
Beringia (Brassicaceae), a New Genus of Arabidopsoid Affinities from Russia and North America

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ABSTRACT. The new monotypic genus *Beringia* is proposed to include the extremely similar taxa previously treated as *Halimolobos mollis* from northern North America and Greenland, *H. virgata* from western North America, and *Arabidopsis bursifolia* from the Russian Far East. The new combinations *B. bursifolia* and *B. bursifolia* subsp. *virgata* are proposed, and a key to taxa and synopsis of the genus are presented.

Key words: *Arabidopsis*, *Beringia*, Brassicaceae, *Halimolobos*, North America, Russia.

As previously delimited (Schulz, 1924; Al-Shehbaz, 1988; Rollins, 1993), *Arabidopsis* (DC.) Heynhold included a heterogeneous assemblage of unrelated taxa that superficially resemble each other. Molecular studies using chloroplast DNA restriction site or sequence variation (Price et al., 1994; Price, unpublished data), and using the internal transcribed spacer (ITS) regions of nuclear ribosomal DNA (Koch et al., 1999; O'Kane & Al-Shehbaz, in press), coupled with detailed morphological comparisons (see Al-Shehbaz et al., 1999), clearly support the division of the 59 species previously assigned to *Arabidopsis* into smaller, better defined genera. As a result, *Arabidopsis* as now recognized consists of only nine species distributed primarily in Europe, with *A. thaliana* (L.) Heynhold being a cosmopolitan weed, and the range of *A. halleri* (L.) O'Kane & Al-Shehbaz extending into boreal and eastern Asia, while that of *A. lyrata* (L.) O'Kane & Al-Shehbaz extends into boreal and eastern Asia and northern and central North America (O'Kane & Al-Shehbaz, 1997). The generic placement of the great majority of the remaining 50 species of *Arabidopsis* is addressed by Al-Shehbaz et al. (1999), with the exception of the Siberian *A. bursifolia* (DC.) Botschantsev, the northern North American

Halimolobos mollis (Hooker) Rollins, and the morphologically extremely similar *Halimolobos virgata* (Nuttall ex Torrey & A. Gray) O. E. Schulz from the western United States and Canada. Here we reexamine the relationships of these species and propose a revised treatment under the new genus *Beringia*.

The correct generic placement of the three species treated here in *Beringia* has been a matter of controversy. They have in the past been variously assigned to the genera *Arabidopsis* (Rydberg, 1922; Schulz, 1933; Hultén, 1945; Botschantsev, 1957, 1959; Jurtsev et al., 1975; Berkutenko, 1983, 1988; Czerepanov, 1995), *Arabis* L. (Hopkins, 1937; Busch, 1939; Porsild, 1943; Jurtsev, 1974), and *Halimolobos* Tausch (Schulz, 1924; Rollins, 1943, 1952, 1993; Porsild, 1957; Hultén, 1968). A major cause for this taxonomic confusion is the fact that generic classification in the Brassicaceae has tended to heavily emphasize fruit and seed morphology, which are apparently subject to frequent homoplasy or retained symplesiomorphy (see e.g., Price, 1996, 1997; Koch et al., 1999; Bailey et al., in press). Sequence data from both the chloroplast and nuclear genomes strongly suggest that in addition to a highly heterogeneous group of lineages having been previously placed in *Arabidopsis* sensu lato, both *Arabis* and *Halimolobos* as circumscribed by Rollins (1993) are polyphyletic assemblages, including multiple, well-separated lineages (see Price, 1997; Koch et al., 1999; Bailey et al., in press). All sequence comparisons conducted to date support the exclusion of *Halimolobos virgata* and *H. mollis* from the clade of southwestern North American, Mexican, and South American taxa (halimolobine clade, Bailey, 2001; Bailey et al., in press) that includes the type of *Halimolobos* and the majority of currently recognized species from

the genus. Sequence comparisons of the chloroplast gene *ndhF* (Price, unpublished data) and the nuclear ribosomal DNA ITS regions (O'Kane & Al-Shehbaz, in press; Bailey et al., in press) indicate that the taxa that we are placing in *Beringia* are much more closely related to one another than to any other genus, and that their closest generic relative is the sister genus *Crucihimalaya* Al-Shehbaz, O'Kane & Price. The three taxa of *Beringia* differ in their *ndhF* sequences by a maximum of two base substitutions across a 1523 base pair region of this rapidly changing chloroplast gene, while differing from *Crucihimalaya* by a minimum of 22 base substitutions. ITS sequences for the two taxa assigned to *Beringia* and examined to date (*Arabidopsis bursifolia* from the Russian Far East and *Halimolobos virgata* from Colorado) are identical, providing additional evidence of their close genetic relationship (O'Kane & Al-Shehbaz, in press; D. Bailey, pers. comm.).

