; calyces not closing; flowers chasmogamous and allogamous; South America (_E. glabrata_ ranges into North America). Base chromosome number = 15.

3. **Guttata group**

Subgroup A, the Guttata subgroup (_E. corallina_, _E. grandis_, _E. arenicola_^{A}, _E. guttata_, _E. thermalis_*^{A}, _E. glaucescens_^{A}, _E. unimaculata_^{A}, _E. lagunensis_^{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. Base chromosome number = 14 (7), perhaps 16 (8). Reports for _E. corallina_ are $2n = 48$ and 56; these need to be restudied. Placement of _E. corallina_ in the Guttata group rather than theTilingii group is based on unpublished observations by Megan Peterson and John Willis.

Subgroup B, the Microphylla subgroup (_E. microphylla_^{A}, _E. marmorata_^{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 (_E. marmorata_) and broader (_E. microphylla_). Base chromosome number = 14 (7).

Subgroup C, the Nasuta subgroup (_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_). Base chromosome number = 14 (7).

Subgroup D, the Arvensis subgroup (_E. arvensis_*^{A}, _E. brachystylis_*^{A}, _E. charlestonensis_*^{A}, _E. hallii_^{A}). Annual, sometimes rooting at lower nodes (_E. arvensis_) but not rhizomatous; flowers often cleistogamous, all autogamous, produced from distal nodes; western USA. Base chromosome number = 14; _E. hallii_ is reported as $n = 16$, perhaps through dysploidy. The Arvensis subgroup may constitute a single variable and widespread species (_E. arvensis_) with several peripheral isolates.

Subgroup E, the Nudata subgroup (_E. nudata_^{A}, _E. filicifolia_^{A}, _E. percaulis_^{A}). Annual; leaf blades of reduced surface area; flowers produced mostly from distal nodes, chasmogamous, small and autogamous in _E. filicifolia_ and _E. percaulis_; California. Base chromosome number = unknown.

Subgroup F, the Tilingii subgroup

Series 1 (_E. tilingii_, _E. minor_, _E. caespitosa_). Perennial; flowers large, chasmogamous and allogamous; filiform rhizomes profusely produced; mostly high elevation (except for _E. utahensis_); western USA. Base chromosome number = 14 (7) (_E. tilingii_: $2n = 28$, 56).

Series 2 (_E. decora_, _E. scouleri_). Perennial; flowers large; rhizomes numerous; leaf margins closely toothed; styles densely hairy; Washington and Oregon. Base chromosome number = unknown.

Table 1. Infrasectional classification of _Erythranthe_ sect. _Simiola_. Modified from Nesom (2012). Plants are allogamous and perennial unless otherwise noted: * = autogamous; ^{A} = annual duration.

