AN OVERVIEW OF NEW MEXICAN *BOECHERA* (BRASSICACEAE) INCLUDING THREE NEW SPECIES AND THIRTEEN NEW NOMENCLATURAL COMBINATIONS

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ABSTRACT

To provide a nomenclatural foundation for the treatment of *Boechera* in the soon-to-be-published *Flora of New Mexico*, we here discuss the current taxonomic situation in the genus, name three new species (**B. austromontana**, **B. pseudoconsanguinea**, and **B. quadrangulensis**), provide new combinations for **B. kelseyana**, **B. thompsonii**, and **B. villosa** as subspecies of *B. crandallii*, and propose subspecific names under *B. perennans* for nine taxa currently treated as species.

RESUMEN

Para proporcionar una base nomenclatural para el tratamiento de *Boechera* en la *Flora of New Mexico*, que pronto se publicará, discutimos aquí la situación taxonómica actual en el género, nombramos tres nuevas especies (**B. austromontana**, **B. pseudoconsanguinea** y **B. quadrangulensis**), proporcionamos nuevas combinaciones de **B. kelseyana**, **B. thompsonii** y **B. villosa** como subespecies de *B. crandallii*, y proponemos nombres subespecíficos bajo *B. perennans* para nueve taxones tratados actualmente como especies.

INTRODUCTION

Over its relatively short evolutionary history, the mustard genus *Boechera* has experienced a phenomenal amount of evolutionary diversification (Rushworth et al. 2011). Although the most recent broad-scale taxonomic treatment for the genus (Al-Shehbaz & Windham 2010) recognized just 111 taxa in North America, ongoing genus-wide microsatellite analyses paint a very different picture (Li et al. 2017). These studies reveal that, in addition to ±83 genetically recognizable sexual diploid taxa, the genus includes 400+ polyploid and/or apomictic hybrids representing diverse combinations of at least 64 of the known sexual entities. Clearly, significant adjustments to the current taxonomy will be needed if we hope to produce a classification useable by a diversity of stakeholders. This effort will require both significant expansion of existing species boundaries as well as the segregation and naming of new species that cannot otherwise be accommodated in the classification. Here we discuss the application of these concepts to the *Boechera* taxa of New Mexico.

Sexual diploids and their intra-clade apomictic derivatives.—The *Flora of New Mexico* will recognize four species of *Boechera* for the state that consist primarily of sexual diploids: *B. crandallii* (B.L. Rob.) W.A. Weber *s.l.*, *B. perennans* (S. Watson) W.A. Weber *s.l.*, *B. pulchra* (M.E. Jones) W.A. Weber *s.l.*, and *B. stricta* (Graham) Al-Shehbaz. The latter, with its longitudinally aligned, sessile, 2-rayed (malpighiaceous) trichomes on basal leaves, is one of the most distinctive species in the genus, and collections from New Mexico closely resemble the type specimens from western Canada, so no taxonomic adjustments are needed. Most herbarium collections of *B. stricta* were originally identified as *Arabis drummondii* A. Gray, and thus those who annotate specimens should be aware that the correct name for this species in *Boechera* is *B. stricta*, not *B. drummondii* (A. Gray) Á. Löve & D. Löve nor *B. angustifolia* (Nutt.) Dorn (see Al-Shehbaz 2003).

Regarding *Boechera pulchra s.l.*, we here adopt a broader circumscription of the species coinciding with the pubescent-fruited clade belonging to the "*B. pulchra* group" of Alexander et al. (2013). Although the three sexual diploid taxa split from *B. pulchra* by Windham and Al-Shehbaz (2006) are morphologically recognizable and largely allopatric, they exhibit convergent reticulate relationships that make it nearly impossible to

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determine which of the three was involved in the origin of a particular hybrid. Restoring these three sexual diploids to infraspecific status within *B. pulchra s.l.* simplifies the species level taxonomy of *Boechera* and focuses attention on the hybrids occurring between clades, which are often recognizable by variations in fruit pubescence [e.g., *B. duchesnensis* (Rollins) Windham & Al-Shehbaz or *B. xylopoda* Windham & Al-Shehbaz; see Al-Shehbaz and Windham 2010]. For the New Mexican flora, the expansion of *B. pulchra* simply involves resurrecting the name *B. pulchra* (M.E. Jones ex S. Wats.) W.A. Weber subsp. *pallens* (M.E. Jones) W.A. Weber for the taxon called *B. formosa* (Greene) Windham & Al-Shehbaz in the Flora of North America (Al-Shehbaz & Windham 2010).

The most significant realignment of species boundaries involves *Boechera perennans s.l.* In this case, we have chosen to rename all species belonging to the *B. fendleri* (S. Watson) W.A. Weber group (Alexander et al. 2013, 2015) as subspecies under the oldest available species name, *B. perennans*. Our rationale for this rests on the clear unsustainability of our current taxonomic trajectory. This group includes nine sexual diploid taxa treated as species in the Flora of North America (Al-Shehbaz & Windham 2010). These appear to be quite recently diverged and can be difficult to distinguish morphologically (e.g , the long-running controversy over whether *Arabis* (*Boechera*) *pendulina* is conspecific with *A. demissa*; see Welsh 2003). What makes the current taxonomy untenable is the extensive hybridization among these sexual diploids, which has given rise to at least 25 genetically distinct diploid and triploid lineages that reproduce via apomixis and have ranges equaling or exceeding those of many sexual diploids (Windham et al. in prep.). Treating all such hybrids as species (which is required if their sexual diploid parents are considered separate species; see Article H.5.1 in the Shenzhen Code, Turland et al. 2018) would result in a completely unworkable species-level classification. Renaming all recognized taxa in the *B. perennans* clade as subspecies represents a compromise that attempts to balance the interests of diverse taxonomic stakeholders. On the one hand, it provides the nomenclature needed by users who are detail-driven (e.g., evolutionary biologists) and, in fact, it facilitates the description of new taxa whose distinguishing features would be considered insufficient for species recognition. At the same time, it highlights the major morphological characters defining the group (i.e , widely pendent fruits, sparingly branched trichomes, mostly biseriate seeds; Alexander et al. 2013), thus facilitating the recognition of hybrids among major clades. More details regarding this approach, plus the necessary new combinations for the entire North American flora, will be presented in a separate paper (Windham et al , in prep.). Considering only those taxa present in New Mexico, this expanded circumscription of *B. perennans s.l.* (see nomenclatural details below) encompasses nine taxa treated as species by Alexander et al. (2015): four sexual diploids [*B. fendleri, B. gracilipes* (Greene) Dorn, *B. perennans*, and *B. spatifolia* (Rydb.) Windham & Al-Shehbaz), four apomictic diploids (*B. carrizozoensis* P.J. Alexander, *B. centrifendleri* P.J. Alexander, *B. sanluisensis* P.J. Alexander, and *B. zephyra* P.J. Alexander), and one apomictic triploid [*B. porphyrea* (Wooton & Standl) Windham, Al-Shehbaz & P.J. Alexander). An additional eight unnamed apomictic taxa (four diploids, three triploids, and one tetraploid) documented for New Mexico in the *Boechera* Microsatellite Website (Li et al. 2017) are also subsumed under this concept of *B. perennans s.l.* We here make the following new combinations for the named taxa present (or very likely to occur) in New Mexico:

Boechera perennans (S. Wats.) W.A. Weber subsp. **carrizozoensis** (P.J. Alexander) Windham, **comb. et stat. nov.** Basionym: *Boechera carrizozoensis* P.J. Alexander, Syst. Bot. 40:592. 2015. Type: U.S.A. New Mexico. Socorro Co.: Oscura Mts., Garden Spring Canyon, slopes on NW side of Chicken Spring, 9.2 mi NNE of Oscura Peak, 29 Apr 2010, *P.J. Alexander 1160* (holotype: NMC; isotypes: BRY, DUKE!, MO).

