

***Arabidopsis kamchatica* (Fisch. ex DC.) K. Shimizu & Kudoh
and *A. kamchatica* subsp. *kawasakiana* (Makino) K. Shimizu &
Kudoh, New Combinations**

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New combinations for two taxa, *Arabidopsis kamchatica* (Fisch. ex DC.) K. Shimizu & Kudoh and *A. kamchatica* subsp. *kawasakiana* (Makino) K. Shimizu & Kudoh, are proposed. The lectotypes of both names were chosen. The former taxon was previously recognized as either *Arabis kamchatica*, *Cardaminopsis kamchatica* or an infraspecific taxon under *Arabis lyrata* or *Arabidopsis lyrata*. The latter was previously recognized as either *Arabis kawasakiana*, *Arabis lyrata* subsp. *kawasakiana* or a synonym of *Arabidopsis lyrata* subsp. *kamchatica*. We here report the bivalent nature of meiotic chromosome of *A. kamchatica* subsp. *kawasakiana*, $n = 16_{II}$ and $2n = 32$. We also provide a molecular evidence of allotetraploidy using a nuclear Chalcone Synthase (*CHS*) sequence. In conjunction with former chromosomal and morphological studies, we considered that both taxa should be placed under the genus *Arabidopsis* but distinct from *Arabidopsis lyrata*. *Arabidopsis kamchatica* will provide a unique opportunity for the molecular genetic analysis of genome duplication, by utilizing the genetic and genomic information on a model species *Arabidopsis thaliana*.

Key words: *Arabidopsis*, *Arabis*, bivalent chromosome, *Cardaminopsis*, *CHS*, *kamchatica*, *kawasakiana*, *lyrata*, tetraploid

Arabidopsis thaliana (L.) Heynh. has been extensively studied as a model organism for genetic and genomic research. Recently, other species of the genus *Arabidopsis* (DC.) Heynh. have also been studied as model systems for evolutionary and ecological studies. The wide array of natural variation in morphology, phenology, and physiology found in these species can be a rich source for molecular

genetic studies, given the huge amount of information already available for *Arabidopsis thaliana* (Alonso-Blanco & Koornneef 2000, Mitchell-Olds 2001, Meyerowitz 2002, Shimizu 2002, Weigel & Glazebrook 2002, Shimizu & Purugganan 2005). *Arabidopsis lyrata* (L.) O’Kane & Al-Shehbaz subsp. *lyrata* and subsp. *petraea* (L.) O’Kane & Al-Shehbaz are often used as reference taxa in evo-

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lutionary and population genetic studies of *A. thaliana* (Bustamante *et al.* 2002, Shimizu *et al.* 2004). *Arabidopsis suecica* (Fr.) Norrl. is allotetraploid and studied as a model for speciation by genome duplication (Madlung *et al.* 2002). Because of the extensive use of diverse *Arabidopsis* species in ecology, evolution and genetics, additional taxonomic and phylogenetic information about the species in *Arabidopsis* is critical. For example, phylogenetic information is necessary to choose the accession or species to be used in interspecific crosses for genetic analysis.

However, the taxonomy and phylogeny of *Arabidopsis* species is still unresolved. Like other members of the Brassicaceae, the paucity of informative morphological characters in this genus has hampered its taxonomic analysis. Based on molecular information, major revision of *Arabidopsis*, *Arabis* L., *Cardaminopsis* (C. A. Mey.) Hayek is underway (O’Kane & Al-Shehbaz 1997, Koch *et al.* 2000, 2001). In this article, we propose new combinations for two tetraploid taxa of *Arabidopsis* that were originally described as *Arabis lyrata* var. *kamchatica* Fisch. ex DC. and *Arabis kawasakiana* Makino.

Taxonomic History

The taxon corresponding to *Arabis lyrata* var. *kamchatica* is a perennial distributed across eastern Eurasia and northernmost North America (Hoffmann 2005). Since its original description, it has been treated either as an infraspecific taxon of *Arabis lyrata* L., or as a distinct species. Candolle (1821), Hopkins (1937), Hultén (1928, 1937, 1968), Ohwi (1953), Kitamura & Murata (1961), Kitagawa (1982), Lan (1987), and Rollins (1993) considered it as an infraspecific taxon of *Arabis lyrata*. In contrast, Ledebour (1841), Busch (1939), and Mulligan (1995) treated it as a species, *Arabis kamchatica* (Fisch. ex DC.) Ledeb. Schulz (1936) treated this taxon as a species of *Cardaminopsis*, *C. kamchati-*

ca (Fisch. ex DC.) O. E. Schulz [note that the genus *Cardaminopsis* is based on *Arabis* L. sect. *Cardaminopsis* C. A. Mey. in Ledeb. Fl. Altaica 3: 19 (1831)]. Both diploid ($2n = 16$) and tetraploid ($2n = 32$) chromosome numbers were reported from taxon corresponding to *Arabis lyrata* var. *kamchatica* (Ihara 1976, Zhukova & Petrovsky 1984, Rollins 1993, Dart *et al.* 2004), as well as from samples representing other varieties and subspecies of *Arabis lyrata* (*Arabis lyrata* by Mulligan 1964, *Arabis lyrata* var. *lyrata* by Rollins 1993, *C. petraea* and *C. lyrata* by Berkutenko *et al.* 1984, *Arabidopsis lyrata* subsp. *petraea* from Austria by Dart *et al.* 2004, which seems to be autotetraploid with tetrasomic inheritance shown by Mable *et al.* 2004).

