Sorbus quernea: taxonomic confusion caused by the naturalization of an alien species, *Sorbus mougeotii*

Sorbus quernea – taxonomický omyl vyvolaný naturalizací nepůvodního druhu _Sorbus mougeotii_

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Sorbus quernea, a hybridogenous species described in 1996 as an endemic in two places in Prague (Czech Republic), is revised. A wide range of contemporary biosystematic techniques, including molecular (nuclear microsatellite markers) and karyological analyses (chromosome counts, DAPI flow cytometry) along with multivariate morphometric and elliptic Fourier analyses, were used to assess its taxonomic status. The revision revealed that *S. quernea* is taxonomically identical to *S. mougeotii*, a western-European hybridogenous species with a large distribution area, which was described from the Vosges Mts in France in 1858. Plants from localities given in the protologues of both taxa and from the German Alps, French Alps, the Massif Central and those of unknown origin planted in the Czech Republic, were shown to be taxonomically, karyologically and genetically consistent. A negligible variation in the microsatellite pattern partly combined with variation in leaf shape was recorded only at Grand Ballon Mt. (Vosges Mts). This variability is probably caused by introgressive hybridization with diploid *S. aria* s. str. Specimens of *S. mougeotii* from woodland show more deeply lobed and broader leaves compared with those from subalpine areas. This variability is ascribed to the ecologically conditioned plasticity of the species. The type material of *S. mougeotii* deposited in Nancy is regarded as taxonomically consistent. At the Prague localities, *S. mougeotii* (the populations erroneously described as *S. quernea*) is considered to be an escaped and recently naturalized alien species. *Sorbus mougeotii* is occasionally planted in the Czech Republic and also in other European countries as a roadside, street or garden tree. In Europe, several other species of *Sorbus* that were planted escaped and became established in (semi-)natural, often relict (rocky) vegetation, which when combined with poor knowledge of taxonomy of the planted species, may give an impression of a natural origin for an escaped population and lead to serious taxonomic misinterpretations. An overview is provided of alien and often or occasionally cultivated hybridogenous *Sorbus* species in European countries.

Keywords: apomixis, Czech Republic, endemic, France, geometric morphometrics, hybridization, karyology, microsatellites, multivariate morphometrics, *Rosaceae*, *Sorbus hybrida* agg., subg. *Soraria*, taxonomy.

Introduction

In Europe, the genus *Sorbus* is a taxonomically difficult group of vascular plants. The main reason for this taxonomic complexity is the high number of taxa, which is the result of relatively frequent interspecific hybridization often combined with polyploidy and apomixis.

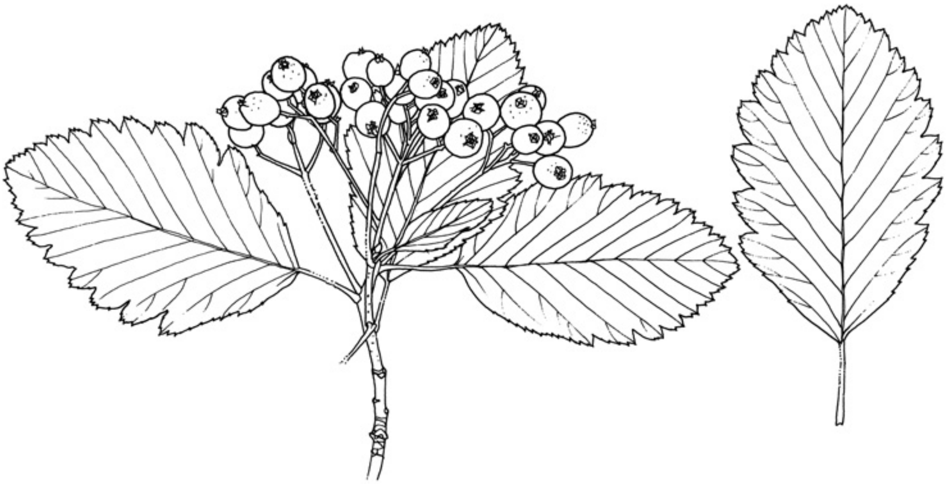

Fig. 1. – *Sorbus mougeotii*, a short fructiferous shoot (left) and a leaf from the middle part of a short sterile shoot (right). Drawing by A. Skoumalová.

These apomictic hybrids are usually treated as independent species (microspecies, agamospecies) primarily because they are morphological and genetically unique and stable (e.g. Meyer et al. 2005, Rich et al. 2010, Németh 2012, Velebil 2012, Vít et al. 2012). They often arise from the same parental combination and therefore are morphologically very similar. This fact, combined with considerable ecologically mediated phenotypic plasticity, causes significant taxonomic difficulties. The taxonomic complexity in the field may also be increased by a sympatric occurrence of microspecies and F1 hybrids or hybrid swarms.

Escapes of cultivated species of *Sorbus* are another and, up to now probably underestimated phenomenon, which may cause taxonomic problems. *Sorbus* species escape from cultivation quite easily and inhabit (semi-)natural, often relict rocky vegetation. If these plants become established at a locality where a native *Sorbus* species occurs (e.g. their parental species), they may give the impression of having evolved naturally at that location and as a result give rise to serious floristic or taxonomic misinterpretations. This article seeks to draw attention to this issue based on an example of a Czech taxon, *Sorbus quernea* Kovanda.

Sorbus quernea was described in 1996 as an endemic hybridogenous species occurring at two places in Prague (Kovanda 1996). It was regarded as an important discovery, because it was the only endemic member of the subg. *Soraria* Májovský & Bernátová (= *S. hybrida* agg. – parental combination *S. aria* s. lat. × *S. aucuparia*) known to occur in the Czech Republic (Kovanda 1996, Kubát et al. 2002). The occurrence of a new species in such a botanically well searched area as Prague (Špryňar & Münzbergová 1997) together with a complete lack of old herbarium specimens (Kovanda 1996), must have aroused suspicion about the origin of this species. The first doubts were expressed in 2006 (Turoňová in Vít 2006). This author mentioned the possibility that this species was not native to the Czech Republic but was previously cultivated for ornamental purposes in the surroundings of the type locality and had escaped and naturalized. But there was no evidence of the

Fig. 2. – Fructiferous fertile shoot of *Sorbus mougeotii* growing on a wall of the Landsberg Castle ruins near Barr in France (photograph by A. Jírová 2010).

cultivation of this species in Prague or elsewhere within the Czech Republic to support this hypothesis. However, the discovery of over 20 individuals of *S. quernea* planted in an urban settlement Šumava in České Budějovice in 2009 prompted a thorough revision of this species. Our comparative study of European floras (Warburg & Kárpáti 1968, Kutzelnigg 1995) and monographs on *Sorbus* (Hedlund 1901, Meyer et al. 2005, Rich et al. 2010) indicated that *S. quernea* is probably identical to *S. mougeotii* Soy.-Will. et Godr. (Fig. 1–2), a species described in the 19th century from the Vosges Mts in France (Godron 1858) and recently reported from a large area extending from the Pyrenees to the western Alps (Kutzelnigg 1995). This species is also known to be planted for ornamental purposes and occasionally escapes (Meyer et al. 2005, Rich et al. 2010). Considering these circumstances, it seemed plausible that *S. quernea* is, in fact, merely escaped and naturalized *S. mougeotii*. However our study of the type material of *S. mougeotii* in the herbarium in Nancy (NCY) gave rise to uncertainty about this determination. The leaves of most of the type specimens seem to be less lobed than most of the individuals of *S. quernea*. The depth of leaf lobes varied also within the type material, thus specimens appeared to be morphologically inconsistent. It was apparent that an additional field investigation of this species at localities given in the protologue was necessary to obtain a more complete knowledge of the phenotypical and genetic variability of the species. Therefore, field observations, molecular analyses, karyological studies, multivariate morphometric and elliptic Fourier analyses were carried out to clarify the variability of *S. mougeotii* and the identity of *S. quernea.* The results of this investigation are presented in this paper.

