Taxonomic study on infraspecific taxa of *Lespedeza maximowiczii* and hybrids with related species

Dong-Pil JIN, Jong-Won PARK and Byoung-Hee CHOI*

Department of Biological Sciences, Inha University, Incheon 22212, Korea

(Received 12 November 2019; Revised 14 December 2019; Accepted 25 December 2019)

ABSTRACT: Many infraspecific taxa within *Lespedeza maximowiczii* and hybrids with related species have been described, but taxonomic verification remains controversial. We examined the morphological traits of hybrids (*L. chiisanensis* and *L. patentibicolor*) and infraspecific taxa (var. *tomentella*, *elongata*, and *tricolor*) and analyzed their genetic structures using microsatellite loci. Flower and leaflet shapes in var. *tomentella* and *elongata* were within the range of variation of those in var. *maximowiczii*, and individuals in the two former varieties were grouped into var. *maximowiczii*. *Lespedeza maximowiczii* var. *tricolor* was similar to *L. buergeri* in terms of the structure and flower color, whereas the leaflet and bracteole shapes of var. *tricolor* were similar to those of var. *maximowiczii*. Based on the genetic structure ($K = 3$), var. *tricolor* had a mixed lineage with *L. maximowiczii* and *L. buergeri*. In addition, these formed a distinct lineage at $K = 5$. For two hybrids, the flower and leaflet structure in *L. chiisanensis* did not differ from those in *L. maximowiczii*, whereas the flowers of *L. patentibicolor* were within the range of variation of *L. bicolor*. In addition, *L. chiisanensis* and *L. patentibicolor* were assigned to *L. maximowiczii* and *L. bicolor*, respectively, based on the genetic structure. We treated var. *tomentella* and *elongata* as a forma, f. *friebeana*, because *L. friebeana* preceded var. *tomentella*, whereas var. *tricolor* was treated as a distinct species, *L. tricolor*. *Lespedeza chiisanensis* was recognized as a synonym of *L. maximowiczii*. *Lespedeza patentibicolor* was considered to be *L. bicolor*.

Keywords: Hybrid, infraspecific taxa, *Lespedeza maximowiczii*, morphological variation, microsatellites, taxonomic treatment

The genus *Lespedeza* Michx., which belongs to the family Fabaceae, includes approximately 44 species and is disjunctively distributed in Asia and North America (Ohashi and Nemoto, 2014). Within this genus, two subgenera [*Lespedeza* and *Macrolespedeza* (Maxim.) H. Ohashi] were recently circumscribed based on the morphology of seedlings and molecular data (Ohashi and Nemoto, 2014). The former grows in the eastern region of North America, whereas the latter is distributed from East Asia to India. In the subgenus *Macrolespedeza*, the section *Macrolespedeza* is composed of subshrub and shrub that bears only chasmogamous flowers, whereas the section *Junceae* (Maxim.) H. Ohashi & T. Nemoto is composed of herbs and subshrubs that bear both chasmogamous and cleistogamous flowers (Ohashi and Nemoto, 2014). The members of the section *Macrolespedeza*

are morphologically varied (Lee, 1965; Akiyama, 1988), which hinders the identification of some species. Many hybrids in the taxa of this section have been reported based on morphological evidence (Lee, 1965; Akiyama, 1988, 2004). Previous molecular phylogenies showed the signal for hybridization within this section (Xu et al., 2012, 2017), i.e., most species are not supported as monophyletic according to their taxonomic status.

Thirteen *Lespedeza* species have been recognized in Korea and six belong to the section *Macrolespedeza* (Choi, 2007). In this study, we focused on *L. maximowiczii* C. K. Schneid., which is in the section. Until recently, this species was known to be distributed in China, Korea, and Tsushima Island of Japan (Ohashi et al., 2009). However, the Chinese plant was separated into *L. pseudomaximowiczii* D. P. Jin, B. Xu & B.

*Author for correspondence: bhchoi@inha.ac.kr

H. Choi because of its distinct morphology and genetic features (Jin et al., 2018); thus, it is accepted that *L. maximowiczii* grows in Korea and a narrow area of Tsushima Island. Like other *Macrolespedeza* species, many infraspecific taxa of *L. maximowiczii* have been recorded, including var. *elongata* Nakai, var. *tomentella* Nakai, var. *tricolor* Nakai, and f. *albiflora* Uyeki (Nakai, 1927; Uyeki, 1941). The taxonomic ranks of these taxa have been argued by different researchers (Hatusima, 1967; Akiyama, 1988). For example, Hatusima (1967) treated *L. maximowiczii* as a subspecies [= subsp. *praecox* (Nakai) Hatusima] of closely related species, *L. buergeri* Miq., var. *tomentella*, and var. *tricolor* were simultaneously changed to the forma [= f. *tomentella* (Nakai) Hatusima] of subsp. *praecox* and other subspecies [= subsp. *tricolor* (Nakai) Hatusima], respectively. However, Akiyama (1988) treated var. *tomentella* as a synonym of *L. maximowiczii*. Furthermore, *L. maximowiczii* var. *elongata* and var. *tricolor* were thought to be synonyms of *L. maximowiczii* (Akiyama, 1988). Many hybrids related to *L. maximowiczii* have been recognized in Korea (Lee, 1965). In detail, the following hybrids were described: *L. angustifolioides* T. Lee (including *L. maximowiczii* var. *elongata* as its synonym) [*L. maximowiczii* × *L. japonica* L. H. Bailey var. *intermedia* (Nakai) Nakai], *L. chiisanensis* T. Lee (*L. maximowiczii* × *L. bicolor* Trucz.), *L. maritima* Nakai (*L. maximowiczii* × *L. cyrtobotrya* Miq.), *L. patentibicolor* T. Lee (*L. maximowiczii* var. *tomentella* × *L. bicolor*), and *L. patentielongata* T. Lee (*L. maximowiczii* var. *tomentella* × *L. japonica* var. *intermedia*). In Lee's subsequent study, he regarded *L. maximowiczii* var. *tomentella* as a hybrid species, i.e., *L. × tomentella* (Lee, 1980) [= *L. × friebeana* Schindl. in Lee and Lee (1975)], between *L. maximowiczii* and *L. japonica* var. *intermedia* [= *L. thunbergii* (DC.) Nakai subsp. *thunbergii* in Ohashi et al. (2009)]. Furthermore, two hybrids (*L. angustifolioides* and *L. patentielongata*) and *L. maximowiczii* var. *elongata* were circumscribed into *L. × friebeana* in that paper (Lee and Lee, 1975). In the case of *L. patentibicolor*, because one putative parent was treated as a hybrid (Lee and Lee, 1975), this species would be a hybrid between a species (*L. maximowiczii*) and a hybrid (*L. × friebeana*). Although Lee's studies improved our understanding of the Korean *Lespedeza* species (Lee, 1965; Lee and Lee, 1975), flowers have not been sufficiently examined despite their importance for identification (Akiyama, 1988). Genetic evidence regarding hybrids is also lacking. Therefore, resolving this complex taxonomic issue related to *L. maximowiczii* requires morphological and genetic analyses.

To verify hybridization, a putative hybrid needs to be examined by genetic evidence and morphological characters. Partial chloroplast DNA and nuclear ribosomal internal transcribed spacer (nrITS) data do not appropriately delimit the species (Xu et al., 2012, 2017), perhaps because of their frequent hybridization or incomplete lineage sorting. Thus, we applied microsatellite markers developed from *L. maritima* (Jin et al., 2016a) to these taxa. Microsatellite markers are codominant and highly polymorphic. Furthermore, they may cover multiple loci in the nuclear DNA (Duminil et al., 2012). Microsatellite markers show the hybridization and introgression between species, in genera such as *Quercus* L. (Lee et al., 2014; Castillo-Mendoza et al., 2019), *Ulmus* L. (Brunet et al., 2013), and *Populus* L. (Zeng et al., 2016). The genetic traits of *L. pseudomaximowiczii* were also revealed by the comparison with other *Lespedeza* species using microsatellite markers (Jin et al., 2018).

Here, our goals were to (1) examine the morphological characters of infraspecific taxa of *L. maximowiczii* and hybrids with related species, (2) investigate the genetic structure among taxa using microsatellite loci, and (3) discuss the taxonomic entities based on these results.

Materials and Methods

Morphological examination and survey of geographical distribution

To compare the morphological characters of typical *L. maximowiczii* with infraspecific taxa and hybrids, we collected specimens from the field sampling and deposited them in the Herbarium of Inha University (IUI). The sample information is detailed in Table 1. Additional morphological examination was conducted by observing specimens from the Korea National Arboretum (KH), College of Agriculture Life Sciences, Seoul National University (SNUA), Institute of Botany, Chinese Academy of Sciences (PE), and the Herbarium of University of Tokyo (TI). In particular, we observed T. B. Lee's collections to understand how he regarded hybrids in his previous studies (Lee, 1965), i.e., *L. chiisanensis*, *L. patentibicolor*, *L. angustifolioides*, and *L. patentielongata* (Fig. 1). Among these, the latter two were regarded as a hybrid of *L. maximowiczii* and *L. thunbergii* [*L. × friebeana* (= *L. × tomentella*)], including *L. maximowiczii* var. *elongata* (Lee and Lee, 1975). *L. angustifolioides*, *L. patentielongata*, and *L. maximowiczii* var. *elongata* were characterized by acuminate at both ends of the leaflet. The two formers were distinguished based only on the hairs on the inflorescence (appressed vs.

Table 1. Sampling information for *Lespedeza maximowiczii* and its related species in Korea that were used in this study.

