DIPLACUS GRANITICOLA, SP. NOV. (PHRYMACEAE), FROM GRANITE CRACKS AND CREVICES IN THE CALIFORNIA SIERRA

STEVE SCHOENIG

UC Davis Center for Plant Diversity 1026 Sciences Laboratory Building 505 Hutchison Drive Davis, California 95616 seschoenig@gmail.com

> GUY NESOM 2925 Hartwood Drive Fort Worth, Texas 76109 guynesom@sbcglobal.net

ABSTRACT

Diplacus graniticola Schoenig, **sp. nov.**, is segregated from *Diplacus layneae*. The new species is true in habitat to granite cracks and crevices in the California Sierra from Tuolumne Co. south through Mariposa, Madera, Fresno, and Tulare counties to Kern Co. and is partially sympatric with typical *D. layneae* in that area. Typical *D. layneae* occurs in various kinds of soil, including serpentine, and has a broader range in California. *Diplacus graniticola* is morphologically distinct from *D. layneae* in its shorter and more numerous nodes, vestiture of longer hairs, calyces without white-membranous intercostal areas and broadly darkened ribs, and distinctive corolla markings. Further variation within *D. layneae* (after the exclusion of *D. graniticola*) remains to be clarified, especially in the North Coast Ranges.

Significant variation in the California endemic *Diplacus (Mimulus) layneae* (Greene) Nesom was noted by Thompson (2005, p. 120): "In the Yosemite National Park area (Tuolumne and Mariposa counties) and southward, *M. layneae* is differentiated into two forms that are known to co-occur The first is a more elongate-pubescent form with a compact habit, growing almost exclusively from granite crevices. The second is a more puberulent form with an open habit, growing on granitic soils. The crevice-inhabiting form usually has more conspicuous radial markings on its spreading corolla limb and some yellow on the throat floor at the mouth. The form that occurs on soils has much more vague markings on its more weakly spreading corolla limb and a throat floor that is mostly white, washed with yellow only deep within the tube-throat, most resembling *M. layneae* from elsewhere in its range. The crevice-inhabiting form likely contains genes from *M. nanus* var. *mephiticus* [= *Diplacus mephiticus* (Greene) Nesom]."

Further field experience (Schoenig) confirms the distinction in habitat and morphology between these two expressions of *Diplacus layneae*. Thompson was not explicit regarding the evidence for his speculation about the genetic contribution from *D. mephiticus*, (although on specimen labels, he noted that the crevice-inhabiting form probably was a hybrid with *D. mephiticus*), but whatever their origin, the granite-crack plants have a coherent geographical range and are consistently distinct in morphology from typical *D. layneae* as well as other *Diplacus* species, even in areas of sympatry. They are recognized here as a distinct species.

DIPLACUS GRANITICOLA Schoenig, **sp. nov. TYPE: California**. Tuolumne Co.: N of Mather along Evergreen Road, Stanislaus National Forest-Yosemite National Park boundary, granite outcrops below road, 1400 m, growing only from granite crevices; common but local, hundreds of plants seen, 15 Jun 1988, *D.M. Thompson 953*, voucher for chromosome count of n = 8 (holotype: RSA, Figure 1; isotypes: JEPS!, OBI). Label data also include this: "Corolla magenta with 5 red-purple lines radiating from throat onto midveins of lobes and two red-purple

splotches at the 2 sinuses that separate the 2 upper from the 3 lower lobes; the 2 throat floor ridges yellow, at least partially bordered by red-purple. Red-purple markings may fuse partially. Probably a hybrid with *M. nanus* var. *mephiticus*."

Similar to *Diplacus layneae* in its dark-drying herbage, vestiture of gland-tipped hairs, flowers at all nodes and usually 2 per node, calyx strong ribbed and plicate, not inflated, corollas lavender to magenta, nearly regular to weakly bilabiate, and ciliate anthers; different from *D. layneae* in its (1) fidelity to cracks in granite, (2) flowering nodes 4-15(-20) in mature plants, distal internodes shorter than leaves, (3) vestiture of longer hairs, (4) calyces without white-membranous intercostal areas and broadly darkened ribs, and (5) distinctive and consistent corolla markings. See key couplet below for details.