Mulligan (1995) reexamined the specimens used in previous studies. Based on the results, he proposed that *Arabis kamchatica* is a tetraploid species ($2n = 32$), which can be distinguished morphologically from other diploid taxa. We agree with his conclusion.

Close relatedness between the genus *Cardaminopsis* and the genus *Arabidopsis* was pointed out by Hylander (1957) and Ball (1993) based on morphology. It is also supported by the finding that the taxon treated as *C. suecica* (Fr.) Hiitonen ex Hyl. is an allotetraploid species derived from *Arabidopsis thaliana* and *C. arenosa* (L.) Hayek [*Arabidopsis arenosa* (L.) Lawalrée] (Hylander 1957).

Recent molecular analyses have strongly supported the idea that the taxon originally described as *Arabis lyrata* var. *kamchatica* should be placed under the genus *Arabidopsis* (Miyashita *et al.* 1998, Koch *et al.* 2000, 2001, Savolainen *et al.* 2000, Hoffmann 2005), as proposed by O’Kane & Al-Shehbaz (1997). O’Kane & Al-Shehbaz (1997) recognized three subspecies under *Arabidopsis lyrata*, *i.e.*, the North American subsp. *lyrata*, the European subsp. *petraea* (L.) O’Kane & Al-Shehbaz, and the Far East / North American subsp. *kamchatica* (Fisch. ex DC.) O’Kane & Al-Shehbaz. However, the molecular markers used in those studies were not

suitable to analyze polyploid taxa. Here, we propose a new combination *Arabidopsis kamchatica* (Fisch. ex DC.) K. Shimizu & Kudoh as follows in the nomenclatural summary, based on chromosomal data and molecular phylogeny using a nuclear gene.

Populations corresponding to *Arabis kawasakiana* represent a winter annual growing on sandy seashores or lakeshores of Western Japan (Tokai, Hokuriku, Kinki and Shikoku districts). Kitamura & Murata (1961, 1962) treated them as *Arabis lyrata* subsp. *kawasakiana* (Makino) Kitam. They considered that the taxon was derived from a Far-East taxon *Arabis lyrata* subsp. *kamchatica* (Fisch. ex DC.) Hultén and adapted to southern climate, because of its morphological similarity with this taxon and with a North American *Arabis lyrata* subsp. *lyrata*. As we report later in this article, the taxon corresponding to *Arabis kawasakiana* has a chromosome number of $2n = 32$ and $n = 16_{II}$. Molecular analyses supported the idea that the taxon corresponding to *Arabis kawasakiana* should be placed under the genus *Arabidopsis* (Miyashita *et al.* 1998, Savolainen *et al.* 2000). In the treatment by O'Kane & Al-Shehbaz (1997), *i.e.*, transfer of *Arabis lyrata* and its subspecies into the genus *Arabidopsis*, they considered that *Arabis kawasakiana* was a synonym of *Arabidopsis lyrata* subsp. *kamchatica*. However, the former is distinctive as an annual occurring on low-altitudinal sandy shores, while the latter is a mountain perennial, as it has been pointed out in Makino (1913), Kitamura & Murata (1961, 1962) and other Japanese Floras (Ohwi 1953, Kitagawa 1982). Therefore, we propose here a new combination *Arabidopsis kamchatica* subsp. *kawasakiana* (Makino) K. Shimizu & Kudoh as follows in the nomenclatural summary.

Materials and Methods

Chromosome numbers of *Arabidopsis kamchatica* subsp. *kawasakiana* were counted for specimens collected from four localities [Toyama-shi, Toyama

Prefecture, Japan (137°16'E, 36°47'N, alt. 2 m); Takashima-shi, Shiga Prefecture, Japan (136°04'E, 35°27'N, alt. 85 m); Hikone-shi, Shiga Prefecture, Japan (136°10'E, 35°14'N, alt. 85 m); Meiwa-cho, Taki-gun, Mie Prefecture, Japan (136°36'E, 34°36'N, alt. 2 m)]. Root tips were treated with cold water at 0°C for 24 hrs, fixed in 3:1 (in volume) ethanol / acetic acid at 5°C for 1 hr and stained in 1% acetic-orcein. For meiotic chromosome counts, young flower buds were fixed in the same fixative for 1 hr and the pollen mother cells were stained in 1% acetic-orcein.

