

PHRYMACEAE LOPSEED FAMILY

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Annual or perennial herbs. LEAVES simple, opposite, with or without glandular hairs; stipules absent. INFLORESCENCE racemose or of solitary axillary flowers. FLOWERS perfect, actinomorphic or zygomorphic (weakly to strongly bilabiate), ebracteate, hypogynous; calyx synsepalous, the lobes 5, equal or unequal, shorter than the tube; corolla sympetalous, with two lips, the upper lip 2-lobed, external in bud, the lower lip 3-lobed, the lower side of the throat with two elevated longitudinal ridges forming a palate, this sometimes partially or completely closing the orifice, usually bearded; stamens 2–4, when 4, didynamous; anthers with two well-developed sacs, the sacs confluent at the apex and more or less divaricate at the base; ovary with 2 fused carpels, superior, placentation axile, parietal, or basal; style solitary, stigmas 2-lobed, the lobes distinct or united. FRUIT a 2-valved, loculicidal capsule sometimes also splitting at the septum dividing the placentae. —ca. 13 genera, ca. 188 spp., worldwide, most abundant in western N. Amer.

The family includes economically important ornamental species in the genera *Mazus*, *Mimulus*, and *Erythranthe*. Recent phylogenetic studies support a close relationship between *Mimulus* (and relatives) and *Phryma* of the formerly monotypic family Phrymaceae (Beardsley & Olmstead 2002, Tank et al. 2006). The genus *Mimulus* has been dismantled into three distinct lineages (Barker et al. 2012). The Arizona species formally treated as *Mimulus* species are here treated as members of the genera *Mimetanthe*, *Erythranthe* or *Diplacus*. The genera are distinguished from each other in the key below.

1. Flowers sessile to subsessile; corollas persistent in fruit; pedicels usually shorter than calyces ***Diplacus***
- 1' Flowers long-pedicellate; corollas deciduous in fruit; pedicels usually longer than calyces.
 2. Calyx not strongly angled, strongly zygomorphic; capsule glandular; fertile stamens 2(–4); placentation parietal ***Mimetanthe***
 - 2' Calyx usually 5-angled, actinomorphic to zygomorphic; capsule eglandular; fertile stamens 4; placentation axile..... ***Erythranthe***

Diplacus Nutt.

Kimberly Hansen

Annual herbs, taprooted, stipitate glandular, puberulent to villous; stems erect, leafy throughout. LEAVES sessile to subsessile, obovate to narrowly elliptic. FLOWERS pedicellate, ebracteolate; calyx tube 5-angled, inflated in fruit, the lobes

subequal or if unequal the upper lobe distinctly longer and broader than others; corolla nearly actinomorphic to bilabiate, magenta to violet or yellow, persisting in fruit; fertile stamens four, included. CAPSULES apically attenuate, glabrous, placentation parietal, the placentae not fused; seeds oblong, finely reticulate. —Ca. 46 species distributed in w N. Amer. WA to MT s to AZ, CA and CO with one species endemic to Mex. From the Greek *diploos* for double, in reference to capsule splitting and exposing two separate placentae.

Diplacus is easily separated from *Mimulus* (and *Erythranthe*) based on presence of sessile to subsessile flowers. It also has apically attenuate capsules and parietal placentation, features it shares with *Mimetanthe*.

1. Calyx teeth subequal, acuminate to attenuate; base of calyx and leaf axils villous; hairs greater than or equal to 1 mm long; corolla violet to magenta*D. bigelovii*
- 1' Calyx teeth unequal, the upper lobe distinctly the largest and broadest, broadly rounded to acute; base of calyx and leaf axils puberulent; hairs less than 0.5 mm long; corolla yellow or violet.....*D. parryi*

Diplacus bigelovii (A. Gray) G.L. Nesom (for Jacob Bigelow [1787–1879], physician and botanist). Bigelow's Monkeyflower. —Annual herbs, (1–)2.5–15(–24) cm tall, glandular-pubescent; stems simple to highly branched. LEAVES 11–30(–39) long, 4–14(–17) wide. FLOWERS (1–)2 per node; pedicels 1–6(–10) mm long; calyx (6–)9–10(–13) mm long, often inflated in fruit, villous at least at base with stipitate-glandular multicellular hairs; lobes subequal, acuminate to attenuate, the sinuses cuneate (rarely rounded); corolla (16–)20–28(–31) mm long, magenta to violet with two yellow patches on palate, the throat yellow with magenta to violet speckles, the lobes broadly rounded. CAPSULES exerted slightly past calyx teeth at maturity. (Figs. 1F–H; 5A). [*Mimulus bigelovii* (A. Gray) A. Gray] —2 vars. in AZ; Inyo co. CA, s NV, sw UT s to n Baja CA.

1. Distal leaf apices acute.....*D. bigelovii* var. *bigelovii*
- 1' Distal leaf apices aristulate to cuspidate *D. bigelovii* var. *cuspidatus*

var. *bigelovii* —LEAVES 11–25(–31) mm long, 4–8(–15) mm wide, the proximal ones obovate, with an acute or rounded apex, the distal ones narrowly elliptic to lanceolate, with an acute apex. (Fig. 1H). [*Mimulus bigelovii* (A. Gray) A. Gray var. *bigelovii*] —Prefers rocky outcroppings but also found in sand and gravel soils in the Mohave and w Sonoran deserts: Mohave and La Paz cos. (Fig. 6A); 150–2200 m (500–7200 ft); Feb–Oct.

var. *cuspidatus* (A. L. Grant) G. L. Nesom —LEAVES 12–30(–39) mm long, (5–)7–17 mm wide, the proximal ones obovate to oblanceolate, with a rounded, acute, or acuminate apex, the distal ones orbicular, with an aristulate to cuspidate apex. (Fig. 1G). [*Mimulus bigelovii* (A. Gray) A. Gray var. *cuspidatus* A. L. Grant] —Often on rocky outcroppings but also found in sand, gravel and cinder soils in the Mohave Desert: Mohave co. (Fig. 6A); 400–2000 m (1300–6500 ft); Mar–Sep.

In Arizona, this variety is usually found on the south side of the Colorado River. Nesom (2013) suggested that *D. bigelovii* var. *cuspidatus* may be more closely related

to other species of *Diplacus* with similar leaf shape than to *Diplacus bigelovii* var. *bigelovii*. Further experimental work is needed.

Previous treatments have recognized *Mimulus spissus* A. L. Grant as a distinct taxon. However, Thompson (2005) suggested that it is merely a form of *Diplacus bigelovii* var. *cuspidatus* that results from high drought stress and it is therefore not recognized here.

Diplacus parryi (A. Gray) G. L. Nesom & N. S. Fraga (for Charles Parry [1823–1890], surgeon and naturalist on Mexican Boundary Surveys). Annual Redspot Monkeyflower. —Annual herbs, 1.5–6(–10.5) cm tall, stipitate glandular-puberulent; stems usually unbranched. LEAVES (6.5–)8–14(–26) mm long, (1–)1.6–4(–7.5) mm wide. FLOWERS (1–)2 per node; pedicels (0.5–)1–3(–4) mm long; calyx (6–)8–12 mm long, inflated in fruit, sparsely stipitate glandular-puberulent (rarely glabrous); lobes unequal, rounded to acute, the upper central lobe distinctly longer and broader, the remaining lobes reduced, sometimes to apicules; corolla (14–)17–22(–27) mm long, magenta or violet with two yellow patches on the palate, or yellow with 6–8 violet spots on the palate; throats yellow with purple to reddish speckling in both forms, the lobes equal, broadly rounded to truncate. CAPSULE more or less included in calyx, visible in sinuses but not exceeding the calyx teeth. (Figs. 1D–E). [*Mimulus parryi* A. Gray] —Mohave Desert in dry sandy washes and on gravel slopes: Mohave Co. (Fig. 6B); 500–1100 m (1700–3600 ft); Apr–Jun; sw UT and Inyo Co., CA.

Diplacus parryi is unusual in having two distinct color morphs, which often occur within the same population without gradation.

Erythranthe Spathe

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Annual or perennial herbs, taprooted to rhizomatous or stoloniferous, glabrous to glandular-pubescent; stems creeping to erect, leafy throughout or scapose. LEAVES sessile to petiolate, linear to orbicular or ovate. FLOWERS pedicellate, ebracteolate; calyx tube usually 5-angled, sometimes inflated in fruit, the lobes subequal or if unequal the upper lobe distinctly longer and broader than others; corolla nearly actinomorphic to strongly bilabiate, yellow, red, pink, purple to blue, deciduous in fruit; fertile stamens four, included or exerted. CAPSULES aristate to acuminate, glabrous in ours, placentation axile; seeds oblong to oval or fusiform. —111 species distributed in British Columbia, Can., to SD, s to n Mex. From Greek *erythros* (red) and *anthos* (flower).