Figure 1. Diplacus graniticola, holotype (rearranged for the illustration), RSA.

Herbs, annual, herbage usually drying distinctly darkened. **Stems** erect, 6-12(-15) cm, villous with gland-tipped hairs 10–16 mm. Leaves mostly cauline, relatively even-sized, 20–40 x 4– 12 mm; petiole weakly delimited; blade mostly lanceolate to ovate-lanceolate, margins entire, rarely with a few shallow teeth distally, apex rounded to obtuse or acute, surfaces of proximal often glabrate and purplish abaxially, distal green, vestiture. Flowers 2 per node, or 1 or 2 per node on a single plant, commonly at all nodes, chasmogamous. Fruiting pedicels 1-3 mm. Calyces 8-12 mm, not inflated in fruit, glandular-villous, ribs narrow, strongly raised, sometimes darkened, tube strongly plicate, intercostal areas green to purple, not membranous, lobes subequal, triangular, erect, lobe apex acute, not indurate. **Corollas** nearly white or pale lavender to pinkish or pale to dark magenta, each lobe consistently with a dark medial line extending to near the lobe tip, throat with a dark red or purple splotch at the junction of each abaxial lobe and adjacent lateral lobe, throat floor sometimes with two adjacent white splotches at lateral lobe bases, palate ridges yellow, sparsely villous, tubethroat 15–20 mm, limb 10–16 mm wide, weakly bilabiate. Anthers included, ciliate. Styles glandular-puberulent; stigma included, lobes weakly unequal, abaxial 1.5 times as long as adaxial. **Capsules** 6–10 mm. **Chromosome number**, 2n = 16 (*Thompson 889*, Fresno Co.; *Thompson 953*, Tuolumne Co.). See Figures 3-13 for morphological and ecological contrasts with D. layneae.

Flowering Apr–Sep. Granite cracks and crevices; 300–2134 m; Calif. (Fresno, Madera, Mariposa, Tulare [rare], and Tuolumne cos.).

