

**RECOGNITION AND SYNOPSIS OF MIMULUS  
SECT. TROPANTHUS AND SECT. LEUCOCARPUS (PHRYMACEAE)**

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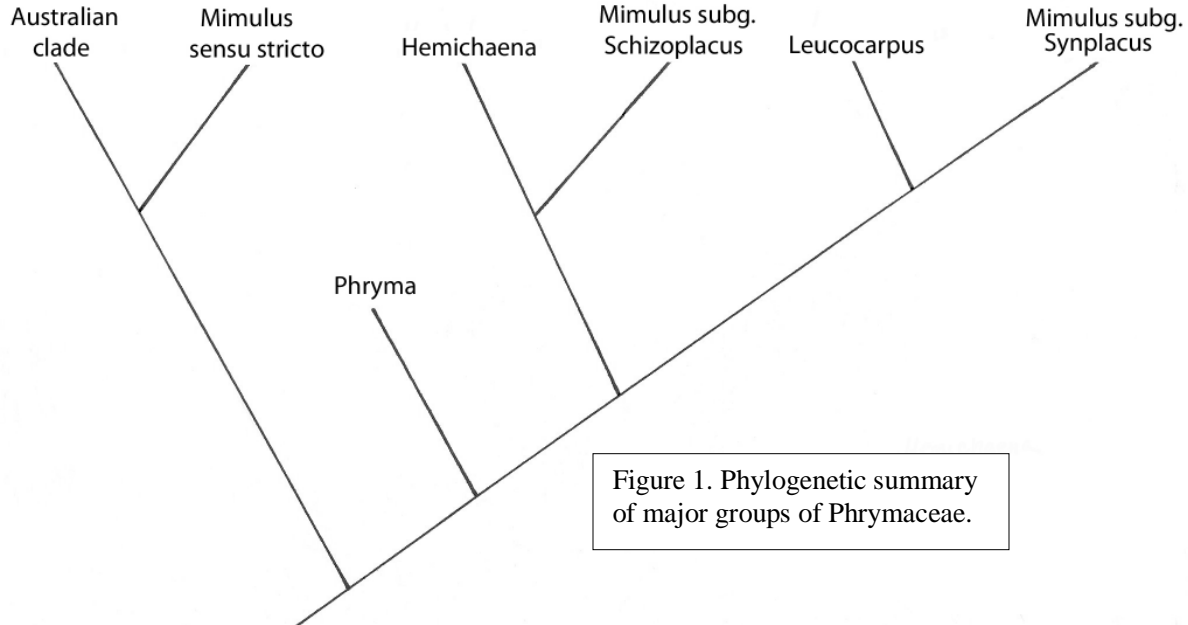
**ABSTRACT**

The American genera *Hemichaena* (5 species) and *Leucocarpus* (1 species) are formally brought into *Mimulus* as *Mimulus* sect. *Tropanthus* A.L. Grant and ***Mimulus* sect. *Leucocarpus*** (D. Don) Nesom, comb. et stat. nov. Sect. *Leucocarpus* includes only *M. perfoliatus* Kunth. Thieret (1972) united the five species of *Berendtiella* and *Hemichaena* into the single genus *Hemichaena* and all five species are formally transferred here to *Mimulus*. The original *Mimulus* sect. *Tropanthus* of Grant (1924) included only the single species *M. treleasei* (= *Hemichaena levigata*) and the section as revived here and expanded includes these: ***Mimulus coulteri*** (A. Gray) Nesom, comb. nov., ***Mimulus fruticosus*** (Benth.) Nesom, comb. nov., ***Mimulus levigatus*** (B. Rob. & Greenm.) Nesom, comb. nov., ***Mimulus spinulosus*** (S. Wats.) Nesom, comb. nov., and ***Mimulus rugosus*** (Benth.) Nesom, comb. nov. A lectotype is designated for *Hemichaena fruticosa* Benth. Sect. *Tropanthus* and sect. *Leucocarpus* are shown by molecular data to have originated as sister to one or the other of the two main clades of American *Mimulus*, and for consistency, recognition of *Hemichaena* and/or *Leucocarpus* would require that western American *Mimulus* be divided into at least two genera. In contrast to the single-flowered inflorescences characteristic of most *Mimulus* species, *Hemichaena* and *Leucocarpus* both produce pedunculate multi-flowered bracteolate cymes, which are interpreted as a primitive feature. The shrubby habit of *Hemichaena* is paralleled in species of *Mimulus* sect. *Diplacus* and the baccate fruits diagnostic of *Leucocarpus* are a specialization approached in function by initially indehiscent capsules in some groups of western USA *Mimulus*.