Material and methods

Plant material and field work

Between one and 60 individuals were collected from 12 populations of *Sorbus* between 2004 and 2006, and 2009 and 2010. Between one and nine (but usually two) well developed leaves per individual mature tree were selected for the study of phenotypic and genetic variation following the recommendations of Kutzelnigg (1995) and Meyer et al. (2005). *Sorbus quernea* was sampled at both the localities in Prague given in the protologue (Kovanda 1996). Samples of *S. mougeotii* were collected in the Vosges Mts in France at all four localities given in the original description of the species (Godron 1858). In addition, samples from the Allgäu Alps in Germany, French Alps, Massif Central and three populations of planted individuals in the Czech Republic (Prague, České Budějovice, Bezděz) were added to determine the variability of this taxon at a larger geographical scale and to corroborate the identity of the Czech plants in cultivation (see Fig. 3 and Table 1 for details). The number of plants collected per locality was dependent upon their abundance, e.g. the sampling at Rothenbachkopf Mt. was limited because *S. mougeotii* is rare there. Samples from the French Alps and Massif Central were kindly provided by Mr. B. Cornier from his garden (the cultivated plants originate from seeds collected at the given natural localities). For the molecular analyses (nuclear microsatellite markers), 14 individuals of *S. quernea*, 35 of *S. mougeotii* and six planted individuals were sampled. For the multivariate morphometric and Elliptic Fourier analyses, 33 individuals of *S. quernea*, 41 of *S. mougeotii* and 22 of planted individuals were used. Voucher specimens were deposited in the CB and PRC herbaria (Holmgren et al. 1990). Altitudes and geographic coordinates (WGS-84) were determined using Garmin eTrex and GPSmap 60CSx instruments.

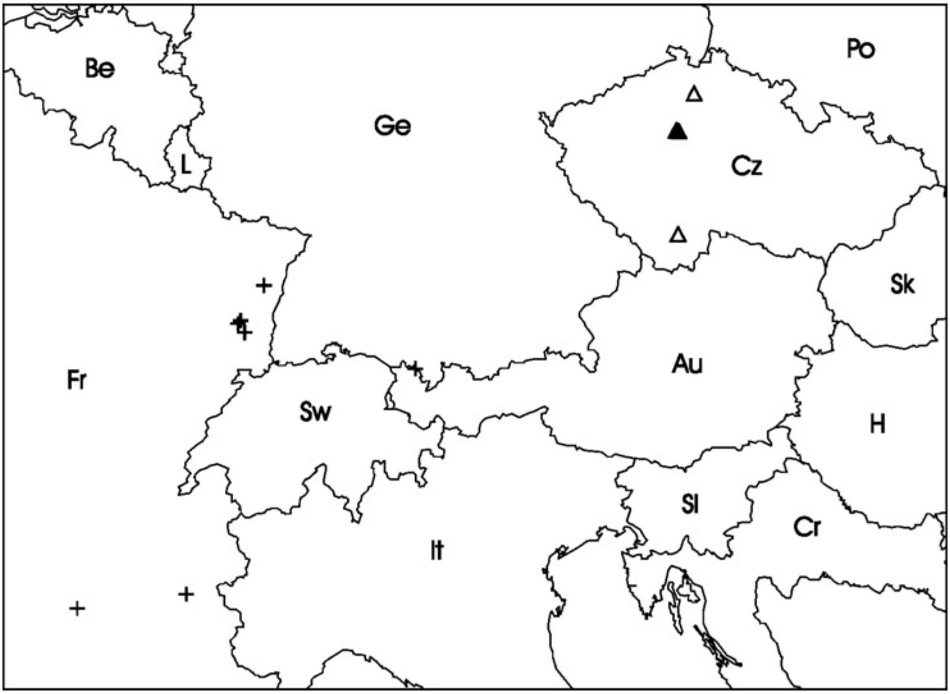

Fig. 3. – Areas sampled with natural populations of *Sorbus mougeotii* in the Alps, Vosges and Central Massif (cross), naturalized populations described as *S. quernea* (filled triangle) and cultivated populations in the Czech Republic of unknown origin (triangle).

Digitalization and elliptic Fourier analysis

Detailed elliptic Fourier analysis was applied to elucidate the variation in leaf shape. Only well developed, mature and intact leaves from the centre of short sterile shoots were collected, carefully flattened and dried and subsequently scanned at 300 dpi using Epson scan 1.11E software. Elliptic Fourier approximation (Kuhl & Giardina 1982) incorporated in the SHAPE 1.2 software package (Iwata & Ukai 2002) was employed to describe the variation in leaf shape of the three groups selected (populations of *S. mougeotii*, *S. quernea* and cultivated plants in the Czech Republic whose exact origin was unknown). The chain-coded contour of each leaf was approximated using the first 20 harmonics and the elliptic Fourier descriptors (EFDs) were normalized to avoid variations related to size, rotation and starting point of the contour trace. Subsequently, principal component (PC) scores for each specimen were calculated from the standardized EFDs and the variation in shape associated with each PC was visualized using the procedure described by Furuta et al. (1995). The discriminant power of the principal component scores (from the above mentioned PCA) used as discriminating variables was tested by a forward selection algorithm in the Linear discrimination analysis (LDA) in Canoco (Lepš & Šmilauer 2003), using the Monte Carlo permutation test (999 permutations; only axes with P-level < 0.05 were considered).

Table 1. – Locality details of *Sorbus mougeotii* populations included in morphometric (classical and geometric morphometry, MM), molecular (nuclear microsatellite markers, SSR) and flow cytometry (FCM) analyses; n = number of individuals analysed, n/n = number of individuals/leaves analysed.

Locality	Geographic coordinates (WGS-84)	Note	Altitude (m a.s.l.)	n (SSR)	n (FCM/ chromosome counting)	n/n (MM)
Czech Republic, Bezděz, ca 1 km SSE of the centre of the village	50°31'42"N, 14°43'25"E	planted along road	370	–	–/1	1/6
Czech Republic, České Budějovice, in Šumava urban settlement	48°58'57"N, 14°26'46"E	planted in urban vegetation	400	6	1/–	21/42
Czech Republic, Praha (Troja), near the western border of the Jabloňka Nature Monument, woody steep slope, the type locality of *S. quernea*	50°07'06"N, 14°26'06"E	naturalized	240–250	7	58/1	16/31
Czech Republic, Praha (Troja), rocky slope near the boarder of the Bílá skála Nature Monument, a locality given in the protologue of *S. quernea*	50°06'54"N, 14°27'24"E	naturalized	260	5	11/–	14/28
Czech Republic, Praha (Troja), the Botanical Garden near Fata Morgana greenhouse	50°07'16"N, 14°24'52"E	naturalized	240	–	–	3/14
France, Barr, the ruin of the castle of Landsberg and the close surroundings, a locality given in the protologue of *S. mougeotii*	48°25'13"N, 07°25'22"E	native	520–650	8	5/–	13/30
France, Gérardmer, the area between the summit of le Hohneck Mountain and le Petit Hohneck Mountain, a locality given in the protologue of *S. mougeotii*	48°01'54"N, 07°01'54"E	native	1170–1250	7	6/–	11/24
France, Gérardmer, the subsummit area of Rothenbachkopf mountain, a locality given in the protologue of *S. mougeotii*	48°00'03"N, 06°58'53"E	native	1200–1300	3	3/–	–
France, St-Amarin, the subsummit area of Grand Ballon mountain, a locality given in the protologue of *S. mougeotii*	47°53'59"N, 07°05'51"E	native	1250–1400	9	9/–	13/28
France, Rhone-Alpes, French Alps, Mont-de-Lans, foot of the cliff, S of the spot height 989, by the road 91	45°02'26"N, 06°05'57"E	native	1010	2	2/–	–
France, Rhone-Alpes, Massif Central range, Ardeche, Saint-Martial village, Les Trabuts (near Suc de Sara)	44°53'03"N, 04°14'55"E	native	920	3	3/–	–
Germany, Oberstaufen, Dreiländerblicks near Hagspiel village	47°30'59"N, 09°59'22"E	native	1060–1080	3	3/–	2/8
Total				53	101/2	94/218

