

SOME COMMENTS ON THE TAXONOMY OF *DELPHINIUM* (RANUNCULACEAE) IN WESTERN OREGON

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ABSTRACT

In preparing the treatment of *Delphinium* for a future volume of *Flora of Oregon*, some taxonomic decisions were made that conflict with the 1997 treatment of the genus by Warnock in *Flora of North America*. The choice of groups to be recognized is based on the present author's opinion that rapid evolution of *Delphinium* taxa occurred in the Willamette Valley following habitat disturbance caused by catastrophic flooding from the late-glacial-age Spokane Floods. *Delphinium pavonaceum* Ewan, *D. leucophaeum* Greene, and *D. oregonum* Howell, which are endemic to the Willamette Valley, may have evolved in the ca. 12,000 years since the floods occurred. These 3 groups are here given species rank, unlike their treatment in *Flora of North America*. This is in line with how the taxa are viewed by Oregon botanists concerned with the rare and endangered species of the state. Lectotypification is necessary for *D. pavonaceum*. A further taxonomic change is the reduction of *D. basalticum* M.J. Warnock to synonymy under *D. glareosum* Greene.

RESUMEN

En la preparación del tratamiento del género *Delphinium* para un futuro volumen de *Flora of Oregon*, se realizaron algunas decisiones taxonómicas que están en conflicto con el tratamiento de 1997 del género por Warnock en *Flora of North America*. La elección de grupos a reconocer se encuentra basada en la opinión del presente autor de que la rápida evolución del taxón *Delphinium* ocurrió en el Valle Willamette debido a la perturbación del hábitat causada por la catastrófica inundación de finales de la edad del hielo de Spokane Floods. *Delphinium pavonaceum* Ewan, *D. leucophaeum* Greene, y *D. oregonum* Howell, endémicas del Valle de Willamette, pudieron haber evolucionado cerca de 12.000 años desde que las inundaciones ocurrieron. Estos tres grupos son aquí dados en el rango de especie, a diferencia del tratamiento dado en *Flora of North America*. Esto se encuentra en la línea de como son vistos estos taxones por los botánicos de Oregon preocupados con las especies raras y amenazadas del estado. La leptotipificación es necesaria para *D. pavonaceum*. Un cambio taxonómico más lejano es la reducción de *D. basalticum* M.J. Warnock a la sinonimia de *D. glareosum* Greene.

INTRODUCTION

Three rare taxa of Oregon *Delphinium* occur in the Willamette Valley, 1 in the northern portion and 2 in the central and southern parts of the valley. In all 3, the root system is fleshy and tuberous, as is characteristic of such Oregon species as *D. menziesii* DC., *D. nuttallii* A. Gray, and *D. nuttallianum* Pritz. Taxonomic treatment of these populations has varied among recent authors. Ewan (1945) and Peck (1961) recognized all 3 as species: *D. leucophaeum*, *D. pavonaceum*, and *D. oregonum*. Hitchcock (1964) gave species rank to the first 2 taxa but placed *D. oregonum* as a synonym of *D. nuttallii*. Sutherland (1967) made *D. pavonaceum* a variety of *D. menziesii*, *D. leucophaeum* a variety of *D. nuttallii*, using a different epithet, and *D. oregonum* a synonym of *D. menziesii*. More recently, Warnock (1995, 1997) gave subspecific rank to *D. pavonaceum* as *D. menziesii* ssp. *pallidum* M.J. Warnock and to *D. leucophaeum* as *D. nuttallii* ssp. *ochroleucum* (Nutt.) M.J. Warnock, but he synonymized *D. oregonum* under *D. menziesii* ssp. *menziesii* (Warnock 1997, p. 235).

Delphinium pavonaceum, which has white sepals, appears to have as its closest relative the blue-sepaled species *D. menziesii*. These taxa are alike in having their lower petals fringed with short, straight hairs. In this respect, they differ from the second white-flowered species *D. leucophaeum*, which is morphologically more similar to the blue-sepaled *D. nuttallii*. The latter 2 taxa have long, crisped (wavy) hairs fringing their lower petals. *Delphinium leucophaeum* and *D. nuttallii* are usually found in rocky sites such as cliffs or stony soils, but for the most part they are well separated geographically. *Delphinium pavonaceum*, on the other hand, is a species of low-elevation prairies, in deep loam soil, while *D. menziesii* is widespread and occurs in a variety of habitats, from prairies to forest edges, rocky hillsides, and high elevation meadows.