Boechera perennans (S. Wats.) W.A. Weber subsp. **centrifendleri** (P.J. Alexander) Windham, **comb. et stat. nov.** Basionym: *Boechera centrifendleri* P.J. Alexander, Syst. Bot. 40:593. 2015. Type: U.S.A. New Mexico. Cibola Co.: Ojo Redondo in the eastern Zuni Mts., 13 mi W of Grants, 1.3 mi SSW of Mount Sedgwick, 19 May 2014, *P.J. Alexander 1450* (holotype: NMC; isotypes: ARIZ, ASU, BRY, DUKE!, MO, TEX, UNM).

Boechera perennans (S. Wats.) W.A. Weber subsp. **fendleri** (S. Wats.) Windham, **comb. et stat. nov.** Basionym: *Arabis holboellii* Hornem. var. *fendleri* S. Wats. in A. Gray, Synop. Fl. N. Amer. 1:164. 1895. Type: U.S.A. New Mexico: from Santa Fe E to Rabbit Ear Creek, 10–20 Aug 1847, *A. Fendler 27* (holotype: GH!; isotypes: MO!, NY, UC).

Boechera perennans (S. Wats.) W.A. Weber subsp. **gracilipes** (Greene) Windham, **comb. et stat. nov.** Basionym: *Arabis gracilipes* Greene, Pittonia 4:193–194. 1900. Type: U.S.A. Arizona. Coconino Co.: Flagstaff, May 1893, *N.C. Wilson s.n.* (holotype: NDG 4325!; isotype: NDG 4359!).

Boechera perennans (S. Wats.) W.A. Weber subsp. **perennans**. Basionym: *Arabis perennans* S. Wats. Proc. Amer. Acad. Arts 22:467. 1887. Type: U.S.A. Arizona. Pima Co.: Santa Catalina Mts., 15 Apr 1881, *C.G. Pringle s.n.* (holotype GH!; isotypes MO!, NY!).

Boechera perennans (S. Wats.) W.A. Weber subsp. **porphyrea** (Wooton & Standl.) Windham, **comb. et stat. nov.** Basionym: *Arabis porphyrea* Wooton & Standl., Contr. U.S. Natl. Herb. 16:123. 1913. Type: U.S.A. New Mexico. Doña Ana Co.: in the Organ Mountains at the Cueva, 25 Apr 1907, *E.O. Wooton & P.C. Standley s.n.* (holotype: US!).

Boechera perennans (S. Wats.) W.A. Weber subsp. **sanluisensis** (P.J. Alexander) Windham, **comb. et stat. nov.** Basionym: *Boechera sanluisensis* P.J. Alexander, Syst. Bot. 40:594. 2015. Type: U.S.A. New Mexico. Taos Co.: Carson National Forest, S side of F.R. 97 on the W side of US Hwy 285, ±7.5 mi SSE of Tres Piedras, 19 May 2008, *P.J. Alexander 752* (holotype: NMC; isotypes: DUKE!, MO).

Boechera perennans (S. Wats.) W.A. Weber subsp. **spatifolia** (Rydb.) Windham, **comb. et stat. nov.** Basionym: *Arabis spatifolia* Rydb., Fl. Rocky Mts. 361. 1917. Type: U.S.A. Colorado. Larimer Co.: Estes Park, 20 July 1903, *G.E. Osterhout 2808* (holotype: NY!; isotype: RM!).

Boechera perennans (S. Wats.) W.A. Weber subsp. **texana** (Windham & Al-Shehbaz) Windham, **comb. et stat. nov.** Basionym: *Boechera texana* Windham & Al-Shehbaz, Harvard Pap. Bot. 11:85. 2006. Type: U.S.A. Texas. Culberson Co.: San Antonio Peak, Sierra Tinaja Pinta, 26 Apr 1961, *R.C. Rollins & D.S. Correll 61142* (holotype: GH!; isotype: LL!).

Boechera perennans (S. Wats.) W.A. Weber subsp. **zephyra** (P.J. Alexander) Windham, **comb. et stat. nov.** Basionym: *Boechera zephyra* P.J. Alexander, Syst. Bot. 40:594–595. 2015. Type: U.S.A. New Mexico. Otero Co.: Cornudas Mountains, NE side of Wind Mountain, 0.9 mi NE of the summit, 2.2 mi N of the Texas state line, 10 Apr 2010, *P.J. Alexander 1136* (holotype: NMC; isotypes: BRY, DUKE!, MO, TEX, UC).

The taxonomic situation in *Boechera crandallii s.l.* is only slightly less complex than that encountered in *B. perennans s.l.*, but New Mexico is at the southeastern edge of its distribution and taxon diversity is relatively low here. Locally, the group includes three sexual diploid taxa currently treated under the specific names *B. kelseyana* Windham & Allphin (Windham et al. 2015), *B. thompsonii* (S.L. Welsh) N.H. Holmgren (see Holmgren 2005), and *B. villosa* Windham & Al-Shehbaz (see Windham & Al-Shehbaz 2006), plus an apomictic diploid hybrid between the first two. The recognition of these taxa as separate species greatly complicates the taxonomy of *Boechera* in the region because they are involved in numerous inter-clade hybridization events but are too similar for one to be able to determine morphologically which taxon was involved in the origin of a particular hybrid. A full taxonomic overview of *B. crandallii s.l.* (Windham et al., in prep.) cannot be completed prior to publication deadlines for the *Flora of New Mexico* so, to provide the necessary names, we here make the following new nomenclatural combinations:

Boechera crandallii (B.L. Rob.) W.A. Weber subsp. **kelseyana** (Windham & Allphin) Windham & Allphin, **comb. et stat. nov.** Basionym: *Boechera kelseyana* Windham & Allphin, Syst. Bot. 40:1041–1042. 2015. Type: U.S.A. Arizona. Apache Co.: SSE of Nazlini on bench of Red Mesa near Indian Route 27 ca. 2.35 road mi NW of its junction with Indian Route 26. (35.8752N 109.4433W; WGS84 Datum), 6,825 ft. elev., in sandy duff soil under *Juniperus* on gentle NW-facing slope with *Artemisia, Cercocarpus* & *Pinus* nearby, 21 Apr 2001, *M.D. Windham & D. Roth 2320* (holotype: DUKE 398927!; isotypes: ARIZ!, ASC!, ASU!, BRY!, GH!, MO!, NMC 77565!, NY!, RM!, RSA!, SJNM!, UC!, UNM!, UT!).

Boechera crandallii (B.L. Rob.) W.A. Weber subsp. **thompsonii** (S.L. Welsh) Windham & Allphin, **comb. et stat. nov.** Basionym: *Arabis thompsonii* S.L. Welsh, Utah Fl., ed. 3. 260. 2003. Type: U.S.A. Utah. San Juan Co.: south [according to labels on type specimens; incorrectly cited as "north" in protologue] of Beef Basin, head of South Canyon below Wild Cow Point (T33S, R18E, S9), 2250 m elev., sandy soil in alcove, 5 Jun 1985, *N.D. Atwood & B. Thompson 11154* (holotype: BRY 288242!; isotype: BRY 510589!).

Boechera crandallii (B.L. Rob.) W.A. Weber subsp. **villosa** (Windham & Al-Shehbaz) Windham & Allphin, **comb. et stat. nov.** Basionym: *Boechera villosa* Windham & Al-Shehbaz, Harvard Pap. Bot. 11:86–87. Type: U.S.A. New Mexico. Taos Co.: Sangre de Cristo Mts., bottom of Rio Grande Canyon, 2 mi N of confluence with Red River, 6800 ft, pinyon-juniper woodland on Quaternary basalt, 17 May 1979, *W.L. Baker 1113* (holotype: NMC 51277!).