Morphometric data and analyses

The leaves used in the Fourier analysis were also used to obtain eight quantitative characters. Subsequently, one ratio character was computed (for a summary and abbreviation of the characters measured, see Fig 6). The character set was chosen on the basis of published determination keys and floras (e.g. Kutzelnigg 1995, Meyer et al. 2005, Rich et al. 2010) and included those used in our previous studies (Lepší et al. 2008, 2009, Vít et al. 2012). Data were log-transformed to improve homogeneity of variance. Depending on which of the analyses below was used the operational units used were either (i) the values of the characters of the individual plants, (ii) the average values of the characters for the individuals or (iii) the average values of the characters for the populations. The principal component analyses (PCA) of samples collected from all the populations (the values of the characters of the individuals were used) provided an insight into the overall pattern of morphological variation and indicated a potential separation of *S. mougeotii*, *S. quernea* and the planted population in the Czech Republic. Redundancy analysis (RDA) was used to test the separation of the three French populations of *S. mougeotii*, two populations of *S. quernea* and additionally one population of cultivated plants in České Budějovice. Linear discrimination analyses (LDA) were used to determine the discriminating power of the morphometric characters used following the methodology described in Lepš & Šmilauer (2003). For RDA and LDA, 11 individuals (the average values of the characters for the individuals were used) from each population were randomly selected and subsequently analysed in a split-plot design: six whole plots (population, free permutation) and 11 split plots (individuals within population, no permutation). Another separate RDA (the average values of the characters for the populations were used, unrestricted permutation) was computed to confirm the results of the RDA given above and tested the potential morphometric differences between the remaining populations (i.e. the Allgäu Alps, Prague, Bezděz). Prior to the PCA and RDA described above, the data were standardized to have zero mean and unit standard deviation. Seven individuals of *S. mougeotii* from Grand Ballon Mt., which showed, according to field observations and molecular analyses, a potential introgession from *S. aria*, were not included in the above analyses but were analysed in a separate PCA (the values of the characters of the individuals were used) to support the occurrence of a putative hybridization event.

All multivariate analyses were carried out using Canoco (Lepš & Šmilauer 2003). Box-and-whisker plots of nine morphological characters measured on leaf laminae of both species were carried out in Statistica (StatSoft 2010).

Karyology

Two samples of short, two-year old branches with well-developed leaf buds of *S. quernea* were collected from the type locality (Jabloňka hill) in February 2006. Additionally, two samples were taken from a tree planted by the road to Bezděz in 2010. Actively growing vegetative tissue was pre-treated with a saturated water solution of p-dichlorbenzen (2–3 hours at RT) and fixed in ice-cold 3:1 ethanol acetic acid overnight. The tissue was then macerated for 30–60 seconds in 1:1 solution of ethanol : HCl at 22 °C. Meristematic tissues were squashed in a drop of lacto-propionic orcein. Chromosomes were counted under a light microscope (Carl Zeiss NU, Jena, Germany) at a magnification of 1000 times.

Estimation of DNA ploidy level

DAPI flow cytometry was used to assess the variation in relative genome size and infer DNA ploidy levels (Suda et al. 2006) of *S. quernea* and *S. mougeotii*. Sets of individuals from each taxon were analysed individually, then bulk samples were analysed (i.e. five individuals simultaneously) from 69 different trees of *S. quernea* and 26 of *S. mougeotii*. *Bellis perennis* (2C = 3.38 pg; Schönswetter et al. 2007) was selected as a suitable internal reference standard (with genome size similar to, but not the same as, that of *Sorbus* species). Nuclei were isolated using a modified two-step procedure (Doležel et al. 2007), stained with DAPI fluorochrome and analysed using the method described by Lepší et al. (2008).

Nuclear microsatellite markers (SSR)

Total genomic DNA was extracted from silica-dried leaves (55 samples in total) following the CTAB protocol (Doyle & Doyle 1987) with minor modifications as described by Pfosser et al. (2005). Microsatellite primers developed for the genera *Sorbus* (Mss1, Mss5, Mss6, Ms6g and Ms14; Oddou-Muratorio et al. 2001, Nelson-Jones et al. 2002) and *Malus* (CH02D11 and CH01H10; Gianfranceschi et al. 1998) were used for the determination of intraspecific genetic variation, following the methodology provided by the original authors. For details see Lepší et al. (2008). Final visualization of fluorescently labelled fragments (NED, 6-FAM, HEX; Applied Biosystems, Foster City, CA, USA) was carried out using an automatic sequencer Avant Genetic Analyser 3100 (Applied Biosystems, Foster City, CA, USA). The microsatellite pattern was scored as “allele phenotypes” (Becher et al. 2000).

Results

Descriptive morphometric analyses

Sorbus mougeotii (French and German populations), *S. quernea* and planted individuals in the Czech Republic were not clearly separated by the PCA (Fig. 4). The RDA of the above mentioned dataset (the average values of the characters for the population were used) also did not reveal any significant difference between either species studied (data not shown). Another separate RDA was carried out to determine differences between the populations cited in the protologues (the average values of the characters for the individuals were used), but the result of the permutation test was nonsignificant (data not shown). The result of an additional RDA of the same data set to which cultivated plants from České Budějovice were added was also nonsignificant. None of the nine morphometric characters of leaves of *S. quernea* and *S. mougeotii* (originating only from the localities given in protologues) that were measured and subjected to a LDA discriminated between the two species (the average values of the characters for the individuals were used; Fig. 5). The box-and-whisker plots delineated the variability in quantitative characters of the species studied and revealed only negligible differences between these taxa (Fig. 6). The PCA, in which two groups of genetically distinct individuals (delimited based on the molecular analyses, see below) from Grand Ballon Mt. were also included, showed a partial separation of only one of these groups (Fig. 7). Width of lamina (LW), length of lamina (LL) and incision between the second and the third lobe from lamina base (INC) were the most closely correlated with the first component axis, which separates this group from the rest of the individuals sampled. These results concur with our field observations – some individuals on Grand Ballon Mt. had indistinctly lobed and narrow leaves compared with typical individuals of *S. mougeotii*. The second genetically delimited group did not appear to be morphologically distinct. Univariate statistics (minimum, maximum, quartiles, median, 5 and 95 percentiles) of quantitative characters for all the individuals collected (excluding potentially introgressed individuals) were calculated and are summarized in Table 2.

