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# A New Combination in *Holodiscus* (Rosaceae, Amygdaloideae, Spiraeeae)

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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, Spiraeeae), 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., Kuntze 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. *micropyllus* (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* (Greenm.) Hitchcock (in Hitchcock & Cronquist 1961: 116), which were treated by Lis (1990, 1993, 2014) as *H. microphyllus* var. *glabrescens* (Greenm.) 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.

| | Collection | GenBank | Reference | Variety (species for 08) | County | 01 | 02 | 03 | 04 | 05 | 06 | 07 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 01 | Potter 710 | MT811053 | This study | *cedrorum* | Sonoma | | | | | | | |
| 02 | Potter 708 | MT811052 | This study | *discolor* | Sonoma | 0 | | | | | | |
| 03 | Potter 712 | MT811054 | This study | *glabrescens* | Butte | 1 | 1 | | | | | |
| 04 | Potter 714 | MT811055 | This study | *glabrescens* | Plumas | 1 | 1 | 0 | | | | |
| 05 | Potter 715 | MT811056 | This study | *glabrescens* | Plumas | 1 | 1 | 0 | 0 | | | |
| 06 | Potter 970517-07 | AF348546 | Potter et al. 2002 | *discolor* | Island (WA) | 0 | 0 | 1 | 1 | 1 | | |
| 07 | Potter 060711-01 | DQ897573 | Potter et al. 2007b | *microphyllus* | El Dorado | 2 | 2 | 1 | 1 | 1 | 2 | |
| 08 | Yi14219 (KUN) | KY420013 | Zhang et al. 2017 | *argenteus* | Alameda (cult.) | 9 | 9 | 8 | 8 | 8 | 9 | 9 |

**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.

| | Collection | GenBank | Reference | Variety | County | 01 | 02 | 03 | 04 | 05 | 06 | 07 | 08 | 09 | 10 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 01 | Potter 709 | MT814044 | This study | *cedrorum* | Sonoma | | | | | | | | | | |
| 02 | Potter 710 | MT814045 | This study | *cedrorum* | Sonoma | 1 | | | | | | | | | |
| 03 | Potter 711 | MT814046 | This study | *cedrorum* | Sonoma | 1 | 0 | | | | | | | | |
| 04 | Potter 708 | MT814043 | This study | *discolor* | Sonoma | 1 | 1 | 1 | | | | | | | |
| 05 | Potter 712 | MT814047 | This study | *glabrescens* | Butte | 4 | 4 | 4 | 3 | | | | | | |
| 06 | Potter 713 | MT814048 | This study | *glabrescens* | Butte | 2 | 2 | 2 | 1 | 2 | | | | | |
| 07 | Potter 714 | MT814049 | This study | *glabrescens* | Plumas | 2 | 2 | 2 | 1 | 1 | 0 | | | | |
| 08 | Potter 715 | MT814050 | This study | *glabrescens* | Plumas | 2 | 2 | 2 | 1 | 0 | 0 | 0 | | | |
| 09 | Wen 7257 (US) | EU669091 | Wen et al. 2008 | *discolor* | Jeff Davis (TX) | 2 | 2 | 2 | 1 | 2 | 0 | 0 | 0 | | |
| 10 | Potter 970702-03 | DQ886361 | Potter et al. 2007a | *microphyllus* | Yolo (cult.) | 8 | 7 | 7 | 7 | 7 | 6 | 6 | 5 | 6 | |
| 11 | Potter 060711-01 | DQ897603 | Potter et al. 2007b | *microphyllus* | El Dorado | 11 | 11 | 11 | 10 | 11 | 9 | 9 | 9 | 9 | 15 |

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 Spiraeeae (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. discolo*r 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.*

Basionym: *Holodiscus dumosus* (Nutt. ex Hook.) A. Heller var. *cedrorum* Raiche & Reveal (2011).

Type:—USA. California: Sonoma County: The Cedars, Central Canyon area NE of Latón [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!).