Inter-clade apomictic hybrids.—In addition to the four sexual *Boechera* species and their intra-clade apomictic derivatives discussed above, the *Flora of New Mexico* will recognize seven exclusively apomictic species arising from hybridization between or among divergent clades. These consist of four previously named hybrid species [*B. consanguinea* (Greene) Windham & Al-Shehbaz, *B. lignifera* (A. Nelson) W.A. Weber, *B. gracilenta* (Greene) Windham & Al-Shehbaz], and *B. selbyi* (Rydb.) W.A. Weber] plus three new species (*B. austromontana, B. pseudoconsanguinea,* and *B. quadrangulensis*) described below. *Boechera consanguinea* was treated as a distinct species by Al-Shehbaz and Windham (2010), who hypothesized that it represented an apomictic hybrid between *B. fendleri* (herein *B. perennans* subsp. *fendleri*) and *B. retrofracta* (Graham) Á. Löve & D. Löve. Recently obtained simple sequence repeat (SSR) DNA data analyzed using the *Boechera* Microsatellite Website (Li et al. 2017) disprove this hypothesis. These analyses reveal that *B. consanguinea* is a trigenomic apomictic triploid incorporating genomes from *B. perennans* subsp. *gracilipes, B. retrofracta*, and *B. exilis* (A. Nelson) Dorn (recently shown to be distinct from *B. retrofracta*; Schilling et al. 2018). This is a unique combination of genomes, and it is clear from our studies that *B. consanguinea* (represented in our DNA analyses—data not shown here—by the holotype at NDG plus 47 other specimens scattered from Colorado to California) is one of the most successful hybrids in the genus. As such, it will be maintained as a separate species in the *Flora of New Mexico.*

Based on integrated morphological, cytological, and microsatellite DNA analyses, Windham et al. (2015) separated specimens previously identified as *Boechera lignifera* into two species, *B. lignifera s.s.* and *B. kelseyana* (herein called *B. crandallii* subsp. *kelseyana*). All New Mexican plants attributed to *B. lignifera* by Al-Shehbaz and Windham (2010) represent *B. crandallii* subsp. *kelseyana*. However, *B. lignifera s.s.* occurs within 2.3 km of the New Mexico border (Windham et al. 2015) and will almost certainly be found in the state. Therefore, *B. lignifera s.s.*, now known to be an apomictic diploid hybrid between *B. exilis* and *B. crandallii* subsp. *thompsonii* (Windham et al., in prep.) will be included in the *Flora of New Mexico.*

Boechera gracilenta, often considered a synonym of *B. perennans* (e.g., Holmgren 2005), was treated as a distinct species [a probable hybrid between *B. fendleri* and *B. pallidifolia* (Rollins) W.A. Weber] in the Flora of North America (Al-Shehbaz & Windham 2010). Simple sequence repeat (SSR) DNA data analyzed using the *Boechera* Microsatellite Website (Li et al. 2017) reveal that the original Windham and Al-Shehbaz (2007b) hypothesis regarding the parentage of *B. gracilenta* requires modification. Analyses of the holotype and isotype curated at NDG indicate that *B. gracilenta s.s.* is an apomictic diploid hybrid incorporating genomes from the taxa herein called *B. perennans* subsp. *fendleri* and *B. crandallii* subsp. *kelseyana*. Hybridization between *B. perennans s.l.* and *B. crandallii s.l.* as defined here has been rampant in the region of geographic overlap (the Colorado Plateau and Great Basin), leading to the formation of at least 32 genetically distinct apomicts (nine of which occur in New Mexico). Treating each of these as a distinct species (as would be required under the taxonomy adopted by Al-Shehbaz and Windham 2010; Alexander et al. 2015; and Windham et al. 2015) is untenable. We therefore combine them under the oldest available name for an interspecific hybrid between *B. perennans s.l.* and *B. crandallii s.l.*, which is *B. gracilenta*.

Boechera selbyi, another previously named hybrid species to be included in the *Flora of New Mexico*, has a complex history of misapplication. Rollins (1941, 1993) associated the epithet *selbyi* with the taxon that we here call *B. crandallii* subsp. *thompsonii*. Holmgren (2005) referred to this same entity as var. *selbyi* and broadened the concept by including (as varieties) plants formerly recognized as *Arabis perennans* S. Watson var. *thorneae* S.L. Welsh and *Boechera inyoensis* (Rollins) Al-Shehbaz. In the *Flora of North America*, Al-Shehbaz and Windham (2010) took a radically different approach and treated *B. selbyi* as a synonym of *Boechera gracilenta*. Recent analyses using the *Boechera* Microsatellite Website (Li et al. 2017) indicate that none of these previous taxonomic treatments accurately reflect the relationships of *B. selbyi*. DNA data from the holotype (curated at NY) and ten other populations from Colorado, New Mexico, and Utah reveal that this taxon is an apomictic diploid hybrid between *B. perennans* subsp. *gracilipes* and *B. retrofracta* (Windham et al., in prep.). The presence of a genome derived from *B. retrofracta* in *B. selbyi* distinguishes it from all other taxa with which it has been associated in the past and, as such, *B. selbyi* will be recognized as a distinct species in the *Flora of New Mexico.*

A new hybrid species involving *Boechera stricta*.—With its distinctive sessile, appressed, 2-rayed (i.e., malpighiaceous) trichomes oriented along the axis of the basal leaves, *Boechera stricta* is one of the most recognizable species in the genus. It occurs in every state and province in western North America (Al-Shehbaz & Windham 2010) and, as a result, its distribution overlaps with many other taxa in the genus. This has resulted in a complex array of apomictic hybrids, the taxonomy of which has been difficult to resolve. In his species compilation for North America, Rollins (1993) united most of these hybrids under the name *Arabis divaricarpa* A. Nelson, an approach also taken by Mulligan (1995) in his work on the Canadian and Alaskan species. Following the transfer of this species group to *Boechera* (Al-Shehbaz 2003), Windham and Al-Shehbaz (2007b) addressed some of the nomenclatural problems by parsing collections assigned to *B. divaricarpa* (A. Nelson) Á. Löve & D. Löve among six species based on hypothesized parentage. More recently, microsatellite DNA analyses of a broad sampling of *Boechera* collections (Beck et al. 2011) have identified a distinctive taxon from the southwestern United States that arose through hybridization between *B. stricta* and *B. perennans* subsp. *fendleri*. This stable, apomictic diploid hybrid occurs in New Mexico and has not been previously named. Here we describe it as:

Boechera austromontana Windham & Allphin, **sp. nov. (Fig. 1)**. Type: U.S.A. Colorado. Archuleta Co.: SSE of Pagosa Springs near edge of Kenney Flats along Forest Route 006B ca. 0.4 road mi NE of its intersection with US Route 84 (37.1078N 106.9145W; WGS84 Datum), 7,700 ft. elev., in duff-covered clay loam on gentle, SE-facing slope with *Quercus*, *Pinus*, *Delphinium*, *Berberis*, *Lupinus* & *Antennaria*, 14 May 2014, *M.D. Windham 4182 & P.J. Alexander* (holotype: DUKE 405276!; isotypes: ASU!, BRY!, COLO!, GH!, MO!, NMC!, NY!, UC!, UNM!, US!, UT!, UTC!).

Most like *Boechera grahamii* (Lehm.) Windham & Al-Shehbaz *s.s.* but differing (see Fig. 2) in having 1) mature fruits mostly ascending (vs. divaricate-descending or pendent), 2) basal leaves with sessile to subsessile trichomes with appressed branches (rays), at least some of these malpighiaceous with two, ± equal rays diverging at 180° (vs. short stalked, ± spreading, mostly 3- to 4-rayed and none malpighiaceous), 3) middle cauline leaves generally glabrous (vs. sparsely hirsute), and 4) sepals glabrous or, if exhibiting a few trichomes (< 20%), these 2-rayed (vs. 3- to 4-rayed).