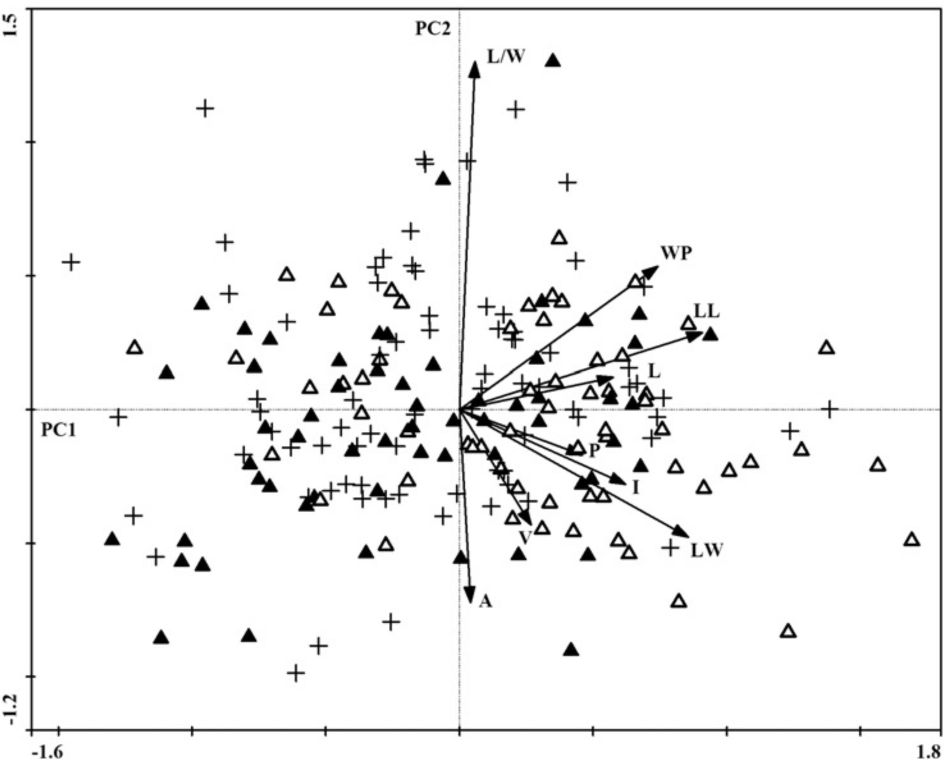

Fig. 4. – Principal component analysis based on nine morphological characters of the leaves of nine populations of *Sorbus mougeotii*: cross – three populations from France (Vosges Mts – Grand Ballon Mt., Hohneck Mt., Landsberg near the town of Barr) given in the protologue of *S. mougeotii* and one population from the German Alps (Hagspiel); filled triangle – two populations of *S. quernea* from the Czech Republic (Prague – Bílá skála nature monument, Jabloňka nature monument); triangle – three cultivated populations in the Czech Republic (České Budějovice, Prague and Bezděz). The first and second ordination axes are displayed, which explain 36.0% and 15.3% of the overall variation, respectively. The potentially introgressed individuals were excluded. For abbreviation of characters see Table 2.

Elliptic Fourier analysis of leaf laminae

Whilst descriptive morphometrics allows the separation of objects studied on the basis of quantitative characters, an elliptic Fourier analysis allows the separation of objects using shape as a diagnostic characteristic. The PCA performed on standardized Fourier coefficients did not reveal any distinct differences between the species studied (Fig. 8). Only a slight trend in shape associated with the first principal component was detected – *S. mougeotii* tended to have narrower leaves than *S. quernea*. Variation along the second axis did not indicate any tendency towards differentiation of either taxon (Fig. 8) and no clear pattern was observed along the other PCA axes (data not shown). No PCA axis was found to improve significantly the discriminant power of the LDA during forward selection in Canoco.

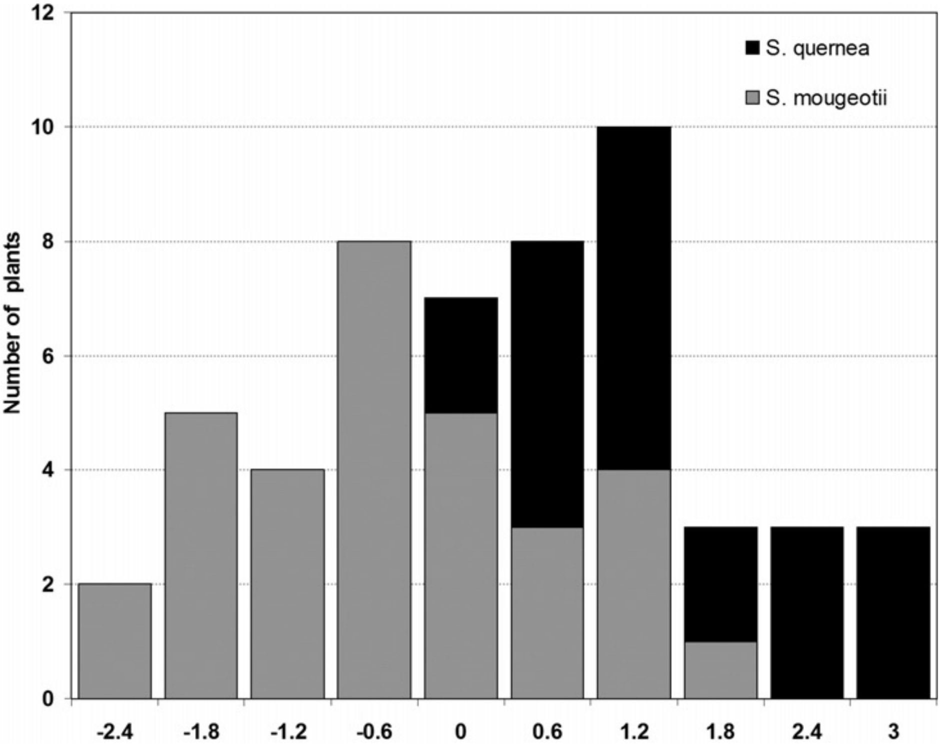

Fig. 5. – Histogram of canonical scores of linear canonical discriminant analysis based on nine morphological characters of the leaves of five populations of *Sorbus mougeotii* – three populations given in the protologue of *S. mougeotii* (France, Vosges Mts – Grand Ballon Mt., Hohneck Mt., Landsberg near the town of Barr) and two populations of *S. quernea* (Czech Republic, Prague – Bílá skála nature monument, Jabloňka nature monument). The first canonical axis explains 47.6% of the variation. None of characters measured showed any discriminate power for separating the two taxa.

Table 2. – Descriptive statistics of morphological characters of leaves of *Sorbus mougeotii* collected from the centres of short sterile shoots. The values are based on the measurements of leaves from nine populations (Czech Republic, Germany and France) excluding potentially introgressed plants.