Taxa	Code	Population locality	Coordinates	No. of samples
<i>Lespedeza maximowiczii</i> f. <i>maximowiczii</i> (조록싸리)	JR	Jirisan Mt., Namwon, Jeonbuk, Korea	35°17'N, 127°31'E	8
	SD	Deoksung Mt., Yesan, Chungnam, Korea	36°40'N, 126°37'E	8
<i>L. maximowiczii</i> var. <i>tomentella</i> (= f. <i>friebeana</i>) (털조록싸리)	CC	Cheomchalsan Mt., Uisin, Jindo, Jeonnam, Korea	34°28'N, 126°19'E	9
	DY	Hyangsan 7-gil, Danyang, Chungbuk, Korea	37°03'N, 128°26'E	1
	JR	Jirisan Mt., Namwon, Jeonbuk, Korea	35°17'N, 127°31'E	12
	SD	Deoksungdsn Mt., Yesan, Chungnam, Korea	36°40'N, 126°37'E	8
	JS	Jeoksangsan Mt., Muju, Cheonam, Korea	35°56'N, 127°41'E	22
<i>L. maximowiczii</i> var. <i>elongata</i> (= f. <i>friebeana</i>) (늑싸리)	JR	Jirisan Mt., Namwon, Jeonbuk, Korea	35°17'N, 127°31'E	3
	JS	Jeoksangsan Mt., Muju, Cheonam, Korea	35°56'N, 127°41'E	4
<i>L. maximowiczii</i> var. <i>tricolor</i> (= <i>L. tricolor</i>) (삼색싸리)	CC	Cheomchalsan Mt., Uisin, Jindo, Jeonnam, Korea	34°28'N, 126°19'E	10
<i>L. patentibicolor</i> (진도싸리)				12
<i>L. chiisanensis</i> (= <i>L. maximowiczii</i> f. <i>maximowiczii</i>) (지리산싸리)	JR	Jirisan Mt., Namwon, Jeonbuk, Korea	35°17'N, 127°31'E	2
<i>L. bicolor</i> (싸리)	DY	Hyangsan 7-gil, Danyang, Chungbuk, Korea	37°03'N, 128°26'E	7
<i>L. buergeri</i>	TB	Taibaisan Mt., Lushi, Henan, China	33°52'N, 111°19'E	14
	O	Kayagasan Mt., Hokuto, Yamanashi, Japan	35°47'N, 138°30'E	15
<i>L. thunbergii</i> subsp. <i>thunbergii</i> (풀싸리)	BS	Jangsangbongsan Mt., Busan, Korea	35°6'N, 129°6'E	5
	CC	Cheomchalsan Mt., Uisin, Jindo, Jeonnam, Korea	34°28'N, 126°19'E	8
	SD	Deoksungsan Mt., Yesan, Chungnam, Korea	36°40'N, 126°37'E	3

patent) (Lee, 1965). Thus, we considered them to be *L. maximowiczii* var. *elongata*. Additional specimen examination was conducted using the website of the Royal Botanical Garden Kew (K), Naturalis (L), and Global Biodiversity Information Facility (GBIF) dataset published by the T. B. Lee herbarium (Chang and Kim, 2019). We could not observe specimens of *L. maximowiczii* f. *albiflora*; therefore, this taxon was not included in this study. All observations of morphological characters were made with a stereomicroscope (Leica MZ8; Wetzlar, Germany), and floral features were measured following criteria that were stipulated by Akiyama (1988).

Sampling, DNA extraction, and the microsatellite polymerase chain reaction (PCR)

Leaves were sampled from the voucher specimens shown in Table 1 and preserved using silica gel. The dried leaves from *Lespedeza* species were used for genomic DNA extraction. We used an MG Plant Genomic DNA Extraction SV Miniprep Kit (MGmed, Seoul, Korea). Although we mostly followed the manufacturer's instructions, initial incubation and ice incubation times were extended to acquire sufficient DNA.

We used the following 11 microsatellite loci (Jin et al., 2016a): LMS3, LMS7, LMS11, LMS18, LMS28, LMS33, LMS39, LMS45, LMS47, LMS53, LMS55, LMS58, and LMS61. The PCR protocol utilized these markers with a GeneAmp PCR System 2700 Thermal Cycler (Applied Biosystems, Foster City, CA, USA). Each reaction mixture (10 µL total volume) contained 5 ng of DNA, plus 5 µL of 2× Plus Mix (Dongsheng Biotech, Guangdong, China) that comprised 0.4 mM dNTPs, 2× PCR buffer with 4 mM MgSO₄, and 0.4 U/µL of Taq DNA polymerase. The mixtures also contained the appropriate 0.08 µM forward M13 (-21)-tagged primer, a 0.3 µM reverse primer, and a 0.3 µM M13 (-21) labeled fluorescent marker (NED, PET, VIC, or 6-FAM). Conditions included initial denaturation at 94°C for 3 min, 30 cycles at 94°C for 30 s, 53°C for 30 s, and 72°C for 45 s, without a final extension. Afterward, the PCR products were visualized on 2% agarose gels and resolved to genotype on an ABI 3730XL sequencer with GeneScan 500 LIZ size standards (Applied Biosystems). This fragment analysis was performed by MacroGen, Inc. (Seoul, Korea). The sizes of the alleles were manually determined using the program GENEMAPPER 3.7 (Applied Biosystems).

Microsatellite data analyses

The fragment sizes of all loci were genotyped according to the individual. To determine the assignment pattern of the six taxa, Bayesian clustering was conducted using our genotypic data. This analysis was performed with STRUCTURE 2.3.4 (Pritchard et al., 2000), selecting the admixture ancestry and correlated allele frequency models. Ten iterations were run for each cluster ($K = 1$ to 20), with 30,000 burn-ins followed by 300,000 Markov chain Monte Carlo repetitions. The optimum K value was determined based on ΔK according to the number of clusters, which was estimated using STRUCTURE HARVESTER (Earl and von Holdt, 2012). The results from each run were generated to a representative stacked bar chart using the Clustering Markov Packager Across K (CLUMPAK) on the web (Kopelman et al., 2015) to summarize and generate representative pie charts associated with each K value. To represent the relationship among species, we reconstructed the neighbor-joining (NJ) tree based on Nei's genetic distances (D_A) (Nei et al., 1983). D_A between individuals was calculated with the POPULATIONS 1.2.32 (Langella, 2011).

Results

Morphological examination on infraspecific taxa of *L. maximowiczii* and hybrids with related species

We compared morphological characters to reconsider the taxonomic position of taxa related to *L. maximowiczii*. The measured values of the infraspecific taxa and hybrids are shown in Tables 2 and 3, respectively.

The results for the infraspecific taxa (Fig. 2, Table 2) showed that *L. maximowiczii* var. *tomentella* (8.9–[10.1]–11.2 mm) had slightly longer flowers than those of var. *elongata* (9.0–[9.6]–10.2 mm) and var. *maximowiczii* (8.2–[9.5]–10.9 mm). Flowers of var. *tricolor* (8.4–[9.0]–9.5 mm) were slightly shorter than those of var. *maximowiczii*, which were similar to those of *L. buergeri* (8.2–[9.0]–9.7 mm). The color of standard petals (purple) was almost identical among the infraspecific taxa, whereas var. *tricolor* had a pale-yellow standard petal with purple dots inside, which was similar to that of *L. buergeri*. The order of the length of petals [K (keel petal) $\approx$ S (standard petal) > W (wing petal)] was the same in var. *maximowiczii*

Table 2. Comparison of morphological traits of *Lespedeza maximowiczii* and its infraspecific taxa.

	<i>L. maximowiczii</i> var. <i>maximowiczii</i>	var. <i>tomentella</i> (= <i>f. friebeana</i>)	var. <i>elongata</i> (= <i>f. friebeana</i>)	var. <i>tricolor</i> (= <i>L. tricolor</i>)	<i>L. buergeri</i>
Hair on inflorescence	Adpressed to patent hair	Adpressed to patent hair	Adpressed to patent hair	Adpressed hair	Adpressed hair
Length of flower (mm)	8.2–(9.5)–10.9	8.9–(10.1)–11.2	9.0–(9.6)–10.2	8.4–(9.0)–9.5	8.2–(9.0)–9.7
Color of standard petal	Purple with denser purple dot inside	Purple with denser purple dot inside	Purple with denser purple dot inside	Pale yellow with purple dot inside	Pale yellow with purple dot inside
Length of standard petal (mm)	7.0–(8.5)–10.0	8.2–(9.3)–10.4	8.0–(8.9)–9.6	6.7–(7.6)–8.6	6.8–(7.6)–8.4
Length of standard petal claw (mm)	0.7–(1.1)–1.5	0.8–(1.2)–1.5	0.8–(1.1)–1.4	1.0–(1.2)–1.7	0.8–(1.0)–1.2
Length of wing petal (mm)	6.4–(7.5)–9.2	7.1–(8.6)–9.9	7.4–(8.3)–9.0	6.5–(7.4)–8.3	6.1–(7.6)–8.8
Length of wing petal claw (mm)	1.7–(2.4)–2.9	1.6–(2.4)–2.9	2.1–(2.5)–2.9	2.0–(2.5)–2.9	1.7–(2.2)–2.9
Length of wing petal lamina (mm)	4.5–(5.4)–6.7	4.8–(6.3)–7.3	5.0–(6.0)–6.8	4.5–(5.0)–5.6	4.6–(5.5)–5.6
Length of keel petal (mm)	7.8–(8.8)–9.8	8.8–(9.5)–10.7	8.2–(9.0)–9.7	8.3–(8.7)–9.0	8.0–(8.7)–9.5
Length of keel petal claw (mm)	2.0–(2.6)–3.3	2.4–(2.8)–3.3	2.3–(2.6)–2.8	2.1–(2.6)–2.9	2.1–(2.4)–2.7
Length of keel petal lamina (mm)	5.6–(6.3)–7.0	6.2–(6.9)–7.5	6.1–(6.6)–7.0	5.4–(6.1)–6.4	5.9–(6.3)–6.8
Length of calyx tube (mm)	1.2–(1.5)–2.1	1.4–(1.8)–2.2	1.2–(1.4)–1.6	1.3–(1.5)–1.6	1.3–(1.6)–2.1
Length of calyx lobe (mm)	1.5–(2.3)–3.5	1.8–(3.1)–4.1	2.5–(3.0)–3.2	0.7–(0.9)–1.1	0.6–(0.9)–1.1
Length of bracteoles (mm)	0.5–(1.1)–2.1	0.4–(1.0)–1.9	1.2–(1.5)–1.8	0.8–(1.1)–1.4	1.3–(1.6)–1.8
Width of bracteoles (mm)	0.2–(0.5)–1.0	0.2–(0.4)–0.6	0.3–(0.4)–0.6	0.6–(0.7)–0.8	0.6–(1.0)–1.3
Shape of leaflets at apex	Mostly acute to acuminate	Mostly acute to acuminate	Acuminate	Mostly acute to acuminate	Acute to obtuse
Density of hairs on upper surface of leaflet (number per 4 mm ²)	1–(8)–59	38–(51)–90	27–(54)–80	0–(0)–1	0–(0)–1

Note: The number in parenthesis indicates mean value.

