TAXONOMIC NOTES ON DIPLACUS (PHRYMACEAE)

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ABSTRACT

An update to the infrageneric classification of Diplacus is provided. The genus includes 48 species, only one of which does not occur in the USA, distributed among five sections. Three species are returned here to sectional positions where earlier placed by Thompson (2005): *D. parryi* and *D. torreyi* to sect. *Eunanus* and *D. rupicola* to sect. *Oenoe*. Sect. *Diplacus* is recognized to comprise ten species and two relatively abundant and formally named hybrids. *Diplacus rutilus* is tentatively maintained at specific rank — it differs from *D. longiflorus* in its red to red-orange corollas and apparently is endemic to Los Angeles County. Distributions of the species and hybrids of sect. *Diplacus* in the USA are mapped at county level.

KEY WORDS: Diplacus, Phrymaceae, infrageneric taxonomy

Since the taxonomic overview of the genus *Diplacus* presented by Barker et al. (2012), several species have been added to the account and a few relegated to synonymy. Sectional disposition of three species is modified. These changes are reflected in the present update of infrageneric taxonomy.


Species with strongly 2-lipped corollas show as a distinct clade in the molecular analysis by Beardsley et al. (2004). *Diplacus nanus* 4, 5, 6, and 7 are part of the 2-lipped clade, but *Diplacus nanus* 1, 2, and 3 weakly cluster as sister to the non-2-lipped species. Reduction of flowers to one per node apparently has occurred independently, because those species (*, one flower per node) do not appear to be monophyletic in the molecular analysis. *Diplacus parryi* and *D. torreyi* are placed outside of sect *Eunanus* in the molecular analysis but are included here on the basis of morphology (comments below).

   9a. *Diplacus bigelovii* var. *bigelovii*
   The two varieties are distinct in leaf shape. Thompson (2005) mapped them as very closely parapatric and noted that they show "limited intergradation" near their contiguous occurrence. It seems at least a hypothesis worth investigating that var. *cuspidatus* is more closely related to species with a similar leaf shape (*D. cusickii*, *D. cusickioides*, *D. deschutesensis*, *D. ovatus*) than to var. *bigelovii*.
   Strongly two-lipped corollas
   *Diplacus cusickii* proves to be a narrow endemic of Malheur Co., Oregon, and immediately adjacent Idaho (Nesom 2013). The remainder of what has previously been identified as *Mimulus cusickii* is treated as *D. cusickioides*.
   SYN = *Mimulus coccineus* Congd.; *Mimulus angustifolius* (Greene) A.L. Grant; *Mimulus densus* A.L. Grant (*Diplacus densus* (A.L. Grant) Nesom)
   Placement here of synonyms agrees with Thompson (2005). *Mimulus coccineus* (mostly California Sierra from Tulare to Eldorado counties, and apparently including *Eunanus angustifolius* Greene from Mt. Rose, Nevada) includes small, tufted plants at high elevations with small calyces and small, dark red-purple, strongly 2-lipped corollas with nearly filiform tubes and prominently exserted stamens. *Mimulus densus* (mostly Nevada counties and Lassen, Nevada, and Plumas counties, California) includes taller plants at lower elevations with a strong tendency to produce populations with all individuals with larger, yellow, nearly regular (non 2-lipped) corollas with more nearly included stamens. Typical *Diplacus mephiticus* has moderate-sized plants at medium elevations with magenta, 2-lipped corollas. There appear to be no clear discontinuities in variation among these expressions, but this needs to be studied in more detail.
   Incertae sedis
   *Diplacus parryi* and *D. ripicola* were treated together as sect. *Ereminimimus* by (Barker et al. 2012), but both are returned here to where Thompson (2005) placed them. Though the two species differ in a number of striking features, their relationship as sister species (100% bootstrap confidence) in the molecular analysis by Beardsley et al. (2004) was weighted in placing them within the same section. Morphologically, however, *D. parryi* can hardly be separated from sect. *Eunanus* and various, apparently derived features of *D. ripicola* place it with sect. *Oenoe*. *Diplacus parryi* is not known to hybridize with any other species.
   Molecular data indicate that *Diplacus torreyi* is sister to the five species of sect. *Cleisanthus* but there appears to be no morphological evidence in support of this hypothesis. Placement of *D. torreyi* (as well as *D. parryi*) in sect. *Eunanus* may reflect plesiomorphic similarities. *Diplacus torreyi* is distinct among the other species sect. *Eunanus* in its chromosome number of $2n = 20$ (vs. $2n = 16$). It is not known to hybridize with any other species.

