
Transfer of Most North American Species of *Arabis* to *Boechea* (Brassicaceae)

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ABSTRACT. Based on extensive molecular, cytological, and morphological studies, most of the North American species of *Arabis* (Brassicaceae) are recognized herein as members of the genus *Boechea*. Morphological differences between the two genera are discussed, and species formerly placed in *Arabis* and not included here in *Boechea* are assigned to other genera. Thirty-two new combinations in *Boechea* are proposed: *B. bodiensis* (Rollins) Al-Shehbaz, *B. breweri* (S. Watson) Al-Shehbaz, *B. canadensis* (L.) Al-Shehbaz, *B. constancei* (Rollins) Al-Shehbaz, *B. cusickii* (S. Watson) Al-Shehbaz, *B. dispar* (M. E. Jones) Al-Shehbaz, *B. falcifructa* (Rollins) Al-Shehbaz, *B. fruticosa* (A. Nelson) Al-Shehbaz, *B. glaucovalvula* (M. E. Jones) Al-Shehbaz, *B. hastatula* (Greene) Al-Shehbaz, *B. hirshbergiae* (S. Boyd) Al-Shehbaz, *B. hoffmanii* (Munz) Al-Shehbaz, *B. inyoensis* (Rollins) Al-Shehbaz, *B. johnstonii* (Munz) Al-Shehbaz, *B. koehleri* (T. J. Howell) Al-Shehbaz, *B. laevigata* (Muhlenberg ex Willdenow) Al-Shehbaz, *B. missouriensis* (Greene) Al-Shehbaz, *B. ophira* (Rollins) Al-Shehbaz, *B. parishii* (S. Watson) Al-Shehbaz, *B. patens* (Sullivant) Al-Shehbaz, *B. perstellata* (E. Braun) Al-Shehbaz, *B. pinzlae* (Rollins) Al-Shehbaz, *B. platysperma* (A. Gray) Al-Shehbaz, *B. pygmaea* (Rollins) Al-Shehbaz, *B. rectissima* (Greene) Al-Shehbaz, *B. repanda* (S. Watson) Al-Shehbaz, *B. rigidissima* (Rollins) Al-Shehbaz, *B. rollei* (Rollins) Al-Shehbaz, *B. shortii* (Fernald) Al-Shehbaz, *B. stricta* (Graham) Al-Shehbaz, *B. subpinnatifida* (S. Watson) Al-Shehbaz, and *B. tiehmii* (Rollins) Al-Shehbaz. Three recently described species, *Arabis calderi* G. A. Mulligan, *A. murrayi* G. A. Mulligan, and *B. glareosa* Dorn, are reduced to synonymy of *B. divaricarpa* (A. Nelson) A. Löve & D. Löve, *B. lyallii*, and *B. gunnisoniana* (Rollins) W. A. Weber, respectively.

Key words: *Arabidopsis*, *Arabis*, *Boechea*, Brassicaceae, *Pennellia*, *Turritis*.

As traditionally delimited by recent North American botanists (e.g., Hopkins, 1937; Rollins, 1941, 1993b; Mulligan, 1996), the genus *Arabis* L. (Bras-

sicaceae) was rather broadly circumscribed to include species now placed in *Arabidopsis* Heynhold, *Boechea* A. Löve & D. Löve, *Pennellia* Nieuwland, and *Turritis* L. (see below). Several European botanists also adopted such a broad concept. For example, Busch (1939) included in *Arabis* species now placed in *Alyssopsis* Boissier; *Arabidopsis*; *Crucihimalaya* Al-Shehbaz, O’Kane & R. A. Price; *Neotorularia* Hedge & J. Léonard; *Rhammatophyllum* O. E. Schulz; and *Turritis*. By contrast, the recent treatment of *Arabis* by Jones and Akeroyd (1993) included species now assigned to *Arabidopsis*, *Diplotaxis* DC., *Fourraea* Greuter & Burdet, and *Turritis* (author’s compilation). All of the above authors delimited *Arabis* exclusively on a combination of latiseptate siliques (fruits flattened parallel to the septum), branched trichomes, and accumbent cotyledons. However, this combination of characters evolved independently many times within the Brassicaceae (Appel & Al-Shehbaz, 2002), and it characterizes some or all species of the ten genera above (minus *Diplotaxis*), as well as those of *Aplanodes* Marais (South Africa), *Aubrieta* Adanson (Europe), *Desideria* Pampanini (central Asia and Himalayas), *Draba* L. (several Asian species), *Eremobium* Boissier (northern Africa, Middle East), *Erysimum* L. (some Eurasian species), *Eurycarpus* Botschantzev (Himalayas), *Lepidostemon* J. D. Hooker & Thomson (Himalayas), *Matthiola* R. Brown (Africa, Eurasia), *Pachycladon* J. D. Hooker (New Zealand and Tasmania), *Pennellia* (some North American members), *Phoenicaulis* Nuttall (U.S.A.), *Sibara* Greene (North America), *Sisymbriopsis* Botschantzev & Tzvelev (central Asia), *Smelowskia* C. A. Meyer ex Ledebour (Far East representatives), and *Stevenia* Adams & Fischer (eastern and central Asia).

Rollins (1993b) recognized 80 North American species in *Arabis*, of which 24 were further divided into 40 varieties, while Mulligan (1996) accepted 30 species and 6 varieties in Alaska, Canada, and Greenland. As shown below, extensive molecular studies on members of North American *Arabis* clearly indicate that the genus, as circumscribed

by Rollins (1993b) and Mulligan (1996), is polyphyletic and represents a heterogeneous assemblage of four genera: *Arabidopsis*, *Boechera*, *Pennellia*, and *Turritis*. First, *Arabis lyrata* L., including *A. media* N. Busch and *A. kamchatica* (Fischer) Ledebour, has been shown by Al-Shehbaz and O'Kane (2002), O'Kane and Al-Shehbaz (1997, 2003), Koch et al. (1999, 2000, 2001), Heenan et al. (2002), and Miyashita et al. (1998) to belong to *Arabidopsis*. Second, *Arabis glabra* (L.) Bernhardt was shown by Koch et al. (1999, 2000, 2001) and Heenan et al. (2002) to be unrelated to *Arabis* and to belong to *Turritis*, as originally treated by Linnaeus (1753) and as accepted in a number of monographic, floristic, and systematic accounts of the family (e.g., Torrey & Gray, 1838; Hayek, 1911; Burdet, 1967; Schulz, 1936; Schultze-Motel, 1986; Zhou et al., 2001; Appel & Al-Shehbaz, 2002). Third, *Arabis microsperma* Rollins and *A. tricornuta* Rollins belong to *Pennellia* (Bailey et al., 2002; Price et al., 2001; Fuentes-Soriano, 2002), a genus most closely related to *Halimolobos* Tausch, *Mancoa* Weddell, *Boechera*, and *Sphaerocardamum* Shauer, and clearly unrelated to *Arabis*. Finally, the bulk of North American *Arabis* is recognized here as *Boechera*.

The genus *Boechera* was segregated from *Arabis* by Löve and Löve (1976) and was said to differ by having a base chromosome number of $x = 7$ instead of $x = 8$. These authors did not provide any morphological characters that otherwise distinguished the two genera. Rollins (in Rollins & Rüdénberg, 1977) strongly disagreed with the splitting of *Arabis* based on chromosome numbers, though he admitted (p. 102) that species with $x = 7$ have "a somewhat different circle of close affinity" from those with $x = 8$, which are related to the Eurasian members of the genus. Weber (1982: 369) concluded that "The difference in basic chromosome number [in *Arabis*] . . . does represent a divergent phylogenetic line, and the genetic barrier that it presents to interbreeding of the units is sufficient justification for thinking in terms of discrete genera."