Delphinium oregonum, the third rare species, has blue sepals and is in many respects intermediate between *D. nuttallii* and *D. menziesii*. A study of this species group by Boyer (1999), which included a morphological comparison supplemented by a Principal Components Analysis, is discussed below in support of the hypothesis of a hybrid origin for *D. oregonum*.

Delphinium basalticum M.J. Warnock was described from a basalt slope near Oneonta Gorge on the Oregon side of the Columbia River Gorge. Specimens at OSC that are referable to *D. basalticum*, including 8 approximate topotypes, were compared with 31 collections of *D. glareosum* Greene, a variable species of higher elevations in the Olympic Mountains and the Washington and Oregon Cascades. It was concluded that *D. basalticum* is best placed as a synonym of the morphologically variable and wide-ranging *D. glareosum*.

It has been noted previously that the isolating mechanisms for species of *Delphinium* are principally ecological, geographic, and/or temporal (Warnock 1995, p. 74). These principles are clearly applicable to the species of western Oregon that form the basis for the present paper, Except for occasional sympatry between *D. pavonaceum* and *D. menziesii*, mentioned below, the taxa are primarily allopatric in distribution. An additional factor, the difference in sepal color between the white- and blue-flowered species, is also discussed, due to its possible effect on the behavior of insect pollinators, thereby limiting gene flow should geographical and ecological barriers become less effective.

TAXONOMIC NOTES

Lectotypification of *Delphinium pavonaceum*

Delphinium pavonaceum Ewan, Univ. Colorado Stud., Ser. D 2(2):110–111. 1945. TYPE: OREGON: fields, W of Corvallis, H.C. Gilbert 1135, 8 May 1916 (LECTOTYPE, selected here: OSC 4173, right-hand plant, labeled “a.” Two plants, complete except for a lack of roots, are present on the sheet (Fig. 1).

Note.—When there are 2 or more plants to choose from on a holotype sheet, it is necessary to select just one of these as a lectotype for the species name.

In his description of *Delphinium menziesii* DC. subsp. *pallidum* (Warnock 1995), the author states “Hybrids are known with *D. trolliifolium* and have been named *D. × pavonaceum*.” This interpretation of *D. pavonaceum* as a hybrid is repeated in *Flora of North America* (Warnock 1997, p. 235). The holotype sheet of *D. pavonaceum* at OSC is not annotated by Warnock, but he probably saw it, or a photograph of it, to make the judgment that one plant or the other is a hybrid with *D. trolliifolium*, a blue-flowered species with thick, branching roots, which is common in woodlands in the Corvallis area. To the present author there is no justification for assuming a hybrid origin for either plant on the type sheet, although the left-hand plant “b,” at first glance, appears to have a stem base wide enough to have been attached to a *D. trolliifolium*-type root. The stem base is curled back, however, and the true tip is only 5 mm wide, which is well within the range of *D. pavonaceum* stem tips. The flowers of both plants on the holotype sheet are white with blue upper petals. Lectotypification by plant “a” will remove any excuse for proposing a hybrid origin of the species.

Relationships of *Delphinium pavonaceum*

Delphinium pavonaceum occupies a limited region of the southern Willamette Valley in Benton, Lane, Marion, and Polk Counties. Populations were sampled by Goodrich (1983) for a morphological study of rare western Oregon delphiniums. She found that the most common habitat for the species is in remnant prairies, in deep silty loam soil, sometimes near vernal pools and marshes, the plants often being inundated by standing water following spring rains (op. cit., pp. 30–31). Other sites in which she observed the species were on roadsides and at the edge of oak-ash woodlands. The related *D. menziesii* is much more widespread, being found at low to high elevations from the Cascade Range to the Coast. Its range extends from the Siskiyou Mountains in the south to British Columbia in the north. It may be sympatric with *D. pavonaceum* (see Discussion, below), but most often it is in drier sites, including conifer forests and mixed woodlands, on hillslopes, and in mountain meadows.

Flower color differences between *Delphinium pavonaceum* and *D. menziesii* in sampled populations from the southern Willamette Valley are described in detail by Goodrich (op. cit., t. 15). Sepal color, white in *D.*



Fig. 1. Holotype sheet of *Delphinium pavonaceum*. The annotation by Joseph Ewan does not indicate which plant he intended as the holotype. Plant 'a,' on the right, is here designated as the lectotype.

pavonaceum and blue or purple in *D. menziesii*, is the most obvious difference. The upper petals are consistently white in *D. menziesii* and blue, lavender, or purple in the majority of *D. pavonaceum* individuals. The lower petals are consistently purple in *D. menziesii* and white in *D. pavonaceum*. As a target for pollinating bees, therefore, flowers of *D. menziesii* appear blue or purple with a white center, and in *D. pavonaceum*, they are white with a blue or purple center.