Additional specimens examined:—USA. California: Sonoma County: N of Cazadero, The Cedars, Big Austin Creek. drainage, near site of Layton Mine processing bldgs., 38.61905°N, 123.1273°W, 259 m, 20 May 1987, *Raiche 70194* (UCJEPS); The Cedars, serpentine area at head of Big Austin Creek N of Cazadero, ca 20 airmiles due W of Healdsburg, along south side of creek, 23 June 1994, *Barbara Ertter, R. Raiche, J. Shevock, & R. Bittman 12850* (UCJEPS); The Cedars, across from Magazines. Lower Russian River, Big Austin Creek watershed., 38.621277°N, 123.132873°W, 273m, 11 June 2010, *Roger Raiche 019.10* (UCJEPS); The Cedars, Campbell Ranch, Lower Russian River, Big Austin Creek watershed, 38.598985°N, 123.130976°W, 165 m, 16 June 2010, *Roger Raiche 021.10* (UCJEPS); The Cedars, lower Russian River, Big Austin Creek watershed, 38.613376°N, 123.134278°W, 217 m, 16 June 2010, *Roger Raiche 022.10* (UCJEPS); The Cedars, 38.6213°N, 123.1329°W, 284 m, 5 August 2014, *Daniel Potter 709* (DAV); The Cedars, 38.62292°N, 123.1357°W, 358 m, 5 August 2014, *Daniel Potter 710* (DAV); The Cedars, 38.61122°N, 123.13654°W, 201 m, 5 August 2014, *Daniel Potter 711* (DAV).

Representative specimens of other taxa (all at DAV):—***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*

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## References

Chan, R., Baldwin, B.G. & Ornduff, R. (2002) Cryptic goldfields: a molecular phylogenetic reinvestigation of *Lasthenia californica* sensu lato and close relatives (Compositae: Heliantheae sensu lato). *American Journal of Botany* 89: 1103–1112. https://doi.org/10.3732/ajb.89.7.1103

Coulter, J.M. (1885) *Manual of the botany (Phænogamia and Pteridophyta) of the Rocky mountain region, from New Mexico to the British boundary.* American Book Company, New York, 452 pp. https://doi.org/10.5962/bhl.title.29024

Greenman, J.M. (1899) Northwestern plants, chiefly from Oregon. *Erythea* 7: 115–120.

Hitchcock, C.L. & Cronquist, A. (1961) *Vascular plants of the Pacific Northwest, pt. 3: Saxifragaceae to Ericaceae.* University of Washington Press, Seattle, 614 pp.

Jepson, W.L. (1925) *A manual of the flowering plants of California*. Sather Gate Bookshop, Berkeley, 1238 pp.

Jepson, W.L. (1936) *A flora of California*. Volume 2. *Capparidaceae to Cornaceae.* Cunningham, Curtiss & Welch, San Francisco, 684 pp.

Koch, K. (1869) *Dendrologie; Bäume, Sträucher und Halbsträucher, welche in Mittel- und Nord- Europa im Freien kultivirt warden. Erster Theil*. Ferdinand Enke, Erlangen, 735 pp. https://doi.org/10.5962/bhl.title.20459

Kress, W.J., Wurdack, K.J., Zimmer, E.A., Weigt, L.A. & Janzen, D.H. (2005) Use of DNA barcodes to identify flowering plants. *Proceedings of the National Academy of Sciences, USA* 102: 8369–8374. https://doi.org/10.1073/pnas.0503123102

Kumar, S., Stecher, G., Li, M., Knyaz, C. & Tamura, K. (2018) MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution* 35: 1547–1549. https://doi.org/10.1093/molbev/msy096

Kuntze, O. (1891) *Schizonotus. Revisio Generum Plantarum* 1. A. Felix, Leipzig, pp. 225–226.

Ley, A. (1943) A taxonomic revision of the genus *Holodiscus* (Rosaceae). *Bulletin of the Torrey Botanical Club* 70: 275–288. https://doi.org/10.2307/2481437

Linnaeus, C. von (1781) *Supplementum plantarum Systematis vegetabilium editionis decimae tertiae, Generum plantarum editionis sextae, et Specierum plantarum editionis secunda.* Impensis Orphanotrophae, Brunsvigae, 468 pp. https://doi.org/10.5962/bhl.title.555

Lis, R.A. (1990) *A taxonomic revision of* Holodiscus *Maxim. (Spiraeoideae: Rosaceae) based upon numerical analyses of leaf morphometric variation.* Ph.D. Dissertation, University of California, Berkeley.