Plant materials for phylogenetic analysis were collected at following localities: *Arabidopsis halleri* subsp. *gemmaifera* (Matsum.) O'Kane & Al-Shehbaz at Inagawa-cho, Kawabe-gun, Osaka Prefecture, Japan; *A. lyrata* subsp. *lyrata* in Wilkes County, North Carolina, USA; *A. kamchatica* subsp. *kamchatica* at Kamikochi, Azumi-mura, Minamiazumi-gun, Nagano-Prefecture, Japan; and *A. kamchatica* subsp. *kawasakiana* at Takashima-shi as described in the material for chromosome observation.

Genomic DNA was isolated from leaf tissues by using the Plant DNeasy Mini kit (Qiagen, Valencia, CA, USA). Primers were designed for the homeolog-specific amplification of Chalcone Synthase (*CHS*) nuclear gene. The reverse primer CHSR1 (5'-AGAGGAACGCTGTGCAAGAC-3') was designed in the conserved sequence near the end of the gene, and forward primers in the promoter region were designed for homeolog-specific amplification. CHSgemFU1 (5'-GAAATCTCCG-TAGTCCGTATGGTG-3') was used for the specific amplification of *halleri* type homeolog of both subspecies of *Arabidopsis kamchatica*. CHSFU1 (5'-TGGAGTTAAGTATGCACGTG-3') and CHSlyrFU1 (5'-TGGGAAGTGAAATCTCCT-TATGGTG-3') were used to amplify the *lyrata* type homeolog of subsp. *kamchatica* and subsp. *kawasakiana*, respectively. The *CHS* genes of *A. lyrata* subsp. *lyrata* and *A. halleri* subsp. *gemmaifera* were amplified by the primer CHSFU1. Polymerase

chain reaction (PCR) was carried out using an ABI 9700 (Applied Biosystems). DNA fragments amplified by ExTaq (TaKaRa) were purified with the QIAquick PCR Purification and Gel Extraction kits (QIAGEN) and sequenced directly, or amplified by high-fidelity PfuUltra polymerase (Stratagene) and cloned in the case of *A. lyrata* subsp. *lyrata*. DNA sequencing was conducted at the North Carolina State University Genome Research Laboratory with a Prism 3700 96-capillary automated sequencer (Applied Biosystems). All singletons were visually confirmed, and the sequences were visually aligned. The alignment of 1403 sites includes part of the promoter region, exon 1, intron 1 and most of exon 2. Neighbor-joining trees were generated with MEGA 2.1 software (Kumar *et al.* 2001) using the Kimura 2-parameter model with the option of complete deletion of gap positions (1385 sites were used). Bootstrap values of 1000 replicates are shown on the nodes of the branches. The *CHS/TT4* gene of *A. thaliana* Col-0 accession (Genbank accession no. AB005230) was included as an outgroup sequence.

Results and Discussion

Chromosome numbers of *Arabidopsis kamchatica*

subsp. *kawasakiana* were counted in the plants collected from four localities. All plants had a chromosome number of $2n = 32$ and $n = 16_{II}$ (Fig. 1). The bivalent nature of the chromosome suggests that the taxon originated by allotetraploidy and is distinct from the diploid species *A. lyrata*.

To obtain further evidence that the two taxa represent a species distinct from *Arabidopsis lyrata*, the nuclear gene Chalcone Synthase (*CHS*) was sequenced. Consistent with the tetraploidy, two copies of *CHS* were amplified from both subspecies (Fig. 2). One of the copies was highly homologous to the *CHS* gene of *A. halleri* subsp. *gemmifera* and then named halleri type, and the other copy was similar to *A. lyrata* subsp. *lyrata* and was named lyrata type. In both subspecies, the divergence between the halleri and lyrata type was 0.014 (20/1391 sites). These molecular data, together with the morphological and chromosomal study by Mulligan (1995) and with the presence of bivalent chromosomes, indicate that *A. kamchatica* is an allotetraploid species and is distinct from *A. lyrata*.

