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Authors: Al-Shehbaz, Ihsan A., and O'Kane, Steve L.

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Taxonomy and Phylogeny of Arabidopsis (Brassicaceae)

Ihsan A. Al-Shehbaz^a and Steve L. O’Kane, Jr.^b

^aMissouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. (e-mail: ihsan.al-shehbaz@mobot.org)

^bDepartment of Biology, University of Northern Iowa, Cedar Falls, Iowa 50614-0421, U.S.A. (e-mail: Steve.Okane@uni.edu)

ABSTRACT

Detailed taxonomic, cytological, and phylogenetic accounts of *Arabidopsis* are presented. As currently delimited, the genus consists of nine species all of which are indigenous to Europe, with the ranges of two species extending into northern and eastern Asia and North American into central United States. A survey of chromosome numbers in the genus is presented, and the country of origin for each count is given. Detailed descriptions of all species and subspecies and keys to all taxa are provided. Generic assignments are updated for the 50 species previously included in *Arabidopsis*. A cladogram of the species of *Arabidopsis* based on molecular phylogenetic studies by the authors is given.

Introduction

The significance of *Arabidopsis* in every aspect of plant biology is known to all biologists and therefore needs no introduction here. The interested reader should consult Meyerowitz and Somerville (1994) and articles and references therein for leads. The present contribution attempts to provide an up-to-date historical, taxonomic, cytological, and phylogenetic information on the genus not found in any other single publication.

Nomenclature and Generic Limits

Nomenclatural history of *Arabidopsis*

The name *Arabidopsis* was first proposed by de Candolle (1821) as a section of the genus *Sisymbrium* Linnaeus, and the seven species he assigned to that section were *S. bursifolium* Linnaeus [now *Rorippa dentata* (Linnaeus) O. Bolós & Vigo], *S. pinnatifidum*

(Lamarck) de Candolle [now *Murbeckiella pinnatifida* (Lamarck) Rothmaler], *S. erysimoides* Desfontaines [same], *S. ramulosum* Delile [now *S. irio* Linnaeus], *S. cinereum* Desfontaines [now *Ammosperma cinereum* (Desfontaines) J.D. Hooker], *S. torulosum* Desfontaines [now *Neotorularia torulosa* (Desfontaines) Hedge & J. Léonard], and *S. contortuplicatum* Willdenow [now *N. contortuplicata* (Willdenow) Hedge & J. Léonard]. When Heynhold (in Holl and Heynhold, 1842) raised *Arabidopsis* to the generic rank, he listed *A. thaliana* as the sole member of the genus. Prior to the Berlin International Code of Botanical Nomenclature (Greuter et al., 1988), many botanists took *A. thaliana* as the type of the genus. However, such typification is erroneous because *A. thaliana* was not one of the original species that de Candolle (1821) assigned to section *Arabidopsis*. According to the Code (for the latest version, see Greuter et al., 2000), the genus must be typified by the type of the sect. *Arabidopsis*. However, de Candolle (1821) did not typify the section, and none of the original seven species he placed in it is now retained in *Arabidopsis*. Celakovsky (1872) retained one of the

seven original de Candolle species, *S. bursifolium*, in *Arabidopsis*, thereby automatically lectotypifying the genus. However, this action would mean that *Arabidopsis* should be reduced to synonymy of the earlier published *Rorippa* Scopoli. The choice of any of the other six original de Candolle species as the type of *Arabidopsis* would mean that either *Arabidopsis* be reduced to synonymy of *Sisymbrium*, or *Ammosperma* J.D. Hooker, *Murbeckiella* Rothmaler, or *Neotorularia* Hedge & J. Léonard be reduced to synonymy of the earlier published *Arabidopsis*. Because of the importance of *Arabidopsis thaliana* in plant biology, taxonomists wanted to find a permanent solution to maintain this name regardless to the complicated nomenclatural past. The only solution was to conserve *Arabidopsis* with a conserved type, as proposed Stepánek (1983) and discussed by Al-Shehbaz (1988). The Berlin Code (Greuter et al. 1988) did just that.

Generic limits of Arabidopsis

The generic limits of *Arabidopsis* were expanded considerably by Busch (1909), and the five species he recognized in the genus (*A. thaliana*, *A. pumila*, *A. toxophylla*, *A. verna*, *A. huetii*) are currently placed in five different genera see the list of species excluded from *Arabidopsis*. Schulz (1924) accepted the first three species of Busch in *Arabidopsis*, but he expanded the limits of the genus further and added eight other species, of which one (*A. parvula*) was transferred by Al-Shehbaz and O’Kane (1995) to *Thellungiella* and the remaining seven to *Crucihimalaya* (Al-Shehbaz et al., 1999). Many other authors transferred to *Arabidopsis* dozens of species that were previously placed in the genera *Arabis*, *Braya*, *Cardaminopsis*, *Cymatocarpus*, *Halimolobos*, *Microsisymbrium*, *Nasturtiopsis*, *Neotorularia*, or *Torularia*. As pointed out by Al-Shehbaz (1988), the limits of *Arabidopsis* became highly artificial because of the transfer of many species (with linear fruits and branched trichomes) that did not fit appropriately in other genera. As a result, *Arabidopsis* became so heterogeneous morphologically (see for example, the accounts of Hedge, 1968; Jafri, 1973; Ball, 1993) that it became almost impossible to delimit it.

The artificially delimited boundaries of *Arabidopsis* are reflected by numerous other cases in the mustard family (Brassicaceae). We believe that principal reasons for such artificiality is the heavy reliance by taxonomists on a few fruit and seed characters that show high convergence, and their placement of much less value on aspects of flowers, trichomes, and vegetative characters. In fact, convergence in the family is so common in almost every morphological character that superficially very similar genera might prove to be unrelated or remotely related. Because fruit and seed morphology has traditionally been used in taxonomy of the Brassicaceae, the problem becomes more acute among the numerous genera with apparently similar linear fruits and branched trichomes.

The pioneering molecular work on the genus and its presumed relatives (Price et al., 1994) stimulated subsequent studies on the taxonomy and phylogeny of the genus. Initial taxonomic attempts by Al-Shehbaz (1994) and Al-Shehbaz and O’Kane (1995, 1997) to exclude some of the anomalous species from *Arabidopsis* have paved the way for thorough morphological studies that led to the recognition of only nine species in this genus (O’Kane and Al-Shehbaz, 1997) and to the exclusion of the remaining species to several other genera (Al-Shehbaz et al., 1999). The latter two taxonomic studies went in parallel with extensive molecular phylogeny (O’Kane and Al-Shehbaz, in press) on the genus and almost all the species previously assigned to it. Subsequent molecular studies (e.g., Koch et al., 1999, 2000) provided full support to the taxonomic conclusions reached by O’Kane and Al-Shehbaz (1997) and Al-Shehbaz et al. (1999).

Distinguishing characters

The genus *Arabidopsis* can be distinguished from the related genera (see also the key below) by the presence of short petiolate but never auriculate or amplexicaul stem leaves, an indumentum of simple trichomes mixed with few-forked but never stellate ones, usually well-defined basal rosettes, white to lavender or rarely purple but never yellow flowers, at least slightly torulose, glabrous, compressed or rarely terete fruits with a distinct midvein, uniseriate, wingless or rarely winged seeds, and accumbent or rarely incumbent cotyledons. *Arabidopsis* can easily be confused with several genera, and the following key should readily separate the genus from those that currently house species previously placed in *Arabidopsis*.

Key to the genera with species previously placed in *Arabidopsis*

- 1a. Plants completely glabrous; leaves and stems glaucous; plants often restricted to strongly saline soils*Thellungiella*
- 1b. Plants sparsely to densely hairy; leaves and stems usually not glaucous; plants (except *Pseudoarabidopsis*) typically on other soil types.
- 2a. Trichomes sessile and completely appressed, malpighiaceus and/or stellate with unbranched rigid straight rays.....*Erysimum*
- 2b. Trichomes short or long stalked, simple or branched, if stellate and sessile then rays slender and/or branched.
- 3a. Scapose annuals without stem leaves; fruiting pedicel nearly as thick as fruit.....*Drabopsis*
- 3b. Nonscapose annuals, biennials, or perennials with few to many stem leaves; very rarely perennials without stem leaves; fruiting pedicels much narrower than fruit (except some *Neotorularia*).
- 4a. Fruits flattened; cotyledons accumbent.
- 5a. Stem leaves short petiolate, neither sagittate nor auriculate at base; trichomes simple and 2- or 3(or 4)-forked, never dendritic or stellate; fruit valves with a prominent midvein; seeds usually wingless.....*Arabidopsis*
- 5b. Stem leaves sagittate or auriculate at base, rarely petiolate; at least some of leaf trichomes dendritic or stellate; fruit valve without or with obscure midvein; seeds often winged.....*Arabis*
- 4b. Fruits terete or 4-angled; cotyledons incumbent.
- 6a. Racemes rachis flexuous; leaves divided into 3 or 5 filiform to narrowly linear segments.....*Ianhedgea*
- 6b. Racemes rachis not flexuous; leaves various but never divided into filiform or narrowly linear segments.
- 7a. Flowers yellow.
- 8a. Stem leaves petiolate; fruit apex strongly recurved or contorted; fruiting pedicels stout, nearly as thick as fruit.....*Neotorularia*
- 8b. Stem leaves auriculate, rarely sessile; fruit apex neither recurved nor contorted; fruiting pedicels slender, narrower than fruit*Olimarabidopsis*
- 7b. Flowers white, lavender, or purple, very rarely creamy white.
- 9a. Fruits glabrous.
- 10a. Stem leaves petiolate; branched trichomes forked, rays always simple.
- 11a. Fruiting pedicels slender, narrower than fruit; seeds mucilaginous when wetted; fruits straight.....*Arabidopsis*
- 11b. Fruiting pedicels stout, nearly as thick as fruit; seeds not mucilaginous when wetted; fruits often twisted.....*Neotorularia*
- 10b. Stem leaves sessile, often auriculate, sagittate, or amplexicaul, if short petiolate then plants canescent; at least some of the trichomes dendritic or stellate with some branched rays.
- 12a. All branched trichomes sessile; petals (6–)6.5–8(–9) mm; fruit short stipitate.....*Pseudoarabidopsis*
- 12b. At least some of the branched trichomes distinctly stalked; petals 1.5–4(–5) mm; fruit sessile.
- 13a. Seeds uniseriate; Himalayas.....*Crucihimalaya*
- 13b. Seeds biseriata; North and South America, Russian Far East
- 14b. Perennial with caudex and persistent basal leaf rosette; stem leaves entire or rarely minutely toothed; Russian Far East, Alaska, N Canada, and northern USA.....*Beringia*
- 14b. Biennials without caudices or persistent basal leaf rosette; stem leaves coarsely dentate to sinuate; USA, Central and South America.....*Halimolobos*
- 9b. Fruit pubescent.
- 15a. Racemes bracteate at least along lower half.....*Crucihimalaya*
- 15b. Racemes ebracteate.
- 16a. Fruit with submalpighiaceus or short-stalked to subsessile stellate trichomes; septum lacking or often perforated.....*Olimarabidopsis*
- 16b. Fruit with other trichome types; septum complete.
- 17a. Seeds not mucilaginous when wetted, uniseriate; fruit often strongly torulose and/or twisted; stems often decumbent; predominantly Old World.....*Neotorularia*
- 17b. Seeds mucilaginous when wetted, mostly biseriata; fruit often smooth; stems not decumbent; exclusively New World.....*Halimolobos*

Cytology

This section includes a summary of the chromosome counts made thus far on the species presently assigned to *Arabidopsis*. Matters relating to meiotic irregularities can easily be obtained by consulting the references cited in Table 1, and the space herein does not permit full coverage of that and the meiosis in artificial interspecific hybrids.