Several phylogenetic studies (Galloway et al., 1998; Koch et al., 1999, 2000, 2001, 2003; Heenan et al., 2002; O'Kane & Al-Shehbaz, 2003) have clearly demonstrated that *Boechera* is unrelated to *Arabis alpina* L., the type species of *Arabis*, or to the Eurasian and North American species with $x = 8$. Therefore, molecular, cytological, and morphological data (see below) strongly support the recognition of *Boechera* as a genus well-defined from the rest of *Arabis*, hereafter *Arabis* s. str., with $x = 8$. Only about ten native North American species belong to *Arabis* s. str. (Mitchell-Olds, unpub-

lished): *A. aculeolata* Greene, *A. arenicola* (Richardson & Hooker) Gelert, *A. blepharophylla* Hooker & Arnott, *A. hirsuta* L., *A. macdonaldiana* Eastwood, *A. modesta* Rollins (if indeed different from the next species), *A. oregana* Rollins, *A. crusisetosa* Constance & Rollins, *A. furcata* S. Watson, and *A. nuttallii* B. L. Robinson. Chromosome counts based on $x = 8$ are known for all except the last three species, which are retained in this genus on the basis of the nuclear ribosomal DNA ITS region (Mitchell-Olds, pers. comm.), leaf indumentum, and fruit morphology. Whether or not the western North American *A. eschscholtziana* Andrzejowski ex Ledebour should be recognized as a distinct species (Mulligan, 1996), as a variety of *A. hirsuta* (Rollins, 1993b), or as a subspecies or synonym of the latter is a matter of judgment and will be dealt with in a separate paper. With the exclusion of the ten North American species of *Arabis* s. str., as well as those transferred to *Arabidopsis* (*A. lyrata*), *Turritis* (*A. glabra*), and *Pennellia* (*A. microsperma* and *A. tricornuta*), the remaining species assigned to *Arabis* by Rollins (1993b) and Mulligan (1996, 2002) should be segregated as *Boechera*.

A critical comparison of the Eurasian and North American species of *Arabis* s. str. and *Boechera* reveals that there are a number of morphological characters that readily distinguish the two. No species of *Arabis* s. str. has falcate, secund, widely spreading, pendent, or strongly reflexed fruits, but the majority of *Boechera* species have at least one of these aspects of fruit morphology. Species of *Arabis* s. str. have erect, ascending, or divaricate-ascending, straight fruits. Furthermore, no species of *Arabis* s. str. has dendritic, irregularly bifurcate, or sessile trichomes on the leaves, and the vast majority of *Boechera* species have at least one of these trichome types. In *Arabis* s. str., the trichomes are stalked and either forked, 3-rayed, or cruciform, and their rays are almost always unbranched. The present author and Sara Fuentes-Soriano are preparing a detailed atlas of trichome morphology of *Arabis* s.l. A few Eurasian species assigned to *Arabis* have dendritic trichomes, and they are to be transferred to other genera (Al-Shehbaz, unpublished). In species with glabrous leaves, characters of the fruit, seed, or leaf morphology (see below) help in assigning them to either of the two genera.

A few other characters have some limited use in the separation of *Arabis* s. str. and *Boechera*. For example, the fruits in *Arabis* s. str. are generally narrow (often less than 2 mm wide) and always glabrous. Although many species of *Boechera* have narrow and glabrous fruits, several others

have fruits 3–8 mm wide or fruit valves sparsely to moderately pubescent. The seeds in *Arabis* s. str. are uniseriate and either narrowly winged or wingless, just as in a number of *Boechera* species. However, several species of *Boechera* have broadly winged seeds (wing 1–3 mm wide) and/or biseriate seeds.

Weber (1982) indicated that *Arabis* is separated from *Boechera* by having loose, slender root systems (instead of shortly clustered caudices) and large, numerous, and often toothed (instead of smaller, fewer, and entire) leaves. These differences were not recognized by Al-Shehbaz (1988), Rollins (1993b), and Mulligan (1996). A closer examination of the caudex and leaves in *Arabis* s.l. worldwide further shows that the caudex, which is absent in the annual and biennial species, is not useful taxonomically and only the leaves are occasionally helpful in the separation of the two genera.

To my knowledge, *Arabis* s. str. does not include any species with both polyploidy and apomixis. Apomixis in *Arabis* s.l. was first reported by Böcher (1947) in *A. holboellii* and subsequently confirmed in other critical studies (Böcher, 1951, 1954, 1966, 1969). Mulligan (1996) suggested that sexual and apomictic populations are found within *A. columbiana* Macoun, *A. divaricarpa* A. Nelson, *A. drummondii* A. Gray, *A. exilis* A. Nelson, *A. lemmonii* S. Watson, *A. lyallii* S. Watson, *A. microphylla* Nuttall, *A. pinetorum* Tidestrom, and *A. sparsiflora* Nuttall. These species, recognized here as members of *Boechera*, include triploid plants based on $x = 7$, and they exhibit some meiotic irregularities, including univalents, multivalents, and B-chromosomes (Böcher, 1947, 1969; Johnson, 1970; Mulligan, 1964, 1996; Packer, 1964; Rollins, 1993b; Rollins & Rüdénberg, 1971; Roy, 1995; Vorobik, 1985).

Jones and Akeroyd (1993) recognized three species in *Arabis* s.l. with strongly falcate and/or reflexed fruits: *A. laxa* Smith (eastern Europe and southwestern Asia), *A. turrata* L. (central and eastern Europe), and *A. pendula* L. (Eurasia). *Arabis laxa* has long been recognized as *Turritis laxa* (Smith) Hayek in several other floristic works (e.g., Cullen, 1965; Hedge, 1968; Meikle, 1977), and on the basis of overall morphology (e.g., glaucous cauline leaves, creamy white or yellowish flowers, slightly 4-angled fruits) and a chromosome number of $n = 6$ (Maassoumi, 1980), it is perfectly at home in *Turritis*. *Arabis turrata*, with $2n = 16$ (e.g., Burdet, 1967; and numerous subsequent counts), is the only species in the genus with bracteate racemes and fruits to 9 cm long. Molecular studies (Koch et al., 2000, 2001) strongly support the separation of

this species to a distinct genus. In addition to its chromosome number of $2n = 21$ (Berkutenko & Gurzenkov, 1976; Berkutenko et al., 1984), *A. pendula* is anomalous in *Arabis* s. str. because it has sessile stellate trichomes with an erect central ray much coarser than the other rays. One might be tempted to place it in *Boechera*, but molecular data (O’Kane & Al-Shehbaz, 2003) place it in a clade well separated from both *Arabis* s. str. and *Boechera*. It may well represent an independent genus, though it is beyond the scope of this paper to deal with it. Another anomalous European *Arabis* recognized by Jones and Akeroyd (1993) is *A. brassica* (Leers) Rauschert, a species with $2n = 14$ (Polatschek, 1966; Burdet, 1967; Titz, 1967; van Loon et al., 1971) often reported as *A. pauciflora* (Grimm) Gracke. However, molecular data (Koch et al., 2001) indicate that this species is unrelated to *Arabis* s. str., and a closer examination of morphology supports Greuter and Burdet (1984) in transferring it to the monotypic *Fourraea* Greuter & Burdet, as *F. alpina* (L.) Greuter & Burdet.

The present account of *Boechera* was prepared during work on the genus for an upcoming volume of the *Flora of North America*, and the new combinations are proposed herein to make the species names available for phylogenetic studies in progress. Of the 40 additional varieties recognized by Rollins in *Arabis* s.l., 35 fall within the present circumscription of *Boechera*. Mulligan (1996) raised 4 of these 35 varieties to the species rank and reduced 9 others to synonymy of other taxa. The status of these infraspecific taxa will be addressed in a subsequent publication following the examination of all types. A key to all species of *Boechera* will be presented when we have a better understanding of the taxa involved, especially the representatives from the Russian Far East.

Under each species of *Boechera*, its synonym in *Arabis* is given regardless whether or not its basionym is in *Arabis*. This is important for comparing the names in *Boechera* with those in Rollins (1993b) and Mulligan (1996). Löve and Löve (1976, 1982), Weber (1982, 1989, 1996), and Dorn (2003) have already transferred several species of North American *Arabis* to *Boechera*, and these are listed below with full information on the type collections because this information was not given by these authors. Types marked “not seen” were compiled from Hopkins (1937), Rollins (1941), and Mulligan (1996).

