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Taxonomy and variability of selected *Sorbus* taxa

Ph.D. Thesis

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České Budějovice 2017

This thesis should be cited as:
Lepší M., 2017: Taxonomy and variability of selected *Sorbus* taxa. Ph.D. Thesis Series, No. 3. University of South Bohemia, Faculty of Science, School of Doctoral Studies in Biological Sciences, České Budějovice, Czech Republic, 321 pp.

Annotation

This thesis is a biosystematic study focusing on the taxonomy and variability of selected taxa of the genus *Sorbus*, one of the most diverse and taxonomically complicated plant groups in Europe. Classical and modern biosystematic methods – comparative study, chromosome counting, analysis of nuclear microsatellite markers, flow cytometry, and traditional multivariate and outline morphometric analyses – were used to assess the morphological, karyological and genetic variability of the genus. The final synthesis of these approaches led to the description of several new taxa (species, hybrids and a subgenus) and the correction of several taxonomic misinterpretations. To reveal ongoing evolutionary processes responsible for the generation of the observed variability, the reproductive modes of 42 *Sorbus* taxa were examined using flow-cytometric seed and pollen screens. Apart from revealing major trends, the study estimates the frequency of rare events and provides several novel conclusions that are relevant both specifically to *Sorbus*/Rosaceae and to apomixis in general.

Key words: apomixis, Czech Republic, endemic, DAPI flow cytometry, flow-cytometric seed and pollen screen, outline morphometrics, Great Britain, hybridization, karyology, microsatellites, traditional multivariate morphometrics, reproductive mode, Rosaceae.

Declaration [in Czech]

Prohlašuji, že svoji disertační práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury. Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své disertační práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

České Budějovice, 1. 1. 2017

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Martin Lepší

Financial support

This work was supported by the Grant Agency of the University of South Bohemia (grants no. 138/2010/P and no. 04-107/2013/P), the Czech Ministry of Education (institutional research support no. MSM-6007665801), the Academy of Science of the Czech Republic (long-term research development project no. RVO 67985939, project no. AV0Z60050516 and project no. IAAX00050801), the Grant Agency of Charles University (project no. 1584414), the Czech Science Foundation (project no. 14-36079G, Centre of Excellence PLADIAS), the Institute of Physical Biology, University of South Bohemia in České Budějovice (M6 Small student projects, 2011), and by financial resources of the South Bohemian Museum in České Budějovice and the Department of Botany, Faculty of Science, University of South Bohemia in České Budějovice.

"Nothing in nature looks simple and there is no reason why we should expect it to be simple".

D. Briggs and S. M. Walters,
Plant Variation and Evolution

Acknowledgements

Special thanks go to my brother Peter for his great support, unwavering enthusiasm for *Sorbus* and perfect professional partnership.

It is my pleasure to thank Petr Koutecký for his kind help with flow-cytometric analyses and for his flawless cooperation. I thank Petr Vít and Jana Bílá for the performance of flow-cytometric and molecular analyses, and once again to Petr Vít for his long-term collaboration in studying the genus *Sorbus*. Milan Štech is acknowledged for his general support since the beginning of my studies. Bruno Cornier (France), Alma Hajrudinović-Bogunić (Bosnia and Herzegovina), Michael Hohla (Austria), Gábor Mészáros (Hungary), Norbert Meyer (Germany) and Csaba Németh (Hungary) generously shared valuable information, kindly provided samples or guided me in the field in their countries. I am also grateful to Tim Rich for his warm care and attention he gave me during my internship in Wales. Jiří Zázvorka is acknowledged for his kind help with latin terms, Jitka Štěpánková and Z. Kaplan for valuable comments on the manuscript in appendix I and Frederick Rooks for advising me on the English of this thesis.

I thank all those who contributed in some other way to this thesis. They are F. Bogunić, K. Boublík, T. Dixon, M. Dolejš, C. D. Drechsler, M. Ducháček, K. Edwards, R. Evans, D. Green, J. Hadinec, L. Houston, V. Jarolímová, Z. Kaplan, J. Kirschner, L. Kirschnerová, F. Kolář, J. Kos, P. Kron, J. Lepš, M. Lučanová, S. Ludwig, T. Mahevas, J. Mottl, Z. Musil, J. Pellicer, P. Petřík, I. Prchlík, J. Sádlo, G. Seznec, A. Skoumalová, J. Šefl, M. Škorpík, P. Šmilauer, J. Štěpánek, T. Tichý, T. Urfus, J. Velebil and M. Zrzavá.

Finally, I extend my gratitude to my life partner Alena Jírová, who encouraged me to start the Ph.D. study.

List of papers and author's contribution

The thesis is based on seven papers and can be divided into two parts. The first part deals with *Sorbus* taxonomy and chorology (papers I–VI), and the second closely related part is a comprehensive biosystematic study on the reproductive modes of selected *Sorbus* taxa (paper VII):

I. Lepší M., Lepší P., Koutecký P., Bílá J. & Vít P. (2015): Taxonomic revision of *Sorbus* subgenus *Aria* occurring in the Czech Republic. – Preslia 87: 109–162. (IF = 4.104).

Martin Lepší wrote the draft of the manuscript, took comments from the co-authors, collected samples for all analyses, conducted multivariate analyses and a majority of flow-cytometric analyses. P. Lepší prepared the distribution maps, compiled the list of herbarium specimens and significantly participated in sample collection and manuscript revision. P. Koutecký and P. Vít participated in flow-cytometric analyses. Jana Bílá provided unpublished molecular data.

II. Lepší M., Lepší P. & Vít P. (2013): *Sorbus quernea*: taxonomic confusion raised by the naturalisation of the alien species, *S. mougeotii*. – Preslia 85: 159–178. (IF = 2.778).

Martin Lepší wrote the draft of the manuscript, took comments from the co-authors, sampled and analysed morphometric data (multivariate and outline analyses), sampled data for molecular and flow-cytometric analyses. P. Lepší significantly participated in data collection and manuscript revision. P. Vít conducted molecular and flow-cytometric analyses.

III. Vít P, **Lepší M.** & Lepší P. (2012): There is no diploid apomict among Czech *Sorbus* species – a biosystematic revision of *Sorbus eximia*, and the discovery of *Sorbus barrandienica*. – Preslia 84: 71–96. (IF = 2.833).

Martin Lepší wrote a considerable part of the draft of the manuscript, took comments from the co-authors, and contributed to data sampling and analysis (outline analysis). He collected distribution and ecological data and suggested nomenclatural and taxonomic solutions. P. Vít was responsible for molecular, flow cytometry and classical morphometric analyses, including the sampling and the writing of sections dealing with these analyses. Petr Lepší prepared the distribution map, compiled the list of herbarium specimens and significantly participated in data collection and manuscript revision.

IV. Lepší M., Lepší P., Sádlo J., Koutecký P., Vít P. & Petřík P. (2013): *Sorbus pauca* species nova, the first endemic species of the *Sorbus hybrida* group for the Czech Republic. – Preslia 85: 63–80. (IF = 2.778).

Martin Lepší wrote a considerable part of the draft of the manuscript, took comments from the co-authors, sampled and analysed morphometric data (multivariate and outline analyses) and participated in flow-cytometric seed screening (sampling and analyses) and collecting of ecological data. P. Lepší prepared the distribution map, compiled the list of herbarium specimens and significantly participated in data collection and manuscript revision. J. Sádlo wrote the section 'The historical context of the occurrence of this species' and contributed to the section 'Ecology'. P. Koutecký and P. Vít were responsible for flow-cytometric analyses, and P. Petřík summarized and analysed ecological data.

V. Kaplan Z., Danihelka J., **Lepší M.**, Lepší P., Ekrt L., Chrtek J. Jr., Kocián J., Prančl J., Kobrlová L., Hroneš M. & Šulc V. (2016): Distributions of vascular plants in the Czech Republic. Part 3. – Preslia 88: 459–544. (IF in 2015 = 4.104).

Martin Lepší wrote the draft of the manuscript dealing with Sorbus *and* Amelanchier *and took comments from the two first authors. Petr Lepší excerpted and imported distribution data into the database. The* *contributions of both authors to the performance other tasks were comparable. The remaining authors wrote the parts concerning other genera included in the paper and did not contribute to sections dealing with* Sorbus *and* Amelanchier.

VI. Rich T. C. G., Green D., Houston L., **Lepší M.**, Ludwig S. & Pellicer J. (2014): British *Sorbus* (Rosaceae): Six new species, two hybrids and a new subgenus. – New Journal of Botany 4 (1): 2–12. (Peer-reviewed journal of the Botanical Society of Britain & Ireland without IF).

Martin Lepší participated in sample collection and writing of sections 'New hybrids and New subgenus'. Tim Rich wrote the remainder of the paper, drew the illustrations and collected some original material. David Green collected material for S. greenii *and* S. herefordensis *and provided the data for 'Figures 5 and 8'. Libby Houston collected original material of* S. richii *and* S. spectans *and provided background data. Shanna Ludwig carried out molecular analyses of* S. spectans. *Jaume Pellicer provided flow-cytometric ploidy estimates.*

VII. Lepší M., Koutecký P., Bílá J., Lepší P., Urfus T. & Rich T. C. G. (2016): Versatility of reproductive modes and ploidy level interactions in *Sorbus* (Malinae, Rosaceae): playful youth and serious adults. – Manuscript.

Martin Lepší wrote the first draft of the manuscript, took comments from the co-authors, collected samples and conducted flow-cytometric analyses. P. Koutecký supervised and conducted flow-cytometric analyses, analysed data, created graphs, revised and considerably rephrased and supplemented the first draft of the manuscript, and wrote the 'Material and methods' section. Jana Bílá and Tomáš Urfus collected and analysed ca 40% of samples. P. Lepší participated in the field work. T. Rich initiated the sampling, provided samples of British taxa and edited the English of the text.

Co-author agreement:

Zdeněk Kaplan, Petr Koutecký, Petr Lepší, Tim Rich and Petr Vít, the main co-authors of all presented papers, fully acknowledge the contribution of Martin Lepší as stated above, consent the publication of the papers in this PhD. thesis and support it by their signatures:

Zdeněk Kaplan, Z. Kaplan

Petr Koutecký

Petr Lepší

Tim Rich

Timothy Rich

Petr Vít

Contents

Introduction

Picture on previous page *Sorbus eximia*, Koda

Introduction

The genus Sorbus *– description, distribution and species diversity*

Sorbus in the broad sense is a genus of deciduous trees or shrubs with simple or pinnate leaves. Flowers of its members are arranged in compound corymbs or rarely panicles and consists of persistent or deciduous sepals, white or rarely reddish or pinkish petals, (10)–15–25(–40) stamens, 2–5 partly free or connate carpels with 2 ovules and 2–5(–7) free or connate styles. Fruits are usually small pommes of various colours (Aldasoro et al. 2004, Rich et al. 2010). The genus is confined to the Northern Hemisphere and has a circumpolar distribution, being found throughout Europe, Asia and North America, and marginally occurring in North Africa. The centres of highest diversity occur in Europe and East Asia (Aldasoro et al. 2004, McAllister 2005). The genus *Sorbus* s.l. comprises about 250 species worldwide (Aldasoro et al. 2004), of which 160 are reported from Europe (Kurtto 2009).

Sorbus *within the Rosaceae*

The Rosaceae are a moderately large family of angiosperms comprising ca 100 genera with ca 3,000 species (Kalkman 2004). A new molecular-based classification distinguishes three subfamilies within the family – Dryadoideae, Rosoideae and Amygdaloideae (Potter et al. 2007). Pomme-bearing plants, traditionally recognized as subfamily Maloideae and including the genus *Sorbus*, are newly classified in the monophyletic subtribe Malinae within the subfamily Amygdaloideae. The Malinae, together with three related dry capsule-bearing American genera *Lindleya*, *Kageneckia* and *Vauquelinia*, represent the tribe Maleae, which is sister to the ancestral genus *Gillenia*, endemic to eastern North America (Potter et al. 2007). The latest hypothesis, based on phylogenetic, morphological and fossil evidence, suggests that the Malinae (base chromosome number n=17) originated from chromosome doubling in the *Gillenia* (n=9) lineage, followed by the aneuploid loss of one pair of homologous chromosomes (Evans & Campbell 2002, Evans & Dickinson 2005). An older competing hypothesis states that the Malinae could have evolved from hybridization between ancestors of the Rosaceae with base chromosome numbers of n=9 and n=8 (Phips et al. 1991). The Malinae include ca 28 genera with ca 950 species with worldwide distribution and a centre of species diversity in the temperate Northern Hemisphere. Some members of the subtribe are commercially important for their edible fruit, ornamental value, or both, such as apple trees (*Malus*), chokeberry (*Aronia*), pears (*Pyrus*), serviceberry (*Amelanchier*), cotoneasters (*Cotoneaster*), hawthorns (*Crataegus*) and *Sorbus*.

Intergeneric variability and classification of Sorbus

Sorbus is traditionally classified into five subgenera – *Aria*, *Chamaemespilus*, *Cormus*, *Sorbus* and *Torminaria* (Kutzelnigg 1995, Meyer et al. 2005, Rich et al. 2010; Fig. 1). The most diverse and widespread subgenera are *Aria* and *Sorbus*, both of which include both amphimictic and apomictic species (Aldasoro et al. 2004, McAllister 2005, Kurto 2009). Their members occur in vast areas of Eurasia and the subgenus *Sorbus* is also distributed in North America. The subgenus *Aria* is morphologically very variable and is divided into 6–14 sections and/or subsections (Gabrielian 1978, Aldasoro et al. 2004) occurring mainly in the South and Southeast of China. The number of sections and their delimitation vary considerably depending on the taxonomic conception of the author. For example, some taxonomists treat sect. *Micromeles* as an independent subgenus or genus (Gabrielian 1978, Kovanda 1981, Phips et al. 1990, Robertson et al. 1991) or consider the subgenus *Chamaemespilus* as a mere section of the subgenus *Aria* (Aldasoro et al. 2004). It is apparent that the use of modern biosystematic methods is necessary for a more objective classification of intra-generic variation of the genus *Sorbus* s.l. (see further). There is a consensus regarding the division of the subgenus *Sorbus*, which is classified into two main groups – *Sorbus* and *Albocarmesinae*, which have the greatest diversity in south-western China and the Sino-Himalayan region, respectively (McAllister 2005).

The remaining subgenera are monotypic and comprise diploid amphimictic species with the exception of the subgenus *Chamaemespilus*, in which diploids, triploids and tetraploids are reported (Warburg & Kárpáti

1968, Meyer et al. 2005). The subgenus *Chamaemespilus* is represented by the European endemic *S. chamaemespilus*, the subgenus *Cormus* by the south-European-to-west-Asian *S. domestica* and the subgenus *Torminaria* by the European-to-west-Asian *S. torminalis* (including *S. tiliifolia*, Rich et al. 2010). In addition to these three species, *S. aucuparia* from the subgenus *Sorbus* and sect. *Aria* of the subgenus *Aria* occur in Europe. The section *Aria* comprises the diploid amphimictic *S. aria*, possibly also the diploid and amphimictic *S. umbellata*, and an intricate complex of many transitional taxa between these two species, which are believed to be apomictic and polyploid (Aldasoro et al. 2004, Rich et al. 2010).

Five Sorbus *subgenera in Europe*

From a morphological point of view, the five basic European *Sorbus* taxa can be divided in two groups – pinnate-leaved (*S. domestica* and *S. aucuparia*) and simple-leaved species (*S. chamaemespilus*, *S. torminalis*, *S.* subg. *Aria*). *Sorbus domestica* is characterized by a fissured and flaky bark, glabrous and brown-green buds, 5(–7) pistils and large, up to 50 mm long unevenly green or brownish-red tinged fruits. By contrast, *S. aucuparia* has smooth bark, usually hairy and dark brown buds, (2–)3–4(–5) pistils, and small, up to 14 mm long and orange-red to dark red fruit. *Sorbus torminalis* has simple lobed leaves with deep and acute lobes, an inferior ovary and brown fruits with a homogenous mesocarp and a withering calyx. *Sorbus* subg. *Aria* and *S. chamaemespilus*, unlike *S. torminalis*, have entire or shallowly lobed leaves, semi-inferior ovary and orange-red to dark red fruit with a heterogeneous mesocarp and a persistent calyx. *Sorbus* subg. *Aria* is differentiated from *S. chamaemespisus* by taller growth, tomentose leaves underneath with craspedromous venation and spreading white petals. *Sorbus chamaemespilus* is a small shrub, with glabrous leaves with camptodromous venation and erect red petals.

The five basic European *Sorbus* taxa differ also in their ecology. *Sorbus chamaemespilus* is an alpine species strictly confined to mountains. *Sorbus torminalis* and *S. domestica* inhabit termophilous woodland communities and are missing in Northern Europe. The subgenus *Aria* is rather termophilous, but diploid *S. aria* and some polyploids occur in mountains or in Scandinavia. Finally, the widespread *S. aucuparia* occurs from the Arctic region to mountains of Southern Europe, avoiding the warmest and driest regions (Rich et al. 2010).

Intersubgeneric hybridization and classification of its products

European members of the genus *Sorbus* are well known for extensive interspecies hybridization. *Sorbus aucuparia*, *S. chamaemespilus, S. torminalis* and *S. aria* hybridize relatively frequently with polyploid members of the subgenus *Aria* and produce polyploid intersubgeneric taxa that are largely viewed as separate apomictic species (see further). By contrast, the former three basic taxa do not hybridize with each other, and *S. domestica* does not participate in natural hybridogenous processes at all. According to the parental combination, intersubgeneric hybrids are grouped into three hybridogenous subgenera: *Soraria* – subg. *Sorbus* × subg. *Aria*, *Tormaria* – subg. *Torminaria* × subg. *Aria* and *Chamaespilaria* – subg. *Chamaemespilus* × subg. *Aria* (Májovský & Bernátová 2001). Complex hybrids originating from crossing of an existing hybrid with a third species are also known: *Chamsoraria* – subg. *Chamaemespilus* × subg. *Sorbus* × subg. *Aria* (Májovský & Bernátová 2001) and *S. intermedia* – subg. *Sorbus* × subg. *Torminaria* × subg. *Aria* (Fig. 1). These hybridogenous groups differ in their distribution and ecological demands, which are related to traits of their parental taxa. The subgenera *Chamaespilaria* (parental species subg. *Aria* and *S. chamaemespilus*) and *Chamsoraria* (parental species subg. *Aria*, *S. chamaemespilus* and *S. aucuparia*) encompass alpine species that are confined to European mountains. By contrast, the subgenus *Tormaria* (subg. *Aria* and *S. torminalis*) includes thermophilous species, which are absent from mountains and northern parts of Europe. The subgenus *Soraria* (subg. *Aria* × *S. aucuparia*) is abundant in Northern Europe and European mountains but occurs only rarely in warm regions of Central Europe (Kutzelnigg 1995). Finally, the complex hybridogenous group including *S.* subg. *Aria*, *S. torminalis* and *S. aucuparia* is represented by *S. intermedia* and its backcrosses with *S. aucuparia*, which are native to the Baltic region and southern Scandinavia (Lemche 1999, Nelson-Jones et al. 2002). The subgenus *Aria* (parents *S. aria* s. str. and diverse polyploids of the subgenus *Aria* and in Southern Europe possibly also *S. umbellata*) consists of many thermophilous species, but it also occurs in Scandinavia and certain mountain areas.

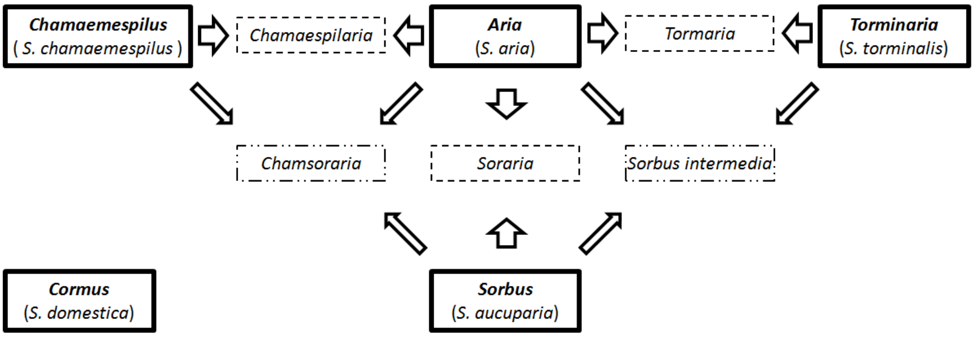

Fig. 1. – European subgenera of the genus *Sorbus* and their relationships. Basic subgenera are bordered by the bold lines, hybridogenous subgenera with two parental species are delimited by the dashed lines and hybridogenous taxa with three parents by the ghosted line. Diploid species are given in parentheses.

Phylogeny of Sorbus

Despite relatively common intersubgeneric hybridization, modern phylogenetic studies indicate that at least some of the basic subgenera should be treated as independent genera. The substantial extent of crossbreeding is ascribed to weak barriers to hybridization rather than close evolutionary relationships (Robertson et al. 1991, Li et al. 2012). In other words, the traditional subgeneric division probably does not satisfactorily reflect the phylogeny of *Sorbus* within the Malinae (Robertson et al. 1991, Cambell et al. 2007, Potter et al. 2007, Li et al. 2012, Lo & Donoghue 2012). It is already clear that pinnate-leaved (*Sorbus*, *Cormus*) and simple-leaved (*Aria*, *Torminaria* and *Chamaemespilus*) species form two distinct monophyletic groups (Potter et al. 2007, Lo & Donoghue 2012). However, the relationships within these two groups are not sufficiently understood and deserve further investigation. Therefore, the traditional broad delimitation of *Sorbus* in Europe still remains in use in systematics and taxonomy (Cornier 2008, Lepší et al. 2009b, Németh 2012, Pellicer et al. 2012, Raimondo et al. 2012, Velebil 2012, Ludwig et al. 2013, Meyer et al. 2014) as well as in national and supranational botanical compendia and databases (e.g. Kurtto 2009, Rich et al. 2010, Grundt & Salvesen 2011) and is adopted in this thesis.

Diversification within Sorbus

As outlined above, the principal mechanism of diversification in the genus *Sorbus* is hybridization accompanied by polyploidization and apomixis. These processes are documented in several cytological and embryological studies (Liljefors 1953, 1955, Jankun & Kovanda 1986, 1987, 1988) and later confirmed by molecular methods (Proctor et al. 1989, Nelson-Jones et al. 2002, Chester et al. 2007, Robertson et al. 2004a, b, 2010). Some taxa might also arise by autopolyploidization or mutation subsequently conserved by apomixis (Liljefors 1955, Rich et al. 2010), but direct evidence of these two evolutionary processes is missing. The residual sexuality in apomictic species enables ongoing hybridization and genesis of new biotypes. The genus *Sorbus* therefore represents an excellent model that provides opportunities to observe the formation of new taxa, reveal the origins of stabilized apomictic species and study the roles of polyploidization and apomixis in the formation of the observed diversity.

Apomixis in Sorbus

While diploid species are all amphimictic, polyploidy is accompanied by diverse degrees of apomixis. Apomixis in *Sorbus* usually comprises two coupled events: the development of an unreduced embryo sac and growth of the egg cell into an embryo without fertilization (parthenogenesis). However, these two processes are at least partly independent and may occur individually. Fertilization of an unreduced egg (so-called B_{III} hybrid production or chromosome summation) is rather rare (Liljefors 1953) but probably plays a considerable role in ongoing speciation (Robertson et al. 2004b). By contrast, the production of reduced seeds without fertilization (haploid parthenogenesis) has been reported only once (Jankun & Kovanda 1986) and no polyhaploids have been reported so far. Most *Sorbus* apomicts follow the aposporous pattern (Liljefors 1953). The two other detected apomictic pathways are infrequent – diplospory was detected independently by Jakun & Kovanda (1987, 1988) and Liljefors (1953), and adventitive embryony was reported by Jakun & Kovanda (1986, 1987, 1988) and Jankun (1994) as the only case of this event known in the Malinae (Campbell et al. 1991). The distinction between diplospory and apospory is of high evolutionary importance because diplospory may enable genetic recombination (Campbell et al. 1991). Unfortunately, the differentiation between these two processes is not always clear (Lijefors 1953). The embryo sac is of the standard 8-nucleate *Polygonum* type (Liljefors 1953), which consist of an egg cell accompanied by two synergids, a central cell containing two polar nuclei, and three 1-nucleate anthipodas (Lijefors 1953). Fertilization of polar nuclei, which initiates endosperm development, is required for the seed set (pseudogamy); available data suggest fusion of two polars and either one or two reduced sperms or one unreduced sperm (Liljefors 1953, Jankun & Kovanda 1987, 1988, Ludwig et al. 2013, Hajrudinović et al. 2015b).

A tendency towards a balanced endosperm (maternal-to-paternal genome ratio of 2:1), which is a crucial condition for seed development in most flowering plants, has been observed in diploid and tetraploid *Sorbus* regardless of their sexual or apomictic origin; in triploids, by contrast, there is some tolerance of endosperm imbalance (Hajrudinović et al. 2015b). The fertility of *Sorbus* pollen, tested by germination experiments, was found to be related to ploidy in Scandinavia. The pollen germination percentage was high in most diploids, very low or zero in triploids and variable but usually relatively good in tetraploids (Lijefors 1953). Similar results were obtained by observing pollen stainability of British *Sorbus*. Diploids demonstrated the highest pollen stainability, followed by tetraploids, and the lowest stainability were observed in triploids (Rich 2009). Considerable differences related to ploidy level were observed also with regard to the mating system, as was shown on the example of a natural diploid and polyploid *Sorbus* population in the Avon gorge in Britain (Ludwig 2013). Diploids were shown to be outcrossing and self-incompatible. Triploids exhibited nearly obligate self-incompatibility and thus dependence on pollen from other co-occurring taxa. By contrast, tetraploid taxa exhibit self-compatibility, so they do not require any inter-taxon pollination.

Sorbus *among other apomictic plants*

Taxonomically widespread apomixis occurs sporadically among flowering plants, being reported from 293 genera out of about 13,000. Half of these genera shows sporophytic apomixis (adventitious embryony) and the rest are gametophytic apomicts (Hojsgaard et al. 2014). Sporophytic apomixis is frequent in tropical or subtropical woody plants of the Rutaceae, Celastraceae and Orchidaceae. By contrast, three-fourths of gametophytic apomicts occur in perennial herbs, shrubs and trees of the Rosaceae, Poaceae and Asteraceae (Asker & Jerling 1992, Carman et al 2011). However, adventitious embryony is also rarely reported from these three plant groups, including *Sorbus* (Asker & Jerling 1992, Jankun 1994). The type of gametophytic apomixis differs among these families. Apomictic members of the Rosaceae and Poaceae frequently exhibit apospory and pseudogamy whereas Asteraceae are often diplosporous with autonomous endosperm development (Whitton et al. 2008). Within the Rosaceae, apomixis is most commonly found in the tribe Maleae (Campbell et al. 1991), where it is documented in many genera such as *Aronia*, *Amelanchier*, *Cotoneaster*, *Crataegus*, *Malus*, *Photinia* and *Sorbus* (Campbell et al. 1991), and in the subfamily Rosoideae, where it is found in *Potentilla*, *Rubus*, *Alchemilla* and *Rosa* (Asker & Jerling 1992).

Many genera from which apomixis is reported create so-called agamic complexes. These typically include a series of polyploid sexual and facultatively or obligately agamospermous taxa, which are largely the result of various hybridizations between sexuals or between sexuals and apomicts of the complex (Bayer 1987). The complexity of agamic complexes varies across different taxonomic groups. European *Rubus fruticosus* agg. and *Taraxacum officinale* agg. are examples of highly complex apomictic groups. Both aggregates show a high diversity of apomictic lineages even at local level. Several tens of microspecies per locality are no exception. Members of these two genera have a very good ability to spread and the current landscape provides large areas of suitable habitats such as conifer plantations and intensively managed meadows, respectively. *Sorbus* populations, by contrast, are usually species-poor and confined to rare and often relict habitats such as open (semi-)natural forest and rocks. The rarity of these habitats limits significantly their dispersal, so *Sorbus* apomicts are often confined to the region of their origin and usually have a regional or more often only local distribution. The low within-locality diversity of apomictic species often makes the taxonomic situation rather clear, and in local intersubgeneric hybridogenous *Sorbus* populations (e.g. subgenus *Tormaria*, *Soraria*), is even possible to infer the parental combination. The determination of both or at least one parental species is also made possible by the fact that parents belong to morphologically well defined subgenera. In some apomictic complexes such as *Poa* or *Amelanchier*, low morphological differentiation between parental taxa and partly also high rates of residual sexuality preclude the delimitation of even microspecies (Dickinson 1999, Hörandl 2009). Another aspect contributing significantly to the low local diversity of intersubgeneric hybridogenous *Sorbus* is probably the predominance of obligate apomixis. Within the subgenus *Aria*, the situation is more complex because several polyploid taxa can participate in diversification and because hybridization is more frequent due to close relationships between parental species (Ludwig et al. 2013). Diverse interactions can also be expected between the phylogenetically close subgenera *Aria* and *Chamaemespilus* in European mountains (Gömöry & Krajmerová 2008) or in the subgenus *Soraria* in Scandinavia (Grundt & Salvesen 2011).

The relatively low complexity of many European *Sorbus* populations is also partly caused by the absence of sympatric occurrences of closely related sexual diploids or tetraploids. In American *Amelanchier* and *Crataegus*, morphologically similar diploids cross mutually and also with co-occurring tetraploids, in both cases producing triploids (Burgess et al. 2014, Talent & Dickinson 2007). Such an interaction between diploids does not occur in *Sorbus* – diploids are distantly related, and products of their rare hybridization are predominantly also diploid (Rich et al. 2010). However, the formation of triploids in mixed populations of diploids and tetraploids is very common in *Sorbus* (Ludwig et al. 2013). In *Rubus fruticosus* agg., diversification is driven by high rates of facultative apomixis at the tetraploid level (*R.* ser. *Glandulosi*) or by existence of tetraploid sexual species (*R. caesius*), both hybridizing with polyploids to produce new apomictic lineages (Šarhanová et al. 2012). Fully or predominantly sexual and widely distributed tetraploids are uknown in *Sorbus*, so the formation of new apomicts is a rare event compared to some other agamic complexes. In *Taraxacum officinale* agg., the relatively common hybridization within mixed populations of asexual triploids and sexual diploids is probably the predominant pathway maintaining diversification of this group (den Nijs 1997). Micro-evolutionary processes are extremely complex also within the genus *Pilosella* due to high rates of facultative apomixis and common production of hybrid swarms, which may include aneuploids and viable polyhaploids (Krahulec et al. 2011).

Agamic *Sorbus* does not reach high ploidy levels (2n=3x, 4x, rarely 5x), unlike other apomictic groups. For example, in the genus *Potentilla* sexual plants are tetraploid, while apomicts are pentaploid or octoploid (Dobeš et al. 2013). In European *Rubus fruticosus* agg., 3x–6x ploidy levels are known in apomictic taxa (Krahulcová et al. 2013). The genus *Taraxacum* consists mostly of triploids, but plants up to the decaploid level are encountered (den Nijs 1997), and in *Pilosella* tetraploids to octoploids are reported (Krahulcová et al. 2009).

Other characteristic features of the genus *Sorbus* are their woody perennial life form and tight link to relic habitats. These two characters facilitate the long-term persistence and stability of *Sorbus* populations. Woody perennials have high competitive ability and live longer compared to herbaceous perennials. In addition, relict habitats are very stable. On the other hand, their greater demands for space coupled with the rarity of suitable habitats mean that *Sorbus* populations often consist of a few individuals only. Other agamic groups, such as *Hieracium* or *Potentilla*, inhabit stable communities, too, whereas *Rubus*, *Taraxacum* and *Pilosella* occur at disturbed and often ruderal habitats that are evanescent in character.

Species concept in apomictic Sorbus

The species concept which treats apomictic lineages as independent species has recently dominated (Meyer et al. 2005, Cornier 2008, Grundt & Salvesen 2011, Castellano et al. 2012, Németh 2012, Raimondo et al. 2012, Velebil 2012, Hajrudinović et al. 2015a). However, some authors advocate the broader morphology-based species approach which avoids delimitations of many species but, on the other hand, groups together unrelated taxa (cf. Aldasoro et al. 2004). In this thesis the narrow species concept is adopted, mainly for its natural approach.

Only a few current proponents of the narrow approach have set out explicitly what species within *Sorbus* should be. However, all are in general congruence with the definition by Rich et al. (2010), who defined their ideal apomictic *Sorbus* species as follows: morphologically recognizable entities with cytological and molecular support which are monophyletic, biologically successful and obligate apomicts. However, not all the conditions are met in practice. For example, it is already apparent that some *Sorbus* taxa are of multiple origin from the same parents (e.g. *S. pseudofennica* may have arisen at least five times independently from *S. arranensis* Hedl. and *S. aucuparia*; Robertson et al. 2004a, b), and some or perhaps many are probably facultatively apomictic mothers to varying extents (Robertson et al. 2010). Another problematic part of the definition is how numerous species have to be in order to be considered biologically successful. Meyer et al. (2005) did not accept singular apomicts or groups of plants of vegetative origin (via root suckers) as species. Similarly, Májovský & Bernátová (2001) stated that singular individuals should not be subject to taxonomic classification and recommended that apomictic species should have a regional or wider distribution. The problem of how large a distribution area an apomictic lineage should have to be treated as a species or how many individuals make an apomictic species has not been addressed in *Sorbus*. Generally, in other apomictic groups more widespread, abundant or distinctive clones are named whereas rare and restricted clones remain unnamed. Only in *Rubus* has there been any attempt to rationalize the taxonomy of European members of *R. fruticosus* agg. by applying the arbitrary definition of a species as an apomictic clone with a distribution range of at least (20–)50 km (Holub 1997, Weber 1999, 2002). Further *Sorbus* research will show whether the species concept outlined by Rich et al. (2010) is tenable for the whole of Europe, including regions with high rates of facultative apomixis, which is usually combined with a high diversity of apomictic clones and blurred differences between them.

Research of hybridogenous Sorbus *taxa in Europe*

Hybridogenous and apomictic *Sorbus* species have long been recognized in Europe, especially in its northern and central part and in the British Isles. The first hybridogenous *Sorbus* species were recognized in the 18th century. They are two Scandinavian species *S. hybrida* (subg. *Soraria*) and *S. intermedia* (subg. *Sorbus* × subg. *Torminaria* × subg. *Aria*) and the French species *S. latifolia* (subg. *Tormaria*). During the 19th century several other species recognized to this day were described in various part of Europe, for example *S. sudetica* (subg. *Chamaespilaria*) from the Czech Republic in 1834, *S. rupicola* (subg. *Aria*) from Great Britain in 1864, *S. mougeotii* (subg. *Soraria*) from France in 1868 and *S. austriaca* (subg. *Soraria*) from Austria in 1892 (Kutzelnigg 1995). At the turn of the 19th and 20th century, T. Hedlund, a Scandinavian botanist summarized findings on the genus *Sorbus* into a worldwide monograph where he published description of several new hybridgenous species and reclassified many previously distinguished taxa from lower taxonomic ranks to the species level (Hedlund 1901). In the 50s of the 20th century, A. Liljefors continued Hedlund's work in Scandinavia by publishing comprehensive cytological and embryological studies (Liljefors 1953, 1955). Around the same time, other authors begin to study the genus in Central Europe. They were M. Kovanda in the Czech Republic (Kovanda 1961a–c), R. P. G. Düll in Germany (Düll 1961) and Z. Kárpáti in Hungary, whose extensive monograph of *Sorbus* in Hungary and adjacent areas (Kárpáti 1960) had a lasting influence on the taxonomy of Central European *Sorbus.* At that time E. F. Warburg studied *Sorbus* in Great Britain (Warburg 1952). He and Z. Kárpáti compiled knowledge about 103 European species into the fundamental European botanical compendium Flora Europaea (Warburg & Kárpáti 1968). In the following second half of the 20th century, J. Challice, A. Jankun and M. Kovanda conducted several embryological and chemotaxonomic studies and significantly contributed to the understanding of the variability and relationships within the genus (Challice & Kovanda 1978, 1986, Jankun & Kovanda 1986, 1987, 1988, Jankun 1994). At the end of the millennium, a treatment of Central European *Sorbus* was published in the flora of Central Europe (Illustrierte Flora von Mittel-Europe, Kutzelnigg 1995), and the first molecular studies of British species began to emerge (Proctor et al. 1989, Proctor & Groenhof 1992, Lemche 1999). At the beginning of the 21st century, a systematic review of the subgenera *Aria* and *Torminaria* was published (Aldasoro et al. 2004) where many previously accepted hybridogenous species were included into broadly morphologically delimited species, often regardless of their origin and without any support of molecular methods. However, this broad taxonomical concept is not accepted by most of European taxonomists. Due to the advent of new biosystematic methods and increased general interest in hybridization, polyploidization and alternative reproductive modes, the genus *Sorbus* was subjected to detailed research in Great Britain and the Czech Republic, which resulted in the descriptions of several dozen new taxa (Rich et al. 2009, Rich & Proctor 2009, Lepší et al. 2008, 2009b). These studies and ongoing taxonomical research prompted the edition of several regional *Sorbus* monographs and determination keys – in Great Britain and Ireland (Rich et al. 2010), Bavaria (Meyer et al. 2005), Norway (Grundt & Salvesen 2011), Hungary (Németh 2009) and the Czech Republic (Kovanda

2002). These countries are among the best researched regions in Europe as far as the genus *Sorbus* is concerned. From the United Kingdom, four dozen apomictic, predominantly endemic, species are reported, including not only taxa from the subgenera *Tormaria* and *Soraria,* but also many taxa from the polymorphic and less understood subgenus *Aria* (Rich et al. 2010). The Norwegian *Sorbus* monograph presents ten apomictic species, two from the subgenus *Aria* and the rest from the subgenus *Soraria* (Grundt & Salvesen 2011). The Flora of Germany has about 30 native mostly endemic species of five subgenera (*Tormaria*, *Aria*, *Soraria*, *Chamaespilaria*, *Chamsoraria*) whereas the richest species groups are the subgenera *Tormaria* (18 species) and *Soraria* (8 species; Meyer 2016). In Hungary, the most diversified groups are the subgenus *Tormaria*, numbering about 30 species, and the insufficiently explored subgenus *Aria*, with ca 15 currently distinguished species (Németh 2009). By contrast, the taxonomy of hybridogenous *Sorbus* in other European regions, especial in Southern Europe have yet to be studied comprehensively. However, several taxonomic works evaluating *Sorbus* diversity appeared recently in France (Cornier 2008), Italy (Castellano et al. 2012, Raimondo et al. 2012), and Bosnia and Herzegovina (Hajrudinović et al. 2015a).

Hybridogenous taxa in the Czech Republic

Research into the genus *Sorbus* has a strong tradition in the Czech Republic thanks to the lifelong interest of M. Kovanda, who conducted several taxonomical and embryological studies in the second half of the twentieth century (Kovanda 1961a–c, Challice & Kovanda 1978, 1986, Kovanda 1984, Jankun & Kovanda 1986, 1987, 1988, Kovanda 1996a, b, 1997a). These works and later on also treatments of *Sorbus* in two principal national botanical monographs – the Flora of the Czech Republic (Kovanda 1992) and the Key to the Flora of the Czech Republic (Kovanda 2002) – aroused interest of other researchers, and several taxonomic revisions and novelties were published, predominantly with support of modern biosystematics methods (Šefl 2000, Boublík et al. 2002, Vít 2006, Šefl 2007, Lepší et al. 2008, 2009a, b).

Before the beginning of this thesis in 2011, there were 21 *Sorbus* species recorded in the Czech Republic. *Sorbus torminalis*, *S. aria* and *S. danubialis* were reported from warm to moderately warm areas of Bohemia and Moravia (Kovanda 1992). The widespread species *S. aucuparia* was known to be abundant throughout the country apart from largely deforested lowlands of Bohemia and Moravia, where it is rare or even absent (Kovanda 1992, Slavík 1998). *Sorbus domestica* was listed as a casual neophyte that escaped and naturalized in several areas of southern Moravia and in north-western Bohemia (Kovanda 1992, Pyšek et al. 2012). *Sorbus austriaca* and *S. carpatica* were included in the Czech flora in 1996 and were viewed as diploid sexual transitional taxa between *S. aria* and *S. aucuparia* (Kovanda 1996b). They were found in the valley of the river Dyje south of the town of Vranov nad Dyjí in southern Moravia, and *S. austriaca* was also found in the karstic area of Moravský kras (Kovanda 1996b, 1997b, 2002). The name *S. subdanubialis* was applied to plants intermediate between *S. danubialis* and *S. aria*, discovered in the valley of the river Dyje south of the town of Vranov nad Dyjí in southern Moravia (Šefl 2007). *Sorbus graeca* was included in the Czech flora in 1997 based on observations made in the karstic area of Moravský kras and the Podyjí region (Kovanda 1997a, 2002). Apart from the predominantly widespread species mentioned above, 11 (sub-)endemic hybridogenous taxa were described from the country. The first hybridogenous *Sorbus* to be distinguished in the Czech Republic was *S. sudetica* (Tausch 1834), a product of hybridization between *S. chamaemespilus* and a member of the subgenus *Aria* (subg. *Chamaespilaria*), confined to (sub-)alpine areas of the Krkonoše Mts (Kovanda 1992). It should be noted that *S. chamaemespilus* is absent in the whole area of the Czech Republic at present. The most diverse subgenus in the Czech Republic is the subgenus *Tormaria* (*S. torminalis* and subg. *Aria* parentage). It includes (1) *S. albensis*, known at 12 localities in the wide surroundings of the deep valley of the river Labe in the České středohoří Mts east of the town of Litoměřice (Lepší et al. 2009b); (2) *S. alnifrons*, confined to Jihlava river valley near Ivančice in southern Moravia (Kovanda 1996b); (3) *S. bohemica*, the most widespread hybridogenous *Sorbus* species in the

Czech Republic recorded at 31 localities in the central part of the České středohoří Mts in north-western Bohemia (Lepší et al. 2009b), (4) *S. eximia*, endemic to the karst area of Český kras (Kovanda 1984), (5) *S. gemella*, recorded at 12 localities in the Džbán hills in the southern surroundings of the town of Louny in north-western Bohemia (Kovanda 1996a, Lepší et al. 2009a), (6) *S. hardeggensis*, described from the valley of the river Dyje south of the town of Vranov nad Dyjí in southern Moravia and Lower Austria (Kovanda 1996b); (7) *S. milensis*, a stenoendemic of Milá hill north of the town of Louny in the southern part of the České středohoří Mts (Lepší et al. 2008); (8) *S. portae-bohemicae*, confined to the Porta bohemica gorge and the Oparenské údolí valley in the northern surroundings of the town of Lovosice in the České středohoří Mts (Boublík et al. 2009, Lepší et al. 2009b); and finally (9) *S. rhodanthera*, endemic to Chlumská hora hill near the town of Manětín in western Bohemia (Kovanda 1996a). The only endemic representative of the subgenus *Soraria* known in the Czech Republic was *S. quernea*, described from two places in Prague (Kovanda 1996a). *Sorbus intermedia*, a native species in southern Scandinavia and parts of the Baltics, is commonly planted for ornamental purposes and along highways in the Czech Republic, and occasionally escapes from cultivation (Kovanda 1992). Based on old literature records and herbarium specimens from the 19th century from the subalpine belt of the Krkonoše Mts, Kovanda (1997c) regards *S. intermedia* as possibly native, explaining its presence by long-distance dispersal by birds from the Baltic countries.

Conservation

Many European apomictic *Sorbus* species have restricted distribution areas and most of them are endemic to one or two countries and are therefore of great importance for national nature conservation. The proportion of *Sorbus* species among endemic plants in some national floras is significant; in the Czech Republic, for example, *Sorbus* accounts for ca 20% of all endemic vascular plants (Kaplan 2012). This is especially true in the northern half of Europe, where the diversity of the endemic flora was repeatedly reduced by considerable climatic and vegetation changes caused by glaciations, and most endemic plants are of quaternary age as a result of repeated re-colonization, migration, isolation and lately also landscape fragmentation due to human activity. *Sorbus* is an example of a plant group that underwent intensive diversification in the Quaternary period and especially in the Holocene (neo-endemism).

The well documented currently ongoing diversification within *Sorbus* (e.g. Robertson et al. 2004b, Hajrudinović et al. 2015a) is another strong argument for the protection of this genus because the processes leading to increased diversity (and eventually speciation) are at least as important as their products (species). The conservation of evolutionary processes places new demands on conservation efforts because management plans should protect habitats where two or more *Sorbus* species co-occur as potential parents of new endemics to enable the generation of new taxonomic diversity by hybridization in the future. Analogically, singular or rare apomicts should also be protected because they can act as evolutionary 'stepping stones' towards more successful lineages by hybridizing with other co-occurring *Sorbus* individuals. It is necessary to mention that some *Sorbus* triploids require pollination by other *Sorbus* taxa in order to produce seeds (Ludwig et al. 2013), so the presence of other species is a precondition for their long-term survival.

Most Central European *Sorbus* species of lower altitudes are now significantly endangered by spontaneous colonization of open habitats (rocks, dry grasslands, open forests) by trees. The spread of trees is caused by the cessation of traditional landscape management (e.g. grazing on low-productive dry and steep slopes) and supported also by eutrophication. Traditional management of woodlands used to maintain open and oligotrophic forests, which are the main habitat type for many *Sorbus* species. However, the shady conditions that prevail in present-day forests are unfavourable for the long-term survival and regular reproduction of light-demanding *Sorbus*. Particular attention should be paid to their protection in future, and appropriate forest management should be implemented.

Endemism, the production of new biological diversity and the decline of their habitats make *Sorbus* very interesting from the nature conservation perspective. Moreover, *Sorbus* species can be used as umbrella or flagship species in conservation strategies because they mostly inhabit relict or semi-natural habitats of high biological value, and their tree life form makes them conspicuous and attractive for the general public.

Objectives of the thesis

The main aim of this thesis is to evaluate the variability of the genus *Sorbus* in the Czech Republic in a Central European context and to reveal the causes of the observed diversity based on traditional and modern biosystematic methods – nuclear microsatellite markers, chromosome counts, flow cytometry, and multivariate morphometric and outline analyses. Most previous taxonomic treatments in Central Europe are based solely on morphology, i.e. with little or no knowledge of the ploidy structure or genetic variability of delimited taxa and could therefore be to some extent burdened by subjectivity and therefore required a revision based on modern methods (paper I–VI). The taxonomic conclusions presented here formed a suitable basis for the second part of this thesis – comprehensive study of reproductive modes using flow-cytometric seed and pollen screens. The main aim of this second section is to reveal the principle mechanism of diversification and evolution in *Sorbus* (paper VII).

Paper I presents a revision and reassessment of the taxonomic diversity of the subgenus *Aria* (probably the least understood and most complex group of the genus *Sorbus* in Europe) occurring in the Czech Republic.

The aim of paper II is a taxonomic revision of *S. quernea*, a hybridogenous species described from two places in Prague (Czech Republic). The hypothesis that the species is taxonomically identical with *S. mougeotii* (a western-European hybridogenous species) is tested.

The objectives of paper III is to assess the variation of *S. eximia* (a Czech endemic hybridogenous taxon well known for apomixis at the diploid level), evaluate its taxonomic status and reassess its exceptional reproductive mode.

In paper IV, a newly discovered hybridogenous population of *S.* subg. *Soraria* (parental combination subg. *Sorbus* × subg. *Aria*) is evaluated taxonomically.

The aim of paper V is to revise and update all available distribution data on Czech *Sorbus* taxa and to subsequently compile them into the form of commented grid maps.

The aim of paper VI is to evaluate taxonomically eight *Sorbus* taxa newly discovered in Britain and to accommodate *S. intermedia* and its relatives into a system of hybridogenous subgenera.

Paper VII focuses on the variability of reproductive pathways in *Sorbus*. The main aims are to answer the following questions: What is the extent and variation of reproductive modes at individual ploidy levels? Are reproductive characteristics associated with the evolutionary success of particular taxa? Can the ongoing evolution and diversification in the genus be driven by variability in reproductive systems?

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Paper I

Taxonomic revision of *Sorbus* subgenus *Aria* occurring in the Czech Republic.

Lepší M., Lepší P., Koutecký P., Bílá J. & Vít P. (2015) Preslia 87: 109–162.

Picture on previous page *Sorbus moravica*, Lažánky

Preslia 87: 109–162, 2015

Taxonomic revision of *Sorbus* subgenus *Aria* occurring in the Czech Republic

Taxonomická revize jeřábů z podrodu *Aria* vyskytujících se v České republice

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Lepší M., Lepší P., Koutecký P., Bílá J. & Vít P. (2015): Taxonomic revision of *Sorbus* subgenus *Aria* occurring in the Czech Republic. – Preslia 87: 109–162.

Results of a taxonomic revision of *Sorbus* subg. *Aria* occurring in the Czech Republic are presented in a central-European context. Flow cytometry and multivariate morphological analyses were employed to assess the taxonomic diversity within the group. Diploid, triploid and tetraploid taxa were detected. Diploids are represented by a single species, *Sorbus aria*, which is morphologically very variable. This extensive variability is specific to this species and separates it, among other characters, from polyploid taxa. An epitype for *S. aria* is designated here. In the Czech Republic, *S. aria* has been recorded only in southern Moravia, and published records from Bohemia relate to other polyploid taxa of the subg. *Aria*. Native occurrencies previously recorded for *S. austriaca* and *S. carpatica* in the Czech Republic are erroneous and relate to individuals of *S. aria* with lobed leaves. Three new triploid species are described: *S. cucullifera* M. Lepší et P. Lepší from the Podyjí and Thaytal National Parks between the towns of Znojmo and Vranov nad Dyjí, and *S. moravica* M. Lepší et P. Lepší and *S. pontis-satani* M. Lepší et P. Lepší from the Moravian Karst area near the city of Brno. Tetraploid taxa include *S. danubialis* and two newly distinguished taxa: *S. thayensis* M. Lepší et P. Lepší and *S. collina* M. Lepší, P. Lepší et N. Meyer. *Sorbus thayensis* is endemic to the Podyjí and Thayatal National Parks and in a similar manner as a triploid species varies very little morphologically, which indicates that these polyploid taxa reproduce apomictically. All these new species are assumed to have originated from interbreeding between *S. danubialis* and *S. aria*. Up until now, *Sorbus collina* has been referred to as *S. aria* in the Czech Republic, as *S. pannonica* in Germany and as *S. graeca* in Austria and Hungary. Records refering to *S. graeca* in southern Moravia (Czech Republic) do not belong to *S. collina*, but are untypical individuals of *S. danubialis*. In the Czech Republic, *S. collina* occurs in central and north-western Bohemia. *Sorbus danubialis* is confined to central and north-western Bohemia and southern Moravia, and is taxonomically uniform. Old records of the existence of diploid individuals of *S. danubialis* in Bohemia are incorrect. Detailed distribution maps for all stenoendemics, photographs of the type specimens and line drawings of all polyploid species known from the Czech Republic are presented.

Keywords: apomixis, DAPI flow cytometry, hybridization, multivariate morphometrics, *Rosaceae*, subg. *Aria*, taxonomy

Introduction

European members of the genus *Sorbus* are traditionally classified into five subgenera – *Aria*, *Chamaemespilus*, *Cormus*, *Sorbus* and *Torminaria* (Kutzelnigg 1995, Rich et al. 2010). The first subgenus includes the diploid amphimictic *Sorbus aria*, possibly also the diploid and amphimictic *S. umbellata* and an intricate complex of many transitional taxa between these two species, which are believed to be apomictic and polyploid. The remaining subgenera are monotypic in Europe and comprise diploid amphimictic species with the exception of subg. *Chamaemespilus* in which diploids, triploids and tetraploids are reporeted (Warburg & Kárpáti 1968, Meyer et al. 2005). Subgenus *Chamaemespilus* is represented by *S. chamaemespilus*, subg. *Cormus* by *S. domestica*, subg. *Sorbus* by *S. aucuparia* and subg. *Torminaria* by *S. torminalis*. All of these monotypic subgenera except for subg. *Cormus* hybridize relatively frequently with subg. *Aria* and produce polyploid intersubgeneric taxa that are largely viewed as separate apomictic species (Meyer et al. 2005, Cornier 2008, Rich et al. 2010, Grundt & Salvesen 2011, Németh 2012, Vít et al. 2012).

Despite relatively common intersubgeneric hybridization, modern phylogenetic studies indicate that at least some of the subgenera should be treated as independent genera. The substantial extent of crossbreeding is ascribed to weak barriers to hybridization rather than close evolutionary relationships (Robertson et al. 1991, Li et al. 2012). In other words, the traditional subgeneric division probably does not satisfactorily reflect the phylogeny of *Sorbus* within the *Pyrinae* (Robertson et al. 1991, Potter et al. 2007, Li et al. 2012, Lo & Donoghue 2012). It is already clear that pinnate-leaved (*Sorbus*, *Cormus*) and simple-leaved (*Aria*, *Torminaria* and *Chamaemespilus*) species form two distinct monophyletic groups (Potter et al. 2007, Lo & Donoghue 2012). However, the relationships within these two groups are not sufficiently understood and deserve further investigation. Therefore, the traditional broad delimitation of *Sorbus* in Europe still remains in use in systematics and taxonomy (Cornier 2008, Lepší et al. 2009, Németh 2012, Pellicer et al. 2012, Raimondo et al. 2012, Velebil 2012, Ludwig et al. 2013, Meyer et al. 2014, Rich et al. 2014) as well as in national and supranational botanical compendia and databases (e.g. Király 2009, Kurtto 2009, Rich et al. 2010, Grundt & Salvesen 2011, Jäger 2011, Danihelka et al. 2012), and is adopted in this study.

From the taxonomic and evolutionary perspective, the most challenging group of the genus *Sorbus* in Europe is subg. *Aria*. It is distinguished from other subgenera of the genus *Sorbus* in Europe by the following combination of characters: leaves simple, serrate or shallowly lobed, greenish-grey to snowy white tomentose on lower surface, with craspedodromous venation (with veins running directly from the midrib and ending at the leaf margin); flowers proterogynous; petals white to yellowish-white, patent; styles 2–3 connate or free and tomentose at base; ovary semi-inferior, tomentose; fruit medium-sized or large, orange, red to dark red, with lenticels and persistent sepals, with heterogeneous mesocarp and cartilaginous endocarp and without sclereids.

Subgenus *Aria* is widely distributed in Europe and Asia, and comprises about 20–130 species, depending on the subgeneric and species delimitation (Gabrielian 1978, Phipps et al. 1990, Aldasoro et al. 2004, Kurtto 2009). The narrow species concept adopted already by Hedlund (1901) has recently dominated (Meyer et al. 2005, Cornier 2008, Grundt & Salvesen 2011, Castellano et al. 2012, Németh 2012, Raimondo et al. 2012, Velebil 2012, Lepší et al. 2013a, Rich et al. 2014); however, some authors do not treat apomictic lineages as independent species and advocate broader species delimitations (cf. Aldasoro et al. 2004).

Members of the subg. *Aria* are classified into seven sections based mainly on morphological and anatomical characters (Aldaroso et al. 2004). All European species of the subg. *Aria* are assigned to the section *Aria*; the other sections occur in East Asia and adjacent regions (Aldaroso et al. 2004). Depending on the species delimitation, the section *Aria* includes 11 (Aldaroso et al. 2004) to 48 species (Phipps et al. 1990). In Europe, about 30 species are distinguished within this section when the narrow species concept is used, i.e. when apomictic species are accepted (Kurtto 2009).

Subg. *Aria* plays a crucial role in microspeciation within the genus, and due to the high diversity of its taxa and ongoing evolution, causes significant taxonomic problems in Europe. Hybridization with members of the subgenera *Torminaria*, *Sorbus* and *Chamaemspilus* has produced numerous intersubgeneric apomictic taxa. However, even more taxonomic diversity has been generated by extensive hybridization within the subgenus. The weak reproductive barriers between its members have resulted in cases of great local diversity and complicated taxonomic situations (Feulner et al. 2013). It is therefore not surprising that, compared to other groups of the genus, subg. *Aria* is the least understood European group of the genus *Sorbus*.

It is hypothesized that most species distinguished within the subg. *Aria* in Europe stem from auto- or allopolyploidization of two basic species: the south-to-central-European species *S. aria* and the south-European and west-Asiatic species *S. umbellata* (Liljefors 1953, Kutzelnigg 1995). Polyploids originating from hybridization or polyploidization of these two basic species may have relatively large distribution areas, as is the case, for example, of the north-to-west-European endemic *S. rupicola*, known from Scandinavia and the British Islands. Other such polyploids can be confined to very small areas, such as *S. cheddarensis* L. Houston et Ashley Robertson, an endemic in the Cheddar Gorge in England (Rich et al. 2010). Local endemics are generally considered to be the results of hybridization between widely distributed polyploids and *S. aria* s. str. (Rich et al. 2010). For example, the above mentioned *S. cheddarensis* is supposed to have arisen from hybridization between *S. aria* and *S. porrigentiformis* E. F. Warb., a species with a scattered distribution in England and Wales (Rich et al. 2010).

A similar scenario is described for central Europe by the author of the fundamental *Sorbus* monograph of the region (Kárpáti 1960). He distinguished several basic (widely distributed) species connected by many morphologically transitional taxa. His concept influenced *Sorbus* taxonomy in central Europe for many years and is still at least partially accepted in many national compendia (Kovanda 1992, 2002, Májovský 1992, Fischer 2008, Király 2009, Jäger 2011). However, most of his taxonomic conclusions are based only on morphology, i.e. with little or no knowledge of the ploidy structure or genetic variability of delimited taxa. His treatments may therefore be to some extent burdened by subjectivity and therefore require revision using modern biosystematic methods.

The lack of the use of more objective methods in the taxonomy of subg. *Aria* also applies to the Czech Republic. Initially, only two species were reported from this country – *S. danubialis* and *S. aria* (Klika 1937, Kovanda 1961, 1992). Both were reported from Bohemia and Moravia, and both were regarded as species with relatively little variability (Kovanda 1992). Kovanda (1961) distinguished *S. danubialis* var. *apiculata*, a leaf morphotype confined mainly to Bohemia, and assigned most plants of *S. aria* from Bohemia to var. *cyclophylla* Beck, stating that they differ from the Moravian population (Kovanda 1992). Later, Kovanda (1997a) reports, again based on leaf morphology only, *S. graeca* from Moravia. Finally, Šefl (2007) recognized triploid individuals transitional between *S. aria* and *S. danubialis* in Moravia. In 2009, we started a taxonomic revision of the group and revealed several taxonomic novelties and serious misinterpretations.

The goal of this paper is to clarify the taxonomy of subg. *Aria* within the Czech Republic based on a combination of classical taxonomic approaches and modern biosystematic methods and provide a basis for further modern biosystematic research of this challenging group in central Europe.

Material and methods

Plant material and field work

Samples for morphometric analyses, flow cytometry and herbarium specimens were collected between 2009 and 2014, following the recommendations of Meyer et al. (2005), Rich et al. (2010) and papers published by Lepší et al. (2008, 2009). Flowering and fructiferous parts were collected in mid-May and September, respectively, and stored in 70% ethanol.

A revision of relevant *Sorbus* material kept in the following herbarium collections was undertaken: BRNM, BRNL, BRNU, CB, CHEB, CHOM, Herbarium of the Museum of Ústí nad Labem, HOMP, HR, LIM, LIT, MP, OL, OLM, OP, PL, PR, PRA, PRC, ROZ, SOKO, ZMT. For abbreviations of public herbaria, see Holmgren et al. (1990). Species nomenclature was unified according to Danihelka et al. (2012) except for *Sorbus* names, which follow Kutzelnigg (1995); otherwise, authorities are provided. Phytosociological nomenclature follows Chytrý et al. (2001).

Multivariate analyses

Multivariate morphometric analyses were used to reveal the species-specific characters of all the species delimited. For numbers and localities of the individuals sampled, see Table 1. A set of 16 quantitative and 2 qualitative characters was chosen on the basis of published determination keys and floras (e.g. Kutzelnigg 1995, Meyer et al. 2005, Rich et al. 2010), including those used in our previous studies (Lepší et al. 2008, 2009, Vít et al. 2012). The characters are: AT – angle of the lamina top, AB – angle of the laminar base, AV – angle between the third lateral vein from the laminar base and the midrib, A3L – angle of the tooth in which the 3rd lateral vein terminates, FL – length of fruit, FW – width of fruit, INC – depth of the incision between the 2nd and the 3rd lateral vein from the laminar base, LL – length of lamina, LL/LW – lamina length/width ratio, LW – width of lamina, NL – number of lenticels per 25 mm^2 of fruit, NT3L – number of teeth between the 2nd and 3rd lateral vein, NV – number of lateral laminar veins, PET – length of petiole, PL – length of petals, PW – width of petals, WP – the distance along the main nerve from the laminar base to the widest laminar width, WP/LL – ratio of the distance along the main nerve from the laminar base to the widest laminar width/length of lamina. Only well developed, mature and intact leaves from the centre of short sterile shoots were

Table 1. – Locality details of populations of *Sorbus* subg. *Aria* included in morphometric analyses.

Taxon	Locality	Geographic coordinates (WGS-84)	Altitude (m a.s.l.)	Number of individuals analysed
S. aria	Czech Republic/Austria – Podyjí and Thayatal National Parks, Dyje/Thaya river valley around Hardegg	48°51'20"N, 15°51'40"E	330–540	20
S. collina	Czech Republic, Bohemian Karst, Beroun, SE of the town	49°55'40"N, 14°07'40"E	350–380	10
S. collina	Czech Republic, Horní Povltaví region, valley of Vltava and Sázava rivers around Štechovice	49°49'50"N, 14°27'20"E	250–400	10
S. cucullifera	Czech Republic/Austria – Podyjí and Thayatal National Parks, Dyje/Thaya river valley around Hardegg	48°51'20"N, 15°51'40"E	310–390	20
S. danubialis	Czech Republic, Moravian Karst, Blansko, E–NE of the town	49°21'60"N, 16°42'50"E	400–500	20
S. moravica	Czech Republic, Moravian Karst, Blansko, Suchý žleb gorge	49°21'40"N, 16°42'50"E	400–490	20
S. pontis-satani	Czech Republic, Moravian Karst, Blansko, Suchý žleb gorge	49°21'40"N, 16°42'50"E	410–470	17
S. thayensis	Czech Republic/Austria – Podyjí and Thayatal National Parks, Dyje/Thaya river valley around Hardegg	48°51'20"N, 15°51'40"E	310–440	20

collected, flattened, dried and scanned at 300 dpi using Epson scan 1.11E software, and then measured using tpsDig software (Rohlf 2006). Reproductive organs (fruit, flowers) were analysed separately and used only for separating triploid species because characters of leaves overlapped considerably within this group. Flowers were measured manually using a stereo zoom microscope and fruit using a digital vernier calliper.

One measurement of each character per individual was recorded and used as the value for the individual in all morphometric analyses. Non-parametric Pearson correlation coefficients were calculated for pairs of characters of each species and for the whole dataset in order to reveal relationships among characters. Principal component analyses (PCA) were performed to provide an insight into the overall pattern of morphological variation and to reveal potential separation of the ploidy groups analysed. Prior to the PCA, the data were log-transformed and standardized to have a zero mean and unit standard deviation.

Linear discrimination analyses (LDA), which maximize differences between a priori defined groups (cytotypes and species characterized by SSR patterns, Vít et al., in prep.), were used to test the discriminating power of morphometric characters, following the methodology described by Lepš & Šmilauer (2003) using forward selection of characters with non-parametric Monte Carlo permutation tests (999 permutations; only axes with P-level < 0.05 were considered). A cross-validated classificatory linear discriminant analysis based on probabilities using only characters selected as discriminating variables by the previous analysis was performed in R version 2.12.2 (R Development Core Team 2011) using the "lda" function in the MASS package (Venables & Ripley 2002). PCA and LDA were carried out using CANOCO (Lepš & Šmilauer 2003). Univariate statistics

Table 2. – Overall results of flow cytometric analyses of all taxa of *Sorbus* subg. *Aria* delimited in this study. *Bellis perennis* was used as the internal standard.

Taxon	*S. aria*	*S. cucullifera*	*S. moravica*	*S. pannonica*	*S. pontis-satani*	*S. collina*	*S. danubialis*	*S. thayensis*
Number of individuals analysed	53	26	8	5	6	45	51	13
Average sample:standard ratio	0.37	0.56	0.56	0.55	0.56	0.75	0.75	0.74
Average coefficient of variation of the sample	3.65	2.87	2.55	3.17	2.39	2.69	2.66	2.73
Average coefficient of variation of the standard	1.82	1.54	1.66	1.57	1.68	1.99	1.83	1.61
Estimated DNA ploidy level	2n~2x	2n~3x	2n~3x	2n~3x	2n~3x	2n~4x	2n~4x	2n~4x

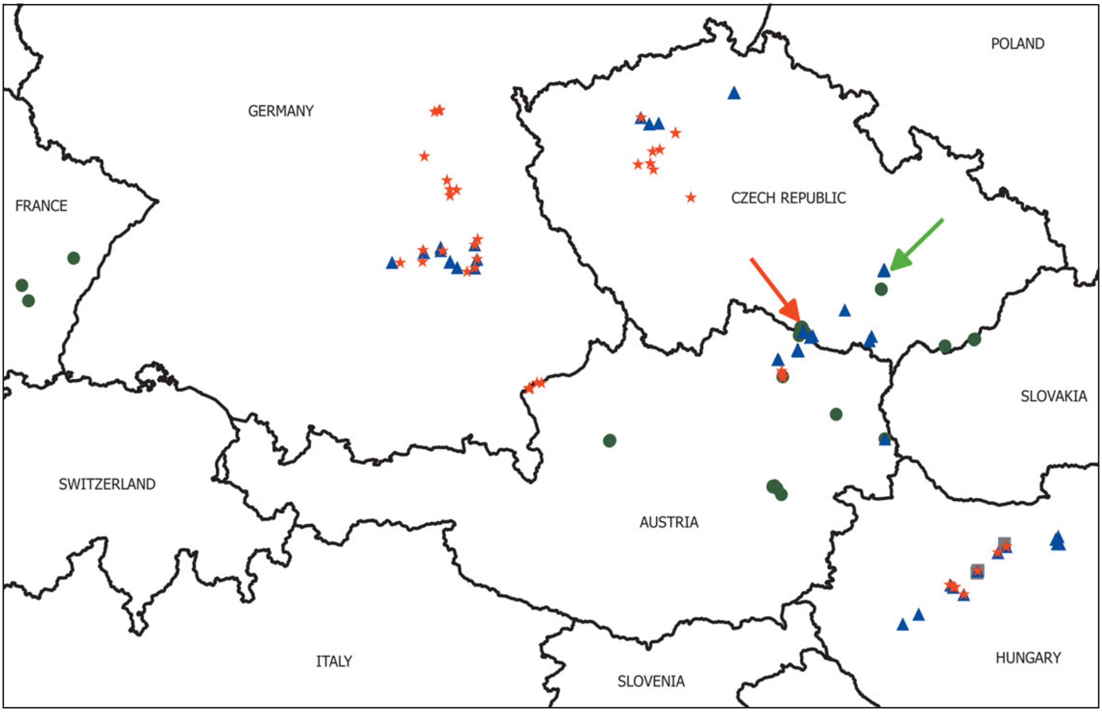

Fig. 1. – Map showing the distribution of the localities of members of *Sorbus* subg. *Aria* sampled for this study. ▲ *S. danubialis*, ● *S. aria*, ★ *S. collina*, ■ *S. pannonica*, → *S. cucullifera* and *S. thayensis*, → *S. moravica* and *S. pontis-satani*.

(minimum, maximum, quartiles) of quantitative characters of all individuals were calculated and used in the description of the species.

DNA ploidy level estimation

DAPI flow cytometry was used to assess DNA ploidy levels (Suda et al. 2006) of members of the subg. *Aria*. Bulked samples from 207 individuals were analysed (i.e. up to four individuals simultaneously) following the methodology described in Lepší et al. (2008). *Bellis perennis* L. (2C=3.38 pg; Schönswetter et al. 2007) was used as the internal standard. The numbers of individuals per species are summarized in Table 2. The general distribution of cytotypes is apparent from the map in Fig. 1, and locality details are given in Appendix 1.

Results

Based on extensive field observations and a detailed investigation of herbarium material, we delimited seven taxa within the subg. *Aria* in the Czech Republic. Results of flow cytometry and morphometric analyses are congruent with each other and support this taxonomic solution.

Ploidy level

The DAPI flow cytometry screening revealed that there are diploids, triploids and tetraploids in subg. *Aria* in the Czech Republic. The diploid level is represented by a single taxon, and triploids and tetraploids each comprise three taxa (see Table 2 for details). Null intraspecific variation was detected.

