

## UPDATE 2019: CLASSIFICATION AND HYPOTHETICAL PHYLOGENY OF *ERYTHRANTHE* SECT. *SIMIOLUS* (PHRYMACEAE)

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### ABSTRACT

An informal classification and phylogenetic diagram of the species of *Erythranthe* sect. *Simiolus* is updated, with revisions in the Guttata group, especially emphasizing new information on the presence/absence of the inverted DIV1 sequence on chromosome 8. The perennial, rhizomatous habit is hypothesized to have arisen only once in the Guttata group, with one exception. The rhizomatous clade includes the sister pair *E. tilingii* and *E. caespitosus* and a sister clade characterized by the inverted DIV1 sequence, including *E. guttata*, *E. grandis*, *E. corallina*, and *E. decora* (and its hypothesized sister, *E. scouleri*). *Erythranthe glaucescens*, which is predominantly non-rhizomatous but includes rhizomatous populations, is hypothesized to be primitively non-rhizomatous and most closely related to the annuals *E. nudata*, *E. percaulis*, and *E. filicifolia*. The remaining species of the section are annuals and are known or hypothesized to have the non-inverted DIV1 sequence. Plants previously identified as *Erythranthe arenicola* (Pennell) Nesom are considered here to be depauperate individuals of *E. grandis*.

An infrasectional classification of sect. *Simiolus* is outlined here (modified from earlier ones: Nesom 2012, 2014b), based primarily on presence/absence of the inverted DIV1 sequence, chromosome number, morphological similarity, and geography. An accompanying phylogenetic diagram also is updated (previous ones in Nesom 2013, 2014b, 2014c). The phylogenetic diagram provides a visualization of the classification and incorporates characters hypothesized to show evolutionary polarity.

Discovery by Lowry and Willis (2010) of an inversion sequence on chromosome 8 (the DIV1 inversion) in species of the *Erythranthe guttata* group has provided a significant character toward understanding phylogenetic relationships among the species of the Guttata group of *Erythranthe* sect. *Simiolus*. Further studies have revealed the sequence orientation in additional species. Major observations are these:

- a. The DIV1 inversion sequence in *E. guttata* and *E. grandis* is in reverse order from that of *E. microphylla* and *E. nasuta* (Lowry & Willis 2010).
- b. The *guttata/grandis* DIV1 sequence also occurs in *E. decora* (Coughlan & Willis 2018) (and can be inferred to occur in its putative sister *E. scouleri*) and in *E. corallina* (Peterson et al. 2015), which shares the UV bulls-eye floral pattern with other perennials of the *E. guttata* group as well as their rhizomatous habit, flowering phenology, and constantly moist or wet habitat.
- c. The *microphylla/nasuta* DIV1 sequence occurs in *E. tilingii* (Oneal et al. 2016; Garner et al. 2016) and in *E. nudata*, *E. laciniata*, and *E. glaucescens* (Coughlan & Willis 2018). It is possible to infer, at least as a reasonable hypothesis, from O'Neal et al. (2014 — from patterns of clustering patterns of microsatellite markers in the DIV1 inversion region) that it also occurs in *E. arvensis* and *E. pardalis*. The authors noted in caution (p. 2855) that “we currently have no direct evidence of the orientation of the inversion in the larger sample of the populations that we sampled here.”

Rhizome production and associated perennial duration in sect. *Simiolus* are hypothesized to be specialized (Nesom 2012–p. 9, 2014b–p. 4, 2014c–pp. 3–4; also comments below regarding *E.*

*glaucescens*) — non-rhizomatous annuals are the prevalent life form in species regarded as most closely related to sect. *Simiolus*, and the developmental origin of rhizomes is simple. Earlier (Nesom 2014b), I suggested that rhizomes perhaps arose independently in *E. guttata*, *E. corallina*, and *E. tilingii*, but data reviewed here support the hypothesis of a single origin of the rhizomatous habit.