**KEY WORDS:** *Hemichaena*, *Berendtiella*, *Mimulus* sect. *Tropanthus*, *Leucocarpus*, *Mimulus* sect. *Leucocarpus*, Phrymaceae

Molecular-phylogenetic studies of *Mimulus* (Beardsley and Olmstead 2002; Beardsley et al. 2004; Beardsley & Barker 2005) have provided insights into its phylogenetic structure and putative relatives. *Mimulus* sensu stricto, including *M. ringens* L., *M. alatus* Ait., and two Southern Hemisphere species, is sister to a clade of primarily Australian taxa, including several generally recognized genera (Fig. 1). Sister to the Australian clade is a branch of two mostly American clades — *Mimulus* subg. *Synplacus* A.L. Grant and *Mimulus* subg. *Schizoplacus* A.L. Grant, together including about 140 species — with the monotypic *Phryma* L. at their base. *Leucocarpus* D. Don (1 species) is sister to subg. *Synplacus*, while *Hemichaena* Benth. (5 species) is sister to subg. *Schizoplacus*.

In order to retain the name *Mimulus* for the large number of well-known American species, an initial step is taken here to bring *Hemichaena* and *Leucocarpus* into *Mimulus*. Other actions will be necessary, since the species identified as *Mimulus* sensu stricto are sister to the Australian clade. In case that it proves desirable to maintain the Australian segregate genera, and to maintain *Phryma* as a distinct genus, the suggestion by Beardsley and Barker (2005) to conserve the name *Mimulus* with a species from within the American lineage is being followed (Nesom and N. Fraga, in prep.). The much diminished *Mimulus* sensu stricto will then require a different name. Nesom and Fraga (in manuscript) also have substantially revised the infrageneric classification of American *Mimulus* in conjunction with preparation of the taxonomic treatment of the genus for the Flora of North America North of Mexico.



The current concept of *Hemichaena* was formulated by Thieret (1955, 1972), who consolidated the species of *Berendtiella* Wettst. & Harms and *Hemichaena* — with the observation that they are "much alike in habit, habitat, vestiture, foliage, inflorescence, flowers, fruits, and seeds, all of which convince me that the taxa are congeneric" (1972, p. 89). His observations of their similarity followed those of Burt (1965). Argue (1982) found that species of *Hemichaena* and *Berendtiella* could not be distinguished by pollen morphology, and further support for the close relationship of *Berendtiella* and *Hemichaena* has come from molecular-phylogenetic studies (Beardsley & Olmstead 2002; Beardsley et al. 2004; Oxelman et al. 2005; Xia et al. 2009).

Pennell (1935) placed *Berendtiella* along with *Mimulus* L. and the monotypic *Leucocarpus* D. Don in the Scrophulariaceae-Gratiolaeae, "because the flowers and especially the plate-like stigmas show a clear kinship to *Mimulus*" (p. 47). In an earlier treatment, however, Pennell (1920) had constituted the tribe Scrophulariaceae-Mimuleae with *Mimulus* and *Leucocarpus* (the treatment included only Colombian taxa). Burt (1965) revived the Mimuleae, noting similarities among *Mimulus*, *Hemichaena*, and *Leucocarpus* in their bilamellate stigmas, campanulate to tubular 5-ribbed calyces, and loculicidal capsules.

Thieret (1967, p. 93) noted that "*Leucocarpus*, even though it possesses a baccate fruit, is obviously closely related to *Hemichaena* as is evidenced not only by its distinctive stigmas and calyx but also by its reticulate seeds with intra-reticular lines of a type apparently found nowhere else in the Scrophulariaceae except in these two genera." Slightly later, Thieret (1972) again recognized that floral characteristics of *Hemichaena* and *Leucocarpus* suggest an alliance with *Mimulus*, but he hypothesized on the basis of fruit and seed morphology that *Leucocarpus* is more distant and placed it as a relative of the Malaysian *Cyrtandromoea* Zoll. Interpretations of evidence from floral morphology are confirmed by the molecular data, which place *Leucocarpus* as sister to *Mimulus* subg. *Synplacus* — indicating that baccate fruits are a singular specialization evolved within this group of species that otherwise have capsular fruits.