   *Diplacus mohavensis* and *D. pictus* were treated together by Thompson (2005) as *Mimulus* sect. *Mimulastrum* because of their remarkably similar and obviously highly derived corollas — radially symmetric, salverform-rotate with an abrupt tube-throat transition and vein-patterned limb. Grant (1924) separated each as a monotypic section. Despite the remarkable similarity in corolla morphology and color patterning, molecular data show *D. mohavensis* to be derived from within sect. *Eunanus*, and pollen morphology also indicates that the two are distinct (Argue 1980; Thompson 2005). Further study is warranted to test this hypothesis of convergent evolution.


   **TYPE:** *Mimulus pictus* (Curran ex Greene) A. Gray [= *Diplacus pictus*]


   **LECTOTYPE** (Thompson 2005): *Mimulus tricolor* Hartweg ex Lindley [= *Diplacus tricolor*]


   **Diplacus rupicola** is similar to species of sect. *Oenoe* in its leaves in a persistent basal rosette, hypogeous hypocotyls, linear cotyledons, calyx asymmetrically attached to pedicel, subequal stigma lobes, capsules indurate-walled and tardily dehiscent, and corollas colored with a pattern similar to *D. tricolor*. It differs in its perennial duration (vs. annual), habitat of cliff crevices (vs. characteristically of vernally wet depressions or seepages), flowers 2 per node (vs. 1 per node), and chromosome number of 2n = 16 (vs. 2n = 20 in *D. pygmaeus* and 2n = 18 in *D. angustatus*, *D. pulchellus*, and *D. tricolor*).

   Although molecular data (Beardsley et al. 2004) cluster *Diplacus rupicola* with *D. parryi* and not with the other four species of sect. *Oenoe*, morphological evidence is pervasively strong in suggesting that the closest ancestry of *D. rupicola* is with the species of sect. *Oenoe*. The chromosome number of 2n = 16 is the most common in *Diplacus* and probably is the base number of the genus, but the sister to sect. *Oenoe* is sect. *Cleisanthus*, with a base of 2n = 18; thus 2n = 16 may be a specialized feature in *D. rupicola*. Just as *D. pygmaeus* is indicated by molecular data to be sister to *D. angustatus*, *D. pulchellus*, and *D. tricolor*, it seems reasonable to hypothesize that *D. rupicola* may prove to be sister to the other four species.


   **TYPE:** *Mimulus cleistogamus* J.T. Howell [= *Diplacus douglasii*]


   **SYN = Diplacus latifolius** (A. Gray) Nesom


5. **Diplacus** sect. **Diplacus** **LECTOTYPE** (Thompson 2005): *Diplacus glutinosus* (J.C.Wendl.) Nutt. [= *Diplacus aurantiacus*]

   An alternative to the conservative treatment of sect. *Diplacus* by Thompson (2005) was revived and further documented by Tulig and Nesom (2012). Eleven species are recognized here to comprise sect. *Diplacus*. Two hybrids are relatively abundant and formally named. *Diplacus rutilus*, which was tentatively recognized at specific rank by Tulig and Nesom, is maintained here (with
commentary) as a distinct species. The distributions of the species and hybrids in the USA are mapped at county level in Figure 1.

   Molecular data (Beardsley et al. 2004) indicate that the yellow-flowered *Diplacus aridus* is sister to red-flowered *D. puniceus*; red-flowered *D. parviflorus* is sister to both.