Fig. 2. Comparison of floral characters of *Lespedeza maximowiczii* (including infraspecific taxa) and *L. buergeri*. A–C. *L. maximowiczii* var. *maximowiczii* (= f. *maximowiczii*). D–F. var. *tomentella* (= f. *friebeana*). G–I. var. *elongata* (= f. *friebeana*). J–L. var. *tricolor* (= *L. tricolor*). M–O. *L. buergeri*. A, D, G, J, M. flower. B, E, H, K, N. calyx. C, F, I, L, O bracteole.

(S, mean 8.5 mm; W, mean 7.5 mm; K, mean 8.8 mm), var. *tomentella* (S, mean 9.3 mm; W, mean 8.6 mm; K, mean 9.5 mm), and var. *elongata* (S, mean 8.9 mm; W, mean 8.3 mm; K, mean 9.0 mm). *L. maximowiczii* var. *tricolor* presented a different order ($K > W \approx S$), and this order was also observed in *L. buergeri*. Calyx lobes were longer than the calyx tube in var. *maximowiczii* (lobe, 1.2–[1.5]–2.1 mm; tube, 1.5–[2.3]–3.5 mm). *L. maximowiczii* var. *tomentella* and var. *elongata* also harbored longer calyx lobes (var. *tomentella*, 1.8–[3.1]–4.1 mm; var. *elongata*, 2.5–[3.0]–3.2 mm) than calyx tubes (var. *tomentella*, 1.4–[1.8]–2.2 mm; var. *elongata*, 1.2–[1.4]–1.6 mm). However, *L. maximowiczii* var. *tricolor* had shorter calyx lobes than calyx tubes (lobe, 0.7–[0.9]–1.1 mm; tube, 1.3–[1.5]–1.6 mm). The shape of the calyx lobes at the apex was acuminate for var. *maximowiczii*, var. *tomentella*, and var. *elongata*, whereas that of var. *tricolor* was acute, similar to that of *L. buergeri*. In all taxa, the ratio of claw to lamina in the wing and keel petals was 1:2–2.9. In the case of bracteoles, the infraspecific taxa of *L. maximowiczii*, except for var. *tricolor*, were ovate to elliptic; thus, the length was generally approximately two times longer than the width. Bracteoles of var. *tricolor* were also ovate, but the narrow form was not observed (width vs. length $\approx$ 1:1.7). Bracteoles of the Chinese *L. buergeri* generally were normal to broadly ovate, whereas those of Japanese individuals were almost round. Their ratio of width to length

was similar to that of *L. maximowiczii* var. *tricolor*. Regarding hairs, the upper surface of the leaflets of *L. maximowiczii* was almost glabrous (1–[8]–59 per 4 mm²), whereas var. *tomentella* had more appressed hairs on the surface of leaflets (38–[51]–90 per 4 mm²). *L. maximowiczii* var. *elongata* also showed a similar density as the former two (27–[54]–80 per 4 mm²), whereas *L. maximowiczii* var. *tricolor* harbored almost glabrous and light green colored leaflets, similar to those of *L. buergeri*.

Regarding the hybrids, *L. chiisanensis* and *L. maximowiczii* showed similar flower structures. Flowers of *L. patentibicolor* and *L. bicolor* were also similar in shape (Fig. 3, Table 3). For standard petal, *L. maximowiczii* and *L. chiisanensis* had a distinct claw, whereas *L. patentibicolor* and *L. bicolor* had no obvious claw, which gradually decreased from the middle to bottom (Fig. 3). Wing petals of *L. maximowiczii* (6.4–[7.5]–9.2 mm) and *L. chiisanensis* (7.4–[8.3]–9.0 mm) were shorter than their keel petals (*L. maximowiczii*, 7.8–[8.8]–9.8 mm; *L. chiisanensis*, 8.8–[9.5]–10.7 mm). Although *L. bicolor* had longer keel petals (8.6–[10.1]–11.2 mm) than wing petals (8.6–[9.5]–11.0 mm), the difference in their length (mean 0.6 mm) was smaller than that of *L. maximowiczii* (mean 1.3 mm) and *L. chiisanensis* (mean 1.2 mm). In the case of *L. patentibicolor*, wing petals (7.1–[8.3]–8.9 mm) were longer than the keel petals (6.4–[7.6]–8.5 mm). For the ratio of claw to lamina in wing and keel petals, *L. maximowiczii* and *L. chiisanensis* had lamina

Table 3. Comparison of morphological traits of typical *Lespedeza maximowiczii* and hybrids with related species.

	<i>L. maximowiczii</i>	<i>L. chiisanensis</i>	<i>L. patentibicolor</i>	<i>L. bicolor</i>
Length of flower (mm)	8.2–(9.5)–10.9	10.2–(11.1)–12.0	8.1–(9.4)–11.5	10.5–(11.7)–12.7
Length of standard petal (mm)	7.0–(8.5)–10.0	9.6–(10.0)–10.3	8.9–(9.2)–9.8	10.2–(11.3)–12.1
Length of standard petal claw (mm)	0.7–(1.1)–1.5	1.2–(1.5)–1.7	1.8–(2.0)–2.1	1.8–(2.0)–2.4
Width of standard petal (mm)	4.4–(5.6)–6.8	5.2–(5.8)–6.4	5.5–(5.6)–5.8	6.0–(7.7)–10.2
Claw of standard	Distinct	Distinct	No distinct	No distinct
Length of wing petal (mm)	6.4–(7.5)–9.2	7.4–(8.3)–9.0	7.1–(8.3)–8.9	8.6–(9.5)–11.0
Length of wing petal claw (mm)	1.7–(2.4)–2.9	2.4–(2.6)–3.0	2.5–(3.1)–3.8	3.2–(3.5)–3.7
Length of wing petal lamina (mm)	4.5–(5.4)–6.7	4.8–(5.8)–6.2	4.8–(5.3)–5.9	5.5–(6.1)–7.2
Length of keel petal (mm)	7.8–(8.8)–9.8	8.9–(10.3)–11.1	6.4–(7.6)–8.5	8.6–(10.1)–11.2
Length of keel petal claw (mm)	2.0–(2.6)–3.3	2.6–(2.9)–3.2	2.9–(3.3)–3.8	3.3–(3.7)–4.2
Length of keel petal lamina (mm)	5.6–(6.3)–7.0	6.5–(7.5)–8.1	3.7–(4.5)–5.7	6.5–(6.8)–7.2
Length of calyx tube (mm)	1.2–(1.5)–2.1	0.7–(2.1)–2.9	2.0–(2.3)–2.8	2.0–(2.2)–2.3
Length of calyx lobe (mm)	1.5–(2.3)–3.5	1.1–(2.1)–2.9	0.9–(1.2)–1.7	1.0–(1.4)–1.8
Shape of calyx lobe at apex	Mostly acuminate	Mostly acuminate	Mostly obtuse to round	Mostly obtuse to round
Shape of leaflets at apex	Mostly acute to acuminate	Acute to obtuse	Obtuse to emarginate	Obtuse to emarginate

Note: The number in parenthesis indicates mean value.

Fig. 3. Comparison of floral characters among hybrids suggested by Lee (1965, 1980) and parents. **A–C.** *L. bicolor*. **D–F.** *L. patentibicolor*. **G–I.** *L. chiisanensis* (= f. *maximowiczii*). **J–L.** *L. maximowiczii*. **A, D, G, J.** Standard petal. **B, E, H, K.** Ratio of length (wing petal vs. keel petal). **C, F, I, L.** Calyx.

that was approximately two times longer than the claw, but the lamina of *L. bicolor* and *L. patentibicolor* were not much longer than the claw. Calyx lobes diverged below the middle of the calyx in *L. maximowiczii* and *L. chiisanensis*, whereas the lobes of *L. bicolor* and *L. patentibicolor* did not. The shapes of the calyx lobes at their apex were also considerably different: acuminate to acute in *L. maximowiczii* and *L. chiisanensis* and obtuse to round in *L. bicolor* and *L. patentibicolor*.

Genotypic analyses of *Macrolespedeza* taxa concerning *L. maximowiczii*

Regarding the Bayesian clustering results performed by STRUCTURE, the optimum cluster number was determined to be three because the highest ΔK was at this value (Fig. 4). At $K = 3$ (Fig. 5), most of *L. bicolor*, *L. patentibicolor*, and *L. thunbergii* subsp. *thunbergii* were assigned to the same lineage (orange). The infraspecific taxa of *L.*

maximowiczii (except for var. *tricolor*) and *L. chiisanensis* were assigned into the same lineage (light blue). Most of *L. buergeri* were grouped into a distinct lineage (dark purple), although some individuals appeared to be closer to *L. maximowiczii*. In the case of *L. maximowiczii* var. *tricolor*, all individuals appeared to have mixed genetic features from other infraspecific taxa (var. *maximowiczii*, var. *tomentella*, and var. *elongata*) and *L. buergeri*. Since $K = 5$ (Fig. 5), *L. maximowiczii* var. *tricolor* was assigned to an independent lineage (purple).