Lis, R.A. (1993) *Holodiscus. In*: Hickman, J.C. (Ed.) *The Jepson Manual: higher plants of California.* University of California Press, Berkeley, p. 953.

Lis, R.A. (2014) *Holodiscus* (K. Koch) Maximowicz, Trudy Imp. S.-Peterburgsk. Bot. Sada. 6: 253. 1879 *In*: Flora of North America Editorial Committee (Eds.) *Flora of North America north of Mexico, vol. 9: Magnoliophyta: Picramniaceae to Rosaceae.* Oxford University Press, New York and Oxford, pp. 415–421.

Maximowicz, C.J. (1879) Adnotationes de spiraeaces. *Trudy Imperatorskago S.-Peterburgskago Botaniceskago Sada. Acta Horti Petropolitani. St. Petersburg* 6: 105–261.

Potter, D. (2012) *Holodiscus. In*: Baldwin, J.C., Goldman, D.H., Keil, D.J., Patterson, R., Rosatti, T.J. & Wilken, D.H. (Eds.) *The Jepson manual: vascular plants of California. Second edition.* University of California Press, Berkeley, pp. 1179–1180.

Potter, D., Eriksson, T., Evans, R. C., Oh, S., Smedmark, J., Morgan, D.R., Kerr, M., Robertson, K.R., Arsenault, M., Dickinson, T.A. & Campbell, C.S. (2007a) Phylogeny and classification of Rosaceae. *Plant Systematics and Evolution* 266: 5–43. https://doi.org/10.1007/s00606-007-0539-9

Potter, D., Gao, F., Bortiri, P.E., Oh, S.-H. & Baggett, S. (2002) Phylogenetic relationships in Rosaceae inferred from chloroplast *matK* and *trnL-trnF* nucleotide sequence data. *Plant Systematics and Evolution* 231: 77–89. https://doi.org/10.1007/s006060200012

Potter, D., Still, S.M., Grebenc, T. Ballian, D. Božič, G. Franjiæ, J. & Kraigher, H. (2007b) Phylogenetic relationships in tribe Spiraeeae (Rosaceae) inferred from nucleotide sequence data. *Plant Systematics and Evolution* 266: 105–118. https://doi.org/10.1007/s00606-007-0544-z

Pursh, F.T. (1814) *Flora Americae Septentrionalis, or a systematic arrangement and description of the plants of North America, vol. 1.*White, Cochrane, and Co., London, 358 pp.

Rafinesque, C.S. (1836) *New flora and botany of North America, part 3.* Printed for the author and publisher, Philadelphia, 96 pp.

Rafinesque, C.S. (1838) *Sylva Telluriana. Mantis Synoptica. New genera and species of trees and shrubs of North America and other parts*. Printed for the author and publisher, Philadelphia, 184 pp. https://doi.org/10.5962/bhl.title.22070

Raiche, R. & Reveal, J.L. (2011) A new variety of *Holodiscus dumosus* (Rosaceae: Spiraeoideae) from coastal northwestern California. *Journal of the Botanical Research Institute of Texas* 5: 25–32.

Rydberg, P.A. (1904) Studies on the Rocky Mountain Flora-XII. *Bulletin of the Torrey Botanical Club* 31: 555–575. https://doi.org/10.2307/2478571

Rydberg, P.A. (1908) *Sericotheca*. *In*: *North American Flora*, vol. 22, part 4. The New York Botanical Garden, New York, pp. 261–266.

Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F. & Higgins, D.G. (1997) The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* 25: 4876–4882. https://doi.org/10.1093/nar/25.24.4876

Wen, J., Berggren, S.T., Lee, C-H., Ickert-Bond, S., Yi, T-S., Yoo, K-O., Xie, L., Shaw, J. & Potter, D. (2008) Phylogenetic inferences in *Prunus* (Rosaceae) using chloroplast *ndhF* and nuclear ribosomal ITS sequences. *Journal of Systematics and Evolution* 46: 322–332.

Zhang, S.D., Jin, J.J., Chen, S.Y., Chase, M.W., Soltis, D.E., Li, H.T., Yang, J.B., Li, D.Z. & Yi, T.S. (2017) Diversification of Rosaceae since the Late Cretaceous based on plastid phylogenomics. *New Phytologist* 214: 1355–1367. https://doi.org/10.1111/nph.14461