Beringia is readily distinguished morphologically from *Crucihimalaya* by having biseriate seeds, fruit valves with prominent marginal veins, and dendritic trichomes especially on its basal leaves. *Crucihimalaya*, which consists of nine primarily Himalayan species (Al-Shehbaz et al., 1999), has uniseriate seeds, fruit valves with obscure marginal veins, and predominantly forked leaf trichomes. *Beringia* is easily distinguished from the more distantly related *Arabidopsis* by having sagittate to auriculate cauline leaves, biseriate seeds, dendritic leaf trichomes, and fruit valves with prominent marginal veins. *Arabidopsis* has petiolate to subsessile but neither sagittate nor auriculate cauline leaves, uniseriate seeds, valves with obscure marginal veins, and leaves with only simple and forked trichomes.

The similarities between *Beringia* and *Halimolobos* are striking, especially in most aspects of flower and fruit morphology. However, the two genera can easily be separated by habit and leaf morphology. Plants of *Beringia* are perennials with a distinct caudex, persistent basal leaf rosettes, entire or rarely minutely toothed cauline leaves, and glabrous fruits. By contrast, species of *Halimolobos* are mostly biennials without distinct caudices or basal leaf rosettes, and they have coarsely dentate to sinuate cauline leaves and stellately or dendritically pubescent fruits. Only two species of *Halimolobos*, *H. palmeri* (Hemsley) O. E. Schulz and *H. parryi* (Hemsley) Rollins, have glabrous fruits, but the other aspects of these two species are clearly characteristic of the genus. As delimited here, *Halimolobos* consists of 12 Mexican species (2 ranging north into the southwestern United States), of which

1 (*H. hispidula* (DC.) O. E. Schulz) extends southward into Argentina, and 3 South American species.

The degree of taxonomic distinctness between the three taxa that we are placing in *Beringia* has also been a matter of controversy. While Rollins (1943, 1952, 1993) recognized *Halimolobos virgata* and *H. mollis* as distinct species, he (1943: 256) suggested that "The similarity between *H. virgata* and *H. mollis* is striking enough so that the two entities might easily be considered to be varieties of the same species." Porsild (1943) took the other extreme by treating the two taxa as conspecific under *Arabidopsis hookeri* Lange. Jurtzev (1975) listed the North American *Turritis mollis* Hooker (= *H. mollis*) as a questionable synonym of the Siberian *Arabidopsis bursifolia*. Berkutenko (1983) placed *H. mollis* in synonymy under *A. bursifolia*, although she later (Berkutenko, 1988) treated their relationship as unresolved, and she indicated that *A. tschuktschorum* Jurtzev is probably an abnormal form of *A. bursifolia*. A critical examination of *A. bursifolia* and *H. mollis* from a wide range of herbarium specimens failed to uncover any consistent morphological differences, and thus we treat *H. mollis* as a synonym of *B. bursifolia*. The finding that ITS sequences for *A. bursifolia* and *H. virgata* are identical (O'Kane & Al-Shehbaz, in press) is also entirely consistent with the treatment of all three taxa as conspecific.

Most of the differences (e.g., stems simple vs. branched at base, plants caespitose or not, fruits terete vs. compressed) given by Rollins (1993) for the separation of *Halimolobos mollis* from *H. virgata* clearly do not hold across the range of currently available herbarium specimens, and the only reliable character that separates them is the distribution and type of trichomes on the upper stems and racemes of the plants, which are glabrous or sparsely pubescent with simple trichomes in *H. mollis* (and *Arabidopsis bursifolia*) and pubescent with branched subappressed trichomes (sometimes mixed with simple ones) in *H. virgata*. Because of this one-character difference and their different geographic distributions (see key), we propose the recognition of the two taxa of the new genus *Beringia* at the rank of subspecies.

