SPECIES AND HYPOTHESIZED RELATIONSHIPS WITHIN ERYTHRANTHE SECT. SIMIOLUS

An informal infrasectional classification of sect. *Simiola* is outlined here. The current version is published in Nesom (2019), modified from the original presented in the revision of sect. *Simiola* (Nesom 2012d, 2014b). The associated phylogram also is from Nesom 2019, modified from the original one shown as part of a commentary (Nesom 2013h) which noted that assumptions regarding patterns of relationships within sect. *Simiola* should have an objective basis and be considered in context of the larger group of species.

The arrangement of species is primarily based on morphological similarities (the main characters emphasized in defining the groups are noted), geography, chromosome number, and presence/absence of the DIV1 inversion.

![Hypothetical phylogeny of *Erythranthe* sect. *Simiolus*. The 50 species are divided into 3 main groups: *Madrensis* (base chromosome number, *x* = 8), *Glabrata* (*x* = 15), and *Guttata* (*x* = 7). Taxa of the Guttata group are highlighted in yellow. Gene flow is inferred from morphological patterns. Extra branches within *E. decora*, *E. grandis*, *E. guttata*, *E. microphylla*, *E. nasuta*, and *E. pardalis* indicate the existence of regional morphological and/or cytological variants.](image)
Informal infrasectional classification of sect. *Simiolus*

Plants are allogamous and perennial unless otherwise noted: *a* = autogamous; *A* = annual duration.

1. Madrensis group

**Subgroup A** (*E. madrensis, E. pallens, E. calciphila*a*A, E. pennellii, *E. visibilis*a*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*a*, *E. dentiloba, E. diminuens*a, 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. geyeria*, *E. inamoena*, *E. cordata*a*A, E. regni*a*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. Perennial and annual; leaves oblong or elliptic to obovate, margins remotely or closely 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.

**Series 1** (*E. corallina, E. guttata, E. grandis, E. thermalis*a*A*). It is hypothesized that the annual *E. thermalis* is derived from perennial *E. guttata* (see commentary and references in Nesom 2012, p. 44–45) — both annuals are thus predicted to have the DIV1 inversion of their progenitor.

Molecular studies continue to assert/assume that “*Mimulus guttatus*” (without specifying whether the annual or perennial form) is the progenitor of the “species complex” (without specifying what is meant by that phrase) (e.g., Ferris et al. 2015; Ferris & Willis 2018). Figure 1 above indicates why this view is problematic (and see Nesom 2013–p. 4–5 and 2014b–p. 4 for discussion).

**Series 2** (*E. decora, E. scouleri*). Perennial; flowers large; rhizomes numerous; leaf margins closely and regularly toothed; styles densely hairy; Washington and Oregon. Base chromosome number unknown. Coughlan et al. (2018, Fig. 1) found that diploids and tetraploids occur within *E. decora* (diploids southern, tetraploids mostly northern) and that two geographic clades exist among the diploids. Strong post-zygotic reproductive barriers exist between the northern and southern diploids and between each of these and the tetraploids. The three races are indistinguishable in morphology.

*Erythranthe scouleri* is hypothesized to share the inverted DIV1 sequence with *E. decora*, in view of their morphological and geographical coherence, suggesting immediate common ancestry. Field studies by Lomer (2019) have contributed to an understanding of the morphology, geography, and ecology of *E. scouleri*.

**Subgroup B**, the Tilingii subgroup (*E. tilingii, E. caespitosa*). Perennial; flowers large, chasmogamous and allogamous; filiform rhizomes profusely produced; mostly high elevation; western USA (see range extension in Nesom 2019a). Base chromosome number = 14 (7) (*E. tilingii: 2n = 28, 56*).

In a STRUCTURE analysis of noninversion microsatellite markers (Oneal et al. 2014, Fig. 1), *E. tilingii* clusters (K2) with samples of *E. guttata* from Colorado and Washington and some in Oregon. For the markers in the inverted sequence (Fig. 2), *E. tilingii* unambiguously appears to cluster (K2 and K3) with the other perennials, although Oneal et al. noted (p. 2851) that “it is difficult to tell whether *E.* tilingii clusters more with the annuals or the perennials for the inverted markers, however, as it appears to harbour variation segregating within both.”
The placement here of *E. tilingii* at the base of the clade with other perennials reflects the interpretation of rhizomes as specialized and (parsimoniously) their origin in the clade’s ancestor. Alternatively, as in *E. glaucescens*, it is not implausible that rhizomes evolved independently in *E. tilingii/caesipt奥斯*

Earlier (Nesom 2014b), I placed “E. minor” in the *E. tilingii* group, but further study shows that plants identified as that species are best considered within the widespread and variable, perennial *E. guttata*, and *E. minor* is now treated as a synonym of it (Nesom 2019b).