Boechera beckwithii (S. Watson) Dorn, Brittonia 55: 3. 2003. Basionym: *Arabis beckwithii* S. Watson, Proc. Amer. Acad. Arts 22: 467.

1887. TYPE: U.S.A. Nevada: Quartz Mts., W of Great Salt Lake, *Lieutenant Beckwith s.n.* (lectotype, designated by Rollins (1941: 452), GH).

Watson (1887) cited four syntypes under the original description of *Arabis beckwithii*. Rollins (1941) listed Beckwith's collection as the type, and this was taken as the lectotype.

Boecheira bodiensis (Rollins) Al-Shehbaz, comb. nov. Basionym: *Arabis bodiensis* Rollins, Contr. Gray Herb. 212: 113. 1982. TYPE: U.S.A. California: Mono Co., 2 mi. NW of Masonic, 5.9 mi. from Bridgeport-Sweetwater highway, loose soil of old mine, 8100 ft., 3 Aug. 1945, *I. L. Wiggins & R. C. Rollins 536* (holotype, GH; isotypes, DS, GH, UC).

Boecheira breweri (S. Watson) Al-Shehbaz, comb. nov. Basionym: *Arabis breweri* S. Watson, Proc. Amer. Acad. Arts 11: 123. 1875. TYPE: U.S.A. California: [Contra Costa Co.], rocky summit of eastern peak of Mt. Diablo, 4 May 1862, *W. H. Brewer 1086* (lectotype, designated by Rollins (1941: 408), GH; isotypes, DS, MO, UC [2], US).

Watson (1875) cited four syntypes under the original description of *Arabis breweri*. Rollins (1941) listed Brewer's collection as the type, and this was taken as the lectotype of the species.

Boecheira canadensis (L.) Al-Shehbaz, comb. nov. Basionym: *Arabis canadensis* L., Sp. Pl. 2: 665. 1753. TYPE: lectotype, designated by Reveal in Cafferty & Jarvis (2002: 531), *J. Clayton 400*, left-hand specimen, Herb. Linn. No. 842.12 (LINN; isotype, BM).

Boecheira cobrensis (M. E. Jones) Dorn, Vasc. Pl. Wyom. ed. 3: 375. 2001. Basionym: *Arabis cobrensis* M. E. Jones, Contr. W. Bot. 12: 1. 1908. TYPE: U.S.A. Nevada: Elko Co., Cobre, clay hills, 6000 ft., 16 June 1906, *M. E. Jones s.n.* (holotype, POM; isotypes, BM, CAS, MO, POM, US [2]).

Boecheira constancei (Rollins) Al-Shehbaz, comb. nov. Basionym: *Arabis constancei* Rollins, Contr. Gray Herb. 201: 5. 1971. TYPE: U.S.A. California: Plumas Co., 7.6 mi. SE of Quincy (at Spring Garden overpass) on road to Blairsden, near rocks on open serpentine, W-SW facing gentle slope, 4100 ft., 11 July 1969, *L. Constance & T. I. Chuang 3875* (holotype, GH; isotype, UC).

Boecheira crandallii (B. L. Robinson) W. A. Weber, Phytologia 51: 369. 1982. Basionym: *Arabis crandallii* B. L. Robinson, Bot. Gaz. 28: 135. 1899. TYPE: U.S.A. Colorado: Montrose Co., Cimarron, 7000 ft., 18 May 1898, *C. S. Crandall 6* (holotype, GH; isotype, NY not seen).

Boecheira cusickii (S. Watson) Al-Shehbaz, comb. nov. Basionym: *Arabis cusickii* S. Watson, Proc. Amer. Acad. Arts 17: 363. 1882. TYPE: U.S.A. Oregon: Union Co., rocky ridges, early spring 1879, *W. C. Cusick 727* (holotype, GH; isotype, US).

Boecheira demissa (Greene) W. A. Weber, Phytologia 51: 370. 1982. Basionym: *Arabis demissa* Greene, Pl. Baker. 3: 8. 1901. TYPE: U.S.A. Colorado: Gunnison Co., Cimarron, stony riverbed, 4 June 1901, *C. F. Baker 16* (holotype, NDG 5264).

Boecheira dispar (M. E. Jones) Al-Shehbaz, comb. nov. Basionym: *Arabis dispar* M. E. Jones, Contr. W. Bot. 8: 41. 1898. TYPE: U.S.A. California: Inyo Co., Panamint Mts., Pleasant Canyon, 5500 ft., 6 May 1897, *M. E. Jones s.n.* (holotype, POM; isotypes, MO, POM, US, UTC not seen).

Boecheira divaricarpa (A. Nelson) A. Löve & D. Löve, Bot. Not. 128: 513. 1976. Basionym: *Arabis divaricarpa* A. Nelson, Bot. Gaz. 30: 193. 1900. TYPE: U.S.A. Wyoming: Yellowstone National Park, Yellowstone Lake, stony and sandy banks of lake, *A. & E. Nelson 6622* (lectotype, designated by Hopkins (1937: 132), RM; isotype, GH).

Arabis calderi G. A. Mulligan, Rhodora 97: 144. 1996. Syn. nov. TYPE: Canada. British Columbia: Indian River at Mile 34 from Alaska Hwy. on Atlin road, ca. 59°54'N, 133°48'W, open grassy flats on bench above river, 9 June 1960, *J. A. Calder & J. M. Gillett 25180* (holotype, DAO).

Nelson (1900) cited two collections (6352 and 6622) in his original description of *Arabis divaricarpa*, but Rollins (1941) indicated that the type is *A. & E. Nelson 6332*, apparently a typographical error. However, Hopkins (1937) was the first to designate a lectotype for the species.

An examination of the holotype of *Arabis calderi* clearly shows that the plant is quite similar to those cited by Mulligan (1996) as *A. divaricarpa* var. *divaricarpa*, including the type collection of *A. pratincta* Greene. There is no single character that supports the maintenance of *A. calderi* as a distinct species, and the trichomes of basal leaves are indistinguishable in the two. As shown by Rollins (1983), *Boecheira divaricarpa* (as *Arabis*) is quite

variable in leaf indumentum and fruit orientation, and various populations of this species show morphological tendencies toward one of its closely related species, *B. stricta* (as *A. drummondii*) and *B. holboellii*.

Boechera falcatoria (Rollins) Dorn, *Brittonia* 55: 3. 2003. Basionym: *Arabis falcatoria* Rollins, *Contr. Gray Herb.* 212: 106. 1982. TYPE: U.S.A. Utah: Box Elder Co., 3.8 mi. N of Grouse Creek on road to Oakley, Idaho, marble chip rock, 9 June 1981, R. C. & K. W. Rollins 81259 (holotype, GH; isotypes, GH, LE, RM, RSA, UC).

Boechera falcifructa (Rollins) Al-Shehbaz, comb. nov. Basionym: *Arabis falcifructa* Rollins, *Contr. Gray Herb.* 212: 112. 1982. TYPE: U.S.A. Nevada: Elko Co., near U.S. Hwy. 93, betw. Thousand Springs & Jackpot, 37 mi. S of Jackpot, rock crevices, sagebrush area on slope of a high ridge, 18 June 1979, R. C. & K. W. Rollins 79267 (holotype, GH; isotype, MO).

Boechera fecunda (Rollins) Dorn, *Brittonia* 55: 3. 2003. Basionym: *Arabis fecunda* Rollins, *Contr. Gray Herb.* 214: 1. 1984. TYPE: U.S.A. Montana: Ravalli Co., big game range E of Corvallis, rocky terrain near sagebrush, 4000 m, 13 June 1976, *Jaculyn Cory* 1611 (holotype, MONTU not seen; isotype, GH).

Boechera fendleri (S. Watson) W. A. Weber, *Phytologia* 51: 370. 1982. Basionym: *Arabis holboellii* var. *fendleri* S. Watson, in A. Gray, *Synop. Fl. N. Amer.* 1: 164. 1895. TYPE: U.S.A. New Mexico: without locality, 1847, A. Fendler 27 (holotype, GH; isotypes, MO, NY not seen, UC).