Morphometric analyses

No highly correlated characters ($r > |0.95|$) were found and all characters were used in the multivariate analyses. PCA of leaf characters indicated a certain level of morphological differentiation between diploids and polyploids. In addition, diploids turned out to be morphologically more variable than polyploids (Fig. 2). Tetraploids and triploids overlapped considerably when 36 individuals of 12 predominantly singular triploids, which we do not treat taxonomically here, were included in the analyses (data not shown). PCAs of individuals delimited here as species (i.e. without singular triploids) revealed that triploids and tetraploids are morphologically different (Fig. 2). The characters contributing most to the morphological distinctiveness of triploids and tetraploids (i.e. the most tightly correlated characters with the first component axis) were: angle of laminar base (AB), ratio length of lamina/width of lamina (LL/LW), angle between the third lateral vein from the laminar base and the midrib (AV), width of lamina (LW) and angle of lamina top (AT). The most strongly correlated characters with the second component axis, which separated diploids from polyploids, were: length of lamina (LL), number of lateral laminar veins (NV), number of teeth between the 2nd and 3rd lateral vein (NT3L) and width of lamina (LW). The subsequent LDA also showed these three groups to be morphologically distinct. No overlap of the canonical scores of diploids and triploids was detected. Both diploids and triploids overlapped slightly with tetraploids (Fig. 3). The forward selection procedure identified 8 characters with a significant conditional effect – length of lamina (LL), width of lamina (LW), angle between the third lateral vein from the laminar base and the midrib (AV), number of teeth between the 2nd and 3rd lateral vein (NT3L), number of lateral laminar veins (NV), length of petiole (PET), angle of laminar base (AB) and ratio of the distance along the main nerve from the laminar base to the widest laminar width/length of lamina (WP/LL); all characters had significant marginal effects

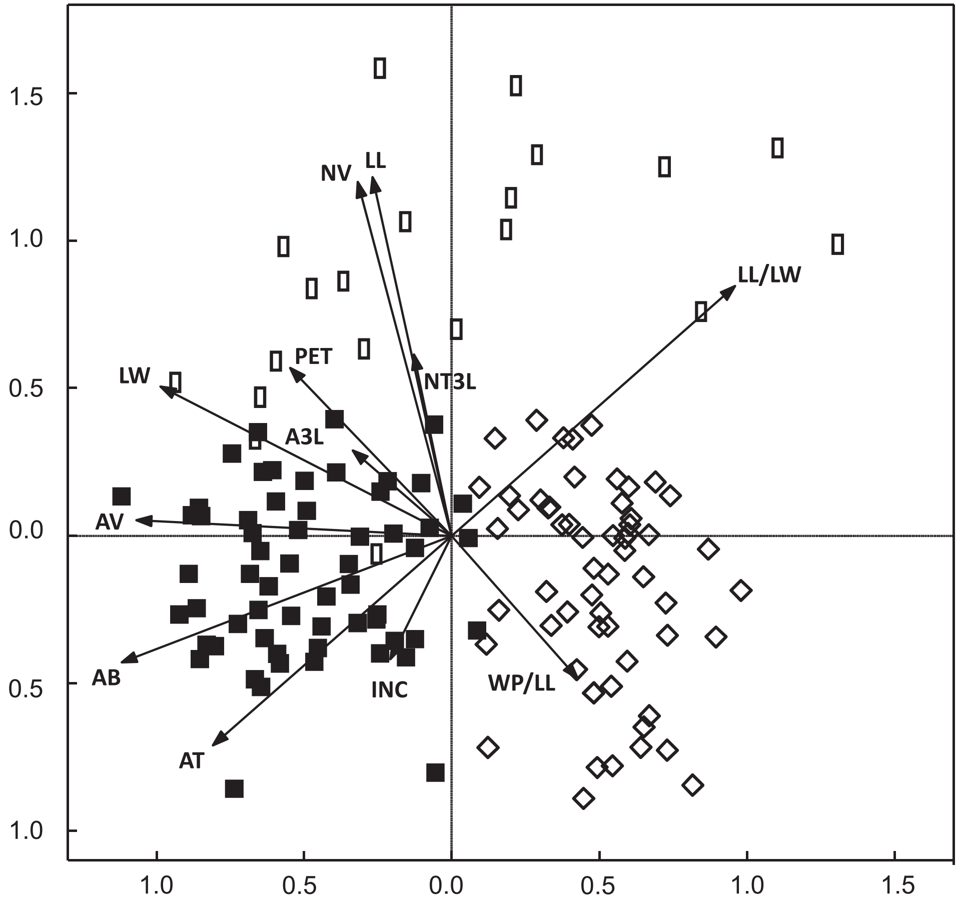

Fig. 2. – Results of the principal component analysis based on twelve morphological characters of leaves of the three ploidy groups of *Sorbus* subg. *Aria*: ▯ diploids; ◇ triploids; ■ tetraploids. The first and second ordination axes are displayed. These explain 30.3% and 22.3% of the overall variation, respectively. Individually occurring triploids, which are not treated taxonomically here, were excluded from this analysis. For abbreviation of characters, see the Material and methods.

(Table 3). The classificatory discriminant analysis resulted in an incorrect classification only in three out of a total of 140 cases (2.1%; Table 4).

The LDA of the three triploid taxa showed that the two sympatrically occurring species, *S. moravica* and *S. pontis-satani*, are clearly separated along the first discriminant axes and that they can be distinguished primarily using the number of lateral laminar veins (NV), the angle of the tooth in which the 3rd lateral vein terminates (A3L) and the length of lamina (LL), characters that have higher values in *S. moravica*. The morphological separation of *S. cucullifera* from the remaining triploids is not so clear. This species falls between the other two species and overlaps somewhat with both of them (Fig. 4). However, *S. cucullifera* differs in fruit and flower morphology, as confirmed by a separate LDA (Table 3). This species has fewer lenticels on fruits (NL) and smaller petals (PL, PW).

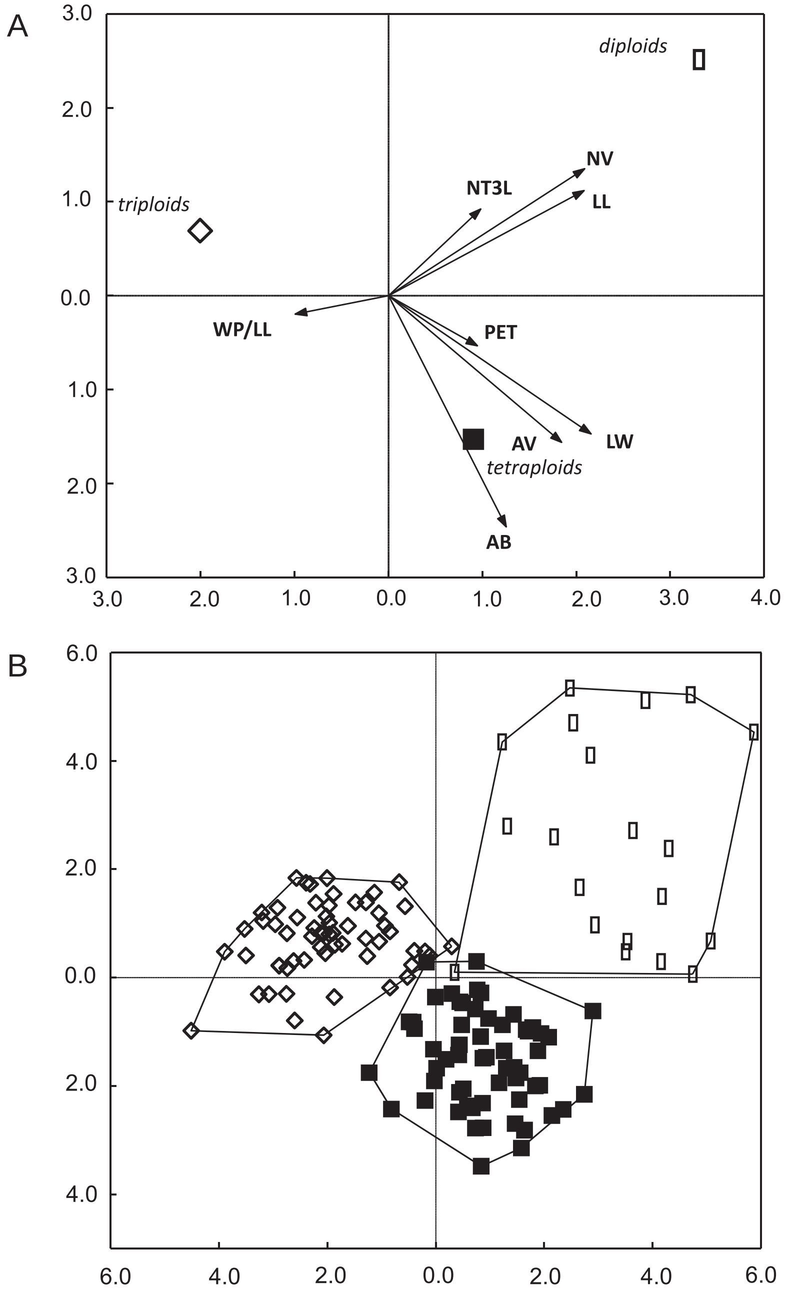

Fig. 3. – Results of the linear discriminant analysis based on 8 morphological characters of leaves of the three ploidy groups of *Sorbus* subg. *Aria*. The characters were selected in a forward selection procedure, and only characters with significant discriminating power for separating the three ploidy groups were used. The first and second canonical axes are displayed, and explain 39.2% and 33.9% of the variation, respectively. The top diagram (A) shows the discriminating characters and centroids of classes and the bottom one (B) the canonical scores of individual plants on the first two discriminating axes. For abbreviation of characters, see the Material and methods.

Table 3. – Morphological characters of cytotypes of *Sorbus* subg. *Aria* with a significant conditional effect (i.e. the effect of the variable in addition to other variables already included in the model) in forward selection of four separate linear discriminant analyses: (i) leaf characters of all cytotypes (diploid, triploid, tetraploid), (ii) leaf characters of triploid taxa (*S. cucullifera*, *S. moravica*, *S. pontis-satani*), (iii) reproductive characters of triploid taxa and (iv) leaf characters of tetraploids taxa (*S. danubialis*, *S. collina*, *S. thayensis*). Individuals were used as OTUs in all LDAs. Significance was tested using the Monte Carlo permutation test (999 permutations). λ – eigenvalue, i.e. discriminant force of a particular character, P – significance level (conditional effect), marg. – characters with significant marginal effects (i.e. the effect of the variable when alone in the model) are given. The contributions of characters to the ordination axes for particular analyses are depicted in Figs 3B, 4B and 5B.

	All			Triploids		Triploids reproductive organs				Tetraploids	
Character	λ	P		λ	P		λ	P		λ	P
LL	0.6	0.001	NV	0.77	0.001	NL	0.78	0.001	AT	0.74	0.001
LW	0.54	0.001	A3L	0.33	0.001	PL	0.37	0.001	LL	0.69	0.001
AV	0.2	0.001	LL	0.13	0.002	PW	0.08	0.031	PET	0.13	0.001
NT3L	0.05	0.001	WP/LL	0.08	0.006	-	-	-	AB	0.06	0.001
NV	0.03	0.023	LL/LW	0.06	0.01	-	-	-	LL/LW	0.05	0.001
PET	0.02	0.005	NT3L	0.04	0.044	-	-	-	NT3L	0.03	0.007
AB	0.02	0.036	-	-	-	-	-	-	NV	0.02	0.015
WP/LL	0.01	0.04	-	-	-	-	-	-	AV	0.02	0.041
marg.: all			marg.: all			marg.: all except for FL			marg.: all except for WP/LL, NV		

Table 4. – Results of cross-validated linear discriminant analyses using only morphological characters selected as discriminating variables in the forward selection procedure (see Table 3). Four separate analyses were conducted: (i) leaf characters of all cytotypes (diploid, triploid, tetraploid), (ii) leaf characters of triploid taxa (*Sorbus cucullifera*, *S. moravica*, *S. pontis-satani*), (iii) reproductive characters of triploid taxa and (iv) leaf characters of tetraploids taxa (*S. danubialis*, *S. collina*, *S. thayensis*).

All				Triploids				Reproductive organs of triploids				Tetraploids			
	Diploids	Triploids	Tetraploids		*S. cucullifera*	*S. moravica*	*S. pontis-satani*		*S. cucullifera*	*S. moravica*	*S. pontis-satani*		*S. danubialis*	*S. collina*	*S. thayensis*
Diploids	19	1	0	*S. cucullifera*	18	1	1	*S. cucullifera*	15	0	0	*S. danubialis*	20	0	0
Triploids	0	59	1	*S. moravica*	2	18	0	*S. moravica*	1	12	2	*S. collina*	0	20	0
Tetraploids	0	1	59	*S. pontis-satani*	1	0	19	*S. pontis-satani*	0	3	12	*S. thayensis*	0	0	20
Total			140				60				45				60

Moreover, the range in the most distinctive character, the number of lenticels (NL) does not overlap with the ranges in either of the other two species, *S. moravica* or *S. pontis-satani* (see the descriptions of these species). The results of the classificatory discriminant analysis of all three triploid taxa were similar to those of the LDA: incorrect classification was detected in five out of a total of 60 cases (8.3%) in terms of leaf characters and in six out of a total of 45 (13.3%) cases in fruit and flower characters (Table 4).

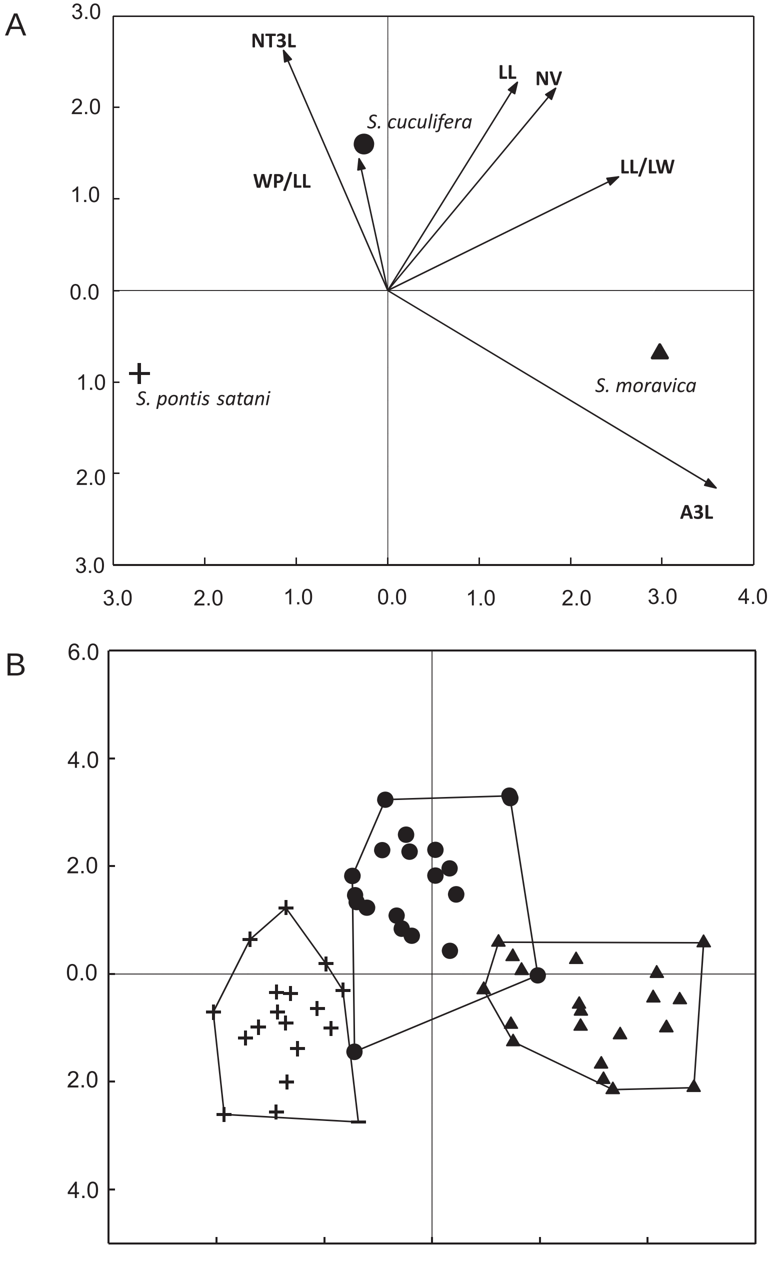

Fig. 4. – Results of the linear discriminant analysis based on 6 morphological characters of leaves of the three triploid taxa of *Sorbus* subg. *Aria*. The characters were selected in a forward selection procedure, and only those that were significantly different and could be used to distinguish the three taxa were used. The first and second canonical axes are displayed, and explain 42.2% and 28.2% of the variation, respectively. The top diagram (A) shows the discriminating characters and centroids of classes and the bottom one (B) canonical scores of individual plants on the first two discriminating axes. For abbreviation of characters, see the Material and methods.

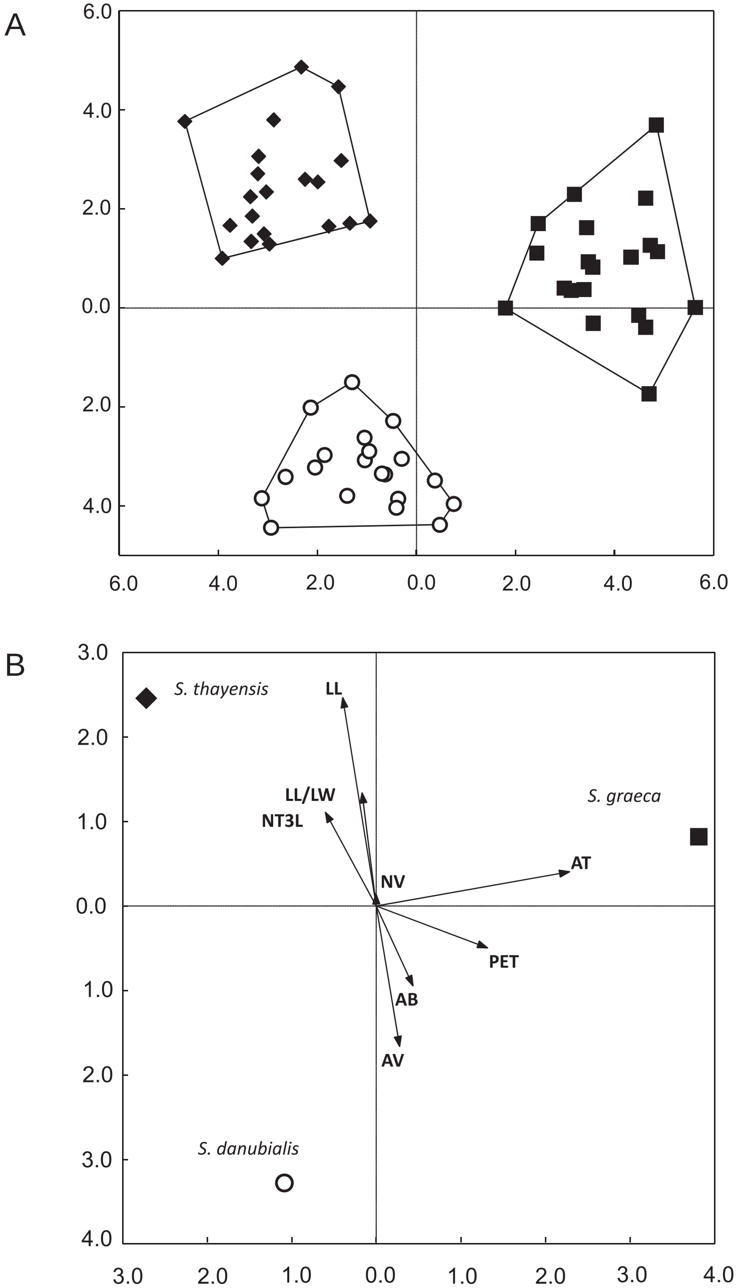

Fig. 5. – Results of the linear discriminant analysis based on 8 morphological characters of leaves of three tetraploid taxa of *Sorbus* subg. *Aria*. The characters were selected in a forward selection procedure, and only those that were significantly different and could be used to distinguish the three taxa were used. The first and second canonical axes are displayed, and explain 44.3% and 42.7% of the variation, respectively. The top diagram (A) shows the discriminating characters and centroids of classes and the bottom one (B) the canonical scores of individual plants on the first two discriminating axes. For abbreviation of characters, see the Material and methods.

The LDA of the three delimited tetraploid taxa (*S. collina*, *S. danubialis*, *S. thayensis*) confirmed their clear morphological separation. No overlap of the canonical scores of the species was detected (Fig. 5, Table 3). The classificatory discriminant analysis using these characters resulted in correct classification in all cases (Table 4).

Discussion and taxonomic treatment

Results of all biosystematic methods employed in this study are congruent with results of SSR analyses, which are part of a broader study on genetic variation in the genus *Sorbus* and will be published elsewhere (Vít et al., in prep.). With respect to the present study, all taxa described below possess different genotypes and are clearly separated.

Diploid species

Diploid members of the subg. *Aria* are relatively rare in the Czech Republic. We detected their occurrence only in three regions of Moravia (Fig. 1). They occur scattered in the Podyjí National Park between the towns of Znojmo and Vranov nad Dyjí, very rarely on the Moravian Karst near the city of Brno, and rarely in the Bílé Karpaty Mts near the villages of Javorník and Starý Hrozenkov. The populations analysed were both morphologically (Figs 2, 3) and genetically (Vít et al., in prep.) very diverse even at the same sites, and this feature combined with their ploidy level confirms the finding that these diploid plants belong to the amphimictic *S. aria* s. str.

This taxon is known to be an extremely variable and sexually reproducing diploid species (Liljefors 1953, 1955, Robertson et al. 2010, Feulner et al. 2013) distributed in central and southern Europe from Spain to the Balkans with outlying localities along the Black Sea coast and in northern Africa (Meusel et al. 1965). *Sorbus aria* is also cultivated for ornamental purposes and reported as a naturalized alien species in many European countries (Lepší et al. 2013b).

Sorbus aria s. str. has been reported as a native species in several areas of the Czech Republic with the alleged centre of its distribution in Bohemia (Kovanda 1992, 2002, Kutzelnigg 1995). Our results, however, do not support this claim. We show that all Bohemian members of the subg. *Aria* are tetraploids and that *S. collina*, a common species of warm and rocky areas of Bohemia (newly described below), has been mistaken for the diploid *S. aria* s. str. The only region where *S. aria* is native in the Czech Republic is Moravia. However, some other records from Moravia may also be dubious, such as the record from the valley of the river Jihlava (Kutzelnigg 1995), which probably actually refer to *S. danubialis*, the only member of the subg. *Aria* known to us in this area. Localities of *S. aria* in the Podyjí National Park and on the Moravský Karst appear as exclaves – they are isolated from each other and from the continuous distribution areas in the Alpine and Carpathian regions, where the species is rather common. The localities in Bílé Karpaty Mts lie probably at the western border of a scattered distribution of this species in Slovakia. All Moravian populations are small except in the Podyjí National Park. It should be added that *S. aria* can occasionally be found in the wild in Bohemia, but they are plants that have escaped from cultivation (e.g. Liberec, Mladá Boleslav, Mcely, Klecany, Nové Hrady).

In the past, the exceptional variability of *S. aria* was overestimated or improperly understood. Many taxa were recognized at the specific and lower levels (Kárpáti 1960), but considering the continuous and reticulate morphological variation in the structure of these taxa, their delimitation is of little if any value. On the other hand, underestimating the range of morphological variation in these species has lead to several other misidentifications. For example, some individuals of *S. aria* from the Podyjí National Park (Czech Republic) were mistakenly determined as *S. austriaca* and *S. carpatica* because of their lobed or conspicuously double serrate leaves (Kovanda 1996, 1997b, 2002). These two transitional taxa between the subg. *Aria* and subg. *Sorbus* were described from Austria and Slovakia, respectively, and do not, to our knowledge occur naturally in the Czech Republic. In addition, *S. austriaca* was recently found to be tetraploid (M. Lepší & P. Lepší, unpublished data).

In addition to their ploidy level, a conspicuous feature that distinguishes *S. aria* from polyploid members of the subgenus is the considerable variation in fruit and leaf morphology that is recorded in every population. Polyploids, by contrast, are morphologically uniform due to prevailing apomixis. There is no universal morphological character that would allow a clear separation of *S. aria* from polyploids within the whole of Europe, but its determination is mostly possible at the regional level. For example, Czech polyploids differ from the dominant morphotype of *S. aria* in having smaller and leathery leaves with fewer veins, while the common features of most individuals of *S. aria* in the Czech Republic are relatively large, thin and elliptic to longish leaves with many veins. However, there are rare individuals that do not fit this pattern and cannot be identified without establishing their ploidy levels (e.g. in the Podyjí National Park). In addition to Moravia, we confirmed the occurrence of *S. aria* in France and Austria (Fig. 1, Appendix 1).

In some regions, the exceptional morphological variability of *S. aria* causes problems with distinguishing this species from polyploids, which in some cases is quite impossible without testing for polyploidy (see Rich et al. 2010), the Czech Republic being no exception (Figs 2, 3). This fact may have some bearing on the nomenclature of this species because its type specimen comes from a tree of unknown origin and ploidy level that was cultivated in G. Clifford's garden in Holland in the 18th century. Despite the fact that the type specimen corresponds morphologically quite well to diploid morphotypes, which are recently uniformly called *S. aria* in Europe, we consider it advisable to select an interpretative epitype of known ploidy from a wild population. In this way, we hope to stabilize the nomenclature of this species in the future.

Sorbus aria (Linnaeus) Crantz, Stirp. Austr. 2: 46, 1763. (Fig. 6)

Basionym: *Crataegus aria* L., Sp. Pl. 1: 475, 1753.
≡ *Mespilus aria* (L.) Scop., Fl. Carniol., ed. 2, 1: 345, 1771.
≡ *Pyrus aria* (L.) Ehrh., Beitr. Naturk. 4: 26, 1789.
≡ *Hahnia aria* (L.) Medik., Geschich. Bot. 81, 1793.
≡ *Azarolus aria* (L.) Borkh., Handb. Forstbot. 2: 1229, 1803.
= *Aria nivea* Host, Fl. Austriac. 2: 8, 1831.

Lectotype: Hortus Cliffordianus 187, BM, No. 000628615, designated by Aldasoro et al. (2004).

Epitype: Lower Austria, Hardegg, "pine forest I" on slopes of Dyje valley, ca 180 m SE of bridge over Dyje river, pine forest with *Sesleria*; 390 m a.s.l., 48°51'4.1"N, 15°51'52.16"E; scattered; tree ca 7 m high; 12. 9. 2011 leg. M. Lepší, P. Lepší; 2n ~ 2x – DNA ploidy level was determined using the flow cytometer Partec PA II

(DAPI fluorochrome); ratio with the internal standard (*Bellis perennis* L.) is 0.375; Analysed 19. 9. 2011, Department of Botany, University of South Bohemia, Č. Budějovice (**epitype designated here:** CB, No. 79814, Fig. 6).

Names previously used for this taxon in the Czech Republic: *Sorbus austriaca* sensu Kovanda, Acta Mus. Morav., Sci. Nat. 81: 202, 1997 p.p.; sensu Kovanda, Klíč ke květeně ČR: 385, 2002 p.p. – *S. carpatica* sensu Kovanda, Verh. Zool.-Bot. Ges. Österreich 133: 360 p. p; sensu Kovanda, Klíč ke květeně ČR: 385, 2002 p.p.

Description: Small tree or shrub up to 12 m high. Bark grey to dark grey, smooth when young, with fissures (particularly at the trunk base) when mature. Twigs thick, brownish-grey; young shoots brown, glabrous to sparsely tomentose when young, glabrous or glabrescent when mature, with pale brown to ochraceous lenticels. Buds turbinate or ovoid, pointed; scales green, glabrescent, with narrow brown sparsely tomentose margins. Leaves on short sterile shoots simple; laminas elliptical to broadly elliptical, oblong elliptical, ovate to oblong ovate, (9.6–) 11.5–12.7 (–15.6) cm long and (5.0–) 6.3–7.8 (–8.4) cm wide, (1.4–) 1.5–2.1 (–2.5) times as long as wide, widest at (43–) 49–54 (–64)% of the lamina length (from the base), with broadly acute, acute to acuminate apex with angle (70–) 85–115 (–135)°, cuneate to broadly cuneate and partly serrate at base, with angle of base (50–) 70–95 (–115)°, usually flat at margins, regularly finely to coarsely simply or double (to triple) serrate or dentate, or deeply serrate to shallowly lobed, with broadly acute, acute or acuminate teeth terminating the main veins (other teeth somewhat smaller), with (6–) 9–12 (–16) teeth between the 2nd and 3rd main veins from the base, with angle of the teeth terminating the 3rd main veins of (50–) 60–85 (–95)°, with incision between the 2nd and the 3rd main vein from the base of (0.7–) 1.6–3.0 (–5.6) mm, thin, more or less glossy, pale or dark green, sparsely tomentose when young, later glabrescent on upper surface, evenly greenish-grey-tomentose on lower surface, with (8–) 11–12 (–13) veins on each side, with the 3rd vein at an angle of (20–) 30–40 (–45)° to midrib; petioles (11–) 14–18 (–20) mm long, tomentose. Leaf laminas on short fertile shoots similar in shape and size. Inflorescences compact, convex, with tomentose branchlets. Sepals triangular, acute or acuminate, tomentose on both surfaces, patent or reclinate at flowering, erect, persistent and dry at fruiting. Petals (5.0–) 6.5–7.5 (–8.5) mm long and (3.8–) 5.0–6.0 (–6.5) mm wide, broadly elliptical to rotund, concave, white, patent, sparsely tomentose at base of upper surface, glabrous on lower surface, with a short claw. Stamens ca 20; anthers pale yellow. Ovary semi-inferior. Styles 2 (–3), free or connate and tomentose at base. Fruit ellipsoid to subglobose, (11.5–) 12.5–14.5 (–16.0) mm long and (9.0–)11.5–13.5(–15.0) mm wide, red to dark red, rarely orange-red when ripe, tomentose at top and base, otherwise glabrescent, glossy, with (1–) 4–9 (–23) lenticels per 25 mm^2; mesocarp heterogeneous; endocarp cartilaginous. Seeds fuscous. DNA ploidy level: diploid (inferred using FCM). Reproduction sexual. Flowering V.

Diagnostic characters: Individuals in every population are very variable in their fruit and leaf morphology, with almost every individual morphologically unique. Common characters of most Czech plants of this species are relatively thin, large and elliptical to oblong elliptical leaves with relatively many veins on short sterile shoots.

Triploid species

Triploids occur in two Moravian regions in the Czech Republic (Fig. 1). We revealed three morphologically (Fig. 4) and genetically (Vít et al., in prep.) distinct lineages: one

BARIUM MUSEI REGIONALIS BOHEMIAE MERIDIONALIS
ČESKÉ BUDĚJOVICE

ra: Lower Austria

CB/79814

Sorbus aria (L.) Crantz

Hardegg (distr.), "pine forest I" on slopes of Dyje valley, ca 180 m SE of bridge over Dyje river, pine forest with Sesleria

Frequence: scattered; tree ca 7 m high

Note: 2n ~ 2x; DNA ploidy level was detected using the flow cytometer Partec PA II (DAPI fluorochrome); ratio to the internal standard (Bellis perennis L.) is 0.375; Analysed 19. 9. 2011, Department of Botany, University of South Bohemia, Č. Budějovice.

Altitude: 390 m **WGS 84:** 48°51'4,1''N; 15°51'52,16''E

Quadrant: 7161acd **ID GPS:** 700

Phytogeographical distr.:

Date: 12.9. 2011 **Collected:** Martin Lepší, Petr Lepší

Quadrant according to Ehrendorfer et Hamann 1965, Ber. Deutsch. Bot. Ges.; Phytogeographical distr. - Skalický 1988, Květena ČR 1

Fig. 6. – Epitype of *Sorbus aria.*

in the Podyjí National Park and two on the Moravian Karst. Below, we describe each of these lineages as a separate species because they are morphologically and genetically uniform, and exhibit all the characteristics of apomictic species. In addition, we detected about 40 triploid individuals in the Podyjí National Park and four on the Moravian Karst associated with the three taxa delimited but clearly differing from them in their morphology and genetic structure (Vít et al., in prep.). Because these triploids occurr usually as single or very rare individuals and do not form significant populations, we do not treat them as separate species. We suppose that they are products of hybridization between tetraploid *S. danubialis* and diploid *S. aria* or in the Podyjí National Park the tetraploid parent might be also *S. thayensis*. This hypothesis is probably valid at least in the case of the Podyjí National Park, where the supposed parental species are present. The situation on the Moravian Karst is not so clear, because *S. aria* does not occurr in this area, and only tetraploid *S. danubialis* and two triploid species are found there. The four triploid individuals might either be the results of former hybridizations between *S. aria* and *S. danubialis* when *S. aria* occurred at this locality, or may be the descendants of crosses between *S. danubialis* and the two triploid species. The third, but less probable, option is that these taxa could have originated somewhere else and later spread by birds or other agents to this locality. A similar scenario applies to the origin of the two triploid species described below, *S. moravica* and *S. pontis-satani*. They could have either evolved at this locality as a result of hybridization between *S. aria* and *S. danubialis* in the past, or less likely, reached there by dispersal.

The first record of the occurrence of subg. *Aria* triploids in the Czech Republic is for the Podyjí National Park (Šefl 2007). The author assigned these plants to *S. subdanubialis* (Soó) Kárpáti, a transitional taxon between *S. aria* and *S. danubialis* described from Hungary. However, *S. subdanubialis* differs from the triploids in the Podyjí National Park in having longer triangular leaf apices, fewer teeth between the 2nd and 3rd main veins from the base and coarsely serrate leaf margins (cf. Kárpáti 1960, Király 2009).

Sorbus cucullifera M. Lepší et P. Lepší, **spec. nova** (Figs 7–8)

Description: Shrub or rarely small tree up to 12 m high. Bark grey or dark grey, smooth when young, with fissures (particularly at the trunk base) when mature. Twigs thick, brownish-grey; young shoots brown, tomentose when young, glabrescent when mature, with pale brown to ochraceous lenticels. Buds ovoid, pointed; scales green, glabrescent, with narrow brown sparsely tomentose margins. Leaves on short sterile shoots simple, when in the sun held more or less upright and overlapping each other; laminas more or less (broadly) elliptical to obovate, (7.2–) 8.4–8.9 (–10.5) cm long and (4.7–) 5.0–5.5 (–6.2) cm wide, (1.5–) 1.6–1.7 (–1.8) times as long as wide, widest at (51–) 54–60 (–65)% of the lamina length (from the base), with acuminate apex with an angle of 100–115 (–125)°, cuneate and partly serrate at base, with angle of base (65–) 70–80 (–85)°, usually flat to slightly undulate margins, regularly, finely, double to triple serrate, with acute teeth terminating the main veins (other teeth somewhat smaller), with (7–) 9–10 (–12) teeth between the 2nd and 3rd main veins from the base, with angle of the teeth terminating the 3rd main veins (40–) 45–65 (–75)°, with incision between the 2nd and the 3rd main vein from the base (1.5–) 2.0–3.0 (–4.0) mm long, leathery, more or less

HERBARIUM MUSEI REGIONALIS BOHEMIAE MERIDIONALIS
ČESKÉ BUDĚJOVICE

Flora: Southern Moravia

CB/83095

Sorbus cucullifera M. Lepší et P. Lepší **HOLOTYPE!**

Čížov (distr. Znojmo), Dyje valley, Sloní hřbet ridge, ca 2.1 km SSE of chapel in village, on cliff

Frequence: scattered; small tree ca 7 m high

Note: No. 246; 2n ~ 3x; DNA ploidy level detected using the flow cytometer Partec PA II (DAPI fluorochrome); ratio to the internal standard (Bellis perennis L.) is 0,564; Analysed 13. 5. 2011, Department of Botany, University of South Bohemia, Č. Budějovice.

Altitude: 340 m **WGS 84:** 48°51'39,53''N; 15°52'40,48''E

Quadrant: 7161adc **ID GPS:** 246

Phytogeographical distr.: Moravské podhůří Vysočiny

Date: 13.6. 2011 **Collected:** Martin Lepší, Petr Lepší

Quadrant according to Ehrendorfer et Hamann 1965, Ber. Deutsch. Bot. Ges.; Phytogeographical distr. - Skalický 1988, Květena ČR 1

Fig. 7. – Holotype of *Sorbus cucullifera*.

Fig. 8. – *Sorbus cucullifera*: short fructiferous shoot (left) and leaf from the middle part of a short sterile shoot (right). Scale bar 2 cm. Drawn by A. Skoumalová.

matt, pale green, sparsely tomentose when young, later glabrescent on upper surface, evenly greenish-grey-tomentose on lower surface, with (8–) 9–10 (–11) veins on each side, with the 3rd vein at an angle of (20–) 25–35° to midrib; petioles (12–) 14–16 (–17) mm long, tomentose. Leaf laminas on short fertile shoots relatively broader, broadly elliptical and more distinctively undulate at margin. Inflorescences compact, convex, with tomentose branchlets. Sepals triangular, acute or acuminate, tomentose on both surfaces, patent at flowering, erect, persistent and dry at fruiting. Petals (5.5–) 6.5–7.0 (–7.5) mm long and (4.2–) 5.0–5.5 (–6.2) mm wide, broadly ovate or broadly elliptical, concave, white, patent, sparsely tomentose at base of upper surface, glabrous on lower surface, with a short claw. Stamens ca 20; anthers pale yellow or pale rose. Ovary semi-inferior. Styles 2, connate and tomentose at base. Fruit ellipsoid to almost subglobose, (11.0–) 12.0–13.0 (–13.5) mm long and 10.5–12.0 (–13.5) mm wide, never wider than long, red when ripe, tomentose at top and base, otherwise glabrescent, matt, with (1–) 3–4 (–7) lenticels per 25 mm^2; mesocarp heterogeneous; endocarp cartilaginous. Seeds fuscous. DNA ploidy level: triploid (inferred using FCM). Reproduction probably apomictic. Flowering V.

Holotype: southern Moravia, Čížov (distr. Znojmo), Dyje valley, Sloní hřbet ridge, ca 2.1 km SSE of chapel in village, on cliff; 340 m a.s.l., 48°51'39.53"N, 15°52'40.48"E; scattered; small trees ca 7 m high; 13. 6. 2011 leg. Martin Lepší, Petr Lepší; CB, No. 83095 (Fig. 7). – Isotypes: PR, 83095/a; PRA, 83095/b; W, 83095/c.

Name previously used for this taxon in the Czech Republic: *Sorbus subdanubialis* sensu Šefl, Thayensia 7: 139, 2007 p.p.

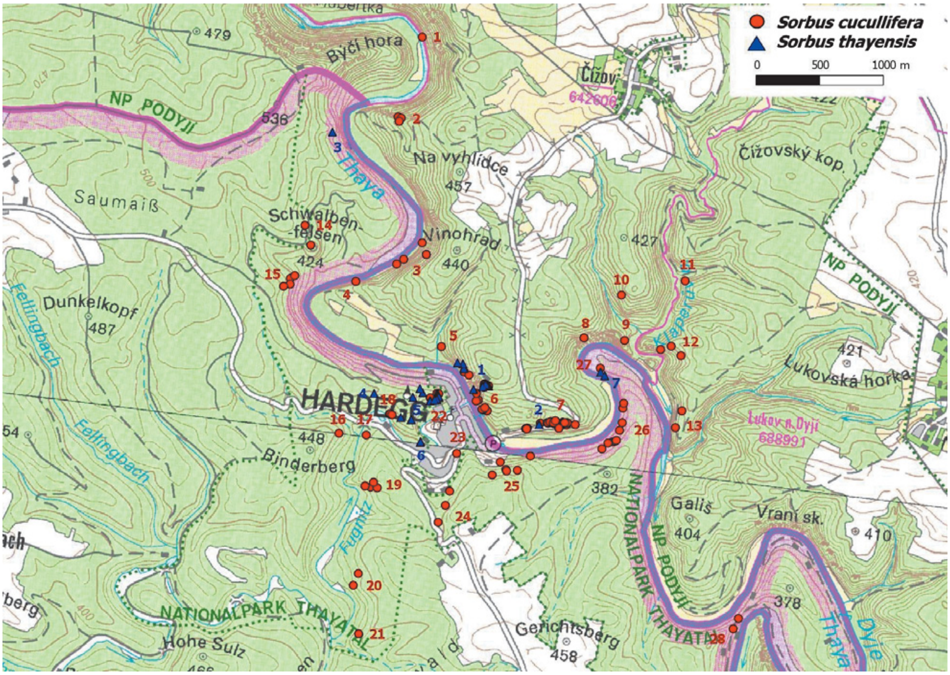

Fig. 9. – Map showing the distribution of *Sorbus cucullifera* and *S. thayensis* (map source © ČÚZK 2014).

Diagnostic characters: Leaf laminas on short sterile shoots more or less (broadly) elliptical to obovate, relatively small, regularly, finely, double (to triple) serrate. Flowers relatively small. Fruit ellipsoid to almost subglobose, never wider than long, red, only with (1–) 3–4 (–7) lenticels per 25 mm^2. Leaves on short sterile shoots of individuals at sunny sites are held more or less upright and overlap each other and therefore resemble a cornet.

Etymology: The epithet "*cucullifera*" refers to the characteristic arrangement of leaves on short sterile shoots of individuals at sunny sites that resemble cornets (in Latin *cucullus*). We propose the name "kornoutolistý" for the Czech name.

Ecology: *Sorbus cucullifera* is a light-demanding species that prefers open habitats such as forest-steppes, rocky steppes, shrubs, open thermophilous oak forests and their fringes. Less often it occurs in other types of open forests and also on rocks and screes. The species grows mainly on calcareous soils on limestone, but frequently also on acid bedrocks such as gneisses and schists. In phytosociological terms, vegetation with common occurrence of *S. cucullifera* belongs to peri-Alpidic basiphilous thermophilous oak forests (*Quercion pubescenti-petraeae*), central-European thermophilous oak forests (*Quercion petraeae*), tall xeric scrub (*Berberidion*), narrow-leaved continental dry grasslands (*Festucion valesiacae*) and vegetation of dry herbaceous forest fringes (*Geranion sanguinei*). Less often, this species is recorded in vegetation in oak-hornbeam forests (*Carpinion*), ravine forests (*Tilio-Acerion*), rock pine forests (*Dicrano-Pinion*), peri-Alpidic basiphilous pine forests (*Erico-Pinion*), acidophilous oak forests (*Genisto germanicae-Quercion*), and low xeric scrub (*Prunion spinosae*).

Distribution and population size: *Sorbus cucullifera* was recorded at 28 localities in the wide surroundings of the town Hardegg, which is located on the border between Lower Austria and southern Moravia (Czech Republic). This species occurs in the valley of the river Dyje and that of its tributary, Fugnitz. Along with *S. aria* it is the most abundant species in the subg. *Aria* in this area. The distance between the two most remote localities, which are Umlaufberg hill (Austria) in the south and Pašerácká stezka trail (Czech Republic) in the north, is almost 5.4 km (Fig. 9). The total number of individuals is estimated to be around 150 in the Czech Republic and 300 in Austria. Some populations consist of about 40 or more individuals (localities 6, 7, 19, 26). *Sorbus cucullifera* is recorded in two quadrants (7161a and 7161c) of the central-European mapping grid (Ehrendorfer & Hamann 1965). All localities are situated in a moderately warm climatic region (Quitt 1971) with a mean annual temperature of about 8–9 °C and mean annual precipitation of 450–500 mm (Tolasz et al. 2007). Czech localities are in the supracolline vegetation belt (Chytrý 2012) in the phytogeographical district of Moravské podhůří Vysočiny (Skalický 1988). The altitudinal range of this species spans from 300 (near Pašerácká stezka trail, Czech Republic) to 420 m a.s.l. (Schwalbenfelsen cliff, Austria).

Herbarium specimens

Czech Republic, southern Moravia, 68. Moravské podhůří Vysočiny, 7161a: 1. Pašerácká stezka path: Čížov village, Dyje valley, Pašerácká stezka path, ca 1.7 km WNW of chapel in village, acidophilous oak forest, shrub ca 5 m high, 48°52'50.9"N, 15°51'00.4"E, 330 m a.s.l. (leg. ML et PL 8. 5. 2011, CB 79750). **2. Na Vyhlídce hill:** Čížov village, slopes on left-hand bank of Dyje river, ca 400 m W of summit Na Vyhlídce hill, a gap in Pine wood, two juvenile plants, 48°52'29.0"N, 15°50'55.4"E, 400 m a.s.l. (leg. ML et PL 23. 7. 2010, CB 74000). – Čížov village, Dyje valley, NW slopes of Na Vyhlídce hill, ca 1.8 km WSW of chapel in village, edge of scree and scree forest, rare, tree ca 2 m high, 48°52'30.1"N, 15°50'54.7"E, 380 m a.s.l. (leg. ML et PL 8. 5. 2011, CB 79762). – Čížov village, Dyje valley, NW slopes of Na Vyhlídce hill, ca 1.8 km WSW of chapel in village, rocky acidophilous oak forest, rare, tree ca 2 m high, 48°52'29.9"N, 15°50'56.0"E, 390 m a.s.l. (leg. ML et PL 8. 5. 2011, CB 79764). – Čížov village, Dyje valley, NW slopes of Na Vyhlídce hill, ca 1.8 km WSW of chapel in village, gap in acidophilous oak forest, rare, shrub ca 1.5 m high, 48°52'28.9"N, 15°50'55.3"E, 390 m a.s.l. (leg. ML et PL 8. 5. 2011, CB 79763). **3. Vinohrad hill I:** Čížov village, Dyje valley, NW slopes of Vinohrad hill, ca 2 km SW of chapel in village, oak-hornbeam forest on steep slope, tree ca 4 m high, 48°51'59.1"N, 15°51'09.6"E, 360 [315] m a.s.l. (leg. ML et PL 8. 5. 2011, CB 79766). – Čížov village, Dyje valley, NW slopes of Vinohrad hill, ca 2.3 km SW of chapel in village, steep woody slope, ca 3 m high, 48°51'52.9"N, 15°51'00.8"E, 300 m a.s.l. (leg. ML et PL 8. 5. 2011, CB 79767). – Čížov village, slopes above Dyje river between Vinohrad hill and Ledové sluje chasm, oak forest, 48°51'54.4"N, 15°51'03.3"E, 350 [330] m a.s.l. (leg. ML et PL 5. 8. 2009, CB 73719). – Čížov village, slopes above Dyje river between Vinohrad hill and Ledové sluje chasm, oak forest, 48°51'56.3"N, 15°51'11.7"E, 360 m a.s.l. (leg. ML et PL 5. 8. 2009, CB 73744–73745). **4. Vinohrad hill II:** Čížov village, Dyje valley, NW slopes of Vinohrad hill, ca 2.6 km SW of chapel in village, acidophilous oak forest with abundant *Pinus sylvestris*, only two individuals, ca 6 m high, 48°51'47.4"N, 15°50'46.0"E, 310 m a.s.l. (leg. ML et PL 8. 5. 2011, CB 79768). **5. Hardeggská vyhlídka outlook I:** Čížov village, Dyje valley, ca 0.5 km SE of summit of Vinohrad hill, pine-oak forest, tree ca 5 m high, 48°51'33.5"N, 15°51'21.7"E, 330 m a.s.l. (leg. ML 21. 8. 2011, CB 79613). **6. Hardeggská vyhlídka outlook II:** Čížov village, slopes with rocks and scree below Hardeggská vyhlídka outlook, ca 0.5 km NE of centre of Hardegg, 48°51'19.4"N, 15°51'41.0"E, 340 m a.s.l. (leg. ML et PL 6. 8. 2009, CB 73673). – Čížov village, slopes with rocks and scree below Hardeggská vyhlídka outlook, ca 0.5 km NE of centre of Hardegg, 48°51'24.9"N, 15°51'41.5"E, 390 m a.s.l. (leg. ML et PL 6. 8. 2009, CB 73672). – Čížov village, Hardeggská vyhlídka outlook, ca 260 m NNW of bridge over Dyje river, edge of oak forest and steppe, scattered, shrub ca 3 m high, 48°51'18.6"N, 15°51'42.1"E, 330 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79675). – Čížov village, Hardeggská vyhlídka outlook, ca 280 m NNW of bridge over Dyje river, forest-steppe, scattered, tree ca 3 m high, 48°51'18.8"N, 15°51'40.4"E, 310 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79847). – Čížov village, Hardeggská vyhlídka outlook, ca 280 m NNW of bridge over Dyje river, rocky forest-steppe, scattered, tree ca 3.5 m high, 48°51'18.9"N, 15°51'40.0"E, 310 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79693). – Čížov village, Hardeggská vyhlídka outlook, ca 350 m NNW of bridge over Dyje river, limestone cliff, shrub ca 2 m high, 48°51'20.8"N, 15°51'37.4"E, 350 [315] m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79687). – Čížov village, Hardeggská vyhlídka outlook, ca 360 m NNW of bridge over Dyje river, scattered, 48°51'21.1"N, 15°51'38.2"E, 360 [340] m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79692, CB 79846). – Čížov village, Hardeggská vyhlídka outlook, ca 410 m NNW of bridge over Dyje river, rocky forest-steppe, scattered, shrub ca 4 m high, 48°51'22.8"N, 15°51'37.2"E, 340 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79689). – Čížov village, Hardeggská vyhlídka outlook, ca 450 m NNW of bridge over Dyje river, scree, shrub ca 3 m high, 48°51'24.5"N, 15°51'39.7"E, 390 m a.s.l. (leg. ML et PL 10. 9. 2011, CB 79806). – Čížov village, Hardeggská vyhlídka outlook, ca 470 m NNW of bridge over Dyje river, scree, shrub ca 7 m high, 48°51'25.4"N, 15°51'39.7"E, 380 m a.s.l. (leg. ML et PL 14. 5. 2011, CB 79849). – Čížov village, Hardeggská vyhlídka outlook, ca 470 m NNW of bridge over Dyje river, oak forest on cliff, shrub ca 3.5 m high, 48°51'25.3"N, 15°51'40.2"E, 400 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79683). – Čížov village, Hardeggská vyhlídka outlook, ca 560 m NNW of bridge over Dyje river, rocky forest-steppe, rare, shrub ca 2 m high, 48°51'27.1"N, 15°51'33.5"E, 380 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79678). – Čížov village, Hardeggská vyhlídka outlook, ca 600 m NNW of bridge over Dyje river, pine forest on acidophilous rock, shrub ca 1 m high, 48°51'27.8"N, 15°51'31.5"E, 340 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79690). **7. Hardeggská stráň hillside:** Čížov village, limestone NE of custom house (leg. B. Trávníček 20. 6. 1991, OL 26154, 26155, 26157). – Čížov village, calcareous slopes above Dyje river ca 400 [560] m SE of the 417 m a.s.l. spot height with Hardeggská vyhlídka outlook, above road to Hardegg, edge of shrubs and steppe, 1 individual ca 2.5 m high, 48°51'17.8"N, 15°52'06.6"E, 350 m a.s.l. (leg. ML et PL 23. 7. 2010, CB 74004). – Čížov village, calcareous slopes above Dyje river ca 500 [600] m SE of spot height of 417 m with Hardeggská vyhlídka outlook, above road to Hardegg, steppe, scaterred, 48°51'17.6"N, 15°52'08.1"E, 350 m a.s.l. (leg. ML et PL 23. 7. 2010, CB 74017). – Čížov village, calcareous slopes above Dyje river ca 500 [600] m SE of spot height of 417 m with Hardeggská vyhlídka outlook, above road to Hardegg, steppe, scaterred, 48°51'17.8"N, 15°52'08.5"E, 350 m a.s.l. (leg. ML et PL 23. 7. 2010, CB 74018). – Čížov village, slopes above Dyje river ca 0.5 to 0.9 km SE of Hardegg, open oak forests on southern slope, 48°51'15.3"N, 15°51'58.0"E, 340 m a.s.l. (leg. ML et PL 6. 8. 2009, CB 73696). – Čížov village, slopes above Dyje river ca 0.5 to 0.9 km SE of Hardegg, open oak forests on southern slope, 48°51'17.6"N, 15°52'07.9"E, 360 m a.s.l. (leg. ML et PL 6. 8. 2009, CB 73692). – Čížov village, slopes above Dyje river ca 0.5 to 0.9 km SE of Hardegg, open oak forests on southern slope, 48°51'18.2"N, 15°52'08.6"E, 370 [350] m a.s.l. (leg. ML et PL 6. 8. 2009, CB 73682). – Čížov village, Hardeggská stráň hillside, above road ca 300 m ENE of bridge over Dyje river, open forest, scattered, shrub ca 6 m high, 48°51'15.3"N, 15°51'57.6"E, 320 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79674). – Čížov village, Hardeggská stráň hillside, above road ca 600 m ENE of bridge over Dyje river, open thermophilous oak forest, plentiful, tree ca 5.5 m high, 48°51'18.0"N, 15°52'12.2"E, 350 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79671). – Čížov village, Hardeggská stráň hillside, above road, ca 300 m ENE of bridge over Dyje river, open forest, scattered, shrub ca 6 m high, 48°51'15.5"N, 15°51'58.2"E, 320 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79673). – Čížov village, Hardeggská stráň hillside, above road, ca 400 m ENE of bridge over Dyje river, forest-steppe, plentiful, tree ca 3 m high, 48°51'17.2"N, 15°52'02.9"E, 350 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79662). – Čížov village, Hardeggská stráň hillside, above road, ca 470 m ENE of bridge over Dyje river, forest-steppe, plentiful, 48°51'17.4"N, 15°52'05.9"E, 350 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79666). – Čížov village, Hardeggská stráň hillside, above road, ca 500 m ENE of bridge over Dyje river, forest-steppe, plentiful, tree ca 2 m high, 48°51'17.5"N, 15°52'05.5"E, 350 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79665). – Čížov village, Hardeggská stráň hillside, above road, ca 500 m ENE of bridge over Dyje river, forest-steppe, plentiful, shrub ca 5 m high, 48°51'17.8"N, 15°52'06.8"E, 350 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79667). – Čížov village, Hardeggská stráň hillside, above road, ca 500 m ENE of bridge over Dyje river, forest-steppe, plentiful, tree ca 3 m high, 48°51'17.6"N, 15°52'07.4"E, 350 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79668). – Čížov village, Hardeggská stráň hillside, above road, ca 520 m ENE of bridge over Dyje river, forest-steppe, plentiful, ca 4 m high, 48°51'17.5"N, 15°52'08.3"E, 350 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79669). – Čížov village, Hardeggská stráň hillside, above road, ca 530 m ENE of bridge over Dyje river, forest-steppe, scattered, shrub ca 3 m high, 48°51'17.4"N, 15°52'09.1"E, 360 [340] m a.s.l. (leg. ML et PL 14. 5. 2011, CB 79850). – Čížov village, Hardeggská stráň hillside, above road, ca 600 m ENE of bridge over Dyje river, forest-steppe, scattered, tree ca 6 m high, 48°51'18.0"N, 15°52'12.2"E, 350 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79851). – Čížov village, Hardeggská stráň hillside, above road, ca 620 m ENE of bridge over Dyje river, forest-steppe, plentiful, tree ca 3.5 m high, 48°51'18.1"N, 15°52'13.3"E, 360 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79672). – Čížov village, Hardeggská stráň hillside, below road ca 550 m ENE of bridge over Dyje river, open oak forest, rare, shrub ca 4 m high, 48°51'16.4"N, 15°52'10.2"E, 320 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79659). – Čížov village, Hardeggská stráň hillside, below road ca 680 m ENE of bridge over Dyje river, forest-steppe, scattered, tree ca 5 m high, 48°51'17.8"N, 15°52'16.3"E, 310 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79848). – Čížov village, Hardeggská stráň hillside, ca 520 m ENE of bridge over Dyje river, forest-steppe, plentiful, shrub ca 4 m high, 48°51'17.6"N, 15°52'08.5"E, 350 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79649). – Čížov village, Hardeggská stráň hillside, ca 530 m ENE of bridge over Dyje river, forest-steppe, scattered, 48°51'17.6"N, 15°52'08.5"E, 350 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79722). – Čížov village, Hardeggská stráň hillside, ca 530 m ENE of bridge over Dyje river, forest-steppe, scattered, shrub ca 3.5 m high, 48°51'17.4"N, 15°52'09.1"E, 350 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79721). – Čížov village, Hardeggská stráň hillside, ca 550 m ENE of bridge over Dyje river, forest-steppe, plentiful, 48°51'17.4"N, 15°52'09.5"E, 350 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79647). – Čížov village, Hardeggská stráň hillside, ca 550 m ENE of bridge over Dyje river, forest-steppe, plentiful, shrub 4 m high, 48°51'17.6"N, 15°52'09.9"E, 350 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79650). – Čížov village, Hardeggská stráň hillside, ca 550 m ENE of bridge over Dyje river, forest-steppe, plentiful, shrub ca 3.5 m high, 48°51'17.7"N, 15°52'09.9"E, 350 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79646). – Čížov village, Hardeggská stráň hillside, ca 550 m ENE of bridge over Dyje river, forest-steppe, plentiful, shrub ca 4 m high, 48°51'17.7"N, 15°52'10.7"E, 350 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79651). – Čížov village, Hardeggská stráň hillside, ca 550 m ENE of bridge over Dyje river, forest-steppe, plentiful, shrub ca 4 m high, 48°51'17.6"N, 15°52'11.1"E, 350 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79652). – Čížov village, Hardeggská stráň hillside, ca 570 m ENE of bridge over Dyje river, forest-steppe, plentiful, shrub ca 4 m high, 48°51'18.0"N, 15°52'11.4"E, 360 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79653). – Čížov village, Hardeggská stráň hillside, ca 600 m ENE of bridge over Dyje river, forest-steppe, plentiful, shrub ca 5 m high, 48°51'17.9"N, 15°52'11.7"E, 350 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79654). – Čížov village, Hardeggská stráň hillside, ca 600 m ENE of bridge over Dyje river, forest-steppe, plentiful, shrub ca 3.5 m high, 48°51'17.6"N, 15°52'12.4"E, 350 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79655). – Čížov village, Hardeggská stráň hillside, ca 600 m ENE of bridge over Dyje river, open oak forest, plentiful, shrub ca 5.5 m high, 48°51'17.6"N, 15°52'13.0"E, 350 m a.s.l. (leg. ML et PL 6. 5. 2011, CB 79656). – Podyjí region, slope above road from Hardegg to Čížov village, ca 400 m ENE of bridge over Dyje river, 48°51'16.2"N, 15°52'03.5"E (leg. J. Brabec 29. 5. 2012, CHEB). **8. Kozí stezky cliff I:** Čížov village, Dyje valley, Kozí stezky slopes, ca 2 km SSW of chapel in village, open forest on rocky slopes, rare, 48°51'39.9"N, 15°52'15.8"E, 360 m a.s.l. (leg. ML 22. 5. 2011, CB 79792). **9. Kozí stezky cliff II:** Čížov village, ca 2 km S of chapel in village, ridge between Dyje river and Klaperův potok brook, rocky oak forest, rare, shrub ca 5 m high, 48°51'40.5"N, 15°52'31.4"E, 350 m a.s.l. (leg. ML et PL 15. 6. 2012, CB 82893). **10. Mufloní kopec hill:** Čížov village, ca 1.6 km S of chapel in village, Mufloní kopec hill, edge of scree, rare, shrub ca 6 m high, 48°51'51.8"N, 15°52'28.2"E, 410 [380] m a.s.l. (leg. ML et PL 15. 6. 2012, CB 82892). **11. Urbanova cesta road:** Čížov village, ca 1.6 km SE of chapel in village, above Urbanova cesta road, oak-hornbeam forest, rare, tree ca 6 m high, 48°51'57.3"N, 15°52'51.9"E, 360 m a.s.l. (leg. ML et PL 15. 6. 2012, CB 82891). **12. Sloní hřbet hill:** Čížov village, S slopes ca 0.4 km N of confluence of Klaperův potok brook (leg. B. Trávníček 3. 9. 1992, OL 26177). – Čížov village, Dyje valley, Sloní hřbet ridge, ca 2.1 km SSE of chapel in village, edge of pine and oak-hornbeam forest, three individuals, shrub ca 7 m high, 48°51'38.3"N, 15°52'53.7"E, 360 m a.s.l. (leg. ML 22. 5. 2011, CB 79796). – Čížov village, Dyje valley, Sloní hřbet ridge, ca 2.1 km SSE of chapel in village, forest-steppe, scattered, shrub ca 3.5 m high, 48°51'40.4"N, 15°52'49.5"E, 360 m a.s.l. (leg. ML 22. 5. 2011, CB 79795). – Čížov village, on Sloní hřbet ridge, ca 2.2 km SSE of centre of village, forest-steppe, scattered, 48°51'39.3"N, 15°52'45.6"E, 330 m a.s.l. (leg. ML 3. 6. 2011, CB 79595). – Podyjí region, Čížov village, Sloní hřbet ridge, ca 1.4 km NE of bridge over Dyje river in Hardegg, 48°51'39.8"N, 15°52'40.3"E (leg. J. Brabec 29. 5. 2012, CHEB, leg. D. Abazid 29. 5. 2012, CHEB). **13. Mouth of Lukovský potok:** Čížov village, ca 2.8 [2.6] km SSE of centre of village, western steep slopes of spur between Dyje river and Lukovský potok brook, by a rock in oak-hornbeam forest, scattered, 48°51'24.4"N, 15°52'56.5"E, 330 m a.s.l. (leg. ML 3. 6. 2011, CB 79593). – Čížov village, ca 2.8 km SSE of centre of village, western steep slopes of spur between Dyje river and Lukovský potok brook, edge of oak-hornbeam forest and open patch, scattered, tree ca 5 m high, 48°51'20.1"N, 15°52'54.8"E, 330 m a.s.l. (leg. ML 3. 6. 2011, CB 79592).

Austria, Lower Austria: 14. Schwalbenfelsen hill I, 7161a: Hardegg, Dyje valley, Schwalbenfelsen cliff, ca 2.1 km NW of bridge over Dyje river, on cliff, ca 10 individuals, shrub ca 3 m high, 48°51'55.2"N, 15°50'27.1"E, 430 m a.s.l. (leg. ML et PL 15. 6. 2011, CB 79612). – Hardegg, Schwalbenfelsen in Dyje valley ca 2.2 km NW of bridge over Dyje river, on cliff in ravine forest, shrub ca 2.5 m high, 48°52'00.0"N, 15°50'24.0"E, 420 m a.s.l. (leg. ML 1. 6. 2012, CB 82853). **15. Schwalbenfelsen hill II, 7161a:** Hardegg, Dyje valley between Hardegg and Felling gamekeepers lodge, ca 2 km NW of bridge over Dyje river, oak-hornbeam forest on rock ridge, rare, tree ca 10 m high, 48°51'46.2"N, 15°50'20.9"E, 420 m a.s.l. (leg. ML et PL 15. 6. 2011, CB 79704). – Hardegg, Dyje valley, ca 2 km NW of bridge over Dyje river, oak-hornbeam forest, shaded tree ca 4 m high, 48°51'47.1"N, 15°50'22.4"E, 400 m a.s.l. (leg. ML et PL 25. 7. 2012, CB 82909). **16. Binderberg hill, 7161a:** Hardegg, Binderberg hill, ca 1.2 km W of bridge over Dyje river, slopes above

Fugnitz stream, acidophilous oak forest, tree ca 3 m high, 48°51'08.6"N, 15°50'46.4"E, 400 m a.s.l. (leg. ML et PL 13. 9. 2011, CB 79632). **17. Fugnitz brook I, 7161a:** Hardegg, W slopes of Fugnitz valley opposite Binderberg hill, ca 990 m W of bridge over Dyje river, edge of scree and *Fagus* and *Carpinus* forest, tree ca 6 m high, 48°51'08.9"N, 15°50'56.9"E, 340 m a.s.l. (leg. ML et PL 12. 6. 2011, CB 79731). **18. Above swimming pool, 7161a:** Hardegg, S slopes of Maxplateau hill above swimming pool, ca 830 m WNW of bridge over Dyje river, rock steppe, scattered, shrub ca 4 m high, 48°51'14.9"N, 15°51'04.9"E, 360 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79770). – Hardegg, S slopes of Maxplateau hill above swimming pool, ca 830 m WNW of bridge over Dyje river, rocky forest-steppe, scattered, tree ca 3 m high, 48°51'14.8"N, 15°51'05.9"E, 360 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79700). – Hardegg, S slopes of Maxplateau hill, above swimming pool, ca 800 m WNW of bridge over Dyje river, rock steppe, scattered, shrub 4.5 m high, 48°51'15.1"N, 15°51'05.1"E, 360 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79643). **19. Fugnitz brook II, 7161c:** Hardegg, slopes of Fugnitz valley opposite Binderberg hill, ca 1 km SW of bridge over Dyje river, forest-steppe, scattered, shrub ca 3 m high, 48°50'56.0"N, 15°51'00.9"E, 400 m a.s.l. (leg. ML et PL 12. 6. 2011, CB 79730). **20. Fugnitz brook III, 7161c:** Hardegg, Kreuzmaiss, slopes above Fugnitz stream, ca 1.5 km SSW of bridge over Dyje river, shrubby edge of rock steppe, shrub ca 2.5 m high, 48°50'30.7"N, 15°50'58.7"E, 380 m a.s.l. (leg. ML et PL 9. 5. 2011, CB 79781). – Hardegg, slopes of Fugnitz valley ca 1.5 km SW of bridge over Dyje river, *Bromion*, tree ca 6 m high, 48°50'33.8"N, 15°51'00.1"E, 390 m a.s.l. (leg. ML et PL 9. 5. 2011, CB 79769). **21. Kreuzmaiss, 7161c:** Hardegg, Kreuzmaiss, slopes above Fugnitz stream, ca 1.8 km SSW of bridge over Dyje river, edge of cliff, shrub ca 1 m high, 48°50'18.7"N, 15°51'02.9"E, 380 m a.s.l. (leg. ML et PL 9. 5. 2011, CB 79779). **22. Maxplateau hill, 7161a:** Hardegg, Maxplateau hill, ca 550 [600] m NW of bridge over Dyje river, oak-hornbeam forest, tree ca 3 m high, 48°51'20.3"N, 15°51'19.7"E, 360 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79639). – Hardegg, Maxplateau hill, ca 570 m NW of bridge over Dyje river, rocky forest-steppe, scattered, shrub ca 8 m high, 48°51'21.6"N, 15°51'22.1"E, 360 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79702). – Hardegg, Maxplateau hill, ca 570 m NW of bridge over Dyje river, rock, tree ca 5 m high, 48°51'21.5"N, 15°51'22.8"E, 360 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79701). **23. Hardegg East, 7161a:** Hardegg, ca 300 m SW of bridge over Dyje river, small rock above road, shrub ca 3 m high, 48°51'07.1"N, 15°51'32.3"E, 320 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79644). **24. Hardegg South, 7161c:** Hardegg, ca 500 m SW of bridge over Dyje river, mixed forest, several individuals, 48°50'57.3"N, 15°51'31.3"E, 380 m a.s.l. (leg. ML et PL 13. 9. 2011, CB 79631). – Hardegg, ca 600 m SW of bridge over Dyje river, *Pinus nigra* plantation on limestone, rare, tree ca 12 m high, 48°50'53.6"N, 15°51'30.4"E, 410 m a.s.l. (leg. ML et PL 13. 9. 2011, CB 79628). – Hardegg, ca 750 m SW of bridge over Dyje river, mixed forest, scattered, ca 6 m high, 48°50'49.1"N, 15°51'28.3"E, 420 m a.s.l. (leg. ML et PL 13. 9. 2011, CB 79629). **25. Hardegg above bridge, 7161a**: Hardegg, "pine forest I" on slopes of Dyje valley, ca 180 m SE of bridge over Dyje river, pine forest with *Sesleria*, scattered, shrub ca 3 m high, 48°51'06.2"N, 15°51'49.4"E, 350 m a.s.l. (leg. ML et PL 15. 5. 2011, CB 79859). – Hardegg, "pine forest I" on slopes of Dyje valley, ca 180 [230] m SE of bridge over Dyje river, pine forest with *Sesleria*, scattered, shrub ca 7 m high, 48°51'04.5"N, 15°51'51.9"E, 380 m a.s.l. (leg. ML et PL 15. 5. 2011, CB 79858). – Hardegg, "pine forest I" on slopes of Dyje valley, ca 180 [250] m SE of bridge over Dyje river, pine forest with *Sesleria calcaria*, tree ca 5 m high, 48°51'04.1"N, 15°51'52.2"E, 390 m a.s.l. (leg. ML et PL 12. 9. 2011, CB 79813). – Hardegg, "pine forest II" on slopes of Dyje valley, ca 300 m SE of bridge over Dyje river, pine forest with *Sesleria*, scattered, shrub ca 6 m high, 48°51'04.6"N, 15°51'56.3"E, 400 m a.s.l. (leg. ML et PL 15. 5. 2011, CB 79860). – Hardegg, ca 250 m SSE of bridge over Dyje river, pine forest with *Anthericum*, tree ca 10 m high, 48°51'02.7"N, 15°51'46.9"E, 400 m a.s.l. (leg. ML 29. 5. 2012, CB 82833). – Hardegg, slopes above Dyje river, ca 320 m ESE of bridge over Dyje river, on rock in forest, tree ca 5 m high, 48°51'08.6"N, 15°52'00.6"E, 300 m a.s.l. (leg. ML et PL 12. 9. 2011, CB 79808). **26. Thayatalweg path, 7161a:** Hardegg, slopes above Dyje river ca 0.87 km E of bridge over Dyje river, cliff with dom. *Sesleria*, shrub ca 6 m high, 48°51'12.5"N, 15°52'27.6"E, 350 m a.s.l. (leg. ML 29. 5. 2012, CB 82841). – Hardegg, slopes above Dyje river ca 0.9 km ENE of bridge over Dyje river, oak-hornbeam forest, shrub ca 4 m high, 48°51'14.2"N, 15°52'29.7"E, 340 m a.s.l. (leg. ML 29. 5. 2012, CB 82840). – Hardegg, slopes above Dyje river ca 1 km ENE of bridge over Dyje river, cliff with dom. *Anthericum*, sapling ca 2 m high, 48°51'17.7"N, 15°52'33.5"E, 340 m a.s.l. (leg. ML 29. 5. 2012, CB 82838). – Hardegg, slopes above Dyje river ca 1.1 km ENE of bridge over Dyje river, edge of forest and rocky steppe, tree ca 5 m high, 48°51'19.7"N, 15°52'34.2"E, 320 m a.s.l. (leg. ML 29. 5. 2012, CB 82837). – Hardegg, slopes above Dyje river ca 1.1 km ENE of bridge over Dyje river, foot of cliff in oak-hornbeam forest, tree ca 8 m high, 48°51'23.4"N, 15°52'33.8"E, 330 m a.s.l. (leg. ML 29. 5. 2012, CB 82836). – Hardegg, slopes above Dyje river ca 1.1 km ENE of bridge over Dyje river, cliff with *Sesleria*, tree ca 5 m high, 48°51'24.7"N, 15°52'33.9"E, 330 m a.s.l. (leg. ML 29. 5. 2012, CB 82835). – Hardegg, slopes above Dyje river, ca 0.9 km ENE of bridge over Dyje river, cliff in forest, scattered, tree ca 7 m high, 48°51'14.6"N, 15°52'31.4"E, 360 m a.s.l. (leg. ML et PL 9. 5. 2011, CB 79773). – Hardegg, slopes above Dyje river, ca 0.9 km ENE of bridge over

Dyje river, oak-hornbeam forest, scattered, tree ca 5 m high, 48°51'14.9"N, 15°52'32.4"E, 360 m a.s.l. (leg. ML et PL 9. 5. 2011, CB 79774). – Hardegg, slopes above Dyje river, ca 1 km NE of bridge over Dyje river, oak-hornbeam forest, tree ca 4 m high, 48°51'15.1"N, 15°52'32.8"E, 360 m a.s.l. (leg. ML et PL 15. 5. 2011, CB 79835). **27. Einsiedler, 7161a:** Hardegg, open woodland on right-hand bank of Dyje river (near tourist footpath), ca 1.5 km E of town (leg. B. Trávníček 25. 5. 1990, OL 26164). – Hardegg, slopes above Dyje river, ca 1 km NE of bridge over Dyje river, on rock, scattered, shrub ca 3.5 m high, 48°51'31.9"N, 15°52'23.5"E, 310 m a.s.l. (leg. ML et PL 15. 5. 2011, CB 79852). **28. Umlaufberg hill, 7161c:** Hardegg, Umlaufberg hill, acid rock, *Cotoneasteretum*, rarely, shrub ca 1.5 m high, 48°50'31.1"N, 15°53'25.9"E, 340 m a.s.l. (leg. ML 30. 5. 2012, CB 82846). – Hardegg, Umlaufberg hill, on cliff in oak forest, 48°50'33.8"N, 15°53'27.4"E, 320 m a.s.l. (leg. ML 30. 5. 2012, CB 82845).

