***Mimulus aurantiacus* W. Curtis** bush monkeyflower
PHRYMACEAE (formally in SCROPHULARIACEAE)

Synonyms: *Diplacus aurantiacus* Jeps.
M. glutinosus Wendl.
D. latifolius Nutt.
D. leptanthus Nutt.

General Description.—Bush monkeyflower, or sticky monkeyflower, is a beautiful, erect to sprawling subshrub, that is named for its woody habit and typical "monkey-faced" flowers. Bush monkeyflower represents a complex assemblage of hybridizing forms with intergrading floral colors and morphologies. For this reason, the most recent taxonomic treatment lumps together all the species of woody monkeyflowers from California, excepting *M. clevelandii* Brandegee, under *M. aurantiacus* (Thompson 1993). The various taxa, sensu Munz and Keck (1968), are distinguished by stature, flower size and color, and range, but share similar leaf morphology. Given the taxonomic uncertainty, we describe *M. aurantiacus* sensu Munz and Keck. Then under "Range and Taxonomy," we provide a brief description of diagnostic differences and distributions of their other taxa that were treated as a single species complex by Thompson (1993).

Shrubs are erect, 6 to 12 dm tall, and the specific epithet "*aurantiacus*" refers to the often deep orange corollas (sometimes yellowish) that are 3.5 to 4.5 cm long. The simple, opposite, leaves are elliptic to narrowly-elliptic, with entire to serrulate margins that are often rolled under. Leaves are 2 to 8 cm long and dark green, and resinous above. Smaller leaves are clustered on shortened shoots in the axils of larger leaves. The lighter underside of leaves and the 2 to 2.5 cm long green, pleated calyx are covered with sticky glandular and nonglandular hairs. Flowers have a long floral tube, spreading limbs, and a large, two-lobed stigma. Plants are often sticky with glandular secretions.

Range and Taxonomy.—Recent phylogenetic work favors placement of woody monkeyflowers (section *Diplacus*) in *Mimulus* and transfers the genus from family Scropulariaceae to the Phrymaceae (Beardsley and Olmstead 2002). Bush monkeyflower (broad sense) ranges from the coast to coastal ranges to interior foothills from northwestern Baja California, northward to Mendocino County, California below 1,600 m and along the western foothills of the Sierra Nevada range. The underlying topography of coastal hills, interior valleys, and foothills is complex, as are the west to east and north to south gradients in temperature and rainfall. The correspondingly complex pattern of variation in bush monkeyflower may reflect once isolated and differentiated populations that have come into secondary contact and hybridized. The resulting patterns of genetic diversity do not match the patterns of morphological diversity (Beardsley and others 2003). The taxonomy is necessarily complex and may be resolved with detailed phylogeographic analysis. See Munz and Keck (1968) and Tulig (2000) for details of the geographic distribution of the following color forms (narrow sense).

The small, orange-flowered *M. aurantiacus* occurs in the foothills and coastal ranges north of Santa Barbara County. *M. a.* ssp. *australis* (McMinn) Munz has orange-yellow to buff or white corollas and occurs in interior San Diego County to Baja California. *M. aridus* (Abrams) A.L. Grant, the lowbush monkeyflower, has a yellow corolla, low, spreading habit to 4 dm tall, and occurs farther east in San Diego County to Baja Calfornia. *M. bifidus* Pennel has a larger orange corolla with larger, deeply-notched lobes, a somewhat spreading habit to 1 m tall, and occurs from coastal San Luis Obispo to Monterey County and along the western base of the Sierra Nevada from Placer into Butte and Plumas Counties. *M. flemingii* Munz has red corollas with limbs about half as long as other forms, is low growing from 1 to 6 dm tall, and is restricted to the Channel Islands. *M. longiflorus* (Nutt.) A. L. Grant, the southern bush monkeyflower (see figure), has an orange-yellow to salmon corolla, a long

and pubescent calyx (to 3.5 cm), is 3 to 12 dm tall, and occurs from central San Diego County through Riverside to San Bernardino County. A shorter, pale-yellow form [*M. l.* ssp. *calycinus* (Eastw.) Munz] occurs primarily farther inland in Riverside and western San Bernardino Counties. A red-corolla form (*M. l.* var. *rutilus* Grant) occurs mostly in interior Los Angeles County. Finally, *M. puniceus* (Nutt.) Steudel, the red bush monkeyflower, has a red corolla, short calyx (to 2.5 cm), and erect habit from 5 to 15 dm tall. It occurs on Catalina Island, coastal Orange County, and inland through the Santa Ana Mountains to southwestern Riverside County south into Baja California.