Boechera fernaldiana (Rollins) W. A. Weber, *Phytologia* 51: 370. 1982. Basionym: *Arabis fernaldiana* Rollins, *Rhodora* 43: 430. 1941. TYPE: U.S.A. Nevada: Nye Co., Toiyabe Mts., E slope of Toiyabe Dome, among rocks & around sagebrush, 10,000 ft., 13 July 1938, R. C. Rollins & T. S. Chambers 2520 (holotype, GH; isotypes, DS, MO, UC).

Arabis vivariensis S. L. Welsh, *Great Basin Naturalist* 46: 263. 1986. *Boechera vivariensis* (S. L. Welsh) W. A. Weber, *Phytologia* 67: 425. 1989. TYPE: U.S.A. Utah: Uintah Co., Jones Hole, National Fish Hatchery, T3S, R25E, Sec. 1, 6000 ft., 16 May 1979, S. L. Welsh & E. Neese 18341 (holotype, BRY not seen; isotypes, CAS, GH, RM, RSA, UC, US).

Welsh (1986) indicated that *Arabis vivariensis* differs from *A. fernaldiana* in style length, fruit width, and petal length, and Weber (1989) trans-

ferred the species to *Boechera*. Although I have not examined the holotype of *A. vivariensis* at BRY, the study of six isotypes supports Rollins (1993b) in reducing the species to synonymy of *A. fernaldiana*. The differences on which *A. vivariensis* was based are rather minor and show continuous variation.

Boechera fruticosa (A. Nelson) Al-Shehbaz, comb. nov. Basionym: *Arabis fruticosa* A. Nelson, *Bot. Gaz.* 30: 190. 1900. TYPE: U.S.A. Wyoming: Yellowstone National Park, Undine Falls, dry roadsides, 6 July 1899, A. & E. Nelson 5681 (holotype, RM; isotypes, GH, MO, NY not seen, US).

Rollins (1983, 1993b) suggested that this species is most likely a variant and possibly synonym of *Arabis divaricarpa*. The two taxa differ considerably in habit as well as the trichomes of basal leaves and merit their recognition as distinct species. The base of *Boechera fruticosa* is somewhat woody and with a few to several stems, and the trichomes are dendritic on minute stalks. By contrast, *B. divaricarpa* is herbaceous and simple at the base, and the trichomes are sessile and often with undivided branches.

Boechera glaucovalvula (M. E. Jones) Al-Shehbaz, comb. nov. Basionym: *Arabis glaucovalvula* M. E. Jones, *Contr. W. Bot.* 8: 40. 1898. TYPE: U.S.A. California: Inyo Co., Darwin Mesa, Argus Mts., 5000 ft., 8 May 1897, Marcus E. Jones s.n. (holotype, POM; isotypes, BM, DS, GH, MO, NY not seen, PH, POM [2], RM, UC [3], US [2], UTC not seen).

Boechera gracilipes (Greene) Dorn, *Brittonia* 55: 3. 2003. Basionym: *Arabis gracilipes* Greene, *Pittonia* 4: 193. 1900. TYPE: U.S.A. Arizona: Coconino Co., Flagstaff, May 1893, N. C. Wilson s.n. (holotype, NDG 4325).

Boechera gunnisoniana (Rollins) W. A. Weber, *Phytologia* 51: 370. 1982. Basionym: *Arabis gunnisoniana* Rollins, *Rhodora* 43: 434. 1941. TYPE: U.S.A. Colorado: Gunnison Co., 6 mi. E of Gunnison, near Saguache Creek, barren rocky knoll, 8000 ft., 21 May 1938, R. C. Rollins 2090 (holotype, GH; isotypes, BM, DAO, GH, RM, UC).

Boechera glareosa Dorn, *Brittonia* 55: 1. 2003. Syn. nov. TYPE: U.S.A. Utah: Uintah Co., ca. 14 mi. E of Jensen, 40°21.077'N, 109°04.117'W, 6700 ft. (2040 m), 12 May 2002, R. D. Dorn 9106 (holotype, RM not seen; isotype, MO).

I have critically examined an isotype of *Boechera glareosa* and compared it with the type collection

and extensive material of *B. gunnisoniana*. There is not a single character that reliably separates the two taxa, especially if the overall variation of the latter is taken into account. The type collection of *B. glareosa* represents the first record of *B. gunnisoniana* from Utah.

Boechea hastatula (Greene) Al-Shehbaz, comb. nov. Basionym: *Arabis hastatula* Greene, Leaf. Bot. Obs. Crit. 2: 79. 1910. TYPE: U.S.A. Oregon: mountains of Imnaha National Forest, 6000 ft., 25 June 1907, A. W. Sampson & G. A. Pearson s.n. (holotype, US).

Boechea hirshbergiae (S. Boyd) Al-Shehbaz, comb. nov. Basionym: *Arabis hirshbergiae* S. Boyd, Aliso 17: 203. 1998. TYPE: U.S.A. California: San Diego Co., Cuyamaca Mts., E of Cuyamaca Reservoir along Sunrise Hwy. (S-1), 0.5 mi. SE of junction with Hwy. 79, about 50 ft. N of the road near the Pedro Fages Trail marker, near 33°00'N, 116°30'W, ca. 1400 m, 19 Mar. 1995, Hirschberg s.n. (holotype, RSA; isotype, GH).

Boechea hoffmanii (Munz) Al-Shehbaz, comb. nov. Basionym: *Arabis maxima* var. *hoffmanii* Munz, Bull. S. Calif. Acad. Sci. 31: 63. 1932. TYPE: U.S.A. California: Santa Cruz Island, ledges in sea cliffs E of Dick's Harbor, 28 Feb. 1932, R. Hoffmann 653 (holotype, POM).

Boechea holboellii (Hornemann) A Löve & D. Löve, Bot. Not. 128: 513. 1976. Basionym: *Arabis holboellii* Hornemann, Fl. Danica 11 (Heft 32): tab. 1879. 1827. TYPE: Greenland. "In-sulae Disco ad Jacobshavn detexit Inspector Grönland," C. Holböll s.n. (holotype, C not seen).

The plate accompanying the original description is superb and shows all the fine details of the flowers, seeds, trichomes, and fruits. *Boechea holboellii* is one of the most complex species in the genus, and Rollins (1993b) divided it into five varieties. Löve and Löve (1976, 1982) treated some of those as *B. collinsii* (Fernald) A. Löve & D. Löve, *B. retrofracta* (Graham) A. Löve & D. Löve, and *B. tenuis* (Böcher) A. Löve & D. Löve, whereas Mulligan (1996) recognized *Arabis boivinii* G. A. Mulligan, *A. exilis* A. Nelson, and *A. pinetorum* Tidestrom.

Boechea inyoensis (Rollins) Al-Shehbaz, comb. nov. Basionym: *Arabis inyoensis* Rollins, Rhodora 43: 457. 1941. TYPE: U.S.A. California: Inyo Co., Sierra foothills W of Big Pine, near rocks in coarse granite sand, 15 May 1906, A. Heller 8259 (holotype, GH; isotypes, CAS, MO, NY not seen, US).

Boechea johnstonii (Munz) Al-Shehbaz, comb. nov. Basionym: *Arabis johnstonii* Munz, Bull. S. Calif. Acad. Sci. 31: 63. 1932. TYPE: U.S.A. California: Riverside Co., Kenworthy, Thomas Valley, San Jacinto Mts., 4500 ft., 19 May 1922, P. A. Munz & I. M. Johnston 5485 (holotype, POM; isotypes, CAS, GH).

Boechea koehleri (T. J. Howell) Al-Shehbaz, comb. nov. Basionym: *Arabis koehleri* T. J. Howell, Fl. Northw. Amer. 1: 44. 1897. TYPE: U.S.A. Oregon: Douglas Co., Cost Mts., along Umpqua River at Roseburg, cliffs, 17 Apr. 1887, T. J. Howell s.n. (holotype, ORE not seen; isotypes, GH, NY not seen, US, WTU not seen).

Although no chromosome count is known for the species, the presence of falcate fruits and subdendritic trichomes supports the assignment of the species to *Boechea*.