Coughlan & Willis (2018, p. 1344) have tentatively agreed with this assessment of polarity. “In perennials, diversity is much lower than in annuals inside of the inversion, although measurements of diversity throughout the rest of the genome [are] relatively similar between these ecotypes (Twyford & Friedman, 2015), in line with the hypothesis that the perennial orientation of the inversion is derived and experienced a relatively old selective sweep.”

In this phylogenetic hypothesis (Fig. 1), the rhizomatous, perennial habit has arisen twice in the Guttata group: (a) In the *Erythranthe guttata* sensu stricto clade, where all species are rhizomatous — here the inverted DIV1 sequence characterizes the species group sister to *E. tilingii/caespitosa*. Annual *E. thermalis* is hypothesized to be secondarily derived from a perennial. (b) In *E. glaucescens*, independently, which is primarily annual but has rhizomatous populations at the western periphery of its range (see further comments below).

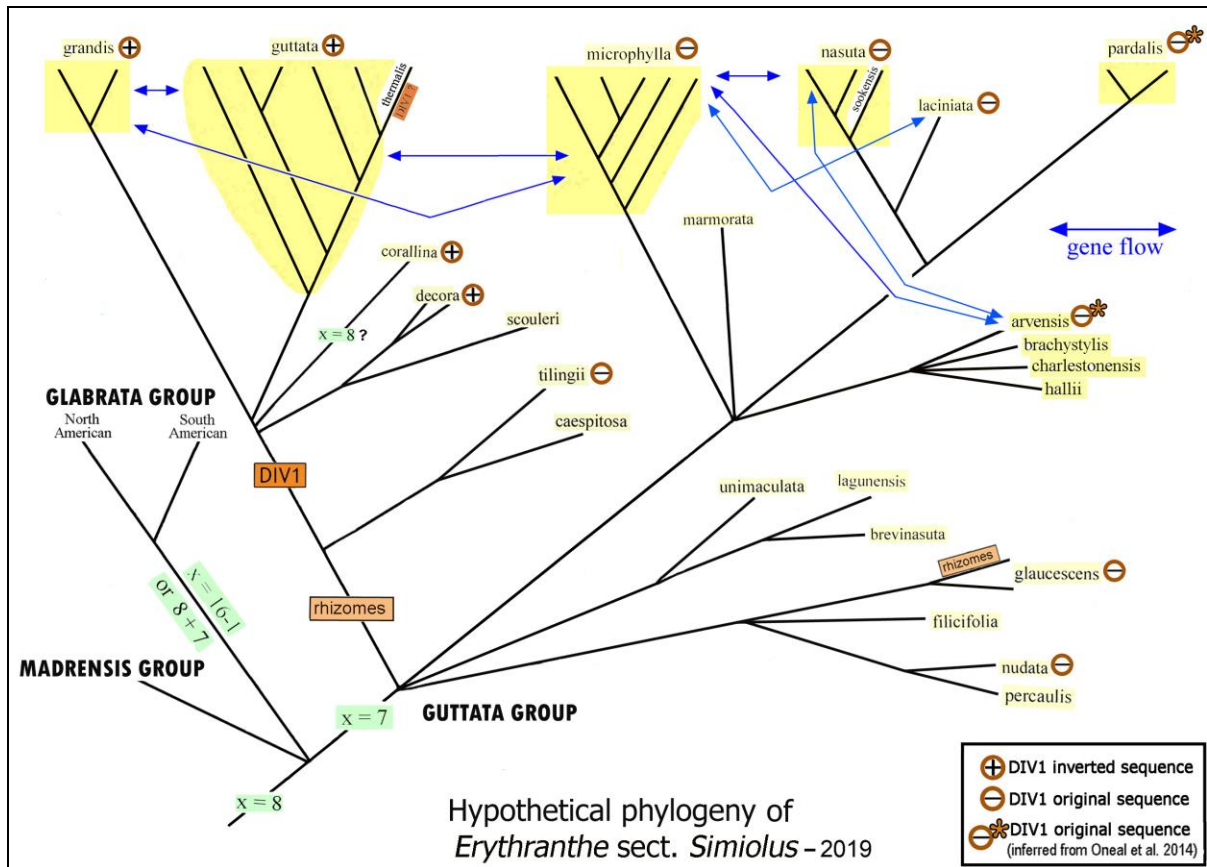


Figure 1. Hypothetical phylogeny of *Erythranthe* sect. *Simiolus*. The 50 species are divided into 3 main groups: **Madrensis** (base chromosome number,  $x = 8$ ), **Glabrata** ( $x = 15$ ), and **Guttata** ( $x = 7$ ). Taxa of the Guttata group are highlighted in yellow. Gene flow is inferred from 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.