Haploid chromosome numbers $n = 5, 8, 13,$ and 16 have been reported in the genus (Table 1). Only *Arabidopsis thaliana* is known to have $n=5$. The count $n=13$ characterizes *A. suecica*, an amphidiploid species originated through hybridization between *A. thaliana* and *A. arenosa*. Diploid and tetraploid counts based on $x=8$ are known in *A. neglecta* and the various subspecies of *A. lyrata* and *A. arenosa*. All three subspecies of *A. halleri* show $2n=16$, but additional counts are needed, especially from populations in eastern Asia. The remaining species of *Arabidopsis*, *A. cebennensis*, *A. croatica*, and *A. pedemontana*, have not yet been investigated cytologically. Counts deviating from the norm (see Table 1) probably represent rare aberrations. Only the normal diploid counts are listed under each species.

Taxonomy

The present formal taxonomic account of *Arabidopsis* includes full descriptions of the genus and all of its nine species and eight subspecies, keys to all taxa, distributions, and habitats. It also includes a list of the species previously included in *Arabidopsis* but currently assigned to other genera, with full citations of the original publications of those species and their current assignments.

Arabidopsis (DC.) Heynhold in Holl & Heynhold, Fl. Sachsen 1: 538. 1842; nom. cons. Type: *A. thaliana* (L.) Heynhold, typ. cons.

Cardaminopsis (C. A. Meyer) Hayek, Fl. Steiermark 1: 477. 1908. Basionym: *Arabis* sect. *Cardaminopsis* C. A. Meyer in Ledeb., Fl. Altaic. 3: 19. 1831. Type not designated.

Hylandra Á. Löve, Svensk Bot. Tidskr. 55: 214. 1961. Type: *H. suecica* (Fries) Á. Löve.

Plants annual, biennial, or perennial herbs with stolons or woody caudex. **Trichomes** unicellular, eglandular,

simple mixed with stalked 1-3-forked or rarely 4-rayed trichomes. **Roots** forming a taproot system, very rarely adventitious. **Stems** erect to ascending or decumbent, 1 or frequently several to many from base, few branched above, always leafy, usually glabrous above. **Basal leaves** petiolate, forming well-developed rosettes, simple, entire toothed, lyrate, to pinnately lobed. **Stem leaves** petiolate to subsessile and cuneate to attenuate at base, never auriculate or sagittate, entire, dentate, or rarely lyrate. **Racemes** few to several flowered, dense or lax, ebracteate, corymbose, elongated considerably in fruit; **rachis** straight. **Fruiting pedicels** slender, terete, ascending to divaricate or slightly reflexed. **Sepals** oblong, free, erect to ascending, glabrous or pubescent, equal, margin membranous or not, base of inner pair slightly saccate or not saccate. **Petals** white, pink, or purple, erect at base with flaring blade, longer than sepals; **blade** obovate to spatulate or oblanceolate, apex obtuse to emarginate, entire; **claw** obscurely differentiated from blade or distinct, glabrous, entire. **Stamens** 6, exerted, erect, tetradynamous; **filaments** filiform, wingless, unappendaged, glabrous, base slightly dilated or not dilated; **anthers** oblong, rounded to sagittate at base, obtuse at apex, not coiled after dehiscence. **Nectar glands** confluent and subtending bases of all stamens; median nectaries sometimes distinct and not confluent; lateral nectaries lunar or annular. **Ovules** 15-80 per ovary. **Fruit** dehiscent, capsular siliques, linear, terete or latiseptate (flattened parallel to the septum), not inflated, short stipitate to rarely subsessile, unsegmented; **valves** papery, veinless or with a distinct midvein, glabrous, not keeled, smooth or somewhat torulose, wingless, unappendaged; **gynophore** to 1 mm long; **replum** rounded; **septum** complete, membranous; **style** obsolete or to 1 mm long, cylindrical, persistent, glabrous; **stigma** capitate, entire. **Seeds** numerous per locule, uniseriate, wingless or margined, oblong to ellipsoid, plump or flattened; **seed coat** minutely reticulate, mucilaginous or not mucilaginous when wetted; **cotyledons** accumbent or rarely incumbent.

Number of species and distribution: nine species distributed primarily in Europe, with two extending into northern and eastern Asia and one into northern North America. *Arabidopsis thaliana* is naturalized throughout the world. The distribution of the European taxa follows closely the account of Jalas & Suominen (1994), that of North American taxa follows Hopkins (1937) and Rollins (1941, 1993), and that of Asian taxa follows Berkutenko (1988), Busch (1939), and Tolmachev (1975).

Table 1. Chromosome count in *Arabidopsis* species

Species	<i>n</i>	<i>2n</i>	Country	Counted as	References
<i>A. arenosa</i> subsp. <i>arenosa</i>	14		Austria	<i>Cardaminopsis arenosa</i>	Mattick in Tischler (1950)
		32	Austria	<i>C. arenosa</i>	Polatschek (1966)
	16		Austria	<i>C. arenosa</i>	Teppner (1980)
		32	Belarus	<i>C. arenosa</i>	Dmitrieva et al. (1977)
		16	Bulgaria	<i>C. arenosa</i>	Loon & Setten (1982), Ancev & Goranova (1997)
	8	16+ (0-4B)	Slovakia, Poland	<i>C. nitida</i> (invalid name)	Mesíček (1970)
	16	32	Czech Republic	<i>C. arenosa</i>	Mesíček (1970)
		32	Germany, Switzerland	<i>C. arenosa</i>	Mesíček (1970)
		32	Czech Republic	<i>C. carpatica</i> (invalid)	Hindáková in Májovský et al. (1978)
		16, 32, 34	Czech Republic	<i>C. carpatica</i> (invalid)	Mesíček in Májovský et al. (1974)
	8, 14-16	16, 18, 32, 34	Slovakia	<i>C. carpatica</i> (invalid)	Mesíček (1970)
	16	16, 28-32, 39, 40	Slovakia	<i>C. petrogena</i>	Mesíček (1970)
		30	Finland	<i>C. arenosa</i>	Hämäl-Ahti & Virrankoski (1970), Uotila & Pellinen (1985)
	16		France	<i>Arabis arenosa</i>	Ritter (1972)
		32	Germany	<i>C. arenosa</i>	Löve (1961), Lippert & Heubl (1988)
		16	Hungary	<i>C. arenosa</i>	Baksay (1956)
		32	Sweden	<i>C. arenosa</i>	Hylander (1957)
		32	Switzerland	<i>C. arenosa</i>	Burdet (1967)
	subsp. <i>borbasii</i>		16, 32	Slovakia	<i>C. arenosa</i> subsp. <i>borbasii</i>
		32	Czech Republic	<i>C. arenosa</i> subsp. <i>borbasii</i>	Mesíček et al. (1992)
		32	Poland	<i>C. arenosa</i>	Skalinska in Skalinska et al. (1966)
<i>A. halleri</i> subsp. <i>halleri</i>	8		Austria	<i>Cardaminopsis halleri</i>	Mattick in Tischler (1950)
		16	Austria	<i>C. halleri</i>	Polatschek (1966)
		16	Slovakia	<i>C. halleri</i>	Váchová & Májovský (1980)
	8		Germany	<i>C. halleri</i>	Jaretsky (1928)
		16	Germany	<i>C. halleri</i>	Buttler (1985)
		16	Poland	<i>C. halleri</i>	Skalinska in Skalinska et al. (1968)
		16	Ukraine	<i>C. halleri</i>	Pashuk (1987)
subsp. <i>ovirensis</i>		16	Austria	<i>C. halleri</i> subsp. <i>ovirensis</i>	Dobes & Hahn (1997)
		16	Ukraine	<i>C. ovirensis</i>	Pashuk (1987)
subsp. <i>gemmifera</i>		16	Korea	<i>Arabis halleri</i>	Lee (1970)
<i>A. lyrata</i> subsp. <i>lyrata</i>		16	Canada	<i>Arabis lyrata</i>	Böcher (1969), Mulligan (1964, 1995)
	8		USA	<i>A. lyrata</i>	Rollins (1941), Smith (1938)
subsp. <i>kamchatica</i>		16	Canada	<i>A. lyrata</i> subsp. <i>kamchatica</i>	Packer & Witkus (1982), Dawe & Murray (1979)
		16	Canada	<i>Cardaminopsis kamchatica</i>	Löve & Löve (1982)
		32	Canada	<i>A. lyrata</i>	Mulligan (1964)
		32	Canada	<i>A. lyrata</i> subsp. <i>kamchatica</i>	Mulligan & Porsild (1969, 1970), Taylor & Mulligan (1968)
		16	Russia	<i>C. lyrata</i>	Berkutenko et al. (1984)
		32	Russia	<i>A. kamchatica</i>	Zhukova & Petrovsky (1984)
		16	USA (Alaska)	<i>A. lyrata</i> var. <i>kamchatica</i>	Rollins (1966)
		32	USA (Alaska)	<i>A. lyrata</i>	Johnson & Packer (1968)
		32	USA (Alaska)	<i>A. lyrata</i> subsp. <i>kamchatica</i>	Knaben (1968)
		12	Taiwan	<i>A. morrisonensis</i>	Hsu (1968)
subsp. <i>petraea</i>		16, 32	Austria	<i>Cardaminopsis petraea</i>	Polatschek (1966)
		16	Slovakia	<i>C. petraea</i>	Burdet (1967)
		16	Iceland	<i>C. petraea</i>	Knaben in Löve & Löve (1948), Löve & Löve (1956)
		16	Iceland	<i>Arabis petraea</i>	Böcher (1966), Böcher & Larsen (1950)
		16	Norway	<i>C. petraea</i>	Knaben (1950)

Table 1. Chromosome count in *Arabidopsis* species (continued)