Boechea laevigata (Muhlenberg ex Willdenow) Al-Shehbaz, comb. nov. Basionym: *Turritis laevigata* Muhlenberg ex Willdenow, Sp. Pl. 3(2): 543. 1801. *Arabis laevigata* (Muhlenberg ex Willdenow) Poir. Encycl. Suppl. 1: 411. 1810. TYPE: U.S.A. Pennsylvania: without locality, G. H. E. Muhlenberg s.n. (holotype, PH not seen).

On the basis of having a chromosome number of $2n = 14$ (Rollins, 1993b) and falcate fruits, the species is easily assigned to *Boechea*.

Boechea lasiocarpa (Rollins) Dorn, Brittonia 55: 3. 2003. Basionym: *Arabis lasiocarpa* Rollins, Syst. Bot. 6: 58. 1981. TYPE: U.S.A. Utah: Rich Co., 6 mi. W of Garden City, off U.S. Hwy. 89, Wasatch Range, high ridge, sedimentary rock, 22 June 1979, R. C. & K. W. Rollins 79307 (holotype, GH; isotypes, MO [2], RM, UC).

Boechea lemmonii (S. Watson) W. A. Weber, Phytologia 51: 370. 1982. Basionym: *Arabis lemmonii* S. Watson, Proc. Amer. Acad. 22: 467. 1887. TYPE: U.S.A. California: Lassen Peak, Sep. 1872, J. G. Lemmon 23 (lectotype, designated by Rollins (1941: 383), GH).

Watson (1887) cited nine syntypes under the original description of *Arabis lemmonii*. Rollins (1941) listed Lemmon's collection as the type, and this was taken as the lectotype. Rollins (1993b) recognized four varieties, of which two were treated by Mulligan (1996) as distinct species, *A. depauperata* A. Nelson & Kennedy and *A. drepanoloba*

Greene. I have not examined the holotypes of these two and therefore refrain from recognizing them at any rank. The accounts in Rollins (1993b) and Mulligan (1996) of these two species, as well as *A. lemmonii*, *A. lyallii*, and *A. microphylla*, hardly show any agreement. For example, Mulligan listed *A. nubigena* J. F. Macbride & Payson as a synonym of *A. depauperata*, whereas Rollins treated it as a variety of *A. lyallii* and recognized *A. depauperata* as a variety of *A. lemmonii*. Furthermore, Mulligan described the new species *A. codyi* G. A. Mulligan, but this is morphologically indistinguishable from *A. nubigena*.

Boechera lignifera (A. Nelson) W. A. Weber, *Phytologia* 51: 370. 1982. Basionym: *Arabis lignifera* A. Nelson, *Bull. Torr. Bot. Club* 26: 123. 1899. TYPE: U.S.A. Wyoming: Sweetwater Co., Green River, 4 June 1898, *A. Nelson 4711* (holotype, RM; isotypes, GH, MO, US).

Boechera lyallii (S. Watson) Dorn, *Vasc. Pl. Wyom.* ed. 3: 376. 2001. Basionym: *Arabis lyallii* S. Watson, *Proc. Amer. Acad.* 11: 122. 1875. TYPE: U.S.A. Washington: Fort Coville to the Rocky Mts., 1861, *Lyall s.n.* (lectotype, designated by Rollins (1941: 367), GH).

Arabis murrayi G. A. Mulligan, *Rhodora* 97: 151. 1996. Syn. nov. TYPE: Canada. Yukon: Kaskawulsh nunatak, junction N & Central arms Kaskawulsh Glacier, W of Kluane Lake, 6000 ft., unstable slopes, 1 July–1 Aug. 1965, *D. F. & D. B. Murray 91b* (holotype, DAO).

Watson (1871) cited four collections (two of his and one each by Lyall and Brewer) under *Arabis drummondii* var. *alpina* S. Watson. However, in the original description of *A. lyallii*, he (Watson, 1875) listed *A. drummondii* var. *alpina* as a synonym but did not cite any collections. It is possible that *A. lyallii* was intended as a new name at the specific rank because of the pre-existence of *A. alpina* L. Both Hopkins (1937) and Rollins (1941) indicated that the type of *A. lyallii* is Lyall's specimen above, and this should be an effective lectotypification of the species. Hopkins also indicated that *Watson 75* (GH) is the type of *A. drummondii* var. *alpina*, and this led Mulligan (1996) to take this collection as the lectotype of both *A. lyallii* and *A. drummondii* var. *alpina*. In my opinion, the typification of *A. lyallii* by both Hopkins (1937) and Rollins (1941) should be accepted.

Mulligan (1996) reduced *Arabis davidsonii* Greene to synonymy of *A. lyallii*, whereas Rollins (1941, 1993a, b) treated these as distinct species. An examination of the types of both taxa shows that

they are not sufficiently distinct, and I tend to agree with Mulligan's opinion.

A critical study of the type collections of *Boechera lyallii* and *Arabis murrayi*, along with a very broad spectrum of material from throughout the range of the former, clearly shows that the alleged difference on which *A. murrayi* is based (cauline leaves minutely auriculate or not auriculate vs. leaves strongly auriculate in *B. lyallii*) does not hold at all. The development of auricles in this species, as well as several others (including *B. holboellii*), can be dramatic and can vary within a single population. If this character is taken at face value, one would have to recognize *A. murrayi* within populations of the entire range of *B. lyallii*, not just in Canada and neighboring Washington. The alleged differences in the trichomes of both species (Mulligan, 1996: 153), "mostly 0.125 mm wide" in *A. murrayi* versus "mostly 0.25 mm wide" in *A. lyallii*, cannot be justified as a reliable difference either. Trichomes, just as other characters, can vary in size within the same population. For these reasons, I do not find adequate grounds that support the recognition of *A. murrayi*.

Boechera microphylla (Nuttall) Dorn, *Vasc. Pl. Wyom.* ed. 3: 376. 2001. Basionym: *Arabis microphylla* Nuttall, in *Torrey & A. Gray, Fl. N. Amer.* 1: 82. 1838. TYPE: U.S.A. Rocky Mountains, *T. Nuttall s.n.* (holotype, PH; isotype, BM).

Boechera missouriensis (Greene) Al-Shehbaz, comb. nov. Basionym: *Arabis missouriensis* Greene, *Repert. Sp. Nov. Regni Veg.* 5: 244. 1908. TYPE: U.S.A. Missouri: Montier, 15 May 1894, *B. F. Bush 31* (holotype, NDG 4416; isotype, GH).

Mulligan (1996) reduced this species to synonymy of *Arabis laevigata*, but the differences in leaf shape, margin, and apex, as well as petal length in relation to sepals (see Rollins, 1993b: 117) justify the recognition of two closely related species.

Boechera ophira (Rollins) Al-Shehbaz, comb. nov. Basionym: *Arabis ophira* Rollins, *Syst. Bot.* 6: 56. 1981. TYPE: U.S.A. Nevada: Nye Co., Toiyabe Range, near Ophir Pass, T13N, R41E, open rocky area, 13 June 1979, *R. C. & K. W. Rollins 79231* (holotype, GH; isotype, GH).

Boechera oxylobula (Greene) W. A. Weber, *Phytologia* 51: 370. 1982. Basionym: *Arabis oxylobula* Greene, *Pittonia* 4: 195. 1900. TYPE: U.S.A. Colorado: Garfield Co., Glenwood Springs, 18 June 1899, *G. E. Osterhout* (holotype, NDG 4427; isotype, RM).

