

**Observations on the comparative morphology of
Boechea horizontalis (Greene) Windham & Al-Shehbaz
and some of its nearest relatives**

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OBJECTIVES OF WORK:

The project was designed to provide information to aid rare plant management within Fremont-Winema National Forest, Rogue River-Siskiyou National Forest, and Crater Lake National Park, and specifically to provide useful comparisons of plant morphology to be used to distinguish *Boechea horizontalis* (the Crater Lake rockcress previously named *Arabis suffrutescens* var. *horizontalis*) from *Boechea lemmonii* (*Arabis lemmonii*), *Boechea suffrutescens* (*Arabis suffrutescens* var. *suffrutescens*), and other rockcresses with which it could be confused. A second objective was to gather and evaluate available evidence of the Crater Lake rockcress occurring in California or parts of Oregon outside of Crater Lake National Park.

WORK PERFORMED:

Literature was reviewed for *Boechea horizontalis* and related taxa. The most recent publication revising this genus is *Flora North America*, Volume 7, 2010, *Boechea*, by I.A. Shehbaz and M. Windham, available on line at:
http://www.efloras.org/flora_page.aspx?flora_id=1; search on *Boechea*

Nomenclature used in this report follows this treatment by Al Shehbaz and Windham. See Table 1 for synonymy.

Herbarium specimens of *Boechea horizontalis* and related taxa were examined from the following herbaria: CAS, CLRA, JEPS, OSC, ORE, UC, USNH, WILLU, and WTU (See Table 2). Specimens at WSU were not reviewed as they were on loan to Windham. Only the type specimens of *Arabis horizontalis* (= *Boechea horizontalis*) were borrowed from USNH (the United States National Herbarium, at the Smithsonian, Washington DC) and examined (see Figure 1).

Field studies were made with Wayne Rolle on 17 July 2009 to Liao Rock and Cloud Cap populations of *Boechea horizontalis* and to the Crater Lake National Park herbarium. Numerous photographs were taken on this date, both of field specimens and of herbarium material. A selection of these photographs were used in figures 3-9.

RESULTS:

Comments on *Boechea horizontalis* populations

Based on the examination of herbarium specimens and the Crater Lake visit on 17 July 2009, it was determined that the most recent *Flora North America* (referred to hereafter as FNA) treatment of *Boechea* cited above (Al Shehbaz and Windham, 2010) accurately describes the *Boechea horizontalis* morphology and geographic range, except for three items. Their description of this species is as follows:

45. ***Boechea horizontalis*** (Greene) Windham & Al-Shehbaz, Harvard Pap. Bot. 11: 266. 2007.

Arabis horizontalis Greene, Leaflet Bot. Observ. Crit. 2: 74. 1910; *A. suffrutescens* S. Watson var. *horizontalis* (Greene) Rollins

Perennials; long-lived; (ces-pitose); apomictic; caudex woody. **Stems** usually 1 per caudex branch, arising from center of rosette, near ground surface or somewhat elevated on woody base, or 1-3.5 dm, sparsely pubescent proximally, trichomes short-stalked, 3-6-rayed, 0.1-0.3 mm, glabrous distally. **Basal leaves**: blade narrowly oblanceolate, 1-5 mm wide, margins entire, ciliate near petiole base, trichomes (simple), to 0.4 mm, surfaces densely pubescent, trichomes short-stalked, 3-6-rayed, 0.1-0.3 mm. **Cauline leaves**: 3-13, often concealing stem proximally; blade auricles 0.5-1.5 mm, surfaces of distalmost leaves glabrous. **Racemes** 5-32-flowered, usually unbranched. **Fruiting pedicels** horizontal to descending, straight or slightly curved downward, 4-11 mm, glabrous. **Flowers** divaricate-ascending at anthesis; sepals pubescent; petals lavender to purple, 5-6 × 1.5-2 mm, glabrous; pollen spheroid. **Fruits** horizontal or descending, not appressed to rachis, secund, straight, edges slightly undulate (not parallel), 2-4 cm × 2-3 mm; valves glabrous; ovules 40-54 per ovary; style 0.2-0.5 mm. **Seeds** uniseriate, 2-2.5 × 1.7-2 mm; wing continuous, 0.5-1 mm wide.

Flowering Jul-Aug. Dry pumice slopes; Oreg.

Morphological evidence suggests that *Boechea horizontalis* is an apomictic species that arose through hybridization between *B. lemmonii* and *B. suffrutescens* (M. D. Windham and I. A. Al-Shehbaz 2007). *Boechea horizontalis* is known only from the vicinity of Crater Lake in south-central Oregon.

Observed difference 1: The basal leaves of this taxon can be glabrate to glabrous, as seen in specimens from near Cloud Cap, shown in Figure 4.