In the southern Willamette Valley, where the range of *Delphinium menziesii* approaches that of *D. pavonaceum*, the latter species is, on average, taller and has a longer raceme and more numerous flowers than the former (Goodrich 1983, t. 13, p. 55). My hypothesis is that *D. pavonaceum* is derived from *D. menziesii* by mutations in floral pigments and growth form, allowing adaptation to novel habitats following the Spokane Floods (Chambers 2000a, b). A succession of at least 40 short-lived lakes formed in the valley after a massive amount of water suddenly drained from Lake Missoula, sweeping across eastern Washington and down the Columbia River to the Portland basin. Environmental disturbance by the valley floods included the destruction of existing vegetation, an abundant deposition of silt, and an increase in the amount of wet habitat. The mutational changes here postulated for *D. pavonaceum* would have favored its ecological separation and partial reproductive isolation from *D. menziesii*.

Relationships of *Delphinium leucophaeum*

As mentioned above, *Delphinium leucophaeum*, except for its white flower color, is morphologically more similar to *D. nuttallii* than to *D. pavonaceum*. Ewan (1945, p. 110) believed that *D. leucophaeum* was “obviously related” to *D. pavonaceum* and that the latter “may very possibly represent an (sic) hybrid between (*D. leucophaeum*) and . . . *D. menziesii*.” Most recently, however, Warnock (1995) placed *D. leucophaeum* as a subspecies of *D. nuttallii* (subsp. *ochroleucum*), noting that “(s)epal color is the only feature consistently separating the two subspecies” and that “a given population typically contains plants of only one flower color” (op. cit. p. 99).

The distribution and habitats of *Delphinium leucophaeum* are described in the Discussion, below. The species very likely evolved from *D. nuttallii* in the past 12,000 years, through mutational changes in flower color and adaptation to specialized post-floods habitats that were not reoccupied by its parental species. The difference between blue and white flower colors is distinguishable by bee pollinators through the strong reflection of ultraviolet light by the sepals and petals of *D. leucophaeum*, as discussed below. According to K. Karoly (in litt.), white sepals are the result of a dominant mutation that blocks the metabolic pathway producing anthocyanin pigments in the blue-flowered species.

Species status of *Delphinium oreganum*

Delphinium oreganum Howell, Fl. NW. Amer. 1:22. 1897. TYPE: OREGON: near Brooks, Willamette Valley, Jun 1882, T. Howell s.n. (ORE 96539).

In his publication of the species in 1897, Howell gave the distribution as “open plains and hillsides of the Willamette Valley.” On the holotype specimen at ORE, Howell wrote Brooks with a capital “B,” referring to a small town on Hwy. 99E north of Salem. Ewan (1945, p. 178) misread this as “brooks,” small “b,” but the species is seldom a stream-side plant. The type shows the inflorescence raceme widening toward the base, the lowest flowers with pedicels up to 7 cm long, unlike the narrow racemes characteristic of *D. nuttallii*. The crisp hairs fringing the lower petals of the holotype plants are up to 2 mm long, as is true also for the latter species. Other collections of *D. oreganum* may have petal margins with short, straight hairs, however (Goodrich 1983, p. 60).

In a Principal Components Analysis of the 3 taxa by Boyer (1999, pgs. 50–54), *D. oreganum* is well separated from the other 2 taxa in the first component and is intermediate between them in the second component. The PCA1 in this comparison involved mostly flower size, sepal cupping, petal hair length, and spreading of the follicles. The PCA2 reflects mostly plant height, leaf nodal distance, and upper petal color. Morphological differences, shown photographically by Boyer (op. cit., pgs. 55–60), illustrate the intermediacy of *D. oreganum* in such features as inflorescence structure, leaf lobing, color of upper petals, spreading of sepals, and divergence of follicles. Details of this study are discussed below.