Plants mostly short-lived perennials, the caudices branched or unbranched, rarely woody and usually not raised above ground level, producing a cluster of ± decumbent rosette leaves distally, these largely deciduous in fruiting individuals. Rosette leaves oblanceolate, 18–40 × 3.8–8 mm, entire or slightly dentate, with enlarged, simple, spurred, and 2-rayed cilia to 0.8 mm long extending from petiole to proximal half (sometimes all) of blade margins; rosette blade surfaces appressed pubescent with subsessile, predominantly (60–90%) 2-rayed trichomes to 0.8 mm long and lesser numbers (10–40%) of 3-rayed trichomes. Sterile short shoots with tuft of ascending leaves often present, the leaves narrowly oblanceolate, 30–53 × 3.5–7 mm, similar to rosette leaves except with fewer (< 5%) simple cilia and a somewhat higher density (5–15 per mm^2) of surface trichomes. Fertile stems 1(2–4) per caudex branch, terminal or arising laterally below sterile short shoot, 3–7 dm long, 1.1–2.8 mm in diameter at base, lower parts glabrous or occasionally with a variable mixture of simple and 2-rayed, mostly spreading trichomes to 0.6 mm long; upper parts of stems glabrous. Cauline leaves 7–28, those at the middle of the stem predominantly glabrous, the uppermost with auricles 0.8–3.2 mm long. Inflorescences simple racemes or sparingly branched, the main axis 12–34-flowered, not secund; lowermost fruiting pedicels 8–16 mm long, ascending, straight or gently up-curved distally, glabrous (rarely with sparse trichomes). Flowers: sepals 3.0–5.4 mm long, greenish to dull lavender, predominantly glabrous but, when sparsely hirsute (< 20%), the trichomes 2-rayed (a few simple); petals 6–9 × 0.9–1.6 mm, mostly pale lavender, glabrous; anthers cream-colored, producing variable percentages of malformed and well-formed pollen grains, the latter mostly ovoid-spheroid and averaging 20 µm wide with 4 or more asymmetrically arranged apertures; ovaries glabrous, usually with 40–84 ovules per fruit, forming seeds apomictically through both diplosporous and aposporous pathways in the type collection. Fruits (the largest) 4.2–8.0 cm × 1.5–2.0 mm at maturity, ascending, curved slightly downward or straight, glabrous; styles 0.15–0.4 mm long. Seeds in two irregular rows near center of fruit, 1.2–1.7 × 0.7–1.1 mm, with pale marginal wing 0.15–0.3 mm wide, the wing continuous from funiculus along radicle side for 2/3 of circumference (rarely confined to distal 1/2). Chromosome number (from the type collection) $2n = 14$, with variable pairing during microsporogenesis (ranging from 14 univalents to 7 bivalents).

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PLANTS OF **COLORADO**, U.S.A.

Boechera austromontana Windham & Allphin (apomictic diploid hybrid)

ARCHULETA CO.: SSE of Pagosa Springs near edge of Kenney Flats along Forest Route 006B ca. 0.4 road miles NE of its intersection with US Route 84. Lat./Long.: 37.1078N 106.9145W (WGS84 Datum). Elev. 7700 ft.

In duff-covered clay loam on gentle, SE-facing slope with Quercus, Pinus, Delphinium, Berberis, Lupinus & Antennaria.

M.D. Windham (4182) 14 May 2014
P.J. Alexander Brassicaceae

Vascular Plant Herbarium, Duke University, Durham, NC
ASU; BRY; COLO; DUKE; GH; MO; NMC; NY; UC; UNM; US; UT; UTC

BOECHERA AUSTROMONTANA HYBRID COMPLEX

Haploid OTUs inferred: fendleri; stricta (1:1)

Species name available for plants with this genomic composition:

Boechera fendleri (S. Wats.) W.A. Weber × B. stricta (Graham) Al-Shehbaz (apomictic diploid)

M.D. Windham (2015) Extrac#: FW1543 DUKE Herbarium

Fig. 1. Holotype of *Boechera austromontana*.

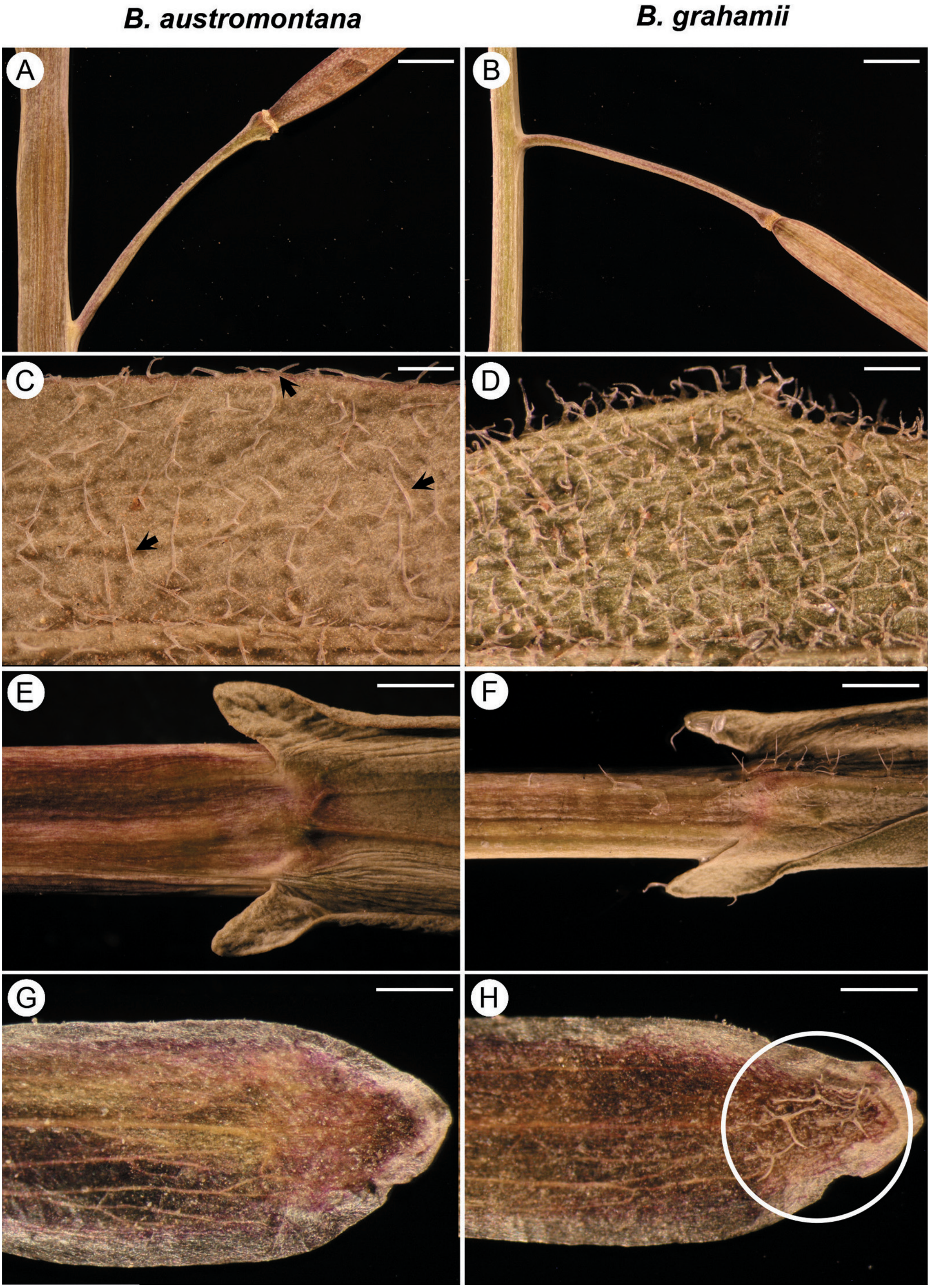

Fig. 2. Morphological comparisons of *Boechera austromontana* (left column) and *B. grahamii* (right column). (**A–B**) Orientation of lower fruiting pedicels relative to rachises; scale bars = 2 mm. (**C–D**) Pubescence on abaxial surfaces of lower leaves; scale bars = 0.5 mm; arrows in C identify malplghiaceous trichomes. (**E–F**) Stem and proximal portion of middle cauline leaves showing pubescence on abaxial surfaces; scale bars = 1 mm. (**G–H**) Sepal pubescence; scale bars = 0.5 mm; circle in H highlights location of trichomes.