Sorbus moravica M. Lepší et P. Lepší, **spec. nova** (Figs 10–11)

Description: Shrub or small tree up to 12 m high. Bark grey or dark grey, smooth when young, with fissures (particularly at the trunk base) when mature. Twigs thick, brownish-grey; young shoots brown, tomentose when young, glabrescent when mature, with pale brown to ochraceous lenticels. Buds ovoid, pointed; scales green, glabrescent, with narrow brown sparsely tomentose margins. Leaves on short sterile shoots simple; laminas elliptical to oblong elliptical, (7.0–) 8.1–9.2 (–10.4) cm long and (3.9–) 4.7–5.6 (–6.2) cm wide, (1.5–) 1.7–1.8 (–1.9) times as long as wide, widest at (50–) 53–56 (–59)% of the lamina length (from the base), with acute to acuminate apex with an angle of (75–) 100–110 (–125)°, cuneate and partly serrate at base, with angle at base (65–) 70–85 (–90)°, usually flat at margins, regularly, double to triple serrate, with acute teeth terminating the main veins (other teeth also acute but somewhat smaller), with (5–) 6–8 (–11) teeth between the 2nd and 3rd main veins from the base, with angle of the teeth terminating the 3rd main veins (60–) 70–90 (–100)°, with incision between the 2nd and the 3rd main vein from the base (1.4–) 1.9–2.6 (–3.3) mm long, leathery, more or less glossy, green, sparsely tomentose when young, later glabrescent on upper surface, evenly greenish-grey-tomentose on lower surface, with (8–) 9 (–10) veins on each side, with the 3rd veins at an angle of (20–) 25–35° to midrib; petioles (9–) 12–15 (–17) mm long, tomentose. Leaf laminas on short fertile shoots more or less the same size and shape as leaf laminas on short sterile shoots. Inflorescences compact, convex, with tomentose branchlets. Sepals triangular, acute to acuminate, tomentose on both surfaces, patent or rarely bent to hypanthium at flowering, erect, persistent and dry at fruiting. Petals broadly ovate to broadly elliptical, (6.5–) 7.5–8.5 (–9.5) mm long and (5.0–) 6.0–6.5 (–7.0) mm wide, concave, white, patent, sparsely tomentose at base of upper surface, glabrous on lower surface, with a short claw. Stamens ca 20; anthers pale yellow. Ovary semi-inferior. Styles 2 (–3), free and tomentose at base. Fruit more or less subglobose, (10.5–) 11.5–12.5 (–13.5) mm long and (10.5–) 11.5–12.5 (–13.5) mm wide, slightly wider than long or slightly longer than wide, red at maturity, tomentose at top and base, otherwise glabrescent, matt, with (10–) 13–18 (–24) lenticels per 25 mm^2; mesocarp heterogeneous; endocarp cartilaginous. Seeds fuscous. DNA ploidy level: triploid (inferred using FCM). Reproduction probably apomictic. Flowering V.

Holotype: southern Moravia, Lažánky (distr. Blansko), Suchý žleb gorge, S slopes, edge of forest and cliff; 440 m a.s.l., 49°21'46.55"N, 16°43'3.11"E; scattered; tree ca 8 m high; 22. 7. 2011 leg. Martin Lepší; CB, No. 79868 (Fig. 10). – Isotype: PR, 79868/a.

Name previously used for this taxon in the Czech Republic: *Sorbus aria* sensu Kovanda, Acta Mus. Morav., Sci. Nat., 81: 196, 1997.

HERBARIUM MUSEI REGIONALIS BOHEMIAE MERIDIONALIS
ČESKÉ BUDĚJOVICE

Flora: Southern Moravia

* C B / 7 9 8 6 8 *

Sorbus moravica M. Lepší et P. Lepší **HOLOTYPE!**

Lažánky (distr. Blansko), Suchý žleb gorge, S slopes, edge of forest and cliff

Frequence: scattered; tree ca 8 m high

Note: 2n ~ 3x; DNA ploidy level was detected using the flow cytometer Partec PA II (DAPI fluorochrome); ratio to the internal standard (Bellis perennis L.) is 0.554; Analysed 28. 7. 2011, Department of Botany, University of South Bohemia, Č. Budějovice.

Altitude: 440 m **WGS 84:** 49°21'46,55''N; 16°43'3,11''E

Quadrant: 6666ada **ID GPS:** 545

Phytogeographical distr.: Moravský kras

Date: 22.7. 2011 **Collected:** Martin Lepší

Quadrant according to Ehrendorfer et Hamann 1965, Ber. Deutsch. Bot. Ges.; Phytogeographical distr. - Skalický 1988, Květena ČR 1

Fig. 10. – Holotype of *Sorbus moravica*.

Fig. 11. – *Sorbus moravica*: short fructiferous shoot (left) and leaf from the middle part of a short sterile shoot (right). Scale bar 2 cm. Drawn by A. Skoumalová.

Diagnostic characters: Leaf laminas on short sterile shoots are elliptical to oblong elliptical, regularly, double (to triple) serrate, with (5–) 6–8 (–11) teeth between the 2nd and 3rd main veins from the base. Fruit are more or less subglobose, slightly wider than long or slightly longer than wide, red.

Etymology: The name "*moravica*" is derived from the Latin name of the Czech land Morava (Moravia), where the species occurs. We propose the epithet "moravský" for the Czech name.

Ecology: *Sorbus moravica* is a light-demanding species that prefers sunny or at least partly open habitats such as cliffs, screes, ravines and steep woody or shrubby slopes of canyons in karst areas. Besides semi-natural to relic vegetation, it also grows in *Picea abies* and *Pinus nigra* plantations or in their clearings. This species occurs on calcareous, dry and shallow soils developed on limestone, and inhabits slopes of all aspects (most individuals were found on slopes facing south, northeast or northwest). This species was mainly recorded in a mixture of communities associated with cliffs and rocky slopes, i.e. in *Sesleria* grasslands (*Diantho lumnitzeri-Seslerion albicantis*), tall xeric scrubs (*Berberidion*), chasmophytic vegetation on calcareous cliffs and screes (*Cystopteridion*) and dry herbaceous fringes (*Geranion sanguinei*). It is also common in ravines, screes and rock forests (*Tilio-Acerion*) or in fringes and gaps in limestone beech forests (*Cephalanthero-Fagenion*). Rarely it was found in broad-leaved dry grasslands (*Bromion erecti*).

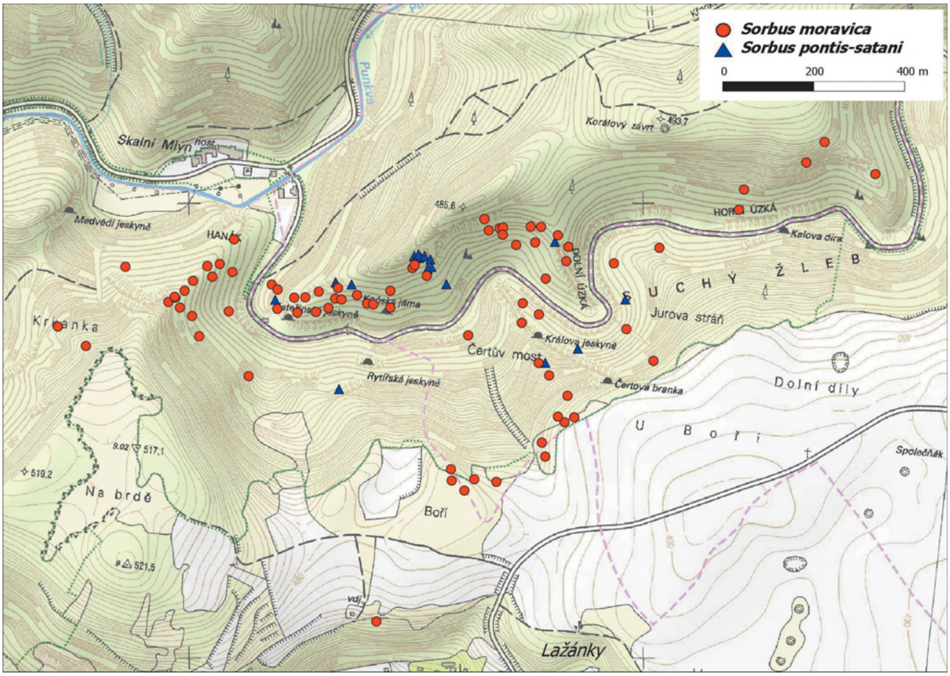

Fig. 12. – Map showing the distribution of *Sorbus pontis-satani* and *S. moravica* (map source © ČÚZK 2014).

Distribution and population size: *Sorbus moravica* is a stenoendemic in the Suchý Žleb gorge by the village of Lažánky (distr. Blansko) on the Moravian Karst (quadrant 6666a of the central-European grid mapping, Ehrendorfer & Hamann 1965). About 200 trees and shrubs are known in the western part of the gorge and the adjacent valley of the Punkva River. A few individuals also occur on the plateau between the gorge and Lažánky (Fig. 12). Most individuals are confined to southern slopes in the Suchý žleb gorge between the settlement of Skalní Mlýn and Chobot hill. Despite being locally abundant, it was not found in adjacent areas such as the Pustý žleb, Lažánecký žleb and Veselý žleb gorges and Punkevní údolí valley. It is even absent in the northern part of the Suchý žleb gorge where there are many suitable habitats. The altitudinal range of this species spans from 360 to 490 m a.s.l. In terms of Czech phytogeography and climatology, the distribution area is in the supracolline vegetation belt (Chytrý 2012), the phytogeographical district Moravian Karst (Skalický 1988) and a moderately warm climatic region (Quitt 1971) with a mean annual temperature of about 7–8 °C and mean annual precipitation of 550–600 mm (Tolasz et al. 2007).

Herbarium specimens

Czech Republic, southern Moravia, 70. Moravský kras, 6666a: Moravian Karst, Vilémovice, W of village (leg. K. Kubát 14. 7. 1980, LIT 1884/41878). – Moravian Karst, edge of arable field above village of Vilémovice (leg. Nováková 14. 7. 1980, MP). – Lažánky village, NE edge of village, fringe of *Pinus sylvestris* plantation, a tree ca 5 m high, 49°21'17.5"N, 16°42'50.9"E, 480 m a.s.l. (leg. ML 12. 5. 2012, CB 82950). – Lažánky village, N-facing slopes of Suchý žleb gorge, top of cliff in *Fagus* and *Picea* forest, rare, tree ca 8 m high, 49°21'46.0"N, 16°43'17.3"E, 410 m a.s.l. (leg. ML 12. 5. 2012, CB 82953). – Lažánky village, N-facing slopes of Suchý žleb gorge, open *Picea abies* plantation, rare, tree ca 8 m high, 49°21'40.0"N, 16°43'14.6"E, 410 m a.s.l. (leg. ML 12. 5. 2012, CB 82958). – Lažánky village, N-facing slopes of Suchý žleb gorge, cliff with *Sesleria* in *Fagus* and *Picea* forest, rare, tree ca 4 m high, 49°21'33.9"N, 16°42'34.2"E, 430 m a.s.l. (leg. ML 12. 5. 2012, CB 82954). – Lažánky village, Skalní Mlýn mill, ca 200 m SSE of mill, bushy cliff, scattered, tree ca 6 m high, 49°21'43.5"N, 16°42'31.1"E, 410 m a.s.l. (leg. ML et PL 28. 8. 2011, CB 79909). – Lažánky village, Skalní Mlýn mill, ca 300 m SW of mill, edge of scree, tree ca 13 m high, 49°21'40.7"N, 16°42'19.6"E, 410 m a.s.l. (leg. ML et PL 28. 8. 2011, CB 79906). – Lažánky village, Skalní Mlýn mill, ca 500 m SW of mill, in beech forest with *Pinus sylvestris*, tree ca 15 m high, 49°21'34.8"N, 16°42'16.2"E, 480 m a.s.l. (leg. ML et PL 28. 8. 2011, CB 79900). – Lažánky village, Skalní Mlýn mill, ca 500 m SW of mill, pine forest with *Sesleria caerulea*, tree ca 5 m high, 49°21'35.9"N, 16°42'13.0"E, 470 m a.s.l. (leg. ML et PL 28. 8. 2011, CB 79902). – Lažánky village, Skalní Mlýn mill, rock ridge ca 300 m SSW of mill, on rock, scattered, tree ca 7 m high, 49°21'38.8"N, 16°42'25.4"E, 470 m a.s.l. (leg. ML et PL 28. 8. 2011, CB 79907). – Lažánky village, Suchý žleb gorge, N edge of gorge, clearing, tree ca 12 m high, 49°21'28.8"N, 16°42'57.2"E, 480 m a.s.l. (leg. ML et PL 26. 7. 2012, CB 82928). – Lažánky village, Suchý žleb gorge, N edge of gorge, *Pinus nigra* and *Pinus sylvestris* plantation, tree ca 6 m high, 49°21'28.2"N, 16°43'02.3"E, 480 m a.s.l. (leg. ML et PL 26. 7. 2012, CB 82927). – Lažánky village, Suchý žleb gorge, N edge of gorge, scrub at forest edge, tree ca 5 m high, 49°21'33.4"N, 16°43'09.9"E, 490 m a.s.l. (leg. ML et PL 26. 7. 2012, CB 82926). – Lažánky village, Suchý žleb gorge, N slopes, scrub in clearing, tree ca 8 m high, 49°21'37.9"N, 16°43'17.9"E, 480 m a.s.l. (leg. ML et PL 26. 7. 2012, CB 82925). – Lažánky village, Suchý žleb gorge, S slopes, bushy clearing, tree ca 3.5 m high, 49°21'54.8"N, 16°43'33.9"E, 480 m a.s.l. (leg. ML 22. 7. 2011, CB 79875). – Lažánky village, Suchý žleb gorge, S slopes, edge of *Pinus* plantation, scattered, a small tree, 49°21'53.2"N, 16°43'32.2"E, 480 m a.s.l. (leg. ML 22. 7. 2011, CB 79876). – Lažánky village, Suchý žleb gorge, S slopes, *Corylus* scrub, scattered, 49°21'45.4"N, 16°43'07.4"E, 420 m a.s.l. (leg. ML 27. 8. 2011, CB 79867). – Lažánky village, Suchý žleb gorge, S slopes, edge of forest and cliff, scattered, tree ca 8 m high, 49°21'46.5"N, 16°43'03.1"E, 440 m a.s.l. (leg. ML 22. 7. 2011, CB 79868). – Lažánky village, Suchý žleb gorge, S slopes, ravine forest with *Tilia*, tree ca 7 m high, 49°21'46.8"N, 16°42'57.9"E, 440 m a.s.l. (leg. ML et PL 27. 8. 2011, CB 79898). – Lažánky village, Suchý žleb gorge, S slopes, rock ridge with *Corylus* and steppe, shrub ca 4.5 m high, 49°21'46.2"N, 16°43'06.1"E, 440 m a.s.l. (leg. ML et PL 27. 8. 2011, CB 79899). – Lažánky village, Suchý žleb gorge, S slopes, gap in forest, shrub ca 4 m high, 49°21'50.8"N, 16°43'25.8"E, 460 m a.s.l. (leg. ML et PL 26. 7. 2012, CB 82923). – Lažánky village, Suchý žleb gorge, S slopes, beech forest on cliff, tree ca 3 m high, 49°21'44.4"N, 16°43'07.3"E, 410 m a.s.l. (leg. ML 27. 8. 2011, CB 79871). – Lažánky village, Suchý žleb gorge, S slopes, edge of basiphilous beech forest and cliff, scattered, tree ca 6 m high, 49°21'38.8"N, 16°42'36.5"E, 400 [360] m a.s.l. (leg. ML et PL 27. 8. 2011, CB 79880). – Lažánky village, Suchý žleb gorge, S slopes, rock ridge, scattered, tree ca 6 m high, 49°21'39.8"N, 16°42'38.3"E, 400 [380] m a.s.l. (leg. ML et PL 27. 8. 2011, CB 79881). – Lažánky village, Suchý žleb gorge, S slopes, bushy cliff, scattered, tree ca 4 m high, 49°21'39.9"N, 16°42'39.4"E, 410 [390] m a.s.l. (leg. ML et PL 27. 8. 2011, CB 79883). – Lažánky village, Suchý žleb gorge, S slopes, cliff, scattered, tree ca 6 m high, 49°21'40.4"N, 16°42'40.8"E, 420 [390] m a.s.l. (leg. ML et PL 27. 8. 2011, CB 79884). – Lažánky village, Suchý žleb gorge, S slopes, edge of limestone beech forest and rocky steppe, scattered, multi-trunk tree ca 7 m high, 49°21'40.8"N, 16°42'42.9"E, 430 m a.s.l. (leg. ML et PL 27. 8. 2011, CB 79886). – Lažánky village, Suchý žleb gorge, S slopes, edge of beech forest and scrub on scree, scattered, shrub ca 6 m high, 49°21'42.7"N, 16°42'50.7"E, 460 m a.s.l. (leg. ML et PL 27. 8. 2011, CB 79891).

Sorbus pontis-satani M. Lepší et P. Lepší, **spec. nova** (Figs 13–14)

Description: Shrub or small tree up to 12 m high. Bark grey or dark grey, smooth when young, with fissures (particularly at the trunk base) when mature. Twigs thick, brownish-grey; young shoots brown, tomentose when young, glabrescent when mature, with pale brown to ochraceous lenticels. Buds ovoid, pointed; scales green, glabrescent, with narrow brown sparsely tomentose margins. Leaves on short sterile shoots simple; laminas broadly elliptical, (5.8–) 6.5–7.8 (–8.8) cm long and (3.8–) 4.4–5.1 (–6.1) cm wide, (1.3–) 1.5–1.6 times as long as wide, widest at (50–) 54–57 (–61)% of the lamina length (from the base), with acute to acuminate apex with angle (100–) 110–125 (–140)°, cuneate and partly serrate at base, with angle at base of (70–) 75–85 (–95)°, usually undulate to

HERBARIUM MUSEI REGIONALIS BOHEMIAE MERIDIONALIS
ČESKÉ BUDĚJOVICE

Flora: Southern Moravia

CB/83096

Sorbus pontis-satani M. Lepší et P. Lepší **HOLOTYPE!**

Lažánky (distr. Blansko), S slopes of Suchý žleb gorge, above entrance of Kateřinská jeskyně cave, on cliff

Frequence: rarely, shrub ca 5 m high

Note: No. 144; 2n ~ 3x; DNA ploidy level was detected using the flow cytometer Partec PA II (DAPI fluorochrome); ratio to the internal standard (Bellis perennis L.) is 0.564; Analysed 31. 8. 2011, Department of Botany, University of South Bohemia, Č. Budějovice

Altitude: 390 m **WGS 84:** 49°21'38,8''N; 16°42'33,9''E

Quadrant: 6666adc **ID GPS:** 60

Phytogeographical distr.: Moravský kras

Date: 16. 8. 2013 **Collected:** Martin Lepší

Quadrant according to Ehrendorfer et Hamann 1965, Ber. Deutsch. Bot. Ges.; Phytogeographical distr. - Skalický 1988, Květena ČR 1

Fig. 13. – Holotype of *Sorbus pontis-satani*.

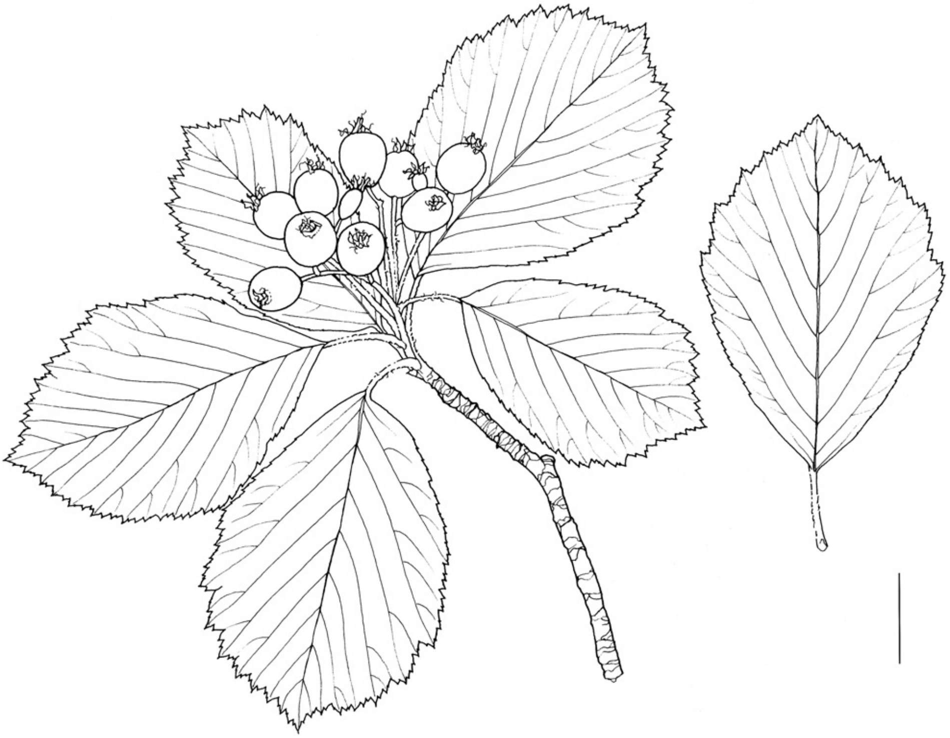

Fig. 14. – *Sorbus pontis-satani*: short fructiferous shoot (left) and leaf from the middle part of a short sterile shoot (right). Scale bar 2 cm. Drawn by A. Skoumalová.

crispate at margins apically, regularly, finely double to triple serrate, with acute teeth terminating the main veins (other teeth also acute but somewhat smaller), with (6–) 8–10 (–11) teeth between the 2nd and 3rd main veins from the base, with angle of the teeth terminating the 3rd main veins (35–) 45–55 (–65)°, with incision between the 2nd and the 3rd main vein from the base (2.1–) 2.7–3.5 (–5.0) mm long, leathery, more or less glossy, green, sparsely tomentose when young, later glabrescent on upper surface, evenly greenish-grey-tomentose on lower surface, with (7–) 8 (–9) veins on each side, with the 3rd veins at an angle of 25–30 (–35)° to midrib; petioles (9–) 10–14 (–17) mm long, tomentose. Leaf laminas on short fertile shoots relatively wider than leaf laminas on short sterile shoots. Inflorescences compact, convex, with tomentose branchlets. Sepals triangular, acuminate, tomentose on both surfaces, patent or rarely bent to hypanthium at flowering, erect, persistent and dry at fruiting. Petals broadly elliptical, (5.5–) 7.0–8.2 (–8.5) mm long and (5.0–) 5.5–6.0 (–6.5) mm wide, concave, white, patent, sparsely tomentose at base of upper surface, glabrous on lower surface, with a short claw. Stamens ca 20; anthers pale yellow. Ovary semi-inferior. Styles 2, free and tomentose at base. Fruit more or less subglobose, (7.0–) 11.0–12.5 (–13.5) mm long and (5.0–) 10.5–12.0 (–12.5) mm wide, slightly wider than long or slightly longer than wide, red when mature, tomentose at top and base, otherwise glabrescent, matt, with (2–) 7–10 (–16) lenticels per 25 mm^2;

mesocarp heterogeneous; endocarp cartilaginous. Seeds fuscous. DNA ploidy level: triploid (inferred using FCM). Reproduction probably apomictic. Flowering V.

Holotype: southern Moravia, Lažánky (distr. Blansko), S slope of Suchý žleb gorge, above entrance of Kateřinská jeskyně cave; 390 m a.s.l., 49°21'38.8"N, 16°42'33.9"E; rarely; shrub ca 5 m high; 16. 8. 2013 leg. Martin Lepší; CB, No. 83096 (Fig. 13). – Isotype: PR, 83096/a.

Name previously used for this taxon in the Czech Republic: *Sorbus austriaca* sensu Kovanda, Acta Mus. Morav., Sci. Nat. 81: 201, 1997 p.p.

Diagnostic characters: Leaf laminas on short sterile shoots broadly elliptical, usually undulate to crispate at margins apically, regularly and finely double (to triple) serrate. Fruit more or less subglobose, slightly wider than long or slightly longer than wide, red.

Etymology: The name "*pontis-satani*" relates to a natural bridge called Čertův most (Devil's bridge) in whose surroundings the species occurs. We propose the epithet "čertův" for the Czech name.

Ecology: *Sorbus pontis-satani* appears to have very similar ecological demands as the sympatric species, *S. moravica*. It is a light-demanding, rupicolous and calcareous species that prefers semi-natural or relic vegetation on cliffs or their close surroundings, but rarely grows in open *Picea abies* plantations or man-made clearings. It was mostly recorded on south-facing and west-facing slopes, exceptionally also on slopes with a northern aspect. It occurs in vegetation consisting of tall xeric shrubs (*Berberidion*), *Sesleria* grasslands (*Diantho lumnitzeri-Seslerion albicantis*), ravine forests (*Tilio-Acerion*) and gaps in limestone beech forests and their fringes (*Cephalanthero-Fagenion*).

Distribution and population size: This species occurs in the Suchý žleb gorge by the village of Lažánky (distr. Blansko) on the Moravian Karst (quadrant 6666a; sensu Ehrendorfer & Hamann 1965). Most of the 30 known individuals of different ages occur mainly on south-facing slopes opposite the Čertův most natural bridge and are very rare on north-facing slopes (Fig. 12). The altitudinal range of this species spans from 380 to 450 m a.s.l. The phytogeographical and climatic data for the distribution of this species are the same as for *S. moravica*.

Herbarium specimens

Czech Republic, southern Moravia, 70. Moravský kras, 6666a: Lažánky village, N-facing slopes in Suchý žleb gorge, open *Picea abies* plantation, rare, tree ca 8 m high, 49°21'42.1"N, 16°43'14.2"E, 400 m a.s.l. (leg. ML 12. 5. 2012, CB 82959). – Lažánky village, N-facing slopes in Suchý žleb gorge, wooded rocky steep slopes, rare, 49°21'38.3"N, 16°43'09.6"E, 410 m a.s.l. (leg. ML 12. 5. 2012, CB 82956). – Lažánky village, N-facing slopes in Suchý žleb gorge, rocky slopes, rare, 49°21'33.7"N, 16°42'44.2"E, 440 m a.s.l. (leg. ML 12. 5. 2012, CB 82955). – Lažánky village, Suchý žleb gorge, N edge of gorge, cliff in clearing, tree ca 2 m high, 49°21'37.0"N, 16°43'05.8"E, 430 m a.s.l. (leg. ML et PL 26. 7. 2012, CB 82929). – Lažánky village, Suchý žleb gorge, S slopes, on cliff, scattered, tree ca 8 m high, 49°21'45.7"N, 16°43'05.9"E, 440 m a.s.l. (leg. ML 22. 7. 2011, CB 79869). – Lažánky village, Suchý žleb gorge, S slopes, shrub-steppe, 49°21'42.8"N, 16°42'52.4"E, 425 m a.s.l. (leg. ML et PL 26. 7. 2012, CB 82931). – Lažánky village, Suchý žleb gorge, S slopes, edge of forest and shrub, tree ca 4 m high, 49°21'43.5"N, 16°42'52.6"E, 425 m a.s.l. (leg. ML et PL 26. 7. 2012, CB 82930). – Lažánky village, Suchý žleb gorge, S slopes, forest-steppe, tree ca 6 m high, 49°21'43.6"N, 16°42'51.5"E, 460 m a.s.l. (leg. ML 22. 7. 2011, CB 79870). – Lažánky village, Suchý žleb gorge, S slopes, cliff, shrub ca 5 m high, 49°21'39.5"N, 16°42'36.3"E, 390 m a.s.l. (leg. ML et PL 27. 8. 2011, CB 79879). – Lažánky village, Suchý žleb gorge, S slopes, in beech forest, tree ca 3 m high, 49°21'41.2"N, 16°42'42.6"E, 420 m a.s.l. (leg. ML et PL 27. 8. 2011, CB 79887). – Lažánky village, Suchý žleb gorge, S slopes, thermophilous shrubs, tree ca 3.5 m high, 49°21'41.1"N, 16°42'44.4"E, 440 m a.s.l. (leg. ML et PL 27. 8. 2011, CB 79888). – Lažánky village, Suchý žleb gorge, S slopes, on rock ridge, tree ca 6 m high, 49°21'43.3"N, 16°42'50.9"E, 470 m a.s.l. (leg. ML et PL 27. 8. 2011, CB 79892). – Lažánky village, Suchý žleb gorge, S slopes, edge of ravine forest, scattered, tree ca 5.5 m high, 49°21'43.6"N, 16°42'50.8"E, 470 m a.s.l. (leg. ML et PL 27. 8. 2011, CB 79893). – Lažánky village, Suchý žleb gorge, S slopes, edge of rocky forest-steppe, scattered, tree ca 7 m high, 49°21'43.8"N, 16°42'51.3"E, 470 m a.s.l. (leg. ML et PL 27. 8. 2011, CB 79894). – Lažánky village, Suchý žleb gorge, S slopes, gap in limestone beech forest, tree ca 5 m high, 49°21'43.5"N, 16°42'51.3"E, 470 m a.s.l. (leg. ML et PL 27. 8. 2011, CB 79895). – Lažánky village, Suchý žleb gorge, S slopes, gap in limestone beech forest, tree ca 7 m high, 49°21'43.7"N, 16°42'51.9"E, 460 m a.s.l. (leg. ML et PL 27. 8. 2011, CB 79896). – Lažánky village, Suchý žleb gorge, S slopes, rocky forest-steppe, scattered, shrub ca 8 m high, 49°21'42.9"N, 16°42'52.8"E, 450 [420] m a.s.l. (leg. ML et PL 27. 8. 2011, CB 79897). – Lažánky village, Suchý žleb gorge, S slopes, in beech forest, tree ca 2 m high, shaded, 49°21'41.9"N, 16°42'54.6"E, 410 m a.s.l. (leg. ML et PL 26. 7. 2012, CB 82918).

Tetraploid species

According to our investigation, the most common ploidy level in the subg. *Aria* in the Czech Republic is tetraploid (Fig. 1). They occur in two separate regions. The first and larger area is situated in central and north-western Bohemia, and the second in southern Moravia. Tetraploids are usually confined to climatically warm regions and inhabit relic habitats such as cliffs and rocky slopes with steppe vegetation. Their local abundance closely depends on the presence and range of these habitats. Tetraploids seem to have played a crucial role in speciation of the Czech *Sorbus* by hybridising with diploid members of other subgenera giving rise to apomictic microspecies. Up until now, there are 13 hybridogenous miscrospecies in the Czech Republic (Danihelka et al. 2012, Lepší et al. 2013a), and each of them probably have genes of a tetraploid of the subg. *Aria* (e.g. Challice & Kovanda 1978, 1986).

Based on the results of our field investigation and morphological analyses, we distinguished three taxa among Czech tetraploids – two widespread species, *S. danubialis* and *S. collina*, and one stenoendemic, *S. thayensis*. The latter two species are for the first time described below as new taxa. *Sorbus danubialis* is a traditionally recognized and widely accepted species in central Europe (Kovanda 1992, Májovský 1992, Kutzelnigg 1995, Meyer et al. 2005, Fisher 2008, Király 2009, Kurtto 2009, Jäger 2011). To verify the classification of Czech plants treated as *S. danubialis*, we analysed the ploidy levels and morphology of four individuals from the type locality (Sas-hegy hill, Budapest, Hungary; Kováts 1998). All of them turned out to be tetraploid, and morphologically similar to Czech plants in PCA (data not shown).

In the Czech Republic, *S. danubialis* is reported from Bohemia and Moravia (Kovanda 1992, 2002), and our findings are mostly in accordance with this general knowledge. However, there are some erroneous records, which deserve closer attention because they were accepted in national compendia such as determination keys or the Red List of the Flora of the Czech Republic (Holub & Procházka 2000, Kovanda 2002). All records of *S. graeca* in the Czech Republic (Podyjí National Park and Moravian Karst) cited by Kovanda (1997a, 2002) apply in reality to untypical, round-leaved individuals of *S. danubialis*, and in a similar way, records of *S. austriaca* from the Moravian Karst (Kovanda 1997b) are partly based on misidentification of shaded individuals of *S. danubialis*. Other errors concern the ploidy level of the species. *Sorbus danubialis* is reported to be a diploid based on an analysis of plants from Hradiště hill in the Lounsko-Labské středohoří phytogeographical district (Jankun & Kovanda 1987, Kovanda 1992).

This region is located in Bohemia, where we did not find any diploid members of the subg. *Aria* (except several escaped plants of *S. aria*). We therefore conclude that *S. danubialis* is tetraploid and that Jankun's and Kovanda's records are incorrect. An erroneous ploidy level is reported by the same authors also for *S. eximia* (Vít et al. 2012).

Sorbus danubialis exhibits a certain level of morphological variation within the Czech Republic. Plants from the Moravian Karst and Bohemian Karst have more rounded leaf laminas compared to most plants from other regions. Individuals from the Dolní Povltaví region and the České středohoří Mts are described as var. *apiculata* due to markedly rhombic leaves (Kovanda 1961), and some individuals from the České středohoří Mts are remarkable in having deeply serrate to shallowly lobed laminas, yet they occur sympatrically with the dominant typical morphotype. This variability can be explained either as a reaction of the species to diverse ecological conditions or a result of genetic variation caused by facultative sexuality or mutation. However, we have not observed any significant variability which would demand taxonomic classification, so we conclude that it is not essential to delimit infraspecific taxa within *S. danubialis* in the Czech Republic. In addition to the Czech Republic, we studied *S. danubialis* also in Bavaria, Lower Austria and Hungary (see Fig. 1 and Appendix 1).

Several different names were used for the second widespread tetraploid *S. collina* in the past. In the Czech Republic, this species was believed to be diploid *S. aria*, as is apparent not only from herbarium specimens, but also from descriptions of its distribution (Klika 1937, Kovanda 1961, 1992, 2002) and a drawing in the Flora of the Czech Republic (Kovanda 1992).

In Bavaria, this taxon was at first called *S. graeca* (Bornmüller 1918). Later, Bresinsky (1978) introduced the name *S. pannonica* following Düll's evaluation of this taxon as a transitus and translating Düll's name "*S. aria* ssp. (*aria-cretica*)" into Karpati's nomenclatural system (Kárpáti 1960). This approach was finally adopted by recent authors (Meyer et al. 2005, Feulner et al. 2013). In fact, *S. pannonica* is the name for the transitional species between tetraploid *S. graeca* and diploid *S. aria* (Kárpáti 1960). We have analysed two populations of *S. pannonica* from Hungary and shown them to be triploid (Table 2, and Appendix 1), which supports the initially suggested origin (Kárpáti 1960). In Austria and Hungary, *S. collina* along with other similar taxa are classified as *S. graeca* (Király 2009, Jäger 2011).

Sorbus graeca is a widespread species distributed in central and southern Europe, Northern Africa and Asia Minor. It is a very variable complex of mutually similar tetraploid and also diploid taxa (cf. Gabrielian 1961, Kutzelnigg 1995, Kurtto 2009, Gabrielian & Balayan 2013). Central-European plants are all tetraploid and morphologically fit within the broadly delimited *S. graeca*. On the other hand, they are more or less morphologically uniform and well separated from *S. graeca* s. str., including several taxa that are regarded as taxonomic synonyms (for details, see Table 5). Based on our thorough comparative study of type material, protologues and other relevant sources on these related taxa, we conclude that the central-European populations represent a unique and well defined apomictic taxon, which deserves delimitation at the species level. To this end the new species *Sorbus collina* is described below. The species *Sorbus danubialis* was separated from the aggregate of *S. graeca* in a similar way (Kovanda 1992). Intraspecific variation within *S. collina* is insignificant in the Czech Republic, Bavaria and the regions of Austria sampled. Hungarian plants differ slightly from this main

Table 5. – Principal values and character states allowing the separation of *S. collina* from *S. graeca* and other taxa that are regarded as synonyms.

Species	Principal differences between taxa and *S. collina*	Characters of *S. collina*	Source
S. graeca var. *cuneifolia* Zinserl.	fruit red with few lenticel located only at the base, petioles 3–15 mm long	fruit dark red with scattered and evenly distributed lenticels, petioles (13–) 16–20 (–22) mm long	protologue, Zinserling 1939, Gabrielian 1961
S. cretica (Lindley) Fritsch et Rech.	leaf lamina 4.2–6.2 cm long, coarsely serrate	leaf lamina (8.4–) 9.0–9.9 (–12.5) cm long, serrate to finaly serrate	lectotype in CGE, No. 06506
S. cyclophylla Gand.	leaf lamina 2–3 cm wide	leaf lamina (5.7–) 7.0–7.5 (–9.8) cm wide	protologue, Gandoger 1875
S. graeca (Loddiges ex Spach) Loddiges ex Schauer	leaf lamina 5.0–6.6 cm long, elliptical subrhomboidal	leaf lamina (8.4–) 9.0–9.9 (–12.5) cm long, broadly elliptical to almost rotund	lectotype in P, No. P00680357
S. graeca var. *orbiculata* Gabr.	fruit red, petioles 3–15 mm long, leaf lamina base rounded to broadly cuneate, 2n = 34	fruit dark red, petioles (13–) 16–20 (–22) mm long, leaf lamina base cuneate to broadly cuneate, 2n = 68	protologue, Zinserling 1939, Gabrielian 1961, Gabrielian & Balayan 2013
S. meridionalis Guss.	petioles 10–13 mm long, leaf lamina base narrowly cuneate	petioles (13–) 16–20 (–22) mm long, leaf lamina base cuneate to broadly cuneate	comparison chart, Castellano et al. 2012
S. migarica Zinserl.	leaf lamina 4–5 cm long	leaf lamina (8.4–) 9.0–9.9 (–12.5) cm long	protologue, Zinserling 1939
S. obtusidentata Zinserl.	leaf lamina obovate, teeth more or less obtuse to crenate	leaf lamina broadly elliptical to almost rotund, teeth acute	protologue, Zinserling 1939
S. schemachensis Zinserl.	leaf lamina with 7–9 pairs of veins	leaf lamina with 9–10 pairs of veins	protologue, Zinserling 1939
S. stankovii Juz.	leaf lamina lobate and crispate at margins	leaf lamina regularly simply or double (to triple) serrate, flat at margins	protologue, Juzepczuk 1950

morphotype in leaf morphology. *Sorbus collina* occurs very often with *S. danubialis* at the same localities, but no transitional plants were observed. This species occasionally hybridizes with *S. aria*, generating transitional morphotypes between the two species (Hungary, Bavaria).

For the sake of completeness, it should be pointed out that *S. graeca* is also reported from the Czech Republic. These records, however, do not relate to *S. collina*. The first reports of the occurrence of *S. graeca* in the Czech Republic were published by Kovanda (1997a). He reported the species from two regions in southern Moravia (the Moravian Karst and Podyjí National Park) and soon these records were included in national compendia (Holub & Procházka 2000, Kovanda 2002). We revised all the herbarium specimens that this author collected (deposited in PRA) and subsequently carried out a detailed field survey of all reported localities, which indicate he mistakenly assigned some untypical individuals of *S. danubialis* to *S. graeca*. Incorrect information on the distribution of

S. graeca in the Czech Republic is presented also in the Flora of Central Europe (Flora von Mitteleuropa; Kutzelnigg 1995). It is obvious that this author did not distinguish *S. danubialis* correctly and reports *S. graeca* from localities where we were later able to confirm only *S. danubialis* occurs (e.g. all localities in Moravia).

The third tetraploid detected, *S. thayensis*, is an endemic species in the Podyjí National Park and is described below.

Sorbus danubialis (Jávorka) Kárpáti, Borbásia Nova 25: 23, 1944. (Fig. 15)

Basionym: *Sorbus cretica* f. *danubialis* Jávorka, Bot. Közl. 14: 104, 1915.
≡ *S. aria* subsp. *cretica* var. *danubialis* (Jávorka) Soó, Acta Geobot. Hung. 1 (2): 223, 1937.
≡ *S. cretica* subsp. *danubialis* (Jávorka) Jávorka, Magyar flóra, 481, 1924.
≡ *S. cretica* var. *danubialis* (Jávorka) Soó, Tisia 2: 223, 1937.
≡ *S. graeca* var. *danubialis* (Jávorka) Kovanda, Dendrol. Sborn. 3: 58, 1961.
= *S. graeca* var. *apiculata* G. Beck ex Kovanda, Dendrol. Sborn. 3: 60, 1961.
= *S. apiculata* (G. Beck ex Kovanda) Mikoláš, Thaiszia 13 (2): 130, 2004.

Neotype: Budapest: in monte Sashegy. 5. 5. 1911 herbarium S. Jávorka; BP, No 562679 (Kováts 1998).

Names previously used for this taxon in the Czech Republic: *Sorbus aria* subsp. *cretica* sensu Dostál, Klíč k úplné květeně ČSR: 319, 1958. – *S. austriaca* sensu Kovanda, Acta Mus. Morav., Sci. Nat. 81: 201, 1997 p.p. – *S. cretica* sensu Klika, Sborn. Čs. Akad. Zeměď. 12: 202, 1937. – *S. graeca* sensu Dostál, Nová Květena ČSR 1: 497, 1989 p.p. – *S. graeca* sensu Kovanda, Verh. Zool.-Bot. Ges. Österreich 134: 306, 1997 p.p.; sensu Kovanda, Klíč ke květeně ČR: 384, 2002 p.p.

Description: Shrub or small tree up to 10 m high. Bark grey, smooth when young, with fissures (particularly at the trunk base) when mature. Twigs thick, brownish-grey; young shoots brown, tomentose when young, glabrescent when mature, with pale brown to ochraceous lenticels. Buds ovoid, pointed; scales green, glabrescent, with narrow brown sparsely tomentose margins. Leaves on short sterile shoots simple; laminas almost rotund less often broadly elliptical or rounded rhombic, (6.5–) 7.4–8.6 (–10.8) cm long and (5.2–) 5.8–6.6 (–7.9) cm wide, (1.1–) 1.2–1.3 (–1.5) times as long as wide, widest at (45–) 50–56 (–62)% of the lamina length (from the base), with broadly acute to obtuse apex with an angle of (95–) 110–130 (–145)°, broadly cuneate and partly serrate at base, with angle at base of (75–) 90–105 (–120)°, usually undulate at margins, coarsely and often deeply serrate or double (to triple) serrate (rarely shallowly lobed), with more or less acute teeth terminating the main veins (other teeth smaller), with (4–) 6–8 (–12) teeth between the 2nd and 3rd main veins from the base, with angle of the teeth terminating the 3rd main veins (55–) 65–80 (–95)°, with incision between the 2nd and the 3rd main vein from the base (1.7–) 2.7–3.4 (–4.5) mm, leathery, more or less glossy, dark green, sparsely tomentose when young, later glabrescent on upper surface, evenly greenish-grey-tomentose on lower surface, with (8–) 9–10 (–11) veins on each side, with the 3rd vein at an angle of (30–) 35–45 (–50)° to midrib; petioles (11–) 13–16 (–21) mm long, tomentose. Leaf laminas on short fertile shoots rounded rhombic, less often broadly elliptical to almost rotund, more distinctively undulate and more deeply serrate at margin. Inflorescences compact, convex, with tomentose branchlets. Sepals triangular, acute or acuminate, tomentose on both surfaces, patent at flowering, erect, persistent and dry at fruiting. Petals (7.0–) 7.5–8.2 (–8.8) mm long and (4.5–) 5.3–6.0 (–6.5) mm wide, broadly elliptical to almost rotund, concave, white, patent, sparsely tomentose at base of upper surface, glabrous on lower surface, with a short claw. Stamens ca 20; anthers pale

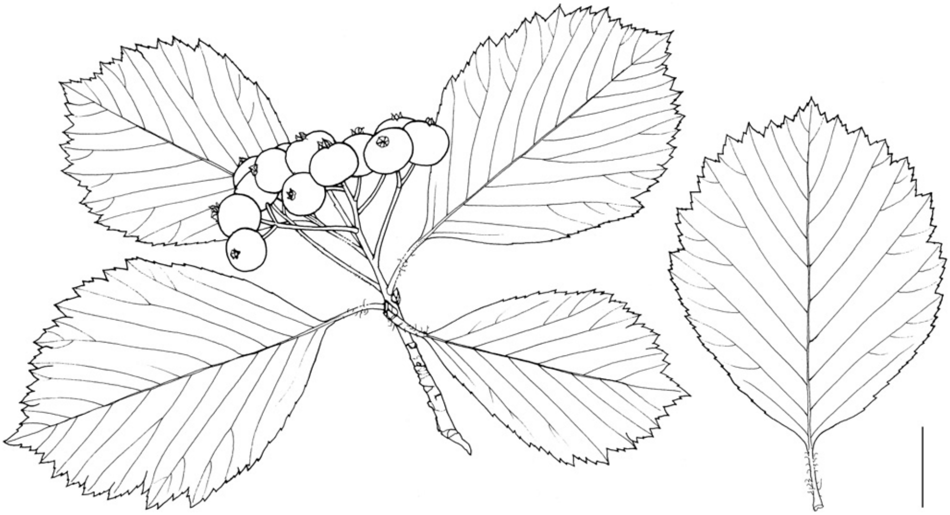

Fig. 15. – *Sorbus danubialis*: short fructiferous shoot (left) and leaf from the middle part of a short sterile shoot (right). Scale bar 2 cm. Drawn by A. Skoumalová.

yellow or pale rose. Ovary semi-inferior. Styles 2, free or connate and tomentose at base. Fruit subglobose, (10.5–) 11.0–12.5 (–13.0) mm long and (12.0–) 12.5–14.0 (–15.0) mm wide, always wider than long, dark red at maturity, tomentose at top and base, otherwise glabrescent, matt, with (1–) 3–5 (–9) lenticels per 25 mm^2; mesocarp heterogeneous; endocarp cartilaginous. Seeds fuscous. DNA ploidy level: tetraploid (inferred using FCM). Reproduction probably mostly apomictic. Flowering V.

Diagnostic characters: leaf lamina on short sterile shoots almost rotund, less often broadly elliptical or rounded rhombic, relatively small, with broadly acute to obtuse apex, undulate and coarsely and often deeply serrate or double (to triple) serrate (rarely shallowly lobed) at margins, with only (4–) 6–8 (–12) teeth between the 2nd and 3rd main veins from the base; leaf lamina on fertile short shoots often rounded rhombic with acute apex; fruit always wider than long, dark red when ripe.

Sorbus collina M. Lepší, P. Lepší et N. Meyer, **spec. nova** (Figs 16–17)

Description: Shrub or small tree up to 18 m high. Bark grey to dark grey, smooth when young, with fissures (particularly at the trunk base) when mature. Twigs thick, brownish-grey; young shoots brown, tomentose when young, glabrescent when mature, with pale brown to ochraceous lenticels. Buds ovoid, pointed; scales green, glabrescent, with narrow brown sparsely tomentose margins. Leaves on short sterile shoots simple; laminas broadly elliptical to almost rotund, (8.4–) 9.0–9.9 (–12.5) cm long and (5.7–) 7.0–7.5 (–9.8) cm wide, (1.2–) 1.3–1.4 (–1.5) times as long as wide, widest at (49–) 52–58 (–64)% of the lamina length (from the base), with obtuse, rounded or truncate apex with an angle of (130–) 140–160 (–170)°, cuneate to broadly cuneate and partly serrate at base, with angle at base of (85–) 90–105 (–120)°, flat at margins, regularly simply or double (to triple) serrate, with acute teeth terminating the main veins (other teeth smaller),

HERBARIUM MUSEI REGIONALIS BOHEMIAE MERIDIONALIS
ČESKÉ BUDĚJOVICE

Flora: Central Bohemia

CB/83296

Sorbus collina M. Lepší, P. Lepší et N. Meyer **HOLOTYPE!**

Nalžovické Podhájí (distr. Příbram), ca 130 m NNE of summit of Na Vyhlídce hill, edge of woodland

Frequence: tree ca 7 m high; scattered

Note: No. 57; 2n ~ 4x; DNA ploidy level was detected using the flow cytometer Partec PA II (DAPI fluorochrome); ratio to the internal standard (Bellis perennis L.) is 0.766; Analysed 2. 10. 2014, Department of Botany, University of South Bohemia, Č. Budějovice.

Altitude: 390 m **WGS 84:** 49°43’30,9’’N; 14°22’13,2’’E

Quadrant: 6252cad **ID GPS:** 57

Phytogeographical distr.: Střední Povltaví

Date: 7. 8. 2013 **Collected:** Martin Lepší, Petr Lepší

Quadrant according to Ehrendorfer et Hamann 1965, Ber. Deutsch. Bot. Ges.; Phytogeographical distr. - Skalický 1988, Květena ČR 1

Fig. 16. – Holotype of *Sorbus collina*.

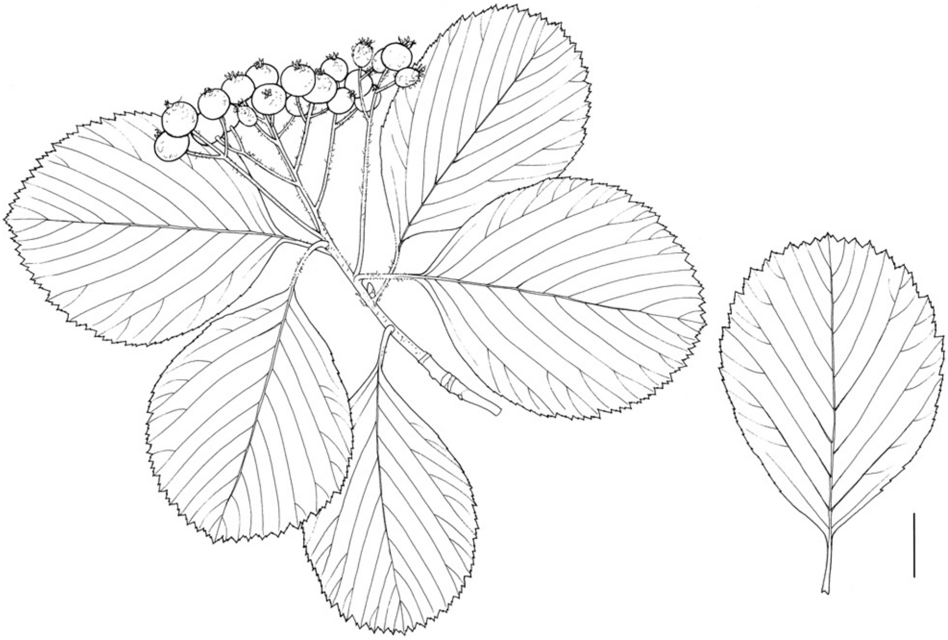

Fig. 17. – *Sorbus collina*: short fructiferous shoot (left) and leaf from the middle part of a short sterile shoot (right). Scale bar 2 cm. Drawn by A. Skoumalová.

with (5–) 8–9 (–10) teeth between the 2nd and 3rd main veins from the base, with angle of the teeth terminating the 3rd main veins (60–) 65–85 (–100)°, with incision between the 2nd and the 3rd main vein from the base (1.3–) 1.8–2.8 (–3.7) mm, leathery, more or less glossy, dark green, sparsely tomentose when young, later glabrescent on upper surface, evenly greenish-grey-tomentose on lower surface, with 9–10 veins on each side, with the 3rd veins at an angle of 30–40 (–45)° to the midrib; petioles (13–) 16–20 (–22) mm long, tomentose. Leaf laminas on short fertile shoots almost rotund with acute to rounded acute apex. Inflorescences compact, convex, with tomentose branchlets. Sepals triangular, acute or acuminate, tomentose on both surfaces, patent at flowering, erect, persistent and dry at fruiting. Petals (6.0–) 6.5–7.5 (–8.0) mm long and (4.0–) 4.5–5.0 (–5.5) mm wide, broadly elliptical, concave, white, patent, sparsely tomentose at base of upper surface, glabrous on lower surface, with a short claw. Stamens ca 20; anthers pale yellow, pale rose or rose. Ovary semi-inferior. Styles 2, free or connate and tomentose at base. Fruit subglobose, (10–) 11–12 (–13) mm long and (10.5–) 12.5–13.5 (–14.5) mm wide, always wider than long, dark red when ripe, cobwebby tomentose at top and base, otherwise usually glabrescent, matt or glossy, with (3–) 5–11 (–15) lenticels per 25 mm^2; mesocarp heterogeneous; endocarp cartilaginous. Seeds fuscous. DNA ploidy level: tetraploid (inferred using FCM). Reproduction probably mostly apomictic. Flowering V.

Holotype: Central Bohemia, Nalžovické Podhájí (distr. Příbram), ca 130 m NNE of summit of Na Vyhlídce hill, edge of woodland; 390 m a.s.l., 49°43'30.9"N, 14°22'13.2"E; scattered; tree ca 7 m high; 7. 8. 2013 leg. Martin Lepší, Petr Lepší; CB, No. 83296 (Fig. 16). – Isotypes: BP, 83296/f; LI, 83296/e; M, 83296/g; PR, 83296/a; PRA, 83296/b; PRC, 83296/c; W, 83296/d.

Names previously used for this taxon in the Czech Republic: *Sorbus aria* sensu Klika, Sborn. Čs. Akad. Zeměď. 12: 204 p.p.; sensu Dostál, Klíč k úplné květeně ČSR: 319, 1958 p.p.; sensu Dostál, Nová Květena ČSR 1: 497, 1989 p.p.; sensu Kovanda, Květena ČR 3: 476, 1992 p.p. – *S. aria* var. *cyclophylla* sensu Klika, Sborn. Čs. Akad. Zeměď. 12: 205; sensu Kovanda, Květena ČR 3: 476, 1992 p.p. – *S. graeca* sensu Dostál, Nová Květena ČSR 1: 497, 1989 p.p.

Diagnostic characters: Leaf lamina on short sterile shoots relatively large, broadly elliptical to almost rotund, resembling a tennis racket, with obtuse, rounded or truncate apex, uniserrate to biserrate (to triserrate), with flat margins; fruit wider than long, dark red.

Etymology: The Latin name refers to the dominant shape of the relief within the distribution area of the species. We propose the epithet “chlumní” for the Czech name.

Ecology: *Sorbus collina* prefers open or semi-open habitats such as cliffs, screes, steppes, rocky slopes, woodland and shrubby fringes, open woodlands and their gaps or clearings. It is recorded in a wide range of different types of vegetation in open mesophilous to thermophilous broadleaved and coniferous forests and shrubs, including contact or transitional vegetation in non-forest communities. It favours natural (often relic) or semi-natural habitats, but also grows in pine and spruce plantations. This species occurs on both acidic and base-rich bedrocks. The centre of its occurrence lies in hilly lands at medium altitudes, but exceptionally reaches the submontane vegetation belt. The altitudinal range of this species spans from 220 (river Kamp, Lower Austria) to 800 m a.s.l. (Milešovka mountain, northwestern Bohemia).

Distribution and population size: *Sorbus collina* is recorded in large areas of central, north-eastern, eastern, south-eastern Bavaria, central, western and north-western Bohemia, in the valleys of the rivers Kamp in Lower Austria and Salzach in Upper Austria, and in the north-western part of Hungary (Central Transdanubia; for individuals sampled, see Fig. 1 and Appendix 1). This species is also rarely cultivated for ornamental purposes in the Czech Republic (e.g. in Domažlice, Strakonice, Rojšín near Křemže, Třebíč, Kuřim). A comprehensive description of this species' distribution in the Czech Republic, including a distribution map and list of herbarium specimens revised, will be published in a separate paper (Lepší et al. in prep.).

Sorbus thayensis M. Lepší et P. Lepší, **spec. nova** (Figs 18–19)

Description: Shrub or rarely a small tree up to 6 (–10) m high. Bark grey or dark grey, smooth when young, with fissures (particularly at the trunk base) when mature. Twigs thick, brownish-grey; young shoots brown, tomentose when young, glabrescent when mature, with pale brown to ochraceous lenticels. Buds ovoid, pointed; scales green, glabrescent, with narrow brown sparsely tomentose margins. Leaves on short sterile shoots simple; laminas more or less broadly elliptical to almost rotund, (9.0–) 10.0–11.6 (–12.8) cm long and (6.3–) 7.1–8.3 (–9.5) cm wide, (1.2–) 1.3–1.5 times as long as wide, widest at (46–) 51–55 (–62)% of the lamina length (from the base), with broadly acute to obtuse apex with an angle of (100–) 110–125 (–140)°, cuneate to broadly cuneate and partly serrate at base, with angle at base (70–) 80–100 (–115)°, flat at margins, regularly, finely, sharply, double to triple serrate, with more or less acute teeth terminating the main veins (other teeth acute and somewhat smaller), with (6–) 8–11 (–15) teeth between the 2nd and 3rd main veins from the base, with angle of the teeth terminating the 3rd main

HERBARIUM MUSEI REGIONALIS BOHEMIAE MERIDIONALIS
ČESKÉ BUDĚJOVICE

Flora: Southern Moravia

CB/83094

Sorbus thayensis M. Lepší et P. Lepší **HOLOTYPE!**

Čížov (distr. Znojmo), Hardeggská vyhlídka outlook, ca 630 m NNW of bridge over Dyje river, acid cliff

Frequence: rarely; shrub ca 4 m high

Note: No. 39; 2n ~ 4x; DNA ploidy level was detected using the flow cytometer Partec PA II (DAPI fluorochrome); ratio to the internal standard (Bellis perennis L.) is 0,709; Analysed 13. 5. 2011, Department of Botany, University of South Bohemia, Č. Budějovice.

Altitude: 350 m **WGS 84:** 48°51’28,69’’N; 15°51’31,25’’E

Quadrant: 7161acd **ID GPS:** 42

Phytogeographical distr.: Moravské podhůří Vysočiny

Date: 15. 6. 2011 **Collected:** Martin Lepší, Petr Lepší

Quadrant according to Ehrendorfer et Hamann 1965, Ber. Deutsch. Bot. Ges.; Phytogeographical distr. - Skalický 1988, Květena ČR 1

Fig. 18. – Holotype of *Sorbus thayensis*.

Fig. 19. – *Sorbus thayensis*: short fructiferous shoot (left) and leaf from the middle part of a short sterile shoot (right). Scale bar 2 cm. Drawn by A. Skoumalová.

veins (30–) 45–65 (–75)°, with incision between the 2nd and the 3rd main vein from the base (2.2–) 3.0–4.4 (–6.5) mm long, leathery, more or less glossy, dark green, sparsely tomentose when young, later glabrescent on upper surface, evenly greenish-grey-tomentose on lower surface, with (8–) 9–10 (–11) veins on each side, with the 3rd vein at an angle of (25–) 30–35 (–40)° to the midrib; petioles (9–) 12–14 (–19) mm long, tomentose. Leaf laminas on short fertile shoots relatively broader, almost rotund, with broadly acute apex, undulate margins apically. Inflorescences compact, convex, with tomentose branchlets. Sepals triangular, acuminate to acute, tomentose on both surfaces, patent at flowering, erect, persistent and dry at fruiting. Petals broadly elliptical rarely almost rotund, (7.0–) 7.5–8.0 (–9.0) mm long and (5.0–) 5.5–6.0 (–6.5) mm wide, concave, white, patent, sparsely tomentose at base of upper surface, glabrous on lower surface, with a short claw. Stamens ca 20; anthers pale yellow. Ovary semi-inferior. Styles 2, free or connate and tomentose at base. Fruit ellipsoid to almost subglobose, (13.0–) 13.5–14.5 (–15.0) mm long and (11.0–) 12.5–14.0 (–14.5) mm wide, never wider than long, dark red when ripe, tomentose at top and base, otherwise glabrescent, matt, with (1–) 4–6 (–10) lenticels per 25 mm^2; mesocarp heterogeneous; endocarp cartilaginous. Seeds fuscous. DNA ploidy level: tetraploid (inferred using FCM). Reproduction probably apomictic. Flowering V.

Holotype: southern Moravia, Čížov (distr. Znojmo), Hardeggská vyhlídka outlook, ca 630 m NNW of bridge over Dyje river, acid cliff; 350 m a.s.l., 48°51'28.69"N, 15°51'31.25"E; rare; shrub ca 4 m high; 15. 6. 2011 leg. Martin Lepší, Petr Lepší; CB, No. 83094 (Fig. 18). Isotypes: PR, 83094/a; PRA, 83094/b.

Diagnostic characters: Leaf laminas on short sterile shoots broadly elliptical to almost rotund, relatively large, regularly finely, sharply, double (to triple) serrate. Flowers relatively large. Fruit large, ellipsoid to almost subglobose, never wider than long, dark red, only with (1–)4–6(–10) lenticels per 25 mm^2.

Etymology: The name "*thayensis*" refers to the Czech-Austrian border river whose German name is Thaya and Czech name is Dyje. This species is confined to the valley of this river. We propose the epithet "podyjský" for the Czech name.

Ecology: This species frequently occurs in open habitats such as fringes and steppes with cliffs; less often it grows in open thermophilous forests and on screes. It is mainly recorded in vegetation of low xeric shrubs on cliffs (*Prunion spinosae*), forest-steppe (mixture of *Quercion pubescenti-petraeae*, *Geranion sanguine*, *Festucion valesiacae*) and open oak-hornbeam forests (*Carpinion*). Occasionally it occurs in ravine forest communities (*Tilio-Acerion*), acidophilous oak forests (*Genisto germanicae-Quercion*) and on open screes (*Asplenion septentrionalis*). *Sorbus thayensis* is tolerant of a range of soils as it grows in both acidic (gneisses) and base-rich (limestone) soils. It is recorded on slopes of all aspects.

Distribution and population size: *Sorbus thayenis* appears to be confined to the valley of the river Dyje (= Thaya) in the surroundings of Hardegg (quadrant 7161a of the central-European grid mapping; Ehrendorfer & Hamann 1965). A total of 33 individuals of various ages were mapped at seven localities. Two of these localities are located in the Czech Republic and five in Austria. The northernmost locality by the Heimatkreuz outlook and the southernmost by the place called Einsiedler are 3.2 km apart, and both are in Austria (Fig. 9). The main population, consisting of about 20 individuals, is on Maxplateau hill (Austria). A smaller population of about 10 individuals occurs by the Hardeggská vyhlídka outlook (Czech Republic). At the remaining localities, one or two individuals are found. The phytogeographical and climatic data for the distribution of this species are the same as for *S. cucullifera*. The altitudinal range of this species spans from 310 (Einsiedler, Austria) to 440 m a.s.l. (Heimatkreuz, Austria).

Herbarium specimens

Czech Republic, southern Moravia, 68. Moravské podhůří Vysočiny, 7161a: 1. Hardeggská vyhlídka outlook: Čížov village, Hardeggská vyhlídka outlook, ca 450 m NNW of bridge over Dyje river, open scree, rare, shrub ca 2.5 m high, 48°51'25.0"N, 15°51'41.2"E, 390 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79681). – Čížov village, Hardeggská vyhlídka outlook, ca 450 m NNW of bridge over Dyje river, edge of scree, scattered, shrub ca 2.5 m high, 48°51'24.6"N, 15°51'39.2"E, 380 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79685). – Čížov village, Hardeggská vyhlídka outlook, ca 450 m NNW of bridge over Dyje river, oak-hornbeam forest, scattered, tree ca 1.5 m high, 48°51'23.7"N, 15°51'35.9"E, 320 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79686). – Čížov village, Hardeggská vyhlídka outlook, ca 460 m NNW of bridge over Dyje river, open scree, shrub ca 6 m high, 48°51'24.9"N, 15°51'41.2"E, 390 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79679, 12. 6. 2011, CB 79726). – Čížov village, Hardeggská vyhlídka outlook, ca 460 m NNW of bridge over Dyje river, scattered, tree ca 1 m high, 48°51'25.1"N, 15°51'40.9"E, 400 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79682). – Čížov village, Hardeggská vyhlídka outlook, ca 470 m NNW of bridge over Dyje river, rocky oak forest, scattered, tree ca 3.5 m high, 48°51'25.3"N, 15°51'40.2"E, 390 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79684). – Čížov village, Hardeggská vyhlídka outlook, ca 630 m NNW of bridge over Dyje river, acidic rock, scattered, shrub ca 4 m high, 48°51'28.7"N, 15°51'31.3"E, 350 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79676). – Čížov village, Hardeggská vyhlídka outlook, ca 660 m NNW of bridge over Dyje river, oak-hornbeam forest, sapling ca 1.5 m high, 48°51'29.8"N, 15°51'30.7"E, 360 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79688). – Čížov village, Hardeggská vyhlídka outlook, ca 680 m NNW of bridge over Dyje river, oak forest, scattered, sapling ca 0.75 m high, 48°51'29.9"N, 15°51'28.6"E, 350 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79691). – Čížov village, slopes with cliffs and screes below Hardeggská vyhlídka outlook, ca 0.5 km SE of the centre of Hardegg, 48°51'24.9"N, 15°51'41.5"E, 390 m a.s.l. (leg. ML et PL 6. 8. 2009, CB 73679). – Podyjí region, cliff close to Hardeggská vyhlídka outlook, ca 60 m SE of gazebo, 48°51'25.1"N, 15°51'41.8"E (leg. J. Brabec 29. 5. 2012, CHEB). **2. Hardeggská stráň hillside:** Čížov village, Hardeggská stráň hillside, ca 420 m ENE of bridge over Dyje river, forest-steppe, a shrub ca 6 m high, 48°51'16.8"N, 15°52'02.5"E, 340 m a.s.l. (leg. ML et PL 11. 6. 2011, CB 79723).