Characters measured	Abbreviation	Minimum	5% percentile	Lower quartile	Median	Upper quartile	95% percentile	Maximum
Petiole length (cm)	P	1.2	1.5	1.7	1.8	2.0	2.4	2.8
Lamina length (cm)	LL	7.3	8	8.8	9.4	10.0	10.9	12.0
Lamina width (cm)	LW	4.5	5.2	5.7	6.0	6.5	7.1	8.1
Lamina length/width ratio	L/W	1.4	1.4	1.5	1.5	1.6	1.7	1.8
Widest part of lamina, from the base (cm)	WP	3.1	3.6	4.1	4.5	5.0	5.6	6.3
Incision between 2nd and 3rd lobes (cm)	I	0.3	0.4	0.5	0.6	0.7	0.8	1.1
Width of 3rd lobe (cm)	L	0.9	1.1	1.2	1.3	1.4	1.6	1.7
Vein angle (°)	A	32.0	35.9	38.0	39.0	41.8	44.2	48.0
Number of veins	V	8	9	10	10	11	12	12

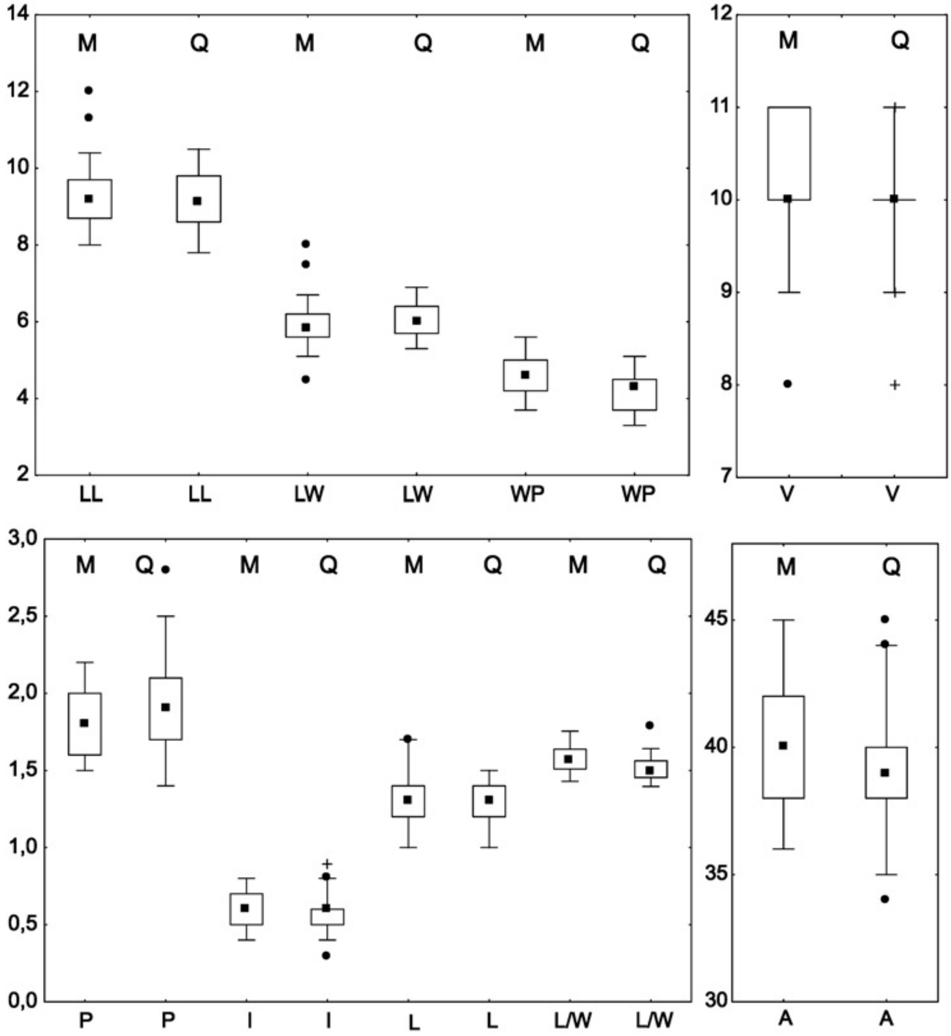

Fig. 6. – Box-and-whisker plots (showing median, 25–75% percentiles, 5–95% percentiles, outlier and extremes) of nine morphological characters of the leaves of five populations of *Sorbus mougeotii* – three populations given in the protologue of *S. mougeotii* (France, Vosges Mts – Grand Ballon Mt., Hohneck Mt., Landsberg by the town of Barr) and two of *S. quernea* (Czech Republic, Prague – Bílá skála nature monument, Jabloňka nature monument). M – *S. mougeotii* (n = 82), Q – *S. quernea* (n = 89). Measured characters: LL – lamina length (cm); LW – lamina width (cm); WP – widest place of lamina from the base (cm); V – vein number; P – petiole length (cm); INC – incision between the second and the third lobe (cm); L – width of the 3rd lobe (cm); L/W – lamina length/width ratio; A – vein angle (°).

Chromosome variation and ploidy level

Somatic cells of *S. quernea* and the cultivated plant at Bezděz have tetraploid chromosome numbers (2n = 4x = 68). DAPI flow cytometry detected only tetraploid DNA ploidy levels in *S. mougeotii* and *S. quernea*. The average sample:standard ratio was 0.75 for *S. mougeotii*

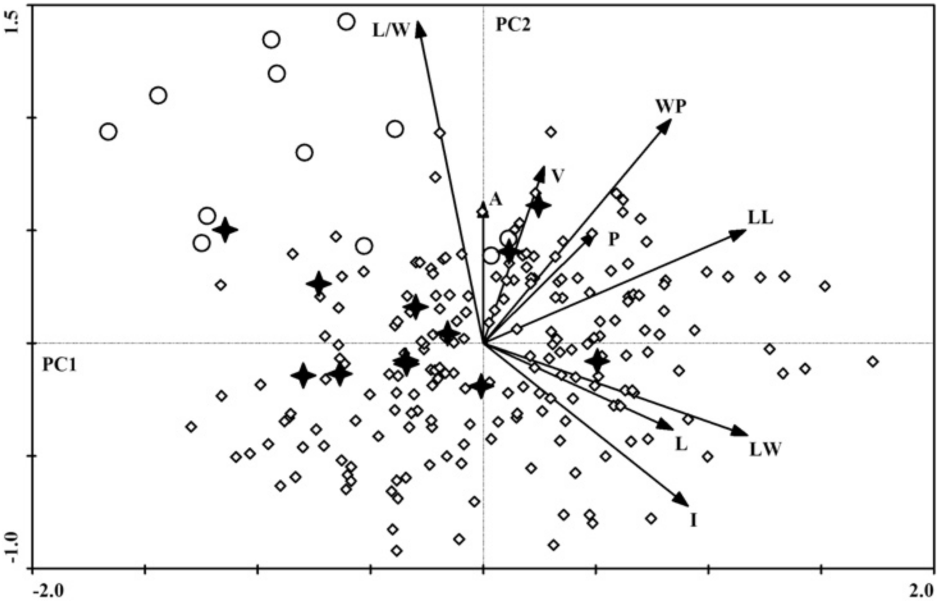

Fig. 7. – Principal component analysis based on nine morphological characters of the leaves of nine populations of *Sorbus mougeotii*: diamonds – three populations from France (Vosges Mts – Grand Ballon Mt., Hohneck Mt., Landsberg near the town of Barr) given in the protologue of *S. mougeotii* and one from the German Alps (Hagspiel), two populations of *S. quernea* from the Czech Republic (Prague – Bílá skála nature monument, Jabloňka nature monument), three cultivated populations in the Czech Republic (České Budějovice, Prague and Bezděz); stars and circles – two genetically distinct groups of potentially introgressed individuals from Grand Ballon Mt. (Vosges Mts, France). The first and second ordination axes are displayed, which explain 35.5% and 17.6% of the overall variation, respectively. For abbreviation of characters see Table 2.

Table 3. – The microsatellite patterns detected in all the individuals analysed. The dominant microsatellite pattern of *Sorbus mougeotii* and *S. quernea* is given in the first line. In the lines below are samples which showed microsatellite variability. The microsatellite loci unique for particular groups are in bold.