The neighbor-joining tree (Fig. 2) suggests that plants similar to *Arabidopsis halleri* and *A. lyrata* are the candidate parental species of the tetraploid *A. kamchatica*. Further analyses using population samples are necessary to reveal the

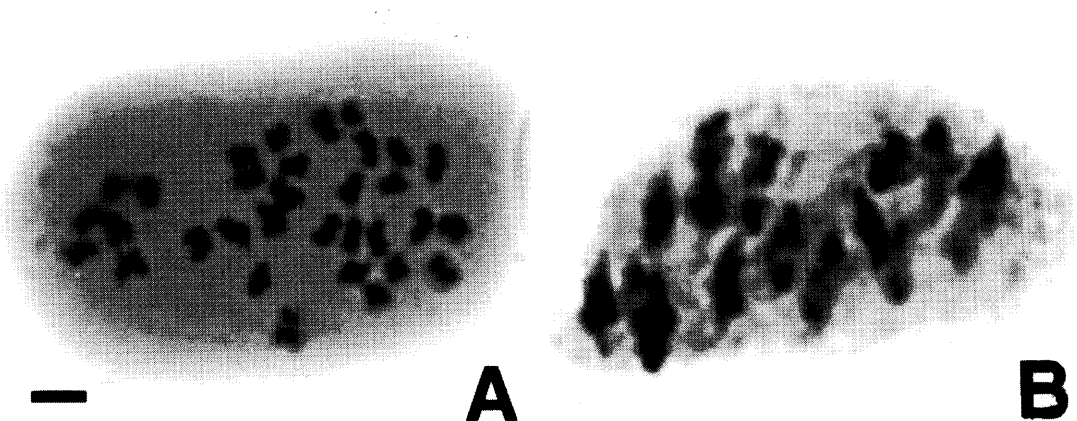


FIG. 1. Mitotic and meiotic chromosomes in *Arabidopsis kamchatica* subsp. *kawasakiana*. Mitotic metaphase, $2n = 4x = 32$ (A) and meiotic metaphase, $n = 16_{II}$ (B). Scale, 2 μm .

parental origin, since gene flow between European subspecies of the two species, namely *A. lyrata* subsp. *petraea* and *A. halleri* subsp. *halleri* is possible (Macnair *et al.* 1999, Ramos-Onsins *et al.* 2004).

Furthermore, our analysis suggested that *Arabidopsis kamchatica* has unique and attractive characteristics for future molecular genetic analysis. Since it belongs to the same genus as a model species *A. thaliana*, the huge amount of genetic and genomic information available for *A. thaliana* can be readily exploited (Mitchell-Olds 2001, Shimizu 2002, Shimizu & Purugganan 2005). While statistical methods for tetraivalent inheritance are still primitive (Wu *et al.* 2001), the observation of bivalent chromosome of *A. kamchatica* subsp. *kawasakiana* means that the mapping methods developed for diploid species can be readily applied. As a tetraploid species in the genus *Arabidopsis*, *A. kamchatica*, along with another species *A. suecica* (Madlung *et al.* 2002), will provide an opportunity to study the evolution and speciation by genome duplication from a molecular genetic viewpoint.

Nomenclatural Summary

- Arabidopsis kamchatica*** (Fisch. ex DC.) K. Shimizu & Kudoh, **comb. nov.**
- ≡ [Basionym] *Arabis lyrata* var. *kamchatica* Fisch. ex DC., Syst. Nat. 2: 231 (1821). Ind. loc.: “in Kamchatkâ”. **Lectotype (designated here):** Kamtschatka, *Fisher s. n.* (G-DC, IDC Microfiche Candolle Herbarium 68/1!).
 - ≡ *Arabis kamchatica* (Fisch. ex DC.) Ledeb., Fl. Ross. 1: 121 (1841), “kamtschatica”.
 - ≡ *Arabis lyrata* subsp. *kamchatica* (Fisch. ex DC.) Hultén, Fl. Aleutian Isl. 202 (1937), “kamtschatica”.
 - ≡ *Cardaminopsis kamchatica* (Fisch. ex DC.) O. E. Schulz in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 17b: 541 (1936), “kamtschatica”.
 - ≡ *Arabidopsis lyrata* subsp. *kamchatica* (Fisch. ex DC.) O’Kane & Al-Shehbaz, Novon 7: 326 (1997).
 - = *Arabis ambigua* ([var.] *glabra* DC., Syst. Nat. 2: 231 (1821). Ind. loc.: “in Kamchatkâ et insulis Kurilensibus”. **Lectotype (designated here):**