The NJ tree was almost consisted of the Bayesian

clustering results (Fig. 6), despite this tree was weakly supported by low bootstrap value. Within clade A, *L. thunbergii*, *L. bicolor*, and *L. patentibicolor* were mainly clustered. The individuals of *L. buergeri* were included within clade B and C. In case of *L. chiisanensis*, this taxon was clustered with infraspecific taxa of *L. maximowiczii* (clade F and H).

Discussion

Taxonomic reconsideration of infraspecific taxa of *L. maximowiczii*

We examined the morphological traits of *L. maximowiczii* and its infraspecific taxa and analyzed their relationships using 11 microsatellite markers. Although morphological differences among *L. maximowiczii* var. *maximowiczii*, var. *tomentella*, and var. *elongata* were observed, the variation ranges mostly overlapped (Table 2). The width of leaflets showed a gradual change from narrow (represented as var. *elongata*) to wide (represented as var. *maximowiczii*). According to Nakai (1927), var. *elongata* is characterized by oblong or oblong-lanceolate leaflets that are acuminate at both ends. This leaflet form is also observed regardless of the presence of hair on the upper surface. *L. maximowiczii* var. *tomentella* bears hairs on the upper surface of leaflets, whereas the upper surface of the leaflet of var. *maximowiczii* becomes glabrous (Lee, 1965; Akiyama, 1988). Patent hair on inflorescences and branches

Fig. 4. ΔK statistics versus the number of clusters (K) calculated based on Bayesian clustering analysis using STRUCTURE.

Fig. 5. Results of Bayesian clustering for *Lespedeza maximowiczii* and other *Lespedeza* species. This analysis was conducted based on 11 microsatellite loci. Lineage assignments are the probability of individuals at $K = 3$, and 5. Population codes along the x-axis are identical to those in Table 1, after code of species name. Numbers along the y-axis indicate posterior probability of belonging to the cluster.

Korean Journal of Plant Taxonomy Vol. 49 No. 4 (2019)

of var. *tomentella* has been suggested to be a specific trait (Lee and Lee, 1975) and this taxon has even been inferred to be a hybrid between *L. maximowiczii* and *L. thunbergii* (Lee and Lee, 1975). When we examined the specimens (ca. 1,100) that are deposited in KH to determine this hypothesis, patent hairs on inflorescences and branches were observed regardless of the pubescent on the upper surface of the leaflets. Appressed hairs on inflorescences were even observed in individuals bearing pubescent leaflets. Thus, we concluded that these two morphological traits were not correlated. In the Bayesian clustering results (Fig. 5), nearly all individuals of *L. maximowiczii* var. *tomentella* shared the same genetic lineage as *L. maximowiczii* var. *maximowiczii*; however, var. *tomentella* did not share a genetic lineage with *L. thunbergii*. Thus, *L. maximowiczii* var. *tomentella* could not be considered a hybrid, as suggested by Lee and Lee (1975). This result of the genetic analysis also applied to *L. maximowiczii* var. *elongata* (Fig. 5). As previously mentioned, *L. maximowiczii* var. *elongata* has been treated as a synonym for *L. × friebeana* [= *L. × tomentella* in Lee (1980)] (Lee and Lee, 1975), including *L. angustifolioides* and *L. patentielongata* that were described as new hybrids in Lee (1965). We determined that *L. angustifolioides* and *L. patentielongata* were also not hybrids. However, *L. maximowiczii* var. *tomentella* was not morphologically different from var. *maximowiczii*, except for the hair on the upper surface of the leaflets (Fig. 2, Table 2). The pubescent form (var. *tomentella*) often grows with the glabrous form (var. *maximowiczii*) in the same place. Considering its resemblance with var. *maximowiczii* in both morphology and geographic distribution, var. *tomentella* should be ranked at the level of forma. However, the species epithet was changed because *L. friebeana* preceded *L. oldhamii* var. *tomentella* Nakai (= *L. maximowiczii* var. *tomentella*) (Lee and Lee, 1975). Both taxa were observed to bear villous leaflets. Therefore, we named the forma *L. maximowiczii* f. *friebeana* (Schindl.) D. P. Jin, J. W. Park & B. H. Choi.

However, *L. maximowiczii* var. *tricolor* is different from other infraspecific taxa in morphology. Its pale-yellow standard and keel petals appeared to be closer to *L. buergeri*. In the original description of this taxon (Nakai, 1923), the color of the keel petals was mentioned as rosy, but it is white or pale yellow in both field and herbarium specimens. In the order of the length of petals, *L. maximowiczii* var. *tricolor* ($K > W \approx S$) resembles that of *L. buergeri* ($K > W \approx S$) and some individuals even showed longer wing petals than

standard petals (Table 2). Although length of wing and standard petals were similar in some individuals of *L. maximowiczii*, no individuals were observed to bear wing petals longer than the standard petals. Calyx lobes at the apex for var. *tricolor* (acute) were within the variation of *L. buergeri* (acute to obtuse). However, bracteoles of var. *tricolor* appeared close to those of var. *maximowiczii* because these taxa do not have the round shape that is regarded as the synapomorphy of *L. buergeri* (Akiyama, 1988; Jin et al., 2016b). Taking into account the intermediate features of var. *tricolor* and the migration history, we suggest that *L. maximowiczii* var. *tricolor* originated from an ancient hybridization between *L. buergeri* and *L. maximowiczii* (Jin et al., 2016b). Genotypes of var. *tricolor* were of mixed lineage of var. *maximowiczii* and *L. buergeri* ($K = 3$) (Fig. 5). In addition, most individuals of var. *tricolor* were determined to have a lineage that was distinguished from var. *maximowiczii* and *L. buergeri* from $K = 5$, which was supported by the low ΔK (Figs. 4, 5). Therefore, we treated *L. maximowiczii* var. *tricolor* as a distinct species, *L. tricolor* (Nakai) D. P. Jin, J. W. Park & B. H. Choi.

Taxonomic reconsideration of hybrids between *L. maximowiczii* and its related taxa

Hybrids between *L. maximowiczii* and its related taxa were analyzed based on morphological and genetic traits. Although both *L. patentibicolor* (*L. maximowiczii* var. *tomentella* × *L. bicolor*) and *L. chiisanensis* (*L. maximowiczii* × *L. bicolor*) are related to *L. bicolor* (Lee, 1965, 1980), their external appearance varies greatly (Figs. 1, 3). The flower of *L. patentibicolor* was within the morphological variation of *L. bicolor*. In detail, the length of claws and lamina of wing and keel petals of *L. patentibicolor* were approximately equal, and standard petals had no distinct claw, as does *L. bicolor* (Akiyama, 1988). In particular, Lee (1965, 1980) described the calyx lobes of *L. patentibicolor* as an intermediate form between its putative parents. However, our observations were opposed to what Lee (1965, 1980) suggested. The inflorescence of *L. bicolor* is generally glabrous (Lee, 1965, 1980; Akiyama, 1988), whereas that of *L. patentibicolor* is covered with hairs (Lee, 1965, 1980). The morphotype of *L. patentibicolor* could be considered *L. bicolor* var. *sericea* Nakai (Nakai, 1927), which has been treated as a synonym or forma of *L. bicolor* by other researchers (Hatusima, 1967; Akiyama, 1988). *L. patentibicolor* could be also be regarded as *L. melanantha* Nakai, characterized by semicircular calyx lobes at the apex and wing petals longer than keel petals (Nakai, 1927; Akiyama, 1988). Although the shape of the calyx is different in both

taxa, the order of the petals in length is the same for both (Lee, 1978). In the case of *L. melanantha*, the width of the calyx lobes is longer than their length (Akiyama, 1988); however, morphological variation must be examined. In Bayesian clustering analysis (Fig. 5), most of *L. patentibicolor* were assigned to the same lineage as *L. bicolor*, but they did not share a genetic lineage with *L. maximowiczii* var. *tomentella*. On the NJ tree (Fig. 6), *L. patentibicolor* was clustered into a clade with *L. bicolor* and *L. thunbergii*, supporting the result of the Bayesian clustering analysis. Although the discussion regarding the relationship among infraspecific taxa of *L. bicolor* and taxonomic delimitation of *L. melanantha* is limited in this study, based on our data, we believe that *L. patentibicolor* is circumscribed into *L. bicolor*.

L. chiisanensis has acute to obtuse leaflets (or emarginate) at the apex and acuminate calyx lobes (Lee, 1965). Its inflorescence is thin, similar to that of *L. bicolor* (Lee, 1965). However, *L. chiisanensis* bears appressed hair, similar to that of *L. maximowiczii* (Lee, 1965). However, these characters were not well separated from *L. maximowiczii*. Although the inflorescence of some specimens was thin in the upper part, the lower part was not different from that of the common *L. maximowiczii*. The corolla of *L. chiisanensis* resembled that of *L. maximowiczii* rather than *L. bicolor* (Fig. 3, Table 3). Standard petal of *L. chiisanensis* showed definite claw and auricular shapes that were similar to those of *L. maximowiczii*. Acuminate calyx lobes appeared to be typical of *L. maximowiczii*. Additionally, the wing and keel petals were in the form of *L. maximowiczii*, i.e., the lamina was two times longer than the claw. In Bayesian clustering analysis (Fig. 5), the individuals, identified as *L. chiisanensis*, were grouped into *L. maximowiczii*. Hence, both morphological and genetic traits suggested that *L. chiisanensis* was within the variation of *L. maximowiczii*. When considering these facts, it is likely that this hybrid should be treated as a synonym of *L. maximowiczii*.