Species	<i>n</i>	<i>2n</i>	Country	Counted as	References
		16	Norway	<i>C. petraea</i>	Engelskjon (1979)
		16	Scotland	<i>C. petraea</i>	Hedberg & Hedberg (1961)
		16, 32	Russia	<i>C. petraea</i>	Berkutenko et al. (1984)
		32	Russia	<i>A. petraea</i> subsp. <i>septentrionalis</i>	Zhukova et al. (1973)
		16	Russia	<i>A. septentrionalis</i>	Petrovsky & Zhukova (1983), Zhukova & Petrovsky (1984, 1987)
		16	Russia	<i>C. petraea</i> subsp. <i>umbrosa</i>	Krogulevich (1978)
		32	Russia	<i>A. umbrosa</i>	Zhukova & Petrovsky (1987)
		16	Russia	<i>A. umbrosa</i>	Krogulevich (1976), Zhukova (1980), Zhukova & Petrovsky (1980, 1984)
		16	Russia	<i>A. petraea</i> subsp. <i>umbrosa</i>	Zhukova & Petrovsky (1977), Zhukova et al. (1973, 1977)
		16	Russia	<i>A. media</i>	Zhukova (1967, 1968), Zhukova & Tikhonova (1971)
		16	USA (Alaska)	<i>A. lyrata</i>	Rollins (1966)
<i>A. neglecta</i>		16	Poland	<i>Cardaminopsis neglecta</i>	Skalinska in Skalinska et al. (1966)
		16	Slovakia	<i>C. neglecta</i>	Májovský & Váňová (1982), Murin & Pačlová (1986)
<i>A. suecica</i>		(20, 22), 26	Finland	<i>Arabisopsis suecica</i>	Harmaja & Pellinen (1991)
		26	Sweden	<i>Cardaminopsis suecica</i>	Hylander (1957)
		(25), 26, (27, 28)	Sweden	<i>Hylandra suecica</i>	Löve (1961)
	14	unknown	unknown	<i>Stenophragma suecicum</i>	Jaretsky (1932)
		26-28	unknown	<i>Arabisopsis suecica</i>	Manton (1932)
		26	unknown	<i>C. suecica</i>	Mesicek (1967)
<i>A. thaliana</i>		10	Austria	<i>Arabidopsis thaliana</i>	Leute (1974)
		10	Belarus	<i>A. thaliana</i>	Dimitrieva (1985)
		10	Bulgaria	<i>A. thaliana</i>	Ancev & Goranova (1997)
		10	Canada	<i>A. thaliana</i>	Mulligan (1964)
	5		Canada	<i>A. thaliana</i>	Mulligan (1984)
	5		China	<i>A. thaliana</i>	Lan & Cheo (1989)
		10	Czech Republic	<i>A. thaliana</i>	Mesicek (1967, 1992)
		10	Czech Republic	<i>A. thaliana</i>	Kirschner et al. (1982)
				<i>A. thaliana</i>	Murin in Májovský et al. (1978).
		10	Denmark	<i>A. thaliana</i>	Böcher & Larsen (1958), Winge (1925)
		10	Ethiopia	<i>A. thaliana</i>	Jonsell (1976)
		10	Finland	<i>A. thaliana</i>	Arohonka (1982), Sorsa (1963), Uotila & Pellinen (1985)
		10	France	<i>A. thaliana</i>	Böcher & Larsen (1958)
		10	Germany	<i>Stenophragma thaliana</i>	Tischler (1935)
	5		India	<i>A. thaliana</i>	Raj (1965)
	5	10	Japan	<i>A. thaliana</i>	Murata & Motoyoshi (1995), Murata et al. (1994)
		10	Netherlands	<i>A. thaliana</i>	Gadella & Kliphuis (1971)
		10	Portugal	<i>A. thaliana</i>	Böcher & Larsen (1958)
		10	Russia	<i>A. thaliana</i>	Polyakova (1964)
	5		Spain	<i>A. thaliana</i>	Ruiz de Clavijo (1994)
		10	Spain	<i>A. thaliana</i>	Luque & Diaz Lifante (1991)
		10	Sweden	<i>A. thaliana</i>	Lövkvist & Hullgård (1999)
	5	10	unknown	<i>A. thaliana</i>	Steinitz-Sears (1963)
		10	Yugoslavia	<i>A. thaliana</i>	Gadella & Kliphuis (1972)
	5		unknown	<i>A. thaliana</i>	Matick in Tischler (1950)
	5		unknown	<i>S. thaliana</i>	Laibach (1907)
	5		unknown	<i>S. thaliana</i>	Jaretsky (1928)
		12	Russia	<i>A. thaliana</i>	Titova (1935)
	7		Iran	<i>A. thaliana</i>	Maassoumi (1980)

Key to the species of *Arabidopsis*

- 1a. Fruits terete; petals 2-3.5(-4) mm long; seeds 0.3-0.5 mm long, usually plump; cotyledons incumbent 1. *A. thaliana*
- 1b. Fruits strongly flattened, rarely subterete (*A. suecica*); petals (4-)5-10 mm long; seeds longer, usually flattened; cotyledons accumbent, rarely obliquely incumbent (*A. suecica*).
- 2a. Replum constricted between seed; plants stoloniferous perennials; basal leaves orbicular or often with an orbicular terminal lobes 9. *A. halleri*
- 2b. Replum not constricted between seeds; plants annuals or almost always non-stoloniferous perennials with or without branched caudices; basal leaves lanceolate, spatulate, oblanceolate, obovate, or rarely suborbicular, without orbicular terminal lobes.
- 3a. Lower and middle stem leaves distinctly petiolate, suborbicular to ovate, nearly as long as wide, dentate with few large teeth.
- 4a. Petals 7-10 mm long, violet or very rarely white; plants (25-)40-80 cm tall, sparsely pubescent; basal leaves acute at apex, longer than wide6. *A. cebennensis*
- 4b. Petals 6-7 mm long, white; plants 10-30 cm tall, plants usually glabrous; basal leaves obtuse at apex, " as long as wide 7. *A. pedemontana*
- 3b. Lower and middle stem leaves subsessile or attenuate to a narrow base, much longer than broad, entire, dentate, lyrate, to pinnatifid.
- 5a. Basal and stem leaves similar in shape and size (rarely stem leaves larger than basal) 5. *A. croatica*
- 5b. Basal and stem leaves dissimilar in shape and size, basal leaves always larger.
- 6a. Stems glabrous or rarely subglabrous; fruits horizontally spreading to slightly reflexed; petals becoming deep lilac; alpine areas in the Carpathian Mountains (Czech Republic, Slovakia, Romania, Poland, and adjacent Ukraine)4. *A. neglecta*
- 6b. Stems sparsely to densely hairy at least below; fruits erect-ascending to subdivaricate; petals white or rarely pale lilac; sea level to various altitudes in Eurasia and North America.
- 7a. Fruits weakly compressed to subterete; petals white, 4-5(-6) mm long; cotyledons obliquely incumbent2. *A. suecica*
- 7b. Fruits strongly compressed; petals white to lilac, (5-)6-8 mm long; cotyledons accumbent.
- 8a. Petals with two small lateral teeth on the claw; basal leaves pinnatisect to pinnatifid3. *A. arenosa*
- 8b. Petals without lateral teeth on the claw; basal leaves lyrate-pinnatifid, lyrate, dentate, or entire 8. *A. lyrata*

1. *Arabidopsis thaliana* (Linnaeus) Heynhold in Holl & Heynhold, Fl. Sachsen 1: 538. 1842.

Synonyms: *Arabis thaliana* Linnaeus, Sp. Pl. 2: 665. 1753; *Conringia thaliana* (Linnaeus) Reichenbach, Fl. Germ. Excurs. II. 686. 1826; *Crucifera thaliana* (Linnaeus) E.H.L. Krause, in Sturm, Fl. Deutschland, ed. 2, 6: 86. 1902; *Erysimum thalianum* (Linnaeus) Kittel, Taschenb. Fl. Deutschl. ed. 2, 899. 1844; *Hesperis thaliana* (Linnaeus) Kuntze, Rev. Gen. 2: 935. 1891; *Pilosella thaliana* (Linnaeus) Kosteletzky, Ind. Pl. Hort. Prag. 104. 1844; *Sisymbrium thalianum* (Linnaeus) J. Gay & Monnard, Ann. Sci. Nat. Bot., ser. 1, 7: 399. 1826; *Stenophragma thalianum* (Linnaeus) Celakovsky, Kvet. Ok. Prazs. 75. 1870. Type: "Hab. in Europae septentrionalis sabulosis" (lectotype, LINN 842.5).

Cardamine pusilla A. Richard, Tent. Fl. Abyss. 1: 18. 1847; *Arabidopsis thaliana* var. *pusilla* (A. Richard) O.E. Schulz in Engler, Pflanzenr. IV. 105(Heft 86): 274. 1924; *Sisymbrium pumilio*, Oliver, Fl. Trop. Afr. 1: 64. 1868; *Sisymbrium thalianum* (Linnaeus) Gay & Monnard var. *pusillum* (A. Richard) T. Durand & Schinz, Conspl. Fl. Afr.

1(2): 99. 1898; *Stenophragma thaliana* (Linnaeus) Celakovsky var. *pusilla* (A. Richard) Engler, Hochgebirgfl. Trop. Afr. 226. 1895. Type: Ethiopia, Begemdir, *Schimper II.1311* (holotype, P; isotype, K).

Annual herbs (2-)5-30(-60) cm tall. Stems erect, 1 to many from the base, simple or branched above, basally pilose with predominantly simple trichomes, apically glabrous. Basal leaves shortly petiolate, rosulate; leaf blade obovate, spatulate, ovate, or elliptic, 0.8-3.5(-4.5) × (0.1-)0.2-1(-1.5) cm, adaxially with predominantly simple and stalked 1-forked trichomes, margin entire, repand, serrulate, or dentate, apex obtuse. Stem leaves subsessile or sessile, usually few; blade lanceolate, linear, oblong, or elliptic, middle ones (0.4-)0.6-1.8(-2.5) × 0.1-0.6(-1) cm, margin entire or rarely sparsely dentate, apex acute to obtuse. Fruiting pedicels slender, divaricate, straight, 3-10(-15) mm long. Sepals 1-2(-2.5) mm long, glabrous or distally sparsely pubescent with simple trichomes, lateral pair not saccate. Petals white, spatulate, 2-3.5(-4) × 0.5-1.5 mm, apex obtuse, base attenuate to a short claw. Filaments white, 1.5-2 mm long. Ovules 40-70 per ovary. Siliques linear, terete, smooth, (0.8-)1-1.5(-2) cm × 0.5-0.8 mm; valves with a distinct midvein; style to 0.5 mm long.

Seeds ellipsoid, plump, light to reddish brown, 0.3–0.5 mm long; cotyledons incumbent. Flowering and fruiting January–June(–October). $2n=10$.

Distribution: native range almost all Europe to central Asia, now naturalized worldwide. Throughout Europe (excluding Iceland), most of Asia (excluding Bahrain, Bangladesh, Bhutan, Cambodia, Iraq, Israel, Jordan, Kuwait, Kyrgyzstan, Laos, Malaysia, Myanmar, Nepal, New Guinea, Oman, Philippines, Qatar, Sri Lanka, Taiwan, Thailand, Turkmenistan, United Arab Emirates, Vietnam, Yemen), Australia and New Zealand, Africa (Algeria, Eritrea, Ethiopia, Kenya, Libya, Morocco, South Africa, Tanzania, Tunisia, Uganda, Zaire), North America (Canada, U.S.A.), and South America (Argentina, Uruguay).

Habitats: open or disturbed habitats, sandy soil, river banks, roadsides, rocky slopes, waste places, cultivated ground, meadows, slightly alkaline flats, under shrubs, open areas; sea level to 4250 m.

2. *Arabidopsis suecica* (Fries) Norrlin, Meddel. Soc. Fauna Fl. Fenn. 2: 12. 1878.

Synonyms: *Arabis suecica* Fries, Summ. Veget. Scand. I, 30, 147. 1846; *A. arenosa* (Linnaeus) Scopoli subsp. *suecica* (Fries) Ahlfvengren in Neuman & Ahlfvengren, Sveriges Flora 453. 1901; *A. arenosa* var. *suecica* (Fries) Cajander in Mela, Suomenkasvio, ed. 5, 295. 1906; *Cardaminopsis suecica* (Fries) Hiitonen ex Hylander, Forteckn. Skand. Vaxt., 1. Karlvaxter, 62, 139. 1941; *Hylandra suecica* (Fries) Å. Löve, Svensk Bot. Tidskr. 55: 215. 1961; *Sisymbrium suecicum* (Fries) Nyman, Consp. Fl. Europ. 44. 1878; *Stenophragma suecicum* (Fries) Celakovsky ex Prantl in Engler & Prantl, Pflanzenfam. 3(2): 192. 1891. Type: Sweden. Prov. Södermanland: Strängnäs, *Fries s. n.* (lectotype, UPS; see Löve, 1961).