Austria, Lower Austria, 7161a: 3. Heimatkreuz: Hardegg, Dyje valley by Heimatkreuz outlook, ca 2.7 km NNW [NW] of bridge over Dyje river, rocky oak forest, shrub ca 2 m high, 48°52'24.3"N, 15°50'30.3"E, 440 [400] m a.s.l. (leg. ML et PL 15. 6. 2011, CB 79606). **4. Below Hardegger Rundweg path:** Hardegg, Maxplateau hill, ca 990 m WNW of bridge over Dyje river, acidophilous oak forest, tree ca 5 m high, 48°51'19.7"N, 15°50'58.1"E, 400 m a.s.l. (leg. ML et PL 12. 6. 2011, CB 79732). **5. Maxplateau hill:** Hardegg, SE slopes of Maxplateau hill at W edge of town, edge of woody and rocky steppe, shrub ca 2.5 m high, rare, 48°51'20.3"N, 15°51'21.9"E, 360 m a.s.l. (leg. ML et PL 23. 7. 2010, CB 74020). – Hardegg, SE slopes of Maxplateau hill at W edge of town, rocky terraces, individual ca 5 m high, 48°51'20.0"N, 15°51'22.2"E, 350 m a.s.l. (leg. ML et PL 23. 7. 2010, CB 74019). – Hardegg, SE slopes of Maxplateau hill at W edge of town, on limestone cliff, shrub ca 5 m high, rare, 48°51'20.0"N, 15°51'21.6"E, 350 m a.s.l. (leg. ML et PL 23. 7. 2010, CB 74021). – Hardegg, SE slopes of Maxplateau hill at W edge of town, close to rocky spur with outlook, on shaded cliff, one individual ca 6 m high, 48°51'14.2"N, 15°51'13.5"E, 360 m a.s.l. (leg. ML et PL 23. 7. 2010, CB 74023). – Hardegg, Maxplateau hill, ca 550 m NW of bridge over Dyje river, edge of forest and rocky steppe, scattered, 48°51'20.8"N, 15°51'22.7"E, 360 [330] m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79697). – Hardegg, Maxplateau hill, ca 550 m NW of bridge over Dyje river, edge of forest and rocky steppe, scattered, 48°51'20.8"N, 15°51'23.0"E, 350 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79696). – Hardegg, Maxplateau hill, ca 550 m NW of bridge over Dyje river, in *Junipero-Cotoneasteretum* on rock, scattered, 48°51'20.1"N, 15°51'22.3"E, 350 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79638). – Hardegg, Maxplateau hill, ca 560 m NW of bridge over Dyje river, edge of forest and rocky steppe, scattered, shrub ca 3 m high, 48°51'20.4"N, 15°51'22.0"E, 350 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79695). – Hardegg, Maxplateau hill, ca 560 m NW of bridge over Dyje river, limestone cliff, scattered, shrub ca 4 m high, 48°51'19.9"N, 15°51'21.4"E, 360 [340] m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79694). – Hardegg, Maxplateau hill, ca 570 m NW of bridge over Dyje river, edge of gap in oak-hornbeam forest, scattered, 48°51'21.4"N, 15°51'22.4"E, 360 [330] m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79698–79699, CB 79817). – Hardegg, Maxplateau hill, ca 650 m NW of bridge over Dyje river, ravine forest, tree ca 15 m high, 70 cm DBH, 48°51'21.3"N, 15°51'16.6"E, 380 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79640). – Hardegg, Maxplateau hill, ca 650 m NW of bridge over Dyje river, ravine forest, shrub 6 m high, 48°51'22.3"N, 15°51'15.3"E, 370 m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79641). – Hardegg, Maxplateau hill, ca 650 m WNW of bridge over Dyje river, cliff, shrub ca 5 m high, 48°51'14.2"N, 15°51'13.3"E, 360 m a.s.l. (leg. ML et PL 14. 5. 2011, CB 79818). – Hardegg, Maxplateau hill, ca 700 m NW of bridge over Dyje river, on rock, shrub ca 4 m high, 48°51'19.9"N, 15°51'13.0"E, 420 [380] m a.s.l. (leg. ML et PL 7. 5. 2011, CB 79642). – Hardegg, E rocky slopes of Maxplateau hill, forest-steppe, 48°51'19.5"N, 15°51'19.8"E, 350 m a.s.l. (leg. ML et PL 6. 8. 2009, CB 73703–73704). **6. Reginafelsen:** Hardegg, SE slopes of Maxplateau hill at W edge of town, below outlook on rocky spur, small cliff in wood, one shrub ca 3 m high, 48°51'08.7"N, 15°51'17.7"E, 320 m a.s.l. (leg. ML et PL 23. 7. 2010, CB 74025). – Hardegg, E rocky slopes of Maxplateau hill, forest-steppe, 48°51'08.9"N, 15°51'17.9"E, 320 m a.s.l. (leg. ML et PL 6. 8. 2009, CB 73705–73706). **7. Einsiedler:** Hardegg, slopes above Dyje river, ca 1 km NE of bridge over Dyje river, oak forest, tree ca 8 m high, 48°51'31.8"N, 15°52'23.7"E, 310 m a.s.l. (leg. ML et PL 15. 5. 2011, CB 79815). – Hardegg, slopes above Dyje river, ca 1 km NE of bridge over Dyje river, edge of scree, sapling ca 1 m high, 48°51'31.0"N, 15°52'25.4"E, 310 m a.s.l. (leg. ML et PL 15. 5. 2011, CB 79816).

Conservation

All four stenoendemic species were found in protected areas, *Sorbus cucullifera* and *S. thayensis* in the Podyjí and Thayatal National Parks, and *S. moravica* and *S. pontis-satani* in the Vývěry Punkvy National Nature Reserve, which is part of the Moravian Karst protected landscape area. Despite this, the protection of these species is insufficient because all of these protected areas are currently being left unmanaged and left to spontaneous succession. The species prefer open forests, which were previously provided by traditional management of woodlands. The shady conditions that prevail in recent woodlands are unfavourable for the long-term survival and regular reproduction of light-demanding *Sorbus* species. The general colonization of open (rocky and steppe) habitats by trees is another serious threat to these endemics. Moreover, populations of *S. thayensis* and *S. pontis-satani* are so sparse that they may be endangered even by a random event such as a rock or tree fall. The reproduction and establishment of these species should therefore be supported by restoration or simulation of traditional landscape management, at least at selected localities. All four species should be included among the critically endangered plants of the Czech flora (C1; sensu Grulich 2012) and critically endangered species (Table 6) according to the IUCN (2001). *Sorbus cucullifera* and *S. thayensis* should be added to the Red List of Austrian Flora among the most endangered species (Category 1 sensu Niklfeld & Schratt-Ehrendorfer 1999). The widely distributed *S. collina* meets the criteria for vulnerable species according to the IUCN (2001), and the same level of endangerment is applicable in the Czech Republic (C3; sensu Grulich 2012) and Germany (3; sensu Korneck et al. 1996). The level of threat faced by these species in other regions is unknown, due to the lack of distribution data.

Table 6. – Threatened categories assigned to the newly delimited taxa of *Sorbus* subg. *Aria* according to the IUCN (2001) and their degree of endangerment in the Czech Republic according to Grulich (2012).

Taxon	IUCN 2001	Grulich 2012
S. collina	VU A4abce; C2a (i)	C3
S. cucullifera	CR B1b (i,iii)	C1b
S. moravica	CR B2ab (i,iii,iv,v); C2a (ii)	C1r
S. pontis-satani	CR B2b (i,iii,iv,v); D	C1r
S. thayensis	CR B2b (i,iii,iv,v); D	C1r

Key for identification of the species of Sorbus subg. Aria occurring in the Czech Republic.

For safe identification, it is essential to use mean values of 3–5 measurements of the same character from the same individuals. Leaves have to be from middle part of short sterile shoots unless stated otherwise.

1a Leaf lamina more or less thin, relatively large, (9.6–) 11.5–12.7 (–15.6) cm long, veins on each side (8–) 11–12 (–13) .... ***S. aria***

1b Leaf lamina more or less stiff, smaller, (5.8–) 6.5–11.6 (–12.8) cm long, veins on each side (7–) 8–10 (–11) 2

2a Leaf lamina (3.8–) 4.4–5.6 (–6.2) cm wide, elliptical to broadly elliptical, oblong elliptical, ovate, obovate; fruit red, sometimes dark red 3

2b Leaf lamina (5.2–) 5.8–8.3 (–9.8) cm wide, broadly elliptical to almost rotund; fruit always dark red 7

3a Leaf lamina undulate and coarsely and often deeply serrated or double (to triple) serrated (rarely shallowly lobed) at margins; leaf laminae from fertile short shoots often rounded rhombic with acute apex .... ***S. danubialis***

3b Leaf lamina flat and finely or shalowlly serrated at margins, if undulate then finely serrated; leaf laminae from fertile short shoots of differend shape 4

4a Fruit with (2–) 7–18 (–24) lenticels per 25 mm^2, Moravský kras Karst only 5

4b Fruit with (1–) 3–6 (–10) lenticels per 25 mm^2, Podyjí National Park only 6

5a Leaf lamina broadly elliptical, regularly finely double (to triple) serrated, angle of tooth in which the 3rd lateral vein terminates (35–) 45–55 (–65)°, usually undulate to crispate at margins apically, with (6–) 8–10 (–11) teeth between the 2nd and 3rd main veins from the laminar base, incision between the 2nd and 3rd lateral vein from the laminar base (2.1–) 2.7–3.5 (–5.0) mm long .... ***S. pontis-satani***

5b Leaf lamina elliptical to oblong elliptical, regularly double (to triple) serrated, angle of tooth in which the 3rd lateral vein terminates (60–) 70–90 (–100)°, mostly flat at margins apically, with (5–) 6–8 (–11) teeth between the 2nd and 3rd main veins from the laminar base, incision between the 2nd and 3rd lateral vein from the laminar base (1.4–) 1.9–2.6 (–3.3) mm long .... ***S. moravica***

6a Leaf lamina (broadly) elliptical to obovate, (7.2–) 8.4–8.9 (–10.5) cm long, (4.7–) 5.0–5.5 (–6.2) cm wide, (1.5–) 1.6–1.7 (–1.8) times as long as wide, cuneate at base, with angle at base (65–) 70–80 (–85)°; leaves on short sterile shoots of plants growing at sunny sites held more or less upright and overlapping and resembling cornets; fruit medium-sized, (11.0–) 12.0–13.0 (–13.5) mm long, 10.5–12.0 (–13.5) mm wide, red .... ***S. cucullifera***

6b Leaf lamina (broadly) elliptical to almost rotund, (9.0–) 10.0–11.6 (–12.8) cm long, (6.3–) 7.1–8.3 (–9.5) cm wide, (1.2–) 1.3–1.5 times as long as wide, cuneate to broadly cuneate at base, with angle at base (70–) 80–100 (–115)°; leaves on short sterile shoots of plants growing at sunny sites more or less patent; fruit large, (13.0–) 13.5–14.5 (–15.0) mm long, (11.0–) 12.5–14.0 (–14.5) mm wide, dark red .... ***S. thayensis***

7a Leaf lamina relatively small, (6.5–) 7.4–8.6 (–10.8) cm long (those of exposed plants even smaller), especially in upper half undulate and coarsely and often deeply serrated or double (to triple) serrated (rarely shallowly lobed) at margins; leaf laminae from fertile short shoots often rounded rhombic with acute apex .... ***S. danubialis***

7b Leaf lamina large, (8.4–) 9.0–11.6 (–12.8) cm long, flat and regularly serrated to biserrated (to triserrated) at margins, leaf laminae from fertile short shoots almost rotund, with broadly acute to rounded acute apex 8

8a Leaf lamina serrated or double (to triple) serrated at margins, incision between the 2nd and 3rd lateral vein from the laminar base (1.3–) 1.8–2.8 (–3.7) mm long, with obtuse, rounded or truncate apex with angle of (130–) 140–160 (–170)°; fruit medium-sized, (10–) 11–12 (–13) mm long, always wider than long, Bohemia only .... ***S. collina***

8b Leaf lamina double (to triple) serrated at margins, incision between the 2nd and 3rd lateral vein from the laminar base (2.2–) 3.0–4.4 (–6.5) mm long, with broadly acute to obtuse apex with an angle of (100–) 110–125 (–140)°; fruit large, (13.0–) 13.5–14.5 (–15.0) mm long, never wider than long, Podyjí National Park only .... ***S. thayensis***

Acknowledgements

We are grateful to N. Meyer and J. Zázvorka for their valuable comments on earlier drafts of this manuscript. We thank M. Hohla, G. Mészáros and N. Meyer for helping us with the field work in Austria, Hungary and Germany, respectively, and Cs. Németh for valuable information on the distribution of Hungarian *Sorbus* taxa. We thank A. Hajrudinović and F. Bogunić, who provided samples from the type locality of *Aria nivea* var. *cyclophylla* Beck. M. Lučanová kindly performed FCM analyses of the samples from the Kamp valley. J. Kos (Administration of the Podyjí National Park) and Z. Musil (Administration of the Moravský kras Protected Landscape Area), who kindly provided accommodation for us during field work. We are also grateful to M. Škorpík and J. Šefl for information on the distribution of whitebeams and guidance in the field in the Podyjí National Park. J. Kirschner and Z. Kaplan kindly provided guidance on nomenclature. A. Skoumalová is the author of line illustrations and F. Rooks and T. Dixon kindly edited our English. The administration of the Podyjí and Thayatal National Parks are acknowledged for granting permits for entering the national parks. We could not have undertaken this study without the financial support of the Grant Agency of Charles University (project No. 1584414; JB). Additional support was provided by the Academy of Science of the Czech Republic (long-term research development project No. RVO67985939; PV) and the Czech Science Foundation (project no. 14-36079G, Centre of Excellence PLADIAS).

Souhrn

V příspěvku jsou představeny výsledky taxonomické revize jeřábů podrodu *Aria* v České republice. Prezentované taxonomické závěry jsou podpořeny výsledky průtokové cytometrie a mnohorozměrných morfologických analýz. V rámci studované skupiny byly detekovány diploidní, triploidní a tetraploidní taxony, které se vzájemně liší i morfologicky. Diploidní skupina je reprezentovaná pouze jedním druhem – *Sorbus aria*, který vykazuje vysokou morfologickou variabilitu a to dokonce i v rámci jedné populace. Tato vlastnost je druhově specifická a mimo jiné odlišuje druh od polyploidních zástupců podrodu. *Sorbus aria* byl zaznamenán na území jižní Moravy (Podyjí, Moravský kras, Bílé Karpaty), údaje dříve publikované z ostatních oblastí státu (Kovanda 1992, 2002, Kutzelnigg 1995) se vztahují k polyploidním taxonům z podrodu *Aria*. *Sorbus aria* se běžně

v ČR pěstuje a příležitostně zplaňuje. Dříve byly v Podyjí někteří jedinci *S. aria* s laločnatými listy mylně považovány za *S. austriaca* a *S. carpatica* (Kovanda 1996, 1997b, 2002), taxony, které se v ČR dle našich poznatků přirozeně nevyskytují. V rámci triploidních jeřábů byly rozlišeny a nově popsány 3 druhy – *S. cucullifera* M. Lepší et P. Lepší (jeřáb kornoutolistý) z Podyjí a *S. moravica* M. Lepší et P. Lepší (j. moravský) a *S. pontis-satani* M. Lepší et P. Lepší (j. čertův) z Moravského krasu. Tetraplodní jeřáby jsou zastoupeny třemi druhy *S. thayensis* M. Lepší et P. Lepší (jeřáb podyjský), *S. collina* M. Lepší, P. Lepší et N. Meyer (j. chlumní) a *S. danubialis*. *Sorbus thayensis* a *S. collina* jsou zde popsány jako nové druhy. *Sorbus thayensis* je endemický druh Podyjí a stejně jako zmíněné triploidní druhy vykazuje minimální morfologickou variabilitu, což ukazuje na apomiktický způsob reprodukce těchto polyploidních taxonů. *Sorbus collina* byl doposud v ČR považován za *S. aria*, v Německu za *S. pannonica* a v Rakousku a Maďarsku za *S. graeca*. Údaje o výskytu *S. graeca* z jižní Moravy (Kovanda 1997a, 2002) se nevztahují k *S. collina*, ale k netypickým exemplářům *S. danubialis*. *Sorbus collina* se na území ČR vyskytuje pouze ve středních a severozápadních Čechách a velmi vzácně je pro okrasu pěstován. Pozorovaná mírná morfologická vnitrodruhová variabilita v rámci středoevropského prostoru pravděpodobně nezasluhuje taxonomické hodnocení. *Sorbus danubialis* je svým výskytem vázaný na střední a severozápadní Čechy a jižní Moravu. V rámci studovaného území vykazuje jistou morfologickou variabilitu, které však nepřisuzujeme žádný taxonomický význam. Údaje o diploidním počtu chromosomů rostlin z Čech jsou mylné. Nové druhy vykazují malou morfologickou variabilitu a jsou dobře diferencované vzájemně i od ostatních v ČR se vyskytujících zástupců podrodu. Nově popsané endemické jeřáby z Moravy navrhujeme zařadit mezi kriticky ohrožené taxony ČR a druh *S. collina* do kategorie C3 (podle Grulich 2012). Všechny jeřáby z podrodu *Aria* jsou v ČR ohroženy zarůstáním světlých lesů a lesostepních biotopů, které byly dříve udržovány tradičním obhospodařováním krajiny. K odlišení jednotlivých druhů na území ČR poslouží následující klíč (čepel listů musí pocházet ze střední části sterilních brachyblastů, je vhodné používat průměrné hodnoty získané z 3–5 různých orgánů stejného jedince).

1a Čepel listu ± tenká, velká, (9,6–) 11,5–12,7 (–15,6) cm dlouhá, žilek na každé straně (8–) 11–12 (–13) .... ***S. aria***
1b Čepel listu ± tuhá, menší, (5,8–) 6,5–11,6 (–12,8) cm dlouhá, žilek na každé straně v počtu (7–) 8–10 (–11) 2
2a Čepel listu (3,8–) 4,4–5,6 (–6,2) cm široká, eliptická až široce eliptická, podlouhle eliptická, vejčitá, obvejčitá; plody červené, někdy tmavě červené 3
2b Čepel listu (5,2–) 5,8–8,3 (–9,8) cm široká, široce eliptická až téměř okrouhlá; plody vždy tmavě červené 7
3a Čepel listu na okraji, obzvláště v horní polovině, zprohýbaná a hrubě, často zastřihovaně 1–2 (–3)× pilovitá (vzácně až mělce laločnatá); čepel listů fertilních brachyblastů často zaokrouhleně kosočtverečná .... ***S. danubialis***
3b Čepel listu na okraji plochá, jemně pilovitá nebo mělce pilovitá, pokud zprohýbaná, pak jemně pilovitá; čepel listů fertilních brachyblastů jiného tvaru 4
4a Lenticely na plodech v počtu (2–) 7–18 (–24) na 0,25 cm^2, Moravský kras 5
4b Lenticely na plodech v počtu (1–) 3–6 (–10) na 0,25 cm^2, Podyjí 6
5a Čepel listu široce eliptická, pravidelně jemně 2 (–3)× pilovitá, s vrcholovým zubem na konci třetí žilky od báze o úhlu (35–) 45–55 (–65)°, na okraji zpravidla zprohýbaná až kadeřavá, se (6–) 8–10 (–11) zuby mezi 2. a 3. žilkou od báze čepele, zářez mezi 2. a 3. žilkou od báze (2,1–) 2,7–3,5 (–5,0) mm dlouhý .... ***S. pontis-satani***
5b Čepel listu eliptická až podlouhle eliptická, pravidelně 2 (–3)× pilovitá, s vrcholovým zubem na konci třetí žilky od báze o úhlu (60–) 70–90 (–100)°, na okraji plochá, se (5–) 6–8 (–11) zuby mezi 2. a 3. žilkou od báze čepele, zářez mezi 2. a 3. žilkou od báze (1,4–) 1,9–2,6 (–3,3) mm dlouhý .... ***S. moravica***
6a Čepel listu (široce) eliptická až obvejčitá, (7,2–) 8,4–8,9 (–10,5) cm dlouhá, (4,7–) 5,0–5,5 (–6,2) cm široká, (1,5–) 1,6–1,7 (–1,8)× delší než široká, na bázi klínovitá o úhlu (65–) 70–80 (–85)°; listy na osluněných větvích vztyčené, tvořící „kornoutky“; plody, středně velké, (11,0–) 12,0–13,0 (–13,5) mm dlouhé, 10,5–12,0 (–13,5) mm široké, červené .... ***S. cucullifera***
6b Čepel listu široce eliptická až téměř okrouhlá, (9,0–) 10,0–11,6 (–12,8) cm dlouhá, (6,3–) 7,1–8,3 (–9,5) cm široká., (1,2–) 1,3–1,5× delší než široká, na bázi klínovitá až široce klínovitá o úhlu (70–) 80–100 (–115)°; listy na osluněných větvích nejsou vztyčené a netvoří kornoutky; plody velké, (13,0–) 13,5–14,5 (–15,0) mm dlouhé, (11,0–) 12,5–14,0 (–14,5) mm široké, tmavě červené .... ***S. thayensis***
7a Čepel listu poměrně malá, (6,5–) 7,4–8,6 (–10,8) cm dlouhá (u více osluněných jedinců i menší), na okraji, obzvláště v horní polovině, zprohýbaná a hrubě, často zastřihovaně, 1–2 (–3)× pilovitá (vzácně až mělce laločnatá); čepel listů fertilních brachyblastů často zaokrouhleně kosočtverečná se špičatým vrcholem .... ***S. danubialis***

7b Čepel listu větší, (8,4–) 9,0–11,6 (–12,8) cm dlouhá, na okraji plochá, nikdy zastřihovaně pilovitá, čepel listů fertilních brachyblastů téměř okrouhlá, s tupě špičatým až zaokrouhleně špičatým vrcholem 8

8a Čepel listu na okraji 1–2(–3)× pilovitá, se zářezem mezi 2. a 3. žilkou od báze (1,3–) 1,8–2,8 (–3,7) mm dlouhým, s hrotitým, zaokrouhleným nebo až uťatým vrcholem o úhlu (130–) 140–160 (–170)°; plody středně velké, (10–) 11–12 (–13) mm dlouhé, vždy širší než dlouhé, Čechy .... ***S. collina***

8b Čepel listu na okraji ostře 2 (–3)× pilovitá, se zářezem mezi 2. a 3. žilkou od báze (2,2–) 3,0–4,4 (–6,5) mm dlouhým, s tupě špičatým až hrotitým vrcholem o úhlu (100–)110–125 (–140)°; plody velké, (13,0–)13,5–14,5 (–15,0) mm dlouhé, nikdy širší než dlouhé, Podyjí .... ***S. thayensis***

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Received 24 November 2014
Revision received 4 February 2015
Accepted 11 February 2015

Appendix 1. – List of localities of *Sorbus aria*, *S. danubialis*, *S. collina* and *S. pannonica* analysed using flow cytometry during this study. Localities are sorted according to taxa and subsequently according to countries. The localities from the Czech Republic are further sorted according to the regional-phytogeographical classification system (Skalický 1988). The format of the data is: Town or village, localization, habitat, height of individual, abundance, quadrant of the Central-European mapping grid according Ehrendorfer & Hamann (1965), coordinates of WGS-84, altitude (collector, collection date); number of individuals analysed; in *Sorbus collina* accession number of specimens. The specimens of all analysed trees are deposited in herbarium CB. Abbreviations of collectors: ML – Martin Lepší, PL – Petr Lepší, GM – Gábor Mészáros, NM – Norbert Meyer.

Sorbus aria

Austria. Gmunden, Traunstein Mt., W base of mountain, rocky slopes, tree ca 10 m high, 8148b, 47°51'34.0"N, 13°48'58.8"E, 550 m a.s.l. (ML 7. 8. 2011); 1. – Gmunden, Traunstein Mt., W base of mountain, open forest, tree ca 3 m high, 8148b, 47°52'32.7"N, 13°48'50.8"E, 430–550 m a.s.l. (ML 7. 8. 2011); 2 – Gmunden, Traunstein Mt., W slopes of mountain, 8148b, 47°51'54.7"N, 13°49'22.2"E, 860–1140 m a.s.l. (ML 7. 8. 2011); 4. – Hainburg an der Donau, NW slopes of Hundsheimer Berg, 7867d, 48°08'07.8"N, 16°55'58.5"E, 350–380 m a.s.l. (ML, PL 16. 7. 2011); 3. – Hardegg, "pine forest I" on slopes of Dyje valley, ca 180 m SE of bridge over Dyje river, 7161a, 48°51'05.4"N, 15°51'49.6"E, 350–400 m a.s.l. (ML, PL 15. 5. 2011); 3. – Hardegg, "pine forest II" on slopes of Dyje valley, ca 300 m SE of bridge over Dyje river, tree ca 12 m high, 7161a, 48°51'04.9"N, 15°51'57.6"E, 400 m a.s.l. (ML, PL 15. 5. 2011); 1. – Hardegg, Dyje valley, ca 2 km NW of bridge over Dyje river, cliff in oak-hornbeam forest, tree ca 10 m high, 7161a, 48°51'46.6"N, 15°50'20.3"E, 420 m a.s.l. (ML, PL 25. 7. 2012); 1. – Hardegg, Dyje valley, ca 2.8–2.9 km NW of bridge over Dyje river, 7161a, 48°52'26.1"N, 15°50'26.5"E, 420–440 m a.s.l. (ML, PL 17. 6. 2012); 2. – Hardegg, Dyje valley, Schwalbenfelsen ca 2.1 km NW of the bridge over Dyje river, on cliff, shrub ca 4 m high, 7161a, 48°51'54.8"N, 15°50'28.1"E, 390 m a.s.l. (ML, PL 15. 6. 2011); 1. – Hardegg, Kreuzmaiss, slopes above Fugnitz stream, ca 1.8 km WSW of bridge over Dyje river, edge of rock, tree ca 2.5 m high, 7161c, 48°50'18.4"N, 15°51'02.9"E, 370 m a.s.l. (ML, PL 9. 5. 2011); 1. – Hardegg, Maxplateau hill, ca 700 m WNW of bridge over Dyje river, on rock in forest, tree ca 7 m high, 7161a, 48°51'21.6"N, 15°51'14.2"E, 400 m a.s.l. (ML, PL 14. 5. 2011); 1. – Hardegg, S slopes of Maxplateau hill above swimming pool, ca 830 m WNW of bridge over Dyje river, forest-steppe, scattered shrub ca 7 m high, 7161a, 48°51'14.6"N, 15°51'06.9"E, 360 m a.s.l. (ML, PL 14. 5. 2011); 1. – Hardegg, slopes above Dyje river, ca 0.9 km ENE of bridge over Dyje river, oak-hornbeam forest, shrub ca 5 m high, 7161a, 48°51'14.6"N, 15°52'31.4"E, 360 m a.s.l. (ML, PL 9. 5. 2011); 1. – Hardegg, slopes of Fugnitz valley opposite of Binderberg hill, ca 1 km SW of bridge over Dyje river, rocky forest-steppe, shrub ca 3.5 m high, 7161c, 48°50'55.5"N, 15°50'59.1"E, 380 m a.s.l. (ML, PL 12. 6. 2011); 1. – Hardegg, Umlaufberg hill, edge of scree and acidophilous oak forest, tree ca 6 m high, 7161c, 48°50'41.4"N, 15°53'33.7"E, 330 m a.s.l. (ML 30. 5. 2012); 1. – Heufurth, near quarry at W edge of village, scrub, tree ca 6 m high, 7160d, 48°49'08.8"N, 15°49'32.4"E, 390 m a.s.l. (ML, PL 15. 6. 2012); 1. – Heufurth, woody slopes above village, 7160d, 48°49'24.1"N, 15°49'34.3"E, 390–430 m a.s.l. (ML, PL 15. 6. 2012); 5. – Klosterneuburg, S slopes of Leopoldsberg hill, 7764a, 48°16'35.9"N, 16°20'56.9"E, 310–330 m a.s.l. (ML, PL 16. 7. 2011); 5. – Prein an der Rax, below the Preiner Wand cliff, in a growth of *Pinus mugo*, rarely a tree ca 4 m high, 8360a, 47°41'51.6"N, 15°44'26.1"E, 1420 m a.s.l. (ML, PL 18. 9. 2010); 1. – Prein an der Rax, ca 0.5 km NE of the Waxriegelhaus, 8360a, 47°41'34.4"N, 15°43'20.2"E, 1470 m a.s.l. (ML, PL 18. 9. 2010); 1. – Prein an der Rax, close by the Waxriegelhaus, a *Picea abies* and *Larix decidua* forest, a tree ca 5 m high, 8360a, 47°41'17.1"N, 15°43'20.6"E, 1380 m a.s.l. (ML, PL 18. 9. 2010); 1. – Prein an der Rax, the N periphery of the village, along a road, scattered, 8360b, 47°40'49.8"N, 15°46'20.3"E, 780 m a.s.l. (ML, PL 18. 9. 2010); 1. – Semmering, in the southern part of the village, an edge of a forest, scattered, a tree ca 8 m high, 8360d, 47°38'22.0"N, 15°49'46.3"E, 940 m a.s.l. (ML, PL 19. 9. 2010); 1. – Schönberg am Kamp, in valley of Kamp river (right-hand bank), ca 600 m NE of summit of Kogelberg hill, rocky and shrubby slopes, rarely, 7460c, 48°30'19.7"N, 15°41'27.1"E, 260 m a.s.l. (ML, PL 14. 8. 2010); 1.

Czech Republic. 19. Bílé Karpaty stepní: Velká nad Veličkou, Javorník, shrubby slope near railway stop Javorník nad Veličkou, mosaic of shrubs and *Bromion* grasslands, 7171a, 48°51'43.4"N, 17°31'13.3"E, 345 m a.s.l. (PL 20. 5. 2013); 3. – **68. Moravské podhůří Vysočiny:** Čížov, Dyje valley, NW slopes of Na Vyhlídce hill, ca 1.8 km WSW of chapel in village, 7161a, 48°52'29.3"N, 15°50'55.6"E, 370–410 m a.s.l. (ML, PL 15. 5. 2011); 4. – Čížov, Dyje valley, Pašerácká stezka path, ca 1.5 km W of chapel in village, 7161a, 48°52'49.3"N, 15°51'05.8"E, 380–470 m a.s.l. (ML, PL 11. 9. 2011); 4. – Čížov, Hardeggská stráň hillside, below road, ca 560 m ENE of bridge over Dyje river, open oak forest, scattered, 7161a, 48°51'16.3"N, 15°52'10.7"E, 320 m a.s.l. (ML, PL 6. 5. 2011); 1. – Čížov, Hardeggská vyhlídka outlook, ca 280 m NNW of bridge over Dyje river, 7161a, 48°51'19.2"N, 15°51'40.9"E, 320–330 m a.s.l. (ML, PL 7. 5. 2011); 3. – Čížov, calcareous left-hand bank slopes of Dyje river valley, ca 400–500 m SE of spot height of 417 m with Hardegg outlook, edge of shrub and steppe, a small tree, 7161a, 48°51'18.4"N, 15°52'08.6"E, 330–360 m a.s.l. (ML, PL 23. 7. 2010); 3. – Čížov, near ridge in meander of Dyje river (left-hand bank), ca 250 m WSW of obelisk above Ledové sluje chasms, ravine forest, tree ca 6 m high, 7161a, 48°53'00.5"N, 15°50'32.1"E, 400 m a.s.l. (ML, PL 23. 7. 2010); 1. – Čížov, rocky slope on left-hand bank of Dyje river, ca 100 m WNW of obelisk above Ledové sluje chasms, rocky woodland with dominant lime tree, individual ca 9 m high, 7161a, 48°53'04.9"N, 15°50'36.6"E, 390 m a.s.l. (ML, PL 23. 7. 2010); 1. – Čížov, summit area of Býčí hora hill, edge of forest road, one individual ca 7 m high, 7161a, 48°52'35.8"N, 15°50'12.8"E, 540 m a.s.l. (ML, PL 23. 7. 2010); 1. – Vranov nad Dyjí, ca 550 m NNW of summit of Býčí hora hill, on cliff, one small tree, 7160b, 48°52'45.8"N, 15°49'57.6"E, 510 m a.s.l. (ML, PL 21. 7. 2010); 1. – Vranov nad Dyjí, right-hand bank slopes of Dyje river valley, opposite meander with place called Ledové sluje chasms, ca 0.7 km NW of summit of Býčí hora hill, woodland on rocky slope, one small tree ca 2 m high, 7160b, 48°52'51.7"N, 15°49'56.4"E, 420 m a.s.l. (ML, PL 21. 7. 2010); 1. – **70. Moravský kras:** Horákov, ca 400 m SE of summit of Hornek hill, cliff in forest, ca 20 individuals, 6766c, 49°13'43.8"N, 16°43'11.1"E, 350–360 m a.s.l. (ML 13. 5. 2012); 7. – Horákov, summit of Hornek hill, upper edge of former quarry, shrub ca 1 m high, 6766c, 49°13'51.9"N, 16°42'56.2"E, 410 m a.s.l. (ML 13. 5. 2012); 1. – **78. Bílé Karpaty lesní:** Starý Hrozenkov, Vyškovec village, between settlements Kykula and Vlčí, fringe of broadleaves forest, near road ca 800 m SE of bell tower (near sharp curve), trees with many trunks, 7073c, 48°55'51.4"N, 17°50'55.2"E, 660 m a.s.l. (PL 24.5. 2013); 2. – Starý Hrozenkov, Vyškovec village, Vlčí settlement, in shrubby growth along road, ca 1.5 km E of bell tower (near sharp curve), shrub ca 2 m high, 7073c, 48°56'02.1"N, 17°51'33.7"E, 560 m a.s.l. (PL 24. 5. 2013); 1.

France. Barr, the close surroundings of the castle of Landsberg, a rock in an oak forest, rarely, 7510d, 48°25'11.4"N, 07°25'20.3"E, 580 m a.s.l. (ML, PL 28. 7. 2010); 1. – Gérardmer, ca 1.5 km S of Gerbépal village, a clearing by the road, rarely, 7807c, 48°07'57.6"N, 06°54'56.8"E, 710 m a.s.l. (ML, PL 27. 7. 2010); 1. – Gérardmer, the area between the summit of le Hohneck Mountain and le Petit Hohneck Mountain, subalpine open shrubs, rarely, a tree ca 10 m high, 7908c, 48°02'02.0"N, 07°01'42.4"E, 1180 m a.s.l. (ML, PL 29. 7. 2010); 1.

Sorbus danubialis

Austria. Lower Austria: Hainburg an der Donau, NW slopes of Hundsheimer Berg, 7867d, 48°08'10.7"N, 16°56'04.6"E, 370 m a.s.l. (ML, PL 16. 7. 2011); 1. – Hardegg, "pine forest I" on slopes of Dyje valley, ca 180 m SE of bridge over Dyje river, pine forest with *Sesleria caerulea*, shrub ca 4 m high, 7161a, 48°51'5.58"N, 15°51'50.22"E, 360 m a.s.l. (ML, PL 12. 9. 2011); 1. – Hardegg, "pine forest II" on slopes of Dyje valley, ca 300 m SE of bridge over Dyje river, pine forest with *Sesleria*, rarely tree ca 7 m high, 7161a, 48°51'04.5"N, 15°51'56.1"E, 400 m a.s.l. (ML, PL 15. 5. 2011); 1. – Pulkau, Pulkau valley, young forest of *Carpinus* and *Quercus* on left-hand bank of Pulkau river, ca 2.3 km NW of Pulkau town, rarely, tree ca 6 m high, 7260d, 48°42'53.3"N, 15°49'58.9"E, 370 m a.s.l., (PL 26. 9. 2012); 1. – Pulkau, Pulkau valley, open forest of *Quercus pubescens* on left-hand bank of Pulkau river, ca 2.1 km WNW of Pulkau town, above Peschtamühle, rarely, tree ca 4 m high, 7261c, 48°42'39.9"N, 15°50'02.8"E, 370 m a.s.l. (PL 26. 9. 2012); 1. – Pulkau, Pulkau valley, open forest on left-hand bank of Pulkau river, ca 1.9 km WNW of Pulkau town, rarely, shrub ca 2 m high, 7261c, 48°42'32.6"N, 15°50'07.8"E, 316 m a.s.l. (PL 26. 9. 2012); 1. – Pulkau, Pulkau valley, upper edge of scree on right-hand bank of Pulkau river, ca 2.9 km SE of Theras village, near Hammerschmiede, rarely, shrub ca 2 m high, 7260d, 48°42'54.3"N, 15°49'22.0"E, 346 m a.s.l. (PL 26. 9. 2012). – Rosenburg, wodded slope in valley of Kamp river, ca 1 km WNW of castle in village, rock in woodland, rarely, one individual ca 3 m high, 7359d, 48°37'43.7"N, 15°37'08.6"E, 350 m a.s.l. (ML, PL 14. 8. 2010); 1. – Rosenburg, in valley of Kamp river, ca 1.8 km W of castle in village, top of cliff, rarely, 7359d, 48°37'38.2"N, 15°36'32.5"E, 330 m a.s.l. (ML, PL 14. 8. 2010); 1.

Czech Republic. 6. Džbán: Třeboc, ca 1–2 km NE of village, Babí hora hill, *Larix* plantation and edge of clearing, scattered, 5748d, 50°13'13.4"N, 13°45'43.9"E, 490–510 m a.s.l. (ML 30. 6. 2011); 3. – Třeskonice, ca 1.3 km S of village, on Výrov hill, 5747b, 50°15'26.1"N, 13°39'04.3"E, 480–520 m a.s.l. (ML 30. 6. 2011); 3. – Zbečno, Milská stráň nature reserve, forest-steppe and open forest on S slope, scattered, 5749c, 50°14'10.6"N, 13°52'15.2"E, 450 m a.s.l. (ML 30. 6. 2011); 3. – **16. Znojemsko-brněnská pahorkatina:** Moravský Krumlov, slopes of Rokytná river at N edge of town, cliff, 6963d, 49°02'51.5"N, 16°19'10.1"E, 300 m a.s.l. (ML, PL 5. 7. 2011); 2. – Znojmo, valley of Dyje river, ca 1.5 km N of former mill called Papírna, oak woodland, one individual ca 1.5 m high, 7161d, 48°49'49.7"N, 15°58'54.3"E, 270 m a.s.l. (ML, PL 22. 7. 2010); 1. – Znojmo, valley of Dyje river (right-hand bank) ca 1.5 km W of centre of area called Šóbes, pine-oak woodland, several individuals, 7161d, 48°49'00.9"N, 15°57'21.3"E, 380 m a.s.l. (ML, PL 22. 7. 2010); 1. **17b. Pavlovské kopce:** Pavlov, northern part of ruin castle Dívčí hrady (Děvičky) west of village, edge of shrubs, shrub ca 2 m high, 7165b, 48°52'34.3"N, 16°39'43.9"E, 420 m a.s.l. (PL 16. 9. 2014); 1. – Klentnice, rocks on the west part of castle ruin Sirotčí hrádek west of village, limestone cliff, 7165d, 48°50'43.1"N, 16°38'24.9"E, 425 m a.s.l. (PL 17. 9. 2014); 2. – **52. Ralsko-bezdězská tabule:** Bezděz, Malý Bezděz hill, base of S slope, edge of clearing, shrub ca 6 m high, 5454c, 50°32'15.5"N, 14°42'45.4"E, 420 m a.s.l. (ML, PL 17. 5. 2011); 1. – Bezděz, Velký Bezděz hill, SE slopes, on cliff, scattered, 5454c, 50°32'23.8"N, 14°43'17.7"E, 560–590 m a.s.l. (ML, PL 16. 5. 2011); 5. – Bezděz, Velký Bezděz hill, SW slopes, scattered, 5454c, 50°32'17.4"N, 14°43'03.5"E, 530–540 m a.s.l. (ML, PL 16. 5. 2011); 4. – **68. Moravské podhůří Vysočiny:** Čížov, Hardeggská stráň hillside, above road, ca 550 m ENE of bridge over Dyje river, forest-steppe, rarely, shrub ca 2 m high, 7161a, 48°51'17.5"N, 15°52'08.9"E, 370 m a.s.l. (ML, PL 14. 5. 2011); 1. – Čížov, calcareous slopes above Dyje river (left-hand bank), ca 500 m SE of spot height of 417 m with Hardeggská vyhlídka outlook, above road to Hardegg, steppe, shrub ca 2 m high, rarely, 7161a, 48°51'17.6"N, 15°52'08.9"E, 350 m a.s.l. (ML, PL 23. 7. 2010); 1. – **70. Moravský kras:** Lažánky, near Blansek castle ruine, 6666a, 49°22'14.8"N, 16°43'12.4"E, 440–470 m a.s.l. (ML 23. 7. 2011); 3. – Lažánky, Suchý žleb gorge, S slopes, 6666a, 49°22'02.8"N, 16°43'40.0"E, 420–460 m a.s.l. (ML 22. 7. 2011); 5. – Vilémovice, Pustý žleb gorge, Koňský spád cliff, 6666a, 49°22'44.6"N, 16°43'45.5"E, 480–490 m a.s.l. (ML 23. 7. 2011); 3.

Germany. Dietfurt, ca 1.5 km NW of centre of village, 6935c, 49°02'26.9"N, 11°33'51.2"E, 460 m a.s.l. (ML 27. 6. 2011); 1. – Essing, rocky slopes above village, 7036d, 48°56'20.7"N, 11°47'11.8"E, 410–440 m a.s.l. (ML 28. 6. 2011); 3. – Gundelshausen, slopes of Danube ca 1.5 km NNW of centre of village, 7037b, 48°57'31.8"N, 11°59'14.0"E, 340 m a.s.l. (ML 28. 6. 2011); 1. – Hebersdorf, ca 0.3 km E of centre of village, 6935a, 49°03'50.0"N, 11°33'27.6"E, 490–580 m a.s.l. (ML 27. 6. 2011); 2. – Heitzenhofen, Naab valley, woody slopes at NW edge of village, 6837d, 49°07'37.8"N, 11°56'37.7"E, 390–410 m a.s.l. (ML 26. 6. 2011); 3. – Kinding, NW of village, forest-steppe, 6934c, 49°00'13.9"N, 11°22'27.9"E, 450 m a.s.l. (ML, NM 24. 6. 2011); 1. – Regensburg, ca 0.7 km SSE of the centre of the village of Goldberg, in the valley of the Naab river, in a woody edge, rarely, 6937d, 49°01'31.0"N, 11°59'51.3"E, 360 m a.s.l. (ML, PL 26. 7. 2010); 1. – Riedenburg, E edge of town, open pine forest, 7036a, 48°58'06.9"N, 11°41'29.4"E, 500 m a.s.l. (ML, NM 24. 6. 2011); 2. – Riedenburg, slopes NE of town, 7036a, 48°58'26.8"N, 11°41'33.7"E, 460 m a.s.l. (ML 28. 6. 2011); 2. – Schönfeld, ca 1.5 km SW of centre of village, 7132a, 48°53'20.3"N, 11°01'51.6"E, 450–470 m a.s.l. (ML, NM 26. 6. 2011); 2. – Thalheim, ca 1.7 km SE of centre of village, 6935a, 49°03'51.1"N, 11°33'27.9"E, 510 m a.s.l. (ML 27. 6. 2011); 1.

Hungary. Balatongyörök, Balaton region, ca 3.5 km NNW of centre of village, 9270a, 46°47'18.6"N, 17°20'12.4"E, 260–270 m a.s.l. (ML, PL, GM 21. 7. 2011); 2. – Budapest, Kecske hegy, 8479d, 47°32'12.3"N, 18°59'36.7"E, 310 m a.s.l. (ML, PL, GM 17. 7. 2011); 3. – Budapest, Ördög oron, 8579b, 47°28'55.1"N, 18°59'13.2"E, 280 m a.s.l. (ML, PL, GM 17. 7. 2011); 1. – Budapest, Sas hegy, 8580a, 47°28'59.2"N, 19°01'01.3"E, 230–270 m a.s.l. (ML, PL, GM 17. 7. 2011); 4. – Budapest, Tündér hegy, 8479d, 47°30'54.2"N, 18°58'03.2"E, 370–390 m a.s.l. (ML, PL, GM 17. 7. 2011); 3. – Csákvár, Vértes Mts, Nagy-Vasak hegy, 8576c, 47°25'50.3"N, 18°24'58.4"E, 390 m a.s.l. (ML, PL, GM 18. 7. 2011); 1. – Csákvár, Vértes Mts, Szedres völgy, 8675b, 47°22'49.1"N, 18°19'44.0"E, 360 m a.s.l. (ML, PL, GM 19. 7. 2011); 1. – Szentkirályszabadja, Balaton region, Malomvölgy, 8973d, 47°02'57.6"N, 17°59'09.9"E, 260 m a.s.l. (ML, PL, GM 20. 7. 2011); 2. – Tapolca, Balaton region, Csobánc hill, 9171a, 46°52'21.7"N, 17°30'12.2"E, 340 m a.s.l. (ML, PL, GM 21. 7. 2011); 1. – Várpalota, Bakony Mts, N of town, 8774d, 47°13'58.1"N, 18°07'05.8"E, 290–380 m a.s.l. (ML, PL, GM 19. 7. 2011); 3. – Veszprém, ca 3.8 km W of centre of town, 8973a, 47°05'43.1"N, 17°51'36.9"E, 280 m a.s.l. (ML, PL, GM 20. 7. 2011); 1. – Veszprém, Márkó, Malom hegy, 8872d, 47°06'33.3"N, 17°49'43.0"E, 360 m a.s.l. (ML, PL, GM 20. 7. 2011); 1.

Sorbus collina

Austria. Upper Austria: Braunau am Inn, in valley of Salzach river (right-hand bank) ca 0.5 km SSW of bridge in Heiligen Kreuz village, wooden slopes, 7842d, 48°08'54.4"N, 12°49'17.5"E, 420 m a.s.l. (ML, M. Hohla 12. 10. 2014, CB 83297); 2. – Braunau am Inn, in valley of Salzach river (right-hand bank) ca 0.5 km ESE of bridge in Heiligen Kreuz village, wooden slopes, 7842b, 48°09'05.5"N, 12°49'44.2"E, 420 m a.s.l. (ML, M. Hohla 12. 10. 2014, CB 83298–83300); 3. – Braunau am Inn, in valley of Salzach river (right-hand bank) S edge of Duttendorf village, cliff, 7843a, 48°09'20.0"N, 12°50'05.6"E, 413 m a.s.l. (ML, M. Hohla 12. 10. 2014, CB 83301); 3. – Braunau am Inn, in valley of Salzach river (right-hand bank) ca 2.3 km ENE of Überackern village, small cliff, 7743c, 48°12'07.8"N, 12°54'13.6"E, 370 m a.s.l. (ML, M. Hohla 12. 10. 2014, CB 83302–83304); 3. – Braunau am Inn, in valley of Inn river (right-hand bank) ca 1 km WSW of Oberrothenbuch village, wooded slope, 7743d, 48°12'19.9"N, 12°57'13.3"E, 380 m a.s.l. (ML, M. Hohla 12. 10. 2014, CB 83305); 2. – **Lower Austria:** Plank am Kamp, in valley of Kamp river (right-hand bank) ca 0.6 km NE of church in village Thürneustift, wooded cliff, tree ca 6 m high, 7460c, 48°32'47.2"N, 15°40'16.8"E, 250 m a.s.l. (ML, PL 14. 8. 2010, CB 74060); 1. – Schönberg am Kamp, in valley of Kamp river (right-hand bank), ca 1.6 km NW of church in village, top of cliff in rocky and shrubby slope of valley, shrub ca 4 m high, 7460c, 48°31'36.6"N, 15°40'49.7"E, 300 m a.s.l. (ML, PL 14. 8. 2010, CB 74058); 1. – Schönberg am Kamp, in valley of Kamp river (right-hand bank), ca 350 m NE of summit of Kogelberg hill, dry and rocky slope above river, tree ca 6 m high, scattered in the surroundings, 7460c, 48°30'00.4"N, 15°41'30.5"E, 220 m a.s.l. (ML, PL 13. 8. 2010, CB 74047); 1. – Schönberg am Kamp, in valley of Kamp river (right-hand bank), ca 600 m NE of summit of Kogelberg hill, rocky and shrubby slopes of valley, rarely, 7460c, 48°30'19.5"N, 15°41'25.9"E, 280 m a.s.l. (ML, PL 14. 8. 2010, CB 74050); 1.

Czech Republic. 6. Džbán: Třeskonice, ca 1.3 km S of village, on Výrov hill, scattered, 5747b, 50°15'23.8"N, 13°39'12.8"E, 510–520 m a.s.l. (ML 30. 6. 2011, CB 82672–82674); 3. – **7c. Slánská tabule:** Kladno, Vinařická hora nature reserve, ca 750 m NW of centre of village, marlstone slope, ca 30 individuals shrub ca 3 m high, 5850b, 50°10'49.2"N, 14°5'3.6"E, 350 m a.s.l. (ML 17. 5. 2011, CB 79944); 1. – Kladno, Vinařická hora nature reserve, ca 700–750 m NW–NNW of centre of village, 5850b, 50°10'53.9"N, 14°05'15.8"E, 380–400 m a.s.l. (ML 17. 5. 2011, CB 79942–79943); 2. – **32. Křivoklátsko:** Branov, Berounka valley, ca 0.9 km NE of centre of village, Nezabudické skály nature reserve, 5949c, 50°01'15.8"N, 13°50'49.9"E, 250–270 m a.s.l. (ML 29. 6. 2011, CB 82657–82659); 3. – Broumy, 2.7 km SSW of centre of village, Jouglovka nature reserve, rarely, 6049c, 49°55'54.2"N, 13°50'19.3"E, 540–560 m a.s.l. (ML 29. 6. 2011, CB 82657–82659); 3. – Terešov, 1.5 km N of centre of village, V Horách nature reserve, rarely, 6048c, 49°54'36.3"N, 13°41'50.4"E, 430 m a.s.l. (ML 29. 6. 2011, CB 82654–82656); 3. – Točník, Točník hill, below castle, 6149a, 49°53'23.4"N, 13°53'11.4"E, 430 m a.s.l. (ML 29. 6. 2011, CB 82647–82649); 3. – Zbečno, Berounka valley, cliffs above town, scattered, 5949d, 50°2'35.5"N, 13°55'38.6"E, 400–410 m a.s.l. (ML 29. 6. 2011, CB 82660–82662); 3.

Germany. Böhming, ca 1.3 km SE of village, cliff, 7034c, 48°56'05.7"N, 11°22'38.5"E, 480–490 m a.s.l. (ML, NM 24. 6. 2011, CB 82557–82559); 3. – Dietfurt, slopes above town, 6935d, 49°2'25.84"N, 11°35'8.38"E, 460–480 m a.s.l. (ML 28. 6. 2011, CB 82625–82627); 3. – Gundelshausen, slopes of Danube ca 1.5 km NNW of centre of village, 7037b, 48°57'33.4"N, 11°59'15.2"E, 340–360 m a.s.l. (ML 28. 6. 2011, CB 82637–82639); 3. – Hartmannshof, slopes at N edge of town, 6535a, 49°29'50.8"N, 11°32'54.5"E, 400–420 m a.s.l. (ML 27. 6. 2011, CB 82613–82615); 3. – Heitzenhofen, Naab valley, woody slopes at NW edge of village, 6837d, 49°7'36.2"N, 11°56'39.8"E, 370–400 m a.s.l. (ML 26. 6. 2011, CB 82602–82603, CB 82605); 3. – Högen, edge of forest ca 2 km NE of centre of village, 6435d, 49°30'09.3"N, 11°37'37.9"E, 460–470 m a.s.l. (ML 27. 6. 2011, CB 82611–82612, CB 82641); 3. – Kallmünz, Naab valley, slopes ca 1.2 km NW of centre of town, 6837b, 49°10'16.5"N, 11°57'59.3"E, 370–390 m a.s.l. (ML 26. 6. 2011, CB 82608–82610); 3. – Kelheim, slopes of Danube NE of centre of town, 7037c, 48°55'15.9"N, 11°54'24.8"E, 350–380 m a.s.l. (ML 28. 6. 2011, CB 82634–82636); 3. – Kinding, 2.8 km NW of centre of village, forest-steppe, 6934c, 49°01'09.59"N, 11°21'33.08"E, 440 m a.s.l. (ML, NM 24. 6. 2011, CB 82554); 1. – Leutenbach, ca 1.2 km SE of town, 6233c, 49°42'14.1"N, 11°11'13.6"E, 480 m a.s.l. (ML, NM 25. 6. 2011, CB 82581, CB 82583); 2. – Obereichstätt, slopes above village, 7132b, 48°53'50.1"N, 11°07'30.7"E, 460–470 m a.s.l. (ML, NM 26. 6. 2011, CB 82595–82596); 2. – Regensburg, ca 0.7 km SSE of the centre of the village of Goldberg, in the valley of the Naab river, an open forest and a dry grassland, scattered, 6937d, 49°01'35.3"N, 11°59'51.0"E, 390–410 m a.s.l. (ML, PL 26. 7. 2010, CB 79558–79559); 2. – Thalheim, ca 1.4–1.7 km SE of centre of village, 6535a, 49°27'10.6"N, 11°33'48.4"E, 420–460 m a.s.l. (ML 27. 6. 2011, CB 82619–82620, CB 82777); 3. – Vorra, slopes at E edge of town, 6434b, 49°33'35.6"N, 11°29'53.4"E, 420–460 m a.s.l. (ML 27. 6. 2011, CB 82616–82618); 3. – Wallersberg, slopes below village, 5933c, 50°02'32.2"N, 11°12'52.7"E, 390–400 m a.s.l. (ML, NM 25. 6. 2011, CB 82570–82571); 2. – Wunkendorf, ca 1.9 km NE of village, 5933b, 50°03'41.2"N, 11°16'27.7"E, 500 m a.s.l. (ML, NM 25. 6. 2011, CB 82578–82580); 3. – Wunkendorf, ca 600 m NE of village, 5933b, 50°03'10.7"N, 11°15'41.4"E, 460 m a.s.l. (ML, NM 25. 6. 2011, CB 82573, CB 82575–82576); 3.

Hungary. Csákvár, Vértes Mts, Nagy-Vasak hegy (NW of village), 8576c, 47°25'44.799"N 18°25'11.571"E, 380–410 m a.s.l. (ML, PL, GM 18. 7. 2011, CB 82513–82514, CB 82448, CB 82450, CB 82453, CB 82455); 7. – Csákvár, Vértes Mts, Szedres völgy, 8675b, 47°22'47.7"N, 18°19'42.5"E, 360–370 m a.s.l. (ML, PL, GM 19. 7. 2011, CB 82517–82519); 3. – Várpalota, Bakony Mts, ca 2.5–4.1 km N–E of town, 8774d, 47°12'57.4"N 18°06'54.0"E, 260–380 m a.s.l. (ML, PL, GM 19. 7. 2011, CB 82462–82463, CB 82469, CB 82524); 4. – Veszprém, Bakony Mts, rock at N edge of town, 8973a, 47°05'50.7"N, 17°53'00.4"E, 240 m a.s.l. (ML, PL, GM 20. 7. 2011, CB 82479); 1. – Veszprém, Bakony Mts, Tekeres völgy, 8973a, 47°05'53.8"N, 17°51'39.4"E, 260–270 m a.s.l. (ML, PL, GM 20. 7. 2011, CB 82535, CB 82537); 2. – Veszprém, Márkó, Malom hegy, 8872d, 47°06'38.7"N, 17°48'59.8"E, 310–360 m a.s.l. (ML, PL, GM 20. 7. 2011, CB 82472, CB 82528); 2. – Szentkirályszabadja, Balaton region, Malomvölgy, 8973d, 47°02'57.0"N, 17°59'9.04"E, 240–250 m a.s.l. (ML, PL, GM 20. 7. 2011, CB 82474–82477); 4. – Veszprém, N of town, 8973a, 47°05'43.3"N, 17°51'36.9"E, 270 m a.s.l. (ML, PL, GM 20. 7. 2011, CB 82449); 1.

Sorbus pannonica

Hungary. Csákvár, Vértes Mts, Fejér megye, Köhányás, Németh-völgy, 8576c, 47°26'58.3"N, 18°23'39.7"E, 360–370 m a.s.l. (ML, PL, GM 19. 7. 2011); 3. – Várpalota, Bakony Mts, N of town, 8774d, 47°13'06.1"N, 18°06'43.2"E, 280 m a.s.l. (ML, PL, GM 19. 7. 2011); 2.

Paper II

Sorbus quernea: taxonomic confusion raised by the naturalisation of the alien species, *S. mougeotii*.

Lepší M., Lepší P. & Vít P. (2013) Preslia 85: 159–178.

Picture on previous page *Sorbus mougeotii*, planted in České Budějovice

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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Lepší M., Lepší P. & Vít P. (2013): *Sorbus quernea*: taxonomic confusion caused by the naturalization of an alien species, *Sorbus mougeotii*. – Preslia 85: 159–178.

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.

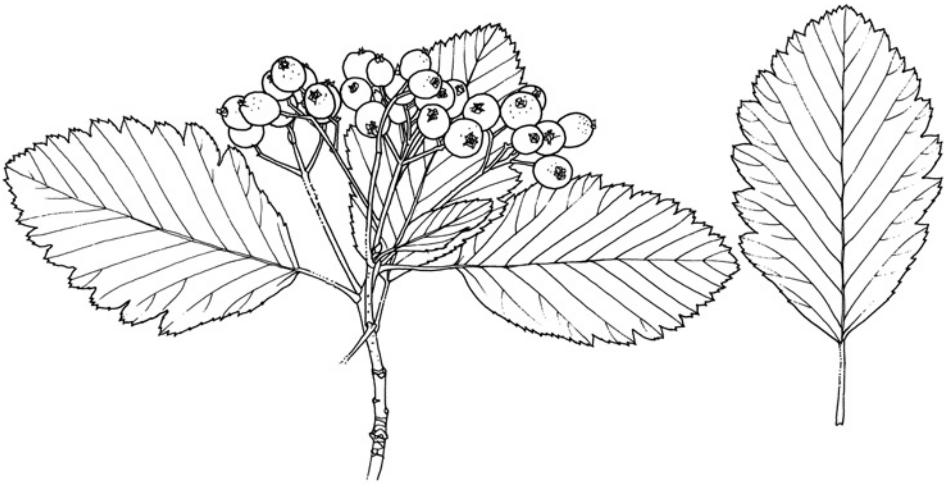

Fig. 1. – *Sorbus mougeotii*, a short fructiferous shoot (left) and a leaf from the middle part of a short sterile shoot (right). Drawing by A. Skoumalová.

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.

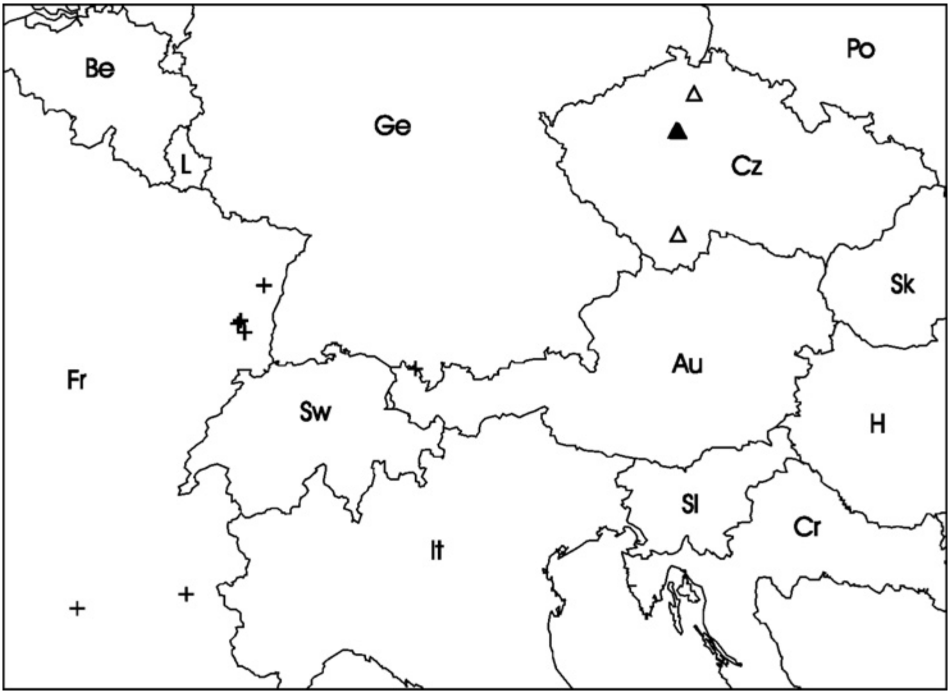

Fig. 3. – Areas sampled with natural populations of *Sorbus mougeotii* in the Alps, Vosges and Central Massif (cross), naturalized populations described as *S. quernea* (filled triangle) and cultivated populations in the Czech Republic of unknown origin (triangle).

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.

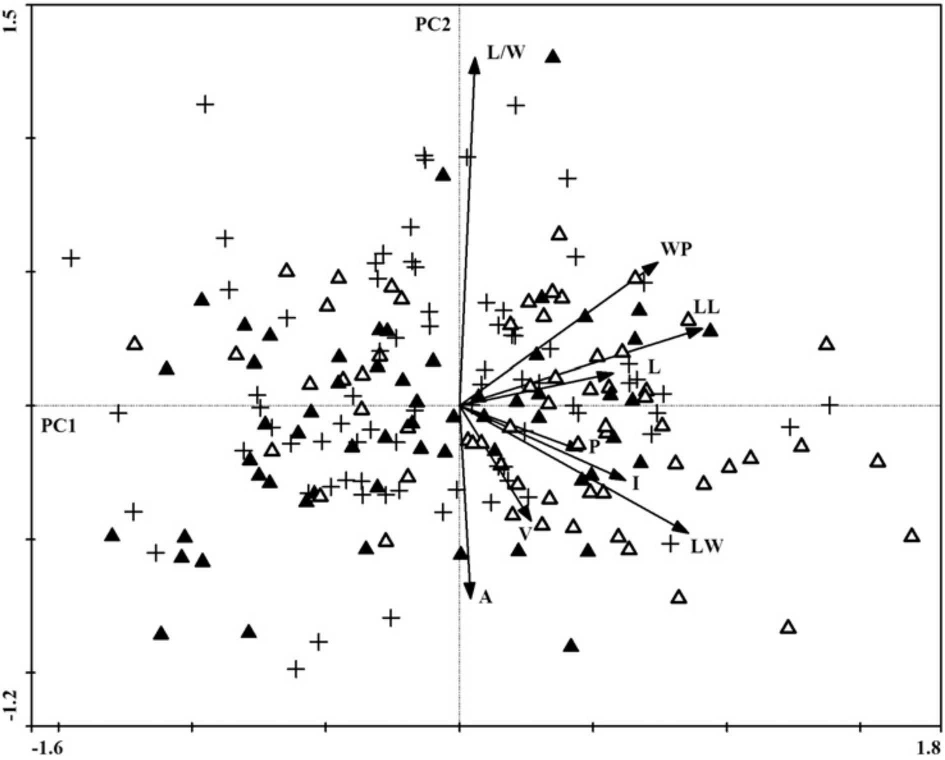

Fig. 4. – Principal component analysis based on nine morphological characters of the leaves of nine populations of *Sorbus mougeotii*: cross – three populations from France (Vosges Mts – Grand Ballon Mt., Hohneck Mt., Landsberg near the town of Barr) given in the protologue of *S. mougeotii* and one 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.

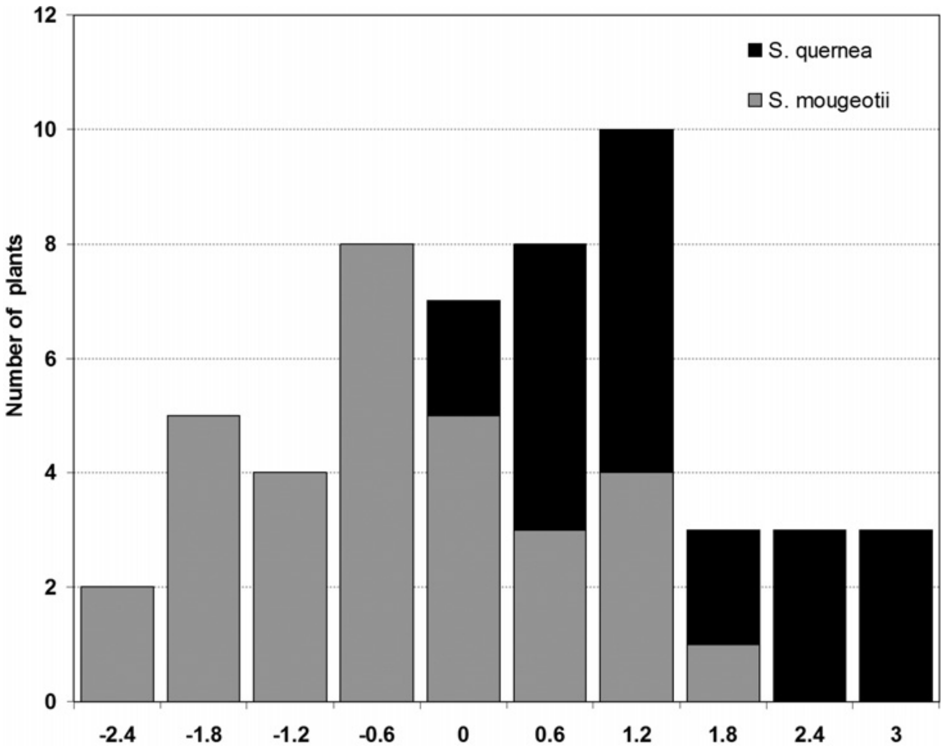

Fig. 5. – Histogram of canonical scores of linear canonical discriminant analysis based on nine morphological characters of the leaves of five populations of *Sorbus mougeotii* – three populations given in the protologue of *S. mougeotii* (France, Vosges Mts – Grand Ballon Mt., Hohneck Mt., Landsberg 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

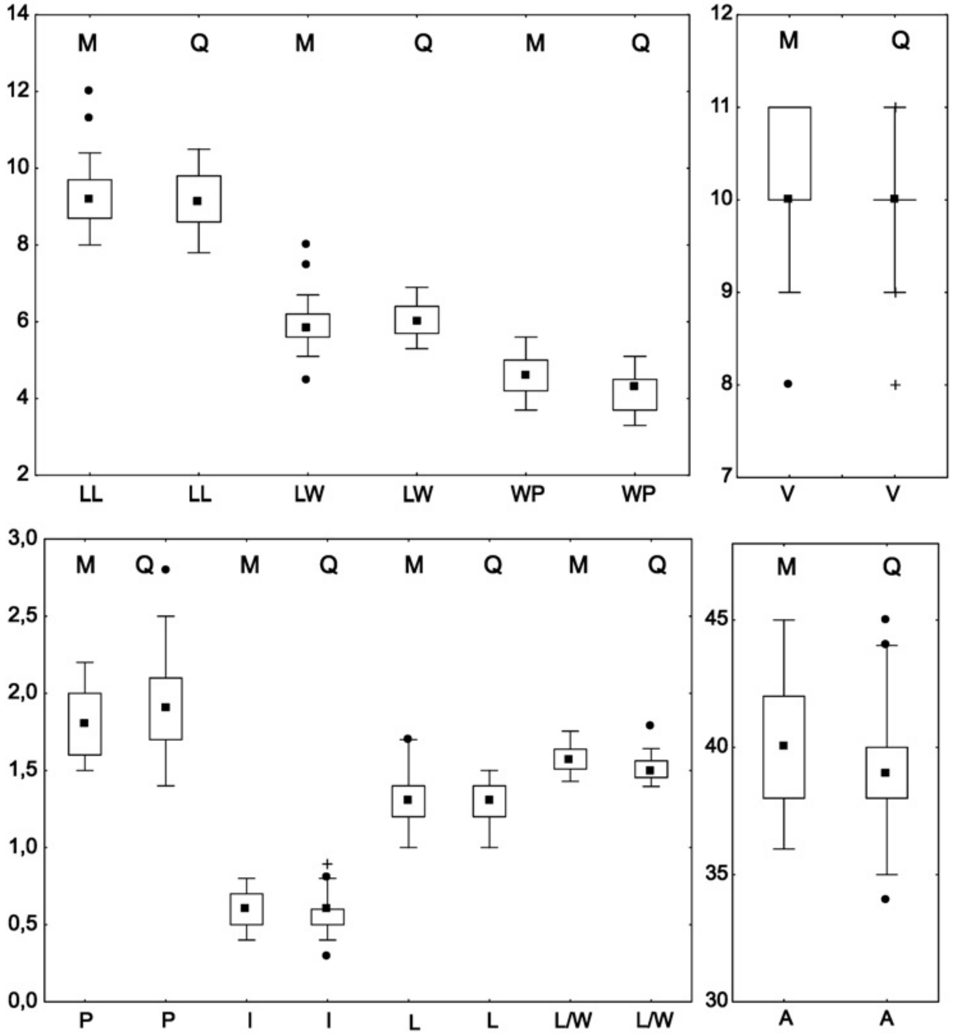

Fig. 6. – Box-and-whisker plots (showing median, 25–75% percentiles, 5–95% percentiles, outlier and extremes) of nine morphological characters of the leaves of five populations of *Sorbus mougeotii* – three populations given in the protologue of *S. mougeotii* (France, Vosges Mts – Grand Ballon Mt., 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*

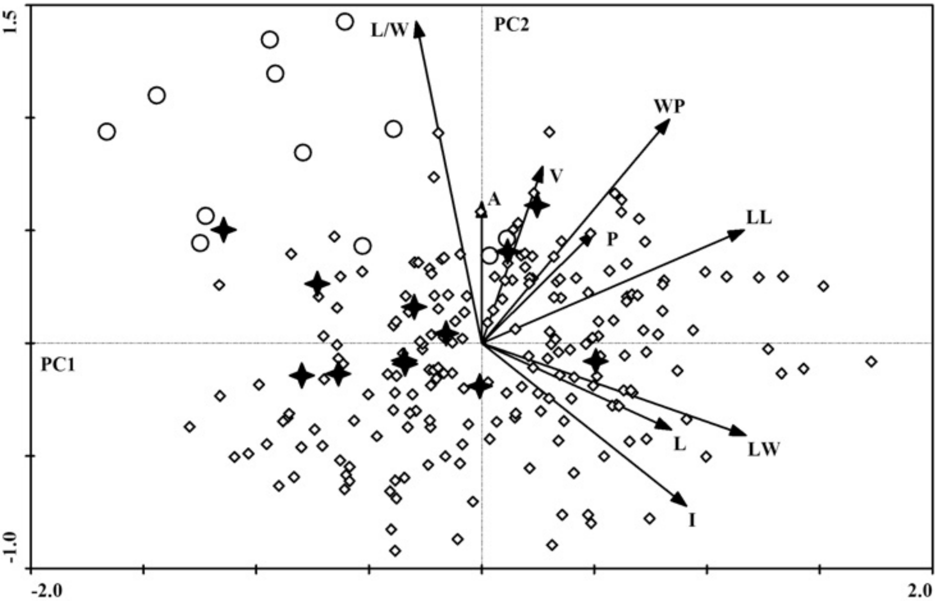

Fig. 7. – Principal component analysis based on nine morphological characters of the leaves of nine populations of *Sorbus mougeotii*: diamonds – three populations from France (Vosges Mts – Grand Ballon Mt., Hohneck Mt., Landsberg near the town of Barr) given in the protologue of *S. mougeotii* and one 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

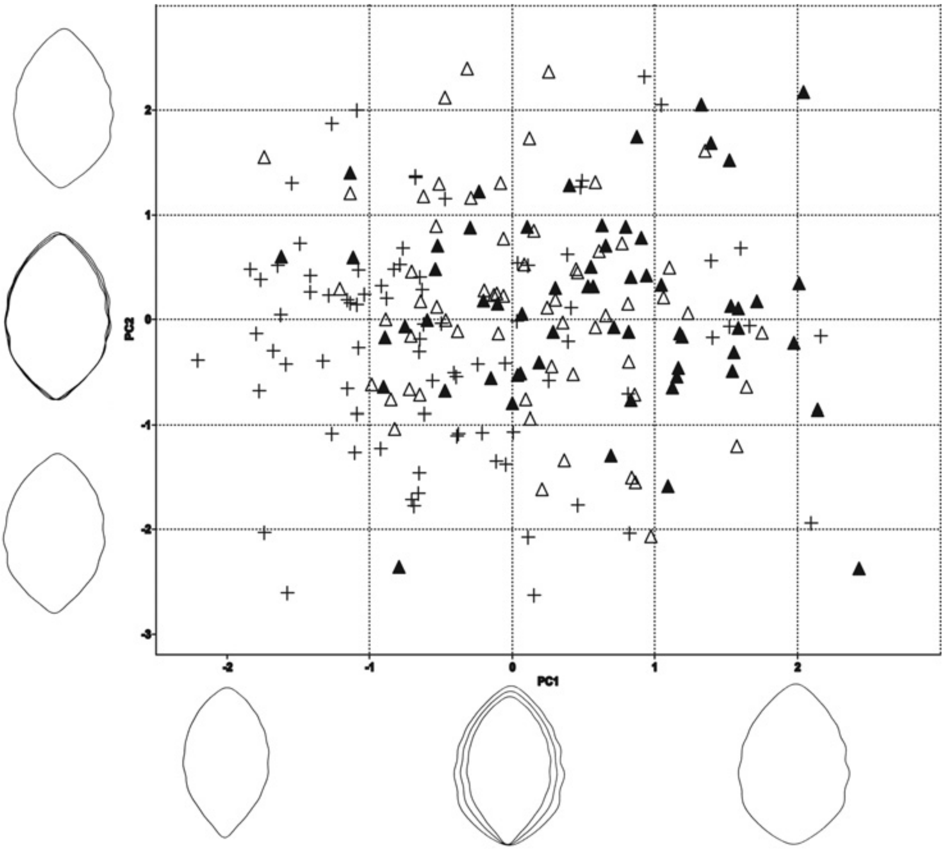

Fig. 8. – PCA of Fourier coefficients describing the total leaf lamina shape of the eight populations of *Sorbus mougeotii*. Cross – three populations from France (Vosges Mts – Grand Ballon Mt., Hohneck Mt., Landsberg near the town of Barr) given in the protologue of *S. mougeotii*; filled triangle – 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.

