A New Combination in Holodiscus (Rosaceae, Amygdaloideae, Spiraeae)

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Abstract

Holodiscus dumosus var. cedrorum, The Cedars oceanspray, was described in 2011 in recognition of the distinct morphology of populations occurring on serpentine soils in The Cedars area in the Outer Coast Ranges of Sonoma County, California. Morphological and genetic data suggest that this taxon should instead be treated as a variety of Holodiscus discolor, here interpreted broadly as a widespread and highly variable species with several taxonomic varieties that intergrade. The new combination Holodiscus discolor var. cedrorum is made and a key to the varieties that occur in California is provided.

Introduction

Holodiscus (Koch 1869: 309) Maximowicz (1879: 253) (Rosaceae, Amygdaloideae, Spiraeae), a genus of shrubs with simple leaves, is distributed from western Canada to northern South America. The number, rank, and circumscription of taxa within the genus have varied considerably among treatments (e.g., Kunze 1891 [as Schizonotus Rafinesque (1836: 74), nom. illeg.], Rydberg 1908 [as Sericotheca Rafinesque (1838: 152)], Ley 1943; reviewed by Lis 1990), with the distinctions based primarily on differences in leaf size and shape. Previous authors have acknowledged the challenging nature of the taxonomy of this group due to variability and intergradations in morphology across its range.

Lis (1990) recognized five species: two in the Holodiscus discolor (Pursh 1814: 342) Maximowicz (1879: 254) complex, distributed from British Columbia through the western US into Mexico, and three in the H. argenteus (Linnaeus 1781: 261) Maximowicz (1879: 254) complex, distributed from Mexico through Central America to Colombia. His recognition of two species in the western US, H. discolor and H. microphyllus Rydberg (1904: 559), was reflected in his treatments of the genus for The Jepson Manual (Lis 1993) and Flora of North America (Lis 2014). In contrast, in the revised treatment of the genus for the second edition of The Jepson Manual, Potter (2012) recognized only one species, H. discolor, with three varieties (var. discolor, var. glabrescens) (Greenman 1899: 116) Jepson (1925: 479), and var. microphyllus (Rydberg) Jepson (1936: 166), based on the morphological variability within and lack of non-overlapping diagnostic characters separating the recognized taxa in California. Potter’s (2012) treatment of microphyllus as a variety of H. discolor implicitly supported for Lis’s (2014) treatment of dumosus as a variety of H. discolor (i.e., H. discolor var. dumosus) (Watson) Maximowicz ex Coulter (1885: 79) as well, though this was not stated explicitly because it was not relevant to the flora of California.

The most recent taxonomic addition to the genus was the description of Holodiscus dumosus (Nutt. ex Hook.) Heller var. cedrorum Raiche & Reveal (2011: 26, as var. cedrorus), in recognition of a distinctive population occurring on serpentine soils in an area known as The Cedars in western Sonoma County, California. Raiche & Reveal’s (2011) treatment reflected their view that the plants at The Cedars are more closely related to those sometimes treated under H. dumosus (a taxon whose geographic range had been restricted, when recognized in previous treatments, to areas further east including the Great Basin and portions of the Sierra Nevada) than to the more geographically proximate H. discolor sensu stricto, previously accepted as the only species found west of the Inner North Coast Ranges in California, including at localities adjacent to The Cedars. Their decision to recognize the taxon at the varietal, rather than the specific or even subspecific level, reflected their appreciation of the lack of clear morphological distinctions between the plants at The Cedars and those that they considered as H. dumosus var. glabrescens (Greemn.) Hitchcock (in Hitchcock & Cronquist 1961: 116), which were treated by Lis (1990, 1993, 2014) as H. microphyllus var. glabrescens (Greemn.) Ley (1943: 284), and by Potter (2012) as H. discolor var. glabrescens.
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TABLE 1. Pairwise differences between chloroplast *trnL-trnF* sequences. Numbers in the top row correspond to those in the leftmost column, indicating which sequences are compared in each cell. The number in the cell is the number of sites at which the two sequences are different. Counties are in California unless otherwise indicated. Voucher specimens are deposited at DAV unless otherwise noted. Cult. = cultivated in the University of California Botanical Garden, Berkeley.
### Table 2. Pairwise differences between nuclear ITS sequences. Numbers in the top row correspond to those in the leftmost column, indicating which sequences are compared in each cell. The number in the cell is the number of sites at which the two sequences are different. Counties are in California unless otherwise indicated. Voucher specimens are deposited at DAV unless otherwise noted. Cult. = cultivated in the UC Davis Arboretum.