Taxa or locality	No	Fragment length of each microsatellite loci (in bp)						
		Mss1	CH01H10	Mss6	CH02D11	Ms14	Mss5	Ms6g
S. quernea / *S. mougeotii*	12/32	188	102	270, 276, 278, 282	112, 118, 122, 152	110	124, 132	164
Bílá skála (Cz)	1	188	**96**, 102	270, 276, 278, 282	112, 118, 122, 152	110	124, 132	164
Jabloňka (Cz)	1	188	102	270, 276, 278, 282	112, 118, 122, 152	110	124, 132	**162**
Grand Ballon (Fr)	4	188	102	270, 276, 278, **284**	112, 118, 122, 152	110	**122**, 124	164
Grand Ballon (Fr)	3	188	102	270, 276, 278, **288**	112, 118, 122, 152	110	124, **130**	164
French Alps, Hohneck (Fr)	2	188	102	270, 276, 278, 282	112, 118, 122, 152	110	**114**, **120**	164

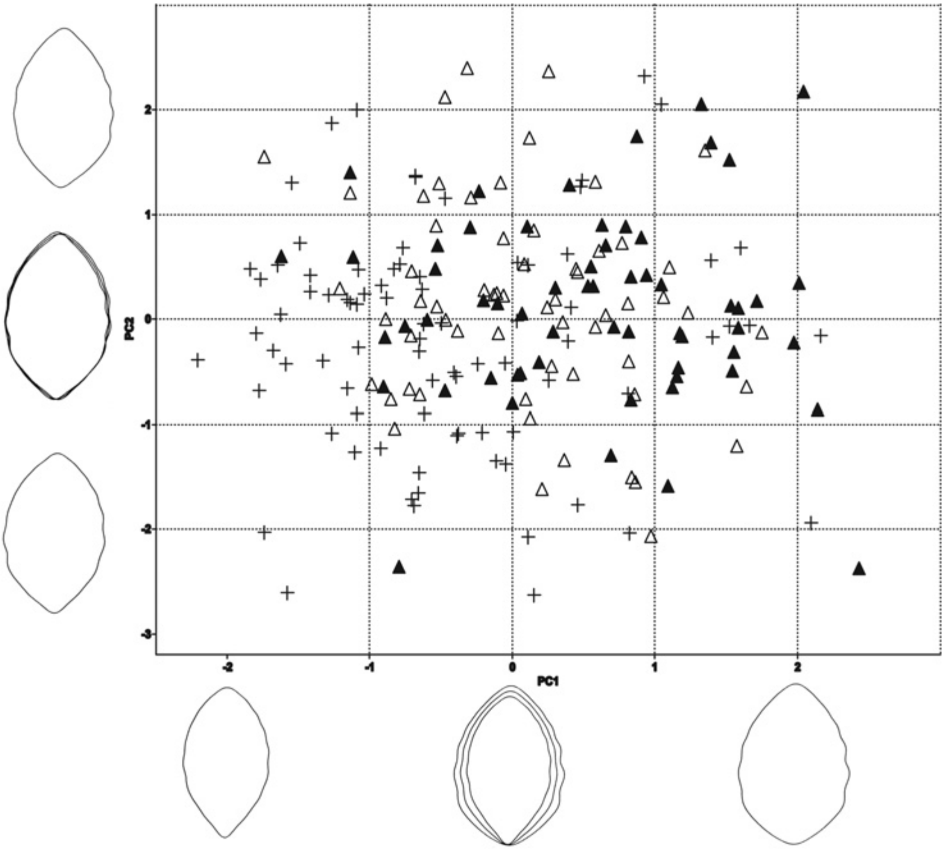

Fig. 8. – PCA of Fourier coefficients describing the total leaf lamina shape of the eight populations of *Sorbus mougeotii*. Cross – three populations from France (Vosges Mts – Grand Ballon Mt., Hohneck Mt., Landsberg near the town of Barr) given in the protologue of *S. mougeotii*; filled triangle – two populations of *S. quernea* from the Czech Republic (Prague – Bílá skála nature monument, Jabloňka nature monument); triangle – three cultivated populations in the Czech Republic (České Budějovice, Prague and Bezděz). The first and second ordination axes are displayed, which explain 48.9% and 10.1% of the overall variation, respectively. Reconstructed contours that correspond to the –2 and +2 SD positions on both axes are visualized along the particular axes (the scale of the plot is in SD units). In the centre, these two contours overlap with the mean leaf shape (corresponds with the [0.0] point of the plot).

(average CV of sample: 3.29 and standard: 1.49) and 0.74 for *S. quernea* (average CV of sample: 3.87 and standard: 2.17). The high values of coefficients of variance recorded are caused by the high level of secondary metabolites in the tissues of plants belonging to the family *Rosaceae*.

Nuclear microsatellite markers (SSR)

Most of the individuals of *S. quernea* and *S. mougeotii* sampled were genetically uniform, i.e. the two taxa did not show any distinct microsatellite pattern (Table 3), which would have allowed their separation. The only considerable genetic variability was recorded for the plants at Grand Ballon Mt. (France), where three genetically distinct groups were delimited. The first group represented by two individuals proved to have the prevailing microsatellite pattern detected in plants at all the sites studied. The second and the third groups (four and three individuals respectively) differ mutually in Mss6 and Mss5 loci and are distinct in the same loci from the dominant microsatellite pattern. The remaining genetic variability relates only to a few discrete individuals from different sites throughout the whole area sampled. There is no geographic pattern in this genetic variation and therefore we attribute it to random somatic mutation or a methodological artefact.

Discussion

Taxonomic and nomenclatural consequences

All biosystematic techniques employed i.e. molecular and karyological analyses (chromosome counts, DAPI flow cytometry) along with multivariate morphometric and elliptic Fourier analyses revealed insignificant differences between *S. quernea* and *S. mougeotii*. We conclude that *S. quernea* and the plants cultivated in the Czech Republic in towns and along roads are taxonomically consistent with *S. mougeotii* and thus we consider the name *S. quernea* to be a taxonomic synonym of *S. mougeotii*.

The elliptic Fourier analyses indicated only a slight but statistically nonsignificant trend in shape associated with the first principal component – *S. mougeotii* tended to have narrower leaves than *S. quernea* (Fig. 8). This trend could be due to ecologically mediated phenotypic plasticity. Many samples of *S. mougeotii* were collected in subalpine areas, where plants are very often exposed and therefore tend to have narrower and less lobed leaves. Leaves of *S. mougeotii* from semi-shady habitats (subalpine shrubs, forests) are broader and more deeply lobed, being similar to those of *S. quernea* coming mostly from oak forests. Individuals of *S. quernea* from rocky and other sunny places in towns have narrow and indistinctly lobed leaves similar to those of exposed plants growing at high altitudes.

There is some indication that the lectotypification of *S. mougeotii* made by Aldasoro et al. (2004) is illegitimate and a new type should be designated (B. Cornier, pers. comm.). Our study of *S. mougeotii* from the localities given in the protologue of this species (Godron 1858) provided an insight into the morphological variation of the type specimens. The lectotype (originated from Barr) and syntypes (Barr and Hohneck Mt.) deposited in NCY are not uniform in terms of leaf morphology. Specimens collected in the woodland in the surroundings of Barr (including the lectotype) have more deeply lobed and broader leaves compared with those from subalpine areas on Hohneck Mt. in the Vosges Mts. This distinct variation in leaf morphology is probably ecologically determined, which is in accordance with our field observations, and morphometric and molecular analyses. A different situation exists at Grand Ballon Mt., where the variability in leaf shape corresponds, at least partly, with the genetic variability and is probably caused by hybridization with *S. aria*. Some of these potentially introgressed plants had less distinctly lobed and somewhat narrower leaves even when compared with typical individuals of *S. mougeotii* from alpine areas. All sampled and observed plants from Hohneck Mt. were genetically and morphologically consistent. Therefore, we consider all the syntype specimens in NCY to be taxonomically uniform and correspond to the original description and we recommend selecting one of these as a lectotype instead of the specimen designated by Aldasoro et al. (2004).