A key to *Lespedeza maximowiczii* and its related taxa

1. Standard and keel petal purple, standard longer than wing petal in length; calyx lobe acuminate and elongated at apex; leaflets glabrous or pubescent on upper surface, usually green to dark green. ... *Lespedeza maximowiczii*
1. Standard and keel petal pale yellow to white, standard slightly longer or the same as wing petal in length; calyx lobe acute to obtuse and not elongated at apex; leaflets glabrous on upper surface, usually green to light green.
 2. Bracteoles ovate to orbicular; leaflet apex usually acute to acuminate. *L. tricolor*

2. Bracteoles elliptic to ovate; leaflet apex usually obtuse to acute. *L. buergeri*

Taxonomic Treatment

Lespedeza maximowiczii C. K. Schneid., Ill. Handb. Laubholz. 2: 113, f. 70–71, 1907.—TYPE: Korea. Gangwon-do: Wonsan-si, Aug 1901, *Faurie 51* (holotype, A, seen as photo!).

L. buergeri Miq. var. *praecox* Nakai, Bot. Mag. Tokyo 25: 55, 1911; *L. praecox* (Nakai) Nakai ex Koidz., Bot. Mag. Tokyo 39: 24, 1925; *L. buergeri* Miq. subsp. *praecox* (Nakai) Hatus., Mem. Fac. Agr. Kagoshima Univ. 6: 6, 1967.

L. densiflora Uyeki, Bull. Nat. Hist. Soc. Corea 20: 17, 1935.

L. chiisanensis T. Lee, Bull. Seoul Nat. Univ. For. no. 2: 11, 1965. syn. nov.—TYPE: Korea. Jeollanam-do: Gurye-gun, Jirisan Mt., from Manbokdae to Nogodan, 10 Aug 1964, T. Lee et al. s.n. (lectotype, designated here, SNUA, see Fig. 1A).

A key to the forma of *Lespedeza maximowiczii*

1. Leaflet upper surface pubescent during fruiting season, sparsely hairy during flowering season. f. *maximowiczii*
1. Leaflet upper surface glabrous during fruiting season, densely hairy during flowering season. f. *friebeana*

f. *maximowiczii*

Korean name: Jo-rok-ssa-ri (조록싸리).

Shrub, erect, up to 2.5 m tall, much branched at upper part. Bark brown to grayish-brown, clefted when old. Branches terete, glabrous, reddish brown to brown, stretched slightly in zigzag pattern; young branches with appressed or patent hairs. Stipules linear triangular to linear, brown, 2–3 mm long. Leaves (based on upper branches) trifoliate, petiolate, stipulate, usually larger at lower part of plant; petioles 9–25 mm long, with sparse to dense appressed to patent hairs; rachises 5.5–15.5 mm long, with sparse to dense appressed or patent hairs; terminal leaflets green to dark green, petiolulate; petiolules ca. 2 mm long, swollen, appressed to patent hair; lamina 3–6 cm long, 1–4 cm wide, elliptic to broad ovate, entire, acute to acuminate (to obtuse) at apex, rounded or obtuse (to acuminate) at base, upper surface with sparsely appressed hairs during flowering season, becoming glabrous during fruiting, lower surface with more densely appressed hairs; lateral leaflets slightly smaller than terminal. Inflorescence axillary pseudo-raceme, usually one (rarely two or three) per leaf, similar length with subtending leaf, 3–7 cm long, 12–18 (to 32) flowered, with appressed to

patent hair. Flowers 8–11 mm long, purple to reddish purple. Bracteoles at base of calyx, ovate to oblong-ovate, pubescent, ca. 1 mm long. Calyx 2.7–6.3 mm long, campanulate, pubescent, four-lobed below middle part; lobes subequal in length, acuminate at apex, usually elongated; lower lobe longest in length; lateral ones ovate, 1.5–3.5 mm long, shortest in length; upper one broad ovate with two clefts at middle part. Standard petal similar with keel petal in length, longer than wing petal; standard petal 7.0–10.5 mm long, 4.4–6.9 mm wide, with auricles, purple to reddish purple; lamina elliptic to obovate, slightly emarginate at apex, deep purple dot inside, paler outside; auricle well developed; claw 0.7–1.5 mm long; wing petal 6.4–9.9 mm long, 1.3–2.7 mm wide, auriculate, deep or reddish purple; lamina oblong or elliptic, 4.5–7.3 mm long, deep or reddish purple, with auricle at base; claw 1.6–2.9 mm long, white; keel petal 7.5–10.7 mm long, 2.2–3.7 mm wide; lamina slightly falcate, reddish or light purple, 5.6–7.5 mm long; claw 2.0–3.3 mm long, white. Stamens 10, similar to keel petal in length, diadelphous (9 + 1), white; filaments equal length; anthers elliptic, retuse at both sides, ca. 0.4 mm long, ca. 0.2 mm width, yellow. Pistil same length as stamen, with appressed hairs from base to middle; style elongated above anthers; ovary narrow elliptic during flowering season, hairy. Legume slightly distorted elliptic, compressed, stalked, subsessile, ca. 13 mm long, ca. 5 mm wide, pilose, elongated spine-tip. Seed reniform, ca. 5 mm long, ca. 3 mm wide, glabrous.

Flowering: (May–) June–July (–August).

Fruiting: September–October.

Distribution: Korea (all provinces), and Japan (north area of Tsushima Isl.).

Taxonomic note: *Lespedeza maximowiczii* (sect. *Heterolespedeza* Nakai) is distinguished by buds (flatted and alternatively arranged scales) from sect. *Macrolespedeza* Maxim. sens. str. (Ohashi et al., 2009). This species is woodier than other sect. *Macrolespedeza* species. Sometimes *L. thunbergii* subsp. *thunbergii* is erroneously identified as *L. maximowiczii* because of its acute leaflet apex and acuminate calyx lobe, but flower length is usually longer in the former (ca. 13 mm) than the latter (ca. 10 mm). *L. buergeri* resembles *L. maximowiczii* in bud and arrangement of leaves, but differs in the petals (pale yellow), and in length of petal ($K > S \approx W$). In 1942, *L. maximowiczii* f. *albiflora* was recorded based on a specimen collected from Nangok (North Korea, Gangwon-do) by Uyeki. This form was characterized by a white corolla. However, herbarium specimens identified as this forma in KH and SNUA are *L. tricolor* or *L. maximowiczii*. We observed no individual which bore a white corolla in the field.

Representative specimens examined: KOREA. Busan-si: Nam-gu, Igidae, 4 Sep 2015, *D. P. Jin & W. B. Cho* 159169, 159176 (IUI). Chungcheongbuk-do: Danyang-gun, Sobaeksan Mt., 28 Jun 2016, *D. P. Jin* DP166309–166312 (IUI). Chungcheongnam-do: Yesan-gun, Deoksungsan Mt., 9 Sep 2016, *D. P. Jin* DP169004, DP16007, DP169017 (IUI). Gangwon-do: Jeongseon-gun, Buk-myeon, Nochusan Mt., 27 Jun 2007, *J. O. Hyun et al.* NAPI-0205 (KH); Hwacheon-gun, Gwangdoegsan Mt., 21 Jun 2004, *E. H. Jung & H. K. Moon* K0721-057 (KH); Wonju-si, Chiaksan Mt., 27 Jun 2016, *D. P. Jin* DP166201, DP166204, DP166216 (IUI). Gyeonggi-do: Anyang-si, Manan-gu, Surisan Mt., 4 Jul 2007, *S. C. Ko et al.* HNHM-A-0788 (KH); Gapyeong-gun, Buk-myeon, Myoungjisan Mt., 20 Jun 2012, *W. K. Paik* PWK-2013-291 (KH); Dongducheon-si, Sangbongam-dong, Soyosan Mt., 20 Jul 2012, *W. K. Paik* PWK-2013-097 (KH); Namyangju-si, Hwado-eup, Cheonmasan Mt., 20 Jun 2016, *D. P. Jin* DP166101–166140 (IUI); Paju-si, Yeongjang-ri, Temple Bogwangsa, 31 May 1998, *Y. M. Lee & D. H. Kim* S-1349 (KH); Pocheon-si, Jikdong-ri, Korean national arboretum, *S. H. Park* ParkSH51431 (KH). Gyeongsangbuk-do: Yeongju-si, Murya-myeon, Seondalsan Mt., 8 Jul 2006, *B. O. Oh et al.* CBU-070571 (KH). Gyeongsangnam-do: Geoje-si, Gaemyeong-ri, 24 Jul 2013, *D. C. Son & B. K. Park* HNHM-S-130288 (KH); Geoje-si, Mangsan Mt., 3 Sep 2015, *D. P. Jin & W. B. Cho* 159033, 159036, 159040, 159066 (IUI); Miryang-si, Danjang-myeon, way to Temple Pyochungsa, 30 May 2007, *H. J. Choi et al.* ChoiHJ 70121 (KH); Namhae-gun, Samdong-myeon, Nogu, 18 Oct 2007, *H. J. Choi et al.* ChoiHJ 70465 (KH); Namhae-gun, Gamabong Mt., 20 Jun 2015, *D. P. Jin* DP156001, DP156009, DP156013 (IUI); Sancheong-gun, Jungsan-ri, Jirisan Mt., 21 Jul 2012, *H. J. Choi* 120721-hjchoi023 (KH); Sancheong-gun, Samjang-myeon, Wangdeungjae wetland, 30 Jun 2004, *J. M. Jeong* 04060222 (KH). Jeollabuk-do: Namwon-si, Deokdong-ri, 10 Oct 2004, *C. Y. Yoon s.n.* (KH); Jinan-gun, Jinan-eup, Jinan technical high school to Temple Gorimsa, 14 Oct 2005, *Y. M. Lee & G. H. Nam* LYM & NGH 50279 (KH); Namwon-si, Jirisan Mt., Manbokdae, 14 Aug 2016 *D. P. Jin* DP168206, DP168217, DP168233 (IUI). Jeollanam-do: Boseong-gun, Hoechun-myeon, Illimsan Mt., 30 Aug 2019, *D. P. Jin* 198429 (IUI); Haenam-gun, Seoheung-ri, Dalmasan Mt., 8 Aug 2005, *H. J. Choi* CHJ 50140 (KH); Jangheung-gun, Anyang-myeon, Jangjaedo Isl., 5 Jul 2006, *Y. H. Cho et al.* WR-060705-058 (KH). Seoul-si: Dobong-gu, Dobongsan Mt., 6 Jun 2005, *S. H. Park* Park SH51399 (KH); Achaasan Mt., Seongdong-gu, 23 Jul 2006, *E. S. Jeon* ESJeon60915 (KH).

f. *friebeana* (Schindl.) D. P. Jin, J. W. Park & B. H. Choi, comb. & stat. nov.; *L. friebeana* Schindl., Repert. Sp. Nov. Regni Veg. 9: 514, 1911; T. Lee et M. Lee, Seoul Natl. Univ. Fac. Pap. Vol. 4: 3, 1975, *pro parte* (as *L. × friebeana*).—TYPE: KOREA. Busan-si: 1859, *C. Wilford s.n.* (holotype, K, seen as photo!).