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Here we transfer var. cedrorum to H. discolor, maintaining Potter’s (2012) view that only one species of Holodiscus occurs in California. Our treatment implicitly agrees with Lis (2014) that H. dumosus should not be recognized as a distinct species, but also supports Potter’s (2012) interpretation that this is also true of H. microphyllus, which Lis did recognize as a distinct species. We further agree with Raiche & Reveal (2011) that the plants occurring at The Cedars are morphologically distinctive enough to warrant taxonomic recognition at the infraspecific level and that the rank of variety is most appropriate. Our conclusions are based on comparisons of morphological characters as well as nucleotide sequences of the chloroplast trnL-trnF and nuclear ITS regions from representatives of The Cedars oceanspray and related taxa. Both regions have been used extensively in phylogenetic analyses of closely related angiosperm species, including Spiraeae (Potter et al. 2007b) and both, especially ITS, have been used to detect cryptic species (e.g., Chan et al. 2002) and for DNA barcoding (Kress et al. 2005) in angiosperms. Our analysis is based on the expectation that sequence divergence in these regions should increase with increasing reproductive isolation of populations due to geographic separation and/or other factors that may lead to speciation.

Materials & methods

Morphological comparisons among the three taxa of Holodiscus here recognized as occurring in California were based on field observations as well as herbarium specimens. In order to test the hypothesis that the three are conspecific using genetic data, we determined chloroplast trnL-trnF and nuclear ITS sequences for three and one individuals of The Cedars Holodiscus, respectively, and compared them to new and previously published sequences of H. discolor var. discolor, H. discolor var. glabrescens, and H. discolor var. microphyllus from various locations (Tables 1, 2). In total, we generated 5 new trnL-trnF sequences and 8 new ITS sequences for this study. Methods for DNA extraction, PCR, and sequencing followed those described in Potter et al. (2007b). Sequences were edited with Sequencher (Gene Codes Corporation) and aligned in ClustalX 2.1 (Thompson et al. 1997) along with several published sequences downloaded from Genbank (Tables 1, 2). Numbers of differences between sequences were calculated in MEGA (Kumar et al. 2018) with gaps were treated as a fifth state; no gap was longer than a single base. Base calls at some sites in some sequences were ambiguous due to presence of two or more overlapping peaks. Such sites were considered identical for two sequences unless there were no shared possible bases for that site.

Results & discussion

Individuals of Holodiscus that occur on serpentine soils at The Cedars, here treated as H. discolor var. cedrorum, differ from other members of the genus in California in several characteristics, most strikingly the red-flushed appearance of the young twigs and adaxial surfaces of young leaves (vs. twigs brown and leaves green in the other varieties). The adaxial leaf surfaces in var. cedrorum are usually shiny and consistently glabrous, while in the other varieties they are dull and range from glabrous to densely hairy. In other respects, the plants at The Cedars fall within the range of morphological variation described for Holodiscus discolor (Potter 2012), supporting their treatment as a variety of that species.

This treatment is also supported by genetic data from chloroplast trnL-trnF and nuclear ITS nucleotide sequences. To the limited extent that the observed DNA sequence variation showed any meaningful patterns, they were not consistently correlated with either morphology or geography (Tables 1, 2). Very little variation was observed in the chloroplast trnL-trnF regions among samples here assigned to H. discolor. The sequence for the accession of the plant from The Cedars was identical to those of H. discolor var. discolor from a non-serpentine site adjacent to The Cedars and a published sequence for that taxon determined from a plant in Washington; these differed at one or two sites from sequences of varieties glabrescens and microphyllus. All of these sequences differed from the published sequence of H. argenteus, a species native to Central America, at 8 or 9 sites. This species is clearly distinguished from H. discolor by stamens equal to or shorter than (vs. longer than) the sepals, evergreen (vs. winter-deciduous) leaves, and several other characters (Ley 1943, Lis 1990). For nuclear ITS, only sequences from North American taxa were available. The most divergent sequences were the two published sequences for H. discolor var. microphyllus; however, each of those sequences was more similar to sequences of other varieties than they were to each other, and the two did not share any mutations that distinguished them from the remaining sequences. The ITS sequences of three individuals of The Cedars Holodiscus were identical or differed at one site; they differed at one site from the sequence of var. discolor.
from a non-serpentine site adjacent to The Cedars, at two sites from the published sequence of var. discolor from Texas, and at 2–4 sites from sequences for three individuals of var. glabrescens.

The limited diversity observed in trnL-trnF and ITS sequences provided no evidence of consistent genetic differentiation between morphological variants or geographic regions, suggesting that gene flow occurs freely among Holodiscus populations throughout the California Floristic Province and likely into the Great Basin and the Pacific Northwest as well. Thus, the morphological variants that have been given taxonomic recognition do not represent distinct evolutionary lineages, supporting their treatment as varieties rather than at any higher taxonomic rank.

Conclusion

Based on available morphological and genetic evidence, we have concluded that:

a) all populations of Holodiscus in California should be treated as conspecific;

b) the existence of several distinct, albeit intergrading, morphological variants makes recognition of several varieties useful for classification and communication, even though they probably do not correspond to genetically distinct groups;

c) plants occurring on serpentine soil at The Cedars in Sonoma County are sufficiently distinct to warrant recognition at the varietal level.