Inflorescences of both *Hemichaena* and *Leucocarpus* tend to be bracteolate cymes, (consistently reduced in two species of *Hemichaena* to single flowers), while flowers of all species of American *Mimulus* are produced singly. The multiple-flowered inflorescences are distinctive but are reasonably interpreted as a primitive expression. Taxa closely related to *Mimulus-Hemichaena-*

*Leucocarpus* (Tank et al. 2006; Xia et al. 2009; Albach et al. 2009; Schäferhoff et al. 2010) — *Rehmannia*, *Triaenophora*, *Paulownia*, *Lancea*, and *Mazus* — usually produce flowers in racemes or a thyrse of cymes, sometimes reduced to axillary and solitary flowers in *Rehmannia*.

Apart from the inflorescence, *Hemichaena* is not distinct from *Mimulus* in any consistent features. Thieret (1972) emphasized the apparent distinction in *Hemichaena* of superposed inflorescences, which result from a bud and supernumerary bud in each leaf axil. Supernumerary buds, however, also occur in *M. gemmiparus* W.A. Weber (the proximal bud becomes a brood bulbil) and *M. guttatus* Fischer ex DC. (the proximal bud is dormant) (Beardsley 1997; Moody et al. 1999). The shrubby habit and revolute leaf margins of *Hemichaena* apparently evolved convergently or in parallel with species of *Mimulus* sect. *Diplacus*. Beardsley and Olmstead (2002) stated that "*Hemichaena* and *Berendtiella* have united placentae thus making divided placentae a synapomorphy for *Schizoplacus*" but Grant (1924) observed that *Hemichaena levigata* (as *Mimulus treleasei*, see next paragraph) is characterized by a separated placenta similar to species of sect. *Diplacus* (and all species of subg. *Schizoplacus*) — my observations support this for the other species of *Hemichaena* as well.

The clearly specialized, baccate fruits of *Leucocarpus* have a parallel, near-analog in those of the ten species of *Mimulus* sect. *Oenoe* (sensu Thompson 2005), where the capsules are initially indehiscent, opening along the inner suture after senescence of the plants and after being wet by fall or winter rains.

Species of *Mimulus* and Phrymaceae relatives are generally characterized by five major types of pollen morphology (Argue 1980, 1983, 1984, 1986; Chadwell et al. 1992). Pollen of both *Hemichaena* and *Leucocarpus* is tricolporate (type II), as is that of *Mimulus* subg. *Synplacus* (excluding sect. *Simiolus*, which has highly specialized and derivative type I). Pollen of *Mimulus* sensu stricto and some of the Australian clade also is tricolporate — *Glossostigma* has (3)4–6(–7)-colpate pollen; Barker 1982; Argue 1986) and *Peplidium* and *Microcarpaea* have tricolpate pollen (Argue 1986). Pollen of *Mimulus* subg. *Schizoplacus* (including sect. *Diplacus*) is tricolpate or stephanocolpate (types III, IV, and V). The pollen of *Phryma* is tricolpate, tectate-perforate to microreticulate, with simple columellae (type III). Tricolporate pollen is characteristic of close relatives of Phrymaceae (e.g., *Dodartia* L., *Lancea* J.D. Hook. & Thomson, *Mazus* Lour.; Argue 1984) and it appears to be the primitive type in Phrymaceae.

The morphological similarity of *Hemichaena* and *Leucocarpus* to *Mimulus* has been reflected in earlier species-level taxonomy. *Leucocarpus perfoliatus* (Kunth) Benth. was originally described by Kunth as *Mimulus perfoliatus*. *Hemichaena rugosa* (Benth.) Thieret was originally described by Bentham (1846) as *Diplacus rugosus* Benth. *Mimulus* sect. *Tropanthus*, as originally described by Grant (1924), included only the single species *M. treleasei* A.L. Grant, which is a synonym of *Hemichaena levigata* (returned to *Mimulus* as *M. levigatus*, as treated here). Grant (p. 325) noted that *M. treleasei* is "a peculiar species, combining the calyx characters of *Eumimulus* with the shrubbiness, the pubescent style, and the separated placentae of *Diplacus*." McMinn (1951, p. 114) observed a resemblance between *M. flemingii* Munz (= *Diplacus parviflorus* Greene) and *Berendtiella levigata* "in the configuration of the leaves and flowers" and admitted the possibility that *Diplacus*, which he treated at generic rank, and *Berendtiella* are derived from a common ancestor.