L. buergeri var. *typica* Nakai, Chosen Shokubutsu I: 260, 1914.

L. oldhamii Miq. var. *tomentella* Nakai, Bot. Mag. Tokyo 33: 203, 1919; *L. maximowiczii* C. K. Schneid. var. *tomentella* (Nakai) Nakai, Lesp. Jap. Korea, 39, 1927; *L. buergeri* Miq. subsp. *praecox* (Nakai) Hatus. f. *tomentella* (Nakai) Hatus., Mem. Fac. Agr. Kagoshima Univ. 6: 6, 1967.—TYPE: KOREA. Jeollanam-do: Wando-gun, 20 Jun 1913, *Nakai 592* (lectotype of *L. oldhamii* Miq. var. *tomentella* Nakai, TI, seen as photo!).

L. maximowiczii C.K. Schneid. var. *elongata* Nakai, Lesp. Jap. Korea: 40, 1927.—TYPE: KOREA. Gyeongsangnam-do: Deoksan, Aug 1912, *T. Mori 183* (holotype, TI, seen as photo!).

L. angustifolioides T. B. Lee, Bull. Seoul Nat. Univ. For. no. 2: 3, 1965. *pro parte, quoad specim.* Tanyang (= Danyang-gun), Jecheon (= Jecheon-gun), Yeunkok (= Yeongok, Jirisan Mt., Gurye-gun).—TYPE: KOREA. Chungcheongbuk-do: Danyang-gun, 21 Jun 1964, *T. Lee s.n.* (lectotype, designed here, SNUA, see Fig. 1C).

L. patentielongata T. B. Lee, Bull. Seoul Nat. Univ. For. no. 2: 26, 1965. *excl. specim.* Temple Soodeuk (= Temple Sudeoksa, Yesan-gun).—TYPE: KOREA. Jeollanam-do: Gurye-gun, Pia valley, around Yeongok, 23 Jul 1963, *T. Lee s.n.* (holotype, SNUA!; isotype, SNUA!, see Fig. 1D).

Korean name: Teol-jo-rok-ssa-ri (털조록싸리).

This form bears adpressed hairs on the surface of leaflets until the fruiting period.

Taxonomic note: During the flowering period, this taxon is hardly distinguished from *f. maximowiczii* because the latter could also bear adpressed hair on the upper surface of leaflets during that time. However, the upper surface of leaflets in *f. friebeana* is generally more pubescent than *f. maximowiczii* (>51 hairs per 2 mm²) (Table 2). Except for hairs on upper surface of leaflets, the morphological characters of *f. friebeana* are included in the variation of *f. maximowiczii*. Lee mentioned that patent hair on the inflorescence is an important key to identify this taxon when considering Schindler's description (Lee 1965; Lee and Lee 1975). The patent hair on the inflorescence is usually observed in *f. friebeana*, but this character is sometimes observed in *f. maximowiczii*. Therefore, caution is required, when this forma is identified based on this

character.

This form has been known as *tomentella* since Nakai named it as *L. oldhamii* Miq. var. *tomentella* Nakai (Nakai, 1919). Although he mentioned *L. tomentella* Nakai based on the hairs of leaflets in his previous study (1914), he stopped publishing *L. tomentella*. This was because he knew *L. friebeana* before the publication of *L. tomentella* (Nakai, 1914). *Lespedeza friebeana* was described based on Wilford's collection (Schindler, 1911), which bears sparse hairs on the upper surface of leaflets. The hairs of the form are not different from those of *L. maximowiczii* var. *tomentella* (including *L. oldhamii* var. *tomentella*) (Nakai, 1919, 1927), and this was written in the original description. In addition, *L. friebeana* (Schindler, 1911) predate *L. oldhamii* var. *tomentella* (Nakai, 1919). The history of the species epithet was according to Lee and Lee (1975). Hence, we chose *f. friebeana* as the epithet of the form that bears sparse hairs on the upper surface of leaflets.

Representative specimens examined: KOREA. Chungcheongbuk-do: Danyang-gun, Daegang-myeon, Sobaeksan Mt., Jungnyeong → Yeonhwabong 1, 28 Jun 2016, *D. P. Jin DP166314, DP166317, DP166320* (IUI); Jincheon-gun, Baekgok-myeon, Yangbaek-ri, Baetiseongji, 5 Oct 2008, *S. H. Park & J. C. Yang ParkSH83007* (KH); Yeongdong-gun, Sangchon-myeon, Minujisan Mt., Temple Hwangnyongsa → top, 8 Sep 2009, *Y. J. Chung & J. C. Ahn SGU 1549* (KH). Chungcheongnam-do: Cheongyang-gun, Daechi-myeon, Janggok 1 bridge, 29 Aug 2009, *E. S. Jeon ESJeon90896* (KH); Geumsan-gun, Nami-myeon, Baegamsan Mt., Nami Natural Recreation Forest → Peak Sunyabong, 24 Aug 2008, *H. S. Lee HNU2243* (KH); Gongju-si, Banpo-myeon, Oncheon-ri, Gapasan Mt., 4 Oct 2008, *J. I. Jeon & H. S. Lee JEON12618* (KH); Nonsan-si, Sangwol-myeon, Yanghwa-ri, Gyeryongsan Mt., Temple Sinwon → Peak Yeoncheonbong, 2 Sep 2008, *H. S. Lee HNU2315* (KH); Yesan-gun, Deoksungsan Mt., 9 Sep 2016, *D.P. Jin DP169013–166315* (IUI). Gangwon-do: Donghae-si, Samhwa-dong, 9 Oct 2011, *K. S. Lee et al. 534* (KH); Gangneung-si, Yeongok-myeon, Samsan-ri, Odaesan Mt., 5 Jul 1989, *B. H. Choi IUI 18284* (KH); Hwacheon-gun, Yonghwasan Mt., 26 Sep 2010, *B. O. Oh 100926-002* (KH); Jeongseon-gun, Yeoryang-myeon, Goyangsan Mt., 25 Jun 2010, *J. H. Choi et al. K0601018* (KH); Pyeongchang-gun, Yongpyeong-myeon, Gyeongbongsan Mt., 4 Jul 2000, *B. H. Choi et al. IUI 37168* (KH); Yeongwol-gun, Sangdong-eup, Naedeok-ri, Jangsan Mt., 13 Oct 2010, *J. C. Yang et al. C101474* (KH); Wonju-si, Chiaksan Mt., 27 Jun 2016, *D. P. Jin DP166220–166225* (IUI). Gyeonggi-do: Pocheon-si, Idong-myeon, Yeongbuk-ri, Baegunsan Mt., 1 Jul 2008, *D. H. Lee Lee-80701012* (KH). Gyeongsangbuk-do: Cheongsong-gun,

Andeok-myeon, Munggeo-ri, 20 Jun 2010, *H. T. Shin et al.* 1450–1453 (KH); Gyeongju-si, Danseoksan Mt., 10 Oct 2006, *S. C. Go s.n.* (KH); Bonghwa-gun, Chunyang-myeon, Guryongsan Mt., 28 Jun 2008, *J. O. Hyun et al.*, 801028, 803010 (KH); Uljin-gun, Tonggosan Mt., 27 Aug 2014, *D. P. Jin* DP1408801, DP1408805, DP1408814, DP1408827, DP1408829 (IUI); Yeongcheon-si, Hwasan Mt., 3 Jun 2006, *C. Y. Yoon* Yoon 555 (KH); Yeongdeok-gun, Byeonggok-myeon, Chilbosan Mt., Temple Yugeumsa, 10 Jun 2006, *G. Y. Jeong* Jeong 558 (KH). Gyeongsangnam-do: Goseong-gun, Hail-myeon, Jwaisan Mt., 12 Sep 2009, *K. H. Tae* 2009-0754 (KH); Changnyeong-gun, Changnyeong-eup, Hwawangsan Mt., 17 Aug. 2009, *S. C. Ko* S. C. Ko 908040 (KH); Haman-gun, Yeohang-myeon, Yeohangsan Mt., 26 Sep 2009, *J. I. Jeon* JEON13147 (KH); Hapcheon-gun, Gayasan Mt., Baegundae, 15 Jun 2010, *D. H. Lee* D. H. Lee106334 (KH); Miryang-si, Danjang-myeon, Jaeyaksan Mt., 10 Oct 2009, *S. C. Ko* S. C. Ko 910031 (KH); Yangsan-si, Cheonseongsan Mt., Hwaemneup swamp, 21 Aug 2008, *S. H. Park & J. C. Yang* ParkSH81176 (KH). Gwangju-si: Eodeungsan Mt., Seobong-dong, Gwangsan-gu, 12 Oct 2010, *D. O. Lim & E. K. Che* Kar LIM2610 (KH). Incheon-si: Michuhol-gu, Munhaksan Mt., 13 Jul 2016, *J.S. Park & J.W. Park* 167001–167002 (IUI); Ongjin-gun, Deokjeokdo Isl., Guksubongsan Mt., 13 Jul 2010, *J. H. Lee & I. S. Choi* J. H. Lee 107107 (KH). Jeollabuk-do: Namwon-si, Jirisan Mt., Manbokdae, 14 Aug 2016 *D. P. Jin* DP168221, DP168239 (IUI); Muju-gun, Jeoksangsang Mt., 22 Jun 2012, *D. P. Jin* DP1206015, DP1206019, DP1206046, DP1206047, DP1206065, DP1206008, DP1206011, DP1206016, DP1206020, DP1206042 (IUI); Jangsu-gun, Jangsu-eup, Deoksan-ri, Jangansan Mt., 19 Jul 2008, *J. I. Jeon et al.* JEON12372 (KH); Jangsu-gun, Jangsu-eup, Palgongsan Mt., 28 Aug 2008, *H. I. Lim & H. K. Kim* LHI499 (KH); Jinan-gun, Jinan-eup, Gunsang-ri, Bugwisan Mt., 6 Sep 2019, *D. P. Jin* 199004, 199016, 199021 (IUI); Wanju-gun, Unju-myeon, Sanbuk-ri, Cheondeungsan Mt., 3 Oct 2008, *H. I. Lim* LHI1734 (KH). Jeollanam-do: Boseong-gun, Nodong-myeon, Hakdong-ri, near Yeje tunnel, 9 Sep 2009, *Y. H. Cho et al.* WR-090909-024 (KH); Hwasun-gun, Dongbok-myeon, Yucheon-ri, Yucheonjeosuji, 23 Sep 2009, *Y. H. Cho et al.* WR-090909-025 (KH); Jangseong-gun, Bugi-myeon, Ibamsan Mt., 30 May 2008, *K. H. Kim* IUI 46679 (KH); Jindo-gun, Cheomchalsan Mt., 12 Aug 2016, *D. P. Jin* DP168101 (IUI); Muan-gun, Seungdalsan Mt., 29 Aug 2019, *D. P. Jin* 198401 (IUI); Mokpo-si, Dal-dong, Dallido Isl., 16 Sep 2010, *Y. H. Cho et al.* YI01233 (KH); Sinan-gun, Songgong-ri, Aphaedo Isl., Songgongsan Mt., 17 Jun 2010, *Y. H. Cho et al.* YI00430 (KH); Suncheon-si, Songgwang-myeon, Sinheung-ri, Jogyesan Mt.,