Reduction to synonymy of *Delphinium basalticum*

The name *Delphinium basalticum*, as mentioned in the Introduction, is based on a type specimen collected by M.J. Warnock on the old Columbia River Highway, 0.1 miles W of Oneonta Gorge, Multnomah County, Oregon. In the original description (Warnock 1995, p. 91), the new species is compared to *D. glareosum* with respect to stem and petiole pubescence (puberulent vs. glabrous or glaucous in the latter species), sepal spur length (14–18 mm long vs. 16–20 mm), depth of lower petal cleft (4–5 mm vs. 2–4 mm in *D. glareosum*), and ratio of fruit length to width (3.5–4.0 times longer than wide vs. 2.5–3.0 times longer than wide in *D. glareosum*). The leaves of *D. basalticum* are “basal and cauline,” while the key to species in Warnock (1997, p. 228) says leaves of *D. glareosum* are “clustered on proximal portion of stem.”

Examination of 8 OSC collections from near Oneonta Gorge revealed that the stems of *Delphinium basalticum* may be glabrous rather than puberulent and the petal clefts may be only 2–3 mm deep. Additionally, from locations outside the Olympic Mountains, the fruits in *D. glareosum* may be up to 4 times longer than wide and the leaves may be both basal and cauline, as in *D. basalticum*. As described by Warnock (1995, p. 91), lobes of the basal leaves of *D. basalticum* are 3–15 mm wide, and those of the cauline leaves are 1–12 mm wide. Lobe tips range from broadly to narrowly acute in Columbia Gorge specimens at OSC, which is similar to the leaves of *D. glareosum* from mountainous areas of Washington. Supposed differences in leaf succulence between *D. basalticum* and *D. glareosum* cannot be evaluated in dried specimens, but considering the extensive variability of other traits in *D. glareosum* throughout its wide range, it seems unlikely that leaf succulence could be a consistent feature of the species.

Delphinium basalticum shares with *D. glareosum* a root system in which the taproot may split lengthwise into elongate, separate or partly fused, ropy cords. This feature is most likely an adaptation to the species' habitats on cliffs, rock slides, and stony streambeds. Despite its low-elevation occurrence, therefore, *D. basalticum* should be included taxonomically in *D. glareosum*. Other species that may occur at higher elevations, such as *Delphinium nuttallii* (e.g. OSC 198429, Hood River Co., 4,760 feet), *Columbadoria hallii* (A. Gray) G.L. Nesom (e.g. OSC 70628, Linn Co., 4,600 feet), and *Erigeron howellii* (A. Gray) A. Gray (e.g. OSC 173084, Clackamas Co., 3600 feet), also grow near the Columbia River in cool, moist habitats on the north-facing side of the Gorge. Farther south in the high Oregon Cascades, *D. glareosum* intergrades with the tuber-rooted species *D. menziesii* and its roots become partly thickened and tuber-like (vouchered by numerous specimens at OSC).

DISCUSSION

The name *Delphinium menziesii* subsp. *pallidum* (Warnock 1995) is placed here as a synonym of *D. pavonaceum*. Its holotype is A.N. Steward 6351, 20 May 1953, “(O)pen fields 12 miles S of Corvallis, Benton County, Oregon” (US). Numerous isotypes are cited, among which are 4 at OSC. All were initially identified as *D. pavonaceum*. Also collected by Steward under number 6351 and housed at OSC are 7 sheets of plants that resemble *D. pavonaceum* but have pale-blue sepals, together with 7 sheets of *D. menziesii*. These collections were all made on the same day from a large mixed population. The most likely explanation for the pale-blue-flowered plants of the Steward 6351 population is through hybridization, perhaps including introgression, with sympatric plants of *D. menziesii*. This population is now extinct, the fields at this site having been brought under cultivation.

Partial genetic isolation between *D. pavonaceum* and *D. menziesii* is suggested by the differences in flower color, which would be recognizable to bee pollinators. Flower color differences in visible light are described above. Ultraviolet wave-lengths, which can be sensed by bees, also differentiate the species. Both the sepals and petals of *D. pavonaceum* are strongly reflective of ultraviolet light, whereas the sepals of *D. menziesii* absorb rather than reflect in these wavelengths (Goodrich op. cit., fig. 19, p. 92).