Introgression in Sorbus mougeotii

Sorbus mougeotii showed minimal intraspecific genetic variation at seven nuclear microsatellite loci, indicating a monotopic origin and apomictic mode of reproduction. These observations are consistent with results for several other apomictic *Sorbus* taxa of hybrid origin (Liljefors 1953, Jankun & Kovanda 1986, 1987, 1988, Meyer et al. 2005, Lepší et al. 2008, 2009, Vít et al. 2012). The genetic variability detected on Grand Ballon Mt. corresponds, at least partly, with the external morphology of the plants and is probably a consequence of introgressive hybridization between *S. aria* and *S. mougeotii*. One genetically distinct group of these potentially introgressed plants has, compared with typical *S. mougeotii*, more shallow leaf lobes. This character was probably inherited from *S. aria*, whose leaves lack lobes or are slightly lobed. *Sorbus aria* is common at Grand Ballon Mt., which makes the likelihood of hybridization plausible. It is necessary to note that we only studied leaf morphology and therefore the second group of plants, which were genetically but not morphologically unique, might differ in form of their flowers or fruits. Alternatively, introgressive hybridization is not always reflected in the external morphology as concluded by Rieseberg & Ellstrand (1993). The observed genetic variability at Grand Ballon Mt. could also be caused by sexual reproduction or mutation. These two options are given as probable explanations for genetic variations of several polyploid species of the *S. aria* aggregate (Nelson-Jones et al. 2002). In our case, these two alternatives cannot be excluded but they seem to be less likely. Multiple origin, which is hypothesized based on molecular analysis of *S. arranensis* Hedl. and *S. pseudofenica* E. F. Warb. (Robertson et al. 2004), is another possible reason for the genetic variability recorded in *S. mougeotii*. However this appears to be unlikely because *S. mougeotii* was shown to be virtually homogenous both genetically and morphologically within the whole sampled area with the exception of the Grand Ballon Mt., the locality where the dominant genotype occurs sympatrically with two genetically distinct groups and *S. aria* s. str. Moreover, molecular analysis and morphology indicated that *S. mougeotii* is a result of hybridization between *S. aucuparia* and *S. graeca* (Nelson-Jones et al. 2002) and *S. graeca* is absent from Grand Ballon Mt.

As the plants of all of these mutually introgressed groups are tetraploids it is likely that they originated from an unreduced gamete of the diploid sexual species *S. aria* merging with a reduced diploid gamete of tetraploid *S. mougeotii*. Another possibility is that an unreduced gamete of a triploid hybrid (which originated from the merger of a haploid gamete of *S. aria* and a diploid gamete of *S. mougeotii*) fused with a reduced gamete of *S. aria*.

The relatively common hybridization between polyploids and diploids plays a crucial role in the ongoing evolution of the genus and produces genetic and morphological variability (Rich et al. 2010). The widespread species *S. mougeotii* is not the exception as several cases of its hybridization with other *Sorbus* species are reported. For example, *S.* ×*arioides* Michalet is described as a backcross of *S. mougeotii* with *S. aria* s. str. and *S.* ×*schnitzii* Düll as a hybrid with *S. chamaemespilus*. Each of the above taxa is considered to be sexual or an unstable hybrid. Another taxon *S. doerriana* N. Mey. is presumed to have originated from hybridization of *S. mougeotii* with *S. chamaemespilus* and is regarded as an apomictic species endemic to the Allgäu Alps (Kutzelnigg 1995, Meyer et al. 2005). The results of our analyses suggest the existence of backcrosses between *S. mougeotii* and *S. aria* and indicate the ability of the species to participate in ongoing evolutionary events. Further research at Grand Ballon Mt is required to clarify the detected variability and investigate the theory of the occurrence of introgression there.

Naturalization of Sorbus mougeotii in Prague

We consider that the *Sorbus quernea* described from two localities in Prague to be nothing more than naturalized populations of the alien species *Sorbus mougeotii*. There are at least four main circumstances that support the naturalization of this species and make its native occurrence improbable: (i) this species has been cultivated in the region of Prague for at least 90 years, i.e. long enough to make naturalization possible; (ii) there are no written records or herbarium specimens that predate the description of the new species in 1996; (iii) this species has escaped and naturalized in several other European countries (see Table 4); (iv) the nearest native occurrence of *S. mougeotii* is in the Austrian Alps, which is ca 300 km from Prague.

The first evidence of the cultivation of *S. mougeotii* in the Czech Republic dates from 1923. Specimens from the botanical gardens in München and Göteborg were introduced to Průhonice near Prague by the Dendrological society in Průhonice. The society produced and advertised the species for sale between 1935 and 1941 (Businský 2009). At present, the species is occasionally cultivated in parks, gardens and along roadsides throughout the Czech Republic. Excluding both the populations described as *S. quernea*, the species was recorded as naturalized in the area of the botanical garden of the town of Prague (Sekerka 2008).

Relatively rare cultivation was probably the reason why *S. mougeotii* was overlooked and not recognized in the Czech botanical literature (Kovanda 1992, Kubát et al. 2002). The massive naturalization at the Prague localities (ca 70 individuals excluding seedlings), along with the co-occurrence of native, potentially parental *Sorbus* species, probably gave rise to the impression that *S. mougeotii* was a native plant, which resulted in this taxonomic error (Kovanda 1996). There was similar taxonomical confusion associated with *Sorbus austriaca* (Beck) Prain et al. in western Bohemia where an escaped population was also thought to be a new undescribed species (Kovanda 1999), but the true identification was revealed before it was formally described (Lepší et al. 2011). The main reason for this misinterpretation, was again, a complete lack of information about the cultivation of this species in the Czech Republic and probably also an incorrect taxonomical concept of *S. austriaca* throughout Europe (Lepší et al. 2011).

Alien and occasionally cultivated Sorbus in Europe

There are 26 species of the subgenera *Soraria* (*S. hybrida* agg.), *Tormaria* Májovský & Bernátová (*S. latifolia* agg.) and *Aria* Pers. (*S. aria* agg.) that are grown for ornamental or other purposes in Europe (Table 4). Seventeen of them are known to have escaped or even participated in an initial speciation processes (hybridization). The northern European hybridogenous polyploid species *S. intermedia* (Ehrh.) Pers. and European diploid species *S. aria* s. str. are the species most often cultivated and naturalized in western and central Europe (Meyer et al. 2005, Rich et al. 2010). Both of them are able to hybridize there with native *S. aucuparia* as recorded in Great Britain (Rich et al. 2010). Another taxonomically interesting example of alien hybridogenous *Sorbus* (Rich et al. 2010) is *S. croceocarpa* P. D. Sell, which is naturalized in Great Britain and was distinguished and formally

Table 4. – Overview of alien and occasionally cultivated species of the subgenera *Soraria* (*S. hybrida* agg.), *Tormaria* (*S. latifolia* agg.) and *Aria* (*S. aria* agg.) in European countries. Species planted in special collections such as botanical gardens and arboretums were not included. Au – Austria, Be – Belgium, Cz – Czech Republic, De – Denmark, Es – Estonia, Fi – Finland, Fr – France, GB – Great Britain, Ge – Germany, H – Hungary, Ir – Ireland, La – Latvia, No – Norway, Po – Poland, Ro – Romania, Sw – Sweden.