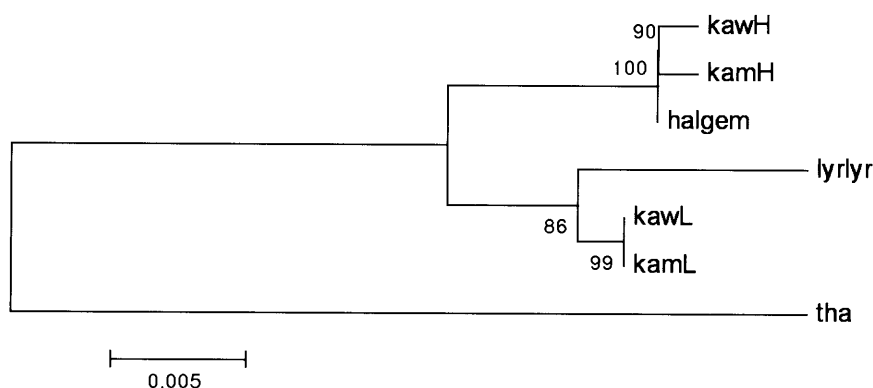


FIG. 2. Neighbor-joining tree of Chalcone Synthase (*CHS*) gene. halgem: *Arabidopsis halleri* subsp. *gemmifera* collected at Inagawa-cho, kamH: halleri type allele of *A. kamchatica* at Kamikochi, kamL: lyrata type allele of *A. kamchatica* at Kamikochi, kawH: halleri type allele of *A. kamchatica* subsp. *kawasakiana* at Takashima-shi, kamL: lyrata type allele of *A. kamchatica* subsp. *kawasakiana* at Takashima-shi, lyrlyr: *A. lyrata* subsp. *lyrata* collected at Wilkes Co., USA, tha: *A. thaliana* Col-0. Bootstrap values of 1000 replicates are shown on the nodes of the branches. Bar, 0.005 substitutions / site.

- Kamtschatka, *Fischer s. n.* (G-DC, IDC Microfiche Candolle Herbarium 67/21!)
- ≡ *Arabis lyrata* var. *glabra* (DC.) Hopkins, *Rhodora* 39: 93 (1937).
- ≡ *Arabis kamchatica* var. *glabra* (DC.) N. Busch, *Fl. Sib. Orient. Extrem.* 4: 468 (1926), “*kamtschatica*”.
- = *Arabis ambigua* β [var.] *intermedia* DC., *Syst. Nat.* 2: 231 (1821). Ind. loc.: “in Unalaska”. Holotype: Unalaska (G-DC, IDC Microfiche Candolle Herbarium 67/22!)
- ≡ *Arabis lyrata* var. *intermedia* (DC.) Farw., *Annual Rep. Mich. Acad. Sci. Rep.* 256 (1917).
- ≡ *Arabis kamchatica* var. *intermedia* (DC.) N. Busch, *Fl. Sib. Orient. Extrem.* 4: 468 (1926), “*kamtschatica*”.
- = *Arabis lyrata* var. *occidentalis* S. Watson in A. Gray, *Syn. Fl. N. Amer.* 1: 159 (1895). Ind. loc.: “From Alaska to British Columbia and the eastern side of the Rocky Mts. in Brit. America; Point Pelee on Lake Erie, *Macoun*. (Kamtshchatka, *Wright*).” Type not designated.
- ≡ *Arabis occidentalis* (S. Watson) Nelson, *Univ. Wyoming Pub.* 3: 111 (1937).

Nomenclatural notes: (1) The specimen from herbarium LE from Fischer’s collection was chosen as a lectotype of the name *Arabis lyrata* var. *kamchatica* Fisch. ex DC. by Mulligan (1995). We have seen only a photograph of this specimen (thanks to Gisèle Mitrow, DAO) as it is, at least for the time being, lost. After being on loan in DAO herbarium it was sent back to LE in 1991, but most probably never reached LE herbarium in St. Petersburg, or if it did it was misplaced after arrival. The specimen undoubtedly comes from the Fischer’s collection, but was not annotated by Candolle, which would make it part of the original material. There were multiple specimens identified as “*Arabis kamtschatica*” collected by Fischer in herbarium LE (includ-

ing four specimens sent to DAO for loan and now at least temporarily lost) and there is no proof that particularly the specimen selected by Mulligan (1995) is a duplicate of one of the three specimens sent by Fischer to Candolle and deposited now in the Candolle’s herbarium in Genève (G-DC). Therefore, according to our opinion, specimen selected by Mulligan has no standing as original material of the name *Arabis lyrata* var. *kamchatica* [see Art. 9.2, Note 2 of the Code, Greuter *et al.* 2000] and therefore was not legitimate for the choice of lectotype. This, together with the fact that the aforementioned specimen selected by Mulligan (1995) is at least temporarily lost, led us to the decision to select a new lectotype. The true original material of the name *Arabis lyrata* var. *kamchatica* in the herbarium of Candolle (G-DC) consists of three plants (three plants on the right in Fig. 3A). There are two labels on the three plants, written very likely in Fischer’s hand, with annotation by Candolle “Mis[it] Fischer 1819” on the sheet. In addition, the specimen is annotated by Candolle as “*Arabis kamchatica* Fisch. / *lyrata* var. DC.” As this seems to be the only extant original material connected with this name we formally designate the second plant from the right side of the sheet as a lectotype (arrows in Fig. 3A and 3B). The particular plant had both flowers and siliques, and is consistent with the description by Candolle (1821) “β A. Kamchatica. *Fischer! in litt.* Var. β in posterum forsan distinguenda differt flore minore, petalis nempe calyce duplò nec triplò longioribus et siliquis longioribus crassioribus.” There is another plant on the same sheet in addition to the three plants, but it is apparently a different collection because it was collected in 1820 and not by Fischer judged from its label (the plant at the far left in Fig. 3A).