Hybridization.—All bush monkeyflowers have n = 10 chromosomes and crosses among them produce viable progeny. Natural, putative hybrids between forms have been hypothesized based on morphology (Munz and Keck 1968, Wells 1980, Grant 1993, Tulig 2000). Preliminary phylogenetic work suggests widespread introgression among forms (personal communication with Paul Beardsley, Colorado College, CO). Grant (1993) examined pollinators in relation to several floral forms (equals species of *Diplacus* in his paper) and postulated that the populations with different floral forms would be partially reproductively isolated. He hypothesized that the red-colored *D. puniceus* Nutt. and salmon *D. longiflorus* Nutt. were primarily hummingbird-pollinated, and that *D. calycinus* Eastw. (*M. l.* var. *calycinus*) with pale yellow flowers and long tube) were hawkmoth-pollinated. He found that habitats interdigitated and resulted in *D. puniceus* and *D. calycinus* populations overlapping in distribution, with *D. longiflorus* habitat forming a connecting link between the different forms. He hypothesized that the intermediate nature of *D. longiflorus* suggested past hybridization of *D. puniceus* and *D. calycinus*.

Tulig (2000) analyzed floral and vegetative variation throughout the geographic range of bush monkeyflowers and found statistical evidence for hybrid populations that were intermediate between parental forms. For example, in San Diego County, putative hybrid populations were intermediate between *M. puniceus* (coastal form) and *M. aurantiacus* ssp. *australis* (inland form), consistent with analysis of Waayers (1996). In the region between the San Gabriel and San Bernardino Mountains, putative hybrids were intermediate between *M. longiflorus* ssp. *calycinus* (lemon yellow corolla) and *M. longiflorus* (salmon corolla).

Ecology.—Bush monkeyflowers occur in areas with cool moist winters and warm to hot, dry summers. They grow on rocky hillsides and cliffs, usually on the border of chaparral or sage scrub, or in open foothill-woodland forest. The roots are fibrous, less than 2 m deep, with feeder roots concentrated within the first 8 cm of soil (Hellmers and others 1955). There is evidence for differentiation and local adaptation in morphological and physiological characters relating to water use. For example, differences in wood anatomy among forms and among populations are correlated with habitat (Michener 1983). Plants from mesic habitats have relatively few, large vessel-elements, while plants from xeric habitats have many, small vessel-elements. Under humid, low-stress conditions, both mesic-adapted and xeric-adapted populations had high water-use efficiency and maintained a high rate of photosynthesis relative to transpiration (Mooney and Chu 1983). Plants from xeric populations had high water-use efficiency under low relative humidity, while the efficiency of coastal plants diminished rapidly with decreasing relative humidity.

The primary herbivore of bush monkeyflower is a specialist butterfly *Euphydryas chalcedona* Doubleday and Hewitson. The timing of growth of both plants and the butterfly is linked to water availability. Emergence of larvae from diapause is synchronized with the initiation of leaf growth. The leaves produce a resin that inhibits the growth of the larvae. During the growing season the youngest leaves have the highest nitrogen (N) content, the highest carbon gain, and the highest resin content. Growth rate of the larvae increases with increasing N but decreases with increasing resin content (Lincoln and others 1982). Larvae feed initially on young leaves with high nutritional value, then switch to older leaves with lower resin content. During flowering, N is translocated from the leaves, and larvae stop feeding (Mooney and others 1981).

Such studies demonstrate physiological trade-offs in resource allocation to growth, reproduction, or defense. Han and Lincoln (1994) found significant heritability and maternal effects for resin content within one population, and they found negative genetic and phenotypic correlations between resin production and growth rate. This indicates potential trade-offs between traits during selection. Leaf resin content varies among populations, but little is known about geographic differentiation in such trade-offs.

Hare (2002) found that nearly 30 percent of the dry weight of leaves is resin. In a common garden experiment, he examined the chemistry and relative quantities of important resin components for six populations of bush monkeyflower from a range of environments and that differed in attack by *E. chalcedona*. The populations differed in chemical components of the resins but not in the pattern of insect attack. This study followed Thompson's (1993) classification and did not mention if there were differences in floral morphology among the

populations. The collection locations could have represented at least three species or subspecific taxa following Munz and Keck (1969) or Tulig (2000).