Representative collections examined. California. Fresno Co. Dunlap, 1850 ft, 9 May 1954, Barneby & Howell 11413 (CAS); along San Joaquin River at Kerckhoff Reservoir bridge, 1050 ft, 10 May 1954, Barneby & Howell 11444 (CAS); 1 mi NW Auberry, Mariposa Quadrangle, 2300 ft, 5 Jun 1935, Bullard 24 (UC); Huntington Lake, 6986 ft, 1 Jul 1926, McDonald s.n. (CAS); overlooking Big Sandy Valley (summit of small ridge on E face of mountain, property of (adjacent to) Ella Carter), Black Mountain, 2500 ft, 14 May 1955, Bacigalupi et al. 5096 (JEPS); Jose Basin Sierra Natl Forest, San Joaquin River watershed, 3600 ft, 11 May 1959, Bacigalupi et al. 7113 (JEPS); near road summit between Shaver Lake and Dinkey Creek, 5 Aug 1944, Quick 68 (CAS); vicinity of Fence Meadow Lookout, Sierra Nevada, ca. 0.1 mi off W side of Forest Service Road 10S69 and 1.25 mi S of junction of Fence Meadow Lookout Road, 4300 ft, 8 Jul 1977, Rubtzoff 9104 (CAS); Sequoia Natl Forest, 100 meters W of Hume Lake Rd, where USFS campground road forks off at Hume Lake, 5300 ft, 14 Jun 1998, Schoenig 98 (UC): 1.7 road mi E of USFS Sugarloaf Road jct, along Auberry Road, 1.0 rd mi E of Meadow Lakes, 0.7 rd mi E of Alva Snow Road jct, 4428 ft, 19 Jul 1986, Thompson 662 (JEPS, RSA); Huntington Lake, between and around Kinnikinnick and Catavee Campgrounds, 6986 ft, 20 Jul 1986, Thompson 668 (RSA); 0.7 mi W Dunlap along Dunlap Road, 1820 ft, 12 May 1988, Thompson 889 (JEPS, RSA); 0.5 mi S USFS Road 10S69 along USFS Hwy 9 (Hwy 7 on map), Haslett Basin, 2132 ft, 9 May 1992, Thompson 1051 (JEPS, RSA); 1/4 mi E Auberry Mission Road (Jose Basin Road), 2000 ft, 13 May 1966, Walker 66013 (JEPS 53963); above Trimmer Springs, 16 May 1937, Winblad s.n. (CAS); 0.4 mi W Dunlap (w slope of Sierra), Sierra Nevada, 1900 ft, 16 May 33, Wolf 4751 (RSA, UC); ca. 40 km NE of Fresno (FSC), Sierra Natl Forest, 2.0 km NE of Tollhouse, Dry Creek drainage, top of Tollhouse Rock, 2935 ft, 1 Jun 1996, York 784 (CAS); ca. 42 km NE of Fresno (FSC), 4.3 km NE of Tollhouse, Sierra Natl Forest, near end of Cripe Road, 3526 ft, 18 Apr 1997, York 1714 (CAS); ca. 15 km NE of Fresno (FSC), Dry Creek basin, midslope on Owens Mountain, 754 ft, 29 May 1998, York 2148 (CAS). Madera Co.: 2 mi W of Oakhurst, 2200 ft, 11 May 1954, Barneby & Howell 11451 (CAS); 2 mi S of Rd. 415 (on Rd. 400), 7 May 1960, Broome & Olsen s.n. (JEPS); Raymond, 9 May 1925, Eastwood 12593 (CAS); along the 4 WD road between Little Shuteye Pass and Shuteye Peak Lookout, Chiquito Ridge, second switchback above saddle, 6900 ft, 2 Jul 1988, Shevock 11848 (CAS 2 sheets). Mariposa Co.: Mormon Bar, 26 May 1895, Congdon s.n. (UC); due E of Silver Bar Rd. (0.3 mi from jct with Ben Hur-Mormon Bar Rd. between sources of Humbug and Mariposa Creeks), Greenamyers Hill, 2000 ft, 11 May 1980, Hamon 80 (UC); Yosemite Natl Park, 4500 ft, no date, Moncrief & Mowbray 74 (UC). Tulare Co.: N of Bear Creek (probably S of Badger near Adams Flat and Dry Creek), 1900 ft, 1 May 1896, Purpus 1765 (UC). Tuolumne Co.: near Wapama Falls, Yosemite Natl Park, Hetch-Hetchy, 4050 ft, 17 May 1986, Botti 267 (JEPS); Yosemite Natl Park, along the Hetch-Hetchy Trail, N side of Hetch-Hetchy Valley, 4050 ft, 16 May 1989, Botti 314 (JEPS, RSA); road to Hetch Hetchy 2.8 mi NE of Mather, 5100 ft, 5 Aug 1980, Ertter & Strachan 3938 (CAS); HetchHetchy, 3700 ft, 27 Jul 1909, *Jepson 3417* (JEPS); Mather, 4592 ft, 3 Jun 1931, *Keck 1205* (CAS); Mather, 4592 ft, 3 Jun 1931, *Keck 1206* (CAS, RSA); N of Hetch Hetchy, Sierra Nevada, Yosemite Natl Park, Miguel Meadows, 4050 ft, 21 Jul 1937, *Mason 11559* (UC); Stanislaus Natl Forest 0.2 mi W of Hetch Hetchy Rd, 1.0 mi NE of Mather (across from Natl Park Sign), 4921 ft, 24 May 1998, *Schoenig 98* (UC).