Annual herbs (5–)10–45(–60) cm tall. Stems erect, 1.5(–8) from the base, usually branched above, basally pilose with simple trichomes to 1 mm long, apically glabrous. Basal leaves rosulate; petiole (0.3–)0.6–2(–2.8) cm long, ciliate; leaf blade obovate to oblanceolate, (0.3–)0.7–3(–4) × (0.1–)0.2–1.4(–1.7) cm, sparsely to densely pubescent with simple and short-stalked forked trichomes, rarely subglabrous, margin lyrate to pinnatifid on each side with 3–6 lateral lobes much smaller than terminal one, rarely dentate, apex obtuse to subacute. Stem leaves 3–8, short petiolate or uppermost sessile; blade lanceolate, oblong, or linear, middle ones (0.3–)1–2.5(–4) × 0.1–0.8(–1.3) cm, margin dentate on lower leaves, entire on upper ones, apex acute to obtuse. Fruiting pedicels slender, divaricate, straight, 5–10(–15) mm long. Sepals 1.5–2.2(–2.5) mm

long, glabrous or distally sparsely pilose with simple trichomes, lateral pair saccate. Petals white to lavender, spatulate, 4–5(–6) × 1.5–2.5 mm, apex obtuse or truncate, base attenuate to a short claw. Filaments white, 2.5–4 mm long. Ovules 40–70 per ovary. Siliques linear, subterete to slightly compressed, smooth to slightly torulose, (2–)2.5–3.5(–4.5) cm × 0.5–0.8 mm; valves with a distinct or obscure midvein; style to 0.5 mm long; gynophore to 0.5 mm long. Seeds oblong, slightly compressed, light to reddish brown, 0.5–0.8 mm long; cotyledons obliquely incumbent. Flowering and fruiting May–July. $2n = 26$.

Distribution: Fennoscandinavia and the Baltic region but perhaps native only in Finland, adventive in adjacent northwestern Russia, Estonia, northeastern Denmark, Sweden, Norway, and north Germany (see Jalas & Suominen, 1994).

Habitats: fields, roadsides, slopes, moist forest margins, grassy areas; near sea level to 600 m.

Arabidopsis suecica is an amphidiploid produced since the last glacial maximum from the hybridization of *A. thaliana* and diploid *A. arenosa* (Mummenhoff and Hurka, 1994, 1995; O’Kane et al., 1997, and references therein).

3. *Arabidopsis arenosa* (Linnaeus) Lawalrée, Bull. Soc. Roy. Bot. Belgique 92: 242. 1960.

Biennial or short-lived perennial with a caudex, (5–)8–80(–100) cm tall. Stems erect, simple or with few to many branches from the base, usually branched above, basally pilose to subhirsute with simple trichomes to 1 mm long, apically glabrous. Basal leaves rosulate; petiole (0.3–)0.7–2(–3) cm long, pilose; leaf blade obovate to oblanceolate, 1–4.5(–6.5) × 0.5–1.3(–1.7) cm, sparsely to densely pubescent with simple and short-stalked forked trichomes, margin pinnatifid to lyrate-pinnatifid and with 3–11 lateral lobes on each side, rarely dentate, apex obtuse to subacute; terminal lobe considerably larger or nearly as large as adjacent lateral lobes. Stem leaves 3–10, short petiolate or uppermost sessile; blade lanceolate to narrowly oblong, middle ones 1–4 (–5) × 0.3–1.5 cm, margin pinnatifid to dentate on lower leaves, dentate or entire on uppermost ones, apex acute to obtuse. Fruiting pedicels slender, divaricate, straight, 4–10(–15) mm long. Sepals 2.2–3 mm long, glabrous or distally sparsely pilose with simple trichomes, lateral pair saccate. Petals white to lavender, obovate, 5–8 × 2.5–4 mm, apex obtuse or truncate, base attenuate to a short claw often apically with a pair of minute teeth. Filaments white, 3–4 mm long. Ovules 28–74 per ovary. Siliques linear, distinctly compressed, smooth to slightly torulose, (1–)2–4(–5) cm ×

(0.8–)1–1.5 mm; valves with a distinct midvein; style to 0.5 mm long; gynophore to 0.5 mm long. Seeds oblong, compressed, light to reddish brown, (0.6–)0.8–1.2 mm long, obscurely to prominently winged distally; cotyledons accumbent. Flowering and fruiting April–July or rarely to August. $2n=16, 32$.

- 1a. Basal leaves with terminal lobe larger than the 1–6 lateral lobes on each side; seeds very narrowly winged distally or rarely wingless; ovules 36–74 per locule.....3a. *A. arenosa* subsp. *arenosa*
 1b. Basal leaves with terminal lobe subequal to or scarcely larger than the 4–11 lateral lobes on each side; seeds conspicuously winged distally; ovules 28–38 per locule.....3b. *A. arenosa* subsp. *borbasii*

3a. *Arabidopsis arenosa* subsp. *arenosa*

Synonyms: *Sisymbrium arenosum* Linnaeus, Sp. Pl. 2: 658. 1753; *Arabis arenosa* (Linnaeus) Scopli, Fl. Carniol., ed. 2, 2: 32. 1772; *Arabis petraea* (Linnaeus) Lamarck var. *arenosa* (Linnaeus) Neireich, Nachtr. Fl. Wein. 262. 1851; *Cardamine arenosa* (Linnaeus) Roth, Man. Bot. 291. 1830; *Cardaminopsis arenosa* (Linnaeus) Hayek, Fl. Steiermark 1: 478. 1908. Type: “In Germania, Helvetica” (holotype, LINN 836.22).

Arabis petrogena A. Kerner, Oesterr. Bot. Z. 13: 141. 1863; *Arabis arenosa* var. *petrogena* (A. Kerner) Borbás; *Cardaminopsis arenosa* subsp. *petrogena* (A. Kerner) Soó, Acta Bot. Acad. Sci. Hung. 16: 371. 1971; *C. petrogena* (A. Kerner) Mesicek, Preslia 42: 246. 1970. Type: “in locis petrosis mintium circa Budam; communissima in monte Adlersberg et in rupibus dolmaticis vallis Auwinkel” (syntypes, WU).

Arabis segetalis Schur, Enum. Pl. Transsilv. 45. 1866; *Cardaminopsis arenosa* var. *segetalis* (Schur) E.I. Nyárády in Savulescu, Fl. Reipubl. Popularis Roman. 3: 291. 1955. Type: “Auf Aeckern unter Saaten, an der Strasse nach Schellenberg bei Hermannstadt.” (holotype, not located).

Arabis arenosa var. *simplex* Neireich, Fl. N.-Öster. 715. 1859; *Cardaminopsis arenosa* var. *simplex* (Neireich) Hayek, Fl. Steiermark 1: 479. 1908. Type: “in ihrer typischen Gestalt am schönsten auf den Inseln und in den Auen dr Donau” (syntypes, W).

Cardaminopsis arenosa var. *peregrina* Lawalrée, Bull. Jard. Bot. État Bruxelles 26: 350. 1956; *Arabidopsis arenosa* var. *runcinata* (Godron) Lawalrée f. *peregrina* (Lawalrée) Lawalrée, Bull. Soc. Roy. Bot. Belgique 9: 243. 1960. Type: Belgium, Etterbeek, Etterbeek-Cinquantenaire, May 1924, *E. Michel s.n.* (holotype, BR).

Plants annual or biennial, rarely perennial. Basal leaves

pinnatisect, with 1–6 lateral lobes on each side, rarely dentate; terminal lobe considerably larger than adjacent lateral lobes. Petals white to lilac. Ovules 36–74 per locule. Seeds very narrowly winged at least distally or rarely wingless. $2n=16, 32$; for aneuploid series, see Table 1.

Distribution: Europe: native in Austria, Belarus, Bosnia Herzegovina, Bulgaria, Croatia, Czech Republic, NE France, Germany, Hungary, N Italy, Latvia, Lithuania, Macedonia, Poland, Romania, Slovakia, Slovenia, Switzerland, Ukraine, and Yugoslavia; naturalized in Belgium, Denmark, Estonia, Finland, Holland, Norway, Russia and W Siberia, and Sweden; absent in Albania, Greece, C and S Italy, and Turkey.

Habitats: forest margins, roadsides, railroad tracks, river banks, disturbed areas, slopes, fields, grassy areas; near sea level to 2000 m.

This subspecies includes a multitude of chromosomal races that were recognized by Mesicek (1970) as distinct species. However, his taxa are weakly defined and were not legitimately published. Therefore, they have no taxonomic status. Subspecies *arenosa* is easily confused with *Arabidopsis suecica* but can be readily distinguished by having narrowly winged seeds, accumbent cotyledons, strongly flattened fruits, and petals with a pair of minute teeth between the blade and claw. By contrast, *A. suecica* differs by having wingless seeds, obliquely incumbent cotyledons, subterete to slightly flattened fruits, and toothless petals.

3b. *Arabidopsis arenosa* (Linnaeus) Lawalrée subsp. *borbasii* (Zapalowicz O’Kane & Al-Shehbaz, Novon 7: 325. 1997.

Synonyms: *Arabis arenosa* (Linnaeus) Scopli subsp. *borbasii* Zapalowicz, Rozpr. Wydz. Mat.-Przyr. Acad. Umiejtn., Dzial B, Nauki Biol. 52: 31. 1912; *Cardaminopsis arenosa* (Linnaeus) Hayek subsp. *borbasii* (Zapalowicz Pawlowski ex H. Scholz, Willdenowia 3: 139. 1962; *C. arenosa* var. *borbasii* (Zapalowicz E.I. Nyárády in Savulescu, Fl. Reipubl. Popularis Roman. 3: 288. 1955; *C. borbasii* (Zapalowicz H. Hess, Landolt & Hirzel, Fl. Schweiz, Fl. Schweiz. 3: 778. 1972. Type: Poland. Carpathians, Babia Góra monte, 1285–1725 m, *Zapalowicz s. n.* (lectotype, designated by O’Kane & Al-Shehbaz (1997), KRAM).

Arabis arenosa var. *dependens* Borbás, Math. Term. Közl. 15: 156. 1878; *Cardaminopsis arenosa* var. *dependens* (Borbás) Jávorka, Magyar Fl. 436. 1924; *C. arenosa* subsp. *borbasii* var. *dependens* (Borbás) Soó, Acta Bot. Acad. Sci. Hungar. 13: 304. 1967; *C. dependens*

(Borbás) Kotov, comb. invalid.

Arabis arenosa var. *multiceps* Neilreich, Fl. N. Öster. 715. 1859; *Arabis multiceps* (Neilreich) Favarger & Rch., Abh. Zool. Bot. Ges. Wien 3: 31. 1905, not *A. multiceps* Greene, Leaflets Bot. Obs. 2: 76. 1910. Type: “Flussgebieten der Peisting, Schwarza, Traisen” (syntypes, W).

Arabis arenosa var. *runcinata* Godron, Fl. de Lorraine, ed. 2, 1: 60. 1857; *Arabidopsis arenosa* var. *runcinata* (Godron) Lawalrée, Bull. Soc. Roy. Bot. Belgique 92: 242. 1960. Type: “Nancy, aux Fonds Saint Barthélémy et à Liverdun (Soyer-Willemet); Pont-à-Mousson (Léré); Rosières-aux Salines; Lunéville” (syntypes, NCY).

Arabis arenosa var. *sarmentosa* Schur, Enum. Pl. Transsilv. 44. 1866. Type: “Auf dem Königstein bei Kronstadt, kalk., Aug., 6000” (holotype, not located).