Acknowledgements

The Conservatoire et Jardins Botaniques de Nancy (NCY), namely T. Mahevas, C. Denjean Drechsler and G. Seznec are acknowledged for kind herbarium assistance. We are also grateful to B. Cornier for valuable information about the type material of *S. mougeotii* and for providing some samples from France. We thank N. Meyer for information about the occurrence of *S. mougeotii* in Germany. Cs. Németh, N. Meyer and B. Cornier generously added important information to the list of cultivated *Sorbus*. Our appreciation goes to R. Evans and K. Edwards who kindly improved our English. Tony Dixon kindly improved the English of the final version of the text. J. Lepš and P. Šmilauer are acknowledged for their valued advice on the multivariate statistical analyses. We extend our gratitude to A. Jírová who kindly cooked for us during the expedition to France and supplied the image of the species. We could not have undertaken this study without the financial support of grant 138/2010/P from the Grant Agency of the University of South Bohemia, Institutional research support MSM-6007665801 from the Czech Ministry of Education and long-term research development project no. RVO 67985939.

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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Received 21 June 2012
Revision received 19 November 2012
Accepted 19 November 2012

Paper III

There is no diploid apomict among Czech *Sorbus* species – a biosystematic revision of *Sorbus eximia*, and the discovery of *Sorbus barrandienica*.

Vít P., Lepší M. & Lepší P. (2012) Preslia 84: 71–96.

Picture on previous page *Sorbus eximia*, Koda

There is no diploid apomict among Czech *Sorbus* species: a biosystematic revision of *S. eximia* and discovery of *S. barrandienica*

Mezi českými jeřáby se nevyskytuje diploidní apomikt – biosystematická revize *Sorbus eximia* a objevení *S. barrandienica*

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Vít P., Lepší M. & Lepší P. (2012): There is no diploid apomict among Czech *Sorbus* species: a biosystematic revision of *S. eximia* and discovery of *S. barrandienica.* – Preslia 84: 71–96.

Sorbus eximia Kovanda, a hybridogenous species that originated from the parental combination *S. torminalis* and *S. aria* s.l., is thought to be an apomictic species, which includes diploid and tetraploid individuals. The present study confirmed the existence of only triploid individuals. A new tentatively apomictic triploid ($2n = 3x = 51$) species from the *S. latifolia* group: *S. barrandienica* P. Vít, M. Lepší et P. Lepší is described based on a revision of *S. eximia*. This species is assumed to have originated from a cross between *S. danubialis* or *S. aria* s.l. and *S. torminalis*. A wide palette of biosystematic techniques, including molecular (nuclear microsatellite markers) and karyological analyses (chromosome counts, DAPI flow cytometry) as well as multivariate morphometric and elliptic Fourier analyses, were used to assess the variation in this species and justify its independent taxonomic status. Allopatric occurrences of both species were recorded east of the town of Beroun in the Český kras, central Bohemia (Bohemian Karst). A distribution map of the two species is provided. *Sorbus eximia* occurs at four localities (the total number of adults and juveniles is 100 and 200, respectively) in basiphilous thermophilous oak forests (*Quercion pubescenti-petraeae*), mesic oak forests (*Melampyro nemorosi-Carpinetum*), woody margins of dry grasslands (*Festucion valesiacae*) and pine plantations. *Sorbus barrandienica* has so far been recorded at 10 localities (ca 50 adults). Recent field studies failed to verify two of these localities. It is mainly found growing on the summits of hills, usually in thermophilous open forests (*Primulo veris-Carpinetum*, *Melampyro nemorosi-Carpinetum*, *Quercion pubescenti-petraeae*) and woody margins of dry grassland. Its populations exhibit minimal genetic variation and are phenotypically homogeneous and well separated from other Bohemian hybridogenous *Sorbus* species. The epitype of *S. eximia* is designated here, and a photograph of the specimen is included. Photographs of the type specimens and in situ individuals, and line drawings of both species are presented.

Keywords: apomixis, Czech Republic, endemic, geometric morphometrics, hybridization, karyology, multivariate morphometrics, *Rosaceae*, *Sorbus latifolia* agg., SSR markers, taxonomy

Introduction

In recent years, taxonomic research on agamospermous groups in the Czech Republic has led to the description of many new taxa. This especially applies to the genera *Taraxacum* (e.g. Øllgaard 2003, Vašut & Trávníček 2004, Vašut et al. 2005, Trávníček et al. 2008) and

Rubus (e.g. Zieliński & Trávníček 2004, Trávníček et al. 2005, Trávníček & Zázvorka 2005, Žíla & Weber 2005, Lepší & Lepší 2006, 2009, Žíla 2009). A recent increase in taxonomic novelties is also recorded in the genus *Sorbus* s.l. Three new species of the *S. latifolia* group – *S. milensis*, *S. albensis* and *S. portae-bohemicae* – have been described from the České středohoří hills in northern Bohemia. The finding of scattered plants recognized as *S. milensis* during extensive floristic research prompted a subsequent detailed taxonomic revision of *S. bohemica*, which in addition resulted in distinguishing two new species, *S. albensis* and *S. portae-bohemicae* (Lepší et al. 2008, 2009). Over the last few years, taxonomic research has focused on another apomictic species – *S. eximia* Kovanda.

Sorbus eximia was described in 1984 as a hybridogenous species endemic to the Český kras karst (Kovanda 1984). Subsequent chemotaxonomical research indicated that it most probably originated from a back-cross between the F1 hybrid *Sorbus torminalis* × *Sorbus aria* s.l. and *Sorbus aria* s.l. (Challice & Kovanda 1986). The species was subsequently studied embryologically and was presented as an apomict comprising two cytotypes: diploid and tetraploid, combined with apospory and diplospory (Jankun & Kovanda 1988). The most surprising result of that study is the discovery of apomixis at the diploid level. Apomixis in *Maloideae* is, with a few exceptions, associated with polyploidy (Campbell & Dickinson 1990). The only reported cases of diploid apomicts are some individuals of *Crataegus calpodendron* (Ehrh.) Medikus, one individual of an apple cultivar, *Sorbus eximia* and possibly *S. subfusca* Boiss. (Campbell et al. 1991). Jankun & Kovanda (1988) found diploid individuals of *S. eximia* at a single locality nearby the settlement of Koda and observed that diploids had leaf laminas more obtusely and more shallowly lobed than tetraploids.

Between 2004 and 2005, a revision of the morphological, karyological and genetic variation in *S. eximia* over its entire distribution area revealed new facts (Vít 2006) that affirmed the karyological results obtained by Jankun & Kovanda (1988). By contrast, morphometrics and molecular techniques confirmed the unique character of the Koda population (Vít 2006), which called for a new taxonomical evaluation of the species. Our additional studies of the type material indicated that the name *S. eximia* relates to the Koda morph and that the remainder of the known populations belong to a new taxon yet to be described. Detailed field work in 2009 and a revision of voucher specimens in major Czech herbaria revealed or confirmed four localities for *S. eximia* and 10 for the new apomictic taxon.

This paper presents a formal description of the newly delimited taxon based on the results of field observations, molecular analyses, karyology, multivariate morphometric and elliptic Fourier analyses. Furthermore, an epitype of *S. eximia* is designated, and its description is revised and emended here. An updated distribution map and a list of revised herbarium specimens of both taxa are also provided.

Material and methods

Plant material and field work

Mature and well developed individuals were selected for the study of phenotypic and genetic variation. For molecular analyses (nuclear microsatellite markers), 12 individuals of *S. eximia* and 10 of *S. barrandienica* were sampled. For the multivariate morphometric analyses, 45 individuals of *S. eximia* and 19 of *S. barrandienica* were used (see Table 1 for locality details). In addition, six other hybridogenous taxa of the *S. latifolia* group occurring in Bohemia, which are closely related to the *Sorbus* species currently under study, were included in the multivariate morphometric analyses in order to assess phenotypic variation within the group and determine species-specific characters. These were *S. albensis* (84), *S. bohemica* (111), *S. gemella* (10), *S. milensis* (15), *S. portae-bohemicae* (13) and *S. rhodanthera* (12) (see Lepší et al. 2008, 2009 for locality details). Elliptic Fourier analysis was carried out to reveal species-specific characters of leaves of *S. eximia* (96 leaves analysed) and *S. barrandienica* (93) and also of the holotype of the name of *S. eximia* (see Table 1 for locality details). Specimens were collected during 2004–2009 following the recommendations of Kutzelnigg (1995) and Meyer et al. (2005), for details see Lepší et al. (2009). To describe the phytosociological affinities of *S. eximia* and *S. barrandienica*, relevés were recorded in subjectively selected plots using the Braun-Blanquet approach. The relevés are stored in the Czech National Phytosociological Database (Chytrý & Rafajová 2003) under the numbers 348308, 203571–203584. Altitudes and geographic coordinates (WGS-84) were determined using Garmin eTrex and GPSmap 60CSx instruments.

Table 1. – Details of the localities of *Sorbus* species included in the morphometric, molecular and ploidy level analyses.

Locality	Geographic coordinates	Altitude (m a.s.l.)	Number of individuals analysed			
			Nuclear microsatellite markers	Classical morphometry	Elliptic Fourier analysis	Ploidy level
Taxon *S. eximia*						
Koda hill near Srbsko	49°56'03.6"N, 14°07'09.5"E	360–370	12	45	15	73
Kotýz prehistoric settlement near Tmaň	49°54'57.5"N, 14°02'56.5"E	390	–	–	10	–
Taxon *S. barrandienica*						
Paní hora hill near Bubovice	49°57'43.1"N, 14°09'52.3"E	410	3	8	5	5
Mokrý vrch hill near Bubovice	49°57'22.2"N, 14°09'44.2"E	390	–	–	1	–
Doutnáč hill near Srbsko	49°57'23.5"N, 14°09'09.5"E	430	–	1	3	1
Haknová hill near Karlštejn	49°56'15.7"N, 14°11'55.7"E	410	5	5	2	5
Plešivec hill near Karlštejn	49°56'04.2"N, 14°11'24.5"E	340	2	5	–	2

A taxonomic revision of the relevant *Sorbus* material kept in the following herbarium collections was undertaken: BRNM, BRNL, BRNU, CB, CHEB, CHOM, Herbarium of the Museum of Ústí nad Labem, HOMP, HR, LIM, LIT, MP, PL, PR, PRA, PRC, ROZ, SOKO and ZMT. For abbreviations of public herbaria, see Holmgren et al. (1990). Revised herbarium specimens were sorted by locality and then according to the year of collection. Information in Czech on herbarium labels was translated into English. Each locality was numbered and named. Coordinates missing on herbarium sheets were obtained using on-line maps (http://www.mapy.cz). Locality numbers were used for displaying localities on the distribution map. Names of the most frequent collectors are abbreviated: ML = M. Lepší, PL = P. Lepší, PV = P. Vít. Species nomenclature is unified according to Kubát et al. (2002) except for, *S. albensis*, *S. portae-bohemicae*, *S. milensis* and *S. latifolia*, which follow Kutzelnigg (1995) and Lepší et al. (2008, 2009). Phytosociological nomenclature follows Chytrý et al. (2001).

Digitalization and elliptic Fourier analysis

Detailed elliptic Fourier analysis was applied to elucidate the variation in leaf shape. Leaves for analysis were predominantly selected from the middle part of short sterile shoots, because most of the *Sorbus* studied were sterile in 2009. Several fertile short and terminal shoots were also included in the analysis to span the leaf variation of the type specimen of *S. eximia,* which only has fertile shoots. Well developed, mature and intact leaves were collected, carefully flattened and dried, and subsequently scanned at 300 dpi using Epson scan 1.11E software. The method of 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 both hybridogenous species. The chain-coded contour of each leaf was approximated using the first 20 harmonics, and the elliptic Fourier descriptors (EFDs) 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 shape variation associated with each PC was visualized using the procedure described by Furuta et al. (1995).

A cross-validated linear discriminant analysis using principal component scores (from the above mentioned PCA analysis) as discriminating variables was performed in R, version 2.0.0 (R Core Development Team 2004) using the MASS package (Venables & Ripley 2002). Only the scores of selected PCA axes were used for the discriminant analysis. These axes were selected by a forward selection algorithm in the CVA analysis in Canoco (Lepš & Šmilauer 2003), using the Monte Carlo permutation test (999 permutations; only axes with P level < 0.05 were considered).

Karyology

Three samples each of short, two-year old branches with well-developed leaf buds of each species were collected from the type localities of *S. eximia* and *S. barrandienica* in February 2006. Actively growing vegetative tissue was pre-treated in a saturated water solution of p-dichlorbenzen (2–3 hours at RT) and fixed in ice-cold 3:1 ethanol acetic acid overnight. The maceration lasted for 30–60 s in 1:1 ethanol : HCl at 22 °C. Meristematic tissues were squashed in a drop of lacto-propionic orceine. Chromosomes were counted under a light microscope (Carl Zeiss NU, Jena, Germany) at a magnification of 1000 times.

Estimate of the DNA ploidy level

DAPI flow cytometry was applied to assess the variation in relative genome size and to infer DNA ploidy levels (Suda et al. 2006) in *S. eximia* and *S. barrandienica*. A group of individuals were analyzed individually, then bulked samples were analysed (i.e. five individuals simultaneously) from 73 different trees of *S. eximia* and 13 trees of *S. barrandienica*. *Bellis perennis* (2C = 3.38 pg; Schönswetter et al. 2007) was selected as a suitable internal reference standard (with genome size close to, but not overlapping that of the *Sorbus* species). Nuclei were isolated using a modified two-step procedure (Doležel et al. 2007), stained with DAPI fluorochrome and analysed following the method of Lepší et al. (2008).

Morphometric data and analyses

Seventeen quantitative characters were measured and scored for all of the hybridogenous apomictic *Sorbus* species studied (for a summary of the characters measured, see Lepší et al. 2008). Two new characters were included: “style length” and “length of the fused part of the style”. This character set was chosen on the basis of published determination keys, floras and our own observations. The dataset was analysed using the SAS package (version 9.1; SAS Institute, Cary, NC, USA) with CANDIS and DISCRIM procedures, following the methodology described in Klecka (1980). For details see Lepší et al. (2008).

Nuclear microsatellite markers (SSR)

Total genomic DNA was extracted from silica-dried leaves (22 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). Based on the different ploidy levels of samples analysed (both species studied are triploids, putatively parental taxa are diploid and tetraploid), the microsatellite pattern was scored as “allele phenotypes” (Becher et al. 2000). The data set was converted to a binary matrix and analysed with procedures recommended for dominant markers (i.e. PCoA). Intraspecific variation was measured using the Arlequin ver. 3.01 computer programme (Excoffier et al. 2005), which computes the average gene diversity of all loci (AGD, Nei 1987).

Results

Typification of Sorbus eximia

The type specimen of *Sorbus eximia* consists only of a fertile terminal shoot and a short fertile side shoot, both bear untypical or (partly) damaged leaves (Fig. 1). The shape of the laminas, the shallow incision between lobes and the results of elliptic Fourier analysis indicate that the type specimen is more likely to belong to the Koda type than the second taxon. The determination, however, is not certain. Information on the label does not help much in this sense because the locality is quite broad: slopes of a hill by the village of Srbsko, which may include both the locality of the Koda population and the distribution area of the second taxon.

Because the determination of the type specimen is ambiguous we consider it advisable to select an interpretative epitype. – Holotype: Herbar. Beck., Böhmen Berghänge bei Srbsko, Kalk, leg. [Beck] 17. 8. 1918, PRC (Fig. 1). – Epitype: Bohemia centralis, distr. Beroun, pagus Srbsko (6050d): ca 300 m situ sept.-orientali a pago Koda, in rupibus in declivibus meridionalibus cotae 393 m, solo calcareo; 360 m s.m., 49°56'03.8"N, 14°07'13.6"E; disperse; leg. M. Lepší 2. 8. 2007 (**epitype designated here:** CB, No. 65278, Fig. 2).

When Kovanda described *S. eximia* he had only three specimens of the Koda taxon and had not seen it in the field. On the other hand, he observed the second taxon (*S. barrandienica* described herein) at three localities in the field and cited nine specimens clearly belonging to it. In addition, the pen drawing of a flowering shoot in the original paper (Kovanda 1984) belongs to the new species of *Sorbus*. Consequently, we can assume that the original diagnosis is based on both taxa but mainly on the formally undescribed taxon, at least for the flowers, which are not present on the specimens of the Koda type. It is apparent that a new description of *S. eximia* is needed.

Sorbus eximia Kovanda, Preslia 56: 170, 1984 emend. P. Vít, M. Lepší et P. Lepší
(Figs 1–4)

Description: Trees (or shrubs) up to 16 m high. Trunk up to 1.1 m in circumference. Bark grey, smooth when young, with vertical fissures (particularly at the trunk base) at maturity, with scattered (4–) 8–11 (–16) mm long and (4–) 6–9 (–16) mm wide lenticels. Twigs brownish-grey; young shoots brown, sparsely tomentose when young and almost glabrous at maturity, with numerous elliptical or subrotund pale brown to ochraceous lenticels. Buds 6–14 mm long and 3–6 mm wide, narrowly ovoid to turbinate; scales green, with narrow brown sparsely tomentose margins. Leaves (on short fertile shoots) simple; laminas more or less broadly ovate to broadly elliptical, cochleariform to more or less flat, somewhat glossy, pale to dark green above, yellowish-greyish-green beneath, usually not undulated at margins, more or less broadly rounded acute to obtuse at apex, usually rounded or broadly cuneate and partly serrate at base, almost glabrous on upper surface, evenly tomentose on lower surface, (7.5–) 8.6–9.3 (–11.3) cm long and (5.0–) 6.7–7.5 (–9.4) cm wide, widest at (39–) 51–58 (–64)% of the lamina length (from the tip), double serrate to regularly shallowly lobed (serrate to double serrate apically); lobes serrate or doubly serrate with sharply acuminate teeth terminating the main veins, other teeth smaller, acuminate; sides of lobes more or less arcuate; the third lobe (from the base) (1.0–) 1.1–1.3 (–1.7) cm broad; incision between the second and the third lobe (0.25–) 0.40 (–0.55) cm; lobes broader than 1 cm (2–) 3–4 on each side; main veins terminating in lobes or teeth (6–) 7–8 (–9) on each side; petioles (1.5–) 1.9–2.1 (–2.6) cm long, more or less tomentose. Inflorescences with (16–) 25–42 (–70) flowers, (5.5–) 6.0–9.5 (–10.5) cm in diameter, convex; branchlets more or less tomentose. Hypanthium turbinate, tomentose. Sepals (1.7–) 2.1–2.5 (–3.0) mm long and (2.2–) 2.7–2.9 (–3.3) mm wide, triangular,

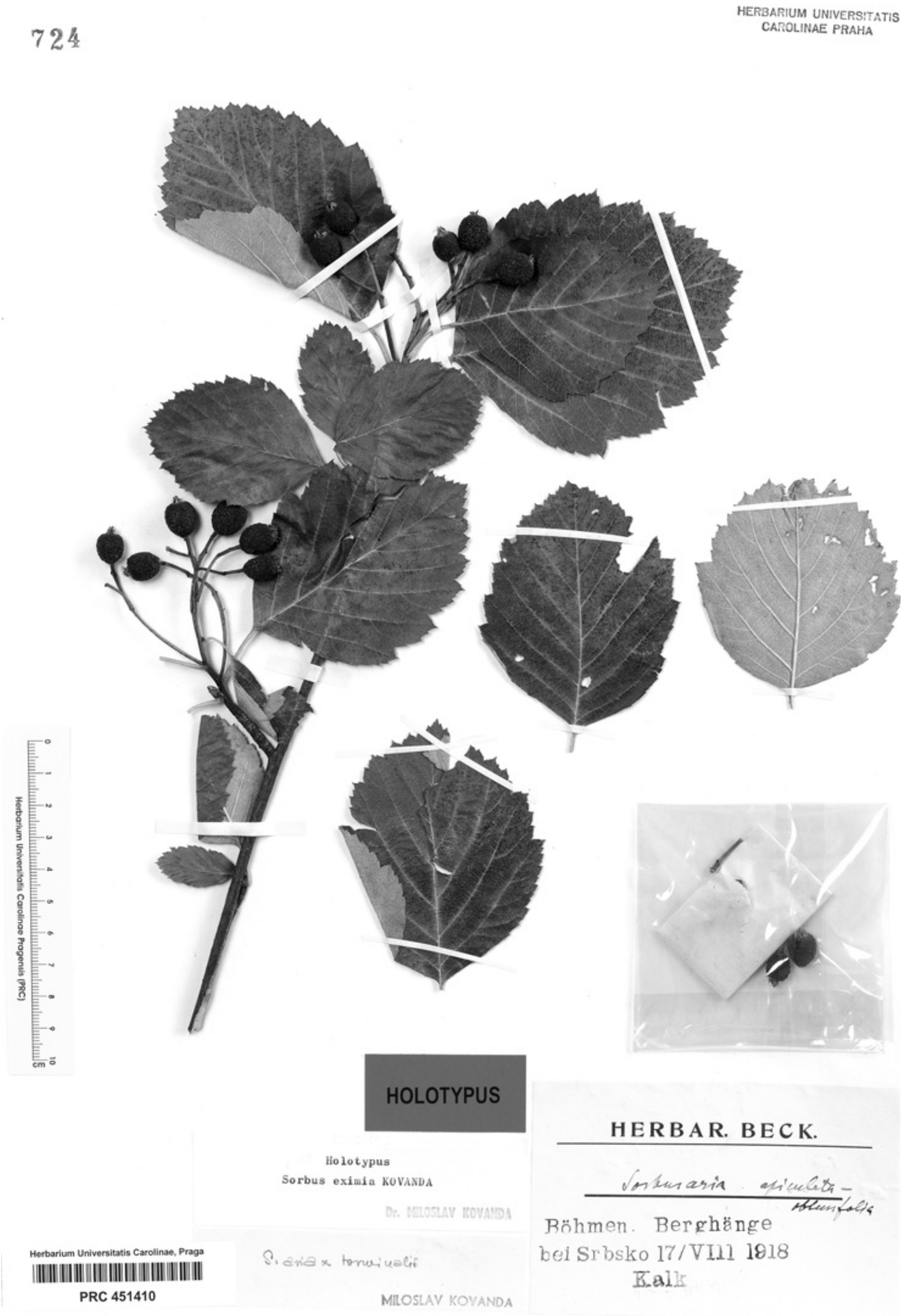

Fig. 1. – Holotype of *Sorbus eximia* Kovanda.

HERBARIUM MUSEI REGIONALIS BOHEMIAE MERIDIONALIS
ČESKÉ BUDĚJOVICE

Flora: Bohemia centralis

EPITYPUS!
No. 65278

Sorbus eximia Kovanda

Habitat:
Distr. Beroun, pagus Srbsko (6050d): ca 300 m situ sept.-orientali a pago Koda, in rupibus in declivibus meridionalibus cotae 393 m, solo calcareo; 360 m s. m., 49°56'3.8''N, 14°7'13.6''E; disperse.

Die: 2. 8. 2007

Legit: Martin Lepší

Fig. 2. – Epitype of *Sorbus eximia* Kovanda.

acuminate or acute, densely tomentose on both surfaces, patent, reclinate after anthesis, persistent, dry, erect. Petals (5.1–) 5.7–6.2 (–6.8) mm long and (3.8–) 4.6–4.9 (–5.2) mm wide, broadly ovate to broadly elliptical, concave, whitish, patent, sparsely hirsute at base of upper surface, with a short claw. Stamens ca 20; filaments whitish; anthers pale yellow, (1.0–) 1.2–1.4 (–1.6) mm long. Ovary semi-inferior. Styles (1–) 2, greenish-cream, (3.0–) 3.4–3.8 (–4.6) mm long, hairy at the base, connate up to (27–) 44–49 (–59)%. Stigma greenish-cream, more or less flat, 0.6–0.7 (–0.8) mm wide. Fruits (11–) 12–13 (–15) mm long and (11–) 12–13 (–15) mm wide, subglobose, often as wide as long or wider than long, orange to orange-red at maturity, glabrous or almost glabrous, glossy, with (8–) 16–32 (–64) ochraceous lenticels per 0.25 cm^2, mesocarp heterogeneous; endocarp cartilaginous. Seeds fuscous. Somatic chromosome number 2n = 51 (triploid). Reproduction tentatively apomictic. Flowering V.

There are pen drawings of a flowering shoot and a leaf in the Flora of the Czech Republic (Kovanda 1992). The same drawing of the leaf is used in the Key to the flora of the Czech Republic (Kubát et al. 2002).

Diagnostic characters

Leaf laminas are broadly ovate to broadly elliptical, (7.5–) 8.6–9.3 (–11.3) cm long and (5.0–) 6.7–7.5 (–9.4) cm wide, often cochleariform, more or less rounded acute to obtuse at apex, usually rounded or broadly cuneate at base, double serrate to regularly shallowly lobed; incision between the second and the third lobe terminating the main veins (0.25–) 0.40 (–0.55) cm long, teeth or lobe terminating the main veins sharply acuminate. Anthers are pale yellow. Styles connate up to (27–) 44–49 (–59)% of their length. Fruits are subglobose, often as wide as or wider than long, orange to orange-red at maturity (Fig. 4).

Ecology

Sorbus eximia occurs in open (woody margins of dry grasslands) and (semi)shaded habitats (forests) on base-rich soils on limestone. In forests, it usually grows in the understorey. Exceptionally it may reach the high tree layer or form monospecific stands (such as by the settlement of Koda). It is recorded on slopes of all aspects. Most individuals grow on southeast, south and southwest slopes. It inhabits mainly basiphilous thermophilous oak forests (*Quercion pubescenti-petraeae*) and mesic oak forests (*Melampyro nemorosi-Carpinetum*). It is rarely also found in narrow-leaved dry grassland (*Erysimo crepidifolii-Festucetum valesiacae*). A majority of individuals occur in semi-natural forests or grasslands with a high abundance of relic species, but it is also found in man-made habitats such as plantations of *Pinus nigra*, long-abandoned quarries (in *Sesleria* grassland – *Diantho lumnitzeri-Seslerion*) or at sites of prehistoric settlements (in species-poor dry grasslands – *Festucion valesiacae*). The species grows sympatrically with *S. aria* s.l., *S. danubialis* and *S. torminalis*. *S. aria* s.l. and *S. danubialis* are a little more heliophilous and xerothermophilous, while *S. torminalis* is a more mesophilous species.

Geographical distribution

Sorbus eximia is recorded at four localities in the Bohemian Karst between Prague and Beroun (Central Bohemia). The largest stand of this species, which includes tens of adults

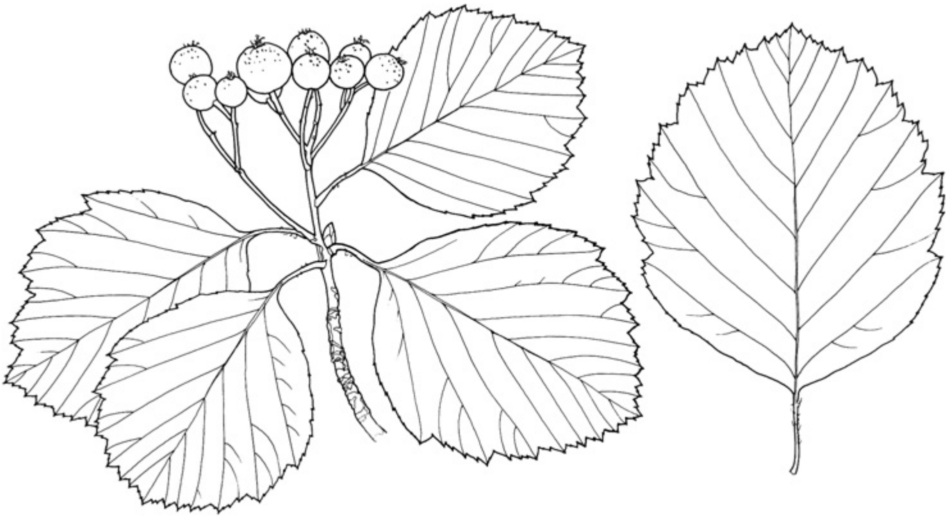

Fig. 3. – *Sorbus eximia*: short fructiferous shoot (left) and leaf from the middle part of short sterile shoot (right). Drawing by A. Skoumalová.

Fig. 4. – Fructiferous short fertile shoot of *Sorbus eximia* at the type locality (photograph taken by P. Lepší, 2009).

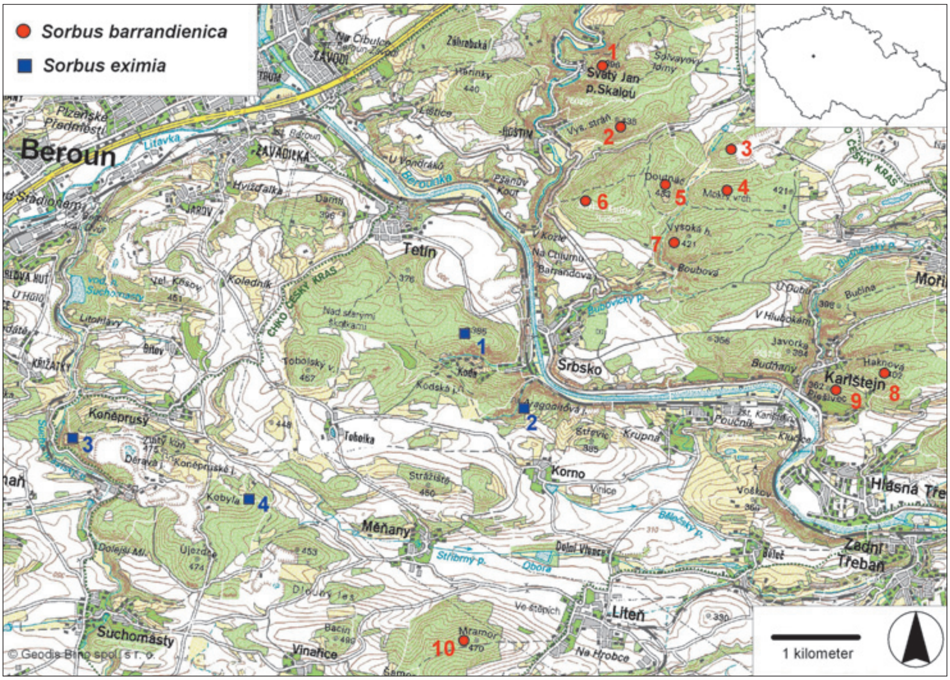

Fig. 5. – Distribution map of *Sorbus eximia* and *S. barrandienica*. The numbers on the map correspond to the locality numbers in the list of revised herbarium specimens and recorded localities (the use of the map was approved by the Ministry of Environment of the Czech Republic).

and ca 200 young trees of different ages, is located by the settlement of Koda near the village of Srbsko within the boundaries of the Koda national nature reserve and covers ca 5 ha. This locality was documented by G. Beck for the first time as far back as in 1918 (holotype in PRC). By contrast, the occurrence of this species nearby Tmaň and Koněprusy was discovered recently in 2009. These two sites harbour a distinctly smaller population, 10 individuals by the village of Tmaň and 20 by the village of Koněprusy. Both of these localities extend over a few tens of square meters. The forth locality in the Císařská rokle gorge is an ex situ conservation plot and houses 11 juveniles. The distance between the localities that are furthest apart is ca 6 km (excluding the locality Císařská rokle) (Fig. 5). *Sorbus eximia* grows in two quadrants (6050d, c) of the Central-European mapping grid (Ehrendorfer & Hamann 1965). The localities are situated in the colline vegetation belt in the phytogeographical district of Český kras (Bohemian Karst) (Skalický 1988). This species grows in a warm and moderately warm climatic region (Quitt 1971) with a mean annual temperature of about 7–9 °C and mean annual precipitation of 500–600 mm (Tolasz et al. 2007). Its altitudinal range spans from 350 m (Koda hill) to 460 m a.s.l. (Kobyla hill). The species has also been planted along the road between the villages of Řevnice and Mořina ca 8 km to the east of its nearest native occurrence (Koda hill).

Herbarium specimens and records:

Czech Republic. Central Bohemia, Bohemian Karst: 1. Koda hill: Herbar. Beck., Böhmen Berghänge bei Srbsko, Kalk (leg. [Beck] 17. 8. 1918, PRC, HOLOTYPE). – Böhmen auf Kalkfelsen bei Koda, nächst Srbsko, häufig (leg. B [=Beck] 1920, PRC). – Koda (leg. J. Klika 4. 10. 1942, PR). – Koda, the plateau (leg. J. Klika 11. 8. 1944, PR 174901). – The S face of the plateau of Koda hill (the reserve) (leg. J. Klika 11. 10. 1944, PR 174899). – On the plateau at the top of Koda hill above the gorge by Koda settlement, growing in association with *Quercus pubescens*, *S. cretica* [= *Sorbus danubialis*], *S. torminalis* and *Carpinus* (leg. J. Klika 5. 7. 1945, two identical specimens in PR). – The plateau of Koda hill by Beroun town (leg. [J. Klika] 2. 4. 1946, PR). – Koda settlement (leg. M. Kovanda 27. 9. 1985, PRA). – Srbsko, rocks and forest-steppe NE of Koda settlement, S slopes at this spot at a height of 393 m, scattered, 6050d: 49°56'03.2"N, 14°07'17.5"E 370 m a.s.l. (leg. ML 2. 8. 2007, PRC 65280/a, CB 65280/b), 49°56'03.8"N, 14°07'13.6"E, 360 m a.s.l. (leg. ML 2. 8. 2007, CB 65278, EPITYPE), 49°56'02.2"N, 14°07'13.6"E, 360 m a.s.l. (leg. ML 2. 8. 2007, CB 65277; leg. PL 19. 9. 2009, CB 71605), 49°56'03.6"N, 14°07'09.5"E, 370 m a.s.l. (leg. ML 19. 8. 2009, CB 71584), 49°56'03.9"N, 14°07'09.5"E, 360 m a.s.l. (leg. PL & ML 10. 5. 2009, CB 71590, CB 71592), 49°56'03.9"N, 14°07'09.6"E, 360 m a.s.l. (leg. PL & ML 10. 5. 2009, CB 71591), 49°56'04.2"N, 14°07'09.9"E, 370 m a.s.l. (leg. PL & ML 10. 5. 2009, CB 71593), 49°56'02.0"N, 14°07'13.3"E, 360 m a.s.l. (leg. PL & ML 10. 5. 2009, CB 71594). – Koda, ca 400 m WNW of the spot at a height of 390 m NE of the settlement, in a oak-hornbeam forest, 6050d, 49°56'09.5"N, 14°07'02.5"E, 375 m a.s.l., scattered (leg. PV, PL, ML & J. Mottl 19. 6. 2009, CB 71595). – Koda, ca 260 m ENE of the spot at a height of 393 m, NE of the settlement, an oak-hornbeam forest, 6050d, 49°56'17.1"N, 14°07'03.4"E, 350 m a.s.l. (leg. PL 21. 6. 2009, CB 71605). This large locality also includes Kovanda's record: Koda forest, N slope (N. of point 390 m), 360–380 m a.s.l. (Jankun & Kovanda 1988). **2. The Císařská rokle gorge:** Srbsko, ca 1 km S of the bridge across the Berounka river, on the right-hand side of the Císařská rokle gorge, 6050d, 49°55'39.5"N, 14°07'56.9"E, 360 m a.s.l., planted in lines, 11 ca 0.5 m high juveniles (leg. PV, PL, ML & J. Mottl 19. 6. 2009, CB 71596). The first record at this locality provided by Schlägelová (2006). **3. Kotýz prehistoric settlement:** Tmaň, the area of Kotýz prehistoric settlement, open thermophilous scrubland, 6050c, 49°54'57.5"N, 14°02'56.5"E, 390 m a.s.l., ca 10 individuals (leg. PL, ML & J. Mottl 19. 6. 2009, CB 71597). A new locality. **4. Kobyla hill:** Koněprusy, SE slopes of Kobyla hill, in the undergrowth of a *Pinus nigra* plantation, 6050d, 49°54'38.5"N, 14°05'05.8"E, 450 m a.s.l., ca 20 individuals of different age (not. J. Mottl 4. 8. 2009, leg. ML 20. 8. 2009, CB 71582). – Koněprusy, the wall of an abandoned quarry on N slope of Kobyla hill, 6050c, 49°54'43.6"N, 14°04'54.4"E, 460 m a.s.l., 1 young tree (leg. ML 20. 8. 2009, CB 71583). A new locality.

Sorbus barrandienica P. Vít, M. Lepší et P. Lepší, **spec. nova** (Figs 6–8)

Descriptio: Arbores usque 12 m alti; foliis (in brachyblastis fertilibus) simplicibus, laminis ambitu fere ellipticis, regulariter pinnato-lobatis (lobis acuminatis, serratis), in parte superiore tantum duplicato-serratis, (8.1–) 8.8–10.3 (–11.6) cm longis et (5.4–) 6.7–7.4 (–8.9) cm latis, ad basin cuneatis usque raro late cuneatis, subintegris vel remote serratis, obscure viridibus, subtus ochro-griseo-viride tomentosis, nervis ab utroque latere (7–) 8 (–9) in numero; petiolis (1.9–) 2.1–2.4 (–2.7) cm longis; corymbothyrsis multifloris, convexis, ramis plus minusve tomentosis. Dentibus calycinis triangularibus, acuminatis usque acutis, (2.3–) 2.5–3.5 (–3.8) mm longis et (2.7–) 2.8–3.0 (–3.2) mm latis, patentibus usque reclinatis, post anthesin reclinatis, dense tomentosis, tempore fructificationis siccis, persistentibus; petalis late ovatis usque late ellipticis, breviter unguiculatis, (6.1–) 6.2–6.9 (–7.5) mm longis et (4.4–) 4.5–4.9 (–5.2) mm latis, albidis, superne ad basin sparse villosis, patentibus; staminibus ca 20, antheris pallide luteis, (1.0–) 1.2–1.3 (–1.5) mm longis; ovario semi-infero; stylis 2 (–3) ad (16–) 29–42 (–57)% coalescentibus, ad basin villosis, albo-viridis, (3.5–) 3.7–3.9 (–4.0) mm longis, stigmatibus plus minusve planis; fructibus subglobosis, (11.5–) 12.0–13.0 (–14.0) mm longis et (11.0–) 12.0–12.5 (–14.0) mm latis, maturitate aurantiacis usque rubris, glabris vel fere glabris, nitidis, cum (4–) 16–32 (–36) lenticellis parvis, ochraceis ad 0.25 cm^2; mesocarpio heterogeneo; endocarpio cartillagineo, seminibus atro-fuscis. Numerus chromosomatum triploideus 2n = 51. Probabiliter planta apomicta. Floret V.

Holotypus: Bohemia centralis, distr. Beroun, pagus Srbsko (6050b): in summo collis Doutnáč, in querceto, solo calcareo; 430 m s.m., 49°57'23.5"N, 14°09'09.5"E; disperse; leg. M. Lepší 2. 8. 2007; CB, No. 65274 (Fig. 6). – Isotypus: PRC, No. 65274/a.

Description: Trees up to 12 m high. Trunk up to 0.55 m in circumference. Bark grey, smooth when young, with vertical fissures (particularly at the trunk base) at maturity, with scattered (3–) 7–11 (–14) mm long and (3–) 7–11 (–14) mm wide lenticels. Twigs

HERBARIUM MUSEI REGIONALIS BOHEMIAE MERIDIONALIS
ČESKÉ BUDĚJOVICE

Flora: Bohemia centralis

HOLOTYPUS!
No. 65274a

Sorbus barrandienica P. Vít, M. Lepší et P. Lepší

Habitat:
Distr. Beroun, pagus Srbsko (6050b): in summo collis Doutnáč, in querceto, solo calcareo; 430 m s. m., 49°57'23.5''N, 14°9'9.5''E; disperse.

Die: 2. 8. 2007

Legit: Martin Lepší

Fig. 6. – Holotype of *Sorbus barrandienica* P. Vít, M. Lepší et P. Lepší.

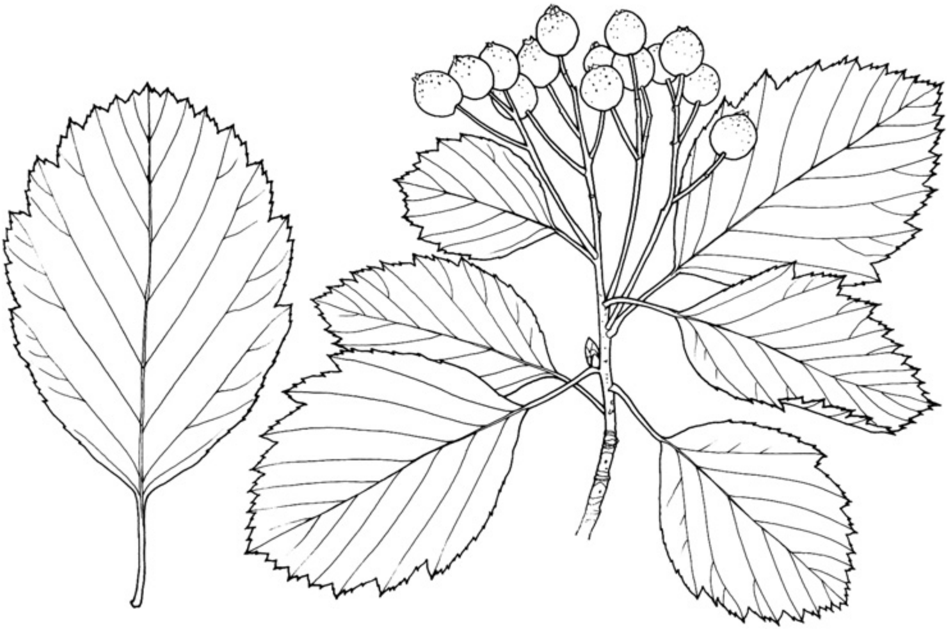

Fig. 7. – *Sorbus barrandienica*: leaf from the middle part of short sterile shoot (left), short fructiferous shoot (right). Drawing by A. Skoumalová.

Fig. 8. – Sterile shoots of *Sorbus barrandienica* growing at Doutnáč hill (photograph taken by P. Lepší 2009).

brownish-grey; young shoots brown, sparsely tomentose when young and almost glabrous at maturity, with elliptical or subrotund pale brown to ochraceous lenticels. Buds 7–14 mm long and 3–6 mm wide, narrowly ovoid to turbinate; scales green, with narrow brown sparsely tomentose margins. Leaves (of short fertile shoots) simple; laminas more or less elliptical, more or less flat, somewhat glossy, dark green above, yellowish-greyish-green beneath, usually flat at margins, more or less rounded acute at apex, usually cuneate rarely broadly cuneate and partly serrate at base, almost glabrous on upper surface, evenly tomentose on lower surface, (8.1–) 8.8–10.3 (–11.6) cm long and (5.4–) 6.7–7.4 (–8.9) cm wide, widest at (16–) 29–42 (–64)% of the lamina length (from the tip), regularly lobed (double serrate apically); lobes serrate or doubly serrate with sharply acuminate teeth terminating the main veins, other teeth smaller, acuminate; sides of lobes more or less arcuate; the third lobe (from the base) (0.95–) 1.15–1.35 (–1.80) cm broad; incision between the second and the third lobe (0.40–) 0.45–0.6 (–0.75) cm; lobes broader than 1 cm (2–) 3–4 on each side; main veins terminating in lobes or teeth (7–) 8 (–9) on each side; petioles (1.9–) 2.1–2.4 (–2.7) cm long, more or less tomentose. Inflorescences with (44–) 50–60 (–66) flowers, (7–) 8–9 (–10) cm in diameter, convex; branchlets more or less tomentose. Hypanthium turbinate, tomentose. Sepals (2.3–) 2.5–3.5 (–3.8) mm long and (2.7–) 2.8–3.0 (–3.2) mm wide, triangular, acuminate or acute, densely tomentose on both surfaces, patent, reclinate after anthesis, persistent, dry, erect. Petals (6.1–) 6.2–6.9 (–7.5) mm long and (4.4–) 4.5–4.9 (–5.2) mm wide, broadly ovate to broadly elliptical, concave, whitish, patent, sparsely hirsute at base of upper surface, with a short claw. Stamens ca 20; filaments whitish; anthers pale yellow, (1.0–) 1.2–1.3 (–1.5) mm long. Ovary semi-inferior. Styles 2 (–3), greenish-cream, (3.5–) 3.7–3.9 (–4.0) mm long, hairy at the base, connate up to (16–) 29–42 (–57)%. Stigma greenish-cream, more or less flat, (0.6–) 0.7 (–0.8) mm wide. Fruits (11.5–) 12.0–13.0 (–14.0) mm long and (11.0–) 12.0–12.5 (–14.0) mm wide, subglobose, orange to orange-red at maturity, glabrous or almost glabrous, glossy, with (4–) 16–32 (–36) ochraceous lenticels per 0.25 cm^2, mesocarp heterogeneous; endocarp cartilaginous. Seeds fuscous. Somatic chromosome number 2n = 51 (triploid). Reproduction tentatively apomictic. Flowering V.

There is also a pen drawing of a flowering shoot in Kovanda (1984).

Diagnostic characters

Leaf laminas are more or less elliptical, (8.1–) 8.8–10.3 (–11.6) cm long and (5.4–) 6.7–7.4 (–8.9) cm wide, more or less rounded acute at apex, usually cuneate, rarely broadly cuneate at base, shallowly lobed; incision between the second and the third lobe terminating the main veins (0.4–) 0.45–0.6 (–0.75) cm long, teeth or lobe terminating the main veins sharply acuminate. Anthers are pale yellow. Styles connate up to (16–) 29–42 (–57)% of their length. Fruits are subglobose, orange to orange-red at maturity.

Etymology

The name "*barrandienica*" derives from the Barrandien, a geologically and paleontologically conspicuous region located between Prague and Pilsen. This species is recorded growing on the Bohemian Karst, which is known as the most significant part of the Barrandien region. The authors propose the epithet "barrandienský" for the Czech name.

Ecology

Sorbus barrandienica occurs mainly on base-rich soils that develop on limestone. It occurs most frequently on the summits of hills, usually in thermophilous open forests or woody margins of dry grassland, and exceptionally in dry grassland, thermophilous scrub or rocks. In most cases, it grows in thermophilous and mesophilous oak-hornbeam forests (*Primulo veris-Carpinetum* and *Melampyro nemorosi-Carpinetum*) and in transition vegetation between these communities. It is also recorded in basiphilous thermophilous oak forests (*Quercion pubescenti-petraeae*) and their mesophilous derivatives. On one occasion, it was recorded in an acidophilous thermophilous oak forest (*Sorbo torminalis-Quercetum*). In the undergrowth of forests, it is very often sterile and does not produce fruits. When it is overshadowed by taller trees, it usually dies. It is recorded on slopes of all aspects save for eastern-facing slopes. Most localities are situated on south and southwest slopes. It does not occur in man-made biotopes. The species grows sympatrically with *S. danubialis*, *S. aria* s.l. and *S. torminalis* at most localities. *Sorbus danubialis* and *S. aria* s.l. are a little more heliophilous and xerothermophilous, while *S. torminalis* is a more mesophilous species.

Geographical distribution

Sorbus barrandienica was recorded at 10 localities in the Bohemian Karst located between Prague and Beroun (Central Bohemia). The centre of its current distribution is located close to Doutnáč hill between the villages of Srbsko and Bubovice (localities 3, 4, 5, 7). This species is not abundant and is represented by small populations in this area. At other localities there are only a few scattered individuals (localities 2, 6, 8 and 9) or the species has not been seen recently (locality 1, 10). The distance between localities that are furthest apart is ca 8 km. The easternmost locality is close to Karlštejn, both the northernmost and westernmost close to the village of Svatý Jan pod Skalou and the southernmost at a very isolated locality located on Mramor hill at the village of Liteň (Fig. 5). *Sorbus barrandienica* is recorded in five quadrants (6050b, d; 6051a, c; 6151a) of the Central European mapping grid (Ehrendorfer & Hamann 1965). The first record of this species is that of V. Krajina in 1926 near Svatý Jan pod Skalou (PRC). These localities are situated in the colline vegetation belt in the phytogeographical district of Český kras (Bohemian Karst) (Skalický 1988). This species grows in a warm and moderately warm climatic region (Quitt 1971) with a mean annual temperature of about 7–9 °C and mean annual precipitation of 500–600 mm (Tolasz et al. 2007). Its altitudinal range spans from 340 m a.s.l. (Plešivec hill) to 450 m a.s.l. (Mramor hill).

Herbarium specimens and records:

Czech Republic. Central Bohemia, Bohemian Karst: 1. Svatý Jan pod Skalou (49°58'10.2"N, 14°08'04.3"E): Karlštejn, Svatý Ivan (leg. Vladimír Krajina 1. 5. 1926, PRC). – Svatý Jan pod Skalou – rocks above the monastery (leg. Štěpánková 4. 6. 1962, CB). The last record for this locality was in 1985: the summit area of U Kříže hill, near Svatý Jan pod Skalou village, 396 m a.s.l. (no specimen available) (Jankun & Kovanda 1988). A locality with unconfirmed occurrence. **2. Vysoká stráň hill:** Svatý Jan pod Skalou, Vysoká stráň hill, ca 950 m NW of the summit of Doutnáč hill, in a thermophilous oak forest, 6050b, 49°57'47.1"N, 14°08'38.0"E, 390 m a.s.l., 2 fertile and 1 sterile individual (leg. ML & Karel Boublík 28. 7. 2007, CB 65276). The first record for this locality was in 1986: the summit area of Vysoká stráň hill, near Hostim village, 435 m a.s.l. (no specimen available) (Jankun & Kovanda 1988). **3. Paní hora hill:** In colle Paní hora prope pagum Bubovice haud procul ab oppido Beroun, solo calcareo, alt. 410 m (leg. M. Kovanda 23. 6. 1964, PRA). – Bubovice, the summit area of Paní hora hill, the scrubby margins of dry grassland, scattered, 6050b: 49°57'43.1"N, 14°09'52.3"E, 410 m a.s.l. (leg. ML & PL 19. 6. 2009, CB 71600), 49°57'43.9"N, 14°09'51.3"E, 410 m a.s.l. (leg. PL 19. 9. 2009, CB 71606). **4. Mokrý vrch hill:** Karlštejn, forester's lodge N 5, Mokryj verch [= Mokrý vrch hill] (leg. B. Augstová 6. 6. 1957, PR 5900946; 24. 5. 1958, PR 590377). – Bubovice, SW slopes of Mokrý vrch hill, the woody margins of grassland, 6050b, 49°57'22.2"N, 14°09'44.2"E, 390 m a.s.l., ca 10 individuals (leg. ML 5. 5. 2009, CB 71585). – Bubovice, W slopes of Mokrý vrch hill, the undergrowth of an oak-hornbeam forest, 6050b, 49°57'24.3"N, 14°09'32.5"E, 380 m a.s.l., 1 sterile individual (leg. ML 5. 5. 2009, CB 71586). – Bubovice, ca 200 m SE of the summit of Mokrý hill, the undergrowth of an oak-hornbeam forest, 6051a, 49°57'22.6"N, 14°10'06.9"E, 420 m a.s.l., 2 old dying individuals (leg. ML 10. 5. 2009, CB 71587). – Bubovice, Mokrý vrch hill, ca 0.6 km WNW of the centre of the Malá Amerika quarry, along a forest road, 6051a, 49°57'17"N, 14°10'02"E, 400 m a.s.l. (leg. PL 20. 6. 2009, CB 71602). This locality probably includes also Kovanda's record: the forest margin in the shallow valley ca 0.8 km NW of the Amerika quarry, 300 m a.s.l. (Kovanda 1999). **5. Doutnáč hill:** Doutnáč hill by Srbsko village (sine coll. IX. 1935, PR 174743). – Distr. Beroun, in nemore ad declivia occid.-merid. montis Doutnáč supra vic. Srbsko, 370 m s.m., No 10868 (leg. Domin & Dostál 28. 6. 1939, PRC). – Beroun: in nemore ad declivia occ.-merid. montis Doutnáč supra vic. Srbsko, 370 m s.m. (leg. Domin & Dostál 28. 6. 1939, PRC). – Central Bohemia, Bohemian Karst, Bubovice, NE slopes of Doutnáč hill, above the valley at an altitude of 350 m; the margin of an open forest and stony steppe, S slope orientation (leg. R. Businský 5. 6. 1977, ROZ 31764-31772). – Doutnáč hill (leg. M. Kovanda 3. 6. 1980, October 1980, 26. 5. 1982, PRA). – Srbsko, the summit area of Doutnáč hill, an oak forest, 6050b, 49°57'23.5"N, 14°09'09.5"E, 430 m a.s.l., ca 10 individuals (leg. ML 2. 8. 2007, CB 65274, HOLOTYPE; PRC 65274/a, ISOTYPE). Some specimens listed in Kovanda (1984) (i.e. in dumetis in clivo austr. collies Doutnáč prope pagum Srbsko, leg. M. Kovanda 1963 PR; in dumetis in summo collis Doutnáč prope pagum Srbsko, leg. M. Kovanda 1964 PR, 1965 PR) are probably lost. **6. Boubová hill:** Svatý Jan pod Skalou, the SW slope of Boubová hill, 400-410 m a.s.l. [not. M. Kovanda (Kovanda 1999)]. – Boubová hill, ca 0.3 km WSW of the summit, the margin of a forest road in an oak-hornbeam forest, 6050b, 49°57'11.9"N, 14°08'17.9"E, 400 m a.s.l., one ca 0.75 m high juvenile individual (not. 19. 6. 2009 J. Mottl, ML & PL). No specimen from this locality is available. **7. Velká hora hill:** Srbsko, W slopes of Velká hora hill, ca 200 m SW of the summit, in thermophilous scrub, 6050d, 49°56'58.6"N, 14°09'24.4"E, 420 m a.s.l., 3 juvenile individuals (leg. ML 4. 7. 2009, CB 71603). – Srbsko, ca 80 m SW of the summit of Velká hora hill, near the margin of the summit plateau, the margin of a forest gap, 6050b, 49°57'01.7"N, 14°09'28.2"E, 420 m a.s.l., one ca 6 m high individual (leg. ML 16. 7. 2009, CB 71601). – Srbsko, W slopes of Velká hora hill, ca 250 m W of the summit, in thermophilous oak forest, 6050b, 49°57'03.7"N, 14°09'18.6"E, 350 m a.s.l., one ca 1.5 m high juvenile individual (not. J. Mottl 2. 8. 2009, leg. ML 29. 10. 2009, CB 71604). A new locality. **8. Haknová hill:** Karlštejn, S slopes of Haknová hill, near the summit, a thermophilous oak forest, 6051c: 49°56'15.7"N, 14°11'55.7"E, 410 m a.s.l., 1 small tree (leg. PL & ML 10. 5. 2009, CB 71588), 49°56'15.8"N, 14°11'55.9"E, 410 m a.s.l., 1 small tree (leg. PL & ML 10. 5. 2009, CB 71589). – Karlštejn, ca 100 m ENE of the summit of the Haknová hill, 6051c, 49°56'17.9"N, 14°12'01.0"E, 420 m a.s.l., one overshadowed ca 4 m high individual (leg. PL & ML 10. 5. 2009, CB 71599). The first record for this locality is 1986: the summit area of Haknová hill near Karlštejn, 402 m a.s.l. (no specimen available) (Jankun & Kovanda 1988). **9. Plešivec hill:** Plešivec hill (leg. M. Kovanda 16. 10. 1985, PRA). – Karlštejn, ca 120 m SE of the summit of Plešivec hill, the margin of steppe, 6051c, 49°56'04.2"N, 14°11'24.5"E, 340 m a.s.l., one overshadowed ca 3 m high individual (leg. ML & PL 10. 5. 2009, CB 71598). **10. Mramor hill** (49°53'54.1"N, 14°07'43.3"E): Beroun: in nemore ad declivia collis Mramor prope pag. Měňany et Liteň, 450 m s.m., s. calcareo (leg. Domin & Dostál 2. 8. 1939, PRC). The specimens listed in Kovanda (1984) (i.e. in nemore in clivo septentr. collis Mramor prope pagum Liteň, leg. M. Kovanda 1980, 1981 PR) are probably lost and are the last records for this locality. A locality with unconfirmed occurrence.

Poorly localized specimens: Karlštejn (leg. M. Řezáč 2001, ROZ).

Herbarium specimens and records not confirmed

In 2005 (Vít 2006) and 2009, we repeatedly failed to confirm the two records cited for *S. eximia* by Jankun & Kovanda (1988) and Kovanda (1999) listed below (herbarium specimen not cited, see below). Considering the rather poor delimitation of these localities, we cannot rule out that the species was overlooked and is still present there. The distribution pattern of both species indicates that these records refer rather to *S. barrandienica* than *S. eximia*, but a field observation is needed to confirm this hypothesis. The specimen collected by Hostim and mentioned below, which Kovanda (1984) referred to as *S. eximia*, we find impossible to identify with certainty. It consists of a sterile, probably epicormic shoot with lobed leaves with a greyish indumentum on the abaxial surface. Lobes are characteristic of hybrid *Sorbus* species, but *S. aria* s.l. can also have exceptionally lobed leaves, particularly on long sterile shoots. A greyish indumentum without any yellowish tinge is typical of *S. aria* s.l. A search carried out by us in the vicinity of the village in 2007 yielded many records of *S. aria* s.l., but no hybrid was recorded there.

Herbarium specimens and records:

Unconfirmed records: 1. Along the road from Hostim to Bubovice, 1 km from Bubovice, 350 m a.s.l. (Jankun & Kovanda 1988). **2.** The surroundings of the Králova studně spring (Kovanda 1999).
Uncertain determination: Böhmen, gehänge bei Hostín [= Hostim], Kalk (leg. Beck 21. 8. 1918, PRC).

Phenotypic variation and species-specific characters

Sorbus eximia and *S. barrandienica* populations are fertile. The plants produce fully developed seeds and are morphologically homogeneous both in vegetative and generative characters. There are no records based on our field observations of morphologically intermediate types between the species (they do not occur at the same localities). The taxa belong to the *S. latifolia* aggregate (parental combination *S. aria* s.l. × *S. torminalis*). The *S. aria* group is represented by *S. danubialis* and *Sorbus aria* s.l. in this region, and both of these taxa (along with *S. torminalis*) often occur sympatrically with the species studied. Plants intermediate between the hybrid species and their putative parents have not been observed. For morphological differences between *S. danubialis*, *S. aria* s.l. and the two hybrid species, see the key in Appendix 1. *Sorbus torminalis* is not included in the key because *S. eximia* and *S. barrandienica* are apparently closer to the *S. aria* group. The species studied differ from other Bohemian members of the *S. latifolia* agg. (*S. albensis*, *S. bohemica*, *S. gemella*, *S. rhodanthera*, *S. portae-bohemicae* and *S. milensis*) in having paler (orange to orange-red) fruits and shallowly lobed leaves. All Bohemian species except for *S. gemella* have darker (orange-red) fruits. *Sorbus gemella* differs in having rhomboidal and more deeply incised laminas. In *S. eximia* the leaves often have cochleariform lamina, which is a unique character for taxa of *Sorbus* occurring in the Czech Republic.

Chromosome variation and ploidy level of S. eximia

Sorbus eximia is cited as an example of a rare diploid apomictic species in several publications (Campbell & Dickinson 1990, Campbell et al. 1991, Nelson-Jones et al. 2002, Meyer et al. 2005, Dickinson et al. 2007, Rich et al. 2010). Our investigations have revealed that somatic cells of *S. eximia* and *S. barrandienica* have a triploid chromosome number ($2n = 3x = 51$). The diploid number previously reported for *S. eximia* (Jankun & Kovanda 1988) was not confirmed in the current study, not even for the populations cited by Kovanda (Koda hill near Srbsko; Jankun & Kovanda 1988). Screening the DNA ploidy levels of *S. eximia* and *S. barrandienica* using DAPI flow cytometry also did not detect any intraspecific variation. Observed sample/standard ratio for *S. eximia* was 0.60 (average CV of sample: 3.04 and standard: 1.66) and for *S. barrandienica* 0.60 (average CV of sample: 3.67 and standard: 2.35). Our recent study indicates the existence of only tetraploid cytotypes in the *S. aria* agg. in the Bohemian Karst (Lepší et al. in prep.), thus occurence of diploid *S. eximia* is improbable. It is therefore concluded that both species studied are triploids and the existence of diploids or tetraploids as reported by Kovanda (1984) and Jankun & Kovanda (1988) must be regarded as dubious. Other hybrid species of the *S. latifolia* group in Bohemia (Jankun & Kovanda 1987, Lepší et al. 2008, 2009, P. Vít, unpubl.) also have the triploid number of chromosomes. The diploid chromosome number has thus so far only been reported with certainty for sexual species of *Sorbus*.

Genetic variation

Sorbus eximia and *S. barrandienica* showed minimal intra-specific genetic variation at seven nuclear microsatellite loci, indicating a monotopic origin (i.e., each species is a single evolutionary lineage). This phenomenon is common in several other agamospermous *Sorbus* taxa occurring in the Czech Republic (e.g., *S. albensis*, *S. portae-bohemicae*, *S. rhodanthera* and *S. milensis*; Lepší et al. 2008, 2009, P. Vít et al., unpubl.). While intra-specific variation was low, inter-specific differentiation is considerable as both of these species have distinct microsatellite patterns. Prevailing fragment length of each of the loci analysed and average gene diversity are presented in Table 2. The species differ from one another in six of the seven loci analysed. Average gene diversity of hybrid species is considerably (about tenfold) lower than that of species reproducing sexually (e.g. *S. torminalis* or *S. aria* s. str.; Vít 2006). This observation supports the independent status of each of the endemic *Sorbus* species as unique evolutionary units. The predominant, if not sole mode of reproduction of the taxa studied, which is inferred from the low morphological and genetic variation, is probably apomixis. These observations are consistent with the results for several other apomictic *Sorbus* taxa of hybrid origin (Liljefors 1953, Jankun & Kovanda 1986, 1987, 1988, Meyer et al. 2005).

Table 2. – Fragment length of each microsatellite loci (in bp) and average gene diversity over all loci (AGD) for each *Sorbus* species.

Taxon	N	Locus Mss1	Locus CH01H10	Locus Mss6	Locus CH02D11	Locus Ms14	Locus Mss5	Locus Ms6g	AGD	S.E.
S. eximia	10	172	78	254	120, 144, 178	128	112, 124	130	0.002405	0.003011
	2	172	78, 82	254	120, 144, 178	128	112, 124	130		
S. barrandienica	9	156	78	250	120, 144, 168	120	112, 124	126	0.008219	0.008045
	1	152	78	250	120, 144, 168	120	112, 124	126		

Morphometric analyses

Sorbus eximia and *S. barrandienica* were well separated in the canonical discriminant analysis (results not shown) from other Bohemian *Sorbus* species of the *S. latifolia* group (for details see Vít 2006, p. 55–61). In separate analysis of *S. eximia* and *S. barrandienica* (see Fig. 9), the species were also well separated. The incision between the 2nd and 3rd lobe of the leaf lamina and calyx length were the variables most tightly correlated with the first discriminant axis. When all of the characters measured are included, 62 (96.87%) of the 64 specimens of *S. eximia* and *S. barrandienica* tested were correctly classified in

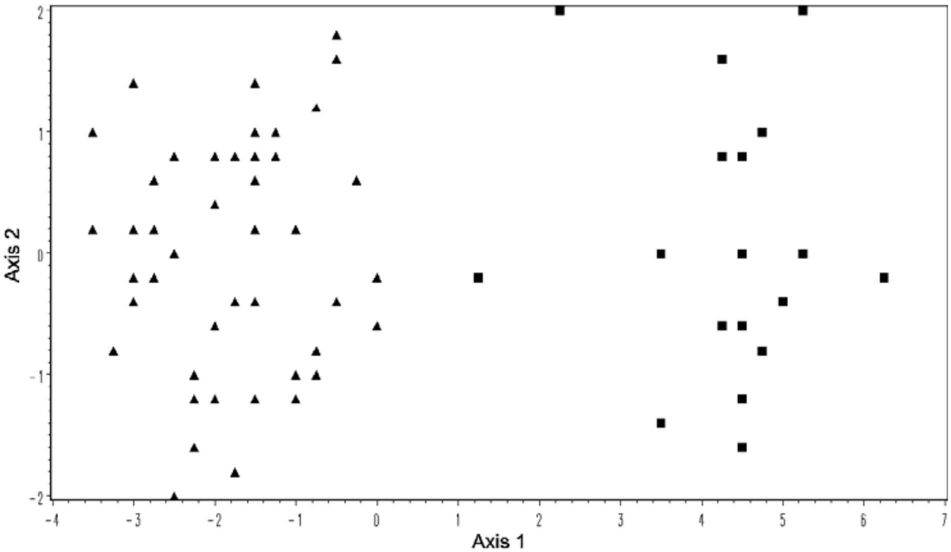

Fig. 9. – Canonical discriminant analysis of *Sorbus eximia* ▲ and *S. barrandienica* ■ using a morphometric data set of 17 characters.

a classificatory discriminant analysis (data not shown). The incorrectly classified samples may be a result of the phenotypic variation and/or problems of standardising sampling.