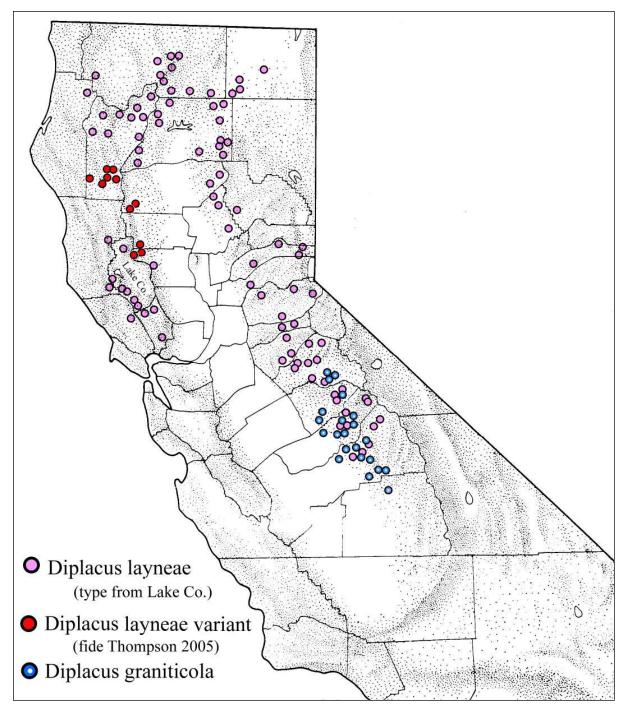


Figure 2. Distribution of *Diplacus graniticola*, typical *D. layneae*, and a variant of *D. layneae* hypothesized by Thompson (2005) to be a *D. layneae/D. nanus* hybrid. Distributions are drawn from published records from Thompson (2005), specimen records summarized in the California Consortium of Herbaria, and study of collections at UC-JEPS and CAS-DS. The type of *D. layneae* and its synonym, *D. brachiatus*, are from Lake County.

Diplacus graniticola occurs in the California Sierra from Tuolumne Co. south through Mariposa, Madera, and Fresno counties to Tulare Co.; it is partially sympatric with typical *D. layneae* in that area (Fig. 2). Exposed granite occurs in California both to the south and north of the range of *D. graniticola*, thus absence of substrate does not appear to limit its distribution. Where sympatric, *D. layneae* commonly occurs in granite-derived sand and gravel immediately adjacent to granite rock providing habitat for *D. graniticola*. Elsewhere in its range, *D. layneae* has been documented from soils from serpentine, metamorphic, and other types of volcanic rocks besides granite. Label data suggest that *D. graniticola* continues flowering later than sympatric *D. layneae*: Apr–Sep(–Oct) vs. Apr–Jul (–Aug).

Distinctions between *Diplacus graniticola* and *D. layneae* are summarized in the couplet below.

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Variation in typical Diplacus layneae

Thompson (2005, p. 119) noted that "*Mimulus layneae* is one of the most complex and variable species in subg. *Schizoplacus*. It hybridizes with *M. nanus* in several parts of its geographic range and produces intermediates that detract from the otherwise distinctive concepts represented by each of these taxa. Fortunately, the problematic hybrid zones are limited in their size." Recognition of *Diplacus graniticola* as a distinct species significantly reduces the taxonomic complexity.

The major putative hybrid zone between *Diplacus layneae* and *D. nanus* (var. *nanus*) mapped and discussed by Thompson (his Figure 48, p. 117) is the region of southern Trinity Co., southwestern Tehama Co., and (perhaps slightly disjunct to) the vicinity of Snow Mountain on the Glenn/Colusa Co. line (see Fig. 2, here) — the High North Coast Ranges. A collection series showing "all degrees of intermediacy" (fide Thompson, p. 120) was collected west of Paskenta, Tehama Co.: *Baker & Wagnon 12748* (nearest *M. layneae*), *12621* (center of variation), and *12676b* (nearest *M. nanus* var. *nanus*) — the series is available at CAS, JEPS, and RSA. Thompson noted (p. 120) that "The two species have little altitudinal overlap in northwestern California, a factor that may limit the spread of the hybrids and some of the backcross progeny beyond these limited regions of sympatry." The current authors have not studied this situation.