- Boechea pallidifolia** (Rollins) W. A. Weber, *Phytologia* 79: 65. 1996. Basionym: *Arabis pallidifolia* Rollins, *Cruciferae of Continental North America* 181. 1993. TYPE: U.S.A. Colorado: Gunnison Co., high hill above Sapinero, steep hillside among rocks & low sagebrush, 18 June 1983, R. C. Rollins, K. W. Rollins & A. G. Roads 8376 (holotype, GH; isotypes, GH, UC).
- Boechea parishii** (S. Watson) Al-Shehbaz, comb. nov. Basionym: *Arabis parishii* S. Watson, *Proc. Amer. Acad. Arts* 22: 468. 1887. TYPE: U.S.A. California: San Bernardino Co., Bear Valley, San Bernardino Mts., 6500 ft., June 1886, S. B. Parish 1793 (holotype, GH; isotype, UC).
- Boechea patens** (Sullivant) Al-Shehbaz, comb. nov. Basionym: *Arabis patens* Sullivant, *Amer. J. Sci.* 42: 49. 1842. TYPE: U.S.A. Ohio: rocky banks of Scioto River, near Columbus, 1840, W. S. Sullivant s.n. (holotype, PH; isotype, GH).
- Boechea pendulina** (Greene) W. A. Weber, *Phytologia* 51: 370. 1982. Basionym: *Arabis pendulina* Greene, *Leaf. Bot. Obs. Crit.* 2: 81. 1910. TYPE: U.S.A. Nevada: Clark Co., Charleston Mts., 7000–8000 ft., May–Oct. 1898, C. A. Purpus 6104 (holotype, US; isotypes, RM, UC [2]).
- Boechea perennans** (S. Watson) W. A. Weber, *Phytologia* 51: 370. 1982. Basionym: *Arabis perennans* S. Watson, *Proc. Amer. Acad. Arts* 22: 467. 1887. TYPE: U.S.A. Arizona: Pima Co., Santa Catalina Mts., rocky canyon, 15 Apr. 1881, C. G. Pringle s.n. (holotype, GH; isotype, MO).
- Boechea perstellata** (E. Braun) Al-Shehbaz, comb. nov. Basionym: *Arabis perstellata* E. Braun, *Rhodora* 42: 47. 1940. TYPE: U.S.A. Kentucky: Franklin Co., Elkhorn Creek, wooded hillsides, 6 May 1936, E. L. Braun 1226 (holotype, GH).
- Boechea pinzlae** (Rollins) Al-Shehbaz, comb. nov. Basionym: *Arabis pinzlae* Rollins, *Contr. Gray Herb.* 212: 110. 1982. TYPE: U.S.A. Nevada: Esmeralda Co., White Mts., bowl on NE side of Boundary Peak, near center of bowl, ca. 11,200 ft., A. Pinzl 4442 (holotype, GH; isotype, GH).
- Boechea platysperma** (A. Gray) Al-Shehbaz, comb. nov. Basionym: *Arabis platysperma* A. Gray, *Proc. Amer. Acad. Arts* 6: 519. 1865. TYPE: U.S.A. California: Alpine Co., Ebbetts Pass, 1863, W. H. Brewer 1989 (lectotype, designated by Rollins (1941: 473), GH; isotypes, UC, US).
- Gray (1865) cited two syntypes under the original description of *Arabis platysperma*. Rollins (1941) listed Brewer's collection as the type, and this was accepted as the lectotype of the species.
- Boechea puberula** (Nuttall) Dorn, *Brittonia* 55: 3. 2003. Basionym: *Arabis puberula* Nuttall, in Torrey & A. Gray, *Fl. N. Amer.* 1: 82. 1838. TYPE: U.S.A. Oregon?: Blue Mts., T. Nuttall s.n. (holotype, PH).
- Boechea pulchra** (M. E. Jones ex S. Watson) W. A. Weber, *Phytologia* 51: 370. 1982. Basionym: *Arabis pulchra* M. E. Jones ex S. Watson, *Proc. Amer. Acad. Arts* 22: 468. 1887. TYPE: U.S.A. Nevada: Ormsby Co., Empire City, 19 June 1882, M. E. Jones 3765 (lectotype, designated by Rollins (1941: 459), GH; isotypes, DS, MO, NY not seen, POM, UC, US [2]).
- Watson (1887) cited seven syntypes under the original description of *Arabis pulchra*. Rollins (1941) listed Jones 3765 collection as the type, and this was taken here as the lectotype.
- Boechea pusilla** (Rollins) Dorn, *Vasc. Pl. Wyom.* ed. 3: 376. 2001. Basionym: *Arabis pusilla* Rollins, *Contr. Gray Herb.* 212: 107. 1982. TYPE: U.S.A. Wyoming: Fremont Co., off Wyoming State Hwy. 28, 39 mi. SW of Lander, cracks & crevices of huge metamorphosed rocks, 20 June 1981, R. C. & K. W. Rollins 81366 (holotype, GH; isotypes, GH, MO, RM, UC).
- Boechea pygmaea** (Rollins) Al-Shehbaz, comb. nov. Basionym: *Arabis pygmaea* Rollins, *Rhodora* 43: 476. 1941. TYPE: U.S.A. California: Tulare Co., basin of the Upper Kern River, Volcano Meadows (formerly Whitney Meadows), 21 July 1904, H. M. Hall & H. D. Babcock 5465 (holotype, GH; isotypes not seen, MO, NY, OSC, US).
- Boechea rectissima** (Greene) Al-Shehbaz, comb. nov. Basionym: *Arabis rectissima* Greene, *Pittonia* 4: 191. 1900. TYPE: U.S.A. California: Fresno Co., 1890, Peckinpah s.n. (holotype, NDG 4469; isotype, NY not seen).
- Boechea repanda** (S. Watson) Al-Shehbaz, comb. nov. Basionym: *Arabis repanda* S. Watson, *Proc. Amer. Acad. Arts* 11: 122. 1875. TYPE: U.S.A. California: Mariposa Co., Yosemite Valley, 1866, H. N. Bolander 4881 (holotype, GH; isotype, UC).

Boechera rigidissima (Rollins) Al-Shehbaz, comb. nov. Basionym: *Arabis rigidissima* Rollins, *Rhodora* 43: 380. 1941. TYPE: U.S.A. California: Trinity Co., Mary Blaine Mt., gravely or rocky soil, 6400 ft., 3 Aug. 1935, *J. P. Tracy* 14469 (holotype, GH; isotype, DS).

Boechera rollei (Rollins) Al-Shehbaz, comb. nov. Basionym: *Arabis rollei* Rollins, *Harvard Pap. Bot.* 4: 43. 1993. TYPE: U.S.A. California: Siskiyou Co., divide betw. Applegate & Klamath Rivers, Red Butte-Kangaroo Mt.–Lilypad Lake–Towhead Lake area, T47N, R12W, Sec. 13, 5400–5900 ft., 4 Aug. 1983, *W. E. Rolfe* 831 (holotype, GH; isotypes, GH, JEPS).

Boechera schistacea (Rollins) Dorn, *Brittonia* 55: 3. 2003. Basionym: *Arabis schistacea* Rollins, *Contr. Dudley Herb.* 3: 370. 1946. TYPE: U.S.A. Nevada: Nye Co., 15 mi. W of Round Mt., Toiyabe Mts., open slope, 9000 ft., 11 July 1938, *R. C. Rollins* & *T. S. Chambers* 2512 (holotype, DS; isotype, GH).

Boechera selbyi (Rydberg) W. A. Weber, *Phytologia* 51: 371. 1982. Basionym: *Arabis selbyi* Rydberg, *Bull. Torr. Bot. Club* 31: 557. 1904. TYPE: U.S.A. Colorado: Ouray Co., W of Ouray, 9 Sep. 1901, *L. M. Underwood* & *A. D. Selby* 207 (holotype, NY not seen).

Boechera shockleyi (Munz) Dorn, *Brittonia* 55: 3. 2003. Basionym: *Arabis shockleyi* Munz, *Bull. S. Calif. Acad. Sci.* 31: 62. 1932. TYPE: U.S.A. Nevada: Esmeralda Co., Mellin Mt., near Candelaria, May 1884, *W. H. Shockley* 366 (holotype, GH; isotypes, JEPS, NDG, US).

Boechera shortii (Fernald) Al-Shehbaz, comb. nov. Basionym: *Arabis perstellata* var. *shortii* Fernald, *Rhodora* 48: 208. 1946. *Sisymbrium dentatum* Torrey, in Short, 3rd Suppl. Cat. Pl. Kentucky 338. 1833, non *S. dentatum* Allioni, *Fl. Pedem.* 1: 275. 1785. TYPE: U.S.A. Kentucky: sandy banks of the Ohio River, *C. W. Short* s.n. (lectotype, designated by Mulligan (1996: 143), DWC; isotype, GH).

For full synonymy of the species, see Rollins (1993b).