### Informal infrasectional classification of sect. *Simiolus*

Plants are allogamous and perennial unless otherwise noted: \* = autogamous; <sup>A</sup> = annual duration.

#### 1. Madrensis group

**Subgroup A** (*E. madrensis*, *E. pallens*, *E. calciphila*<sup>\*A</sup>, *E. pennellii*, *E. visibilis*<sup>\*A</sup>). Perennial or annual; calyces 5-lobed or mostly 3-lobed; flowers small (allogamous or autogamous); western Mexico into southwestern USA. Base chromosome number  $x = 16$  (or 8).

**Subgroup B** (*E. chinatiensis*<sup>\*</sup>, *E. dentiloba*, *E. diminuens*<sup>\*</sup>, *E. parvula*<sup>\*</sup>). Perennial, mat-forming; calyces 5-lobed or with tendency toward 3-lobed; flowers relatively small, allogamous or autogamous; corolla lobes lacinate to fimbriate; southwestern USA and northwestern Mexico. Base chromosome number  $x = 16$  (or 8).

#### 2. Glabrata group

**Subgroup A** - North American (*E. michiganensis*, *E. geyeri*<sup>\*</sup>, *E. inamoena*<sup>\*</sup>, *E. cordata*<sup>\*A</sup>, *E. regni*<sup>\*A</sup>, *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  $x = 15$

**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  $x = 15$ .

#### 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) for *E. guttata*, *E. grandis*, *E. decora*, and *E. tilingii*.

Reports for *E. corallina* are  $2n = 48$  and 56, perhaps based on  $x = 8$ ; these need to be restudied/confirmed, particularly the count of  $2n = 48$ .

**Series 1** (*E. grandis*, *E. guttata*, *E. thermalis*<sup>\*A</sup>, *E. corallina*). It is hypothesized that the annual *E. thermalis* is derived from perennial *E. guttata* (see commentary and references in Nesom 2012, p. 44–45) and is thus predicted to have the DIV1 inversion of its progenitor. Plants previously identified as *Erythranthe arenicola* (Pennell) Nesom are considered here to be within the range of variation of *E. grandis* (see comments below).

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  $x = 7$ . 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  $x = 14$  (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/caespitosus*.

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  $x = 14$  (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  $x = 14$  (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  $x = 14$  (7); *E. hallii* is reported as  $n = 16$ . The Arvensis subgroup might reasonably be 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 *M[imulus] 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.

***Erythranthe arenicola* is a synonym of *E. grandis***

I recognized at specific rank (Nesom 2012) depauperate, small-flowered plants from sandy, seaside habitats in Monterey Co., California, originally described by Pennell (1947) as *Mimulus guttatus* subsp. *arenicola*. I interpreted their duration as annual and hypothesized that they were evolutionarily derived from stoloniferous *Erythranthe grandis*. After studying a set of collections at PH from the same area, it now seems clear that they also are stoloniferous and range in sizes typical of *E. grandis* down to depauperate individuals (stems 6–15 cm tall, calyces 10–12 mm long) similar to those originally named by Pennell. All are encompassed within the range of variability of *E. grandis*.

Similarly, another "beach form" described in the same publication by Pennell as *Mimulus guttatus* subsp. *litoralis* is a variant of *Erythranthe grandis*. These include plants from seaside habitats in northern California and Oregon, with prostrate or decumbent-ascending stems that often root at the nodes. They have been collected from cliffs and bluffs, wet banks, and dunes.

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