(2) Al-Shehbaz & O’Kane (2002) include the name *Sisymbrium tilesii* Ledeb., *Mem. Acad. Imp. Sci. St. Pétersbourg. Hist. Acad.* 5: 548, 1815, in the synonymy of the name *Arabidopsis lyrata* subsp. *kamchatica*. If this were true, then the epithet “*tile-*

sii” would have priority at the species level for this particular taxon. We have checked the original material (most probably holotype) of this name in herbarium LE (*S. Tilesii* mihi, In Camtchatca ..., Tilesius [18]13). Although the plants were collected early in the flowering season and so characteristics of mature plants such as silique width cannot be analyzed, the petals of the specimen were larger (up to 7.3 mm) than the range of the petal size of *Arabis kamtschatica* (4.0–5.5 mm) described by Mulligan (1995). In addition, Ledebour himself, who described *S. tilesii*, later considered the material as a variety of *Arabis petraea* (β . *floribus majoribus*) (Ledebour 1841). Thus, it seems most

likely that this specimen belongs to another taxon, namely *Arabidopsis lyrata* subsp. *petraea*.

(3) The original material of the name *Arabis ambigua* α [var.] *glabra* DC. in the herbarium of Candolle (G-DC) consists of three plants. Each plant has its own label. All the three labels were written very likely in Fischer’s hand, with an annotation by Candolle “Mis[it] Fischer”. In addition, the sheet is annotated by Candolle as “*Arabis ambigua* α DC.” There seems to be no locality for the left-hand plant. That of the middle plant was “E 2ou ins. Curil” and that of the right-hand plant was “Kamtschatka?” We formally designate the right-hand plant as a lectotype. The particular plant is the



FIG. 3. Lectotype specimen. (A) Specimen sheet including the lectotype of *Arabidopsis kamtschatica* shown by an arrow. (B) Reverse side of the two plants in the center in (A). The lectotype is again shown by an arrow.

only one with rosette leaves, which appeared in the description by Candolle (1821).

Arabidopsis kamchatica (Fisch. ex DC.) K. Shimizu & Kudoh subsp. **kamchatica**

Japanese name: Miyama-hatazao

Distribution: EAST ASIA (Far East Russia, China, Korea, Taiwan, Japan) and NORTH AMERICA (Alaska, Canada, Northwestern United States). In Japan, the subspecies occurs in montane, sub-alpine, and alpine habitats.

Arabidopsis kamchatica subsp. **kawasakiana** (Makino) K. Shimizu & Kudoh, **comb. nov.**

≡ [Basionym] *Arabis kawasakiana* Makino, Bot. Mag., Tokyo 27: 24 (1913). Ind. loc.: “Prov. Ise: Yokkaichi”. **Lectotype (designated here):** Japan. Prov. Ise: Yokkaichi, Umaokoshi, June 1905, *M. Kawasaki s. n.* (MAK 118231!).

≡ *Arabis lyrata* subsp. *kawasakiana* (Makino) Kitam. in Kitam. & Murata [Col. Ill. Herb. Pl. Jap. 2: 181 (1961), *nomen*] Acta Phytotax. Geobot. 20: 201 (1962).

≡ *Arabis petraea* var. *nipponica* Makino in Inuma, Somoku-Dzusetsu (ed. 3), 3 (12): 10, pl. 11 (1912), “*nipponicum*”. Ind. loc.: “Abundant in the vicinity of rice fields near the eastern coast of Yokkaichi [in Japanese]”. **Lectotype (designated here):** Japan. Prov. Ise: Yokkaichi, Umaokoshi, June 1905, *M. Kawasaki s. n.* (MAK 118231!).

Nomenclatural note: There is one sheet collected by M. Kawasaki in 1905 in herbarium in MAK annotated as “*Arabis petraea* var.” As cited in the original description, Makino had tentatively used either *Arabis petraea* var.? [Bot. Mag., Tokyo 11: 157 (1897)] or *Arabis petraea* var. *nipponica* Makino [Inuma’s Somoku-Dzusetsu ed. 3, 3 (12): 10 (1912)] for *Arabis kawasakiana* prior to the original description. As the specimen collected by

M. Kawasaki in 1905 seems to be the only extant original material connected with this name (no original material was found in TI) and in the absence of evidence that any other original material existed at the time where the description was prepared, we formally designate this specimen as a lectotype. Three more sheets that were collected by M. Kawasaki in 1913 were found in the survey of the herbarium in MAK (MAK 118230, 116251 and 116298), but they were collected during the flowering season in 1913, apparently after Makino published the description in February 1913 and thus they have no standing as the original material of the name.

Japanese name: Tachi-suzushirosho

Distribution: Western Honshu (Tokai, Hokuriku, Kinki and Shikoku districts), Japan. The subspecies grows in sandy open habitats along seashores or the shore of Lake Biwa.