   The type of *Diplacus calycinus* is from Tulare County and the concept of the species is perhaps best restricted to the Sierran population system in Fresno, Tulare, and Kern counties, disjunct from *D. longiflorus*, which occurs primarily in coastal counties. The Sierran system, which apparently is free from the genetic influence of any other species, is characterized by distinct abaxial leaf vestiture –– the hairs are unbranched, broad, and vitreous, compared to the branched, thinner, and dull hairs of *D. longiflorus*. Plants of *D. calycinus* parapatric with *D. longiflorus* also show a tendency toward the characteristic vestiture and also have lighter-colored (but more variable in color) corollas with narrower (but slightly shorter) tubes. Intergradation between *D. calycinus* and *D. longiflorus* occurs in the region connecting the San Gabriel and San Bernardino mountains (in San Bernardino County).

41. **Diplacus clevelandii** (Brandeg.) Greene, Erythea 4: 22. 1896.

   *Diplacus grandiflorus* (Sierran counties: Butte, Eldorado, Nevada, Placer, Plumas, Sierra, Tehama, Yuba) and *D. linearis* (coastal counties: Monterey, San Benito, San Luis Obispo) are remarkably similar, so much so that it seems likely they are vicariants. In addition to the disjunction in distribution, leaves of *D. linearis* have narrower limbs and both pairs of anthers and the stigma are at the same level and relatively deeply included. In *D. grandiflorus*, the anther pairs are separated and the stigma is above the upper anther pair at or near the throat opening.

43. **Diplacus linearis** (Benth.) Greene, Pittonia 2: 156. 1890.
   *Diplacus linearis* was allied by Pennell (1947) with the Sierran *D. grandiflorus* as a narrower-leaved and smaller-flowered subspecies. The two were considered synonymous by Thompson (2005), but they are disjunct in geography and ecology. *Diplacus linearis* and *D. grandiflorus* appear to be distinct as a pair particularly in the deep notching of the corolla lobes and the minutely hirtellous, eglandular stem vestiture. The molecular analysis by Beardsley et al. (2004), however, suggests that *D. grandiflorus* is related as a sister to *D. aurantiacus*. Treatment of *D. linearis* as a nothospecies is speculative.


   See comments below on the distinctiveness of *D. rutilus*.

46. **Diplacus parviflorus** Greene, Pittonia 1: 36. 1887.


Hybrids:

a. **Diplacus × australis** (McMinn ex Munz) Tulig, Phytoneuron 2012-45: 16. 2012. [= *Diplacus longiflorus* × *D. puniceus*]
   Many plants and populations intermediate between *Diplacus longiflorus* and *D. puniceus* are found where their ranges meet in Los Angeles, Orange, Riverside, and San Diego counties. The intermediate morphology and geography indicate that these are hybrids (as has been hypothesized by, for example, Thompson 2005; Streisfeld & Kohn 2005; Tulig & Nesom 2012), which have been identified as *Diplacus × australis*. Streisfeld and Kohn found that in San Diego County, *D. longiflorus* and *D. puniceus* are discrete in morphology and separate in geography, separated by a narrow zone of hybrids and putative introgressants.
   In Riverside County in 1920, I.M. Johnston observed and documented (16 sheets total, MO!) what he probably saw as a hybrid swarm between *Diplacus longiflorus* and *D. puniceus*. Riverside Co.: due W of Lakeview, 2000 ft, 8 May 1920, I.M. Johnston 2284-2298 (MO). His collection numbers 2280-2283, 2289-
2294, and 2297 show a range of intermediacy in leaf shape, vestiture, and corolla form and color. Most plants are glabrous or with reduced vestiture. His collection numbers 2284, 2286, 2295, and 2298 (MO!) are more or less typical *D. puniceus*. None of the 16 sheets show what would be interpreted here as typical *D. longiflorus*.