Boechera sparsiflora (Nuttall) Dorn, *Vasc. Pl. Wyom.* ed. 3: 376. 2001. Basionym: *Arabis sparsiflora* Nuttall, in Torrey & A. Gray, *Fl. N. Amer.* 1: 81. 1838. TYPE: U.S.A. Rocky Mts., toward sources of Oregon, *T. Nuttall* s.n. (holotype, BM; photo, GH; isotype, PH).

Rollins (1941) indicated that Nuttall's sheet at PH is the isotype, whereas Mulligan (1996) considered that sheet a mixture of more than one species

and designated the specimen to the far right as the lectotype. I have examined the type at BM and agree with Rollins's conclusion.

Boechera stricta (Graham) Al-Shehbaz, comb. nov. Basionym: *Turritis stricta* Graham, *Edinburgh New Philos. J.* 7: 350. 1829. *Arabis drummondii* A. Gray, *Proc. Amer. Acad. Arts* 6: 187. 1864. TYPE: U.S.A. Rocky Mts., grown from seeds, *Drummond* s.n. (holotype, E).

The nomenclature of this species is confusing, and the species epithet has not been used since the mid 19th century. The species is far better known as *Arabis drummondii* A. Gray, a name proposed by Gray (1864) to avoid the creation of a later homonym that would have resulted from the transfer of *Turritis stricta* to *Arabis* because of the existence of *A. stricta* Hudson published in 1777 (*Fl. Angl.* 1: 292. 1777). The transfer by Löve and Löve (1976) of *A. drummondii* to *Boechera* is illegitimate because these authors did not use *T. stricta*, the legitimate, validly published, and earliest basionym for the species.

Boechera subpinnatifida (S. Watson) Al-Shehbaz, comb. nov. Basionym: *Arabis subpinnatifida* S. Watson, *Proc. Amer. Acad. Arts* 20: 353. 1885. TYPE: U.S.A. Oregon: Josephine Co., Waldo, 3 June 1884, *T. Howell* s.n. (lectotype, designated by Rollins (1941: 454), GH; isotypes, NY not seen, US).

Watson (1885) cited two syntypes under the original description of *Arabis subpinnatifida*. Rollins (1941) listed Howell's collection as the type, and this was taken as the lectotype of the species.

Boechera suffrutescens (S. Watson) Dorn, *Brittonia* 55: 3. 2003. Basionym: *Arabis suffrutescens* S. Watson, *Proc. Amer. Acad. Arts* 17: 362. 1882. TYPE: U.S.A. Oregon: Baker Co., bluffs of Snake River & vicinity, Apr. 1881, *W. C. Cusick* 919 (holotype, GH).

Boechera tiehmii (Rollins) Al-Shehbaz, comb. nov. Basionym: *Arabis tiehmii* Rollins, *J. Arnold Arbor.* 64: 496. 1983. TYPE: U.S.A. Nevada: Washoe Co., Sierra Nevada, Carson Range, ridge N of Mt. Rose, 3/4 air mi. N-NW of peak, T17N, R18E, Sec. 11, 10,200 ft., near rock outcrops on decomposed granite, 19 Aug. 1982, *A. Tiehm* 7561 (holotype, GH; isotypes, CAS, GH, RSA).

Boechera williamsii (Rollins) Dorn, Vasc. Pl. Wyom. ed. 3: 376. 2001. Basionym: *Arabis williamsii* Rollins, Syst. Bot. 6: 62. 1981. TYPE: U.S.A. Wyoming: Fremont Co., off Wyoming Hwy. 28, E of Continental Divide on SE approach to Wind River Mts., coarse granitic soil, 7800 m, 26 June 1979, R. C. & M. L. Rollins 79332 (holotype, GH; isotypes, GH, MO, RM, UC).

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Literature Cited

Al-Shehbaz, I. A. 1988. The genera of Arabideae (Cruciferae; Brassicaceae) in the southeastern United States. *J. Arnold Arbor.* 69: 85–166.

——— & S. L. O’Kane, Jr. 2002. Taxonomy and phylogeny of *Arabidopsis* (Brassicaceae). (22 August 2002), in C. R. Somerville & E. M. Meyerowitz (editors), *The Arabidopsis Book*. American Society of Plant Biologists, Rockville, Maryland. Doi/10.1199/tab.0001 at <http://www.aspb.org/publications/arabidopsis>.

Appel, O. & I. A. Al-Shehbaz. 2002. Cruciferae. In: K. Kubitzki (editor), *Families and Genera of Vascular Plants* 5: 75–174. Springer-Verlag, Berlin, Heidelberg.

Bailey, C. D., R. A. Price & J. J. Doyle. 2002. Systematics of the halimolobine Brassicaceae: Evidence from three loci and morphology. *Syst. Bot.* 27: 318–332.

Berkutenko, A. N. & N. N. Gurzenkov. 1976. Chromosome numbers and distribution of Cruciferae in the south of the Magadan Region. I. *Bot. Zhurn. (Moscow & Leningrad)* 61: 1595–1603.

———, S. I. Tzytlenok & S. V. Pulkina. 1984. Chromosome numbers and dispersal of the Brassicaceae family in the Magadan District. *Bot. Zhurn. (Moscow & Leningrad)* 69: 75–80.

Böcher, T. W. 1947. Cytological studies of *Arabis holboellii*. *Hereditas* 33: 573.

———. 1951. Cytological and embryological studies in the amphi-apomictic *Arabis holboellii* complex. *Biol. Skr.* 6: 1–59.

———. 1954. Experimental taxonomic studies in the *Arabis holboellii* complex. *Svensk Bot. Tidsskr.* 48: 31–44.

———. 1966. Experimental and cytological studies on plant species IX. Some arctic and montane crucifers. *Biol. Skr.* 14: 1–74.

———. 1969. Further studies in *Arabis holboellii* and allied species. *Bot. Tidsskr.* 64: 141–161.

Burdet, H. M. 1967. Contribution à l’étude caryologique des genres *Cardaminopsis*, *Turritis* et *Arabis* en Europe. *Candollea* 22: 107–156.

Busch, N. A. 1939. *Arabis*. In: V. L. Komarov (editor), *Fl. URSS* 8: 172–197. Academy of Sciences of USSR, Moscow and Leningrad.

Cafferty, S. & C. F. Jarvis (editors). 2002. Typification of Linnaean plant names in Brassicaceae (Cruciferae). *Taxon* 51: 529–537.

Cullen, J. 1965. *Turritis*. In: P. H. Davis (editor), *Flora of Turkey and the East Aegean Islands* 1: 429–430. Univ. Press, Edinburgh.

Dorn, R. D. 2003. A new species of *Boechera* (Brassicaceae) from Utah and Colorado. *Brittonia* 55: 1–3.

Fuentes-Soriano, S. 2002. Taxonomic Revision of the Genus *Pennellia* (Brassicaceae). Master’s Thesis, University of Missouri, St. Louis.

Galloway, G. L., R. L. Malmberg & R. A. Price. 1998. Phylogenetic utility of the nuclear gene arginine decarboxylase: An example from Brassicaceae. *Molec. Biol. Evol.* 15: 1312–1320.

Gray, A. 1864. On *Streptanthus*, Nutt., and the plants which have been referred to that genus. *Proc. Amer. Acad. Arts.* 6: 182–188.

———. 1865. Characters of some new plants of California and Nevada, chiefly from the collections of Professor William H. Brewer, botanist of the State Geological Survey of California, and of Dr. Charles L. Anderson, with revisions of certain genera or groups. *Proc. Amer. Acad. Arts* 6: 519–556.

Greuter, W. & H. Burdet. 1984. Med-checklist notulae, 8. *Willdenowia* 13: 277–288.

Hayek, A. 1911. Entwurf eines Cruciferensystems auf phylogenetischer Grundlage. *Beih. Bot. Centralbl.* 27: 127–335.

Hedge, I. C. 1968. Arabideae. In: K. H. Rechinger (editor), *Flora Iranica* 57: 193–218. Akademische Druck- u. Verlagsanstalt, Graz.