Most Arizona species formerly included in *Mimulus* are now included in the genus *Erythranthe*. The primary character separating *Erythranthe* from *Mimulus* is the leaf venation; *Mimulus* in North America is weakly brochidodromous (veins arising from a prominent midvein and merging at the margin with the adjacent veins), whereas *Erythranthe* has basal acrodromous venation (multiple parallel veins separating at base of leaf and fusing at the apex). Base chromosome number also separates *Mimulus* from *Erythranthe*. *Mimulus* has a base chromosome number of $x = 8, 11, 12$ and *Erythranthe* has $x = 14, 15, 16$. Many of the species have showy, handsome flowers. *Erythranthe*

cardinalis, *E. cuprea*, *E. guttata*, *E. lutea*, and *E. primuloides* are cultivated. Most of the Arizona species grow in wet soil. Herbarium specimens without mature fruit and calyx are often difficult to identify.

1. Corollas red; calyx tubes 16 mm or longer (Sect. *Erythranthe*).
 2. Basal leaves fan-shaped, with apices rounded with prominent teeth; pedicels 1–3(–4.5) cm long; capsules ca. 8 mm long *E. eastwoodiae*
 - 2' Basal leaves oblanceolate, with apices acute without prominent teeth; pedicels 3–10 cm long; capsules 14–18 mm long.
 3. Anther sacs spreading *E. cinnabarina*
 - 3' Anther sacs reflexed, forming a horseshoe-shape..... *E. verbenaceus*
- 1' Corollas yellow, pink, purple or blue; calyx tubes less than 16 mm long.
 4. Calyx teeth subequal; calyx not or only moderately inflated in mature fruit.
 5. Perennials, mat-forming, stoloniferous, eglandular (Sect. *Monantha*)..... *E. primuloides*
 - 5' Annuals, erect, taprooted, stipitate-glandular.
 6. Leaves green, ovate, widest below the middle; stems with soft, tangled hairs; corolla lobes entire to slightly notched; calyx teeth triangular and acute–acuminate (Sect. *Mimulosa*) *E. floribunda*
 - 6' Leaves suffused purplish-red, especially the lower surface, widest at or above the middle; stems sparsely glandular-puberulent; corolla lobes notched; calyx teeth rounded, often mucronate (Sect. *Paradantha*)
 7. Plants 1–3(–7) cm tall; internodes usually shorter than leaves; flowering pedicels 2–7(–10) mm long..... *E. suksdorfii*
 - 7' Plants 3–32 cm tall; internodes usually longer than leaves; flowering pedicels 6–22 mm long *E. rubella*
 - 4' Calyx teeth not equal, upper calyx tooth longer than the others; calyx inflated in mature fruit (Sect. *Simiola*)
 8. Lateral calyx teeth not closing over orifice in fruit..... *E. geyeri*
 - 8' Lateral calyx teeth closing over orifice in fruit.
 9. Stems mat-forming; corolla lobes fimbriate; calyx tube 2.5–4.5 mm long *E. parvula*
 - 9' Stems decumbent to erect; corolla lobes entire; calyx tube 3–14 mm long.
 10. Stems 1–12.5 cm long; calyx tube 3–6 mm long.
 11. Fruiting pedicels 10–40 mm long; leaves not much reduced distally; rare, Huachuca and Chiricahua Mountains *E. calciphila*
 - 11' Fruiting pedicels 2–23(–34) mm long; leaves reduced distally, widespread *E. guttata (in part)*
 - 10' Stems 5–60(–90) cm long; calyx tube (3–)6–14 mm long.
 12. Stems 30–60(–90) cm long; leaves reduced distally; plants 1–many flowered; usually below 3000 m (10,000 ft); common..... *E. guttata (in part)*
 - 12' Stems 5–11 cm long; leaves not much reduced distally; plants 1–5(–6) flowered; usually above 3000 m (10,000 ft); rare..... *E. tilingii*

Erythranthe calciphila (Gentry) G. L. Nesom (limestone loving). —Annual herbs, fibrous rooted without rhizomes or stolons, glabrous to villosulous, stipitate glandular. STEMS usually erect, 1–12.5 cm long. LEAVES short-petiolate or the distal sub-sessile, glabrous to sparsely short villous, sometimes with stipitate glands; petioles 1–4 mm long; blades palmately 3–5 veined, orbicular to ovate, 0.5–2.2 cm long, 0.5–2 cm wide, the distal leaves barely reduced; apex subacute to rounded; base cuneate to rounded; margins shallowly serrulate, sometimes denticulate, usually with 5–7 teeth per side. FLOWERS axillary, from most axillary nodes; fruiting pedicels 1–4 cm long; calyx zygomorphic, glabrous to sparsely short-villous and stipitate glandular, pale-green to green, the tube 3–6 mm long, inflated in fruit, the dorsal teeth 0.5–2 mm long, acute, closing over orifice in fruit, the lateral teeth 0.5–0.75 mm long, acute, the upper tooth 1.5–3 mm long, acute; corolla bilabiate, yellow, sometimes sparsely red-spotted, the tube cylindrical–funnelform, 5–10 mm long, exerted 1–2.5 mm beyond longest calyx tooth, the lobes entire; anthers included, the anther sacs reflexed, glabrous; stigma club-shaped. CAPSULES oblong, aristate, 4–5 mm long, included in calyx. SEEDS oval, brown. [*Mimulus calciphilus* Gentry, *Mimulus minutiflorus* Vickery] —Moist spots under rock ledges, rare, from Chiricahua and Huachuca Mountains in Cave Creek Canyon and Gance Canyon respectively: Cochise Co. (Fig 6C); 1500–2000 m (5000–6500 ft); Aug–Sep; AZ; nw Mex..

Erythranthe cinnabarina G. L. Nesom (reference to the resin of *Pterocarpus*). Cinnabar Monkeyflower. —Perennial herbs, rhizomatous, sparsely villous with sessile or stipitate glands. STEMS erect or ascending, 25–60 cm long. LEAVES sessile, glabrous to sparsely villous, the blades palmately veined, elliptic to broadly lanceolate, 6–13 cm long, 2.5–4.5 cm wide; apex acute; margins serrate. FLOWERS in pairs; fruiting pedicels 5–9.9 cm long; calyx actinomorphic, hispid, often red-tinged on veins, the tube 27–34 mm long, not inflated in fruit, the teeth subequal, 7–10 mm long, ovate, abruptly attenuate to linear-caudate; corolla bilabiate, deep orange to orange-red, the tube funnelform, 29–36 mm long, exerted 7–12 mm beyond calyx teeth, the throat yellow with hairy ridges, the lobes entire; anthers exerted, the anther sacs spreading, densely white-villous; stigmas 2-lobed. CAPSULES oblong, acuminate, 14–18 mm long, slightly exerted from calyx. SEEDS oval, brown to black. (Figs. 2E–F; 5B). —Canyons in mixed conifer forest: Cochise, Graham, and Pima, cos. (Fig. 6D); 2450–3300 m (8000–10,800 ft); Jun–Sep; AZ endemic.

Erythranthe cinnabarina is a recent segregate from *E. cardinalis* (Dougl. ex Benth.) Spach based on calyx lobes 7–10 mm long with an “abruptly attenuate to linear-caudate apex” (vs. calyx lobes 4–7 mm long with lobes that are apically attenuate–acute but not caudate in *E. cardinalis*). The corolla tubes are also longer in *E. cinnabarina* [29–36 mm vs. (15–)20–30 mm in *E. cardinalis*]. The range of *E. cinnabarina* is limited to se Arizona in the Chiricahua, Pinaleno, and Santa Catalina Mtns. while *E. cardinalis* is restricted to CA and Baja C., Mex. In Arizona this species can easily be confused with *E. verbenacea*. *Erythranthe verbenacea* has reflexed anther sacs, more cylindrical corolla tubes, and grows at or below 2600 meters (vs. divaricate or spreading anther sacs, more funnelform corolla tubes, and grows between 2450–3300 meters) (Nesom 2014).

Erythranthe eastwoodiae (Rydb.) G. L. Nesom (for Alice Eastwood [1859–1953], western botanist). Eastwood’s Monkeyflower. —Perennial herbs, stoloniferous, glandular-puberulent or viscid-villous. STEMS often pendent, usually unbranched, 7–30(–45) cm long, densely villous with stipitate glands. LEAVES sessile, glandular puberulent, the blades palmately veined; proximal blades fan-shaped, 0.5–2 cm long, 1–1.5 cm wide; distal blades obovate to oblanceolate, 2.5–4.5 cm long, (0.5–)1–2 cm wide; apex acute; margins coarsely toothed. FLOWERS solitary or in pairs; pedicels 1–3(–4.5) cm long; calyx actinomorphic, hispid, often red-tinged on veins, the tube 20–30 mm long, not inflated in fruit, the teeth subequal, 3–6 mm long, lanceolate, acuminate; corolla bilabiate, dropping after anthesis, scarlet to orange-red, the tube narrowly funnelform, 30–45 mm long, exerted 15–20 mm beyond calyx teeth, the throat with hairy ridges, the lobes entire; anthers exerted, the anther sacs divaricating or reflexed, edges pilose; stigma 2-lobed. CAPSULES oblong, acuminate, ca. 8 mm long, included in calyx. SEEDS oval, brown to black. (Figs. 2A–B; 5C). [*Mimulus eastwoodiae* Rydb.] —Wet alcoves or hanging garden communities in sandstone rock walls: Apache, Coconino, Navajo cos. (Fig. 7A); 700–2500 m (2500–8000 ft); May–Oct; AZ, CO, NM, UT.