Elliptic Fourier analysis of leaf laminas

While descriptive morphometrics separated the two species on the basis of quantitative characters, an elliptic Fourier analysis allowed the separation of the two species by using the shape of the leaf lamina as a diagnostic character. Principal component analysis (PCA) performed on standardized Fourier coefficients revealed distinct differences between the species studied (Fig. 10). A morphological shape trend associated with the first principal component separates the two species based on the overall shape of the lamina. *S. eximia* has a broadly ovate to broadly elliptical leaf lamina, while that of *S. barrandienica* is more or less elliptical. Variation along the second (data not shown) and third axis demonstrated a tendency towards differentiation in the curve of the lamina base and apex. In *S. barrandienica* it tends to be rounded acute at the apex and cuneate at the base, while in *S. eximia* the apex is more or less broadly rounded acute to obtuse and the base rounded or broadly cuneate. The results of these analyses confirmed our field observations. No clear pattern was observed along the other PCA axes (data not shown). In total, seven PCA axes were found to significantly improve the discriminant power of the CVA analysis during forward selection in Canoco. A cross-validated discriminant analysis was performed on the principal component scores of these seven axes. The discriminant analysis resulted in an incorrect classification in eight of a total 194 cases (6 individuals of *S. eximia* were assigned to *S. barrandienica* and 2 individuals of *S. barrandienica* to *S. eximia*). These incorrectly classified samples were leaves untypically developed due to phenotypic varia-

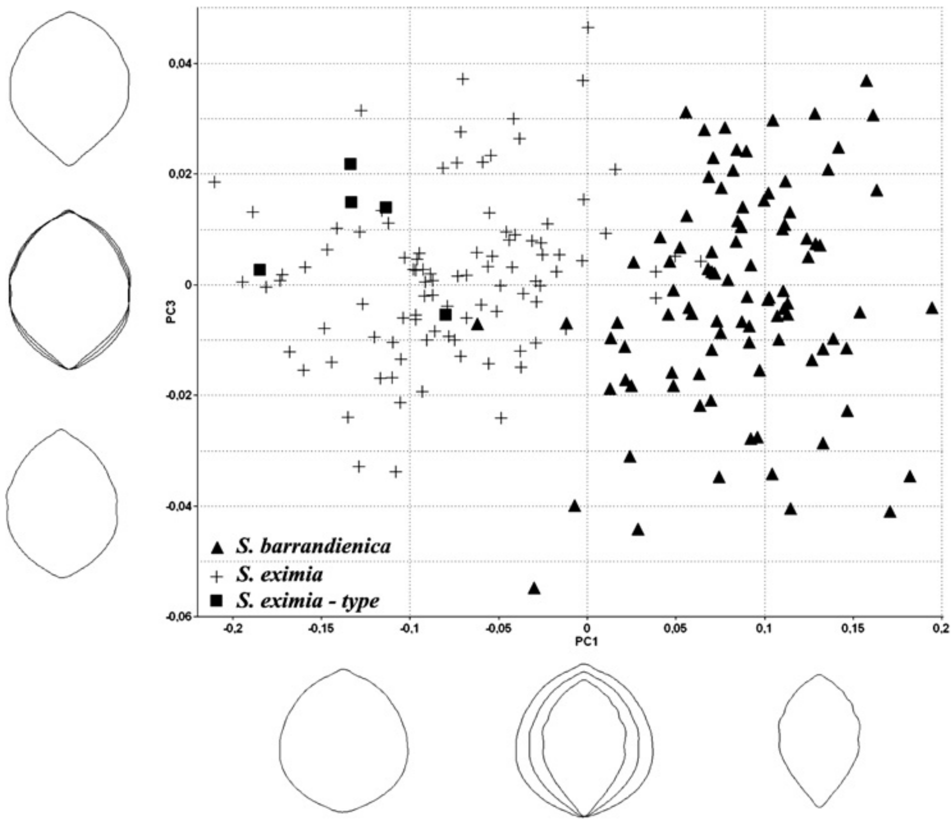

Fig. 10. – PCA of Fourier coefficients describing the total leaf lamina shape of *S. eximia* and *S. barrandienica*. The first and third ordination axes are displayed, which explain 81.8% and 2.5% of the overall variation, respectively. Reconstructed contours corresponding to the –2 and +2 SD positions on both axes are visualized along the particular axes. In the middle, these two contours are overlapped with the mean leaf shape (corresponding to the [0.0] point of the plot).

tion in this species (too overshadowed or exposed plants). All 5 leaves from the type specimen of *S. eximia* were determined as *S. eximia*. Neither the relative position nor the shape of the laminar lobes contributed to the discrimination of these two species, even when the shape of the lobes was more accurately described by using a greater (40) number of harmonics (data not shown).

Conservation status

All the specimens of the two taxa studied are found within the area of the Bohemian Karst protected landscape area and are (except the locality of *S. barrandienica* at Mramor hill) part of small-scale protected areas (in particular, Koda and Karlštejn national nature reserves, Kotýz national nature monument and Kobyla nature reserve). Despite this, the protection of the two endemic species is insufficient. The main threat stems from the cessation of traditional forest management, which previously maintained open forests stands. The shady conditions that prevail in recent so-called tall forests are unfavourable for the long-term survival and regular reproduction of light-demanding *Sorbus* species. The general expansion of woods (especially of *Fraxinus excelsior*) into open (rocky and steppe) habitats represents another serious threat to these endemics.

Even before the taxonomic revision presented here, *Sorbus eximia* was regarded as a strongly endangered species (Holub & Procházka 2000). The new species *Sorbus barrandienica* should be included among the critically endangered plants of the Czech flora (C1; sensu Holub & Procházka 2000), as there are few individuals, frequent occurrence of old or dying trees and lack of juveniles at most localities. *Sorbus eximia* is considered strongly endangered (category C2) because there are considerably larger populations with lots of juveniles at its localities. Moreover, this species is able to spread into man-made non-relic biotopes, e.g. into abandoned quarries or pine plantations. Such habitats are now common in the Bohemian Karst. On the other hand, it is only recorded at three localities and the biggest one, Koda hill, is significantly affected by the spread of *Fraxinus excelsior*. Both endemic species should also be added to the list of species protected by law. According to the IUCN (2001), *S. eximia* and *S. barrandienica* rank among critically endangered species [status criteria B2b (iii) and B2b (iii,iv,v);C2a (i), respectively]. Particular attention should be paid to protecting these species in the future. Appropriate forest management (which would facilitate reproduction of these endemics) should be implemented at selected localities. Three localities are recommended: Koda hill for protection of *S. eximia* and Paní hora hill and/or Doutnáč hill for *S. barrandienica*. Supposed parental species occurring at the same localities as the endemics should also be included in the management plan, since they may generate new taxonomic diversity (by hybridization and introgression) in the future and thus play an important role in the ongoing evolutionary processes (cf. Ennos et al. 2005).

Acknowledgements

We are grateful to J. Zázvorka for valuable comments on earlier drafts of the manuscript, J. Mottl, T. Tichý (Administration of the Český kras Protected Landscape Area) for guidance in the field and J. Mottl for information about new localities of the taxa under study. We thank V. Jarolímová for her help with chromosome counting, K. Boublík for help with elaboration of the phytosociology of the taxa, F. Kolář for help with cross-validated analysis, J. Velebil for information about the cultivation of *S. eximia* by Řevnice, and M. Ducháček, J. Hadinec and L. Kirschnerová for technical and herbarium assistance. The Herbarium of the Department of Botany (PRC), in particular J. Štěpánek, is acknowledged for permission to use the photograph of the type specimen of *S. eximia*. F. Rooks kindly improved our English. The study was supported by grant 138/2010/P from the Grant Agency of the University of South Bohemia, Institutional research support MSM-6007665801 from the Czech Ministry of Education and project AV0Z60050516 from the Academy of Sciences of the Czech Republic.

Souhrn

V příspěvku je popsán nový apomiktický triploidní ($2n = 3x = 51$) druh jeřábu *Sorbus barrandienica* P. Vít, M. Lepší et P. Lepší (jeřáb barrandienský), náležející do skupiny *S. latifolia* agg. (rodičovská kombinace *S. aria* s.l. × *S. torminalis*). Byl rozlišen na základě taxonomické a chorologické revize jeřábu krasového (*Sorbus eximia*), hybridogenního druhu stejné rodičovské kombinace, který byl popsán v roce 1984 z Českého krasu (Kovanda 1984). Pomocí moderních biosystematických metod byly v rámci *S. eximia* rozlišeny dvě apomiktické linie, lišící se zřetelně morfologicky a geneticky. Průzkum ploidie pomocí průtokové cytometrie ukázal, že oba rozlišené taxony jsou triploidní. To je v rozporu s dřívějšími studiemi, kde byl u *S. eximia* zjištěn diploidní a tetraploidní stupeň

(Jankun & Kovanda 1988). Dokonce byla na diploidní úrovni pozorována i apomixie, jež je dodnes udávaná pouze v jednom nejistém případě u *S. subfusca*. Naše výsledky tyto závěry vyvracejí. Studium typového materiálu odhalilo, že jméno *S. eximia* se vztahuje k rostlinám na lokalitě v NPR Koda, populace udávané ze zbylých lokalit v Českém krasu náleží novému, zde popsanému druhu *S. barrandienica*. Terénním průzkumem bylo dodatečně zjištěno, že *S. eximia* roste na 4 lokalitách, z toho jedna vznikla výsadbou. Velikost populace je odhadována na 100 dospělých exemplářů a ca 200 juvenilních jedinců. *S. barrandienica* byl nalezen na 10 lokalitách, z toho dvě historické se nepodařilo potvrdit. Celá populace dnes čítá ca 50 exemplářů. Oba druhy nejčastěji rostou v teplomilných doubravách a dubohabřinách a v lesních lemech suchých trávníků. Vykazují malou genetickou a morfologickou variabilitu a jsou dobře diferencovaní od jeřábů vyskytujících se v Čechách. Nejvíce jsou ohroženy zánikem světlých lesů. *Sorbus barrandienica* navrhujeme zařadit do červeného seznamu taxonů ČR do kategorie kriticky ohrožený druh, *S. eximia* mezi silně ohrožené druhy (Holub & Procházka 2000). Pro přežití druhů je nutné na vybraných lokalitách zavést speciální management, k tomuto účelu doporučujeme lokality Doutnáč nebo Paní hora a Koda. K odlišení společně se vyskytujících jeřábů v Českém krasu poslouží následující klíč (čepel listů musí pocházet ze střední části fertilních brachyblastů):

1a Čepel listů mělce nebo pouze v horní třetině zastřihovaně dvojitě pilovitá (až mělce laločnatá), na rubu šedozelená, plody (korálově) červené **2**
1b Čepel alespoň některých listů laločnatá, na rubu nažloutle šedozelená, plody oranžové až oranžově červené **3**
2a Čepel listů široce eliptická až okrouhlá, mělce dvojitě pilovitá, s plochým okrajem, 6–12 cm dlouhá .... ***S. aria* s.l.**
2b Čepel listů víceméně kosočtverečná až zaokrouhleně kosočtverečná, v horní třetině zastřihovaně dvojitě pilovitá (někdy až mělce laločnatá), se zvlněným okrajem, 4–10 cm dlouhá .... ***S. danubialis***
3a Čepel listů víceméně eliptická, plochá, na bázi klínovitá vzácněji široce klínovitá, mělce laločnatá; zářez mezi druhým a třetím lalokem (0,40–) 0,45–0,60 (–0,75) cm dlouhý, kališní cípy (2,3–) 2,5–3,5 (–3,8) mm dlouhé, plody často delší než široké .... ***S. barrandienica***
3b Čepel listu široce vejčitá až široce eliptická, často lžícovitě prohnutá, na bázi většinou zaokrouhlená nebo široce klínovitá, dvojitě pilovitá až pravidelně mělce laločnatá, zářez mezi druhým a třetím lalokem (0,25–) 0,40 (–0,55) cm dlouhý, kališní cípy (1,7–) 2,1–2,5 (–3,0) mm dlouhé, plody často stejně široké jako dlouhé nebo širší .... ***S. eximia***

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Received 18 February 2011
Revision received 30 May 2011
Accepted 31 May 2011

Appendix 1. – Key for determining the species of the *Sorbus latifolia* agg. and *S. aria* s.l. occurring in the Český kras Karst.

1a Leaf lamina shallowly or coarsely double serrate (to shallowly lobed) distally, greyish-green beneath, fruits red 2
1b Leaf lamina (at least some) shallowly lobed, yellowish-greyish-green beneath, fruits orange to orange-red ... 3
2a Leaf lamina broadly elliptical to rounded, shallowly double serrate, with flat margin, 6–12 cm long .... ***S. aria* s.l.**
2b Leaf lamina more or less rhomboidal to round rhomboidal, coarsely double serrate (to shallowly lobed) distally, with folded margin, 4–10 cm long .... ***S. danubialis***
3a Leaf lamina more or less elliptical, flat, cuneate rarely broadly cuneate at base, shallowly lobed; incision between the second and the third lobe terminating the main veins (0.40–) 0.45–0.60 (–0.75) cm long, sepals (2.3–) 2.5–3.5 (–3.8) mm long, fruits often longer than wide .... ***S. barrandienica***
3b Leaf lamina broadly ovate to broadly elliptical, often cochleariform, usually rounded or broadly cuneate at base, double serrate to regularly shallowly lobed, incision between the second and the third lobe terminating the main veins (0.25–) 0.40 (–0.55) cm long, sepals (1.7–) 2.1–2.5 (–3.0) mm long, fruits often as wide as or wider than long .... ***S. eximia***

Paper IV

Sorbus pauca species nova, the first endemic species of the *Sorbus hybrida* group for the Czech Republic.

Lepší M., Lepší P., Sádlo J., Koutecký P., Vít P. & Petřík P. (2013) Preslia 85: 63–80.

Picture on previous page *Sorbus pauca*, Bezděz (photo by A. Jírová)

Sorbus pauca species nova, the first endemic species of the *Sorbus hybrida* group for the Czech Republic

Sorbus pauca species nova – první endemický druh z okruhu Sorbus hybrida pro Českou republiku

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Lepší M., Lepší P., Sádlo J., Koutecký P., Vít P. & Petřík P. (2013): *Sorbus pauca* species nova, the first endemic species of the *Sorbus hybrida* group for the Czech Republic. – Preslia 85: 63–80.

We describe a newly distinguished apomictic tetraploid (2n = 4x = 68) species *Sorbus pauca* M. Lepší et P. Lepší. We classify this new species as a member of the *Sorbus hybrida* group because we presume that it has originated from a cross between *S. danubialis* and *S. aucuparia*. *Sorbus pauca*, a stenoendemic that occurs on Bezděz and Malý Bezděz hills (Doksy region, northern Bohemia), is the first species of the *S. hybrida* group to be described for the Czech Republic. Multivariate morphometrics and elliptic Fourier analyses reveal that it is distinct from the morphologically close *S. danubialis.* The new taxon is phenotypicaly homogenous, morphologically well separated from the sympatrically occurring *S. danubialis* and European taxa of *S. hybrida* agg. It does not show any karyological variation. Apomixis was detected as the species' sole mode of reproduction. The two known populations of *S. pauca* consist of 14 adult individuals. The species is restricted to rocky grasslands, rocky scrub and open woodlands on rocks with *Festuca pallens* and *Cotoneaster integerrimus*.

Keywords: apomixis, DAPI flow cytometry, geometric morphometrics, hybridization, karyology, multivariate morphometrics, *Rosaceae*, subg. *Soraria*, taxonomy

Introduction

European hybridogenous species of the genus *Sorbus* L. comprise four main species groups, which arose from crosses between polyploid members of the *Sorbus aria* aggregate and five basic diploid *Sorbus* species (Kutzelnigg 1995, Rich et al. 2010). These species groups differ in their morphology, distribution and ecological demands, which are related to the characters of their parental taxa.

The *Sorbus sudetica* group (diploid parent *S. chamaemespilus*) encompasses alpine species that are confined to European mountains. In contrast, the *S. latifolia* group (diploid parent *S. torminalis*) includes thermophilous species, which are absent from mountains and northern parts of Europe. The *Sorbus aria* group (diploid parents *S. aria* s. str. and in southern Europe possibly also *S. umbellata*) consists of many thermophilous species, but it also occurs in Scandinavia and certain mountain areas in Europe. Finally, the *S. hybrida* group (diploid parent *S. aucuparia*) is abundant in northern Europe and European mountains but occurs only rarely in warm regions of central Europe (Kutzelnigg 1995).

In the Czech Republic, the distribution of endemic, hybridogenous *Sorbus* species follows this pattern. Only *S. sudetica*, which occurs at high altitudes in the Krkonoše Mts, is a descendant of *S. chamaemespilus* and an unknown member of the *S. aria* group, both of which are now extinct in this mountain range (Kovanda 1992). Other taxa are confined to lower altitudes. The *Sorbus latifolia* group is the most abundant and the most studied group within the Czech Republic and currently includes 11 taxa (Kubát et al. 2002, Lepší et al. 2008, 2009, Velebil 2012, Vít et al. 2012). According to our unpublished data, their tetraploid parents are *S. danubialis* and a taxonomically unclear member of the *S. aria* group. The *S. aria* group has not yet been adequately examined from a taxonomical perspective and some taxonomic novelties are likely to occur in the lowlands of Moravia.

There are no native species of the *S. hybrida* agg., in the Czech Republic, but two species have been reported as garden escapes: *S austriaca* (Lepší et al. 2011, Pyšek et al. 2012) and *S. mougeotii*, which was initially described by Kovanda (1996) from Prague as *S. quernea* (Lepší et al. 2013). This paper provides a taxonomic evaluation of a unique population of the *S. hybrida* group discovered in the Bezděz hills in 2008 and described here as a new species, *S. pauca*.

Material and methods

Plant material and field work

Samples for morphometric analyses, flow cytometry and herbarium specimens were collected in 2009 and 2011, following the recommendations of Meyer et al. (2005), Rich et al. (2010) and papers published by Lepší et al. (2008, 2009). The two co-occuring species, *S. pauca* and *S. danubialis,*were studied. Flowering and fructiferous parts were collected in mid-May and September, respectively.

Nine relevés with the presence of *S. pauca* were recorded using the Braun-Blanquet approach, located using Garmin eTrex instruments (WGS-84) and stored in the Czech National Phytosociological Database (CNFD) under relevé numbers 203585–203591, 335307–335308 (Chytrý & Rafajová 2003). Furthermore, 78 relevés from the Bezděz hills were added from CNFD, which describe the habitat preferences of both the supposed parental species (*S. aucuparia* and *S. danubialis*). Considering the lengths of the gradient (over 5.5 SD), the unimodal ordination method DCA was chosen to explain variability in species composition of relevés within the ordination space. The analysis was done using CANOCO for Windows 4.5 (Lepš & Šmilauer 2003).

A revision of relevant *Sorbus* material kept in the following herbarium collections was undertaken: BRNM, BRNL, BRNU, CB, CHEB, CHOM, Herbarium of Museum of Ústí nad Labem, HOMP, HR, LIM, LIT, MP, PL, PR, PRA, PRC, ROZ, SOKO, ZMT. For abbreviations of public herbaria, see Holmgren et al. (1990). Species nomenclature was unified according to Kubát et al. (2002) except for *Sorbus* names, which follow Kutzelnigg (1995), otherwise authorities are provided.

Multivariate and elliptic Fourier analyses

Multivariate morphometric and geometric morphometric analyses were used to reveal species-specific characters in two sympatrically occurring species: *S. pauca* (12 individuals) and *S. danubialis* (10 individuals). Only well developed branches of mature individuals were studied. In total, 24 leaves from *S. pauca* and 15 from *S. danubialis* were used for morphometric analyses. The determination of individuals analysed was based on the shape of lobes or main teeth on leaves – *S. pauca* obtuse lobes, *S. danubialis* acute lobes or teeth. A set of 18 quantitative characters was chosen on the basis of published determination keys and floras (e.g. Kutzelnigg 1995, Meyer et al. 2005, Rich et al. 2010), including those used in our previous studies (Lepší et al. 2008, 2009, Vít et al. 2012). The characters are: ANG – angle between the third lateral vein from the laminar base and the midrib, ANT – length of anther, FL – length of fruit, FW – width of fruit, FWFL – ratio width of fruit/length of fruit, INC – incision between the second and the third lobe from the laminar base, length of lamina, LLLW – ratio length of lamina/width of lamina, LOW – width of the third lobe from the laminar base, LW – width of lamina, NL – number of lenticels per 25 mm^2 on fruit, NV – number of lateral laminar veins, PET – length of petiole, PL – length of petals, PW – width of petals, SL – length of sepals, SW – width of sepals, WP – widest width of lamina from the base. Two measures of each character per individual were recorded and the arithmetic mean was calculated and used as the value for the operational unit for an individual in all morphometric analyses.

Pearson correlation coefficients were calculated for pairs of characters for each species and for the whole data set in order to reveal the relationship among characters. It was necessary to exclude laminar length from subsequent analyses because of its high correlation with laminar width ($r > 0.95$). Principal component analyses (PCA) were performed to provide an insight into the overall pattern of morphological variation and show a potential separation of *S. danubialis* and *S. pauca*. Prior to PCA, the data were standardized to have a zero mean and unit standard deviation. Linear discrimination analyses (LDA), which maximize differences between a priori defined groups, were used to test the discriminating power of morphometric characters, following the methodology described by Lepš & Šmilauer (2003) using forward selection of characters with non-parametric Monte Carlo permutation tests (999 permutations; only axes with P-level < 0.05 were considered).

A cross-validated linear discriminant analysis based on probabilities using only characters selected as discriminating variables by the previous analysis was performed in R, version 2.12.2 (R Development Core Team 2011) using the lda function in the MASS package (Venables & Ripley 2002). PCA and LDA were carried out using Canoco (Lepš & Šmilauer 2003). Box-and-whisker plots of selected morphological characters of each species were carried out in Statistica version 9.1 (StatSoft, Inc. 2010). Univariate statistics (minimum, maximum, quartiles) of the quantitative characters of all the individuals of *S. pauca* collected were calculated and used in the description of the species.

Elliptic Fourier analysis was used to find differences in leaf shape of *S. pauca* and *S. danubialis*, based on the method of elliptic Fourier approximation (Kuhl & Giardina 1982) incorporated in the SHAPE 1.2 software package (Iwata & Ukai 2002). This procedure is described in Vít et al. (2012).

Karyology and DNA ploidy level estimation

For the purpose of counting chromosomes, four specimens from Bezděz and Malý Bezděz hills were collected in March 2010 and subsequently analysed using the procedure described in Lepší et al. (2008). DAPI flow cytometry was used to assess DNA ploidy levels (Suda et al. 2006) in *S. pauca* and *S. danubialis*. Bulked samples from 13 individuals of *S. pauca* and 10 of *S. danubialis* were analysed (i.e. three or four individuals simultaneously) following the methods of Lepší et al. (2008).

Mode of reproduction

To determine the mode of reproduction, embryo/endosperm DNA ploidy levels of seeds were analysed using the flow cytometric seed screening method of Matzk et al. (2000). In total, we analysed 40 seeds originating from 13 different individuals. Twelve seeds were analysed individually and then bulked samples of up to five seeds were used. Sample preparation followed the simplified two-step procedure (Doležel et al. 2007). Only the apical part (2–3 mm) of each seed, which contains the embryo, was used for nucleus isolation. The remainder of the seed, which contains mainly cotyledon tissue, was excluded. The apical part was cut up along with the internal standard (*Bellis perennis* leaf tissue) in 0.5 ml of ice-cold Otto I buffer. The suspension was filtered through a 42-μm nylon mesh and incubated for at least 10 minutes at room temperature. After incubation, 1 ml of the staining solution (Otto II buffer supplemented with 2 μl/ml of 2-mercaptoethanol and 4 μg/ml of the DAPI fluorochrome) was added. Samples were run on a Partec PA II flow cytometer after up to 10 minutes of staining and the fluorescence intensity of 5000 particles recorded. Resulting fluorescence histograms were analysed using FloMax 2.6 software (Partec GmbH, Germany) and the ratios between the mean fluorescence of the embryo, the endosperm and the internal standard recorded.

Results

Multivariate morphometric analyses

PCA revealed a distinct morphological difference between *Sorbus pauca* and *S. danubialis* (Fig. 1). The strongest contribution to the morphological distinctiveness of both species (i.e., the most strongly correlated characters with the first component axis) was the width of the lamina (LW), length of petiole (PET), incision between the second and third lobe from the laminar base (INC) and the length of lamina/width of lamina ratio (LLLW).

The LDA analysis also confirmed that these species are morphologically different. No overlap in the canonical scores of the species was detected. A forward selection procedure identified two characters (LLLW and INC) with a significant conditional effect and six other characters with significant marginal effects (LW, ANG – angle between the midrib and the third lateral vein from the laminar base, PET, FWFL – ratio width of fruit/length of fruit, LOW– width of the third lobe from the laminar base and NV – number of lateral veins per leaf). The species were well separated by the values of the two characters LLLW and INC with only a slight overlap in these values (Fig. 2). The cross-validated discriminant analysis using these two characters resulted in correct classification in all cases.

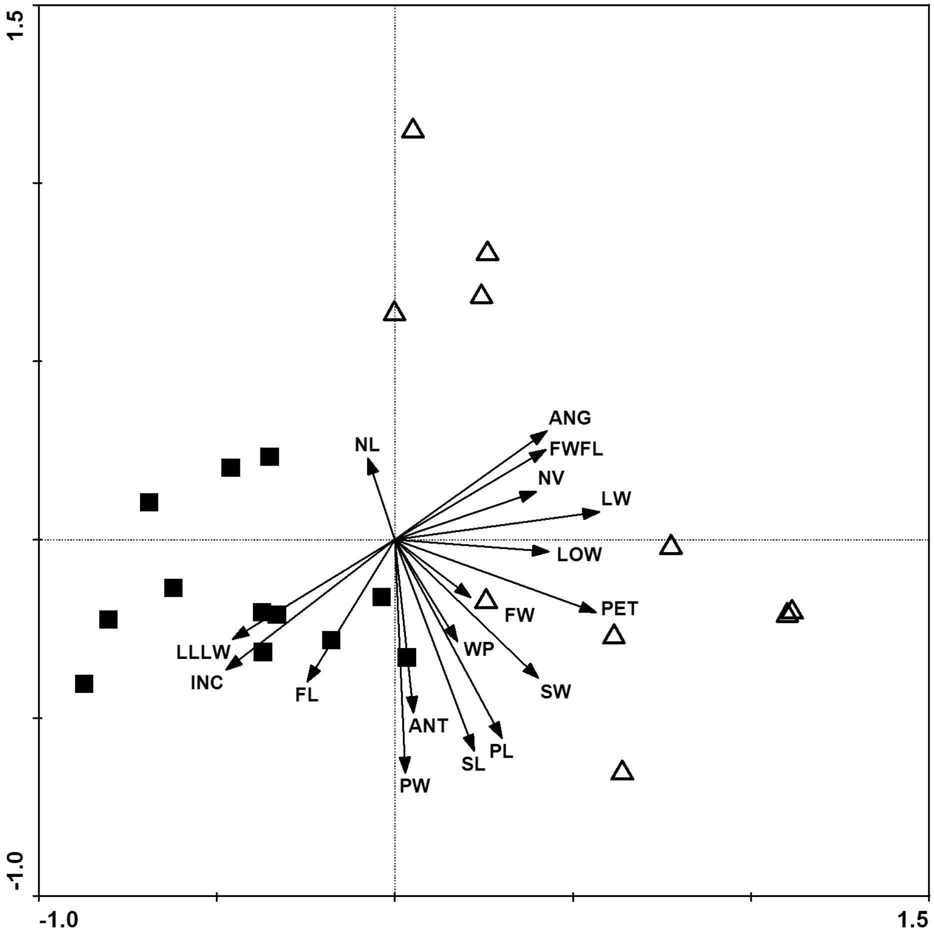

Fig. 1. – PCA of individuals of *Sorbus pauca* and *S. danubialis* using 17 characters. ■ *S. pauca*, △ *S. danubialis*. The first and the second ordination axes are depicted and account for 30.3% and 19.0% of the variation, respectively. See text for character codes.

Elliptic Fourier analysis of leaf laminas

Principal component analysis (PCA) performed on standardized Fourier coefficients revealed distinct differences between the species studies (Fig. 3). A trend in shape associated with the first principal component separates the two species based on the width of the lamina; *S. pauca* has oblong obovate leaves, whereas those of *S. danubialis* are more or less round rhomboidal. Other axes did not facilitate the differentiation between the two taxa (Fig. 3). Only the first two PCA axes were found to improve significantly the discriminant power of the LDA during forward selection. A cross-validated discriminant analysis, which was performed on the principal component scores of the first and second axis, confirmed the classification in all cases.

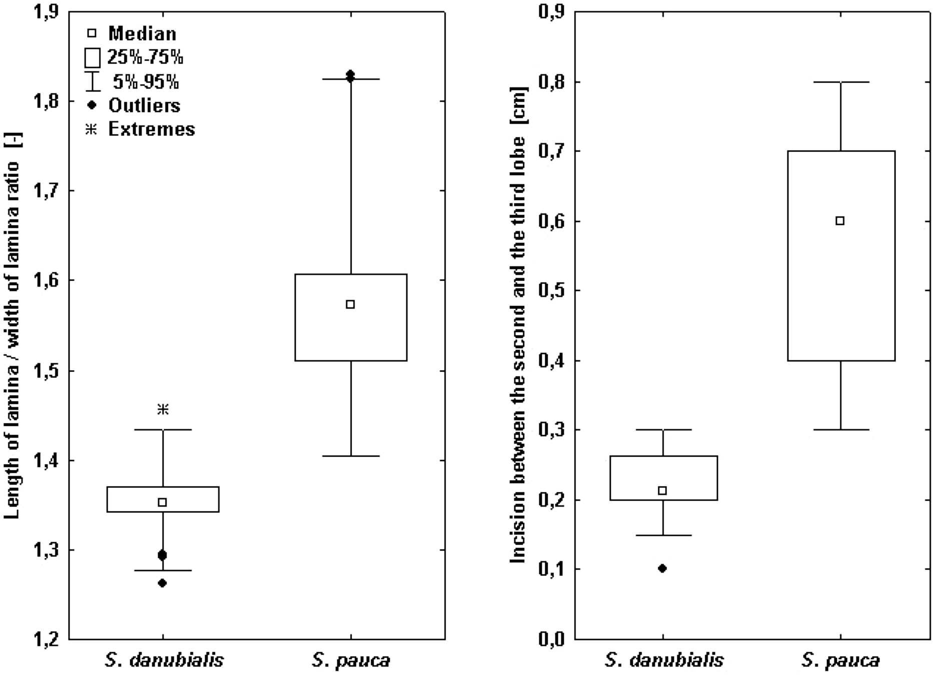

Fig. 2. – Box-and-whisker plots of LLLW (leaf length/width ratio) and INC (incision between the second and the third lobe from the lamina base) characters of *Sorbus danubialis* and *S. pauca*. Only these two characters, which were identified by a forward selection procedure, have significant discriminating power in the linear discriminant analysis.

Chromosome variation and ploidy level

Somatic cells of *S. pauca* have a tetraploid chromosome number (2n = 4x = 68, Fig. 4). No intra-specific variation within *S. pauca* and *S. danubialis* was detected by DAPI flow cytometry and both species are tetraploids. The sample/standard ratio was 0.78 for *S. pauca* (average coefficient of variation for samples: 3.36 and the standard: 2.42) and 0.74 for *S. danubialis* (average CV of samples: 2.77 and standard: 1.82).

Mode of reproduction

The DNA ploidy level of the embryo is tetraploid in all the seeds analysed, the embryo/standard ratio of DAPI fluorescence was 0.78. The endosperm/embryo ratio of DAPI fluorescence was 2.95–3.03, which corresponds closely with the value of 3.00 expected for a 2C (tetraploid) embryo and 6C (dodecaploid) endosperm, most likely consisting of two unreduced maternal chromosome complements and one unreduced paternal chromosome complement. We therefore conclude that *S. pauca* is an apomictic tetraploid with an endosperm formed through pseudogamy via unreduced (tetraploid) pollen.

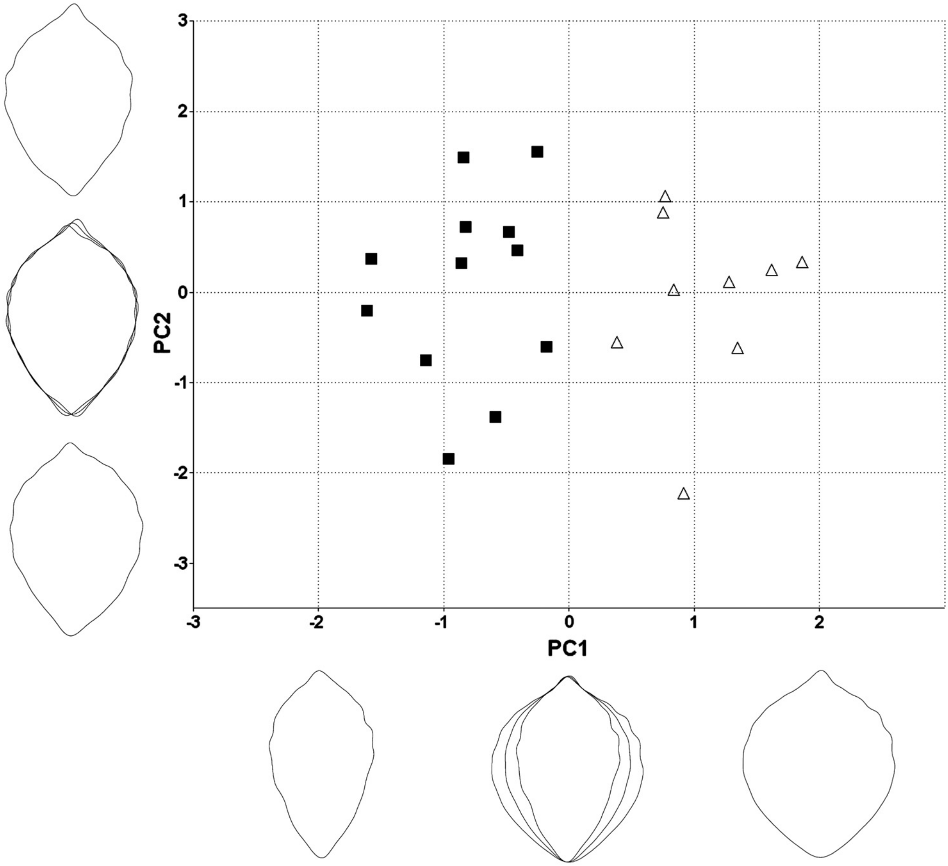

Fig. 3. – PCA of Fourier coefficients describing the total leaf lamina shape of ■ *Sorbus pauca* and △ *S. danubialis*. The first and second ordination axes are displayed and account for 71.1% and 7.6% of the overall variation, respectively. Reconstructed contours corresponding to the –2 and +2 SD positions on both axes are visualized along the axes (the scale of the plot is in SD units). In the middle, these two contours overlap the mean leaf shape (corresponding to the [0.0] point of the plot).

Sorbus pauca M. Lepší et P. Lepší **spec. nova** (Figs 5–7)

Diagnosis: Frutices humiles usque 4 m alti; foliis (in brachyblastis sterilibus) simplicibus, laminis ambitu conspicue polymorphis, i. e. obovatis, oblonge obovatis vel ellipticis et saepe in parte inferiore usque centrali paulo incisis, irregulariter pinnato-lobatis, in parte superiore tantum duplicato-dentatis, margine undulatis, parvis, (62–) 70–76 (–97) mm longis et (38–) 45–50 (–59) mm latis, (1.4–) 1.5–1.6 (–1.8) plo longiores quam latiores, basi cuneatis, apice plus minusve acutis usque acuminatis, subtus griseo-viride tomentosis, lobis parvis, obtusis, variabiles in magnitudine et forma, contingens usque partim coincidens, incisionibus inter secundis et tertis lobis (2–) 4–7 (–10) mm, petiolis (9–) 10–12 (–17) mm longis; fructibus subglobosis, (11–) 12 (–13) mm longis et (12–) 13–14 mm latis, (0.85–) 0.91–0.93 (–0.98) plo longiores quam latiores, maturitate rubris, cum (1–) 2–3 (–5) lenticellis parvis ad 25 mm^2. Numerus chromosomatum tetraploideus 2n = 68. Planta apomicta.

Holotypus: Bohemia septentrionalis, distr. Česká Lípa, pagus Bezděz (5454c): in rupe phonolithica sub cacumine collis Bezděz; 580 m s. m., 50°32'23.3"N, 14°43'18.0"E; raro; frutex ca. 2.5 m altus; 23. 7. 2011 leg. M. Lepší et P. Lepší; CB, No. 79599 (Fig. 5). – Isotypus: PR, 79599a.

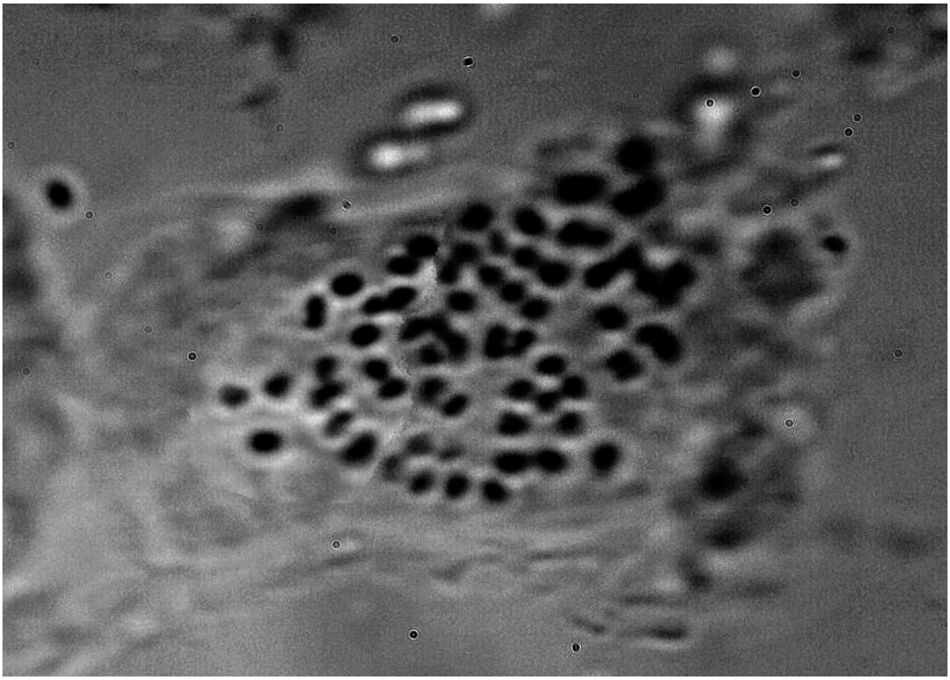

Fig. 4. – Microphotograph of the somatic chromosomes (2n = 4x = 68) of *Sorbus pauca* from Malý Bezděz hill (photo V. Jarolímová).

Description: Shrubs up to 4 m high. Bark grey, with scattered lenticels. Twigs brownish-grey; young shoots brown, sparsely tomentose when young and almost glabrous at maturity, with elliptical or sub-rotund pale brown to ochraceous lenticels. Buds 5.5–9.0 mm long and 3.0–4.5 mm wide, ovoid; scales brownish green, with brown sparsely tomentose margins. Leaves (in the centre of short sterile shoots) simple; laminas conspicuously polymorphic, obovate, oblong-obovate or elliptical, with sides in the lower part often concave, somewhat glossy, dark green above, greyish-green beneath, undulate at margins, more or less acute to acuminate at apex, cuneate and partly serrate at base, almost glabrous on upper surface, evenly tomentose on lower surface, (62–) 70–76 (–97) mm long and (38–) 45–50 (–59) mm wide, (1.4–) 1.5–1.6 (–1.8) times as long as wide, widest at (29–) 33–40 (–47)% of the laminar length (from the tip), irregularly shallowly lobed, double dentate apically with more or less outwardly directed teeth; lobes small, obtuse, often overlapping each other, serrate or doubly serrate with acute to obtuse, outwardly directed teeth terminating the main veins, other teeth usually smaller, acute, forwardly directed; sides of lobes more or less arcuate; the third lobe (from the base) (7–) 8–11 (–14) mm broad; some opposite lobes unequal in size and shape owing to asymmetrically pinnate (curved, forked or even crossed lateral veins); incision between the second and the third lobe (2–) 4–7 (–10) mm; lobes broader than 10 mm (0–) 1–2 (–4) on each side; lateral veins (7–) 9 (–11) on each side, at an angle of (27–) 34–37 (–44)° to midrib at centre of the leaf; petioles (9–) 10–12 (–17) mm long, tomentose. Inflorescences convex; branchlets more or less tomentose. Hypanthium turbinate, tomentose. Sepals (2.4–) 2.9–3.3 (–4.1) mm long and (2.4–)

HERBARIUM MUSEI REGIONALIS BOHEMIAE MERIDIONALIS
ČESKÉ BUDĚJOVICE

Flora: Bohemia septentrionalis

HOLOTYPUS!
No. **CB 79599**

Sorbus pauca M. Lepší et P. Lepší

Habitat

Distr. Česká Lípa, pagus Bezděz (5454c): in rupe phonolithica sub cacumine collis Bezděz; 580 m s. m., 50°32'23.3"N, 14°43'18.0"E; raro; frutex ca. 2.5 m altus.

Die: 23. 7. 2011

Legit: M. Lepší et P. Lepší

Fig. 5. – Holotype of *Sorbus pauca*.

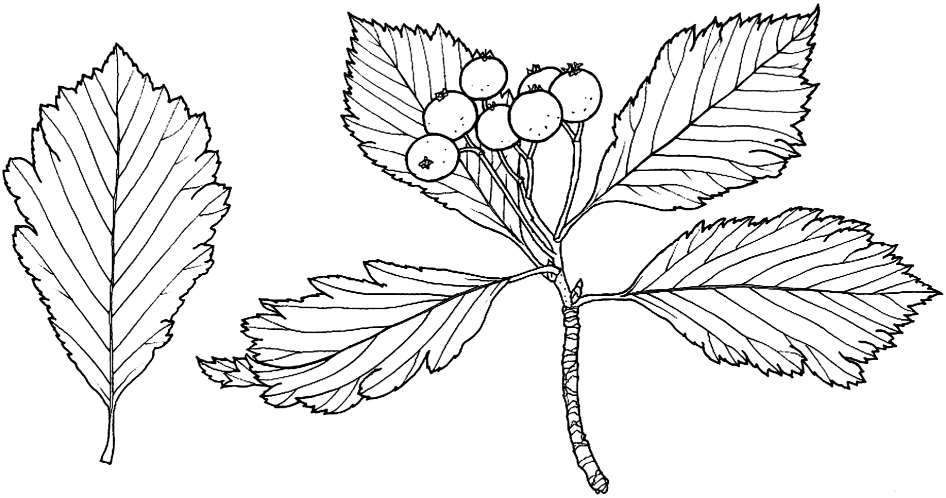

Fig. 6. – *Sorbus pauca*: short fructiferous shoot (right) and leaf from the centre of a short sterile shoot (left). Drawing by A. Skoumalová.

Fig. 7. – Short fertile shoot of *Sorbus pauca* growing on Malý Bezděz hill (photo P. Lepší 2009).

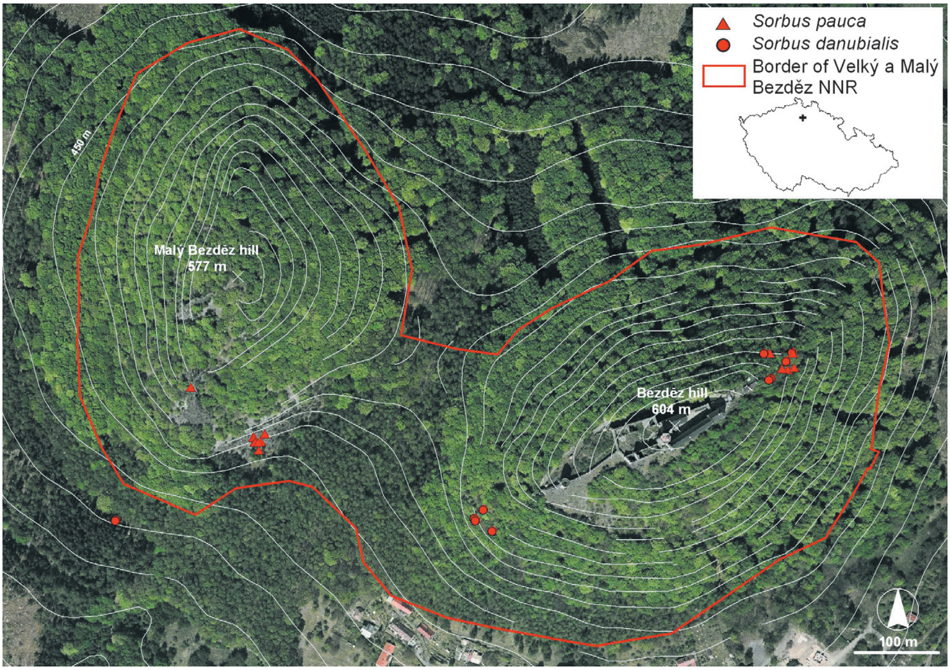

Fig. 8. – Map showing the distribution of *Sorbus pauca* and the individuals of *S. danubialis* sampled (the use of the map was approved by the Ministry of the Environment of the Czech Republic).

2.9–3.3 (–3.5) mm wide, triangular, acuminate, tomentose on both surfaces, patent, persistent, dry, erect. Petals (5.7–) 6.5–7.4 (–8.4) mm long and 4.9–5.3 (–5.7) mm wide, broadly ovate to broadly elliptical, concave, whitish, patent, sparsely hirsute at base of upper surface, with a short claw. Stamens ca 20; filaments whitish; anthers pale yellow to pale rose, 1.3–1.5 (–1.7) mm long. Ovary semi-inferior. Styles 2 (–3), greenish-cream, connate and hairy at base. Stigma greenish-cream, more or less flat. Fruit (11–) 12 (–13) mm long and (12–) 13–14 mm wide, (0.85–) 0.91–0.93 (–0.98) times as long as wide, sub-globose, red at maturity, sparsely tomentose to almost glabrous, matt, with (1–) 2–3 (–5) ochraceous lenticels per 25 mm^2; mesocarp heterogeneous; endocarp cartilaginous. Seeds fuscous. Somatic chromosome number 2n = 68 (tetraploid). Reproduction apomictic. Flowering V.

Distribution and population size

Sorbus pauca occurs on Bezděz and Malý Bezděz hills near the town of Doksy in northern Bohemia (Fig. 8). At these sites, which are ca 0.6 km apart, five and nine mature individuals were found, respectively. We did not record any seedlings at the localities because their determination is problematic. The age of older individuals cannot be determined because of their clonality (re-sprouting from the base). The population on Bezděz hill occurs on a large rock with relict vegetation. Nine individuals on Malý Bezděz hill occur in an abandoned quarry, except for one shrub growing on rock at the summit. The altitudinal range of the species spans from 440 to 580 m a.s.l. In terms of Czech phytogeography and climatol-

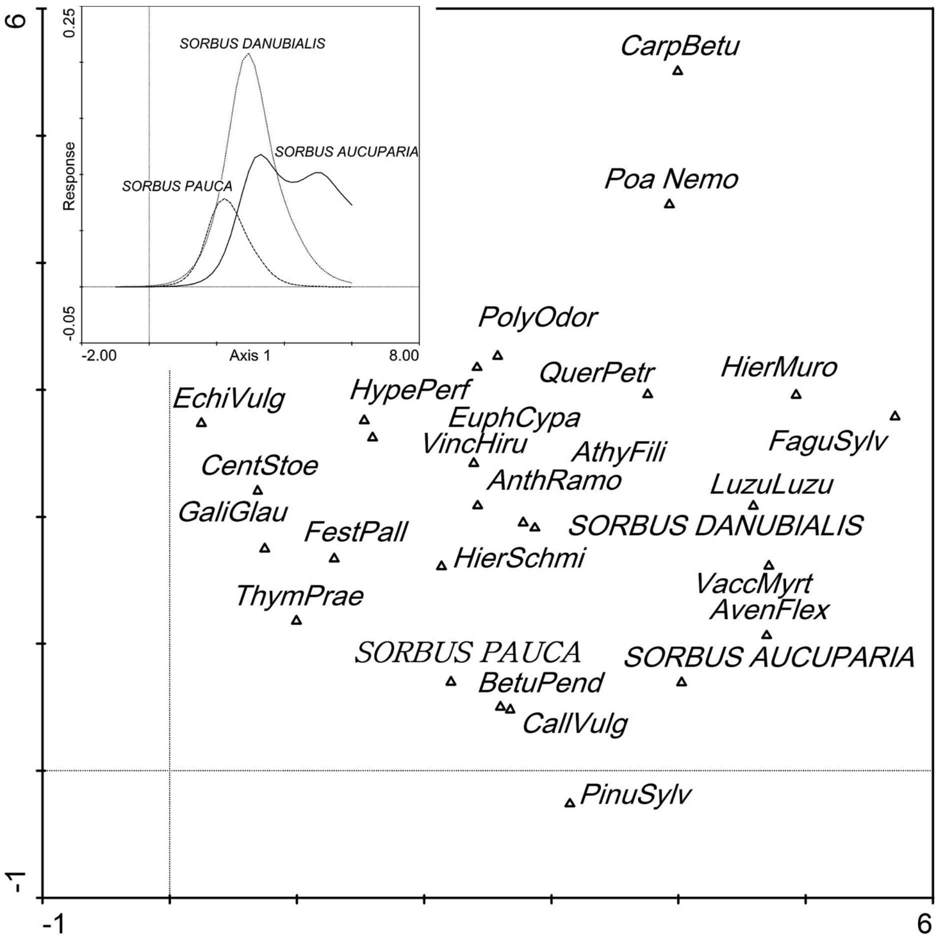

Fig. 9. – DCA diagram depicting the position of species best fitting the ordination axes. The diagram was constructed using 18 of our own and 60 published relevés of vegetation where *Sorbus pauca* or its parental species occur at the study locality (Bezděz and Malý Bezděz hills). The first and second DCA axes account for 10.4% and 5.2% of the variability in species composition, respectively. The picture in the upper left corner shows the species response curves for the three *Sorbus* species based on the generalized additive model (GAM) along the first DCA axis with Poisson distribution. The abbreviations correspond with these names: *Anthericum ramosum*, *Athyrium filix-femina*, *Avenella flexuosa*, *Betula pendula*, *Calluna vulgaris*, *Carpinus betulus*, *Centaurea stoebe*, *Echium vulgare*, *Euphorbia cyparissias*, *Galium glaucum*, *Hieracium murorum*, *H. schmidtii*, *Fagus sylvatica*, *Festuca pallens*, *Hypericum perforatum*, *Luzula luzuloides*, *Pinus sylvestris*, *Poa nemoralis*, *Polygonatum odoratum*, *Quercus petraea*, *Thymus praecox*, *Vaccinium myrtillus*, *Vincetoxicum hirundinaria.*

ogy, the hills belong to the supracolline vegetation belt (Chytrý 2012), the phytogeographical district Ralsko-bezdězská tabule (Skalický 1988) and a moderately warm climatic region (Quitt 1971) with a mean annual temperature of about 7–8 °C and mean annual precipitation of 600–650 mm (Tolasz et al. 2007).

Herbarium specimens:

Czech Republic. Northern Bohemia, 52. Ralsko-bezdězská tabule/table, CEBA 5454c: 1. Bezděz hill: Bezděz village, a protruding rock ridge on NE slope of Bezděz hill, low shrubs, three individuals, 50°32'23.1"N, 14°43'18.2"E, 560 m a.s.l. (leg. M. Lepší & P. Lepší 27. 8. 2009, CB 73616, CB 73617). – Bezděz village, a rocky slope connected with the summit castle area of Bezděz hill, one shrub, 50°32'23.9"N, 14°43'17.3"E, 560 m a.s.l. (leg. M. Lepší & P. Lepší 26. 3. 2010, CB 79422). **2. Malý Bezděz hill:** Bezděz village, lower parts of walls of abandoned quarry on the SE slope of Malý Bezděz hill, 5 shrubs ca 1 m high, 50°32'18.3"N, 14°42'51.6"E, 440 m a.s.l. (leg. M. Lepší & P. Petřík 20. 8. 2009, CB 73768). – Bezděz village, the upper parts of walls of abandoned quarry on the SE slope of Malý Bezděz hill, several shrubby individuals, 50°32'18.9"N, 14°42'52.1"E, 450 m a.s.l. (leg. M. Lepší & P. Lepší 28. 8. 2009, CB 73618). – Bezděz village, the bottom of an abandoned quarry on the SE slope of Malý Bezděz hill, 1 shrub ca 3 m high, 50°32'18.3"N, 14°42'51.6"E, 440 m a.s.l. (leg. M. Lepší & P. Petřík 20. 8. 2009, CB 73767; leg. M. Lepší & P. Lepší 23. 3. 2010, CB 79421; leg. P. Lepší & M. Lepší 16. 5. 2011, CB 79600, PRC, PRA, LI).

History of finds

We did not find any herbarium specimens belonging to *S. pauca* in any of the herbarium collections studied. Klika (1937) reports *S. franconica* (a hybridogenous species of the presumed parental combination *S. aria* agg. × *S. torminalis*) from Bezděz hill, but both the specimens that this record is based on refer to *S. danubialis* (Lepší et al. 2009). The first known record of this species was therefore, reported by J. Sádlo in 2008.

Ecology

A striking feature of the localities investigated is the spatial heterogeneity of habitats caused by local differences in the relief and diversity of microclimates, substrate properties and current vegetation. This heterogeneity allows the *Sorbus* species studied to co-occur despite their different habitat requirements.

Populations of *Sorbus pauca* inhabit dry phonolite cliffs and stony slopes. The species occurs mainly in sparse xerophilous vegetation consisting of scattered woody plants such as *Betula pendula*, *Calluna vulgaris*, *Cotoneaster integerrimus*, *Juniperus communis* and *Pinus sylvestris*, and low herbaceous plants such as *Festuca pallens*, *Hieracium schmidtii*, *Thymus praecox* and *Vincetoxum hirundinaria* (see Appendix 1). In phyto-sociologal terms, the vegetation belongs to the units *Alysso-Festucion pallentis* Moravec in Holub et al. 1967 (grassland), *Berberidion vulgaris* Br.-Bl. ex Tüxen 1952 (scrub) and *Festuco-Pinion sylvestris* Passarge et Hofmann 1968 (sparse woodland). Both parental species of *S. pauca* also occur abundantly in these habitats, but their environmental range is broader (Fig. 9). Whereas *S. danubialis* resembles *S. pauca* in its range of habitats, the second ancestor, *S. aucuparia*, is more mesophilous and tolerant of shade and plentiful nutrients.

Discussion

Phenotypic variation, diagnostic characters and the origin of this species

Individuals of *S. pauca* are morphologically homogeneous in both vegetative and generative characters and produce fully developed seeds. Plants intermediate between *S. pauca* and supposed parental species have not been recorded.

Considering the principal morphological features of this species (i.e. oblong-obovate leaves with obtuse lobes), we conclude that it belongs to the *S. hybrida* group and its most probable ancestors are *S. danubialis* of the *S. aria* group and *S. aucuparia*, which are the only native *Sorbus* species occurring at present at the localities studied and in the adjacent area of northern Bohemia.

Sorbus pauca differs markedly from other European species of the *S. hybrida* group in having small undulating leaves with irregular shallow (but distinct) lobes and average sized fruit with scattered lenticels. The leaves of related species is either partly pinnate (e.g. *S. borbasii* Jávorka, *S. hybrida*, *S. meinichii* Hedl., *S. pseudofennica* E. F. Warb.) or deeply lobed (e.g. *S. arranensis* Hedl., *S. austriaca*, *S. dacica*, *S. pulchra* N. Mey., *S. scepusiensis* Kovanda or *S. schwarziana* N. Mey.). Other species with comparably shallow lobes have larger leaves or smaller fruit (e.g. *S. anglica* Hedl., *S. cuneifolia* T. C. G. Rich, *S. minima* (Ley) Hedl., *S. mougeotii*). The few taxa reported from Hungary and adjacent regions (such as *S. buekkensis*, *S. hungarica*, *S. javorkae* or *S. velebitica*) have indistinctly lobed leaves and therefore seem to belong to the *S. aria* group rather than the *S. hybrida* group.

Sorbus pauca more closely resembles *S. danubialis* than *S. aucuparia* in the above mentioned characters. *Sorbus danubialis* is characterized by rhomboidal to round rhomboidal leaves, with a coarsely double serrate to indistinctly lobed margin to the upper part of the lamina, with acute lobes or main teeth and average sized fruit with scattered lenticels. Many species of the *S. hybrida* group resemble *S. aucuparia* in having pinnatifid to pinnatisect leaves and small fruit with few or no lenticels. We assume that the absence of these characters reflects an increased portion of genetic information from *S. danubialis* in the genome of the new species.

The ploidy level of *S. pauca* seems to support this concept. *Sorbus pauca* most probably arose from two hybridization events. A triploid hybrid could have arisen from a cross between the tetraploid *S. danubialis* and diploid *S. aucuparia* and subsequently a reduced diploid gamete of this triploid ancestor fused with a reduced diploid gamete of *S. danubialis* giving rise to a tetraploid species. Another hypothetical option concerns direct hybridization of an unreduced gamete of *S. aucuparia* with a reduced gamete of *S. danubialis*, which, considering the lack of information about the production of unreduced gametes in *S. aucuparia* is less probable. Also the morphology of *S. pauca* indicates that the contribution from *S. aucuparia* is less than one half of the genome.

The historical context of the occurrence of this species

In addition to *Sorbus pauca*, a considerable number of endemic plants occur in the Doksy region. *Dactylorhiza bohemica* (Businský 1989) and *Pinguicula vulgaris* subsp. *bohemica* (Kubát et al. 2002) occur in local fens (the latter also previously occurred in fens by the river Elbe ca 45 km away). Pale-flowered and small-leaved populations of *Pulsatilla pratensis* occurring in dry calcic soils in pine forests were named as var. *albida* (Domin) Skalický (Skalický 1988). *Potentilla psammophila* Soják is a recently missing hybridogeneous species of the *P. collina* group (Soják 2009). Local populations of *Minuartia cespitosa* differ considerably from other populations in terms of the physiology of the individual plants, which can grow in calcic soils, whereas those of other populations are associated with metaliferous soils where calcium carbonate is almost absent (Brooks

1987). In addition, two species forming peculiar local populations are restricted to hills of volcanic origin, including Bezděz hill, namely *Cardaminopsis petraea* (rosy flowered plants with a pilose stem, Měsíček et al. 1992) and *Viola tricolor* subsp. *polychroma* (plants with large blue-violet flowers lacking a yellow tint, Kirschner & Skalický 1990).

This endemism might be due to the stability of the vegetation in the area in which the biome of boreal forests (lowland taiga) persisted since the early Holocene (Chytrý 2012, Novák et al. 2012). In the landscape surrounding the Doksy region, the vegetation has undergone major changes. Relatively stable conditions, however, may have persisted on the rocks of the Bezděz hills and some other volcanic hills in the region. Our hypothesis that the rocks were not forested throughout the Holocene is supported by the local occurrence of presumably relict species such as *Allium strictum*, *Arctostaphylos uva-ursi*, *Aster alpinus*, *Calamagrostis varia*, *Dianthus gratianopolitanus*, *Festuca pallens* and *Hieracium schmidtii*. These species are unable to spread either under a forest canopy or in open habitats of a cultural landscape, and their survival is dependent on harsh conditions on open rocks.

The picturesque cultural history of the Bezděz hills (Žemlička 1980, Durdík 1999) sharply contrasts with the relic character of their rocky slopes and the general stability of the vegetation in the region. For at least eight centuries, stable conditions in natural habitats alternated in space and time with human-made stages of disturbances, abandonment and repeated afforestation.

Summits of hills were undoubtedly utilized as partly deforested lookouts since ancient times. The establishment of the monarch's church of St. Aegidius in the foothills implies an early colonization during the middle ages. During the 13th century, construction of the king's castle Bezděz, a fortification on Malý Bezděz hill and a generous but utterly failed attempt to turn the village into a town resulted in extensive deforestation and, without doubt, also soil erosion on both hills although the steepest slopes were probably never deforested. Both hills were grazed to different extents by goats and sheep until the first half of the 20th century. Between the 16th and 18th centuries, several attempts to restore the castle, which was later used as a monastery, were interrupted by repeated fires and vandalism. The ruins were repaired in several stages after the beginning of the 19th century (Flegl 1983). A phonolite quarry, where *S. pauca* currently occurs, was opened on the south-eastern slope of Malý Bezděz hill no later than the beginning of the 19th century. In the last hundred years, hill slopes covered by sparse vegetation, with clusters of trees and shrubs, developed into a closed forest with some rocky patches. It is possible that this decline in the extent of open rocky habitats is the main cause of the current scarcity of *S. pauca*. Though *S. pauca* has survived the intensive human pressure at the Bezděz hills, it is absent on roughly twenty similar, but more natural, volcanic hills in a radius of 20 km. It is therefore probable that the current distribution of *S. pauca* is not a remnant of a previous (e.g. early Holocene) wide distribution. Rather, it might be a historically young species that never managed to spread. Like its parents, the species is a weak competitor against trees and only manages to survive owing to human-made disturbances, which reduce the competition and release nutrients. Conversely, the population of this species could have been reduced considerably by the construction of the castle or intensive grazing in the past. Besides its biological value (e.g. as an example of stenoendemism, see Kaplan 2012), this species might also have a cultural value as a possible unforeseen consequence of the effect of humans on the Bezděz hills.

Conservation

All specimens were found within the area of the Velký a Malý Bezděz National Nature Reserve, which ensures their protection. Current human activities do not seem to threaten directly this species except for the occasional cutting of shrubs. Conversely, the population is so sparse that it may be endangered even by a random event such as a rock fall or a long term process such as succession resulting in the growth of tall shrubs or trees. Therefore the reproduction and establishment of the species should be supported by partial removal of surrounding woody vegetation. The species should be included among the critically endangered plants of the Czech flora (C1; sensu Grulich 2012) and critically endangered species (status criteria B2a; D) according to the IUCN (2001) and it seems to be a very good candidate for *ex situ* conservation in a seed bank and/or a botanical garden.

Appendix 1 (page 155)

Acknowledgements

We are grateful to J. Zázvorka for valuable comments on earlier drafts of the manuscript. We thank V. Jarolímová for her help with chromosome counting. We wish to thank A. Skoumalová for drawing the illustration, I. Prchlík for consultation on the Latin species name and M. Dolejš for technical assistance. R. Evans and F. Rooks kindly improved our English, and Tony Dixon edited the final manuscript. The study was supported by grant 138/2010/P from the Grant Agency of the University of South Bohemia, Institutional research support MSM-6007665801 from the Czech Ministry of Education, long-term research development project (RVO 67985939) and a grant from the Academy of Sciences of the Czech Republic (IAAX00050801).

Souhrn

Nově rozeznaný jeřáb bezdězský (*Sorbus pauca*) je endemitem dvou blízkých vrchů, Bezdězu a Malého Bezdězu v Ralsko-bezdězské pahorkatině. Je to hybridogenní apomiktický tetraploidní (2n = 4x = 68) druh z okruhu *S. hybrida* agg., do nějž jsou řazeni potomci křížení *S. aria* agg. a *S. aucuparia*. Z tohoto okruhu byly doposud v České republice známy dva nepůvodní druhy, *S. austriaca* a *S. mougeotii*, ale žádný druh původní. Na příslušnost k okruhu *S. hybrida* ukazuje podlouhle obvejčitý obrys a zaokrouhlené (tupé) laloky listové čepele. Od ostatních evropských druhů tohoto okruhu se *S. pauca* odlišuje poměrně drobnými listovými čepelemi s nepravidelně vyvinutými a mělkými, avšak dobře patrnými laloky a středně velkými plody s roztroušenými lenticelami. Druhým rodičovským taxonem je pravděpodobně *S. danubialis*, který se vyskytuje na obou lokalitách společně s novým druhem. *Sorbus danubialis* má na rozdíl od *S. pauca* kosočtverečné až zaokrouhleně kosočtverečné čepele listů, které jsou v horní polovině zastřihovaně dvojitě pilovité, někdy až mělce laločnaté, laloky či hlavní zuby jsou špičaté nikoliv tupé. Vysoká podobnost obou druhů nás vede k hypotéze, že *S. pauca* vznikl zpětným křížením hybrida *S. aucuparia* × *S. danubialis* s druhem *S. danubialis*. *Sorbus pauca* je morfologicky i karyologicky homogenní a morfologicky dobře vymezený od *S. danubialis* i od ostatních v Evropě doposud popsaných taxonů jeřábů. Druh je vázán na skalnaté biotopy (trávníky, křoviny, lesy) s *Festuca pallens* a *Cotoneaster integerrimus*. Z lokality jsou známy dvě populace se 14 plodnými jedinci jeřábu bezdězského. Vzhledem k jeho malé početnosti a tudíž pravděpodobnému ohrožení ho navrhujeme zařadit do kategorie kriticky ohrožených druhů cévnatých rostlin (C1 podle Grulich 2012).

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Received 15 August 2012
Revision received 27 November 2012
Accepted 30 November 2012

Appendix 1. – Phytosociological relevés with *Sorbus pauca*.

Relevé number	1	2	3	4	5	6	7	8	9
Area (m^2)	20	20	9	16	8	16	25	21	21
Altitude (m a.s.l.)	460	450	450	440	450	550	560	550	580
Aspect	S	S	SE	SE	SSE	NWW	EES	EES	NE
Slope (°)	30	90	80	80	80	80	90	90	20
Cover E_2 (%)	40	0	0	0	0	5	10	20	10
Cover E_1 (%)	60	30	10	15	5	5	8	10	50
Cover E_0 (%)	0	5	5	5	1	10	5	5	3
E_2 – shrub layer									
Sorbus pauca	2	.	.	.	.	.	.	2	1
Cotoneaster integerrimus	.	.	.	.	.	.	1	2	1
Rosa canina agg.	2	.	.	.	.	.	.	1	.
Betula pendula	.	.	.	.	.	1	1	.	.
Crataegus ×fallacina	.	.	.	.	.	.	1	2	.
E_1 – herb layer									
Campanula rotundifolia agg.	+	+	1	1	+	+	+	+	1
Vincetoxicum hirundinaria	3	1	+	1	+	.	1	1	1
Sorbus pauca	.	1	2	1	1	+	+	.	.
Galium glaucum	.	1	+	+	+	.	+	.	r
Hieracium schmidtii	.	+	.	r	+	.	+	+	r
Euphorbia cyparissias	.	.	r	+	+	.	+	+	+
Festuca pallens	.	1	.	1	1	.	1	1	.
Anthericum ramosum	.	1	+	1	+	.	.	.	.
Thymus praecox	.	1	+	+	+	.	.	.	.
Polygonatum odoratum	.	.	.	.	+	.	+	+	+
Calluna vulgaris	.	+	r	.	.	1	.	.	.
Danthonia decumbens	.	+	.	+	r	.	.	.	.
Centaurea stoebe	.	+	.	r	.	.	+	.	.
Cardaminopsis sp.	.	.	.	.	.	.	1	+	+
Calamagrostis varia	2	.	.	.	.	.	.	.	1
Viola riviniana	r	+	.	.	.	.	.	.	.
Leontodon hispidus	.	+	.	r	.	.	.	.	.
Asplenium ruta-muraria	.	+	.	.	r	.	.	.	.
Polygala vulgaris	.	r	.	r	.	.	.	.	.
Potentilla filiformis	.	.	.	r	+	.	.	.	.
Cotoneaster integerrimus	1	.	.	.	.	+	.	+	.
Rubus idaeus	.	.	.	.	.	+	.	.	2
Avenella flexuosa	.	.	.	.	.	+	.	.	+
Rosa canina agg.	.	.	.	.	.	.	1	+	.
Hieracium sabaudum	.	.	.	.	.	.	.	r	+
Hylotelephium maximum	.	.	.	.	.	.	.	r	+
Sorbus aucuparia	.	.	.	.	.	+	.	.	r

In one relevé only: **Shadowing trees out of the plot:** *Malus sylvestris* 9: 2, *Fagus sylvatica* 9: 2, *Tilia cordata* 9: 1. **E_2:** *Pinus sylvestris* 1: 2, *Euonymus europaea* 1: 2, *Quercus petraea* 1: 2, *Juniperus communis* 6: 1, *Sorbus aucuparia* 6: +, *S. danubialis* 9: 1. **E_1**: *Euonymus europaea* 1: +, *Rubus franconicus* 1: +, *Parthenocissus inserta* 1: r, *Prunus avium* 1: r, *Potentilla tabernaemontani* 2: +, *Viola collina* 2: +, *Epilobium collinum* 2: r, *Festuca* sp. 3: 1, *Pinus sylvestris* 3: 1, *Pinus nigra* 4: 1, *Hypericum perforatum* 4: r, *Asplenium septentrionale* 5: r, *Festuca ovina* 6: 1, *Sorbus danubialis* 6: +, *Quercus robur* 6: r, *Fagus sylvatica* 6: r, *Echium vulgare* 7: +, *Sedum reflexum* 7: +, *Jovibarba globifera* subsp. *globifera* 7: r, *Geranium sanguineum* 8: 1, *Convallaria majalis* 9: 1, *Dianthus gratianopolitanus* 9: 1, *Polypodium vulgare* 9: 1, *Poa nemoralis* 9: 1, *Stellaria holostea* 9: 1, *Hieracium murorum* 9: 1, *Dryopteris filix-mas* 9: 1, *Lonicera xylosteum* 9: 1, *Brachypodium pinnatum* 9: 1, *Vaccinium myrtillus* 9: 1, *Achillea millefolium* 9: +, *Mercurialis perennis* 9: +, *Fragaria* sp. 9: +, *Festuca rubra* 9: +, *Viola* sp. 9: +, *Silene nutans* 9: +, *Luzula luzuloides* 9: +, *Poa pratensis* s. l. 9: +, *Campanula rapunculoides* 9: +, *Lilium martagon* 9: +, *Digitalis grandiflora* 9: r, *Quercus petraea* 9: r.