Species	Native	Cultivation only	Alien	Source
S. aria (L.) Crantz	Europe	Au, Ge, H, Fr	Be, Cz, De, Fi, GB, Ir, No, Sw	Meyer et al. 2005, DAISIE 2009, Rich et al. 2010, B. Cornier pers. comm. 2012, Cs. Németh pers. comm. 2012, Lepší et al. unpubl.
S. arranensis Hedl.	GB		GB	Rich et al. 2010
S. austriaca (Beck) Prain et al.	Au		Cz, No	Lepší et al. 2011, Cs. Németh pers. comm. 2012, Gederaas et al. 2012
S. bakonyensis (Jáv.) Kárpáti	H	H		Cs. Németh pers. comm. 2012
S. bodajkensis Barabits	H	H		Cs. Németh pers. comm. 2012
S. borbasii Jáv.	Ro	H		Cs. Németh pers. comm. 2012
S. bristoliensis Wilmott	GB		GB	Rich et al. 2010
S. croceocarpa P. D. Sell	unknown		GB, Ir	Rich et al. 2010
S. decipiens (Bechst.) Petzold et Kirchner	Ge		GB	Rich et al. 2010
S. degenii Jáv.	H	Au, H		Cs. Németh pers. comm. 2012, Lepší et al. unpubl.
S. devoniensis E. F. Warburg	GB, Ir		Ir	Rich et al. 2010
S. eugenii-kelleri Kárpáti	H	H		Cs. Németh pers. comm. 2012
S. eximia Kovanda	Cz	Cz		Lepší et al. 2011
S. graeca s.l.	Eastern and Central Europe	Ge, Cz	Cz, Sw	Lepší et al. unpubl., N. Meyer pers. comm. 2012
S. hibernica E. F. Warb.	Ir		Ir	Rich et al. 2010
S. hybrida L.	De, Fi, La, No, Sw	Ge, H	GB, Ir, La, No	DAISIE 2009, Rich et al. 2010, Cs. Németh pers. comm. 2012, Grundt & Salvesen 2011
S. intermedia (Ehrh.) Pers.	De, Es, Fi, Ge, La, Po, Sw	Fr	Au, Be, De, Cz, GB, Ge, H, Ir, La, No, Po, Pyrenees	Kovanda 1992, Kutzelnigg 1995, Meyer et al. 2005, DAISIE 2009, Rich et al. 2010, B. Cornier pers. comm. 2012, Cs. Németh pers. comm. 2012
S. latifolia (Lam.) Pers.	Fr	Fr	Be, Cz, De, Fi, GB, Ge, Ir, No, Sw	Kutzelnigg 1995, Meyer et al. 2005, DAISIE 2009, Rich et al. 2010, Cornier pers. comm. 2012, Lepší et al. unpubl.
S. mougeotii Soyer-Willemet et Godron	Western Europe	Au, Ge	Cz, GB, Ir, No	Meyer et al. 2005, Rich et al. 2010, Gederaas et al. 2012, Lepší et al. unpubl.
S. norvegica Hedl.	No, Sw		No	Grundt & Salvesen 2011
S. redliana Kárpáti	H	H		Cs. Németh pers. comm. 2012
S. rupicola (Syme) Hedl.	Es, Ir, De, La, No, Sw, GB	No		Grundt & Salvesen 2011
S. subsimilis Hedl.	No		No	Grundt & Salvesen 2011
S. meinichii (Lindeb.) Hedl.	Scandinavia	No	La	DAISIE 2009, Grundt & Salvesen 2011
S. ×*thuringiaca* Düll	Europe	Au, Cz, Fr, GB, Ge, H	GB	Meyer et al. 2005, Rich et al. 2010, B. Cornier pers. comm. 2012, Cs. Németh pers. comm. 2012, Lepší et al. unpubl.
S. ×*tomentella* Gand.	Europe	Ge, H		N. Meyer pers. comm. 2012, Cs. Németh pers. comm. 2012

described based on specimens in cultivation there without knowledge of its native occurrence (Sell 1989). *Sorbus mougeotii*, *S. latifolia* (Lam.) Pers. and *S.* ×*thuringiaca* Düll are some of the other often cultivated and escaped species. Some hybridogenous *Sorbus* are already considered as potentially invasive species. For example in Norway, *Sorbus intermedia* and *S. mougeotii* have recently been evaluated as representing a very high risk of becoming invasive, and *Sorbus austriaca* and *S. latifolia* as having a high risk potential (Gederaas et al. 2012). The remainder of the species listed in Table 4 are probably planted and escaped only occasionally or locally.

It is likely that the list in Table 4 is not exhaustive and many other *Sorbus* microspecies will in the future be proposed and sold by modern garden companies specialising in the production of unconventional flora. The issue is that the knowledge of planted species of *Sorbus* is poor, especially in garden literature and promotional catalogues. However botanical floras and keys also do not provide sufficient information. Some species are unrecognized and/or incorrect names are commonly used. Therefore, closer attention must be paid to planted hybridogenous *Sorbus* species in the future in order to avoid taxonomic or floristic confusion when these species become naturalized.

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Souhrn

Sorbus quernea byl popsán jako hybridogenní endemický druh Prahy v roce 1996. Taxonomická revize druhu však ukázala, že se jedná o zplanělý západoevropský druh *S. mougeotii*, který byl popsán v 19. století z oblasti pohoří Vogézy a dnes je udáván od Pyrenejí po západní Alpy. Pro bezpečné ověření totožnosti *S. quernea* se *S. mougeotii* byly studovány typové položky a následně navštíveny všechny lokality uvedené v protologu obou druhů. Žádná z použitých biosystematických metod – cytometrie, klasická a geometrická morfometrie a molekulární analýzy – neodhalila prokazatelné rozdíly mezi oběma taxony. Rovněž pěstované rostliny v České republice a přírodní populace v německých Alpách se od francouzských populací významně neliší. *Sorbus mougeotii* vykazoval na typových lokalitách variabilitu ve tvaru listové čepele – oslunění jedinci měli užší a méně laločnaté listy oproti jedincům středně zastíněným. Úzkolisté a méně laločnaté typy byly nalézány hlavně v subalpínském pásmu, v doubravách v kolinním stupni se více vyskytovali jedinci se širšími a více laločnatými listy. Tuto variabilitu přičítáme ekologicky podmíněné plasticitě druhu. Morfologicky částečně variabilní typový materiál *S. mougeotii* uložený v NCY je dle našeho názoru taxonomicky konzistentní a vhodný k lectotypifikaci. Výjimkou je lokalita *S. mougeotii* na hoře Grand Ballon, kde byla u některých málo laločnatých a úzkolistých rostlin detekována genetická variabilita. Domníváme se, že tato variabilita je způsobena introgresivní hybridizací *S. mougeotii* se *S. aria*. Výskyt *S. mougeotii* na území Prahy považujeme za druhotný, tj. druh zde zplaněl a zdomácněl. *Sorbus mougeotii* byl do České republiky introdukován již v první polovině 20. století a byl následně distribuován Dendrologickou společností v Průhonicích. Dnes je občas pěstován podél komunikací nebo jako součást městské zeleně. V Praze je nyní pěstován a zdomácnělý na území Botanické zahrady města Prahy, což je asi 2 km daleko od lokalit uvedených v protologu *S. quernea*. Na příkladu *S. mougeotii* a dalších v Evropě zplaňujících druhů je ukázáno, že

některé pěstované jeřáby mají tendenci se šířit na přirozené biotopy a vytvářet smíšené populace s domácími druhy jeřábů. Zdomácnělá populace může vyvolávat dojem původního výskytu, což může bez znalosti pěstovaných druhů vést k floristickým nebo taxonomickým omylům. Proto je v článku vypracován přehled v Evropě zplaňujících nebo častěji pěstovaných jeřábů.

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