Erythranthe floribunda (Lindl.) G. L. Nesom (profusely flowering). Many-flowered Monkeyflower. —Annual herbs, taprooted, sticky, with long, tangled, stipitate glandular hairs. STEMS erect, 4–40 cm long. LEAVES petiolate, villous, the petiole 1–7 mm long, the blades pinnately to subpalmately 3-veined, lanceolate to deltoid, 0.4–3 cm long, 0.2–1.6 cm wide; apex acute; base rounded; margins usually serrate. FLOWERS axillary, 1–many in leafy racemes; pedicels 1–3 cm long; calyx actinomorphic, more or less glandular-pubescent, green to purple, often darker on veins, often spotted, the tube 0.4–0.8 cm long, not or only moderately inflated in fruit, the teeth subequal, 0.5–1 mm long, triangular and acute–acuminate, sometimes ciliate; corolla actinomorphic, yellow, red-spotted, the tube cylindrical, 6–12 mm long, exerted 1–8 mm beyond calyx teeth, the lobes entire to slightly notched; anthers included, the anther sacs reflexed, glabrous; stigma 2-lobed. CAPSULES oblong to fusiform, aristate, 3.5–5 mm long, included in calyx. SEEDS oval, yellow to tan. (Figs. 3B; 5D). [*Mimulus floribundus* Lindl., *Mimulus deltoides* Gandog., *Mimulus membranaceus* A. Nelson, *Mimulus multiflorus* Pennell, *Mimulus peduncularis* Douglas ex Benth., *Mimulus pubescens* Benth., *Mimulus serotinus* Suksd., *Mimulus subulatus* (A. L. Grant) Pennell, *Mimulus trisulcatus* Pennell] —Crevices, seeps around granite outcrops, near streams: Apache, Cochise, Coconino, Gila, Graham, Pima, Santa Cruz, Yavapai cos. (Fig. 7B); 550–2500 m (1900–7300 ft); Mar–Jul; British Columbia, Can., MT, CA, AZ, NM, SD; Mex. (Chih.). *Erythranthe floribunda* is extremely variable in size and ours are often depauperate.

Erythranthe geyeri (Torrey) G. L. Nesom (for Karl Andreas Geyer [1809–1853], German botanist). Geyer’s Monkeyflower. —Perennial herbs, often creeping and sometimes mat-forming, mostly or entirely glabrous, if hairs present, sparsely short-villous and stipitate glandular distally or on pedicels only. STEMS usually prostrate to decumbent–ascending, 3–27(–50) cm, often rooting at the nodes. LEAVES petiolate to sessile, glabrous, the proximal leaves with petioles 1–14 mm long, the distal

leaves sub-sessile to sessile, the blades palmately 3–5 veined, orbicular to ovate (reniform), 0.3–2.2(–3.2) cm long, 0.4–2.5(–4) cm wide; apex rounded to sub-acute; base cordate to rounded; margins shallowly serrulate to serrate (rarely erose) with 5–10 teeth per side. FLOWERS axillary, 2–12, usually from distal nodes but sometimes also from proximal ones, racemose; fruiting pedicels 0.3–3.5 cm long; calyx zygomorphic, the tube 4–8 mm long, glabrous to sparsely short-villous and stipitate glandular, green to purple tinged, inflated in fruit; dorsal and lateral teeth usually obsolete to 1 mm long, acute to mucronate, the upper tooth 0.5–3 mm long, acute to mucronate, teeth not closing over orifice in fruit; corolla bilabiate, yellow, sometimes sparsely red spotted, the tube funnelform, 7–15 mm long, exerted 2–4 mm beyond longest calyx tooth, the lobes entire, the palate only partially closing throat; anthers included, glabrous, reflexed; stigma club-shaped. CAPSULES oblong, aristate, 3–5 mm long, included in calyx. SEEDS oval, brown. (Figs. 4C–D; 5E–F). [*Mimulus glabratus* Kunth, *Mimulus glabratus* var. *jamesii* (Torr. & A. Gray ex Benth.) A. Gray, *Mimulus geyeri* Torr.] —Wet places, both in water and along stream margins, in hanging gardens, nearly vertical rock faces: Apache, Cochise, Pinal, Santa Cruz cos. (Fig. 7C); 1500–2600 m (4900–8500 ft); May–Oct; AZ; Mex.

Herbarium specimens of *E. geyeri* are easily confused with *E. guttata* when the calyx teeth are folded during pressing.

Erythranthe guttata (DC.) G. L. Nesom (spotted). Seep Monkeyflower. — Annual or perennial herbs, rhizomatous, glabrous to minutely villous; hairs eglandular to glandular. STEMS decumbent to erect, (4–)30–60(–90) cm, stout and fistulose to slender, up to 13 mm wide. LEAVES variable, petiolate often becoming sessile distally, mostly glabrous to hispidulous to minutely villous-hirsute, eglandular or glands sessile or stipitate; petioles (1–)5–60(–90) mm long, the blades palmately to sub-pinnately (3–)5–9(–11)-veined, cordate to ovate to orbicular to elliptic, (0.1–)1–8(–11) cm long, (0.15–)0.5–5(–7.5) cm wide; apex subacuminate to acute to obtuse; base cordate to truncate to cuneate; margins denticulate to dentate, serrulate to serrate, or erose, with 5–many teeth per side. FLOWERS axillary, 1–many; fruiting pedicels (0.2–)0.5–4(–7.2) cm long; calyx zygomorphic, the tube (3–)6–14 mm long, glabrous to minutely villous, green to purple, sometimes spotted, inflated in fruit, the dorsal and lateral teeth 0.5–2.5 mm long, acute to mucronate, closing over orifice in fruit, the upper tooth 1–5.5 mm long, acute to mucronate; corolla bilabiate, yellow, sometimes red-spotted, the tube funnelform, (6–)10–22 (–26) mm long, exerted 1–10 mm beyond longest calyx tooth, the palate raised and closing throat, the lobes entire; anthers included, glabrous, reflexed; stigma club-shaped. CAPSULES oblong, aristate, 3–8 mm long, included within closed calyx teeth. SEEDS oval, brown. (Figs. 5G–H). [*Mimulus guttatus* Fischer ex DC., *Mimulus langsdorfii* var. *guttatus* (Fischer ex DC.) Jepson *Mimulus nasutus* Greene, *Mimulus cordatus* Greene, *Mimulus unimaculatus* Pennel, *Erythranthe nasuta* (Greene) G. L. Nesom, *Erythranthe cordata* (Greene) G. L. Nesom, *Erythranthe unimaculata* (Pennell) G. L. Nesom] —Wet places, creeks, streams, canyon bottoms, washes, seeps, wet meadows, pools, tanks, places with intermittent water, sandy soils, limestone, bedrock: Apache, Cochise, Coconino, Gila, Graham, Greenlee, La Paz, Maricopa, Mohave, Navajo, Pima, Pinal, Santa Cruz, Yavapai cos.

(Fig. 7D); 400–3050 m (1350–10000 ft.); Dec–Oct; w U.S.; w Can.; Mex. (Baja C., Son.); introduced in CT, DE, IN, MI, NY, PA; Can. (New Bruns.); Europe.

The *Erythranthe guttata* complex is taxonomically troublesome with four to more than 20 recognized species (Grant 1924; Campbell 1950; Kearney & Peebles 1951; Pennell 1951; Barker et al. 2012; Nesom 2012, Nesom 2015). Due to the huge amount of morphological variation in this group in Arizona, and little consistency across suites of taxonomically informative characters, the morphologically variable *E. guttata* segregates recently recognized by Nesom in his treatment of the genus *Erythranthe* are not recognized here. After examining specimens from all major Arizona herbaria, the characters recently used to delineate Nesom's species are unreliable and cannot be used to put specimens into consistent groupings. The treatment presented here follows that of Thompson (1993) in the Jepson Manual regarding *M. guttatus*—"Exceedingly complex: local populations may be unique but their forms intergrade over geograph[ic region] or elevation; variants not distinguished here."

Beardsley et al. (2004) developed a phylogeny of *Mimulus s.l.* using chloroplast and nuclear DNA. Sect. *Simiola*, which is now a part of *Erythranthe*, proved to be a well-supported clade. However, within the clade the genetic distances between species were very short, suggesting the groups are very closely related and possibly very young. Characters may not yet be fixed, which may be why possible segregate taxa, closely related to *E. guttata*, have proven so difficult taxonomically.

Sect. *Simiola* in Arizona contains *E. guttata*, *E. tilingii*, *E. parvula*, *E. geyeri*, and *E. calciphila*, all recognized in this treatment. We do not recognize *E. cordata* (Greene) Nesom, *E. nasuta* (Greene) Nesom, or *E. unimaculata* (Pennell) Nesom, which are considered synonyms of *E. guttata* in this treatment. For a discussion of the characters used to distinguish these taxa see Nesom (2012, 2015).