Emergence and Growth.—Seedlings emerge in the cool rainy season, and most growth is in winter and spring. Plants can reach reproductive maturity in a single growing season, with flowering primarily from mid spring to early summer. The capsules mature in summer, and the many, tiny seeds (about 1 mm long, half as wide and nearly flat) disperse by gravity and wind. Plants become dormant in the summer dry season and shed many leaves by fall. Leaf production begins after the first fall rain and ends near the beginning of July (Mooney and others 1981). A large and relatively constant proportion of carbon and nitrogen are allocated to reproduction, and reproductive structures supply some of their own carbon (Alpert and others 1985). Both growth and reproduction are primarily water limited.

Reproduction.—Bush monkeyflowers are pollinated by diverse flower visitors, and the dominant pollinators vary with color form and location. This may reflect local differentiation, or the relative abundances of pollinators. Fetscher and Kohn (1999) reported Anna's hummingbird as the primary pollinator of a red flower form in San Diego County, California, with black-chinned, Costa's, and rufous hummingbirds as occasional visitors. Bromer and others (1990) reported that *M. longiflorus* was "generally but not exclusively" pollinated by Black-chinned and Anna's hummingbirds. Six populations from the Santa Monica Mountains varied in floral form, sucrose content of nectar, and anther-stigma separation. Populations with high pollinator diversity but low visitation rates had shorter corolla tubes and lower sucrose:hexose ratios in nectar than populations with less diverse pollinators. In a different population of *M. longiflorus*, Eckert (1970) found that almost all pollination was done by solitary bees and that Anna's hummingbirds were only occasional visitors. Most pollination was effected by bees in the genus *Osmia* and carpenter bees in *Ceratina*. Both visited multiple flowers per plant, and self-pollination appeared common. Eckert also found that selfed flowers produced fewer capsules per plant and had more aborted ovules than outcrossed flowers.

Horticulture.—The bush monkeyflowers and their horticultural hybrids have striking flower colors, produce masses of flowers, and are popular ornamental plants (Schmidt 1980, Perry 1992, Keator 1994). Plants can be grown from seeds or cuttings, but plants grown from seed tend to live longer (personal communication with Steve Morgan, University of California Riverside Botanic Garden, CA). The shrubs grow best in full sun to light shade. Flowering and leaf production may be extended by summer watering in more arid regions. However, Atkinson and others (1988) found that watering may increase susceptibility to atmospheric pollution in the dry season. In summer, unwatered plants drop most leaves, are not photosynthetically active, and take up little SO_2, while watered plants retain their leaves, are photosynthetically active, and take up SO_2.

Growth and Management.—Bush monkeyflowers have been planted along highways corridors and are used in habitat restoration. There are about 145 million seeds/kg (Mirov and Kraebel 1939). Seeds will germinate without pretreatment (Mirov and Kraebel 1939, Schmidt 1980), but seeds need to be exposed to light and leachate from charred wood may improve germination slightly (Keeley 1987). For pot culture, the tiny seeds should be sown on the surface of the soil and kept moist until seedlings emerge. Outdoors, they should be planted with shallow broadcasting methods. The phylogenetic relationships among populations and the fitness effects of translocations and hybridization are not yet known, and there are no published studies on population genetic patterns. However, there is a complex pattern of geographic variation, genetic differentiation of floral form and resin chemistry, local adaptation to moisture environments, and extensive ability to hybridize. Consequently, attention should be made of flower color and habitat matching when obtaining seeds for large planting projects. Use of regionally local seed sources for planting projects can mitigate unknown fitness consequences of out of range plantings. A careful analysis of hybrid zones and the fitness of hybrids is needed to understand if hybridization following translocations will cause decreases in fitness of adjacent wild populations.

Benefits.—Bush monkeyflowers are important plants for water-wise landscaping and revegetation projects. They provide nectar to hummingbirds and large bees and are an important larval host of the checkerspot butterfly.

References

Alpert, P., E.A. Newell, C. Chu, J. Glyphis, S.L. Gulmon, D.Y. Hollinger, N.D. Johnson, H.A. Mooney, and G. Puttick. 1985. Allocation to reproduction in the chaparral shrub, *Diplacus aurantiacus*. Oecologia 66: 309-316.

Atkinson, C.J., W.E. Winner, and H.A. Mooney. 1988. Gas exchange and SO_2 fumigation studies with irrigated and unirrigated field grown *Diplacus*

aurantiacus and *Heteromeles arbutifolia*. Oecologia 75: 386-393.

Beardsley, P.M. and R.G. Olmstead. 2002. Redefining Phrymaceae: the placement of *Mimulus*, tribe Mimuleae, and *Phryma*. American Journal of Botany 89: 1093-1102.

Beardsley, P.M., S.E. Schoenig, J.B. Whittall, and R.G. Olmstead. 2003. The radiation of *Mimulus* (Phrymaceae) in western North America. American Journal of Botany. In Press.