A similar color difference between *D. leucophaeum* vs. *D. nuttallii* was illustrated by Goodrich (op. cit., fig. 19 continued, p. 93), with flowers of the former species reflecting ultraviolet light and those of the latter being absorptive of ultraviolet wavelengths. *Delphinium leucophaeum* is found principally in a small region of the lower Willamette River south of Portland, with outliers in Clackamas County and SW Washington (K. Karoly, in litt.). Such areas were scoured by the late-glacial-age Spokane Floods (Allen & Burns 1986). Examples of its habitats, described by Goodrich (1983, pp. 36–40), are in thin soil over a rocky substrate at Camassia Natural

Area, on basalt cliffs by Lake Oswego (a kolk lake that was carved by the floods), and on small rocky islands in the Willamette River south of West Linn. Elk Rock, a basalt cliff by the river at the town of Milwaukie, is another reported site. *Delphinium nuttallii*, on the other hand, occurs in the Columbia River Gorge and in gravelly outwash prairies of SW Washington (Hitchcock 1964, p. 360). At only one known site does it grow in a mixed population with *D. leucophaeum* (K. Karoly, in litt.). Populations of *D. nuttallii* are also found above 1200 m in Wasco and Hood River Counties (OSC 164337, 178338), indicating sites at which the species could have survived the Spokane Floods that swept the Gorge.

Boyer (1999) performed a detailed comparison of *Delphinium oregonum* with *D. menziesii* and *D. nuttallii*. A total of 22 morphological characteristics were measured for OTUs in the 3 taxa. In the Principal Components Analysis referred to earlier, 60.01 percent of the variance in the OTUs was accounted for by Component 1 and 16.21 percent by Component 2. *Delphinium oregonum* was well separated from the 2 putative parental species in Component 1 and was intermediate between them, with considerable overlap, in Component 2 (op. cit. fig. 6, p. 51). Examples of morphological traits used in the analysis are illustrated by Boyer (op. cit., pp. 55–60). The inflorescence of *D. nuttallii* is a narrow raceme, that of *D. oregonum* is a raceme with long-pedicelled lower flowers, and *D. menziesii* has short- or long-pedicelled flowers in a usually more open inflorescence. Leaflets of *D. nuttallii* and *D. oregonum* have acute apices while *D. menziesii* has obtuse apices. Sepals of *D. nuttallii* are angled forward, those of *D. oregonum* are spreading, and those of *D. menziesii* are reflexed. The upper petals of *D. nuttallii* and *D. oregonum* are white with a blue tip, but in *D. menziesii* they are white throughout. The lower petals of all 3 species are blue. The follicles of *D. nuttallii* are erect and appressed, those of *D. menziesii* and widely spreading, and in *D. oregonum*, the follicles are spreading in their upper half.

According to Boyer (1999, p. 74), *Delphinium oregonum* grows primarily in well-drained grassy meadows and on roadsides. Additional sites recorded on recent collections are in open woodlands, wetlands, and fence-rows. The species ranges from Clackamas County south to Lane County and westward in Yamhill and Polk Counties. Its distribution overlaps that of *D. menziesii*, but according to Boyer (op. cit., p. 84), the peak flowering period for low elevation populations of *D. menziesii* is mid-late April, approximately 1 month earlier than that of *D. oregonum* (late May–July). The range of *D. nuttallii*, at least at present, is well north of *D. oregonum* and includes the Columbia Gorge, SW Washington, and higher elevations in Wasco and Hood River counties (see above).

CONCLUSIONS

Delphinium pavonaceum and *D. leucophaeum* are here given taxonomic status as distinct species, separate from their closest relatives *D. menziesii* and *D. nuttallii* respectively. Both species are localized endemics of the Willamette Valley and are found primarily below the 400-foot contour marking the depth of valley lakes formed by overflow from the late-glacial Spokane Floods. This separation of the white-flowered taxa as named species supports their treatment given by regional botanists concerned with the conservation of rare and endangered species (e.g. U.S. Fish & Wildlife Service 2010). A third endemic species, *D. oregonum*, has previously been confused with either *D. nuttallii* or *D. menziesii*. However, a morphological analysis of the 3 taxa provided strong evidence that *D. oregonum* is intermediate between these taxa and is probably a product of interspecies hybridization. Because *D. oregonum* is also found principally in areas below the height of valley floods, it too may have arisen in the past 12,000 years, after that period of extreme habitat disturbance. The postulated rapid divergence of western Oregon *Delphinium* taxa is consistent with the molecular studies of Koontz et al. (2004), which led to their conclusion that “recent and rapid radiation” was the rule in western North American *Delphinium* (op. cit. p. 354).

Delphinium basalticum, once thought to be a localized endemic of the Columbia River Gorge, occupies sites that are similar to those characteristic of *D. glareosum*, a widespread montane species of the Pacific Northwest. The Gorge plants can readily be accommodated in the morphological variability of the latter species, whose elongated, ropy roots probably are an adaptation to its characteristic rocky habitats.

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