Erythranthe parvula (Woot. & Standl.) G. L. Nesom (small form). —Perennial herbs, rhizomatous, mat-forming, glabrous to villous, eglandular to glandular. STEMS prostrate, 3–15 cm long. LEAVES petiolate, glabrous (scurfy) to glandular villous-hirsute, sometimes more so on adaxial surface; petioles 1–3(–7) mm long; blades palmately 3-veined, ovate to deltoid to reniform, 2–9 mm long, 2–8 mm wide; apex acute to obtuse; base cordate to truncate to cuneate; margins shallowly denticulate to dentate or serrulate to serrate, with 3–5 teeth per side. FLOWERS axillary, 1–many; fruiting pedicels 0.5–1.3 cm long; calyx zygomorphic, glabrous to villous, green to dark purple, the tube 2.5–4.5 mm long, inflated in fruit, the dorsal and lateral teeth 1–1.5 mm long, acute to mucronate, closing over orifice in fruit, the upper tooth 2–3 mm long, acute to mucronate; corolla bilabiate, yellow, sometimes red-spotted, the tube funnellform, 6–9 mm long, exerted 3–5 mm beyond longest calyx tooth, the lobes fimbriate; anthers included, glabrous, reflexed; stigma club-shaped. CAPSULES oval, aristate, 2–3 mm long, included within closed calyx teeth. SEEDS oval, brown. (Figs. 4E–H). [*Mimulus parvulus* Woot. & Standl.] —Seepy springs on cliff faces, seepage cliffs above creeks, wet soils at base of small shallow alcoves, riparian canyons and hillsides, wash banks with seeps, rocky canyon walls just above water: Coconino, Graham, Greenlee, Maricopa, Yavapai cos. (Fig. 8A); 500–1500 m (1600–5000 ft.); (Jan–)Apr–Sep; AZ, NM; Mex. (Son.).

This taxon is a recent segregate of *Erythranthe dentiloba* (B. L. Rob. & Fernald) G. L. Nesom (*Mimulus dentilobus* B. L. Rob. & Fernald), which is now believed to only occur in nw Mex.

Erythranthe primuloides (Benth.) G. L. Nesom & N. S. Fraga (primrose-like). Primrose Monkeyflower. —Perennial herbs, stoloniferous, mat-forming, glabrous to sparsely villous, eglandular. STEMS erect, 1–12 cm. LEAVES sessile or tapering into a petiolate base, glabrous to sparsely villous on adaxial side, the petioles 1–3 mm long, the blades pinnately 3-veined, oblong to obovate, 0.5–3 cm long, 0.4–1 cm wide; apex acute; base cuneate; margins entire to minutely serrate. FLOWERS solitary or in pairs on a short scape; pedicels 2–8 cm long; calyx actinomorphic, glabrous, green to purple, often darker on veins, the tube 5–9 mm long, not or only moderately inflated in fruit, the teeth subequal, 0.5–1.5 mm long, acuminate, ciliate; corolla actinomorphic, yellow, brown-spotted, the tube funnelform, 7–19 mm long, exserted 4–12 mm beyond calyx teeth, the lobes notched; anthers included, the anther sacs reflexed, woolly; stigma club-shaped. CAPSULES oblong, aristate, 5–7 mm long, included in calyx. SEEDS oval, tan to brown. (Figs. 3D; 5I). [*Mimulus primuloides* Benth., *Mimulus primuloides* var. *pilosellus* Benth., *Mimulus pilosellus* Greene, *Mimulus primuloides* var. *minus* Benth.] —Wet meadows, seeps, streamsides, high elevation: Apache, Coconino, Greenlee cos. (Fig. 8B); 2400–2900 m (8000–9400 ft); Apr–Sep; AZ to WA.

Erythranthe linearifolia (A. L. Grant) G. L. Nesom & N. S. Fraga of CA is considered by some to be conspecific with this species and was formerly recognized as a variety of this species in *Mimulus* (*M. primuloides* var. *linearifolius* A. L. Grant).

Erythranthe rubella (A. Gray) N. S. Fraga (reddish). Little Redstem Monkeyflower. —Annual herbs, taprooted, glabrous to sparsely villous, sparsely stipitate glandular-puberulent. STEMS erect, 2–25 cm, often purplish-red; internodes usually longer than leaves. LEAVES subsessile except proximal ones, glabrous to sparsely villous on upper side, the petioles 1–10 mm long, the blades pinnately 1–3-veined, oblanceolate to rhombic, 0.3–2.7 cm long, 0.1–1.2 cm wide, purplish-red; apex acute; base cuneate; margins entire to serrate. FLOWERS axillary, 1–many, in leafy racemes; pedicels 0.5–2.2 cm long; calyx actinomorphic, stipitate-glandular, green to purple, often darker on veins, the tube 3–9 mm long, not or only moderately inflated in fruit, the teeth subequal, 0.5–1 mm long, rounded and often mucronate, often ciliate; corolla actinomorphic, yellow, purple, pink or white, red-spotted, the tube funnelform, 6–12 mm long, exserted 2–9 mm beyond calyx teeth, the corolla lobes notched; anthers slightly exerted to included, the anther sacs divaricate to slightly reflexed, glabrous; stigma 2-lobed. CAPSULES oblong, aristate, 4–5.5 mm long, included in calyx. SEEDS oval, brown. (Figs. 3A; 5J–K). [*Mimulus rubellus* A. Gray, *Mimulus gratioloides* Rydb.] —Generally in and along washes: Apache, Cochise, Coconino, Gila, Graham, Greenlee, La Paz, Maricopa, Mohave, Navajo, Pima, Pinal, Santa Cruz, Yavapai, Yuma cos. (Fig. 8C); 450–2500 m (1480–7800 ft); Jan–Aug; CA, CO, NM, NV, TX, UT, WY; n Mex.

Erythranthe suksdorfii (A. Gray) N. S. Fraga (for Wilhelm Suksdorf [1850–1932], German American botanist). Suksdorf's Monkeyflower. —Annual herbs,

taprooted, sparsely stipitate glandular-puberulent. STEMS erect, 1–3(–7) cm, purplish-red; internodes usually shorter than leaves. LEAVES sessile to subsessile, stipitate-glandular, the blades pinnately 3-veined, linear to oblanceolate, 0.3–1.5 cm long, 0.1–0.5 cm wide, purplish-red; apex rounded; base truncate; margins entire. FLOWERS axillary, 1–many, in leafy racemes; pedicels 2–7(–10) mm long; calyx actinomorphic, stipitate-glandular, purple, often darker on veins, the tube 3–6 mm long, not or only moderately inflated in fruit, the teeth subequal, 1 mm long, rounded and often mucronate; corolla actinomorphic, yellow, red-spotted, the tube tubular–funnelform, 4–7 mm long, exserted 2–4 mm beyond calyx teeth, the corolla lobes notched; anthers slightly exserted to included, the anther sacs divaricate, glabrous; stigma 2-lobed. CAPSULES oblong, aristate, 3.5–5.5 mm long, included to slightly exserted from the calyx. SEEDS oval, tan. (Figs. 3C; 5L). [*Mimulus suskendorfii* A. Gray, *Mimulus montioides* A. Gray] —Moist, generally clay soils in full sun: Apache, Coconino cos. (Fig. 8D); 1500–2500 m (5500–8000 ft); May–Jun; CO, ID, MT, NV, OR, UT, WA, WY.

Erythranthe tilingii (Regel) G. L. Nesom (for Heinrich Sylvester Theodor Tiling [1818–1871], Latvian physician). Tiling’s Monkeyflower. —Low creeping perennial herbs, stoloniferous, emerging from thick yellowish rootstocks, glabrous to stipitate-glandular on pedicels and calyces. STEMS procumbent to erect, 5–11 cm long. LEAVES petiolate, glabrous, the proximal petioles 1–10 mm long, the distal petioles generally sessile, the blades palmately 3–5-veined, elliptic to ovate, 0.5–2.5 cm long, 0.5–1.5 cm wide; apex acute to rounded; base cuneate; margins serrulate with about 5–6 teeth per side. FLOWERS axillary, 1–6; fruiting pedicels 0.9–2 cm long; calyx zygomorphic, glabrous to sparsely short-villous, green, the tube 6–9 mm long, inflated in fruit, the dorsal and lateral teeth 0.5–2 mm long, acute to mucronate, the dorsal teeth slightly longer than lateral teeth, closing over orifice in fruit, the upper tooth 2–4 mm long, acute to mucronate; corolla bilabiate, yellow, sometimes red-spotted, the tube funnelform, 14–23 mm long, exserted 4–7 mm beyond longest calyx tooth, the lobes entire, the palate raised and mostly closing throat; anthers included, glabrous, reflexed; stigma club-shaped. CAPSULES oblong, aristate, 5–8 mm long, included within closed calyx teeth. SEEDS oblong, brown. (Figs. 4A–B). [*Mimulus tilingii* Regel] —Stream channels: Coconino, Graham cos. (Fig. 9A); ca. 3050 m (10000 ft.); July; CA, CO, ID, MT, NV, WY; Can.