Arabis hispida Mygind var. *intermedia* Freyn, Österr. Bot. Z. 39: 133. 1889; *A. freynii* Brügger, Österr. Bot. Z. 39: 231. 1889. Type: Salzburg, J. Freyn s.n. (holotype, BRNM?).

Arabis multijuga Borbás, Linnaea, 41: 604. 1877; *Arabis arenosa* subsp. *multijuga* (Borbás) Kulczyński in Szafer, Fl. Polska 3: 162. 1927; *A. arenosa* var. *multijuga* (Borbás) Zapalowicz, Rozpr. Wydz. Mat.-Przyr. Acad. Umiejetn., Dzial B, Nauki Biol. 52: 35. 1912; *Cardaminopsis multijuga* (Borbás) Czerepanov, Plantae Vasculares URSS 127. 1981; *C. arenosa* var. *multijuga* (Borbás) Kotov in Klukov & E.D. Wissjulina, Fl. RSS Ucr. 5: 290. 1953. Type: Gutin, *Borbás* s.n. (holotype, BP or BPU).

Arabis petraea (Linnaeus) Lamarck var. *intermedia* Neilreich, Nachtr. Fl. Wien. 262. 1851; *Cardaminopsis arenosa* var. *intermedia* (Neilreich) Hayek, Fl. Steiermark 1: 479. 1908. Type: “Gemein auf Felsen der kalkgebirge und in Sand subalpiner Bäche in der höhern Berg- und Voralpenregion besonders im Flossgebiete des kaltenganges und der Schwarza steigt nicht über 3000” (syntypes, W).

Plants usually perennial. Basal leaves pinnatisect, with 4–11 lateral lobes on each side; terminal lobe about as large as adjacent lateral lobes. Petals bright lilac. Ovules 28–38 per locule. Seeds broadly winged at least distally. $2n=16, 32$.

Distribution: E Belgium, Czech Republic, NE France, Germany, Hungary, Poland, Romania, Slovakia, Switzerland, Ukraine. Doubtfully occurring in Denmark.

Habitats: forest margins, slopes, stream banks, trails; 400–2100 m.

Unlike the many other segregates of *Arabidopsis arenosa*, subsp. *borbasii* is a well-defined taxon that can be consistently distinguished from subsp. *arenosa* (see key). Subspecies *borbasii* has variously been split into poorly defined races, but none of those merits recognition.

Zapalowicz (1912) indicated that interspecific hybridization between *Arabidopsis* (as *Arabis*) *arenosa* subsp. *borbasii* and *A. halleri* occurs in Tatra mountains (Poland).

4. Arabidopsis neglecta (Schultes) O’Kane & Al-Shehbaz, Novon 7: 326. 1997.

Synonyms: *Arabis neglecta* Schultes, Oestr. Fl. 2: 248. 1814; *Arabis arenosa* (Linnaeus) Scopli subsp. *neglecta* (Schultes) Zapalowicz, Rozpr. Wydz. Mat.-Przyr. Acad. Umiejetn., Dzial B, Nauki Biol. 52: 36. 1912; *Cardaminopsis neglecta* (Schultes) Hayek, Fl. Steiermark 1: 480. 1908. Type: Carpathians, ?Schultes s.n. (holotype, M).

Arabis floribunda Schur, Enum. Pl. Transsilv. 44. 1866. Type: “Auf steinigen Abhängen der Rodnaer Alpen, 6,500c, in Gesellschaft von Lychn.” (holotype, not located)

Arabis glareosa Schur, Verh. Mitth. Siebenbürg. Vereins. Naturwiss. Hermannstadt 1: 106. 1850; *Cardaminopsis neglecta* subsp. *glareosa* (Schur) Soó, Acta Bot. Acad. Sci. Hung. 16: 371. 1971. Type: “Auf den Rodnaer Alpen von Herrn Albert Bielz, auf den Arpáscher Alpen von mir 1847” (holotype, not located).

Arabis transsilvanica Schur, Enum. Pl. Transsilv. 43. 1866. Type: “Auf feuchtem schlammigen Boden der Hochalpen, Glimmerschiefer, 6,000c, an Quellen und kleinen Bächen der Arpaser Alpen” (holotype, not located).

Perennial herbs, with a distinct caudex, 5–15(–20) cm tall. Stems erect, simple or few branched, glabrous. Basal leaves rosulate; petiole to 2 cm long; leaf blade obovate to oblanceolate, 0.5–2 × 0.3–1 cm, fleshy, glabrous or sparsely pubescent with simple and fewer, short-stalked forked trichomes, margin subentire to lyrate-pinnatifid with up to 4 teeth or small lateral lobes on each side. Stem leaves 3–6, attenuate to a short petiole; blade ovate to oblanceolate, usually glabrous, entire or basally minutely 2-toothed. Fruiting pedicels slender, recurved or reflexed, 8–12 mm long. Sepals 2.5–3.5 mm long, glabrous or distally sparsely pilose with simple trichomes, lateral pair saccate. Petals purple, 5–6 × 2–3 mm, apex obtuse, base attenuate to a short claw. Filaments lavender, 3–4.5 mm long. Ovules ca. 30 per ovary. Siliques linear, distinctly compressed, smooth to slightly torulose, (1–)1.5–2.5(–3) cm × 1.2–1.8 mm; valves with a distinct midvein or obscurely veined; style to 1 mm long, slender. Seeds oblong, compressed, light brown, 1–1.2 mm long, wingless; cotyledons accumbent. Flowering and fruiting May–July. $2n=16, 32$.

Distribution: Carpathian Mountains (Poland, Romania, Slovakia, and adjacent Ukraine).

Habitats: mountain slopes, forest margins; 1200–2660 m.

5. Arabidopsis croatica (Schott) O’Kane & Al-Shehbaz, Novon 7: 325. 1997.

Synonyms: *Arabis croatica* Schott, in Schott, Nyman, & Kotschy, *Analect. Bot.* 44. 1854.

Cardaminopsis croatica (Schott) Jávorka, *Magyar Fl.* 435. 1924. Type: Croatia, *F. Maly s. n.* (holotype, BP?).

Perennial herbs, with a distinct caudex, 8–18(–20) cm tall. Stems erect, divaricately branched, flexuous, glabrous. Basal leaves rosulate; petiole to 3 cm long; leaf blade obovate, 0.5–2 × 0.4–1.5 cm, glaucous, fleshy, glabrous or sparsely pubescent with simple and fewer, short-stalked forked trichomes, margin entire to denticulate, rarely lyrate-pinnatifid. Stem leaves similar to basal ones, sometimes larger. Fruiting pedicels slender, horizontal or reflexed, 7–10 mm long. Sepals 2.5–3.5 mm long, glabrous or distally sparsely pilose with simple trichomes, lateral pair saccate. Petals lavender to purplish, 4–6 × 2–2.5 mm, apex obtuse, base attenuate to a short claw. Filaments lavender, 2.5–3.5 mm long. Ovules ca. 50 per ovary. Siliques linear, compressed, smooth to slightly torulose, 1.8–5 cm × 0.9–1.1 mm; valves obscurely veined; style to 1 mm long, slender. Seeds oblong, compressed, light brown, ca. 1 mm long, wingless; cotyledons accumbent. Flowering and fruiting May–July.

Distribution: Bosnia, Croatia.

Habitats: Rocky areas, crevices.

Arabidopsis croatica is morphologically very close to and might represent a subspecies of the earlier published *A. arenosa*. Only a limited material was available for our study, and more collections are needed to understand the variation within the species. No chromosome counts have been made thus far.

6. Arabidopsis cebennensis (de Candolle) O’Kane & Al-Shehbaz, *Novon* 7: 325. 1997.

Synonyms: *Arabis cebennensis* de Candolle, *Syst. Nat.* 2: 234. 1821; *Cardaminopsis cebennensis* (de Candolle) Burdet in Greuter & Raus, *Willdenowia* 13: 86. 1983. Type: [France], “in locis asperis subumbrosis montium Cebennorum in horto Dei et Bramabioi” (holotype, G-DC).

Perennial herbs (25–)40–80 cm tall. Stems erect, simple at base, branched above, pilose with simple trichomes mixed with stalked forked ones. Basal leaves rosulate; petiole (1–)1.5–4 cm long; leaf blade ovate to ovate-lanceolate, 2–7 × 1.5–4.5 cm, sparsely to densely pubescent with stalked, forked or 3-rayed trichomes, base cuneate, margin coarsely and irregularly few toothed, apex acute. Stem leaves 7–15, similar to basal leaves, becoming smaller, short petiolate, and basally attenuate upward. Fruiting pedicels divaricate, slender, 6–12(–15) mm long. Sepals oblong, 2.5–3.5 mm long, lateral pair saccate.

Petals deep purple, lavender, or very rarely white, obovate, 7–10 × 2.5–4 mm, slightly spreading. Filaments usually lavender, 3–4.5 mm long. Ovules 30–44 per ovary. Fruit linear, (2–)2.5–4.5(–5) cm × 1–1.5 mm, strongly compressed, torulose; valves with a distinct midvein; gynophore to 1 mm long; styles slender, 0.8–1.2 mm long. Seeds reddish brown, compressed, 1.2–1.6 mm long, narrowly winged distally; cotyledons accumbent. Flowering and fruiting June–August.

Distribution: SE France.

Habitats: slopes, forest margins; 600–2300 m.

A very rare and poorly known species for which no chromosome counts have been made. It is most closely related to the following species

7. Arabidopsis pedemontana (Boissier) O’Kane & Al-Shehbaz, *Novon* 7: 326. 1997.

Synonyms: *Arabis pedemontana* Boissier, *Diagn. Pl. Orient.* 1: 69. 1843; *Arabis cebennensis* de Candolle subsp. *pedemontana* (Boissier) P. Fournier, *Quatre Fl. France* 421. 1936; *Cardaminopsis pedemontana* (Boissier) Burdet in Greuter & Raus, *Willdenowia* 13: 86. 1983. Type: [Switzerland], “In regione alpina montium Pedemontii, legi Aug. supra limitem arborum in collo inter Crissolo et Luzerna sitio” (holotype, G).

Perennial herbs 10–30 cm tall. Stems erect, simple or branched above, glabrous or subglabrous. Basal leaves rosulate; petiole (1.5–)2.5–6(–7) cm long; leaf blade orbicular to broadly ovate-cordate, (1.5–)2–5 × (2–)2.5–5.5 cm, glabrous or very rarely sparsely pubescent with simple and stalked forked trichomes, base truncate to cordate, margin coarsely and irregularly few toothed or entire, apex obtuse to subacute. Stem leaves 3–6, smaller than basal ones, petiolate, broadly ovate or uppermost subsessile and lanceolate, gradually reduced in size upward, base cuneate, margin coarsely dentate, apex acute. Fruiting pedicels divaricate to ascending, slender, 7–12(–15) mm long. Sepals oblong, 2.5–3.5 mm long, lateral pair saccate. Petals white, obovate, 6–7 × 2–3.5 mm. Filaments white, 2.5–4 mm long. Ovules 20–30 per ovary. Fruit linear, 1.5–3 cm × 1–1.5 mm, strongly compressed, slightly torulose; valves with a distinct midvein; gynophore to 0.5 mm long; styles slender, to mm long. Seeds reddish brown, compressed, 0.9–1.4 mm long, broadly winged at least distally; cotyledons accumbent. Flowering and fruiting June–August.

Distribution: northwestern Italy and, presumably extinct, in adjacent SW Switzerland.

Habitats: mountain slopes, forest margins.