Heenan, P. B., A. D. Mitchell & M. Koch. 2002. Molecular systematics of the New Zealand *Pachycladon* (Brassicaceae) complex: Generic circumscription and relationships to *Arabidopsis* sens. lat. and *Arabis* sens. lat. *New Zealand J. Bot.* 40: 543–562.

Hopkins, M. 1937. *Arabis* in eastern and central North America. *Rhodora* 39: 63–98, 106–148, 155–186.

Johnson, T. F. 1970. Investigations in the Floral Biology of the *Arabis holboellii* Complex. Unpublished M.S. Dissertation, University of Washington, Seattle.

Jones, B. M. G. & J. R. Akeroyd. 1993. *Arabis*. In: T. G. Tutin, N. A. Burges, A. O. Chater, J. R. Edmondson, V. H. Heywood, D. M. Moore, D. H. Valentine, S. M. Walters & D. A. Webb (editors), *Fl. Europaea* ed. 2, 1: 359–369. Cambridge Univ. Press, Cambridge.

Koch, M., J. Bishop & T. Mitchell-Olds. 1999. Molecular systematics and evolution of *Arabidopsis* and *Arabis*. *Pl. Biol.* 1: 529–537.

———, B. Haubold & T. Mitchell-Olds. 2000. Comparative analysis of chalcone synthase and alcohol dehydrogenase loci in *Arabidopsis*, *Arabis* and related genera (Brassicaceae). *Molec. Biol. Evol.* 17: 1483–1498.

———, ——— & ———. 2001. Molecular systematics of the Brassicaceae: Evidence from coding plastidic *matK* and nuclear *chs* sequences. *Amer. J. Bot.* 88: 534–544.

———, C. Dobes & T. Mitchell-Olds. 2003. Multiple hybrid formation in natural populations: Concerted evolution of the internal transcribed spacer of nuclear ribosomal DNA (ITS) in North American *Arabis divaricarpa* (Brassicaceae). *Molec. Biol. Evol.* 20: 338–350.

Linnaeus, C. 1753. *Species Plantarum. Impensis laurentii Salvii, Holmiae* [Stockholm].

Loon, J. C. van, T. W. J. Gadella & E. Kliphuis. 1971.

- Cytological studies in some flowering plants from southern France. *Acta Bot. Neerl.* 20: 157–166.
- Löve, A. & D. Löve. 1976. Nomenclatural notes on Arctic plants. *Bot. Not.* 128: 497–523.
- & ———. 1982. In: A. Löve (editor), IOPB chromosome number reports LXXXV. *Taxon* 31: 119–128.
- Maassoumi, A. A. R. 1980. *Crucifères de la Flore d'Iran. Étude Caryosystematique*. Doctoral Dissertation, Strasbourg, France.
- Meikle, R. D. 1977. *Flora of Cyprus*, Vol. 1. Royal Botanic Gardens, Kew.
- Miyashita, N. T., A. Kawabe, H. Innan & R. Terauchi. 1998. Intra- and interspecific DNA variation and codon bias of the alcohol dehydrogenase (Adh) locus in *Arabidopsis* species. *Molec. Biol. Evol.* 15: 1420–1429.
- Mulligan, G. A. 1964. Chromosome numbers of the family Cruciferae. *Canad. J. Bot.* 42: 1509–1519.
- . 1996. Synopsis of the genus *Arabidopsis* (Brassicaceae) in Canada, Alaska and Greenland. *Rhodora* 97: 109–163.
- . 2002. Chromosome numbers determined from Canadian and Alaskan material of native and naturalized mustards, Brassicaceae (Cruciferae). *Canad. Field-Naturalist* 116: 611–622.
- Nelson, A. 1900. Contributions from the Rocky Mountain herbarium. *Bot. Gaz.* 30: 189–203.
- O'Kane, S. L., Jr. & I. A. Al-Shehbaz. 1997. A synopsis of *Arabidopsis* (Brassicaceae). *Novon* 7: 323–327.
- & ———. 2003. Phylogenetic position and generic limits of *Arabidopsis* (Brassicaceae) based on sequences of nuclear ribosomal DNA. *Ann. Missouri Bot. Gard.* 90: 603–612.
- Packer, J. G. 1964. Chromosome numbers and taxonomic notes on western Canadian and Arctic plants. *Canad. J. Bot.* 42: 473–494.
- Polatschek, A. 1966. Cytotaxonomische Beiträge zur Flora der Ostalpenländer, I. *Österr. Bot. Z.* 113: 1–46.
- Price, R. A., C. D. Bailey & I. A. Al-Shehbaz. 2001. Transfer of the cupulate-flowered *Arabidopsis microsperma* and *A. tricornuta* to *Pennellia* (Brassicaceae). *Novon* 11: 337–340.
- Rollins, R. C. 1941. A monographic study of *Arabidopsis* in western North America. *Rhodora* 43: 289–325, 348–411, 425–485.
- . 1983. Interspecific hybridization and taxon uniformity in *Arabidopsis* (Cruciferae). *Amer. J. Bot.* 70: 625–634.
- . 1993a. New taxa and names in the Cruciferae of California. *Harvard Pap. Bot.* 4: 43–48.
- . 1993b. The Cruciferae of Continental North America. Stanford Univ. Press, Stanford.
- & L. Rüdénberg. 1971. Chromosome numbers of Cruciferae II. *Contr. Gray Herb.* 201: 117–133.
- & ———. 1977. Chromosome numbers of Cruciferae III. *Contr. Gray Herb.* 207: 101–116.
- Roy, B. A. 1995. The breeding systems of six species of *Arabidopsis* (Brassicaceae). *Amer. J. Bot.* 82: 869–877.
- Schultze-Motel, W. 1986. Cruciferae. In: G. Hegi, *Illustrierte Flora von Mittel-europa* 4(1): 73–514. Verlag Paul Parey, Berlin and Hamburg.
- Schulz, O. E. 1936. Cruciferae. In: A. Engler & H. Harms (editors), *Die Natürlichen Pflanzenfamilien*, ed. 2, 17B: 227–658. Verlag von Wilhelm Engelmann, Leipzig.
- Titz, W. 1967. Zur Cytologie und Systematik einiger österreichischer *Arabidopsis*-Arten (einschliesslich *Turritis glabra* L.). *Ber. Deutsch. Bot. Ges.* 49: 474–488.
- Torrey, J. & A. Gray. 1838. *A Flora of North America*, Vol. 1. Wiley & Putnam, New York.
- Vorobik, L. A. 1985. Hybridization and Reproductive Isolation between Sympatric *Arabidopsis* (Cruciferae) in Southwestern Oregon. Unpublished Ph.D. Dissertation, University of Oregon.
- Watson, S. 1871. Botany. In: C. King, *United States Geological Exploration of the Fortieth Parallel*, Vol. 5. Government Printing Office, Washington, D.C.
- . 1875. Botanical contributions VI. *Proc. Amer. Acad. Arts* 11: 105–148.
- . 1885. Contributions to American botany XIV. *Proc. Amer. Acad. Arts* 20: 324–378.
- . 1887. Contributions to American botany XXI. *Proc. Amer. Acad. Arts* 22: 396–481.
- Weber, W. A. 1982. New names and combinations, principally in the Rocky Mountain flora—II. *Phytologia* 51: 369–376.
- . 1989. New names and combinations, principally in the Rocky Mountain flora—II. *Phytologia* 67: 425–428.
- . 1996. New names and combinations, principally in the Rocky Mountain flora—IX. *Phytologia* 79: 65–67.
- Welsh, S. L. 1986. New taxa in miscellaneous families from Utah. *Great Basin Naturalist* 46: 261–264.
- Zhou, T. Y., L. L. Lu, G. Yang & I. A. Al-Shehbaz. 2001. Brassicaceae. Pp. 1–193 in Z. Y. Wu & P. H. Raven (editors), *Flora of China*, Vol. 8. Science Press, Beijing, and Missouri Botanical Garden Press, St. Louis.



Al-Shehbaz, Ihsan A. 2003. "Transfer of most North American species of Arabis to Boechera (Brassicaceae)." *Novon a journal of botanical nomenclature from the Missouri Botanical Garden* 13, 381–391.

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