Erythranthe verbenacea (Greene) G. L. Nesom & N. S. Fraga (verbena-like). Scarlet Monkeyflower. —Perennial herbs, rhizomatous, sparsely villous with sessile or stipitate glands. STEMS erect or sometimes decumbent, 25–40 cm long. LEAVES sessile, glabrous to sparsely villous, the blades palmately veined, oblanceolate to narrowly lanceolate, 2–9(–13) cm long, 1–3.8(–7.5) cm wide; acute at the apex; margins irregularly serrate, sometimes with distinct reddish-brown to black zonation (Fig. 2D) across the middle of the blades. FLOWERS solitary or in pairs, the pedicels 3–11 cm long, villous; calyx actinomorphic, hispid, with darker veins, the tube 12–20 mm long, not inflated in fruit, the teeth subequal, 4–7 mm long, triangular, acuminate; corolla bilabiate, scarlet to orange-red, the tube narrowly funnelform, 25–35 mm long, exserted 10–20 mm beyond calyx teeth, the lobes entire; anthers exserted, the anther

sacs reflexed, combined horseshoe-shaped, white-villous; stigmas 2-lobed. CAPSULES oblong, acuminate, 12–16 mm long, included in calyx. SEEDS oval, brown to black. (Figs. 2C–D). [*Mimulus verbenaceus* Greene, *Mimulus cardinalis* var. *verbenaceus* Kearny & Peebles] —Moist to wet soil, usually by streams or lakes in the shade: Apache, Cochise, Coconino, Gila, Graham, Greenlee, Maricopa, Mohave, Pima, Pinal, Yavapai cos. (Fig. 9B); elevation 600–2500 m (2000–8000 ft); Mar–Oct; UT; Mex.

This species is very similar to *E. cinnabarina* but can be easily distinguished by the presence of reflexed or horseshoe-shaped anther sacs. The unique leaf zonation, common in plants from the Sycamore and Oak Creek drainages, can also be used to distinguish *E. verbenacea* from other red-flowered species. This taxon was often treated as a synonym or variety of *E. cardinalis*. Genetic studies (Beardsley et al. 2003) confirm its specific status and support *E. eastwoodiae* as its sister species, not *E. cardinalis* or *E. cinnabarina*.

Mimetanthe Greene

Kimberly Hansen

Annual herbs, 3–32(–48) cm tall, taprooted, glandular-pubescent to viscid-villous; STEMS erect, leafy throughout, unbranched to highly branched. LEAVES sessile, lanceolate to oblong, 1.5–10 mm wide; apex obtuse to acuminate; base cuneate to rounded. FLOWERS two per node, ebracteolate; pedicels 5–23 mm long; calyx (2–)4–11 mm long, not strongly inflated in fruit, bilabiate, the tube not angled, the lobes lanceolate, subequal, with apices acute; corolla nearly actinomorphic, 6.2–9 mm long, yellow, with two red to brown spots on lower lip, sparsely pilose inside tube throat, deciduous in fruit; fertile stamens 2(–4), included, didynamous, often with lower pair reduced to staminodes. CAPSULES more or less exserted from calyx at maturity, loculicidally dehiscent along distal 1/3 to 1/2 of both sutures, apically attenuate, glandular-puberulent, placentation parietal, the placentae fused at least proximally; seeds oblong to oval, reticulate. Monotypic genus distributed in w N. Amer. From Greek *mimetes* (an imitator) and *anthos* (flower) due to similarity to *Mimulus*.

Mimetanthe is easily separated from *Mimulus* (and *Erythranthe*) based on presence of parietal placentation and apically attenuate capsules, features it shares with *Diplacus*. *Mimetanthe* also has pustulate-glandular capsules, a unique feature not seen in the other Arizona species of Phrymaceae.

Mimetanthe pilosa (Benth.) Greene (hairy). Hairy Mimetanthe. (Figs. 1A–C). [*Mimulus pilosus* (Benth.) S. Watson] —Moist habitats such as stream banks, often growing in sandy soils: Gila, Graham, Maricopa, Mohave, Pima, Pinal, Yavapai cos. (Fig. 9C); 300 to 1900 m (980 to 6300 ft); Apr–Oct; WA to UT, and CA.