Arabidopsis pedemontana is morphologically similar to *A. cebennensis* except for being smaller (10–30 cm instead of (25–)40–80 cm) and glabrous or subglabrous instead of sparsely to densely pubescent. It has not yet been studied for chromosome numbers, and little is known about its morphological variation.

8. *Arabidopsis lyrata* (Linnaeus) O’Kane & Al-Shehbaz, *Novon* 7: 325. 1997.

Herbs biennial or perennial with a caudex and stolons, (5–)10–30(–45) cm tall. Stems erect or decumbent, 1 to numerous from base, usually branched and straight or flexuous above, basally pilose or subhirsute with simple and forked trichomes, apically glabrous. Basal leaves rosulate; petiole 0.4–2(–6) cm long; leaf blade oblanceolate or ovate, (0.5–)1–3(–8) × (0.3–)0.5–1.5 cm, adaxially with a mixture of simple and stalked, 1-forked trichomes, rarely glabrous, margin entire, dentate, lyrate, or pinnatifid with 1–3 lateral lobes on each side, apex obtuse. Stem leaves shortly petiolate and uppermost often sessile, several; blade of middle ones oblanceolate, (0.5–)1–3.5(–5.5) × (0.1–)0.2–0.7(–1.3) cm, entire, repand, or obscurely toothed, rarely lower ones lobed, gradually reduced in size upward. Fruiting pedicels slender, ascending to divaricate, straight, (0.4–)0.7–1.2(–1.5) cm long. Sepals 2–3 mm long, glabrous or densely pubescent, lateral pair saccate. Petals white, rarely lavender or purplish, spatulate or obovate, 4–8(–9) × 1.5–3(–3.5) mm. Filaments white, 2–3 mm long. Ovules 20–36 per ovary. Siliques linear, flattened, torulose, (1–)2–4.5(–6) cm × 0.5–1.5 mm; valves with a distinct midvein extending full length; gynophore to 0.5 mm long; style obsolete or to 1 mm long. Seeds oblong, flattened, light brown, 0.8–1.2 mm long, wingless, sometimes distally margined; cotyledons accumbent. Flowering and fruiting March–October. $2n=16, 32$.

Arabidopsis lyrata is a circumboreal species divided here into three subspecies that can distinguished with some difficulty, especially in areas where their distribution ranges overlap. Busch (1939) and Mulligan (1995) treated the three subspecies of *A. lyrata* as distinct species, but as shown in the key above, the morphological differences between them do not support such a treatment.

- 1a. Basal leaves entire or toothed; older plants with an obvious, somewhat thickened, often branched caudex.....9b. *lyrata* subsp. *petraea*
 1b. Basal leaves mostly lyrate to lyrate-pinnatifid; older plants with a slender, simple or rarely branched caudex.
 2a. Basal leaves usually pubescent and sparsely

- hirsute on petiole margins; petals 6–8 mm long; fruit to 1 mm wide; style slender, 0.5–1 mm long.....8a. *A. lyrata* subsp. *lyrata*
 2b. Basal leaves glabrous to sparsely pubescent, petioles usually glabrous; petals (4–)5–6 mm long; fruit ca. 1.5 mm wide; style obsolete or rarely to 0.5 mm long.....8c. *A. lyrata* subsp. *kamchatica*

8a. *Arabidopsis lyrata* subsp. *lyrata*

Synonyms: *Arabis lyrata* Linnaeus, *Sp. Pl.* 2: 665. 1753; *Cardaminopsis lyrata* (Linnaeus) Hiitonen, *Mem. Soc. Faun. Fl. Fenn.* 25: 75. 1950. Type: Canada, *D. Kalm s.n.* (holotype, LINN 842.8).

Biennial or perennial herbs, with slender or rarely branched caudex. Basal leaves lyrate-pinnatifid; petioles pilose to subhirsute, often ciliate; lateral lobes 1–5 on each side, entire of few toothed; terminal lobe considerably larger than lateral lobes. Petals 6–8 mm long. Fruits 0.7–1 mm wide; styles slender, 0.5–1.1 mm long, distinctly longer than broad. $2n=16, 32$.

Distribution: NE European Russia, Alaska, Canada (Ontario west into British Columbia), and southeastern and central United States (Vermont south into northern Georgia and Mississippi northward into Missouri and Minnesota).

Habitats: cliffs, calcareous ledges, rock crevices, sandy areas in open woods, river banks; near sea level to 2200 m.

8b. *Arabidopsis lyrata* subsp. *petraea* (Linnaeus) O’Kane & Al-Shehbaz, *Novon* 7: 326. 1997.

Synonyms: *Cardamine petraea* Linnaeus, *Sp. Pl.* 2: 654. 1753; *Arabis arenosa* (Linnaeus) Scopli subsp. *petraea* (L.) Celakovsky, *Prodr. Fl. Böhm.* 455. 1875; *A. petraea* (Linnaeus) Lamarck, *Encycl.* 1: 221. 1783; *Cardaminopsis petraea* (Linnaeus) Hiitonen in Hylander, *Förteckn. Scand. Växt. 1, Kärleväxt.*, ed. 3, 62. 1941. Type: “In Angliae, Arvoniae, Mervinae, Sueciae, rupibus excelsis” (holotype, LINN-835.5).

Arabis amurensis N. Busch, *Bot. Mater. Gerb. Glav. Bot. Sada RSFSR* 3(3–4): 12. 1922; *Cardaminopsis amurensis* (N. Busch) O.E. Schulz in Engler & Prantl, *Nat. Pflanzenfam.* ed. 2, 17B: 541. 1936. Type: “Ad flumen Amur et ejus confluentis (Schilka Kur) et in Sachalin (contra ostium fl. Amur)” (syntypes, LE).

Arabis crantziana Ehrhart, *Beitr. Naturk.* 5: 177. 1796

(nomen. nud.), Ehrhart ex Willdenow, Sp. Pl. 3: 535. 1802; *A. petraea* var. *crantziana* (Ehrhart) de Candolle, Syst. Nat. 2: 229. 1821. Type: "in monte Katzenstein," Ehrhart 78 (holotype, not located).

Arabis hispida Mygind in Linnaeus, Syst. Veg., ed. 13, 501. 1774, not *A. hispida* Moench, Methodus 258. 1794; *Cardaminopsis hispida* (Mygind) Hayek, Fl. Steiermark 1: 478. 1908. Type: Austria (holotype, LINN-842.9).

Arabis media N. Busch, Bot. Mater. Gerb. Glav. Bot. Sada RSFSR 3(3-4): 11. 1922; *Cardaminopsis media* (Busch) O.E. Schulz in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17B: 541. 1936; *C. petraea* subsp. *media* (N. Busch) Hämet-Ahti, Ann. Bot. Fenn. 7: 293. 1970. TYPE: [East Siberia]. "Zona arctica et subarctica ab ostio Lenae usque ad Anadyr, montes Sajansenses orientales, montes cis-et transbaicalenses atque Jacutenses" (holotype, LE).

Arabis septentrionalis N. Busch, Bot. Mater. Gerb. Glav. Bot. Sada RSFSR 3(3-4): 10. 1922; *A. petraea* subsp. *septentrionalis* (N. Busch) Tolmachev & Bloomintal, Trudy Bot. Muz. 23: 204. 1931; *Cardaminopsis septentrionalis* (N. Busch) O.E. Schulz in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17B: 541. 1936. Type: "Zona arctica a Novaja Zemlja usque ad ostia Lenae fluminis" (holotype, LE).

Arabis umbrosa Turczaninow in Ledebour, Fl. Ross. 1: 120. 1842, not *A. umbrosa* Crantz, Stirp. Austr. Fasc. ed. 1, 1: 43. 1762, ed. 2, 1: 41. 1769; *A. petraea* subsp. *umbrosa* Tolmachev, Fl. Arctica URSS 7: 97. 1975; *Cardaminopsis umbrosa* Czerepanov, Plantae Vasculares URSS 127. 1981; *C. petraea* subsp. *umbrosa* Peschkova, Fl. Tsentral'noi Sibiri 1: 396. 1979. Type: "in sabulosis ad fl. Irkut," Turczaninow s.n. (holotype, KW).

Perennial herbs, with stout, often several-branched caudex, rarely also stoloniferous. Basal leaves entire or dentate, rarely lyrate-dentate; petioles glabrous or pilose to subhirsute, often ciliate. Petals 4-7(-9) mm long. Fruits 1-1.5(-2) mm wide; styles slender to stout, to 0.6 mm long, slightly longer than broad. $2n=16, 32$.

Distribution: Austria, Czech Republic, England, Germany, Hungary, Iceland, Ireland, N. Italy, Norway, Russia (NW Russia, Siberia and Far East), Scotland, Sweden, Ukraine, boreal North America (Alaska and Yukon). Apparently extinct in Poland.

Habitats: Rocky and gravelly ground, sandy creek beds or banks, tundra slopes, tundra tussocks, sand dunes; near sea level to 2000 m.

Beginning in central Siberia, the taxon is increasingly similar to subspecies *kamchatica*, and many collections can only doubtfully be assigned to one or the other taxon. North American plants of subsp. *petraea* have been placed in *Arabis media* by Mulligan (1995).

8c. *Arabis lyrata* (Linnaeus) O'Kane & Al-Shehbaz

subsp. **kamchatica** (Fischer ex de Candolle) O'Kane & Al-Shehbaz, Novon 7: 326. 1997.

Synonyms: Linnaeus var. Fischer ex de Candolle, Syst. Nat. 2: 231. 1821; (Fischer ex de Candolle) Ledebour, Fl. Ross. 1: 121. 1842; *A. lyrata* subsp. *kamchatica* (Fischer ex de Candolle) Hultén, Fl. Aleut. Isl. 202. 1937, (Fischer ex de Candolle) O.E. Schulz in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17B: 541. 1936. TYPE: [Russia], Kamchatka, Fischer s.n. (holotype, LE).

Arabis ambigua de Candolle var. *glabra* de Candolle, Syst. Nat. 2: 231. 1821; *A. kamchatica* var. *glabra* (de Candolle) N. Busch, Fl. Sib. Orient. Est. 4: 468. 1926; *A. lyrata* Linnaeus var. *glabra* (de Candolle) M. Hopkins, Rhodora 39: 93. 1937. Type: "in Kamchatka et insulis Kurilensis" (holotype, G).

Arabis ambigua de Candolle var. *intermedia* de Candolle, Syst. Nat. 2: 231. 1821; *A. kamchatica* (Fischer ex de Candolle) Ledebour var. *intermedia* (de Candolle) N. Busch, Fl. Sib. Orient. Est. 4: 468. 1926; *A. lyrata* Linnaeus var. *intermedia* (de Candolle) Farwell, Annual Rep. Michigan Acad. Sci. 19: 256. 1917. Type: "insulis Kurilensibus," (holotype, G).

Arabis kawasakiana Makino, Bot. Mag. (Tokyo) 27: 24. 1913. Type: Japan. Prov. Ise: Yokkaichi, M. Kawasaki s. n. (holotype, MAK).

Arabis lyrata var. *occidentalis* S. Watson in A. Gray, Syn. Fl. N. Amer. 1: 159. 1895; *A. occidentalis* (S. Watson) A. Nelson, Univ. Wyoming Publ. 3: 111. 1937. Type: not designated.

Arabis morrisonensis Hayata, J. Coll. Sci. Imp. Univ. Tokyo 30(1): 29. 1911. Type: Taiwan, monte Morrison, 13,094 ft., Nov. 1905, S. Nagasawa 680 (holotype, TI).