Observed difference 2: The fruits and fruiting pedicels can be divaricately ascending as well as spreading, secund, to divaricately descending. See Figure 4.

Observed difference 3: The geographic range may extend into California, as evidenced by the CAS specimen L. Ahart 5356 (see Figure 2 and Table 2). I agree with the Al-Shehbaz and Windham annotation that this probably is a plant of *Boechea horizontalis*, but think that a field visit is warranted in order to check the field population for floral characters and variability of fruit position, etc.

Comparison of *Boechera horizontalis* morphology with similar *Boechera* species

The FNA treatment also accurately describes the morphological differences between taxa considered in this report. However, due to the scope of the treatment and large number of taxa considered in the FNA treatment, this author will present simplified comparisons and images that will facilitate Rare Plant Botanists to differentiate between *B. horizontalis* and similar taxa which occur in the same environments.

For example, excerpting from the FNA treatment, *B. horizontalis* is compared with *B. lemmonii* as follows:

- 44. Cauline leaves with auricles 0.5--1.5 mm; petals 1.5--2 mm wide; fruiting pedicels 4--11 mm; fruits 2--3 mm wide; ovules 40--54 per fruit; seeds 2--2.5 x 1.7--2 mm; sc Oregon
44. *Boechera horizontalis* (in part)
- 44. Cauline leaves with auricles to 0.5 mm; petals 1--1.5 mm wide; fruiting pedicels 2--6 mm; fruits 1.6--2.3 mm wide; ovules 28--44 per fruit; seeds 1.3--2 x 1--1.5 mm; widespread in w North America 52. *Boechera lemmonii* (in part)

but is not directly compared with the other taxa (Table 1) considered in this report. Even in the example above, it is not readily apparent which are the critical characters one uses in order to differentiate these two taxa, but in the field *B. horizontalis* and *B. lemmonii* are readily distinguished from one another.

Presented below are suggested morphological characters to compare in order to differentiate between the taxa considered in this study. These comparisons are presented in Table 3; photographic images taken from Crater Lake populations of all taxa considered in this report are shown in Figures 3 through 9.

Boechera horizontalis* compared with *Boechera suffrutescens

The first comparison is logical, in that *B. horizontalis* was considered a subspecies of *B. suffrutescens* (see Table 1). Although the two taxa have similar leaf and fruit shapes, the two taxa can be readily distinguished by the elongate branching caudex found in *B. suffrutescens* (Figure 6b), but absent in *B. horizontalis* (Figure 3b, 4a, 4c, 5c), and by the "horizontal", or at least near-horizontal fruit position in *B. horizontalis* compared with that of *B. suffrutescens* (Figures 3f and 2g compared with Figures 6a, 6b, and 6d).

Boechera horizontalis* compared with *Boechera retrofracta

Boechera retrofracta is not represented in this report with images as it is easily distinguished from *B. horizontalis*: the former has pendant fruits (usually straight and numerous)

arising from strictly reflexed pedicels. In contrast *B. horizontalis* fruits are less numerous, broader, and their position is spreading ascending to horizontal or spreading descending.

Boechea horizontalis* compared with *Boechea lemmonii

It would be difficult to confuse these two taxa: fruits *Boechea horizontalis* (Figures 3a, 3f, and 3g) are wider, straighter, and usually less numerous compared with those of *B. lemmonii* (Figure 7a). In addition the leaves of *B. horizontalis* (Figures 3c, 3d, 4c, and 5b), while varying from hairy in the Llao Rock populations to glabrate in the Cloud Cap populations, are never whitish hairy with the fine white vestiture typically seen in the leaves of *B. lemmonii* (Figure 7b).

Boechea horizontalis* compared with *Boechea lyallii* and *Boechea platysperma

Boechea lyallii and *B. platysperma* each are very similar in form to *B. horizontalis* with respect to overall aspect, leaf shape, vestiture, and fruit shape, but *B. lyallii* and *B. platysperma* have ascending to erect fruits and pedicels (Figures 8b and 9d respectively). It is difficult to distinguish between *Boechea lyallii* and *B. platysperma* except for the broader fruits in *B. platysperma* (Figures 9e) and the relatively showy pink flowers of *B. lyallii* (Figure 5a).

Some plants of *Boechea horizontalis* were seen with spreading to ascending fruits (see Figure 4b). These may be distinguished from *Boechea lyallii* plants by the larger flowers with broader petal blades found in *B. lyallii* (see Figure 8a). They may be distinguished from plants of *B. platysperma* by the broader fruits found in *B. platysperma* (see Figure 9e).