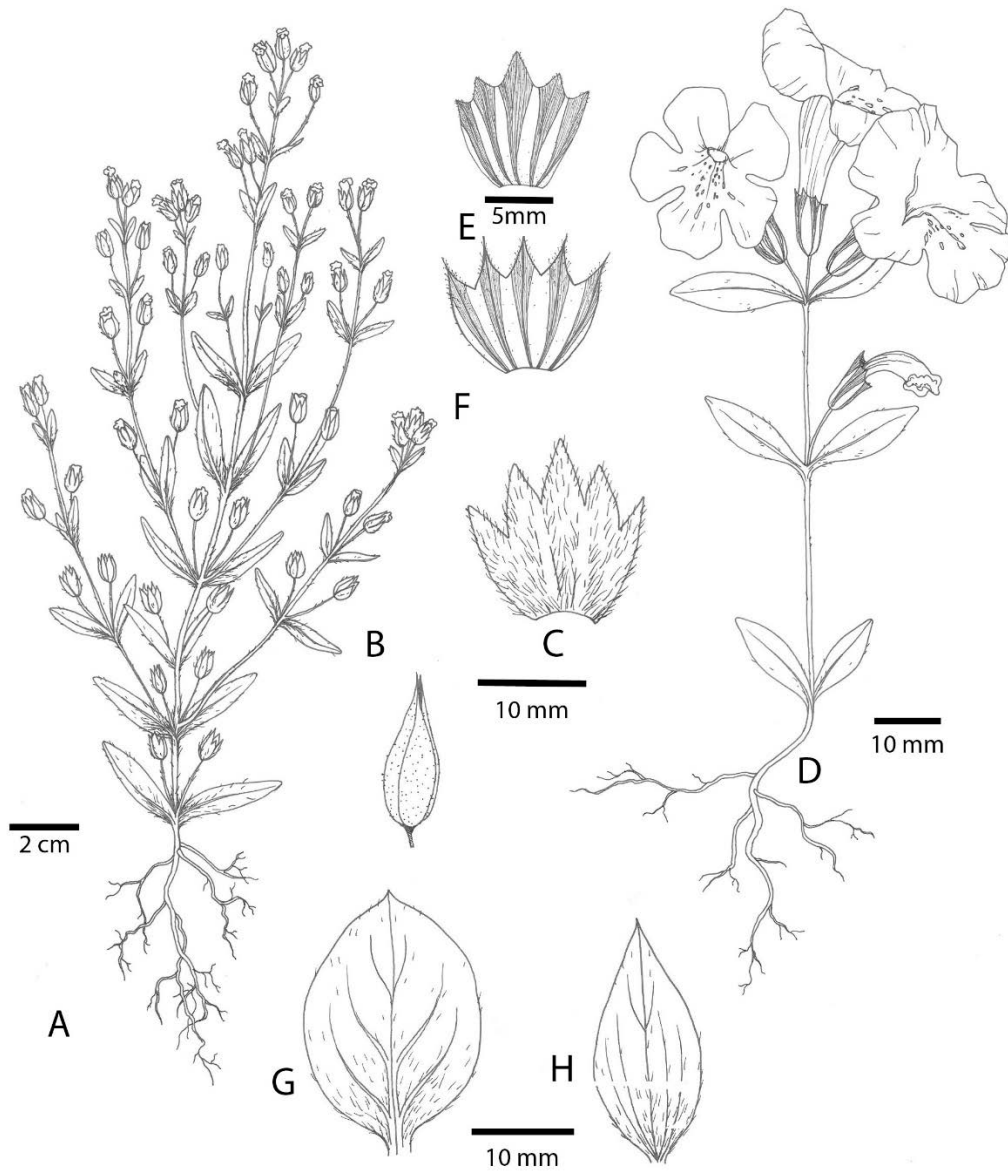
ACKNOWLEDGEMENTS

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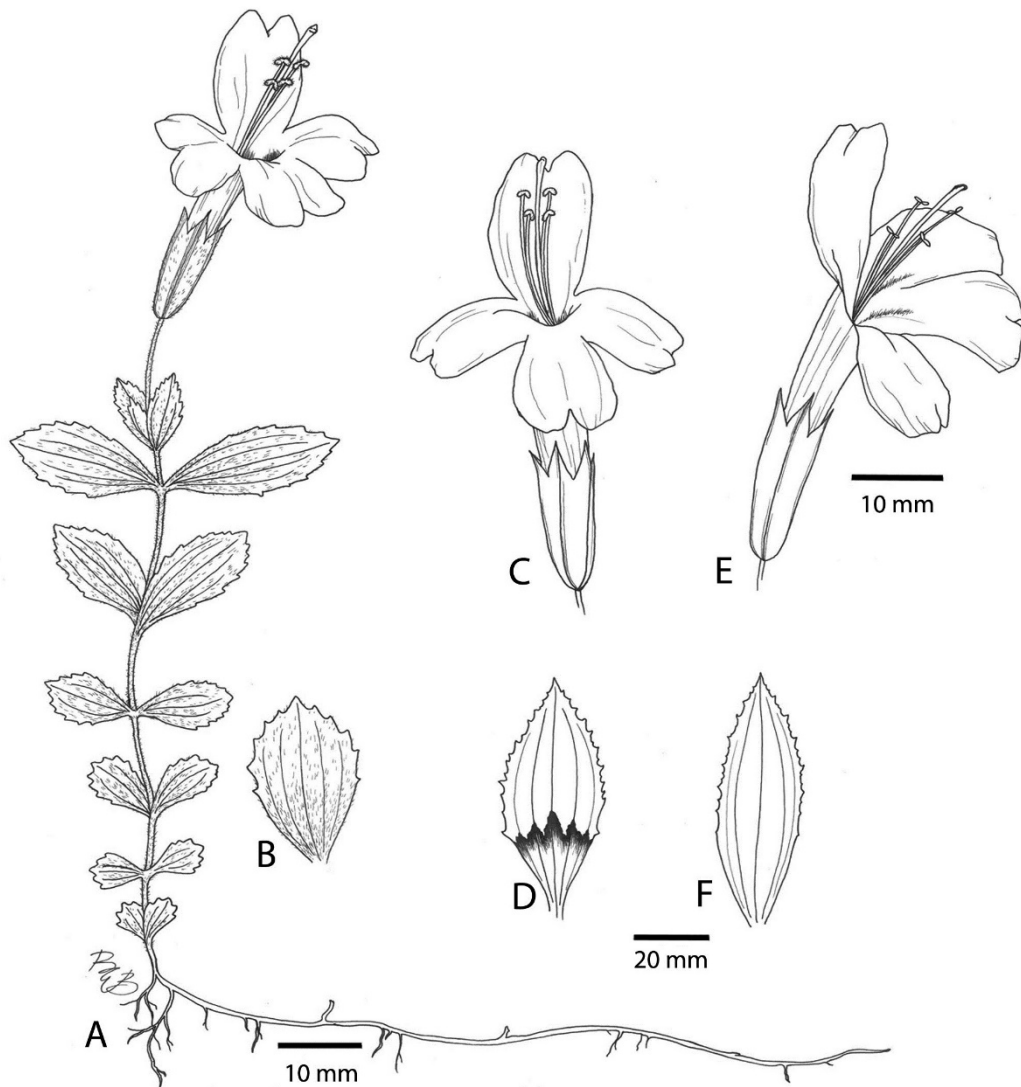
provided the digital images for the photo plate. We would also like to acknowledge the ASC and ASU staff, whose comments have helped to improve the quality of this publication.

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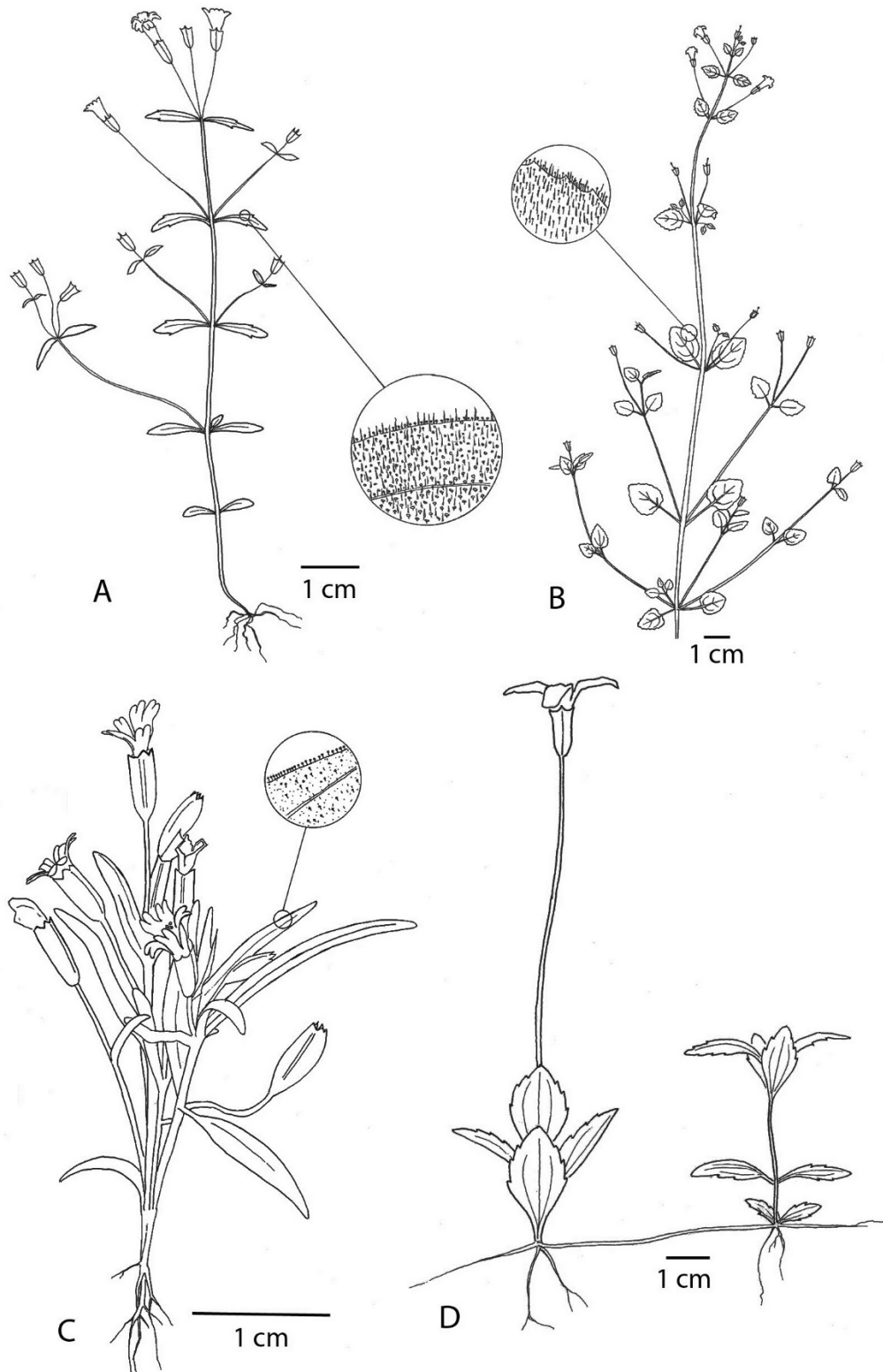
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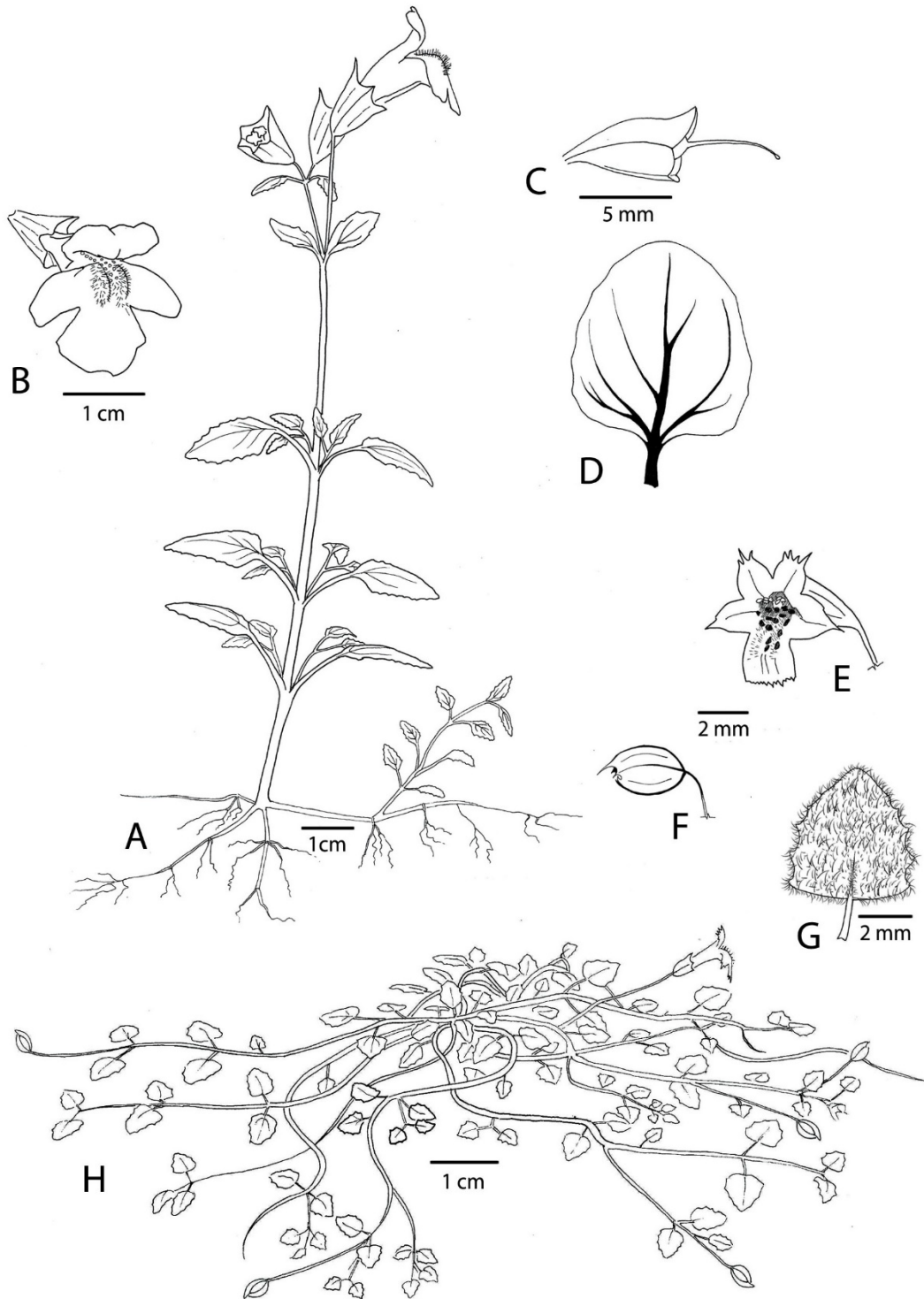
Phrymaceae. Figure 1. (A–C) *Mimetanthe pilosa*. (A) habit; (B) capsule; (C) calyx. (D–E) *Diplacus parryi*. (D) habit; (E) calyx. (F–H) *Diplacus bigelovii*. (F) calyx; (G) *D. bigelovii* subsp. *cuspidatus* leaf; (H) *D. bigelovii* subsp. *bigelovii* leaf.