Beringia R. A. Price, Al-Shehbaz & O'Kane, gen. nov. TYPE: *Beringia bursifolia* (DC.) R. A. Price, Al-Shehbaz & O'Kane.

Herba perennis; pili ramosi minute stipitati et pilis simplicibus vel furcatis praesentibus; folia basalia rosulata, petiolata, dentata vel integra; folia caulina sessilia, sagittata vel auriculata; racemi ebracteati, valde elongati; se-

pala oblonga, nonsaccata; petala alba; ovulae 35–75 per locula; fructus lineares, teretes, valvae manifeste trinervae; septum completum; semina biseriata, oblonga, mucilaginoso; cotyledones incumbentes.

Herbs perennial, basally hirsute with simple and some forked trichomes, often with dendritic and forked trichomes on other parts. Stems erect to ascending, single or several from the caudex, simple or branched. Basal leaves rosulate, petiolate, simple, dentate to entire. Cauline leaves sessile, sagittate to auriculate, entire to rarely minutely dentate. Racemes several-flowered, ebracteate, corymbose, elongated considerably in fruit; rachis straight. Sepals oblong, deciduous, erect, glabrous or pubescent, base of inner pair not saccate. Petals white, oblanceolate, short clawed. Stamens 6, slightly tetradynamous; anthers oblong, cordate at base, short apiculate at apex. Nectar glands confluent and subtending bases of all stamens. Ovules 35–75 per locule. Fruit dehiscent, linear, terete, glabrous, not torulose; valves with a prominent midvein and marginal veins, secondary veins anastomosing, distinct or obscure; gynophore absent to obsolete; septum complete; style distinct, to 1 mm long; stigma capitate, entire. Seeds biseriata, wingless, oblong, plump; seed coat minutely reticulate, mucilaginous when wetted; cotyledons incumbent.

Beringia is named after the Bering Sea, in relation to the distribution of its plants across both sides of that sea.

Beringia bursifolia (DC.) R. A. Price, Al-Shehbaz & O'Kane, comb. nov. Basionym: *Nasturtium bursifolium* DC., Syst. Nat. 2: 194. 1821. *Arabidopsis bursifolia* (DC.) Botschantsev, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 19: 106. 1959. TYPE: [Russia], Kamtchatka, *Fischer s.n.* (holotype, G-DC).

Turritis mollis Hooker, Fl. Bor.-Amer. 1: 40. 1829. *Arabidopsis mollis* (Hooker) O. E. Schulz, Bot. Jahrb. Syst. 66: 97. 1933. *Halimolobos mollis* (Hooker) Rollins, Rhodora 43: 480. 1941. *Arabis hookeri* Lange, Consp. Fl. Groenland 3: 50. 1880, not *A. mollis* Steven, Mem. Soc. Nat. Moscou 3: 270. 1812. TYPE: "shores of the Arctic Sea, between long. 107° and 130°," *Richardson s.n.* (holotype, K).

Arabis trichopoda Turczaninow, Bull. Soc. Imp. Naturalistes Moscou 13: 63. 1840. *Arabidopsis trichopoda* (Turczaninow) Botschantsev, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 18: 104. 1957. TYPE: [Russia.] Yakutia, between Yakutsk and Aldan, *Turczaninow s.n.* (holotype, LE).

Arabis tschuktschorum Jurtzev, Bot. Zhurn. (Moscow & Leningrad) 59: 1452. 1974. *Arabidopsis tschuktschorum* (Jurtzev) Jurtzev, Bot. Zhurn. (Moscow & Leningrad) 60: 240. 1975. TYPE: Russia. "Peninsulae

Tschukotskij, ad fl. Putukunei-veem," 22 July 1972, *B. Jurtzev s.n.* (holotype, LE).

Arabidopsis bursifolia var. *beringensis* Jurtzev, in A. I. Tolmatchev, Fl. Arctica URSS 7: 58. 1975. TYPE: Russia. Peninsulae Tschukotskij, near Czegitun, 8 Aug. 1972, *Jurtzev, Sekretareva & Sytin s.n.* (holotype, LE).