The geographic distribution of *Hemichaena* and *Leucocarpus* is primarily subtropical, but radiations in traditionally recognized *Mimulus* have produced species that occur within the geographic range of *Hemichaena* — *M. pachystylus* A.L. Grant (endemic to Chiapas; sect. *Paradanthus* fide Grant 1924) and *M. rupestris* Greene (endemic to Morelos; sect. *Erythranthe*).

Other species (e.g., *M. glabratus* Kunth and *M. guttatus* Fischer ex DC.) have ranges that extend from the western USA through Mexico and Central America to South America.

In summary, *Hemichaena* and *Leucocarpus* are both justifiably accommodated as groups within the bounds of *Mimulus* — each at the base of one or the other of the two major clades of the primarily western American species, subg. *Schizoplacus* and subg. *Synplacus*. This provides a first step toward retaining *Mimulus* as the generic name for these two subgenera, which together include about 140 species. If *Phryma* and Australian segregate genera of Phrymaceae are to be maintained, the next step is to conserve the name *Mimulus* with a species from within a western American group and adopt an alternative name for the four species of *Mimulus* sensu stricto.

**MIMULUS** sect. **LEUCOCARPUS** (D. Don) Nesom, comb. nov. **Leucocarpus** D. Don in Sweet, Brit. Flower Gard. ser. 2, 2: pl. 124. 1831. Type: *Conobea alata* Graham (= *Mimulus perfoliatus*).

**Plants** shrubs or suffrutescent perennial herbs, glabrous or subglabrous, eglandular. **Stems** 0.4–1.8(–2.5) m high, strongly 4-angled to shallowly winged. **Leaves** thickened, elliptic-oblongate to narrowly lanceolate or narrowly oblanceolate, 9–21(–28) cm x 1.3–4.2(–5.6) cm, margins closely serrate to serrate-dentate, basally auriculate-clasping and perfoliate. **Flowers** on short, bracteate pedicels in axillary, pedunculate cymes of (1–)2–7(–14). **Calyces** tubular-campanulate, 6–12 mm long. **Corollas** 15–22 mm long, deciduous, yellow or white with a yellow throat, bilabiate. **Fruits** baccate, 10–18 mm wide, white, with thin skin and with most of the substance of the fruit derived from the fleshy placenta, septicidally sulcate, indehiscent. **Chromosome number** apparently not reported.

A single species.

**Mimulus perfoliatus** Kunth, Nov. Gen. Sp. (quarto ed.) 2: 371. 1817 [1818]. *Leucocarpus perfoliatus* (Kunth) Benth., Prodr. (DC.) 10: 335. 1846. **TYPE: Colombia.** Crescit in Regno Novo-Granatensi, no date, *Humboldt & Bonpland s.n.* (holotype: P).

*Conobea alata* J. Graham, Edinburgh New Philos. J. 10: 168. 1830. *Leucocarpus alatus* (J. Graham) Benth., Brit. Flower Gard. ser. 2, 2: pl. 124. 1833[1831]. **TYPE: Mexico.** "This plant was raised in the garden of P. Neill, Esq. at Canonmill [Scotland], from Mexican seeds communicated by Mr. D. Don as a species of *Conobea*, and flowered in the greenhouse in Sept." (from the protologue).

*Mimulus perfoliatus* ranges from Mexico (Chiapas, Guerrero, Hidalgo, Jalisco, [Michoacan?], Oaxaca, Puebla, Querétaro, San Luis Potosí, Veracruz) and Central America (Panama, Nicaragua, Honduras, Guatemala) southward to South America (Bolivia, Colombia, Ecuador, Peru, Venezuela). It has been collected at elevations of 1500–10,200 feet.

**MIMULUS** sect. **TROPANTHUS** A.L. Grant, Ann. Missouri Bot. Gard. 11: 324. 1924. **TYPE: *Mimulus treleasei* A.L. Grant (= *Mimulus levigatus*).**

*Hemichaena* Benth., Pl. Hartw. 78. 1841. **TYPE: *Hemichaena fruticosa* Benth. (= *Mimulus fruticosus*).**

*Berendtia* A. Gray, Proc. Amer. Acad. Arts 7: 379. 1868 (non Goeppert 1845). *Berendtiella* Wettst. & Harms in Engler et Prantl, Nat. Pflanzenfam., Gesamtreg. 2-4: 459. 1899 [a replacement name for *Berendtia* A. Gray]. **LECTOTYPE** (Thieret 1972, p. 92): *Berendtia ghiesbreghtii* A. Gray (= *Mimulus rugosus*). Gray did not cite a type for his new genus, in which he included *B. ghiesbreghtii*, *B. coulteri*, and *B. rugosa*. Thieret cited *B. ghiesbreghtii* as the type.