Phrymaceae. Figure 2. *Erythranthe*. (A–B) *E. eastwoodiae*, (A) habit; (B) leaf; (C–D) *E. verbenacea*; (C) flower showing distinct reflexed anther sacs; (D) leaf with zonation; (E–F) *E. cinnabarina*; (E) flower; (F) leaf.



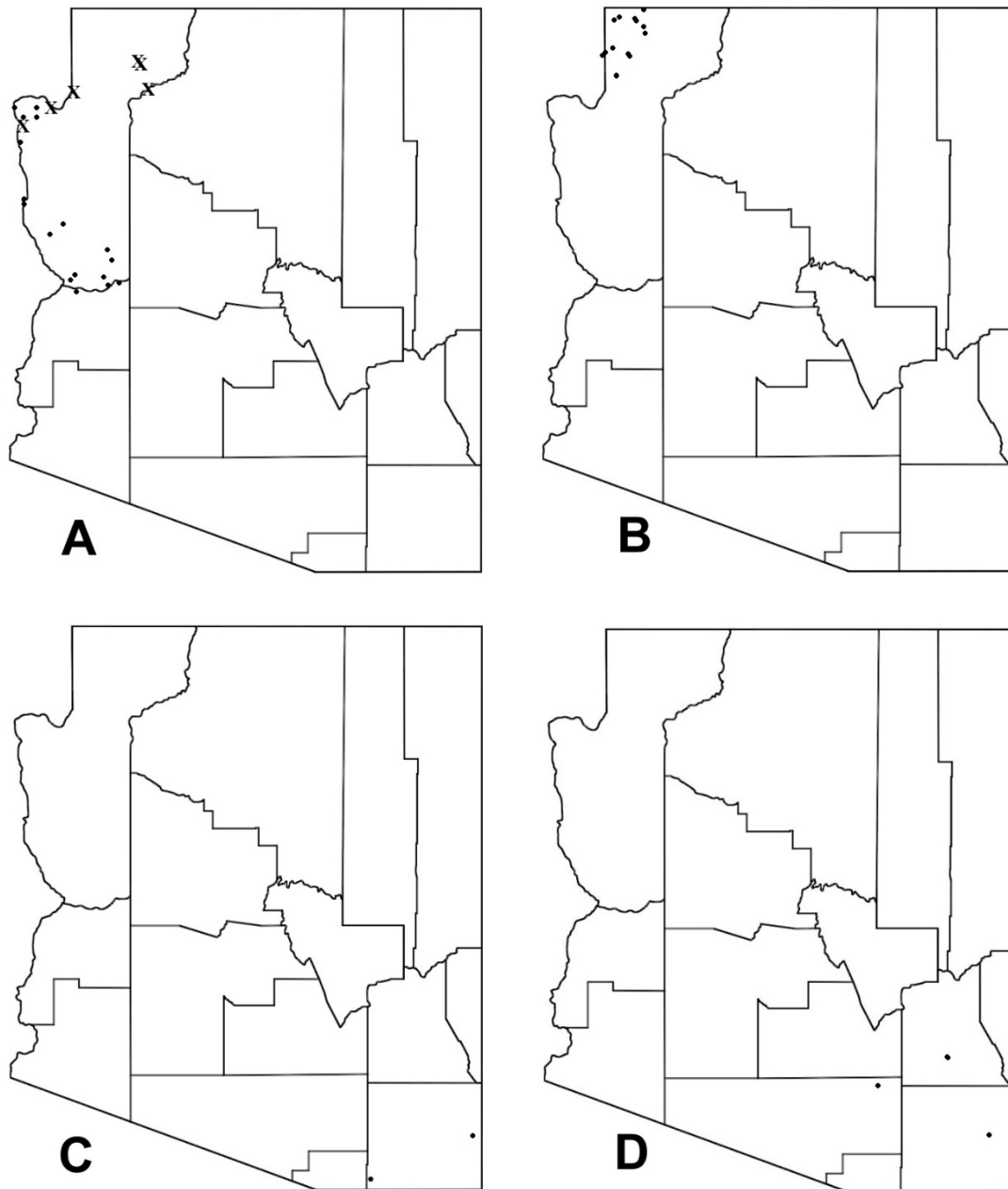
Phrymaceae. Figure 3. *Erythranthe* habit. (A) *E. rubella*; (B) *E. floribunda*; (C) *E. suksdorfii*; (D) *E. primuloides*. Insets vestiture.



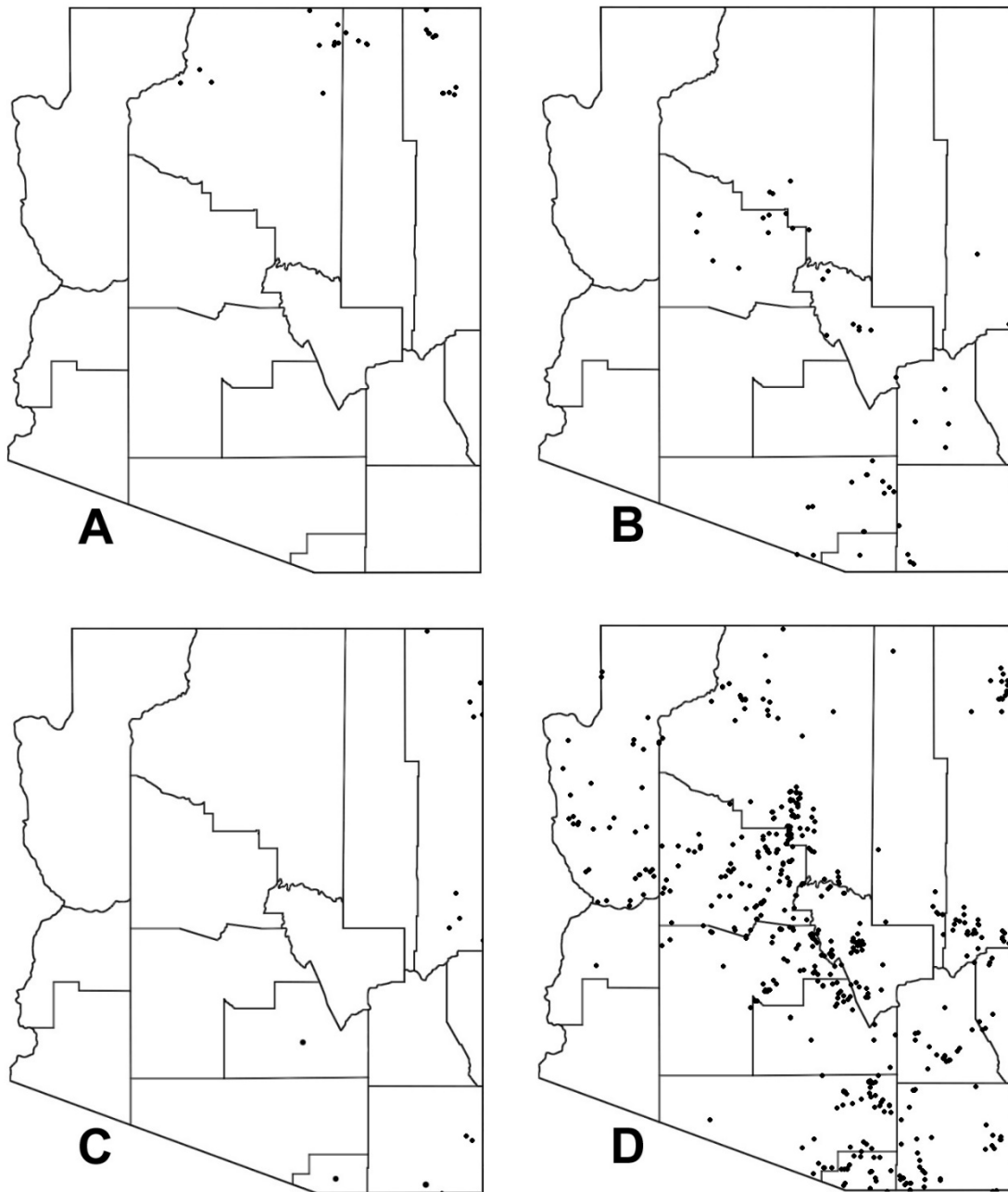
Phrymaceae. Figure 4. *Erythranthe* (A–B) *E. tilingii*; (A) habit; (B) flower; (C–D) *E. geyeri*; (C) calyx in fruit; (D) leaf; (E–H) *E. parvula*; (E) flower; (F) calyx in fruit; (G) leaf; (H) habit.