b. *Diplacus × lompocensis* McMinn, Madroño 11: 62. 1951. [= *Diplacus aurantiacus* × *D. longiflorus*]

*Diplacus × australis* and *D. × lompocensis* are similar to each other in most features. There are no obvious qualitative morphological distinctions between them and they are only easily separated by geographic range. *Diplacus × lompocensis* occurs in San Luis Obispo and Santa Barbara counties. *Diplacus longiflorus* is generally distinct from both in its larger corolla features and villous calyx pubescence.
c. *Diplacus parviflorus* × *longiflorus*

Grant (1924) found these to be fairly common on Santa Cruz Island on open hillsides near Friar’s Harbor and Valdez, where the two species grew near each other though apparently separated in habitat, typical *D. parviflorus* mostly in canyons, *D. longiflorus* on open hillsides. She noted that the apparent hybrids were variable in all possible combinations of features of the leaves, calyces, and corollas, including color.

**Status of *Diplacus rutilus***

*Diplacus rutilus* was treated at species rank among those taxa recognized by Tulig and Nesom (2012) as members of sect. *Diplacus*. McMinn (1951) also regarded it as a species, but Munz (1973) followed Grant’s original assessment (1925) in treating it as a variety of yellow-flowered *D. longiflorus*, while Beeks (1951) and Thompson (2005) regarded it only as a populational variant of *D. longiflorus*, without formal rank. The present commentary tentatively maintains *D. rutilus* as a distinct, geographically localized, red- to red-orange-flowered species (Fig. 1). The variation in corolla color is suggestive of a difference in pollination biology, but similar variation occurs in other species of *Diplacus* where both yellow and magenta forms are produced dimorphically. In any case, the distinctive color and localized geography of these red-flowered plants warrant further study, especially in the field.


Grant made two collections at Santa Susanna Pass (Los Angeles Co.) in 1920 — *Grant 1650*, the type of *Mimulus longiflorus* var. *rutilus*, which had dark red corollas, and *Grant 1651*, which she noted had "salmon-red" corollas. Wolf in 1936 at the "base of Santa Susanna Pass" made three collections closely matching the type of var. *rutilus* and identified by him as var. *rutilus* — a dark red-flowered plant (*Wolf 7772*), one with "fls in shades of reddish orange (*Wolf 7773*)", and an apparently orange-flowered plant (*Wolf 7774*). Numerous other plants with red to dark orange flowers and otherwise closely matching the "rutilus" type have been collected in the area of Santa Susana Pass (e.g., *Dittes 1388*, *Peirson 1146*, *Thompson 1078*) as well as other nearby localities in Los Angeles Co. (e.g., San Dimas, Griffith Park, near Pomona and Claremont; see citations below; Also see other collections from the Santa Susana Pass area (via California Consortium — IRVC, SBBG, SD, SFV, UC, UCR), all currently identified fide D.W. Thompson as *Mimulus aurantiacus* var. *pubescens*.