Paratypes. **ARIZONA. Coconino Co.:** Big Springs, North Rim, Grand Canyon National Park, *Machina & Huisinga 2432* [ASC 70958]. **COLORADO. Archuleta Co.:** FS Road 006 ca. 1/2 mi from US 84 ca. 14 mi S of Pagosa Springs (37°06'29cN 106°54'50"W), *Heil & Heil 21882* [SJNM 46443]. **Conejos Co.:** 3.3 mi W of Aspen Glade Campground along highway from Antonito to Chama, *Mosquin & Mosquin 4575* [DAO 599488]; Conejos Campground, campsite #12, on S side of F.R. 250 in bottom of Conejos River Canyon ±5.6 mi NW of jct. with CO Hwy 17, ±0.15 mi WNW of Spectacle Lake, *Alexander 761* [DUKE, MO NMC]; Conejos Campground, along Conejos River ca. 4 mi NW of junction with Cumbres Pass Road, *Weber 7845* [GH]. **NEW MEXICO. Taos Co.:** W base of the Taos Mountains along an unlabeled forest road, ±3 mi S of Questa, ±1.2 mi NE of Lama, *Alexander 615* [DUKE 398992, NMC 78599]. UTAH. **Kane Co.:** W of Long Valley Junction along Strawberry Creek near UT 14 ca. 0.78 km WSW of Cold Spring (37°30'29"N 112°37'18"W; WGS84 Datum), *Windham 3600* [DUKE 400113]

Distribution, Habitat and Phenology.—*Boechera austromontana* is known from northern Arizona and New Mexico, as well as southern Colorado and Utah. It favors clay loam soils in open pine-oak woodland or semi-riparian habitats at elevations of 2300–2700 m. The species blooms from early May to early July and produces mature seeds in July and August.

Etymology and additional comments.—The specific epithet chosen is a combination of *austro-* (southern) and *montana* (mountain), highlighting its exclusive occurrence in the southern Rocky Mountain region. Although future studies may reveal a broader distribution, *B. austromontana* does not appear to overlap with *B. grahamii*, which occurs to the north and east and has not been collected south of El Paso County, Colorado. In addition to the characters mentioned in the diagnosis above, one other morphological trend can help distinguish *B. austromontana* from *B. grahamii*. In the latter species, a single flowering stem arises from the center of each fertile leaf rosette and sterile short shoots with tufted ascending leaves are absent. By contrast, about half of the *B. austromontana* plants observed have sterile short shoots terminating the caudex branches and, in these cases, the flowering stem (occasionally more than one) arises lateral to the short shoot (between the decumbent rosette leaves and the ascending leaf tuft).

A new hybrid species segregated from *Boechera consanguinea*.—Microsatellite DNA analyses of *Boechera* collections from the Four Corners region reveal that some specimens previously identified as *B. consanguinea* by Windham and Al-Shehbaz (2007a) cannot be classified as such given their divergent parentage. Typical specimens of *B. consanguinea* are stable, apomictic triploids containing genomes from *B. exilis, B. perennans* subsp. *gracilipes*, and *B. retrofracta* (Windham et al., in prep.). However, there are a few populations from northern New Mexico and Arizona in which the *B. retrofracta* genetic contribution is replaced by a genome from *B. crandallii* subsp. *kelseyana*. To acknowledge this genomic difference, we herein name this newly documented hybrid:

Boechera pseudoconsanguinea Windham & Allphin, **sp. nov. (Fig. 3)**. Type: U.S.A. New Mexico. San Juan Co.: NE of Aztec in Hart Canyon on slope above Hart Canyon Road (Route 2770) ca. 1.0 road mi ESE of its intersection with U.S. Route 550 (36.8672N 107.9328W; WGS84 Datum), 5925 ft. elev., among cobbles (igneous) in sandy alluvial soil on NW-facing slope with *Artemisia, Juniperus, Yucca, Pleuraphis & Aristida*, 15 May 2014, *Windham 4187, Allphin & Alexander* (holotype: DUKE 406710!; isotypes: BRY!, COLO!, GH!, MO!, NY!, NMC!, RM!, US!, UT!, UTC!).

Most similar to *Boechera consanguinea* but differing (see Fig. 4) in having 1) mature fruits widely pendent with their bases positioned 6.5–15 mm from rachises (vs. closely pendent with bases positioned 1–6 mm from rachises), 2) basal leaves mostly entire (vs. denticulate), 3) shorter sepals (2.5–3.5 vs. 3.3–5.1 mm at full anthesis), and 4) less pubescent fruiting pedicels (< 25% pubescent and these with < 20 trichomes attached to the visible surfaces vs. > 90% pubescent with 20–140 trichomes).

Plants mostly short-lived perennials, the caudices usually unbranched, non-woody and not raised above ground level, producing a cluster of rosette leaves distally, these mostly deciduous in fruiting individuals, the caudices lacking crowded, persistent leaf bases. Rosette leaves oblanceolate, 20–48 × 3.5–7 mm, entire or denticulate with 1–2 pairs of teeth to 0.2 mm, most with enlarged, simple and 2-rayed cilia (and often a few 3–4-rayed) to 0.7 mm near petiole base; rosette leaf blades subappressed pubescent, the abaxial surfaces with 3–8-rayed trichomes to 0.4 mm (4- to 6-rayed always present). Sterile short shoots with tuft of ascending leaves rare, when present the leaves narrowly oblanceolate, 40–60 × 4–7 mm, otherwise similar to rosette leaves. Fertile stems 1(rarely 2) per caudex branch, mostly terminal but occasionally arising laterally below

PLANTS OF **NEW MEXICO**, U.S.A.

Boechera pseudoconsanguinea Windham & Allphin
(apomictic triploid hybrid)

SAN JUAN CO.: NE of Aztec in Hart Canyon on slope above Hart Canyon Road (Route 2770) ca. 1.0 road mile ESE of its intersection with U.S. Route 550. Lat./Long.: 36.8672N 107.9328W (WGS84 Datum). Elev. 5925 ft.

Among cobbles (igneous) in sandy alluvial soil on NW-facing slope with Artemisia, Juniperus, Yucca, Pleuraphis & Aristida.

M.D. Windham (4187),
L. Allphin & P.J. Alexander

15 May 2014
Brassicaceae

Vascular Plant Herbarium, Duke University, Durham, NC
BRY; COLO; DUKE; GH; MO; NY; NMC; RM; US; UT; UTC

Fig. 3. Holotype of *Boechera pseudoconsanguinea*.

