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

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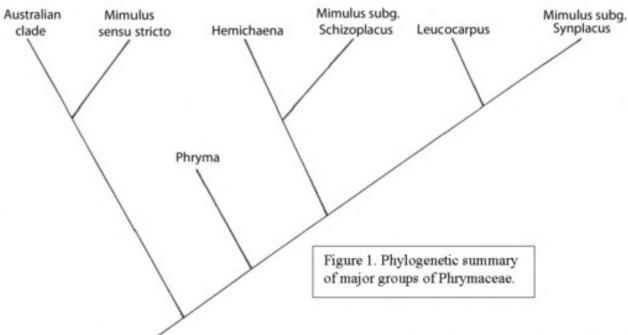
ABSTRACT

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 Burtt (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-Gratioleae, "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). Burtt (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. pachystyhus 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-oblanceolate 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 ghiesbrechtii A. Gray (= Mimulus rugosus). Gray did not cite a type for his new genus, in which he included B. ghiesbrechtii, B. coulteri, and B. rugosa. Thieret cited B. ghiesbrechtii 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 calvces. 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 subsessile, 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 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 stipitateglandular adaxially; inflorescence usually terminal, bracteate; corollas vellow
 - 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
 - 4. Corollas yellow, tube 13-15 mm long, included in or slightly longer than the calyx; 4. Corollas red to orange, tube 25-35 mm long, 2.5-3.5 times longer than the calyx, stamens
- 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. Calvces 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. Calvees 9-15 mm long. Corollas reddish orange, 2.5-3.5 cm long, tube 3 times longer than the calyx. Stamens barely or not exserted, anthers 2-2.5 mm long.

Ledges and rocky soil, limestone slopes, materral 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, Cieba 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 exserted, 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 Dasylirion-Agave-Cercocarpus-Fraximus 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!). 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. Calvees 5-8 mm long. Corollas yellow, tube 13-15 mm long, included in or slightly longer than the calyx. Stamens exserted, 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.

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 exserted, anthers 1.5-2 mm long.

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

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