Herbs perennial from a simple or branched caudex, densely hirsute basally with primarily simple trichomes to 1 mm long, these often mixed with smaller, forked and/or dendritic trichomes, distally glabrescent or with simple and/or short-stalked, subappressed dendritic trichomes. Stems (5–)10–45(–60) cm tall, 1 to several from the base, erect, simple or branched near base and above. Basal leaves rosulate; petiole 0.3–3 cm long, flattened at base, ciliate; blade oblanceolate to obovate or linear-lanceolate, (0.5–)1.2–6.5(–10) cm long, (2–)3–8(–15) mm wide, pubescent primarily with branched trichomes on both surfaces, base cuneate to attenuate into petiole, margin entire or sometimes dentate, very rarely sinuate, apex obtuse to subacute. Cauline leaves lanceolate to linear-lanceolate or narrowly oblong, middle ones (0.5–)1–3(–4.2) cm long, (1–)2.5–7(–10) mm wide, sessile, strongly sagittate to auriculate, pubescent as basal leaves, margin entire or very rarely minutely few toothed, apex obtuse to subacute. Sepals oblong, 1.2–2.5 × 0.6–1 mm, with a distinct membranous margin, sparsely to densely pubescent with simple and/or branched trichomes. Petals white, oblanceolate, (2.5–)3–4(–4.5) mm long, (0.8–)1–1.5 mm wide, obtuse at apex. Filaments white, slender, 2–2.5 mm long; anthers oblong, 0.4–0.5 mm long. Fruiting pedicels ascending to subdivaricate, slender, straight, (3–)5–14(–18) mm long, glabrous or pubescent with simple or branched trichomes. Fruit linear, erect to erect-ascending, terete, glabrous, smooth, (1.5–)2–3.3(–3.8) cm long, (0.7–)0.9–1.2 mm wide; valves with a prominent midvein and marginal veins, not torulose. Style slender, 0.2–0.8(–1) mm long. Seeds narrowly oblong, 0.8–1 × 0.4–0.5 mm.

KEY TO THE SUBSPECIES OF *BERINGIA BURSIFOLIA*

- 1a. Upper parts of stem and inflorescence rachis glabrous or sparsely pubescent with simple trichomes; plants of the Russian Far East, Alaska, Yukon, Saskatchewan, and Greenland
 subsp. *bursifolia*
- 1b. Upper parts of stem and inflorescence rachis with branched subappressed trichomes sometimes mixed with simple ones; plants of Alberta, Saskatchewan, Colorado, Utah, Idaho, and Wyoming subsp. *virgata*

***Beringia bursifolia* subsp. *bursifolia*.**

Representative specimens examined. RUSSIA (all from Yakutsky Region and deposited at LE). Niznekolymsky District: Kolyma river basin, 22 June 1973, *Petrovsky s.n.*; Ponteleyka, *Nepli 593*. Abysky District: Indigirskaya lowland, 2 km S of Ozshochino, *Kondratyeva 192*. Yakutia District: near Yakutsk, *Drobov 16*, *Sokolov 151*; vicinity of Yakutsk Mts. on the Vilyuisky rd. near River Lena, *Abolin 6*, *Abolin 53*; near Pantelenhy, *Nepli 120*; Kolimsky, on way from Pohodka to Pantelenhy, *Shulga 304*. Tiksi District: near port Tiksi, 3 Aug. 1956, *Shamurin s.n.*; Lena River basin, near Tiksi, 17 July 1955, *Tikhomirov & Shamurin s.n.*; banks of Bolshoy Buluikan, near Tiksi, 9 July 1955, *Tikhomirov, Shamurin & Dorogostayskaya s.n.* Verhoyansky District: basin of Yani river, *Yarovoi 41*. Oymyakonsky District: near Tomtor settlement, S slope of Lisiy Mt., 21 July 1958, *Yutzev s.n.* Churapchinsky District: 20 km from Xhrapchi, *Kuvaev 58-3*; near Sredny-Kolymsk, 15 June 1964, *Permjakova s.n.* CANADA. **Yukon Territory:** Whitehorse, *Gillett & Mitchell 3260* (MO); W slope of Moosehide Mt., Dawson, *Calder & Billard 2902* (MO); Klondike River, Dawson, *Eastwood 117* (NY). **Saskatchewan:** Lipton, *Clokey 1804* (MO). GREENLAND. Qaersuarssuk, 26 July 1927, *Porsild s.n.* (MO); Qeqertat, 11 July 1929, *M. & R. Porsild s.n.* (MO); Etah, *Robinson 31* (GH); Ikerasak i Umanaq Distrikt, 30 July 1935, *Porsild s.n.* (MO); Sydostbugten, N of Qarajaq, *Feilberg 2600* (MO); Itivdleq-Fjord, Qingua, 5 July 1926, *Porsild s.n.* (MO); Foulke Fjord, *Simmons 1466* (GH); Argersiorfik Fjord, 20 July 1924, *Porsild s.n.* (MO).