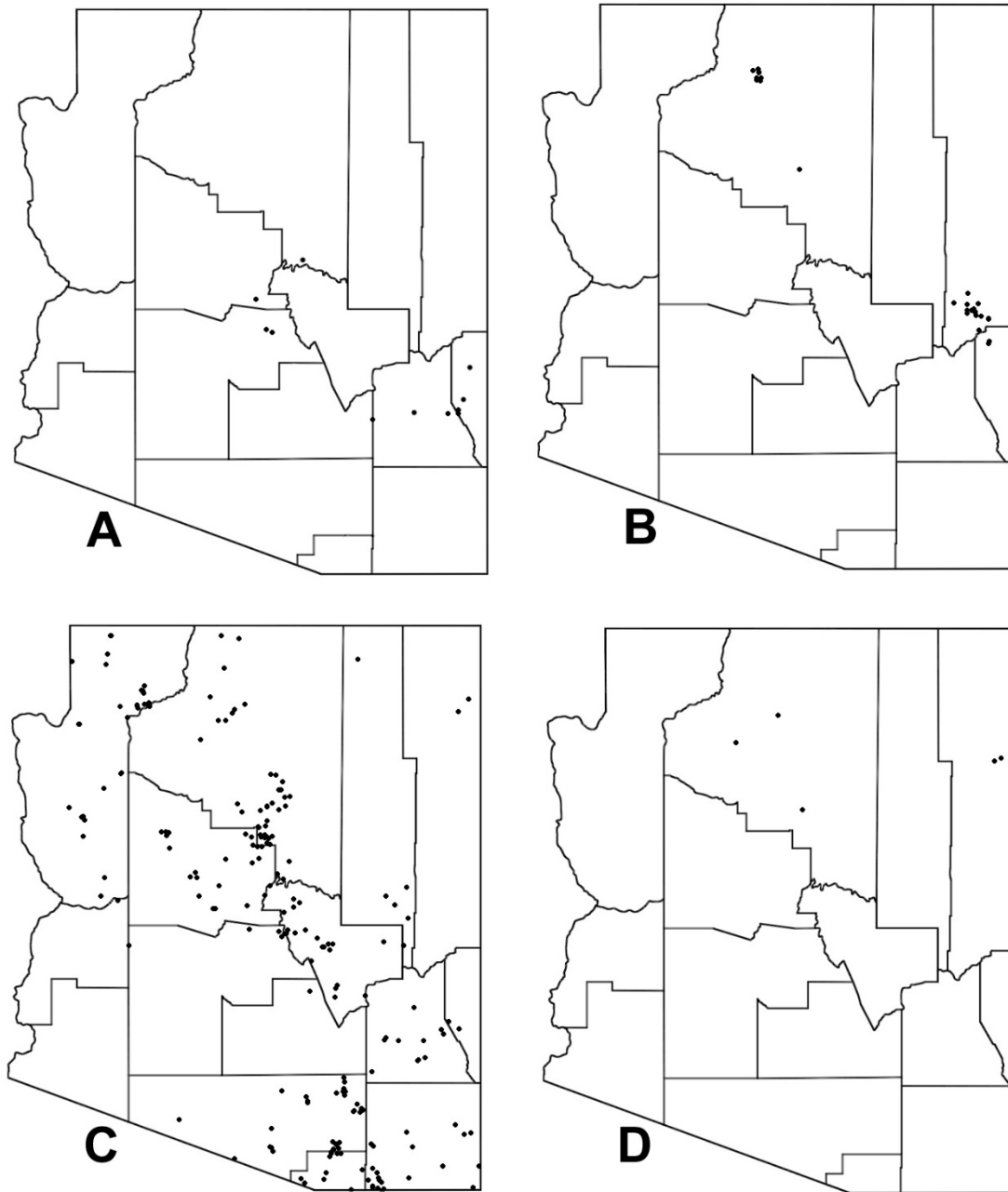
Phrymaceae. Figure 5. (A) *Diplacus bigelovii*; (B) *Erythranthe cinnabarina*; (C) *Erythranthe eastwoodiae*; (D) *Erythranthe floribunda*; (E–F) *Erythranthe geyeri*; (G–H) *Erythranthe guttata*; (I) *Erythranthe primuloides*; (J–K) *Erythranthe rubella*, (J) pink morph, (K) yellow morph; (L) *Erythranthe suksdorfii*. (all photos ©M. Licher)



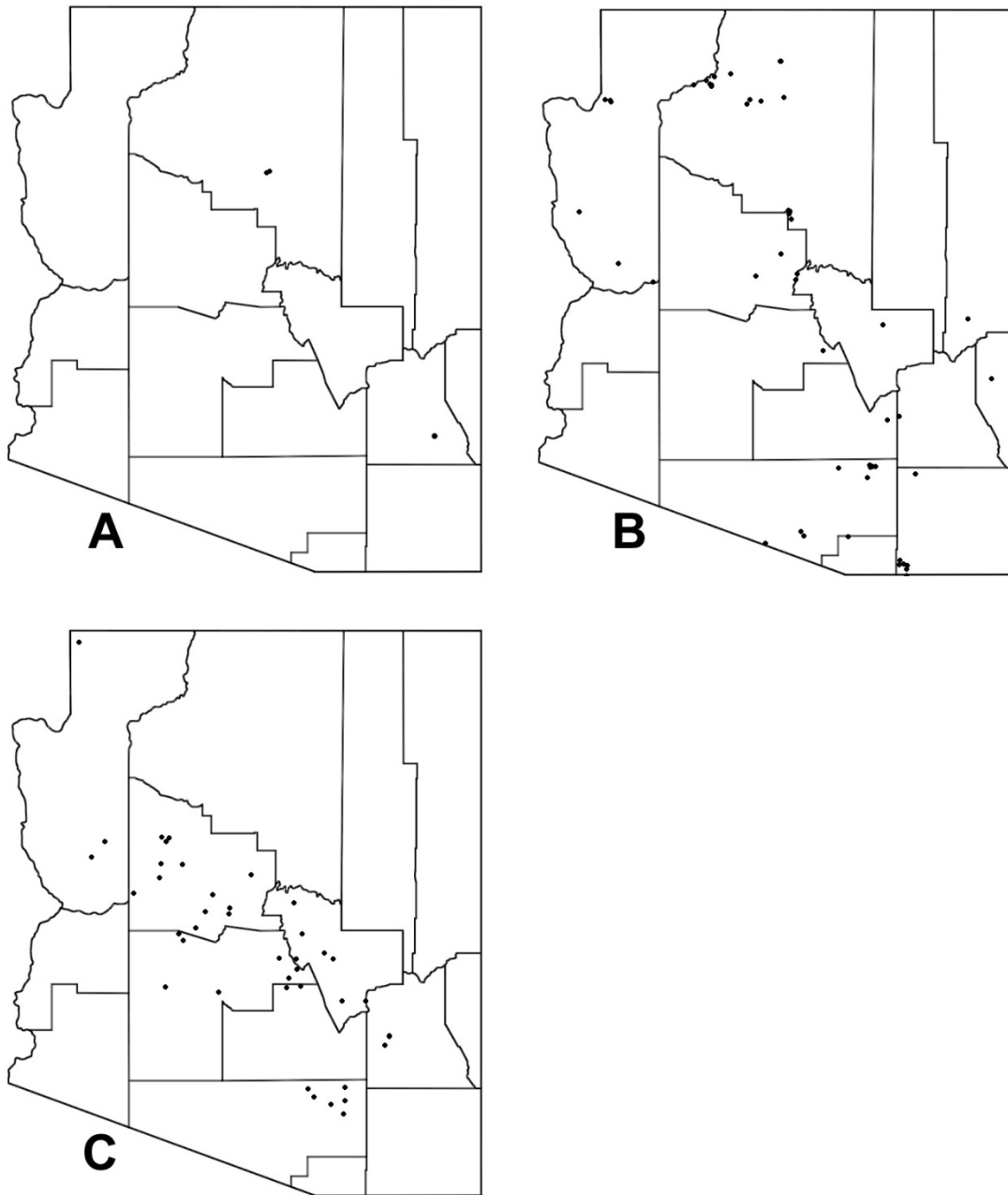
Phrymaceae. Figure 6. Distribution of: (A) *Diplacus bigelovii* var. *bigelovii* (circles) and *Diplacus bigelovii* var. *cuspidatus* (Xs) (B) *D. parryi*; (C) *Erythranthe calciphila*; (D) *E. cinnabarina*.



Phrymaceae. Figure 7. Distribution of: (A) *Erythranthe eastwoodiae*; (B) *E. floribunda*; (C) *E. geyeri*; (D) *E. guttata*.



Phrymaceae. Figure 8. Distribution of: (A) *Erythranthe parvula*; (B) *E. primuloides*; (C) *E. rubella*; (D) *E. suksdorfii*.



Phrymaceae. Figure 9. Distribution of: (A) *Erythranthe tilingii*; (B) *E. verbenacea*; (C); *Mimetanthe pilosa*.