**Plants** perennial, shrubs, stipitate-glandular or glabrous to vernicose. **Stems** woody, erect. **Leaves** pinnately nerved, margins slightly to strongly revolute. **Inflorescences** axillary cymes, solitary or superposed, 1-flowered or 2–12-flowered; pedicels shorter to slightly longer than the calyces. **Corollas** tubular, yellow to orange or red, sometimes with dotted throat, marcescent, bilabiate. **Anthers** glabrous, style pubescent. **Capsules** dehiscent halfway to completely to the base along both sutures, placentae separating completely or nearly so. **Chromosome number** apparently not reported.

1. Leaves auriculate-clasping; corollas yellow; stamens included ..... **Mimulus fruticosus**  
 1. Leaves short-petiolate to sessile, bases cuneate to attenuate or acute, not clasping; corollas yellow to orange or red; stamens exserted (slightly so in *M. levigatus* and *M. rugosus*).

2. Stems and leaves glabrous, vernicose; petiole bases hardly swollen and indurate, blade margins prominently decurrent as stem wings; corollas orange to yellow ..... **Mimulus levigatus**  
 2. At least adaxial leaf surfaces stipitate-glandular; petiole bases swollen and indurate, persistent after abscission of the blade and upper petiole, blade margins not prominently decurrent; corollas yellow to orange or red.

3. Leaves 5–22 mm x 1–3(–5) mm; young stems densely hirtellous, eglandular, leaves stipitate-glandular adaxially; inflorescence usually terminal, bracteate; corollas yellow  
 ..... **Mimulus spinulosus**  
 3. Leaves 20–80 mm x 10–35(–50) mm; young stems and both leaf surfaces stipitate-glandular; inflorescence of axillary flowers arising among large cauline leaves; corollas yellow to orange or red.

4. Corollas yellow, tube 13–15 mm long, included in or slightly longer than the calyx; stamens long-exserted ..... **Mimulus coulteri**  
 4. Corollas red to orange, tube 25–35 mm long, 2.5–3.5 times longer than the calyx, stamens slightly exserted ..... **Mimulus rugosus**

**1. Mimulus fruticosus** (Benth.) Nesom, comb. nov. *Hemichaena fruticosa* Benth., Pl. Hartw., 78. 1841. *Leucocarpus fruticosus* (Benth.) Benth., Prodr. (DC.) 10: 336. 1846. **LECTOTYPE** (designated here): **Guatemala**. Prope Quetzaltenango, 1840, *K.T. Hartweg 549* (K digital image!). Other very similar specimens cannot be assumed to be exact duplicates of the type because of differences in the date or collection number: 1839, *Hartweg 549* (LD digital image!); no date, *Hartweg 548* (BM digital image!); 1841, *Hartweg 548* (NY digital image!); 1840, *Hartweg 548* (PH not seen). The protologue cited only "Quetzaltenango."

Erect herbaceous, suffrutescent, or shrubby plants to 2 m, young stems and leaf surfaces stipitate-glandular. **Leaves** sessile, ovate or elliptic, sometimes narrowly so, 4–16 cm long, 1.5–5.5 cm wide, margins coarsely to finely toothed, usually less so or even entire toward the base, base slightly clasping to cordate-amplexicaul, sometimes slightly pandurate; petioles 0–1 mm long, bases swollen and indurate, persistent after abscission of the blade and upper petiole. **Inflorescence** axillary, arising among large cauline leaves; peduncles 1–12-flowered, to 4 cm long; pedicels to 20 mm long. **Calyces** 14–17 mm long. **Corollas** yellow, 2.5–3.2 cm long, tube 2 times longer than the calyx. **Stamens** included, anthers 3 mm long.

Roadsides and road banks, disturbed and open slopes, cliff faces, river banks, sandbars, rocky places, clay over limestone, oak-pine zones, pine forests, broadleaf cloud forest, evergreen cloud forest with *Quercus*, *Pinus*, *Abies*, *Drimys*, *Photinia*, *Clethra*, *Cornus*, and *Symplocos*; ca. 3000–11,500 ft; Oaxaca, Chiapas, Guatemala, Honduras, Nicaragua, Costa Rica, Panama.