There apparently are other small areas of overlap between *Diplacus layneae* and typical *D. nanus*, although the two are allopatric in most of northern California. Thompson, however, did not recognize (cite) putative hybrids from any other areas besides the one noted above.

Thompson (2003, 2005) regarded *Mimulus brachiatus* Penn. as a synonym of *Diplacus layneae* (both taxa are typified by collections from Lake Co.), but Pennell (1951) treated them as separate species, his key separating them primarily on the basis of smaller corollas with unequal lobes in *M. brachiatus* vs. larger corollas with nearly equal lobes in *M. layneae*. We agree with Thompson's assessment that both names represent the same entity. The type locality of *Mimulus brachiatus* is over serpentine substrate; the type of *Eunanus layneae* was collected on Bartlett Mountain, which apparently is without serpentine outcrops (LCAQMD 2016), thus *D. layneae* is tolerant of serpentine but not restricted to it.

- Diplacus layneae (Greene) Nesom, Phytoneuron 2012-39: 29. 2012. Eunanus layneae Greene, Bull. Calif. Acad. Sci. 1: 104. 1885. Mimulus layneae (Greene) Jepson, Fl. W. Calif. (ed. 1), 405. 1901. LECTOTYPE (Thompson 2005, p. 115): California. Lake Co.: Bartlett Mtn., 1884, M.K. Curran s.n. (BM digital image!; isolectotypes: F digital image!, UC [Katherine Brandegee as collector]!; probable isolectotype: GH digital image!).
- Mimulus brachiatus Pennell, Notul. Nat. Acad. Nat. Sci. Philadelphia, No. 235: 2. 1951. **TYPE**: **California**. Lake Co.: NE of Middletown, serpentine barrens, 1000 m, 19 Jun 1945, *H.D. Ripley* & *R.C. Barneby* 6886 (holotype: PH digital image!).

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Figure 3. *Diplacus graniticola* (left) and *Diplacus layneae* (right) ventral view of corolla tube-throats showing color and pattern differences. These plants were 3 meters apart in granitic crevices and on adjacent scree respectively. Hetch-Hetchy area, Tuolumne Co. Photos © Steve Schoenig, May 2016.



Figure 4. *Diplacus graniticola*. Eleven out of 18 nodes stripped of leaves and calyces showing the extremely close distal internode lengths in a mature plant. Hetch-Hetchy area. Photo © Steve Schoenig, September 2016.



Figure 5. Diplacus graniticola, Hetch-Hetchy, Tuolumne Co. Photo © Steve Schoenig, 1 July 1993.



Figure 6. Diplacus graniticola, Hume Lake, Fresno Co. Photo © Steve Schoenig, 2 June 2007.



Figure 7. Diplacus graniticola, Hume Lake, Fresno Co. Photo © Neal Kramer, 2 June 2007.



Figure 8. *Diplacus graniticola*, San Joaquin River Gorge BLM Management Area, Fresno Co. Photo © Aaron Schusteff, 20 April 2013.



Figure 9. Diplacus graniticola, Yosemite National Park. Photo © Keir Morse, 15 July 2005.



Figure 10. Diplacus graniticola, Yosemite National Park. Photo © Keir Morse, 15 July 2005.



Figure 11. *Diplacus layneae* in gravelly soil immediately derived from granite, Yosemite National Park. Photo © Keir Morse, 12 July 2005.



Figure 12. *Diplacus layneae* in granite gravel, Yosemite Valley, Bridal Veil Fall Vista, Mariposa Co. Photo © Jean Pawek, 23 July 2011.



Figure 13. Diplacus layneae near Angwin, Napa Co. Photo © Steve Schoenig, May 1998.