The classification adopted here treats H. discolor as a widely distributed and highly variable species in which morphological variants that have been given taxonomic recognition represent phenotypic combinations that occur independently at multiple locations throughout the range and likely reflect random genetic variation and/or adaptation to local environmental factors, rather than separate evolutionary lineages, and are therefore most appropriately treated as varieties of a single species rather than separate species or subspecies.

Taxonomy

Holodiscus discolor (Pursh) Maxim. var. cedrorum (Raiche & Reveal) D. Potter & Raiche, comb. nov.


Type:—USA. California: Sonoma County: The Cedars, Central Canyon area NE of Laton [or Layton] slopes, 38°37'16"N, 123°08'00"W, 270 m, 7 June 2010, J.L. Reveal & R. Raiche 8999 (holotype NY!; isotypes ARIZ!, ASU!, BH, BM!, BRY!, CAS!, COLO!, GH!, LL!, MICH!, MO!).

Representative specimens of other taxa (all at DA V):

— Holodiscus discolor var. discolor. USA. California: Solano County: Mix Canyon Road, 4.6 miles west of Pleasants Valley Road, 767 m, 38.413052°N, 122.109234°W, 20 July 2015, Daniel Potter 832; Sonoma County: Goat Rock, S side of King Ridge Rd., NW of Cazadero, 38.57986°N, 123.1161°W, 113 m, 5 August 2014, Daniel Potter 708; Oregon: Josephine County: Sunny Valley/Wolf Creek, along driveway at 181 Brimstone Road, 42.6312°N, 123.44392°W, 22 August 2017, Daniel Potter 925; Washington: Island County: Guemes Island, 17 May 1997, Daniel Potter 970517-07. Holodiscus discolor var. glabrescens. USA. California: Butte County: about 50 m east of Humboldt Road and ¼ mile west of the top of Humboldt Peak on the Pacific Crest Trail, 40.15174°N, 121.43515°W, 2024 m, 9 August 2014, Daniel Potter 712; about 10 m east of Humboldt Road and ¼ mile west of the top of Humboldt Peak on the Pacific Crest Trail, 40.1521°N, 121.43607°W,
2011 m, 9 August 2014, Daniel Potter 713; Plumas County: Caribou Wilderness, Indian Meadow trail to Beauty Lake, ca. ¼ mile west of the trail, 40.43915°N, 121.19913°W, 10 August 2014, 2031 m, Daniel Potter 714; Caribou Wilderness, along Indian Meadow trail to Beauty Lake, 40.44714°N, 121.20337°W, 2028 m, 10 August 2014, Daniel Potter 715. *Holodiscus discolor* var. *microphyllus*. USA. California: Alpine County: along Pacific Crest trail, east of Wet Meadows Reservoir, 38.622506°N, 119.848483°W, 31 July 2010, Daniel Potter 100731-02; El Dorado County: Desolation Wilderness, Eldorado National Forest, Twin Lakes (near Wright’s Lake), ca. 50 m N of the first lake on rocky slope, 11 July 2006, Daniel Potter 060711-01; Inyo County: Inyo National Forest, John Muir Wilderness, along Shepherd’s Pass Trail, 21 August 2000, Daniel Potter 000821-04; John Muir Wilderness, along Shepherd’s Pass trail, along trail descending from the pass, between Anvil Camp and Mahogany Flat, 21 August 2000, Daniel Potter 000821-01.

**Key to the Varieties of Holodiscus discolor in California:**

1. Leaf blades glabrous, shiny adaxially, flushed red, base wedge-shaped; on serpentine ........................................ var. *cedrorum*
   - Leaf blades glabrous to densely hairy adaxially, dull, not flushed red, base wedge-shaped or truncate to rounded; usually not on serpentine ................................................................. 2.

2. Leaf blade 1.5–8 cm, teeth toothed, base usually truncate to rounded; inflorescence 5–25 cm, 5–25 cm wide, branches usually many ............................................................................................................. var. *discolor*
   - Leaf blade 0.3–3 cm, teeth entire, above middle, base usually wedge-shaped; inflorescence 2–8 cm, 1.5–5 cm wide, branches 0–few .................................................................................................................. 3.

3. Leaf puberulent to glabrous on both surfaces, glands visible ........................................................................................................... var. *glabrescens*
   - Leaf ± long-hairy on one or both surfaces, glands 0 or usually obscured by hairs ................................................................................. var. *microphyllus*

**Acknowledgements**

We thank Kai Battenberg and Mark Jaradeh for performing lab work needed to generate the new DNA sequences analyzed here and Peter Fraissinet (BH) and Teri Barry (DAV) for assistance in locating and distributing the type specimens, which had not been distributed prior to the death of Dr. James Reveal in 2015. This study was supported by funding to DP from the UC Davis Agricultural Experiment Station (Project Number CA-D-PLS-6273-H).

**References**