24 Jun 2009, *Y. H. Cho et al.* WR-090624-020 (KH). JAPAN. Nagasaki Pref.: Tsushima Isl., Waniura, 25 Jul 2012, *J. Y. Lee & I. S. Choi* TS003 (IUI).

L. tricolor (Nakai) D. P. Jin, J. W. Park & B. H. Choi, stat. nov. (Fig. 7); *L. oldhamii* Miq. var. *tricolor* Nakai, Bot. Mag. Tokyo 37: 78, 1923; *L. maximowiczii* Schneid. var. *tricolor* (Nakai) Nakai, Lesp. Jap. Korea: 40, 1927; *L. buergeri* Miq. subsp. *tricolor* (Nakai) Hatus., Mem. Fac. Agr. Kagoshima Univ. 6: 6, 1967.—TYPE: KOREA. Jeollanam-do: Wando-gun, 20 Jun 1913, *Nakai* 600 (lectotype, TI, seen as photo!; isolectotype, TI, seen as photo!).

Korean name: Sam-saek-ssa-ri (삼색싸리).

Shrub, erect, 1–2 m tall, much branched at the upper part. Bark light brown to gray, vertically clefted when old. Branch terete, glabrous, light brown to brown, sometimes stretched in a zigzag pattern; young branches with appressed hairs. Stipules linear triangular to linear, brown, 2–3 mm long. Leaves trifoliate, petiolate, stipulate, usually bigger at lower part of plant; petioles 9–30 mm long, with appressed hairs; rachises 9–20 mm long, similar to petioles; terminal leaflets green, petiolulate; petiolules ca. 2 mm long, swollen, with densely appressed hair; lamina 3–7 cm long, 2–4 cm wide, elliptic to ovate, entire, acute to acuminate (to obtuse) at apex, rounded or obtuse (to acute) at base, upper surface glabrous, lower surface pubescent; lateral leaflets similar to terminal ones but relatively smaller in size. Inflorescence axillary pseudo-raceme, usually one (rarely two or three) per leaf, 2.6–8 cm long, similar or longer than subtending leaf, 18–38 flowered, with appressed to somewhat patent hairs. Bracts ovate to narrowly triangular, ca. 1 mm long. Flowers 8.4–9.6 mm long, pale yellow and purple mixed; pedicel 1–2 mm long, with appressed to somewhat patent hairs. Bracteoles at base of calyx, ovate to elliptic, pubescent at outside, ca. 1 mm long. Calyx 2.1–2.7 mm long, campanulate, pubescent, four-lobed until middle part; lobes subequal in length, similar to tube in length, acute at apex (not elongated like *L. maximowiczii*); lateral ones ovate, shortest in length, 0.7–1.1 mm long; upper ones broad ovate, slightly two-clefted. Keel petal longest among petals in length, standard longer or equal to wing; standard 6.7–8.6 mm long, 3.9–5.1 mm wide, with auricles; lamina oblong to obovate, slightly emarginate at apex, purple or reddish purple dot inside, pale yellow outside; auricle well developed, pale yellow; claw 1.0–1.7 mm long, pale yellow; wing petal 6.5–8.3 mm long, 1.6–1.8 mm wide, auriculate, purple and reddish purple at base; lamina oblong to elliptic, 4.8–5.6 mm long, auricle at base; claw 2.5–2.8 mm long; keel petal 8.3–9.0 mm long, 2.1–

Fig. 7. *Lespedeza tricolor* (Nakai) D. P. Jin, J. W. Park & B. H. Choi. **A.** Habit. **B.** Bark. **C.** Bud. **D.** Branch and leaves. **E.** Flower (front). **F.** Flower (side). **G.** Fruit.

2.8 mm wide, pale yellow to white (similar or paler than standard petal); lamina 5.4–6.4 mm long, slightly falcate, obtuse at apex, sometimes purple dotted at apex; claw 2.2–2.9 mm long. Stamens 10, similar to keel petal in length, diadelphous (9 + 1), white; filaments equal in length; anthers elliptic, retuse at both sides, ca. 0.4 mm long, ca. 0.2 mm wide, yellow. Pistil as long as stamen, with appressed hairs from base to middle, glabrous at apex; style elongated above anther; ovary narrow elliptic during flowering season, hairy. Legume slightly distorted elliptic, compressed, sessile, ca. 13 mm long, ca. 5 mm wide, pilose, elongated spine-tip. Seed reniform, ca. 5 mm long, ca. 3 mm wide, glabrous.

Flowering: July–August.

Fruiting: September–October.

Distribution: Restricted to Korea (south-western regions of Jeollanam-do). Endemic.

Taxonomic note: This species resembles *L. buergeri* in color of flowers, order of petal length, shape of calyx, and glabrous

upper surface of leaflets. However, the bracteole of each taxon is different. *L. tricolor* bears an ovate to elliptic form, whereas *L. buergeri* bears a round to elliptic form. In addition, bracteoles of *L. buergeri* could almost cover the calyx tube. Apex of leaflets of *L. tricolor* are generally acute to acuminate, but that of *L. buergeri* are usually obtuse to acute. Nakai (1923, 1927) and other researchers (Lee, 1965; Akiyama, 1988) mentioned that *L. tricolor* bears rosy keel petals, but our examination found that the color of keel petals was similar or paler than that of standard petal. On the other hand, *L. maximowiczii* has a purple standard petal, acute to acuminate leaflet apex, and elliptic bracteoles. Although *L. maximowiczii* is distinct from *L. tricolor* in the color of standard petal, the former is similar to the latter in shape of leaflets and bracteoles. Regarding genetic structure, *L. tricolor* harbors a mixed genetic lineage between *L. buergeri* and *L. maximowiczii* ($K = 3$) (Fig. 5), even *L. tricolor* shows an independent lineage from the latter two ($K = 5$) (Fig. 5). In a previous study (Jin et al.,

2016b), *L. tricolor* was originated from *L. buergeri* that had migrated from Japan, which experienced gene flow with *L. maximowiczii* in Korea during the Quaternary. Therefore, we considered *L. tricolor* as a distinct species from *L. maximowiczii* and *L. buergeri*.

Representative specimens examined: KOREA. Jeollanam-do: Jindo-gun, Galdu, 20 Jun 2002, *J. O. Hyun & H. K. Park* 2002128–2002129 (KH); Jindo-gun, Seomang, 19 Jul 2006, *Y. H. Cho et al.* WR-060719-098 (KH); Jindo-gun, Cheomchalsan Mt., 11 Jul 2013, *D. P. Jin* 1307001–1307030 (IUI); Jindo-gun, Cheomchalsan Mt., 28 Sep 2008, *E. S. Jeon* ESJeon81409 (KH); Jindo-gun, Temple Ssangyesa, 8 Aug 1964, *T. Lee s.n.* (SNUA); Haenam-gun, Dalmasan Mt., 8 Aug 2005, *H. J. Choi* CHJ 50159 (KH); Haenam-gun, Duryunsan Mt., 13 Aug 2003, *E. S. Jeon* ESJeon32119-1 (KH); Wando-gun, Sangwangbong Mt., 12 Jul 2013, *D. P. Jin* 1307031–1307042, 1307044–1307049, 1307051–1307053 (IUI); Wando-gun, Bogildo Isl., 22 Jul 2014, *D. P. Jin & I. S. Choi* 1407127–1407131 (IUI); Wando-gun, Bogildo Isl., 22 Jul 2014, *D. P. Jin & I. S. Choi* 1407127–1407131 (IUI); Wando-gun, Saengildo Isl., 23 Jul 2008, *Y. H. Cho et al.* WR-080723-239 (KH); Wando-gun, Daemodo Isl., 22 Jul 2010, *S. C. Ko et al.* HNHM-2010-0209 (KH); Gangjin-gun, Udubong peak, 25 Jul 2007, *Y. H. Cho et al.* WR-070725-222 (KH).