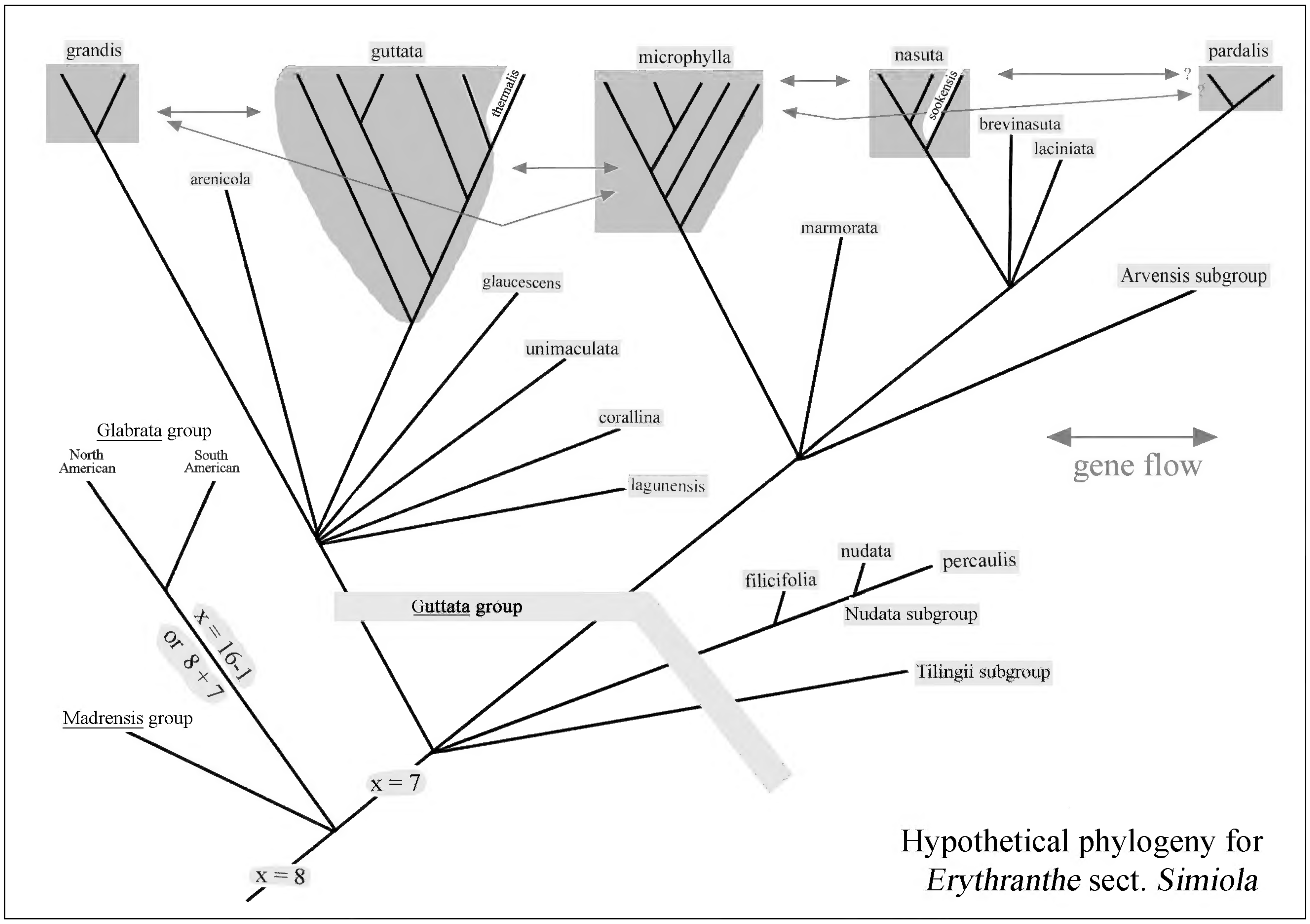

Figure 1. Hypothetical phylogeny of *Erythranthe* sect. *Simiola* (modified from Nesom 2013). The 50 species are divided into 3 main groups: Madrensis (x = 8), Glabrata (x =15), and Guttata (x = 7). Taxa of the Guttata group are highlighted in light yellow. Gene flow is inferred from morphological patterns. Extra branches within *E. grandis*, *E. guttata*, *E. microphylla*, *E. nasuta*, and *E. pardalis* indicate the existence of regional variants.

2. The Madrensis group. The species of Subgroup A are mostly restricted to montane regions of western Mexico and have a tendency to produce 3-lobed calyces. Morphological similarities between *E. madrensis* and *E. pallens* suggest that they may be sister species — they are broadly sympatric but apparently intergrade little if at all. In Subgroup A, *E. calciphila*, *E. pennellii*, and *E. visibilis* presumably are interrelated — they do not overlap in geography or morphology. Prior to 2012, *E. dentiloba*, *E. chinatiensis*, and *E. parvula* (Subgroup B) mostly had generally been identified collectively as *E. dentiloba* because of their laciniate to fimbriate corolla lobes, but each of the three has a distinct combination of biology and morphology and each is allopatric with both of the others. It seems a reasonable hypothesis that the range of an original, widespread, fimbriate-lobed species was fragmented into three geographic segments and at least two of them subsequently diverged evolutionarily. The disjunct population system of *E. dentiloba* in Baja California Sur might be expected to have significant genetic differences from the system in mainland Mexico but the two systems apparently have not diverged in morphology.

3. The Glabrata group. The division between subgroups A and B may prove to be arbitrary, but it seems likely that the species of the Andean cluster are more closely related among themselves. All chromosome counts for *Erythranthe cordata* (except one) have been 2*n* = 60, a strong indication that it belongs in the Glabrata group. The chromosome number of the narrow endemic *E. regni* is unknown, but the species occurs on the range periphery of *E. cordata* and perhaps arose from a population of the latter. See comments on *E. utahensis* under the Tilingii group.

4. The Guttata group (the "*Mimulus guttatus* species complex," e.g., see Oneal et al. 2014, as inferred and extrapolated from their limited sampling of species) comprises about 26 species in the account here — all those above the 'x = 7' node on the phylogenetic diagram (Fig. 1). The present classification divides these 26 species into six subgroups (Guttata, Microphylla, Nasuta, Arvensis, Nudata, Tilingii).

5. *Erythranthe guttata* has often been referred to in molecular genetics literature as ancestor to the others of sect. *Simiola* or as the sister species to one or another species. Such observations are founded on phylogenetic study of a very small set of species or else they are assumptions without basis. The only statement (that I am aware of) explicitly in justification of ancestral status for *E. guttata* apparently is this: "Because of its wide geographical range and high levels of intraspecific genetic diversity it is likely that *Mimulus guttatus* is the progenitor of the other self-fertilizing species with restricted ranges" (Ferris et al. 2014, p. 9) — but this is flawed as a rationale (see Nesom 2014).