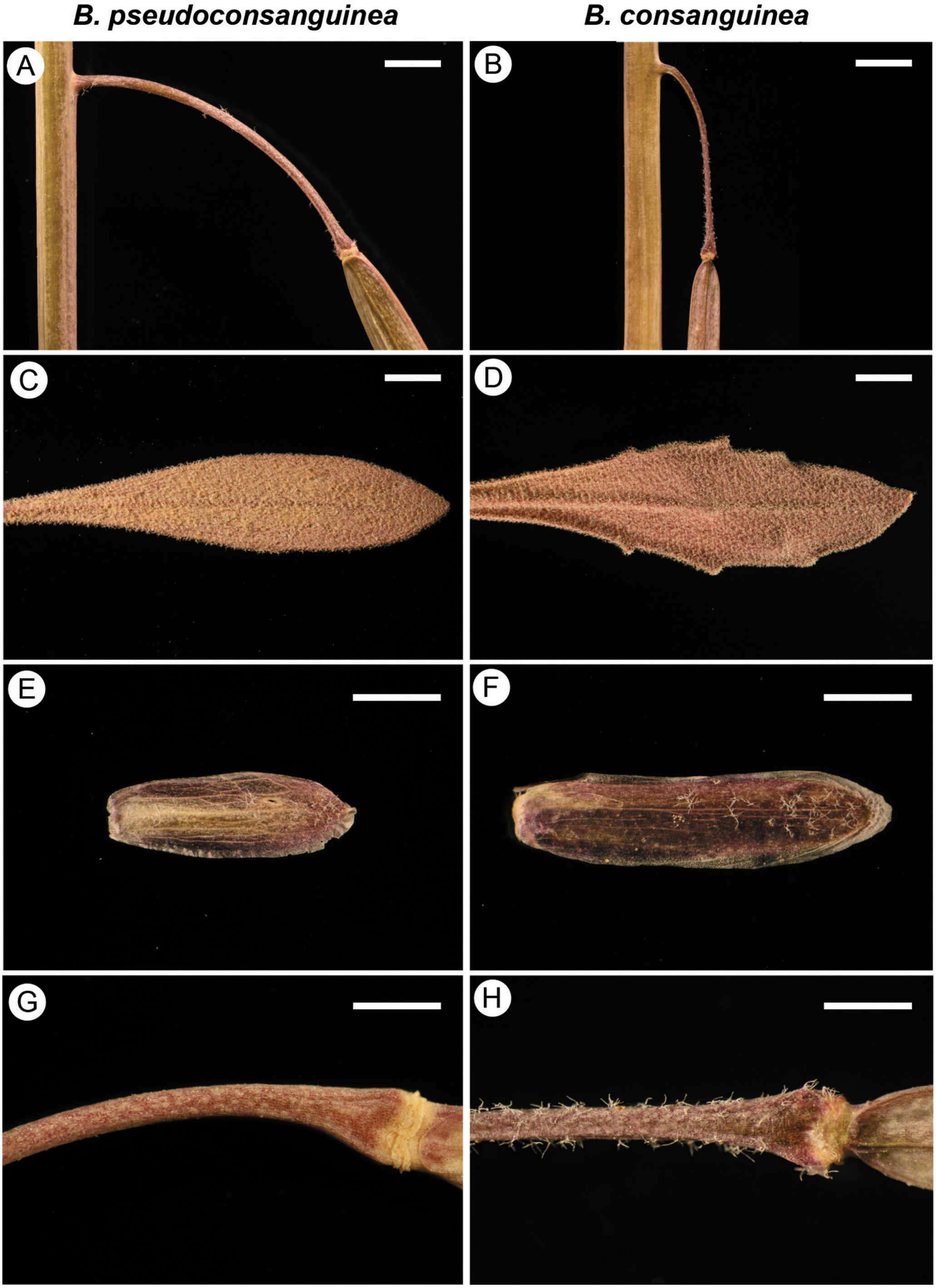

Fig. 4. Morphological comparisons of *Boechera pseudoconsanguinea* (left column) and *B. consanguinea* (right column). (**A–B**) Orientation of lower fruiting pedicels relative to rachises; scale bars = 2 mm. (**C–D**) Lower leaf dentition; scale bars = 2 mm. (**E–F**) Sepal length and pubescence; scale bars = 1 mm. (**G–H**) Distal portion of lower fruiting pedicels documenting trichome density; scale bars = 1 mm.

sterile short shoot, 4–7 dm tall, 1.2–4 mm in diameter at base, lower internodes moderately pubescent with 2–6-rayed trichomes to 1 mm (3- to 5-rayed always present); uppermost internodes and rachises usually glabrous. Cauline leaves 9–38, most pubescent with 2–7-rayed trichomes to 0.3 mm (4- and 5-rayed always present), the uppermost occasionally glabrous, all but the lowermost with auricles 0.9–2.5 mm. Inflorescences simple racemes, rarely sparingly branched, the main axis 14–45-flowered, not secund; lowermost fruiting pedicels 13–17 mm, perpendicular to slightly descending, gently downcurved distally, most glabrous but a few with 4–7-rayed trichomes concentrated distally. Flowers: sepals 2.5–3.5 mm, mostly dull lavender, with trichomes similar to those of rosette leaf surfaces; petals 5–7.5 × 0.8–1.2 mm, whitish but turning pale lavender with age, glabrous; anthers cream-colored, producing variable percentages of malformed and well-formed pollen grains, the latter mostly ovoid-spheroid and averaging 22 μm wide with 4 or more asymmetrically arranged apertures; ovaries glabrous, usually with 52–80 ovules per fruit, forming seeds apomictically through diplospory. Fruits 4.8–5.6 cm × 1.6–2.1 mm at maturity, straight to curved downward, pendent, bases of lower fruits positioned 6.5–15 mm from rachises, all glabrous; styles 0.15–0.3 mm. Seeds in two irregular rows near center of fruit, 1.1–1.5 × 0.8–1.2 mm; marginal wing ± continuous or from funiculus along cotyledon side for 2/3 of circumference and most prominent distally, to 0.25 mm wide. Chromosome number (from the type collection) n = 2n = 21, with variable pairing during microsporogenesis (ranging from 21 univalents to 7 trivalents).

Paratypes. **ARIZONA. Navajo Co.:** Skeleton Mesa W of Keet Seel Ruins (UTM Zone 12S: 4068948N by 544256E), *Rink & Bungart 3105* [NY]. **NEW MEXICO. Rio Arriba Co.:** SSW of Lybrook below mesa near head of Blanco Wash (36°13′19″N 107°34′12″W; WGS84 Datum), *Windham 3069* [DUKE 400844]. **San Juan Co.:** NE of Aztec in Hart Canyon on slope above Road 2770 ca. 1.0 road mi E of its junction with U.S. Route 550 (36.8683N 107.9332W; WGS84 Datum), *Windham et al. 3945* [DUKE 404003].

Distribution, Habitat and Phenology.—*Boechera pseudoconsanguinea* currently is known from a single population in northern Arizona (Navajo Co.) and two populations in northern New Mexico (Rio Arriba and San Juan Cos.). It occurs in sandy alluvial soils, typically associated with *Artemisia* and *Juniperus* at elevations of 1750–2300 m. The species blooms from early April to late May and produces mature seeds in June and July.

Etymology.—The epithet references its similarity to, and initial confusion with, *Boechera consanguinea*.