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References

Al-Shehbaz, I. A. & S. L. O’Kane (2002). Taxonomy

- and phylogeny of *Arabidopsis* (Brassicaceae). In: Somerville C.R. & E.M. Meyerowitz (eds.), *The Arabidopsis book*. American Society of Plant Biologists, Rockville, MD, doi/10.1199/tab.0001, <http://www.aspb.org/publications/arabidopsis/>.
- Alonso-Blanco, C. & M. Koornneef. 2000. Naturally occurring variation in *Arabidopsis*: an underexploited resource for plant genetics. *Trends Pl. Sci.* 5: 22-29.
- Ball, P. W. 1993. *Arabidopsis*. In: T. G. Tutin *et al.* (eds.) *Flora Europaea* 2nd ed. 1: 322-323. Cambridge Univ. Press, Cambridge.
- Berkutenko, A. N., S. I. Tzyltenok & S. V. Pulkina. 1984. Chromosome numbers and dispersal of the Brassicaceae family in the Magadan district. *Bot. Zhurn. (Moscow & Leningrad)* 69: 75-80. (in Russian)
- Busch, N. A. 1939. *Arabis* L. In: V. L. Komarov & N. A. Busch (eds.) *Flora of the U.S.S.R.* 8: 172-197. Publishing House of the Academy of Sciences of the U.S.S.R., Moscow & Leningrad. (in Russian)
- Bustamante, C. D., R. Nielsen, S. A. Sawyer, K. M. Olsen, M. D. Purugganan & D. L. Hartl. 2002. The cost of inbreeding in *Arabidopsis*. *Nature* 416: 531-534.
- Candolle, A. P., de 1821. *Regni vegetabilis systema naturale*. Vol. 2. Treuttel & Würtz, Paris.
- Dart, S., P. Kuron & B. K. Mable. 2004. Characterizing polyploidy in *Arabidopsis lyrata* using chromosome counts and flow cytometry. *Canad. J. Bot.* 82: 185-197.
- Greuter, W., J. McNeill, F. R. Barrie, H. M. Burdet, V. Demoulin, T. S. Filgueiras, D. H. Nicolson, P. C. Silva, J. E. Skog, P. Trehane, N. J. Turland & D. L. Hawksworth (eds.). 2000. International code of botanical nomenclature (Saint Louis Code) adopted by the Sixteenth International Botanical Congress, St. Louis, Missouri, July-August 1999. *Regnum Veg.* 138: 1-474.
- Hoffmann, M. H. 2005. Evolution of the realized climatic niche in the genus *Arabidopsis* (Brassicaceae) Evolution. (in press)
- Hopkins, M. 1937. *Arabis* in eastern and central North America. *Rhodora* 39: 63-98.
- Hultén, E. 1928. *Flora of Kamtchatka and the Adjacent Islands*. Vol. 2. Almqvist & Wiksells Boktryckeri A. B., Uppsala.
- . 1937. *Flora of the Aleutian Islands*. Thule, Stockholm.
- . 1968. *Flora of Alaska and Neighboring Territories*. Stanford University Press, Stanford.
- Hylander, N. 1957. *Cardaminopsis suecica* (Fr.) Hiit., a northern amphidiploid species. *Bull. Jard. Bot. État* 27: 591-604.
- Ihara, K. 1976. Mode of local differentiation in *Arabis lyrata* and *A. gemmifera* (Cruciferae) in Japan. *Journ. Fac. Sci. Univ. Tokyo, Section III, Botany* 12: 1-36.
- Kitagawa, M. 1982. *Cruciferae* (Brassicaceae). In: Satake, Y. *et al.* (eds.) *Wild Flowers of Japan, Herbaceous Plants* 2: 127-138. Heibonsha, Tokyo. (in Japanese)
- Kitamura, S. & G. Murata. 1961. *Colored Illustration of Herbaceous Plants in Japan II (Choripetalae)*. Hoikusha, Osaka. (in Japanese)
- & ———. 1962. New names and new conceptions adopted in our coloured illustrations of herbaceous plants of Japan II (Choripetalae). *Acta Phytotax. Geobot.* 20:195-208. (in Japanese)
- Koch, M., B. Haubold & T. Mitchell-Olds. 2000. Comparative evolutionary analysis of chalcone synthase and alcohol dehydrogenase loci in *Arabidopsis*, *Arabis*, and related genera. *Molec. Biol. Evol.* 17: 1483-1498.
- , ——— & ———. 2001. Molecular systematics of the Brassicaceae: evidence from coding plastidic matK and nuclear Chs sequences. *Amer. J. Bot.* 88: 534-544.
- Kumar, S., K. Tamura, I. B. Jakobsen & M. Nei. 2001. MEGA2: Molecular evolutionary genetics analysis software. *Bioinformatics* 17: 1244
- Lan, Y. Z. 1987. *Arabis* L. In: T. Y. Cheo (ed.) *Fl. Repub. Popul. Sinicae*. 33: 253-278. Science Press, Beijing. (in Chinese)
- Ledebour, C. F. 1815. *Decades sex plantarum novarum in imperio rossico indigenarum*. *Mem. Acad. Imp. Sci. St. Pétersbourg. Hist. Acad.* 5: 514-578.
- . 1841. *Flora Rossica*. Vol. 1. E. Schweizerbart, Stuttgart.
- Mable, M. B., J. Beland & C. D. Berardo. 2004. Inheritance and dominance of self-incompatibility alleles in polyploidy *Arabidopsis lyrata*. *Heredity* 93: 476-486.
- Macnair, M. R., V. Bert, S. B. Huitson, P. Saumitou-Laprade & D. Petit. 1999. Zinc tolerance and hyperaccumulation are genetically independent characters. *Proc. R. Soc. Lond. B* 266: 2175-2179.
- Madlung, A., R. W. Masuelli, B. Watson, S. H. Reynolds, J. Davison, & L. Comai. 2002. Remodeling of DNA