When the concept of ancestral "*Mimulus guttatus*" includes 2 or 3 or more different species, its meaning is ambiguous and interpretations of related speciation events are correspondingly ambiguous, misdirected, or meaningless. Similarly, assumptions of sister relationships between species of sect. *Simiola* often appear to be baseless and conclusions dependent on such assumptions also are invalid.

6. Evolutionary change from perennial (rhizomatous) to annual and from annual to perennial apparently has occurred multiple times among species of *Erythranthe* (as well as in the Phrymaceae as a whole). It is suggested here that rhizomes and stolons in *E. guttata*, *E. corallina*, and *E. grandis* and in the *E. tilingii* group probably are derived features, arising from ancestors of annual duration. All other x = 7 sect. *Simiola* species are annual, without rhizomes or stolons, as are most other species of *Erythranthe*. See related earlier comments (Nesom 2012).

Conceivably it is developmentally simple for lower branches to become rhizomelike or stolonlike by production of adventititous roots. Plants of *E. arvensis* and *E. cordata* characteristically are of annual duration (without rhizomes or stolons), but large plants in wet habitats sometimes become proximally decumbent or prostrate and develop adventitious roots at lower nodes and along the internodes. *Erythranthe glaucescens* is characteristically annual, but at least one rhizomatous population is known (Nesom 2012, p. 61; Taylor 2013) — the rhizomes (or runners) either arising independently from within the species or perhaps their genetic basis acquired by hybridization with *E. guttata*. Given the topology of Figure 1, it is likely that the rhizomes of *E. tilingii*, *E. guttata*, and *E. corallina* are not strictly homologous but rather have arisen independently in each instance. The distinctiveness of the numerous, very slender, rhizomelike, mostly above-ground runners originating from lowermost stem nodes characteristic of many populations of *E. guttata* in Colorado even suggests that they may have a different genetic basis than rhizomes of *E. guttata* from other regions.

7. The Arvensis subgroup may constitute a single variable and widespread species (*E. arvensis*) with several peripheral isolates. Annual duration, similar patterns of leaf shape and vestiture, and small autogamous flowers in this subgroup suggest a close relationship to *E. nasuta*. Occasional collections are encountered suggesting that gene flow occurs between *E. arvensis* and *E. nasuta*, although flowers of both species are autogamous.

8. All three species of the Nudata subgroup (*E. nudata*, *E. percaulis*, *E. filicifolia*) are annual in duration, completely glabrous to glabrate, and have slightly succulent leaves with prominently reduced surface area. All are narrow endemics and there is no morphological indication of genetic influence from any other species that might be suspected to have a close relationship. *Erythranthe nudata* and *E. percaulis* probably are sister species, with *E. percaulis* the more specialized.

9. The Tilingii subgroup (Series 1) can be interpreted as a widespread species divided, perhaps vicariantly, into three geographic units — *E. tilingii*, *E. caespitosa*, and *E. minor*. *Erythranthe decora* and *E. scouleri* are distinct from the *E. tilingii* trio and perhaps are sister species. There is no morphological indication of gene flow between species of the Tilingii subgroup and any others of the x = 7 lineage.

Erythranthe corallina was associated with *E. tilingii* in the 2012 account of sect. *Simiola* because of its slender rhizomes, similar to those of *E. tilingii*, but unpublished crossing data from John Willis and Megan Peterson suggest that it instead may be more closely related to the Guttata group. As a member of the Tilingii subgroup, it would be morphologically isolated.

Erythranthe utahensis, like *E. corallina*, is characterized by production of slender rhizomes and recently was associated with *E. tilingii* (Nesom 2012). It was originally described, however, as *Mimulus glabrata* var. *utahensis* Pennell (1935), emphasizing the calyx that remains open at maturity, and an allozyme analysis by Vickery (1990) placed *E. utahensis* as most similar to Andean taxa of the Glabrata group. The original assessment of relationship probably was correct. For the sect. *Simiola* revision, I examined vouchers at UT for chromosome counts of *E. utahensis* reported by Vickery: **2*n* = 28** (California, Mono Co.; Nevada, Mineral Co.; Utah, Juab Co.); **2*n* = 30** (Nevada, Elko Co. and White Pine Co.; Utah, Tooele Co. and Wayne Co.). A base number of x = 15 supports placement of *E. utahensis* with the Glabrata group; the counts of 2*n* = 28 should be reexamined — they might reflect a dysploid reduction or, particularly for the Californian populations, might suggest that those plants are better identified as a different taxon.