A new hybrid species segregated from *Boechera duchesnensis*.—In the *Flora of North America* treatment of *Boechera*, Al-Shehbaz and Windham (2010) broadly defined *B. duchesnensis* to encompass a diversity of pubescent-fruited hybrid populations that were thought to include a genome from *B. formosa* (herein called *B. pulchra* subsp. *pallens*). Subsequent work has revealed that typical *B. duchesnensis* is a stable apomictic diploid hybrid between *B. pulchra* subsp. *pallens* and *B. crandallii* subsp. *thompsonii* (Allphin & Windham, in prep.). These studies also indicate that *B. duchesnensis s.s.* is confined to the Uintah Basin in northern Utah. Specimens previously attributed to *B. duchesnensis* from the Four Corners region are stable apomictic triploids containing genomes from *B. pulchra* subsp. *pallens, B. crandallii* subsp. *kelseyana*, and *B. perennans* subsp. *perennans*. Analyses conducted using the *Boechera* Microsatellite Website (Li et al. 2017) indicate that this trigenomic triploid arose in the Four Corners region through hybridization between *B. pulchra* subsp. *pallens* (a sexual diploid) and an apomictic diploid lineage belonging to *B. gracilenta s.l.* (Windham et al., unpubl.). Here we name this newly documented hybrid as:

Boechera quadrangulensis Windham & Allphin, **sp. nov. (Fig. 5)**. TYPE: U.S.A. NEW MEXICO. San Juan Co.: NE of Aztec in Hart Canyon on slope above Hart Canyon Road (Route 2770) ca. 1.0 road mi ESE of its intersection with U.S. Route 550 (36.8672N 107.9328W; WGS84 Datum), 5925 ft. elev., among cobbles (igneous) in sandy alluvial soil on NW-facing slope with *Artemisia, Juniperus, Yucca, Pleuraphis & Aristida*, 15 May 2014 *Windham 4186, Allphin & Alexander* (HOLOTYPE: DUKE 405280!; ISOTYPES: ASU!, COLO!, GH!, MO!, NMC!, NY!, UNM!, UT!).

Most similar to *Boechera duchesnensis* but differing (see Fig. 6) in having 1) ovaries with few or rarely no trichomes (vs. relatively abundant and always present) that are sporadically distributed (vs. concentrated distally), 2) petals with mostly non-flaring, pale lavender blades (vs. flaring and usually whitish), 3) fruits with largely deciduous (vs. persistent) trichomes and some ovules clearly biseriate (vs. irregular to uniseriate), 4) middle cauline leaves usually wider (> 2 vs. < 2 mm) with fewer trichomes (< 25 vs. > 25 per mm^2) on abaxial surfaces, and

BOECHERA QUADRANGULENSIS HYBRID COMLEX

Haploid OTUs inferred: formosa; kelseyana; perennans (1:1:1)

Species name available for plants with this genomic composition:

Boechera formosa (Greene) Windham & Al-Shehbaz × B. kelseyana Windham & Allphin × B. perennans (S. Wats.) W.A. Weber (apomictic triploid)

M.D. Windham (2015) Extrac#: FW1549 DUKE Herbarium

PLANTS OF **NEW MEXICO**, U.S.A.

Boechera quadrangulensis Windham & Allphin (apomictic triploid hybrid)

SAN JUAN CO.: NE of Aztec in Hart Canyon on slope above Hart Canyon Road (Route 2770) ca. 1.0 road mile ESE of its intersection with U.S. Route 550. Lat./Long.: 36.8672N 107.9328W (WGS84 Datum). Elev. 5925 ft.

Among cobbles (igneous) in sandy alluvial soil on NW-facing slope with Artemisia, Juniperus, Yucca, Pleuraphis & Aristida.

M.D. Windham (4186),
L. Allphin & P.J. Alexander

15 May 2014
Brassicaceae

Vascular Plant Herbarium, Duke University, Durham, NC
ASU; COLO; DUKE; GH; MO; NMC; NY; UNM; UT

Fig. 5. Holotype of *Boechera quadrangulensis*.

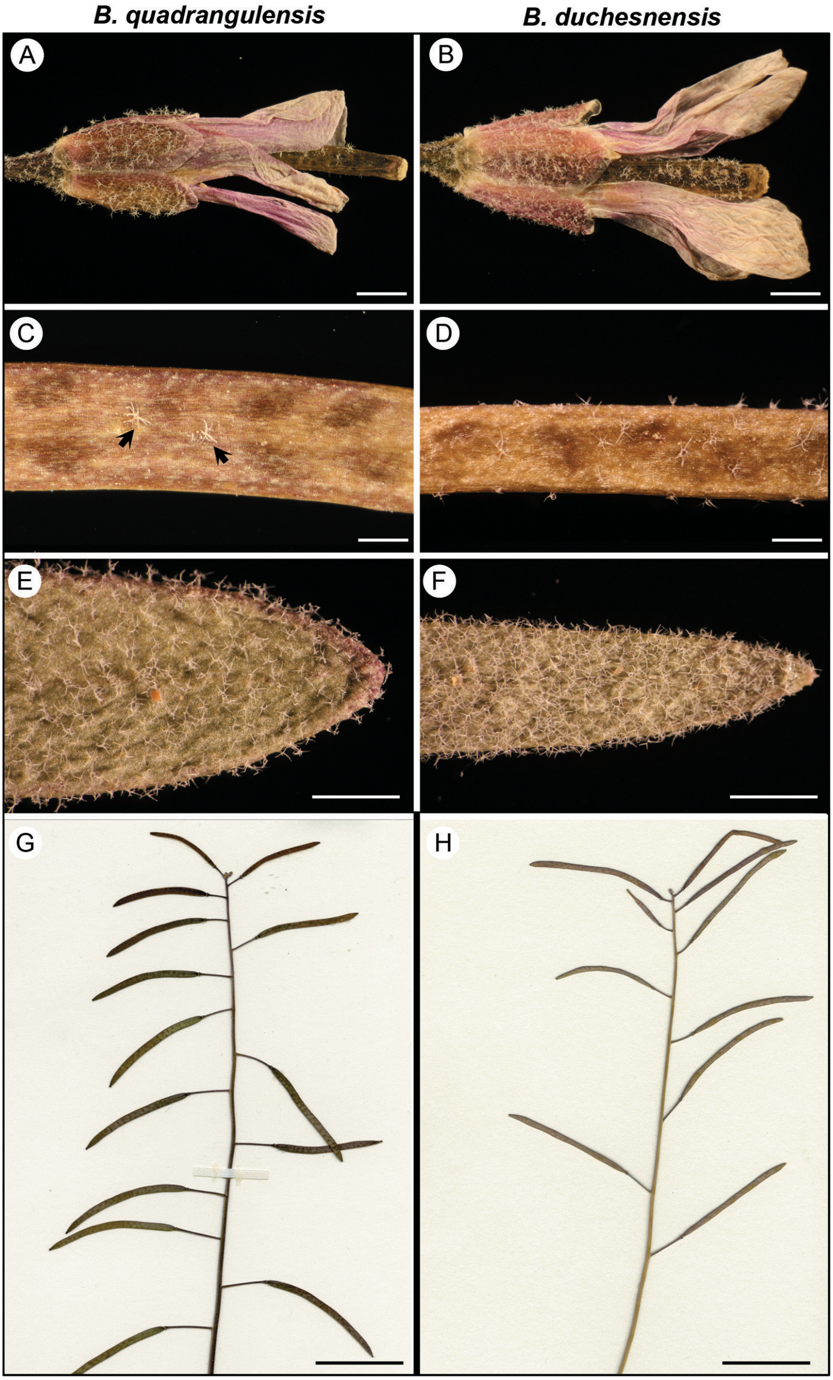

Fig. 6. Morphological comparisons of *Boechera quadrangulensis* (left column) and *B. duchesnensis* (right column). (**A–B**) Individual flowers at full anthesis; scale bars = 1 mm. (**C–D**) Immature fruits highlighting ovule arrangements and trichome abundance/persistence; arrows in C identify few remaining trichomes on *B. quadrangulensis* fruit; scale bars = 0.5 mm. (**E–F**) Distal portion of middle cauline leaves emphasizing density of trichomes on abaxial surfaces; scale bars = 1 mm. (**G–H**) Infructescences showing mature fruit orientation; G from DUKE holotype of *Boechera quadrangulensis*, H from RM isotype of *Arabis pulchra* var. *duchesnensis*; scale bars = 2 cm.