ORCID: Dong-Pil JIN <https://orcid.org/0000-0002-3617-952X>; Jong-Won PARK <https://orcid.org/0000-0002-5877-4696>; Byoung-Hee CHOI <https://orcid.org/0000-0002-9234-9052>

Acknowledgments

The authors are grateful to the persons concerned at the KH, SNUA, PE and TI herbaria for permitting the examination of specimens. We also thank our colleague J.S. Park, Plant Systematics Laboratory of Inha University, for commenting on this manuscript and editing the figures. This work was supported by the National Research Foundation of Korea (NRF) (No. NRF — 2018R1D1A1B07043030).

Conflict of Interest

The authors declare that there is no conflict of interest.

Literature Cited

- Akiyama, S. 1988. A revision of the genus *Lespedeza* section *Macrolespedeza* (Leguminosae). The University Museum, The University of Tokyo, Bulletin 33: 1–170.
- Akiyama, S. 2004. A new hybrid *Lespedeza* × *miquelii* (Leguminosae). Journal of Japanese Botany 79: 230–234.
- Brunet, J., J. E. Zalapa, F. Pecori and A. Santini. 2013. Hybridization and introgression between the exotic Siberian elm, *Ulmus pumila*, and the native Field elm, *U. minor*, in Italy. Biological Invasions 15: 2717–2730.
- Castillo-Mendoza, E., D. Salinas-Sánchez, L. Valencia-Cuevas, A. Zamilpa and E. Tovar-Sánchez. 2019. Natural hybridisation among *Quercus glabrescens*, *Q. rugosa* and *Q. obtusata* (Fagaceae): microsatellites and secondary metabolites markers. Plant Biology 21: 110–121.
- Chang, C. S. and H. Kim. 2019. Flora of the Korean Peninsula. Version 1.16. TB Lee Herbarium. Occurrence dataset. Retrieved Nov. 12, 2019, available from <https://doi.org/10.15468/fyxnsd>.
- Choi, B. H. 2007. *Lespedeza* Michx. In The Genera of Vascular Plants of Korea. Park, C.-W. (ed.), Academy Publishing Co., Seoul. Pp. 614–618.
- Duminil, J., D. Kenfack, V. Viscosi, L. Grumiau and O. J. Hardy. 2012. Testing species delimitation in sympatric species complexes: the case of an African tropical tree, *Carapa* spp. (Meliaceae). Molecular Phylogenetics and Evolution 62: 275–285.
- Earl, D. A. and B. M. von Holdt. 2012. STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conservation Genetics Resources 4: 359–361.
- Hatusima, S. 1967. *Lespedeza*: sects. *Macrolespedeza* and *Heterolespedeza* from Japan, Korea and Formosa. Memoirs of the Faculty of Agriculture, Kagoshima University 6: 1–17.
- Jin, D.-P., W.-B. Cho, I.-S. Choi and B.-H. Choi. 2016a. Isolation and characterization of 28 microsatellite loci for a Korean endemic, *Lespedeza maritima* (Fabaceae). Applications in Plant Sciences 4: 1500089.
- Jin, D.-P., J.-H. Lee, B. Xu and B.-H. Choi. 2016b. Phylogeography of East Asian *Lespedeza buergeri* (Fabaceae) based on chloroplast and nuclear ribosomal DNA sequence variations. Journal of Plant Research 129: 793–805.
- Jin, D.-P., B. Xu and B.-H. Choi. 2018. Taxonomic reconsideration of Chinese *Lespedeza maximowiczii* (Fabaceae) based on morphological and genetic features, and recommendation as an independent species *L. pseudomaximowiczii*. Korean Journal of Plant Taxonomy 48: 153–162.
- Kopelman, N. M., J. Mayzel, M. Jakobsson, N. A. Rosenberg and I. Mayrose. 2015. CLUMPAK: a program for identifying clustering modes and packaging population structure inferences across K. Molecular Ecology Resources 15: 1179–1191.
- Langella, O. 2011. Populations 1.2.32. Retrieved Dec. 9, 2019 available from <http://www.bioinformatics.org/project/>

?group_id=84.

- Lee, J.-H., D.-P. Jin and B.-H. Choi. 2014. Genetic differentiation and introgression among Korean evergreen *Quercus* (Fagaceae) are revealed by microsatellite markers. *Annales Botanici Fennici* 51: 39–48.
- Lee, M. H. 1978. Studies on the genus *Lespedeza* in Korea: characteristics chosen for an identification of the genus *Lespedeza*. *Bulletin of the Arboretum Seoul National University* 2: 7–28.
- Lee, T. B. 1965. The *Lespedeza* of Korea (1). *Bulletin of the Seoul National University Forests* 2: 1–43.
- Lee, T. B. 1980. *Illustrated Flora of Korea*. Hyangmunsa, Seoul. Pp. 468–472.
- Lee, T. B. and M. H. Lee. 1975. The *Lespedeza* of Korea (2): trichomes for an identification of *Lespedeza*. *Seoul National University Faculty Papers* 4: 1–5.
- Nakai, T. 1914. Vegetation of Island Wando (Wangto shokubutsu hokokusho). Governor-General of Korea (Chosen sotokufu). 35 pp. (in Japanese)
- Nakai, T. 1919. Notulae ad plantas Japoniae et Coreae XXI. *Botanical Magazine Tokyo* 33: 193–216.
- Nakai, T. 1923. Notulae ad plantas Japoniae et Coreae XXX. *Botanical Magazine Tokyo* 37: 69–82.
- Nakai, T. 1927. *Lespedeza* of Japan and Korea. The Forestal Experiment Station of Government General of Chosen 6: 1–101.
- Nei, M., F. Tajima and Y. Tateno. 1983. Accuracy of estimated phylogenetic trees from molecular data. II. Gene frequency data. *Journal of Molecular Evolution* 19: 153–170.
- Ohashi, H. and T. Nemoto. 2014. A new system of *Lespedeza* (Leguminosae tribe Desmodieae). *Journal of Japanese Botany* 89: 1–11.
- Ohashi, H., T. Nemoto and K. Ohashi. 2009. A revision of *Lespedeza* subgenus *Macrolespedeza* (Leguminosae) in China. *Journal of Japanese Botany* 84: 197–223.
- Pritchard, J. K., M. Stephens and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155: 945–959.
- Schindler, A. K. 1911. *Lespedezae novae et criticae*. I. Repertorium novarum specierum regni vegetabilis 9: 514–523. (in German)
- Uyeki, H. 1941. Trees and forests (Jumoku to shinrin). *Bulletin of Forestry Society of Korea (Chosen sanrin kaiho)* 194: 7–13. (in Japanese)
- Xu, B., N. Wu, X.-F. Gao and L.-B. Zhang. 2012. Analysis of DNA sequences of six chloroplast and nuclear genes suggests incongruence, introgression, and incomplete lineage sorting in the evolution of *Lespedeza* (Fabaceae). *Molecular Phylogenetics and Evolution* 62: 346–358.
- Xu, B., X.-M. Zeng, X.-F. Gao, D.-P. Jin and L.-B. Zhang. 2017. ITS non-concerted evolution and rampant hybridization in the legume genus *Lespedeza* (Fabaceae). *Scientific Reports* 7: 40057.
- Zeng, Y.-F., J.-G. Zhang, A.-G. Duan and B. Abuduhamiti. 2016. Genetic structure of *Populus* hybrid zone along the Irtysh River provides insight into plastid-nuclear incompatibility. *Scientific Reports* 6: 28043.

조록싸리 종내분류군과 잡종의 분류학적 연구

진동필 · 박종원 · 최병희*

인하대학교 생명과학과

적 요: 조록싸리(*Lespedeza maximowiczii*) 내에 많은 종내분류군들 및 근연분류군과의 잡종들이 기록되었지만, 이들의 분류학적 실체에 대해서는 학자들간에 이견이 있다. 본 연구는 조록싸리와 근연분류군간 잡종인 지리산싸리(*L. chiisanensis*), 진도싸리(*L. patentibicolor*) 및 조록싸리의 종내분류군인 털조록싸리(var. *tomentella*), 늦싸리(var. *elongata*), 삼색싸리(var. *tricolor*)의 실체를 규명하기 위해, 외부형태를 관찰하고 microsatellite를 이용하여 유전적 구조를 분석하였다. 연구 결과 털조록싸리와 늦싸리의 꽃과 잎의 형태는 조록싸리의 변이폭에 속했고, 유전적으로도 두 분류군이 조록싸리와 같이 묶였다. 삼색싸리는 꽃의 구조와 색에서 근연종인 *L. buergeri*와 유사한 반면 소엽 정단부와 소포엽의 형태는 조록싸리와 가까웠다. 유전적 구조에서도 삼색싸리의 개체들은 조록싸리와 *L. buergeri*의 계통이 혼합된 형태를 보이거나($K=3$), 독립되었다($K=5$). 잡종들의 경우, 지리산싸리의 꽃과 잎의 형태는 조록싸리와 구별되지 않는 반면, 진도싸리의 꽃 형질은 싸리(*L. bicolor*)의 변이폭에 속했는데, 유전적 계통도 각각 조록싸리와 싸리로 지정되었다. 본 연구결과를 종합하여 저자들은 털조록싸리와 늦싸리를 조록싸리의 품종, f. *friebeana* (Schindl.) D. P. Jin, J. W. Park & B. H. Choi로 처리하였는데, 이는 *L. friebeana*가 var. *tomentella* 보다 먼저 발표되었기 때문이다. 또한 삼색싸리는 독립종, *L. tricolor* (Nakai) D. P. Jin, J. W. Park & B. H. Choi로 처리하였고, 지리산싸리는 조록싸리의 이명으로 처리하였다. 한편 진도싸리는 싸리의 이명으로 판단된다.

주요어: 잡종, 종내분류군, 조록싸리, 형태 변이, microsatellite, 분류학적 처리