Molecular and genetic study

Oneal et al. (2014, p. 2857) are pessimistic regarding the potential for phylogenetic reconstruction in sect. *Simiola*.

> "Nesom (2012) argued that his hypothesized taxonomy of the species complex could be tested with a molecular phylogeny, but this is unlikely for two reasons. First and foremost, gene flow is widespread across the complex, and no phylogenetic methods currently exist which satisfactorily account for the confounding factor of hybridization (Eckert & Carstens 2008; Meng & Kubatko 2008; Liu *et al.* 2009), although one possible way forward is through new methods that evaluate population splits and mixtures in a tree-based framework (Pickrell & Pritchard 2012). Second, we have demonstrated convincingly that different regions of the genome, particularly the inversion, experience different patterns of introgression and shared ancestry. Together, these features suggest that the difficulty inherent in resolving relationships among the diverse members of the *M. guttatus* species complex is not merely a technical problem, but instead reflects the true nature of the speciation process, whereby clear genome-wide divergence does not occur until well after species are first identifiable."

Implication that knowledge of evolutionary processes ("the true nature of the speciation process") characterizing "the diverse members of the *M. guttatus* species complex" is at hand is a gross over-generalization, unjustified by any published research that I am aware of. The Oneal et al. sample apparently includes only about 10 species of the currently known 26 in the Guttata group of sect. *Simiola*, and their generalizations about the speciation process appear to be further restricted in purview, as they are based mostly on studies of interactions between *E. guttata* and *E. microphylla*, and in some cases *E. nasuta*. Judging from the geography and patterns of morphological variation for many (or most) of the remaining species, the guttata-microphylla model probably will not apply to them.

The Oneal et al. study (using a Bayesian clustering algorithm) includes *Erythranthe arvensis* (their "*Mimulus micranthus*" is a synonym), *E. caespitosa* (samples of "*Mimulus tilingii*" from Washington, as inferred), *E. guttata*, *E. laciniata*, *E. microphylla* (samples of annual "*Mimulus guttata*," as inferred), *E. minor* (samples of "*Mimulus tilingii*" from Colorado, as inferred), *E. nasuta*, *E. nudata*, *E. pardalis* (their "*Mimulus cupriphilus*" is a synonym), and *E. tilingii* in the strict sense (collections from California and Oregon, as inferred). I am cited in the Acknowledgements as having "helped to confirm identification of many collection samples" but their identifications of "*M. guttatus*," "*M. micranthus*," "*M. cupriphilus*," and "*M. tilingii*" are not consistent with the way I would have identified them.

Well supported and plausible molecular phylogenies across many families have been reconstructed for species groups where gene flow occurs, and the possibility remains that reasonable hypotheses for the evolutionary history of the Guttata group and the larger sect. *Simiola* also can be formulated. Given the diversity of the group, there has not yet been any serious attempt to understand sect. *Simiola* phylogeny through either a molecular or genetic approach. Knowledge of species yet unsampled but obviously closely related to *E. guttata* and *E. microphylla* (Fig. 1) should be expected to provide insight into the phylogenetic positions of the latter two.

LITERATURE CITED

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

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

Ferris, K.G., J.P. Sexton, and J.H. Willis. 2014. Speciation on a local geographic scale: The evolution of a rare rock outcrop specialist in *Mimulus*. Philos. Trans. Roy. Soc. B. 369 2014, 20140001.

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

Nesom, G.L. 2013. Review: Brandvain, Kenney, Flagel, Coop, and Sweigart. "Speciation and introgression between *Mimulus nasutus* and *Mimulus guttatus*." Phytoneuron 2013-97: 1–9.

Nesom, G.L. 2014. Commentary: Speciation on a local geographic scale in *Mimulus*. Phytoneuron 2014-72: 1–4.

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

Pennell, F.W. 1935. *Mimulus* Linnaeus. The Scrophulariaceae of eastern temperate North America. Proc. Acad. Nat. Sci. Philadelphia 1: 112–136.

Sexton, J.P., K.G. Ferris, and S.E. Schoenig. 2013. The fern-leaved monkeyflower (Phrymaceae), a new species from the northern Sierra Nevada of California. Madroño 60: 236–242.

Taylor, D.W. 2013. Shield-bracted monkeyflower (*Erythranthe glaucescens*) is probably 2 species. California botany blog. <http://californiabotany.blogspot.com/2013/08/shield-bracted-monkeyflower-erythranthe.html>

Vickery, R.K., Jr. 1990. Close correspondence of allozyme groups to geographic races in the *Mimulus glabratus* complex (Scrophulariaceae). Syst. Bot. 15: 481–496.