Bromer, W., J. Barnette, J. Lee, D. Green, and V. Ervin. 1990. Genetic variation within and among populations of *Mimulus longiflorus* in the Santa Monica Mountains, CA: consequences of breeding system and pollination. Bulletin of the Ecological Society of America 71: 103.

Eckert, J.R. 1970. Pollination studies in *Mimulus longiflorus* (Nutt.) Grant. Master's thesis. California State University, Los Angeles. 88 p.

Fetscher, A.E. and J.R. Kohn. 1999. Stigma behavior in *Mimulus aurantiacus* (Scrophulariaceae). American Journal of Botany 86: 1,130-1,135.

Grant, V. 1993. Origin of floral isolation between ornithophilous and sphingophilous plant species. Proceedings of the National Academy of Sciences of the United States of America 90: 7729-7733.

Han, K. and D.E. Lincoln. 1994. The evolution of carbon allocation to plant secondary metabolites: a genetic analysis of cost in *Diplacus aurantiacus*. Evolution 48: 1,550-1,563.

Hare, J.D. 2002. Geographic and genetic variation in the leaf surface resin components of *Mimulus aurantiacus* from southern California. Biochemical Systematics and Ecology 30: 281-296.

Hellmers, H., J.S. Horton, G. Juhren, and J. O'Keefe. 1955. Root systems of some chaparral plants in southern California. Ecology 36: 667-678.

Keator, G. 1994. Complete Garden Guide to the Native Shrubs of California. Chronicle Books, San Francisco, CA. 314 p.

Keeley, J.E. 1987. Role of fire in seed germination of woody taxa in California chaparral. Ecology 68: 434-443.

Lincoln, D.E., T.S. Newton, P.R. Ehrlich, and K.S. Williams. 1982. Coevolution of the checkerspot butterfly *Euphydryas chalcedona* and its larval food plant *Diplacus aurantiacus*: larval response to protein and leaf resin. Oecologia 52: 216-223.

Michener, D.C. 1983. Systematic and ecological wood anatomy of Californian Scrophulariaceae. I. *Antirrhinum*, *Castilleja*, *Galvezia*, and *Mimulus* sect. *Diplacus*. Aliso 10: 471-487.

Mirov, N.T. and C.J. Kraebel. 1939. Collecting and handling seeds of wild plants. Civilian Conservation Corps, Forestry Publication 5. United States Government Printing Office, Washington, D.C.

Mooney, H.A., and C. Chu. 1983. Stomatal responses to humidity of coastal and interior populations of a Californian shrub. Oecologia 57: 148-150.

Mooney, H.A., K.S. Williams, D.E. Lincoln, and P.R. Ehrlich. 1981. Temporal and spatial variability in the interaction between the checkerspot butterfly, *Euphydryas chalcedona* and its principal food source, the Californian shrub, *Diplacus aurantiacus*. Oecologia 50: 195-198.

Munz, P.A. and D.D. Keck. 1968. A California Flora with Supplement. University of California Press, Berkeley, CA. 1,681 + 224 p.

Perry, B. 1992. Landscape Plants for Western Regions: an Illustrated Guide to Plants for Water Conservation. Land Design Publishing, Claremont, CA. 318 p.

Schmidt, M.G. 1980. Growing California Native Plants. University of California Press, Los Angeles.

Thompson, D.M. 1993. *Mimulus.* In: J.C. Hickman, ed. The Jepson Manual: Higher Plants of California. University of California Press, Ltd., Los Angeles, CA. p. 1,037-1,046.

Tulig, M. 2000. Morphological variation in *Mimulus* section *Diplacus* (Scrophulariaceae). Masters Thesis, Department of Biological Sciences, California State Polytechnic University, Pomona, CA. 82 p.

Waayers. 1996. Hybridization, introgression, and selection in *Mimulus aurantiacus* ssp. a*ustralis* and *M. puniceus*. Master's thesis. San Diego State University, San Diego, CA. 77 p.

Wells, H. 1980. A distance coefficient as a hybridization index: an example using *Mimulus*

longiflorus and *M. flemingii* (Scrophulariaceae) from Santa Cruz Island, California. Taxon 29: 53-65.

Arlee M. Montalvo, Plant Population Biologist, Department of Botany and Plant Sciences, University of California, Riverside, CA 92521-0124 and Paul A. McMillan, Coordinator, Biology Department, Capilano College, 2055 Purcell Way, North Vancouver, British Columbia, Canada V7J 3H5