SUMMARY AND COMMENTS:

Based on examination of herbarium specimens and especially of plants studied in the field, it is concluded that *Boechea horizontalis* is a valid taxon, and very rare: known only from the vicinities of Crater Lake and Mount McLoughlin. The only specimens seen of this taxon outside of this region was the Ahart 5356 collection (see Figure 2 and Table 2); I recommend field checks of this population, and recommend further protection of the Crater Lake habitat and study of *Boechea horizontalis* genetic background.

It has been proposed that *Boechea horizontalis* is of hybrid origin, and this hypothesis is now supported by Windham genetic research using microsatellites (personal communication via Wayne Rolle). Windham's comments are included below:

1) We got true *B. horizontalis* (similar to the type collection) at three locations: Llao Rock, Cloudcap, and Victor View. The microsatellite analyses reveal that all are apomictic triploid hybrids (as Ihsan and I had predicted based on pollen), but the parentage isn't quite what we expected. In Windham & Al-Shehbaz (2007), we hypothesized that *B. horizontalis* contained genomes from *B. suffrutescens* and *B. lemmonii*; it turns out that it also contains a genome derived from *B. lyallii*. Looking back at the morphology, this makes a lot of sense. Thus, *B. horizontalis* joins the ever expanding number of trigenomic triploids (a class of hybrids we originally thought were uncommon).

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2) The other "form" of *B. horizontalis* (the nearly glabrous type with more ascending fruits) that you pointed out along the access road to Cloudcap is very interesting. This turns out to be an apomictic diploid(!) hybrid between *B. suffrutescens* and *B. lyallii*...again, congruent with morphology. A genetically identical plant was collected by Wynd in 1929, suggesting that this unnamed taxon is capable of reproducing itself. Looking at range-wide microsatellite variability in the parents, it's pretty clear that this thing originated in the vicinity of Crater Lake...in fact, our collections of *B. lyallii* (Llao Rock) and *B. suffrutescens* (Rim Drive overlooking Kerr Valley) contain nearly all the alleles found in the hybrid.

3) Integrating items 1 and 2 above, the origin of a trigenomic triploid (Item 1) basically requires (predicts) the existence of a digenomic diploid hybrid (Item 2), which produces the trigenomic taxon by hybridizing with an unrelated sexual diploid. In the case of *B. horizontalis*, the unnamed diploid hybrid from Cloudcap could be a "stepping stone" that led to the formation of the triploid (by hybridizing with *B. lemmonii* which, interestingly, is present at Cloudcap). As with all trigenomics, however, there are three possible digenomic "stepping stones" leading to *B. horizontalis*: a) *suffrutescens* x *lyalli* [the taxon you found], b) *suffrutescens* x *lemmonii*, and 3) *lemmonii* x *lyallii*. The microsatellite data clearly indicate that the genotype of *suffrutescens* x *lyallii* that we have in hand was NOT involved in the origin of *B. horizontalis*. So, we still have some work to do (more intensive DNA sampling of local plants) with regard to the genomic diversity of Crater Lake *Boechea* and the origin of *B. horizontalis*.

My own hesitation at describing apomictic *Boechea* species or infraspecific taxa is that there are many small localized populations which may represent hybrid clones such as described above. I observed this for many taxa in my research (Vorobik, 1985. *Hybridization and reproductive isolation between sympatric Arabis (Cruciferae) in southwestern Oregon*. PhD Dissertation. University of Oregon, Eugene.), and of specimens or photographs which have been sent to me for determination. It would seem imprudent to name all of these populations, especially if each commanded Federal protection due to its small geographic range. I will leave this problem for others to weigh in on.

Table 1. Scientific Names, authorities, and latest publication for cited name of *Boechera* taxa considered for this report.

Taxonomy according to Shehbaz, I.A. and M. Windham, Flora North America, Volume 7, 2010, available on line (3/14/2010) at:
http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=104152

Boechera horizontalis (Greene) Windham & Al-Shehbaz, Harvard Pap. Bot. 11: 266. 2007

Previous name: *Arabis suffrutescens* var. *horizontalis*

Boechera lemmonii (S. Watson) W. A. Weber, Phytologia. 51: 370. 1982.

Previous name: *Arabis lemmonii*

Boechera lyallii (S. Watson) Dorn, Vasc. Pl. Wyoming ed. 3. 376. 2001.

Previous name: *Arabis lyallii*

Boechera platysperma (A. Gray) Al-Shehbaz, Novon. 13: 388. 2003.

Previous name: *Arabis platysperma*

Boechera retrofracta (Graham) Á. Löve & D. Löve, Taxon. 31: 125. 1982.

Previous name: *Arabis holboellii* var. *retrofracta*

Boechera suffrutescens (S. Watson) Dorn, Brittonia. 55: 3. 2003.

Previous name: *Arabis suffrutescens* var. *suffrutescens*