The name "*Hemichaena oaxacana*" applied to a collection of *Mimulus fruticosus* at NY apparently was never published.

- 2. *Mimulus levigatus*** (B. Rob. & Greenm.) Nesom, comb. nov. *Berendtia levigata* B. Rob. & Greenm., Proc. Amer. Acad. Arts 32: 39. 1897. *Hemichaena levigata* (B. Rob. & Greenm.) Thieret, Fieldiana, Bot. 34: 96. 1972. *Berendtiella levigata* (B. Rob. & Greenm.) Thieret, Ceiba 4: 305. 1955. **TYPE: Mexico. Puebla.** Calcareous ledges near Tehuacan, 5500 ft, 24 Dec 1895, C.G. Pringle 6294 (holotype: US digital image!; isotypes: A, CAS digital image!, F digital image!, GH-2 sheets, K digital image!, MO digital image!, PH digital image!, US). *Mimulus treleasei* A.L. Grant, Ann. Missouri Bot. Gard. 11: 325. 1924 [1925]. **TYPE: Mexico. Puebla.** Tehuacan, 2 Jun 1905, W. Trelease 68 (holotype: MO digital image!).

Erect shrubs to 0.9 m, glabrous, vernicose especially in the younger parts. **Leaves** opposite or fascicled, sometimes clustered on spur shoots, elliptic, ovate, or rhombic, sometimes narrowly so, 1.5–5 cm long, 0.4–2.2 cm wide, margins usually revolute, entire to distally serrate with widely spaced teeth, base acute to attenuate, petioles 0–8 mm long, winged distally, petiole bases neither strongly swollen nor indurate. **Inflorescence** axillary, arising among large cauline leaves; peduncles 1-flowered, to 20 mm long; pedicels as peduncles. **Calyces** 9–15 mm long. **Corollas** reddish orange, 2.5–3.5 cm long, tube 3 times longer than the calyx. **Stamens** barely or not exerted, anthers 2–2.5 mm long.

Ledges and rocky soil, limestone slopes, matorral with *Morkillia mexicana*, *Erythroxylon compactum*, *Bursera glabrifolia*, *Sophora secundiflora*, *Krameria cytisoides*, *Hintonia latiflora*; ca. 5000–6000 ft; Oaxaca, Puebla, Veracruz.

- 3. *Mimulus spinulosus*** (S. Wats.) Nesom, comb. nov. *Berendtia spinulosa* S. Wats., Proc. Amer. Acad. Arts 25: 159. 1890. *Hemichaena spinulosa* (S. Wats.) Thieret, Fieldiana, Bot. 34: 98. 1972. *Berendtiella spinulosa* (S. Wats.) Thieret, Ceiba 4: 305. 1955. **TYPE: Mexico. Nuevo León.** Dry limestone cliffs of the Sierra Madre near Monterey, 27 Jun 1888, C.G. Pringle 1952 (holotype: US digital image!; isotypes: F digital image!, GH, K digital image!, USJ).

Erect, pendent, or trailing shrubs to 0.9 m, young stems and leaf surfaces stipitate-glandular. **Leaves** opposite or fascicled, elliptic, ovate, or obovate; sometimes narrowly so, 5–22 mm long, 1–3(–5) mm wide, margins entire to several toothed, teeth widely spaced, base acute to attenuate, petioles 1–2 mm long, bases swollen and indurate, persistent after abscission of the blade and upper petiole. **Inflorescence** usually terminal, bracteate; peduncles 1-flowered, to 10 mm long, sometimes persisting and "thornlike" on dead branches; pedicels as peduncles. **Calyces** 5–6.5 mm long. **Corollas** yellow, tube 13–18 mm long, 1.5–2 times longer than the calyx. **Stamens** exerted, anthers 0.7–1 mm long.

Outcrops, cliff faces, crevices, talus, slopes, arroyo banks, limestone, gypsum, cemented gravel, oak-pine forest, scrub-oak zone, oak chaparral with *Garrya-Rhus-Agave-Nolina-Pinus* or with *Dasyllirion-Agave-Cercocarpus-Fraxinus greggii* and *Pinus*, matorral of *Acacia*, *Leucaena*, *Pistacia*, *Vauquelinia*, and *Dodonea*; ca. 2000–5000 ft; Coahuila, Nuevo León.

Collections in herbarium TEX-LL that have been recognized by the unpublished name "*Mimulus cebollanus*" are within the range of variation of *M. spinulosus*. Similarly, the name "*Berendtiella pendens*" applied to a collection of *M. spinulosus* at K apparently was never published.