Sisymbrium tilesii Ledebour, Mem. Acad. Imp. Sci. St. Pétersbourg Hist. Acad. 5: 548. 1815; *Arabis tilesii* (Ledebour) Karavaev ex V.N. Voroshilov, Byull. Glavn. Bot. Sada (Moscow) 134: 36. 1984. Type: Kamtschatka, 1806, *Tilesius* s.n. (holotype, LE?; isotype, MW).

Perennial herbs, with slender or rarely branched caudex. Basal leaves lyrate-pinnatifid; petioles glabrous or rarely very sparsely pilose; lateral lobes 1-5 on each side, entire or few toothed; terminal lobe considerably larger than lateral lobes. Petals 4-5(-5.5) mm long. Fruits (1-)1.2-1.5 mm wide; styles obsolete or distinct, stout, rarely to 0.5 mm long, distinctly wider than long. $2n=32$.

Distribution: boreal Alaska, Canada (Yukon, Mackenzie District, British Columbia, northern Saskatchewan), Aleutian Islands, eastern Siberia, the Russian Far East, Korea, northern China, Japan, and Taiwan.

Habitats: gravelly slopes, forests, alpine regions, roadsides, flooded areas; near sea level to 3500 m.

In the Russian Far East, subsp. *kamchatica* tends to

grow closer to the sea than does subsp. *petraea*, which is a more continental taxon. Plants of subsp. *kamchatica* growing in sandy, ocean-side localities tend to have massive leaves and seem indistinguishable from those described as *Arabis kawasakiana* of Japan. Mulligan (1995) treated subsp. *kamchatica* as a species of *Arabis*, whereas Rollins (1993) treated it as a variety of *Arabis lyrata*.

9. Arabidopsis halleri (Linnaeus) O’Kane & Al-Shehbaz,
Novon 7: 325. 1997.

Herbs perennial, stoloniferous, (10–)20–65(–80) cm tall. Stems decumbent, few from base, simple or branched above, basally with simple and 1-forked trichomes, apically glabrous. Basal leaves rosulate; petiole (5–)1–2.5(–5) cm long; leaf blade orbicular to broadly ovate, (1–)2–4.5(–9) × (0.5–)1–1.5(–2.5) cm, adaxially with a mixture of simple and stalked, 1- or 2-forked trichomes, margin pinnatifid to lyrate-pinnatifid and with (1 or)2–4(–7) suborbicular lateral lobes on each side; terminal lobe suborbicular, much larger than lateral ones, sometimes coarsely dentate, rarely entire or repand, apex obtuse. Stem leaves shortly petiolate, several; blade of middle and lower ones ovate to oblong or lanceolate, (0.5–)1–2.5(–8) × (0.2–)0.5–1.5(–3) cm, coarsely toothed or rarely lobed, gradually reduced in size upward. Fruiting pedicels slender, divaricate or slightly reflexed, straight, (0.5–)0.8–1.3(–2) cm long. Sepals 1.5–2 mm long, glabrous or apically with few simple trichomes, lateral pair saccate. Petals white, lilac, or purplish, obovate, 4–5(–6.5) × 2–2.5(–3.5) mm. Filaments white, 2–2.5 mm long. Ovules 14–18 per ovary. Siliques linear, flattened, torulose, (0.9–)1–2(–2.5) cm × 0.6–1 mm; replum constricted between seeds; valves not veined or with an obscure midvein; gynophore slender, to 0.7 mm long; style slender, to 1 mm long. Seeds oblong, flattened, light brown, 0.8–1.2 mm long, wingless; cotyledons accumbent. Flowering and fruiting June–August. $2n=16$.

Arabidopsis halleri is widely distributed from central Europe into northern Russia, the Far East, and Japan south into Taiwan. It is highly variable in leaf morphology, flower color, and the degree of development of stolons. The three subspecies, however, are quite distinct.

- 1a. Basal leaves entire or with weakly developed lateral lobes; lower stem leaves orbicular to ovate, entire or crenate; flowering stems few, sparsely branched above; petals light purple to pale lavender
.....9b. *A. halleri* subsp. *ovirensis*
- 1b. Basal leaves pinnatifid or lyrate; lower stem leaves oblong and dentate; flowering stems numerous,

branched at base and often also above; petals white or pale lavender.

2a. Basal leaves pinnatifid, with 1–7 lateral lobes; petals white or lavender; plants 20–45 cm tall;

Europe.....9a. *A. halleri* subsp. *halleri*

2b. Basal leaves lyrate; petals white; plants 40–80 cm tall; Russian Far East, northeastern China, Korea,

Japan, and Taiwan.....9c. *A. halleri* subsp. *gemmifera*

9a. Arabidopsis halleri subsp. *halleri*

Synonyms: *Arabis halleri* Linnaeus, Sp. Pl. ed. 2, 2: 929. 1763; *Cardamine halleri* (Linnaeus) Prantl, Exkursionflora v. Bayern, ed. 2, 229. 1884; *Cardaminopsis halleri* (Linnaeus) Hayek, Fl. Steiermark 1: 479. 1908. Type: an epitype needs to be designated. O’Kane and Al-Shehbaz (1997) indicated that the type is LINN 842.11, but that typification is incorrect.

Arabis besseri Zapalowicz subsp. *proseocarpatica* Zapalowicz, Rozpr. Wydz. Mat.-Przyr. Acad. Umiejtn., Dzial B, Nauki Biol. 52: 31. 1912. Type: “in rupibus calcareis Carpatorum orientaliu locis siccioribus: Budyowska Wielka, 1555 m,” *Zapalowicz s.n.* (lectotype, KRAM).

Arabis halleri Linnaeus var. *pilifera* Beck, Fl. Nieder-Österreich 2: 458. 1892; *Cardaminopsis halleri* var. *pilifera* (Beck) E. Schmid in Hegi, Ill. Fl. Mitel-Eur., ed. 1, 424. 1919. Type: Austria, *Beck s.n.* (holotype, PRC or W).

Arabis tenella Host, Fl. Austriac. 2: 273. 1831. Type: “in Styria superiore in humidis alpinum judenburgensium” (holotype, W).

Plants with few stolons. Stems 20–45 cm tall, branched below and above. Basal leaves pinnatifid, with 1–7 lateral lobes on each side; lower stem leaves often oblong, dentate. Fruiting pedicels 5–10 mm long. Petals white or rarely lavender. $2n=16$.

Distribution: Austria, Croatia, Czech Republic, Germany, N and C Italy, Poland, Romania, Slovakia, Slovenia, Switzerland, and S Ukraine. Probably introduced in N France and extinct in Belgium.

Habitats: mountain slopes, forest margins, rocky crevices; 600–2200 m.

9b. Arabidopsis halleri subsp. *ovirensis* (Wulfen)

O’Kane & Al-Shehbaz, *Novon* 7: 325. 1997.

Synonyms: *Arabis ovirensis* Wulfen in Jacquin, *Collectanea* 1: 196. 1787; *A. halleri* Linnaeus subsp. *ovirensis* (Wulfen) Klástersky, *Preslia* 8: 30. 1929; *Cardaminopsis halleri* subsp. *ovirensis* (Wulfen) Hegi & E. Schmid in Hegi, Ill. Fl. Mittel-Eur. 4(1): 424. 1919; *C. ovirensis* (Wulfen) Thellung ex Jávorka, *Magyar Fl.* 436. 1924; *C. ovirensis* (Wulfen) O. Schwarz, *Mitt. Thuring. Bot. Ges.* 1(1): 101. 1949, comb. superfl. Type: [Austria] *Ovirensis* supra *Ebriacum* in Valle Junonia percurrerem alpes, *Wulfen s.n.* (holotype, W).

Arabis halleri Linnaeus subsp. *transilvanica* Klástersky, *Preslia* 8: 29. 1929. Type: not designated, several syntypes cited.

Cardamine stolonifera Scopoli, *Fl. Carniol.* ed. 2, 2: 22. 1772; *Arabis stolonifera* (Scopoli) Hornemann, *Hort. Hafn.* 2: 618. 1815. Type: “in Carnioliae distritu Vipaccensi” (holotype, LINN?).

Plants with numerous stolons. Stems 10-20 cm tall, few branched above. Basal leaves entire or with weakly developed lateral lobes; lower stem leaves orbicular to ovate, often entire. Fruiting pedicels 10-14 mm long. Petals lavender or purple. $2n=16$.

Distribution: Albania, Austria, NE Italy, Romania, Slovakia, Slovenia, SW Ukraine, Yugoslavia.

Habitats: rocky slopes and crevices; 1200-2400m.

According to Jones & Akeroyd (1993), intermediates between subsp. *halleri* and subsp. *ovirensis* occur in the Tatra Mountains (Poland).

9c. Arabidopsis halleri subsp. gemmifera (Matsumura) O’Kane & Al-Shehbaz, *Novon* 7: 325. 1997.

Synonyms: *Cardamine gemmifera* Matsumura, *Bot. Mag. (Tokyo)* 13: 49. 1899; *Cardaminopsis gemmifera* (Matsumura) Berkutenko, *Novosti Sist. Vyssh. Rast.* 15: 154. 1978. Type: Japan. Prov. Shinano: monte Norikura, 1891, *K. Fuji s.n.* (holotype, TI).

Arabis coronata Nakai, *Bot. Mag. (Tokyo)* 28: 302. 1914. Type: Korea, “in silvis Laricis pede montis Paiktusan, Aug. 1913, *T. Mori s.n.* (holotype, TI).

Arabis gemmiferæ var. *alpicole* H. Hara, *J. Jap. Bot.* 12: 901. 1936. Type: Japan, Honshu, Prov. Omi, Mt. Ibuki, May 1914, *G. Koidzumi s.n.* (holotype, TI).

Arabis halleri Linnaeus var. *senanensis* Franchet & Savatier, *Enum. Pl. Jap.* 2: 279. 1879; *A. senanensis* (Franchet & Savatier) Makino, *Bot. Mag. (Tokyo)* 24: 224.

1910. Type: Prov. Senano, ubi Rein, *Savatier 2802* (holotype, P).

Arabis maximowiczii N. Busch, *Bot. Mater. Gerb. Glav. Bot. Sada RSFSR* 3(3-4): 13. 1922; *Cardaminopsis maximowiczii* (N. Busch) O.E. Schulz in Engler & Prantl, *Nat. Pflanzenfam.*, ed. 2, 17B: 541. 1936. Type: Manschuria, “Ussuri et ejus confluentes, Vladivostok, insula Putjatin,” *Maximowicz s.n.* (holotype, LE).

Cardamine greatrexii Miyabe & Kudo, *Trans. Sapporo Nat. Hist. Soc.* 6: 169. 1917; *Arabis greatrexii* (Miyabe & Kudo) Miyabe & Tatewaki, *Trans. Sapporo Nat. Hist. Soc.* 13: 379. 1934. Type: Japan, Hokkaido, Prov. Oshima, Hakodate, 10 June 1916, *Greatrex s.n.* (holotype, SAPA).

Plants with few to several stolons. Stems 40-65(-80) cm tall, branched below and above. Basal leaves often lyrate; lower stem leaves often ovate, dentate. Fruiting pedicels (8-)10-20 mm long. Petals white. $2n=16$.

Distribution: Russian Far East, northeastern China, Korea, Japan, and Taiwan.

Habitats: gravelly or grassy slopes, forests, shaded and most areas; near sea level to 2600 m.

Generic placement of species excluded from Arabidopsis

The following species previously placed in *Arabidopsis* (italics) are currently considered as synonyms of those in boldface.