5) mature fruits mostly horizontal to divaricate-descending (vs. divaricate-ascending); differing from *B. pulchra* subsp. *pallens* (its pubescent-fruited parent) by the fruit trichome characters indicated above as well as having fewer trichomes (< 10 vs. > 10 per mm^2) on rachises; differing from *B. gracilenta s.l.* (its apomictic diploid, glabrous-fruited parent) by having sparse to abundant trichomes on > 90% of ovaries at anthesis and 30–150 (vs. mostly < 30) trichomes on lowermost fruiting pedicels, these trichomes often concentrated distally (vs. widely scattered).

Plants long- to short-lived perennials, the caudices mostly branched, usually somewhat woody and often raised above ground level, producing a cluster of rosette leaves distally, these largely deciduous in fruiting individuals. Rosette leaves oblanceolate, 20–56 × 4.2–8.5 mm, entire or dentate with 1–2 pairs of teeth to 0.8 mm, often with enlarged, simple and/or 2–4-rayed cilia (2-rayed always present) to 0.9 mm near petiole base; rosette leaf blades subappressed pubescent, the abaxial surfaces with 3–8-rayed trichomes to 0.3 mm long (5- and 6-rayed trichomes always present). Sterile short shoots with tuft of ascending leaves often present, the leaves narrowly oblanceolate, 16–52 × 1.7–5.8 mm, similar to rosette leaves except the cilia often larger (to 1.3 mm) and extending farther up the petiole. Fertile stems 1(2–7) per caudex branch, terminal or arising laterally below sterile short shoot, 1.5–6 dm long, 1–3 mm in diameter at base, lower parts moderately pubescent with mostly 2–6-rayed trichomes to 1 mm; upper parts of stems with scattered, 2–8-rayed trichomes (some 5-rayed always present). Cauline leaves 6–15, all pubescent with 2–9-rayed trichomes to 0.4 mm (5- and 6-rayed trichomes always present), the uppermost (> 95%) with auricles 0.2–2 mm. Inflorescences simple racemes or sparingly branched, the main axis 7–31-flowered, not secund; lowermost fruiting pedicels 6–21 mm, divaricate-ascending to horizontal (rarely slightly descending), straight or gently down-curved distally, with 3–10-rayed trichomes concentrated distally (5-, 6-, and 7-rayed trichomes always present). Flowers: sepals 2.5–4.5 mm, mostly dull lavender, with trichomes similar to those of the fruiting pedicels; petals 5–10 × 1–3 mm, usually pale lavender but darkening with age, glabrous; anthers cream-colored, producing variable percentages of well-formed and malformed pollen grains, the former mostly ovoid-spheroid and averaging 25 µm wide with 4 or more asymmetrically arranged apertures; ovaries (> 90%) with at least a few, sporadically-distributed trichomes, usually with 30–56 ovules per fruit, forming seeds apomictically predominantly through diplospory. Fruits (the largest) 3.2–6.0 cm × 1.3–2.1 mm at maturity, ± horizontal to slightly descending, gently curved downward to straight, > 50% with a few 3–10-rayed trichomes on distal 1/3 of valve surfaces, not extending to replum; styles 0.3–0.8 mm long. Seeds in two irregular rows near center of fruit, ca. 1.5 – 0.8 mm, with pale marginal wing up to 0.2 mm wide, wing continuous except near funiculus. Chromosome number (from the type collection) n = 2n =21, with variable pairing during microsporogenesis (but most cells exhibiting 21 univalents).

Paratypes. **ARIZONA. Apache Co.:** Carrizo Mountains; between Red Goat Spring and Tse abeii Point ca. 1.5 mi S of Red Goat Spring, *Clifford AC-63* [SJNM 14726]. **Coconino Co.:** top of Leche-E Rock, *Jenness s.n.* [ASC 53203]; U.S. 89, 10 mi S of Page, *Nash & Nash 70* [ASU 55985]; Cape Solitude, near rim of Grand Canyon, *Bowers et al. 1682* [ARIZ 222921]. **Navajo Co.:** jct. of Little Capitan Valley road and road cutting through Comb Ridge (36°47′32″N 110°05′27″W), *Heil & Clifford 16352* [SJNM 37460]; ca. 3 mi N of Kayenta on US 163, ca. 2 mi E of Chaistla Butte along Little Capitan Valley near Porros Dikes (36°46′48″N 110°10′02″W), *Heil & Clifford 16299* [SJNM 37413]. **COLORADO. Montezuma Co.:** Ute Mtn. Indian Res. 5 mi S of Towaoc and 4 mi W of Highway 666, *Porter 1767* [SJNM 4714]. **NEW MEXICO. Rio Arriba Co.:** ca. 2 mi W of Floyd Miles #1 well site, top of mesa, *Heil 8706* [SJNM 21277]. **Sandoval Co.:** S of Lybrook on mesa near head of Escrito Canyon ca. 3.16 km SSE of Escrito Spring (36.2065N 107.5618W; WGS84 Datum), *Windham 3067* [ARIZ, ASC, BRY, DUKE 405275]. **San Juan Co.:** San Juan College Nature Trail, *Jenksin [Jenkins?] et al. 25* [SJNM 8630]; NNE of Aztec on slope above Animas River floodplain near Ruins Road ca. 3.1 road mi NE of its junction with State Route 516 (36.8622N 107.9798W; WGS84 Datum), *Windham et al. 3942* [DUKE 403974]; Navajo Nation, ca. 4.5 mi SW of Shiprock Diatreme (T28N, R19W), *Clifford 18263* [SJNM 40119]; B-Square Ranch; Hammond Canal (T29N, R12W, S30, SE), *Heil 12984* [SJNM 31217]; Navajo Indian Reservation; Beclahbito Dome ca. 1.75 mi S of trading post (T30N, R21W), *Clifford 01-197* [SJNM 40129]; Chaco Canyon National Monument; on mesa W from South Gap, *Hastings s.n.* [ARIZ 47484.2]. UTAH. Grand Co.: NW of Moab near base of Courthouse Rock (38°42′01″N 109°43′17″W; WGS84 Datum), *Windham et al. 99-045* [DUKE 400773, MO, NMC, UT]; 8 mi W of Dead Horse Point, *Cottam 12139* [UT 71294]. **Kane Co.:** Hurricane Wash, 35 mi SE of Escalante (T39S, R7E, S26; SW), *Albee 1260* [UT 80022]. **San Juan Co.:** E of Bluff along small canyon tributary of San Juan River ca. 3.89 km E of Sunbonnet Rock (37°17′09″N 109°30′12″W; WGS84 Datum), *Windham 3366* [BRY, DUKE 400710, MO, NMC, UT]; **Navajo Nation:** Road 480 to ca. 1 mi S of Lake Powell along Piute Canyon (37°08′47″N 110°41′58″W), *Heil et al. 18437* [SJNM 41811]. **Wayne Co.:** VABM 6190 - Clyde (1 mi SW); T28S, R16E, S14), *Welsh & Holland 21942* [RM 364692].

Distribution, Habitat and Phenology.—*Boechera quadrangulensis* is known from northern Arizona and New Mexico, as well as southern Colorado and Utah. It favors sandy loam soils in pinyon-juniper woodland or sagebrush flats at elevations of 1150–2300 m. The species blooms from early April to early June and produces mature seeds in July and August.

Etymology.—The epithet is a combination of *quadranguli-* (having four angles/corners), and *-ensis* (from), highlighting its exclusive occurrence in what is known as the Four Corners region of the southwestern United States.

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