Collections examined (or cited by Grant 1925). California. Los Angeles Co.: Claremont, San Antonio Canyon, 23 May 1909, *Baker 5354* (POM fide Grant 1925); Griffith Park, 11 Jun 1902, *Braunton 472* (US fide Grant 1925); Santa Susanna Mts., Feb 1861, *Brewer 208* (GH, US, both fide Grant 1925); Simi Hills, 118º 37' 12.9" W, 34º 16' 25.7" N, N of Santa Susana Road, ca. 2.3 air mi NW of Chatsworth High School, ca. 0.9 air mi W of Topanga Blvd., ca. 0.8 air mi ENE of Santa Susana Pass, recently burned chaparral, 1250 ft, 4 Jun 2006, *Dittes 1388* (CHSC, OSC); Santa Susana Pass, 10 Apr 1926, *Epling s.n.* (MO, OSC); Santa Susana Pass, dry hillsides, flrs salmon-red, 10 Jun 1920, *Grant 1651* (DS, MO); hills near Chatsworth Park, 3 Apr 1917, *Grinnell s.n.* (POM fide Grant 1925); Santa Susana Pass, 29 May 1931, *Howell 6575* (CAS); W of Pomona, 16 Mar 1926, *Jones s.n.* (CAS); Lone Hill, near San Dimas Canyon, sunny hillside, 1100 ft, 17 Mar 1920, *Munz 3362* (MO, OSC); Santa Ana Mts., Sierra Canyon, rocky hillside, 1200 ft, 24 Apr 1920, *Munz & Harwood 3758* (ORE); Lone Hill near San Dimas, 19 Apr 1919, *Parish 19266* (MO); W foot of Santa Susana Pass, 5 May 1918, *Peirson 1146* (RSA fide Grant 1925); Brea Canyon near Pomona, 12 Apr 1940, *Thomas s.n.* (CHSC); Santa Susana Pass, road at jct with Hwy 118 access road (summit), 479 m, 23 May 1992, *Thompson 1078* (JEPS); San Gabriel Mts, Monroe Canyon, 1800 ft, 12 Jun 1936, *Wheeler 4146* (CAS); near Pomona, 23 Apr 1937, *Winblad s.n.* (CAS); base of Santa Susana Pass, 24 Apr 1936, *Wolf 7772* (DS, MO, OSC, TEX), *Wolf 7773* (CAS, DS), *Wolf 7774* (MO).
Those collections I have studied apparently cannot be separated in any feature except corolla color from typical *Diplacus longiflorus*, and they might reasonably be considered infrapopulational variants of *D. longiflorus*. Red corollas have not been observed in the species outside of Los Angeles County (and perhaps Riverside County) and perhaps can be interpreted as reflecting local introgression in this area from *D. puniceus*. On the other hand, the distinctive linear geographical distribution (see below) of these red-flowered plants and their apparent absence elsewhere in the area where *D. x australis* occurs suggest that the origin of *D. rutilus* is different from that of the highly variable *D. x australis*.

Of collections cited by Grant as var. *rutilus*, *Parish 19266* from "Lone Hill near San Dimas" has vegetative morphology and vestiture of typical *Diplacus longiflorus*, but the red corollas are relatively narrowly tubular with a narrow limb. *Parish 19264* (MO!), also from "Lone Hill" on the same day, is vegetatively like 19266 but has narrow-limbed yellow corollas. The Parish collections from Lone Hill might be interpreted as *Diplacus x australis* (hybrid variants), but the plants from
around Santa Susanna Pass mostly do not show similar variability. An exception apparently is a plant collected at Santa Susanna Pass in 1926 (Epling s.n., MO!) with an orange, relatively narrow corolla tube and limb and with linear-lanceolate leaves sparsely pubescent abaxially, identified by Grant as a hybrid between *M. longiflorus* and *M. puniceus*.

McMinn (1951) cited collections of *Diplacus rutilus* from Ventura, Los Angeles, and Riverside counties. Susanna Pass, however, although said by Grant (1924) to be in Ventura County, is in Los Angeles County, and I have not seen collections *D. rutilus* from Riverside County. Munz (1973) noted that *D. rutilus* (as *Mimulus longiflorus* var. *rutilus*) occurs in Riverside County but Roberts et al. (2004) did not include it even as a synonym. *Diplacus rutilus* was included by Beauchamp (1986) for San Diego County as occurring on Mt. Palomar, but Rebman and Simpson (2006) apparently reidentified those plants either as *M. puniceus* or *M. australis*.

Information from Bert Wilson of Las Pilitas Nursery in Escondido, California, has been especially helpful in tentatively assessing the evolutionary status of *Diplacus rutilus*. According to him, and from his contacts and other sources, *D. rutilus* seems to occur in pockets in a strip from about Whittier [and Pomona] through North Pasadena westward to near the Ventura County line (the Santa Susana area), a distance of almost 60 miles. This distribution essentially matches the herbarium records.

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**LITERATURE CITED**