**4. *Mimulus coulteri*** (A. Gray) Nesom, comb. nov. *Berendtia coulteri* Gray, Proc. Amer. Acad. Arts 7: 380. 1868. *Hemichaena coulteri* (A. Gray) Thieret, Fieldiana, Bot. 34: 94. 1972. *Berendtiella coulteri* (Gray) Thieret, Ceiba 4: 305. 1955. **TYPE: Mexico.** No other information, *T. Coulter 1335* (holotype: GH; isotype: K-2 sheets digital images!). A collection labeled as *Coulter 1334* (fide JSTOR) at K apparently is not an isotype.

Erect shrubs to 2 m, young stems and leaf surfaces stipitate-glandular. **Leaves** elliptic, (25–)30–80 mm x 15–35(–50) mm, margins entire to obscurely toothed or undulate, base acute to rounded, the apex acute to obtuse, petioles 1–2 mm, bases swollen and indurate, persistent after abscission of the blade and upper petiole. **Inflorescence** axillary, arising among large cauline leaves; peduncles 1–5-flowered, to 15 mm long; pedicels to 5 mm long. **Calyces** 5–8 mm long. **Corollas** yellow, tube 13–15 mm long, included in or slightly longer than the calyx. **Stamens** exerted, anthers 1.6–1.8 mm long.

Rocky or shale to clay or loam slopes, canyons, xerophytic matorral with juniper and oak, deciduous tropical forest, disturbed cloud forest with pine and juniper; ca. 4000–6000 ft.; Guanajuato, Hidalgo, Querétaro.

**5. *Mimulus rugosus*** (Benth.) Nesom, comb. nov. *Diplacus rugosus* Benth., Prodr. (DC.) 10: 368. 1846. *Hemichaena rugosa* (Benth.) Thieret, Fieldiana, Bot. 34: 96. 1972. *Berendtia rugosa* (Benth.) A. Gray, Proc. Amer. Acad. Arts 7: 380. 1868. *Berendtiella rugosa* (Benth.) Thieret, Ceiba 4: 305. 1955. **TYPE: Mexico. Chiapas.** "In Mexico australi in prov. Chiapas," *J.J. Linden 201* (holotype: K, fide Thieret 1972).

*Berendtia ghiesbrechtii* A. Gray, Proc. Amer. Acad. Arts 7: 380. 1868. **TYPE: Mexico. Chiapas.** *Ghiesbrecht & Berendt 134* (holotype: GH, fide Thieret 1972).

Erect, arching, or sometimes pendent shrubs to 4 m, young stems and both leaf surfaces stipitate-glandular. **Leaves** opposite or fascicled, ovate or elliptic, sometimes narrowly so, 20–70 mm long, 10–35 mm wide, margins coarsely to finely many to few toothed, the base cuneate to attenuate, petioles 1–7 mm long, bases swollen and indurate, persistent after abscission of the blade and upper petiole. **Inflorescence** axillary, arising among large cauline leaves; peduncles 1–3-flowered, to 15 mm long; pedicels to 12 mm long. **Calyces** 8–14 mm long. **Corollas** orange to red, tube 25–35 mm long, 2.5–3.5 times longer than the calyx. **Stamens** exerted, anthers 1.5–2 mm long.

Rocky slopes, ridges, cliff faces, roadsides and roadbanks, matorral, oak and pine-oak-juniper-arbutus woodlands; ca. 4600–10,000 ft; Chiapas, Guatemala, Honduras.

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#### LITERATURE CITED

- Albach, D.C., K. Yan., S.R. Jensen, and H.Q. Li. 2009. Phylogenetic placement of *Triaenophora* (formerly Scrophulariaceae) with some implications for the phylogeny of Lamiales. *Taxon* 58: 749–756.
- Argue, C.L. 1980. Pollen morphology in the genus *Mimulus* (Scrophulariaceae) and its taxonomic significance. *Amer. J. Bot.* 67: 68–87.
- Argue, C.L. 1983. A biometric and taxonomic study of pollen character variation in *Berendtiella* and *Hemichaena* (Scrophulariaceae). *Canad. J. Bot.* 61: 53–62.