Localitites of the relevés: 1. Malý Bezděz hill, under the quarry wall, 19. 8. 2009, 50°32'18.5"N, 14°42'51.4"E. **2.** ditto, wall at the base of the quarry, 19. 8. 2009, 50°32'23.5"N, 14°42'39.1"E. **3.** ditto, in the middle part of the quarry wall on SE site of the hill, 16. 5. 2011, 50°32'18.9"N, 14°42'52.1"E. **4.** ditto, close to the base of the wall of the quarry, 16. 5. 2011, 50°32'18.9"N, 14°42'52.1"E. **5.** ditto, lower third of the quarry wall, 16. 5. 2011, 50°32'18.9"N, 14°42'52.1"E. **6.** ditto, rock under the summit part, 16. 5. 2011, 50°32'20.8"N, 14°42'48.5"E. **7.** Bezděz hill, rock in the SE part of the summit, 16. 5. 2011, 50°32'23.1"N, 14°43'18.2"E. **8.** ditto, 16. 5. 2011, 50°32'23.1"N, 14°43'18.2"E. **9.** ditto, 23. 5. 2011, 50°32'23.8"N, 14°43'17.6"E.

Paper V

Distributions of vascular plants in the Czech Republic. Part 3.

Kaplan Z., Danihelka J., Lepší M., Lepší P., Ekrt L., Chrtek J. Jr., Kocián J.,
Prančl J., Kobrlová L., Hroneš M. & Šulc V. (2016) Preslia 88: 459–544.

Picture on previous page *Sorbus bohemica*, Plešivec

Distributions of vascular plants in the Czech Republic. Part 3

Rozšíření cévnatých rostlin v České republice. Část 3

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Kaplan Z., Danihelka J., Lepší M., Lepší P., Ekrt L., Chrtek J. Jr., Kocián J., Prančl J., Kobrlová L., Hroneš M. & Šulc V. (2016): Distributions of vascular plants in the Czech Republic. Part 3. – Preslia 88: 459–544.

The third part of the publication series on the distributions of vascular plants in the Czech Republic includes grid maps of 105 taxa of the genera *Acorus*, *Amelanchier*, *Asplenium*, *Calla*, *Cerastium*, *Ceratophyllum*, *Eichhornia*, *Hieracium*, *Hippuris*, *Hottonia*, *Lemna*, *Limosella*, *Peplis*, *Pistia*, *Pontederia*, *Sorbus*, *Spirodela*, *Symphytum*, *Trapa*, *Valerianella* and *Wolffia*. The maps were produced by taxonomic experts based on all available herbarium, literature and field records. Three of the studied genera include Czech endemics, which are confined to small geographic areas, mostly have small population sizes and thus are of conservation concern. These maps resulted from detailed fieldwork and herbarium revisions by monographers of the respective groups and for many of these endemics they are first available maps. The endemic species of *Hieracium* occur mainly in the subalpine habitats in the Krkonoše, Králický Sněžník and Hrubý Jeseník Mts. By contrast, a great majority of *Sorbus* endemics are found mainly in thermophilous open broad-leaved and pine forests on rocky habitats at middle altitudes. *Cerastium alsinifolium* is confined in its total distribution to serpentine outcrops in western Bohemia. *Asplenium* is another ecologically specialized group, which includes petrophytes, some of which are restricted to specific substrates, such as siliceous, limestone, basalt or serpentine rocks. The plants studied include 53 taxa classified in the Red List of vascular plants of the Czech Republic, some of which have shown remarkable declines. *Symphytum bohemicum*, distributed mainly in central Europe, is confined to calcareous fens in the lowlands. There are many endangered and vulnerable species amongst aquatic plants, which are threatened mainly by fish-farming intensification, eutrophication and habitat destruction. Populations of some of the most endangered and attractive aquatics, including *Hippuris vulgaris* and *Trapa natans*, have been lost and locally replaced by plants of unknown provenance purchased in garden stores, which causes a potential threat of genetic erosion of native populations. Attractive appearance is the reason why alien aquatics, such as

Eichhornia crassipes, *Pistia stratiotes* and *Pontederia cordata*, are sometimes planted not only in garden pools but also in wetlands in the countryside; each has been recorded at about a dozen such sites during the past 25 years. *Lemna turionifera*, by contrast, has been introduced and dispersed by waterfowl and is now widespread in the country. The histories of the introduction and subsequent spread are also described and analysed for the widespread neophyte *Acorus calamus* and for the alien species of *Amelanchier* and *Symphytum*. Spatial distributions and temporal dynamics of individual species are shown in maps and documented by records included in the Pladias database and available in electronic appendices. The maps are accompanied by comments, which include additional information on the distribution, habitats, taxonomy and biology of the species.

Keywords: alien species, central Europe, chorology, Czech Republic, distribution atlas, distribution patterns, endangered species, endemic, flora, grid maps, herbaria, introduction, phytogeography, plant record, vascular plants

Introduction

Since the project of mapping plant distributions in the Czech Republic was launched in 2014, a modern plant record database Pladias has been established and 162 grid distribution maps have been produced by taxonomic experts, based on critically evaluated and sorted records, and published in two papers (Kaplan et al. 2015, 2016). The ultimate aim of this effort, started within the PLADIAS project (www.pladias.org) and planned to continue as a series of publications, is to prepare the basis for a complete atlas of the distribution of vascular plants in the Czech Republic.

From April to August 2016 the Pladias database has increased by about 2,900,000 new records. Of these almost 11,000 records resulted from critical examination of herbarium specimens by taxonomic experts. Maps of further 105 taxa were finished at the beginning of August 2016 and these are published in this paper. These maps include both native and alien species, rare species confined to small geographic areas as well as widespread species, and endangered as well as common species. About one third of the Czech endemics (Kaplan 2012), which is a group of plants that deserves the highest attention and conservation priorities, are mapped. A great majority of the maps resulted from recent detailed revisions of taxonomically critical groups, such as *Amelanchier* (Lepší & Lepší 2008), *Asplenium* (Ekrt 2008b, Ekrt & Štech 2008), *Cerastium* (Letz et al. 2012, Vít et al. 2014), *Hieracium* (e.g. Chrtek 2004, Chrtek et al. 2007), *Lemna* (Kaplan 2010), *Sorbus* (e.g. Lepší et al. 2015) and *Symphytum* (Kobrlová et al. 2016), which have refined taxonomic concepts and the delimitation of taxa, and in some cases also led to the discovery of new species or first country records.

Materials and methods

Taxonomic scope

The following groups of vascular plants are mapped: native taxa, naturalized aliens and most casuals, and selected hybrids. Distribution maps are produced for species and subspecies, and in exceptional cases also for varieties or infrageneric taxa (e.g. sections). Plants of species groups that are difficult to assign to species may be mapped as species aggregates. Field crops and plants deliberately cultivated in gardens and parks are not included in the mapping project. Nomenclature, taxonomic concepts and delimitation of species aggregates mostly follow Danihelka et al. (2012), with differences indicated where necessary. For taxa not included in that checklist, a taxonomic reference is given. Publication of maps does not follow any alphabetical or systematic order but those maps that have resulted from recent revisions are printed preferentially.

Data sources

All relevant floristic data sources are used. Major national herbaria and some local and foreign collections, incl. BRA, BRNL, BRNM, BRNU, CB, CBFS, CESK, CHEB, CHOM, FMM, GM, HOMP, HR, KHMS, LIM, LIT, MJ, MMI, MP, MZ, NJM, OH, OL, OLM, OMJ, OP, OSM, OVMB, PL, PR, PRA, PRC, ROZ, SAV, SOB, SOKO, SUM, VM, WRSL, WU and ZMT (acronyms follow Thiers 2016), were consulted as the main source of taxonomically revised records. Most records for maps of common and easy-to-identify taxa come from the recently developed Pladias database (hosted at the Institute of Botany, Průhonice), which has integrated all available records on the distribution of the vascular plants in the Czech Republic. Among the most important incorporated databases are the Database of the Distribution of Vascular Plants in the Czech Republic (FLDOK), the Czech National Phytosociological Database (CNPD), plant records from the Floristic Summer Schools and other activities of the Czech Botanical Society, the Species Occurrence Database of the Nature Conservation Agency of the Czech Republic (NDOP) and the Database of Forest Typology of the Forest Management Institute of the Czech Republic (DLT). Unpublished field records previously entered into the Pladias database by the authors of maps or regional contributors were also considered.

Procedure of mapping

All records used for mapping are entered into the Pladias database and geographically sorted according to the traditionally used CEBA (Central European Basic Area) grid template (Niklfeld 1999) divided into quadrants of 5 × 3 arc minutes (corresponding to approximately 5.5 × 5.9 km). The territory of the Czech Republic is covered by 2551 quadrants, of which 2181 are completely within the border of the country. Individual records as well as the whole distribution pattern of each taxon are checked and evaluated by the author of a particular map in a web-based mapping interface of the Pladias database. Maps of taxonomically critical groups are based solely or mainly on herbarium records revised by taxonomic experts; these cases are indicated in the text accompanying the particular map. Maps of all other taxa are based on records from databases, literature and herbaria, which were scrutinized by the authors of the respective maps. Records used for producing maps are listed in Electronic Appendices 1–105. In selected maps, native versus introduced occurrences are distinguished and corresponding records in the database classified accordingly. Draft distribution maps and the background records are released in a web-based review process for scrutiny to field botanists, regional collaborators and members of the Czech Botanical Society. Their comments and additional records are collected in the database and returned to the responsible specialists for consideration before producing final distribution maps.

Final maps and comments

The treatment of each taxon consists of a grid distribution map and an accompanying text; authors of maps are indicated in the figure captions, and they also took the major part in preparing the first drafts of the respective texts. Maps are displayed using spherical Mercator projection (EPSG:3857) where meridians and parallels are shown perpendicularly, and the mapping CEBA grids are thus nicely displayed. The background relief was derived from the SRTM data (http://www2.jpl.nasa.gov/srtm/, the version provided by http://srtm.csi.cgiar.org), and the river network was adapted from data provided by CENIA (www.cenia.cz). When appropriate, different symbols are used in the maps in order to distinguish one of the following attributes of the plant distribution records: (1) recent versus old records, (2) native occurrences versus introductions, or (3) records based on revised herbarium specimens versus all other records. These classifications of records are used only for those taxa where such distinction provides important information and, in addition, the amount and quality of records are sufficient. The mapping symbols used to indicate the different attributes of the records in the particular grid cell are shown in Table 1. Symbols specific to individual maps are explained in their captions. To save space, rare taxa of the genera *Hieracium* and *Sorbus* with distinct distributions are shown in maps in groups of 2–4, with symbols and annotations of individual taxa in the maps distinguished using different colours. In the caption to each map, counts of occupied quadrants are indicated according to the symbols used in the map; uncertain occurrences are not included in the counts. The accompanying text includes the accepted scientific name, a brief outline of the total distribution, information on habitats occupied by the species and a description of its distribution in the Czech Republic. Where appropriate, comments on the taxonomy, biology and details of the spatial and temporal dynamics of the distribution are given.

Table 1. – The mapping symbols used in the distribution maps to indicate the different attributes of the occurrence in a particular grid cell.

Attribute distinguished	Symbol	Attribute state
None	●	all records
Time	●	recent occurrence (at least one record since 2000)
	○	old occurrence (all records before 2000, or demonstrably being extirpated from all localities after 2000, or all records undated)
Origin	●	native (at least one record)
	×	alien
Source data	●	a revised herbarium specimen (at least one record)
	▲	all other
All	?	only record(s) uncertain regarding identification and/or locality

al. 1997, Rojas-Sandoval et al. 2013). In Europe it has been recorded as escaped in Portugal, Spain, France, Belgium, the Netherlands, Germany, the Czech Republic, Hungary, Italy, Slovenia, Romania, Ukraine and Russia, but only in Slovenia it is considered as invasive (Pieterse et al. 1981, Georges & Pax 2002, Kaplan 2002, Rojas-Sandoval et al. 2013). *Pistia stratiotes* is intolerant of low temperatures, which limits its distribution. In countries with cold climates only scattered ephemeral populations have been reported. In the Czech Republic *P. stratiotes* is a popular aquarium plant, which is sometimes discarded in water bodies during the summer season. It acts like an annual, dying during the winter, and it can re-appear only as a result of re-introductions. It was first recorded in a fish storage pond near the village of Ponědraž in southern Bohemia in 1999 (Kaplan 2002). So far it has been found at 12 sites in ponds and slow-flowing stretches of rivers in Bohemia and at 3 sites in Moravia. It is classified as a casual neophyte (Pyšek et al. 2012).

Pontederia cordata (Fig. 56)

Pontederia cordata is native to North and South America, from south-eastern Canada and eastern USA southwards as far as Argentina and Uruguay (Lowden 1973, Horn 2002). In Europe it is cultivated as an ornamental in pools and ponds and as a bog plant (Jäger et al. 2011). It is sometimes planted in water bodies outside gardens and parks or it survives as a cultivation relic, and locally it has become naturalized (Verloove 2016b). So far it has been recorded as escaped in the British Isles, Spain, France, Belgium, the Netherlands, Switzerland and Italy (Wallentinus 2002, DAISIE 2016b). In the Czech Republic *P. cordata* has been available in garden stores and plant nurseries since the 1990s. In 2004 it was first found in a pond in the village of Býkev near the town of Mělník in central Bohemia (Rydlo 2006, Kaplan 2009). Since then it has been recorded at 7 other sites in the shallow edges and on the banks of ponds, oxbow lakes and slow-flowing rivers. In rivers it may be transported to new sites by water currents, which appears to be the case on the Labe river near the village of Chvalovice near the town of Poděbrady. *Pontederia cordata* is classified as a casual neophyte (Pyšek et al. 2012).

Sorbus subg. *Aria* (*S. aria* agg.)
Sorbus aria (Fig. 57), *S. collina* (Fig. 58), *S. cucullifera* (Fig. 59), *S. danubialis* (Fig. 60), *S. moravica* (Fig. 59), *S. pontis-satanae* (Fig. 61) and *S. thayensis* (Fig. 61)

Sorbus subg. *Aria* is widely distributed from Europe to Central Asia (Aldasoro et al. 2004). It is a complex of sexual and agamospermous taxa, in Europe comprising two diploid species (*S. aria* and *S. umbellata*), widely distributed tetraploids and local polyploid endemics, which are generally considered to be results of hybridization between *S. aria* and the tetraploids (Kutzelnigg 1995, Rich et al. 2010). In the Czech Republic the subgenus includes seven species: *S. aria*, two widely distributed tetraploids, *S. danubialis* and *S. collina*, and four local endemics, all apart from the first two being described only recently (Lepší et al. 2015). All are light-demanding species and prefer open habitats such as rocks and screes, rock steppes, rock scrub, forest-steppes, thermophilous and open pine, oak, hornbeam and ravine forests and their fringes. Besides semi-natural to relic vegetation, they occasionally grow in *Picea abies*, *Pinus nigra* and *P. sylvestris* plantations or in their clearings. The closed canopy that now prevails in woodlands in the Czech Republic is unfavourable for the long-term survival and regular reproduction of such species. The spread of trees and shrubs into open rocky and steppe habitats represents another major threat.

Sorbus aria is a widely distributed species occurring mainly in the mountains of central and southern Europe and possibly also of northern Africa; northwards it reaches south-eastern England, northern France, central Germany and the Western Carpathians (Kutzelnigg 1995, Rich et al. 2010). Its occurrence beyond this northern limit (e.g. in Scandinavia and most of the British Isles) is ascribed to escapes from cultivation (Rich et al. 2010, Grundt & Salvesen 2011). The native occurrence of *S. aria* in the Czech Republic is confined to the supracolline to submontane vegetation belts at altitudes of 300–660 m in four areas of southern Moravia: slopes of the Dyje river valley between the towns of Vranov nad Dyjí and Znojmo, the karst area of Moravský kras, Bílé Karpaty Mts and Pavlovské vrchy hills. These localities are situated at the northern limit of the species' distribution range. In the valley of the Dyje river *S. aria* is scattered, whereas all other Moravian populations are small and that in the Pavlovské vrchy hills no longer extant. It occasionally escapes from cultivation. The literature records of *S. aria* from other parts of the country (Kovanda 1992, 2002, Kutzelnigg 1995) are dubious and refer to *S. danubialis* or *S. collina* (Lepší et al. 2015). *Sorbus aria* is classified as endangered because of its scarcity (Grulich 2012).

Sorbus collina is probably endemic to central Europe but its distribution is insufficiently known. Up to now it has been recorded in Bavaria, Bohemia and Lower and Upper Austria, and similar plants are also found in north-western Hungary (Lepší et al. 2015). In the Czech Republic *S. collina* occurs only in warm to moderately warm parts of central, western and north-western Bohemia. It grows particularly in areas with rocky slopes and rock outcrops such as deep river valleys, karst areas and solitary volcanic hills. It mainly occurs in the karst areas of Český kras, the Křivoklátsko region, the central part of the České středohoří Mts and in the valley of the Vltava river south of Prague. Elsewhere it is rare, often being confined to isolated sites. Some of these outposts harbour only one individual or a very small population and may be actually garden escapes, as it is also rarely grown for ornamental purposes. Most of the records are from the colline and supracolline vegetation belts and only exceptionally was it recorded from the submontane belt, with an altitudinal maximum at 800 m on Mt Milešovka in the České středohoří Mts. The species was described only recently (Lepší et al. 2015) and was therefore not included in the third edition of the Red List (Grulich 2012); it deserves the category of vulnerable.

Sorbus cucullifera and *S. thayensis* are endemic to the valley of the Dyje river in the surroundings of the town of Hardegg along the border between Lower Austria and Moravia, while the latter occurs also in the adjacent valley of the Fugnitz stream, a right-hand tributary of the Dyje river. The appropriate threat status of both species would be critically threatened. *Sorbus cucullifera* has been recorded at 13 sites in the Czech Republic and 15 in Austria, all in the colline vegetation belt. The distance between the two most distant localities is almost 5.4 km and the estimated total number of individuals is around 150 in the Czech Republic and 300 in Austria. *Sorbus thayensis* is known from two sites in the Czech Republic and five in Austria, the most distant ones being 3.2 km apart. Ten of thirty-three known individuals are found in the Czech Republic (Lepší et al. 2015).

Sorbus danubialis is a central-European species known from Bavaria, Lower Austria, the Czech Republic, Slovakia and Hungary (Lepší et al. 2015), in Bohemia reaching the northern limit of its distribution range. In the Czech Republic it occurs particularly in

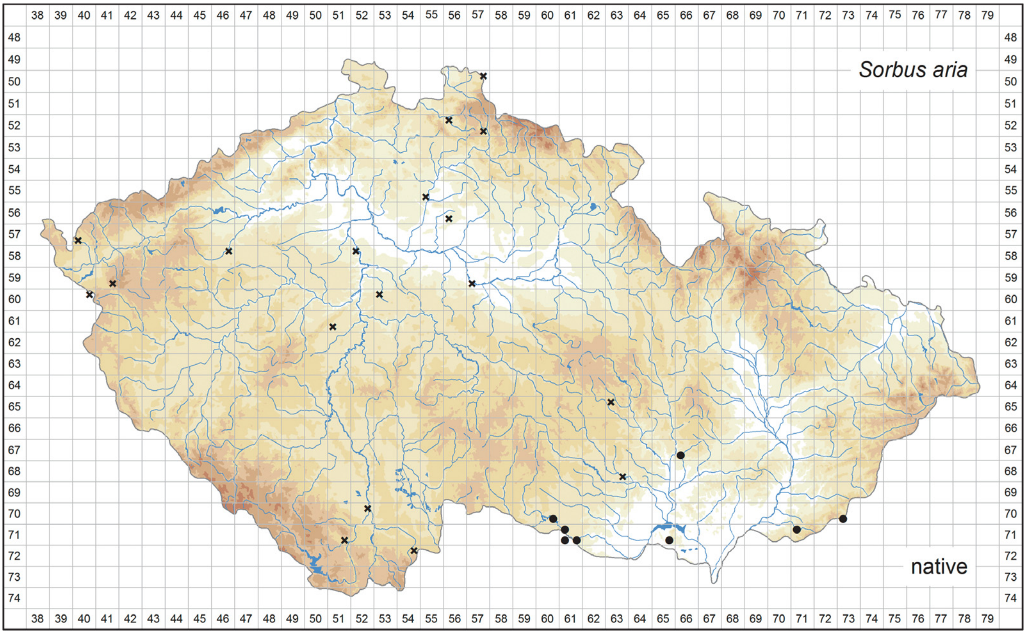

Fig. 57. – Distribution of *Sorbus aria* in the Czech Republic: ● native (8 quadrants), × alien (18 quadrants). Prepared by Martin Lepší & Petr Lepší.

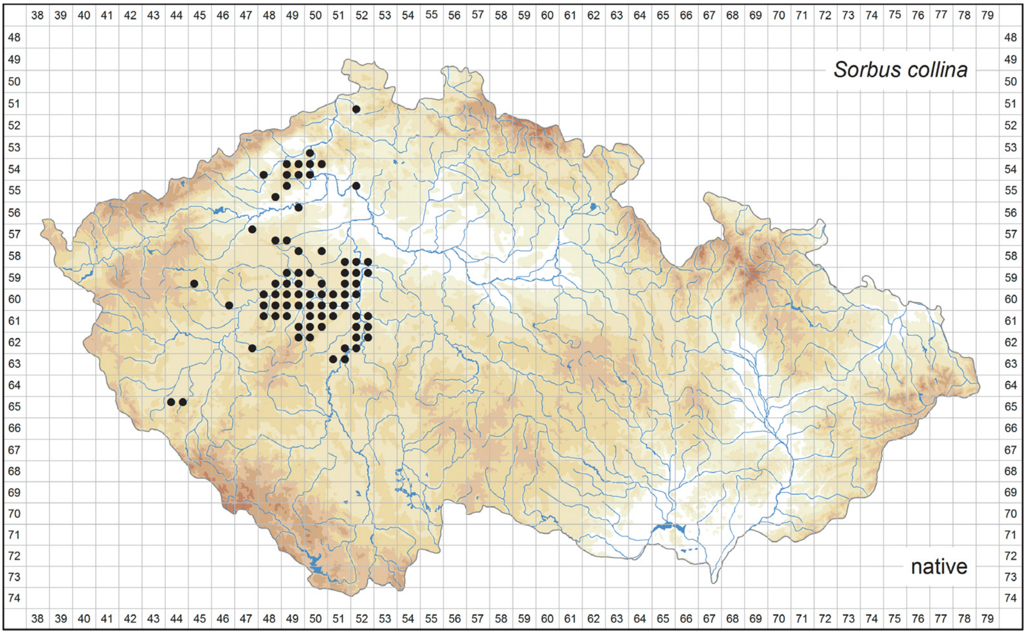

Fig. 58. – Distribution of *Sorbus collina* in the Czech Republic (77 occupied quadrants). Prepared by Martin Lepší & Petr Lepší.

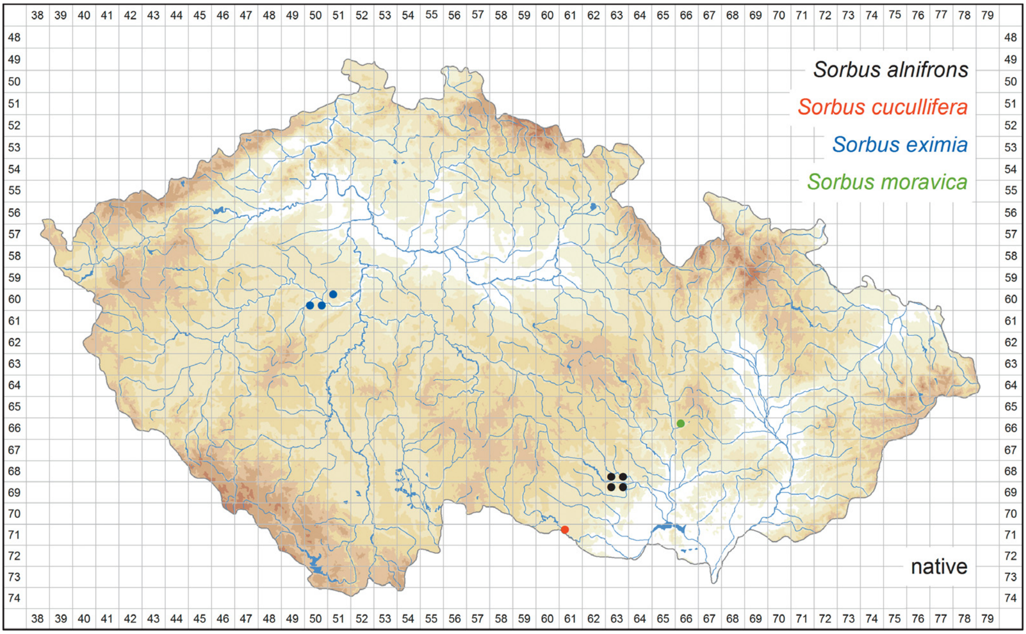

Fig. 59. – Distribution of *Sorbus alnifrons* (4 occupied quadrants), *S. cucullifera* (1 occupied quadrant), *S. eximia* (3 occupied quadrants) and *S. moravica* in the Czech Republic (1 occupied quadrant). Prepared by Martin Lepší & Petr Lepší.

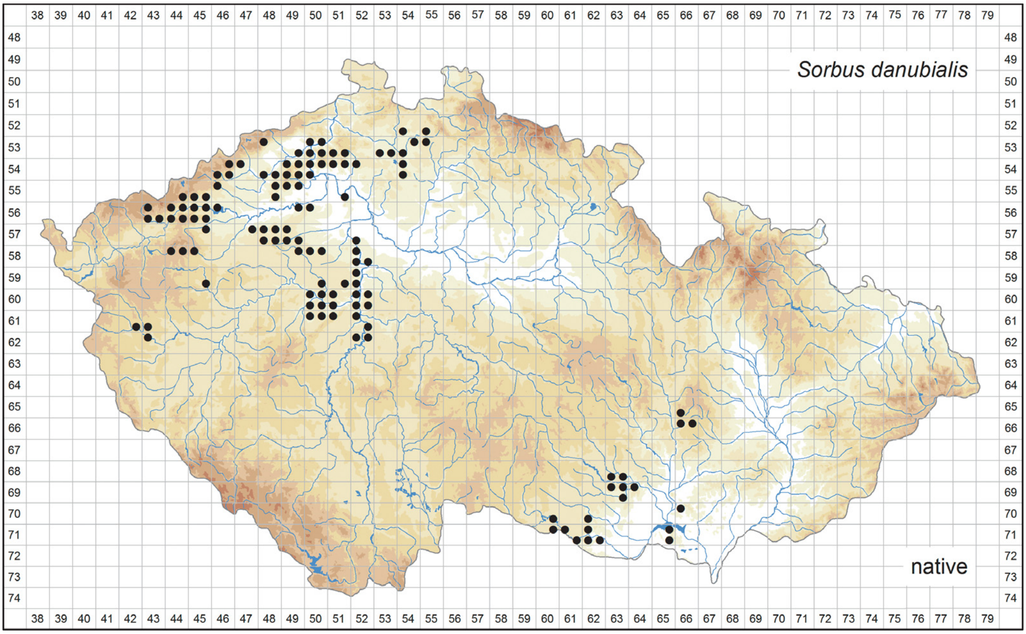

Fig. 60. – Distribution of *Sorbus danubialis* in the Czech Republic (120 occupied quadrants). Prepared by Martin Lepší & Petr Lepší.

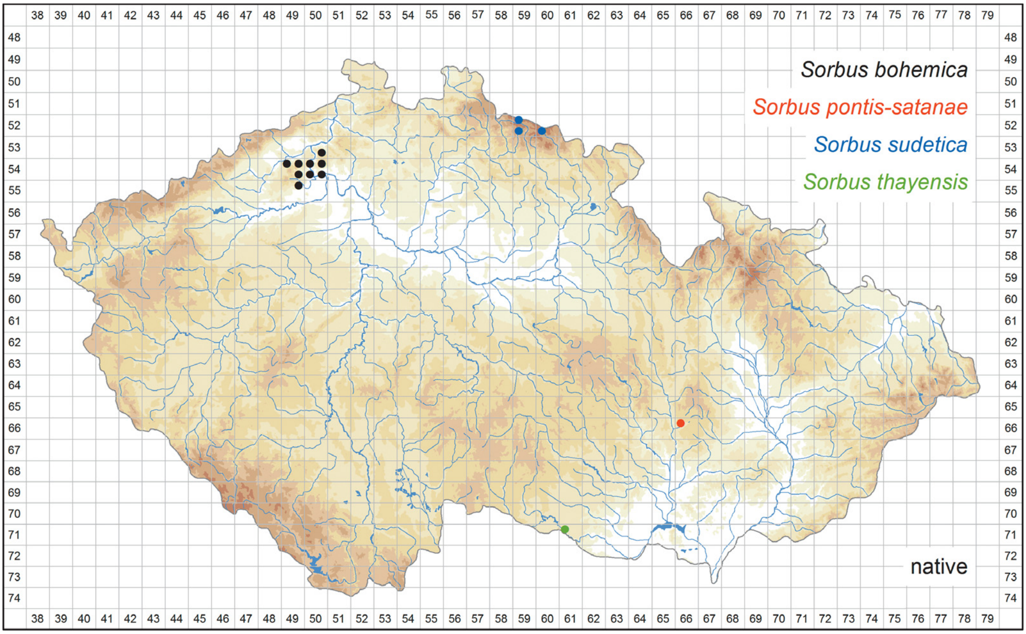

Fig. 61. – Distribution of *Sorbus bohemica* (9 occupied quadrants), *S. pontis-satanae* (1 occupied quadrant), *S. sudetica* (3 occupied quadrants) and *S. thayensis* in the Czech Republic (1 occupied quadrant). Prepared by Martin Lepší & Petr Lepší.

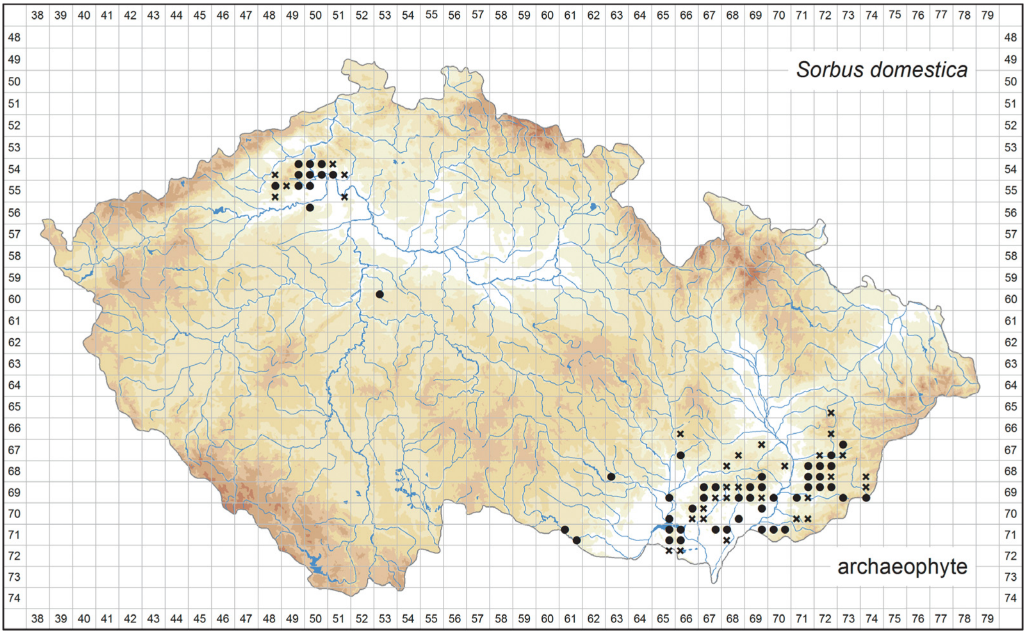

Fig. 62. – Distribution of *Sorbus domestica* in the Czech Republic: ● spontaneous escapes (52 quadrants), × deliberately planted in the countryside and uncertain origin (32 quadrants). Prepared by Martin Lepší, Petr Lepší, Zdeněk Špíšek & Karel Kubát.

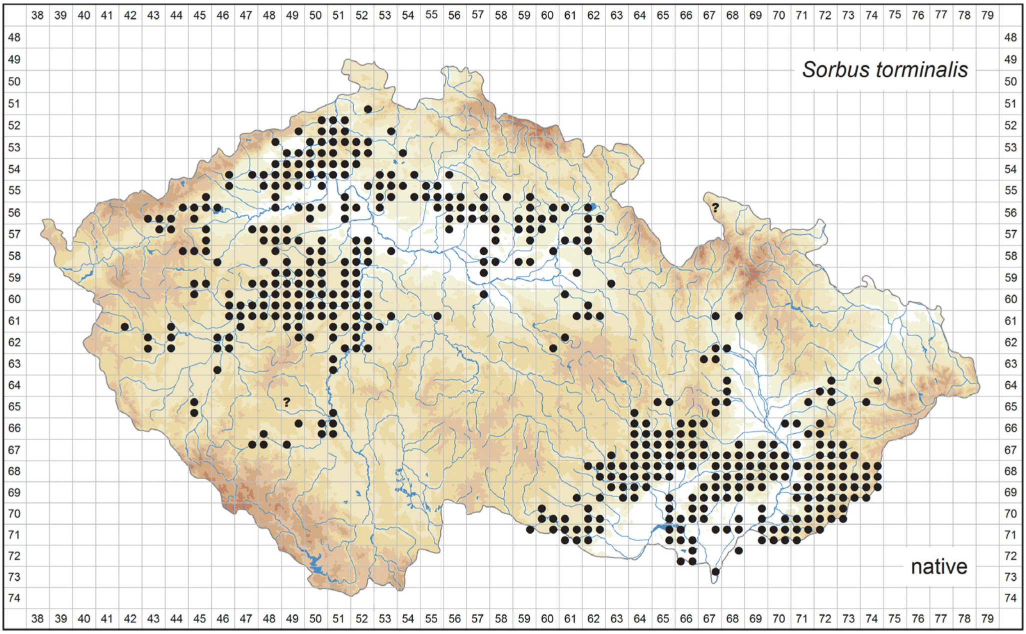

Fig. 63. – Distribution of *Sorbus torminalis* in the Czech Republic (475 occupied quadrants). Prepared by Martin Lepší & Petr Lepší.

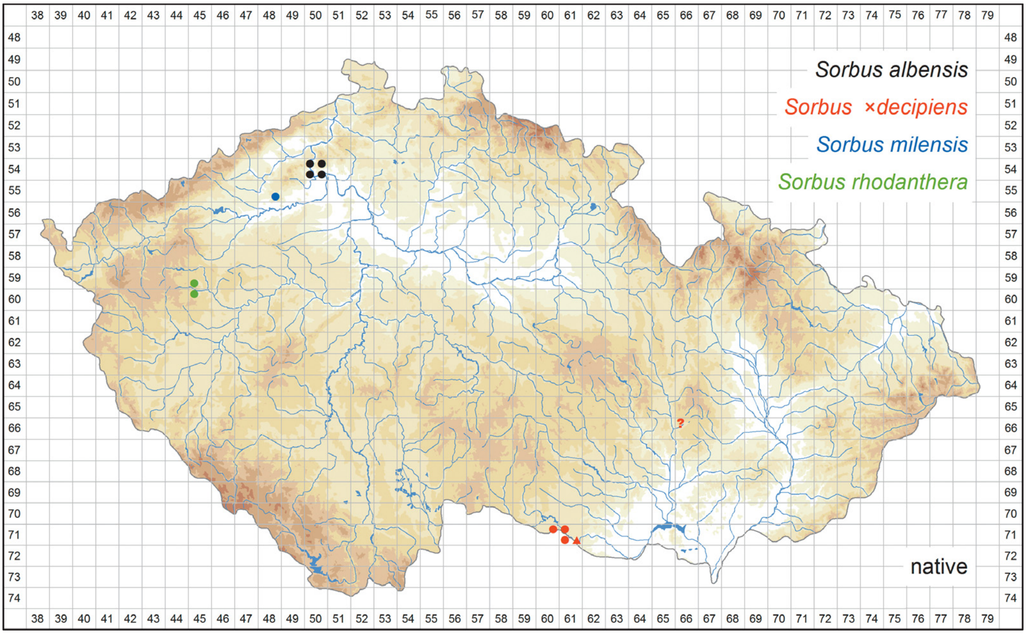

Fig. 64. – Distribution of *Sorbus albensis* (4 occupied quadrants), *S. milensis* (1 occupied quadrant), *S. rhodanthera* (2 occupied quadrants) and *S. ×decipiens* in the Czech Republic (● occurrence documented by herbarium specimens: 3 quadrants, ▲ occurrence based on other records: 1 quadrant). Prepared by Martin Lepší & Petr Lepší.

warm to moderately warm areas of central, western and north-western Bohemia and of southern Moravia. Its populations are scattered throughout these areas, depending on the presence of rocky slopes and rock outcrops. It was recorded particularly in the deep river valleys of the middle stretches of the Vltava, Dyje and Jihlava rivers and in areas with calcareous rocks (the karst areas of Český kras and Moravský kras, the Pavlovské vrchy hills and Džbán hills) or other base-rich, usually volcanic bedrocks (Doupovské hory Mts, České středohoří Mts, the surroundings of the town of Doksy). It grows in the colline and supracolline, and rarely also in the montane vegetation belts. The altitudinal range of the species extends from 175 m to 940 m. It is classified as vulnerable because of its scarcity (Grulich 2012).

Sorbus moravica and *S. pontis-satanae* are narrow endemics of the Suchý žleb gorge near the village of Lažánky in the karst area of Moravský kras. The populations, found at altitudes of 360–490 m, consist of about 200 and 30 individuals, respectively. Both species should be classified as critically threatened (Lepší et al. 2015).

With the exception of *Sorbus domestica*, *S. torminalis* and *S. aucuparia*, the distribution maps of the *Sorbus* taxa were based solely on revised herbarium specimens and our own field records.

Sorbus subg. *Chamaespilaria*
Sorbus sudetica (Fig. 61)

Sorbus subg. *Chamaespilaria* includes taxa that have arisen from hybridizations between the species of *S.* subg. *Aria* and *S.* subg. *Chamaemespilus*. It occurs in the subalpine and alpine belts of mountains in the southern half of Europe (Kutzelnigg 1995).

Sorbus sudetica is endemic to the Krkonoše Mts, representing there an outpost at the northern limit of the distribution range of the subgenus. Unlike most other species of this subgenus, at present it occurs there without its parental species, *S. chamaemespilus* and an unknown member of *S.* subg. *Aria*. In the Czech Republic it has been recorded in the Labský důl valley and the Obří důl valley, which are about 13.5 km apart. The small population once present near the Mały Staw lake in Poland does not exist any more (Kovanda 1998). *Sorbus sudetica* grows on steep slopes of glacial cirques at altitudes of about 1060–1350 m. It inhabits rocks, screes, subalpine grasslands, montane to subalpine heathland, scrub and the fringes of forest gaps. The species has probably vanished from four of its ten sites and the number of individuals at the remaining localities has declined. Currently, the estimated total number of individuals is about 110, including 10 planted individuals in the Labský důl valley (J. Zahradníková, pers. comm. 2014). It is classified as critically threatened because of its rarity and population decline (Grulich 2012).

Sorbus subg. *Cormus*
Sorbus domestica (Fig. 62)

Sorbus domestica, the only member of *S.* subg. *Cormus*, is distributed in central and southern Europe from eastern Spain to southern Great Britain, northern France, Germany, Slovakia, Hungary and the Balkan Peninsula, with outposts in the Black Sea area, Anatolia and in Morocco and Algeria in northern Africa (Rotach 2003, George et al. 2016). The species has been planted in some warm areas of the Czech Republic as a fruit tree since the Medieval period (Pyšek et al. 2012) and it has become widely naturalized in the České středohoří Mts in north-western Bohemia and in several parts of southern Moravia (e.g. the Pavlovské vrchy, Ždánický les, Chřiby and Vizovická vrchovina hills and the Bílé Karpaty Mts). The southernmost and easternmost localities in Moravia are close to the northern limit of its assumed native distribution area in Slovakia or Hungary (Kurtto 2009) and perhaps some of them may be native. However, direct evidence of its native occurrence in southern Moravia is lacking. In the České středohoří Mts it is almost solely confined to areas where *Quercus pubescens* also grows. Because it has been grown not only in villages but commonly also planted in vineyards and elsewhere, it is often difficult to distinguish intentionally planted individuals from bird-sown escapes. The map therefore distinguishes spontaneous escapes and naturalized populations from trees of uncertain origin, including those planted outside settlements. The trees planted in gardens and parks are not mapped. The escaped plants are found in thermophilous oak and open hornbeam forests, forest edges and scrub. Most of the records are from the planar to colline, rarely up to the supracolline vegetation belts, with an altitudinal maximum at 470 m. *Sorbus domestica* is classified as a casual archaeophyte in the Czech Republic (Pyšek et al. 2012).

Sorbus subg. *Tormaria*
Sorbus torminalis (Fig. 63)

There are two taxa within *S.* subg. *Tormaria*: the widespread *S. torminalis* and the Iranian species *S. tiliifolia* (Rich et al. 2010). The distribution range of *S. torminalis* extends from the British Isles and the Baltic countries southwards to northern Africa and eastwards to the Caspian Sea (Meusel et al. 1965). In the Czech Republic it occurs in warm to moderately warm areas of Bohemia and Moravia but it is usually absent from the largely deforested lowlands. *Sorbus torminalis* grows in oak, hornbeam, calcareous or open beech forests, forest fringes and scrub and occasionally colonizes abandoned dry grasslands. It is rarely planted in the countryside by foresters and grown as an ornamental in parks and towns. Most of the records are from the colline and supracolline vegetation belts, and several from the submontane belt, with an altitudinal maximum at 760 m on Mt Milešovka in the České středohoří Mts. It is classified as near threatened (Grulich 2012) because its habitats disappear as open forests develop a dense canopy, or are replaced by conifer and *Robinia pseudoacacia* plantations.

Sorbus subg. *Torminaria* (*S. latifolia* agg.)
Sorbus albensis (Fig. 64), *S. alnifrons* (Fig. 59), *S. barrandienica* (Fig. 65),
S. bohemica (Fig. 61), *S. eximia* (Fig. 59), *S. gemella* (Fig. 65), *S. latifolia* (Fig. 66),
S. milensis (Fig. 64), *S. omissa* (Fig. 65), *S. portae-bohemicae* (Fig. 65),
S. rhodanthera (Fig. 64), *S.* ×*decipiens* (Fig. 64) and *S.* ×*kitaibeliana* (Fig. 67)

This subgenus contains species that have originated as hybrids and backcrosses between *S.* subg. *Aria* and *S.* subg. *Tormaria*. It occurs in western, central and southern Europe and in Anatolia, where the distribution of *S. torminalis* overlaps with that of members of *S.* subg. *Aria* (Rich et al. 2010, Zieliński & Vladimirov 2013). The Czech species of the subgenus inhabit mainly open oak, hornbeam, ravine and pine forests, forest fringes and rock scrub and occasionally also rocks, screes and rock and forest steppes. Besides seminatural forests, *S. alnifrons*, *S. eximia*, *S. gemella* and *S. rhodanthera* occasionally grow in *Larix decidua*, *Picea abies*, *Pinus nigra*, *P. sylvestris* and rarely *Robinia pseudoacacia* plantations or in their clearings. The main threat to these hybridogenous species stems from the cessation of coppicing and hay making, which maintained open forests. High forests, the currently prevailing forest management practice, creates stands with a closed canopy, which are too shady for the long-term survival and reproduction of light-demanding *Sorbus* species. The members of this subgenus occur from the planar to the supracolline vegetation belts in the Czech Republic.

Sorbus albensis, *S. bohemica* and *S. portae-bohemicae* are endemic to the České středohoří Mts in north-western Bohemia, occurring in the surroundings of the deep valley of the Labe river between the town of Lovosice and the city of Ústí nad Labem (Lepší et al. 2009). *Sorbus bohemica* is the most widespread hybridogenous *Sorbus* species in the Czech Republic with a distribution area of about 16 × 15 km. It has been recorded at 36 localities and the total population is about 1100 trees. The species has disappeared from four sites and its natural reproduction is poor and therefore it is classified as endangered (Grulich 2012). *Sorbus albensis* grows at 15 localities east of the town of Litoměřice and the population consists of about 600 individuals. The distance between the most distant localities is nearly 6 km. The species is classified as endangered (Grulich 2012). *Sorbus portae-bohemicae* is confined to two sites about 1.2 km apart in the northern surroundings of the town of Lovosice in the Oparenské údolí valley and on Lovoš hill. Only about 30 trees are currently known. The species is listed as critically threatened (Grulich 2012). *Sorbus milensis* is a narrow endemic of the basaltic hill of Milá in the southern part of České středohoří Mts. At least 60 individuals of diverse age have been recorded (Lepší et al. 2008). It is classified as critically threatened because of its rarity and sparse regeneration (Grulich 2012).

Sorbus alnifrons is endemic to the valley of the Jihlava river near the town of Ivančice in south-western Moravia. The population consists of about 200 individuals and spans a length of valley of about 2.5 km. It is classified as critically threatened because of its scarcity (Grulich 2012).

Sorbus barrandienica and *S. eximia* are central-Bohemian endemics recorded in the karst area of Český kras between Prague and the town of Beroun, the latter species being described only recently (Vít et al. 2012). About 330 individuals of the former are documented at 5 sites, and only 50 plants at 10 sites are reported for the latter. *Sorbus barrandienica* is classified as critically threatened (Grulich 2012) as there are few individuals, many of them old or dying, while juveniles are lacking at most localities. *Sorbus eximia* is considered endangered (Grulich 2012).

Sorbus gemella, an endemic of the Džbán hills, has been recorded at 13 localities and the estimated total number of individuals is 300. The distance between the localities that are furthest apart is about 9 km. The species is classified as critically threatened due to its rare regeneration (Grulich 2012).

Sorbus latifolia is native to France, while the records from other European countries require confirmation (Kutzelnigg 1995). Escapes from cultivation are reported in several European countries (Lepší et al. 2013b). In the Czech Republic it has been rarely planted in towns and parks and from there it has escaped near Prague and the towns or villages of Strakonice, Nečtiny, Březina, Orlík nad Vltavou, Ivančice and Valtice. Its habitats include scrub, rocks, open woodland and parks. It is classified as a casual alien (Pyšek et al. 2012).

Sorbus omissa is confined to the deep valley of the lower stretches of the Vltava river north of Prague in central Bohemia. At least 149 plants are known at two sites 3.6 km apart (Velebil 2012). The species is classified as critically threatened due to the small population size, poor regeneration and lack of other suitable habitats for further spread (Grulich 2012, Velebil 2012).

Sorbus rhodanthera is now known to be an endemic confined to Chlumská hora hill near the town of Manětín in western Bohemia, where there are at least 700 individuals. The species is classified as critically threatened (Grulich 2012).

Sorbus ×decipiens is a diploid hybrid between *S. torminalis* and *S. aria*. It occurs in Europe where the parents grow sympatrically (Rich et al. 2010). In the Czech Republic it is very rare due to the scarcity of *S. aria*. Approximately 15 individuals are found in the valley of the Dyje river south of the town of Vranov nad Dyjí in southern Moravia. These individuals together with plants from adjacent Lower Austria were mistakenly described as a hybridogenous species *S. hardeggensis* (Kovanda 1996). The taxonomic identity of a single diploid tree in the Suchý žleb gorge near Lažánky in the karst area of Moravský kras is uncertain as *S. aria* s. str. does not occur at the locality and the *S.* subg. *Aria* parent may have been one of the co-occurring polyploids, i.e. *S. danubialis*, *S. moravica* or *S. pontis-satanae*.

Sorbus ×kitaibeliana is a rare hybrid between *S. danubialis* and *S. torminalis*, hitherto known only from its type locality in northern Hungary (Kárpáti 1960). In the Czech Republic one individual has been recorded near the city of Ústí nad Labem in northern Bohemia. This name was misapplied by Kovanda (1996) to an individual of *S. latifolia* escaped at Pekárka hill near Ivančice in south-western Moravia.

Sorbus subg. *Soraria* (*S. hybrida* agg.)
Sorbus austriaca (Fig. 68), *S. mougeotii* (Fig. 69), *S. pauca* (Fig. 67), *S. ×abscondita* (Fig. 70) and *S. ×thuringiaca* (Fig. 67)

This subgenus involves European and Asian taxa that originated from hybridizations between the species of *S.* subg. *Sorbus* and those of *S.* subg. *Aria*. In Europe the subgenus includes hybrids and hybridogenous species with the parentage of *S. aucuparia* and *S. subg. Aria*, usually found in the areas where the parental species co-occur. They are most frequent in northern Europe and in the mountains of central and southern Europe. In the Czech Republic three native and two alien taxa occur.

Sorbus austriaca in the narrow circumscription is endemic to the Austrian Alps. In the Czech Republic it has rarely been grown and found as rare garden escapes in parks, hedges in towns and in scrub in the countryside near or in the towns of Český Krumlov, Průhonice, Benešov, Krahulčí near Telč and Rokycany. Previous reports on its native occurrence in the Dyje river valley between the towns of Vranov nad Dyjí and Znojmo and the karst area of Moravský kras (Kovanda 1996, 1997a) have been shown to be dubious (Lepší et al. 2015).

Sorbus mougeotii, a montane western-European species, is occasionally planted in the Czech Republic and also in other European countries as a roadside, street or garden tree. It has become naturalized in scrub and open oak-hornbeam woodland at three sites in Prague and has escaped in the city of České Budějovice. Two Prague populations, together consisting of about 100 individuals, were superfluously described as *S. quernea* (Lepší et al. 2013b).

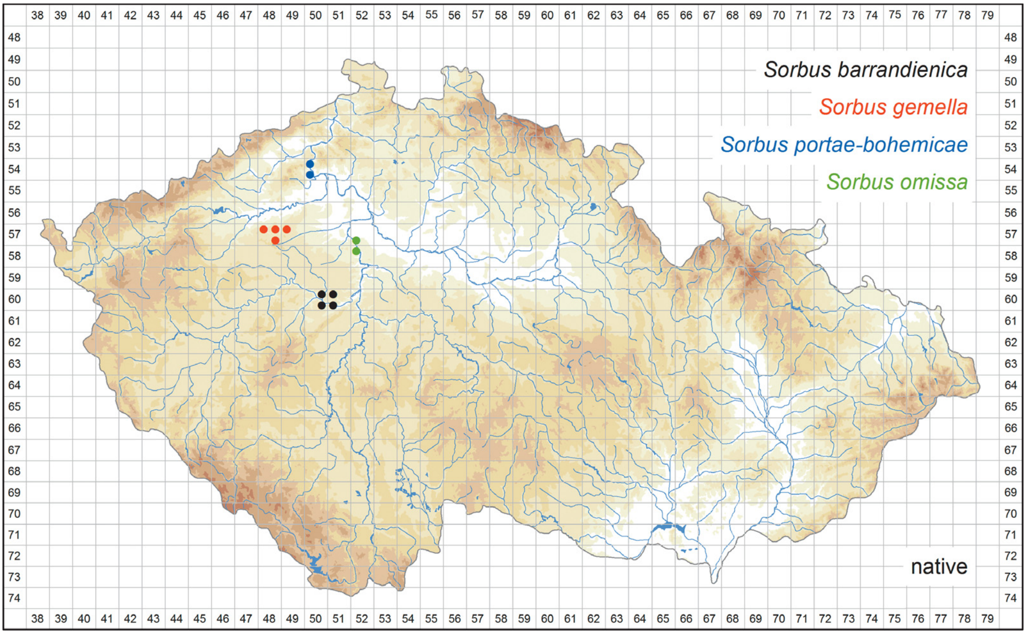

Fig. 65. – Distribution of *Sorbus barrandienica* (4 occupied quadrants), *S. gemella* (4 occupied quadrants), *S. omissa* (2 occupied quadrants) and *S. portae-bohemicae* in the Czech Republic (2 occupied quadrants). Prepared by Martin Lepší & Petr Lepší.

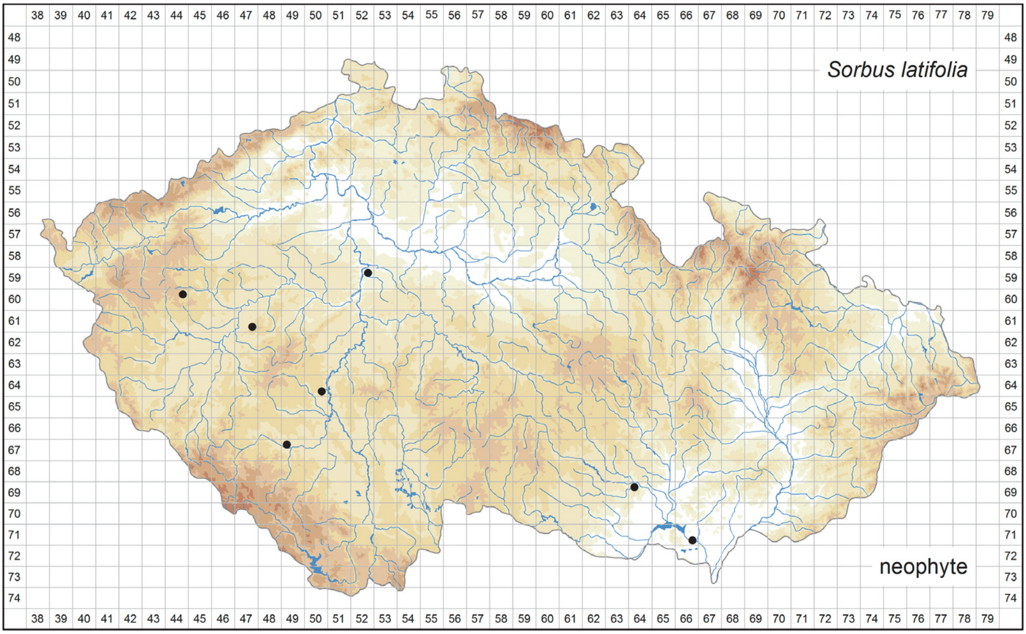

Fig. 66. – Distribution of *Sorbus latifolia* in the Czech Republic (7 occupied quadrants). Prepared by Martin Lepší & Petr Lepší.

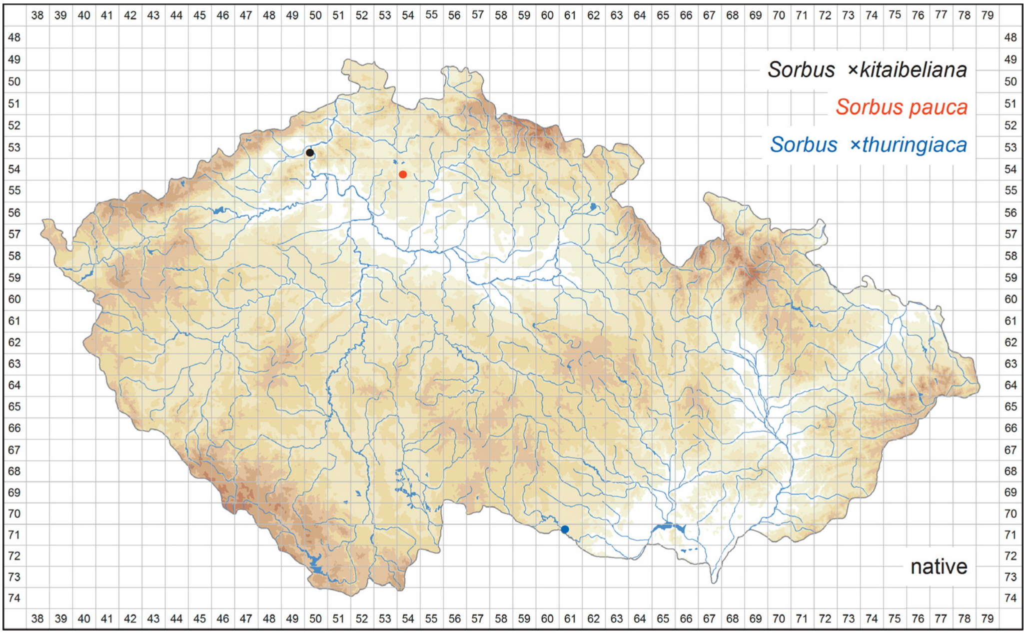

Fig. 67. – Distribution of *Sorbus pauca* (1 occupied quadrant), *S. ×kitaibeliana* (1 occupied quadrant) and *S. ×thuringiaca* in the Czech Republic (1 occupied quadrant). Prepared by Martin Lepší & Petr Lepší.

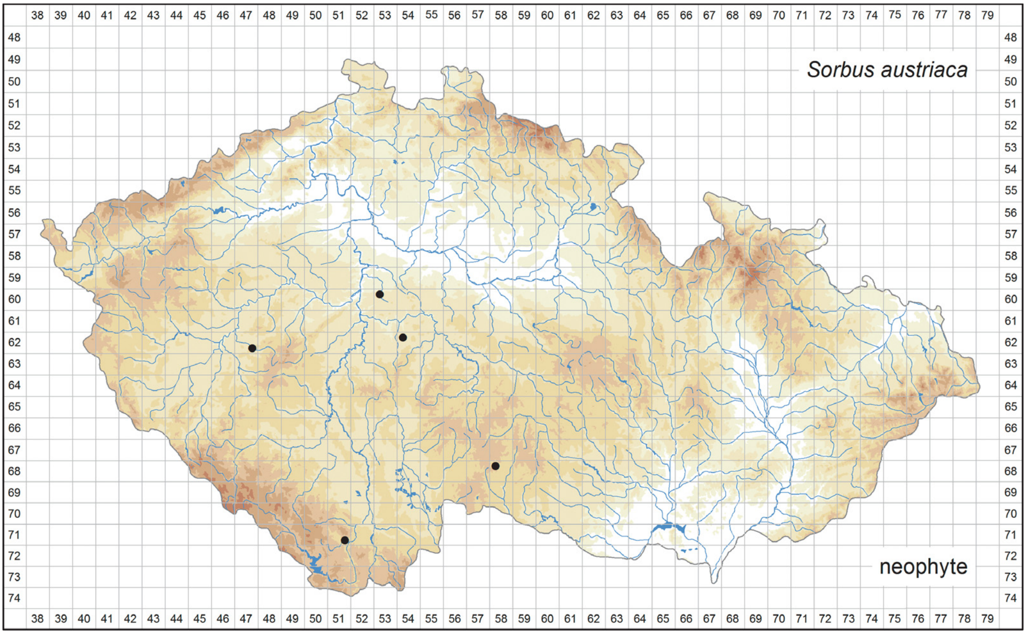

Fig. 68. – Distribution of *Sorbus austriaca* in the Czech Republic (5 occupied quadrants). Prepared by Martin Lepší & Petr Lepší.

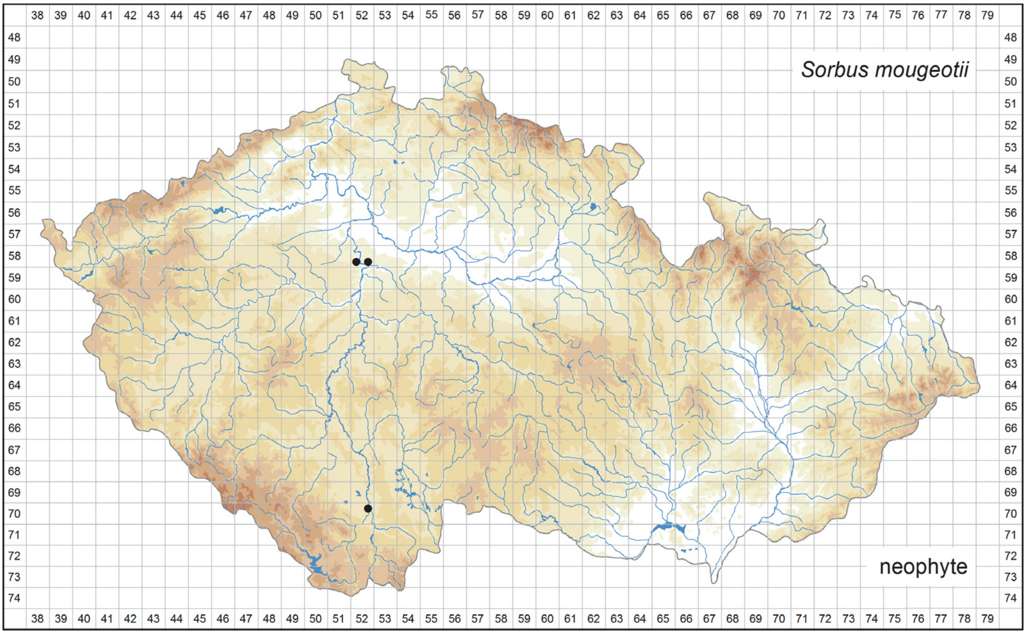

Fig. 69. – Distribution of *Sorbus mougeotii* in the Czech Republic (3 occupied quadrants). Prepared by Martin Lepší & Petr Lepší.

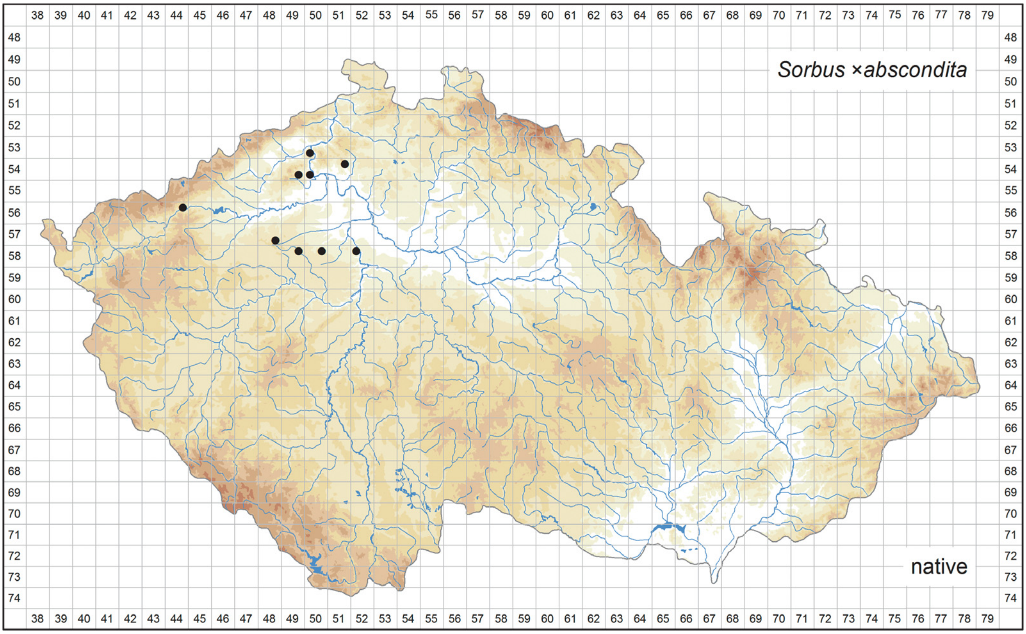

Fig. 70. – Distribution of *Sorbus ×abscondita* in the Czech Republic (9 occupied quadrants). Prepared by Martin Lepší & Petr Lepší.

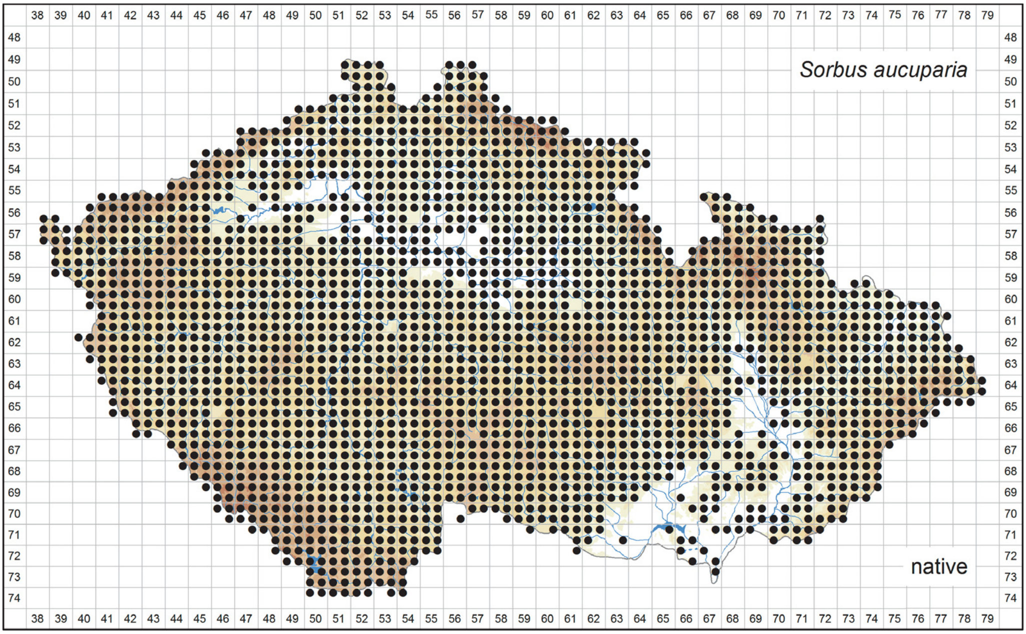

Fig. 71. – Distribution of *Sorbus aucuparia* in the Czech Republic (2334 occupied quadrants). Prepared by Petr Lepší & Martin Lepší.

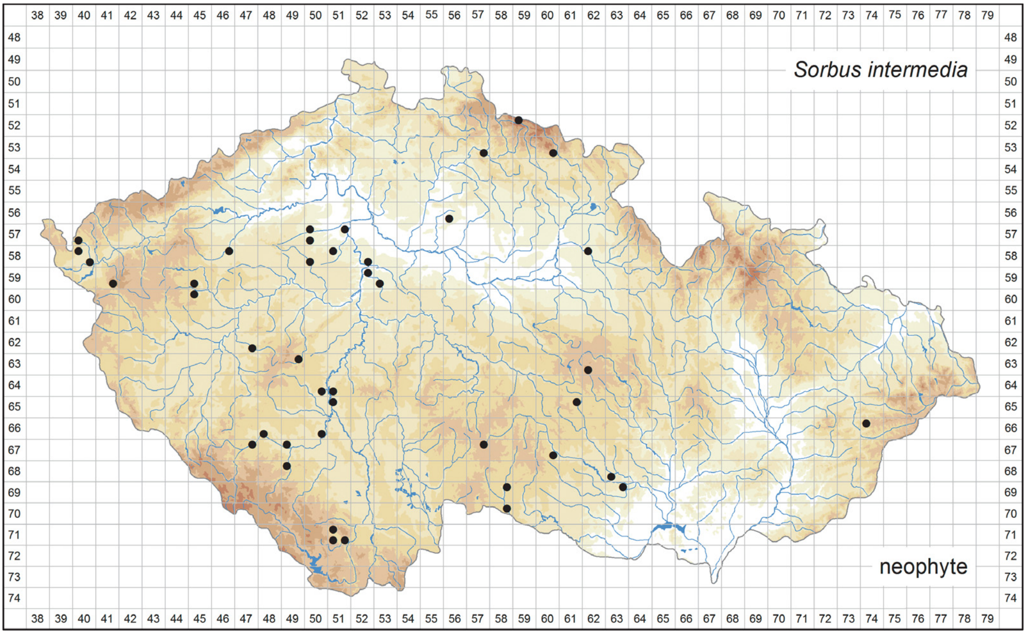

Fig. 72. – Distribution of *Sorbus intermedia* in the Czech Republic (42 occupied quadrants). Prepared by Martin Lepší & Petr Lepší.