- methylation and phenotypic and transcriptional changes in synthetic *Arabidopsis* allotetraploids. *Pl. Physiol.* 129: 733-746.
- Makino, T. 1913. Observations on the flora of Japan. *Bot. Mag., Tokyo* 27: 21-30.
- Meyerowitz, E. M. 2002. Plants compared to animals: the broadest comparative study of development. *Science* 295: 1482-5.
- Mitchell-Olds, T. 2001. *Arabidopsis thaliana* and its wild relatives: a model system for ecology and evolution. *Trends Ecol. Evol.* 16: 693-700.
- Miyashita, N. T., A. Kawabe, H. Innan & R. Terauchi. 1998. Intra- and interspecific DNA variation and codon bias of the alcohol dehydrogenase (*Adh*) locus in *Arabis* and *Arabidopsis* species. *Molec. Biol. Evol.* 15: 1420-1429.
- Mulligan, G. A. 1964. Chromosome numbers of the family Cruciferae I. *Canad. J. Bot.* 42: 1509-1519.
- . 1995. Synopsis of the genus *Arabis* (Brassicaceae) in Canada, Alaska and Greenland. *Rhodora* 97: 109-163.
- O'Kane, S. L. & I. A. Al-Shehbaz. 1997. A synopsis of *Arabidopsis* (Brassicaceae). *Novon* 7: 323-327.
- Ohwi, J. 1953. Flora of Japan. Shibundo, Tokyo. (in Japanese)
- Ramos-Onsins, S. E., B. E. Stranger, T. Mitchell-Olds & M. Agaudé. 2004. Multilocus analysis of variation and speciation in the closely related species *Arabidopsis halleri* and *A. lyrata*. *Genetics* 166: 373-388.
- Rollins, R. C. 1993. The Cruciferae of continental North America. Stanford University Press, Stanford.
- Savolainen, O., C. H. Langley, B. P. Lazzaro & H. Fréville. 2000. Contrasting patterns of nucleotide polymorphism at the alcohol dehydrogenase locus in the outcrossing *Arabidopsis lyrata* and the selfing *Arabidopsis thaliana*. *Molec. Biol. Evol.* 17: 645-655.
- Schulz, O. E. 1936. *Cardaminopsis*. In: A. Engler & K. Prantl (eds.) Die Natürlichen Pflanzenfamilien 2nd ed. 17b: 541. Verlag von Wilhelm Engelmann, Leipzig. (in German)
- Shimizu, K. K. 2002. Ecology meets molecular genetics in *Arabidopsis*. *Popul. Ecol.* 44: 221-233.
- & M. D. Purugganan. 2005. Evolutionary and ecological genomics of *Arabidopsis*. *Plant Phys.* 138: 578-584.
- , J. M. Cork, A. L. Caicedo, C. A. Mays, R. C. Moore, K. M. Olsen, S. Ruzsa, G. Coop, C. D. Bustamante, P. Awadalla & M. D. Purugganan. 2004. Darwinian selection on a selfing locus. *Science* 306: 2081-2084.
- Weigel, D. & J. Glazebrook. 2002. *Arabidopsis: a laboratory manual*. Cold Spring Harbor Press, Cold Spring Harbor, New York.
- Wu, S. S., R. Wu, C.-X. Ma, Z.-B. Zeng, M. C. K. Yang & G. Casella. 2001. A multivalent pairing model of linkage analysis in autotetraploids. *Genetics* 159: 1339-1350.
- Zhukova, P. G. & V. V. Petrovsky. 1984. A cytotaxonomical study of some species of the family Brassicaceae in northern Asia. *Bot. Zhurn. (Moscow & Leningrad)* 62: 236-240. (in Russian)

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