- Argue, C.L. 1984. Pollen morphology in *Dodartia*, *Lancea*, *Leucocarpus*, and *Mazus* and an analysis of pollen morphotypes in the Mimuleae (Scrophulariaceae). *Canad. J. Bot.* 62: 1287–1297.
- Argue, C.L. 1986. Pollen morphology of *Amphianthus*, *Artanema*, *Curanga*, *Glossostigma*, and *Peplidium* (Scrophulariaceae - Gratiolaeae). *Amer. J. Bot.* 73: 1570–1576.
- Barker, W.R. 1982. Evolution and biogeography of arid Australian Scrophulariaceae. Pp. 341–350, in W.R. Barker and P.J.M. Greenslade (eds.), *Evolution of the Flora and Fauna of Arid Australia*. Peacock Publications, Adelaide, South Australia.
- Beardsley, P.M. 1997. Colorado's rare endemic plant, *Mimulus gemmiparus*, and its unique mode of reproduction. M.S. thesis (Botany), Colorado State Univ., Ft. Collins.
- Beardsley, P.M. and R.G. Olmstead. 2002. Redefining Phrymaceae: The placement of *Mimulus*, tribe Mimuleae, and *Phryma*. *Amer. J. Bot.* 89: 1093–1102.
- 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.
- Beardsley, P.M. and W.R. Barker. 2005. Patterns of evolution in Australian *Mimulus* and related genera (Phrymaceae similar to Scrophulariaceae): A molecular phylogeny using chloroplast and nuclear sequence data. *Austral. Syst. Bot.* 18: 61–73.
- Bentham, G. 1846. Scrophulariaceae. *Prodr. (DC.)* 10: 186–586. *Diplacus* (p. 368), *Mimulus* (pp. 368–373), *Eunanus* (p. 374).
- Burt, B.L. 1965. The transfer of *Cyrtandromoea* from Gesneriaceae to Scrophulariaceae, with notes on the classification of that family. *Bull. Bot. Survey India* 7: 73–88.
- Chadwell, T.B., S.J. Wagstaff, and P.D. Cantino. 1992. Pollen morphology of *Phryma* and some putative relatives. *Syst. Bot.* 17: 210–219.
- Grant, A.L. 1924. A monograph of the genus *Mimulus*. *Ann. Missouri Bot. Gard.* 11: 99–388.
- McMinn, H.E. 1951. Studies in the genus *Diplacus* (Scrophulariaceae). *Madroño* 11: 33–128.
- Moody, A., P.K. Diggle, and D.A. Steingraeber. 1999. Developmental analysis of the evolutionary origin of vegetative propagules in *Mimulus gemmiparus*. *Amer. J. Bot.* 86: 1512–1522.
- Oxelman, B., P. Kornhall, R.G. Olmstead, and B. Bremer. 2005. Further disintegration of Scrophulariaceae. *Taxon* 54: 411–425.
- Pennell, F.W. 1920. Scrophulariaceae of Colombia. *Proc. Acad. Nat. Sci. Philadelphia* 72: 136–188.
- Pennell, F.W. 1935. The Scrophulariaceae of eastern temperate North America. *Proc. Acad. Nat. Sci. Philadelphia* 1: 1–650. *Mimulus* Linnaeus (pp. 112–136).
- Schäferhoff, B., A. Fleischmann, E. Fischer, D.C. Albach, T. Borsch, G. Heubl, and K.F. Müller. 2010. Towards resolving Lamiales relationships: Insights from rapidly evolving chloroplast sequences. *BMC Evol. Biol.* 10: 352 (22 pages).
- Tank, D.C., P.M. Beardsley, S.A. Kelchner, and R.G. Olmstead. 2006. L.A.S. Johnson Review No. 7. Review of the systematics of Scrophulariaceae s.l. and its current disposition. *Austral. Syst. Bot.* 19: 289–307.
- Thieret, J.W. 1954. The tribes and genera of Central American Scrophulariaceae. *Ceiba* 4: 164–184.
- Thieret, J.W. 1955. The status of *Berendtia* A. Gray. *Ceiba* 4: 304–305.
- Thieret, J.W. 1967. Supraspecific classification in the Scrophulariaceae: A review. *Sida* 3: 87–106.
- Thieret, J.W. 1972. Synopsis of *Hemichaena*, including *Berendtiella* (Scrophulariaceae). *Fieldiana Bot.* 34: 89–99.
- Xia, Z., Y.-Z. Wang, and J.F. Smith. 2009. Familial placement and relations of *Rehmannia* and *Triaenophora* (Scrophulariaceae s.l.) inferred from five gene regions. *Amer. J. Bot.* 96: 519–530.