Sorbus pauca is a narrow endemic of two close phonolite hills Malý Bezděz and Bezděz near the town of Doksy in northern Bohemia (Lepší et al. 2013a). Its parents are *S. aucuparia* and *S. danubialis*. It grows in scrub and grasslands on sunny rocks and on the slopes of an abandoned quarry in the supracolline vegetation belt at altitudes of 440–580 m. Its population consists of only 16 individuals and it is therefore classified as critically threatened (Grulich 2012).

Sorbus ×*abscondita* is a rare hybrid between *S. danubialis* and *S. aucuparia*. So far it has been recorded at 9 localities in Bohemia and at all except two only one individual was present.

Sorbus ×*thuringiaca* is a diploid sexual hybrid between *S. aucuparia* and *S. aria*. It is widespread but sporadic in Europe where its parents co-occur (Rich et al. 2010). In the Czech Republic it is very rare due to the scarcity of *S. aria*. Only two trees and three saplings at three sites have been recorded in ravine and oak forests in the valley of the Dyje river south of the town of Vranov nad Dyjí in southern Moravia.

Sorbus subg. *Sorbus*
Sorbus aucuparia (Fig. 71)

This subgenus is widely distributed in the temperate zones of the Northern Hemisphere and includes about 70 species (McAllister 2005).

Sorbus aucuparia occurs from Iceland, Madeira and northern Africa eastwards to northern China and Kamchatka and as an alien it is reported from North America (McAllister 2005). In the Czech Republic it is widespread throughout the country but with different frequencies. It is abundant primarily in rather cold and largely forested regions but rare in or even absent from the largely deforested lowlands of Bohemia and Moravia. At least some of these gaps represent true absences, while the others may be due to low frequency or under-recording. It is frequent in open broadleaved and coniferous forests and their fringes, forest openings and clearings and on rocks and screes. It is a pioneer tree able to colonize abandoned pastures, waste ground, railways and roadsides. *Sorbus aucuparia* is often grown as a street, roadside and fruit tree, and it is therefore hardly possible to distinguish native occurrences from escaped trees. It is distributed from the planar to subalpine vegetation belts with an altitudinal maximum at 1450 m in the Krkonoše Mts (Kovanda 1992).

Sorbus subg. *Triparens*
Sorbus intermedia (Fig. 72)

Sorbus subg. *Triparens* includes *S. intermedia* and *S.* ×*liljeforsii*, which both originated from the crossing of three taxa: a species of *S.* subg. *Aria*, *S. torminalis* and *S. aucuparia* (Rich et al. 2014).

Sorbus intermedia is generally regarded as native to southern Sweden and parts of the Baltics and it has occasionally become naturalized elsewhere in Europe (Kurtto 2009). In the Czech Republic it is commonly planted for ornamental purposes in towns and parks and along highways. It occurs rarely across the country in scrub, forest fringes, open mixed and oak forests, *Pinus sylvestris* plantations, on rocks, in dry grasslands, on stony walls and in quarries, usually as an escape from cultivation. Based on old literature records and 19th-century herbarium specimens from the subalpine areas of the Krkonoše

Mts, Kovanda (1997b) considers *S. intermedia* as possibly native, explaining its presence by long-distance dispersal by birds from the Baltic countries.

Spirodela polyrhiza (Fig. 73)

Spirodela polyrhiza is a nearly cosmopolitan species. It is found in most of Europe except its northern and north-eastern parts, in Asia it is rare in Siberia but more frequent in south-western, southern and south-eastern Asia eastwards as far as the Russian Far East and Japan and southwards through islands as far as Australia. It also occurs in most of North America, extending south to Colombia, Ecuador and Peru in South America. In Africa it is found in its northernmost, central and southern parts (Hultén & Fries 1986, Landolt 1986, Crawford et al. 2006). In the Czech Republic *S. polyrhiza* grows in ponds and small concrete reservoirs in villages, in fishponds, fish storage ponds, alluvial pools, oxbow lakes, drainage ditches, sometimes also in flooded sand-pits and along banks of slowly flowing lowland rivers. It mostly occurs in eutrophic to hypertrophic water above a thick layer of sapropelic mud or organic silt on the bottom. It tolerates eutrophication and organic pollution (Šumberová 2011g). It is most frequent at middle altitudes, particularly in Bohemia and in the Českomoravská vrchovina highlands, while in the warm and dry lowlands it is restricted to river floodplains. It is rare in or locally absent from the mountains, dry areas with base-rich to saline soils and from most of Moravia, where suitable habitats are missing.

Symphytum asperum (Fig. 74)

Symphytum asperum is probably native to the Caucasus and Anatolia or to adjacent regions (Bucknall 1913, Kurtto 1982). It has become widely naturalized all over Europe (Pawłowski 1972, Smejkal 1978, Hultén & Fries 1986), in North America (Gadella 1984) and Japan (Fedorov 2001), mainly as a nectar-bearing and forage plant. The earliest records from the Czech Republic date back to the second half of the 19th century when it was grown mainly as livestock fodder (Smejkal 1978). Since then it has escaped several times and became locally naturalized (Pyšek et al. 2012). The records of *S. asperum* are scattered throughout Bohemia, mainly in the surroundings of the towns of Klatovy, Strakonice and Prachatice. The species was collected in ruderal grasslands in settlements, parks, castle gardens, railway stations, and along roads and railways. In the Czech Republic it was recorded particularly in the 1970s, and there have been only two finds since 2000. The map is based solely on revised herbarium specimens because some literature records may be wrong, based on misidentifications of *S. officinale* or *S. ×uplandicum*.

Symphytum bohemicum (Fig. 75)

Symphytum bohemicum is a diploid member of the *S. officinale* group. It is quite well defined morphologically by its greenish or yellowish white flowers and only shortly decurrent leaves. It was described from central Bohemia by F. W. Schmidt as early as the late 18th century (Kirschner et al. 2007). Further records of the diploid white-flowered "*S. officinale*" that we consider to be *S. bohemicum* are from eastern England, the Netherlands, Germany, southern Poland, south-eastern Slovakia, northern Hungary, south-western Slovenia and northern Italy (Gadella & Kliphuis 1969, 1972, Májovský &

natans, mizí a místo nich se v krajině objevují vysazené rostliny neznámého původu, často zakoupené v zahradnických velkoprodejnách. Takové výsadby mohou způsobit genetickou erozi našich původních populací. Atraktivní vzhled je příčinou stále častější výsadby i nepůvodních okrasných druhů, zejména *Eichhornia crassipes*, *Pistia stratiotes* a *Pontederia cordata*. Všechny tři byly u nás zaznamenány jako vysazené do přírody během posledních 25 let, poté co se objevily ve specializovaných obchodech. Naproti tomu okřehek *Lemna turionifera* k nám byl zavlečen a dále rozšířen vodními ptáky a dnes se již nachází téměř po celém území státu. Popis zavlečení a šíření je uveden i u dnes zdomácnělého a velmi rozšířeného puškvorce *Acorus calamus* a zavlečených druhů rodů muchovník (*Amelanchier*) a kostival (*Symphytum*). Celkový obraz rozšíření jednotlivých zpracovávaných taxonů poskytují mapy; konkrétní floristické údaje odrážející odlišné trendy v různých oblastech a v různých obdobích jsou uloženy v databázi Pladias a dostupné v elektronických přílohách. Každou mapu doprovází textový komentář, který obsahuje nástin celkového rozšíření, výčet nejčastějších stanovišť a stručnou charakteristiku rozšíření v České republice, případně i doplňující informace k taxonomii, biologii, změnám v rozšíření a míře ohrožení.

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Received 9 September 2016
Revision received 11 November 2016
Accepted 13 November 2016

Paper VI

British *Sorbus* (Rosaceae): Six new species, two hybrids and a new subgenus.

Rich T. C. G., Green D., Houston L., Lepší M., Ludwig S. & Pellicer J.
(2014) New Journal of Botany 4 (1): 2–12.

Picture on previous page *Sorbus intermedia*, planted in Lovosice

British *Sorbus* (Rosaceae): six new species, two hybrids and a new subgenus

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Six new *Sorbus* species are described in *Sorbus* subgenus *Aria*; *S. evansii* T.C.G. Rich, sp. nov., *S. greenii* T.C.G. Rich, sp. nov., *S. herefordensis* D. Green, sp. nov., *S. richii* L. Houston, sp. nov., *S. sellii* T.C.G. Rich, sp. nov., and *S. spectans* L. Houston, sp. nov. The occurrence of two new subgeneric hybrids is noted – *S. aucuparia* × *minima* (subgenus *Soraria*) and a distinct member of subgenus *Tormaria* of unknown parentage – which do not merit binomials. Subgenus *Triparens* M. Lepší & T.C.G. Rich is described to accommodate taxa that originated as crosses between *Sorbus* subgenus *Aria*, subgenus *Sorbus* and subgenus *Torminaria*.

Keywords: Britain, *Sorbus decipiens*, whitebeam

Introduction

Following publication of our monograph of British and Irish *Sorbus* (Rich *et al.*, 2010), we have continued working on *Sorbus* and have re-examined some taxonomic problems and discovered some new taxa. The more significant of these new taxa are described as new species below. In addition, for consistency of the infra-generic classification, as set out by Rich *et al.* (2010, p.29), we have described a new subgenus to cover the triple hybrids in the *S. intermedia* group.

These six species and two hybrids add more to the existing centres of *Sorbus* diversity and evolution in the Avon Gorge, Brecon Beacons and Wye Valley (Rich *et al.*, 2009, 2010). Like the other polyploid *Sorbus* species they are all likely to be apomictic, although this has only been demonstrated for *S. spectans* whose microsatellite profile is uniform (S. Ludwig, unpublished).

Descriptions have been drawn up following the format of Rich *et al.* (2010) to allow comparisons to be made. Flow cytometry data are either as reported in Pellicer *et al.* (2012) or are new records estimated using the same methods. Conservation statuses are drawn up following the IUCN (2001) guidelines.

New species

1. ***Sorbus evansii*** T.C.G. Rich, **sp. nov**.

TYPE. Carboniferous Limestone outcrop, Seven Sisters, Great Doward, Herefordshire (v.c. 36), England, SO5470215312, 100 m altitude, *T.C.G. Rich,* 16 October 2013 (holotype **NMW**, accession no. V.2013.1.185).

Vernacular name: Evans's Whitebeam.

Description. Large tree or shrub to at least 6 m tall. Bark greyish-brown. Leaf buds lanceoloid, acute, pilose with white hairs on margins. Broad leaves of short sterile shoots (13–)14–25 × 9.5–12.5 cm, obovate, 1.3–1.7 times as long as wide and widest 56–70% of way along leaf length, usually unlobed or occasionally with a few very shallow lobes, apex rounded to obtuse, base cuneate and untoothed in lowest 1–2 cm, margins with acuminate, uniserrate to weakly biserrate outwardly directed acuminate teeth, veins 19–23 held at an angle of 29–40(–42)° to midrib at centre of the leaf, dark green above, greyish-green tomentose below. Petioles 13–25 mm. Flowers not seen. Largest fruit 9–13 × 11–15 mm, (0.7–)0.8–0.9 times as long as wide and usually looking globose or wider than long, red to dark red at maturity with few to occasional lenticels mainly at base of fruit.

Chromosome number: flow cytometry indicates this clone is triploid (11 samples; Pellicer *et al.* (2012), as *S. porrigentiformis* 'Symonds Yat clone').

Notes. *Sorbus evansii* belongs to subgenus *Aria* Pers., with simple leaves white-tomentose underneath and red fruits. This taxon is noted in Rich *et al.* (2010, p.16) as the fourth unresolved taxon from Seven Sisters Rocks in the *S. porrigentiformis* aggregate.

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DOI 10.1179/2042349714Y.0000000036

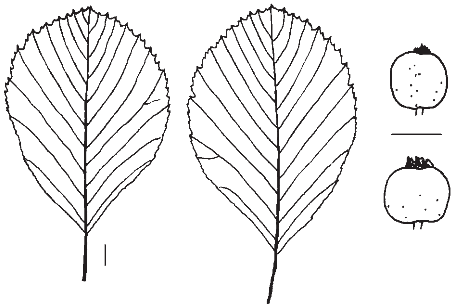

Figure 1 ***Sorbus evansii*** **showing typical leaves from short sterile shoots and ripe fruit. Scale bars 1 cm.**

The plants form a distinctive local group characterised by the usually unlobed, obovate leaves with rounded apices and cuneate bases and neat uniserrate acuminate teeth projecting around the margin with greyish-green undersides, and the small globose to wider than long fruits with few lenticels (Fig. 1).

The neat obovate leaves, greyish-green underneath, and the broad fruit distinguish this triploid from diploid *S. aria* (L.) Crantz. The relatively large leaves with neat uniserrate teeth but lacking lobes separate it from the tetraploid *S. porrigentiformis* E. F. Warb. sensu stricto. *Sorbus rupicola* (Syme) Hedl. has oblong, obtuse leaves and larger fruit. *Sorbus saxicola* T.C.G. Rich has narrower, more strongly lobed leaves. The tetraploids *S. eminens* E. F. Warb. and *S. eminentiformis* T.C.G. Rich have rotund or rotund-ovate leaves.

Isozyme analysis by Proctor & Groenhof (1992, as *S. graeca* (Spach) Kotschy sensu lato) showed this taxon was genetically different from the other *S. porrigentiformis* taxa that they studied. Studies of chloroplast types of two trees, including the type tree, by Chester *et al.* (2007) with updated identifications following Rich *et al.* (2010), revealed it had the 'Aria R' chloroplast type otherwise found in *Sorbus aria* and *S. eminentiformis* and it may well be of this hybrid origin.

Etymology. Named after the great Monmouthshire botanist Trevor G. Evans, whose broad botanical knowledge is admired greatly by T. Rich, a long-time friend. Trevor first showed us the type tree on the BSBI *Sorbus* meeting in September 1982, and it has been visited and studied much since.

Distribution. English endemic (Fig. 2). About 70 trees are known on the west side of the Great Doward, Herefordshire, v.c. 36, especially on Seven Sisters Rocks with more in the quarry near King Arthur's Cave, and in Gloucestershire, v.c. 34, around Symonds Yat Rock and on Coldwell Rocks. So far it has not been found across the Wye in Monmouthshire, v.c. 35, but could occur on the cliffs of Lady Park Wood.

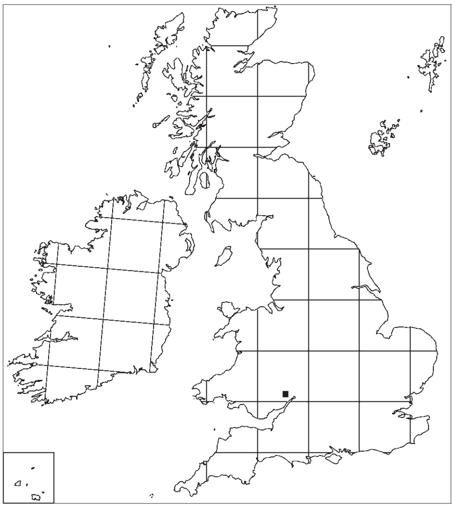

Figure 2 Distribution of *Sorbus evansii* in Britain.

Sorbus evansii occurs on the Carboniferous Limestone cliffs and rocks, associated with other *Sorbus* species *(S. aria, S. eminentiformis, S. greenii, S. rupicola, S. saxicola), Fraxinus excelsior, Quercus petraea, Taxus baccata* and *Tilia platyphyllos.*

Conservation status. IUCN (2001) threat category: Endangered.

2. ***Sorbus greenii*** T.C.G. Rich, **sp. nov.**

TYPE. Car Park Quarry, Great Doward, Herefordshire (v.c. 36), England, SO5471615669, 147 m altitude, *T.C.G. Rich,* 16 October 2013 (holotype **NMW**, accession no. NMW.V.2013.1.183; isotype **BM**).

Vernacular name. Green's Whitebeam.

Description. Tree to at least 15(–18) m. Bark brownish-grey. Leaf buds ovoid-conical, acute, pilose. Broad leaves of short sterile shoots (5.5–)7.0–10.0(–10.5) × (4.5–)5.0–7.0(–7.5) cm, 1.2–1.6 times as long as wide, obovate to broadly obovate, and widest 55–65% of way along leaf length, apex usually truncate in outline but sometimes acute or often mucronate with strong biserrate, forward-pointing acute lobes and teeth, base cuneate, veins (12–)14–20(–21) held at an angle of 25–35° to midrib at the centre of the leaf, upper side of leaf dark green, lower side greyish-green tomentose. Petioles (6–)7–17 mm. Inflorescences to 7 cm across, crowded, flat-topped. Flowers 12–15 mm across. Sepals green, narrowly triangular, eglandular. Petals 5.5–6.0 mm long, orbicular to oval, white. Anthers cream with slight reddening on edges. Styles 2, free to base, pilose. Largest fruits (9.5–)10–11 × 10–12 mm, (0.83–)0.85–1.05(–1.1) times as long as wide, mostly looking globose but a few may look longer than wide or wider than long, dark red at maturity (R.H.S. colour chart 46A, 46B) with few to frequent small lenticels.

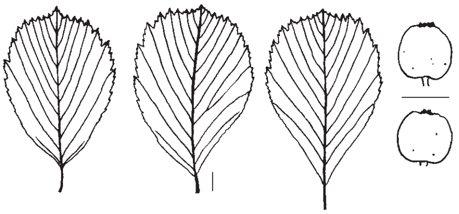

Figure 3 ***Sorbus greenii*** **showing typical leaves from short sterile shoots and ripe fruit. Scale bars 1 cm.**

Chromosome number: flow cytometry indicates this clone is triploid (3 samples; J. Pellicer, unpublished).

Notes. *Sorbus greenii* is a member of subgenus *Aria* with simple leaves white-tomentose underneath and red fruits, and has clear affinities to the *S. porrigentiformis* group (cf. Rich *et al.*, 2010). It is easily distinguished from all other *Sorbus* species by its leaves which are truncated at the apex but with strong biserrate, forward pointing acute lobes and a central mucronate lobe, though sometimes the central lobe is not that pronounced. The leaves are otherwise broadly obovate and cuneate at the base, with greyish-green tomentum underneath (Fig. 3).

Etymology. The tree is named after David Green who found it in 2009 and then first recognised it as a distinct clone in 2011.

Distribution. English endemic. It appears to be endemic to the Great Doward, Herefordshire, v.c. 36 (Figs. 4, 5). The earliest collection traced was on the BSBI *Sorbus* meeting on 18 September 1982 when a series of fallen leaves were collected by T. Rich as *S. porrigentiformis* (**NMW**, accession no. V1998.31.68). Surveys by D. Green between 2011 and 2013 revealed at least 59 individuals on the Great Doward, mainly in the quarries at SO547157 and SO546163 with a few larger trees scattered between. It has not yet been found in the adjacent calcareous woodlands in West Gloucestershire or Monmouthshire, Wales but should be looked for there.

It occurs with a range of age classes on the open sides of quarries and cliffs in *Fraxinus*-dominated secondary woodland with *S. aria, S. eminens, S. evansii, S. eminentiformis* and *S. saxicola.*

3. *Sorbus herefordensis* D. Green, sp. nov.

TYPE. Multi-stemmed tree on edge of field, Miners Rest, Great Doward, Herefordshire (v.c. 36), England, SO5524815784, 155 m altitude, *T.C.G. Rich*, 16 October 2013 (holotype **NMW**, accession no. V.2013.1.182; isotype **BM**).

Vernacular name. Herefordshire Whitebeam.

Description. Single or multi-stemmed coppiced tree to 20 m. Bark of larger trunks grey. Leaf buds ovoid, acute with white hairs on margins. Broad leaves of short sterile shoots thick and leathery, (8.0–)9.0–13.0(–15.0) × (5.5–)6.5–9.0(–9.5) cm, mostly elliptic or occasionally obovate, (1.25–)1.3–1.7 times as long as wide and widest (45–)48–61% of way along leaf, shallowly but distinctly and sometimes asymmetrically lobed 10–20(–25)% of way to midrib at centre of the leaf with broadly acute lobes, apex acute, base cuneate to broadly rounded, margin biserrate, veins (19–)20–25 held at an angle of (27–)30–40(–42)° to midrib in centre of leaf, upper surface dark green, lower surface densely white-tomentose. Petioles 12–30 mm. Inflorescences to 14 cm across, lax. Flowers to 20 mm across. Sepals narrowly triangular, green, eglandular. Petals 5.5–7 mm, round to oval, white. Anthers cream with hint of red on edges. Styles 2, free to base, pilose. Largest fruits 12–13 × 12–14 mm, 0.86–1.0 times as long as wide, broadly obovoid, red at maturity (R.H.S. colour chart 45A, 46B) with frequent small lenticels scattered over surface of fruit.

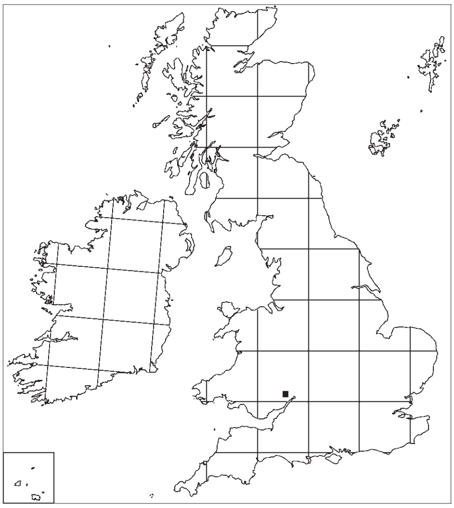

Figure 4 **Distribution of** ***Sorbus greenii*** **in Britain.**

Chromosome number: flow cytometry indicates this clone is triploid (4 samples; J. Pellicer, unpublished).

Notes. *Sorbus herefordensis* is a characteristic member of subgenus *Aria* with simple leaves which are densely white-tomentose underneath and red berries. It is characterised by its large, lobed, usually elliptic or sometimes obovate leaves, with broadly cuneate bases and weakly acuminate to acute apices, densely tomentose underneath and dark green and glossy above, with fruits broader than long (Fig. 6).

Sorbus herefordensis is most likely to be confused with the diploid *S. aria*, but differs in being triploid with coarser, thicker, lobed leaves with cuneate bases, slightly fewer veins which are more prominent below,

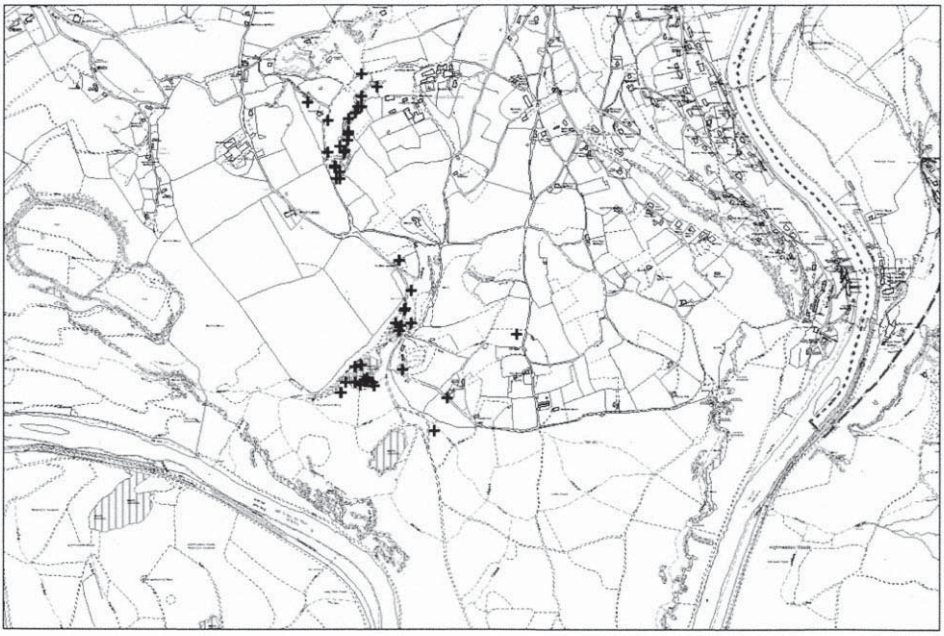

Figure 5 Distribution of *Sorbus greenii* (+) on the Great Doward, Herefordshire, v.c. 36.

the denser white tomentum underneath and the upper surface which is typically darker green and more glossy than *S. aria.* The tetraploids *Sorbus eminens* and *S. eminentiformis* both also occur in tall woodland but have rotund to rotund-ovate leaves. It is possible that the triploid *S. herefordensis* may have originated through hybridisation between the diploid *S. aria* and one of the tetraploids *S. eminens* or *S. eminentiformis* all of which occur in the same area.

Sorbus herefordensis was first found by D. Green in 2010 and initially included in *S. aria* until it was noticed that the woodland trees were consistent in leaf shape. Flow cytometry subsequently showed it to be a triploid clone.

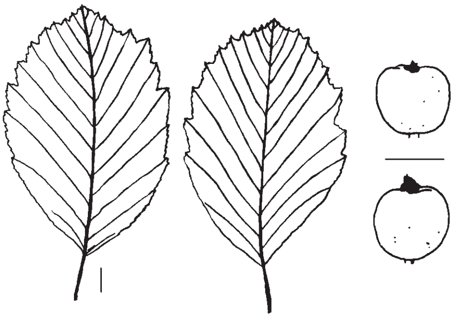

Figure 6 *Sorbus herefordensis* showing typical leaves from short sterile shoots and ripe fruit. Scale bars 1 cm.

Etymology. The tree is named after the English county of Hereford, to which it appears to be endemic.

Distribution. English endemic. This whitebeam is unusual in that it occurs predominantly in tall, closed Carboniferous Limestone woodlands on the centre of the Great Doward dome and has not yet been found on the open cliffs like the other rare whitebeams. The main population is centred on the Miners Rest Reserve and the Woodside Reserve of the Herefordshire Wildlife Trust with its frequency reducing towards the edges of the Doward (Figs. 7, 8). These *Fagus-Fraxinus* woodlands have a history of management for charcoal and coppice rotation, and some areas were mined for metals and quarried in the 17th and 18th Centuries which may have provided the generally open conditions required for regeneration of light-demanding *Sorbus* taxa. It can also colonise unmanaged, old pastures. A total of 118 trees were mapped between 2010 and 2012. Despite being abundant in the Nature Reserves it has been overlooked due to its similarity to *Sorbus aria*, and most botanists interested in *Sorbus* have visited the well-known cliffs at Seven Sisters and around the Doward (cf. Rich *et al.*, 2010).

Conservation status. IUCN (2001) threat category: Endangered.

4. ***Sorbus richii*** L. Houston, **sp. nov.**

TYPE: Top of cliff above shore by Fisherman's Steps, Kilkenny Bay, Portishead, Somerset (v.c. 6), England, ST4977176798, *T.C.G. Rich, L. Houston &*

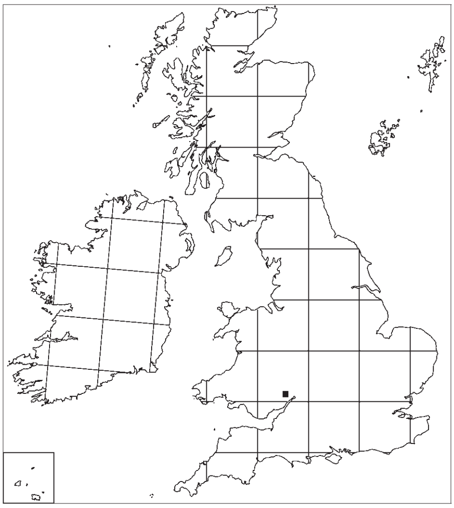

Figure 7 Distribution of *Sorbus herefordensis* in Britain.

C.M. Lovatt, 15 October 2013 (holotype **NMW**, accession no. V.2013.1.186; isotypes **BRISTM**, **BM**).

Vernacular Name: Rich's Whitebeam.

Description. Tree to at least 15 m, usually much less in exposed situations. Bark dark brownish-grey. Buds ovoid, acute, pilose on margins with white hairs. Broad leaves of short shoots 8.5–12.5(–13) × 6–9(–9.5) cm, usually obovate, sometimes elliptic, 1.3–1.55 times as long as wide and widest (45–)47–61(–65)% of way along leaf length, apex broadly obtuse to rounded, base cuneate, entire in lowest 2–3 cm, unlobed, margins more or less uniserrate with outwardly and slightly forwardly-directed acuminate teeth, veins (17–)18–22(–23) held at an angle of 22–30(–31)° to midrib at centre of leaf, upper surface mid green, lower surface greenish-greyish tomentose. Petioles 11–22 mm. Flowers not seen. Fruits (9–)10–12 × (10–)13–15 mm, 0.7–0.85 times as long as wide and looking clearly wider than long, dark red, lenticels few, medium-sized, mainly at base of fruit.

Chromosome number: flow cytometry shows this species is tetraploid (19 samples; Pellicer *et al.* (2012), as 'Portishead taxon').

Notes. *Sorbus richii* is a member of subgenus *Aria* with simple leaves white-tomentose below and small red fruits. It is characterised by the large, unlobed, obovate, more or less uniserrate leaves with broad fruits, and is tetraploid (Fig. 9). It is similar to the diploid *S. aria* but differs from this as the leaves are cuneate with generally fewer veins, greenish-greyish tomentum underneath and regular, uniserrate toothing, and it has broad fruits. It has some similarities to the tetraploid *S. eminens* but that has rotund to rotund-ovate leaves. It differs from *S. porrigentiformis* in having larger, unlobed leaves.

Figure 8 Distribution of *Sorbus herefordensis* (+) on the Great Doward, Herefordshire, v.c. 36.

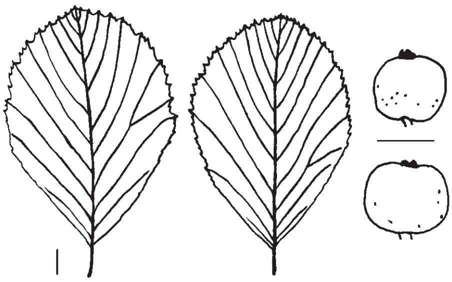

Figure 9 ***Sorbus richii*** **showing typical leaves from short sterile shoots and ripe fruit. Scale bars 1 cm.**

Sorbus richii was first collected in 2001 at Church Hill, Clevedon by T. Rich when it was doubtfully attributed to the *S. porrigentiformis* group (**NMW**). The much larger population at Kilkenny Bay, Portishead was found in 2007 by L. Houston who noted its closer affinity to *S. eminens*, and further populations along the coast nearby were soon found. These Portishead plants were noted under *S.* × *robertsonii* T.C.G. Rich (=*S. aria* × *eminens*) by Rich *et al.* (2010, p.107) who suggested they might be of *S. aria* × *eminens* origin. When sampling for flow cytometry in 2011 we found it was consistently tetraploid (Pellicer *et al.*, 2012) and thus not of direct *S. aria* × *eminens* parentage. However, as *S. richii* shares the '*Aria A*' chloroplast type with *S. aria* and *S. eminens* (cf. Clevedon plant listed under *S. eminens* sensu lato in Chester *et al.* (2007)), it is clearly related to these species. Whilst sampling for the flow cytometry work we realised the Clevedon and Portishead plants were the same taxon.

Distribution. *Sorbus richii* has been recorded from five localities along the shores of the Severn Estuary from Portishead to Clevedon (Fig. 10). At East Wood, Portishead (ST4777), at least four trees occur with *S. aria, S. eminens* and *S. torminalis* (L.) Crantz; one triploid tree may be *S. aria* × *richii* but requires further investigation. Two trees occur on the cliffs at the east end near the pier (ST4777) and one at the west end on cliffs at Battery Point (ST4677). At Kilkenny Bay (ST4576), it is frequent along the top edge of the Old Red Sandstone cliffs above the shore and occasional on the cliffs themselves, with at least 20 plants. At Redcliffe Bay (ST4476), there are five trees on the sandstone cliff edges with *S. aria.* At Church Hill, Clevedon (ST3971), at least nine trees are scattered along the upper sea cliffs in Carboniferous Limestone woodland. Although the remaining cliffs between Portishead and Clevedon look suitable, LH has been unable to find any further populations.

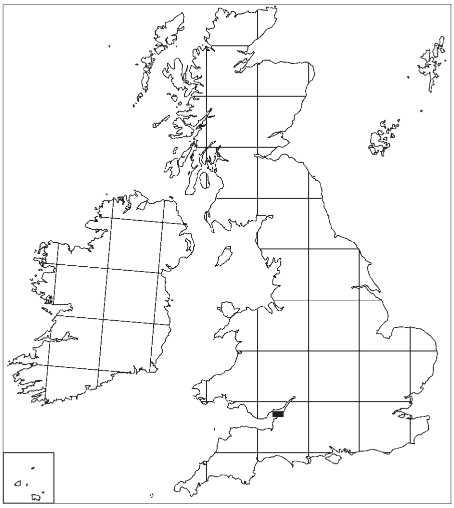

Figure 10 **Distribution of** ***Sorbus richii*** **in Britain.**

The identity of trees at Worlebury Hill, Weston-Super-Mare remains to be clarified. Herbarium material collected by M.C.F. Proctor in 1989 from above the Toll Road, from a spur (c. ST3162) and from Helen's Steps (ST3262) (cf. Proctor & Groenhof, 1992), and material we collected in 2007 and 2011, is currently attributed to *S. eminens* but some trees differ from typical *S. eminens* in having obovate-elliptic rather than rotund leaves. These trees, which grow with *S. aria* and typical *S. eminens*, do not quite match our *S. richii* description and may be of local hybrid derivation; DNA studies are required to clarify their identity.

Etymology. *Sorbus richii* is named after T.C.G. Rich, the original collector.

Conservation status. IUCN (2001) threat category: Endangered.

5. ***Sorbus sellii*** T.C.G. Rich, **sp. nov.**

TYPE: Cambridge Botanic Garden s.n., origin unknown, *T.C.G. Rich,* 18 September 2001 (holotype **NMW**, accession no. V.2001.25.309).

Misapplied name: *S. decipiens* (Bechst.) Irmisch sensu Sell (1989).

Vernacular name: Sell's Whitebeam.

Description. Tree to at least 20 m tall but often smaller, not rhizomatous. Bark of larger trunks grey, brownish-grey in young twigs. Leaf buds ovoid to lanceoloid, acute or obtuse, with white hairs on margins of scales. Broad leaves of short sterile shoots (6–)7–11(–12.5) cm × 5–8(–9.5) cm, ovate or elliptic, 1.2–1.6 times as long as wide and widest 30–50% of way along leaf length, with narrowly triangular to triangular, acute lobes cut (5–)8–19(–21)% of way to midrib at centre of the leaf, apex acute, base rounded to broadly cuneate, margins weakly biserrate with forward pointing, acute teeth, and (17–)20–27(–28) veins held at an angle of (25–)27–38(–43)° to the midrib at centre of the leaf, upper surface dark green,

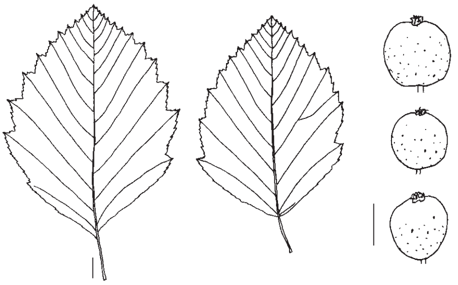

Figure 11 ***Sorbus sellii*** **showing typical leaves from short sterile shoots and ripe fruit. Scale bars 1 cm.**

lower surface greyish-green. Petioles 1.3–3.2(–3.5) cm, slender. Inflorescences to 15(–20) cm across, dense, branchlets tomentose. Sepals narrowly triangular, with many brown glands on margins. Petals (6–)6.5–10 mm × (4–)5–7 mm, white. Anthers creamy yellow. Styles 2, split to base. Largest fruits 12–17 × (11–)13–16(–17) mm but markedly variable in size as a whole, 0.9–1.1(–1.2) times as long as wide but mostly looking wider than long or globose, turning orange or yellowish when ripe (R.H.S. colour chart 21B, 25A, 28A, ripening 169A, 169C) with many small and fewer medium lenticels, and rarely a few large lenticels, scattered over fruit.

Chromosome number: 2n=51, triploid (Bailey *et al.*, 2008).

Notes. *Sorbus sellii* is an obvious member of *Sorbus* subgenus *Tormaria* Májovský & Bernátová with its shallowly but sharply lobed leaves which are greyish-green underneath and orangey fruits. It is characterised by the ovate, sharply lobed leaves with many (20–27) veins, acute apices and rounded to cuneate bases, and the orangey fruits (Fig. 11). Further details and photographs are given in Rich *et al.* (2010, p.200).

When P.D. Sell reviewed the *Sorbus latifolia* aggregate (i.e. subgenus *Tormaria*) in the British Isles (Sell, 1989), he attributed British members of an occasionally cultivated taxon with acute lobes to *S. decipiens* (Bechst.) Irmisch, having had much trouble trying to determine the correct name for the taxon. He designated a neotype for *S. decipiens* as the illustration in Bechstein's *Forstbotanik* 5th edition as herbarium material was unavailable. In our monograph of British and Irish *Sorbus*, we followed Sell's (1989) application of the name but noted Sell's concept of *S. decipiens* did not match that of Düll (1961) in his review of Bavarian and Thuringian *Sorbus*.

Recently, Meyer *et al.* (2014) investigated seven presumed apomictic microspecies in subgenus *Tormaria* from Thuringia including *S. decipiens* from the type locality (Bechstein's plant came from a mountain at Walterhausen near Gotha, Germany). Surprisingly, all seven 'microspecies' were found to be diploid and thus either primary or early hybrids between *S. aria* and *S. torminalis.* Meyer *et al.* (2014) point out two consequences of this finding for *S. decipiens*; first, the name *S.* × *decipiens* (Bechst.) Petz & G. Kirchn. is now the earliest combination for the hybrid (note corrected authorities) and predates *S.* × *tomentella* Gand. which has only come into use recently (e.g. Rich *et al.*, 2010), and second, the triploid taxon *S. decipiens* sensu Sell (1989) and Rich *et al.* (2010) required a new name.

Etymology. Peter Sell (1930–2013) was one of the Britain's greatest critical botanists. Peter had a particular interest in *Sorbus* and it gives T. Rich great pleasure to name this tree, with which Peter is associated, in his honour. The holotype is selected from the large tree in the Cambridge University Botanic Garden which we discussed together in 2001 and which Peter mentioned in his 1989 paper. The tree from which the type was collected was in good health in 2013 (T. Upson, pers. comm. 2013).

Distribution. Like *S. croceocarpa* P. D. Sell, which is also a widely cultivated member of sect. *Tormaria*, the geographical origin of *S. sellii* is unknown. It does not match any described species clearly, and is currently unknown in Germany (N. Meyer, pers. comm. 2013), Czech Republic (M. Lepší, pers. obs.) and Hungary (Cs. Németh, pers. comm. 2013). It might have originated elsewhere in central Europe, as this is one of the centres of diversity of subgenus *Tormaria.*

A map showing the naturalised distribution in Britain was given in Rich *et al.* (2010); since then it has also been confirmed in Yorkshire, v.c. 64.

The two Avon specimens sampled in our chloroplast DNA survey (Chester *et al.*, 2007) had the widespread 'Torminalis M' chloroplast type. Microsatellite studies by Robertson *et al.* (2010) showed the slightly anomalous position in PCO plots relative to other British members of subgenus *Tormaria* was probably due to its parent taxa not being sampled for the analysis, suggesting it did not originate in the Avon Gorge and probably not in Britain.

Conservation status. IUCN (2001) threat category: as this is a cultivated species in Britain only rarely naturalised, it is of Least Concern.

6. *Sorbus spectans* L. Houston, sp. nov.

TYPE: Edge of cliffs overlooking Avon Gorge, tree no. 22 of Observatory clone, Observatory, Clifton, Bristol, England, ST565732, *L. Houston & T.C.G. Rich,* 15 October 2013 (holotype **NMW**, accession no. V.2013.1.184; isotype **BM)**.

Vernacular name: Observatory Whitebeam.

Description. Shrub or small tree to 9 m. Bark of larger trunks greyish-brown. Leaf buds ovoid-conical, acute, pilose with white hairs on margins. Broad leaves of short sterile shoots (7.0–)7.5–10.0(–10.5) × 5.0–7.5 cm, rhombic, elliptic or slightly obovate or ovate,

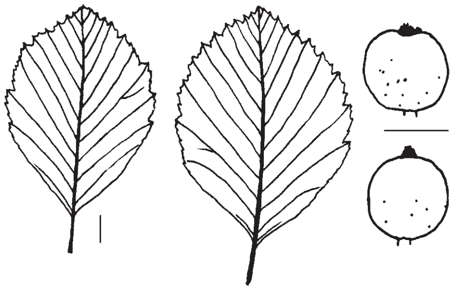

Figure 12 ***Sorbus spectans*** **showing typical leaves from short sterile shoots and ripe fruit. Scale bars 1 cm.**

1.3–1.6(–1.65) times as long as wide and widest (42–)45–58% of way along leaf length, apex acute to obtuse, base cuneate, margins weakly biserrate, usually with shallow obtuse or sometimes acute lobes at middle of leaf to 16(–18)% of way to midrib or sometimes unlobed, veins (14–)16–20(–22) held at an angle of (28–)30–42° to the midrib at the centre of leaf, upper surface mid to dark green, lower surface densely white-tomentose. Petioles 13–20(–22) mm. Inflorescences to c. 8 cm across, crowded. Branchlets tomentose. Flowers to c. 20 mm across. Sepals narrowly triangular, greenish at tip, tomentose, margins eglandular. Petals c. 5–6 × 5 mm, broadly elliptic to orbicular, white. Anthers cream. Styles 2–4, split to base, pilose. Largest fruits 9–14(–15.5) × (8.5–)9.0–13.5(–15.0) mm, 0.83–1.1 times as long as wide, generally looking globose or longer than wide, dark red at maturity (RHS colour chart 45A, 46A, 46B) with a few small lenticels mainly at the base.

Chromosome number: flow cytometry indicates this clone is triploid (12 samples; Pellicer *et al.* (2012), as 'Observatory Hill taxon').

Notes. *Sorbus spectans* belongs to subgenus *Aria* with simple leaves white-tomentose underneath and red fruits. It is characterised by the small, elliptic or rhombic, biserrate shallowly lobed leaves which are dark green above and densely white-tomentose underneath (sometimes almost 'bluish-white' tomentose), and the more or less globose fruits. There are often smaller secondary veins branching off from the lateral veins.

Sorbus spectans is most similar to the triploid *S. wilmottiana* E.F. Warb. which differs in having larger, narrower, more deeply lobed leaves and fruits longer than wide. It differs from the ubiquitous diploid *S. aria* in having consistently smaller elliptic or rhombic leaves with 16–20 veins, cuneate bases and shallow acute lobes and small ± globose fruits (Fig. 12). It is otherwise similar to the tetraploid *S. porrigentiformis* which has fruits broader than long and obovate leaves which are greyish-white tomentose underneath, and to *S. whiteana* T.C.G. Rich & L. Houston which differs in having larger obovate leaves and fruits longer than wide. *Sorbus leighensis* T.C.G. Rich differs in having obovate, more or less truncate leaves. The hybrid *S.* × *avonensis* T.C.G. Rich differs in having obtuse leaves.

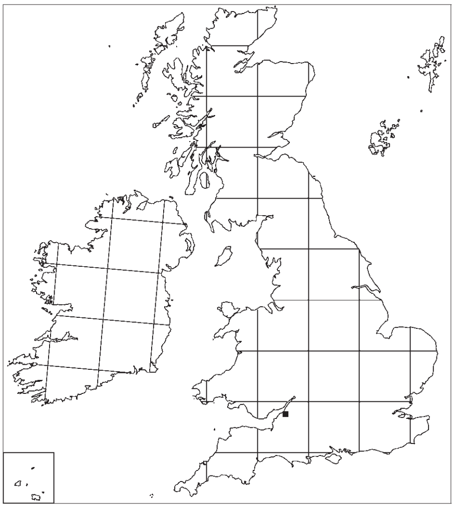

Figure 13 **Distribution of** ***Sorbus spectans*** **in Britain.**

Like some other Avon Gorge endemic *Sorbus* taxa, it is likely to have arisen as *S. aria* × *porrigentiformis*. Microsatellite DNA analysis show this taxon has a unique combination of loci (S. Ludwig, unpublished).

Etymology. The epithet *spectans* relates to looking out or observing, due to its proximity to the Avon Gorge Observatory, and was suggested by C. M. Lovatt.

Distribution. English endemic. Over 60 trees belonging to this clone have been found on the rocks, cliffs and slopes of St Vincent's Rocks, below the Observatory at the south end of the Avon Gorge near Brunel's suspension bridge (Fig. 13). It was first recognised as a distinct taxon by L. Houston on 11 October 1999 (**NMW**).

Conservation status. IUCN (2001) threat category: Endangered.

New hybrids

The following two hybrids are presented below to document their occurrence, but we will not provide binomials for them until they are found more widely.

Sorbus aucuparia L. × *S. minima* (Ley) Hedl.

Description. Shrub to c. 3 m high. Leaf buds lanceoloid with long white hairs on margins of bud scales. Broad leaves of short sterile shoots 5.5–10 × 4.2–5.8 cm, oblong-ovate, 2.0–2.6 times as long as wide and widest 38–50% of way along leaf, variably pinnate

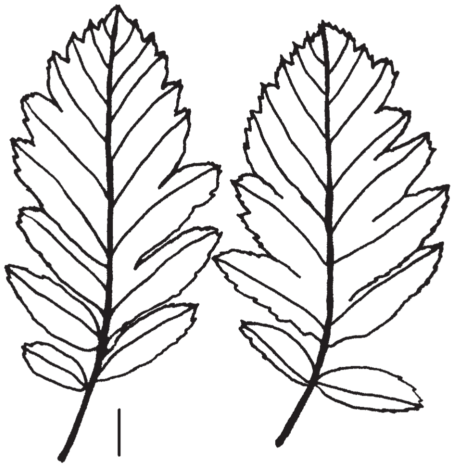

Figure 14 *Sorbus aucuparia* × *minima* showing typical leaves from short sterile shoots. Scale bar 1 cm.

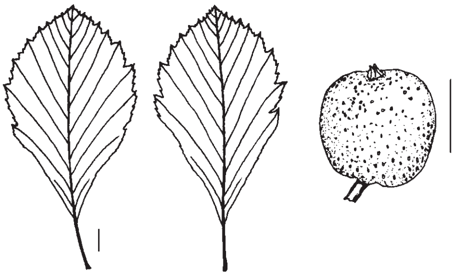

Figure 15 The Cwmyoy *Sorbus porrigentiformis* sensu lato × *torminalis* showing typical leaves from short sterile shoots and one fruit. Scale bars 1 cm.

below with 2–5 free leaflets, the lowest pair 'pinched' at the base with the lamina not joined to the midrib, and decreasingly pinnatifid above with rounded to acute lobes, lobes cut 36–100% way to midrib at centre of the leaf, apex acute or rarely just obtuse, basal leaflets spreading, leaf margin uniserrate with forward-directed teeth, veins 14–17 held at an angle of 34–45° to midrib at centre of the leaf, upper surface dark green, lower surface greyish-green tomentose. Petioles 14–21 mm. Flowers and fruit not seen.

Chromosome number: flow cytometry shows this taxon is tetraploid (1 sample; J. Pellicer, unpublished).

Notes. This hybrid is a member of subgenus *Soraria* Májovský & Bernátová, with lobed leaves which are greenish-white tomentose underneath and small red fruits (Fig. 14). It is clearly intermediate between its parents: *S. aucuparia* differs in having regularly pinnate leaves and *S. minima* differs in having simple leaves lobed up to 35% of way to midrib. Like other tetraploid taxa derived from crosses between *S. aucuparia* and triploid members of subgenus *Soraria* (e.g. *S. pseudofennica* E.F. Warb., *S.* × *motleyi* T.C.G. Rich) it has partly pinnate leaves which become less lobed above. The Scottish endemic *Sorbus pseudofennica* (derived from the triploid *S. arranensis* Hedl. × *S. aucuparia*) differs in having relative broader leaves 1.3–1.9 times as long as wide. The Welsh endemic hybrid *S.* × *motleyi* (=*S. aucuparia* × *leyana* Wilmott) differs in having more free leaflets (usually 4–7) reflecting the more deeply lobed leaves of *S. leyana* compared to *S. minima.*

Distribution. This hybrid was first found on 18 September 2012 by M. Lepší (**NMW**). One shrub occurred on a relatively inaccessible Carboniferous Limestone cliff at Craig-y-Cilau, Brecon Beacons (v.c. 42), Wales with both parents (SO187157). So far only one shrub has been found, despite regular surveys at the three *S. minima* sites since 2002 (cf. Rich *et al.*, 2005).

Sorbus porrigentiformis E.F. Warb. *sensu lato* × *S. torminalis* (L.) Crantz

Description. Trees to at least 10 m in height. Bark greyish-brown. Buds lanceoloid, acute, with white hairs on margins. Broad leaves of short shoots (8.5–)9–10.5 × 5.5–6.5(–7) cm, obovate, 1.5–1.7 times as long as wide and widest 52–65% of way along leaf length, lobed 12–22% of way to midrib at centre of leaf with acute lobes, obtuse, base cuneate or slightly curving outwards and entire on lowest 2–3 cm, margins with acuminate, outwardly directed teeth, veins 18–19 held at an angle of 26–32(–33)° to the midrib, upper surface dark green, lower surface greenish-white tomentose. Petioles 16–24 mm. Flowers not seen. Fruits 13–15 × 13–15 mm, globose, orangey-brown with many large lenticels over most of fruit.

Chromosome number: flow cytometry indicates this clone is triploid (2 samples; J. Pellicer, unpublished).

Notes. This hybrid is a clear member of subgenus *Tormaria* with acutely-lobed leaves which are greenish-white underneath and with long petioles, and with brownish fruits with many lenticels (Fig. 15). The obovate leaves distinguish it from most other British members of subgenus *Tormaria* except for *S. bristoliensis* Wilm., of *S. eminens* × *torminalis* parentage (Robertson *et al.*, 2010), which differs in having less lobed leaves and smaller, orangey-red fruit.

It was first collected on 23 May 1990 by M.C.F. Proctor when sampling members of the *S. porrigentiformis* group for isozyme analysis (**NMW**). Proctor & Groenhof (1992) reported that, as the anomalous tree with rather narrow rhomboid leaves at Cwmyoy, it had a peroxidase phenotype similar to but not identical with *S. wilmottiana*. Given that the sample was collected before the leaves were fully developed and flowers still in early bud, it is not surprising that it was not recognised as subgenus *Tormaria* rather than subgenus *Aria*. It was immediately recognised as subgenus *Tormaria* when independently refound in fruit on 9 September 2012 by M. Lepší (**NMW; CB** accession no. 83061).

Microsatellite DNA analysis will be required to determine the exact parentage of this triploid. *Sorbus torminalis* is clearly one parent, presumably as the female parent as in other *S. torminalis* hybrids (cf. Chester *et al.*, 2007). The similarity of the isozymes profile to that of *S. wilmottiana* suggests that the male parent is likely to be tetraploid *S. porrigentiformis*. However, we have been unable to find either putative parent at the site suggesting it may not have originated there; the nearest known locality of *S. porrigentiformis* is *c*. 8 km away in the Usk valley whilst the nearest *S. torminalis* tree is *c*. 1.5 km away. *Sorbus cambrensis* M. Proctor and *S. stenophylla* M. Proctor both occur reasonably frequently with it at Cwmyoy but, as these are pentaploids (Pellicer *et al.*, 2012), they are not involved in its origin.

Distribution. Two trees occur on the top edge of the Old Red Sandstone cliff at Cwmyoy, Monmouthshire (v.c. 35), Wales, SO296243.

New subgenus

Sorbus subgenus ***Triparens*** M. Lepší & T.C.G. Rich, **subg. nov.**

[*Sorbus* subg. *Sorbus* × subg. *Aria* × subg. *Torminaria* (DC.) C. Koch]

Holotype species: *Sorbus intermedia* (Ehrh.) Pers., *Syn. Pl.* 2: 38, 1806.

Description. Trees or shrubs. Leave lobed, pinnatifid to subpinnate, yellowish-green-tomentose underneath with relatively few (10–20) veins, the lobes or leaflets subacute to obtuse with few or very few teeth towards the base. Petals white. Styles 2–3. Fruit small to big, orange to red with sparse to absent small to medium size lenticels.

Notes. Subgenus *Triparens* includes taxa which originated as hybrids and backcrosses between subgenus *Aria*, subgenus *Sorbus* and subgenus *Torminaria*. The most similar subgenus to subgenus *Triparens* is subgenus *Soraria* which has leaves with generally more veins and with greyish-white indumentum underneath and red or deep red fruits. Subgenera *Tormaria* and *Torminaria* are distinguished by having acute or acuminate leaf lobes and red, orange or brown fruit. Subgenus *Aria* has serrate to shallowly lobed leaves which are white to greyish-white underneath. Subgenera *Chamaemespilus* (DC.) C. Koch., *Chamsoraria* Májovský & Bernátová and *Chamaespilaria* Májovský & Bernátová differ in having pink petals and serrate to shallowly lobed leaves which are glabrous or greyish-white underneath.

There are currently two taxa which belong to subgenus *Triparens*: *S. intermedia* and its backcross with *S. aucuparia* (=*S.* × *liljeforsii* T.C.G. Rich (Rich, 2008)). The distribution of the subgenus is identical with the general distribution of *S. intermedia* which is known as native around the Baltic in Denmark, Sweden, Baltic Islands, Poland, North Germany, Estonia, Latvia and Finland. *Sorbus intermedia* is also commonly planted throughout the Europe and is reported as naturalised in 12 countries (Lepší *et al.*, 2013). *Sorbus* × *liljeforsii* occurs naturally scattered around the Baltic but may also originate spontaneously where *S. intermedia* has been planted outside the native distribution area. Such spontaneous hybrids have been reported from Britain and Ireland (Rich *et al.*, 2010) and Norway (P. Salvesen, pers. comm. 2009).

From their morphology, two Romanian species – *S. dacica* Borbás and *S. paxiana* Jávorka – may also belong to subgenus *Triparens* but their parentage has not been elucidated yet (Cs. Németh, pers. comm. 2012).

Acknowledgements

We would like to thank Sandra Clermont, Mike Fay, the Forestry Commission, Alan Foulds, Herefordshire Wildlife Trust, Simon Hiscock, Sarah Lendrum, Doug Lloyd, Clive Lovatt, Csaba Németh, Frances Simpson and Tim Upson for their help. We would like to thank Norbert Meyer for drawing attention to the *S. decipiens* problem and allowing us to publish the new name. Martin Lepší was funded by the European Union's Erasmus programme.

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Paper VII

Versatility of reproductive modes and ploidy level interactions in *Sorbus* (Malinae, Rosaceae): playful youth and serious adults.

Lepší M., Koutecký P., Bílá J., Lepší P., Urfus T., Rich T. C. G. (2016) manuscript

Picture on previous page *Sorbus albensis*, Bídnice

Versatility of reproductive modes and ploidy level interactions in *Sorbus* (*Malinae*, Rosaceae): playful youth and serious adults

Annotation

To reveal ongoing evolutionary processes responsible for the generation of the observed variability in the genus *Sorbus* , the reproductive modes of 42 *Sorbus* taxa were examined using flow-cytometric seed and pollen screens. Apart from revealing major trends, the study estimates the frequency of rare events and provides several novel conclusions that are relevant both specifically to *Sorbus/*Rosaceae and to apomixis in general.

Abstract

- **Background and Aims** The genus *Sorbus* includes four ploidy levels and both sexual and apomictic taxa and represents an excellent model for studying the role of polyploidization and apomixis in formation of diversity in plants. Our study is focussed on the extent and variation of reproduction modes at individual ploidy levels and the role of reproductive modes in diversification and evolutionary success of individual taxa.
- **Methods** In total, 3663 seeds of 42 taxa were analysed by flow cytometry. We infer reproductive modes/origin of seeds from ploidy levels of embryo and endosperm. Our sampling covers all ploidy levels known in the genus and includes both stabilised taxa and evolutionary young biotypes. Flow cytometry of pollen was conducted to reveal occurrence of unreduced pollen.
- **Key Results** The genus *Sorbus* show high variability in reproduction pathways (sexuality, apomixis, chromosome summation, haploid parthenogenesis). Diploids are sexual while polyploids showed predominantly obligate or facultative apomixis of pseudogamic type. Surprisingly, in half of the polyploids studied, several reproductive modes were present and even intra-individual variation was detected. Diploids, tetraploids and pentaploids are pollinated by conspecific pollen while triploids are largely but not fully dependent on pollen of other species. Production of unreduced pollen was not confirmed at any ploidy level. In pseudogamic seeds, fertilisation of the central cell by both sperms is dominant, which is unlike all other Rosaceae genera

studied so far. Several cases of rare process of heterofertilization (pollination by two pollen) are documented.

- **Conclusions** The principal mechanisms of diversification in *Sorbus* are residual sexuality in apomicts, production of triploid taxa from diploid-tetraploid crosses and production of BIII hybrids from triploid-diploid/tetraploid crosses. Evolutionary success of *Sorbus* taxa is largely dependent on the breeding system and is determined by self-(in-)compatibility and the interplay between stabilising apomixis and variation-generating sexuality.

Key words: apomixis, breeding system, diversification, flow cytometric seed and pollen screen, endosperm balance, hybridization, Malinae, pollen, polyploidy, Rosaceae, *Sorbus*.

This part is the subject of unpublished manuscript, which was submitted to Annals of botany in September 2016. The full version of the Chapter VII is archived by the Faculty of Science, University of South Bohemia in the printed version of the Ph.D. Thesis. Author's contribution is given above in the introductory section List of papers and author's contribution.

Summary of Results and Conclusions

Picture on previous page *Sorbus rhodanthera*, Chlumská hora

Summary of Results and Conclusions

The taxonomy, genetic and morphological variability, and reproductive modes of most *Sorbus* taxa occurring in the Czech Republic and selected taxa from Great Britain were examined and evaluated using classical approaches and modern biosystematic methods (nuclear microsatellite markers, chromosome counts, flow cytometry, traditional multivariate morphometrics and outline analyses).

The synthesis of the obtained results led to the confirmation of many previous taxonomic conclusions, but also to several significant taxonomic and phytogeographical novelties (Table 1). Taxonomic novelties include the discovery and description of several new species and hybrids for science – seven species and three hybrids from the Czech Republic, including a complete taxonomic reassessment of the taxonomically least understood subgenus *Aria* in the Czech Republic (papers I–V), the description of a new subgenus (paper VI), and a revision of *Sorbus quernea* and *S. hardeggensis*. The two latter species, originally described as (sub-)endemics of the Czech Republic, were shown to be the naturalized alien species *S. mougeotii* (paper II) and a population of the sexual hybrid *S.* ×*decipiens* (paper VII), respectively. The observation of apomixis at the diploid level in *S. eximia* was refuted (paper III). Another result of this thesis is the finding that broadly accepted records about native occurrences of *S. austriaca*, *S. carpatica*, *S. subdanubialis* and *S. graeca* in the Czech Republic are predominantly based on misidentifications. These taxa should be therefore excluded from the checklist of the Czech native flora (paper I). Instead, *S. mougeotii*, *S. latifolia* and *S. austriaca* are added to the species list of the Czech alien flora (papers I, II, V). A comprehensive taxonomic revision of the complex subgenus *Aria* (paper I) also showed that diploid *S. aria* is confined to Moravia and that previous records of its occurrence in Bohemia relate to the tetraploid species *S. collina*, newly described within this work (paper I and V). The revised *Sorbus* flora of the Czech Republic now includes three native (*S. aria*, *S. aucuparia*, *S. torminalis*) and one naturalized (*S. domestica*) sexual species, two widely distributed facultative

Table 1. – Major taxonomic and phytogeographical conclusions regarding Czech *Sorbus* made in this thesis.

Revised taxa previously reported from the Czech Republic (CZ)	Taxonomic and other conclusions reached in this thesis	Type of findings	Source
S. aria p.p.	= *S. collina*	taxonomic novelty	paper I
	= *S. moravica*	taxonomic novelty	paper I
S. austriaca	= *S. aria*	misidentification	paper I
	= *S. pontis-satanae*	taxonomic novelty	paper I
S. carpatica	= *S. aria*	misidentification	paper I
S. eximia p.p.	= *S. barrandienica*	taxonomic novelty	paper III
S. graeca	= *S. danubialis*	misidentification	paper I
S. hardeggensis	= *S.* × *decipiens*	incorrect taxonomic assessment	paper V, VII
S. quernea	= *S. mougeotii*	incorrect taxonomic assessment	paper II
S. subdanubialis	= *S. cucullifera*	taxonomic novelty	paper I
S.× *kitaibeliana*	= *S. latifolia*	misidentification	paper V
-	*S. thayensis*	taxonomic novelty	paper I
-	*S. pauca*	taxonomic novelty	paper IV
-	*S. austriaca*	new alien for CZ	paper V
-	*S. mougeotii*	new alien for CZ	paper II, V
-	*S. latifolia*	new alien for CZ	paper V
-	*S.*× *kitaibeliana*	new native taxon for CZ	paper V
-	*S. gemella* × *torminalis*	taxonomic novelty	appendix I
-	*S. barrandienica* × *torminalis*	taxonomic novelty	appendix I
-	*S. collina* × *torminalis*	taxonomic novelty	appendix I

apomicts (*S. danubialis* and *S. collina*), 15 (sub-)endemic hybridogenous polyploid species, four apomictic alien species, and two diploid and six polyploid hybrids (paper V, appendix I). Annotated distribution maps for most of taxon were created as a basis for the future complete atlas of the distribution of vascular plants in the Czech Republic (paper V). To make all the above information accessible to the botanical public, the nomenclature, descriptions, distribution and ecology of all Czech *Sorbus* taxa were updated, unified and compiled into chapters of the Flora of the Czech Republic (appendix I). The results of a flow-cytometric seed screen indicate that the mode of endosperm and embryo formation is species-specific and may be used as an additional taxonomic character, particularly for delimitation of regional hybridogenous taxa (paper VII).

The genetic variability of all regional apomictic species under study is low and suggests their monotopic and single-event origin. By contrast, morphological variability may be relatively high depending on the diversity of environmental conditions, but it is significantly lower than the genetically controlled morphological variability of sexual species. It is concluded that despite the considerable morphological plasticity of apomictic taxa, it is still possible to distinguish closely related apomictic species using morphological characters (paper I and III).

The comprehensive taxonomic treatment of *Sorbus* taxa presented above established a suitable basis for a subsequent flow-cytometric study (paper VII). Thanks to the detailed taxonomic knowledge, the sampling included not only widespread taxa, but also narrow endemics and several unique singular biotypes, represented by one or a few individuals only. Flow cytometry proved to be an appropriate tool for assessing variability in the ploidy levels and reproductive modes of all Czech and selected European taxa. Diploid, triploid, tetraploid and pentaploid taxa were detected and their reproductive modes examined. The flow-cytometric seed screen method revealed the principle mechanism of diversification in *Sorbus* and provided several novel conclusions that are significant both specifically for *Sorbus*/Rosaceae and for apomixis in general. Four basic reproductive pathway were recorded – sexuality, apomixis, chromosome summation and haploid parthenogenesis. Regardless of the detected reproductive modes and ploidy levels of taxa, only the production of reduced pollen was observed. Diploids are sexual whereas polyploids showed predominantly obligate or facultative apomixis of the pseudogamic type. Surprisingly, in half of the polyploids studied, more than one reproductive pathway was present at the species and also at the individual level. In pseudogamic seeds, fertilization of the central cell by both sperms is dominant, unlike in all other Rosaceae genera studied so far. Several cases of heterofertilization (pollination by two pollen grains), a rare process in plants, were documented. Tetraploids showed greater evolutionary potential than triploids due to their facultative apomixis (and the resulting potential for adaptation) or, in addition or alternatively, the ability to accept their own pollen (independence of other taxa). Triploid species, by contrast, are largely apomictic and mainly but not fully dependent on pollen of other species. It is concluded that the principal mechanisms of diversification in *Sorbus* are residual sexuality in apomicts, production of triploid taxa from diploid-tetraploid crosses and production of B_{III} hybrids from triploid-diploid/tetraploid crosses. The evolutionary success of *Sorbus* taxa is largely dependent on the breeding system and is determined by self-(in-)compatibility and the interplay between stabilizing apomixis and variation-generating sexuality (paper VII).

Appendix I

Sorbus L. – jeřáb in Štěpánková J., Chrtek J. & Kaplan Z. (eds): Dodatky ke Květeně České republiky, svazkům 1–9.

Lepší M. & Lepší P. (submitted 2017) Academia.

Appendix I contains a revised and updated treatment of the genus *Sorbus* for the Flora of the Czech Republic, a comprehensive national botanical compendium intended for the general botanical public. Because it is written in Czech, it was excluded from the thesis. It is attached for the sake of completeness and for its widespread impact on Czech botany. The text covers the nomenclature, description, variability, distribution, ecology and biology of particular species. The treatment was compiled based on conclusions presented in this thesis and other published and also own unpublished information. The contributions of both authors were comparable.

This part is the subject of unpublished manuskript, which was submitted to editors in January 2017. The full version of the Appendix I is archived by the Faculty of Science, University of South Bohemia in the printed version of the Ph.D. Thesis.

Picture on previous page *Sorbus danubialis*, Templštejn

Professional Curriculum Vitae

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Education and Qualification

1995–1998 – Faculty of electrical engineering Plzeň of University of West Bohemia in Plzeň;
– BSc. thesis: Evaluation of quality of water in the Úhlava river for water supply purposes.
1998–2000 – Faculty of Environment of Jan Evangelista Purkyně University in Ústí nad Labem;
– MSc. thesis: Determination of relationship between age and impedance in common spruce (*Picea abies*) by the Mervit instrument.
2003–2004 – Sydney college of English;
– English courses
since 2010: University of South Bohemia, Faculty of Science;
– Ph.D. thesis: Taxonomy and variability of selected *Sorbus* taxa

Employment

since 2000: South Bohemian Museum in České Budějovice, curator of herbarium, botanical field researcher (vegetation and flora mapping), popularizer of botany (exhibitions, excursions for public and students), co-leader of South Bohemian branch of Czech Botanical Society.

Research interests

- taxonomy and chorology of vascular plants
- biosystematics of *Sorbus* and *Rubus*
- nature protection

Publications

Papers in impact factor journals

Lepší M. & Lepší P. (2006): *Rubus kletensis*, a new species from South Bohemia and Upper Austria. – Preslia 78, 103–114.

Ekrt L., **Lepší M.**, Boublík K. & Lepší P. (2007): *Dryopteris remota* rediscovered for the flora of the Czech Republic. – Preslia 79: 69–82.

Lepší M. & Lepší P. (2009): *Rubus silvae-norticae*, a new species from Bohemia, Austria and Bavaria and the significance of brambles for regional migrations and phytogeography. – Preslia 81: 43–62.

Lepší M., Vít P., Lepší P., Boublík K. & Kolář F. (2009): *Sorbus portae-bohemicae* and *Sorbus albensis*, two new endemic apomictic species recognized based on a revision of *Sorbus bohemica* – Preslia 81: 63–89.

Vít P.**, Lepší M.** & Lepší P. (2012): There is no diploid apomict among Czech *Sorbus* species – a biosystematic revision of *Sorbus eximia*, and the discovery of *Sorbus barrandienica*. – Preslia 84: 71–96.

Lepší M., Lepší P., Sádlo J., Koutecký P., Vít P. & Petřík P. (2013): *Sorbus pauca* species nova, the first endemic species of the *Sorbus hybrida* group for the Czech Republic. – Preslia 85: 63–80.

Lepší M., Lepší P. & Vít P. (2013): *Sorbus quernea*: taxonomic confusion raised by the naturalisation of the alien species, *S. mougeotii*. – Preslia 85: 159–178.

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Papers in non-impact factor journals

Boublík K., Kubát K., **Lepší M.** & Lepší P. (2000): Příspěvek ke květeně severozápadních Čech se zvláštním zřetelem k území Českého středohoří. – Severočeskou přírodou 32: 101–104.

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Taxonomy and variability of selected *Sorbus* taxa
Ph.D. Thesis Series, 2017, No. 3

Printed in the Czech Republic by Typodesign
Edition of 20 copies

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