A. bactriana Ovczinnikov & Junussov, *Fl. Tadzhitskoi SSR* 5: 626. 1978. No material has been seen, but according to the original description, the species cannot be assigned to *Arabidopsis* because it is pulvinate, scapose perennial with cylindrical fruits, subbiseriate seeds, and leafless stems.

A. brevicaulis (Jafri) Jafri, *Fl. W. Pakistan* 55: 272. 1973. = **Crucihimalaya himalaica** (Edgeworth) Al-Shehbaz, O’Kane & R.A. Price, *Novon* 9: 301. 1999.

A. bursifolia (de Candolle) Botschantsev, *Not. Syst. Herb. Inst. Bot. Acad. Sci. URSS* 19: 106. 1959. = **Beringia bursifolia** (de Candolle) R.A. Price, Al-Shehbaz & O’Kane, *Novon* 11: 2001 (in press).

A. campestris O.E. Schulz, *Notizbl. Bot. Gart. Berlin-Dahlem* 9: 1059. 1927. = **Crucihimalaya wallichii** (J.D. Hooker & Thomson) Al-Shehbaz, O’Kane & R.A. Price, *Novon* 9: 301. 1999.

A. dentata (Allioni) Dalla Torre, *Alpenfl.* 115. 1899. = **Murbeckiella pinnatifida** (Lamarck) Rothmaler, *Bot. Notiser* 1939: 469. 1939.

- A. drassiana* Naqshi & Javeid, J. Econ. Taxon. Bot. 7: 624. 1986. No material has been seen, and the species is excluded from *Arabidopsis* because it has sessile amplexicaul leaves (Naqshi and Javeid, 1986).
- A. erysimoides* Hedge & Kit Tan, Pl. Syst. Evol. 156: 202. 1987. = **Erysimum hedgeanum** Al-Shehbaz, Novon 4: 1. 1994.
- A. esepata* Hedge, Fl. Iran. 57: 334. 1968. = **Olimarabidopsis umbrosa** (Botschantsev & Vvedensky) Al-Shehbaz, O'Kane & R.A. Price, Novon 9: 303. 1999.
- A. gamosepala* Hedge, Fl. Iran. 57: 334. 1968. = **Neotorularia gamosepala** (Hedge) Al-Shehbaz & O'Kane, Novon 7: 93. 1997.
- A. glauca* (Nuttall ex Torrey & A. Gray) Rydberg, Fl. Rocky Mt. 342. 1917. = **Thellungiella salsuginea** (Pallas) O.E. Schulz, Pflanzenz. IV. 105(Heft 86): 252. 1924.
- A. griffithiana* (Boissier) N. Busch, Fl. Cauc. Crit. 3(4): 457. 1909. = **Olimarabidopsis pumila** (Stephan) Al-Shehbaz, O'Kane & R.A. Price, Novon 9: 303. 1999.
- A. himalaica* (Edgeworth) O.E. Schulz, Pflanzenreich IV.105(Heft 86): 283. 1924. = **Crucihimalaya himalaica** (Edgeworth) Al-Shehbaz, O'Kane & R.A. Price, Novon 9: 301. 1999.
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Molecular phylogeny

Molecular studies on the nine species presently recognized in *Arabidopsis* and most of the 50 species previously assigned to the genus (O'Kane and Al-Shehbaz, 2001; Koch et al., 1999, 2000, 2001; Price et al. 1994) show beyond doubt that previous delimitation of the genus and the alleged phylogenetic relationships and tribal classifications (Schulz, 1924, 1936) are untenable. The artificiality of the tribal classifications of the family and the polyphyly of most tribes have been pointed out by many workers (e.g., Price et al., 1994; Koch et al., 2001) and need not be repeated here.

Arabidopsis forms a well-defined, monophyletic clade somewhat closely related to the recently segregated genus *Olimarabidopsis* (O'Kane and Al-Shehbaz, 2001; Price et al., 1994; Koch et al., 2001). The latter genus consists of three species distributed in Eurasia but mainly in central and southwestern Asia (Al-Shehbaz et al., 1999). Depending on the taxa studied, the various molecular phylogenies proposed thus far (Price et al., 1994; Koch, 1999, 2000, 2001; O'Kane and Al-Shehbaz, 2001) show different topologies and relationships between *Arabidopsis* and other genera, including *Crucihimalaya*, *Pseudoarabidopsis*, *Capsella*, *Camelina*, and *Arabis sensu lato*. However, the lack of comprehensive phylogenetic studies on the entire family makes it difficult to point out definitively what the nearest relatives of *Arabidopsis* really are. Because *Arabidopsis* is most highly diversified in Europe, it would be highly desirable to concentrate on the taxa there that share the same morphological and cytological aspects, especially those with base chromosome numbers of $x=8$, branched trichomes, and linear fruits. Species of the European *Arabis sensu lato* and *Olimarabidopsis* are good candidates to concentrate on. It should be kept in mind, however, that the molecular studies cited above clearly demonstrated the polyphyly of *Arabis*, and that concentrated efforts should be made to establish a monophyletic genus by assigning unrelated species to other, possibly new, genera. In fact, such attempts (Koch et al., 1999; Price et al., 2001) have already been made.

Molecular studies (Mummenhoff and Hurka, 1994, 1995; O'Kane et al., 1997) within *Arabidopsis* have demonstrated that *A. sucecica* ($2n=26$) is an allopolyploid formed by hybridization between the maternal parent *A. thaliana* ($2n=10$) and a diploid paternal parent not very different from *A. arenosa* or *A. neglecta* ($2n=16$). More recent work indicates that *A. arenosa* is in fact the maternal parent (O'Kane, unpub. data) as indicated in Fig. 1. For taxonomic and experimental studies related to the origin of *A. sucecica*, the interested reader should consult the

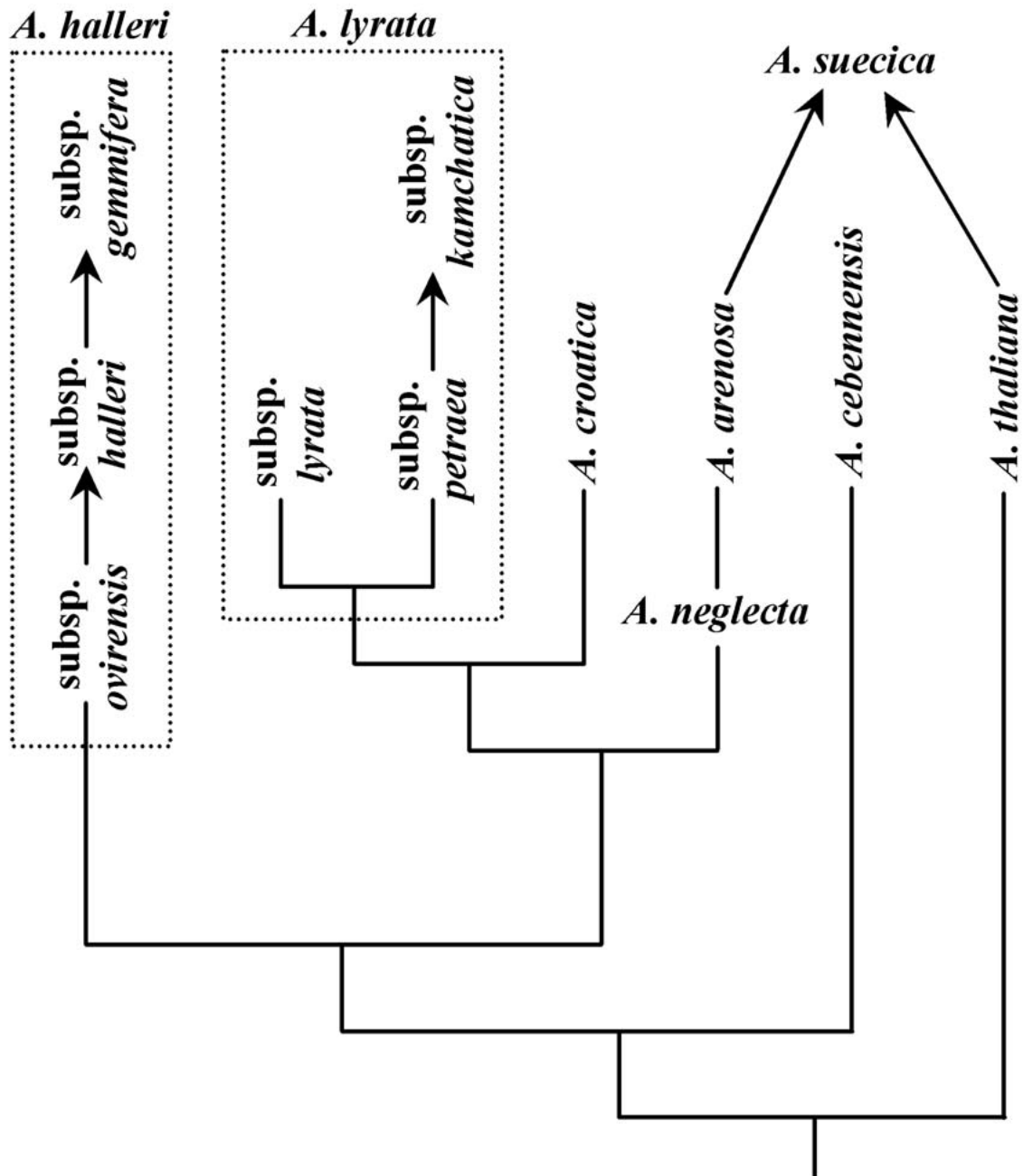


Figure 1. Phylogenetic relationships within *Arabidopsis* based on ITS data.

references in the three works above.

Detailed molecular studies of the taxa of *Arabidopsis*, summarized in Fig. 1, based on DNA sequences of the internal transcribed spacers of nuclear ribosomal DNA (O’Kane and Al-Shehbaz, 2001) show that *A. lyrata* (and its subspecies) form a well supported clade in a sister group relationship to *A. croatica*. *Arabidopsis lyrata* is circumboreal with relict populations of subsp. *kamchatica* occurring at high elevations in Taiwan. Its presence on Taiwan is likely a consequence of southward range expansion during the last major glaciation when a land bridge was formed with mainland Asia (Voris, 2000).

Arabidopsis halleri subsp. *ovirensis* is an alpine plant of the southeastern Alps, the Carpathians, and the northern Balkan Peninsula. From this subspecies evolved the lowland, stolon-producing subspecies *halleri*, which is distributed in central Europe and northern Asia. The species is represented in the eastern Asia (Russian Far East, eastern China, Korea, Japan, and Taiwan) by subsp. *gemmifera*. The latter evolved from subsp. *halleri*, and its migration into Taiwan apparently followed the same pattern as that of *A. lyrata* subsp. *kamchatica*.

Arabidopsis arenosa and *A. neglecta* together form a monophyletic group, but each of these species is paraphyletic with respect to the other in one or more molecular analyses. One-step statistical parsimony analysis (Templeton et al., 1992), however, indicates that the alpine *A. neglecta* is directly ancestral to *A. arenosa*, a species with weedy tendencies that grows at elevations below the alpine. These two species must have diverged so recently that paraphyly in the nrDNA ITS gene tree is still seen, i.e., not enough time has elapsed for drift and fixation to convert the lineage from paraphyletic to monophyletic (Rieseberg and Brouillet, 1994). It appears that evolutionary innovation in these two species, as in the subspecies of *A. halleri*, progressed from high to low elevations. As shown in Fig. 1, the broad-leaved *A. cebennensis* is basal to the clade including the rest of the species of the genus excluding *A. thaliana*. (*Arabidopsis pedemontana* was not included in the molecular analyses for lack of adequate material.)

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