Subgroup C, the Unimaculata subgroup (*E. unimaculata*<sup>A</sup>, *E. lagunensis*<sup>A</sup>, *E. brevinasuta*<sup>A</sup>). Annual; sw USA and nw Mexico (*E. unimaculata*) and Baja California Sur (*E. lagunensis*, *E. brevinasuta*). *E. unimaculata* and *E. lagunensis* have large corollas and are morphologically similar to *E. guttata* in many features but are annuals, without rhizomes. *E. brevinasuta* has small flowers (cleistogamous, autogamous) but produces denticulate calyx margins, an unusual character shared with *E. lagunensis*, and it is hypothesized that the latter two are sister species. The corolla palate of *E. unimaculata* dries a distinctive blue-green — the UV pattern almost certainly is “runway” (sensu Peterson et al. 2015), implying that it has the non-inverted DIV1 sequence.

Subgroup D, the Microphylla subgroup (*E. microphylla*<sup>A</sup>, *E. marmorata*<sup>A</sup>). 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 more broadly distributed (*E. microphylla*). Base chromosome number = 14 (7).

Subgroup E, the Nasuta subgroup (*E. nasuta*<sup>A</sup>, *E. laciniata*<sup>A</sup>, *E. pardalis*<sup>A</sup>). 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 more broadly distributed (*E. nasuta*). Base chromosome number = 14 (7).

Subgroup F, the Arvensis subgroup (*E. arvensis*<sup>A</sup>, *E. brachystylis*<sup>A</sup>, *E. charlestonensis*<sup>A</sup>, *E. hallii*<sup>A</sup>). 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. The Arvensis subgroup might reasonably considered a single variable and widespread species (*E. arvensis*) with several peripheral isolates.

Subgroup G, the Nudata subgroup (*E. nudata*<sup>A</sup>, *E. percaulis*<sup>A</sup>, *E. filicifolia*<sup>A</sup>, *E. glaucescens*<sup>A</sup>). Annual; leaf blades of reduced surface area; flowers produced mostly from distal nodes, small and autogamous in *E. filicifolia* and *E. percaulis*; narrow endemics of north-central California, hypothesized here to represent a single clade, emphasizing their geographic coherence. Base chromosome number unknown. *E. nudata* and *E. percaulis* probably are sister species; *E. percaulis* has smaller cauline leaves and distinctly smaller, autogamous flowers. *E. filicifolia* and *E. glaucescens* each have distinctive leaf morphology.

The newly described *Erythranthe filicifolia* was hypothesized (Nesom 2013a, 2014a, 2014b) to be most closely related to *E. nudata* and *E. percaulis*. Ferris and Willis (2018) found a strong hybrid sterility barrier between *E. filicifolia* and both *E. guttata* and *E. laciniata* and that *E. filicifolia* is more genetically distant from *E. laciniata* than from *E. guttata* and *E. nasuta* — concluding that *E. filicifolia* may have arisen from an ancestor other than the “wide-ranging *Mimusus* guttatus,” offering no contradiction to the hypothesis of relationship summarized here. Oneal et al. (2016) characterized the hybrid seed inviability that underlies reproductive isolation between *E. nudata* and *E. microphylla*.

Plants in most populations of *Erythranthe glaucescens* are annual but those of at least two populations in Butte County (ca. 7 miles apart) are rhizomatous (Nesom 2012, p. 61; Taylor 2013). If the species were interpreted as primitively rhizomatous, it would be placed here as a 3rd subgroup in the ‘guttata’ sensu stricto clade (following the parsimonious view that rhizomes have arisen only once in the Guttata group), but the tentative interpretation here is that the rhizomatous populations of *E. glaucescens* have arisen (probably in a single event) from a conspecific, non-rhizomatous one.

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