To our knowledge, the type specimen of *Beringia bursifolia* subsp. *bursifolia* is the single known collection from Kamchatka (Berkutenko, 1988). Although Rollins (1943) reported the subspecies (as *Halimolobos mollis*) from Alaska, we have not seen material from that state. The above material from Saskatchewan was annotated by Rollins as *Halimolobos virgata*, but the plants are glabrous above and their middle parts are exclusively with simple trichomes. Therefore, they should be assigned to subspecies *bursifolia*.

Beringia bursifolia* subsp. *virgata (Nuttall ex Torrey & A. Gray) R. A. Price, Al-Shehbaz & O'Kane, comb. nov. Basionym: *Sisymbrium virgatum* Nuttall ex Torrey & A. Gray, Fl. N. Amer. 1: 93. 1838. *Hesperis virgata* (Nuttall ex Torrey & A. Gray) Kuntze, Revis. Gen. Pl. 2: 935. 1891. *Stenophragma virgata* (Nuttall ex Torrey & A. Gray) Greene, Pittonia 3: 138. 1896. *Pilosella virgata* (Nuttall ex Torrey & A. Gray) Rydberg, Torrey 7: 160. 1907. *Arabidopsis virgata* (Nuttall ex Torrey & A. Gray) Rydberg, Fl. Rocky Mt. 342. 1917. *Halimolobos virgata* (Nuttall ex Torrey & A. Gray) O. E. Schulz, in Engler, Pflanzenr. 86(IV. 105): 290. 1924. TYPE: U.S.A. Rocky Mts. [probably Wyoming], "sources of Sweet Water of the Platte," *Nuttall s.n.* (holotype, BM; isotypes, GH, NY, PH).

Arabis berberiana A. Nelson, Bull. Torrey Bot. Club 25: 383. 1898. TYPE: U.S.A. Wyoming: Carbon Co., Fort Steele, A. Nelson 3135 (holotype, RM; isotype, NY).

Pilosella stenocarpa Rydberg, Torrey 7: 161. 1907. *Arabidopsis stenocarpa* Rydberg, Fl. Rocky Mt. 342. 1917. TYPE: Canada. Saskatchewan: Wood Mt., Assiniboia, *Macoun 10007* (holotype, NY; isotypes, GH, MO, US).

Representative specimens examined. U.S.A. **Colorado:** Park Co., 4 mi. SW of Fairplay, *Rollins, Weber & Livingston 5169* (GH, MO); 1/4 mi. S of Fairplay, off U.S. hwy. 285, *R. & K. Rollins 83334* (GH, MO). **Utah:** Daggett Co., 12 mi. SW of Manila, *Rollins 2269* (GH). **Idaho:** Butte Co., Big Creek, *Davis 178* (MO). **Wyoming:** Albany Co., Laramie, A. & E. Nelson 6827 (GH, MO, NY, US), *Porter 3192* (MO); Laramie Hills, *Nelson 1902* (GH, MO, NY, US); Pole Mt., *Porter 3247* (MO); Telephone Canyon, *Williams 2229* (GH, MO); Uinta Co., near Henrys Fork River, between Lonetree and McKinnon, *Rollins 1682* (GH, MO, NY); Sweetwater Co., Leucite Hills, *Merrill & Wilcox 480* (GH, MO, NY). CANADA. **Alberta:** vicinity of Rosedale, *Moodie 949* (GH, MO).

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